

THE GEOGRAPHICAL DISTRIBUTION OF NEOTROPICAL AND ANTARCTIC COLLEMBOLA

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Abstract: Observations are made on (i) geographical gradients in the proportions of dark and pale species, (ii) the present knowledge of the collembolan faunas in the different regions, (iii) the splitting and lumping criteria, (iv) specific and generic endemism, (v) "paleantarctic" lines, and (vi) the relationships between the Neotropical Region and other regions of the world.

Springtails: an example of ancient distribution

Collembola is the most abundant—in number of individuals—and the best dispersed group of insects. Its biogeography, however, is poorly known. Handschin (1926, 1927) and Salmon (1949, 1951) published short papers on the subject, and other brief observations were made (Bödvarsson 1957, 1966; Carpenter 1916; Folsom 1901; Hammer 1953a, 1953b; Massoud 1967; Mills 1939; Schött 1893; Skorikow 1900; Uchida 1954; Womersley 1939). As occurs with the majority of invertebrate taxa, the knowledge we have on the collembolan fauna of the world is far from being complete and therefore the conclusions presented here are rather tentative.

The order Collembola is very primitive. The most ancient fossil record of insects, i.e., *Rhyniella praecursor* from the middle Devonian belongs to this group. Unfortunately, between this finding and that of the Baltic amber, or Tertiary, there is a hiatus which does not permit any clear idea of the possible evolution and migration of these animals. Between the above two findings we have only *Protentomobrya walkeri*, from the Cretaceous of Cedar Lake (Manitoba) which, by itself, constitutes a separate family—Protentomobryidae (Folsom 1937; Delamare & Massoud 1968). Although this specimen seems to be a juvenile it is undoubtedly related to the Entomobryidae and Isotomidae despite the fact that the antennae are similar to the more primitive Poduridae. On the other hand, the Baltic amber fossils belong to living genera and even to living species, such as *Hypogastrura protoviatica*, *H. intermedia*, *Isotoma protocinerea*, *I. crassicornis*, *Tomocerus taeniatus*, *Entomobrya pilosa*, *Lepidocyrtus ambricus*, *Orchesella eocaena*, *Sminthurus succineus*, *Allacma plumosetosa*, *A. plumosa*, and *A. setosa*. Contrary to the situation with other insect groups, the species mentioned above are of boreal distribution and do not show indications of foreign elements such as those identified as Gondwanian by Jeannel (1961). Noteworthy among the Baltic amber springtails are, in fact, the typically northern-hemispheric genera *Tomocerus* and *Orchesella*.

The particular case of *Palaeosminthurus juliae* (Pierce & Gibron 1962) discovered in Miocene nodules from California merits a special comment. This anomalous specimen has such singular characteristics as (i) four simple ocelli between the ocular patches, (ii) reduction or disappearance of the second and third pair of legs, (iii) presence of ensiform mandibles in the suborder Symphyleona, (iv) spiracular openings in mesothorax, metathorax, and first abdominal segment, and (v) absence of a ventral tubus. All of these characteristics are unknown in the Collembola; moreover, judging from the author's drawing, one has the impression that the remains, con-

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sidered by Pierce & Gibron to be of an entire body, only correspond to a thorax, and, that the "furcula" seems to be a hind leg.

The Problematics

Northern and Southern Hemisphere Forms

The center of origin of Collembola is unknown, although this does not present an obstacle to drawing conclusions on the possible origin of some families and genera. We do not believe there are well-founded reasons to suppose that Collembola originated in southern Europe or Asia, as suggested by Salmon, especially if we consider that insect paleontology has scarcely been studied in large areas of southern continents. Analyzing the family Pseudachorutidae (Stach 1949) we see that it is composed of 23 genera—57% of these belong to the Southern Hemisphere, 26% are shared or cosmopolitan, and the remaining 17% are distributed in the Northern Hemisphere although concentrated in the tropical and subtropical fringe. Of the family Brachystomellidae, 60% are austral, 25% boreal, and 15% cosmopolitan genera.

Although the above-mentioned families are not universally accepted, they illustrate certain tendencies which should not be overlooked. Certainly there are some almost typically northern-hemispheric taxa such as Dicyrtomidae, Tomocerini, and Neogastruridae. The latter, for example, has 56% northern, 33% cosmopolitan, and 11% southern species. However, here, it is convenient to concentrate on austral forms. A subfamily, Spinothecinae, is found only in the Southern Hemisphere, distributed in New Zealand and Araucania. "Araucania" is used here to designate the southern Andean forests and moorlands, including Tierra del Fuego and Malvinas (Falkland) Islands. Also, the Katiannini group of the family Sminthuridae is predominantly southern.

Geographical gradients

The term "Gloger's Rule" was originally used to compare forms belonging to the same species and it has proven especially valid for warm-blooded animals. Apparently, a sort of "inverse Gloger's Rule" is observed in collembolans, that is, at higher latitudes the pigmentation is darker and more intense. In our collections we had opportunity to compare faunulae from tropical (Amazonian rain-forest, Venezuelan savannas), temperate (pampas) and cold (Antarctica) climates and were surprised to note a predominance of light colors in the tropical samples and strong melanism in the Antarctic ones. There are certainly exceptions, as *Sminthurinus mime*, a totally black species from central Argentina, and *Cryptopygus caecus*, a totally unpigmented blind species from the Subantarctic islands. The general aspects, however, of the samples or collections taken in different areas were at first sight plainly unlike.

In order to verify this impression, a roughly semiquantitative method was applied by classifying the species into four degrees of pigmentation—dark, medium dark or somber, light or pale, and white. Published data provided valuable information used to compare material from different latitudes (Arlé 1939; Bödvarsson 1957, 1966; Bonet 1934; Cassagnau 1963; Cassagnau & Rapoport, 1962; Christiansen 1963; Delamare Deboutteville 1951; Rapoport & Najt 1966; Rapoport & Rubio 1963; Wise & Shoup 1967; Yosii 1959). In Table 1 the percentages of species with a different degree of pigmentation are given separately for each locality. In some cases the method seemed rather subjective, the main problem being the classification of mottled and patchy species and the bordering cases. In any case, the surface covered by pigment patches or bands was taken into account by a cursory inspection of the iconography available in the literature.

Table 1. Degree of pigmentation at different latitudes: Species percentage

	dark	somber	pale	white
Venezuelan savannas	4.3	21.7	30.5	43.5
Ivory Coast	0	16.0	20.0	64.0
Malay and Singapore	6.7	20.0	53.3	20.0
Bahia Blanca (Argentina)	21.9	25.0	15.6	37.5
Pyrénées (France)	18.4	26.3	21.1	34.2
Bretagne (France)	12.5	25.0	31.2	31.3
Patagonian woodlands	27.4	17.7	25.5	29.4
Santiago (Chile) and La Plata (Arg.)	30.3	20.9	20.9	27.9
Iceland	20.0	32.8	23.6	23.6
Cape Hallett (An- tarctica)	100.0	0	0	0

The percentage of the four different degrees of pigmentation does not give a completely clear picture of the problem, but with a summing-up of the figures given under "dark" and "somber" on one side, and "pale" and "white" on the other, a correlation does seem clearly established between degree of pigmentation and geographical situation. Fig. 1, to which four other local faunulae were added, illustrates the relationship.

