THE ARYTAININI OF THE SUBFAMILY PSyllINAE, HEMIPTERA–HOMOPTERA, FAMILY PSyllIDAE.—II.

By G. Heslop-Harrison.

CORRIGENDA AND ADDENDA TO PART I.*

The genus Livilla Curtis, was unfortunately omitted from the preliminary consideration of the scope of the Agytainini, although it was already known that it possessed all the characters necessary to place it in this tribe and in a position close to Agytaina itself. Both the genus and its species will therefore receive the full treatment in this series.

Dr. J. de Beaumont of Lausanne, Switzerland, has presented the author with paratypes of Cerutti’s species Agytaina montana, and another series of the same species has been received from Dr. Livio Tamanini from Trento, Italy.

Examination of both series in a detailed fashion has left the present author with no doubts whatsoever that the species was correctly placed in the genus Agytaina. Although the costal margin of the wing is slightly thickened in the region where R₁ merges into it, no pterostigma is formed and a costal nodal break is absent. Cerutti was therefore in error when he described this form as having a pterostigma.

Dr. Wilhelm Wagner and Prof. L. D. Tuthill have both corrected the author on a point of nomenclature in respect to the use of a homonym. It would appear that the rules of nomenclature are quite definite, so that the species referred to in Part I (3), Ann. Mag. nat. Hist. Ser. 12, vol. iv, May 1951, p. 444, as Agytaina (Spartina) spartii (Guérin) should have been known as Agytaina (Spartina) spartiophila (Forst.).

This may well be the most convenient place, however, to indicate that there are very good reasons now, why the new subgenus Spartina Heslop-Harr. (1951) should be raised to a full genus. The original description of it as a subgenus of Agytaina Forst. will stand for the purpose of defining it, but in raising its status, a type species must be designated. It is proposed that the species Spartina spartiophila (Forst.) be henceforth recognised as the designated type species of the genus Spartina Heslop-Harr.

Several authors have indicated that the name afforded to the new genus of psyllids, Neopsylla Heslop-Harr. (Ent. mon. Mag., June, 1949) which the author has since recognised as of the Agytainini was not available since Neopsylla Wagner (1903), is a recognised genus of fleas. In correspondence as well as in a recent publication, Professor L. D. Tuthill has also indicated that the method of changing this to Acizzia Heslop-Harr. (Ann. Mag. nat. Hist., Ser. 12, vol. iv, p. 417) was informal, and not acceptable under the current rules of nomenclature.

* Part I was published in the Annals and Magazine of Natural History, Ser. 12, vol. IV, May, 1951.
It is now proposed to amend the position officially. *Neopylla* Heslop-Harr. 1949 (see Wagner 1903, *nomen preoccupatum = Acizzia* Heslop-Harr., *n.n.*

Work on subfamily separation which the author is also undertaking has now reached a point where the Psyllinae as a subfamily of the Psyllidae has received a full investigation. As the Arytainini of Crawford is only one of several integral parts receiving tribal status within the Psyllinae, much more is now known concerning its status and limits within the latter. *Psyllopis* Löw, *Diaphorina* Löw and *Euphalara* Schwarz, and several derivative genera, have no place in the Arytainini although they were considered to have when Part I of this series was written. Although it may be necessary to refer to them all in passing, they will not receive any full treatment in this series, that being reserved for more appropriate places in the treatment of the additional tribes concerned.

(5) PRELIMINARY NOTES ON THE NORTH AMERICAN PSYLLIDAE
HITHERTO REFERRED TO THE GENUS ARYTAINA FORSTER, 1848.

Whilst being immediately concerned with the North American "species" pertaining largely to the United States North of Mexico, of which the author possesses examples sufficient in number to have made this investigation possible, there are others recently described from the West Indies, Florida, etc. and zones bordering on the semi-tropical, south-eastern Central American region of the U.S.A. These, although omitted from present consideration, undoubtedly need further investigation, which they will receive, if and when the author is in a position to give it to them. It would seem that some of them are not even congeneric with any of the sections distinguished as separate genera in the present work. Unfortunately, examples of such species are not immediately available, and their further discussion at this place is therefore out of the question. Indeed, in some cases, the paucity of essential detail in the original descriptions coupled with a lack of adequate illustrations, renders even subsequent identification a doubtful procedure.

In Part I (2) pp. 420–425 a general historical review of the Arytainini was presented when it was indicated that it was thought that no American species had hitherto been referred to the genus *Arytaina* Förster, correctly. At the time no adequate reasons were given upholding this belief, but it would now appear that further discussion of the Arytainini would be facilitated if this American section is given immediate treatment. That this should be done now is particularly important in view of the numerous new species that have to be added to *Arytaina* (*sensu stricto*) in the near future, and again if ever a true understanding of the genus *Acizzia* Heslop-Harr. is to be gained. *Acizzia* has come in for much comment in its Australian and New Zealand range, when it appears to have been overlooked that it also has a large number of additional species distributed through the Indo-Malayan Archipelago and Africa. In this connection and before proceeding any further it should also be borne in mind that it was never intended or implied that all the Australian species hitherto referred to *Peylla* should now be referred to *Acizzia*, and that when the genus was first defined under the *nomen preoccupatum*, *Neopylla*, only five species could be referred to it with some degree of certainty, and three of these, only because of the very detailed illustrations and descriptions that had been given by Ferris and Klyver (1932: Trans. N.Z. Inst., 63 pp. 34–61).

However, to return to the discussion of the North American forms hitherto referred to the genus *Arytaina*, except for the introduced European *Arytaina genistae* Lattr. and *Spargina spartiophila* (Först.), it should be indicated at once that many of them may not be considered to be the in the strict sense; such forms represent complexes of several. An apparent variability is manifest which several authors seem to have noted in these complex species, and this variability seems to have been attributed primarily to habitat difference, geographical variation, etc., etc., but what is believed to be the true state of affairs by the present author has been completely ignored by all the American workers in this field except perhaps by Miss Louise M. Russell, and now by Prof. D. D. Jensen.

Owing to the terms in which the pre-existing descriptions have been couched, and without the further critical examinations which are needed in both the laboratory and the field, many must thus remain unrecognised as complexes and not species. For the time being it is necessary to treat the sections as if they were individual species, and to refer to them under the specific names that have already been afforded to them. The ultimate elucidation and separation of the component parts must be left to interested American systematists, but warning must be given to the effect that this is decidedly not a task for the amateur.

Long before this work was begun, an impression had been gained that it would become necessary to provide one, or at most, two new generic names for the members of this section of the American Psyllidæ hitherto referred to *Arytaina*; it was not understood then that there were no fewer than four distinct genera through which the twelve species or species complexes concerned were distributed.

No pretence is maintained at a complete understanding of how this peculiar situation had arisen, but it seems to have begun with an initial misunderstanding of generic limits as afforded by Crawford in 1914, in a work which, because of its comprehensive American application, seems to have precluded the use of any other.

This may be coupled with a failure to recognise the nature of *Arytaina genistae* Lattr., the type species of *Arytaina* when the latter was discovered as an introduction to the North American psyllid fauna as early as 1911. It was then associated with indigenous forms which it superficially resembled, and the nature of the genus *Psyllopis* Craw., in which it were then placed was such, that it bore little or no apparent relationship to the original *Arytaina*. The nature of *Psyllopis* is recognised now, only
It is now proposed to amend the position officially. *Neopsylla* Heslop-Harr. 1949 (see Wagner 1903), *nomen pro corruptum = Acizzia* Heslop-Harr., *n.n.*

Work on subfamily separation which the author is also undertaking has now reached a point where the Psyllinae as a subfamily of the Psyllidae has received a full investigation. As the Arytainini of Crawford is only one of several integral parts receiving tribal status within the Psyllinae, much more is now known concerning its status and limits within the latter. *Psyllopsis* Löw, *Diaphorina* Löw and *Euephyalus* Schwarz, and several derivative genera, have no place in the Arytainini although they were considered to have when Part I of this series was written. Although it may be necessary to refer to them all in passing, they will not receive any full treatment in this series, that being reserved for more appropriate places in the treatment of the additional tribes concerned.

(5) **PRELIMINARY NOTES ON THE NORTH AMERICAN PSYLLIDAE HITHERTO REFERRED TO THE GENUS ARYTAINA FORSTER, 1848.**

Whilst being immediately concerned with the North American "species" pertaining largely to the United States North of Mexico, of which the author possesses examples sufficient in number to have made this investigation possible, there are others recently described from the West Indies, Florida, etc. and zones bordering on the semi-tropical, south-eastern Central American region of the U.S.A. These, although omitted from present consideration, undoubtedly need further investigation, which they will receive, if and when the author is in a position to give it to them. It would seem that some of them are not even congeneric with any of the sections distinguished as separate genera in the present work. Unfortunately, examples of such species are not immediately available, and their further discussion at this place is therefore out of the question. Indeed, in some cases, the paucity of essential detail in the original descriptions coupled with a lack of adequate illustrations, renders even subsequent identification a doubtful procedure.

In Part I (2) pp. 420–425 a general historical review of the Arytainini was presented when it was indicated that it was thought that no American species had hitherto been referred to the genus *Arytaina* Förster, correctly. At the time no adequate reasons were given upholding this belief, but it would now appear that further discussion of the Arytainini would be facilitated if this American section is given immediate treatment. That this should be done now is particularly important in view of the numerous new species that have to be added to *Arytaina* (*sensu stricto*) in the near future, and again if ever a true understanding of the genus *Acizzia* Heslop-Harr. is to be gained. *Acizzia* has come in for much comment in its Australian and New Zealand range, when it appears to have been overlooked that it also has a large number of additional species distributed through the Indo-Malayan Archipelago and Africa. In this connection and before proceeding any further it should also be borne in mind that it was never intended or implied that all the Australian species hitherto referred to *Psylla* should now be referred to *Acizzia*, and that when the genus was first defined under the *nomen pro corruptum, Neopsylla*, only five species could be referred to it with some degree of certainty, and three of these, only because of the very attractive illustrations and descriptions that had been given by Ferris and Klyver (1932: *Trans. N.Z. Inst.*, 63 pp. 34–61).

However, to return to the discussion of the North American forms hitherto referred to the genus *Arytaina*, except for the introduced European *Arytaina genistae* Latr. and *Spartina spartiophila* (Först.), it should be indicated at once that many of them may not be considered to be the true *Arytaina*; such forms represent complexes of several. An apparent variability is manifest which several authors seem to have noted in these complex species, and this variability seems to have been attributed primarily to habitat difference, geographical variation, etc., etc., but what is believed to be the true state of affairs by the present author has been completely ignored by all the American workers in this field except perhaps by Miss Louise M. Russell, and now by Prof. D. D. Jensen.

Owing to the terms in which the pre-existing descriptions have been couched, and without the further critical examinations which are needed in both the laboratory and the field, many must thus remain unrecognised as complexes and not species. For the time being it is necessary to treat the sections as if they were individual species, and to refer to them under the specific names that have already been afforded to them. The ultimate elucidation and separation of the component parts must be left to interested American systematists, but warning must be given to the effect that this is decidedly not a task for the amateur.

Long before this work was begun, an impression had been gained that it would become necessary to provide one, or at most, two new generic names for the members of this section of the American Psyllidae hitherto referred to the genus *Arytaina*; it was not understood then that there were no fewer than four distinct genera through which the twelve species or species complexes concerned were distributed.

