Quaestiones entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

VOLUME VIII 1972

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Editorial – One Eye on the Pot

The year 1972 marks the fiftieth anniversary of the establishment of the Department of Entomology at the University of Alberta. Anniversary –the turning of the year– is perhaps an unfortunate term, and especially so in relation to a university, the function of which is the unification –or turning into one– of knowledge. For, though history may repeat itself, it is to be hoped that a university does not. Perhaps it is the celebration of centennials and other major anniversaries that encourages history to repeat itself, for such celebrations are often preoccupied with the events of a hundred years earlier. If we should not be preoccupied with the past, then, trapped in the tunnel of time, our only remaining option is to look forwards. But gazing into crystal balls is fraught with perils for these without an anchor in history, so perhaps we need to take a quick glance backward to see whence we have come before viewing the horizon ahead to chart a course for the future. Oh for a pair of compound eyes, each able, though plastered on to the head, to look both ways without asking it to turn for them. Too little attention has been paid to this feature of the structure of insects, in attempts to understand their ability to stay on course in migration.

In 1921 E. H. Strickland, then working for the Canada Department of Agriculture at Lethbridge, visited Edmonton to consider an offer made to him by the University of Alberta. It must have been later in the year than this issue of *Quaestiones entomologicae* will appear, for the then Dean of Agriculture took him out on to some rough ground at the north end of the campus overlooking the valley of the North Saskatchewan River –like stout Cortez– and showed him the place where a building which would house the proposed department of entomology was to be built. We do not know whether Strickland was swayed by what he saw on that day, but in April 1922 the Department was created and twenty-five years later the staff increased by 100 per cent and he and I each occupied a roomlet, at either end of a modest room in the medical building. Our supporting staff consisted of half a stenographer and $12 a month worth of part time student help. Professor Strickland's budget for entomological books for the library in 1923 was $20, and the entire budget for the department in 1947-8 was $9,401. Although nobody saw fit to calculate it, the cost of a "teaching unit" was $18, a fifth of the cost today; we now teach four times the "units" with three times the staff and twenty times the money. In 1958, four years after Professor Strickland retired, the Department of Entomology moved into its present quarters in the Agriculture and Bio-Sciences building, which is just about where the Dean had said it would be. Two years later these quarters proved inadequate and a migratory branch of the department finally came to

an uneasy rest in the basement of Athabasca Hall.

So much for the backward glance. What of the future? When the first issue of *Quaestiones entomologicae* appeared a caustic reader remarked that he had no use for fly-by-night periodicals which usually folded up in five years. We have outlived that one. Some other pen than mine, I predict, will write an editorial for the volume which marks the centennial of the Department of Entomology. The editor who writes it may well have something caustic to say about this editorial for some of my predictions will be wrong; but if this one is, at least he will not say so.

It is customary to predict, by direct extrapolation of a smoothed curve of human population, that there will be 7.5 billion of us by the year 2000. With rather less reliability it might be predicted that by 2022 there will be double that number. But the curve of human population is based on close approximations for less than 300 years and we do know that *Xenopsylla cheopis* was indirectly responsible for putting several dents in the curve before that time and glacial epochs probably did likewise. Furthermore at least some drafts of the early part of the curve have been based on several species of hominid. Add to this Deevey's (1) elegant demonstration that this is man's third population explosion and the first to have its roots in non-renewable resources, and any applied entomologist might be expected to predict an end to the outbreak before 2022. A successful prediction of such an event should lead to a return to favour of entomologists, among both their biological colleagues and the population at large. Indeed, since a reduction in the number of insect species will almost certainly have resulted from the activities of the peak population of man, perhaps the economy of a declining population will support enough taxonomists to catch up a bit with the task of describing these species.

Sparked by the shortage of food and specifically of animal protein, man will have returned to eating insects. His smaller population will have been able to retreat from monoculture so that insect pest problems will have been reduced –perhaps to a point where eating the troublesome species will provide adequate control. Of course the arts of the kitchen should have so progressed that even a swarm of hoary old horseflies might be transformed into a delectable dish, and we can but imagine the succulent delight a skilled cook could render from the abdomens of queen termites forcibly fed on proof copies of last quarter's *Quaestiones entomologicae*. Or perhaps by then it will be last month's.

Clearly, as compared with today, the relative importance of the positive and the negative aspects of applied entomology will be reversed. Benefactory entomology will transcend pest control.

The Department of Entomology at the University of Alberta will be re-united under one roof –perhaps that of Athabasca Hall– but it will be understood that the roof will be demolished in the following year.

And so, like the cross-eyed cook in the English folk-song, we look briefly back and soberly forward from the first issue of volume eight –'with one eye on the pot and the other up the chimney...'

(1) Scientific American 203:195, 1960

Brian Hocking

A CHIRONOMID (DIPTERA) LARVA ATTACHED TO A LIBELLULID (ODONATA) LARVA

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While identifying libellulid larvae collected in 1966-1968 from two sloughs located about 9 miles southeast of Edmonton, Canada, I found one specimen with the tube of a chironomid larva attached to its prothorox. (See photograph below; inset magnification is approximately 35x). The libellulid was a *Sympetrum* sp. probably *internum* Montogomery and the chironomid within the tube was a *Paratanytarsus* sp.

s The association is probably not truly phoretic like those reported by Steffan (1965a, 1965b, 1967) between chironomid larvae and other aquatic invertebrates, mainly insects, but more probably is accidental like those reported by Lewis et al (1960) and Corbet (1962) between immature simuliids and odonate larvae. I have reached this conclusion because only one of the few hundred libellulid larvae I examined carried a chironomid larva and because *Paratanytarsus* sp. larvae are one of the most common, free living chironomid larvae in the sloughs I studied. Such associations, however, may represent a stage in the development of phoresis and as Corbet (1962) wrote: "further attention paid to anomalous cases of this kind might throw light on the way in which the well-known [examples of] phoresis originated".

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DIGESTIVE PROCESSES OF HAEMATOPHAGOUS INSECTS
I. A LITERATURE REVIEW

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About 240 papers published between 1903 and early 1971, providing information on more than 150 species of haematophagous insects, are reviewed. Aspects of digestive physiology covered are size of the blood meals and their distribution within the alimentary canal, properties of the salivary glands, gross and histological changes in the gut and its contents, the enzyme content of the gut and the properties of the digestive enzymes. The relationship of digestive processes to vectoring ability is discussed briefly.

Environ 240 articles publiés entre 1903 et 1971 donnant des informations sur plus de 150 espèces d'insectes hématophages, sont revisés dans cet ouvrage. Les aspects de la physiologie de la digestion qui sont couverts sont: la quantité de sang que contiennent les repas et sa distribution dans le tractus alimentaire, les caractéristiques des glandes salivaires, les changements histologiques et l'ensemble des changements de l'intestin et de son contenu, le contenu enzymatique de l'intestin et les caractéristiques propres des enzymes digestives. La relation qui existe entre le processus digestif et l'aptitude qu'ont certains insectes à être vecteur de maladies est décrite brièvement.

The primary objectives of this paper are to summarize the knowledge of the digestive physiology of blood-sucking insects and to indicate some unsolved problems. Aspects considered include the size of the blood meals, the fate of these within the digestive tract, and the sources and nature of the enzymes involved in their breakdown. Sources of the blood meals and the mechanisms of ingestion and absorption are not considered except where these appear to have a bearing on digestion.

A comparative study of digestion in blood-sucking insects is of interest primarily for two reasons. First, blood feeding has evolved several times in the insects and a comparison of digestive processes may reveal that different species have overcome problems presented by the blood meal in different ways. Conversely, the nature of their food may have resulted in convergence in the digestive processes of different haematophagous species. A second and more practical reason is that many blood-sucking arthropods are vectors of pathogenic organisms. Since most of these pathogens spend some time in the gut of the vector, digestive processes of the insect could influence vectoring ability. The possible importance of the digestive processes of insects in studies of host relationships, nuisance created by blood-sucking insects, or the efficiency of disease transmission, has been suggested by several authors (West and Eligh, 1952; O'Gower, 1956; Detinova, 1962).

There are several general reviews of digestive physiology of insects (Day and Waterhouse, 1953a, b, c; Gilmour, 1961; House, 1965; Uvarov, 1929; Waterhouse, 1957; Waterhouse and Day, 1953; Wigglesworth, 1965). Related material has also appeared in articles by Barrington (1962), Fallis (1964), House (1958, 1961, 1962), Lipke and Fraenkel (1956), Snodgrass (1935), Vonk (1964), Waldbauer (1968) and Wigglesworth (1952). The digestive physiology of mosquitoes was reviewed briefly by Clements (1963) and this and the chapter on digestion in Wigglesworth (1965) constitute the most extensive reviews published on digestion by haematophagous insects. Chapters 20 and 22 in Christophers (1960) contain some relevant material but the discussion of digestion by adult mosquitoes (pp. 707-708) is very brief. Much of the work on digestion by tsetse flies was reviewed by Buxton (1955).

Within each of the following sections an attempt has been made to arrange the material more or less taxonomically; the exopterygotes (Hemiptera and Siphunculata) are discussed first followed by the Diptera (Nematocera, Brachycera, then Muscoid flies) and finally the Aphaniptera. However, to facilitate comparisons it occasionally has been necessary to deviate from this arrangement.

SIZE OF THE BLOOD MEAL

Several methods have been used to estimate blood meal size. The simplest and most widely employed involves weighing individuals before and immediately after feeding. Some workers have weighed batches of insects before and after feeding to obtain the average weight of the meal, particularly in studies involving very small insects, or in those undertaken with inadequate equipment. A further modification has been to compare the weights of batches of fed and unfed insects; this has been particularly useful when dealing with insects which will not readily feed under laboratory conditions, the data being obtained from field-caught insects. Blood meal volumes have usually been estimated by dividing the weight of the meal by the specific gravity of the blood. However in at least one case the volume was estimated by mixing midguts of blood-fed insects with a known volume of fluid and measuring the resulting volume (O'Connor and Beatty, 1937). This method gave an unusually low estimate of meal size. One difficulty encountered with all these procedures is that some species defecate during or immediately after feeding.

The first material defecated is generally from a previous meal or the serum of the meal just consumed (Boorman, 1960). Since erythrocytes are rarely defecated, tagging these with radioactive cesium or iron and then comparing radioactivity in the fed insect with aliquots of the host's blood has yielded estimates of the meal size which are usually not influenced by defecation during the act of feeding. Using the cesium tagging method the blood meal size of *Aedes aegypti* (L.) was estimated to be 4.21 μl compared with 2.47 to 2.71 μl by the gravimetric method (Boorman, 1960). A similar discrepancy in meal size was obtained with *Culex pipiens quinquefasciatus* Say (10 μl by Fe^{59} method, and 3.3 μl by gravimetric method) but not with *Triatoma infestans* (Klug) or *Panstrongylus megistus* (Burmeister) (de Freitas and Guedes, 1961). Chemical determination of the amount of hemoglobin (by conversion to alkaline hematin) in the engorged insect compared with the hemoglobin content of the host's blood (Kershaw et al, 1956) also yields estimates which are not influenced by defecation.

In some insects *Mansonia richiardii* (Ficalbi) and *Aedes cinereus* Meigen there is a correlation between pre-feeding weights and the amount of blood ingested, but in others (*Aedes cantans* (Meigen), *Aedes detritus* (Haliday) and *Aedes punctor* (Kirby), there is not (Service 1968a). This may explain some of the variation in meal sizes reported by different workers for the same insect species. Environmental temperature apparently influences the amount of blood consumed by fifth instar *Triatoma dimiata* (Latreille) (174.5 mg at 26.5 C, 281.6 mg at 23 C) but not by other instars (Zeledon et al, 1970). The source of the blood meal may influence the quantity of blood ingested by *Pediculus humanus* L. (Krynski et al, 1952), *Cimex lectularius* L. (Johnson, 1937) and *A. aegypti* (Bennett, 1965). The physiological state of *Stomoxys calcitrans* (L.) may influence the size of the meal ingested (Anderson and Tempelis, 1970). *Glossina austeni* Newstead irradiated with 10 krad as pupae or 15 krad as teneral adults consumed as much blood as non-irradiated flies (Langley and Abasa, 1970). Environmental humidity does not influence the meal size of *Glossina tachinoides* Westwood (Buxton and Lewis, 1934) or *Glossina palpalis* (Robineau-Desvoidy) (Mellanby, 1936). In the latter species the second meal is larger than the first and older females tend to take

larger meals than young females (Mellanby, 1936).

The blood meal sizes for several species of insects are presented in Table I. The values recorded are the averages reported in the literature; where a range is given this represents the range of average meal sizes reported in the literature. Nymphal instars are indicated by Roman numerals.

The quantity of blood ingested by the insect is influenced by two physiological factors: a chemical in the blood which stimulates the insect to continue feeding and stretch receptors in the abdomen which inhibit further feeding. Adenosine-5′- phosphate and related compounds stimulate *Culex pipiens* (issp) *pallens* Coquillett to engorge upon blood (Hosoi, 1959). Diphosphates and triphosphates of cytosine, guanine, inosine, and uridine; creatine phosphate, sodium pyrophosphate, riboflavin-5′-phosphate, 5′-adenylic acid and 3′, 5′-cyclic adenylic acid stimulate *R. prolixus* to engorge (Friend, 1965; Friend and Smith, 1971). Termination of feeding by *R. prolixus* nymphs is apparently determined by stretch receptors in the abdomen (Maddrell, 1963). Nymphs whose nerve cord is severed between the pro-, and mesothoracic ganglia will consume much larger meals than normal nymphs; nymphs with a fistula in the midgut (which permits draining the midgut during the act of feeding) will consume more blood over a longer period of time than the controls (Maddrell, 1963). By cutting the ventral cord of *A. aegypti* between various ganglia and then giving the mosquitoes a blood meal, Gwadz (1969) demonstrated that the quantity of blood ingested is determined by segmental stretch receptors. Similar, but less extensive, experiments led to the same conclusions for *A. taeniorhynchus, A. triseriatus, A. subalbatus, C. pipiens quinquefasciatus* and *A. quadrimaculatus* (Gwadz, 1969). Lea (1967) reported that ablation of the median neurosecretory cells did not affect the amount of blood ingested by *A. taeniorhynchus, A. sollicitans* or *A. triseriatus* but reduced the blood meal size of *A. aegypti* by 35%.

The nature of the hunger mechanism has not been elucidated but it has been suggested that some blood-sucking insects have an optimal frequency of feeding (Gooding, 1960). Such an optimum could result from an interaction of meal size with the rates of digestion, absorption, and utilization of some component of the meal. The respiratory rate of *G. morsitans* reaches a maximum about 24 hours after feeding on a guinea-pig. At 12, 24, and 48 hours after feeding there is a high correlation between the meal size and the respiratory rate. Rajagopal and Bursell (1966) interpreted this increased oxygen consumption as being linked to the metabolic processes associated with digestion, absorption, deamination, detoxication, uric acid synthesis and excretion.

DISTRIBUTION OF MEALS WITHIN THE ALIMENTARY CANAL

In the lice, fleas, and blood-sucking bugs the digestive tract has no oesophageal diverticula and the blood meal is conveyed directly to the midgut. Blood is stored in the expanded anterior part of the midgut in bugs and is digested only in its posterior reaches (Bacot, 1915; Wigglesworth, 1936).

Flies, however, have from one to three oesophageal diverticula. Mosquitoes usually dispatch sugar solutions to the diverticula and blood to the midgut. The subject has been reviewed by Trembley (1952) and Megahed (1958). Trembley also presented data on the distribution of blood and sugar solutions in the various parts of the alimentary canal of 9 species of mosquitoes (*Anopheles freeborni* Aitken, *Anopheles aztecus* Hoffman, *Anopheles quadrimaculatus, Anopheles albimanus, Aedes albopictus* Skuse, *Aedes aegypti, Aedes atropalpus* (Coquillet) *Aedes vexans,* and *Culex pipiens* Linnaeus). The effects of interrupted feedings, time after feeding and the method of obtaining the blood meal (i.e. from a droplet

Table 1A. Blood meal sizes of some hemimetabolous insects.

Species	Stage					Sex		References
	I	II	III	IV	V	♂	♀	
Pediculus humanus L.	-	-	-	-	-	-	0.85-1.2	Buxton, 1947; Kryński *et al.*, 1952
Cimex hemipterus Fabricius	0.5	1.3	3.1	4.5	6.8	2.6	5.8	Wattal and Kalra, 1961
Cimex lectularius L.	0.26 -0.9	0.48 -1.7	1.09 -2.9	2.86 -5.0	5.53 -10.1	3.81 -6.2	6.48 -9.47	Jones, 1930; Johnson, 1937 Tawfik, 1968
Panstrongylus megistus (Burmeister)	4.*	-	-	-	-	-	-	de Freitas and Guedes, 1961
Rhodnius prolixus Stål	3.2 -5.9	13.8 -15.8	38.3 -48.7	108 -127	237 -284	130	187 -210	Buxton, 1930; Friend *et al.*, 1965 Goodchild, 1955; Pippin, 1970
Triatoma dimiata (Latreille)	4.5 -5.4	11.1 -13.3	42.3 -47.1	87.6 -89.5	174 -282	220	283	Zeledón *et al.*, 1970
Triatoma gerstaeckeri (Stål)	3.9 -4.0	7.4 -8.6	27.4 -34.4	56.8 -61.2	186 -192	133	218	Pippin, 1970; Thurman, 1945
Triatoma infestans (Klug)	1.5	4.0	10.0	107 -186	195 -382	440 *	307	de Freitas and Guedes, 1961 Goodchild, 1955
Triatoma sanguisuga (LeConte)	-	-	-	-	-	43	61	Hays, 1965
Triatoma sanguisuga texana Usinger	1.2	4.2	11.6	46.2	129.7	52.6	79.4	Pippin, 1970

* Indicates a μl value, all others are in mg.

Table 1B. Blood meal size of female mosquitoes.

Species	Meal size	References
Aedes aegypti (L.)	2.1- 4.5 mg	Garnham, 1947; Gwadz, 1969; Howard, 1962; Jeffery, 1956; Lea, 1967; Roy, 1936
	1.6- 4.2 µl	Bennett, 1965; Boorman, 1960; Jeffery, 1956
Aedes cantans (Meigen)	5.9 mg	Service, 1968a
Aedes cinereus Meigen	2.6 mg	Service, 1968a
Aedes detritus (Haliday)	3.5 mg	Service, 1968a
Aedes hexodontus Dyar	⩽5.5 mg	Barlow, 1955
Aedes infirmatus Dyar and Knab	4.9 mg	Woodard and Chapman, 1965
Aedes punctor (Kirby)	4.0 mg	Service, 1968a
Aedes sollicitans Walker	3.9- 8.5 mg	Lea, 1967; Woodard and Chapman, 1965
Aedes sticticus (Meigen)	2.1 mg	Stage and Yates, 1936
Aedes taeniorhynchus (Wiedemann)	3.2- 3.8 mg	Gwadz, 1969; Lea, 1967; Woodard and Chapman, 1965
Aedes triseriatus (Say)	3.93 mg	Gwadz, 1969
Aedes vexans (Meigen)	2.1- 4.7 mg	Stage and Yates, 1936; Woodard and Chapman, 1965
Anopheles albimanus Wiedemann	2.6 mg	Jeffery, 1956
Anopheles litoralis King	2.1 mg	Laurel, 1934
Anopheles ludlowae (Theobald)	2.1 mg	Laurel, 1934
Anopheles maculatus Theobald	2 mg	Laurel, 1934
Anopheles minimus Theobald	1 mg	Laurel, 1934
Anopheles quadrimaculatus Say	2.3- 5.5 mg	Gwadz, 1969; Jeffery, 1956; Woodard and Chapman, 1965
Armigeres subalbatus (Coquillett)	3.7 mg	Gwadz, 1969
Culex pipiens quinquefasciatus Say	2.0- 5.0 mg	Rachou *et al.*, 1957; Wharton, 1960; Jordon and Goatly, 1962; Gwadz, 1969
	1.0-10. µl	O'Connor and Beatty, 1937; de Freitas and Guedes, 1961
Culex salinarius Coquillett	2.1 mg	Woodard and Chapman, 1965
Culiseta annulata (Schrank)	7.0 mg	Service, 1968a
Culiseta inornata (Williston)	4.5 µl	Owen and Reinholz, 1968
Mansonia perturbans (Walker)	4.3 mg	Woodard and Chapman, 1965
Mansonia richiardii (Ficalbi)	3.3 mg	Service, 1968a
Psorophora ciliata (Fabricius)	25.0 mg	Woodard and Chapman, 1965
Psorophora confinnis (Lynch Arribalzaga)	6.0 mg	Woodard and Chapman, 1965
Psorophora cyanescens (Coquillett)	9.2 mg	Woodard and Chapman, 1965
Psorophora ferox (Humboldt)	5.1 mg	Woodard and Chapman, 1965

Table 1C. Blood meal sizes of some flies. Data are from females except where otherwise indicated.

Species	Meal size	References
Ceratopogonidae		
Phlebotomus papatasi Scopoli	0.1 mg	Adler and Theodor, 1926
Leptoconops kerteszi Kieffer	0.23 mg	Foulk, 1967
Simuliidae		
Prosimulium decemarticulatum (Twinn)	2.2 µl	Bennett, 1963
Simulium aureum Fries	2.9 µl	Bennett, 1963
Simulium croxtoni Nicholson and Mickel	3.26 µl	Bennett, 1963
Simulium damnosum Theobald	1.08 µl	Crosskey, 1962
Simulium latipes (Meigen)	2.65 µl	Bennett, 1963
Simulium quebecense Twinn	2.14 µl	Bennett, 1965
Simulium rugglesi Nicholson and Mickel	1.36 mg 1.94 µl	Anderson *et al.*, 1962; Bennett, 1963
Tabanidae		
Chrysops dimidiata Van der Wulp	19.7 µl	Kershaw *et al.*, 1956
Chrysops silacea Austen	24.2 - 30 µl	Gordon and Crewe, 1953; Kershaw *et al.*, 1956
	40 mg	Kershaw *et al.*, 1954
Hybomitra frontalis (Walker) (= *T. septentrionalis*)	27 mg	Miller, 1951
Hybomitra affinis (Kirby)	156 mg	Miller, 1951
Tabanus quinquevittatus Wiedemann	71 mg	Tashiro and Schwardt, 1949
Tabanus sulcifrons Macquart	344 mg	Tashiro and Schwardt, 1949
Muscidae		
Glossina austeni Newstead (♂)	11.4 mg	Langley and Abasa, 1970
(♀)	19.9 mg	Langley and Abasa, 1970
Glossina brevipalpis (♂) Newstead	107. mg	Moloo and Kutuza, 1970
Glossina morsitans (♂)	34 mg	Lester and Lloyd, 1928
Westwood (♀)	37 mg	Lester and Lloyd, 1928
Glossina palpalis (♂)	22.74- 33.70 mg	Mellanby, 1936
(Robineau-Desvoidy) (♀)	25.13- 41.67 mg	Mellanby, 1936
Glossina tachinoides (♂)	30 mg	Lester and Lloyd, 1928
Westwood (♀)	28 mg	Lester and Lloyd, 1928
(?)	8.94- 14.00 mg	Buxton and Lewis, 1934
Stomoxys calcitrans (L.) (♂)	6.9 - 9.45 mg	Anderson and Tempelis, 1970; Suenaga, 1965
(♀)	10.5 - 16.43 mg	Anderson and Tempelis, 1970; Suenaga, 1965
(?)	25.8 mg	Parr, 1962

or through a membrane) were investigated. The results showed that the major factor in determining the destination of the meal in the alimentary canal was its composition. Similar results were reported for *Phlebotomus papatasi* (Adler and Theodor, 1926), *Simulium damnosum* (Lewis, 1953), *Simulium venustum* Say (Yang and Davies, 1968b), *Culicoides nubeculosus* Meigen (Megahed, 1956, 1958), *Chrysops* and *Tabanus* (Wigglesworth, 1931). Although *Anopheles maculipennis* Meigen generally dispatched blood to the midgut only, about 1/3 of the mosquitoes also had some blood in the ventral diverticulum (Wright, 1924). It has been claimed that *A. aegypti* but not *A. albimanus* (reported as *Anopheles tarsimaculatus*) passed blood first into the diverticula and then within half an hour of feeding into the midgut (Pawan, 1937). A honey - citrated blood mixture fed to *A. maculipennis, C. pipiens,* and *A. aegypti* (recorded as *Aedes argenteus*) went to the diverticula. The ventral diverticulum filled first, followed by the dorsal diverticula after unusually large meals (MacGregor and Lee, 1929). Radiographic studies *in situ* of the distribution of sugar solutions and blood meals in the digestive tract of *A. aegypti* showed that sugar meals could be moved from one diverticulum to another and that during ingestion of a blood meal the hind most part of the midgut filled first (Guptavanij and Venard, 1965).

Among some flies however, (*Glossina* sp., Wigglesworth, 1931; *Stomoxys calcitrans,* Champlain and Fisk, 1956; *Hippelates pallipes* (Loew), Kumm, 1932) the blood meal goes first to the oesophageal diverticulum and then to the midgut. In the eye gnat, *H. pallipes,* only a small quantity of blood goes directly to the midgut. Within 30 mins of feeding the gnats begin transfering blood from the crop to the midgut and by 6 hours after feeding about half of the meal is transferred. The blood blackens in the midgut as digestion takes place. By 2 days after feeding the crop is empty (Kumm, 1932). The first portion of a blood meal ingested by tsetse flies (*Glossina morsitans* and *Glossina tachinoides*) is conveyed to the midgut where it is localized in 3 regions, a clot forming in the most posterior. Additional blood is dispatched to the crop (esophageal diverticulum) but it does not clot there. By 2.5 hours after feeding most of the blood passes from the crop into the midgut which is now more or less continuously full of blood. The blood at the posterior end of the midgut clots and progressively darkens while the blood in the anterior of the midgut does not clot and is bright red. By 24 hours after the meal the crop is empty and the blood in the midgut is again divided into regions by folds in the gut. The blood in the anterior part of the midgut forms a pasty mass as a result of absorption of most of the serum but a true clot does not form. The blood cells in this region of the midgut are contained in a mucilaginous secretion from the gut cells. By 48 hours the blood mass in the gut greatly decreases and the dark mass progressively contracts posteriorly (Lester and Lloyd, 1928).

When blood only is fed to *A. aegypti* it is dispatched to the midgut in all individuals, traces being found in the diverticula of only 6% of the mosquitoes (Day, 1954). Increasing the concentration of glucose in a blood-glucose mixture increases the frequency with which meals go to the diverticula. At concentrations above 0.46 M glucose all mosquitoes send the meal to the diverticula, only 7 to 10% also convey food to the midgut. These results indicate that there are receptors in this mosquito for both glucose and some component of blood. *A. aegypti* can detect sucrose and probably arabinose, mannose, and raffinose but not lactose when mixed with blood. Although both plasma and erythrocytes are detected solutions of haemoglobin and albumin with glucose go mainly to the diverticulum. Mosquitoes feeding on very dilute erythrocyte suspensions in sugar dispatch the sugar solution to the diverticulum and the erythrocytes to the midgut. This is apparently accomplished by a group of spines in the neck of the diverticulum which are capable of acting as a seiving mechanism when particles are sparse. Experiments with red cell ghosts and fly sarcosomes in water indicate that the particulate nature of the erythrocytes is one factor in blood detected by

the mosquito. Day (1954) explained the distribution of fluids by proposing that the pit organs in the buccal cavity detect sugars and the resulting impulses mediate the relaxation of the diverticula sphincter muscles. Similarly, the papillar sense organs detect components of the blood and relaxation of the cardiac sphincter permits blood to enter the midgut.

Hosoi (1954) reported upon the mechanism by which *Culex pipiens* (issp) *pallens* distributes fluids to the midgut and diverticula. As in other mosquitoes, sugary solutions go to the diverticula and blood to the midgut. Dilute suspensions of erythrocytes in saline go to the midgut but if glucose is added to the meal there is an increased tendency to dispatch the meal to the diverticula. Replacing the erythrocytes with other particulate matter in a 5% glucose solution generally results in the meal being dispatched to the diverticula - thus indicating that the particulate nature of a blood meal is not the only stimulus for dispatching food to the midgut. Hosoi suggested that erythrocytes have, adsorbed to their surfaces, substances which are responsible for stimulating certain sense organs. Sensory receptors on the labium respond to glucose but not to erythrocytes while the reverse is true for receptors on the fascicle. However the existence of other sense organs capable of differentiating the meal composition was not excluded.

Theories concerning the biological importance of the retention of sugars in the diverticula were reviewed by Trembley (1952), Megahed (1958), and Christophers (1960, p. 489). Two of these theories pertain to digestive physiology. One is that the carbohydrate meal is stored in the diverticula so that the hunger mechanism, which is presumed to originate in the midgut, is not interfered with, and the mosquito is thus always ready to take blood (Day, 1954). The other is that by storing carbohydrate solutions in impervious structures the mosquito carries with it a supply of water which may be passed to the midgut for absorption as needed. If the second theory is correct, then the mosquito's physiology is adapted to conserving water from a carbohydrate meal while disposing of much of the water in a blood meal (Boorman, 1960; Howard, 1962). Denisova (1949) investigated the function of horsefly diverticula by injecting water and salt solutions into the flies. She concluded that the diverticula store water which is supplied in small amounts to the midgut minimizing rapid drops in haemolymph osmotic pressure. However, it seems doubtful that nectar solutions, with their high sugar content, would significantly lower the osmotic pressure of insect haemolymph if dispatched directly to the midgut.

The inhibition of honeybee proteolytic enzymes by honey (Bailey, 1952) suggests that nectar may contain substances which inhibit insect proteinases. The diverticula of insects which consume both nectar and blood may thus function as a mechanism for separating inhibitors present in one type of meal from the digestive enzymes required to digest another type of meal. MacGregor (1930) stated that "Poisonous fluids invariably enter the diverticula" of mosquitoes and gave as an example the ingestion of 20% formalin. The mosquitoes died immediately after the diverticula filled and traces of formalin passed into the midgut. This was interpreted as indicating that absorption did not take place from the diverticula.

THE SALIVARY GLANDS AND THEIR SECRETIONS

Since saliva is usually the first insect secretion to which the blood meal is exposed there has been considerable interest in the effects of saliva upon blood. Bates (1949) suggested that anticoagulins and haemagglutinins from the salivary glands of mosquitoes assist in the preliminary breakdown of the blood meal. Fisk (1950) suggested that coagulation or agglutination of the blood meal denatures its proteins sufficiently to permit attack by mosquito proteinases. Regrettably these suggestions have not been investigated.

Aedes aegypti feeding upon suckling mice left an average of 4.7 μg of saliva in the mice

during consumption of a meal (Devine et al, 1965). Probably because of the minute amount of saliva secreted by blood-sucking insects, most investigators have used homogenates of the salivary glands to test for a variety of enzymes, haemolysins, agglutinins, and anticoagulins. The most commonly encountered are agglutinins and anticoagulins; a summary of their occurrence among the blood-sucking insects is given in table 2.

The ability of salivary gland emulsions to cause agglutination sometimes depends upon the source of the erythrocytes. *A. maculipennis* salivary glands agglutinate erythrocytes from man, donkey, rabbit, and dogs, but not those from mice, guinea-pigs, or monkey (York and Macfie, 1924; confirmed for white mice by Shute, 1935). The agglutinin from *A. quadrimaculatus* is effective against red blood cells of man, mule, cow, pig, dog, rabbit, guinea-pig, rat, and mouse but not chicken or turtle (Metcalf, 1945).

Agglutinins are restricted to the median acinus of the salivary glands of *A. maculipennis* (de Buck 1937) and *A. quadrimaculatus* (Metcalf, 1945) but occur in all three acini of *C. annulata* salivary glands (de Buck 1937). Solutions of these agglutinins are heat labile (York and Macfie, 1924; de Buck 1937; Metcalf, 1945). The agglutinin from *A. maculipennis* was reported by York and Macfie (1924) to be inactivated by desiccation, but by de Buck (1937) to be stable for several months at room temperature or for 1 hour at 99 C when dried. Similar properties for the agglutinin from *C. annulata* were reported by de Buck (1937).

Baptist (1941) reported that the anticoagulin in *R. prolixus* salivary glands was inactivated by heating to 70 C but Hellmann and Hawkins (1964) reported this anticoagulin was stable at 60 or 80 C for 30 mins, was not affected by 0.1 N HCl or 0.1 N NaOH at R.T. or 60 C for 30 mins but was completely destroyed by heating to 100 C for 5 mins. It was not precipitated by centrifuging at 100,000 g for 30 mins but was removed from solution by dialysis in the cold. This anticoagulin (designated Prolixin-S by Hellmann and Hawkins, 1965) did not inhibit thrombin, but acted mainly upon factor VIII (the antihaemophilic factor). Prolixin-S retained its activity upon freezing, freeze drying or dialysis but was inactivated by trypsin.

Anticoagulin cannot be detected in *R. prolixus* midgut immediately after feeding but is found 4 hours later. Fractionation of the gut contents indicate that the anticoagulin is probably present but inhibited by some component of the blood meal (Hellmann and Hawkins, 1965). A salivary gland anticoagulin from *T. rubofasciata* is inactivated by normal rabbit serum but not by serum from a rabbit used as a host for one year (Cornwall and Patton, 1914). A salivary gland anticoagulin from *T. maculata* is not an anti-thrombin and is slightly less heat stable than that of *R. prolixus* (Hellmann and Hawkins, 1966).

Anticoagulin occurs in all three acini of the salivary glands of *C. pipiens* (de Buck 1937), *A. quadrimaculatus* (Metcalf, 1945), *A. plumbeus* and *A. maculipennis* (de Buck, 1937). However, in the latter species its concentration in the lacteral acini is very low. The anticoagulin from *A. maculipennis* is stable at R.T. for several months when dried and is heat stable as either a desiccated preparation (99 C for 1 hr) or saline solution (100 C for 35 mins) (de Buck, 1937). Anticoagulins from *C. pipiens* and *C. annulata* are stable when desiccated but are more heat labile than the anticoagulin from *A. maculipennis* (de Buck 1937). The *A. quadrimaculatus* anticoagulin is thermostable (Metcalf, 1945).

The anticoagulins from the salivary glands of *G. tachinoides* and *G. morsitans* are non-dialyzable and that of the former species is not markedly affected by 0.1 N KOH or 0.1 N HCl. They are stable at temperatures up to 90 C but at this temperature lose half their activity in 15 mins and all activity in 30 mins; at 100 C all activity is lost in 15 mins. From experiments with fibrinogen solutions and citrated blood, Lester and Lloyd (1928) suggested that the tsetse fly anticoagulin is an antikinase. They found that although the delay

Table 2. Agglutinins, coagulins and anticoagulins in some blood-sucking insects.

Species	Salivary Glands		Midgut		References
	Agglutinin	Anticoagulin	Coagulin	Anticoagulin	
Lice					
Pediculus humanus L.		+			Nuttall, 1917a
Pthirus pubis (L.)		+[1]	+[2]		Grúsz, 1923
Bugs					
Cimex lectularius L.		+			Puri, 1924; Baptist, 1941
Cimex hemipterus Fabricius (= *Cimex rotundatus*)		–	–		Cornwall and Patton, 1914
Rhodnius prolixus Stål		+			Baptist, 1941
		+		+	Hellmann and Hawkins, 1964, 1965
Triatoma infestans (Klug)		+			Baptist, 1941
Triatoma maculata (Erichson)		+		+	Hellmann and Hawkins, 1966
Triatoma rubrofasciata (DeGeer)		+		+	Cornwall and Patton, 1914
Sandflies					
Phlebotomus papatasi Scopoli	–	+		+	Adler and Theodor, 1926
Mosquitoes					
Aedes aegypti (L.)	–	–			Yorke and Macfie, 1924; Metcalf, 1945
		–			McKinley, 1929
	–				Gorden and Lumsden, 1939
Aedes aegypti (= *Aedes calopus*)	–				Shute, 1935
Aedes detritus (Haliday)	–				Shute, 1935
Aedes rusticus (Rossi)	–				Shute, 1935
Aedes vexans (Meigen)	–	–			Metcalf, 1945

Present +, not found –, those not checked for are left blank; [1] present in head and thorax, [2] present in abdomen.

Table 2 (continued)

Species	Salivary Glands		Midgut		References
	Agglutinin	Anticoagulin	Coagulin	Anticoagulin	
Mosquitoes (continued)					
Anopheles claviger (Meigen)	–				Shute, 1935
Anopheles crucians Wiedemann	+	+			Metcalf, 1945
Anopheles jamesii (Theobald)	+	+			Cornwall and Patton, 1914
Anopheles labranchiae atroparvus VanThiel (= *An. m.* var. *atroparvus*)	+				Shute, 1935
Anopheles maculatus (Theobald)	–				Shute, 1935
Anopheles maculipennis Meigen	+	+			Yorke and Macfie, 1924
	+	+	–		de Buck *et al.*, 1932
	+	+		+	de Buck, 1937
	+				Shute, 1948
Anopheles maculipennis Meigen var. *maculipennis*	+				Shute, 1935
Anopheles maculipennis var. *messeae* Falleroni	+				Shute, 1935
Anopheles plumbeus Stephens	–				Shute, 1935
	–	+			de Buck, 1937
Anopheles punctipennis (Say)	+	+			Metcalf, 1945
Anopheles quadrimaculatus Say	+	+			Metcalf, 1945
Anopheles rossi Giles	+	+			Cornwall and Patton, 1914
Anopheles stephensi Liston	–				Shute, 1948
Anopheles subpictus Grassi	+	+			Cornwall and Patton, 1914
Culex pipiens quinquefasciatus Say	–				Shute, 1935
Culex pipiens L.		–			Nuttall and Shipley, 1903 Yorke and Macfie, 1924
	–				Shute, 1935
	–	+	+		de Buck, 1937

Table 2 (continued)

Species	Salivary Glands		Midgut		References
	Agglutinin	Anticoagulin	Coagulin	Anticoagulin	
Mosquitoes (continued)					
Culex restuans Theobald	–	–			Metcalf, 1945
Culex salinarius Coquillett	–	–			Metcalf, 1945
Culiseta annulata (Schrank)			+		de Buck *et al.*, 1932; de Buck, 1937
	+	+			de Buck, 1937
	–				Shute, 1935
		–			Yorke and Macfie, 1924
Psorophora discolor (Coquillett)	–	–			Metcalf, 1945
Mansonia richiardii (Ficalbi)	–				Shute, 1935
Horse flies					
Tabanus albimedius Walker	+				Cornwall and Patton, 1914
Muscoid flies					
Gasterophilus intestinalis (DeGeer)		+			Tatchell, 1958
Glossina morsitans Westwood		+	+	+	Lester and Lloyd, 1928
Glossina tachinoides Westwood		+			Yorke and Macfie, 1924
		+			Lloyd, 1928
		+	+	+	Lester and Lloyd, 1928
Hippobosca L. sp		–			Wigglesworth, 1930
Musca convexifrons Thomson		–	+		Cornwall and Patton, 1914
Musca crassirostris Stein (= *Philoematomyia insignis*)		+	+	–	Cornwall and Patton, 1914
Musca nebulo Wiedemann		–	–		Cornwall and Patton, 1914
Musca pattoni Austen		+	+		Cornwall and Patton, 1914
Stomoxys calcitrans (L.)		–	+		Cornwall and Patton, 1914
Stomoxys (probably *indica* Picard)		–	+		Cornwall and Patton, 1914

in clotting of sheep's blood is a function of the number of glands present, a simple straight line relationship is not obtained.

The anticoagulin in the salivary glands of *M. crassirostris* (reported as *Philoematomyia insignis*) is only slightly inactivated by heating to 100 C for 10 mins. This anticoagulin is probably non-antigenic in rabbits and rats. However normal sera of calf, rat, and rabbit contain one or more substances which inactivate the anticoagulin. Unlike sodium citrate inhibition of coagulation, the anticoagulin from *M. crassirostris* is not overcome by addition of $CaCl_2$. Anticoagulin activity of female salivary glands is greater than that of males. Newly emerged adults appear to have less anticoagulin than older adults which have had an opportunity to feed (Cornwall and Patton, 1914).

Hemolytic activity of salivary gland emulsions has never been demonstrated, although it has been tested for in *C. pipiens* (Nuttall and Shipley, 1903; Yorke and Macfie, 1924), *A. aegypti* (Yorke and Macfie, 1924; McKinley, 1929), *C. annulata,* and *G. tachinoides* (Yorke and Macfie, 1924), and *P. papatasi* (Adler and Theodor, 1926).

Although salivary glands have frequently been examined for digestive enzymes these have rarely been demonstrated. Salivary glands of *C. lectularius, R. prolixus,* and *T. infestans* do not have demonstrable amounts of protease, lipase, invertase, or amylase (Baptist, 1941). Although esterases occur in the salivary gland tissues of *Anopheles freeborni* and *A. aegypti* they are not demonstrable in the salivary secretions (Frevogel, Hunter and Smith, 1968). Roy (1937) examined the salivary glands of *G. intestinalis* and found no amylase, lipase, maltase, lactase, pepsin or trypsin, but he did find a milk-clotting (proteolytic) enzyme. The existance of this milk clotting enzyme was confirmed by Tatchell (1958) who also demonstrated invertase, maltase, and amylase; the later with a pH optimum at 6. Wigglesworth (1929) reported that *Glossina morsitans submorsitans* Newstead and *G. tachinoides* salivary glands did not contain amylase, invertase, maltase, lactase, trypsin, pepsin, or peptidase. However, the salivary glands of *Glossina austeni* contain a factor which activates plasminogen (Hawkins, 1966). This or a similar material is also found in the crop, midgut, and hindgut where presumably it contributes to the lysis of the blood clot. A weak amylase occurs in *S. calcitrans* salivary glands (Champlain and Fisk, 1956). However, Roston and Gamal-Eddin (1961) found no evidence for amylase or proteinase (active at pH 6, 7, or 8.3) in the salivary glands of *S. calcitrans, Stomoxys sitiens* Rondani, or *Musca vitripennis* Meigen. The salivary glands of larvae of *Protocalliphora avium* Shannon and Dobroscky (reported as *Apaulina avium*) contain butyrase and a weak maltase (Rockstein and Kamal, 1954).

Metcalf (1945) found no evidence of protease, lipase, amylase, or lecithinase-A in the salivary glands of *A. quadrimaculatus.* Wigglesworth (1931) reported that *Chrysops* and *Glossina* salivary glands contained a lipase. No invertase occurs in the salivary glands of *Prosimulium fuscum* Syme & Davies, or *Simulium venustum* (Yang and Davies, 1968c).

No cytological changes were detected in the salivary glands of *A. aegypti* immediately after feeding on sugar or human blood but histochemical changes observed in the glands during the 24 hours following a blood meal led to the conclusion that "feeding depletes the glands and that this depletion leads to the resynthesis of secretory products" (Orr, Hudson and West, 1961).

The salivary glands of female blackflies (probably *S. venustum*) contain a Periodic acid-Schiff positive material prior to the time a blood meal is taken. This material is present in only small amounts in the glands immediately after feeding, but reappears during the next 96 hours (Gosbee, Allen, and West, 1969).

A major function of anticoagulins in saliva appears to be the prevention of premature clotting of the blood meal. Lloyd (1928) reported that removal of the salivary glands of *G.*

tachinoides did not prevent feeding on humans, but sooner or later the flies died with a blood clot in the proboscis or oesophagus. *Aedes stimulans* (Walker) whose salivary ducts had been cut ingested blood in a normal manner and developed eggs. No observable difference between the blood clot in the midgut of operated and control mosquitoes could be detected (Hudson, Bowman, and Orr, 1960).

GROSS CHANGES IN QUANTITY & QUALITY OF THE GUT CONTENTS.

Mosquitoes feeding on chicks with heavy *Plasmodium gallinaceum* Brumpt infections may defecate 20 to 50% of the meal within a few hours (Howard, 1962). The discharge of blood during and following feeding seems to favour the elimination of gametocytes thus reducing the intensity of the infection in the mosquitoes (Mitzmain, 1917). When undisturbed *Anopheles gambiae* Giles and *Anopheles funestus* Giles will engorge until blood is passed from the anus; sometimes the amount of blood passed is at least half the volume ingested (Hocking and MacInnes, 1949). Neither the coagulation time nor the blood corpuscles are affected by this rapid passage through these mosquitoes. The fluid defecated by *Aedes aegypti* during and just after feeding contains uric acid, simple proteins or amino acids, and occasionally red blood corpuscles but no reducing sugars (Boorman, 1960). The volume of the fluid passed is approximately 1.5 μl; some of this comes from the serum while the remainder (actually the first few drops passed) containing uric acid, is probably present in the hind gut at the time of feeding.

The discharge of material from the anus during and just after feeding has been observed in *Pediculus humanus* (Nuttall, 1917b), tsetse flies (Lester and Lloyd, 1928), and *Culicoides nubeculosus* (Megahed, 1958).

The relatively great changes in the size and shape of the abdomens of some blood-sucking insects occurring during feeding and the translucence of the abdominal pleura have permitted observations on digestion with no more than a dissecting scope or hand lens. Frequently, these observations could be made in more detail by simply dissecting the insect and without the use of elaborate histological techniques.

Sella (1920a) divided the digestion of blood and the development of the ovaries into 7 stages. These stages were summarized by Detinova (1962, p. 57) who also reviewed aspects of blood digestion relating to age-grouping methods and studies of ovarian development. Modification of Sella's (1920a) method have been developed by several workers (Hocking and MacInnes, 1949 for *Anopheles*; Jackson, 1933 for *Glossina*; Linley, 1965 for *Leptoconops*).

Blood ingested by *Culex pipiens quinquefasciatus (C. fatigans)* turns black within 6 hours and the abdomen is 3/4, 2/3, 1/2, slightly less than 1/2, and less than 1/3 distended at 12, 24, 36, 48 and 60 hours after a blood meal (O'Gower, 1956). In the tropics *Anopheles* species generally take 2 days to digest a blood meal and develop eggs but *Anopheles vagus* Dönitz requires only 24 hours to accomplish these same processes in Assam, India (Muirhead-Thomson, 1951).

Chicken blood ingested by *A. aegypti* clots in about 30 minutes compared to 25 minutes for the same volume on a glass slide (Howard, 1962). By 45 minutes a clear yellowish border forms around ingested blood and this adheres to the surfaces of both the midgut cells and the blood meal. This adherence persists for about 12 hours by which time the peritrophic membrane is being formed. By 24 hours the meal becomes a comparatively firm clot, and although its volume decreases its consistency does not change after that time. By 72 hours after feeding the midgut is usually empty.

Gross changes in the appearance of the blood meal of *A. aegypti* fed on a rat have

been reported by Akov (1965). The blood is bright red immediately after ingestion. As digestion proceeds inwards from the periphery the blood meal turns brown. By 24 hours the meal is brown except for the center. Akov considered digestion to be complete and elimination of the residue to begin when the color of the blood was brown throughout. On this basis digestion is complete and defecation begins by 36 hours. The size of the blood clot decreases and the midgut wall becomes folded. By 42 hours after feeding 2/3 of the females have empty midguts and 1/3 contain small residues of blood. By 48 hours about 1/4 of the mosquitoes contain residues in the midgut or hindgut. Elimination of blood residues is complete in all mosquitoes by 54 hours after feeding.

Feeding increasing concentrations of 5-fluorouracil (5-FU) to *A. aegypti* for 2 days prior to a blood meal results in an increasing tendency for the mosquitoes to retain undigested blood in the midgut (Akov 1965). However, the rate of digestion of a subsequent blood meal is normal. Similar results are produced with *A, aegypti* (1) fed metepa, apholate, or tepa for 2 days prior to a blood meal, (2) held in contact with a metepa treated glass surface or (3) irradiated with from 2,000 to 32,000 r (from a Co^{60} source) (Akov, 1966). Irradiation of the mosquitoes does not influence the rate at which Evan's blue stained Dextran passes from the midgut. This indicates that the delay in emptying the midgut of a blood meal, by *A. aegypti* treated with irradiation or chemosterilants, is due not to an effect upon the gut mobility but upon the rate at which the digestion products are absorbed and utilized (Akov, 1966). In mosquitoes of the same age, the evacuation rate is lower during the second meal than during the first.

There are individual differences in the rate of digestion by *Anopheles punctulatus* Dönitz (MacKerras and Roberts, 1947). In this species about 25% of the females still have blood in the midgut 72 hours after feeding. MacKerras and Roberts suggested that if a large amount of blood is present at 48 hours the *Plasmodium* Marchiafava and Celli ookinetes may be imprisoned in this mass. The mean time for gut emptying is 48 hours for *A. gambiae* and 60 hours for *A. funestus* with considerable variation in the rate of digestion in both species (Hocking and MacInnes, 1949). In *A. gambiae* evacuation time varies from 24 to 72 hours; in *A. funestus* from 24 to 96 hours. *Anopheles maculipennis* whose ovaries are developing digest their blood meal in 73.4 to 87.1 hours, while parous females whose ovaries are not developing require 57.7 to 60 hours (Detinova, 1962). These findings led Detinova to suggest that neuro-hormonal regulation of digestion may occur in mosquitoes. There is a slight but significant decrease in the digestion rate with aging and Detinova (1962) reported that it takes longer to digest the first meal than to digest subsequent meals. This latter finding is the opposite of that reported for *A. aegypti* (Akov, 1966).

Digestion of blood is quite different in "long winged" and "short winged" *A. maculipennis* when they are overwintering (de Buck, Shoute, and Swellengrebel, 1932). For at least the first 24 hours, the blood ingested by the "long winged" females is divided into an anterior translucent half and a posterior, opaque, cellular mass. The erythrocytes show very little agglutination when the midgut is dissected in saline. At 24 to 26 C, digestion of the meal proceeds very slowly, requiring 5 or 6 (occasionally 10) days before the red colour (indicating undigested blood) disappears. In the "short-winged" females the sequence of events is quite different. Within half an hour of feeding the serum is absorbed from the lumen of the midgut leaving the cells in close contact with the gut epithelium. There is a marked agglutination of red cells and the digestion of the meal proceeds rapidly if the temperature is sufficiently high. If given more than one meal, a certain portion of the "long winged" population digests blood in the same manner as the "short-winged" females (de Buck, Torren, and Swellengrebel, 1933). The differences in digestion by "long-winged" and "short-winged" *A. maculipennis* are not observed during the summer.

Variations in digestion rate occur in *Anopheles claviger.* These are correlated with the season (Sella, 1920a) and with environmental temperature (Sella, 1920b). In *A. maculipennis* the rate of digestion of the blood meal slows down as the temperature falls in the autumn, (Guelmino, 1951). The unchanged condition of the red cells suggests that digestion and absorption in the fall are limited to water soluble materials that can be used to develop adipose tissue (Guelmino, 1951).

Detinova (1962 p. 57), reviewing some aspects of the digestive process in *A. maculipennis,* stated that "if the temperature rises to the optimum the speed of the processes increases, but at temperatures above the optimum they slow down".

Culiseta annulata taken from the Poole area of Dorset, southern England require 4 weeks to digest a blood meal "at temperatures experienced in November - February" (Service, 1968b). Other species (*A. claviger, C. annulata, Mansonia richiardii, Aedes dorsalis* (Meigen), *Aedes geniculatus* (Olivier), *Aedes detritus, Aedes punctor, Aedes cantans,* and *Aedes cinereus*) in this same area (Brownsea Island, Dorset) take 5 to 8 days to digest a meal of human blood during May to August or September (Service, 1968a).

Australasian anophelines complete digestion of a blood meal in 3 to 4 days under summer conditions (Roberts and O'Sullivan, 1949). Büttiker (1958) observed *Anopheles culicifacies* Giles and *Anopheles aconitus* Dönitz in several locations in southeast Asia which were in a quiescent state and whose midguts contained a blood meal which was "dark red, coagulated, very hard and almost completely dessiccated."

The digestion of blood by a mosquito may be influenced by other materials fed to the mosquito. When various species of *Anopheles* are fed alternately upon gametocyte carriers and bananas, many mosquitoes die with undigested masses of blood in their midguts (Darling, 1910). Some *A. aegypti* fed upon $CaCl_2$, $MgCl_2$, or either of these plus oxytetracycline before and after ingesting blood from a chicken, still have a residue of blood in the midgut four days later when held at 26.5 C and 75% R.H., conditions under which digestion is normally complete in 3 days (Terzian, 1958). In mosquitoes with inhibited digestive processes these undigested residues are about 1/3 the size of the original clot, are orange-red, contain no intact red cells and give a positive heme test (benzidine reaction). (The positive benzidine test indicating the presence of intact heme groups is not surprising in view of O'Gower's (1956) finding that mosquito feces give a positive benzidine test). Inhibition of digestion can be prevented by adding the chelating agent ethylene diamine tetraacetic acid to the salt-antibiotic mixture. Since mosquitoes with a large residue of undigested blood are able to produce large numbers of eggs, Terzian (1958) concluded that it was "reasonable to assume that only digestion of the hemoglobin fraction, of all the fractions contained in the original blood meal, is affected by the cations, or cation antibiotic mixture." The validity of this assumption is questionable in view of the finding that the *in vitro* activity of *A. aegypti* proteinase upon both hemoglobin and serum albumin is inhibited by $CaCl_2$, $MgCl_2$, and $MnCl_2$ (Gooding, 1966a). Terzian (1963) expanded the *in vivo* inhibition studies to include both *A. aegypti* and *Anopheles quadrimaculatus,* 4 cations, and 4 antibiotics. Digestion of blood is inhibited to varying degrees in both species by the presence of calcium, magnesium, manganese or iron in sugar solutions consumed prior to the blood meal. The action of the antibiotics is very complex. Oxytetracycline by itself has very little effect on digestion by *A. aegypti* but potentiates the action of calcium, magnesium, and manganese. It supresses inhibition by iron. However, oxytetracycline has a marked inhibitory effect on *A. quadrimaculatus* digestion, potentiates manganese only and inhibits the effect of iron. Penicillin reduces the effects of calcium and magnesium upon *A. aegypti,* but has itself an inhibitory effect on *A. quadrimaculatus* digestion. A mixture of chloramphenicol and dihydrostreptomycin in the diet of *C. pipiens quinquefasciatus* slows down

digestion of canary blood infected with *Plasmodium relictum* Grassi and Feletti to such an extent that about 1/3 of the mosquitoes still have blood in the midgut after 7 days (Micks and Ferguson, 1961). The results of these experiments with antibiotics are interesting in view of Arnal's (1950) claim that digestion of blood is initiated in *Culex pipiens* by bacteria which cause the haemolysis of the red blood cells.

Terzian and Stahler (1964) confirmed Terzian's (1963) findings and extended the observations as indicated below. *A. aegypti* completes digestion of a meal of chicken blood in about 72 hours at 26.7 C and 75% R.H. while *A. quadrimaculatus* required "at least 96 hours". Neither NaCl nor KCl at concentrations up to 0.3 M have any inhibitory effect upon digestion. Penicillin suppresses the inhibitory effects of oxytetracycline and neomycin in both species. Streptomycin inhibits digestion in *A. aegypti;* does not interact with oxytetracycline, but is suppressed by penicillin. Neomycin inhibits digestion by *A. aegypti* and *A. quadrimaculatus* and enhances the effects of calcium and magnesium markedly in the former but only slightly, of at all, in the latter. Neomycin enhances the inhibitory effect of manganese in both species. Iron suppresses the inhibitory effect of neomycin in *A. aegypti* but the inhibition by iron and neomycin are additive in *A. quadrimaculatus*. The inhibitory effects of the cations upon digestion in these mosquitoes led Terzian and Stahler (1964) to conclude that "the process of blood digestion is fundamentally the same in both species". However they suggested that the effects of the antibiotics upon a given physiological process vary with the species. Apparently these mosquitoes are able to produce viable eggs despite the inhibition of the digestion (Terzian and Stahler, 1964). This led Terzian and Stahler to conclude that the "effective inhibitory compounds do not interfere with the digestion or absorption of the plasma fraction of the blood but rather interfere with some one phase of the digestion of hemoglobin". This is essentially the same conclusion reached earlier by Terzian (1958) although no critical experiments were done to see if digestion of the serum proteins had, in fact, taken place.

Usually only female mosquitoes bite, although biting males have also been recorded (reviewed by Bates, 1949, p. 79). Whether or not the blood ingested by males is digested may vary with the species. Chao and Wistreich (1959) referred to the results of unpublished experiments indicating that male *Culex tarsalis* Coquillett could not digest force-fed blood meals and died shortly after the experimental meal. However, Russell (1931) was able to induce *C. pipiens quinquefasciatus, A. aegypti* and *Anopheles ludlowae* males to take blood meals which were dispatched to the midgut. In one male *C. pipiens quinquefasciatus* a single oocyst of *Plasmodium cathemerium* Hartman developed. No mention was made of unduly high mortality among the males. Males of *A. aegypti* and *C. pipiens quinquefasciatus* force-fed repeatedly, digested these blood meals in the same time as did the females (MacGregor, 1931).

Twenty-one of 23 blood-fed *Leptoconops (Holoconops) becquaerti* (Kieffer) held at 29.4 C emptied their guts by 40 hours after the meal. At 36.7 C 1 midge of 9 had an empty gut at 24 hours and by 28 hours 4 of the 9 midges had empty guts (Linley, 1965). Service (1968c) estimated the time for digestion of human blood by two species of midges (*Culicoides impunctatus* Goetghebuer and *Culicoides obsoletus* (Meigen) under field conditions in Dorset (southern England). During April (mean temperature 8.9 C) *C. obsoletus* took an average of 8.09 ± 0.63 days to digest its meal while in May (mean temperature 11.6 C) and June (mean temperature 15.9 C) the times were 5.79 ± 0.31 and 5.14 ± 0.39 days respectively For *C. impunctatus* the time in June was 5.15 ± 0.33 days, in July (15.6 C) 5.27 ± 0.66 days; August (15.4 C) 5.09 ± 0.22 days, in September (15.8 C) 7.38 ± 1.05 days.

Stomoxys calcitrans which are hungry at the time they are offered blood will gorge until the abdomen is "not only more than twice its usual depth, but is also about half as broad

again as the normal breadth" (Hewitt, 1914). Within half an hour the abdomen may return to its normal size and by 2 hours the red color of the gut contents will no longer be visible externally. Brown feces are first passed about 6 hours after a blood meal and these were interpreted by Hewitt as being excretion of digested blood. Defecation of brown material usually ends about 72 hours after the blood meal and this time was interpreted as the period necessary for digestion of the blood meal. Digestion time varies from 50 to 95 hours and depends in part upon the size of the meal ingested. From the number and size of fecal deposits Hewitt concluded that digestion is most rapid 26 to 52 hours after feeding. Bishop (1913) reported that the rate of digestion by *S. calcitrans* is affected by weather. On the basis of the gross appearance of the abdomen at 24 hours after a blood meal 5 of 8, at 46 hours 9 of 10, and at 70 hours 8 of 8 wild caught male *S. calcitrans* had digested their meals (Anderson and Tempelis, 1970). The corresponding figures for females were 0 of 20, 5 of 20, and 7 of 24. Anderson and Tempelis (1970) summarized previous reports of the digestive rate of *S. calcitrans* and concluded that "the host source of the blood meal and the temperature at which flies are held both also affect digestion rates". They also reported (but without presenting the data) that with nulliparous *S. calcitrans* "the time elapsing between ingestion and digestion varies according to which state of a gonotrophic cycle she is in".

Vanderplank (1947), stated that with *Glossina swynnertoni* Austen age can probably affect the duration of the hunger-cycle and "young flies in the laboratory take smaller meals and digest them quickly".

Small clear globules of unknown composition appear in the ventriculus of *Diamanus montanus* (Baker) and *Xenopsylla cheopis* (Rothschild) (but not *Polygenis gwyni* (Fox), within an hour of a blood meal but usually disappear within a day (Holenreid, 1952). Unfed *P. gwyni* (but not *D. montanus* or *X. cheopis*) have bubbles in the ventriculus which disappear 1 to 24 hours after a blood meal. The flea ventriculus is swollen and bright red just after a blood meal but shrinks and darkens as digestion proceeds and in *D. montanus* is devoid of blood residue 1 to 10 days after the meal. None of these species defecate undigested blood. Parker (1958) observed that fleas (*Cediopsylla inaequalis inaequalis* (Baker), *Thrassis bacchi gladiolis* Jordan and *Pulex irritans* L.) fed on a variety of small mammals infected with *Pasteurella tularensis* (McCoy & Chapin) generally clear their digestive tracts of the bulk of the blood meal by 36 hours.

Nuttall (1917b) reported that the rate of digestion by *P. humanus* is influenced by temperature. The ingested blood remains red and the abdomen swollen for 4 days when the insects are kept at 12 C. At 31-37 C the size of the abdominal contents decreases rapidly in a few hours and as the blood is digested it turns from red to reddish-brown and finally to black.

HISTOLOGICAL CHANGES IN THE GUT AND BLOOD MEAL

Secretory and absorptive cells are not differentiated in the midgut of the hog louse, *Haematopinus suis* (L.) and these activities apparently are carried out by all gut cells (Florence, 1921). Within an hour of feeding, erythrocytes are vacuolated but leucocytes and platelets are not. Platelets are destroyed after 2 hours. The staining properties of leucocyte cytoplasm is slightly affected within 2 hours of feeding and by 6 hours after the meal the nuclei begin to disintegrate. By 8 hours the blood is an amorphous mass.

Pediculus humanus humanus L. (= *Pediculus humanus corporis* de Geer) at 30-32 C completely destroy the erythrocytes within 4 hours of feeding on humans (Cabasso, 1947). However, when lice are fed on guinea pigs the erythrocytes remain intact for 48 hours, about which time the lice die, many with ruptured guts. The mortality rates of unfed lice and

those fed human or guinea pig blood indicate that those fed guinea pig blood starve to death. Lice consuming a single meal on guinea pigs and subsequently feeding on man live a normal life span. Cabasso concluded that *P. humanus* can not digest guinea pig blood. Kryński, Kuchta and Becla (1952) claimed that guinea pig erythrocytes rapidly haemolyzed within the gut of *P. humanus*. Using a hanging-drop technique they showed that the haemoglobin crystallized in "trigonal pyramids of various size". Crystal formation began during the feeding period and within 6 hours the gut was filled with crystals which mechanically damaged the midgut epithelium. Guinea pig haemoglobin also crystallized in the gut of *Cimex lectularius* and *Ornithodorus moubata* (Murray) but in these species the crystals decomposed without injuring the gut wall (Kryński et al, 1952).

Davies and Hansens (1945) proposed the hypothesis that "the digestive enzymes of the louse were immunologically specific and developed to act upon the blood taken by the young insect in its first meal". This hypothesis was tested by rearing *P. humanus* for 10 days on either a man or a rabbit and then transferring half of each group to another man or another rabbit. Mortality during the next 9 days was independent of whether the lice had switched host species and thus the data did not support the hypothesis.

The rate at which mouse erythrocytes and *Spirochaeta duttoni* (Novy and Knapp) are destroyed in the gut of *C. lectularius* depends upon temperature. At 12, 14, 16, 20 and 24 C erythrocytes are still intact at 278, ?122 (sic), 42, 31, and 8-24 hours after ingestion of the blood meal (Nuttall, 1908).

Erythrocytes from a sickle-cell anemia patient all exhibited the sickling form after 24 hours in the midgut of *Panstrongylus megistus* compared with only 1/3 "sickle-form" in a sealed control (Pick, 1955). Haemolysis began in 3 days and was complete by 6 days after feeding. By 15 days crystals of sickle-cell haemoglobin were observed. Crystals of normal hemoglobin were never observed in the gut of *P. megistus.*

Blood meals are stored in the expanded, anterior portion of the midgut ('stomach') of *Rhodnius prolixus* (Wigglesworth, 1936). Here the blood cells remain intact for several days and the haemoglobin red for several weeks indicating that no digestion is taking place (Wigglesworth, 1936). In the narrow, posterior portion of the midgut ('intestine') the blood turns dark brown or black indicating that this is the site of digestion.

Digestion of the blood meal by mosquitoes begins at the outer edge of the meal and proceeds inward (Davies and Philip, 1931). This occurs in *Culex pipiens* (Huff, 1934), *Aedes aegypti* (Stohler, 1957; Howard, 1962; Akov, 1965; Freyvogel and Staubli, 1965; Gander, 1968), *Anopheles stephensi, Anopheles gambiae* and *Anopheles labranchiae atroparvus* (reported as *A. maculipennis atroparvus*) (Freyvogel and Staubli, 1965).

Before engorgement the midgut epithelial cells of *A. aegypti* are columnar; during engorgement they become squamous with convex internal borders (Howard, 1962). As digestion proceeds, the cells return to their original shape. These observations were confirmed by Freyvogel and Staubli (1965) and were extended to *A. stephensi, A. gambiae* and *A. labranchiae atroparvus* (Staubli, Freyvogel and Suter, 1966). Although the shape of the epithelial cells changes in a reversible manner the shape of the tracheoles serving the midgut cells is irreversibly changed from a tight spiral before the first meal to slightly curved after the meal (Detinova, 1962).

A whorled granular endoplasmic reticulum, is present near each nucleus in the midgut cells of fasting or sugar-fed *A. aegypti*. During the ingestion of blood (by *A. aegypti* and *Aedes togoi* (Theobald), these whorls unfold. The whorls reform upon completion of digestion, and the endoplasmic reticulum may be involved in the secretion and transport of proteolytic enzymes (Bertram and Bird, 1961). These changes in *A. aegypti* were confirmed by Staubli, et al (1966). In unfed *A. labranchiae atroparvus, A. gambiae* and *A. stephensi* the

whorls found in *A. aegypti* are replaced by apical granules which disappear at the time secretions are detectable in the midgut lumen. The large globules of RNA- containing material found between the nuclei and the lumen borders of midgut epithelial cells of unfed *A. aegypti* by Dasgupta and Ray (1955) may be the whorls of endoplasmic reticulum reported by the workers cited above.

Staubli et al (1966) suggested four possible functions for the whorled endoplasmic reticulum. First, the midgut secretions (e.g. digestive enzymes) could be synthesized and stored in the whorls prior to ingestion of the blood meal, although the appearance of the whorls was not consistent with this. Second, immediately after feeding the whorls could rapidly synthesize the secreted material. Since the whorls break down into vesicles (Staubli et al, 1966) within 9 minutes of feeding it was suggested that synthesis was completed by this time. Third, synthesis of the secretory material could take place on the vesicles which arise from the whorls and fourth, the endoplasmic whorls could be concerned rather, with the absorption process. The first and second and, possibly, the second and third suggestions could be distinguished from each other by experiment. However, as far as I know the critical experiments on mosquitoes have not been done.

In *Anopheles maculipennis* the anterior midgut cells secrete a fairly large amount of a mucous-like material within 7 minutes of a blood meal. Although this mucous forms a plug at both ends of the stomach and often completely surrounds the meal the mucous "does not appear to exert any important effect on digestion, as the erythrocytes in its vicinity are hardly broken down at all" (Freyvogel and Staubli, 1965). Other species of *Anopheles* appear to produce a smaller quantity of mucus a little later than *A. maculipennis.*

In mouse-fed *A. aegypti* the midgut epithelium produces a granular secretion for up to 15 hours after feeding and the peritrophic membrane (PM) is apparently formed from this (Bertram and Bird, 1961). However, with chicken-fed *A. aegypti*, secretions in the form of discrete hemispherical droplets on the internal border of the cells first appear about 12 hours after engorgement (Howard, 1962). These droplets increase to a maximum size at about 40 hours, after which each appears to be attached to a cell by a stock. In contrast Dasgupta and Ray (1955) observed in blood fed *A. aegypti* a holocrine secretion which disintegrated when discharged into the gut lumen. Howard (1962) interpreted the droplets he observed in *A. aegypti* as the substance from which the PM forms. The PM first appears about 12 hours after the mosquitoes feed. This membrane increases in size until about 36 hours, and by 48 hours is rather brittle. As the amount of blood in the midgut decreases the PM is fragmented by the contraction of the midgut muscles. In *A. aegypti* the PM forms several hours after ingestion of the blood meal but before digestion begins (Stohler, 1957). As digestion proceeds the PM becomes harder and more brittle but subsequently softens and as the meal is digested the PM adheres to the blood meal, not the midgut cells.

Yaguzhinskaya (1940) demonstrated the presence of a chitin-containing PM in blood-fed *A. maculipennis*. The membrane forms after a blood meal and is occasionally open at the posterior end. The remnants of the membrane are defecated after the meal is digested.

A chitin containing PM forms around the blood meal in the mosquito midgut (Waterhouse, 1953a). If, after partial digestion of the first blood meal, a second meal is taken, the second meal surrounds the first and a second peritrophic membrane is formed around the entire mass of blood.

The development of the PM has been studied in *A. aegypti, A. stephensi, A. labranchiae atroparvus,* and *A. gambiae* (Freyvogel and Staubli, 1965). In the first two species age and number of blood meals have no effect on the development of the PM. However, some specimens do not develop a complete PM and in these digestion is usually abnormal. In *A. aegypti* and *A. stephensi* feeding upon man, guinea pigs, rabbits or chicken the source of the

blood meal does not affect the formation of the PM. *A. gambiae* formed a PM but *A. labranchiae atroparvus* produce nothing more than a viscous material surrounding the blood meal. However, unlike the *A. stephensi* which lack a PM, *A. labranchiae atroparvus* digest the blood meal in a normal manner. In *A. aegypti* the PM forms in 5 to 8 hours after the meal and remains until digestion is practically complete (48 hrs). In *A. gambiae* PM formation requires at least 13 hours but may persist up to 60 hrs. The corresponding times for *A. stephensi* are 32 and 72 hours. The membrane in *Aedes* spp. passes through stages described as viscous, elastic, solid and finally fragile, but in anophelines it never develops beyond a delicate membrane.

Three species (*A. aegypti, A. gambiae, A. stephensi*) which normally form a PM do not do so completely if they ingest only a small quantity of blood (Freyvogel and Staubli, 1965). Mosquitoes feeding upon a chicken injected with heparin, or upon defibrinated blood, form a PM. *A. aegypti* and *A. gambiae*, feeding upon guinea-pig serum, form the membrane but *A. stephensi* usually do not. When *A. aegypti* are given an incomplete meal on guinea pigs, followed after 10 hours by a meal on chickens, they form a PM around each meal. The PM around the anterior (chicken blood) meal is thinner than around the posterior meal.

Ringer's solution will not dissolve the *A. aegypti* PM but does dissolve those of *A. gambiae* and *A. stephensi* (Freyvogel and Staubli, 1965). However Van Wisselingh's chitosan-iodine test is positive for PM of all three species.

A. aegypti consuming less than 0.1 mg of guinea-pig blood form no PM and they must ingest at least 0.5 mg before forming a complete PM (Freyvogel and Jaquet, 1965). However, there is no correlation between blood meal size and the condition of the PM in *A. stephensi* and probably not in *A. gambiae*. Both *A. aegypti* and *A. gambiae* produce a PM when they are given an enema of physiological saline or air. The PM formed in both species after a meal of blood or serum reacts positively to Van Wisselingh's chitosan-iodine test. However Freyvogel and Jaquet reported that the results of this test on the PM formed after a saline or air enema were inconclusive.

Formation of the PM and digestion of the blood meal in *A. aegypti* and *A. stephensi* have been studied in frozen sections by Gander (1968). The PM of these species have different structural features: in *A. aegypti* it is laminar while in *A. stephensi* it consists of a granular material imbedded in a Periodic acid-Schiff (PAS-) positive substance. In their initial stages of formation the PM of both species contain Periodic acid-Schiff positive material but during blood digestion this material disappears completely from the *A. aegypti* PM and partially from that of *A. stephensi*. Histochemical tests demonstrate the presence of carbohydrates and lipids in both PM's. In *A. aegypti* cells throughout the midgut epithelium undergo an apocrine secretion while in *A. stephensi* there is a modified merocrine secretion proceeding from the posterior to the anterior end of the midgut. Gander (1968) divided blood meal digestion by *A. aegypti* and *A. stephensi* into 2 phases. Early in phase I the midgut secretes carbohydrates and lipids. In the first 10 hours after a blood meal, carbohydrates are not detectable in the epithelial cells of *A. aegypti* but can be found in those of *A. stephensi*. Enzymes are probably secreted also during this phase but only erythrocytes at the very edge of the meal show signs of breakdown. Phase I ends when the PMs form, 16 hours in *A. aegypti* and 30 hours in *A. stephensi* after feeding, and no further secretion by the midgut epithelial cells occurs. Formation of lipid droplets within the blood meal and accumulation of these on the lumen side of the PM marks the beginning of Phase II. Digestion of the blood meal proceeds inward from the periphery and the epithelial cells accumulate carbohydrates and lipids. In *A. aegypti* the peak of lipid absorption occurs before the peak of carbohydrate absorption while the reverse is true for *A. stephensi*. Peroxidases occur in the midgut epithelial cells of both species of mosquitoes during digestion of blood; their concen-

tration remains constant in *A. stephensi* but in *A. aegypti* reaches a maximum 40 hours after feeding. Gander felt that there was a descrepency between his observation that digestion proper did not begin in *A. aegypti* until about 16 hours after feeding, and the results of Fisk and Shambaugh (1952) and Gooding (1966b) which showed considerable proteinase in the gut by this time. He suggested that this discrepency was connected with the presence of trypsin inhibitors within the blood meal.

Digestion of blood by *C. pipiens* was studied by deBoissezon (1930a, 1930b), Huff (1927, 1934) and Arnal (1950) using histological techniques. Huff's observations on *C. pipiens* are similar to those made on *A. aegypti.* The rate of digestion depends upon the amount of blood ingested and upon ambient temperature (deBoissezon, 1930a, 1930b). Hemolysis of the erythrocytes is followed by crystallization of their hemoglobin. The hemoglobin crystals are dissolved by the digestive juices and absorbed and digested by cells in the floor of the wide part of the midgut. Cells in the anterior, narrow part of the midgut produce a vitreous secretion from the nucleolar region and a granular secretion from their cytoplasm. Cells in the wide part of the midgut secrete vesicles which occasionally included their nucleolei. In *C. pipiens* Arnal (1950) observed merocrine secretion in two regions of the midgut during fasting and three types of secretion after a blood meal. He concluded that digestion of blood was initiated by symbiotic bacteria which penetrated the blood meal, caused the red cells, but not the leucocytes, to swell and eventually to lyse and which also prevented clotting. Simultaneously, the midgut cells began secreting. The cells in the narrow, anterior region released granules, those at the beginning of the wide portion of the midgut released vacuoles and holocrine secretion occurred in the cells in the floor of the widest part of the midgut. Arnal stated that the pH during digestion was 6.5 to 7, and speculated that the secretions observed were trypsins capable of acting in a slightly acid medium. Stroma and the leucocytes resisted digestion, but the bacteria apparently did not as they disappeared. Iron was detected in the young cells in the floor of the midgut with the Liesegang technique. As absorption took place, the midgut contents thickened, and the haemoglobin crystallized in the midgut lumen. Haemoglobin could not be detected in the hindgut.

In *Culicoides nubeculosus* the midgut epithelium of the unfed midge has columnar cells which become more or less cuboidal on ingestion of a blood meal (Megahed, 1956). A PM, not present in the unfed insect, forms within 5 hours of feeding on blood. The membrane varies in thickness and appearance in different parts of the stomach, having villi-like structures in some regions and a laminar appearance in others. The PM is apparently secreted by the midgut epithelial cells. By 24 hours, the PM develops a perforation at its posterior end through which material may pass from the midgut to the hindgut. The PM completely surrounds the blood meal except at its posterior end but a partial disintegration of one or more layers is evident in some regions. By 48 hours the blood meal is almost completely digested but the gut still contains haematin and some evidence of the PM. After 72 hours the midgut is empty of both blood residues and the remains of the PM.

During the first 2 days after *Culicoides obsoletus* feed on human blood the gut contents solidify and become opaque but change little in volume (Jamnback, 1961). Undigested blood and small black pigment granules and rods, presumably digestion products, occur in the gut by the third day. By the fourth day the blood meal is completely digested and the gut is empty when the midges are held at 21 C.

Feng (1951) examined the formation of the PM in *Phlebotomus mongolensis* Sinton and *Phlebotomus chinensis* Newstead fed on Chinese hamsters and in *Sergentomyia squamirostris* (Newstead) (reported as *Phlebotomus squamirostris*) fed on a toad. He studied also the influence of the PM upon establishment of trypanosomes in these sandflies. In *P. mongolensis* the PM completely envelopes the blood meal and is very tough. As in mosquitoes, digestion of

the blood meal begins at the periphery and progresses inward. Digestion of the blood meal requires 5-6 days and as material is digested and absorbed, the PM shrinks to a small spindle which is passed complete into the hindgut. *Leishmania donovani* Laveran and Mesnil flagellates live only within this peritrophic sac and pass into the hindgut within it. In *P. chinensis* a PM is formed but begins to break down 3 days after feeding, fragments of it passing into the hindgut with the blood meal residue. Digestion of a blood meal in *P. chinensis* takes about 7 days. The disintegration of the PM releases the flagellates which move forward and establish themselves in the proventriculus. Ultimately they migrate forward to the mouth parts. The PM of *S. squamirostris* appears to be open at the posterior end. Digestion of a blood meal by this species is complete within 3 days. Crithidia of *Trypanosoma bocagei* França leave the midgut through the open posterior end of the PM and establish themselves in the hindgut.

In *Phlebotomus papatasi* digestion is very slow and haemolysis of the erythrocytes takes place 3 or 4 days after feeding (Adler and Theodor, 1926). "Unaltered haemoglobin is never found in the epithelial cells of the stomach but it is passed in the feces" and it was concluded that it is the plasma which is the essential component of blood and not the erythrocytes. A PM is present a day or two after a blood meal.

Peritrophic membranes occur in *Simulium anatinum* Wood, *Simulium rugglesi, Simulium aureum, Simulium latipes, Simulium quebecense, Simulium croxtoni, Simulium venustum, Prosimulium decemarticulatum, Prosimulium hirtipes* (Fries) and *Cnephia ornithophilia* Davies, Peterson and Wood, (Bennett and Fallis, unpublished work cited by Fallis, 1964); *Simulium griseicolle* Becker, and *Simulium damnosum* (Lewis, 1950), and *Simulium neavei* Roubaud (Lewis, 1960). In *S. damnosum* the PM gives a positive chitosan test (Lewis, 1950, 1953) and is formed after ingestion of blood but not sugar (Lewis, 1953). Flies interrupted during feeding have blood in both the tubular (anterior) portion and the expanded (posterior) portion of the midgut. Engorged flies have all the blood in the posterior part of the midgut. During consumption of a blood meal some of the contents of the crop apparently pass into the anterior part of the midgut. A delicate membrane forms within half a minute of completion of engorgement and this membrane is quite distinct by 30 minutes after feeding. By an hour after engorgement the laminar nature of the PM is evident, particularly in the knob of the membrane at the posterior end of the midgut. The membrane gradually turns yellow and then brown. Between 24 and 72 hours after the meal, the blood mass decreases in size and the PM breaks up (Lewis, 1953). In blackflies, digestion proceeds from the periphery toward the centre of the blood meal (Fallis, 1964, citing unpublished work of Bennett and Fallis). Cells at the centre of the blood mass may remain intact for more than 48 hours.

"Resting" cells are columnar in the 'stomach' portion of the midgut of *Tabanus albimedius* (and other *Tabanus* spp.) but are converted to flattened pavement epithelium when the midgut fills with blood (Cragg, 1920). Secretory cells casting off large droplets are seen in the midgut most frequently during the 5 minutes after feeding and are rarely found more than 1 hour after a meal. The digestive substances acting on the erythrocytes cause the formation of dark pigments, beginning at the surface of the blood meal. One day after a blood meal and later, the epithelial cells become columnar again and secrete minute droplets of undetermined fate. Cells in the anterior portion of the midgut (cardia) secrete continuously. Columnar cells reform as digestion of the meal proceeds. There is no PM. Red blood cells are normal for a short time after ingestion but soon become distorted, shrunken, and poorly stained. Stroma are detectable for 24 hours in the gut. Pigments form early and by 2 hours the stomach contents are a purple, tarry mass. About 8 hours after feeding residue from the meal begins to pass into the hindgut.

No PM forms in the gut of *Chrysops silacea* (Wigglesworth, 1931; Crewe, 1961) and observations of the gut histology of this species made at various times after a blood meal "agree exactly with those of Cragg (1920) on *Tabanus*" (Wigglesworth, 1931).

The midguts of *Glossina palpalis, Glossina submorsitans* and *Glossina tachinoides* can each be divided into 3 sections on a histological basis (Wigglesworth, 1929). In all species the anterior half has an irregular columnar epithelium and includes a narrow band of giant cells containing bacteroids. In this region the blood is concentrated by removal of water but there is no digestion of the blood components. In the next region of the midgut there are large, deeply staining cells which, during digestion of blood, produce and release large vacuolated buds of cytoplasm from their apical surfaces; these buds later disintegrate in the lumen of the midgut. Blood in this region turns dark and becomes amorphous. The posterior region of the midgut has regular, columnar epithelial cells which become vacuolated late in the digestive process - probably indicating a role for them in absorption. A PM surrounds the blood meal and it is secreted by cells of the proventriculus. Hoare (1931) confirmed in *G. palpalis*, the existence of a PM consisting of a continuous, open-ended cylinder reaching from the proventriculus to the hind gut with new material being secreted at its anterior end each time a blood meal is consumed. Yorke, Murgatroyd and Hawking (1933) also reported PM's surrounding the blood meals of *Glossina morsitans* and *G. palpalis*. Weitz and Buxton (1953) cited unpublished observations of Jackson indicating that blood remains microscopically recognizable longer in laboratory held tsetse flies than in marked flies in the field.

The anterior part of the midgut of *Stomoxys calcitrans* consists of a blood reservoir with columnar epithelial cells (Lotmar, 1949). Although these cells secrete material (probably anticoagulins), the blood cells in a meal remain unchanged and no digestion takes place. Digestion proceeds as the blood moves posteriorly through the digestive region of the midgut and cyclic changes in merocrine secretion, absorption and cell regeneration occur. The formation of fat globules in isolated epithelial cells is observed 1 to 2 hours after ingestion of blood and these cells become more numerous as digestion proceeds. Digestion is more or less complete in 24 hours.

Minchin and Thomson (1915) described the histological changes occurring in the midgut of the flea *Nosopsyllus fasciatus* (Bosc) (reported as *Ceratophyllus fasciatus*) during digestion of *Trypanosoma lewisi* (Kent) infected blood meals. After the fleas feed, the midgut cells are flattened but become columnar as the meal is digested. Within a few hours of feeding the red blood cells break down and by 24 hours the blood meal is viscous and brick-red and contains large "grains". By 48 hours the stomach contents are watery and brownish-black and contain fewer smaller "grains". By use of an iron-haematoxylin-Lichtgrün-picric acid combination the stomachs of the fleas may be divided into 2 classes - a grey-black series with a greenish tinge and a bright lemon-yellow series. In the grey-black series there are many grains and spherules suspended in the greenish "coagulated albuminous matrix" by 18-24 hours after the meal. The centre of the gut contents lacks the coarse grains and is clear. The grains become smaller as digestion proceeds and by 36 hours only greenish-grey debris next to the epithelial cells remains. Leucocytes are recognizable 24 hrs, but not 36 hours after the blood meal. Minchin and Thomson concluded that "digestion, or more probably the passage backwards toward the rectum of the undigestible remnants, of the blood-debris appears to proceed from the center... towards the periphery". The stomachs of the yellow series contain a closely packed granular material and this and the matrix are stained by the picric acid. Digestion in this series is slower than in the grey-black series and Minchin and Thomson considered the yellowish stomachs to be abnormal.

The midgut epithelium of adult fleas (*Ctenophthalmus* Kolenati sp) has intranuclear crystals in about 10% of the cells (Richards and Richards, 1969). The existence of these crystals

in the blood-feeding adult but not in the scavenging larva led to the suggestion that they are derived from the hemoglobin of the blood meal.

Waterhouse (1953b) presented data on PM's based on a rather extensive survey of insect midguts. He classified the PM's as type I, if they consisted of 1 or more layers "produced mainly or entirely by a ring of cells at the anterior end of the midgut" and as type II, if they consisted "typically of a series of thinner, coaxial layers and arises by periodic delamination from the surface of the striated border of a layer of material secreted from the whole midgut epithelium". Type II PM's occur in adult mosquitoes (*A. aegypti, Culex pipiens quinquefasciatus*) and tabanids (*Dasybasis froggatti* (Ric.), *Scaptia jacksoniensis* (Guer.) and *Scaptia gattata* (Don) while type I PM's are found in the Nycteribiidae (*Nycterebosca falcozi* Jobl.) and some Hippoboscidae (*Ortholfersia macleayi* Leach and *Ornithomyia* Latreille sp but not *Melophagus ovinus* (L)).

SEROLOGICAL AND CHEMICAL ANALYSIS OF GUT CONTENTS DURING DIGESTION OF THE BLOOD MEAL

The precipitin technique has been used most frequently in host preference studies of mosquitoes but has also yielded data on digestion rates. Most of the latter demonstrate that after a certain length of time depending on environmental conditions, the midgut contents do not give a positive reaction (Bull and King, 1923; Davis and Philip, 1931; Weitz and Buxton, 1953; West, 1950). Bates (1949, p. 90) cites unpublished observations of Balfour on digestion rates in *Anopheles superpictus* Grassi, *Anopheles maculipennis* and *Anopheles sacharovi* Favre in Greece. The latter two species were similar and 100%, 91% and 79% of the mosquitoes gave positive tests after 2, 12, and 14 hours respectively. *A. superpictus* digested blood more rapidly and 96%, 72% and 39% gave positive reactions after 2, 12, and 14 hours.

Schubert and Kelley (1950) correlated the appearance of the blood meal with the precipitin reaction. *Aedes aegypti* were divided into three groups 17 hours after feeding on a bird (species not stated). Of the mosquitoes containing digested and haemolized blood 67% gave positive precipitin tests, 83% of the partially fed mosquitoes were positive and 96-100% of the fully engorged mosquitoes were positive.

West and Eligh (1952) studied the digestion rates in *A. aegypti* under laboratory conditions and in *Aedes hexodontus* under field conditions with the precipitin test. They showed that digestion in *A. aegypti* held in total darkness occurred more rapidly at higher temperatures (6 to 27 C). The rate of digestion of guinea-pig serum by *A. aegypti* has a $Q_{10} = 2.0$ in the temperature range 20 to 30 C (Williams, 1953). West and Eligh suggested that the rate of digestion could be influenced by light, and by the species of mosquito and host. It was pointed out that serological techniques indicate alteration of the blood meal proteins and not completion of digestion, and West and Eligh (1952) suggested that measurement of protease activity as done by Fisk (1950) "might give a more accurate indication of completion of blood digestion than would any other known method". In this respect the results of Akov (1965) are interesting. She found that in untreated *A. aegypti* as well as in those treated with 5-FU that there was a good correlation (coef. corr.= 0.872) between the amount of proteinase in the midgut and average stage of development of the ovaries in the mosquito. Confirmation of this was obtained by feeding mosquitoes citrated sheep blood containing 1.25 μg crystalline soybean trypsin inhibitor/2 mg blood; this inhibited both midgut proteinase and the development of the ovaries.

Weitz and Buxton (1953) ran precipitin tests at irregular intervals on mosquitoes kept at 25 C and 80% R.H. Two species, *Anopheles labranchiae atroparvus* and *A. aegypti*, fed on

man, were all positive after 16 hours and 9% and 27% were positive after 3 days. All were negative on the fourth and fifth day. All *Culex pipiens* (issp) *molestus* Forskal fed on man, gave positive precipitin reactions 24 hours after the blood meal but all were negative on the third and fifth days. The percentage of ox-fed *Anopheles aquasalis* Curry giving a positive precipitin test also declined as digestion proceeded (95% after 16 hours, 26% at 20 hours, 4% at 30 hours, and 0% at 40 hours).

Differences in the rate of digestion of human blood by five species of mosquito were observed when they were held under identical conditions of temperature (27 C), photoperiod (ratio of light to dark was 1:1), and humidity (saturation deficit was 2±1 mm Hg) (O'Gower, 1956). The time required for half of the mosquitoes to complete digestion to a point where the precipitin test was negative was 31 hours for *Aedes scutellarus* (Walker), 36 hours for *Aedes notoscriptus* (Skuse), 38 hours for *A. aegypti*, 46 hours for *Culex pipiens quinquefasciatus* and 48 hours for *Aedes australis* (Erichson). Since the intraspecific variation in the size of females was almost as great as the interspecific variation, O'Gower felt that "the different rates of digestion of human blood by the species of mosquitoes tested would seem to be due to specific differences in the digestive processes and not to specific difference in the size of the adults". O'Gower investigated the effect of photoperiod on *A. notoscriptus*. Mosquitoes were held under five conditions, ranging from continuous light to continuous dark and precipitin tests were run at 36 and 40 hours after the blood meal. As the ratio of dark to light increased so did the rate of digestion. O'Gower also stated (without supporting data) that one week old and three week old mosquitoes (species not stated) digested blood at the same rate.

Downe, Goring and West (1963) used the precipitin test to study the effect of both meal size and meal source on the rate of digestion by several species of mosquito. The time required for 50% or 100% of the mosquitoes to completely digest or denature human serum proteins were reported for *A. aegypti* and *Aedes trichurus* (Dyar). Using these criteria it appeared that females of both species given a small blood meal (i.e. where ratio of weight of blood ingested to weight of mosquito was less than one) digested the meal much more rapidly than those given a large blood meal. For *A. aegypti* the "50% digestion time" and the "100% digestion time" for small blood meals were 16 and 36 hours and for large blood meals were 40-44 hrs and 52-56 hours. The corresponding values for *A. trichurus* were 28 and 48 hours, and 64 and 76 hours.

The source of the blood meal (man, guinea pig, dog, or chicken) had little effect upon digestion rates in several species of *Aedes*, but did affect those of *Mansonia perturbans* (Downe, Goring, and West, 1963). In this species the "50% digestion time" and "100% digestion time" were 36 and 44 hours for chicken blood, 48 and 56 hours for guinea pig blood, 48 and 60 hrs for dog blood and 52 and 60 hours for human blood.

Templis and Lofy (1963) showed that *Culex tarsalis* digests blood meals from three different species of bird at three different rates. Positive reactions were obtained with mosquitoes fed on all three species of birds up to 18 hours after feeding, but at 24 and 36 hours the percentages were 70 and 29 for those fed on the white crown sparrow; 56 and 50 for those fed on the cow bird; and 100 and 73, for those fed on the English sparrow.

In *A. aegypti* given a small meal of human blood followed in 2 to 12 hours by a larger meal of guinea pig blood digestion of the human blood was prolonged (Downe, 1965). This probably occurred because the human blood meal was surrounded by the guinea pig blood meal and thus protected from digestion, which proceeded from the periphery toward the centre of the midgut contents.

Using agar double diffusion and immunoelectrophoretic analysis Mattern et al (1967) found that laboratory reared *C. pipiens quinquefasciatus* digested human albumin within 24

to 48 hours but retained the human immunoglobulin, IgG, in the midgut for 4 to 5 days. Wild caught mosquitoes fed on man and then kept in a tube for 4 days gave the same results. On the other hand, wild caught mosquitoes left free in a room for 48 hours after feeding on man were negative for IgG but gave strong positives for albumin. Even though a positive reaction for IgG was found in the midguts of caged *C. pipiens quinquefasciatus* for 4 or 5 days the appearance of a second precipitin band indicated that digestion of IgG began about 5 hours after the mosquitoes fed. Using the agar double diffusion technique these authors compared the IgG digestion products in the mosquito stomach with those produced by digestion of IgG with papain and trypsin. They concluded that "protein cleavage occurring in the stomach of mosquitoes is quite different from that produced by papain or trypsin". All these results were, however, based on a small number of mosquitoes.

Zaman and Chellappah (1967) studied digestion of human blood by *Armigeres subalbatus* using gel-diffusion and immunoelectrophoresis and concluded that the serum albumins persisted in the midgut longer than the serum globulins. The precipitin band for the former persisted for 48 but not 56 hours while for the latter it lasted 12 but not 18 hours. A similar pattern of digestion was obtained with *A. aegypti* digesting guinea-pig blood (Williams, 1953).

Herndon and Ringle (1967) used the double diffusion technique in microtubes to determine the length of time host antigens were detectable in the midgut of blood-fed *Anopheles quadrimaculatus* and *Culex pipiens.* Refrigerated (6-9 C) *C. pipiens* had identifiable antigens in the midgut for 12 days while in *A. quadrimaculatus* the antigens remained identifiable for only 1 week. At 25-28 C the antigens were identifiable for only about 1 day.

With precipitin tests Edman (1970a) showed that 2 and 4 day old *A. aegypti* digested human blood at about the same rate (at 27 C and 70% R.H.) while mosquitoes 6, 8, and 10 days old digested it at a slower rate. There was no difference in the rate of digestion by 8 and 22 day old mosquitoes. With 6 day old mosquitoes digestion was slower in virgin than in mated females. Digestion by 10 day old parous females was slower than by 10 day old nulliparous females. However digestion rates of the second blood meal in 10 day old mosquitoes were the same as of the third blood meal in 18 day old mosquitoes. This last finding differs from Akov's (1966) for the rate of emptying of the midgut of *A. aegypti*. Using immunological techniques and antisera of high titre, Edman (1970b) found no consistent differences in the rate of digestion of human albumin, γ-globulin, and α-globulin by *A. aegypti.* Complete denaturation of the proteins occurred between 60 and 66 hours after ingestion of the meal.

Of the *Culicoides nubeculosus* fed on man, 80% gave positive precipitin reactions after 24 hours, but all were negative after 3 days (Weitz and Buxton, 1953). In the same study it was reported that laboratory reared *Glossina morsitans* fed on man, ox, sheep, or goat were all positive for 2 days and on the third day gave 100%, 100%, 75%, and 90% positive reactions respectively. In contrast wild caught *Glossina swynnertoni* estimated as having fed on mammals 3 days earlier, gave only 28% positives and those estimated as having fed four days earlier gave only 7% positives.

Downe (1957) used serological techniques to follow the digestion of horse and guinea-pig blood (actually the serum) by several species of black-flies (*Simulium venustum, Simulium vittatum* Zetterstedt, *Prosimulium hirtipes* and *Simulium parnassum* Malloch). The rates of digestion were similar in all these species and were not markedly affected by the source of the blood. At 19.4 - 21.1 C and 75 - 80% R.H. precipitin reactions were obtained in nearly 100% of the insects 24 hrs after feeding. This declined to about 74% by 32 hours, 40% by 40 hours, and to 3% by 48 hours, after which no positives were obtained. The digestion rate in insects maintained under field conditions was retarded at lower temperatures. By using the Meyer reduced phenolphthalein test Downe could detect blood in 5 out of 8 *S. venustum*

50 hours after they were fed on a horse but similar tests on 11 *S. venustum* made 60 hours after feeding were all negative. Downe (1957) stressed that the serological test indicated only when serum proteins were modified and not when the blood meal was actually digested.

Holstein (1948) studied methods of producing specific antisera and presented some data on the length of time after a blood meal at which positive precipitin reactions could be detected. For *Pediculus humanus* positive reactions were obtained with 1/10 dilutions of antisera up to 13 days, with 1/100 up to 10 days and with 1/1000 up to 2 days after the lice had fed on humans. However it is not clear whether the lice lived for the full 15 days of the experiment after the blood meal. For *Cimex lectularius* positive reactions were obtained (dilutions of sera given in brackets) for 36 days (1/10), 30 days (1/100), 20 days (1/1,000), 14 days (1/2,000), 11 days (1/5,000), 6 days (1/10,000), and 1 day (1/15,000). Evidence that *C. lectularius* digested human blood slowly was obtained by Weitz and Buxton (1953) who found 100% were positive after 5 days, 97% positive after 10 days, 40% positive after 20 days, and 22% positive after 30 days.

Positive precipitin tests for human blood could be obtained in *Phlebotomus argentipes* Annadale and Brunetti for up to 8 days after they had fed once on human and then on mouse blood (Lloyd and Napier, 1930). Although the number of sandflies tested at each time after ingestion of the meal was small, the results indicated that the rate of positive reactions was unaffected by the duration of the digestion period! This suggests to me that some component of human blood, with which the anti-serum was reacting, was not digested by these sandflies.

By using the precipitin test on male *Stomoxys calcitrans* fed an unknown volume of citrated human blood Anderson and Tempelis (1970) obtained the following frequencies of positives: 1 of 2 at 12 hours, 3 of 4 at 24 hours, and 3 of 4 at 30 hours. The corresponding values for females were: 2 of 2 at 12 hours, 4 of 5 at 24 hours, and 2 of 3 at 30 hours. In one experiment, the weight of material ingested was known: males consumed 6.9 mg and females 10.5 mg of citrated human blood. Precipitin tests on these gave the following frequencies of positive for males: 6 of 11 at 25 hrs, 5 of 9 at 30 hrs and 0 of 10 at 33 hours after feeding. The data for females were 10 of 10 at 25 hours, 5 of 5 at 30 hours and 9 of 10 at 33 hours.

By spectroscopic examination of the gut contents of *Rhodnius prolixus* a month or more after feeding on a rabbit, Wigglesworth (1943) found evidence of oxyhaemoglobin, methaemoglobin and traces of acid haematin and concluded that "even after storage for this length of time in the stomach [=anterior mid-gut] digestion of haemoglobin has scarcely begun". A similar examination of the "coiled intestine" [=posterior mid-gut] showed that oxyhaemoglobin occurs only in the region near the stomach whereas acid haematin exists throughout. The haemoglobin is rapidly digested. The black residue remaining in the rectum consists of free haematin. Globulin apparently is digested leaving the unchanged iron porphyrin which is excreted. Some intact haemoglobin is absorbed from the digestive tract, but this is apparently not due to excessive stretching of the stomach, since bugs given a partial meal also absorb haemoglobin. Some of the absorbed haemoglobin passes into the haemolymph and some is digested in the midgut cells to form a modified haem pigment and free iron.

Digestion in the 'intestine' of *Triatoma infestans* is reported to "follow the same lines as in Rhodnius" (Wigglesworth, 1943). In *C. lectularius* "Digestion in the lumen of the gut proceeds as in *Rhodnius* but no brown or green pigments can be seen in the epithelium of the stomach or the intestine" (Wigglesworth, 1943).

The human body louse, *P. humanus humanus* digests its blood meal in the midgut but does pass undigested haemoglobin in the feces as evidenced by the presence of methaemoglobin and oxyhaemoglobin in the excreta (Wigglesworth, 1943). A positive reaction with

benzidine occurs, both with mosquitoes (*A. aegypti, A. scutellaris, A. notoscriptus, A. australis* and *C. pipiens quinquefasciatus*) 90 hours after feeding upon human blood and with the material defecated by blood fed mosquitoes. Thus O'Gower (1956) concluded that the haem of the haemoglobin was not broken down in the mosquito. The flea *Nosopsyllus fasciatus* apparently passes undigested haemoglobin in the feces (Wigglesworth, 1943).

Wigglesworth (1943), using spectroscopic techniques, found no evidence for absorption of undigested haemoglobin in mosquitoes (*A. maculipennis* and *A. aegypti*) or the flea (*N. fasciatus*). However evidence was obtained for its absorption in *Rhodnius, Triatoma, Eutriatoma, Cimex* and *Pediculus.*

The hematin crystals in the feces of *P. humanus* fed on man are rhombic plates whereas those in feces of *P. humanus* fed on rabbits are smaller and cubic (Davis and Hansens, 1945). Whether this difference is attributable entirely to the source of the blood or to possible differences in the way *P. humanus* digests human and rabbit blood was not mentioned.

Gooding (1966b) determined the amount of water soluble protein in the midguts of *A. aegypti* and *C. pipiens quinquefasciatus* fed on chickens. Assuming that the decline in midgut protein content represents digestion of protein by the mosquitoes two criteria can be applied for comparing the rates of digestion: (1) the decrease in protein content in mg/midgut/time interval or (2) the time required for a certain percentage of the protein in the meal to be removed. Using the first criterion *C. pipiens quinquefasciatus* digests its meal faster than *A. aegypti.* With the second criterion the reverse is true. The time required for a 50% and a 90% decrease in the protein content of the midgut was approximately 18 and 40 hours respectively for *A. aegypti* and 23 and 48 hours for *C. pipiens quinquefasciatus.* (Briegel (1969) reported that half the protein in a blood meal disappears from the midgut of *Culex pipiens* within 24 hours of feeding and that digestion was completed by 72 to 96 hours). These experiments were done under essentially the same environmental conditions as those of O'Gower (1956) except that the mosquitoes were fed on chickens by Gooding, (1966b) and on humans by O'Gower, (1956). O'Gower found that 50% of the *A. aegypti* and of the *C. pipiens quinquefasciatus* gave negative precipitin tests by 38 and 46 hours respectively. Gooding estimated that 90% of the water soluble protein had been removed from the midguts of *A. aegypti* and *C. pipiens quinquefasciatus* by 40 and 48 hours respectively. O'Gower in fact studied the denaturation of serum proteins and Gooding the decline of total water soluble proteins in both serum and hemoglobin. Although the two studies were done with blood-meals from different sources the results were consistant since *in vitro* studies showed that these mosquitoes hydrolyzed serum proteins slower than hemoglobin (Gooding, 1966a).

During the digestion of guinea-pig blood by *A. aegypti* the ratio of protein nitrogen to total nitrogen in the midgut declines during the first 48 hours after feeding indicating digestion of the meal (Williams, 1953). However during this period there is no decrease in the total nitrogen content of the midgut indicating either that there is no absorption or that nitrogenous materials are being secreted into the midgut.

Fisk (1950) estimated the pH of the midguts of *A. aegypti* and *A. quadrimaculatus* with indicators. Stomachs of unfed mosquitoes of both species had a pH of 6.5 while those of *A. aegypti* fed on human blood had a pH of 7.3. With a microelectrode, Micks, deCaires, and Franco (1948) found the pH's of the stomachs of unfed *C. pipiens, C. pipiens quinquefasciatus, A. aegypti,* and *A. quadrimaculatus* to be 7.27, 7.43, 7.31, and 7.59. When these species were fed upon chicks the pH values of the stomachs were 7.52, 7.60, 7.67 and 7.75. Similar measurements of blood from the stomachs of *A. aegypti* fed on chickens gave values ranging from pH 7.47 to pH 7.90 (Bishop and McConnachie, 1956). Twenty-four of the 30 samples had pH values between 7.60 and 7.76 and there was no correlation between the duration of the digestion (up to 70 minutes) and the pH value. From these pH estimates, it

may be inferred that the proteinases responsible for digestion of the blood meal must function in a slightly alkaline medium. MacGregor (1931) reported that the midgut of *A. aegypti* and *C. pipiens quinquefasciatus* fed upon a solution (pH 7) of bacto-peptone and B.D.H. universal pH indicator had a pH of approximately 3 to 4. Roy (1937), examining dissected *Gasterophilus intestinalis* larvae with indicators, determined the pH of various parts of the alimentary canal to be: salivary glands pH 7.1, proventriculus pH 7, middle part of midgut pH 7.4 and hindgut pH 6.8. The pH of the midgut of blood fed *Glossina submorsitans* was about 6.6. The exact mechanism for controlling the gut pH and the contribution of the buffering capacity of the ingested blood to its control have not been elucidated, nor has the relationship between gut pH and the pH optimum of all the enzymes functioning in the gut.

DeFreitas and Campos (1961) studied the rate of elimination of Fe^{59} by fifth instar and adult *T. infestans* and by first instar *Panstrongylus megistus* fed upon a chicken which had had Fe^{59} incorporated into its haemoglobin. The results indicated the rate of digestion of haemoglobin by these bugs. There was little or no excretion of Fe^{59} during the first six days after feeding on the radioactive blood. The time required for elimination of 50% of the Fe^{59} was 40 days for 1st instar *P. megistus*, 31 days for 5th instar, and 16 days for adult *T. infestans.*

The major nitrogenous wastes in the feces of *G. morsitans* are uric acid, arginine, histidine, and hematin (Bursell, 1965). A reasonably close agreement existed between the quantities of these compounds excreted after the first hunger cycle and the amount which would theoretically be produced from a blood meal. The differences between these amounts during the first hunger cycle were accounted for by the development of the flight muscles during this period. Bursell (1965) also found a correlation between the amount of blood consumed and the amount of uric acid produced. Thus one can use the rate of excretion to estimate the rate of digestion.

Langley (1966b) used this technique to show that male *G. morsitans* digests chicken and lizard blood faster than mammalian blood. However, the rates for digestion of blood from rat, guinea-pig, sheep, cow, bushpig, or man do not differ significantly. Digestion of impala blood is also at about the same rate as that of other mammals (Langley, 1968a). Laboratory reared, non-teneral males feeding on guinea-pigs digest their meal more slowly than field-caught, non-teneral, males. Digestion is fastest in males which are caught after they have fed upon oxen (Langley, 1966b). These differences led Langley (1966b) to propose that the prefeeding behaviour of the flies affected the subsequent rate of digestion. Non-teneral, field-caught males feeding upon guinea-pigs digest this meal at the same rate when held in continuous light as when held in total darkness, even though the males are less active in total darkness.

Field-caught male and female *G. morsitans,* feeding on oxen, digest their blood meals more rapidly than laboratory reared males and females feeding on bovine or guinea-pig blood (Langley, 1967a). Laboratory-reared, fertilized females digest their blood meal more rapidly than unfertilized females. Male *G. morsitans* feeding on ox blood in the field, excrete their blood meal more rapidly than field-caught males feeding upon guinea-pigs in the laboratory (Langley, 1967c). There is no difference between rate of digestion of guinea-pig blood and cow blood (Langley, 1967b). Field-caught males fed several times on guinea pigs in the laboratory digest each meal more slowly than the preceeding one until by the third meal the rate of digestion is only slightly greater than for laboratory-reared flies (Langley, 1966c). The digestion rate in male *G. morsitans* is not affected by the sex or reproductive condition of the guinea-pigs upon which they feed (Langley, 1968b).

DIGESTIVE ENZYMES AND THEIR PROPERTIES

A variety of digestive enzymes have been found in blood-sucking insects. Interpretation of the literature is straight forward except for the frequent occurrence of the word "trypsin" to describe a proteinase with maximum activity in an alkaline medium. There are several proteinases (carboxypeptidase, amino-peptidase, chymotrypsin, etc) which are not readily distinguished from trypsin on the basis of the pH-activity curve alone. Therefore, in this discussion, the term "trypsin" will be reserved for an alkaline proteinase which cleaves peptide bonds on the carboxyl side of a basic amino acid and "chymotrypsin" for one which cleaves on the carboxyl side of an aromatic amino acid. Such designations are based upon the use of synthetic substrates. Proteolytic enzymes active in the alkaline region, without adequate demonstration of the bond specificity, shall be referred to as proteinases or, if necessary, alkaline proteinases.

Two proteolytic enzymes occur in whole *Aedes aegypti* adults (Wagner, Tenorio and Terzian, 1961). One of the enzymes is a trypsin found in the midgut of the female but not in the rest of the mosquito nor in any part of the male. This enzyme separates into two fractions on a DEAE-cellulose column, the 2 fractions have similar properties. The other enzyme hydrolyzes denatured hemoglobin. It has maximum activity at pH 7.5, but functions almost as well up to pH 9. The purified enzyme is quite stable in acid, losing none of its activity at pH 3 when heated to 96 C for ten minutes. Wagner et al ran 2 experiments with females to determine whether the activity was localized in the midgut; in one all of the activity was in the gut; in the second 53% of the activity was in the gut homogenate. Thus, the authors concluded that this proteinase was primarily a digestive enzyme.

The tryptic & chymotryptic activities of *A. aegypti, Culex pipiens quinquefasciatus* and *Pediculus humanus* are due to 2 different enzymes and for each species the chymotrypsin has a higher molecular weight than the trypsin (Gooding, 1968, 1969). The major chymotrypsin fractions from the midguts of larval and adult *A. aegypti* are approximately the same molecular weight (Yang and Davies, 1971). Trypsin from adult *A. aegypti* has a molecular weight of 21,500 (Huang, 1971a). The proteinases in *Rhodnius prolixus* and *Cimex lectularius* have a high molecular weight ($\geqslant$160,000) (Gooding, 1968, 1969).

On paper electrophoresis, using a barbital buffer at pH 8.0, 3 cationic bands of proteolytic activity were found in *Stomoxys calcitrans* midguts (Patterson and Fisk, 1958). However, using starch gel electrophoresis, cationic bands were never found but 3 bands of proteinase activity were found migrating toward the anode at pH 7.6 (tris-citrate buffer) and pH 8.0 (barbital buffer). By comparing different electrophoretic fractions (from the starch gel electrophoresis) with respect to the relative rates of hydrolysis of azocasein and azoalbumin Patterson and Fisk concluded that at least two "trypsin-like" enzymes existed in the midguts of *S. calcitrans.*

Crystallized hemoglobin is hydrolyzed almost as rapidly by *A. aegypti* and *C. pipiens quinquefasciatus* as denatured hemoglobin (Gooding, 1966a). However it is not known whether the crude midgut homogenates used in these experiments contained substances which denatured the hemoglobin. If no denaturing agents were present, then the proteinases of these mosquitoes may differ significantly from mammalian trypsins which do not readily attack native proteins (Sumner and Somers, 1947, p. 175). Denaturation of the proteins within the mosquito's midgut prior to digestion has not been demonstrated and Fisk (1950) wondered whether the proteinases of mosquitoes normally attacked native proteins or proteins denatured by some as yet unknown mechanism. He suggested that coagulation and agglutination of blood denature the proteins sufficiently to permit attack by mosquito trypsin.

With proteinases from *A. aegypti* and *C. pipiens quinquefasciatus* assayed at pH 7.9, the following are the K_m values (in mg/ml) for blood proteins: denatured hemoglobin, 1.51 and 1.32; crystallized hemoglobin, 1.84 and 3.15; bovine serum albumin fraction V, 19.3 and 8.51; and γ-globulin fraction II, 374, and 6.22 (Gooding, 1966a). At pH 9.5 there is little hydrolysis of the serum proteins by either species. The K_m values for *A. aegypti* and *C. pipiens quinquefasciatus* are: denatured hemoglobin 2.75 and 2.10, and crystallized hemoglobin 4.08 and 2.17. Using purified *A. aegypti* midgut trypsin, the K_m values at pH 7.9 are 2.24 mM for denatured hemoglobin and 0.47 mM for benzoyl-DL-arginine-p -nitroanilide (BAPNA) (Huang, 1971a). Davies and Yang (1968) reported trypsin with a pH optimum of 8.4 from the midguts of 6 simuliid species (*Cnephia dacotensis* (Duar and Shannan), *Prosimulium decemarticulatum, Prosimulium fuscum, Simulium rugglesi, Simulium venustum* and *Simulium vittatum*). The K_m values for tosyl-L-arginine methyl ester (TAME) are 2.4 mM for *S. venustum* and 3.1 mM for *S. rugglesi* (Yang and Davies, 1968b).

The *in vitro* temperature optima for *A. aegypti* and *C. pipiens quinquefasciatus* proteinases are in the range 46 to 50 C (Gooding, 1966a, 1968), that for *S. calcitrans* near 50 C (Patterson and Fisk, 1958), and for *C. lectularius* and *R. prolixus* about 45 to 50 C (Gooding, 1968). These optima are typical of alkaline proteinases. The temperature optima for mammalian trypsins range from 45 to 55 C (Buck, Bier, and Nord, 1962). For the housefly the optimum is 45 C (Lin and Richards, 1956), and for the larval blowfly it is 44 C (Evans, 1958). The *A. aegypti* proteinase experiments of Fisk (1950), Fisk and Shambaugh (1952), and Shambaugh (1954), were carried out at approximately 40 C, a temperature at which the enzyme is functioning at only half its maximum rate. Wagner et al (1961) carried out assays with *A. aegypti* proteinase at 30 C, a temperature at which the enzyme has about one quarter the activity it has at its temperature optimum.

The activity of the non-trypsin proteinase from *A. aegypti* is increased by diisopropylfluorophosphate (DFP), p-chloromercuribenzoate and sometimes cystine. Crystalline soybean trypsin inhibitor gives some inhibition, as do several cations (magnesium, calcium, mercury, and manganese) (Wagner et al, 1961). The alkaline proteinase activity of *A. aegypti* and *C. pipiens quinquefasciatus* is inhibited to some extent by calcium, magnesium, and manganese when denatured hemoglobin or bovine serum albumin are used as the substrates (Gooding, 1966a). However the proteinase from *S. calcitrans* is not affected by several ions (calcium, magnesium, sodium, chloride, or fluoride), penicillin G, or dialysis against distilled water (Patterson and Fisk, 1958).

Cations have varying effects upon partially purified *A. aegypti* trypsin (Wagner et al, 1961). Magnesium and manganese have no effect, but calcium, mercury, cadmium, and zinc inhibit the enzyme to varying degrees. The enzyme is inhibited by p-chloromercuribenzoate but cystine has no effect. This enzyme is not inhibited by crystalline soybean trypsin inhibitor (Wagner et al, 1961). However, Akov (1965) stated that soybean trypsin inhibitor inhibited *A. aegypti* trypsin *in vitro* and presented data to show that mosquitoes fed on citrated sheep blood containing 0.625 μg/ml had less than half the proteinase activity found in the controls 24 hours after the meal. Gooding (1969) reported inhibition of trypsin from *A. aegypti* and *C. pipiens quinquefasciatus* and chymotrypsin from *P. humanus* by soybean trypsin inhibitor.

A. aegypti trypsin is inactivated by DFP (Wagner et al, 1961). Phenylmethane sulphonyl fluoride (PMSF) inhibits trypsin from *A. aegypti* and *C. pipiens quinquefasciatus* and chymotrypsin from *P. humanus* (Gooding, 1968, 1969). (These inhibitors are known to inhibit mamalian trypsin and chymotrypsin by reaction with serine at the active center of the enzyme; therefore, it may be inferred that the mosquito and louse enzymes studied have serine at their active centers.) Tosyl-L-lysine chloromethyl ketone (TLCK) inhibits *A. aegypti* and

C. pipiens quinquefasciatus trypsin but not *P. humanus* chymotrypsin, while tosyl-amide-phenylethylchloromethyl ketone (TPCK) inhibits *P. humanus* chymotrypsin but not *A. aegypti* or *C. pipiens quinquefasciatus* trypsin (Gooding 1968, 1969) (TLCK is a specific inhibitor of mammalian trypsin while TPCK is a specific inhibitor of mammalian chymotrypsin. Both compounds react with histidine at the active center and therefore it may be inferred that the insect enzymes studied have histidine at their active centers).

Although Fisk (1950) used heparinized whole rabbit blood as a substrate for most of his experiments he used a 1% solution of serum albumin for his studies on the effects of pH. Fisk calculated that during the assay only 0.34% of the available protein in the rabbit blood was hydrolyzed and concluded that the presence of 4 mg of blood per midgut was saturating the enzyme with substrate. He noted that the reaction rate when serum albumin was used was almost 3 times as great as when blood was used as the substrate. He suggested that blood from the rabbit may contain some substances which inhibit the midgut proteinase of *A. aegypti* and that some of the mosquito proteinase may combine with the inhibitor to neutralize it in the midgut. Gooding (1966a) demonstrated that serum from both normal and *Plasmodium gallinaceum* infected chicks will inhibit the *in vitro* activity of proteinases from *A. aegypti* and *C. pipiens quinquefasciatus* when denatured hemoglobin is used as the substrate. To obtain a 50% inhibition of the proteinases, from 1 to 7 μl serum/ml reaction mixture was required.

The sera of 17 vertebrate species and the hemolymph of *Periplaneta americana* (L.) inhibit *A. aegypti* midgut trypsin (Huang, 1971a). The inhibition capacity of whole serum varies from a low of 0.01 μg trypsin inhibited/μg serum for the dogfish to a high of 0.21 μg trypsin inhibited/μl serum for the chicken. Huang used G-200 Sephadex gel filtration to determine the minimum number of inhibitors in serum and estimate their molecular weights. *P. americana* hemolymph has 1 inhibitor with a molecular weight of $\leqslant$11,000. All of the vertebrate species examined have an inhibitor with a molecular weight between 31,800 and 66,100. This is the only inhibitor in 4 species (dogfish, turkey, chicken, and rat). All other vertebrate species have a second inhibitor with molecular weight $\geqslant$160,000. A third inhibitor with a molecular weight between 77,600 and 107,000 occurs in 4 species (man; turtle, frog, and pike).

Huang (1971b) partially purified two inhibitors of *A. aegypti* trypsin from bovine serum. One of these, inhibitor I, is electrophoretically associated with the α_1-globulin fraction of serum, has a molecular weight of about 43,500 and combines with trypsin in the molar ratio of 3.5 inhibitor I molecules to 1 trypsin molecule. Hill plots indicate that 2 molecules of inhibitor I inactivate 1 enzymic site of trypsin. Inhibition of trypsin by inhibitor I is competitive when haemoglobin is the substrate at 37 C. When BAPNA is the substrate inhibition is competitive at 30 and 34 C and non-competitive at 37 and 44.5 C. Inhibitor II is electrophoretically associated with α_2 -macroglobulin, has a molecular weight of $\geqslant$160,000 (possibly as high as 1,000,000) and forms a complex with *A. aegypti* trypsin in the ratio 1.7 molecules inhibitor II/molecule of trypsin. Hill plots indicate that 2 molecules of inhibitor II inactivate 1 enzymatic site of trypsin. Huang demonstrated the complex of trypsin and inhibitor II electrophoretically and by gel filtration. This complex has very little proteolytic activity when hemoglobin is the substrate but retains most of the esterolytic activity when BAPNA is the substrate. Inhibitor II has the interesting property of protecting the mosquito trypsin against inhibition by inhibitor I, soybean trypsin inhibitor and PMSF but not against inactivation by TLCK. Although the pH optimum is similar for free trypsin and trypsin-inhibitor II complex, the K_m for BAPNA is lower for the trypsin-inhibitor II complex (0.21 $\pm$ 0.007 mM) than for free trypsin (0.47 $\pm$ 0.01 mM). When hemoglobin is used as a substrate, inhibitor II is a competitive inhibitor at 37 C but when BAPNA is used as the

substrate inhibition is competitive at 30 and 34 C and non-competitive at 37 and 44.5 C.

The chymotrypsin from *A. aegypti* larvae is inhibited by human and horse sera and in both cases inhibition is associated with the α-globulin fraction (Yang and Davies, 1971). Inhibition by human α-globulin is competitive. The inhibitors are unaffected by heating to 60 C but are inactivated at 100 C.

In view of the presence of a trypsin inhibitor in the hemolymph of *P. americana* (Huang, 1971a) it is interesting that the trypsin activity of the midgut of blackflies is approximately the same as homogenates of whole flies (Yang and Davies, 1968b). This latter observation led Yang and Davies to conclude that blackfly tissues probably do not contain materials inhibiting their trypsin.

The midguts of several insects have substances which influence the clotting of blood. The occurrence of coagulins and anticoagulins among various species of insects is summarized in table 2.

The anterior third of the midguts of *Glossina tachinoides* and *Glossina morsitans* contains an anticoagulin, but by removing the salivary glands it can be demonstrated that this anticoagulin is derived from the salivary glands (Lester and Lloyd, 1928). However, the anticoagulin found in the midgut of *Anopheles maculipennis* probably does not originate in the salivary glands, since it is destroyed by heating to 80 C while the salivary gland anticoagulin is stable at 100 C for 35 mins (de Buck, 1937).

R. prolixus midgut anticoagulin is stable at 60 and 80 C for 30 mins, is not affected by treatment with 0.1 N HCl or 0.1 N NaOH at R.T. or 60 C for 30 mins, but is destroyed by heating to 100 C for 5 mins (Hellmann and Hawkins, 1964). It is not precipitated by centrifuging at 100,000 g for 30 mins but is removed from solution by dialysis in the cold. It prevents clotting of rat, guinea-pig, cat, and human blood. The gut anticoagulin was designated Prolixin-G by Hellmann and Hawkins (1965). Prolixin-G inhibits thrombin and has a molecular weight between 100,000 and 200,000, is soluble in saline but is insoluble in water and is therefore possibly a euglobulin. It is less stable than the salivary anticoagulin, Prolixin-S (which also occurs in the midgut) when tested by storage at -20 C for 24 hours, freeze-drying or dialysis. It is, however, more stable than Prolixin-S when exposed to dilute trypsin solutions (Hellmann and Hawkins, 1965).

An antithrombin in the midguts of *Triatoma maculata* is distinct from the salivary anticoagulin (Hellmann and Hawkins, 1966). The gut anticoagulin is not affected by incubation with protamine sulfate, is fairly stable at 60 and 80 C, but loses about half its activity at 100 C in 2 mins and all its activity in 30 mins. Anticoagulin activity is not lost by treatment with 0.1 N HCl for 10 mins at R.T. or 60 C, but is lost in 0.1 N NaOH at 60 C in 10 mins. Freezing and freeze-drying cause a loss of activity but the anticoagulin is stable in the refrigerator. This antithrombin has a molecular weight between 100,000 and 200,000, is resistant to trypsin but loses some activity when dialyzed against saline (Hellmann and Hawkins, 1966).

Hellmann and Hawkins (1966) found no indication of fibrinolytic activity in the salivary glands of *T. maculata*. The gut, however, contains a plasminogen-activating factor but no active fibrinolytic enzymes. Guts with low anticoagulin activity have high fibrinolytic activity and visa versa. Freeze-drying decreases the fibrinolytic activity of the gut preparation but storage of dry preparations under refrigeration and storage at -20 C does not cause a loss of activity. The activity is not destroyed at 60 C but is in 2 mins at 80 C or 100 C and in 5 mins at R.T. in 0.1 N HCl or 0.1 N NaOH. The properties of the gut antithrombin from *T. maculata* are very similar to the gut antithrombin from *R. prolixus*. (Hellmann and Hawkins 1966).

The gut homogenates, but not the salivary gland homogenates, of *R. prolixus* contain

fibrinolytic activity. The gut contains a fibrinolytic activator and there is evidence that it also contains some weak fibrinolytic enzyme (Hellmann and Hawkins, 1964). The fibrinolytic activity in the gut is destroyed by heating to 100 C for 5 mins and by treating with 0.1 N NaOH or 0.1 N HCl for 30 mins at R.T. A 5 minute exposure to 0.1 N HCl causes a 70% loss of activity while 0.1 N NaOH has no effect in 5 mins. A single gut contains 1 N.I.H. unit of urokinase. A dialyzable fibrinolytic inhibitor is also present in the midguts of fed *R. prolixus*; the source of this inhibitor (insect or host) is unknown. The addition of soybean trypsin inhibitor to the *R. prolixus* gut extract does not inhibit the lysis of fibrin and it was concluded that "it is therefore unlikely that the fibrinolytic activity of the gut extract is due to trypsin".

Hawkins and Hellmann (1966) demonstrated that the midgut of *R. prolixus* contains a plasminogen activator which is detectable by measuring either fibrinolysis or caseinolysis and they proposed the name "rhokinase" for this material. Rhokinase activates plasminogen directly and its activity in the assay systems increases with time. The source of rhokinase in the midgut is unknown but it is not detectable in the blood of the guinea-pig on which the bugs fed, the salivary glands, the midgut cells of the bug, or in cultures of the bug's symbiont, *Nocardia rhodnii* (Erikson).

Lysis of the blood clot in the digestive tract of *Glossina austeni* is accomplished by two agents (Hawkins, 1966). The salivary glands and crop contain a substance presumably from the salivary glands, which activates plasminogen, resulting in lysis of the clot. The midgut and hindgut also contain an enzyme which is inhibited by soybean trypsin inhibitor. This enzyme was presumed by Hawkins (1966) to be trypsin. Hawkins showed that this same enzyme was responsible for clot formation of oxalated plasma.

A coagulin found in the abdomen (presumably in the midgut) of *Pthirus pubis* can neutralize the anticoagulin found in the head and thorax (presumably in the salivary glands) (Grusz, 1923). Similarly, the coagulins in the midguts of *Culiseta annulata* and *Culex pipiens* hasten clotting of both normal blood and that which was treated with the salivary glands of *A. maculipennis, C. pipiens quinquefasciatus,* or *C. annulata* (de Buck, 1937). Presumably, the coagulins neutralize the salivary anticoagulins. The coagulin from *C. annulata* is not destroyed by drying or by heating dry material to 99 C for 1 hour but saline solutions are inactivated by heating to 50 C for 15 mins.

The midgut coagulin from *G. morsitans* is completely inactivated by treating with 0.1 N KOH for 10 mins, or by heating to 80 C for 15 mins, while treating with 0.1 N HCl for 10 mins destroys about half the activity (Lester and Lloyd, 1928). By mixing salivary gland and midgut homogenates in various ratios and by adding these mixtures to sheep blood, the clotting time may be prolonged or shortened. If the salivary anticoagulin is added to blood 1 min before adding varying amounts of coagulin, the clotting time can be shortened, but not to the same extent as when the coagulin is added to the anticoagulin before mixing with the blood. Lester and Lloyd interpreted these findings as indicating that the midgut coagulin inactivates the salivary gland anticoagulin and they suggested that the midgut coagulin was similar to vertebrate kinase (i.e. the enzyme which converts prothrombin to thrombin). Lloyd (1928), speculating on the relationship between the function of the midgut coagulin and clot formation, stated that the "main function of this clot appears to be that it puts a brake on to the fluid meal and holds it in the proper region of the gut while digestion begins". The coagulin from *Musca crassirostris* is destroyed by heating to 100 C for 10 mins and its concentration in the midgut reaches a maximum 20 to 44 hours after a meal (Cornwall and Patton, 1914).

In invertases from *P. fuscum* and *S. venustum* have maximum activity at pH 6.2 (Yang and Davies, 1968c; Davies and Yang, 1968). The synthesis of oligosaccharides by the invert-

ase of *S. venustum* was detected by Yang and Davies but the products were not identified so it was not established whether the invertase was of the α-glucosidase or β-fructosidase type.

Gasterophilus intestinalis midgut amylase has optimal activity at pH 6 and is activated by chloride (Tatchell, 1958). Maltase and invertase have optimal activity at pH 6. Tatchell demonstrated that lipase hydrolysing tributyrin had maximal activity at pH 7 but no hydrolysis of olive oil or ethyl butyrate was demonstrated. The amylase from both male and female *S. venustum* has a pH optimum at approximately pH 6.5 (Yang and Davies, 1968a). The K_m (starch) is 0.65 mg/ml for female *S. venustum* amylase (Yang and Davies, 1968a).

ENZYME CONTENT OF THE GUT

Proteolytic activity in the midgut of *Aedes aegypti* is significantly higher in mosquitoes one or two hours after a partial blood meal than in sugar-fed mosquitoes (Fisk, 1950). The addition of homogenates of crops and/or salivary glands does not markedly increase the proteolytic activity of midgut homogenates of unfed mosquitoes. Immediately after *A. aegypti* feed on human blood, the proteinase activity in the midgut drops below the level of the unfed midgut. When mosquitoes are kept at 26.6 C and 50% R.H. the activity rises to a maximum about 18 hours after feeding and then slowly declines (Fisk and Shambaugh, 1954). Fisk and Shambaugh proposed that the initial decline in proteinase activity in the midgut was due either to depletion of enzyme due to an excess of substrate or to the presence of an antitrypsin in the serum. Feeding on sugar causes a slight increase in proteolytic activity after one hour, but the level returns to normal by two hours. Secretion of the proteolytic enzymes is primarily in response to serum proteins in the meal and there is a direct correlation between the amount of blood ingested and the proteinase activity of the midgut homogenate (Shambaugh, 1954). Incubation of *A. aegypti* midgut homogenates with blood for 18 hours at 40 C does not result in production of detectable quantities of proteinase, but midguts dissected from mosquitoes 18 hours after feeding on human blood have a large quantity of proteinase.

A. aegypti feeding on 5-fluorouracil (5-FU) in sugar solutions prior to, or with, the blood meal have lower midgut proteinase levels than controls 24 hours after the blood meal (Akov, 1965). The suppression of the proteinase level decreases with time when the mosquitoes are taken off the 5–FU diet. Mosquito proteinase is not inhibited *in vitro* by 5-FU.

A. aegypti treated with metepa (applied topically or fed a sugar solution), apholate (sugar solution) or gamma irradiation have a normal amount of midgut proteinase one day after feeding on a rat (Akov, 1966). The treated mosquitoes, however, retain blood in their midguts longer than the controls and two days after feeding have much more midgut proteinase than the controls (which, incidently, have empty midguts). When metepa is mixed with citrated sheep's blood and fed to *A. aegypti* through a membrane, the midgut proteinase activity is higher than in the controls but even so the blood meal is retained longer in the metepa treated insects.

Gooding (1966a) found much more proteinase in the midguts of *A. aegypti* and *Culex pipiens quinquefasciatus* 24 hours after feeding on chicks than in the midguts of unfed mosquitoes. In these experiments denatured hemoglobin was used as the substrate and the elevated proteinase levels in the fed mosquitoes were found at all pH values from 4 to 11. Proteinase activity in *C. pipiens quinquefasciatus* reached a maximum 36 hours after feeding and in *A. aegypti* usually 24 hours (but on 1 occasion 36 hours) after feeding (Gooding, 1966b). The time at which the maximum concentration of proteinase was present in the midgut was not influenced by holding the mosquitoes in continuous light or continuous darkness. In a single experiment in which *A. aegypti* and *C. pipiens quinquefasciatus* were

fed on normal or *Plasmodium gallinaceum* infected chicks, those mosquitoes which fed on the infected bird had a higher proteinase content in their midgut. Two experiments were run comparing normal *A. aegypti* with those having oocysts of *P. gallinaceum* on the midgut at the time of the second blood meal. In both experiments the infected groups of mosquitoes had higher proteinase activity than the uninfected groups. The maximum proteinase activity in all six infected groups occurred 36 hours after the blood meal while in the two uninfected groups it occurred at 24 hrs for one and at 36 hours for the other. Yang and Davies (1971) found that trypsin activity but not chymotrypsin activity in the midguts of *A. aegypti* rose after a blood meal. Combre et al (1971) reported that adult *A. aegypti* have lower chymotrypsin activity than the larvae.

Although the complete mechanism for the control of proteinase secretion in the mosquito is not known, it is clear that serum proteins stimulate proteinase secretion in *A. aegypti* (Shambaugh, 1954). The greatest secretion results when mosquitoes consume a mixture of serum proteins, but the presence of any one serum protein in the meal also stimulates secretion.

Fisk and Shambaugh (1952) and Shambaugh (1954) began studies to elucidate the mechanism which controls the production of midgut proteinase in *A. aegypti* following a blood meal, but attempts to stimulate enzyme secretion by injection of hemolymph from fed to unfed mosquitoes failed. Detinova (1962, p. 59), from studies of digestion and ovarian development in *Anopheles maculipennis* concluded that "the process of ovarian development slows down the speed of digestion. Neurohormonal regulation of the duration of the digestive process may therefore be postulated for mosquitoes." Autogenous *Aedes atropalpus* generally do not take a blood meal during the first gonotrophic cycle (Hudson, 1970). Those which feed utilize neither the protein nor the carbohydrate in the blood meal during production of the first batch of eggs. The results reported by Detinova (1962) and Hudson (1970) suggest that mosquitoes with mature, or nearly mature, eggs are incapable of synthesizing or releasing normal quantities of digestive enzymes.

The amount of midgut proteinase present in *A. aegypti* 27 to 28 hours after engorging on chicks is much lower in mosquitoes decapitated within six hours of feeding than in dewinged individuals (Gooding, 1966b). These results are consistent with but not proof of, humoral control of proteinase secretion. However, using net synthesis of triglycerides as a criterion for digestion of the blood-meal, Lea (1967) concluded that ablation of the median neurosecretory cells of mosquitoes does not affect digestion or absorption. The results of experiments with 5-FU (Akov, 1965) suggest, but do not prove, that the midgut proteinase secreted by *A. aegypti* is formed *de novo* after the ingestion of the blood meal.

In *Simulium venustum* the trypsin activity is higher in midguts of blood-fed females than in females fed on sucrose only (Yang and Davies, 1968b). In *Simulium rugglesi* fed on a duck, the trypsin level rises steadily for 18 hours after feeding, and remains essentially unchanged at 24 hours. In *Prosimulium decemarticulatum* feeding on a chicken, the trypsin level rises sharply by 5 hours then drops slightly during the next 19 hours. *S. venustum* adults feeding on a 50% human blood - 0.5 M sucrose solution, and kept at 15 C nearly double their trypsin activity within 24 hours and maintain this level for about 8 days (Yang and Davies, 1968b). At 30 C the trypsin level is nearly triple that of sugar fed controls and is also maintained at this elevated level for 8 days. Males feeding on the blood-sucrose mixture and maintained at 15 C have a slightly depressed trypsin level for 4 days. *S. venustum* females feeding on duck erythrocytes have only slightly less trypsin than those feeding upon whole duck blood; the reverse is true when feeding on material of bovine origin. The blood meal stimulates trypsin secretion in the midgut of *P. decemarticulatum, S. rugglesi* and *S. venustum* (Davies and Yang, 1968).

In *Stomoxys calcitrans* the proteinase activity reaches a maximum about 13 hours after a blood meal but remains essentially unchanged after a sucrose meal (Champlain and Fisk, 1956). No depletion of the midgut proteinase below the level of unfed flies occurs. These authors attributed this difference in pattern between *A. aegypti* and *S. calcitrans* to the different ways in which these species distribute the blood meal between the midgut and crop diverticula.

There is a positive linear relationship between meal size and proteinase activity in the midgut of *Glossina morsitans* at 6, 18, 24, 48, 72, and 96 hours after the blood meal (Langley, 1966a). When the concentration of defibrinated blood in the meal is varied from 10% to 100% but the specific gravity remains relatively constant (1.00-1.05), the amount of proteinase activity varies with the volume of the meal and not the concentration of the blood in the meal. However, since flies consuming saline alone do not secrete proteinase it appears that some blood must be present for proteinase to be produced. The stimulus for proteinase production is in the serum rather than in the erythrocyte. Langley proposed that stimulation of stretch receptors in the crop duct causes impulses to pass along the oesophageal nerves to the neuroendocrine system, resulting in the production and/or release of hormones which cause the middle portion of the midgut to produce the precursors of the proteinase. He further suggested that the enzyme is then activated by some component of the serum portion of the meal. The frequency of feeding of *G. morsitans* (every 48, 72 or 96 hours) does not affect the production of proteinase (Langley, 1969a). Females have a higher maximum proteinase level in the midgut than males. In females the maximum amount of proteinase occurs 24 to 48 hours after a meal while in males it occurs between 12 and 24 hours after the meal. The maximum level of proteinase in field caught males is about 1.5 times the maximum level in laboratory reared males. This latter finding is consistant with the fact that field caught flies excrete the blood meal more rapidly than laboratory reared flies (Langley, 1966b, 1967a).

The amount of proteinase in the midgut of unfed *G. morsitans* rises during the first 24 hours of adult life, remains constant until the fly is 96 hours old, and declines by 120 hours, the flies die from starvation by 144 hours (Langley, 1967b). The rise in proteinase activity during the first 24 hours is not caused by either crawling up through sand or flight activity. Results of experiments involving puncturing the ptilinum, and injecting material into the teneral fly suggest that distension of the crop (possibly in combination with the presence of protein in the crop) is responsible for the rise in proteinase activity. Experiments involving ligaturing, nerve sectioning, and injection of tissue homogenates, demonstrated that the brain is involved in the production and/or secretion of the midgut proteinase in the unfed teneral fly.

During the first 24 hours of adult life in *Glossina austeni* there is a 50% increase in the midgut proteinase (Langley and Abasa, 1970). This increase occurs in normal males and females and in flies irradiated with 10 krad as pupae. Twenty-four hours after the first blood meal there is a positive correlation between meal size and the amount of midgut proteinase activity. The slope of the regression line is not significantly affected in flies given 10 krad as pupae or 15 krad as 0 to 3 hr old adults. However, the irradiated flies have much lower correlation coefficients (0.49) than the unirradiated controls (0.74), indicating greater variation in the irradiated flies.

Schaefer (1968), largely on the basis of work by Langley (1967a) proposed that the reactions of hosts in the wild, to attack by blood-sucking insects cause stress in the latter. This stress heightens the activity of the neurosecretory processes of the brain and corpora cardiaca and the resulting neurosecretions stimulate the early release of proteolytic enzymes into the midgut.

The invertase activity of *A. aegypti* midguts increases from 2 to 4 hours after the mosquitoes feed on blood (Fisk and Shambaugh, 1954). A depression in invertase activity in both the midgut and diverticula after a sugar meal persists for at least 24 hours. The invertase activity is always higher in the midgut than in the diverticula regardless of the nature of the meal or the time after feeding, indicating that the midgut is the source of this enzyme.

There is no significant difference in the invertase content of sucrose-fed and water-fed *S. venustum* but the invertase level rises immediately after a blood meal and remains elevated for 48 hours (Davies and Yang, 1968; Yang and Davies, 1968c).

Some of the amylase activity in *A. aegypti, Culex pipiens, S. venustum* and *Simulium vittatum* occurs in the midgut, but most occurs elsewhere principally in the hemolymph (Yang and Davies, 1968a). With *A. aegypti* there is a 3 to 4 fold increase in amylase activity immediately after feeding on man; this activity declines as the blood is digested. By comparing the amylase activity of blood-fed mosquitoes and human blood Yang and Davies concluded that most of the amylase activity in the fed mosquito came from the blood meal.

Freyvogel, Hunter, and Smith (1968) suggested that esterases demonstrated in the midgut of *Anopheles freeborni, Anopheles stephensi* and *A. aegypti* may have a role in digestion of the blood meal.

Longevity studies indicate that *A. aegypti* can utilize the disaccharides sucrose, maltose, trehalose, and melibiose, the trisaccharides raffinose, and melizitose, and the polysaccharide dextrin, but not the disaccharides lactose or cellobiose, the polysaccharides starch, glycogen, or inulin or the glycosides α-methylglucoside or α-methylmannoside (Galun and Fraenkel, 1957). Homogenates of whole *A. aegypti* hydrolyze sucrose, maltose, trehalose, raffinose, melezitose, and dextrin but not melibiose, lactose, cellobiose, starch, glycogen, inulin, α-methylglucoside or α-methylmannoside. The results of the feeding experiments and the enzyme tests are consistent except in the case of melibiose, for which no hydrolytic enzyme could be demonstrated.

RELATIONSHIP OF DIGESTIVE PROCESSES TO VECTORING ABILITY.

The discovery of insect transmission of vertebrate pathogens was followed within a few years by the demonstration of numerous examples of vector-parasite specificity. An early hypothesis advanced to explain this phenomenon was that the digestive processes of the insect determine which parasites develop. This hypothesis has been investigated several times beginning with Nuttall (1908) and has remained an attractive explanation. Although tested several times without experimental confirmation, the role of the gut in vector-parasite specificity is still occasionally mentioned. For example Day and Waterhouse (1953a) in a review article stated that "The physiology of the mosquito midgut is of exceptional importance in that it is one of the factors controlling the establishment of malarial parasites within the insect vector". In considering the differences in the digestive rates of *Anopheles sacharovi, Anopheles maculipennis,* and *Anopheles superpictus,* Bates (1949, p. 90) wrote "It has been suggested that such specific differences in the digestive process might be a factor in determining the susceptibility of a mosquito to plasmodium invasion." Wigglesworth (1930) wrote "there is, at the present time, a common but indefinite impression that some simple demonstrable difference in the chemistry of the digestive tract (for instance, in salt content or in hydrogen-ion concentration) may be at the back of specificity in the insect host as a vector of pathogenic micro-organisms. Although of course it cannot be denied that this may be so, I do not myself see any *a priori* reason why specificity in the insect host should be due to causes any less subtle than say natural immunity among vertebrates."

The influence of agglutinins can be seen by comparing the distribution of *Plasmodium*

oocysts in the midguts of *A. maculipennis* and *Anopheles stephensi* (Shute, 1948). Both species have anticoagulins but only the former has an agglutinin which causes the red blood cells to clump and settle out. As a result when *A. maculipennis* is in its normal, head-up, vertical position after a blood meal, the erythrocytes settle to the posterior part of the midgut and most *Plasmodium* oocysts are found in this region. However, in *A. stephensi* the erythrocytes do not settle out and the oocysts are more or less uniformly distributed over the midgut.

Lavoipierre (1958) reviewed the relationships between filarial nematodes and their arthropod vectors, including a brief discussion of the possible role of digestive physiology of the vector in limiting the intensity of infection.

Chamberlain and Sudia (1961), in a review of virus transmission by mosquitoes, listed several hypotheses to explain the "gut barrier" to infection including two related to digestive physiology (virus inactivation by digestive fluids and impermeability of the PM). They emphasized that arguments could be presented to support or refute each hypothesis and that no mechanism has been completely proved. For example the suggestion that digestive fluids inactivate the virus can be argued against on the grounds that viable WEE virus is detectable in mosquito midgut for as long as a day after the infectious meal. On the other hand, since digestion commences at the periphery of the blood meal, the virus particles next to the gut wall may be inactivated while those deeper in the clot may be unaffected. Similarly, the pore sizes of the peritrophic membrane may explain differences in susceptibility to viruses of different sizes but not to those of the same size.

Young *Cimex lectularius*, feeding upon mice infected with *Pasturella pestis* (Lehmann and Neumann) fail to reduce the size of the ingested meal within a few days and usually die (Bacot, 1915). Bacot stressed that digestion of blood is very rapid in the midgut of the flea and that with the destruction of both the red blood cells and the leucocytes, the midgut becomes very much like an artificial culture medium in which *P. pestis* may develop rapidly. However, in the crop of the bug *P. pestis* development "differs generally from that which takes place in the stomach of the flea in respect of its slower and looser growth, this limitation of activity being accompanied by and possibly due to the preservation of the structural character of the blood for many days after its ingestion into the crop".

Duncan (1926) ran tests for bactericidal activity in the gut contents and feces of several blood-sucking insects (*Stomoxys calcitrans, Anopheles bifurcatus* (L.), *Aedes cinereus*, *C. lectularius Rhodnius prolixus*) and on blood fed *Musca domestica* L. Activity was found against 8 of the 18 species of bacteria used. The bactericidal material from *S. calcitrans* was heat stable (100 C for 30 minutes) and was not destroyed by trypsin. St. John, Simmons, and Reynolds (1930) found no evidence of bactericidal material in the digestive tract of *Aedes aegypti*.

Packchanian (1948a) found that *Leishmania tropica* (Wright) and *Leishmania donovani* fed to several species of *Triatoma* (*T. gerstaeckeri, Triatoma lectularia* (Stal) (=*T. heidemanni*), *T. protracta* (Uhler), and *T. uhleri* Neiva) died in the gut within 3 days. Similarly he showed that *Trypanosoma brucei* Plimmer and Bradford, *Trypanosoma gambiense* Dutton, and *Trypanosoma evansi* (Steel) (reported as *T. hippicum*) died within 10 days of ingestion by *Triatoma* spp. (*T. gerstaeckeri, T. sanguisuga, T. protracta* and *T. rubrofasciata*) (Packchanian, 1948b).

The spirochaete *Treponema pertenue* Castellani remains mobile much longer in the oesophageal diverticulum than in the stomach of *Hippelates pallipes* indicating that this spirochaete may be affected by the fly's digestive secretions (Kumm, Turner, and Peat, 1935).

A possible influence of defecation, during the act of feeding, upon intensity of infection was shown by Kartman (1953a) who fed five species of mosquitoes (*A. aegypti, Aedes*

albopictus, Culex pipiens quinquefasciatus, Culex pipiens and *Anopheles quadrimaculatus*) on a dog infected with *Dirofilaria immitis* (Leidy). As the mosquitoes became replete, the only species observed to defecate a drop of fluid was *A. quadrimaculatus*. By counting the microfilaria in this drop and in the midguts of the fed mosquitoes, it was estimated that about 7% of the microfilaria were lost from the midgut by defecation.

Kartman (1953b) showed that the clotting of the blood in the mosquito midgut (in for example *Aedes* and *Culex*) reduced the number of microfilaria of *D. immitis* which could leave the midgut. Degeneration of microfilaria in the midgut was observed, and although it was concluded that this destruction was due to the digestive process, it was pointed out that death may not have been caused by the digestive enzymes but rather by other factors in the midgut or salivary secretion.

Huff (1927) fed *C. pipiens* and *Aedes sollicitans* upon canaries infected with *Plasmodium cathemerium* and, at various times after the meal, made smears of the gut contents and observed the appearance of the erythrocytes and the sexual and asexual forms of the parasites. In *C. pipiens*, a susceptible species, the asexual forms began to stain abnormally after 3 hours, and after 6 hours were not found. In *A. sollicitans* the asexual forms had not disappeared after 6 hours and some were found until the end of the series 20 hours after feeding. The fate of the sexual forms was the same as that of the asexual forms. Huff also injected homogenates of the midguts of both species into normal birds at intervals after the mosquitoes had fed on an infected bird. The resulting infections in the birds showed that the asexual forms lose their infectivity after 5 or 6 hours in the gut of both the susceptible and the refractory species. During this study Huff noted that some mosquitoes of both species differed greatly from the others in the rate of digestion of blood. Huff (1934) attempted to determine whether intraspecific variation in the rate of digestion was correlated with the degree of susceptibility to malaria parasites in *C. pipiens*. The mosquitoes were fed upon canaries infected with either *P. cathemerium* or *Plasmodium relictum*. A second meal on an infective bird was given 5 to 8 days later, the mosquitoes then being dissected and their midguts removed and examined microscopically. With this technique, each mosquito served as its own control -- those which had large oocysts were susceptible, and the others were considered refractory. No differences were observed in digestion in the susceptible and refractory individuals.

However, de Buck, Schoute, and Swellengrebel (1930, 1932), and deBuck, Torren, and Swellengrebel (1933), suggested that refractoriness in *A. maculipennis* was correlated with slow digestion of the blood meal in certain varieties during overwintering. Ookinetes were formed in both the undigested meal of the "long winged" and in the partially digested meal of the "short winged" mosquitoes and it was proposed that the difference in susceptibility may be due to differences in the ease with which ookinetes can work their way out of the blood meal.

Bishop and McConnachie (1956) found no evidence that exflagellation of *Plasmodium gallinaceum* took place any faster in the stomach of *A. aegypti*, a susceptible mosquito, than under a coverslip on a glass slide.

Attempts have been made to correlate the development of oocysts with the diet of the mosquito. The first was the observation that *Anopheles*, fed alternately upon bananas and gametocyte carriers, often failed to digest their blood meal or to develop oocysts (Darling, 1910). Feeding several salts, including 0.1 M solutions of $CaCl_2$ or $MgCl_2$ to *A. aegypti* decreased the number of *P. gallinaceum* oocysts developing on the gut wall (Terzian and Stahler, 1960). However, the same study showed that $MgCl_2$ fed at a concentration of 0.4 M increased susceptibility to *P. gallinaceum*. The presence of $CaCl_2$ and $MgCl_2$ in the diet of *A. aegypti* and *A. quadrimaculatus* inhibited the *in vivo* digestion of blood (Terzian, 1958,

1963), and these same salts had an inhibitory effect upon the *in vitro* activity of *A. aegypti* proteinase (Wagner, Tenorio and Terzian, 1961; Gooding, 1966a). On the other hand, feeding a chloramphenicol-dihydrostreptomycin-sugar solution to *C. pipiens quinquefasciatus* inhibited digestion of blood by this species, but increased its susceptibility to *P. relictum* (Micks and Ferguson, 1961). There was a slight increase in the per cent of the mosquitoes infected (74% in controls, 85%, in treated mosquitoes) and a considerable increase in the intensity of the infection (56 oocysts/midgut in controls and 110 oocysts/midgut in the antibiotic treated mosquitoes).

Attempts have been made to influence the level of infection by decapitating the mosquitoes after a blood meal. Rozeboom (1961) found a decrease in the percentage of mosquitoes infected, in the number of oocysts per midgut, and in the size of the oocysts (*P. gallinaceum*) when *A. aegypti* were decapitated within 6 hours of feeding. These results may indicate a lower nutritive environment for the *P. gallinaceum* oocyst in the decapitated mosquitoes, since decapitation was subsequently shown to influence the amount of proteinase in the midgut of *A. aegypti* (Gooding, 1966b). However, Rozeboom (1961) stated that "blood digestion does proceed in the decapitated females which survive 3 to 5 days. In many specimens a residue of the blood meal may remain in the gut; in others the gut becomes completely empty as in normal mosquitoes. Thus a sufficient degree of normal digestive processes, including changes in the epithelium, continued to take place in decapitated mosquitoes to permit a somewhat reduced number of zygotes to be taken up by the epithelium". Yoeli, Upmanis, and Most (1962) found that decapitation of *A. quadrimaculatus* after a blood meal did not interfere with the normal development of the larvae of *D. immitis*.

Stohler (1961) considered in some detail the relationship between the PM of Diptera and the role of the latter as vectors of blood parasites. He concluded that the PM could influence the intensity of an infection by imprisoning a portion of the parasites within the blood meal but that the parasites can usually escape from the meal through the viscous portion of the PM, through its open, posterior end or at the time the PM breaks up if the parasites have not already been killed. He stated, however, that the full role of the PM in influencing vectoring ability of flies was not completely resolved, and that a study of closely related species which differed widely in their vectoring abilities could be very useful.

Bates (1949, p. 229) considered the critical stage in determining the susceptibility of the mosquito to be the penetration of the gut wall by the ookinete. Mariani (1961) suggested that the PM in *Anopheles labranchiae* Falleroni may hinder the passage of malaria zygotes from the blood meal into the mosquito. He discussed the importance of the PM in vectoring ability of mosquitoes.

Ookinetes of *P. gallinaceum* that fail to penetrate the PM between 20 and 30 hours after *A. aegypti* feeds will perish. After considering the frequency with which ookinetes are found near the PM, Stohler (1957) suggested that the PM constitutes a physical barrier to the penetration of the ookinetes and that penetration of the gut epithelium does not constitute a significant barrier to infection. During the early stages of its formation, the PM does not constitute a barrier to ookinete penetration, but with subsequent hardening it becomes progressively more impenetrable.

Interpretation of the role of digestion in vector-plasmodia specificity is complicated by our uncertainty about the course of development of the malaria parasite within the gut of the mosquito and by the paucity of information on the stage at which development of the parasite stops. Most of the evidence suggests that decreased susceptibility is correlated with a decreased rate of digestion. It thus appears that if the digestive processes of the mosquito play a role in the infection of the mosquito by plasmodia, it would be by providing nutrients to the developing parasite. The possibility that the digestive enzymes of a refractory species

act directly on the parasite has, however, not been adequately investigated and thus cannot be eliminated at this time.

The influence of the PM upon the establishment of *Trypanosoma grayi* (Novy) in *Glossina palpalis* has been studied by Hoare (1931). *T. grayi* are confined to the midgut lumen by the PM for 2 or 3 days after an infective meal. They then migrate back to the hind gut and escape from the PM taking up residence between the PM and the gut wall by 6 to 8 days after the infective meal and eventually migrating foreward in this space. The trypanosomes continue to occupy this space for the remainder of their residence in the tsetse fly. Lewis (1950) observed that the blackfly PM prevented many microfilaria from entering the body cavity and he concluded that "Frequently therefore, the membrane protects the fly itself from heavy infection without preventing it from transmitting the parasite".

CONCLUDING REMARKS

The blood-sucking insects are parasites ingesting a meal which is well defined both in respect of its composition and the time it is consumed. As such these insects should be ideal for studies of digestive physiology and nutrition as they relate to parasitism in general and host-parasite relationships in particular.

The size of a blood-sucking insect ultimately determines the size of the blood meal it can ingest. In general the blood meal is rather large compared with the size of the insect, and all the greater when one considers it in relation to the amount of tissue available for synthesis of the digestive enzymes and absorption of the products of digestion. It then appears that blood-sucking insects can digest relatively larger quantities of blood at a time. This however is more apparent than real for most of them have some mechanism which limits the amount of blood being digested at any time. In some there are no anticoagulins and the blood clots in the midgut, while many of those which do have anticoagulins also have agglutinins. The meal is further concentrated by removal of water during or just after feeding. Enzymes are then secreted onto the surface of the meal. In bugs and many of the higher flies most of the meal is stored (and in some species concentrated) in the anterior part of the midgut without any digestion taking place and then passes to the posterior part of the midgut in small quantities for digestion. The net result of both of these methods is that only a small portion of the meal is digested at any one time and that the digestive enzymes are never mixed with the total, freshly ingested, meal.

Digestion of only a small fraction of the meal at a time has several advantages to the insect. One advantage is that if the enzymes were mixed thoroughly with the entire meal there may be such an excess of substrate that substrate inhibition would significantly reduce the rate of digestion. The proteinase inhibitors in serum may also inhibit most of the digestive proteinases thus reducing the rate of digestion or necessitating secretion of increased amounts of enzyme. Thus another advantage of having only a small portion of the meal exposed to the digestive enzymes is that the serum proteinase inhibitors may be titrated out by the digestive enzymes or destroyed by a concerted attack by the midgut proteinases. A third advantage to digesting small quantities of blood close to the midgut epithelium is that the products of digestion are readily available for absorption rather than having to move from the center of the midgut.

Salivary gland anticoagulins and agglutinins are widespread, but not universal, characteristics of blood-sucking insects. Whether these substances indicate a degree of convergence selected for by the nature of the blood meal or the retention of primitive characters is unknown. It would indeed be interesting to examine the saliva of several non-haematophagous insects for anticoagulins and agglutinins. The specific contribution of sali-

vary agglutinins and anticoagulins to the denaturation and digestion of the blood meal has not been investigated. There are however reports that mosquitoes and tsetse flies can digest blood without saliva. Whether the efficiency of the process is unaltered in surgically modified insects is not definitely established. One might expect some effect on digestion in *Glossina austeni* whose salivary ducts have been cut since a plasminogen activator from the salivary glands probably contributes to clot lysis in the midgut.

The role of digestive physiology in host parasite relations has not been systematically examined. The work on digestion by *Pediculus humanus* indicates that this highly host specific ectoparasite encounters difficulties in digesting guinea pig blood. To what extent these difficulties are peculiar to the *P. humanus* – guinea pig system is unknown. Insufficient work has been done on comparison of digestive physiology of insects varying in the degree of host specificity. Vertebrate serum contains some proteins necessary for the secretion or activation of digestive proteinases and others which inhibit proteinases. The relative concentrations or activities of these two kinds of proteins in various vertebrate sera are unknown, as are the responses of various insects to these. It is conceivable that certain highly host specific blood-sucking insects could have very precise requirements with respect to both the proteinase stimulators and the inhibitors. The fate of these stimulators and inhibitors in the digestive tracts of either specific or non-specific blood-sucking insects is unknown but worthy of investigation.

On the basis of work with synthetic substrates as well as specific inhibitors it appears that most of the proteinase activity in the mosquito midgut is due to a trypsin, with much smaller amounts of chymotrypsin also being present. However, immunological studies indicate that digestion products from at least some blood proteins in the midgut of *Culex pipiens quinquefasciatus* are different from those produced by mammalian trypsin. These findings indicate that either the small amount of chymotrypsin may have a marked qualitative influence upon digestion in the mosquito or that the mosquito trypsin has a different bond specificity than mammalian trypsin when whole proteins are used as the substrate.

In this article I have summarized a substantial portion of the literature on digestion in blood-sucking insects and indicated some areas in which further research would be profitable. In subsequent articles in this series I propose to report on digestion in a variety of blood-sucking insects and on contributions to the solution of some of the problems indicated in this article.

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RAPID ORIENTATION OF WAX EMBEDDED SPECIMENS

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Quaestiones entomologicae
8 : 61-62 1972

A rapid method for orientation of wax embedded specimens in precast wax blocks with an electrical heat probe is given.

Pour l'orientation de spécimens imbibés au préalable de cire dans des blocs de cire moulés d'avance, une méthode simple est décrite ne nécessitant qu'un simple fil métallique chauffé électriquement.

A procedure for the rapid, accurate embedding and orientation of simuliid (Diptera) embryos and larval heads in wax has been developed which should prove useful for other small animals.

The specimens are impregnated with wax in a small container on a hot plate adjacent to a stereoscopic microscope. Then a previously cast squared wax block is positioned in the optical axis of the microscope. Next, each specimen is lifted from the molten wax with a fine needle. On removal the wax solidifies rapidly around the needle and specimen. Then the specimen is carried to the top of the wax block and held there while a small pool of molten wax is formed in the top of the block with an electrically heated probe. Then the probe is touched to the needle above the specimen. This melts the wax and the specimen slides off into the pool.

The probe consists of part of a straightened wire paper-clip with one end inserted in a glass rod. Three inches of oxide coated, 0.008 inches diameter resistance wire is twisted around the clip near the tip and the ends of the wire are connected to the secondary winding of a variable transformer for a microscope lamp which allows the temperature of the probe to be controlled.

The specimen is oriented with the needle, while the probe prevents the pool of wax from solidifying and determines the depth of the specimen in it (Fig. 1). During final cooling the wax solidifies from the bottom and holds the specimen steady. If the specimen has been maintained in the microscope's optical axis, the orientation of the specimen is known in relation to the sides of the wax block and any required orientation can be repeated. The block is sectioned in the normal manner with particular care given to its orientation to the microtome knife.

With this technique it is possible to get perfect transverse, sagittal, and frontal sections. Fig. 2 shows a sagittal section of the recurrent nerve (r.n) in *Cnephia dacotensis* and Fig. 3, the stomodaeum (st.) of *Gymnopais* sp.

ACKNOWLEDGEMENTS

I wish to thank B.S. Heming for constructive criticism and J.S. Scott for photographic assistance. The work was supported by the National Research Council of Canada.

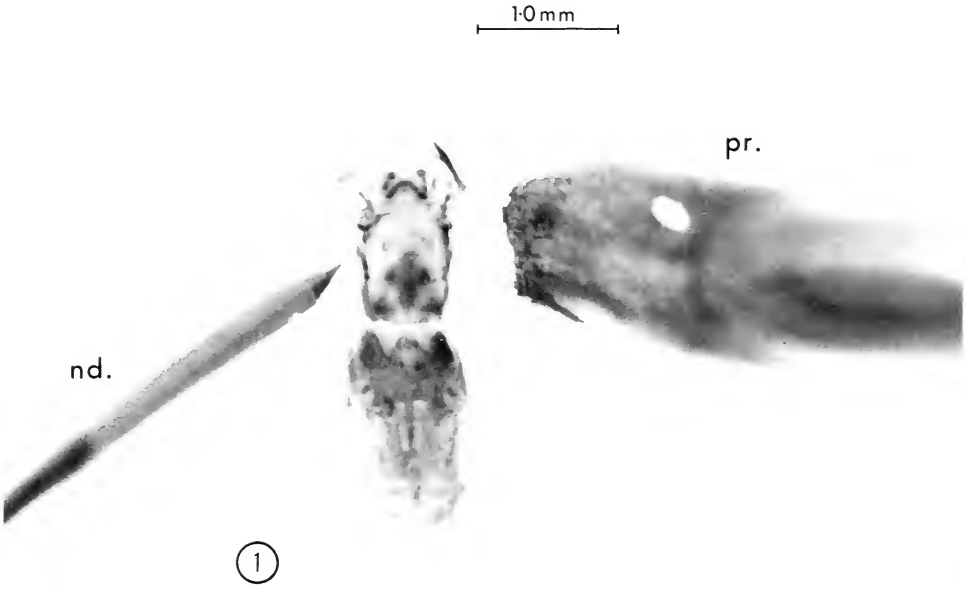

Figure 1. Larval head of *Cnephia dacotensis* during orientation. pr = probe, nd = needle.

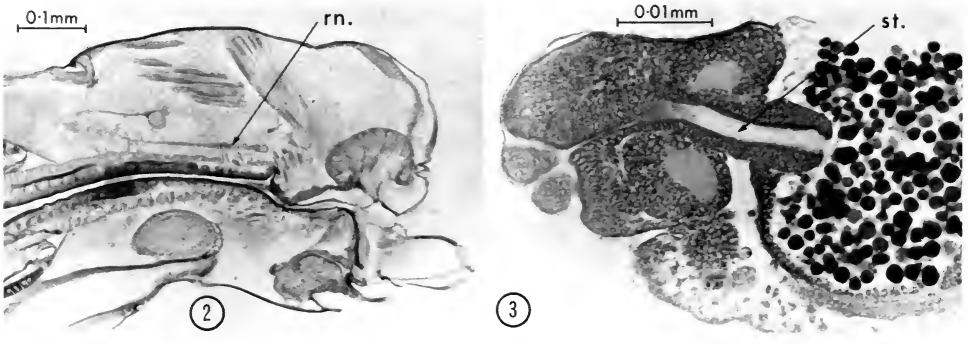

Figure 2. Sagittal section of larval head of *Cnephia dacotensis* showing recurrent nerve (rn). Figure 3. Sagittal section of embryo of *Gymnopais* sp. showing stomodaeum (st.).

Book Review

HODGES, R.W. 1971. Sphingoidea. Fascicle 21. In The moths of America north of Mexico, including Greenland. FERGUSON, R.B. FRANCLEMONT, J.G. HODGES, R.W. MUNROE, E.G. DOMINICK, R.B. EDWARDS, C.R. Editors. E.W. Classey Ltd. & R.B.D. Publications Inc., London, xii + 158 pp., 4 black & white, 14 color plates; 2 pages of line drawings at the end, 19 groups of line drawings in the text. Size 8-7/8" x 11½", wrap cover, 103 references. Price: £-10.00; $24.00.

Printed in England, "The Sphingoidea" section of this encyclopaedic work on North American moths is the first of 41 planned. The work is scheduled for completion in about twelve years and the "Announcement" of publication states: "it is intended that a similar work on skippers and butterflies will follow."

"The moths of America north of Mexico, including Greenland" will be the first comprehensive treatise on more than 10,000 moth species known from that region. It is superbly illustrated and the 14 color plates contained in fascicle 21 deserve special mention. The plates were reproduced from 4" x 5" transparencies taken by R.B. Dominick and C.R. Edwards and printed by offset lithography in four colors. Credit must be given to them as well as to The Curwen Press of London.

Dr. R.W. Hodges, of the U.S.D.A., Systematic Entomology Laboratory in Washington, D.C., the author of "Sphingoidea", earned his doctorate at Cornell University in insect taxonomy. "Sphingoidea" is a synthesis of past revisionary studies of the group. One species is described as new and one new genus is proposed, along with 13 new combinations.

The work is intended for use by both the professional and the amateur entomologist. Two pages of line drawings at the end together with fig. 1, provide a good introduction to structural characteristics. The text figures by Dr. Hodges' wife Elaine R. Hodges are fully labelled and self explanatory; scales apparently vary but are not indicated. It is unfortunate that genital armatures are not pictured for all the species described.

The book begins with an introductory note followed by the introduction to and supraspecific classification of North American Sphingidae. It contains a key to genera based on adults, a partial key to genera based on pupae (after Mosher, 1918), and a partial key to genera based on mature larvae (after Forbes, 1911). For each genus, a complete citation of its original description, type species designation, synonymy, generic description and key to its species are given. For each species, a complete citation of its original description, synonymy, type locality, and where applicable an official common name are given. Species are briefly and unevenly discussed. A review of important literature on the group concludes the text. The color plates portray life size 199 specimens of all species described and the major polymorphs. Each plate is faced by legend and followed by explanatory notes. The book is concluded by indices to animal names and to plant names.

According to the "Announcement", the completed work will include an introduction, to be published last. This part is intended to include sections on morphology, phylogeny, ecology, faunal history, distribution, variation, migration, and dispersal. These are aspects either not covered in "Sphingoidea" or discussed only briefly. I fear that when published, years from now, they may not be adequate for the whole work. For example, species zoogeography is briefly discussed here and there in "Sphingoidea" but no distribution maps are given. For zoogeographic or dispersal studies, all specimens must be examined again. The omission of illustrations of immature stages is another of the few weaknesses. Minor errors include, on p. 47 penultimate line: "*Isoparce* is a monotypic genus." A genus proposed for a single species is better described as monobasic since all genera have, by rule, only one type species. A little more serious is incorrect binominal nomenclature, as on p. 149, "*Pluto* has

been taken in Southern Texas....". I believe the author meant: "Representatives of *Xylophanes pluto* have been taken in Southern Texas....".

Further sections of "The moths of America north of Mexico, including Greenland" are impatiently awaited. They will become indispensable for any lepidopterist interested in the North American fauna. But it is to be hoped that the text in succeeding volumes might be fuller. The cutting of corners in such an important part of such an important work cannot be justified.

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ANNOUNCEMENT

In connection with the 50th Anniversary of the Department of Entomology at the University of Alberta two symposia are being organised for the third week in May 1972. Readers who wish to be kept advised of developments should write to the person named.

1) Biting fly control and environmental quality 16-18 May: Dr. Susan B. McIver, Department of Parasitology, School of Hygiene, University of Toronto, Toronto 181, Ontario, Canada.

2) Entomology in education and education in entomology 19 May: Dr. Brian Hocking, Department of Entomology, University of Alberta, Edmonton 7, Alberta.

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

Copy should conform to the Style Manual for Biological Journals published by the American Institute of Biological Sciences, Second Edition, 1964, except as regards the abbreviations of titles of periodicals which should be those given in the World List of Scientific Periodicals, 1964 Edition. The appropriate abbreviation for this journal is *Quaest. ent.* An abstract of not more than 500 words is required. All manuscripts will be reviewed by referees.

Illustrations and tables must be suitable for reproduction on a page size of $9\frac{3}{4} \times 6\frac{3}{4}$ inches, text and tables not more than $7\frac{3}{4} \times 4\frac{3}{4}$ inches, plates and figures not more than $8\frac{1}{2} \times 5$ inches. Reprints must be ordered when proofs are returned, and will be supplied at cost. Subscription rates are the same for institutions, libraries, and individuals, $4.00 per volume of 4 issues, normally appearing at quarterly intervals; single issues $1.00. An abstract edition is available, printed on one or both sides (according to length) of 3×5 inch index cards (at $1.00 per volume) or on 5×8 inch standard single row punched cards ($1.50 per volume).

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CONTENTS

Editorial – Dissection of Science

Politicians – in the sense of those who would make policy – seem to have it in for science. Commissions, councils, and advisory bodies, in Canada as in many other countries, have come into being in the last few years, with instructions to take a pragmatic look at scientists and their activities. Such groups have been busy dissecting "science" in every conceivable way and attempting to fit the pieces into categories of likenesses. But no matter how they dissect it they seem to wind up with a number of bits such as technology, and industrial research –which are hardly science at all– and to be left with an amorphous mass of true science which they can divide no further, a sort of Lucretius' atom of knowledge. This should not surprise us, for science –true science– is but weakly represented, if at all, among the membership of such groups: a true scientist and a politician are a world apart.

Science once meant knowledge; *scientific*, making knowledge. It has now come to mean new knowledge 'made' by the scientific method of hypothesis and experiment; or at most knowledge susceptible of verification by experiment. Your narrow-minded scientist may consider this the only true knowledge. Research, often synonymized with scientific method, by derivation means having another look –a small step from verification by experiment. While repetition resulting from inadequate literature (re)search is justly frowned upon, usually for sound economic reasons, it can cost more today to retrieve published information than to repeat the work. Repetition for confirmation of results which have been called in question is another matter and is often necessary.

Most research is an extension from previous research; if it has an avowed purpose this is sometimes referred to as applied research. The application of science or research is technology, which uses existing knowledge rather than making new. Research which breaks new ground and is not an extension from previous research cannot, by its nature, have a purpose beyond the creation of new knowledge. Indeed the term research is clearly inappropriate here and such work is often referred to as pure, basic, or fundamental science. None of these terms is without objection. Pure, because although most other work may be biassed by economic purpose it is unjust to imply that it is all impure. Basic, because to a physical scientist other work may then become acid. Fundamental, because of its implications to a biologist. The description 'free basic science' has recently become current for this type of

study, and free is certainly apposite, in both its meanings. For who can regulate where all are ignorant? And contrary to popular belief, basic discoveries are not usually expensive, though the minds that can make them are rare, and the rewards often wanting or posthumous. We might perhaps call this kind of study foundation science.

In the field of entomology, taxonomy, despite the slender support it gets, is close to foundation science, for although the structure, functions, and even relationships of undescribed species have been worked on, and molecular studies are sometimes reported without reference to a species, it is usually otherwise. The discovery and description of a "new" species is new knowledge, allowing the further extension of knowledge by the morphologist, physiologist, –and even the molecular biologist. If, as sometimes happens, a new species is discovered by chance, however, though foundation it is not science, in the derived sense. Often, of course, the existence of a new species can be hypothesized from known species; its discovery is then truly scientific –but no longer quite foundation.

Though technological virtuosity now allows us to erect a large building on a small base, if the edifice of science is to serve us well its foundations must outspan its superstructure. This is not now so. The economic rewards of technology have tempted it too far beyond its foundation science in too many directions –dust bowls, pollution, oil spills, thalidomide babies, the drug problem– are some of the consequences.