With respect to Bergmann's rule (body-size increase in colder regions) and Allen's rule (shortening of appendages in colder regions), we could not prove their applicability to spring-tails. In general, it appears that latitude does not influence the size of collembolans, but the habitat indeed does. Prairie species are generally smaller than forest species, as forests are normally where giant species are found. At least, this is applicable to Argentina where the larger species abound in the Patagonian and subtropical northern forests and none of the kind are found in the Pampa's steppes.

Present knowledge of the Collembolan faunas

If we begin with the world index of Collembola compiled by Salmon (1964) where 396 genera and 3424 species are registered, and include our file data to 1968, we have a total of 416 genera and 3874 species. Due to the fact that Salmon's work is scarcely a critical one, it is almost certain that the above-mentioned figures may be somewhat reduced. The mean number of species per genus for the total order Collembola would be 9.3.

The number of subspecies—which sometimes gives an indication of the evolutionary potentialities—greatly varies in the different families. Table 2 shows the number of subspecies described, taken from Salmon's index.

Although the concept of subspecies and of geographical race is not always agreed upon among collembologists, it is in general possible to appreciate a certain relationship between the evolutionary position of the group and its rate of subspeciation. Tomocerids are believed to have evolved further than Entomobryids; the suborder Symphypleona is always considered as modern when compared with Arthropleona; and, the same seems valid for Isotomids and Onychiurids, and for Sminthurids and Neelids. In all of these cases the subspeciation degree is higher in the more evolved groups. It is remarkable, however, that one of the most primitive families of Poduromorpha, i.e., Hypogastruridae, has one of the highest ratios in Table 2. This perhaps explains why they are so abundant and still have success. Today they continue to exhibit a high variability among populations as, for example, with *Hypogastrura manubrialis*, a very primitive but variable and ubiquitous species (Rapoport & Izarra 1962).

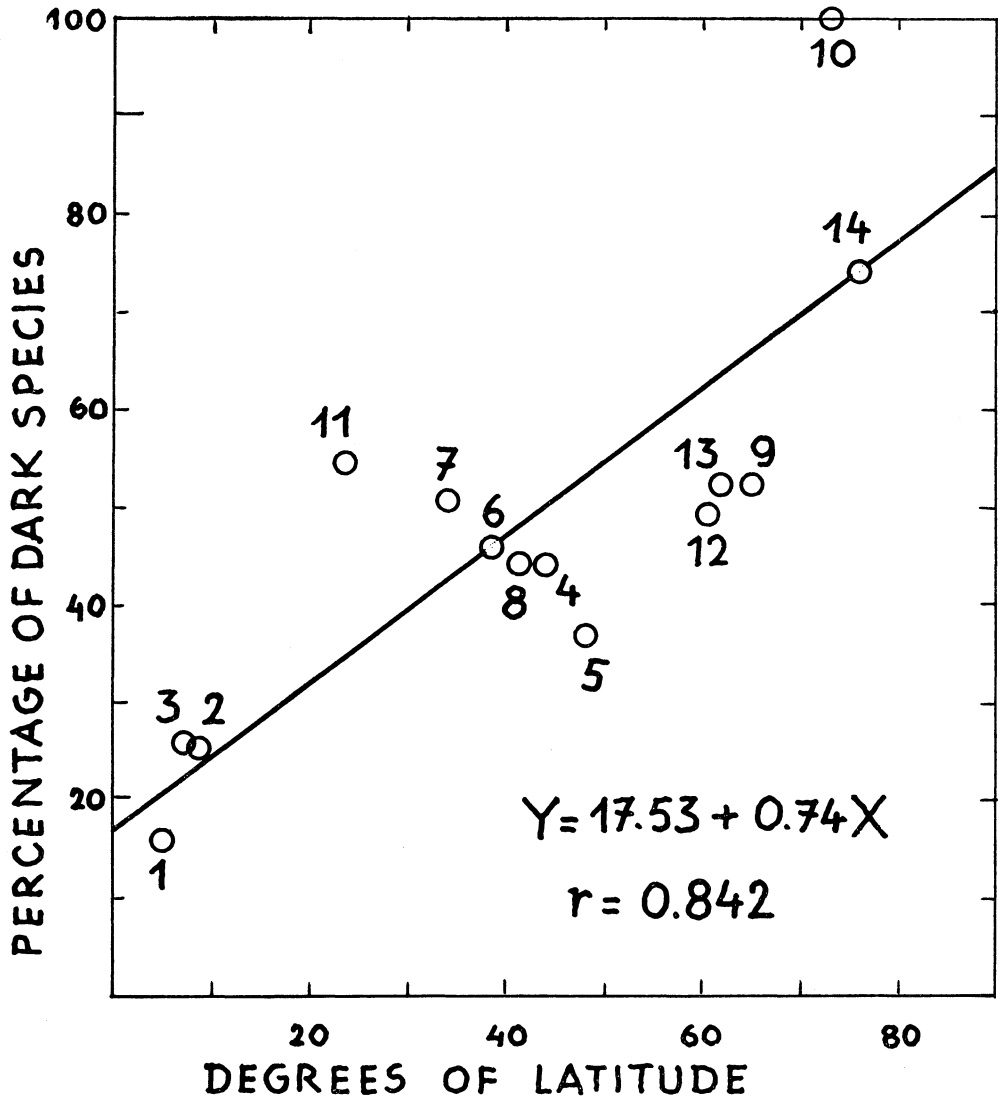


Fig. 1. Degree of pigmentation as a function of latitude. Localities are numbered as follows: (1) Ivory Coast, (2) Venezuelan savannas, (3) Singapore and Malay, (4) Pyrénées, (5) Bretagne, France, (6) Bahia Blanca, Argentina, (7) 34°-35° SL at Santiago (Chile) and La Plata (Argentina), (8) Araucanian forests, (9) Iceland, (10) Cape Hallett, Antarctica, (11) Rio de Janeiro, Brazil, (12) South Orkney Is., (13) South Shetland Is., (14) South Victoria Land, Antarctica. The coefficient of correlation is significant for $P < 0.001$.

To date we know 130 genera and 535 species living in the Neotropical Region and, although it seems surprising, the best studied locality up to the first quarter of our century was Tierra del Fuego. This is, of course, not the first case in the history of zoology where an exotic and remote region is first studied, discovering there taxonomic groups later found to

Table 2. Subspecies described for some selected families of Collembola

taxon	number of species	number of subspecies	subspecies percentage
Hypogastruridae	283	63	22.3
Brachystomellidae	74	2	2.7
Anuridae	149	16	10.7
Neanuridae	235	19	8.1
Onychiuridae	271	37	13.7
Isotomidae	653	123	18.8
Oncopoduridae	18	0	0
Entomobryidae	1084	189	17.4
Tomoceridae	73	17	23.3
Neelidae	18	1	5.6
Arthropleona (totals)	2881	482	16.7
Symphyleona (totals)	542	174	32.1
Grand Total	3423	656	19.2