No pretense is maintained at a complete understanding of how this peculiar situation had arisen, but it seems to have begun with an initial misunderstanding of generic limits as afforded by Crawford in 1914, in a work which, because of its comprehensive American application, seems to have precluded the use of any other.

This may be coupled with a failure to recognise the nature of *Arytaina genistae* Latr., the type species of *Arytaina* when the latter was discovered as an introduction to the North American psyllid fauna as early as 1911. It was then associated with indigenous forms which it superficially resembled, and the nature of the genus *Psylllopsis* Crawf., in which they were then placed was such, that it bore little or no apparent relationship to the original *Arytaina*. The nature of *Psylllopsis* is recognised now, only
on the basis of its original inclusions, from the time of its inception until it was finally abandoned; it has never been defined but will be seen to have included representatives of now fewer than six genera, some of these occurring in the Indo-Malayan and Pacific regions!

Maintaining this situation since then in American circles, has been a persistent conventional use of the Crawford plan of classification and, for the most part, the genera he used in the form originally conceived by him. With regard to North American species of the Arytainini, subsequent authors have done little more than provide the names and descriptions of new species as they were recognized in collections, tacking them on willy-nilly, to the "genera" already recognized. Few American systematists have bothered to examine Arytaina genista in this connection, and as that species seems to have been restricted to one known locality in North America (Woods Hole, Massachusetts), its consequent inaccessibility no doubt explains this in part.

At first sight, the present problem seemed simply to be one of providing definitions for the new genera, and then designating type species for them; unfortunately there is much more involved than this.

As the author has been aware of the complex nature of the indigenous North American arytainine psyllids for a number of years, it has been natural that he should have conveyed his opinions to several interested American collaborators. It would appear from the replies he has received that there exists a considerable amount of prejudice not only towards the present views concerning generic limits and the characterising of genera, but also a very strong dislike to break convention of such long standing. It is therefore necessary to give this American section of the Arytainini more detailed consideration than otherwise would have been necessary.

As a start, it might be as well to draw attention to the existence of several "manuscript names" for some of the "species" and, these names, since they existed long before Crawford's work appeared, indicate that the earlier American systematists neither considered the complex to be uniformly congeneric within itself, nor for any part of it to be congeneric with Arytaina Först. Perhaps it might then be argued that this earlier attitude was the outcome of ignorance, but there is an abundance of evidence in support of the view now expressed, that entomologists of the Schwarz and Riley class were extremely well informed at least in matters pertaining to the Psyllidae. Support to this view is manifest by the obvious collaboration that existed between them and their European contemporaries; there has been an equally obvious lack of such collaboration, until quite recently, on matters pertaining to the Psyllidae by their successors.

When the twelve representatives of the American species and species complexes of the Arytainini available to the author are displayed together, there is manifest a lack of homogeneity, a lack which it seems that these earlier systematists had in part recognised. If these "species" are then reviewed in conjunction with an even longer chain of true

**Arytaina** species from Europe and North Africa, the original opinion expressed in Part I, to the effect that they were not congeneric, is very apparent, and this difference was already expressed in part by the nature of the species and species complexes referred to under pre-existing American manuscript names.

In presenting this declaration, it is necessary to point out that the Palaearctic **Arytaina** covers an area perhaps more than equal in extent to that occupied by its North American relatives and that it is now known to include more than twice as many species and species complexes, and that throughout them all there is exhibited a uniformity of type. This uniformity of type is considered to be a necessary attribute of a genus, no matter how large or how small it may be. In the latter respect this has obviously not been considered to be necessary when the North American Arytainini of the present section have been referred, to **Arytaina**, en masse, and apparently in error.

Although the Palaearctic area covered by **Arytaina** is so great, its forty or so species are invariably associated with a group of related species of closely related genera of the Genistee (see Part I, (4), p. 449). This fact has been confirmed by personal investigation into the biology of some twenty of the species concerned, coupled with published and other data concerning the hosts of most of the remaining. By comparison the North American section of the Arytainini under consideration shows no such uniformity of host choice.

The significance to be attached to this, lies in the fact that in the main, the speciation of the modern Psyllidae has followed closely on the speciation of the host groups to which they have become attached. The members of the various genera of psyllids, with significant frequency, are thus seen to be attached uniformly to the species of closely related genera. Whilst there are exceptions, these are not so numerous as to detract from the general truth of this statement, and acceptable explanations are available for the exceptions.*

* Therefore, that the present American complex has long been recognised to have such a wide host range as it has, in the first instance, suggested possible primary lines of subdivision according to the differing host attachments.

Three "species" are known to be attached to members of the genus *Amorpha*, and the latter are papilionate shrubs which are not too distantly related to the Genistee to preclude them, from the host standpoint, having affinities with species of the genus *Arytaina*. Although undoubtedly related, it will be shown later that these American species are not congeneric with members of the European genus *Arytaina*.

Of the remainder, two "species" representing another section are attached to the members of the genus *Purshia*, a genus of shrubs referable to the Rosaceae. A third section, the largest, is associated with species

* Some of the exceptions to this general rule in the arytainine genus *Acleis* have been discussed at length in a more appropriate place, and it is hoped that the publication in which this discussion was effected will be in print by the time that the present account is in the press.
on the basis of its original inclusions, from the time of its inception until it was finally abandoned; it has never been defined but will be seen to have included representatives of now fewer than six genera, some of these occurring in the Indo-Malayan and Pacific regions!

Maintaining this situation since then in American circles, has been a persistent conventional use of the Crawford plan of classification and, for the most part, the genera he used in the form originally conceived by him. With regard to North American species of the Arytainini, subsequent authors have done little more than provide the names and descriptions of new species as they were recognized in collections, tackling them on willy nilly, to the "genera" already recognised. Few American systematists have bothered to examine Arytaina genistae in this connection, and as that species seems to have been restricted to one known locality in North America (Woods Hole, Massachusetts), its consequential inaccessibility no doubt explains this in part.

At first sight, the present problem seemed simply to be one of providing definitions for the new genera, and then designating type species for them; unfortunately there is much more involved than this.

As the author has been aware of the complex nature of the indigenous North American arytainine psyllids for a number of years, it has been natural that he should have conveyed his opinions to several interested American collaborators. It would appear from the replies he has received that there exists a considerable amount of prejudice not only towards the present views concerning generic limits and the characterising of genera, but also a very strong dislike to break convention of such long standing. It is therefore necessary to give this American section of the Arytainini more detailed consideration than otherwise would have been necessary.

As a start, it might be as well to draw attention to the existence of several "manuscript names" for some of the "species", and these names, since they existed long before Crawford's work appeared, indicate that the earlier American systematists neither considered the complex to be uniformly congeneric within itself, nor for any part of it to be congeneric with Arytaina Först. Perhaps it might then be argued that this earlier attitude was the outcome of ignorance, but there is an abundance of evidence in support of the view now expressed, that entomologists of the Schwarz and Riley class were extremely well informed at least in matters pertaining to the Psyllidae. Support to this view is manifest by the obvious collaboration that existed between them and their European contemporaries; there has been an equally obvious lack of such collaboration, until quite recently, on matters pertaining to the Psyllidae by their successors.

When the twelve representatives of the American species and species complexes of the Arytainini available to the author are displayed together, there is manifest a lack of homogeneity, a lack which it seems that these earlier systematists had in part recognised. If these "species" are then reviewed in conjunction with an even longer chain of true

Arytaina species from Europe and North Africa, the original opinion expressed in Part I, to the effect that they were not congeneric, is very apparent, and this difference was already expressed in part by the nature of the species and species complexes referred to under pre-existing American manuscript names.

In presenting this declaration, it is necessary to point out that the Palaearctic Arytaina covers an area perhaps more than equal in extent to that occupied by its North American relatives and that it is now known to include more than twice as many species and species complexes, and that throughout them all there exists a uniformity of type. This uniformity of type is considered to be a necessary attribute of a genus, no matter how large or how small it may be. In the latter respect this has obviously not been considered to be necessary when the North American Arytainini of the present section have been referred latterly, to Arytaina, en masse, and apparently in error.

Although the Palaearctic area covered by Arytaina is so great, its forty or so species are invariably associated with a group of related species of closely related genera of the Genistee (see Part I, (4), p. 449). This fact has been confirmed by personal investigation into the biology of some twenty of the species concerned, coupled with published and other data concerning the hosts of most of the remaining. By comparison the North American section of the Arytainini under consideration shows no such uniformity of host choice.

The significance to be attached to this, lies in the fact that in the main, the speciation of the modern Psyllidae has followed closely on the speciation of the host groups to which they have become attached. The members of the various genera of psyllids, with significant frequency, are thus seen to be attached uniformly to the species of closely related genera. Whilst there are exceptions, these are not so numerous as to detract from the general truth of this statement, and acceptable explanations are available for the exceptions.*

Therefore, that the present American complex has long been recognised to have such a wide host range as it has, in the first instance, suggested possible primary lines of subdivision according to the differing host attachments.

Three "species" are known to be attached to members of the genus Amorpha, and the latter are papilionate shrubs which are not too distantly related to the Genistee to preclude them, from the host standpoint, having affinities with species of the genus Arytaina. Although undoubtedly related, it will be shown later that these American species are not congeneric with members of the European genus Arytaina.

Of the remainder, two "species" representing another section are attached to the members of the genus Pusdia, a genus of shrubs referable to the Rosaceae. A third section, the largest, is associated with species

* Some of the exceptions to this general rule in the arytainine genus Acizia have been discussed at length in a more appropriate place, and it is hoped that the publication in which this discussion was effected will be in print by the time that the present account is in the press.
of the genus *Ceanothus* of the Rhamnaceae. In the latter instance the shrubs concerned are ornamental plants restricted to the western area of the North American continent, so far as it has been possible to ascertain, and they do not appear to have any close relatives in the Palaearctic region. *Ceanothus* seems to be a recent genus, and one having evolved in an area west of the Rockies, in North America.

Although so far only eight "species" of arytainine psyllids are known to be attached to species of *Ceanothus*, it is perhaps in this section that the greatest number of new forms may be discovered. It is already apparent that two genera are involved and it is estimated that perhaps as many as twenty or more true species have yet to be separated in the several obvious complexes that are now known to exist.

On the evidence of their distribution on such a range of unrelated host groups, and without any further information being available, it was deduced as early as 1934 that it was possible that as many as three genera may be involved, one of which was considered to be *Arytaina*, sensu Förster, the other two, new. At that time the present author believed that morphological distinction should be sought between the sections associated with the differing host groups, but how great such morphological distinction may have been he had no means of estimating; no amount of description in psyllid literature can ever compensate for the absence of critical illustrations of the necessary structures. Reference is now being made particularly to frontal views of the head which have never been adequately considered in this group.

Justification for the original and subsequent contentions (See Part I) held by the present author concerning the inter- and intra-generic relationships existing in this section of the Arytainini could thus only be determined by reference to the actual psyllid material. The necessary investigation was held in abeyance until this became available, and in providing it, it is now very necessary to acknowledge with gratitude, the help afforded, first, by Dr. Louise M. Russell, of the United States Department of Agriculture, Washington, Professor L. D. Tuthill of the University of Hawaii, and Professor D. D. Jensen, College of Agriculture, University of California.

