## TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XX.

THE DISTRIBUTION AND COMPARATIVE MORPHOLOGY OF THE ORDER EMBIOPTERA.
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(Four Text-figures.)<br>[Read 27th November, 1940.]

In the preceding nineteen parts of the present series, the available knowledge of the various genera of the Order Embioptera has been summarized, and certain new data added. In all, thirty-six genera have been allowed or described as new, while five (Antipaluria, Dityle, Euembia, Aposthonia and Monotylota) have been listed as untenable. Systematic order has not been followed in the treatment of genera, for several reasons. It has been desirable from the point of view of publication to treat the Order in a number of short papers rather than in one or a few large ones, so that the sequence followed is in part dependent on the avoidance of nomina nuda in cross-references. Moreover, the earlier parts were compiled at a time when it appeared that circumstances might preclude completion of the work, so that, where possible, the readily-available data were put on record regardless of sequence. It is the purpose of the present paper to arrange the genera in systematic order, with suggestions as to family classification, and to note certain points in the distribution of the Order, and evolutionary trends in the comparative morphology of its members.

Much of the work in the preceding papers of this series was of necessity carried out under hurried conditions. The types, and certain other material, of the Museum of Comparative Zoology, the British Museum, the Paris Museum, and the Oxford University, Genoa, Geneva and Congo Museums, were examined in a working time of three weeks, and the study of the unworked material from the first three of the above Museums, and the Colombo Museum, was carried out during several months, interspersed with academic duties and the compilation of the papers of this series for publication. These facts are offered both as an extenuation of the inadequacy which is apparent in certain parts of the series, and as a suggestion to future workers on the Order that a considerable amount of work still remains to be done even on the collections listed above, both in the study of points untouched by the writer and in checking the facts adduced.

## Generic Key.

The following key, based on the characters of the mature males, serves to distinguish between the known genera. Structures referred to in the key are figured at some place in the earlier parts of the present series. The greatest difficulty lies in the separation of the genera Rhagadochir and Pararhagadochir, especially in the aberrant species $P$. argentina Navás (two hind metatarsal bladders), and in the supposedly East African species $R h$. carpenteri 'Davis, which has terminalia generically inseparable from Pararhagadochir. This question has been discussed earlier (Part xv of this series). Another difficulty arises in that Calamoclostes End. may be based on a venational aberration.

The interpolation of several genera in the key between Embia Latr. and the very closely related Parembia Davis (separated only on the hind metatarsal bladders and on the distribution) illustrates the extremely arbitrary nature of the key. Again, the key might be rendered unworkable by the discovery of wingless forms of the male in genera now known only from winged males, e.g. Mesembia. The key is drawn up merely on the available data, and may require considerable modification in the light of future
records. In several cases, for convenience, a dichotomy has been formed on a character of relatively little importance, such as would not be allowed as a generic character unless supported by additional characters. Such supplementary characters, though omitted in the key, are of course included under the generic diagnoses in the earlier parts of the series.

1. Permian ; cerci composed of numerous annular segments. (if probably winged) ...... 2 Tertiary-Recent; cerci with two segments or less. (f wingless) ...................... 3
2. North American .............................................................. Protembia Tillyard Russian ..................................................................... . . . . Tillyardembia Zalessky
3. Left cercus two-segmented, not echinulate . . . . . . . . . . . . .................................... 4

Left cercus echinulate (rarely smooth; if so, then the two segments fused to a composite structure)
4. Tenth abdominal tergite entire, or, if divided, processes of hemitergites small, not prominent ; ventral parts of terminalia almost symmetrical

Clothoda Enderlein (syn. Antipaluria Enderlein)
Tenth abdominal tergite wholly or partly cleft, processes of hemitergites large, prominent, often complex; ventral parts of terminalia markedly asymmetrical

5
5, $\mathrm{R}_{4+5}$ (or macrotrichia representing vein) forked . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
$R_{4+5}$ simple, or wingless


$\mathrm{R}_{2+3}$ simple, or wingless
8
8. Right hemitergite with an inner ventral flap-like process .................................. 9

Right hemitergite without any process on the inner side ............. Saussurembia Davis
9. Hind metatarsus with two prominent ventral bladders

