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# The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera)

## I. General questions of taxonomy, biology and evolution

With 10 plates (Figs. 1—38) and 2 graphs

**Contents**

## Introduction

This paper is intended to be the first of a series of papers on the Alysiinae parasites of the Agromyzidae. The work will mainly refer to the tribe Dacnusini, as there are only a few Agromyzid parasites which do not belong to this tribe, but, particu-

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larly in this first paper, some questions will be discussed in the context of the sub-family as a whole. The succeeding papers will give detailed host records for particu-lar groups of hosts and parasites, with descriptions of new species and taxonomic revision where necessary.

The need for this work has been apparent for some time. Large collections of bred Dacnusini have been accumulated in recent years by several workers as a by-product of the effort which has been put into breeding Agromyzidae. In writ-ing this paper I have had before me material bred by Professor E. M. HERING (Berlin), Dr. J. T. NOWAKOWSKI (Warsaw), the late FRANZ GROSCHKE (Stuttgart), Mr. K. A. SPENCER (London), Mr. A. LUNDQVIST (Lund), the late NILS RYDÉN (Hälsinborg), Miss MARIA BEIGER (Poznan), the late Mr. A. H. HAMM (Oxford) and myself. The total number of specimens runs into several thousand, and their hosts include the majority of European Agromyzidae. This material demonstrates beyond all reasonable doubt that the great majority of Dacnusini are highly host specific. There are many instances of the same species having been bred repeatedly from a narrow range of hosts: and Agromyzid species collected in different parts of Europe have in most cases yielded the same species of parasites.

The connection between host and parasite is evidently such an intimate one that keys to the parasites of given groups of hosts can be constructed, much in the same way as keys to mining insects are broken down according to plant genera and families. Such keys will be given in later papers in this series. It is my view that new species in the more difficult groups, particularly some *Chorebus* and *Dacnusa*, ought not to be described from caught material because a degree of overlap in the morphological characters of some species makes it difficult to be sure of the iden-tity of isolated individuals; in bred series individuals are automatically associated with others of their kind and the range of individual variation can be seen much more clearly. There are unfortunately no characters in adult Dacnusini which are at all comparable in value with the male genitalia of the Agromyzidae in deter-mining the specific identity of individuals.

It has been necessary to make certain nomenclatorial changes in this paper, both as a result of revision of the generic concepts and on purely formal grounds. In particular a change in the application of the name *Dacnusa* has been unavoid-able because the type-designation accepted by NIXON (1937 and 1943—54) in his revisionary work was invalid. This change is confusing but necessary: the applica-tion of the rules is clear, and the appropriate synonymy and type-designation has already been established in the American literature (MUESEBECK & WALKLEY, 1951).

I am using my revised generic classification consistently throughout this paper, and in reading the earlier sections the reader may find it necessary to turn forward to the section headed "Summary of proposed Classification of the Dacnusini" to clarify the application of the generic names.

The characters which I have used in classifying the Dacnusini are derived from the external morphology of the adult, as have been used by previous authors. At

the start of the work I examined the male and female genitalia of a number of representative species of Dacnusini, as well as *Dapsilarthra* and *Opius*, but found that they were remarkable by their uniformity. I observed differences only in the proportions of the various parts, and could find no clear-cut apomorph characters which were useful for the generic classification. However at specific level the length of the ovipositor is sometimes important, and RIEGEL (1950) has found specific differences in the male genitalia of *Chaenusa* spp. The most likely source of new characters which will throw further light on the phylogeny of the group lies in the larval morphology. Only a few Alysiine larvae have so far been described, but they show considerable morphological differences in both first and last instars.

In revising the classification I have tried to follow the principles of phylogenetic systematics as defined by HENNIG (1950). I am in agreement with him that zoological nomenclature should as far as possible reflect such a system. Following the same author the terms apomorph and plesiomorph are used to denote the degree of divergence of morphological characters from a given ancestral condition (a plesiomorph character is one which is close to a given ancestral condition; an apomorph character one which is divergent from it). These terms are preferable to such terms as "primitive" and "specialised", or "conservative" and "progressive", because they do not have the other conflicting meanings and overtones of those terms. In a phylogenetic system only synapomorphy can be used to justify the association of species in a genus or other supraspecific grouping. Convergence (the independent evolution of similar apomorph characters) and symplesiomorphy (agreement in some plesiomorph character) cannot be used to justify such an association. An important concept in phylogenetic systematics is the sister-group relationship which exists when two monophyletic groups of equal rank (i.e. age) are associated in a higher monophyletic group. The relationship can be demonstrated by an alternance of apomorph and plesiomorph characters (i. e. each of the two groups is apomorph in some respect in which the other is plesiomorph). It is important to note that it is not valid to split a group simply on the presence or absence of a particular character, as is often done in conventional systems of classification.

I am adopting a high standard of verification before accepting any breeding records in the literature. Before NIXON's work more species of Dacnusini were undescribed than described and many of the names available must have done credit for a number of distinct species. Consequently most earlier breeding records cannot be accepted at their face value, and I will only accept them if I have been able to see the specimens concerned or if the record has subsequently been confirmed. In addition there are a number of records in the literature which appear to be misassociations of host and parasite, and it is my intention in later papers in this series to clear these up as far as possible and produce reliable lists of the parasites of particular Agromyzid hosts.

In writing this paper I have had before me a considerable material of Dacnusini and *Dapsilarthra*, but for the other genera I have relied on a sample range of spe-

cies which were made available to me from the collection in the British Museum (Natural History). This sample included:

*Prosapha speculum* (HALIDAY)

*Orthostigma pumilum* (NEES)

*Aspilota microcera* THOMSON and two other *Aspilota* spp.

*Alloea contracta* HALIDAY

*Chasmodon apterus* (NEES)

*Aphaereta* sp.

*Cratospila circe* (HALIDAY)

*Trachyusa aurora* (HALIDAY)

*Tanycarpa gracilicornis* (NEES) and *Tanycarpa* sp.

*Alysia manducator* (PANZER), *A. fuscipennis* HALIDAY, *A. incongrua* NEES, *A. frigida* HALIDAY and *A. punctigera* HALIDAY

*Coelalysia bicolor* (SZÉPLIGETI)

*Pentapleura pumilio* (NEES) and *P. fuliginosa* (HALIDAY)

*Phaenocarpa pullata* (HALIDAY), two species identified as "*P. ruficeps* (NEES)", *P. tabida* (NEES) and *Phaenocarpa* sp.

*Grandia cynaraphila* (RICCHELLO)

The determinations of these species were mostly by G. E. J. NIXON, J. A. J. CLARK and CH. FERRIÈRE. Observations in this paper on the distribution of particular characters in the Alysiinae apart from the Dacnusini and *Dapsilarthra* should be interpreted as based solely on the above range of species, unless it is otherwise clear from the context.

## Previous Taxonomic Literature on the Dacnusini

The first author to describe a species now included in the Dacnusini was GRA-VENHORST (1807). Then NEES ab ESENBECK published a number of descriptions in a series of papers which appeared in 1811, 1814, 1816 and 1818. His major work "Hymenopterorum Ichneumonibus affinium Monographiae" (1834) superseded these earlier papers, which need only be consulted on nomenclatorial questions. In his work of 1834 he divided his "Ichneumonides adsciti" (the present Braconidae) into two groups, the Ichneumonides Braconoidei and the Ichneumonides Alysioidei, on the basis that the Braconoidei had five segments of their maxillary palpi but the Alysioidei six. Most of the present Dacnusini were included with other Alysiinae in the genus *Alysia*, except for *Symphya* (placed as Sectio II of *Sigalphus* LATREILLE), *Chaenusa* (included in *Perilitus* NEES) and *Coelinius*. WESMAEL (1835) criticised NEES' classification and drew attention to the importance of the mandibles. On this basis he divided his Braconides into two subtribes, the "Braconides endodontes" and the "Braconides exodontes". The latter group has been accepted as a homogeneous unit by all subsequent authors and is the Alysiinae of this paper. But his concept of "Braconides endodontes", being based on plesiomorph characterisation, is heterogeneous. WESMAEL did not publish any specific descriptions of his Exodontes. Other isolated descriptions of species during this period appeared in the works of CURTIS (1829), SCHIÖDTE (1837) and ZETTERSTEDT (1838).

The other main body of specific descriptions from the early 19th century is found in the work of HALIDAY. After a short summary of his generic classification published in 1833, he published detailed descriptions of English and Irish species in 1838 and 1839. He included all the present Alysiinae in a single genus *Alysia*, which he divided into the subgenera *Alysia*, *Chasmodon*, *Alloea*, *Oenone*, *Dacnusa*, *Chorebus*, *Chaenusa* and *Coelinius*. This classification was used with minor modification by many subsequent authors. Its main drawback was the heterogeneous nature of *Dacnusa*.

Both NEES' and HALIDAY's work contain reasonably full descriptions and, although a few characters which are now considered important were unfortunately omitted, they contrast very favourably with the inadequate descriptions of a number of later authors. After their work little interest was shown in the Dacnusini for some time. Descriptions of individual species were published by RATZEBURG (1852)[2] and RUTHE (1859), and some very inadequate descriptions of bred species by GOUREAU (1851). GOUREAU's names have not since been used, but now that extensive bred material is available it will be possible to clear up the identity of his species.

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[2] RATZEBURG (1852) described his *Alysia gedanensis* from specimens sent to him supposedly bred from galls of the coleopteron *Saperda populnea* (L.) on twigs of *Populus tremula* L. The possibility that the true host was dipterous did however occur to him, and, to judge from his description, it is very probable that NIXON's (1944) *Dacnusa anguligena*, bred from galls of *Melanagromyza* on the same tree, is a synonym. GIRAUD (1861, Verh. zool.-bot. Ges. Wien, **11**, 486) also refers to parasites bred from *Melanagromyza* galls on *Salix* and *Populus* under the nomen nudum "*Dacnusa agromyzae*".

FÖRSTER (1862) proposed eighteen new generic names with only the briefest descriptions. By this action he caused considerable nomenclatorial confusion and it is painfully apparent that he had no more than a very superficial knowledge of the group. The fact that a few of these names are the first available for tenable generic concepts is largely fortuitous and reflects little credit on their author. Subsequent workers were unable to understand much of his key and continued largely to follow HALIDAY's system. It was necessary for me to reexamine the type material (see Appendix IV) in order to clarify the application of many of his names.

Apart from the description of a new genus by GIRAUD (1863) and a single species by VOLLENHOVEN (1878), the next workers on European Dacnusini were MARSHALL (1891 and 1897) and THOMSON (1895). MARSHALL gives reasonably full descriptions, but THOMSON's species were all inadequately described and many of the names have not since been used. I have tried to clarify their application in Appendix V following my reexamination of his types. SZÉPLIGETI (1901) described two species from Asiatic Russia, but one of these has been synonymised with a HALIDAY species.

For more recent times I am content to indicate only the more important taxonomic papers. MORLEY (1924) proposed six new specific names on hopelessly inadequate descriptions, and none have been used since. Unless his type material can be found, it seems preferable to consider all his names as nomina dubia. TELENGA (1935) has described a number of new Russian species, but I feel uneasy about interpreting at least his *"Dacnusa"* species from the descriptions given, since his concept (after HALIDAY) can now be seen to have been heterogeneous and some of the characters which I consider significant for the generic classification are omitted from the descriptions. A reexamination of his material in the light of more recent knowledge of the group is desirable, and until this can be done I have preferred not to use his names.

The most important contribution to our knowledge of the Dacnusini since NEES' and HALIDAY's time is the work of NIXON (1937, 1942 and 1943—54). In my view NIXON is the first worker who has had a sufficiently representative material of the group before him to form an adequate basis for an overall revision. His careful delimitation of the species I consider in general to be very reliable, and my criticisms of his work on various points of detail must not be taken as implying any disrespect of the whole. His generic classification represents a considerable improvement on that of previous authors, particularly because the heterogeneous elements previously included in *"Dacnusa"* have been largely disentangled. My rejection of a number of features of his system should again not be taken as implying disrespect. It is inevitable that any attempt to base the classification of a group on rigourously phylogenetic principles will result in rather different generic nomenclature being adopted than in a non-phylogenetic system.

A number of short papers giving descriptions of new European Dacnusini have been published in recent years by STELFOX (1952, 1954 and 1957), BURGHELE (1959a, 1959b, 1960a and 1960b) and FISCHER (1961). The first two authors are particularly interested in the so-called "Wasserhymenopteren" (i. e. *Chaenusa* and

certain *Chorebus* spp.). Earlier papers on these groups which have not been mentioned in this account can easily be traced from the references in BURGHELE's works. TOBIAS (1962) has produced a long paper in Russian on the fauna of the Leningrad region, including descriptions of new species, but owing to linguistic difficulty I have been unable to study this fully before going to press. His new genus *Paragyrocampa* however clearly falls within my concept of *Chorebus*.

The Dacnusine fauna of areas other than temperate Europe is very little known. For the mediterranean region there are only a few scattered references in the main European literature and recent papers on the Spanish fauna by DOCAVO ALBERTI (1955 and 1962).

The only Japanese literature of which I am aware is WATANABE's (1963) description of two new *Coelinius* (Coelinidea) spp.

The North American literature on Dacnusini is very scattered, but the descriptions of all the species can be traced easily from MUESEBECK & WALKLEY's (1951) synoptic catalogue. The total number of species listed there, thirty-three, is very small by comparison with the known European fauna and doubtless large numbers of species await description. RIEGEL's (1950) description of a new species which I include in *Chaenusa* was not included in that catalogue, but there has been no subsequent published work on the North American fauna of which I am aware.

The information for the tropical regions is even more meagre. For the old world there is only WALKER's (1860) description of two genera from Ceylon. The records for South America, refering to four species in all, are summarised in RIEGEL's (1952) catalogue.

It may be useful for future reference to append a few notes on the location of some collections. All remaining NEES types at Bonn were destroyed during the last war, and Dr. B. MANNHEIM of the Zoologisches Universitäts-Museum there has stated, in a letter to Dr. M. FISCHER, that his authority can be quoted to this effect. Mr. M. W. R. DE V. GRAHAM has recently discovered a few of NEES' Proctotrupoid and Chalcidoid types, originally sent on loan to WESTWOOD, in the Hope Department at Oxford, but there are no Braconids there.

HALIDAY's material is in the Irish National Museum at Dublin. It was studied by NIXON and his interpretation of HALIDAY's species can be taken as authoritative. FÖRSTER's Dacnusini types are in the Zoological Museum of the Humboldt University at Berlin, and an account of my reexamination of them is given in Appendix IV. THOMSON's types are all in the Zoological Institute of Lund University and an account of my reexamination of his *"Dacnusa"* types is given in Appendix V. MARSHALL's and NIXON's material is all in the British Museum (Natural History).

### Terminology

The terminology used in this paper largely follows that proposed by RICHARDS (1956) and incorporates several changes in the traditional terminology used in previous papers on this group.

For the wing venation a modified version of the COMSTOCK-NEEDHAM system is used. The abbreviations for the veins are given on fig. 3 and for the cells on fig. 4.

The mesopleuron of previous authors is here called the mesepisternum (after RICHARDS, 1956). The names used for the sutures found on this also follow RICHARDS (see fig. 27). The "furrow" which is frequently mentioned in NIXON's (1937 and 1943—54) descriptions accordingly becomes the "precoxal suture". In some of the descriptions I will have cause to refer to the slightly raised part of the mesepisternum which lies beneath the wing base (immediately above the epicnemial suture, when this is present): this I have called the subalar callus.

It has generally been the practice in taxonomic papers to number the abdominal segments from the petiole as "segment 1", because in the Apocrita the true first segment (the propodeum) is functionally part of the thorax. This system is very confusing, particularly when the genitalia are studied, and I am abandoning it. In my descriptions the first two abdominal tergites will, as is customary, be termed the propodeum and petiole, while the succeeding tergites will be numbered 3, 4, 5 etc. according to their true homology. The term "gaster" is used when necessary as a collective term for segments 2 onwards (the functional abdomen).

The numbering of antennal segments is the same as in most previous works, and includes the scape (segment 1), the pedicel (segment 2) and a variable number of flagellar segments. The small annellus is not included in the count.

Teeth on the mandibles are numbered from front to rear (as in NIXON's works).

Although the larvae might more precisely be termed "parasitoids", as the host is invariably killed, I have preferred to retain the less precise term "parasite" in this paper, largely on stylistic grounds.

## The Characterisation and Relationship of the Alysiinae

The Alysiinae (including the "Dacnusinae" of most authors) are established beyond doubt as a monophyletic group by the form of the mandibles (fig. 1). These can be opened at right angles to the head and their teeth are curved outwards. This condition is known as the exodont condition, and the terms "exodont Braconids" or "Exodontes" (following WESMAEL, 1835) have been generally used by authors who recognised two subfamilies as the generic term to include them both. This terminology becomes superfluous if only one subfamily is recognised as in the present paper. The only character which has ever been put forward to justify the separation of the "Alysiinae" in the restricted sense and "Dacnusinae" as separate subfamilies is the presence or absence of vein 2 r-m. This separation was first proposed by FÖRSTER (1862) who recognised two families — the Dacnusoidae and Alysioidae. Most subsequent authors have retained these coordinate concepts, though they have accorded them only subfamily or tribal rank.

While the bulk of the "Dacnusinae" as thus defined (the exceptions are discussed under the heading "Genera excluded from the Dacnusini" below) have every appearance of being a monophyletic group, the same is not true of the "Alysiinae". No apomorph character has ever been put forward which can justify the "Alysiinae" bereft of the "Dacnusinae" as a monophyletic group. While it is arguable that nomenclature need not always follow phylogeny absolutely and it may sometimes be desirable to retain stage groups, at least provisionally, as taxa, I think

that such exceptions should be minimal and I cannot see that one is justifiable in the present case. In a phylogenetic system only the old "Dacnusinae" (with certain reservations) can be justified as a monophyletic group within the larger monophyletic group of the exodont Braconids as a whole. To give nomenclatorial expression to this situation I am using the term Alysiinae in the wide sense to include all exodont Braconids, and am provisionally proposing within this subfamily a subordinate tribe Dacnusini to include (with three exceptions) those genera formerly included in the "Dacnusinae". More work will be needed to show whether the subdivision of the Alysiinae into a number of tribes is a convenient arrangement (at present the overall picture is very obscure). In the meantime the use of the term Dacnusini as a subordinate tribe of the Alysiinae has the advantage of continuing a well-known terminology in only a slightly modified form, but without the misleading implications of coordinate terms. (Some authors have used the terms Alysiini and Dacnusini to denote coordinate tribes within the subfamily. This is of course equally objectionable to coordinate subfamilies and merely removes the above argument to a lower level.)

The wider relationship of the Alysiinae probably lies with some groups included in the Opiinae which are likewise parasites of Diptera and pupate within their host's puparium. Dr. MAX FISCHER (personal communication) has expressed the following views on the evolution of the Alysiine mandibles:

> „Nun gibt es eine Reihe von *Opius*-Arten bei denen die Mandibeln „an der Basis erweitert" sind. In extremen Fällen bildet diese Erweiterung einen mehr oder minder deutlichen Zahn. Man kann sich u. U. vorstellen, daß diese basale Erweiterung der Mandibeln zum dritten Mandibelzahn der Alysiinae geworden ist. Übrigens zeigen manche *Opius*-Arten an Stelle dieser Erweiterung am unteren Rand der basalen Hälfte bloß eine scharfe Kante, die als Vorstufe zu einer Basalerweiterung und zum Basalzahn gedeutet werden kann. Der primäre Schritt zur Entstehung der Alysiinae ist also wohl nicht die Verkürzung der Mandibeln oder die Veränderung ihrer Lage, sondern die zusätzliche Bildung eines dritten Zahnes von der Basis her (nicht durch Spaltung an der Spitze, wie es bei den Bassini bei den Ichneumoniden der Fall ist)."

The evidence of the wing venation and larval morphology does not conflict with this view. The wing of *Opius caelatus* (HALIDAY) (fig. 3) for instance is virtually identical with that of some genera of Alysiinae and agrees with my postulated plesiomorph form for that group. The larvae of *Dapsilarthra* and *Alysia*, clearly plesiomorph forms for the Alysiinae, resemble those of the Opiinae according to SHORT (1952). But it must be remarked that these resemblances could be the result of symplesiomorphy, and too much reliance should not be placed on them until more detailed studies have been made on the family as a whole.

I have confined my present study to the Alysiinae and mainly to the tribe Dacnusini within the subfamily. Nevertheless I have considered the existence of some form of close relationship between the Alysiinae and some Opiinae (the latter may

not be a monophyletic group) sufficiently clear to throw light in some cases on which characters are plesiomorph for the Alysiinae.

## The Characterisation and Relationship of the Dacnusini

The most important apomorph character of the Dacnusini is the loss of the cross-vein 2 r-m. With this is associated the characteristically sinuate vein $R_s$ (fig. 14) (in species with 2r-m retained this normally runs straight to the wing-margin (figs. 3 and 4)), except that in a few groups this is secondarily evenly curved. Apart from these features the Dacnusini contain species which are as plesiomorph as . any in the Alysiinae and I have been unable to find any other clear-cut apomorph feature in the adult morphology characterising the group. The two known first-instar larvae (those of *Dacnusa areolaris* (NEES) and *Chorebus gracilis* (NEES)) develop within a distended trophamnium retained from the egg stage, an important apomorph character which is of considerable phylogenetic as well as biological interest. But obviously a representative range of species will need to be studied before it will be possible to rely on this character for purposes of classification. As the sinuation of vein $R_s$ is clearly linked with the loss of 2r-m and cannot be considered an independent character, the validity of the Dacnusini as a concept rests for the present on whether 2r-m has been lost once only or more than once independently. Certainly one species, *Grandia cynaraphila* (RICCHELLO), appears to demonstrate an independent loss of 2r-m and I have therefore excluded it from the Dacnusini (see below). But the great majority of the old "Dacnusinae" have all the appearance of being a monophyletic group because there is a continuous range of forms leading to all the more obviously apomorph groups and the characters of the latter give no reason to think that any of them is more closely related to any group outside the Dacnusini than it is to the rest of the tribe. I have analysed some of the characters of the tribe below to establish which conditions are plesiomorph. As can be seen from the results the common ancestor of the Dacnusini cannot have looked very different from many groups alive today and there are many species which diverge from the plesiomorph pattern in only one or two of the characters analysed.

The existence of a large number of predominantly plesiomorph species little removed from the ancestral form is the reason why the tribe has proved difficult to classify generically. It also indicates that the group is relatively young (a conclusion which is also reached from considerations of host association — see under "The Connection between Phylogeny and Host Association" below).

The conception of Dacnusini as a monophyletic group derives some support from the elongate form of pterostigma characteristic of all except a few apomorph groups such as *Coelinius* where it is secondarily modified, but I am not sure whether this can be described as an apomorph character. Many other Alysiinae have short broad pterostigmata (for instance *Alysia, Cratospila, Coelalysia, Pentapleura, Grandia, Idiasta* and some *Phaenocarpa*). In others such as *Synaldis, Aspilota* and "*Phaenocarpa*" *tabida* (NEES) the pterostigma is very weak. An elongate pterostigma comparable with that typical of the Dacnusini is found only in *Orthostigma*,

*Trachyusa*, *Tanycarpa* and *Dapsilarthra* (fig. 6) among the genera I have examined. I am doubtful whether this character really indicates an affinity of *Orthostigma*, *Trachyusa* and *Tanycarpa* with the Dacnusini. *Orthostigma* in particular appears close to *Aspilota* and its allies in respect of the elongate petiole and very small mandibles.

The biology of *Dapsilarthra* suggests a possible affinity with the Dacnusini. All the species are parasites of leaf-mining Diptera (including *Philophylla* (Trypetidae), Agromyzidae, Muscidae and *Chylizosoma* (Cordyluridae)) and are in northern Europe the only group of Alysiinae apart from the Dacnusini known to attack Agromyzidae (published records to the contrary I view with suspicion). It can be established that the original hosts of the Dacnusini were leaf-mining Agromyzidae (see under the heading "The Connection between Phylogeny and Host Association" below). Thus the circumstantial evidence of host selection suggests that a possible relationship between *Dapsilarthra* and the Dacnusini would merit investigation, but I must admit that I have been unable to find any apomorph characters which throw light on the affinities of *Dapsilarthra*. Several *Dapsilarthra* spp. (such as *D. balteata* (THOMSON), fig. 6) have an obviously sinuate $R_s$, similar to that of the Dacnusini, but this seems to be the result of convergence as in other species a straight $R_s$ is retained.

The conception of Dacnusini put forward in this paper is strengthened by the occurrence of two distinct evolutionary trends which are not apparent in other Alysiinae. These are (i) that when vein $Cu_1$ is reduced so that cell 2Cu is open at its lower distal corner, reduction occurs through the weakening or loss of $Cu_{1b}$ (figs. 11 and 14) (the base of $Cu_{1a}$ never migrates towards the junction of $Cu_1$ with 1m-cu); (ii) the development of extensive pubescence in many groups on various parts of the thorax and abdomen (and sometimes the head and hind coxae too). These trends are discussed further in the section headed "Evolutionary Trends".

## Plesiomorph Characters

In attempting to reconstruct the phylogenetic relationships between members of a monophyletic group it is necessary first to consider which characters are plesiomorph for that group — in other words the original characters of the ancestor of that group. In some cases the plesiomorph character may be so obvious that explanation is unnecessary (no one would doubt for instance that wingless Alysiinae are derived from winged ancestors). But there are a number of characters which are important in the classification of the Dacnusini where I think some further explanation of my interpretation may be needed. I have therefore given a list of such characters under thirteen headings below. In arriving at my interpretation I have considered the distribution of these characters within the Dacnusini, within the Alysiinae as a whole and sometimes also in the Opiinae and other Braconids.

### (i) Mandibles 3-toothed

Within the Dacnusini mandibles with three about equally developed teeth are found in *Dacnusa*, *Amyras*, *Priapsis*, *Coloneura*, *Tates* and *Exotela* (except *E. interstitialis* (THOMSON)). In other Alysiinae apart from the Dacnusini this type

of mandible is almost universal (of the material before me only the two *Tanycarpa* spp. have more or less 4-toothed mandibles, and the apterous *Lodbrokia hirta* HEDQVIST is described as possessing a mandible with about 7 teeth). In view of the wide distribution of this character within the Dacnusini and its almost universal presence in other Alysiinae I am confident that it is plesiomorph.

### (ii) Clypeus flat with a differentiated apical rim (fig. 1)

As well as in most Dacnusini clypei of this type are found in the majority of other Alysiinae. Because of this wide distribution it is my opinion that this character must be considered plesiomorph. Conspicuously projecting clypei are found only in some species in the *Coelinius* genus-group (Dacnusini), and among other Alysiinae in *Alysia, Coelalysia, Aphaereta* and some *Phaenocarpa*.

### (iii) Maxillary palpi long, 6-segmented (fig. 1)

Elongate palpi similarly proportioned to those of *Chorebus lateralis* (HALIDAY) are found among the Dacnusini in *Dacnusa, Tates, Exotela* and many *Chorebus*. Substantially shorter palpi are found in *Coloneura, Priapsis, Dacnusa, Chaenusa, Protodacnusa* and some *Chorebus*. In the *Dacnusa* genus-group, which contains species with both long and obviously shortened palpi, species which have otherwise the most plesiomorph features, for instance *Dacnusa laeta* (NIXON), *D. abdita* HALIDAY, *D. metula* (NIXON) and *Amyras clandestina* (HALIDAY), have long palpi. However I would not press this argument. Clearer justification for the view that elongate palpi are a plesiomorph feature for the Dacnusini lies in this condition being general in other Alysiinae. Of course there is variation between different groups and I do not claim to be able to define the plesiomorph character with any precision. But I consider the evidence sufficient to show that the possession of palpi considerably shorter than those figured (fig. 1) is an apomorph character.

The maxillary palpi have 6 segments except in the single species *Coloneura stylata* FÖRSTER.

### (iv) Labial palpi 4-segmented

This is the general condition both within the Dacnusini and in other Alysiinae. A reduction to three segments appears to have occurred twice in the Dacnusini — in a group of *Chorebus* spp. which are strongly apomorph in other characters ("*Chorebus*" in the restricted sense of previous authors, and "*Gyrocampa*" *miodes* NIXON) and in some *Chaenusa* (the species hitherto included in *Chorebidea* and *Chorebidella*).

### (v) Mean number of antennal segments in the order of 26—34

The number of antennal segments in the Dacnusini ranges from over 50 to as few as 15. Consideration of the range shown by other Alysiinae and Opiinae has led me to the conclusion that the plesiomorph condition for the Dacnusini must lie somewhere between these two extremes, and furthermore the species which exhibit the more extreme conditions are strongly apomorph in other respects (e. g. *Chorebus ampliator* (NEES), *Chorebus thisbe* (NIXON) and *Coelinius* spp.). I have tried to assess the plesiomorph number of segments by considering the range shown by the more plesiomorph species in the larger monophyletic groups of Dacnusini, i. e.

*Chorebus*, the *Dacnusa* genus-group, the *Coelinius* genus-group, *Chaenusa* and *Exotela*. In *Chorebus* *C. nydia* (NIXON) has 29—35 segments, *C. spenceri* sp. nov. 32—34 and *C. lugubris* (NIXON) 30—36: in the *Dacnusa* genus-group *Amyras clandestina* (HALIDAY) has 33—35 and *Dacnusa metula* (NIXON) 27—28: in the *Coelinius* genus-group *Laotris striatula* (HALIDAY) as 25—28 and *Synelix semirugosa* (HALIDAY) 33—37: *Chaenusa orghidani* BURGHELE has 20—25 and *C. punctulata* BURGH. 23: *Exotela hera* (NIXON) has 28—32 and *E. flavicoxa* (THOMSON) 28—34. From the above figures it seems reasonable to suppose that the plesiomorph mean number was something in the order of 26 to 34, but it is probably unwise to attempt to be more precise. I consider that species whose mean number lies outside this range may be characterised as apomorph in this respect.

In most species of Dacnusini the males have on average a few more antennal segments than the females. This is a general tendency in the Hymenoptera and is doubtless plesiomorph for the Alysiinae. But in *Tates heterocera* (THOMSON) and *Coelinius* spp. the dimorphism is exceptionally great and represents an apomorph character.

### (vi) Mesoscutum with distinct notaulices: largely bare with hairs only along the course of the notaulices and on its anterior face

Notaulices are a well-known feature of many Hymenoptera. In the Dacnusini they are well developed in many species belonging to *Chorebus*, the *Coelinius* genus-group and *Dacnusa*, but are weak or absent in many species in those same groups and in *Priapsis*, *Coloneura* and most *Chaenusa*. In the other Alysiinae I have examined well developed notaulices are shown by *Aphaereta*, *Cratospila circe* (HALIDAY), *Coelalysia bicolor* (SZÉPLIGETI), *Alysia punctigera* HALIDAY, two *Phaenocarpa* spp., *Tanycarpa aurora* (HALIDAY) and *Alloea contracta* HALIDAY. In view of this wide distribution in nearly all groups of Alysiinae and many other Braconids, the presence of well-developed notaulices must clearly be regarded as plesiomorph.

Most Dacnusini have pubescence over at least the middle lobe of the mesoscutum. But in other Alysiinae the mesoscutum is almost always bare and shining with hairs only along the course of the notaulices (of the species I have examined only the two *Tanycarpa* have pubescence over the central lobe of the mesoscutum). In this respect they agree with the great majority of Braconidae. It is clear therefore that the more extensive pubescence shown by many Dacnusini is an apomorph feature (see further below under "Evolutionary Trends"), and that the possession of a bare mesoscutum is plesiomorph.