(6) THE MORPHOLOGICAL AND BIOLOGICAL DIFFERENCES THAT EXIST BETWEEN THE EUROPEAN AND NORTH AMERICAN SECTIONS OF THE ARYTAININI.

At this point it is very necessary to take measures that will preclude any further possibility of confusing the members of the several American genera in this complex hitherto referred collectively to *Arytaina*, sensu Crawford, with the European-Palaearctic *Arytaina*, sensu Förster and its derivatives the genera *Spartina* Heslop-Harrison, Lindbergia Heslop-Harrison, *Floria* Löw, *Allooneura* Löw, *Amblyrhina* Löw and *Limula* Curtis.

It is maintained that the members of a single genus cannot possess either a pterostigma or alternatively none without some further sub-

division. No matter what previous opinions have been voiced concerning the validity for using the presence or absence of a pterostigma as a character of generic significance, the present opinion is one which is upheld by the meaning, origin and evolution of the pterostigma in the Psyllidae. These are aspects which do not seem to have been considered previously when the contrary views have been expressed, but which are now to be given some discussion in Section 7.*

Crawford's view, and therefore that also expressed by Tuthill et al., gives an overriding significance to the character and method of division of the propulerites as they are expressed in the Arytainini (See Part I, p. 417). By using this character without considering any others of significance, the typical genus *Arytaina* Förster has been combined with additional distinct genera of the North American and other regions, into the larger "genus" as at present recognised in American circles under the same name.

In this fashion, the original definition of Förster has ceased to have significance in such circles, but it should be remarked that if such a practice becomes universal, which is not now at all likely, this larger "genus", whilst it remains of *Arytaina* Förster, may not be known correctly as *Arytaina* Förster.

If the logical extension of the views expressed by the American systematicist, E. P. Van Duzee, (cf. Tuthill, 1943, p. 454) is maintained, then the details, within limits, of the species referred to a given genus must agree with the published generic details of its designated type. If such a contention is rigidly applied, rather than cause confusion, much confusion is liable to be obviated. In respect to the confusion now existing amongst the arytainine psyllids under discussion, this most certainly would have been so.

It has been necessary to use the qualification, "within limits" in expressing this belief, since modern standards require rather more detail in generic and other definitions than the earlier systematists offered. One may now restrict the scope of a genus by reference to structures not mentioned in the first published definition. The literature is full of such examples, and indeed, *Arytaina* Förster was so modified by Löw in 1878 when he removed *Allooneura* from its compass by this means. On the other hand, the scope may not be increased by omitting details and terms of reference included in the original definition, if such details and terms of reference are applicable to its type and possibly also to a reasonable range of its species. If, however, this should be done, then the new version must not pass under its original name, for it then ceases to have the same significance. As in the case of certain published versions of *Arytaina* to which reference will be made later, it is possible that even the designated type species may be excluded!

*It is obvious that any discussion of this sort afforded at this place cannot be made complete, but the Hemipteroid pterostigma has been made the subject of special study by the author in his attempt to elucidate its significance in the Psyllidae. Appropriate parts of this study are now being prepared for publication in the Annals and Magazine of Natural History, and it is hoped that the contribution concerned will be in the hands of the editors within the year.
of the genus *Ceanothus* of the Rhamnacese. In the latter instance the shrubs concerned are ornamental plants restricted to the western area of the North American continent, so far as it has been possible to ascertain, and they do not appear to have any close relatives in the Palaearctic region. *Ceanothus* seems to be a recent genus, and one having evolved in an area west of the Rockies, in North America.

Although so far only eight "species" of arytainine psyllids are known to be attached to species of *Ceanothus*, it is perhaps in this section that the greatest number of new forms may be discovered. It is already apparent that two genera are involved and it is estimated that perhaps as many as twenty or more true species have yet to be separated in the several obvious complexes that are now known to exist.

On the evidence of their distribution on such a range of unrelated host groups, and without any further information being available, it was deduced as early as 1934 that it was possible that as many as three genera may be involved, one of which was considered to be *Arytaina*, *sensu* Förster, the other two, new. At that time the present author believed that morphological distinction should be sought between the sections associated with the differing host groups, but how great such morphological distinction may have been he had no means of estimating; no amount of description in psyllid literature can ever compensate for the absence of critical illustrations of the necessary structures. Reference is now being made particularly to frontal views of the head which have never been adequately considered in this group.

Justification for the original and subsequent contentions (See Part I) held by the present author concerning the inter- and intra-generic relationships existing in this section of the Arytainini could thus only be determined by reference to the actual psyllid material. The necessary investigation was held in abeyance until this became available, and in providing it, it is now very necessary to acknowledge with gratitude, the help afforded, first, by Dr. Louise M. Russell, of the United States Department of Agriculture, Washington, Professor L. D. Tuthill of the University of Hawaii, and Professor D. D. Jensen, College of Agriculture, University of California.

(8) The morphological and biological differences that exist between the European and North American sections of the *Arytainini*.

At this point it is very necessary to take measures that will preclude any further possibility of confusing the members of the several American genera in this complex hitherto referred collectively to *Arytaina*, *sensu* Crawford, with the European-Palaearctic *Arytaina*, *sensu* Förster and its derivatives the genera *Spartina* Heslop-Harrison, *Lindbergia* Heslop-Harrison, *Floria* Löw, *Allooneura* Löw, *Amblyrhina* Löw and *Linulla* Curtis.

It is maintained that the members of a single genus cannot possess either a pterostigma or alternatively none without some further sub-

division. No matter what previous opinions have been voiced concerning the validity for using the presence or absence of a pterostigma as a character of generic significance, the present opinion is one which is upheld by the meaning, origin and evolution of the pterostigma in the *Psyllidae*. These are aspects which do not seem to have been considered previously when the contrary views have been expressed, but which are now to be given some discussion in Section 7.*

Crawford's view, and therefore that also expressed by Tuthill et al., gives an overriding significance to the character and method of division of the propleurites as they are expressed in the Arytainini (See Part I, p. 417). By using this character without considering any others of significance, the typical genus *Arytaina* Förster has been combined with additional distinct genera of the North American and other regions, into the larger "genus" at present recognised in American circles under the same name.

In this fashion, the original definition of Förster has ceased to have significance in such circles, but it should be remarked that if such a practice becomes universal, which is now not at all likely, this larger "genus", which is the sense of *Arytaina* Förster, may not be known correctly as *Arytaina* Förster.

If the logical extension of the views expressed by the American systematist, E. P. Van Duzee, (cf. Tuthill, 1943, p. 454) is maintained, then the details, within limits, of the species referred to a given genus must agree with the published generic details of its designated type. If such a contention is rigidly applied, rather than cause confusion, much confusion is liable to be obviated. In respect to the confusion amongst the arytainine psyllids under discussion, this most certainly would have been so.

It has been necessary to use the qualification, "within limits" in expressing this belief, since modern standards require rather more detail in generic and other definitions than the earlier systematists offered. One may now restrict the scope of a genus by reference to structures not mentioned in the first published definition. The literature is full of such examples, and indeed, *Arytaina* Förster was so modified by Löw in 1878 when he removed *Allooneura* from its compass by this means. On the other hand, the scope may not be increased by omitting details and terms of reference included in the original definition, if such details and terms of reference are applicable to its type and possibly also to a reasonable range of its species. If, however, this should be done, then the new version may not pass under its original name for it then ceases to have the same significance. As in the case of certain published versions of *Arytaina* to which reference will be made later, it is possible that even the designated type species may be excluded!

* It is obvious that any discussion of this sort afforded at this place cannot be made complete, but that the Hemipteroid pterostigma has been the subject of special study by the author in his attempt to elucidate its significance in the Psyllidae. Appropriate parts of this study are now being prepared for publication in the Annals and Magazine of Natural History, and it is hoped that the contribution concerned will be in the hands of the editors within the year.
On the basis of the American acceptance of forms within a genus purporting to be *Arytaina* both with and without a pterostigma, it is immediately obvious that this cannot be *Arytaina* Förster. Having ignored the terms of reference given by the author of the original *Arytaina* the species of these wider versions lack the necessary homogeneity desired in a genus. Furthermore, in the light of a more critical examination of the details of the designated type species of *Arytaina*, additional information has been revealed, and on considering this, it becomes very necessary to preclude all of the indigenous American species.

*Arytaina genistae* (Latreille) is of the designated type species of the genus, not because it happened to be the first species in it to be defined, but because Scott made it so in 1876. This species although included in his 1943 treatment of a genus purporting to be *Arytaina* Förster is actually excluded by Tuthill, by his new definition of the "genus". It is similarly excluded, but for different reasons by Crawford's 1919 definition. The circumstances of these exclusions will be discussed more fully later.

In view of the current variable attitude towards the significance to be afforded to the presence or absence of a pterostigma and although this character will have to be used in generic capacity later, at this place it has not been considered as expedient to use it in the separation of those certain American forms that could be separated by this means, from *Arytaina*, *sensu* Förster. Some more positive character, and one with sufficient generality that was applicable to all the American species in this complex, and which could not be denied in American cireles, had to be found.

*Arytaina*, *Floria*, *Allasoneura*, *Amblyrhina*, *Lutilia* and latterly *Lindbergia* and *Spartina*, in European usage, have long been known to be very close genera, but nevertheless, have always been considered to be distinct by systematists. The known genera were so considered by Crawford in 1914, but that author did not apparently appreciate that if he included *Arytaina* *genistae* in his version of *Arytaina*, then the representatives of all of these additional genera would be dragged into it, willy nilly; there was nothing left to exclude them.

Although not generally known, the very character which related the representatives of European arytainine genera, is that which may now be used to separate them from their not-so-close American relatives.

So far as is now known, none of the species of the above-mentioned European-Palaearctic genera, with the possible exception of the genus *Floria* (which has a seeming range as far south in Africa as Durban) are known to occur naturally outside of the Palaearctic region, and in the latter region they form a natural syngenetic group of psylline-Psyllidae quite distinct from all others of the same region.

They alone constitute the only known group of Palaearctic genera whose species in that region uniformly possess only one basal metatarsal spine.

No indigenous American species of the present complex of the Arytainini has been described with only one basal metatarsal spine, but that fact alone could not be considered as significant; this character was rarely or never mentioned in specific descriptions until the present author gave it the significance it truly merits in this connection several years ago.

Despite this, however, Tuthill, 1943, defined "Arytaina" as with the "Basal segment of the metatarsus with two black clawlike spines"—a condition which then excluded both *Arytaina* *genistae* the type of the genus, and its European relative *Spartina spartiophila* (both European introductions in America) but which, it has now been ascertained, is a condition which applied uniformly to all other "species" he then placed in the "genus".

In defining *Arytaina* thus, Tuthill was perhaps more specific than Crawford (1914), who simply stated "In other respects not differing markedly from *Psylla*...including claw-like spines of basal tarsus of hindlegs." The character, that is, the absence, presence and number when present, of the basal metatarsal spines, is frequently considered on a higher level, than the generic in the American psyllid literature. (cf. Crawford, 1914 1919; Tuthill, 1943, and others). Then it is usually discussed in the various texts on a subfamily level.

Crawford, for example, seemed to attach "...a good deal of importance taxonomically to the claw-like spines on the basal tarsus of hindlegs" and asserted that "...in *Psyllinae* there are two such claws, in *Trioxinae* none, while in *Carsiadinae* (i.e. *Ciriacerinae*) there is only one such claw."

