The geographical distribution of the Dermaptera (Insecta) with reference to continental drift

EDWARD J. POPHAM†

26 Branch Road, Mellor Brook, Blackburn BB2 7NU, England

In this exercise, the centres of evolution of the main forficuline taxa have been determined using the techniques of Nelson and Rosen (1981). This has shown that the Forficulina arose in an area of land now comprising north east Brazil and north west Africa. From here some taxa spread westwards into the Americas and others going eastwards to the rest of Africa, Madagascar, and Australia. The Cretaceous separation of India from Africa and its subsequent drift across the Indian Ocean to fuse with south east Asia resulted in the Oriental Region becoming a secondary centre of forficuline evolution, from whence various taxa have subsequently spread into Burma, China, Japan and Micronesia. Other taxa spread through the East Indies into New Guinea, Australia and associated islands. A few migrated from central Gondwanaland into Antarctica and thence to New Zealand and associated Polynesian islands. During the Miocene orogenesis of the Sea of Tethys, some families spread from north Africa into southern Europe and the Middle East. An analysis the geographical distributions of the various families indicates the main migration routes used by forficuline taxa as aspects of Dermapteran systematics in need of further study and consideration.

Introduction

The original Dermapteran classifications of Verhoeff (1902), Zacher (1911) and Burr (1911) have subsequently been the basis of those by Steinmann (1974), Sakai (1982) and others workers. Sakai (1982) has also produced a list of the then known forficuline species giving their recorded occurrence. This work has been used for the present investigation.

The Dermaptera comprise nearly 2000 species, which are mainly distributed throughout the southern continents, with a minority of species in North America, Europe and Southern Asia.

Some species are wingless, but the majority live in secluded habitats such as litter, thick vegetation, under bark or detritus. Many species seldom or never fly. The present distribution of the world's species is, therefore, almost entirely due to their migration from the centres of evolution across adjacent land masses, which have subsequently split and been moved by continental drift. The virtual absence of

†Deceased.

earwigs from the volcanic oceanic islands of the eastern Pacific Ocean, except for the cosmopolitan species introduced by man, supports this view.

Those environment and ecological factors, which have produced the existing range of forficuline genera and species have also been responsible for their present geographical distributions. The techniques of Nelson and Rosen (1981) have been used to determine the centres of evolution of the main forficuline taxa, while a detailed study of the distributions of the genera and species has revealed the main distribution routes of these insects. Ideally, a natural classification should agree with the geographical evidence, but it can never prove that a given classification is correct. Differences between the two approaches, indicate matters needing further study and consideration. It is with these matters that this paper is concerned.

Materials and methods

In this paper, the paleocontinental world maps of Smith *et al.* (1981) have been used in preference to the views of Shields (1979), which are based upon the expanding Earth theory. These paleocontinental maps show that by the early Permian, the western end of the Sea of Thethys had become virtually obliterated by the south coast of Europe, lying close to the north coast of South America. By the late Triassic, both North America and Europe had drifted eastwards to produce a line of contact between the northern and southern land masses ranging from Peru, along the north coast of South America, and the north west coast of Africa. These inter continental contacts would have enabled insects of Laurasian origin to invade Gondwanaland. The centre of this north–south land connection seems to have been between Morocco and eastern Brazil or north-west Gondwanaland.

After the Jurassic disintegration of the southern presentiment, the fusion of India with the Oriental Region created a secondary centre of evolution, from whence forficuline taxa invaded Burma to China, Japan, Micronesia and Polynesia. Others spread through the East Indies to New Guinea and Australia. Some South American taxa spread through the Caribbean area to Central and North America, while others went southwards and either reached South Africa, or invaded northern Antarctica and from there were able to reach New Zealand and the associated islands. The taxa in these eastern land masses have not been used to determine the primary centre of forficuline evolution, for the simple reason that before the Jurassic no direct land connection existed between them and Gondwanaland.

The centre of each forficuline subfamily has been determined by constructing a phylogenetic tree for each forficuline family. Where the systematics of a family are in a state of flux, the order in which Sakai (l982) listed the subfamilies has been used. The present known geographical distributions of each genus or subfamily are then duly noted. By working from the ends of the branches of the tree to its base, the most likely centre of evolution of that taxon is determined. At each stage of this process, the smallest areas or those with the least number of species are eliminated. The centre of evolution is assumed to be smallest area, from which the largest number of taxa could have originated. The smaller the resultant area, the more accurate it is likely to be. When the evolutionary centres of each family have been determined, the process is repeated to deduce that of the Forficulina as a whole.

A difficulty arises in the Apachyidae and Chelisochidae, which have a relatively small number of species and a restricted area of distribution. In such cases, the present species distribution has been considered against the facts of continental drift and the distributions of related subfamilies.

A study of the distributions of all the forficuline genera has been used to determine their main migration routes from both their primary and secondary centres of evolution.

Finally, the deduced evolutionary centres of each family have been used to determine that of the Forficulina, using the traditional classifications (figure 8), that of Popham (1965). The cladogram of Haas (1995) (figure 9) is also given. In spite of their differences, the results obtained must contain some common elements of truth, but the main value of their differences lies in indicating those aspects of forficuline systematics possibly requiring further study and investigation.

The difficulty of studying the geographical distribution of any group of organisms is that it has to be based upon the existing records of their occurrence. The discovery of new species and new geographical records is an on going process and provides a more accurate picture of the distribution of each taxon. This means that no geographical study can be definitive, while the absence of any taxon from given area is no proof that that is not, nor previously been, present.

The main forficuline taxa

Haas (1995) has claimed that the pygidicranid earwigs are paraphyletic, with the Karschiellidae, Haplodiplatys and Diplatyidae being independent taxa. Not unreasonably, he also questions whether the Pygidicranidae is a monophyletic taxon. In view of the importance of his approach, the arrangement of the main taxa by Haas (1995) has been followed, but the detailed classification of the taxa is that of Sakai (1982–1997).

KARSCHIELLIDAE
(Map 1)

The absence of this family in any other land mass (table 1) suggests that this family originated in Africa.
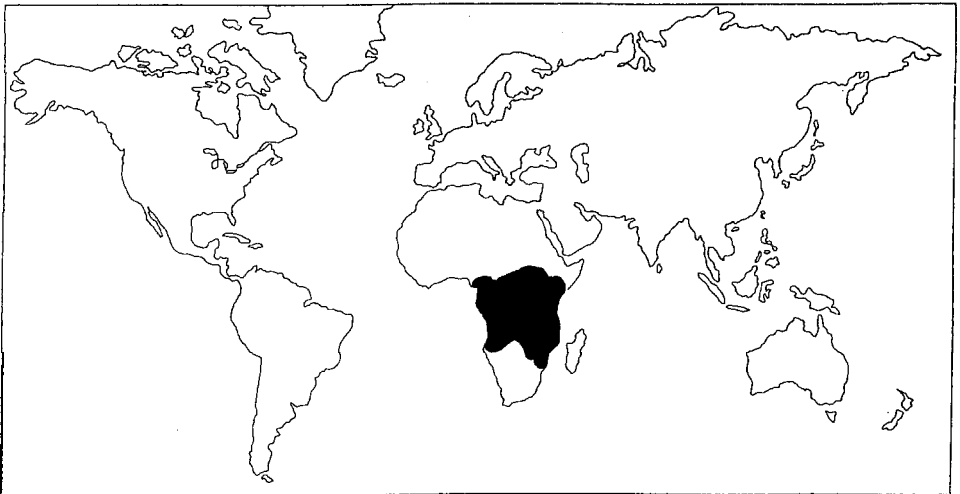
Map 1.   Distribution of the Karschiellidae.