Politicians, policy, and police are words of common origin, collectively implying regulation, and a settled course of action. But foundation science is born of curiosity in the face of ignorance and leads none knows where. To regulate it is to destroy it. Direct policy for foundation science is thus a contradiction in terms. But in a favorable intellectual climate it thrives. And such an intellectual climate can be created. If policy would encourage technology it must first provide the climate for foundation science. Failing this it must restrain technology within the existing foundations of science. Advisory bodies concerned with science policy should devote less of their time to shuffling funds around among the varyingly squeaky wheels at various levels of technology and applied and industrial research, and more of it seeking ways and means of creating a climate for foundation science. Industry can afford its own research. Never since the Renaissance has the world been in such dire need of new thought at a basic level –of enlarged foundations of knowledge.

Brian Hocking

STUDIES ON BOREAL AGROMYZIDAE (DIPTERA). I.
PHYTOMYZA MINERS ON SAXIFRAGACEAE

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8 : 67-80 1972

Five species of Phytomyza *are known as leaf-miners of Saxifragaceae. Three of these are confined to* Saxifraga, *as follows:* Phytomyza deirdreae *n. sp. (Western Canada, Alaska and Japan, type-locality Sitka),* P. saxifragae *Hering (Central Europe and Balkans) and* P. aizoon *Hering (Central Europe). On other genera of Saxifragaceae two new species are recorded:* Phytomyza tiarellae *n. sp. on* Tiarella *and* Tolmiea *(type-locality Sitka, Alaska) and* P. mitellae *n. sp. on* Mitella *(type-locality Edmonton, Alberta).*

Cinq espèces de Phytomyza *sont connues comme mineuses dans les feuilles des Saxifragacées. Trois de ces espèces sont limitées à la* Saxifraga, *tel que:* Phytomyza deirdreae *n. sp. (L'ouest du Canada, Alaska et Japon, localité-type Sitka),* P. saxifragae *Hering (Europe centrale et Balkans) et* P. aizoon *Hering (Europe centrale). Sur les autres genres de Saxifragacées deux espèces nouvelles sont rapportées:* Phytomyza tiarellae *n. sp. sur* Tiarella *et sur* Tolmiea *(localité-type Sitka, Alaska) et* P. mitellae *n. sp. sur* Mitella *(localité-type Edmonton, Alberta).*

Fünf Phytomyza-*Arten sind als Blattminierer von Saxifragaceae bekannt. Drei von diesen sind auf* Saxifraga *beschränkt, wie folgt:* Phytomyza deirdreae *n. sp. (Westlich Kanada, Alaska und Japan, Fundort vom Typus Sitka),* P. saxifragae *Hering (Mitteleuropa und Balkanhalbinsel) und* P. aizoon *Hering (Mitteleuropa). An anderen Saxifragaceen-Gattungen werden zwei neue Arten besprochen:* Phytomyza tiarellae *n. sp. an* Tiarella *und an* Tolmiea *(Fundort vom Typus Sitka, Alaska) und* P. mitellae *n. sp. an* Mitella *(Fundort vom Typus Edmonton, Alberta).*

The present paper is the first of a series dealing with boreal and arctic Agromyzidae, both from the Palaearctic and Nearctic regions. The distinction between these regions becomes unnatural at the level of the boreal forest, because many of the species found here are distributed in both regions or have their closest relatives in the other region. I will be particularly concerned in this series with making critical comparisons between European and North American material, in order to establish which species are holarctic. The Agromyzidae are well suited for studies of historical biogeography, because their restricted choice of larval host-plants allows hypotheses about their dispersal to be correlated with the likely dispersal of their host-plants.

The references listed in this series with the synonyms of each species will refer only to works which contain nomenclatural proposals or present substantial new information on the species. References in catalogues, faunal lists and summarizing works will not be listed in synonymies unless meeting the above criteria.

In the present paper I deal with the miners of Saxifragaceae *sensu stricto*. I do not treat the miners of the Hydrangeaceae (including *Philadelphus, Deutzia* and *Hydrangea*), which are included in Saxifragaceae in some botanical classifications. Names of plants are used in the sense of Webb (1964) for European species, and of Hultén (1968) for North American species.

The holotypes of the new species described in this paper will be deposited in the Canadian National Collection (Ottawa). Other North American material is in the University of Alberta collections and in my personal collection. Leaf mines of the North American species are preserved in my herbarium of mines.

TERMS APPLIED TO MALE GENITALIA

I have discussed elsewhere (Griffiths, in press) the terms applied to the male postabdomen and genitalia of cyclorrhaphous Diptera in general. The proposals in that book entail modifications of the terms in use for some parts of the male genitalia of Agromyzidae. Table 1 sets out the terms used in the present series of papers, with the equivalent term or terms used in recent literature on Agromyzidae.

Table 1. Equivalence of terminology.

Equivalent previous terminology	Revised terms
Areas of aedeagus	
basal section (basiphallus) and phallophore	basal section
distal and median sections	distal section
hypophallus	medial lobe(s)
Sclerites of aedeagus	
arms of basiphallus, or sclerites of basiphallus	basal sclerites or paraphalli
paraphalli	paramesophalli
sclerites of hypophallus	sclerites of medial lobe(s)
(The application of the terms phallophore, distiphallus and mesophallus is unchanged.)	
Other parts of genital segment	
epandrium	periandrium
surstyli	telomeres
(The application of the terms epiphallus, aedeagal hood, hypandrium, pregonites and postgonites is unchanged.)	

I now consider the narrow dorsal band of sclerotization found after the 6th tergum in some agromyzid species as a remnant of the inverted 8th sternum (a large sclerite in many other families of Schizophora).

A special difficulty already recognized by other authors (Nowakowski, 1964; von Tschirnhaus, 1969) involves the application of the terms "dorsal" and "ventral" to the aedeagus. In Agromyzidae and many other families of Schizophora, the aedeagus is swung by muscular action through a wide arc from a posteriorly directed copulatory position to an anteriorly directed rest position (Griffiths, in press). Which side of the aedeagus is dorsal and which ventral thus depends on the position of the organ. The convention in descriptions of Agro-

myzidae is to apply these terms with reference to the rest position of the aedeagus. Probably little would be gained by attempting to change this convention. But the ambiguity of these terms should be appreciated. In discussions where an equivalent application of such terms as "dorsal" and "ventral" throughout the Diptera is needed these terms should be applied to the copulatory position of the aedeagus in those groups of Schizophora which show the swinging mechanism.

ABBREVIATIONS

The following conventional abbreviations are used in descriptions:

acr	acrostichal setulae
dc	dorsocentral bristle(s)
ia	intra-alar setulae
mg_2, mg_3, mg_4	second, third and fourth costal sections
ori	lower orbital bristle(s)
ors	upper orbital bristle(s)
pa	postalar bristle(s)

RELATIONSHIPS OF SPECIES TREATED

In my discussion of the *Phytomyza syngenesiae* group (Griffiths, 1967) I alluded to the possibility of defining as one of the segregates of *Phytomyza* in the present sense a group containing the *syngenesiae* group, the *milii* group and *P. nigra* Meigen. The species now treated in this paper, as well as some of the *Phytomyza* miners of Gentianaceae and Caprifoliaceae, may be added to this list. Hardy's (1849) name *Chromatomyia* may be applied to this group (whether as genus or subgenus), when a division of *Phytomyza* in the present wide sense is proposed (see Griffiths, 1967). But such a formal proposal would be premature at the present time, as the male genitalia of many European species have still not been described. The structure of the distal section of the aedeagus in this group is strongly modified (apomorphous). Most characteristic is the presence of a pair of dorsal "supporting sclerites", arising from the base of the distal section (Fig. 8). I accept von Tschirnhaus' (1969) opinion that these sclerites should not be called the "distiphallus" (as in my 1967 paper), and follow him in calling them supporting sclerites ("Stützsklerite"). The medial lobe ("hypophallus") is poorly or not at all differentiated. And it is doubtful whether a true distiphallus (containing a bifid terminal portion of the ejaculatory duct) is retained in any members of this group. Von Tschirnhaus uses the term distiphallus for the distal tubule containing the ejaculatory duct in the *syngenesiae* group; but since this is unpaired it more probably represents the mesophallus (as assumed in my 1967 paper) or a secondary sclerotization.

All species with the type of aedeagus described above also show a characteristic apomorphous type of puparium. The puparium remains within the host plant, with its anterior spiracles bent downwards so that they project through the epidermis. Hardy (1849) characterized his proposed genus *Chromatomyia* on the basis of this puparium type. However this puparium type has a wider distribution than the type of aedeagus described above. Either the apomorphous puparium type indicates a wider monophyletic group inclusive of the group characterized by the apomorphous type of aedeagus; or the puparium type has evolved more than once. The latter possibility cannot be evaluated without studies of additional groups of species. But I am confident that the species which show both the modified form of aedeagus and the *Chromatomyia*-type of puparium form a monophyletic group, deserving eventually of nomenclatural recognition.

DIAGNOSIS

The species treated in this paper can be identified most readily as larvae or puparia. The three species on *Saxifraga* show obvious differences in the form of the posterior larval (and puparial) spiracles (Fig. 3-5). In the new species *tiarellae* (on *Tiarella* and *Tolmiea*) and *mitellae* (on *Mitella*) these spiracles have a characteristic crescentic form (Fig. 6-7). No other agromyzid larvae are known to mine the leaves of Saxifragaceae.

Caught males of these species can be identified by study of their genitalia, particularly the form of the distal section of the aedeagus. I am doubtful whether reliable diagnosis is possible on the basis of the external form of the adult.

The three new species may be included in Spencer's (1969:219) key to *Phytomyza* species of Canada and Alaska by the following extensions.

56.	Sides of thorax bright yellow	*notopleuralis* Spencer
–	Sides of thorax predominantly dark	56a
56a.	Aedeagus as in Spencer's Fig. 395, with membranous distal section	*agromyzina* Meigen
–	Aedeagus as in Figs. 13 and 15-17	56b
56b.	Mesonotum strongly shining; aedeagus as in Fig. 13	*mitellae* n. sp.
–	Mesonotum weakly shining; aedeagus as in Fig. 17	*tiarellae* n. sp.

58.	Distal section of aedeagus with cylindrical mesophallus and distiphallus consisting of divergent tubules (Spencer's Fig. 442)	*ilicis* Curtis
–	Aedeagus not of this type	59
59.	Aedeagus as in Spencer's Figs. 447-448	*involucratae* Spencer
–	Aedeagus as in Spencer's Fig. 460	*milii* Kaltenbach
–	Aedeagus as in Figs. 8-9	*deirdreae* n. sp.

TREATMENT OF SPECIES

Phytomyza deirdreae new species

"*Phytomyza saxifragae* Hering". Sasakawa, 1956:105. – 1961:467.

Adult. – Head (Fig. 2) with orbits not or only very narrowly projecting above eyes in lateral view; genae in middle about ¼ of eye height; eye pubescence fine and inconspicuous. Frons at level of front ocellus about twice width of eye. Two ors, of equal length, posteriorly directed; two ori, inwardly directed, anterior at least half as long as posterior; orbital setulae one-rowed. Peristomal margin with vibrissa and 6-8 upcurved peristomal setulae. Third antennal article rounded distally, with only short pubescence.

3 + 1 dc; acr numerous, in 5-7 rows anteriorly, 4-5 rowed posteriorly; presutural ia numerous; 11-16 postsutural ia; inner pa long, over half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 2.9-3.1 in type series (about 3.5 in Japanese material according to Sasakawa, 1956). Wing length about 2.5 mm (both sexes).

Colour largely dark. Centre of frons dark brown, only slightly paler than black orbits and ocellar plate; genae dark brown. Antennae black. Palpi black; labella brown or yellow-brown. Thorax finely grey-dusted, only weakly shining, completely black except whitish seams of notopleural and mesopleural sutures; squamal margin and fringe infuscated; wing base infuscated. Legs dark, with tips of femora yellow-brown (but only those of front legs

distinctly so). Basal cone of ovipositor (♀) dusted on about basal two-thirds.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not delimited from periandrium, indicated by dense group of short setulae. Aedeagus as in Fig. 8-9, with large ventral area enclosed by membrane, without medial lobe; supporting sclerites fused basally, in form of Y-shaped structure with base confluent with short stretch of sclerotization of ejaculatory duct; other distal sclerites (? mesophallus or paramesophalli) better developed than in *saxifragae* and *aizoon*, extending anteriorly below supporting sclerites. Ejaculatory apodeme (Fig. 10) very small.

Additional figures and information on the female genitalia (not considered here) are given by Sasakawa (1961).

Puparium and third instar larva. – Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles two-horned, with at least 25 bulbs. Posterior spiracles (Fig. 3) with about 40-45 bulbs, with two very long and slender horns which are directed more or less vertically on puparium. Colour of puparium variable (white, brown or blackish). Length of puparium 2.3-2.5 mm.

Other figures are given by Sasakawa (1961).

Mine. – Larvae leaf-miners on certain *Saxifraga* species (see records below). Mine (Fig. 22) at origin with short linear channel, but soon broadened into irregular blotch (the latter in some cases enclosing the initial linear channel), appearing white or greenish white in incident light; faeces scattered as discrete particles throughout mine; main part of mine normally formed on upper surface of leaf, with pupation following at end of short channel without faeces on lower surface (but a few mines formed entirely on the lower surface were also found). Puparium with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Types. – Holotype ♂, 3 ♀♀ paratypes from larvae and puparia 19.viii.69 on *Saxifraga ferruginea* Graham, Harbour Mountain (1900 feet elevation), Sitka, Alaska, emerged 1.ix.69, 2.ix.69, 5.v.70 (holotype) and 6.v.70, leg. D. E. and G. C. D. Griffiths.

Additional records. – I hope to obtain further material from larvae and puparia collected 15-23.viii.71 on *Saxifraga lyallii* Engler, *S. nivalis* L. and *S. punctata* L. on the slopes above the Mount Cavell chalet, Jasper National Park, Alberta, at elevations between 5900 and 7900 feet.

Additional records for North America, based on my own collections of larvae and puparia which yielded parasites, are as follows:

Puparia 20.viii.69 on *Saxifraga punctata* L., same locality as type series (1000 feet elevation); puparia 27.viii.69 on *Saxifraga punctata* L., Chilkat Pass (3000 feet elevation), Haines highway, British Columbia; larvae and puparia 17-19.vii.68 on *Saxifraga hieracifolia* Waldst. and Kit. and *S. punctata* L., Eagle Summit (3900 feet elevation), Steese highway, Alaska.

Sasakawa (1956) described material bred from *Saxifraga sachalinensis* Fr. Schm., Jyôzankei, Hokkaido, Japan (leg. Y. Nishijima). In his 1961 work he also records this species on *S. fusca* Maxim., Mount Hakusan, Toyama Prefecture (Japan).

Dedication. – I am pleased to dedicate this species to my wife Deirdre, who has assisted me ably on field work.

Discussion. – The description of this species brings the total of known *Phytomyza* miners of *Saxifraga* to three. The other two species (*saxifragae* and *aizoon*) are known only from Europe. The three species are probably monophyletic, as evidenced by the similar form of the aedeagus. The most obvious differences between them are in the form of the posterior larval (and puparial) spiracles (Fig. 3-5). There are also slight differences in the form of the distal section of the aedeagus. There are probably some statistical differences in the external

form of the adult, for instance in the costal ratio and numbers of thoracic setulae; but the available material of all species is too limited for reliable statistical treatment.

The occurrence of *Phytomyza* miners on *Saxifraga* in Finland is indicated by Linnaniemi's (1913, Fig. 29) photograph of mines on *Saxifraga nivalis* L. I think these mines may well be those of *deirdreae*, but no firm opinion can be given in the absence of information on the form of the puparia. Hering (1957) includes Linnaniemi's record as no. 4648 in his key to miners of *Saxifraga*.

I regard the Japanese material described by Sasakawa (1956, 1961) as probably conspecific with my North American material, not with the Central European species *Phytomyza saxifragae* Hering. Sasakawa's (1961) Fig. 143n indicates long and slender horns on the posterior larval spiracles, and his figure of the aedeagus (143d) also agrees substantially with that of the holotype of *deirdreae*. I detect a discrepancy only in his figure (143c) of the telomeres ("surstyli"). The group of short spines indicated by Sasakawa are represented by rather longer setulae in the holotype.

The known distribution of *Phytomyza deirdreae* is indicated on Fig. 19.

Phytomyza saxifragae Hering 1924

Phytomyza saxifragae Hering. Hering, 1924:38. –1927:135. De Meijere, 1926:289. –1941: 25. Hendel, 1928:99. –1935:473. Holotype ♀, Herculesbad (Roumania), in the Zoologisches Museum, Humboldt Universität, Berlin.

Adult. – Hendel (1935) has described the external form of the adult in detail. I am unable to separate this species from *deirdreae* on external characters. The costal ratio mg_2/mg_4 is 3.3-3.5 in the specimens I examined. The sclerites of the wing base are paler than in *deirdreae*, but Hendel's (1935) description "Flügelwurzel weisslichgelb, kontrastierend" seems exaggerated. The colour difference is not so great that I would rely on it for identification.

Male postabdomen and genitalia similar to those of *deirdreae*, but with some difference in form of distal section of aedeagus (Fig. 11); base of supporting sclerites not confluent with short stretch of sclerotization of ejaculatory duct; area below supporting sclerites membranous.

Puparium and third instar larva. – Differing from *deirdreae* in form of posterior spiracles, which have 22-25 bulbs in a widely open bow (Fig. 5), with only one prominent horn which is directed more or less horizontally on puparium. See further the descriptions and figures of de Meijere (1926, 1941). Puparium black ventrally, red dorsally (Hering, 1927).

Mine. – Larvae leaf-miners on *Saxifraga rotundifolia* L. Mine (Fig. 23) primarily linear according to Hering (1924, 1927) and Hendel (1928, 1935), but seldom extended, usually crossing itself or blending to form secondary blotch, appearing whitish in incident light. Hendel gives the length of the mine as about 14 cm, and its greatest terminal width as 2.75-3.0 mm. Faeces scattered as discrete particles on either side of mine channel (separated by about 5 mm in terminal part of mine). Main part of mine normally formed on upper surface of leaf (but sometimes on lower surface according to Hering), with pupation normally following on lower surface. Puparium (when internal) with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Hering (1924, 1927) stated that puparia were found inside the leaf, which I think must be their normal location in view of their morphological adaptation to this end (anterior spiracles turned downwards). However Hendel (1928) reported that larvae may also leave the leaf to pupate.

A photograph of the leaf mine is given by Hendel (1928, Tafel V).

Material examined. – 1 ♀ from mine on *Saxifraga rotundifolia* L., West Rila mountains,

Bulgaria, emerged 31.viii.39, leg. H. Buhr. 1 ♂ from mine on *Saxifraga rotundifolia* L., Vals, Switzerland, emerged 8.vii.29, leg. W. Hopp. 1 ♂ from mine on *Saxifraga rotundifolia* L., Rigi, Switzerland, emerged 2.viii.25, leg. M. Hering.

Additional records. – This species was originally described from Herculesbad in the Banat region of Roumania (Hering, 1924) (holotype ♀ emerged 30.v.22 from puparium collected 13. v.22). Hering also refers in that paper to the finding of mines at Königssee, near Berchtesgaden in Bavaria (Germany). There are also sheets in Hering's mine herbarium (now in the British Museum) for the Plöckenpass, Carinthia (Austria), 27.vi.29, leg. Hedicke; and for Brunnsteinsee, Warscheneck-Gebirge, Austria (1600 metres elevation), 28.viii.60, leg. E. M. Hering.

Discussion. – The above records indicate that this species is widely distributed at high elevations in the mountains of central Europe and the Balkans (Fig. 20). Buhr (reported by de Meijere, 1941) gives its altitudinal range in the West Rila mountains as 1600 to 2200 metres. Webb (1964) indicates that the host-plant is widely distributed in the mountains of central and southern Europe, but does not occur in northern Europe.

Phytomyza aizoon Hering 1932

Phytomyza aizoon Hering. Hering, 1932:162. Hendel, 1934:337. De Meijere, 1938:87. Syntypes ♂ ♀, Mauthen (Carinthia, Austria), in the Zoologisches Museum, Humboldt Universität, Berlin.

Adult. – Hering (1932) and Hendel (1934) have described the external form of the adult in detail. Adults of this species are substantially similar on external characters to those of the previous two species (*saxifragae* and *deirdreae*), but I note the following points. According to Hendel the orbits in *aizoon* are distinctly projecting above the eye in lateral view (his Fig. 345), and the arista is thickened to about its middle (only on about its basal third in the other two species). 8-11 postsutural ia. The costal ratio mg_2/mg_4 is only 2.4 in the paratype examined by me; the value 3.0 in the original description (Hering, 1932) is probably an overestimate, as already implied by Hendel's (1935) placement of *aizoon* in his key (p. 511). Size smaller (wing length about 1.75 mm).

Male postabdomen and genitalia similar to those of *deirdreae* and *saxifragae*, but with some difference in form of distal section of aedeagus (Fig. 12); base of supporting sclerites not confluent with short stretch of sclerotization of ejaculatory duct; area below supporting sclerites membranous, not extending so far anteriorly as in *saxifragae*.

Puparium and third instar larva. – Differing very obviously from *saxifragae* and *deirdreae* in form of spiracles. Anterior spiracles knob-shaped, with only 9-10 bulbs (Hering, 1932). Posterior spiracles (Fig. 4) small, knob-shaped, with only 9-12 bulbs. Puparium white, 2.3 mm long.

Mine. – Larvae leaf-miners on *Saxifraga paniculata* Miller (= *aizoon* Jacq.). Hering (1932, 1957) describes the mine as a gradually widening upper-surface channel, sometimes branching, often becoming blotch-like terminally; appearing greenish or brownish in incident light; with mine channel sometimes becoming swollen subsequently due to formation of callus tissue; faecal particles present. Puparium remaining in mine, with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Material examined. – 1 ♂ paratype from mine 24.vii.29 on *Saxifraga paniculata* Miller, Mauthen, Carinthia, Austria, emerged 3.viii.29, leg. O. Hering.

Additional records. – Hering (1932) records this species for Mauthen (Carinthia, Austria) and Zernez, Switzerland (adult emerged 16.viii.29 from mines collected 12.vii.29, leg. Hopp). The only additional collection which I have traced is by Zavřel on 12.ix.52 at Berg Kotouč, Stramberg, Eastern Moravia (Czechoslovakia) (sheet in Hering's mine herbarium).

Discussion. – The above records suggest a restricted distribution for this species in the mountains of central Europe (Fig. 21), where it is sympatric with *saxifragae*. But the real distribution may well be much wider, for Webb (1964) indicates that the host-plant is widely distributed also in southern Europe, Asia Minor and the Caucasus, and occurs locally in Norway. A "variety" of the host-plant occurs in North America (mainly in the East), but has not yet been examined for leaf miners.

Phytomyza tiarellae new species

Adult. – Head (compare Fig. 1) with proportionately large eyes; orbits not projecting above eyes in lateral view; genae in middle less than ¼ of eye height; eye pubescence fine and inconspicuous. Frons at level of front ocellus about twice width of eye. Two ors, of equal length, posteriorly directed; two ori, inwardly directed, anterior pair variable in length (only slightly shorter than posterior pair in holotype, but less than half as long in paratype); orbital setulae one-rowed. Peristomal margin with vibrissa and 5-6 upcurved peristomal setulae. Third antennal article rounded distally, slightly longer than high, with fairly long pale pubescence.

3 + 1 dc; acr numerous, in 5-6 rows anteriorly, becoming 4-5 rowed posteriorly; presutural ia numerous; 6-10 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 3.0 in male holotype, 3.5 in female paratype. Wing length 2.1 mm (holotype), 2.5 mm (paratype).

Colour largely dark. Centre of frons partly brown (paler than black orbits and ocellar plate); genae brown. Antennae black. Palpi black; labella yellow. Thorax finely grey-dusted, only weakly shining, completely black except whitish seams of sutures (especially notopleural and mesopleural sutures); squamal margin and fringe infuscated, but wing base contrastingly whitish. Legs with coxae, trochanters and femora largely dark, but with tips of femora and whole of tibiae and tarsi contrastingly deep yellow or yellow-brown. Abdomen largely dark brown. Basal cone of ovipositor (♀) dusted on about basal two-thirds.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not delimited from periandrium, indicated by dense group of short setulae. Aedeagus as in Fig. 15-17, with medial lobe weakly differentiated; supporting sclerites closely approximated, parallel; small membranous lobe present distal to supporting sclerites; sclerites below supporting sclerites (? paramesophalli) appearing broad basally in lateral view, extending distally almost as far as supporting sclerites. Ejaculatory apodeme (Fig. 18) very small.

Puparium and third instar larva. – Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles two-horned, with about 20 bulbs. Posterior spiracles (Fig. 6) one-horned, with 18-23 bulbs arranged more or less in crescent. Puparium brown or white, with darker strip on ventral surface. Length of puparium 1.9-2.1 mm.

Mine. – Larvae leaf-miners on *Tiarella trifoliata* L. and *Tolmiea menziesii* (Pursh). Mine (Fig. 24) entirely linear, appearing white in incident light, up to 20-25 cm long, about 2 mm wide terminally; faeces scattered as discrete particles (mostly separated by over 1 mm), or forming short "threads" (Fadenstücke) in terminal part of mine; mine formed entirely on upper surface of leaf, but with puparium formation following on lower surface at end of mine channel. Puparium with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Types. – Holotype ♂, 1 ♀ paratype from larvae and puparia 22-24.viii.69 on *Tiarella trifoliata* L., Starrigavan, Sitka, Alaska (near sea level), emerged 9.ix.69 and 8.v.70 (holotype), leg. G. C. D. Griffiths.

Discussion. – Puparia were also collected at the type locality on *Tolmiea menziesii*

(Pursh), but only parasites obtained from this sample.

The known host-plants of *tiarellae* are both distributed mainly in the rain forest of the Pacific coast of North America, with ranges from Alaska to northern California (Hultén, 1968). A similarly restricted distribution may also be expected for the fly. The mean annual rainfall at the type locality is probably about 100 inches, on the basis of data for the Sitka Magnetic weather station.

The emergence of one of the adult flies soon after collection of the puparia indicates that this species is at least partly multivoltine, unlike the species next to be described.

Phytomyza mitellae new species

Adult. – External form of adult as described for *tiarellae*, except as follows. Frons about 1.5 times eye width at level of front ocellus. Anterior pair of ori well developed in all specimens, at least half as long as posterior pair (Fig. 1). Costal ratio mg_2/mg_4 2.4 in male holotype, 2.7-3.0 in female paratypes. Wing length 1.9-2.2 mm. Ocelli bright red in most specimens, but yellow in two females (as normally in *Phytomyza*, including all other species treated in this paper). Mesonotum strongly shining, with only very fine dusting; sides of mesonotum brown; mesopleuron with dorsal and posterior margins narrowly white; squamae pale, with only their fringe infuscated. Abdomen brown, in some specimens yellowish on sides at base.

Male postabdomen and genitalia very similar to those of *tiarellae*, but with some difference in form of distal section of aedeagus (Fig. 13); sclerites below supporting sclerites (? paramesophalli) appearing narrower in lateral view, not extending so far distally (with their apices well short of apices of supporting sclerites).

Puparium and third instar larva. – Very similar to *tiarellae*; posterior spiracles (Fig. 7) one-horned, with 14-17 bulbs arranged more or less in crescent. Puparium uniformly brown or yellow-brown. Length of puparium 1.7-2.1 mm.

Mine. – Larvae leaf-miners on *Mitella nuda* L. Mine (Fig. 25) entirely linear, appearing white in incident light, 10-11 cm long, 1.5-2.0 mm wide terminally; faeces deposited as fine particles, forming more or less continuous strip in early part of mine, separated (but mostly by less than 1 mm) in terminal part of mine; mine formed entirely on upper surface of leaf, but with puparium formation following on lower surface at end of mine channel. Puparium with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Types. – Holotype ♂, 6 ♀♀ paratypes from larvae and puparia 21.viii-27.ix.70 on *Mitella nuda* L., Edmonton (White Mud Creek and north-facing slopes of river valley), Alberta, emerged 14-26.v.71 (holotype 14.v.71), leg. D. C. Christophel, V. K. Sehgal, D. E. and G. C. D. Griffiths.

Additional records. – This species also occurs at Elk Island National Park, Alberta (mines with larvae noted on 21.ix.71).

Discussion. – The host plant is common in the ground layer of forest in the Edmonton district. It is one of the few herbs whose leaves remain green through the winter beneath the snow cover. The fly seems to be univoltine, since no mines have been found before late August. Feeding larvae continued to be found up to September 27th, the last pupating in the insectary on October 1st. This is well after leaf fall and the onset of frost.

I have no doubt that *mitellae* and *tiarellae* are monophyletic; for instance, the crescentic form of the hind spiracles of the puparium and the presence on the male aedeagus of a membranous lobe distal to the supporting sclerites, are both synapomorphous characters of these two species.

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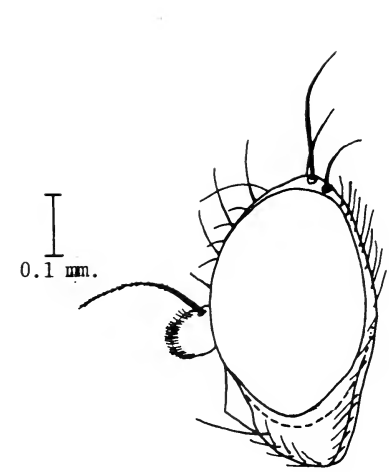

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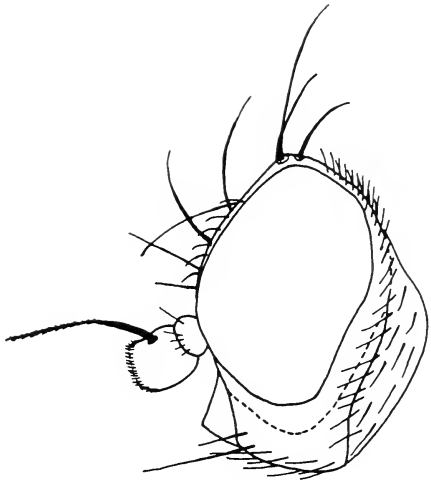

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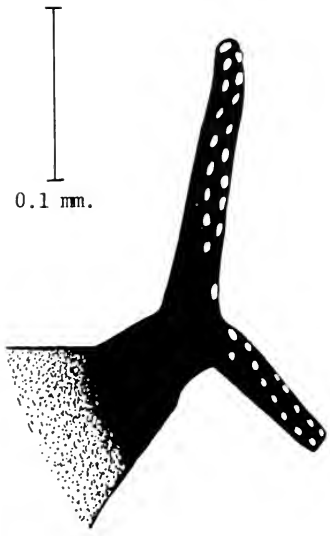

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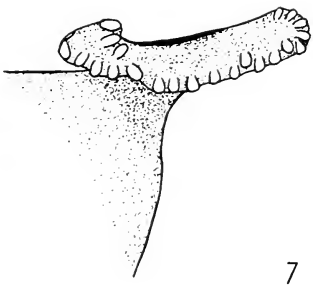

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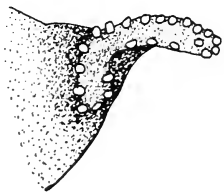

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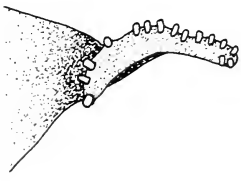

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Fig. 1. *Phytomyza mitellae* n. sp., head in left lateral view. Fig. 2. *Phytomyza deirdreae* n. sp., head in left lateral view. Fig. 3. *Phytomyza deirdreae* n. sp., posterior spiracles of puparium in left lateral view. Fig. 4. *Phytomyza aizoon* Hering, posterior spiracles of puparium in caudal view. Fig. 5. *Phytomyza saxifragae* Hering, posterior spiracles of puparium in left lateral view. Fig. 6. *Phytomyza tiarellae* n. sp., posterior spiracles of puparium (± dorsal view). Fig. 7. *Phytomyza mitellae* n. sp., posterior spiracles of puparium (± dorsal view).

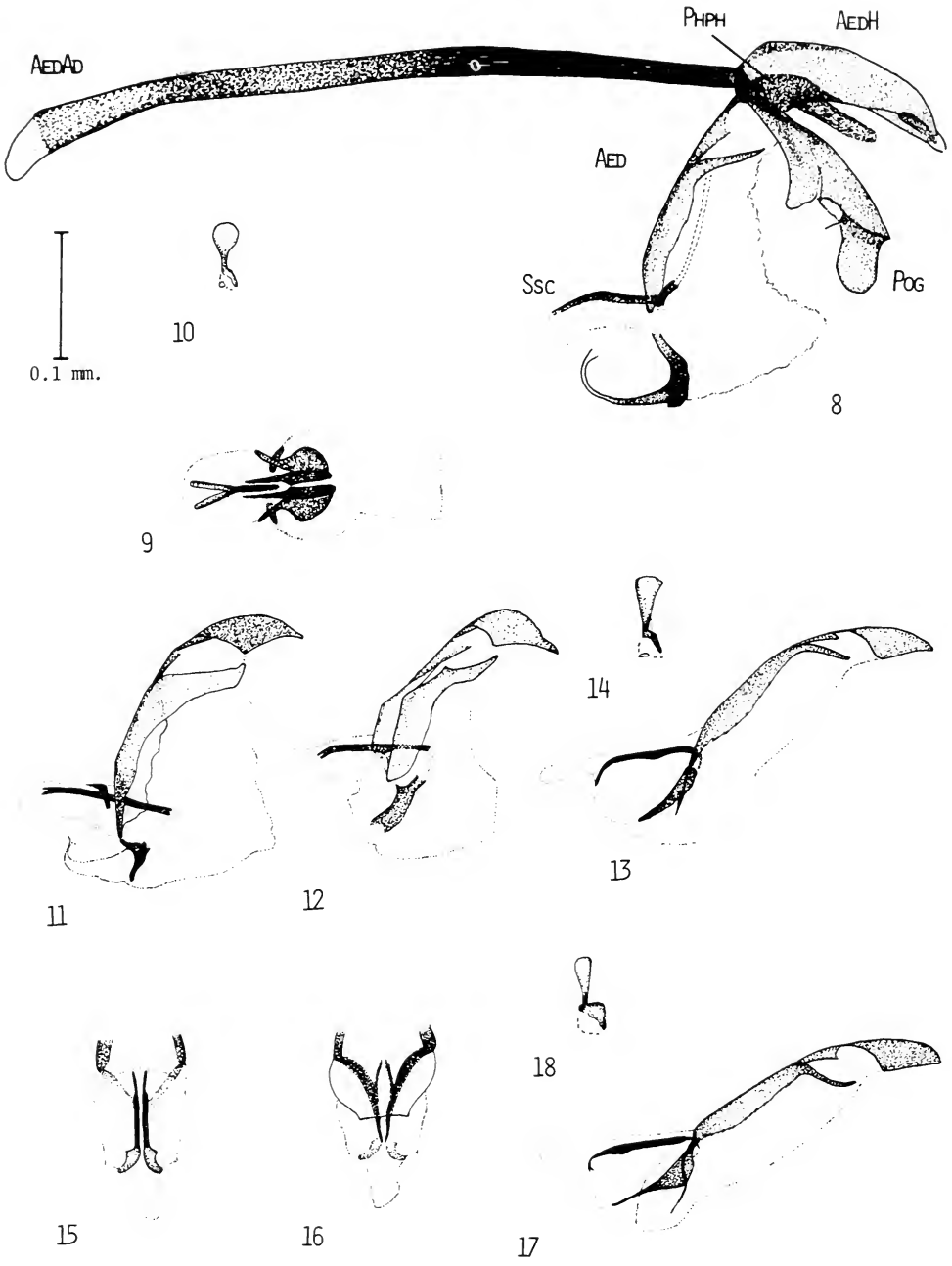
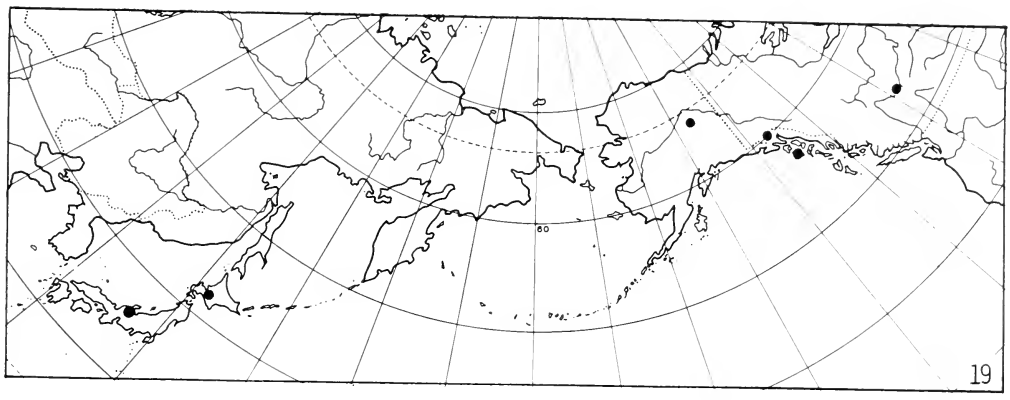
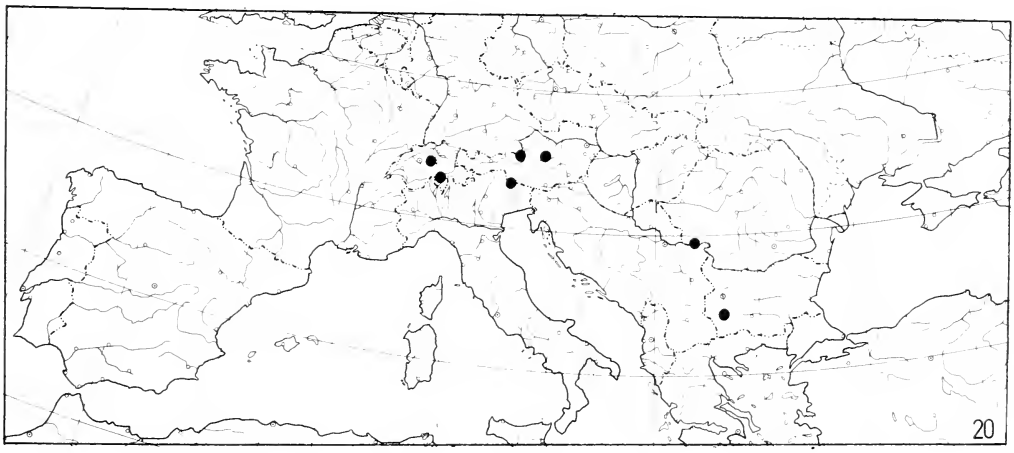


Fig. 8-10. *Phytomyza deirdreae* n. sp., holotype ♂: 8, aedeagus and associated structures in lateral view (AED aedeagus, AEDAD aedeagal apodeme, AEDH aedeagal hood, PHPH phallophore, POG postgonite, SSC supporting sclerite); 9, aedeagus in ventral view; 10, ejaculatory apodeme. Fig. 11. *Phytomyza saxifragae* Hering, Vals (Switzerland), aedeagus (♂) in lateral view. Fig. 12. *Phytomyza aizoon* Hering, paratype ♂, Mauthen (Austria), aedeagus in lateral view. Fig. 13-14. *Phytomyza mitellae* n. sp., holotype ♂: 13, aedeagus in lateral view; 14, ejaculatory apodeme. Fig. 15-18. *Phytomyza tiarellae* n. sp., holotype ♂: 15, distal section of aedeagus in dorsal view; 16, distal section of aedeagus in ventral view; 17, aedeagus in lateral view; 18, ejaculatory apodeme.





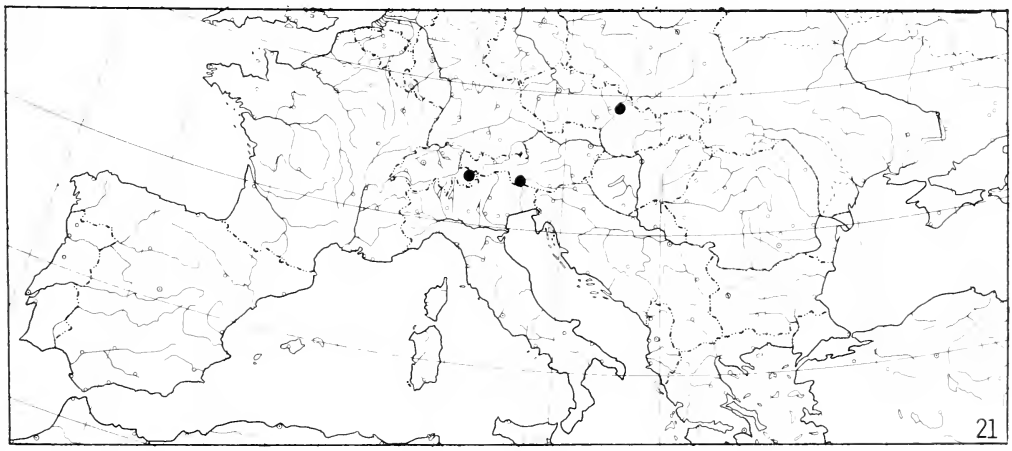
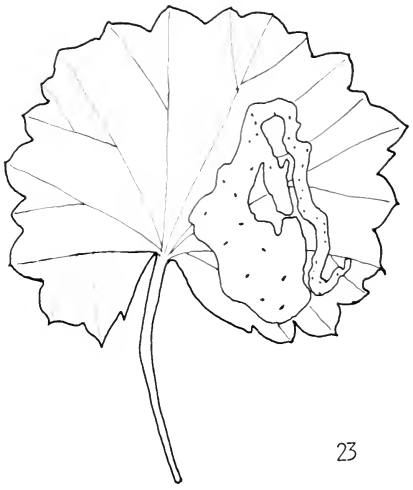


Fig. 19. Collection sites for *Phytomyza deirdreae* n. sp. Fig. 20. Collection sites for *Phytomyza saxifragae* Hering. Fig. 21. Collection sites for *Phytomyza aizoon* Hering.



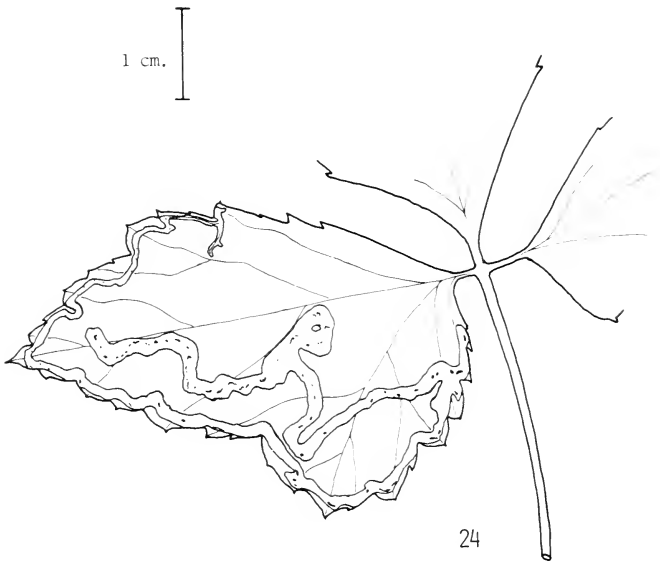


Fig. 22. Leaf-mine of *Phytomyza deirdreae* n. sp. on *Saxifraga punctata* L. Fig. 23. Leaf-mine of *Phytomyza saxifragae* Hering on *Saxifraga rotundifolia* L. (after Hering, 1927). Fig. 24. Leaf-mine of *Phytomyza tiarellae* n. sp. on *Tiarella trifoliata* L. Fig. 25. Leaf-mine of *Phytomyza mitellae* n. sp. on *Mitella nuda* L.

THE PARASITOID COMPLEX OF *EUXOA OCHROGASTER* (GUENEE) (LEPIDOPTERA: NOCTUIDAE)

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Twenty-seven species of parasitoids have been recorded as being reared from Euxoa ochrogaster *(Guenée). Three of these records are not valid because they are based on misidentifications. Descriptions of the available immature stages of 15 species are provided. Of the remaining species, four had been previously described, two could not be studied because of taxonomic difficulties, and no material was available of three more. A brief discussion of the host specificity and the role of the parasitoids in regulating* E. ochrogaster *populations is given.*

*Vingt-sept espèces de parasitoids ont été spécifiées comme faisant partie de l'*Euxoa ochrogaster *(Guenée). Cependant, trois de ces spécifications se sont relevées fausses à cause de certaines erreurs d'identification. Des descriptions de 15 espèces à l'état précoce sont publiées. Concernant le reste, quatre ont été antérieurement décrites, deux de ces espèces n'ont pas pu être observées encore de façon spécifique à cause de difficultés d'ordre taxonomique et les trois autres demeurent inconnues par manque de matériels. Une brève discussion sur la spécificité et le rôle des parasitoids en relation avec le contrôle des groupes d'*E. ochrogaster *a été pourvue.*

The red-backed cutworm, *Euxoa ochrogaster* (Guenée) is a well-known, destructive ground cutworm native to the prairie provinces of Canada. The purpose of this study is to provide a method of identifying some of the immature stages of the parasitoids of the red-backed cutworm. Some groups of parasitoids are difficult to identify to species as adults but may be identified using morphological or behavioural characters of immature stages. The advantages of recognizing the immature stages of the parasitoids of any host species are: 1. If research with live adult parasitoids is necessary, identification using the remains of the immature stages prevents damage to the living specimens. 2. It is not necessary to rear either the host or the parasitoids to maturity to obtain data on the host-parasitoid relations. This allows analysis of host specimens which died, and of hosts killed to enlarge a sample size when there was no time to rear all the hosts or parasitoids to maturity. 3. Super-, hyper-, or multiple parasitoid attack can usually be recognized only by the dissection of host material before any of the parasitoids can mature and emerge. Analysis of inter-specific and intra-specific competition of parasitoids as well as the interactions with predators and disease is possible from the results of such dissections.

The term parasitoid is used in this paper rather than parasite which is usually used when referring to entomophagous groups which attack single host units. The need for the term parasitoid arises from the fact that ecologically the action of such entomophagous species is different from that of either predators or true parasites. Doutt (1964) outlined the ways in which parasitoids differ from parasites.

PROCEDURES AND REVIEW

Materials and methods

This research was started during the summer of 1967 in conjunction with the work of Dr. J. H. Frank (1971a, b) on the predator complex attacking *E. ochrogaster*. The field research was carried out at Calahoo, Alberta on the farm of Mr. C. Bergstreiser. The location

of the field site was South-west 8, Township 55 – Range 27: West 4th Meridian. This site was first investigated June 22, 1967 following a report of a cutworm outbreak to the Alberta Department of Agriculture. The outbreak was limited in both cutworm numbers and in area attacked and little damage was caused. Most of the cutworms were in the final instar. The center of the outbreak was used as a test area and the balance of the field was sprayed with insecticide. During the spring and summer of 1968, plots were established in an oat field adjacent to the barley field in which the outbreak had occurred the year before. The oat field was summer-fallowed the year before. Cutworms were collected in two types of pitfall traps: 3.05 m x 0.12 m eavestroughs and plastic containers 8.7 cm diameter at the top x 10.2 cm depth, by hand collecting, and by systematic sieving of quadrat samples. The numbers of cutworms captured were higher than the season before but inadequate for a meaningful population study of either the host or its parasitoids. All live hosts were reared in both 1967 and 1968. A small number of cutworms was collected in 1969 at Calahoo using 3.05 m eavestroughs as pitfall traps and preserved for further study.

Captured cutworms were reared in the laboratory in individual plastic petri dishes. Each dish was provided with moist filter paper and fresh dandelion (*Taraxacum officinale* Weber) leaves on at least every second day. The dishes were changed when feces had badly contaminated the filter paper. To prevent or reduce the spread of disease in the laboratory new dishes were used as much as possible or the old dishes were sterilized with a KOH solution. Forceps used to handle specimens were rinsed in 95% ethyl alcohol after each specimen was handled. Dishes infested with mites were changed but mites were still a serious source of mortality in laboratory reared cutworms. Specimens were reared in a controlled temperature cabinet at between 18 and 21 C. All specimens which were found dead in the field (usually drowned) and most of those which died in the laboratory were preserved in 70% ethyl alcohol. Some of the hosts which showed obvious stages of parasitoid attack were killed and stored in alcohol for further study. All hosts which failed to produce either adults or parasitoids were checked by dissection for evidence of parasitoid attack.

The basic parasitoid list was formed using three sources of information. A literature review was carried out to establish all the recorded parasitoids. The best sources of information were King and Atkinson (1928), Thompson (1945), and Graham (1965). Specimens of adult parasitoids which had been reared in my study were compared with known specimens or were identified by Dr. Mason or Dr. Peck of the Entomology Research Institute, Ottawa. The final source of information was host labels on reared specimens in the Canadian National Collection (C.N.C.). The host labels aided by allowing me to find specimens which had originally been recorded at the generic level only, or which were not previously recorded at all.

Specimens of most of the species studied were borrowed from the C.N.C. The only bombyliid personally examined was *Poecilanthrax alcyon* (Say). The only other parasitoid species which I did not borrow specimens of was *Copidodoma bakeri* (Howard).

The methods of differentiating species and the preparation of the specimens for study will be discussed in the sections dealing with each family of parasitoids.

Biology of *E. ochrogaster*

The biology of the red-backed cutworm has been discussed by King (1926), McMillan (1930), and Strickland (1923). Jacobson (1970) gives details of the laboratory ecology. Hardwick (1965) reviews the taxonomy and the geographical range of *E. ochrogaster.*

One useful character is the appearance of the pupa before and after the parasitoids emerge. Fig. 60 shows a typical pupa which would produce an *E. ochrogaster* adult. Directly after the prepupa has molted to the pupa, the cuticle is a pale off-white. The cuticle darkens

quickly to a light brown and remains this color. As the normal pupa develops, it gradually darkens and shortens until just before emergence, when it is very black and the surface is distorted. The adult emerges through the dorsal side and many of the sutures release, leaving the pupal remains badly damaged. The abdominal segments of the pupa are often telescoped anteriorly at emergence (Fig. 61). After emergence, the pupa returns to a light brown color.

Predators, diseases, and non-insect parasitoids

King and Atkinson (1928) list several predators of *E. ochrogaster* immature stages. Frank (1971a) studied the carabid predators of *E. ochrogaster* extensively. I found that the lycosid spider, *Trichosa terricola* Thorell, killed many cutworms in pitfall traps. From its ability to kill even the largest cutworms, it is probably an important predator at Calahoo.

The role of diseases in the control of the red-backed cutworm is in need of study. King and Atkinson (1928) carried out a preliminary study but did not have the pathogen identified. I also found extensive mortality from an unidentified disease in my laboratory colonies.

The only non-insect parasitoid found attacking the red-backed cutworm was a single nematode. It was reared from a fifth instar red-backed cutworm in late June, 1969 from material collected at Calahoo. This specimen was examined by Dr. H. E. Welch, who stated that it probably belongs to the genus *Agamermis* Cobb, Steiner, and Cristie. Positive identification was not possible because the specimen was immature.

TACHINIDAE

The morphology of immature tachinids

The morphology of the final instar larvae and puparia of tachinids, as well as of other higher Diptera, is poorly understood. A recent work by Menees (1962) offers an explanation of the origins of the cephalopharyngeal structures of the various larval instars. In his work he shows that the mouth hooks are chiefly maxillary in origin, and that beyond the first instar there is no evidence of vestigial mandibular structures. Various authors describing these structures use different terminologies which assume different origins of the structures (Zuska, 1963; Sanjean, 1957). Others based their terminologies on convenient names (Finlayson, 1960). The system which I use is outlined in Fig. 1-4 and includes arbitrary terms not based on any morphological assumptions.

The final instar tachinid larva has 12 segments, but the puparium has only 11 due to the invagination of the pseudocephalon and part of the first thoracic segment when the larval skin becomes the puparium (Zuska, 1963). This leaves the cephalopharyngeal structures lying in the immediate anterior end of the puparium, attached to part of the unsclerotized final instar larval skin. Horizontal and vertical sutures in the puparium release when the adult emerges. The flaps which are formed at emergence are connected at their midpoints to the rest of the puparium. The dorsal flap, carrying the anteiror spiracles, often is lost. The ventral flap is less often lost and contains the cephalopharyngeal structures.

The puparium retains many of the characters of the final instar larva. One of these characters is the pattern of spinules. Zuska (1963) states that these patterns may vary due to different hosts and other factors, and that thus is not a good taxonomic character. Colour is often used as a character in the description of the puparium (Greene, 1921; Strickland, 1923), but as pointed out by Zuska (1963) and from my observation, the variation is too great for it to be of much use. The most reliable puparium characters to work with are the posterior spiracles (Fig. 3). Unfortunately, the difference between closely related species is not always sufficient. While all of the species in this study had three orificia, some groups

of tachinids have four or more. The cicatrix, remnants of the second instar spiracle, was evident in all specimens studied. As the anterior spiracles are often lost, they are not a good character to base general classifications on. In addition, the number of openings or pori varies intraspecifically.

The cephalopharyngeal structures (Fig. 2) found inside the puparium are generally good characters, but the variability of some of the parts must be considered. Basically, the cephalopharyngeal structures are formed of three sclerites: the anterior, median, and posterior. These may be fused to their adjacent members so that only one or two sclerites are apparent and functional. The anterior parts appear to be very constant whereas the posterior portion may vary a great deal in shape or degree of sclerotization. As the posterior sclerite is the least sclerotized portion of the structure, it may be twisted or bent in such a way as to obscure its true appearance.

Sclerites in addition to the basic three, occur in some species. Sanjean (1957) offers names for three such sclerites in sarcophagid larvae, but there is no evidence to show which are present in my specimens. As the true origin of these sclerites is not known, I have called them auxiliary sclerites. While dissecting the host, the cast cephalopharyngeal structures of earlier instars may be found but not often enough to be of use in identifying a species.

Gonia Meigen

The concept of the genus *Gonia* has been reviewed by Tothill (1924), Morrison (1940), and Brooks (1943). Brooks regarded *Gonia* as a composite of several genera which he separated and described. His work separated the species which I am considering into three genera: *Gonia (capitata, sequax); Reaumuria (aldrichi)*, and *Fuscigonia (fuscicollis).* Sabrosky and Arnaud (1965) restored *Gonia* to its original concept, which will be used in this paper. As will be shown in the discussion of the species of this genus, more work is needed on their taxonomy.

The characteristics of *Gonia* puparia are as follows. The puparia are robust, larger than 9 mm in length, and are patterned or completely covered with spinules. The posterior spiracles are large, protruding, and heavily sclerotized while the anterior spiracles are diverse in character. The anal protuberance is small and insignificant. The cephalopharyngeal structure is two-articled with the anterior and median sclerites being fused. The dorsal anterior portion of the posterior sclerite forms an arm which projects forward to the anterior sclerite. A sclerotized band of different widths surrounds the inner angle between the dorsal and ventral processes of the posterior sclerite. The entire structure of the cephalopharyngeal apparatus has a triangular form with the lines of the anterior-median and posterior sclerites being nearly straight.

The females of this genus typically lay their eggs on vegetation which may be eaten by host larvae. The eggs hatch in the host gut and the larvae penetrate into the body cavity. The larvae develop to the second instar in the host larva and complete development after the host pupates. The puparium is found in the host pupa. Strickland (1923) provides a detailed account of the life-cycle of a species he called *Gonia capitata*. King and Atkinson (1928) did not differentiate between three species of *Gonia* which they found but stated that as a group, they tended to select plants which were most likely to be eaten by host cutworms. None of these authors believed that *Gonia* species would ever show a high effective rate of parasitism in *E. ochrogaster* populations as has been found in *Agrotis orthogonia* Morrison populations.

When the cutworm is attacked by *Gonia* sp., the pupa darkens to a deep brown because of the presence of the puparium. The emerging adult causes a transverse break across the head

of the host pupa. (Fig. 62). The break usually closes and the host pupa remains intact. The abdominal segments remain very much like those of a normal pupa. In some specimens, the host pupa is expanded around the puparium and is slightly collapsed directly behind it.

Gonia aldrichi Tothill

King and Atkinson (1928) recorded *Gonia aldrichi* as reared from *E. ochrogaster*. They stated that *aldrichi* is the most important parasitoid of *E. ochrogaster* in the genus *Gonia* and is widely distributed in Saskatchewan. It appears that at least two species are currently included in the concept of *G. aldrichi* and both have been reared from *E. ochrogaster*. These species will be designated here as *G. aldrichi* No. 1 and *G. aldrichi* No. 2.

Description of puparia. – The puparia are similar in both of these species. The exit hole from the host pupa is a transverse, irregular break across the head of the pupa (Fig. 62). After the adult has emerged, the break is usually only slightly open except in the unusual cases where the anterior region of the host pupa is broken off. The posterior spiracles (Fig. 9, 10) are large and the orificial ridges are high and prominent. The orificial ridges occur very close to the edge of the spiracular plate and the ventral ridge often appears continuous with the edge. The cicatrix is usually poorly developed but varies in size and prominence from specimen to specimen. Spinules cover most of the puparium in indistinct bands. The spinules occur singly, and are randomly distributed (Fig. 11). The anterior spiracles have two very different shapes, one of which consists of two or three pori on a distinct pedicel (Fig. 8), and the other with 12 or more pori (Fig. 7) surrounding and partially obscuring the pedicel. The difference in anterior spiracle shape could not be correlated to other characters. Also, the number of pori vary on the same specimen though never from one type to the other.

Description of larvae. – The main difference between the two species lies in the shape of the cephalopharyngeal structures. The entire structure of *G. aldrichi* No. 1 (Fig. 5) is a wider triangle than that of *G. aldrichi* No. 2 (Fig. 6). The angle between the dorsal and ventral arms of the posterior sclerite is greater in No. 1 than in No. 2. The inner angle of No. 1 is only lightly, if at all sclerotized, whereas in No. 2 a definite band of up to one-quarter the width of the dorsal arm extends around the inner angle from near the tip of the dorsal arm to past the widened area of the lower arm. The lower arm of No. 1 lacks any definite widening along its length. The fused anterior and median sclerite of No. 1 is shorter than that of No. 2. The blade of the mouth hooks of No. 2 has a definite S-curve shape whereas in No. 1 the curve is a simple arc. The overall sizes of No. 1 and 2 are similar.

The second instar larvae of *Gonia* sp. (Fig. 12) were found in my dissections of dead host larvae. As the puparia and cephalopharyngeal structures of all the reared specimens were similar to the two *G. aldrichi* species, it is safe to call these second instar larvae *G. aldrichi* also. The cephalopharyngeal structures of these larvae are fused into a single sclerite (Fig. 13). The larva is 5 to 6 mm long, curved ventrally and patterned by black papillae. The patterns of papillae were not constant.

Biology. – While no adults were obtained from reared specimens in my study, several puparia were found in reared host pupae. The reared *Gonia* puparia compared favorably with borrowed specimens. It is likely that faulty rearing conditions caused the failure of adult emergence. During the dissection of dead host larvae, five specimens were found to contain from one to five second instar *Gonia* larvae. In one of these host larvae, two of the five *Gonia* larvae were damaged and partially disintegrated, while in another only the cephalopharyngeal structures of a larva were found, as well as a healthy *Gonia* larva.

Hosts. – Specimens of *G. aldrichi* examined were reared from *E. ochrogaster* and *A. orthogonia*.

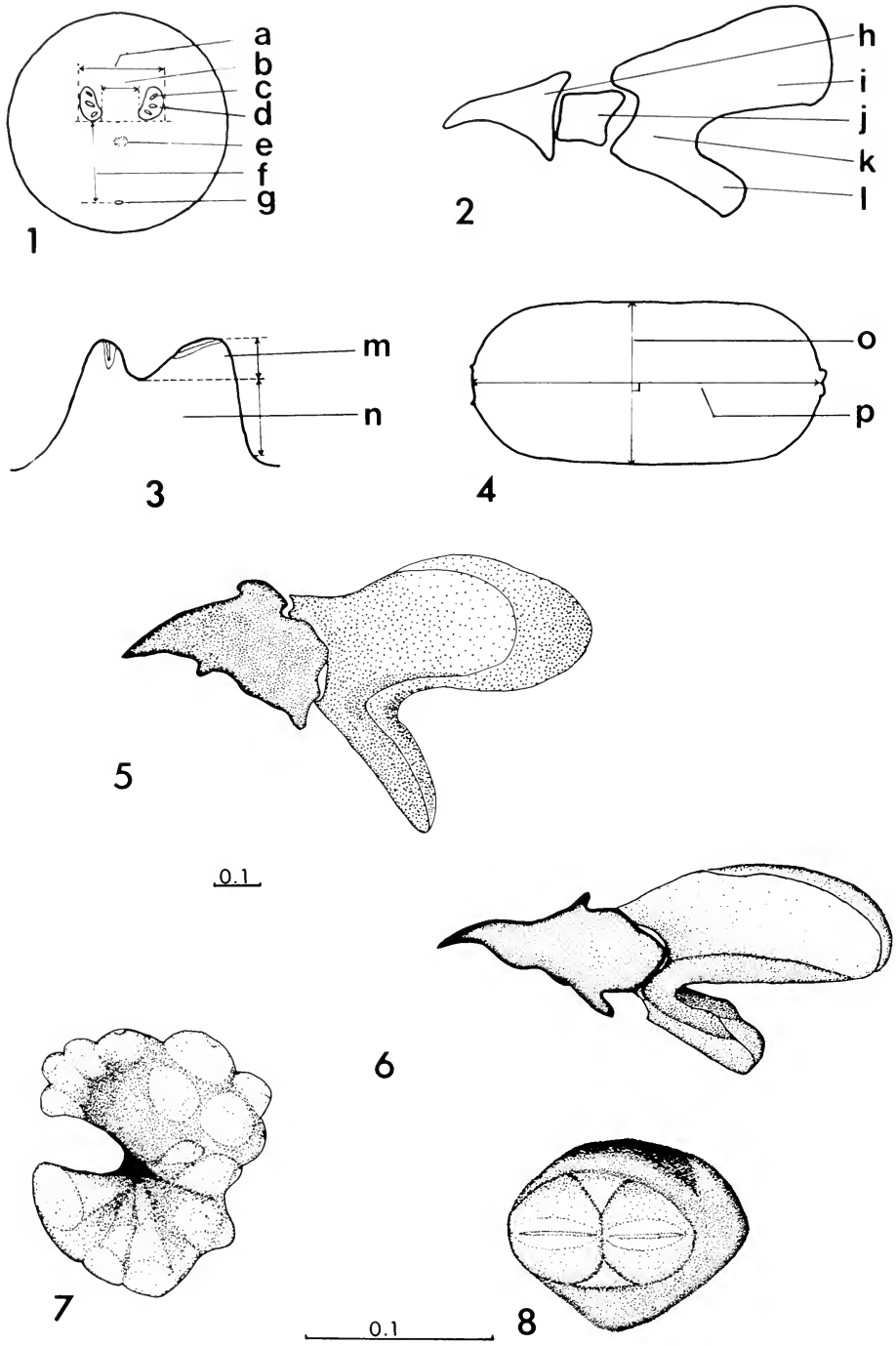


Fig. 1–4. Immature tachinids. 1. posterior view of puparium. a, b, maximum and minimum distance between posterior spiracles; c, orificium; d, spiracular plate; e, supra-anal protuberance; f, distance of anus from posterior spiracles; g, anus. 2. cephalopharyngeal structures of 3rd instar larva. h, anterior sclerite; i, dorsal process of posterior sclerite; j, median sclerite; k, posterior sclerite; l, ventral arm of posterior sclerite. 3. side view of posterior spiracle. m, orificial ridge; n, stigmatophore; (from Zuska, 1963). 4. dorsal view of puparium. o, p, width and length of puparium. Fig. 5–8. *Gonia aldrichi*. 5. cephalopharyngeal structures of *G. aldrichi* No. 1. 6. *G. aldrichi* No. 2. 7, 8. anterior spiracles. Scales in millimeters.

Gonia capitata (De Geer)

Gonia capitata was recorded as being reared from *E. ochrogaster* by Strickland (1923). Strickland noted that this could be a mistaken identification and that the species studied could be divided into five groups. It is now recognized that *G. capitata* is exclusively a European species (Brooks, 1943; Sabrosky and Arnaud, 1965). This invalidates the figures and descriptions of Greene (1921). The biological work of Strickland must now be regarded as being of *Gonia* sp. but is nevertheless a valuable source of information.

Gonia fuscicollis Tothill

Gonia fuscicollis was recorded as being reared from *E. ochrogaster* by King and Atkinson (1928). Brooks (1943) regarded this species as being so different from the other species of *Gonia* that he created the genus *Fuscigonia* for it. Unfortunately, no specimens were available for study.

Nothing is known of the biology of this species and it is likely that it is not an important parasitoid of any of the economic cutworms. The description of the immature stages is necessary in the future, however, to help separate the large number of species in this genus.

Gonia sequax Williston

Gonia sequax has not been recorded as being reared from *E. ochrogaster*. I am including *G. sequax* in this study as I am sure that it is a potential, if not actual parasitoid of *E. ochrogaster*, as well as to represent the *capitata* species group (Brooks, 1943).

Description of puparia. – The puparium of *G. sequax* is very similar to that of *G. aldrichi* in size and shape. The posterior spiracles (Fig. 15) differ in that the orificial ridges are set further in from the edge of the spiracular plate than those of *G. aldrichi*. The orificial ridges enclose the cicatrix which is fairly prominent. The anterior spiracles (Fig. 16) have only one porus on the end of a long pedicel. Only one specimen was examined so that this may not be characteristic of all members of this species. The spination of the puparia differs sharply from that of *G. aldrichi*. The spines (Fig. 17) tend to be in groups or series of three or more and often form long, irregular rows.

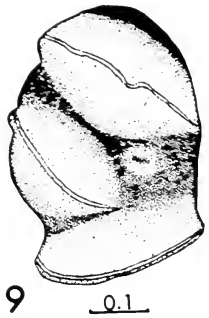
Description of larvae. – The cephalopharyngeal structures (Fig. 14) are similar to both *G. aldrichi* No. 1 and No. 2 but differ from both enough to be separated. The blade of the mouth hooks is a simple arc as in *G. aldrichi* No. 1 but the overall shape is closer to that of No. 2. Distinct from both *G. aldrichi* No. 1 and No. 2 is the anterior projection of the dorsal arm of the posterior sclerite. It is long, distinct, and well developed, and usually has a large open space between it and the anterior-median sclerite.

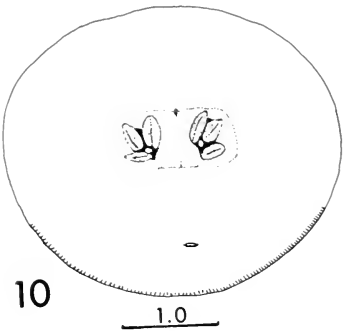
Biology. – Little is known of the biology of this species and how it differs from other members of the genus.

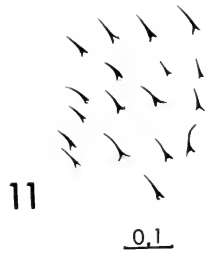
Hosts. – This species has been reared from *Agrotis orthogonia* from Alberta and Saskatchewan.

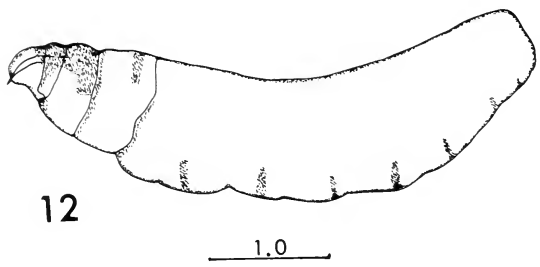
Bonnetia comta (Fallen)

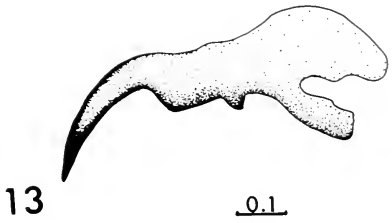
The puparia and posterior spiracles of *Bonnetia comta* were described by Greene (1921) and all the life stages including the above structures were described by Strickland (1923). Allen (1926) described the first instar larvae. Greene's drawings either are not clear enough or are of a different species than what is now called *B. comta*.

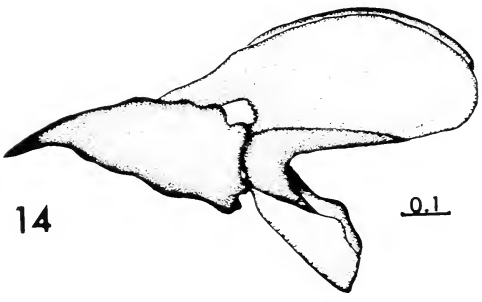


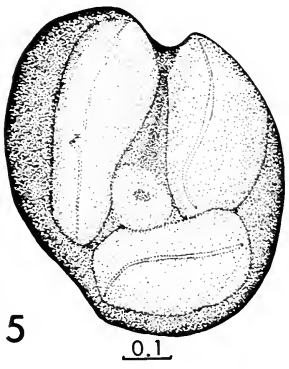


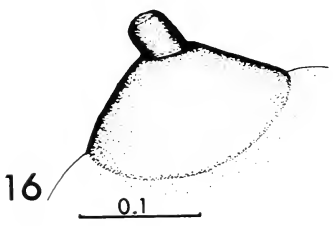












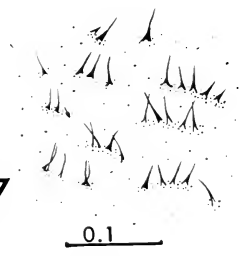


Fig. 9–13. *Gonia aldrichi*. 9. posterior spiracle. 10. posterior view of puparium. 11. spine pattern of puparium. 12. second instar larva. 13. cephalopharyngeal structures of second instar larva. Fig. 14–17. *Gonia sequax*. 14. cephalopharyngeal structures. 15. posterior spiracle. 16. anterior spiracle (side view). 17. spine pattern of puparium. Scale in millimeters.

Description of puparia. – The puparia are large, sub-elliptical, smooth-surfaced without any trace of spination, and show only vague segmentation marks (Fig. 22). The anterior stigmata (Fig. 20) are raised and show either five or six pori which are arranged in a curvilinear pattern with the axes of the individual porus pointing towards the center of the curve. Both the stigmatal plates and the supraanal protuberance are widely separated from the true anus and occur high on the dorsal surface of the puparium (Fig. 21). The stigmatal plates of the posterior spiracles (Fig. 19) are low and flat with the orificial ridges being only slightly raised but quite wide. The cicatrix is also low but is large and distinct. Occasionally, especially with transmitted light, a weakly sclerotized region can be seen between the inner and medial orificial ridges. The supraanal protuberance is pronounced and in some specimens is higher than are the stigmatal plates. From it runs a distinct ridge which separates the stigmatal plates.

Description of larvae. – Strickland (1923) describes the life stages and gives figures for them. The following passage is taken from his paper to describe the final instar larvae, which I have not examined.

> "The smallest specimen seen measures 12 mm. long and 4 mm. wide; the largest, which was almost mature, was 15.75 mm. by 4.25 mm. While living, the larvae that were dissected from their host constantly changed their shape by violent muscular contractions. The transparent cuticle revealed the yellow and brown viscera in strong contrast to the voluminous white fat-body. When killed . . . the larva is arcuate, dorsum concave, tapering cephalad and slightly so to the bluntly rounded caudal extremity. Eleven segments, only, were seen. Dorso-laterally between segments I and II there are a pair of blackened spiracles . . . each of which possesses six respiratory papillae that open into a short constricted felt-chamber, behind which are a pair of stout trachea which run the length of the body and connect with the caudal spiracles. The cuticle is almost destitute of armature, though minute simple spines are present on all of the intersegmental areas. These are most numerous in the anterior and posterior segments where they form a fine network of rows that encircle the body. In addition there are traces of intersegmental hooks between the four anterior segments. The buccal-pharyngeal armature . . . differs little from that of the preceding stage except in size. The over-all measurement is 1.0 mm. to 1.1 mm., the mandibular hooks being 0.17 mm. to 0.18 mm. long."

Strickland's drawings of the cephalopharyngeal structures provide the appropriate general impressions but are inaccurate in one aspect. Ventral to the anterior sclerite lies an auxiliary sclerite as shown in Fig. 18. This sclerite is always shown as being solidly fused to the anterior sclerite in Strickland's paper. I have examined 12 borrowed specimens and three slides which were part of Strickland's study and my interpretation is as follows: The posterior sclerite is very slightly sclerotized and while it has a characteristic shape, it is often twisted or bent in the puparium. The anterior process of this structure becomes progressively less sclerotized until it terminates in a ligament-like structure which connects with the posterior process of the anterior sclerite. The articulation between the median and posterior sclerite is very weak and usually releases when the entire structure is being removed from the puparium. In contrast, the anterior articulation is very solid and it is often difficult to find the division between the two sclerites except at the tip of the posterior process of the anterior sclerite.

Biology. – The life history and behavior of *B. comta* is well outlined by Strickland (1923). This species belongs to the tachinids which either larviposit or oviposit in an area where the first instar larvae can actively attach themselves to a host and enter from the outside of the body. Strickland found that the cutworms were attacked in the third or fourth instar and death resulted during the prepupal stage when the mature larva emerged to enter

the soil and pupate.

Hosts. – Two generations occur per year with the larvae of the second generation overwintering in their hosts. The hosts recorded for this species in Strickland's (1923) paper are as follows: *Euxoa tristicula* Morrison, Montana; *E. messoria* Harris, Washington; *Agrotis ypsilon* L., California; *A. orthogonia* Morrison, Alberta; *Copablepharon viridisparsa* Dod., Alberta; *Polia acutermina* Sm., Alberta (induced parasitism). King and Atkinson (1928) recorded *B. comta* as reared from *E. ochrogaster* but found it to be an insignificant parasite during their studies in Saskatchewan.

Periscepsia Gistel

This genus has been handled in several different ways by various authors. Sabrosky and Arnaud (1965) list six different synonyms of *Periscepsia*. The confusion with regard to *P. helymus* and *P. laevigata* lies in the fact that the former has been placed in seven different name combinations and the latter in eight. In addition, many authors confused *P. laevigata* with *P. helymus* and named it as the latter. The major generic names in which both species have been placed and which have been used in the literature are *Phorichaeta, Metachaeta,* and *Wagneria. P. helymus* has also had the specific names *helyma* and *sequax,* while *P. laevigata* has been known as *helymus, atra,* and *carbonaria.* The character recognized by Reinhard (1955) and Wood (pers. comm.) to separate these species is the presence of setae on the median portion of the first wing vein in *P. laevigata* as opposed to a bare first wing vein in *P. helymus*. Because of the confusion which has existed about these two species, one must regard the host lists from the literature with caution.

Periscepsia helymus (Walker)

The puparia of *P. helymus* were described by Greene (1921) under two synonymous names, *Phorichaeta sequax* (Williston) and *Metachaeta helymus,* but the puparia were different from each other.

Description of puparia. – Greene's (1921) descriptions and figures of the puparia under the name *Metachaeta helymus* closely resemble *P. helymus*, while those of *Phorichaeta sequax* differ sufficiently from the other two to be considered different. Also, the puparia which I measured were significantly larger (4.5 x 2.1 mm) than the dimensions given by Greene for *Phorichaeta sequax* (3.5 x 1.5 mm). Even the ranges of the specimens I studied (4.08 mm - 4.88 mm x 1.92 mm - 2.16 mm) did not include his dimensions. *M. helymus* dimensions were 4.75 mm x 1.75 mm and hence are similar to the measurements taken from my study series.

From a lateral view of the puparium, the posterior regions carrying the stigmatal plates and anus appear extended (Fig. 24). From a posterior view the puparia appear nearly circular with a raised central region (Fig. 25). The spiracular plates are terminal in position. The spiracular plates of the posterior spiracles (Fig. 26) are narrowly separated, only slightly raised and are quite flat. The cicatrix is large, round, and slightly concave in the central region. The entire shape of the spiracular plate varies from oblong to slightly curved. The anterior spiracles are especially poor characters in this group because they are often lost at emergence. The stigmata are small and tuberculate with a cluster of pori in a crescent (Fig. 28). The number of pori is not constant.

Description of larvae. – No specimens of the final instar larvae were available for study, therefore I am relying on the cephalopharyngeal structures recovered from the puparia for characters. The cephalopharyngeal structure (Fig. 23) is very distinctive but the variations

which occur tend to confuse its appearance. The anterior sclerite is heavily sclerotized with the ventral process being almost as long as the actual mouth hooks. Behind the ventral process lies an auxiliary sclerite which may be concealed or lie in several different positions in the same general region. The median and posterior sclerites are fused but with adequate lighting, the suture can be seen. Projecting dorsally from the median sclerite is a hook-like process which curves anteriorly. The posterior sclerite varies considerably in the degree of sclerotization from a dark colour which nearly obscures the hook, to a very weakly sclerotized, clear structure. In the latter case, many structural differences appear but are probably insignificant. In this species the anterior process of the posterior sclerite is very weak or lacking. In some specimens a membranous connection may be seen between the anterior and posterior sclerites in the dorsal regions.

Biology. – Little is known of the biology of this species except that it attacks cutworm larvae and that more than one may emerge from a single host (Reinhard, 1955). Guppy (1967) records three or four *P. helymus* as being reared from a single sixth instar *P. unipuncta* Haworth larva.

Hosts. – In the literature, *P. helymus* has been recorded as reared from the following hosts: *Heliophila commoides* Guenée (Tothill, 1913), Ontario; *Pseudaletia unipuncta* Haworth (Baker, 1914), Ontario; *Euxoa ochrogaster* (King and Atkinson, 1928), Saskatchewan. Reinhard (1955) lists the following hosts not recorded above: black army cutworm, *Actebia fennica* Tausch, Michigan; *Peridroma saucia* Hübner, California; *Cirphis* sp. Hampson, Washington; *Euxoa auxiliaris*, Alberta; *Polia adjuncta; Grapholitha* sp. *Conistra devia* Grote; *Lithophane innominata* Smith, Maine. Specimens which I examined were reared from: *H. commoides,* Ontario; *A. eliminata* Gn., New Brunswick; *Rhynchagrotis cupida* Grote, New Brunswick; *Andropolia vancouvera* Strand, British Columbia; *Andropolia* sp. Grote, Alberta; *A. contacta* Walker, Alberta.

Periscepsia laevigata (Van der Wulp)

There appears to be no previous description of the immature stages of this species in the literature.

Description of puparium. – Only the puparium of one specimen was studied and it lacked the anterior flaps so that neither the cephalopharyngeal structures nor the anterior spiracles were available for study. The posterior spiracles are similar to those of *P. helymus* but the orificial ridges tend to be higher, wider, and more rounded (Fig. 27). The orificia follow the top of the ridges almost to the level of the spiracular plates. While the cicatrix is large and round it is not as distinct as that of *P. helymus*. The best differentiating character is the median orificium which is very curved in *P. laevigata* but nearly straight in *P. helymus*. The rounded shape of the orificial ridge of *P. laevigata* contrasts well with the long, narrow shape in *P. helymus*.

Biology. – Little is known of the biology of this species except that it attacks fifth instar cutworm larvae (Guppy, 1967). The range of the species is from Guatemala to Canada (Reinhard, 1955).

Hosts. – The problem of host records is important in regards to this species. As one cannot be sure of the accuracy of earlier identifications, it is possible that the following list is either incomplete or inaccurate. Reinhard (1955) lists the following hosts: *Pseudaletia unipuncta, Euxoa auxiliaris, Grapholitha* sp. Hübner; *Lascoria ambigualis* Walker, *Elaphria nucicolora* Grote, and unidentified cutworms. Guppy (1967) records *P. unipuncta* from Ontario as a host. The specimen I examined was reared from an unidentified 'phalaenid' from Big Beaver, British Columbia.

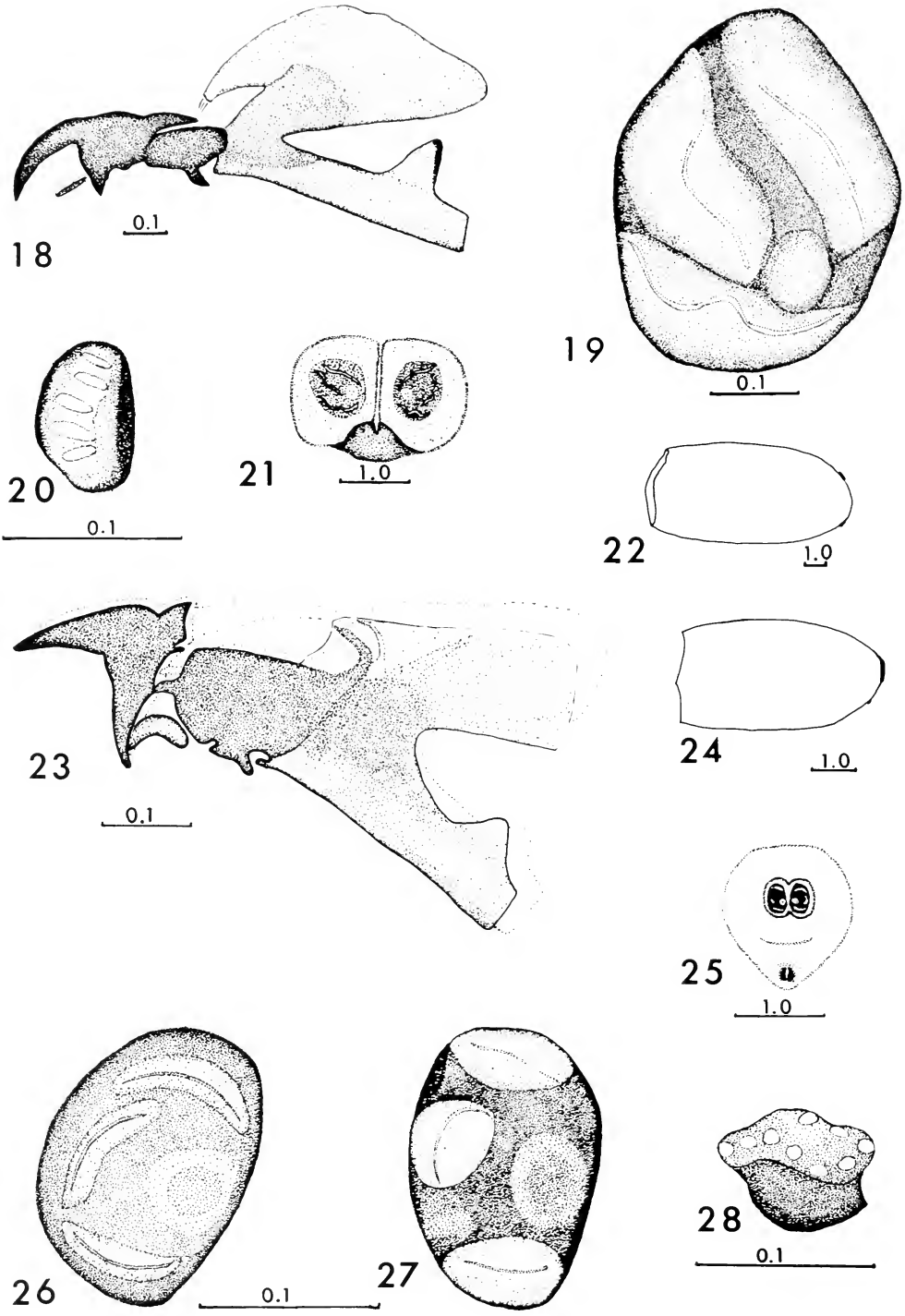


Fig. 18–22. *Bonnetia comta*. 18. cephalopharyngeal structures. 19. posterior spiracle. 20. anterior spiracle. 21. posterior view of puparium. 22. puparium. Fig. 23–26, 28. *Periscepsia helymus*. 23. cephalopharyngeal structures. 24. puparium. 25. posterior view of puparium. 26. posterior spiracle. 28. anterior spiracle. Fig. 27. Posterior spiracle of *P. laevigata*. Scale in millimeters.

BOMBYLIIDAE

Biology and morphology of immature bombyliids

Five species in two genera of Bombyliidae have been recorded as primary parasitoids, and one other species as a hyperparasitoid of *Euxoa ochrogaster*. Brooks (1952) illustrated the final instar larvae and the pupae of five of these six species and provided keys for their identification. Painter and Hall (1960) provide keys for adults to the genera of Bombyliidae, to the subgenera of *Villa*, and to the known species of *Poecilanthrax*. Generally, little is known of the biology of bombyliids. No comprehensive work has been done on the biology of any species attacking Lepidoptera. The terminology used for the morphology of the immature stages is based on Berg (1940) in his work on the immature stages of *Systoechus vulgaris* Loew.

While Bohart *et al.* (1960) suggest that there may be four larval instars, other authors have only described three (Hynes, 1947; Berg, 1940; Clausen, 1928). The first instar larva is active, vermiform, and adapted to move through the soil and seek out its host (Clausen, 1928; Bohart *et al.*, 1960; Berg, 1940). In parasitoid species the first instar larvae penetrate their host and develop internally. The second instar larva is far less mobile than the first and is more maggot-like (Clausen, 1940; Bohart *et al.*, 1960). It has lost its adaptations for moving through the soil and likely can only move in open areas. In species which are internal parasitoids, the larva likely molts immediately after attacking the host due to the radically different environment in which it then lives. Because the cast skin of the final instar larva can be found in the pupal case of the host, descriptions of this stage are available for several species. Brooks (1952) reviews the taxonomically important characters of both the final instar larvae and the pupae of noctuid-attacking bombyliids. In the final instar larvae he found the structure of the mouth parts and the head sclerites to be important. In the pupae he found that the head tubercles and mouth part sizes were of specific use, whereas the apical segments were of little use due to the general uniformity in the group and the variability within the species involved.

Bombyliids have been observed apparently ovipositing in loose sand or dust, but this has not been confirmed (Painter and Hall, 1960). Brooks (1952) noted that the species attacking noctuids fly from the latter half of July through to September, but the hosts are not attacked until their fourth, fifth or sixth instars the next season. He felt that the species overwinters as eggs in the soil or old vegetation. Painter and Hall feel that the first instar larvae seek out small caterpillars as hosts and remain inactive until the host pupates, when they rapidly develop and kill the host. The bombyliid pupa breaks out of the host pupal remains, and with the use of directed spines and bristles moves to the soil surface where the adult emerges quickly (Painter and Hall, 1960; Allen, 1921; Snow, 1925). It is likely that the abrasion from moving through the soil accounts for much of the intraspecific differences which have been observed in the shape of the head tubercles, apical segments, and spines.

Other than Allen's (1921) report that *Poecilanthrax lucifer* (Fabr.) attacked 25% of the fall army worm, *Spodoptera frugiperda* (Smith) in Mississippi, bombyliids have been regarded as minor parasitoids of noctuids (Brooks, 1952; King and Atkinson, 1928).

Villa Lioy

This genus has a wide host range as internal or external parasites of Diptera, Lepidoptera, Hymenoptera, and Coleoptera. Painter and Hall (1960) provide a key to the adult subgenera. Two of these, *Villa* and *Hemipenthes*, are of interest to us.

Villa (Villa) alternata (Say)

This species was recorded by Brooks (1952) as a parasite of *E. ochrogaster* which was collected as fourth, fifth, and sixth instar larvae in May and June. Records show this species to range across the prairies of Canada. Brooks provides illustrations of the mouth hooks, head capsule, and apical platelets of the mature larvae as well as of the entire pupa, its head, and apical structures.

Hosts. – *Euxoa flavicollis* Sm., *E. tesselata* Harris, *Agrotis orthogonia, Feltia ducens* Walker, *E. ochrogaster*, (Brooks, 1952); tenebrionid larvae (Clausen, 1940).

Villa (Villa) fulviana (Say)

This species was recorded by King and Atkinson (1928) as reared from *E. ochrogaster,* but only from *Euxoa* sp. Hübner by Brooks (1952). It has been collected in host pupae from June 30 to July 12 and found to emerge as adults in the autumn. King and Atkinson felt that it overwinters in alternative hosts. Illustrations of the larvae and pupae are provided by Brooks.

Hosts. – *E. ochrogaster* (King and Atkinson, 1928), *Euxoa* sp. Hübner (Brooks, 1952).

Villa (Villa) lateralis (Say)

King and Atkinson (1928) record this species as having attacked two specimens of *E. ochrogaster* and emerging in the autumn. No reference is made to this species by Brooks (1952). No drawings of any of the life stages are known and no material appears to be available at the present time.

Villa (Hemipenthes) moroides (Say)

Species of the subgenus *Hemipenthes* are hyperparasitic upon the primary parasites of Lepidoptera (Clausen, 1940). Clausen refers to members of this subgenus as attacking ichneumonid parasitoids, but Brooks (1952) records three species as reared from tachinid hosts. *V. moroides* was reared from *Gonia* spp. and *Bonnetia comta*, which were reared from noctuid hosts. Clausen stated that the exact relationship between the host, parasitoid, and hyperparasitoid was not established and that it was possible that the ichneumonids were attacked in the pupal stage independently of the host. It appears that a true hyperparasitoid role has been established for *V. moroides.*

Poecilanthrax Osten Sacken

This is a widespread genus which attacks chiefly noctuid larvae. Painter and Hall (1960) list 15 species of cutworms and army worms which are attacked by eight species of *Poecilanthrax.*

Poecilanthrax alcyon (Say)

This species was recorded as a parasitoid of *E. ochrogaster* by King and Atkinson (1928) under the name of *halcyon*. Painter and Hall (1960) give the distribution of the species in southern Canada and the United States, but fail to show the correct boundaries of northern distribution. The range extends from Texas to the Northwest Territories, and with the ex-

ception of Southern California, east of the Rocky Mountains to the Atlantic Ocean.

Brooks (1952) illustrated the final instar larva (Fig. 32) and pupa. Painter and Hall (1960) discuss the entire species at length, as *P. alcyon* is the type of the genus, and give a detailed description of the adult. Fig. 29, 30, 31 and 33 are original drawings of a specimen of *P. alcyon* reared from *E. ochrogaster.*

Only one specimen of a pupa attacked by *Poecilanthrax alcyon* (Fig. 63) was examined. This specimen was a light brown similar to one from which a moth had emerged. The adult *P. alcyon* emerges from the dorsal surface behind the head, leaving the pupa intact. The abdominal segments are fully extended after emergence.

Hosts. – *E. ochrogaster, E. flavicollis, Chorizagrotis thanatologia, Pseudaletia unipuncta,* (Brooks, 1952); *peridroma margaritosa* (Walkden, 1950).

Poecilanthrax willistonii (Coquillet)

The adults of this species were reported by King and Atkinson (1928) to emerge either in the autumn or the following June. They felt that the species overwinters as larvae in noctuid hosts which overwinter in the larval stage. Painter and Hall (1960) show the distribution as from south of the United States to the middle of the prairie provinces of Canada, and from the west coast through to the central great plains. Figures of the larvae and pupae are given by Brooks (1952) and those of the pupae are reprinted by Painter and Hall (1960).

Hosts. – *Agroperina dubitans* Walker, *Chorizagrotis thanatologia* Dyar, *S. devestator, Euxoa flavicollis, E. ochrogaster, E. tessellata, Feltia ducens,* (Brooks, 1952); *Chorizagrotis auxiliaris* Grote, *Euxoa scandens* Riley, (Walkden, 1950).

ICHNEUMONIDAE

Morphology of immature ichneumonids

The ichneumonid parasitoids have many taxonomic characters which are useful to separate their immature stages. The terminology and approach to description follows that of Finlayson (1960). The cocoons, if present, can be separated using: size, color and shape, and location of the adult emergence hole from the cocoon. The spiracles were of limited use when studying these species as the differences I found were insignificant. The best separating characters for the final instar larvae were found in the cephalic structures (Fig. 34). To differentiate between species, the presence or absence of sclerites, and the shape of mandibles were the best characters found.

Preparation of specimens. – After having been soaked in water for at least 24 hours, the final instar larval skins were removed from the cocoons by means of fine forceps or a hooked pin. The larval skin was gently unfolded and removed from the adult meconium which covered many of the specimens. The skin was then placed in 10% KOH for 24 hours at room temperature, or longer if it was not cleared enough. Boiling in KOH was found to disarticulate the cephalic structures resulting in the loss of sclerites, and so was not used. The cleared larval skin was mounted in polyvinyl lactophenol on microscope slides for further examination. Polyvinyl lactophenol was chosen because it is a mild clearing agent and thus aids in the ease of sclerite recognition.

Four species of the tribe Ichneumonini have been recorded as parasitoids of *E. ochrogaster.* Three species, *Eutanyacra suturalis, Diphyus* No. 1, and *Spilichneumon superbus* were examined and found to be similar in the following ways. The females lay their eggs in the cutworm larvae but the host is not killed until it reaches the pupal stage. None spin any apparent cocoon and all use the host pupa for protection during their pupal stage. All have

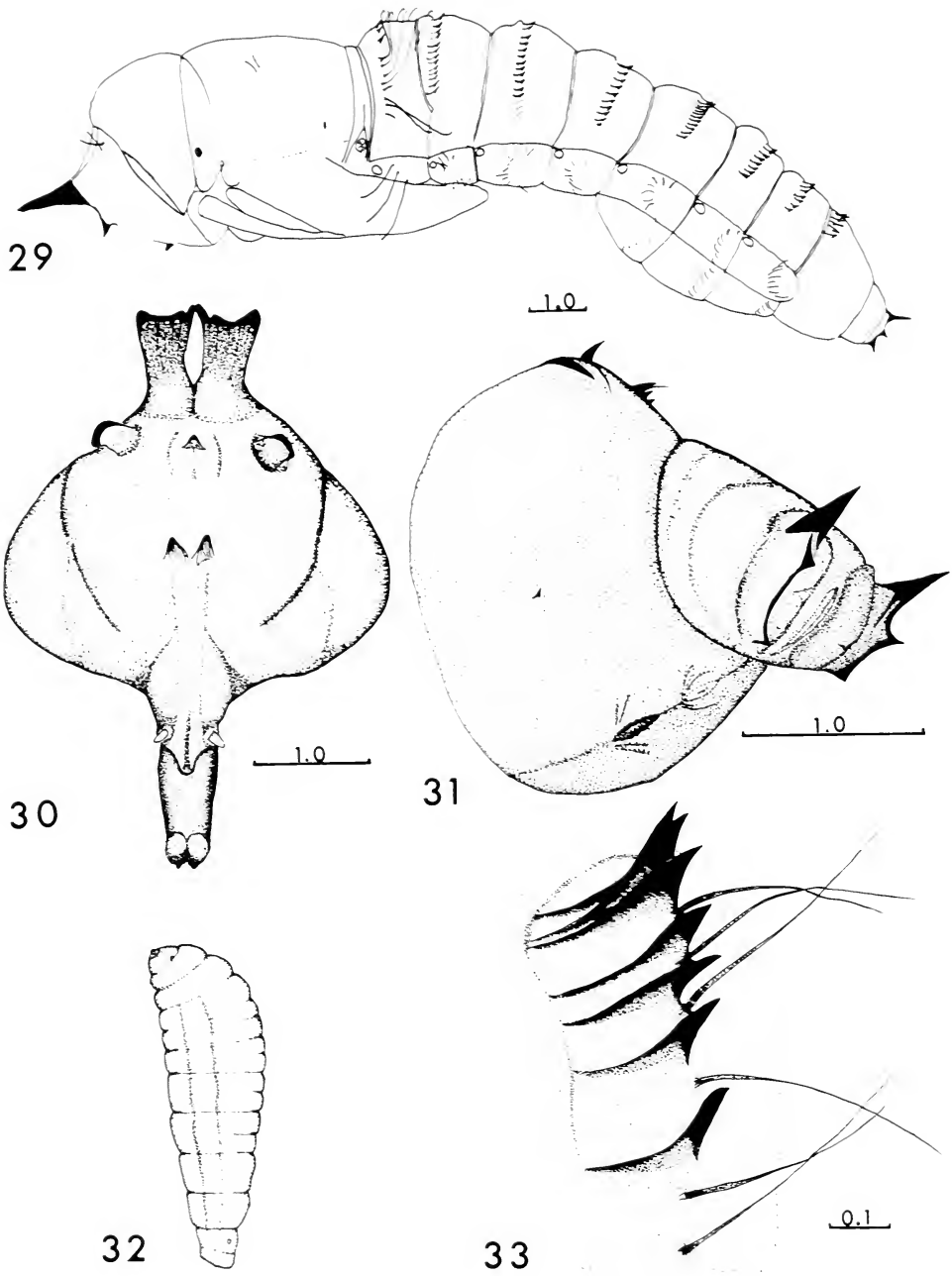


Fig. 29–33. *Poecilanthrax alcyon*. 29. pupa. 30. ventral view of pupal head. 31. ventro-lateral view of posterior end of pupa. 32. final instar larva (Brooks, 1952). 33. spine and setal pattern of third abdominal segment of pupa. Scale in millimeters.

greatly reduced larval mouth parts which differ between species mainly in the mandible shape. One pair of sclerites located behind the mandibles do not conveniently fit into the Finlayson (1960) sclerite classification. It is possible that these are modified from the suspensorial sclerite. In all these species, the stipital and labial sclerites are lost. The shape of the spiracles is quite constant (Fig. 37), and is of no use to separate species. Several ichneumonine larvae were dissected from final instar cutworm larvae and one was removed from a host pupa. Those removed from the cutworms were an early instar (Fig. 36) and could be either *Diphyus* No. 1 or *S. superbus*. The one removed from the pupa had cephalic structures which were clearly those of *Diphyus* No. 1. When attacked by any of these species, the host pupa does not darken as it normally does, but remains the shiny brown of a healthy 3 to 7 day old pupa. The anterior portion of the host pupa is chewed and broken by the emerging ichneumonine adult (Fig. 64). The pupal remains are distinct from those from which a moth has emerged (Fig. 61). The unexamined species, *Pseudambly teles subfuscus*, is likely similar to the examined species.

Eutanyacra suturalis (Say)

Description of larvae. – The cephalic structures (Fig. 35) of the final instar larva with incomplete epistoma. Pleurostoma wide, heavily sclerotized, and with a very irregular, poorly defined edge. Superior mandibular process wide and short, inferior mandibular process reduced to one. Pleurostoma and hypostoma closely connected but limited movement between them possible. Hypostomal arms heavy and of irregular width. Stipital and labial sclerites missing. Labial and maxillary palpi small and difficult to see. Silk press small and very lightly sclerotized. Mandibles large, robust, heavily sclerotized with slightly curved blades which continued into base without clear marking. Behind or above mandibles, the two sclerites heavily sclerotized and irregularly larger dorsally than ventrally.

Biology. – *E. suturalis* females were observed, collected, and reared during the *Actebia fennica* outbreak at Worsley, Alberta in 1967. The females were seen to fly and hunt during the late afternoon and early evening. They were found hunting in fields which had been defoliated several days before by the passing cutworm army. The hunting females ran rapidly on the soil surface and searched around soil clods and in large cracks in the soil. While hunting, they could be easily approached and could be captured by hand. Captured females would attack field-caught *A. fennica* larvae, but oviposition was never observed. The attack consisted of mounting the cutworm lengthwise and curling the tip of the abdomen under so that the ovipositor touched the cutworm. At this point, every attacking female was flipped off the cutworm by a violent twisting movement of the cutworm. In no instance was such a cutworm reattacked, and I never succeeded in rearing an *E. suturalis* adult from an offered cutworm. In the laboratory, adult *E. suturalis* emerged 10 to 14 days after host pupation.

Hosts. – Whitehouse (1922) recorded *E. suturalis* as reared from *E. ochrogaster* in Alberta. The following hosts were found by examining host labels in the C.N.C.: *Actebia fennica,* British Columbia; *E. ochrogaster*, Saskatchewan; *E. flavicollis*, Saskatchewan; *Scotogramma trifolii* Rottenburg, Saskatchewan.

Spilichneumon superbus (Provancher)

Description of larvae. – The cephalic structures of the final instar larva (Fig. 39) are similar to those of *E. suturalis* and *Diphyus* No. 1. The size is closer to that of *Diphyus* No. 1 than to that of *E. suturalis*. The mandibles are short and broad with a wide, straight

blade which is continuous in appearance with the base. The edge of the pleurostoma is well defined as in *Diphyus* No. 1.

Biology. – This species was reared from *A. fennica, E. ochrogaster* and *F. ducens* during the current study. Because it was not recognized as being different from *Diphyus* No. 1 while live adults were available, the adults were mixed and little data on either behavior or biology was obtained. The adults emerged from the host about 3 weeks after host pupation.

Hosts. – The following hosts of *S. superbus* have been recorded (Heinrich, 1960): *Chorizagrotis auxiliaris*, Alberta; *E. ochrogaster*, Manitoba; *E. scandens, E. flavicollis, E. messoria, Feltia ducens*, Saskatchewan; *Pseudaletia unipuncta*, Hawaii (introduced).

Pseudamblyteles subfuscus (Cresson)

Strickland (1923) recorded *Amblyteles subfuscus* as reared from *E. ochrogaster*. This species was subsequently transferred to *Pseudamblyteles* which is now considered to be congeneric with *Diphyus* Kriechbaumer (Heinrich, 1961). The genus *Diphyus* is now being reworked and the different species are currently denoted by numbers in the C.N.C. In the C.N.C. only *Diphyus* No. 1 of the genus *Diphyus* had host labels associating it with *E. ochrogaster*. Dr. Mason (pers. comm.) states that *Diphyus* No. 1 does not include what was *P. subfuscus*. There is no other evidence currently available to determine which of the *Diphyus* species was *P. subfuscus*.

Strickland (1923) described the biology of *P. subfuscus* from his research. Unfortunately little of the data which he presents is of use to separate *P. subfuscus* from any of the other ichneumonines which attack *E. ochrogaster*. The major biological fact which he describes is that the eggs are laid in the salivary glands of the host cutworm. During my dissections of *E. ochrogaster* larvae, I have seen neither the eggs which he describes nor the resulting scar on the salivary glands. Until the taxonomy of *Diphyus* is better understood, the status of *P. subfuscus* as a parasitoid of *E. ochrogaster* will be unclear.

Hosts. – Strickland (1923) reared *P. subfuscus* from *Chorizagrotis auxiliaris* and *E. ochrogaster* in Alberta, while Gibson (1917) reared it from *Euxoa excellans* Grote in British Columbia.

Diphyus No. 1

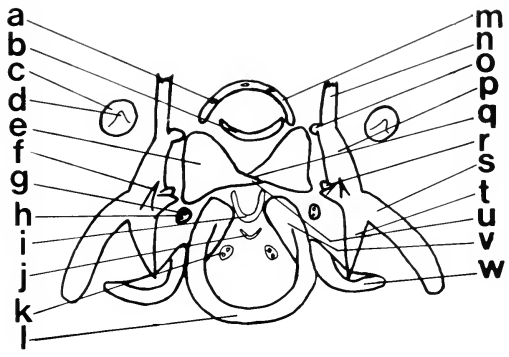
Description of larvae. – The cephalic structures of the final instar larvae (Fig. 38) of *Diphyus* No. 1 are similar to those of *E. suturalis*. The mandibles differ from those of *E. suturalis* in that they have a long narrow blade which is well marked off from the base. When rotated the blades appear to be curved posteriorly. The sclerites above the mandibles tend to be more squared than those of *E. suturalis*. The edge of the epistoma in *Diphyus* No. 1 is well defined.

Biology. – Using the final instar cephalic structures, it was found that this species was a parasitoid of *E. ochrogaster* at Calahoo. Adults emerged from the host pupae about 3 weeks after host pupation.

Hosts. – The following hosts were found by examining *Diphyus* No. 1 specimens in the C.N.C.: *E. ochrogaster*, Alberta; *C. auxiliaris*, Alberta; unidentified cutworm, British Columbia.

Campoletis atkinsoni (Viereck)

King and Atkinson (1928) reported *C. atkinsoni* as reared from *E. ochrogaster*. This



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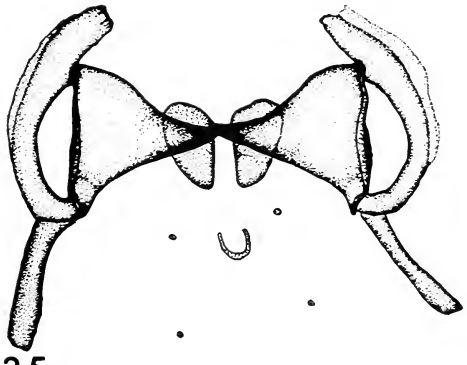

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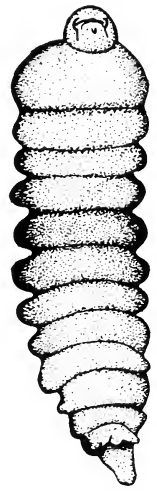

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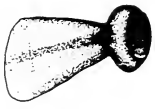

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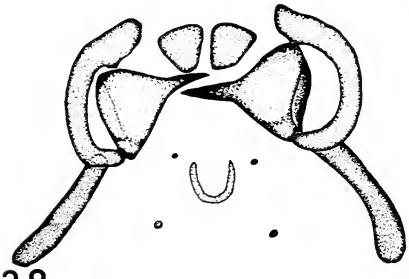

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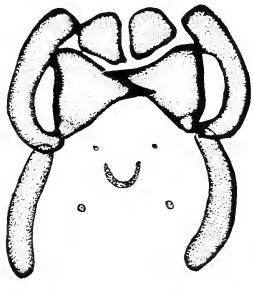

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Fig. 34. Generalized cephalic structures of final instar ichneumonoid larva (from Finlayson, 1960). a, vacuole; b, suspensorial sclerite; c, antennal socket; d, antenna; e, mandible; f, lacinial sclerite; g, sensorium; h, maxillary palp; i, silk press; j, prelabial sclerite; k, labial palp; l, labial sclerite; m, labral sclerite; n, epistoma (incomplete); o, superior mandibular process; p, pleurostoma; q, teeth; r, inferior mandibular process; s, hypostoma; t, hypostomal spur; u, blade of mandible; v, dorsal arm of labial sclerite; w, stipital sclerite. Fig. 35. Cephalic structures of final instar larva of *Eutanyacra suturalis*. Fig. 36. Ichneumonine larva. Fig. 37. Larval spiracle of *Spilichneumon superbus*. Fig. 38. Cephalic structures of final instar larva of *Diphyus* No. 1. Fig. 39. Cephalic structures of final instar larva of *S. superbus*. Scale in millimeters.

species appears to be one of the more important parasitoids of *E. ochrogaster*. This will be discussed later.

Description of cocoon. – The cocoon (Fig. 40) (2.1-2.4 x 5.4-6.2 mm) consists of two layers: a very thin outer layer of silk which is also used to secure the cocoon to the substrate, and a tough inner parchment-like layer. The freshly spun cocoon is a light yellowish white but the mature cocoon varies from a dark tan to a dull brown. Some of the specimens reared in this study were observed to spin their cocoons with the host remains attached to the posterior end. In other cases, the larva would crawl a few centimeters before spinning a cocoon. In all cases the cocoon took 12 to 18 hours to complete. The exit hole is on the dorsal edge of the anterior end of the cocoon. It is irregular in outline as the adult chews its way out. The remains of the final instar larva are stuck to one side near the end of the cocoon. These remains are often difficult to find and remove. The remains of the pupa and the meconium tend to obscure the larval remains so that care must be taken not to lose the cephalic structures in any of the study procedures.

Description of larva. – The cephalic structures of the final instar larva (Fig. 42) with a complete epistomal arch which is very lightly sclerotized and difficult to recognize. Superior mandibular processes sclerotized and small. Inferior mandibular processes well developed. Lacinial sclerite absent. Hypostoma long, narrow, straight, and heavily sclerotized. Hypostomal spur about 1½ times as long as wide at base and meets straight, well-developed stipital sclerite at about midpoint. Stipital sclerite meets top of labial sclerite. Labial sclerite widest at one-third of way from base and narrowed to a rounded point at end. End of labial sclerite very lightly sclerotized and may appear lost. Silk press large, wide, well developed and terminated by a long narrow spur. Mandibles small with a short blade which curves directly from base. Labral sclerite absent. Suspensorial sclerite short and narrow. Maxillary palpi large and well developed and protrude in a large membranous sack. Antennae large and well developed.

Biology. – *C. atkinsoni* is the only recorded parasitoid of *E. ochrogaster* which attacks the early instar larvae. It usually kills the host in the third or fourth instar. For this reason, this species is usually overlooked or not found in studies based solely on outbreak conditions. The first evidence of the presence of a *C. atkinsoni* larva in a host appears 2 to 4 days before the host is killed. At this point, the host is noticeably more sluggish, eats less than normal, and tends to bulge abnormally. Subsequently, the host stops eating, loses its mobility, and begins to lose its normal shape. Just before the parasitoid emerges, it can be seen moving about in the host, as the host's integument is very limp. The *C. atkinsoni* larva devours the entire contents of the host so that after it rips its way out of the host, the remains lie very flat and are nearly transparent. The parasitoid larva begins to spin its cocoon immediately after emergence and usually needs some object to crawl against so that it can complete its cocoon. The cocoon is stuck to the substrate with silk fibers. The adult *C. atkinsoni* emerge 7 to 10 days after the completion of the cocoon. All the specimens studied in 1968 emerged from the host during the last few days of May and the first week of June, and the adults emerged during the first 3 weeks of June. Although all available cutworm species found in the test area were reared in both 1967 and 1968, no alternative host was found later in the season.

Hosts. – *E. ochrogaster* appears to be the only recorded host of *C. atkinsoni*. Graham (1965) lists several noctuid hosts of *Campoletis* spp. and one yponomeutid, the diamondback moth, *Plutella maculipennis* Curtis. As *C. atkinsoni* attacks only the early instars of its cutworm hosts, its host range will likely only be found in studies which are based upon endemic cutworm populations rather than epidemic populations.

Netelia Gray

The genus *Netelia* formerly was named *Paniscus* Schrank. The name change was necessitated because of the misapplication of the name *Paniscus* by Gravenhorst (Townes *et al.*, 1961). Townes *et al.* provide taxonomic information on the adults of this genus and give keys and characters to separate specimens to the sub-generic level. Using his characters, it was found that the specimens reared from *E. ochrogaster* were in the sub-genus *Netelia.*

Description of cocoon. – The cocoons of three borrowed specimens of *Netelia* sp. were examined but none contained any larval remains. One cocoon found in the field study at Calahoo closely resembled those of *Netelia*, and it also lacked any larval remains. It is possible that the larval exuviae were removed from the borrowed specimens by a previous worker. It is also possible that the remains are left loose in the cocoon and easily lost. While the literature contains generalized descriptions of *Netelia* larvae, no mouth part drawings appear to be available. Cushman (1926) and Strickland (1923) provide illustrations of larvae and eggs of various members of the genus.

The cocoons studied averaged 4 x 12 mm in size. The cocoon (Fig. 41) consists of a very sparse outer covering of silk which appears as a fluffy mass at the ends, and a tough, tightly constructed inner layer. The over-all color is shiny black, but Strickland (1923) noted that it is originally a light color which changes with maturity. When viewed laterally, the cocoons had a slightly curved shape. The adults emerged from the end of the cocoon leaving a very ragged and irregular exit hole.

Biology. – *Netelia* sp. is the only recorded external parasitoid of *E. ochrogaster*. Cushman (1926), Vance (1927), and Strickland (1923) provided information on the biology of species in this genus. Only a generalized summary of the life history of *Netelia* spp. is given here.

The females deposit one to four stalked eggs on the thoracic region of late instar lepidopterous larvae. Of these only one survives to maturity. Strickland (1923) showed that the egg would remain attached even though the host molted. Cushman (1926) stated that the host larvae were attacked when they were very large and when they were about to pupate in some protective medium. The egg hatches generally after the host has entered a pupation site. The parasitoid larva feeds by puncturing the host integument, attaching its mouthparts, and remaining in one place until new punctures are made necessary. The parasitoid larva remains attached to the egg for most of its life, at least till the final instar. Attachment to the egg shell is accomplished by a special spined area on the terminal abdominal segment. The cast larval skins all remain attached to the egg shell and provide a convenient record of the larval morphology of each instar. The parasitoid develops rapidly and kills the host leaving a dry skin. Shortly after this it spins a cocoon.

As the species which has been reared from cutworms has not been identified, it is not possible to construct a host list. The genus is too large and widespread to be considered in this paper. Townes *et al.* (1961) state that the hosts of *Netelia* are exposed, medium-sized lepidopterous larvae that pupate in the ground. As *Netelia* spp. attack the larvae just before they are to pupate, it is likely that any species is a potential host if it crawls on the soil looking for a pupation site. The examined specimens reared from *E. ochrogaster* were from Saskatoon and Red Deer, Saskatchewan. One empty cocoon which likely was of *Netelia* was found at Calahoo.

Gravenhorstia propinqua (Cresson)

Originally, King and Atkinson (1928) recorded *Erigorgus* sp. as being reared from *E.*

ochrogaster. Erigorgus is now considered to be a synonym of *Gravenhorstia* (Townes *et al.*, 1961). Specimens of *Gravenhorstia propinqua* which were reared from *E. ochrogaster* were found in the C.N.C.

Description of cocoon. – The cocoon of this species is spun inside the host pupa. It appears to be lightly constructed of a single layer of silk which likely offers little protection to the parasitoid pupa. The emerging adult destroys the entire anterior end of the host pupa and leaves much of the cocoon visible (Fig. 65). The larval remains are stuck in the posterior end of the cocoon and are easily recovered and handled.

Description of larva. – The cephalic structures of the last larval instar (Fig. 43) are distinct from the other pupal parasitoids and are described as follows: The epistoma is heavy and complete, with superior mandibular processes short, wide and directed ventrally. Inferior mandibular processes are reduced to one which is broad and heavy. Lacinial sclerite is absent. Long, heavy hypostomal arms are curved ventrally in a wide semi-circle so that the ends form a nearly straight line with ends of the labial sclerite. Hypostomal spur absent. Stipital sclerite long, narrow, extending from one-third of way along the hypostoma ventromedially to a point three-quarters along its length, where it bends sharply dorso-medially to touch the labial sclerite. Labial sclerite incomplete with long narrow arms extending ventrally. Silk press present, very lightly sclerotized forming a wide U-shape. Labral sclerite straight, short and irregular in outline with several vacuoles. Suspensorial sclerite very wide and well developed. Mandibles large, well developed, with distinct blade clearly marked off from base. Maxillary and labial palps clearly distinct. Antennae not observed.

Biology. – Except that it kills the pupal stage of *E. ochrogaster*, little is known of the biology of *Gravenhorstia propinqua*. King and Atkinson (1928) noted that the species they recorded overwintered in the host pupa. One interesting fact appears in the host lists for the genus. Two tortricids have been recorded as hosts, and both larvae were killed by the *Gravenhorstia* sp. In both noctuid hosts, the pupal stage was killed. It is possible that when this genus is studied more carefully, more than one genus will be found within the present concept.

Hosts. – The following hosts have been recorded for *Gravenhorstia* spp.: *Polia purpurissata* Grote (Wood *et al.*, 1954), New Brunswick; *Archips argyrospilus* Walker (Paradis, 1960), Quebec; *Tortrix alleniana* Fern (Martin, 1958), Ontario; *Agrotis orthogonia* (King and Atkinson, 1928). The specimens reared from *E. ochrogaster* were from Saskatchewan.

BRACONIDAE

Morphology of immature braconids

Basically, the methods used to separate the immature stages of ichneumonids apply to those of braconids. In addition, important characters are found in the color, size, shape, and number of cocoons per host in each species. The appearance of the cocoon mass is also of importance.

Four species, *Microplitus kewleyi, Apanteles laeviceps, A. griffini,* and *A. acronyctae,* from the subfamily Microgastrinae have been recorded as reared from *E. ochrogaster*. Short (1952) stated that the final instar larvae are characterized as follows: hypostoma, stipital sclerite, and labial sclerite present; hypostomal spur reduced; pleurostoma weakly sclerotized; epistoma always absent; antennae not distinct; setae present on body but spines not present. Capek (1970) gives the same basic characters but makes no definite statement about the epistoma. I believe that Short is incorrect in stating that the epistoma is always missing, as it is present in *M. kewleyi*. Capek states that members of the group of genera to which *Apanteles* and *Microplitus* belong are endoparasites of lepidopterous larvae, are often

gregarious, emerge as mature larvae to pupate, and that the emergence hole is regular due to a cap.

Apanteles Foerst

Apanteles acronyctae Riley

Apanteles acronyctae was recorded as being reared from *E. ochrogaster* by King and Atkinson (1928). The record was based on only two specimens reared by the authors. *A. acronyctae* is normally associated only with arctiid hosts and likely does not attack cutworms (Mason, pers. comm.). This record is likely based on a mistaken identification.

Apanteles laeviceps Ashmead

Apanteles laeviceps was recorded as reared from *E. ochrogaster* by Strickland (1923).

Description of cocoon. – The cocoon mass (Fig. 45) contains 22 to 28 individual cocoons. The mass is compact and only rarely was an isolated cocoon observed. The cocoons are tightly woven together and are united in a single irregular deep mass. The individual cocoon (Fig. 46) is 3.0 to 3.2 mm long, cylindrical with bluntly rounded ends, and is lightly constructed. When treated with a mild KOH solution the cocoon structure is completely destroyed. The loose outer layer of silk is tightly interwoven with that of the other cocoons. As with the other braconids, a distinct cap is formed and breaks off when the adult emerges. The color of the mass changes from a pale yellow to white as the cocoons mature. In many cocoons, the contents can be seen through their walls.

Description of larvae. – The penultimate larval stage of *A. laeviceps* (Fig. 47), which is found in the host, differs from the same stage of *Meteorus vulgaris* in the following ways. The cephalic region of *A. laeviceps* is more clearly defined than that of *M. vulgaris*. The body of *A. laeviceps* is long, narrow, and terminated by a bulbous caudal appendage. Overall length is approximately 5 mm, with the widest point measuring 1.8 mm. As in *M. vulgaris,* the larvae molt to the final instar as they escape from the host. The final instar larva was described by Strickland (1923). It differs from that of *M. vulgaris* in that it lacks a definite caudal appendage and has a series of small black spines on its body. It differs from the penultimate stage by not having the globular caudal appendage. In both of the last two larval instars of *A. laeviceps* the mouthparts appear similar. The cephalic structures of the final instar larva with epistoma missing, pleurostoma apparently missing, lower mandibular process blunt and rounded (Fig. 44). Hypostoma heavily sclerotized, long, narrow and curved medially. Hypostomal spur small, distinct, pointed. Stipital sclerite heavily sclerotized, wide with a distinct twist in the mid-area. Labial sclerite complete, well developed, thick at top, narrowed at bottom, sometimes widened at end. Silk press very obscure but large. Maxillary and labial palpi small. Mandibles with long curved blade arising low on mandibular base. Antennae and spiracles not apparent.

Biology. – The females of *A. laeviceps* oviposit in early instar host larvae. This was demonstrated in the current study by rearing early instar cutworms which had been captured in the field, and finding them to be attacked by *A. laeviceps*. The earliest instar cutworm found attacked was an early third instar. The host is usually killed in the fifth or early sixth instar. The larvae of *A. laeviceps* exert a strong influence over the behaviour of the host. Strickland (1923) noted that until the *A. laeviceps* larvae began to attach to the host's cuticle, no ill effects were evident. At this stage, the host leaves the soil and climbs some convenient object such as a grain stem or a large clod of earth. I have observed *E. ochro-*

gaster larvae climbing only when attacked by *A. laeviceps*. While the host is on the object, the parasitoid larvae emerge from all sides of it. The host then crawls away leaving the parasitoids behind. The parasitoids begin to spin their cocoons almost immediately. When studying cutworm outbreaks, cocoon masses of *A. laeviceps* are easily found by examining marker stakes or emergence traps, both of which serve as climbing points for the hosts. The host larva returns to the soil but always dies within a short time. In the laboratory, I have seen *E. ochrogaster* larvae live up to 3 days following *A. laeviceps* emergence. These host larvae are recognizable by the presence of the exuvia-plugged emergence holes of the parasitoid, the presence of one or more *A. laeviceps* larvae in the body cavity which failed to emerge, and by the general lack of damage to the muscles and nerves.

Hosts. – The following hosts have been recorded in the literature: *Eucirrhoidea pampina* Gn. (Wood and Nielson, 1957), New Brunswick; *Spaelotis clandestina* Harrison (Wood, 1951), New Brunswick; *Syngrapha epigaea* Grote (Wood, 1951), New Brunswick; *E. ochrogaster, Chorizagrotis auxiliaris* (Strickland, 1923), Alberta; *Meliana albilinea* Hübner (Webster, 1911); *Loxostege sticticalis* L. (Vierick, 1916), *Pseudaletia unipuncta* (Guppy, 1967) Ontario. During the current study *A. laeviceps* was reared from *E. ochrogaster* in 1967 and 1968 and from *Feltia ducens* in 1967.

Apanteles griffini Viereck

Schaffner and Griswold (1934) recorded *Apanteles griffini* as being reared from *E. ochrogaster* in the north-eastern part of the United States.

Description of cocoon. – The cocoon mass of *A. griffini* (Fig. 49) is deeply divided longitudinally so that two distinct but connected portions are evident. The construction and density of the mass is very similar to that of *A. laeviceps*. The groove is likely formed because the larvae pupate almost immediately after emergence and do not move together. The groove corresponds to the location of the host at the time of emergence of the parasitoid larvae.

Description of larvae. – No specimens of the entire larvae were available for study. Cephalic structures of final instar larvae (Fig. 48) similar to those of *A. laeviceps*. Hypostoma less distinctly curved than in *A. laeviceps*. The labial sclerite more narrowly developed than that of *A. laeviceps*. Mandible with a long narrow blade which arises near the center of the base. The base is more triangular than that of *A. laeviceps*. The hypostomal spur is short and bluntly developed.

Biology. – *A. griffini* is generally found in the more southern range of *E. ochrogaster* (Mason, pers. comm.). Little is known of the biology of this species.

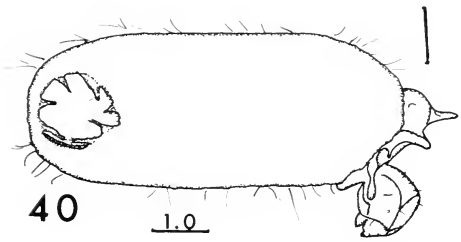
Hosts. – Walkden (1950) recorded the following hosts of *A. griffini* from the central great plains, U.S.A.: *Agrotis orthogonia, A. gladiaria* Morrison, *Chorizagrotis auxiliaris, Peridroma margaritosa* Haworth.

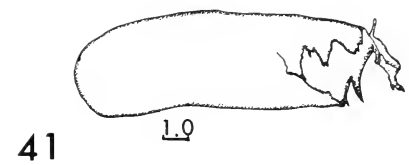
Microplitus kewleyi Muesebeck

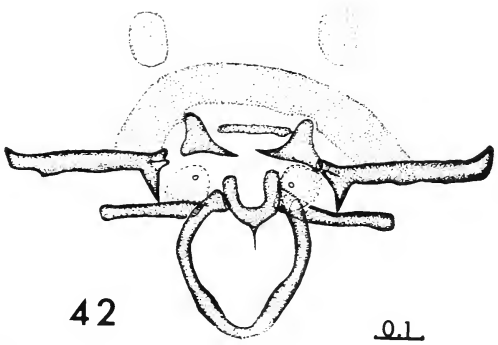
Schaffner and Griswold (1934) recorded *Microplitus kewleyi* as being reared from *E. ochrogaster*. Only one specimen was available for study.

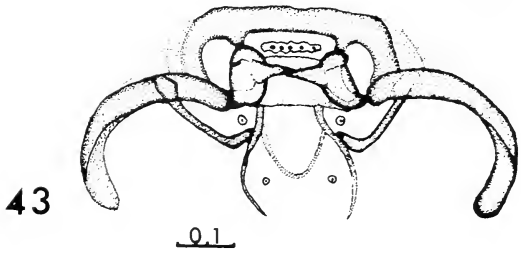
Description of cocoon. – The cocoon (Fig. 51) is solitary, small (3.1 x 1.4 mm), has very little outer silk, has a very tough inner layer of silk, and is an opaque buff color.

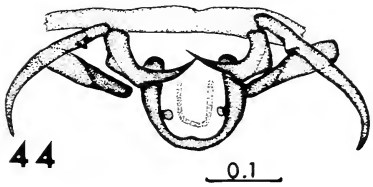
Description of larvae. – Cephalic structures (Fig. 50) of the final instar larva with a very weakly sclerotized, incomplete epistoma. Superior mandibular process very indistinct, as well as the rest of pleurostoma. Inferior mandibular processes each small and bluntly devel-

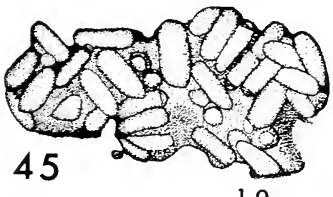


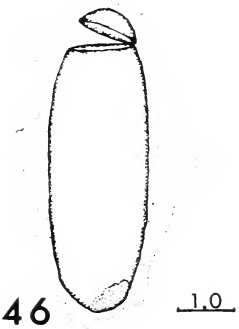












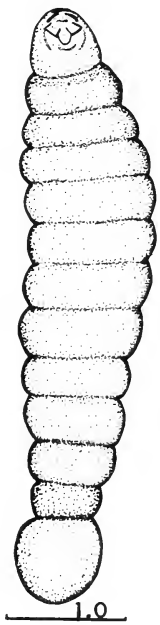


Fig. 40, 42. *Campoletis atkinsoni*. 40. cocoon. 42. cephalic structures of final instar larva. Fig. 41. Cocoon of *Netelia* sp. Fig. 43. *Gravenhorstia propingua* final instar larva cephalic structures. Fig. 44–47. *Apanteles laeviceps*. 44. cephalic structures of final instar larva. 45. cocoon mass. 46. individual cocoon. 47. penultimate larva. Scale in millimeters.

oped. Hypostoma heavily sclerotized, curved medially, with a reduced, pointed hypostomal spur. Stipital sclerite long, narrow, and with irregular outline. Labial sclerite heavily sclerotized, widest at midpoint and narrowed to a point at distal end. Silk press lightly sclerotized, long and narrow. Suspensorial sclerite lightly sclerotized and irregular in form. Mandibles with short narrow blades arising from bottom of mandible bases. The mandible open posteriorly in a distinct groove.

Biology. – Extremely little is known of the biology of this species other than that it attacks larval cutworms. The examined specimen was reared from a cutworm at College Park, Maryland.

Meteorus Haliday

Two species of *Meteorus, dimidiatus* Cresson and *vulgaris* Cresson have been recorded as reared from *E. ochrogaster*. Strickland (1923) recorded the former as being a common parasitoid of prairie cutworms. He noted, however, that difficulty had been encountered when the series were identified in distinguishing them from *M. vulgaris*, and Dr. W.R.M. Mason also is sceptical of this record. The current host lists (Graham, 1965) do not include *M. dimidiatus*. All of the *Meteorus* specimens reared from *E. ochrogaster* in my study were *M. vulgaris*. Strickland dealt at length on the biology, hosts, and development of *M. dimidiatus*. This information on the biology of *M. dimidiatus* appears now to be valid for *M. vulgaris*.

Meteorus vulgaris Cresson

This species was recorded as reared from *E. ochrogaster* by King (1926), and has subsequently been recorded several times.

Description of cocoon. – The cocoons are 4.9-5.4 mm x 1.9-2.3 mm, elliptical in shape with the widest point between the posterior one-third and the midpoint (Fig. 55). The anterior end of the cocoon terminates in a distinct cap which breaks off at adult emergence. Specimens which were observed spinning their cocoons formed the cap only after the rest of the cocoon was completed. While the rest of the cocoon turns brown with maturity, the cap remains a much lighter color. The cocoons are usually translucent so that the contents are easily seen. An outer layer of fine silk binds the cocoon to the substrate and to surrounding cocoons. The cocoon mass (Fig. 54) is very loose and irregular, and it is common to find cocoons completely separated from the rest of the mass. The larval remains are easily found and removed from the cocoons.

Description of larvae. – Cephalic structures of the final instar (Fig. 52) with incomplete, lightly sclerotized epistoma. Each superior mandibular process well developed, inferior mandibular processes small and blunt, lacinial sclerite small and pointed. Hypostomal arms short, narrow curved, and only lightly sclerotized. Pleurostoma distinctly sclerotized as opposed to light sclerotization of the epistoma and hypostoma. Stipital sclerite long, narrow, almost straight, reaching upper end of labial sclerite. Labial sclerite large, heavy and greatly thickened in ventral portion. Silk press well developed and moderately sclerotized. Well-developed pharyngeal region with lightly sclerotized ridges behind silk press and top of labial sclerite. Mandibles small, with short, pointed, conical blades well set off from base. Maxillary palps large and with well-developed membranous projection. Antennae large and well developed.

Strickland provided figures of the entire final instar larva and of the penultimate larva. The larva normally molts as it emerges from the host leaving the exuvia of penultimate larva in the emergence hole. The penultimate larva as shown by Strickland has a long caudal

appendage whereas the final instar larva has a much reduced caudal appendage. No larvae similar to that described by Strickland as the penultimate instar were found during my study. The shape of the final instar larva (Fig. 53) changes as the cocoon is spun. The larva shortens and thickens, the segmentation becomes less defined, and the caudal appendage becomes more obscure. When dissecting host specimens from which *M. vulgaris* larvae had emerged, it was found that one to three larvae were usually remaining in the host. These appeared the same as the final instar larvae and likely molted even though they failed to emerge.

Biology. – The biology of the immature stages of *M. vulgaris* is well documented by Strickland (1923). Normally, 24 to 28 pupae were reared from a single host but as many as 36 were reached during my study. The hosts killed by *M. vulgaris* during 1967 and 1968 were in the late stages of the sixth instar. In most cases, the host larva crawled away from the *M. vulgaris* pupae and died. Dissection of the host cutworm after the emergence of the *M. vulgaris* larvae revealed that the muscle layers were partially destroyed, as is the case with other parasitoids. The exuviae of the penultimate instar larvae formed blackened areas on the cutworm integument indicating the emergence points. These usually occur on the ventro-lateral portion of the cutworm's body. The presence of the cast exuviae gives the cutworm a characteristic appearance, aiding in recognition of the cutworm after the *M. vulgaris* larvae have emerged, but before the death of the host. In two cases, *M. vulgaris* pupal masses were found in the loose upper soil. The adults emerge from the pupae 14 to 17 days after pupation.

Hosts. – The following hosts have been recorded for *M. vulgaris: Euxoa ochrogaster* (King and Atkinson, 1928; King, 1926) Saskatchewan; *E. tristicula* (King, 1926) Saskatchewan; *Peridroma saucia* (Fletcher, 1901); *Syngrapha epigaea* (Wook and Nielson, 1960) New Brunswick. Strickland (1923) reared *M. vulgaris* (or *dimidiatus*) from the following hosts captured in Alberta: *A. orthogonia, E. ochrogaster, C. auxiliaris, E. tristicula, S. devestator* Brace, *Actebia fennica.* Walkden (1950) listed the following hosts of *M. vulgaris* from the central great plains, U.S.A.: *A. orthogonia, A. gladiaria, A. ypsilon, C. auxiliaris, Feltia subgothica* Haworth, *Euxoa messoria, Peridroma margaritosa.* I reared *M. vulgaris* from *Feltia ducens* in the summer of 1967.

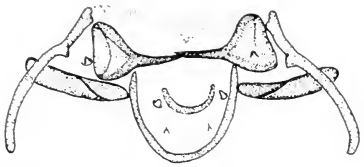
ENCYRTIDAE

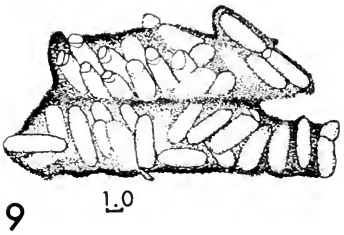
Copidosoma bakeri (Howard)

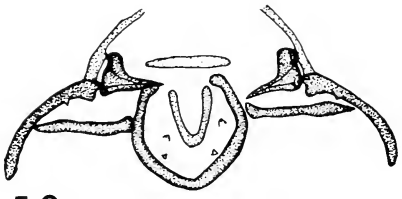
Copidosoma bakeri is probably the most important single parasitoid of *E. ochrogaster* over most of its range. This species was first described in the genus *Berecyntus* and most of the literature associated with this species is found under *Berecyntus bakeri.* Originally *C. bakeri* was described as a single species with several varieties including *gemma* Girault, *arizonensis* Girault, *euxoae* Strickland, and *bakeri* Girault. Other workers gave these varieties subspecific rank (Gibson, 1917; Peck, 1951). Peck (1963) states that *C. bakeri* cannot be subdivided into varieties or subspecies, as the earlier groupings are merely a reflection of color patterns and not of population differences.

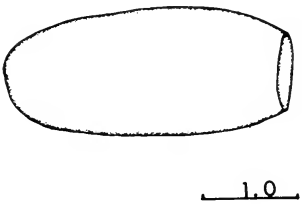
Biology. – Work on the biology and development of *C. bakeri* has been published by Gibson, 1915; Strickland, 1916; King and Atkinson, 1928; and Cook, 1930. The most extensive work done on this species was that of McMillan (1930) in an unpublished masters thesis.

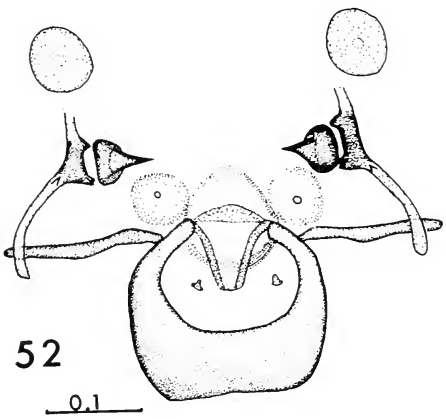
C. bakeri oviposits in the eggs of its many hosts but the host is not killed until the approximate time that host pupation occurs. The polyembryonic development of *C. bakeri*

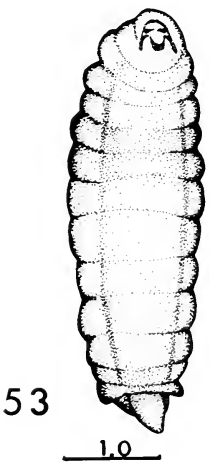


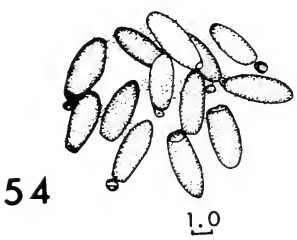












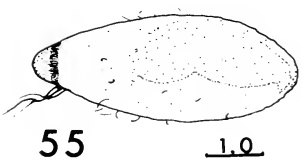


Fig. 48, 49. *Apanteles griffini*. 48. cephalic structures of final instar larva. 49. cocoon mass. Fig. 50, 51. *Microplitus kewleyi*. 50. cephalic structures of final instar larva. 51. cocoon. Fig. 52–55. *Meteorus vulgaris*. 52. cephalic structures of final instar larva. 53. final instar larva. 54. cocoon mass. 55. cocoon. Scale in millimeters.

will be discussed later.

McMillan (1930) observed *C. bakeri* adults in the field in central Saskatchewan from early May until the end of August, while I observed them during the latter portion of July and most of August. The great length of time during which adults occur in the field is due to the emergence from different host species completing development at different times during the summer. *C. bakeri* adults emerge from *E. ochrogaster* larvae at approximately the same time as do the *E. ochrogaster* adults. In the laboratory the maximum time which *C. bakeri* adult females can be kept alive is 16 days, with a mean of 11 days (McMillan, 1930). It is likely that eggs of *E. ochrogaster* are exposed to only a small portion of the *C. bakeri* adults which emerged from *E. ochrogaster* larvae because of the long preoviposition period of *E. ochrogaster* females. A detailed biology of adult *C. bakeri* may be found in McMillan (1930).

The parasitic egg develops for approximately 45 days within the host egg till it reaches an overwintering stage. During this time it has approximately doubled in size and is transformed into a syncytium of cleavage nuclei surrounded by a trophamnion (McMillan, 1930). The trophamnion provides nutriment for the embryonic mass from the host tissues as the eggs of polyembryonic parasitoids are relatively free of yolk (Chapman, 1969). After the host emerges from its egg, the growth of the polyembryonic mass resumes. The actual mechanism of polyembryonic development is described by McMillan (1930) and Leiby (1922).

The earliest that a polyembryonic body (p.e.b.) was detected in my dissections of red-backed cutworms was in the third instar of the host. The polyembryonic body at this time is very small, compact and is usually flattened and little internal differentiation is apparent. It grows in size in the next instars of the host until it fills a major portion of the area between the gut and the muscle layer under the integument. At this point it may be present as a simple flattened structure or it may be lobed or divided into smaller bodies. If more than one p.e.b. is present in the host then one is usually much more developed than the other. There were never two distinct p.e.b.'s in the same area of the host's body. The body remains largely undifferentiated until either the sixth or seventh instar of the host, depending upon whether an extra instar occurs. The p.e.b. then begins to divide into smaller embryonic units which are marked by density changes in the p.e.b. These embryonic units change to spherical structures and give the entire p.e.b. the appearance of a bag of marbles. These structures change into the form of larvae while still in the intact p.e.b. The p.e.b. in the meantime becomes larger and more deformed till it is very lobed. When the larvae are fully developed within the body, they begin to escape from it. Several dissections were made at the time when the p.e.b. had begun to disintegrate and the larvae spread throughout the host body. Not all the larvae appeared to leave the p.e.b. simultaneously; in fact, some of the remaining larvae were less developed and likely did not complete their development before the earlier-developing larvae destroyed both the host and the remains of the p.e.b. Occasionally, some larvae were found free of the p.e.b. before the majority of the larvae were mature enough to leave the p.e.b. These likely correspond to the pseudolarvae referred to by Leiby (1922, 1926). The pseudolarvae are actually larvae which failed to obtain sufficient nutrition while in the p.e.b., and will not survive to the pupal stage.

Once the larvae break free of the p.e.b., they begin to actively ingest the host body contents. This is a very rapid process taking 2 to 4 days.

The behaviour of the host changes radically during the last stages of intact p.e.b. and the beginning of the parasitoid larval attack. The host eats more during the last period than does the normal cutworm (McMillan, 1930). As the p.e.b. breaks down the host is very active and restless. Strong turning and twisting activity is often noticed. Feeding ceases during this period. The parasitoid larvae distribute themselves throughout the body and rapidly

destroy the internal organs leaving the external musculature and nerve network until last. The host is usually capable of reflexes i.e. curling movements even if the entire internal structure is destroyed. Finally, the muscles, brain, and nervous system are eaten leaving only a 'plastic' bag of host integument full of parasitoid larvae. In one case, even this integument bag was destroyed. The external appearance also changes radically from the attack of the larvae. Sometimes the intact p.e.b. can be seen through the intersegmental membranes of the host as a solid white mass which does not move like the surrounding fat body. The host at this stage is a typical dorsal red and ventral clear light grey. The crawling and curling movements appear normal. As the p.e.b. begins to break down, the color of the body changes. The reds become lighter and pass through a pale pink and then become an off-grey. The ventral surface changes from the clear grey to a mottled grey as the parasitoid larvae can be seen through the integument (Fig. 59). As the last muscle and nerve tissue is destroyed, a fluid discharge is emitted from the body of the host which leaves a brown stain on the filter paper of a culture dish. The host is now a uniform buff-grey shade and the larvae are packed into every portion of the body including the prolegs, brain and eyes (Fig. 58). The body of the host sags to the most stable shape, which in culture dishes fits the pattern of the objects on which it lies. Specimens found in the field were flattened, screw-shaped, or almost normally curved. The *C. bakeri* larvae pupate within 2 days of the host body collapse.

As the pupae mature, the color of the host carcass darkened noticeably due to the color change of the individual pupae. After 14 to 26 days the adults emerge in a period of 6 to 12 hours. The host carcass is perforated with holes on all sides except the bottom. Each adult does not form a new hole but will use an old hole if one exists near it. After emergence the host resumes a dull grey or tan color.

The individual larvae (Fig. 56) of *C. bakeri* have very few distinctive characters. McMillan (1930) gives a figure of the mandibles of the larvae, but I found the mandibles so hard to obtain and study that I regard them as being essentially useless as an identifying character. *C. bakeri* larvae are easily distinguished from other larvae likely to be found attacking *E. ochrogaster* by their great numbers and by their lack of sclerotized characters. Late larvae or prepupae (Fig. 57) are also easily recognized as the host is essentially destroyed by the time of their appearance.

Hosts. – *C. bakeri* has a wide range of natural hosts. The following hosts were recorded by Peck (1963) with the authors he cited and additional references. Location by province or state is included to provide additional information on the distribution of both the host and the parasitoid: a. *Agrotis orthogonia* (Cook, 1930), Montana; b. *A. venerabilis* Walker (King and Atkinson, 1928), Saskatchewan; c. *Amathes smithi* Snellen (Wood and Nielson, 1957), New Brunswick; d. *Chorizagrotis auxiliaris* (Strickland, 1916; Girault, 1917), Alberta; (Snow, 1925), Utah; (Walkden, 1950), Kansas; e. *C. thanatologia* (King and Atkinson, 1928), Saskatchewan; f. *Chorizagrotis* sp. Sm. (Girault, 1916), Arizona; g. *Crymodes devastator* (Gibson, 1915, 1917; Girault, 1916; Treherne, 1915), Ontario; h. *Euxoa detersa* Walker (King and Atkinson, 1928), Saskatchewan; i. *E. flavicollis* (King and Atkinson, 1928), Saskatchewan; j. *E. intrita* Morrison (Cook, 1930), Montana; k. *E. messoria* (Walkden, 1950), Kansas; l. *E. ochrogaster* (King and Atkinson, 1928), Saskatchewan; m. *E. scandens* (Walkden, 1950), Kansas; n. *E. tristicula* (Strickland, 1921; Whitehouse, 1922), Alberta; (King and Atkinson, 1928), Saskatchewan; o. *Euxoa.* sp. (Girault, 1916; Gibson, 1917), Ontario; p. *Feltia ducens* (King and Atkinson, 1928), Saskatchewan; q. *Feltia subgothica* (Walkden, 1943, 1950), Kansas; (Peck, 1951), Kansas, Alberta, New Mexico; r. *Lacinopolia renigera* Stephens (Walkden, 1950), Kansas, s. *Pissodes strobi* (Taylor, 1929), Massachusetts.

McMillan's (1930) thesis lists nine of the above species as hosts of *C. bakeri.* In addition

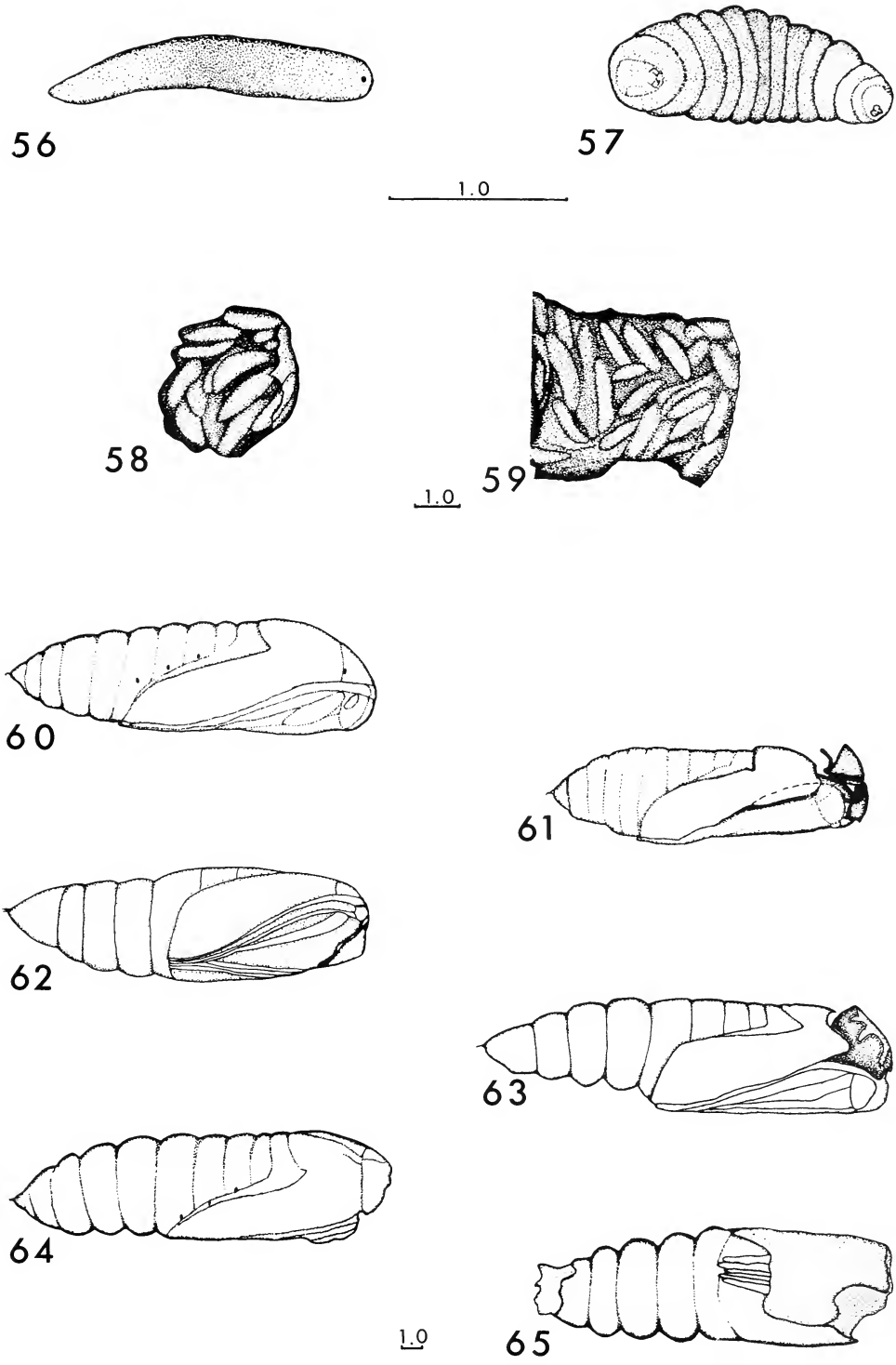


Fig. 56–59. *Copidosoma bakeri*. 56. feeding larva. 57. prepupa. 58. cross-section of host at completion of *C. bakeri* feeding. 59. surface view of above. Fig. 60–65. *E. ochrogaster* pupae. 60. normal before moth emergence. 61. normal after moth emergence. 62. after *Gonia* spp. emergence. 63. after *Poecilanthrax alcyon* emergence. 64. after ichneumonine emergence. 65. after *Gravenhorstia propingua* emergence. Scale in millimeters.

six more species are given in which parasitism was induced. They are *Euxoa tesselata, E. verticalis* Grote, *E. dargo* Stkr., *E. divergens* Walker, *E. campestris* Grote, L. renigera. McMillan felt that natural parasitism does not occur in these species because they normally lay their eggs in hard packed prairie soil. He proved that firmly packed soil provides an effective barrier to *C. bakeri* oviposition.

Of the 20 species which I have listed as recorded hosts, I believe that one is in error. The species *Pissodes strobi,* the white pine weevil, attacks the shoots of white pine trees. (*Pinus strobus*). The list from which Peck (1963) derived his information is headed 'Parasites reared from *P. strobi* or weeviled material' (Taylor, 1929) and is data from several different workers. All other recorded hosts are cutworms which are typically found in open areas and whose eggs are laid on or near the soil, while *P. strobi* is a weevil and occurs in wooded areas. Also, *P. strobi* lays its eggs in the tips of white pine shoots so that it is very unlikely that one parasitoid would attack such a wide range of hosts in such divergent habitats.

During the present study *C. bakeri* was reared from *Feltia ducens* during the summer of 1967, and from *E. ochrogaster* in 1967 and 1968 and was dissected from *E. ochrogaster* larvae in 1969.

DISCUSSION

Twenty-seven species of parasitoids have been recorded as reared from *Euxoa ochrogaster.* Three of these records, *Gonia capitata, Apanteles acronyctae,* and *Meteorus dimidiatus* are incorrect. Of the 24 species of confirmed parasitoids, the immature stages of 15 are described. Of the remaining species, Brooks (1952) has provided descriptions of four of the bombyliids. *Pseudamblyteles subfuscus* and *Gonia* sp. were not described as I was not able to find what species these records are now valid for and thus could not locate specimens. *Gonia fuscicollis, Villa lateralis,* and *Agamermis* sp. were not described because I could obtain no specimens of any of the immature stages. Because of the possibility that both *Periscepsia laevigata* and *Gonia sequax* are parasitoids of the red-backed cutworm, descriptions of the available immature stages of these species have been included.

The known biology of each species of parasitoid is given in the text and some of this information is summarized in Table 1. It should be noted that the stage of the host in which the parasitoid lays its egg was determined either by literature records or by using rearing data from field-collected specimens. The earliest instars selected by the parasitoid can be calculated by determining both the instar and the time of the season in which the host, which later produced a parasitoid, was captured. The latest instars can be found by dissections of host material and sometimes by observing the oviposition behaviour of the parasitoid. For example, no specimens of the red-backed cutworm collected before the fourth instar produced ichneumonine adults. When sixth instar cutworms were attacked in the laboratory, the ichneumonine females were unable to lay eggs in the host because of its defense reactions.

Figure 66 summarizes the parasitoid complex and the stages at which the parasitoid eggs are laid and those at which the hosts are killed.

Alternative hosts

All the better known species of parasitoids in this study have several hosts from which they have been reared and recorded. Indubitably, for each of these species of parasitoids, there are more hosts which have yet to be recorded. Most host records for parasitoids result from the rearing of economic species, and there is little reason to suspect that these parasitoids attack only hosts which are of economic importance. With the exception of *Villa*

Table 1. Summary of the biology of *E. ochrogaster* parasitoids.

Species	Status	Stage attacked	Stage killed	No. of known hosts
Tachinidae				
Gonia aldrichi	confirmed	IV, V, VI	pupa	2
Gonia capitata	rejected	–	–	–
Gonia fuscicollis	confirmed	IV, V, VI	pupa	1
Gonia sequax	suspected	IV, V, VI	pupa	1
Bonnetia comta	confirmed	III, IV	prepupa	7
Periscepsia helymus	confirmed	larva	VI	17
Periscepsia laevigata	suspected	larva	V	5
Bombyliidae				
Villa alternata	confirmed	IV, V, VI	pupa	6
Villa fulviana	confirmed	IV, V, VI	pupa	1
Villa lateralis	confirmed	IV, V, VI	pupa	1
Villa moroides	hyper parasitoid	–	–	–
Poecilanthrax alcyon	confirmed	IV, V, VI	pupa	5
Poecilanthrax willistonii	confirmed	IV, V, VI	pupa	9
Ichneumonidae				
Eutanyacra suturalis	confirmed	IV, V, ?VI	pupa	4
Diphyus No. 1	confirmed	IV, V, ?VI	pupa	3
Spilichneumon superbus	confirmed	IV, V, ?VI	pupa	6
Pseudamblyteles subfuscus	?	–	–	–
Compoletis atkinsoni	confirmed	I, II	III, IV	1
Netelia sp.	confirmed	V, VI	prepupa	–
Gravenhorstia propingua	confirmed	larva	pupa	1
Braconidae				
Apanteles acronyctae	rejected	–	–	–
Apanteles laeviceps	confirmed	II, III	V	8
Apanteles griffini	confirmed	?II, III	?V	4
Microplitus kewleyi	confirmed	?III, IV	?IV, V	1
Meteorus vulgaris	confirmed	III, IV	VI	14
Meteorus dimidiatus	rejected	–	–	–
Encyrtidae				
Copidosoma bakeri	confirmed	egg	VI or VII	19
Nematoda Merinthidae				
Agamerimis sp.	confirmed	?	–	–

alternata, all parasitoids recorded as reared from *E. ochrogaster* were mainly restricted to noctuid larvae as additional hosts. I believe it is necessary to consider the type of habitat in which all of the species in this host-parasitoid complex existed before agricultural practices modified large areas. Large numbers of cutworm species probably existed in low densities in the prairie and parkland areas of Canada. The densities of individual host species were probably low enough to prevent host-parasitoid complexes restricted to small numbers of species from occurring. In order to survive, each parasitoid species probably had to attack any host in a given taxonomic range in a given habitat type. The hosts of some of the species include ground cutworms and climbing cutworms which are found in grasslands, fields or low bush open areas.

Cutworms such as *E. ochrogaster* were probably adapted to feeding in areas of recently disturbed soil. This is reflected by the preference of the female to lay her eggs in loose soil. One of the parasitoids, *Copidosoma bakeri*, is also restricted to areas of loose soil. McMillan (1930) showed that *C. bakeri* was capable of completing development in species normally found only in packed soil but that in the field they are unable to penetrate the soil and find the eggs. It is likely that the high degree of polyembryony in *C. bakeri* is the result of the unstable nature of the habitat it requires and the relative difficulty of finding such a habitat. As agriculture has increased the amount of disturbed soil and at the same time made the cutworm habitat more stable, the densities of both the host species and their parasitoids have probably increased.

Regulation of *E. ochrogaster* populations by parasitoids

Nine species of parasitoids were reared from *E. ochrogaster* during this study. The estimated percentages of hosts killed in the 1967 and 1968 seasons are given in Table 2. These estimates were calculated using the number of hosts killed by a parasitoid (or which contained immature stages of that parasitoid) out of the total number of hosts entering the stage which the parasitoid normally killed. As was found by King and Atkinson (1928), *Gonia aldrichi, Meteorus vulgaris, Campoletis atkinsoni*, and *Copidosoma bakeri* were important parasitoids. Interestingly, King and Atkinson found no ichneumonine species as parasitoids of *E. ochrogaster*, while I found three. Of these, *Spilichneumon superbus* was the most important species and *Diphyus* No. 1 may be important in other years. The total ichneumonine complex is an important regulatory factor in the population fluctuations of the red-backed cutworm. *A. laeviceps* was recorded by Strickland (1923) as killing 5% of the red-backed cutworms in 1915 and less than 1% in 1916. In 1967, the number of fifth instar larvae collected was too low to permit estimation of the mortality caused by *A. laeviceps*. In 1968, only one collected red-backed cutworm was killed by *A. laeviceps*. It does not appear as if this species was important in regulating the numbers of *E. ochrogaster* during 1967 and 1968.

It appears from my study and from the work of King and Atkinson (1928), that the parasitoids are not the chief controlling factors of *E. ochrogaster* populations, but are important regulating factors.

Figure 67 shows the decrease in size of the *E. ochrogaster* population at Calahoo in the summer of 1968. The population estimates were made weekly and were based on 20 one-half square meter samples. These samples were taken using a modified random sampling plan within a 100 quadrat sampling area. The sampling area was 100 meters square. The soil was removed to a depth of 15 cm and sieved using a mechanical shaker.

The decrease shown is far more rapid than if parasitoids were the most important regulating factors. Frank (1971a) does not feel that carabid predators are the controlling factor either. It is likely that the reduction of population is due to a complex interaction of

predators, diseases, and parasitoids. All of these factors are likely directly influenced by the weather conditions within any season. Until more intensive research is carried out on the total regulatory complex, the most important controlling factor must remain in doubt.

Table 2. The estimated mortality caused by the species of parasitoids reared from *E. ochrogaster* at Calahoo in 1967 and 1968.

Species	1967	1968
Gonia aldrichi	5 - 10%	9%
Eutanyacra suturalis	< 5%	3%
Diphyus No. 1	< 5%	5%
Spilichneumon superbus	5 - 10%	10%
Campoletis atkinsoni	–	9%
Apanteles laeviceps	≅ 5%	< 1%
Meteorus vulgaris	10%	5%
Copidosoma bakeri	35%	22%
Agamermis sp.	< 1%	0

Economic benefits of parasitoids

In addition to analyzing the effect of any parasitoid on the yearly population fluctuations of *E. ochrogaster* the influence of this parasitoid on the amount of damage caused in any given year must be considered. To reduce the damage done, feeding by the cutworms must be reduced or prevented. Because it kills the early instar larvae *Campoletis atkinsoni* essentially prevents economic damage, and its rate of killing hosts is its rate of economic return. *Apanteles laeviceps*, which kills during the host's fifth instar, reduces the damage done by the hosts which it attacks. *A. laeviceps* has shown a very low rate of attack during my study. While *C. atkinsoni* and *A. laeviceps* reduce the loss caused by their hosts, *Copidosoma bakeri* increases the loss by the current generation. McMillan (1930) found that hosts attacked by *C. bakeri* consumed 27.5% more food than did normal hosts. If a seventh instar occurs, this extends the feeding period of each host. As *C. bakeri* attacks at a fairly high rate, the increased loss due to its presence probably exceeds that prevented by *C. atkinsoni* and *A. laeviceps*. The other parasitoids kill at such low rates, or kill after the host damage has occurred and appear to be economically neutral i.e. they neither increase nor decrease the loss during that season.

Future research

My approach has been to study each of the known parasitoids of *E. ochrogaster* and its geographic range. The knowledge of the parasitoid complex is a reflection of the area where this host is most commonly a pest, namely western Canada. It appears that *E. ochrogaster*, or in fact any economic cutworm, is attacked by the normal parasitoid complex which attack cutworms. The parasitoid complex of any given host could change or be very different in different regions. I believe that it is very difficult at this point to study all the parasitoids of any host which covers a wide geographic range. A more valuable approach may be to

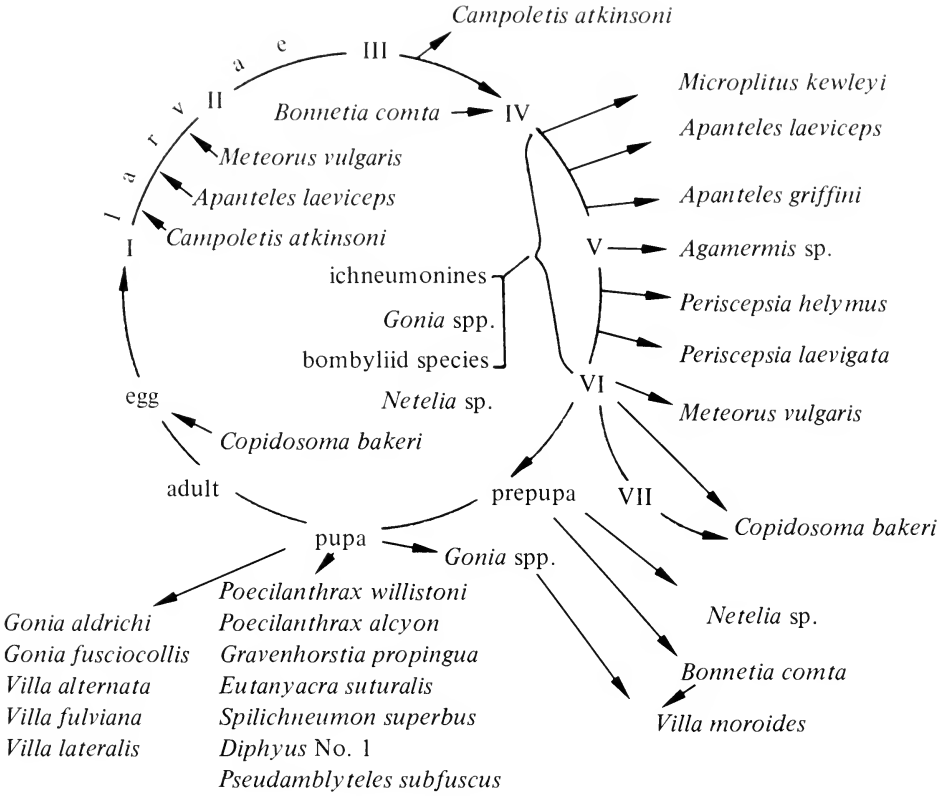


Fig. 66. The parasitoid complex of *Euxoa ochrogaster*. Arrows entering the circle indicate oviposition by the parasitoids. Arrows leaving the circle indicate the stage at which the host is killed.

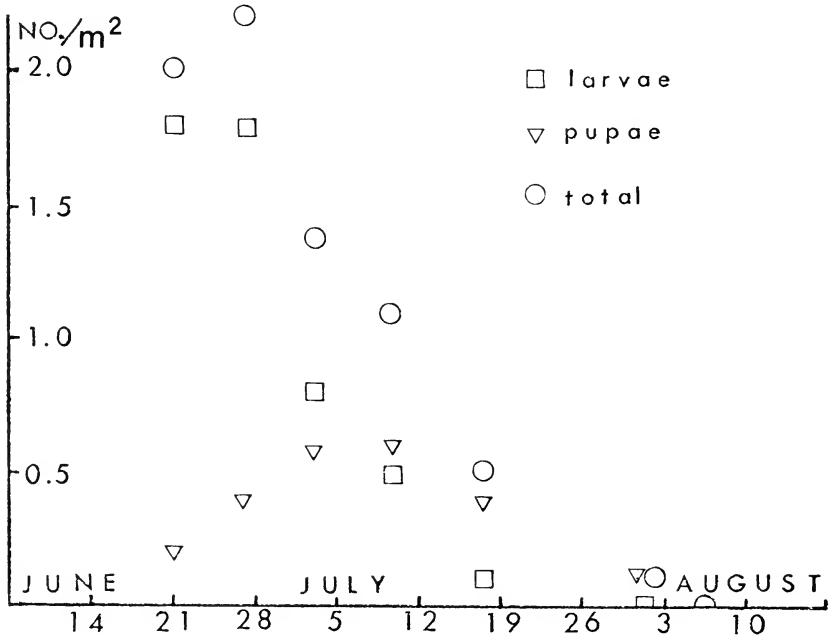


Fig. 67. The decline of the *Euxoa ochrogaster* population at Calahoo, Alberta in the summer of 1968.

study the complex of hosts and parasitoids in any given region. In such a study, all of the parasitoids of all the cutworm hosts which are found in that region would be studied and described. As a result of such a study, all the potential parasitoids of any cutworm species found within that region would be known. The advantages of such an approach are that when any one species is studied some of its actual parasitoids may not be present in sampled populations. If several species of hosts are studied than any one parasitoid is less likely to be overlooked and thus will be recognized in a future outbreak of cutworms. Also, if a different species of cutworm appears in a region, most of the potential parasitoids will be easily recognized, allowing a meaningful analysis of the role of the parasitoids as regulation factors.

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COLLEMBOLA ON FLOWERS ON BANKS ISLAND, N. W. T.

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Quaestiones entomologicae
8 : 121 1972

Two species of Collembola, Entomobrya comparata *Folsom and* Corynothrix borealis *Tullberg (Entomobryiidae) were collected from the flowers of* Lesquerella arctica *(Wormskjöld) S. Watson (Cruciferae) where they were feeding on pollen directly from the anthers. The observations compare well with those reported earlier from northern Ellesmere Island.*

Deux espèces de collembole, Entomobrya comparata *Folsom et* Corynothrix borealis *Tullberg (Entomobryiidea) ont été recueillis alors qu'ils se nourrissaient du pollen directement des anthères des fleurs de* Lesquerella arctica *(Wormskjöld) S. Watson (Cruciferae). Ces observations sont en accord avec celles rapportées précédement du nord de l'ile d'Ellesmere.*

Kevan and Kevan (1970) have reviewed the literature on Collembola as visitors to flowers and pollen feeders, and reported on observations from around Lake Hazen, Ellesmere Island, N. W. T. On 5 July 1970 on Banks Island, N. W. T., I collected 11 Collembola associated with the flowers of *Lesquerella arctica* (Wormskjöld) S. Watson (Cruciferae), the same plant species as for the Lake Hazen Collembola-flower association. The following observations were made on a stony well-drained ridge of the coastal escarpment 2 km east of the village of Sachs Harbour (71° 59′N., 125° 11′W.). *Lesquerella arctica* was flowering elsewhere, but Collembola were not found in association.

Two specimens of *Entomobrya comparata* Folsom (Entomobryiidae) were collected and observed, in the same circumstances as described for this species around Lake Hazen. Another was seen, but it escaped. Eight specimens of the darker *Corynothrix borealis* Tullberg (Entomobryiidae) were collected from the flowers. Of these, six were inside the corolla and two were crawling on the outside of the petals. One other was found on the ground beside a flowering plant. Of the six within the corollas, three were watched as they fed on pollen directly from the anthers. Their postures were different from those assumed by *E. comparata.* They gripped the anther and filament of the stamen being fed at so that their bodies were parallel to the filament, rather than curled around the anther as *E. comparata.* One other individual of *C. borealis* was in a similar posture but its mouthparts were applied to the stigma and its body parallel to the style.

Dr. K. Christiansen, Grinnell College, Iowa, kindly identified the specimens for me and examined their gut contents according to my suggestions. Both specimens of *E. comparata* and seven of the specimens of *C. borealis* had pollen of *L. arctica* in their guts, and most were well stuffed. One individual of *C. borealis* had also ingested some xylem vessel elements and fungal hyphae.

The dates of these records coincide almost exactly with the suggested "sensitive period" for *E. comparata* around Lake Hazen (Kevan and Kevan, 1970). Data are insufficient to make a statement about *C. borealis* in this regard. *Corynothrix borealis* is the first species in this genus recorded visiting flowers and feeding on pollen and fits within the group of light coloured Collembola (albeit a little browner than *E. comparata*) in exposed flowers where they would be least conspicuous. The day on which the Banks Island collection was made was heavily overcast, so that there would have been no raised intra-floral temperature to hold the Collembola in the flowers.

REFERENCE

Kevan, P. G. and D. K. McE. Kevan. 1970. Collembola as pollen feeders and flower visitors with observations from the high arctic. Quaest. ent. 6:311-326.

Book Review

JACOT-GUILLARMOD, C. F. Catalogue of the Thysanoptera of the World. Annals of the Cape Provincial Museums (Natural History). Vol. 7, Part 1 (1970), p. i-iii, 1-216; Part 2 (1971), p. 217-515. Published jointly by the Cape Provincial Museums at the Albany Museum, Grahamstown, South Africa. (No price given.)

Judging by the treatment given them in most textbooks of general entomology, one might think the Thysanoptera to be a poorly known order of insects. That they are at least as studied as other groups of comparable size should quickly become apparent on perusal of these, the first two of a projected six- or seven- part catalogue of the order.

In his introduction to Part 1, Jacot-Guillarmod outlines his methods and indicates that his goal is to list all literature on the species treated in each part up to the time of publication. The rest of Part 1 treats the sub-order Terebrantia except for the family Thripidae, and Part 2 the subfamilies Panchaetothripinae (=Heliothripinae), and Thripinae (in part) in the family Thripidae. Systematically-arranged are the names of superorder, order, suborder, superfamilies, families, subfamilies, tribes and subtribes. Generic names are listed alphabetically under the next higher category; specific names under the genus or subgenus, and subspecific names under the species. Every publication that cites a name is listed under the valid name of the species in chronological order and each reference is complete except for title. Type-species for valid and invalid genera are indicated; the locations of type-specimens are shown, and distribution, type-locality and habitat are given for each species. Invalid names are cross-indexed.

This is a very difficult work to use because there is no index and because the headings of all categories above the genus are printed in similar-sized type. For the benefit of my readers I here list the names of the higher categories and the pages on which they are found: Part 1. Thysanoptera = p.1; Terebrantia = 9; Aeolothripoidea = 15; Aeolothripidae = 17; Melanthripinae = 22; Mymarothripinae = 60; Aeolothripinae = 62; Orothripini = 63; Franklinothripini = 86; Aeolothripini = 94; Mesothripidae (fossil) = 174; Palaeothripidae (fossil) = 174; Permothripidae (fossil) = 175; Merothripoidea = 176; Merothripidae = 176; Erotidothripinae = 177; Merothripinae = 178; Thripoidea = 185; Heterothripidae = 186; Heterothripini = 188; Opadothripini = 211; Uzelothripidae = 216. Part 2. Thripidae = 217; Panchaetothripinae = 225; Thripinae = 322; Dendrothripini = 324; Sericothripini = 356; Sericothripina = 358; Chirothripini = 436.

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Book Review

GILLETT, J. D. 1971. Mosquitos. (The World Naturalist Series, Ed. Richard Carrington). pp. xiii + 274 + 22 Figs + 38 plates. 468 refs. London, Weidenfeld and Nicolson. Price £5.90.

Professor Gillett has given us a readable and well-illustrated account of the life of mosquitos and their effects on human affairs. The emphasis is on their ecology and behaviour, and on the need to consider the population as well as the individual.

An introductory chapter gives an outline classification of mosquitos and notes on the history and distribution of the family. One chapter each is devoted to eggs, larvae, pupae, adults, and flight. The next three chapters, on the ovarian cycle, the circadian rhythm, and strains and species, are especially interesting as Professor Gillett has worked extensively in these fields. After two more chapters, on parasites and predators and mosquitos as nuisance, the remainder of the text, about one fifth of the book, is devoted to mosquitos and disease and mosquitos and history. The author worked for many years at the East African Virus Research Institute, Entebbe, Uganda, and was one of those responsible for elucidating the roles of *Aedes africanus* and *Aedes simpsoni* in sylvan yellow fever. The account of this work, and of other mosquito-borne viruses is well worth reading. Malaria, by contrast, is rather briefly dealt with.

The author states that he set out to draw on personal experience wherever possible, and the book is enhanced by some accounts of the practical difficulties of studying mosquitos in nature, such as building tree platforms 25 meters above the forest floor to study biting cycles in the canopy.