Whilst the latter is neither a complete nor accurate statement of the position with regard to the basal metatarsal spines in the groups he mentioned, a fact which will be amply demonstrated in other places in the near future, its acceptance is sufficiently wide in America for the character to be considered there at the lower generic level in which it is now to be used.

Expressions concerning this character as it occurs in the Psyllinae are common. Tuthill, for example, in defining the subfamily Psyllinae stated, "Crawford considered the presence of two black claws on the basal segment of the metatarsi as of great importance, which indeed it is...".

If, therefore, some of the upholders of similar beliefs are confronted with the possibility of generic distinction being based on the uniform possession of one basal metatarsal spine in psylline—Psyllidae as opposed to two in the subfamily, or even if such a condition is complicated by other considerations which will become apparent later, it is hardly likely that they can raise legitimate objection.

Thus, all the indigenous American species of this complex hitherto referred to *Arytaina* and examined in the present connection possess two basal metatarsal spines and are therefore uniformly similar in this respect to all other known American psylline—Psyllidae. *Tetragonoccephala* Cwrf., an American genus which has previously been placed in the
On the basis of the American acceptance of forms within a genus purporting to be *Arytaina* both with and without a pterostigma, it is immediately obvious that this cannot be *Arytaina* Förster. Having ignored the terms of reference given by the author of the original *Arytaina* the species of these wider versions lack the necessary homogeneity desired in a genus. Furthermore, in the light of a more critical examination of the details of the designated type species of *Arytaina*, additional information has been revealed, and on considering this, it becomes very necessary to preclude all of the indigenous American species.

*Arytaina genistae* (Latreille) is of the designated type species of the genus, not because it happened to be the first species in it to be defined, but because Scott made it so in 1876. This species although included in his 1943 treatment of a genus purporting to be *Arytaina* Förster is actually excluded by Tuthill, by his new definition of the "genus". It is similarly excluded, but for different reasons by Crawford's 1919 definition. The circumstances of these exclusions will be discussed more fully later.

In view of the current variable attitude towards the significance to be afforded to the presence or absence of a pterostigma and although this character will have to be used in generic capacity later, at this place it has not been considered as expedient to use it in the separation of those certain American forms that could be separated by this means, from *Arytaina, sensu Förster*. Some more positive character, and one with significant in generic capacity that was applicable to all the American species in this complex, and which could not be denied in American circles, had to be found.

*Arytaina, Floria, Alloœneura, Amblyrhina, Lutilla* and latterly *Lindbergia* and *Spartina*, in European usage, have long been known to be very close genera, but nevertheless, have always been considered to be distinct by systematists. The known genera were so considered by Crawford in 1914, but that author did not apparently appreciate that if he included *Arytaina genistae* in his version of *Arytaina*, then the representatives of all of these additional genera would be dragged into it, willy nilly; there was nothing left to exclude them!

Although not generally known, the very character which related the representatives of European *arytainine* genera, is that which may now be used to separate them from their not-so-close American relatives.

So far as is now known, none of the species of the above-mentioned European-Palaearctic genera, with the possible exception of the genus *Floria* (which has a seeming range as far south in Africa as Durban) are known to occur naturally outside of the Palaearctic region, and in the latter region they form a natural syngenetic group of psylline-Psyllidae quite distinct from all others of the same region.

They alone constitute the only known group of Palaearctic genera whose species in that region uniformly possess only one basal metatarsal spine.

No indigenous American species of the present complex of the *Arytainini* has been described with only one basal metatarsal spine, but that fact alone could not be considered as significant; this character was rarely or ever mentioned in specific descriptions until the present author gave it the significance it truly merits in this connection several years ago.

Despite this, however, Tuthill, 1943, defined " *Arytaina* " as with the "basal segment of the metatarsus with two black clawlike spines"—a condition which then excluded both *Arytaina genistae* the type of the genus, and its European relative *Spartina spatiiophila* (both European introductions in America) but which, it has now been ascertained, is a condition which applied uniformly to all other "species" he then placed in the "genus".

In defining *Arytaina* thus, Tuthill was perhaps more specific than Crawford (1914), who simply stated "In other respects not differing markedly from *Psylla* ... including claw-like spines of basal tarsus of hindlegs."

The character, that is, the absence, presence and number when present, of the basal metatarsal spines, is frequently considered on a higher level, than the generic in the American psyllid literature. (cf. Crawford, 1914 1919; Tuthill, 1943, and others). Then it is usually discussed in the various texts on a subfamily level.

Crawford, for example, seemed to attach "... a good deal of importance taxonomically to the claw-like spines on the basal tarsus of hindlegs" and asserted that "... In Psyllinae there are two such claws, in Trioxinae none, while in Carsidarinae (i.e. Ciriacerininae) there is only one such claw."

Whilst the latter is neither a complete nor accurate statement of the position with regard to the basal metatarsal spines in the groups he mentioned, a fact which will be amply demonstrated in other places in the near future, its acceptance is sufficiently wide in America for the character to be considered there in the lower generic level in which it is now to be used.

Expressions concerning this character as it occurs in the *Psyllinae* are common. Tuthill, for example, in defining the subfamily *Psyllinae* stated, "Crawford considered the presence of two black claws on the basal segment of the metatarsi as of great importance, which indeed it is . . . ."

If, therefore, some of the upholders of similar beliefs are confronted with the possibility of generic distinction being based on the uniform possession of one basal metatarsal spine in *Psyllidae*—Psyllinae as opposed to two in the *arytainines* even if such a condition is complicated by other considerations which will become apparent later, it is hardly likely that they can raise legitimate objection.

Thus, all the indigenous American species of this complex hitherto referred to *Arytaina* and examined in the present connection possess two basal metatarsal spines and are therefore uniformly similar in this respect to all other known American psylline—Psyllidae. *Tetragonoscelphala* Crawf., an American genus which has previously been placed in the
Psyllinae for want of any other place suitable, is seen to possess no basal metatarsal spines, but it does not constitute an exception to the general rule applicable to the American Psyllinae; its position lies in the Spondylasinae rather than the Psyllinae, and in the former subfamily the absence of basal metatarsal spines is not of infrequent occurrence.

It is extremely doubtful at the present time if Förster ever noted the presence, absence, or number when present, of the basal metatarsal spines in the Psyllidae when his monograph was being produced, and he certainly did not mention them in connection with his simple definition of Arytaina. Even so, the restriction imposed by considering this character in connection with his genus Arytaina, as it applies to the type species and all of its true congenors, is quite in order.

The little we know about the North American psyllids under discussion would suggest that they are also biologically distinct from those European-Palaearctic forms with which they have been confused.

Without considering the biological distinction as manifest in their obvious differences in host preference, although the latter alone may contribute much in supporting the present contention regarding them, we have reference to the nymphal habits of three American "species" providing additional support. (cf. Klyver, Entomological News, vol. 33, 1932, pp. 39, 40 and 71).

For part of the complex then passing under the name "Arytaina robusta"(there would now appear to be as many as seven species confused under that name!) we read, "The nymphs occur on the ventral side of the leaves in individual cells constructed of white wax secretion, in which the nymphal stages occur. The last stage nymph leaves its cell a short time before the last moult." 

The details afforded for the form passing under the name of "Arytaina ribesiae" Crawford, are significantly similar to those given above. Although Tuthill has referred an "Arytaina ribesiae" to the genus Peysila, it should also be borne in mind that Enderlein was condemned by the same author for having referred all of the American species under discussion to Peysila for much better reasons; it is certain that Enderlein knew of the condition of the basal metatarsal spines, and therefore felt justified in his action.

On the other hand, the discussion (p. 488) afforded by Tuthill in 1943 suggested confusion between several distinct forms, some of his own conception of Arytaina and some of Peysila, the position being rendered quite difficult because of the obscurity of the condition of the propuritres in all arytainine species, without special preparatory treatment.

Even so, it seems quite clear that the form or forms discussed by Klyver under the name Arytaina ribesiae did pertain to the Arytainini. First, there is the cell-forming habit of the nymphs he described and second, the fact that these were observed on Ceanothus thyrsiflorus.

Crawford illustrated two "forms" of the "species", but there are at least four involved, and whilst one of these is possible, but not certainly of the genus Peysila, Klyver's information loses none of its significance to the present argument.

The nymphs of the "species" pubescens (Klyver, loc. cit., p. 71) representing another and different section of the American Arytainini, are described as follows:--"The nymphs are found among the younger branches and leaves, where they produce large amounts of wax secretion." This statement has a different but parallel significance.

The production of wax in quantity by all three of these psyllid nymphs, or in sufficient quantity to be available for individual cell production, indicates the presence of complex surface pore characters, and these, it should be remarked, when occurring on the bodies of neotenic female coccids—which are, strictly speaking, adventitious nymphs—have been regarded as sufficiently significant by the Ferris school of American Coccidologists to be worthy of consideration at the family level! Since the author's investigation of the phylogeny of the Psyllidae has necessitated a detailed consideration of the younger but derivative forms, however, he is certainly not in agreement with any views attaching to much importance to juvenile characters which, in part, can change when the same individuals are transferred to different hosts! On the other hand he is of the opinion that some importance may be attached to such characters, and, since the two families, the Psyllidae and the Coccidae have a common origin, whatever value this may be given in the one may not be considered in any major degree different in the other. Pore characters are seemingly worthy of remarking as offering considerable support to the present argument, but at generic rather than family level.

Some twenty or more species of the true Arytaina occurring in the Palaearctic region have been studied in the field in connection with this and related work. None of these has been distinguished by copious wax secretion, and the presence of their nymphs on the various host species has been detected only by beating. In them, the pore characters involved are of a much more simple nature, but pores are not absent; they are limited to the production of a fine, thin, dusting of wax over the general body surface, and the tubular filament secreted by the circum- anal pore-ring.

Copious wax production by nymphal psyllids leaves the surfaces of the host plants sticky or gummy for a considerable period after the adults have emerged. The survival of the latter, depending on the quantity of the gummy material involved, may be hazardous in the extreme unless they are provided with means to overcome the difficulties of entanglement.

The North American arytainine psyllids under discussion are all provided with such means, and therefore differ from all of the known Palaearctic forms of the same complex.

It has been known since 1949 that those spondylaspine psyllids of Australia living under similar conditions, possess contractile tarsal pads, and similar tarsal pads are now found in the adults of these American arytainine psyllids, where, perhaps, they have been developed by the same processes of evolution and perhaps for the same reasons.

In concluding Section 6, it is necessary to remark that no matter how one may consider the division of the North American arytainine psyllids
Psyllinae for want of any other place suitable, is seen to possess no basal metatarsal spines, but it does not constitute an exception to the general rule applicable to the American Psyllinae; its position lies in the Spondylaspinidae rather than the Psyllinae, and in the former subfamily the absence of basal metatarsal spines is not of infrequent occurrence.

It is extremely doubtful at the present time if Förster ever noted the presence, absence, or number when present, of the basal metatarsal spines in the Psyllidae when his monograph was being produced, and he certainly did not mention them in connection with his simple definition of *Arytaina*. Even so, the restriction imposed by considering this character in connection with its genus *Arytaina*, as it applies to the type species and all of its true conegers, is quite in order.

The little we know about the North American psyllids under discussion would suggest that they are also biologically distinct from those European-Palaearctic forms with which they have been confused.