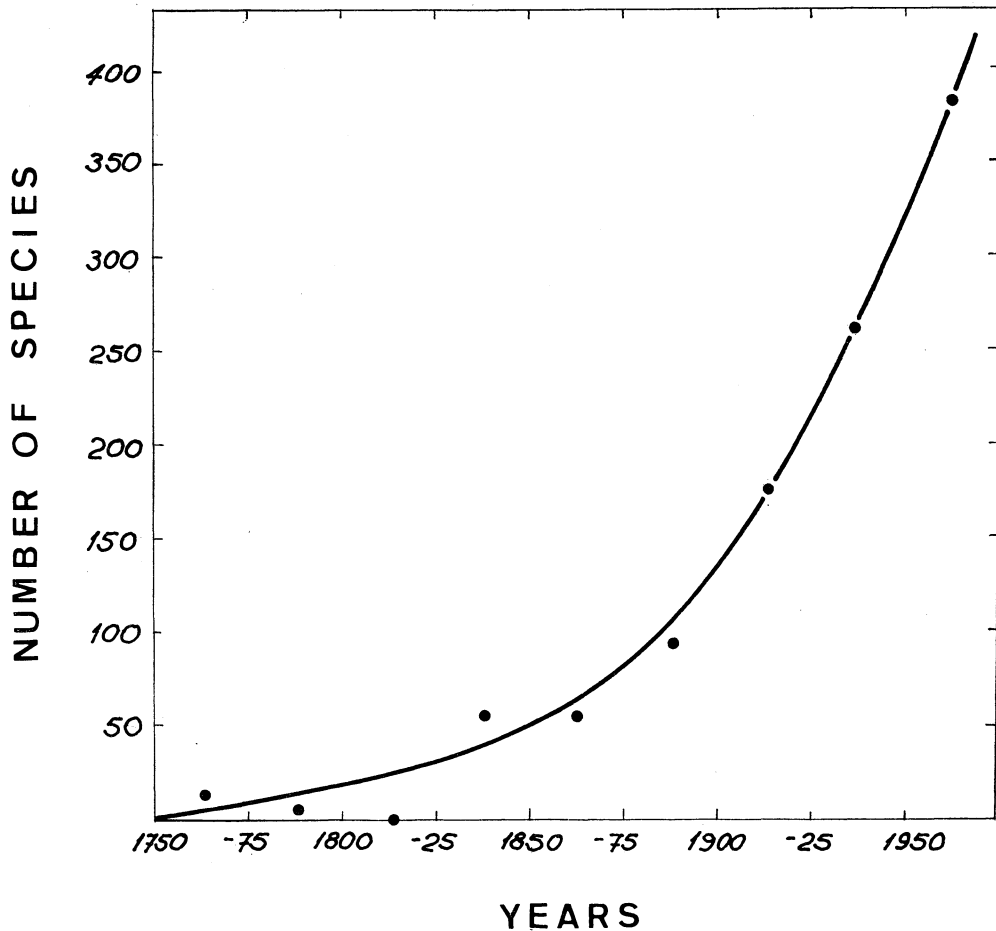


Fig. 2. Number of European species described from Linné to present.

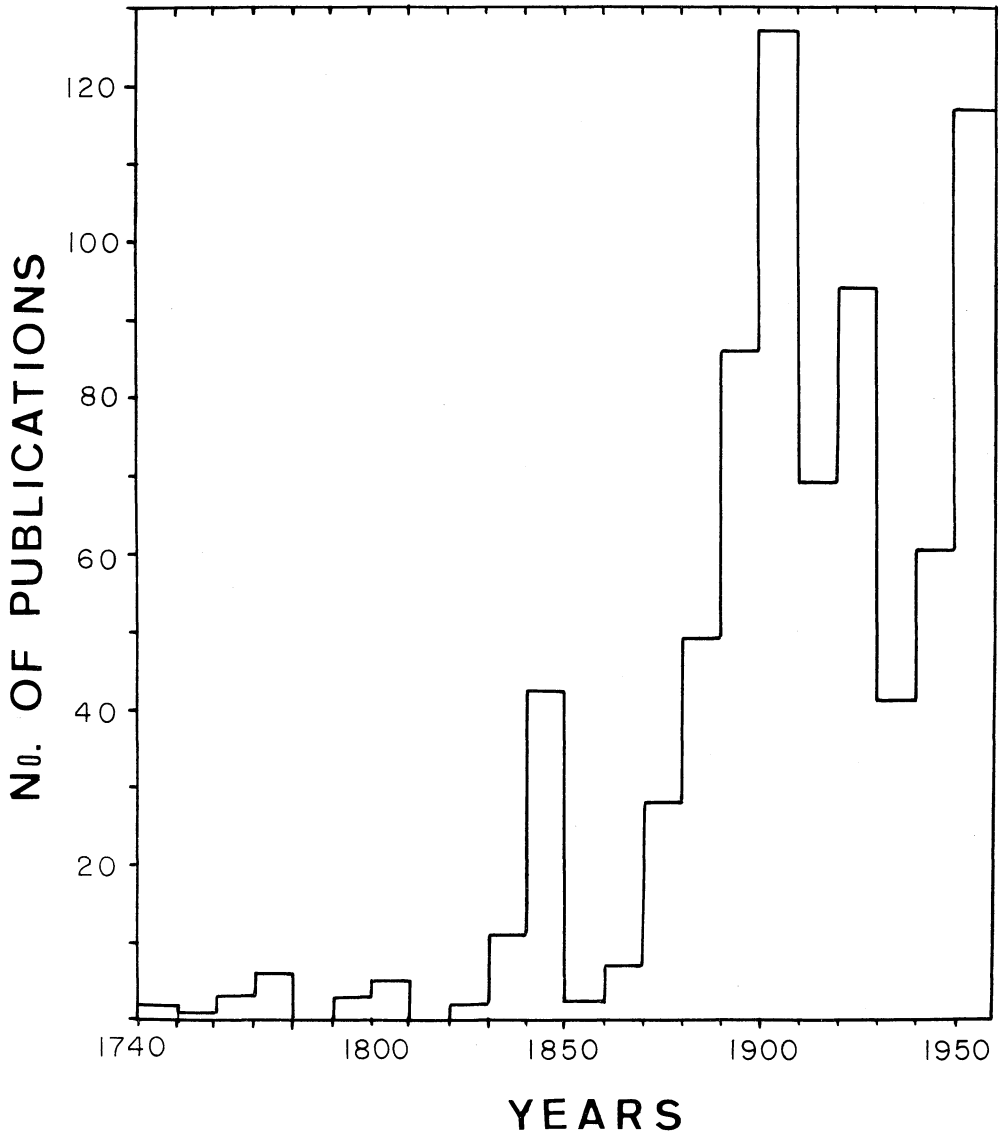


Fig. 3. Number of papers containing information on *Entomobrya nivalis* L. from first mention by DeGeer in 1740. The first notorious decrease (1850-60) corresponds to the withdrawal of Bourlet's and Nicolet's contributions, the second and third ones correspond to World War I & II.

be widely distributed in the world as a whole. Several Central American species described by Denis are examples of this. Other taxonomically studied localities are Rio de Janeiro, Costa Rica, La Plata, Bahia Blanca, some parts of Peru, Patagonian forests, and some superficially explored points in Guiana, Trinidad, Puerto Rico, Cuba, Chile, Venezuela, Bolivia, and Mexico (south of the Anahuac line). Thus far we know only one species from Paraguay and there are

countries still completely unknown such as Colombia and Ecuador.