Table 1.   Distribution of the genera of the Karschiellidae.

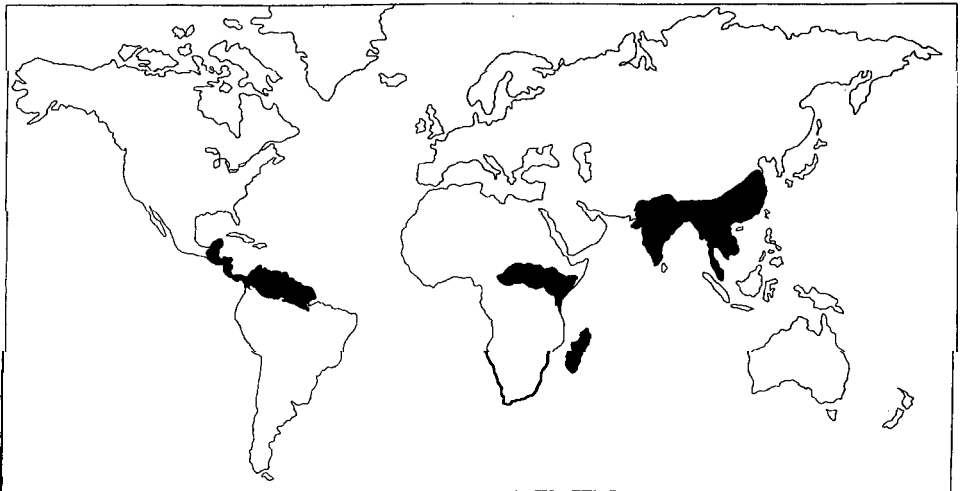| Taxon	Number of species	Occurrence of species
Karschiellidae		
Bormansia	8	East and Southern Africa
Karschiella	5	West and Central Africa

HAPLODIPLATYS
(Map 2)

Of the 39 species of Haplodiplatys, seven occur in South America, four in Africa, six in Madagascar and the remaining 22 species in the Oriental Region.
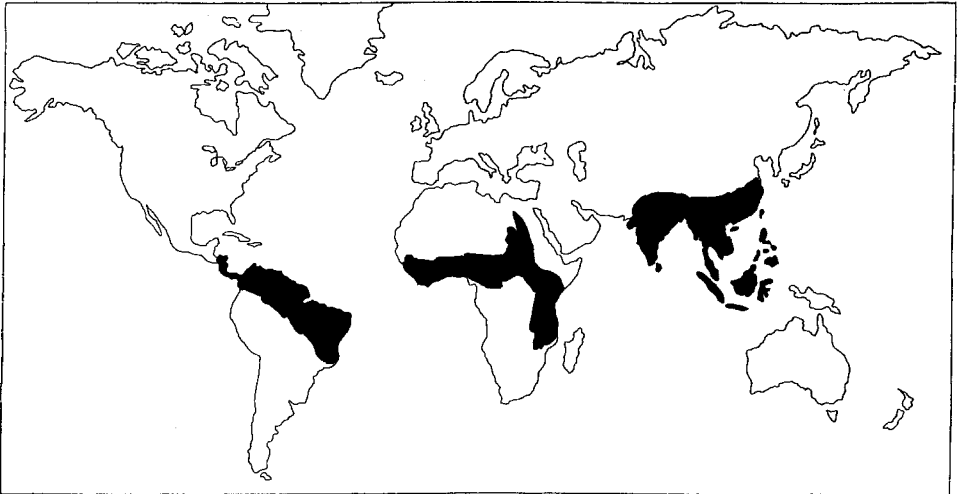
DIPLATYIDAE
(Map 3)

The study of Haas (1995) was based upon several species of *Diplatys*, but in his figure 7 of forficuline phylogeny, he does not use the family name, but that of *Diplatys jacobsoni*. In this study, the name 'Diplatyidae' is used to include the subfamily Cylindrogastrinae, but not the genus *Haplodiplatys*.

The penis lobes of the Cylindrogastrinae possess a single virga, in contrast to the double virga of other diplatyid earwigs. The restricted occurrence of this subfamily to South America (table 2), along with some species of the *Haplodiplatys*, suggests a neotropical evolutionary centre for two of the three of these taxa. Figure 1 gives a possible tree for the Diplatyidae and *Haplodiplatys*. The occurrence of these taxa in South America, Africa, Madagascar and India suggests that both the Diplatyinae and *Haplodiplatys* were widely distributed in these land masses, before the disintegration of Gondwanaland. This means that those taxa present in the Oriental Region and East Indies could only have been derived from Gondwanaland taxa and that no means existed for migration in the opposite direction. If these Oriental species are not considered, the 'diplatyid' originally evolved in either South America or Africa.

Map 2.   Distribution of *Haplodiplatys*.

MAP 3.   Distribution of the Diplatyidae.

Table 2.   The occurrence of the species of the Diplatyidae.

| Taxon	Total number of species	Occurrence and number of species
Cylindrogastrinae	7	South America
Diplatyinae		
Schizodiplatys	14	Africa (2), South East Asia (6), Philippines (4), Sumatra (2) and Celebes (1)
Diplatys	55	Africa (13) South East Asia (39), Sumatra (1), Borneo (3), Philippines (1)
Lobodiplatys	11	Africa (9) and India (2)
Circodiplatys	1	Philippines
Paradiplatys	10	Africa (8)and Orient (2)
Diplatymorpha	1	East Indies
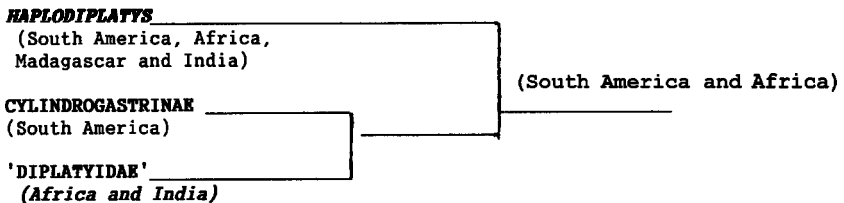
FIG. 1.   A possible tree for the 'Diplatyid' taxa.

PYGIDICRANIDAE
(Map 4)

Of the seven genera of Pygidicraninae, *Pygidicrana* is restricted to South America, the genus *Dacnodes* mainly occurs in South America and Africa, while the other five genera all occur east of India in South East Asia, the East Indies and Australia (table 3). The Echinosomatinae comprise 36 species, 10 in Africa, three in

Map 4.   Distribution of the Pyidicranidae.

Table 3.   The occurrence of the species of the Pygidicranidae.