Without considering the biological distinction as manifest in their obvious differences in host preference, although the latter alone may contribute much in supporting the present contention regarding them, we have reference to the nympha1 habits of three American "species" providing additional support. (cf. Klyver, Entomological News, vol. xxxii, 1932, pp. 39, 40 and 71).

For part of the complex then passing under the name " *Arytaina robusta* " (there would now appear to be as many as seven species confused under that name! we read, "The nymphs occur on the ventral side of the leaves in individual cells constructed of white wax secretion, in which the nympha1 stages occur. The last stage nymph leaves its cell a short time before the last moulting.""

The details afforded for the form passing under the name of " *Arytaina ribesiae* " Crawford are significantly similar to those given above. Although Tuthill has referred an " *Arytaina ribesiae* " to the genus *Psylla*, it should be borne in mind that Enderlein was condemned by the same author for having referred all of the American species under discussion to *Psylla* for much better reasons; it is certain that Enderlein knew of the condition of the basal metatarsal spines, and therefore felt justified in his action.

On the other hand, the discussion (p. 488) afforded by Tuthill in 1943 suggested confusion between several distinct forms, some of his own conception of *Arytaina* and some of *Psylla*, the position being rendered quite difficult because of the obscurity of the condition of the propurrites in all arytainine species, without special preparatory treatment.

Even so, it seems quite clear that the form or forms discussed by Klyver under the name *Arytaina ribesiae* did pertain to the *Arytaini*ni. First, there is the cell-forming habit of the nymphs he described and second, the fact that these were observed on *Ceanothus thyrsiflorus*.

Crawford illustrated two "forms" of the "species", but there are at least four involved, and whilst one of these is possibly, but not certainly, of the genus *Psylla*, Klyver's information loses none of its significance to the present argument.
amongst themselves, sufficient evidence has been presented, it is thought, to have established that they are biologically as well as morphologically quite distinct from their European-Palaearctic counterparts, and the least measure of such distinction that can be afforded under the circumstances, must clearly be generic.

(7) Characters to be considered as of generic significance amongst the North American Arytainine Psyllidae

Without considering the genera Psyllopsis Löw and Euphalarus Schwarz, which are now referred to other tribes than this, the North American arytainine-Psyllinae, have all hitherto been referred to the genus Arytaina. When this work was commenced and for the reasons already expressed, satisfaction would have been gained simply by the establishment of the fact long suspected, that these species were not congeneric with the type and related Palaearctic species strictly pertaining to Förster's version of that genus. To do so clearly deprived these American species of a genus name, and under the circumstances the erection of four new genera is necessary.

To provide that many for a group of species and species complexes hitherto referred to one genus has caused considerable misgiving, and no doubt will arouse certain consternation amongst American specialists in the group. More particularly is this so in view of the fact, that, with one exception (Miss Russell) nowhere in the literature or by correspondence has such a situation been hinted at since Crawford's time.

Further subdivision, however necessary amongst these American psyllids, is subject to difficulty, but this difficulty explains perhaps why this situation has remained undetected for so long. The use of certain characters is necessitated which are apparently considered as of little or no taxonomic significance at generic level in American circles. Therefore before anything else can be accomplished in this direction, it is necessary to justify their use in the present connection.

(a) The pterostigma and the associated costal nodal break.

It has long been known that the American species hitherto referred to Arytaina can be subdivided morphologically on the basis of the presence or absence of a pterostigma. Amongst European systematists, almost without exception, the presence or absence of a pterostigma would constitute sufficient basis for such a generic separation, but it has never been considered at this level by the American systematists interested in the group.

Crawford did not, apparently, investigate the meaning and origin of the pterostigma of the psyllids, nor did he consider its possible significance as a basic Homopterous character. His failure in this respect and his consequent neglect of it as a taxonomic character at generic level constitute no reasons why others should continue to neglect it.

In both his personal correspondence and in his writings Prof. L. D. Tuthill appears to have adopted the Crawford point of view, and he, like numerous other American systematists interested in the Psyllidae), has thus accepted without question, a number of the Crawford genera which, for this reason, are undoubtedly complex.

Thus, whilst being fully aware that the European conception of Arytaina was invariably one in which only species could be included that did not possess a pterostigma, and that the genus was, as he said, "Originally separated from Psylla by the lack of a pterostigma in the forewing," Tuthill (1943, p. 594) continued by remarking that this "...... was a character which is not of sufficient importance in itself to warrant such distinction." Further, that "Both Förster and Scott separated the genera on this basis, then, with no explanation proceeded to describe species of Psylla such as buxi in which there is no pterostigma."

A great deal more is known about psyllid systematics since the pioneer days of Förster (1848) and Scott (1876). A lot of changes have been made on both sides of the Atlantic, and most of them are valid.

"Psylla" buxi was referred to another genus by Enderlein in 1921, the genus Asphagidella, and whilst wrong in his supposition that "Psylla" buxi was devoid of a pterostigma, its separation seems to be valid for other reasons. Tuthill himself has described buxi as with the "pterostigma almost entirely lacking." Whilst it is understood what he means, i.e. that the pterostigma was small in that species, there can be no degrees of its presence. A pterostigma in the Psyllinae is present or absent, and confirmation of its presence is invariably found in the associated character of the costal nodal break.

For the present purposes it is necessary to explain briefly what the pterostigma is and why it is herein considered to have generic significance.

An analysis of the precursory tracheation within the wing-buds of psyllids and other Homoptera reveals the presence of a basic venational system which appears to have developed before the Homoptera became a distinct suborder. Venational specialisation within the suborder has subsequently followed two lines, (a) complication by the secondary development of supernumerary veins and the duplication of various secondaries subdivided by the basic primordials, or (b), reduction effecting the secondaries themselves or their principal secondaries.

Without modification by either (a) or (b), a basically complete type is also evident, and this is regarded as primitive.

In such a primitive type, a true pterostigma is seen to be the product of the secondary division of the principal of the radial system, namely R1 into R1a and R1b. As such a division occurs in various sections throughout the Homoptera with the formation of a true pterostigma, the latter may not be regarded as a simple specialisation occurring at random in some psyllids only. Rather, it is the inheritance by some, of a basic character possessed by their protopsyllid ancestors, which they in their turn had retained from their protohomopteran ancestors, long before. The fossil evidence supports this conclusion.

The presence of a true pterostigma in the Psyllidae is almost invariably accompanied by another character, the costal nodal break, a discon-
amongst themselves, sufficient evidence has been presented, it is thought, to have established that they are biologically as well as morphologically quite distinct from their European-Palaearctic counterparts, and the least measure of such distinction that can be afforded under the circumstances, must clearly be generic.

(7) **Characters to be considered as of generic significance amongst the North American Arytainine Psyllidae**

Without considering the genera *Psyllopsis* Löw and *Euphalanus* Schwarz, which are now referred to other tribes than this, the North American arytainine-Psyllinae, have all hitherto been referred to the genus *Arytaina*. When this work was commenced and for the reasons already expressed, satisfaction would have been gained simply by the establishment of the fact long suspected, that these species were not congeneric with the type and related Palaearctic species strictly pertaining to Förster's version of that genus. To do so clearly deprived these American species of a genus name, and under the circumstances the erection of four new genera is necessary.

To provide that many for a group of species and species complexes hitherto referred to one genus has caused considerable misgiving, and no doubt will arouse certain consternation amongst American specialists in the group. More particularly is this so in view of the fact, that, with one exception (Miss Russell) nowhere in the literature or by correspondence has such a situation been hinted at since Crawford's time.

Further subdivision, however necessary amongst these American psyllids, is subject to difficulty, but this difficulty explains perhaps why this situation has remained undetected for so long. The use of certain characters is necessitated which are apparently considered as of little or no taxonomic significance at generic level in American circles. Therefore before anything else can be accomplished in this direction, it is necessary to justify their use in the present connection.

(a) **The pterostigma and the associated costal nodal break.**

It has long been known that the American species hitherto referred to *Arytaina* can be subdivided morphologically on the basis of the presence or absence of a pterostigma. Amongst European systematists, almost without exception, the presence or absence of a pterostigma would constitute sufficient basis for such a generic separation, but it has never been considered at this level by the American systematists interested in the group.

Crawford did not, apparently, investigate the meaning and origin of the pterostigma of the psyllids, nor did he consider its possible significance as a basic Homopterous character. His failure in this respect and his consequent neglect of it as a taxonomic character at generic level constitute no reasons why others should continue to neglect it.

In both his personal correspondence and in his writings Prof. L. D. Tuthill appears to have adopted the Crawford point of view, and he, like numerous other American systematists interested in the *Psyllidae*),

G. Heslop-Harrison on Arytainini of the family Psyllidae.—II has thus accepted without question, a number of the Crawford genera which, for this reason, are undoubtedly complex.

Thus, whilst being fully aware that the European conception of *Arytaina* was invariably one in which only species could be included that did not possess a pterostigma, and that the genus was, as he said, "Originally separated from *Psylla* by the lack of a pterostigma in the forewing," Tuthill (1943, p. 594) continued by remarking that this "...... was a character which is not of sufficient importance in itself to warrant such distinction." Further, that "Both Förster and Scott separated the genera on this basis, then, with no explanation proceeded to describe species of *Psylla* such as *buxi* in which there is no pterostigma."

A great deal more is known about psyllid systematics since the pioneer days of Förster (1848) and Scott (1876). A lot of changes have been made on both sides of the Atlantic, and most of them are valid.

"*Psylla* *buxi* was referred to another genus by Enderlein in 1921, the genus *Asphagidella*, and whilst wrong in his supposition that "*Psylla* *buxi* was devoid of a pterostigma, its separation seems to be valid for other reasons. Tuthill himself has described *buxi* as with the "pterostigma almost entirely lacking." Whilst it is understood what he means, i.e. that the pterostigma was small in that species, *there can be no degrees of its presence.* A pterostigma in the *Psyllidae* is present or absent, and confirmation of its presence is invariably found in the associated character of the costal nodal break.

For the present purposes it is necessary to explain briefly what the pterostigma is and why it is herein considered to have generic significance. An analysis of the precursory tracheation within the wing-buds of psyllids and other Homoptera reveals the presence of a basic venational system which appears to have developed before the Homoptera became a distinct suborder. Venational specialisation within the suborder has subsequently followed two lines, (a) complication by the secondary development of supernumerary veins and the duplication of various secondaries subdivided by the basic primaries, or (b), reduction effecting the secondaries themselves or their principal secondaries.

Without modification by either (a) or (b), a basically complete type is also evident, and this is regarded as primitive.

In such a primitive type, a true pterostigma is seen to be the product of the secondary division of the principal of the radial system, namely *R₁* into *R₁a* and *R₁b*. As such a division occurs in various sections throughout the Homoptera with the formation of a true pterostigma, the latter may not be regarded as a simple specialisation occurring at random in some psyllids only. Rather, *it is the inheritance by some, of a basic character possessed by their protopsyllid ancestors, which they in their turn had retained from their protohomopteran ancestors, long before. The fossil evidence supports this conclusion.*

The presence of a true pterostigma in the *Psyllidae* is almost invariably accompanied by another character, the costal nodal break, a discon-
tinuity of the costal marginal vein occurring just in front of the junction R₁₄ effects with the costal margin of the wing.

