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On the Taxonomy and Geographical Distribution of the Lithobiomorpha

by

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Abstract: The families, subfamilies and many genera of the Lithobiomorpha are defined and their distribution is described. Suggestions are made as to the possible faunistic connexions at subfamilial and generic levels indicated by the distribution of these taxa. An attempt is made to explain the distribution of the principal genera in terms of their evolution.

1. Introduction:

I will pass over the early attempts to classify *Lithobius* (s.l.), notably those of STUXBERG (1875) and GARBOWSKI (1897), because they have been adequately summarized by ANDERSSON (1979) who reviewed the whole subject of classification. The only aspect about which there is no dispute is the division of the order Lithobiomorpha into two principal taxa, one based on *Lithobius* LEACH in which the forcipular pleurites do not meet each other ventrally and the male gonopods are stout and usually short, and the other based on *Henicops* NEWPORT in which the forcipular pleurites form a ventral collar and the male gonopods are flagelliform. These taxa are regarded variously as either suborders, families or subfamilies.

LEWIS (1981) reviewed the nominal families of the order and their distribution and I will expand on the general outline which he has given. The simplest scheme I can devise to show all the essential relationships is:

Order Lithobiomorpha
- Family Lithobiidae
  - Subfamilies
    - Lithobiinae (to include Watobiidae and Gosibiidae)
    - Pseudolithobiinae
    - Pterygoterginae
    - Ethopolyinae
- Family Henicopidae
  - Subfamily Henicopinae
    - Tribes
      - Henicopini
      - Zygethobiini
  - Subfamily Anopsobiinae

2. Lithobiinae:

The vast majority of species and nominal genera of Lithobiidae, which is an essentially holarctic family, belong to the Lithobiinae and, as I said at Manchester during our second Congress (EASON 1974 a), their generic classification is bedevilled by a number of factors. Some generic names were proposed in the past without designation of type-species, and may have been adopted by subsequent authors to apply to groups of species other than those originally intended: even where a type-species was designated the genus may have been redefined to exclude it. Other genera are based on characters which may be reasonably stable intraspecifically but, when used to define a genus, lead to the grouping together of a number of unrelated species. Yet others are based on unstable characters of even on single abnormal specimens.

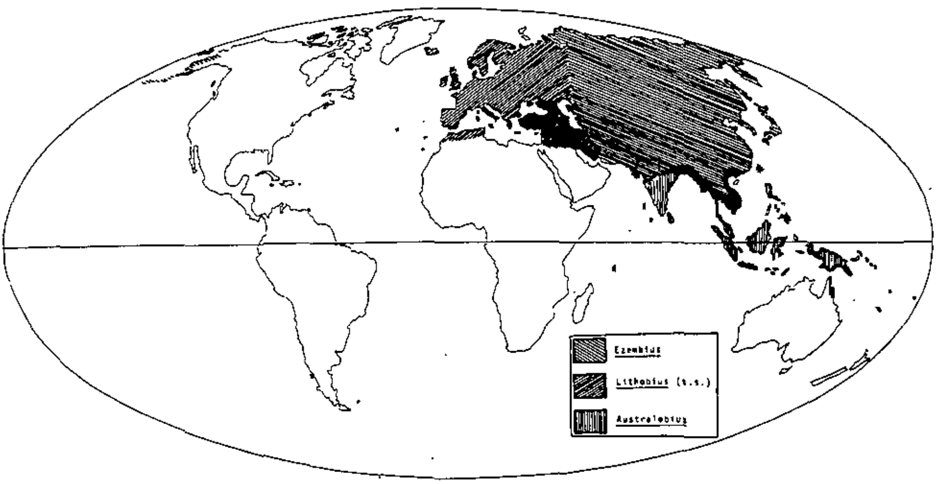
Lack of co-operation between authors on either side of the Atlantic is a further source of confusion. CHAMBERLIN, by far the most prolific American author who also wrote on Middle Eastern, oriental and Australian species, gave an account of Turkish species (CHAMBERLIN 1952) and subjected them to a system of classification which I find partly acceptable but which is not accepted by other European authors. VERHOEFF, the most prolific European author who also wrote on American and oriental species, took little account of CHAMBERLINs work and duplicated some of it, naming a number of redundant taxa. Add to this the fact that palaearctic species of *Lithobius* have been introduced to America and elsewhere, some being placed by CHAMBERLIN in genera to which they do not belong, others being made type-species of new genera by CHAMBERLIN, and one can understand how such vast confusion has arisen. For example the ubiquitous *Lithobius obscurus* MEINERT has spread from its natural range in the western Mediterranean region to New Zealand, Australia, South Africa, Bermuda and most of the maritime countries of South America: this species has been given six different names in the genus *Lithobius* and, under yet more specific names, has been made the type-species of three other genera (EASON 1974 b).