The drawings and photographs are well chosen and the jacket design, a painting of the Brazilian *Sabethes belisarioi* Neiva, is strikingly attractive. There are no tables of data in the text but for those looking for more detail there is a list of some 500 references. A curious feature of the book is a series of 9 appendices listing by geographical region the 2,500 or so known species, with symbols to indicate if they have been found to transmit filariae, malaria, or viruses over any part of their range. Since these appendices cover 32 pages, an extra page or two of analysis of their contents would have been helpful.

I noticed few typographical errors. The name of Dr. C. B. Cuellar is misspelled on page ix and that of Jack Colvard Jones on page 104. Male *Culiseta inornata* (Will.) do not find their females only by touch, as stated on page 104. Kliewer et al. (1966. Ann. Ent. Soc. Amer. 59: 530) have shown that the female produces a pheromone which attracts the male and releases his sexual response.

In his final chapter Professor Gillett reminds us that in spite of the great expenditure of money and effort on mosquito eradication schemes no species has actually been eradicated by man. The only complete success was the eradication of *Anopheles gambiae* from Brazil, a species introduced there only ten years previously. Only by understanding the ways of mosquitos can man learn to avoid their ravages. It is noteworthy that four of the most severe biters and transmitters of disease, *A. gambiae, Aedes aegypti, Culex pipiens fatigans,* and *Culex tarsalis* owe much of their present success to conditions that man has created for them. The case of *C. tarsalis* will be particularly hard to solve since its spread is associated with irrigation schemes, otherwise worthwhile ventures. Insecticides are hardly mentioned in this book, a refreshing change for those of us who are accustomed to seeing mosquitos as figures on mortality tables.

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Book Review

WEISS, E. (Editor). 1971. Arthropod cell cultures and their application to the study of viruses. Current topics in Microbiology and Immunology. Vol. 55. Springer-Verlag, Berlin, Heidelberg, New York. xx + 288 pp., 151 figs., author and subject indices. Cloth. $22.60 (U. S.).

Although this book presents the proceedings of a symposium, it is much more than the collection of papers on rather unrelated topics that usually emanates from such conferences. Its contents are organized into 11 chapters with the following titles: 1. The culture of cells from insects and ticks; 2. Analysis of cells from established insect cell lines; 3. Physiology of cultivated arthropod cells; 4. Arthropod tissue culture in the study of arboviruses and Rickettsiae: A review; 5. Propagation of arboviruses in Singh's *Aedes* cell lines; 6. Growth of arboviruses in arthropod cell cultures: comparative studies; 7. Growth of viruses in arthropod cell cultures: applications; 8. Homoptera cell culture and its application to the study of plant pathogens; 9. Lepidoptera cell culture and its application to the study of plant viruses and animal parasites; 10. *Drosophila* cell culture and its application for the study of genetics and virology; and 11. New opportunities in biological research offered by arthropod cell cultures.

Each chapter contains several papers on topics related to the chapter title. References are gathered together at the end of the book. The approach of different authors varies: some contributions are short research reports, while others are full accounts with summaries of previous work and discussion of implications for other fields and for the future.

In Chapter 2, J. L. Vaughn emphasizes the difficulties inherent in research in invertebrate tissue culture. Accidental contamination of cell lines with microorganisms or with cells from other lines will probably become a problem as more lines are introduced and as the use of these proliferates. Since cells in culture look similar regardless of their source, contamination of this kind cannot be recognized by differences in cell morphology. A. E. Greene and J. Charney received a cell culture supposedly from *Aedes aegypti* in their lab in 1967. Using agar gel immunodiffusion and isoenzyme analysis they showed that this culture had been contaminated and replaced by cells of a moth, *Antherea eucalypti.* They indicate also how these techniques can be used in identifying cultures of mammalian, piscine and avian origin and in separating these from cells of arthropod origin.

Since the organs and tissues of animals are comprised of cells organized and specialized in particular directions and because the form of these structures is determined by the genetic makeup of the cells interacting with the environment during and after embryonic development, T.D.C. Grace suggests that a good way to study these phenomena is in tissue culture where the investigator has some control over the cells' surroundings. R. L. Seecof and R. L. Teplitz monitored the development of individual cells from dissociated embryos of *Drosophila.* Some of these divided unequally and produced long extensions in culture. Events similar to these occur in the development of the central nervous system from neuroblasts during normal embryogenesis. When the neuro endocrine organs of the cockroach, *Leucophaea maderae* were explanted in culture, they continued to function *in vitro* for some time (E. P. Marks).

J. H. Conover and his colleagues succeeded in producing bi-nucleate, somatic cell hybrids between mosquito (*Aedes aegypti*) and human (He La) cell lines. When control He La cultures were innoculated with polio virus, they died within three days whereas mosquito-human hybrids persisted until day 10. Mosquito (*Aedes aegypti*) cell cultures were little affected when treated with organo-phosphate, carbamate, chlorinated hydrocarbon, arsenical, nicotine and pyrethrin insecticides, but similar amounts of these chemicals applied to larvae killed them (T.D.C. Grace and J. Mitsuhashi).

There are two reviews in the book: one by C. E. Yunker on the culture of arboviruses and Rickettsiae in cultured cells and the other by H. Hirumi on the use of homopteran cell cultures in the study of plant pathogens. Yunker points out that two thirds of all published work in the area of his review was done in 1968 and 1969. From this work he concludes, among other things, that primary cultures of arthropod tissues will support growth of viruses that that particular donor arthropod or a relative can transmit. Arboviruses may propagate to a higher degree in cultures of vector tissues than in the cells of the intact arthropod. Since primary tick cultures and established insect cell lines are very sensitive to many arboviruses and Rickettsiae, they may be used to detect these pathogens at lower concentrations than do techniques (animal, egg, or vertebrate culture) now used.

Since there is little knowledge of how plant virus particles penetrate and multiply in the cells of their vector species, Hirumi suggests that the successful culture of these microorganisms in vector cell cultures is a promising avenue of research. Both virus-vector and mycoplasma-vector interactions have been studied in cultured embryonic cells of leafhoppers, aphids and planthoppers.

Although most articles in the book deal with virus-cell culture interactions, one by T. J. Kurtti and M. A. Brooks summarizes their successful culture of *Glugea disstriae*, a microsporidian protozoan, in cell cultures of *Malacosoma disstria* and *M. americanum*. Since this microorganism is a naturally-occurring parasite of these insects, eventually we may be able to use tissue-culture techniques in the mass-production of this and other protozoan parasites for biological control of pest species.

C. Barigozzi summarizes the advantages of using *Drosophila* cell culture for genetical studies. Molecular biologists are beginning to switch their activities from procaryote to eucaryote organisms because of their increasing interest in the factors controlling development in higher organisms. *Drosophila* cell lines have advantages over vertebrate ones for biochemical studies of this kind because the genetics of this genus is so well understood. Particularly useful is the occurrence of somatic pairing and the ability to induce crossing-over in these cells by X-ray irradiation as has been shown by H. A. Schneiderman and his students at Irvine, California. Such techniques could be put to good advantage in *Drosophila* cell lines since an accurate genetic analysis is aided by crossing-over.

The future of tissue culture is speculated upon by B. W. Schlesinger and W. Trager in the final chapter. Schlesinger suggests that culture work with viruses may eventually shed some light on the evolutionary origin and relationships between different, arthropod-transmitted plant and animal viruses. These viruses, as he emphasizes, are the only ones known to bridge the evolutionary gaps between kingdoms (animals and plants) and phyla (arthropods and vertebrates). The ability to switch such viruses back and forth between vertebrate and arthropod cells under controlled conditions should help us to understand both of these subjects. He speculates on the evolutionary origin of viruses and asks questions which may be answered with culture techniques.

Since Trager was the first (1935) to culture viruses (nuclear polyhedrosis) in invertebrate (*Bombyx mori*) tissue culture, it is fitting that he should have the final say in this book. He predicts that major breakthroughs in the understanding of parasitic protozoan life cycles (e.g. malaria, sleeping sickness), insect mycetomes and their function, and insect development will follow from increased work in insect tissue culture. Why, he asks, do the cells of larval Cyclorrhapha stop dividing in the egg and subsequently develop through an increase in cell size and chromosomal polyteny? This does not occur when embryonic cells of these insects are cultured; when explanted they continue to increase in number by mitosis. He completes his discussion with reference to the work of Hadorn and his students on determination and transdetermination in *Drosophila*. The whole theory of structural homology, so

important in comparative morphological, palaentological, evolutionary, and systematic studies, can be thrown into question, if, as has been shown experimentally, cells determined to form one structure, can be "transdetermined" in nature to form almost any other in the body.

This book should have wide appeal. Plant pathologists, microbiologists, parasitologists, medical entomologists, and developmental biologists will profit from a careful reading of pertinent parts of it. The book is well produced and is amazingly free of typographical errors (I found three) considering that its English text was printed in Germany. With a few exceptions, the photomicrographs are excellent. However the price ($22.60) indicates why it is that violation of copyright is an increasing problem.

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ANNOUNCEMENT

An English translation of Rohdendorf's Historical Development of the Diptera edited by Harold Oldroyd and Brian Hocking will be published by the University of Alberta Press in the Fall of 1972. A further announcement concerning price and details will follow.

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

Copy should conform to the Style Manual for Biological Journals published by the American Institute of Biological Sciences, Second Edition, 1964, except as regards the abbreviations of titles of periodicals which should be those given in the World List of Scientific Periodicals, 1964 Edition. The appropriate abbreviation for this journal is *Quaest. ent.* An abstract of not more than 500 words is required. All manuscripts will be reviewed by referees.

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Book Review

WILSON, Edward O. 1971. *The Insect Societies.* The Belknap press of Harvard University Press, Cambridge, Massachusetts, U.S.A. pp. x + 548. $22.00.

This book is a very impressive achievement for a single author. E.O. Wilson states at the beginning of the work that he is attempting to provide a modern synthesis of insect sociology, and to present the knowledge within the framework of the concepts of population biology. I think he has succeeded to a remarkable degree. Almost all of the information reviewed is from the works of other authors and the range covered is enormous. The bibliography extends over 55 pages and includes references published from the seventeenth century up to 1971. Such coverage has often resulted in books becoming a dull catalogue of abstracts, but the author's control of his material has produced a very readable and coherent account, which is consistently interesting and clear. In some parts the book is even compulsive.

Michener's classification of the degrees of social behavior *(Ann. Rev. Ent., 14:299-342)* is adopted for use throughout the book. Four chapters are devoted to descriptions of the social organizations found among wasps, ants, bees and termites respectively. The accounts also include the taxonomy of the social species, what is known of the fossil records, and current and previous hypotheses about the evolution of sociality within the groups.

An interesting chapter on pre-social insects follows, bringing together information on parental, co-operative, sub- and quasi-social behavior among several orders of insects and in spiders.

Three chapters are given to caste in ants, bees and wasps, and termites, respectively, in which the evolution and determination of castes and the division of labor among them are discussed. As in other parts of the book, the limits of current knowledge are always stressed.

The sensory physiology and mental capacities of the social insects are reviewed as a prelude to discussions of the communication systems employed in alarm and assembly, recruitment, recognition, food exchange and grooming which make up the next three chapters. The author emphasizes the way in which complex social behavior is created out of the relatively simple individual reactions of colony members to stimuli from the rest of the colony and from the environment. These discussions lead into the chapters on group effects and the control of nestmates and on social homeostasis and the superorganism.

Wilson gives considerable attention to the historical importance of the idea of an insect colony as a superorganism and concludes that the concept has lost popularity not because it is wrong but because it has become irrelevant. It was valuable in stimulating interest and research, but does not itself contribute towards understanding the phenomena which have

been discovered through that research.

Hamilton's idea of the importance of haplodiploidy in the development of insect sociality *(J. Theoret. Biol., 7:1-52, 1964)* is among those dealt with in a chapter on the genetic theory of social behavior. The intriguing suggestion that because hymenopteran males are haploid, and a female thus shares more genes with her sisters than with her offspring, social behavior improves her chances of perpetuating her own genes, is subjected to close scrutiny. Predictions which should follow from it are examined using available data, and Wilson concludes that the idea can be provisionally accepted. But he stresses that multiple mating by the queen can cancel the bias unless the population shows low dispersal or much interbreeding.

A chapter entitled "Compromise and Optimization in Social Evolution" discusses how social organization is affected by the environmental circumstances of the colony. It includes a review of Wilson's own earlier work on the hypothesis that the proportions of castes in a mature colony represent an 'optimal mix' which minimizes the 'production cost' of the new virgin queens. The constitution of the optimal mix depends on the degree of specialization of the castes and varies with changes in the environment. The small amount of data which supports the hypothesis is quoted, but it will be very difficult to prove or disprove.

Two chapters on symbioses follow, treating relationships among the social insects and with other arthropods respectively. Wilson thinks that permanent parasitism of one ant species on another can be reached by any of three routes: via the slave-making habit, via temporary parasitism in colony foundation, or via xenobiosis, the habit of one species of living within the nest of another. He gives examples to support his opinion.

The penultimate chapter is on the population dynamics of colonies, a study which the author considers to be the next essential stage in accounting for the observed social phenomena of insects, following work on their physiology. The chapter covers survivorship of colony members and of colonies, regulation of colony growth, competition and territoriality, control of colony destiny and species diversity, and dispersal of colonies.

The concluding chapter relates the study of insect societies to that of vertebrate societies and looks forward to the founding of a general theory of sociobiology.

Throughout the text entomological terms are explained where they occur and no assumptions are made about the reader's background. A glossary is provided. It is clear that the book is intended for wider readership than entomologists only. Each chapter can be read and understood independently, although references are made to other chapters which discuss in detail themes mentioned in passing. This design leads to some repetition of data, especially in the section on behavior, although on most occasions a new facet of interest is revealed.

All the many illustrations are borrowed from earlier works, either reproduced directly or modified, and are mostly good. Some take the form of original drawings by Sarah Landry composed from one or more sources, and these are both clear and pleasing.

Wilson also quotes many passages of description or argument directly from earlier authors. Such inserts provide a valuable change of pace for the reader and enhance the author's own style. He also gives his personal assessment of the value of other people's work, and in cases where no data are available to enable a mystery to be explained, makes a suggestion of his own towards a solution.

I estimate that it took me about thirty-one hours to read through the entire book. The price of the volume may seem high, but for so much solid entertainment and enlightenment it compares well with other media, even without counting re-reading time. I would recommend *The Insect Societies* to anyone. You would actually read it.

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CLASSIFICATION, PHYLOGENY, AND ZOOGEOGRAPHY OF *SCHIZOGENIUS* PUTZEYS (COLEOPTERA: CARABIDAE: SCARITINI)*

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Quaestiones entomologicae
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North and Middle American species of Schizogenius *Putzeys are reviewed in detail, and South American species are treated provisionally. The genus is redefined, characterized, and illustrated. Two subgenera are* Genioschizus *new subgenus, with three species groups, and* Schizogenius s. str., *with 21 species groups. In all, I recognize 68 species and two subspecies. Keys are given to: subgenera; described species groups, species, and subspecies of* Genioschizus; *same of North and Middle American* Schizogenius s. str.; *and species groups and most described species of South American* Schizogenius s. str.

I describe as new the following 27 taxa: S. crenulatus chiapatecus, S. sculptilis, S. impuncticollis, S. suturalis, S. jacarensis, S. bicolor, S. cearaensis, S. negrei, S. costipennis, S. reichardti, S. ocellatus, S. lindrothi, S. brevisetosus, S. seticollis vandykei, S. plurisetosus, S. kulti, S. dilatus, S. tibialis, S. ozarkensis, S. planuloides, S. neovalidus, S. chiricahuanus, S. pacificus, S. emdeni, S. scopaeus, S. falli, *and* S. ochthocephalus. *Synonymies proposed for the first time are:* S. peninsularis *Van Dyke (=* S. auripennis *Bates),* S. angusticollis *Putzeys (=* S. arechavaletae *Putzeys),* S. validus *Fall (=* S. longipennis *Putzeys), and* S. championi *Kult (=* S. pygmaeus *Van Dyke).*

Given for each species are, as appropriate: synonymic list, diagnostic combination, description, discussion of variation, etymological derivation, geographic distribution list, collecting notes, taxonomic notes, and illustrations of important structural characteristics. Geographic distributions are mapped for all North and Middle American species. Descriptions of most North and Middle American species are augmented with tables of descriptive statistics. Results of detailed statistical analyses of geographic variation for members of some North and Middle American species groups are tabulated, mapped, and discussed.

A phylogeny is reconstructed for the genus, and carefully integrated with historical zoogeography. No geographic evidence is used to reconstruct the phylogeny of major groups and lineages; phylogenies derived from contrasting phyletic and phenetic techniques are favorably compared. To derive the phylogeny of members of the truquii *lineage, which includes most North and Middle American species of* Schizogenius, *use of zoogeographic evidence is essential; simple cladistic techniques are not used because character states of too many characteristics are reversible. An average time between dichotomies in the reconstructed phylogeny of* Schizogenius *is about 3,000,000 years. This interval is used to integrate* Schizogenius *phylogeny and zoogeography. On the same basis, phylogenies and zoogeographies of* Brachinus *and* Evarthrus *are compatible. Zoogeographies of* Brachinus, Evarthrus, *and* Schizogenius *are compared for North and Middle American faunas.*

Ancestral Schizogenius *evolved in South America about Middle Eocene. Ancestors of the* ferrugineus *group, the* truquii *lineage, and the* crenulatus *group entered North America in Late Eocene, Middle Oligocene, and Middle Miocene. The ancestor of the* truquii *lineage ultimately evolved into eight species groups, and their evolutionary zoogeographies are discussed in detail. Since Early Pleistocene, members of the* tenuis, optimus, *and* lindrothi *groups have crossed the Panamanian land bridge to Middle America, and members of the* depressus *group have spread southward into South America.*

* Revised version of thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of requirements for the degree of Doctor of Philosophy at the University of Alberta. The author's present address is c/o Department of Entomology, United States National Museum, Washington, D. C. 20560.

En este trabajo se revisan, en detalle, las especies de Schizogenius *Putzeys de Norte y Centro América, en tanto que las especies de Sur América son revisadas provisionalmente. El género es redefinido, señalado, e ilustrado. Dos subgéneros son el* Genioschizus*, subgénero nuevo, con tres grupos de especies; y el* Schizogenius s. str.*, con 21 grupos. En total, yo reconozco 68 especies y dos subespecies. Se han ofrecido claves para los subgéneros, grupos de especies, especies, y subespecies del* Genioschizus*; lo mismo que para el* Schizogenius s. str. *de Norte y Centro América, asi como para los grupos de especies, y la mayor parte de las especies descritas en Sur América.*

Yo describo como nuevos los siguientes: S. crenulatus chiapatecus, S. sculptilis, S. impuncticollis, S. suturalis, S. jacarensis, S. bicolor, S. cearaensis, S. negrei, S. costipennis, S. reichardti, S. ocellatus, S. lindrothi, S. brevisetosus, S. seticollis vandykei, S. plurisetosus, S. kulti, S. dilatus, S. tibialis, S. ozarkensis, S. planuloides, S. neovalidus, S. chiricahuanus, S. pacificus, S. emdeni, S. scopaeus, S. falli, *y* S. ochthocephalus. *Son sinonimias nuevas:* S. peninsularis *Van Dyke (=* S. auripennis *Bates),* S. angusticollis *Putzeys (=* S. arechavaletae *Putzeys),* S. validus *Fall (=* S. longipennis *Putzeys), y* S. championi *Kult (=* S. pygmaeus *Van Dyke).*

Para cada especie se ha ofrecido, como conviene: lista de sinonimias, combinación de diagnóstico, descripción, discurso de variación, derivación etimológica, lista de localidades, notas sobre colección y taxonomía, e ilustraciones de características esenciales. Igualmente se dan cartas de distribución para las especies de Norte y Centro América. Las especies de Norte y Centro América han sido provistas, en su descripción, con tablas de estadísticas descriptivas; y los resultados de análisis estadísticos detallados, son catalogados, delineados en cartas, y discutidos.

Se ha reconstruido una filogenia para el género, y, cuidadosamente, se ha integrado ésta con una zoogeografía histórica. No se ha usado ninguna evidencia geográfica para la reconstrucción de la filogenia de grupos y los linajes mayores; las filogenias derivadas de técnicas filéticas y fenéticas son comparadas favorablemente. Para derivar la filogenia de miembros del linaje truquii*, que contiene la mayor parte de las especies del* Schizogenius *de Norte y Centro América, el uso de evidencia zoogeográfica es indispensable. No se han usado técnicas fenéticas sencillas debido a que los estados de carácter con demasiadas características, son reversibles. Un intervalo proporcional entre dicotomías en la filogenia reconstruida del* Schizogenius *se aproxima a los 3,000,000 de años. Este intervalo es usado para integrar la filogenia con la zoogeografía del* Schizogenius*. Igualmente, las filogenias y zoogeografías del* Brachinus *y el* Evarthrus *son compatibles. Las zoogeografías del* Brachinus*, el* Evarthrus*, y el* Schizogenius *son comparadas para las faunas de Norte y Centro América.*

El Schizogenius *ancestral se desarrolló en Sur América alrededor del Eoceno Medio. Los predecesores del grupo* ferrugineus*, del linaje* truquii*, y del grupo* crenulatus*, penetraron en Norte América durante el Eoceno Último, Oligoceno Medio, y Mioceno Medio. El predecesor del linaje* truquii *finalmente desarrollado en ocho grupos de especies, y sus zoogeografías evolutivas son discutidos en detalle. Desde el Pleistoceno Primario, miembros de los grupos* tenuis, optimus, *y* lindrothi *han atravesado el puente de tierra de Panamá hacia Centro América, y miembros del grupo* depressus *se han distribuido en el interior de Sur América.*

CONTENTS

Introduction. – Small American beetles of the tribe Scaritini have received little careful attention. This is unfortunate since as a result no other aspects of their biologies have been studied, but fortunate in that comparatively few taxonomic errors have been introduced into the literature. Lindroth (1961) wrote a fine revision of the Canadian and Alaskan members of this fascinating group of beetles. His treatment of *Schizogenius*, the subject of my investigations, is excellent for the limited Canadian fauna but is not adequate to identify specimens from most regions in the United States. The genus, after all, is mainly Neotropical, and in fact a good taxonomy for it must be based on the entire fauna. Except for Lindroth's (1961) key to described species from America north of Mexico, the most recent full revisions of *Schizogenius* were done by Putzeys (1866) for Mexico and southward, and by LeConte (1879) for America north of Mexico.

How much is known about these beetles? Since Thomas Say named the first species in 1823, little more than descriptive morphological work has been done. Immature stages remain completely unknown, and aside from collector's notes on habitat we have no information on adult biology. The earliest names for species now placed in *Schizogenius* were proposed by Say (1823), Castelnau (1835), and Haldeman (1843). Putzeys (1846) introduced the generic name *Schizogenius*, and in this and subsequent important papers (1863, 1866, 1878) he named numerous species. Meanwhile, LeConte (1848, 1852, 1857, 1863) studied Nearctic species, and in 1879 summarized his knowledge about them in a key and synonymic list. Bates (1881, 1891) treated species of the Mexican and Middle American faunas as known to him. Darlington (1934, 1939), Fall (1901), Kirsch (1873), Steinheil (1869), and Van Dyke (1925, 1949) each introduced one or more new names to the literature. Kult (1950) produced the first major report on the Neotropical fauna since the nineteenth century, and Lindroth (1961) did likewise for the Nearctic fauna. Since I began my studies on the genus I have named two South American *Schizogenius* species as new (1966a), and transferred Darlington's *S. arenarius* to *Halocoryza*, a closely related genus which I revised and characterized (1966b, 1969).

In this study I treat in detail the taxonomy and distribution of *Schizogenius* in North and Middle America, and provide the basis for a similar study of the South American fauna. I define "North America" as America north of Guatemala, "Middle America" as America from Guatemala to Costa Rica plus the West Indies, and "South America" as South America proper plus Panama. I hope that my work will not only make possible the identification of specimens, but that it will stimulate more detailed investigations into the many problems in evolutionary biology that render members of this genus so interesting. Thus, I attempt to unravel some of the myriad puzzles in speciation in North and Middle American *Schizogenius*, and point out others that particularly demand attention.

MATERIALS

This revision is based on the study of 9326 adult specimens of North and Middle American *Schizogenius,* plus 932 adults from South America. I have collected these insects along streams in much of the United States and Mexico, and other collections were made especially for this study by G. E. Ball, T. L. Erwin, D. H. Kavanaugh, D. J. Larson, and H. B. Leech. Other specimens were loaned to me by various museums and private collectors; the following abbreviations represent these collections and their respective curators.

AMNH American Museum of Natural History, New York, New York 10024; P. Vaurie.
ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; H. R. Roberts.
BMNH British Museum (Natural History), London, England; P. Hammond, R. D. Pope.
CAS California Academy of Sciences, San Francisco, California 94118; H. B. Leech.
CNC Canadian National Collection of Insects, Entomology Research Institute, Ottawa,

Ontario; E. C. Becker, W. J. Brown.

CNHM Chicago Natural History Museum, Chicago, Illinois 60605; H. Dybas.

CPBo C. Bolívar y Pieltain, Instituto Politecnico Nacional, Mexico, D. F.

CUNY Cornell University, Ithaca, New York 14850; H. Dietrich, L. L. Pechuman.

DHKa D. H. Kavanaugh, University of Alberta, Edmonton 7, Alberta.

DJLa D. J. Larson, University of Calgary, Calgary, Alberta.

DRWh D. R. Whitehead, University of Alberta, Edmonton 7, Alberta.

FDAG Florida Department of Agriculture, Gainesville, Florida 32601; R. E. Woodruff.

GRNo G. R. Noonan, University of Alberta, Edmonton 7, Alberta.

HFHo H. F. Howden, Carleton University, Ottawa, Ontario.

HGou H. Goulet, University of Alberta, Edmonton 7, Alberta

INHS Illinois State Natural History Survey, Urbana, Illinois 61803; L. K. Gloyd.

IRSB Institut Royal des Sciences Naturelles de Belgique, 31, Rue Vautier, Bruxelles 4, Belgium; R. Damoiseau.

JHen J. Hendrichs S., Apartado Postal 11-774, Mexico 11, D. F.

JNeg J. Nègre, 9, Boulevard de Lesseps, Versailles, France.

KHSt K. H. Stephan, 3038 East Eastland, Tucson, Arizona 85716.

KSUM Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.

LACM Los Angeles County Museum, Exposition Park, Los Angeles, California 90007; C. L. Hogue.

LBSC Long Beach State College, Long Beach, California 90804; E. L. Sleeper.

MCZ Museum of Comparative Zoology, Cambridge, Massachusetts 02138; P. J. Darlington. Jr., J. F. Lawrence.

MGFT Museum G. Frey, Entomologisches Institut, Tutzing bei Munchen, Germany; M. von Falkenhayn.

MHNG Museum d'histoire Naturelle, Geneva, Switzerland; C. Besuchet.

MNHP Museum National d'histoire Naturelle, Paris, France; A. Bons, J. Nègre.

MSUL Michigan State University, East Lansing, Michigan 48823; T. F. Hlavac.

MZSP Museu de Zoologia da Universidade de Sao Paulo, Caixa Postal 7172, Sao Paulo, Brazil; H. Reichardt.

OSUC Ohio State University, Columbus, Ohio; C. A. Triplehorn.

PSUU Pennsylvania State University, University Park, Pennsylvania 16802; W. W. Boyle, S. W. Frost.

RTBe R. T. Bell, University of Vermont, Burlington, Vermont 05401.

RUNB Rutgers University, New Brunswick, New Jersey 08903; J. B. Schmitt.

TCBa T. C. Barr, University of Kentucky, Lexington, Kentucky 40506.

TLEr T. L. Erwin, United States National Museum, Washington, D. C. 20560.

UAFA University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.

UASM University of Alberta, Strickland Museum, Edmonton 7, Alberta; G. E. Ball.

UATA University of Arizona, Tucson, Arizona 85721; F. G. Werner.

UCB University of California, Berkeley, California 94720; J. A. Powell.

UCD University of California, Davis, California 95616; R. O. Schuster.

UKSM University of Kansas, Snow Museum, Lawrence, Kansas 66045; G. W. Byers.

UMCG University of Miami, Coral Gables, Florida 33124; H. F. Strohecker.

USNM United States National Museum, Washington, D. C. 20560; P. J. Spangler.

UWLW University of Wyoming, Laramie, Wyoming 82070; N. L. Marston.

VMKi V. M. Kirk, North Grain Insects Research Laboratories, Brookings, South Dakota 57006.

ZMLS Zoological Institut, University of Lund, Lund, Sweden; C. H. Lindroth.

METHODS

Dissecting techniques

Representative female specimens of subgenera and some species groups were relaxed in boiling water, then dissected with fine forceps; mouthparts, wings, and ovipositors were mounted in Hoyer's medium on slides, studied with a compound microscope, and drawn. As I found no characteristics useful in species recognition, these dissections were not done routinely at species level.

Male genitalia including parameres were dissected from the abdominal apices of relaxed specimens, examined for peculiarities in form, and mounted in Hoyer's medium on slides. Proper positioning was obtained by spreading the drop of mountant to a thin layer before placing the cover slip. Two or three days after mounting, each preparation had cleared sufficiently for study, and no additional clearing techniques were used. The endophallus was everted in at least one specimen of nearly every North and middle American species, specimens permitting, by hooking and pulling the apex of the virga with a fine pin. I did not attempt this for most South American species, because in older material, particularly specimens collected in other than ethyl acetate, incidence of damage was prohibitive. Nor was this procedure used routinely for members of the *depressus* group, because of their generally small sizes. After genitalia were studied and drawn, they were removed from slides, glued to cards, and pinned with the specimens.

Measurements and statistics

Mensurable and meristic data. – Certain routine measurements used in species descriptions and in variation analyses were made with a Leitz stereoscopic microscope at a magnification of 50 diameters, using a micrometer eyepiece with a scale interval of 0.025 mm. These measurements and their abbreviations are: DP, maximum depth of thorax from intercoxal process of prosternum to basal carina of pronotum; LE, length of left elytron along suture from basal tubercle to apex; LH, length of head from base of eye to anterolateral angle of clypeus; LP, length of pronotum along midline; PS, minimum distance from apex of left paramedian longitudinal sulcus to base of pronotum. Ta, length of hind tarsus, claws excluded; Ti, length of hind tibia; TL, total length, combining LH, LP, and LE; WE, maximum width across closed elytra; WF, minimum width of head between eyes; WH, maximum width of head across eyes; WP, maximum width of pronotum, hind angles excluded.

Most of these measurements can be made accurately, but fixed reference points are not available for intercoxal process in DP, apex of paramedian sulcus in PS, or base of tibia in Ti, and thus these measurements are less accurate. Least accurate is the Ta measurement, made from base of article one to apex of article five regardless of expansion or contraction between articles.

Some of these measurements were used to obtain ratios which help express body proportions. These ratios are: DP/LP, relative depth or convexity of thorax; LE/WE, form of elytra; LP/WE, relative size of pronotum; LP/WP, form of pronotum. PS/LP, relative length of paramedian pronotal sulcus; Ta/Ti, relative length of hind tarsus; and WF/WH, relative eye size. The range of variation in any given sample depends in part on the accuracy of measurements used to form ratios; for example, Ta/Ti is quite inaccurate and thus too variable for use in infraspecific comparisons. Except for LE/WE, a ratio used only for species and species groups for which it had been used before (Kult, 1950), these proportions are intended to represent different, independent aspects of body form.

In those species having more than three or four setae on the elytral disc, counts were

made of numbers of setae on intervals three, five, and seven of the left elytron. These counts were totalled when used for statistical analysis. Similar counts were made of numbers of marginal pronotal setae, in the few forms having more than the standard two pairs.

Although I am not sure that variation in numbers of elytral setae exactly follows a normal distribution, especially when numbers are small, I treated these data in the same way as I did the mensurable data. Sokal and Rohlf (1969) suggest, as a rule of thumb, that the number of unit steps in a range of variables should range from about 30 to 300. Such a broad range in the proportion variables would require greater accuracy in the original measurements than I found practical. Nor do numbers of setae per elytral disc, at least in most species, vary to this amount. But, since I use statistics more to discern relationships than to determine similarities, I believe descriptive statistics based on these data are adequate.

Descriptive statistics. – Except for the poorly known and unusually variable *S. tibialis,* I give a comprehensive set of descriptive statistics for one sample of each described North and Middle American species; I do not do so for South American species because of inadequate material. Mensurable and meristic data so treated include, where appropriate, TL, LE, WH, WP, WE, setae on intervals three, five, and seven of the left elytron and their total, WF/WH, LP/WP, DP/LP, LP/WE, LE/WE, Ta/Ti, and PS/LP. When at least eight specimens made up a sample, I give range of variation, mean, 1.5 standard deviations and two standard errors (Hubbs and Hubbs, 1953), and coefficient of variability. I use 1.5 rather than one standard deviation, since it is more critical as an analytical tool (Mayr, *et al.,* 1953). When fewer than eight specimens were used in a sample, I give only range and mean. I do not use coefficient of difference, a statistic suggested by Mayr (1969) for subspeciation analysis, because my criteria for subspecies differ from his.

Ideally, each sample included at least 20 males collected at one time and place. These conditions were often not entirely satisfied, usually because of inadequate numbers. In those species belonging to species groups which do not have reliable external characteristics to distinguish sexes, sex was ignored. For some species, samples of adequate size could be made only by combining specimens collected over a more or less extensive area. When too few specimens were available for adequate statistical treatment, the sample comprised all specimens on hand regardless of sex or provenance.

These statistics complement species characterizations, and are used for comparisons between closely related species or between species groups. They are not intended for comparisons between less closely related species. Thus, the statistical treatment is as uniform as possible for species within a species group, but sample compositions or characteristics studied may differ for different species groups.

Analysis of geographic variation. – Where problems in species recognition were evident, I carefully studied variation among population samples before making taxonomic decisions. I chose for analysis characteristics which could be easily and accurately measured, and which promised to tell the most about geographic variation. These were LE, WF/WH, LP/WP, total number of setae on disc of left elytron, and, for the *pluripunctatus* group, PS/LP and LP/WE. If two samples differ from one another by non-overlap of two standard errors from the means, I term them "statistically significantly different;" this is equivalent to the t-test at 0.05 probability. I use the term "taxonomically significantly different" if two samples differ from one another by non-overlap of 1.5 standard deviations from the means, to imply that 90% or more specimens from one sample can be distinguished from 90% or more from the other sample (Mayr *et al.,* 1953).

Samples were composed of equal numbers of females and males, despite probably increasing sample variance and thereby decreasing statistical sensitivity, in order to increase

the numbers of samples suitable in size for useful comparisons. These samples, designated by numbers, are plotted on maps; details of locality and composition may be derived by consulting maps and distribution lists. Ideally, each sample included at least ten of each sex, and samples having fewer than five of each were not analyzed. To insure that samples represented biological populations, I tried to form each sample from specimens collected at one time and place. If this could not be done, then date of collection was ignored. When still no adequate sample could be made, I drew from a wider geographic area. These latter samples probably represent composite biological populations, but are approximations which can be modified after additional collections are made. Henceforth, I use the word "population" to mean the statistical population from which a sample was drawn, unless otherwise specified. Because samples were limited by numbers and distributions of available specimens, geographic coverage is less than ideal. Samples form a loose network over the geographic area covered, and proximate samples may not represent truly proximate biological populations. Thus, statistical data among proximate samples only approximately suggest biological relationships, and should be reinterpreted if geographically intermediate samples become available.

Understanding relationships between taxa requires knowledge of similarities, but within a species, or between closely related allopatric phena, similarity alone may not be a useful yardstick of relationship (Mayr, 1969). Statistical analysis of single characteristics yields limited direct information about relationships. If statistics are used to obtain such direct information, statistical data should represent the total phenotype and be studied by various procedures of multivariate analysis or numerical taxonomy (e.g., Sokal and Sneath, 1963). In an analysis of geographic variation, however, each characteristic should first be considered independently, since characteristics within a species may vary independently. This is clinal variation, or the geographic variation of single characteristics (e.g., Mayr, 1969). Only after characteristics have been studied separately may they be profitably studied in combination, as for example by hybrid index techniques (e.g., Freitag, 1965). I limited my statistical studies of geographic variation to clinal analyses; more sophisticated procedures were unnecessary.

Statistically significant differences in one or more characteristics between population samples of a species, or between closely related allopatric phena, are evidence of evolutionary divergence between them. Indeed, if evolution is a dynamic continuing process, some evolutionary divergence between any two biological populations of a species should take place, given sufficient time. Its extent would depend on geographic relationships of the populations, duration and completeness of their isolation, and various environmental factors. Speciation occurs when two populations or groups of populations have diverged sufficiently to acquire reproductive isolation, and when they have lost reproductive links through other populations.

Statistically or taxonomically significant differences in one or more characteristics between samples of geographically distant populations provide no information about presence, absence, or amount of gene flow between them. They do give information about amount of divergence or similarity, but not about biological relationships, and without additional data from intermediate population samples they yield little useful evidence either for or against conspecificity. Furthermore, since any two proximate samples may not represent contiguous biological populations, the biological significance of whatever statistical difference, or indeed or any difference, between them cannot readily be interpreted. More meaningful comparisons may be made of two samples via one or more intermediate samples. From them, one may predict the relative extent of gene flow between populations represented by these samples. The intent of this discussion is to emphasize that the terms "statistically significant"

and "taxonomically significant" indicate amount of difference or similarity, not any precise relationship. These points are illustrated in my analysis of *S. pygmaeus* and *S. scopaeus.*

I use statistics to study clinal relationships among populations within species and between closely related allopatric species or phena, in order to determine probable biological relationships of samples rather than similarities or differences. These clinal studies yield evidence about possible gene flow, and consequently about possible reproductive isolation. From them, one can reasonably predict whether or not populations are conspecific, given sufficient data. Mayr (1969) states that isolated allopatric populations may be either species or subspecies, and that a taxonomic decision may be arbitrary; he suggests that such isolates are best treated as subspecies. However, I think information on clinal variation is relevant in such decisions. If the nearest populations in two isolated groups of populations are the most similar, or at least show no evidence of divergence, then I would expect that some gene exchange does exist and that the populations are conspecific. If these two populations are the most different in one or more characteristics, or even if only one of them is divergent, then I think that gene flow is unlikely and that the two groups of populations are not conspecific. Within the *pluripunctatus* group, an example of the former situation is the taxon *S. seticollis,* with two subspecies; and as an example of the second, I regard the taxa *S. plurisetosus* and *S. multisetosus* as separate species. If intermediate samples diverge in one or more characteristics, then the more distant samples, regardless how similar, may not be conspecific; see for example my treatment of the taxa *S. pygmaeus* and *S. scopaeus.* And if the intermediate samples converge, then the more distant samples probably are conspecific, regardless how dissimilar; see my disposition of the names *S. pygmaeus* and *S. championi.*

In a statistical study of character clines, I think the most useful statistic is the sample mean, compared with means of proximate samples. Statistics of dispersion from the mean are more useful to estimate the relative significance of observed differences between means than to estimate absolute differences. They suggest whether differences between means are or are not the result of coincidence. If two samples differ significantly in a particular characteristic, but an intermediate sample differs significantly from neither, I conclude not only that the first two populations have diverged but also that gene flow still exists between them. I think this pattern is unlikely to result from coincidence.

Illustrations

Line drawings were made on paper squared to a one cm grid, with the aid of an ocular grid mounted in a Leitz stereoscopic dissecting microscope. I used much care in preparing these drawings, since I used them to make direct comparisons of details of form and structure, and to supplant verbal description. Homologous structures are drawn consistently to the same scale to facilitate comparisons. Male genitalia, endophalli, and other small organs mounted on slides were drawn from an optical magnification of 150 diameters, and their details checked at still higher magnifications with a compound microscope. Partial and entire habitus drawings were made from a magnification of 50 diameters, and fine detail and shading added as needed.

Distribution maps are given for all North and Middle American species; I do not give such maps for South American species since most are known from too few localities to even begin to picture their distributions. Special maps were prepared to illustrate clinal relationships, where studied, and also to illustrate broad zoogeographic patterns.

Criteria for species-group and genus-group taxa

For deciding interrelationships of specimens and populations at species level, I follow a

slightly qualified version of the biological species definition proposed by Mayr (1963, 1969): species are populations or groups of populations through which gene flow actually or potentially exists, but which are reproductively isolated from all other populations. The biological species, if bisexual, is the only taxon which has nonarbitrary boundaries at any given time and place; it is nonarbitrary as to what is included and as to what is excluded (Simpson, 1961). However, in contemporary, bisexual organisms, nonarbitrariness may be difficult to demonstrate for geographically distant populations, since information about gene flow or potential reproductive isolation may not be available. For example, consider a series of populations the most distant of which are similar to one another and may not be reproductively isolated, while the most proximate, especially when parapatric or sympatric, are dissimilar and reproductively isolated. The entire aggregate of populations may fit the biological species definition, but the most potent available taxonomic evidence is the reproductive isolation of the near populations. The biological species definition cannot here be strictly applied, for lack of evidence, and I think the best taxonomic solution is to recognize two biological species where there may really be only one. But, while sympatry is a test for reproductive isolation between two populations, it may not always indicate specific distinctness. If, for example, the two sympatric populations were shown to be end points in a circle of races, then I would regard them as members of a single species.

Beyond the question of species definition is that of practical species recognition. For *Schizogenius,* the only data presently available are from adult morphology and distribution; there is no direct information about reproductive isolation, at least between allopatric populations, and indeed the limits of populations are unknown. In carabid beetles, the structures of greatest use in species recognition, because of diversity in form, are often in the male genitalia. In *Schizogenius,* major differences in male genitalia among related species are exceptional, and so I could not rely upon finding them to distinguish species. In the few species groups where major differences were found, however, and assuming no contrary evidence, I accept them as suitable criteria for species recognition. When species are sympatric, there is usually little difficulty in their recognition. If two forms differ constantly in one or more ways, and if there is no geographic or biologic evidence to the contrary, I assume the differences are maintained through reproductive isolation and treat the two forms as separate species. Generally, differences between sympatric species are numerous and well marked. When similar differences distinguish allopatric forms, and again if there is no contrary evidence, I consider the allopatric forms to represent distinct species. When allopatric forms differ less markedly, I use analytical statistics to determine if reproductive isolation is likely, specimens permitting. When two allopatric forms cannot be linked in some reasonable geographic way because adjacent or intermediate samples are divergent in one or more characteristics, I regard them as separate species. If these samples do not diverge, and particularly if they converge, I regard the allopatric forms they represent as conspecific.

I use the subspecies category only for taxa of uncertain status, and then only for completeness. All or nearly all individuals of a subspecies are morphologically distinguishable from those of an allopatric form, yet no judgement may yet be made as to biological status in terms of reproductive isolation. That is, there is a substantial statistical or morphological gap between the two forms, but one which could easily be bridged by collections made in intermediate areas if the two forms are truly conspecific. If, on the other hand, I have strong evidence of gene flow between allopatric forms, or if I have the direct evidence of hybridization between them, I recognize only one geographically variable taxon, the species. Aside from this use of the subspecies category as an expression of uncertainty, I share

Erwin's (1970) view that naming subspecies is undesirable.

Unlike species-group taxa, genus-group taxa are arbitrarily limited as to inclusiveness (Simpson, 1961). Most taxonomists agree that the subgenus or genus should contain an aggregate of related species separated from similar aggregates by a gap. It is not agreed how large this gap should be, nor is it agreed how inclusive should be the aggregates so separated. In the study of single genera, I think the existing concept of the genus should be accepted unless it is poorly defined or clearly unreasonable. I have elsewhere (1966b) segregated and defined the genus *Halocoryza.* I see no reason to otherwise modify Putzeys' (1846, 1863, 1866) concept of *Schizogenius*.

A supraspecific taxon should be strictly monophyletic, according to Hennig (1966). However, especially when no fossil evidence is available, I doubt that monophyly can be definitely demonstrated for all groupings; and other objections to this strict requirement for monophyly have been expressed by Mayr (1969). I have already (1966b) suggested that *Halocoryza* and *Schizogenius* share a common ancestry. I think that *Schizogenius* really is monophyletic but *Halocoryza* may be either paraphyletic or monophyletic, and if my interpretations of its origin and relationships were correct it is indeed paraphyletic. If so, the requirement for monophyly indicates: 1, a single genus comprising *Halocoryza* + *Schizogenius;* 2, the Old World genus *Halocoryza* and the New World genus *Schizogenius;* or 3, three genera, the Old World *Halocoryza*, New World "*Halocoryza*," and *Schizogenius*. I chose none of these, since my separation of *Halocoryza* and *Schizogenius* better reflects known biological and zoogeographic peculiarities. Also, the relationships I suggested are based more on conviction than on demonstrable fact; quite possibly the two genera, as I define them, really are monophyletic assemblages.

Lindroth (1969) notes that recognition of subgenera may lead to chaos, and he uses informal "species groups." I agree that one should not formally recognize numerous closely related subgenera, but believe that use of the category may be justified for larger genera if done sparingly and carefully, and in accord with Simpson's (1961) suggestions about ranking taxa. I use the subgenus category for major monophyletic lineages which are approximately equally divergent from one another, yet subordinate in my concept of the genus. I use the informal species group category for minor monophyletic lineages within subgenera.

Taxonomic methods

Specimens of North and Middle American *Schizogenius* were first sorted into presumptively related or conspecific complexes based on external morphological similarity. These complexes were further sorted by geographic locality, and the original sorting then refined. A preliminary survey of the male genitalia within each complex was then made, and the complexes refined further, as necessary. Relationships and status of specimens within each complex were then decided, based on my criteria for species and subspecies. If sufficient specimens were available, and if there was a problem in deciding whether forms were conspecific or not, I used statistical methods to analyze variation and to determine probable gene flow patterns. I examined at least six male genitalia for each species, specimens permitting, and as many more as necessary to reach appropriate conclusions about variation. Naming of specimens was based on knowledge of type specimens of all previously described taxa, and lectotypes were designated as required. The diacritical mark "(!)" is used to indicate that I examined the type specimen.

Similar methods could not be applied throughout to the South American specimens studied, because of insufficient numbers. More reliance was placed on absolute superficial or genitalic similarity, and none on statistical methods, but criteria for species recognition

remained the same. No subspecies were recognized. When taxonomic decisions could not be made, specimens were left undescribed or unassigned to species. I studied type material of some, but not all, described South American species, and may therefore have made some errors in association. I think this fault is outweighed by the need to provide the basis for future study of the South American fauna, and also to aid in understanding the North and Middle American faunas.

Simpson (1961) clearly defined zoological classification: it is the ordering of animals into groups based on their relationships. Accordingly, it should reflect the evolutionary history of animals. Mayr (1969) wrote that the major purpose of zoological classification is to provide a system for maximum information storage and retrieval, and that the most efficient classification for that purpose is based on evolutionary relationships. I believe that the classification should allow one to make and test predictions about zoogeographic, biochemical, chromosomal, larval, or other relationships not already directly embodied in the classification. For this purpose, a classificaiton based on hypotheses about evolutionary relationships is the most efficient, since only it can theoretically contain and yield more information than was used in its creation. The difference between a classification based on suspected or real relationships and one based only on similarities is that the former is structured around evolutionary theory, while the latter is a mechanical structure with no intended theoretical basis. This difference may be not or scarcely evident in the end product, but I think it important. I have tried to provide for *Schizogenius* a classification with, I hope, some predictive value, and I hope it will be tested in future investigations.

Mayr (1969) summarized methods used in zoological classification. I have used various of them in various combinations, depending on the particular problem at hand. I obtained much useful information about relationships of components of some species complexes by using methods of analytical statistics. These methods did not, however, give useful information about less closely related forms. Perhaps some of the various techniques of multivariate analysis would be useful to detect these more distant relationships, but I remain unconvinced of either their validity or utility (Mayr, 1969). Similarly, I have not used other numerical or deliberately phenetic methods, except some methods of numerical cladistics (Camin and Sokal, 1965). I did use some of the weighted character methods suggested by Mayr (1969), together with some of the more rigidly cladistic approaches preferred by Hennig (1966). I give a more detailed discussion of phylogenetic methods, and discuss relationships between classification and phylogeny, in later sections.

Taxonomic literature and synonymic lists

Pertinent taxonomic works are listed for all previously described taxa in *Schizogenius* in synonymic lists for those taxa. These synonymic lists do not pretend to completeness. In particular, most faunal and catalogue listings are excluded.

I made no effort to verify locality records cited in faunal works, and unless such records are particularly important and probably correct, references to those works are excluded. Many old records are doubtless erroneous; for example, some reports of *S. lineolatus* from eastern North America are doubtless based on specimens of *S. sulcifrons*. Important faunal works that I normally omitted from synonymic lists include those by Blatchley (1910), Brimley (1938), Fattig (1949), Leonard (1926), and Smith (1910).

Catalogue listings are excluded, since they neither contribute new taxonomic information nor contain useful summaries of then available taxonomic information other than literature references. Such catalogues are those by Blackwelder (1944), Csiki (1927), Gemminger and Harold (1868), Leng (1920), and Leng and Mutchler (1933).

TAXONOMY

Genus *Schizogenius* Putzeys

Schizogenius Putzeys 1846:650. *Type species.* – *Schizogenius strigicollis* Putzeys 1846: 650 (subsequent designation by Lindroth, 1961:164). LeConte 1857:82. Putzeys 1863: 24. Putzeys 1866:222. LeConte 1879:34. Kult 1950:139. Lindroth 1961:164.

Diagnostic combination. – Clypeus tridentate apically; frons with four or five pairs of longitudinally directed carinae between eyes; lacinia plurisetose on inner and outer margins; gula not more than 0.3 width of mentum; pygidium with numerous longitudinally directed crenulate carinae near middle; stylus and coxite of ovipositor fused, plurisetose.

Description. – Small to medium size, LE 1.65 to 5.00 mm. Body pedunculate, elongate, depressed to cylindrical. Color various, maculate or not, not to strongly aeneous or metallic. Integument shiny or dull; microsculpture varied in extent, isodiametric, often useful in species recognition.

Head. Large, prognathous. Labrum Fig. 1-3, biemarginate to deeply emarginate; dorsal surface with seven setae in front, median and two outer ones longest; lateral margins each with five to about fifteen pairs of frayed or bifid setae, anterior pairs curved forward and inward over mandibles. Clypeus with two strong paramedian teeth; median tooth prominent in most species; paramedian carinae varied, oblique or arcuate, joined at apex with median tooth or not; median field triangular or hemicircular, basal width varied; clypeus with one pair of setae basad and laterad to carinae. Clypeal suture obsolete to sharply engraved. Frontal lobes prominent. Frons with four or five pairs of longitudinally directed carinae between eyes, neither perfectly equidistant nor equally raised, appearance of frons not evenly convex; median sulcus broader than outer paramedian sulci, with or without median carina; carina five variable, obsolete or not; carina six obsolete except on frontal lobes, not raised above dorsal margin of eye. Anterior supraorbital seta set in front of carina five; posterior seta set between bases of frontal carinae four and five. Eyes varied in size, prominence, and size and number of facets. Neck punctate at least on sides, orbit extended laterad along posterior margin of eye. Antennal articles five to ten slightly transverse to quite elongate, moniliform to filiform; scape with one subapical dorsal seta; pedicel with one ventral seta, or bisetose or plurisetose in some species; articles three to four plurisetose or pubescent; articles five to eleven pubescent, without glabrous areas. Mandibles Fig. 5-7, stout and broadly curved along lateral margin; inner ventral margin of right mandible with small tooth near middle; scrobe oblique. Maxilla Fig. 9-11, terminal article of palpus swollen basally; lacinia with apex acute and abruptly bent, setose on outer and inner margins. Labium Fig. 13-15, penultimate article of palpus bisetose. Mentum Fig. 17-20, deeply emarginate at middle, with one anterior pair of paramedian setae; median tooth obsolete to acute; lateral lobes truncate or with antero-lateral angles acutely produced; ventral surface with broad, abruptly depressed concave area, limited behind by arcuate carina; base of mentum with one pair of large, pouch-like sensory pits, and one pair of paralateral setae. Submentum with one paramedian and one postero-lateral pair of setae, plurisetose in *S. strigicollis* Putzeys. Gula narrow, at narrowest part 0.05-0.30 width of mentum.

Thorax. Pronotum slightly to moderately transverse; median longitudinal sulcus not bordered by carinae; paramedian longitudinal sulci well developed in most species, hooked basally; paralateral sulci present in some species; lateral grooves shallow, bordered by distinct carinae in some species; anterior and posterior pairs of marginal setae present, additional marginal setae present in some species; basal carina moderately to strongly elevated above margin; disc flattened to moderately convex. Prothoracic pleuron smooth, without longi-

tudinal ridge, rugose or punctate in some species. Prosternum strongly compressed between front coxae; posterior process broadened and convex, without setae or carinae. Metepisternum slender, elongate. Anterior coxal cavities closed-separated-unbridged; middle and hind coxal cavities disjunct-confluent (see Bell, 1967).

Elytra. Lateral channel varied in form, slightly narrowed at apex, or flared and with one or more deep subapical pits (Fig. 22); umbilicate series of punctures unbroken. Elytron with whip-like seta at base of interval three; disc in most species with two or more setigerous punctures on interval three, in many species with variable numbers on intervals five and seven. Intervals one to six flat to convex, in some species with short apical carinae, in some species entirely carinate; interval seven carinate or not; interval eight carinate at apex, in most species not joined at apex by other intervals. Striae punctate at least basally, faintly so in some species; striae evident to apex, in most species deeply impressed, outer and inner striae equally engraved.

Hind wings. Macropterous and probably functional in all North and Middle American species, brachypterous in at least one South American species. Venation (Fig. 31-34) of usual carabid type except wedge cell absent and oblongum cell hooked in front.

Legs. Front tibia anisochaetous, with four evident external teeth; subapical spurs varied in size and form, not grossly unequal; ventral-basal margin with three or four setae. Middle and hind tibiae with apical spurs slender, inconspicuous. Anterior and middle tarsi of males of many species slightly dilated and more densely pubescent ventrally than in females, but without distinctive adhesive pads. Hind tarsi narrow and nearly glabrous. Tarsi moderately to markedly elongate, hind tarsus more than 0.55 length of hind tibia; article one of hind tarsus 2.0 to 4.0 times as long as article two. Paronychia obsolete to nearly as long as tarsal claws.

Abdomen. Sternum three with one pair of strong, oblique paramedian carinae, in many species strongly curved outward at apices. Sterna four to six each with one pair of paramedian ambulatory setae. Sternum seven with or without one pair of paramedian ambulatory setae, sexually dimorphic or not, and two pairs of approximately equidistant apical marginal setae. Sterna four to seven without basal transverse impressions. Pygidium (Fig. 23-25) with two or more pairs of paramedian setae, one pair of large setae near pygidial glands, variable numbers of microsetae, and conspicuous crenulate carinae along midline; margin of pygidium entire in males, but serrate or crenulate in some or all females of many species.

Male genitalia. Parameres subequal, slightly asymmetric, each with one to three large apical setae. Median lobe arcuate to angulate, in most species nearly symmetric, not constricted near base, base not lobate; apical third compressed, varied in form, in many species strongly deflected. Endophallus doubly invaginated; basal stylets of varied form; no flagellum; apical brush or virga without large spines; dorsal cap sclerite present; basal collar spines present in some species (see Whitehead, 1966a). Abdominal segment nine of normal carabid type, ring sclerite complete.

Female genitalia and ovipositor. Internal genitalia without sclerotized structures, not studied in detail. Ovipositor (Fig. 27-29) with stylus and coxite fused, plurisetose at middle; setae of posterior margin of valvifer normally in two groups; paraprocts absent; proctiger articulated with upper margin of valvifers.

Immature stages. Unknown; see Vinson (1956) for description of the presumably similar larva of *Halocoryza*.

Etymology. — Greek, *schizo* = split, plus *genio* = chin or mentum; in reference to form of mentum.

Distribution. — Members of this genus are known from continental North, Middle, and South America, from southern Canada to central Argentina; one species is endemic to Cuba.

Separation of *Schizogenius* and *Halocoryza*

In my review of *Halocoryza* (Whitehead, 1966b), I stated that members of the genus *Schizogenius* were best distinguished by uni- or bisetose antennal pedicels and striate pygidia. However, at least one South American species has plurisetose antennal pedicels, probably secondarily so. Also, American *Halocoryza* species have striate pygidia, but the striations are inconspicuous and weakly developed (Fig. 26). These striae are actually rows of tubercles, file-like ridges possibly used for stridulation; in this work I call them "crenulate carinae."

Several other differences listed in that paper are apparently without exception. The lacinia of *Schizogenius* is setose only on the outer margin. The gula of *Schizogenius* is much narrower than that of *Halocoryza* (Fig. 21). Another important difference, not recognized previously, is that in *Halocoryza* the fused stylus and coxite of the ovipositor has one large seta (Fig. 30). I found no characters in labrum (Fig. 4), mandibles (Fig. 8), labium (Fig. 16), or wing useful to distinguish *Schizogenius* from *Halocoryza,* but in some forms of *H. arenaria* the apical part of the wing is reduced.

Key to subgenera of *Schizogenius*

I here recognize two subgenera, *Genioschizus* new subgenus and *Schizogenius s. str.,* both represented in North, Middle, and South America. *Genioschizus* is a small, mainly South American subgenus, composed of three closely related species groups. *Schizogenius s. str.* is much larger and more varied, and particularly in North America is the dominant subgenus.

1. Lateral channel of elytron flared near apex, with one or more deep subapical pits . . . . . *Genioschizus*, new subgenus, p. 144
1' Lateral channel of elytron narrowed near apex, without deep subapical pits . . . . . *Schizogenius s. str.*, p. 165

Subgenus *Genioschizus* new subgenus

Type species. – *Schizogenius crenulatus* LeConte 1849:197, here designated.

Diagnostic combination. – Lateral channel of elytron flared near apex and with one or more deep subapical pits. Also: paramedian clypeal carinae tuberculate, not joined to median clypeal tooth; clypeal suture not sharply engraved; antennae moniliform; paralateral longitudinal sulci present on pronotum or not; front tarsi slightly dilated in males only; paramedian ambulatory setae on sternum seven in both sexes; and pygidium not serrate or crenulate in either sex.

Description. – Small beetles, LE 1.65-2.75 mm. Body cylindrical. Color testaceous to piceous, aeneous or not, elytra sellate or not. Integument shiny; microsculpture reduced on or absent from median frontal sulcus, prothoracic pleura, and middle of abdominal sterna, present in small patches in coxal depressions of sternum three.

Head. Labrum (Fig. 1) slightly emarginate or biemarginate apically, margined laterally with five or six pairs of setae. Clypeus with median tooth reduced; paramedian carinae short, ended before median tooth, either oblique and tuberculate or arcuate and with apices nearly joined in an arc; median field triangular or hemicircular, at base more than 1.5 greatest width of median frontal sulcus. Clypeal suture obsolete. Frontal carinae one to four irregular, nearly parallel, confused basally or not, carinae one and four more strongly raised, carina five reduced or obsolete; median sulcus wider than at least outer paramedian sulci, not limited in front by transverse carina, with no trace of median carina, sides parallel or slightly divergent behind. Eyes prominent (WF/WH, 0.49-0.63), multifaceted, facets uniform

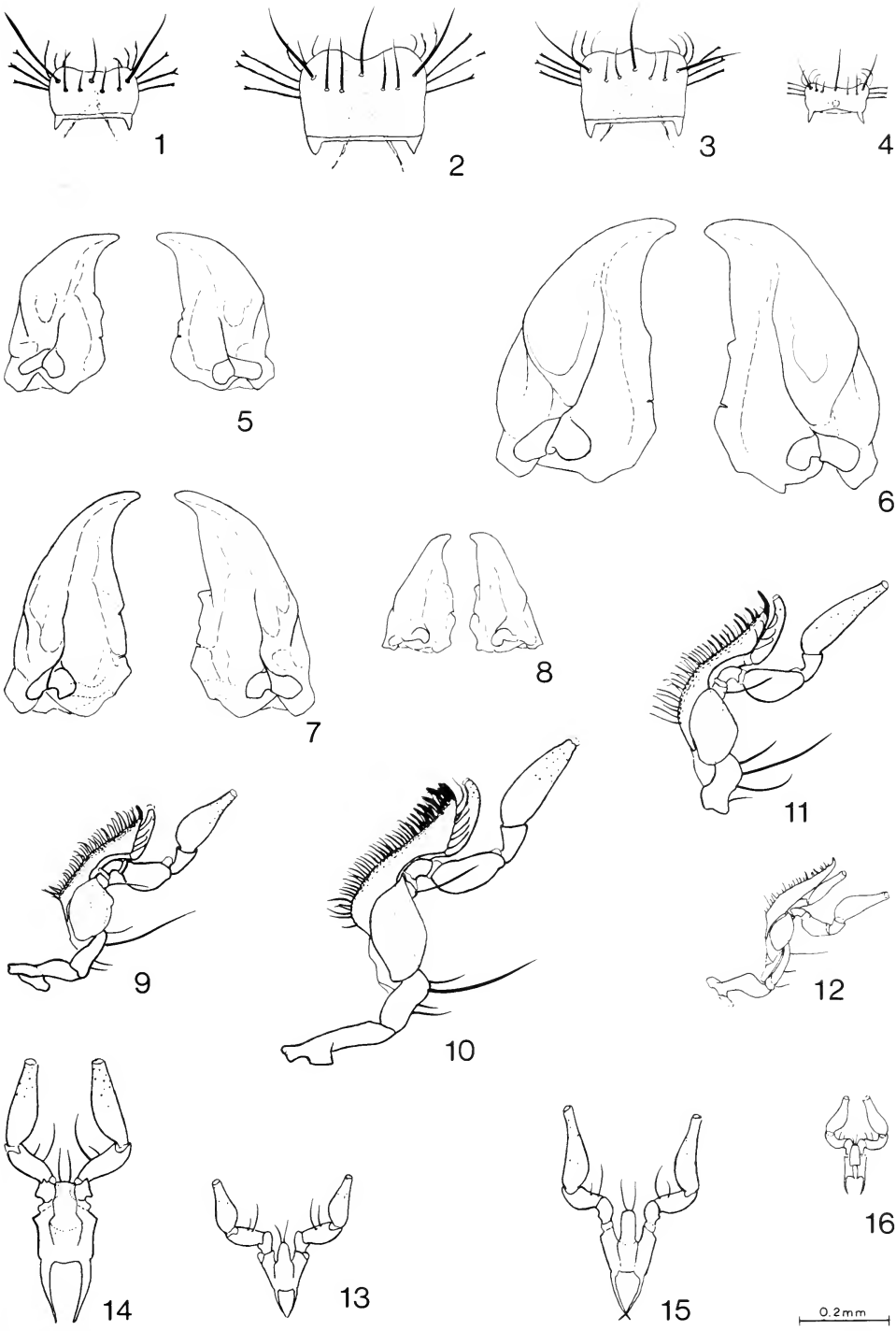


Fig. 1-4. Labrum, dorsal aspect. 1. *Schizogenius crenulatus* LeConte. 2. *S. optimus* Bates. 3. *S. sallei* Putzeys. 4. *Halocoryza acapulcana* Whitehead. Fig. 5-8. Mandibles, dorsal aspect. 5. *S. crenulatus* LeConte. 6. *S. optimus* Bates. 7. *S. sallei* Putzeys. 8. *H. acapulcana* Whitehead. Fig. 9-12. Left maxilla, ventral aspect. 9. *S. crenulatus* LeConte. 10. *S. optimus* Bates. 11. *S. sallei* Putzeys. 12. *H. acapulcana* Whitehead. Fig. 13-16. Labium, ventral aspect. 13. *S. crenulatus* LeConte. 14. *S. optimus* Bates. 15. *S. sallei* Putzeys. 16. *H. acapulcana* Whitehead.

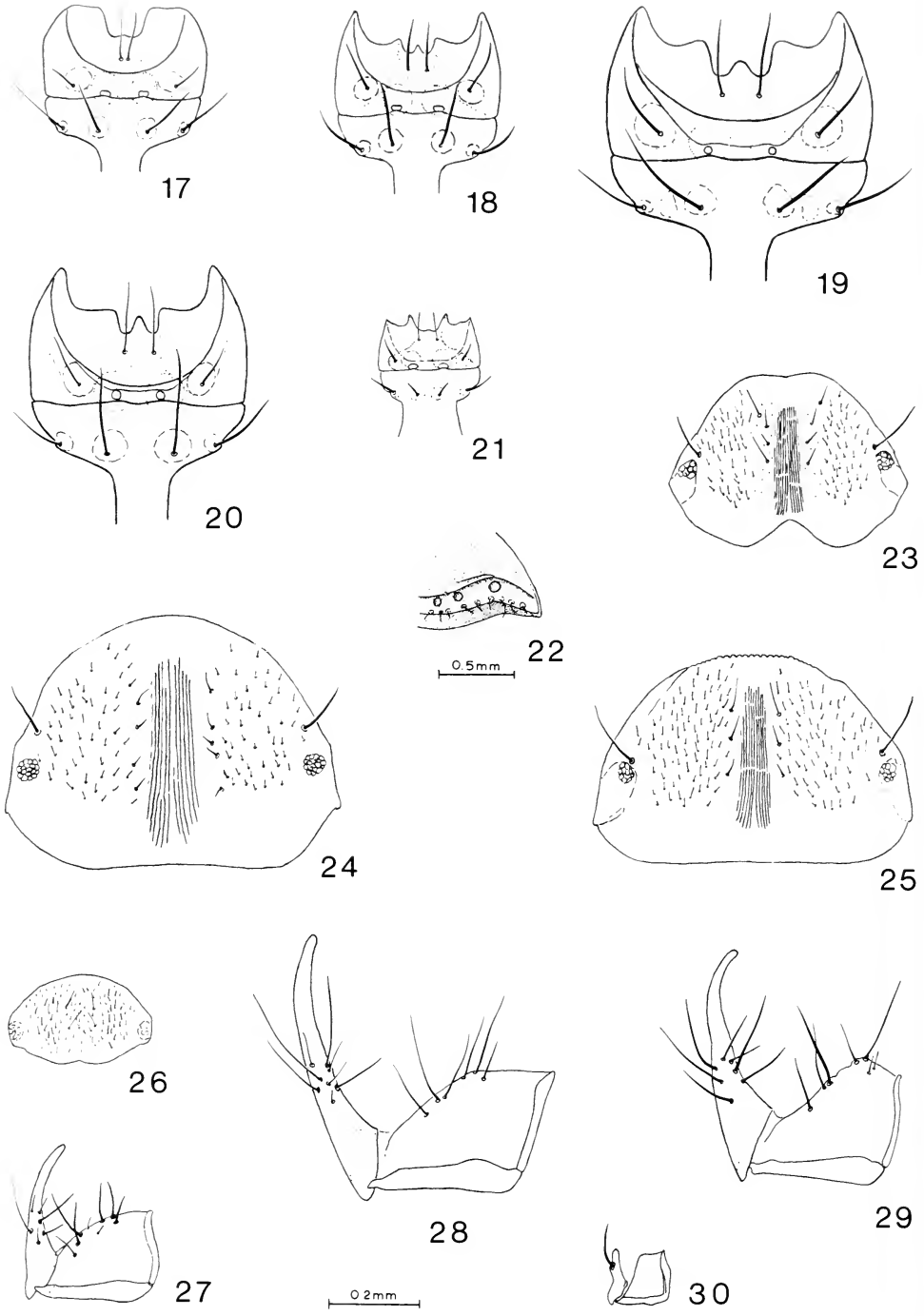


Fig. 17-21. Mentum, ventral aspect. 17. *S. crenulatus* LeConte. 18. *S. tenuis* Bates. 19. *S. optimus* Bates. 20. *S. sallei* Putzeys. 21. *H. acapulcana* Whitehead. Fig. 22. Elytral apex, postero-lateral aspect, *S. crenulatus* LeConte. Fig. 23-26. Female pygidium, dorsal aspect. 23. *S. crenulatus* LeConte. 24. *S. optimus* Bates. 25. *S. sallei* Putzeys. 26. *H. arenaria* Darlington. Fig. 27-30. Ovipositor, lateral aspect. 27. *S. crenulatus* LeConte. 28. *S. optimus* Bates. 29. *S. sallei* Putzeys. 30. *H. arenaria* Darlington.

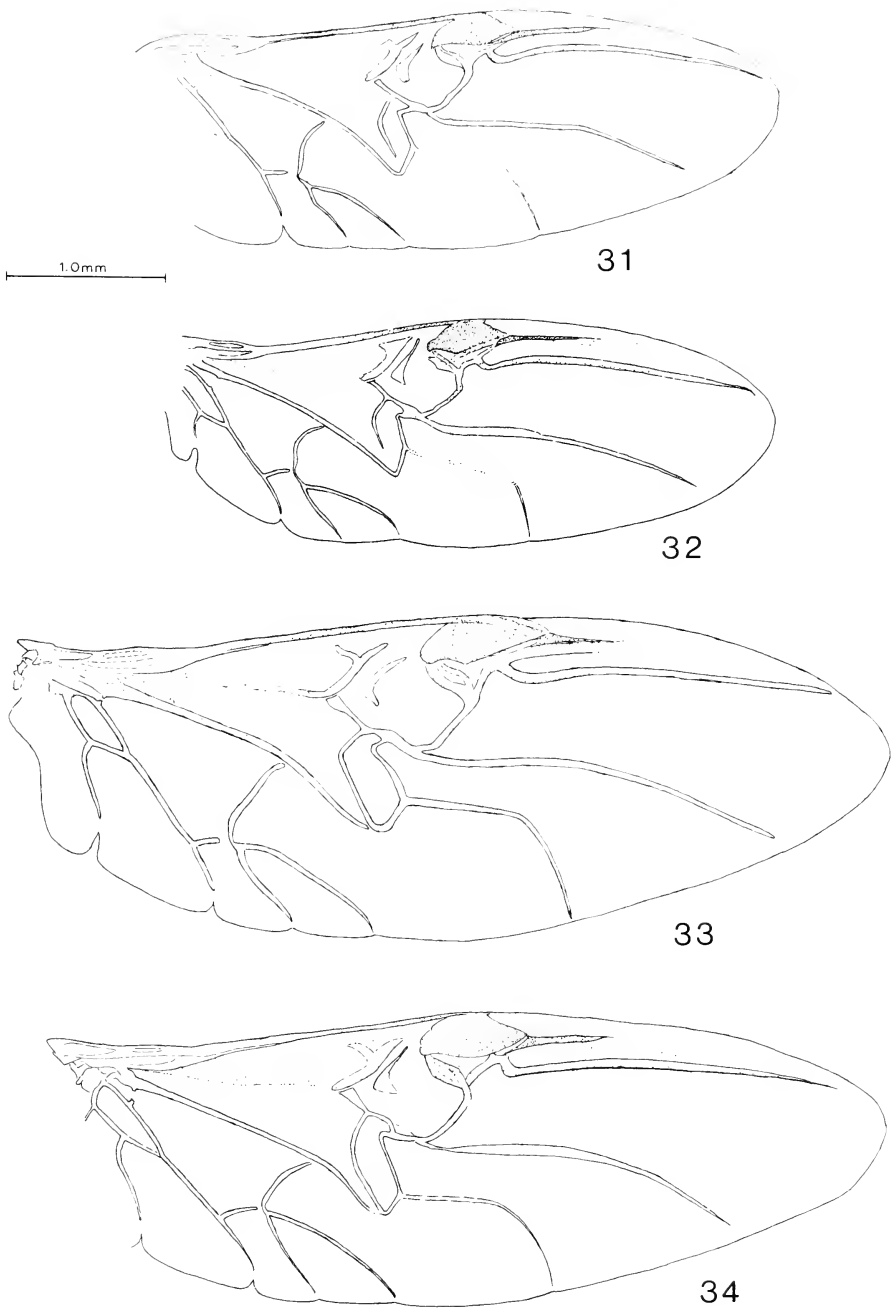


Fig. 31-34. Hind wing. 31. *S. crenulatus* LeConte. 32. *S. tenuis* Bates. 33. *S. optimus* Bates. 34. *S. sallei* Putzeys.

or inner facets enlarged. Antennal articles five to ten square to slightly elongate, moniliform; pedicel unisetose; articles three to eleven pubescent. Mandibles (Fig. 5) stout. Mentum (Fig. 17-18) deeply emarginate at middle; median tooth either small and sharp or obsolete; antero-lateral angles of lateral lobes either broadly rounded or acutely produced; anterior paramedian setae close together. Submentum without accessory setae. Gula narrow, its narrowest part 0.15-0.20 width of mentum.

Thorax. Pronotum in most species slightly transverse (LP/WP, 0.91-1.01); paramedian sulci well developed; paralateral sulci present or absent; lateral grooves not bordered by distinct carinae; accessory marginal setae absent; hind angles reduced or nearly obsolete. Prothoracic pleuron impunctate.

Elytra. Lateral channel broad and deep at apex, with one to three or four large pits near apex above umbilicate series (Fig. 22). Disc with two to four setae on interval three, zero to two basally on interval five, and none on interval seven. Interval eight strongly carinate, especially near apex; interval seven carinate at least in basal half; intervals two to seven subequal in width, convex, sharply carinate at extreme apices or not; interval eight joined by combined apices of intervals five and seven or not; interval seven normally joined by apex of interval five and either ended before apex of interval three or joined to it. Striae deeply engraved and, particularly near base of elytron, coarsely punctate.

Hind wings. Fully developed and probably functional in all species. Venation, Fig. 31-32.

Legs. Front and middle tarsi at most slightly more dilated and densely pubescent ventrally in male than in female; hind tarsus narrow, moderately elongate (Ta/Ti, 0.59-0.75); article one of hind tarsus 2.0-2.5 times as long as article two. Paronychia conspicuous, about as long as tarsal claws. Front tibia narrowed evenly to base where much narrower than at level of subapical spur; distal tooth nearly straight, stout, and blunt; apical and subapical spurs subequal, slender and acute; posterior ventral margin with three setae proximad to spur.

Abdomen. Sternum seven with paired paramedian ambulatory setae in both sexes. Paramedian carinae of sternum three not rounded at apices. Margin of pygidium entire in both sexes.

Male genitalia. Median lobe arcuate, symmetric. Endophallus without distinct basal collar spines; membrane around virga reduced; basal stylets various, useful in species recognition.

Female ovipositor. Number and position of setae variable, of no value in species recognition (Fig. 27).

Etymology. – *Genioschizus* is an anagram of *Schizogenius,* and bears the same meaning: Greek, *genio* = mentum; *schizo* = split.

Distribution. – Members of this subgenus range from southern Arizona and New Mexico in the north, southward at least to northern Argentina and Brazil. None are known from the West Indies. I examined 326 specimens of this subgenus.

Taxonomic notes. – Members of this subgenus are here placed in three quite easily distinguished and apparently natural groups, but some species are difficult to distinguish. The *crenulatus* group contains one polytypic species found from southwestern United States to Honduras. The *quinquesulcatus* group, known only from South America, includes three recognized species. The *tenuis* group includes one species distributed from Mexico to Colombia, one species endemic to southern Mexico, and three additional species described from Colombia. Six additional specimens of the *tenuis* group from Argentina, Bolivia, Brazil, and Peru probably represent at least two undescribed species, but I defer formal treatment until more material is available for study. I tentatively assign to the *tenuis* group a species described from Brazil, *S. maculatus* Kult, but I have seen neither the type nor any other specimens which match its description.

Key to described species groups, species, and subspecies of the subgenus *Genioschizus*

1. Pronotum with two pairs of paramedian longitudinal sulci 2
1' Pronotum with one pair of paramedian longitudinal sulci (*tenuis* group) 6
2.(1). Lateral lobes of mentum truncate, broadly rounded in front; median tooth of mentum obsolete. North and Middle America (*crenulatus* group) 3
2' Lateral lobes of mentum angulate, acutely produced; median tooth of mentum sharp, prominent. South America (*quinquesulcatus* group) 4
3.(2). Abdominal sterna without coarse lateral microsculpture; base of interval five normally asetose. Arizona and California to Sinaloa and Nayarit . . . . . *S. crenulatus crenulatus* LeConte, p. 150
3' Abdominal sterna with coarse lateral microsculpture; base of interval five normally with one or two setae. Jalisco to Honduras . . . . . *S. crenulatus chiapatecus* new subspecies, p. 152
4.(2'). Elytra uniformly dark. Brazil, Ecuador . . . . . *S. quinquesulcatus* Putzeys, p. 153
4' Elytra pale, with dark sutural macula 5
5.(4'). Sides of pronotum broadly rounded (Fig. 37). Colombia, Argentina . . . . . *S. szekessyi* Kult, p. 155
5' Sides of pronotum not strongly rounded (Fig. 38). Brazil . . . . . *S. janae* Kult, p. 155
6.(1'). Base of interval five asetose; elytra with sutural macula. Brazil . . . . . *S. maculatus* Kult, p. 165
6' Base of interval five with one seta. Colombia and northward (specimens from south of Colombia not keyed) 7
7.(6'). Interval six of elytron conspicuously narrowed and carinate in apical third; abdominal sterna normally with coarse lateral microsculpture. Chiapas and Tabasco. . . . . *S. sculptilis* new species, p. 156
7' Interval six of elytron not narrowed in apical third, finely carinate only at extreme apex if at all; abdominal sterna four to six usually without continuous, coarse lateral microsculpture 8
8.(7'). Median longitudinal sulcus of frons not narrowed toward apex; median lobe of male genitalia with apex sharply deflexed (Fig. 53). Colombia . . . . . *S. impressicollis* Putzeys, p. 161
8' Median longitudinal sulcus of frons narrowed toward apex; median lobe of male genitalia with apex not sharply deflexed 9
9.(8'). Head with neck nearly or quite impunctate along midline. Colombia . . . . . *S. impuncticollis* new species, p. 161
9' Head with neck distinctly punctate along midline 10
10.(9'). Disc of elytron with distinct sutural macula. Colombia . . . . . *S. suturalis* new species, p. 162
10' Disc of elytron without sutural macula; eyes with inner facets larger than outer facets. Mexico to Colombia . . . . . *S. tenuis* Bates, p. 158

The *crenulatus* group

Diagnostic combination. – Clypeal carinae strongly arcuate; mentum with median tooth obsolete, lateral lobes truncate; pronotum with short but evident paralateral longitudinal sulci; elytron with three or four conspicuous pits near apex of lateral channel; interval five with or without basal setae; intervals two to seven not carinate apically; interval eight free

to apex; and parameres normally uni- or bisetose.

The mentum, with lateral lobes truncate, is diagnostic within the genus. Members of this group differ from other North and Middle American members of the subgenus by ecarinate apices of elytral intervals two to seven.

Distribution. – This group includes one species, *S. crenulatus* LeConte, with two subspecies distributed from extreme southwestern United States to Honduras. Other groups of the subgenus have more tropical distributions, though one species of the *tenuis* group ranges nearly as far northward. I studied 64 specimens of the *crenulatus* group.

Schizogenius crenulatus LeConte

Diagnostic combination. – Specimens of *S. crenulatus* differ from other *Schizogenius* by truncate mentum lateral lobes. I recognize two subspecies, distinguished by extent of microsculpture on abdominal sterna.

Schizogenius crenulatus crenulatus new combination

Schizogenius crenulatus LeConte 1852:197. *Type locality* "California," here restricted to the Colorado River opposite Yuma, Yuma County, Arizona; type in MCZ, specimen labelled MCZ 5480 here designated lectotype (!). LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:223. LeConte 1879:34. Lindroth 1961:165.

Diagnostic combination. – From specimens of the other subspecies, specimens of this form are distinguished by reduced microsculpture on sides of abdominal sterna. Also, most are paler, and most lack basal setae on elytral interval five.

Description. – Color rufopiceous, legs paler, palpi, antennae, and tarsi testaceous; without strong aeneous luster, elytra not sellate or maculate.

Integument. Fine but conspicuous microsculpture on genae, gula, mouthparts, front tibiae and apical half of anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two thirds, and in coxal depressions of sternum three; paramedian frontal sulci obscurely microsculptured.

Head. Fig. 35. Eyes prominent, subglobose, coarsely and uniformly faceted. Neck densely and coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum (Fig. 17) lateral lobes truncate, median tooth obsolete. Antennae short, moniliform, article five 1.0-1.1 times as long as wide.

Pronotum. Fig. 35. Paramedian sulci faintly punctate, shallow apically, deep and broadly hooked basally, basal tips abruptly limited; paralateral sulci usually deep, coarsely punctate, no more than half length of paramedian sulci; anterior transverse impression finely to coarsely punctate; base transversely rugose.

Elytra. Three discal setigerous punctures on interval three adjacent to second stria; interval five asetose or in some specimens with one basal seta. Intervals one to six convex; interval seven carinate in basal two-thirds; interval eight carinate throughout, sharply so in apical third. Interval eight fused with interval one at apex, otherwise free; intervals three and five joined to apex of interval seven in most specimens. Lateral channel with three or four large pits near apex.

Male genitalia. Median lobe (Fig. 44) variable, some specimens as in *chiapatecus* (Fig. 45), apical portion suddenly deflexed; basal stylets, Fig. 58-59; virga (Fig. 57) without distinguishing spines or scales. Seven specimens studied.

Measurements and proportions. See Table 1.

Table 1. Descriptive statistics for *S. crenulatus*, based on 28 specimens of undetermined sex from Arizona and California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.52-4.25	3.962	0.272	0.068	4.57
LE	2.16-2.60	2.426	0.172	0.043	4.47
WH	0.69-0.83	0.776	0.048	0.012	4.08
WP	0.94-1.16	1.075	0.081	0.021	5.05
WE	1.10-1.35	1.246	0.089	0.022	4.74
B. Proportions.					
WF/WH	0.54-0.59	0.569	0.023	0.006	2.78
LP/WP	0.94-1.01	0.975	0.025	0.006	1.70
DP/LP	0.80-0.86	0.831	0.025	0.006	2.00
LP/WE	0.81-0.87	0.842	0.022	0.006	1.73
Ta/Ti	0.63-0.73	0.691	0.038	0.010	3.69
PS/LP	0.62-0.69	0.651	0.025	0.006	2.55

Variation. – One specimen from Blythe, California, has a basal seta on interval five of left elytron, but in all other specimens interval five is asetose on both elytra. Paralateral pronotal sulci of some specimens are quite weakly impressed. Paramedian clypeal carinae of some specimens are short and widely separated at apices. There is no pronounced external sexual dimorphism, though some males are distinguished by slightly broader front tarsi. Among specimens studied, extremes in size were found in two females from Rio San Lorenzo in Sinaloa (LE, 1.89-2.61 mm). Variation in selected characteristics in specimens from the Colorado River drainage basin of Arizona and California is given in Table 1.

Etymology. – Latin, *crenulatus* = minutely toothed, in reference to the minutely toothed elytral apices.

Distribution. – Specimens of *S. crenulatus crenulatus* have been collected at low elevations in the lower reaches of the Colorado River and environs in southern California and Arizona, south to southern Sinaloa and northern Nayarit (Fig. 74). I studied 57 specimens from the following localities.

UNITED STATES

No locality (1; ANSP). ARIZONA (7; CAS, INHS, USNM): Gila Co., Salt River (2; ANSP, MCZ); Maricopa Co., Phoenix (1; CUNY); Pima Co. (1; USNM); Yuma Co. (10; CAS, USNM), Yuma (9; CAS, MCZ, USNM). CALIFORNIA: Riverside Co., Blythe (2; CAS).

MEXICO

NAYARIT: Jesus Maria (2; UCB). SINALOA: 30.6 mi. s. Culiacan (18; DRWh, UASM), 21 mi. e. Villa Union (2; CNC), 26 mi. ne. Villa Union 1000' (1; LBSC). SONORA: 7.2 mi. se. Alamos (1; GRNo).

Collecting notes. – The most recently collected specimens seen from the United States are from Blythe and Phoenix, taken in 1917. Perhaps, because of environmental changes resulting from manipulation of the Colorado River system, *S. crenulatus* may now be extinct or nearing extinction in the southwestern United States. All Mexican specimens, however, were collected more recently.

According to label data, adults of *S. crenulatus* are probably active throughout the year. Several specimens were taken at lights, so no doubt wings are functional. I have no field experience with adults of this subspecies, but suspect they normally live in sandy river banks rather than gravel bars. G. E. Ball, T. L. Erwin, and R. E. Leech collected 19 specimens near Culiacan, Sinaloa, under litter on moist sand along the Rio San Lorenzo.

Taxonomic notes. – I treat the old name *S. crenulatus* as a new combination, *S. crenulatus crenulatus,* because I recognize, as a new subspecies, *S. crenulatus chiapatecus*. Available specimens of the two forms are well distinguished morphologically, and hence I think that recognition of separate subspecies is well justified. Proximate localities of these allopatric forms are not greatly distant, but I can neither reject nor defend a proposition of reproductive isolation.

Schizogenius crenulatus chiapatecus new subspecies

Type material. – Holotype, female, labelled "MEXICO. Chiapas. 3.2 mi. n. Arriaga 400' Rte. 195 III.2.1966" and "George E. Ball, D. R. Whitehead collectors" (MCZ). Four females and one male from various localities in Chiapas, Guerrero, Jalisco, and Oaxaca are paratypes (FDAG, MCZ, UASM).

Diagnostic combination. – Sterna four to six with continuous microsculpture on each side. All specimens seen have one or two basal setigerous punctures on interval five on at least one elytron.

Description. – As in *S. crenulatus crenulatus* except as follows. Color darker, most specimens with faint aeneous luster, strongest in Chiapas specimens; antennae, maxillae, labial palpi, and tarsi dark testaceous.

Integument. Conspicuous microsculpture on sternum two, sternum three except median field, sterna four to six at sides, and sternum seven along margin.

Pronotum. Anterior transverse impression more finely punctate; base of pronotum often more strongly rugose, basal tips of paramedian sulci not sharply limited.

Elytra. Interval five normally with one or two basal setae.

Male genitalia. Median lobe, Fig. 45; basal stylets, Fig. 60; virga as in *S. crenulatus crenulatus*. One specimen studied.

Measurements and proportions. Holotype: TL, 4.36 mm; LE, 2.72 mm; WH, 0.85 mm; WP, 1.14 mm; WE, 1.38 mm; WF/WH, 0.55; LP/WP, 0.98; DP/LP, 0.84; LP/WE, 0.81; Ta/Ti, 0.72; PS/LP, 0.67. Holotype plus paratypes: TL, 3.80-4.09-4.31 mm; LE, 2.35-2.54-2.67 mm; WH, 0.75-0.80-0.85 mm; WP, 1.02-1.11-1.18 mm; WE, 1.17-1.29-1.36 mm; WF/WH, 0.55-0.57-0.58; LP/WP, 0.94-0.96-0.98; DP/LP, 0.82-0.85-0.86; LP/WE, 0.81-0.82-0.84; Ta/Ti, 0.65-0.70-0.75; PS/LP, 0.63-0.68-0.70.

Variation. – Variations in numbers of discal setae on elytra include: absence of middle seta of interval three of left elytron in Chiapas paratype; absence of seta of interval five of left elytron in Oaxaca male; and presence of two setae near base of fifth interval on both elytra in Acapulco specimen. Otherwise I found no noteworthy variation.

Etymology. – The name *chiapatecus* is given in reference to the type locality, in Chiapas.

Distribution. – Seven specimens of *S. crenulatus chiapatecus* have been collected at low elevations from Jalisco south to Honduras (Fig. 74).

MEXICO

CHIAPAS: 3.2 mi. n. Arriaga (2; MCZ, UASM). GUERRERO: Acapulco (1; MCZ). JALISCO: Pitillal (1; UASM). OAXACA: Rio Jaltepec (2; FDAG).

HONDURAS

CORTES: La Lima (1; FDAG).

Collecting notes. – Specimens of this subspecies have been collected in January, March, May, June, and August. The Chiapas specimens were taken in coarse sand along a small stream. Other specimens were collected at lights, and probably arrived by flight.

Taxonomic notes. – Since the Chiapas locality is distant from the known range of *S. crenulatus crenulatus*, I chose one of the two females from there as holotype. I found no diagnostic characteristics in the male genitalia. *S. crenulatus chiapatecus* may be a biologically distinct species, but evidence from morphological characteristics reported here is inconclusive. That the possibility exists, however, is sufficient reason to distinguish this form taxonomically. As all known specimens of this subspecies are distinguishable from all known specimens of the other, the names refer to distinctive phena which may eventually prove to be reproductively isolated.

The *quinquesulcatus* group

Diagnostic combination. – Head with clypeal carinae straight to moderately arcuate; mentum with median tooth small and sharp, lateral lobes acutely produced at antero-lateral angles; pronotum with short but evident paralateral longitudinal sulci; elytron with at least two conspicuous pits near apex of lateral channel; interval five with basal seta; intervals two to seven finely carinate at extreme apices; interval eight free to apex; and parameres normally unisetose.

The acutely produced lateral lobes of the mentum and the deep paralateral sulci of the pronotum are, in combination, diagnostic of the group within the genus.

Distribution. – I here recognize three species, all closely related, from nearly throughout continental South America. I studied 20 specimens of the group from northern Colombia south to northern Argentina.

Schizogenius quinquesulcatus Putzeys

Schizogenius quinquesulcatus Putzeys 1863:26. *Type locality* "Amazone", Brazil; type female in IRSB (!). Putzeys 1866:232.

Schizogenius exaratus Putzeys 1863:27. *Type locality* Nova Friburgo, Brazil; type female in IRSB (!). Putzeys 1866:232, established synonymy.

Diagnostic combination. – Within the *quinquesulcatus* group, specimens of this species are distinguished by dark, non-sellate elytra.

Description. – Color dark piceous; femora rufous or infuscated, legs and antennae otherwise ferrugineous; palpi testaceous; elytra with slight aeneous luster, not sellate or maculate, apex pale or not.

Integument. Fine microsculpture on genae, gula, mouthparts, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, sides of sterna two to six, and apex of sternum seven; paramedian frontal sulci obscurely microsculptured.

Head. Fig. 36; paramedian clypeal carinae straight to arcuate, apices widely separated, median field triangular or hemicircular; inner paramedian frontal carinae nearly parallel. Eyes prominent, subglobose, coarsely and uniformly faceted. Neck densely, finely to coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum with lateral lobes acutely produced, median tooth conspicuous but short and sharp. Antennae short, moniliform, article eight 1.0-1.2 times as long as wide.

Pronotum. Fig. 36; sides broadly rounded; paralateral longitudinal sulci and anterior transverse impression punctate; base transversely rugose.

Elytra. Three discal setigerous punctures on interval three, near or adjacent to stria two; interval five with one seta near base. Striae deep and sharply engraved throughout, evidently punctate except near apex of elytron, coarsely punctate in basal half. Intervals one to six broad, convex, narrowed and finely carinate at apices; interval six not carinate basally; interval seven carinate throughout; interval eight carinate in apical half. Interval eight free to apex; intervals seven, five, and three joined at apices in most specimens. Lateral channel with two large conspicuous pits near apex.

Male genitalia. Median lobe, Fig. 46-47; basal stylets. Fig. 61-63; virga without distinguishing spines or scales. Three specimens studied.

Measurements and proportions. Ranges of variation in measurements and proportions among eight specimens studied are: TL, 3.24-3.95 mm; LE, 1.99-2.50 mm; WH, 0.65-0.76 mm; WP, 0.92-1.07 mm; WE, 1.00-1.28 mm; WF/WH, 0.57-0.62; LP/WP, 0.88-0.91; DP/LP, 0.84-0.91; LP/WE, 0.74-0.82; LE/WE, 1.94-1.99; Ta/Ti, 0.67-0.79; PS/LP, 0.64-0.73.

Variation. – The specimen from Ecuador differs from Brazilian specimens by more coarsely punctate neck, longer antennae, and shorter paramedian pronotal sulci, but is otherwise not distinctive. Paramedian clypeal carinae vary in form, but this variation is probably not taxonomically important since it forms no evident geographic pattern.

Etymology. – For *quinquesulcatus*, Latin, *quinque* = five, plus *sulcatus* = grooved, in reference to the five longitudinal grooves on the pronotum. For *exaratus*, Latin, *ex* = out, plus *aratus* = plow, in reference to the fossorial habitus.

Distribution. – I studied 14 specimens of this species from Atlantic and Pacific drainage systems from the following continental South American localities.

BRAZIL

"Amazones" (1; IRSB, Type of *quinquesulcatus*). CEARA: Fortaleza (1; IRSB). RIO DE JANEIRO: Nova Friburgo (1; IRSB, type of *exaratus*). SANTA CATARINA (2; IRSB): Nova Teutonia (6; DRWh, MCZ). SAO PAULO: Piracicaba (2; OSUC, UASM).

ECUADOR

EL ORO: 9 mi. s. Santa Rosa (1; CAS).

Collecting notes. – Specimens of this species have been collected in January, February, April, August, September, October, and November, and individuals may therefore be active throughout the year.

Taxonomic notes. – The names *quinquesulcatus* and *exaratus* were both originally proposed for unique specimens. The specimen listed here as type of *S. quinquesulcatus* is certainly so, but label data on the *S. exaratus* specimen ("S. exaratus. P," handwritten on green paper, and "Dup. 8/8 47 Bres.," handwritten on white paper) are equivocal. Neither specimen matches its original description in detail, but since Putzeys often erred in his descriptions I think this may be ignored. My reasons for suggesting that the *S. exaratus* specimen is indeed the type are the following. Putzeys gave no indication that the type was deposited elsewhere than in his collection, and no other specimen in IRSB can be the type. The specimen was collected well before the date of the original description, and thus was likely available to Putzeys since he corresponded with Dupont. Most important, the specimen is the only one labelled as *S. exaratus* in Putzeys' own hand, something he probably would not have done with subsequent material as his discovery of a third specimen of the species prompted him to synonymize the two names. Quite possibly the third specimen mentioned by Putzeys (1866) is the Ceará specimen.

I believe all of the Brazilian specimens are conspecific, despite variation in form of clypeal carinae. The Ecuadorian specimen may well not be conspecific, but I am unable to decide without additional material.

Schizogenius szekessyi Kult

Schizogenius szekessyi Kult 1950:144. *Type locality* Aracataca, Colombia; type in Budapest Museum, not studied.

Diagnostic combination. – From specimens of *S. janae*, the only other described member of the *quinquesulcatus* group having pale elytra with a dark sutural macula, specimens of this form are distinguished by broadly rounded pronotal sides.

Description. – As in *S. quinquesulcatus* except: body paler, rufopiceous; elytron rufotestaceous, with dark sutural macula extended outward to interval three or four; head and pronotum, Fig. 37, clypeal carinae straight and neck coarsely punctate in all specimens studied; male median lobe (Fig. 48) and basal stylets (Fig. 64-65) as illustrated; three specimens studied.

Measurements and proportions. Ranges of variation in measurements and proportions among five specimens studied are: TL, 3.52-3.78 mm; LE, 2.20-2.35 mm; WH, 0.65-0.79 mm; WP, 0.96-1.08 mm; WE, 1.14-1.24 mm; WF/WH, 0.55-0.58; LP/WP, 0.89-0.92; DP/LP, 0.85-0.87; LP/WE, 0.76-0.78; LE/WE, 1.90-2.00; Ta/Ti, 0.65-0.73; PS/LP, 0.63-0.73.

Variation – The specimen from Argentina differs from Colombian specimens by smaller sutural macula and relatively narrower elytra. This specimen has only two setae on interval three of the left elytron.

Etymology. – This species was named in honor of the Hungarian entomologist, Dr. W. Szekessy.

Distribution. – I assign the name *S. szekessyi* to four topotypic specimens from Colombia, and one specimen from Argentina.

ARGENTINA

SALTA: Oran (1; MCZ).

COLOMBIA

MAGDALENA: Aracataca (4; DRWh, MCZ).

Collecting notes. – Colombian specimens were collected from January to May, and the Argentinian specimen was taken in September; thus, individuals are probably active as adults throughout the year.

Taxonomic notes. – I have not studied type material of this species, but think there is no question of identity since topotypic material agrees with the original description. I see no reason to treat the specimen from Argentina as other than conspecific.

Schizogenius janae Kult

Schizogenius janae Kult 1950:145. *Type locality* Brazil; type in Kult Collection, not studied.

Diagnostic combination. – The sides of the pronotum are less broadly rounded in specimens of *S. janae* than in those of *S. szekessyi*, the only other member of the *quinquesulcatus* group having a sutural macula on the elytra; differences in form of median lobe of male genitalia may also be useful in species recognition.

Description. – As in *S. quinquesulcatus* except as follows. Color of body paler, rufopiceous; elytra rufotestaceous, each with a dark sutural macula extended outward to interval three or four. Head and pronotum, Fig. 38; pronotal sides weakly rounded, clypeal carinae straight, and neck coarsely punctate. Male median lobe (Fig. 49) and basal stylets (Fig. 66) as illustrated; one specimen studied.

Measurements and proportions. TL, 3.25 mm; LE, 2.00 mm; WH, 0.68 mm; WP, 0.92

mm; WE, 1.02 mm; WF/WH, 0.59; LP/WP, 0.91, DP/LP, 0.80; LP/WE, 0.82; LE/WE, 1.96; Ta/Ti, 0.68; PS/LP, 0.72.

Etymology. – This species was dedicated by Kult to his wife.

Distribution. – I studied one specimen of this species from Brazil.

BRAZIL

MATO GROSSO: Jacare (1; MGFT).

Collecting notes. – The Brazilian specimen reported here was collected in September.

Taxonomic notes. – I have not studied the type, but think this specimen represents *S. janae* because it agrees well with the original description and comes from a suitable locality. In particular, the specimen is smaller and paler than specimens of *S. szekessyi*, and the form of the pronotum is correct. Other characters given in the original description are unreliable.

I think it highly probable that the names *S. janae* and *S. szekessyi* are synonyms, despite differences illustrated for form of pronotum and male median lobe. More specimens are needed from throughout the range to determine extent of individual and geographic variation.

The *tenuis* group

Diagnostic combination. – Head with clypeal carinae normally arcuate; mentum with median tooth prominent, lateral lobes acutely produced; pronotum without paralateral sulci; elytron with one to three conspicuous subapical pits in lateral channel; interval five with or without basal seta; intervals two to seven carinate apically; interval eight free to apex or not; and parameres in most species bi- or trisetose.

The lack of paralateral longitudinal sulci from the pronotum is unique within the subgenus.

Distribution. – Specimens of this group have been collected from northern Mexico to northern Argentina. I here recognize one species known only from Mexico, another from Mexico to Colombia, and three others from Colombia. Six unplaced specimens from widely separated localities elsewhere in South America probably represent at least two additional, undescribed, species. I tentatively place as a member of this group a species described by Kult from Brazil, *S. maculatus*. I examined 244 specimens of the *tenuis* group.

Schizogenius sculptilis new species

Type material. – Holotype, male, and allotype, female, labelled "MEXICO. Chiapas San Quintin 700′ 91°20′-16°24′ stream margins II. 5-20. 1966" and "George E. Ball D. R. Whitehead collectors" (MCZ). Twenty additional specimens from two localities in Chiapas and Tabasco are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. – Most reliably distinguished from *S. tenuis* by narrowed, carinate apices of elytral interval six, and by characteristic form of basal stylets of median lobe. On most specimens, the abdomen is microsculptured laterally, while in most Middle American specimens of *S. tenuis* the abdomen lacks extensive microsculpture.

Description. – Color dark piceous, legs, palpi, and antennae paler; no definite aeneous luster; elytra not sellate or maculate, apices normally not pale.

Integument. As described for *S. tenuis* except on abdomen; sides of sterna four to six and margin of sternum seven strongly microsculptured in most specimens.

Head. Fig. 39. Generally as described for *S. tenuis*. Frontal carina one broad, carinae two to four narrow, carina five short but well developed. Inner facets of eyes much larger than marginal facets. Mentum with median tooth minute.

Pronotum. Fig. 39. Generally as described for *S. tenuis* except disc flatter, paramedian sulci longer, and anterior transverse impression coarsely punctate.

Elytra. Discal setae and striae as in *S. tenuis*. Intervals one to five broad, convex, carinate at extreme apices; interval six narrowed, carinate in apical third; interval seven carinate throughout; interval eight carinate in apical half. Apex of interval eight fused with interval one, nearly fused with interval two, otherwise free; intervals three, five, and seven in many specimens more or less fused at apex. Lateral channel with one small but conspicuous subapical pit.

Male genitalia. Median lobe (Fig. 50) arcuate, apical part not suddenly deflexed; basal stylets (Fig. 67) characteristic; virga without distinguishing spines or scales. Four specimens studied.

Measurements and proportions. See Table 2. Holotype: TL, 3.83 mm; LE, 2.30 mm; WH, 0.78 mm; WP, 1.08 mm; WE, 1.21 mm; WF/WH, 0.59; LP/WP, 0.96; DP/LP, 0.82; LP/WE, 0.86; Ta/Ti, 0.73; PS/LP, 0.71. Allotype: TL, 3.82 mm; LE, 2.30 mm; WH, 0.78 mm; WP, 1.11 mm; WE, 1.24 mm; WF/WH, 0.60; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.83; Ta/Ti, 0.63; PS/LP, 0.74.

Table 2. Descriptive statistics for *S. sculptilis*, based on 22 unsexed specimens from Chiapas and Tabasco.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.33-3.98	3.658	0.271	0.077	4.93
LE	1.94-2.44	2.210	0.184	0.052	5.56
WH	0.70-0.81	0.749	0.048	0.014	4.27
WP	0.93-1.12	1.036	0.078	0.022	5.02
WE	1.09-1.26	1.176	0.075	0.021	4.28
B. Proportions.					
WF/WH	0.57-0.63	0.592	0.028	0.008	3.15
LP/WP	0.91-0.99	0.945	0.027	0.008	1.91
DP/LP	0.80-0.89	0.830	0.037	0.011	3.00
LP/WE	0.81-0.86	0.834	0.021	0.006	1.67
Ta/Ti	0.59-0.73	0.666	0.053	0.015	5.32
PS/LP	0.68-0.74	0.715	0.029	0.008	2.67

Variation. – Two specimens from Chiapas and one from Tabasco have reduced abdominal microsculpture. Another Chiapas specimen has an extra seta on interval three of the left elytron, and one Tabasco specimen has pale elytral apices. Aside from slightly broader front tarsi in males, there is no evident secondary sexual differentiation.

Etymology. – Latin. *sculptilis* = carved, in reference to form of apices of elytral intervals.

Distribution. – Specimens of this species have been collected at two localities (Fig. 75) in lowland rain forests of Chiapas and Tabasco. I studied 22 specimens from the following localities.

MEXICO
CHIAPAS: San Quintin (20; BMNH, CAS, CNC, IRSB, MCZ, UASM, USNM).
TABASCO: 59.4 mi. se. Villahermosa (2; DRWh).

Collecting notes. – Adults of *S. sculptilis* are probably active throughout the year, since specimens were collected in February and June. No specimens were seen to fly, and none were taken at lights, but like other North and Middle American *Schizogenius*, adults of *S. sculptilis* probably are capable of flight. Among North and Middle American members of *Schizogenius*, habits of this species are unusual in that the preferred habitat is in sand, along shaded forest streams. Three specimens were taken under leaf litter on sand along the Rio Jatate, but all other San Quintín specimens were collected in deep forest in a sand-gravel substrate along stream margins. Specimens of *S. tenuis* also found at San Quintín were collected on sandy, sunlit shores of the Rios Jatate and Perlas.

Taxonomic notes. – In addition to characters mentioned in the diagnostic combination, specimens of *S. sculptilis* generally differ from specimens of *S. tenuis* by: uniformly dark elytra; second and eighth elytral intervals united at apex; and subapical pit in lateral channel smaller. Ecological and morphological differences, and sympatry at least in Chiapas, indicate reproductive isolation. *S. sculptilis* agrees with *S. tenuis*, and differs from other South American species, by having enlarged inner eye facets, a peculiarity suggesting possible close relationship with *S. tenuis*. But *S. tenuis* is otherwise more similar to other South American species, and I suspect the relationship between *S. sculptilis* and *S. tenuis* is remote.

Schizogenius tenuis Bates

Schizogenius tenuis Bates 1881:38. *Type locality* Paso Antonio, Guatemala; type in BMNH, specimen labelled as holotype here designated lectotype (!).

Diagnostic combination. – Specimens of this species differ from those of *S. sculptilis*, the only other member of the *tenuis* group known from Middle America, most conspicuously by differences in elytral structure: interval six not carinate except finely at extreme apex, and subapical pits of lateral channel larger. Also, the basal stylets of the median lobe are strikingly different. Specimens of *S. tenuis* differ from other South American specimens of the group seen by me by the combination of: neck punctate medially; elytra not sellate or maculate; and eyes in most specimens with inner facets enlarged.

Description. – Color dark piceous, legs, palpi, antennae, and in most specimens elytral apices paler; elytra with slight aeneous luster, not sellate.

Integument. Fine but conspicuous microsculpture on paramedian sulci of frons, genae, gula, mouthparts, sides and base of pronotum, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, and coxal depressions of sternum three. Abdomen without extensive microsculpture on sides of sterna four to six or margin of sternum seven.

Head. Fig. 40. Clypeus with apices of paramedian carinae fused to form an arc, or nearly so; median field hemicircular, width at base more than 2.0 apical width of median field of frons. Frons with median longitudinal sulcus narrowed in front. Eyes prominent, subglobose, coarsely faceted, inner facets usually larger than marginal facets. Neck densely and coarsely punctate. Genae strongly punctate, finely rugose in front. Mentum (Fig. 18) with lateral

lobes acutely produced, median tooth conspicuous but short and sharp. Antennae short, moniliform, article five 1.0-1.1 times as long as wide.

Pronotum. Fig. 40. Disc convex, slightly transverse, greatest width near middle; paramedian sulci short, faintly punctate, deep and abrupt apically, deep and broadly hooked basally, basal tips normally confused laterad with basal rugosity; paralateral sulci absent; anterior transverse impression impunctate to finely punctate.

Elytra. Three discal setigerous punctures on interval three, first adjacent to second stria, others in middle of interval; interval five with one seta at base. Intervals one to six broad, convex, carinate at most at extreme apices, interval six not carinate basad of posterior discal seta; interval seven carinate throughout; interval eight carinate in apical half. Apex of interval eight often fused with apices of intervals three, five, and seven, as well as with interval one. Lateral channel with at least one large subapical pit, some specimens with one or more additional smaller pits, or with two or three large pits.

Male genitalia. Median lobe (Fig. 51) arcuate, apical part not suddenly deflexed; basal stylets, Fig. 68; endophallus without distinguishing spines or scales on virga. Thirteen specimens studied.

Measurements and proportions. See Table 3.

Table 3. Descriptive statistics for *S. tenuis*, based on 22 unsexed specimens from San Quintín, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.38-3.98	3.645	0.263	0.075	4.82
LE	2.09-2.49	2.255	0.169	0.048	5.00
WH	0.68-0.92	0.747	0.055	0.016	4.89
WP	0.88-1.05	0.957	0.072	0.021	5.05
WE	1.04-1.25	1.135	0.084	0.024	4.93
B. Proportions.					
WF/WH	0.49-0.57	0.544	0.031	0.009	3.78
LP/WP	0.95-1.00	0.968	0.015	0.004	1.06
DP/LP	0.80-0.87	0.828	0.032	0.009	2.58
LP/WE	0.79-0.85	0.818	0.027	0.008	2.16
Ta/Ti	0.60-0.75	0.675	0.070	0.020	6.87
PS/LP	0.62-0.68	0.655	0.027	0.008	2.73

Variation. – I found no important geographic variation in size or body proportions, and because of paucity of material did no statistical analysis of variation. The smallest specimen studied (LE, 1.86 mm) is from Paso Antonio, Guatemala, and the largest (LE, 2.50 mm) is from Villahermosa, Tabasco. Variation in discal setae on elytra includes reduction, with the middle seta of interval three lacking from both elytra in one specimen from San Luis Potosí, and addition, with four setae on interval three of one or both elytra in several specimens. All specimens have at least one large subapical pit in the lateral channel of the elytron.

Many have one or more additional, but much smaller, pits as well. Small specimens, especially from the Paso Antonio and El Coyul samples, tend to have unusually large secondary pits, and a strongly marked tendency for the apices of elytral intervals three, five, and seven to converge on interval eight. I think these differences lack geographic significance. In some Colombian specimens, and less noticeably in some Costa Rican specimens, the inner eye facets are not as distinctly enlarged as in specimens from more northern areas, but the transition is gradual.

Etymology. – Latin, *tenuis* = thin, in reference to body form.

Distribution. – The known distribution of *S. tenuis* (Fig. 76) extends from northern Mexico to Colombia, from low elevations to as high as 4000′ in Puebla. I studied 203 specimens from the following localities.

MEXICO

CHIAPAS: San Quintin (23; UASM). DURANGO: Ventanas (1; BMNH). JALISCO: 18 km. n. Puerto Vallarta (25; UASM). NAYARIT: Acaponeta (1; CAS), Jesus Maria (5; UCB), Rio Santiago Ferry (2; CAS), 5 mi. s. Rio Santiago Ferry (4; CAS). OAXACA: 17.7 mi. w. El Camaron (2; DRWh), 29.4 mi. e. El Coyul (3; AMNH, CNC), 11.1 mi. n. Matias Romero (34; MGFT, UASM), Valle Nacional (5; UASM). PUEBLA: Tepexco (7; UASM). SAN LUIS POTOSI: Tamazunchale (3; CNHM, DRWh). SINALOA: 30.6 mi. s. Culiacan (2; IRSB). SONORA: 10 mi. w. Alamos (1; AMNH). TABASCO: Teapa (3; BMNH), Villahermosa (2; MCZ). VERACRUZ: 20 mi. nw. Huatusco (1; FDAG).

GUATEMALA

ESCUINTLA: Paso Antonio (2; BMNH). IZABAL: Los Amates (2; MCZ).

HONDURAS

CORTES: La Lima (24; FDAG).

COSTA RICA

GUANACASTE: Las Canas (2; UASM). LIMON: Los Diamantes (18; FDAG), Reventazon (9; USNM). PUNTARENAS: Palmar Sur (2; UAFA).

PANAMA

CANAL ZONE: San Pablo (1; USNM). CHIRIQUI: Tole (6; IRSB, MCZ).

COLOMBIA

MAGDALENA: Aracataca (2; MCZ), Rio Frio (10; MCZ). TOLIMA: Coyaima (1; CAS).

Collecting notes. – I have seen specimens of *S. tenuis* collected nearly throughout the year, except during the latter part of the dry season from early April to mid-June. Numerous specimens were taken at black lights, which probably indicates flight.

I collected numbers of this species only at Matias Romero and San Quintín. Specimens of several species were collected along the Rio Malatengo in gravel bars, but the *S. tenuis* were found alone, in sand. All but three of the San Quintín specimens were found along the Rio Jatate in sandy banks; the others were collected on the Rio Perlas a short distance away, perhaps also in sand. One specimen from Tamazunchale, two from Culiacan, and three from El Coyul were also taken in silt or fine sand; other specimens were hand collected by G. E. Ball or me at El Camaron and Valle Nacional, but whether in sand or not is unrecorded. *S. tenuis* thus probably agrees with other species of the subgenus by living in a sandy habitat, but, unlike those of *S. sculptilis*, specimens are more likely to be found along open rivers.

Taxonomic notes. – Mexico, this species is sympatric with both *S. crenulatus*, at Jesus Maria and Culiacan, and *S. sculptilis*, at San Quintín. In Colombia, it is sympatric with at least two other members of the *tenuis* group; specimens of *S. tenuis*, *S. impuncticollis*, and *S. suturalis* were taken at Aracataca by P. J. Darlington.

Possibly related but probably distinct are a female from Tucuman, Argentina (JNeg), a male (Fig. 52, 69) from Santa Isabel do Araguaia, Brazil (CAS), and a specimen of unde-

termined sex from Tabilas, Salta, Argentina (CAS). In addition to differences in male genitalia as illustrated, eyes are uniformly faceted, and elytral apices are pale in sharp contrast to the rest of the elytron.

Schizogenius impressicollis Putzeys

Schizogenius impressicollis Putzeys 1846:653. *Type locality* Colombia; lectotype here designated, male in the Institut Royal des Sciences Naturelles de Belgique, so labelled (!). Putzeys 1863:24. Putzeys 1866:223.

Diagnostic combination. – Within the *tenuis* group, basal stylets (Fig. 70), form of median lobe (Fig. 53), and form of median frontal sulcus (Fig. 41), of the lectotype are distinctive. Also, lateral lobes of male genitalia are broad and trisetose apically, rather than bisetose as in other members of the group. The elytra probably are not sellate, the eyes are uniformly faceted, and the neck is sparsely punctate along the midline. Since I examined only one old, discolored specimen, I prefer not to give a detailed description.

Distribution. – The specific locality at which the type specimens were collected in Colombia is unknown, and I have seen no additional specimens.

Etymology. – Latin, *impressus* = impressed, plus *collum* = neck in reference to the sulcate pronotum.

Taxonomic notes. – In the original description of this species, Putzeys wrongly stated it to have three or four setae on intervals three, five, and seven; this was an error he repeated in several other species descriptions.

Schizogenius impuncticollis new species

Type material. – Holotype, male, labelled "Aracataca, Mgd. Colombia III 2 29 Darlington" (MCZ). Allotype female, label data same as in holotype except III 3 29 (MCZ). Two additional specimens from the same locality are paratypes (MCZ).

Diagnostic combination. – Specimens of this species are readily distinguished from other members of the *tenuis* group by combination of: neck nearly or quite impunctate along midline; basal transverse impression of pronotum greatly deepened; body strongly aeneous or metallic; and elytral apices contrastingly pale.

Description. – Color rufopiceous, strong aeneous or metallic green luster; front femora rufous; antennae, palpi, elytral apices, and legs except front femora testaceous.

Integument as described for *S. tenuis.*

Head and pronotum. Fig. 42. Generally as described for *S. tenuis,* except eyes uniformly faceted, neck not or hardly punctate along midline, anterior transverse impression strongly punctate, and basal transverse impression unusually deep.

Elytra. As in *S. tenuis* except more strongly bicolored.

Male genitalia. Median lobe, Fig. 54; basal stylets, Fig. 71; virga without distinguishing spines or scales. Three specimens studied.

Measurements and proportions. Holotype: TL, 3.35 mm; LE, 2.05 mm; WH, 0.69 mm; WP, 0.90 mm; WE, 1.09 mm; WF/WH, 0.62; LP/WP, 0.98; DP/LP, 0.77; LP/WE, 0.81; Ta/Ti, 0.70; PS/LP, 0.69. Holotype plus paratypes: TL, 3.23-3.36-3.49 mm; LE. 1.99-2.06-2.15 mm; WH, 0.65-0.68-0.70 mm; WP, 0.88-0.90-0.92 mm; WE, 1.05-1.10-1.16 mm; WF/WH, 0.59-0.60-0.62; LP/WP, 0.93-0.96-0.98; DP/LP, 0.77-0.79-0.82; LP/WE, 0.76-0.78-0.81; Ta/Ti, 0.66-0.70-0.72; PS/LP, 0.67-0.68-0.70.

Etymology. – Latin, *im* = not, plus *punctus* = punctate, plus *collum* = neck, in allusion to one diagnostic characteristic of specimens of this species, lack of punctures along midline

of neck.

Distribution. – Only the type specimens from Aracataca, in northern Colombia, are known.

Collecting notes. – Specimens of this species were collected in March. As wings are fully developed, adults probably can fly.

Taxonomic notes. – The range of this species overlaps that of at least *S. tenuis* and *S. suturalis* among other members of the *tenuis* group. Also, specimens of this species differ sufficiently from those of other described members of the group that they undoubtedly represent a distinct species.

A female from Yoay, Bolivia (CAS), a male from Yurac, Peru (CAS), and an unsexed specimen from El Cidral, Bolivia (MCZ) agree with the Colombian specimens in having the neck impunctate. These specimens are much less strongly metallic and have less strongly bicolored elytra, and the basal transverse impression of the pronotum is shallower. The female (LE, 2.43 mm) is markedly larger than specimens from Colombia, and the male differs in form of median lobe (Fig. 55) and basal stylets (Fig. 72). For these reasons I doubt that these specimens represent *S. impuncticollis.* Final judgment as to their relationships must await study of additional material.

Schizogenius suturalis new species

Type material. – Holotype, male, and allotype, female, labelled "Aracataca, Mgd. Colombia III 2 29 Darlington" (MCZ). Five additional specimens from the same locality are paratypes (DRWh, MCZ, UASM).

Diagnostic combination. – Specimens of this species differ from others in the *tenuis* group by having, in combination, sellate elytra and one seta near base of interval five.

Description. – Color rufopiceous, with strong aeneous or metallic green luster; front femora rufous; elytra rufotestaceous, central macula aeneopiceous; antennae, palpi, and legs except front femora testaceous.

Integument. As described for *S. tenuis.*

Head and pronotum. Fig. 43. Generally as described for *S. tenuis* except eyes uniformly faceted.

Elytra. Except for coloration, as described for *S. tenuis.*

Male genitalia. Median lobe, Fig. 56; basal stylets, Fig. 73; virga without distinguishing spines or scales. Two specimens studied.

Measurements and proportions. Holotype: TL, 3.56 mm; LE, 2.18 mm; WH, 0.70 mm; WP, 0.94 mm; WE, 1.15 mm; WF/WH, 0.57; LP/WP, 0.97; DP/LP, 0.81; LP/WE, 0.79; Ta/Ti, 0.62; PS/LP, 0.60. Holotype plus paratypes: TL, 3.19-3.58-3.77 mm; LE, 1.96-2.21-2.35 mm; WH, 0.65-0.70-0.75 mm; WP, 0.83-0.95-1.02 mm; WE, 1.01-1.15-1.23 mm; WF/WH, 0.55-0.57-0.61; LP/WP, 0.94-0.95-0.97; DP/LP, 0.81-0.82-0.84; LP/WE, 0.77-0.79-0.81; Ta/Ti, 0.62-0.67-0.71; PS/LP, 0.57-0.62-0.66.

Variation. – One paratype has an extra seta on left margin of pronotum, and another has four setae on interval three of right elytron.

Etymology. – Latin, *sutura* = seam, in reference to sutural macula.

Distribution. – The only known specimens are from Aracataca, in northern Colombia.

Collecting notes. – Specimens of this species were collected in March and May. Wings are fully developed, so individuals probably fly.

Taxonomic notes. – *S. suturalis, S. tenuis,* and *S. impuncticollis* are sympatric in Colombia, so are undoubtedly specifically distinct. The only other described species included in the *tenuis* group which has the sutural macula is *S. maculatus* Kult. If that species really

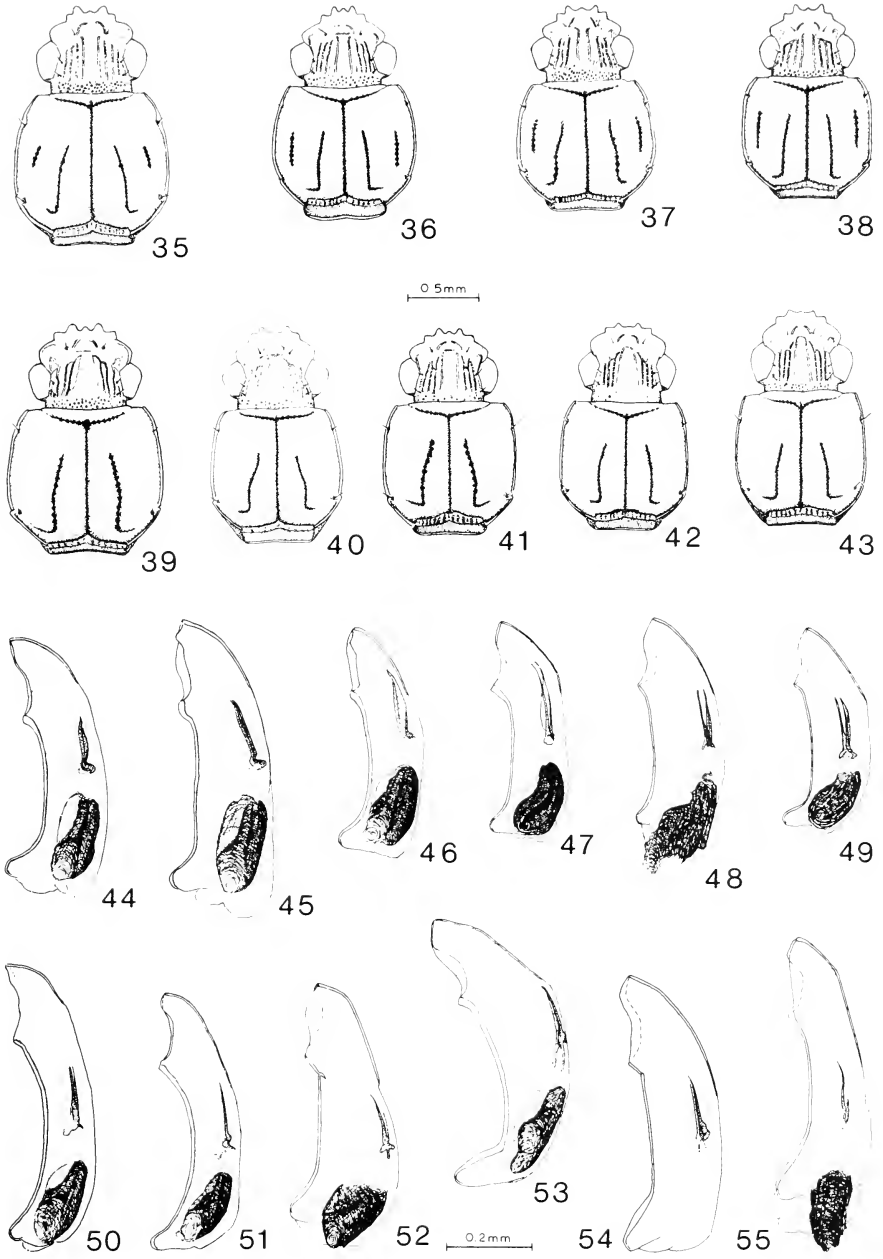


Fig. 35-43. Head and pronotum, dorsal aspect. 35. *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. 36. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 37. *S. szekessyi* Kult, Aracataca, Columbia. 38. *S. janae* Kult, Jacare, Brazil. 39. *S. sculptilis* new species, San Quintin, Chiapas. 40. *S. tenuis* Bates, Matias Romero, Oaxaca. 41. *S. impressicollis* Putzeys, Columbia. 42. *S. impuncticollis* new species, Aracataca, Columbia. 43. *S. suturalis* new species, Aracataca, Columbia. Fig. 44-55. Male median lobe, lateral aspect. 44. *S. crenulatus crenulatus* LeConte, Yuma, Arizona. 45. *S. crenulatus chiapatecus* new subspecies, Rio Jaltepec, Oaxaca. 46. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 47. Same, Santa Rosa, Ecuador. 48. *S. szekessyi* Kult, Aracataca, Columbia. 49. *S. janae* Kult, Jacare, Brazil. 50. *S. sculptilis* new species, San Quintin, Chiapas. 51. *S. tenuis* Bates, Rio Santiago, Nayarit. 52. *S.* nr. *tenuis* Bates, Santa Isabel, Brazil. 53. ***S. impressicollis*** Putzeys, Colombia. 54. *S. impuncticollis* new species, Aracataca, Colombia. 55. *S.* nr. *impuncticollis* new species, Yurac, Peru.

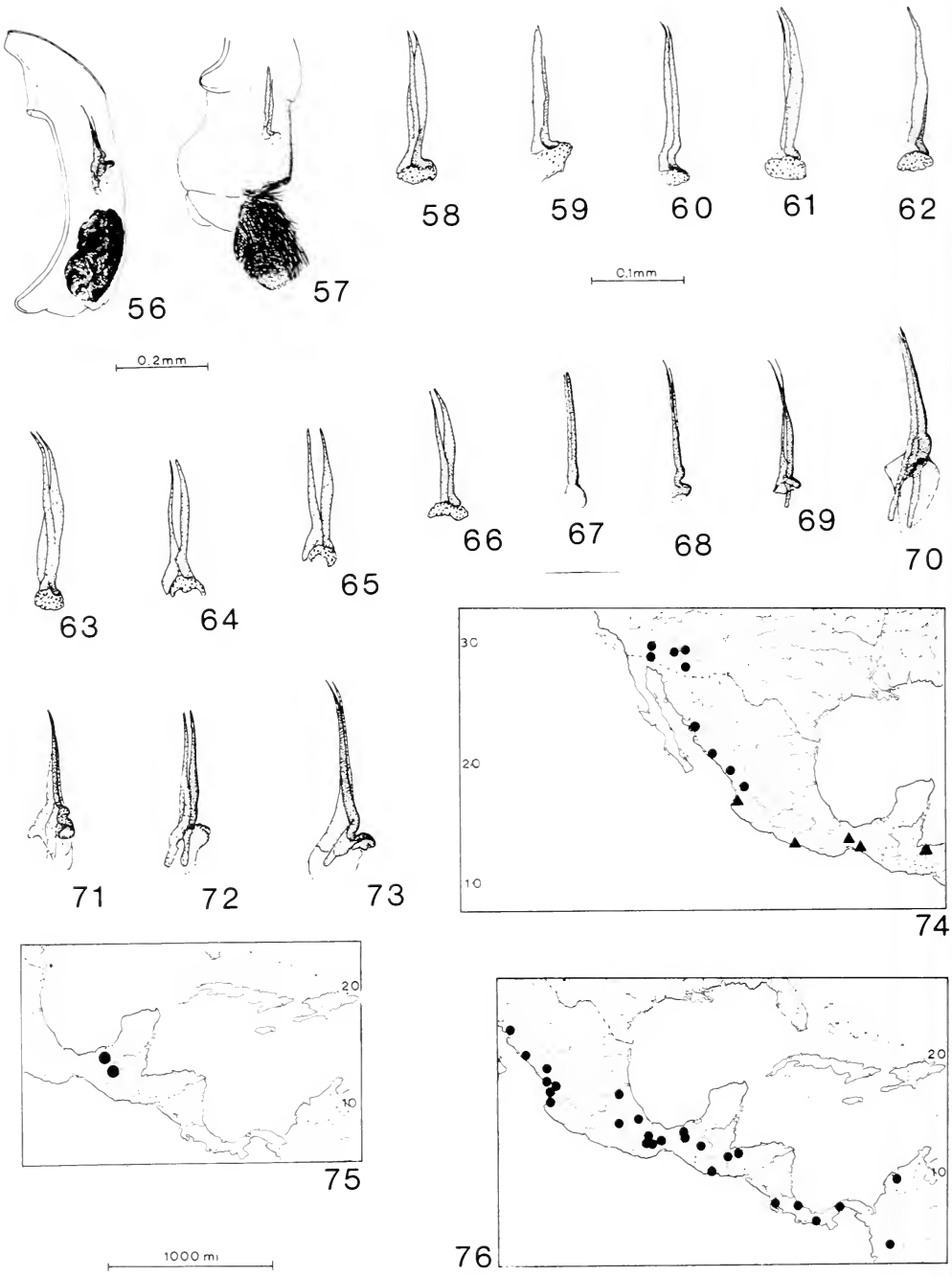


Fig. 56. Male median lobe, lateral aspect, *S. suturalis* new species, Aracataca, Colombia. Fig. 57. Male endophallus, *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. Fig. 58-73. Basal stylets of male endophallus. 58, 59. *S. crenulatus crenulatus* LeConte, Culiacan, Sinaloa. 60. *S. crenulatus chiapatecus* new subspecies, Rio Jaltepec, Oaxaca. 61, 62. *S. quinquesulcatus* Putzeys, Nova Teutonia, Brazil. 63. Same, Santa Rosa, Ecuador. 64, 65. *S. szekessyi* Kult, Aracataca, Colombia. 66. *S. janae* Kult, Jacare, Brazil. 67. *S. sculptilis* new species, San Quintin, Chiapas. 68. *S. tenuis* Bates, Rio Santiago, Nayarit. 69. *S.* nr. *tenuis* Bates, Santa Isabel, Brazil. 70. *S. impressicollis* Putzeys, Colombia. 71. *S. impuncticollis* new species, Aracataca, Columbia. **72.** *S.* nr. *impuncticollis* new species, Yurac, Peru. **73.** *S. suturalis* new species, Aracataca, Colombia. Fig. 74-76. Known distributions. 74. *S. crenulatus crenulatus* LeConte, circles, and *S. crenulatus chiapatecus* new subspecies, triangles. 75. *S. sculptilis* new species. 76. *S. tenuis* Bates.

belongs in the group, and if the original description is correct, then it differs from *S. suturalis* by not having a basal seta on interval five.

Schizogenius maculatus Kult

Schizogenius maculatus Kult 1950: 143. *Type locality* Para, Amazonas, Brazil; type in Kult collection, present location not known, not seen by me.

Diagnostic combination. – Assuming the original description is correct, and if this species really is a member of the *tenuis* group, specimens of it should be readily recognized by not having a basal seta on elytral interval five. The only other described species in the group having a dark sutural macula is *S. suturalis,* which may differ further by having the striae coarsely punctate basally.

Taxonomic notes. – Since I have not studied specimens which I could identify with this name, I am unable to give further data on *S. maculatus.* My allocation to the *tenuis* group, and indeed to the subgenus *Genioschizus,* is tentative, since critical subgeneric characteristics were not mentioned in Kult's description. However, the only small species of *Schizogenius* with a sutural macula, reduced elytral setation, and moniliform antennae known to me are *Genioschizus,* and absence of paralateral pronotal sulci indicates placement in the *tenuis* group. Absence of basal setae from interval five of the elytron is not otherwise known in this group, but is characteristic of *S. crenulatus crenulatus* in the *crenulatus* group. I do not suspect Kult misinterpreted this characteristic, since he correctly described it in *S. szekessyi* and *S. janae*. The names *S. maculatus* and *S. suturalis* may be synonymous, but the information available to me indicates otherwise.

Subgenus *Schizogenius sensu stricto*

Type species. – *Schizogenius strigicollis* Putzeys 1846:650, subsequent designation by Lindroth, 1961: 164.

Diagnostic combination. – Lateral channel of elytron not flared near apex, without deep subapical pits; and females, except of *S. pluripunctatus*, and species of *basalis* group, normally without paramedian ambulatory setae on sternum seven. Also: paramedian clypeal carinae tuberculate or not; antennae moniliform to filiform; front tarsi markedly dilated in many species, more strongly so in males than females; male endophallus of many species with well developed basal collar spines; paralateral longitudinal sulci not present on pronotum; clypeal suture obsolete to sharply engraved; and pygidium serrate or crenulate in females of many species.

Description. – Size variable, LE 1.65-3.70 mm in North and Middle America, up to 5.00 mm in South America. Body cylindrical to strongly depressed. Color testaceous or ferrugineous to dark piceous, aeneous or metallic in some species, elytra maculate or sellate in some South American species. Integument shiny in most species, dorsum without extensive microsculpture except in some South American species; coxal depressions of sternum three of most species with small patches of particularly coarse microsculpture; microsculpture isodiametric or nearly so.

Head. Labrum (Fig. 2-3) weakly emarginate or biemarginate apically, or in some South American species deeply emarginate; margined laterally with six or seven pairs of setae, to about fifteen pairs in *S. optimus*. Clypeus with median tooth prominent, nearly or quite as large as paramedian teeth, except in some South American species; paramedian carinae straight or arcuate, joined to median tooth or not; median field triangular or hemicircular, base of varied width. Clypeal suture obsolete to deeply engraved at middle. Frons with

carinae one to four straight and nearly parallel, or arcuate in some South American species; carinae one and four more strongly elevated or not; carina five distinct or not; median sulcus wider than at least outer paramedian sulci, limited in front by transverse carina or not, with median longitudinal carina in some species; sides of median sulcus parallel, divergent behind, or bowed outward at middle. Eyes flat to prominent, multifaceted, inner facets not enlarged in most species; eyes in *S. ocellatus* each reduced to an apparently single, bubble-like facet. Antennal articles five to ten moniliform to elongate; pedicel unisetose, or bisetose or plurisetose in some South American species; articles three and four pubescent, or plurisetose in some South American species; articles five to eleven pubescent. Mandibles (Fig. 6-7) elongate, prominent. Mentum (Fig. 19-20) deeply emarginate at middle, or shallowly in some South American species, median tooth large and sharp, or blunt in some South American species; antero-lateral angles of lateral lobes acutely produced; anterior paramedian setae widely spaced. Submentum without accessory setae, except in *S. strigicollis*. Gula narrow, its narrowest part 0.15-0.30 width of mentum, or less than 0.10 in some South American species.

Thorax. Pronotum convex to flat, transverse to elongate; paramedian longitudinal sulci usually present, paralateral sulci absent; lateral grooves narrow and deep, or broad and shallow in some South American species; lateral grooves not bordered internally by carinae, except in some South American species; accessory marginal setae present or absent; hind angles obsolete to prominent. Prothoracic pleura impunctate except in *S. amphibius*.

Elytra. Lateral channel narrow to broad at apex, shallow, not flared, without foveae or pits above umbilicate series. Disc without setae, with setae on interval three, intervals three and five, or on intervals three, five, and seven. Elytral intervals broad, flat to moderately convex, carinate in some South American species; interval eight and in some species intervals five and seven carinate at apex; interval eight free, interval seven in most species joined by apices of intervals three and five. Striae in most species deeply engraved, in most species distinctly punctate at least in basal half.

Hind wings. Fully developed except in *S. ocellatus*. Venation as in Fig. 33-34; oblongum cell broad, proximal transverse vein not broken.

Legs. Front and middle tarsi expanded and with relatively dense ventral pubescence in many species, particularly in males, or narrow in both sexes. Hind tarsi slender, short to elongate; article one of hind tarsus 2.5-4.0 times as long as article two. Paronychia varied from about half to quite as long as tarsal claws, or obsolete in some South American species. Front tibia narrowed evenly to base or not; distal tooth varied in form; spurs subequal, slender and acute; posterior ventral margin with three setae proximad to spur, or four in some South American species.

Abdomen. Sternum seven with paramedian ambulatory setae present in males of most species, absent from females except of *S. pluripunctatus* and of members of *basalis* group. Paramedian carinae of sternum three curved outward at apices or not. Margin of pygidium (Fig. 24-25) crenulate or not in females, not in males.

Male genitalia. Median lobe arcuate, nearly symmetric in most species, form of apex various. Endophallus with distinctive basal collar spines in many species; membrane around virga reduced or not; basal stylets various, distinctive in some species.

Female ovipositor. Number and position of setae variable, of no value in species recognition (Fig. 28-29).

Distribution. – Members of this subgenus range from southern Canada southward to central Argentina. One species is known from Cuba in the West Indies. I examined 9930 specimens of the subgenus *Schizogenius*.

Taxonomic notes. – The subgenus is most diverse in South America. Since I treat only

the North and Middle American fauna in detail, I deliberately mention characteristics peculiar to South American forms in the description. These characteristics are not repeated in species descriptions, except in species groups where appropriate.

Key to described North and Middle American species groups, species, and subspecies of subgenus *Schizogenius*

1. Pronotum with paramedian longitudinal sulci obsolete; clypeal suture obsolete; neither sex with paramedian ambulatory setae on sternum seven (*optimus* group) ..... *S. optimus* Bates, p. 173
1' Pronotum with deep paramedian longitudinal sulci; clypeal suture sharply engraved; at least males with paramedian ambulatory setae on sternum seven 2
2.(1'). Paramedian clypeal carinae tuberculate, not or hardly extended to median tooth; antennal articles four to ten moniliform (*ferrugineus* group) 3
2' Paramedian clypeal carinae extended to median tooth; antennal articles four to ten moderately to strongly elongated, filiform 4
3. (2). Abdomen strongly microsculptured; body without metallic luster ..... *S. ferrugineus* Putzeys, p. 179
3' Abdomen not extensively microsculptured; body with distinct aeneous luster ..... *S. auripennis* Bates, p. 182
4.(2'). Paramedian pronotal sulci extended forward nearly to anterior transverse impression; front tarsi slender in both sexes (*truquii* group) ..... *S. truquii* Putzeys, p. 204
4' Paramedian pronotal sulci shorter; front tarsi slightly to strongly dilated, at least in males 5
5.(4'). Interval seven with at most one seta, usually with none (*lindrothi* group) ..... *S. lindrothi* new species, p. 199
5' Interval seven of elytron with at least three discal setae 6
6.(5'). Discal setae of elytra average 1.2 or more times longer than maximum width of interval two; striae usually indistinctly punctate; body form cylindrical to subcylindrical; pronotum with or without accessory marginal setae (*pluripunctatus* group) 7
6' Discal setae of elytra average no more than 1.0 times longer than maximum width of interval two; striae usually distinctly punctate; body form various; pronotum without accessory marginal setae 12
7.(6). Pronotum with accessory marginal setae 8
7' Pronotum without accessory marginal setae 10
8.(7). Front and middle tarsi strongly expanded in both sexes. California and Baja California 9
8' Front and middle tarsi not strongly expanded. Northeastern Mexico ..... *S. plurisetosus* new species, p. 214
9.(8). Disc of elytron with fewer than 60 setae. California ..... *S. seticollis seticollis* Fall, p. 209
9' Disc of elytron with more than 60 setae. Southern Baja California ..... *S. seticollis vandykei* new subspecies, p. 212
10.(7'). Females with paramedian ambulatory setae; apex of median lobe weakly deflected; disc of elytron with 35 or more setae. Arizona and New Mexico south to Durango and northern Nayarit, north of Rio Grande de Santiago drainage basin ..... *S. pluripunctatus* LeConte, p. 221

10' Females without paramedian ambulatory setae; apex of median lobe arcuate or sharply deflected. Not known from north of Rio Grande de Santiago drainage basin 11

11.(10'). Apex of median lobe sharply deflected; elytron normally with more than 40 discal setae, none seen with fewer than 37. San Luis Potosí south to Puebla and Oaxaca ..... *S. multisetosus* Bates, p. 216

11' Apex of median lobe not angularly deflected; elytron normally with fewer than 35 setae, none seen with more than 41. Central Nayarit in west and Veracruz in east, south at least to Guatemala, near coasts or not ..... *S. kulti* new species, p. 223

12.(6'). Elytron with 35 or more short discal setae; abdomen not extensively microsculptured; body strongly depressed; color castaneous; eyes prominent (*brevisetosus* group) ..... *S. brevisetosus* new species, p. 206

12' Elytron with fewer than 35 discal setae, or abdomen extensively microsculptured 13

13.(12'). Abdomen with entire ventral surface microsculptured, or nearly so; paramedian frontal sulci not or hardly closed behind; body moderately to strongly depressed; not in West Indies (*tristriatus* group) 14

13' Abdomen not with entire ventral surface microsculptured, or paramedian frontal sulci strongly closed behind, or in West Indies 20

14. (13). Prothoracic pleura distinctly punctate; small, LE under 2.50 mm ..... *S. amphibius* Haldeman, p. 236

14' Prothoracic pleura not distinctly punctate; larger, LE over 2.50 mm 15

15.(14'). Prothoracic pleura strongly microsculptured ..... *S. tibialis* new species, p. 234

15' Prothoracic pleura not or weakly microsculptured 16

16.(15'). Range, United States; eyes flattened, WF/WH 0.65 or more; each elytron normally with 25 or more discal setae 17

16' Range, Mexico; eyes prominent, WF/WH 0.65 or less; each elytron normally with fewer than 25 discal setae 19

17.(16). Range, east of Mississippi River; median lobe, Fig. 175 ..... *S. planulatus* LeConte, p. 238

17' Range, west of Mississippi River 18

18.(17'). Range, north of Red River; median lobe, Fig. 176 ..... *S. ozarkensis* new species, p. 240

18' Range, south of Red River; median lobe, Fig. 177 ..... *S. planuloides* new species, p. 241

19.(16'). Elytra rufopiceous, apices reddish; front tibia not dilated proximally ..... *S. tristriatus* Putzeys, p. 231

19' Elytra castaneous, concolorous; front tibia distinctly expanded proximally ..... *S. dilatus* new species, p. 232

20.(13'). Abdomen distinctly microsculptured along midline (*sallei* group) ..... *S. sallei* Putzeys, p. 229

20' Abdomen not distinctly microsculptured along midline, or if so then entire abdomen microsculptured 21

21.(20'). Sternum three without small paralateral patch of distinct microsculpture on each side (*longipennis* group) 22

21' Sternum three with small paralateral patch of distinct microsculpture on each side 25

22.(21). Range, Arizona and New Mexico; front femur piceous; frontal carina three in most specimens abbreviated behind; apex of median lobe (Fig. 197) deflected at nearly right angle ..... *S. neovalidus* new species, p. 252

22' If in Arizona and New Mexico, then front femur reddish; frontal carina three in most specimens not abbreviated behind; median lobe with apex less sharply deflected 23

23.(22'). Elytra rufous to rufopiceous; endophallus (Fig. 204) with basal collar spines broad. Southern Arizona ..... *S. chiricahuanus* new species, p. 257

23' Elytra normally piceous 24

24.(23'). Endophallus (Fig. 203) with basal collar spines broad; virga small; most specimens smaller, stockier, and with tibiae paler. Western Mexico ..... *S. pacificus* new species, p. 258

24' Endophallus (Fig. 205) with basal collar spines narrow; virga large. Arizona and Tamaulipas south to Costa Rica ..... *S. longipennis* Putzeys, p. 254

25.(21'). Pronotal hind angles sharply developed; elytra, except in specimens from Rio Grande drainage, piceous with aeneous tinge (in Rio Grande area, elytra castaneous with clearly paler apices). Rio Grande drainage and northward, east of Rocky Mountains (*lineolatus* group) ..... *S. lineolatus* Say, p. 246

25' Pronotal hind angles not sharply developed, or if so then elytra pale, unicolorous (*depressus* group) 26

26.(25'). Paramedian frontal sulci strongly closed behind by fused paramedian carinae; elytra testaceous to brunneous 27

26' Paramedian frontal sulci not or hardly closed behind, or elytra piceous 28

27.(26). Abdomen extensively microsculptured. Northern and central California ..... *S. ochthocephalus* new species, p. 285

27' Abdomen not extensively microsculptured. Not in northern and central California ..... *S. falli* new species, p. 281

28.(26'). Abdomen extensively microsculptured. Color piceous. West Indies ..... *S. arimao* Darlington, p. 264

28' Abdomen not extensively microsculptured. Not in West Indies 29

29.(28'). Elytra piceous, and range United States and Canada 30

29' Elytra testaceous to brunneous, or range Mexico and southward 31

30.(29). Range, east of Mississippi River ..... *S. sulcifrons* Putzeys, p. 265

30' Range, Pacific coastal drainage systems ..... *S. litigiosus* Fall, p. 268

31.(29'). Pronotal hind angles normally prominent; color brunneous; larger, LE normally over 2.15 mm ..... *S. depressus* LeConte, p. 287

31' Pronotal hind angles normally rounded; color various; size various, LE under or over 2.15 mm 32

32.(31'). Piceous; sternum three with paralateral patches of microsculpture reduced, indistinct; elytron with 12 to 14 discal setae. Guatemala to Costa Rica; median lobe, Fig. 223 ..... *S. emdeni* new species. p. 265

32' Color various; sternum three with paralateral patches of microsculpture distinct; elytron with 14 or more discal setae 33

33.(32'). Color testaceous to brunneous, not piceous; range, northeastern Mexico, and United States from Rio Grande River northward, east of Rocky Mountains; median lobe, Fig. 226, 227 ..... *S. scopaeus* new species, p. 278

33' Color various; range, United States west of Rocky Mountains, and Mexico south to Colombia; in northeastern Mexico, color piceous; median lobe, Fig. 228, 229 ..... *S. pygmaeus* Van Dyke, p. 270

Partial key to South American species groups and species of the subgenus *Schizogenius*

1. Hind tarsi elongate, Ta/Ti 0.75 or more; paramedian frontal sulci not microsculptured; clypeal suture not strongly engraved; elytral disc asetose or with setae on interval three only 2
1' Hind tarsi shorter, Ta/Ti under 0.75; paramedian frontal sulci microsculptured in most species; clypeal suture weakly to strongly engraved 6
2.(1). Paramedian pronotal sulci well developed; interval three of elytron bi- or trisetose (*jacarensis* group) ..... *S. jacarensis* new species, p. 172
2' Combination of characters not as above (*optimus* group) 3
3.(2'). Paramedian pronotal sulci obsolete or nearly so 4
3' Paramedian pronotal sulci well developed; elytral disc asetose 5
4.(3). Elytra piceous, metallic; clypeal carinae straight, apices abbreviated; elytra ovate ..... *S. dyschirioides* Putzeys, p. 175
4' Elytra brunneous, unmetallic; clypeal carinae arcuate, apices joined and extended by stem to median tooth; elytra elongate, not ovate ..... *S. clivinoides* Putzeys, p. 176
5.(3'). Elytron with large sutural macula ..... *S. grossus* Whitehead, p. 176
5' Elytron not maculate ..... *S. bicolor* new species, p. 177
6.(1'). Elytral disc with setae on intervals three, five, and seven; antennal articles five to ten nearly moniliform; paramedian clypeal carinae tuberculate, apices not extended to median tooth; clypeal field broad, at base more than 1.5 apical width of median frontal sulcus (*basalis* group) 7
6' Combination of characters not as above 10
7.(6). Pygidium not strongly crenulate in either sex; color ferrugineous, not or slightly aeneous ..... *S. negrei* new species, p. 186
7' Pygidium strongly crenulate in females; at least pronotum aeneopiceous to metallic 8
8.(7'). Elytral striae not distinctly punctate in basal half; occiput densely punctate ..... *S. multipunctatus* Kult, p. 185
8' Elytral striae distinctly punctate in basal half; occiput not densely punctate 9
9.(8'). Elytral disc with more than 40 setae; elytral length over 2.25 mm; pronotum piceous, metallic at sides and base only ..... *S. basalis* Putzeys, p. 184
9' Elytral disc with fewer than 40 setae; elytral length under 2.25 mm; pronotum entirely metallic green *S. cearaensis* new species, p. 185
10.(6'). Paramedian pronotal sulci evident only at base; elytral intervals three, five, and seven asetose (*elongatus* group) 11
10' Paramedian pronotal sulci more elongated, developed well in front of base 12
11.(10). Metallic green; total length over 5 mm ..... *S. costiceps* Steinheil, p. 188
11' Less strongly metallic; total length about 4 mm ..... *S. elongatus* Kult, p. 188
12.(10'). Elytral disc asetose, intervals carinate (*carinatus* group) 13
12' Elytral disc with setae at least on interval three 14
13.(12). Body color piceous ..... *S. carinatus* Whitehead, p. 189
13' Body color rufotestaceous ..... *S. costipennis* new species, p. 190
14.(12'). Elytral disc with setae on interval three only 15
14' Elytral disc with setae on interval five 16
15.(14). Eye normal, multifaceted (*quadripunctatus* group) ..... *S. quadripunctatus* Putzeys, p. 202

15' Eye ocellate, reduced to one bubble-like facet (*ocellatus* group) ..... *S. ocellatus* new species, p. 196
16.(14'). Elytral disc with setae on intervals three and five only 17
16' Elytral disc with setae on intervals three, five, and seven 21
17.(16). Elytral interval five with setae in basal half only (*arechavaletae* group)..... 18
17' Elytral interval five with setae evenly distributed 19
18.(17). Humeral angles of elytra prominent ..... *S. reichardti* new species, p. 193
18' Humeral angles of elytra rounded ..... *S. arechavaletae* Putzeys, p. 192
19.(17'). Inner paramedian frontal carinae grossly enlarged; median frontal sulcus microsculptured, with or without median carina .....(*darlingtoni* group), p. 197
19' Inner paramedian frontal carinae normal; median frontal sulcus not microsculptured, without median carina 20
20.(19'). Antennal articles five to ten short, nearly moniliform (*lindrothi* group) ..... *S. banningeri* Kult, p. 201
20' Antennal articles five to ten elongate, filiform .....(*capitalis* group), p. 198
21.(16'). Submentum with numerous accessory setae; pronotum with lateral grooves bordered internally by distinct carinae (*strigicollis* group) ..... *S. strigicollis* Putzeys, p. 191
21' Submentum with two standard pairs of setae only; pronotum without lateral carinae ..... (*depressus* group), p. 263

As I am unfamiliar with some named South American species of subgenus *Schizogenius* and cannot evaluate their characteristics from original descriptions, this key is provisional and incomplete. In particular, I have no useful concepts of forms named *S. canaliculatus* Putzeys, *S. gracilis* Putzeys, *S. leprieuri* Castelnau, *S. sellatus* Putzeys, and *S. sulcatulus* Putzeys, and cannot place them to species group. From original descriptions, I associate the names *S. clivinoides* Putzeys and *S. interstriatus* Putzeys with species groups, but not with specimens. I tentatively associate the names *S. costiceps* Steinheil and *S. putzeysi* Kirsch with actual specimens. All other associations are based either on type material or on topotypic or nearly topotypic specimens which closely match good original descriptions. I did not key South American species belonging to the *darlingtoni, capitalis,* or *depressus* groups, since I am insufficiently familiar with them.

The *jacarensis* group

Diagnostic combination. – Members of this group may be distinguished by the following combination of characters: hind tarsi elongate, Ta/Ti over 0.75; clypeal suture weakly engraved; paramedian frontal sulci not microsculptured; elytral disc with two or three setae on interval three; paramedian pronotal sulci well developed; basal sensory bristles of terminal article of maxillary palpus arranged transversely; and apex of median lobe of male genitalia neither elongate nor strongly deflexed. Also: size large (LE over 2.75 mm); integument not extensively microsculptured; labrum strongly biemarginate, fringed laterally with six or seven pairs of setae; clypeal carinae straight and abbreviated; clypeal field at base more than 1.5 apical width of median frontal sulcus; clypeus with median tooth reduced; frontal carinae not arcuate; antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent; mentum deeply emarginate, median tooth blunt; front and middle tarsi slender in both sexes; paronychia nearly obsolete; posterior ventral margin of front tibia with three setae near base; paramedian carinae of sternum three straight; paramedian ambulatory setae present on sternum seven of males only; pygidium not crenu-

late in either sex; and endophallus without enlarged basal collar spines.

Distribution. – This monobasic group is known only from three specimens from central Brazil.

Schizogenius jacarensis new species

Type material. – Holotype male and allotype female labelled "Jacare P. N. Xingu M. Grosso – Bras. XI.1961 leg. M. Alvarenga" (MGFT). A specimen from Goias state is a paratype (DRWh).

Diagnostic combination. – *S. jacarensis* is the only known member of the *jacarensis* group.

Description. – Body stout, subcylindrical, head proportionately large. Color rufocastaneous, elytra strongly aeneous or weakly metallic, not maculate; legs and mouthparts rufous; tarsi and antennae testaceous.

Integument. Fine microsculpture on genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, sterna two and three, sides of sterna four to six, and margin of sternum seven. Sternum three without patches of particularly coarse microsculpture in coxal depressions.

Head. Fig. 77. Labrum strongly biemarginate, fringed laterally with six or seven pairs of setae. Paramedian clypeal carinae straight, attenuate; median clypeal field triangular, width at base much more than 1.5 apical width of median field of frons; median clypeal tooth much shorter than paramedian teeth. Clypeal suture obsolete or nearly so. Frontal carinae weakly arcuate, median frontal sulcus narrowed from base to apex. Antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent. Eye subglobose, uniformly faceted. Terminal article of maxillary palpus with basal sensory bristles arranged transversely. Mentum deeply emarginate, median tooth blunt.

Pronotum. Fig. 77. Sides bisetose, hind angles reduced; base not rugose; paramedian sulci sharply engraved; anterior transverse impression impunctate. Pronotum widest well in front of middle.

Legs. Front and middle tarsi slender in both sexes, without dense ventral pubescence; hind tarsus slender, elongate. Front tibia narrowed evenly to base; postero-ventral margin with three setae near base. Front femur not strongly constricted near apex. Paronychia much less than half length of tarsal claws.

Elytra. Disc with two or three setigerous punctures on interval three. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to eight broad, convex, apices not carinate; intervals three, five, and seven joined at apices.

Abdomen. Paramedian carinae of sternum three straight. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 81, apex neither elongate nor sharply deflexed; endophallus without distinctive spines. One specimen examined.

Measurements and proportions. Of holotype: TL, 5.36 mm; LE, 3.25 mm; WH, 1.42 mm; WP, 1.60 mm; WE, 1.68 mm; WF/WH, 0.75; LP/WP, 0.80; DP/LP, 1.02; LP/WE, 0.76; Ta/Ti, 0.81; PS/LP, 0.60. Of allotype: TL, 4.94 mm; LE, 3.07 mm; WH, 1.24 mm; WP, 1.43 mm; WE, 1.56 mm; WF/WH, 0.73; LP/WP, 0.82; DP/LP, 1.06; LP/WE, 0.75; Ta/Ti, 0.83; PS/LP, 0.58.

Variation. – Two specimens have three setae on interval three of the left elytron.

Etymology. – *S. jacarensis* is named after the type locality, Jacaré National Park.

Distribution. – I studied three specimens of this species, from the following localities.

BRAZIL

GOIAS: Santa Isabel do Morro (1; DRWh). MATO GROSSO: Jacare P. N. Xingu (2; MGFT).

Collecting notes. – Specimens of this species were collected in June and November.

Taxonomic notes. – This species probably represents an early side branch of the *optimus* group, since the weakly engraved clypeal suture, elongate hind tarsi, and unmicrosculptured paramedian frontal sulci are all characteristics shared with members of that group. Males do not have the elongated apex characteristic in genitalia of members of the *optimus* group, and the head is proportionately much larger, the eyes smaller, and the pronotum more transverse. As in all other members of *Schizogenius* except those of the *optimus* group, basal sensory bristles of terminal articles of maxillary palpi in *S. jacarensis* are transversely arranged.

The *optimus* group

Diagnostic combination. – Members of this group are distinguished by the following combination of characters: hind tarsi elongate, Ta/Ti over 0.75; clypeal suture weakly engraved; paramedian frontal sulci not microsculptured; elytral disc asetose or with setae on interval three only; if interval three setose, then paramedian pronotal sulci obsolete or nearly so; basal sensory bristles of terminal article of maxillary palpus arranged longitudinally; and apex of median lobe of male genitalia elongate and strongly deflexed. Also: size medium to large (LE 2.75-5.00 mm); integument extensively microsculptured or not, testaceous to dark piceous, metallic or not, elytra maculate in one species; labrum weakly to strongly emarginate or biemarginate, fringed laterally with six or seven to about 15 pairs of setae; clypeal carinae straight and abbreviated, or fused in an arc and joined to median tooth by common stem; clypeal field at base more than 1.5 apical width of median frontal sulcus; clypeus with median tooth reduced or not; antennal articles five to ten moniliform, pedicel uni- or bisetose, articles three and four plurisetose to pubescent; mentum shallowly to deeply emarginate, median tooth blunt to sharp; gula 0.05-0.20 width of mentum; anterior and middle tarsi slender in both sexes; paronychia obsolete to about half length of tarsal claws; posterior ventral margin of front tibia with three to four setae near base; paramedian carinae of sternum three straight; paramedian ambulatory setae present on sternum seven of males only, or absent; pygidium not crenulate in either sex; and endophallus without enlarged basal collar spines.

Distribution. – One Middle American species extends from Chiapas south to Costa Rica. Four other species occur in Panama and much of continental South America. I studied 117 specimens of the *optimus* group.

Schizogenius optimus Bates

Schizogenius optimus Bates 1881:37. *Type locality* Rio Naranjo, Guatemala; type in BMNH, specimen labelled lectotype by G. E. Ball here so designated (!).

Diagnostic combination. – This is the only Middle American species of *Schizogenius* having obsolete paramedian pronotal sulci. Specimens of *S. optimus* are distinguished from others in the *optimus* group by the following character combination: elytra piceous, metallic, not extensively microsculptured, not maculate; antennal pedicel unisetose; clypeal carinae arcuate, fused apically and joined by common stem to median tooth; elytral interval three asetose; and labrum not deeply emarginate, margined laterally with no more than seven pairs of setae.

Description. – Body stout, subcylindrical. Color piceous, elytra and pronotum strongly metallic, legs, mouthparts, and antennae testaceous.

Integument. Fine microsculpture on gena, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, sternum two, coxal depressions of sternum three, sides of sterna four to six, and margin of sternum seven. Sternum three without patches of particularly coarse microsculpture in coxal depressions.

Head. Fig. 78. Labrum strongly emarginate, fringed laterally with six or seven pairs of setae. Paramedian clypeal carinae arcuate, fused apically and extended by common stem to median tooth; median clypeal field hemicircular, width at base over 1.5 apical width of median field of frons; median clypeal tooth shorter than paramedian teeth. Clypeal suture obsolete to weakly engraved. Frontal carinae not arcuate, median frontal sulcus narrowed from base to apex. Antennal articles five to ten moniliform, pedicel unisetose, articles three and four pubescent. Eyes subglobose, uniformly faceted. Terminal article of maxillary palpus with basal sensory bristles longitudinally arranged. Mentum deeply emarginate, median tooth sharp.

Pronotum. Fig. 78. Sides bisetose, hind angles reduced; base not rugose; paramedian sulci absent or barely evident at base; anterior transverse impression finely punctate.

Legs. Front and middle tarsi slender in both sexes, without dense ventral pubescence; hind tarsus slender, elongate. Front tibia narrowed evenly to base where much narrower than at base of antennal cleaner; posterior ventral margin of front tibia with three setae near base. Front femur not strongly constricted near apex. Paronychia short, about half length of tarsal claws.

Elytra. Disc without setigerous punctures, one seta at base of interval three. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to eight broad, convex; intervals five, seven, and eight carinate apically; interval seven joined by apex of interval five, otherwise free.

Abdomen. Paramedian carinae of sternum three straight. Sternum seven without paramedian ambulatory setae in either sex. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe (Fig. 82) with form of apex characteristic; endophallus (Fig. 85) with enlarged scales on dorsal side of virga. Four specimens examined.

Measurements and proportions. See Table 4.

Variation. – I found two males with one paramedian ambulatory seta on sternum seven.

Etymology. – Latin, *optimus* = best, a reference to the large size of individuals of this species.

Distribution. – The known range of *S. optimus* extends from southern Chiapas to Costa Rica (Fig. 86). I studied 46 specimens from the following localities.

MEXICO

CHIAPAS: Pijijiapan (31; CAS, CNC, DRWh, IRSB, UASM).

GUATEMALA

GUATEMALA: Agua Caliente (2; MCZ). SAN MARCOS: Rio Naranjo (2; BMNH).

HONDURAS

COMAYAGUA: Rancho Chiquito (2; FDAG). CORTES: La Lima (1; FDAG). EL PARAISO: El Paraiso (1; UCD).

COSTA RICA

No locality (1; USNM). LIMON: Rio Reventazon (2; BMNH, USNM).
PUNTARENAS: 3-7 mi. ne. Puerto Viejo (4; UAFA).

Table 4. Descriptive statistics for *S. optimus*, based on 31 unsexed specimens from Pijijiapan, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.98-6.17	5.634	0.390	0.093	4.61
LE	3.00-3.70	3.387	0.238	0.057	4.69
WH	1.12-1.42	1.258	0.095	0.023	5.03
WP	1.43-1.88	1.668	0.128	0.031	5.11
WE	1.58-2.06	1.803	0.146	0.035	5.41
B. Proportions					
WF/WH	0.66-0.69	0.675	0.012	0.003	1.20
LP/WP	0.86-0.92	0.892	0.022	0.005	1.66
DP/LP	0.85-0.91	0.876	0.021	0.005	1.62
LP/WE	0.78-0.87	0.826	0.030	0.007	2.41
Ta/Ti	0.80-0.92	0.849	0.053	0.013	4.16

Collecting notes. – I found specimens of this species at Pijijiapan, Chiapas, in gravel along a river. They were concentrated near the edge of the water in a strip only a few feet in length, for no reason apparent to me; specimens of several other *Schizogenius* species were found along the same stream but were not so concentrated. Adult individuals of *S. optimus* are probably active throughout the year, and I have seen specimens collected in March, May, June, August, and October.

Schizogenius dyschirioides Putzeys

Schizogenius dyschirioides Putzeys 1863:28. *Type locality* "Amazone," Brazil; type specimens not seen, probably in the Chevrolat Collection of the Hope Museum at Oxford, or in the Bates Collection in MNHP. Putzeys 1866:222.

Diagnostic combination. – Specimens of the *optimus* group with combination of metallic elytra, bisetose second antennal articles, bisetose elytral interval three, and obsolete paramedian pronotal sulci probably all represent this species.

Description. – Body form, color, and integument generally as described for *S. optimus*, except sides of sterna four to six more strongly and extensively microsculptured.

Head. Fig. 79. As described for *S. optimus* except clypeal carinae straight, neither fused apically nor extended to median tooth; and antennal pedicel bisetose.

Pronotum. Fig. 79; generally as described for *S. optimus*.

Legs. As in *S. optimus* except paronychia shorter, much less than half length of tarsal claws.

Elytra. As described for *S. optimus* except interval three bisetose, and intervals three, five, and seven joined at apices.

Abdomen. As in *S. optimus* except males with paramedian ambulatory setae on sternum seven.

Male genitalia. Median lobe, Fig. 83; endophallus not studied in detail, without conspicuously enlarged spines. Two specimens studied.

Measurements and proportions. Based on five specimens from Brazil, Colombia, and Panama. TL, 4.66-5.10-5.33 mm; LE, 2.85-3.10-3.23 mm; WH, 0.98-1.09-1.15 mm; WP, 1.32-1.48-1.56 mm; WE, 1.54-1.66-1.72 mm; WF/WH, 0.63-0.65-0.67; LP/WP, 0.87-0.90-0.92; DP/LP, 0.85-0.86-0.86; LP/WE, 0.79-0.80-0.82; Ta/Ti, 0.82-0.88-0.91.

Variation. – The Pará specimen, a female, is much smaller than specimens from Colombia and Panama, and has an extra seta on interval three of left elytron.

Etymology. – Latin, *dyschirioides* = *Dyschirius*-like, a reference to the quite oval elytra.

Distribution. – I refer to this species 16 specimens from the following South American localities.

BRAZIL

PARA: Belem (1; USNM).

COLOMBIA

MAGDALENA: Rio Frio (13; MCZ), Sevilla (1; MCZ).

PANAMA

CANAL ZONE: San Pablo (1; USNM).

Collecting notes. – Specimens of *S. dyschirioides* were collected in March and May.

Taxonomic notes. – Though I have not seen type specimens of *S. dyschirioides,* there is little doubt that this association is correct. The specimens well match the original description, and the Pará specimen may even by topotypic.

I suspect that presence of paramedian ambulatory setae on sternum seven in males is secondary; these setae are present in some specimens of *S. optimus*. The extra seta on the antennal pedicel clearly is a novelty. Other than these features, form of clypeal carinae, and presence of setae on elytral interval three, *S. dyschirioides* is not greatly different from *S. optimus.*

Schizogenius clivinoides Putzeys

Schizogenius clivinoides Putzeys 1866:229. *Type locality* "Pampas," Argentina; type not seen, possibly in the Chaudoir collection in MNHP.

Diagnostic combination. – From the description, specimens of this species should have the following combination of characteristics: paramedian pronotal sulci obsolete; color yellowish or brownish, unmetallic; elytral interval three bisetose; elytral striae punctate to apex; and paramedian frontal carinae arcuate, apices fused and extended to median tooth.

Taxonomic notes. – I have seen no specimens of this species. Specimens of it should be readily identified from my diagnosis, if the original description is accurate.

Schizogenius grossus Whitehead

Schizogenius grossus Whitehead 1966:3. *Type locality* Rio Madeira, Brazil; holotype male in USNM (!).

Diagnostic combination. – Specimens of this species are the only members of the *optimus* group with maculate elytra. They are the only members of the genus known to have four rather than three postero-ventral setae near the base of the front tibia, and the only ones to have more than ten pairs of marginal setae on the labrum. Other characteristics are: color castaneous, unmetallic; integument extensively microsculptured; labrum weakly biemarginate; paramedian clypeal carinae straight, attenuate; antennal articles three and four plurisetose; paramedian pronotal sulci present; paronychia much less than half length of tarsal

claws; elytral disc asetose, elytral striae shallow; and sternum seven with paramedian ambulatory setae in neither sex.

Description. – The original description and illustrations (Whitehead, 1966a) are adequate.

Etymology. – Latin, *grossus* = gross, a reference to the large size of these insects.

Distribution. – In addition to the type series from Bolivia and Brazil, I studied the following two specimens.

ARGENTINA

SALTA: Aguas Blancas (1; MZSP), San Martin (1; MZSP).

Schizogenius bicolor new species

Type material. – Holotype male and allotype female labelled "Jacare P. N. Xingu M. Grosso – Bras. XI.1961 leg. M. Alvarenga" (MGFT). An additional 40 specimens from two localities in the Brazilian state of Mato Grosso are paratypes (CAS, DRWh, IRSB, MCZ, MGFT, MZSP, UASM).

Diagnostic combination. – Specimens of this species have in combination: characters of *optimus* group; no setae on elytral disc; plurisetose antennal articles three and four; elytra paler than pronotum, not metallic, not maculate; and pronotum with strong paramedian sulci.

Description. – Body stout, subcylindrical. Color castaneous, elytra and appendages rufotestaceous, unmetallic, elytra not maculate.

Integument. As described for *S. optimus*, except elytra faintly microsculptured.

Head. Fig. 80. As in *S. optimus* except: paramedian carinae straight, attenuate; details of paramedian frontal sulci and carinae differ; antennal articles three and four plurisetose.

Pronotum. Fig. 80. Side margins indented at anterior marginal setae as in *S. grossus*. Paramedian longitudinal sulci well developed. Sides bisetose, hind angles reduced; base not rugose; anterior transverse impression with longitudinal rugae.

Legs. As in *S. optimus* except paronychia much less than half length of tarsal claws.

Elytra. As in *S. optimus* except more parallel sided; intervals three, five, and seven not carinate, joined at apices; and striae finely punctate in basal half.

Abdomen. As described for *S. optimus*.

Male genitalia. Median lobe, Fig. 84; endophallus not studied in detail. Two specimens studied.

Measurements and proportions. Of holotype: TL, 5.19 mm; LE, 3.19 mm; WH, 1.10 mm; WP, 1.50 mm; WE, 1.64 mm; WF/WH, 0.66; LP/WP, 0.93; DP/LP, 0.83; LP/WE, 0.85; Ta/Ti, 0.88; PS/LP, 0.60. Of allotype: TL, 5.48 mm; LE, 3.40 mm; WH, 1.17 mm; WP, 1.61 mm; WE, 1.72 mm; WF/WH, 0.66; LP/WP, 0.91; DP/LP, 0.87; LP/WE, 0.85; Ta/Ti, 0.91; PS/LP, 0.65.

Variation. – Six specimens from Piaui state are darker and less distinctly bicolored than specimens in the type series.

Etymology. – Latin, *bi* = two, plus *color* = color, in reference to the distinctive coloration of individuals of this species.

Distribution. – Specimens of this species have been taken in the Brazilian states of Mato Grosso and Piaui. I studied 48 specimens from the following localities.

BRAZIL

MATO GROSSO: Barra de Tapirape (2; MZSP), Jacare P. N. Xingu (40; CAS, DRWh, IRSB, MCZ, MGFT, UASM). PIAUI: Terezina (6; MGFT).