The development of the costal nodal break undoubtedly preceeded the development of a pterostigma in the evolutionary history of the Homoptera, and whilst it may occur without the formation of a true pterostigma, in the psyllids at least, it has never been known to be absent in those possessing a true pterostigma.* This fact has to do with the apparent function and meaning of both.

A primary division of the North American species under discussion by means of these two associated characters is absolute and certain, but the members of the two groups, however superficially similar they may appear, do not involve or imply direct syngeny amongst themselves.

The pterostigmatic differences amongst the Psyllidae must have evolved long before the syngeneric aggregates of species we now distinguish as genera. As a failure to give at least generic status to the presence or absence of a pterostigma implies that arytainine psyllid species evolved before their respective hosts, further comment seems unnecessary.

(b) Head form

A more or less globular head with all three ocelli visible in dorsal view and of which the anterior member is located upon a clearly defined frons is now regarded as approximating the primitive head form of not only the Psyllidae but the Homoptera as a whole. Naturally, when this primitive head form is in evidence other characters are sought to offset it, but as it appears in the present group of American arytainine psyllids and before full use can be made of it in their classification, the details involved in this condition have to be analysed in order to assess their significance, both individually and collectively.

In degree of significance the "details" involved are then (i) the exposure of the frons (ii) the development of the genus into conical or tubular protrusions and (iii) the degree of deflection of the head.

The frons and the development of the genus: In his recent treatment of the New Zealand representatives of the Psyllidae he referred to the genus *Psylla* which then included members of the genus *Acizzia* Heslop-Harr.), Prof. L. D. Tuthill has commented upon the variable condition of the frons. This, since he was dealing with a composite group, (part of which is still undergoing very active evolution), rather than a single genus, cannot be regarded as significant in the way then implied. The author remarked "... The tendency for the genital processes to cover the frons only incompletely is also not universal... several North American species exhibit this trait."

It seems most likely that he was referring to the present section of the North American Arytainini, for the present author is quite unaware of

* Apparent exceptions appear to exist in certain ciriacidine genera, e.g. as *Homotoma* Guér., *Coriaria* Walker and *Paracacarida* Heslop-Harr., but these special cases need detailed discussion. It will be shown for them that R₁₄ remains undivided, and therefore that no true pterostigma is formed, however much the wing margin may be thickened.

G. Heslop-Harrison on Arytainini of the family Psyllidae.—II 431 any other North American psylline-Psyllidae to which such remarks could have applied.

Although there are exceptions, the degree of exposure of the frons (not its degree of development) in any psyllid is almost invariably the outcome of the degree of development of the gene into swellings of various shapes and sizes.

However considered in other insects, the existence of a frons as a basic taxonomic unit of the Homopterous head, must be recognised; Ferris himself had regarded it as such in the Psyllidae in 1932, although he had conveniently forgotten this by the time he came to introduce his peculiar conceptions of cephalic metamorhism for insects generally (cf. *Microentomology*, 7(2), 1942; 8(1), 1943).

The true development of the exposed frons is an expression of primitive character in the Psyllidae, whilst its partial or complete suppression is evidence of subsequent evolution. The presence of the exposed frons is thus worthy of consideration at generic level in the classification of the group. Since it is natural that the degree of development of the gene into lobes or swellings which obscure the frons should be variable, effective division on this basis is not absolute, but we try to use it as if it were, as far as it is possible to do so.

The presence of more or less well-developed genital protrusions with an associated suppression of the frons, is ordinarily considered to be a typical psylline trait, but in that subfamily, and in particular, within the tribe Arytainini, it is quite evident that the frons may exist in a graded series of degrees of suppression or exposure dependent on the variable degrees of development of the geneae. It is not, however, within the nature of the Psyllidae, that the extremes of complete exposure or complete suppression of the frons will exist side by side in species placed correctly within the same genus. No cases have been examined in which they do, and the North American arytainine psyllids under discussion therefore present no exception.

The deflection of the head: The question of how a globular head can be regarded as either deflexed or horizontal would seem to present an enigma. However, no matter how globular the head may be, the vertex in the Arytainini is invariably flattened or excavated to some extent, so that a line drawn through its median axis will make a variable angle with a similar line drawn through the median axis of the thorax. If the two are more or less on the same plane, then the head is to be regarded as horizontal, and if a distinct angle is made at their point of intersection, then the head is to be regarded as more or less deflexed.

This is a character of convenience rather than of significant taxonomic standing, but in its application in the present complex it helps in associating those forms which possess an exposed frons and undeveloped gene, distinguishing them from the others.

(c) The male genitalia.

How far one is to regard the details of the genitalia as providing characters of generic or even higher significance in any group of insects is
tinuity of the costal marginal vein occurring just in front of the junction of the wing.

The development of the costal nodal break undoubtedly preceded the development of a pterostigma in the evolutionary history of the Homoptera, and whilst it may occur without the formation of a true pterostigma, in the psyllids at least, it has never been known to be absent in those possessing a true pterostigma.* This fact has to do with the apparent function and meaning of both.

A primary division of the North American species under discussion by means of these two associated characters is absolute and certain, but the members of the two groups, however superficially similar they may appear, do not involve or imply direct syngeny amongst themselves.

The pterostigmatic differences amongst the Psyllidae must have evolved long before the syngenetic aggregates of species we now distinguish as genera. As a failure to give at least generic status to the presence or absence of a pterostigma implies that arytainine psyllid species evolved before their respective hosts, further comment seems unnecessary.

(b) Head form

A more or less globular head with all three ocelli visible in dorsal view and of which the anterior member is located upon a clearly defined frons is now regarded as approximating the primitive head form of not only the Psyllidae but the Homoptera as a whole. Naturally, when this primitive head form is in evidence other characters are sought to offset it, but as it appears in the present group of American arytainine psyllids and before full use can be made of it in their classification, the details involved in this condition have to be analysed in order to assess their significance, both individually and collectively.

In degree of significance the “details” involved are then (i) the exposure of the frons (ii) the development of the gene into conical or tubular protrusions and (iii) the degree of deflection of the head.

The frons and the development of the gene: In his recent treatment of the New Zealand representatives of the Psyllidae he referred to the genus *Psylla* and the then included members of the genus *Aecisia* Heslop-Harr., Prof. L. D. Tuthill has commented upon the variable condition of the frons. This, since he was dealing with a composite group, (part of which is still undergoing very active evolution), rather than a single genus, cannot be regarded as significant in the way then implied. The author remarked “... The tendency for the genital processes to cover the frons only incompletely is also not universal... several North American species exhibit this trait.”

It seems most likely that he was referring to the present section of the North American Arytainini, for the present author is quite unaware of any other North American psylline-Psyllidae to which such remarks could have applied.

Although there are exceptions, the degree of exposure of the frons (*not its degree of development*) in any psyllid is almost invariably the outcome of the degree of development of the gene into swellings of various shapes and sizes.

However considered in other insects, the existence of a frons as a basic taxonomic unit of the Homopterous head, must be recognised; Ferris himself had regarded it as such in the Psyllidae in 1932, although he had conveniently forgotten this by the time he came to introduce his peculiar conception of cephalic metamerism for insects generally (cf. *Microentomology*, 7(2), 1942; 8(1), 1943).

The deflection of the exposed frons is an expression of primitive character in the Psyllidae, whilst its partial or complete suppression is evidence of subsequent evolution. The presence of the exposed frons is thus worthy of consideration at generic level in the classification of the group. Since it is natural that the degree of development of the gene into lobes or swellings which obscure the frons should be variable, effective division on this basis is not absolute, but we try to use it as if it were, as far as it is possible to do so.

The presence of more or less well-developed genal protrusions with an associated suppression of the frons, is ordinarily considered to be a typical psylline trait, but in that subfamily, and in particular, within the tribe Arytainini, it is quite evident that the frons may exist in a graded series of degrees of suppression or exposure dependent on the variable degree of development of the genes. It is not, however, within the nature of the Psyllidae, that the extremes of complete exposure or complete suppression of the frons will exist side by side in species placed accurately within the same genus. No cases have been examined in which they do, and the North American arytainine psyllids under discussion therefore present no exception.

The deflection of the head: The question of how a globular head can be regarded as either deflexed or horizontal would seem to present an enigma. However, no matter how globular the head may be, the vertex in the Arytainini is invariably flattened or excavated to some extent, so that a line drawn through its median axis will make a variable angle with a similar line drawn through the median axis of the thorax. If the two are more or less on the same plane, then the head is to be regarded as horizontal, and if a distinct angle is made at their point of intersection, then the head is to be regarded as more or less deflexed.

This is a character of convenience rather than of significant taxonomic standing, but in its application in the present complex it helps in associating those forms which possess an exposed frons and undeveloped gene, distinguishing them from the others.

(c) The male genitalia.

How far one is to regard the details of the genitalia as providing characters of generic or even higher significance in any group of insects is...
no doubt a matter of opinion, but no pertinent opinions on this matter seem to have been expressed so far, in this, or any other group. In reaching some conclusion, it has been borne, in mind that the characters of the genitalia may provide mechanical barriers to cross-mating and thus initiate the isolation of forms, which, by proliferation, may ultimately give rise to the syngeneric groups of species we call genera. No real objection may thus be raised in using genitalial characters in generic separation—particularly when supported in other ways.

(d) Other minor characters.

The R M-Cu petiole ratio: This character was used in part in the Lövian system of classification of the Psyllidae. Despite all that has been said to the contrary by Crawford and others, no character used since has had the same efficacy in the primary classification of the European Psyllidae. Bearing this fact in mind, and despite the evidence that its use may break down on wider application than that for which it was primarily intended, the groupings effected by this means suggest that, as a character, it possesses a high degree of phylogenetical significance in the Psyllidae. We may not ignore it and it is at least worthy of consideration at lower levels, e.g. the generic, particularly when it appears to be supported in other ways.

The pigmental patterns of the forewings: The conditions which lead to the formation of significant pigmental patterns in the forewings of the Psyllidae may be mainly physiological when variation within the species is being considered. At a specific level there is considerable evidence that these patterns in basic character, are genetically controlled, and that groups of species, frequently constituting genera, may be distinguished by the basic uniformity of the pigmental patterns of their forewings. There is no contrary evidence in any group of known arytainine psyllids hitherto distinguished as a genus, which may be used as suggesting that we may not use pigmental patterning of the forewings as of generic import when it is expedient to do so.

The radular areas: The radular areas of the forewings of the Psyllidae are areas of heavier microsculpturing found in the margins of the apical cells. In one form in the Triozinae they have been considered as constituting a subfamily character, and there is no particular reason why they may not be given other values where they occur in other groups. In the present, they are to be considered at generic level.

The basal metatibial spurs: As a general rule, the species of a genus uniformly possess these spurs or they do not. When there appears to be some lack of uniformity, as there does in at least one section of the present arytainine psyllids, then it is found that it is not a question of the variable absence or presence of a somewhat obscure character in the species concerned, but rather the degree of their presence in them all. The small tubercles called “spurs” in the Arytainini have little phylogenetical significance.
no doubt a matter of opinion, but no pertinent opinions on this matter seem to have been expressed so far, in this, or any other group. In reaching some conclusion, it has been borne, in mind that the characters of the genitalia may provide mechanical barriers to cross-mating and thus initiate the isolation of forms, which, by proliferation, may ultimately give rise to the syngeneric groups of species we call genera. No real objection may thus be raised in using genitalial characters in generic separation—particularly when supported in other ways.