Haploembia Verhoeff (syn. Dityle Friederichs)
Hind metatarsus not as above ........... Oligotoma Westwood (syn. Aposthonia Krauss)
10. Second segment of left cercus reduced, wholly or partly fused to first segment ....... 11

Second segment of left cercus distinct, subcylindrical, at least three times as long as thick

16
11. $R_{4+5}$ forked . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12
$R_{4+5}$ simple, or wingless . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13
12. Second segment of left cercus represented by a small obtuse protuberance on outer side of end of first segment ............................................ . Ptilocerembia Friederichs
Second segment of left cercus represented as a subacute incurved extension of first segment
Embonycha Navás
13. Right hemitergite with an internal echinulate process directed forward . . Notoligotoma Davis Right hemitergite not as above

14
14. Left cercus smooth; veins strong, with some oblique cross-veins; Miocene ................ Burmitembia Cockerell
Left cercus echinulate (rarely almost smooth) ; veins weaker, with cross-veins weak, or wingless; Recent

15
15. Right hemitergite with a dorsal flap-like process directed inward; Australian .............

Metoligotoma Davis
Right hemitergite not as above; American ................................. Anisembia Krauss
16. $\mathrm{R}_{4+5}$ simple in all wings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Mesembia Ross
$R_{4+5}$ forked, at least in hindwings, or wingless . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17
17. Left hemitergite with a short rounded dorsal protuberance on the right, but with main process simple ........................................................... . . . Pseudembia Davis
Left hemitergite and process not as above .................................................. 18
18. Process of left hemitergite simple, without an additional lateral or dorsal lobe ........ 19

Process of left hemitergite with an additional lateral or dorsal lobe .................. 26
19. First segment of left cercus with an internal echinulate hook directed forward, longer than thick

Leptembia Krauss
First segment of left cercus not as above ..................................................... . . . . 20
20. Hind metatarsus with two ventral bladders ................................................ . . . 21

Hind metatarsus with one ventral bladder
Embia Latreille (syn. Euembia Verhoeff and Monotylota Enderlein)
21. Right hemitergite without any process on inner side; wingless

Dictyoploca Krauss
Right hemitergite with an inner process; winged .......................................... . . 22
22. Cubitus with three or more branches ...................................... Berlandembia Davis

Cubitus two-branched
23
23. First segment of left cercus with inner margin carrying a row of large sharp forwardlydirected teeth, practically uniseriate

Dinembia Davis
First segment of left cercus not as above
24. First segment of left cercus with inner margin produced into two lobes armed with strong teeth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Metembia Davis First segment of left cercus with only one internal lobe, with rather small teeth ...... 25
25. Inner process of right hemitergite flap-like, elliptical; medial hind metatarsal bladder large, rounded ..................................................................... Parembia Davis Inner process of right hemitergite not as above; medial hind metatarsal bladder small,

26. $\mathrm{R}_{4+5}$ simple in forewing, shortly forked in hindwing ............... . Calamoclostes Enderlein
$R_{4+5}$ forked in all wings, the fork at least as long as the stem
$\mathrm{R}_{4+5}$ forked
27
27. Mandibles huge, overlying labrum ................................................. . Enveja Navás

Mandibles not as above ............................................................................. . . . . 28
28. Teeth on first segment of left cercus less than ten, very large . .......................... . . . 29

Teeth on first segment of left cercus small, more than ten in number .................. 30
29. Hind metatarsus with one ventral bladder; M tending to fork ..... Donaconethis Enderlein Hind metatarsus with two ventral bladders; M simple .................. Odontembia Davis
30. First segment of left cercus with more than one internal echinulate lobe; cubitus threebranched .......................................................... . Dihybocercus Enderlein First segment of left cercus with one internal echinulate lobe ; cubitus two-branched .. 31
31. $R_{4+5}$ obsolescent beyond fork . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Navásiella Davis
$R_{4+5}$ not as above .................................................................................... . . . . 32
32. Process of left hemitergite with a distal concavity between lobes ...................... 33

Process of left hemitergite with lateral lobe very short, no distal concavity between it and main part of process ................................................. . . Parachirembia Davis
33. Inner process of right hemitergite a flat subelliptical flap separated from hemitergite by membrane except at posterior limit
Inner process of right hemitergite not as above ............................................. 35
34. Hind metatarsus with two large ventral bladders; right cercus-basipodite very large ....