### (vii) Mesepisternum with rugose precoxal suture extending more or less to its rear margin

A rugose precoxal suture, broad anteriorly and extending narrowly more or less to the rear margin of the mesepisternum (see fig. 27 and RICHARDS, 1956, fig. 35) is found in the other Alysiinae before me in *Alysia*, *Cratospila* and *Phaenocarpa* (except *P. tabida* (NEES)): in the Dacnusini this type of suture is found for instance in the *Chorebus nydia* group and widely in the *Coelinius* genus-group. In *Chaenusa*,

*Tates*, many *Chorebus* and *Exotela hera* (NIXON) the anterior part of the suture is narrower and the posterior part leading to the rear margin of the mesepisternum more or less smooth. A clearly apomorph feature derived from this is the long completely smooth suture shown by some *Chorebus* spp. (the *leptogaster* and *cytherea* groups and most species hitherto included in "*Chorebus*" in the restricted sense and "*Gyrocampa*").

I think it can be accepted that the extension of the suture towards the rear margin of the mesepisternum is plesiomorph on the grounds that the feature is shown by several disjunct groups: but it is not altogether clear from this distribution whether a broader or narrower form of suture is plesiomorph for the Dacnusini. But the presence of a broad suture in the other Alysiinae listed in the previous paragraph inclines me to the view that it is plesiomorph.

In *Coloneura*, *Protodacnusa tristis* (NEES), many *Chorebus* (the *lateralis*/*ovalis* complex), some *Exotela* and some *Dacnusa* the suture is shorter and does not extend towards the rear margin of the mesepisternum. Complete elimination of the suture is characteristic of many species of *Dacnusa*, *Priapsis dice* NIXON and one *Exotela* (undescribed).

### (viii) Metapleuron sparsely clothed with hairs which are directed downwards towards the coxa (fig. 16)

In the Alysiinae apart from the Dacnusini (except *Phaenocarpa tabida* (NEES) which has a completely bare metapleuron), hairs of the metapleuron occur sparsely and are directed downwards towards the coxa. Within the Dacnusini this condition is found in *Priapsis*, *Coloneura*, *Exotela*, *Tates*, *Protodacnusa*, *Chaenusa*, the *Coelinius* genus-group and widely in *Dacnusa*. Markedly different conditions are found in *Chorebus* and some *Dacnusa*, but they are not the same conditions. In some *Dacnusa* the pubescence of the metapleuron may be very dense indeed, but it remains directed mostly downwards towards the coxa (compare also *Amyras*). In most *Chorebus* however the hairs tend to be directed outwards around a raised area (smooth or with rugose sculpture) on the lower half of the metapleuron (figs. 22 and 23). This condition when fully developed is very characteristic and allows immediate diagnosis of a species as belonging to that genus. I think that the restricted distribution shown by these different conditions clearly establishes that they are apomorph, and that the plesiomorph condition is the one found widely in other Alysiinae, i. e. that the hairs of the metapleuron are sparse and directed downwards towards the coxa.

The interpretation of the presence or absence of sculpture on the metapleuron is not so clear. Many unrelated groups have the metapleuron more or less smooth, but the presence of obvious sculpture over at least the lower half is also widespread (in the material before me I have noted this in *Alysia*, *Coelalysia*, *Phaenocarpa*, *Pentapleura*, *Grandia* and *Alloea*, and among the Dacnusini in the *Coelinius* genus-group and *Chaenusa*). However the presence of a clearly defined rugose swelling in some *Chorebus* spp. can clearly be characterised as apomorph, as this feature is not found in other groups.

### (ix) Propodeum bare

Conspicuous pubescence of the propodeum is characteristic of *Dacnusa* and *Chorebus* and is associated with dense pubescence of the metapleuron (see above): as with the metapleuron the pubescence is of a different kind in the two genera and must be considered to have evolved separately. The great majority of Alysiinae and nearly all other Braconidae have a bare propodeum, so that this must clearly be regarded as a plesiomorph feature.

### (x) Petiole short (less than twice as long as broad), more or less bare

I do not think it possible to identify the plesiomorph form of petiole with any precision, as this part is subject to considerable variation in nearly all groups. But conspicuously elongate (more than twice as long as wide) forms of petiole can clearly be characterised as apomorph, as they are confined to *Chorebus, Chaenusa* and *Tates* among the Dacnusini and *Aspilota, Orthostigma, Prosapha, Cratospila* and *Tanycarpa gracilicornis* (NEES) among the other Alysiinae examined. The petiole is bare or almost so in the great majority of Alysiinae and this is clearly the plesiomorph condition. Only in three groups of Dacnusini which are strongly apomorph in other respects are extensively hairy petioles found. These are *Chorebus, Dacnusa* and the *Coelinius* genus-group. The pubescence is usually evenly distributed over the entire surface, but very characteristic apical tufts are formed in some *Chorebus* spp.

I am inclined to think that longitudinally striate sculpture of the petiole may be a plesiomorph feature, being found in many disjunct groups, but I do not wish to press this point in view of the obvious variation in this character between species and even individuals.

### (xi) 1m-cu widely rejected from cell $R_s$ (figs. 11 and 14)

It is clear from RIEGEL's (1949) study of Braconid wings that in the groundplan of the Braconidae 1m-cu[3] was received into $R_s + M$ before the separation of the distal segments of those veins (for descriptive purposes this condition is described as "1m-cu rejected from cell $R_s$"). This is very obviously the case for instance in *Helcon*, the Braconid genus possessing the most plesiomorph known wing in that it retains the anal cross-vein. Although apomorph conditions are widely distributed in other Alysiinae, the plesiomorph condition is retained by the great majority of Dacnusini. As the extreme condition — "trapping" of the distal segments of M by 1m-cu (fig. 13) — is a substantial change in the venation which must be assumed, in the absence of contrary evidence, to be irreversible, it clearly follows that in the ground-plan of the Alysiinae 1m-cu was rejected from cell $R_s$, as is the case with most Dacnusini and a few other genera. The more detailed distribution of these characters in the Dacnusini is as follows.

1m-cu is widely rejected from cell $R_s$ in the majority of species of all genera of Dacnusini except *Exotela*. In a number of species and species-groups (e.g. the *Dacnusa abdita* group (fig. 9) and *Chorebus merella* (NIXON) and a few related species) 1m-cu is rather closely approximated to cell $R_s$ or is interstitial, but these all

[3] Following RICHARDS (1956) I am calling the cross-veins 1m-cu and 2r-m, not 2m-cu and 3r-m as in RIEGEL (1949).

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fall within larger monophyletic groups containing species with 1m-cu widely rejected, so that the approximation of 1m-cu to cell $R_s$ must be considered to have evolved independently on a number of occasions. This same change is the primary character of the genus *Exotela* (fig. 12), but many species of this genus show a more extreme apomorph condition in which 1m-cu is received into cell $R_s$ (fig. 13). No other genus of Dacnusini shows this condition, but it occurs widely in other Alysiinae (e.g. *Prosapha, Orthostigma, Aspilota, Coelalysia, Pentapleura, Tanycarpa* and *Dapsilarthra apii* (Curtis)). In *Alysia* (except *A. punctigera* (Haliday)) and *Phaenocarpa* (except *P. tabida* (Nees)) 1m-cu is more or less interstitial. It is widely rejected from cell $R_s$, as in most Dacnusini, only in *Cratospila*, some *Dapsilarthra, Alysia punctigera* (Haliday) and *Phaenocarpa tabida* (Nees). It is probably necessary to assume convergent development of the extreme apomorph character (1m-cu received into cell $R_s$) outside the Dacnusini on at least three occasions (see below under "Evolutionary Trends").

### (xii) Cell 2Cu more or less closed, vein Cu$_1$ branching into Cu$_{1a}$ and Cu$_{1b}$ near the bottom of the cell (cf. fig. 3)

This condition is found widely in the Dacnusini (all species of *Dacnusa*, some *Chaenusa*, most of the *Coelinius* genus-group, most *Exotela* and some *Chorebus*). In the other Alysiinae before me it occurs in *Orthostigma pumilum* (Nees), *Aspilota* spp., *Alysia* spp. and some *Dapsilarthra* spp. It must clearly be accepted as the plesiomorph condition for the Alysiinae because it is the most usual condition in the Opiinae and many other Braconids, and the apomorph conditions found in the Alysiinae can easily be interpreted as simplifications of it. Furthermore it is noteworthy that the apomorph conditions found in the Dacnusini and in certain non-Dacnusine genera (*Cratospila, Coelalysia, Pentapleura, Phaenocarpa, Grandia, Tanycarpa, Trachyusa* and some *Dapsilarthra*) are not the same and have been evolved separately. The distribution of each apomorph character is, as would be expected, more restricted than that of the plesiomorph. See further below under "Evolutionary Trends".

### (xiii) Body length (excluding antennae) about 2–3 mm

The majority of Dacnusini (including nearly all the more plesiomorph species listed in the discussion of the number of antennal segments above) fall more or less within this size range. Exceptionally large species (notably *Coelinius* spp. which range up to 8 mm., and *Chorebus petiolatus* (Nees) which reaches 5 mm.) are all strongly apomorph in other respects. At the other end of the scale some very small species (in the 1.2–1.3 mm. range) are found in *Chorebus, Priapsis* and *Dacnusa*. In view of this distribution I think it reasonable to suppose that the plesiomorph size-range for the Dacnusini is something in the order of 2–3 mm., although it is not possible to be precise.

## Evolutionary Trends

The purpose of this section is to indicate certain widespread trends in the Dacnusini which give rise to similar or identical apomorph characters through convergence. The existence of a common evolutionary trend in different branches within

a monophyletic group may indicate some similarity in the genetic make-up of these branches. Such trends may therefore be valuable additional evidence in support of a group concept, although they do not admit of such precise analysis as the presence or absence of clear-cut apomorph characters. The taxonomist will also need to recognise such common trends as early as possible in his enquiry because they may have given rise to convergent apomorph characters which could lead him to misleading conclusions. In this section I have outlined some important evolutionary trends concerning the wing-venation and pubescence which are common to a number of the main branches of the Dacnusini. Two of these trends — the manner of reduction of vein $Cu_1$ and the tendency to develop extensive pubescence — are confined to the Dacnusini among the Alysiinae and thus lend support to the conception of the tribe as a monophyletic group. Finally two less important trends to eliminate certain thoracic sutures are briefly mentioned.

### (i) Wing Venation

The plesiomorph form (ground-plan) of wing venation in the Alysiinae was probably almost identical with the wing of *Opius caelatus* (HALIDAY) (Opiinae) figured at fig. 3. However it is not clear whether the pterostigma was elongate as shown or of a shorter form such as that figured for *Phaenocarpa ruficeps* (NEES) (fig. 4). The ground-plan of the Dacnusini thus differs from that of the Alysiinae by the loss of 2r-m and sinuation of vein $R_s$, and possibly also by the elongate pterostigma, if a short pterostigma belonged to the ground-plan of the Alysiinae (see the section headed "The Characterisation and Relationship of the Dacnusini").

The form of the pterostigma varies considerably and there does not appear to be a trend common to different groups of the Alysiinae. But there are two important trends in the wing-venation which produce convergent apomorph characters in different genera of Alysiinae. These are (a) reduction of veins $Cu_1$ and 1 a; and (b) "trapping" of the distal sections of M by 1m-cu, which takes on more of the appearance of a long vein.

The manner in which reduction of $Cu_1$ has occurred in the Dacnusini is different from that found in other Alysiinae. In the Dacnusini the transverse section of $Cu_1$ is always retained and the point of origin of $Cu_{1a}$ never migrates towards the junction of $Cu_1$ with 1m-cu; but the apical branches of $Cu_1$ ($Cu_{1a}$ and $Cu_{1b}$) tend to become weakened or lost, leaving cell 2Cu open at its lower distal corner (figs. 11 and 14). This tendency is found in many *Chorebus* spp., *Priapsis, Coloneura, Tates* and two *Protodacnusa* spp. In a few unrelated species 1a is also shortened. Many species of *Chorebus* however retain a closed cell 2Cu (for instance almost all the left-hand branch of the dichotomy of *Chorebus* on graph 1) and it is clear that the identical reduction found in other *Chorebus* spp. and *Priapsis* represents convergence. The open cell in the *Protodacnusa* species too must represent convergence, as the plesiomorph condition is retained in the other members of this genus (see Appendix VI).

Among other Alysiinae species which retain the closed cell 2 Cu from the ground-plan of the subfamily are in the minority. But the manner in which reduction has

occurred is in most cases by the migration of the base of $Cu_{1a}$ towards the junction with 1m-cu, followed only later by the weakening and loss of $Cu_{1b}$ and 1a. The following examples may be given of these two main stages (although there are of course many intermediate conditions);

(i) *Phaenccarpa pullata* (Haliday) and *Cratospila circe* (Haliday) in which $Cu_{1a}$ continues more or less directly from the junction of $Cu_1$ with 1m-cu, but cell 2 Cu, although much narrowed, remains closed apically by $Cu_{1b}$;

(ii) *Grandia cynaraphila* (Ricchello) (fig. 5), *Dapsilarthra balteata* (Thomson) (fig. 6) and *Aphaereta* spp. in which $Cu_{1a}$ is as stated above but the transverse segment of $Cu_1$ has been lost and 1 a shortened.

It is clear that the extreme condition in the latter three cases is the result of convergence because *Grandia* and *Dapsilarthra balteata* are each more closely related to species which are more plesiomorph in respect of cell 2Cu (e.g. *Phaenocarpa pullata* (Haliday) and *Dapsilarthra rufiventris* (Nees) respectively) than they are respectively to either of the remaining two genera which are apomorph in this respect.

The other important trend which manifests itself in several disjunct groups of Alysiinae concerns the junctions at the centre of the wing, where the plesiomorph condition is that $R_s + M$ first meets 1m-cu and then forks into the separate distal sections of $R_s$ and M. In the Dacnusini and to a lesser extent in other Alysiinae the veins are conspicuously weakened between these junctions. There appears to be a line of weakness running across the wing from the gap before the pterostigma through this junction. It is clear that in the ground-plan of the Dacnusini 1m-cu met $R_s + M$ well removed from the separation of the distal sections of those veins (figs. 11 and 14) (for descriptive purposes I describe this condition as "1m-cu remote from cell $R_s$"), but there is a tendency in several disjunct groups (see the section headed "Plesiomorph Characters") for the junction with 1m-cu to approach the bifurcation of $R_s$ and M. A further development of this is the "interstitial" condition, shown for instance by *Dacnusa abdita* Haliday (fig. 9), where the two junctions coincide. In many *Exotela* spp. a still more apomorph condition is found in that 1m-cu has "trapped" the distal segments of M and now functions as its base (fig. 13) (for descriptive purposes this is termed "1m-cu received into cell $R_s$").

In other Alysiinae this same tendency is widespread, the extreme apomorph condition shown by *Exotela* occuring in *Prosapha*, *Orthostigma*, *Aspilota*, *Coelalysia*, *Pentapleura*, *Tanycarpa* and *Dapsilarthra apii* (Curtis). Unfortunately it is not clear which of these genera can be associated with each other to form monophyletic groups, but I would certainly suppose a closer relationship of *Coelalysia* and *Pentapleura* to *Alysia* and *Idiasta* than to the other genera mentioned, and *Dapsilarthra* contains species which retain the plesiomorph form of these junctions. Thus convergence must be postulated on at least three occasions.

The tendency to reduce veins $Cu_1$ and 1a needs no special explanation in the context of the Alysiinae, as it is an instance of the almost universal tendency in the higher orders of insects to reduce the venation of the anal and cubital fields. The reason for the changes in the arrangement of the junctions at the centre of the

wing is not clear: they may be seen as a strengthening of the longitudinal element in the venation, or alternatively may be connected with the manner in which the wing is folded before emergence.

### (ii) Pubescence

Braconids are typically bare and shining insects. In the ground-plan of the Alysiinae hairs on the mesoscutum were confined to the notaulices and its anterior face, and the metapleuron was at most sparsely haired. The propodeum, petiole, gastral tergites, mesepisternum and head were completely or almost bare. Apart from the Dacnusini the other Alysiinae have changed little in this respect (of the genera I have examined only *Tanycarpa* shows pubescence over the central lobe of the mesoscutum).

The ground-plan of the Dacnusini is unchanged from that of the Alysiinae but there is throughout the tribe a strong tendency in all the major groups to develop more extensive pubescence. This manifests itself very commonly on the mesoscutum and the majority of Dacnusini have pubescence over at least its central lobe. The development of pubescence on other parts varies between the different groups. In the *Coelinius* genus-group the thoracic pubescence does not show any striking changes, but in *Coelinius* and *Aristelix*, and to a lesser extent in *Symphya* and *Epimicta*, the entire surface of the gaster is densely covered with short hairs. In *Dacnusa* there is a complete range of variation from largely bare forms to the highly apomorph species of the *areolaris* group, which have long dense pubescence covering their metapleuron, propodeum and petiole. *Chorebus* shows a still more extensive range of variation. Apomorph conditions of the pubescence and sculpture of the metapleuron are of considerable importance in recognising the genus. The mesoscutum varies from being largely bare to very densely pubescent, and there is a wide range of variation in the pubescence of the propodeum and petiole. Characteristic apomorph conditions of the latter are the "apical tufts" exhibited by many species and the fringe of outwardly directed hairs found only in the *cytherea* group. In some species the sides of the pronotum (e.g. *C. misellus* (MARSHALL)) or the back of the head (e.g. many species of the *senilis* group) are clothed with dense pile. Dense tufts of hair on the hind coxae are characteristic of many species in the lefthand branch of the dichotomy of the genus on graph 1 and, presumably by convergence, in a very few species (e.g. *C. nana* (NIXON)) of the *lateralis/ovalis* complex.

Thus although the tendency to develop extensive pubescence is very widespread in the Dacnusini and a good deal of convergence has occurred in the development for instance of the mesoscutal pubescence, the parts of the body affected and the type of pubescence developed is characteristically different in the apomorph species of the different genera. Some excellent apomorph characters which are of major importance for the classification are derived from the pubescence.

### (iii) Sutures of mesoscutum and mesepisternum

The prescutal sutures or notaulices are weak or suppressed in many groups of Alysiinae, undoubtedly in many cases as a result of convergence. In the Dacnusini

all groups except *Priapsis* and *Coloneura* contain species with well-developed notaulices retained, but there are many in which they are weak or lost. The tendency to eliminate the notaulices is particularly strong in *Chaenusa* and *Dacnusa*, where they have been lost by the majority of species.

The variation in the precoxal suture has been outlined in the section headed "Plesiomorph Characters". There is a strong tendency to eliminate this suture in *Dacnusa* (it is completely lost in the majority of species), but this is not general in the other main groups of Dacnusini. However *Priapsis dice* NIXON and an undescribed *Exotela* sp. have also lost this suture.

## Nixon's (1943) Separation of a Tribe "Dacnusini" within his Subfamily "Dacnusinae"

NIXON (1943) separated his tribe "Dacnusini" from the rest of his "Dacnusinae" on the grounds that the hairs of at least tergites 5 to 7 were arranged more or less to form a row on each segment. But the arrangement of hairs in single rows on the gastral segments, being found in almost all other Alysiinae and many other Braconidae, is beyond doubt plesiomorph. In a phylogenetic system such characterisation is unacceptable.

What then is the relationship between the genera included in NIXON's Dacnusini and those exluded ? I think the simplest way to approach the problem is to consider one obviously apomorph character which is found in all the excluded genera[4] — the extension of longitudinal striation similar to that of the petiole over tergite 3 (tergite 2 in NIXON's terminology). This feature is also shown by two genera included by NIXON in his Dacnusini — *Ectilis* and *Laotris* — and two species attributed to *Chorebus* by STELFOX (1957) — *striolus* STELFOX and *scabrifossus* STELFOX. The question now to be answered is whether other characters support the association of some or all of these genera in a monophyletic group, or whether there is reason to suppose that this striate sculpture has been evolved more than once.

If STELFOX was right in ascribing his two species to *Chorebus*, their evolution of longitudinal striation on tergite 3 must be considered independent, because the genus *Chorebus* is a monophyletic group, the majority of whose species are plesiomorph in that they lack this feature. If on the other hand these species form a monophyletic group with other species showing longitudinal striation of tergite 3, then their reduction of the labial palpi to three segments must represent convergence with certain *Chorebus* spp. Through the kindness of Mr. A. W. STELFOX I have examined these species and am satisfied that they are correctly included in *Chorebus*. They possess the typical metapleural pubescence of that genus and similar mandibles to the group of species hitherto known as "*Chorebus*" (in the restricted sense) and "*Gyrocampa*". Their independent evolution of longitudinal striation of tergite 3 has been associated with the development of extensive sculpturation on other parts of the body, particularly the frons, mesoscutum and mesepisternum.

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[4] Except some *Coelinius* spp. where its loss seems to be secondary.

But the evidence for the other genera supports their association in a large mono-phyletic group. *Laotris striatula* (HALIDAY) is in most respects a plesiomorph species, but it possesses an unusual mandible which shows a small additional tooth before the original tooth 2 (fig. 37). This agrees with some species of *Coelinius*, which were excluded from NIXON's "Dacnusini". *Synelix* (= *Ectilis*) has two obvious apomorph features — an evenly curved $R_s$ and a female gaster which is strongly laterally compressed towards its apex — which are both shared with *Sarops rea* NIXON, which was excluded from the "Dacnusini". I think it untenable to place these species in different tribes, and I have proposed below their inclusion in the same genus.

The genus *Coelinius* stands well apart from the other genera by reason of its wing venation, but the plesiomorph form of mandible for the genus seems identical with that of *Laotris*. *Aristelix* agrees with *Coelinius* in respect of its densely pubescent gaster, but retains a more plesiomorph wing venation. The two remaining genera, *Symphya* and *Epimicta*, are similar to *Coelinius* in respect of their wing venation (fig. 8) and gastral pubescence, although this may be the result of convergence (see below). But there is no evidence that they are more closely related to any other group than to the other genera showing sculpture of tergite 3.

To summarise, it appears certain that longitudinal striation of tergite 3 has been evolved independently by two species of *Chorebus*, but there is no reason to think that the other genera exhibiting this feature do not form a monophyletic group. I will therefore refer to them as the *Coelinius* genus-group. This I consider to be one monophyletic group within my Dacnusini (the equivalent of NIXON's "Dacnusinae"). A more detailed discussion of this group is found below.

### Genera excluded from the Dacnusini

There are three European genera, each with a single species, which have recently been attributed to the "Dacnusinae" but are excluded from my Dacnusini. These are *Grandia*, *Pterusa* and *Lodbrokia*. The reasons for this action are as follows.

#### (i) *Grandia cynaraphila* (RICCHELLO)

This species has two apomorph features of the wing-venation (fig. 5) which do not occur in the Dacnusini. These are the large spindle-shaped pterostigma which is abruptly cut off apically, and the reduction of the veins $Cu_1$ and 1a (the branch $Cu_{1b}$ and the transverse segment of $Cu_1$ which normally close the distal end of cell 2Cu have been lost, and $Cu_{1a}$ continues more or less directly from the longitudinal segment of $Cu_1$: vein 1a is shortened so that the former cell 2Cu is completely open below).

Similar pterostigmata are found in the material before me in *Alysia, Cratospila, Coelalysia, Pentapleura fuliginosa* (HALIDAY) and *Phaenocarpa* (fig. 4) (except *P. tabida* (NEES)). Furthermore in all these groups except *Alysia* there is a distinct approach to the condition of vein $Cu_1$ shown by *Grandia* (see above under "Evolutionary Trends"). The nearest approach of all to the venation of *Grandia* is shown by *Phaenocarpa pullata* (HALIDAY) which has a similarly short cell $2R_1$.

I therefore suspect that the affinities of *Grandia* lie with *Phaenocarpa* and its allies, and that its loss of vein 2r-m has been independent of that of the Dacnusini.

The characters put forward by Nixon (1954) to support his inclusion of this species in his Dacnusini — the form of the clypeus and the arrangement of the abdominal hairs — are both plesiomorph.

### (ii) *Pterusa crassiceps* (Fischer)

This is a brachypterous species with highly modified wing venation ascribed by Fischer (1958) to the Dacnusinae. I can see no similarity to the venation of the Dacnusini and suggest that the affinities of this species should be investigated in the context of the other brachypterous or apterous genera, in particular *Alloea contracta* (Haliday). Mr. Karl-Johan Hedqvist informs me (personal communication) that some males of *Alloea* have identical wing venation to that Fischer describes.

### (iii) *Lodbrokia hirta* Hedqvist

This is an apterous species which was ascribed by Hedqvist (1962) to the Dacnusinae, although he in fact compares it with the other apterous or brachypterous genera. *Lodbrokia* is remarkable in possessing a mandible with about 7 teeth, but this does not resemble the condition found in any of the Dacnusini and is doubtless an independent development. I can see no other character which might suggest the inclusion of this species in the Dacnusini.

## The *Coelinius* genus-group

The *Coelinius* genus-group is established as a monophyletic group by the extension of longitudinal striation or sculpture similar to that of the petiole over the surface of tergite 3. The absence of this feature in a few *Coelinius* spp. is considered to be secondary, as it is shown clearly by the majority of species in the genus. The condition found in *Chorebus talaris* (Haliday), where rugose sculpture is found at the extreme base only of tergite 3, has clearly been evolved independently, as the mandibles of this species clearly show that it is a *Chorebus*. Other noteworthy features of this group (although I am not able to characterise them as apomorph or plesiomorph) are the strongly sculptured metapleuron with evenly distributed pubescence which shows little variation between the different genera of the group, and the tendency for 2r to branch off from the pterostigma well distal of its base. The mandibles exhibit various apomorph features, and no species retains the simple 3-toothed form which is plesiomorph for the Dacnusini. All genera of this group show a more or less clear separation of tergites 3 and 4.

The *Coelinius* genus-group appears easier to classify than most of the Dacnusini as its members show no lack of apomorph characters. Because of their considerable diversity of appearance their affinity with each other has not generally been recognised, and the number of genera accepted has in my view been excessive and out of proportion with the classification of the rest of the Dacnusini. I am therefore proposing to amalgamate certain genera which have been considered separate by previous authors.

The most obviously plesiomorph genus of the group is *Laotris*, erected by NIXON (1943) for the single species *L. striatula* (HALIDAY). This species retains the short abdomen which is typical of most Dacnusini attacking leaf-mining Agromyzidae and is probably plesiomorph for the Dacnusini as a whole: the hairs are confined to single bands on each segment, as in the vast majority of Alysiinae. It is also the only species in the *Coelinius* genus-group which is known to be a parasite of a leaf-mining Agromyzid, a long series having been bred by the late FRANZ GROSCHKE from *Cerodontha (Dizygomyza) effusi* (KARL) on *Juncus effusus* L. There is reason to believe that this biology is primitive (see under "The Connection between Phylogeny and Host Association" below). But the form of mandible is unusual in that an additional tooth has been developed between the original teeth 1 and 2 (fig. 37): in this respect it resembles the plesiomorph form for *Coelinius*.

The name *Synelix* is used here to include the species attributed to *Ectilis* NIXON and *Sarops* NIXON. The genus in this new wide sense is established on the following apomorph characters: (i) $R_s$ not sinuate but evenly curved throughout; and (ii) female gaster very elongate, strongly laterally compressed towards its apex. These species lack the dense pubescence of the gaster found in other genera of the *Coelinius* genus-group (except *Laotris*), but the apical gastral tergites tend to have more than one row of hairs. The mandibles of this genus are distinctly apomorph, dominated by a large tooth 2, and it is not clear whether they can have evolved from the 4-toothed *Laotris* type, as appears to be the case with *Coelinius*. BURGHELE (1960 b) figures a clearly 4-toothed mandible for her *"Ectilis" brevicornis*, but unfortunately the position of the additional tooth is not clear, as she does not state which mandible has been figured. The biology of one *Synelix* sp. is known, *S. semirugosa* (HALIDAY) having been bred from the Cordylurid *Amaurosoma armillatum* ZETTERSTEDT.

Apart from *Laotris* and *Synelix* all the remaining genera of this group are characterised by more extensive pubescence of the gaster. A single species of unknown biology, *Aristelix phaenicrura* (HALIDAY), retains a largely plesiomorph wing venation, but has characteristic apomorph very small mandibles. The remaining genera (three are here recognised — *Coelinius*, *Epimicta* and *Symphya*) are all further characterised by the short broad pterostigma (fig. 8), but it seems likely that this represents convergence in the case of *Coelinius* as *Symphya* and *Epimicta* retain a relatively short gaster, which is not laterally compressed in the female. The elongate form of gaster, strongly laterally compressed in the female, which is shown by *Coelinius* suggests a closer relationship with *Aristelix* and *Synelix*, and this is supported by the known host association of the latter genus with a Gramineae-feeding Dipteron. The association of *Symphya* in a monophyletic group with *Coelinius* would probably imply that the association of *Symphya* with *Phytobia* spp. had been reached by way of an association with some non-Agromyzid Gramineae-feeding Dipteron. It seems more reasonable to suppose convergent development in the wing venation, as is implied by the arrangement given on graph 1.

*Coelinius* is characterised as a monophyletic group by the form of the pterostigma, the elongate gaster and the strong sexual dimorphism in the number of antennal segments (a mean difference of at least 6, often much more). The large

size (up to 8 mm.) is also a characteristic feature of many species. In most species the clypeus is clearly projecting beyond the face in profile, and in *C. liparae* (GI-RAUD) it is still more strongly projecting as a thickened lamella. The development of sculpture on tergite 3 is variable: in *C. anceps* (CURTIS) strong longitudinal striation is present on the base of that tergite, but in many species it bears only shallow rugose sculpture or punctulation: in a few species tergite 3 appears completely smooth. This reduction is considered to be secondary as *C. anceps* (CURTIS), which shows strong striation of tergite 3, is in other respects the most plesiomorph species.

The mandibles of *Coelinius* are of fundamental importance for my interpretation of the *Coelinius* genus-group as a whole. In most species the mandibles appear more or less 3-toothed, dominated by the large elongate tooth 2. This is an apomorph condition which is not to be confused with the plesiomorph form of mandibles for the Dacnusini, which is not retained by any member of the *Coelinius* genus-group. It is my view that these mandibles are secondarily 3-toothed and derived from the type of mandible shown by the plesiomorph species *C. anceps* (CURTIS), in which a well-defined additional tooth can be seen between the original teeth 1 and 2. Through kindness of Mr. A. W. STELFOX I have been able to examine a wide range of species of the subgenus *Coelinidea* and have found two — *C. procera* HALIDAY and an unidentified species — in which some indication of this additional tooth can clearly be seen. The importance of establishing this point lies in this form of 4-toothed mandible being virtually identical with that of *Laotris*. The presence of the same feature in the ground-plan of *Coelinius* is thus an important piece of evidence for my conception of the *Coelinius* genus-group.

The species of *Coelinius* all show a high degree of morphological similarity in other respects apart from the apomorph characters, and there seems little doubt of their monophyly. All are as far as known parasites of Chloropidae, and are the only Dacnusini known to me to be parasites of that family. It has been the custom to divide the group into three genera — *Coelinius* s. s. (= *Chaenon*), *Coelinidea* (= *Eriocoelinius*) and *Polemochartus* (= *Polemon*). This division may be tenable in a phylogenetic system, but I have preferred to establish my genus at a higher level, as this seems to me to correspond better with the generic level I have taken for other groups of Dacnusini. In addition there is a danger that the division may break down if further relatively plesiomorph species are discovered, because the characterisation of *Coelinius* s. s., now based on a single species, seems plesiomorph for the genus. I have decided therefore to reduce these concepts to subgenera. *Coelinidea*, containing many species, is clearly a monophyletic group, distinguished from the ground-plan of the genus by its evenly curved vein $R_s$. The two remaining subgenera are plesiomorph in retaining a sinuate $R_s$. *Polemochartus*, containing two species both parasites of *Lipara*, has several distinctive apomorph features, including its clypeus which projects as a thickened lamella, the extension of longitudinal striation onto the base of tergite 4 and its large, broad petiole. *Coelinius* s. s. however contains only a single species which appears to be plesiomorph in all these respects, unless its elongate petiole represents synapomorphy with *Coelinidea*.