Therefore, compared with other parts of the world, the collembolan fauna of Latin America has been studied very little. In decreasing order the most studied regions are probably Europe, Japan, New Zealand, Antarctica, North America, South America, Australia, Asia, and Africa. However, if we analyze the general trend in Europe from Linné to the present day (Fig. 2) it is possible to say that far from being stabilized, there is a clear tendency towards increase in the number of new species. Despite the amount of work done there, Europe is far from being well-known from the taxonomical viewpoint. An informative case concerning the progress of knowledge is provided by *Entomobrya nivalis* (Linné, 1758). From its first mention by DeGeer in 1740 to the end of 1959 this species has been cited in 765 publications. The histogram of Fig. 3 represents the number of papers in 10-year periods in which this species has been mentioned. *Entomobrya nivalis* is probably the most frequently mentioned species of Collembola; yet, the knowledge we have about it is still fairly deficient.

At the present time, about 1000 species are recognized for Europe. If we follow the lumping criterium of Gisin, these species can be grouped in 54 genera with a mean of 18.5 species per genus. There are genera with up to 134 (167?) species, this being the case of *Onychiurus*. The splitting criterium is possibly best represented by Stach in his revision of Polish and world fauna. In a comparison of both tendencies we have:

Table 3. Splitting and lumping criteria in Collembolan taxonomy

	number of genera		percentage accepted by Gisin
	Stach	Gisin	
Poduridae	37	15	41
Onychiuridae	14	3	21
Isotomidae	27	17	63
Symphyleona	21	7	33

To compute Poduridae it was necessary to sum up Neogastruridae, Brachystomellidae, Anuridae, Pseudachorutidae, and Bilobidae with 15, 6, 4, 4, and 8 genera, respectively. The mean percentage, accepted by Gisin is 39.5, or, in other words, he made a reduction of almost 60 percent of the genera recognized by Stach. Using the same lumping criterium, we could further reduce the number of Neotropical genera from 130 to about 52, and if we apply the ratio of 18.5 species per genus given in Europe we would then have a total of 962 species in the Neotropics. This presumes, of course, a faunistic knowledge in Latin America equivalent to that of the Old World. This figure of 962, however, does seem rather low since Latin America is not only bigger than Europe but also possesses a wider climatic range—from tropical to cold temperate. Moreover, according to data provided by Schaller (1961) on the Peruvian rain-forest, collembolans present the same phenomenon as plants which, in tropical regions tend to exhibit a greater number of genera with a small number of very dispersed species, that is, with low density of individuals. For this reason the calculation on the possible number of species and genera of Neotropical collembolans is subjected to many variables, and risks unreliability for any purpose.

The Neotropical collembolan fauna is highly endemic, if it is possible to speak of endemism in such a large region. In Table 4 the Araucanian subregion (or region) is separated for comparison. By Neotropical *sensu lato* we understand the Neotropical *sensu stricto* plus Araucania.

As could be predicted from its larger surface area, the Neotropical Region *sensu lato* has a higher

Table 4. Species, genera, and endemism

region	no. of genera	no. of species	no. of endemic genera	no. of endemic species	generic endemism (%)	specific endemism (%)	spp/gen
Araucanian	52	104	8	58	15.4	55.8	2.0
Neotropical s. str.	115	341	18	222	15.7	65.1	3.0
Neotropical s. l.	130	535	32	418	24.6	78.1	4.1
Antarctic continent & islands	39	80	7	58	17.9	72.5	2.1

proportion of generic and specific endemism. It is remarkable, however, that the Antarctic continent and islands immediately follow in degree of specific endemism, a fact that gives a good idea of the isolation of these lands. For the sake of comparison it can be contrasted with the 10.3% of specific endemism obtained by Womersley (1939) for Australia, and the 34.2% generic endemism and 85.4% specific endemism shown by the New Zealand fauna, according to data obtained by Salmon. Moreover, if we consider the Antarctic continent separately we have 10 genera, 5 of them endemic, thus giving the highest degree of generic endemism. Of the 17 recorded Antarctic continental species, 8 are endemic, 6 are shared with periantarctic islands, and 3 are shared with these islands and other regions of the world (Fig. 4). This means that Antarctica does not share with other biogeographical regions any species which is not also found in the periantarctic islands. The number of genera and species annotated by us differs from that of Wise (1967) and Gressitt (1967) in that we also included Marion, Crozet, Amsterdam and St. Paul Islands. Despite its proximity to the continent we also considered the South Shetland Islands as part of the periantarctic group.

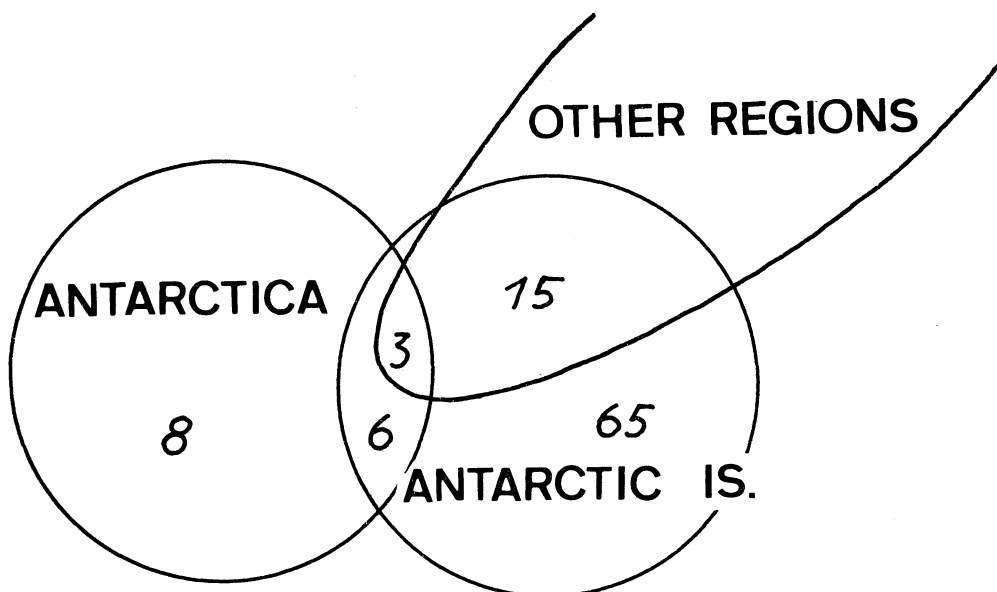


Fig. 4. Number of species shared among Antarctica, periantarctic islands, and other regions of the world.

In summary, the present knowledge of the different subregions is: Araucanian 104, Chilean-Patagonian 173, Guyano-Brazilian 279, Central-American 120, and Antillean 39 species. This last figure clearly shows the lack of knowledge we have of the Caribbean Islands.

Composition of the Neotropical and Antarctic fauna

South America seems to be the center of origin of several genera, and considered together with Antarctica and Australia, it has given origin to at least one family and several lower taxa of Collembola, i.e., Spinothecinae. Probably from the beginnings of the Tertiary, or even earlier, the more important center of speciation moved from the Araucanian to the Guyano-Brazilian biome. As seen in Table 5 both subregions are almost equally abundant in species and genera. Figures indicate the total number of species, and, between brackets, the number of shared species. The following dubious genera, some of them under revision, were not included: *Americotrimeria*, *Biclavella*, *Brachygastrura*, *Handschinia*, *Neorganella*, *Neotropiella*, *Organella*, *Paranurella*, *Portachorutes*, *Pseudostachia*, and *Rapoportina*.