Macrembia Davis
Hind metatarsus with only one ventral bladder; right cercus-basipodite small
Chirembia Davis
35. Hind metatarsus with two ventral bladders; African ................ Rhagadochir Enderlein

Hind metatarsus with one ventral bladder (two in one species) ; Neotropical
Pararhagadochir Davis

## Family Classification.

The following major groupings are advanced:
Sub-Order Protembioptera (Protembiaria of Tillyard 1937).
Family Protembiidae Tillyard 1937: Protembia Till., Tillyardembia Zal.
Sub-Order Euembioptera (Euembiaria of Tillyard 1937).
Family Clothodidae Tillyard 1937: Clothoda End.
Family Oligembiidae, n. fam.: Oligembia Davis, Diradius Fried.
Family Teratembiidae Krauss 1911: Teratembia Krauss.
Family Oligotomidae Krauss 1911: Oligotoma Westw., Haploembia Verhoeff.
Family Notoligotomidae, n. fam.: Notoligotoma Davis, Metoligotoma Davis, Burmitembia Ckll., Embonycha Nav., Ptilocerembia Fried.
Family Anisembiidae, n. fam.: Anisembia Krauss, Mesembia Ross, Saussurembia Davis.
Family Embiidae auct.: Remaining 20 genera.
In several cases (Oligembiidae, Notoligotomidae) prior genera (Diradius, Embonycha, Burmitembia, Ptilocerembia) have been passed over in the selection of the family stem, merely because existing descriptions of those genera do not allow their structure and relationship to be fully gauged.

The characteristics of the families are summarized below. Convergence prohibits the drawing up of a satisfactory family key based on structure alone, but in all except one genus the family sequence has been kept in the generic key. In the case of Saussurembia, which differs from Mesembia only in the lack of nodules on the left cercus, the desired sequence cannot be accomplished in the generic key.
(1) Protembiidae: Permian Embioptera, obviously very generalized in structure; the state of preservation of the fossils does not allow any very definite conclusions to be drawn. The venation is not much less reduced than in some recent Embioptera; the cerci were apparently multi-articulate. These fossils may form a link with the Protoperlaria. It seems probable that the female was winged.
(2) Clothodidae: The most generalized of recent Embioptera, Neotropical in range; the series Clothoda nobilis (Gerst.) $\rightarrow$ C. intermedia Davis $\rightarrow$ C. urichi (Sauss.) illustrates the division of the tenth tergite followed by the loss of the third cubital branch, the cerci remaining unchanged. The ventral structures of the male terminalia emphasize the primitive nature of the family, and its far removal from other recent forms. The Miocene C. florissantensis (Ckll.) has been provisionally referred to the genus Clothoda. The number of hind metatarsal bladders in this species is unknown; in the recent species, two bladders are present. This appears to be primitive, the medial bladder possibly representing the former point of articulation of two segments now fused.
(3) Oligembiidae: A Neotropical series including Oligembia and Diradius. The venation is greatly reduced in strength, although reduction in the number of veins is less marked than in some other genera, the traces of $R_{4}$ and $R_{5}$ remaining distinct. No hind metatarsal bladders seem to be present, but whether this is primitive is very doubtful. The terminalia agree with the Oligotomidae in the incomplete fission of the tenth abdominal tergite and the lack of nodules on the left cercus in the adult male. The structures at the base of the left cercus are complex in Oligembia, as they are in Oligotoma; details for Diradius are lacking. Oligembia appears to be derived from Diradius by the forking of the process of the left hemitergite, a frequently-recurrent evolutionary step in the Order. The family is probably not very close to the Oligotomidae, in spite of superficial resemblance. The general weakness of the veins in both families may be associated with small size.
(4) Teratembiidae: This Neotropical family is based on a single specimen, so that generalizations on the structure are unsafe. It appears to have $R_{2+3}$ forked and $R_{4+5}$ simple. If this is a constant feature, it indicates family distinction from the Oligembiidae. If, however, it represents an individual aberration ( $R_{4}$ detached from $R_{4+5}$ and secondarily attached to $R_{2+3}$ ), the Teratembiidae should be enlarged to include the Oligembiinae as a sub-family.