Taxon	Total number of species	Occurrence and number of species
Pygidicraninae		
Pygidicrana	9	Brazil (5), Paraguay (1), Venezuela (2), and Honduras (1)
Cranopygia	15	India (7), Sumatra (2), Java(1), Borneo (2), Philippines (2), Celebes (2), New Guinea (1), Solomon Islands (1) and Australia (2)
Macrocranopygia	3	Java (1), Sumatra (1) and Borneo (1)
Paracranopygia	16	India (3), South East Asia (2), Sumatra (1), Java (2), Borneo (1) and Philippines (2)
Epicranopygia	7	India (6) to Assam (1)
Tagalina	11	Philippines (1), Borneo (1), Celebes (1), Solomon Islands (2), New Guinea (8)
Dacnodes	17	Africa (14), Madagascar (1),India (1), Australia (2), South America (1)
Anataelinae	2	Canary Islands and Brazil
Challinae	1	Korea (1), China (1)
Echinosomatinae	36	Africa (10), Madagascar (3), Seychelles (1), South East Asia (9), India (5), Sumatra 4), Java (4), Borneo (3), Philippines (1), Celebes (1), New Guinea (3) and Solomon Islands (1)
Blandicinae	6	South Africa (4) and Madagascar (2)
Esphalmeninae		
Esphalmenus	14	South America (13) and Cape Colony (3)
Echinopsalis	1	South and Central America
Pyragopsalis	5	Caribbean area (5)
Pyragra	6	North. Central and South America (6)

Madagascar, Seychelles and 26 in the Oriental Region and East Indies. The distribution of these species resembles that of the Diplatyid subfamilies, but their absence from South America, may indicate a possible African origin for this subfamily.

The Anataelinae occur in the Canary Islands and Brazil (Sakai, 1996), the Challinae in Korea and north east China, while the Pygidicraninae are represented in South America by the genus *Pygidicrana*, the majority of species occur east Asia and the East Indies, except for the African genus *Dacnodes*. The Echinosomatinae are distributed from Africa through Madagascar, the Seychelles to south east Asia, the East Indies and New Guinea. In contrast, the Esphalmeninae is predominantly a neotropical family, which has spread into the Caribbean area, whilst the few species in South Africa, probably arrived there before the Cretaceous opening of the southern Atlantic Ocean. The Blandicinae are restricted to south east Africa and Madagascar.

The occurrence of the genus *Pygidicrana* in South America indicates that the Pygidicranids like the Diplatyids are of neotropical cum Ethiopian origin, while the presence of some genera and species in the Oriental Region and East Indies, implies that this is a secondary evolutionary centre for this family. The occurrence of a small number of species of the genus *Tagalina* in the East Indies, New Guinea and the Solomon Islands probably explains the occurrence of this genus in Northern Australia.

The phylogenetic and geographical relationships between these taxa are summarized in figure 2. Taking the Pygidicranidae, *Haplodiplatys* and the Diplatyidae together, it is reasonable to assume, that even if they may not be a monophyletic group, they could have evolved from a common ancestor with a 'blattoid' neck and two penis lobes, which are folded forwards when not in use. Figure 2 and map 4 suggest that the Pygidicranidae arose in an area of north-west Gondwanaland. The occurrence of the Anataelinae in Brazil and the Canary Islands supports this view and that the present discontinuous distribution of this subfamilies due to the Cretaceous opening of the Atlantic Ocean. The Challinae of Korea and south east Asia occur on the northern edge of the distribution of the Pygidicranidae.
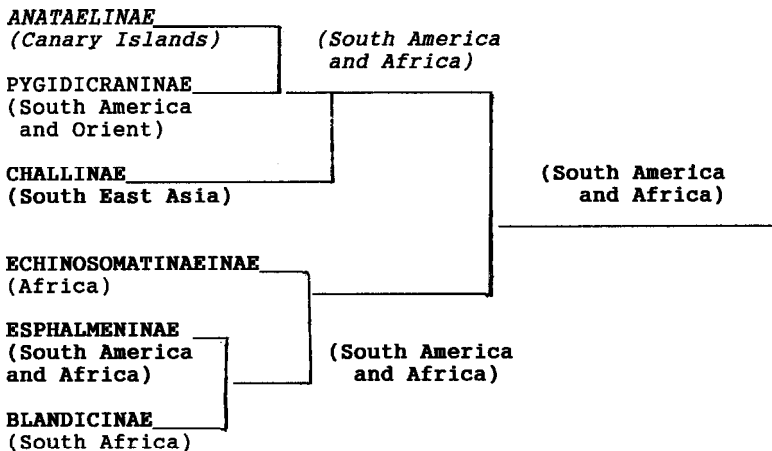

FIG. 2.   A possible tree for the subfamilies of the 'Pygidicranidae'.

APACHYIDAE
(Map 5)

This subfamily is distributed from Africa to New Guinea (table 4). There are four species in Africa, one in India and Burma and eleven in the East Indies and Australasia. The widespread occurrence of this family in Africa and Madagascar suggests that its primary evolutionary centre was Africa and that the family had reached India before that subcontinent became united with southern Asia, from whence this family spread into the East Indies and Australasia. The presence of six species of *Apachys* in Australia may either represents a migration across with a united Gondwanaland or one from New Guinea, during a period of low sea level (Jackson, (1995).
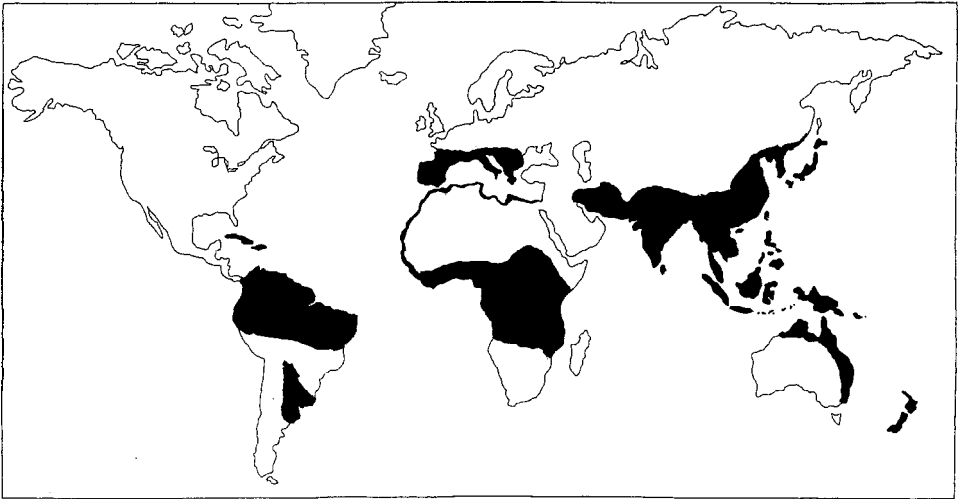
LABIDURIDAE
(Map 6)