The Antarctic continent and islands contain the following endemic genera: *Antarcticinella*, *Biscoia*, *Gomphiocephalus*, *Gressittacantha*, *Lepidiaphanus*, *Lepidobrya*, *Neocryptopygus*, *Parakatianna*, and

Table 5. Neotropical endemic genera

	Araucanian	Chilean-Patagonian	Guyano-Brazilian	Central-American	Antillean
Araucanocyrtus	1	-	-	-	-
Austrosminthurus	1	-	-	-	-
Brachystomellides	2	-	1	-	-
Brasilimeria	-	-	2	-	-
Cassagnaurida	1	-	-	-	-
Collophora	-	-	1	1	-
Ctenocyrtinus	-	-	2	-	-
Delamarellina	2	-	-	-	-
Dicranocentrella	-	-	-	(1)	(1)
Dicranocentrophia	-	-	-	-	1
Dicranocentrua	-	-	-	-	1
Folsomiella	1	1	3 (1)	(1)	-
Guacharia	-	-	1	-	-
Halachorutes	-	-	1	-	-
Haploisotoma	-	(1)	(1)	-	-
Jacksoniella	-	-	1	-	-
Katiannellina	1	-	-	-	-
Mastigoceras	-	-	1	-	-
Metasinella	-	-	-	1	2
Microgasturella	-	-	-	-	1
Micronella	(1)	2 (1)	(1)	(1)	-
Mucrotoma	(1)	(1)	-	-	-
Notachorudina	1	-	-	-	-
Nothobrya	-	-	1	-	-
Pachytullbergia	1	-	-	-	-
Parastomella	1	-	-	-	-
Probrachystomella	1	2	1	-	2
Setogaster	-	-	1	-	-
Spelaeogastrura	-	-	-	1	-
Tullbergiella	-	1	-	-	-
Winterella	-	-	1	-	-
Yosiella	-	-	1	-	-

Parasinella, the latter being shared with some Pacific islands. In Antarctica there are 17 species, and a total of 80 species including the periantarctic islands embracing Campbell and Macquarie Islands.

In 1962 Salmon reported the most austral² finding of a terrestrial animal, the collembolan *Biscoia sudpolaris* living among filamentous lichens at 83°55' SL. This is an exceptional finding not only from the geographical but also from the evolutionary viewpoint, because the animal represents a relict link between the more primitive Poduridae and the more evolved Onychiuridae. There are also two intermediate genera between the families—*Pachytullbergia* Bonet from the Araucanian subregion, and *Paleotullbergia* Delamare from the Ivory Coast. The former has been considered as Onychiuridae by Bonet and as Poduridae by Cassagnau and Rapoport due to a certain mixture of characters. On the other hand, *Paleotullbergia* seems to be a case of extreme regression among the Poduridae, because of the loss of postantennal organs, eyes, furcula and unguiculus, and by the absence of pseudocelli and anal spines. This genus could be somehow related to Tullberginae but it has nothing in common with Onychiurinae.

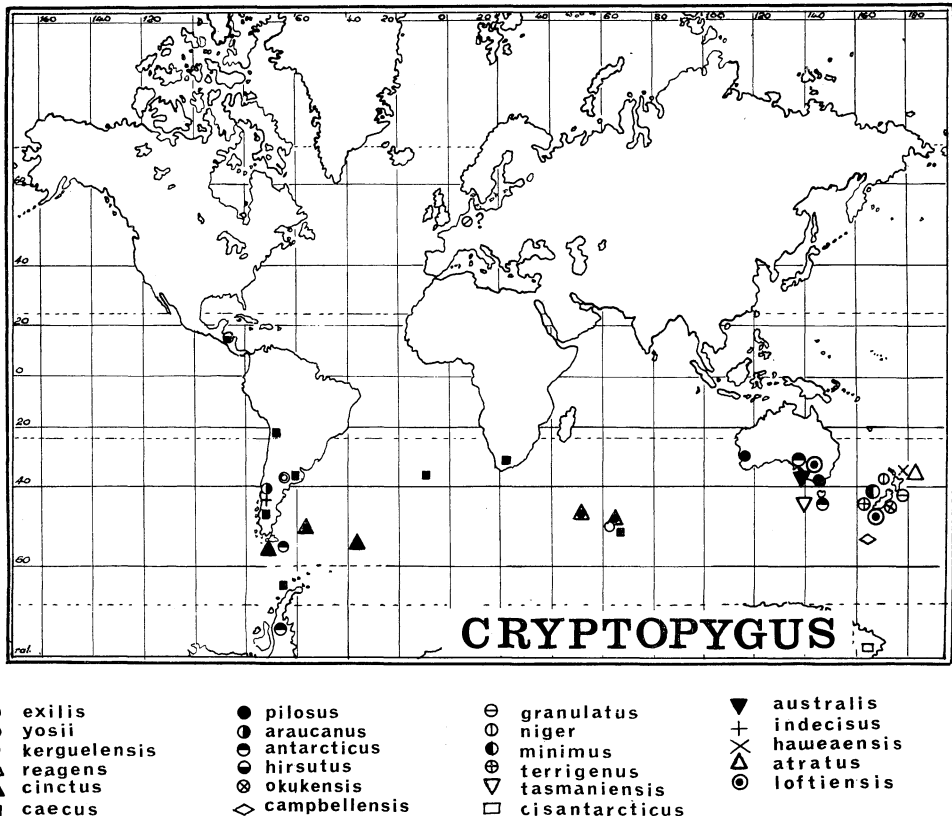


Fig. 5. Geographical distribution of the species of *Cryptopygus* s. str.

2. More southern records have been reported (Wise & Gressitt 1965; Gressitt 1967; Wise 1967): Collembola to 84°47'; Acarina to 85°32' SL (Ed.).

At the same time there is *Tullbergiella* Izarra, a subgenus of *Tullbergia* with an extremely primitive postantennal organ, circular in shape, not elongated as in the other Tullbergines, and composed of numerous perpendicular rods as commonly occurs in Poduridae.

There are three genera, one from Antarctica (*Biscoia*), another from Araucanian forests (*Pachytullbergia*), and a third from the arid Patagonia (*Tullbergiella*) which, because of their intermediate characteristics, suggest the possibility that the southern American cone or perhaps the ancient Paleantarctic continent was the center of origin of the whole family Onychiuridae, or at least the subfamily Tullberginae. This might have occurred during a more favorable climate, and from the Paleantarctic continent this family dispersed over the entire world and diversified.

Another Paleantarctic line is represented by the genus *Cryptopygus* s. str. (Isotomidae). In a recent revision of this genus Massoud & Rapoport concluded that *Cryptopygus* and *Isotomina* are synonyms. However, there is still a small difference between them—*Cryptopygus* has dentes equal to or smaller than the manubrium, a peculiarity which can be ascribed to a subgeneric level. The distribution of species of *Cryptopygus* with this characteristic is depicted in Fig. 5. There are good reasons to suppose that *Cryptopygus* s. str. dispersed from the Paleantarctic continent towards Australia and New Zealand on one hand, and towards South Africa on the other hand; thus, it was the major migration wave through South America. It reached Costa Rica along the Andes by means of the species *C. hirsutus*. The most widely distributed species *C. caecus*, inhabits practically all the periantarctic islands including Campbell, Kerguelen, and Tristan da Cunha; it penetrates South Africa, and South America to Bolivia and Peru in the west, and to central Argentina in the east, or more precisely the Sierra de la Ventana. This is a small group of very old mountains—mainly Paleozoic—completely surrounded and isolated by the flat Pampean steppes, located at the borderlines of the Guyano-Brazilian and the Chilean-Patagonian subregions. A mixture of Brazilian and Araucanian elements are seen there, not only in the invertebrate fauna, but also in such typically austral plants as the *Blechnum* ferns. In addition, there are some Araucanian elements which probably arrived there in one of the Paleantarctic "pulsations" to use Jeannel's terminology. Segregation there produced the genus *Haploisotoma* which is clearly derived from *Cryptopygus* s. str.