The structure of the terminalia has been discussed earlier (Part xix of this series). They agree with Oligembia in the lack of nodules on the left cercus, and the complex structures at the base of this cercus; in other respects they seem to differ markedly, but the exact structure and homologies are doubtful.
(5) Oligotomidae: The genus Oligotoma has as its indigenous range the warmer parts of the Asiatic region, extending throughout Australia, and possibly to East Africa. It is now tropicopolitan, due apparently to human transport. The recent species of Haploembia are distributed around the coasts of the Mediterranean and Black Seas.

Haploembia may temporarily be assigned to the Oligotomidae, a course suggested by Krauss. The family characters may be summarized as follows: Winged or wingless; if winged, veins weakly developed, $R_{4+5}, M$, and $\mathrm{Cu}_{1 \mathrm{a}}$ simple. Hind metatarsus with one or two ventral bladders. Male terminalia with tenth abdominal tergite incompletely separated into hemitergites; right hemitergite with an elongate posterior process and a ventral flap-like inner process; first segment of left cercus without' nodules, second segment distinct, elongate-subcylindrical. Structures at base of left cercus often complex.

Some members of the next two families agree with the winged examples of Oligotoma in the absence of $R_{5}$, which cannot therefore be taken as a family character, as it has been in the past.
(6) Notoligotomidae: This name is selected for an apparently monophyletic series of Indo-Malayan and Australian distribution (Miocene to Recent), the common character of which is the partial or total fusion of the segments of the left cercus. The composite structure is usually echinulate (not in Burmitembia; only very weakly in Metoligotoma rileyi Davis). In some cases, $\mathbf{R}_{5}$ is lost (Burmitembia, Notoligotoma pars), or winglessness supervenes (Notoligotoma pars, Metoligotoma). The processes of the hemitergites of the male terminalia are variable, but show no affinity to the Oligotomidae. Two hind metatarsal bladders probably characterize all members. The close relationship between Ptilocerembia and Notoligotoma indicates the impossibility of using the lack of $R_{5}$, unsupported by other factors, as the basis for a major dichotomy.
(7) Anisembiidae: This family culminates in the Sonoran genus Anisembia; forms linking this genus to more generalized types are probably the Antillean and Central American genera Mesembia and Saussurembia. These three genera are characterized by the loss of $R_{5}$ or of the entire wings, convergent to the two preceding families. Anisembia is further specialized by the fusion of the segments of the left cercus in the adult male. It is closely convergent to the two endemic Australian genera, but its ancestor (cf. Mesembia) would appear to have had $\mathrm{R}_{4+5}$ simple and the second segment of the left cercus distinct, whereas the ancestor of the Australian genera (cf. Ptilocerembia) would seem to have had $R_{4+5}$ forked and the second segment of the left cercus fused to the first segment.

The processes of the hemitergites of the male terminalia are variable in the Anisembiidae, but the right hemitergite is always very clearly separated from the left, and lacks any marked trace of an inner process. One hind metatarsal bladder is probably the characteristic of the family as at present constituted. Nodules are present on the first segment of the $\delta$ left cercus in Mesembia and in Anisembia (sometimes weakly so), but absent in Saussurembia, possibly a secondary loss.
(8) Embiidae: This is very probably a polyphyletic group, but subdivision on the present data seems impossible. On this understanding, it may be retained as an artificial unit for members of the Order in which the venation and terminalia have reached a common stage in evolution. If wings are present, $\mathrm{R}_{4+5}$ is forked; in some cases $M$ is normally or exceptionally forked, in others the cubitus has more than the usual two branches. The hind tarsi have one or two bladders on the first segment. In the male terminalia, the tenth tergite is always completely separated into, hemitergites; the left hemitergite varies very considerably, but the right has a process on the inner margin except in Dictyoploca. The left cercus is two-segmented, the first segment being echinulate in all cases, the second elongate, subcylindrical and distinct.