The genus *Symphya* is plesiomorph in respect of the clypeus and antennae, but characterised by the broad pterostigma (fig. 8), a spiniform projection on the postscutellum, the large tergites 3 and 4 (covering at least two-thirds of the gaster beyond the petiole) and the strong 4-toothed mandibles (it is unfortunately not clear which is the additional tooth). The latter two characters are probably connected with the unusual biology of the genus — its species are parasites of *Phytobia* s. s. (= *Dendromyza* HENDEL) (Agromyzidae) whose larvae bore in the cambium of trees.

The single species of *Epimicta* known to me, *E. marginalis* (HALIDAY), might perhaps be included in *Symphya* as the most plesiomorph species of that genus, as it possesses a small but distinct spur on the postscutellum. NIXON (1943) considers that it is closely related to *Symphya* and forms with it a "natural group". Tergites 3 and 4 are not enlarged as in *Symphya* and the mandibles are different, showing a wide blunt tooth 3. The former feature is plesiomorph and the latter apomorph, so that it is possible that *Symphya* and *Epimicta* can be justified as sister-groups. I have thought it preferable to leave the existing nomenclature unchanged and accept *Epimicta* provisionally as a distinct genus. Its host association is unfortunately unknown.

### *Chaenusa* HALIDAY

The genus *Chaenusa* sensu lato is well characterised as a monophyletic group by the hairy eyes — an apomorph character found only in this group among the Alysiinae. The form of the pterostigma is also a clearly apomorph feature: although varying from species to species it is always distinctly broader than is normally the case in the Dacnusini (other exceptions are *Coelinius*, *Symphya* and *Epimicta* in the *Coelinius* genus-group, *Chorebus ampliator* (NEES) and *Tates heterocera* (THOMSON)).

Hitherto it has been the custom to divide this group into two genera — *Chorebidea* and *Chaenusa* — and RIEGEL (1950) has proposed a third, *Chorebidella*, for the American species *bergi* RIEGEL. This subdivision causes difficulty because the definition of *Chaenusa* which it entails — 4-segmented labial palpi and cell 2Cu closed below by a vein (see RIEGEL, 1950) — is completely plesiomorph. (RIEGEL also gives the form of the pterostigma as a character, but the species since described by BURGHELE (1960a) do not differ significantly in this respect from *Chorebidea*.) I can therefore see no reason to believe that *Chaenusa* in the customary restricted sense is a monophyletic group, and cannot accept the concept for a phylogenetic system of classification. If the subdivision of *Chaenusa* s. l. is to be retained, it is clear that its basis needs revision.

Apart from the question of the validity of the existing subdivision, I prefer on more general grounds to include all this group in a single genus *Chaenusa*. The number of described species is less than twenty. The life-history of most of them is known, and these are all parasites of the single host genus *Hydrellia* (Ephydridae). To subdivide this small well-defined group into a number of genera seems to me unnecessary and probably involves using the generic concept at a lower level than in most other groups of Dacnusini.

*C. conjungens* (NEES) and *C. bergi* (RIEGEL) show a degree of sexual dimorphism of the pterostigma. But, as this is not the case with all species, it is probably to be regarded as an independent development, not representing synapomorphy with *Dacnusa*.

### *Chorebus* HALIDAY

The generic name *Dacnusa*[5] was widely used before NIXON's work to include all Dacnusini which did not fall within any of the other recognised genera, which were all small strongly apomorph groups. For instance SCHMIEDEKNECHT (1930) included in *Dacnusa* all my *Dacnusa* except "*Liposcia* FÖRSTER" (i. e. the male sex only of *Dacnusa discolor* (FÖRSTER)) and much of *Chorebus* in the sense proposed in this paper. The disentanglement of these two heterogeneous groups from each other is perhaps the most important advance made in NIXON's (1943) generic system. But in spite of this very considerable improvement he states (1944, Ent. mon. Mag., 79, 159) "it could not be claimed that *Dacnusa* (i. e. most of *Chorebus* in the sense of this paper), as defined above, is a homogeneous unit".

The important apomorph feature characterising NIXON's "*Dacnusa*" is, as given in his key, the form of the mandibles (figs. 24 and 25), which show an additional tooth arising from the base of tooth 2 between the original teeth 2 and 3. The strength of this tooth varies in different species and individuals: sometimes it is as large as tooth 2 so that the mandibles are fully 4-toothed, but often it is no more than a projection arising from the base of tooth 2. In a few species, for instance *Chorebus resa* (NIXON) and *C. transversa* (NIXON), the mandibles of many individuals appear completely 3-toothed, but this must be secondary reduction as the affinity of these species is clear on other characters. I fully support NIXON's view of the importance of the form of the mandibles and am using this as the primary character to define my *Chorebus* (including NIXON's *Chorebus*, *Gyrocampa*, *Etriptes* and most *Dacnusa*). The elongate mandibles (fig. 26) of the species formerly included in the first two genera are clearly secondary, as a number of intermediate conditions between this and the plesiomorph 4-toothed mandibles are found (e. g. "*Gyrocampa*" *affinis* (NEES)).

Another characteristic feature of the majority of species in this genus is the dense adpressed pubescence of the propodeum and metapleuron. NIXON (1943) in his key gives "Propodeum invariably densely clothed with coarse woolly pubescence which completely obscures the surface of the sculpture beneath or, if the outstanding rugosities are visible, then the hairs form a closely adpressed greyish pubescence . . ." as a character of his "*Dacnusa*", although he included in the genus certain species (e. g. the *nydia* group) to which that description does not apply. I have preferred to place more emphasis on the pubescence of the metapleuron for descriptive purposes, because I think it can be described more intelligibly than that of the propodeum, and can be figured in what I hope is a recognisable fashion. The development of dense metapleural pubescence is clearly linked

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[5] I regret that the unfortunate change in the application of the name *Dacnusa* may have made this passage difficult to follow. The interplay of *Dacnusa* and *Chorebus* in two senses has been unavoidable.

with that of the propodeal, so that this difference of treatment is largely one of description not interpretation.

In the majority of species in NIXON's "*Dacnusa*" the metapleural pubescence is of a very characteristic apomorph type. The lower part of the metapleuron bears a more or less raised swelling or callus which is surrounded by a very dense fringe of short radiating hairs (figs. 22 and 23): the centre of the swelling, which may be smooth or rugose, often bears a few longer outstanding hairs but is sometimes almost bare. All the species which show this feature also have dense adpressed propodeal pubescence. The "genera" *Chorebus* (in the restricted sense), *Gyrocampa* and doubtless also the recently described *Paragyrocampa* (although I have seen no specimen) are synapomorph with the majority of NIXON's "*Dacnusa*" in these respects, and they can be united in a wide monophyletic group with the *cytherea, senilis, leptogaster, gracilis* and *merella* groups of "*Dacnusa*" (see below). The customary concept of "*Chorebus*" amounts in fact to breaking off a small group of more obviously apomorph species from a larger whole which is rendered heterogeneous thereby. This is not acceptable in a phylogenetic system. The definition of *Gyrocampa* is very obviously untenable as it consists of a curious com-bination of apomorph characters which are shared with "*Chorebus*" (the evenly curved radius and elongate mandibles) and plesiomorph features such as the bare mesoscutum and 4-segmented labial palpi (except *G. miodes* NIXON). The form of the precoxal suture and the hind-coxal tufts are good apomorph characters but are shared with many of the "*Dacnusa*" groups just mentioned and cannot therefore justify the existing conceptions of "*Chorebus*" or "*Gyrocampa*". "*Chorebus*" has been further defined by its 3-segmented labial palpi and dense pubescence of the mesoscutum, but, as there are "*Gyrocampa*" species which possess each of these characters (i. e. *miodes* NIXON and *lanigera* STELFOX), this definition is not even satisfactory for a non-phylogenetic system of classification. Thus apart from my objection to the separation of *Gyrocampa* and "*Chorebus*" as being unacceptable in a phylogenetic system of classification, the concepts have already been breaking down because of the difficulty of incorporating new species into them, and there can be no objection on grounds of practical convenience to formally abandoning them. The name *Chorebus* is therefore used in this paper in a wider sense to include most of NIXON's (1943—54) "*Dacnusa*" and the whole of his *Etriptes, Gyrocampa* and *Chorebus*. (The application of the name *Dacnusa* to this group is formally invalid.)

The detailed classification of my *Chorebus* as now defined is difficult because of the lack of clear-cut apomorph characters in many species of the genus. But there appears to be a fundamental dichotomy.

The species included by NIXON (1943—54) in his *senilis* (except *C. fallax* (NIXON)), *lepiogaster, cytherea, gracilis* and *merella* groups, the "genera" *Chorebus* and *Gyrocampa*, and *C. petiolatus* (NEES) appear to be a monophyletic group although clear-cut justification in terms of apomorph characters is lacking. All the species I include in this group have cell 2Cu closed at its lower distal corner by a clearly-developed vein $Cu_{1b}$ (fig. 15) (except for *C. nixoni* BURGHELE in which the

vein closing the cell beneath has been lost) and vein $R_s$ generally only feebly, if at all, sinuate. Within this group the *senilis*, *leptogaster*, *cytherea* and *gracilis* groups, "*Gyrocampa*" and some "*Chorebus*" all show a very long narrow precoxal suture (rugose in the *gracilis* and *senilis* groups but smooth in nearly all species in the other groups)[6] and well developed tufts of hair on the hind coxae. *C. merella* (NIXON) and a few related species (including *C. transversa* (NIXON)) are plesiomorph in these respects but are connected by intermediate species with the *cytherea* group (all being parasites of the single host subgenus *Dizygomyza*). I therefore regard the *merella* group as rightly associated with the others but being probably the most plesiomorph group. NIXON's *gracilis* group consists of two species agreeing with his *senilis* group but characterised by the additional apomorph character of the long laterally compressed female gaster. The evolution of this latter feature has probably been connected with a change in host association from stemboring *Melanagromyza*-species, the hosts of the *senilis* group, to the larger stemborer *Psila* (Psilidae). *Chorebus petiolatus* (NEES) is a species of unknown life-history, which can hardly be an Agromyzid parasite on account of its large size. I have little doubt that it is related to the *senilis*-group. The individuals which I have examined show a tuft of hairs on their hind coxae, approaching the condition in that group and a number of species in that group have like *petiolatus* markedly elongate petioles. I also suspect that *C. abnormiceps* (NIXON) is related to the *senilis* group, but this opinion will require checking: this species shows no trace of hind-coxal tufts.

A suggested outline phylogeny for this part of *Chorebus* is given on graph 1. The definition and delimitation of the groups used (after NIXON, 1943—54) may need some revision, but I have thought they are a sufficiently good approximation for this present purpose. The arrangement given postulates that the smooth form of precoxal suture has been evolved twice as I have associated the *leptogaster* group with the *senilis* group, not with the other groups with a smooth suture. The reason for this is that the *senilis* and *leptogaster* groups have a very distinct biology in that they are all parasites of *Melanagromyza* and *Ophiomyia* spp. (mainly stemborers, stem-miners and gall-causers) and to split such an apparently homogeneous group appears unnatural. NIXON's inclusion of a species with a rugose suture in his *leptogaster* group would also imply the independent evolution of the character in question.

The second half of my dichotomy of *Chorebus* may be broadly termed the *lateralis/ovalis* complex, using NIXON's (1943—54) group names. These species retain an obviously sinuate vein $R_s$, but are characterised by the apomorph form of cell 2Cu in that vein $Cu_{1b}$ is feeble or lost so that the cell is widely open at its lower distal corner (fig. 14). I include here all the species included by NIXON in his *lateralis* and *ovalis* groups, *resa* (NIXON), *diremtus* (NEES), *aphantus* (MARSHALL), *iphias* (NIXON), *atis* (NIXON), *abaris* (NIXON), *thecla* (NIXON), *tamiris* (NIXON), *nana* (NIXON), *fallax* (NIXON), *innana* (NIXON), *dagda* (NIXON), *albipes* (HALIDAY), *misellus* (MARSHALL), *sativi* (NIXON), *rufimarginatus* (STELFOX) and *solstitialis* (STELFOX). This complex contains large numbers of species often poorly characterised, many of

[6] The very broad rugose suture shown by *Chorebus striolus* STELFOX and *C. scabrifossus* STELFOX may be secondary as it is associated with an extensive development of sculpturation on the head, mesoscutum and tergite 3.

which are undescribed. They are all as far as known Agromyzid parasites, mainly of leaf-mining species. In view of the difficulty of delimiting and identifying the species it is desirable that bred material should be used as far as possible for designating types so that the specific names are linked with known biologies. The further subdivision of this group is problematical. NIXON's "*ovalis* group" was acknowledged to be heterogeneous. The species in his "*lateralis* group" (with which I also associate *C. resa* (NIXON)) are characterised by their elongate antennae, but it is unfortunately not possible to draw a clear-cut distinction on the basis of this character. The other character he gives — the evenly distributed pubescence of the petiole — may be an intermediate stage between the sparsely haired petiole of some species (e. g. *C. lugubris* (NIXON)) included in his *ovalis* group and the characteristic apomorph condition found in others where not only is the petiole densely haired but dense apical tufts are formed. Nevertheless in spite of the weakness of its morphological justification the *lateralis*-group concept appears to be a natural one in terms of biology as all its members are parasites of *Agromyza*. In general the *lateralis/ovalis* complex appears lacking in clear-cut apomorph characters which would allow the phylogeny of the group to be established in detail.

I do not intend to elaborate any subdivision here, but it is useful for the purposes of the discussion below on "The Connection between Phylogeny and Host Association" to indicate which species are probably the most plesiomorph members of this group. The development of the pubescence of the mesoscutum and propodeum varies considerably between different species of the group and in terms of these characters the most plesiomorph species appear to be *lugubris* (NIXON), *angelicae* (NIXON), *glabriculus* (THOMSON) and *raissa* (NIXON) (corresponding to the *raissa* group of NIXON, 1937). The hosts of these species are *Agromyza albipennis* MEIGEN, *Phytomyza angelicae* KALTENBACH, unknown and *Cerodontha (Dizygomyza) iraeos* (ROBINEAU-DESVOIDY) respectively. Thus not a very clear picture emerges, though the association of two species with *Agromyza* and *Dizygomyza* does not conflict with the situation in other groups.

It is probable that these two main divisions of my present *Chorebus* may eventually be recognised as genera or subgenera, but I have refrained from making any nomenclatorial proposals at this stage because I am very conscious of the limitations of our present knowledge of these groups and have no wish to impose what might prove a premature generic structure on them before the fauna of other areas of the world outside Europe is better known.

Apart from these two main groups there were some fifteen other species included by NIXON (1943—54) in his "*Dacnusa*". Three of these were in my opinion misplaced (the reasons are set out below under the heading "Species excluded from *Chorebus*"); the remaining twelve possess the characteristic mandibles of *Chorebus*, but are plesiomorph in respect of the absence or poor development of the metapleural rosette which is so characteristic of most species in this genus. A further species — *talaris* (HALIDAY) — was raised by NIXON to generic rank although he states (NIXON, 1954) "it is doubtful if this genus has any genuine validity . . .

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I exclude the single species *talaris* from *Dacnusa* solely on its having the base of tergite (2 + 3) rugulose". The rugulosity at the base of tergite 3 (NIXON's 2) is a distinctive apomorph character of this single species but I see no grounds for maintaining a separate genus on this account in a phylogenetic system (for this it would be necessary to indicate some plesiomorph character which justified this species as the sister-group of *Chorebus*). The characters of the mandibles and metapleura (fig. 20) in particular are similar to those of the *Chorebus nydia* group.

As well as *talaris* and the *nydia* group, other species with a conspicuous rugose swelling on the lower half of the metapleura are *phaedra* (NIXON) and *rhanis* (NIXON). All these species show no tendency to develop a fringe of hairs around the metapleural swelling, and any hairs that may be present are more or less evenly distributed over it. They also all lack the dense propodeal pubescence characteristic of most *Chorebus* spp. They are in my opinion the most plesiomorph species in the genus and are therefore of considerable interest for my study of the connection between phylogeny and host association. A key to these species is given in Appendix III. The small aberrant *freya* (NIXON), whose metapleura are largely bare (fig. 19), is also included in that key.

Another small group outside my main dichotomy of *Chorebus* is represented by three species *cyclops* (NIXON), *cybele* (NIXON) and *didas* (NIXON) which stand well apart from the rest by reason of their elongate form and narrow mandibles. Their densely haired propodeum approaches the condition of most other *Chorebus*, but their metapleural pubescence (fig. 21) is highly plesiomorph, more or less evenly distributed with only a weak tendency towards differentiation in the direction of the hairs. The resemblance between *cybele* and *didas* and the *senilis*-group because of their elongate facies is in my view misleading and to be classed as convergence. Both groups are *Melanagromyza*-parasites, but there is a completely clear-cut distinction between them in respect of their metapleural pubescence and the pubescence of the hind coxae.

There remain five species of doubtful affinity — *acco* (NIXON), *thusa* (NIXON), *myles* (NIXON), *anita* (NIXON) and *ampliator* (NEES) — whose metapleuron bears only a poorly defined more or less smooth swelling, but its pubescence shows a distinct tendency to form a partial rosette at least around its lower or posterior edge. The existence of these species has made me unable to draw any clear-cut distinction between the bulk of *Chorebus* and the more plesiomorph groups, and for that reason I am retaining a very wide generic concept.

## Species excluded from *Chorebus*

Three species were included by NIXON (1943—54) in his "*Dacnusa*" which I am excluding from *Chorebus*. The reasons for this action are as follows.

(i) *Priapsis ate* (NIXON) **comb. nov.** When NIXON (1943) described this species he had assumed that the sole specimen had 4-toothed mandibles, but in his later description (NIXON, 1946) corrected this to 3-toothed. I have examined the holotype (now unfortunately headless) and confirmed that the pubescence of the metapleuron is plesiomorph (evenly distributed and directed downwards towards the

coxa). The species thus lacks any apomorph character which would include it in *Chorebus*. The open cell 2Cu and the short maxillary palpi agree with the characterisation of the genus *Priapsis*, where I believe this species should be placed.

(ii) *Exotela interstitialis* (THOMSON) (= *Dacnusa mamertes* NIXON, see Appendix V). The generic position of this species is difficult. Its metapleuron is plesiomorph, agreeing completely with that of *Exotela flavicoxa* (THOMSON) (fig. 16), but the mandibles have more than three teeth (fig. 35). If the mandibles are taken as a modification of the type characterising *Chorebus* this species might be included in that group as the only species retaining a plesiomorph form of metapleural pubescence. But on the other hand no member of that genus has mandibles closely resembling those of *interstitialis* and it seems likely that this condition has arisen independently by indentation of the original tooth 3. The species has two undoubtedly apomorph features, the close approximation of vein 1m-cu to cell $R_s$ and the even distribution of hairs over tergite 3, which suggest that it is correctly placed in *Exotela*.

(iii) The species hitherto known as *Dacnusa tristis* (NEES) cannot be included in *Chorebus*. Its mandibles (fig. 2) are very distinctive in that tooth 3 is represented by a long milled edge. This is a very different condition from that found in any species of *Chorebus* and I see no reason to think that it represents a modification of the 4-toothed mandibles of that group as NIXON (1946) implies. The metapleuron of this species is plesiomorph, being almost smooth with sparse pubescence directed downwards towards the coxa. The propodeum is clothed with sparse somewhat long hairs. I have found no apomorph characters which support the inclusion of this species in any of the existing genera, and a new genus *Protodacnusa* with *tristis* as genotype is therefore described below in Appendix VI.

### The *Dacnusa* genus-group

The *Dacnusa* genus-group is primarily characterised by a single apomorph character — sexual dimorphism of the pterostigma. This feature is also found in a few *Chaenusa* spp. but it seems likely that this is by convergence. Within the group there is a wide range of variation from species which are highly plesiomorph in other respects to the strikingly apomorph species of the *Dacnusa areolaris* and *stramineipes* groups. NIXON (1943—54) is to be congratulated for extricating this group from the grossly heterogeneous "*Dacnusa*" of previous authors, but his division into two main genera "*Rhizarcha*" and "*Pachysema*" is clearly not tenable in a phylogenetic system, because *Pachysema* contains all the more plesiomorph species and is not a monophyletic group. Even for a purely morphological system this division causes difficulties, for instance *D. monticola* (FÖRSTER) has been ascribed under different synonyms to both genera (see Appendix IV) and *D. nitetis* (NIXON), placed in "*Rhizarcha*", is clearly an ecological vicariant of *D. cercides* (NIXON), *D. comis* (NIXON) and *D. discolor* (FÖRSTER), all placed in "*Pachysema*". I have therefore united NIXON's two concepts into a single large genus *Dacnusa* (the name being restored to this group on formal grounds).

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I have also included in *Dacnusa* the species *hospita* (Förster) and *adducta* Haliday which have generally been accepted (following Förster, 1862) as monobasic genera on account of peculiarities in the wing venation. These apomorph features do not justify their retention as genera in a phylogenetic system as there are no corresponding plesiomorph features to suggest that they are sister-groups of *Dacnusa*.

The genus *Amyras*, erected by Nixon (1943) for the single species *A. clandestina* (Haliday), has been retained in this paper, as it may genuinely represent a sister-group of *Dacnusa*. To the extent that the short high cell 2Cu of *Dacnusa* represents a degree of apomorphy, its replacement by a long narrow cell in *Amyras* may represent a genuine alternance of plesiomorph and apomorph characters. There is nothing in the other characters of *clandestina* which casts doubt on this interpretation by suggesting a close relationship with any particular group of species within *Dacnusa*.

### *Priapsis* Nixon and *Coloneura* Förster

Included in *Priapsis* are so far only three species (including *Priapsis ate* (Nixon), see above). They lack any apomorph characters which will include them in any of the main monophyletic groups of Dacnusini and are probably to be recognised as a distinct group in their own right. The apomorph features which can be used to characterise *Priapsis* are (i) the short maxillary palpi, and (ii) the open cell 2Cu. Both these characters are found in other groups within the major genera but, as these genera also contain species plesiomorph in respect of these characters, their evolution there must have been independent, and their validity in characterising *Priapsis* is not thereby prejudiced.

The two apomorph features of *Coloneura stylata* Förster, the only species of the genus, — 5-segmented maxillary palpi and the completely open cell 2Cu due to the loss of the vein which previously closed it beneath — can be seen as more extreme developments of the characters of *Priapsis*. But there is a considerable gap between the characters of this species and the known species of *Priapsis*, and it may be that Nixon (1954) was right in thinking that there was no close relationship. My association of these two genera is therefore provisional.

### *Tates* Nixon

Like Nixon (1954) I am unable to associate the single species *Tates heterocera* (Thomson) with any other group. I consider its more important apomorph characters to be (i) the high degree of sexual dimorphism in the number of antennal segments ($\male$, 42—48; $\female$, 29—33), (ii) the long narrow cell 2Cu which is open at its lower distal corner, and (iii) the elongate petiole.

### *Exotela* Förster

Most of the species I am including in this genus can readily be recognised as belonging here by a characteristic apomorph condition of the wing-venation — the reception of vein 1m-cu into cell $R_s$ (fig. 13). This occurs in no other genus of

Dacnusini, and was used by Förster (1862) and Nixon (1943) to characterise their respective genera *Exotela* and *Toxelea*. But it is difficult to maintain this definition as there are a few species in which 1m-cu is closely approximated to cell $R_s$ (fig. 12) which are morphologically very similar to the species in which 1m-cu is received into that cell. Furthermore in *Exotela hera* (Nixon) 1m-cu is only interstitial in many individuals. This continuous range of variation has led me to the view that the species with the more plesiomorph venation — *flavicoxa* (Thomson), *melanocera* (Thomson) and *interstitialis* (Thomson) — should be included in the genus *Exotela*, not in a separate genus (i.e. Nixon's *Antrusa*). The sole apomorph characterisation of this generic concept which I can see is the approximation of 1m-cu to cell $R_s$ (the reception of 1m-cu into that cell being a further development of this). Apart from the venation the only additional apomorph feature which may have some significance is the presence of pubescence on tergite 3 in several species, although this character is also found in *Protodacnusa*. Clearly my present characterisation of *Exotela* cannot be claimed to be satisfactory, but in the absence of any further apomorph features in the characters analysed, for the present nothing better can be offered.

The approximation of 1m-cu to cell $R_s$ does of course occur in a number of other groups of Dacnusini (see the section headed "Plesiomorph Characters"), but they all fall within monophyletic groups established on other characters and must therefore be considered to have evolved this character through convergence.

The generic position of Nixon's species *vaenia* causes some difficulty, but in view of its close overall resemblance to *Exotela flavicoxa* (Thomson) I am placing it in this genus, although it is not significantly apomorph in respect of an approximation of 1m-cu to cell $R_s$. I think it unlikely that its feeble longitudinal striation of tergite 3 represents synapomorphy with the *Coelinius* genus-group.

The new genus *Protodacnusa* is distinguished from *Exotela* by the form of its head and mandibles (figs. 2, 36 and 38). *Exotela vaenia* (Nixon) has relatively large mandibles, but as normally in *Exotela* teeth 1 and 3 are of about equal size (in *Protodacnusa* tooth 3 is much expanded laterally). The maximum width of the mandibles of *vaenia* is 0.19 mm., while the minimum in the *Protodacnusa* material examined is 0.21 mm. Also the head of *vaenia* is more transverse and its temples are clearly narrower than the eye-width (in dorsal and lateral views).

As far as known all species of *Exotela* are parasites of Agromyzidae. The more plesiomorph species in which 1m-cu is not received into cell $R_s$ have been bred only from the *Agromyza nigripes/ambigua* groups and *Cerodontha* subg. *Poemyza*, while the apomorph species in which 1m-cu is received into that cell are known to me as parasites of other *Agromyza* spp., *Phytagromyza* and *Phytomyza*.

### Summary of proposed Classification of the Dacnusini

The diagnoses given below are intended to summarise the main characters on which I have tried to base the concepts for the purposes of phylogenetic systematics. A practical key for identifying the genera is given in Appendix II.

The synonymies include all names proposed for Palaearctic and Nearctic genera as far as I am aware, but omit the two names *Heratremis* and *Nebartha* proposed by WALKER (1860) for Ceylonese species.

### Subfamily Alysiinae (NEES, 1834)
### Tribe Dacnusini (FÖRSTER, 1862)

Diagnosis: The primary apomorph characters of the Dacnusini are (i) the loss of vein 2m-cu, (ii) the sinuation of vein $R_s$, and (iii) the development of the first-instar larva within a distended trophamnium retained from the egg stage. The first two characters are also shown by *Grandia cynaraphila* (RICCH.) but I suspect that this represents convergence (see under "Genera excluded from the Dacnusini" above). The third character requires confirmation over a wider range of species, as the first-instar larvae of only two species have been described.

A plesiomorph character retained by many Dacnusini in contrast with many other groups of Alysiinae is the closed cell 2Cu, with vein $Cu_{1b}$ retained. In groups where $Cu_{1b}$ has been lost, the transverse segment of $Cu_1$ is always retained and $Cu_{1a}$ never migrates towards the top of cell 2Cu.

A prominent evolutionary tendency within the tribe is the development of extensive pubescence on various parts of the body.

### The *Coelinius* genus-group

Diagnosis: Longitudinal striation or sculpture similar to that of the petiole generally extending over tergite 3 (this is completely lost only in a few *Coelinius* spp.). Mandibles with at least some indication of an additional tooth, or, if secondarily 3-toothed, they are dominated by a large pointed tooth 2. Metapleuron with rugose sculpture, but its pubescence always plesiomorph, sparse and directed mostly downwards towards the coxa. Cell 2Cu elongate.

Six genera are here recognised — *Laotris, Synelix, Aristelix, Coelinius, Symphya* and *Epimicta.*

### *Laotris* NIXON, 1943

*Laotris* NIXON, 1943, Ent. mon. Mag., 79, 30. Type-species: *Alysia (Dacnusa) striatula* HALIDAY, 1839, by original designation and monotypy.
Diagnosis: This genus is based on a single species which appears to be the most plesiomorph member of the *Coelinius* genus-group in respect of (i) its gaster, which is short, dorso-ventrally compressed in both sexes, with a single row of hairs near the margin of each segment; and (ii) its wing venation (elongate pterostigma and sinuate $R_s$ retained). The mandibles are apomorph in respect of showing a distinct additional tooth between the original teeth 1 and 2 (fig. 37).

### *Synelix* FÖRSTER, 1862

*Synelix* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 9, 276. Type-species: *Synelix agnata* FÖRSTER, 1862 [= *Alysia (Dacnusa) semirugosa* HALIDAY, 1839, see Appendix IV] by original designation and monotypy.

*Sarops* NIXON, 1942, Ent. mon. Mag., 78, 133. Type-species: *Sarops rea* NIXON, 1942, by original designation and monotypy. **Syn. nov.**

*Ectilis* NIXON, 1943, Ent. mon. Mag., 79, 29. Type-species: *Alysia (Dacnusa) semirugosa* HALIDAY, 1839, by original designation and monotypy. **Syn. nov.**

Diagnosis: The apomorph characters are (i) vein $R_s$ evenly curved (fig. 7), (ii) the strongly laterally compressed female gaster, and (iii) that the apical segments of the gaster in both sexes tend to have more than one row of hairs. The mandibles show an elongate tooth 2, and sometimes an additional fourth tooth.

## *Aristelix* NIXON, 1943

*Aristelix* NIXON, 1943, Ent. mon. Mag., 79, 27. Type-species: *Alysia (Dacnusa) phaenicrura* HALIDAY, 1839, by original designation and monotypy.

Diagnosis: The apomorph characters are (i) the elongate gaster which is densely haired beyond the petiole, (ii) thorax, back of head and clypeus punctate, and (iii) mandibles very small and narrow, obviously 4-toothed (tooth 2 being the longest). This genus is based on a single species which resembles *Coelinius* in respect of (i) and (ii), but retains more plesiomorph wing venation in respect of the elongate pterostigma.

## *Coelinius* NEES, 1818

*Coelinius* NEES ab ESENBECK, 1818, Nov. Act. Acad. Nat. curios, 9, 301. Type-species: *Stephanus parvulus* NEES, 1811 [= *Chaenon anceps* CURTIS, 1829 and *Ichneumon circulator* GRAVENHORST, 1807 according to VIERECK, 1914] by monotypy; not *Coelinius niger* NEES, 1834 [*Stephanus niger* NEES, 1811][7] by designation of FÖRSTER, 1862.

*Chaenon* CURTIS, 1829, Brit. Ent., 6, 289. Type-species: *Chaenon anceps* CURTIS, 1829, by original designation and monotypy.

*Copisura* SCHIÖDTE, 1837, Nat. Tidskr., 1, 603. Type-species: *Copisura rimator* SCHIÖDTE, 1837 [= *Chaenon anceps* CURTIS, 1829 according to FÖRSTER, 1862] by monotypy.

?*Lepton* ZETTERSTEDT, 1838, Ins. Lapp., 1, 403. Type-species: *Lepton attenuator* ZETTERSTEDT, 1838 [? = *Ichneumon circulator* GRAVENHORST, 1807 according to VIERECK, 1914] by monotypy.

*Polemon* GIRAUD, 1863, Verh. zool.-bot. Ges. Wien, 13, 1267. Type-species: *Polemon liparae* GIRAUD, 1863, by designation of VIERECK, 1914 (preoccupied). **Syn. nov.**

*Copidura* DALLA TORRE, 1898, Catalogus Hymenopterorum, 4, 20 (emendation of *Copisura*).