According to Table 6 the Antarctic continent and islands have more affinities between them

Table 6. Number of shared species and the correspondent coefficient of similarity (between brackets)

	Arauc- anian	Chilean Patagon.	Guyano Brazil.	Central American	Antillean	Antarc- tica	Periantarctic islands
Araucanian	—	(9.49)	(5.80)	(3.33)	(1.42)	(2.54)	(5.29)
Chilean-Patag.	24	—	(16.20)	(5.78)	(1.44)	(0.53)	(2.06)
Guyano-Brazil.	21	63	—	(7.26)	(2.58)	(0.34)	(0.85)
Cent.-American	7	16	27	—	(6.71)	(0)	(0)
Antillean	2	3	8	10	—	(0)	(0)
Antarctic	3	1	1	0	0	—	(8.24)
Periantarctic	9	5	3	0	0	7	—
Nearctic	1	3	11	16	3	0	0
Palaearctic	5	13	12	8	1	0	2
Ethiopian	0	2	5	7	3	0	0
South African	1	1	1	0	0	1	2
Oriental	0	0	3	2	0	0	0
Australian	2	0	2	1	0	1	4
Cosmopolitan	13	34	26	14	1	0	4

than any other region; above all, they are more related to the Araucanian than with the Neotropical s. str. or the Australian regions. The coefficient of similarity used was that of Sørensen, $Ca = Pab / (Pa + Pb - Pab)$, Pab being the number of shared species, Pa and Pb the number of species living in A and B regions, respectively.

The Palearctic influence, as it was already mentioned, is also seen in South Africa and Tristan da Cunha. In this group of oceanic islands the composition of the collembolan fauna (Rapoport, in press) has been decisively influenced by the European colonization, with 60% European and cosmopolitan species introduced by man. In decreasing order this is followed by endemic species (20%), Holantarctic species (10%), and species of uncertain origin (10%). If we take into account not only the present affinities but also the distribution of the nearest relatives of the endemic species, three migratory waves are outlined: (i) Palearctic, (ii) Araucanian or perhaps Neotropical s.l., and (iii) Holarctic, the latter being mainly man-introduced species.

Relationship of the Neotropical Region to other regions of the world

Relationship to the Nearctic Region: A certain degree of interchange has occurred between these continents via the Antilles and Central America. Wray (1959), for instance, mentions the Central American character of the fauna of Florida. Likewise, Handschin (1927) claims Nearctic influence of the Mexican fauna, especially notable at high altitudes. Thus, he found a variety of *Tomocerus flavescens*, a typical Holarctic element, in the Desierto de los Leones.

Other examples are *Friesea magnicornis*, first discovered in Costa Rica and later in northern Canada. *Willemia intermedia* has been cited for the United States and El Salvador. *W. persimilis* has been found in Mexico north and south of the "Anahuac line" of separation between the Nearctic and Neotropical regions, and has been recently reported in El Salvador and the Cordillera Negra (Peru) at 3480 m above sea level. *Neelides minutus* is also found on both sides of the Anahuac line, extending from the United States to Costa Rica, and in Europe. We have the same situation with *Megalothorax minimus* and *M. incertus*, which are found from Brazil to the United States and Europe in the latter case, and from the United States to southern Mexico in the former. On the contrary, *M. tristani* is restricted to the New World in Cuba, Costa Rica, and the United States. *Micracurida pygmaea* has been mentioned for Europe, the United States and Peru; *Entomobrya atrocincta pseudoperpulchra* for the United States and Argentina. *Seira mexicana* inhabits northern Mexico, Peru and Argentina excluding the Guyano-Brazilian sub-region. *Onychiurus encarpatus* is found in the United States, Costa Rica and Brazil. Sometimes a series of related species are present without, however, constituting a real cline. This is the case of *Isotoma martiniquae*, from Martinica, which is intermediate between *I. pentatoma* from Brazil and *I. constricta* from Florida. *Harmonillsia oculata* is found in Peru, Mexico, and Florida; *Entomobrya cubensis* in Cuba, Puerto Rico, and Florida. The genus *Ptenothrix* also has species covering areas north and south of the Anahuac line.

According to Folsom (1901) 25% of the Nearctic species are also found in the Palearctic Region, but Mills (1939) considers possible an increase in this figure of up to 31% if cosmopolitan species are added. Marshall (1967) reported that 46% of the Canadian species of Collembola are also present in Europe. It is evident that the degree of similarity between Nearctic and Palearctic Regions, although remarkable, is not higher in the Collembola than in other taxa. From Table 6, however, it is possible to extract an interesting point—while the Palearctic influence on South America is stronger than the Nearctic, the reverse occurs in Central America and the Antilles. This is an outstanding example of "vicinity effect", partly due perhaps to

the direct influence of man but mainly to its close proximity to North America.

A notable case of bipolarity is that of the genus *Tomocerura*, probably of austral origin. This genus has four species in the Australian Region, one in the periantarctic islands, two in the Araucanian and one species in Toronto (Canada).

Relationship to the Palearctic Region: As early as 1897 Giard wrote a paper called "Sur le faciès paléarctique des thysanoures du sud de l'Amérique méridionale" in which again he observes—and, as he stated three years earlier—the surprising similarities between Chilean and European collembolan fauna. He supposed correct the ideas of Parona (1895) who suggested that 95% of the Argentinian species of Collembola were Palearctic. Several authors justifiably thought that these species were imported. But the fact is that more than half of Parona's "palearctic" species were really new to science, as was demonstrated by Bonet. A considerable number of imported species were also found, especially within the cities and their surroundings. Of the 83 species known for Bahia Blanca 39.7% correspond to exotic ones, mainly European. Even *Isotoma antennalis*, never cited outside the British Isles, was found by us in the Sierra de la Ventana, a locality where some English farmers live. We have not, however, an explanation for the case of *Friesea oligorhopala* first found in Tripoli and Malta, and later in Bahia Blanca (Argentina) and Santiago (Chile). On the other hand, *Andiella quinquefasciata* was probably exported as it is found in Germany, Switzerland, and France.

The cases of genera and even species shared between the Palearctic and Neotropical Regions are numerous. An example is *Acherontides*, with a species north and south of the Anahuac line and with representatives in Afghanistan and Japan. *Actaetes* has only two known species—*A. neptuni* in Europe and *A. calcarius* in Jamaica. *Caecarrhopalites* extends over Europe, Japan and Araucania. The genus *Folsomia* seems to be typically Palearctic, with 29 species in the Old World, 9 in North America, 6 in Australia and one in the Oriental Region. In the Neotropics there are four species, two of them cosmopolitan, one in Peru and one in Puerto Rico. *Triacanthella* is interesting due to its peculiar distribution. Of the 17 known species, 6 are Mediterranean (mainly France and Italy), 5 are periantarctic, 6 are from New Zealand and Australia, one from Tierra del Fuego and another is shared by Tierra del Fuego and New Zealand. If we follow the arguments of Jeannel, this genus seems to be the relict of a group inhabiting the northern (Tethyan) and southern coasts of the ancient Gondwanaland. Other shared, typically Palearctic genera are *Anurida*, *Hypogastrura*, *Friesea*, *Onychiurus*, *Isotoma*, *Oncopodura*, *Pseudosinella*, *Ptenothrix*, *Sminthurus* and *Arrhopalites*, including also several cosmopolitan species. Conversely, Neotropical genera shared by both regions are *Brachystomella*, *Seira* and perhaps *Cyphoderus*.