The genera comprising the family occur in South America (one species reaching Central America) and Africa, extending thence east to East India and north to the southern parts of Europe. In spite of apparent structural homogeneity, the Embiidae may well be an unnatural group, e.g. Embolyntha may well be a link between the Clothodidae and the Anisembiidae, and more closely related in its ancestry to these families than to Old-World Embiidae. To follow this course would possibly seem to be giving prominence to zoogeography at the expense or exclusion of morphology.

The above eight families may be artificially keyed as follows; the key can be used only by considering locality* as well as structure:

1. Permian

Protembiidae
Tertiary-Recent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Tenth abdominal tergite entire in the male or, if divided, processes of hemitergites small, not prominent; ventral parts of terminalia almost symmetrical .......... Clothodidae
Male terminalia with processes of hemitergites prominent, often complex; ventral parts markedly asymmetrical
3. Indo-Malayan and Australian; left cercus one-segmented in the male .... Notoligotomidae Not as above
. . . . . . . . .
4. Central and North American and Antillean, $R_{4+5}$ simple, or wingless ....... Anisembiidae Not as above
... 5
5. Male terminalia with hemitergites clearly separated ............................ Embiidae Male terminalia with suture between hemitergites obsolescent basally, or if complete, hemitergites in contact



$R_{4+5}$ simple or wingless ( $\sigma^{t}$ ) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Oligotomidae
Note.-Navás (1918) divided the Order into two Sub-Orders, Oryttica and Netica,
one for the genus Cylindracheta, the other for the remaining genera. This seems quite unnecessary, as Cylindracheta is a Gryllotalpid.

## Comparative Morphology and Evolutionary Trends.

In Figures 1-4, an attempt has been made to illustrate schematically the comparative morphology of those characters used in the Order as taxonomic criteria. The fact that

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Fig. 1.


Fig. 2.
Figs. 1-4.-Comparative anatomy and possible evolutionary trends in the Order Embioptera. (1) New-World groups exclusive of the more advanced Embiidae. (2) Embiidae. (3) Oligotomidae. (4) Notoligotomidae. For codification of characters see text.

## AMCESTRAL OLTGOTOMID




RAPLDEMDIA SOLIERI
(CIRCUM-MEDITERRANRAN).

haplommbia taurica (CRDIEA).
these characters are selected by systematists is sufficient indication that little profit can accrue from a comparative study of most other characters; the internal anatomy is almost constant throughout the widely-separated members of the Order which have been studied. Possible supplementary characters for comparative purposes are to be found in the thoracic and anterior abdominal sternites, and in the female terminalia; these characters show little indication of differences useful for comparative purposes, at least at this stage of our knowledge; they may be found useful when further studies on the Order are carried out.

The scheme previously advanced (Davis, 1938, fig. 120) is obviously unsound in many places, particularly in the treatment of the 'Oligotomidae' and in the consideration of Haploembia and 'Monotylota'. This scheme was prepared with very little first-hand knowledge of exotic genera. It was advanced to illustrate a theory of convergence, rather than as an attempt to solve the evolutionary problems in different lines of descent in the Order.

In the present schemes, and in the discussion below, the males alone are referred to. The schemes (Figs. 1-4) are primarily to show the comparative morphology of existing types; they may also indicate evolutionary relationships. In several cases, recent species are placed in the ancestral line of other recent species; this course has been explained previously (1938, fig. 120).