*Polemochartus* SCHULZ, 1911, Zool. Ann., 4, 61. New name for *Polemon* GIRAUD. **Syn. nov.**

*Coelinidea* VIERECK, 1913, Proc. U.S. nat. Mus., 41, 555. Type-species: *Stephanus niger* NEES, 1811, by original designation and monotypy. **Syn. nov.**

[7] The date of the original description is given in brackets after the later description which is specifically given in the type designation.

*Eriocoelinius* VIERECK, 1913, Proc. U.S. nat. Mus., 41, 555. Type-species: *Coelinius longulus* ASHMEAD, 1888, by original designation and monotypy. **Syn. nov.**

Diagnosis: The apomorph characters of this genus are (i) the elongate gaster (laterally compressed towards its apex in the female) whose at least apical tergites bear several rows of hairs, (ii) the short broad pterostigma (compare fig. 8), and (iii) the strong sexual dimorphism in the number of antennal segments (mean difference of at least 6 segments, often much more). The plesiomorph form of mandible for this genus shows an additional tooth between the original teeth 1 and 2 (as in *Laotris*), but in most species the mandibles are more or less 3-toothed, dominated by the large elongate tooth 2. The development of sculpture on tergite 3 is variable and in a few small species this tergite may appear completely smooth. Three subgenera are provisionally recognised:

### *Coelinius* s. s. [= *Chaenon, Copisura*, ? *Lepton, Copidura*]

Diagnosis: Plesiomorph sinuate $R_s$ and broad 4-toothed mandibles retained. Petiole elongate.

### *Coelinidea* [= *Eriocoelinius*]

Diagnosis: $R_s$ evenly curved. Petiole elongate. Mandibles dominated by tooth 2, with a distinct additional tooth between teeth 1 and 2 retained only in a few species.

### *Polemochartus* [= *Polemon*]

Diagnosis: Plesiomorph sinuate $R_s$ retained. Petiole massive, less than twice as long as broad. Mandibles dominated by very large tooth 2. Longitudinal striation extending over tergite 3 and part of tergite 4.

## *Symphya* FÖRSTER, 1862

*Aenone* HALIDAY, 1838, Ent. Mag., 5, 214 (subgenus of *Alysia* LATREILLE, 1805). Type-species: *Sigalphus mandibularis* NEES, 1814, by designation of WESTWOOD, 1840 ( ? preoccupied).

*Oenone* HALIDAY, 1839, Hym. Brit., 2, 3 (subgenus of *Alysia* LATREILLE, 1805) (preoccupied). Emendation of *Aenone* HALIDAY.

*Symphya* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 9, 273. Type-species: *Sigalphus mandibularis* NEES, 1834 (1814)[8] by original designation and monotypy.

The names *Ænone* and *Œnone* were used by LAMARCK (1818) for a genus of Annelida (according to that author the name *Ænone* was first proposed by SAVI in a paper published in 1817, but I have been unable to trace this work). The form first used by LAMARCK is *Ænone* in a key on page 321, but in the descriptions on page 326 the form *Œnone* is used five times. Clearly the latter spelling is intentional and preoccupies *Oenone* HALIDAY, 1839. It could perhaps be argued that the use of *Ænone* on the earlier page is a typographical error, but in the circumstances it seems preferable to regard both spellings of HALIDAY's name as preoccupied, and to retain the now customary use of the name *Symphya* for this genus.

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[8] The date of the original description is given in brackets after the later description which is specifically given in the type designation.

Diagnosis: The apomorph characters are (i) the gaster beyond the petiole densely haired, (ii) tergites 3 and 4 large, together covering at least two thirds of the gaster beyond the petiole, (iii) postscutellum bearing a spiniform projection, (iv) pterostigma and cell $2R_1$ short (fig. 8), and (v) mandibles strongly 4-toothed.

## *Epimicta* FÖRSTER, 1862

*Epimicta* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 9, 274.
   Type-species: *Alysia (Dacnusa) marginalis* HALIDAY, 1839, by original designation and monotypy.
Diagnosis: Two species have been attributed to this genus, only one of which is known to me. This agrees with *Symphya* in respect of wing venation and the postscutellum bears a small spur. But the gaster is more plesiomorph in that segments 3 and 4 are not enlarged. The mandibles are 4-toothed with a wide blunt tooth 3. The validity of this concept as a distinct genus from *Symphya* is doubtful.

## *Chaenusa* HALIDAY, 1839

*Chaenusa* HALIDAY, 1839, Hym. Brit., 2, 19 (subgenus of *Alysia* LATREILLE, 1805).
   Type-species: *Bracon conjungens* NEES, 1811, by monotypy.
*Chorebus* sensu HALIDAY, 1839, FÖRSTER, 1862, MARSHALL, 1891 and 1897 etc.
   (nec HALIDAY, 1833).
*Chorebidea* VIERECK, 1914, Proc. U.S. nat. Mus., 45, 32. Type-species: *Alysia
   (Chorebus) nereidum* HALIDAY, 1839 by original designation and monotypy.
   **Syn. nov.**
*Chorebidea* NIXON, 1943, Ent. mon. Mag., 79, 28. Type-species: *Alysia (Chorebus)
   najadum* HALIDAY, 1839 by original designation and monotypy (preoccupied by
   *Chorebidea* VIERECK). **Syn. nov.**
*Chorebidella* RIEGEL, 1950, Ent. News, 61, 125. Type-species: *Chorebidella bergi*
   RIEGEL, 1950 by original designation and monotypy. **Syn. nov.**
Diagnosis: The genus is apomorph in respect of (i) the hairy eyes, (ii) the form of the pterostigma (variable between species, but always broader than normally in the Dacnusini), and (iii) the narrow mandibles with elongate tooth 2. There is a strong tendency within the genus to simplify the wing venation by the loss or shortening of various veins. The metapleuron is strongly sculptured but its pubescence is plesiomorph.

## *Chorebus* HALIDAY, 1833

*Chorebus* HALIDAY, 1833, Ent. Mag., 1, 264 (subgenus of *Alysia* LATREILLE, 1805).
   Type-species: *Alysia (Chorebus) affinis* (NEES) sensu HALIDAY, 1833 [= *Alysia
   (Dacnusa) uliginosa* HALIDAY, 1839, not *Bassus affinis* NEES, 1814] by monotypy;
   not *Alysia (Chorebus) nereidum* HALIDAY, 1839 by designation of WESTWOOD,
   1840; nor *Alysia (Chorebus) najadum* HALIDAY, 1839, by designation of FÖR-
   STER, 1862; nor *Bassus affinis* NEES, 1814 by designation of VIERECK, 1914.
*Dacnusa* sensu FÖRSTER, 1862 and NIXON (1943—54) etc. (nec HALIDAY, 1833),

*Ametria* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., **19**, 274. Type-species: *Alysia (Dacnusa) uliginosa* HALIDAY, 1839 by original designation and monotypy. **Syn. nov.**

*Gyrocampa* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., **19**, 276. Type-species: *Alysia affinis* NEES, 1834 [*Bassus affinis* NEES, 1814][9] by original designation and monotypy. **Syn. nov.**

*Stiphrocera* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., **19**, 276. Type-species: *Stiphrocera nigricornis* FÖRSTER, 1862 [ = *Alysia ampliator* NEES, 1834, see Appendix IV] by original designation and monotypy. **Syn. nov.**

*Phaenolexis* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., **19**, 276. Type-species: *Alysia petiolata* NEES, 1834, by original designation and monotypy. **Syn. nov.**

*Etriptes* NIXON, 1943, Ent. mon. Mag., **79**, 30. Type-species: *Alysia (Dacnusa) talaris* HALIDAY, 1839, by original designation and monotypy. **Syn. nov.**

*Paragyrocampa* TOBIAS, 1962, Trudy Zool. Inst. Akad. Nauk URSS, **31**, 119. Type-species: *Paragyrocampa ophthalmica* TOBIAS, 1962 by original designation and monotypy. **Syn. nov.**

Diagnosis: The primary apomorph feature characterising *Chorebus* is the development of an additional mandibular tooth arising from the posterior side of the base of tooth 2 (figs. 24 and 25) (contrast *Laotris* and *Coelinius anceps* (CURTIS) in which the additional tooth is developed between the original teeth 1 and 2, and *Exotela interstitialis* (THOMSON) and certain *Dacnusa* species in which an additional tooth is formed by the indentation of the original tooth 3). The majority of species are in addition characterised by apomorph pubescence of the metapleuron and propodeum — the pubescence of the lower half of the metapleuron forming a dense rosette of radiating hairs around a raised swelling (figs. 22 and 23), which may be smooth or rugose, and the propodeal pubescence being adpressed, normally short and dense. Species in which the mandibles are secondarily elongate and apparently 3-toothed, or otherwise modified, may be recognised by this pubescence. The precoxal suture is always retained, at most reduced to a narrow groove.

### The *Dacnusa* genus-group

Diagnosis: The two genera *Amyras* and *Dacnusa* are associated as the *Dacnusa* genus-group as being synapomorph in respect of their sexually dimorphic pterostigmata.

### *Dacnusa* HALIDAY, 1833

*Dacnusa* HALIDAY, 1833, Ent. Mag., **1**, 264 (subgenus of *Alysia* LATREILLE, 1805). Type-species: *Bracon areolaris* NEES, 1811, by designation of MUESEBECK & WALKLEY, 1951; not *Alysia petiolata* NEES, 1834 by designation of WESTWOOD, 1840 (not originally included); nor *Alysia (Dacnusa) lateralis* HALIDAY, 1839 by designation of FÖRSTER, 1862 (not originally included).

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[9] The date of the original description is given in brackets after the later description which is specifically given in the type designation.

*Aphanta* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 273.
Type-species: *Aphanta hospita* FÖRSTER, 1862 by original designation and mono-
typy.

*Agonia* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 274.
Type-species: *Alysia (Dacnusa) adducta* HALIDAY, 1839, by original designa-
tion and monotypy.

*Pachysema* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 274.
Type-species: *Alysia (Dacnusa) macrospila* HALIDAY, 1839 by original designa-
tion and monotypy.

*Brachystropha* FÖSRTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19,
274. Type-species: *Brachystropha monticola* FÖRSTER, 1862 by original designa-
tion and monotypy.

*Tanystropha* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19,
275. Type-species: *Tanystropha haemorrhoa* FÖRSTER, 1862 by original designa-
tion and monotypy.

*Rhizarcha* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 275.
Type-species: *Alysia areolaris* NEES, 1834 [*Bracon areolaris* NEES, 1811][10] by
original designation and monotypy.

*Liposcia* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 276.
Type-species: *Liposcia discolor* FÖRSTER, 1862 by original designation and mono-
typy.

*Radiolaria* PROVANCHER, 1886, Addit. Corr. Faune ent. Canada Hym., 2, 154.
Type-species: *Radiolaria clavata* PROVANCHER, 1886, by monotypy [synonymy
following MUESEBECK & WALKLEY, 1951].

Diagnosis: The primary apomorph features characterising *Dacnusa* are (i) the
sexual dimorphism in the shape and colour of the pterostigma, which is broader
and darker in the male, and (ii) the short high cell 2Cu. The dimorphism of the
pterostigma is less noticeable in the *stramineipes* and *areolaris* groups, where the
pterostigma is secondarily narrow and elongate (fig. 10) in both sexes. Most species
are in addition characterised by the reduction or loss of the precoxal suture. Plesio-
morph features to be noted are (i) vein $Cu_{1b}$ retained, and (ii) the simple 3-toothed
mandibles (except for a few species in the *stramineipes* group).

### *Amyras* NIXON, 1943

*Amyras* NIXON, 1943, Ent. mon. Mag., 79, 30. Type-species: *Alysia (Dacnusa)
clandestina* HALIDAY, 1839 by original designation and monotypy.

Diagnosis: Thes genus is based on a single species synapomorph with *Dacnusa*
in respect of its sexually dimorphic pterostigma. But unlike *Dacnusa* cell 2Cu is
elongate. Its other characteristic apomorph features are the enlarged mandibles
and (♀) elongate ovipositor.

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[10] The date of the original description is given in brackets after the later description which is specifically given
in the type designation.

### *Exotela* FÖRSTER, 1862

*Exotela* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 274.
   Type-species: *Exotela cyclogaster* FÖRSTER, 1862 by original designation and
   monotypy.
*Mesora* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 275.
   Type-species: *Dacnusa gilvipes* (HALIDAY) sensu FÖRSTER, 1862 (nec *Alysia*
   (*Dacnusa*) *gilvipes* HALIDAY, 1839) by original designation and monotypy.
   **Syn. nov.**
*Toxelea* NIXON, 1943, Ent. mon. Mag., 79, 29. Type-species: *Alysia* (*Dacnusa*)
   *gilvipes* HALIDAY, 1839 by original designation and monotypy.
*Antrusa* NIXON, 1943, Ent. mon. Mag., 79, 30. Type-species: *Dacnusa melanocera*
   THOMSON sensu NIXON, 1937 [= *Dacnusa* (*Dacnusa*) *flavicoxa* THOMSON, 1895,
   see Appendix V] by original designation and monotypy. **Syn. nov.**
Diagnosis: In most respects this genus is plesiomorph. The apomorph feature
on which the concept is based is the approximation of vein 1m-cu to cell $R_s$ (in more
plesiomorph species), leading to its reception into that cell (fig. 13) in more apo-
morph species. Another apomorph character of most species, though admittedly
trivial, is the presence of hairs at least at the base of tergite 3.

### *Priapsis* NIXON, 1943

*Priapsis* NIXON, 1943, Ent. mon. Mag., 79, 31. Type-species: *Priapsis dice* NIXON,
   1943, by original designation and monotypy.
Diagnosis: Plesiomorph in most respects. Apomorph characters are (i) cell 2Cu
widely open at its lower distal corner following the loss of vein $Cu_{1b}$, and (ii) maxil-
lary palpi shortened.

### *Coloneura* FÖRSTER, 1862

*Coloneura* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 276.
   Type-species: *Coloneura stylata* FÖRSTER, 1862 by original designation and mono-
   typy (priority hereby accorded in spite of the page precedence of *Isomerista*
   and *Trisisa*, see Appendix IV).
*Isomerista* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 275.
   Type-species: *Isomerista oligomera* FÖRSTER, 1862 [= *Coloneura stylata* FÖRSTER,
   1862, see Appendix IV] by original designation and monotypy. **Syn. nov.**
*Trisisa* FÖRSTER, 1862, Verh. naturh. Ver. preuss. Rheinl. & Westph., 19, 275.
   Type-species: *Trisisa exilis* FÖRSTER, 1862 [= *Coloneura stylata* FÖRSTER, 1862,
   see Appendix IV] by original designation and monotypy. **Syn. nov.**
*Merites* NIXON, 1943, Ent. mon. Mag., 79, 28. Type-species: *Merites taras* NIXON,
   1943 [= *Coloneura stylata* FÖRSTER, 1862, see Appendix IV] by original designa-
   tion and monotypy. **Syn. nov.**
Diagnosis: The apomorph characters of the single species are (i) maxillary palpi
5-segmented, and (ii) vein 1a shortened so that cell 2Cu is not closed beneath by
a vein.

### Tates Nixon, 1943

*Tates* Nixon, 1943, Ent. mon. Mag., 79, 31. Type-species: *Dacnusa* (*Dacnusa*)
   *heterocera* Thomson, 1895 by original designation and monotypy.
Diagnosis: The apomorph characters of the single species are (i) the high degree
of sexual dimorphism in the number of antennal segments, and (ii) cell 2Cu very
elongate, open at its lower distal corner.

### *Protodacnusa* gen. nov.

The description of this new genus is given in Appendix VI.

### Significance of the Mandibles of the Alysiinae

The function of the characteristic Alysiine mandibles has puzzled many Hymeno-
pterists, mainly because they thought of the mouthparts solely as feeding organs.
They have in fact another at least equally important function in Parasitica which
pupate inside their host's pupa or puparium — to assist the mature parasite in
escaping to the outside world. The characteristic Alysiine mandibles clearly repre-
sent an adaption to secure escape from the puparia of cyclorrhaphous Diptera. Most
such puparia present a very hard concave surface to their inmates, but there are
preformed fissures at the anterior end which are ruptured by the adult fly in
emergence.[11]

The first published observation on the emergence of an Alysiine appears to
have been by Graham-Smith (1916), who states refering to *Alysia manducator*
(Panzer) that "the Braconid emerges by gnawing an irregular oval hole near the
anterior end of the puparium" and gives photographs of vacated puparia. The
term "gnawing" is however misleading in this context. Excellent and detailed
accounts of this same species were subsequently given by Altson (1920) and
Myers (1927). Altson's account begins as follows:

"The adult emerges from the host puparium and its cocoon by breaking away that part
directly in contact with the head. It is furnished with a very powerful pair of mandibles
beautifully adapted for the work in hand. It breaks away the cocoon and puparium by an
outward movement and does not bite the obstruction . . . In the outward movement of
the mandibles a small fracture appears on the puparium, generally between the second
and fourth segment, gradually increasing in size until the perfect insect has created an
aperture large enough to enable it to escape. Observation has failed to disclose any use for
the mandibles other than breaking out of the host puparium, which operation, when in
progress by several insects, has been distinctly audible by putting the ear over the mouth
of the jar in which they were confined".

Myers (1927), commenting on Altson's account, states that "more often than not,
in my experience, *Alysia* seems to break off a cap like that of the emerging fly
itself".

[11] Laing's (1935) description of the emergence of *Calliphora erythrocephala* (Meigen) is as follows. "The puparium
is ruptured in two fissures — a longitudinal and a circular. The former extends around the anterior end along its sides,
external to but in the same line as the main tracheal trunk of the larva, until it meets the circular fissure which runs
completely around the anterior margin of the fourth visible segment. The ruptured anterior end may hinge back,
or break off, in two pieces, a dorsal and a ventral, or more rarely it may separate as a single bowl-shaped portion.
The ruptures are effected by inflation and retraction of the ptilinum . . ."

In spite of this careful and reliable work, the significance of the mandibles has not penetrated the main taxonomic literature, and most taxonomists (with the exception of BURGHELE and DOCAVO ALBERTI) have remained innocent of any conception of their function.

Turning to the Dacnusini, it is my experience from breeding many hundreds of specimens of many species from Agromyzidae that emergence has always taken place by rupturing the fissures.[12] Unlike *Alysia* the pupae of Dacnusini have no cocoon and the vacated puparia cannot readily be distinguished from those from which the host fly has emerged. The parasite generally crawls out upwards and the lower portion of the anterior end of the puparium is often left intact. This contrasts very strikingly with the emergence of other parasites obtained from the puparia of cyclorrhaphous Diptera. The many *Opius* spp. which I commonly obtain from Agromyzid puparia generally emerge downwards, leaving the dorsal edge of the puparium intact, through a large opening which may partially coincide with the vertical circular fissure, but has at least in part an irregular outline indicating that some cutting action has taken place. Chalcidoid parasites generally emerge through a circular hole which they carve usually on the lower side of the puparium and make no use of the fissures.

The exact manner of operation of the mandibles, whether as piercing or cutting instruments or as levers requires further investigation. The very large heads of some species and the very clean split along the fissures produced by the species emerging from Agromyzid puparia suggest to me that the fissures are broken by upward pressure from the head with the mandibles functioning as levers. The pressure thus exerted would correspond closely with that exerted by the host fly in inflating its ptilinum. But it is probable that there is variation in the exact method of emergence in different groups, associated with variation in the form of the head and mandibles. (An additional function of large heads may also be the penetration of earth or plant material surrounding the puparium.)

RICCHELLO (1928) observed that *Grandia cynaraphila* (RICCHELLO) also emerges by splitting the fissures of its host's puparium, although he did not realise the function of the mandibles and attributed the splitting to the action of the hind legs. (This suggestion has not been confirmed subsequently and I find it incredible: but the possibility that RICCHELLO observed an abnormal emergence cannot of course be excluded). Puparia associated with many other Alysiinae which I have examined also show a clean split along the fissures, and this is clearly the normal manner of emergence of the great majority of species. The only exceptions known to me are a small group of species which are multiple parasites (including *Aphaereta* (or *Phaenocarpa*) *minuta* (NEES) and the American *A. auripes* PROVANCHER) which emerge through irregular holes of variable position (EVANS, 1933, and CAPEK, personal communication). This manner of emergence is clearly secondary, dictated by the circumstances of multiple parasitism.

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[12] As an isolated exception I have one example of an undescribed *Chorebus* sp. which succeeded in emerging from a puparium of *Cerodontha* (*Poemyza*) *pygmaea* (MEIGEN) by a vertical more or less circular rupture around the entire 8th abdominal segment of the puparium, presumably after developing within the puparium facing the wrong direction.

My conclusion is that the apomorph mandibles which characterise the Alysiinae as a monophyletic group are an adaptive feature to enable them to escape from cyclorrhaphous puparia. In the most plesiomorph species studied (*Alysia manducator* (Pz.)) there is some variation in the precise manner of emergence but in the great majority of species, including all members of the tribe Dacnusini which have been studied, emergence is almost invariably effected by splitting the pre-formed fissures. The existence of such a specialised adaption indicates a long-standing and specialised association with this particular group of hosts and may constitute a barrier against any radical change in host selection. The exception of the *Aphaereta* species mentioned above is secondary and does not detract from the main conclusion.

It obviously follows from the above conclusion that Alysiinae must in general be expected to be parasites of Diptera Cyclorrhapha (or Musciformia), and, if this were not the case, the conclusion would be open to serious doubt. A search of the literature has revealed no more than two or three records of the breeding of Alysiinae from non-cyclorrhaphous Diptera, but there are a few records refering to non-Dipterous hosts. Most of these are isolated records not subsequently confirmed and some are doubtless erroneous: but nevertheless there are a few records refering to *Aspilota* which must be accepted. Most refer to leaf-mining Lepidoptera, not-ably *Lithocolletis*, but WATANABE (1957) has described a species bred from the Cynipid (Hymenoptera) *Dryocosmus kuriphilus* YASUMATSU in Japan. The major-ity of *Aspilota* species are however known to be parasites of Diptera Cyclorrhapha and these examples of different selection are doubtless secondary. Records of *Orthostigma* from large lepidopterous larvae require checking, as it is known for Alysiinae to attack Tachinid larvae within their lepidopterous hosts.

## Some general biological Comments

Apart from the interesting question of the function of the mandibles, there are a number of other general points concerning the biology of the Alysiinae which it is useful to make at the start of this series of papers.

The Alysiinae attack the larva of their host. Wright, Geering and Ashby (1947) state that *Chorebus gracilis* (NEES) probably attacks all three instars of its host *Psila rosae* (F.). According to EVANS (1933) *Aphaereta minuta* (NEES) attacks only the first two instars of Calliphorid larvae, but *Alysia manducator* (PANZER) only the third. Emergence of the adult Hymenopteron always takes place from the host puparium. Puparia parasitised by Dacnusini are not readily distinguishable from those containing the host, except in the case of translucent puparia when the parasite can be seen developing within.

The plesiomorph form of first-instar larva for the Alysiinae possesses setate appendages on the trunk segments and a large head-capsule with well-developed mandibles (see the discussion in EVANS, 1933, who considers these features to have been retained from a previous ectoparasitic way of life). Such larvae are described for *Alysia manducator* (PANZER) (EVANS, 1933), *Grandia cynaraphila* (RICCH.) (RICCHELLO, 1928) and *Dapsilarthra gahani* (BAUME-PLUVINIEL) (DE LA BAUME-

PLUVINIEL, 1914). In *Aspilota* sp. and *Aphaereta minuta* (NEES) the appendages have been lost, and the complexity of the framework of the head-capsule reduced (EVANS, 1933). In addition the *Aphaereta* has reduced mandibles. HAVILAND (1922) says that the first-instar larva of *Dacnusa areolaris* (NEES) develops by absorbing food through the distended trophamnium retained from the egg-stage and does not rupture this until it moults some 36 hours after the host has pupated. WRIGHT, GEERING and ASHBY (1947) have shown the same to be the case with *Chorebus gracilis* (NEES), but do not state the time of the first moult.

It is evident that the pupation of the host has a considerable effect on the development of the parasite. In *Aphaereta minuta* (NEES) hatching from the egg is closely connected with the host's pupation (EVANS, 1933). In *Dacnusa areolaris* (NEES) (see above) it is the first moult and the shedding of the trophamnium which is so induced. *Grandia cynaraphila* (RICCHELLO) oviposits in the first-instar larva of its host (RICCHELLO, 1928), but the resulting larva does not develop beyond the first instar until after the host's pupation. The synchronisation of host-parasite development in *Dapsilarthra gahani* (BAUME-PLUVINIEL) is not altogether clear from DE LA BAUME-PLUVINIEL's (1914) account, but his statement that he obtained the first-instar larva from both host larvae and puparia presumably implies that the parasite larva does not reach its second instar until after the host's pupation. It thus appears to be general in the Alysiinae that development of the immature stages is retarded until the host pupates.

This synchronisation has the effect of allowing the host to reach its full size before it suffers serious injury, thus ensuring a plentiful supply of food for the parasite's further development. A possible exception is an *Aphaereta* sp. which I have bred from *Pegomyia dentiens* PANDELLÉ (Muscidae) in *Filipendula* stems: in this case the parasitised puparia were less than half the volume of normal puparia. Also in the plesiomorph *Alysia manducator* (Pz.) the adult, according to EVANS (1933), only oviposits in the third-instar larva of its host, so that a mechanism for delaying larval development may be unnecessary.

The number of larval instars in *Chorebus gracilis* (NEES) has been shown to be four (WRIGHT, GEERING & ASHBY, 1947), but according to EVANS (1933) *Alysia manducator* (Pz.) and *Aphaereta minuta* (NEES) have only three larval instars.

The following papers should be consulted for detailed larval descriptions:

DE LA BAUME-PLUVINIEL (1914) — *Dapsilarthra gahani* (BAUME-PLUVINIEL)
ALTSON (1920) — *Alysia manducator* (PANZER)
HAVILAND (1922) — *Dacnusa areolaris* (NEES)
RICCHELLO (1928) — *Grandia cynaraphila* (RICCHELLO)
MORGAN (1929) — *Alysia manducator* (PANZER)
EVANS (1933) — *Alysia manducator* (PANZER), *Aphaereta minuta* (NEES) and *Aspilota* sp.
WRIGHT, GEERING & ASHBY (1947) — *Chorebus gracilis* (NEES)
SHORT (1952) — *Alysia manducator* (PANZER), *Aspilota vesparum* STELFOX and *Coelinius liparae* (GIRAUD).

ALTSON (1920) and MYERS (1927 and 1929) have made excellent studies of the habits of *Alysia manducator* (PANZER).

All Dacnusini are solitary parasites, and the same is generally the case with other Alysiinae. HAVILAND (1922) in her work on *Dacnusa areolaris* (NEES) concluded that the female would never oviposit in a host larva which already contained an egg. Only a small group of *Aphaereta* species are known to be multiple parasites.

The emergence of Dacnusini from Agromyzid puparia takes place generally from a few days to up to two or three weeks later than host flies from the same breeding. Their appearance thus tends, as might be expected, to coincide with the appearance of host larvae.

There seem to have been no investigations made on whether the Dacnusini parasites of Agromyzidae support any hyperparasites. WRIGHT, GEERING & ASHBY (1947) have shown that larvae of *Loxotropa tritoma* THOMSON (Proctotrupoidea, Diapriidae) will develop as hyperparasites of larvae of *Chorebus gracilis* (NEES), as well as primary parasites of its host *Psila rosae* (F.) (Psilidae), but as far as I am aware no Diapriids have ever been bred from Agromyzid puparia. GRAHAM-SMITH (1916 and 1919) bred *Melittobia acasta* WALKER (Chalcidoidea, Eulophidae) freely from Calliphorid puparia containing larvae of *Alysia manducator* (PANZER), though the species could also develop in unparasitised puparia.

At the time of emergence the adults of the higher Diptera have a very soft cuticle and change in form considerably before they finally mature. In particular they take in quantities of air with the result that the mature fly is of greater volume than the puparium from which it issued. Agromyzid species which emerge from elongate flattened puparia (for instance many *Ophiomyia* spp.) do not retain this shape but contract in length after emergence. The external shape of the mature individual is not affected by the form of its puparium. But Dacnusini emerge from the host's puparium in a much more mature state. At the time of emergence the overall shape of the individual has already been determined except for the wings which are unexpanded. The result is that the shape of the parasite, particularly its thorax, reflects the shape of the host puparium.

There is no evidence for any except sexual dimorphism in the Dacnusini. Certain characters, such as size, the shape of the thorax and to a lesser extent other parts of the body (as explained above) are influenced by the physical limitations of the host puparium, but apart from these characters individuals of the same species from different hosts are readily comparable. Obvious differences in characters other than shape or size in series bred from different hosts I regard as indicating that different species are concerned. In all long series which I have bred males have occurred freely, giving no reason to suspect that other than normal sexual reproduction has occurred.

## Host Specificity in the Dacnusini

The possible causes of host specificity have been analysed by SALT (1938), who expressed the three possible limiting factors in the following form:

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(1) Host not found,

(2) Host found but not accepted, and

(3) Host found and accepted but not suitable.

He then subdivides the third heading into two: (A) attack frustrated, and (B) parasitism unsuccesful because (i) host physically unsuitable, (ii) chemically unsuitable, or (iii) biologically unsuitable.

The great majority of Dacnusini exhibit an extraordinarily high degree of host specificity, as will be apparent from the detailed records in succeeding papers in this series. I am not aware of any experiments having been performed with Dacnusini which shed light on the factors responsible for this phenomenon and can therefore only offer at this time deductions from the known host distributions.

It seems to me impossible that adult Dacnusini fail to find alternative hosts. There are many instances in the breeding records where the same or related hosts are attacked on different plants growing in different biotopes — e.g. *Chorebus nana* (NIXON) attacking the *Phytomyza obscura* group in subaquatic habitats (on *Mentha*, *Myosotis* and *Lycopus*) or chalk downs (*Clinopodium* and *Origanum*): *Chorebus cinctus* (HALIDAY) attacking *Agromyza lucida* HENDEL on *Deschampsia* in woodlands and *Glyceria* in subaquatic habitats: *Chorebus perkinsi* (NIXON) attacking *Agromyza albitarsis* MEIGEN on *Populus tremula* and *A. lygophaga* HERING on *Salix repens*: *Chorebus lateralis* (HALIDAY) and *Dacnusa abdita* HALIDAY attacking the *Agromyza reptans* group on *Urtica* and various Boraginaceae. If host finding were the main limiting factor one would not expect to find host distributions of this type predominating, but rather a much closer correspondance with the host's food-plants and the habitats in which they grow. The existence of such restricted host distributions which appear independent of habitat in fact suggests that the Dacnusini have their host-finding faculties very well developed. Furthermore there are a number of Dacnusini which are monophagous parasites of hosts which, although widespread, are numerically uncommon in Britain, e.g. *Exotela phryne* (NIXON) attacking *Agromyza alnibetulae* HENDEL, or very localised, such as *Phytomyza scabiosae* HENDEL (attacked by an undescribed *Chorebus* sp.), *Phytomyza silai* HERING (*Priapsis dice* NIXON), *P. gentianae* HENDEL (*Chorebus dagda* (NIXON)) and *P. ramosa* HENDEL (*Chorebus tanis* (NIXON) and *Dacnusa metula* (NIXON)). It is difficult to believe that monophagy would be maintained in such circumstances except by a group possessing considerable powers of host finding.