Of the 74 species of this family, no less than 48 (65%) occur in the Oriental Region (table 5). There are three species in South America and nine in Africa. Comparison with the distributions of other dermapteran families suggests that the Labiduridae arose in North Africa and then spread eastwards into Africa and India, where a secondary evolutionary centre developed enabling this family to colonise the East Indies, New Guinea and northern Australia. If this is so, then the occurrence of few species in South America represents a westward spread of this family from its centre of evolution before the end of the Jurassic.
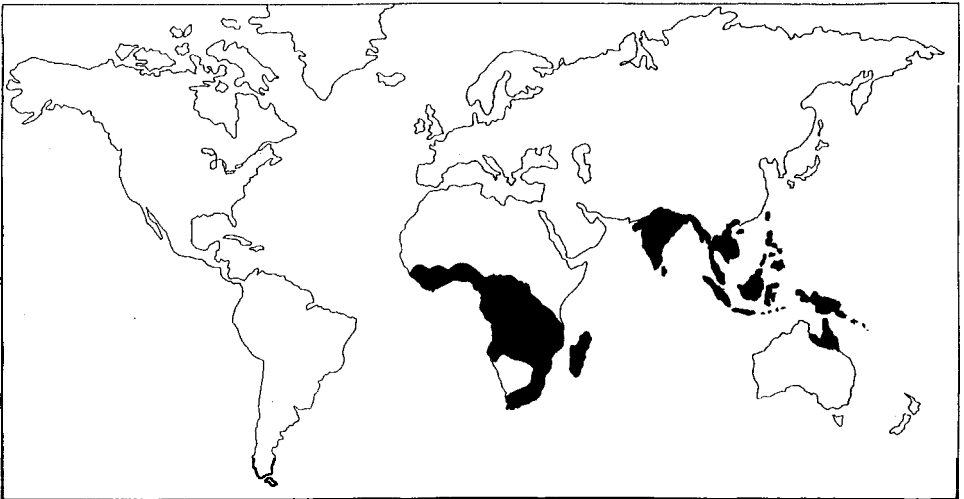
MAP 5.   Distribution of the Apachyidae.

Table 4.   The distribution of the genera of the Apachyidae with number of species.

Taxon	Number of species	Distribution with number of species
Apachys	13	Africa (4), Orient (2), Australia (6) and East Indies
Dendroiketes	4	Sri Lanka, Orient, East Indies, Bismarck Islands and New Britain

MAP 6.   Distribution of the Labiduridae.

Table 5.   The distribution of the genera of the Labiduridae with numbers of species.

Taxon	Total number of species	Distribution of Genera with number of species
Nalinae		
Nala	11	Africa (4), Orient (2), East Indies, New Guinea (1) and Australia (4)
Labidurinae		
Labidura	9	Africa (2), Orient (4), East Indies (1), Australia (1), South America (1), Cosmopolitan (1)
Tomopygia	1	Java
Forcipula	33	Africa (3), Orient (24), East Indies, New Guinea (1) and South America (2)
Allostethinae		
Allostethus	17	Orient and East Indies (15)
Gonolabidura	5	Orient (3) and East Indies (2)

Figure 3 has been constructed using Steinmann's (1974) arrangement of the subfamilies and points to an African origin of this family. In this figure occurrence of subfamilies east of India have not been used to determine the primary evolutionary centre of this family.
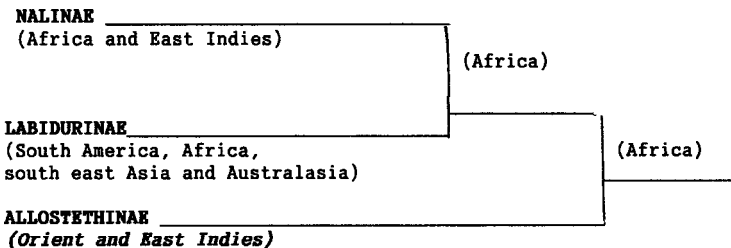

FIG. 3.   A possible tree for the subfamilies of the Labiduridae.

ANISOLABIDAE
(Map 7)

Recent authors have created new genera and subgenera, without indicating their mutual affinities of these subfamilies. As the systematics of this family is in a state of flux, Sakai's (1982) list of subfamilies has been followed (table 6).

In figure 4 the subfamilies are given in the order as listed by Sakai (1982). Of the ten subfamilies of the Anisolabiidae, one is restricted to the Galapagos Islands, two to South America, the Platylabinae to the Oriental Region with six occurring in South America. This points to a neotropical origin for this family, which first spread eastwards to Africa, India, the Orient and from there to Australasia and

MAP 7.　Distribution of the Anisolabiidae.

Table 6.　List of subfamilies and number of species of the Anisolabidae in areas indicated.

Subfamily	Occurrence of each subfamily with the number of species given in brackets
Parisolabinae	Greece (1), India (2), East Indies (1) Australia (1) and New Zealand (8)
Idolopsalinae	Mexico (1), South America (11)
Isolaboidinae	Turkey (1), Lebanon (1), India (1)
Anophthalmolabinæ	Galapagos Islands (1)
Gonolabinae	Peru (3) and Chile (1)
Brachylabinae	South America (7), Africa (4), Madagascar (4), Orient (5), East Indies (1), New Zealand (1), Polynesia (13)
Antisolabinae	Africa (1), Seychelles (1), India (1), Australia,(1), New Zealand (1), New Guinea (1) and Fiji (1)
Isolabinae	South America (5), Africa (22), Orient (15), East Indies (2), Australia (1)
Platylabinae	Burma (1) and India (2)
Anisolabidinae	North America (2), South America (20), Europe (3), Africa (93), Madagascar (2), Orient (68), East Indies (21), New Guinea (12), Australia (13), New Zealand (5), Polynesia (16) and Cosmopolitan (2)

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PARISOLABINAE_____
(Greece,India)                        (Greece to
                                      India)

ISOLABOIDINAE
(Turkey, India)_____

IDOLOPSALINAE_____
(South America)
                                      (South
                                      America)
ANOPHTHALMOLABINAE_____
(Galapagos Islands)

GONOLABINAE_____
(South America)
                                               (South
BRACHYLABINAE_____                        America)
(South America, Africa
and India)

ANISOLABINAE_____
(Africa and India)

ISOLABINAE_____
(South America and Africa)

PLATYLABINAE_____
(India)
CARCINOPHORIDAE_____
(South America and Africa)
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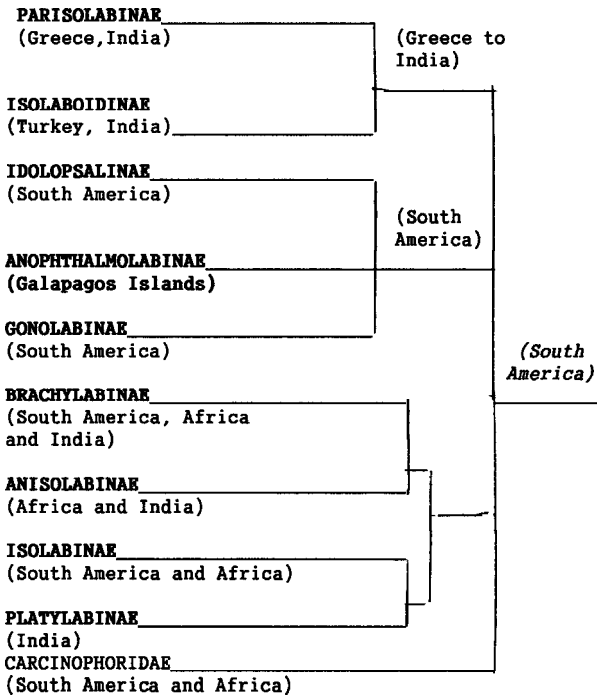
FIG. 4.   A possible tree for the subfamilies of the Anisolabiidae.