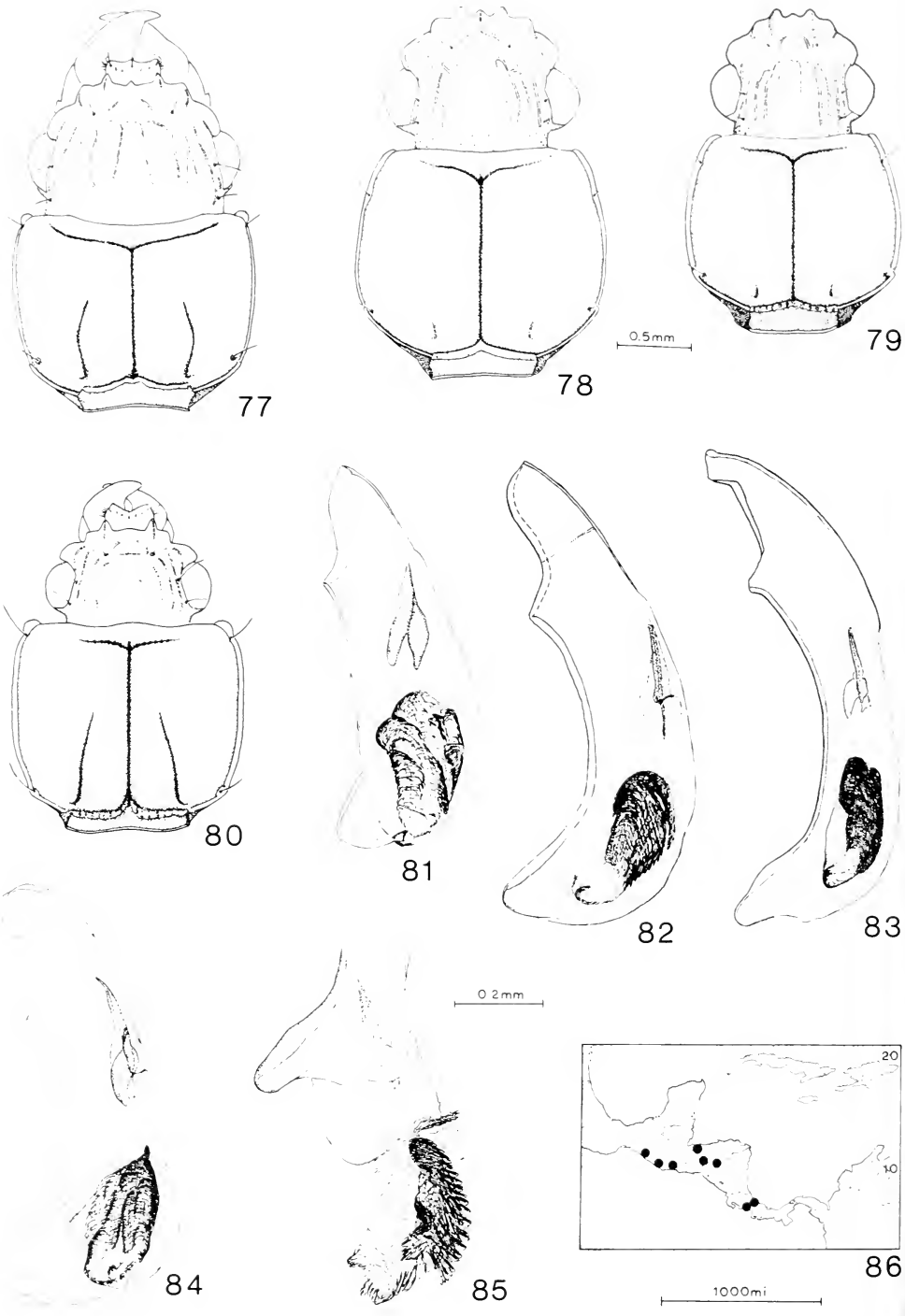


Fig. 77-80. Head and pronotum, dorsal aspect. 77. *S. jacarensis* new species, Jacare, Brazil. 78. *S. optimus* Bates, Pijijiapan, Chiapas. 79. *S. dyschirioides* Putzeys, Sevilla, Colombia. 80. *S. bicolor* new species, Jacare, Brazil. Fig. 81-84. Male median lobe, lateral aspect. 81. *S. jacarensis* new species, Jacare, Brazil. 82. *S. optimus* Bates, Pijijiapan, Chiapas. 83. *S. dyschirioides* Putzeys, Rio Frio, Colombia. 84. *S. bicolor* new species, Jacare, Brazil. Fig. 85. Male endophallus, *S. optimus* Bates, Pijijiapan, Chiapas. Fig. 86. Known distribution of *S. optimus* Bates.

Collecting notes. – Specimens of this species were collected in November and January.

Taxonomic notes. – This species is most closely related to *S. grossus* Whitehead, but is less specialized. Specimens are less extensively microsculptured, have more sharply engraved elytral striae, have a deeply emarginate mentum, have just three postero-ventral setae on the front tibia, and have only six or seven pairs of marginal setae on the labrum. But they are similar in habitus, distribution of discal setae, and non-pubescent third and fourth antennal articles.

The *ferrugineus* group

Diagnostic combination. – Within the subgenus, members of this group are characterized by the following combination of characters: paramedian clypeal carinae tuberculate, apices nearly or quite obsolete; clypeal field triangular, its base 1.0 to more than 1.5 times apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten moniliform; anterior tarsi slender in both sexes; elytral disc with setae on intervals three, five, and seven; paramedian carinae of sternum three straight; paramedian ambulatory setae present in males only; pygidium not crenulate in either sex; and endophallus without enlarged basal collar spines.

This group contains the only North and Middle American *Schizogenius* species whose members each have tuberculate clypeal carinae in combination with discal setae present on intervals three, five, and seven.

Distribution. – One species ranges throughout much of eastern North America, southwestward to Arizona. A second species overlaps the first in Arizona, and ranges southward in Pacific drainage systems to at least Costa Rica. I examined 631 specimens of the *ferrugineus* group.

Taxonomic notes. – The two species included in this group are similar in habitus but are not closely related. They may even not form a monophyletic group, as I have found no assuredly synapomorphic characteristics except perhaps loss of paramedian anal setae from sternum three of females, but I have no reason to treat them otherwise.

Schizogenius ferrugineus Putzeys

Schizogenius ferrugineus Putzeys 1846:653. *Type locality* Galveston, Texas; location of type unknown. LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:223. LeConte 1879: 34. Lindroth 1961:168.

Clivina sulcata LeConte 1848:214. *Type area* New York State; type in LeConte Collection, MCZ.

Schizogenius sulcatus, LeConte 1857:83, suggested synonymy.

Diagnostic combination. – Specimens of this species are readily distinguished from those of *S. auripennis*, the only other known species of the group, by ferrugineous coloration and extensively microsculptured abdomen.

Head. Fig. 87. Clypeal carinae tuberculate, not or weakly extended to median clypeal tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of frons. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted. Neck densely but finely punctate. Gena rugose in front. Antennal articles four to ten moniliform.

Pronotum. Fig. 87. Sides bisetose, hind angles reduced, base not rugose. Paramedian sulci long, impunctate, shallow and indistinct apically, deep and strongly hooked basally. Anterior transverse impression impunctate or finely punctate.

Legs. Front and middle tarsi slender, without dense ventral pubescence; hind tarsus slender, short. Paronychia inconspicuous, about half length of tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Five to seven setigerous punctures each on intervals three and five, and three to five on interval seven. Striae deep and sharply engraved, finely punctate in basal two thirds. Intervals one to seven broad and convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven.

Abdomen. Sternum three with paramedian carinae straight at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 93; endophallus, Fig. 98, without enlarged basal collar spines. Six specimens examined.

Measurements and proportions. See Table 5.

Table 5. Descriptive statistics for *S. ferrugineus*, based on 20 males from Round Mountain, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.13-3.76	3.434	0.297	0.089	5.77
LE	1.89-2.27	2.072	0.180	0.054	5.80
WH	0.66-0.82	0.738	0.067	0.020	6.07
WP	0.83-1.05	0.944	0.099	0.030	7.03
WE	0.91-1.14	1.006	0.102	0.031	6.79
B. Setae on left elytron.					
Interval 3	5- 7	6.2			
Interval 5	5- 7	6.3			
Interval 7	3- 4	3.5			
Total	14-18	16.0	1.6	0.5	6.72
C. Proportions.					
WF/WH	0.66-0.72	0.688	0.023	0.007	2.27
LP/WP	0.95-1.01	0.982	0.033	0.010	2.22
DP/LP	0.80-0.86	0.824	0.023	0.007	1.86
LP/WE	0.88-0.96	0.918	0.036	0.011	2.61
Ta/Ti	0.64-0.75	0.708	0.052	0.015	4.86
PS/LP	0.63-0.76	0.701	0.050	0.015	4.75

Variation. – Among specimens studied, the largest female (LE, 2.48 mm) and male (LE, 2.41 mm) are from Long Beach, New York, the smallest female (LE, 1.66 mm) is from Columbus, Texas, and the smallest male (LE, 1.69 mm) is from Clark Co., Kansas. There is an apparent slight tendency for larger size toward the northeast than toward the southwest,

but population samples generally are too small for worthwhile comparisons.

Etymology. – Latin, *ferrugineus* = rust colored, in reference to the body color; Latin, *sulcatus* = sulcate, in reference to the sulci on the frons and pronotum.

Distribution. – *S. ferrugineus* ranges at low elevations in sandy places from southern Ontario south to northern Florida and west to southeastern Arizona (Fig. 100). I examined 507 specimens from the following localities.

CANADA

No locality (1; UKSM). ONTARIO (1;CAS): Tilbury (1; KHSt); Toronto (5; CAS, CUNY, KSUM, MCZ).

UNITED STATES

No locality (3; ANSP, IRSB). ALABAMA: Washington Co., Leroy (2; CUNY). ARIZONA: Cochise Co., Douglas (1; UCB); Graham Co., Aravaipa (1; CAS); Pima Co., Robles Ranch (1; UCD). ARKANSAS: Carroll Co., Eureka Springs (1; UKSM); Hempstead Co., Hope (3; CUNY, USNM); Washington Co., Mount Sequoyah (1; INHS). COLORADO: Logan Co. (1; USNM). DELAWARE (1; MCZ). FLORIDA: Nassau Co., Fernandina Beach (2; USNM). GEORGIA (2; ANSP). ILLINOIS: Mason Co., Havana (1; USNM); Pike Co., Pittsfield (2; UCD). INDIANA (1; CNHM): Lake Co., Pine (6; CNHM, MGFT): Steuben Co., Fremont (1; CNHM); Tippecanoe Co. (1; UCD). IOWA: Johnson Co., Iowa City (4; USNM); Des Moines Co., Burlington (2; MCZ). KANSAS (14; CNHM, CUNY, KSUM, MCZ, USNM): Clark Co. (1; UKSM); Douglas Co. (1; UKSM), Lawrence (4; INHS); Kiowa Co. (1; UKSM); Leavenworth Co. (3; USNM); Pottawatomie Co., Onaga (1; UASM); Reno Co. (8; CAS, MCZ, USNM), Medora (2; KSUM); Riley Co. (7; KSUM, USNM), Manhattan (1; KSUM); Sedgwick Co. (6; USNM); Mount Hope (9; CAS, USNM). KENTUCKY (1; AMNH). LOUISIANA: Winn Co., Winnfield (1; MCZ). MAINE: Oxford Co., Paris (1; MCZ). MARYLAND: Difficult (4; CUNY, MCZ); Calvert Co., Chesapeake Beach (19; USNM), Kenwood Beach (14; DRWh, JNeg, UCD, USNM); Montgomery Co., Great Falls (1; CAS), Plummers Island (2; USNM). MASSACHUSETTS: Essex Co., Ipswich (4; MCZ); Hampden Co., Chicopee (3; MCZ), Springfield (1; MCZ); Middlesex Co., Tewksbury (1; MCZ), Tyngsboro (13; MCZ). MICHIGAN: Huron Co. (1; MSUL); Monroe Co., Monroe (10; MCZ, MSUL, USNM). MINNESOTA: Houston Co., Mississippi Bluff (1; MSUL). MISSISSIPPI: George Co., Lucedale (2; CUNY). MISSOURI (1; ANSP). NEBRASKA: Cuming Co., West Point (2; USNM); Thomas Co., 2.5 mi. w. Halsey (1; CAS). NEW HAMPSHIRE: Grafton Co., Rumney (10; CNC, DRWh, MCZ). NEW JERSEY (2; ANSP, MCZ): Atlantic Co., Atlantic City (1; MCZ), Brigantine (3; CAS, RUNB); Burlington Co., Atsion (8; CAS); Camden Co., Cramer Hill (1; USNM), Westville (10; ANSP, MCZ, RUNB, USNM); Cape May Co., Anglesea (18; ANSP, LACM, MCZ, RUNB), Five Mile Beach (4; USNM), Ocean City (1; CAS); Gloucester Co., Woodbury (1; ANSP); Warren Co., Phillipsburg (1; CAS). NEW MEXICO: Curry Co., Clovis (2; UKL). NEW YORK (8; CAS, USNM): New York City and vicinity (13; AMNH, CAS, RUNB); Long Island (4; CAS, UNSM); Brooklyn Co., Coney Island (7; CAS, MCZ); Nassau Co., Long Beach (17; AMNH, CAS, USNM); Queens Co., Rockaway Beach (10; CAS, CUNY, USNM); Suffolk Co., Plum Island (1; MCZ), Riverhead (2; CUNY), Sound Beach (1; AMNH); Tompkins Co., Groton (2; CAS). NORTH CAROLINA (1; MSUL). OHIO: Athens Co., Athens (2; UWLW), Hamilton Co., Cincinatti (1; MCZ). OKLAHOMA: Caddo Co., Hinton (6; MSUL); Love Co., Oswalt (2; MSUL); McCurtain Co., Sherwood (1; MSUL); Woodward Co., Woodward (3; USNM). PENNSYLVANIA (1; USNM). SOUTH CAROLINA (2; CAS, MCZ): Charleston Co., Charleston (1; CAS), Folly Beach (1; USNM), Isle of Palms (5; ANSP, RUNB, USNM). TEXAS (65; AMNH, ANSP, CAS, CNHM, INHS, IRSB, KSUM, MCZ, MSUL, UKSM, USNM): Bexar Co., San Antonio (2; CAS); Blanco Co., Cypress Mills (6; CAS, USNM), Rome Mountain (16; CAS), Round Mountain (25; CAS, MCZ, RUNB); Brown Co., Brownwood (1; AMNH); Burnet Co. (2; USNM); Comal Co. (1; CAS); Colorado Co., Columbus (21; USNM); Harris Co., Hockley (2; AMNH, CAS); Lee Co. (2; MCZ), Fedor (6; CAS), Lexington (1; MCZ); Llano Co., Enchanted Rock (1; CNC); McCulloch Co., 16 mi s. Brady (1; CAS); Travis Co., Austin (1; USNM); Wharton Co., Wharton (2; CUNY). VIRGINIA: Elisabeth City, Fort Monroe (1; USNM); Fairfax Co., Arlington (1; USNM); Nelson Co. (1; USNM); Princess Anne Co., Cape Henry (5; AMNH), Virginia Beach (2; USNM). WISCONSIN: Grant Co., Boscobel (1; FDAG).

Collecting notes. – *S. ferrugineus* differs from most other species of the subgenus *Schizogenius* in that individuals live in sand rather than in gravel bars. Specimens from Iowa City, Iowa, are labelled "Butler's Landing sand area." Specimens from Kenwood Beach, Maryland, were found "under wash-up." P. J. Darlington collected specimens "under log on beach" at Ipswich, Massachusetts, and others in "galleries in dry sand under logs, Baker River" at Rumney, New Hampshire. Additional specimens were collected in "drift" along the Merrimack River at Tyngsboro, Massachusetts.

Specimens of this species have been collected from 13 March at Charleston, South Carolina, to 16 October at Lawrence, Kansas. Many flew in to lights at various localities. I can add no additional observations, having collected no specimens of this species.

Schizogenius auripennis Bates

Schizogenius auripennis Bates 1881:38. *Type locality* Teleman, Guatemala; type in BMNH, specimen labelled "holotype" here designated as **lectotype** (!).

Schizogenius peninsularis Van Dyke 1949:50. *Type locality* 5 mi. s. Miraflores, Baja California; type in CAS, not studied. NEW SYNONYMY.

Diagnostic combination. – The shiny, unmicrosculptured abdomen separates specimens of *S. auripennis* from those of *S. ferrugineus*, the only other known member of the group. The apex of the male median lobe is strikingly different in form from that of any other species in the genus.

Description. – Body cylindrical. Color dark rufopiceous above and dark rufous below, elytral apices, legs, palpi, and antennae testaceous or rufotestaceous; dorsal surface with slight to strong aeneous luster.

Integument. Smooth, shiny. Fine microsculpture on paramedian frontal sulci, genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at extreme base, and at least small patch in coxal depression of sternum three; some specimens with microsculpture on sternum two, sides of sterna three and four, and margin of sternum seven.

Head. Fig. 88. As described for *S. ferrugineus* except: median field of clypeus narrower at base, between 1.0 and 1.5 apical width of median field of frons; second frontal carina broadened at base, fifth nearly obsolete; eye larger, globose; neck densely and coarsely punctate; and gena strongly rugose in front.

Pronotum. Fig. 88. Smaller, more transverse than in *S. ferrugineus*, paramedian sulci shorter and slightly hooked basally, anterior transverse impression finely punctate.

Legs. Paronychia more conspicuous, slightly shorter than tarsal claws.

Elytra. Five to eight setigerous punctures on interval three, five to seven on interval five, and four to seven on interval seven. Otherwise as in *S. ferrugineus.*

Abdomen. As in *S. ferrugineus.*

Male genitalia. Median lobe (Fig. 94) with form of apex diagnostic; endophallus, Fig. 99. Eleven specimens examined.

Measurements and proportions. See Table 6.

Variation. – Since *S. auripennis* has no known close relatives, and as available material was limited, I did not study geographic variation in detail. Specimens from the south tend to have more abdominal microsculpture, more elytral setae, more elongate paramedian pronotal sulci, and more cylindrical body form, but this variation seems gradual. The smallest specimens seen are males and females from Arizona and Baja California (LE, 2.07 mm) and the largest is a female from Tucson, Arizona (LE, 2.88 mm).

Etymology. – Of *auripennis*, Latin, *aurum* = gold plus *penna* = wing, in reference to elytral coloration of the slightly teneral type; of *peninsularis*, Latin, *peninsula* = peninsula, a reference to the type locality in peninsular Baja California.

Distribution. – The known distribution of this species (Fig. 101) extends from southern Arizona south to Costa Rica in Pacific drainage areas, from elevations near sea-level to as high as 4500′ in Guatemala. I studied 124 specimens from the following localities.

UNITED STATES

ARIZONA: Cochise Co., Douglas (1; CAS); Graham Co., Aravaipa (1; CAS); Maricopa Co., Phoenix (2; CUNY, DRWh), Wickenburg (5; MCZ, MSUL); Pima Co., Arivaca (1; KHSt), Organ Pipe National Monument (1; LBSC), Quitobaquito (1; UATA), Tucson (3; AMNH, CAS, USNM); Santa Cruz Co., Nogales (2; CAS, UCD), Peña Blanca (4; UASM, UATA).

MEXICO

BAJA CALIFORNIA: 5 mi. s. Miraflores (17; CAS), 5 mi. w. San Bartolo (3; CAS), 6 mi. sw. Santiago (4; UATA), Triunfo (3; CAS). CHIAPAS: 20.9 mi. n. Arriaga (1; UASM), Puente Macuilapa (2; FDAG). JALISCO: Pitillal (1; UASM). NAYARIT: Jesus Maria (1; UCB), San Blas (1; CAS). PUEBLA: Tepexco (2; UASM). SINALOA: 19 mi. s. Culiacan (2; UCB), Real de Piaxtla (2; AMNH), 4 mi. s. Villa Union (1; UCB), 26 mi. ne. Villa Union (2; LBSC). SONORA: Alamos (6; CAS, LACM), 5 mi. w. Alamos (2; UATA), 10 mi. w. Alamos (4; AMNH), 7 mi. se. Alamos (5; GRNo, UCB), Hermosillo (34; CAS), Minas Nuevas (1; AMNH), 10 mi. e. Navajoa (1; UATA).

GUATEMALA

ALTA VERAPAZ: Teleman (1; BMNH). EL QUICHE: Sacapulas (1; AMNH).

HONDURAS

CORTÉS: La Lima (3; FDAG, INHS).

COSTA RICA

PUNTARENAS: Palmar Sur (1; UAFA). SAN JOSE: Barranca (1; JNeg), 3-7 mi. n. Puerto Viejo (1; UAFA).

Collecting notes. – Nearly all specimens were taken at lights, so little is known of the biology of *S. auripennis*. I collected one specimen from Arriaga along a small stream, and G. E. Ball collected one in gravel along a stream at Pitillal. Probably, individuals of this species normally live in sand rather than gravel bars, as do those of *S. ferrugineus*; this supposition is supported by the cylindrical body form, which is not suited for life in gravel bars. If the normal habitat is sand, and particularly if it is dry sand, then the distribution of this species is likely to be unaffected by location and substrate of drainage systems. Specimens have been collected throughout the year.

Table 6. Descriptive statistics for *S. auripennis*, based on 20 males from Hermosillo, Sonora.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.46-4.23	3.824	0.329	0.098	5.73
LE	2.14-2.60	2.362	0.194	0.058	5.47
WH	0.73-0.88	0.789	0.071	0.021	5.98
WP	0.97-1.21	1.080	0.108	0.032	6.64
WE	1.10-1.34	1.201	0.105	0.031	5.85
B. Setae on left elytron.					
Interval 3	6- 8	6.7			
Interval 5	5- 7	6.3			
Interval 7	4- 7	5.4			
Total	16-22	18.4	1.6	0.7	8.64
C. Proportions.					
WF/WH	0.60-0.66	0.623	0.029	0.009	3.13
LP/WP	0.88-0.95	0.914	0.027	0.008	0.95
DP/LP	0.84-0.88	0.866	0.018	0.005	1.42
LP/WE	0.79-0.86	0.822	0.032	0.010	2.59
Ta/Ti	0.63-0.73	0.680	0.053	0.016	5.18
PS/LP	0.56-0.63	0.599	0.035	0.011	3.94

Taxonomic notes. – I have seen topoparatypes of both *S. auripennis* and *S. peninsularis.* These names are clearly synonyms. Southern specimens differ slightly as noted, but male genitalia are constant throughout the known range. Exact relationships of this species with *S. ferrugineus* are unclear, but are quite apparently not close.

The *basalis* group

Diagnostic combination. – Specimens referred to this group have the following combination of characters: body convex; paramedian clypeal carinae not extended to median tooth; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten short but filiform, distinctly longer than wide; submentum without accessory setae; pronotum without distinct paralateral carinae, with well developed paramedian sulci; front and middle tarsi quite narrow in both sexes; elytra with discal setae on intervals three, five, and seven, intervals not carinate; sternum seven with paramedian ambulatory setae in both sexes; paramedian carinae of sternum three not or slightly curved at apices; and pygidium apex weakly to strongly crenulate in females.

Distribution. – Members of this group are known only from Brazil, Uruguay, and Argentina. I examined 18 specimens of the *basalis* group.

Taxonomic notes. – I assign to this group four species, two described here as new. I examined the type of *S. basalis* Putzeys, and saw some Brazilian specimens which agree well with the original description of *S. multipunctatus* Kult, but I doubt that any additional described species belong to this group. I have not provided full species descriptions, as none of the species are well represented in collections.

This group seems an important phylogenetic link, as it seems to share a common ancestry with the *ferrugineus* group (which has no clear derivatives), and probably also with all remaining groups of *Schizogenius.*

Schizogenius basalis Putzeys

Schizogenius basalis Putzeys 1866:230. *Type locality* Santa Lucia River, 12 leagues north of Montevideo, Uruguay; holotype female in IRSB (!). Kult 1950:148.

Diagnostic combination. – The only specimen of this species seen by me differs from specimens of *S. multipunctatus* by larger size (LE about 2.5 mm), less metallic coloration, and sparsely punctate occiput. It differs from specimens of *S. cearaensis* by larger size, more numerous discal setae, and less metallic pronotal coloration, and from specimens of *S. negrei* by larger size, more numerous discal setae, and darker coloration.

Description. – With characters of the *basalis* group. Body coloration faded from aging, but according to original description aeneopiceous, with elytral base fuscous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum. Fig. 89; antennal article five about 1.3 times longer than wide; occiput sparsely punctate. Elytral striae distinctly punctate in basal half; left elytron with 16, 17, and 14 setae on intervals three, five, and seven, respectively. Male genitalia not known.

Measurements and proportions. TL, 4.01 mm; LE, 2.50 mm; WH, 0.79 mm; WP, 1.16 mm; WE, 1.33 mm; WF/WH, 0.67; LP/WP, 0.87; DP/LP, 0.86; LP/WE, 0.76; PS/LP, 0.61.

Etymology. – Latin, *basilaris* = at the base, in reference to the pale elytral base.

Distribution. – I examined only the type specimen from near Montevideo, Uruguay.

Schizogenius cearaensis new species

Type material. – Holotype male and allotype female labelled "Fortaleza Ceara, BRAZIL III -29/IV-2-63 F. G. Werner" (MCZ). Nine additional specimens with the same label data are paratypes (DRWh, IRSB, MCZ, UASM).

Diagnostic combination. – Within the *basalis* group, specimens of this species are distinguished by the combination of: occiput sparsely punctate; elytra uniformly pale; pronotum strongly metallic; and elytral disc with fewer than 40 setae.

Description. – With general characters of *basalis* group. As in *S. basalis* except as follows. Color ferrugineous; pronotum strongly aeneopiceous to metallic green; elytra, antennae, palpi, front tibiae and tarsi, and middle and hind legs testaceous. Head and pronotum, Fig. 90. Left elytron with 10 to 12 setae on interval three, 12 to 14 on interval five, and 9 to 13 on interval seven, total 33 to 38 in specimens examined. Male genitalia, Fig. 95; one specimen examined.

Measurements and proportions. Of holotype, the smallest specimen: TL, 3.07 mm; LE, 1.88 mm; WH, 0.65 mm; WP, 0.87 mm; WE, 1.07 mm; WF/WH, 0.65; LP/WP, 0.90; DP/LP, 0.88; LP/WE, 0.73; PS/LP, 0.54; Ta/Ti, 0.65. Of allotype, the largest specimen: TL, 3.37 mm; LE, 2.09 mm; WH, 0.67 mm; WP, 0.85 mm; WE, 1.12 mm; WF/WH, 0.67; LP/WP, 0.89; DP/LP, 0.88; LP/WE, 0.76; Ta/Ti, 0.73.

Etymology. – I name this species for its type locality, in the Brazilian state of Ceará.

Distribution. – *S. cearaensis* is known only from the type series from Fortaleza, Ceará, Brazil.

Taxonomic notes. – I distinguish *S. cearaensis* as a species distinct from the related *S. basalis* because all known specimens are smaller, have fewer elytral setae, and differ in coloration. It remains possible, however, that the two forms are merely geographic variants. More material of the group is required to study geographic variation, and to obtain more information about *S. basalis* including information about male genitalia.

Schizogenius multipunctatus Kult

Schizogenius multipunctatus Kult 1950:147. *Type locality* Corumba, Mato Grosso, Brazil; holotype and paratype in Kult collection, present location not known.

Diagnostic combination. – Within the *basalis* group, specimens with occiput densely punctate belong to this species. All known specimens of this species differ further from the type of *S. basalis* by smaller body size (LE under 2.3 mm), and from specimens of *S. cearaensis* and *S. negrei* by the dark elytra.

Description. – With characters of *basalis* group. Body bright aeneopiceous to metallic green, elytra unicolorous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 91; antennal article five about 1.3 times longer than wide; occiput densely punctate. Elytral striae finely punctate in basal half; left elytron with about 14-18 setae on interval three, 15-17 on interval five, 11-13 on interval seven; total 41-46 in specimens examined. Male genitalia, Fig. 96; one specimen examined.

Measurements and proportions. Largest specimen, female: TL, 3.55 mm; LE, 2.24 mm; WH, 0.73 mm; WP, 0.98 mm; WE, 1.15 mm; WF/WH, 0.62; LP/WP, 0.87; DP/LP, 0.91; LP/WE, 0.74; Ta/Ti, 0.66; PS/LP, 0.59. Smallest specimen, male: TL, 3.17 mm; LE, 2.00 mm; WH, 0.66 mm; WP, 0.85 mm; WE, 1.02 mm; WF/WH, 0.60; LP/WP, 0.88; DP/LP, 0.92; LP/WE, 0.74; Ta/Ti, 0.58; PS/LP, 0.57.

Etymology. – Latin, *multus* = much, plus *punctum* = small hole, in reference to the numerous discal setae on the elytra.

Distribution. – Specimens of this species have been collected in various localities in central Brazil. I studied three specimens from the following localities.

BRAZIL
GOIAS: Santa Isabel do Morro (1; DRWh). PIAUI: Terezina (2; MGFT).

Collecting notes. – As these specimens were collected in January and June, adults of *S. multipunctatus* are probably active throughout the year.

Taxonomic notes. – Specimens here identified as *S. multipunctatus* differ from specimens of *S. basalis* and *S. cearaensis* in coloration and in punctation of occiput, and doubtless are reproductively isolated from them. Although I did not see type material of *S. multipunctatus*, the specimens reported here fit the original description quite well and seem correctly assigned.

Schizogenius negrei new species

Type material. – Holotype male (MNHP) and allotype female (JNeg) labelled "Tucuman Concepcion 31-xii-46 Coll A. Golbach" ex collection J. Nègre. One female specimen with the same label data is a paratype (DRWh).

Diagnostic combination. – Specimens of this species are distinguished from all others in the group by entirely ferrugineous body coloration. Further, known females have the pygidium apex only indistinctly crenulate.

Description. – With characters of the *basalis* group. As in *S. basalis* except as follows. Color ferrugineous, pronotum slightly aeneous; antennae, palpi, front tibiae and tarsi, and middle and hind legs testaceous. Head and pronotum, Fig. 92; antennal article five about 1.2 times longer than wide. Left elytron with 12-13 setae on interval three, 13-17 on interval five, and 10-13 on interval seven, total 35-41 in specimens examined. Male genitalia, Fig. 97; one specimen examined.

Measurements and proportions. Of holotype: TL, 3.38 mm; LE, 2.08 mm; WH, 0.71 mm; WP, 0.93 mm; WE, 1.07 mm; WF/WH, 0.66; LP/WP, 0.91; DP/LP, 0.88; LP/WE, 0.79; Ta/Ti, 0.73; PS/LP, 0.62. Of allotype: TL, 3.48 mm; LE, 2.15 mm; WH, 0.72 mm; WP, 0.99 mm; WE, 1.13 mm; WF/WH, 0.65; LP/WP, 0.89; DP/LP, 0.89; LP/WE, 0.78; Ta/Ti, 0.71; PS/LP, 0.63.

Etymology. – It is with pleasure that I name this species for my friend, J. Nègre.

Distribution. – This species is known only from the type series of three specimens, collected at Concepcion, Tucuman, Argentina. It is the only member of the group known from Argentina.

Taxonomic notes. – *S. negrei* is morphologically well differentiated from other members of the *basalis* group, and is no doubt reproductively isolated from them.

The *elongatus* group

Diagnostic combination. – Specimens of this group have the following combination of characters: body convex; paramedian clypeal carinae extended to median tooth or not; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten moniliform, slightly longer than wide; submentum without accessory setae; pronotum with paramedian sulci distinct at base only, and with distinct paralateral carinae; front and middle tarsi slightly broadened in both sexes; elytra without discal setae, intervals not carinate; sternum seven with paramedian ambulato-

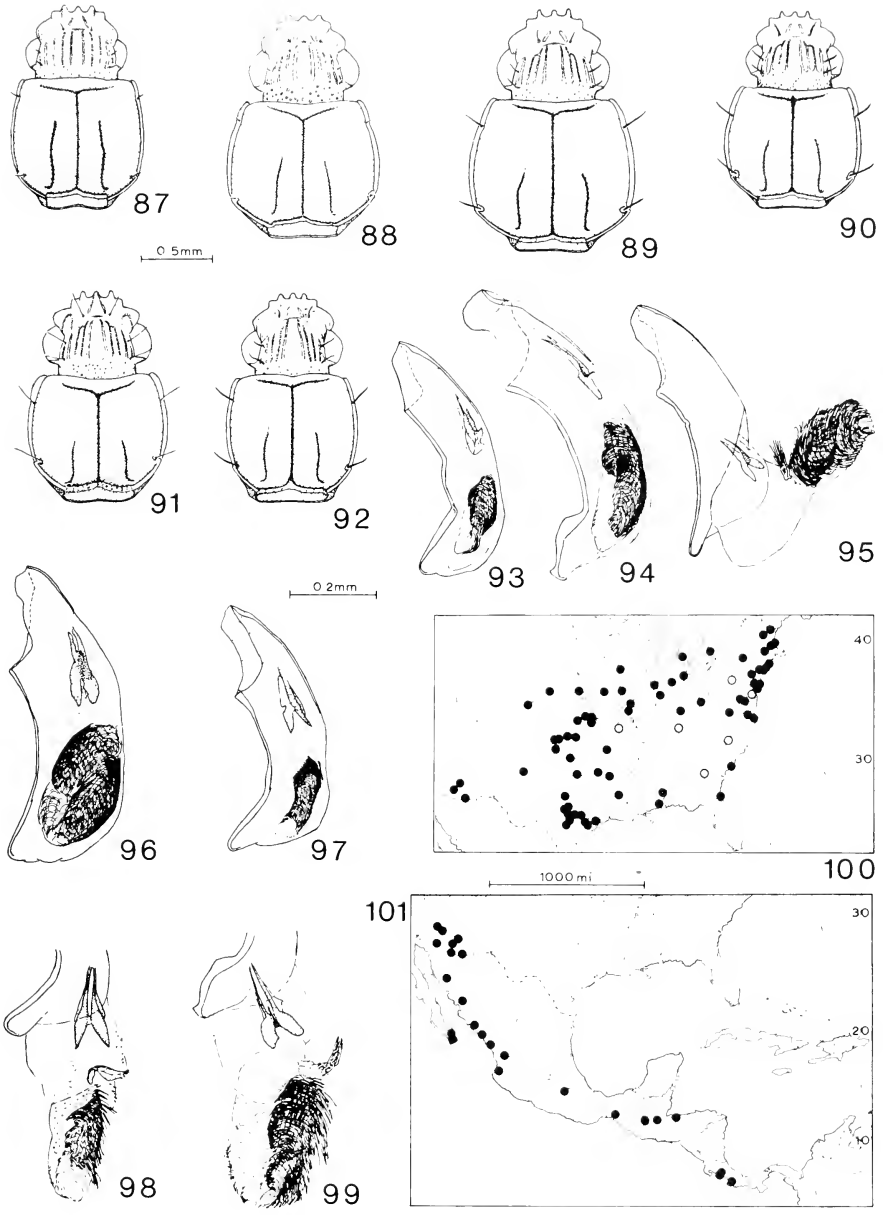


Fig. 87-92. Head and pronotum, dorsal aspect. 87. *S. ferrugineus* Putzeys, Kenwood Beach, Maryland. 88. *S. auripennis* Bates, Arriaga, Chiapas. 89. *S. basalis* Putzeys, Rio Santa Lucia, Uruguay. 90. *S. cearaensis* new species, Fortaleza, Brazil. 91. *S. multipunctatus* Kult, Terezina, Brazil. 92. *S. negrei* new species, Concepcion, Argentina. Fig. 93-97. Male median lobe, lateral aspect. 93. *S. ferrugineus* Putzeys, Logan County, Colorado. 94. *S. auripennis* Bates, Miraflores, Baja California. 95. *S. cearaensis* new species, Fortaleza, Brazil. 96. *S. multipunctatus* Kult, Terezina, Brazil. 97. *S. negrei* new species, Concepcion, Argentina. Fig. 98-99. Male endophallus. 98. *S. ferrugineus* Putzeys, Kenwood Beach, Maryland. 99. *S. auripennis* Bates, Hermosillo, Sonora. Fig. 100-101. Known distributions. 100. *S. ferrugineus* Putzeys; hollow symbols represent state records only. 101. *S. auripennis* Bates.

ry setae in males, not in females; paramedian carinae of sternum three not or hardly curved at apices; and pygidium apex strongly crenulate in females.

Distribution. – Members of this group are known only from Argentina and Brazil. I studied 13 specimens of the *elongatus* group.

Taxonomic notes. – I assign here two described species, *S. costiceps* Steinheil and *S. elongatus* Kult, though I have seen type material of neither. Specimens from near the type locality of *S. elongatus* agree well with its original description. My association of a specimen from Argentina with the name *S. costiceps* is less definite, but I have no reason to doubt the association. As I have seen no type material of the group, I give no detailed redescriptions of the two described species here assigned to it.

Schizogenius costiceps Steinheil

Schizogenius costiceps Steinheil 1869:242. *Type locality* San Luis, Argentina; location of type unknown.

Diagnostic combination. – One specimen seen by me which may belong to this species differs from specimens of *S. elongatus* by larger size (LE over 2.9 mm), brighter green color, more elongated paramedian pronotal sulci, and less distinctly punctate elytral striae.

Description. – With characters of *elongatus* group. Body piceous, strongly metallic green; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 102; clypeal carinae extended to median tooth, but weakly developed in apical third; antennal article five about 1.1 times longer than wide. Elytral striae indistinctly punctate. Male genitalia not known.

Measurements and proportions. TL, 4.69 mm; LE, 2.96 mm; WH, 0.91 mm; WP, 1.27 mm; WE, 1.50 mm; WF/WH, 0.62; LP/WP, 0.93; DP/LP, 0.91; LP/WE, 0.79; Ta/Ti, 0.66; PS/LP, 0.49.

Etymology. – Latin, *costa* = rib, plus *caput* = head, in reference to the frontal carinae.

Distribution. – Two specimens are known, both from central Argentina. The type is from San Luis, San Luis province. The specimen reported here is labelled "Rep. Arg. Pronunciamento Pro-Entre Rios XI-63." (JNeg).

Taxonomic notes. – The original description of *S. costiceps* is inadequate, as Steinheil thought that the eight longitudinal carinae on the frons were distinctive. But the Entre Rios specimen fits the description in other characteristics recorded, such as the size and bright green color, and is from a sufficiently close locality that it may well be conspecific. Steinheil's description indicates a more pale body color, but his specimen was probably teneral. Further evidence that the Entre Rios specimen is conspecific with or closely related to the type of *S. costiceps* is in what Steinheil did not say: he particularly omitted any mention of discal setae on the elytra.

Schizogenius elongatus Kult

Schizogenius elongatus Kult 1950:146. *Type locality* Corumba, Mato Grosso, Brazil; type and paratype in Kult collection, present location not known.

Diagnostic combination. – Within the *elongatus* group, specimens of this species are distinguished by small body size (LE under 2.5 mm), narrow body, aeneopiceous coloration, nearly obsolete paramedian pronotal sulci, and finely but distinctly punctate elytral striae.

Description. – With characters of *elongatus* group. Body piceous, strongly aeneous; legs and antennae ferrugineous; palpi testaceous. Head and pronotum, Fig. 103; clypeal carinae broken in apical third; antennal article five about 1.1 times longer than wide. Elytral striae

finely but distinctly punctate in basal half. Male genitalia, Fig. 108; 1 specimen examined.

Measurements and proportions. Largest specimen, male: TL, 3.88 mm; LE, 2.40 mm; WH, 0.79 mm; WP, 1.07 mm; WE, 1.20 mm; WF/WH, 0.59; LP/WP, 0.94; DP/LP, 0.86; LP/WE, 0.84; Ta/Ti, 0.61; PS/LP, 0.22. Smallest specimen, female: TL, 3.39 mm; LE, 2.13 mm; WH, 0.71 mm; WP, 0.94 mm; WE, 1.04 mm; WF/WH, 0.58; LP/WP, 0.91; DP/LP, 0.92; LP/WE, 0.83; Ta/Ti, 0.64; PS/LP, 0.26.

Etymology. – Latin, *elongatus* = prolonged, in reference to the elongate body form.

Distribution. – Specimens of *S. elongatus* have been collected in two states in central Brazil. I studied 12 specimens from the following localities.

BRAZIL

GOIAS: Santa Isabel do Morro (8; DRWh, MGFT, UASM). MATO GROSSO: Barra do Tapirape (1; MZSP), Caceres (2; MGFT), Jacaré (1; MGFT).

Collecting notes. – Adults of this species have been collected in June, November, and December, and thus are probably active throughout the year.

Taxonomic notes. – Although I did not study type material of *S. elongatus*, the specimens here reported agree well with the original description and were collected near the type locality. Kult erred in suggesting a relationship with members of the *optimus* group, which lack distinct clypeal suture and differ in numerous additional ways.

The *carinatus* group

Diagnostic combination. – Members of this group are readily recognized by the following combination of characters; antennal articles five to ten filiform; elytral intervals strongly carinate; and elytral disc without setae. Also: body convex; paramedian clypeal carinae extended to median tooth or not; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; median frontal sulcus strongly microsculptured, with median carina distinct; submentum without accessory setae; pronotum with paramedian sulci well developed and with distinct paralateral carinae; front and middle tarsi distinctly expanded, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three not curved at apices; and pygidium apex crenulate in females.

Distribution. – Seven specimens of this group are known from Brazil.

Taxonomic notes. – I assign here two quite different species, *S. carinatus* Whitehead and a new species described below. Characteristics of members of this group are so distinctive that all described species not seen by me may safely be excluded from the group.

Schizogenius carinatus Whitehead

Schizogenius carinatus Whitehead 1966:2. *Type locality* Santa Isabel, Mato Grosso, Brazil; holotype male in CAS (!).

Diagnostic combination. – Within the *carinatus* group, specimens of this species are distinguished from the only known specimen of *S. costipennis* by the following: body color piceous; clypeal carinae clearly extended to median tooth; dorsum not extensively microsculptured; pronotum not rugose; and elytral intervals more distinctly carinate.

Description. – I have nothing to add to the original description (Whitehead, 1966a), except pygidium apex crenulate in female.

Etymology. – Latin, *carina* = keel, in reference ot the carinate elytra.

Distribution. – I studied six specimens of *S. carinatus* from the following localities in central Brazil.

BRAZIL
GOIAS: Santa Isabel do Morro (2; DRWh). MATO GROSSO: Jacaré (3; MGFT), Santa Isabel (1; CAS).

Collecting notes. – Adults of this species probably are active throughout the year, as specimens have been collected in June, August, and November.

Schizogenius costipennis new species

Type material. – Holotype female labelled "S. Isabel do Morro Ilha do Bananal Bras. Goias VI. 1961 leg. M. Alvarenga" (MGFT).

Diagnostic combination. – The only known specimen of this species differs from specimens of *S. carinatus*, the only other known member of the *carinatus* group, by the following: body color rufotestaceous; integument extensively microsculptured; pronotum strongly rugose; paramedian clypeal carinae interrupted before median tooth; and elytral intervals distinctly but weakly carinate.

Description. – Body broad, moderately convex. Color rufotestaceous, without metallic luster.

Integument. Entire body apparently microsculptured, but under surface not examined in detail; median frontal sulcus as well as paramedian sulci coarsely microsculptured. Pronotum strongly rugose.

Head. Fig. 104. Paramedian clypeal carinae straight, parallel, abbreviated at apices; median field triangular, no wider at base than apex of median field of frons. Clypeal suture sharply defined. Median frontal sulcus divided by longitudinal carina. Eye uniformly faceted. Neck rugose-punctate. Antennal articles four to ten elongate, filiform, article five about 1.8 times longer than wide.

Pronotum. Fig. 104. Sides bisetose, hind angles strongly reduced, entire surface rugose. Paramedian longitudinal sulci long, impunctate, sinuate, shallow toward apices, strongly hooked basally. Anterior transverse impression finely punctate. Paralateral longitudinal carinae strongly developed.

Legs. Front and middle tarsi strongly dilated; hind tarsi slender, short. Paronychia about half as long as tarsal claws. Front tibia narrowed evenly to base. Front femur strongly constricted near apex.

Elytra. Discal setae absent. Striae deep, sharply engraved, finely punctate in basal two-thirds. Interval one moderately convex; intervals two to seven strongly raised, finely carinate; interval eight sharply carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles moderately prominent.

Abdomen. Sternum three with paramedian carinae straight. Sternum seven without paramedian ambulatory setae. Pygidium with apical margin crenulate.

Male genitalia. Not known.

Measurements and proportions. Holotype: TL, 4.15 mm; LE, 2.68 mm; WH, 0.92 mm; WP, 1.21 mm; WE, 1.56 mm; WF/WH, 0.63; LP/WP, 0.76; DP/LP, 0.96; LP/WE, 0.59; PS/LP, 0.70.

Etymology. – Latin, *costa* = rib, plus *penna* = wing, in reference to the strongly sculptured elytra.

Distribution. – This species is known only from the holotype, from central Brazil.

Collecting notes. – The holotype was collected in June. Specimens of the following

additional species were taken at the same time and place: *S. carinatus*, *S. elongatus*, *S. jacarensis*, and *S. multipunctatus*. I presume that adults of *S. costipennis* are active throughout the year, as adults of the other species probably are, and that they probably live in riparian gravel bars.

Taxonomic notes. – *S. costipennis* is peculiar in numerous ways, and perhaps is not closely related to *S. carinatus*. In addition to characteristics mentioned in the diagnostic combination, the form of the thorax is quite different, and the elytra are much more strongly ovate. However, I doubt that the peculiar combination of elytral intervals carinate, elytral disc without setae, and pronotum with strong paralateral carinae is the result of convergence. And the two species are sympatric, so at least there is no evidence that this combination of characteristics had independent origins in separate areas. If these two species indeed are related, then additional species of the group should exist and, if found, should verify the relationship.

The strigicollis group

Diagnostic combination. – Specimens of this group are distinguished from all others of the genus by numerous accessory setae on submentum. They have the following additional combination of characters: body convex; paramedian clypeal carinae extended to median tooth, moderately elevated basally; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform, distinctly longer than wide; pronotum with well developed paralateral carinae and paramedian sulci; front and middle tarsi moderately dilated in males and females; elytra with numerous discal setae on intervals three, five, and seven, intervals not carinate; sternum seven with paramedian ambulatory setae in male only; paramedian carinae of sternum three not curved at apices; and pygidium apex not crenulate in females.

Distribution. – This group is known only from three specimens from Colombia.

Taxonomic notes. – Lindroth (1961) designated *S. strigicollis* as the type species of the genus, as it was the first species of the genus listed by Putzeys (1846). This species is the only known member of the group.

Schizogenius strigicollis Putzeys

Schizogenius strigicollis Putzeys 1846:650. *Type locality* Colombia, here restricted to Aracataca, Magdalena; male specimen in IRSB (!) labelled lectotype here so designated. Putzeys 1863:24. Putzeys 1866:222. Bates 1881:38. Lindroth 1961:164.

Diagnostic combination. – *S. strigicollis* is the only known species of *Schizogenius* characterized by numerous accessory setae on submentum.

Description. – With characters of *strigicollis* group. Body convex, bright aeneopiceous, elytra margined in metallic green; legs, antennae, and mouthparts rufotestaceous. Head and pronotum, Fig. 105; antennal article five about 1.8 times longer than wide; pronotum distinctly rugose at sides and base. Elytral striae indistinctly punctate basally; left elytron with about 13-15 setae on interval three, 13 on interval five, 9-10 on interval seven; total 35-38 in specimens examined. Male median lobe, Fig. 109; one specimen examined.

Measurements and proportions. Largest specimen, a female: TL, 4.90 mm; LE, 3.12 mm; WH, 1.06 mm; WP, 1.35 mm; WE, 1.67 mm; WF/WH, 0.59; LP/WP, 0.84; DP/LP, 0.91; LP/WE, 0.68; Ta/Ti, 0.63; PS/LP, 0.53. Smallest specimen, a male: TL, 4.69 mm; LE, 2.88 mm; WH, 1.10 mm; WP, 1.35 mm; WE, 1.62 mm; WF/WH, 0.61; LP/WP, 0.86; DP/LP, 0.89; LP/WE, 0.72; Ta/Ti, 0.62; PS/LP, 0.59.

Etymology. – Latin, *strigosus* = strigose, plus *collum* = neck, in reference to the rugose pronotum.

Distribution. – I studied three specimens of this species, all from Colombia.

COLOMBIA

No locality (1; IRSB). MAGDALENA: Aracataca (2; MCZ).

Collecting notes. – Specimens from Aracataca were collected by P. J. Darlington in March and May.

Taxonomic notes. – Records of this species from Mexico (Putzeys, 1846; Bates, 1881) are no doubt erroneous.

The *arechavaletae* group

Diagnostic combination. – Specimens of this group differ from other members of the subgenus by having three or four setae on interval three of elytron, and two setae only on basal half of interval five. They have the following additional characters: body moderately convex; paramedian clypeal carinae abbreviated before median tooth; clypeal field triangular, at base more than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform, distinctly longer than wide; pronotum without paralateral carinae, with short paramedian sulci; front and middle tarsi moderately dilated in both sexes; elytral intervals not carinate; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three curved outward at apices; and pygidium apex crenulate in females.

Distribution. – Two species are known, one from Uruguay and the other from northeastern Brazil. I studied ten specimens of the *arechavaletae* group.

Taxonomic notes. – The two species included in this group are quite different in body form, but as they agree in all important ways except length of paronychia they probably are quite closely related.

Schizogenius arechavaletae Putzeys

Schizogenius arechavaletae Putzeys 1866:227. *Type locality* Santa Lucia River, north of Montevideo, Uruguay; male specimen in IRSB labelled lectotype (!), here so designated.

Schizogenius angusticollis Putzeys 1866:231. *Type locality* Santa Lucia River, north of Montevideo, Uruguay; holotype male in IRSB (!). NEW SYNONYMY.

Diagnostic combination. – Specimens of *S. arechavaletae* are distinguished from specimens of *S. reichardti*, the only other known member of the *arechavaletae* group, by longer paramedian pronotal sulci, more convex body form, and rounded humeral angles of elytra.

Description. – Body broad, convex. Color of type specimens faded; originally described by Putzeys as aeneocupreous, appendages fuscous.

Integument. Microsculpture generally as in *S. reichardti* except on abdomen: less developed on sternum two, in coxal depressions and on small paralateral patches on sternum three, otherwise largely unmicrosculptured.

Head. Fig. 106. Clypeal carinae tuberculate, in some specimens evidently but weakly extended to median tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of frons. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted. Neck densely, coarsely punctate. Gena rugose in front. Antenna filiform, short, article five about 1.5 times wider than long.

Pronotum. Fig. 106. Sides bisetose, hind angles weakly developed, base and sides moderately rugose. Paramedian sulci short, impunctate, distinctly engraved apically, deep and broadly hooked basally. Anterior transverse impression distinctly punctate.

Legs. Front and middle tarsi distinctly dilated, particularly in males, in males with dense ventral pubescence; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Three or four setigerous punctures on interval three, two on basal half of interval five. Striae deep and sharply engraved, finely punctate in basal half. Intervals one to seven broad and convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven. Humeral angles rounded.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with paired paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in females.

Male genitalia. Median lobe, Fig. 110, 111; three specimens studied.

Measurements and proportions. Largest specimen, a female: TL, 4.66 mm; LE, 2.95 mm; WH, 0.91 mm; WP, 1.34 mm; WE, 1.60 mm; WF/WH, 0.65; LP/WP, 0.82; DP/LP, 0.93; LP/WE, 0.69; Ta/Ti, 0.67; PS/LP, 0.58. Smallest specimen, a male: TL, 3.61 mm; LE, 2.27 mm; WH, 0.75 mm; WP, 0.99 mm; WE, 1.27 mm; WF/WH, 0.65; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.67; Ta/Ti, 0.69; PS/LP, 0.59.

Etymology. – The name *arechavaletae* was given in honor of the collector, M. Arechavaleta. The name *angusticollis* is derived from Latin, *angustus* = narrow, plus *collum* = neck, in reference to the narrowly prominent pronotal front angles.

Distribution. – I studied seven specimens of this species from Uruguay, all from type series (IRSB) of *S. arechavaletae* and *S. angusticollis.*

Taxonomic notes. – If the holotype specimen of *S. angusticollis* is correctly labelled, it unquestionably is conspecific with specimens named *S. arechavaletae*, and was from the same series. According to original descriptions, however, there is some possibility of error; the description of *S. angusticollis* suggests an animal more like *S. reichardti* than *S. arechavaletae*. This question cannot be resolved until other specimens of the type series are found, and, for the present, I prefer to place the names *S. angusticollis* and *S. arechavaletae* in synonymy.

Paronychia apparently are primitively short in the subgenus *Schizogenius*, and secondarily elongate in *S. arechavaletae* and all following species groups. I suspect that the ancestor of the *arechavaletae* group has secondarily elongated paronychia, and that the shortened paronychia of *S. reichardti* represents a reversion to the ancestral condition.

Schizogenius reichardti new species

Type material. – Holotype female labelled "PARAIBA Corema – VI-1957 Exp. Dep. Zoologia" (MZSP). Two additional females with the same label data, from Brazil, are paratypes (MZSP, DRWh).

Diagnostic combination. – Specimens of this species are readily distinguished from others in the *arechavaletae* group by numerous characteristics, including prominent humeral angles of elytra.

Description. – Body broad, dorsum flattened. Color dark castaneous, elytra with slight aeneous luster; legs, antennae, and palpi ferrugineous.

Integument. Distinct microsculpture on paramedian frontal sulci, genae, mouthparts, base of pronotum, anterior surfaces of front legs, middle legs except trochanters, hind tibiae and

posterior surfaces of hind femora, elytral epipleura on base and apical two-thirds, sternum two, and portions of sterna three to seven.

Head. Fig. 107. Clypeal carinae tuberculate, convergent, nor or weakly extended to median tooth; median clypeal field triangular, broad, width at base about 1.5 apical width of median field of front. Clypeal suture sharply engraved. Eye prominent, subglobose, uniformly faceted. Neck densely, coarsely punctate. Gena rugose in front. Antenna filiform, short, article five about 1.3 to 1.4 times longer than wide.

Pronotum. Fig. 107. Sides bisetose, hind angles weakly developed, base and sides moderately rugose. Paramedian sulci short, impunctate, shallow and indistinctly engraved apically, deep and broadly hooked basally. Anterior transverse impression distinctly punctate.

Legs. Front and middle tarsi distinctly dilated, without dense ventral pubescence; hind tarsus slender, short. Paronychia distinct, about half length of tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Three or four setigerous punctures on interval three, two on basal half of interval five. Striae deep and sharply engraved, distinctly punctate in basal three-fourths. Intervals one to seven broad and moderately convex, interval eight carinate at apex; intervals three and five broadly joined apically with interval seven. Humeral angles prominent.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven without paramedian ambulatory setae in female. Pygidium with apical margin crenulate in female.

Male genitalia. Unknown.

Measurements and proportions. Largest specimen: TL, 4.99 mm; LE, 3.09 mm; WH, 1.15 mm; WP, 1.42 mm; WE, 1.65 mm; WF/WH, 0.65; LP/WP, 0.88; DP/LP, 0.90; LP/WE, 0.73; Ta/Ti, 0.73; PS/LP, 0.44. Smallest specimen: TL, 4.47 mm; LE, 2.75 mm; WH, 1.02 mm; WP, 1.28 mm; WE, 1.58 mm; WF/WH, 0.66; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.70; Ta/Ti, 0.68; PS/LP, 0.49.

Variation. – On one paratype basal halves of all femora are strongly rugose.

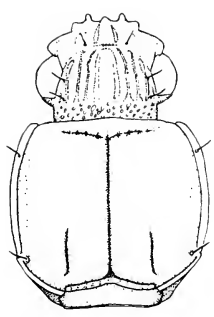
Etymology. – I take pleasure in naming these distinctive beetles for my friend, Hans Reichardt, who made specimens of them available for study.

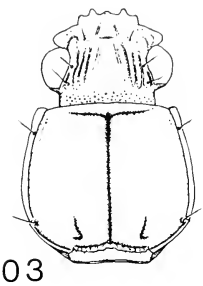
Distribution. – Only the type specimens from northeastern Brazil are known.

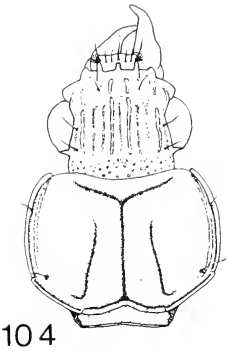
The *ocellatus* group

Diagnostic combination. – Specimens of this group differ from all others of the genus by remarkably reduced, bubble-like eyes, and plurisetose antennal pedicels. They have the following additional combination of characters: body flattened; prothoracic pleura and abdominal sterna microsculptured; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus, clypeal suture sharply impressed; inner paramedian frontal carinae not grossly thickened; median frontal sulcus not or weakly microsculptured, without median longitudinal carina; antennal articles five to ten filiform, elongate; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on interval three only; hind wings brachypterous; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three strongly curved at apices; and pygidium apex crenulate in females.

Distribution. – Eight specimens of one species were collected in a cave in southern Brazil.







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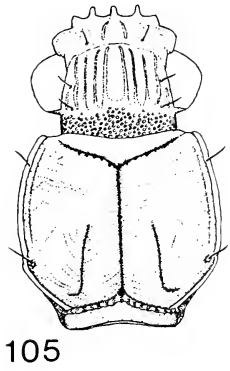
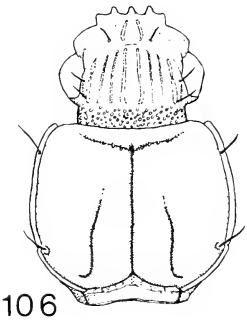
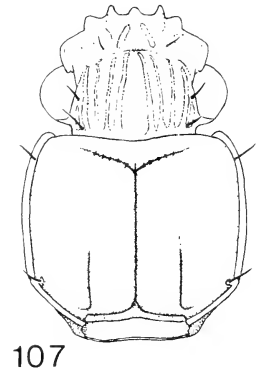
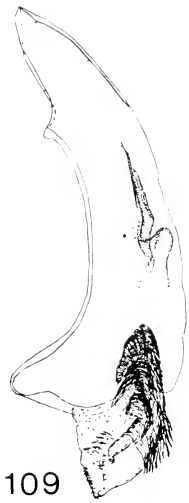






0.2 mm



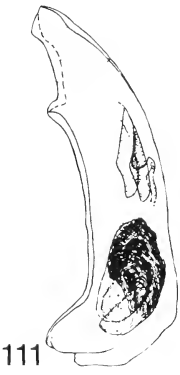


Fig. 102-107. Head and pronotum, dorsal aspect. 102. *S. costiceps* Steinheil, Entre Rios, Argentina. 103. *S. elongatus* Kult, Caceres, Brazil. 104. *S. costipennis* new species, Santa Isabel do Morro, Brazil. 105. *S. strigicollis* Putzeys, Aracataca, Colombia. 106. *S. arechavaletae* Putzeys, Rio Santa Lucia, Uruguay. 107. *S. reichardti* new species, Corema, Brazil. Fig. 108-111. Male median lobe, lateral aspect. 108. *S. elongatus* Kult, Santa Isabel do Morro, Brazil. 109. *S. strigicollis* Putzeys, Aracataca, Colombia. 110, 111. *S. arechavaletae* Putzeys, Rio Santa Lucia, Uruguay.

Taxonomic notes. – The plurisetose pedicel is reminiscent of antennae in *Halocoryza* species, but is clearly a secondary adaptation. Relationships are uncertain; castaneous color, ventral microsculpture, prominent hind angles, curved sternal carinae, reduced elytral setation, and other characteristics suggest relationship with members of the *darlingtoni* group. The reduced eyes are quite unlike any others seen by me in Carabidae, and lend the head a peculiar appearance.

Schizogenius ocellatus new species

Type material. – Holotype male and allotype female labelled "Grutas das Areias Sao Paulo Bresil 30.VII.68 P. Strinati" (MHNG). Six additional specimens with the same label data are paratypes (DRWh, MHNG, MZSP, UASM).

Diagnostic combination. – The peculiarly reduced eyes readily distinguish members of this species from all others of the genus so far known.

Description. – Body flattened, elytra ovate. Color castaneous, no aeneous luster, appendages paler.

Integument. Conspicuous microsculpture on paramedian frontal sulci, genae, mouthparts, prothoracic pleura, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and most of abdomen except on midline of sternum seven.

Head. Fig. 112. Paramedian clypeal carinae straight, extended to median tooth; median field narrow, not or hardly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye reduced, bubble-like, not apparently faceted. Neck coarsely punctate. Gena rugose-punctate. Antennal articles five to ten elongate, article five about 2.0 times longer than wide.

Pronotum. Fig. 112. Sides bisetose, hind angles prominent, base not rugose. Paramedian longitudinal sulci elongate, impunctate, deep throughout, slightly hooked basally. Anterior transverse impression punctate. Front angles sharply produced.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in females, strongly so in males; hind tarsus slender, short. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Three or four setae on interval three, none on intervals five or seven. Striae deep and sharply engraved, distinctly punctate in basal two-thirds. Intervals one to seven broad and convex, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Hind wings brachypterous.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with paired ambulatory setae in males, not in females. Apex of pygidium entire in males, crenulate in females.

Male genitalia. Median lobe, Fig. 116; one specimen examined.

Measurements and proportions. Holotype: TL, 3.65 mm; LE, 2.10 mm; WH, 0.50 mm; WP, 1.07 mm; WE, 1.17 mm; WF/WH, 0.79; LP/WP, 0.98; DP/LP, 0.78; LP/WE, 0.90; Ta/Ti, 0.64; PS/LP, 0.67. Allotype: TL, 3.82 mm; LE, 2.24 mm; WH, 0.80 mm; WP, 1.08 mm; WE, 1.21 mm; WF/WH, 0.81; LP/WP, 1.00; DP/LP, 0.80; LP/WE, 0.89; Ta/Ti, 0.63; PS/LP, 0.67.

Etymology. – Latin, *ocellatus* = having little eyes, in reference to the ocellus-like eye.

Distribution. – Only the type series of eight specimens is known, from a cave in southeastern Brazil.

Taxonomic notes. – The only true troglobitic scaritines heretofore described are *Spelaeodytes mirabilis* Miller and *Italodytes stammeri* Müller from Europe and *Antroforceps*

bolivari Barr from Mexico (see Barr, 1967). Specimens of *S. ocellatus* differ from all other known specimens of *Schizogenius* by brachyptery, plurisetose antennal pedicel, and greatly modified eye structure, and in these ways are reminiscent of *A. bolivari*. Specimens of other *Schizogenius* species have been taken in caves, and in particular specimens of *S. tibialis* from Indian Creek Cave in Texas have markedly reduced eyes. But though measures of relative eye size (WF/WH) for *S. ocellatus* and cavernicolous *S. tibialis* are similar, they are not comparable because of grossly different eye structures.

The *darlingtoni* group

Diagnostic combination. – Specimens of this group have the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed or not; inner paramedian frontal carinae grossly thickened; median frontal sulcus microsculptured, with or without median longitudinal carina; antennal articles five to ten filiform; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on intervals three and five only; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three strongly curved at apices; and pygidium apex crenulate in females or not.

Distribution. – *S. darlingtoni* Kult was described from Panama. I studied ten specimens of other species from Colombia, Venezuela, and Peru.

Taxonomic notes. – I studied type material of no members of this group, and am therefore unable to review them at this time. As here defined, the group contains specimens with enlarged inner paramedian frontal carinae, microsculptured frontal sulcus, normally developed eyes, and setae on elytral intervals three and five. The type specimens of *S. darlingtoni* Kult (1950:140), described from Volcan de Chiriquí, Panama (BMNH), have strong microsculpture on the apical two-thirds of the elytra. I judge from original descriptions that *S. interstriatus* Putzeys (1878:54, from Medellin, Colombia) and *S. riparius* Putzeys (1878:54, from Ibague, Colombia) are members of this group. These descriptions are not adequate, and I do not know the present location of type specimens. However, as an aid to future students, I made tentative identifications of the following specimens.

Seven specimens from Rio Frio, Magdalena, Colombia (DRWh, MCZ) agree well with Putzeys' description of *S. interstriatus* in all characteristics reported. Additional characteristics are: paramedian pronotal sulci elongate (PS/LP, 0.76-0.81); front femur strongly angulate on midventral margin; elytral interval three with four setae, interval five with five or six setae; abdomen without extensive microsculpture; and female pygidium not crenulate at apex. No other known species in the genus have the angulate front femur characteristic of this species.

Three additional specimens are in general agreement with Putzeys' description of *S. riparius*, but may represent at least two different species, and as none are from Colombia perhaps none are conspecific with *S. riparius*. These specimens are from the following localities: Chanchamayo, Peru (MCZ); Cueva Alfredo Jahn Miranda, Venezuela (MNHG); and El Valle, Venezuela (CNHM). The Venezuelan specimens (LE, 2.53-2.66 mm) agree in the body size reported for *S. riparius*, but the Peruvian specimen is much larger (LE, 3.04 mm). Additional characteristics of these specimens are: paramedian pronotal sulci less elongate (PS/LP, 0.68-0.71); front femur not angulate midventrally; elytral interval three with five or six setae, interval five with six setae; abdomen extensively microsculptured; and female pygidium crenulate at apex.

The *capitalis* group

Diagnostic combination. – Specimens referred to this group have the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; clypeal field triangular, at base less than 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; inner paramedian frontal carinae not grossly thickened; median frontal sulcus not microsculptured, without median longitudinal carina; antennal articles five to ten elongate, filiform; submentum without accessory setae; pronotum with elongate paramedian sulci, without paralateral carinae; front and middle tarsi broadened in both sexes, particularly in males; elytra with discal setae on intervals three and five only; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three strongly curved at apices; and pygidium apex not crenulate in either sex. Members of this group differ most notably from members of the related *lindrothi* group by less convex body and much more strongly filiform antennae.

Distribution. – I have seen 12 specimens of this group from the following countries in western South America: Argentina, Bolivia, Colombia, Ecuador, and Peru.

Taxonomic notes. – A female specimen in IRSB (!) is labelled as the type of *S. capitalis* Putzeys (1863:25, from Carracas, Venezuela), and is labelled "capitalis P." in Putzeys' script. However, the specimen is labelled "Medellin" (Colombia), and differs from the original description by having four setae each on intervals three and five rather than five setae each on intervals three, five, and seven. Despite these discrepancies, the specimen otherwise fits the description, and until shown otherwise I think it best to regard this specimen as holotype of *S. capitalis*.

I have not seen type material of *S. putzeysi* Kirsch (1873:129, from Peru), but this seems quite clearly from the original description to be a member of the *capitalis* group, and I suspect the type specimen is teneral. I have tentatively identified as *S. putzeysi* six specimens, all smaller (LE, 2.50-2.79 mm) than the specimen of *S. capitalis* (LE, 3.05 mm) reported above, and all with distinct microsculpture on the sides of the pronotum. These specimens are from the following localities.

BOLIVIA

BENI: Huachi (2; USNM).

ECUADOR

EL ORO: 9 mi. s. Santa Rosa (3; CAS).

PERU

HUANUCO: 24 mi. e. Yurac (1; CAS).

I labelled five additional specimens as an undescribed species near *S. putzeysi*. These are also smaller (LE, 2.54-2.84 mm) than the specimen of *S. capitalis*, but lack distinct microsculpture on the sides of the pronotum. These specimens are from the following localities.

ARGENTINA

TUCUMAN (1; MCZ): Tacanas (3; MGFT), Villa Monti (1; CAS).

As I have seen no definite type material of the *capitalis* group, and few specimens from a broad geographic area, I attempt no detailed revision. Specimens reported above may represent as few as one to as many as three species; tentative identifications are intended as an aid to future students, but the group requires additional study before definite identifications are possible.

The *lindrothi* group

Diagnostic combination. – This group includes those species with three to six evenly distributed setae in elytral intervals three and five, but none in interval seven; antennal articles five to ten submoniliform, not strongly elongated; median field of frons not microsculptured, not bounded by unusually thickened carinae; and pygidium not crenulate in either sex. Also: body nearly cylindrical; paramedian clypeal carinae extended to median tooth, not strongly raised in basal half; clypeal field not or hardly wider at base than apex of median frontal sulcus; clypeal suture sharply impressed; anterior tarsi of males broadened and with dense ventral pubescence; abdomen not extensively microsculptured; paramedian carinae of sternum three curved at apices; sternum seven with paramedian ambulatory setae normally in males only; and endophallus with short basal collar spines.

Distribution. – I have seen 38 specimens of this group, representing at least two species, from Florida, Guatemala, Costa Rica, Venezuela, and Brazil.

Schizogenius lindrothi new species

Type material. – Holotype male and allotype female labelled "FLORIDA. Bay Co. 7 mi. n. Southport 10 July 1967 D. R. Whitehead" (MCZ). An additional 18 specimens from various localities in Florida are paratypes (BMNH, CAS, CUNY, DRWh, IRSB, UASM, USNM).

Diagnostic combination. – Specimens of this species are the only known specimens of North and Middle American *Schizogenius* with three or four setae each on elytral intervals three and five but none or only one on interval seven.

Description. – Body nearly cylindrical, elytra convex. Color dark rufopiceous, without strong aeneous luster; legs ferrugineous; palpi and antennae testaceous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, genae, mouthparts, pronotal base, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura in apical two-thirds and at extreme base, part of sternum two, and coxal depressions of sternum three.

Head. Fig. 113. Paramedian clypeal carinae straight, evenly elevated, extended to median tooth; median field narrow, not or hardly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye globose, finely and uniformly faceted. Neck densely punctate. Gena rugose in front, strongly punctate. Antennal articles five to ten slightly but distinctly elongate, submoniliform, article five 1.3 times as long as wide.

Pronotum. Fig. 113. Sides bisetose, hind angles not prominent, base not rugose. Paramedian longitudinal sulci moderately elongate, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in male, less so in female; hind tarsus slender, rather short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Three to four setae each on intervals three and five, none or rarely one on interval seven. Striae deep and sharply engraved, distinctly punctate in basal two-thirds. Intervals one to seven broad and convex, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined.

Abdomen. Sternum three with paramedian carinae curved at apices. Sternum seven with ambulatory setae in males, normally not in females. Apex of pygidium entire in both sexes.

Male genitalia. Median lobe, Fig. 117; endophallus, Fig. 120, with short basal collar spines; nine specimens examined.

Measurements and proportions. See Table 7. Of holotype: TL, 4.19 mm; LE, 2.52 mm; WH, 0.85 mm; WP, 1.15 mm; WE, 1.30 mm; WF/WH, 0.57; LP/WP, 0.95; DP/LP, 0.83; LP/WE, 0.84; Ta/Ti, 0.69; PS/LP, 0.76. Of allotype: TL, 4.15 mm; LE, 2.52 mm; WH, 0.68 mm; WP, 1.15 mm; WE, 1.32 mm; WF/WH, 0.59; LP/WP, 0.92; DP/LP, 0.85; LP/WE, 0.80; Ta/Ti, 0.62; PS/LP, 0.71.

Table 7. Descriptive statistics for *S. lindrothi*, based on nine males from northern and central Florida.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.76-4.32	4.006	0.275	0.122	4.58
LE	2.28-265	2.419	0.180	0.080	4.97
WH	0.78-0.90	0.840	0.053	0.024	4.20
WP	1.01-1.20	1.084	0.096	0.043	5.90
WE	1.18-1.38	1.258	0.095	0.042	5.01
B. Setae on left elytron.					
Interval 3	3-4	3.3			
Interval 5	3-4	3.3			
Interval 7	nil				
Total	6-8	6.7	1.3	0.6	1.30
C. Proportions.					
WF/WH	0.55-0.58	0.564	0.013	0.006	1.54
LP/WP	0.94-0.99	0.958	0.025	0.011	1.73
DP/LP	0.83-0.86	0.841	0.016	0.007	1.26
LP/WE	0.80-0.85	0.830	0.022	0.010	1.81
Ta/Ti	0.63-0.69	0.663	0.029	0.013	2.91
PS/LP	0.72-0.79	0.748	0.031	0.014	2.75

Variation. – There is not enough material in collections to study geographic variation. but if *S. lindrothi* is restricted to Florida such variation is probably negligible. In addition to variation in the Florida specimens listed in Table 7, I noted one female from Southport with a single seta on interval seven of the left elytron, and one female from Enterprise with a pair of paramedian ambulatory setae on sternum seven.

I tentatively associate with this species single females from Guatemala and Costa Rica. The Guatemala specimen differs by having a broad (LP/WP, 0.88), deep (DP/LP, 0.89), and relatively smaller (LP/WE, 0.70) thorax, and by having more prominent pronotal hind angles and stronger humeral angles on the elytra. The Costa Rican specimen falls outside the observed range of variation in Florida specimens by having a smaller thorax (LP/WE, 0.71), sharper hind angles and prominent humeral denticles, legs darker with femora rufopiceous, and more elytral setae: four or five setae each on intervals three and five.

Etymology. – I take pleasure in naming this new species after C. H. Lindroth, who first mentioned its existence in his 1961 review of the genus.

Distribution. – If all specimens listed here are conspecific, then the distribution of *S. lindrothi* is disjunct, in Florida and southern Middle America but not in Mexico (Fig. 121). Inclusion of the Middle American specimens is, however, tentative. I studied 31 specimens which I include under the name *S. lindrothi*, from the following localities.

UNITED STATES

FLORIDA (2; CAS, USNM): Bay Co., 7 mi. n. Southport (9; BMNH, DRWh, IRSB, MCZ, UASM); De Soto Co., Arcadia (1; CUNY); Hernando Co., Weeke Wachee Springs (2; CNC); Highlands Co., Lake Placid (1; CAS); Marion Co. (1; CAS); Orange Co., Winter Park (3; MCZ); Sumpter Co. (1; USNM); Volusia Co., Enterprise (1; MCZ, USNM).

GUATEMALA

ALTA VERAPAZ: Trece Aguas (1; USNM).

COSTA RICA

LIMON: Los Diamantes (1; FDAG).

Collecting notes. – I collected the Southport specimens in the sandy margins of a small, spring-fed pond, and most probably *S. lindrothi* is exclusively an inhabitant of sand. Specimens of this or related species are not likely to be found in Mexico or far west of Florida along the Gulf of Mexico, if, as I suspect, their distribution agrees with that of the so-called Carribean pines (Mirov, 1967). For the same reason, it would be no surprise to find specimens of the *lindrothi* group in the West Indies.

Taxonomic notes. – Specimens of this species differ sufficiently from those of *S. banningeri* in details of male genitalia that there is no reason to suspect them conspecific. Whether Middle American specimens are conspecific with *S. lindrothi*, or even with one another, is a question that cannot now be satisfactorily answered.

Schizogenius banningeri Kult

Schizogenius banningeri Kult 1950:148. *Type locality* Corumba, Mato Grosso, Brazil; type in Kult Collection, present location not known; type not seen.

Diagnostic combination. – I assign to this species all specimens of the *lindrothi* group seen from South America. They differ from specimens of *S. lindrothi* by details of male genitalia (median lobe, Fig. 118; one specimen examined), and form and sculpture of head and pronotum (Fig. 114). In particular, the median frontal sulcus is less sharply defined and is more strongly narrowed in front. As I have seen only seven specimens of the *lindrothi* group from South America, I am not certain they are all conspecific and I therefore do not give a detailed description here.

Variation. – I did not study these specimens closely for variation, but only the Mato Grosso specimen is as small as specimens reported by Kult.

Etymology. – Kult named this species in honor of M. Bänninger.

Distribution. – Just as limits of the species are unknown, so is the extent of its distribution. I studied the following seven specimens.

BRAZIL

MATO GROSSO: Cerceres (1; MGFT). PIAUI: Terezina (5; DRWh, MGFT).

VENEZUELA

CARACAS: Caracas (1; IRSB).

Collecting notes. – Specimens of this species were collected in January and December.

Taxonomic notes. – Though I have not seen type material, the specimen from Cerceres

matches the original description and is from an appropriate locality. Whether specimens from the other two localities are conspecific is not certain.

The Caracas specimen is labelled as the type of *S. sellatus* Putzeys (1866:228, from Caracas, Venezuela), but perhaps incorrectly. It does not have maculate elytra, though this may be the result of aging. More important, it does have a prominent median clypeal tooth, in contradiction to Putzeys' description. This is the specimen that Kult (1950) believed was the type of *S. sellatus*, and the one with which he compared his *S. banningeri*. The differences he noted in body size and convexity of elytral intervals are probably not important. If this Caracas specimen really is the type of *S. sellatus*, then the name *S. banningeri* may be a synonym. A re-examination of all material studied by Putzeys will be required to resolve this question. For now, I regard the Caracas specimen as one of *S. banningeri*, not as the type of *S. sellatus*.

The *quadripunctatus* group

Diagnostic combination. – Specimens of the only known species of this group have the following combination of characters: body moderately flattened; paramedian clypeal carinae extended to median tooth; antennal articles five to ten filiform; eyes normal; discal setae present on interval three only, intervals not carinate; and abdomen extensively microsculptured. Also: clypeal suture sharply impressed; clypeal field triangular, less than 1.5 apical width of median frontal sulcus; submentum without accessory setae; pronotum with distinct paramedian sulci, without paralateral carinae; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved at apices; pygidium not crenulate at apex in either sex; and endophallus with basal collar spines distinct.

Distribution. – One species of this group is known from southern Brazil and northern Argentina. I examined 200 specimens.

Schizogenius quadripunctatus Putzeys

Schizogenius quadripunctatus Putzeys 1866:225. *Type locality* Parana, Brazil; location of type male unknown. Whitehead 1966a:5.

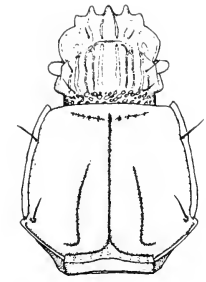
Diagnostic combination. – Specimens of *S. quadripunctatus* are readily distinguished by large size, dark color, filiform antennae, microsculptured abdomen, and normally developed eyes.

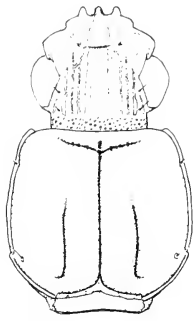
Description. – Since *S. quadripunctatus* is the only known member of the *quadripunctatus* group, and since specimens may readily be identified from the original description, a detailed redescription is not required. Head and pronotum, Fig. 115. Left elytron with four or five discal setae on interval three. Male genitalia, Fig. 119; three specimens examined.

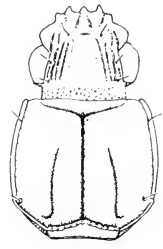
Measurements and proportions. Largest specimen, female: TL, 6.20 mm; LE, 3.97 mm; WH, 1.20 mm; WP, 1.65 mm; WE, 2.06 mm; WF/WH, 0.59; LP/WP, 0.88; DP/LP, 0.87; LP/WE, 0.70; Ta/Ti, 0.69; PS/LP, 0.61. Smallest specimen, female: TL, 5.35 mm; LE, 3.37 mm; WH, 1.05 mm; WP, 1.39 mm; WE, 1.81 mm; WF/WH, 0.60; LP/WP, 0.91; DP/LP, 0.86; LP/WE, 0.70; Ta/Ti, 0.65; PS/LP, 0.59.

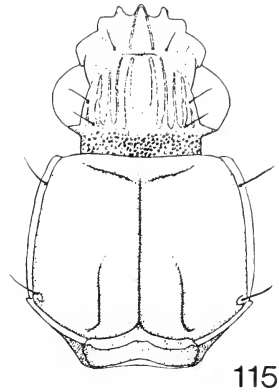
Etymology. – Latin, *quadri* = four, plus *punctum* = small hole, in reference to the normal number of setae on each elytron.

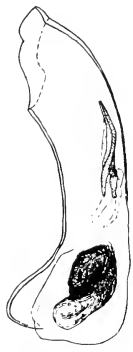
Distribution. – *S. quadripunctatus* is known from two localities in southern Brazil, including the type locality in Parana state, and from one locality in Argentina. I examined 199 specimens from Nova Teutonia, Santa Catarina, Brazil (DRWh, MCZ, MGFT), and one specimen from Pico, La Pampa, Argentina (MCZ).

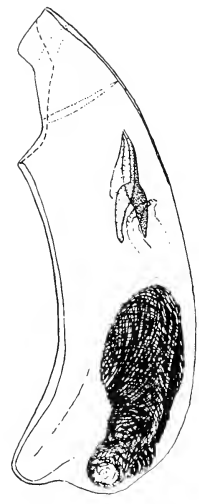












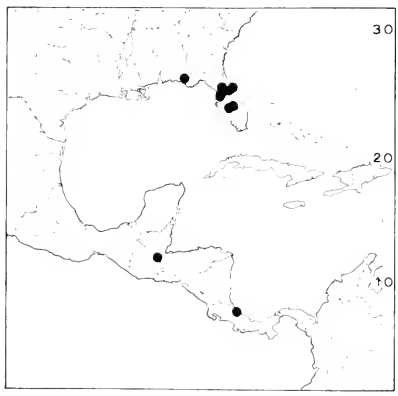


Fig. 112-115. Head and pronotum, dorsal aspect. 112. *S. ocellatus* new species, Grutas das Areias, Brazil. 113. *S. lindrothi* new species, Southport, Florida. 114. *S. banningeri* Kult, Terezina, Brazil. 115. *S. quadripunctatus* Putzeys, Nova Teutonia, Brazil. Fig. 116-119. Male median lobe, lateral aspect. 116. *S. ocellatus* new species, Grutas das Areias, Brazil. 117. *S. lindrothi* new species, Southport, Florida. 118. *S. banningeri* Kult, Terezina, Brazil. 119. *S. quadripunctatus* Putzeys, Nova Teutonia, Brazil. Fig. 120. Male endophallus, *S. lindrothi* new species, Southport, Florida. Fig. 121. Known distribution of *S. lindrothi* new species.

Collecting notes. – Fritz Plaumann collected specimens of this species in January, February, March, April, August, September, and November, so adults probably are active throughout the year.

Taxonomic notes. – Although I saw no type material, specimens seen well match the original description of this distinctive species, and as the locality in Santa Catarina is near the type locality I have no doubt that I have associated the name correctly.

The *truquii* group

Diagnostic combination. – Members of this group are distinguished from all other in the genus by unusually elongated paramedian pronotal sulci, which extend nearly to the anterior transverse impression. They are further characterized by the following additional characters: body subcylindrical; paramedian clypeal carinae extended to median tooth, but more strongly raised in basal half; clypeal field triangular, its base over 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten submoniliform, slightly elongate; anterior tarsi slender in both sexes; elytral disc with setae on intervals three, five, and seven; sternum seven with paramedian ambulatory setae in males only; paramedian carinae of sternum three usually curved at apices; pygidium not crenulate in either sex; and endophallus without enlarged spines.

Distribution. – The only known species in the group, *S. truquii* Putzeys, is probably restricted to the southern edge of the Trans-Volcanic Sierra of central Mexico, and northward along western slopes of the Sierra Madre Occidental to Sinaloa. I examined 42 specimens of the *truquii* group.

Schizogenius truquii Putzeys

Schizogenius truquii Putzeys 1866:224. *Type locality* Mexico, here restricted to Cuernavaca, Morelos; type in IRSB, female specimen labelled lectotype here so designated (!). Bates 1881:37.

Diagnostic combination. – *S. truquii* is the only species of the genus known to have paramedian pronotal sulci extended forward nearly to anterior transverse impression.

Description. – Body subcylindrical. Color dark rufopiceous, without metallic luster, appendages rufous.

Integument. Fine microsculpture on paramedian frontal sulci, genae, mouthparts, anterior surfaces of front tibiae and femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, and small patch near coxal depressions of sternum three.

Head. Fig. 122. Clypeal carinae extended to median tooth, more strongly raised in basal half; clypeal field triangular, narrow, wider at base than apex of median frontal sulcus. Clypeal suture sharply engraved. Frons with median field smooth, without median carina. Eye globose, finely and uniformly faceted. Neck sparsely, rather coarsely punctate. Gena rugose in front. Antennal articles five to ten distinctly elongate, submoniliform; article five 1.2-1.3 times as wide as long.

Pronotum. Fig. 122. Sides bisetose, hind angles prominent, base not rugose. Paramedian sulci elongated nearly to anterior transverse impression, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression punctate. No evident paralateral carinae.

Legs. Front and middle tarsi slender, without dense ventral pubescence; hind tarsus slender, short. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia evenly narrowed to base where much narrower than at base of antennal cleaner. Front femur not strongly constricted near apex.

Elytra. Six to eight setigerous punctures on interval three, five to eight on interval five, and three to five on interval seven. Striae deep and sharply engraved, distinctly punctate except at apex. Intervals one to eight broad, convex; interval eight carinate at apex; intervals three, five, and seven broadly joined at apices.

Abdomen. Sternum three with paramedian carinae usually suddenly curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 127; endophallus, Fig. 137, with poorly developed basal collar spines; five specimens examined.

Measurements and proportions. See Table 8.

Variation. – The smallest (LE, 2.15 mm) and largest (LE, 2.56 mm) specimens are females from La Garita, Jalisco. A female from Sinaloa has a flatter body (DP/LP, 0.77) and much smaller eyes (WF/WH, 0.67) than do other specimens.

Etymology. – *S. truquii* was named to honor E. Truqui, who collected the specimens which Putzeys first reported as this species.

Distribution. – Specimens of *S. truquii* have been found in central and western Mexico at moderate elevations, from about 1500′ to 4000′ (Fig. 145). I studied 42 specimens from the following localities.

MEXICO

JALISCO: San Diego Cocula (1; USNM), 0.4 mi. w. Cocula (2; DRWh), 8.5 mi. n. Juchitlan (2; MCZ), La Garita (32; BMNH, CAS, CNC, IRSB, UASM). MICHOACAN: 8.5 mi. n. Nueva Italia (1; USNM). MORELOS: Cuernavaca (2; BMNH). SINALOA: 21 mi. e. Villa Union (1; CNC).

Table 8. Descriptive statistics for *S. truquii*, based on 20 males from La Garita, Jalisco.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.67-4.06	3.854	0.188	0.056	3.26
LE	2.25-2.48	2.347	0.125	0.037	3.54
WH	0.75-0.85	0.805	0.039	0.012	3.26
WP	0.93-1.08	1.000	0.063	0.019	4.19
WE	1.15-1.27	1.204	0.060	0.018	3.40
B. Setae on left elytron.					
Interval 3	6- 8	6.4			
Interval 5	5- 8	6.6			
Interval 7	3- 5	4.2			
Total	14-20	17.3	2.0	0.6	7.74
C. Proportions.					
WF/WH	0.60-0.64	0.621	0.017	0.006	2.22
LP/WP	0.96-1.02	0.988	0.026	0.008	1.75
DP/LP	0.78-0.85	0.807	0.024	0.007	1.97
LP/WE	0.79-0.86	0.819	0.028	0.008	2.28
Ta/Ti	0.62-0.73	0.672	0.052	0.015	5.12
PS/LP	0.85-0.90	0.882	0.022	0.007	1.66

Collecting notes. – At La Garita, the only locality at which a long series of this species was taken, I found no other species of *Schizogenius*. I noted nothing peculiar about the locality, and other carabid beetles taken there are found abundantly elsewhere along similar gravel streams. At other localities in Jalisco and Michoacan where I found specimens of *S. truquii*, the *Schizogenius* fauna included representatives of two or three additional species. Specimens from these states include nearly twice as many males as females, possibly because of the season; all were collected in January or March, and none of the collecting localities were revisited at a later season. The Sinaloa specimen was taken in July, at light.

Taxonomic notes. – Putzeys (1866) described the body as strongly convex, and the elytron as having 12 setae each on intervals three, five, and seven. These observations are clearly erroneous. The lectotype specimen agrees with my description, and is undoubtedly one of the specimens studied by Putzeys; it has a printed label, "Truqui Mexique," as well as Putzeys' handwritten green determination label.

The *brevisetosus* group

Diagnostic combination. – Specimens of this group are distinguished by the following combination of characters: elytron with 35 or more short discal setae; abdomen without extensive microsculpture; body depressed; color castaneous; size large, LE over 2.70 mm in all specimens seen. Also: paramedian clypeal carinae extended to median tooth, more strongly raised in basal half; clypeal field triangular, its base under 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; discal setae present on intervals three, five, and seven; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae curved at apices; pygidium not crenulate in either sex; and endophallus with basal collar spines distinct.

Distribution. – *S. brevisetosus* is known from Coahuila, New Mexico, and Texas. The group is probably most closely allied to the *pluripunctatus* group, but differs in various ways, notably by short elytral setae. The two groups are allopatric but proximate in geographic distribution. I examined 42 specimens of the *brevisetosus* group.

Schizogenius brevisetosus new species

Type material. – Holotype male and allotype female labelled "Sanderson, TEX. April 27, 1959 Becker & Howden" (CNC). An additional 32 specimens collected at various times and places in Texas are paratypes (CAS, CNC, CUNY, DRWh, LACM, MCZ, UASM, USNM).

Diagnostic combination. – Specimens of this distinctive species are readily distinguished from all others in the genus by the combination of large size, pale coloration, deplanate body, numerous short discal setae on elytra, and lack of extensive microsculpture on abdomen.

Description. – Body deplanate. Color dark castaneous, without definite aeneous luster, appendages paler.

Integument. Conspicuous microsculpture on paramedian sulci of frons, genae, mouthparts, front tibiae and anterior surfaces of front femora, middle legs except trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura in apical two-thirds and at extreme base, and coxal depressions of sternum three.

Head. Fig. 123. Labrum weakly biemarginate. Paramedian carinae of clypeus straight, extended to median tooth, strongly raised in basal half; median field triangular, narrow, slightly wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye globose, finely and uniformly faceted. Neck densely, coarsely punctate. Gena coarsely

punctate, rugose in front. Antennal articles four to ten elongate, filiform; article five 1.7 times as long as wide.

Pronotum. Fig. 123. Sides bisetose, hind angles sharp and prominent, base not rugose. Paramedian sulci elongate, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi slightly but distinctly dilated and pubescent ventrally; hind tarsus slender, quite short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 13-20 setae on interval three, 12-18 on interval five, and 10-14 on interval seven. Striae deep, sharply engraved, finely but distinctly punctate nearly to apex. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles sharp and prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe, Fig. 128; endophallus (Fig. 138) with well developed basal collar spines. Three specimens examined.

Measurements and proportions. See Table 9. Of holotype: TL, 4.87 mm; LE, 3.05 mm; WH, 0.95 mm; WP, 1.26 mm; WE, 1.62 mm; WF/WH, 0.64; LP/WP, 0.95; DP/LP, 0.79; LP/WE, 0.74; Ta/Ti, 0.59; PS/LP, 0.72. Of allotype: TL, 4.63 mm; LE, 2.98 mm; WH, 0.85 mm; WP, 1.17 mm; WE, 1.17 mm; WF/WH, 0.66; LP/WP, 0.92; DP/LP, 0.79; LP/WE, 0.72; Ta/Ti, 0.62; PS/LP, 0.68.

Table 9. Descriptive statistics for *S. brevisetosus,* based on 16 males from Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.40-4.97	4.699	0.187	0.062	2.65
LE	2.79-3.12	2.949	0.188	0.039	2.66
WH	0.82-0.97	0.913	0.051	0.017	3.75
WP	1.11-1.32	1.220	0.064	0.021	3.48
WE	1.46-1.63	1.549	0.068	0.023	2.92
B. Setae on left elytron.					
Interval 3	13-20	15.6			
Interval 5	12-18	14.9			
Interval 7	10-14	11.9			
Total	35-50	42.4	5.3	1.8	8.35
C. Proportions.					
WF/WH	0.63-0.67	0.650	0.017	0.006	1.77
LP/WP	0.90-0.95	0.929	0.022	0.007	1.54
DP/LP	0.76-0.80	0.791	0.017	0.006	1.42
LP/WE	0.69-0.76	0.729	0.028	0.009	2.52
Ta/Ti	0.57-0.61	0.591	0.021	0.007	2.38
PS/LP	0.67-0.74	0.694	0.029	0.010	2.83

Variation. – Available material is too limited to permit study of geographic variation in this species. Males average about 0.2 mm smaller than females. The largest (LE, 3.33 mm) and smallest (LE, 2.83 mm) females are from Hope, New Mexico, and Limpia Canyon, Texas, respectively; the largest (LE, 3.05 mm) and smallest (LE, 2.74 mm) males are both from Sanderson, Texas.

Etymology. – Latin, *brevis* = short, plus *setosus* = bristly, in reference to the short discal elytral setae.

Distribution. – Specimens of *S. brevisetosus* have been collected from eastern New Mexico, east to central Texas, and south to Coahuila, from the Colorado River in the north to the Rio Grande drainage system in the south (Fig. 146). I examined 42 specimens from the following localities.

UNITED STATES

NEW MEXICO: Eddy Co., Hope (2; UKSM). TEXAS (1; USNM): Blanco Co., Cypress Mills (1; USNM); Brewster Co. (1; MCZ), Alpine (3; CUNY, MCZ); Jeff Davis Co., Davis Mountains (3; CAS), Limpia Canyon (6; DRWh, UASM), Barrel Springs Creek (1; DRWh), Fort Davis (4; CNC); Kerr Co., Kerrville (4; CNC); Terrell Co., Lozier Canyon (3; MCZ), Sanderson (6; CNC); Uvalde Co., Garner State Park (2; LACM).

MEXICO

COAHUILA: La Gloria, s. of Monclova (3; AMNH).

Collecting notes. – Specimens of this species have been collected from April to August, frequently at light, apparently not always near streams (e.g., Lozier Canyon and La Gloria). I collected two specimens in typical gravel streams near Fort Davis, Texas, along with specimens of *S. scopaeus.*

The *pluripunctatus* group

Diagnostic combination. – The most obvious diagnostic feature of members of this North and Middle American group is unusual length of discal setae on elytron; these setae generally are about 1.2 times as long as the maximum width of interval two, or longer. Specimens of some South American species also have long setae; from these, members of the *pluripunctatus* group are distinguished by the following additional characters in combination: setae present on intervals three, five, and seven of elytra; pronotum without marginal carinae; mentum without accessory setae; and pygidium of female not crenulate. Most included forms are densely setose, with more than ten setae on elytral interval three. Additional characters of members of the group are: form cylindrical to subcylindrical; paramedian clypeal carinae extended to median tooth, sometimes strongly raised in basal half; clypeal field triangular, its base under 1.5 apical width of median frontal sulcus; clypeal suture sharply impressed; antennal articles five to ten filiform; anterior and middle tarsi slightly to strongly broadened, especially in males; sternum seven with paramedian ambulatory setae in males, sometimes in females; paramedian carinae of sternum three curved at apices; abdomen without extensive microsculpture; endophallus with distinct basal collar spines. The group contains the only known species in the genus with more than two pairs of lateral setae on the pronotum.

Distribution. – This group includes several similar, allopatric forms, in two geographic subgroups. One subgroup ranges from northern California south to southern Baja California. The second subgroup ranges from southern Arizona and New Mexico, south to Guatemala, and north in the east to Nuevo Leon and Tamaulipas. I examined 585 specimens of the *pluripunctatus* group.

Taxonomic notes. – The two geographic subgroups could be termed "superspecies," and

I relied in part on statistical analyses to sort out taxonomic relationships within them. The Californian subgroup, with two allopatric forms here treated as subspecies, is distinguished by more flattened body form and short deflexed apex of male median lobe. The second subgroup, with four allopatric forms here recognized as species, is distinguished by more cylindrical body form and relatively longer deflexed apex of male median lobe.

Schizogenius seticollis Fall

Diagnostic combination. – Specimens of this species, one of two species in the genus characterized by accessory marginal setae on the pronotum, differ from those of *S. plurisetosus* by form of male median lobe. *S. plurisetosus* is intermediate between the two subspecies of *S. seticollis* in numbers of elytral setae, but has fewer pronotal setae and normally only one seta in recessed pits at pronotal hind angles rather than two or three. The form of the median lobe, with deflexed apical portion proportionately short, is diagnostic of specimens of *S. seticollis* within the *pluripunctatus* group.

Schizogenius seticollis seticollis new combination

Schizogenius seticollis Fall 1901:209. *Type locality* Pomona, California; type in MCZ; specimen labelled MCZ type 23859 here designated lectotype (!). Lindroth 1961:165.

Diagnostic combination. – Specimens of this subspecies are distinguished by fewer than 60 setae per elytron, and most specimens have fewer marginal pronotal setae.

Description. – Body subcylindrical. Color piceous; mandibles, mentum, front coxae, trochanters, tibiae, femoral apices, and in some specimens margin and apex of elytron rufopiceous; antennae, at least at base, rufous; and labial palpi, maxillae, and tarsi testaceous; no pronounced metallic or aeneous luster.

Integument. Fine but conspicuous microsculpture on mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, extreme bases of epipleura, and small areas in coxal depressions of sternum three. Microsculpture irregular and indistinct in paramedian frontal sulci.

Head. Fig. 124. Clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, globose, finely and uniformly faceted. Neck densely, coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.6 times as long as wide.

Pronotum. Fig. 124. Sides plurisetose, generally with seven to 11 setae on each side, two or three setae in pits recessed from hind angles; hind angles obsolete; base not rugose. Paramedian sulci rather short, impunctate, nearly straight, deep throughout, slightly hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi dilated and pubescent ventrally in both sexes, slightly more so in males; hind tarsus slender, rather short. Paronychia conspicuous, more than half length of tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Discal setae about 1.2 times as long as maximum width of interval two. Among 20 specimens examined, 10-17 setae on interval three, 12-19 on interval five, and 11-23 on interval seven; most setae adjacent to corresponding inner striae, but up to 25% irregular, slightly biseriate. Striae deep and sharply engraved, finely to indistinctly punctate in basal half or two-thirds. Intervals one to seven broad and slightly convex, interval eight carinate at apex;

apices of intervals three, five, and seven broadly joined. Humeral denticles small, sharp.

Abdomen. Sternum three with paramedian carinae straight or curved outward at apices. Sternum seven with paramedian ambulatory setae in male only. Pygidium with apical margin entire in both sexes.

Male genitalia. Median lobe (Fig. 129) elongate, narrow; apex deflected at weak angle, relatively short; endophallus with well developed basal collar spines (Fig. 139); four specimens examined.

Measurements and proportions. See Table 10.

Table 10. Descriptive statistics for *S. seticollis seticollis*, based on 11 males from Los Angeles County, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.73-4.68	4.381	0.404	0.162	6.14
LE	2.29-2.86	2.686	0.238	0.096	5.91
WH	0.78-0.95	0.896	0.080	0.032	5.97
WP	1.00-1.26	1.187	0.111	0.045	6.23
WE	1.22-1.57	1.451	0.136	0.055	6.24
B. Setae on left elytron.					
Interval 3	12-17	13.8			
Interval 5	13-19	16.2			
Interval 7	12-23	17.3			
Total	40-58	47.3	8.6	3.5	12.11
C. Proportions.					
WF/WH	0.60-0.65	0.625	0.020	0.008	2.18
LP/WP	0.87-0.94	0.919	0.029	0.012	2.09
DP/LP	0.81-0.87	0.838	0.025	0.010	1.98
LP/WE	0.72-0.78	0.752	0.029	0.012	2.58
Ta/Ti	0.61-0.74	0.659	0.059	0.024	5.96
PS/LP	0.62-0.68	0.643	0.029	0.012	3.04

Variation. – I found little noteworthy variation in this subspecies. In five selected samples (samples one to five), I found little significant clinal variation in size (Fig. 148, Table 11); slightly increased numbers of discal elytral setae to the south (Fig. 149, Table 12); slightly increased eye size to the south (Fig. 150, Table 13); and slightly narrowed pronotum to the south (Fig. 151, Table 14).

Etymology. – Latin, *seta* = bristly, plus *collis* = hill, in reference to the marginal setae of the pronotum.

Distribution. – Specimens of *S. seticollis seticollis* have been collected in central and western California, from Shasta County in the north to San Diego County in the south (Fig. 147). I examined 232 specimens from the following localities.

Table 11. Variation in body size (LE, in mm) in selected samples of the *seticollis* subgroup; see Fig. 148.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	2.72-3.19	2.935	0.204	0.068	4.64
2	16	8	2.65-3.26	2.942	0.272	0.091	6.17
3	10	5	2.63-3.35	3.095	0.315	0.133	6.97
4	18	9	2.50-3.18	2.827	0.314	0.099	7.41
5	22	11	2.29-2.96	2.747	0.231	0.066	5.61
S. s. vandykei.							
6	10	5	2.54-3.34	2.886	0.406	0.171	9.39

Table 12. Variation in numbers of discal setae on left elytron in selected samples of the *seticollis* subgroup; see Fig. 149.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	35- 49	39.9	5.4	1.8	9.05
2	16	8	33- 46	37.4	5.9	2.0	10.47
3	10	5	42- 51	46.3	4.8	2.0	6.98
4	18	9	33- 53	41.2	7.7	2.4	12.39
5	22	11	40- 53	46.7	7.6	2.2	10.91
S. s. vandykei.							
6	10	5	71-104	83.5	16.4	6.9	12.85

Table 13. Variation in eye size (WF/WH) in selected samples of the *seticollis* subgroup; see Fig. 150.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	0.62-0.66	0.631	0.017	0.006	1.81
2	16	8	0.62-0.66	0.639	0.018	0.006	1.88
3	10	5	0.62-0.65	0.633	0.017	0.007	1.83
4	18	9	0.59-0.65	0.629	0.023	0.007	2.41
5	22	11	0.60-0.65	0.626	0.018	0.005	1.89
S. s. vandykei.							
6	10	5	0.61-0.66	0.640	0.022	0.009	2.33

Table 14. Variation in pronotal form (LP/WP) in selected samples of the *seticollis* subgroup; see Fig. 151.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. s. seticollis.							
1	16	8	0.88-0.94	0.914	0.028	0.009	2.07
2	16	8	0.90-0.95	0.918	0.023	0.008	1.66
3	10	5	0.89-0.95	0.917	0.029	0.012	2.12
4	18	9	0.88-0.96	0.924	0.030	0.009	2.17
5	22	11	0.87-0.94	0.920	0.026	0.007	1.91
S. s. vandykei.							
6	10	5	0.89-0.98	0.938	0.039	0.016	2.74

UNITED STATES

CALIFORNIA (9; ANSP, CAS, USNM): Colorado Desert (1; MCZ); Alameda Co., Berkeley (1; CUNY), 17.5 mi. s. Livermore (1; CAS), Sunol Valley (1; GRNo); Calaveras Co., Mokelumne Hill (9; CAS); Colusa Co., Cooks Springs (1; CAS); El Dorado Co., Latrobe (2; CAS); Fresno Co., Camp Greeley (5; CAS, CNC, KSUM), Le Ferre Creek (2; CAS), Trimmer (1; CAS), 3.5 mi. e. Trimmer (8; DRWh, TLEr, UASM), 11.6 mi. s. Tollhouse (3; TLEr); Glenn Co., Elk Creek (1; CAS); Humboldt Co., Garberville (1; CAS); Kings Co., Stratford (1; CAS); Lake Co. (2; CAS), Kelsey Creek (2; CAS), Middle Creek (2; CAS); Los Angeles Co. (6; CAS, USNM), Azuza (1; CAS), 4½ mi. ne. Claremont (1; INHS), La Canada (1; CAS), Los Angeles (1; INHS), Palmdale (1; CAS), Pasadena (5; CAS), Pomona (3; MCZ, RUNB), Pomona Mountains (5; CUNY, MCZ), San Gabriel Mountains (2; TCBa), Saugus (1; CAS); Tujunga (4; MCZ); Mendocino Co. (5; JNeg), Dry Creek (13; CAS); Monterrey Co., Arroyo Seco Camp (1; TLEr), Bradley (3; MCZ, UCB); Napa Co. (1; CNHM), Monticello (1; UCD), Pope Creek (2; CAS), Rutherford (3; TLEr), Santa Helena (2; MCZ, CAS); Riverside Co., Riverside (3; CAS, USNM), San Jacinto Mountains (1; CAS); San Benito Co., Pinnacles National Monument (1; CAS), San Benito River (2; CAS); San Bernadino Co., 0.9 mi. ne. Cedar Springs (3; GRNo, LBSC), Lytle Creek (4; MCZ), Mojave River (1; GRNo), San Bernadino (1; CAS), San Bernadino Mountains (3; MGFT); San Diego Co., San Diego (5; MCZ, CAS), Warners (3; UKSM); San Joaquin Co., Manteca (4; CAS); San Luis Obispo Co., Paso Robles (3; CAS, UKSM), Santa Margarita (4; CAS); San Mateo Co., Foster (1; CAS); Santa Barbara Co. (1; CAS), Santa Inez Mountains (3; CAS); Santa Clara Co., Gilroy Hot Springs (10; DJLa, TLEr), Mount Hamilton (5; CAS, TLEr); Santa Cruz Co. (1; CNHM); Shasta Co., Redding (15; CAS), 10 mi. ne. Redding (1; DHKa); Sonoma Co. (1; AMNH), Duncan Mills (2; CAS), Healdsburg (3; CAS), 2 mi. e. Healdsburg (1; CAS), Russian River (8; CAS, MCZ), Santa Rosa (2; MCZ), 2.5 mi. w. Skaggs Springs (8; CAS), Sobre Vista (2; CAS), Sylvania (3; CAS, MCZ); Stanislaus Co., 22 mi. w. Patterson (4; CAS); Tehama Co. (2; CAS); Tulare Co., Kaweah (1; CAS), Ventura Co., 9 mi. sw. Stauffer (1; UCB); Yolo Co., Davis (2; UCD), Rumsey (1; UCD).

Collecting notes. – Specimens have been collected from March through October, most of them along gravel streams. Some were taken at lights, indirect evidence that adults can fly. I have not collected specimens of this subspecies.

Taxonomic notes. – See discussion for *S. seticollis vandykei*.

Schizogenius seticollis vandykei new subspecies

Type material. – Holotype male and allotype female labelled "MEX. B.Cal. 3 mi. NW of Miraflores 19–I–1959" and "Canon San Bernadino. Boca de la Sierra" and "H. B. Leech Collector" (CAS). Nine additional specimens from various localities in southern Baja California are paratypes (CAS, DRWh, UASM).

Diagnostic combination. – All known specimens of this subspecies have more than 60 discal setae per elytron, and thus differ from specimens of *S. seticollis seticollis.*

Description. – As in *S. s. seticollis* except as follows. Base of frons (Fig. 125) more

strongly calloused. Pronotum with 10-14 setae on each side. Elytron with 18-36 setae on interval three, 27-35 on interval five, and 22-37 on interval seven; arrangement of setae on intervals three, five, and seven strongly biseriate; discal setae about 1.5 times as long as the maximum width of interval two. Male genitalia (Fig. 130) not distinctive, two specimens examined.

Measurements and proportions. See Table 15. Of holotype: TL, 4.63 mm; LE, 2.83 mm; WH, 0.92 mm; WP, 1.18 mm; WE, 1.48 mm; WF/WH, 0.61; LP/WP, 0.98; DP/LP, 0.82; LP/WE, 0.78; Ta/Ti, 0.66; PS/LP, 0.65. Of allotype: TL, 4.81 mm; LE, 2.96 mm; WH, 0.95 mm; WP, 1.28 mm; WE, 1.57 mm; WF/WH, 0.65; LP/WP, 0.93; DP/LP, 0.82; LP/WE, 0.76; Ta/Ti, 0.65; PS/LP, 0.65.

Table 15. Descriptive statistics for *S. seticollis vandykei*, based on six males and five females from southern Baja California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.14-5.40	4.625	0.666	0.268	9.60
LE	2.54-3.34	2.856	0.414	0.166	9.67
WH	0.83-1.05	0.915	0.117	0.047	8.52
WP	1.06-1.38	1.199	0.179	0.072	9.97
WE	1.34-1.78	1.505	0.208	0.083	9.20
B. Setae on left elytron.					
Interval 3	18- 36	24.0			
Interval 5	27- 35	30.4			
Interval 7	22- 37	30.0			
Total	71-104	84.4	16.3	6.5	12.86
C. Proportions.					
WF/WH	0.61-0.66	0.639	0.022	0.009	2.25
LP/WP	0.89-0.98	0.940	0.038	0.015	2.69
DP/LP	0.82-0.90	0.845	0.041	0.017	3.27
LP/WE	0.70-0.79	0.747	0.040	0.016	3.59
Ta/Ti	0.61-0.69	0.659	0.035	0.014	3.49
PS/LP	0.61-0.67	0.637	0.028	0.011	2.90

Variation. – See Tables 11-14.

Etymology. – I dedicate this subspecies to E. C. Van Dyke, who provided much of our knowledge about the Coleoptera of southwestern United States.

Distribution. – Specimens of this subspecies are known only from a few localities in southern Baja California (Fig. 147). I studied 11 specimens from the following localities.

MEXICO

BAJA CALIFORNIA: Arroyo Saltito near Las Cruces (5; CAS, DRWh, UASM), 20 mi. n. Comondu (1; CAS), Hamilton Ranch (1; CAS), 3 mi. nw. Miraflores (2; CAS).

Collecting notes. – Adults of *S. seticollis vandykei* are probably active throughout the year, as I have records for January, July, and August. I know nothing about their habits, but suspect they may be found along intermittent streams. Aside from *S. auripennis, S. falli,* and *S. pygmaeus*, the subspecies is the only member of the genus known from Baja California.

Taxonomic notes. – I recognize *S. seticollis vandykei* as a distinct subspecies because it clearly is closely related to *S. seticollis seticollis*, there is no evidence of reproductive isolation between them, and all known specimens of each subspecies are distinguished by numbers of discal elytral setae. I suspect that the ranges of the two subspecies are disjunct in central and northern Baja California, or at least they are joined only by steeply stepped character clines.

As shown in Tables 11-14 and Fig. 148-151, sample six, *S. seticollis vandykei* does not differ significantly in body size from samples one to five, *S. seticollis seticollis*; it is more different from southern than northern samples of *S. s. seticollis* in eye size, but not significantly different from any of them; and the pronotum is narrower than in any of the *S. s. seticollis* but not statistically significantly different from the southernmost samples. In the number of discal elytral setae, however, despite a slightly greater similarity of *S. s. vandykei* to southern rather than northern samples of *S. s. seticollis*, the differences are large, indeed are taxonomically significant at 1.5 standard deviations from means. Numbers of discal elytral setae are, in general, directly correlated with body size. From Tables 11 and 12, ratios formed of the mean values for number of setae to elytral length are, for samples one to six, respectively: 13.6, 12.7, 15.0, 14.6, 17.0, and 29.6 setae per mm. A definite increase from north to south is evident from samples one to five, but a large hiatus still exists between samples five and six. I conclude from these observations that reproductive isolation between the two subspecies is indeterminate, but that they are at least isolated geographically. Collections from central and northern Baja California are needed to better define geographic and reproductive relationships.

Schizogenius plurisetosus new species

Type material. – Holotype male and allotype female labelled "MEX. Tamaulipas Rio Purificacion nr. El Barretal Rte. 85 800′ X. 19. 65" and "George E. Ball D. R. Whitehead collectors" (MCZ). An additional 15 specimens from various localities in Nuevo Leon and Tamaulipas are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. – Specimens of this species are readily distinguished from specimens of *S. seticollis* by having fewer accessory marginal pronotal setae, and only one seta in pit near hind angle. Also: apical portion of male median lobe proportionately longer and more sharply deflexed; front and middle tarsi less expanded; and range, in northeastern Mexico, sharply disjunct.

Description. – As in *S. seticollis seticollis*, except as follows. Legs paler, femora uniformly rufopiceous. Form and sculpture of head and pronotum, Fig. 126; genae less coarsely sculptured; pronotum with five to seven setae on each side, usually with only one in a pit recessed from the hind angle; basal impression distinctly punctate; anterior transverse impression nearly impunctate. Elytron with 18-24 setae on interval three, 17-30 on interval five, and 17-22 on interval seven; setae moderately biseriate; discal setae about 1.5 times as long as the maximum width of interval two; striae indistinctly punctate. Front and middle tarsi much narrower. Male genitalia with apex of median lobe (Fig. 131, slightly distorted) sharply deflexed, proportionately long; endophallus, Fig. 140; four specimens examined.

Measurements and proportions. See Table 16. Of holotype: TL, 3.98 mm; LE, 2.43 mm; WH, 0.80 mm; WP, 1.06 mm; WE, 1.24 mm; WF/WH, 0.61; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.80; Ta/Ti, 0.60; PS/LP, 0.63. Of allotype: TL, 4.25 mm; LE, 2.65 mm; WH, 0.83 mm; WP, 1.11 mm; WE, 1.35 mm; WF/WH, 0.62; LP/WP, 0.92; DP/LP, 0.83; LP/WE, 0.76; Ta/Ti, 0.66; PS/LP, 0.66.

Table 16. Descriptive statistics for *S. plurisetosus*, based on seven males from Nuevo Leon and Tamaulipas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.78-4.69	4.234	-	-	-
LE	2.33-2.92	2.546	-	-	-
WH	0.76-0.91	0.824	-	-	-
WP	0.98-1.25	1.086	-	-	-
WE	1.18-1.48	1.293	-	-	-
B. Setae on left elytron.					
Interval 3	18-24	21.0			
Interval 5	17-30	21.7			
Interval 7	17-23	20.7			
Total	52-74	63.4			
C. Proportions.					
WF/WH	0.60-0.64	0.613	-	-	-
LP/WP	0.92-0.95	0.936	-	-	-
DP/LP	0.80-0.82	0.810	-	-	-
LP/WE	0.77-0.80	0.784	-	-	-
Ta/Ti	0.59-0.69	0.633	-	-	-
PS/LP	0.63-0.70	0.661	-	-	-

Variation. – See Table 16. Two specimens have two setae in a recessed pit on one side of the pronotum; all others have only one seta per pit.

Etymology. – Latin, *pluralis* = more than one, plus *setosus* = bristly, in reference to the large numbers of setae which characterize members of this species.

Distribution. – Specimens of this species have been collected only in Nuevo Leon and Tamaulipas, from the Rio Salinas, a tributary of the Rio Grande, south to the Rio Corona, a tributary of the Rio Soto la Marina (Fig. 147). The species is not known to range into the United States, but may do so. I studied 17 specimens, all collected by G. E. Ball or me during 1964 to 1966, from the following localities.

MEXICO

NUEVO LEON: Cienega de Flores (5; UASM), Linares (2; DRWh). TAMAULIPAS: El Barretal (6; CAS, CNC, MCZ). 15.2 mi. n. Ciudad Victoria (1; BMNH), 21.3 mi. n. Ciudad Victoria (3; IRSB; USNM).

Collecting notes. – Specimens of *S. plurisetosus* were collected in riparian gravel bars, in July, September, and October, at elevations ranging from 500 to 1200′. At all stations there were fewer specimens of this species than of others in the genus.

Taxonomic notes. – Despite accessory pronotal setae, this species is not closely related to *S. seticollis*, as judged from form of male genitalia. It is most closely related to the geographically proximate *S. multisetosus*, with similar male genitalia. Even so, the form of the apex is slightly but apparently constantly more broadly rounded. This detail, together with the apparently constant accessory pronotal setae, indicates that *S. plurisetosus* and *S. multisetosus* are reproductively isolated. Statistical comparisons between them confirm this distinction. Thus, as shown in Tables 18-23 and Fig. 152-157, samples one to four, there is no important difference in body size, eye size, or relative pronotal size, but numbers of discal elytral setae are much greater in sample one, *S. plurisetosus*, than in any sample (see Fig. 153) of *S. multisetosus*. Also, the northernmost sample of *S. multisetosus* differs by having statistically significantly broader pronota and statistically significantly longer paramedian pronotal sulci.

Schizogenius multisetosus Bates

Schizogenius multisetosus Bates 1891:233. *Type locality* Huitzo, Oaxaca; type in BMNH, male specimen labelled holotype here designated lectotype (!).

Diagnostic combination. – The combination of two pairs of marginal setae on the pronotum, sharply deflexed apical portion of the median lobe, and lack of paramedian ambulatory setae in females, distinguishes this species from other members of the *pluripunctatus* group. Also, numbers of setae on the elytral disc, in specimens examined, range from 37 to 56.

Description. – As in *S. seticollis seticollis* except: legs paler, femora uniformly rufous to rufopiceous, tibiae paler; abdomen often paler toward apex. Form and sculpture of head and pronotum as in *S. plurisetosus*, Fig. 126, except sides of pronotum bisetose and basal transverse impression less distinctly punctate. In specimens studied, elytron with 12-18 setae on interval three, 12-21 on interval five, and 12-20 on interval seven; setae mostly adjacent to corresponding inner striae, not markedly biseriate. Male genitalia with median lobe (Fig. 132-134) with apical portion sharply deflexed, proportionately long; endophallus, Fig. 141-142; 24 specimens examined.

Measurements and proportions. See Table 17.

Variation. – Samples of sufficient size for statistical analysis were available from only three localities. Data on variation in six characteristics in these samples, numbered two to four as in Fig. 152-157, are given in Tables 18-23. All three samples differ significantly from one another in body size (Fig. 152, Table 18). Other statistically significant differences are: sample two, shorter paramedian pronotal sulci (Fig. 157, Table 23); sample three, proportionately smaller thorax (Fig. 156, Table 22); and sample four, broader pronotum (Fig. 155, Table 21). These samples therefore represent populations which are equally well isolated from one another geographically, so no analysis of clinal relationships is feasible. The median lobe, especially at base, varies in form; most specimens from the Rio Moctezuma at 300′ have a reduced basal lobe, and those from the Rio Balsas usually have a less sharply angulate apical deflection. A male from Hidalgo, collected at 5300′ in the Rio Moctezuma drainage system, is in most ways similar to the Rio Balsas specimens but has the large thorax characteristic of Tamazunchale specimens; it may represent a truly intermediate population.

Etymology. – Latin, *multus* = most, plus *setosus* = setose, in reference to the numerous discal setae of the elytra.

Table 17. Descriptive statistics for *S. multisetosus*, based on 14 males from 72.5 miles south of Valle Nacional, Oaxaca.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.84-4.44	4.093	0.315	0.112	5.13
LE	2.34-2.78	2.546	0.201	0.072	5.27
WH	0.75-0.90	0.816	0.068	0.024	5.51
WP	0.95-1.15	1.049	0.096	0.034	6.07
WE	1.20-1.45	1.304	0.112	0.040	5.72
B. Setae on left elytron.					
Interval 3	12-17	14.5			
Interval 5	15-20	17.1			
Interval 7	12-18	15.9			
Total	40-54	47.5	5.9	2.1	8.27
C. Proportions.					
WF/WH	0.60-0.64	0.621	0.020	0.007	2.14
LP/WP	0.93-0.97	0.944	0.020	0.007	1.42
DP/LP	0.81-0.87	0.841	0.027	0.010	2.15
LP/WE	0.74-0.78	0.761	0.024	0.009	2.12
Ta/Ti	0.62-0.68	0.649	0.026	0.009	2.67
PS/LP	0.62-0.69	0.654	0.030	0.011	3.09

Distribution. – Specimens of *S. multisetosus* have been collected at altitudes ranging from near sea level in the north to at least 5300′. They are from four river systems in central Mexico (Fig. 147): the Rios Moctezuma and Papaloapan on the Atlantic slopes, and the Rios Balsas and Atoyac on the Pacific. I studied 73 specimens from the following localities.

MEXICO

GUERRERO: 5 mi. s. Iguala (1; CAS). HIDALGO: Rio Tula near Tasquillo 5300′ (1; UASM). MORELOS: Tetecala 2800′ (6; CNC, MCZ, UASM), Yautepec (1; BMNH). OAXACA: Huitzo (2; BMNH), 72.5 mi. s. Valle Nacional 4100′ (25; UASM). PUEBLA: Tehuitzingo 3700′ (1; MGFT), Tepexco (22; UASM). SAN LUIS POTOSÍ: Tamazunchale 300′ (14; CAS, DRWh, IRSB, UASM, USNM).

Collecting notes. – Specimens of *S. multisetosus* were collected during June, August, September, and October. Some, including the entire Tepexco series, were collected at black lights, having doubtless flown there. Others were hand collected in riparian gravel bars, the normal habitat for most species in the subgenus, but on the average in slightly drier places. Some inhabited streams, at least in Puebla, are dry during winter.

Taxonomic notes. – *S. multisetosus*, so far as known, is allopatric with respect to all other members of the group. It does share at least one drainage system, the Rio Papaloapan, with *S. kulti*, and may be sympatric with it. Lack of known sympatry and close similarity of members of the *pluripunctatus* subgroup provide no direct evidence of reproductive isolation between them, but statistical data provide indirect evidence that reproductive isolation exists. Selected samples of *S. plurisetosus, S. multisetosus, S. pluripunctatus,* and

Table 18. Variation in body size (LE, in mm) in selected samples of the *pluripunctatus* subgroup; see Fig. 152.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	2.33-2.93	2.625	0.320	0.114	8.14
S. multisetosus.							
2	14	7	2.50-3.10	2.734	0.251	0.089	6.12
3	22	11	2.33-2.90	2.575	0.227	0.064	5.87
4	20	10	2.07-2.60	2.342	0.232	0.069	6.62
S. pluripunctatus.							
5	18	9	2.05-2.70	2.402	0.251	0.079	6.95
6	10	5	2.15-2.65	2.382	0.228	0.096	6.39
7	18	9	2.09-2.68	2.407	0.218	0.069	6.04
8	8	5	1.98-2.75	2.372	-	-	-
9	10	5	2.15-2.71	2.445	0.237	0.100	6.47
S. kulti.							
10	10	5	2.00-2.55	2.278	0.263	0.111	7.70
11	20	10	1.96-2.65	2.234	0.237	0.071	7.07
12	22	11	1.75-2.25	2.050	0.205	0.058	6.65
13	12	6	2.07-2.44	2.283	0.183	0.070	5.34
14	10	8	2.16-2.60	2.299	-	-	-

Table 19. Variation in numbers of discal setae on left elytron in selected samples of the *pluripunctatus* subgroup; see Fig. 153.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	52-74	64.4	7.4	2.6	7.62
S. multisetosus.							
2	14	7	42-56	48.8	6.0	2.1	8.16
3	22	11	42-55	47.4	5.6	1.6	7.91
4	20	10	37-54	47.0	7.9	2.4	11.28
S. pluripunctatus.							
5	18	9	39-56	47.2	7.4	2.3	10.50
6	10	5	41-57	47.1	8.1	3.4	11.40
7	18	9	39-55	45.3	7.1	2.2	10.51
8	8	5	35-55	43.0	-	-	-
9	10	5	45-61	52.3	8.0	3.4	10.20
S. kulti.							
10	10	5	28-41	34.6	6.0	2.6	11.66
11	20	10	18-28	22.6	3.6	1.1	10.55
12	22	11	19-26	21.8	3.8	1.1	11.72
13	12	6	21-27	22.9	3.0	1.1	8.62
14	10	8	23-31	26.3	-	-	-

Table 20. Variation in eye size (WF/WH) in selected samples of the *pluripunctatus* subgroup; see Fig. 154.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.70-0.66	0.622	0.025	0.009	2.68
S. multisetosus.							
2	14	7	0.59-0.65	0.620	0.027	0.010	2.89
3	22	11	0.60-0.66	0.625	0.021	0.006	2.25
4	20	10	0.60-0.64	0.620	0.015	0.004	1.61
S. pluripunctatus.							
5	18	9	0.61-0.66	0.631	0.020	0.006	2.14
6	10	5	0.59-0.66	0.627	0.030	0.013	3.19
7	18	9	0.61-0.66	0.633	0.022	0.007	2.27
8	8	5	0.61-0.67	0.642	-	-	-
9	10	5	0.60-0.63	0.614	0.013	0.005	1.37
S. kulti.							
10	10	5	0.59-0.63	0.606	0.019	0.008	2.08
11	20	10	0.58-0.63	0.604	0.020	0.006	2.24
12	22	11	0.60-0.65	0.617	0.020	0.006	2.20
13	12	6	0.58-0.61	0.595	0.013	0.005	1.52
14	10	8	0.58-0.63	0.605	-	-	-

Table 21. Variation in pronotal form (LP/WP) in selected samples of the *pluripunctatus* subgroup; see Fig. 155.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.90-0.95	0.932	0.019	0.007	1.34
S. multisetosus.							
2	14	7	0.93-1.00	0.959	0.032	0.012	2.25
3	22	11	0.93-0.98	0.950	0.021	0.006	1.51
4	20	10	0.92-0.95	0.936	0.013	0.004	0.93
S. pluripunctatus.							
5	18	9	0.88-0.93	0.907	0.017	0.005	1.25
6	10	5	0.91-0.94	0.919	0.016	0.007	1.19
7	18	9	0.87-0.93	0.910	0.022	0.007	1.64
8	8	5	0.90-0.93	0.915	-	-	-
9	10	5	0.90-0.96	0.931	0.027	0.011	1.92
S. kulti.							
10	10	5	0.90-0.93	0.916	0.018	0.007	1.28
11	20	10	0.89-0.95	0.925	0.024	0.007	1.76
12	22	11	0.90-0.97	0.932	0.025	0.007	1.80
13	12	6	0.90-0.95	0.925	0.021	0.008	1.49
14	10	8	0.88-0.94	0.913	-	-	-

Table 22. Variation in pronotal length relative to elytral width (LP/WE) in selected samples of the *pluripunctatus* subgroup; see Fig. 156.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.74-0.80	0.775	0.027	0.010	2.30
S. multisetosus.							
2	14	7	0.73-0.82	0.789	0.050	0.018	4.19
3	22	11	0.73-0.78	0.752	0.027	0.008	2.42
4	20	10	0.74-0.80	0.776	0.022	0.007	1.88
S. pluripunctatus.							
5	18	9	0.75-0.83	0.790	0.028	0.009	2.34
6	10	5	0.74-0.81	0.781	0.039	0.016	3.33
7	18	9	0.71-0.80	0.764	0.034	0.011	2.95
8	8	5	0.76-0.81	0.785	-	-	-
9	10	5	0.74-0.79	0.779	0.036	0.015	3.11
S. kulti.							
10	10	5	0.74-0.81	0.784	0.035	0.015	3.01
11	20	10	0.75-0.83	0.784	0.034	0.010	2.87
12	22	11	0.75-0.84	0.780	0.035	0.010	3.00
13	12	6	0.77-0.81	0.792	0.021	0.008	1.79
14	10	8	0.75-0.82	0.786	-	-	-

Table 23. Variation in length of paramedian pronotal sulcus relative to pronotal length (PS/LP) in selected samples of the *pluripunctatus* subgroup; see Fig. 157.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
S. plurisetosus.							
1	14	7	0.63-0.70	0.664	0.026	0.009	2.61
S. multisetosus.							
2	14	7	0.58-0.65	0.629	0.028	0.010	3.02
3	22	11	0.62-0.69	0.658	0.025	0.007	2.51
4	20	10	0.63-0.70	0.656	0.032	0.009	3.21
S. pluripunctatus.							
5	18	9	0.61-0.68	0.647	0.030	0.009	3.09
6	10	5	0.63-0.73	0.663	0.042	0.018	4.27
7	18	9	0.63-0.71	0.653	0.030	0.010	3.09
8	8	5	0.63-0.68	0.660	-	-	-
9	10	5	0.63-0.70	0.673	0.032	0.013	3.14
S. kulti.							
10	10	5	0.59-0.68	0.656	0.039	0.017	4.01
11	20	10	0.61-0.68	0.646	0.029	0.009	3.02
12	22	11	0.59-0.66	0.628	0.028	0.008	2.93
13	12	6	0.63-0.70	0.658	0.034	0.013	3.42
14	10	8	0.58-0.66	0.628	-	-	-

S. kulti are compared for six different characteristics in Tables 18-23 and Fig. 152-157. Satisfactory comparisons of *S. multisetosus* with the other species are made difficult by lack of good information on clinal variation. Still, certain facts support the notion that *S. multisetosus* is reproductively isolated from the other three forms.

S. plurisetosus is known from rivers just north of the Moctezuma drainage basin, and a direct comparison between those specimens (sample one) and those of *S. multisetosus* from Tamazunchale (sample two) is therefore relevant. The apex of the median lobe of the male genitalia is more broadly rounded; accessory pronotal setae are present in all specimens; and the number of discal elytral setae (Fig. 153, Table 19) is much greater. Additional, statistically significant, differences are in the form of the pronotum (Fig. 155, Table 21) and in the length of the paramedian pronotal sulci (Fig. 156, Table 23). In these two features, the *S. plurisetosus* sample is similar to one or both of the two southern *S. multisetosus* samples (samples three and four); the Tamazunchale sample may thus be considered divergent, indicating a lack of gene flow between it and *S. plurisetosus.* Differences in these five characteristics, and the geographic proximity of the two samples, indicate reproductive isolation of *S. multisetosus* from *S. plurisetosus.*

Known geographic ranges of *S. pluripunctatus* (samples five to nine) and *S. multisetosus* are so widely separated that statistical differences are equivocal. However, constant differences in form of male genitalia, constant presence of paramedian ambulatory setae on sternum seven in females of *S. pluripunctatus*, and apparent geographic isolation are sufficient reasons to recognize *S. pluripunctatus* and *S. multisetosus* as separate species.

S. kulti (samples 10 to 14), particularly in the south, is characterized by fewer elytral setae and smaller body size than is *S. multisetosus*. Sample 13 of *S. kulti,* Valle Nacional and sample three of *S. multisetosus*, 72.5 mi. s. Valle Nacional, are from the same river system. Statistically significant differences in eye size, pronotal form, and relative size of thorax represent divergences in these features, so there is little doubt that the two samples represent reproductively isolated taxa. Similar, though less conclusive, comparisons between other population samples of the two forms give similar results, even though northern samples of *S. kulti* (samples 10 and 14) are characterized by large body size and increased numbers of elytral setae. These facts, together with constant differences in form of male median lobe, strongly support the conclusion that *S. kulti* is reproductively isolated from *S. multisetosus.*

Schizogenius pluripunctatus LeConte

Schizogenius pluripunctatus LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, specimen labelled MCZ 5484 here designated lectotype (!). LeConte 1857: 82. Putzeys 1863:24. Putzeys 1866:225. LeConte 1879:34. Lindroth 1961:165.

Schizogenius simplex LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, specimen labelled MCZ 5485 here designated lectotype (!). LeConte 1857:83, established synonymy.

Diagnostic combination. – Within the *pluripunctatus* group, specimens of this species are distinguished by the following combination of characters: pronotum without accessory marginal setae; females as well as males each with paramedian ambulatory setae on sternum seven; apex of median lobe deflected at a weak angle; and elytron with 35 or more discal setae.

Description. – As in *S. seticollis seticollis*, except: legs paler, femora uniformly rufous, tibiae paler; abdomen often paler toward apex. Form and sculpture of head and pronotum as in *S. plurisetosus* (Fig. 126), except sides of pronotum bisetose and basal transverse

impression less distinctly punctate. In specimens studied, elytron with 12-18 setae on interval three, 12-23 on interval five, and 11-19 on interval seven; setae mostly adjacent to corresponding inner striae, not markedly biseriate; total number of setae per elytron 35-61; striae usually indistinctly punctate. Females and males each with a pair of ambulatory setae on sternum seven. Male genitalia: median lobe (Fig. 135) with apical portion proportionately long, deflected at weak angle; endophallus, Fig. 143; 23 specimens examined.

Measurements and proportions. See Table 24.

Table 24. Descriptive statistics for *S. pluripunctatus*, based on nine males from 18.6 miles southeast of Tonalá, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.38-4.26	3.819	0.418	0.186	7.29
LE	2.05-2.60	2.334	0.260	0.116	7.43
WH	0.72-0.89	0.800	0.090	0.040	7.52
WP	0.93-1.19	1.063	0.127	0.057	7.98
WE	1.06-1.33	1.206	0.147	0.065	8.13
B. Setae on left elytron.					
Interval 3	13-17	14.2			
Interval 5	12-20	16.1			
Interval 7	13-19	14.8			
Total	39-56	45.1	5.5	2.4	8.10
C. Proportions.					
WF/WH	0.61-0.65	0.630	0.021	0.009	2.24
LP/WP	0.88-0.91	0.903	0.015	0.007	1.11
DP/LP	0.81-0.85	0.830	0.018	0.008	1.47
LP/WE	0.77-0.83	0.797	0.026	0.012	2.17
Ta/Ti	0.62-0.72	0.664	0.054	0.024	5.38
PS/LP	0.62-0.68	0.650	0.031	0.014	3.17

Variation. – Data on variation in six characteristics among five samples (samples five to nine) are given in Tables 18-23 and Fig. 152-157. Three samples from Arizona and New Mexico (samples five to seven) are quite uniform, and are intermediate in most ways to the two Mexican samples. I therefore suspect that sample nine from Sinaloa and Nayarit is geographically isolated from sample eight from Durango, and that these two samples represent populations near the ends of a partial circle of races. This is a reasonable hypothesis, since these areas are well separated by high ranges of the Sierra Madre Occidental, but should be tested through additional collections.

One female specimen from Prescott, Arizona, has only one left paramedian ambulatory seta on sternum seven. I otherwise found this character to be constant, and presume that it remains stable southward where the range of *S. pluripunctatus* approaches that of *S. kulti*.

Etymology. – Latin, *plurimus* = most, plus *punctum* = small holes, in reference to the numerous discal setae on the elytron.

Distribution. – Specimens of *S. pluripunctatus* have been collected in the Gila and Colorado River drainages in Arizona and New Mexico, south to the Rio Acaponeta drainage basin in northern Nayarit, and in the interior Rio Nazas drainage in Durango (Fig. 147). One specimen labelled "N.Y." (UKSM) is no doubt erroneous. I studied 130 additional specimens from the following localities.

UNITED STATES

ARIZONA (14; AMNH, CAS, UASM, USNM): Cochise Co., Cochise Stronghold (1; UATA), Fairbanks (1; CAS); Coconino Co., Bill Williams Fork (9; KSUM, MCZ, UKSM); Gila Co., Carrizo Creek (12; UASM), Globe (1; CAS), Roosevelt Lake (1; AMNH), Salt River Canyon (3; ANSP, MCZ, UASM), Verde River (1; MCZ); Graham Co., Aravaipa (12; BMNH, CAS, CNC, DRWh, IRSB, KHSt), San Carlos Reservoir (1; MCZ); Maricopa Co., Phoenix (2; LACM); Pima Co., Collosal Cave Park (2; KHSt), Madera Canyon (1; UASM), Tucson (6; AMNH, CAS, JNeg, KHSt, UATA); Santa Cruz Co., Nogales (3; CNHM, UASM), 5 mi. n. Nogales (1; MCZ), Patagonia (8; AMNH, CAS, UATA), 2 mi. sw. Patagonia (5; UATA), Peña Blanca (1; UASM); Yavapai Co., Bumble Bee (2; CAS), Haslampa District (2; CAS), Prescott (2; UASM). NEW MEXICO: Catron Co., Glenwood (1; UASM); Grant Co., Cliff (8; UASM), 26 mi. n. Silver City (9; TLEr), 36.4 mi. ne. Silver City (1; MGFT).

MEXICO

DURANGO: 12.2 mi. s. El Banco (8; UASM). NAYARIT: Acaponeta (1; UASM), 2.4 mi. s. Acaponeta (6; UASM), 8 mi. nw. Acaponeta (1; CAS). SINALOA: 26 mi. ne. Villa Union (3; LBSC). SONORA: 7.2 mi. se. Alamos (1; GRNo).

Collecting notes. – Specimens of *S. pluripunctatus* have been collected from March to September in the United States, and in January, July, and September in Mexico. Many specimens were taken at lights, to which they no doubt flew. I have collected specimens in gravel bars along streams, usually further from water than specimens of most other species.

Taxonomic notes. – The type of *S. simplex*, taken at the same time and place as that of *S. pluripunctatus*, is a small specimen of the same species and was so recognized subsequent to its description. Though the name has line priority, it was treated as a junior synonym of *S. pluripunctatus* by LeConte (1857) and by all subsequent authors.

Though known distributions are allopatric, specimens of *S. pluripunctatus* and *S. kulti* have been taken within 75 miles of each other, and the two river systems involved, Acaponeta and Grande de Santiago, approach each other even more closely in places. Scarcity of material from this area precludes definite statements about reproductive relationships, but available evidence suggests reproductive isolation. In specimens seen, all females of *S. pluripunctatus* have paramedian ambulatory setae on sternum seven, and males have the apical portion of the median lobe deflected at a slight but evident angle.

Statistical evidence of distinctness of *S. pluripunctatus* and *S. kulti* is given in Tables 18-23 and Fig. 152-157. Northern specimens of *S. kulti* (sample ten) approach *S. pluripunctatus* in body size and in numbers of elytral setae, but the Nayarit sample of the latter (sample nine) is divergent in these ways. Northern specimens of *S. kulti* approach specimens of *S. pluripunctatus* from Nayarit, but diverge from those from Durango (sample eight), in eye size. And, they diverge from Nayarit *S. pluripunctatus* in pronotal form. It is unlikely that there is any actual or potential gene flow between northern *S. kulti* and either southern form of *S. pluripunctatus*, and I therefore treat these taxa as distinct species.

Schizogenius kulti new species

Type material. – Holotype male and allotype female labelled "MEXICO. Chiapas. 18.6 mi. se. Tonala. Rte. 200 100′ III.2.1966" and "George E. Ball D. R. Whitehead collectors" (MCZ). Thirty additional specimens from various localities in Chiapas are paratypes (CNC,

DRWh, UASM, USNM).

Diagnostic combination. – The following characters combine to distinguish specimens of this species from all others in the *pluripunctatus* group: median lobe arcuate, apical deflection not angulate; females without paramedian ambulatory setae; and pronotum without accessory marginal setae. Most specimens have fewer than 30 setae on the disc of each elytron, a feature unique within the group, but some specimens from northern parts of the range cannot be so distinguished.

Description. – As in *S. seticollis seticollis* except: color paler, testaceous to rufopiceous; front femora, coxae, and trochanters ferrugineous; maxillae, labial palpi, antennae, front tarsi and tibiae, middle and hind legs except coxae, and apical margins of elytra and abdomen rufotestaceous; no metallic luster. Form and sculpture of head and pronotum as in *S. plurisetosus* (Fig. 126), except sides of pronotum bisetose and basal and anterior transverse impressions nearly impunctate. Elytral intervals three, five, and seven in specimens examined with 6-14, 6-14, and 4-14 setae, respectively; striae nearly impunctate. Male genitalia: median lobe, Fig. 136, nearly or quite arcuate, apical portion proportionately long and deflexed at a slight angle or not angulate; endophallus, Fig. 144; 11 specimens examined.

Measurements and proportions. See Table 25. Of holotype: TL, 3.43 mm; LE, 2.09 mm; WH, 0.71 mm; WP, 0.92 mm; WE, 1.04 mm; WF/WH, 0.63; LP/WP, 0.93; DP/LP, 0.83; LP/WE, 0.83; Ta/Ti, 0.65; PS/LP, 0.61. Of allotype: TL, 3.45 mm; LE, 2.10 mm; WH, 0.72 mm; WP, 0.92 mm; WE, 1.08 mm; WF/WH, 0.60; LP/WP, 0.95; DP/LP, 0.83; LP/WE, 0.82; Ta/Ti, 0.65; PS/LP, 0.59.

Table 25. Descriptive statistics for *S. kulti*, based on 14 males from 18.6 miles southeast of Tonalá, Chiapas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	2.85-3.53	3.280	0.349	0.140	7.09
LE	1.75-2.14	1.987	0.205	0.082	6.87
WH	0.62-0.75	0.696	0.066	0.027	6.34
WP	0.76-0.96	0.884	0.097	0.039	7.31
WE	0.92-1.09	1.016	0.090	0.036	5.93
B. Setae on left elytron.					
Interval 3	6- 9	7.5			
Interval 5	7-10	8.0			
Interval 7	5- 7	5.9			
Total	19-25	21.5	3.9	1.6	11.99
C. Proportions.					
WF/WH	0.60-0.65	0.620	0.024	0.010	2.60
LP/WP	0.90-0.97	0.935	0.029	0.012	2.04
DP/LP	0.81-0.85	0.832	0.018	0.007	1.41
LP/WE	0.75-0.84	0.807	0.040	0.016	3.32
Ta/Ti	0.60-0.71	0.668	0.051	0.020	5.04
PS/LP	0.61-0.65	0.629	0.020	0.008	2.07

Variation. – Date on variation in six characteristics are given in Tables 18-23, for samples numbered 10 to 14 as in Fig. 152-157. Toward the north in both Atlantic and Pacific drainage basins, body size, pronotal width, and numbers of elytral setae increase, eye size decreases, and except for the Veracruz sample paramedian pronotal sulci lengthen. Northern populations are geographically isolated from one another, so that their similarities may be interpreted either as convergences or as relict characteristics. I suspect the latter is more likely, since related species are larger and more setose. I found no specimens with accessory pronotal setae, and no females with paramedian ambulatory setae on sternum seven. The form of the median lobe is constantly arcuate, the apical portion not or hardly deflected at an angle.

Etymology. – The name *S. kulti* is dedicated to the Czechoslovakian entomologist, K. Kult, whose numerous papers on the Scaritini contributed much to our knowledge of the group. A specimen from Rio Maria Linda, Guatemala, was treated by Bates (1881) as *S. tristriatus*, but was subsequently labelled as a paratype of *"S. brittoni"* Kult, a pin label name never published.

Distribution. – Specimens of *S. kulti* have been collected at altitudes ranging from near sea level to 4100′, from the Rio Grande de Santiago system in Nayarit and Zacatecas and the Rio Atoyac system in Veracruz, south to Guatemala (Fig. 147). I studied 122 specimens of this species from the following localities.

MEXICO

CHIAPAS: 3.2 mi. n. Arriaga (1; USNM), 12.2 mi. ne. Chiapa de Corzo (4; DRWh, UASM), Pijijiapan (4; CNC), Tonalá (1; USNM), 18.6 mi. se. Tonalá (23; MCZ, UASM). GUERRERO: 41.4 mi. n. Acapulco (3; UASM), Coyuca (2; UASM). JALISCO: 0.4 mi. w. Cocula (1; UASM), Talpa de Allende (1; UASM). NAYARIT: Jesus Maria (2; UCB), 14 mi. e. San Blas (1; UASM). OAXACA: 17.7 mi. w. El Camaron (10; MGFT, UASM), 29.4 mi. e. El Coyul (33; UASM), 11.1 mi. n. Matias Romero (1; CAS), Valle Nacional (14; UASM), Zanatepec (3; IRSB). TABASCO: Teapa (3; BMNH). VERACRUZ: Córdoba (1; CAS), Fortín de las Flores (9; DRWh, FDAG), Catemaco (1; JNeg). ZACATECAS: 0.9 mi. n. Jalpa (1; UASM).

GUATEMALA

ESCUINTLA: Rio Maria Linda (1; BMNH). IZABAL: Los Amates (1; MCZ).

Collecting notes. – Adults of *S. kulti* are active throughout the year in gravel bars along streams. I noted no special habits, and found them together with specimens of one or more other *Schizogenius* species. Specimens from Fortín de las Flores, Veracruz, were taken at black lights, and no doubt flew there. None of the Fortín specimens were collected by hand, although suitable habitats are in the vicinity and numerous specimens of *S. tristriatus* were collected there.

The *sallei* group

Diagnostic combination. – Members of this monotypic group are distinguished by the following combination of characters: body strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum without paralateral carinae; discal setae present on intervals three, five, and seven, total normally less than 30, average length less than 1.0 times maximum width of interval two; abdomen microsculptured along midline, and with microsculpture in small lateral patches near coxal depressions of sternum three; endophallus with basal collar spines distinct. Also: clypeal suture sharply impressed; antennal articles five to ten filiform, elongate; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved outward at

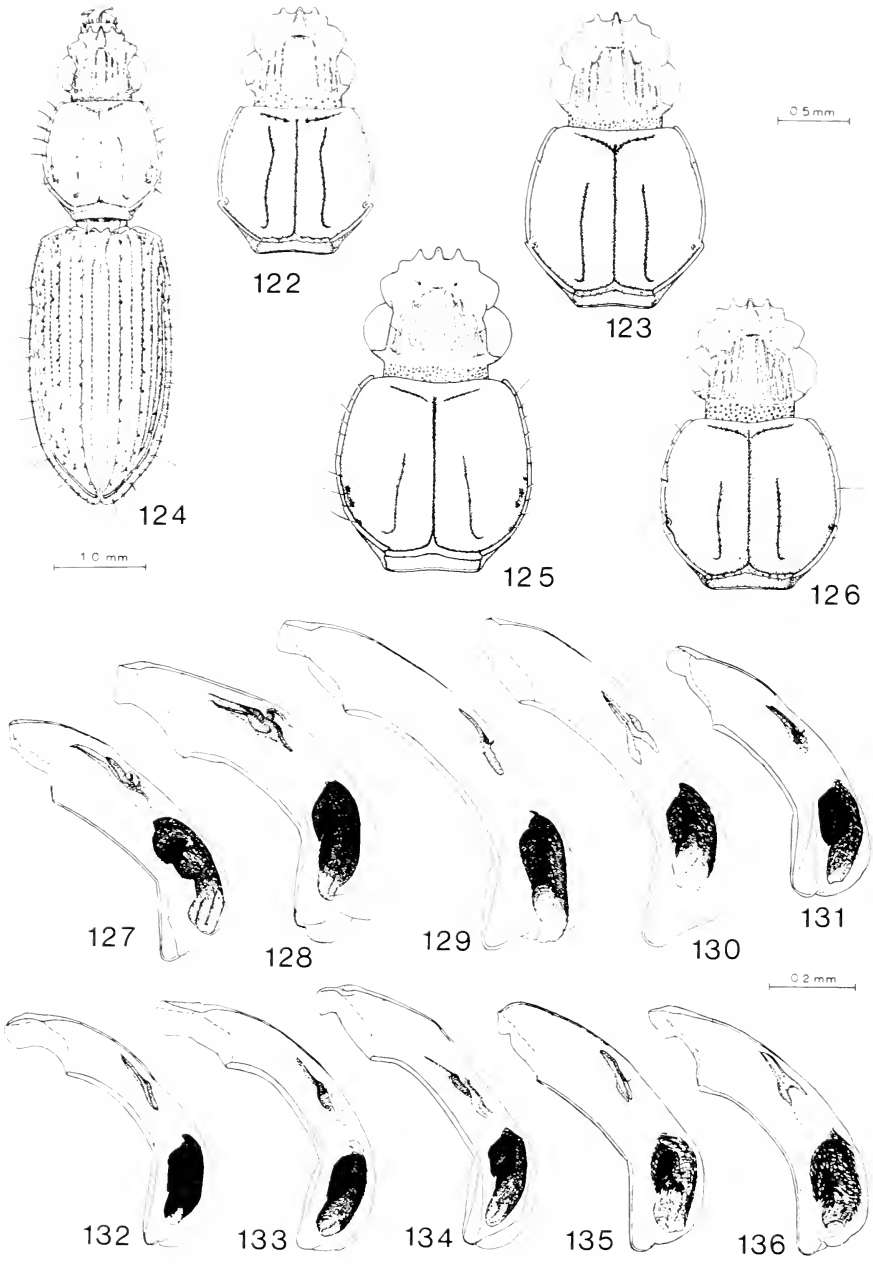


Fig. 122-123. Head and pronotum, dorsal aspect. 122. *S. truquii* Putzeys, Cocula, Jalisco. 123. *S. brevisetosus* new species, Barrel Springs Creek, Texas. Fig. 124. Habitus, dorsal aspect, *S. seticollis seticollis* Fall, Mokelumne Hill, California. Fig. 125-126. Head and pronotum, dorsal aspect. 125. *S. seticollis vandykei* new subspecies, Arroyo Saltito, Baja California. 126. *S. plurisetosus* new species, Linares, Nuevo Leon. Fig. 127-136. Male median lobe, lateral aspect. 127. *S. truquii* Putzeys, Cocula, Jalisco. 128. *S. brevisetosus* new species, Sanderson, Texas. 129. *S. seticollis seticollis* Fall, Dry Creek, California. 130. *S. seticollis vandykei* new subspecies, Arroyo Saltito, Baja California. 131. *S. plurisetosus* new species, Cienega de Flores, Nuevo Leon. 132. *S. multisetosus* Bates, Tepexco, Puebla. 133. Same, 72.5 mi. s. Valle Nacional, Oaxaca. 134. Same, Tamazunchale, San Luis Potosi. 135. *S. pluripunctatus* LeConte, Patagonia, Arizona. 136. *S. kulti* new species, Valle Nacional, Oaxaca.

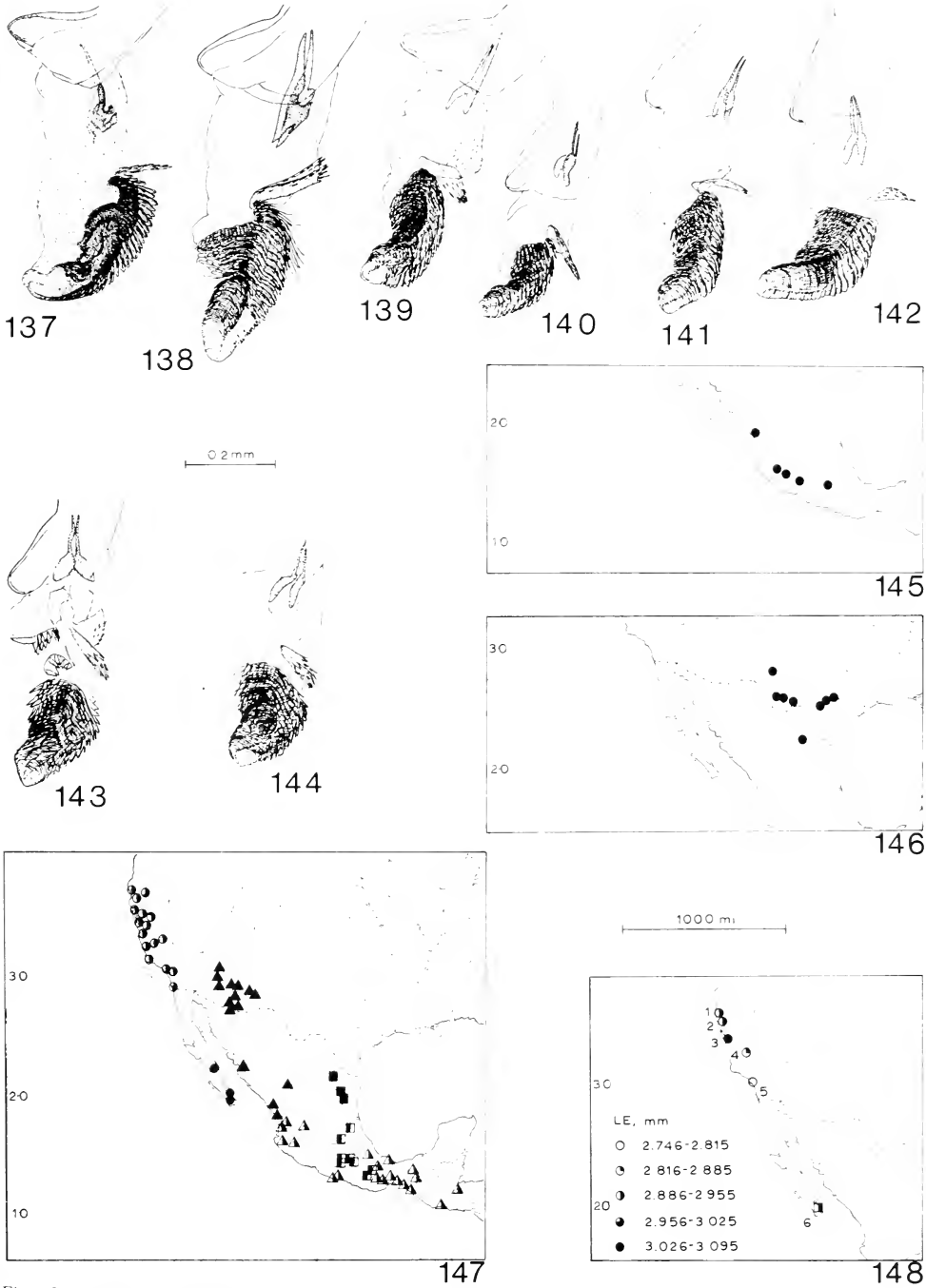


Fig. 137-144. Male endophallus. 137. *S. truquii* Putzeys, La Garita, Jalisco. 138. *S. brevisetosus* new species, Lozier Canyon, Texas. 139. *S. seticollis seticollis* Fall, Trimmer, California. 140. *S. plurisetosus* new species, El Barretal, Tamaulipas. 141. *S. multisetosus* Bates, 72.5 mi. s. Valle Nacional, Oaxaca. 142. Same, Tepexco, Puebla. 143. *S. pluripunctatus* LeConte, Acaponeta, Nayarit. 144. *S. kulti* new species, 41.4 mi. n. Acapulco, Guerrero. Fig. 145-147. Known distributions. 145. *S. truquii* Putzeys. 146. *S. brevisetosus* new species. 147. *S. seticollis seticollis* Fall, half-filled circles; *S. seticollis vandykei* new subspecies, filled circles; *S. pluripunctatus* LeConte, filled triangles; *S. kulti* new species, half-filled triangles; *S. multisetosus* Bates, half-filled squares; *S. plurisetosus* new species, filled squares. Fig. 148. Geographic variation in *S. seticollis seticollis* Fall, circles, and *S. seticollis vandykei* new subspecies, square; means of body size, Table 11.

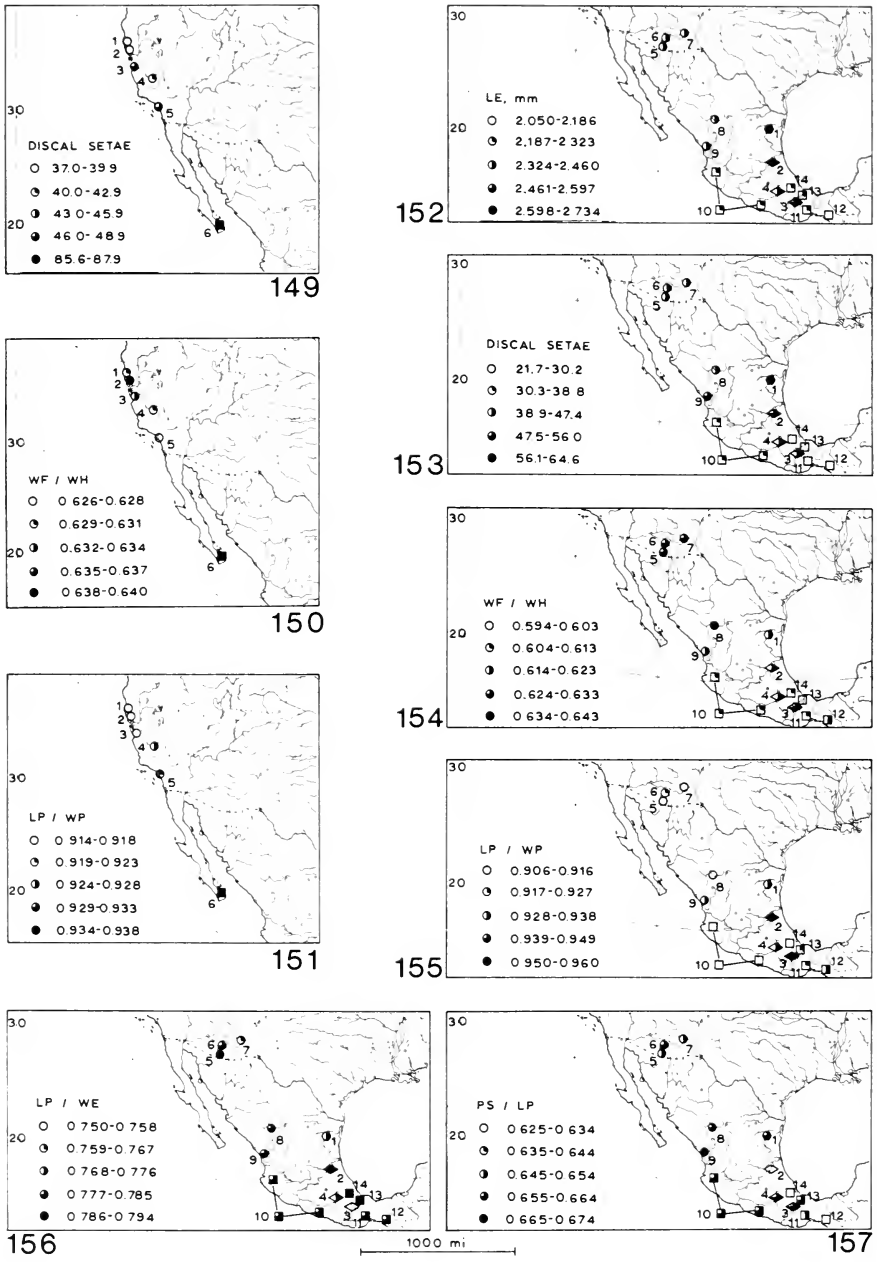


Fig. 149-151. Geographic variation in *S. seticollis seticollis* Fall, circles, and *S. seticollis vandykei* new subspecies, square. 149. Means of numbers of discal setae on left elytron, Table 12. 150. Means of relative eye size, Table 13. 151. Means of pronotal form, Table 14. Fig. 152-157. Geographic variation in *S. plurisetosus* new species, hexagon; *S. multisetosus* Bates, diamonds; *S. pluripunctatus* LeConte, circles; and *S. kulti* new species, squares. 152. Means of body size, Table 18. 153. Means of numbers of discal setae on left elytron, Table 19. 154. Means of relative eye size, Table 20. 155. Means of pronotal form, Table 21. 156. Means of relative pronotal size, Table 22. 157. Means of relative length of paramedian pronotal sulci, Table 23. Accompanying legends are for all included taxa.

apices; pygidium crenulate at apex in females; color rufocastaneous; and pronotal hind angles sharply developed.

S. sallei is the only *Schizogenius* species characterized by strong microsculpture along the midline but not the margins of the abdomen.

Distribution. – *S. sallei* is known from the Great Plains region of North America, from Kansas south to the Rio Grande. I examined 374 specimens.

Schizogenius sallei Putzeys

Schizogenius sallei Putzeys 1866:228. *Type locality* Texas; type male in IRSB, specimen labelled lectotype by me so designated (!). LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. – Abdomen microsculptured along midline, otherwise mostly unmicrosculptured.

Description. – Body flattened. Color castaneous, unmetallic, legs and palpi paler.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two-thirds, sternum three in coxal depressions and small paralateral patches, and middle of abdomen on sterna three to five or six.

Head. Fig. 158. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.7-1.8 times longer than wide.

Pronotum. Fig. 158. Sides bisetose; base not rugose; hind angles prominent. Paramedian longitudinal sulci moderately long, nearly straight, strongly hooked basally. Anterior transverse impression strongly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 7-9 setae on interval three, 6-8 on interval five, 3-5 on interval seven; total 17-23 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in females, entire in males.

Male genitalia. Median lobe, Fig. 169; endophallus, Fig. 178; 8 specimens examined.

Measurements and proportions. See Table 26.

Variation. – See Table 26. I found no significant geographic variation in relative eye size, pronotal form, body size, or in numbers of elytral setae.

Etymology. – This species was named after Auguste Sallé, who made important early collections of Coleoptera in Mexico.

Distribution. – The known range of this species extends from Kansas south to the Rio Grande Valley in Texas (Fig. 185). This is a peculiar distribution, especially since there is no evidence of restricted gene flow either between the Rio Grande and Colorado River systems, or north and south of the Red River. I have two doubtful records of unspecified localities in Canada (UKSM) and Ohio (CAS); both require confirmation. I studied 374 additional specimens from the following localities.

UNITED STATES

No locality (7; ANSP, LACM). KANSAS: Butler Co., Leon (6; UKSM); Riley Co. (1; USNM). OKLAHOMA: Carter Co., 10.7 mi. s. Drake (2; TLEr); Murray Co., 10.3 mi. n. Drake (6; TLEr). TEXAS (55; AMNH, ANSP, CAS, CNHM, INHS, IRSB, KSUM, MCZ, MSUL, RUNB, UKSM, USNM, ZMLS): Andrews Co., Fullerton (3; CAS, USNM); Bexar Co., San Antonio (1; MCZ); Blanco Co., Cypress Mills (3; USNM), Johnson City (8; UASM), Twin Sisters (7; UASM); Brown Co., Brownwood (1; AMNH); Comal Co., New Braunfels (1; USNM); Colorado Co., Columbus (1; MSUL); Cooke Co., 4 mi. sw. Era (3; BMNH); Dallas Co. (1; INHS), Dallas (7; INHS, MCZ, MSUL, RTBe); Erath Co., Morgan Mill (2; IRSB); Guadalupe Co., Seguin (3; UKSM); Kerr Co., Kerrville (7; CNC); Kinney Co., 23 mi. sw. Brackettville (107; AMNH, ANSP, CAS, CUNY, DJLa, FDAG, HGou, INHS, JHen, JNeg, MCZ, MGFT, MZSP, TCBa, UAFA, UASM, UATA, UCB, ZMLS); Lampasas Co., Adamsville (10; UASM); Maverick Co., 8 mi. n. Quemado (1; DHKa); McCulloch Co., 16 mi. s. Brady (4; CAS); McLennan Co., Waco (1; DHKa); Randall Co., Canyon (2; MSUL); Real Co., Leakey (1; UASM), 2 mi. s. Leakey (34; UASM); Taylor Co., 25 mi. sw. Abilene (14; CNHM); Terrell Co., Chandler Ranch (7; UASM); Travis Co., Austin (4; UASM, USNM); Uvalde Co., Garner State Park (15; UASM), Sabinal (2; USNM), 17 mi. nw. Uvalde (1; UASM); Val Verde Co., 26 mi. n. Comstock (7; DRWh), Devil's River (1; UATA), 9 mi. se. Del Rio (8; UASM), 13 mi. nw. Del Rio (24; UASM), 14 mi. se. Del Rio (6; UASM).

Table 26. Descriptive statistics for *S. sallei*, based on 20 males from 23 miles southwest of Brackettville, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.04-4.50	4.278	0.189	0.056	2.95
LE	2.51-2.80	2.660	0.126	0.038	3.16
WH	0.82-0.91	0.866	0.036	0.011	2.79
WP	1.05-1.14	1.096	0.041	0.012	2.52
WE	1.29-1.44	1.372	0.060	0.018	2.90
B. Setae on left elytron.					
Interval 3	7- 9	7.8			
Interval 5	6- 8	7.4			
Interval 7	3- 5	4.0			
Total	17-21	19.2	1.9	0.6	6.62
C. Proportions.					
WF WH	0.59-0.64	0.610	0.022	0.007	2.40
LP WP	0.91-0.96	0.935	0.023	0.007	1.61
DP LP	0.78-0.84	0.804	0.025	0.007	2.03
LP WE	0.71-0.77	0.743	0.027	0.008	2.43
Ta Ti	0.59-0.68	0.636	0.033	0.010	3.51
PS LP	0.66-0.72	0.692	0.030	0.009	2.86

Collecting notes. – Specimens of this species have been collected from March to September, in riparian gravel bars and at lights. At least in southern Texas, I found them abundant. The lack of pronounced geographic variation implies that *S. sallei* is a particularly vagile species.

Taxonomic notes. – This species is not closely related to any other, and I found no problems in infraspecific variation.

The *tristriatus* group

Diagnostic combination. – Members of this group are distinguished by the following combination of characters: body flattened; paramedian clypeal carinae extended to median tooth; bases of paramedian frontal carinae not broadly fused; antennal articles five to ten filiform; discal setae present on intervals three, five, and seven; and abdomen extensively microsculptured. Also: clypeal suture sharply impressed; clypeal field triangular, less than 1.5 apical width of median frontal sulcus; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved at apices; pygidium crenulate at apex in most females and some males; and endophallus with basal collar spines distinct.

Distribution. – Members of this group range from southeastern Canada, through the eastern and central United States, south to southern Mexico. I studied 398 specimens of the *tristriatus* group.

Schizogenius tristriatus Putzeys

Schizogenius tristriatus Putzeys 1846:651. *Type locality* Mexico; location of type unknown, possibly Hope Museum, Oxford. Putzeys 1863:24. Putzeys 1866:227. Bates 1881:37. Kult 1950:140.

Diagnostic combination. – Specimens of this species are readily recognized by characteristics given in the key to North and Middle American species of the subgenus *Schizogenius*. *S. tristriatus* is the only Mexican member of the *tristriatus* group which does not have basally broadened front tibiae.

Description. – Body flattened. Rufopiceous; elytral apices, abdomen, and legs rufous; palpi testaceous; no metallic luster. Microsculpture as in *S. dilatus*. Otherwise as in *S. tibialis* except as follows. Form and sculpture of head and pronotum, Fig. 159; eyes prominent; antennal article five 1.6-1.7 times longer than wide. Front tibia (Fig. 164) strongly tapered, distal tooth not spatulate. Left elytron with 6-8 setae on interval three, 5-7 on interval five, and 2-4 on interval seven, total 14-18 in specimens studied. Male genitalia with median lobe, Fig. 17-; endophallus, Fig. 179; 6 specimens examined.

Measurements and proportions. See Table 27.

Variation. – Two specimens from San Luis Potosí and Queretaro are slightly paler in color, but may simply be teneral.

Etymology. – Latin, *tres* = three, plus *stria* = furrow, in reference to the median and paramedian pronotal sulci.

Distribution. – Specimens of this species have been collected in eastern Mexico from San Luis Potosí and Queretaro south to Veracruz, at elevations ranging from 2900 to 4100′ (Fig. 186). I studied 78 specimens from the following localities.

MEXICO

No locality (4; IRSB, MCZ). QUERETARO: Escanelilla (1; UASM). SAN LUIS POTOSÍ: Xilitla (2; CNC). VERACRUZ: 3.2 mi. sw. Coscomatepec (22; BMNH, CAS, CNHM, DRWh, IRSB, MCZ, MGFT, UASM, USNM): Fortín de las Flores (49; FDAG, UASM).

Collecting notes. – Specimens of *S. tristriatus* have been collected nearly throughout the year, from March to November, either in gravel bars along streams or at lights. Where I have collected them in numbers, I did not find specimens of other species, though at Fortín de las Flores specimens of other species were collected at lights.

Table 27. Descriptive statistics for *S. tristriatus*, based on 20 males from Fortín de las Flores, Veracruz, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.16-4.84	4.574	0.258	0.077	3.76
LE	2.60-3.02	2.854	0.154	0.046	3.59
WH	0.84-1.00	0.928	0.058	0.018	4.20
WP	1.10-1.30	1.215	0.081	0.024	4.44
WE	1.43-1.62	1.531	0.079	0.024	3.43
B. Setae on left elytron.					
Interval 3	6- 8	6.7			
Inteval 5	5- 7	6.0			
Interval 7	3- 4	3.2			
Total	14-18	16.0	1.8	0.5	7.31
C. Proportions.					
WF/WH	0.59-0.63	0.604	0.018	0.005	2.02
LP/WP	0.87-0.93	0.905	0.024	0.007	1.77
DP/LP	0.78-0.84	0.814	0.020	0.006	1.66
LP/WE	0.69-0.74	0.719	0.024	0.007	2.25
Ta/Ti	0.60-0.67	0.625	0.034	0.010	3.62
PS/LP	0.62-0.71	0.668	0.030	0.009	2.95

Taxonomic notes. – There are two specimens of *S. tristriatus* in the Putzeys collection in the Institut Royal des Sciences Naturelles de Belgique labelled as syntypes, but I think these probably are the specimens mentioned in a subsequent paper (Putzeys, 1863). However, they were identified by him, and do match the original description, notably in coloration, and no doubt are conspecific with the types. *S. longipennis* Putzeys was described as a variety of *S. tristriatus* and was considered as such by Bates (1881), but as noted by Kult (1950) is not closely related.

Schizogenius dilatus new species

Type material. – Holotype male and allotype female labelled "MEX. Nuevo Leon Rio Sabinas Hidalgo, 4.8 mi. e. Sabinas Hidalgo 800′ X.22-23. 65" and "George E. Ball D. R. Whitehead collectors" (MCZ). An additional 26 specimens from various localities in Nuevo Leon and Tamaulipas are paratypes (BMNH, CAS, CNC, DRWh, IRSB, UASM, USNM).

Diagnostic combination. – Specimens of this species are distinguished from others in the group by front tibia strongly broadened basally and femur distinctly constricted near the apex, but no pronounced microsculpture on prothoracic pleura.

Description. – Strong microsculpture on paramedian frontal sulci, mouthparts, genae, sides and base of pronotum, front legs, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and entire abdomen. Otherwise as in *S. tibialis* except as follows. Eyes prominent; antennal article five about

1.6-1.7 times longer than wide. Front tibia (Fig. 165) slightly more tapered, distal tooth not spatulate. Left elytron with 8-11 setae on interval three, 7-10 on interval five, and 3-5 on interval seven, total 18-23 in specimens studied. Male genitalia with median lobe, Fig. 171; and endophallus, Fig. 180; 6 specimens examined.

Measurements and proportions. See Table 28. Of holotype: TL, 4.57 mm; LE, 2.81 mm; WH, 0.90 mm; WP, 1.18 mm; WE, 1.45 mm; WF/WH, 0.61; LP/WP, 0.97; DP/LP, 0.74; LP/WE, 0.79; Ta/Ti, 0.65; PS/LP, 0.74. Of allotype: TL, 5.05 mm; LE, 3.10 mm; WH, 0.98 mm; WP, 1.33 mm; WE, 1.60 mm; WF/WH, 0.63; LP/WP, 0.95; DP/LP, 0.74; LP/WE, 0.79; Ta/Ti, 0.65; PS/LP, 0.65.

Table 28. Descriptive statistics for *S. dilatus*, based on 12 males from Nuevo Leon and Tamaulipas, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.41-5.08	4.727	0.316	0.122	4.46
LE	2.74-3.11	2.903	0.176	0.068	4.03
WH	0.84-1.00	0.928	0.073	0.028	5.22
WP	1.12-1.33	1.227	0.095	0.037	5.17
WE	1.38-1.62	1.499	0.110	0.042	4.89
B. Setae on left elytron.					
Interval 3	8- 9	8.7			
Interval 5	7- 9	7.5			
Interval 7	3- 5	4.1			
Total	18-22	20.3	1.8	0.7	6.00
C. Proportions.					
WF/WH	0.60-0.65	0.624	0.023	0.009	2.51
LP/WP	0.94-1.00	0.967	0.027	0.010	1.84
DP/LP	0.74-0.77	0.755	0.016	0.006	1.44
LP/WE	0.76-0.81	0.789	0.019	0.007	1.57
Ta/Ti	0.58-0.65	0.618	0.037	0.014	3.95
PS/LP	0.65-0.74	0.702	0.039	0.015	3.74

Etymology. – Latin, *dilatus* = expanded, in reference to the form of the front tibia.

Distribution. – I studied 28 specimens from the following localities in northeastern Mexico (Fig. 187).