I think therefore that the problem can be narrowed down to the question of whether the limiting factor is host selection (i.e. SALT's alternative (2)) or host suitability (alternative (3)). A definite answer to this question can only be given by controlled breeding experiments. SALT's alternative 3(A) is very unlikely to apply to mining larvae which are relatively immobile compared with free-living forms and in no position to escape from or physically resist the attack of a parasite whose ovipositor is suitably adapted to reach them (though the mining habit does of course protect them from attack by most parasites and predators which are not specially adapted). For most Dacnusini with very restricted host ranges there will be little difficulty in finding prospective hosts which show no great physical or biological difference

from the normal hosts, so that experiments could be devised to demonstrate whether chemical unsuitability or host selection is the factor which limits the host range of particular species. If the latter is the case it may be possible to breed Dacnusini on a wider range of hosts in the laboratory than their known host-range in nature. Such results, if obtained, should not be confused with normal selection, which can only be established by systematic breeding of host larvae collected in the wild, like the records which will form the basis of the succeeding papers in this series. It is well known that laboratory host lists of many parasitic insects include hosts on which they never occur in the wild.

An interesting possibility worth experimental investigation is that the host specificity of the Dacnusini is associated with physiological specialisation of the larva, particularly the first instar. In *Dapsilarthra*, which like the Dacnusini contains parasites of leaf-mining Diptera, the plesiomorph mobile first-instar larva is retained and host specificity much less developed. Unfortunately the first-instar larva of only two species of Dacnusini has been studied, so that it is not possible to evaluate this suggestion at present. The importance of host defence reactions has been demonstrated by SALT (1955) with respect to lepidopterous larvae, and could possibly have some significance in this present context.

Experimental work would also of course be valuable in confirming the validity of individual species by attempting to cross-breed presumed distinct species and strains which are believed to belong to the same species obtained from different hosts. The latter would be particularly valuable in the case of the apparently polyphagous *Dacnusa* spp. But it would be idle to suppose that this work will be done on more than a few of the many species in the tribe in the foreseeable future, and the taxonomy of the group will doubtless remain based almost entirely on morphology for a long time to come.

Appendix I defines the terms used to describe different degrees of host specificity.

## The Connection between Phylogeny and Host Association

Graph 1 sets out in diagrammatic form my views on the phylogeny of the Dacnusini. I have not attempted at this time to link together the eight main branches at the bottom of the tree. Graph 2 shows in broad terms the known host association and should be read as if superimposed on graph 1 (graph 1: see p. 894, graph 2: p. 895).

With the aid of this data it is possible to draw certain conclusions about the host association of the common ancestor of the group. My analysis is founded upon two principles. The first is what HENNIG (1950) calls his "Progressionsregel" or the "Gesetz vom Parallelismus zwischen morphologischer und chorologischer Progression". The fundamental postulate of this rule is that when a species divides into two daughter-species the most strongly changed (apomorph) species is that which is "räumlich" (i. e. spatially in the widest possible sense) the furthest removed from the parent species. The result of this process is that where the pattern has not been disturbed by other factors, the morphologically most plesiomorph species in a group will be the least removed

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from the common ancestor in spatial (chorological) terms. Host association is in my view the most important single spatial factor for the Dacnusini, and, as a reasonably complete picture of the range of morphological variation in the fauna of boreal Europe now seems available, I believe that valid comparison of the morphological data and the host association can be made in terms of this rule. My second principle is that the original host-selection, like a plesiomorph morphological character, may be shown by a number of disjunct groups, but a significantly different host association must, like an apomorph morphological character, indicate monophyly unless the same change has occurred more than once. When the phylogeny of a group has been established on morphological grounds, the application of this principle can also assist in indicating the priority of different types of host association.

If these two principles are applied to graph 2 it must inevitably be concluded that the earliest hosts of the Dacnusini were leaf-mining Agromyzidae. Of the seven different stems whose biology is known, the most plesiomorph species of six have this biology. Except in the case of *Chaenusa* selection of other families as hosts is clearly seen to be secondary. The known cases for Europe may be summarised as follows.[13]

### 1. *Psila* (Psilidae)

*Chorebus gracilis* (NEES), the well-known parasite of *Psila rosae* (F.), is an apomorph species which should be associated with the *senilis* group, all parasites of *Melanagromyza* and *Ophiomyia*. It is clear that a transference has occurred from a stem-boring *Melanagromyza* to the larger *Psila* larva with similar habits.

### 2. *Scaptomyza* (Drosophilidae)

The two leaf-mining species of *Scaptomyza* — *S. graminum* FALLÉN and *S. apicalis* HALIDAY [= *flaveola* MEIGEN] have each a host specific Dacnusine parasite, *Dacnusa faeroensis* (ROMAN) [= *lestes* NIXON] on the former and *Dacnusa temula* HALIDAY on the latter. All other *Dacnusa* spp. are as far as known parasites of Agromyzidae and Dacnusini are not known to attack other Drosophilidae. Again a change in host association from an Agromyzid leaf-miner appears certain.

### 3. Chloropidae

Excluding doubtful records all the Dacnusini parasites of the Chloropidae belong to a highly apomorph monophyletic group which I have considered as the single genus *Coelinius*. Several different biologies are shown within the *Coelinius* genus-group and their priority is not altogether clear. But the most plesiomorph species, *Laotris striatula* (HALIDAY), is a *Dizygomyza*-parasite.

### 4. *Amaurosoma* (Cordyluridae)

Only a single species known to me[14], *Synelix semirugosa* (HALIDAY), is known to attack this genus. This also belongs to the *Coelinius* genus-group.

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[13] In addition to the instances given RUSCHKA (1926, Dtsch. ent. Ztschr., **6**, 45) described his *Dacnusa lonchopterae* from a single specimen which he states was bred from *Lonchoptera lutea* PANZER (Lonchopteridae). I have not discussed this species, as its generic position is not known to me.

[14] *Dacnusa amaurosomae* TELENGA (1935) has been left out of consideration until its generic position can be confirmed

### 5. *Hydrellia* (Ephydridae)

The Dacnusini parasites of *Hydrellia* belong to two disjunct groups. One (*Chorebus* sensu NIXON, BURGHELE etc.) is a highly apomorph group belonging to *Chorebus* s. l. and related to the more plesiomorph *merella*-group which are parasites of *Dizygomyza* spp. The transference to *Hydrellia* is clearly an innovation which has occurred within the genus. The small genus *Chaenusa* is however shown as a separate stem of the Dacnusini in its own right, with all its members as far as known being parasites of *Hydrellia*. Until the relationships between the different main stems are better understood (perhaps as a result of larval studies) it is not clear whether this group too has derived from ancestors which attacked Agromyzidae.

Within the Agromyzidae there are some clear differences between the Dacnusine fauna bred from different genera, and it is informative to compare these and to consider what conclusions can be drawn. Two groups of unusual biology may be considered first. The larvae of *Phytobia* s. s. (= *Dendromyza* HENDEL) bore in the cambium of trees, where they are attacked by species of *Symphya* FÖRSTER. That genus belongs to the *Coelinius* genus-group, whose most plesiomorph species is, as already stated, a *Dizygomyza*-parasite. I think it must be deduced from the fact that *Phytobia* is only parasitised by this single highly apomorph genus that this host association is an innovation. Thus if the hypothesis suggested by NOWAKOWSKI (1962) that Agromyzidae originally fed in the cambium of some primitive arboreous Angiosperms is correct, there is no reason to think that they were attacked by Dacnusini at that stage.

The genera *Melanagromyza* and *Ophiomyia* (mainly stem-feeders, but containing a few gall-causers and leaf-miners) have a characteristic Dacnusine fauna belonging to two disjunct groups of *Chorebus* — the *senilis/leptogaster* complex and the small *cybele* group. The former group at least is strongly apomorph and related to the more plesiomorph *merella*-group, which are *Dizygomyza*-parasites. My interpretation of the different biologies shown by the left-hand branch of *Chorebus* on graph 1 is that the association with *Dizygomyza* is prior to an association with *Melanagromyza/Ophiomyia* or *Hydrellia*. The *cybele* group, though relatively plesiomorph in respect of its metapleural pubescence, is in several respects strongly apomorph, certainly much more so than some *Chorebus* spp. associated with leaf-miners on Gramineae. I think it can be accepted therefore that an association with *Melanagromyza* or *Ophiomyia* represents an innovation and that the original association of the Dacnusini was with Agromyzid leaf-miners. This conclusion corresponds well with the rather obvious hypothesis that the leaf-mining habit is prior to stem-boring in the Agromyzinae, because the genera in which the latter biology is dominant, *Melanagromyza* and *Ophiomyia*, form a strongly apomorph monophyletic group.

Turning to the rest of the family (mainly leaf-miners but including a few with different biologies), the known Dacnusine parasites of the major genera for which adequate material is available belong to the groups listed below. For the purposes

of this table *Exotela* has been divided into the apomorph species in which 1m-cu is received into cell $R_s$, and plesiomorph species in which it is not.

| | |
|---|---|
| *Agromyza nigripes/ambigua* group (Gramineae-feeders) | Plesiomorph *Exotela* spp., *Protodacnusa*, *Chorebus nydia* group, *Chorebus ovalis/lateralis* complex. |
| Other *Agromyza* spp. | Apomorph *Exotela* spp., *Dacnusa*, *Chorebus ovalis/lateralis* complex. |
| *Cerodontha* subg. *Dizygomyza* (monocotyledons other than Gramineae) | *Laotris*, *Dacnusa* (polyphagous sp. only), *Chorebus merella/cytherea* groups, *Chorebus ovalis/lateralis* complex. |
| *Cerodontha* subg. *Poemyza* (Gramineae) | Plesiomorph *Exotela* spp., *Chorebus talaris* (HALIDAY), *Chorebus ovalis/lateralis* complex. |
| *Liriomyza* | *Priapsis* and *Coloneura*, *Dacnusa*, *Chorebus ovalis/lateralis* complex. |
| *Phytomyza* | Apomorph *Exotela* spp., *Priapsis*, *Dacnusa*, *Chorebus ovalis/lateralis* complex. |

Now it is very striking from the above table that the parasite fauna of *Phytomyza*, *Liriomyza* and the "other *Agromyza* spp." is largely identical. The only differences are that no *Exotela* has yet been bred from *Liriomyza*, and no *Priapsis* from *Agromyza*. But the fauna of the three main groups which are exclusively leaf-miners of monocotyledons is significantly different. Only the *Chorebus lateralis/ovalis* complex is common to all Agromyzid leaf-miners. The differences between the Dacnusine fauna of the primary monocotyledon-feeders[15] and other leaf-mining Agromyzidae may be summarised as in the table on page 873.

It is very remarkable that, apart from the *Chorebus merella/cytherea* groups, the other four groups exclusive to the primary monocotyledon-feeders are all strongly plesiomorph, and it may be concluded that this host association is less removed from that of the common ancestor of the Dacnusini than an association with other groups of leaf-mining Agromyzidae. There is particularly clear evidence of vicariance in the case of *Exotela* where the plesiomorph species in which 1m-cu is not received into cell $R_s$ have been bred only from these hosts, while the species which are apomorph in this respect only from other leaf-mining Agromyzidae. It is also tempting to conjecture that *Protodacnusa* is a vicariant of *Dacnusa*, although definite morphological evidence for this is lacking.

It now remains to project the conclusions reached on the phylogeny and host association of the Dacnusini back into their chronological setting. I am not aware of any direct fossil evidence for the age and evolution of the Dacnusini, but once the priorities of the different types of host selection have been established, it is possible to draw certain broad conclusions from the evolution of their hosts.

[15] Under this term I include *Cerodontha* s. l. and the *Agromyza nigripes/ambigua* group which are both very large groups exclusively associated with monocotyledons. The few *Liriomyza* and *Phytomyza* spp. which also feed on Gramineae are all closely related to species feeding on dicotyledonous hosts and they have a similar parasite fauna to other members of their genera.

| Groups associated exclusively with the primary monocotyledon-feeders | Groups associated only with other leaf-mining Agromyzidae |
|---|---|
| Plesiomorph species of *Chorebus* (the *nydia* group on the *Agromyza nigripes/ambigua* group and *talaris* (HALIDAY) on *Cerodontha* subg. *Poemyza*) | *Dacnusa* (except that one polyphagous species sometimes attacks *Cerodontha* subg. *Dizygomyza*) |
| *Protodacnusa* (on the *Agromyza nigripes/ambigua* group) | Apomorph species of *Exotela* |
| Plesiomorph species of *Exotela* (on the *Agromyza nigripes/ambigua* group and *Cerodontha* subg. *Poemyza*) | *Priapsis* and *Coloneura* |
| *Laotris* (on *Cerodontha* subg. *Dizygomyza*) | |
| *Chorebus merella/cytherea* groups (on *Cerodontha* subg. *Dizygomyza*) | |

I would however emphasise at this stage that existing accounts of the evolution of the Agromyzidae may need to be modified considerably as the phylogeny of the family is better understood. But with this reservation I think it informative to attempt to link the phylogeny of the Dacnusini with that of their hosts.

The most recent account of the evolution of the Agromyzidae is given by NOWA-KOWSKI (1962). According to that author[16] it is likely that the Agromyzidae originally fed in the cambium of some primitive arboreous Angiosperms during the upper Cretaceous period. Subsequently the leaf-mining habit was evolved and during the Tertiary, when large numbers of arboreous plants changed into herbaceous, the family spread over all continents and speciated widely in association with many families of these herbaceous plants.

It is clear that there is no reason to suppose the association of Dacnusini with the Agromyzidae during the cambium-feeding stage (because the only known Dacnusini parasitic on the present-day *Phytobia* belong to a single highly apomorph genus). It appears therefore that the end of the Cretaceous is the earliest date for the association of the ancestral Dacnusine with an Agromyzid host or hosts. From the present-day distribution of plesiomorph species it is clear that we should seek this host or hosts among the ancestors of one or both of the primary monocotyledon-feeding genera — *Cerodontha* s. l. and the *Agromyza nigripes/ambigua* group. The group then spread to other Agromyzidae and certain other graminivorous Diptera Schizophora and speciated extensively. The association of a few species with *Psila* and *Scaptomyza* and of certain *Chorebus* spp. with *Hydrellia* is clearly of more recent origin.

[16] I am disregarding the alternative suggestion he gives — that the origin of the Agromyzidae consisted of a change from saprophagy to feeding in the thallus of liver-mosses — as it is founded on what I believe to be a false premise, that the larval characters of *Liriomyza mesnili* D'AGUILAR are plesiomorph.

More detailed comments on the relationship between speciation and host association within the genera will be included in later parts of this paper after detailed breeding records have been given. I think it probable that the *Chorebus ovalis/ lateralis* complex has resulted from the fragmentation of a single oligophagous species. All its species show a high degree of host specificity, but they are remarkably evenly spread over *Agromyza* and almost all Phytomyzinae except *Phytobia* s. s. Yet there are few hosts from which more than one species of the group can be bred. The phenomenon of secondary oligophagy or polyphagy is well-known in the Agromyzidae and a contemporary case is shown in the Dacnusini by *Dacnusa maculipes* THOMSON, which freely attacks most leaf-mining Phytomyzinae.

## Appendix I — Definition of Terms used to describe Host Association

The terms used for describing the host ranges of phytophagous insects have been standardised by HERING (1951). These same terms are appropriate for describing the host ranges of parasitic insects, and will be used with HERING's definitions in this series of papers. The apparently new term "Disjunctive Monophagy" has been adopted to correspond at a lower level with Disjunctive Oligophagy. The definitions are as follows:

I Systematic Monophagy — attacking a single "natural genus" or species of host

  (a) Monophagy (first degree) or Specific Monophagy — restriction to a single species of host

  (b) Monophagy (second degree) or Superspecific Monophagy — restriction to a closely related group or pair of species

  (c) Monophagy (third degree) or Generic Monophagy — restriction to a single "natural genus"

II Systematic Oligophagy — attacking a related range of hosts

  (a) Oligophagy (first degree) — restriction to related "natural genera" in the same family

  (b) Oligophagy (second degree) — attacking different but related families

  (c) Oligophagy (third degree) — attacking different but related orders

III Disjunctive Monophagy — having a host range which exhibits monophagy around two or more host species, species-groups or "natural genera" which are not closely related

  (i) A special case of Disjunctive Monophagy is Combined Generic Monophagy, where Generic Monophagy is combined with a lower category (i. e. Specific or Superspecific Monophagy)

IV Disjunctive Oligophagy — having a host range which exhibits oligophagy around two or more groups of hosts which are not closely related

  (i) A special case of Disjunctive Oligophagy is Combined Oligophagy, where the host range combines oligophagy with monophagy.

Xenophagy is the term used to denote an abnormal choice of host: in the sense that the above four categories are all descriptive of normal host selection, they

may be considered subordinate to the term Euphagy, denoting normal selection in opposition to Xenophagy.

HERING's broader categories of Polyphagy and Pantophagy are not needed for this work. There is also no need to define terms denoting temporary parasitism or alternating generations on different hosts, as I know of no such cases in the Alysiinae.

I have chosen for the purposes of this terminology to depart from the existing generic classification of the Agromyzidae in many cases. This is necessary because some of the existing concepts are unsatisfactory, and others are at widely differing levels. There is no species of Dacnusini with a host range corresponding to the present wide and heterogeneous concepts of *Agromyza* and *Phytomyza*, and, if the formal classification were rigidly adhered to, the (meaningless) conclusion would be drawn that generic monophagy occurs only in the parasites of small genera such as *Phytagromyza* s. s. (i. e. the Salicaceae-feeders). Hence my use of the term "natural genus" in the table above to denote large species-groups (such as the *Agromyza ambigua/nigripes* group and the *Phytomyza obscura* group), which may eventually become recognised as genera or subgenera when the classification of the Agromyzidae is better understood.

## Appendix II — Practical Key to the Genera of Dacnusini

This key departs from the phylogenetic arrangement of genera notably because the difficulty of characterising some *Exotela* spp. makes it preferable to approach them by a process of elimination when constructing a practical key which may be used by inexperienced students. The same applies to *Dacnusa* since its primary character, sexual dimorphism of the pterostigma, cannot be confirmed from single specimens considered in isolation. A few of the couplets in this key are based on NIXON (1943), but most of it is new.

### Key to the genera of Dacnusini

1 Longitudinal striation generally extending over tergite 3 (and sometimes more extensively). Metapleuron sculptured with sparse hairs directed more or less downwards towards the coxa. Mandibles either 4-toothed or, if more or less 3-toothed, dominated by a large, often long and pointed, tooth 2 (the plesiomorph form of mandible with 3 about equally developed teeth is never retained) . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . *Coelinius* genus-group    2

> Notes: (i) Some *Coelinius* spp. in which tergite 3 bears only shallow rugose sculpture or is even completely smooth may be readily recognised by their enlarged pterostigma (cf. fig. 8), evenly curved $R_S$ and elongate mandible with long pointed tooth 2.
> (ii) All species in which the additional mandibular tooth is situated before the original tooth 2 (fig. 37) belong to this group, but species in which the additional tooth is situated after tooth 2 may belong either here or to *Chorebus*, *Dacnusa* or *Exotela*.

— Tergite 3 generally smooth, at most sculptured at its extreme base . . . . . . . .    7

> Notes: (i) In *Exotela vaenia* (NIXON) tergite 3 bears shallow longitudinal striation, but unlike any member of the *Coelinius* genus-group this species has broad 3-toothed mandibles with the teeth about equally developed.
> (ii) Two species of *Chorebus* in which tergite 3 bears longitudinal striation may be recognised by their characteristic metapleural pubescence (a rosette of short dense hairs around a raised swelling) (figs. 22 and 23).

2     Pterostigma (fig. 8) short and broad: cell $2R_1$ short . . . . . . . . . . . .    3

—     Pterostigma and cell $2R_1$ more elongate . . . . . . . . . . . . . . . . .    5

3     Species of very slender build, the gaster at least two and a half times as long as wide, laterally compressed towards the apex in the female. Mandibles dominated by a large pointed tooth 2 in most species; if 4-toothed the additional tooth is small and situated before the original tooth 2 . . . . . . . . . . . . . . . *Coelinius* Nees

Three subgenera may be distinguished as follows.

(i) $R_s$ sinuate. Petiole elongate (over twice as long as broad). Mandibles obviously 4-toothed, with the additional tooth before the original tooth 2. Tergite 3 with longitudinal striation at base. . . . . . . . . . . . . . . . . . . . *Coelinius* Nees s.s.

(ii) $R_s$ sinuate. Petiole massive (less than twice as long as broad). Mandibles dominated by very large tooth 2. Longitudinal striation extending over tergite 3 and part of tergite 4 . . . . . . . . . . . . . . . . . . . *Polemochartus* Schulz

(iii) $R_s$ evenly curved. Petiole elongate (over twice as long as broad). Mandibles dominated by large, usually long and pointed, tooth 2: additional tooth poorly developed or absent. Sculpture of tergite 3 variable, sometimes absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Coelinidea* Viereck

—     Species of stout build, the gaster not more than twice as long as wide, dorso-ventrally compressed in both sexes. Mandible broad, obviously 4-toothed . . . . .    4

4     Postscutellum with a strong medial spiniform projection. Tergites 3 and 4 very large, both covered with longitudinal striation, occupying at least two-thirds of the gaster beyond the petiole and in some species forming a carapace which covers almost the whole of the gaster. Mandibles massive with 4, all about equally developed, strong teeth . . . . . . . . . . . . . . . . . . . . . *Symphya* Förster

—     Postscutellum with only a weak medial spur. Tergites 3 and 4 not enlarged: longitudinal striation not extending beyond tergite 3. Mandibles 4-toothed with tooth 3 wide and blunt . . . . . . . . . . . . . . . . . . . . . . . *Epimicta* Förster

5     Mandibles very small, 4-toothed with tooth 2 the longest. Gaster elongate with tergites 3 onwards bearing numerous hairs over their entire surface. Vein $R_s$ sinuate. Clypeus, thorax and temples punctate . . . . . . . . . . . . *Aristelix* Nixon

—     Gaster not so extensively hairy, at most the more apical tergites bearing more than one row of hairs. Clypeus and temples more or less smooth . . . . . . .    6

6     Mandibles bearing a small additional tooth before the original tooth 2 (fig. 37). Gaster short, about as long as the thorax, without any indication of more than one row of hairs on any tergite, dorso-ventrally compressed in both sexes. $R_s$ sinuate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Laotris* Nixon

—     $R_s$ evenly curved (fig. 7). Gaster elongate, strongly laterally compressed in the female, with more than one row of hairs on the apical tergites . . *Synelix* Förster

7     Eyes hairy (this is best seen in dorsal view). Metapleuron sculptured with sparse hairs mostly directed downwards. Pterostigma short and broad (in some species very markedly so) . . . . . . . . . . . . . . . . . . . . . *Chaenusa* Haliday

—     Eyes bare . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .    8

8     Mandibles generally 4-toothed, the additional tooth situated between the original teeth 2 and 3 (figs. 24 and 25), sometimes represented by little more than a projection from the posterior side of the base of tooth 2. In addition most species are characterised by their metapleural pubescence, which forms a dense rosette of radiating hairs around a raised swelling (figs. 22 and 23) (which may be smooth or rugose), and short adpressed propodeal pubescence. Precoxal suture always present, but sometimes represented only by a long smooth groove. *Chorebus* Haliday

Note: Species with elongate apparently 3-toothed (fig. 26) or otherwise modified mandibles can be recognised as belonging to this genus by their metapleural and propodeal pubescence. No species in this genus retains the plesiomorph form of mandible with 3 about equally developed teeth.

—     Mandibles generally 3-toothed. Metapleural pubescence sparse or, if dense, evenly distributed and directed downwards towards the coxa, not adpressed. . . . . .    9

Notes: (i) *Exotela interstitialis* (THOMSON) which has 4-toothed mandibles (fig. 35) may be recognised by its plesio-
morph metapleural pubescence (cf. fig. 16) and the presence of pubescence over the surface of tergite 3.
(ii) A few species of the *Dacnusa stramineipes* group which have 4-toothed mandibles may be recognised
by their very elongate pterostigma, and the long evenly-distributed pubescence of their metapleuron,
propodeum and petiole.

9   Vein 1m-cu received into cell $R_s$ (fig. 13) . . . . . . . . . . . .*Exotela* FÖRSTER (in part)
—   Vein 1m-cu generally received into cell $1R_1$ (interstitial in a few *Dacnusa* spp.
which may be recognised by their large pterostigmata (fig. 9) and the absence of the
precoxal suture)  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .   10
10  Head massive, 1.4—1.6 times as wide as the thorax, with the temples (in dorsal
and lateral views) at least as broad as the eye-width (figs. 2 and 36). Mandibles con-
siderably enlarged (0.21—0.3 mm. wide) with tooth 3 expanded laterally, not or
weakly angulate. Metapleural and propodeal pubescence sparse. Pterostigma not
dimorphic. ♀ ovipositor concealed  . . . . . . . . . . . *Protodacnusa* gen. nov.
—   Head about 1.4 times as wide as the thorax. Mandibles very much enlarged (over
0.2 mm. wide) with tooth 3 not or only weakly angulate. Ocellar triangle unusually
small. Metapleuron and propodeum clothed with long whitish pubescence. Ptero-
stigma wedge-shaped, darker in the male. ♀ ovipositor projecting far beyond the
apex of the gaster. Cell 2Cu narrow. . . . . . . . . . . . . . . . . . *Amyras* NIXON
—   Mandibles rarely so large, and, if so, tooth 3 is not more expanded than tooth 1   11
11  Cell 2Cu open, at least at its lower distal corner  . . . . . . . . . . . . . . . .   12
—   Cell 2Cu closed by vein $Cu_{1b}$ at its lower distal corner  . . . . . . . . . . .   14
12  Length 2.8—3 mm. Cell 2Cu about three times as long as wide. Antennae strongly
sexually dimorphic (♂, 42—48 segments: ♀, 29—33). Petiole about twice as long as
apically wide, more or less parallel-sided. . . . . . . . . . . . . . . . *Tates* NIXON
—   Smaller species with cell 2Cu not more than twice as long as wide. Number of anten-
nal segments not strongly dimorphic . . . . . . . . . . . . . . . . . . . . . . . .   13
13  Cell 2Cu not closed below by a vein. Maxillary palpi very short, 5-segmented.
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Coloneura* FÖRSTER
—   Cell 2Cu closed below by vein 1a, open only at its lower distal corner. Maxillary
palpi short, but 6-segmented . . . . . . . . . . . . . . . . . . . . *Priapsis* NIXON
14  Pterostigma sexually dimorphic, darker and often larger in the male, varying consi-
derably in shape between species. Species with exceptionally elongate pterostig-
mata (the *stramineipes* and *areolaris* groups, see fig. 10) are also characterised by
dense metapleural and propodeal pubescence. Precoxal suture often lost. . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Dacnusa* HALIDAY

Note: The few species retaining a rugose precoxal suture and sparsely pubescent metapleuron can be distinguished
from *Exotela* by their wedge-shaped or otherwise enlarged pterostigmata.

—   Pterostigma identical in both sexes, never enlarged or wedge-shaped. Metapleural
pubescence sparse (fig. 16). Rugose precoxal suture present. . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Exotela* FÖRSTER (in part)

## Appendix III — The *Chorebus nydia* group

On the basis of the form of the mandibles I have included in *Chorebus* a number
of species which lack the apomorph metapleural pubescence characteristic of most
species of the genus. These species are particularly important for my study of the
relationship between phylogeny and host association, and were therefore studied
carefully. Three species included by NIXON (1937, 1943 and 1946) under the name
*nydia* probably represent a monophyletic group (here termed the *nydia* group)
and have been redescribed and discussed below. The apomorph characters which
lead me to consider these species monophyletic are their slightly projecting clypeus
and somewhat shortened maxillary palpi, whose proportions are identical in all

three species (fig. 24). Their association is supported by a very high degree of morphological resemblance (see the table of biometric data below).

The delimitation of the species included in the key below from the rest of *Chorebus* on the basis of metapleural pubescence is not as clear-cut as might be wished because there are a few species (e. g. *acco* (NIXON), *anita* (NIXON), *ampliator* (NEES) and *myles* (NIXON)) in which the metapleural pubescence shows only a weak tendency to be differentiated in the form of a rosette and the propodeum is largely bare. Nevertheless these species can with experience be distinguished from those included in the key below because the raised area on the lower half of the metapleuron is largely bare or if bearing hairs these are noticeably longer than the surrounding hairs and tend to radiate. *Chorebus cybele* (NIXON) and a few related species also have more or less plesiomorph metapleural pubescence (fig. 21), but can be readily distinguished from the species keyed below by their narrow mandibles, elongate form and short dense propodeal pubescence.

### Key to some plesiomorph species of *Chorebus*

(including species whose metapleural pubescence shows little tendency to form a rosette around a more sparsely haired central swelling. All except *freya* show a conspicuous rugose swelling on the lower half of the metapleuron. Propodeum bare or with only a few inconspicuous scattered hairs.)

1  20—21 antennal segments. Metapleuron (fig. 19) only feebly sculptured on its lower half with two or three long hairs. Maxillary palpi brown, very short. Coxae and hind femora and tibiae darkened . . . . . . . . . . . . . *freya* (NIXON) **comb. nov.**
—  Antennae with at least 29 segments. Metapleuron (figs. 17, 18, 20) with a clearly defined rugose swelling on its lower half . . . . . . . . . . . . . . . . . . . . .     2

2  Antennae with 39—46 segments. Mandibles very much enlarged (width about 0.3 mm.), with tooth 3 showing as a projection on the lower side of 2 and often much reduced. Notaulices well-defined to middle of mesoscutum. Metapleural swelling clothed with long hairs. Length about 3 mm. . . . . . . *phaedra* (NIXON) **comb. nov.**
—  Antennal segments fewer. Mandibles narrower, always with a distinct tooth 3 . . .     3

3  Base of tergite 3 with rugose sculpture similar to that of the petiole. Mandible narrow with tooth 2 sharply pointed. Precoxal suture narrow, feebly rugose. Metapleuron (fig. 20) with well-defined rugose swelling clothed with long hairs. Notaulices absent. Legs obscurely brownish yellow with the hind coxae dark. *talaris* (HALIDAY) **comb. nov.**
        Host: *Cerodontha* (*Poemyza*) *pygmaea* MEIGEN
—  Tergite 3 without sculpture . . . . . . . . . . . . . . . . . . . . . . . .     4

4  32 antennal segments (1 ♀). Hind tarsus very slightly shorter than its tibia; hind coxa conspicuously rugose. Anterior face of mesoscutum clearly rugose: hairs extending all over the anterior half of the lateral lobes. Legs and palpi largely dark
   . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *rhanis* (NIXON) **comb. nov.**
—  Palpi yellow. Femora and tibiae yellow . . . . . . . . . . . . . *nydia* group    5

5  Coxae yellow. Mesoscutum densely clothed with short hairs (fig. 30) over almost its entire surface. Metapleural pubescence rather dense (fig. 18) . . . ***spenceri* sp. nov.**
        Host: *Agromyza phragmitidis* HENDEL
—  Coxae dark. Metapleural pubescence sparser (fig. 17) . . . . . . . . . . . . .     6

6  At least the four apical tarsal segments darkened. . . . . *nydia* (NIXON) **comb. nov.**
        Host: *Agromyza nigripes* MEIGEN
—  Tarsal segments 1—4 yellow, but segment 5 contrastingly black. . . . . . . . . .
   . . . . . . . . . . . . . . . . . . . . . . . . . . *coxator* (THOMSON) **comb. nov.**
        Hosts: *Agromyza phragmitidis* HENDEL and *hendeli* GRIFFITHS

*Chorebus nydia* (Nixon), **comb. nov.**

*Dacnusa nydia* Nixon, 1937, 1943 and 1946 (in part)

Colour.[17] Antennae dark, except for a small ring at the base of the flagellum. Mandibles dark red with black teeth. Labrum black, but labial and maxillary palpi contrastingly yellow. Coxae and usually trochanters of all legs shining black. Femora and tibiae of all legs golden yellow. Tarsal segments progressively darkened.