Polynesia. An alternative explanation is that this large family originated in Africa and then spread westwards into South America and eastwards to India and western Australia. The exceptionally wide distribution of this family, from the Galapagos Islands to Polynesia (map 7) shows that it is probably the oldest forficuline family, with a predominantly circumtropical distribution.
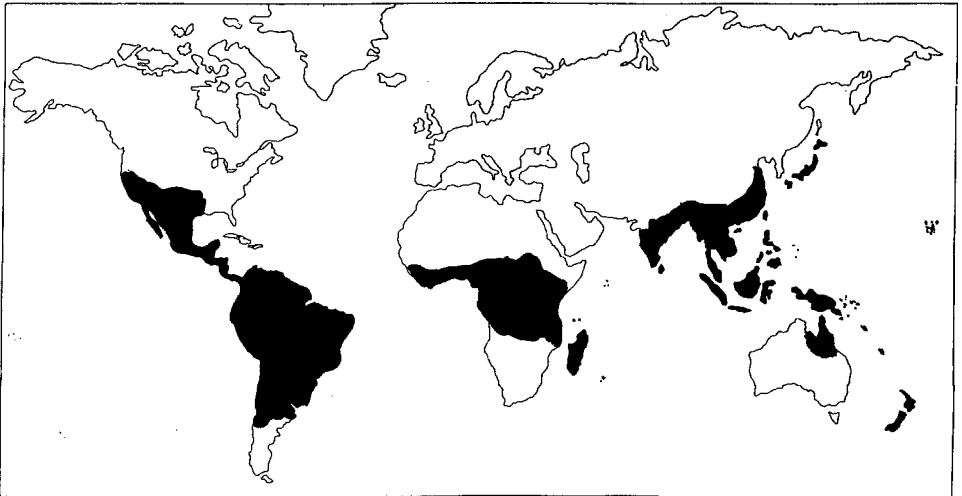
SPONGIPHORIDAE (= LABIIDAE)
(Map 8)

The order of these subfamilies (table 7) is that of Sakai (1982).

The centre of evolution of the subfamilies has been determined with reference only to those countries, which were once part of Gondwanaland. The family tree is shown in figure 5. This figure shows that six of the eight subfamilies occur in South America, four in Africa and three in the Orient. This with the occurrence of 172 out of 418 (41%) species in South America suggests that this family had a neotropical origin and then spread eastwards through Gondwanaland to reach Australia, before the proto-continent started to be divided (map 8). Only the Anisolabidae has a slightly wider geographical circumtropical distribution than the Spongiphoridae, implying that these are probably the oldest forficuline families.

CHELISOCHIDAE
Map (9)

This family occurs in Africa and India, but after India became joined to Asia, it spread to south east Asia, the East Indies, Australasia and Polynesia (map 9).

MAP 8.   Distribution of the Spongiphoridae.

Table 7.   The list of subfamilies and number of genera of the Spongiphoridae in the areas indicated.

Subfamily	Occurrence of each subfamily with the number of species given in brackets
Pericominae	Peru (1)
Vandicinae	Africa (8)
Strongylopsalinae	South America (12)
Isopyginae	Madagascar (1)
Nesogastrinae	Orient (2), East Indies (13, New Guinea (5), Australia (3) and Polynesia (7)
Sparratinae	North America (3), South America (37), East Indies (8), New Guinea (3)
Spongiphorinae	North America (7), South America (73), Africa (23), Madagascar (6), Orient (17), East Indies (8), New Guinea (7), Australia (1), New Zealand (4), Polynesia (4)
Labinae	North America (3), South America (44), Europe (1), Africa (33), Madagascar (18), Mauritius (1), Seychelles (1), Orient (46), East Indies (32), New Guinea (11), Australia (5), New Zealand (2) Polynesia (31), Cosmopolitan (2)
Geracinae	South America (28), Africa (10), Mauritius (1), Orient (2), and East Indies (2)

Out of the 74 species of this family, 44 (59%) occur in Australasia and the East Indies and 13 (14%) from the Solomon and Bismarck Islands, which lie close to New Guinea (table 8). The small number of species in some areas, makes it difficult to determine the centre of evolution of this family, but a comparison with the distribution of the related forficuline subfamilies suggests that the Chelisochidae originated in Africa, then spread into India, the East Indies, Australia and Polynesia. The presence of *Chelisoches lilyanus* Holdhaus on Samoa implies that this family formerly had a wider Polynesian distribution.
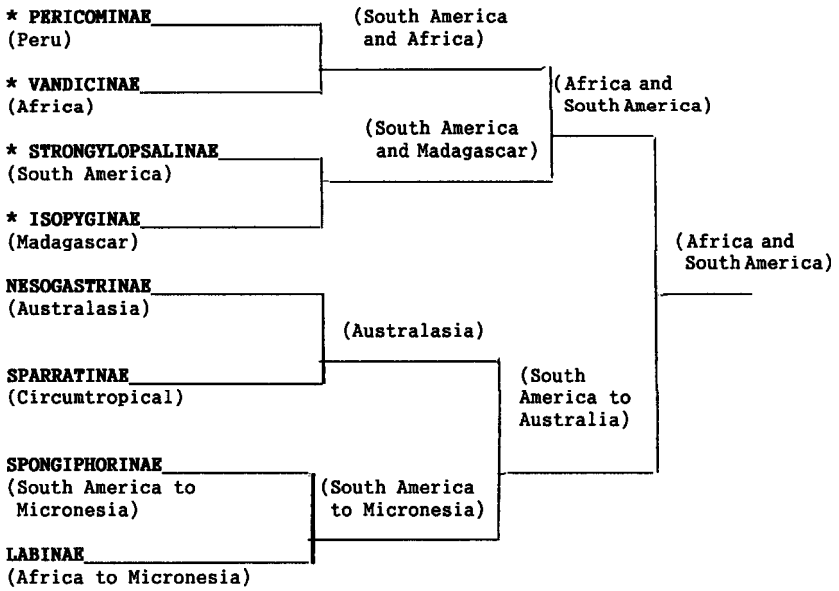
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* PERICOMINAE_____        (South America
 (Peru)                        and Africa)
                                              (Africa and
* VANDICINAE_____                           South America)
 (Africa)
                             (South America
* STRONGYLOPSALINAE_____   and Madagascar)
 (South America)
                                                        (Africa and
* ISOPYGINAE_____                                     South America)
 (Madagascar)

NESOGASTRINAE_____
 (Australasia)
                             (Australasia)
SPARRATINAE_____                      (South
 (Circumtropical)                         America to
                                          Australia)

SPONGIPHORINAE_____
 (South America to          (South America
  Micronesia)                to Micronesia)

LABINAE_____
 (Africa to Micronesia)
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FIG. 5.   A possible tree for the subfamilies of the Spongiphoridae. (*Endemic subfamily.)
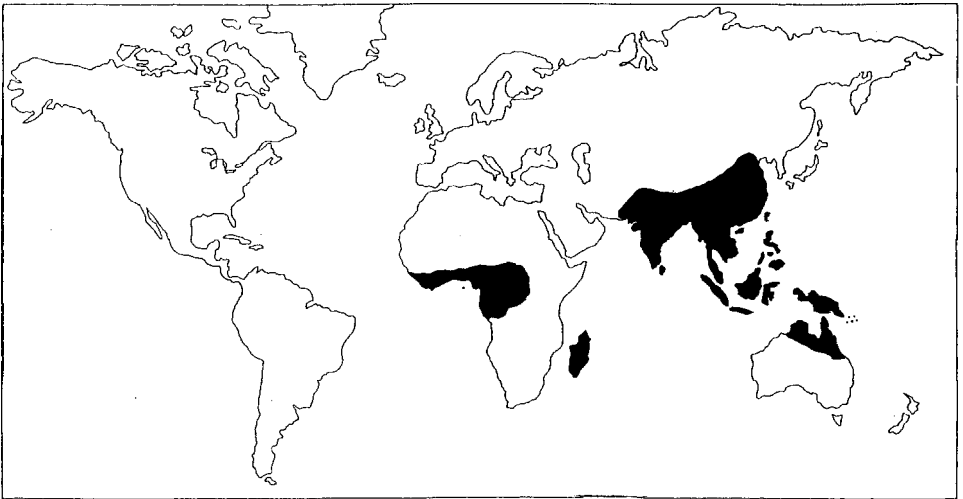
MAP 9.   Distribution of the Chelisochidae.