Two assumptions open to a considerable amount of doubt must be made if the schemes are taken as evolutionary, and not merely as comparative. The New- and OldWorld Embiidae are shown as parallel developments, rather than as a unit; and the Old-World Embiidae are divided by the primary dichotomy on one or two hind metatarsal bladders. The second of these two steps is even less defensible than the first. It cannot be said whether one or two bladders represent the primitive condition; perhaps it is significant that all Tertiary fossils in which the character is preserved have two such bladders. In any case, a reversion to the primitive type (whatever it is), in such a simple character, may well have occurred in several instances. This would be in opposition to the so-called Dollo's Law, which is in any case not accepted. The artificiality of the dichotomy is illustrated in Figure 2 thus (Embia $\leftrightarrows$ Parembia).
Notes on Figures 1-4.
1.-This scheme shows the comparatively straightforward development within the Clothodidae; several possible courses for the development of the Anisembiidae; and an attempt to relate the difficult groups Teratembiidae and Oligembiidae to a more primitive form. The last-named is too hypothetical to discuss further. The course most favoured for the development of Anisembia is Clothoda-Embolyntha-Mesembia-Anisembia, with Saussurembia derived from Mesembia by a secondary degeneration of the nodules of the left cercus (by neoteny, since the larval cerci are smooth throughout).
2.-This tentative scheme would make the Embiidae polyphyletic. Convergence is frequently invoked, especially in the forking of the process of the left hemitergite, the loss of wings, and to a less extent the modification in several ways of the first segment of the left cercus.
3.-Assuming the Oligotomidae as at present constituted to be monophyletic, the comparison of its various component lines offers little difficulty, but the origin of the family as a whole from any other known type is shrouded in obscurity. Loss of wings, and development of a terminal hook on the process of the left hemitergite, are the most frequently-recurring parallel steps.
4.-The evolution of the Notoligotomidae offers less difficulty than that of other families. The ancestor might well resemble the Indian genus Parembia; on Figure 4, it has been assumed that the left cercus was not echinulate, but this difference from Parembia can be resolved by considering the loss of nodules on the left cercus as a secondary feature of Burmitembia and Metoligotoma rileyi, as suggested under Saussurembia.

The fusion of the segments of the left cercus is convergent to the genus Anisembia; an exactly parallel step (in both cerci) has occurred within the Nemouridae, in the closely-related Order Perlaria. The motive force in each case may well have been
surface tension acting on the cercus during the last ecdysis. This is not an implication of somatic induction; the growth mechanics of the left cercus, as of other parts of the complex terminalia, during the last ecdysis, must be complicated, and may include such factors as pressure of body fluid, muscular contraction, differential hardening, differential adherence to the exuvium, etc.; as soon as these forces were relaxed, by a genetic change, however caused, surface tension would tend to promote reduction in the area of the cercus or other structure.

Teratological failure of the segments of the left cercus to fuse has been noted in Metoligotoma extorris (Davis 1938); this probably resulted from failure to separate cleanly from the exuvium. A regular failure to fuse would represent an example of neoteny, and a definite contradiction to Dollo's 'Law'.

I am indebted to Mr. E. S. Ross, of the University of California, for the suggestion that the larval setae retain their position when the segments of the left cercus fuse. No exact study of the chaetotaxy has been made, but the setae of the left cercus of the adult male in Notoligotoma, Metoligotoma and Anisembia certainly seem to be very dense at the place where the larval second segment has been wholly or partly resorbed.

## Codification of Characters, Figs. 1-4.

Unless annotated, males winged; $\pm W$, winged and wingless forms of male known; $-W$, males wingless.
$R_{4}, R_{5}$, veins distinct; $R-$, vein simple ; $R_{4} \rightarrow R-$, apparent secondary attachment of $R_{4}$ to anterior branch of sector ; $\left.\frac{R \overline{{ }_{4+5}}}{R_{4}, R_{5}}\right\}$, $R_{4+5}$ simple in forewing, forked in hindwing; 2 M , media regularly forked, simple by anomaly. $1-2 \mathrm{M}$, media usually simple, forked in one or more wings by venational aberrations of moderate frequency; 1 M , media regularly simple.

3 Cu , cubitus with more than two branches; 2 Cu , cubitus with two branches.
$\ldots$. after any vein represents weakening or partial obsolescence; $2 \mathrm{Cu} . .$. indicates that only the anterior branch $\left(\mathrm{Cu}_{1 \mathrm{a}}\right)$ is weakened, as the stem $\left(\mathrm{Cu}_{1^{\mathrm{b}}}\right)$ is always strong.