Morphology. Ocellar triangle with its base longer than its sides. Frons bare apart from a few hairs along the eye-margins. Face conspicuously pitted, with short adpressed pubescence, but becoming bare and smooth along its central line. Clypeus somewhat projecting in profile (compare fig. 24). Antennal segments: ♂, 29(2), 30(2), 31(2), 32(1), 33(1); ♀, 28(2), 29(4), 30(7), 31(2). Mandibles with tooth 1 somewhat expanded in most specimens.

　Central lobe of mesoscutum (fig. 29) with distinct microsculpture, covered with short hairs: lateral lobes usually with fewer hairs and bare at their centre (in a few Irish specimens however the pubescence is more extensive): notaulices rugose, clearly defined to the middle of the mesoscutum, often with long outstanding hairs along their course. Sides of pronotum and mesepisternum with distinct scaly reticulation: both the precoxal and epicnemial sutures of the mesepisternum are broad and rugose-costate (compare fig. 27): subalar callus with only a few hairs. Metapleuron largely bare and shining, with a coarsely rugose swelling on its lower half from which arise a few weak hairs (fig. 17).

　Wing (compare fig. 34) with veins $Cu_{1a}$ and $Cu_{1b}$ both virtually eliminated, and 1a a little shortened: cell 2Cu is therefore widely open at its lower distal corner. $R_s$ more or less evenly curved.

　Propodeum reticulate-rugose, with very sparse short fine hairs which in no way conceal the surface beneath. Petiole almost bare, with longitudinal striation and generally a distinct central keel (fig. 32), similar to that of *coxator*.

Breeding Records

　　　Host — *Agromyza nigripes* Meigen

　　from larvae and puparia 5. ix. 53 and 5. ix. 60 on *Glyceria maxima*, Ash Vale, Surrey, England, emerged 14. ix. 53, 3. x. 60, 10. iii. 61, 20. v. 54 and 22. v. 54: from puparia on the same plant, Buckingham Palace Gardens, London, emerged 19. iii. 62 (2) (Spencer).

Some of these records have already been published in Griffiths (1956) and Griffiths (1963a).

Other material examined

　The holotype ♀, Byfleet, Surrey, 17. vii. 32 (Coe) is the only other English specimen seen apart from the bred material. But Mr. A. W. Stelfox has sent me Irish material with the following data:

　1♀,　　Bahana Wood, Carlow, 9. vi. 35
　1 ♂ 1 ♀, Bushfoot, Antrim, 3. vi. 38

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[17] In all descriptions the general body colour is black unless otherwise stated. Characters which admit of simple numerical expression are given in the table of biometric data and omitted from the verbal descriptions.

| | |
|---|---|
| 1 ♀, | River Boyne, Meath, 30. vii. 39 |
| 2 ♂♂, | Clondalkin, Dublin, 29. vi. 41 |
| 1 ♀, | Three Castles, Wicklow, 31. vii. 46 |
| 1 ♀, | Lucan, Dublin, 26. v. 48 |
| 1 ♂, | Golliestown, Dublin, 4. viii. 48 |
| 1 ♂, | The Murrough, Killoughter, 16. viii. 40: 1 ♂ 2 ♀♀, same locality, 5. vi. 49 |
| 1 ♂ 1 ♀, | Inch Abbey, Down, 21. vi. 57 |
| 1 ♀, | Lough Gill, Leitrim, 11. vi. 59 |
| 1 ♀, | Shriff, near Drumahaire, Leitrim, 11. vi. 60 |

Location of material. Holotype and three bred specimens in the British Museum (Natural History): other bred material in my personal collection: Mr. STELFOX's material in his personal collection.

NIXON's (1937) original description of this species is considered to be composite and two of his three paratypes are now referred to C. *spenceri* sp. nov. and one to C. *coxator* (THOMSON).

### Chorebus coxator (THOMSON), comb. nov.

*Dacnusa* (*Dacnusa*) *Coxator* THOMSON, 1895

*Dacnusa nydia* sensu NIXON, 1937, 1943 and 1946 (in part)

This species is to be compared with *nydia* in the following respects.

Colour. Labrum yellow-brown. Coxae of all legs shining black or dark brown, but the trochanters golden yellow. Femora, tibiae and first four tarsal segments of all legs yellow, but tarsal segment 5 contrastingly black.

Morphology. Clypeus strongly projecting in profile (fig. 24). Antennal segments: ♂, 31(1), 33(2), 35(2); ♀, 29(1), 30(2), 32(2), 33(2).

Microsculpture of mesoscutum extending over the lateral and central lobes: notaulices feebly developed, the hairs along their course not obviously outstanding: lateral lobes (fig. 28) as well as central lobe covered by short hairs. Sides of pronotum bare, but with distinct scaly reticulation.

Petiole very broad, similar to that of *nydia*, deeply longitudinally striate but usually without any central keel.

## Breeding Records

### Host 1 — *Agromyza phragmitidis* HENDEL

from larvae 28. ix. 60 on *Phragmites communis*, Woodwalton Fen, Huntingdon, England, emerged 4. v. 61, 10. v., 14. v., 22. v. and 21. vi. 61: from larva 23. viii. 60, same plant and locality, emerged 14. v. 61: from larva 13. ix. 54 on same plant, Slapton, South Devon, England, emerged iv. 55 (SPENCER): from puparium 7. x. 24 on same plant, Hogley Bog, Oxford, England, emerged 30. v. 25 (HAMM) (designated a paratype of *nydia* by NIXON, 1937).

### Host 2 — *Agromyza hendeli* GRIFFITHS [= *lucida* auctt.]

from larvae and puparia 23. viii. 60 on *Phragmites communis*, Woodwalton Fen, Huntingdon, emerged 18—20. ix. 60 (3 specimens).

Some of these records have already been published in GRIFFITHS (1963a) where this species is refered to as "*Dacnusa* spec. *b*" and in GRIFFITHS (1963b).

Other material examined

Lectotype ♀ (by present designation), Lille, France
Woodwalton Fen, Huntingdon, England, 1949 (FORD)
Löderup, Skåne, Sweden, 24. vii. 38 (PERKINS)

Location of material. Lectotype in the THOMSON collection at Lund: HAMM's specimen in the Hope Department, Oxford: remaining material divided between my personal collection and the British Museum (Natural History).

This species agrees with *nydia* in most respects, but it can readily be distinguished by the colour of the tarsi: also the notaulices are generally less well developed. The southern English material of *nydia* can also be distinguished from *coxator* by the sparser mesoscutal pubescence (see figs. 28 and 29), but some Irish specimens which I consider to be *nydia* have more extensive pubescence. The separation of these two species as ecological vicariants is probably very recent (and perhaps not yet complete) and the coxal coloration (clearly apomorph in *coxator*) is the only reliable diagnostic criterion I have found.

### *Chorebus spenceri* sp. nov.

*Dacnusa nydia* sensu NIXON, 1937, 1943 and 1946 (in part)

Colour. Antennal scape yellow beneath, but flagellum entirely dark. Centre of mandibles orange. Labrum orange-yellow. Labial and maxillary palpi yellow. Legs orange-yellow, except for the progressively darkened tarsal segments. Gaster with tergite (3 + 4) dark brown, the following tergites black.

Morphology. Ocelli forming a triangle whose base is only slightly longer than its sides: in the centre of the triangle is a rugose longitudinal impression. Frons bare above the antennae, but with 3—4 rows of hairs along the eye-margins and a band of two rows across from the upper eye-margin to the ocellar triangle: ocellar triangle with about 8 short hairs. Face shallowly pitted, with dense pubescence except along its central line. Antennal segments: ♂, 32(2), 34 (holotype). Mandibles narrower than those of *coxator* (compare fig. 24) with tooth 1 small, not expanded.

Mesoscutum covered with reticulate sculpture, especially on its central lobe: notaulices visible to about its middle: its entire surface covered with short dense hairs in the holotype (fig. 30), but the two paratypes show a small bare area on the hind part of the lateral lobes. Propleuron and sides of pronotum covered with short hairs (these are conspicuous in the holotype and the Inverness paratype, but not in the other paratype). Precoxal and epicnemial sutures of the mesepisternum (fig. 27) very broad and rugose-costate: subalar callus densely haired. Metapleuron (fig. 18) bearing a very coarse rugose swelling, from which arise a few long hairs: the area around the swelling is rather densely clothed with hairs but no rosette is formed.

Wing (fig. 33) with $R_s$ obviously sinuate (unlike *nydia* and *coxator*). Vein $Cu_{1a}$ virtually eliminated; $Cu_{1b}$ is still more or less developed in the holotype (so that cell 2Cu is only narrowly open at its lower distal corner), but has been eliminated in the two paratypes.

Propodeum deeply and coarsely rugose, with fine hairs which, though denser than in *nydia* and *coxator,* in no way obscure the surface beneath. Petiole more elongate (fig. 31), bearing irregular more or less reticulate sculpture and two apical rows of about 4 short hairs.

Breeding Records
        Host — *Agromyza phragmitidis* HENDEL

Holotype ♂ from larva 13. ix. 54 on *Phragmites communis*, Slapton, South Devon, England, emerged iv. 55 (SPENCER).

This record has already been published in GRIFFITHS (1963a), where this species is refered to as "*Dacnusa* spec. *a*". In addition two caught males are designated paratypes, with the following data:

Loch Garten, Inverness, Scotland, 21. vi. 33 (COE)
Isle of Wight, England, ix. 31 (BLAIR) (British Museum 1937—2)

Both these specimens were previously designated as paratypes of *nydia* by NIXON (1937).

Location of material. Holotype in my personal collection: the two paratypes in the British Museum (Natural History).

This species differs from *nydia* and *coxator* most obviously in the very extensive thoracic pubescence and the yellow coxae. Other differences worthy of note are the retention of an obviously sinuate $R_s$, the narrower petiole and the narrower mandibles.

### Discussion

The species of the *nydia* group show a high degree of host specialisation. The host range of *coxator* is classed as superspecific monophagy (see Appendix I) and the other two species, as far as known, exhibit specific monophagy. In the case of *nydia* the evidence for specific monophagy is strongly supported by the fact that large numbers of *Agromyza albipennis* MEIGEN were bred along with the host *A. nigripes* MEIGEN at the Ash Vale locality, but only puparia of the latter species yielded *nydia*. *A. albipennis* and *A. nigripes* are a monophyletic pair of species (i. e. superspecies) according to GRIFFITHS (1963a). However in the case of *spenceri* only a single specimen has been bred and the classification of its host range as specific monophagy can only be provisional.

Within the *nydia* group I consider that *nydia* and *coxator* are monophyletic since their morphological differentiation is in general very slight and they are clearly synapomorph in respect of vein $R_s$, whose sinuation has been virtually eliminated (fig. 34), while *spenceri* retains a plesiomorph obviously sinuate $R_s$.

In the diagram below (on p. 883) the phylogeny of the *nydia* group is compared with that of their hosts. The diagram of host phylogeny is taken from GRIFFITHS (1963a).

Two of the *Agromyza* spp. — *A. albipennis* and *A. lucida* — have been bred frequently but have not yielded parasites of the *nydia* group. This makes it seem improbable that the vicariance of *nydia* and *coxator* has arisen through simultaneous speciation of host and parasite. Consideration of the time factor also tells

Agromyza                                                          Chorebus
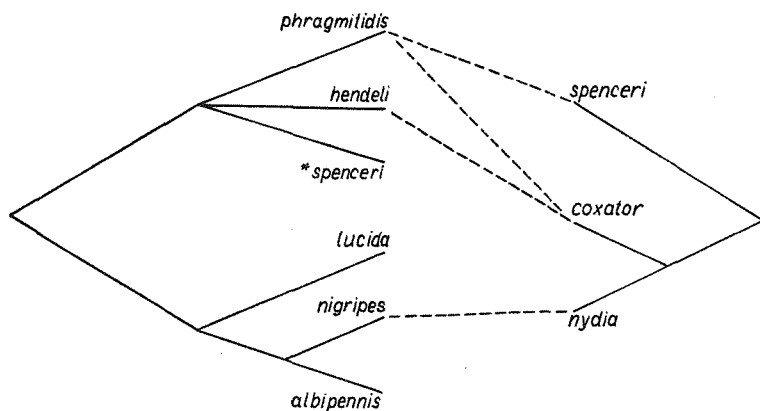


\* The parasites of *Agromyza spenceri* GRIFFITHS are not known.

against the possibility of simultaneous speciation. While there is no clear criterion for comparing the age of the branching of the two phylogeny trees, it seems unlikely in view of the minimal morphological differences of the two parasite species that their separation can correspond with the earliest branching of the host tree. The available evidence thus suggests that their speciation has followed upon a secondary expansion of host range, though which association is the earlier is not clear.

### Appendix IV — Notes on the types of some of FÖRSTER's (1862) species

FÖRSTER (1862) proposed a number of new generic names for the Dacnusini (his "Dacnusoidae"), but the descriptions he gave were very inadequate. As a result the application of nearly all his new names has been doubtful, and most have not been used by subsequent authors. In revising the generic classification of the Dacnusini it was necessary for me to check from FÖRSTER's types the application of some of his generic names which were based on his own new species. Notes of the results of my examination are given below.

The type locality (not given in FÖRSTER's paper) of these species is Aachen except for *Brachystropha monticola*, which is labelled "Celerina" (where this is I have not been able to trace, but the specific name doubtless implies that it is in a mountainous area), and *Isomerista oligomera*, which bears no locality label.

*Synelix agnata*

The three specimens sent me are all males of *semirugosa* HALIDAY, and the following synonymy is therefore established:

**Synelix semirugosa** (HALIDAY), **comb. nov.**

*Alysia (Dacnusa) semirugosa* HALIDAY, 1839
*Synelix agnata* FÖRSTER, 1862 **syn. nov.**
*Dacnusa semirugosa* (HALIDAY), MARSHALL, 1891 and 1897, NIXON, 1937
*Ectilis semirugosa* (HALIDAY), NIXON, 1943 and 1954

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*Exotela cyclogaster*

The single specimen sent me is a female of the species subsequently described as *Dacnusa bellina* by NIXON (1937). The following synonymy is therefore established:

**Exotela cyclogaster** FÖRSTER

*Exotela cyclogaster* FÖRSTER, 1862
*Dacnusa bellina* NIXON, 1937 **syn. nov.**
*Toxelea bellina* (NIXON), NIXON, 1954

*Coloneura stylata, Isomerista oligomera* and *Trisisa exilis*

Incredible as it may seem FÖRSTER has described these three so-called new genera from a short series of the female sex of a single species (the species subsequently described by NIXON (1943) as *Merites taras*).

I received two specimens as *Coloneura stylata*, with 19 and 18 antennal segments respectively. A further specimen (with 17 antennal segments) was sent as *Isomerista oligomera*. As *Trisisa exilis* I received a mount bearing two insects, one of which was a further female (with 18 antennal segments) of this same species, but the other a male of a small *Dacnusa* species. As this latter clearly does not fit FÖRSTER's description, I designate the female as lectotype.

As first reviser I give priority to *Coloneura stylata*, because its types are in good condition, notwithstanding the page precedence of the other two names. The following synonymy is established:

**Coloneura stylata** FÖRSTER

*Coloneura stylata* FÖRSTER, 1862
*Isomerista oligomera* FÖRSTER, 1862 **syn. nov.**
*Trisisa exilis* FÖRSTER, 1862 **syn. nov.**
*Merites taras* NIXON, 1943 and 1954 **syn. nov.**

*Brachystropha monticola*

I have received a single male of a *Dacnusa* sp. with characteristically short cell $2R_1$, largely bare mesoscutum and dark legs. I consider it to be the same species as NIXON's *mutia*, and therefore establish the following synonymy:

**Dacnusa monticola** (FÖRSTER), **comb. nov.**

*Brachystropha monticola* FÖRSTER, 1862
*Rhizarcha mutia* NIXON, 1948 **syn. nov.**
*Dacnusa (Rhizarcha?) coracina* STELFOX, 1954 **syn. nov.**
*Pachysema coracina* (STELFOX), NIXON, 1954
*Pachysema mutia* (NIXON), STELFOX, 1957

The synonymy of *coracina* with *mutia* was established by STELFOX (1957).

*Stiphrocera nigricornis*

The four specimens sent me are all *ampliator* NEES sensu NIXON. Accepting NIXON's interpretation of NEES' species I established the following synonymy:

**Chorebus ampliator** (NEES), **comb. nov.**

*Alysia ampliator* NEES, 1834

*Alysia (Dacnusa) ampliator* NEES, HALIDAY, 1839

*Stiphrocera nigricornis* FÖRSTER, 1862 **syn. nov.**

*Dacnusa ampliator* (NEES), MARSHALL, 1891 and 1897, NIXON, 1937, 1943
    and 1946

## *Tanystropha haemorrhoa*

The single specimen is a male of the *Dacnusa stramineipes* group. Probably it is *stramineipes* HALIDAY, a synonymy already suggested by MARSHALL (1891). Its antennae are broken with 22 segments remaining — I judge there to have been originally at least 25 segments. I refrain from establishing a formal synonymy without more detailed study of the group.

## *Mesora gilvipes*

The single female of FÖRSTER's misidentified type-species (i. e. not *Alysia (Dacnusa) gilvipes* HALIDAY, 1839) clearly belongs to *Exotela* in the sense proposed in this paper, not to the *Dacnusa abdita* group as has sometimes been assumed. As it is in poor condition I am not certain which species it represents, but I suspect that it is a small specimen of *hera* NIXON. The question of its precise specific identity is unimportant, as the species-name was not new. The generic name has been formally synonymised with *Exotela*, which has page priority and a better type, in my summary of proposed classification (above).

## Appendix V — Notes on THOMSON's (1895) new species of *Dacnusa*

THOMSON (1895) described a number of new species of Dacnusini, but his descriptions unfortunately omit several important characters. Consequently subsequent authors have had difficulty in interpreting his names, and many of them have not since been used. Through kindness of Dr. SVEN JOHANSSON of the Zoological Institute at Lund University, I have been able to examine the material in THOMSON's collection of all his new species of his subgenus *Dacnusa*, and have summarised the results of my examination in this Appendix.

Besides the species on whose identity I am giving a definite opinion, there are a number (at the end of the list below) on whose specific identity I have not wished to make any definite statement without more detailed study of the groups to which they belong. Nevertheless I have thought it useful in these cases too to indicate the species-group concerned for future reference, as THOMSON's subdivision of his subgenus *Dacnusa* into eight Sectiones can now be seen to have little merit, all except Sectiones 1 and 2 being heterogeneous.

*albicoxa*

The single female sent me from the type locality (Ringsjön) confirms the synonymy of this name with *lateralis* HALIDAY established by NIXON (1937). The synonymy now reads:

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### Chorebus lateralis (Haliday), comb. nov.

*Alysia (Dacnusa) lateralis* Haliday, 1839
*Dacnusa lateralis* (Haliday), Marshall, 1891 and 1897, Nixon, 1937 and 1944
*Dacnusa (Dacnusa) albicoxa* Thomson, 1895

### albilabris

I have received a male from Mölle and a female from Yddinge (both localities being named in the original description). The female is clearly *Exotela gilvipes* (Haliday), but the male probably another *Exotela* species. In order to confirm the synonymy established by Nixon (1937) I designate the female as lectotype. The synonymy now reads:

### Exotela gilvipes (Haliday), comb. nov.

*Alysia (Dacnusa) gilvipes* Haliday, 1839
*Dacnusa gilvipes* (Haliday), Marshall, 1891 and 1897, Nixon, 1937
*Dacnusa (Dacnusa) albilabris* Thomson, 1895
*Toxelea gilvipes* (Haliday), Nixon, 1954

### aridula

The single specimen represents a *Protodacnusa* species, which is redescribed in Appendix VI.

### aterrima

I have received a single female from Kävlinge (the type-locality) which I designate as lectotype (there is also another male in the collection in bad condition which I have not examined). This is a very characteristic species, not otherwise known to me, which I refer to the genus *Dacnusa*. Its outstanding features are its uniform black colour, very short palpi, short antennae (17 segments), large wedge-shaped pterostigma, vein 1m-cu interstitial and enlarged sternite projecting beyond the apex of the ovipositor sheaths. As in most *Dacnusa* the precoxal suture has been eliminated.

### brevicornis

The single female from Lund belongs to the species since described by Nixon (1944) under the names *ea* and *chrysippe*. After examining Nixon's types I establish the following synonymy:

### Chorebus brevicornis (Thomson), comb. nov.

*Dacnusa (Dacnusa) brevicornis* Thomson, 1895
*Dacnusa chrysippe* Nixon, 1944 **syn. nov.**
*Dacnusa ea* Nixon, 1944 **syn. nov.**

The two females described as *ea* bred from *Melanagromyza cirsii* (Rondani) have their ovipisitor sheaths projecting a little beyond the apical tergite, but in two specimens I have bred from the same host these do not project. I consider this to be individual variation and, as I can see no other difference between the

type series of *ea* and *chrysippe*, have concluded that they represent the same species.

### castaneiventris

Two specimens were sent me as this species. One is a male (with 42 antennal segments) which I consider to be *cincta* HALIDAY, whose locality label cannot be interpreted. The second specimen is labelled Yddinge (not the type locality) and belongs to a different species. As the Yddinge specimen does not fit THOMSON's description, clearly the identity of his species must be taken from the former, which I therefore designate as lectotype. The following synonymy is established:

> **Chorebus cinctus** (HALIDAY), **comb. nov.**
> *Alysia (Dacnusa) cincta* HALIDAY, 1839
> *Dacnusa cincta* (HALIDAY), MARSHALL, 1891 and 1897, NIXON, 1937 and 1944
> *Dacnusa (Dacnusa) castaneiventris* THOMSON, 1895 **syn. nov.**

### coxator

This species has been redescribed in Appendix III.

### crenulata

There is only a single female (with 30 antennal segments) from the type locality Örtofta (there is no male in the collection although THOMSON's description gives "♂♀"): this is therefore designated lectotype. Following comparison with NIXON's material of *elegantula* I establish the following synonymy:

> **Chorebus crenulatus** (THOMSON), **comb. nov.**
> *Dacnusa (Dacnusa) crenulata* THOMSON, 1895
> *Dacnusa elegantula* NIXON, 1937 and 1945 **syn. nov.**

### facialis

The single male (not female as stated in the description) from the type locality Ringsjön represents an *Exotela* species with vein 1m—cu received into cell $R_s$. Its characteristic features are its yellow face, 24 antennal segments and elimination of the precoxal suture. I am not able to associate this specimen with any species known to me. The first antennal segment is shorter than in the common *E. cyclogaster* FÖRSTER.

### flavicoxa

The single female from Pålsjö, the type locality, has 30 antennal segments and belongs to the species called *Antrusa melanocera* (THOMSON) by NIXON. The true *melanocera* (see below) is the smaller species which NIXON (1954) distinguished as *Antrusa persimilis*. The following synonymy is established:

> **Exotela flavicoxa** (THOMSON), **comb. nov.**
> *Dacnusa (Dacnusa) flavicoxa* THOMSON, 1895
> *Dacnusa melanocera* THOMSON sensu NIXON, 1937 (nec *Dacnusa (Dacnusa) melanocera* THOMSON, 1895) **syn. nov.**

Antrusa melanocera (THOMSON) sensu NIXON, 1943 and 1954 (nec Dacnusa
(Dacnusa) melanocera THOMSON, 1895)

## glabricula

The female (with 29 antennal segments) from the type locality Gualőv agrees
with the paratypes of NIXON's cortipalpis in the British Museum, and I therefore
establish the following synonymy:

**Chorebus glabriculus** (THOMSON), **comb. nov.**
Dacnusa (Dacnusa) glabricula THOMSON, 1895
Dacnusa cortipalpis NIXON, 1937 and 1945 **syn. nov.**

## heterocera

I received a male and female from Yddinge in Skåne, both agreeing with NIXON's
(1937, 1943 and 1954) interpretation of this species.

## incidens

The named localities in THOMSON's paper are Yddinge and Pålsjő. I received
three specimens, a pair on a mount labelled "Yst." (presumably Ystad) and a fe-
male from Pålsjő. Dr. JOHANSSON considers that the specimens labelled "Yst."
must be those on which the Yddinge record in THOMSON's paper was based (i. e.
either the label or the reference is erroneous), so that all three specimens are
equally available for the purpose of type fixation. The two Ystad specimens are
abdita HALIDAY, but the Pålsjő female with 40 antennal segments is referable to
the large race or possibly species parasitising Agromyza abiens ZETTERSTEDT des-
cribed by FISCHER (1961) as Pachysema maximum. In order to preserve the
synonymy of incidens with abdita established by NIXON (1937) without compli-
cations, I designate the Ystad female as lectotype. The synonymy now reads:

**Dacnusa abdita** (HALIDAY)
Alysia (Dacnusa) abdita HALIDAY, 1839
Dacnusa lepida MARSHALL, 1891 and 1897
Dacnusa (Dacnusa) incidens THOMSON, 1895
Dacnusa abdita (HALIDAY), NIXON, 1937
Pachysema abdita (HALIDAY), NIXON, 1954
Pachysema abditum (HALIDAY), FISCHER, 1961

## interstitialis

I received under this name two females from the type locality Ringsjőn, but
one of these is a Chorebus sp. with completely yellow legs, thus not agreeing with
the description. I therefore designate as lectotype the other specimen, which
accords with the description. After examining NIXON's type of mamertes I establish
the following synonymy:

**Exotela interstitialis** (THOMSON), **comb. nov.**
Dacnusa (Dacnusa) interstitialis THOMSON, 1895
Dacnusa mamertes NIXON, 1943 and 1946 **syn. nov.**

*melanocera*

I received a pair from the type locality Mölle, the female certainly and the male probably referable to the species described by NIXON (1954) as *Antrusa persimilis* (antennal segments: ♂, 28; ♀, 24). The larger species which NIXON called *melanocera* is in fact *flavicoxa* THOMSON (see above). I designate the female as lectotype and establish the following synonymy:

### *Exotela melanocera* (THOMSON), comb. nov.

*Dacnusa (Dacnusa) melanocera* THOMSON, 1895
*Antrusa persimilis* NIXON, 1954 **syn. nov.**

*4-dentata*

I received four specimens attributed to this species. Two of them are *Amyras clandestina* (HALIDAY) (one of each sex) and two are a *Chorebus* sp. (compare *lugubris* NIXON). One of the *Chorebus* bears a label ''4-dentata'' and one of the *Amyras* a label ''caudata''.

THOMSON's description obviously refers to *Amyras* (in particular the phrase "terebra crassa, subrecurva, dimidio abdomine fere breviore" must exclude the *Chorebus*). The type locality given is Alnarp, which is the locality of the *Amyras* female labelled ''caudata'', but of none of the other specimens. The only puzzling feature is the name *4-dentata* itself (*Amyras* being 3-toothed). But the application of the name, however inappropriate it may seem, can only be judged from the description and data given. Being completely satisfied that the female *Amyras* is the specimen used by THOMSON for his description of *4-dentata*, I formally designate it as lectotype. The existing labelling is presumably of later date as the label ''caudata'' must refer to *Dacnusa caudata* SZÉPLIGETI, which has been synonymised with *clandestina* by TELENGA (1935).

The following synonymy is established:

### *Amyras clandestina* (HALIDAY)

*Alysia (Dacnusa) clandestina* HALIDAY, 1839
*Dacnusa clandestina* (HALIDAY), MARSHALL, 1891 and 1897, NIXON, 1937
*Dacnusa (Dacnusa) 4-dentata* THOMSON, 1895 **syn. nov.**
*Dacnusa caudata* SZÉPLIGETI, 1901
*Amyras clandestina* (HALIDAY), NIXON, 1943 and 1954

*rotundiventris*

I received a single female of a very characteristic *Chorebus* species which has not been recorded in the literature since THOMSON's day. But I have before me another specimen bred from *Agromyza distorta* GRIFFITHS in Britain, and there are five males in the HALIDAY collection probably from Lough Neagh (Northern Ireland) (found by Mr. A. W. STELFOX in a series of insects above a general label "L. Neagh" in HALIDAY's writing).

**Species for whose specific identity a definite opinion is not offered**

*dentifera*

The single female from Yddinge (the type locality) represents a large species related to *Chorebus petiolatus* (NEES) and *C. gracilis* (NEES). It is probably a male (the abdomen unfortunately is shrivelled). The antennae are broken, but with 41 segments remaining — probably there were at least 45 segments originally. Unlike *petiolatus* and *gracilis* this is a completely yellow-legged species: the basal third of the antennae are also bright yellow.

*gracilipes*

I received two specimens, both belonging to a *Chorebus* species with elongate secondarily 3-toothed mandibles. It would fall within NIXON's (1949) concept of *Gyrocampa*.

*laevipectus*

Two specimens have been sent me from the type locality Pålsjö, both *Dacnusa*, but probably not the same species. I do not wish to comment further without more detailed studies of this group.

*liopleuris*

I received a single female of a small *Dacnusa* sp. with fairly dense pubescence of metapleuron, propodeum and petiole, to be compared with *D. melicerta* (NIXON).

*longicauda*

Two specimens were sent me, one labelled Bohuslän (not the type locality) and one whose locality label is not legible. They represent two different species in the *Dacnusa stramineipes* group.

*maculipes*

I have received five specimens of *Dacnusa* on the same mount from the type locality Örtofta. They are heterogeneous, but two of them I think agree with NIXON's (1948) interpretation of the name. The next reviser of the group should be able to select a lectotype confirming NIXON's use of the name.

*obliqua*

The specimen (or specimens) from the type locality Fågelsång has been destroyed. I received four other specimens from THOMSON's collection, all being *Chorebus* with elongate secondarily 3-toothed mandibles (fig. 26), falling within NIXON's (1949) concept of *Gyrocampa*.

*parvungula*

The female received from the type locality Örtofta is very similar to *Chorebus cyclops* (NIXON), but may possibly represent a different species as the pubescence of the mesoscutum and shape of the petiole are somewhat different.

*stenocentra*

The female sent me is unfortunately without legs and antennae. It clearly belongs to the *senilis* group sensu NIXON (1944), now referred to the genus *Chorebus*, but I am unable to comment further without more detailed study.

*stenocera*

There are no specimens in the collection from the type locality Ringsjön. I have received a male from Örtofta and a female from Lund, both belonging to the *Chorebus senilis* group. The male (with 35 antennal segments) may well be NIXON's *praeclara*, but I am not proposing to establish any synonymy without more detailed study of the group.

*tarsalis*

Under this name I have received two females from the type-locality Örtofta. One is a small *Chorebus* species (compare *C. armida* (NIXON) and *C. turissa* (NIXON)) and the other a *Dacnusa* species with long pterostigma (compare *D. nitetis* (NIXON)). Both these specimens fit THOMSON's description, so the choice between them for fixing the identity of the species is arbitrary. But as the *Chorebus* has broken antennae, I prefer to designate the *Dacnusa* (which has its antennae intact with 23 segments) as lectotype.

*tomentosa*

There is only a male in the collection from the type locality Pålsjö. In colour this agrees with *Chorebus marsyas* (NIXON) (see NIXON, 1944), not *C. senilis* (NEES), the previously established synonymy. I do not propose to establish any formal synonymy without more detailed study of the *senilis* group.

### Appendix VI

### *Protodacnusa* gen. nov.

(Derivation: πρωτο-"first", δακνοῦσα "biting", after *Dacnusa* HALIDAY, 1833: gender feminine)

Type-species: *Alysia tristis* NEES, 1834, Hym. Ichn. aff., 1, 258.