A case of bipolarity is provided by *Vertagopus arboreus*, from Europe and Tierra del Fuego, although the possibility of it being a man-introduced species is also feasible. Certainly, the frequently mentioned example of *Archisotoma besselsi* from northern Atlantic coasts and periantarctic islands, is no longer merely bipolar due to its recent discovery in Trinidad and Rio de Janeiro.

Although the Palearctic influence upon the Neotropical fauna is appreciable, its real significance is overlooked due to the fact that the European fauna is better studied. In general, the areas best studied in South America are surrounding the cities where the number of imported species is higher. Supposedly, as new undisturbed localities are studied the ratio Palearctic/Neotropical forms will decrease. By illustration, 20.6% of the 97 species studied by Winter (1963) in Peru are common to Europe, and 52.6% are new to science; and, of the 125 species

mentioned in the series "Biologie de l'Amérique Australe" only 16.0% are European or Palearctic and 43.2% are new. One must acknowledge the introduction of living plants, with their complete associated faunulae, which has been carried out in Latin America since the Spanish conquest and colonization and sometimes it is difficult to determine whether a species is a cosmopolitan or a man-introduced one. It is significant that in the Pampean area, for example, almost all the ornamental trees are European or Asiatic. For purposes of comparison, it is useful to know that the number of European species of Collembola introduced into Australia, according to Womersley, is 29.8% of a total of 208 species. In some way confirming the above-mentioned ideas of Giard, it is possible to conclude from Table 6 that the amount of Palearctic elements is higher in the Chilean-Patagonian subregion than in the rest of South America.

Relationship to the Ethiopian Region: Leaving aside the Palearctic interference, the closest affinities of South America are with Africa and Australia. The following are some examples: *Sminthurinus stenognathus* has two subspecies, one near Zanzibar and the other in the Pampean area. *Aethiopella* comprises 13 African species, one from Lebanon and one from Brazil. *Friesea reducta* is a case similar to *Isotomina martiniquae* already mentioned; it has been found in Costa Rica and the Ivory Coast. In Sierra de la Ventana (Argentina) there is a different subspecies which seems to be intermediate in position between the "forma principalis" and *F. africana* of Mt. Kilimanjaro, the latter being the most primitive. *Cyphoderus limboxiphius* has two subspecies, one in East Africa, Mozambique and Southern Rhodesia, the other in Buenos Aires Province (Argentina). If the identity (synonymy) of this species and *C. innominatus* were confirmed, their chorology would increase embracing central Argentina, Rio de Janeiro, Recife (Brazil) and Yucatan (Mexico). Another species, *C. similis*, has been reported in Iowa, Costa Rica, Panama, Peru and the Ivory Coast. *Dicranocentrus gracilis* is shared by Cameroun, Peru and Puerto Rico; *Proisotoma centralis* by Yucatan, Costa Rica, Cuba, Brazil, Peru and Annobon Island (Gulf of Guinea); *Salina bidentata* by Costa Rica and the Ivory Coast. The genus *Andiella* is also shared with two very closely related species, *A. spathacea* from Fundu Is. and *A. carreensis* from Santa Fé (Argentina). Without showing a perfect correspondence, we can mention the case of *Choreutinula* which has three species, one in Argentina, another in South Africa and a third in northern Africa, penetrating Europe. *Temeritas macroceros* has been found in Costa Rica and Gambia. The genus *Arlesia* has two species in Brazil, one species in Bolivia, one in Surinam and Central America, one in Angola and one in Gambia. Also the genus *Kenyura* has different species in Kenya, the Ivory Coast, Brazil and Peru.

Relationship to the Australian Region: Strictly between New Zealand and South America, according to Salmon, the zoogeographical relationships are weak, as exemplified by the genera *Ceratrimeria*, *Lepidophorella*, *Lepidocyrtus*, *Katianna* and *Tomocerura*. Salmon states that New Zealand has its closest affinities with Australia and the Indomalayan Region. This is not surprising for they are relatively close to one another especially if we consider the "modern" influences received by New Zealand from Australia, and both of them, in turn, from the Oriental Region which have obscured in some way the ancient relationships. A furthering of knowledge of the invertebrate fauna of the Neotropical and Australian regions produced a change of focus with respect to the geographical distribution of lower taxa, among them the collembolans. Some of the above-mentioned genera are by no means valid any longer, and new relationships have been established. The genus *Paronellides* (= *Pericrypta*) spreads over Australia, Tasmania and Brazil. *Cryptopygus*, too, has representatives in both regions and in Antarctica; one of them, *C. indecisus*, from the Araucanian woodlands is practically identical to *C. tasmaniensis*.

Other shared genera are: *Delamarellina* (Araucania and New Zealand), *Setocerura* (Brazil, New Zealand, Australia), *Zealandella* (New Zealand, Araucania), *Setanodosa* (Peru, Brazil, Araucania, Australia, New Zealand), and *Sorensia* (Campbell I., Possession I., New Zealand, Araucania). New Zealand and Araucania also possess a common subfamily, Spinothecinae, with one genus and two species.

Relationship to the Oriental Region: The relationship to this region is poor and rather constitutes a zoogeographical curiosity. If we take into account all of the observations and data recorded—some of which are very well-known such as that regarding the Tapirids—it could have some paleogeographical significance and not be merely due to chance. In the case of collembolans we are inclined to think, in the first place, that genera or species limited to both regions are the result of a lack of knowledge of the intermediate areas. If this hypothesis were not valid, we would be disposed to follow the position of hologenists.

An example of Oriental-Neotropical distribution is provided by *Alloscopus*, with two Indomalayan, one Brazilian and one Peruvian species. *Cyphoderus javanus* has been reported in Java, Israel, Buenos Aires and Tucuman (Argentina) although it might be another case of a man-introduced species. *Dicranocentrus problematicus* from Viet Nam is supposedly synonymus with *D. silvestri* from Central and South America. The genus *Cyphoderodes* has three species, one from India, one from Ceylon and one from Brazil. *Paronella carpenteri* from the Guianas and Costa Rica has its closest relative in Viet Nam with *P. subcarpenteri*. *Dicranocentroides fasciculatus* was mentioned for India and Puerto Rico. *Setogaster* has five known species, three from southeast Asia and two from the tropical forest of Peru.

Collembola of holotropical distribution

The chorology of these animals is clearly governed by climatic factors, though it is necessary to point out that temperature and humidity alone cannot explain the presence of a taxon in widely separated areas within the tropics. The factors which may have intervened in such a type of distribution could be classified as (i) primitively cosmopolitan groups later adapted to humid [tropical environments, suffering extinction in the less adequate areas, (ii) South America, Africa and SE Asia being somehow connected in the past, (iii) polar wandering and climatic changes forcing slow and massive migrations pushing the animals to the more "comfortable" milieus of the tropical belt, (iv) migration and active interchange along recent and modern contact points (Panama isthmus, Bering, Suez, Indomalayan archipelago, etc.) and (v) accidental transport by natural rafts, icebergs, winds, marine currents, phoresis on migratory animals.