MEXICO

NUEVO LEON: Cienega de Flores (4; CAS, IRSB), Linares (1; DRWh), 14.8 mi. w. Linares (2; USNM), 5 mi. s. Monterrey (1; CNC), 4.8 mi. e. Sabinas Hidalgo (17; MCZ, UASM). TAMAULIPAS: El Barretal (1; BMNH), 21.3 mi. n. Ciudad Victoria (1; CNC), 39 mi. s. Ciudad Victoria (1; DRWh).

Collecting notes. – Specimens of *S. dilatus* have been collected from June to October, in

riparian gravel bars. The specimens from 14.8 miles west of Linares were taken at black lights. The facts that one good series was taken along a stream, and that the eyes are not reduced, indicate epigean habits.

Taxonomic notes. – The only other species having broadened front tibiae, *S. tibialis*, is well separated morphologically, and is also sympatric at least in Nuevo Leon. *S. dilatus* is otherwise most similar to *S. tristriatus*, but is clearly distinct.

Schizogenius tibialis new species

Type material. – Holotype male and allotype female labelled "MEXICO S.L.P. Rte. 85, 19.3 mi. n.w. Tamazunchale 500′ XI.14&20.65" and "George E. Ball D. R. Whitehead collectors" (MCZ). Ten additional specimens from various localities in San Luis Potosí, Mexico, are paratypes (CAS, CNC, DRWh, IRSB, UASM, UKSM).

Diagnostic combination. – Specimens of this species differ from all others in the genus by the following combination of characteristics: prothoracic pleura strongly microsculptured; front tibia strongly broadened basally; and front femur strongly constricted near apex.

Description. – Body flattened. Color castaneous to rufopiceous, without metallic luster, legs and antennae ferrugineous, tarsi and palpi testaceous.

Integument. Strong microsculpture on paramedian frontal sulci, mouthparts, genae, sides and base of pronotum, prothoracic pleura, front legs, middle legs except anterior surfaces of trochanters, hind legs, elytral epipleura, and entire abdomen.

Head. Fig. 160, 161. Generally as in *S. amphibius*, except eyes prominent to strongly flattened, and antennal article five about 1.7-1.8 times longer than wide.

Pronotum. Form and sculpture, Fig. 160. Otherwise as in *S. amphibius* except anterior transverse impression strongly punctate.

Legs. Front and middle tarsi strongly dilated and pubescent ventrally in males, less so in females; hind tarsus slender. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia (Fig. 166) parallel sided, not or hardly narrowed toward base; distal tooth (Fig. 167-168) varied in form. Front femur strongly constricted near apex.

Elytra. Left elytron with 8-11 setae on interval three, 7-10 on interval five, and 3-6 on interval seven. Striae deep, sharply engraved, strongly punctate in basal two-thirds. Otherwise as in *S. amphibius*.

Male genitalia. Median lobe, Fig. 172, 173; endophallus, Fig. 181; eight specimens examined.

Measurements and proportions. Of holotype: TL, 4.56 mm; LE, 2.77 mm; WH, 0.87 mm; WP, 1.17 mm; WE, 1.45 mm; WF/WH, 0.63; LP/WP, 1.00; DP/LP, 0.75; LP/WE, 0.81; Ta/Ti, 0.65; PS/LP, 0.65. Of allotype: TL, 4.87 mm; LE, 2.95 mm; WH, 0.92 mm; WP, 1.25 mm; WE, 1.54 mm; WF/WH, 0.66; LP/WP, 1.01; DP/LP, 0.74; LP/WE, 0.82; Ta/Ti, 0.61; PS/LP, 0.72.

Variation. – As *S. tibialis* is poorly represented in collections, a statistical analysis of geographic variation is not yet possible. I do not suspect important variation in body size, body form, or in numbers of elytral setae. The largest (LE, 3.12 mm) and smallest (LE, 2.70 mm) males are from Encarnacion de Diaz and Saltillo, respectively, and the largest (LE, 3.06 mm) and smallest (LE, 2.73 mm) females are from Monterrey and the Rio Balsas, respectively.

Despite paucity of material, a geographic pattern is evident from unusually pronounced variation in two characteristics. The distal tooth of the front tibia is swollen or spatulate apically in specimens from San Luis Potosí, Veracruz, Oaxaca, and Chiapas (Fig. 167), less so in specimens from Jalisco, and hardly or not at all in specimens from Coahuila, Guerrero,

Tamaulipas, and Texas (Fig. 168). Relative eye sizes (WF/WH) are summarized in Fig. 188; eyes are prominent in specimens from San Luis Potosí and Veracruz (Fig. 160), less so in specimens from Oaxaca, decrease in prominence northward, and are especially flattened in specimens from Indian Creek Cave in Texas (Fig. 161). Only forms with prominent eyes have been taken in series, in San Luis Potosí and Oaxaca, and even they were not found as abundantly as were specimens of other species. The distribution of *S. tibialis* is probably correlated with the distribution of limestone, and perhaps of limestone caves, as all samples were obtained in regions in or near limestone outcroppings.

Probably there are no important barriers to gene flow along the Atlantic slope from San Luis Potosí south to Oaxaca, then back north along the Pacific slope to the Trans-Volcanic Sierra and inland along its northern drainages. As there is more similarity between Jalisco and San Luis Potosí samples in form of distal tooth of front tibia than between the latter and the Guerrero specimen, there may be some gene flow there. And the eye size pattern suggests that there is no serious barrier to gene flow between Jalisco and Atlantic drainage systems in Coahuila, Tamaulipas, and Texas. The particularly small eye of Indian Creek Cave specimens suggests a steeply stepped cline; those specimens might be of a reproductive isolate, but the existence of a reasonable geographic cline argues otherwise. However, large-eyed populations from San Luis Potosí are structurally isolated from smaller-eyed forms from Texas and Tamaulipas, and may be reproductively isolated and even sympatric. Thus, samples of *S. tibialis* probably represent a circle of races, as shown in Fig. 188. This hypothesis requires further investigation. In particular, further collections should be made in Tamaulipas, in the Sierra de Guatemala and Sierra de Tamaulipas, to determine whether sympatry exists.

Etymology. – Latin, *tibialis* = of the tibia, a reference to the peculiar structure of the front tibia.

Distribution. – Specimens of this species have been collected from the Nueces River system in southern Texas, south to southeastern Oaxaca (Fig. 188) and northern Chiapas, in a pattern strongly suggesting a circle of races. I studied 35 specimens of this species from the following localities.

UNITED STATES

TEXAS: Uvalde Co., Indian Creek Cave (2; TCBa); Val Verde Co., 9 mi. se. Del Rio (1; USNM).

MEXICO

CHIAPAS: 31 mi. w. Lázaro Cárdenas (1; CNC). COAHUILA: 14 mi. n. Saltillo (1; BMNH). GUERRERO: Rio Balsas (1; MCZ). JALISCO: 9.7 mi. e. Encarnacion de Diaz (3; UASM). NUEVO LEON: 5 mi. s. Monterrey (2; CNC). OAXACA: 11.1 mi. n. Matias Romero (1; UASM), Tapanatepec (9; UKSM). SAN LUIS POTOSÍ: El Salto de Agua (1; CNC), Huichihuayan (3; UKSM), 17 mi. n. Palitla (1; DRWh), Rio Verde (1; IRSB), 2 mi. e. Tamazunchale (1; UASM), 5 mi. n. Tamazunchale (1; CAS), 19.3 mi. nw. Tamazunchale (4; DRWh, MCZ, UASM). TAMAULIPAS: 73.1 mi. n. Manuel (1; UASM). VERACRUZ: 20 mi. nw. Huatusco (1; FDAG).

Collecting notes. – Specimens of this species have been collected nearly throughout the year. Some were taken at lights. Both specimens from Indian Creek Cave were taken in a deep cave, and at that locality the species may be troglobitic. Elsewhere I suspect individuals are found near the surface only incidentally, and live at a much wider range of depths in gravel bars than do most other species in the genus.

Taxonomic notes. – The only other species known to have broadened front tibiae, *S. dilatus*, is sympatric with *S. tibialis* at least in Nuevo Leon, and lacks marked subepigean adaptations. Specimens of *S. tibialis* have more strongly constricted front femora, and coarser microsculpture on the prothoracic pleura.

Specimens from Indian Creek Cave may represent a truly troglobitic species, reproductively isolated from the more southern epigean or subepigean forms. Or, they may represent a distinctive subspecies, since they are visibly distinct in eye size, and geographically are from an adjacent drainage system, But I think the eye size character varies in a direct, though steeply stepped, cline.

Schizogenius amphibius Haldeman

Clivina amphibia Haldeman 1843:299. *Type locality* southeastern Pennsylvania; type in MCZ, specimen labelled "amphibius 2" here designated lectotype (!). LeConte 1848: 215.

Schizogenius amphibius, LeConte 1857:83. Putzeys 1863:24. Putzeys 1866:224. LeConte 1879:34. Lindroth 1961:168.

Clivina frontalis LeConte 1848:215. *Type locality* Westchester County, New York; type male MCZ, specimen labelled MCZ 5482 here designated lectotype (!).

Schizogenius frontalis, LeConte 1857:83, suggested synonymy.

Diagnostic combination. – Specimens of this species are easily distinguished from all others in the group by small size and coarsely punctate prothoracic pleura.

Description. – Body flattened. Color testaceous, without metallic luster.

Integument. Coarse microsculpture in paramedian frontal sulci and on sides of abdomen. Fine but conspicuous microsculpture on mouth-parts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura, and middle of abdomen. Indistinct microsculpture sometimes on median portion of frons and on prothoracic pleura. Prothoracic pleura coarsely punctate.

Head. Fig. 162. Paramedian clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, no wider at base than apex of median field of frons. Clypeal suture sharply defined. Eye small, slightly flattened, finely and uniformly faceted. Neck densely and coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.4 times longer than wide.

Pronotum. Form and sculpture, Fig. 162. Sides bisetose, hind angles sharp and prominent, base not rugose. Paramedian longitudinal sulci long, impunctate, nearly straight, deep throughout, in most specimens sharply hooked basally. Anterior transverse impression finely punctate.

Legs. Front tarsus slightly dilated and pubescent ventrally in both sexes; middle and hind tarsi slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with 9-14 setae each on intervals three and five, and 5-10 on interval seven, adjacent to corresponding inner striae. Striae deep, sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles sharp and prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in both sexes, or finely crenulate in a few females.

Male genitalia. Median lobe, Fig. 174, apex not sharply deflexed; endophallus with elongate basal collar spines; 6 specimens examined.

Measurements and proportions. See Table 29.

Table 29. Descriptive statistics in *S. amphibius*, based on 10 males from Ithaca, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.18-3.38	3.307	0.101	0.042	2.03
LE	1.95-2.10	2.045	0.078	0.033	2.53
WH	0.62-0.68	0.651	0.024	0.010	2.45
WP	0.81-0.88	0.840	0.039	0.016	3.07
WE	0.99-1.05	1.025	0.039	0.016	2.51
B. Setae on left elytron.					
Interval 3	11-14	12.5			
Interval 5	10-14	11.5			
Interval 7	6-10	7.7			
Total	29-36	31.7	4.0	1.7	8.42
C. Proportions.					
WF/WH	0.68-0.71	0.698	0.021	0.009	2.00
LP/WP	0.93-0.98	0.952	0.024	0.010	1.70
DP/LP	0.76-0.81	0.781	0.024	0.010	2.05
LP/WE	0.76-0.81	0.781	0.029	0.012	2.45
Ta/Ti	0.55-0.65	0.607	0.045	0.019	4.91
PS/LP	0.69-0.78	0.742	0.039	0.017	3.52

Variation. – I noted no obvious important variation, and because the only good population samples are clustered in a small geographic area, I did not study variation in detail. The largest (LE, 2.80 mm) and smallest (LE, 1.80 mm) specimens are females from New York.

Etymology. – For *S. amphibius*, Greek, *amphibios* = amphibius, a reference to the habitat. For *S. frontalis*, Latin, *frons* = frons, a reference to the sculpture of the frons.

Distribution. – *S. amphibius* is known to range from Michigan and Quebec south to Tennessee and North Carolina (Fig. 190). An isolated form may exist in Texas, as I have seen four specimens from there but without definite locality data (ANSP, UKSM, USNM), but confirmation is needed; no other specimens are known from west of the Mississippi River. I studied 188 additional specimens from the following localities.

CANADA

QUEBEC: Montreal (1; USNM). See Lindroth (1961) for additional records.

UNITED STATES

No locality (6; ANSP, IRSB, USNM). CONNECTICUT: Hartford Co., West Hartford (1; MCZ). DISTRICT OF COLUMBIA: Washington (10; AMNH, ANSP, MCZ, USNM). ILLINOIS: Pike Co., Pittsfield (1; UCD). INDIANA: Tippecanoe Co. (1; UCD). KENTUCKY: Ballard Co., Wickliffe (2; TCBa); Jackson Co., Sand Gap (1; TCBa); Metcalfe Co., Edmonton (2; DRWh); Powell Co., Slade (1; TCBa). MAINE (1; MCZ); Oxford Co., Paris (2; MCZ). MARYLAND (4; INHS, USNM): Frederick Co., Frederick (1; RTBe). MICHIGAN (2; CAS). NEW HAMPSHIRE: Grafton Co., Franconia (4; AMNH, MCZ). NEW JERSEY: Burlington Co., Riverside (1; MCZ), Camden Co., Camden (1; MCZ), Cramer Hill (1; USNM); Essex Co., Irvington (1; CAS). NEW YORK (13; CAS, CNHM, INHS, KSUM, USNM): New York City vicinity (5; AMNH, CAS, MCZ); Long Island (1; USNM); Albany Co., Altamont (1; CUNY); Dutchess Co., Hyde Park (4; CAS); Herkimer Co., Newport (1; MCZ); Orange Co., West Point (21; USNM); Tompkins Co., Groton (4; CAS), Ithaca (20; CAS, CUNY, USNM, VMKi),

Varna (2; UASM); Ulster Co., Esopus (2; CUNY), Phoenicia (3; CAS, CNHM); Westchester Co., Peekskill (20; CAS, CUNY, MCZ, PSUU), Tarrytown (3; LACM); Wyoming Co., Pike (2; MCZ). NORTH CAROLINA: Buncombe Co., Black Mountains (7; AMNH, CAS, MCZ). OHIO: Mohican Point (1; UMCG); Ashtabula Co., Ashtabula (1; MSUL), Jefferson (1; MSUL). PENNSYLVANIA (1; ANSP): Allegheny Co. (1; MCZ); Bucks Co., Parkland (3; RUNB); Philadelphia Co., Frankford (2; USNM); Pike Co., Milford (1; USNM); Warren Co., Warren (3; CAS); Gray's Ferry (2; RUNB). RHODE ISLAND: Providence Co., Providence (1; USNM). TENNESSEE: Jackson Co., Blackman Fork (2; TCBa); Smith Co., Lancaster (1; TCBa), Monoville (1; TCBa). Vermont: Franklin Co., East Georgia (1; RTBe); Rutland Co., Clarendon (1; USNM); Windham Co., Brattleboro (2; RTBe). VIRGINIA: Alexandria Co. (5; USNM); Fairfax Co., Mount Vernon (1; USNM); Spotsylvania Co., Fredericksburg (1; USNM). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (3; CAS, MCZ).

Collecting notes. – Specimens of *S. amphibius* have been collected from April until September, generally in small numbers. I collected two specimens near Edmonton, Kentucky, together with specimens of *S. sulcifrons*, *S. lineolatus*, and *S. planulatus*. But a long series of this species only was taken at West Point, New York, so habitat requirements of *S. amphibius* must differ in some way from those of other, sympatric species. Its range is more completely restricted to limestone regions than those of either *S. sulcifrons* or *S. lineolatus*, and reduced eyes suggest a more subterranean habitat.

Taxonomic notes. – Haldeman's types are supposed to be in the LeConte Collection, at the head of each relevant series. However, the only specimens eligible for recognition as type material of *S. amphibius* are specimens 2, 3, 4, and 5, each so labelled and from Pennsylvania. The first specimen in the series is the only specimen representing type material of *S. frontalis* LeConte, and is the lectotype. I selected specimen 2 as lectotype of *amphibius*.

S. amphibius has no known close relatives, nor did I find any interesting patterns of variation within the species. If, however, specimens labelled "Texas" really were found there, they may not be conspecific. I doubt that *S. amphibius* will be found in any area between Texas and the Mississippi River, so that Texan populations, if they exist, would be markedly disjunct.

Schizogenius planulatus LeConte

Schizogenius planulatus LeConte 1863:5. *Type area* New York; type in MCZ; female labelled MCZ 5481 here designated lectotype (!). Putzeys 1866:224. LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. – Body strongly flattened. Dark testaceous to castaneous, unmetallic.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, apex of gula, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, extreme base and sides of pronotum, apical two-thirds of elytral epipleura, and entire abdomen. Fine microsculpture on basal third of elytral epipleura, and sometimes on prothoracic pleura and median frontal sulcus.

Head. Fig. 163. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye small, slightly flattened, finely and uniformly faceted. Neck densely and coarsely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 2.2 times longer than wide.

Pronotum. Fig. 163. Sides bisetose; base not rugose; hind angles small. Paramedian longitudinal sulci long, nearly straight, deep, sharply hooked basally. Anterior transverse impression finely punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in

females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with 10-14 setae on interval three, 9-12 on interval five, 6-9 on interval seven; total 27-34 in specimens examined. Striae deep and sharply engraved, finely punctate in basal three-fourths. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles sharp but not prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paired paramedian ambulatory setae in males only. Pygidium with apical margin strongly serrate in females, entire in males.

Male genitalia. Median lobe, Fig. 175, apex characteristic; endophallus, Fig. 182; 5 specimens examined.

Measurements and proportions. See Table 30.

Table 30. Descriptive statistics for *S. planulatus*, based on 11 females plus four males from New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.85-5.30	5.133	0.236	0.081	3.06
LE	3.00-3.28	3.190	0.128	0.044	2.67
WH	0.97-1.08	1.042	0.052	0.018	3.34
WP	1.28-1.42	1.357	0.067	0.023	3.30
WE	1.55-1.68	1.629	0.060	0.021	2.44
B. Setae on left elytron.					
Interval 3	10-14	11.6			
Interval 5	9-12	10.5			
Interval 7	6- 9	7.3			
Total	27-34	29.3	3.0	1.0	6.78
C. Proportions.					
WF/WH	0.66-0.71	0.687	0.023	0.008	2.25
LP/WP	0.88-0.94	0.909	0.026	0.009	1.88
DP/LP	0.74-0.81	0.777	0.028	0.009	2.37
LP/WE	0.71-0.78	0.755	0.026	0.009	2.29
Ta/Ti	0.53-0.65	0.605	0.049	0.017	5.42
PS/LP	0.69-0.74	0.708	0.020	0.007	1.92

Etymology. – Latin, *planus* = flat, in reference to body form.

Distribution. – I have seen specimens of this species only from Kentucky, New York, and West Virginia (Fig. 189) but it has been reported from Georgia (Fattig, 1949) and probably ranges throughout the Appalachian region at least in limestone areas. I studied 20 specimens from the following localities.

UNITED STATES

KENTUCKY: Metcalfe Co., 9 mi. e. Edmonton (3; DRWh, IRSB). NEW YORK: Erie Co., North Evans (2; CAS, MCZ); Tompkins Co., Ithaca (13; CAS, CUNY, UASM), Groton (1; JNeg). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (1; MCZ).

Collecting notes. – Specimens of this species have been collected from May to September. I collected the Kentucky specimens in a gravel bar, along with specimens of *S. amphibius*, *S. lineolatus*, and *S. sulcifrons*. Specimens of this species probably tend to be subepigean, as so few have been collected.

Taxonomic notes. – Specimens of this species differ radically from the related *S. ozarkensis* and *S. planuloides* in form of male genitalia, but otherwise probably are indistinguishable. As I found no important geographic variation in form of male genitalia in any of these species, I conclude that form of genitalia is constant and that the three geographic segregates truly represent distinct species. See discussion for *S. planuloides*.

Schizogenius ozarkensis new species

Type material. – Holotype male and allotype female labelled "5 mi. n. Stringtown Atoka Co. OKLAHOMA 7.IX.1964 Awram-Whitehead" (MCZ). 24 additional specimens from various localities in Arkansas, Missouri, and Oklahoma are paratypes (BMNH, CAS, CNC, DRWh, INHS, IRSB, UASM, USNM).

Diagnostic combination. – Males of this species differ strikingly from those of *S. planulatus* and *S. planuloides* in form of apex of median lobe. This species is the only member of the *tristriatus* group known from the Ozark region, north of the Red River and west of the Mississippi River.

Description. – Superficially as in *S. planulatus*, except frontal lobes prominent. Left elytron with 10-14 setae on interval three, 9-12 on interval five, and 6-9 on interval seven; total 25-32. Male genitalia with median lobe, Fig. 176, apex characteristic; endophallus, Fig. 183; 6 specimens examined.

Measurements and proportions. See Table 31. Of holotype: TL, 4.74 mm; LE, 2.92 mm; WH, 0.95 mm; WP, 1.24 mm; WE, 1.48 mm; WF/WH, 0.68; DP/LP, 0.74; LP/WP, 0.93; LP/WE, 0.78; PS/LP, 0.76; Ta/Ti, 0.61. Of allotype: TL, 4.68 mm; LE, 2.90 mm; WH, 0.94 mm; WP, 1.18 mm; WE, 1.45 mm; WF/WH, 0.68; DP/LP, 0.76; LP/WP, 0.96; LP/WE, 0.81; PS/LP, 0.69; Ta/Ti, 0.65.

Etymology. – I name this species after the Ozark Mountains, as this species is known only from in or near this area.

Distribution. – *S. ozarkensis* is known from only a small area in eastern Oklahoma, western Arkansas, and southern Missouri (Fig. 189). I studied 27 specimens from the following localities.

UNITED STATES

ARKANSAS: Carroll Co., 5 mi. w. Berryville (4; BMNH, CNC), Eureka Springs (2; UKSM); Van Buren Co., Formosa (2; IRSB); Washington Co. (1; INHS), 7 mi. s. Fayetteville (8; UASM). MISSOURI: Butler Co., 12 mi. se. Elsinore (4; CAS). OKLAHOMA: Atoka Co., 5 mi. n. Stringtown (5; DRWh, MCZ, USNM); Ottawa Co., Wyandotte (1; MCZ).

Collecting notes. – Adults of this species have been found from June to September, in riparian gravel bars.

Taxonomic notes. – Although adults of this species cannot be distinguished from those of *S. planulatus* and *S. planuloides* by external morphology, details of the male genitalia differ radically and show no sign of intergradation. Hence, I think that *S. ozarkensis* is a reproductive isolate.

Table 31. Descriptive statistics for *S. ozarkensis*, based on 10 females and seven males from northwestern Arkansas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.50-5.16	4.848	0.249	0.081	3.43
LE	2.80-3.22	3.006	0.155	0.050	3.44
WH	0.90-1.04	0.978	0.059	0.019	4.03
WP	1.10-1.32	1.225	0.062	0.020	3.40
WE	1.38-1.58	1.502	0.076	0.025	3.37
B. Setae on left elytron.					
Interval 3	10-14	11.2			
Interval 5	9-12	10.4			
Interval 7	6- 9	7.2			
Total	26-32	28.8	3.5	1.1	8.01
C. Proportions.					
WF/WH	0.64-0.74	0.671	0.038	0.012	3.76
LP/WP	0.92-0.98	0.948	0.024	0.008	1.69
DP/LP	0.73-0.77	0.751	0.017	0.006	1.52
LP/WE	0.74-0.80	0.771	0.027	0.009	2.29
Ta/Ti	0.60-0.68	0.643	0.041	0.014	4.28
PS/LP	0.66-0.74	0.690	0.033	0.011	3.16

Schizogenius planuloides new species

Type material. – Holotype male labelled "Cypress Mills 7/1/88 Texas" and "2048" (USNM). An additional 19 specimens from various localities in Texas are paratypes (ANSP, CAS, CNHM, DHKa, DRWh, MSUL, UASM, UKSM, USNM).

Diagnostic combination. – Specimens of this species are readily distinguished from those of the related *S. planulatus* and *S. ozarkensis* only by form of male genitalia and by the allopatric geographic distribution.

Description. – Superficially as in *S. planulatus*, except eyes in most specimens more strongly flattened and frontal lobes more prominent. Left elytron with 9-13 setae on interval three, 9-12 on interval five, and 6-8 on interval seven; total 26-31. Male genitalia with median lobe, Fig. 177, apex characteristic; endophallus, Fig. 184; 3 specimens examined.

Measurements and proportions. See Table 32. Of holotype: TL, 5.20 mm; LE, 3.20 mm; WH, 1.06 mm; WP, 1.34 mm; WE, 1.69 mm; WF/WH, 0.71; DP/LP, 0.75; LP/WP, 0.95; LP/WE, 0.76; PS/LP, 0.69; Ta/Ti, 0.70.

The claw-bearing article of the left hind tarsus of the type is lacking.

Etymology. – Latin, *planulatus* + *oides* = like *planulatus*, in reference to the great external similarity of this species to *S. planulatus*.

Distribution. – This species is known from only six definite localities throughout much of Texas (Fig. 189). Specimens labelled simply "Texas" may well have been collected at the

type locality, since that was a favorite early collecting locality in Texas. I studied 22 specimens of this species from the following localities.

UNITED STATES

TEXAS (15; ANSP, CAS, MSUL, UKSM, USNM): Blanco Co., Cypress Mills (1; USNM); Coryell Co. (1; MCZ); Dallas Co., Dallas (1; MCZ); Kinney Co., 23 mi. sw. Brackettville (1; DRWh); McLennon Co., Waco (1; DHKa); Taylor Co., 25 mi. sw. Abilene (1; CNHM); Terrell Co., Independence Creek (1; UASM).

Table 32. Descriptive statistics for *S. planuloides*, based on six females and 12 males from Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.94-5.54	5.194	0.244	0.077	3.13
LE	3.05-3.45	3.204	0.160	0.050	3.33
WH	1.02-1.15	1.084	0.050	0.016	3.07
WP	1.22-1.40	1.322	0.076	0.024	3.82
WE	1.50-1.75	0.628	0.095	0.030	3.88
B. Setae on left elytron.					
Interval 3	9-13	11.0			
Interval 5	9-12	10.4			
Interval 7	6- 8	6.9			
Total	26-31	28.3	2.3	0.7	5.25
C. Proportions.					
WF/WH	0.68-0.73	0.703	0.022	0.007	2.13
LP/WP	0.93-0.98	0.956	0.021	0.007	1.49
DP/LP	0.72-0.78	0.752	0.024	0.008	2.16
LP/WE	0.75-0.79	0.776	0.019	0.006	1.67
Ta/Ti	0.63-0.68	0.645	0.021	0.007	2.19
PS/LP	0.64-0.73	0.675	0.033	0.011	3.30

Collecting notes. – Specimens of this species have been collected from March through July, some at lights distant from water. I collected one specimen near Brackettville in a riparian gravel bar, along with several specimens of *S. scopaeus* and over 100 of *S. sallei*. Scarcity of specimens, and more strongly reduced eyes, suggest that this species is more strongly subepigean than either *S. planulatus* or *S. ozarkensis*. As in those species, I suspect that geographic distribution depends on surface and subsurface limestone.

Taxonomic notes. – The well differentiated male genitalia of this species indicates reproductive isolation from *S. planulatus* and *S. ozarkensis*. The geographically intermediate *S. ozarkensis* has less specialized male genitalia, but the genitalia of *S. planulatus* and *S. planuloides* are specialized in different ways. As shown in Tables 30-32, the sample of *S. planulatus* is characterized by statistically significantly broader pronota, the sample of *S. ozarkensis* by statistically significantly smaller body size, and the sample of *S. planuloides*

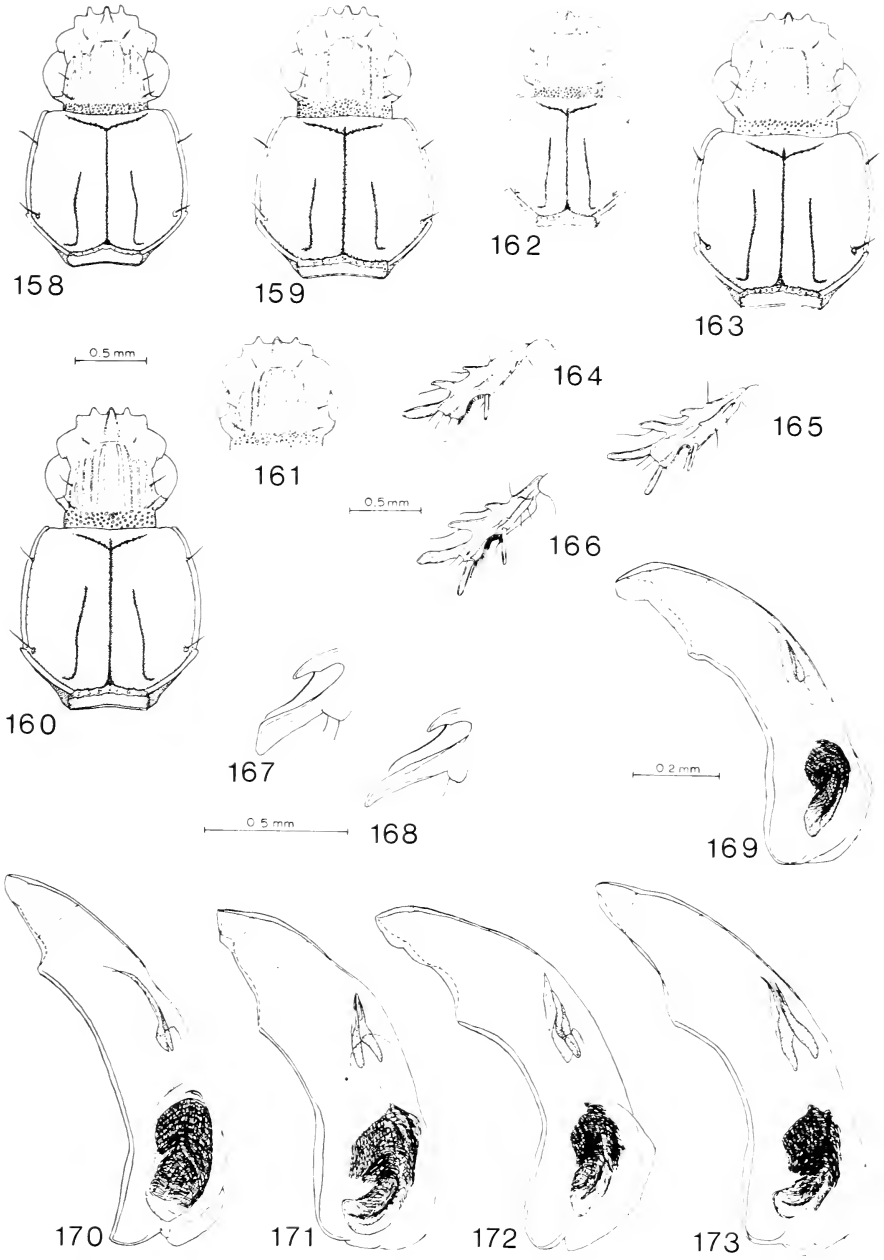


Fig. 158-163. Head and pronotum, dorsal aspect. 158. *S. sallei* Putzeys, Comstock, Texas. 159. *S. tristriatus* Putzeys, Coscomatepec, Veracruz. 160. *S. tibialis* new species, Tamazunchale, San Luis Potosi. 161. Same, Indian Creek Cave, Texas. 162. *S. amphibius* Haldeman, Edmonton, Kentucky. 163. *S. planulatus* LeConte, Edmonton, Kentucky. Fig. 164-166. Left front tibia, posterior aspect. 164. *S. tristriatus* Putzeys, Coscomatepec, Veracruz. 165. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 166. *S. tibialis* new species, Tamazunchale, San Luis Potosi. Fig. 167-168. Distal portion of left front tibia, posterior aspect. 167. *S. tibialis* new species, Tamazunchale, San Luis Potosi. 168. Same, Indian Creek Cave, Texas. Fig. 169-173. Male median lobe, lateral aspect. 169. *S. sallei* Putzeys, Austin, Texas. 170. *S. tristriatus* Putzeys, Fortin de las Flores, Veracruz. 171. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 172. *S. tibialis* new species, Encarnacion de Diaz, Jalisco. 173. Same, Indian Creek Cave, Texas.

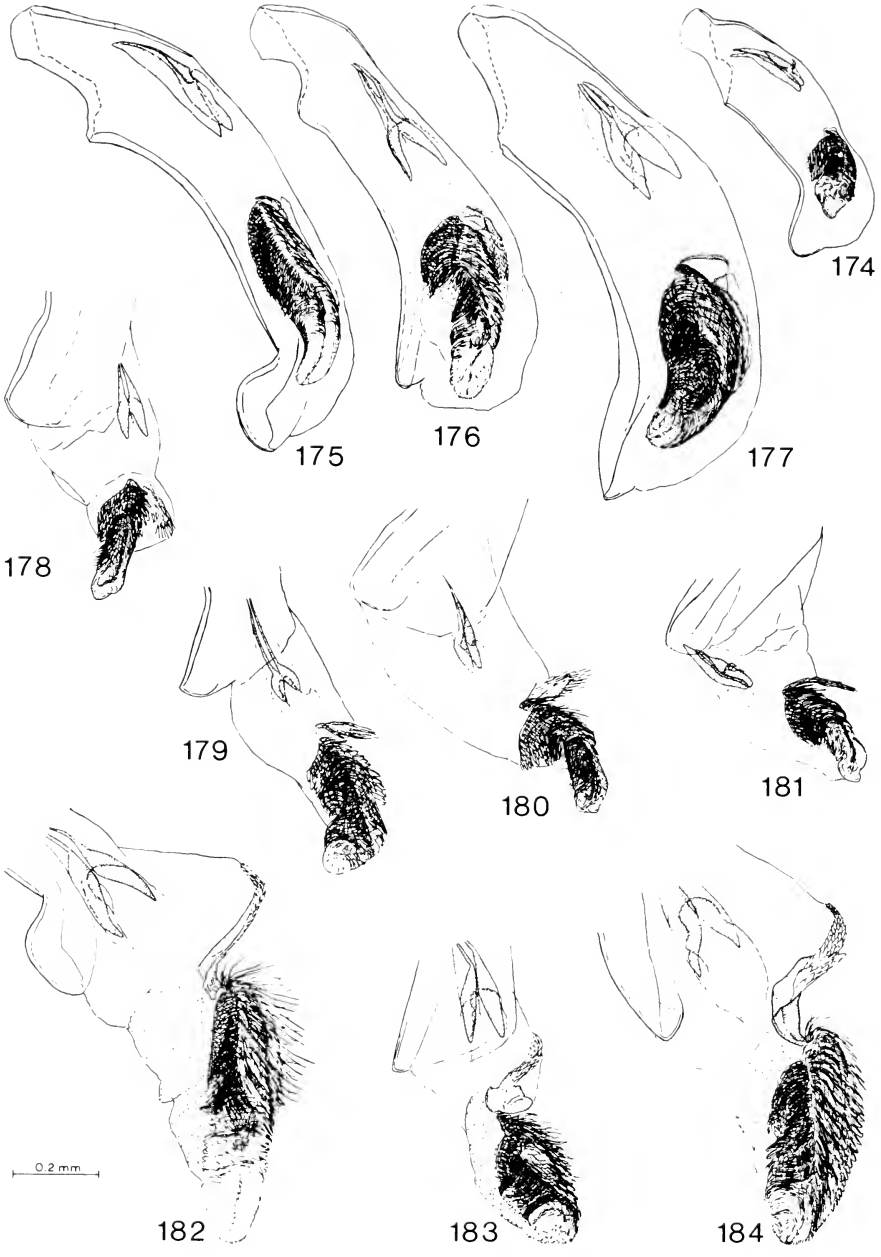
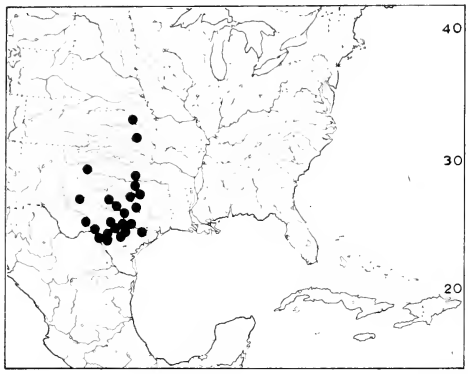


Fig. 174-177. Male median lobe, lateral aspect. 174. *S. amphibius* Haldeman, West Point, New York. 175. *S. planulatus* LeConte, North Evans, New York. 176. *S. ozarkensis* new species, Elsinore, Missouri. 177. *S. planuloides* new species, Texas. Fig. 178-184. Male endophallus. 178. *S. sallei* Putzeys, Sabinal, Texas. 179. *S. tristriatus* Putzeys, Fortin de las Flores, Veracruz. 180. *S. dilatus* new species, Sabinas Hidalgo, Nuevo Leon. 181. *S. tibialis* new species, Tapanatepec, Oaxaca. 182. *S. planulatus* LeConte, Ithaca, New York. 183. *S. ozarkensis* new species, Stringtown, Oklahoma. 184. *S. planuloides* new species, Cypress Mills, Texas.



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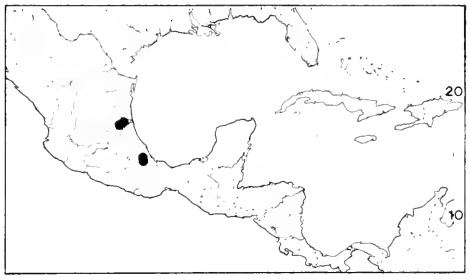

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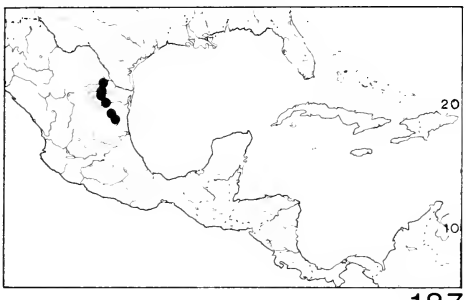

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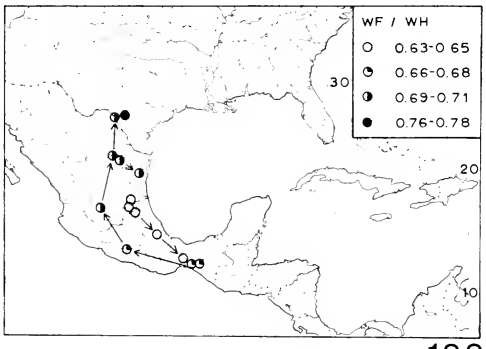

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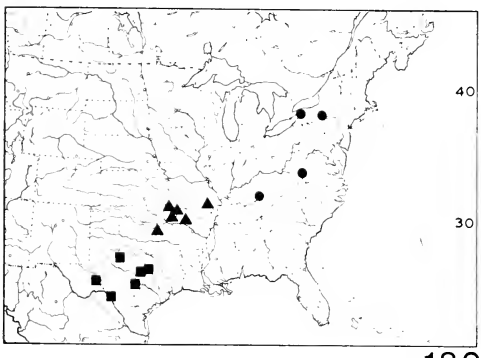
1000 mi



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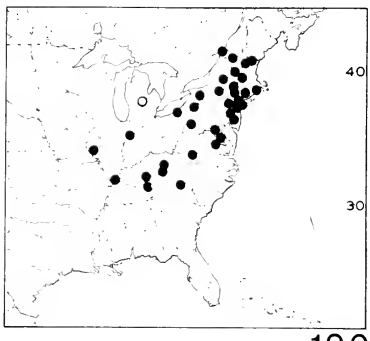

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Fig. 185-190. Known distributions. 185. *S. sallei* Putzeys. 186. *S. tristriatus* Putzeys. 187. *S. dilatus* new species. 188. *S. tibialis* new species (with clinal variation in relative eye size). 189. *S. planulatus* LeConte, circles; *S. ozarkensis* new species, triangles; *S. planuloides* new species, squares. 190. *S. amphibius* Haldeman; open symbol represents state record only.

by statistically significantly smaller eye size. As judged from comparisons with other members of the *tristriatus* group, the ancestor of the *planulatus* subgroup probably had larger eyes as in *S. planulatus* and *S. ozarkensis*, smaller size as in *S. ozarkensis*, and narrower pronota as in *S. ozarkensis* and *S. planuloides*. In all of these ways, *S. ozarkensis* is most like the probable ancestor of the subgroup.

Since I have no females from the type locality, I designate no allotype for *S. planuloides*.

The *lineolatus* group

Diagnostic combination. – From other members of the genus with antennae elongate, pronotal hind angles prominent, discal setae on intervals three, five, and seven, and paramedian sternal carinae curved at apices, members of this group are distinguished by the following combination of characters: body strongly flattened; elytra aeneopiceous, or rufocastaneous with pale apices; paramedian pronotal sulci not extended forward nearly to anterior transverse impression; elytron with total discal setae fewer than 30, their average length less than 1.0 times maximum width of interval two; and abdomen unmicrosculptured except in small patches near coxal depressions of sternum three. Also paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; clypeal suture sharply impressed; frontal carinae not confused at base; submentum without accessory setae; pronotum without paralateral carinae, without accessory marginal setae; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; pygidium crenulate at apex or not in females; and endophallus with basal collar spines distinct.

Distribution. – The range of the single included species, *S. lineolatus*, covers much of eastern North America south to the Rio Grande. I examined 897 specimens.

Schizogenius lineolatus Say

Clivina lineolata Say 1823:22. *Type locality* Allegheny, Pennsylvania (designated by Lindroth, 1961); neotype male designated by Lindroth and Freitag (1969). LeConte 1848: 214.

Schizogenius lineolatus, LeConte 1857:82. Putzeys 1863:24. Putzeys 1866:228. LeConte 1879:34. Lindroth 1961:166.

Diagnostic combination. – Specimens of this species are best distinguished by characteristics given in the key. In eastern North America, the only other dark species of *Schizogenius* with setae on elytral interval seven is *S. sulcifrons*. Specimens of that species generally have less sharply developed pronotal hind angles, more elytral setae, and concolorous elytra and pronotum.

Description. – Body flattened. Color light to dark castaneous; legs rufous; tarsi and palpi testaceous; elytra rufopiceous and in most specimens strongly aeneous, except in Rio Grande Valley where castaneous, paler toward apices, and weakly aeneous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on apical two-thirds and in most eastern specimens on shoulder and on basal third, and sternum three in coxal depressions and small paralateral patches.

Head. Fig. 191. Paramedian clypeal carinae straight, moderately elevated in basal half,

extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.7-1.8 times longer than wide.

Pronotum. Fig. 191. Sides bisetose; base not rugose; hind angles prominent. Paramedian longitudinal sulci quite long, nearly straight, strongly hooked basally. Paralateral carinae absent. Anterior transverse impression strongly punctate in most specimens.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about six to nine setae on interval three, five to eight on interval five, two to five on interval seven; total 13-20 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin crenulate in some females, entire in males.

Male genitalia. Median lobe, Fig. 196; endophallus, Fig. 201, virga small; 20 specimens examined.

Measurements and proportions. See Table 33.

Table 33. Descriptive statistics for *S. lineolatus*, based on 20 males from 5 miles north of Stringtown, Oklahoma.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.80-4.44	4.412	0.288	0.077	4.15
LE	2.35-2.74	2.558	0.153	0.046	4.00
WH	0.81-0.95	0.875	0.052	0.016	3.97
WP	1.00-1.20	1.092	0.083	0.025	5.08
WE	1.20-1.42	1.324	0.084	0.025	4.22
B. Setae on left elytron.					
Interval 3	6- 8	6.8			
Interval 5	5- 8	6.2			
Interval 7	2- 4	3.1			
Total	14-19	16.1	1.9	0.6	7.78
C. Proportions.					
WF/WH	0.55-0.59	0.567	0.017	0.005	1.99
LP/WP	0.87-0.94	0.910	0.021	0.006	1.55
DP/LP	0.80-0.86	0.830	0.024	0.007	1.93
LP/WE	0.73-0.77	0.749	0.019	0.006	1.73
Ta/Ti	0.60-0.69	0.643	0.037	0.011	3.85
PS/LP	0.76-0.82	0.786	0.025	0.007	2.08

Variation. – Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 34-37 for 17 samples of *S. lineolatus* (Fig. 211-214). Body size (Table 34, Fig. 211) decreases quite regularly from northeast to southwest, with no geographically proximate samples statistically significantly distinct from one another. Numbers of elytral setae (Table 35, Fig. 212) tend to increase from northeast to southwest, and the Rio Grande sample (number 17) barely is statistically significantly distinct from the Guadalupe River sample (number 16). Eye size (Table 36, Fig. 213) increases generally southwest to the Guadalupe River (sample 16), with a statistically significant increase in the east between samples four and five, but is sharply reduced between samples 16 and 17. The pronotum (Table 37, Fig. 214) narrows from northeast to southwest, with statistically significant gaps between the Red River (sample 14), the Guadalupe River (sample 16), and the Rio Grande (sample 17).

Variation in extent of evident microsculpture on basal third of elytral epipleura and on shoulder follows a pattern of gradual reduction from east to west. Microsculpture on the basal third of the epipleura is present on most specimens from east of the Appalachians, absent from most specimens from west of the Mississippi River, and varied in specimens from intermediate areas. Microsculpture is evident on the shoulder of most specimens from all areas except in many from the most western localities such as in western Oklahoma and eastern Wyoming, but is most strongly developed in eastern specimens.

Specimens from the Rio Grande Valley (sample 17) differ from all others, except some teneral specimens, in elytral coloration: reddish rather than blackish, and paler toward apices. In this characteristic, these specimens do not intergrade with those from the nearest localities where *S. lineolatus* is known to exist, in the Guadalupe River system (sample 16) some 125-150 miles distant. These two samples also are statistically distinct in the number of elytral setae, relative eye size, and pronotal form, but are not distinct in epipleural microsculpture or in body size. Lack of differentiation in some characteristics, evidence of clinal continuity in others, and in particular the fine clinal sequence in variation in pronotal form shown by samples 14-16-17 strongly indicate that the Rio Grande population is not reproductively isolated. But the difference in coloration is constant, statistically significant differences exist for numbers of elytral setae, relative eye size, and pronotal form, and the direction of clinal variation is reversed in the relative eye size characteristic. I conclude from these facts that the Rio Grande form is geographically isolated from populations to the north, and predict that truly intermediate populations do not exist.

Etymology. – Latin, *lineola* = fine line, probably in reference to the presence of paramedian pronotal sulci.

Distribution. – Four specimens are labelled "Fla." I doubt that *S. lineolatus* really occurs in Florida, as I think there is no suitable habitat there. Otherwise, the known range of this species extends west from southern Canada and eastern United States to at least eastern Wyoming, and south to the Rio Grande Valley (Fig. 206). I studied 893 additional specimens from the following localities.

CANADA

No locality (5; ANSP, CNHM, MCZ, UKSM). ONTARIO: 16 mi. w. Bondhead (1; UASM), London (20; CNHM, UASM), Ottawa (1; TLEr), Port Credit (1; CUNY), Port Stanley (1; UASM), Saint Catherines (3; JNeg), Toronto (5; MCZ, UASM), Wheatley (1; KHSt). QUEBEC: Montreal (1; MCZ), Potton Springs (10; MCZ). For other Canadian records, see Lindroth (1961).

UNITED STATES

No locality (8; ANSP, CUNY, IRSB, USNM). ALABAMA: Tuscaloosa Co., 15 mi. n. Tuscaloosa (11; DJLa). ARKANSAS: Carroll Co., Berryville (1; MCZ), 4 mi. w. Berryville (27; UASM); Newton Co., Jasper (1; BMNH); Sevier Co., 6 mi. n. Lockesburg (1; MCZ); Van Buren Co., Formosa (2; IRSB); Washington Co. (2; INHS), 7 mi. s. Fayetteville (7; UASM).

Table 34. Variation in body size (LE, in mm) in selected samples of *S. lineolatus*; see Fig. 211.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	2.82-3.08	2.902	0.127	0.053	2.91
2	10	5	2.65-3.08	2.844	0.218	0.092	5.12
3	18	9	2.55-3.15	2.828	0.197	0.062	4.68
4	12	6	2.58-2.98	2.813	0.212	0.082	5.03
5	28	14	2.40-3.04	2.735	0.252	0.064	6.14
6	16	8	2.55-2.95	2.756	0.178	0.069	4.30
7	12	6	2.62-3.02	2.802	0.178	0.069	4.24
8	12	6	2.55-3.00	2.750	0.184	0.071	4.46
9	10	5	2.40-2.92	2.663	0.237	0.100	5.93
10	10	5	2.55-2.98	2.766	0.199	0.084	4.81
11	14	7	2.45-2.90	2.643	0.189	0.067	4.76
12	14	7	2.48-2.88	2.677	0.156	0.056	3.90
13	22	11	2.42-3.00	2.703	0.200	0.057	4.94
14	26	13	2.35-2.85	2.629	0.197	0.052	5.00
15	16	8	2.38-2.98	2.619	0.273	0.091	6.96
16	18	9	2.38-2.85	2.616	0.206	0.065	5.26
17	20	10	2.32-2.88	2.630	0.195	0.058	4.94

Table 35. Variation in numbers of discal setae on left elytron in selected samples of *S. lineolatus*; see Fig. 212.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	13-17	15.3	1.7	0.7	7.58
2	10	5	16-19	16.6	1.6	0.7	6.48
3	18	9	15-19	15.9	1.6	0.5	6.62
4	12	6	15-17	16.2	1.3	0.5	5.16
5	28	14	14-17	15.6	1.2	0.3	5.04
6	16	8	15-17	15.6	1.2	0.4	5.23
7	12	6	15-18	15.9	1.5	0.7	6.26
8	12	6	13-17	15.5	1.9	0.7	8.02
9	10	5	14-17	15.6	1.3	0.5	5.41
10	10	5	15-18	16.0	1.6	0.7	6.58
11	14	7	15-20	17.1	1.5	0.9	9.60
12	14	7	14-17	16.1	1.1	0.4	4.77
13	22	11	14-19	16.3	1.7	0.5	7.17
14	26	13	14-18	16.2	1.5	0.4	6.30
15	16	8	15-19	16.5	1.5	0.5	6.26
16	18	9	14-18	16.0	1.8	0.6	7.43
17	20	10	16-19	17.2	1.4	0.4	5.28

Table 36. Variation in eye size (WF/WH) in selected samples of *S. lineolatus*; see Fig. 213.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	0.59-0.63	0.614	0.023	0.010	2.57
2	10	5	0.60-0.62	0.612	0.012	0.005	1.29
3	18	9	0.58-0.63	0.607	0.021	0.006	2.26
4	12	6	0.58-0.62	0.601	0.016	0.006	1.80
5	28	14	0.56-0.61	0.590	0.016	0.004	1.87
6	16	8	0.58-0.61	0.592	0.017	0.006	1.87
7	12	6	0.57-0.60	0.582	0.015	0.006	1.77
8	12	6	0.56-0.60	0.579	0.020	0.008	2.26
9	10	5	0.56-0.60	0.579	0.022	0.009	2.50
10	10	5	0.56-0.59	0.577	0.014	0.006	1.64
11	14	7	0.54-0.59	0.579	0.023	0.008	2.70
12	14	7	0.55-0.59	0.574	0.018	0.006	2.12
13	22	11	0.56-0.59	0.576	0.015	0.004	1.75
14	26	13	0.55-0.59	0.569	0.017	0.004	1.95
15	16	8	0.55-0.58	0.565	0.015	0.005	1.83
16	18	9	0.54-0.60	0.564	0.020	0.006	2.37
17	20	10	0.57-0.60	0.579	0.015	0.004	1.67

Table 37. Variation in pronotal form (LP/WP) in selected samples of *S. lineolatus*; see Fig. 214.

Sample	N	Males	Range	Mean	1.5SD	2SE	CV(%)
1	10	5	0.86-0.90	0.880	0.022	0.009	1.69
2	10	5	0.84-0.91	0.880	0.030	0.012	2.14
3	18	9	0.85-0.91	0.882	0.025	0.008	1.92
4	12	6	0.84-0.94	0.883	0.041	0.016	3.07
5	28	14	0.85-0.93	0.888	0.015	0.006	1.87
6	16	8	0.86-0.93	0.886	0.023	0.008	1.74
7	12	6	0.86-0.94	0.898	0.033	0.013	2.46
8	12	6	0.84-0.92	0.882	0.037	0.014	2.82
9	10	5	0.87-0.94	0.899	0.035	0.015	2.59
10	10	5	0.87-0.91	0.885	0.019	0.008	1.43
11	14	7	0.88-0.93	0.901	0.023	0.008	1.73
12	14	7	0.88-0.94	0.909	0.026	0.009	1.90
13	22	11	0.86-0.93	0.903	0.030	0.008	2.19
14	26	13	0.87-0.93	0.902	0.025	0.007	1.85
15	16	8	0.89-0.95	0.912	0.022	0.007	1.63
16	18	9	0.88-0.94	0.922	0.023	0.007	1.64
17	20	10	0.90-0.98	0.940	0.031	0.009	2.18

DISTRICT OF COLUMBIA: Washington (16; AMNH, CAS, MCZ, MSUL, USNM). ILLINOIS (8; INHS, MCZ, USNM). Cook Co., Palos Park (1; CNHM); La Salle Co., Ottawa (1; RTBe); McLean Co., Normal (1; INHS); Peoria Co., East Peoria (2; CNHM); Vermilion Co., Fairmount (1; RTBe). INDIANA (1; MSUL): Parke Co. (9; UCD), The Shades State Park (3; RTBe); Tippicanoe Co. (2; MCZ), 1 mi. ne. Lafayette (1; GRNo), Wabash River (2; CAS). IOWA: Herrold (1; USNM); Boone Co., Boone (6; UASM); Cedar Co. (1; USNM); Johnson Co., Iowa City (1; USNM). KANSAS: Bourbon Co., Fort Scott (2; USNM); Douglas Co., Lawrence (1; DJLa); Pottawatomie Co., Onaga (5; KSUM, USNM); Riley Co., Manhattan (1; KSUM); Wilson Co., Benadict (2; CAS). KENTUCKY: Ballard Co., Wickliffe (9; TCBa); Cumberland Co., Marrowbone Creek (7; TCBa); Green Co., Greasy Creek (1; TCBa); Jackson Co., Sand Gap (2; TCBa); Jessamine Co., Indian Falls (2; TCBa); Metcalfe Co., 8 mi. e. Edmonton (20; UASM); Powell Co., Slade (2; TCBa); Hockcastle Co., Crooked Creek (1; TCBa). MARYLAND (3; CAS, MSUL, USNM): Difficult (1; MCZ); Baltimore Co., Baltimore (2; CAS); Frederick Co., Frederick (7; DRWh, RTBe); Harford Co., Edgewood (7; DRWh); Prince Georges Co., Bladensburg (1; CUNY). MISSOURI: Barry Co., Cassville (1; USNM); Boone Co., Columbia (3; USNM); Crawford Co., Meramec River (2; USNM); Laclede Co., Bennet Springs (7; USNM); McDonald Co., 3 mi. n. Noel (3; CAS); Ozark Co., Gainesville (18; UASM); Reynolds Co., Bunker (1; USNM); Ripley Co., Buffalo Creek (1; CAS), Doniphan (2; USNM); Saint Louis Co., Saint Louis (2; UMCG); Taney Co., 5 mi. e. Forsythe (2; MGFT); Wright Co., Mountain Grove (14; TCBa). MONTANA: Roosevelt Co., Wolf Point (1; CAS). NEW JERSEY (2; ANSP): Bergen Co., Westwood (1; CAS); Camden Co., Camden (9; CAS, LACM, RUNB), Cramer Hill (1; USNM); Essex Co., Irvington (2; AMNH); Gloucester Co., Westville (2; MCZ); Middlesex Co., Jamesburg (3; CUNY); Morris Co., Boonton (6; USNM): Somerset Co. (1; USNM); Warren Co., Phillipsburg (11; CAS, MSUL). NEW YORK (5; CAS, CNHM, INHS, USNM); New York City (2; CAS); West Hebron (3; CAS); Albany Co., Altamont (1; CUNY); Broome Co., Chenango Valley State Park (13; GRNo); Cattaraugus Co., Allegany State Park (1; USNM); Dutchess Co., Fishkill (6; CAS); Erie Co., Buffalo (2; CAS), North Evans (3; CAS); Greene Co., Ashland (4; CUNY, MCZ); Rockland Co., Hillburn (2; USNM); Tompkins Co., Groton (7; JNeg, UATA), Ithaca (28; CAS, CUNY, FDAG, USNM, VMKi); Ulster Co., Phoenicia (1; CAS); Wyoming Co., Pike (2; MCZ). NORTH CAROLINA: (2; MCZ) Buncombe Co., Black Mountains (1; CAS). OHIO: Mohican Point (3; UMCG); Ashtabula Co., Ashtabula (2; MSUL), Conneaut (1; MSUL), Rock Creek (1; MSUL); Athens Co., Athens (1; UATA); Crawford Co., Plankton (1; CAS); Cuyahoga Co., Cleveland (1; FDAG); Knox Co., Gambier (1; UMCG); Preble Co., West Alexandria (1; RTBe); Warren Co., Twenty Mile Strand (19; DJLa). OKLAHOMA: Atoka Co., Atoka (6; CAS, MCZ, USNM), 5 mi. n. Stringtown (80; UASM); Carter Co., 10.7 mi. s. Drake (7; TLEr); Cherokee Co., 15 mi. sw. Talequah (1; BMNH); Comanche Co., Wichita National Forest (13; CAS); Cotton Co. (2; CAS); Craig Co., Grand Lake (6; DHKa); McCurtain Co., 7 mi. sw. Smithville (10; UASM); Murray Co., 10.3 mi. n. Drake (6; TLEr); Washita Co. (1; CAS). PENNSYLVANIA (15; AMNH, ANSP, CAS, MCZ, MSUL): Willow Mills (1; VMKi); Allegheny Co., Allegheny (1; MCZ); Bucks Co. (4; CAS, RUNB), Point Pleasant (1; CAS); Cumberland Co., Lemoyne (3; CAS), New Cumberland (12; CAS, CUNY, MCZ, VMKi), West Fairview (10; CAS); Monroe Co., Delaware Water Gap (12; AMNH, MCZ); Northampton Co., Bethlehem (4; CNHM), Easton (8; CAS, CNHM); Philadelphia Co., Frankford (3; USNM), Mount Airy (1; ANSP), Philadelphia (5; MCZ), Wyoming (1; USNM); Pike Co., Milford (6; USNM); York Co., 5 mi. w. Davidsburg (1; GRNo). SOUTH CAROLINA (1; MCZ). SOUTH DAKOTA: Mellete Co., White River (1; UASM). TENNESSEE: Carter Co., Elizabethton (1; CNHM); Davidson Co., Nashville (4; CAS, CUNY, LACM); Jackson Co., Cummins Mill (7; TCBa); Lincoln Co., 2 mi. n. Howell (5; UASM); Smith Co., Lancaster (2; TCBa); Warren Co., Cardwell Mountain (1; TCBa); White Co., Caney Fork River (2; TCBa), Sparta (1; TCBa). TEXAS (21; ANSP, CAS, MCZ, RUNB, UKSM, USNM); Blanco Co., Cypress Mills (2; USNM), Johnson City (22; UASM); Colorado Co., Columbus (9; USNM); Cooke Co., 4 mi. sw. Era (1; CNC); Erath Co., Morgan Mill (2; INHS); Hamilton Co., 6 mi. n. Hamilton (6; ANSP); Kerr Co., Kerrville (1; CNC); Kinney Co., 23 mi. sw. Brackettville (3; DRWh); Lampasas Co., Adamsville (7; AMNH); McCulloch Co., 16 mi. s. Brady (3; CAS); Maverick Co., 8 mi. n. Quemado (5; UASM); Parker Co., 5 mi. sw. Weatherford (3; CNHM); Val Verde Co., 13 mi. nw. Del Rio (17; UASM). VERMONT: Clarendon (3; RTBe); South Alberg (1; RTBe); Addison Co., North Ferrisburg (5; RTBe); Bennington Co., Pownall (3; RTBe); Chittenden Co., Charlotte (2; RTBe), Shelburne (1; CAS); Franklin Co., East Georgia (13; RTBe); Rutland Co., Fair Haven (9; RTBe); Windham Co., Brattleboro (1; USNM), Newfane (1; RTBe), Townshend (4; RTBe); Windsor Co., (1; RTBe). VIRGINIA: Arlington Co., Rosslyn (4; MCZ, USNM); Fairfax Co. (1; USNM), Alexandria (13; AMNH, CAS, USNM), Black Pond (1; USNM), Glencarlyn (1; USNM), Great Falls (2; AMNH, USNM), Mount Vernon (4; USNM); Loudon Co. (2; AMNH); Roanoke Co., Buffalo Creek (6; CUNY), Roanoke (1; MZSP). WEST VIRGINIA: Greenbrier Co., White Sulphur Springs (1; CAS). WISCONSIN (6; CAS, CNHM, USNM): Milwaukee Co., Milwaukee (1; MCZ), Wauwatosa (1; CNHM). WYOMING: Niobrara Co., 37 mi. n. Lusk (8; UASM).

MEXICO

TAMAULIPAS: 34.9 mi. s. Nuevo Laredo (2; UASM).

Collecting notes. – Specimens of this abundant species have been collected from April to October, most of them in gravel bars along streams.

Taxonomic notes. – This species and *S. sulcifrons* were long confused in the literature, but Lindroth (1961) recognized their distinctness. They are not closely related. A distinctive form of *S. lineolatus* in the Rio Grande Valley does not meet my criteria for recognition as a subspecies, but is no doubt geographically isolated.

The *longipennis* group

Diagnostic combination. – Members of this group are distinguished by the following combination of characters: body moderately to strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum without paralateral carinae; discal setae present on intervals three, five, and seven, total less than 20, average length less than 1.0 times maximum width of interval two; abdomen without extensive microsculpture, and without small lateral patches near coxal depressions of sternum three; endophallus with enlarged basal collar spines. Also: clypeal suture sharply impressed in most specimens; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three not or weakly curved outward at apices; and pygidium crenulate or not at apex in females.

Distribution. – Members of this group range from the Colorado River system in Arizona and New Mexico in the west and from Tamaulipas and Nuevo Leon in the east south to Costa Rica. I examined 1406 specimens of the *longipennis* group.

Taxonomic notes. – I have not critically studied geographic variation in members of this group, as three species are neither widespread nor represented by sufficient material. Four species are distinguished by male genitalic characteristics or by superficial characters. Variation in at least *S. longipennis* is extensive and no doubt is worthy of study, but such study is not required for species recognition.

Schizogenius neovalidus new species

Type material. – Holotype male and allotype female labelled "Gila River, nr. Cliff, Grant Co. NEW MEXICO 26.VIII.1964 Awram-Whitehead" (MCZ). An additional 107 specimens from various localities in Arizona and New Mexico are paratypes (AMNH, ANSP, BMNH, CAS, CNC, CNHM, CUNY, DJLa, DRWh, IRSB, JNeg, MGFT, TLEr, UASM, UATA, USNM).

Diagnostic combination. – Within the *longipennis* group, the following characteristics of the male genitalia are diagnostic of this species: apex of median lobe (Fig. 197) elongate, deflexed at sharp angle, right margin strongly flanged; basal collar spines of endophallus slender, elongate. In Arizona, most matured specimens may be distinguished from matured specimens of *S. longipennis* by rufopiceous rather than rufous femora, and by form of frontal carinae (Fig. 192). From matured specimens of *S. chiricahuanus* matured specimens of *S. neovalidus* are distinguished by piceous or dark rufopiceous rather than rufous or light rufopiceous elytra.

Description. – Body flattened. Color piceous, elytra not to weakly aeneous; femora in most specimens dark rufopiceous; tibiae, tarsi, and antennae rufous; palpi testaceous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, and hind tibiae and posterior surfaces of hind femora. Sternum three without conspicuous paralateral patches of microsculpture.

Head. Fig. 192, frontal carinae three abbreviated in most specimens. Paramedian clypeal carinae straight, not markedly elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture weakly to strongly engraved. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate,

article five about 1.6-1.7 times longer than wide.

Pronotum. Fig. 192. Sides bisetose; base not rugose; hind angles reduced. Paramedian longitudinal sulci moderately long, nearly straight to strongly bent near middle, strongly hooked basally. Anterior transverse impression not or weakly punctate; basal impression impunctate.

Legs. Front tarsus strongly dilated in males, moderately in females; middle tarsus moderately dilated in both sexes; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about 6-8 setae on interval three, 5-8 on interval five, 3-5 on interval seven; total 14-19 in specimens examined. Striae deep and sharply engraved, finely punctate in basal three-fourths. Intervals one to seven broad and weakly convex, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles moderately prominent.

Abdomen. Sternum three with paramedian carinae not or weakly curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin entire in males and females.

Male genitalia. Median lobe, Fig. 197, apex elongate, deflexed at a 50-60 degree angle, right ventral margin strongly flanged; endophallus, Fig. 202, virga 0.42-0.48 length of median lobe, basal collar spines six to eight times longer than wide; 13 specimens examined.

Measurements and proportions. See Table 38. Of holotype: TL, 4.94 mm; LE, 3.09 mm; WH, 1.02 mm; WP, 1.32 mm; WE, 1.64 mm; WF/WH, 0.65; LP/WP, 0.87; DP/LP, 0.85; LP/WE, 0.70; Ta/Ti, 0.63; PS/LP, 0.64. Of allotype: TL, 5.29 mm; LE, 3.35 mm; WH, 1.02 mm; WP, 1.38 mm; WE, 1.78 mm; WF/WH, 0.65; LP/WP, 0.88; DP/LP, 0.86; LP/WE, 0.69; Ta/Ti, 0.64; PS/LP, 0.63.

Variation. – See Table 38. In some specimens, the front femora may be rufous or the third frontal carina not abbreviated basally; I otherwise observed no important variation.

Etymology. – Latin, *neo* = new, plus *validus* = strong. Since the Arizona form of *S. longipennis* was named *S. validus* by Fall, I here name this similar looking new species by the similar name, *S. neovalidus.*

Distribution. – The known range of this species, except for one female specimen collected recently by D. J. Larson on the Verde River, is restricted to upper reaches of the Gila River system in southeastern Arizona and southwestern New Mexico (Fig. 207). I examined 110 specimens from the following localities.

UNITED STATES

ARIZONA: Gila Co., nr. Carrizo (3; UASM), 6 mi. n. Payson (1; DJLa); Graham Co., nr. Aravaipa (35; AMNH, ANSP, BMNH, CAS, CNC, CNHM, CUNY, DRWh, IRSB, JNeg, MGFT, UASM, UATA, USNM); Pinal Co., 9 mi. nw. Payson (1; CAS). NEW MEXICO: Catron Co., Glenwood (11; UASM); Grant Co., Cliff (33; MCZ, UASM), Gila (1; UASM), 26 mi. n. Silver City (15; TLEr), 36.4 mi. ne. Silver City (7; UASM), 71.6 mi. ne. Silver City (3; UASM).

Collecting notes. – Specimens of this species have been collected from late May through late August, in riparian gravel bars.

Taxonomic notes. – Until now, specimens of the *longipennis* group from Arizona have all been named *S. validus* Fall. But these specimens clearly represent three species, and further, the name *S. validus* falls as a synonym of *S. longipennis* Putzeys. Males of all three species are well characterized by details of the male median lobe and endophallus, but females cannot be distinguished with certainty. Two females from Aravaipa are identified as *S. longipennis*, and a female and male of *S. neovalidus* from Payson are well within the range of *S. longipennis*. Thus, these two species are sympatric.

Table 38. Descriptive statistics for *S. neovalidus*, based on 16 males from Cliff, New Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.79-5.49	5.224	0.366	0.122	4.65
LE	3.00-3.41	3.248	0.212	0.071	4.34
WH	0.96-1.14	1.059	0.076	0.025	4.78
WP	1.22-1.50	1.401	0.128	0.043	6.09
WE	1.57-1.86	1.736	0.131	0.044	5.04
B. Setae on left elytron.					
Interval 3	6- 8	6.7			
Interval 5	6- 7	6.2			
Interval 7	3- 5	3.7			
Total	15-18	16.6	1.4	0.5	5.76
C. Proportions.					
WF/WH	0.61-0.65	0.632	0.019	0.006	1.96
LP/WP	0.84-0.92	0.881	0.037	0.012	2.80
DP/LP	0.82-0.89	0.848	0.026	0.009	2.03
LP/WE	0.69-0.73	0.711	0.015	0.005	1.40
Ta/Ti	0.61-0.69	0.654	0.033	0.011	3.40
PS/LP	0.58-0.67	0.614	0.033	0.011	3.56

Schizogenius longipennis Putzeys

Schizogenius tristriatus longipennis Putzeys 1866:227. *Type locality* "Mexique," here restricted to Fortín de las Flores, Veracruz; lectotype female labelled "longipennis. Chd. Mex. (C. Chd.)" on green paper in Putzeys' script, in IRSB (!), specimen labelled lectotype here designated. Bates 1881:37.

Schizogenius longipennis, Kult 1950:140.

Schizogenius validus Fall 1901:210. *Type locality* Rio Verde, central Arizona; type male in MCZ (!), specimen labelled "M.C.Z. Type 23860" here designated lectotype. Lindroth 1961:166. NEW SYNONYMY.

Diagnostic combination. – Males of this species are distinguished from males of other members of the *longipennis* group by the following combination of characters of the male genitalia; apex of median lobe short, deflected at weak angle, ventral margin in most specimens weakly swollen near angulation, not flanged (Fig. 198); endophallus with virga enlarged, about 0.42-0.48 length of median lobe; basal collar spines slender, elongate, about 10 times longer than wide. In Arizona, most matured specimens of *S. longipennis* are distinguished from matured specimens of *S. chiricahuanus* by darker body color, and from those of *S. neovalidus* by reddish front femora. In western Mexico, most specimens of *S. longipennis* are distinguished from most specimens of *S. pacificus* by larger body size, relatively larger eyes, less convex body, indistinct microsculpture on sternum two and basal margin of pronotum, pronotum proportionately smaller in relation to rest of body, elytra less strongly aeneous, and paramedian pronotal sulci shorter, less sharply terminated at apices.

Description. – As in *S. neovalidus* except as follows. Color of legs variable, front femora rufous to piceous. Form and sculpture of head and pronotum, Fig. 193; base of frontal carina three not abbreviated in most specimens; paramedian pronotal sulci in most specimens sharply terminated at apices. Left elytron with 13-21 discal setae in specimens examined. Pygidium with apical margin crenulate in some females.

Male genitalia. Median lobe, Fig. 198; apex short, deflexed at a 30-40 degree angle, right ventral margin not flanged, ventral margin in most specimens distinctly swollen near angulation; endophallus, Fig. 203, virga 0.42-0.48 length median lobe, basal collar spines about 10 times longer than wide; 34 specimens examined.

Measurements and proportions. See Table 39.

Table 39. Descriptive statistics for *S. longipennis*, based on 20 males from Paso de Ovejas, Veracruz, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.87-5.54	5.270	0.305	0.091	3.85
LE	3.04-3.50	3.319	0.192	0.057	3.85
WH	0.97-1.10	1.046	0.058	0.017	3.72
WP	1.26-1.47	1.390	0.095	0.028	4.57
WE	1.61-1.82	1.742	0.098	0.029	3.76
B. Setae on left elytron.					
Interval 3	5- 7	6.1			
Interval 5	5- 7	5.6			
Interval 7	2- 4	3.3			
Total	12-17	15.0	1.5	0.4	6.49
C. Proportions.					
WF/WH	0.58-0.63	0.605	0.017	0.005	1.90
LP/WP	0.86-0.93	0.887	0.028	0.008	2.07
DP/LP	0.83-0.90	0.862	0.026	0.008	2.03
LP/WE	0.68-0.73	0.708	0.022	0.007	2.06
Ta/Ti	0.59-0.69	0.645	0.036	0.011	3.71
PS/LP	0.56-0.66	0.618	0.037	0.011	4.02

Variation. – Geographic variation not studied in detail. In general, there is a trend toward size reduction and reduced numbers of discal elytral setae from north to south. The frequency of crenulate pygidial margins in females is higher from Arizona to Sinaloa than elsewhere. The front femur tends to be reddish from Arizona to Sinaloa, reddish in the apical fourth from Jalisco to Guerrero, and piceous elsewhere. And the tibiae tend to be testaceous to rufous from Arizona to Guerrero, and dusky or piceous elsewhere.

Etymology. – Latin, *longus* = long, plus *penna* = wing, in reference to the elongate elytra.

Distribution. – The known range of this species extends from southern Arizona in the west and from Nuevo Leon and Tamaulipas in the east south at least to Costa Rica (Fig. 208). I studied 1125 specimens from the following localities.

UNITED STATES

ARIZONA (17; AMNH, ANSP, CAS, INHS, USNM): Hot Springs (2; CAS), Riverside (6; ANSP, CAS, USNM); Cochise Co., 2.8 mi. s. Portal (1; TLEr); Gila Co., 33 mi. s. Globe (1; DJLa), Pinal Mountains (1; CUNY), Roosevelt Lake (2; CAS, UKSM), Sierra Ancha Mountains (1; UASM); Graham Co., Aravaipa (2; CUNY, DRWh); Maricopa Co., Phoenix (1; MCZ); Santa Cruz Co., Peña Blanca (2; UASM), Sycamore Canyon (2; CAS); Yavapai Co., Bumble Bee (1; CAS).

MEXICO

No locality (5; IRSB, MCZ); Matamoros (1; CAS). CHIAPAS: 3.2 mi. n. Arriaga (1; CNC), 18.4 mi. ne. Chiapa de Corzo (2; UASM), 32.5 mi. e. Comitan (1; UASM), Huehuetan (10; UASM), Huixtla (2; DRWh), 12.8 mi. nw. Huixtla (1; CNC), 38.2 mi. nw. Huixtla (1; CNC), Pijijiapan (18; UASM), Solosuchiapa (1; UASM), 4.0 mi. s. Solosuchiapa (4; UASM), 18.6 mi. se. Tonalá (45; UASM). COLIMA: 3.4 mi. se. Colima (54; UASM), 8 mi. sw. Colima (3; UASM). GUERRERO: 41.4 mi. n. Acapulco (42; UASM). JALISCO: 4 mi. s. Atenquique (7; UASM), Cocula (3; IRSB), Ixtapa (34; UASM), 8.5 mi. n. Juchitlan (37; UASM), La Garita (1; CAS), 17.9 mi. w. Magdalena (8; UASM), Pitillal (48; UASM), Puerto Vallarta (1; UASM), Talpa de Allende (76; CNHM, CUNY, INHS, JNeg, MCZ, MZSP, UASM, UATA, USNM). MICHOACAN: 8.5 mi. n. Nueva Italia (10; UASM). MORELOS: Puente de Ixtla (1; CBoP), Tejalpa (1; FDAG), Tetecala (9; UASM). NAYARIT: Acaponeta (5; UASM), 2.4 mi. s. Acaponeta (9; UASM), 8 mi. nw. Acaponeta (11; CAS), 13.8 mi. e. San Blas (20; UASM). NUEVO LEON: Linares (1; DRWh), 32.9 mi. n. Montemorelos (2; UASM). OAXACA: 5 mi. w. El Camaron (1; HFHo), 17.7 mi. w. El Camaron (1; BMNH), 25 mi. e. El Camaron (28; UASM), 29.4 mi. e. El Coyul (25; UASM), Juchatengo (3; AMNH), 11.1 mi. n. Matias Romero (1; BMNH), 9.9 mi. n. Pochutla (7; UASM), 18.6 mi. n. Pochutla (3; UASM), 19.1 mi. s. Suchixtepec (1; ANSP), 5 mi. e. Tapanatepec (1; ANSP), Tehuantepec (2; BMNH), Valle Nacional (50; UASM), 72.5 mi. s. Valle Nacional (16; UASM), 97.3 mi. s. Valle Nacional (1; CBoP), Zanatepec (20; UASM), 76 mi. w. Zanatepec (1; UASM), 18.4 mi. w. Zanatepec (4; UASM). PUEBLA: Tehuitzingo (2; CNHM), Tepexco (23; UASM). QUERETARO: Escanelilla (9; UASM), Jalpan (6; UASM), 6.4 mi. e. Pinal de Amoles (1; JHeS). SAN LUIS POTOSÍ: 17 mi. n. Palitla (36; UASM), 2.7 mi. w. Santa Catarina (8; UASM), Tamazunchale (26; UASM). SINALOA: Alamosa (1; CAS), Choix (2; UCD), 5.5 mi. nw. Choix (1; UCD), Chupaderos (2; UCD), Concordia (19; UASM), 11.2 mi. ne. Concordia (1; JHeS), 30.6 mi. s. Culiacan (6; UASM), 8 mi. w. El Palmito (1; CNC), Mazatlan (2; MCZ), 7 mi. n. Mazatlan (2; LBSC), Rio Piaxtla (3; UASM), Rosario (11; UASM), 21-33 mi. e. Villa Union (13; CNC, LBSC, UCB). SONORA: Alamos (1; CAS), 7.2 mi. se. Alamos (5; GRNo), 10 mi. s. Alamos (1; UCD). TABASCO: Teapa (54; MGFT, UASM). TAMAULIPAS: El Barretal (46; UASM), Encino (4; UASM), 15.2 mi. n. Ciudad Victoria (6; UASM), 21.3 mi. n. Ciudad Victoria (30; UASM), 39 mi. s. Ciudad Victoria (25; UASM). VERACRUZ: Coatzacoalcos (2; USNM), Cordova (4; CAS, USNM), Coyame (1; UASM), Fortín de las Flores (7; FDAG, UASM), 20 mi. nw. Huatusco (1; FDAG), Jalapa (3; MCZ, USNM), 21.8 mi. e. Jalapa (1; MCZ), Paso de Ovejas (52; UASM).

GUATEMALA

EL QUICHE: Sacapulas (1; AMNH).

HONDURAS

CORTES: La Lima (2; FDAG).

COSTA RICA

CARTAGO: Turrialba (1; UAFA). LIMON: Guapiles (1; USNM). PUNTARENAS: Palmar Sur (2; UAFA), 6 mi. n. Palmar Sur (22; UAFA), 3 mi. s. Palmar Sur (1; UAFA).

Collecting notes. – Adult specimens of *S. longipennis* have been collected throughout the year, in riparian gravel bars or at lights. In material at hand, teneral adults are most abundant in the months just before and just after the wet season, which, in most of Mexico, extends from June through August.

Taxonomic notes. – Putzeys (1866) indicated that his specimens of *S. longipennis* were collected together with his specimens of *S. tristriatus*. As these must have come from Veracruz, and most likely from the Cordova area, and as I have seen specimens of both species from Fortín de las Flores, I have restricted the type locality to that locality. Despite the treatment of *S. longipennis* as a form of *S. tristriatus* by both Putzeys (1866) and Bates (1881), these names clearly refer to unrelated species.

The range of *S. longipennis* is sympatric with those of the other members of the *longi-*

pennis group, and there hence is no question that *S. longipennis* is a distinct species. I have seen the types of both *S. longipennis* and *S. validus*. Specimens of *S. longipennis* from Arizona do differ in various ways from Veracruz specimens, as noted in my discussion of variation, but I have no evidence to suggest that variation in any characteristic is disjunct. Thus, I think the names *S. longipennis* and *S. validus* are synonyms.

Schizogenius chiricahuanus new species

Type material. – Holotype male and allotype female labelled "Cave Ck., Cochise Co. ChiricahuaMts. Ariz. ca.6000′ Aug. 17, 1960" and "G.E. Ball family & R.B. Madge collectors" (MCZ). An additional 30 specimens from various localities in Arizona are paratypes (AMNH, CUNY, DJLa, DRWh, IRSB, KHSt, UASM, UKSM, USNM).

Diagnostic combination. – Within the *longipennis* group, matured specimens of this species are distinguished by rufous coloration. Also, characteristics of the male genitalia (Fig. 199) are diagnostic.

Description. – As in *S. neovalidus* except as follows. Average size smaller. Color light to dark rufous, not piceous or dark rufopiceous. Form and sculpture of head and pronotum, Fig. 194. Left elytron with about 6-8 setae on interval three, 6-8 on interval five, and 3-5 on interval seven; total 15-20 in specimens examined. Pygidium with apex crenulate in some females.

Male genitalia. Median lobe, Fig. 199, apex short, deflexed at 40-45 degree angle, right ventral margin not flanged, ventral margin not swollen near angulation; endophallus, Fig. 204, virga 0.32-0.38 length median lobe, basal collar spines about five times longer than wide or less; four specimens examined.

Measurements and proportions. See Table 40. Of holotype: TL, 4.52 mm; LE, 2.89 mm; WH, 0.90 mm; WP, 1.20 mm; WE, 1.53 mm; WF/WH, 0.64; LP/WP, 0.85; DP/LP, 0.89; LP/WE, 0.67; Ta/Ti, 0.61; PS/LP, 0.66. Of allotype: TL, 4.91 mm; LE, 3.12 mm; WH, 0.98 mm; WP, 1.30 mm; WE, 1.63 mm; WF/WH, 0.62; LP/WP, 0.86; DP/LP, 0.86; LP/WE, 0.69; Ta/Ti, 0.65; PS/LP, 0.67.

Etymology. – I name *S. chiricahuanus* after the Chiricahua Mountains of southern Arizona, since most specimens known to me were collected there.

Distribution. – Specimens of this species are known only from a few localities in southern Arizona (Fig. 209). I studied 35 specimens from the following localities.

UNITED STATES

ARIZONA: Cochise Co., Cave Creek (19; MCZ, UASM), Chiricahua Mountains (4; UKSM, USNM), Huachuca Mountains (1; KHSt) Portal (2; KHSt), 5 mi. w. Portal (4; AMNH, CUNY, UCB), Rucker Lake (1; IRSB); Gila Co., Roosevelt Lake (1; DJLa), Sierra Ancha Mountains (3; DRWh, MCZ).

Collecting notes. – Specimens of this species have been collected in riparian gravel bars, from June through August.

Taxonomic notes. – *S. chiricahuanus* is sympatric with both *S. longipennis* and *S. neovalidus* in southern Arizona, or at least nearly so. This fact, and well marked differences in structures of male genitalia and in other features, indicate that *S. chiricahuanus* is reproductively isolated from those species. Known ranges of *S. chiricahuanus* and *S. pacificus* do not overlap, and differences in structures of male genitalia are smaller, but well marked differences in body form and in other characteristics indicate that these two forms are also reproductively isolated. Differences in habitus are clearly indicated in Tables 38-41 for the four species of the *longipennis* group.

Table 40. Descriptive statistics for *S. chiricahuanus*, based on 16 males from Cochise County, Arizona.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.23-4.71	4.426	0.210	0.070	3.17
LE	2.68-2.97	2.812	0.119	0.040	2.83
WH	0.85-0.97	0.904	0.046	0.015	3.42
WP	1.08-1.26	1.164	0.068	0.023	3.92
WE	1.43-1.57	1.491	0.070	0.023	3.12
B. Setae on left elytron.					
Interval 3	6- 8	6.9			
Interval 5	6- 7	6.6			
Interval 7	3- 5	3.7			
Total	16-19	17.1	1.6	0.5	6.35
C. Proportions.					
WF/WH	0.59-0.65	0.617	0.026	0.009	2.78
LP/WP	0.83-0.90	0.866	0.030	0.010	2.35
DP/LP	0.84-0.89	0.868	0.028	0.009	2.16
LP/WE	0.63-0.71	0.678	0.030	0.010	2.91
Ta/Ti	0.58-0.69	0.642	0.040	0.013	4.19
PS/LP	0.62-0.69	0.654	0.026	0.009	2.67

Schizogenius pacificus new species

Type material. – Holotype male and allotype female labelled "Acapulco Gro., Mex. Aug. 18, 1938 Lipovsky" (MCZ). An additional 51 specimens from various localities in Guerrero, Jalisco, and Sinaloa are paratypes (CAS, DRWh, MCZ, UASM, USNM).

Diagnostic combination. – Within the *longipennis* group, specimens of *S. pacificus* are distinguished from those of *S. longipennis* and *S. neovalidus* by numerous details of male genitalia (Fig. 200), and from specimens of *S. chiricahuanus* by dark coloration. In addition, specimens of *S. pacificus* differ from specimens of the sympatric *S. longipennis* by distinct microsculpture on base of pronotum and on sternum two, and by a more convex body.

Description. – As in *S. neovalidus* except as follows. Body convex. Color piceous, elytra in most specimens distinctly aeneous; femora in most specimens partly or wholly piceous or dark rufopiceous; front tibia rufous to rufopiceous, hind tibiae rufotestaceous. Additional conspicuous microsculpture at base of pronotum and on sternum two in most specimens. Head and pronotum, Fig. 195. Left elytron with about 5-7 setae on interval three, 5-7 on interval five, 2-4 on interval seven; total 13-17 in specimens examined. Pygidium apex crenulate in females or not.

Male genitalia. Median lobe, Fig. 200, apex moderate, deflexed at a 40-45 degree angle, right ventral margin not flanged, ventral margin not swollen near angulation; endophallus, Fig. 205, virga 0.32-0.38 length median lobe, basal collar spines about five times longer than wide; five specimens examined.

Measurements and proportions. See Table 41. Of holotype: TL, 4.27 mm; LE, 2.62 mm; WH, 0.94 mm; WP, 1.25 mm; WE, 1.45 mm; WF/WH, 0.61; LP/WP, 0.84; DP/LP, 0.91; LP/WE, 0.72; Ta/Ti, 0.65; PS/LP, 0.57. Of allotype: TL, 4.67 mm; LE, 2.90 mm; WH, 0.99 mm; WP, 1.31 mm; WE, 1.57 mm; WF/WH, 0.62; LP/WP, 0.86; DP/LP, 0.93; LP/WE, 0.72; Ta/Ti, 0.71; PS/LP, 0.60.

Table 41. Descriptive statistics for *S. pacificus,* based on 16 males from San Juan Abajo, Jalisco, Mexico.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	4.01-4.92	4.327	0.415	0.138	6.32
LE	2.45-2.99	2.676	0.244	0.081	6.08
WH	0.89-1.02	0.995	0.068	0.023	4.56
WP	1.13-1.38	1.25	0.110	0.037	5.85
WE	1.39-1.63	1.491	0.121	0.040	5.41
B. Setae on left elytron.					
Interval 3	6- 7	6.2			
Interval 5	5- 7	5.8			
Interval 7	2- 4	3.0			
Total	14-17	15.0	1.1	0.4	4.87
C. Proportions.					
WF/WH	0.61-0.64	0.626	0.013	0.004	1.43
LP/WP	0.83-0.91	0.862	0.032	0.011	2.49
DP/LP	0.88-0.94	0.902	0.026	0.009	1.95
LP/WE	0.68-0.77	0.728	0.036	0.012	3.26
Ta/Ti	0.63-0.71	0.685	0.037	0.012	3.58
PS/LP	0.55-0.63	0.597	0.034	0.011	3.75

Etymology. – I name this species after the Pacific Ocean, since most known specimens were collected along Pacific drainage systems.

Distribution. – Specimens of *S. pacificus* have been collected along various rivers of the Pacific slope from southern Sinaloa to southern Oaxaca, and along one river of the Atlantic slope in the Isthmus of Tehuantepec in Oaxaca (Fig. 210). I studied 136 specimens from the following localities.

MEXICO

GUERRERO: Acapulco (7; MCZ), 24.8 mi. e. Acapulco (1; CAS), Coyuca (2; IRSB). JALISCO: 4 mi. s. Atenquique (4; UASM), San Juan Abajo (33; UASM). OAXACA: 22.2 mi. n. Matias Romero (12; UASM). 18.4 mi. w. Zanatepec (70; AMNH, ANSP, BMNH, CNC, CNHM, CUNY, JHeS, JNeg, MGFT, MZSP, UASM). SINALOA: Rosario (4; CAS, DRWh, USNM), Villa Union (2; UASM), 26 mi. ne. Villa Union (1; LBSC).

Collecting notes. – Specimens of this species have been collected in riparian gravel bars,

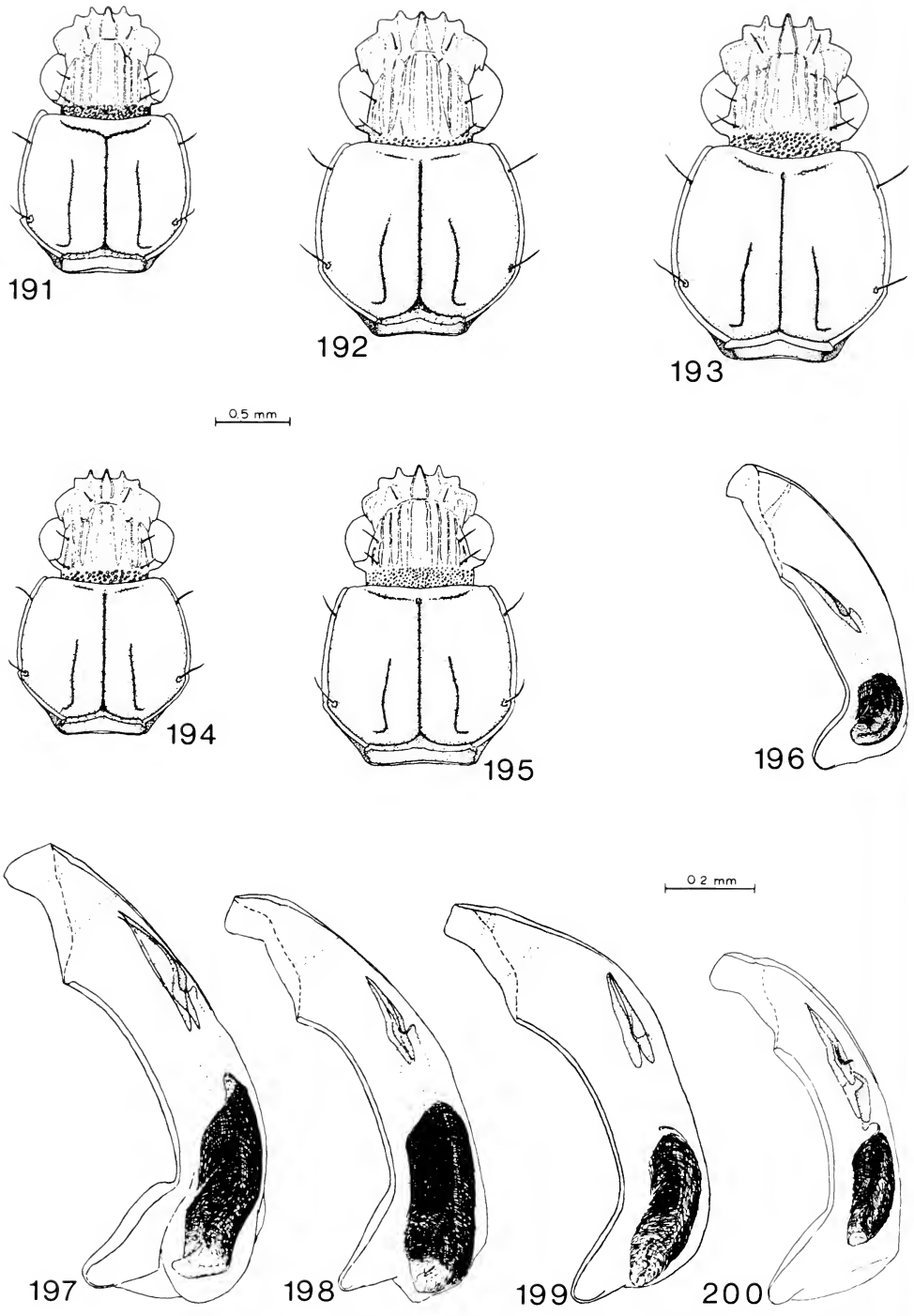
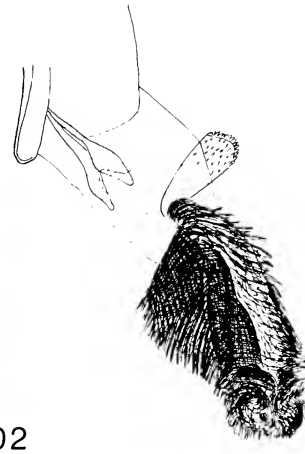
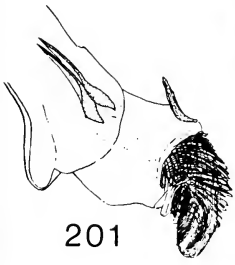
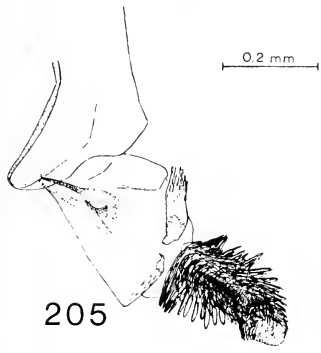
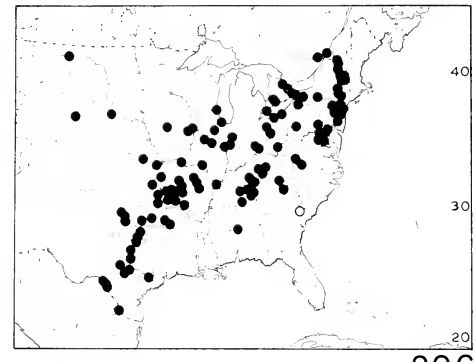


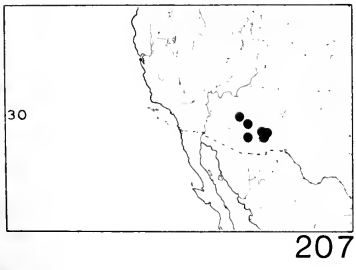
Fig. 191-195. Head and pronotum, dorsal aspect. 191. *S. lineolatus* Say, Frederick, Maryland. 192. *S. neovalidus* new species, Aravaipa, Arizona. 193. *S. longipennis* Putzeys, Linares, Nuevo Leon. 194. *S. chiricahuanus* new species, Portal, Arizona. 195. *S. pacificus* new species, Rosario, Sinaloa. Fig. 196-200. Male median lobe, lateral aspect. 196. *S. lineolatus* Say, Edgewood, Maryland. 197. *S. neovalidus* new species, Glenwood, New Mexico. 198. *S. longipennis* Putzeys, Palitla, Veracruz. 199. *S. chiricahuanus* new species, Sierra Ancha Mountains, Arizona. 200. *S. pacificus* new species, Villa Union, Sinaloa.

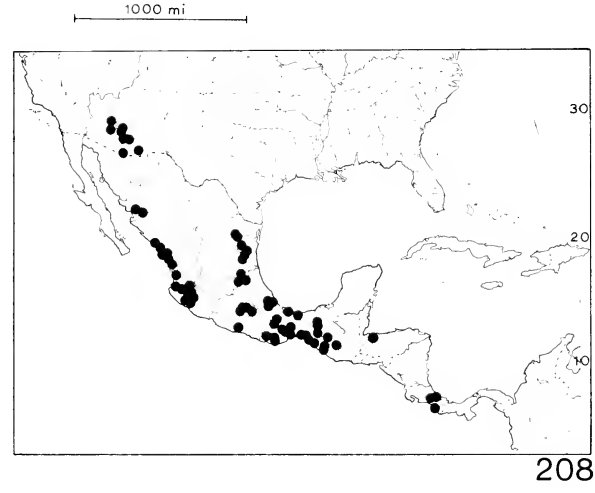




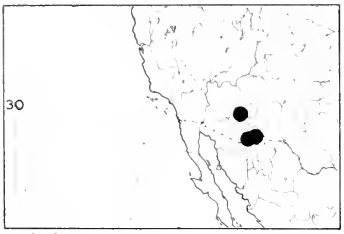








201-205. Male endophallus. 201. *S. lineolatus* Say, Berryville, Arkansas. 202. *S. neovalidus* new species, Carrizo, Arizona. 203. *S. longipennis* Putzeys, Alamos, Sonora. 204. *S. chiricahuanus* new species, Portal, Arizona. 205. *S. pacificus* new species, Acapulco, Guerrero. Fig. 206-208. Known distributions. 206. *S. lineolatus* Say; open symbol represents state record only. 207. *S. neovalidus* new species 208. *S. longipennis* Putzeys.



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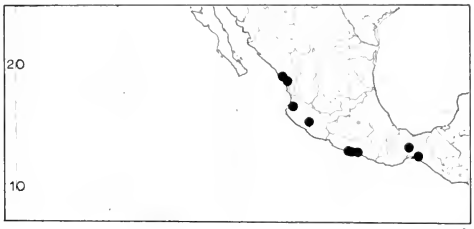

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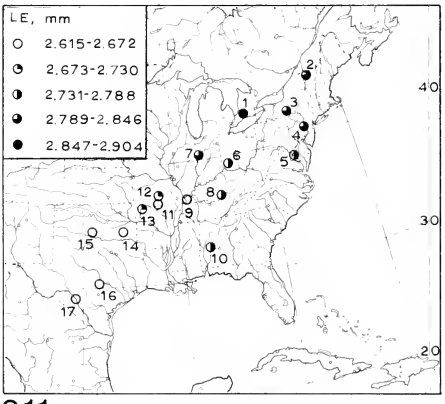
1000 mi



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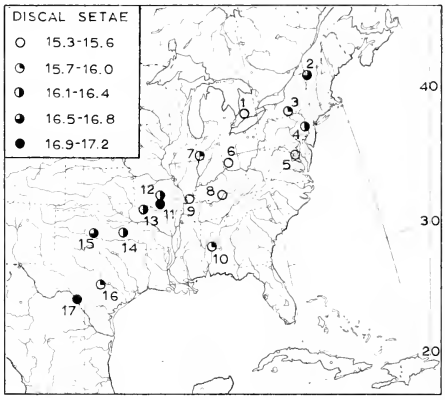

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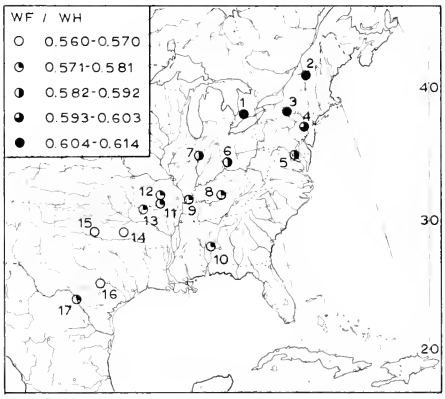

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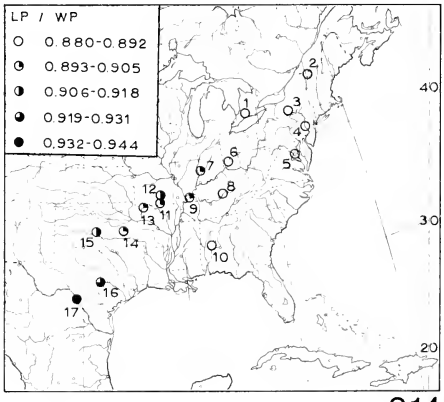


214

Fig. 209-210. Known distributions. 209. *S. chiricahuanus* new species. 210. *S. pacificus* new species. Fig. 211-214. Geographic variation in *S. lineolatus* Say. 211. Means of body size, Table 34. 212. Means of numbers of discal setae on left elytron, Table 35. 213. Means of relative eye size, Table 36. 214. Means of pronotal form, Table 37.

or at lights, in January, March, June, August, and December. I suspect that its habitat differs somewhat from that of *S. longipennis*, since specimens of the two species have been taken together in only four places, and then in quite unequal samples. The more convex body form of *S. pacificus* suggests a sandier habitat than that of *S. longipennis*.

Taxonomic notes. – Specimens of this species are well differentiated from specimens of other members of the *longipennis* group in characters of male genitalia or habitus or both, and are unquestionably reproductively isolated from them.

The *depressus* group

Diagnostic combination. – Members of this group are distinguished by the following combination of characters: body moderately to strongly flattened; paramedian clypeal carinae extended to median tooth; clypeal field narrow, no wider at base than apex of median frontal sulcus; submentum without accessory setae; pronotum with paralateral carinae not or weakly developed; discal setae present on intervals three, five, and seven, total normally less than 30, average length less than 1.0 times maximum width of interval two; elytra concolorous with pronotum if aeneopiceous, not pale at apices if rufocastaneous; abdomen without extensive microsculpture except in small lateral patches near coxal depressions of sternum three, or, if extensively microsculptured then pronotal hind angles not prominent; endophallus with basal collar spines distinct but small. Also; clypeal suture sharply impressed in most species; antennal articles five to ten filiform; front and middle tarsi broadened and with dense ventral pubescence, especially in males; sternum seven with paramedian ambulatory setae in males, not in females; paramedian carinae of sternum three curved outward at apices; and pygidium crenulate or not at apex in females.

Distribution. – The composite range of members of this group is that of the whole genus. I examined 5114 specimens of the *depressus* group.

Taxonomic notes. – I made no attempt to classify South American members of this large and difficult group, as I studied insufficient material to make a worthwhile contribution. The only species of the group known to extend into South America from Middle America is *S. pygmaeus*, which ranges at least to Colombia. Colombian specimens of that species may be distinguished from specimens of other Colombian species of the *depressus* group by details of the male genitalia. Also, they lack distinct microsculpture on the median field of the frons, have little or no microsculpture on the sides of the pronotum, and have a relatively convex pronotum with no indication of paralateral ridges.

In addition to the Colombian specimens of *S. pygmaeus*, I examined 513 specimens of one or perhaps several closely related South American species of the *depressus* group, from a few localities in Argentina, Bolivia, Brazil, and Colombia (AMNH, CAS, DRWh, GRNo, IRSB, JNeg, MCZ, MGFT, MZSP, UASM). All of these have piceous body color, as do southern specimens of *S. pygmaeus* and the Middle American *S. emdeni*. I here refer to these specimens as a single taxon, *S. "apicalis."* Putzeys (1863:24) described *S. apicalis*, based on 12 specimens from the Amazon River. One male from the type series (IRSB) is labelled "Amaz." and "S. apicalis Ptz." on green paper. As this specimen does not agree with the original description in various diagnostic characteristics, I make no lectotype designation until other type material is seen. I have seen type material of no other described South American species of the *depressus* group, and am unable to place other species in that group from original or subsequent descriptions.

Schizogenius arimao Darlington

Schizogenius arimao Darlington 1934:71. *Type locality* Soledad, Cuba; holotype male in MCZ (!).

Diagnostic combination. – Specimens of this species differ from others of the *depressus* group by uniformly piceous elytra, abdomen microsculptured, and frontal carinae basally confused.

Description. – Body moderately flattened. Color piceous, not aeneous; front femora rufopiceous, legs otherwise rufous; palpi testaceous.

Integument. Strong microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura at base and on apical two-thirds, and abdomen.

Head. Fig. 215. Paramedian clypeal carinae straight, extended to median tooth, strongly elevated in basal half; median field triangular, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, filiform, article five about 1.4 times longer than wide.

Pronotum. Fig. 215. Sides bisetose, hind angles obsolete, base not rugose. Paralateral carinae weakly developed. Paramedian longitudinal sulci elongate, hooked basally. Anterior transverse impression strongly punctate.

Legs. Front and middle tarsi slightly dilated and pubescent ventrally in both sexes; hind tarsus slender. Paronychia conspicuous, nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about seven setae each on intervals three and five, and about four on interval seven (Darlington, 1934). Striae deep, sharply engraved, strongly punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; apices of intervals three, five, and seven broadly joined. Humeral denticles prominent.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with a pair of paramedian ambulatory setae in males only (Darlington, 1934). Pygidium not examined.

Male genitalia. Median lobe, Fig. 222; 1 specimen studied.

Measurements and proportions. Based on one male from the type locality. TL, 3.61 mm; LE, 2.23 mm; WH, 0.74 mm; WP, 0.94 mm; WE, 1.19 mm; WF/WH, 0.61; LP/WP, 0.94; DP/LP, 0.81; LP/WE, 0.75; Ta/Ti, 0.65; PS/LP, 0.66.

Etymology. – *S. arimao* was named after the Arimao River.

Distribution. – *S. arimao* is known definitely only from two localities in Cuba (Darlington, 1934) (Fig. 235); I did not confirm a Jamaican record (Darlington, 1941). Although I saw type material in the Museum of Comparative Zoology, my description is based on just one topotypic male given to me by Darlington.

Taxonomic notes. – This species has no known close relatives. Darlington suggested a relationship with *S. tristriatus*, but I think it most closely related to the South American *S. "apicalis"* and the Middle American *S. emdeni*. In particular, the weak but evident paralateral pronotal carinae suggest a relationship with *S. "apicalis"*, a suggestion supported by zoogeographic considerations, reduced hind angles, short antennae, small size, dark color, and comparatively elongate tarsi. Abdominal microsculpture of this species is a characteristic convergent in the taxon *S. ochthocephalus* and in members of the *tristriatus* group.

Schizogenius emdeni new species

Type material. – Holotype female labelled "S. Geronimo. Guatemala. Champion.", "B. C.A. Col. I. 1. Schizogenius tristriatus, Putz.", "TYPE", and "Schizogenius Emdeni Kt. 57 det. K. Kult" (BMNH). Four males and two females from Palmar Sur, Costa Rica are paratypes (DRWh, UAFA, UASM).

Diagnostic combination. – Best distinguished from *S. pygmaeus*, the only other known piceous Middle American member of the *depressus* group without abdominal microsculpture, by details of male genitalia. Also, most specimens have fewer than 15 elytral setae, and reduced paralateral patches of microsculpture on sternum three.

Description. – As in *S. pygmaeus* except as follows. Body color piceous, elytra distinctly aeneous. Patches of microsculpture in coxal depressions of sternum three smaller, less distinct. Head and pronotum, Fig. 216. Left elytron with five or six setae on interval three. five on interval five, and two or three on interval seven; total 12-14 in specimens examined. Male genitalia with median lobe, Fig. 223; one specimen examined.

Measurements and proportions. Of holotype: TL, 4.04 mm; LE, 2.48 mm; WH, 0.80 mm; WP, 1.11 mm; WE, 1.29 mm; WF/WH, 0.61; LP/WP, 0.92; DP/LP, 0.83; LP/WE, 0.79; Ta/Ti, 0.62; PS/LP, 0.66. Of type series: TL, 3.31-3.751-4.04 mm; LE, 2.05-2.316-2.48 mm; WH, 0.65-0.739-0.80 mm; WP, 0.86-1.009-1.11 mm; WE, 1.06-1.196-1.29 mm; WF/WH, 0.60-0.616-0.64; LP/WP, 0.90-0.941-0.98; DP/LP, 0.79-0.814-0.84; LP/WE, 0.76-0.784-0.80; Ta/Ti, 0.62-0.657-0.68; PS/LP, 0.62-0.651-0.70.

Etymology. – K. Kult recognized this species as distinct, and planned to name it after the well known coleopterist Fritz van Emden. As he never published the name, I do so here.

Distribution. – *S. emdeni* is so far known only from two localities in Middle America (Fig. 235). I studied seven specimens from the following localities.

GUATEMALA

BAJA VERAPAZ: San Geronimo (1; BMNH).

COSTA RICA

PUNTARENAS: Palmar Sur (6; DRWh, UAFA, UASM).

Collecting notes. – In Costa Rica, specimens of *S. emdeni* were collected at black lights by R. T. Allen, in August.

Taxonomic notes. – I selected as holotype the specimen earlier selected by Kult, in order to avoid future confusion. There is no doubt that the Costa Rican specimens are conspecific with it.

Reduced numbers of elytral setae and reduced paralateral patches of microsculpture on sternum three superficially suggest placement in the *longipennis* group. I place *S. emdeni* in the *depressus* group because the patches of microsculpture are present, and because of similarities in some statistical characteristics with *S. arimao* and *S. "apicalis"*.

Schizogenius sulcifrons Putzeys

Schizogenius sulcifrons Putzeys 1846:652. *Type locality* "Amerique boreale," restricted to Rumney, New Hampshire by Lindroth (1961); lectotype female designated by Lindroth (1961), in Hope Museum at Oxford, not seen by me, Lindroth 1961:167.

Schizogenius lineolatus, LeConte 1857:83. Putzeys 1863:24. Putzeys 1866:228. Gemminger and Harold 1868:206. LeConte 1879:34. Leng 1920:48. Csiki 1927:551.

Diagnostic combination. – Specimens of *S. sulcifrons* are distinguished from those of

other piceous species of *Schizogenius* found in eastern North America by having in combination: more than 20 discal setae per elytron in most specimens; weakly developed pronotal hind angles; and uniformly piceous pronotum and elytra. Most specimens differ from most of the western *S. litigiosus* by abdomen paler than elytra.

Description. – Body flattened. Color piceous above, rufopiceous below; legs and antennae rufous; palpi testaceous; elytra in most specimens strongly aeneous.

Integument. Conspicuous microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, elytral epipleura on apical two-thirds, and sternum three in coxal depressions and small paralateral patches.

Head. Fig. 217. Paramedian clypeal carinae straight, moderately elevated in basal half, extended to median tooth; median field triangular, narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.6-1.8 times longer than wide.

Pronotum. Fig. 217. Sides bisetose; base not rugose; hind angles weakly developed. Paramedian longitudinal sulci moderately elongate, nearly straight, strongly hooked basally. Paralateral carinae absent. Anterior transverse impression not or weakly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about seven to eleven setae each on intervals three and five, five to eight on interval seven; total 19-30 in specimens examined. Striae deep and sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles moderate.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin normally crenulate in females, entire in males.

Male genitalia. Median lobe, Fig. 224; six specimens examined.

Measurements and proportions. See Table 42. As this sample includes males and females, these data are not directly comparable with data given for other members of the *depressus* group. Males tend to be smaller than females; the mean LE of six males from Rumney, New Hampshire, is 2.505 mm.

Variation. – I had insufficient material of this species for a useful statistical analysis of variation. I noticed no important geographic variation in either pronotal form or in numbers of elytral setae. But, from the midwestern states, through the Washington, D. C. area, through New York state, to New Hampshire, there are definite trends toward larger body size and reduced eyes. These trends agree with those observed for *S. lineolatus* in the same general areas.

Etymology. – Latin, *sulcus* = groove + *frons* = front, in reference to the plurisulcate frons.

Distribution. – The known range of *S. sulcifrons* includes much of North America east of the Mississippi River, from New Brunswick (Lindroth, 1961) to Georgia in the east, and from Wisconsin to Mississippi in the west (Fig. 236). I studied 131 specimens from the following localities.

CANADA

No locality (1; ANSP). ONTARIO: London (6; CNHM, UASM), Saint Augustine (1; USNM), Toronto (3; CUNY, MCZ). See Lindroth (1961) for additional Canadian records.

UNITED STATES

No locality (9; ANSP, CAS, PSUU, UKSM). ALABAMA: Jackson Co., Big Coon Creek (1; TCBa). DISTRICT OF COLUMBIA: Washington (7; CAS, USNM). GEORGIA (1; ANSP). ILLINOIS: Vermilion Co., Kickapoo State Park (2; RTBe). INDIANA (1; CNHM): Parke Co., The Shades State Park (1; RTBe); Tippecanoe Co. (3; CNC, MCZ, UATA). KENTUCKY: Metcalfe Co., 8 mi. e. Edmonton (2; DRWh). MAINE: Oxford Co., Paris (1; MCZ). MARYLAND: Frederick Co., Frederick (1; RTBe); Harford Co., Edgewood (3; CUNY); Prince Georges Co., Bladensburg (1; USNM). MASSACHUSETTS: Franklin Co., Northfield (2; MCZ). MISSISSIPPI: Ireland (1; UKSM). NEW HAMPSHIRE: Carroll Co., North Conway (2; MCZ); Grafton Co., Rumney (15; CNHM, CNC, MCZ, UASM). NEW JERSEY (1; CAS); Warren Co., Phillipsburg (1; CAS). NEW YORK (7; CAS, UKSM, USNM); New Windsor (2; USNM); Erie Co., Lancaster (1; CAS); Schuyler Co., Watkins Glen (3; AMNH, MCZ); Suffolk Co., Riverhead (1; CUNY); Tompkins Co., Groton (5; JNeg), Ithaca (15; CAS, CUNY, USNM); Ulster Co., Esopus (5; CUNY, MCZ). NORTH CAROLINA: Buncombe Co., Black Mountains (1; CAS). OHIO: Knox Co., Gambier (3; UMCG). PENNSYLVANIA (2; CAS); Allegheny Co., Allegheny (1; MCZ); Monroe Co., Delaware Water Gap (2; AMNH); Philadelphia Co., Philadelphia (2; MCZ); Pike Co., Milford (1; USNM). SOUTH CAROLINA (1; MCZ). TENNESSEE: Davidson Co., Nashville (2; CAS, USNM); Monroe Co., Sweetwater (3; AMNH). VERMONT (1; MCZ): Chittenden Co., Milton (1; RTBe); Rutland Co., Poultney (1; RTBe). VIRGINIA: Loudon Co. (4; AMNH). WISCONSIN (1; CUNY).

Table 42. Descriptive statistics for *S. sulcifrons*, based on six males and six females from Rumney, New Hampshire.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.69-4.50	4.128	0.314	0.121	5.08
LE	2.32-2.85	2.601	0.215	0.083	5.50
WH	0.75-0.85	0.808	0.039	0.015	3.20
WP	0.97-1.17	1.086	0.087	0.033	5.33
WE	1.19-1.43	1.329	0.104	0.040	5.24
B. Setae on left elytron.					
Interval 3	8- 9	8.5			
Interval 5	7-10	8.4			
Interval 7	5- 7	6.0			
Total	20-25	22.9	2.8	1.1	8.00
C. Proportions.					
WF/WH	0.62-0.68	0.658	0.026	0.010	2.58
LP/WP	0.85-0.91	0.892	0.023	0.009	1.73
DP/LP	0.80-0.85	0.828	0.024	0.009	1.91
LP/WE	0.70-0.75	0.727	0.021	0.008	1.97
Ta/Ti	0.59-0.66	0.621	0.035	0.013	3.73
PS/LP	0.68-0.76	0.707	0.039	0.015	3.68

Collecting notes. – Specimens of *S. sulcifrons* have been collected from late March through September, generally in riparian gravel bars. I found specimens of this species, *S. lineolatus, S. amphibius*, and *S. planulatus* along a small stream near Edmonton, Kentucky.

Taxonomic notes. – See discussion by Lindroth (1961). As I did not see the lectotype, I accept Lindroth's concept of the species. Though *S. sulcifrons* and *S. lineolatus* have been

confused in the past, they are not really closely related. *S. sulcifrons* is closely related to *S. litigiosus*, but ranges of the two forms are widely separated and there is no evidence of intergradation between them.

Schizogenius litigiosus Fall

Schizogenius litigiosus Fall 1901:210. *Type locality* Sylvania, California; holotype female in MCZ (!). Lindroth 1961:168.

Schizogenius depressus, Hatch 1949:118. Hatch 1953:69.

Diagnostic combination. – Fully colored specimens of this species are distinguished from other members of the *depressus* group in western North America by their piceous coloration. Most specimens are distinguished from most specimens of the eastern *S. sulcifrons* by having concolorous abdomen and elytra.

Description. – Body flat. Color piceous; front femora rufous to rufopiceous; antennae, tibiae, tarsi, and middle and hind femora rufous; palpi testaceous; elytra not or weakly aeneous, rufescent toward apices in many specimens.

Integument, head, pronotum, legs, elytra, and abdomen as in *S. sulcifrons* except as follows. Head and pronotum, Fig. 218. Left elytron with about six to nine setae each on intervals three and five, three to five on interval seven; total 16-22 in specimens examined. Apex of pygidium normally entire in females and males.

Male genitalia. Median lobe, Fig. 225; six specimens examined.

Measurements and proportions. See Table 43.

Table 43. Descriptive statistics for *S. litigiosus*, based on 18 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.43-4.34	4.033	0.315	0.099	5.21
LE	2.13-2.70	2.495	0.191	0.060	5.11
WH	0.71-0.88	0.822	0.061	0.019	4.92
WP	0.87-1.15	1.054	0.107	0.034	6.76
WE	1.10-1.38	1.284	0.098	0.031	5.08
B. Setae on left elytron.					
Interval 3	6- 8	7.2			
Interval 5	6- 8	7.0			
Interval 7	3- 5	4.4			
Total	16-21	18.6	2.1	0.6	7.40
C. Proportions.					
WF/WH	0.60-0.65	0.617	0.022	0.007	2.35
LP/WP	0.90-0.97	0.935	0.024	0.007	1.69
DP/LP	0.78-0.82	0.801	0.020	0.006	1.63
LP/WE	0.74-0.79	0.768	0.022	0.007	1.92
Ta/Ti	0.60-0.70	0.648	0.040	0.013	4.12
PS/LP	0.65-0.73	0.688	0.034	0.011	3.25

Variation. – There is a definite trend toward reduced eye size from northern California to southern British Columbia, and there may also be a trend toward increased body size from south to north. I otherwise found no conspicuous geographic variation. I had insufficient material from most areas for useful statistical analysis of geographic variation.

Etymology. – Latin, *litigiosus* = contentious or quarrelsome; Fall probably suggested this name because this species had previously been confused with *S. pluripunctatus* and *S. depressus.*

Distribution. – The known range of *S. litigiosus* extends from southern British Columbia to southern California, west of the Rocky Mountains (Fig. 237). I studied 629 specimens from the following localities.

CANADA

BRITISH COLUMBIA: Duncan (13; CAS, KSUM, MCZ), Keremeos (8; BMNH, DRWh, IRSB, MGFT). For other Canadian records, see Lindroth (1961).

UNITED STATES

CALIFORNIA (13; AMNH, CAS, KSUM, MCZ, USNM); La Panza (1; CAS); Alameda Co., Alameda Creek (1; CAS), 20 mi. s. Livermore (1; UCB); Amador Co., Cold Creek (2; CAS); Butte Co., Oroville (7; CAS); Paradise (2; CAS); Calaveras Co., Mokelumne Hill (23; CAS, MCZ); Colusa Co., Cooks Springs (2; CAS); Del Norte Co. (3; CNHM); Eldorado Co. (7; CNHM, MGFT), Coloma (6; GRNo); Fresno Co., Camp Greeley (1; CAS); Glenn Co., Elk Creek (1; CAS), 25 mi. w. Elk Creek (1; CAS), Hamilton City (2; UCD); Humboldt Co. (2; CAS), 6 mi. e. Bridgeville (1; TLEr), Garberville (2; CAS), Hoopa (2; CAS, UASM), Larabee Creek (2; CAS), Mad River (1; CAS), North Dobbyn Creek (1; CAS), Redwood Creek (1; UASM), Shively (3; UCD), Willow Creek (2; CAS); Kings Co., Stratford (2; CAS); Lake Co. (2; CAS), Clear Lake (28; CAS), Grossford (1; CAS), Kelseyville (3; CAS), Middle Creek (23; CAS), Middletown (5; CAS), North Fork Cache Creek (10; UCD), Scott Creek (1; CAS); Los Angeles Co., Cole (1; CAS), Pomona (1; USNM), 3 mi. s. Valyermo (1; GRNo); Madera Co., North Fork (1; CUNY); Marin Co. (1; CAS), Fairfax (15; CAS); Mendocino Co. (3; CNHM), Black Butte River (18; CAS), Bloody Run Creek (1; CAS), Dry Creek (4; CAS), Eel River (3; CAS), Longvale (13; CAS), Mailliard (2; CAS), 8 mi. w. Navarro (1; CAS), 2 mi. nw. Philo (1; CAS), Twin Rocks (1; CAS), Williams Creek (13; CAS), 2 mi. s. Yorkville (3; CAS); Modoc Co., 9.5 mi. s. Cedarville (35; CAS), Lake City (2; CAS); Napa Co. (6; CAS, USNM), Monticello (10; CAS, UCD, MCZ), Pope Valley (6; CAS), Saint Helena (6; CAS, KSUM, MCZ, UASM); Placer Co., Auburn (3; UCD), Penryn (1; UCB); Plumas Co., Clio (4; CAS); Sacramento Co., Cosumes River (2; CAS), Fair Oaks (2; UCD); San Bernadino Co., Hesperia (1; CAS), Mojave River (5; GRNo, TLEr); San Diego Co. (2; LACM); San Francisco Co. (3; CAS); San Joaquin Co., San Joaquin River (1; CAS), Santa Clara Co., Anderson Reservoir (1; DHKa), Gilroy Hot Springs (11; CAS, DJLa, TLEr), Los Gatos (1; CAS), Mount Hamilton (3; CAS); Shasta Co., Redding (9; CAS); Siskiyou Co. (1; USNM), 2.3 mi. nw. Callahan (9; CAS), Dillon Creek (6; UASM), Scott River (1; CAS), Yreka (1; MCZ); Sonoma Co. (6; CAS, CUNY, LACM, MCZ), Agua Caliente (2; CNHM), Annapolis (2; CAS), Cloverdale (1; CAS), Duncan Mills (3; CAS), Guerneville (12; CAS), Healdsburg (2; CAS), Preston (1; CAS), Rio Nido (1; CAS), Russian River (6; CAS, MCZ), Santa Rosa (10; CAS, MCZ, MSUL), 2.5 mi. w. Skaggs Springs (2; CAS), Sylvania (5; CAS, MCZ, LACM); Stanislaus Co., 22 mi. w. Patterson (4; CAS); Tehama Co., Red Bluff (29; CNHM); Trinity Co., 2 mi. e. Burnt Ranch (6; CAS, RTBe), Canyon City (1; CAS); Clear Creek (1; TLEr), Douglas City (3; UASM), Hayfork Creek (9; CAS), Hyampton (3; CAS), Mad River (3; CAS, UASM), 4 mi. se. Ruth (22; CAS), 6 mi. s. Ruth (5; CAS), Ruth Dam (3; GRNo, TLEr), Trinity Center (2; CAS), Weaverville (1; CAS); Tulare Co., Fairview (1; UCB), Kaweah (1; CAS); Yolo Co., Davis (13; UCD), Putah Canyon (2; UCD), Rumsey (1; UCD). IDAHO: Nez Perce Co., 6 mi. n. Lenore (1; DHKa); Owahee Co., Hot Creek Falls (3; CNHM). NEVADA (2; ANSP): Lyon Co., Weeks (3; UASM); Washoe Co., Pyramid Lake (1; UCD). OREGON (1; ANSP): Jackson Co., Cow Creek (3; CAS, MCZ), Eagle Point (1; CNHM), Medford (17; CAS, MCZ, UCD, USNM), Talent (2; UCD); Josephine Co. (7; CNHM); Lane Co., Eugene (3; CNHM), Middle Fork of Willamette River (1; CNHM); Malhuer Co., Sucker Creek Canyon (3; CNHM); Umatilla Co., McKay Reservoir (1; CNHM); Wasco Co., The Dalles (1; USNM); Wheeler Co., John Day Gorge (1; CNHM); Yamhill Co., Dayton (2; MCZ). WASHINGTON: Yakima Co., Toppenish (12; KSUM, MCZ, USNM).

Collecting notes. – In the north, specimens of this species have been collected from May to September. In central California, adults may be found throughout the year. Adults are found in riparian gravel bars.

Taxonomic notes. – This species was confused with *S. depressus* by Hatch (1949, 1953), but well distinguished by Lindroth (1961). The range of *S. litigiosus* is entirely included within that of *S. depressus*, and specimens of both species have often been found at the same locality.

Schizogenius pygmaeus Van Dyke

Schizogenius pygmaeus Van Dyke 1925:12. *Type locality* Clear Lake, California; holotype in CAS, not seen by me.

Schizogenius championi Kult 1950:142. *Type locality* Pantaleon, Escuintla, Guatemala; holotype in BMNH, not studied. NEW SYNONYMY.

Diagnostic combination. – Within the *depressus* group, all dark or bicolored specimens seen from Mexico belong to *S. pygmaeus*, and none from the United States or Canada do. In Middle America south of Mexico, dark forms of this species are best distinguished from specimens of *S. emdeni* by characteristics given in the key. In South America, specimens of *S. pygmaeus* are distinguished from other members of the *depressus* group by details of male genitalia. Specimens of pale forms of *S. pygmaeus* are best distinguished from specimens of pale forms of *S. falli*, *S. ochthocephalus*, and *S. depressus* by characteristics given in the key. Ranges of *S. pygmaeus* and *S. scopaeus* are largely allopatric. The latter species is distributed along Atlantic drainage systems; its range extends south of the Rio Grande only in Nuevo Leon and Tamaulipas where it is sympatric with black forms of *S. pygmaeus*. The range of *S. pygmaeus* reaches the Rio Grande drainage basin only in southern Chihuahua, where *S. scopaeus* is not known to occur. Where the two species approach one another or overlap in range, specimens are distinguishable by conspicuous differences in the male genitalia and, in northeastern Mexico, by color.

Description. – Body weakly convex. Color testaceous or ferrugineous to brunneous to piceous, some specimens distinctly bicolored with head and pronotum darker than elytra; some dark specimens slightly aeneous; legs and antennae ferrugineous or testaceous; palpi testaceous.

Integument. Distinct microsculpture on paramedian frontal sulci, mouthparts, genae, front legs except posterior surfaces of femora and trochanters, middle legs except anterior surfaces of trochanters, hind tibiae and posterior surfaces of hind femora, shoulders and apical two-thirds of elytral epipleura, and small areas in coxal depressions of sternum three.

Head. Fig. 219. Clypeus with paramedian carinae straight, extended to median tooth, strongly elevated in basal half; median field narrow, no wider at base than apex of median frontal sulcus. Clypeal suture sharply defined. Eye prominent, finely and uniformly faceted. Neck finely, densely punctate. Gena coarsely punctate, rugose in front. Antennal articles four to ten elongate, article five about 1.4-1.5 times longer than wide.

Pronotum. Fig. 219. Sides bisetose; base not rugose; hind angles weakly developed. Paramedian longitudinal sulci moderately long, nearly straight, strongly hooked basally. Anterior transverse impression weakly to strongly punctate.

Legs. Front and middle tarsi moderately dilated and pubescent ventrally, less so in females; hind tarsus slender, short. Paronychia nearly as long as tarsal claws. Front tibia narrowed evenly to base. Front femur not strongly constricted near apex.

Elytra. Left elytron with about six to ten setae on interval three, five to nine on interval five, three to six on interval seven; total 14-24 in specimens examined. Striae sharply engraved, finely punctate in basal two-thirds. Intervals one to seven broad and flat, interval eight carinate at apex; intervals three, five, and seven broadly joined at apices. Humeral denticles weakly developed.

Abdomen. Sternum three with paramedian carinae curved outward at apices. Sternum seven with paramedian ambulatory setae in males only. Pygidium with apical margin finely crenulate in some females.

Male genitalia. Median lobe, Fig. 226, 227, form of apex variable (Fig. 234); 20 specimens examined.

Measurements and proportions. See Table 44.

Table 44. Descriptive statistics for *S. pygmaeus*, based on 20 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	2.80-3.22	3.032	0.152	0.045	3.35
LE	1.72-1.98	1.861	0.091	0.027	3.25
WH	0.57-0.66	0.629	0.038	0.011	4.03
WP	0.72-0.84	0.792	0.045	0.013	3.79
WE	0.89-1.02	0.958	0.043	0.013	2.98
B. Setae on left elytron.					
Interval 3	7- 9	8.0			
Interval 5	7- 9	7.6			
Interval 7	3- 6	4.6			
Total	17-23	20.2	2.3	0.7	7.46
C. Proportions.					
WF/WH	0.64-0.70	0.660	0.021	0.006	2.11
LP/WP	0.91-0.98	0.936	0.023	0.007	1.67
DP/LP	0.77-0.83	0.802	0.023	0.007	1.91
LP/WE	0.74-0.80	0.771	0.022	0.006	1.88
Ta/Ti	0.55-0.70	0.646	0.052	0.016	5.40
PS/LP	0.66-0.73	0.690	0.027	0.008	2.57

Variation. – As shown in Fig. 242, specimens from interior and Pacific drainage basins south to and including the Rio Balsas are reddish, without conspicuous variation. Mature specimens from coastal lowland Atlantic drainage basins in Mexico, and from most localities south of Mexico, are dark piceous. In Pacific drainage systems in Chiapas and Oaxaca, most specimens are strongly bicolored, but others are piceous or intermediate. Two specimens from La Lima, Honduras are bicolored. In upland areas in Atlantic drainage systems in both Oaxaca and Chiapas, dark and bicolored forms are commonly found together. In Guerrero south of the Rio Balsas, and in upland Atlantic drainage areas in San Luis Potosi, most specimens are dark red and many are slightly bicolored. Specimens from 5000′ on the Rio Tula in Hidalgo are brown. In short, there is a gradation from red forms (*S. pygmaeus*) to dark forms (*S. championi*) in Mexico, both eastward and southward.

Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 45-48. Major discontinuities, representing strong statistically significant differences, are shown in Fig. 243-246 by heavy broken lines. Two or more such gaps are found in central California (setae, LP/WP), between southern California and Arizona (setae, WF/WH), along the Sierra Madre Occidental (LE, setae, WF/WH), and along the Sierra Madre del Sur (LE, setae, LP/WP). These gaps strongly suggest that gene

Table 45. Variation in body size (LE, in mm) in selected samples of *S. pygmaeus*; see Fig. 243. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	1.77-2.00	1.878	0.091	0.029	3.58
2	16	1.70-2.00	1.907	0.130	0.044	4.56
3	14	1.71-2.16	1.907	0.152	0.054	5.32
4	16	1.62-2.03	1.841	0.197	0.066	7.14
5	24	1.87-2.15	2.028	0.128	0.035	4.20
6	12	1.75-2.15	1.970	0.170	0.065	5.74
7	18	1.80-2.16	1.988	0.142	0.047	4.76
8	24	1.81-2.12	1.954	0.125	0.034	4.26
9	12	1.83-2.13	1.962	0.164	0.063	5.57
10	18	1.88-2.20	2.019	0.126	0.040	4.16
11	26	1.80-2.23	1.984	0.164	0.043	5.51
12	16	1.87-2.30	2.078	0.158	0.053	5.08
13	18	1.68-1.95	1.839	0.106	0.033	3.83
14	10	1.70-1.93	1.817	0.115	0.050	4.32
15	12	1.75-2.07	1.957	0.140	0.054	4.77
16	20	1.69-2.02	1.860	0.143	0.043	5.13
17	16	1.82-2.12	1.938	0.115	0.038	3.96
18	12	1.90-2.24	2.027	0.139	0.054	4.58
19	12	1.73-1.95	1.818	0.101	0.039	3.70
20	10	1.80-2.03	1.910	0.132	0.055	4.57
21	12	1.75-2.08	1.951	0.153	0.059	5.24
22	26	1.91-2.25	2.114	0.127	0.033	4.01
23	20	1.86-2.14	2.002	0.114	0.034	3.78
24	16	1.98-2.26	2.103	0.131	0.044	4.14
25	22	1.88-2.25	2.090	0.154	0.044	4.91
26	12	1.99-2.30	2.113	0.149	0.057	4.70
27	12	1.99-2.29	2.170	0.132	0.051	4.04
28	24	1.95-2.28	2.092	0.142	0.039	4.53
29	9	1.96-2.21	2.101			
30	6	2.00-2.21	2.135			
31	6	1.99-2.12	2.038			

Table 46. Variation in numbers of elytral setae in selected samples of *S. pygmaeus*; see Fig. 244. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	18-23	20.6	1.7	0.6	6.30
2	16	19-22	20.5	1.5	0.5	4.94
3	14	16-19	18.4	1.3	0.5	4.62
4	16	19-22	20.2	1.3	0.4	4.23
5	24	17-23	19.6	2.0	0.5	6.85
6	12	18-23	19.4	2.3	0.9	8.06
7	18	15-22	19.2	2.6	0.8	9.02
8	24	17-22	19.0	2.1	0.6	7.54
9	12	17-21	19.0	1.6	0.6	5.50
10	18	16-20	18.6	1.7	0.5	6.19
11	26	15-21	18.7	2.1	0.6	7.68
12	16	17-21	19.2	2.1	0.7	7.18
13	18	14-18	16.3	1.5	0.5	6.30
14	10	15-17	16.2	0.9	0.4	3.90
15	12	15-19	16.8	1.7	0.6	6.62
16	20	15-18	16.8	1.5	0.4	5.44
17	16	14-18	16.1	2.0	0.7	8.44
18	12	16-20	17.5	1.5	0.6	5.71
19	12	14-18	16.0	1.7	0.7	7.05
20	10	15-18	16.9	1.7	0.7	6.51
21	12	16-20	17.5	1.8	0.7	6.67
22	26	16-20	17.4	1.6	0.4	6.11
23	20	16-20	17.8	1.6	0.5	5.93
24	16	18-21	19.1	1.6	0.5	5.57
25	22	16-22	18.6	2.3	0.6	8.07
26	12	18-21	19.5	1.5	0.6	5.13
27	12	19-24	21.9	2.1	0.8	6.29
28	24	19-25	21.8	2.0	0.6	6.20
29	9	19-24	21.4			
30	6	18-21	19.5			
31	6	17-19	18.5			

Table 47. Variation in relative eye size (WF/WH) in selected samples of *S. pygmaeus*; see Fig. 245. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.65-0.67	0.658	0.013	0.004	1.30
2	16	0.64-0.67	0.655	0.017	0.006	1.76
3	14	0.64-0.68	0.659	0.017	0.006	1.73
4	16	0.60-0.66	0.637	0.022	0.007	2.27
5	24	0.60-0.65	0.628	0.018	0.005	1.97
6	12	0.61-0.65	0.631	0.017	0.007	1.85
7	18	0.60-0.64	0.624	0.015	0.005	1.58
8	24	0.60-0.65	0.622	0.019	0.005	2.08
9	12	0.60-0.62	0.610	0.011	0.004	1.21
10	18	0.60-0.64	0.618	0.016	0.005	1.72
11	26	0.59-0.65	0.619	0.024	0.006	2.60
12	16	0.60-0.64	0.623	0.015	0.005	1.63
13	18	0.59-0.63	0.604	0.016	0.005	1.81
14	10	0.59-0.64	0.616	0.025	0.010	2.67
15	12	0.59-0.63	0.608	0.021	0.008	2.31
16	20	0.58-0.62	0.604	0.020	0.006	2.23
17	16	0.59-0.63	0.615	0.015	0.005	1.68
18	12	0.59-0.62	0.603	0.016	0.006	1.78
19	12	0.58-0.62	0.598	0.020	0.008	2.23
20	10	0.58-0.62	0.599	0.019	0.008	2.15
21	12	0.57-0.61	0.595	0.022	0.008	2.43
22	26	0.58-0.61	0.599	0.015	0.004	1.52
23	20	0.58-0.62	0.598	0.018	0.005	1.90
24	16	0.58-0.63	0.606	0.020	0.007	2.16
25	22	0.60-0.64	0.619	0.018	0.005	1.92
26	12	0.62-0.65	0.638	0.016	0.006	1.66
27	12	0.61-0.65	0.634	0.020	0.008	2.07
28	24	0.60-0.66	0.633	0.023	0.006	2.40
29	9	0.60-0.65	0.628			
30	6	0.60-0.63	0.615			
31	6	0.58-0.63	0.600			

Table 48. Variation in pronotal form (LP/WP) in selected samples of *S. pygmaeus*; see Fig. 246. Males and females each 50% in samples 1-28.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.90-0.98	0.934	0.026	0.007	1.86
2	16	0.92-0.97	0.941	0.020	0.007	1.42
3	14	0.89-0.94	0.913	0.022	0.008	1.63
4	16	0.89-0.95	0.922	0.025	0.008	1.84
5	24	0.86-0.94	0.907	0.030	0.008	2.15
6	12	0.87-0.95	0.913	0.036	0.014	2.61
7	18	0.88-0.94	0.909	0.025	0.008	1.83
8	24	0.88-0.93	0.908	0.023	0.006	1.71
9	12	0.88-0.93	0.899	0.022	0.008	1.61
10	18	0.88-0.93	0.906	0.021	0.007	1.53
11	26	0.88-0.91	0.919	0.022	0.006	1.61
12	16	0.89-0.95	0.910	0.028	0.009	2.08
13	18	0.88-0.93	0.904	0.019	0.006	1.38
14	10	0.87-0.94	0.898	0.032	0.014	2.39
15	12	0.88-0.94	0.916	0.023	0.009	1.64
16	20	0.88-0.94	0.906	0.021	0.006	1.54
17	16	0.88-0.93	0.897	0.023	0.008	1.71
18	12	0.89-0.93	0.910	0.019	0.007	1.41
19	12	0.88-0.93	0.908	0.023	0.009	1.70
20	10	0.88-0.91	0.901	0.016	0.007	1.22
21	12	0.87-0.94	0.914	0.027	0.011	2.00
22	26	0.87-0.93	0.902	0.023	0.006	1.73
23	20	0.88-0.93	0.905	0.023	0.007	1.70
24	16	0.88-0.93	0.908	0.023	0.008	1.67
25	22	0.88-0.93	0.904	0.022	0.006	1.66
26	12	0.89-0.95	0.919	0.030	0.012	2.20
27	12	0.88-0.95	0.912	0.031	0.012	2.24
28	24	0.89-0.94	0.920	0.022	0.006	1.60
29	9	0.90-0.96	0.927			
30	6	0.88-0.92	0.905			
31	6	0.88-0.93	0.910			

flow is impeded across these regions.

Fig. 234 portrays observed variation in form of male genitalia in *S. pygmaeus*. Because of considerable individual variation, analysis of geographic variation is difficult. I found no important clinal variation except for a sudden increase in size of apex toward northern California. Specimens from this area cannot be distinguished by form of apex of male genitalia from specimens of *S. scopaeus* from northeastern Mexico and the lower Rio Grande in Texas.

I conclude that some gene flow exists between narrow bodied forms of *S. pygmaeus* in central and northern California and wider bodied forms further south, and between small eyed forms in California and large eyed forms in Arizona. There is little or no gene flow across the higher parts of the Sierra Madre Occidental, but gene flow is unrestricted from north to south on both sides of this mountain range. South of the Rio Balsas and across the Sierra Madre del Sur, gene flow is limited. Across northern Mexico from the eastern side of the Sierra Madre Occidental to the Atlantic coast, there is no evidence that gene flow is restricted. Nor is gene flow restricted along the Atlantic coast to Middle America, across to the Pacific in Chiapas, and west from there to the southern side of the Sierra Madre del Sur. No geographically proximate forms are reproductively isolated, and no forms warrant formal recognition as subspecies.

Etymology. – Latin, *pygmaeus* = dwarf, a reference to the small size of these beetles.

Distribution. – Specimens of *S. pygmaeus* have been found at elevations ranging from near sea level to about 6500′. *S. pygmaeus* ranges from northern California, Arizona, extreme western New Mexico, southern Chihuahua, Durango, Zacatecas, San Luis Potosí, Nuevo Leon, and Tamaulipas, southward at least to Colombia (Fig. 239). I studied 1143 specimens of this species from the following localities.

UNITED STATES

ARIZONA (9; ANSP, CUNY, MCZ, UKSM, USNM): 10 mi. e. Continental (1; UATA), Hot Springs (2; USNM), Riverside (3; CAS, USNM); Cochise Co., Chiricahua Mountains (1; UKSM), Cochise Stronghold (4; TLEr, UATA), Palominas (1; UASM), Portal (1; UCB), 5 mi. w. Portal (4; AMNH, CNC), Rucker Lake (1; UASM); Coconino Co., Bill Williams Fork (1; UKSM); Gila Co., Globe (3; MCZ, UASM), 33 mi. s. Globe (1; DJLa), Pinal Mountains (2; UASM), Rice (3; MCZ, UASM), Salt River (2; USNM), San Carlos Lake (1; UASM); Graham Co., Aravaipa (19; KHSt, UASM), Galiuro Mountains (2; USNM); Graham Mountains (2; UATA), Power's Garden (2; UASM), Thatcher (1; UCD); Greenlee Co., Gila River (1; KHSt); Pima Co., Ajo Mountains (1; CAS), Arivaca (11; CAS, MCZ), Baboquivari Mountains (6; CAS, MCZ), Organ Pipe National Monument (1; CAS), Quitobaquito (17; UASM), Sabino Canyon (38; AMNH, CNC, TCBa, TLEr, UATA, UCD, UKSM), Sahuarita (1; MCZ), Santa Catalina Mountains (4; CAS, KHSt), Tanque Verde (14; UATA), Tucson (8; CAS, KHSt, MCZ, UATA, USNM); Pinal Co., 14 mi. e. Oracle (1; CAS), Superior (1; CAS); Santa Cruz Co., Madera Canyon (4; UATA, UCD), Nogales (6; CAS, CNHM), Patagonia (12; CAS, CNHM, CUNY, KHSt, TLEr, UATA), Peña Blanca (10; CNC, KHSt, UASM, UATA), Santa Rita Mountains (1; KHSt), Tumacacori Mountains (17; CAS); Yuma Co., Fort Yuma (2; USNM). CALIFORNIA (12; ANSP, CAS, MCZ): Alameda Co., 20 mi. s. Livermore (1; TLEr); Butte Co., Oroville (1; CAS); Calaveras Co., Mokelumne Hill (6; CAS), El Dorado Co. (1; CNHM); Fresno Co., La Fevre Creek (3; CAS), 11.6 mi. s. Tollhouse (5; TLEr); Lake Co. (3; CAS), Clear Lake (59; CAS), North Fork Cache Creek (2; UCD); Los Angeles Co., Pasadena (1; CAS), Pomona (1; RUNB), San Gabriel Canyon (2; TCBa), Tujunga Canyon (4; LACM, MSUL); Mendocino Co., Longvale (1; CAS); Orange Co., San Juan Guard Station (3; GRNo); Riverside Co., Palm Springs (15; AMNH, CAS, CNC); San Bernadino Co. (1; MCZ), 10 mi. ne. Earp (2; UCB), Mojave River (1; TLEr), San Bernadino Mountains (1; MGFT); San Diego Co., Elsinore Lake (4; CAS), Julian (4; KHSt), Poway (4; CAS), Warners Hot Springs (1; MSUL); Santa Barbara Co., Santa Barbara (1; CAS); Santa Clara Co., East Palo Alto (1; CAS), Gilroy Hot Springs (3; TLEr), Mount Hamilton (29; CAS); Sonoma Co., Rio Nido (1; CAS); Stanislaus Co., Del Puerto Creek (1; DHKa), Patterson (2; CAS), 20 mi. w. Patterson (1; TLEr); Yolo Co., Davis (9; UCD). NEW MEXICO: Grant Co., Cliff (3; DRWh), 21.9 mi. ne. Pinos Altos (1; UASM).

MEXICO

AGUASCALIENTES: 2.8 mi. s. Aguascalientes (1; UASM). BAJA CALIFORNIA (4; CAS): Catavinia (4; CAS), 20 mi. n. Comondu (1; CAS), Ensenada (1; UKSM), 12.4 mi. e. La Paz (1; CAS), Las Cruces (7; CAS), 5 mi. nw. Miraflores (1; CAS), 5 mi. s. Miraflores (1; CAS), 5 mi. w. San Bartolo (11; CAS), Santa Rosa (2; CNHM, MCZ), Santiago (1; CAS), 6 mi. sw. Santiago (4; UATA), Triunfo (8; CAS). CHIAPAS: 3.2 mi. n. Arriaga (15; UASM), 20.9 mi. n. Arriaga (19; UASM),

5.9 mi. e. Chiapa de Corzo (1; UASM), 12.2 mi. ne. Chiapa de Corzo (13; HFHo, UASM), 32.5 mi. e. Comitan (3; BMNH), Huehuetan (2; IRSB), Huixtla (12; UASM), Macuilapa (6; FDAG), San Quintín (38; UASM), Tonalá (2; UASM), 18.6 mi. se. Tonalá (9; UASM). CHIHUAHUA: Catarinas (7; AMNH), Parral (1; AMNH), 15 mi. e. Parral (1; AMNH). COLIMA: 3.4 mi. se. Colima (5; UASM), 8 mi. sw. Colima (1; UASM). DURANGO: 12.2 mi. s. El Banco (30; UASM), 4.2 mi. w. Vicente Guerrero (8; UASM). GUANAJUATO: 9.8 mi. s. Silao (2; UASM). GUERRERO: Acapulco (4; MCZ), 24.8 mi. e. Acapulco (3; UASM), 41.4 mi. n. Acapulco (8; UASM), Coyuca (4; UASM), 23.7 mi. n. Zumpango del Rio (1; UASM), 30.8 mi. n. Zumpango del Rio (1; UASM). HIDALGO: Tasquillo (6; UASM). JALISCO: Ajijic (1; CAS), Cocula (19; UASM), 9.7 mi. e. Encarnacion de Diaz (8; UASM), 8.5 mi. n. Juchitlan (10; UASM), 10.6 mi. s. La Huerta (1; UASM), 17.7 mi. nw. Los Volcanes (1; UASM), 17.9 mi. w. Magdalena (2; UASM), Pitallal (31; UASM), Puerto Vallarta (5; UASM), Talpa de Allende (4; UASM). MEXICO: Tejupilco (3; MCZ). MICHOACAN: 8.5 mi. n. Nueva Italia (32; UASM), 20 mi. n. Nueva Italia (3; UASM). MORELOS: Tetecala (2; UASM). NAYARIT: 2.4 mi. s. Acaponeta (1; UASM), 20.3 mi. w. Compostela (1; GRNo), 14 mi. e. San Blas (3; UASM). NUEVO LEON: 14.8 mi. w. Linares (3; UASM). OAXACA: 17.7 mi. w. El Camaron (2; UASM), 25 mi. w. El Camaron (11; UASM), 29.4 mi. e. El Coyul (1; UASM), Huitzo (2; BMNH), 11.1 mi. n. Matias Romero (7; UASM), 19 mi. s. Matias Romero (3; CNC), 22.5 mi. w. Oaxaca (2; MGFT), 9.9 mi. n. Pochutla (15; UASM), Rio Jalpan (1; FDAG), Salina Cruz (3; AMNH), Tehuantepec (2; BMNH), Totolapan (1; UKSM), Valle Nacional (1; UASM), Zanatepec (25; UASM), 18.4 mi. w. Zanatepec (17; UASM). PUEBLA: Acatlan (2; UCB), 9 mi. n. Amatitlan (2; CAS), Petlalcingo (17; UASM), Tehuitzingo (4; UASM), Tepexco (13; UASM). QUERETARO: Escanelilla (1; UASM), Jalpan (3; UASM). SAN LUIS POTOSÍ: 14 mi. e. Ciudad del Maiz (1; CAS), Ciudad del Valles (1; CBoP), El Naranjo (1; CAS), Huichihuayan (1; UKSM), 7.5 mi. nw. Mexquitic (1; UASM), 2.7 mi. w. Santa Catarina (23; UASM), Tamazunchale (1; UASM), 19.3 mi. nw. Tamazunchale (1; UASM), Vergel (1; CBoP). SINALOA: Concordia (18; UASM), 11.2 mi. ne. Concordia (1; UASM), 12 mi. s. Mazatlan (5; CAS, TLEr, UCB), Rosario (1; UASM), 28 mi. e. Villa Union. SONORA (4; CNC): 10 mi. s. Agua Prieta (1; KHSt), Alamos (16; CAS), 7 mi. s. Alamos (10; UCB, UCD), 10 mi. s. Alamos (1; UCD), 10 mi. w. Alamos (5; AMNH), 5 mi. w. Alamos (1; UATA), 16 mi. ne. Ciudad Obregon (1; CNC), Hermosillo (4; CAS), 10 mi. e. Navajoa (4; UATA), San Carlos Bay (3; CAS). TAMAULIPAS: Ciudad Victoria (1; USNM), 15.2 mi. n. Ciudad Victoria (1; UASM), 21.3 mi. n. Ciudad Victoria (13; UASM), Encino (2; UASM). VERACRUZ: Bobo (1; BMNH), Catemaco (2; JNeg), Fortín de las Flores (1; FDAG), 20 mi. nw. Huatusco (5; FDAG), 21.8 mi. e. Jalapa (9; UASM), Paso de Ovejas (12; UASM). ZACATECAS: Jalpa (6; UASM), Sain Alto (4; UASM).

GUATEMALA

ALTA VERAPAZ: Trece Aguas (1; USNM). CHIQUIMULA: Chiquimula (5; AMNH). GUATEMALA: Chinautla (1; BMNH). QUICHE: Sacapulas (1; AMNH).

EL SALVADOR

LA PAZ: La Herradura (4; JNeg). SAN SALVADOR: Guzapa (4; JNeg), San Salvador (4; JNeg).

HONDURAS

COMAYAGUA: Rancho Chiquito (4; FDAG). CORTÉS: La Lima (2; FDAG). El Zamarano (1; OSUC).

NICARAGUA

RIVAS: 10 km. nw. Sapoa (1; FDAG).

COSTA RICA

GUANACASTE: 5 km. n. Canas (1; LACM). LIMON: Los Diamantes (1; FDAG). PUNTARENAS: Palmar Sur (1; UAFA), 6 mi. n. Palmar Sur (12; UAFA). 7 mi. nw. Palmar Sur (1; UAFA), Villa Neilly (1; FDAG).

COLOMBIA

MAGDALENA: Aracataca (1; MCZ), Rio Frio (7; MCZ).

Collecting notes. – Specimens of this species have been taken throughout the year, at lights or in riparian gravel bars. At most localities where specimens of *S. pygmaeus* and *S. falli* have been collected together, one of the two species was strongly numerically dominant.

Taxonomic notes. – Although I studied holotypes of neither *S. pygmaeus* nor *S. championi*, I did study paratypes of both and have no doubt that my association of the names is correct. As shown in my analysis of geographic variation above, these two names clearly refer to a single species. Lindroth (1961) suggested that the form in southern California might be a distinct species, but though most specimens are distinguishable from topotypic specimens of *S. pygmaeus*, there is no evidence for reproductive isolation.

Schizogenius scopaeus new species

Type material. – Holotype male and allotype female labelled "Limpia Canyon, 2 mi. n.w. Fort Davis, Texas. 3.VIII.63 D.R. Whitehead" (MCZ). An additional 98 specimens from Jeff Davis County, Texas are paratypes (AMNH, ANSP, BMNH, CAS, CNC, CNHM, DJLa, DRWh, IRSB, MGFT, UASM, UCD, USNM).

Diagnostic combination. – Specimens of this species are reliably distinguished from red specimens of *S. pygmaeus* only by form of apex of male median lobe, and by geographic distribution.

Description. – As in *S. pygmaeus* except as follows. Body color testaceous to ferrugineous, not brunneous, piceous, bicolored, or aeneous. Left elytron with about eight to eleven setae on interval three, seven to ten on interval five, four to seven on interval seven; total 18-27 in specimens examined. Male genitalia with median lobe, Fig. 228-229, apex in most specimens, particularly western specimens, broader than in specimens of *S. pygmaeus* (Fig. 234); 20 specimens examined.

Measurements and proportions. See Table 49. Of holotype: TL, 3.25 mm; LE, 2.00 mm; WH, 0.66 mm; WP, 0.84 mm; WE, 1.04 mm; WF/WH, 0.64; LP/WP, 0.93; DP/LP, 0.81; LP/WE, 0.75; Ta/Ti, 0.60; PS/LP, 0.68. Of allotype: TL, 3.50 mm; LE, 2.18 mm; WH, 0.71 mm; WP, 0.92 mm; WE, 1.12 mm; WF/WH, 0.63; LP/WP, 0.90; DP/LP, 0.78; LP/WE, 0.74; Ta/Ti, 0.64; PS/LP, 0.72.

Table 49. Descriptive statistics for *S. scopaeus*, based on 20 males from Limpia Canyon, Texas.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.04-3.60	3.265	0.199	0.059	4.07
LE	1.86-2.22	2.010	0.144	0.043	4.78
WH	0.64-0.75	0.685	0.040	0.012	3.89
WP	0.79-0.93	0.848	0.050	0.015	3.91
WE	0.97-1.18	1.054	0.078	0.023	4.93
B. Setae on left elytron.					
Interval 3	9-11	9.6			
Interval 5	7-10	8.6			
Interval 7	4- 7	5.4			
Total	20-26	23.5	2.3	0.7	6.55
C. Proportions.					
WF/WH	0.60-0.66	0.628	0.023	0.007	2.47
LP/WP	0.88-0.95	0.924	0.026	0.008	1.86
DP/LP	0.78-0.84	0.804	0.022	0.007	1.86
LP/WE	0.72-0.77	0.747	0.023	0.007	2.04
Ta/Ti	0.60-0.70	0.658	0.044	0.013	4.48
PS/LP	0.64-0.77	0.694	0.038	0.011	3.67

Variation. – Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 50-53 and summarized in Fig. 243-246. From north to south, numbers of elytral setae increase, eyes increase in size, and pronota narrow. Specimens from central Texas tend to be smaller than specimens from the Rio Grande Valley to the South and from Arkansas and Missouri to the north. The form of apex of median lobe of male genitalia (Fig. 234) shows considerable variation; in particular, the apex is much larger in specimens from Colorado and western Texas.

Etymology. – Greek, *skopaios* = dwarf. This word is an etymological synonym of the Latin *pygmaeus*, chosen to indicate the great similarity of these two species.

Distribution. – *S. scopaeus* ranges over an area limited in the north by the Missouri River, in the east by the Mississippi River, in the west by the Rocky Mountains, and in the south by the Rio Grande except for a small area in northeastern Mexico (Fig. 238). I studied 375 specimens of this species from the following localities.

UNITED STATES

No locality (1; ANSP). ARKANSAS: Carroll Co., 5 mi. w. Berryville (15; UASM); Washington Co., 7 mi. s. Fayetteville (7; UASM). COLORADO: Baca Co., Regnier (1; AMNH); Pueblo Co., 38 mi. e. Walsenburg (6; UASM). MISSOURI: Butler Co., 12 mi. se. Elsinore (5; CAS); Crawford Co., Meramec River (1; USNM); McDonald Co., 3 mi. n. Noel (1; CAS); Reynolds Co., Ellington (2; USNM); Ripley Co., 5.5 mi. n. Briar (8; CAS); Wayne Co., Williamsville (1; CNC). OKLAHOMA: Atoka Co., 5 mi. n. Stringtown (4; UASM); Carter Co., 10.7 mi. s. Drake (1; TLEr); Cimarron Co., Black Mesa State Park (1; CAS); Comanche Co., Wichita National Forest (13; CAS); Cotton Co. (1; CAS); Murray Co., 10.3 mi. n. Drake (4; TLEr). TEXAS (11; AMNH, CAS, CNHM, INHS, MCZ, MSUL, UKSM, USNM): Austin Co., Austin (8; CAS, USNM). Bexar Co., San Antonio (1; CAS); Blanco Co., Cypress Mills (2; USNM), Johnson City (12; UASM), Twin Sisters (2; UASM); Brewster Co., Alpine (1; MCZ), Big Bend National Park (1; CNC), Green Valley (1; CAS), 22 mi. s. Marathon (3; UCD); Culberson Co., 2.5 mi. e. Nickle Creek Station (1; CNHM); Jeff Davis Co., Barrel Springs Creek (8; BMNH, DRWh, IRSB, MGFT), Davis Mountains State Park (4; CAS, DJLa), Fort Davis (21; AMNH, ANSP, CAS, CNC, MCZ, UCD), 4 mi. w. Fort Davis (4; CNC), Limpia Canyon (64; AMNH, CNC, CNHM, MCZ, UASM, USNM); Kinney Co., 23 mi. sw. Brackettville (6; UASM); Lampasas Co., Adamsville (2; JNeg); Llano Co., Enchanted Rock (13; CNC); Maverick Co., 8 mi. n. Quemado (9; UASM); McCulloch Co., Brady (2; KSUM), 16 mi. s. Brady (33; CAS), San Saba Camp (1; KSUM); Terrell Co., Chandler Ranch (6; UASM), Independence Creek (14; UASM); Val Verde Co., Del Rio (4; CNC, USNM), 13 mi. nw. Del Rio (17; UASM).

MEXICO

NUEVO LEON: Cienega de Flores (8; UASM), Linares (1; JHeS), Montemorelos (11; UASM), 32.9 mi. n. Montemorelos (1; UASM), 5 mi. s. Monterrey (16; CNC, HFHo), 6 mi. s. Monterrey (1; FDAG), 4.8 mi. e. Sabinas Hidalgo (1; UASM). TAMAULIPAS: 39 mi. s. Ciudad Victoria (1; CBoP), Villagran (11; UASM).

Collecting notes. – Specimens of *S. scopaeus* are abundant in gravel bars along both permanent and intermittent streams. In northeastern Mexico they are found in less protected places than are specimens of *S. pygmaeus*, such as along the intermittent Arroyo Villagran in Tamaulipas. All specimens were collected between April and October. On repeated occasions, specimens have been taken at lights in the vicinity of Fort Davis and Limpia Canyon, Texas.

Taxonomic notes. – I recognize *S. scopaeus* as a new species distinct from *S. pygmaeus* because these taxa overlap in range in northeastern Mexico and because I cannot show that they form a continuous circle of races through Durango, Chihuahua, and western Texas. Such a circle of races is quite possible, and is strongly suggested in statistical comparisons summarized in Fig. 243-246. But male genitalia in this area are divergent (Fig. 234); western forms of *S. scopaeus*, so far as studied, have broad apices while those of *S. pygmaeus* in Durango and Chihuahua have narrow apices. A detailed study of material from the Rio Conchos system in Chihuahua will be required to finally decide whether the forms here separated as *S. scopaeus* and *S. pygmaeus* are conspecific or not. A stepped cline in the genitalic characteristic is surely a possibility. However, *S. scopaeus* is largely replaced by the related *S. falli* in the Big Bend region of Texas, and Chihuahua *S. pygmaeus* and Texas *S. scopaeus* may therefore be geographically isolated along the lower parts of the Rio Conchos.

Table 50. Variation in body size (LE, in mm) in selected samples of *S. scopaeus*; see Fig. 243. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	1.77-2.10	1.940	0.122	0.035	4.19
2	26	1.83-2.15	1.975	0.122	0.032	4.10
3	14	1.82-2.05	1.964	0.096	0.034	3.24
4	22	1.89-2.28	2.068	0.151	0.043	4.86
5	22	1.71-2.01	1.879	0.122	0.035	4.34
6	20	1.71-2.02	1.888	0.140	0.042	4.95
7	20	1.85-2.14	1.971	0.139	0.041	4.71
8	12	1.87-2.18	1.975	0.121	0.047	4.09

Table 51. Variation in numbers of elytral setae in selected samples of *S. scopaeus*; see Fig. 244. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	21-27	23.0	2.6	0.7	7.51
2	26	20-27	23.2	2.4	0.6	7.01
3	14	21-27	22.9	2.8	1.0	8.20
4	22	20-28	23.6	2.4	0.7	6.85
5	22	18-26	21.6	2.6	0.7	8.01
6	20	19-25	21.6	2.0	0.6	6.27
7	20	18-23	20.6	1.7	0.5	5.50
8	12	19-24	21.0	1.9	0.7	6.09

Table 52. Variation in relative eye size (WF/WH) in selected samples of *S. scopaeus*; see Fig. 245. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.59-0.65	0.616	0.019	0.005	2.05
2	26	0.60-0.65	0.624	0.020	0.005	2.18
3	14	0.61-0.64	0.629	0.015	0.005	1.58
4	22	0.60-0.65	0.629	0.023	0.006	2.42
5	22	0.63-0.66	0.640	0.012	0.003	1.23
6	20	0.62-0.67	0.643	0.025	0.008	2.63
7	20	0.63-0.68	0.650	0.020	0.006	2.09
8	12	0.64-0.68	0.654	0.020	0.008	2.00

Table 53. Variation in pronotal form (LP/WP) in selected samples of *S. scopaeus*; see Fig. 246. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	22	0.89-0.96	0.922	0.030	0.009	2.19
2	26	0.88-0.97	0.925	0.028	0.007	1.99
3	14	0.90-0.96	0.931	0.031	0.011	2.22
4	22	0.89-0.96	0.922	0.026	0.007	1.88
5	22	0.87-0.95	0.911	0.030	0.009	2.23
6	20	0.87-0.94	0.914	0.025	0.007	1.82
7	20	0.89-0.93	0.904	0.015	0.004	1.10
8	12	0.87-0.93	0.902	0.026	0.010	1.96

Schizogenius falli new species

Type material. – Holotype male and allotype female labelled "MEX. Nuevo Leon Rio Sabinas Hidalgo, 4.8 mi. e. Sabinas Hidalgo 800′ X.22-23. 65" and "George E. Ball D. R. Whitehead collectors" (MCZ). An additional 34 specimens from various localities in Nuevo Leon are paratypes (BMNH, CAS, CNC, CNHM, DRWh, IRSB, MGFT, UASM, USNM).

Diagnostic combination. – Within the *depressus* group, specimens of this species are recognized by the following combination of characters: pale color; small size; abdomen without extensive microsculpture; and frontal carinae strongly fused basally.

Description. – As in *S. pygmaeus* except as follows. Body color testaceous to ferrugineous, not brunneous, piceous, bicolored, or aeneous. Head and pronotum, Fig. 220; frontal carinae confused basally; pronotal hind angles more prominent. Left elytron with about seven to eleven setae on interval three, six to ten on interval five, four to six on interval seven; total 17-27 in specimens examined. Male genitalia with median lobe, Fig. 230; 10 specimens examined.

Measurements and proportions. See Table 54. Of holotype: TL, 3.80 mm; LE, 2.30 mm; WH, 0.80 mm; WP, 1.02 mm; WE, 1.20 mm; WF/WH, 0.66; LP/WP, 0.94; DP/LP, 0.76; LP/WE, 0.79; Ta/Ti, 0.59; PS/LP, 0.71. Of allotype: TL, 3.78 mm; LE, 2.34 mm; WH, 0.80 mm; WP, 0.99 mm; WE, 1.18 mm; WF/WH, 0.66; LP/WP, 0.93; DP/LP, 0.77; LP/WE, 0.78; Ta/Ti, 0.56; PS/LP, 0.70.

Variation. – Data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 55-58, and summarized in Fig. 247-250. In general, body size increases from west to east, with no important gaps between geographically proximate samples (Fig. 247). Specimens from interior parts of the range tend to have more setae than do those from peripheral areas, and there is a statistically significant difference between the Chihuahua and Durango samples (16 and 17) (Fig. 248). Relative eye size (Fig. 249) tends to decrease from west to east, and there is a statistically significant difference between the Boquillas and Marathon samples (9 and 10). Specimens from the northeast and southwest of the range (Fig. 250) tend to have wider pronota than those from elsewhere, and the samples from Cochise Stronghold and Portal (5 and 6) are statistically significantly different in this characteristic. For a more extended discussion, see the taxonomic notes section under *S. ochthocephalus*.

Table 54. Descriptive statistics for *S. falli*, based on 20 males from 4.8 miles east of Sabinas Hidalgo, Nuevo Leon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.52-4.18	3.858	0.237	0.071	4.10
LE	2.15-2.58	2.358	0.150	0.045	4.25
WH	0.74-0.85	0.794	0.041	0.012	3.40
WP	0.93-1.09	1.019	0.065	0.019	4.27
WE	1.10-1.29	1.203	0.071	0.021	3.91
B. Setae on left elytron.					
Interval 3	7- 9	8.2			
Interval 5	6- 9	7.5			
Interval 7	4- 6	5.3			
Total	19-24	21.0	1.7	0.5	5.44
C. Proportions.					
WF/WH	0.65-0.70	0.671	0.020	0.006	1.99
LP/WP	0.92-0.97	0.942	0.020	0.006	1.40
DP/LP	0.75-0.78	0.762	0.013	0.004	1.09
LP/WE	0.78-0.83	0.801	0.022	0.007	1.85
Ta/Ti	0.56-0.62	0.594	0.024	0.007	2.75
PS/LP	0.67-0.76	0.709	0.032	0.009	3.00

Etymology. – I dedicate the name *S. falli* in recognition of the many important contributions to our knowledge of North American Coleoptera made by the late H. C. Fall.

Distribution. – The known range of *S. falli* extends west from southern Illinois to extreme southern California and south to Colima (Fig. 240). I studied 1069 specimens from the following localities.