The apomorph characters on which this genus has been based are found in the form of the head and mandibles (figs. 2, 36 and 38). The head is massive, 1.4—1.6 times as wide as the thorax, with the temples (in dorsal and lateral view) at least as broad as the eye-width. The mandibles are considerably enlarged (0.21—0.3 mm. wide) with tooth 3 expanded laterally, not (fig. 2) or only weakly (fig. 38) angulate. In other respects the ground-plan of the genus is strongly plesiomorph (see under "Plesiomorph Characters" above).

Noteworthy apomorph characters developed by more than one species within the genus are (i) the suppression of the notaulices (3 species), (ii) the extension of pubescence over the entire surface of tergite 3 (2 species), and (iii) the loss of $Cu_{1b}$ (2 species).

This genus is based on *tristis* NEES, which, as previously stated, cannot be included in *Chorebus*. Further study has revealed three other species which are synapomorph with *tristis* in the form of the head and mandibles, and their high degree of morphological resemblance in many respects (see the table of biometric data) makes me confident that they can be associated with *tristis* as a monophyletic group. They may be distinguished according to the following key:

1  Cell 2Cu widely open (fig. 11) at its lower distal corner ($Cu_{1b}$ lost). Notaulices lost: mesoscutum largely bare and shining. Tergite 3 with at most a few weak hairs at its base. $R_1$ (metacarp) short, much less than half as long as the pterostigma  . . . . .  2
—  Cell 2Cu more or less closed by $Cu_{1b}$ at its lower distal corner. Tergite 3 clothed with many rows of hairs. Metacarp longer  . . . . . . . . . . . . . . . .  3
2  Petiole almost bare. Precoxal suture rugose. Palpi longer . . . . . .  *tristis* (NEES)
—  Petiole clothed with evenly distributed erect hairs. Precoxal suture represented by a smooth groove, or virtually lost. Palpi shorter . . . . . . . . .  *ruthei* **sp. nov.**
3  Head strongly swollen behind the eyes (fig. 36). 26—32 antennal segments  . . .
  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .  *litoralis* **sp. nov.**
—  Head quadrate, in dorsal view not noticeably broadened behind the eyes. 24—25 antennal segments . .  . . . . . . . . . . . . . . . . . . . . . . .  *aridula* (THOMSON)

### *Protodacnusa tristis* (NEES), **comb. nov.**

*Alysia tristis* NEES, 1834
*Dacnusa tristis* (NEES), MARSHALL, 1891 and 1897, NIXON, 1937, 1943 and 1946.

Colour. Antennae dark. Centre of mandibles red-brown. Labrum black. Labial and maxillary palpi infuscated. All coxae and trochanters black: hind and middle femora entirely black, but front femora testaceous in apical half: tibiae testaceous, slightly darkened apically: tarsi testaceous at base, with the distal segments progressively darkened. Wing-membrane with a distinctly milk-white appearance. Morphology. Head massive, clearly broadened behind the eyes in dorsal view. Frons, vertex and temples smooth and strongly shining with fine pubescence. Ocelli forming a more or less equilateral triangle. Face smooth, with sparse white pubescence, bare along its central line. Eyes more narrowly separated than in *litoralis* and *aridula*. Antennal segments: ♂, 30—34; ♀, 25—29. Mandibles (fig. 2) with tooth 3 represented by a long flattened edge with a milled appearance.

Notaulices completely eliminated. Mesoscutum largely bare and shining except for its anterior face, which is pubescent and faintly sculptured: otherwise only a few hairs are present along the former course of the notaulices. Mesepisternum with clearly developed rugose precoxal suture, but the epicnemial suture is more or less smooth. Metapleuron smooth or very feebly sculptured, sparsely pubescent (cf. fig. 16).

Wing (fig. 11) with elongate pterostigma and short metacarp, vein 2m-cu widely rejected from cell $R_s$, and cell 2Cu widely open following the loss of $Cu_{1b}$.

Propodeum finely rugose, largely bare but with a few fine hairs at the sides and across its middle. Petiole subtriangular, almost bare, very finely sculptured. ♀ ovipositor not projecting.

Breeding Records

Host — *Agromyza* sp. (probably *ambigua* group)

2 ♀♀ from larvae 14. vi. 53 on *Hordeum* sp. (cultivated), Cobham, Surrey, England, emerged 1. v. 54 (SPENCER)

The record "probably parasites of *Chlorops* sp." given in NIXON (1946) was originally stated to be doubtful and should now be discarded. The record in DALLA TORRE (1898) of this species being bred by GOUREAU from *Agromyza nigripes* MEIGEN is of little value without further details. (I cannot find this record in GOUREAU's works, but he uses the name *nigripes* for the species now called *A. nana* MEIGEN, a leaf-miner of Papilionaceae, which suggests that the parasite was not *tristis* in the sense used here.)

Other material

There are a number of swept specimens in the British Museum from southern England (the localities are given in NIXON, 1946), where the species seems to be not uncommon. A specimen from near Venice (Italy) has been included in the table of biometric data.

The application of the name *tristis* is traditional (all NEES' types having been destroyed). The species is readily distinguished by the open cell 2Cu, rugose precoxal suture and almost bare petiole.

### *Protodacnusa ruthei* sp. nov.

This species is to be compared with *tristis* as follows.

Colour. Mandibles red-brown. Labrum black. Labial and maxillary palpi infuscated. Legs as in *tristis*.

Morphology. Head similar to *tristis*, very strongly widened behind the eyes. Frons with a conspicuous central groove. Eyes very small and narrowly separated. Face feebly rugulose towards its sides. Antennal segments: ♂, 26, 28; ♀ (holotype), 26. Palpi clearly shorter than in other *Protodacnusa* species.

Mesoscutum as in *tristis*. Mesepisternum with precoxal suture represented by a more or less smooth groove, virtually lost in one male. Metapleuron smooth and shining, a little more densely pubescent than in *tristis*.

Wing venation as in *tristis* with open cell 2Cu and elongate pterostigma (cf. fig. 11). Tarsi distinctly shorter than in other species.

Propodeal pubescence denser than in *tristis*. Petiole with evenly-distributed erect hairs, similar to those of the petiole: these do not obscure the longitudinal striation beneath. A few weak hairs are also found along the base of tergite 3.

Material examined

Holotype ♀ (15. v. 1856) and 4 ♂♂, 1 ♀ paratypes (30. iv — 15. v. 1856), Germany (probably neighbourhood of Berlin) ex RUTHE collection. All are in the British Museum (Natural History) except one male paratype retained in my personal collection.

NIXON (1946) refers to the series from which this species has been described under his description of *tristis*. I am satisfied that they represent a distinct species,

differing from *tristis* most clearly in the form of precoxal suture, the shorter palpi and tarsi, and the clearly pubescent petiole.

### *Protodacnusa aridula* (THOMSON), **comb. nov.**

*Dacnusa (Dacnusa) aridula* THOMSON, 1895

*Antrusa miser* NIXON, 1954 syn. nov.

Colour. Centre of mandibles red-brown. Labrum orange-red. Palpi testaceous or dull yellow. All coxae infuscated, especially the hind pair, but the rest of the legs brown or testaceous. Tergite 3 brown.

Morphology. Head massive, but not broadened behind the eyes in dorsal view. Vertex and temples with fine but rather dense pubescence, lacking the shining appearance of the other species. Ocelli forming a triangle whose base is slightly longer than its sides. Face more densely pubescent than in *tristis*, not shining. Eyes widely separated. Antennal segments: ♀, 24, 25 (broken in the holotype). Mandible similar to that of *litoralis* (fig. 38) with tooth 3 slightly angulate.

Mesoscutum lacking the bare, shining appearance of the other species, with shallow reticulate sculpture mainly on its anterior half; notaulices rugose, reaching
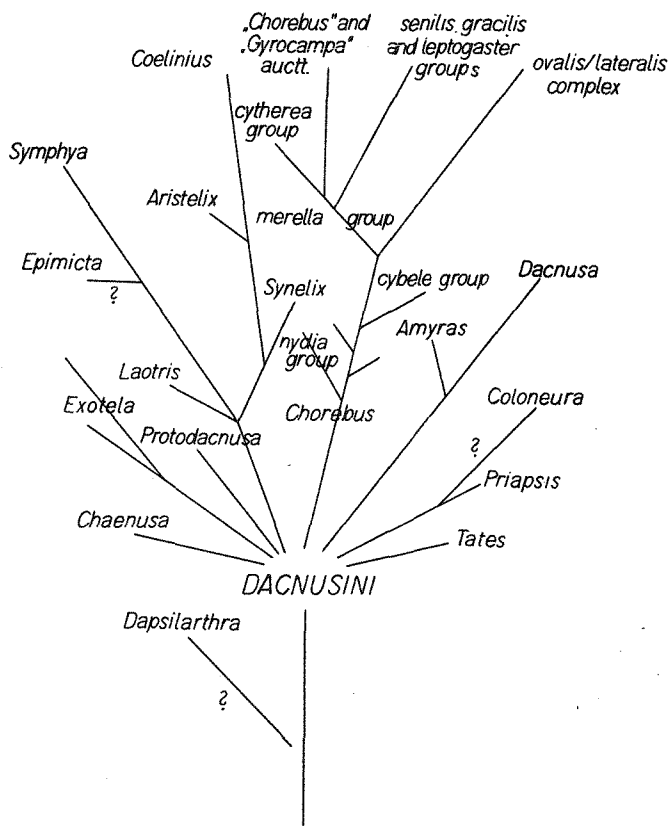


Graph 1. Phylogeny of the Dacnusini

to about half its length: central lobe and anterior part of lateral lobes rather densely pubescent. Mesepisternum with large rugose precoxal suture. Metapleuron evenly regose over its lower half, with long fine pubescence (denser than in *tristis*) directed mainly downwards towards the coxa.

Wing differing obviously from that of *tristis* and *ruthei* by the closed cell 2Cu with vein Cu$_{1b}$ retained, and the approximation of 1m-cu to cell R$_s$ (this is more marked in the holotype than in the other specimens): the pterostigma is shorter and meta-carp longer.

Propodeum rugose, covered with fine inconspicuous pubescence. Petiole sub-triangular, with evenly distributed but inconspicuous pubescence. Tergite 3 evenly covered with hairs over its entire surface, but the succeeding tergites bear only a single apical row of hairs. ♀ ovipositor not projecting.

Material examined

THOMSON's holotype ♀ taken at Ilstorp, Skåne province, Sweden. ♀ holotype of the synonymised *Antrusa miser* NIXON, Degeberga, Skåne, Sweden, 10. vii. 38 (PERKINS). ♀ paratype of *A. miser* NIXON, Germany (probably neighbourhood of
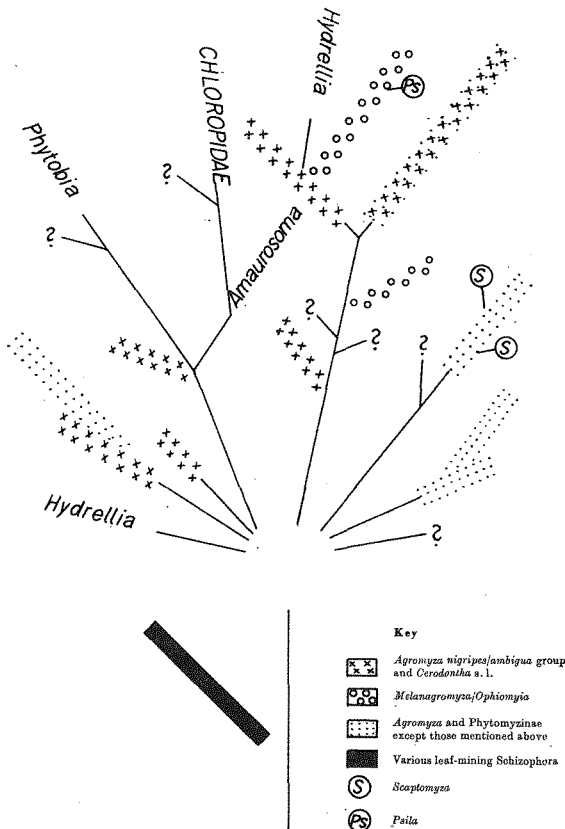


Graph 2. Host selection of the Dacnusini, to be read in conjunction with graph 1

Berlin) ex RUTHE collection. The holotype is in the THOMSON collection at Lund, and the other two specimens in the British Museum (Natural History).

The inclusion of this species in *Protodacnusa* is established by the form of the head and mandibles. It can easily be distinguished from the other species by its more extensive pubescence on various parts of the body, and the retained notaulices. I am reasonably satisfied that *Antrusa miser* NIXON is a synonym, although the German female included in the table of biometric data is much smaller than the holotype.

### *Protodacnusa litoralis* sp. nov.

Colour. Centre of mandibles reddish black. Labrum red-brown. Palpi largely brown. Legs largely testaceous, but the hind coxae are largely black: all tarsi and the extreme apex of the hind tibiae are also dark.

Morphology. Head (fig. 36) much as in *tristis* (broadened behind the eyes, sparsely pubescent and of strongly shining appearance). Antennae 31- and 32-segmented ($\male$). Eyes unusually small and very widely separated. Mandibles very large, rugulose in their centre, with tooth 3 long, but distinctly angulate (fig. 38), lacking the milled appearance of *tristis*.

Mesoscutum with rugose notaulices shortly impressed on about its anterior third: the anterior face and anterior third of the central lobe pubescent and feebly sculptured, but the lateral lobes and posterior part of the central lobe are largely bare and strongly shining, except for the rows of hairs along the former course of the notaulices. Mesepisternum with a large precoxal suture, which is rugose along its entire length. Metapleuron shining, with sparse pubescence, as in *tristis* (cf. fig. 16), but shallowly rugose over its lower half.

Wings with closed cell 2Cu, but 1m-cu not unusually approximated to cell $R_s$. Pterostigma as in *aridula*, less elongate than in *tristis* and *ruthei*.

Propodeum as in *tristis*, finely rugose with only a few fine hairs. Petiole subtriangular, bearing shallow sculpture with a distinct longitudinal element, and a few long fine hairs distributed evenly over its surface. Tergite 3 with four or five rows of fine hairs distributed evenly over its surface: the succeeding tergites bear only an apical row of hairs.

Material examined[18]

$\male$ holotype, Isle of Dough, East Donegal, Ireland, 21. vi. 55 (STELFOX). $\male$ paratype, Ards, West Donegal, 17. vi. 55 (STELFOX). Both in Mr. A. W. STELFOX's personal collection.

I would like to thank Mr. A. W. STELFOX for bringing this large attractive species to my attention. He tells me that both specimens were taken on the coast, the holotype in a sheltered hollow on top of low cliffs, and the paratype at the foot of cliffs behind a fringe of dunes.

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[18] Since writing this description I have seen a further series of 2 $\male\male$ and 4 $\female\female$ (hereby designated paratypes) from Denmark, Hansted reservatet, Jyll, KLITMØLLER, 12. vi. 60 (leg. Copenhagen Zoological Museum Expedition). One pair has been retained in my personal collection and the remainder returned to the Zoological Museum, Copenhagen. Their antennal segments number: $\male$, 30, 32; $\female$, 26, 27, 30 (2). In the larger females of this series the mesoscutal pubescence is rather more extensive than that described and covers the entire central lobe: the degree of approximation of 1m-cu to $R_s$ is variable, so that no clear distinction can be made with *aridula* in this respect.

This species, like *aridula*, retains a closed cell 2Cu, but in the form of its head and the reduction of the notaulices it is synapomorph with *tristis* and *ruthei*. The mesoscutal pubescence is less extensive than in *aridula*.

### Discussion

The expression of the relationship between these four species in the form of a phylogeny tree seems straightforward. The two species *tristis* and *ruthei* are clearly synapomorph in the form of their cell 2Cu and the relative proportions of the pterostigma and metacarp. The new species *litoralis* seems synapomorph with these in the form of its head (which is strongly broadened in dorsal view behind the small eyes) and the reduction of the notaulices. This leaves *aridula* as the most plesiomorph species, retaining both well-developed notaulices and a closed cell 2Cu. The relationships may be expressed thus:
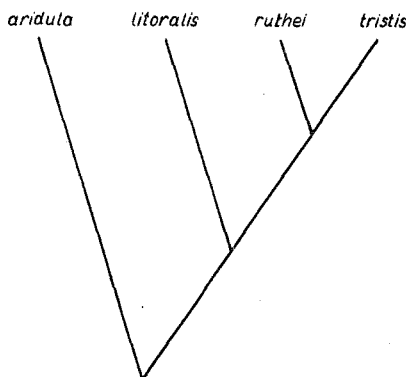
Summary

1. This paper is intended to be the first of a series dealing with the Alysiinae parasites of the Agromyzidae. The majority of these belong to the Dacnusini, and it is with that tribe that this paper is principally concerned.

2. The morphological characters of the Alysiinae are analysed according to the principles of phylogenetic systematics defined by HENNIG (1950) and as a result of this analysis a phylogeny tree is produced and changes are proposed in the previously accepted classification. The significance of the exodont mandibles of the Alysiinae is discussed and it is concluded that their normal function is to help secure the parasite's escape from puparia of cyclorrhaphous Diptera.

3. Most Dacnusini show an exceptionally high degree of host specificity. Comparison of their phylogeny with their host association leads to the conclusion that the common ancestor of the tribe was probably associated with the ancestor(s) of one or both of two groups of Agromyzidae which are leaf-miners of monocotyledons. These are the *Agromyza nigripes/ ambigua* group and *Cerodontha* s. 1.

4. Appendices given include a practical key to the genera of Dacnusini, notes on some of THOMSON's (1895) and FÖRSTER's (1862) types, a revision of the *Chorebus nydia* group and descriptions of the new genus *Protodacnusa* and its species. One new species is described in the *Chorebus nydia* group and two in *Protodacnusa*.

Zusammenfassung

1. Diese Arbeit soll sich als erste einer Veröffentlichungsreihe mit den Alysiinae als Parasiten der Agromyziden befassen. Der größte Teil von ihnen gehört zur Tribus Dacnusini, die in der vorliegenden Arbeit hauptsächlich behandelt wird.

2. Die morphologischen Merkmale der Alysiinae werden nach den Prinzipien der von Hennig (1950) definierten phylogenetischen Systematik untersucht. Als Ergebnis einer solchen Analyse wird ein Stammbaum entwickelt, wobei Änderungen der bisher gebräuchlichen Klassifikation vorgeschlagen werden. Eine Erörterung über die Bedeutung der exodonten Mandibeln der Alysiinae führt zu dem Schluß, daß ihre normale Funktion darin besteht, das Entweichen des Parasiten aus dem Puparium cyclorrhapher Dipteren zu gewährleisten.

3. Die meisten Dacnusini zeigen einen außerordentlich hohen Grad von Wirtsspezifität. Ein Vergleich ihrer Phylogenie mit ihrer Wirtsbindung führt zu dem Schluß, daß der gemeinsame Vorfahre der Tribus wahrscheinlich an den (oder die) Vorfahren von einer oder zwei Gruppen von Agromyziden gebunden war, die in Blättern von Monokotyledonen minieren. Dafür kommen die *Agromyza nigripes/ambigua*-Gruppe und *Cerodontha* s. l. in Betracht.

4. Beigefügt sind ein praktischer Bestimmungsschlüssel der Gattungen der Dacnusini, Bemerkungen über Thomsons (1895) und Försters (1862) Typen, eine Revision der *Chorebus nydia*-Gruppe und Beschreibungen der neuen Gattung *Protodacnusa* und ihrer Arten. Eine neue Art in der *Chorebus nydia*-Gruppe und zwei in der Gattung *Protodacnusa* werden beschrieben.

Резюме

1. Это первая работа из серии публикаций, которая исследует Alysiinae как паразитов Agromyzidae. Большая часть относится к трибе Dacnusini, которая обсуждается в предлагаемой работе.

2. Морфологические признаки Alysiinae исследуются по принципам, сформулированной Хеннигом (1950) филогенетической систематики. В результате этого исследования развивается родословная, причем предлагается внести изменения в применявшуюся до сих пор классификацию. Рассмотрение значения Mandibulae exodont приводит к заключению, что ее нормальная функция заключается в том, что она обеспечивает выход паразита из пупария Diptera Cyclorrhapha.

3. Большинство Dacnusini проявляют чрезвычайно сильную специфичность по отношению к хозяину. Сравнение их филогенеза с их принадлежностью к хозяину приводит к заключению, что общий предок трибы вероятно был связан с предками (или предком) одной или двух групп минирующих мух, которые минировали листья однодольных растений. Во внимание могут быть приняты группа *Agromyza nigripes/ambigua* и *Cerodontha* s.l..

4. Прилагается также ключ для практического определения рода Dacnusini, замечания по поводу типов Томсона (1895) и Фёрстера (1862), ревизия группы *Chorebus nydia* и описание нового рода *Protodacnusa* и его видов. Описывается новый вид из группы *Chorebus nydia* и два вида из рода *Protodacnusa*.

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## Table 1
### Biometric Data

| | | Absolute Measurements (1 = 0.01 mm.) | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | | Head | | | Eye-width (lateral) | Distance between Eyes | Clypeus Width | Mandibles Width | Antennal Segments | | | Maxillary Palpus Segments | | | | Thorax | | | Hind Leg | | | Hind Tarsal Segments | | | | |
| | | Width | Length | Height | | | | | 3 | 4 | 5 | 3 | 4 | 5 | 6 | Length | Width | Height | Femur | Tibia | Tarsus | 1 | 2 | 3 | 4 | 5 |
| 1 | ♂ | 67 | 35 | 50 | 22 | 32 | 22 | 13 | 15 | 11 | 11 | 7 | 9 | 8 | 9 | 95 | 54 | 80 | 65 | 91 | 71 | 25 | 13 | 10 | 10 | 13 |
| 2 | ♂ | 67 | 35 | — | 19 | — | — | 13 | 17 | 11 | 11 | 9 | 11 | 7 | 9 | 104 | 58 | 83 | 65 | 91 | 72 | 26 | 15 | 11 | 9 | 13 |
| 3 | ♂ | 71 | 37 | 58 | 19 | — | — | 13 | 14 | 11 | 11 | 8 | 9 | 9 | 12 | 102 | 56 | 87 | 71 | 96 | 76 | 28 | 15 | 10 | 7 | 12 |
| 4 | ♀ | 65 | 37 | 54 | 19 | 30 | 21 | 13 | 17 | 11 | 11 | 7 | 10 | 7 | 10 | 95 | 59 | 80 | 69 | 89 | 74 | 26 | 13 | 10 | 8 | 14 |
| 5 | ♀ | 61 | 34 | 46 | 17 | 26 | 17 | 13 | 14 | 10 | 9 | 7 | 9 | 6 | 7 | 87 | 50 | 65 | 56 | 78 | 61 | 19 | 12 | 9 | 7 | 12 |
| 6 | ♀ | 65 | 35 | 46 | 17 | — | — | 17 | 17 | 12 | 11 | 9 | 11 | 8 | 10 | 89 | 56 | 76 | 63 | 91 | 72 | 26 | 14 | 11 | 8 | 11 |
| 7 | ♂ | 58 | 32 | 46 | 15 | — | — | 11 | 16 | 11 | 10 | — | — | — | — | 89 | 50 | 69 | 59 | 78 | 63 | — | — | — | 7 | 13 |
| 8 | ♂ | 74 | 41 | 59 | 21 | 35 | 19 | 15 | 15 | 11 | 11 | 9 | 12 | 9 | 9 | 100 | 65 | 87 | 74 | 95 | 76 | 26 | 13 | 11 | 9 | 15 |
| 9 | ♀ | 63 | 35 | 46 | 19 | 35 | 17 | 15 | 13 | 9 | 9 | — | 9 | 7 | 9 | 96 | 54 | 72 | 59 | 76 | 65 | 22 | 11 | 9 | 7 | 13 |
| 10 | ♂ | 65 | 32 | 50 | 17 | 28 | 17 | 15 | 13 | 10 | 10 | — | 9 | 7 | 9 | 83 | 54 | — | 56 | 81 | 65 | 22 | 11 | 9 | 7 | 14 |
| 11 | ♀ | 69 | 37 | 59 | 19 | 30 | 19 | 17 | 14 | 11 | 9 | 9 | 11 | 8 | 9 | 102 | 59 | 83 | 71 | 89 | 74 | 27 | 13 | 9 | 9 | 17 |

Nos. 1—3. *Chorebus spenceri* sp. nov.: 1, Inverness, Scotland; 2, Isle of Wight, England; 3, holotype ex *Agromyza phragmitidis*, Devon, England.

Nos. 4—7. *Chorebus nydia* (NIXON) ex *Agromyza nigripes*, England: 4 and 7, Buckingham Palace Gardens, London; 5 and 6, Ash Vale, Surrey.

## Table 2
### Biometric Data

| | | Absolute Measurements (1 = 0.01 mm.) | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | | Head | | | Eye-width (lateral) | Distance between Eyes | Clypeus Width | Mandible Width | Antennal Segments | | | Maxillary Palpus Segments | | | | Thorax | | | Hind Leg | | | Hind Tarsal Segments | | | | |
| | | Width | Length | Height | | | | | 3 | 4 | 5 | 3 | 4 | 5 | 6 | Length | Width | Height | Femur | Tibia | Tarsus | 1 | 2 | 3 | 4 | 5 |
| 1 | ♀ | 76 | 48 | 59 | 22 | 26 | — | 22 | 13 | 11 | 11 | — | — | — | — | 106 | 54 | 76 | 71 | 95 | 81 | 32 | 17 | 11 | 9 | 13 |
| 2 | ♀ | 74 | 46 | 58 | 23 | 24 | 15 | 25 | 13 | 11 | 11 | — | 9 | 7 | 9 | 104 | 54 | 74 | 71 | 98 | 83 | 34 | 15 | 11 | 9 | 13 |
| 3 | ♂ | 83 | 48 | 58 | 15 | 32 | 21 | 28 | 19 | 13 | 13 | 9 | 11 | 9 | 11 | 111 | 58 | 85 | 72 | 109 | 85 | 34 | 17 | 11 | 9 | 13 |
| 4 | ♀ | 78 | 48 | 56 | 17 | 28 | 17 | 30 | 18 | 11 | 11 | — | 11 | 7 | 10 | 95 | 54 | 74 | 67 | 96 | 81 | 32 | 17 | 11 | 9 | 11 |
| 5 | ♀ | 78 | 50 | 59 | 22 | 37 | 22 | 30 | 13 | — | — | — | 13 | 9 | 11 | 104 | 58 | 74 | 59 | 91 | 74 | 30 | 13 | 11 | 9 | 11 |
| 6 | ♀ | 69 | 41 | 52 | 17 | 30 | 19 | 21 | 13 | 11 | 9 | — | — | — | — | 91 | 50 | 67 | 59 | 78 | 65 | 24 | 13 | 10 | 7 | 13 |
| 7 | ♂ | 93 | 46 | 59 | 15 | 43 | 22 | 30 | 15 | 13 | 12 | — | — | — | — | 111 | 61 | 85 | 69 | 102 | 78 | 30 | 17 | 11 | 9 | 13 |
| 8 | ♂ | 98 | 50 | 63 | 17 | 43 | 24 | 30 | 17 | 11 | 11 | 11 | 14 | 11 | 11 | 115 | 65 | 93 | 67 | 104 | 83 | 34 | 15 | 11 | 9 | 15 |
| 9 | ♂ | 72 | 43 | 48 | 11 | 28 | 17 | 21 | 11 | 10 | 9 | 8 | 7 | 7 | 6 | 91 | 50 | 67 | 52 | 74 | 63 | 21 | 13 | 11 | 7 | 11 |
| 10 | ♀ | 81 | 52 | 56 | 13 | 24 | 19 | 24 | 15 | 11 | 11 | 7 | 9 | 7 | 7 | 104 | 52 | 72 | 65 | 91 | 76 | 26 | 17 | 11 | 9 | 11 |

Nos. 1—4. *Protodacnusa tristis* (NEES): 1 and 2, ex *Agromyza* sp., Surrey, England; 3, Harpenden, Herts., England; 4, Litorale Veneto; Italy.

Nos. 5—6. *Protodacnusa aridula* (THOMSON): 5, holotype, Sweden; 6, Germany.