A total of 140 genera and subgenera (I shall not distinguish between the two) of Lithobiinae have been named, 105 of them by CHAMBERLIN and 70 of these from North America. Many North American species were originally described in the genus *Lithobius*: the few which have not since been removed by CHAMBERLIN to other genera and remain in *Lithobius* (sensu CHAMBERLIN 1925 b) are probably introduced from the Old World and the same may apply to other supposedly amphiatlantic genera (see EASON 1974 a). Some of CHAMBERLINs American genera are well-defined with numerous species, many are monotypic and a few are of doubtful validity: most of them are nearctic but a few genera, all among those placed by CHAMBERLIN in the controversial family "Gosibiidae" (see CHAMBERLIN 1917), are found in the northern part of the neotropical region. All those from the South American continent are, I believe, based on introduced European species such as *L. obscurus* except for *Atethobius* CHAMBERLIN, described originally from Mexico but also represented by *A. weyrauchi* TURK, a species which may be truly indigenous in Peru (see also KRAUS 1957). The small species from southern states of the U.S.A. and Mexico, which CHAMBERLIN (1914) placed in the "Watobiidae", are characterised by almost total absence of spines on the legs: this condition is found in some small European species of Lithobiinae and, by itself, is neither a familial nor a subfamilial character.

In the Eastern Hemisphere the Lithobiinae are found throughout the palaearctic and much of the oriental regions, the most striking feature of their distribution being the difference between the fauna west and east of the Ural Mountains. In Europe and North Africa the larger species with distinct tarsal articulations on the anterior legs have the antennal articles well in excess of 20 with considerable intraspecific variation in their number, and remain at present in *Lithobius* (s.s.) except for a few which belong to other well-defined genera such as *Pleurolithobius* VERHOEFF and *Harpolithobius* VERHOEFF, the latter having been raised to subfamilial status by MATIC (1983). A number of other genera have been named but I do not consider all of them to be valid. On the other hand *Lithobius* (s.s.) as at present constituted is a very heterogeneous assemblage of species and it is possible to recognize several speciesgroups within it worthy of generic or subgeneric status. Among these is *Alokobius* ATTEMS as originally defined (ATTEMS 1926) which most authors disregard but which I now believe I was quite wrong to decry as an unnatural group (EASON 1974 a). However, there remain some species which might have to be placed in monotypic genera, and others which I have not examined and which have been so inadequately described that they cannot be placed at all, so I have hesitated to publish my conclusions.

The smaller species with fused tarsal articulations on the anterior legs are placed by most authors in *Monotarsobius* VERHOEFF regardless of the number of their antennal articles. I have explained in a previous paper (EASON 1974 b: 9) why I believe that only those species with the number of these articles fixed at 20 or thereabouts should be placed in *Monotarsobius*, and that the others with a larger more variable number of articles, which comprise the majority of small European species largely confined to Italy and the Balkans, should be referred to *Sigibius* CHAMBERLIN.

East of the Urals and in the oriental region the picture is quite different. Apart from a few from Formosa, Kyushu (Japan), an area comprising part of southern China and eastern Indo-China (Map 1) and Hawaii (EASON 1977), all the larger known species of Lithobiinae with distinct tarsal articulations on the anterior legs have the number of antennal articles fixed at 20 or thereabouts with little intraspecific variation. One or two very distinctive central Asiatic species have been placed in the genus *Disphaerobius* ATTEMS, others in the rather less well-defined *Schizotergitius* VERHOEFF, also from central Asia (see EASON 1986 a), yet others from Japan, Korea, north-eastern China and the Soviet Far East in *Chinobius* VERHOEFF (see MATIC 1973 a). Most of the larger oriental species of the subfamily, some of which have fused anterior tarsal articulations, belong to the fairly well – defined genus *Australobius* CHAMBERLIN which also occurs in the Seychelles (usually regarded as part of the Ethiopian region but see EASON 1978) and across Wallace's Line in New Guinea and northern Queensland (Map 1): a few palaearctic species have been placed in *Australobius*, all, I believe, by mistake (EASON 1978). ATTEMS (1938) regarded the North American genera *Gonibius* CHAMBERLIN and *Zinapolys* CHAMBERLIN as synonyms of *Australobius* but I find this synonymy unconvincing.