UNITED STATES

No locality (2; ANSP). ARIZONA (13; AMNH, ANSP, INHS, MCZ, USNM): Cochise Co., Bear Canyon (1; CUNY), Benson (1; UATA), Carr Canyon (1; CAS), Cave Creek (4; UASM), Chiricahua Mountains (2; CAS, USNM), Cochise Stronghold (42; DJLa, TLEr, UATA), Douglas (2; CNHM, KHSt), Guadalupe Canyon (1; KHSt), Portal (4; UCB), 5 mi. w. Portal (7; AMNH, CUNY, FDAG, UCB, UCD), Texas Pass (15; CUNY), Whetstone Mountains (2; CAS), Wilcox (1; CAS), 8 mi. e. Wilcox (3; GRNo); Gila Co., Globe (32; CAS, CNC, MCZ, UASM, USNM), 33 mi. s. Globe (2; DJLa), Rice (4; MCZ, UASM), San Carlos Lake (16; CUNY, MCZ, UASM); Graham Co., Aravaipa (2; CAS, UASM), Galiuro Mountains (1; USNM), Marijilda Canyon (2; CAS, UATA), Power's Garden (8; UASM), Thatcher (5; UCD); Maricopa Co., Haslampa District (1; CAS), Phoenix (6; MCZ, USNM), Salt River (2; MCZ), Tempe (1; USNM), Verde River (4; LACM, MCZ), Wickenburg (1; LACM); Mojave Co., Kingman (1; UKSM); Pima Co., Alamo Canyon (3; CAS), Arivaca (8; CAS, MCZ, UKSM), Azo (3; CAS), Baboquivari Canyon (6; CAS), Brown Canyon (4; CAS, UATA), Catalina Springs (2; USNM), Collosal Cave Park (4; KHSt), Elkhorn Ranch (1; CAS), Kits Peak Rincon (2; AMNH), Organ Pipe National Monument (10; UATA, UCD), Pantano (3; CUNY), Pepper Sauce Canyon (1; CAS), 17 mi. w. Quijotoa (1; UASM), Quitobaquito (3; AMNH, UASM), Robles Ranch (3; UCD), Sabino Canyon (15; CAS, RTBe, TCBa, TLEr, UCD, UKSM, USNM), Santa Catalina Mountains (11; CAS, KHSt, UATA), Staghorn Ranch (1; CNC), Tanque Verde (4; UATA), Tucson (101; ANSP, CAS, JNeg, KHSt, UATA, UCB, USNM); Pinal Co., 7 mi. ne. Apache Junction (3; GRNo), 10 mi. w. Casa Grande (1; CAS), Oracle (2; USNM), 14 mi. e. Oracle (1; CAS), Superior (3; UATA); Santa Cruz Co., 11.5 mi. se. Arivaca (1; CAS), Black Dike Prospect (2; AMNH), Calabasas Canyon (3; UASM), Canelo (6; UATA), Madera Canyon (30; DHKa, UATA, UCD), Nogales (32; AMNH, CAS, CNHM, UASM, UCD), Patagonia (10; CAS, CNHM, TLEr, UASM, UATA), Peña Blanca

Table 55. Variation in body size (LE, in mm) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 247. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	2.19-2.50	2.292	0.136	0.053	3.97
2	12	2.09-2.47	2.247	0.167	0.064	4.95
3	24	2.08-2.42	2.211	0.166	0.045	4.99
4	20	2.00-2.38	2.182	0.136	0.041	4.16
5	20	2.05-2.45	2.208	0.145	0.043	4.38
6	14	2.00-2.40	2.229	0.155	0.055	4.64
7	14	2.14-2.40	2.281	0.096	0.042	3.43
8	14	2.17-2.52	2.340	0.136	0.048	3.87
9	20	2.00-2.59	2.309	0.234	0.070	6.75
10	20	2.17-2.47	2.320	0.158	0.047	4.54
11	10	2.10-2.50	2.295	0.192	0.081	5.57
12	18	2.20-2.58	2.368	0.165	0.052	4.64
13	20	1.95-2.35	2.186	0.198	0.059	6.05
14	20	1.87-2.39	2.080	0.201	0.060	6.44
15	20	1.90-2.33	2.170	0.195	0.058	5.97
16	20	2.04-2.55	2.304	0.215	0.064	6.23
17	18	2.15-2.50	2.326	0.140	0.044	4.02
18	20	2.20-2.58	2.396	0.183	0.055	5.09

Table 56. Variation in numbers of elytral setae in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 248. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	18-22	19.9	1.7	0.7	5.85
2	12	19-23	21.0	1.8	0.7	5.74
3	24	19-25	21.2	2.0	0.6	6.37
4	20	19-24	21.0	2.0	0.6	6.29
5	20	19-25	21.5	2.3	0.7	7.16
6	14	20-25	21.9	1.8	0.6	5.50
7	14	20-25	21.7	2.2	0.8	6.62
8	14	20-23	21.6	1.5	0.5	4.71
9	20	19-24	21.8	2.1	0.6	6.48
10	20	19-24	21.1	2.4	0.7	7.52
11	10	20-24	21.3	2.0	0.8	6.28
12	18	18-25	21.2	2.3	0.7	7.29
13	20	18-24	21.4	2.6	0.8	8.08
14	20	17-26	21.0	3.4	1.0	10.73
15	20	18-24	21.1	2.2	0.6	6.86
16	20	17-25	20.4	2.8	0.8	9.06
17	18	19-27	22.1	2.6	0.8	7.85
18	20	19-24	21.4	2.1	0.6	6.68

Table 57. Variation in relative eye size (WF/WH) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 249. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	0.65-0.69	0.671	0.017	0.007	1.74
2	12	0.62-0.66	0.636	0.016	0.006	1.70
3	24	0.62-0.66	0.645	0.015	0.004	1.58
4	20	0.63-0.67	0.651	0.015	0.004	1.49
5	20	0.63-0.66	0.644	0.014	0.004	1.47
6	14	0.62-0.66	0.641	0.017	0.006	1.78
7	14	0.63-0.68	0.654	0.025	0.009	2.52
8	14	0.63-0.68	0.653	0.019	0.007	1.94
9	20	0.63-0.68	0.666	0.021	0.006	2.14
10	20	0.63-0.66	0.648	0.019	0.006	1.91
11	10	0.65-0.69	0.669	0.024	0.010	2.38
12	18	0.64-0.68	0.661	0.014	0.004	1.42
13	20	0.62-0.66	0.647	0.016	0.005	1.67
14	20	0.61-0.67	0.650	0.022	0.007	2.26
15	20	0.63-0.67	0.652	0.019	0.006	1.98
16	20	0.65-0.70	0.669	0.026	0.008	2.61
17	18	0.64-0.68	0.662	0.021	0.007	2.09
18	20	0.65-0.70	0.673	0.026	0.008	2.56

Table 58. Variation in pronotal form (LP/WP) in selected samples of *S. falli* and *S. ochthocephalus* (sample one from Davis, California); see Fig. 250. Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	12	0.93-0.96	0.952	0.014	0.005	0.98
2	12	0.94-0.98	0.958	0.017	0.006	1.16
3	24	0.90-0.99	0.950	0.035	0.010	2.47
4	20	0.92-0.98	0.952	0.024	0.007	1.71
5	20	0.93-0.98	0.956	0.028	0.008	1.96
6	14	0.90-0.97	0.937	0.025	0.009	1.80
7	14	0.92-0.98	0.944	0.023	0.008	1.65
8	14	0.92-0.99	0.950	0.030	0.011	2.11
9	20	0.90-1.00	0.950	0.030	0.009	2.11
10	20	0.94-0.98	0.952	0.015	0.004	1.06
11	10	0.90-0.96	0.936	0.030	0.013	2.15
12	18	0.90-0.96	0.931	0.024	0.008	1.72
13	20	0.93-0.98	0.935	0.017	0.005	1.18
14	20	0.92-0.99	0.947	0.032	0.010	2.25
15	20	0.92-0.97	0.946	0.018	0.006	1.31
16	20	0.91-0.98	0.944	0.025	0.008	1.80
17	18	0.90-0.99	0.944	0.036	0.011	2.57
18	20	0.92-0.98	0.948	0.022	0.007	1.56

(30; CNC, CUNY, UASM); Santa Rita Mountains (9; UKSM, USNM), Sycamore Canyon (12; CAS, KHSt, UATA); Yavapai Co., Bumble Bee (3; CAS), Congress (1; UATA), Jerome (4; CAS), Mayer (1; GRNo); Yuma Co., Yuma (10; UKSM, USNM). ARKANSAS: Caroll Co., Berrytown (7; UKSM), Eureka Springs (7; UKSM); Madison Co., Patrick (1; UKSM); Washington Co. (1; INHS), 7 mi. s. Fayetteville (5; UASM). CALIFORNIA (2; MCZ, USNM): Imperial Co., Potholes (2; CAS); Riverside Co., Palm Springs (1; USNM); San Bernadino Co., 10 mi. ne. Earp (3; UCB). COLORADO: Montrose Co., Cimarron (1; CUNY). ILLINOIS: Pike Co., Pittsfield (1; UCD). MISSOURI: Crawford Co., Meramec River (1; USNM); Ripley Co., 5.5 mi. n. Briar (1; CAS); Wright Co., Mountain Grove (1; TCBa). NEBRASKA: Douglas Co., Omaha (1; CAS). NEW MEXICO: Dona Ana Co., Agustin Pass (2; CAS), Las Cruces (1; CNC), White Sands (1; UKSM); Grant Co., Cliff (1; DRWh), Silver City (1; CNC); Hidalgo Co., Lordsburg (1; CNC); Luna Co., Deming (1; UCD), 7.5 mi. nw. Florida (7; CAS); Rio Arriba Co., San Juan Pueblo (1; DRWh); Torrance Co., 4 mi. w. Abo (4; GRNo). OKLAHOMA: Cimarron Co., Black Mesa State Park (1; CAS). TEXAS (20; AMNH, ANSP, CAS, INHS, MCZ, USNM): Blanco Co., Cypress Mills (3; USNM), Round Mountain (1; MCZ); Brewster Co. (1; MCZ), Black Gap Refuge (1; CNC), Boquillas (62; AMNH, CNC, UCB), Green Valley (1; CAS), Hot Springs (21; AMNH, CNC), Lajitas (2; CNC), 22 mi. s. Marathon (39; UCD), Maverick (3; CNC), Nine Point Draw (1; CNC), Panther Junction (1; CNC), Rio Grande Village (4; CAS, UASM), Terlingua (2; CNC), Tornillo Flat (3; CNC); Jeff Davis Co., Davis Mountains State Park (10; CAS, DHKa, DJLa), Fort Davis (7; CAS, CNC); Llano Co., Enchanted Rock (7; CNC); Presidio Co., 4 mi. w. Lajitas (1; JHeS), 6 mi. e. Presidio (21; UASM); Terrell Co., 10 mi. e. Dryden (1; DJLa), Lozier Canyon (1; MCZ); Val Verde Co., Del Rio (3; CAS, USNM). UTAH: San Juan Co., 8 mi. e. Bluff (1; UATA).

MEXICO

BAJA CALIFORNIA: 10 mi. sw. Canipole (3; UATA), 20 mi. n. Comondu (5; CAS), Conception Bay (1; CAS), 8 mi. nw. El Progreso (1; CAS), La Paz (2; CAS), 25 mi. w. La Paz (1; CAS), Purissima (2; UASM), 5 mi. w. San Bartolo (7; CAS), 12 mi. nw. San Bartolo (3; CAS), 10 mi. sw. San Jose del Cabo (8; UATA), 25 mi. s. Santa Rosalia (1; CAS), 6 mi. sw. Santiago (12; UATA), Triunfo (7; CAS). CHIHUAHUA: 25 mi. sw. Camargo (2; AMNH), Catarinas (5; AMNH), 70-75 mi. n. Chihuahua (2; GRNo, UCB), 33 mi. s. Ciudad Jimenez (3; DJLa), Parral (1; UCB), 15 mi. e. Parral (3; AMNH), 40 mi. ne. Parral (3; UASM), 5 mi. w. Parrita (3; UCB), 63 mi. w. Santa Barbara (4; AMNH), Valle de Olivos (2; AMNH). COAHUILA: Boquillas del Carmen (3; CNC), 15 mi. n. Saltillo (1; UASM). COLIMA: 8 mi. sw. Colima (1; UASM). DURANGO: 12.2 mi. s. El Banco (25; UASM), Las Nieves (3; UASM), 4.2 mi. w. Vicente Guerrero (1; UASM). NAYARIT: Acaponeta (1; CAS), 2.4 mi. s. Acaponeta (2; UASM). NUEVO LEON: Cienega de Flores (2; CAS), 14.8 mi. w. Linares (2; BMNH), 5 mi. s. Monterrey (2; CNC), 4.8 mi. e. Sabinas Hidalgo (30; CNHM, DRWh, IRSB, MCZ, MGFT, UASM, USNM). SINALOA: 30.6 mi. s. Culiacan (1; UASM), 26 mi. n. Pericos (1; CAS), 4 mi. s. Villa Union (1; UCB). SONORA (2; BMNH): Alamos (8; CAS), 5 mi. w. Alamos (3; UATA), 10 mi. w. Alamos (5; AMNH), Hermosillo (40; CAS, UATA), 40 mi. n. Hermosillo (13; CAS), 10 mi. e. Navajoa (21; UATA), San Bernadino (1; CAS), San Carlos Bay (1; CAS), San Lorenzo (1; CNHM), 40 mi. nw. Santa Ana (2; GRNo). TAMAULIPAS: Nuevo Laredo (1; USNM). ZACATECAS: 25 mi. w. Fresnillo (1; CAS), 1.3 mi. se. Sain Alto (1; UASM).

Collecting notes. – Specimens of this species have been collected from April to October, and, in Mexico, in January. Most were found in riparian gravel bars, or were taken at lights.

Taxonomic notes. – Within the *depressus* group, *S. falli* is similar to *S. pygmaeus, S. scopaeus*, and *S. depressus*, and has in the past been confused with them. But these species are sympatric, and specimens are constantly distinguishable by form of frontal carinae and by details of male genitalia. That *S. falli* is specifically distinct is further confirmed by the fact that sympatric population samples of these species are statistically significantly different in various ways.

Schizogenius ochthocephalus new species

Type material. – Holotype male and allotype female labelled "Davis Cal I.17 1956," "Taken in flood debris," and "E. A. Kurtz Collector" (UCD). An additional 16 specimens from various localities in central and northern California are paratypes (CAS, DRWh, UASM, UCD).

Diagnostic combination. – Within the *depressus* group, this is the only known pale species with extensive abdominal microsculpture.

Description. – As in *S. falli* except as follows. Left elytron with about seven to eight setae on interval three, six to eight on interval five, four to six on interval seven; total 18-21 in specimens examined. Abdomen extensively microsculptured. Male genitalia with median lobe, Fig. 231; four specimens examined

Measurements and proportions. See Table 59. Of holotype: TL, 3.64 mm; LE, 2.25 mm; WH, 0.75 mm; WP, 0.93 mm; WE, 1.12 mm; WF/WH, 0.65; LP/WP, 0.96; DP/LP, 0.78; LP/WE, 0.79; Ta/Ti, 0.56; PS/LP, 0.70. Of allotype: TL, 3.88 mm; LE, 2.40 mm; WH, 0.80 mm; WP, 1.02 mm; WE, 1.25 mm; WF/WH, 0.67; LP/WP, 0.94; DP/LP, 0.78; LP/WE, 0.77; Ta/Ti, 0.61; PS/LP, 0.71.

Table 59. Descriptive statistics for *S. ochthocephalus*, based on 11 males from various localities in California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.51-3.77	3.633	0.122	0.049	2.23
LE	2.18-2.34	2.247	0.074	0.030	2.18
WH	0.71-0.77	0.743	0.026	0.010	2.33
WP	0.89-0.97	0.928	0.035	0.014	2.54
WE	1.10-1.17	1.127	0.034	0.014	2.03
B. Setae on left elytron.					
Interval 3	7- 8	7.4			
Interval 5	6- 8	7.1			
Interval 7	5- 6	5.2			
Total	18-21	19.6	1.8	0.7	6.14
C. Proportions.					
WF/WH	0.65-0.69	0.670	0.020	0.008	2.00
LP/WP	0.94-0.97	0.955	0.021	0.009	1.49
DP/LP	0.76-0.81	0.784	0.020	0.008	1.73
LP/WE	0.77-0.80	0.784	0.013	0.005	1.11
Ta/Ti	0.55-0.60	0.580	0.034	0.014	3.93
PS/LP	0.69-0.73	0.706	0.019	0.008	1.78

Etymology. – Greek, *ochthos* = mound, plus *kephalos* = head, in reference to lumpy appearance of head caused by basal coalescence of frontal sulci.

Distribution. – *S. ochthocephalus* is known from only a few localities in central and northern California (Fig. 240). I studied the following 18 specimens.

UNITED STATES

CALIFORNIA: Calaveras Co., Mokelumne Hill (1; CAS); Humboldt Co., Fernbridge (1; UASM); Lake Co., Clear Lake (1; CAS); Sacramento Co., Fair Oaks (1; UCD); Sonoma Co., Guerneville (1; CAS); Yolo Co., Davis (13; DRWh, UCD).

Collecting notes. – I have not collected specimens of this species, but presume they live in riparian gravel bars. Available specimens were collected in January, March, April, and June.

Taxonomic notes. – This species is sympatric with *S. pygmaeus* and *S. depressus*, and differs constantly from them by having abdominal microsculpture and basally confused frontal carinae. *S. ochthocephalus* clearly shares a common ancestry with *S. falli*, and may be only a

geographic isolate of that species, but I think it is reproductively isolated for the following reasons. There is evidently at least one complete morphological discontinuity between the two taxa, as all specimens of the former have the abdomen completely microsculptured, while none of the latter do. Mean eye size in *S. ochthocephalus* (sample one) is taxonomically significantly smaller (Table 57) than in the geographically nearest sample of *S. falli* (sample two, Yuma), and in this characteristic an otherwise continuous cline is interrupted (Fig. 249). These discontinuities indicate that *S. ochthocephalus* is more likely reproductively isolated from *S. falli* than not, and justify my recognition of them as distinct species. The *S. ochthocephalus* sample is further characterized by fewer elytral setae than the Yuma sample of *S. falli* (Table 56, Fig. 248), but the difference is not statistically significant.

Since no related species in the *depressus* group have extensive abdominal microsculpture, presence of such microsculpture in *S. ochthocephalus* must be a specialization. The four characteristics studied by statistical analysis exemplify central-peripheral patterns of variation (Brown, 1958; Ball 1960), in which peripheral character states are best regarded as ancestral. I judge that large body size (Fig. 247) and small numbers of elytral setae (Fig. 248) are peripheral character states, and hence probably ancestral. The small body size character state is evidently spreading outward from the Sonoran Region, but has reached neither *S. ochthocephalus* nor eastern populations of *S. falli*. Increased numbers of elytral setae may be a character state now spreading outward from the Chihuahuan Region, with impeded gene flow between the Chihuahua and Durango samples, and no gene flow between *S. falli* and *S. ochthocephalus*. The evidence for central-peripheral variation in relative eye size (Fig. 249) is stronger; the small eye character state is definitely peripheral, and hence most probably is ancestral. The enlarged eye character state apparently is spreading outward from the Sonoran Region, but does not affect *S. ochthocephalus*, and, curiously, is only weakly evident in the Big Bend part of Texas.

Even more interesting is the pattern of variation in pronotal form (Fig. 250). The wide pronotum, as in samples 12 and 13, is a peripheral character state which I think must be ancestral. Further support for this notion comes from a comparison of two samples from the Dragoon Mountains in Arizona. One sample from Texas Pass, not tabulated or figured, was collected in 1917; the second sample, collected in 1965, is from Cochise Stronghold (sample five). Data for the Texas Pass sample are as follows: N, 12; Range, 0.89-0.98; Mean, 0.936; 1.5SD, 0.030; 2SE, 0.011; CV(%), 2.11. If the statistical data for these two samples properly reflect their respective populations, there must have been a shift in time from broad to narrow pronotal form. The difference is statistically significant, and I therefore interpret it as biologically significant; there has, in the region of the Dragoon Mountains, been a shift from the ancestral to derived character state within a period of less than 50 years. I suggest that in *S. falli* the narrow pronotum character state is spreading from two foci, in the Sonoran Region and along the Rio Grande. If this assertion is correct, then the narrow pronotum in *S. ochthocephalus* must be an independently acquired specialization. However, my interpretation may be overly simplified, in view of the complex pattern of variation in pronotal form. A test of my hypothesis of central-peripheral variation may be made by searching for other shifts in time, from narrow to broad or broad to narrow pronotal form.

Schizogenius depressus LeConte

Schizogenius depressus LeConte 1852:197. *Type locality* Colorado River, California; type in MCZ, male labelled MCZ 5843 here designated lectotype (!). LeConte 1857:83. Putzeys 1863:24. Putzeys 1866:223. LeConte 1879:34. Hatch 1949:118. Hatch 1953:69. Lindroth 1961:168.

Diagnostic combination. – Among pale members of the *depressus* group without ventral microsculpture, specimens of *S. depressus* are distinguished by prominent pronotal hind angles, frontal sulci not or weakly confused basally, and elytral length over 2.0 mm.

Description. – As in *S. pygmaeus* except as follows. Larger, elytral length 2.05 mm or more. Body color testaceous to ferrugineous or castaneous, not piceous, bicolored, or aeneous. Head and pronotum, Fig. 221; eyes uniformly faceted except in some Mexican specimens, where inner facets enlarged; neck densely to sparsely punctate; antennal article five about 1.4 to 1.6 times longer than wide; pronotal hind angles prominent in most specimens; anterior transverse impression finely punctate. Left elytron with six to twelve setae on interval three, six to 11 on interval five, four to seven on interval seven; total 16-30 in specimens examined; humeral denticles moderately sharp and prominent. Male genitalia with median lobe, Fig. 232; endophallus, Fig. 233; 20 specimens examined.

Measurements and proportions. See Table 60.

Variation. – Specimens from the Rio Balsas drainage in the state of Mexico have much larger inner than outer eye facets. Specimens from Zacatecas also have large inner eye facets, though less pronouncedly so. Eyes in all other specimens are uniformly faceted, including those from the Rio Tula drainage in the state of Mexico. The Zacatecas locality is, in a sense, geographically intermediate between the two state of Mexico localities, as it is from an interior drainage system, while the Rio Balsas drains to the Pacific and the Rio Tula to the Atlantic.

Table 60. Descriptive statistics for *S. depressus*, based on 20 males from Clear Lake, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements, in mm.					
TL	3.39-3.92	3.706	0.194	0.058	3.49
LE	2.06-2.40	2.263	0.123	0.037	3.61
WH	0.70-0.81	0.764	0.039	0.012	3.41
WP	0.91-1.05	0.990	0.052	0.016	3.50
WE	1.06-1.24	1.165	0.069	0.020	3.92
B. Setae on left elytron.					
Interval 3	6- 9	7.0			
Interval 5	6- 8	7.2			
Interval 7	4- 6	4.6			
Total	16-22	18.8	2.0	0.6	7.15
C. Proportions.					
WF/WH	0.63-0.68	0.650	0.020	0.006	2.08
LP/WP	0.90-0.96	0.930	0.024	0.007	1.69
DP/LP	0.76-0.81	0.788	0.023	0.007	1.98
LP/WE	0.77-0.83	0.790	0.024	0.007	1.99
Ta/Ti	0.59-0.68	0.634	0.041	0.012	4.31
PS/LP	0.70-0.78	0.735	0.032	0.009	2.88

Statistical data on variation in body size, numbers of elytral setae, relative eye size, and pronotal form are given in Tables 61-64, and summarized in Fig. 251-254. The main features of variation in body size (Fig. 251) are the following. Western samples are varied, but all show clear evidence of clinal relationships with geographically related samples. Eastern samples decrease in mean body size south to the Colorado River, and increase from there south into Mexico. Northern samples are not statistically significantly different from one another, but seem not to be clinally continuous across the Rocky Mountains.

Variation in numbers of elytral setae (Fig. 252) may be summarized as follows. In the United States, samples from the Rio Papigochic, Colorado River, Great Basin, Rio Grande, Canadian River, and Missouri River drainage basins have statistically significantly more elytral setae than any of the western samples. All eastern and all western samples are evidently clinally related to one another. Northern samples do not appear to be clinally continuous across the Rocky Mountains. The Chihuahua sample (number 22) is probably related to the Arizona sample (number 21) via a steep cline. Additional collections are needed to determine relationships between the quite different Chihuahua and Zacatecas samples (22 and 23).

Table 61. Variation in body size (LE, in mm) in selected samples of *S. depressus* (Fig. 251). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	2.22-2.50	2.378			
2	14	2.32-2.92	2.563	0.221	0.079	5.74
3	20	2.16-2.71	2.442	0.226	0.067	6.17
4	12	2.22-2.58	2.432	0.184	0.071	5.09
5	30	2.25-2.78	2.560	0.183	0.044	4.76
6	16	2.32-2.66	2.487	0.165	0.055	4.43
7	4	2.39-2.58	2.482			
8	40	2.05-2.60	2.321	0.154	0.035	4.71
9	16	2.31-2.69	2.501	0.152	0.050	4.04
10	16	2.12-2.56	2.325	0.203	0.068	5.82
11	12	2.29-2.69	2.514	0.181	0.070	4.80
12	14	2.26-2.72	2.461	0.166	0.059	4.50
13	14	2.35-2.75	2.520	0.213	0.076	5.62
14	20	2.28-2.72	2.502	0.169	0.050	4.50
15	6	2.32-2.70	2.558			
16	18	2.30-2.70	2.529	0.167	0.053	4.41
17	16	2.15-2.78	2.530	0.241	0.080	6.34
18	26	2.35-2.69	2.494	0.143	0.037	3.83
19	24	2.25-2.75	2.508	0.200	0.054	5.31
20	48	2.19-2.72	2.449	0.187	0.036	5.10
21	40	2.25-2.78	2.520	0.164	0.035	4.36
22	4	2.65-2.85	2.775			
23	24	2.50-2.92	2.676	0.161	0.044	4.01

Table 62. Variation in numbers of elytral setae in selected samples of *S. depressus* (Fig. 252). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	18-21	19.5			
2	14	18-22	20.4	1.7	0.6	5.65
3	20	17-22	19.8	2.3	0.7	7.61
4	12	18-21	19.5	1.3	0.5	4.09
5	30	18-23	20.4	1.9	0.5	6.12
6	16	18-23	20.1	1.9	0.6	6.43
7	4	17-21	18.8			
8	40	16-22	19.2	1.8	0.4	6.15
9	16	17-21	19.2	1.6	0.5	5.53
10	16	18-23	19.9	1.9	0.6	6.33
11	12	18-22	19.8	1.7	0.7	6.02
12	14	18-22	19.8	1.6	0.6	5.31
13	14	19-22	20.3	1.8	0.6	5.94
14	20	17-22	19.8	2.0	0.6	6.68
15	6	20-23	21.8			
16	18	21-25	23.0	2.3	0.7	6.67
17	16	20-25	22.1	2.1	0.7	6.37
18	26	20-24	22.0	1.7	0.4	5.05
19	24	20-28	23.0	3.2	0.9	9.16
20	48	20-30	22.2	2.9	0.6	8.66
21	40	19-25	22.6	2.0	0.5	6.93
22	4	24-27	25.5			
23	24	19-23	20.5	2.0	0.5	6.44

Variation in relative eye size (Fig. 253) has the following main features. In both east and west, there is a general trend toward increased eye size from north to south, with particularly large eyes characteristic of Mexican samples. In the United States, eye size in eastern samples is quite uniform but in the west a discordant pattern of variation is evident in the north. Northern samples do not appear to be clinally continuous across the Rocky Mountains.

The chief features of variation in pronotal form (Fig. 254) are as follows. The pattern of variation in western samples is complex, and no definite trends are evident, but geographically related samples are probably clinally continuous. Among eastern samples there is a definite cline toward narrower pronotal form from north to south. Across the Rocky Mountains in the north, there is strong evidence of clinal discontinuity in this characteristic.

Among Mexican specimens, only those from Zacatecas were numerous enough to form a good sample for statistical analysis; thus, no detailed account of variation is yet possible. The Chihuahua specimens are evidently related by steep character clines to specimens

Table 63. Variation in relative eye size (WF/WH) in selected samples of *S. depressus* (Fig. 253). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	0.66-0.69	0.675			
2	14	0.63-0.68	0.658	0.021	0.008	2.13
3	20	0.63-0.69	0.670	0.023	0.007	2.24
4	12	0.66-0.69	0.676	0.016	0.006	1.47
5	30	0.63-0.67	0.654	0.017	0.004	1.73
6	16	0.66-0.70	0.674	0.015	0.005	1.63
7	4	0.65-0.68	0.670			
8	24	0.62-0.68	0.655	0.020	0.005	2.01
9	16	0.63-0.68	0.659	0.017	0.006	1.70
10	16	0.65-0.69	0.666	0.016	0.005	1.63
11	12	0.63-0.67	0.650	0.022	0.009	2.27
12	14	0.63-0.67	0.652	0.020	0.007	2.01
13	14	0.65-0.67	0.663	0.012	0.004	1.25
14	20	0.63-0.68	0.657	0.018	0.005	1.79
15	6	0.64-0.67	0.657			
16	18	0.64-0.68	0.661	0.016	0.005	1.63
17	16	0.64-0.69	0.659	0.024	0.008	2.44
18	26	0.62-0.70	0.654	0.026	0.007	2.67
19	24	0.63-0.68	0.664	0.022	0.006	2.26
20	48	0.62-0.68	0.653	0.025	0.005	2.51
21	24	0.63-0.68	0.655	0.022	0.006	2.70
22	4	0.62-0.67	0.642			
23	24	0.62-0.66	0.640	0.018	0.005	1.93

from the Chiricuahua Mountains of Arizona. Specimens from Zacatecas differ markedly from those from Chihuahua, particularly in numbers of elytral setae, but the differences probably reflect mainly a lack of intermediate collections. Specimens from Atlantic and Pacific drainages in the state of Mexico are strongly differentiated. Rio Tula and Guanajuato specimens differ from Rio Balsas specimens by narrower pronota, and by uniformly faceted and much smaller eyes. Zacatecas specimens are intermediate in these characteristics, and may also be considered geographically intermediate since they are from an interior drainage system. I suspect that the Rio Balsas and Rio Tula populations are geographically quite isolated from one another despite their proximity, and that they may even be reproductively isolated.

In America north of Mexico, sample means for numbers of elytral setae in eastern samples of *S. depressus* are statistically significantly greater than in western samples. Eastern samples are similar in all ways measured, and are linked to one another by definite character clines. Western samples are more varied, but are similarly related by character clines. There is no evidence of reproductive isolation between eastern and western forms in the south, but

Table 64. Variation in pronotal form (LP/WP) in selected samples of *S. depressus* (Fig. 254). Males and females each 50%.

Sample	N	Range	Mean	1.5SD	2SE	CV(%)
1	4	0.91-0.94	0.925			
2	14	0.91-0.96	0.939	0.023	0.008	1.64
3	20	0.90-0.95	0.932	0.019	0.006	1.76
4	12	0.91-0.96	0.932	0.026	0.010	1.84
5	30	0.89-0.95	0.928	0.021	0.005	1.53
6	16	0.90-0.96	0.927	0.025	0.008	1.79
7	4	0.93-0.97	0.948			
8	24	0.89-0.98	0.933	0.032	0.009	2.29
9	16	0.89-0.96	0.928	0.029	0.010	2.10
10	16	0.89-0.96	0.929	0.032	0.011	2.27
11	12	0.91-0.98	0.938	0.034	0.013	2.40
12	14	0.92-0.96	0.941	0.017	0.006	1.21
13	14	0.87-0.96	0.936	0.038	0.013	2.67
14	20	0.91-0.95	0.932	0.020	0.006	1.46
15	6	0.88-0.94	0.915			
16	18	0.89-0.95	0.923	0.025	0.008	1.82
17	16	0.89-0.95	0.923	0.022	0.007	1.62
18	26	0.89-0.95	0.923	0.024	0.006	1.76
19	24	0.88-0.96	0.930	0.028	0.008	2.04
20	48	0.89-0.98	0.928	0.024	0.005	1.75
21	24	0.89-0.98	0.939	0.028	0.008	2.06
22	4	0.90-0.97	0.942			
23	24	0.88-0.96	0.928	0.031	0.008	2.23

differences in mean numbers of elytral setae do indicate geographic isolation. In the north, the Montana sample (sample 15) is similar in most ways to some of the more distant western samples, especially samples two and five, but is divergent from them in pronotal form. Western samples geographically closer to the Montana sample, particularly samples three and four, are more differentiated in most or all characteristics measured. In the Pacific Northwest, these characteristics vary in definite geographic patterns, apparently independently of one another but not randomly. Most notably, small eyed forms extend southwest from the Snake River to northern California, thus separating large eyed forms to the north and south (Fig. 253). These facts suggest that the northern populations were once clinally continuous across the Rocky Mountains, but later became geographically and perhaps even reproductively isolated. The eastern form may relatively recently have crossed the mountain barrier to interact with the western form, resulting in character displacement (Brown and Wilson, 1956). This hypothesis of character displacement may be tested by searching for bimodal character state distributions in large samples collected along the western slopes of the Rocky Mountains. Insufficient material is available at

present for such an analysis.

Although I have no direct evidence of character displacement in the northwest, I cannot otherwise explain how such a complex pattern of variation and differentiation may have originated. I assume that my hypotheses are correct, and postulate the following sequence of events. *S. depressus* was once widespread in western North America, with clinal continuity in the south via the Colorado River, in the north via the Columbia and Missouri Rivers, and perhaps also across the Great Basin. With deteriorating climatic conditions in the Pleistocene, and particularly with advances of glaciation southward along the Rocky Mountains, clinal continuity in the north was repeatedly broken by geographic isolation. During subsequent interglaciation, geographic isolation may have been partially maintained. Much later, the retreat of the Wisconsin glaciation was accompanied by a rapid spread of desert conditions in the south (Martin and Mehringer, 1965), and resulted in a break in clinal continuity there. As climates in the north moderated, renewed contact between eastern and western forms was established, but too late for renewed clinal continuity. Possible datings for Late Pleistocene events (Martin and Mehringer, 1965) are: glacial advance, 70,000 years ago; glacial retreat, 12,000 years ago; and reestablishment of contact between eastern and western forms in the north, less than 12,000 years ago.

Etymology. – Latin, *depressus* = flattened, in reference to the flattened body form.

Distribution. – *S. depressus* ranges further north, and reaches higher elevations, than any other species in the genus (Fig. 241). It ranges in the east along upper reaches of the Rocky Mountain drainage systems as far north as Montana, and in the west it occurs in coastal and montane regions north to southern British Columbia. To the south, *S. depressus* extends to both Atlantic and Pacific drainage basins in the state of Mexico, where specimens have been found as high as 8000′ above sea level. One specimen labelled "D. C." belongs to this species and is no doubt incorrectly labelled. I examined 1230 additional specimens of this species from the following localities.

CANADA

BRITISH COLUMBIA: Salmon Arm (2; CAS, MCZ), Vaseaux Lake (1; UASM), Vernon (6; CAS, KSUM); see Lindroth (1961) for additional Canadian records.

UNITED STATES

No locality (4; IRSB, MGFT, USNM). ARIZONA (29; AMNH, ANSP, CAS, CUNY, INHS, USNM): Cochise Co., Bear Canyon (1; CUNY), Bisbee (1; CAS), Cave Creek (22; AMNH, CAS, TCBa, UASM), Chiricahua Mountains (12; CAS, UKSM, USNM), Cochise Stronghold (2; TLEr, UATA), Huachuca Mountains (1; KHSt), Montezuma Pass (1; CNC), Palmerlee (1; USNM), Pinery Creek (2; CNHM), 5 mi. w. Portal (32; AMNH, CNC, CUNY, LBSC, MSUL, TLEr, UCB, UCD), Ramsey Canyon (1; UATA), Rucker Lake (1; UASM), Sierra Vista (1; CNC), South Fork Forest Camp (1; UATA), Texas Pass (1; CAS), Turkey Creek (1; UATA); Coconino Co. (1; CNHM), Flagstaff (6; CAS, UKSM), Oak Creek Canyon (1; UASM); Gila Co., Globe (4; CAS, CNC, KSUM), 6 mi. n. Payson (1; DJLa), Rice (1; UASM), Roosevelt Lake (1; UASM), San Carlos Lake (1; CUNY); Graham Co., Arcadia Forest Camp (1; UATA), Camp Geronimo (1; UATA), Noon Creek (2; UATA), Power's Garden (1; UASM); Greenlee Co., Clifton (1; CAS), Diamond Creek (3; UASM); Pima Co., Rincon Mountains (4; UASM), Sahuarita (3; MCZ); Santa Cruz Co., Madera Canyon (6; DHKa, UATA, UCD), Nogales (2; CAS, MGFT), Peña Blanca (1; UCB), Santa Rita Mountains (3; UKSM), Sycamore Canyon (3; CAS, KHSt); Yavapai Co., Crown King (3; CAS), Prescott (12; CAS, MCZ, UASM). CALIFORNIA (29; AMNH, ANSP, CNHM, INHS, KSUM, MCZ, RUNB, UKSM, USNM): Alameda Co., Arroyo Mocho (7; TLEr, UCB), Berkeley (2; CUNY), Livermore (1; CAS), Sunol (1; UCB); Alpine Co., Markleville (1; CAS); Calaveras Co., Mokelumne Hill (3; CAS); Colusa Co., Cooks Springs (2; CAS); Contra Costa Co., March Springs Creek (3; CAS, MCZ), Moraga (1; CAS), Mount Diablo (2; CAS), San Pablo Valley (1; UCB); Del Norte Co. (2; CNHM); El Dorado Co. (11; CNHM), Pollock Pines (1; UCD); Fresno Co., Kings River (1; CAS), Stevenson Creek (3; CAS), Trimmer (6; CAS); Humboldt Co., 6 mi. e. Bridgeville (1; GRNo), Fernbridge (1; UASM), Frenchman Creek (2; CAS); Inyo Co., Panamint Mountains (1; USNM); Kern Co. (4; USNM); Lake Co., Adams Springs (1; CAS), Clear Lake (90; CAS), Lower Lake (2; CAS), North Fork Cache Creek (33; UCD), Middletown (1; CAS); Los Angeles Co., Arroyo del Valle (1; CAS), Crystal Lake (9; TCBa), Fish Canyon (1; GRNo), Pasadena (4; CAS), San Antonio Canyon (1; GRNo), Santa Monica (3; CAS, INHS), Tanbark Flat (1; UCD), Tapia Park (1; LACM), Tujunga Canyon (7; LACM); Marin Co. (1; KSUM), Camp Taylor (2; CAS, CNHM), Fairfax (5; CAS), Lake Lagunitas (1; CAS), San Anselmo (1; CAS); Mariposa Co. (1; CNHM), Miami Ranger Station (1; CAS), Yosemite Valley (1; INHS); Mendocino Co. (2;

CNHM, MCZ), Bloody Run Creek (1; CAS), 8 mi. w. Navarro (3; CAS), 2 mi. nw. Philo (1; CAS); Modoc Co. (9; CNHM, MGFT), Davis Creek (2; CAS), 4.5 mi. n. Fort Bidwell (3; CAS), 3 mi. s. Lake City (1; CAS); Mono Co., Fales Hot Springs (1; CAS); Napa Co. (1; CNHM), Mount Saint Helena (1; CAS), Rutherford (5; TLEr); Nevada Co. (4; CNHM, MGFT), Truckee (9; CAS, MCZ, USNM); Orange Co., El Toro (1; CAS), Silverado Canyon (1; GRNo); Placer Co. (1; USNM), Bear Valley (2; CAS), Lake Tahoe (20; CAS, MCZ, UASM, UCD), Tahoe City (3; CAS); Riverside Co., Banning (1; CAS), Idyllwild (2; CAS, UCB), Pinon Flat (1; UCB), 15 mi. e. Redlands (1; LBSC), Riverside (2; CAS), San Jacinto Mountains (1; CAS); San Benito Co., Pinnacles National Monument (1; CAS); San Bernadino Co., 5.5 mi. sw. Big Pine Flat (1; GRNo), Cedar Springs (11; GRNo, LBSC), 9 mi. nw. Fawnskin (1; TLEr), San Bernadino Mountains (1; CAS), South Fork Santa Ana River (1; CAS); San Diego Co., Poway (2; CAS, GRNo), Warners Springs (2; CAS); San Luis Obispo Co., La Panza (2; CAS), San Luis Obispo (2; CAS); San Mateo Co. (2; CAS, MCZ); Santa Barbara Co. (1; CAS), Santa Cruz Island (3; CAS, UCD), Santa Inez Mountains (1; CAS); Santa Clara Co., Alum Rock Park (1; TLEr), Arroyo Bayo (1; TLEr), Gilroy Hot Springs (11; CAS, TLEr), Los Gatos (2; CAS), San Martin (23; CAS), Stanford (1; CAS); Siskiyou Co. (2; CAS, USNM), 2.3 mi. nw. Callahan (1; CAS), Dunsmuir (1; USNM), 1.3 mi. e. Grenada (1; CAS), McCloud (1; CAS); Sonoma Co. (4; CAS, CUNY, LACM), Cazadero (1; CAS), Guerneville (1; CAS), Healdsburg (1; CAS), Santa Rosa (1; MSUL); Stanislaus Co., Del Puerto Creek (1; TLEr); Trinity Co., 10 mi. sw. Big Bar (3; CAS), Hyampon (1; CAS), 4 mi. se. Ruth (2; CAS); Tulare Co., Gray Meadow (1; CAS), Kaweah (1; CAS), Sequoia National Park (2; CAS, UCD); Tuolumne Co., Hardin Flat (1; CAS). COLORADO (6; KSUM, USNM): Baca Co., Regnier (1; AMNH); Boulder Co., 6.9 mi. n. Golden (14; TLEr), Lyons (2; UASM), South Boulder Creek (3; DHKa), 2 mi. e. Wonderview (1; DHKa); El Paso Co., Colorado Springs (1; USNM); Fremont Co., Canon City (7; ANSP, CAS, MCZ, USNM); Jefferson Co., Coal Creek Canyon (1; CAS), Golden (3; DHKa), 2 mi. n. Golden (3; TLEr), 2 mi. e. Morrison (10; DHKa), Waterton (5; DHKa); Huerfano Co., La Veta (1; MCZ); La Plata Co., Durango (1; MCZ); Larimer Co., Fort Collins (2; CAS). IDAHO: Idaho Co., 39 mi. e. Lowell (1; HGou); Kootenai Co., Hayden's Lake (1; CAS); Nez Perce Co., Juliaetta (2; CUNY, USNM), 6 mi. w. Lenore (12; DHKa, HGou), Waha Lake (19; AMNH, CAS, KSUM, MCZ, USNM). MONTANA: Blaine Co., Bear Paw Mountains (2; USNM); Cascade Co., Armington (3; DJLa, UASM); Lewis and Clark Co., Helena (1; UASM), 4 mi. s. Wolf Creek (1; UASM). NEW MEXICO (3; UKSM): Bernalillo Co., Albuquerque (1; USNM); Catron Co., 3 mi. s. Beaverhead (28; TLEr), 12.3 mi. n. Glenwood (4; UASM); Grant Co., 4 mi. e. Hillsboro (1; CNHM), 23 mi. n. Mimbres (5; TLEr), Silver City (1; MCZ), 14 mi. n. Silver City (1; MSUL), 26 mi. n. Silver City (16; TLEr), 36.4 mi. ne. Silver City (3; UASM), 71.6 mi. ne. Silver City (1; UASM); Rio Arriba Co., San Juan Pueblo (1; DRWh); Sandoval Co., Jemez Mountains (5; CAS), Jemez Springs (2; TCBa), 6 mi. sw. Jemez Springs (1; GRNo); San Miguel Co., Las Vegas (2; INHS), Porvenir (1; CAS), Sapello (15; UASM); Taos Co., Taos (2; CAS). OREGON: Columbia Co., Portland (1; CUNY); Gilliam Co., Rock Creek (1; CAS); Grant Co., Blue Mountains (2; CAS); John Day Gorge (2; CNHM); Jackson Co., Medford (14; CAS, UCD), Talent (48; UCD), Tolo (1; UCD); Lake Co., Crooked Creek (5; MSUL), Lakeview (1; CNHM), Paisley (2; CNHM); Malhuer Co., Sucker Creek (5; CAS, CNHM); Marion Co., Detroit (1; CAS); Yamhill Co., Dayton (1; MCZ). SOUTH DAKOTA: Lawrence Co., Spearfish (1; DRWh). TEXAS: Randall Co., Canyon (5; MSUL). UTAH (2; JNeg): Beaver Co., Beaver Creek Hills (2; USNM), South Creek (1; USNM); Juab Co., Nephi (1; USNM); San Juan Co., Arch Canyon (2; MCZ); Utah Co., American Fork (30; ANSP, CAS, USNM); Provo (30; CAS, MCZ, USNM); Weber Co., Ogden (23; CNHM, MCZ, USNM); Chad's Ranch (2; MCZ, USNM). WASHINGTON: Seattle (4; KSUM); Franklin Co., Kahlotus (1; USNM); Walla Walla Co., College Place (1; CNC), Walla Walla (21; CAS). WYOMING: Laramie Co., 11 mi. n. Cheyenne (22; UASM).

MEXICO

CHIHUAHUA: Catarinas (2; AMNH), 23.0 mi. s. Miñaca (1; UASM), Santa Barbara (3; AMNH), 63 mi. w. Santa Barbara (1; AMNH). GUANAJUATO (1; BMNH). MEXICO: Temascaltepec (3; MCZ), Villa Carbon (3; JHeS). ZACATECAS: General Enrique Estrada (69; UASM, IRSB, BMNH).

Collecting notes. – I have collected specimens of this species at several localities, all at comparatively high altitudes or latitudes, in gravel bars along unshaded streams. The only locality where I collected a good series was near Laramie, Wyoming, where I found specimens of no other species of the genus. At lower elevations elsewhere, however, specimens have been taken together with specimens of one or more other species. Specimens of *S. depressus* have been taken throughout the year in the more southern parts of the United States.

Taxonomic notes. – *S. depressus* is closely related to *S. pygmaeus*, *S. scopaeus*, *S. ochthocephalus*, and *S. falli*, but is sympatric with all of them and clearly is reproductively isolated. As noted by Lindroth (1961), Hatch (1949, 1953) erred in placing *S. litigiosus* as a synonym of *S. depressus*.

Eastern and western populations of *S. depressus*, in both the northern and southern extremes of its range, may be reproductively isolated. Here is a fertile field for future investigations at the population level.

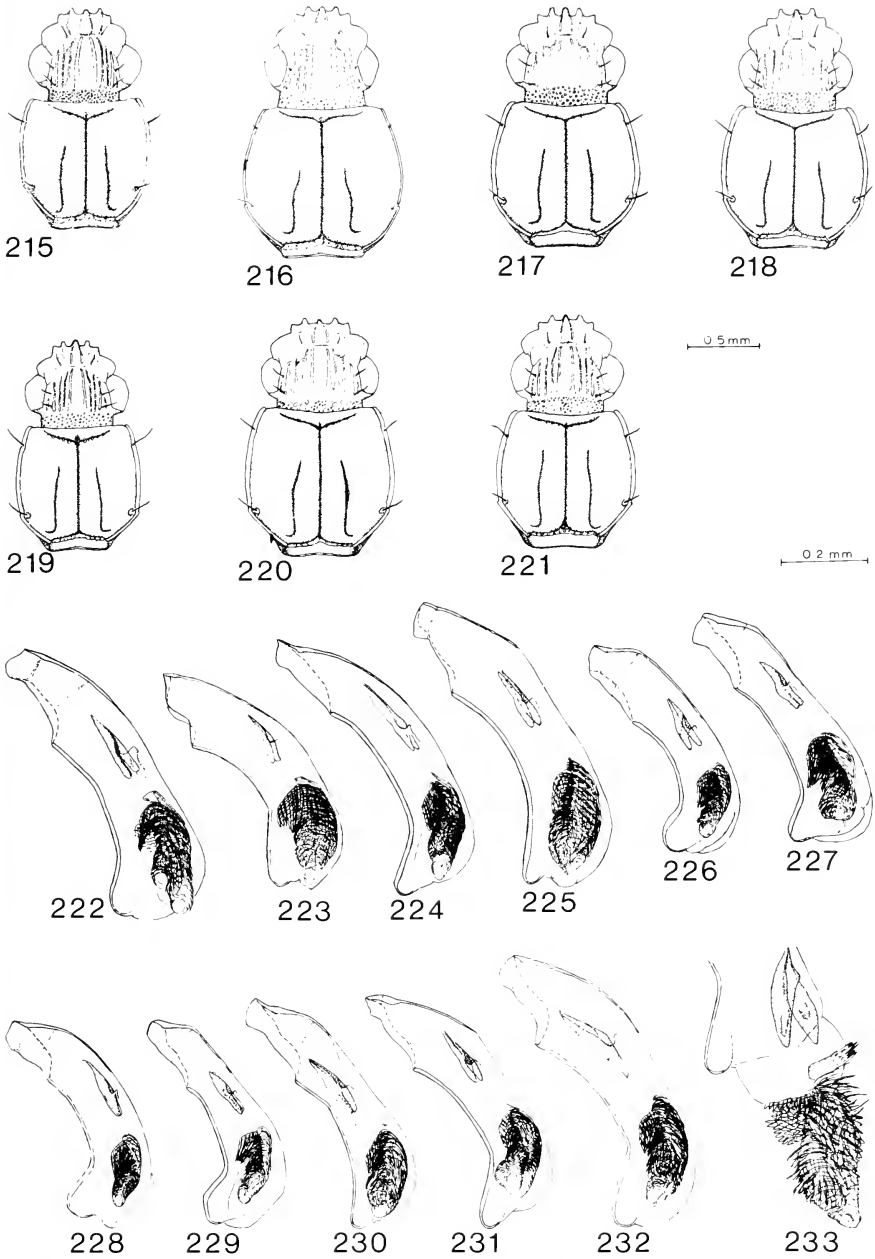


Fig. 215-221. Head and pronotum, dorsal aspect. 215. *S. arimao* Darlington, Soledad, Cuba. 216. *S. emdeni* new species, San Geronimo, Guatemala. 217. *S. sulcifrons* Putzeys, Edmonton, Kentucky. 218. *S. litigiosus* Fall, Gilroy, California. 219. *S. pygmaeus* Van Dyke, Cliff, New Mexico. 220. *S. falli* new species, Sabinas Hidalgo, Nuevo Leon. 221. *S. depressus* LeConte, San Juan Pueblo, New Mexico. Fig. 222-232. Male median lobe, lateral aspect. 222. *S. arimao* Darlington, Soledad, Cuba. 223. *S. emdeni* new species, Palmar Sur, Costa Rica. 224. *S. sulcifrons* Putzeys, Rumney, New Hampshire. 225. *S. litigiosus* Fall, Willow Creek, California. 226. *S. pygmaeus* Van Dyke, Tollhouse, California. 227. Same, Linares, Nuevo Leon. 228. *S. scopaeus* new species, Montemorelos, Nuevo Leon. 229.Same, Brackettville, Texas. 230. *S. falli* new species, Power's Garden, Arizona. 231. *S. ochthocephalus* new species, Fernbridge, California. 232. *S. depressus* LeConte, Power's Garden, Arizona. Fig. 233. Male endophallus, *S. depressus* LeConte, Oliver, British Columbia.

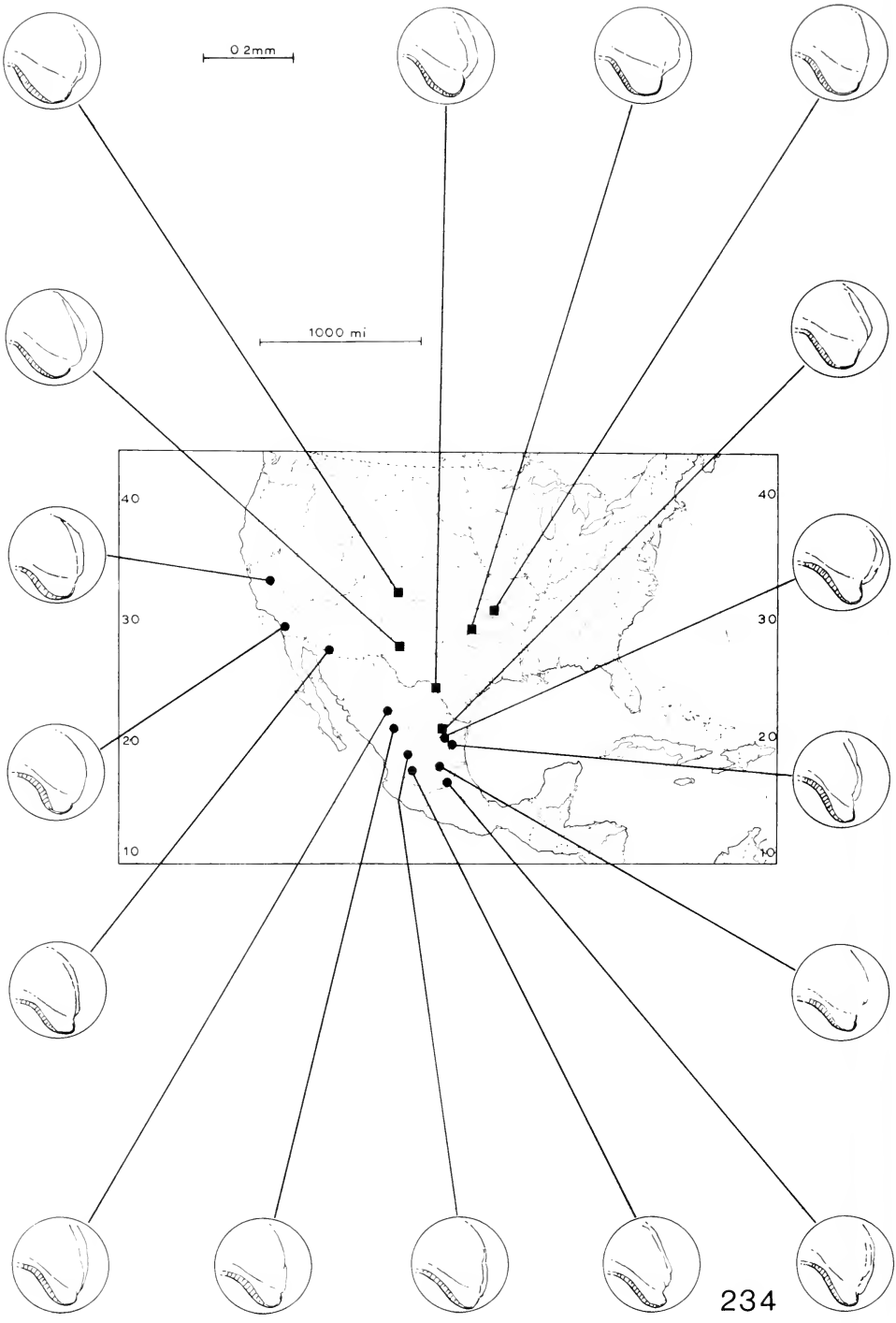
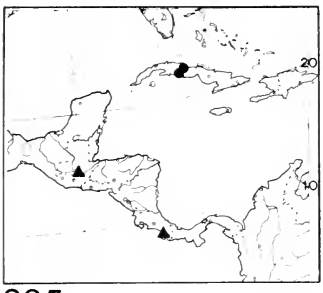


Fig. 234. Geographic variation in form of apex of male median lobe in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares.



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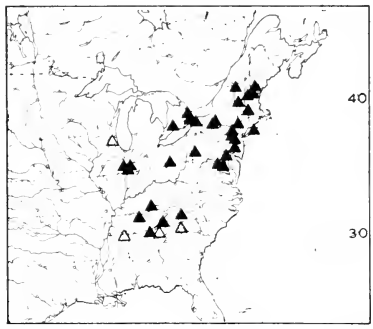

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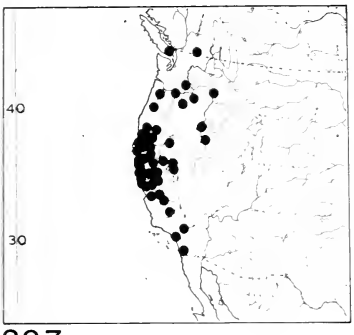
1000 mi



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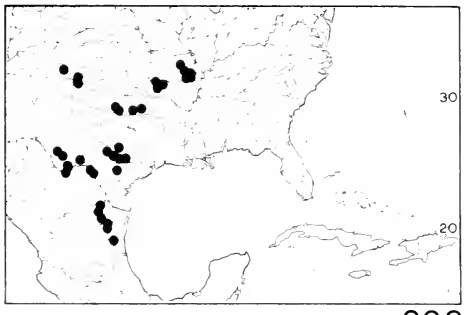

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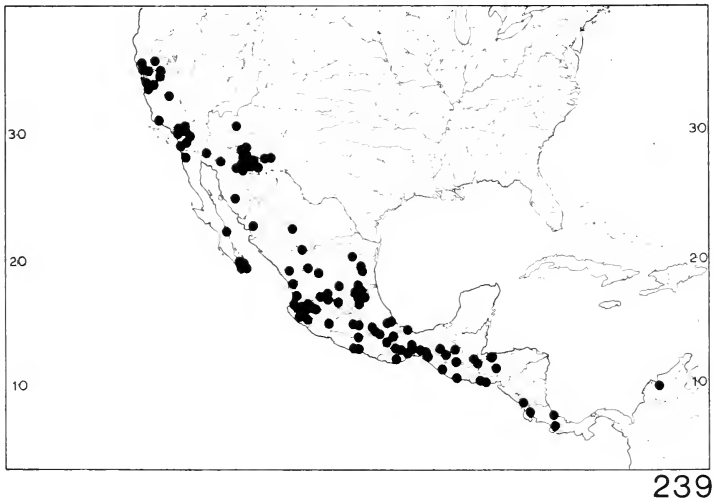

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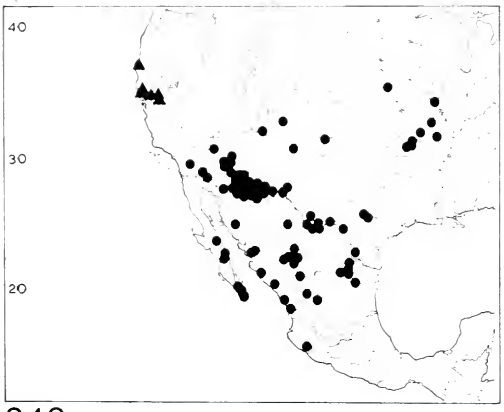
Fig. 235-239. Known distributions. 235. *S. arimao* Darlington, circles, and *S. emdeni* new species, triangles. 236. *S. sulcifrons* Putzeys; open symbols represent state records only. 237. *S. litigiosus* Fall. 238. *S. scopaeus* new species. 239. *S. pygmaeus* Van Dyke.



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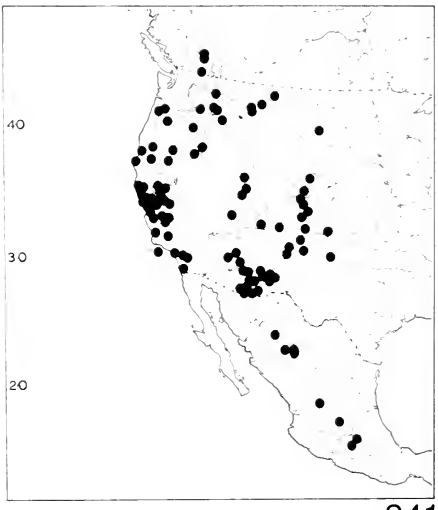

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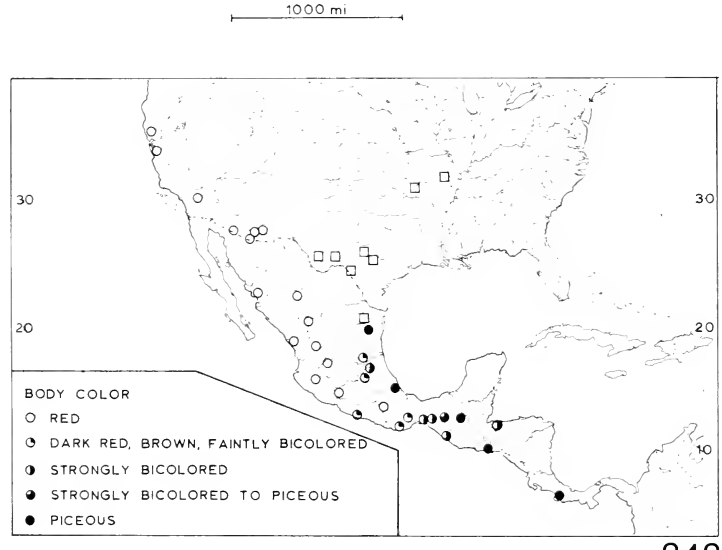

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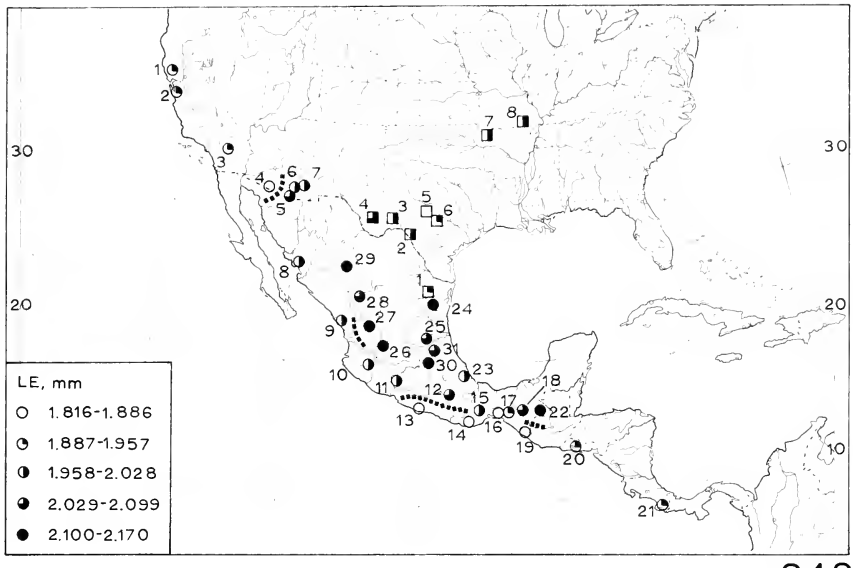
Fig. 240-241. Known distributions. 240. *S. falli* new species, circles, and *S. ochthocephalus* new species, triangles. 241. *S. depressus* LeConte. Fig. 242. Geographic variation in body color of *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; legend applies to both taxa.



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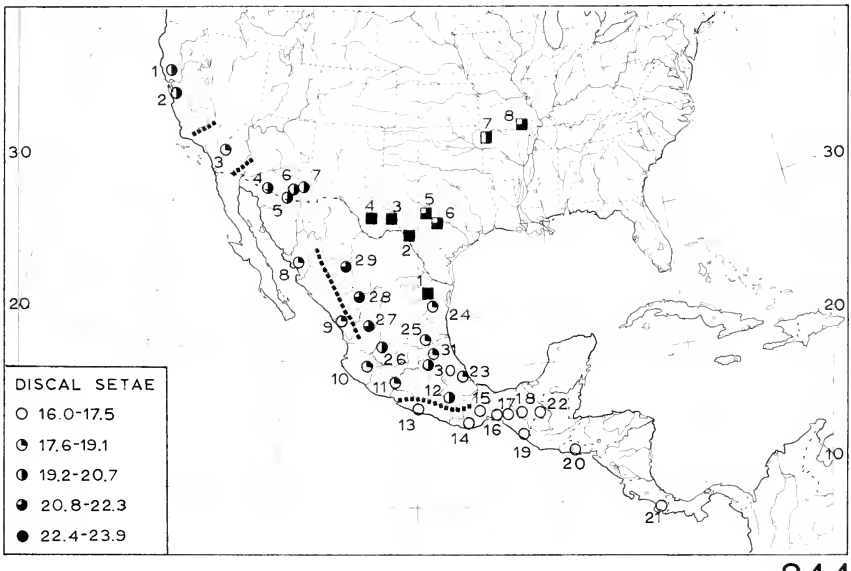

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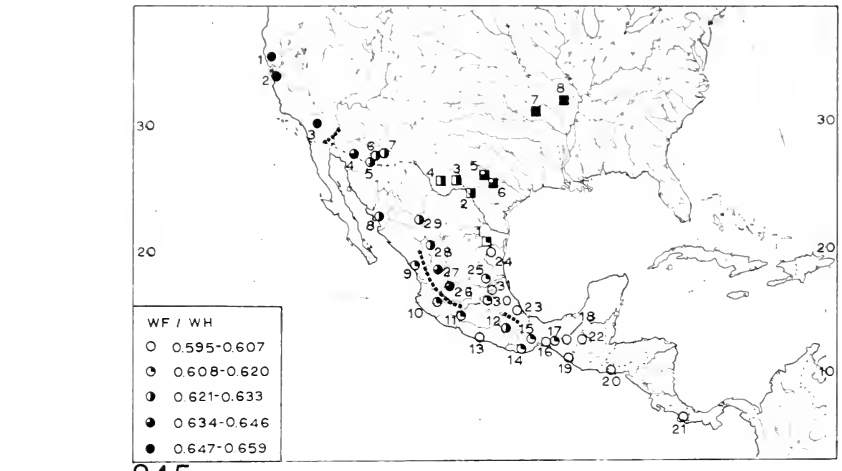
Fig. 243-244. Geographic variation in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; broken lines indicate probable major bariers to gene flow. 243. Means of body size, Tables 45 and 50. 244. Means of numbers of discal setae on left elytron, Tables 46 and 51.



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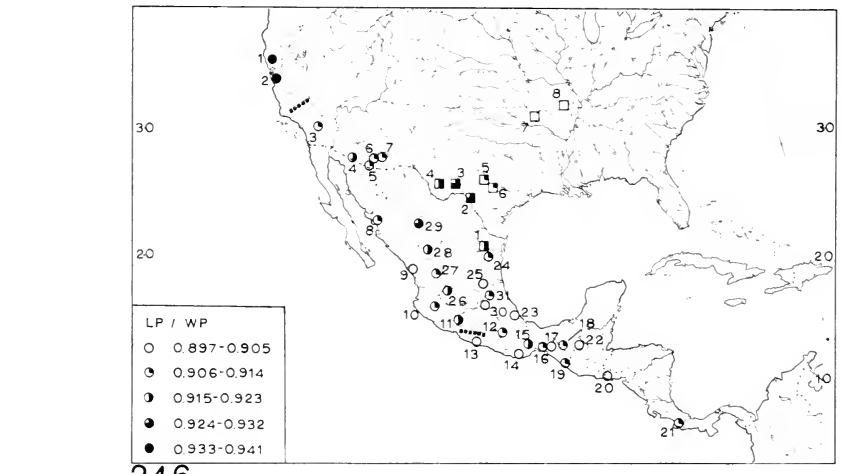

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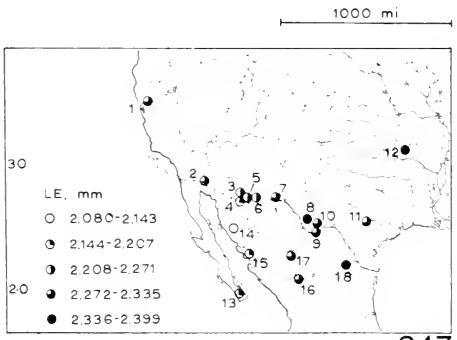

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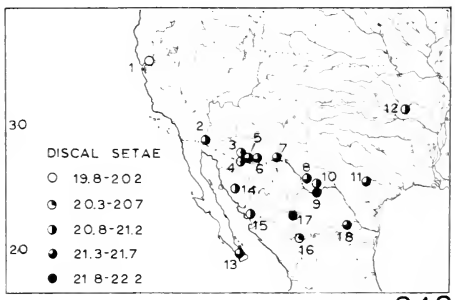

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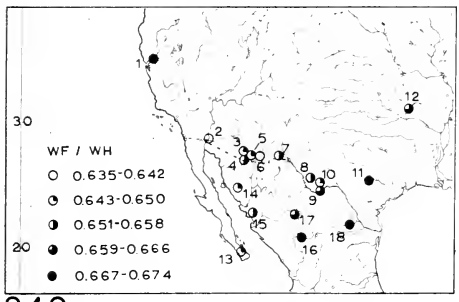
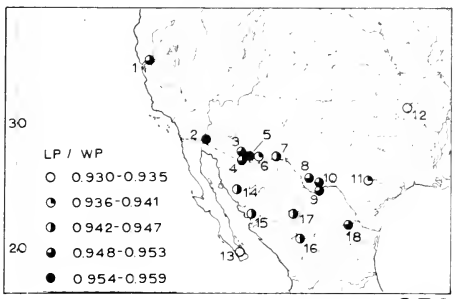
Fig. 245-246. Geographic variation in *S. pygmaeus* Van Dyke, circles, and *S. scopaeus* new species, squares; broken lines indicate probable major barriers to gene flow. 245. Means of relative eye size, Tables 47 and 52. 246. Means of pronotal form, Tables 48 and 53. Fig. 247-248. Geographic variation in *S. ochthocephalus* new species, Sample 1, and *S. falli* new species, Samples 2-18. 247. Means of body size, Table 55. 248. Means of numbers of discal setae on left elytron, Table 56.





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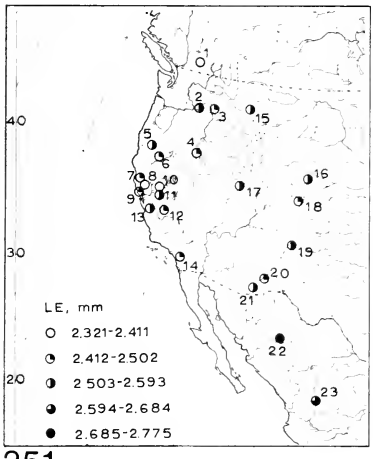
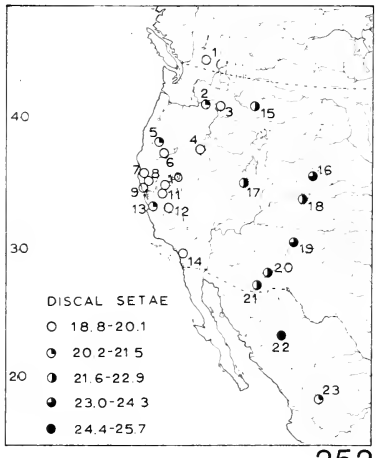
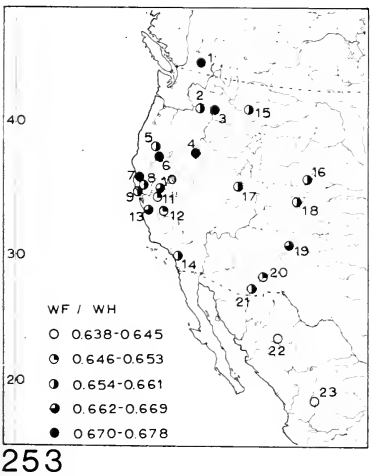






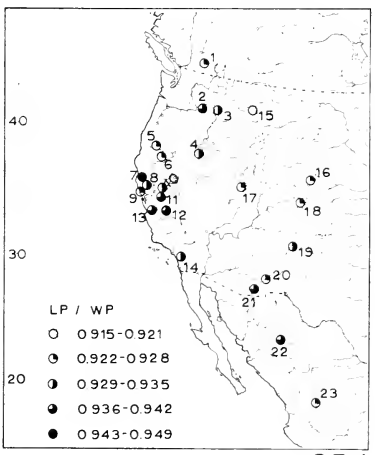


Fig. 249-250. Geographic variation in *S. ochthocephalus* new species, Sample 1, and *S. falli* new species, Samples 2-18. 249. Means of relative eye size, Table 57. 250. Means of pronotal form, Table 58. Fig. 251-254. Geographic variation in *S. depressus* LeConte. 251. Means of body size, Table 61. 252. Means of numbers of discal setae on left elytron, Table 62. 253. Means of relative eye size, Table 63. 254. Means of pronotal form, Table 64.

PHYLOGENY

Introduction

A taxonomic study normally includes aids for identification of specimens, and organizes information for storage and retrieval. I believe it should do much more than this. It should be based on evolutionary theory, and thus furnish sufficient background to predict relationships or similarities in characteristics not yet studied, and to make whatever critical comparisons are needed to test those predictions. Therefore, phylogenetic and biogeographic analyses are important adjuncts to taxonomic work.

I here give a general summary of my philosophical and procedural approaches, which derive from a blending of patristic, cladistic, and even some phenetic philosophies and procedures. I do not claim originality for ideas aired in this section. All have at least been touched upon, and most have been explored in detail, by one or more of the following: Blackwelder (1962); Brundin (1966); Crowson (1970); Darlington (1970); Ehrlich and Raven (1969); Hennig (1966); Hull (1964, 1970); Mayr (1969); Sokal and Crovello (1970); and Tuomikoski (1967). See also Darlington (1971) for an able review of "modern taxonomy, reality, and usefulness". The following discussion amplifies those of my ideas about phylogeny that do not completely agree with those of Darlington and Mayr, with whom I am in closest general agreement; it closes with a series of examples, some from the literature and some from my own work.

Classification, phylogeny, and zoogeography

The evolutionary history of a taxon relates closely to its past and present distribution patterns and to environmental factors responsible for those patterns. Thus, to classify taxa in accordance both with evolutionary theory and with all of the facts known about the organisms, one must determine probable evolutionary pathways and correlate these with probable historical zoogeography. The phylogeny, zoogeography, and classification of a group must be compatible with one another, and a classification is therefore likely to be most useful if completed after a careful consideration of phylogenetic and zoogeographic evidence.

Discussions on phylogeny and zoogeography provide indications of the taxonomist's logic, and may even suggest compatibility tests for evaluating the integrity of his work. Without these discussions, only experience permits users to evaluate a taxonomic work. Thus, the user is entitled not only to know something about the taxonomist's philosophical and procedural approaches, but also to know where compatibility tests may most appropriately be made. In this study of *Schizogenius* I did my best to ensure compatibility. Phylogeny was a major consideration in developing the entire classification, and my original classification was modified repeatedly until all incompatibilities obvious to me were eliminated. Zoogeography was considered in working out relationships at the species level, and among many of the species groups. Relationships among the *truquii, lineolatus, longipennis, depressus, brevisetosus, pluripunctatus, sallei, tristriatus, capitalis, lindrothi, darlingtoni, ocellatus,* and *quadripunctatus* groups were analyzed with zoogeographic considerations in mind. But relationships of all other species groups to these groups and to one another were analyzed independently of zoogeographic considerations, so the user may, if he so desires, test for compatibility between zoogeography and phylogeny among these groups. I give examples of compatibility between phylogeny and zoogeography in the carabid genus *Evarthrus* and the carabid division Brachinida, and an example of noncompatibility in the milliped genus *Cleptoria.*

Phylogenetic methods

In general, my methods for reconstructing a phylogeny conform with Hennig's (1966) holomorphological and chorological methods. No data are available to permit use of paleontological and parasitological methods, so these require no further discussion here. Hennig's principles for working out phylogenetic relationships may be summarized as follows: recognize and define a monophyletic group; determine its sister group; and repeat these processes until the phylogeny of a group is completely reconstructed. I apply these principles by using four closely related procedures. I first develop from morphological data a probable phylogeny which best fits these data. Then I compare this phylogeny with chorological data, and modify as required. From the modified phylogeny, I estimate the most probable morphological and chorological characteristics of the common ancestors of sister groups, and if necessary modify the phylogeny accordingly. Finally, the revised phylogeny is correlated with major paleogeological events, and again revised if necessary.

In general, the simplest system for explanation of all available morphological and chorological data is the system of choice. I believe further that a phylogeny should be reconstructed as completely as possible, so long as sufficient data are available and so long as these data are not to be overruled by rigid *a priori* decisions. Darlington (1970) rightly criticizes Brundin (1966) for gross oversimplifications in interpretation of certain of Hennig's (1966) phylogenetic and zoogeographic procedures and interpretations. But I think cladistic methods are useful as analytical tools, at least to develop broad generalizations.

Monophyly, paraphyly, and polyphyly. – According to Darlington (1970), "the central thesis of cladism is that taxonomic categories [i.e., taxa] must be monophyletic in a special, rigid sense, and that their rank must be determined by time of origin rather than by degree of difference or extent of diversification." Tuomikoski (1967), who otherwise basically agrees with Hennig (1966) and Brundin (1966), suggests that paraphyletic taxa may be acceptable under certain conditions. I (1966b) treated the genus *Halocoryza* as a paraphyletic taxon in disregard of the sister group rule, the rule of monophyly, and the rule of ranking by time of origin. This was done to account for the relative divergence of *Schizogenius* from New World *Halocoryza*; all species of *Halocoryza* are more similar to one another than to any species of *Schizogenius* in known characteristics, and probably also in characteristics not yet studied. This is consistent with my premise that a classification should be based on hypotheses about patristic relationships, rather than cladistic relationships alone. My treatment of the genera *Halocoryza* and *Schizogenius* parallels classifications in which birds are segregated from crocodiles and other reptiles (Darlington, 1970; Hennig, 1966).

Taxa are not always monophyletic in the "special, rigid sense" of Hennig (1966), Brundin (1966), and Tuomikoski (1967). This is clear in botanical diploid-tetraploid systems in which progeny are reproductively isolated from their parents. If tetraploidy may appear once, then it may reappear; obviously, the parent species is then paraphyletic, and the daughter species is polyphyletic. Further, as suggested by Crowson (1970), the tetraploid progeny might in turn spontaneously produce diploid progeny, so that both the diploid and the tetraploid forms are at once paraphyletic and polyphyletic. It is not my intention here to discuss plant speciation, but Crowson does suggest that diploid-tetraploid shifts may have also played some part in animal evolution. If so, and if such diploid-tetraploid pairs are accepted as biological species, then it follows that strictly monophyletic species are not always definable; Hennig's techniques provide no practical way to distinguish stem species from daughter species in such systems.

That the stem species concept, a theoretical element of the cladist's phylogenetic system, should not be confused with the biological species concept is clear. Indeed, the very point of the stem species concept is to make a monophyletic definition of extant biological species

possible. But, as in diploid-tetraploid sister species, the concept fails in practice. And an even more radical departure from the pattern of a stem species resolved into two monophyletic daughter species results when two parent species hybridize successfully to produce an unquestionably polyphyletic hybrid species (Hull, 1964).

What really is wrong with the stem species as a rigid concept, and with the concept of rigidly monophyletic taxa, however, is to be found where species differentiation is gradual, as it must ordinarily be. If geographic isolation develops such that each isolate initially includes two or more populations, those populations of each isolate that once shared the most gene flow are genetically most closely related to one another. If species differentiation follows, daughter species are paraphyletic; and evidence of paraphyletic relationships may remain for some time after completion of reproductive isolation. If geographic isolation results from establishment of a founder population, the parental isolate is paraphyletic because initially some individuals or populations are genetically more closely related to the founder than are other individuals or populations. And if limited gene flow continues in one or both directions even while species differentiation takes place, one or both isolates are polyphyletic in the early stages of species differentiation. Thus, strict monophyly cannot be required of species level taxa, since paraphyly and even polyphyly may be inherent in their evolutionary histories. And if this is so, then by logical extension absolute requirement of strict monophyly even for taxa of higher categories may be voided.

I do not accept as species taxa geographic isolates which are evidently paraphyletic, as judged from character clines, and probably would not do so even if these geographic isolates were known to be reproductively isolated. For instance, in *Schizogenius tibialis*, I suspect that the Indian Creek Cave form is reproductively isolated from its geographically nearest neighbors; but it is more similar and doubtless more closely related genetically to them than to any geographically more distant populations of that species. I look for evidence of propinquity of ancestry at the population level, and, if I find such evidence, I regard the forms in question as conspecific. At some indeterminate time after reproductive isolation is achieved, such evidence of propinquity of ancestry should disappear; I would then treat the forms in question as distinct species, or, where genetic relationships are in doubt, as subspecies. This propinquity of ancestry criterion depends on whether paraphyly remains evident, or whether such evidence is lost. Thus, at species level, I in fact approach the rigidly monophyletic taxa required by Hennig. But having decided that there is no theoretical basis for rigidly monophyletic taxa, I do not insist that higher taxa always be monophyletic, though I think such a criterion is normally desirable.

The important point here is not whether or not taxa should be rigidly monophyletic. The real question is how to devise classifications and reconstructed phylogenies that best show relationships and best suggest hypotheses to be tested by other workers. If they are intended to have maximum heuristic value, their construction cannot be rigidly bound by any concepts other than evolutionary theory. The simplest possible models should be used initially, but should freely be modified for particular situations as complexities in these situations become evident. I accept cladistic concepts as working models, but do not insist that all situations fit a model in all ways. My views on this subject are analogous to my use of the biological species concept as a model.

Secondary cladistic concepts. – Three of Darlington's (1970) criticisms of Hennig's (1966) and Brundin's (1966) methodologies are: that there is no fundamental reason why species should invariably split in a simple, dichotomous fashion; that phylogenies need not be strictly dichotomous; and that rates of evolution and divergence need be neither constant nor the same for different groups. If the range of a species is divided into three or more approximately equal parts by the same or related phenomena, and if rates of

evolution and divergence are constant, then reproductive isolation must develop at nearly equal rates in all geographic isolates. If speciation results from a gradual process, there should be no clearly definable branching points. And if these isolates form a pattern in which the intermediate isolate has undergone the least amount of evident evolutionary change, then it might be difficult or even impossible to determine sister species relationships even if their phylogeny truly was dichotomous. Nevertheless, it may still be possible to realistically simplify most such situations, and, as I prefer a dichotomous system I attempt to do so; an example is given for the species taxa *S. planulatus, S. ozarkensis,* and *S. planuloides.*

That rates of evolutionary change and divergence are neither always constant nor the same in all groups is well known. But, at least for balanced continental faunas, I think it worthwhile to assume an average rate of speciation in the group studied, because on that basis its phylogeny can be tested against known paleogeological events. This assumption, in other words, makes available an analytical method for testing a reconstructed phylogeny for compatibility with historical zoogeography. Some correlated assumptions are the following. Changes in evolutionary rates imposed by gradual environmental change are negligible. In a major taxon whose phylogeny has been worked out, at least one major lineage is sufficiently diverse and complete that extinction patterns may be disregarded. And apparent large gaps between related genus-group taxa are associated with rapid rates of evolutionary change and divergence resulting from exploitation of new habitats and resulting major new adaptations. Analytical methods required to test a reconstructed phylogeny for compatibility with historical zoogeography are the following. The average time required for speciation is determined from what is known about living species taxa of the group in question, and from probable historical factors involved in their evolution. In the phylogeny to be tested, this average time is treated as equal to the time between successive dichotomies in the lineage with the maximum number of known dichotomies. The age of any desired common ancestry is thus the maximum number of dichotomies between that ancestry and the present, multiplied by the average time span required for speciation. These assumptions and methods are generalizations, and perhaps even gross oversimplifications, but the interesting point is that where I have tested them they seem to work. Examples are given for the carabid division Brachinida and the carabid genus *Evarthrus*. I used these techniques to help place such species taxa as *S. arimao* in both classification and reconstructed phylogeny, whenever morphological data suggested two or more equally plausible evolutionary pathways.

Phylogeny, classification, and the biological species

Various relationships among phylogeny, classification, and biological species were discussed by Hull (1970). I here summarize my views about relationships and compatibilities among these, with particular emphasis on the biological species concept as a unifying model of great evolutionary importance. I also discuss how I apply the biological species concept in certain situations in which reproductive relationships are discordant with suspected phylogenetic relationships, and explain my rationale for interpreting these situations. In this discussion, I start from Hull's (1970) restricted definition of "classification," Hennig's (1966) definition of "phylogenetic relationships," and Mayr's (1969) definition of "species".

A concise statement of my interpretation of relationships among phylogeny, classification, and biological species is the following. Organisms are classified into taxa, each of which is based on the hypothesis that included organisms are more closely related to one another than to excluded organisms, at least at any one time. A reconstructed phylogeny is based on hypotheses about how taxa are related to one another. In this system, the species is not a necessarily fundamental evolutionary unit; but the classification and reconstructed phylogeny are unified by the biological species concept, which consequently is a fundamental

evolutionary model.

Compatibility of patristic classification and reconstructed phylogeny. – I prefer patristic classifications over cladistic classifications, because the cladistic relationships implied in the latter may be adequately expressed in a reconstructed phylogeny. Inherent in a patristic classification is the hypothesis that extant elements of a taxon share closer patristic relationships with one another than with extant elements of excluded taxa. A reconstructed phylogeny, on the other hand, must reflect evolutionary history, and is based on hypotheses about cladistic relationships between taxa. The patristic classification and the reconstructed phylogeny are therefore statements based on different sets of hypotheses. For heuristic purposes, however, they are interdependent, and must therefore be compatible with one another.

Compatibility between an evolutionary classification and a reconstructed phylogeny is achieved if units of at least one level are common to both. Taxa of species rank are such units. Higher taxa in an evolutionary classification may not be compatible with the reconstructed phylogeny, and units below species rank do not normally appear in the reconstructed phylogeny. Taxa of species rank are the units best suited to insure compatibility between the evolutionary classification and the reconstructed phylogeny for the following additional reasons.

Hennig (1966) discussed differences between ontogenetic, tokogenetic, and phylogenetic relationships, which apply respectively to semophoronts, individuals, and reproductively isolated groups of individuals or populations. An evolutionary classification is possible because semophoronts, individuals, and populations cluster to form more or less discrete groups which are linked by phylogenetic relationships. Semophoronts, individuals, and populations that share ontogenetic and tokogenetic relationships are conspecific, but these relationships are not sufficient to define a species. Ontogenetic and tokogenetic relationships between geographic isolates are replaced by phylogenetic relationships, but are renewed if gene exchange occurs before reproductive isolation is achieved. This potential instability of phylogenetic relationships is sufficient reason for units of compatibility between an evolutionary classification and a reconstructed phylogeny to be taxa of at least species rank.

A species is a unit of classification based on known or hypothetical relationships among included semophoronts, individuals, and populations; these relationships are interpreted in terms of a model, the biological species concept. Since only for taxa of species rank is there such a model, species level taxa are better suited as units of compatibility between an evolutionary classification and a reconstructed phylogeny than are taxa of higher rank. Thus, species have the important function of unifying facts, hypotheses, and theories, and this is why I consider the biological species concept as a fundamental evolutionary model.

Some problems in applying the biological species concept. – Semophoronts and individuals may be classified (Blackwelder, 1962; Hennig, 1966), but since they are characterized by having ontogenetic or tokogenetic relationships they do not evolve independently from one another and therefore are not fundamental evolutionary units. Some authors believe that species are the real units of evolution (Mayr, 1969). Others (see Hull, 1970) suggest that species are not fundamental evolutionary units, and that populations may be such units (Ehrlich and Raven, 1969; Sokal and Crovello, 1970). Their basic arguments are that selection is the prime factor in evolution and that gene flow normally is negligible. But how can one explain patterns of continuous or nearly continuous geographic variation if gene flow is negligible? One might argue that similarities between geographically proximate populations result exclusively from similar selective regimes. But such an argument is superficial; it does not explain, for example, the circular pattern of variation in relative eye size in *S. tibialis* (Fig. 188). I think that all character clines in *Schizogenius* species studied by me indicate genetic relationships between at least some geographically proximate population

samples, and that these genetic relationships result from relatively recent gene flow. However, though populations must interact with some frequency if there are non-random patterns of geographic variation, they must be sufficiently independent of one another for selection to act to produce this variation. Except in such species that include only one population, species normally are not really fully integrated evolutionary units since included populations are independent of one another to varied degrees.

A problem raised by the notion that species are not necessarily fundamental evolutionary units is that reproductive relationships may not be concordant with suspected phylogenetic relationships. This problem arises as a consequence of loss of tokogenetic relationships between populations or groups of populations (i.e., geographic isolation) before reproductive isolation is attained. These populations or groups of populations have phylogenetic relationships, but according to the biological species concept they are conspecific. If the evolutionary classification and reconstructed phylogeny are to have maximum heuristic value, interpretations of discordant reproductive and phylogenetic relationships must be flexible and must be made at the population level. That some species taxa may not perfectly fit the biological species concept does not diminish the importance or validity of that model. Data compared with a model either fit it or fail to fit it, and models in biology are not exceptionless; why would they be, when life itself has no rigorous, universally accepted definition? Indeed, from evolutionary theory the existence of exceptions is to be predicted. The biological species concept is a good model because most data do fit it, and its importance is that it provides a reasonably consistent basis for species recognition.

Reproductive isolation is a criterion for defining species in terms of discrete evolutionary potential. However, before reproductive isolation is attained, isolates may have a marked evolutionary potential even if that potential is not discrete. An example is found in the taxa *S. pygmaeus* and *S. scopaeus*. Alternatively, if possible reproductive isolates retain evidence of paraphyletic relationships, their evolutionary potential, though discrete, may be of relatively recent origin, and may be limited. An example of this alternative is the taxon *S. tibialis*. I base species taxa on hypotheses about past or present genetic relationships between populations in addition to known or suspected relationships among semophoronts and individuals. Recognition of these taxa depends on evidence about how or perhaps whether populations most probably interact or have interacted with one another. Thus, some species taxa in *Schizogenius* such as *S. tibialis*, *S. pygmaeus*, and *S. scopaeus* do not, or may not, exactly fit the biological species concept. But even if they are not fundamental evolutionary units, these taxa seem more consistent with the differing hypotheses on which I define species, base classifications, and reconstruct phylogenies than they would if redefined in terms of discrete evolutionary potential. I think they should be reclassified if, and only if, underlying hypotheses fail, regardless of additional data on reproductive isolation.

Some examples of phylogenetic analyses

In this section I illustrate with examples, some from the literature and some from my study of *Schizogenius*, certain points raised in preceding sections. These examples are keyed to the pertinent section of discussion. A further reason for including these examples is to give the reader insight into details of my phylogenetic methods. Not all of the *Schizogenius* phylogeny is discussed in detail, but these examples are representative of my methods throughout.

Compatibility of phylogeny and zoogeography. – The examples given here, both from the literature, are chosen to show how compatibility tests between phylogeny and zoogeography can be made. To test techniques outlined above, I examined the phylogeny and historical zoogeography proposed for *Brachinus* (Erwin, 1970) and *Evarthrus* (Ball and

Freitag, *in* Freitag, 1969). For various reasons, the average time required for speciation in the genus *Schizogenius* is considered to be approximately 3,000,000 years. The *Brachinus* and *Evarthrus* examples were selected to find if this time span might be common among North American carabid beetles.

Erwin's proposed phylogeny suggests a maximum of 23 dichotomies to reach the common ancestor of American *Neobrachinus* species. The true number, as determined from known species taxa, may be somewhat less, since Erwin's data suggest that the following taxa form monophyletic groups: *B. oaxacensis, B. patruelis,* and *B. conformis*; *B. ovipennis* and *B. medius*; and *B. tenuicollis* and *B. cyanipennis*. This would reduce the required minimum number of dichotomies to 19. If the 3,000,000 year time span is correct, ancestral *Neobrachinus* entered North America some 57,000,000 to 69,000,000 years ago. This fits Erwin's hypothesis that entry into North America occured at some time before Eocene, probably during Paleocene some 58,000,000 to 63,000,000 years ago. Erwin further suggested that the primitive ancestor of the bombardier beetles of the Division Brachinida evolved in Middle to Late Cretaceous. His phylogeny indicates a minimum of seven and a maximum of ten additional dichotomies to reach back to this brachinine ancestor. At 3,000,000 years per dichotomy, this ancestor evolved between 78,000,000 and 99,000,000 years ago, a period well within Erwin's suggested limits. The only fault I found with Erwin's work is that his phylogeny is incompletely reconstructed. It is sufficiently complete, however, that it can be tested for compatibility and correlation with the zoogeography, and I find that there is indeed a strong, positive correlation. I therefore suggest that Erwin's work may be used with confidence, for heuristic purposes.

There are limits to the applicability of these procedures. Ball and Freitag suggest that the ancestor of the pterostichine genus *Evarthrus* entered North America via the Behring land bridge in Early Tertiary. No dating of this early event by my techniques is possible from the *Evarthrus* phylogeny, because all western lineages, if there were any, have become extinct. Whether this dating can be done from examination of the phylogeny of the Old World sister group cannot be judged until such a phylogeny is reconstructed. However, suggestions about subsequent events can be tested and dated according to the suggested *Evarthrus* phylogeny. Members of the genus spread across temperate Arcto-Tertiary forests in the north, but in Middle Tertiary receded eastward as did those forests. The common ancestor of living *Evarthrus* species evolved after this eastward recession. Depending on how the peculiar taxa *E. gravesi* and *E. hypherpiformis* fit the phylogeny, there may be as few as nine to as many as eleven dichotomies needed to reach that common ancestor. Its age thus falls between 27,000,000 and 33,000,000 years, which corresponds to Oligocene, or Middle Tertiary, in support of Ball and Freitag's ideas. Moreover, members of only the *substriatus* and *torvus* groups extend much westward of southeastern forested regions. Just four dichotomies are required to reach their common ancestor, which may still have been a component of the eastern forest fauna; the timing is about 12,000,000 years ago, in Early Pliocene. This supports Ball and Freitag's idea that Gulf Coast grassland habitats were not entered by *Evarthrus* species before post-Miocene time, because if they were the genus should today be represented in northeastern Mexico. My conclusions are that Ball and Freitag's phylogenetic and zoogeographic analyses are compatible, and so probably correct, and that therefore their work may confidently be used for heuristic purposes.

The data required for these compatibility tests are the authors' suggested phylogenies and suggested timings for zoogeographic events. For both Brachinida and *Evarthrus*, compatibilities were found at two different points in time. General conclusions from these analyses are that for each the phylogeny and zoogeography are compatible, and that both of these taxonomic works are therefore probably highly reliable. The taxonomy must have

been carefully done and well thought out for these compatibilities to be evident. An additional conclusion is that the 3,000,000 year time span between dichotomies may be a useful generalization for North American Carabidae, although in *Evarthrus* this time span may be somewhat shorter as my datings are at upper limits of acceptability.

Incompatibility of taxonomy, phylogeny, and zoogeography. – Hoffman (1967), in his review of the milliped genus *Cleptoria*, proposed aesthetically pleasing phylogenetic and zoogeographic patterns but gave no indication about timing. Thus, my test for compatibility between phylogeny and zoogeography, illustrated above for *Evarthrus* and *Brachinus*, is inapplicable. A user interested in studying relationships between species must assess the reliability of the taxonomy, phylogeny, and zoogeography by other means, if given no firm basis to believe the phylogeny and zoogeography have good heuristic value. Without personal experience with the organisms, the only way he can judge the soundess of their taxonomy is to carefully read and compare all descriptive material, including information about geographic variation. Based on his conclusions about taxonomy, he must then decide for himself about phylogeny and zoogeography.

Hoffman's data indicate that all five species taxa included in *Cleptoria*, except perhaps *C. rileyi* and *C. bipraesidens*, have long been reproductively isolated. These data also support his ideas that the taxon *C. divergens* is the most primitive in the genus, and that the origin of the genus was in the southern Appalachians. But, though I think the taxonomy is sound, I think Hoffman's explanation of the phylogeny and zoogeography (Fig. 259) in *Cleptoria* is improbable. He suggests that the five allopatric species taxa evolved in a "hop-scotch" pattern, from the southern Appalachians southward into the piedmont region. Such a pattern would probably be comparatively recent in development, and some evidence of gene flow patterns should remain; I would expect to find evidence of paraphyletic relationships, as discussed for *Schizogenius tibialis* later in this section. However, no gene flow patterns are evident between species taxa in *Cleptoria*. I think an orderly "hop-scotch" pattern is unlikely, if species taxa really are reproductive isolates, since if isolates are so readily founded they should also be susceptible to replacement or displacement by subsequent founders. The pattern suggests much greater vagility than is reflected in known facts of distribution and morphology. An essentially linear sequence among reproductive isolates would more probably result from a "taxon cycle" system of displacement (Wilson, 1961); but then the taxon *C. divergens* should be the most apomorphic of the genus, not the most plesiomorphic.

A review of Hoffman's data suggests that a more plausible system of evolutionary pathways in the milliped genus *Cleptoria* (Fig. 260) is the following. The first dichotomy in the phylogeny of *Cleptoria* was a split of a piedmont form, with telopodite shortened and thickened and gonopods not interlocked, from the more conservative montane *C. divergens*. The piedmont form developed isolates north and south of the Savannah River, with the peculiarly specialized *C. abbotti* representing the latter. A subsequent extension by the northern isolate southward across the Savannah River resulted in the separation of the northern *C. macra* from the southern ancestor of *C. rileyi* and *C. bipraesidens*, which lost the prefemoral process. These forms diverged somewhere near their present ranges, and displaced *C. abbotti* from the western part of its range. I thus do not think that *C. abbotti* is closest to *C. rileyi*, and in fact suspect that *C. macra* is closer to *C. rileyi* and *C. bipraesidens* than is *C. abbotti*. Support for these suggestions is evident in Hoffman's diagrams of the process of sternum three, which show *C. rileyi* and *C. macra* as intermediate between *C. divergens* and *C. abbotti*; I doubt that this similarity is a coincidence. Thus, though I have not personally studied specimens of *Cleptoria*, my reinterpretations from Hoffman's data seem to explain evolutionary pathways at least as well as do Hoffman's interpretations.

When phylogenetic and zoogeographic analyses are published, they should allow a user to verify for himself the probable correctness of suggested relationships. If an author's own interpretations are compatible with morphological and chorological data, no reinterpretations should be needed. But the heuristic value of an author's interpretations are suspect is his published data suggest more plausible interpretations.

Phylogeny: dichotomous or trichotomous? – The taxa *Schizogenius planulatus, S. ozarkensis*, and *S. planuloides* have ranges now separated by the Mississippi and Red Rivers (Fig. 189). Perhaps these rivers were at one time not effective barriers, but became so because of some major change in climate which increased water loads and thus eliminated suitable habitats by deposition of silt or mud. The three isolates evolved independently, and male genitalia became more specialized in *S. planulatus* (Fig. 175) and *S. planuloides* (Fig. 177) than in the geographically intermediate *S. ozarkensis* (Fig. 176). This sequence of events suggests a trichotomous phylogeny. But other zoogeographic factors suggest that a dichotomous phylogeny is more probable.

The Mississippi River, near its confluence with the Ohio River, should pose no major barrier to these organisms, since limestone uplands in southern Illinois nearly link those of western Kentucky and eastern Missouri. Drainage systems from uplands of this entire region should provide suitable habitats for members of this complex. Indeed, there may be extant populations of one or both of *S. planulatus* and *S. ozarkensis* in southern Illinois. Further, these species range primarily in regions of deciduous forests and may therefore be adapted to cooler conditions than is *S. planuloides*, a species of warmer, more arid regions. I think the ancestor of these taxa evolved in subtropical Texas or northeastern Mexico, since that is the region of greatest diversity among their relatives. The first dichotomy in their phylogeny followed establishment of a northern isolate, which became cool adapted and spread across temperate forested areas in the Ozark and Appalachian regions. Meanwhile, the male genitalia of the southern isolate evolved its specialized characteristics. The second dichotomy developed when Early Pleistocene climatic deterioration caused the northern isolate to subdivide into isolates restricted to the southern Ozark and southern Appalachian regions. Then the Appalachian isolate diverged in characteristics of the male genitalia from the more conservative Ozark isolate. Following retreating Pleistocene glaciations, the ranges of Ozark and Appalachian isolates expanded northward, and may now approach or even overlap one another in the region near the confluence of the Mississippi and Ohio Rivers.

Problem species. – Some species of *Schizogenius* may not fit precisely the biological species concept. Examples are the taxa *S. tibialis, S. pygmaeus,* and *S. scopaeus*. Where evidence from geographic variation indicates relatively recent gene flow between geographically proximate populations, I regard them as conspecific. If no evidence of such gene flow between these populations exists, either directly or through some alternative geographic sequence, and if morphological and chorological evidence suggests reproductive isolation, then I recognize them as distinct species.

Lindsay and Vickery (1967) found from studies of *Mimulus* "a picture of the frequent emergence, change, and disappearance of distinctive populations with only the rare formation of one sufficiently distinct to be on its own evolutionary path." I suspect the same is true in *Schizogenius*.

In the taxon *S. tibialis* (Fig. 188), the Indian Cave Creek form may or may not be a reproductive isolate, but regardless shows evidence of past genetic continuity with geographically proximate populations to the south. It is restricted and peripheral in known distribution, is undoubtedly of comparatively recent origin, and probably has a low potential for survival. Suspected reproductive and phylogenetic relationships are discordant; if this form is recognized as a separate species because of reproductive isolation, the southern form is reduced to

an evidently paraphyletic taxon. I regard the Indian Cave Creek isolate as conspecific with other populations of *S. tibialis* because it is patristically more closely related to geographically proximate populations than to more distant ones. I do not here regard possible reproductive isolation as a useful criterion for species recognition, because though evolutionary potential may be discrete I do not think it is great. I would not recognize the Indian Cave Creek form as a distinct species even if known to be reproductively isolated, unless hypotheses about patristic relationships were found to fail. One such failure would be to find the two forms sympatric; the hypothesis of paraphyletic relationships would then be falsified.

In contrast, certain geographically distant populations of the taxa *S. pygmaeus* (Fig. 239) and *S. scopaeus* (Fig. 238) may well not be reproductively isolated from one another, but geographically proximate populations evidently are. These taxa, both of which are abundant and widespread, are sympatric in northeastern Mexico where they are doubtless reproductively isolated. No certain evidence of paraphyly remains between geographically proximate populations of these taxa, and the possible lack of reproductive isolation between certain distant populations is not a useful criterion for species recognition. These taxa, if marked by a lack of discrete evolutionary potential, seem nevertheless to have such evolutionary potential well developed, and probably have had it so developed much longer than have had the isolates of *S. tibialis*. Along the Rio Conchos and Rio Grande in Chihuahua, clinal continuity between *S. pygmaeus* and *S. scopaeus* is suggested in several statistical characteristics (Fig. 243-246) but not in structures of the male genitalia (Fig. 234). I would treat these taxa as conspecific only if unexpected evidence from a geographically intermediate sample showed my interpretation of differences in the male genitalia to be wrong.

Subgenera and species groups of *Schizogenius*

In this section I attempt to reconstruct the phylogeny of major lineages of the genus *Schizogenius*, using contrasting phyletic and phenetic methods. For purposes of this discussion, the *truquii, lineolatus, longipennis, depressus, brevisetosus, pluripunctatus, sallei,* and *tristriatus* groups are treated as a monophyletic group, the *truquii* lineage. The *capitalis, lindrothi, quadripunctatus, darlingtoni,* and *ocellatus* groups form another monophyletic group, the *capitalis* lineage. All other species groups are considered as separate lineages.

Relationships of the genus *Schizogenius* to other genera were discussed earlier, and in a separate paper (1966b). From those intergeneric comparisons, I judge that ancestral character states in the common ancestor of living *Schizogenius* species included the following: mandibles more or less arcuate laterally; lacinia setose along outer margin; mentum deeply emarginate at middle, median tooth distinct; gula less than 0.3 maximum width of mentum; antennal article two not plurisetose; eyes not bordered by dorsal carinae; frontal carinae not perfectly regular, parallel, equidistant, or equally raised; occiput punctate dorsally, extended laterad along posterior margin of eyes; hind leg with tarsus more than 0.6 length of tibia; paramedian carinae of sternum three strongly developed; and pygidium with well developed median longitudinal rows of files. Additional probable plesiomorphic character states, determined from intergeneric and infrageneric comparisons, are listed in Table 65. Character states so listed are designated or coded as apomorphic or plesiomorphic, based on what I think is primitive in a group or lineage (see Ball and Erwin, 1969). The apomorphic state of several characters arose in more than one lineage, but in this phylogeny none of the characters studied reverted to the plesiomorphic state except the elongate paronychia of the *arechavaletae-truquii-capitalis* and *strigicollis-elongatus-carinatus* lineages.

The genus is most diverse in South America, which I therefore think is the primary center of radiation. Penetration of North and Middle America over the water gap that separated this area from South America during Middle Tertiary is considered an apochoric zoogeo-

graphic characteristic. Ancestors of only the *crenulatus*, *ferrugineus*, and *truquii* lineages made these crossings. These zoogeographic data were not considered in reconstructing the phylogeny, but are not in conflict with it.

Phylogeny reconstructed by phyletic techniques. – The reconstructed phylogeny of major lineages of *Schizogenius* is shown in Fig. 255, and the principal data used are listed in Table 65; the time scale suggested is discussed in a later section. I here summarize principal features of this phylogeny, indicate its weaknesses and strengths, and note apomorphic character states thought to have arisen in more than one lineage. I am confident that all branching points are correctly positioned, and have indicated apomorphic character states for nearly all dichotomies. I think that each lineage is monophyletic, and that this phylogeny is most probably a correct representation of evolutionary relationships; this reconstructed phylogeny should therefore have strong heuristic value for predicting patristic relationships.

Ancestral *Schizogenius* differentiated into two stocks, the subgenera *Genioschizus* and *Schizogenius*. Apomorphic character states in ancestral *Genioschizus* included flared and pitted lateral channel of elytron, and reduced numbers of discal setae on elytron; the latter character state evolved independently in several lineages of *Schizogenius*. In ancestral *Schizogenius*, apomorphic conditions included shortened paronychia, and loss of paralateral pronotal sulci; the latter condition evolved independently in the *tenuis* group of *Genioschizus*.

Genioschizus differentiated into three known groups. This differentiation took place comparatively recently, as *Genioschizus* is far less diverse than is *Schizogenius*. Among known forms, the *crenulatus* group is the most distinctive. Its ancestor entered North America across a water gap between North and South America, and developed the apomorphic condition of truncated mentum lateral lobes. The ancestor of its sister group remained in South America, developed the apomorphic condition of elytral intervals carinate at apices, and differentiated into the *quinquesulcatus* and *tenuis* groups. An apomorphic condition of ancestral *tenuis* group was loss of paralateral pronotal sulci, an apomorphic condition also of ancestral subgenus *Schizogenius*. A weakness in my reconstructed phylogeny of *Genioschizus* is that I found no useful synapomorphic condition to characterize the *quinquesulcatus* group.

The first major dichotomy in the phylogeny of the subgenus *Schizogenius* reflects the differentiation of the *jacarensis-optimus* lineage from the remainder of the subgenus. The ancestor of its sister group had the apomorphic sharply engraved clypeal suture; this condition appeared also in some members of the *optimus* group. Numerous apomorphic features distinguished the ancestor of the *jacarensis-optimus* lineage, but among those indicated in Fig. 255 only the condition of elongate tarsi was not repeated elsewhere in the phylogeny of the genus. The *jacarensis-optimus* lineage subsequently differentiated into the *optimus* and monotypic *jacarensis* groups. Apomorphic features of the ancestor of the *optimus* group included apex of male median lobe abruptly bent, and bristles on terminal palpal articles longitudinally arranged.

The ancestor of the *ferrugineus* group entered Middle and North America where it lost the female paramedian ambulatory setae from sternum seven, but this loss was repeated later in the phylogeny of its sister group. Apomorphic conditions of the ancestor of that sister group were antennae filiform and female pygidial margin crenulate.

The ancestor of the South American *basalis* group differentiated from the ancestor of its sister group when the latter lost the female paramedian ambulatory setae from sternum seven. This apomorphic condition also characterized ancestors of the *jacarensis-optimus* and *ferrugineus* lineages. A weakness in this dichotomy is that I found no synapomorphic characteristic for the *basalis* group. In most members of the sister group the paronychia are elongate as in subgenus *Genioschizus*.

Table 65. Characters and character states used in phyletic analysis of phylogeny of major lineages of *Schizogenius*.

Character	Character state	
	Plesiomorphic	Apomorphic
Head		
(1) Paramedian clypeal carinae:	tuberculate	not tuberculate
(2) Clypeal suture:	shallow	deep
(3) Occiput punctation:	uniform	reduced medially
(4) Antennae:	moniliform	filiform
(5) Arrangement of bristles on terminal palpal articles:	transverse	longitudinal
(6) Mentum lateral lobes:	produced	truncate
Pronotum		
(7) Paralateral sulci:	present	absent
(8) Paramedian sulci:	present	obsolete
(9) Paralateral carinae:	absent	present
(10) Hind angles:	rounded	prominent
Elytra		
(11) Apex of lateral channel:	not foveate	foveate
(12) Apices of intervals:	not carinate	carinate
(13) Setae of interval five:	normal	basal
(14) Setae of intervals three, five, and seven:	present	absent from interval seven (′) interval five (″) interval three (‴)
Legs		
(15) Male front tarsi:	narrow	dilated
(16) Hind tarsi:	short	long
(17) Paronychia:	long	(′) short (″) long
Abdomen		
(18) Sternal carinae:	straight	rounded at apices
(19) Patch of microsculpture in coxal area of sternum three:	present	absent
(20) Female anal ambulatory setae:	present	absent
(21) Female pygidium apex:	entire	crenulate
(22) Basal collar spines of internal sac of male median lobe:	indistinct	distinct

The *strigicollis-elongatus-carinatus* lineage developed the apomorphic condition of strongly developed paralateral pronotal carinae, while the *arechavaletae-truquii-capitalis* lineage had as apomorphic the curved apices of paramedian carinae of sternum three. Some members of the *truquii* lineage have weakly developed paralateral pronotal carinae, obviously an independent apomorphy. Members of the *strigicollis* lineage have accessory setae on submentum, while members of the *elongatus-carinatus* lineage lack discal setae on elytron. Members of *elongatus* lineage have shortened paramedian pronotal sulci, while members of *carinatus* lineage have carinate elytral intervals. Loss of discal setae and reduced pronotal sulci are also characteristic of some members of the *optimus* lineage, and in the *quinquesulcatus-tenuis* lineage of subgenus *Genioschizus* the apices of elytral intervals are carinate.

The ancestor of the *arechavaletae* lineage lost discal setae from the apical half of interval seven, and in the ancestor of the *truquii-capitalis* lineage the paramedian clypeal carinae extended to median clypeal tooth. The ancestor of the *capitalis* lineage lost discal setae from interval seven. A weakness of this dichotomy is that I found no synapomorphic morphological characteristic of the *truquii* lineage. But zoogeographic evidence supports this dichotomy; the ancestor of the *truquii* lineage entered Middle and North America, while the ancestor of the *capitalis* lineage remained in South America. Loss of discal setae from interval seven occurred in ancestors of five lineages: *Genioschizus, jacarensis-optimus, elongatus-carinatus, arechavaletae,* and *capitalis*. Discal setae were lost completely in ancestors of the *jacarensis-optimus* and *elongatus-carinatus* lineages, and in some derived members of *Genioschizus* and the *capitalis* lineage. In the ancestor of *Genioschizus*, setae of interval five were restricted to the base, while in the ancestor of the *arechavaletae* group they were distributed in the basal half. Some members of the *strigicollis-elongatus-carinatus* lineage have the paramedian clypeal carinae weakly extended to median tooth, but this condition is apparently unstable; in the *truquii-capitalis* lineage the condition is synapomorphic, stable, and well developed.

Evident weaknesses in this reconstructed phylogeny concern the relative positions of the *Genioschizus* and *jacarensis-optimus* lineages, and the *ferrugineus* and *basalis* lineages. Justifications for my interpretations are given below. Otherwise, the reconstructed phylogeny appears sound, and requires no further discussion.

On first examination, it is difficult to decide whether the *crenulatus-quinquesulcatus-tenuis (Genioschizus)* lineage or the *jacarensis-optimus* lineage was the first to differentiate from the rest of the genus. Members of the former are plesiomorphic in most characteristics, and thus appear to be the most primitive element of *Schizogenius*. Members of the *jacarensis-optimus* lineage have in combination numerous apomorphic characteristics, and thus appear more strongly differentiated than do members of the *Genioschizus* lineage. My interpretation is based on the following observations. In the *Genioschizus* lineage the apomorphic characteristics of the lateral channel form a complex not found in other carabid beetles. The one apomorphic characteristic of members of the *jacarensis-optimus* lineage that distinguishes them from other members of the genus, the elongate tibiae, seems a much less complex characteristic. These observations alone suggest that the *Genioschizus-Schizogenius* dichotomy is the most likely. An even more compelling reason, if the simplest system of evolutionary pathways is the most probable one, is that at least two extra evolutionary steps are needed if the *jacarensis-optimus* lineage is the first dichotomy. These are: paronychia shortened twice, not once; and paralateral pronotal sulci lost thrice, not twice. No evolutionary steps are saved if the *jacarensis-optimus* lineage is regarded as the sister group of the rest of the genus.

An extra evolutionary step is required if the apomorphic condition of lost female paramedian ambulatory setae evolved independently in the *ferrugineus* and *strigicollis-truquii*

lineages, as well as in the *jacarensis-optimus* lineage. But the evolutionary significance of this character condition is uncertain, for the following reasons. Males of some species of the *optimus* group lack anal ambulatory setae. Occasional females of various species of the *truquii* and *capitalis* lineages have been found with one or even both of these setae. And females of *S. pluripunctatus* of the *truquii* lineage have regained both setae as a clearly apomorphic condition. Future genetic studies may show that some mechanism such as a suppressor gene controls the presence or absence of female ambulatory setae. If so, their loss was apomorphic in the ancestor of the subgenus, and they were regained in both the *basalis* group and in *S. pluripunctatus*. Otherwise, the relative positions of the *ferrugineus* and *basalis* lineages in this reconstructed phylogeny are the most parsimonious. The following apomorphies arose once rather than twice: antennae filiform; female pygidium crenulate; basal collar spines strongly developed; and male front tarsi markedly dilated. Of these apomorphic character states, the most stable is that of the antennae; all members of the *basalis-truquii* lineage have filiform antennae, though of variable length. The other three characters do not appear in the apomorphic condition in all members of the *basalis-truquii* lineage, but most probably were apomorphic in the ancestor of that lineage.

Whatever the phylogeny of the major groups of *Schizogenius* really was, many characteristics of external morphology are convergent. The reconstructed phylogeny proposed here is the most parsimonious, but even so at least the following conditions evolved more than once: apices of elytral intervals carinate, twice; paralateral pronotal sulci lost, twice; paramedian ambulatory setae lost from female sternum seven, three times; setae lost from elytral interval seven, five times; setae lost from apical half of interval five, twice; and setae entirely lost from interval five, twice. The apochoric zoogeographic characteristic, penetration of Middle and North America, happened three times. The paronychia shortened in the ancestor of subgenus *Schizogenius*, but became secondarily elongated in some of the more derived lineages.

Phylogeny reconstructed by phenetic techniques. – Some methods of numerical cladistics were proposed by Camin and Sokal (1965) for deducing phylogeny, one of which was satisfactorily tested for a group of tiger beetles by Willis (1971). Necessary assumptions are that character states are discrete and may be arranged sequentially from primitive to derived, and that while derived character states may have arisen repeatedly, none reverted to the ancestral condition. In the phylogeny of major groups of *Schizogenius* these assumptions appear valid, except that the paronychia are secondarily elongate in some members of the *strigicollis-elongatus-carinatus-arechavaletae-truquii-capitalis* lineage. I used this method to test the logic of my reconstructed phylogeny of major lineages; as a technique for determining the most parsimonious system of evolutionary pathways, it should produce the same result as my phyletic analysis. In the phylogeny of species, as in the *truquii* lineage, character states of many characters have evidently reverted to the ancestral condition, so that numerical cladistics, at least in their simple form (Willis, 1971), cannot be used.

Coded character states are given in Table 66, and fitted to a data matrix in Table 67 and a compatibility matrix in Table 68. The character state of any given character is the one regarded as ancestral in the operational taxonomic unit (OTU) concerned, irrespective of possible specializations in various derived members of that OTU. The secondarily elongate paronychia of some members of the *strigicollis-elongatus-carinatus-arechavaletae-truquii-capitalis* lineage are coded as short. Only those characteristics represented in the derived character state by two or more OTU's were used in this analysis, but additional, autapomorphous, characteristics were used to relate terminal elements in various lineages. If two or more characteristics produced the same cladogram pattern, they are combined and coded accordingly.

Table 66. Characters and coded character states used in phenetic analysis of phylogeny of major lineages of *Schizogenius*.

Character	Character state
(1) Elytral lateral channel:	0, not foveate; 1, foveate
(2) Apices of intervals:	0, not carinate; 1, carinate
(3) Elytral intervals with discal setae:	0, three, five, and seven; 1, three and five; 2, three; 3, none
(4) Setae on interval five:	0, normal or absent; 1, basal
(5) Antennae:	0, moniliform; 1, filiform; 2, long
(6) Male front tarsi + female pygidium apex + basal collar spines:	0, narrow + not crenulate + not developed; 3, dilated + crenulate + developed
(7) Paralateral pronotal sulci:	0, present; 1, absent
(8) Anal ambulatory setae:	0, males and females; 1, males only
(9) Clypeal suture:	0, shallow; 1 deep
(10) Hind tarsi + microsculpture patch in coxal area of sternum three:	0, short + present; 2, elongate + absent
(11) Paralateral pronotal carinae:	0, absent; 1, present
(12) Paramedian clypeal carinae + pronotal hind angles:	0, tuberculate + rounded; 2, not tuberculate + produced
(13) Paronychia:	0, long; 1, short
(14) Paramedian sternal carinae:	0, straight; 1, curved at apices

As seen in Table 68, cladogram patterns one, seven, and thirteen are the most parsimonious; each requires a minimum of four extra evolutionary steps. The first and third of these link all three species groups of *Genioschizus* as a clade, but the second excludes the *tenuis* group. Substudies revealed that pattern seven is less parsimonious than patterns one and thirteen, as in the completed phylogeny extra evolutionary steps are required to account for convergences in characteristics one, three, and four. In patterns one and thirteen, three OTU's cluster on one branch, and ten on the other. Substudies done for the major branch revealed that cladogram pattern ten is the most parsimonious, with two OTU's on one branch and eight on the other. In the final cladogram (Fig. 256), 33 evolutionary steps are needed, 12 more than the 21 minimum steps indicated in Table 67. This cladogram is the same as the reconstructed phylogeny suggested in Fig. 255, as expected, and I arbitrarily fitted it to the same time scale for ready comparison.

The *truquii* lineage

Relationships among species and species groups of the *truquii* lineage are obscured by the lack of evident and strongly developed synapomorphous characteristics. My reconstructed phylogeny (Fig. 257) is provisional, and needs to be tested in future studies by analysis of non-morphological characteristics, but it is supported by zoogeographic evidence. Morphological characteristics, including statistical characteristics obtained from Tables 8-64, are listed in Table 69.

Table 67. Data matrix for phenetic analysis of phylogeny of major lineages of *Schizogenius*.

Characters	OTU: major group or lineage														
	crenulatus group	*quinquesulcatus* group	*tenuis* group	*jacarensis* group	*optimus* group	*ferrugineus* group	*basalis* group	*strigicollis* group	*carinatus* group	*elongatus* group	*arechavaletae* group	*truquii* lineage	*capitalis* lineage	Character states (c)	Minimum steps (c-1)
(1)	1	1	1	0	0	0	0	0	0	0	0	0	0	2	1
(2)	0	1	1	0	0	0	0	0	1	0	0	0	0	2	1
(3)	1	1	1	2	2	0	0	0	3	3	1	0	1	4	3
(4)	1	1	1	0	0	0	0	0	0	0	1	0	0	2	1
(5)	0	0	0	0	0	0	1	2	2	1	1	2	2	3	2
(6)	0	0	0	0	0	0	3	3	3	3	3	3	3	4	3
(7)	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1
(8)	0	0	0	1	1	1	0	1	1	1	1	1	1	2	1
(9)	0	0	0	0	0	1	1	1	1	1	1	1	1	2	1
(10)	0	0	0	2	2	0	0	0	0	0	0	0	0	3	2
(11)	0	0	0	0	0	0	0	1	1	1	0	0	0	2	1
(12)	0	0	0	0	0	0	0	0	0	0	0	2	2	3	2
(13)	0	0	0	1	1	1	1	1	1	1	1	1	1	2	1
(14)	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1
															21

The *truquii* lineage includes eight species groups. Four of them, the *truquii, brevisetosus, sallei*, and *lineolatus* groups, are monobasic. The *pluripunctatus, tristriatus, longipennis*, and *depressus* groups all include several known species taxa. In the following discussion, I treat first the suspected relationships between groups, and then the suspected relationships within the larger groups.

Relationships of species groups. – The *truquii* group, the only group of the lineage not represented north of the Tropic of Cancer, includes one living species from central Mexico. I suspect the ancestor of the *truquii* group entered Pacific areas of southern Mexico, while the ancestor of its sister group penetrated Atlantic areas in northeastern Mexico. Specialized features of the *truquii* group include male front tarsus narrowed, female pygidial crenulations lost, and paramedian pronotal sulci extended nearly to anterior transverse impression. Loss of female pygidial crenulations was probably also ancestral in the *brevisetosus* and *pluripunctatus* groups, and in some species of the *depressus* group. This characteristic, and the narrowed male front tarsi, are secondary specializations convergent with ancestral conditions in the genus. A weakness of this dichotomy is the lack of an evident synapomorphous characteristic of the sister group. But the dichotomy is supported by distributional data,

Table 68. Compatibility matrix for phenetic analysis of phylogeny of major lineages of *Schizogenius*.

	Patterns														Compatibilities	Extra steps
	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
(1)	X	1	0	0	0	0	1	0	0	0	0	0	0	0	11	2
(2)	1	X	1	1	1	1	1	1	1	0	1	0	1	0	3	10
(3)	1	3	X	1	5	2	1	1	2	2	2	1	1	1	0	23
(4)	1	1	0	X	1	1	1	1	1	0	0	0	1	1	4	9
(5)	0	2	4	1	X	1	0	1	0	0	2	2	0	2	6	14
(6)	0	3	6	3	3	X	0	3	0	0	3	3	0	3	5	27
(7)	1	1	3	1	1	1	X	1	1	1	1	1	1	1	0	15
(8)	0	1	3	1	1	1	0	X	1	1	1	1	0	1	3	12
(9)	0	1	2	1	2	1	0	0	X	0	1	1	0	1	5	10
(10)	0	0	0	0	0	0	0	0	0	X	0	0	0	0	13	0
(11)	0	1	1	0	1	0	0	0	0	0	X	0	0	0	10	3
(12)	0	0	2	0	0	0	0	0	0	0	0	X	0	0	12	2
(13)	0	1	3	1	2	1	0	1	1	1	1	1	X	1	2	14
(14)	0	0	1	1	1	0	0	0	0	0	0	1	0	X	9	4
Compatibilities	9	3	3	4	3	6	9	6	7	9	5	5	9	5	83	—
Extra steps	4	15	26	11	18	8	4	9	7	5	12	11	4	11	—	145

and by the amount of phenetic difference between members of the *truquii* group and members of its sister group.

Relationships among the remaining seven species groups are unclear from morphological evidence, and my arrangement is suggested partly by geographic evidence and partly by the rule of parsimony. Probable sister groups are: *brevisetosus* and *pluripunctatus*, increased discal setae; *sallei* and *tristriatus*, abdominal microsculpture; and *longipennis* and *depressus*, reduced hind angles. Members of the *brevisetosus*, *sallei*, and *tristriatus* groups are largely confined to limestone regions, and their pale color may be an adaptation to that habitat. Their ancestor was a Texan vicariant of the Tamaulipan ancestor of the *lineolatus, longipennis,* and *depressus* groups. Ancestors of the *brevisetosus* and *pluripunctatus* groups were Texan-Sonoran vicariants, and ancestors of the *sallei* and *tristriatus* groups were Texan-Tamaulipan vicariants. If the ancestor of the *lineolatus* group was Texan, the ancestor of the *longipennis* and *depressus* groups was Tamaulipan, and in turn the ancestors of those two groups were tropical-Tamaulipan vicariants. These geographic relationships are expressed in

Table 69. Characters and character states in *truquii* lineage.

Character	Character state	
	Plesiomorphic	Apomorphic
General		
(1) Form (mean DP/LP):	0.80-0.84	(a) 0.75-0.79 (b) 0.85-0.89
(2) Size (mean LE, mm):	2.50-2.95	(a′) 2.21-2.49 (a″) under 2.21 (b) over 2.95
(3) Color:	piceous	(′) paler (″) piceous
Head		
(4) Eye size (mean WF/WH):	0.60-0.63	(′) 0.64-0.67 (″) 0.68-0.71
(5) Clypeal field:	narrow	broad
(6) Bases of frontal carinae:	free	confused
(7) Microsculpture of paramedian frontal sulci:	strong	weak
(8) Antennae:	long	short
Prothorax		
(9) Form (mean LP/WP):	0.89-0.96	(a) wider (b) narrower
(10) Relative size (mean LP/WE):	0.75-0.80	(′) smaller (″) reverted
(11) Length of paramedian sulci (mean PS/LP):	0.67-0.74	(a) shorter (b′) 0.75-0.82 (b″) longer
(12) Pronotal hind angles:	prominent	rounded
(13) Paralateral pronotal carinae:	absent	evident
(14) Accessory marginal setae:	absent	present
(15) Pleura:	impunctate	punctate
(16) Pleural microsculpture:	absent or weak	strong
Elytral setae		
(17) Mean number per elytron:	23 or fewer	(′) 24-34 (″) more
(18) Length:	short	long
Legs		
(19) Tarsal length (mean Ta/Ti):	over 0.60	under 0.60
(20) Male front tarsi:	dilated	narrow
(21) Front tibia near base:	narrow	broad
Abdomen		
(22) Microsculpture of coxal depressions of sternum three:	present	absent
(23) Median microsculpture:	absent	present
(24) Lateral microsculpture:	absent	present
(25) Female pygidium apex:	crenulate	not crenulate

Fig. 265-269, and further discussed under "Zoogeography". This is the most parsimonious arrangement I can develop, is consistent with the premise that geographic isolation precedes speciation, and requires the shortest sequence of branching points. Unfortunately, I found no synapomorphous characteristics to justify either main branch, aside from the pale coloration of members of the *brevisetosus*, *sallei*, and *tristriatus* groups.

Among ancestors of species groups of the *truquii* lineage, my reconstructed phylogeny requires at least the following character convergences: color pale, twice, one reversion; pronotum small, twice, one reversion; paramedian pronotal sulci long, twice; pronotal hind angles rounded, twice; and female pygidium not crenulate, twice.

Relationships within larger species groups. — Relationships among species and subspecies taxa of the *pluripunctatus* group are quite straightforward, and vicariant relationships are shown in Fig. 266. If the ancestor of the group was Sonoran, the ancestor of *S. seticollis* and the ancestor of its sister group were Californian-Sonoran vicariants characterized respectively by accessory pronotal setae and relatively short antennae. The taxa *S. seticollis seticollis* and *S. seticollis vandykei* diverged from one another as north-south vicariants. A taxon cycle system of displacement (Wilson, 1961) would account for the general distribution of members of the *pluripunctatus* subgroup and for the presence of accessory pronotal setae in the taxa *S. seticollis* and *S. plurisetosus*. It would not account for various similarities between geographically proximate populations of *S. plurisetosus* and *S. multisetosus*. I suggest that the ancestor of the taxa *S. plurisetosus* and *S. multisetosus* and the ancestor of the taxa *S. pluripunctatus* and *S. kulti* were Sonoran-tropical vicariants, distinguished sharply by differences in form of male median lobe (Fig. 131-136). Subsequently, *S. plurisetosus* and *S. multisetosus* diverged as Tamaulipan-tropical vicariants, and *S. pluripunctatus* and *S. kulti* diverged as Sonoran-tropical vicariants. The apomorphic condition of accessory pronotal setae is convergent in the taxa *S. seticollis* and *S. plurisetosus*.

The *tristriatus* group is divisible into four clearly distinguished subgroups: *S. tristriatus, tristriatus* subgroup; *S. amphibius, amphibius* subgroup; *S. dilatus* and *S. tibialis, dilatus* subgroup; and *S. planulatus, S. ozarkensis*, and *S. planuloides, planulatus* subgroup. Detailed relationships among species taxa of the *planulatus* subgroup were discussed above. The *amphibius, dilatus,* and *planulatus* subgroups share the synapomorphic characteristic of flattened body form; their ancestor and the ancestor of the *tristriatus* subgroup were Tamaulipan-tropical vicariants. Dark coloration is a secondarily acquired characteristic in members of the *tristriatus* subgroup, and relatively enlarged pronota is secondary in the other three subgroups. Members of the *amphibius* and *planulatus* subgroups differ strikingly in size, but agree in increased numbers of elytral setae and reduced eye size. Their ancestor and the ancestor of the *dilatus* subgroup were Texan-Tamaulipan vicariants. And, as judged from the distribution of living species, the ancestors of the *amphibius* and *planulatus* subgroups were temperate-Texan vicariants. Ancestors of the taxa *S. dilatus* and *S. tibialis* were clearly Tamaulipan-tropical vicariants, but some forms of *S. tibialis* reentered the Tamaulipan area from the west, and even entered the Texan area (Fig. 188). These vicariant relationships are shown in Fig. 267.

Among taxa included in the *longipennis* group, *S. longipennis* and *S. neovalidus* are clearly sister species linked by the synapomorphous condition of enlarged virga in the male endophallus, and *S. pacificus* with elongate tarsi and convex body is the most divergent form. My views on vicariant relationships are expressed in Fig. 268. Three of the four included species are represented in Arizona, two apparently as relicts. One might therefore suspect that ancestors of the *depressus* and *longipennis* groups were Tamaulipan-Sonoran vicariants, rather than Tamaulipan-tropical. But no members of the group are known either from Texas or the Mexican Central Plateau, and, further, if the ancestor of the group was

Sonoran one could not convincingly explain the presence of the Arizona relicts. I think a taxon cycle system of displacement (Wilson, 1961) was responsible for present distributions. The ancestor of the group spread across tropical regions of southern Mexico; the ancestor of *S. pacificus* and the ancestor of its sister group were Pacific-Atlantic vicariants. When the ancestor of that sister group again spread to the Pacific slopes, *S. pacificus* was well differentiated, and not subject to displacement. The ancestor of *S. chiricahuanus* and the ancestor of its sister group were Sonoran-tropical vicariants, but the range of *S. chiricahuanus* recessed when its sister group entered the Sonoran region. The ancestors of *S. neovalidus* and *S. longipennis* were again Sonoran-tropical vicariants, and the range of *S. neovalidus* recessed when *S. longipennis* entered the Sonoran region.

The aggregate range of members of the *depressus* group is nearly as great as that of the entire genus. Thus evolutionary relationships are difficult to interpret, and my analysis of vicariant relationships (Fig. 269) is difficult to justify. For purposes of this discussion, I recognize three subgroups: *S. arimao, S. emdeni*, and *S. "apicalis", arimao* subgroup; *S. sulcifrons* and *S. litigiosus, sulcifrons* subgroup; and *S. pygmaeus, S. scopaeus, S. falli, S. ochthocephalus,* and *S. depressus, depressus* subgroup. Members of the *arimao* subgroup agree in the synapomorphous characteristic of shortened pronotal sulci, also characteristic of members of the *pluripunctatus* and *longipennis* groups. I found no clear synapomorphous characteristic of its sister group, but suspect the ancestor of that group had slightly increased numbers of elytral setae. Ancestors of the *arimao* subgroup and its sister group were probably tropical-Tamaulipan-Texan vicariants. I suspect an ancestral condition in the *arimao* subgroup was the presence of weakly developed paralateral pronotal carinae, subsequently lost in *S. emdeni.* The ancestor of *S. arimao* may have entered Cuba via a Middle American land bridge, and its ancestor and the ancestor of its sister group thus may have been Cuban-Middle American vicariants. Whether the ancestors of *S. emdeni* and *S. "apicalis"* were early Middle American-South American vicariants, or whether they diverged in Middle America, is uncertain.

Chorological data suggest that the ancestor of the *sulcifrons* and *depressus* subgroups was Texan, and that their respective ancestors were temperate-Texan vicariants. The ancestor of the latter subgroup was characterized by small size and pale color. The ancestor of the *sulcifrons* subgroup diverged into cool-adapted western and eastern vicariants during Pleistocene time. The common ancestor of *S. falli, S. ochthocephalus,* and *S. depressus* and the common ancestor of *S. pygmaeus* and *S. scopaeus* were Sonoran-Texan vicariants, as suggested particularly by the pattern of geographic variation in *S. falli*. The ancestor of *S. falli, S. ochthocephalus*, and *S. depressus* was characterized by reduced eye size and flattened body, while the ancestor of *S. scopaeus* and *S. pygmaeus* was characterized by reduced body size. The ancestor of *S. depressus* and the ancestor of *S. falli* and *S. ochthocephalus* diverged as temperate-Sonoran vicariants, and the respective ancestors of *S. falli* and *S. ochthocephalus* diverged as Sonoran-Californian vicariants. Simple vicariance does not, however, explain the evolutionary history of the taxa *S. scopaeus* and *S. pygmaeus*. Their distribution patterns are best explained by an early split into Texan-Tamaulipan+tropical vicariants, a later split of the Texan form into Texan-Sonoran vicariants, and a still later reestablishment of reproductive continuity between the tropical and Sonoran vicariants.

The weakest parts of this reconstructed phylogeny (Fig. 257) are in the relationships of the *lineolatus*, *longipennis*, and *depressus* groups, and in relationships within the *depressus* group. In particular, present distributions of all members of both the *arimao* and *sulcifrons* subgroups are far removed from both the Texan and Tamaulipan regions, so that my suggested vicariant relationships are not well justified. In general, however, the suggested vicariant relationships lend support to the reconstructed phylogeny, or at least do not contradict it, and they seem to satisfactorily explain known distributions of modern species and sub-

species taxa. I think they suggest the most probable of an astronomical number of possible evolutionary pathways.

Other groups and lineages

Hypothetical relationships among species and subspecies taxa of the genus *Schizogenius*, excluding members of the *truquii* lineage, are shown in Fig. 258. Most of these taxa are South American, and as the South American fauna is poorly known this reconstructed phylogeny is incomplete, and my comments on it are brief.

Among the three included taxa of the *quinquesulcatus* group, *S. szekessyi* and *S. janae* share maculate coloration. They are at most sister species, and may not even be biologically distinct entities.

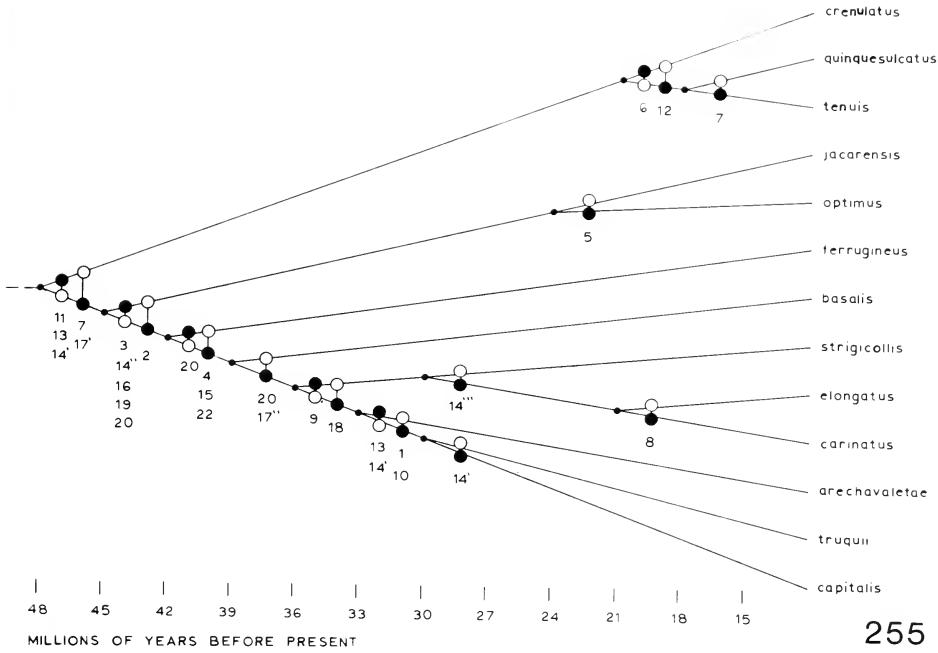
Within the *tenuis* group, *S. impressicollis* is divergent from other taxa in form of male genitalia, but plesiomorphic in having parallel rather than convergent paramedian frontal carinae. Relationships among other taxa in the *tenuis* group are unclear, and cannot be properly interpreted until the South American fauna is better known. I think *S. sculptilis* is least closely related, as judged by amount of phenetic difference; in particular, I doubt that it shares a direct common ancestry with *S. tenuis*. My phylogeny suggests a possible pre-Pleistocene entry into Middle America for the ancestor of *S. sculptilis*, but there may well be an as yet unknown sister species in South America. More probably, the ancestor of *S. sculptilis* entered Middle America in Early Pleistocene, and *S. tenuis* followed in Late Pleistocene.

The ancestor of the *optimus* group gave rise to one line with shortened pronotal sulci, and another with discal setae lost: respectively, *S. optimus, S. dyschirioides,* and *S. clivinoides;* and *S. bicolor* and *S. grossus. S. optimus* and *S. dyschirioides* are evidently sister species, and the ancestor of *S. optimus* was most probably an Early Pleistocene entrant into Middle America.

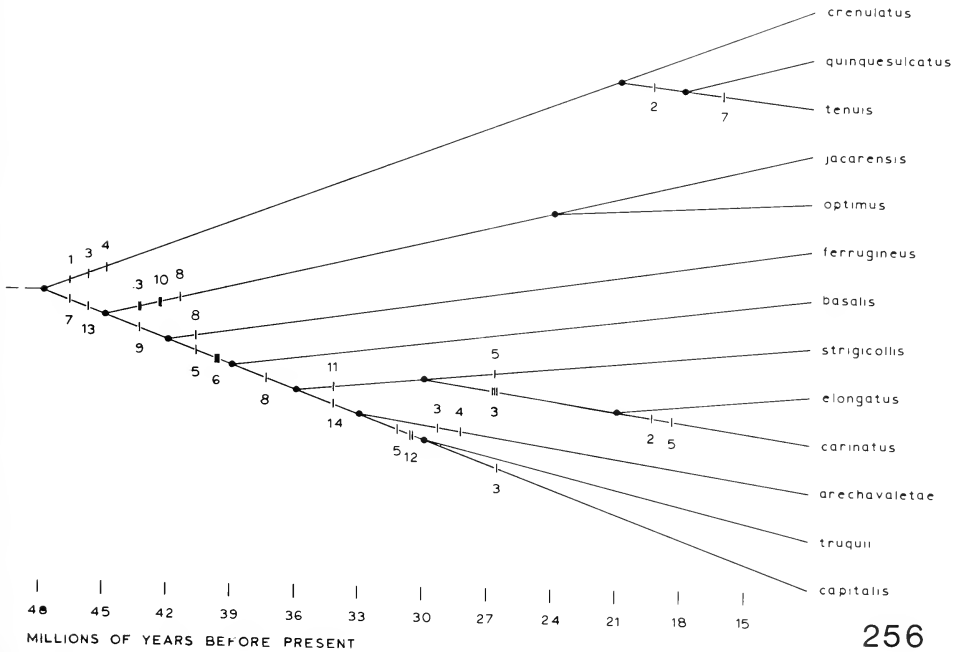
Among the four included taxa of the *basalis* group, *S. basalis* and *S. cearaensis* seem most closely related to one another, and together with *S. negrei* agree in having reduced occiput punctation.

Aside from the *truquii* lineage, the most diverse lineage in *Schizogenius* is the *capitalis* lineage, with five included species groups. Similarities among some members of the *darlingtoni* and *ocellatus* group in size, color, and ventral microsculpture suggest possible relationships, but radical specializations of members of the *ocellatus* group imply considerable antiquity for the common ancestor of these two groups. Within the *darlingtoni* group, the taxa *S. darlingtoni* and *S. interstriatus* agree in having extensive abdominal microsculpture. Of the remaining three species groups, the *quadripunctatus* group is the most divergent and hence probably the oldest. Loss of discal setae from all but elytral interval three in this and the *ocellatus* group is probably convergent. The ancestor of the *lindrothi* group had reduced pronotal hind angles and shortened antennae, as in some groups of the *truquii* lineage. Ancestors of *S. lindrothi* and *S. banningeri* were probably Early Pleistocene Middle American-South American vicariants.

This reconstructed phylogeny suggests the following Middle and South American faunal exchanges. Ancestors of the *crenulatus* group, the *ferrugineus* group, and the *truquii* lineage entered Middle America well before Pleistocene time. Early Pleistocene Middle American immigrants included ancestors of *S. sculptilis, S. optimus,* and *S. lindrothi;* the ancestor of *S. "apicalis"* was a probable Early Pleistocene immigrant. During Late Pleistocene, *S. tenuis* spread into Middle America, and *S. pygmaeus* spread into South America. Thus, three south-north migrations occurred over water, three south-north migrations and one north-south migration occurred soon after establishment of land connections, and one north-south migration and one south-north migration occurred comparatively recently.



255



256

Fig. 255-256. Phylogeny of major groups and lineages of genus *Schizogenius; crenulatus, quinquesulcatus,* and *tenuis* groups are in subgenus *Genioschizus.* 255. Phylogeny reconstructed by phyletic techniques. 256. Phylogeny reconstructed by phenetic techniques.

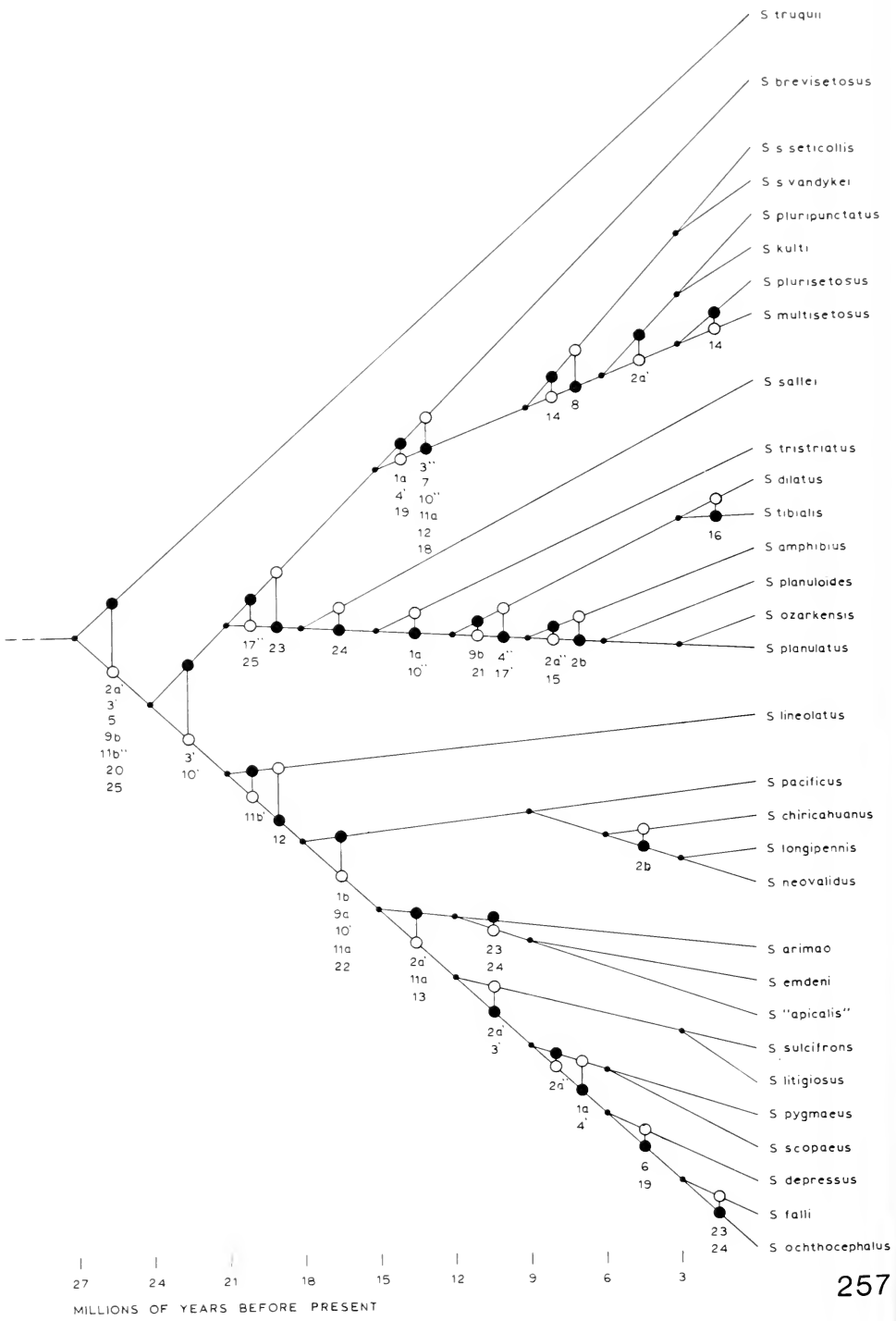


Fig. 257. Reconstructed phylogeny of *truquii* lineage of genus *Schizogenius*.

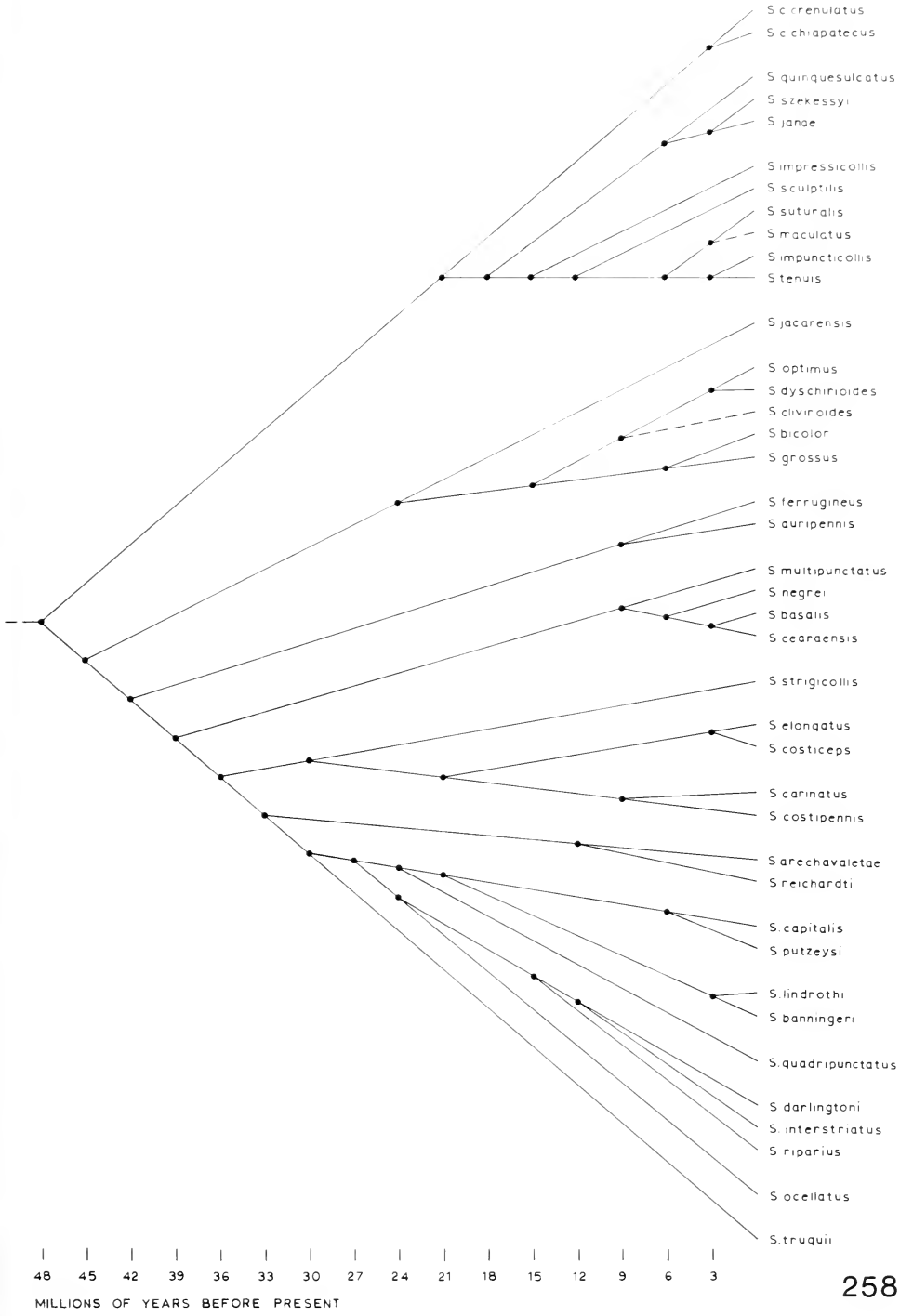


Fig. 258. Reconstructed phylogeny of subspecies and species taxa of genus *Schizogenius*, excluding components of *truquii* lineage.

ZOOGEOGRAPHY

Introduction and general patterns of distribution

Introduction

Various classes of clues available to help assess past movements of animals include number clues, extent of area, continuity of area, degree of differentiation, and vicariance (Darlington, 1957; Erwin, 1970). In my study of *Schizogenius*, I found number clues and vicariance clues especially useful.

I base much of my argumentation of Maldonado-Koerdell's (1964) summary of historical geography of Middle America. His views on locations and times of opening and closing of water gaps, and of land connections with major West Indian islands, are hotly disputed; I here attempt to reconcile various divergent views.

Biogeographers, no doubt correctly, dismiss direct land connections between North and South America before Middle to Late Tertiary as inconsistent with geologic and zoogeographic facts. Yet the possibility of indirect connections *via* islandic chains, i.e., incomplete or only partially effective barriers to dispersal, existing through Paleocene should not be lightly dismissed. As Patterson and Pascual (1968) state, ancestral forms of at least four mammalian lineages appeared in South America in rapid succession about the Cretaceous-Tertiary boundary, while subsequently, during the first half of Tertiary, ancestors of perhaps only three more mammalian lineages did so. Henceforth, when I speak of pre-Eocene land bridges or land connections, I do so of this probable, incomplete, bridge. The geological history of not only Middle America but of the whole circum-Caribbean land mass requires further study.

Patterson and Pascual (1968) doubt that land bridges from Middle America to Cuba ever existed, and doubt further that Middle America was divided into smaller land masses by water portals during Middle Tertiary. Hershkovitz (1969) suspects the existence of both. For riparian species of *Schizogenius*, water gaps such as the supposed Tehuantepec portal are not required for barriers to exist. Had this region been emergent but of sufficiently low relief that riparian gravel bars did not exist, it would have been perfectly effective as a barrier. And this would be so not only for riparian *Schizogenius*, but for upland terrestrial animals of many kinds. The same argument, however, could well apply to the question of Middle American-Cuban land connections; probably, if such land connections did exist, they were not of high relief. I accept Maldonado-Koerdell's (1964) postulations of these land bridges in part for consistency and in part for convenience, but without specific justification. A land bridge to Cuba is useful to explain the distribution of one, and only one, species of *Schizogenius*; it clearly is not a requirement.

Hershkovitz (1969) indicates that the Panamanian portal closed in Late Miocene-Early Pliocene rather than Late Pliocene-Early Pleistocene, and surely is supported in this assertion by evidence from distributions of living mammal species. Again, however, effective land connections for riparian *Schizogenius* species require sufficient uplifting for formation of riparian habitats. I am satisfied that these conditions did not exist before Late Pliocene.

General patterns of distribution

The genus *Schizogenius* is a sister group of New World *Halocoryza*; the ancestor of these organisms diverged from an African ancestor, and all other related genera are of Old World origin. The genus *Schizogenius* is best developed and most diverse in South America, and only three old lineages are restricted to or diversified in North and Middle America. The ancestor of the genus was therefore clearly South American; and it must have differ-

entiated from *Halocoryza* stock no earlier than Eocene, after North and South America became well isolated by truly effective Middle American water barriers. One major water gap was across the Isthmus of Tehuantepec, and another across Panama, closing respectively in Late Miocene and Late Pliocene (Maldonado-Koerdell, 1964). These gaps approximately defined the area I recognize as Middle America: in the south bounded approximately by the Panama-Costa Rica border, and in the north including Pacific drainages of southeastern Chiapas but excluding the Usumacinta and Grijalva Rivers in Guatemala. Known southern limits of two *Schizogenius* species, *S. tenuis* and *S. pygmaeus*, approximate southern limits for Middle America as defined by Hershkovitz (1969). The reality and significance of this geographic boundary as it pertains to members of *Schizogenius* cannot be further assessed at present.

Of 23 species groups in *Schizogenius*, 10 evolved in North America and 13 in South America. North American species groups arose from three early migrations from South America. One early immigrant gave rise to the *crenulatus* group, with one subspecies ranging into northern Middle America. A second early immigrant was the ancestor of the *ferrugineus* group, one species of which extends from North America to the southern limit of Middle America. The third immigrant gave rise to eight species groups, all centered in North America. One species of the *pluripunctatus* group enters the northern part of Middle America. One species of the *tristriatus* group extends to the southern limit of North America. One species of the *longipennis* group extends to the southern limit of North America, and another to the southern limit of Middle America. And in the *depressus* group, three endemic Middle American, Cuban, and South American species form a monophyletic subgroup of old Middle American ancestry, while another extends to northern South America from North America. I judge that the endemic South American form arrived there about Late Pliocene-Early Pleistocene, and that it may have an as yet unknown vicariant sister species in Middle America.

Six of the 13 South American groups are not known from Panama, Colombia, or Venezuela. Some members of the *capitalis, darlingtoni, quinquesulcatus,* and *strigicollis* groups are known from this region but not from Middle America. The *lindrothi* and *optimus* groups include vicariant Middle and South American sister species, but except for Floridian populations of *S. lindrothi* are otherwise unrepresented in North and Middle America. Only the *tenuis* group, with one species endemic in southern North America and another extending through Middle America to northern Mexico, is represented north of the Isthmus of Tehuantepec. The endemic species, *S. sculptilis*, probably also occurs in Middle America; its ancestor probably arrived there soon after re-establishment of land connections, and it may have an as yet unknown vicariant sister species in South America.

Middle America serves as a funnel (Simpson, 1950) between North and South America for *Schizogenius* species, and also shows a notable filter effect at both ends. Tropical insect faunas of Mexico and Middle America derive primarily from South American ancestors (Halffter, 1964), but for *Schizogenius* Halffter's notions about timing of immigrations are inadmissible. If the genus originated in South America after Eocene, the first wave of migrations northward was not earlier than mid-Tertiary. After closure of the Panamanian portal early migrants evolved as endemic Middle American species. Later migrants, *S. tenuis* and *S. pygmaeus*, were more probably Late Pleistocene than Late Pliocene. Despite evidence for two-way mammalian interchanges between Middle and South America since Late Miocene (Hershkovitz, 1966), no evidence of free interchange before Late Pliocene exists for *Schizogenius* species.

The Middle American *Schizogenius* fauna is poorly known, but probably not so poorly as suggested by the limited numbers of known species. Among Mexican species not yet

recorded from Middle America, only *S. sculptilis* is really likely to be found there. Also expected is a sister species of the South American *S. "apicalis"*, and perhaps other South American species enter southern parts of the area. Of 10 species known from the region, five enter from North America, one from South America, and four are endemic; two endemics have South American sister species, while the others differentiated there from an earlier penetration from North America. Through much of Middle Tertiary, Middle America was an isolated, often partitioned land mass, and despite probable continuity with Cuba during much of this period was relatively small in area (Maldonado-Koerdell, 1964). Although the Tehuantepec portal closed in Late Miocene, the Isthmus was not elevated until Late Pliocene; the Isthmus may have been a continuously significant barrier since Early Oligocene. And, since Early Miocene and particularly since Late Pliocene, Middle America suffered much volcanic activity. These observations suggest that the *Schizogenius* fauna of Middle America may never have been really large. Support for this conclusion is evident from known distributions of species in the area. Aside from one species endemic to Cuba, all species except *S. crenulatus* and *S. kulti* are known to be widely distributed from north to south, suggesting lack of barriers and consequent reduced geographic isolation and species diversification. Thus, while mid-Tertiary fracturing of Middle America may have contributed greatly to speciation in Trichoptera (Ross, 1967), it had no apparent effect on speciation in *Schizogenius*. After closure of the Tehuantepec portal in Late Miocene, some North American elements penetrated the area, and may have replaced some endemic forms. Further elimination of endemic forms may have resulted from arrival of South American immigrants after closure of the Panamanian portal in Late Pliocene.

Distribution patterns in North and Middle America

Introduction

The genus *Schizogenius* is represented throughout North and Middle America, south of 52°N in the west and 48°N in the east, except in the West Indies where known only from Cuba and Jamaica. Since this fauna originated in South America, most included species and subspecies are tropical or subtropical, and relatively few have acquired truly temperate adaptations. Their distribution patterns were regulated by the development of Middle and Late Tertiary climatic and physiographic features, and were modified particularly in the north by Pleistocene events. I use number clues to evaluate distribution patterns, generally according to techniques developed by Ball and Freitag (*in* Freitag, 1969) and Erwin (1970), and compare my observations with some of their observations on *Evarthrus* and *Brachinus*, respectively. Then I consider vicariance clues, particularly in relation to the *truquii* lineage, and attempt to reconstruct the historical zoogeography of the genus in North and Middle America.

Methods and general patterns

Following Erwin's (1970) methods, I show on a 5° longitudinal and latitudinal grid map the number of species or subspecies known to occur in each interval (Fig. 261), and list "total interval values" (TIV) and "average landmass interval values" (ALIV) in Table 70. The number of species is maximum in southern and central Mexico, and slightly less in Arizona. Numbers decrease rapidly in all directions from these centers. To the north, numbers decrease least rapidly in the humid forested regions of the Appalachians and the Pacific coast. To the south, numbers decrease sharply near the Panama-Costa Rica border. And the *Schizogenius* fauna of Florida and the West Indies is notably depauperate. The general pattern is similar to that for *Brachinus*, except for absence of an evident east-west lateral asymmetry and reduced numbers in extreme southeastern United States.

These general patterns are readily explained. Few species are cool-adapted, and none are cold-adapted; hence, reduction to the north, particularly in central North America and in the Rocky Mountain region. Most species inhabit riparian gravel bars; hence reduction in extreme southeastern United States, and lack of east-west asymmetry in the United States. The reduction of numbers in Middle America was considered previously.

Maximum linear ranges (Erwin, 1970) are given in Table 71, and compared with data on linear ranges for *Brachinus* species (Erwin, 1970) and *Evarthrus* species (Ball and Freitag, *in* Freitag, 1969). Maximum ranges of *Schizogenius* species are almost exactly intermediate between those of *Brachinus* and *Evarthrus*; average maximum distances between localities were determined as about 700 miles for *Evarthrus*, 1000 miles for *Schizogenius*, and 1300 miles for *Brachinus*. One of the *Schizogenius* species, *S. pygmaeus*, has a linear distribution of more than 1000 miles greater than any species of *Evarthrus* or *Brachinus*.

If barriers limit distributions of *Evarthrus* species, and broad climatic zones limit distributions of *Brachinus* species, barriers and climatic zones together may account for distributions of *Schizogenius* species. Barriers, for inhabitants of riparian gravel bars, include the following: high altitudes; rivers or sections of rivers without gravel bars; and land or water gaps between rivers. Limiting climatic zones correspond roughly to tropical, subtropical, warm temperate, and cool temperate. Another limiting factor in distributions of some *Schizogenius* species and subspecies is almost certainly one of ecological displacement. In North and Middle America, at least, no more than seven species may be taken in gravel bars at a single locality, and normally no more than five. Ecological displacement is particularly obvious in some allopatric sister species, which inhabit adjacent river systems or even separate segments of the same river system.

An example of a mountain barrier is the Sierra Madre Occidental. Species found on both sides of this range, such as *S. pluripunctatus* and *S. pygmaeus*, evidently lack gene flow across the mountains. Others, such as *S. depressus* to the east and *S. longipennis* to the west, have ranges limited by the mountains. Lack of suitable habitat along portions of the Red and Mississippi Rivers probably accounts for limits of ranges in *S. planuloides, S. ozarkensis,* and *S. planulatus.* And the apparent isolation of *S. s. seticollis* and *S. s. vandykei* is probably due to a large gap between suitable habitats in northern Baja California.

Climatic zones are not sharply limited, but nonetheless seem at least partly responsible for range limitations. Of 13 species groups represented in North and Middle America, including representatives of three South American groups, all are represented in tropical or subtropical regions, seven in warm temperate regions, and six in cool temperate regions. Numerous species or subspecies have ranges limited near the Tropic of Cancer; 12 species or subspecies have southern or northern limits within 3½°S, and eight within 3½°N.

Some examples of allopatric sister taxa found in adjacent drainage systems are: *S. kulti* and *S. pluripunctatus*, Rio Grande de Santiago and Rio Acaponeta; *S. multisetosus* and *S. plurisetosus*, Rio Panuco and Rio Tamesi; and *S. c. crenulatus* and *S. c. chiapatecus*, Rio Grande de Santiago and Rio Ameca. Adjacent river systems may also limit sharply differentiated forms within a taxon, as in *S. tibialis*: large eyed forms occur from the Rio Panuco southward, moderate eyed forms from the Rio Panuco to the Rio Grande, and small eyed forms in the Nueces River basin. An example of displacement on a single river system is the occurrence of *S. pygmaeus* on the Rio Conchos, rather than *S. scopaeus* which occurs elsewhere along the Rio Grande. Somewhat less closely related taxa may also be subject to displacement, and an example may be the displacement of *S. dilatus* south of the Rio Tamesi by *S. tristriatus* or large eyed *S. tibialis* and north of the Rio Sabinas Hidalgo by *S. sallei* or *S. planuloides.* Faunal compositions along river systems may vary from downstream to upstream. The taxa *S. multisetosus* and *S. kulti* are known from the same river

Table 70. Total number of species and subspecies, "average landmass interval values" (ALIV), and "total interval values" (TIV) derived from Fig. 261.

Interval	No. spp.	ALIV	TIV	Interval	No. spp.	ALIV	TIV
A	--	--	--	a	1	1.0	1
B	5	4.8	12	b	4	1.7	10
C	5	3.1	14	c	10	3.1	33
D	11	4.9	22	d	14	4.7	45
E	16	6.1	32	e	20	7.7	48
F	20	6.6	43	f	19	9.1	32
G	22	9.2	46	g	20	16.9	38
H	17	6.9	26	h	17	15.2	38
I	13	5.8	23	i	6	12.0	12
J	13	5.7	23	j	7	10.6	8
K	7	4.4	13	k	1	1.3	1
L	6	4.4	10	l	--	--	--

Table 71. Frequency distribution of maximum linear range in miles of species of *Brachinus**, species of *Evarthrus***, and species and subspecies of *Schizogenius* in North and Middle America.

Class	*Brachinus* No.	%	*Evarthrus* No.	%	*Schizogenius* No.	%
3501-3750	0		0		1	
3251-3500	0	0	0	0	0	3
3001-3250	0		0		0	
. . . . .						
2751-3000	0		0		1	
2501-2750	5	19	0	5	2	13
2251-2500	5		0		2	
2001-2250	2		2		0	
. . . . .						
1751-2000	9		1		1	
1501-1750	2	39	3	16	1	24
1251-1500	8		1		1	
1001-1250	5		2		6	
. . . . .						
751-1000	11		8		5	
501- 750	4	42	5	79	5	60
251- 500	3		10		6	
0- 250	8		12		7	
. . . . .						

* From Erwin (1970)

**From Ball and Freitag (*in* Freitag, 1969)

systems but not from the same localities; when both occur on a drainage system, *S. multisetosus* is found upstream from *S. kulti*. Along the Rio Grande, seven species are known from the Del Rio region, three of them from the Big Bend region, and one of them plus another from northern New Mexico. Part of these faunal changes are probably due to lack of suitable habitat, as in the Las Cruces-El Paso segment of the Rio Grande.

Techniques described by Erwin (1970) for finding centers of concentration are not useful for Central America and southern Mexico, because the 5° grid crosses the entire continent and obscures possible Atlantic and Pacific centers. Instead, I plotted centers of geographic distribution of all species and subspecies taxa with ranges less than 1250 miles, and circled these centers to enclose all geographic distributions up to a 300 mile radius (Fig. 262). Not surprisingly, resulting centers of concentration correspond to presence of endemic species. Centers 4 and 8 overlap, but contain quite distinct faunas. Based on these centers of concentration, areas of concentration (Fig. 263) were determined by comparisons of geographic distributions and by notions about barriers. Area 5 is judged to include peninsular Florida, because of the presence there of only the Middle American *S. lindrothi*. Area 6 is of doubtful reality, as it includes only one known species which, though endemic, is related to a species in area 5. Area 7 is also of doubtful reality, because the endemic species there, *S. sculptilis*, most probably ranges into Middle America. Distributions of species and subspecies are compared with these centers and areas in Table 72, dissimilarity values (Erwin, 1970; Ball and Freitag, 1969) are listed in Table 73, and an index of dissimilarity is given in Table 74.

Peripheral areas 1, 6, 11, and 12 are most distinct, as were Erwin's centers 1, 5, and 8. Areas 5 and 7, with a dissimilarity value of 64, are least distinct, and perhaps not distinct at all. In general, more central areas are least distinct, as was found by Erwin for *Brachinus*. All contiguous areas share one or more taxa, but subtraction patterns are evident. Curiously, area 2 is more similar in faunal composition to tropical area 4 than to subtropical or temperate areas 1, 9, 10, and 11. Physical barriers, such as the Sierra Nevada, Rocky Mountains, Mexican Plateau, and Colorado Desert, are probably responsible for this pattern.

In general, my areas of concentration for *Schizogenius* correspond fairly well with Erwin's centers of concentration for *Brachinus*, except for lack of a special area in southeastern United States and division of Mexico and Middle America into several separate areas. They are not, however, as well correlated with general climatic patterns, and a more detailed comparison follows.

My area 1 differs from Erwin's center 1 mainly by including arid regions south of the Tehachapi crest. In *Schizogenius*, the Tehachapi isolates *S. falli* from *S. ochthocephalus*, and also isolates distinctive populations of *S. pygmaeus*, but otherwise is not evidently an important barrier. Area 2 differs from Erwin's center 2 by exclusion of western Texas, southern California (area 1), and Baja California (area 3). Although the endemic form in area 3 is most closely related to one in area 1, another form is shared with area 2 but not area 1, and populations of both other species in area 3 are more similar to populations in area 2 than area 1. Areas 10 and 11 correspond closely with Erwin's centers 4 and 3, except that western Texas is included in area 10. Area 12 includes Erwin's center 6 plus part of center 7.

Erwin's center 5 includes approximately my areas 4, 5, 7, 8, and 9. Area 7, which may be an artifact, and area 5 comprise Middle America plus the rest of the area east of the Isthmus of Tehuantepec. This region is not sharply differentiated climatically from areas 4 and 8 in southern Mexico, but probably reflects the past existence of a water gap. Areas 4 and 8 form the rest of the continental tropical region, their northern limits corresponding closely to northern limits of rain-forest formations. When the distributions of the various taxa of

Table 72. Distribution of North and Middle American species and subspecies of *Schizogenius* in relation to centers of concentration.

Taxon	Centers											
	1	2	3	4	5	6	7	8	9	10	11	12
amphibius												xx
arimao						xx						
auripennis		xx	xx	xx	xx		xx					
brevisetosus									x	xx		
chiapatecus				xx	xx							
chiricahuanus		xx										
crenulatus		xx		x								
depressus	xx	xx		x				x	x	x		
dilatus									xx			
emdeni					xx							
falli	x	xx	xx	x					xx	xx	xx	x
ferrugineus		xx								xx	xx	xx
kulti				xx	x		xx	xx				
lindrothi					xx							
lineolatus										xx	xx	xx
litigiosus	xx											
longipennis		xx		xx	xx		xx	xx	xx			
multisetosus				xx				xx				
neovalidus		xx										
ochthocephalus	xx											
optimus					xx							
ozarkensis											xx	
pacificus		x		xx								
planulatus												xx
planuloides										xx		
pluripunctatus		xx										
plurisetosus									xx			
pygmaeus	xx	xx	xx	xx	xx		xx	xx	xx			
sallei										xx	xx	
scopaeus									xx	xx	xx	
sculptilis							xx					
seticollis	xx											
sulcifrons												xx
tenuis		x		xx	xx		xx	xx				
tibialis				xx				xx	xx	xx		
tristriatus								xx				
truquii		x		xx								
vandykei			xx									
Totals, x and xx	6	13	4	13	9	1	6	8	9	9	6	6

x- in area, but not in center
xx- in center

Table 73. Dissimilarity values among centers of concentration of the genus *Schizogenius* in North and Middle America.

Center	Statistics*	Center 2	3	4	5	6	7	8	9	10	11	12
1	t-c/t x 100	84	70	84	93	100	92	86	80	87	92	92
2	t-c/t x 100	—	82	65	81	100	79	81	86	86	90	90
3	t-c/t x 100	—	—	82	83	100	80	92	85	92	90	90
4	t-c/t x 100	—	—	—	73	100	74	76	77	86	95	95
5	t-c/t x 100	—	—	—	—	100	64	75	88	100	100	100
6	t-c/t x 100	—	—	—	—	—	100	100	100	100	100	100
7	t-c/t x 100	—	—	—	—	—	—	71	87	100	100	100
8	t-c/t x 100	—	—	—	—	—	—	—	76	88	100	100
9	t-c/t x 100	—	—	—	—	—	—	—	—	72	87	93
10	t-c/t x 100	—	—	—	—	—	—	—	—	—	67	80
11	t-c/t x 100	—	—	—	—	—	—	—	—	—	—	75

* t = total taxa, c = taxa in common

Table 74. Index of dissimilarity among areas of concentration of the genus *Schizogenius* in North and Middle America, determined from Table 73.

1*	Area 6	1100
2	Area 12	1015
3	Area 11	996
4	Area 1	980
5	Area 10	968
6	Area 5	957
7	Area 7	947
8	Area 3	946
9	Area 8	945
10	Area 9	931
11	Area 2	924
12	Area 4	907

*Ranked in order from most to least dissimilar.

area 2 are better known, that area may be found divisible into subunits corresponding at least to the subtropical area 9 and the warm temperate area 10.

In summary, *Schizogenius* species are generally less vagile than *Brachinus* species but more vagile than *Evarthrus* species, and their distribution patterns are accordingly influenced by a balance of factors influencing distributions in *Brachinus* and *Evarthrus*. The riparian gravel bar habitat of most of the species is a further restraining variable, but also one which may permit penetration of otherwise unfavorable climatic zones. The westward extension of area 10, for example, is one which simply follows the Rio Grande drainage system; its *Schizogenius* fauna is depauperate, and contains some elements from area 2, but is still most closely related to the fauny of the rest of area 10.

Historical zoogeography

Paleogeography. – According to Maldonado-Koerdell (1964), many important events occurred in Mexico and Middle America during Tertiary and Quarternary time. For purposes of this discussion, I use the following time scale, in millions of years before present: Pleistocene and Recent, 0-3.0; Pliocene, 3.1-13.0; Miocene, 13.1-25.0; Oligocene, 25.1-36.0; Eocene, 36.1-58.0; and Paleocene, 58.1-63.0. North and South America were separated in Late Paleocene by formation of the Peruvian-Venezuelan geosyncline. During Paleocene and Eocene, the Balsas portal was eliminated, the Sierra Madre Oriental was lifted, the Mexican Plateau began to rise, and Middle America bulged northward to include Jamaica but not Cuba. Near Early Oligocene, Middle America became separated from North America by the Tehuantepec portal, and extended further northward to include Cuba. Early Miocene saw the rise of the Sierra Madre Occidental, continued emergence of the Mexican Plateau, beginnings of volcanic activity in Middle America and along the Neo-Volcanic Axis, and approximate delimitation of modern climatic zones. In Late Miocene, the Tehuantepec portal closed, and Cuba and Jamaica became isolated from Middle America. In Middle Pliocene volcanic activity was generally interrupted, but renewed in Late Pliocene. Also in Late Pliocene, South and Middle America were reconnected, and uplands in the Isthmus of Tehuantepec were formed.

Pleistocene events are more difficult to interpret and collate. Presumably, the first two million years of the period were marked by a general deterioration in climate, followed in the last million years by a series of four major glaciations; the last of these glaciations, the Wisconsin, commenced about 100,000 years ago. In Mexico and Middle America, intermittent but intense volcanic activity occurred throughout the Pleistocene. The climate was probably warm humid in Late Pliocene, cool humid in Early Pleistocene, and cool dry during the first glaciation.

Subsequently the climate varied cyclically through warm dry to warm humid during interglacials, returning through cool humid to cool dry during glaciations. Montane glaciers in central Mexico descended to as low as 2450 m, or about half the lower limits of present remnants of these glaciers. These observations suggest that climatic conditions at low elevations even in the south fluctuated, and in particular tropical conditions probably did not extend north of the Neo-Volcanic axis during glacial maxima.

Evolutionary and phylogenetic rates. – Evolutionary and zoogeographic pathways developed interdependently, and phylogenetic and zoogeographic analyses should therefore be compatible with one another. One method for testing for compatibility is to correlate the reconstructed phylogeny with known or suspected paleogeographical events. To do this, I determined an average time between branching points in the reconstructed phylogeny, based on assumptions discussed in the section on phylogeny; this method was tested and found useful for comparing phylogeny and zoogeography in Brachinus (Erwin, 1970) and Evar-

thrus (Ball and Freitag, *in* Freitag, 1969). The average time between branching points was determined to be about 3,000,000 years, from the following lines of reasoning.

For Hawaiian birds, Bock (1970) suggests that time required for speciation may range between 100,000 and 1,000,000 years. For recent European mammals, Kurten (1968) suggested a time range of between 30,000 and 3,000,000 years; his upper limit corresponds to Early Pleistocene, while the lower limit may at least in part reflect inadequate knowledge. According to Halffter (1964), La Brea (Pleistocene) insects are no more than subspecifically distinct from extant species, though their distributions may have changed greatly. For speciation in *Schizogenius* and other continental North American carabid beetle genera except those with highly insular distributions such as *Scaphinotus* (see Ball, 1966), Kurten's upper limit may be close to an average figure.