(d) Other minor characters.

The R M-Cu petiole ratio: This character was used in part in the Lövian system of classification of the Psyllidae. Despite all that has been said to the contrary by Crawford and others, no character used since has had the same efficacy in the primary classification of the European Psyllidae. Bearing this fact in mind, and despite the evidence that its use may break down on wider application than that for which it was primarily intended, the groupings effected by this means suggest that, as a character, it possesses a high degree of phyllogenetical significance in the Psyllidae. We may not ignore it and it is at least worthy of consideration at lower levels, e.g. the generic, particularly when it appears to be supported in other ways.

The pigmental patterns of the forewings: The conditions which lead to the formation of significant pigmental patterns in the forewings of the Psyllidae may be mainly physiological when variation within the species is being considered. At a specific level there is considerable evidence that these patterns in basic character, are genetically controlled, and that groups of species, frequently constituting genera, may be distinguished by the basic uniformity of the pigmental patterns of their forewings. There is no contrary evidence in any group of known arytainine psyllids hitherto distinguished as a genus, which may be used as suggesting that we may not use pigmental patterning of the forewings as of generic import when it is expedient to do so.

The radular areas: The radular areas of the forewings of the Psyllidae are areas of heavier microsculpturing found in the margins of the apical cells. In one form in the Triozinae they have been considered as constituting a subfamily character, and there is no particular reason why they may not be given other values where they occur in other groups. In the present, they are to be considered at generic level.

The basal metathoracic spurs: As a general rule, the species of a genus uniformly possess these spurs or they do not. When there appears to be some lack of uniformity, as there does in at least one section of the present arytainine psyllids, then it is found that it is not a question of the variable absence or presence of a somewhat obscure character in the species concerned, but rather the degree of their presence in them all. The small tubercles called “spurs” in the Aytainini have little phyllogenetical significance.

G. Heslop-Harrison on Aytainini of the family Psyllidae.—II


Before defining the four new genera believed to be involved it is necessary to examine the availability of some of the manuscript and other names that have been used previously to cover some of the species. The type species of Crawford’s “genus” Psyllopa (1911) by usage, was “Psyllopa” magna, but as this was later discovered by its author to be a synonym for Aytaina genistae (Latreille) Crawford naturally thought that this made Psyllopa a non-valid synonym of Aytaina Först. However wide it may have been, Psyllopa was never defined as a genus, but remained as a nomen nudum throughout the several years of its use. With its first species consisting of the type of Aytaina, as it did, Psyllopa can never be used in the present connection, by definition or any other means. The American species known earlier as Psylla amorphae Mally (1894) was apparently represented by a series of insects in the United States National Museum, where it bore Riley’s manuscript name Amblyrhina fracticopercula. This fact was duly noted by Crawford in 1914 when he came to refer it to his conception of a genus Aytaina.

Amblyrhina Löw (1878) is a European-Palaeartic genus and typical of the European arytainine genera in that its species also possess only one basal metatarsal spine. The American species superficially appears to be very close to Amblyrhina, but differs in possessing two metatarsal spines. Riley perhaps showed more understanding in referring the insect to Amblyrhina than Crawford did in referring it to Aytaina, but Amblyrhina is not available for use in this or any other American connection.

According to Crawford, another series of insects, then referred to his “new” species “Aytaina” chelifera (Crawford, 1914) was also held in the United States National Museum, and this series bore the manuscript name Brachysypylla purshiae Schwarz. Whilst it is not at all clear why Crawford made no attempt to validate Schwarz’ manuscript name purshiae when he came to describe this insect, it is perhaps easy to understand why he rejected Brachysypylla as a generic name. He must have been aware that Brachysypylla was a genus defined in connection with Australian species discussed by Froggatt in 1903, and in addition there was a mistaken impression that he held, that this was one of the indigenous American species that should be referred to Aytaina. In this matter also, the earlier author, this time Schwarz, showed a better understanding of the relationships of the species concerned than did Crawford, a circumstance of which the present author has long been aware since he possessed authentic examples of both the American and Australian insects. Brachysypylla is also not available for use in the present instance, but it should be understood that it is an Australian arytainine genus, and that it has closer relatives in America than it has in Europe.

Under the manuscript name Euglyptoneura triatis Schwarz, Crawford also remarked on another series of insects in the United States National
Museum. This series he also referred to *Arytaina* in 1914 under the name *Arytaina fuscipennis* Crawford. The genus name *Euglyptoneura* of Schwarz has no encumbrances, nomenclatorically or otherwise, but the category which it may have covered, had Schwarz defined it, remains unknown. It is therefore proposed to use it as one of the new genus names necessary since the species *fuscipennis* Crawford is representative of one of the present groups to be distinguished as genera.

Three generic names, *Amorphicola*, *Ceanothia* and *Purshiora* have been provided for the remaining three genera that are seen to be involved.

**Euglyptoneura** (Schwarz M.S.) *gen. nov.* (Fig. 1.)

Insects of a general arytainine facies; robust or thickset, with somewhat angulate and broad wings. Veins proportionately thick, membranes more or less uniformly opaque and horny and frequently with a characteristic pigmented pattern. Species attached to the members of the genus *Ceanothus* Linn.

**Wings**

Membrane thickened and coriaceous, veins stout and frequently with their paths paralleled by a double row of setae. Membrane uniformly horn-coloured or with a characteristic heavy pigmented pattern; radial areas diffuse.

**Cubito-medial petiole** extremely short, and scarcely more than one-third of the length of the radial petiole.

**Pterostigmatic area** thickened, but a true pterostigma is absent; costal nodal break absent.

**Legs**

Short and stout, hind tibia usually with a small basal spur. Metatarsal spines two in number.

**Male Genitalia**

Proctiger unipartite, frequently short or broadened in lateral view. Parameres, except in the species *fuscipennis*, where it is bilobed, simple although perhaps dilated slightly at the apex and correspondingly constricted at the base.

**Type of the genus**

*Euglyptoneura minuta* (Crawford), 1914. Species to be referred to the genus: *minuta* Crawf., "robusta" Crawf., *fuscipennis* Crawf., *snowi* Dowell, *montana* Crawf., *robusta-sinuata* Tuthill, and possibly a *Euglyptoneura ribesia* (Crawford, Klyver, etc. propartim).

**Amorphicola** *gen. nov.* (Fig. 2.)

Although of a general arytainine facies, the insects to be referred to this genus are small and slender, with a more or less globular and deflexed head, devoid of prominent genal protrusions. Species attached to representatives of the genus *Amorpha* Linn.

**Head**

Width not exceeding the width of the thorax, more or less horizontal. Genae parallel to the plane of the vertex, usually contiguous at the base, but normally well developed into bluntly rounded, conical protuberances. *Frons* obscured by the contiguous bases of the genae, anterior ocellus thrust up between the latter. Antenna averaging not more than one and one-half times as long as the width of the head.

**Thorax**

Broad, robust and generally strongly arched.
Museum. This series he also referred to Artytaina in 1914 under the name Artytaina fuscipennis Crawford. The genus name Euglyptoneura of Schwarz has no encumbrances, nomenclatorically or otherwise, but the category which it may have covered, had Schwarz defined it, remains unknown. It is therefore proposed to use it as one of the new genus names necessary since the species fuscipennis Crawford is representative of one of the present groups to be distinguished as genera.

Three generic names, Amorphicola, Ceanothia and Purshiora have been provided for the remaining three genera that are seen to be involved.

Euglyptoneura (Schwarz M.S.) gen. nov. (Fig. 1.)

Insects of a general artytainine facies; robust or thickset, with somewhat angulate and broad wings. Veins proportionately thick, membranes more or less uniformly opaque and horny and frequently with a characteristic pigmenal pattern. Species attached to the members of the genus Ceanothus Linn.

**Wings**

Membrane thickened and coriaceous, veins stout and frequently with their paths paralleled by a double row of setae. Membrane uniformly horn-coloured or with a characteristic heavy pigmenal pattern; radial areas diffuse.

Cubito-medial petiole extremely short, and scarcely more than one-third of the length of the radial petiole.

**Pterostigmatic area** thickened, but a true pterostigma is absent; costal nodal break absent.

**Legs**

Short and stout, hind tibia usually with a small basal spur. Metatarsal spines two in number.

**Male Genitalia**

Proctiger unipartite, frequently short or broadened in lateral view. Paramere, except in the species fuscipennis, where it is bilobed, simple although perhaps dilated slightly at the apex and correspondingly constricted at the base.

**Type of the genus**

Euglyptoneura minuta (Crawford, 1914). Species to be referred to the genus: minuta Crawf., "robusta" Crawf., fuscipennis Crawf., snowi Dowell, montana Crawf., robusta-sinuata Tuthill, and possibly a Euglyptoneura ribesiac (Crawford, Klyver, etc. propartim).

Amorphicola gen. nov. (Fig. 2.)

Although of a general artytainine facies, these insects to be referred to this genus are small and slender, with a more or less globular and deflexed head, devoid of prominent genital protrusions. Species attached to representatives of the genus Amorpha Linn.

**Amorphicola**

- **Genitalia**
  - **A**
  - **B**
  - **C**
  - **D**

**Amorphicola**

- **Genitalia**
  - **A**
  - **B**
  - **C**
  - **D**
G. Heslop-Harrison on Atytainini of the family Psyllidae.—II

Head: Scarcely as wide as the thorax, and usually quite strongly deflexed. Genus developed at most into mere rounded swellings, and separated at their bases by the full width of an exposed frons. Antennae: length from one to one and one-third times the width of the head.

Thorax: Flattened laterally, strongly arched dorsally; pronotum almost vertical.

Wings: Nearly three times as long as broad, slender, venation more typically psylline. Veins slender, membrane whitish-opaque or fumate; radial areas diffuse. Cubito-medial petiole slightly more than half the length of the radial petiole. Pterostigma well developed, costal nodal break distinct.

Legs: slender, moderately short. Hind tibia without a basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger broadly tubular in lateral view; unipartite. Genital segment broadly rounded and developed as in Psyllopsis. Parameres more or less hammer-headed at their spines and in lateral view, and adorned with inner teeth and secondary spine-like processes.

Type of genus: Amorphiscus amorphus (Mally), 1894.

Species to be referred to the genus: amorphus Mally, pallida Tuthill. (Also a floridensis Crawford and/or ilicis Crawford?)

CEANOThIA gen. nov. (Fig. 3.)

Species small, uniformly yellowish or brownish in colour, at least in the preserved condition. Forewings semi-opaque, white or fumate. Associated with species of the genus Ceanothus Linn.

Fig. 3.

Ceanothia Heslop-Harrison: A, generalized impression of the whole insect in lateral view; B, generalized impression of head, dorsal view; C, tracheation of forewing showing a true pterostigma; D, male genitalia; E, parameres in dorsal aspect.

G. Heslop-Harrison on Atytainini of the family Psyllidae.—II

Head: Clearly narrower than the thorax, or approximating the width of the latter; partially deflexed. Genus developed into small, non-contiguous lobes; frons reduced, or partially concealed under the bases of the genus. Antennae at most only one and one-half times as long as the width of the head.

Thorax: Strongly arched; not particularly robust; pronotum almost vertical.