Map 1: World distribution of species of *Ezembius*, *Lithobius* (s. s.) and *Australobius*. – Although the distribution of the genera shown is based on recorded localitiers, the exact areas are, to some extent, presumptive.

The remaining larger Asiatic species of Lithobiinae which constitute the majority have been placed by most European authors in *Paobius* CHAMBERLIN, but I have explained (EASON 1974 b: 30) why this group of species should be referred to *Ezembius* CHAMBERLIN which extends from the Urals across Siberia and central Asia to China, Japan and Alaska, and southwards into the northern Indian subcontinent and the northern part of the oriental region where it overlaps the range of *Australobius* but does not extend so far south (Map 1).

Like the European *Lithobius* (s.s.), *Ezembius* (sensu EASON 1974 b) is a rather heterogeneous assemblage of species and may be divisible into a number of more natural groups. But these Asiatic species need to be separated from their European counterparts and *Ezembius* is a useful, though possibly not an altogether natural, division.

The smaller Asiatic species, with fused anterior tarsal articulations, also have the number of antennal articles fixed at 20 or thereabouts, some with the number constant at 17. Apart from *Dakrobius* ZALESSKAYA, a monotypic genus containing an unusual species from the Soviet Far East without coxal pores on the 12 leg (ZALESSKAYA 1975), all the known species belong to *Monotarsobius* whose distribution is much the same as that of *Ezembius* except that several species are known from west of the Urals, the most westerly being *Lithobius curtipes* C.L. KOCH (the type-species of *Monotarsobius*), *L. crassipes* L. KOCH and *L. aeruginosus* L. KOCH which are all common in western Europe. As I have said a number of times (EASON 1976, 1986 b), the distinction between *Monotarsobius* and *Ezembius,* depending as it does on size and the state of the anterior tarsal articulations, is probably artificial though convenient. The only species of *Sigibius* from east of the Urals that I know of, *L.* (*Sigibius*) *bullatus* EASON, is known from Hong Kong (EASON 1991) and has recently been found inland in southern China (EASON unpublished).

Some of CHAMBERLINs genera, as far as one can tell from their brief descriptions, are indistinguishable from *Monotarsobius.* For example *Nipponobius* from Japan which I have already proposed as a synonym of *Monotarsobius* (EASON 1976), *Onebius* from Ocean Is. in the Pacific (see EASON 1977) and *Helembius* from Louisiana, U.S.A. (CHAMBERLIN 1918). But these ill-defined taxa add nothing convincing to our knowledge of the distribution of *Monotarsobius.*

Evidence for essentially North American genera of Lithobiinae occurring in Asia is also unconvincing. *Lithobius* (*Monotarsobius*) *worogowensis* EASON from Siberia is thought by ZALESSKAYA (1978) to be a probable synonym of *Nampabius japonicus* SHINOHARA from Japan: this may well be so but whether SHINOHARA (1972) was justified in referring *japonicus* to *Nampabius* CHAMBERLIN, which is distributed in the eastern and southeastern states of U.S.A. (CHAMBERLIN 1913) is very doubtful (EASON 1976). ZALESSKAYA (1978) also noted the similarity of *Monotarsobius kurchevae* ZALESSKAYA from Asiatic Russia to species of *Pokabius* CHAMBERLIN, a widespread North American genus: but I doubt whether there is sufficient justification for placing *kurchevae* in *Pokabius.* The distribution of *Ezembius* which is an Asiatic genus with only a toehold in North America has already been described and the only other North American genus of Lithobiidae that I know of which has been alleged to occur in Asia is *Arebius* CHAMBERLIN, a Californian genus: two species which I would refer to *Ezembius,* one from Korea and the other from China, were placed in *Arebius* by CHAMBERLIN & WANG (1952) for no apparent reason.