The ancestor of *Schizogenius* entered South America after formation of an effective barrier at the Panamanian portal in Late Paleocene, no more and probably less than 60,000,000 years ago. According to my reconstructed phylogeny (Fig. 257-258), a minimum of 16 branching points are required to reach back to the common ancestor of American *Halocoryza* and *Schizogenius*. Thus the maximum possible time between branching points is 4,000,000 years. According to Halffter (1964), fossils in Upper Oligocene-Lower Miocene amber from Semojovel, Chiapas, about 25,000,000 years in age, include nine species of beetles, all extinct, as so far studied. These are arrayed in seven genera, five of which are extant; none are carabid beetles. In the same amber deposit is a carabid of the bembidiine genus *Tachys*, said to be related to living species (T. L. Erwin, 1971). The extinct genera may represent sideline extinctions, or ancestral forms, and relationships of the extinct species of extant genera are unclear. But the *Tachys* specimen, at least, implies that ancestors of existing species groups of carabid beetles may already have evolved at that time. Therefore, ancestral *Schizogenius* had probably evolved by at least Late Oligocene, and had probably even differentiated into at least the major lineages, such as the *truquii* lineage, by then. If the ancestor of *Schizogenius* had diverged from *Halocoryza* by Late Oligocene, but not yet differentiated into subgenera, the average time between dichotomies would be about 1,500,000 years. If the *truquii* lineage had differentiated by this time from its sister group, but not yet undergone radiation, the time required between dichotomies would be close to 3,000,000 years. In short, clues from Semojovel amber suggest by analogy that at least the ancestor of *Schizogenius* had evolved by Late Oligocene, and that probably some differentiation had taken place.

Matthews (*in* Hopkins, *et al.*, 1971) discussed a Late Pliocene insect fauna from the Bering Strait region, dated at approximately 5.7 million years. Among carabid beetles reported in this paper, some apparently represent extant species, while others probably represent extinct species closely related to extant forms. These data are significant in their implications of old age for living species of carabid beetles.

Faunal exchanges between Middle and South America offer a further clue to the age of the most recent dichotomies. Only three lineages are likely to have crossed over the Panamanian portal, or, perhaps, over emergent land of low relief there. I think that shortly after this barrier disappeared, one invasion of South America and three of Middle America occurred, and resulted in differentiation of distinctive species. I judge that these events took place between three and five million years ago, more probably three million years because there is no reason to believe immigration proceeded immediately. The Panamanian area is still evidently a significant barrier to the dispersal of *Schizogenius* species, as only two modern species are known from both Middle and South America.

Another general line of reasoning concerns Pleistocene events in North America. In *S. falli*, there is statistical evidence of rapid change in a single characteristic over a short period

of time in one area: 50 years, in the Dragoon Mountains of southern Arizona. In *S. depressus,* there is statistical evidence that differentiation of eastern and western groups of populations in the southwestern United States has taken place within the last 10,000 years. Perhaps in the north further differentiation has developed much more recently, as a result of character displacement. Also in the north, however, is evidence that genetic differentiation but not speciation is associated with much earlier Pleistocene events; at least Wisconsin (100,000 years), and more probably Nebraskan (1,000,000 years). My reasoning here presumes that the northern forms became isolated in early Pleistocene because of deteriorating climatic conditions, were subsequently alternately completely and partially isolated, and that by the first interglacial were partly genetically isolated. The common ancestor of the closely related but grossly disjunct *S. sulcifrons* and *S. litigiosus* was probably transcontinental in Early Pleistocene, but with the deterioration of climate formed eastern and western isolates before the Nebraskan glaciation. Similarly, I suspect that geographic isolates of the common ancestor of *S. planulatus* and *S. ozarkensis* formed in Early Pleistocene, before the onset of glaciation. Alternatively, one might date the initial isolations of *S. sulcifrons* from *S. litigiosus* and *S. planulatus* from *S. ozarkensis* as no earlier than the beginning of Wisconsin glaciation. But this would suggest that the entire evolution of the genus may have taken place within the last 2,000,000 years. If these isolations occurred in Early Pleistocene, however, they may be dated as about 3,000,000 years and thus agree with datings from other evidence.

A particularly difficult problem is posed by those species complexes in which included species are allopatric but proximate. If their ranges have long been proximate, and fixed, a period of 3,000,000 years seems difficult to explain. But boundaries unquestionably were not always contiguous, they most likely are not fixed, and there are doubtless interactions along these boundaries. Competitive exclusion (Mayr, 1963) is the probable reason for maintenance of proximate but allopatric distributions in *Schizogenius* species. For instance, *S. pluripunctatus* and *S. kulti* probably were isolated by Late Pliocene or Early Pleistocene vulcanism along the Neo-Volcanic Axis, in agreement with my suggested 3,000,000 year time limit. Subsequently, geographic isolation was maintained by competitive exclusion, but boundaries shifted northward with the northward extension of tropical climates after the end of the Pleistocene. If two species which are closely related or which are particularly similar in ecological requirements inhabit adjacent river systems, or separate segments of a single river, their distributions are unlikely to overlap. Undoubtedly, there is contact on an individual basis, as individuals migrate away from parental habitat. Evidence that this does happen is found in allopatric components of a species complex such as in *S. falli* and *S. ochthocephalus* or in *S. kulti* and *S. pluripunctatus*, or even in eastern and western forms of *S. depressus* in northwestern United States. Where ranges approach one another, proximate populations tend to be the most strongly differentiated, which, I think, is evidence of character displacement (Brown and Wilson, 1956). I have used this observation, of interrupted gene flow, as one criterion for species recognition. But I think such patterns are best explained as the result of interspecific interaction. In northeastern Mexico, where *S. scopaeus* and *S. pygmaeus* are parapatric or sympatric in distribution they are also strongly differentiated morphologically and, probably, ecologically; elsewhere, where less strongly differentiated, they are allopatric. Near their boundary in the Big Bend Region of the Rio Grande, they probably are not strongly differentiated ecologically, and in that region they show evidence of character displacement in form of male median lobe.

In summary, the separation of North and South America in Late Paleocene suggests an upper limit for the age of ancestral *Schizogenius* of 60,000,000 years, and paleontological data from the Semojovel fossils suggests a lower limit of 25,000,000 years. In turn these datings suggest that intervals between dichotomies in the most complete lineage of the

reconstructed phylogeny of the genus are at most 4,000,000 years and at least 1,500,000 years. The timing of overland faunal exchanges between South and Middle America, and Pleistocene events in North America, suggest that this interval is approximately 3,000,000 years. This is a crude approximation, and is an average, not a constant; I accept this interval as a working proposition.

With a 3,000,000 year interval between dichotomies, I judge that the common ancestor of *Schizogenius* evolved some 50,000,000 years ago, about Middle Eocene. Ancestors of the *ferrugineus* group, the *truquii* lineage, and the *crenulatus* group entered North America in Late Eocene, Middle Oligocene, and Middle Miocene, respectively. These suggested historical events are compared with paleogeological events in the following section. This 3,000,000 year interval is the basis of the time scale shown in my reconstructed phylogeny (Fig. 255-258).

Vicariance and historical zoogeography. — In this section, I deal briefly with matters of vicariance and historical zoogeography pertaining to minor groups and lineages of the genus *Schizogenius* that have penetrated North and Middle America, and at some length as they apply to the *truquii* lineage.

The origin of the subgenus *Genioschizus* took place in South America about 48,000,000 years ago. This group is now poorly represented, with three closely related species groups, and extinctions undoubtedly account for its present lack of diversity. The ancestor of the *crenulatus* group entered Middle America in Early to Middle Miocene. The ancestor of living taxa entered southwestern North America after closure of the Tehuantepec portal, probably in Middle to Late Pliocene, and extended northward into the Sonoran region. Southern and northern isolates formed in Early Pleistocene because of orogenic activity in the Neo-Volcanic Axis, but, with northward extension of tropical climates in more recent times, their boundary shifted northward to its present location near the Tropic of Cancer. The two living subspecies of *S. crenulatus* are north-south vicariants. Two other members of the subgenus *Genioschizus* represented in North and Middle America are distantly related members of the *tenuis* group. Ancestral *S. sculptilis* entered Middle America in Early Pleistocene, and extended westward as far as the Usumacinta-Grijalva area; this species probably remains a component of the Middle American fauna. More recently, *S. tenuis* has extended northward from Colombia through Middle America, as far as the northern limits of the tropics in eastern Mexico and the northern limits of the subtropics in western Mexico.

As do members of the subgenus *Genioschizus*, and at least *S. lindrothi* of the *lindrothi* group, members of the *ferrugineus* group are found mainly in sandy habitats. I suggest a particularly early entry into Middle America for this group, perhaps Early Eocene, before the Tehuantepec portal opened. The group is characterized by lack of diversity, no close relationship among existing species, and by widespread distributions of living species. The two existing species are largely allopatric, but are not true sister species and therefore vicariant relationships are doubtful. The group is not represented in far western United States, Florida, or eastern Mexico. These gaps in distribution are difficult to explain. *S. ferrugineus*, or a related form, may until comparatively recently have been represented in subtropical Florida, but displaced by the immigrant *S. lindrothi*. The distribution of *S. lindrothi*, Middle America and Florida, suggests that early distributions of the *ferrugineus* group may have followed a similar pattern. But if my conclusions about timing are correct, Florida did not then exist as such, and, further, there was no barrier to dispersal at the Isthmus of Tehuantepec. The present continuity of range of the two species suggests that Middle America and southern Mexico were depopulated of the group for a long time, with extinction of tropic-subtropic elements initiated in Late Oligocene or Early Miocene. This may have been caused in part by orogenic activity and in part from displacement by newer

immigrants of the *truquii* lineage. Surviving forms became adapted to temperate conditions in northeastern North America. A later isolate subsequently became established in the Sonoran area, from which it successfully penetrated southward along the Pacific coast of Mexico, and beyond to the southern limit of Middle America.

Other minor lineages represented in North and Middle America are the *lindrothi* and *optimus* groups, each with distinctive vicariant sister species in Middle and South America. Ancestors of Middle American species arrived there in Early Pleistocene. *S. lindrothi* subsequently became distributed across the Gulf of Mexico to peninsular Florida, where it may have displaced *S. ferrugineus* from sandy habitats in subtropical regions. Although Middle American and Floridian forms of *S. lindrothi* are quite distinctive, I suspect the species may also be represented in the West Indies, particularly in areas of Caribbean pines as discussed by Mirov (1967).

The ancestor of the *truquii* lineage passed through Middle America into southern Mexico in Middle Oligocene, over the Tehuantepec and Panamanian portals. After reaching tropical Mexico, it gave rise to two lineages, one centered in southwestern Mexico and the other in northeastern Mexico. One lineage is today represented by a single species and species group, *S. truquii*. The other lineage diversified into seven species groups, comprising the main part of the genus represented at present in North and Middle America.

The major part of the evolutionary history of the *truquii* lineage unfolded in Mexico and the southern part of the United States. To analyze the zoogeography of this lineage, I made detailed comparisons between species for geographic distributions, geographic variation, and vicariance, and refined limits for the areas of concentration in Fig. 263 accordingly. Resulting major areas of vicariance are shown in Fig. 264. Vicariance areas 1 and 6 are peripheral, corresponding approximately to concentration areas 1, 5, 6, 7, 11, and 12. High altitude regions of northern and central Mexico form a potent barrier to the dispersal of *Schizogenius* species, as suggested by greater dissimilarity between eastern and western areas of concentration than between northern and southern areas. Area 2 excludes all portions of the Colorado River except the Gila system, in recognition of northern limits of numerous species. Area 5 was recognized as separate from area 2 to account for northern limits of several southern species, to conform with distributional limits of *S. depressus*, and to exclude certain species endemic to area 2. And the northwestern limit of area 3 was refined to exclude *S. depressus*.

Vicariance areas 2 and 3, Sonoran and Texan regions, have similar latitudinal limits, and climates that may be described as warm temperate. Vicariance areas 4, 5, and 6 may be described as subtropical regions, respectively the Baja Californian, Sinaloan, and Tamaulipan regions. All these areas represent broad climatic zones; their boundaries are inexact, and surely have not been constant in the past. Probably, for example, northern boundaries of tropical areas 7 and 8 shifted southward to the Neo-Volcanic Axis during Pleistocene glacial maxima. These suggested boundaries are intended only to describe general, climatically limited, centers of speciation, not specific areas of distribution. Thus, exact locations of some boundaries such as those between areas 5 and 7 in the west and between areas 3 and 6 in the east are quite arbitrary, but this defect is more apparent than real. Other boundaries, as between areas 6 and 8, do represent abrupt faunal limits, but as noted above have not been constant over long periods of time.

Fig. 265-269 are vicariance maps showing evolutionary and zoogeographic pathways for species groups of the *truquii* lineage, and for taxa included in the *pluripunctatus, tristriatus, longipennis*, and *depressus* groups. These vicariance relationships were described in the section on the phylogeny of the *truquii* lineage, and following is a correlation of evolutionary and zoogeographic pathways with paleogeological events.

When the ancestor of the *truquii* lineage arrived in North America in Middle Oligocene, orogenic activity in Mexico was minimal. After divergence into eastern and western lineages in Late Oligocene, distributions of the ancestors of these lineages were maintained initially through competitive exclusion. In Early Miocene, orogenic and volcanic activity commenced along the Neo-Volcanic Axis and Sierra Madre Occidental, rendering vicariance areas 2, 5, and 7 relatively inhospitable for colonization. In areas 3 and 6, however, no mountain building took place then or subsequently, and these areas were thus particularly suitable for speciation of *Schizogenius* species.

Nothing certain can be said of the zoogeographic history of the *truquii* group. Doubtless some species diversification did take place, and doubtless vicariance was a factor, but all species except *S. truquii* subsequently disappeared. Limitations of habitat caused by orogenic disturbances hindered evolution of the group, and when elements of the more progressive sister group entered regions formerly occupied by members of the *truquii* group, the latter were simply eliminated.

Most early diversification in the rest of the *truquii* lineage, before Middle Pliocene volcanic quiescence, took place in Atlantic areas 3, 6, and 8, and resulted from isolations caused by shifts in climatic tolerance. The ancestor of the *arimao* subgroup of the *depressus* group entered Middle America over the Tehuantepec portal in Late Miocene, and spread to Cuba before the West Indies separated from Middle America. Also in Late Miocene or Early Pliocene, the ancestor of the *pluripunctatus* group entered the northern part of area 2, north of the intense tectonic activity in the Sierra Madre Occidental region. In Fig. 265 I show the split of the ancestor of the *truquii* group from its sister group in southern Mexico, latitudinal vicariance shifts in the ancestry of other groups in the lineage, and the immigration to the Sonoran region of the ancestor of the *pluripunctatus* group.

During the long geological quiescence of Middle Pliocene, ancestral elements of the *pluripunctatus* group became firmly entrenched in the Sonoran region, and spread westward and southward from there. One form, the ancestor of *S. seticollis*, became isolated in California, and spread into southern Baja California; in Early Pleistocene, in turn, this southern form became isolated as the ancestor of the living subspecies *S. s. vandykei.* Another form, the ancestor of *S. plurisetosus* and *S. multisetosus*, became isolated in southern Mexico in Late Pliocene, perhaps by renewed volcanic activity in the Neo-Volcanic Axis. Vicariance patterns in the *pluripunctatus* group were completed in Early Pleistocene when ancestral forms of *S. pluripunctatus* and *S. kulti*, and of *S. plurisetosus* and *S. multisetosus* were divided into tropical and subtropical isolates, perhaps also by vulcanism in the Neo-Volcanic Axis. Subsequently, northern limits of the tropical forms shifted northward to their present locations, and the more progressive *S. kulti* displaced the more conservative *S. multisetosus* from most lowland parts of its range. These events are summarized in Fig. 266.

No elements of the *tristriatus* group evolved in Pacific drainage systems (Fig. 267), although one species, *S. tibialis* (Fig. 188), has successfully penetrated the area. The ancestor of one species, *S. tristriatus*, reacquired tropical adaptations in Late Miocene or Early Pliocene, but probably never did penetrate south of the then active Neo-Volcanic Axis. The ancestor of its sister group, which had retained subtropical adaptations, subsequently differentiated into warm temperate and subtropical lineages. Of the subtropical lineage, differentiation into subtropical and tropical forms led to the speciation of *S. dilatus* and *S. tibialis*. Ancestral *S. tibialis* spread southward to the Isthmus of Tehuantepec, from there into the Rio Balsas and Rio Grande de Santiago drainages, and returned northward across the highlands of central Mexico into subtropical area 6 and even into southernmost warm temperate area 3. Zoogeographic history of the warm temperate ancestor of the

amphibius and *planulatus* subgroups was one of a tendency to acquire cool temperate adaptations. In Middle Pliocene, ancestral *S. amphibius* became isolated in cool temperate area 1 and subsequently spread into the Appalachian region, to which it was restricted in Pleistocene time. In Late Pliocene, the ancestor of *S. planulatus* and *S. ozarkensis* was isolated in the cool temperate area, and differentiated into those species in Pleistocene.

The ancestor of the *longipennis* group (Fig. 268) was the first element of the subtropical and warm temperate adapted branch of the *truquii* lineage to return to tropical areas and extend south of the Neo-Volcanic Axis. In Middle Pliocene, a western vicariant, ancestor to *S. pacificus*, spread through western areas 5 and 7. The eastern vicariant followed later, and in Late Pliocene the ancestor of *S. chiricahuanus* was isolated in area 2 by renewed volcanic activity in the Neo-Volcanic Axis. In Early Pleistocene, the ancestor of *S. neovalidus* and *S. longipennis* spread into area 2, and ancestral *S. neovalidus* became isolated there by Pleistocene events. More recently, the progressive *S. longipennis* also extended northward into area 2, and displaced the more conservative *S. chiricahuanus* and *S. neovalidus* from most parts of their ranges except relict higher elevation strongholds.

The ancestor of the *arimao* subgroup (Fig. 269) acquired tropical adaptations in Late Miocene, and was the only member of the *truquii* lineage to enter Middle America over the Tehuantepec portal. Indeed, it was the only North American member of the genus to enter Middle America before Late Pliocene elevation of the Isthmus of Tehuantepec. This ancestral form spread into Cuba before severance of Cuba from the mainland, but since Early Pliocene *S. arimao* evolved in isolation. The ancestor of remaining Middle American forms differentiated into the ancestors of *S. emdeni* and *S. "apicalis"*. In Early Pleistocene, after closure of the Panamanian portal, South America was penetrated and widely colonized by the ancestor of *S. "apicalis"*.

The ancestor of the rest of the *depressus* group entered warm temperate Texas, and differentiated into one line that continued to evolve there and another that became isolated in cool temperate areas. The cool temperate form spread across northern parts of the continent, and differentiated into modern *S. litigiosus* and *S. sulcifrons* in Early Pleistocene. In Middle Pliocene, the long period of volcanic quiescence in the west, one line of the *depressus* subgroup became isolated in the Sonoran Region. The ancestor of *S. depressus* penetrated northward, acquired cool temperate adaptations, and subsequently extended southward through the Sonoran region into high elevation areas of central Mexico. In Early Pleistocene, another cool temperate form, ancestor of *S. ochthocephalus*, was isolated in northern California. Its sister species spread southward through area 5 into northern parts of area 7, northward into the Colorado River area of western part of area 1, and eastward into area 3 from which it spread north into central parts of area 1 and south into area 6. Zoogeographic origins of *S. pygmaeus* and *S. scopaeus* are less well shown in Fig. 269. Their ancestor was widespread in eastern areas 3, 6, and 8 in Middle Pleistocene, but Late Pliocene vulcanism resulted in northern and southern isolates. In Late Pliocene or Early Pleistocene, the ancestor of the northern form spread westward into the Sonoran region, and formed an isolate there. This western form spread northward into California, and southward into southern Mexico where it reestablished genetic contact with the southern isolate. By Late Pleistocene, however, reproductive isolation had developed between the form in Texas, ancestral to *S. scopaeus*, and the southern form which, reconnected with the Sonoran form constitutes modern *S. pygmaeus*. Also in Late Pleistocene, Californian *S. pygmaeus* evolved into statistically differentiated northern and southern isolates.

With this background, more can be said about distribution of the *ferrugineus* group. Probably before entry of the *truquii* lineage into the area, ancestral forms of the *ferrugineus* group were represented throughout Mexico and southern United States. Paleogeological

events in southern and western Mexico from early Miocene contributed to elimination of the group from that area. Concurrently, spread of progressive and actively evolving members of the *truquii* lineage into eastern areas 3, 6, and 8 resulted in displacement of members of the *ferrugineus* lineage from that entire region. One line did reach cool temperate areas of central and eastern United States, and there perfected adaptations to life in sandy habitats, and, consequently, was not eliminated when gravel bar adapted forms of the *truquii* lineage penetrated cool temperate regions. Western United States meanwhile may have been generally untenable for colonization by members of the *ferrugineus* lineage because of tectonic and orogenic activity. Alternatively, members of the group living there lacked special adaptations and were displaced by more progressive elements of the *truquii* lineage from Middle Pliocene onward. In Middle Pliocene, however, the ancestor of *S. auripennis* succeeded in penetrating the Sonoran region, and subsequently extended southward into tropical regions as far as southern Middle America, and special adaptations prevented competitive displacement by members of the *truquii* lineage.

Before Early Pliocene, members of relatives of the *truquii* group may well have occupied the Sonoran region and perhaps even California, but since then and particularly since Middle Pliocene were in competition with members of more advanced lineages, and gradually eliminated. A study of ecological specializations of *S. truquii* might reveal reasons for its apparent success in continued survival.

Little can be said about the evolutionary and zoogeographic histories of the monotypic *brevisetosus*, *sallei*, and *lineolatus* groups, all with probable Texan origins (Fig. 265). *S. brevisetosus* seems a relict species, and other elements of the *brevisetosus* group may have been eliminated through competitive displacement by other forms with better developed limestone adaptations. Curiously, the known distribution of *S. brevisetosus* is allopatric in relation to distributions of members of the *pluripunctatus* group, despite loss of limestone adaptations of the latter. In contrast, distributions of *S. sallei* and *S. lineolatus* are not evidently relict, and within their respective ranges both tend to be numerically dominant over all others in the genus. Perhaps the relatively great vagility of these species is a partial explanation of the absence of close relatives; if new areas are colonized, gene flow tends to continue, and no geographic isolation results. The only clear exception to this pattern is in the Rio Grande isolate of *S. lineolatus*. I suspect this form is a relict from cooler Pleistocene times, when the distribution of the northern form of the species extended further south than it presently does.

In summary, my reconstructed phylogeny seems completely compatible with what is known about paleogeological events, and I think I have described evolutionary and zoogeographic pathways that have a high probability of correctness. It is my hope that future workers will test these hypotheses in comparative studies on ecology, physiology, biochemistry, and larval taxonomy.

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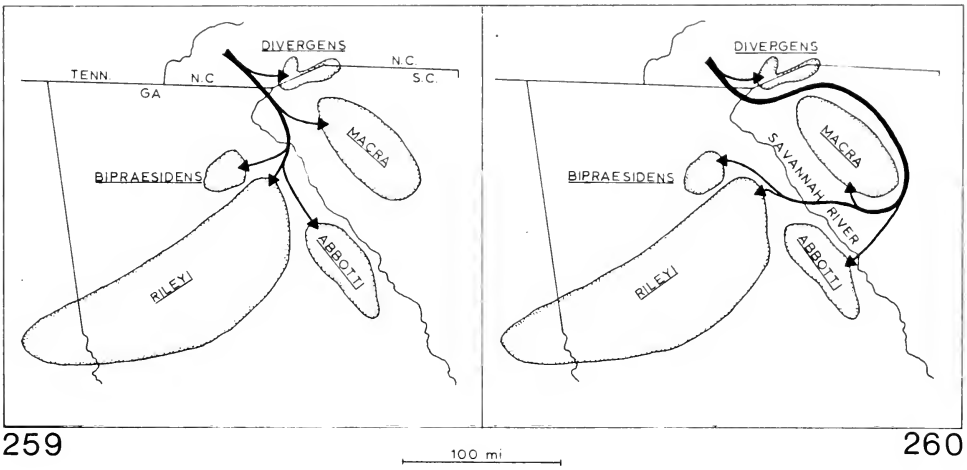


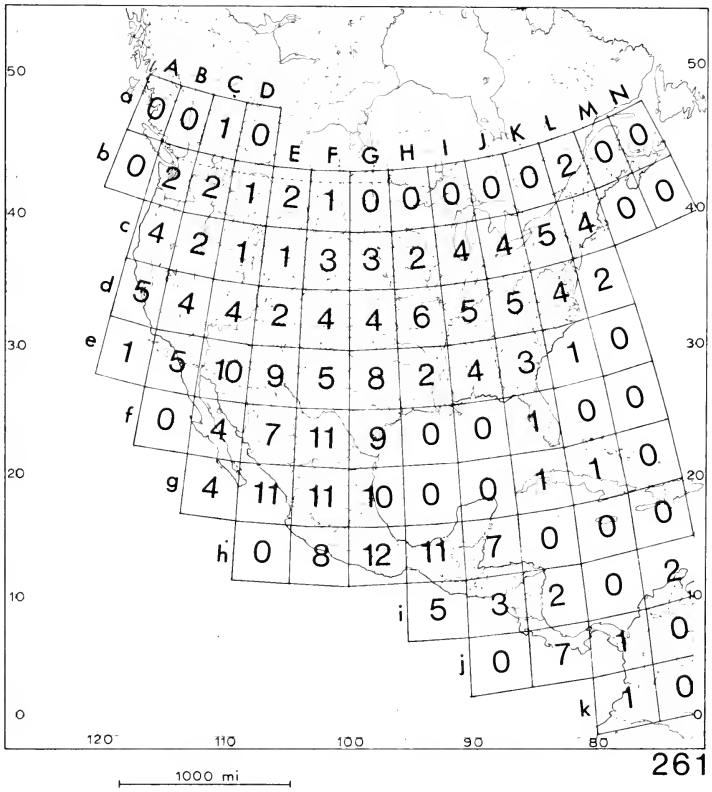
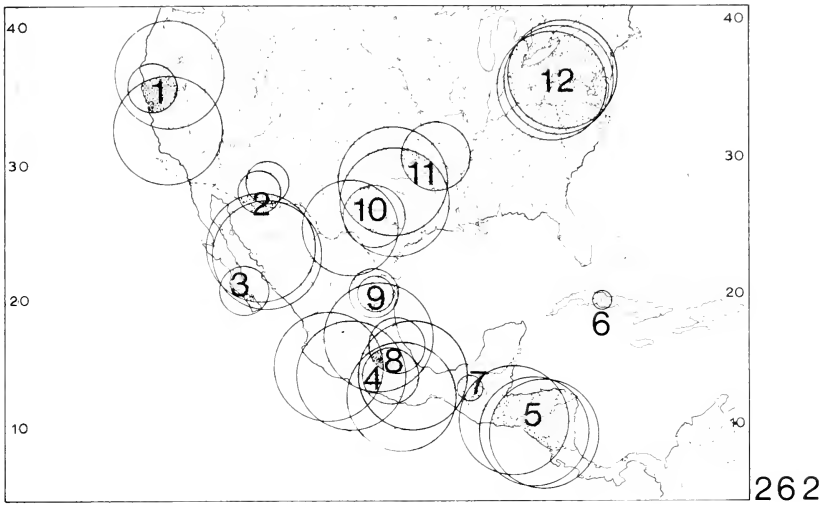
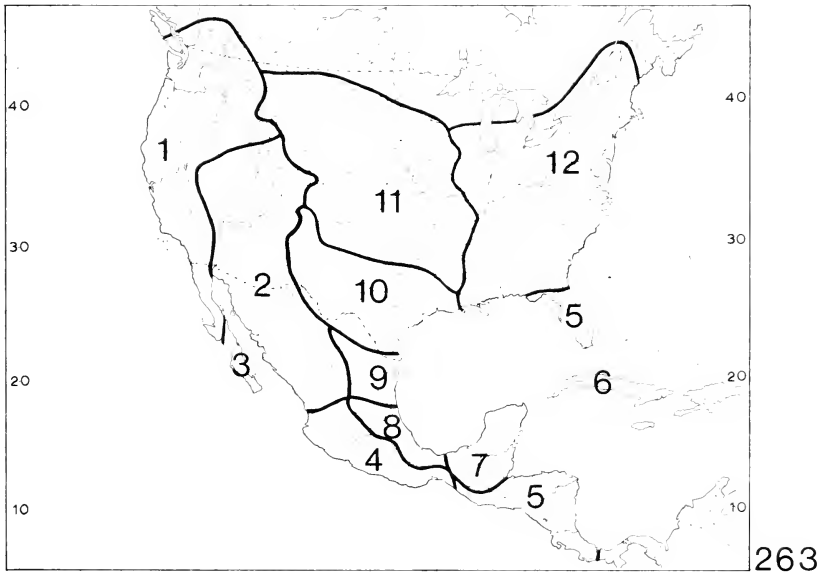


Fig. 259-260. Evolutionary zoogeography of the milliped genus *Cleptoria.* 259. As suggested by R. L. Hoffman (after Hoffman, 1967). 260. As reinterpreted. Fig. 261. Numbers of species of *Schizogenius* in 5° intervals, as used in Table 70.





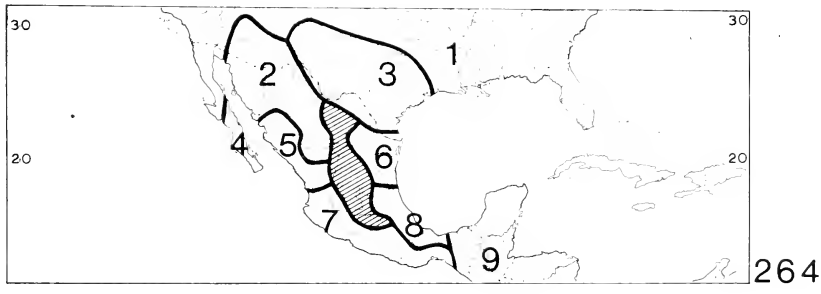
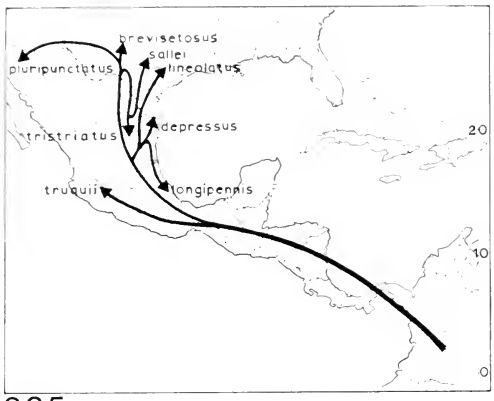


Fig. 262. Centers of concentration of species of the genus *Schizogenius* in North and Middle America. Fig. 263. Areas of concentration of species of the genus *Schizogenius* in North and Middle America. Fig. 264. Areas of vicariance for species of the genus *Schizogenius* in North and Middle America; shaded area represents uplands.



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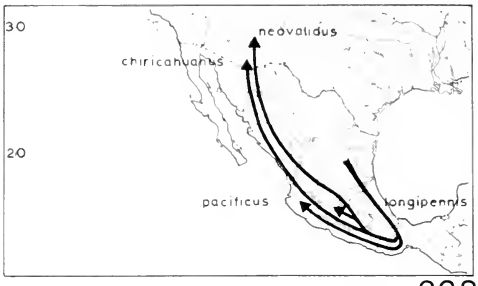

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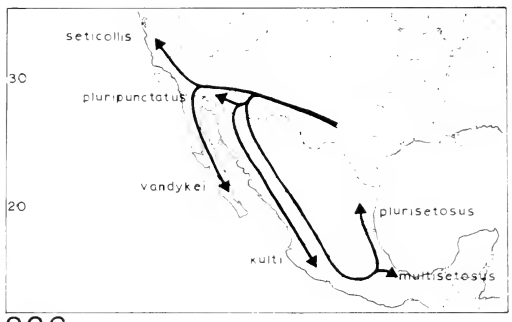

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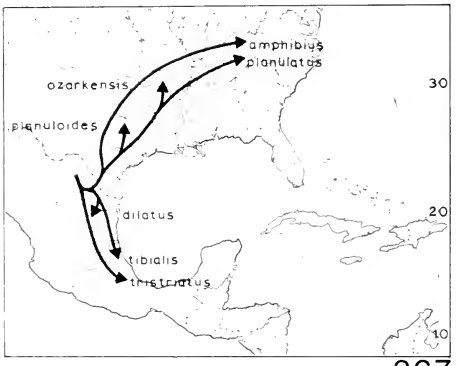

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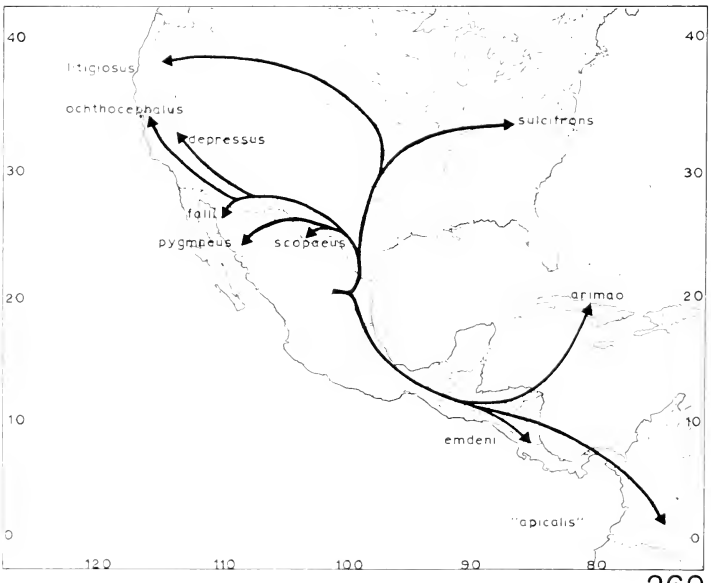

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Fig. 265-269. Evolutionary zoogeography. 265. Species groups of *truquii* lineage. 266. Species and subspecies of *pluripunctatus* group. 267. Species of *tristriatus* group. 268. Species of *longipennis* group. 269. Species of *depressus* group.

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ANNOUNCEMENTS

Biting Fly Control and Environmental Quality – Proceedings of a Symposium held at the University of Alberta in Edmonton, May 16, 17, and 18, 1972.

The proceedings of this symposium, which was organized jointly by the Department of Entomology at the University of Alberta and the Advisory Committee on Entomology of the Defence Research Board, are expected to be published before the end of 1972. A further announcement will follow.

Entomology and Education – Proceedings of a Symposium held at the University of Alberta in Edmonton, May 19, 1972.

The proceedings of this symposium organized by the Department of Entomology at the University of Alberta to mark the 50th anniversary of its foundation are expected to be published as a supplement to Volume 8 of *Quaestiones entomologicae* at no extra cost to subscribers. A further announcement will follow.

An English translation of Rohdendorf's Historical Development of the Diptera edited by Harold Oldroyd and Brian Hocking will be published by the University of Alberta Press before the end of 1972. The estimated purchase price will be approximately $12.00 per copy. A further announcement will follow.

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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A TEMPERATURE CONTROLLED CAPACITANCE-TYPE ACTOGRAPH FOR CRYPTOZOAN ARTHROPODS

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During an investigation of the locomotor activity rhythms of intertidal beetles the need arose for an actograph especially suitable for these animals which spend a great deal of their time in crevices or under stones. The actograph also needed to be kept at a constant temperature without using an expensive and noisy growth chamber. A review of the literature on the many kinds of actographs used with insects indicated that the most suitable way to detect animal movement is through the use of electronic transducers. In the capacitance-type transducer a movement of the test animal causes a change in capacitance which is detected as a frequency change and amplified into a voltage output signal. Therefore, the electronic circuit of the sensing apparatus described by Schechter, Dutky and Sullivan (1963) and later modified by Grobbelaar et al. (1967) was, with minor modification, adapted for the actograph described here.

The sensors, however, differ from those used by the above authors. These formed a part of two parallel 5 mm x 11.5 cm x 11.5 cm plexiglass plates between which the insect is placed as shown in Figure 1. The thin wire forming the electrode on the bottom of the top plate is positioned to form a series of loops starting from one edge of a 10.5 cm circle and ending at the other edge and then going on to a ground terminal. In contrast, in order to obtain a maximum non-uniform electric field between the two plates, the other electrode wire consists of a 10.5 cm spiral starting from the center of the top surface of the bottom plate and eventually leading to the detector circuit. A change in capacitance due to a movement of the test insect is detected at the junction between the top electrode and the bottom one so that the insect need not touch either of the wires. The closer the wire spirals or the loops or the distance between the two electrodes the more sensitive is the actograph to small movements. The 31 gauge electrode wires were placed into grooves scored into the plates and held there by brushing over them a thin layer of plexiglass dissolved in ethyl acetate.

The thickness of the spacer is determined by the height of the insect so that ideally the insect is able to move freely about with the two parallel plates as close as possible to each other. A series of plexiglass spacers were made ranging in thickness from 0.25 to 3.5 mm and any of these, either alone or in combination, can be used for insects of varying heights. A test insect was first measured for height before placing in the actograph by viewing it in the bottom of a narrow glass vial with a micrometer hand lens.

Sometimes the test insect is kept in the actograph for periods of 10 to 14 days and in order to provide the high humidity and water necessary for hygrophilic insects two methods were employed, both involving some modification of the bottom plate. Where very high humidity was necessary, holes were drilled between the wire spirals of the bottom plate which was then tightly connected with screws to a plexiglass container of water. By using a graduated glass tube connected with flexible tubing to this water container the water level could be adjusted so that the holes in the bottom plate were almost filled with water. Loss of water through evaporation was measured by the graduated tube and water was added when necessary during a test. Where high humidity is not critical a cotton wick was inserted into a 2 cm x 0.25 cm inside diameter tube which was inserted into the center of the bottom plate and suspended over a container of water. The top of the wet wick just barely protruded above the top of the bottom plate. A few holes can be drilled between the wires in the top plate to maintain an air supply and a larger hole can be used for placing the insect into the space between the plates. This larger hole is then corked during the operation of the actograph.

The only modification of the electronic circuit described by Grobbelaar et al. (1967) consisted of the use of AC power with two regulated power supplies instead of a battery source. One power supply (± 10 volts) was used for the sensing part of the circuit while the other (± 15 volts) powered an amplifier and a comparator that switched a relay at selected output voltage peaks. In this way the activity record could consist of an analog tracing or a count of voltage peaks per unit time. A potentiometer allowed a range of voltage peaks from 0.1 volts to 10 volts to switch the relay thereby providing a means of sensitivity adjustment. The relay signals were counted and printed at hourly intervals on a Sodeco counter-printer.

Unless walk-in constant-temperature chambers are available, actographs are normally operated in constant-temperature cabinets such as plant growth chambers. Unfortunately with these cabinets the cooling compressor is often exceedingly noisy and the very noticeable on and off cycle of the compressor could influence an activity rhythm of a test animal. Figure 1 shows a non-cyclical constant-temperature container for holding the actograph. The container consists of a fiberglass-encased top and bottom of equal dimensions (34 cm x 34 cm x 14 cm) separated by two 13 mm thick foam rubber pads. A length of 6 mm outside diameter copper tubing, closely coiled in circles to form a 25 cm inside diameter cylinder, was placed in the top and bottom containers with inlet and outlet connections protruding from the sides. The spaces between the tubing and the walls of the containers were filled with poured-in foam insulation. Provided a styrofoam cover or base is used both top and bottom containers can be used alone or they can be used together as shown in Figure 1. In this case the cables from the temperature, humidity and capacitance sensors as well as the flexible tubing for the water supply fit between the two layers of foam rubber. The base of the bottom container is 2.5 cm thick foam insulation encased in fiberglass while the top of the top container which can be used for viewing the actograph consists of two sheets of 6 mm thick plexiglass separated by 1.5 cm of air space. The copper tubing is connected to a constant-temperature circulating bath and equilibrium is usually obtained after about 2 hours depending on the temperature required and ambient temperatures. I have been using two complete actographs in constant-temperature containers as shown in

Figure 1 connected to a Haake circulating water bath maintaining a temperature of 18.0° ± 0.25°.

An example of the kind of results that can be expected with this type of actograph is shown in Figure 2. Specimens of *Alphitobius piceus* (Tenebrionidae) were kept in the dark for two months (group A) while another group was exposed during this period to alternating 12 hours light and 12 hours darkness (group B). After this time five specimens of each group were placed in the actograph under dark conditions for 10 days. As is evident from Figure 2 the group kept in the dark for two months were arhythmic while the other group maintained a periodicity of 23.75 hours (periodogram analysis; *see* Enright, 1965), for the 10 days of activity measurements.

The actograph described here has proved to be very suitable for carabid beetles (a total of 18 species representing members of riparian, forest litter, marsh, intertidal and open-field habitats have been tested so far) and it probably can be used successfully with other cryptozoan animals such as chilopods, diplopods, mites, pseudoscorpions as well as beach-inhabiting isopods and amphipods.

ACKNOWLEDGEMENTS

My thanks go to P. Hardybala and W. Diachuck for constructing the constant-temperature containers and the actograph respectively.

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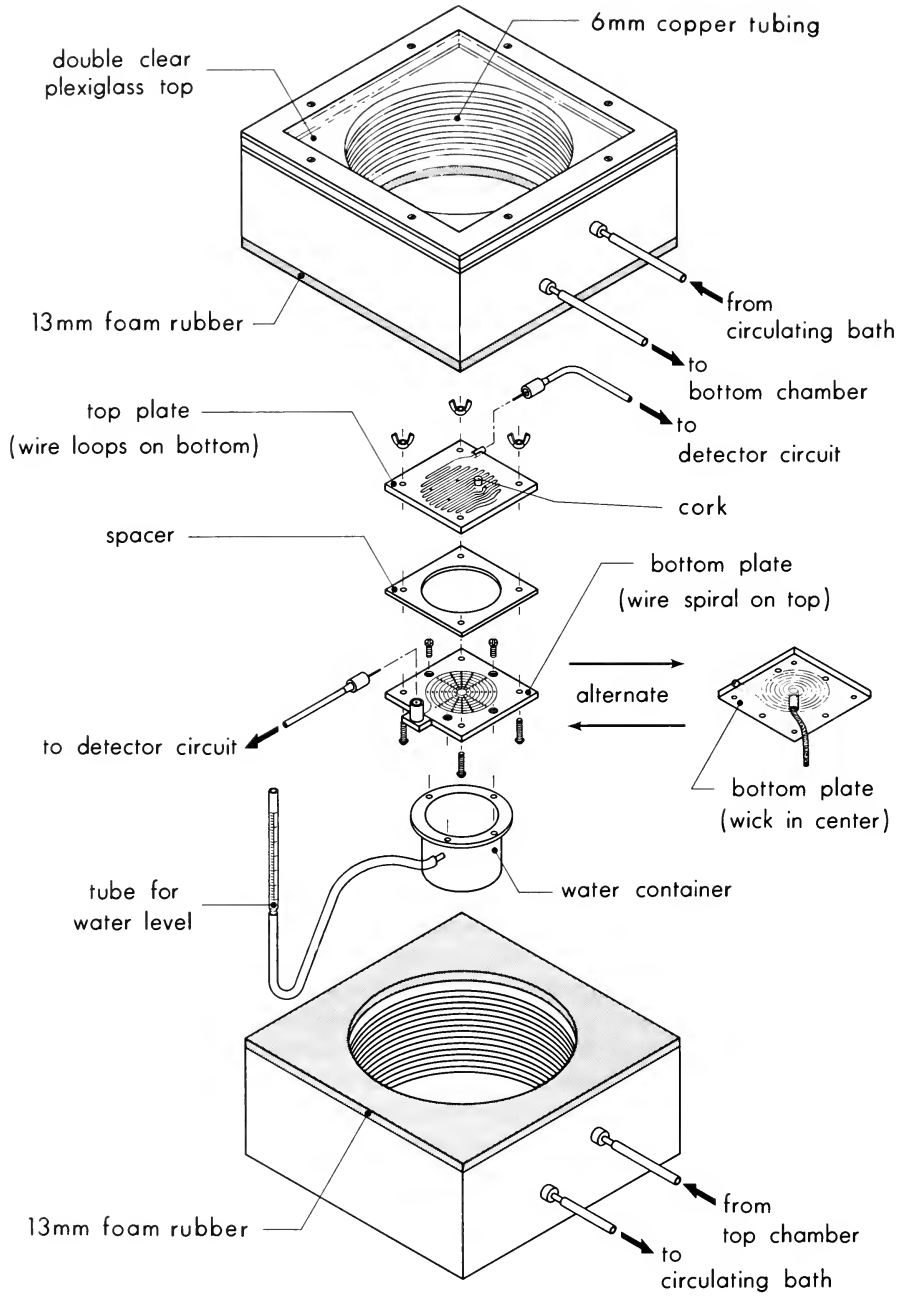

Figure 1. An exploded view of the sensors of the capacitance-type actograph and the constant temperature containers.

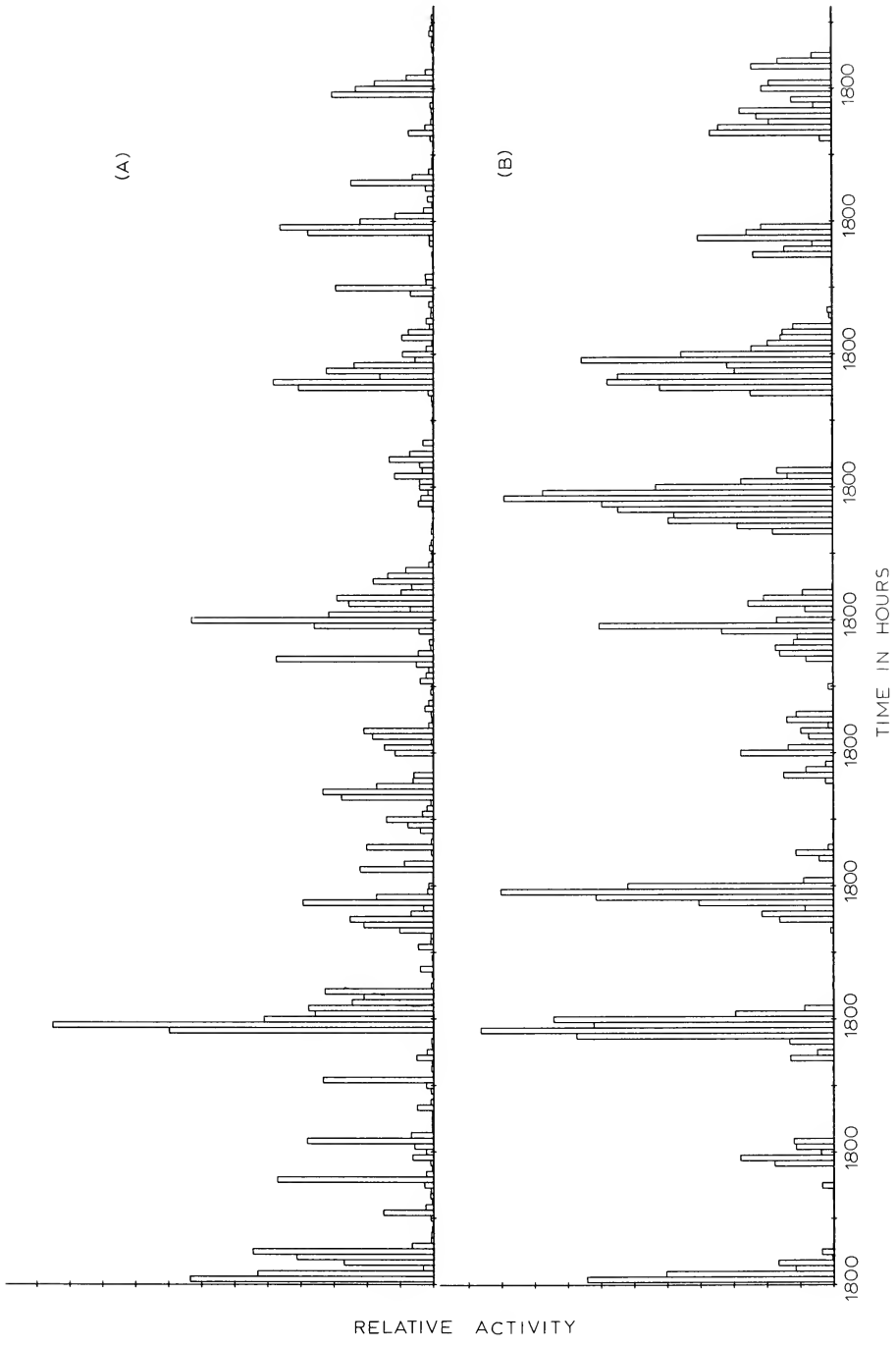

Figure 2. A 10-day activity record of two groups of five specimens of *Alphitobius piceus* obtained with the actograph in darkness. Group A were kept in the dark for two months prior to the test while group B were subjected to a DL 12:12 at the same time.

FAMILIAL AND SUBFAMILIAL CLASSIFICATION OF THE TENEBRIONOIDEA (COLEOPTERA) AND A REVISED GENERIC CLASSIFICATION OF THE CONIONTINI (TENTYRIIDAE)

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The presence of visible membranes between the terminal abdominal sternites of Tenebrionidae and related families is correlated with the presence of defensive glands which empty posterad of sternite 7. Species which lack defensive glands consistently have the aedeagus inverted from the typical position in most Coleoptera. These complex, correlated characters indicate a fundamental division among the Tenebrionoidea and several changes in the classification of these beetles are proposed accordingly.

Morphological comparisons of several tribes, principally the Coniontini, Praocini and Zophosini are summarized. The results indicate that the Zophosini are closely related to other African tribes such as the Adesmiini. The Praocini show close affinities to the South American Nycteliini and Physogasterini. The North American Coniontini and Coelini likewise share great affinity. While the taxa from these geographic regions are superficially similar, they differ in major structural features and are not closely related.

Finally, taxonomic changes intended to simplify the classification of the Coniontini and Coelini are proposed, with a revised generic checklist and key.

La présence de membranes visibles entre les sternites abdominales terminales des Tenebrionidae et des familles apparentées est en rapport avec la présence de glandes défensives qui s'ouvrent derrière le sternite 7. Les espèces dépourvues régulièrement de glandes défensives ont l'aedeage renversé par rapport à la position normale chez l'ensemble des coléoptères. La correspondance de ces caractères complexes indique une division fondamentale parmi les Tenebrionoidea et nous proposons en conséquence plusieurs modifications dans la classification de ces coléoptères.

Nous résumons les comparaisons morphologiques entre plusieurs tribus surtout celles des Coniontini, des Praocini et des Zophosini. Les résultats indiquent que les Zophosini sont en rapport étroit avec d'autres tribus africaines telles que les Adesmiini. Il y a des affinités étroites entre les Praocini et les Nycteliini et les Physogasterini sud-américains. Ces rapports étroits se retrouvent également chez les Coniontini et les Coelini nord-américains. Tandis que les groupes de ces régions géographiques n'accusent que des ressemblances superficielles, ils diffèrent par leurs caractéristiques structurales fondamentales et ne sont pas apparentés de façon étroite.

En fin de compte, nous proposons des modifications taxonomiques qui ont pour but de simplifier la classification des Coniontini et des Coelini et fournissons à l'appui une liste générique modifiée ainsi qu'une clef.

SUBFAMILY CLASSIFICATION OF THE TENEBRIONIDAE

Watt (1966) reviewed and summarized the various classifications which have been proposed for the Tenebrionidae. Consequently, only the most important works will be mentioned here. Tenebrionidae is used in the restricted sense of Crowson (1955) and Watt

(1966, 1967). Based on the structure of the procoxae, mesocoxae and aedeagus they exclude such genera as *Boros*, *Dacoderus*, *Tretothorax*, *Perimylops* and *Zopherus* et al. Watt (1967) also cites evidence indicating a close relationship of the Alleculidae, Lagriidae and Nilionidae to the Tenebrionidae. These families, together with the Zopheridae and Monommidae, are referred to here as Tenebrionoidea. In his analysis of the taxonomic position of *Petria* (Alleculidae: Omophlinae) Lawrence (1971) also mentions several characters which are important in the classification of the Tenebrionoidea.

The most recent classification of the Tenebrionidae treating the world fauna is that of Lacordaire (1859). This century-old work emphasizes external differences, especially in mesocoxal structure and mouthparts. In a broad sense, Lacordaire's primary divisions into Sections and Cohortes correspond to the subfamilies of more recent classifications. However, the Cohortes of his Section II are based on the vestiture of the tarsi. As noted by Watt (1966), this feature is probably related to the substrate on which the beetles walk, and is not a reliable taxonomic character. Consequently, Lacordaire's Section II, Cohorte I contains an assortment of unrelated tribes now assigned to different subfamilies. It should be mentioned that nearly all Lacordaire's tribes and subtribes are recognized as tribes today. Many of the numerous tribes proposed by subsequent workers, especially Casey (1907, 1908) and Reitter (1917) contain very few genera. These small tribes have served mainly to occlude the interrelationships within the family.

LeConte (1862), LeConte and Horn (1883) and Horn (1870), considering primarily the North American fauna, recognized three subfamilies. Their most important contribution was an appreciation of the taxonomic importance of the intersegmental membranes between the terminal abdominal sternites. They delimited the Tenebrioninae by the presence of external intersegmental membranes. The remainder of the family, with internal membranes, they divided between the Tentyriinae (mesocoxal cavities enclosed by the sterna; mesotrochantin concealed) and the Asidinae (mesocoxal cavities open laterally; mesotrochantin visible).

Most recent classifications (Gebien, 1910-11, 1937, 1938-44; Arnett, 1960) combine features of the arrangements of LeConte and Lacordaire, and differ from one another in minor ways. An exception is the proposal by Koch (1955) to divide the Tenebrionidae into only two subfamilies, depending on the condition of the membranes between the terminal abdominal sternites. On this basis, Koch combined the Asidinae with the Tentyriinae, also pointing out that the mesocoxal structure of the African Asidini does not conform to LeConte and Horn's criterion of the presence of a distinct trochantin. Brown (1971) has shown that the condition of the trochantin is also variable in the North American Asidini. Koch's classification is supported by the evidence presented below, and the name Tentyriinae will be used in the sense he advocated.

MORPHOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF THE TENEBRIONOIDEA

Adults

Although most recent workers agree that the presence of external abdominal membranes is important as a diagnostic character, the high correlation with the presence of abdominal glands and reservoirs has not been noticed. The reservoirs are paired, cuticular invaginations surrounded by diffuse glandular tissue. They empty through ducts which open posterad of sternite 7 (visible sternite 5). Morphological studies by Blumberg (1961), Eisner, McHenry, and Salpeter (1964) and Kendall (1968) show that the glands and reservoirs are apparently homologous throughout the Tenebrionidae, Alleculidae and Lagriidae. Dissections made by the author reveal that similar glands are also present in the Nilionidae. The secretions

produced by these glands are probably defensive since they consist largely of quinones and other irritants (*see reviews by* Eisner and Meinwald, 1966; Schildknecht et al., 1964). The structural details of the glands and reservoirs are the subject of a comprehensive comparative study (Tschinkel, *in progress*) which may clarify the relationships among those Tenebrionidae which possess glands.

A survey by the author of over 45 tribes of Tenebrionidae, as well as members of the other families mentioned above, has revealed a nearly perfect correlation between the presence of glands and external membranes between abdominal sternites 5, 6, and 7. The single exception is the Pimeliini, where membranes are visible, as noted by Watt (1966), but reservoirs and glands are absent.

A further correlation exists between the occurrence of glands and the orientation of the aedeagus in the retracted position. As first noted by Sharp and Muir (1912) and elaborated by Blaisdell (1939), the aedeagus is rotated 180° in some Tenebrionidae, so that the primitively ventral surface is dorsal. This rotation, which also occurs in the Dacoderidae (Watt, 1967), some Salpingidae (Spilman, 1952) and the Monommidae (Sharp and Muir, 1912) is rather inappropriately termed inversion by coleopterists. With one known exception, Tenebrionidae with the aedeagus inverted lack defensive glands, while species with the aedeagus in the normal position possess them. The exception is the Cossyphini, a small Palearctic-African tribe whose members are specialized for living beneath bark. In these beetles the aedeagus is oriented with the tegmen dorsad, but defensive glands are absent and the terminal abdominal membranes are internal. This tribe is highly modified morphologically, particularly in thoracic structure, and more detailed studies will be required to clarify its relationships. Possibly the defensive glands have been lost secondarily.

The very high correlations among these highly complex structures is a fundamental difference separating the Tenebrionoidea into two distinct groups. The tenebrionid subfamily Tenebrioninae, together with the Alleculidae, Lagriidae and Nilionidae possess defensive glands and external abdominal membranes and have the aedeagus in the normal position. The subfamily Tentyriinae (*sensu* Koch) and the Monommidae lack defensive glands, have the terminal abdominal membranes internalized, and have the aedeagus inverted. In addition, these two groups seem to have evolved in different ecological situations. The Tenebrioninae, etc., are predominant in woodland habitats in tropical or subtropical climates, and many species are adapted to feeding on fungi or in rotting wood. Most of the species of this group which occur in temperate regions occupy relatively mesic, woodland habitats. Contrastingly, the Tentyriinae occur primarily in arid or subarid habitats in temperate climates, with highly distinct faunas in the deserts of southern Africa, Eurasia, South America, and southwestern North America. Nearly all of the species in this group are soil dwellers. There are exceptions to these generalizations, such as the Eleodini (Nearctic) and the Blaptini (Palearctic), which contain many species adapted to aridity, but clearly belong to the Tenebrioninae. Conversely, the Epitragini (Tentyriinae) are widespread in tropical regions, especially in the western hemisphere. These exceptions, coupled with the fact that the more generalized members of both subfamilies are winged, clearly show that loss of defensive glands and flight are not simply associated with adaptation to arid environments. Indeed, the diverse array of components in the defensive secretions (Tschinkel, *in progress*), and the variability of the associated delivery systems, especially in those Tenebrioninae inhabiting arid environments, suggests that the secretions have been very important in the evolution of these beetles. For instance, some species of *Blaps*, *Eleodes* and *Centronopus* are capable of spraying fine jets of secretion up to 30 cm. The elytra of other species, such as *Cibdelis blaschkei* Mannerheim are impressed with fine canals along which the secretions flow, rapidly coating the posterior portion of the body.

Larvae

The great majority of tenebrionid larvae which have been associated with adults are in the subfamily Tenebrioninae (*see* Korschevsky, 1943; Van Emden, 1947; Hayashi, 1966, 1968). Recently, larvae of several tentyriine tribes have been adequately characterized, including Erodiini, Akidini, Epitragini, Tentyriini, and Asidini, chiefly by Russian workers (Keleynokova, 1963, 1971; Skopin, 1960, 1962, 1964). Schulze (1962, 1964) and Marcuzzi and Rampazzo (1960) have described larvae from some additional tribes (Lepidochorini, Adesmiini, Coniontini, Coelini). Skopin (1964) and Keleynokova (1963) have attempted to use their results to produce larval classifications. Skopin's primary division splits the Tenebrionoidea into two groups, based on the structure of the legs. His Pedobionta includes all soil inhabiting larvae, in which the anterior legs are enlarged and modified for digging. The Pedobionta correspond to the Tentyriinae, with the addition of the Blaptini, Opatrini and Platyscelini of the Tenebrioninae. The Eleodini and Scaurini would also belong to the Pedobionta on the basis of leg structure. Skopin's Heterobionta incorporates the remainder of the Tenebrioninae as well as the families Alleculidae, Lagriidae and Nilionidae.

Clearly, Skopin's primary division is based on a highly adaptive feature. Keleynokova (1963) points out that soil inhabiting larvae are characterized by the absence of urogomphi as well as enlarged forelegs. Urogomphi are commonly present in the Tenebrioninae, and are apparently used in moving backward through the tunnels these larvae excavate in ligneous substrates. In Tenebrioninae which inhabit soil the urogomphi are reduced or absent (e.g., Blaptini, Eleodini, Pedinini). *Tenebrio* (Tenebrionini) is exemplary in this regard. Species of this genus infest stored grain products, which are probably similar to soil in physical properties. The anterior legs of *Tenebrio* are enlarged and the urogomphi are much reduced. For these reasons, Skopin's placement of the Blaptini, Opatrini, etc., in the Pedobionta is judged in error. The same conclusion was reached by Keleynokova (1963), who placed these tribes in a separate subfamily within the "tenebrioid line." In most respects, however, Keleynokova's classification into six subfamilies does not correspond to relationships indicated by adults. As noted by Watt (1966), her subfamilies are not clearly defined, and it is impossible to evaluate them at present.

One larval characteristic which is not stressed by Skopin or Keleynokova is the configuration of the mandibles. In the Tentyriinae the larval mandibles bear a dorsolateral prominence which is densely set with coarse setae. Setae on the mandibles of the Tenebrioninae, Alleculidae, etc., are never restricted to an elevated, dorsolateral region. The distribution of these character states is very highly correlated with the presence of defensive glands and the orientation of the aedeagus, and further supports a primary division of the Tenebrionoidea into two taxa.

Another character which may be of taxonomic importance is egg size. In the few tribes which have been investigated, the eggs are relatively large in the Tentyriinae (Asidini, Coniontini, Nyctoporini, Cryptoglossini) and small in the Tenebrioninae (Tenebrionini, Coelometopini, Ulomini) (Doyen, *unpublished*).

Skopin's (1964) subdivisions of his Heterobionta suggest several interesting relationships which reinforce the conclusions here derived from adult characteristics. His "Ulomimorpha" includes the Alleculidae as well as the Ulomini, and he flatly states that these should be placed in the same family on the basis of larval features. His "Pycnocerimorpha" includes the Goniaderini, Heterotarsini and Pycnocerini, tribes which have always been placed in the Tenebrioninae. On the basis of larval features, however, they are very similar to the Lagriidae. Hayashi (1968) also reached this conclusion from his studies of Japanese members of these taxa.

Evidence concerning the Nilionidae is not clear-cut. The adults greatly resemble members of the Leiochrini (Tenebrioninae), and Böving and Craighead's larval characterization is based on *Leiochrodes* sp. The characters listed by Skopin (1964) for the Nilionidae fit known larvae of the Leiochrini. However, he does not specify the taxa on which his concept is based, and the larva of *Nilio* appears to be unknown.

RECLASSIFICATION OF THE TENEBRIONOIDEA

The major morphological and ecological differences described above, and the extreme diversity in body form in both subfamilies, suggest that they have been evolving separately for a long time, and that the Tenebrionidae as now constituted are probably polyphyletic. Biogeographic evidence also lends tentative support to this conclusion. The Tenebrioninae, Alleculidae and Lagriidae enjoy a world-wide distribution, especially in the tropics. Contrastingly, the Tentyriinae, although widely distributed in temperate regions, are almost entirely absent from Australia and New Zealand, where a few tribes of the Tenebrioninae have radiated extensively into arid habitats. The few Australian genera previously included in the Tentyriinae have mostly been removed to other families (e.g., *Tretothorax*, *Zopherosis*: *see* Böving and Craighead, 1931; Crowson, 1955; Watt, 1966, 1967). These distributions suggest that the evolutionary line producing the Tenebrioninae arose before the separation of the Australian land mass. The Tentyriinae apparently differentiated after the separation of Australia, probably in southern Africa, which unquestionably supports the most diverse and distinct fauna now known (Koch, 1955).

If the correlated differences described above are to be reflected in the classification of the Tenebrionoidea, the Tenebrioninae, Alleculidae, Lagriidae and Nilionidae should be treated as a single taxon, coordinate with the Tentyriinae. I feel that these relationships are best reflected by recognizing a family Tentyriidae and placing the Alleculidae, Lagriidae, Nilionidae and Tenebrioninae as subfamilies of the Tenebrionidae. The Monommidae, which share most of the characters of the Tentyriidae are differentiated by having all the abdominal sternites flexibly connected by internal membranes and the front coxal cavities open, and should clearly be recognized at the family level. The proposed arrangement is compared with previous classifications in Table 1.

In addition, a number of tribes are incorrectly placed in the Tenebrioninae in recent classifications (Gebien, 1938-44; Arnett, 1960). According to the criteria described above, the Coniontini, Coelini, Branchini, Physogasterini, Praocini and Pimeliini are members of the Tentyriidae. Interestingly, all the early American workers agreed that these tribes belonged to the Tentyriinae (Blaisdell, 1939; Casey, 1908; Horn, 1870; LeConte and Horn, 1883). In addition the genera *Eupsophulus* Cockerell and *Alaephus* Horn, currently placed in the Tenebrioninae (Tenebrionini), clearly belong to the Tentyriidae, although their exact affinities are uncertain. Horn (1870) realized that these genera exhibited characteristics of both subfamilies and judged their classification as tentative.

It must be emphasized that the infrafamilial classification of these beetles remains in a confused state. The numerous tribes of the Tentyriidae are frequently very distinct and without intermediates (e.g., Stenosini, Triorophini, Nyctoporini). Conversely, while some of the tribes assigned to the Tenebrioninae are disjunct (e.g., Diaperini, Scaurini, Cossyphini), many are founded on superficial characters which have arisen independently many times (e.g., Coelometopini, which are distinguished from the Tenebrionini by being apterous).

Table 1. Comparison of classifications of the Tenebrionoidea.*

	Lacordaire, 1859	LeConte and Horn, 1883	Gebien 1937-44	Koch, 1955
Tentyriidae	Tenebrionides (Section 1; Section II, Cohorte I, in part)	Tentyriinae, Asidinae	Tentyriinae, Asidinae & Coniontini, Praocini, Pimeliini, etc.	Tentyriinae
Tenebrionidae Tenebrioninae	Tenebrionides (Section II, Cohorte I, in part; Cohorte II)	Tenebrioninae	Tenebrioninae	Tenebrioninae
Alleculinae	Cistelides (=Alleculidae)	Cistelidae (=Alleculidae)	[Alleculidae]	[Alleculidae]
Lagriinae	Lagriides	Lagriidae	[Lagriidae]	[Lagriidae]
Nilioninae	Nilionides	[Nilionidae]	Leiochrini & [Nilionidae]	[Leiochrini & Nilionidae]

* The arrangement proposed here is listed on the left. The characters on which this classification is based are described fully in the text. The Monommidae, considered a distinct family by all workers, is not included. Names in brackets are not specifically mentioned in the works cited because these taxa were outside the geographic or taxonomic scope of the respective classifications.

AFFINITIES OF THE CONIONTINI, COELINI AND BRANCHINI

Say (1824) in his original description of *Eusattus reticulatus*, assigned it to *Zophosis* (Zophosini), an old world genus that is superficially similar. Subsequently, Casey (1908) speculated that the Branchini, Coniontini, Zophosini, Praocini and Nycteliinae comprise a closely related group which he designated the Coniontinae. LeConte and Horn (1883) and Champion (1884) also noticed the superficial similarity of the Branchini to *Praocis* and *Nyctelia*, and suggested a relationship to these South American tribes. In the present study, mouthparts, male and female genitalia, and internal thoracic structures were compared among the following taxa in order to reassess their interrelationships.

Coniontini

Coniontides latus LeConte

Coniontis viatica Eschscholtz

Coniontellus inflatus Casey
Coelotaxis punctulata Horn
Coelosattus fortineri Blaisdell
Eusattus robustus LeConte
erosus Horn
dubius LeConte
reticulatus (Say)
muricatus LeConte
Coelini
Coelus globosus LeConte
ciliatus Eschscholtz
remotus Casey
Coelomorpha maritima Casey
Zophosini
Zophosis plana Fabricius
Praocini
Praocis chiliensis (Gray) (Det. L. E. Peña)
penai Kulzer (Det. L. E. Peña)
pilula Laporte (Det. L. E. Peña)
Nycteliini
Nyctelia varipes Fairmaire (Det. L. E. Peña)
Gyriosomus modestus Kulzer (Det. L. E. Peña)
Physogasterini
Entomochilus varius laevis Kulzer (Det. L. E. Peña)
Branchini
Branchus floridanus LeConte
Branchus woodii LeConte
Oxinthas praocioides Champion

MOUTHPARTS

The mentum is typically large in most Tentyriidae, concealing the maxillae and ligula, which is usually membranous. In the Coniontini and Coelini the mentum is relatively small exposing the maxillae and ligula, which is always ventrally sclerotized and articulated with the mentum by a narrow membrane (Fig. 1). The labial palp hinges with a sclerotized palpifer which is embedded dorsally in the membrane above the ligular articulation. The only appreciable variation in these structures involves the size and pattern of the setae on the dorsal surface of the ligula. The coarse bristles shown in Fig. 1 are characteristic of several fossorial species of *Eusattus* as well as *Coelus*. In more generalized species of *Eusattus* and in *Coniontis* the ligular setae are much finer, more numerous and brush-like, as in *Branchus* (Fig. 2). In general shape and morphology the labial structure of *Branchus* shows no important differences from the Coniontini.

The mentum of the Physogasterini and Praocini is relatively smaller, compared to the ligula, which is articulated by a broad membranous band (Fig. 3). Portions of the ventral surface of the ligula are usually membranous, especially in the Praocini. The greatest divergence from the Coniontini involves the insertion of the labial palps. Whereas these are attached dorsally to sclerotized palpifers in the Coniontini they are articulated with the ventral (external) surface of the ligula in the Praocini and Physogasterini, and the palpifer is absent. The labial structure is very similar in the Nycteliini, but in *Nyctelia* the ligula

is relatively small and retracted beneath the mentum. In *Gyriosomus* the ligula is large and protuberant, as in the Praocini.

The mouthparts of *Zophosis* (Fig. 4) are distinctly tentyrioid in structure. The mentum is large, concealing the ligula and the maxillae. The membranous ligula is relatively small, with the labial palps articulated dorsally. The palpifer is absent. A similar structural arrangement occurs in many other tribes of Tentyriidae, including the Tentyriini, Adesmiini, and Triorophini. *Zophosis* also differs from the other taxa considered here in the structure of the maxilla. In these other tribes, the lacinia is bidentate, and the galea brush-like. In *Zophosis*, both lacinia and galea are densely setate and brush-like.

GENITALIA

The aedeagus and penis of most Tentyriidae are simple fusiform tubes (Koch, 1955). This structure is exemplified by the Coniontini and Coelini. In these tribes the tegmen consists of lateral struts, connected proximally. The sclerotized parts of the penis are narrow, lateral rods (Fig. 5, 6). In *Branchus floridanus* (Fig. 7, 8) the tegmen is a sclerotic tube, with only a small ventral membrane (the homologous membrane is dorsal in the Tenebrionidae). The paramere is strongly ridged proximally, and is apically truncate, with sharp lateral spurs. The penis is exceptionally elongate and distally curved and enlarged. The functional significance of these remarkably modified structures is unknown. In *Branchus woodii* and *Oxinthas* the male genitalia are essentially similar to those of the Coniontini. The Praocini, Nycteliini and Physogasterini are very similar to the Coniontini in respect to male genitalia, with minor differences in the degree of sclerotization and shape and proportions of the aedeagus and penis. It may be significant that the aedeagus bears lateral, subterminal patches of setae in all four tribes. The aedeagus and penis of *Zophosis* (not illustrated) are relatively much shorter and thicker and lack the subterminal setae.

Female genitalia in these beetles consist of an elongate 1st valvifer and short, distally spatulate and strongly sclerotized 2nd valvifer (Fig. 9-11). The 2nd valvifer is distally modified as a sclerotized process in many Tentyriidae (e.g., Adesmiini, Asidini, Cryptoglossini), probably for penetrating the oviposition substrate, and frequently the ovipositor tube is very elongate as compared to that of the Tenebrionidae. In the Coniontini, Coelini and Branchini the 1st valvifer is a weakly sclerotized plate with a marginal baculus (Fig. 9). The second valvifer is continuously sclerotized, with the distal process oriented horizontally. A subterminal membranous area marks the position of the gonostylus, which is recognizable as a group of elongate setae. This configuration is nearly constant throughout these tribes, the only significant variation involving size and slight differences in shape. The ovipositor is similar in the Praocini, Physogasterini and *Nyctelia* (Fig. 10) with the following differences. The ovipositor tube is usually more elongate and the baculus of the 1st valvifer is submarginal. The 2nd valvifer is oriented obliquely or nearly vertically and bears a sulcus about two-thirds of the distance to the base. Two features shared with the Coniontini are the setal clothing of the 2nd valvifer and the median, ventral sclerite situated in the membrane between the 2nd valvifers. In *Gyriosomus* (Nycteliini) the entire ovipositor is densely setate, the sulcus on the 2nd valvifer is very strong, and the median ventral sclerite is absent.

The ovipositor of *Zophosis* (Fig. 11) is relatively short and thick. Both valvifers are densely setate and the 2nd valvifer consists of a basal sclerotized plate and baculus with a narrow, lateral sclerotization articulating with the strongly sclerotized, terminal process. There are no suggestions of the gonostylus or the median, dorsal sclerite.

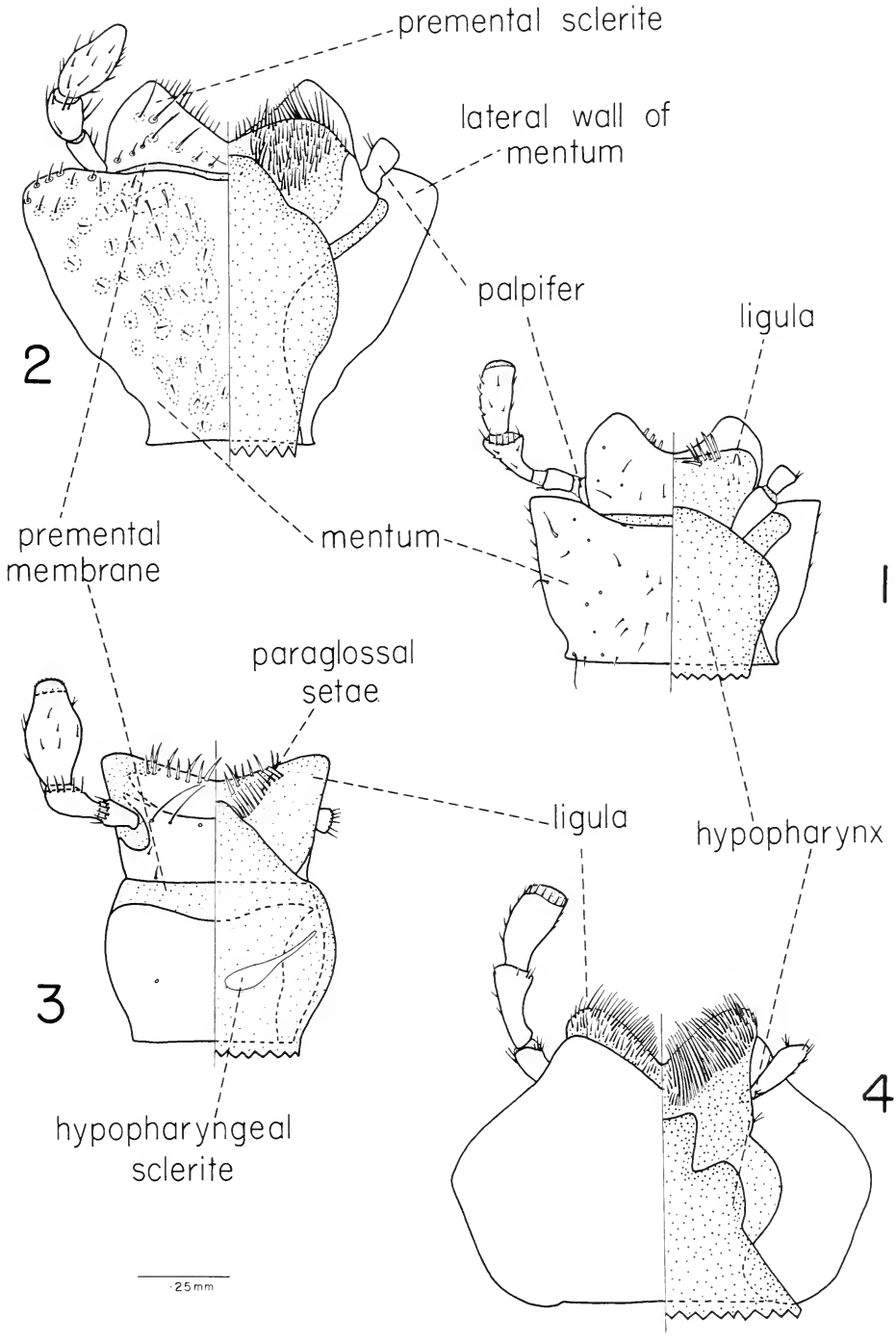

Fig. 1-4. Labial structures. The left side of each figure represents the ventral (external) surface. The right side represents the dorsal (internal) surface. 1, *Eusattus muricatus*; 2, *Branchus floridanus*; 3, *Praocis penai*; 4, *Zophosis plana*.

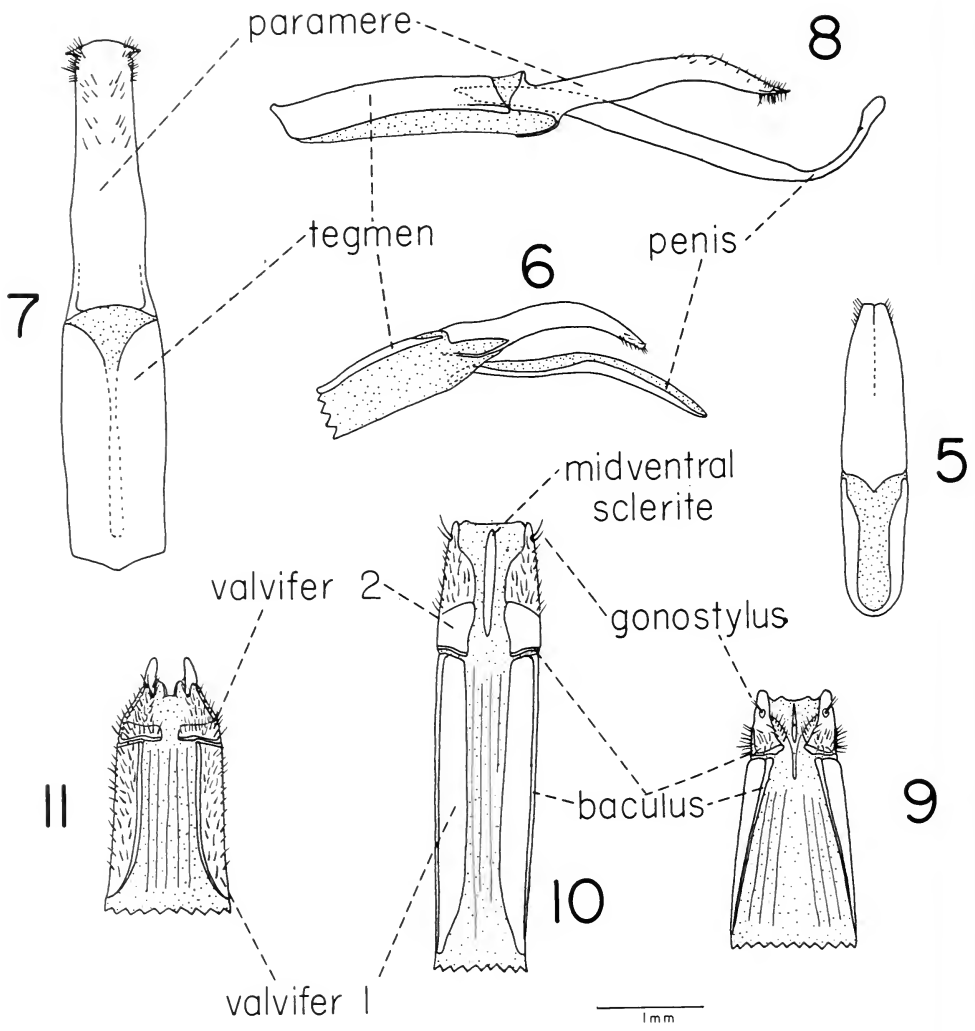

Fig. 5-8. Male genitalia. 5, *Eusattus reticulatus*, ventral aspect of aedeagus; 6, *Eusattus reticulatus*, lateral aspect of aedeagus and penis; 7, *Branchus floridanus*, ventral aspect of aedeagus; 8, *Branchus floridanus*, lateral aspect of aedeagus and penis. Fig. 9-11. Ventral aspect of ovipositors. 9, *Eusattus dubius*; 10, *Praocis penai*; 11, *Zophosis plana*.

INTERNAL THORACIC STRUCTURE

Flightless tenebrionids and tentyriids illustrate extreme modifications of thoracic structure. Smith (1964) described reductions of flight musculature and the accompanying desclerotization and reduction in size of the metathoracic terga in a number of micropterous and apterous beetles. However, most of his examples appear to represent relatively early stages in the specialization for ambulatory life. Many groups of Tentyriidae have apparently been apterous for a very long time. In these the metanotum is completely membranous and the mesonotum is reduced to a narrow, leathery, transverse sclerite which extrudes externally as the scutellum. In highly modified forms (e.g., *Edrotes*, *Epiphysa*; Doyen, 1968) the mesonotum is further reduced, with no external indication of the scutellum, and the mesosterna and prosterna are fused by cuticular extensions of the sternal apophyses. These specializations are usually accompanied by elongation and thickening of the metendosternite, which frequently becomes fused with the mesocoxal inflections and the mesopleura, especially in fossorial species.

Most of the skeletal adaptations described above are represented in the taxa discussed here. In the Coniontini, Coelini and Branchini the arms of the metendosternite are extremely elongate and approximated to the mesocoxal inflections, or fused to the inflections in more highly modified species (Fig. 12, Table 2). The arms extend to the vicinity of the mesepisterna, terminating in muscle disks which are fused with the episterna in the most specialized species. The mesapophyseal arms are relatively short, and may be expanded as vertically oriented flanges in fossorial species (Fig. 12). Structural details of the pterothorax of various species of these tribes are summarized in Table 2.

The Praocini, Nycteliini and Physogasterini share a distinct thoracic structure. The arms of the metendosternite are broadly fused with the mesocoxal inflections, but terminate as short prongs without terminal muscle disks, and never approach the mesopleura (Fig. 13). The elongate, slender arms of the mesendosternite extend dorsolaterally almost to the dorsal margin of the mesepisternum. In *Nyctelia* and *Gyriosomus* the mesothorax and prothorax are rigidly joined by strong, ligamentous thickenings of the intersegmental membrane, while in *Praocis* and *Entomochilus* the prothorax is relatively mobile as in the Coniontini.

The thoracic modifications of *Zophosis* (Fig. 14) are strikingly similar to those of *Adesmia* and *Epiphysa* (*see* Doyen, 1968). The metendosternite is fused with the mesocoxal inflections and the arms extend anterodorsally to the mesopleura, terminating in large muscle disks, but are not fused with the mesopleura. The mesendosternite consists of short, horizontal arms with large terminal muscle disks which are opposed to similar disks formed by the proapophyseal arms. The prothorax is attached to the pterothorax by a stout, ligamentous membrane, permitting little flexibility.

Zophosis has some other noteworthy structural modifications. The anterior three abdominal sternites, which are connate in all tenebrionids, are rigidly fused with the metasternum by continuous cuticular bands laterad of the metacoxal cavities. The pterothorax and abdomen thus become a single, rigid unit. In all other Tentyriidae, Tenebrionidae and other Coleoptera which have been examined, the mesothoracic-abdominal articulation is flexible, although in most apterous tenebrionids movement is prevented by interlocking joints between the elytra and the abdominal sternites and thoracic pleurites. In *Zophosis* there is a pair of sclerotized, dorsolateral projections from the region of the lateral metacoxal articulations. The function of these projections, which are unique among known Coleoptera, is uncertain, but they may help secure the elytra against the abdominal sternites.

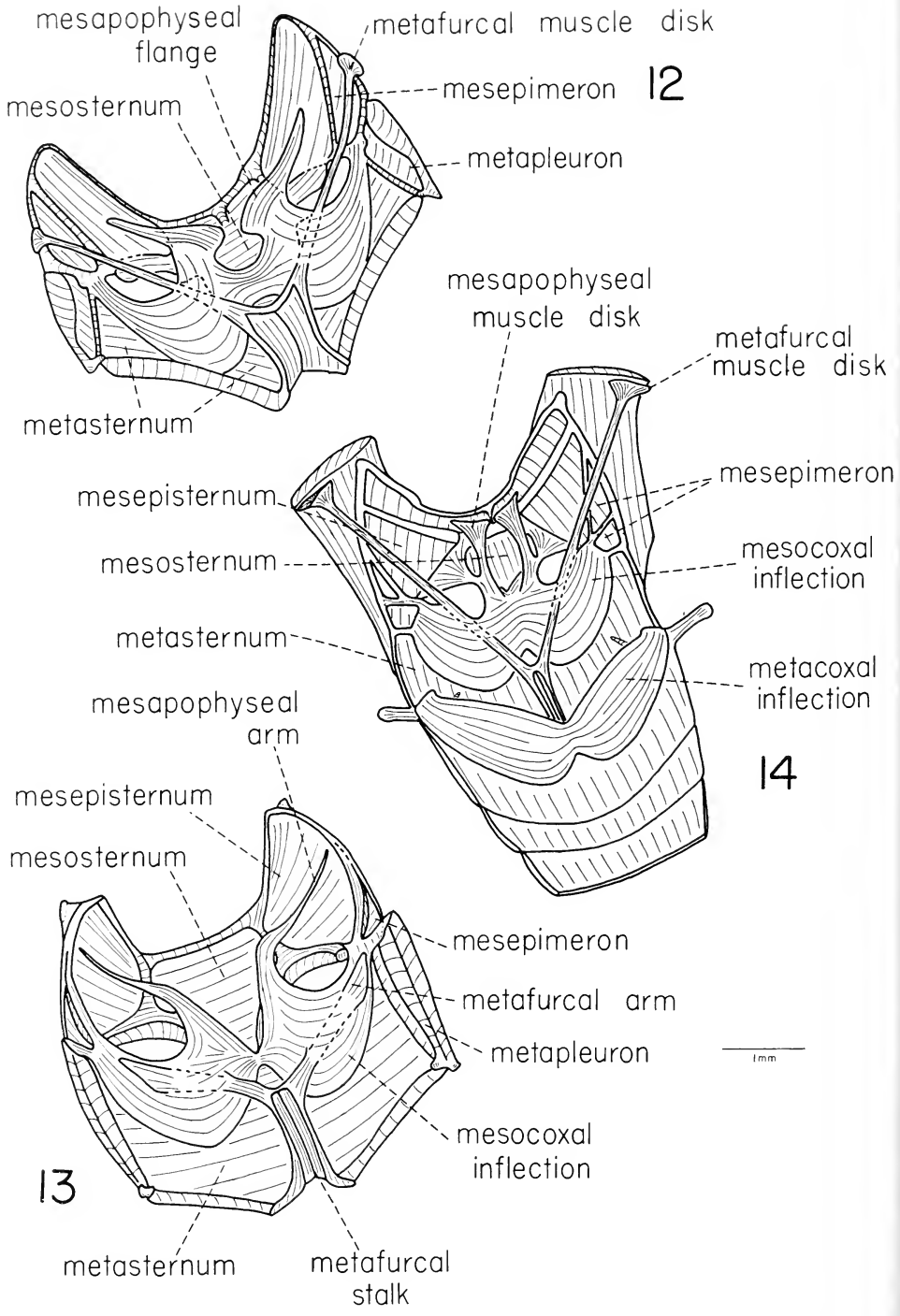

Fig. 12-14. Internal thoracic structures. The figures are from an oblique posterodorsal aspect, with the thoracic nota and dorsal abdominal membranes removed. 12, *Coelosattus fortineri*; 13, *Praocis penai*; 14, *Zophosis plana*.

Table 2. Comparison of certain thoracic features among selected species of Coniontini.*

	mentendosternite			mesapophyseal arms	
	(a) mesocoxal fusion	(b) muscle disks	(c) mesopleural fusion	(d) length	(e) basal flange
Coelus ciliaris	–	–	–	–	–
Coelomorpha maritima	–	–	–	–	–
Coniontellus obesa	–	–	–	–	–
Coelotaxis punctulata	–	+	–	–	–
Coniontides latus	–	+	–	–	–
Coniontis viatica	–	+	–	–	–
Branchus floridanus	–	+	–	+	–
Oxinthas praocioides	–	+	–	+	+
Eusattus dubius	–	+	+	–	–
robustus	–	+	+	+	–
erosus	–	+	+	+	–
reticulatus	–	+	+	+	+
muricatus	+	+	+	+	+
Coelosattus fortineri	+	+	+	+	+

*(a) Arms of metendosternite fused with mesocoxal inflection (+) or free (–); (b) arms terminated as enlarged muscle discs (+) or unmodified (–); (c) muscle disks fused with mesopleuron (+) or free (–); (d) mesapophyseal arms short, thick, extending no more than 1/2 the distance to the mesepisternal process (+) or more slender and extending at least 1/3 the distance to the mesepisternal process (–); (e) mesapophyseal arms expanded as flattened flanges basally (+) or unmodified (–). Taxa are arranged in order of increasing specialization, which has occurred in two ways. In *Branchus* and *Oxinthas*, the mesapophyseal arms are shortened and flanged, while the metafurcal arms are unmodified. Conversely, in all *Eusattus* the metafurcal arms are subject to fusions with other thoracic structures, while the mesapophyseal arms are modified only in fossorial species. Specialization in internal thoracic structures is not always concordant with trends in other characteristics. For example, the protarsi and antennae of *Coelus* and *Coelomorpha* are highly specialized for burrowing (Fig. 19-20).

Externally, *Zophosis* shows some other puzzling structural features. The metepisterna, which are separated from the metasterna by membranous clefts in winged Coleoptera, have apparently coalesced with the sterna. A pair of oblique grooves arising near the lateral metacoxal articulations and terminating near the mesocoxal inflections may represent the metepisternal sutures, but more likely are secondary grooves which strengthen

the metasternum. *Zophosis* also has a pair of "oblique sutures" running anterolaterad from the intercoxal process. These probably strengthen the metasternum. None of the beetles discussed here possess antecoxal grooves, which are almost universally present in winged forms. The antecoxal grooves run from the medial metacoxal articulation to the lateral metacoxal articulation, and probably reinforce the posterior sternal region.

The evidence described above indicates close affinities between geographically related taxa, but does not clarify the relationships among taxa in different zoogeographic regions. *Zophosis* shows clear relationships to *Adesmia* and *Epiphysa*, all inhabiting Africa and southern Eurasia. *Nyctelia*, *Gyriosomus*, *Praocis* and *Entomochilus*, all endemic to South America, share a strong structural consistency, particularly in internal thoracic features. Likewise the Coniontini, Coelini and Branchini (North America) are very similar morphologically. Intermediate forms between the African, South American and North American taxa are unknown, and the adaptations of each of these groups are so different that it is premature to speculate upon their affinities.

CLASSIFICATION OF THE CONIONTINI, COELINI AND BRANCHINI

Current tribal and generic classifications of these beetles largely follow the arrangement of Casey (1908, 1924) which emphasizes external differences in leg and antennal structure and size and shape of the epipleura. These features are variously modified to facilitate burrowing, and intermediate forms sometimes relate the specialized, fossorial species to the more generalized, ambulatory ones. This is especially evident in Casey's group Eusatti, as recognized by Triplehorn (1968), who synonymized all Casey's genera under *Eusattus*, greatly simplifying the previously arbitrary and unworkable classification. Several other generic and tribal changes are proposed here, based on adult characteristics. Larval features are largely concordant, and will be described elsewhere.

As indicated above, the morphological features of coniontine tentyriids strongly reflect their mode of life. Most species of *Coniontis* dwell on substrate surfaces, and the body is oval and relatively elongate. The arms of the metendosternite are elongate, but not fused with the mesocoxal inflections (Table 2). *Coelotaxis*, distinguished by an elongate basal protarsomere and "minute" scutellum, is extremely similar to *Coniontis* in all other external and internal characters. There is considerable variation in the tarsal character, and some individuals are scarcely distinguishable from *Coniontis* (Fig. 15-18). Furthermore, the scutellum is relatively large, but is frequently hidden by the pronotum in pinned specimens. Therefore, *Coelotaxis* is placed as a synonym of *Coniontis*. *Coniontellus* is differentiated from *Coniontis* by having the eyes completely divided by a median canthus. However, there is considerable interspecific variation in the degree of constriction of the eyes in *Coniontis*, and in some specimens of *Coniontellus* the eyes are not completely divided. *Coniontides* and *Conisattus* differ from *Coniontis* only in minor body proportions. These three genera are also placed as synonyms of *Coniontis*. Detailed revisionary studies of *Coniontis* may show that some of these names should be recognized as subgenera, but even in the expanded sense proposed here *Coniontis* is much more monomorphic than *Eusattus* or *Praocis*.

The species of *Eusattus* are usually stouter bodied than *Coniontis*, and several are highly modified for burrowing in aeolian sand (*E. muricatus*, *E. ciliatus* Horn, *E. puberulus* LeC.). Within *Eusattus* (*sensu* Triplehorn) the degree of modification of internal thoracic structure ranges from the generalized condition in *E. dubius* to that in *E. muricatus* (Table 2). *Coelosattus*, which was placed in the Coelini by Blaisdell (1927), differs from *E. muricatus* chiefly in having broadly expanded protibiae (Fig. 22-23) and strongly arcuate middle and hind

tibiae. It lacks the specialized tarsal and antennal characters of the Coelini, while the specialized internal thoracic structure (Fig. 12) is nearly identical to that of *E. muricatus*. The thoracic structure of *Coelus* and *Coelomorpha* is similar to that of *Coniontis*. For these reasons, *Coelosattus* is placed as a synonym under *Eusattus*.

The Coelini comprise a small, monomorphic group of fossorial species restricted to maritime sand dunes along the Pacific coast of North America. Superficially they greatly resemble certain species of *Praocis* (e.g., *P. pilula*), but show distinct differences in mouthparts and internal thoracic structures, as described earlier. The most important characters differentiating the Coelini from the Coniontini are the enlarged, spatulate basal protarsomeres (Fig. 19, 20) and the extremely short antennae. In all other characters they greatly resemble the Coniontini, particularly the fossorial species of *Eusattus*. That they apparently evolved independently, perhaps from *Coniontis*, is indicated by the generalized nature of the internal thoracic structures (Table 2). However, the general similarity to the Coniontini suggests that the Coelini should not be recognized as a separate tribe. This classification was also favored by LeConte (1866), LeConte and Horn (1883) and Horn (1870). One further point concerns the genera *Coelus* and *Coelomorpha*, which show very similar modifications in protarsal and antennal structure, but differ in the number of antennal segments (10 in *Coelomorpha*; 11 in *Coelus*). Because of their overall similarity, I propose that *Coelomorpha* be placed in synonymy under *Coelus*.

The Branchini were originally differentiated from the Coniontini by LeConte (1862). He felt that the anteriorly confluent gular sutures and abrupt basal expansion of the epipleura indicated an affinity to the Nycteliini and Praocini, respectively. Later, LeConte (1866:113) realized that most of the character states he used to separate these tribes were represented in the single genus *Eusattus*, and he suggested that the Nycteliini, Praocini and Branchini should possibly be placed in synonymy under the Coniontini. LeConte was unaware of the internal thoracic differences of the first two tribes, but his judgement concerning the Branchini was undoubtedly correct. The only major structural feature differentiating the Branchini is the absence of the submental sclerite (Fig. 24). However, the submentum is very small in some *Eusattus* (Fig. 25). For these reasons the Branchini are placed in synonymy under the Coniontini.

The taxonomic changes proposed here are intended to consolidate the classification of the Coniontini so that the degree of variation encompassed is similar to that of other differentiated tribes, such as the Adesmiini, Zophosini, Praocini and Eleodini. Extensive elucidation of the generic and tribal relationships will be necessary before the patterns of variation and affinity in the Tenebrionidae and Tentyriidae can be used to reach more general evolutionary and biogeographic conclusions.

The proposed taxonomic changes are summarized in the following checklist.

Tribe Coniontini

Coniontini Lacordaire, 1859:218; Horn, 1870:291; LeConte and Horn, 1883:371; Casey, 1908:55.

Coelini Casey, 1908:150.

Branchini LeConte, 1862:222.

Body stout, oval to subglobose, apterous. Mentum small, trapezoidal, weakly emarginate anteriorly; ligula large, sclerotized, projecting anteriorly beyond mentum; labial palps inserted dorsally on distinct palpifers; maxillae exposed laterad of labium, lacinia dentiform. Metendosternite with arms elongate, extending to region of metapleural wing process. Ovipositor with 1st valvifers elongate, weakly sclerotized; 2nd valvifers prolonged posteriorly

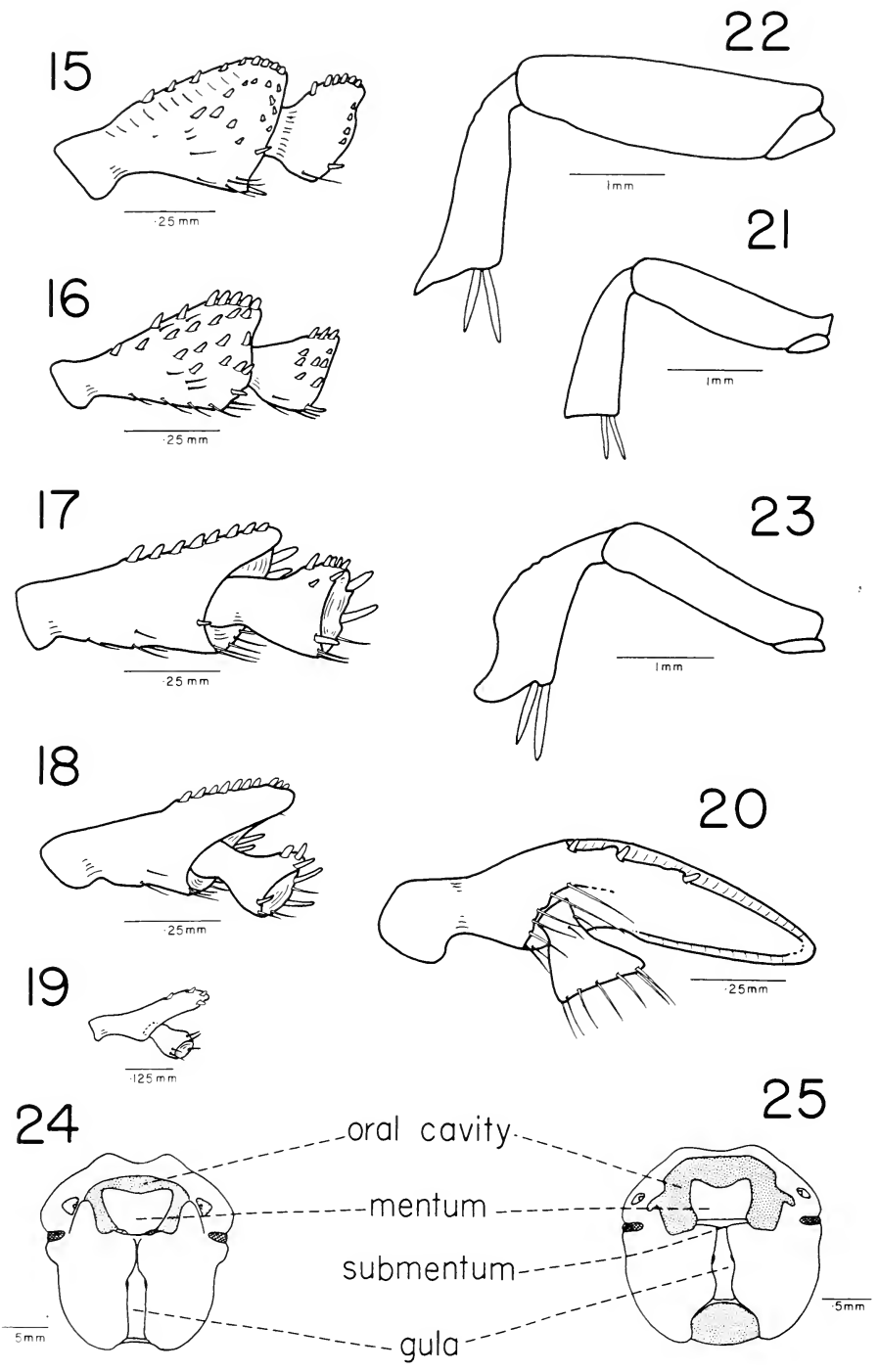

Fig. 15-20. Basal tarsomeres of forelegs, posteroventral aspect; 15, *Coniontis hoppingi* Blaisdell; 16, *Coniontides latus*; 17, 18, *Coelotaxis punctulata*; 19, *Coelomorpha maritima*; 20, *Coelus globosus*. Fig. 21-23. Posterior aspect of forelegs; 21, *Coniontides latus*; 22, *Eusattus reticulatus*; 23, *Coelosattus fortineri*. Fig. 24-25. Ventral aspect of crania; maxillae, mandibles, ligula and clypeus excised; 24, *Oxinthas praocioides*; 25, *Eusattus muricatus*.

as strongly sclerotized, spatulate prongs; gonostyli represented by several elongate setae inserted in membranous foramen situated medially on 2nd valvifers. Aedeagus inverted; tegmen with variable desclerotized area posteroventrally; paramere longer than tegmen, bearing several lateral setae at apex.

Coniontis Eschscholtz, 1829. Type species: *Coniontis viatica* Eschscholtz, Casey designation, 1908:57.

syn. *Coniontellus* Casey, 1890. Type species: *Coniontis obesa* LeConte, 1851, Casey designation, 1908:57.

syn. *Coniontides* Casey, 1908. Type species: *Coniontis lata* LeConte, 1866, by original designation, p. 57.

syn. *Conisattus* Casey, 1908. Type species: *Conisattus rectus* Casey, 1908:57, monobasic.

syn. *Coelotaxis* Horn, 1876. Type species: *Coelotaxis punctulata* Horn, 1876, Casey designation, 1908:57.

Eusattus LeConte, 1851.[1] Type species: *Eusattus difficilis* LeConte, 1852, Casey designation, 1908:56.

syn. *Eusattodes* Casey, 1908. Type species: *Eusattus laevis* LeConte, 1866, Casey designation, 1908:56.

syn. *Megasattus* Casey, 1908. Type species: *Eusattus erosus* Horn, 1870, by original designation, p. 56.

syn. *Nesostes* Casey, 1908. Type species: *Eusattus robustus* LeConte, 1866, by original designation, p. 56.

syn. *Sphaeriontis* Casey, 1908. Type species: *Eusattus muricatus* LeConte, 1851, by original designation, p. 56.

syn. *Coelosattus* Blaisdell, 1927. Type species: *Coelosattus fortineri* Blaisdell, 1927, monobasic.

syn. *Discodemus* LeConte, 1862. Type species: *Zophosis reticulata* Say, 1824, monobasic.

syn. *Conipinus* LeConte, 1862. Type species: *Eusattus dubius* LeConte, 1851, Gebien designation, 1938:284.

Coelus Eschscholtz, 1829. Type species: *Coelus ciliatus* Eschscholtz, 1829, monobasic.

syn. *Coelomorpha* Casey, 1890. Type species: *Coelomorpha maritima* Casey, 1890, Casey designation, 1908:151.

Branchus LeConte, 1862. Type species: *Branchus floridanus* LeConte, monobasic.

Oxinthas Champion, 1892. Type species: *Oxinthas praocioides* Champion, monobasic.

Anectus Horn, 1866. Type species: *Anectus vestitus* Horn, monobasic.

Detailed keys to species will be presented in future revisionary work on each genus. The genera are keyed below.

Key to the genera of Coniontini

1. Submentum clearly defined, though sometimes small, transverse (Fig. 25) 2
– Submentum extremely small, invisible externally (Fig. 24) 4
2. Basal protarsomere truncate or with process shorter than second tarsomere (Fig. 15-18) 3

[1] Generic synonymy for *Eusattus* is adapted from Triplehorn (1968) with the addition of *Coelosattus* Blaisdell.

– Basal protarsomere extending beyond second tarsomere as spatulate process (Fig. 19-20) ..... *Coelus*
3. Protibia abruptly expanded apically as an acute process (Fig. 22-23) ..... *Eusattus*
– Protibia gradually enlarged apically (Fig. 21) ..... *Coniontis*
4. Intercoxal process of abdomen broadly rounded 5
– Intercoxal process of abdomen rectangularly truncate[2] ..... *Anectus*
5. Protibia abruptly expanded apically as a short, acute process ..... *Branchus*
– Protibia gradually enlarged apically ..... *Oxinthas*

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[2] This couplet compiled from Horn, 1866.

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STUDIES ON BOREAL AGROMYZIDAE (DIPTERA). II.
PHYTOMYZA MINERS ON *SENECIO*, *PETASITES* AND *TUSSILAGO* (COMPOSITAE, SENECIONEAE)

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Twelve species of Phytomyza *are known as miners of* Senecio, Petasites *and* Tussilago *in boreal areas. These belong to three species-groups, the* albiceps *group (4 species), the* syngenesiae *group (3 species) and the* robustella *group (5 species). Three new species of the* robustella *group are described, as follows:* Phytomyza hyperborea *n. sp. (type-locality Walker Fork, Alaska),* P. hypophylla *n. sp. (type-locality Eagle Summit, Alaska) and* P. lugentis *n. sp. (type-locality Summit Lake Pass, British Columbia). In the* albiceps *group one new subspecies is described,* Phytomyza tussilaginis kevani *n. ssp. (type-locality Richards Island, Northwest Territories); the North American* P. petasiti *Spencer is considered a geographical subspecies of* P. tussilaginis *Hendel, described from Europe; and* P. alpina *Groschke, previously known from Scotland and the Alps, is recorded for British Columbia, Yukon and Alaska.*

Douze espèces de Phytomyza *sont connues dans les régions boréales comme mineuses du* Senecio, *du* Petasites *et de la* Tussilago. *Ces espèces appartiennent à trois groupes d'espèces, le groupe* albiceps *(4 espèces), le groupe* syngenesiae *(3 espèces) et le groupe* robustella *(5 espèces). Trois nouvelles espèces sont décrites dans le groupe* robustella, *tel que:* Phytomyza hyperborea *n. sp. (localité-type Walker Fork, Alaska),* P. hypophylla *n. sp. (localité-type Eagle Summit, Alaska) et* P. lugentis *n. sp. (localité-type Summit Lake Pass, Colombie britannique). Dans le groupe* albiceps *une nouvelle sous-espèce est décrite,* Phytomyza tussilaginis kevani *n. ssp. (localité-type Richards Island, Territoires du nord-ouest);* P. petasiti *Spencer d'Amérique du nord est considérée comme sous-espèce géographique de* P. tussilaginis *Hendel, d'Europe; et* P. alpina *Groschke, connue dans le passé d'Écosse et des Alpes, est maintenant notée pour la Colombie britannique, pour le Yukon et pour l'Alaska.*

Zwölf Phytomyza-*Arten werden als Minierer von* Senecio, Petasites *und* Tussilago *in borealischen Gebieten besprochen. Diese gehören zu drei Arten-Gruppen, der* albiceps-*Gruppe (4 Arten), der* syngenesiae-*Gruppe (3 Arten) und der* robustella-*Gruppe (5 Arten). Drei Arten der* robustella-*Gruppe sind neu beschrieben, wie folgt:* Phytomyza hyperborea *n. sp. (Fundort vom Typus Walker Fork, Alaska),* P. hypophylla *n. sp. (Fundort vom Typus Eagle Summit, Alaska) und* P. lugentis *n. sp. (Fundort vom Typus Summit Lake Pass, British Columbia). Bei der* albiceps-*Gruppe wird eine geographische Unterart neue beschrieben,* Phytomyza tussilaginis kevani *n. ssp. (Fundort vom Typus Richards Island, Northwest Territories); die nordamerikanische* P. petasiti *Spencer wird als Unterart von* P. tussilaginis *Hendel (aus Europa beschrieben) vermutet;* P. alpina *Groschke, vorher nur aus Schottland und aus den Alpen bekannt, wird für British Columbia, für Yukon und für Alaska besprochen.*

The present paper deals with the *Phytomyza* miners of part of the Senecioneae. All known *Phytomyza* miners of *Tussilago* and *Petasites* are treated; but I leave out of consideration (as outside my geographical area of interest) the following miners of *Senecio*: *Phytomyza burchardi* Hering (Canary Isles) and *P. seneciovora* Spencer (Africa). K. A. Spencer informs me (in correspondence) that he has recently obtained an undescribed species close to *seneciovora* from a tree *Senecio* in Kenya. He will discuss these species in a later work. In his opinion both belong to the *syngenesiae* group.

The species of *Phytomyza* here treated are referred to three groups, the *albiceps* group, the *syngenesiae* group and the *robustella* group.

The flies from Holland described by de Meijere (1924) as *Phytomyza jacobaeae* were almost certainly not bred from *Senecio*. No one has since succeeded in obtaining from *Senecio* flies which agree with his description. I have seen two female syntypes of this species, and in my opinion they belong to *Phytomyza milii* Kaltenbach, a well-known grass-feeder. The puparia from *Senecio jacobaea* L. associated with these flies by de Meijere doubtless belonged to a species of the *Phytomyza syngenesiae* group; for de Meijere (1926: 267) stated that he could find no morphological difference between these puparia and those of that group (as "*atricornis*"). I suggest that the description of "*jacobaeae*" was the result of an error in associating the wrong flies with these puparia.

The presentation followed in this paper is similar to that of the first paper of this series (Griffiths, 1972), which should be consulted for explanation of the terms and abbreviations used in my descriptions. My use of names of North American plants again follows Hultén (1968). The holotypes of the new species and subspecies described in this paper will be deposited in the Canadian National Collection (Ottawa).

DIAGNOSIS

The species treated in this paper all belong to groups in which identification is based largely on the form of the male genitalia, particularly the aedeagus. The new species whose male is unknown (*Phytomyza hyperborea* n. sp.) may be distinguished from its close relatives by its long antennal pubescence. The difference in the form of the aedeagus between the species of the *albiceps* and *robustella* groups treated here is rather striking, as indicated in my figures. No difficulty should be experienced in identifying males of these species, if a suitable technique of dissection is used. For further information on the more difficult *P. syngenesiae* group, only briefly discussed here, see my earlier revision (Griffiths, 1967).

Keys with worldwide coverage to the mines of *Phytomyza* larvae on *Senecio*, *Petasites* and *Tussilago* are given below. Other genera of Agromyzidae whose larvae are known to attack these host genera are *Liriomyza*, *Calycomyza*, *Ophiomyia* and *Melanagromyza*. Some species of the *albiceps* and *syngenesiae* groups cannot be separated on the basis of their mines and larvae, as indicated in the keys.

The new species of the *robustella* group described in this paper may be included in Spencer's (1969b) key to the *Phytomyza* species of Canada and Alaska by the extensions given below. I am not attempting to revise the couplets to which the species of the *albiceps* group would be referred (couplets 12-16 and 18-25), as I think that this part of the key will need to be substantially rewritten. The distinctions in the range of the costal ratio drawn in Spencer's couplets 12 and 18 are a particular source of difficulty, as the range in some species transgresses the boundaries indicated.

26. Third antennal segment with conspicuously long pubescence 26a
Third antennal pubescence normal 27

26a. Third antennal segment enlarged in female (Spencer 1969b, Fig. 450). Aedeagus as in Spencer's Fig. 451 ..... *lactuca* Frost
– Third antennal segment not enlarged in female (Fig. 31). (♂ unknown) ..... *hyperborea* n. sp.

66. Distal section of aedeagus with large distiphallus containing bifid terminal portion of ejaculatory duct 66a
– Aedeagus not of above type; "supporting sclerites" arising from base of distal section 66b
66a. Orbits distinctly projecting above eye; aedeagus as in Figs. 23-24 ..... *hypophylla* n. sp.
– Orbits not projecting above eye; aedeagus as in Figs. 17-18 ..... *lugentis* n. sp.
66b. (as Spencer's couplet 66)

Key to *Phytomyza* mines on *Senecio*

1. Larva normally leaving leaf before formation of strongly arched brown or black puparium (Fig. 26). Posterior spiracles of puparium and third instar larva with 19-36 bulbs (Fig. 28) ..... (*albiceps* group) 2
– Puparium formed inside leaf, with anterior spiracles turned downwards, projecting through epidermis (Fig. 27). Posterior spiracles of puparium and third instar larva with fewer bulbs 3
2. Canary Isles. Linear mines on *S. papyraceus* DC. ..... *P. burchardi* Hering
– Europe. Mines linear throughout, not more than 1.5 mm wide terminally (Fig. 37), on *S. nemorensis* L., *S. fuchsii* Gmel., *S. subalpinus* Koch and *S. fluviatilis* Wallr. ..... *P. senecionis* Kaltenbach
– Europe. Mines initially linear, but blotchy terminally (Fig. 36). On *S. alpinus* (L.) and *S. jacobaea* L. ..... *P. alpina* Groschke
– North America. Linear mines on *S. lugens* Richards and *S. pauperculus* Michx. (Fig. 35) ..... *P. alpina* Groschke
– Japan. Linear mines on *S. palmatus* Pall. ..... *P. ravasternopleuralis* Sasakawa
3. Puparium bright green; hind spiracles distinctly horned, with about 20 bulbs. Africa. ..... *P. seneciovora* Spencer
– Puparium white, brown or black; hind spiracles knob-shaped, with not more than 12 bulbs 4
4. Mine with narrow linear channel, not more than 2 mm wide (if with blotchy areas, these formed by convolutions of mine channel or by coalescence of mines of different larvae) ..... *P. syngenesiae* group

Three species of this group, *P. syngenesiae* (Hardy), *P. horticola* Goureau and *P. senecionella* Sehgal, are reported from *Senecio*.

– Mine channel broader, often with blotchy areas. North America. On *S. lugens* Richards and *S. sheldonensis* Pors. ..... *P. lugentis* n. sp.

Key to *Phytomyza* mines on *Petasites* and *Tussilago*

1. Larva normally leaving leaf before formation of strongly arched brown or black puparium (Fig. 26). Mines linear, on upper surface of leaf. Posterior spiracles of puparium and third instar larva with 19-31 bulbs (Fig. 28) ..... (*albiceps* group) 2
– Puparium formed inside leaf or petiole, with anterior spiracles turned downwards,

projecting through epidermis (Fig. 27) 3

2. Europe. On *Tussilago* and *Petasites* ..... *P. tussilaginis tussilaginis* Hendel
– Japan. On *Petasites* ..... *P. ravasternopleuralis* Sasakawa
– North America. On *Petasites* ..... *P. tussilaginis petasiti* Spencer
..... or *P. tussilaginis kevani* n. ssp.
..... or *P. alpina* Groschke

3. Larvae feeding mainly in petiole of leaf, in some cases also in veins. Posterior spiracles of puparium and third instar larva with 18-22 bulbs. Europe. On *Petasites* and *Tussilago* ..... *P. buhriella* Spencer
– Larvae feeding on parenchyma of leaf, not in veins or petioles (although the mine channel may run *besides* some of the veins). Posterior spiracles of puparium and third instar larva with fewer bulbs 4

4. Posterior spiracles of puparium and third instar larva with about 15 bulbs. Puparium reddish yellow. North America. On *Petasites* ..... *P. hyperborea* n. sp.
– Posterior spiracles of puparium and third instar larva with 7-12 bulbs (Fig. 29). Puparia mostly white (but some overwintering puparia of *syngenesiae* group brown or black) 5

5. Mines mainly on lower surface of leaf, normally convolute within restricted area (Fig. 34). North America. On *Petasites* ..... *P. hypophylla* n. sp.
– Mines on upper surface of leaf, narrowly linear (about 1 mm wide terminally), 24-28 cm long (Fig. 33A). Europe. On *Tussilago* and *Petasites* .....
..... *P. farfarae* Hendel
– Mines linear, on upper or lower surface, much shorter than those of *farfarae* (less than 10 cm long), in most cases over 1 mm wide terminally .....
..... *P. syngenesiae* group

Two species of this group, *P. horticola* Goureau and *P. senecionella* Sehgal, are reported from *Petasites*.

TREATMENT OF SPECIES

(a) the *Phytomyza albiceps* group

Nowakowski (1962b) has already discussed the possibility of defining a "natural group or subgenus" in this sense. In the *albiceps* group the puparia are strongly arched and dark in colour (brown or black), formed outside the mine (Fig. 26); the aedeagus is characterized by narrow, strongly sclerotized basal sclerites ("arms of basiphallus") and in many species also by the presence of spine-like cuticular processes; and the posterior ors is variable in length (in most individuals shorter than the anterior ors or completely absent). The limits of this group have not yet been clarified, but it is evident that numerous species whose larvae mine Compositae and Umbelliferae belong here. The black-frons species which have been referred to as the "*obscurella* group" should in my opinion also be included in the *albiceps* group.

Identification of many species of the *albiceps* group is only possible through study of the male genitalia. Nowakowski (1962b) has rightly remarked that the reliance on colour differences in Hendel's (1935-6) key has led to artificial separation of closely related species. My present study indicates that gross differences in colour can be shown not only by closely related species, but even by races of the same species. Another character whose high variability has not been appreciated is the length of the posterior orbital bristle (ors). For instance, in *Phytomyza tussilaginis* Hendel the range of variation in the development of this bristle varies from equal length to the anterior ors to complete absence (the extremes can even be shown on either side of the same individual!). Therefore all claims that the

length of the posterior ors can be used for differentiating species of the *albiceps* group should be regarded as doubtful.

K. A. Spencer has in press a note on the type specimens of *Phytomyza albiceps* Meigen. The customary use of this name for a species mining *Artemisia* in Europe has proved to be incorrect. Spencer thinks that the female lectotype probably belongs to the species since described as *Phytomyza rydeniana* Hering. Fortunately the latter species is referable to the *albiceps* group in the wide sense here followed, so there is no need to propose a different group name.

Phytomyza tussilaginis Hendel 1925
(synonymy below under subspecies)

Adult. – Head with orbits not or only very narrowly projecting above eye in lateral view; genae in middle 1/4 to 1/3 of eye height; eyes with only sparse fine pubescence or apparently bare. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors variably developed, in most individuals 1/2 to 2/3 as long as anterior ors, but ranging from fully as long (as in the holotype of subspecies *petasiti*) to completely absent; anterior ori usually 1/2 to 2/3 as long as posterior ori (but in some individuals absent on one side according to Hendel, 1935); orbital setulae one-rowed. Peristomal margin with vibrissa and 4-6 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr numerous, in 4-6 rows anteriorly; presutural ia numerous; 7-12 postsutural ia; inner pa 1/3 to 1/2 as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 2.6-4.0. Wing length 2.2-2.8 mm (see below under subspecies).

Colour geographically variable (see below under subspecies).

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from periandrium, bearing only fine setulae. Pregonites extending ventrally, shielding base of aedeagus at rest. Aedeagus as Fig. 6-7; basal sclerites narrow, strongly divergent distally, with row of spinules distally along their dorsal margins; sclerites of medial lobe widely separated anteriorly, convergent and bent upwards posteriorly; distal section with small distiphallus consisting of pair of tubules widely separated from basal section by clear membranous area (without or at most with fine linear traces of pigmentation). Ejaculatory apodeme small (Fig. 8).

A figure of the aedeagus has also been published by Spencer (1969b).

Puparium and third instar larva. – Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with two short horns, with 12-15 bulbs in irregular ellipse. Posterior spiracles borne on short conical processes, with 25-31 bulbs in irregular ellipse. Puparium dark brown or black, 2.0-2.3 mm long (Fig. 26).

Mine. – Larvae leaf-miners on *Tussilago* and *Petasites*. Mine (Fig. 33B) entirely linear, up to 25 cm long, 2-4 mm wide terminally; faeces deposited as discrete particles (separated by over 1 mm in mines on *Tussilago*, but closer together in mines on *Petasites*); mine entirely on upper surface of leaf, appearing white (on *Petasites*) or whitish green (on *Tussilago*) in reflected light; larvae leaving leaf through semicircular slit on upper surface before puparium formation.

A figure has also been given by Beiger (1960) of a mine on *Petasites albus* (L.).

Remarks. – This is the first species of the *albiceps* group in which geographical colour variation has been discovered. Since the colour forms do not differ in morphology or in life-history, I conclude that they are probably geographical races of the same species. Thus I interpret *tussilaginis* as a Rassenkreis or polytypic species. All specimens obtained from forested areas in North America are referable to the yellow subspecies (*petasiti* Spencer), while the new dark subspecies described below was obtained from arctic tundra (see Fig.

38). All European specimens so far described are referable to the nominate subspecies (*tussilaginis* Hendel). However all these specimens are from moderate latitudes, so that the possibility of other races occurring in more northern areas of Europe remains open.

Spencer (1969b) has suggested that the leaf mine of subspecies *petasiti* is shorter and broader than that of subspecies *tussilaginis*. But I can find no such difference in the additional material now available to me. The mine figured by Spencer seems to me untypically short and convolute.

This species has only been bred with certainty from *Tussilago* and *Petasites*. I am doubtful whether Hendel's (1935) record of *Adenostyles* as a host-plant is correct, for that genus does not belong to the Senecioneae. The fly in Hendel's collection bred from *Adenostyles* is a female, whose specific identity will remain uncertain until males can be associated with it.

The type series of *tussilaginis* was bred by Hendel from *Tussilago farfara* L. in Austria. Since only a female from this series has been traced (listed below under subspecies *tussilaginis*), the application of Hendel's name is open to doubt. I here follow the accepted opinion that flies on *Petasites* and *Tussilago* in Europe belong to the same species. But no male has yet been bred from *Tussilago* to confirm this.

Phytomyza tussilaginis tussilaginis Hendel 1925

Phytomyza tussilaginis Hendel. Hendel, 1925:308. –1935:493. Hering, 1927:114. Holotype lost; type-locality, Vienna (Austria).

Adult. – Frons largely clear yellow, but with dark ocellar plate and dark vertex (both vt on dark ground); in some specimens upper part of orbits also slightly infuscated along eye margins. Face partly yellow, but becoming brown in antennal pits and in some specimens also around antennal bases. Genae yellow. Occiput dark. Antennae with first article yellow or yellow-brown, second article brown or black, third article black. Palpi brown or black; labella yellow.

Mesonotum weakly shining, finely grey-dusted, black centrally, brown on sides with traces of brighter coloration (yellow-brown or whitish yellow) around margins of humeral callus and on upper part of sutural triangle. Scutellum black. Pleura black except narrow white band along dorsal margin of mesopleuron and white seam of mesopleural suture. Wing base and squamae contrastingly white, but latter with dark fringe. Legs largely dark, with tips of femora contrastingly yellow; tibiae and tarsi brown.

Abdomen largely brown, becoming yellow-brown on sides at base. Basal cone of ovipositor (♀) grey-dusted on about basal third to half.

Wing length 2.4-2.8 mm. Costal ratio mg_2/mg_4 2.6-4.0.

Material examined. – 1 ♀ paratype from larva 17.x.23 on *Tussilago farfara* L., Vienna University, Austria, emerged 18.iii.24 (in Zoological Museum of Humboldt University, Berlin). 1 ♂, 3 ♀♀ from larvae 29.viii.53 on *Petasites hybridus* (L.), Boxhill, Surrey, England, emerged 16-18.ix.53, leg. G. C. D. Griffiths; 1 ♂, 1 ♀ from larvae 12.ix.54, same plant and locality, emerged 4.x.54 and 29.iii.55, leg. G. C. D. Griffiths. 1 ♂ from larva 21.viii.53 on *Petasites hybridus* (L.), Millers Dale, Derby, England, emerged 10.ix.53, leg. K. A. Spencer.

Other records. – The following records are referred to this subspecies, on the assumption that it is the only member of the *albiceps* group whose larvae mine *Petasites* and *Tussilago* in Europe.

Ireland – Tipperary, 29.viii.69, mines on *Tussilago farfara* L. (K. A. Spencer).

Austria – Volderbad and Haller Strasse (Tirol) on *Tussilago farfara* L. (Hendel, 1925); Mösern (Tirol) on *Tussilago farfara* L. (Griffiths, 1966:807); also sheets in Hering's mine herbarium for Carinthia (Plöckenpass on *Tussilago farfara* L.,

and Mauthen on *Petasites albus* [L.]).

Germany – Neubrandenburg (Mecklenburg) on *Petasites hybridus* (L.) (Buhr, 1941a); Gottesberg, Bad Elster and Oberwiesenthal (Saxony) on *Tussilago farfara* L., *Petasites hybridus* (L.) and *P. albus* (L.) (Buhr, 1964); also sheets in Hering's mine herbarium for Mühlhausen (Thuringia) on *Tussilago farfara* L., Soritz (Bautzen) on *Tussilago farfara* L., Falkenstein (Bavaria) on *Petasites albus* (L.), Tölz (Bavaria) on *Petasites hybridus* (L.), Heimkehle (Alter Stolberg) on *Petasites albus* (L.), and Berlin Botanical Gardens on *Petasites hybridus* (L.).

Italy – Rionero in Vulture, on *Tussilago farfara* L., leg. Ricchello (sheet in Hering's mine herbarium).

Czechoslovakia – Tisová, Orlik and Jesenik (Starý, 1930), mines on *Tussilago farfara* L.

Roumania – Herculesbad (Banat), mines on *Petasites* sp. and *Tussilago farfara* L. (Hering, 1924, nos. 60 and 104); Sinaia, on *Tussilago farfara* L., leg. Sienkiewicz (sheet in Hering's mine herbarium).

Poland – Tatry Mountains, on *Tussilago farfara* L., leg. Nowakowski (Griffiths, 1966: 807); Ojków National Park, on *Petasites albus* (L.) (Beiger, 1960).

Denmark – Hørsholm, on *Petasites hybridus* (L.) (sheet in Hering's mine herbarium).

Finland – mines on *Petasites frigidus* (L.) at Kemi (Ostrobothnia borealis) (Linnaniemi, 1913) and Viborg (Karelia australis) (Frey, 1937).

Russia – Moscow region, mines on *Tussilago farfara* L. (Rohdendorf, 1960).

Hendel (1935) also lists *Petasites paradoxus* (Retz.) as a host-plant, in addition to host species recorded above.

Phytomyza tussilaginis petasiti Spencer 1969, new status

Phytomyza petasiti Spencer. Spencer, 1969b:266. Holotype ♂, Alberta (Canada), in K. A. Spencer's collection.

Adult. – Colour of head as described for subspecies *tussilaginis*, but with dark coloration of vertex less extensive, not enclosing bases of vt in specimens from Alberta and British Columbia (however vte on dark ground in specimens from Yukon and Alaska); face completely yellow, or at most with weak traces of brown in antennal pits.

Mesonotum dark centrally (weakly shining, finely grey-dusted), but with strongly contrasting broad whitish side bands which anteriorly extend inwards along its anterior margin to level of either row of dc, and posteriorly to scutellar suture; outer pa on yellow ground or on boundary between yellow and dark ground; humeral calli with traces of infuscation (a distinct dark spot in some specimens). Scutellum largely dark, but with traces of pale coloration at its basal corners. Pleura extensively whitish, but with dark anteroventral area of variable size on mesopleuron and in some specimens with parts of pteropleuron infuscated; sternopleuron dark ventrally, with pale dorsal band; hypopleuron largely dark. Wing base and squamae white, latter with white or ochreous fringe. Coxae pale apically, dark at base; femora largely dark with contrasting yellow tips; tibiae and tarsi entirely yellow or yellow-brown.

Abdomen extensively yellowish (especially towards sides), in female with contrasting black basal cone of ovipositor (grey-dusted on basal third to half).

Wing length 2.4-2.8 mm. Costal ratio mg_2/mg_4 2.6-4.0.

Material examined. – 1 ♂, 1 ♀ from larvae 4.vii.71 on *Petasites palmatus* (Ait.), Elk Island National Park, Alberta, emerged 27.vii.71 and 28.v.72, leg. G. C. D. Griffiths; 1 ♂, 1 ♀ from larvae 25.vii.71 on *Petasites* (? *palmatus* X *frigidus*), same locality, emerged 13.viii.71 and

15.v.72, leg. G. C. D. Griffiths; 1 ♀ from larva 26.ix.71 on *Petasites sagittatus* (Banks), same locality, emerged 3.vi.72, leg. G. C. D. Griffiths. 1 ♀ from larva 6.viii.70 on *Petasites palmatus* (Ait.), Summit Lake Pass (4200 feet elevation; Alaska Highway mile 392), British Columbia, emerged 19.v.71, leg. G. C. D. Griffiths. 1 ♂, 1 ♀ from larvae 31.viii.69 on *Petasites sagittatus* (Banks), East shore of Lake Teslin, Yukon Territory, emerged 16 & 22.v.70, leg. G. C. D. Griffiths. 1 ♂ from larvae 2-3.viii.68 on *Petasites frigidus* (L.), Walker Fork, Taylor Highway, Alaska, emerged 23.x.68 (forced), leg. G. C. D. Griffiths.

Other records. – The holotype was bred from leaves of *Petasites frigidus* (L.) (= *vitifolius*) collected at Blairmore, Alberta (Spencer, 1969b). Sehgal (1971) records specimens bred from *Petasites sagittatus* (Banks) at Edmonton and Elk Island Park (Alberta).

Phytomyza tussilaginis kevani new subspecies

Adult. – Frons yellow centrally, with ocellar plate and vertex contrastingly shining black (both vt on dark ground); orbits somewhat infuscated, especially along eye margins and around bases of orbital setae. Face clear yellow only on margins, extensively infuscated in antennal pits. Genae yellow. Occiput black, somewhat shining. Antennae with first article brown, second and third articles black. Palpi black; labella yellow.

Thorax weakly shining, finely grey-dusted, almost entirely black, with traces of pale coloration only at margins of humeral calli (especially around anterior spiracles); seams of notopleural and mesopleural sutures white; wing base and squamae contrastingly white, latter with dark fringe. Legs largely dark with tips of femora yellow (but only those of front legs distinctly so in holotype); tibiae and tarsi brown or black. Abdomen entirely dark.

Wing length 2.2-2.3 mm. Costal ratio mg_2/mg_4 2.6-2.7 (lower end of range of values for other subspecies).

Types. – Holotype ♂ from larva 31.vii.70 on *Petasites frigidus* (L.), South shore of Yaya Lake, Richards Island, Northwest Territories (Canada), emerged 6.v.71, leg. P. G. Kevan. 1 ♂ paratype from larva 18.viii.70 on *Petasites frigidus* (L.), Triple Summit (132° 54′ W, 69° 32′ N), Northwest Territories, emerged 4.v.71, leg. P. G. Kevan.

I am pleased to name this subspecies after Dr. Peter G. Kevan, who collected material for me while working in the Arctic.

Phytomyza alpina Groschke 1957

Phytomyza alpina Groschke. Groschke and Hering, 1957:122. Holotype ♂, Bavaria (Germany), in Staatliches Museum für Naturkunde, Ludwigsburg.

Adult. – Head (Fig. 32) with orbits not or only very narrowly projecting above eye in lateral view; genae in middle 1/4 to 1/3 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors variably developed, in most specimens about 2/3 as long as anterior ors, but ranging from fully as long to completely absent; anterior ori in most specimens 1/3 to 1/2 as long as posterior ori, but in some absent or represented only by very small setulae; orbital setulae more or less one-rowed. Peristomal margin with vibrissa and 4-7 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr in 4-5 rows; 5-10 presutural ia; 4-10 postsutural ia; inner pa over half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 2.8-3.4. Wing length 2.2-3.2 mm.

Frons clear yellow centrally, with ocellar plate and vertex contrastingly black (vte on dark ground; vti on boundary between dark and pale ground); orbits largely yellow, but with

traces of infuscation along eye margins and around bases of orbital setae. Face partly yellow, but infuscated in antennal pits. Genae yellow. Occiput black. Antennae with first article yellow-brown, second and third articles black. Palpi black; labella yellow. Thorax largely dark, strongly grey-dusted, scarcely shining; sides of mesonotum with limited area of pale coloration around margins of humeral calli and on upper part of sutural triangle; scutellum dark; mesopleuron with narrow whitish dorsal band along notopleural suture; seam of mesopleural suture whitish; wing base and squamae yellowish white, latter with dark fringe. Legs largely dark, with tips of femora contrastingly yellow. Abdomen largely black or brown. Basal cone of ovipositor (♀) grey-dusted on about basal half.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from periandrium, bearing only fine setulae. Pregonites extending ventrally, shielding base of aedeagus at rest. Aedeagal hood with two pairs of lateral sclerites. Aedeagus as Fig. 1, 2 and 5; basal sclerites narrow, slightly convergent distally; dense group of spinules on left side near dorsal margin of left basal sclerite; on right side less dense group of more dorsally situated spinules nearer centre-line; sclerotization of medial lobe forming loop, confluent anteriorly with basal sclerites; distal section of aedeagus with pair of slender paramesophalli and distiphallus consisting of more or less parallel, paired tubules. Ejaculatory apodeme small (Fig. 3-4).

In most European specimens the tubules of the distiphallus appear rounded dorsally in lateral view (as Fig. 5). But they appear more or less angulate in some British specimens, as in all the specimens from North America (Fig. 1). No clear-cut morphological distinction can be made between populations from the two areas.

Puparium and third instar larva. – Similar to those of *tussilaginis*. In my British series there is an unusually wide range of variation between individuals in the number of spiracular bulbs (anterior spiracles with 14-18 bulbs; posterior spiracles with 22-36 bulbs). The variation is less in North American material (anterior spiracles with 12-15 bulbs; posterior spiracles with 19-25 bulbs) (Fig. 28). Puparium 2.0-2.5 mm long.

Mine. – Larvae leaf-miners on *Senecio* and *Petasites*, leaving leaf through semicircular slit, in most cases on upper surface, before puparium formation. Mines on upper surface of leaf, appearing white or greenish white in reflected light, geographically variable in shape (Fig. 35-36).

In Europe mines have been reported only on *Senecio alpinus* (L.) and *S. jacobaea* L. Mine (Fig. 36) initially linear but becoming progressively broader and more or less blotchy terminally; faeces deposited as discrete particles, well separated (mostly by over 1 mm) in terminal part of mine.

In North America I have bred this species from mines on *Petasites*, as well as on *Senecio* (see records below). Mine (Fig. 35) retaining its linear appearance throughout, up to 15 cm long, 2-3 mm wide terminally; faecal particles separated by about 2 mm in terminal part of mines on *Senecio lugens* Richards, but more numerous and separated by less than 1 mm in mines on *Petasites*.

Material examined. – 1 ♂ paratype from larvae on *Senecio alpinus* (L.), Partnachklamm, Bavaria, Germany, emerged 27.viii.51, leg. F. Groschke. 5 ♂♂, 7 ♀♀ from larvae 30.vii.62 on *Senecio jacobaea* L., Ingleborough, Yorks., England, emerged 26-31.viii.62, leg. G. C. D. Griffiths. 8 ♂♂, 5 ♀♀ from larvae 6.ix.64 on *Senecio jacobaea* L., Gorsdale Scar, Yorks., England, emerged 5-12.x.64 and 22.iv.65 (1 ♂), leg. G. C. D. Griffiths. 6 ♂♂, 1 ♀ from larvae 10.vi.65 on *Senecio jacobaea* L., Mullagh More, Clare, Ireland, emerged 2-8.vii.65, leg. G. C. D. Griffiths. 2 ♂♂ from larvae 31.viii.66 on *Senecio jacobaea* L., Derreen, Clare, Ireland, emerged 6-27.iii.67, leg. G. C. D. Griffiths.

1 ♂, 2 ♀♀ from larvae 31.viii.69 on *Petasites sagittatus* (Banks), on East shore of Lake

Teslin, Yukon Territory, emerged 17-26.v.70, leg. G. C. D. Griffiths. 1 ♂, 1 ♀ from larvae 30.viii.69 on *Senecio pauperculus* Michx., Lake Laberge, Yukon Territory, emerged 17-19.v. 70, leg. G. C. D. Griffiths. 1 ♀ from larvae 19-26.vii.68 on *Petasites frigidus* (L.), Eagle Summit (3900 feet elevation), Steese Highway, Alaska, emerged 8.x.68 (forced), leg. G. C. D. Griffiths. 3 ♂♂, 2 ♀♀ from larvae 3-11.viii.70 on *Senecio lugens* Richards, Summit Lake Pass (4200 feet elevation; Alaska Highway mile 392), British Columbia, emerged 12-13.v.71, leg. G. C. D. Griffiths; 1 ♀ from larva 9.ix.71, same plant and locality, emerged 11.v.72, leg. G. C. D. Griffiths.

Other records. – Groschke's original material was bred from *Senecio alpinus* (L.) in the Bavarian Alps (Partnachklamm and Lenggries). Other localities where mines on *Senecio alpinus* (L.) have been recorded are Tölz (Bavaria), Kleiner Walsertal and Eisenerzer Reichenstein (Austria) (*in* Groschke and Hering, 1957), and Maloja, Switzerland (*in* Griffiths, 1966). The first British record was from Kinlochewe, Ross (Scotland), mines on *Senecio jacobaea* L. collected by O. W. Richards on 10.vii.53 (Spencer, 1956). Other Irish localities (all in the Burren area of County Clare) are given by Griffiths (1968).

Remarks. – The known distribution of this species is indicated on Fig. 39.

I am not able to distinguish the leaf mines of this species on *Petasites* in North America from those of *tussilaginis*. Although the *maximum* length of mines of *tussilaginis* in the available samples is longer, there is overlap between the species in respect of this measurement.

The species described by Nowakowski (1962b) as *Phytomyza aronici* is the sister-species of *alpina*. The aedeagus of *aronici* is very similar to that of *alpina*, particularly in respect of the asymmetrical development of the groups of spinules (an undoubtedly apomorphous character). The only clear differences which I have noted involve the shape of the paramesophalli and the situation of the left group of spinules closer to the left basal sclerite in *aronici*. The type series of *aronici* was bred from mines on *Doronicum clusii* (All.), a member of the Senecioneae, in the Tatry Mountains of Poland (1600-2400 metres elevation).

Phytomyza senecionis Kaltenbach 1869

Phytomyza senecionis Kaltenbach. Kaltenbach, 1869:176. –1874:364. Hendel, 1935:478.

Types lost; type-locality, Germany.

Adult. – Head with orbits not or only narrowly projecting above eye in lateral view; genae in middle about 1/4 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors variably developed, ranging from two-thirds as long as anterior ors to completely absent; anterior ori short, not more than half as long as posterior ori; orbital setulae irregularly one-rowed. Peristomal margin with vibrissa and 4-5 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr in 4-5 rows; 7-10 presutural ia; 8-11 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 3.3-4.1. Wing length 2.1-2.6 mm.

Frons clear yellow except dark ocellar plate (both vt on yellow ground). Face largely or completely yellow, at most infuscated in antennal pits. Genae yellow. Occiput dark. Antennae with first article yellow-brown, second and third articles brown to black. Palpi brown or black; labella yellow. Mesonotum dark centrally (weakly shining, finely grey-dusted), but with strongly contrasting broad whitish side bands which enclose the humeral calli (indicated by small dark spot) and extend posteriorly to the scutellar suture; outer pa on boundary between yellow and dark ground; scutellum dark; mesopleuron whitish on upper third to half, dark ventrally; other pleura largely dark, but with some pale coloration along

sutures. Wing base and squamae white, latter with contrastingly dark fringe. Coxae dark; femora largely dark with contrasting yellow tips; tibiae and tarsi deep yellow or yellow-brown. Abdomen largely brown, but yellow on sides at base. Basal cone of ovipositor (♀) grey-dusted on basal half to two-thirds.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from periandrium, bearing only fine setulae. Ventral extensions of pregonites inconspicuous, more or less membranous. Aedeagal hood with two pairs of lateral sclerites. Aedeagus as Fig. 11; basal sclerites with angular notches (notch on left sclerite lower than that on right) near each of which lies a group of spinules; sclerotization of medial lobe forming loop; distal section small, with conspicuous spine on left side, with poorly differentiated distiphallus (pigmented only around its margins). Ejaculatory apodeme rather large (Fig. 12).

Puparium and third instar larva. – Similar to those of *tussilaginis*. Anterior spiracles with 9-11 bulbs; posterior spiracles with 21-28 bulbs. Puparium 1.7-2.1 mm long.

Mine. – Larvae leaf-miners on *Senecio*. Mine (Fig. 37) entirely linear, up to 23 cm long, in many cases following midrib for long distance, remaining narrow terminally (not more than 1.5 mm wide); faeces deposited as fine particles, in some cases forming short strips; most mines confined to upper surface of leaf (but some beginning on lower side according to Hering, 1957b), appearing contrastingly white in reflected light; larvae leaving leaf through semicircular slit on upper surface before puparium formation.

A figure of the mine has also been given by Hering (1957b).

Material examined. – 1 ♂ from larva 10.vi.54 on *Senecio fuchsii* Gmel., Kunnersdorf (near Görlitz), Germany, emerged 28.vi.54, leg. E. M. Hering (no. 6040). 2 ♀♀ from larvae 23.viii.63 on *Senecio nemorensis* L., North of Como, Italy, emerged 17-22.ix.63, leg. G. C. D. Griffiths.

Other records. – According to Hering (1957b) the larvae of this species occur commonly on *Senecio nemorensis* L. and *S. fuchsii* Gmel. in Central Europe. Records are as follows.

Holland – Berg en Dal and Valkenburg on *Senecio fuchsii* Gmel. (de Meijere, 1926, as "*Phytomyza lappae* Gour.").

Germany – Kaltenbach's original material was bred from *Senecio nemorensis* L. (locality not stated). Buhr (1964) lists localities in Saxony, where he reports this species as common on *Senecio fuchsii* Gmel. Voigt (1929) records mines at Geisenheim and Laacher See (Rheingau); Zoerner (1969) at Saarensee (Middle Elbe region). There are also sheets of *Senecio fuchsii* Gmel. in Hering's mine herbarium for Frankenhausen (Thuringia), Alter Stolberg (Südharz), Siegen (Westphalia), Schlosspark/Torga (Lausitz), Lowenburg/Rhöndorf (Rheinland) and the Mosel Valley (Rheinland).

Austria – Sheets of *Senecio fuchsii* Gmel. in Hering's mine herbarium for Linz (Donau) and Tal der Grossen Mühlviertel.

Czechoslovakia – Starý (1930) lists localities where larvae were collected on *Senecio fuchsii* Gmel. He also reports this species on *Senecio jacobaea* L. at Tisová, which record needs checking as this plant is a host of *Phytomyza alpina* Groschke (not yet described when Starý wrote).

Bulgaria – Rila Mountains, on *Senecio nemorensis* L. (Buhr, 1941b).

Poland – Collected by Nunberg (1948) and Nowakowski (1962a:152) on *Senecio nemorensis* L., *S. fuchsii* Gmel. and *S. subalpinus* Koch at various localities in the Tatry Mountains (see also Griffiths, 1966:797, 807, and 809); also found by Nowakowski on *Senecio fluviatilis* Wallr., near Sztum and Warsaw (Nowakowski, 1962a:152); Beiger (1959, 1965) gives records for the district of Wieliczka (on *Senecio fuchsii* Gmel.) and for the Kraków-Wieluń Jura (on *Senecio nemorensis* L.).

Denmark – Maribo (Sønderup, 1949).

Whether this species occurs in Scandinavia has not been established. Rydén's (1952) record for Sweden is doubtful, since it is based on a caught female.

Phytomyza ravasternopleuralis Sasakawa 1955, new status

Phytomyza senecionis ravasternopleuralis Sasakawa. Sasakawa, 1955:19. –1961a:468. Holotype ♂, Aomori prefecture (Japan), in Entomological Laboratory, Saikyo University.

Adult. – As described for *senecionis*, except as follows.

Sternopleuron entirely dark, without pale dorsal band along suture.

Distal section of aedeagus (Fig. 9) longer, with weakly differentiated paramesophalli and slender distiphallus whose tubules are almost parallel apically. Ejaculatory apodeme small (Fig. 10).

For further description and figures see Sasakawa (1955, 1961a).

Puparium and third instar larva. – Similar to those of *tussilaginis* and *senecionis*. Anterior spiracles with 11-14 bulbs; posterior spiracles with 22-28 bulbs. Puparium about 2 mm long. For further description and figures see Sasakawa (1961a).

Mine. – Larvae leaf-miners on *Senecio* and *Petasites*. Sasakawa (1955) describes the mines as linear throughout ("ophionome"), whitish, yellowish or yellowish green in colour, 7-13.5 cm long, on upper surface of leaf; faeces deposited in short strips or as fine particles; larvae leaving leaf through semicircular slit on upper surface before puparium formation. Figures of the mine are given by Sasakawa (1955, 1961a).

Material examined. – 1 ♂ from larvae on *Petasites japonicus* Miq., Mominoki, Mount Sara, Ehime prefecture (Shikoku), Japan, leg. T. Yano (May 1954).

Other records. – The type series was bred from *Senecio palmatus* Pall. at Towada Park, Aomori prefecture, Japan (Sasakawa, 1955).

Remarks. – I propose to consider *ravasternopleuralis* a full species, rather than a subspecies of *senecionis* (as it was described by Sasakawa), because the form of the distiphallus is substantially different from that of the only male of *senecionis* available to me. But this judgement is only tentative, in view of the limited material available.

Sasakawa (1961a) referred specimens bred from *Petasites japonicus* Miq. to "*Phytomyza lappae* Robineau-Desvoidy". However the aedeagus of the male from this plant lent me by Sasakawa (Fig. 9) does not agree with his figure of "*lappae*", but rather with his figure of *ravasternopleuralis*. I conclude that the Japanese flies from *Petasites* should be referred to the latter taxon.

(b) the *Phytomyza syngenesiae* group

I have discussed the definition of the *Phytomyza syngenesiae* group and given descriptions of species in my 1967 revision. One additional species (*senecionella*) has since been described by Sehgal (1971). In this group the puparia remain inside the leaf, as in the *robustella* group. But the form of the aedeagus is very different, characterized (*inter alia*) by inclusion of the terminal part of the ejaculatory duct in an unpaired distal tubule.

The two polyphagous species of this group, *Phytomyza syngenesiae* (Hardy) and *P. horticola* Goureau, probably occur commonly on *Senecio* (see records below). Whether they also sometimes attack *Tussilago* and *Petasites* requires confirmation. Records of "*Phytomyza atricornis* Meigen" (a name formerly used for species of this group) on *Petasites* and *Tussilago* in Europe were published, for instance, by Hering (1924, 1927), de Meijere (1926) and Starý (1930). But these records antedate the description of *P. farfarae* Hendel,

and confusion with that species must therefore be suspected. In 1967 I dissected three males identified as "*atricornis*" in Hering's collection and they all proved to belong to *farfarae*. The only European record since the description of *farfarae* is Sønderup's (1949) report of "*atricornis*" on both *Tussilago* and *Petasites* in Denmark. This record cannot be checked, as no adult flies are known to have been obtained from his samples.

Phytomyza syngenesiae (Hardy)

I have given firm records for *Senecio jacobaea* L., *S. cruentus* DC. and *S. squalidus* L. in Europe (Griffiths, 1967). There are many other published records of "*Phytomyza atricornis* Meigen" on species of *Senecio* in Europe, but I cannot determine whether they refer to *syngenesiae* or *horticola*. In North America *Senecio cruentus* DC., *S. mikanioides* Otto and *Petasites* sp. are recorded as hosts (Frick, 1959; Griffiths, 1967). The last record requires confirmation in view of possible confusion with species of the *robustella* group.

My previous opinion (Griffiths, 1967) that this species dispersed across the Bering land bridge between Siberia and Alaska is now withdrawn. The most northern locality for *syngenesiae* in North America is the City of Edmonton (Alberta), where it has been collected only once and does not seem established. The species does not occur in the boreal forest nor in coastal regions of Alaska, where trans-Beringian migrants are expected to occur. The only species of the *syngenesiae* group so far found in such northern areas is *senecionella*. I now think it more likely that *syngenesiae* was introduced into North America with horticultural plants.

Phytomyza horticola Goureau

I have given firm records for *Senecio vulgaris* L., *S. vernalis* W. et K. and *S. doria* L. in Europe (Griffiths, 1967). For Japan Sasakawa (1961b) lists *Senecio vulgaris* L., *S. cruentus* DC. and *Petasites japonicus* Miq. as host plants.

Phytomyza senecionella Sehgal

Sehgal (1971) has described this species on the basis of material bred from *Senecio congestus* (R. Br.) var. *palustris* (L.) at Elk Island National Park (shores of Tawayik Lake), Alberta. His figure 123 indicates that the distal tubule of the aedeagus has a characteristic sinuate shape, by which the species may be distinguished from *syngenesiae*. I have figured (Fig. 13) the aedeagus of a male bred from *Petasites frigidus* (L.) at Eagle Summit (3900 feet elevation), Steese Highway, Alaska (emerged 26.vii.68 from puparium collected 19.vii. 68, leg. G. C. D. Griffiths). Probably *Petasites* is only an occasional host of this species, for only a single mine was found. The main host at Eagle Summit was *Senecio atropurpureus* (Ledeb.) subsp. *tomentosus* (Kjellm.) (1 ♂, 2 ♀♀ emerged 24-26.vii.68 from puparia collected 17.vii.68). Mines were also found the same day on *Senecio yukonensis* Pors. While the male genitalia of these Alaskan specimens agree substantially with Sehgal's figure, the coloration of the head is darker than in the original series, with the frons largely orange-brown with grey-dusted orbits.

Leaf mines collected at Eagle Summit are 6-7 cm long, 1.5-2.0 mm wide terminally; faecal particles discrete, mostly separated by 0.75-1.00 mm in terminal part of mine; mines formed mainly on upper surface of leaf, with puparium formation following in most cases on lower surface.

(c) the *Phytomyza robustella* group

The term "*Phytomyza robustella* group" has been used to include certain species whose larvae produce gall-like swellings in the midrib of the leaves of Compositae. However no clear morphological distinction can be drawn between these species and certain other species whose larvae are leaf- or stem-miners on Compositae, not forming swellings. Spencer (1971) has already referred to this group one such species, *P. buhriella* Spencer (as *notabilis*). In the present work I treat that species and some additional leaf-mining species whose male genitalia are of similar type. The puparia of all species referred to this group remain in the plant tissue, with the anterior spiracles turned downwards so that they project ventrally through the epidermis. A similar apomorphous type of puparium is shown by the *Phytomyza syngenesiae* group and related groups, as discussed in the first paper of this series (Griffiths, 1972). Species of the *Phytomyza robustella* group differ from those groups most obviously in respect of the structure of the aedeagus, retaining a forked distiphallus (containing the bifid terminal portion of the ejaculatory duct) and lacking "supporting sclerites". However since these aedeagal characters are probably plesiomorphous for *Phytomyza*, they do not provide a satisfactory indication of the limits of the group. My delimitation of the "*Phytomyza robustella* group" is therefore only tentative.

Phytomyza buhriella Spencer 1969

Phytomyza spec. Hering, 1957a:93. –1957b:746 (no. 3604a).

Phytomyza buhriella Spencer. Spencer, 1969a:21. Holotype ♂, Mühlhausen (Germany), in K. A. Spencer's collection.

Phytomyza notabilis Spencer. Spencer, 1971:182. Holotype ♂, Edinburgh (Scotland), in University Museum, Oxford. New synonymy.

The synonymy of *notabilis* has been pointed out in correspondence by M. von Tschirnhaus.

Adult. – External form and colour as described by Spencer (1969a).

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from periandrium (without suture on outer side), bearing numerous fine setulae. Pregonites not extending ventrally. Aedeagal hood with one pair of lateral sclerites. Aedeagus as in Fig. 15; basal sclerites rather broad, more or less parallel distally; medial lobe large, with distinct sclerites; distal section with broad paramesophalli whose sclerotization is confluent with V-shaped distiphallus. Ejaculatory apodeme as Fig. 16.

Puparium and third instar larva. – See the detailed larval description given by Hering (1957a:93) (as *Phytomyza* spec.). The larvae can be distinguished from those of all other species treated in this paper by the presence of a pair of sclerotized processes of the mandibular adductor apodeme on either side of the labial sclerite (as also in gall-forming species of the *robustella* group), and the large size and annulate appearance of the frontal process. Spiracles (both anterior and posterior) with 18-22 bulbs. Puparia white.

Mine. – Larvae miners on *Petasites* and *Tussilago*. Mines linear, formed mainly in petioles of basal leaves (but in some cases beginning in leaf vein); faecal particles inconspicuous (Hering, 1957b:746). Puparium with its ventral surface adjacent to surface of petiole, with its anterior spiracles projecting ventrally through epidermis.

Material examined. – 5 ♂♂ swept on *Tussilago farfara* L., 28.v.67, Ihlkate, SW Kiel, Germany, leg. M. von Tschirnhaus.

Other records. – The type series of *buhriella* was bred by H. Buhr from *Petasites albus* (L.) at Mühlhausen, Thuringia, Germany. Buhr (1964) has also reported mines from

Oberwiesenthal (Erzgebirge). Von Tschirnhaus has obtained further material (both swept and bred) from *Tussilago farfara* L. in Schleswig-Holstein. In Britain this species is known from a male taken at Edinburgh, Scotland, 2.vi.1905 (holotype of *notabilis*); and 1 found puparia in petioles of *Tussilago farfara* L. at Leeds, Yorks., in October 1964.

Phytomyza farfarae Hendel 1935

Phytomyza farfarae Hendel. Hendel, 1935:400. De Meijere, 1938:90. Holotype ♀, without locality label (presumably Austria), in the Naturhistorisches Museum, Vienna.

Adult. – Head with orbits only very narrowly projecting above eye in lateral view; genae in middle about 1/3 of eye height; eyes with sparse fine pubescence or virtually bare. Frons at level of front ocellus about twice width of eye. Two ors, of equal length, posteriorly directed; only one strong ori, inwardly directed (anterior ori absent or represented by short setula); orbital setulae one-rowed. Peristomal margin with vibrissa and 3-4 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr few, in two rows; ia few (4-5 presutural; 1-3 postsutural); inner pa 1/3 to 1/2 as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio mg_2/mg_4 2.1-2.7. Wing length 2.1-2.7 mm.

Frons deep yellow or brown centrally, with ocellar plate and vertex contrastingly dark (both vt on dark ground, or vti on boundary between dark and pale ground); orbits grey along eye margins. Face largely dark brown, in some specimens becoming yellow towards sides. Genae deep yellow or brown. Occiput black. Antennae with first article yellow-brown or brown, second and third articles dark brown or black. Palpi black; labella yellow. Thorax dark, strongly grey-dusted, scarcely shining, with pale coloration only along notopleural and mesopleural sutures; wing base yellow or ochreous; squamae with dark margin and fringe. Legs largely dark, with tips of femora contrastingly yellow. Abdomen largely brown. Basal cone of ovipositor (♀) grey-dusted on about basal two-thirds.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres delimited from periandrium by distinct suture on outer side, bearing numerous fine setulae. Pregonites not extending ventrally. Aedeagal hood with one pair of lateral sclerites. Aedeagus as in Fig. 20-21; basal sclerites rather broad, divergent distally; medial lobe without or with only weak traces of sclerotization; distal section with pair of small paramesophalli and large Y-shaped distiphallus. Ejaculatory apodeme as Fig. 22.

Puparium and third instar larva. – Mandibles with two alternating teeth; right mandible longer than left. Spiracles as described and figured by de Meijere (1938:90); anterior spiracles knob-shaped, with about 9 bulbs; posterior spiracles also knob-shaped, about same size as anterior spiracles, with 7-11 bulbs. Puparium white, 2.2-2.7 mm long.

Mine. – Larvae leaf-miners on *Tussilago* and *Petasites*. Mine (Fig. 33A) interparenchymal, pale green in reflected light, entirely linear, 24-28 cm long, about 1 mm wide terminally, in many cases with long straight stretches besides some of main veins; faeces deposited in very fine particles, often forming long beaded strips (in Perlschnüren zusammenhängend) on one side of mine; main part of mine formed on upper surface of leaf, but with puparium formed at end of short channel on lower surface. Puparium with its ventral surface adjacent to surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Material examined. – 3 ♂♂, 4 ♀♀ from puparia 19.viii.64 on *Tussilago farfara* L., Mösern (1250 metres elevation), Tirol, Austria, emerged 28.viii-7.ix.64, leg. G. C. D. Griffiths. 1 ♂ from puparium 4.ix.55 on *Petasites* sp., Garmisch, Bavaria, Germany, emerged 21.ix.55, leg. K. A. Spencer.

Other records. – This species can be definitely accepted as occurring only in central Europe and the Balkans. Additional firm records are as follows.

Austria – found "everywhere" according to Hendel (1935); Stanzach im Lechtal, on *Tussilago farfara* L. (de Meijere, 1938); also sheets in Hering's mine herbarium for Mauthen (Carinthia) on *Petasites albus* (L.), Tal der Grossen Mühlviertel on *Petasites paradoxus* (Retz.), Heiligenblüt (Tauern) on *Tussilago farfara* L., and Warscheneck-Gebirge (Linzershaus, 1400 metres elevation) on *Tussilago farfara* L.

Germany – Mühlhausen, Thuringia, on *Petasites albus* (L.) (Buhr, 1960); Lenggries, Bavaria, on *Tussilago farfara* L., leg. Groschke (Griffiths, 1966).

Poland – common in the Tatry Mountains (Nowakowski, in correspondence).

Roumania – Sinaia, ix.57 (sheet in Hering's mine herbarium).

Bulgaria – Rila Mountains, on *Tussilago farfara* L. and *Petasites albus* (L.) (Buhr, 1941b).

Records for Denmark (Rydén, Lyneborg and Nielsen, 1963) and Ångermanland, Sweden (Rydén, 1956) cannot be accepted, as they are based on caught specimens which have not been dissected. Rydén's (1947) record for Jämtland, Sweden, is almost certainly erroneous, since the fly was bred from *Solidago*. Hendel (1935) also referred to this species a series of caught specimens from Jakutsk (Siberia) in the Leningrad Museum. They were misidentified; on dissection I found that they belong to the grass-feeding *Phytomyza fuscula* Zetterstedt, in the sense clarified by Spencer (1969b).

Phytomyza hyperborea new species (♀)

Adult. – As described for *farfarae*, except as follows.

Third antennal article with long upcurved pubescence distally (Fig. 31).

Costal ratio mg_2/mg_4 2.6. Wing length 2.4 mm.

Frons largely deep yellow, slightly grey-dusted along eye-margins, with ocellar plate contrastingly dark; dark coloration of vertex less extensive (vti on yellow ground, vte on boundary between dark and yellow ground). Face deep yellow, only slightly infuscated in antennal pits. Genae deep yellow. Wing base contrastingly yellow; squamae pale with ochreous fringe. Abdomen largely brown, but yellow on sides at base and with yellow bands on hind margins of all terga.

Puparium and third instar larva. – Mandibles with two alternating teeth; right mandible longer than left. Spiracles knob-shaped, anterior with about 20 bulbs, posterior with 15 bulbs. Puparium reddish yellow, 2.6 mm long.

Mine. – The single specimen was bred from a puparium found at the end of a linear mine with widely spaced faecal particles on the upper surface of a leaf of *Petasites frigidus* (L.). Since much of the mine had been destroyed through the feeding of a large tephritid larva in the same leaf, a full description is not possible. Puparium with its ventral surface adjacent to upper surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Type. – Holotype ♀ from puparium 2.viii.68 on *Petasites frigidus* (L.), Walker Fork, Taylor Highway, Alaska, emerged 21.x.68, leg. G. C. D. Griffiths.

Remarks. – Long pubescence on the third antennal article is also shown by *Phytomyza ciliata* Hendel, a European species of the *robustella* group whose larvae mine the leaves of *Chrysanthemum leucanthemum* L. *Phytomyza hyperborea* differs from that species as follows: (1) orbits not projecting above eye in lateral view; (2) higher costal ratio mg_2/mg_4 (less than 2.0 in *ciliata*); and (3) more extensive yellow coloration (vti on yellow ground, face largely yellow, abdomen yellow on sides at base and with yellow bands on hind margins of all terga).

Under natural conditions the holotype would not have emerged until the following spring. The late autumn emergence was due to delay in my obtaining outdoor storage facilities.

Phytomyza hypophylla new species

Adult. – As described for *farfarae*, except as follows.

Head (Fig. 30) with orbits more distinctly projecting above eye in lateral view; genae in middle 1/2 to 2/5 of eye height. Third antennal article with slightly longer pubescence than in *farfarae* (but not so long as in *hyperborea*).

Costal ratio mg_2/mg_4 1.7-2.1 (lower than in both *farfarae* and *hyperborea*). Wing length 2.1-2.7 mm.

Head darker coloured; orbits entirely dark, densely grey-dusted; centre of frons grey-dusted over brown to reddish black ground colour; face largely dark brown or black; genae brown.

Male postabdomen and genitalia very similar to those of *farfarae*, but with some difference in shape of distiphallus (Fig. 23-24). Ejaculatory apodeme larger (Fig. 25).

Puparium and third instar larva. – As in *farfarae*. Spiracles knob-shaped, anterior with 8-10 bulbs, posterior (Fig. 29) with 7-11 bulbs. Puparium white, 2.1-2.7 mm long (Fig. 27).

Mine. – Larvae leaf-miners on *Petasites*. Mine (Fig. 34) formed mainly on lower surface of leaf, basically linear but usually convolute within restricted area, forming irregular secondary blotch, very inconspicuous (virtually concealed in reflected light by dense pile of leaf); on upper surface of leaf at most short stretches of mine channel or area of brownish discoloration visible; faeces deposited as very fine particles, in some cases forming short strips. Puparium with its ventral surface adjacent to lower surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Types. – Holotype ♂; 2 ♂♂, 7 ♀♀ paratypes from larvae and puparia 19-26.vii.68 on *Petasites frigidus* (L.), Eagle Summit (3900 feet elevation), Steese Highway, Alaska, emerged 26.vii-12.viii.68, leg. G. C. D. Griffiths. 3 ♂♂ paratypes from puparia 16-25.viii.71 on *Petasites hyperboreus* Rydb., near Mount Cavell Chalet (5800-7400 feet elevation), Jasper National Park, Alberta, emerged 23.viii-3.ix.71, leg. G. C. D. Griffiths.

Remarks. – I have also bred a female from undersurface mines collected at Walker Fork, Alaska (from larvae and puparia 2-3.viii.68 on *Petasites frigidus* (L.), emerged 20.viii.68, leg. G. C. D. Griffiths). In this specimen the colour of the head is as in *farfarae*, with the frons largely yellow-brown. In the absence of associated males I cannot judge whether this specimen represents an additional undescribed species of the *robustella* group, or a colour variant of *hypophylla*.

Phytomyza lugentis new species

Adult. – As described for *farfarae*, except as follows.

Costal ratio mg_2/mg_4 1.9-2.2. Wing length 2.5-2.8 mm.

Head darker coloured (compare also *hypophylla*); centre of frons brown or ochreous; face largely black; genae brown; antennae entirely black; labella yellow-brown or red-brown. Abdomen black. Basal cone of ovipositor (♀) grey-dusted on about basal third to half.

Male postabdomen and genitalia similar to those of *farfarae* in most respects, but with clear differences in form of aedeagus (Fig. 17-18). Distal section of aedeagus with larger Y-shaped distiphallus, without paramesophalli; medial lobe with loop of unpigmented sclerotization. Ejaculatory apodeme larger (Fig. 19).

Puparium and third instar larva. – As in *farfarae*. Spiracles knob-shaped, anterior with 9-10 bulbs, posterior with 7-10 bulbs. Puparium white, 2.3-2.6 mm long.

Mine. – Larvae leaf-miners on *Senecio lugens* Richards and *S. sheldonensis* Pors. Mine formed on upper or lower surface of leaf (largely on lower surface in most cases), variable in shape (more or less linear throughout, or partly linear with irregular blotchy areas); faeces deposited as discrete particles (separated by over 1 mm in terminal part of mine). Puparium with its ventral surface adjacent to lower surface of leaf, with its anterior spiracles projecting ventrally through epidermis.

Types. – Holotype ♂; 2 ♂♂, 4 ♀♀ paratypes from puparia 3-11.viii.70 on *Senecio lugens* Richards, Summit Lake Pass (4200 feet elevation; Alaska Highway mile 392), British Columbia, emerged 7-15.viii.70, leg. G. C. D. Griffiths. 2 ♂♂ paratypes from puparia 5.viii.70 on *Senecio sheldonensis* Pors., same locality (5000 feet elevation), emerged 12.viii.70, leg. G. C. D. Griffiths.

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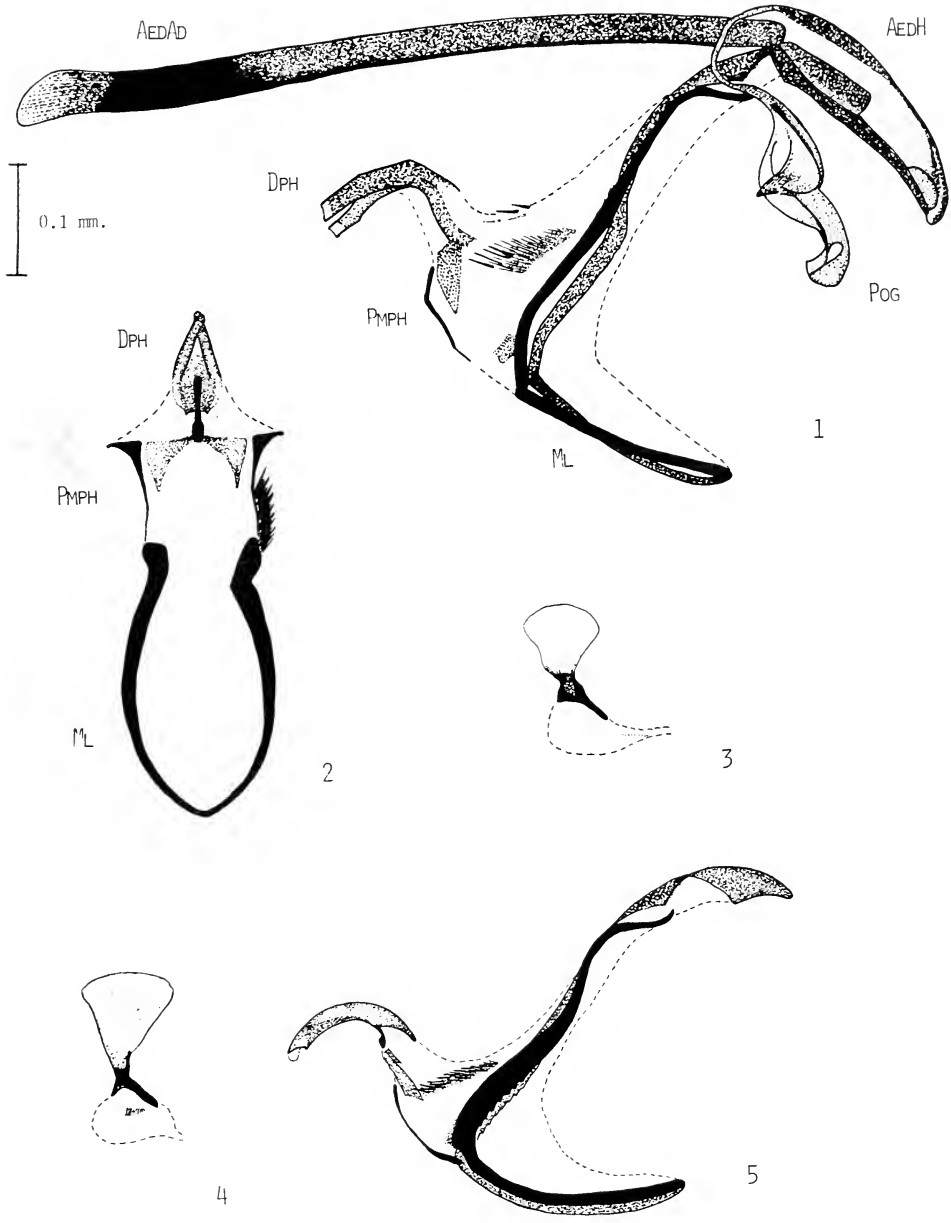


Fig. 1-3. *Phytomyza alpina* Groschke (♂), Lake Teslin, Yukon: 1, aedeagus and associated structures in lateral view (AEDAD aedeagal apodeme, AEDH aedeagal hood, DPH distiphallus, ML medial lobe, PMPH paramesophallus, POG postgonite); 2, distal section and medial lobe of aedeagus in anteroventral view (lettering as Fig. 1); 3, ejaculatory apodeme. Fig. 4-5. *Phytomyza alpina* Groschke (♂), England: 4, ejaculatory apodeme; 5, aedeagus in lateral view.