Table 8.   The distribution subfamilies and numbers of genera of the Chelisochidae, given in brackets.

Subfamily	Occurrence and number of species present
Chelisochellinae	Malaya (1)
Chelisochinae	Africa (3), Madagascar(3), Orienta Region (37), East Indies (22), New Guinea area (19), Australia (5) and Polynesia (9)

FORFICULIDAE
(Map 10)

The occurrence of the species of this widely distributed family is given in table 9. The numbers in brackets indicate the number of species of this family present in that area.

Figure 6 is based upon Sakai's (1982) classification of the Forficulidae to which the Gondwanaland occurrences of each taxon have been added. The given order of the subfamilies is the same as that listed by Sakai (1982).

The geographical distribution of the Forficulidae is summarized on map 10. The occurrence of seven of the eleven subfamilies in South America, with its occurrence in Africa points to this family originating in a area derived from both Africa and South America. The Opisthocosminae spread eastwards to India, South East Asia,

MAP 10.   Distribution of the Forficulidae.

Table 9.   The list of subfamilies of the Forficulidae.

| Subfamily	Number of species	Occurrence with numbers of species
Opisthocosminae	82	Africa, Orient, East Indies (79) Cuba (2)
Cosmiellinae	51	South America (11) Africa (18), Orient, (12) and East Indies (10)
Ancistrogastrinae	33	North, Central and South America
Sarcinastricinae	5	Central and South America
Rhyacolabinae	3	Central America
Eudohrninae	25	Orient and East Indies
Neolobophorinae	13	North and South America
Diaperasticinae	6	Africa
Anechurinae	55	Europe and the Orient
Allodahlinae	17	Eurasia and the Orient
Forficulinae	101	South America (2), Eurasia (25), Africa (27), Orient (42), East Indies (2), Australia (2) and Cosmopolitan (1)
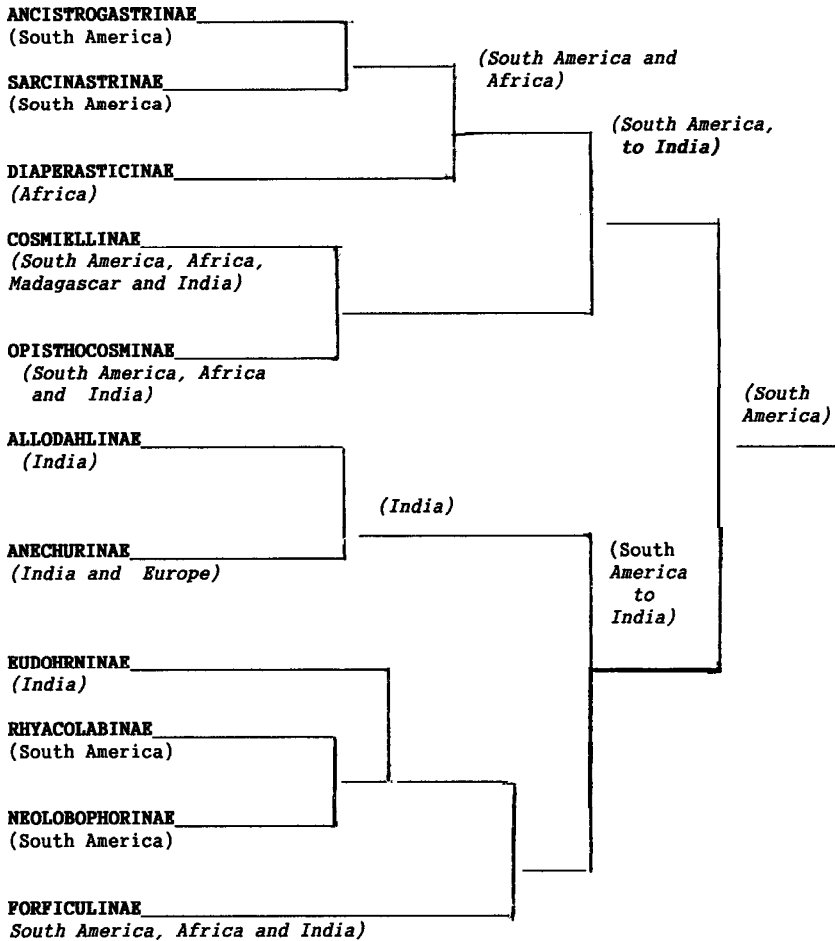
Fig. 6. A possible tree for the subfamilies of the Forficulidae with the areas of Gondwanaland in which they occur.

the East Indies and New Guinea, and where four species of the genus *Acanthorax* are endemic, a fifth species occurs on the Bismarck Islands and in New Britain. Four of the subfamilies are endemic to South America, the Diaperasticinae are restricted to Africa and the Eudohrninae to the Orient and the East Indies. The Anechurinae, which arose in the Oriental Region, also spread northwards into Asia and Europe. The largest subfamily, the Forficulinae, spread eastwards to India, which then became a secondary evolutionary centre, enabling the family to reach New Guinea and Australia. Sakai's (1982) list mentions two Australian species, but the identification of *Doru speculiferum* (Scudder) is doubtful (Brindle personal communication, 1997). The other Australian species is *Forficula vilma* Steinmann (= *F. modesta* Menozzi) from New South Wales. The occurrence of the 157 (40%) species of this family in the Orient is in contrast to the scarcity of the Forficulid species in Australia. The Forficulinae also spread from north Africa into the Mediterranean area and northern Europe. Six species of *Guanchia* occur on the Canary Islands and two of *Forficula* on the islands of Madeira.

Centres of forficuline evolution

Sakai's (1982) arrangement of the main forficuline taxa, which is basically the same as those previously proposed by Zacher (1911), Burr (1911), Hincks (1955, 1959), Steinmann (1974) and other workers, has been used to determine the centre of evolution of the Forficulina in figure 7. This suggests, that the Forficulina originated in an area ranging from South America to India.

In figure 8 the centre of forficuline evolution has been determined using Popham's (1965) classification.

Figure 9 gives the cladogram Haas (1995) produced on the phylogeny of the Forficulina. To his figure has been added the deduced centres of evolution of each of the taxa concerned.

The three figures, 7, 8 and 9, are based upon different approaches and different techniques. The use of the techniques of Nelson and Rosen (1981), for determining the area of the centres of forficuline evolution, results in an appreciably smaller area in figure 8 than in figure 7. The main value of the differences in the results obtained, is that they indicate the following taxonomic problems in need for further consideration.