An area which I shall loosely term the Middle East consisting of Turkey, the Levant, Iraq, western Iran and the Caucasus is of special interest in connexion with the distribution of the Lithobiinae. Here we have the European and Asiatic fauna intermingling so that *Lithobius* (s.s.) and *Ezembius* (= *Archeobius* CHAMBERLIN 1952) exist side by side (Map 1). This area also has its own peculiar genus, *Hessebius* VERHOEFF, which is known throughout the region and in the adjacent part of Egypt (EASON 1981). Another species-group, akin to *Australobius* which has not received a name but can be arranged around *L. stuxbergi* SSELIWANOFF and differs from the typical *Ezembius* in having more than 2 + 2 prosternal teeth, seems to be confined to the Caucasus. A final point of interest about the Middle East is that CHAMBERLIN (1952) described two genera from Turkey, *Ottobius* and *Turkobius,* which he believed to belong to the group he called "Gosibiidae" which extends from Idaho and North Carolina to Costa Rica, with one species as far south as Peru but with its centre of distribution in Mexico. The only species I have examined which certainly belongs to *Turkobius* is the common Greek species *L. carinatus* L. KOCH (= *macrops* KARSCH). The structure of the female gonopod which characterises the "Gosibiidae" might, by itself, have no taxonomic significance but a true faunistic link between the Middle East on the one hand, Central America and the southern part of North America on the other, seems likely when we come to consider the next subfamily.

3. Pseudolithobiinae (Pseudolithobiidae MATIC):

This subfamily consists of two genera: *Pseudolithobius* STUXBERG with one species from California and another from Arizona, with 20 - 22 antennal articles; and the monotypic *Osellaebius* MATIC from eastern Turkey with 64 - 72 antennal articles (MATIC 1973 b). The Pseudolithobiinae are characterised by having coxal pores on the last five pairs of legs and in having the female gonopods of such a shape that CHAMBERLIN (1917) placed *Pseudolithobius* in the "Gosibiidae". Coxal pores on the 11th leg are characteristic of the henicopid genus *Zygethobius* and have been found as an abnormality in the common European *Lithobius forficatus* (L.) by MATIC (1958: Fig. 9). This character does not, therefore, by itself indicate a monophyletic origin for the species possessing it; but the other characters common to the two genera of Pseudolithobiinae leave little doubt that they belong to the same natural group and lend strong support to the idea of an American/Middle Eastern faunistic link.

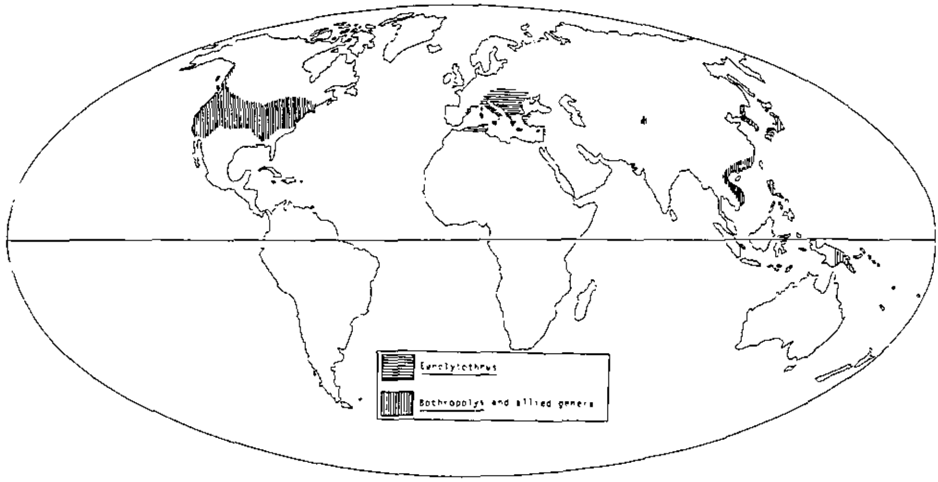
4. Pterygoterginae (Pterygotergidae VERHOEFF):

This subfamily consists of a single monotypic genus, *Pterygotergum* VERHOEFF, from Sinkiang (China), which differs from the Lithobiinae in the shape of the large tergites in the male, notably the enormous lateral expansion of the 12th tergite (VERHOEFF 1934). A similar but less marked modification of the tergites is found in the Asiatic *Disphaerobius* and the Mexican *Atethobius*, both of which remain at present in the Lithobiinae. Like most Asiatic species of Lithobiidae, *Pterygotergum* has only 20 antennal articles.

5. Ethopolyinae (Ethopolidae CHAMBERLIN):

The fourth subfamily, whose species have numerous irregularly arranged pores on the last four pairs of coxae, is divisible into two groups; the European *Eupolybothrus* VERHOEFF with numerous antennal articles on the one hand and the Asiatic/North American *Bothropolys* WOOD and allied genera with 20 antennal articles or thereabouts on the other. 22 genera and subgenera of Ethopolyinae have been named, many of them by VERHOEFF who first used STUXBERGs (1875) system depending on the number of tergites with posterior projections for his classification, without designating type-species, and later an altogether different system based on the structure of the male gonopods. JEEKEL (1963, 1967) has regularised the generic classification of the European species and CHAMBERLIN (1925 a) and CRABILL (1955) that of the others.