Wings: Broadly rounded or slightly rhomboidal. Veins stout, membrane opaque or fumate; radial areas diffuse. From two to two and one-half times as long as broad. Cubito-medial petiole from one-half to one-third the length of the radial petiole. Pterostigma well developed, thickened and elongated. Costal nodal break quite distinct.

Legs: Somewhat slender, but not long. Hind tibia without a basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger slender and tapering; unipartite. Parameres slender and tapering; simple, but strongly acuminate.

Type of the genus: Ceanothia ceanothi* (Crawford), 1914.

Species to be referred to the genus: ceanothi Crawf., aculeata Crawf. Both so-called species are possible complexes.

PURSHIOvRA gen. nov. (Fig. 4.)

A genus of small, slender insects. Specimens examined hitherto are invariably pale and devoid of strong positive colouring. Wings semi-opaque, or fumate at the apices. Species apparently restricted to Purshiia in the Western United States.

Fig. 4.

Purshiovra Heslop-Harrison: A, generalized impression of the whole insect in lateral view; B, generalized impression of head, dorsal view; C, male genitalia of Purshiovra chelifer (Crawf.); D, male genitalia of Purshiovra pubeccens (Crawf.).

* Amended from ceanothae by Tuthill, 1943.
Head: Scarcely as wide as the thorax, and usually quite strongly deflexed. Genus developed at most into mere rounded swellings, and separated at their bases by the full width of an exposed frons. Antennae: length from one to one and one-third times the width of the head.

Thorax: Flattened laterally, strongly arched dorsally; pronotum almost vertical.

Wings: Nearly three times as long as broad, slender, venation more typically psylline. Veins slender, membrane whitish-opaque or fumate; radial areas diffuse. Cubito-medial petiole slightly more than half the length of the radial petiole. Pterostigma well developed, costal nodal break distinct.

Legs: slender, moderately short. Hind tibia without a basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger broadly tubular in lateral view; unipartite. Genital segment broadly rounded and developed as in Psyllopsis. Parameres more or less hammer-headed at their spines and in lateral view, and arched with inner teeth and secondary spine-like processes.

Type of genus: Amorphocole amorphae (Mally), 1894.

Species to be referred to the genus: amorphae Mally, pallida Tuthill. (Also a floridensis Crawford and/or ilicis Crawford?)

CEANOTHIA gen. nov. (Fig. 3.)

Species small, uniformly yellowish or brownish in colour, at least in the preserved condition. Forewings semi-opaque, white or fumate. Associated with species of the genus Ceanothus Linn.

G. Heslop-Harrison on Arytainini of the family Psyllidae.—II

Head: Clearly narrower than the thorax, or approximating the width of the latter; partially deflexed. Genus developed into small, non-contiguous lobes; frons reduced, or partially concealed under the bases of the genus. Antennae at most only one and one-half times as long as the width of the head.

Thorax: Strongly arched; not particularly robust; pronotum almost vertical.

Wings: Broadly rounded or slightly rhomboidal. Veins stout, membrane opaque or fumate; radial areas diffuse. From two, to two and one-half times as long as broad. Cubito-medial petiole from one-half to one-third the length of the radial petiole. Pterostigma well developed, thickened and elongated. Costal nodal break quite distinct.

Legs: Somewhat slender, but not long. Hind tibia without a basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger slender and tapering; unipartite. Parameres slender and tapering; simple, but strongly acuminate.

Type of the genus: Ceanothia cenanathi* (Crawford), 1914.

Species to be referred to the genus: cenanathi Crawf., aculeata Crawf. Both so-called species are possible complexes.

PURSHIVORA gen. nov. (Fig. 4.)

A genus of small, slender insects. Specimens examined hitherto are invariably pale and devoid of strong positive colouring. Wings semi-opaque, or fumate at the apices. Species apparently restricted to Purshia in the Western United States.

Purshivora Heslop-Harrison: A, generalized impression of the whole insect in lateral view; B, generalized impression of head, dorsal view; C, male genitalia of Purshivora cheliferus (Crawf.); D, male genitalia of Purshivora pubescens (Crawf.).

* Amended from ceanothae by Tuthill, 1943.
Head: Nearly or quite as broad as the thorax, more or less horizontally disposed. Genye developed into small, rounded tubercles, depressed below, but in the same plane as the vertex. Not contiguous at their bases. Frons wholly or partially exposed between. Antennae scarcely longer than the width of the head.

Thorax: Quite well arched; robust. Pronotum flattened and depressed slightly towards the anterior margin.

Wings: Broadly rounded apically, scarcely twice as long as broad. Membrane fumate apically, opaque or pigmented; radial areas distinct. Veins only moderately thickened. Cubito-medial petiole, from just less than the length of the radial petiole to slightly more than half its length. Pterostigma narrow but distinct. Costal nodal break, distinct.

Legs: Slender. Hind tibia with a small to quite large basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger short, parallel-sided; tubular and unipartite. Parameres, scarcely approximating the proctiger in length; adorned with subapical, inner spiniform processes of cheliferate appearance.

Type of the genus: Purshivora chelifera (Crawford), 1914.
Species to be referred to the genus: chelifera Crawf., pubescens Crawf.

CONCLUDING NOTES TO PART II.

To those familiar with the recent North American psyllid compilations, it will be evident that included as species to be referred to the new genera are a series of insects covered by several names that appear therein as synonyms only.

However, in such a genus as Euglypnoneura, it is the present opinion that time will prove that their inclusion as distinct species will no doubt have been justified. The indiscriminate collection of Ceanothus psyllids and their treatment without adequate reference to their individual host specificities, it is felt, have inevitably led to some confusion of identity. There has, it would seem, been a consequental and dependent failure to discriminate significantly different forms as more than varietal, when in fact they have been species.

Distinguishable "varietal" differences, if they can be associated with differing host specificities, must now be regarded as specific differences, and the forms recognized accordingly.

There are no fewer than forty indigenous North American species of Ceanothus recognized. Depending on the number of significant distinctions (specific or otherwise), that the associated psyllids may make, there will be a corresponding number of distinct psyllid forms. Considering that two genera of Ceanothus psyllids are involved this ultimate number may very well become doubled.

It is fairly certain that the two species referred to the genus Purshivora are in fact chelifera Crawf. and pubescens Crawf., in which case there will be evident discrepancies between Crawford's original illustrations of the male genitalia and those now presented. The former were not only inadequate, but wholly inaccurate, and consequentially they do not serve to identify the species. The name chelifera is an appropriately apt specific name if it is considered in connection with the form of the male paramere, but the original illustrations do not indicate, any more than the accompanying texts, that it had equal application to the species pubescens! With reference to the latter, the male paramere is not in the form of a bluntly rounded lobe terminating in a long, fine, bristle-point, as depicted by Crawford (and by Tuthill also, who merely reversed the Crawford illustration) but of a cheliferate structure, similar but differing in specific detail to that found in the species chelifera.

It is unlikely that many if any more species are actually involved in the genus Purshivora as it occurs in the United States, but as the host genus extends into the Pacific Islands, additional species may be expected to occur there.

Since the above was written, Prof. D. D. Jensen has added a number of additional species to the complex "Arytaina" of American usage. None of these has yet been seen by the present author, and whilst it seems that the descriptions and illustrations are adequate from the point of view of subsequent determination, neither provides any information of use in their distribution amongst the new genera with any degree of certainty; it is even possible that some new genera are involved.

It has to be remarked in this connection that the technique of providing photographic illustrations from flattened slide mounts of psyllid parts other than wings, is both confusing and misleading; the distortion that may be depicted can be enormous. Prof. Jensen's illustrations are all of this type; except for accurately depicting, for comparative purposes, the micro-details of psyllid wings, this technique was abandoned by the present author years ago, and for the reasons expressed above.

To be continued.
Head: Nearly or quite as broad as the thorax, more or less horizontally disposed. Genae developed into small, rounded tubercles, depressed below, but in the same plane as the vertex. Not contiguous at their bases. Front wholly or partially exposed between. Antennae scarcely longer than the width of the head.

Thorax: Quite well arched; robust. Pronotum flattened and depressed slightly towards the anterior margin.

Wings: Broadly rounded apically, scarcely twice as long as broad. Membrane fumate apically, opaque or pigmented; radial areas distinct. Veins only moderately thickened. Cubito-medial petiole, from just less than the length of the radial petiole to slightly more than half its length. Pterostigma narrow but distinct. Costal nodal break, distinct.

Legs: Slender. Hind tibia with a small to quite large basal spur. Metatarsus with two basal spines.

Male genitalia: Proctiger short, parallel-sided; tubular and uni-partite. Parameres, scarcely approximating the proctiger in length; adorned with subapical, inner spiniform processes of cheliferate appearance.

Type of the genus: Purshivora chelifera (Crawford), 1914.

Species to be referred to the genus: chelifera Crawf., pubescens Crawf.

Concluding Notes to Part II.

To those familiar with the recent North American psyllid compilations, it will be evident that included as species to be referred to the new genera are a series of insects covered by several names that appear therein as synonyms only.

However, in such a genus as Euglyptoneura, it is the present opinion that time will prove that their inclusion as distinct species will no doubt have been justified. The indiscriminate collection of Ceanothus psyllids and their treatment without adequate reference to their individual host specificities, it is felt, have inevitably led to some confusion of identity. There has, it would seem, been a consequental and dependent failure to discriminate significantly different forms as more than varietal, when in fact they have been species.

Distinguishable "varietal" differences, if they can be associated with differing host specificities, must now be regarded as specific differences, and the forms recognized accordingly.

There are no fewer than forty indigenous North American species of Ceanothus recognized. Depending on the number of significant distinctions (specific or otherwise), that the associated psyllids may make, there will be a corresponding number of distinct psyllid forms. Considering that two genera of Ceanothus psyllids are involved this ultimate number may very well become doubled.

It is fairly certain that the two species referred to the genus Purshivora are in fact chelifera Crawf. and pubescens Crawf., in which case there will be evident discrepancies between Crawford's original illustrations of the male genitalia and those now presented. The former were not only inadequate, but wholly inaccurate, and consequently they do not serve to identify the species. The name chelifera is an appropriately apt specific name if it is considered in connection with the form of the male paramere, but the original illustrations do not indicate, any more than the accompanying texts, that it had equal application to the species pubescens! With reference to the latter, the male paramere is not in the form of a bluntly rounded lobe terminating in a long, fine, bristle-point, as depicted by Crawford (and by Tuthill also, who merely reversed the Crawford illustration) but of a cheliferate structure, similar but differing in specific detail to that found in the species chelifera.

It is unlikely that many if any more species are actually involved in the genus Purshivora as it occurs in the United States, but as the host genus extends into the Pacific Islands, additional species may be expected to occur there.

Since the above was written, Prof. D. D. Jensen has added a number of additional species to the complex "Arytaina" of American usage. None of these has yet been seen by the present author, and whilst it seems that the descriptions and illustrations are adequate from the point of view of subsequent determination, neither provides any information of use in their distribution amongst the new genera with any degree of certainty; it is even possible that some new genera are involved.

It has to be remarked in this connection that the technique of providing photogorphic illustrations from flattened slide mounts of psyllid parts other than wings, is both confusing and misleading; the distortion that may be depicted can be enormous. Prof. Jensen's illustrations are all of this type; except for accurately depicting, for comparative purposes, the micro-details of psyllid wings, this technique was abandoned by the present author years ago, and for the reasons expressed above.

To be continued.