(1) The majority of previous authors have divided the forficuline taxa into two groups namely the Anisolaboidea, with two penis lobes and the Forficuloidea, which have lost one. As a result of this procedure the Spongiphoridae, Forficulidae and Chelisochidae are placed in a common taxon. The loss of one penis lobe in each of these families is a negative or absentee character and uniting them in a common taxon is a *non sequitur* argument and its conclusion, therefore, is null and void.

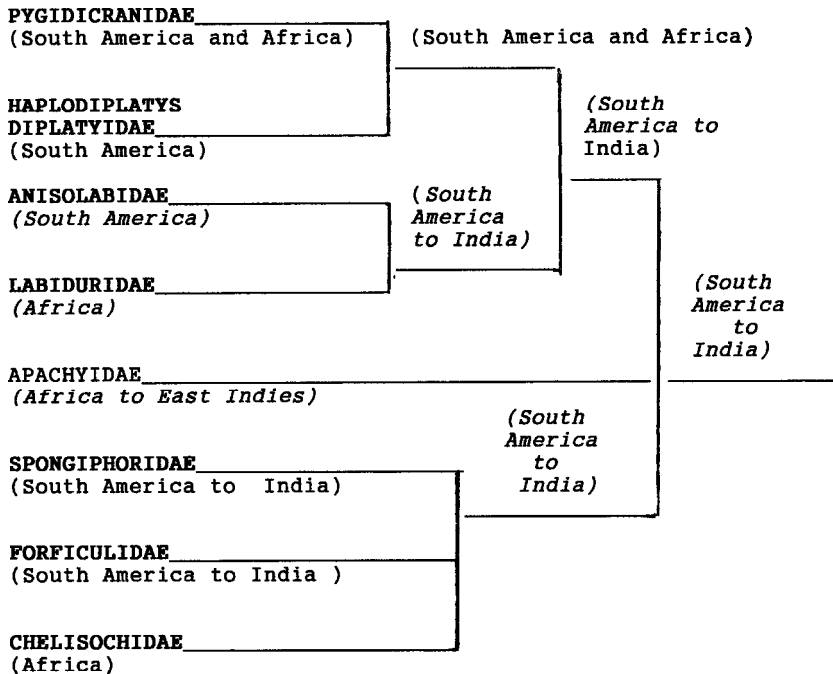(2) The presence of a virgal vesicle in the Apachyidae, Labiduridae,

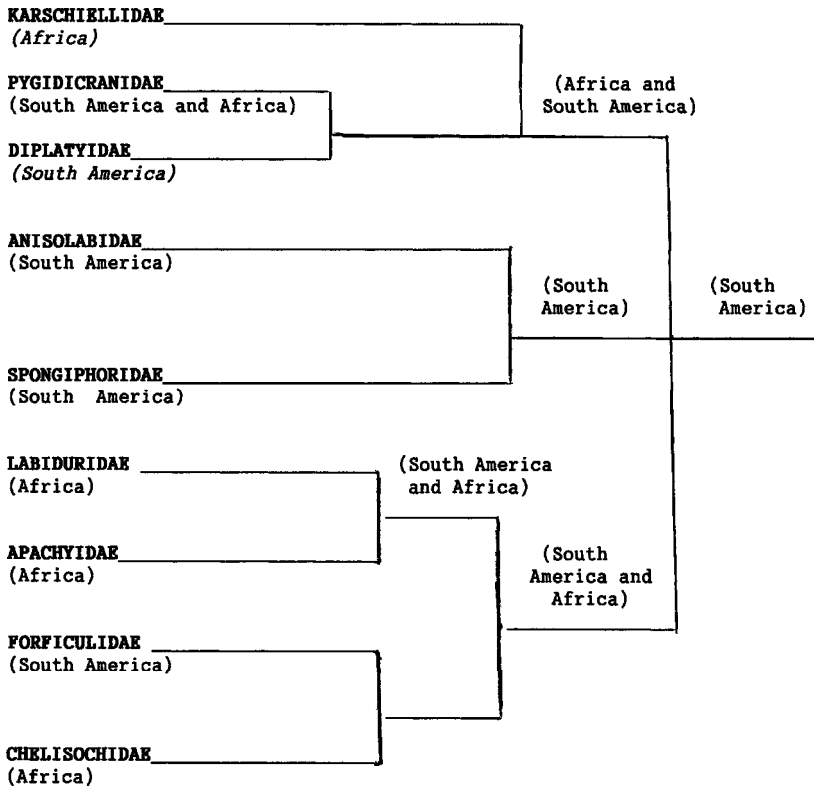FIG. 7.   The Families of the Forficulina based on Sakai's (1982) classification.

KARSCHIELLIDAE
(Africa)

PYGIDICRANIDAE   (Africa and
(South America and Africa)   South America)

DIPLATYIDAE
(South America)

ANISOLABIDAE
(South America)   (South   (South
                                                   America)   America)

SPONGIPHORIDAE
(South America)

LABIDURIDAE   (South America
(Africa)   and Africa)

APACHYIDAE   (South
(Africa)   America and
                                                    Africa)

FORFICULIDAE
(South America)

CHELISOCHIDAE
(Africa)

FIG. 8.   The Families of the Forficulina based on Popham's (1965) classification.

Order
of Haas
  0 ──────────────── ANCESTRAL FORFICULINE EARWIGS
  1 ──────────────── KARSCHIELLIDAE (Africa)
  2 ──────────────── HAPLODIPLATYS (South America)
  3 ──────────────── DIPLATYIDAE (Orient)
  4 ──────────────── PYGIDICRANIDAE (South America and Africa)
  5 ──────────────── APACHYIDAE (Africa)
  6 ──────────────── LABIDURIDAE (Africa)
  7 ──────────────── ANISOLABIDAE (South America)
  8 ──────────────── SPONGIPHORIDAE (South America)
  9 ──────────────── CHELISOCHIDAE (Orient)
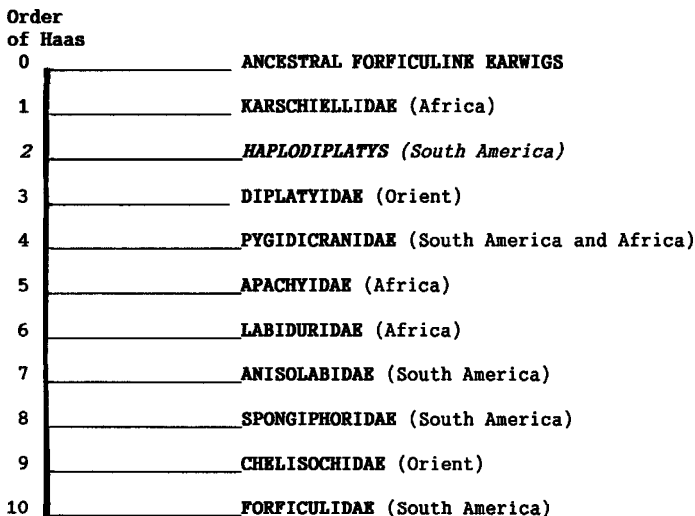 10 ──────────────── FORFICULIDAE (South America)

FIG. 9.   A Cladogram of the Phylogeny of Forficulina Taxa (Haas, 1995).

Chelisochidae and Forficulidae is either due to convergence or it is a homo-
logous apomorphic feature of these four families. Whichever alternative is
correct, it should be reflected in the classification of the Forficulina.