Eupolybothrus occurs in southern and central Europe, the Balkans, the eastern Mediterranean region, Tunisia and Algeria. The commonest species of *Bothropolys, B. multidentatus* (NEWPORT), is widespread in America north of Mexico but the other American species of the genus and those referred to the allied genera *Ethopolys* CHAMBERLIN and *Zygethopolys* CHAMBERLIN are confined to a region west of the Rockies. *Bothropolys* is also found in central Asia around Tashkent (USSR), eastern and southern China, Indo-China, Korea, Japan, the Philippines, New Guinea and the Hawaiian Is. where it may have been introduced (EASON 1977). The Asiatic and oriental distribution of *Bothropolys* shown on Map 2 may reflect the intensity of collecting and will probably be found to be more extensive. The commonest Asiatic species, *B. rugosus* (MEINERT) (= *asperatus* L. KOCH) is so close to *B. multidentatus* that the two species can only be separated with difficulty.



Map 2: World distribution of species of *Eupolybothrus* and *Bothropolys* (and allied genera). - See note to Map 1.

6. Discussion:

It seems significant that the chief difference between the Asiatic *Bothropolys* and the European *Eupolybothrus*, namely the more numerous antennal articles in the latter, is mirrored by the same character difference between the Asiatic *Ezembius* and *Monotarsobius* and the European *Lithobius* (s.s.) and *Sigibius*. GARBOWSKI (1897) regarded 20 antennal articles as the ancestral condition in *Lithobius* (s.l.) and if we accept this view it may be that the Ethopolyinae and Lithobiinae became differentiated from each other in central Asia at a relative early stage of evolution, both retaining primitive antennae of 20 articles, and then spread to Europe, both groups acquiring more articles. It is well known that when lithobiids take to cave-dwelling one of the first distinctive characters they acquire is longer antennae with more articles than their surface-dwelling relatives, presumably in response to their greater need for an efficient tactile organ. It is therefore tempting to assume that the acquisition of more articles, without necessarily any increase in the length of the appendage, makes the antenna more flexible and more efficient in response to some environmental pressure exerted on the European *Eupolybothrus*, *Lithobius* (s.s.) and *Sigibius* but not on the Asiatic *Bothropolys*, *Ezembius* and *Monotarsobius*. The fact that a few species which, by my definition, belong to *Lithobius* (s.s.) and one to *Sigibius* are found in outlying parts of Asia suggests that here too conditions affecting the evolution of lithobiids are similar to those in Europe. Why a few very small species of *Monotarsobius*, mostly from Japan, have the antennal articles reduced to 17 is difficult to explain unless it is a function of the small size of the animal.

If the above speculations have any validity, what is the nature of the environmental pressure leading to an increase in the number of antennal articles? One possibility is that, over the ages, Europe and outlying parts of Asia have suffered more upheavals resulting in more caves and crevices than in Central Asia where conditions are likely to have remained relatively stable. On this assumption species with numerous antennal articles would, of course, have to have cave-dwellers or crevice-dwellers in their ancestry. However this may be, a striking feature of the range in the number of these articles in the Lithobiidae as a whole is its marked discontinuity. There are some species in which the number is fairly constant at 17 or 19, numerous species in which it is 20 with little variation, very few in which it seems typically to be 22 or 23 but very many in which it is 24 or more (often many more) with considerable intraspecific variation. This discontinuity makes it fairly easy to separate *Bothropolys* from *Eupolybothrus*, *Ezembius* from *Lithobius* (s.s.) and *Monotarsobius* from

Sigibius. But, assuming GARBOWSKI to be correct, 20 antennal articles is a plesiomorphic character as ANDERSSON (1979) has pointed out, and does not necessarily indicate a monophyletic origin for the species possessing it. Furthermore, an increased number of these articles is essentially functional and does not indicate a close phylogenetic relationship between *Eupolybothrus* and *Lithobius* (s.s.); nor does it suggest that the few species of *Lithobius* (s.s.) found in Asia must be of European origin; nor yet does it mean that the two genera of Pseudolithobiinae are not closely related because *Osellaebius* with 64 - 72 antennal articles is probably a cave-dweller or may have a recent cave-dwelling ancestor.