MD !, mandibles greatly over-developed. HMT0, HMT1, HMT2, hind metatarsal bladders 0,1 or 2 . HMT(1-2), medial bladder very small.
$\overline{10}$, tenth abdominal tergite entire ; 10 , divided, with processes of hemitergites small; 10L, 10 R , divided, with processes of hemitergites well-developed; 10L, 10R...., divided, with processes prominent, but with suture between hemitergites obsolescent proximally.
$10 \mathrm{LP}(\mathrm{A})$, process of left hemitergite with a terminal hook or claw; 10LP(B), with a nonterminal lateral or dorsal lobe; 10LP(B...), lateral or dorsal lobe weak; 10LP(C), process of left hemitergite slightly expanded and obliquely truncate terminally ; $10 \mathrm{LP}(\mathrm{X})$, left hemitergite with a blunt dorsal inner protuberance, but with main process simple.
$10 \mathrm{RP}_{1}, 10 \mathrm{RP}_{2}(\mathrm{X})$, right hemitergite with an elongate posterior process and an inner ventral flap-like process. $10 \mathrm{RP}_{2}(\mathrm{~A})$, right hemitergite with an inner subelliptical flap; $10 \mathrm{RP}_{2}(\mathrm{~B})$, with a forwardly-directed rod or hook on inner margin; (cf. (A) or cf. (B), approximating to typical form as above) ; $10 \mathrm{RP}_{\mathrm{o}}(\mathrm{C})$, with a membranous, horizontal, inwardly-directed process.
$\mathrm{LC}_{1}, \mathrm{LC}_{2}, \mathrm{RC}_{1}, \mathrm{RC}_{2}$, first and second segments of left and right cerci elongate-cylindrical, without nodules; $\mathrm{LC}_{1}[\mathrm{~A}]$, first segment of left cercus weakly clavate; $\mathrm{LC}_{1}(\mathrm{~A})$, more strongly clavate; $\mathrm{LC}_{1}(\mathrm{~B})$, with two inner lobes ( $\mathrm{LC}_{1}[\mathrm{~B}]$, inner lobes weak); $\mathrm{LC}_{1}(\mathrm{C})$, with a narrow forwardly-directed hook; *, echinulate; **, echinulate, teeth very strong, sharp; -*, secondary loss of nodules; $\overline{\mathrm{LC}}$, two segments of left cercus fused ( $\overline{\mathrm{LC}}(\mathrm{A})$, remains of second segment a terminal incurved extension of first; $\overline{\mathrm{LC}}(\mathrm{B})$, a distal external protuberance of first). $\mathrm{RC}_{1}(\mathrm{~A})$, first segment of right cercus squat.
$\overline{\mathrm{LCB}}$, 'left cercus-basipodite' composite (apparently including left half of larval tenth sternite) ; LCB(A), structures at base of left cercus complex, with the true cercus-basipodite and the supposed left half of the larval tenth sternite distinct, both produced to processes.

RCB !, right cercus-basipodite enlarged ; (RCB), right cercus-basipodite suppressed, probably by fusion to cercus.

Distribution: The recent members of the Order seem to be confined to warm countries, extreme ranges being represented by the Crimea and South-east Tasmania. Some species are recorded from dry regions, especially in the Sonoran and Australian regions and in parts of Africa. Although little is at present known of the ecology of the Order, it appears that its members are 'drought-evading' rather than 'droughtenduring', to borrow the plant ecological terms in a somewhat-altered sense. For
instance, the Sonoran species retreat deep into cracks in the soil during the dry season.

With regard to migration of ancestral lines in the past, it seems fairly evident that the further the migration in space, the greater is the structural modification; members which have failed to migrate, or have become geographically fixed at some point of the migration route, seem to have evolved less rapidly than those which have migrated further. As a general assumption, it is supposed that the more recent migration routes have been directed away from the tropics, especially in the colonization of the Australian and Sonoran regions. The Miocene species Clothoda florissantensis occurred in Colorado, but it is assumed that its descendants, if any, were driven south by the Pleistocene cold, and that the present Sonoran species have more recently migrated north, either by Central America or by the Antilles.

## List of References.

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## Corrigenda.

Part xv.
Page 183, line 13 from bottom, for specimen, read species
Page 190, second line of dichotomy 3, for smaller, less than ten, read smaller, more than ten
Part xvi.
Page 327 , line 24 , for synonyms, read synonymous.
Part xvili.
Page 384, line 6 from bottom, for subspecies, read species


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[^0]:    * The locality in which the group is indigenous, not the range enlarged by artificial spreading.