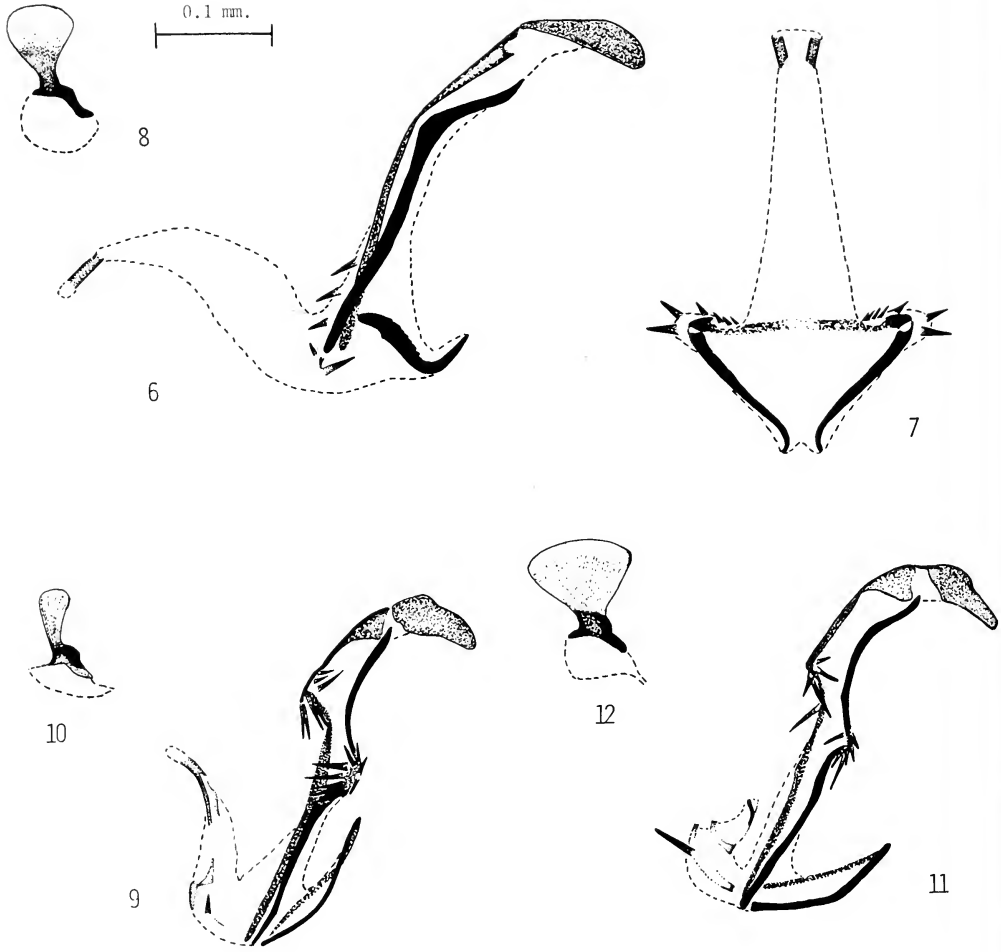
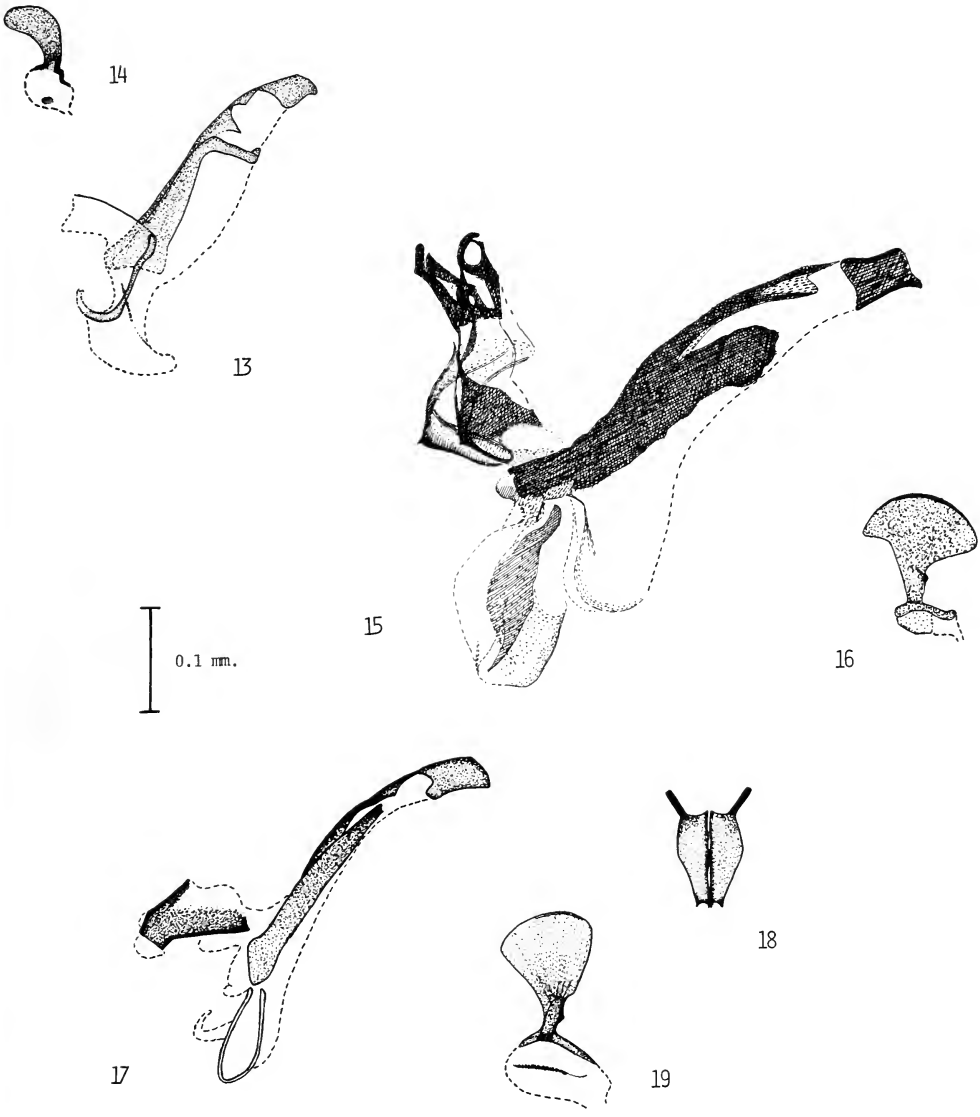


Fig. 6-8. *Phytomyza tussilaginis* Hendel (♂), England: 6, aedeagus in lateral view; 7, distal section and medial lobe of aedeagus in ± ventral view; 8, ejaculatory apodeme. Fig. 9-10. *Phytomyza ravasternopleuralis* Sasakawa (♂): 9, aedeagus in lateral view; 10, ejaculatory apodeme. Fig. 11-12. *Phytomyza senecionis* Kaltenbach (♂): 11, aedeagus in lateral view; 12, ejaculatory apodeme.



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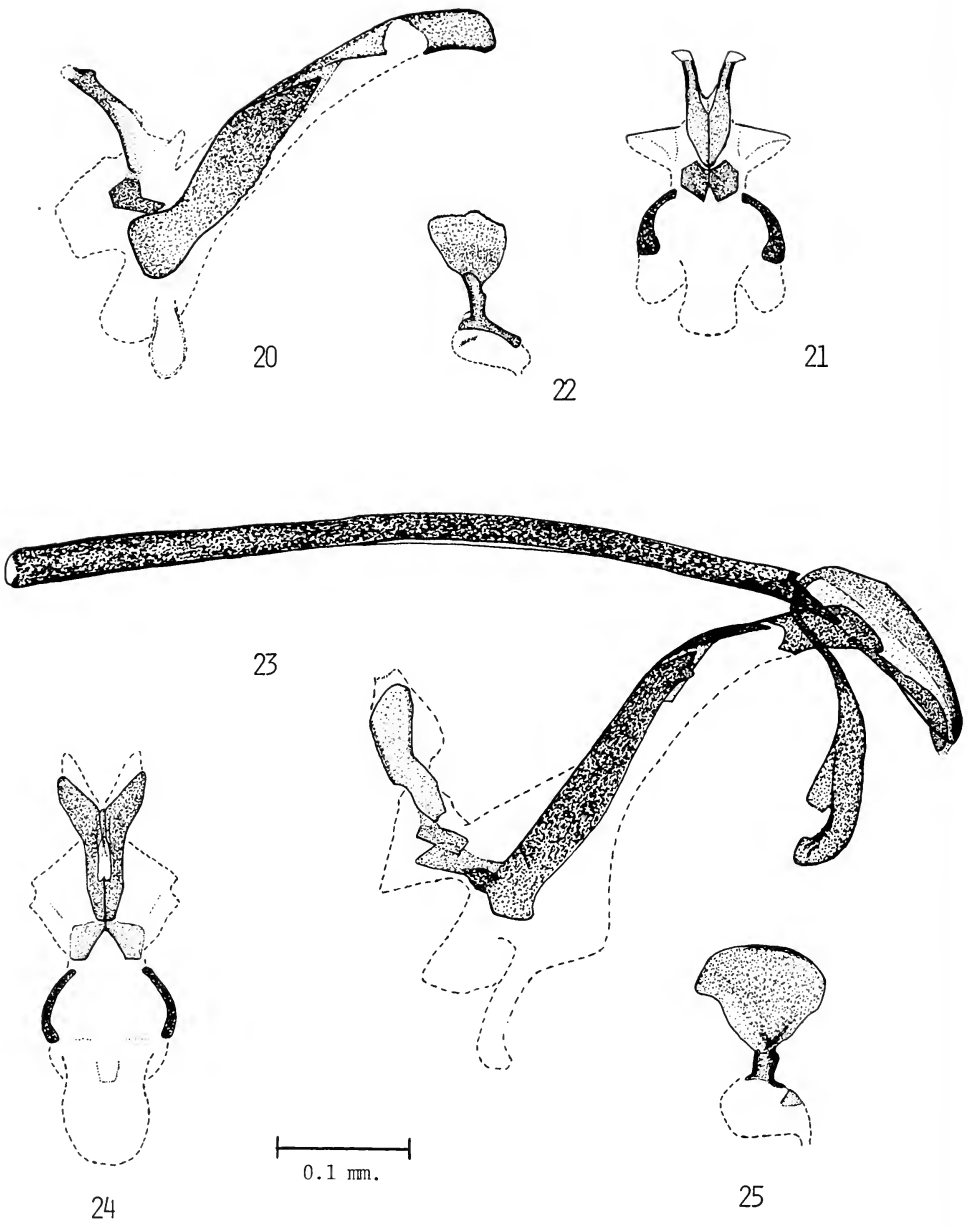

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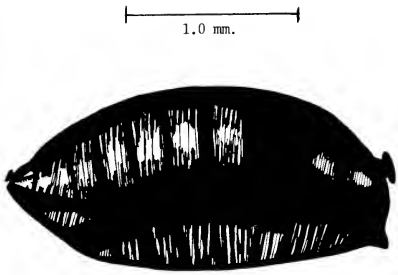

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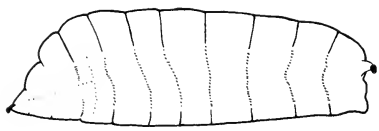

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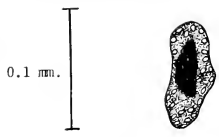

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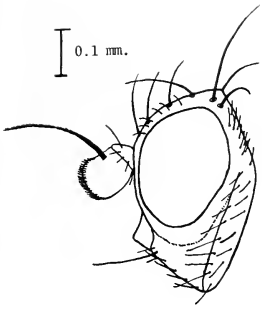

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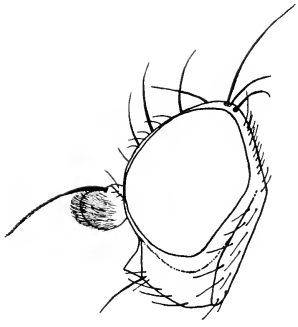

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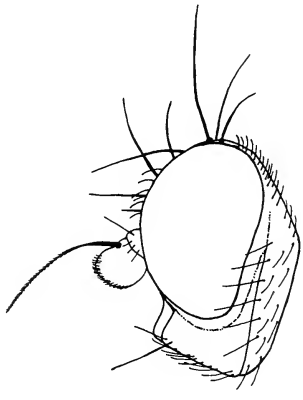

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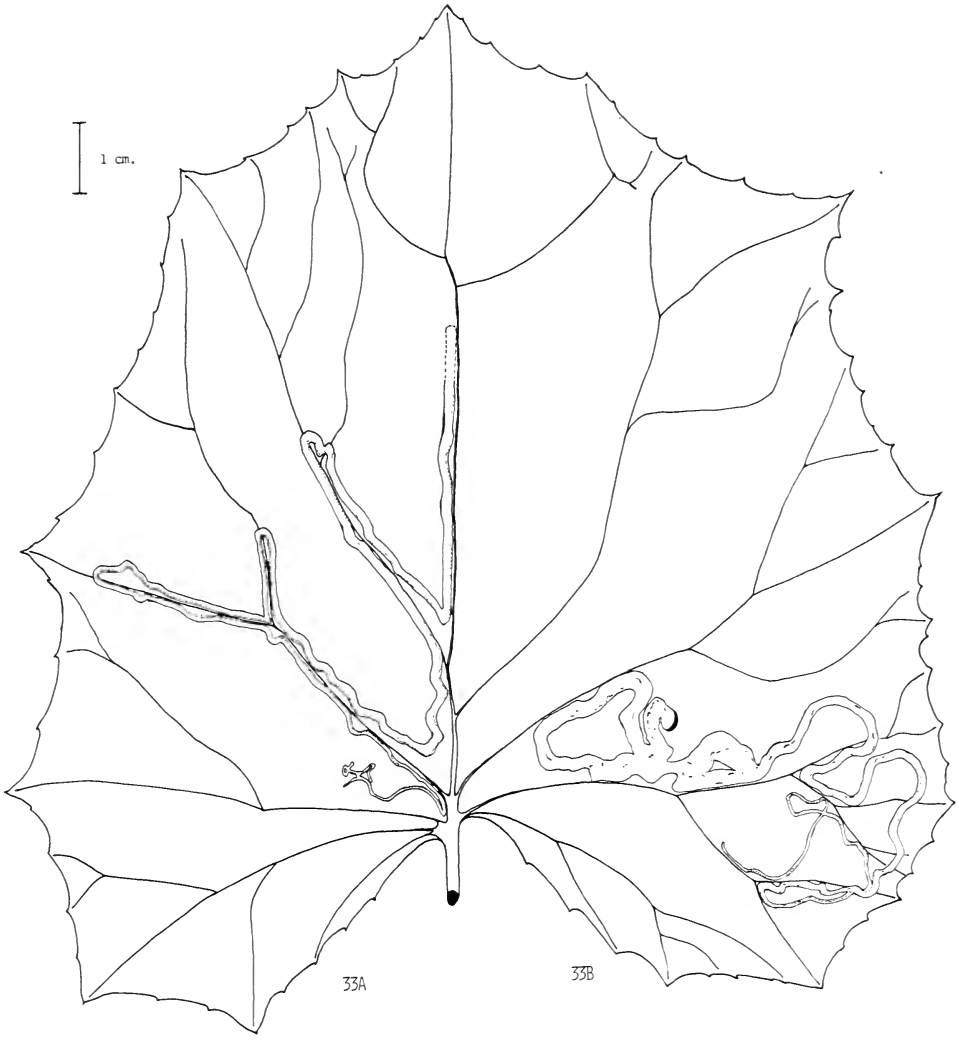

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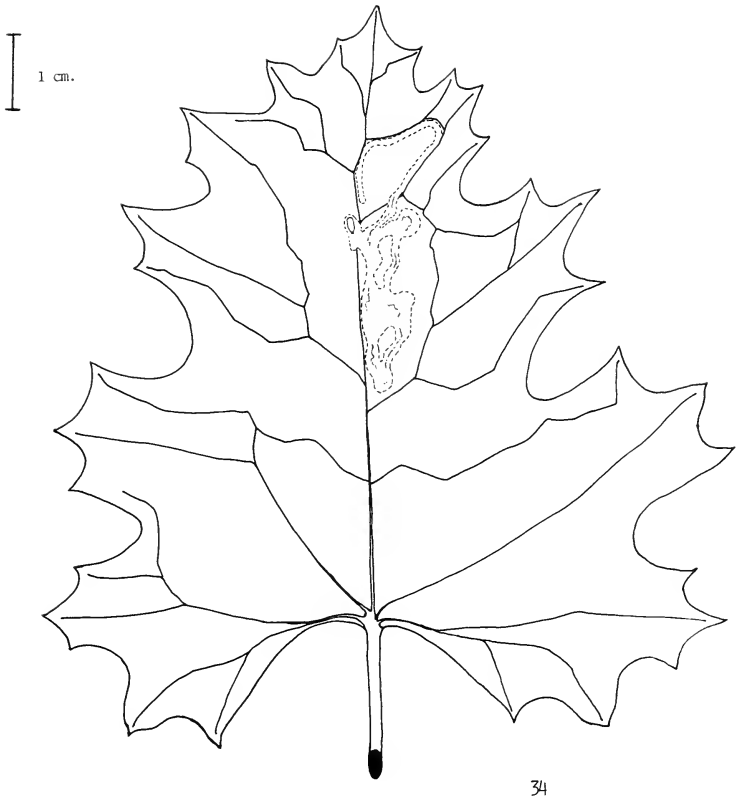

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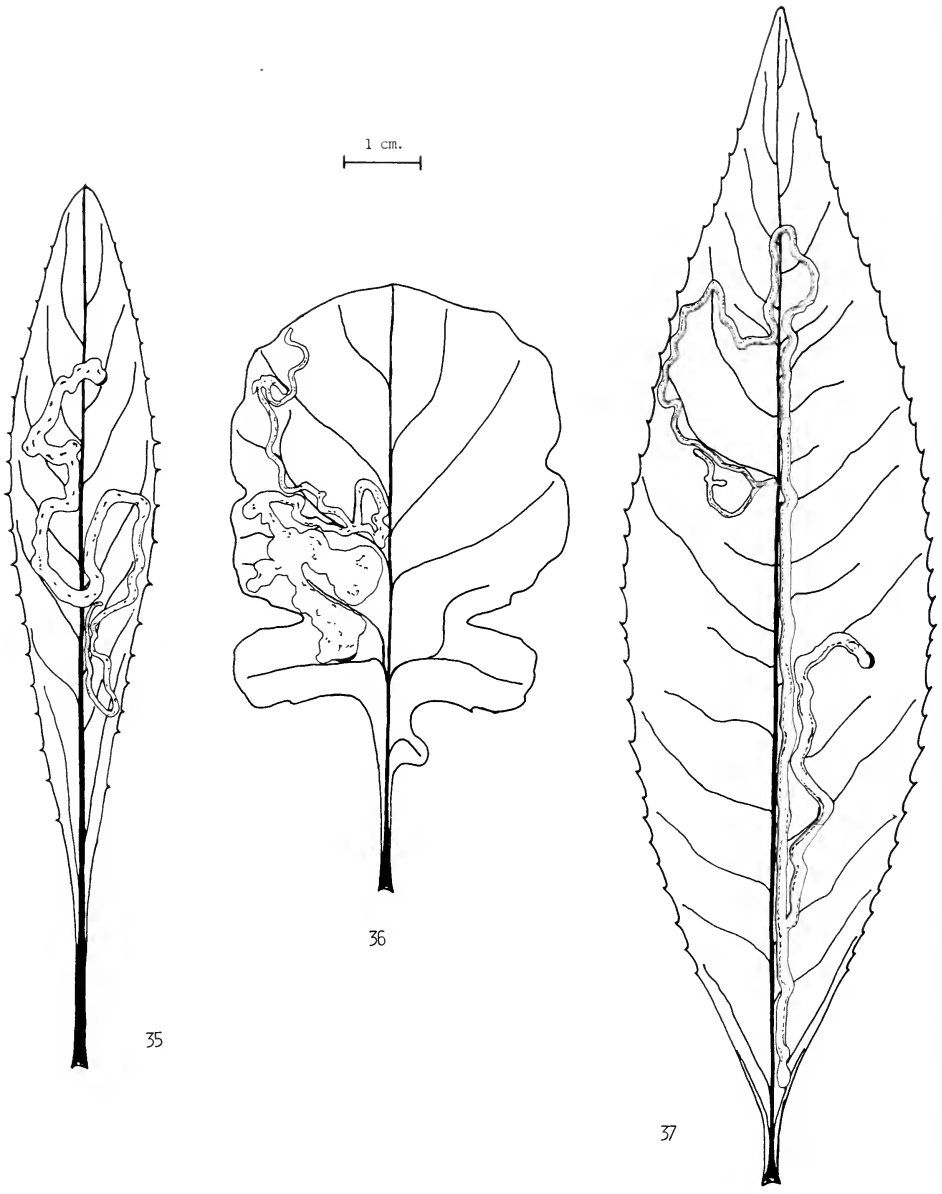

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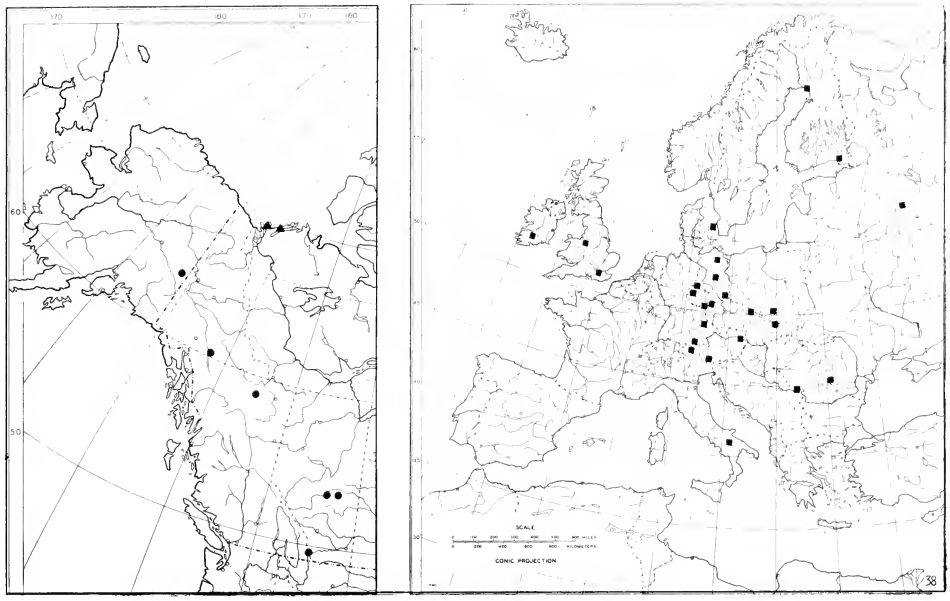

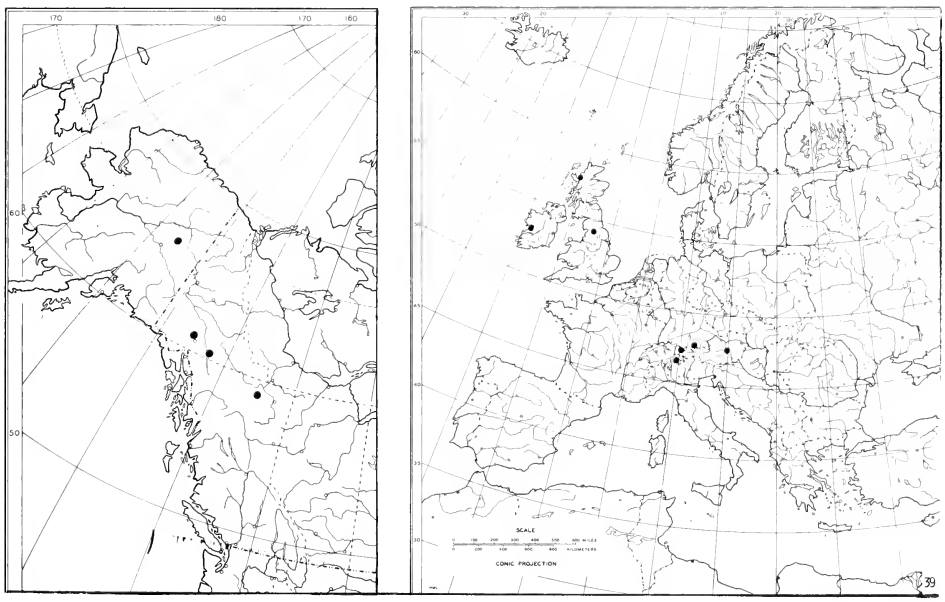

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ANNOUNCEMENT

Biting Fly Control and Environmental Quality – Proceedings of a Symposium held at the University of Alberta in Edmonton, May 16, 17, and 18, 1972.

The proceedings of this symposium, which was organized jointly by the Department of Entomology at the University of Alberta and the Advisory Committee on Entomology of the Defence Research Board, are expected to be published before the end of 1972. A further announcement will follow.

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

Copy should conform to the Style Manual for Biological Journals published by the American Institute of Biological Sciences, Second Edition, 1964, except as regards the abbreviations of titles of periodicals which should be those given in the World List of Scientific Periodicals, 1964 Edition. The appropriate abbreviation for this journal is *Quaest. ent.* An abstract of not more than 500 words is required. All manuscripts will be reviewed by referees.

Illustrations and tables must be suitable for reproduction on a page size of $9\frac{3}{4} \times 6\frac{3}{4}$ inches, text and tables not more than $7\frac{3}{4} \times 4\frac{3}{4}$ inches, plates and figures not more than $8\frac{1}{2} \times 5$ inches. Reprints must be ordered when proofs are returned, and will be supplied at cost. Subscription rates are the same for institutions, libraries, and individuals, $4.00 per volume of 4 issues, normally appearing at quarterly intervals; single issues $1.00. An abstract edition is available, printed on one or both sides (according to length) of 3×5 inch index cards (at $1.00 per volume) or on 5×8 inch standard single row punched cards ($1.50 per volume).

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Quaestiones entomologicae

ENTOMOLOGY & EDUCATION

Proceedings of a Symposium organized by the
Department of Entomology, University of Alberta
on the Occasion of the 50th Anniversary
of its Foundation
May 19, 1972

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

VOLUME VIII **SUPPLEMENT** **1972**

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ACKNOWLEDGEMENTS

We are grateful for financial support from the University of Alberta and for the enthusiasm and concern shown by the speakers, chairmen, discussion leaders, rapporteurs and participants. Special thanks are due to Brian Hocking, Don Whitehead, Ron Gooding, Ollie Frost, Tony Thomas, Doug Craig, George Braybrook, Brian Rolseth, Jack Scott, Natalie Daviduk, Marli Engeland, Linda Meissenheimer, and Lucille Queyrane who kept the symposium running smoothly or who assisted in the preparation of these proceedings.

PREFACE

To celebrate the 50th anniversary of its foundation by E. H. Strickland, the Department of Entomology at the University of Alberta hosted two symposia during the week of May 14, 1972. The proceedings of the first on "Biting Fly Control and Environmental Quality" are to be published by the Defence Research Board of the Canada Department of National Defence. Those of the second are presented here.

The texts of the formal presentations appear here as they did in the authors' final typescripts except for a few changes in grammar and some adjectival deletions. The discussions, as transcribed from tape recordings of the deliberations, have been left colloquial in the hope that some of the heat there generated will come through in the printed text. Much of the excess verbiage typical of spontaneous oral presentation has, however, been removed.

Bruce Heming
June, 1972

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INTRODUCTION

B. S. Heming
Department of Entomology
University of Alberta, Edmonton, Alberta

You might wonder why we are having a symposium on this topic to celebrate our 50 years of operation as a Department of Entomology at the University of Alberta. As most of you are aware, and as was mentioned several times during the last three days, entomology, like science in general, has entered a difficult period in its history. An increasing number of graduates are unable to find worthwhile employment in a world of shrinking job opportunities. Those who should be the most employable members in society are declared useless because of inexperience and "over-qualification." At the same time, the public has lost its faith in the ability of entomologists and other scientists to solve the problems now facing mankind. In addition, some of these problems, for example pesticide pollution, are said to have resulted from the activities of the scientists themselves. As a result of this "crisis-in-confidence" taxpayers are becoming increasingly reluctant to have portions of their incomes appropriated for the support of seemingly useless or even dangerous segments of society. This feeling has been communicated to the granting agencies and has resulted in shrinking financial support for research in universities and government institutes and for education in universities.

Our responsibility in departments of entomology is to educate entomologists. Thus, we thought it worthwhile, on our 50th anniversary, to re-evaluate our role in light of present and future conditions. We felt that this could best be accomplished by contacting practising entomologists in as many fields as was practical. Accordingly, we solicited contributions from six former students of this department: a high school biology teacher, a Canadian biology teacher in a primarily undergraduate university, an American entomologist in a U. S. land grant institution, a Canadian government research taxonomist, a Canadian government researcher in applied entomology, and the technical director of a large industrial concern. Each speaker was asked to comment on the following questions: 1. What is the proper education for entomologists of all kinds? 2. What can entomology contribute to education in general? and 3. What changes should be made in the curriculum of the Department of Entomology at the University of Alberta? Included with these questions were copies of past curricula, budgets, etc. for this department, selected at 10 year intervals to illustrate our development through the years. Thus, all participants, regardless of when they graduated, had a good idea of what the department had been doing in the intervening years.

You will notice that the program consists of two parts; the speakers in the morning session are educators while those in the afternoon are "users" of our graduates. Each group of papers will be followed by a discussion period. In each case we have a discussion leader, also an alumnus or a member of the department, who has received notice of the contents of the papers in advance. He will open the discussion after which we will ask for comments from the floor. We would therefore ask you to hold onto your questions until the open discussion period.

UNIVERSITY EDUCATION AND HIGH SCHOOL BIOLOGY

Don N. Jantzie
County Central High School
Vulcan, Alberta

First of all I would like to congratulate Dr. Hocking and his staff on the unique manner they have chosen to celebrate 50 years of distinguished service since the founding of the Department of Entomology at the University of Alberta. It is an honor and privilege for me to have this opportunity to participate in your celebrations. I would like to compliment you on your choice of topic since I believe that entomology has been almost totally bypassed in the curriculum of the high schools.

At the outset I should point out that the situation may appear more critical to an entomology graduate teaching and administrating in a school system than it would to persons having other specialized training in the biology field. As a science and biology teacher, I often found myself lamenting the fact that, because of the structure and content of the courses, I was unable to utilize my special knowledge and skills to the benefit of the pupils under my charge. This was because high school courses were not structured toward an in-depth study of the insect world nor was there any concerted effort to emphasize the environmental interrelations of insects with other organisms. The students of our school, residing in a rural setting, actively involved in a battle of survival against infestations of grasshoppers, cutworms, wireworms, sawflies, warble flies, lice, mange and so on, were busy studying forms of life that many of them had never seen and would never think of again in their lifetime. The biology courses were excellent according to sequential study of higher life forms in botany and zoology, but were not particularly relevant to the experiences of the students themselves. Then, six years ago, our school began a program that was designed to fill the needs of a large group of these rural students who planned to remain in the agriculture field, and who were negatively motivated toward many of the standard options in the high school curriculum. We developed an agriculture program that encompassed four main areas of study: soils, horticulture, field crops and animal husbandry and in every instance, where it was possible, included a comprehensive study of insects. Our experiment met with such outstanding success that it has become one of the most important options offered in our program, so much so that my instruction time is now totally dedicated to high school agriculture. My enthusiasm has been heightened because of the fulfillment I have received as an entomologist. It has also made me realize how much more effective several other high school courses might be if they too incorporated a study of insects into their curricula.

Unfortunately, most high school students have had little exposure to the world of insects. During their 12 years of primary and secondary education they have looked only briefly at the social habits of Hymenoptera, particularly at those of bees and ants and principally in comparison to human social habits; they have had a short overview of metamorphosis with particular emphasis on Orthoptera and Lepidoptera; and they have briefly considered the disease-carrying ability of Diptera as a health hazard. A brief introduction to rudimentary classification is made at the high school level in biology which only affects those students entered in a matriculation program (approximately 60% of the student body). The overall effect of these references to insects is minimal. There is little emphasis on creating a desire to pursue this interesting study farther, and what we have may even be detrimental to the development of future entomological interest. The average secondary school student in Alberta would be unable to contrast the eating habits or the mouth parts, for example, of

the house fly, the grasshopper, the leaf hopper, the bee and the cutworm and would probably consider all these insects very close relatives. These are the same students who, in their social studies courses, are required to make value judgements on the ecological and environmental effects of man's attempts to control nature, of which one of the prominent hot spots lies in the chemical control of insects.

Since these courses do not create an interest in entomology, how can a student in high school, going through a normal program, ever become interested enough in insects to study them at post-secondary institutions? Another question – How did each of us become interested in entomology to the extent that we specialized in the field? How much opportunity would a student in the faculty of education have of developing an interest in entomology, should he major in biology? These questions are fundamental to our problem at the secondary school level.

There are major inadequacies in our high schools with respect to entomological education. First and foremost, biology teachers, for the most part, are not qualified to teach entomological concepts, since most of them have had no training in entomology at the university level. With a minimum of background in such a diverse and complicated field, it is no wonder that teachers skirt the topic should it arise during the course of a lesson. In addition, it would be extremely unfair to the student should he be subjected to classroom instruction by a person who has no background experience in the field. With these points in mind, it is not surprising that our school curriculum covers only elementary concepts in the study of insects.

Another major inadequacy in our educational system today, is a curriculum that sidesteps any serious exploration of entomology. Keeping in mind what we have already discussed regarding the teacher, this situation follows naturally from the first, for it seems only reasonable that it would be difficult to utilize a curriculum weighted heavily toward an area that could not be adequately presented. Although, at the present time, biology is still taught in the standard pattern, a concerted effort to improve old and innovate new high school and the junior high school courses has been undertaken. With greater professional freedom, the teacher now has the opportunity to stress parts of the curriculum that he feels have more meaning and more relevance to the experiences of his class. There are also provisions for teaching options such as oceanography, entomology, geology, etc. at the junior high level by persons with special interests and background knowledge. It is generally agreed that our curriculum committees have made much progress in developing research-oriented courses that shy away from rote memorization (and regurgitation) of facts, a notable achievement in itself. Despite these improvements, however, the basic problem of including entomology with biology courses is lacking.

Curriculum committees have an additional problem when recommending text and reference books at a reading level suitable for secondary schools. To my knowledge there are no text books available that could be fully utilized in the school system. The problem lies in two areas. First of all, since entomology has been traditionally a university discipline growing out of the zoology pattern, the source books have been written with specific divisions in mind such as in taxonomy, morphology or physiology. The second area of difficulty lies in the reading level at which these texts are written. In both areas, the students would encounter so much difficulty in utilization and comprehension, that the books would be almost useless. Failing to find suitable text books in print, it would be necessary to write our own, thus creating additional economic problems (high publication costs). School boards, staggering under inflationary increases in operating costs, have tightened the educational belt to such an extent that the purchase of new text books, other than those in demand by large numbers of jurisdictions, is prohibited. In addition, writers and publi-

shers hesitate to develop a treatise, unless it has been specifically requested for a large potential market, and particularly if it does not measure up to the professional standards of the author. I believe the problem of finding or producing a suitable text book to be a difficult one to overcome.

Curriculum committees have the responsibility of developing courses that provide a concept structure, suitable as a foundation for the students' future understanding. In the exercise of this duty they must take into consideration economic priorities (very important at the present time); educational priorities, influenced a great deal by post-secondary institutions; and personnel priorities, influenced by the educational backgrounds of the teachers as well as by those of the committee members themselves. Looking at this situation we can only conclude that, at the present time, entomology must take a secondary position in our high school curriculum.

Having looked at two major inadequacies in the fostering of entomological interests in the secondary schools, let us now take a brief look at post-secondary institutions. How many students in the faculties of education or science obtain their major in entomology? In the past, the Faculty of Agriculture supplied virtually the entire body of graduates from the Department of Entomology. While we must agree that the study of insects should be an integral part of the study of agriculture, it should be closely linked to botany and zoology as well. Traditionally, an entomologist is an Aggie and, if we want to enlarge the stereotype farther, he is also a somewhat strange person, dressed in an old fashioned wool suit, and holding the perennial butterfly net over his shoulder. To put it bluntly, entomologists are considered by the average man in society to be a bit weird. This negative attitude harms our image and prevents expansion of the science into the associated field of education. I consider myself fortunate to have graduated in agriculture and especially in entomology. My training in the biological sciences – bacteriology, botany, zoology, genetics, biochemistry, plant pathology and entomology have made my teaching in high school a thrilling experience. It is unfortunate that more teachers could not have had a similar background.

What conclusions can we draw from the obscure role of entomology in the secondary school system? I believe that entomologists must become more involved with education, especially at the teaching and curriculum-planning levels. It is imperative that high school students, whether university bound or otherwise, be given the opportunity to explore and understand the fascinating world of insects and the tremendous impact that these small organisms have on other living things. It is of utmost importance that they learn to distinguish one family from another; that they comprehend the total meaning of biological and chemical control; and that they place this phase of entomology into its proper ecological perspective. To accomplish this our schools need teachers who have background experience in entomology, and we thus need university courses that provide access to this information. At the university level we need greater enrolments and greater participation from faculty of education students planning to work in the biology and ecology fields. Students should be able to recognize and understand the interrelationships that exist in our living world. The current ecological crisis demands that we have knowledgeable people in all walks of life. We need to press for change in the basic pattern of the curriculum at both the secondary and post-secondary levels of education. We need to shorten the educational lag that is an integral part of our education system. We have to provide a foundation of understanding through our teachers and through our schools that produces answers, not doubts, about our ability to solve environmental problems. Progress in the future will depend upon how we, the graduate entomologists of the past, influence the education patterns of tomorrow.

A VIEW OF BIOLOGY AND ENTOMOLOGY FROM THUNDER BAY

Richard Freitag
Department of Biology
Lakehead University, Thunder Bay, Ontario

"The elder statesmen sit on the mats,
And wrangle through half the day;
A hundred plans they have drafted
and dropped,
And mine was the only way."

– from the Book of Songs,
675 B. C. by Confucius

As you probably know, during the last five years almost every university sector has had its share of crises. Most of these have been corrected to some extent, while others persist. Some are growing worse. Two matters of concern to the Ontario university community are a marked decline in student enrolment, and a scarcity of jobs for students following graduation. As a means of offering information toward reaching the objectives of this session, I shall attempt to describe the two conditions, in particular as they affect biology and entomology in Ontario. Then I shall offer some possible remedial concepts for discussion.

It is well known now that most universities in Ontario experienced a shortfall in projected enrolments in September, 1971. At first it was looked upon as a brief dip in a clinal increase in the numbers of students entering universities. The usual observations, analyses and rhetoric followed in the academic and mass media. Concurrently, budgetary adjustments were made and by December, 1971, the crisis had almost been overcome. However, this year the crisis has reappeared with even more vigour (Table 1).

According to a recent report of the Committee on Statistics and Enrolment Projections, of the Ontario Universities' Council on Admissions (February, 1972), evidence from submissions of individual universities indicates that applications from students in Grade 13 are down by 5% compared to those at the same time a year ago. Also, the number of non-grade 13 applicants into first year is less than half of what it was a year ago. Thus, the total number of applications to Ontario universities is down by 7 to 8% from what it was a year ago. There are also major shifts in program preferences of applicants as indicated in Table 2.

Applicants for combined Arts and Science have declined by 16%, for Arts by 14% and for Engineering by 10%, while applicants for Science have increased by 9% and for other programs by 4%. Part of the expected 9% increase in the sciences is due to slightly increased enrolments in the Life Sciences programs, which is probably because of ecological charisma. Increased enrolments in the life sciences are taking place in other Canadian universities as indicated by a survey conducted by Dr. Von Borstel, Chairman of the Department of Genetics at the University of Alberta.

The Minister of Colleges and Universities of Ontario, Mr. George Kerr, recently announced to the legislature that Ontario universities are expecting a 5% drop in enrolment next fall, so there is no reason to believe that the situation will improve by September. The decline in enrolment last year and possibly next year may indicate a trend. If so, it precedes by approximately 20 years a projected decline in enrolment in universities in Ontario provided by the Draft Report of the Commission on Post-secondary Education in Ontario (Queen's Printer, Toronto, 1971). The commission notes this 1972 discrepancy but does not elabo-

rate on its occurrence.

In addition to the problem of enrolment, students are experiencing increasing difficulty in finding employment. Some statistics from student placement offices and unemployment centres show this to be a general trend. Because employment for biology and entomology students is in part what concerns us, I have selected the following table from a report of the committee investigating employment problems of entomologists in Ontario, by Drs. R. L. Edwards and P. S. Corbet (1970), as a more specific example (Table 3).

Table 1*. Total applicants to full-time programs in the Ontario Universities.

UNIVERSITY	1971	1972	DIFFERENCE	TOTAL DIFFERENCE
Brock	2,512	1,883	- 629	- 8,862
Carleton	5,962	5,265	- 697	
Guelph	6,670	6,475	- 195	
Lakehead	1,590	1,684	+ 94	
Laurentian	2,190	2,100	- 90	
McMaster	10,299	10,758	+ 459	
Ottawa	4,941	4,942	+ 1	
Queen's	9,258	8,653	- 605	
Toronto	18,034	17,410	- 624	
Trent	3,525	2,535	- 990	
Waterloo	14,517	12,533	- 1,984	
Western	17,648	15,600	- 2,048	
Windsor	4,796	4,124	- 672	
York	11,164	10,441	- 723	
W. L. U.	2,631	2,472	- 159	

Table 2*. Applicants to first year full-time programs in the Ontario Universities on or about February 15, 1972.

PROGRAM	1971 TOTAL	1972 TOTAL
Arts & Science	13,970	11,688
Arts	28,756	24,708
Science	10,560	11,507
Engineering	5,412	4,856
Other	12,155	12,652

*Tables 1 and 2 adapted from Report of the Committee on Statistics and Enrolment Projections of the Ontario Universities Council on Admissions. Meeting of committee held February 24, 1972.

Table 3*. Numbers of graduate students in entomology at Ontario Universities in 1970-71, and the number of existing positions for entomologists in Ontario from 1969 to 1971.

Number of graduate students in entomology in Ontario Universities:

M.Sc.	33
Ph.D.	21
Total	54

Number of existing positions for entomologists in Ontario:

	1969	1970	1971
Federal Government Service	120	115	115
Ontario Government Service	8	8	4
Industry	2	2	2
Ontario Universities	38	40	40
Total	168	165	161

*Report of the committee investigating employment problems of entomologists in Ontario. Proc. ent. Soc. Ont. 101:89-92, 1971.

The authors conclude that "if the rate of turnover is 3% per annum, we can expect vacancies for entomologists to become available at the rate of approximately five per year. However, the total number of existing positions for entomologists is expected to decline at about the same rate, from 168 in 1969 to a projected 161 in 1971." So opportunities for employment in universities, government and industry do not look too promising for the next few years. The situation is probably not any better for graduate students in other fields of biology. The drop in student numbers and the decline in employment opportunities are probably real and obvious while the underlying reasons seem more elusive. The classes at Lakehead University tend to be small, (no, an optimal size), and teacher and student usually communicate at the individual level. According to some of my students, many high school graduates no longer come to university because they feel taking an undergraduate degree is a wasted effort if it does not help them in getting a good job. Others tell me that many students *drop out* of university for the same reason. One of our top graduating students expressed the view that the increasing drop out rate in universities is mainly due to uninteresting courses and programs, not because students are unable to do the work. He suggested that the three-lecture, one-lab-per-week course becomes a 'drag' by the middle of the second year, and that project courses dealing with up-to-date problems should replace some of the others. He was very enthusiastic about a full-year chemistry course in which the entire second half was devoted to a laboratory project on the DNA molecule.

Some students believe that job-oriented community colleges have attracted high school graduates who would otherwise have gone to university. In order to understand more quantitatively the priorities of gaining qualification for work as opposed to an education, in the minds of biology students, I conducted a brief survey in two of my classes. Of course both processes are hardly separable in a biology degree program but I asked them to give

priority to one or the other. Thirty-nine students stated that they attended university primarily to obtain qualifications for employment and 14 claimed that they were taking the program because they enjoyed biology.

The relationship between job opportunities and education is much more difficult to define than causes of decline in student enrolment. This is clearly expressed in the Draft Report (1971, p. 28) as follows: "An important aspect of post-secondary education is its relationship to the labour market. Paradoxically enough this relationship is in most cases fuzzy. . . . We apparently do not have sufficient data even to describe or evaluate such a relationship. Under such conditions it would be difficult and irresponsible to forecast future linkages of education and manpower needs. It is often said that the majority of jobs our current generation of students will hold in their lifetime have not yet been invented."

Although student enrolments are increasing in biology and entomology programs, there is no evidence that job opportunities are improving for biology graduates. Indeed, increasing numbers of our graduates find employment in fields not related to biology. I was surprised to find two of our biology graduates working as permanent employees in an Ontario liquor store. Hardly a place for biologists, but they seemed to enjoy their work.

What then can we do to improve the situation for our students while remaining committed to our subjects and maintaining the good programs we now have? I suggest that we attempt to increase the development of biology and entomology in a lateral dimension. Surely in our changing society, new and different occupations are developing in which an education in biology or entomology is essential, but not to the extent provided by the programs we now offer. The following recommendations are a list of personal views which have developed from my experiences at Lakehead University. These recommendations are not intended to replace or change any traditional activities or programs. They are proposed rather as possible supplementary avenues of development. I shall give the recommendations and a brief rationale for each.

Recommendations

1. That university biology and entomology departments conduct annual surveys with a view to determining the present scope of entomology and biology.

A few weeks ago Dr. S. Madras, Director of the Liberal Science program at York University, visited Lakehead University to discuss Liberal Science with us. Dr. Madras served on several education advisory committees in Quebec of which part of their terms of reference was to determine the role of educational institutions for the government. He remarked that the conceptual profile of a university changes when the university is observed from varying distances and positions. His experience was that the interactions of universities and society became clear when he communicated with people who were considerably removed from the university milieu. Now this kind of experience is not new to field biologists who in fact use the process as a means of studying a single species in its natural environment, i.e. autecology. In my opinion, a carefully designed and executed autecology of biology and entomology would provide a greater understanding of our relationships to a changing society. It would also reveal possible interactions of our disciplines with academic and other sectors of society which could benefit biology, entomology and our students. Perhaps the survey could be conducted on a larger scale, that is by all life sciences departments in a university or even on a provincial or national scale. The survey could be conducted at two levels. First, an assessment could be made on the relationships of the classical programs, courses and course content to the professional occupations of biologists and entomologists. Second, and probably more important at this time, information could be obtained on occupations which require or should require graduates with some

knowledge of biology and entomology. We could also determine adaptations necessary to ensure that our subjects successfully evolve. Among the many probable advantages deriving from such a study would be ideas for establishing new course programs. Information would accrue that would be valuable in counselling first year students in determining a course program for a specific goal. The data obtained would be of benefit to all biologists across the country.

2. That major (biology, entomology) – minor (business administration, economics, law, political science, chemistry, physics, etc.) programs of study be developed for uncommitted students.

By uncommitted students I mean those who are taking a degree in biology or entomology but who also have special interests in other fields of study. There can be a definite advantage to having a strong training in two subjects with respect to getting a job. One of our students has a diploma in forestry and a B.Sc. degree in biology. He was hired to teach vocational subjects and academic courses in a vocational high school in Swan Lake, Manitoba. He was told that he would not have been offered the job if he had had only a degree in biology or in forestry. Another one of our biology education graduates was just hired to teach science in a high school in North Bay, Ontario. He completed a chemistry program in a community college before coming to Lakehead University. The principal of the high school informed him that he was hired primarily because he had a good background in both biology and chemistry. These are two examples of a possible growing demand for university graduates with such qualifications. Major-minor programs would clearly serve this need not only in education but in other occupations as well.

3. That honours students' research topics be multidisciplinary. A greater effort should be made to hire undergraduates for research being conducted by biology or entomology faculty, especially for multidisciplinary research.

Multidisciplinary research provides a good groundwork for more specialized research. I feel that the third undergraduate year or the honours year is a good level for such research. The student, while completing a program composed of subjects often apparently related, can obtain an appreciation of how they actually do relate. In addition, undergraduate students would greatly benefit from supervised research, particularly if they plan to continue graduate studies in a specific biology. Also, if a student plans to leave university this experience provides potential employers with a more complete picture of the student's abilities.

4. That a major (biology, entomology) – minor (business administration, economics, law, chemistry, physics, etc.) M.Sc., Ph.D., program be developed.

This kind of graduate project would require increased cooperation among university departments which is one of the main reasons for the recommendation. In my view the greatest failing in our society is the colossal human sound barrier among its components. This problem is well illustrated by the present environmental issue on which our political leaders and biologists seem to maintain an impasse. What better way to bridge this gap than with a graduate 'biobarrister' or 'entopolitician.'

SOME OBSERVATIONS: PROGNOSTICATIONS ON TRENDS IN ENTOMOLOGICAL CURRICULA IN U. S. COLLEGES AND UNIVERSITIES

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Before proceeding into the topic for discussion, I would like to extend my sincere appreciation to the committee for the opportunity of appearing on this symposium. This allowed me to make a pilgrimage back to the old Alma Mater after many years of absence. While change is the nature of all living things, and that includes man's institutions, and the University of Alberta is certainly far from an exception, I have pleasant twinges of nostalgia when picking out some old landmarks and reminiscing about my experiences here.

In my years subsequent to the baccalaureate at Alberta, I've retained a very fond memory of Prof. Strickland and have never waivered in the opinion that he was a great teacher, a fine entomologist and one of the most sincere, dedicated and human individuals I have met. Many times I've had cause to reflect on how fortunate I was in being exposed to his particular style of teaching.

And of course we are gathered here today, in part at least, to pay homage to Dr. Strickland, for his establishment of this department in 1922 has provided reason for our celebration these 50 years later. But if we are to honor Dr. Strickland for "creating" and nurturing the Department of Entomology through the earlier years, it would indeed be ungracious of me not to honor equally Brian Hocking, under whose vision and capable direction this department has developed into the significant and prestigious position it now holds among departments of entomology in institutions of higher learning throughout Canada and the United States. Indeed, as an alumus I extend my gratitude to you, Dr. Hocking, and to the other members of the faculty of the Department of Entomology for your outstanding and successful efforts in building this proud and productive entomological unit.

Moving on to the subject matter of the symposium, and referring to Dr. Heming's outline, I view his charge to the symposial participants as a three-part directive. First he asks that we consider the subject of a "proper education for entomologists of all kinds." My, what far reaching import lies in that word "proper"! Secondly, we're asked to direct some thought as to what entomology can contribute to education in general. And finally, if appropriate, to provide some feedback on entomological activities at the U. of A. over the preceding 50 years and perhaps direct some constructive comments as to the future. This is a substantial responsibility.

In public speaking one is cautioned never to provide excuses for the comments or directions he takes in formally presenting his views on a given subject. However, today I choose to avoid such caution and beg your indulgence regarding what might be claimed to be a degree of "tunnel vision," insofar as my direct association with entomological education over the past 20 years has been confined to institutions in the United States and even more specifically to land grant institutions. As most of you know, the land grant institution in the United States was created primarily for the purpose of meeting obligations related to the practical needs of the agricultural and mechanical arts. And while these institutions have embraced the concept of a total university, practical aspects of our field nevertheless commonly dominate in our activities.

I believe that before we can truly attend to the matter of education in entomology, we have to outline some evaluations regarding the contemporary position of the scientific community – at least as it appears in the public mind. Liberally paraphrasing some leading

educators in science, immediately and regrettably we note that, at a time in our history when we most need the talents of specialized intellectuals, they are becoming a drug on the market. Primarily, of course, I am referring to Ph.D.'s who, throughout the 1950's and 60's, were in such short supply and long demand that they could almost name their own salaries as they emerged from graduate school. During that decade, incidentally, Ph.D. production rates soared from 9,400 in the U. S. in 1959 to more than 26,000 in 1969. And entomology generally kept pace.

But now, suddenly, the stampede is over. Education – by far the largest consumer of learned specialists – has moved to a period of contracting activity. Government and industry, caught in a recession, have curtailed those activities that used the greatest shares of such talent. Such fields of particular interest to us as environmental quality control and modern pest management are just two areas which would seem to cry for the intellect and training of Ph.D.'s who are now being turned aside as surplus.

It is proposed today that we must retreat and guide this stream of extraordinary manpower into more productive channels and call for coordinated placement efforts by government and private industry on the one hand, and for greater discipline and imagination by universities on the other. "Should universities judiciously curtail their production in certain areas and steer into new avenues of greater need, government and industry could come together to insure better opportunities for the numerical surplus of Ph.D.'s."

This, however, presents us with our first of a series of dilemmas. On the one hand, entomological educators are almost totally committed time-wise to redirection into the future, replete with all the time-consuming activities of re-organization, re-evaluation, re-education and development of an enthusiasm for broader interdisciplinary involvements. Little time is left, therefore, for political involvement which appears to be becoming increasingly necessary to assure adequate consideration by the body politic and the body public of entomology and attendance to entomological needs within the aegis of "Environmental Issues." While the issue of insecticides has gained substantial public exposure, the vast research efforts needed to develop alternate means of keeping pestiferous species at non-economic levels have been dramatically over-simplified, undersold, or even ignored. And in this regard we, the entomologists, may be substantially to blame. Now is an ideal time for us to emphasize paramount need for research on long term insect control and to see that public interest is translated into fiscal support.

In effect then, entomologists in the field of education must not only be active in modernizing and redirecting the total curriculum, but must also involve themselves in providing the public and government with a clear awareness of the overall needs for entomological expertise. We must be pragmatic enough to learn that it's not sufficient to train and educate people in what we deem a viable entomological curriculum today. If we are remiss in educating the public, government and industry to a need for our product, then we are failing our students, ourselves, our profession and society at large.

In backing our attitude towards political activism we, in entomology, must assume some responsibility in educating the whole man. Granted, we cannot be expected to teach all the courses that contribute to his wholeness, but "the implications of our field for the well being of mankind are too important to be placed in the hands of leaders who lack the capacity for wide judgement." "The role of the biologist has assumed new importance as he has become able to manipulate growth processes and control living organisms in his environment. But to provide this knowledge for biological manipulation without developing an accompanying awareness in the area of human affairs and moral responsibility will render our products ill-prepared for the new role that will surely be thrust upon them." These new professionals must be provided with a breadth of exposure and understanding, for, if our

premise be correct relative to the importance of our field, they will constitute our primary agents in the re-education of the "establishment" to the vital role of entomology. As our banquet speaker, Mr. Coffey, stated the other evening . . . : "We are no longer society's decision makers" – accordingly then, we must maximize communication between ourselves and those who make the final decisions so that their judgements are based upon at least adequate information.

In reflection, it's ironic that just as scientists are on the crest of a wave of achievement, we must plead increasingly strongly for financial support. Just a short time ago, national prestige and well-being seemed to be clearly dependent upon the ever increasing growth of science and technology. Today, in spite of the tremendous impact scientific and technological advances have made on our lives, the layman generally doubts that scientists are doing what they should for mankind. And a lack of concert among ourselves adds to this confusion. The average man on the street sees a dialectic . . . on the one hand he is deeply impressed by the ability of scientists to "create," but on the other hand he is critical that scientists have allowed technological advances to proceed in a way that creates profound environmental and societal problems. Public disappointments have led to cutbacks in financial support for scientific research in many areas. And so it is up to scientists themselves to bridge some so-called "credibility gaps" and to convince the public and government that science is indeed very relevant.

Moving on now to some specifics relating to entomological education . . . first, I believe it self-evident that no single entomology department can be all things to all people. No department can provide all the courses and training experiences we deem necessary in preparing students for all kinds of entomological activities. Obviously, there are too many limits to our resources, both financial and expertise-wise. But to go one step further, while we often point to a need for a certain "critical mass" in terms of faculty numbers for coordinated departmental operation, a department geared in an attempt to do all things might in fact exceed a "maximum desirable mass." One might paraphrase such a situation as "the law of increasing negative returns." Another trap we sometimes fall into without realization is the unconscious acceptance of the concept that there is indeed a perfect entomological curriculum. Perhaps this subtly emerges as a result of conditioning where we think in terms of the individual when, in reality, we must think of a collective group of individuals – students of various interests, ambitions, abilities, for whom we must provide mosaics of educational patterns. If we fix our focus firmly in terms of the collective rather than the individual then we are more inclined to present flexible programs within which we design or at least accommodate for a number of directions of emphasis.

However, when one discusses the total curriculum offered by a department, of necessity it must be recognized that we are talking about two tracks: that of the undergraduate and that of the graduate. And within each are a number of sub-tracks. While I feel that a viable entomology department does need both of these programs (because of the cross-fertilization which is evident for both undergraduate students and graduate students), it is nigh impossible to embrace both programs within a single, common philosophy. Therefore, I believe there is need to consider undergraduate and graduate programs independently.

Let us discuss for the moment the undergraduate program. The premise I offer is a simple one and paraphrases that advanced earlier by Dr. Edward H. Smith. Entomology is a branch of biology and training at the undergraduate level in entomology fares best when closely allied with biological sciences. Specialization is left to the graduate level. Entomology departments, by their very existence with *esprit de corps* and offered capacity for growth, tend to proliferate and fragment a biological curriculum. It's perhaps inevitable that such units become the victims of scientific isolation, replete with all the dangers of reduced

capacity for interdisciplinary effort. Therefore, I agree with Smith when he states that there is little justification for an elaborate undergraduate major in entomology for those students planning graduate training. There are some exceptions to this, to which I would like to turn in a moment, but they still relate primarily to training for a terminal degree at the bachelor level. In order for the student to acquire a firm foundation for an advanced degree program, many hours must be devoted to generalized courses in the biological, physical and social sciences. Consequently, little time is left for specialization in entomology. Courses in mathematics, chemistry, physics, zoology and botany are prerequisites taking precedence over a field of specialization. Specialization then would logically occur at the graduate level. Admittedly, we should retain a minimal core of courses at the undergraduate level. These may be modified in part, both to serve a general service function and to accommodate the student who enters college with a career in entomology already firmly fixed in mind. Alternately, the university curricular regulations must be flexible enough to allow the committed student access to upper divisional and so-called graduate courses.

The point I make should not be construed as a proposal to eliminate entomology as an undergraduate offering. It is more a plea to reduce and ideally eliminate specialization or course proliferation at the undergraduate level.

However, today we must realistically face what appears to be the rapidly-emerging field of pest management. Inherent in the implementation of many pest management programs is the implication that there will be considerable manpower needs at probably the bachelor's level of education to conduct much of the observation and scouting required for constant surveillance of various units within a given agro-ecosystem. Admittedly, this is a very pragmatic approach, but it appears to me that we will be remiss in our responsibilities to society and agriculture if we do not design undergraduate curricula to best prepare individuals for this particular vocation. I envision such a curriculum with the first two years devoted to general courses in the physical and biological sciences (much as we have now) but with the last two years specializing in applied ecology with the added ingredients of economic entomology, weeds, plant diseases, climatology and the like. In addition, a most desirable addendum would be some kind of practicum course (admittedly a harsh term to use in the ivory halls of learning). And should we not be giving greater emphasis to in-service training programs with government and industry? From a mercenary point of view alone, development of new in-service training programs at times constitutes a "job-creating" maneuver.

Obviously, we are again faced with a difficult decision in determining what blend of applied training should be built into a framework of academic study dealing with biological principles. Considering the transient nature of technical knowledge as opposed to fundamental knowledge, I hope that even here we would tend to stress the latter. Regardless of which is emphasized, we must firmly imbue every student with the realization that continuous self-renewal is essential for professional survival.

Incidentally, that constitutes another basic consideration we sometimes allow to slip away from us when focussing our attention on what might constitute a complete and comprehensive curriculum. We must clearly remind ourselves and instill in the minds of our students that academia can only hope to provide an embryogenesis to the profession. Growth, development and even the metamorphosis of an individual in his profession must be carefully and continuously nurtured throughout his career.

Finally, let me phrase a few succinct and pertinent questions being asked today on undergraduate education in general. Are we giving sufficient attention to the content and approach being offered in high school biology courses today and accordingly upgrading our own lower division college courses in light of increasing sophistication of the high school programs? Are we evaluating and considering the need for students, at the upper levels par-

ticularly, to exercise some voice in determining their own curricula and setting their own goals within specific courses? Regardless of the eventual outcome of discussions along these lines, exchanges-of-position-views by itself often promotes mutual enthusiasm and has an inspirational effect.

Turning now to the matter of graduate education, we seem faced with a kind of collage incorporating both clear and obscure elements. Obviously, a graduate curriculum must be built largely upon the areas of expertise of the faculty. This immediately places a substantial burden on an existing faculty and their departmental administrator to plan carefully for additional and replacement faculty positions as well as curricular programs. This is asking both faculty and administration to exercise a considerable degree of clairvoyance in determining the nature of the various specializations within the profession as they relate to the future.

There are, however, a number of remedial steps which I feel should be taken today in graduate educational programs regardless of the direction or redirection of the curriculum. The first of these concerns a critical need for the exposure of students to the continuously newer technologies as they become available. Even the traditional systematist must be competent in the employment of modern physiological tools; the anatomist with the scanning electron microscope; the ecologist with infrared photometry; and all of us with the language and use of the computer. These are but a few examples, but ones which all too frequently are relatively ignored or given only vague consideration by teachers through inattention, preoccupation, or sometimes even downright laziness. It is perhaps fitting at this point, since I have not made reference elsewhere to the variety of graduate degrees offered by institutions, to pose a few additional, pertinent questions. Most of the questions outlined are under serious consideration at a number of U. S. institutions.

1. Does the research-oriented Master's degree program have a viable contemporary purpose? Or does it simply serve as a second prize and a more palatable means of "weeding out" Ph.D. candidates? Some educators refer to this degree as a "dinosaur."

2. Should we be instituting special graduate degree programs which differ in scope and purpose from the traditional M.Sc. and Ph.D. programs? What about a non-thesis M.Sc. for those going into extension, industrial sales, etc.? What about a special doctorate (i.e. Doctor of Arts) wherein we de-emphasize the research aspects and emphasize preparation for teaching or other largely non-research careers?

3. Have our language requirements become passé? Do these so-called "translation competency tests" represent simply another archaic "pseudo-intellectual hoop" through which students must leap to obtain their parchment? We well know that at many institutions the language exam evaluates vocabulary proficiency and preparation for the examination does not often develop any true proficiency in the language, including a knowledge or "feeling" for the culture or ways of thinking of the people for whom that language constitutes their native tongue. It is being suggested that either we require intensive study in a foreign language or allow substitution of other proficiencies. Computer courses have been recommended strongly as one alternative.

But back to the central theme! While, of necessity, we must immerse a student in the details of a particular specialization, we must be careful not to do him the disservice of overchannelling him whereby he has neither time nor opportunity to explore other fields which philosophically or practically might relate directly to his own area of study. Let us use care in not over-emphasizing how entomology relates to other fields, but rather to commence emphasis centering on how such areas as biochemistry, cellular biology, development biology, evolutionary biology, etc. relate to our own field. We must develop our curriculum with a focus on process rather than organism, even though we realize this does impose consider-

able stress on traditional departmental structure. Fortunately, many of our research programs today (at least those receiving substantial portion of total funding) are both mission-oriented and tuned to interdisciplinary team approaches. Consequently and traditionally, as goes research, so often goes the graduate academic program, unless we've withdrawn so far as to consider the Ph.D. degree to be largely a matter of formal course hurdles, language requirements and preliminary examinations. And, I'm afraid there has been a tendency to move in this direction at the expense of maximizing opportunity for both directed and independent research effort.

I realize I'm speaking philosophically and in generalities but today can one be expected to do much more outside of one's institution, what with each institution exhibiting uniqueness relative to philosophy, faculty interests and abilities, fiscal and physical resources, etc.

In spite of all the "soul searching" we are engaged in today, I believe we're very fortunate to be in the field of entomology, a discipline which provides for considerable latitude and opportunity for delving into numerous phases such as physiology, morphology, behavior and the like. I'm frequently impressed with entomologists in general because many have interest in numerous subdisciplines. I honestly feel that the heterosis one finds in our field is what makes it "tick." I'm always concerned that the alternative to general interest and broad involvement is narrow specialization which frequently breeds professional extinction.

And so, again, we are faced at the graduate level with the need for what might first appear to be two antagonistic responsibilities – training the individual in an area of specialization, but also providing him with a continual expansion of his total education. To accomplish the latter does not necessitate saddling the student with a vast array of courses at the graduate level, but only requires that there be a significant cross-fertilization between all members of the department be they staff or student and with additional input from without. What we are endeavoring to do this week is a prime example of a very viable way of approaching this objective. Symposia, seminars, discussion groups, coffee sessions, reports on meetings, presentations of research results and the like, are means by which this can be accomplished. We should also look into the matter of involving those from without the institution in special lectures, programs, etc. This has apparently been successfully used in Law and Medicine. So I would charge all university entomologists to greater involvement in these kinds of activities even at the expense of a few "precious" hours lost from their own research laboratory. To ask a student to "dig it out for yourself" is commonly a good educational procedure, particularly if it generates some frustration followed by satisfaction in having learned by self-instruction (and how better can one really learn?). From such activity comes increased motivation. But to fail to provide the individual with subsequent opportunity to expound and bounce his philosophies and ideas off his teachers, constitutes a breakdown in the educational process.

Turning now to the matter of how entomology can serve education, I'm perhaps being somewhat naive when I state that the picture seems more clear-cut. The insect is an almost ideal critter for illustrating a vast array of biological principles being introduced at all grade levels within our educational system. Personally, I've had considerable success in teaching a rather practical course along these lines to erstwhile grade school and high school biology teachers. Many insect species provide most convenient laboratory animals, and field projects involving these same insects can be easily carried out even under minimal supervision.

The field of entomology provides both the information and the biological tools for studies in many related disciplines, be they biochemistry, genetics, gerentology, or cancer research. May I take the liberty of suggesting perhaps that some of the other participants on this symposium can provide a far more comprehensive outline of this area of our dis-

cussion.

Finally, what can I offer the Department of Entomology here in both reflection and prediction? Very little I'm afraid, particularly in the area of the future over and above what I've already covered. As to the past how can I, one of your alums, be so modest, indeed be so callous as to level any large degree of criticism for past things done or undone. In truth I have only two points of reference – the first being my experiences here some 20 years ago, which I felt were well tuned to my needs, being on the one hand designed to provide me with sufficient breadth as to be aware of, if indeed not capable of, becoming educated. And on the other hand providing me with a fundamental array of courses in botany, zoology, basic and applied entomology, chemistry and the like so that I would experience at least some degree of confidence in my ability to handle a position in entomology or to be prepared (and it so happened I was) for continuing my education at the graduate level.

My second point of reference is not a firm one but revolves around my occasional contact with currently-enrolled or recently graduated students of this department. I have been impressed with both their competency and with their enthusiasm and I could say no more that would constitute a greater endorsement.

DISCUSSION – MORNING SESSION

Leader – D. H. Pengelly
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Upon learning that I had been designated a discussion leader, I tried to find some kind of pattern within previous symposia experienced that would shed some light on my responsibilities in this one. There isn't one. Nevertheless, I do thank the committee for the opportunity of being part of this program held to pay respect to Dr. Strickland and to the department that he started.

The speakers have presented a wide variety of ideas on Entomology and Education. Mr. Jantzie has placed a challenge squarely in front of us as entomologists. We must be represented on the committees that formulate curricula for senior public and high schools and convince those responsible that the insect is far too important to be ignored at any level in an educational program. Our representatives will have the assurance that most, if not all, of the entomologists in this country are solidly behind them. Some competent soul will have to write a book that uses insects to illustrate basic biological principles. We should be encouraged on hearing that Dr. Gittins has such a book in preparation and we are looking forward to seeing it.

It is encouraging too, to see that Mr. Jantzie and his staff have stepped over the time-honoured traces by introducing detailed studies of insects and equating these with local and world problems in food production, health, and other aspects of an environmental nature. If the rest of us sit back and do nothing, there will be little or no progress and there will be a relapse back to the traditional.

The problems of using insects have been covered. In many ways this is a difficult group but the challenge of the difficulties associated with these aliens of Planet Earth should attract those with the keenest minds. Making students aware of insects as early in their life as possible will do much toward getting entomology into its proper place in schools, colleges, universities, and back to the layman. It must not be left in the hands of a chosen few. It is a changing world and we must do our part in bringing about change if it will be to the advantage of the fair-haired youth who someday must pass this way.

Our second speaker exposed a different set of problems associated with declining student numbers. Our concern here should perhaps be directed toward the administrators who in their "crystal balling" have assumed that there are populations having a predictable, continual, and prolonged growth increase. Under the present system of sponsorship that demands speculation, admonishes the seers, and punishes the academic community by limiting funds that they were forced to anticipate, I can see little else other than problems. Dr. Freitag said that the present problems in under-enrolment were overcome by "budgetary adjustments." Perhaps he would enlarge on this and tell us what adjustments were made. I suspect that the academic who survives on a diet of Full-time Teaching Equivalents will be the first to go hungry.

The decline may well continue and in all likelihood be attributable to the lack of employment opportunities for graduates. It does seem a bit much to expect that there will be jobs for everyone who graduates from the vast array of specialties available. Here we see the conflicting points-of-view as to the function or role of a university. To some, one goes to university for the pure joy of learning. To most, it is because specialized training will provide greater returns in a chosen field of endeavour. The latter is the basic philosophy of parents and children as to why an education is necessary. The former reason is a dodging

of responsibilities when it is offered as an explanation to job-seeking, fourth-year students. If this is the basic function of a university then it must be made clear as early as grade one that education and employment are in no way related. The initiative for going to university, whether we wish it to be or not, is associated with the monetary system of a materialistic society. If community colleges with job-oriented programs are attracting or just starting to attract students, the university must do some soul searching. Student-supporting agencies will soon decide where to invest their monies.

Dr. Freitag has made a number of recommendations. Within the next 15 years the majority of the entomologists presently employed in Canada will have retired. What are we doing to ensure that there will be Canadian students in the "mill"? It is going to take 9 or 10 years to produce the kind of product that is being sought occasionally today. An annual survey does not seem to be a very useful undertaking.

Our speaker has illustrated a rather strange phenomenon. He refers to entomology and biology. Why do entomologists accept so passively, their categorization by "zoologists" as being neither biologists nor zoologists? Correcting this would serve a very useful purpose. For what it is worth from one who has been "there and back," so to speak, I am convinced that for entomology to maintain and increase its position in the academic community, which it surely must do, the name "Entomology" must be retained. To be swallowed by the "Zoological Octopus" that does not accept entomologists as being either biologists or zoologists, is sheer folly. How many universities offering degrees in biology or zoology have any extensive courses in entomology as requirements?

To establish programs embracing biology and law, or economics, chemistry, physics, etc., is an admirable idea but somewhat ethereal. Entomology is ignored by such closely associated programs as animal science, crop science, soil science, and landscape architecture, to mention a few.

I envy those whose vantage point is within a smaller university. Research projects in the final year are indeed desirable. In crowded institutions, especially in the three-term system, this is all but impossible. As far as having M.Sc. and Ph.D. programs involving the arts, physical sciences, and biology I am again pessimistic. Students in these areas in universities have the choice right now to elect courses in biology but they choose to do otherwise.

Dr. Gittins has provided much food for thought. One thought was that there be a channelling of Ph.D.'s into more productive or needed areas. Why has this obvious fact been ignored by both government and university? Why have they been immune to planned programming, especially in this age of computers? Education for education's sake may have a place but this should not have priority over education for the sake of service to mankind and to this fragile planet as a whole. During the war years men and women needed for particular jobs, even the "tail-end-Charlies," were obtained; not by the free choice of individuals but by directed training programs.

The need to educate the government and the public has been stressed. The education of the student was referred to by Dr. Gittins as being associated with modernizing and redirecting the total curriculum. I have often wondered what it would be like if we reverted to the courses required and recommended by Dr. Strickland 25 years ago. Frankly, I think the end product would fare very well indeed. Often we are preoccupied with changing and revising (mostly downward) because of the system of government support and the need for self-preservation in an F.T.E.- (Full-time Teaching Equivalents) dominated system.

The need to provide an awareness in the areas of human affairs and moral responsibility is a pressing one. I do not agree that this should be left to the university. If so, there will be no visible improvement. It must occur long before this, preferably in the home.

Perhaps biologists should shoulder some of the responsibilities for the adverse effects of technological progress but there are others who need a jolting with the proverbial "frozen boot." For the lawyers who make laws, chemists and engineers who design processes, equipment and buildings, architects who plan streets, gardens, parks and even universities, the establishment of at least one ecological ethic would be a godsend.

As to leaving specialization to the graduate school, I am in complete disagreement. Had this been the policy in the past, most of us would not be here today. My interest in entomology was aroused and maintained by Dr. Strickland. Had I not been able to specialize in this area, undoubtedly I would have ended up elsewhere. Learning to be an entomologist in the graduate school is next to impossible. By then, it is much too late. Students with the so-called broad and varied background are seldom a match for those who have been reading, observing and experimenting with insects, or any other animals, since childhood. A student who is neither fish nor fowl and tries to become one or the other in graduate school finds himself a student of the lecture room and the text book and not of the library and laboratory.

Dr. Gittins has cautioned us about relating entomology to other fields such as biochemistry, cellular, developmental and evolutionary biology. To me these are as much a part of entomology as they are of any other branch of zoology. There has been, and still is, a tendency to call all entomologists "specialists" and to accept without question the idea that only zoologists have the so-called broad background. I am of the opinion that if a student entered university and studied insects only, as representatives of the animal kingdom, and studied these with respect to morphology, anatomy, histology, embryology, genetics, physiology, behaviour, taxonomy, zoogeography and evolution, he would be at least as good a biologist as those who now graduate in Honours Programs in zoology without so much as looking at a single member of the Class Insecta.

Looking back over the last 20-odd years I do not remember there being an abundance of jobs. There wasn't when I graduated. I think that if we assess the past we will see that our training stood us in good stead by providing us not only with a solid base in entomology but also with an attitude that we could tackle almost anything. If we can come close to instilling the enthusiasm and confidence in our students that Dr. Strickland did in us, we will have made a significant contribution. We must convince the public and government that entomology is academically respectable and in some way establish the study of insects in public and high schools. We must provide the tools and competent, qualified teachers. The rest should follow.

Ladies and Gentlemen, your comments and questions, please.

Gittins – Moscow – When I spoke of leaving specialization to the graduate level, I did not mean to infer that we are leaving out specialization in entomology *per se*. I am in no way convinced that entomology isn't a vital part of an undergraduate curriculum, but specialization in general entomology rather than in systematics, morphology or something like that. One point Dave made is very important and hits us right now. We must resist this full-time equivalent business with all the vehemence that we can muster. I presented the budget for our department to our central administration a week or so ago and suggested that we cease worrying about student credit hours generated, at least within shop. I can think of no more detrimental activity for the university. What would result of course, if this concept were carried to extremes, is a single lecture course with 400 students. Such a course would generate credit hours but at the expense of innovation, of special programs, of seminars, of these kinds of things that don't generate that kind of hour. This is one thing we do have to fight and fight hard.

Freitag – Thunder Bay – There is just one point about budgetary adjustments at Lakehead

University that I'd like to mention. I believe there were about 30 people on staff last year whose term appointments will not be renewed this summer because of the drop in student enrolment in 1971. There were a number of staff released in the summer as well. I have two questions from Dr. Hocking regarding my talk. First, "How were 1972 enrolment predictions arrived at?" These were based on grade 13 and non-grade 13 applications to first year in all Ontario universities. They, in turn, passed this information on to the Ontario Universities Council of Admissions.

The other question was, "What is wrong with a liquor store as an environment for a biologist?" Answer – They were holding jobs for which entomologists were better qualified.
Downer – Waterloo – Several years ago the Entomological Society of Canada recognized many of the problems which we have been discussing this morning and, to find means of alleviating some of them, established a Committee on Student Encouragement. I thought it might be appropriate to mention some of the activities which are presently being pursued by this committee. Like Dr. Gittins, this committee has recognized the need for suitable resource material for teachers. We felt that teachers must be convinced that working with insects is quite feasible in the classroom. To this end the committee is preparing an experimental manual containing information on methods of rearing and maintaining insect cultures in the classroom and some simple experiments that can be used by teachers and students. A note to this effect was placed in the bulletin of the Society a few months ago in which we invited interested people to submit experiments which could be included in this manual. We are still looking for contributions and they will be gratefully received. We are also preparing a list of audio-visual aids, films and other material which might be of use in the classroom. If anyone knows of any films which might be suitable for this purpose, we would be very pleased to hear comments from them. Thirdly, we have established liaison with several provincial science teacher's associations in Ontario with the hope that, by providing articles of interest to these teachers, it will be possible to instill greater interest in things entomological among them. The final approach has been to attempt infiltration of the various provincial committees which formulate school curricula. We have met with mixed success in this regard. I think Doug Craig established some contact with the Alberta authorities and we have been successful in Ontario in getting membership on one of these committees. In Ontario we have been helped by the fact that provincial Bill 145 has limited to a considerable extent the use of non-human vertebrates in the classroom. Teachers are therefore looking desperately for alternative animals to use in traditional experiments.
Pepper – Bozeman – The problems arising out of our current methods of insect control should have been foreseen by many of us at least 15 years ago. The indiscriminate use of insecticides and the resulting environmental problems is only one of these. Our biggest problem has been our failure to recognize that we are dealing with evolutionary units, that we are artificially selecting for undesirable characteristics in pest populations. Do we teach this in our courses? Hopefully we do now.

I used to teach a very specialized course in insect physiology. One of my students asked, "What relevance has this course to the problems I will be confronted with on graduation?" At that time my answer was, "None, but I will give you a grade in it anyway." Entomological education today seems to be comprised of a bunch of fragments: histology, morphology, taxonomy, toxicology, etc. Students graduate with these fragments. Their education started no place, led no place, and ended no place. Yet we send these same students out to be confronted on the job with completely new situations. What are they going to do? What background do they have to do it? Who is going to give them this background? Entomology, as we all know, started out as a hobby with scattered practitioners all over the world. They collected, studied life histories, and in some instances made great contributions. Even-

tually there came a time when these people were replaced by those whose approach was more scientific. We started using tools, every tool we could lay our hands on. All you had to have was something to measure, and by God, you measured it. You measured it so that you could write a paper on it and if you wrote enough papers you got an increase in salary. This was, and unfortunately still is, true. Eventually, we became a group of gadgeteers. This sort of thing continued. Then, along came mathematics. To use mathematics in entomology, we must quantify. We now have at our disposal computers that can do anything – can even put a man on the moon. But, can you quantify a qualitative property of an entity? Can you put a qualitative characteristic into a computer and have it analyzed? That well known phrase, "garbage in, garbage out" answers that question.

All entomology students must take math, physics, chemistry, and so on during their undergraduate years. But what kind of math? They get the math being taught to those who want to go into industry. Statistics? Statistics is said to be based on logic. The best definition I've heard for logic is "an organized procedure for going wrong with competence and certainty." Chemistry? Since I received my undergraduate degree in chemistry, I feel that I can criticize chemical education legitimately. The chemistry taught in university is industrial chemistry. The biochemistry taught in universities is the application of organic chemistry to some industrial product. Physics? We learn about solids. Living systems are liquid ones. Biologists of all kinds should demand from these departments that they teach a type of math, chemistry and physics suited to biological thinking.

Once I visited each of my staff and asked, "How do you use your knowledge of math?" "Well, I don't use it myself but everyone else seems to." I eventually discovered that no one in my department used math. I found the same to be true of chemistry and physics. Then why in the world do we require that our students take these subjects? If a student asks this question we usually answer, "It's in the calendar as a requirement." What I've been trying to say is that the whole educational bag must be re-evaluated as a whole, not fragment by fragment.

Jantzie – Vulcan – I hope I didn't leave you thinking that the current high school biology courses here in Alberta are poor ones. I agree with Dr. Gittins that when students go to university, their high school biology is usually adequate for their first year. In fact, first year biology in Alberta is almost a complete repeat of high school biology. I have sometimes found the high school course, if anything, to be overly sophisticated for the majority of students. They seemed to enjoy it but I sometimes felt that they went into some things a little too deeply for that age level. I think they would have appreciated a look at some of the more simple things in life. We could have spent more time on insects, on plant pathology, etc. and less on DNA. You can talk about fungus all you want, but unless you then go and say, "Okay, let's look at some of the plant diseases of cereal crops," these students aren't going to relate it to anything they already know.

As I think back to the broom closets that comprised the entomology department of the 40's, I see now that entomology occupied a lesser position in the eyes of the administration than did the departments of zoology, botany, etc. I hope that things are different now, but I'm not so sure that they are. This may be because administrators have not appreciated the ubiquitous role that insects have in the living world.

Mr. McGregor has asked about the agriculture program that we have in Alberta high schools. There is no specific program in agriculture. If a person wants to teach it, he must get special permission from the Department of Education. He must have the qualifications to teach it and he must make up his own syllabus. This is nice because he can structure it to his own particular specifications. That is why I am so happy with our program.

Following graduation from the University of Alberta, I worked in the seismograph field

for several years where I didn't use much of my background in entomology. But I had a wonderful time until I took up farming at Vulcan. I farmed there for almost 10 years until I decided to try to do something for our school system which had, at that time, been plagued by a rapid turnover in teachers. That's how I got involved in education, and I must say I have enjoyed every second of it since.

Hocking – Edmonton – I have one or two comments that I would like to add on this question of predictions. I was glad to learn from Rick Freitag that predictions in Ontario are made from high school enrolments. I have been doing this, on behalf of biology and science at this university, for a number of years and the predictions I come up with usually seem to be closer to what actually transpires than the predictions of our office of institutional research and planning. Much of the devastating effect of declining enrolments is not so much the fact that they are declining but that they are declining in the face of growing predictions. To illustrate this point and possibly add a note of optimism, I have three slides here illustrating percentages of enrolments in grades 11, 12 and first year university, taking the three sciences: chemistry, physics and biology since 1963-64. *Grade 11:* Green is biology, red is chemistry, blue is physics, white is science. You will note that until 1968 biology was not a science. *Grade 12:* My only comment here is that the dotted green line is the old biology 32 going down as the new biology 30 comes up – to a higher position in relation to the other sciences than 32. The next one is first year university which I think is perhaps the most encouraging of the three.

I would like to answer two rhetorical questions which the speakers asked. Mr. Jantzie asked how many students in education, agriculture and science get their major in entomology. I haven't precise figures but I would guess that over the last 10 years, there were very few altogether. Science would have the largest number, agriculture next, and education very few. Dr. Gittins asked about the role of the Master's degree. I would like to give you my interpretation of the role of the Master's degree. I consider it a stepping stone between a doubtfully adequate undergraduate program and a Ph.D., or if you like, a trial run for a Ph.D. – specifically for students with a dubious background in language, writing, research and research procedures.

Gurba – Edmonton – One of the problems facing entomology seems to be the same as that confronting other disciplines in university. Too many of the teaching programs there are still research-oriented. This was alright in the days when graduates were filling positions in government research and university teaching, but these positions have now been filled and there is now a surplus of students with this type of background being graduated. Why haven't these curricula been changed? There are interesting opportunities in fields other than research and teaching. There are openings in extension, in agriculture, in forestry, in industry and in parks and recreation. Many of these jobs involve helping other people and are therefore very satisfying.

Dr. Gittins mentioned the need for work and training in pest management. This is something we, in the Department of Agriculture, have been discussing for a long time. What is our entomology department doing about training people in this area? Those of us who came through the University of Alberta in the late 40's and in the early 50's got this sort of thing from Dr. Strickland in his courses in general and economic entomology. This sort of approach is not available today and I am wondering why.

Pengelly – The answer could lie in consideration of administration. My point is this: if they turned out one apiculturist a year and he found a job open somewhere in Canada, they would have served Canada well. Unfortunately, this does not suit present-day systems. You cannot institute a new course without assuring administration that you will have relatively large enrolments in it. Three students might want to take a course in pest manage-

ment. Well, you'll have to be sure of more students than that or you can't offer it. It brings us back to our old problem of full-time teaching equivalents.

Hocking – I entirely agree with what David has just said. I would like to indicate what we are doing about this question here. There *is* one way of getting a course accepted and allowing it to persist in spite of apparently inadequate enrolments. We have a project course in applied entomology. The only way we have been able to keep this course in existence is by having it a catch-all. Anybody wanting pest management can enrol in this course and get it. Unfortunately, the university is now looking very hard at any course with an enrolment of 10 or less. They are trying to weed these courses out to cut costs. If we don't have a demand, there is nothing we can do about it.

Kavanaugh – Edmonton – My question concerns the possibility of channelling students into specific areas of interest. I would like to ask those here with considerable experience in teaching at what point in the education of the individual we can begin this channelling. More importantly, how late in the process can we accomplish this sort of thing? I ask this question as a student realizing that motivation is of prime importance and I wonder where in my own education I would have been susceptible to rechannelling. I might add that I am interested in taxonomy which should put things in perspective for you. Certainly, it had to be pretty early in my case. I would say, in very early grade school. In my experience however, students in entomology are generally pretty turned-on people. I think in biology that to rechannel these people would mean to redirect or change the object of their enthusiasm and I don't think this is going to be too easy, especially later on. You have to remember that we are dealing with people that have motives and are motivated. They are not objects sitting on a conveyor belt that we can manipulate.

Pengelly – I wasn't suggesting manipulation, Dave. What I *was* suggesting in agreeing with Dr. Gittins on channelling is this: most kinds of financial support require that some knowledgeable professor who really knows the art of grantsmanship apply for support from our friendly uncle in Ottawa. The group of people making decisions on research grants will simply say that because there are no job opportunities in taxonomy in the foreseeable 10 years, we are not going to sponsor 55 taxonomists in Canadian universities. This is the kind of channelling that I was envisioning. Funds would be directed into areas of need. Enthusiastic students who followed the dollar sign a little bit might find problems that fitted into these areas. I wasn't saying that you are not going to be what you want to be.

Kavanaugh – If we can accept the fact that we do have some capacity to direct where the funds go and that we are not completely at the mercy of public opinion, I would be reasonably satisfied. I just wanted to know at what point we can really influence a student – interest him in a given field.

Pengelly – In Ontario there is a committee in existence that is going around and visiting various departments in various universities. Members of this committee are asking that each professor justify what he is teaching in relation to those courses offered elsewhere in his university. If he can't, if his entomology course is too specialized for a general biology program, he could be asked to move to another university with strength in entomology. I suspect that we will see, within Ontario at least, different campuses specializing in different disciplines such as engineering or food science or entomology. There will be only one or two "centres of excellence" for entomology. You, as a student, will have to be very careful when choosing an institution to further your education because all will be specialized.

Gittins – Let's not be too gloomy about the future of entomology. I think it looks pretty good. Also, let's eliminate the use of those two terms "basic" and "applied" – they are meaningless today. In Idaho we are now looking at insect control in terms of population suppression. No longer are we going to rely solely on insecticides. We are investigating

instead the fundamental biology of pest insects and seeing how we can manipulate various aspects of these. The 20 years we have just completed were atypical, not typical. As pest management programs develop we are going to require improved insect keys and a fuller understanding of basic biology. Whether we are interested in physiology or taxonomy or toxicology we are all still interested in insects; interested in all of their aspects. Surely we can redirect our activities without instituting a bunch of new courses. Our primary interest may still be systematics but we can practise it with a different emphasis. We are not just taxonomists or physiologists, we are entomologists, all of us, and we should be proud of it.

Morrison – Waterloo – Is the government of Alberta funding the university here in terms of the number of students enrolled? Is the funding reaching down to the department or faculty level as it has in Ontario? This creates very serious problems in the teaching programs that a department tries to implement. It is devastating in many many ways. When Guelph talks of their problems they talk of them in this light, and when *we* talk of our problems we talk of them in this light. Could you please enlighten us?

Hocking – A large part of the funding at the University of Alberta is geared through weekly student hours but, hitherto, this has been on the basis of predicted weekly student hours. Initially, a correction factor applied if enrolment did not meet predictions and this is perhaps one reason why predictions are high. It is, I agree, a terrible system but what is the alternative? I wish there were some way of getting away from this. We resisted it to our cost as a department just about as far as we could go. I think there is an increasing tendency to resist this and hopefully somebody will, sooner or later, really come to grips with it and get something done about it.

Pengelly – You are really fighting Mother when you go after these people because they are the ones with the purse strings and, as Dr. Hocking suggests, this might be to your cost if you challenge them too hard.

W. E. Heming – Guelph – For many years I have had the feeling that a gifted popularizer of science is making as great a contribution as many of the research scientists, and I feel maybe we have reached the point where a gifted popularizer of entomology could reach the public, could reach the granting agencies and make a very real contribution. I wonder what some of the rest of you feel?

Schwab – Edmonton – My name is Betty Schwab and I am a psychiatrist. I like Dr. Heming's comments. Those I am going to make are probably a little philosophical. I am speaking as a person who now realizes that the two years that I spent in entomology were, to a degree, wasted because I did not realize how valuable they were going to be to me as a mother. I think as teachers, that we are waiting much too long to interest children in the fascinating field of entomology. I heard Mr. Jantzie say that he was dealing with a turned off group by the time that they reached high school. This struck me as being very sad because I think that if those children had been motivated to look at insects as kindergarten students, in grade school and high school they would have been a different population of young people. I would suggest that even at the university level, it would be to the advantage of the general public, to the children and to entomology to develop simple programs for kindergarten students.

Pengelly – That's certainly endorsement of Mr. Jantzie's idea that we start teaching entomology a little earlier.

Craig – Edmonton – I would like to speak as a father. We have a daughter four years old and a son two. Our daughter has a number of friends around the place who come and play. Last year we made a breakthrough when our daughter lost her fear of mosquitos. We have had great difficulty, however, in stopping her friends from squashing every bug that they see. Thus, this business of education must be started very early. Our 2-year old son is just

the opposite – he loves everything. He will often lie on the foot path and say "Hi!" to every ant that comes along. In the next few years he is going to see his friends stomping on insects. Perhaps we should be looking at this age group. I am directing these comments to Dr. Downer and also to myself and perhaps to the Student Encouragement Committee of the Entomological Society of Canada. Perhaps we should be attempting kindergarten encouragement rather than student encouragement.

Corbet – Waterloo – I think the last few comments have raised in my mind very clearly, two questions. One relates to communication and one relates to the reason why we recognize entomology as a separate science. I think there is a reason why we recognize entomology as a separate science and it is largely one of convenience. It is particularly related to training in the direction in which we may expect to get professional employment afterwards. I think there is another reason why we should recognize entomology as part of and not separate from biology and, speaking now to the question of communication, why we should teach entomology. I think one of the most compelling reasons we teach entomology is to illustrate biological principles. In this connection it matters not one whit as to whether the person who learns entomology later on becomes a professional entomologist. It is very important however that he become a knowledgeable biologist. The people here who don't already know it, might be interested to hear of one of the small number of resolutions that the founding meeting of the Canadian Committee of University Biology Chairmen made when it met in November (1971) in Montebello. This resolution was that members of the biological disciplines or subdisciplines, and of course that includes entomology, should refer to themselves first as biologists and only second, if necessary and appropriate, as adherents of a subdiscipline.

Pengelly – Thanks, Dr. Corbet. Maybe my comments were not exactly parallel to yours but I still feel the name entomology has to hang around someplace. I sat and watched it going down the drain once.

TAXONOMIC ENTOMOLOGY; GOING, GOING, – WHERE?

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From looking at the program I suspect that my views are supposed to represent the government employment ivory tower segment of entomology. Accordingly, I take it that I can discuss any reasonable aspect of entomology and education. Because of my background, the viewpoint that will come through loud and clear will be that of the basic research worker in a government department. Thus, I will start with a description of the condition of systematic entomology at the present time.

Much of what I have to say about systematic entomology has been stated in a report recently published by the National Science Foundation in the United States (Steere *et al.*, 1971). This report emphasizes that the great systematic biology collections are an irreplaceable and priceless national resource, functioning as the key to all filing and retrieval systems for information on the diversity of living creatures of the world. "These great collections are now in a situation that can only be called desperate. They are suffering from: (1) a great influx of new specimens resulting largely from government financed research projects; (2) stepped-up use of collections in response to specific practical questions as well as intensified research; (3) sky-rocketing inflation on top of a static income base leading to a merciless financial crunch. The result has been substandard salaries, deteriorating personnel strength, reduced activities and deferred expansion. Deficits have been reflected more in deterioration than in actual dollar figures but soon actual deficits will be inevitable." The publication closes with an urgent plea for financial assistance from the federal government but the sum is surprisingly modest considering the means of our neighbours to the south: they want only 198 million dollars over the next 10 years.

The above publication covers conditions in the great systematic collections (exclusive of the U. S. National Museum) in the United States but, nevertheless, much of its content applies equally to the great collections in Canada. Let me tell you what has happened to the Entomology Research Institute, undoubtedly the largest and best financed in the country. Since 1968 our budget has been cut to less than half the number of dollars that were available in 1968. Our staff of professionals has suffered six resignations or retirements and only three have been replaced. During the same four years we have had to increase our identification service from 43,000 to 77,000 identifications per year. And we have had no additional space, although the collections continue to grow at an alarming rate. Fortunately, our Institute experienced rapid growth of staff and facilities during the 1950's and early 1960's and thus things are not as bleak as my figures might indicate.

The more entomological museums one visits the stronger becomes the pervading impression of overcrowding, under-staffing and financial stringency. This, sad to say, is the atmosphere into which the aspiring taxonomist will be heading and it is not likely to change until taxonomists themselves are better able to compete for the budget dollar.

If present trends continue unaltered one can only foresee a continuing deterioration, not only of the great collections themselves, but also of the associated services such as identification and bibliographic advice. The time may well come when identifications will become very slow and difficult to make in some groups and completely impossible in others. Then perhaps, biologists in general, and especially ecologists, will finally awaken to the plight of museums and bring pressure to bear upon governments and granting institutions to make available enough funds to put life back into the museum segment of biological sciences.

Even at that it will take many years to train a new generation of taxonomists to revive ancient and moribund institutions and to modernize their methodology. For some institutions a revival could come too late because museum pests and other natural agencies may have already destroyed large, neglected parts of the collections.

Now this is the kind of thing that might happen and I hope it represents a pessimistic pole for the probabilities available to us. What is more likely, I expect, is that the cries for help, such as the one from the U. S. National Science Foundation that I referred to earlier, will be heeded in time and the museums will be kept going even though on a more stringent scale than they would like. There are plenty of intelligent people in high places who can see the need and urgency and we can only hope that their priorities will include museums. At any rate none of us dare sit back complacently and wait for "George" to do it. It is up to everyone who has an interest in the maintenance of museums in good financial and physical health to do whatever he can in the way of agitation for their better maintenance.

Another great trouble bothering taxonomy is the conservative nature of taxonomists themselves. We tend far too much to cling to old, time-consuming methods of working, necessitated by rules that were originally drawn up in the days when taxonomy was the exclusive field of amateur dilettantes of independent wealth. Consider the amount of time and effort that goes into searching through ancient literature trying to dig out the oldest name and the first combination etc. etc. This is not zoology; it is bibliographic research done by the most old fashioned and time-consuming methods. Furthermore, it is only of historical interest and has very little place in science. Think where the science of chemistry would be today if they had a code of nomenclature that rigorously demanded that the earliest name for every chemical compound be exhumed from the literature and used regardless of all logic. Think also where they would be if all papers had equal value no matter how good or poor the work was. In other branches of science a poor piece of work is quickly read and thrown aside to be forgotten if it is of no value, whereas in taxonomy we are stuck with it forever no matter how ambiguous or unrecognizable or even crazy the work happens to be. And what a horrible condition our cataloguing is in when the chief cataloguing journal for taxonomists, Zoological Record, is six years behind the literature and steadily losing place. If all taxonomic novelties such as new names and new combinations had to be validated by filing with an international bureau (why not the Zoological Record?) there would be little trouble in keeping the catalogues up to date. Some of the money now going into grants for biological research should certainly be put into cataloguing and bibliographic services, fully computerized and internationally available for all zoologists or botanists to draw upon. This kind of thing ought to be a function of a large world organization such as the United Nations. The ancient literature should be fully catalogued once and for all and the data filed in computer banks. Then the old rare and expensive books need never again be consulted except for historical interest. Anything missed in that cataloguing process (after a waiting period during which biologists at large could note deficiencies) should simply be written off because only a rare and valueless publication would be omitted.

A number of computerized systems for use by taxonomists and other biologists are at present being developed in Washington and other centers. Working out suitable techniques for the manipulation of a large body of systematic data is not an easy task, but in the last few years computer technology has evolved to the point where direct application to the management of large amounts of systematic data is feasible. The Smithsonian Information Retrieval system, the Flora of North America Program and the Museum Computer Network system are at present under development. Lack of funds and staff very seriously limit the participation of many museums in these programs but the outlook for computerization of museum technology is bright.

Computerization of taxonomic data has recently achieved a rather bad reputation among taxonomists because of early misapplications toward the study of phylogeny and other relationships. However, in proper applications the computer could revolutionize the abilities of curators to retrieve data. As antipathy toward modernization and fear of the machine give way to the realization of the computers' enormous ability to manipulate data, the advances necessary for the maximum utilization of these great collections will soon follow. Computers can also be very important in making identifications of specimens in reasonably well known groups. Not only can a computer construct a key but it can also run a specimen through the key, needing only an operator to select key characters from observation of the specimen. The computer can even tell the observer what characters to read. This will release highly trained research workers from the routine part of identification activities and enable the latter to be carried on by technicians.

Will the research taxonomist be needed at all in this idyllic future? Yes, indeed he will, because the computer cannot replace the research brain and it cannot extract new data from unworked specimens. Fortunately for insect taxonomists the Insecta are not only the most numerous of all living creatures but also the least known. Many groups of Insecta are five or 10 percent known on a world basis. Some are that poorly known even within such reasonably well studied areas as North America.

Dr. H. K. Townes has recently compiled figures (Townes, 1969) for the world fauna of Ichneumonidae (Table 1). Note his estimate that only 35% of the North American species are presently known. Note also his estimate that between 85 and 90% of all tropical species are unknown and that in the world as a whole there are approximately four undescribed species for every described one. I might also add out of personal knowledge that at least half the described species are known from only one or a very few specimens with no associated ecological data. To put it in other words our acquaintance with at least 90% of the species of Ichneumonidae is limited to a few museum specimens only. Since a modern taxonomist can revise at best only a few hundred species a year even at the alpha level, and since the Ichneumonidae are typical of large parts of the lesser known sections of the Insecta, it is easy to see that there is absolutely no danger of the entomological taxonomist running out of work for generations to come. The real danger is that large parts of the Insecta will be extinct before they are even described.

Now I move from the needs for, and opportunities in, insect taxonomy to the demand for taxonomists – a very different subject.

This graph (Figure 1) is adapted from one published by Kelly (1971). I think it might serve very well as the symbol of the symposium, showing as it does the really outstanding problem facing entomology departments and graduate students today. The contrast in the actual numbers and also the trends of the output of Ph.D.'s and the positions available for them is too obvious to need any further comment, but the plight of the unfortunate individuals who are caught in the gap calls for a lot of hard thinking and action. The reason I show this graph is to serve as background for a story illustrating how badly wrong the common wisdom may be and how desperately we really need accurate forecasts of a type not available to us in the past (nor at present, according to Kelly).

During 1967, the editor of the Canadian Entomologist, Dr. D. P. Pielou asked me if I would write an article, preferably controversial enough to start some correspondence and stimulate interest, for the first number of a popular publication he planned to start for the entomologists of Canada. The publication has since appeared and is now established as The Bulletin of the Entomological Society of Canada. It sounds strange to say it now, but at that time, in 1967, I was trying very hard to recruit Canadian taxonomists for positions in the Entomology Research Institute. Quite a number of well qualified foreign students were

Table 1. World species of Ichneumonidae

	Valid described species	Estimated % described	Estimated total species
Nearctic	2809	35	8026
W. Palaearctic	4023	70	5747
E. Palaearctic	2400	20	12000
Indo-Australian	2424	15	16160
Ethiopian	1618	15	10787
Neotropical	1718	10	17180
	14992		69900
Allowance for duplication (13.5%)	-2025		-9400
Corrected Total	12967	21	60500

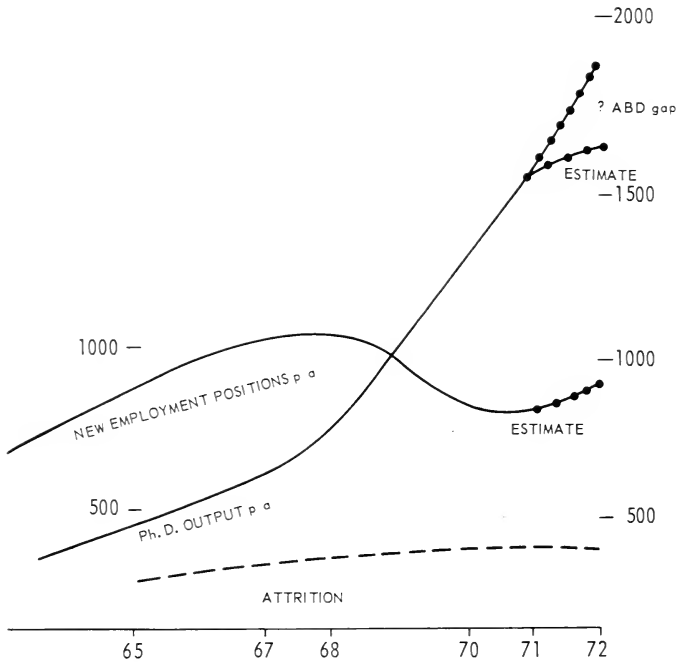

Figure 1. Supply and demand for Ph.D.'s in science and engineering in Canada. ABD – all but dissertation.

available and anxious to take the positions but the executive insisted on having Canadian citizens for the positions if at all possible. There were very few students qualified to work in taxonomy and the few who were qualified seemed disinterested. So in an attempt, which I should in honesty now admit was a little contrived, to bait a few university professors I wrote an article (Mason, 1969) complaining of the lack of Canadian students trained in taxonomy and laid the blame on the shoulders of the Canadian universities. Well, I certainly got a reaction (Kevan, 1969; Scudder, 1969). However, before I elaborate, examine the graph once more and see when the article was written. In 1967 the production of graduate students was well below the accumulation of new positions. Allow a lapse of almost 18

months while the article was in press and then see the result in late 1969 when the letters from the professors came in to the editor. By that time new positions were declining and the output of Ph.D.'s was still rising. This time no one needed experts to tell them what the trends were. Unemployment was screaming at us from every university campus in the country and the federal government was in the midst of reducing its staff by not replacing retirements, by forcing early retirements, and even by a little outright firing.

Well at least I was not alone in my ignorance back in the middle sixties. In those days we were living in an era when all graphs went upwards and upwards forever. The catastrophe of 1929 seemed far away and we were secure in our knowledge that modern economics had now made such an occurrence impossible. We heard no academic voices crying that the production of graduate students should be curtailed because the young hopefuls who were then enrolling in graduate studies would not be able to find jobs in three or four years when they launched themselves upon the market. No, the cry was for Canadian universities to enlarge their graduate departments, train our own Canadian students at home and generally more and more of everything. But the bubble burst, not just as it did in 1929 and not with the same drastic results. Nevertheless, burst it did, and we are now living with the results. Those who should be the most eligible and employable members of our society are declared useless because of inexperience and overqualification. Those with experience are declared obsolete, overaged and unemployable because of pension fund computations. It seems that no matter who you are or what your background the personnel department has a stainless-steel-clad reason for declaring you ineligible for any vacancy.

Well all this gloomy talk serves to indicate that the demand for taxonomists in the near future is likely to be far below what taxonomists themselves believe is the need.

But what is a need? Certainly everybody knows there is a difference between demand and need but what determines it? Well as I see it needs are what you believe you wish to have and demand is what you are willing to pay for. Needs may be divided into necessities and luxuries and of course the dividing line is always a nebulous zone that varies from one individual to another and from one community to another. For instance, I have travelled in primitive parts of the world where the population considers a man who suffers only from malnutrition, intestinal parasites and endemic malaria to be healthy and where they can see no need for any measures to prevent these conditions. In other words, if you are poor enough and ignorant enough, malaria control and sanitation are luxuries, not necessities.

Obviously, if the public and its representatives are to hire entomologists they must be sold on the idea that the services of entomologists are a necessity. To some extent this job has been done but it seems that, at the moment, entomologists above a certain number in the Public Service are regarded as a luxury. In fact the federal government, through its top executives, regards the Public Service of Canada as being presently overloaded with entomologists. Hence, the lack of demand for entomologists in the Public Service. It is quite clearly a disastrous policy for a department such as this one in the University of Alberta to continue to train entomological graduates in numbers larger than the market place will absorb. Only four courses of action seem open: (1) cut down the production of the department; (2) convince employing agencies, chiefly the governmental and university authorities, that more entomologists are needed; (3) direct the graduates into non-entomological employment; or (4) do nothing. The last two alternatives seem silly. The first course of action is a passive one of simply trying to foresee the demand and filling it as closely as possible. The present situation demonstrates how well universities have been succeeding recently. They are not entirely to blame, admittedly, for there is no source of information on which to make reasonable forecasts (Kelly, 1971). The second course of action involves salesmanship and is the kind of thing that has made business expand in a free enterprise system. An effective

enough advertising campaign can convert a luxury into a necessity in the minds of people with enough money to pay for it. The present popularity enjoyed by environmentalists and conservationists should be the key to a sales approach by entomologists. After all, insects are by far the most numerous forms of animal life in Canada or in any other part of the terrestrial world and are the least known.

Should the university be in the advertising business? Well, that is a decision that is up to the university, but it seems to me that there is already tacit admission that something along these lines is necessary when universities maintain placement services to assist their students in obtaining employment. Furthermore; there seems little point in using the university budget to build larger facilities and improved labs and hire more staff if no one will buy the product. Any factory that was glutting the market with an unsalable commodity would very quickly close its production lines and pump increased funds into advertising in order to move the stock. And if universities will not indulge in this messy business of advertising, what then? Well clearly young people are going to look elsewhere and the great facilities so painstakingly built up in the universities will be running at half capacity. Maybe empty classrooms and empty lab space will be a very pleasant novelty for a while but it might also mean reductions in staff (horrible thought) and reductions in budget (more horrible thoughts). Probably the apparently inevitable population growth will catch up with the empty spaces and fill them again but by that time the facilities may well be obsolete.

In spite of all these words of gloom, I can foresee a very bright future for entomologists in general and also for taxonomists if the opportunities inherent in our present situation are correctly handled. Entomology can even be made a popular study with the public. As proof of that one need only examine the number of entomological clubs existing in Japan. I am told that butterfly and dragonfly collecting in Japan are about as popular as snowmobiling is in Canada.

I think the fundamental problem is that the public must be made aware of insects in a pleasant and positive way and thus be made interested in the encouragement of entomologists. At the moment our average fellow Canadian thinks of an insect as almost synonymous with a house fly or a mosquito, in other words an unmitigated nuisance – the only good one being a dead one. With that kind of attitude the good entomologist is the one who can kill insects with the greatest efficiency. But you and I know that the vast majority of insects go about minding their own business in ways that are really beneficial to humanity even though humanity does not appreciate it. I think it behooves all entomologists to think very hard and very seriously about improving our public image as a group and thereby improving our lot and our share of the national budget.

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EDUCATION AND THE PROFESSIONAL ENTOMOLOGIST

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Although entomologists occupy various positions as in teaching, extension, or industry, I wish to limit my discussion to those employed primarily to produce new knowledge that will be applied for the direct benefit of society. I will concentrate mostly on those associated with research in agriculture, because they constitute the largest group of professional entomologists in Canada.

Entomologists have found relatively few positions in most fields in recent years and there is little evidence of much immediate improvement. Better long-term prospects, however, make this an appropriate time to examine their education. As the present generation in universities and elsewhere retire, new entomologists will undoubtedly be hired. It is likely, however, that the largest number of replacements will be required in departments of the federal government either in Agriculture or Forestry, providing that drastic changes are not made as a result of advice from the new Ministry of State for Science and Technology.

Prospects in Agriculture

The Canada Department of Agriculture employed about 140 entomologists in 1944, rising to over 350 in 1956 (2).

By 1964 this number had fallen to 173, which still amounted to over half the entomological force employed in Canada (4). Of the remainder, about 40 were employed by universities and provincial governments, and about 96 by the Department of Forestry (now in Environment Canada).

In 1972 the Canadian Forestry Service employed 87 entomologists plus 15 administrators, some of whom may not be entomologists. The Research Branch, CDA, employed 162 entomologists; five in stored products research, 11 in veterinary-medical entomology, 33 in taxonomy, and 113 mostly in crop entomology.

Most entomologists in the Research Branch were probably hired between 1945 and 1950. Because early retirement after 30 or 35 years of service is encouraged by the federal government, it is likely that by 1980 many will be retired or close to retirement. Allowing for some attrition of positions, the Branch will require 60 to 80 entomologists within the next eight to 13 years. Undoubtedly the Forestry Service will also require some in the same period, bringing the probable total to well over 100.

The demand will depend on entomologists explaining the importance of their research. The belief that the need for entomology was self-evident became obsolete with the advent of tight budgets and cost-benefit analyses of research. Data to show the need for entomological research are scarce. The decision of the Canadian Entomological Society to remain separate from organizations such as the Agricultural Institute of Canada removed us from the places of influence. Until data are obtained to show the potential hazards from insect pests or until we experience more dramatic outbreaks, such as that of the Bertha armyworm in 1971, we will continue to find it difficult to change the current impression that there are too many entomologists.

Another factor has been the success of the control measures that we developed, primarily centering around the use of insecticides. Insecticide use resulted in the expansion of regulatory agencies and increased the numbers of pesticide analysts, but reduced the apparent need for entomological research. Even though insecticides have detrimental side effects

and have not provided permanent insect control, their immediate and evident effectiveness makes it difficult for non-entomologists to understand why entomologists advocate the continued search for better controls. Some support and understanding for our position has been generated by public reaction in recent years.

Even if we had sufficient knowledge to solve all our present problems satisfactorily, the need for entomological research would continue. New insect outbreaks will inevitably follow the introduction of new crops and cultural practices. Environmental changes, the development of resistant strains of insects, the necessity for opening up new agricultural areas, and the increasing demand for food will all have this result. Unless a sufficient number of trained entomologists are available to meet these new problems, Canada could be in serious trouble in the future.

The Entomologist in Agricultural Research

Most entomologists in the Research Branch are engaged in applied research. Although some are in relatively pure research, their numbers are decreasing. At Lethbridge, the work on insect cold-hardiness ended when R. W. Salt retired. The Belleville Institute will be closed and its personnel transferred. The taxonomic work of the Entomology Institute at Ottawa has been more closely related to its service for field entomologists.

The research of the Branch has been reorganized into programs, most of which are aimed at the production of agricultural commodities. Objectives are established and goals are set for attainment within a specified period of time. The programs generally include a wide range of disciplines particularly at the larger research centres. The scientists have thus been drawn into a true interdisciplinary approach in planning and conducting research. Despite early misgivings, we find that we are obtaining a better appreciation of the problems involved, thus providing a more rational approach to research planning.

The research of the applied entomologist is best described by a few examples. In the project on cutworms at our Research Station at Lethbridge, work is proceeding to develop suitable artificial diets and environmental conditions for mass rearing of moths for pheromone studies. Concurrently, the testing of synthetic pheromones is being advanced in conjunction with analyses with the gas chromatograph and mass spectrometer and electroantennal response tests. Studies of the pea aphid on alfalfa involve the collection and identification of the species complex in alfalfa fields, determination of the roles of the species involved, and the effects of insecticides on parasites and predators. Research on the technology of the manipulation of the alfalfa leafcutter bee is accompanied by studies on behavior of bumblebees and of their enemies, the cuckoo bees. The resistance of new wheats to the wheat stem sawfly is being examined along with determination of the influence of plant hormones and quality and quantity of light on host plant resistance and larval behavior.

Although I have described our research as applied, it could as well be classified as research and development, or even as applied and background. Perhaps it defies classification because it is so varied. The entomologist in agricultural research inevitably becomes involved in activities that range from extension, preparation of popular articles, training post-doctoral fellows and undergraduates, developing *ad hoc* controls for unexpected outbreaks of new pests, participating in advisory committees on insecticides, conducting field surveys, and developing computer programs, to keeping up with the scientific literature, designing new experiments, and publishing results in scientific journals.

The primary aim of entomologists in applied research is to develop the knowledge and techniques required for the management of insect populations. To accomplish this aim the ideal entomologist should possess, in addition to an interest in research and insects, the

ability to determine the significant questions, the ingenuity and imagination to design experiments that will answer these questions, the willingness to discard hypotheses proven untenable, and the intelligence to interpret the results of the experiments.

Educating the Entomologist for Applied Research

Now that I have described some of the work and characteristics of the entomologist in applied research, all that remains is to decide how to educate him. Seriously though, his formal education should enable a reduction in the amount of experience required before he can make a significant contribution and it should provide a base of knowledge that will enable a broad selection of strategies for solving research problems.

It would be difficult for anyone to provide a list of the subjects necessary without spending a great deal more time than I have. Research in applied entomology involves a range of sciences and of scientific fields that is probably broader than that for any other single modern scientific specialty. The main branches of the seven major sciences total 88 (3). Applied entomology involves a knowledge of, or at least an association with, 32 of them.

The research entomologist should have a basic grounding in the classical fields of entomology, with a general knowledge of insect behavior and ecology probably ranking first. He must be able to identify rapidly many of the major families of insects and possess instant recognition of a large number of the more common species. He should be knowledgeable in the properties of insecticides and with the methods and equipment of their application. He must have a thorough knowledge of how to find and search the relevant scientific literature.

Knowledge of statistical design and analysis of experiments is essential and a thorough grounding in mathematics related to the study of ecology would be valuable if not essential. He should take chemistry, physics, and economics. Plant taxonomy and ecology, vertebrate and invertebrate zoology, and animal ecology would be important additions. A course in instrumentation would be excellent and computer science would be valuable. Exposure to most of the other agricultural sciences should be required for the agricultural entomologist, with a similar requirement in forestry for the forest entomologist.

Unless he has already taken French or a foreign language, the student will usually benefit little from such training in his graduate program. A foreign language should not be automatically required for an advanced degree. It would be far better to concentrate on English composition and grammar. Only the rare scientist can write with clarity and simplicity. Most spend long and painful hours attempting to write good scientific papers and presentations, and few are able to write decent popular articles. The theses that I have read convince me that professors who act as major advisors deserve hardship pay on the one hand, and on the other, demerit in their pay for allowing the production of what is all too often a dull, verbose, and pretentious composition of interminable length. But perhaps times have changed since I wrote my thesis. It would be preferable if the theses were written as a scientific paper that had to be published in a properly refereed journal. Although the schools have failed, the universities share the failure by allowing its students to graduate with only a rudiment of the skill of communication. If the proper courses for writing and editing scientific and popular articles do not exist, the department should insist that they be created.

The Future Entomologist

Entomological research of the next two or three decades will be similar to that of today because our knowledge of the behavior and ecology of many insects of economic significance is still insufficient. For example, the flea beetles that annually damage a variety of

our crops remain unidentified even to species, and their behavior and habits are almost unknown. Bierne (1) has listed 314 species or species-groups of insects that have been recorded as damaging annual crops in Canada. He covered only three of the 27 orders of insects and did not deal with perennial crops, ornamentals, stored products, animals, households, and forests, nor the beneficial species. It is obvious that the list of all insects of direct importance to Canadians includes many hundreds more. The five species that appear annually as new pests of crops also add to the list. Even with many more entomologists it would take years before we could expect to know all that is required of even 50 percent of these species.

Although cotton insects in the U. S. have received a great deal of attention over the years, only seven years ago an investigative committee decided that little of the essential research had been done on them. In Canada, orchard pests have been studied intensively, yet a recent research planning meeting on these pests listed 11 major research areas still requiring attention including sampling techniques, rearing methods, methodology for use of pheromones, determination of crop losses, and the search for parasites and predators.

Advances have been made in the laboratory in the identification and synthesis of pheromones and other compounds such as hormones. But, as with other new or potential methods of insect control, the entomologist is the only one who can test these advances in the field and develop the proper methods for their application. The lack of adequate research by entomologists and others led us into the difficulties associated with the application of insecticides, and we should try to avoid a similar omission with these new techniques.

The professional entomologist of the future will work more closely with specialists in other scientific disciplines in his attempts to develop integrated controls. He will be required to work with economists to generate more data on the losses caused by insects, and to determine the cost-benefit ratios of his research and the control measures he recommends. He will have to develop methods for accurately forecasting outbreaks as well as for determining the levels of population that require control. He will have to cooperate in studies to determine the effects of his control measures on the biosphere.

The University Department

The department of entomology has a responsibility as a professional department as well as in the liberal arts context. At the University of Alberta this is acknowledged by placing the department in the Faculty of Agriculture and Forestry and by listing entomology as a major in the Faculty of Science. In view of this dual role I would suggest that the department re-examine its 1970 objectives.

Because of its responsibility in applied science, the department should ensure that its staff will continue to include members that have had professional experience as entomologists. This opinion is based on the hypothesis that such members are more likely to know the courses that are best suited for positions outside the university. Professional experience enables the professor to draw on his own experience for counselling students and for the provision of personal anecdotes to embellish his lectures. Additional benefit will be derived from the addition to the department of a point of view not usually acquired in the university environment. The university is such a distinctly separate subculture that selection of faculty solely from those who have spent all of their life in the academic environment is likely to make it difficult for the university to understand the needs of society and vice versa.

The department should encourage the student who is interested in research to seek work at a research establishment during the summer. This would provide the student with a sample of applied research, and exposure to different attitudes concerning the objectives of research. The student who intends to pursue graduate studies with the purpose of getting

a job in applied research would be well advised to take one or two years off to work in such research before proceeding to his terminal degree. This should assist him in selecting the appropriate courses and in determining whether or not he is suited to the job.

Students may wish to pursue a field of entomology primarily of academic interest or of limited potential for future employment. The professor concerned should discover the ultimate goal of the student and advise him accordingly. It is a sincere tribute to any professor that he can make his own field so interesting that many students wish to emulate him. Unfortunately for the student interested in a career, not all of the interesting fields are needed outside the university.

Despite the importance of ecology in entomology, it is my impression that there are few if any universities in Canada noted for their expertise in this field. The field of insect cold-hardiness is now vacant even though it should be an important area of study in a country with our climate. Another orphan, although certainly less appealing scientifically, is the study of insects that inhabit households.

Canada will require substantial numbers of entomologists in the relatively near future. In the past we relied on the U. S. to provide most of the graduate training of entomologists but Canadian universities should be able to carry more of this load. Departments that are part of an applied science faculty should be best suited to fulfill this role.

In Summary

The Department of Entomology of the University of Alberta has a long history of excellence and experience in the education of entomologists, most of whom probably ended up in applied research. Indeed most of the entomologists at the Lethbridge Research Station, including myself, are graduates of the Department. The Crop Entomology Section and the Department had a common progenitor in E. H. Strickland, and close contact has been maintained for the past 50 years. A recently retired member of the Section was the acting Head of the Department for two winters. It would not be surprising therefore, if the ideas that I have presented differ little from those already considered by the Department. Perhaps the major difference, if any exists, is in the attitude toward the purposes and goals of entomology.

Research is becoming more difficult. Many of the easier problems have been solved. Entomologists of the future will have to be better educated. They will have to work closely with scientists of other disciplines, and they will have to be more imaginative in their approach to research. If entomology is to continue as a strong discipline, entomologists will have to educate people outside of the discipline as to the importance of our research. The department is in the ideal position to perform this role.

The public is becoming increasingly reluctant to support science without the promise of social benefit. The measurable benefit from entomology is likely to be demonstrated only by its application. Unless the department makes the error of embarking on an extensive program of applied research on its own, it will have to rely on the success of its graduates in order to obtain public support. The success of applied entomology in turn relies on the education provided by a strong department that continues to maintain the basic fields of entomology. Applied entomology has been and will continue to be important to society. Departments, to serve society and to ensure their own strengths, have to be concerned with providing the most suitable education for applied entomologists.

Departments, as well as entomologists in general, will also have to concern themselves with the new Ministry of State for Science and Technology. The Ministry is likely to have an important voice in the agreements on financing universities that will be re-negotiated within two years between the federal and provincial governments. Currently, the federal

government provides 50% of the operating costs and over 70% of the research grants to the universities. The Ministry has already indicated that it expects to play a major role in decisions of government departments and in planning the science programs of universities (Science Forum 4:16-18, 1971). The practical course will be to determine what we think the future needs for entomology are likely to be and to ensure that our scientific and professional associations present these views to the Ministry. This should be done within the next two years.

The Department of Entomology of the University of Alberta deserves credit for taking the highly unusual step of asking entomologists from outside of the University to offer suggestions and criticisms on the education of the entomologist. While major changes may not be indicated or made, an exchange of ideas between the Department and outside sources at this symposium should benefit all concerned.

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INDUSTRY VIEWS ENTOMOLOGY

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Everyone has experienced events in early childhood, that remain forever imprinted in his mind. Living through the grasshopper invasions around Medicine Hat and Lethbridge during 1920, '21, and '22 was such an experience for me. It was my first major encounter with an insect pest, and the sight of crops disappearing almost overnight will never be forgotten. Grasshoppers were everywhere, and were even eating the cotton clothing hanging on clothes-lines and the bark from the unpeeled fence posts of barbed wire fences. In 1922, about the only green material that survived in some areas was Russian thistle, and in many cases this was harvested for feed for the coming winter. It was during this period that I had the good fortune to meet my first entomologist, E. H. Strickland. I was very young at that time, and was very impressed with the meeting, even though I am certain that this feeling was not mutual. At a much later date that first meeting and its impact on me were discussed. It was through Professor Strickland that the first, large chemical control program in Alberta was started. I was to spend many hours spreading poisoned bait for grasshopper control, and well remember the instructions on how to handle the bran bait.

Professor Strickland was, to me, a practical, economic entomologist. I have always felt that it was his approach to insect control that provided the encouragement necessary to establish a sound pesticide industry in Western Canada. The wide-scale application of arsenicals and strychnine provided incentive to the suppliers of pesticides. During this period, two other economic entomologists also gave support to the young industry. Both Mr. R. (Dick) Painter and Dr. H. E. Gray had a marked impact on the industry through their work on chemical control of insect pests.

Following the war, I enrolled in the Faculty of Agriculture of the University of Alberta rather than in that of Education, a field which I had been following prior to the war. In my first year I had the privilege of taking my first course in economic entomology from Professor Strickland. To those of you who did not have the good fortune of attending his classes may I state that you missed a great and inspiring experience. He was a dedicated and superb teacher, a first-rate practical economic entomologist, and had developed to a very high degree that rare commodity – a sense of humour.

Lack of a sense of humour could be responsible for some of the problems we presently face. If one recalls the highly successful economic entomologists of the past, this one trait is found in all of them. As the years have passed, a marked change in entomologists and in entomology, has occurred. Polarization now exists in both. The economic entomologist no longer has anything in common with the taxonomist, the physiologist, etc. and today, it is difficult at times to realize they are all part of entomology. There has been so little interest, cooperation, and communication between the entomologist interested in the biological control of insects and the entomologist working with chemicals, that at times each has proclaimed that his was the only meaningful work. Rarely has there been any attempt to consider both areas in proper perspective. This fragmentation of entomology by entomologists has been detrimental to all.

For too long entomology has not been an active, integrated part of biology. Little interest has been shown by entomologists in considering their contributions in relation to those of other biologists and little interest in relating these to the needs of agriculture. Entomology and entomologists have tended to remain aloof from other associated disciplines and as a

result, must now make a concerted effort to break out of the web in which they find themselves trapped. In the world of today and tomorrow, the entomologist must become an active participant in applied biology if we are to protect our environment, economy, and social customs.

Just as happened in the period prior to 1950 when chemical control became almost the only love of the economic entomologist, so the period following the early 1950's initiated the trend to basic research. While basic research is essential and will always be so, it is unfortunate that it is now implemented to such an extent that it deters the applied entomologist. Today, industry employs very few entomologists as there are very few good, applied entomologists available. At the same time, there is little opportunity for the employment of basic research entomologists in the pesticide industry in Canada. There is, in fact, a marked shortage of applied entomologists employed by governments too, and I am aware of two positions that are not being filled because of this shortage. Indications are that this shortage will become more acute in the next few years, and this can only result in serious problems for the future. More and more major insect problems are developing as we move into the "Green Revolution," and yet we are not solving these problems. It is time we returned to the concept of cooperation, and worked together in developing a well-balanced, integrated program of insect control that will benefit our entire society. The time for "class distinction" between entomologists is over; each segment is essential, each must be kept in balance, and each must contribute and be given equal recognition for the part it plays in producing programs that are economically sound and give maximum protection to our environment.

In the early days of entomology, the universities offered courses that both introduced the subject broadly and emphasized practical implications. One has only to review the names of noted entomologists occupying important positions in Canada's past, to find that in most instances their basic training was in economic entomology. In the past, graduating entomologists had far more exposure to other areas of biology than many get today. It may be true that most of these courses were then offered by the Faculty of Agriculture, but faculties of science were involved as well. Today, in many universities, "entomology" is no longer being taught.

During the past four or five years, I have interviewed many graduates applying for positions in our company. All too often I find that their training has been restricted to one small phase of entomology and even, at times, to one specific aspect of one specific insect. Although they had taken a course in general entomology, they admitted having little or no interest in insects other than the ones on which they had specialized. This type of specialization might have been acceptable, provided the applicant had received an adequate grounding in basic entomology, but this was apparently lacking. In several instances, I have indicated to the applicant that a broader knowledge of biology and chemistry is essential if employment with industry is expected. A closer check on the quality of graduating students also indicated that many of our universities have, as their main interest, the number of students enrolled, rather than the quality of the students or of the courses they teach. In attempting to take maximum advantage of grants available for student support, universities have ceased being selective when enrolling students. Instances are available of universities encouraging every student to continue on to higher degrees, regardless of the ability they have shown. It would appear that little attempt has been made to encourage students to enter fields in which employment opportunities are available, although this may be partially due to a lack of understanding of such needs or a failure, on the part of student advisors, to be far-sighted when counselling. Many recent graduates are inflexible and seem to think that a university degree is the key to instant success. The phrase: "I was encouraged by my professor to accept the fact that an advanced degree would assure me of employment" has

been too often repeated by job applicants. Graduating students should certainly be made aware of the significance and need of advanced training, but it should also be emphasized to them that obtaining such a degree alone is not the complete answer. They must be versatile, adaptable, tolerant, and realistic in their approach to employment. The entomological departments of universities and the entomological sections of biological departments have a very important role to play in the future training of entomologists. There must be broader exposure to other biological sciences, greater selectivity in accepting candidates for advanced degrees, and more awareness of the immediate and long-range needs for entomologists trained in the various facets of entomology. Only in this way can we keep the supply of and the demand for entomologists in balance, and avoid the serious employment problem that is facing us today.

Entomology should be taught in public school, in high school, and in university at the undergraduate level, to all students. A quick check of schools in the Province of Ontario last year revealed a disturbing ignorance of insects on the part of teachers, a failure of teachers to use insects in biological studies and in fact, a tendency of teachers to create an adverse reaction to anything connected with insects. *Entomophobia* seems to be increasing because of this widespread ignorance of insects. Lately, there has been a revival in superstitions and fables regarding insects that date back to the middle ages. A larger percentage of young people seem to fear insects than was true a few years ago. One contributing factor to this present ignorance and fear of insects is the failure of entomologists to communicate with the public.

When one reviews today's curricula in universities, elementary schools, and high schools, it is apparent that economic entomology and general entomology are no longer present. Compare the programs of the Department of Entomology, University of Alberta, from 1922 to 1936 with those of 1970, and the changes that have been made become apparent.

I have been very critical these last few minutes, and this has been deliberate. While we in industry realize the important role that the entomologist has played in the success of the chemical industry in the past, we also feel that there is a need for change in the future. More economic entomologists must be graduated if the major agricultural problems of the immediate future are to be solved. Chemical control of pest insects is essential now and will remain so for many years. The answer to our insect pest problems surely lies in our acceptance, development and implementation of integrated control programs. Full cooperation by all entomologists is essential. Let us get back to teaching more general and economic entomology before specialization begins.

DISCUSSION – AFTERNOON SESSION

Leader – D. H. Kavanaugh
Department of Entomology
University of Alberta, Edmonton, Alberta

First of all I would like to thank our speakers on behalf of all of us. I would especially thank Dr. Mason for discriminating between the terms "need," "demand," "luxury" and "necessity." It is clear from what has been said that our profession today is diseased. The outstanding symptom of the affliction has been repeatedly described today in graphs and words: namely, that entomologists are, using Dr. Mason's terminology again, "necessary" and yet not in demand. We are confronted today then with the job of diagnosing the disease. Once we have succeeded in doing this we should begin to formulate some treatment for it. If we succeed in this, then perhaps we'll have something which will assist entomology departments in Canada and the U. S., and particularly our department here, in understanding the present situation and possibly even in planning for the future. The papers presented today covered a great variety of points all, I believe, very relevant to the problems at hand. Numerous suggestions have been put forth which should stimulate discussion. In my attempts to relate the various topics discussed to one another, I felt the same frustration that others have mentioned throughout the week. I found it useful to jot the main points down on a flow chart (Fig. 1) and I would like to use this to outline what I think we are facing. I realize that all of you would probably organize your thoughts a little differently but I hope that this approach will promote rather than stifle the discussion to follow.

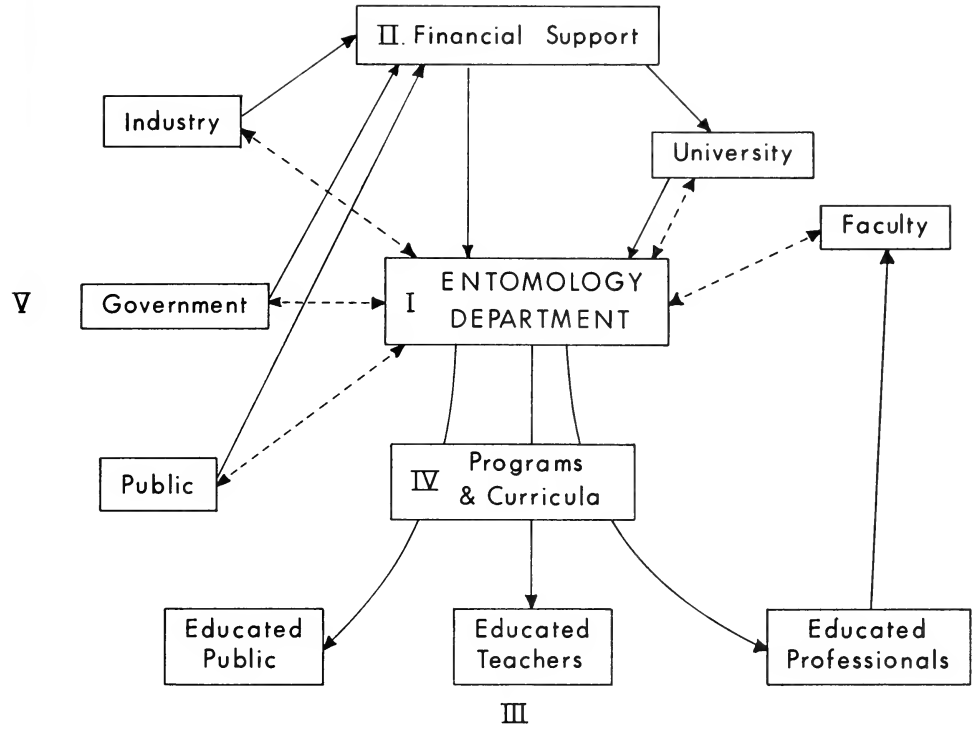
Roman numeral I is the Entomology Department, the focal point for this symposium.

Roman numeral II is financial support. I think we will include in this category our symptoms – the fact that we have lots of entomologists coming along, that we have a need for them but no place for them to go. Related to this topic under Roman numeral II we have the sources of support. Under support I would include not only funds but jobs. We have three sources of these: the public, government and industry which narrow down to one, the public at large. Dr. Mason has aptly presented the position of some of us with regard to job support. The other speakers today have provided us with a good deal of insight into what kind of support we can expect and into what we will have to do if we want to get more.

Under Roman numeral III, I have listed what I consider to be three goals of an entomology department. Their first responsibility is to educate professionals. Here, a big problem seems to be relevance – I use that term in the Madison Avenue sense – getting the background knowledge necessary to engage in interdisciplinary research. Dr. Cooper's talk had surprises for me since I was given a little indication of what he was to say beforehand. He changed much of it – for the better I think. A lot of what he had to say is directly applicable to this responsibility of educating professionals.

The second goal of an entomology department is to educate teachers – not only university educators but primary and secondary school teachers too. Special attention was paid to this topic by Mr. Jantzie and especially by Dr. Gittins. I hope we will hit the topic hard in our discussion because it is related to many of our problems.

Lastly, we have a responsibility to educate the general public. I would suggest that we have two problems here. First, we have to educate young people. We can do this by taking care of some of our other goals, namely by getting some good teachers into the school system at all levels. Secondly and perhaps most difficult, will be to reach the people who control the money; I call them the "post-schoolers."



Flow chart to and from a department of entomology.

Roman numeral IV I have headed Programs and Curricula. The goals I indicated for an entomology department are only achieved through some sort of plan – through specific programs and curricula as emphasized by Dr. Freitag and Dr. Gittins. The distinction made by Dr. Gittins between the goals of graduate and undergraduate programs is very important.

My fifth point doesn't fit into my scheme very well. It involves channelling students into different specialties during their educational process. Here, I include the screening of students to find out whether or not they are really dedicated and to learn to what they are dedicated. We may have to resort to these procedures to handle the imbalance now existing between students available and jobs available.

Next, I would like to consider faculty, a topic pretty well skirted in this symposium so far. In this context I would like to pose a few questions. First, what sort of staff should an entomology department have in light of its goals? At present faculty members must be teachers, researchers, and administrators. Have we left room for our best teachers? We certainly have left lots of room for our best researchers! Can an individual whose forte is teaching keep a job in a university today? The system requires that he carry out research at the same time that he is teaching. What does this drain on his time do to his teaching

potential? Dr. Cooper suggested that there are other aspects of teaching that could be better investigated, i.e. that there are activities outside the classroom just as or more important than those going on inside.

Finally, is the public really getting the education it needs from the entomology department? Here I mean the public; not industry nor government. To link this all together, and I have indicated this on my chart by dotted arrows, we have to communicate. Communication is a problem in any group situation. Looking at the different parts of my scheme, and we all know this from our own experience, we can see the problem: there is little communication between sections. Perhaps this is really the disease I referred to earlier. This lack of communication is the disease we have to cure. All day we have been hearing about this lack of communication between entomology departments, and entomologists, and the public, government and industry but this communication must be a two-way street. Hopefully, this symposium has been a step in the right direction. Intrauniversity and interdepartmental communication needs to be increased and encouraged as well.

Before opening the floor for discussion, I would like to say a few things about the public as a separate entity. The most challenging problem we face as scientists and educators is communicating effectively with the public. Those who supply the funds and jobs for entomologists are not available to educators as students; you can't get them into a classroom to have at them. They are not likely to pick up our point of view from television either, since, even if we had presentations on T.V., they would be watching "All in the Family" instead. Maybe, as Dr. Mason suggested, we will have to adopt Madison Avenue techniques to sell ourselves to the public. For is it not pathetic that Madison Avenue can sell luxuries . . . as necessities when we can't even sell necessities as necessities?

Until Dr. Cooper did so, no one had mentioned one additional barrier to our communicating with the public. I refer here to the increasing problem of *entomophobia. Entomophobia* isn't just squeamishness, it's a real psychiatric problem and I'm sorry to see that our resident psychiatrist, Dr. Schwab has left for the day. *Entomophobia* is an irrational fear of insects. I was an extension entomologist for five minutes a few days ago when Bruce Stewart, our extension expert, was out somewhere. A woman came in with a tiny little insect which she insisted was infesting her bed. She had broken out in a rash and was itching all over the place. The insect she showed me was a *collembolan*, yet I could not convince her that it was harmless. I'm afraid that the problem of *entomophobia* will not be solved by education alone. It will require the integrated efforts of psychologists, sociologists, psychiatrists and maybe even advertising agencies.

I would now like to open the floor to a general discussion. Dr. Cooper made some stiff accusations. Let's answer them.

Craig – Edmonton – Dr. Holmes indicated the need for research on cold-hardiness and household pests. Who's going to provide the funds?

Holmes – Lethbridge – This problem of obtaining support should be considered clearly. We can talk all we like about communicating with the public; but the public does not provide us with funds, at least not directly. In the federal government money is first apportioned to the various agencies. From there it is passed down through various levels of authority. Eventually, we have to compete with people in other disciplines for a certain amount of the money. In other words priorities are established. We are not, as entomologists, able to increase the total amount of money coming to the government; but we can increase the percentage of this amount that comes to us. You have to sell your research proposal to the individuals controlling the purse strings.

Gittins – Moscow – There are ways of getting funds without involving the government at all. In California there are many organizations called commodity groups. Many of these

organizations have funds available for research on the commodity of their concern. I am sure, for example, that Gord Hobbs at Lethbridge has received money from the alfalfa seed association. The sugar beet industry in southern Alberta, I am sure, has such a fund. Many of these agencies provide money for research in insect control. Very often the results can be lucrative for all concerned.

I would like to support Dr. Cooper's plea for entomologists to work together. We have gone through periods when "squirt gun" entomologists were considered to be at the bottom of the totem pole. Let's get away from this – all of us will profit.

One positive result of the student activism of the last few years is this word "relevance." In many of our universities this is the call we hear now. "Publish or perish" is being replaced by "teach or travel". I think this is great.

Cooper – Rexdale – About five years ago we at Cyanamid had money available for research on household insects – but no one was interested – there was no demand for research of this type. There is more misuse of pesticides in the household than anywhere else. No one tells the housewife that a vacuum cleaner is often more useful in controlling insects than the flit gun. If more people were aware of the problems resulting from the misuse of household sprays, funds could be made available to investigate alternate methods for controlling household pests. If I go to a university with some suggestions for research on household insects, pray tell me where do I go? If I do find a university that wishes to do the work, I am then told that I am not allowed to put any strings upon the work which is to be done even though my company is providing the money. In addition, it has been my experience that university personnel seem to think that a student being supported on an industrial grant will become contaminated if he undertakes a project which involves pesticide evaluation or a study of termite habits. Why have the universities stigmatized the student interested in applied entomology?

Pengelly – Guelph – Having had our academic tails twisted slightly, I, as a representative of academe, would like to clarify our position. Dr. Cooper referred to the poor calibre of student he is getting. If he thinks the students graduating now are mediocre, he should wait a couple of years. They have just introduced a system at the University of Guelph called "Pass by Course." If you take 50 courses while at university, and pass 40 of them, then you get your degree. There is nothing that says you have to pass Chem 100 before taking Chem 200 or 400. Why? Our all-wise Senate is composed primarily of "Arts" types because Wellington College (our Faculty of Arts and Science) has the largest student body on campus. These are the people swinging the cat – and their current educational fad is "doing your own thing."

Dr. Cooper mentioned sources of support for students doing research in integrated control. In our Department of Environmental Biology we have a staff member who is interested in integrated control. He was quietly told that research in integrated control of apple pests is now the province of the CDA lab at Vineland. Since he has no money he can't take on a student in integrated control.

At one time it was not academically respectable in most universities for a student to submit a thesis on the use of pesticides. In fact there were graduate schools that refused to accept students with this interest. We have tried to get students to work in applied research but they just said, "Pooh." Dr. Cooper mentioned that when he wanted an applied entomologist, he couldn't get one. Well, I am sympathetic because I would like to have one or two as graduate students. Our educational program here at Alberta was a sensible one and, at one time we did have a sensible one at Guelph. If you came into the department or into the faculty of agriculture you at least got one course called introductory or general entomology. One or two people took on the challenge introduced by this course

and eventually became entomologists. Well, at Guelph, through judicious maneuvering of "zoologists" we ended up with entomology being required by no one. Now how in the world can we interest anyone in entomology when we never get a chance to talk to him? At Guelph, if you are enrolled in animal husbandry, you don't have to take a course in livestock insects. The same is true of students in crop science, and so on. A student must have an "Introduction to Microbiology," and an "Introduction to Zoology" but he doesn't have to have an "Introduction to Entomology."

Heming – Edmonton – Bob Dixon, with the Alberta Department of Agriculture was wondering why it was we didn't have a speaker from the provincial government presenting the point of view of the extension entomologist. His point is well taken. We probably would not have had time to put him on but something that has come through loud and clear throughout this symposium is the need to communicate – and an extension expert's job is communication. We are forewarned next time.

Dixon – Edmonton – I created 13 jobs this year for students. Five students are working on mosquito biology for the city of Edmonton; one at Fort Saskatchewan; four in Calgary and two on blackflies for the provincial government. Three students were turned down. In 1957 there was only one entomologist on staff in the Department of Agriculture. By 1962 there were two and by 1971 three full-time entomologists with the department. In addition, one entomologist transferred to the Department of the Environment. This June I am creating another position for an entomologist to bring our total to four. I suspect that by 1973 there will be need of an additional entomologist in the Department of the Environment. I am not an Albertan. I received my training in Manitoba. Alberta entomology graduates right now are in trouble. The Department of Entomology at the University of Alberta does not have any applied entomology so that their graduates are competing for jobs with people from outside the province who do. I have had to reduce the level of one position in the hope of getting an Alberta graduate to fill it.

Freitag – Thunder Bay – Mr. Dixon, are the entomologists you refer to M.Sc.'s, Ph.D.'s or undergraduates?

Dixon – The students I placed were undergraduates. In this province not one Alberta entomology student got any of these positions. There were none or they did not apply. Where are they? The other positions are for M.Sc.'s and possibly Ph.D.'s if they have an applied bent. Otherwise we don't want them since we can't afford to train them.

Gooding – Edmonton – I am not looking for a job, Bob, but I would love to know where these jobs are being advertised.

Dixon – I phoned your department twice, Ron. I got no response from the Faculty of Agriculture. I did get responses from Physical Education, Zoology, and Education. The professional jobs were and are advertised in the papers. All you have to do is read the classified ads.

Gooding – We have only one undergraduate majoring in entomology and he is employed elsewhere for the summer. Another is working with mosquitoes for the summer but I'm not sure if he is one of your 13. He has four assistants. Surely there are lots of undergraduates who have had some entomology. There is a girl working for the city of Edmonton at $600.00 a month who took one of our courses. The student you have working at Fort Saskatchewan took a course in medical and veterinary entomology. Most of the students you have with you have had some entomology. We have few students majoring in entomology when undergraduates.

Dixon – This is the point I am trying to make. There is no requirement in the Faculty of Agriculture that students take entomology, even though all agriculture graduates should have at least an introduction to the subject. We have 60 district agriculturalists on our

staff, few of whom have any entomological background. I credit you people with teaching the ones that do. This is true too of the students from other faculties who we have employed. Nevertheless, where are the entomologists? We can create jobs but we have to have entomologists to fill them.

Gooding – During his talk Dr. Cooper referred to certain aspects of our entomology curriculum that he did not like. What doesn't he like and what would he like to see added or substituted?

Cooper – Too many of your courses are specialized and too few cover introductory and applied entomology. When I was a student, everybody in agriculture had to take some entomology. What good are agriculture graduates to us if they have had no entomology? All of our chemical salesmen are agriculture graduates but we cannot find enough of them that have had any entomological exposure. We have agriculture graduates that specialize in engineering, crop science, animal husbandry . . . but not entomology. In looking over your number of professors, students and grad students, there are few in what I would call the economic field. I would, therefore, probably have to take a very broad interpretation of what you are calling economic entomology.

Kavanaugh – Dr. Cooper, you have just told us what you would like to see in an agriculture graduate with a Bachelor's degree. What do you want in a postgraduate?

Cooper – We want a student who has had enough general and applied entomology to be flexible. If you talk to a man who has taken nothing but taxonomy, that is the only field he is interested in. All I ask is that he have a good general background upon which he can build. If he has only taxonomy and physiology he is of no use to us. A student should have at least two years exposure to general entomology no matter what his specialty. We have nothing against taxonomists; we have nothing against physiologists; but we do have something against the taxonomist who has so little general background that we must re-train him.

Hocking – Edmonton – The curriculum of the Faculty of Agriculture is decided by democratic process. Many years ago most courses required of all students were eliminated and with them entomology. There was nothing we could or would do about this because we do not believe in teaching entomology to students who are in class only because they have to be. I would like to list the applied courses we offer, since there seems to be some ignorance of this. There are three courses in medical and veterinary entomology, two in forest entomology, one in general agricultural entomology; one in toxicology, and a project course which can be used to cover aspects of applied entomology not included in the courses I have mentioned. We have six research projects in progress on applied aspects, all of these involving at least one graduate student as well as faculty. During the last 10 to 15 years, one quarter of the theses produced were in applied fields.

I would like to thank Dr. Holmes for repeating what I have been saying to graduate students for years about the writing of theses. I have also said it to the chairman of the Department of English here, and on more than one occasion in the hope, so far vain, of getting his department to do something about this. All I have been able to persuade them to do is to intensify their instruction in such fields as the appreciation of the writings of Geoffery Chaucer. Most students in entomology, however, already have a reasonable appreciation of some of his works. However, we have had a real problem, especially with graduate students who have never had to write anything other than the yes's and no's required in high school examination papers, in getting these people to the position where they can write a well written paper. This problem we have tried to solve ourselves by offering, on Saturday mornings in the fall term, a course in scientific writing. I think this is improving the situation, but it takes time.

Dr. Mason showed a graph illustrating Ph.D. production and job openings in science and

technology in Canada. It did not show this information for entomology and for the whole world. It has always been my belief that entomology is international and should be treated as such. If a similar pair of curves were drawn for the life sciences and especially for entomology and on a world-wide basis, the picture would be a different one. It certainly was in the past and I predict that it will be in the future.

Shemanchuk – Lethbridge – Dr. Hocking emphasized that the curriculum of the Faculty of Agriculture here had been derived through democratic process. I would suggest that the curriculum has also become too liberal; that the student is allowed too much freedom to choose to take only what he feels like taking, not, necessarily, what he needs. Everybody knows that a little entomological knowledge is of use to all agriculturalists. Surely none of us would go to a surgeon for surgery if we knew that he had not taken surgical procedure because he did not have to take it when in medical school. Therefore, I refuse to endorse the idea that a student need not take a course because he doesn't want to do so. If he has committed himself to a program in agriculture, or animal science etc., an entomology course should be mandatory.

Evans – Edmonton – Dr. Hocking listed the applied courses that we offer. Ecology is basic science. The textbook I use in this course is by Andrewartha and Birch, two well known economic entomologists. The whole book is a review of the applied entomological literature. Morphology is often considered basic. Our extension entomologist, Bruce Stewart, studied the sense organs of the red turnip beetle as a project in this course. Projects in physiology often involve the use of mosquitos, grain beetles and cockroaches. Thus, a course appearing basic from its description in the calendar is not necessarily so.

Nelson – Lethbridge – I would like to support Dr. Gittins and Dr. Corbet in their emphasis on leaving specialization in entomology until the graduate level. I did this myself and found it very helpful.

At our last meeting of the Entomological Society of Alberta a motion was made that we attempt to hold a joint meeting with the Canadian Society of Zoologists. It was defeated. This was a shame for reasons which are obvious.

Mason – Ottawa – Dr. Hocking, in answer to your statements on my graph, I did not have figures available on life scientists or entomologists, and your remarks about internationalism are to the point. In scientific research, nationality is irrelevant; in employment it surely is not. People who hire entomologists do look at your citizenship. Therefore, the fact that there are entomological jobs in France or Brazil does not help Canadians one bit. These people demand French or Brazilian citizenship of the people they employ.

Dolinsky – Edmonton – I am the latest asset of the Alberta Department of Agriculture – a newly-hired supervisor of entomology. I would suggest that the reason we are not getting the type of people we need out of our universities is because the people who are teaching there are not teachers but researchers. When they graduated with their Ph.D.'s, they knew nothing about teaching. Thus, it's not surprising that they teach only their own little field. They know nothing of cutworms, flea beetles, red turnip beetles or clover mites; in other words, they have no background in general entomology. I would like to see a course in entomology offered at a university that a person could take to learn about pest problems in his own country. What insects are forest pests? What do these insects look like? What are their life cycles?

I have gone to university. I have taken all kinds of introductory courses. Yet, when I graduated a couple of months ago I knew nothing about the behaviour of grasshoppers, about flea beetles, about Bertha armyworms. I came here with a background in grain pests. I knew a little about grain pests and household pests. But when you get into a field like extension you are expected to be a G. P. Every time you get up to talk you shake because

you are aware of your limitations. Nobody can know everything about everything. The CDA in the next five years is going to retire a large number of researchers. Yet, there is no one coming up through the ranks with experience of Canadian pest problems. Last year we had an outbreak of Bertha armyworm on rape but, because for years there had been no problem with this insect, no one knew what to do. In a few years we are not going to have any grasshopper experts in western Canada. Who is going to control the outbreaks to come?

Heming – Mike, you mentioned earlier that we in the universities are researchers not teachers. Since coming here four years ago I have had about 10 students in my two introductory courses who were majoring in education. Seven of them told me that the quality of the teaching in that faculty was lower than in any other they had experience of. Where are we supposed to learn to teach – probably not in the faculty of education.

Henri Goulet – Edmonton – Taxonomists are always the ones singled out as narrow-minded. I have been a student both here and at Macdonald College. I would like to work in applied entomology when I graduate. Students in entomology here do get a broad background. Dr. Ball insists that his students know all aspects of entomology and much in other fields as well. I have had courses in basic and applied entomology and in botany, zoology, anthropology, and geology among others. I will agree with you that there are narrow-minded entomologists, but few of them graduate from this department. Dr. Hocking would not allow it. Mike Dolinsky complained about the lack of courses on specifically Canadian pests. I advise him to get in touch with Macdonald College. They offer a superb course of this type.

O'Keefe – Moscow – We are talking quite frankly to each other today and this is good, but we are also polarizing people in this room who should not be polarized. I came into entomology after having received my B.Sc. degree in agriculture; I was not an amateur entomologist as a five-year-old as many of you seem to have been. This doesn't necessarily mean that I can't be a good entomologist. I also have five years experience in extension entomology – fireline, talk-to-the-people type of entomology. Until about 1965 if you asked an entomologist a question you got an answer, right or wrong. Since then this has ceased to be true. Entomologists won't answer a question now unless they know the answer. Yet, there are tasks to be done that don't require a lot of detailed knowledge. In university we should be learning how to pose questions and how to look for answers. If you learn to do this properly you should have no problem fitting yourself into a new job or situation. Although I have been working in entomology for five years I have never had a course in applied entomology. I have had a commitment to agriculture and, more recently, one to entomology and biology. I am having no trouble in my job.

Dr. Mason mentioned that we had to adopt Madison Avenue techniques if we were to sell entomology. This isn't necessary. If you talk to someone who is having trouble with insects he wants to listen to you. This is why Edmonton is having trouble allocating the right amount of money for mosquito control – because we entomologists are afraid to go down and talk to them not knowing all the answers. If we had the answers we would be more than willing to talk to them and they would be willing to pay us to listen. I talk to people about insects. As a result, both my applied entomology and my insect physiology suffer, but I still take the time to talk. As a result, it helps other entomologists because I am considered to be typical of other entomologists and since I take the time to talk to people, others probably do as well. If a person comes to you with an insect problem you have a chance to sell the subject of entomology to him.

SUMMARY

Morning Session

Rapporteur – D. R. Whitehead
Department of Entomology
University of Alberta, Edmonton, Alberta

Bruce Heming introduced today's discussion by pinpointing what he considers to be the crisis in entomological education. Too many students are graduating to fill too few jobs. In the eyes of the public our product is overqualified and is therefore, paradoxically, useless. To the modern taxpayer it seems that science creates rather than solves problems and taxpayer support is therefore lacking. We must therefore re-evaluate what is required of entomological education and we must also re-educate the public as to our actual goals. The goals of this meeting are, as was noted again later by Dr. Gittins, to answer these three questions. First, what is the proper education for entomologists of all kinds? Second, what can entomology contribute to education in general? Third, what has been done at the University of Alberta and what should be done?

Our first speaker this morning, Don Jantzie, gave us his thoughts as a teacher of high school biology. He lamented that entomology, general and environmental, is not treated in sufficient depth in high schools. Students should not only be stimulated but should have sufficient background to make value judgements when they become taxpayers. They should further, at secondary school level if not perhaps much earlier, be instructed in effect in what I would call insect appreciation or relevant entomology.

Problems in entomological education at secondary levels are lack of adequately trained teachers and lack of suitable texts. The second of these, promised by Dr. Gittins, is about to be resolved. The first, however, seems to be up to us. We need lateral education at university level with participation of faculty of education students in entomology programs. And, entomologists must become more involved with secondary education at teaching and curriculum planning levels.

Rick Freitag gave us his views from a base at a small, mainly undergraduate, Canadian university. He modified the statement of crisis in entomological education given earlier by Dr. Heming to one that university enrolments are decreasing and job placement becoming more difficult. Science enrolments, however, continue to increase, complicating the problem of job placement. Students in science programs seem job oriented – only about 10 to 15% seem interested in education *per se*. Some students drop out because of bleak employment prospects, some prospective students do not even enrol for the same reason, and some opt to take further training at more vocational-oriented institutions. According to Rick we should prepare the entomology or biology student with a broad range of options by (1) continuing surveys designed to acquaint academia with public requirements, (2) offering enhanced opportunities for undergraduates to experience multi-disciplinary research, and (3) insuring at both undergraduate and graduate levels, opportunities for lateral education. This is essentially the reverse of what Mr. Jantzie suggested but completely complementary. Jobs of the future may not now be foreseen and yet provision should be made for their fulfillment.

Art Gittins gave his views from a base that is somewhat larger – a U. S. Land Grant University which I take to be strong in both undergraduate and graduate programs. He noted that while Ph.D. production rates in the U. S. nearly tripled from 1959 to 1969, these Ph.D.'s, though still urgently needed in such areas as environmental quality control

and pest management, are no longer in demand. Entomologists in education must modernize and redirect the total curriculum and must also provide both public and government with a clear awareness of the need for entomologists. At university, broadened education is again called for. At undergraduate levels, training should be closely allied with biological science with specialization left to the graduate level. Exceptions may be when undergraduate training is terminal perhaps as in pest management entomology. Courses should be updated to accommodate today's more sophisticated high school graduate. Above all, students should be made aware that education must continue after graduation through their professional lives.

Graduate level education should be re-examined. Faculties should be carefully structured to meet modern needs. Students should be exposed to new technologies as they become available. Dr. Gittins asked a number of interesting questions. Should we have research-oriented Master's level degree programs? Should we not, in fact, have non-research-oriented Ph.D. programs? Should not superficial foreign language requirements be eliminated or replaced by requirements in computer languages? The student should have an opportunity to be broadened in experienced, not channelled.

Now, to get at the three main questions addressed to this symposium, I shall attempt to put together remarks made by our three morning speakers, by the discussion leader Dr. Pengelly and by members of the audience.

First, "What is the proper education for entomologists of all kinds?" As suggested by Dr. Pengelly, entomology should be clearly defined for the public, including the government. This is up to us as entomologists. Students should be introduced to the subject at an early age, perhaps even before they become students. We must, and it seems we are about to, produce suitable books that can be read in high school level or by the general public. Should the orientation of training be vocational or educational? Again, there seems to be some disagreement. It was suggested first, by Dr. Pengelly I believe, that the current job situation is normal, not depressed. Thus, perhaps continued emphasis on educational aspects may be desirable. Dr. Pepper, however, implied that professional entomological training never has been relevant.

Some members of this symposium have suggested broadened lateral education both for entomologists and for non-entomologists. I gathered that there is not total agreement with this idea though it seems a good one to me. In my opinion, which perhaps is not out of place here, Rick Freitag's suggestion – increased lateral and multidisciplinary education in entomology – does seem appropriate.

I think Mr. Gurba may have alluded to the central problem, in providing more emphasis in communication in entomological training, so that our graduates need not be solely research entomologists.

The second question was, "What can entomology contribute to education in general?" This question, really, is not easily distinguished from the first and perhaps should not be. Entomology should indeed be a part of education in general. The emphasis again is on communication and we as entomologists are responsible for educating the public and the government.

The final question was, "What has been done at the University of Alberta and what should be done?" If my memory serves me correctly, there was general agreement that in Professor Strickland's day entomology at the university was ideal. It was suggested by some participants this morning that entomology at the University of Alberta should return to the form it then took; indeed, perhaps if enrolments continue to decline, entomology here may do just that – but as a discipline it would very probably soon disappear. Again, this question is not really separable from the first and may be similarly answered. It would seem desirable

that future students have broadened, non-entomological training, especially to include exposure to and communication with non-entomologists including professionals in other fields and with the public. Please bear in mind that this is this morning's discussion, however.

I hope that I have done reasonable justice to thoughts given by those involved in the preparation of the product and will now turn this over to Martin Chance whose responsibility will be to summarize views of the users of the product.

Afternoon Session

Rapporteur – M. A. C. Chance
Department of Entomology
University of Alberta, Edmonton, Alberta

Bill Mason began with what he hoped was a pessimistic view of the future of the great systematic biology collections in Canada and the U. S. With static financial support, systematists will be expected to cope with an ever-increasing inflow of new specimens and an ever-increasing number of requests for identification. Eventually, conditions will become such that identification will become slow or impossible. Large portions of valuable collections may be destroyed because they were neglected and large amounts of data will become unretrievable. Dr. Mason points out that to avoid this dismal future those of us interested in the maintenance of museums must agitate for increased museum support. The second problem, he tells us, is the conservative nature of the taxonomists themselves. They retain old, time-consuming nomenclatural and information retrieval methods which could be replaced by a fast, computerized validating service. As well, with the help of computers, much of the routine identification could be carried out by technicians. Will the computer replace the scientist? Dr. Mason thinks not. The computer cannot extract new data from unworked specimens nor can it replace the research brain. Is the taxonomist likely to run out of material? The Insecta are not only the most numerous of all living creatures but are also the least known. Largely due to expansion of Canadian facilities in the 1960's, the production of Canadian Ph.D.'s now far exceeds the demand for them. Continued overproduction is a disastrous policy. Dr. Mason suggested what he feels are two reasonable courses of action. First, lowering production and second, convincing employing agencies that more entomologists are needed. The first has been unsuccessful hitherto as can be seen by the present employment situation. The second involves salesmanship – the conversion of something thought to be a luxury into a necessity in the minds of those with enough money to pay for it. The popularity enjoyed by environmentalists and conservationists should be the key to this sales approach. Dr. Mason thinks the university should be in advertising but also that all entomologists should be involved. Our public image as a group must be improved.

Neil Holmes began by indicating that the CDA has, in the past, been the largest employer of entomologists in Canada and that, within the next eight to 13 years, it will require 60 to 80 new entomologists. This demand will be modified by the capacity of entomologists to explain the importance of their research, by additional dramatic outbreaks of pest species such as that of the Bertha armyworm last summer, and by public reaction to the use of insecticides. Dr. Holmes indicated that most entomologists in agricultural research are in applied fields. Those involved with relatively pure research are decreasing in numbers. There is a general trend towards programs with an interdisciplinary approach. Whatever the research, the agricultural entomologist becomes involved in a wide range of activities directed to the management of insect populations. How should an agricultural entomologist be

trained? Dr. Holmes says that of the 88 main branches of the seven major sciences, applied entomology has associated with it 32. A wide background is thus essential. The study of foreign languages should, perhaps, be replaced by increased emphasis on English composition and grammar. Theses should be written as scientific papers to be published in refereed journals. The skills of communication should be increasingly developed. The entomologist in the next two or three decades, Dr. Holmes feels, will carry on research similar to that of today. Our knowledge of behaviour and ecology of many pest insects is still inadequate. Many pest species remain to be identified. New techniques, such as the use of pheromones, must be adequately tested to avoid past mistakes. Entomologists will integrate their efforts more with those of other specialists. Dr. Holmes feels that the university entomology department should include staff members who have professional experience as entomologists. These members might better understand the needs of society. Students interested in research should be encouraged to seek work at research establishments during the summer. Those entering grad studies should work at such establishments for one or two years before proceeding to terminal degrees. Such experience might help the beginning student in choosing a research proposal.

George Cooper believes that there is a need to reintroduce the study of insects into public and high schools. Little is done at these levels to create a favourable image, or an understanding, of insects. There is probably even a tendency to create an adverse reaction to insects at this level. He believes that entomologists with different specialties have become far too fragmented – far too isolated from the activities of other biologists. Broad biological background no longer seems to be provided to the entomology student. The trend toward basic research is so extensive that applied entomologists are sometimes in short supply. Industry and government need applied entomologists. Dr. Cooper feels that there is a need for a long term survey to determine Canada's future needs for entomologists. With this as a guide, the universities should become more selective when taking on new students. On-the-job training for university students should be encouraged. Dr. Cooper believes that there is a need today and that there will be a need in the future in industry for entomologists with broad backgrounds in biology and chemistry. Today's graduates do not fulfill industry's needs. Advertisement and especially improved communication may overcome this problem. Dr. Cooper believes there is a need for some consideration of psychiatric problems caused by insects. There is also a very large need for the personal counselling of students by university staff. Dr. Cooper is also alarmed by the lack of interest, desire, enthusiasm and salesmanship evidenced by university staff themselves.

I will try and sum up what has transpired this afternoon in four points.

1. Both public and government should be made aware that entomologists are necessary and not a luxury. However, the activities of entomologists should not be directed solely towards solving entomological problems arising in a free enterprise economic system, since some of the assumptions supporting such a system are questionable.

2. A favourable view of insects should be encouraged at all levels of our school system.

3. Input should be provided for graduate schools so that their graduates are of use to those hiring entomologists. I hope, in the future, that we won't again have as much negative feedback from employers as we did today.

4. A narrow education in entomology should be avoided in this day of problems requiring multidisciplinary answers. If the languages of chemistry, physics and mathematics have too strong an industrial accent, then we should develop entomological dialects to fill our requirements.

RESOLUTIONS

B. S. Heming
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This has been a long day. I think you will be surprised to see how small a package everything has salted down to. We have only two resolutions resulting from today's activities. Before presenting them I'd like to thank Brian Hocking and Philip Corbet for helping the rapporteurs and me to put them together. The first resolution is entitled "The Need for Communication."

WHEREAS, There is a lack of appreciation of the social and biological significance of insects and of entomology, especially among parents, educators, employers, the communications media, and governments at all levels, therefore

Be it Resolved, That continuing and increasing efforts be devoted to remedying this lack, in particular by: 1. encouraging children to regard insects as friends rather than foes; 2. emphasizing the increasing value of living insects as classroom material, especially for illustrating biological principles; 3. encouraging the improvement of communication between educators and employers; 4. assisting the media to present, insofar as possible, information about insects and entomological problems that is authoritative and accurate; and 5. making known to governments the benefits and the costs to man of insect activities, and thus the need for entomologists, now and in societies of the future.

The second resolution pertains to the lack of practical experience of today's graduates in entomology.

WHEREAS, Too few graduating entomologists have adequate background in applied fields for immediate employment in them, therefore

Be it Resolved, That greater efforts be made by all concerned to: 1. facilitate summer employment for undergraduates in research especially in these fields, and 2. make additional material in applied fields available in the curriculum both as formal courses and through appropriate invited speakers.

Are there any questions?

Běličěk – Edmonton – Entomology should be made compulsory for students in agriculture and related fields. If you want to be a physicist you have to take math. This should be true also of biologists and agriculturalists with respect to entomology. I suggest that we include a resolution to the effect that in agriculture and other pertinent fields an entomology course be made compulsory for graduation.

Heming – I would like to hear Dr. Hocking speak on this.

Hocking – Edmonton – We don't have the power to institute it. The curriculum in agriculture is decided by agriculture faculty council and that is what I meant when I said curriculum is decided by democratic process – not by democratic process among the students – but by faculty council. Faculty council eliminated a large proportion of required courses some years ago and I see little prospect of convincing them to change their minds.

Corbet – Waterloo – In relation to that last point, Mr. Chairman, we seem to have identified a serious deficiency among agriculture graduates, namely that they can graduate in agricul-

ture and not have been exposed to entomology. Since the present mechanism within universities is not competent to correct this, I think it would be appropriate to see how it can be corrected and I suggest that one way towards this might be for the employers to take a very stern line here and make it clear to the universities that they don't consider in many fields a graduate in agriculture as being trained adequately unless he or she has had entomology.
Heming – Do other people here agree? I wonder if Dr. Corbet's contribution can be rephrased as a resolution? Do you think this would have any impact on the powers that be in our faculty council?
Mary Chance – Edmonton – Perhaps we should include it as a resolution and send it on to the Faculty of Agriculture. Where are these resolutions going anyway?
Heming – I have to admit that I have given little thought about where these resolutions are going to go. They are to appear in the proceedings of this meeting, of course, but I am open for additional suggestions. One target will certainly be the Faculty of Agriculture.
Fredeen – Saskatoon – The Agricultural Institute of Canada and its provincial branches have professional standards committees. If these resolutions are worth anything they should go to these committees.
Rowes – Pinawa, Manitoba – I agree with Dr. Corbet that we should get potential employers involved. I also think that another symposium should be organized involving professors and employers that will get down to the problem of course details etc. What does the employer need? I suggest that an additional resolution should be formulated having to do with such a future symposium.
Gittins – Moscow – Something additional should be added to the resolution soon to come from Dr. Corbet's remarks. Those education students who are majoring in biology and who will be teaching biology at the elementary and high school level should be included. They too should be required to take entomology.
Hocking – I have spent the last few minutes framing a third resolution dealing with the last question to come up. I don't think of itself it will do much good; nevertheless, if there is additional support brought forward from other directions for this sort of thing, it just could bring about some changes.

WHEREAS, Knowledge of insects is considered to be essential in the work of all agriculturalists, foresters, and educators in the life sciences and desirable in the work of educators in all sciences, therefore

Be it Resolved, That faculties of agriculture and forestry be requested to give favourable reconsideration to a requirement for entomology or at least to facilitate increased enrolment in courses in this field and faculties of education be similarly requested in respect of students in science and especially biology majors.

Moved by Evans, seconded by Holmes that the three resolutions be accepted in principle. Passed unanimously.

ENTOMOLOGY AND EDUCATION – POSTSCRIPT TO SYMPOSIUM

Unquestionably, this Symposium has achieved a number of the objectives for which it was organized: it has given us a number of practical suggestions for here and now action, the more important of which have been drawn together in the resolutions. It is our intention to act on these in the widest possible ways; directly, through contributors as intermediaries where appropriate, and more indirectly through wide distribution of these proceedings.

Some of us, I think organizers and contributors alike, had other problems in our minds which never really found explicit expression, but which must have been apparent, by implication, to most sensitive listeners. Collectively, these may perhaps be covered by the expression "Education Sickness," which would include the current wave of anti-education feeling, declining budgets for education, declining enrolments and mounting drop-outs at schools and universities. These problems are difficult to focus on and have so far proved impossible to solve; Hoar (1972) aired some of them in his address to the heads of departments of biological sciences in Canada at Montebello, Quebec in November, 1971.

To me, this sickness shows some of the symptoms of chronic indigestion: a constant sense of fullness – of the head with knowledge rather than the stomach with food –, a feeling of revulsion when confronted with further knowledge, and relief obtainable only by abstention and the passage of time – accelerated perhaps by exercise. Since wisdom may be described as digested knowledge, an approach to a solution to these problems at once suggests itself: a move towards balancing the knowledge we create by research with some wisdom digested from it, and towards teaching the wisdom along with the knowledge. This is really saying no more than that we should be putting more emphasis on education and less on training. Education – leading out – produces wisdom from knowledge, thus curing mental indigestion. Training facilitates and improves the use of knowledge, mainly by repetition, and is thus not far removed from rote learning. While some training is a necessary part of education, training without education is not only possible, but perhaps usual. No man is made wise merely by training his memory. That we talk of training Ph.D.'s is tragic if this is really what we mean, especially since training has as its only *raison d'être*, preparation for a specific job.

As measured by the printed pages recording it, scientific knowledge has been multiplied more than tenfold in the last century. It is said that ninety per cent of the scientists who have ever lived are alive today – busily producing more at an ever increasing rate. The capacity of human brains to absorb knowledge has not increased correspondingly; indeed one may question whether any selection pressure for this still exists. Attempts, in this situation, to continue to teach all that is known, even in a narrowing field, may make a reality of that cynics' specialist – the man who knows everything about nothing. Clearly there is a glut of scientific knowledge and it is no wonder its price in the market place has declined, and the public is disillusioned with its misapplications. Though entomology is a bit of a laggard it is no exception. The sins of technology are being visited upon the world of learning and both knowledge and wisdom are threatened. A man who has taken every course a single university department offers is less well educated than one who has taken the same number of introductory courses in different departments. Wisdom, though not wealth, is more readily distilled from breadth than from depth. Knowledge is already in disgrace but wisdom, synthesis, and the broad view must, in time, prevail over that self-destructive, narrow nationalism which in the present must favour insects over ourselves and in the future threaten them and us through our common environment.

The insect world reflects in miniature so many aspects of mankind that entomology cannot lag for long. In education the insects will illustrate more biological principles for a dollar

than any other class of animal; increasingly so as our pressure on the environment increases. And after education? While our population continues to grow, insects will increasingly threaten our food, fibre, and health; when it shrinks, as it soon must, we shall have them to learn from still.

Hoar, W. S. 1972. Educational patterns and manpower requirements in the biological sciences. Canadian Soc. of Zoologists Newsletter 3(4):1-9.

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June 1972

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MAY 15 - 19, 1972

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