(3) Previous authors have given the Apachyidae a taxonomic status equal to that of the Anisolaboidea Sakai (= Mesodermaptera, Steinmann). In view of this family's limited geographical distribution, and the issues raised in (2) above, it would seem to indicate that the systematic status of this taxon needs to be reconsidered.

The fact that the Anisolabidae and Spongiphorinae have the widest circumtropical geographical distributions, suggests that they represent the main line of forficuline evolution, while the slightly smaller distributions of the pygidicranid and forficulid lines show that they may be later but contemporary developments. Both Popham (1965) and Haas (1995) regard the Karschiellidae as representing an evolutionary line independent of the pygidicranid and diplatid taxa, but further clarification on the status of the pygidicranid subfamilies is probably required.

Forficuline distribution routes
There is ample fossil evidence that several insect orders existed in Laurasia during the Carboniferous, when the Sea of Tethys was partially, if not totally, responsible for preventing any insect migration to Gondwanaland. The paleocontinental maps of Smith *et al.* (1981) show that in the Permian, the southern coast of Europe was sufficiently near the north west corner of South America to allow Laurasian insects to reach north west Gondwanaland. It was here that the Forficulina developed their primary centre of evolution, from whence they spread throughout the southern continents. A study of the distribution of the species of each family suggests that following primary migration routes developed.

From South America earwigs migrated to:

(1) Mexico and North America (Idolopsalinae);
(2) Eastern Caribbean area (Esphaleminae–Pyragra);
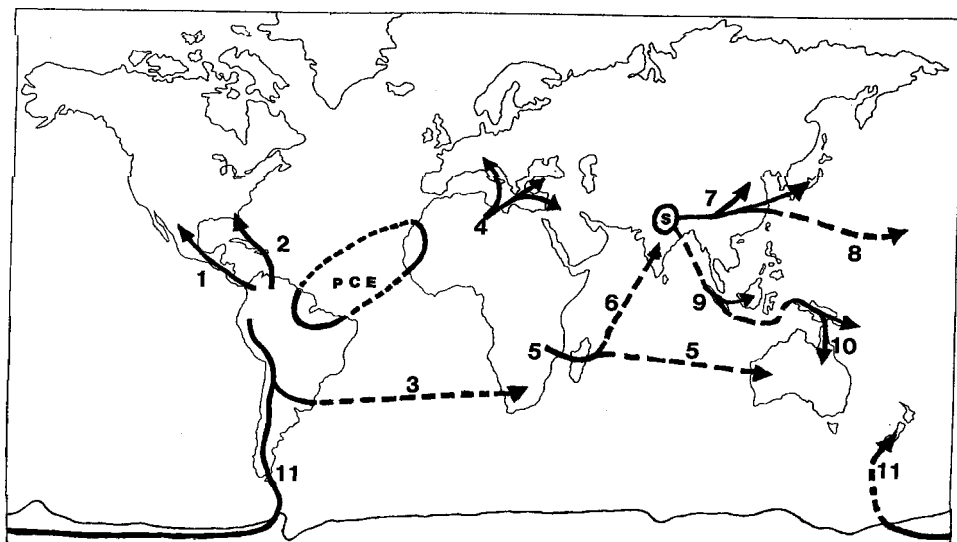
MAP 11.   The main distribution routes of the Forficulina. PCE = Primary centre of forficuline evolution, S = Secondary centre of forficuline evolution, Dotted lines indicate the distribution route of the relevant continental fragment.

(3) Cape Colony–South Africa (Genera Esphalmenus and Blandicinae);
(11) New Zealand and associated islands via Antarctica.

The Anataelinae occur on the Canary Islands and Madeira and was possibly within the primary evolutionary centre of the Forficulina.

From Africa some earwigs migrated to:

(4) Lebanon, Turkey and Greece (Idolopsalinae) and southern Europe;
(5) Madagascar and western Australia;
(6) The Seychelles and Cormora Islands. (Diplatyidae) and India (Labiduridae and Allostethinae).

From India earwigs migrated to:

(7) South of the Himalayas through the deep river valleys of south East Asia, to invade Tibet, China and Japan (Spongiphoridae);
(8) Micronesia and Polynesia (Spongiphoridae);
(9) The East Indies New Guinea (Anisolabiinae and Spongiphorinae).
   From New Guinea to:
(10) Australia (Genera:–Cranopygia, Isolabis, Euborellia, Apachys, Chelisoches, Proreus, and Chaetospania.)

Some species, such as *Forficula auricularia*, L., *Labidura riparia* (Pallas) and *Euborellia annulipes* (Lucas) have become cosmopolitan by being adapted to man made conditions. The main routes of Forficuline distribution are shown on map 11.

In New Zealand, there are eight species of *Parisolabis*, and single species of *Brachylabis*, *Antisolabis*, *Anisolabis* and *Chaetospania*, none of which occur in Australia. The New Zealand species of Parisolabis are allied to the neotropical Idolopsalinae. This suggests that after the Parisolabinae arrived on Antarctica by Route 11, they then migrated south eastwards to reach New Zealand. In contrast, the Australian genera were derived from those in New Guinea by Routes 9 and 10.

In the Cenozoic, New Guinea and Australia drifted northwards, but in the Miocene, the islands of Sumatra and Java were situated immediately to the west of New Guinea and the associated islands. It would seem that a temporary land bridge between these areas then permitted an eastwards emigration of some species of the Anisolabiidae and Spongiphorinae into the area of New Guinea. When this island drifted further northwards to its present position, the temporary land bridge was broken, but the little kink along Wallace's Line in Route 9 proves its previous existence.

The restriction of the Hemimerina to Africa, is consistent with it being a taxon independent of the Forficulina. In contrast, the Arixenina is restricted to the caves of Java, and other nearby islands. The existence of this taxon in a forficulid migration route in the East Indies, along with the large size of the insects, supports the views Popham (1965, 1985) that the Arixenina is a minor forficuline taxon.

Fossil Dermaptera

Vishniakova's (1980) discovery of several species of *Semenoviola* and other similar insects from Turkestam calls for comment. Much depends upon what is meant by the terms Dermaptera and Forficulina. Terrestrial fossils are seldom so perfectly preserved that their relationships with other taxacan be easily determined. For example, *Protodiplatys fortis* Marytinov is frequently cited as being an early

earwig, yet it has five jointed tarsi and segmented cerci: features which are not typical of the Dermaptera. The present study is restricted to the main stem of the forficuline evolution and leaves it an open question as to whether or not the Asiatic fossils belong to the Forficulina. Jhang Jun-feng's (1996) description of the occurrence of a species of the Echinosomatinae from the Upper Jurassic of China, raises the question how this family reached this area. Here it is relevant to quote Smith *et al.* (1981) who consider that parts of Eastern Eurasia may also have been attached to Gondwanaland (p. 61). *Cretolabis cearae* Popham from the Lower Cretaceous of the Amazon Basin is certainly a member of the Forficulina, but its affinities with any of the existing subfamilies are obscure.

Conclusion

The fact that the Forficulina live in secluded microhabitats and seldom fly, makes them ideal subjects for studying the effects of continental drift upon their geographical distributions. This study on the geographical distributions of forficuline subfamilies and families has indicated topics worthy of further investigation and research. It is hoped that this information will be of interest and value to future students of Dermapteran systematics.

Acknowledgements

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