Table headers (columns 26–32 = measurements; A–L = Ratios):

- 26 = Hind Coxa Width; 27 = Hind Coxa Length; 28 = Wing Length; 29 = Gaster Length; 30 = Petiole Width; 31 = Petiole Length; 32 = Total Body Length
- A = Length/Width of Head; B = Length/Height of Head; C = Width of Head/Distance between Eyes/Width of Clypeus; D = Width of Mandibles/Length of Head; E = Antennal Segments (3:4:5); F = Height/Length of Thorax; G = Thorax Width/Head Width; H = Wing Length/Body Length; I = Hind Tibia/Tarsus; J = Hind Tarsal Segments (1:2:3:4:5); K = Lengths of Petiole/Gaster; L = Width/Length of Petiole

| 26 | 27 | 28 | 29 | 30 | 31 | 32 | A | B | C | D | E (3:4:5) | F | G | H | I | J (1:2:3:4:5) | K | L |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | 32 | 291 | 118 | 30 | 43 | 257 | 1.9 | 1.4 | 2.1:1:0.7 | 2.7 | 1.4:1:1 | 1.2 | 1.2 | 0.9 | 0.8 | 1.9:1:0.8:0.7:1.0 | 2.8 | 1.4 |
| 17 | 26 | 286 | 118 | 34 | 41 | 252 | 1.9 | — | — | 2.7 | 1.5:1:1 | 1.2 | 1.1 | 0.9 | 0.8 | 1.8:1:0.8:0.6:0.9 | 2.9 | 1.2 |
| 21 | 28 | 310 | 126 | 35 | 46 | 271 | 1.9 | 1.5 | — | 2.9 | 1.3:1:0.9 | 1.2 | 1.3 | 0.9 | 0.8 | 1.9:1:0.7:0.5:0.8 | 2.7 | 1.3 |
| 17 | 28 | 286 | — | 37 | 39 | — | 1.8 | 1.4 | 2.1:1:0.7 | 2.9 | 1.5:1:0.9 | 1.2 | 1.1 | — | 0.8 | 2.0:1:0.8:0.6:1.1 | — | 1.1 |
| 13 | 22 | 248 | 96 | 30 | 37 | 214 | 1.8 | 1.4 | 2.4:1:0.7 | 2.6 | 1.4:1:0.9 | 1.3 | 1.2 | 0.9 | 0.8 | 1.4:1:0.7:0.6:1.0 | 2.6 | 1.2 |
| 14 | 24 | 286 | 102 | 34 | 41 | 233 | 1.8 | 1.3 | — | 2.1 | 1.4:1:0.9 | 1.2 | 1.2 | 0.8 | 0.8 | 1.8:1:0.8:0.6:0.8 | 2.5 | 1.2 |
| 13 | 22 | 252 | 102 | 28 | 37 | 228 | 1.8 | 1.5 | — | 2.8 | 1.4:1:0.9 | 1.3 | 1.1 | 0.9 | 0.8 | — | 2.7 | 1.3 |
| 21 | 26 | 295 | 124 | 41 | 52 | 276 | 1.8 | 1.5 | 2.1:1:0.5 | 2.7 | 1.3:1:0.9 | 1.1 | 1.1 | 0.9 | 0,8 | 2.0:1:0.9:0.7:1.1 | 2.4 | 1.3 |
| 17 | 22 | 248 | 100 | 34 | 41 | 238 | 1.8 | 1.3 | 1.8:1:0.5 | 2.4 | 1.4:1:1 | 1.3 | 1.2 | 1.0 | 0.9 | 1.9:1:0.8:0.7:1.2 | 2.5 | 1.2 |
| 13 | 22 | 252 | 108 | 32 | 37 | 238 | 2.1 | 1.6 | 2.3:1:0.6 | 2.1 | 1.3:1:1 | — | 1.2 | 0.9 | 0.8 | 2.0:1:0.8:0.7:1.2 | 2.9 | 1.2 |
| 15 | 26 | 267 | — | 39 | 46 | — | 1.9 | 1.6 | 2.2:1:0.6 | 2.2 | 1.2:1:0.8 | 1.2 | 1.1 | — | 0.8 | 2.1:1:0.7:0.7:1.3 | — | 1.2 |

Nos. 8—11. *Chorebus coxator* (THOMSON), England: 8, ex *Agromyza phragmitidis*, Woodwalton Fen, Hunts.; 9, ex *Agromyza hendeli*, Woodwalton Fen, Hunts.; 10, ex *Agromyza phragmitidis*, Devon; 11, ex *Agromyza phragmitidis*, Woodwalton Fen, Hunts.

| 26 | 27 | 28 | 29 | 30 | 31 | 32 | A | B | C | D | E (3:4:5) | F | G | H | I | J (1:2:3:4:5) | K | L |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | 28 | 267 | 135 | 34 | 41 | 257 | 1.6 | 1.2 | 2.9:1:— | 2.2 | 1.2:1:1 | 1.4 | 1.4 | 1 | 0.9 | 2.0:1:0.7:0.6:0.8 | 3.3 | 1.2 |
| 15 | 26 | 291 | — | 32 | 39 | — | 1.6 | 1.2 | 3.1:1:0.6 | 1.9 | 1.2:1:1 | 1.4 | 1.4 | — | 0.8 | 2.1:1:0.7:0.6:0.8 | — | 1.2 |
| 17 | 32 | 333 | 130 | 28 | 39 | 276 | 1.7 | 1.2 | 2.6:1:0.6 | 1.7 | 1.4:1:1 | 1.3 | 1.4 | 0.8 | 0.8 | 2.0:1:0.7:0.6:0.8 | 3.3 | 1.4 |
| 17 | 26 | 271 | 126 | 28 | 37 | 262 | 1.6 | 1.2 | 2.8:1:0.6 | 1.6 | 1.2:1:0.9 | 1.3 | 1.4 | 1 | 0.8 | 1.9:1:0.7:0.6:0.7 | 3.4 | 1.3 |
| 17 | 30 | 248 | 130 | 35 | 44 | 276 | 1.6 | 1.2 | 2.1:1:0.6 | 1.7 | — | 1.4 | 1.4 | 1.1 | 0.8 | 2.3:1:0.9:0.7:0.9 | 2.9 | 1.3 |
| 15 | 26 | 228 | 98 | 28 | 39 | — | 1.7 | 1.3 | 2.3:1:0.6 | 2.0 | 1.3:1:0.9 | 1.4 | 1.4 | — | 0.8 | 1.9:1:0.8:0.6:0.9 | 2.5 | 1.4 |
| 17 | 32 | 319 | 143 | 34 | 44 | 310 | 2.0 | 1.3 | 2.2:1:0.5 | 1.6 | 1.2:1:0.9 | 1.3 | 1.5 | 1 | 0.8 | 1.8:1:0.7:0.6:0.8 | 3.2 | 1.3 |
| 17 | 32 | 333 | 167 | 34 | 46 | 333 | 2.0 | 1.3 | 2.3:1:0.6 | 1.7 | 1.5:1:1 | 1.2 | 1.5 | 1 | 0.8 | 2.2:1:0.8:0.6:1.0 | 3.6 | 1.4 |
| 15 | 24 | 257 | 113 | 28 | 37 | 248 | 1.7 | 1.1 | 2.6:1:0.6 | 1.9 | 1.1:1:1 | 1.4 | 1.4 | 1 | 0.8 | 1.6:1:0.9:0.6:0.9 | 3.1 | 1.3 |
| 15 | 26 | 271 | 118 | 34 | 44 | 276 | 1.6 | 1.1 | 3.4:1:0.8 | 2.2 | 1.4:1:1 | 1.4 | 1.6 | 1 | 0.8 | 1.6:1:0.7:0.6:0.7 | 2.7 | 1.3 |

Nos. 7—8. *Protodacnusa litoralis* sp. nov.: 7, holotype, Ireland; 8, paratype, Ireland.
Nos. 9—10. *Protodacnusa ruthei* sp. nov. paratype ♂ and holotype ♀, Germany.

### Notes on tables 1 and 2 of biometric data

Absolute Measurements. All height, length and width measurements are perpendicular, not point-to-point, measurements. The following notes refer to the method of taking some of the measurements:

1 measured in dorsal view
2 measured in lateral view with the front point of measurement taken from the upper point of the junction of the antennae with the head (i. e. excluding any prominence below the antennae)
3 measured in lateral view with the lower point of measurement taken from the apex of the clypeus
5 minimum distance on lower part of face
6 measurement of the convex part of the clypeus only, excluding any lateral extensions of the depressed rim
7 measured between the apices of the outer teeth
15 refers to the functional thorax and is measured in lateral view from the leading edge of the mesoscutum to the posterior edge of the propodeum
16 the maximum width of the mesoscutum (excluding any prominences associated with the wing muscles)
18 excluding the basal ring or trochantellus
20 & 25 excluding the arolium (foot-pad) and claws
26 — 27 measured in lateral view
29 excluding the ovipositor and its sheaths
30 maximum width at apex
32 excluding the antennae and ovipositor and its sheaths

Ratios. In ratios A, B, D, F, G, H, I, K and L the first measurement given is taken as unity, and not stated in the table. In ratios C, E and J unity is as stated in the table.

A blank entry in the table means that an accurate measurement was not possible (generally because of the manner in which the specimen has been mounted).
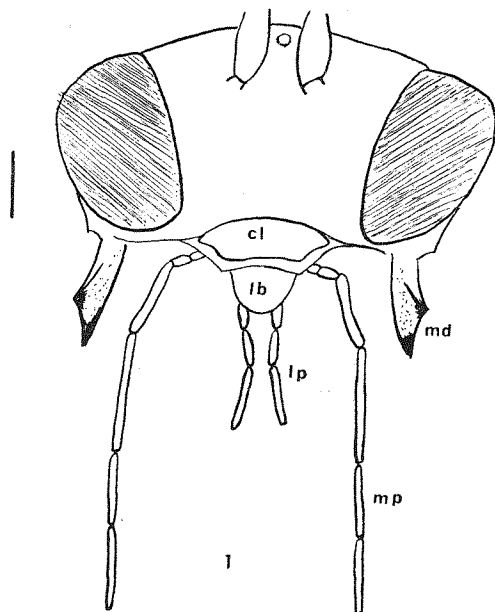
Fig. 1. *Chorebus lateralis* (HALIDAY), head in anterior view. md = mandibles, cl = clypeus, lb = labrum, lp = labial palpi, mp = maxillary palpi (Scale 0.1 mm.)
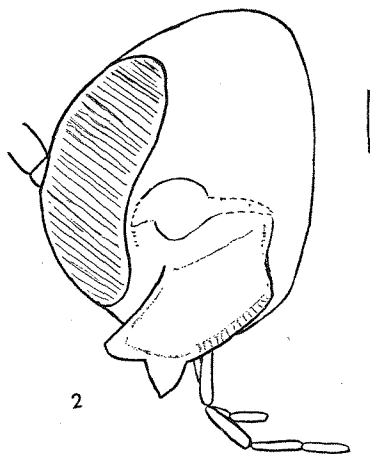


Fig. 2. *Protodacnusa tristis* (NEES), head in lateral view. (Scale 0.1 mm.)
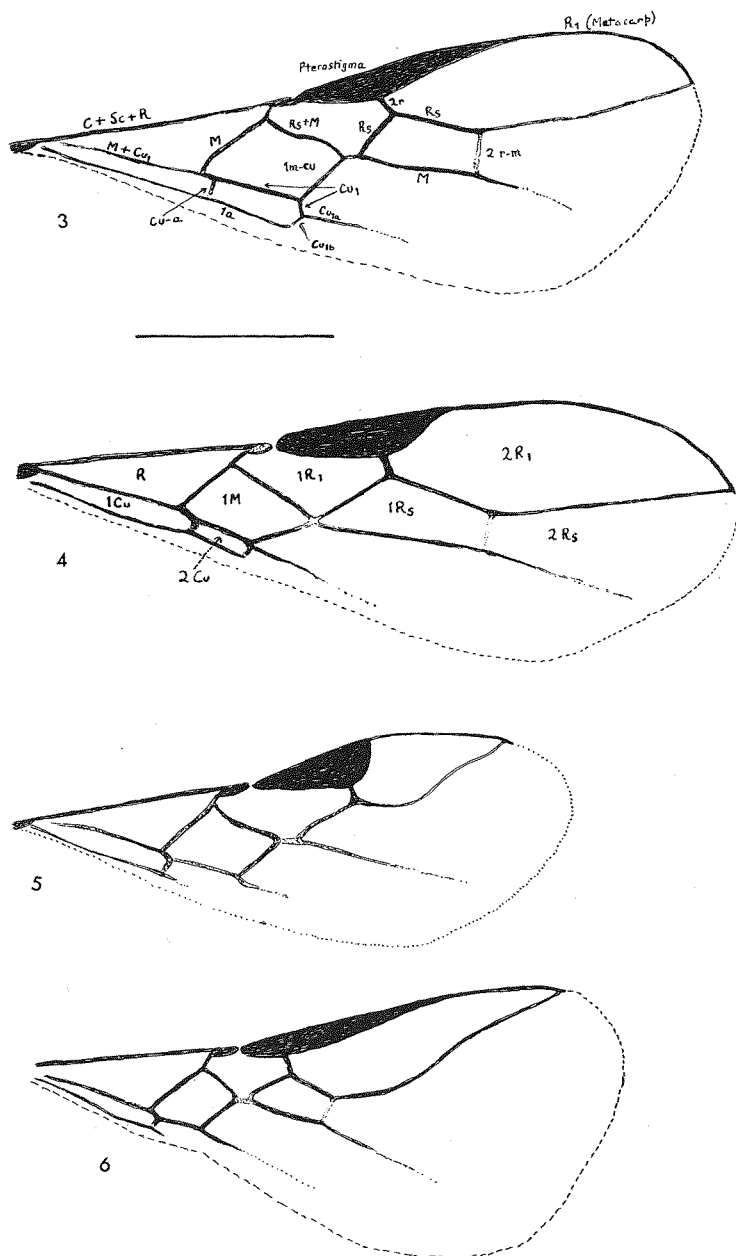
**Plate 1**

**Plate 2**

Figs. 3—6. Wings of: 3 *Opius caelatus* HALIDAY (det. FISCHER), showing termi-
nology used for veins; 4 *Phaenocarpa ruficeps* (NEES) (det. FERRIÈRE), showing
terminology used for cells; 5 *Grandia cynaraphila* (RICCHELLO); 6 *Dapsilarthra
balteata* (THOMSON). (Scale 0.1 mm.)
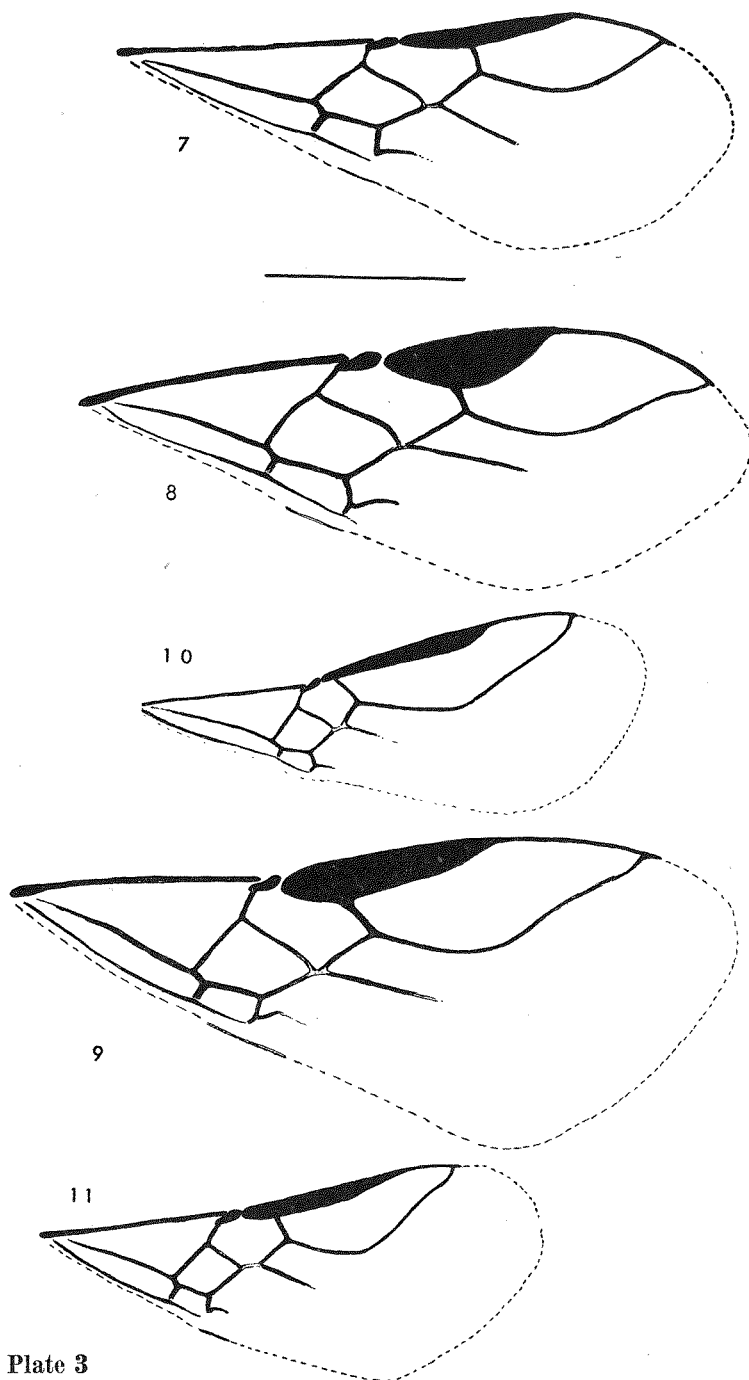
Plate 3

Figs. 7—11. Wings of : 7 *Synelix semirugosa* (HALIDAY); 8 *Symphya hians* (NEES); 9 *Dacnusa abdita maxima* (FISCHER); 10 *Dacnusa areolaris* (NEES); 11 *Protodacnusa tristis* (NEES). (Scale 0.1 mm.)
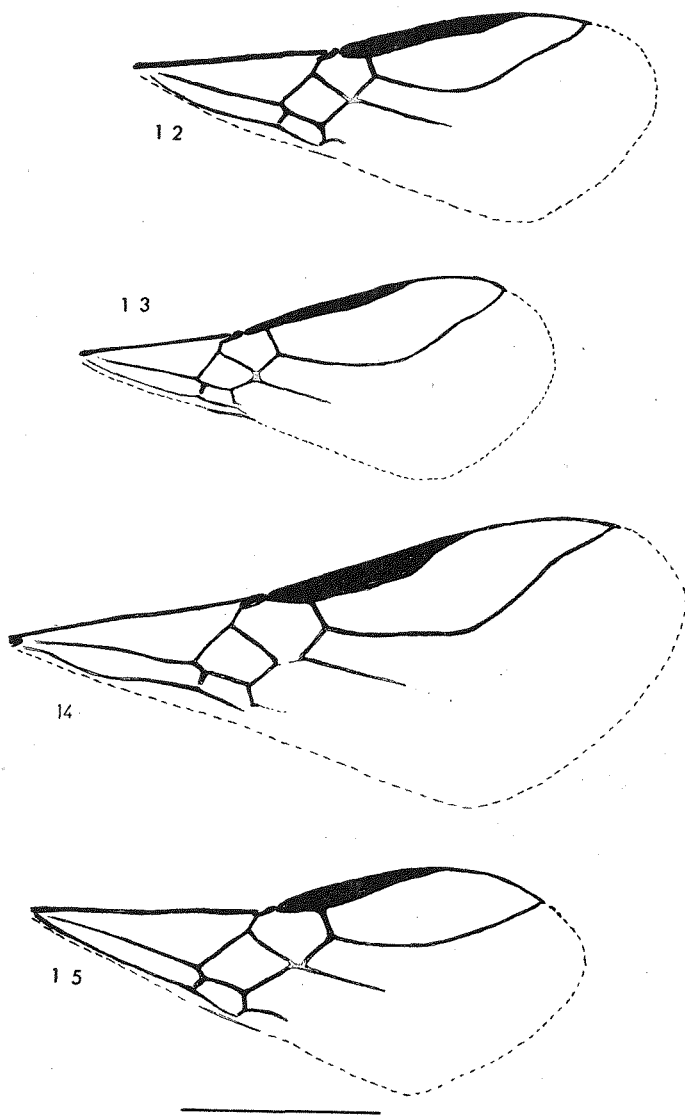
**Plate 4**

Figs. 12—15. Wings of: 12 *Exotela flavicoxa* (THOMSON); 13 *Exotela cyclogaster*
FÖRSTER; 14 *Chorebus lateralis* (HALIDAY); 15 *Chorebus brevicornis* (THOMSON).
(Scale 0.1 mm.)
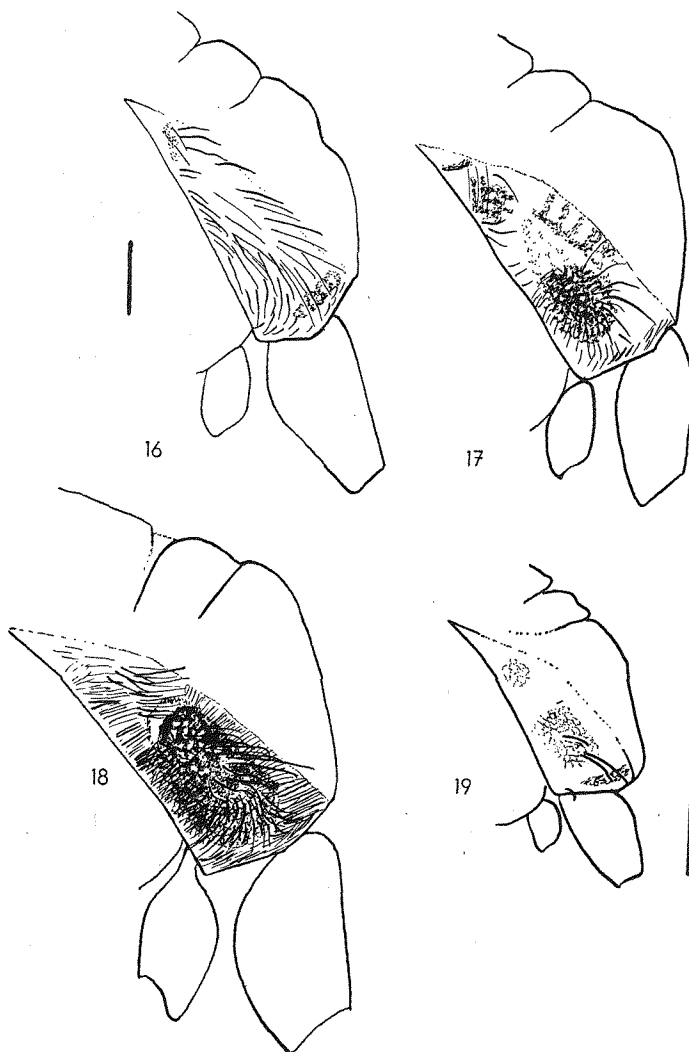
**Plate 5**

Figs. 16—19. Metapleuron of: 16 *Exotela flavicoxa* (THOMSON); 17 *Chorebus nydia* (NIXON); 18 *Chorebus spenceri* n. sp.; 19 *Chorebus freya* (NIXON). (Scale 0.1 mm.)
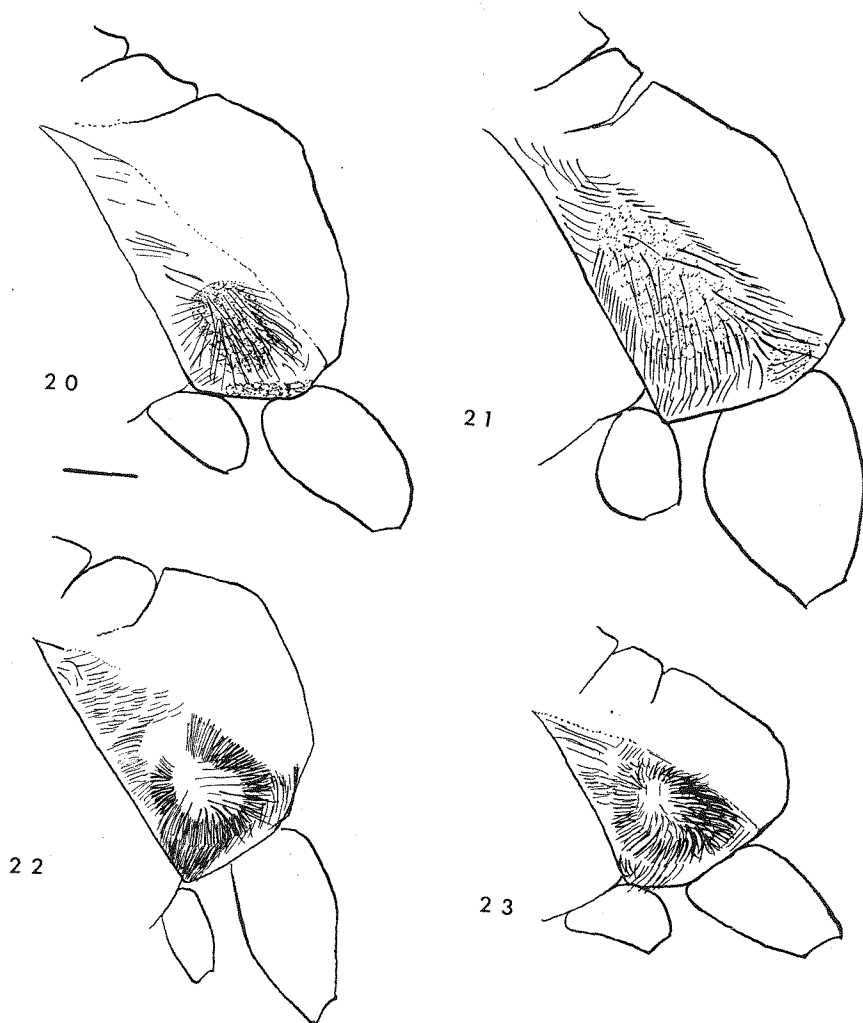
## Plate 6

Figs. 20—23. Metapleuron of: 20 *Chorebus talaris* (HALIDAY); 21 *Chorebus cybele* (NIXON); 22 *Chorebus lateralis* (HALIDAY); 23 *Chorebus esbelta* (NIXON). (Scale 0.1 mm.)
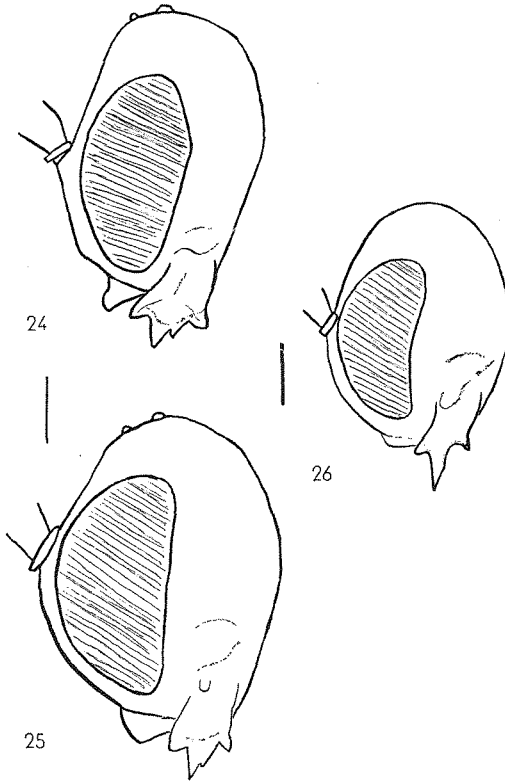
**Plate 7**

Figs. 24—26. Head in lateral view of: 24 *Chorebus coxator* (THOMSON); 25 *Chorebus merella* (NIXON); 26 *Chorebus obliquus* (THOMSON). (Scale 0.1 mm.)
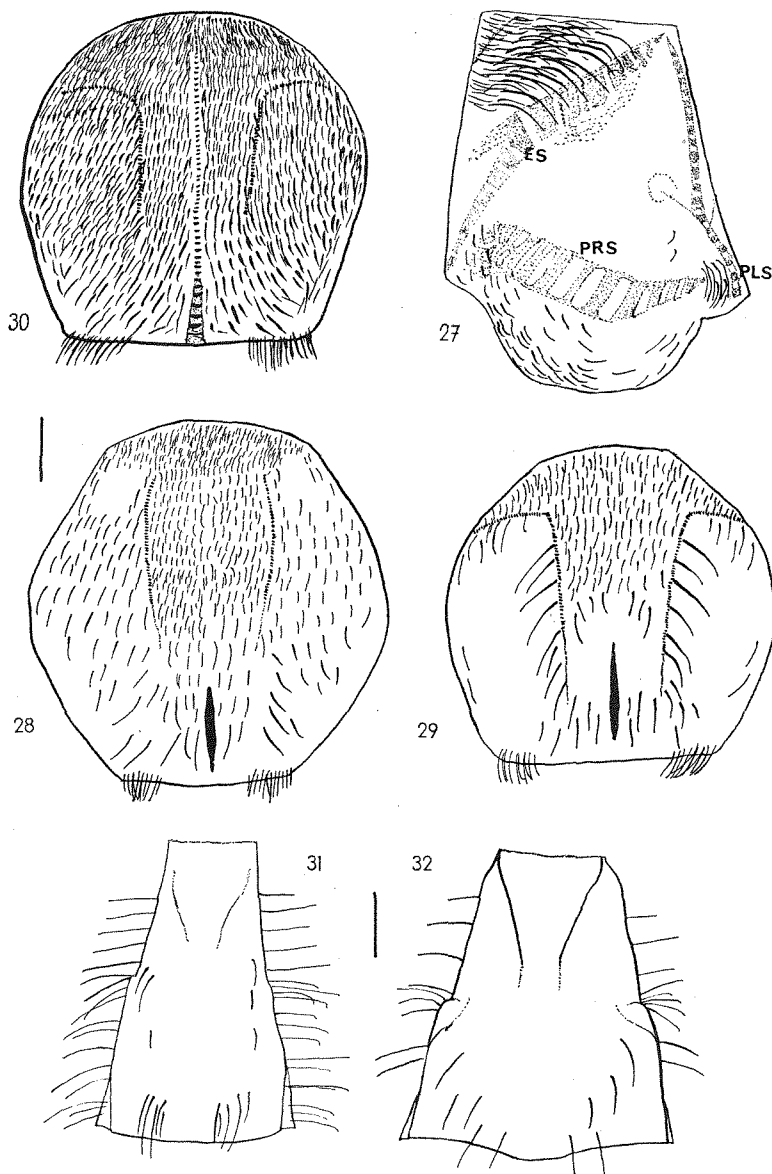
## Plate 8

Fig. 27. Mesepisternum of *Chorebus spenceri* n. sp. PRS = precoxal suture, PLS = pleural suture, ES = epicnemial suture. (Scale 0.1 mm.)

Figs. 28—30. Mesoscutum of: 28 *Chorebus coxator* (THOMSON); 29 *Chorebus nydia* (NIXON); 30 *Chorebus spenceri* n. sp. (Scale 0.1 mm.)

Figs. 31—32. Petiole of: 31 *Chorebus spenceri* n. sp.; 32 *Chorebus nydia* (NIXON). (Scale 0.1 mm.)
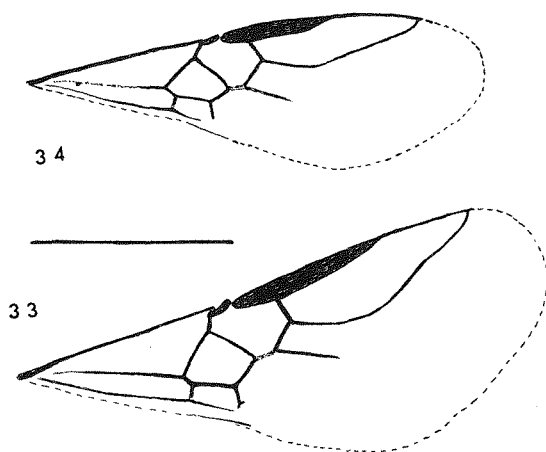
Plate 9

Figs. 33—34. Wings of: 33 *Chorebus spenceri* n. sp.; 34 *Chorebus coxator* (THOM-SON). (Scale 0.1 mm.)
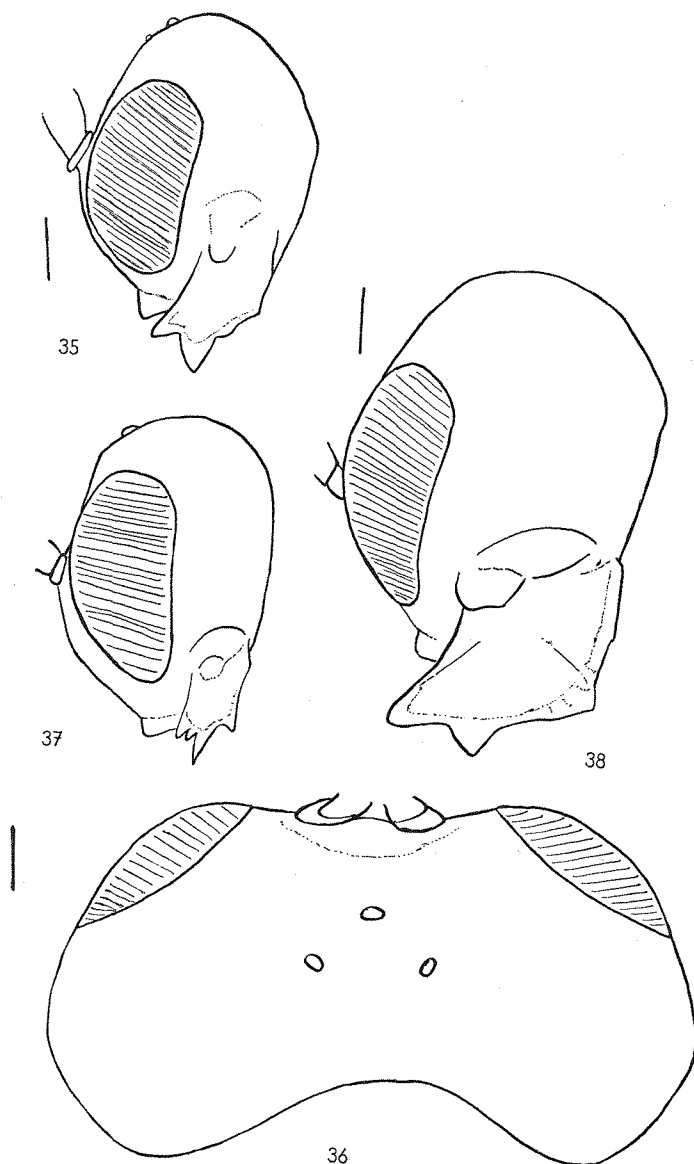
**Plate 10**

Figs. 35—38. Heads of: 35 *Exotela interstitialis* (THOMSON) (lateral view); 36 *Protodacnusa litoralis* n. sp. (dorsal view); 37 *Laotris striatula* (HALIDAY) (lateral view); 38 *Protodacnusa litoralis* n. sp. (lateral view). (Scale 0.1 mm.)