It will be said that a system of classification based largely on either plesiomorphic or functional characters has little value. But it is eminently practical and provides a useful framework pending the definition of smaller more natural taxa. There are, of course, a few species which do not fit in exactly with this rather arbitrary scheme such as *Lithobius hispanicus* MEINERT from Spain with 18 - 27 antennal articles, but they are a small minority and do not alter the overall picture.

The North American Lithobiinae include many genera with antennal articles well in excess of 20 and therefore equivalent, in this respect, to the European *Lithobius* (s.s.) and *Sigibius*, and even more with these articles almost constant at 20 and therefore equivalent to the Asiatic *Ezembius* and *Monotarsobius*. If one considers the geographical distribution of these genera relative to the number of their antennal articles a pattern, albeit a rather vague one, does seem to emerge. The majority of genera confined to a region west of the Rockies have only 20 articles whereas east of the Rockies and elsewhere in North America the two groups of genera are more equally matched. Assuming that the Lithobiinae evolved in Asia it is not too fanciful to suggest that the further they spread east and south after crossing into North America, the more antennal articles many of them acquired.

7. Henicopidae:

Unlike that of the Lithobiidae, the classification of the Henicopidae seems to have met with general agreement except for the inevitable difference of opinion as to what rank should be given to the various taxa. Species of Henicopidae are known from all the continents expect Antarctica and the family replaces the Lithobiidae in the temperate parts of the Southern Hemisphere where the latter family, apart from introduced species, is unknown. There are 20 genera of Henicopidae known to me, about half of them monotypic and most of them summarised by ATTEMS (1928).

The Henicopini comprise nine genera. *Lamyctes* MEINERT is the most widespread and *L. fulvicornis* MEINERT, which may originate in Australia, has been found throughout the temperate parts of Europe and North America including Greenland (BÖCHER & ENGHOFF 1984), probably having spread so widely because throughout most of its range it reproduces parthenogenetically. Other species of *Lamyctes*, some of which are based on variable characters and may be conspecific with *fulvicornis*, are known from the Southern Hemisphere and the tropics. *Lamyctinus* SILVESTRI is widespread in the tropics and subtropics of both the Old and New Worlds but in temperate regions it is usually synanthropic. *Paralamyctes* POCOCK is known from New Zealand, New Caledonia, South America and South Africa where *P. spenceri* POCOCK, a fairly large species, occupies much the same niche as *Lithobius forficatus* in Britain. *Henicops* NEWPORT is known from New Zealand, Australia and Tasmania, *Wailamyctes* ARCHEY from New Zealand and Tasmania and the other genera from one country only: *Haasiella* POCOCK from New Zealand, *Lamyctopristus* ATTEMS from South Africa, *Triporobius* SILVESTRI from India and *Pleotarsobius* ATTEMS from Hawaii.

The six genera of Anopsobiinae are characterised by having pores only on the last two pairs of coxae and a lobate process on the last pair. *Anopsobius* SILVESTRI is known from New Zealand, Tasmania, South America and South Africa, *Dichelobius* ATTEMS from Australia and New Caledonia, *Tasmanobius* CHAMBERLIN from Tasmania, *Catanopsobius* SILVESTRI from South America, *Shikokuobius* SHINOHARA from Japan and *Ghilaroviella* ZALESSKAYA from

Tadzhikistan (USSR). The overall distribution of the Henicopini and Anopsobiinae is not dissimilar, that of *Paralamyctes* and *Anopsobius* indicating a faunistic connexion at generic level between Australasia, South Africa and South America (see BRINCK 1960), although the possibility of introduction must be borne in mind. The controversial genus *Anopsobiella* ATTEMS from Indo-China was placed by ATTEMS (1938) in the Anopsobiinae, but SHINOHARA (1982) believes it may prove to belong to the Henicopini.

The distribution of the Zygethobiini, which differ from the Henicopini in having the first pedal segment without stigmata, is in marked contrast to that of the rest of the Henicopidae, being largely confined to the Northern Hemisphere. Of the four genera, *Zygethobius* CHAMBERLIN which has pores on the last five pairs of coxae, and *Buethobius* CHAMBERLIN are known only from North America and *Hedinobius* VERHOEFF from the Tien Shan Mts. in western China. *Esastigmatobius* SILVESTRI is widespread in Asia, being known from Japan, Formosa, Korea, Indonesia and the central Asiatic Soviet Republics.

This rather fragmentary account of the distribution of the Henicopidae is obviously very incomplete because I am less familiar with the family than I am with the Lithobiidae and may have missed some of the literature. I have collections of Henicopidae from various parts of the world which I have not yet had the competence to identify or describe, but which I am sure to contain new species and probably new genera.

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