This last possibility may have occurred many times and there are no reasons to think it is not presently at work between Africa and South America, with, however, only exceptional cases achieving success. Otherwise, the microarthropod faunae of both continents should resemble each other more than they actually do. In spite of the relatively shorter distances between the Caribbean islands and the eastern coasts of the United States which the tropical hurricanes reach, the fauna of that country has little Antillean influence. Through study of Pacific insular fauna, Gressitt (1956) arrives at the conclusion that winds play a dominant role in the dispersal of many insects and, in such a way, the south Pacific islands have a clear Indomalayan influence. Nonetheless, the absence of similarity between the SE United States collembolan fauna (except Florida which constitutes a special case) and the Caribbean fauna makes one seriously doubt the effectiveness of wind and raft transport from sites with little harmonic faunae (v. gr. islands) to

places with highly diversified ecological niches (v. gr. continents); this is the reverse of the case studied by Gressitt.

The risks to which a wind-transported collembolan is subjected are many. Primarily we have mortality due to fasting and desiccation, for these animals resist few days without food, and only hours or minutes in atmospheres lower than 97–98% relative humidity (Rapoport & Bianco 1966). However, supposing that a great number of individuals of the same species can travel at densities, say, of 100,000 per km², and supposing 1,000 of them could cross the oceanic barrier and land over a surface of 1 km², we would then have 1,000 individuals per square kilometer probably disseminated at random, following a Poisson distribution as occurs with rain drops. Unfavorable factors as inadequate climate or soil, being swept by rain into streams and rivers and into the ocean (Rapoport & Sanchez 1963), and predators should be taken into account in any conjecture. Even surpassing these difficulties we would have only 1,000 individuals per km² or 10 per hectare; 10 individuals whose average length is 1 mm. What is the probability that a male and a female will encounter, as, if they are edaphic they dwell in microcaves and soil fissures to 30 cm in depth, and if they are epiedaphic they climb trees to a height of several meters? It should be very low. To these deterring factors we must add a short life-span, and the natural slowness they adopt when introduced into litter or soil. Supposing the existence of sexual odors or the arrival of a pregnant female, the possibility of success is still slight because their ecological niche is almost surely occupied by other species against which they have to compete. Obviously, through millions of years the probability increases but never in a decisive way, otherwise the number of common species in related continents would be the rule and not the exception as it is. These arguments do not completely satisfy the biogeographer as there remains the problem of cosmopolitan species. In the case of *Collembola* we always tend to suppose introduction by man, but suggestions of their being the result of passive transport nonetheless exist.

Another possible means of faunistic interchange between Africa and South America could be by way of species adapted to floating or to skating on the water surface, as in the case of springtails and other arthropods constituting the epineuston. Rivers and streams constantly cast into the ocean enormous numbers of these animals, from a few thousand to several hundred thousand per hour (Rapoport & Sanchez 1963). Considering the shortest distance between Africa and South America to be about 3,000 km and the direction of winds and oceanic currents, at this point, to be generally from east to west, the possibility of success for neustonic species is not negligible, especially if we consider that in landing they will not spread over a wide area but along a coastal line. This is an advantage over the aerial plankton, but we cannot take it seriously into consideration as a means of interchange between widely separated continents, with the exception of the well-known cosmopolitan species.

Examples of Holotropical genera are: *Campylothorax*, which has 3 species in the Guyano-Brazilian subregion, one in Cameroun and one in Ceylon; *Dicranocentrus* with 5 species in the Neotropical Region (s. str.), 7 in the Ethiopic Region, one in Seychelles Is. and 5 in the Indomalayan Region; *Paronella* with 10 species in the Neotropics (s. str.), 11 in the Ethiopics, 27 in the Indomalayan, 3 in Seychelles Is., 2 in Bismarck Archipelago, and one in Solomon Islands; *Serrodorus* with 8 species in the Ivory Coast, one in Angola, one in Java and one in Araucania. Another two genera which can be included in this list are *Neotropiella* (*sensu* Massoud) and *Rastriopes*, and also the species *Brachystomella contorta*, reported in Costa Rica, Jamaica, Angola and the Malay Peninsula.

A wider pattern of distribution is the so-called Gondwanian, which also includes Australia and

New Zealand. Although it partially overlaps the Holotropical belt, it probably has a different paleogeographical meaning. We can include here such genera as *Acanthocyrthus*, *Arlesia*, *Ceratrimeria* (*sensu* Börner), *Clavontella*, *Katianna*, *Pseudanurida*, *Salina*, and possibly also the species *Cyphoderus serratus* which is distributed through Australia, Indochina and French Guiana, although it is absent from Africa. *Temeritas* has a species shared between Costa Rica and Gambia, 2 species in Argentina (Tucuman and Parana delta), one in Surinam, two in Venezuela (to be published), one in Viet Nam and several more (undescribed, according to Delamare) in Angola and the Ivory Coast. In a revision recently made by Najt (1968), two species are also reported for Australia.

Whatever the causes, the fact is that we have many cases of Holotropical distribution among the invertebrates. The geographical significance of an Holotropical belt is different from that of the Inabresia (Jeannel) because it is wider, and it differs from Gondwania for it excludes Antarctica and Australia and includes the Pacific islands which do not correspond to the stratigraphic series of Gondwanaland. Several authors considered the usefulness of adjectives as "pantropical", "tropicopolitan" and "panequatorial", especially the phytogeographers. The distributional patterns of some taxa, especially invertebrates, suggested the delineation of three principal bands which for the sake of uniformity in nomenclature were designated as Holarctic, Holotropical and Holantarctic (Rapoport 1968).

Conclusion

The complex and numerous relationships of the Neotropical collembolan fauna with practically all of the zoogeographical regions lead us to consider this as an indication of great antiquity. From the Devonian period they had opportunity to follow the geological evolution of continents, thus manifesting a great adaptive capability to different climates and environments, without suffering great morphological changes. This is a typical case of bradytely accompanied by a fairly high constancy of form and low number of chromosomes (Núñez 1962). Not for this fact we had to consider the Neotropical fauna as lacking its own characteristics; the proportion of endemic genera and species is high, although varying in the different subregions. There are clearly two stocks, the Paleantarctic, relegated to the Araucanian subregion and with progressively weakening influences in the remaining areas, and the Neotropical s. str. stock, probably Afro-Brazilian or Holotropical. Both stocks had faunistic interchanges between themselves and also received Holarctic influences. Presently there is a certain degree of segregation between these stocks principally due to climatic factors, i.e., a large desertic fringe called the Andean-Patagonian subregion which extends from the extreme south, up the east side of the Andes to 40° SL, and including the Andes as far as Bolivia and Peru. Real relictual refugia are dispersed along this subregion, especially in Chile. For instance, Cerro El Roble is populated by *Odontella loricata*, *Brachystomellides neuquensis*, *Pachytullbergia scabra* and *Notachorudina castrii*, which are typically Araucanian elements. Winter (1963) also found a species of *Brachystomellides* in the cloudy rain-forest of Peru, one of the possible points of contact and faunistic interchange between these two major stocks.

A negative factor that should be pointed out is the absence of the very common Holarctic genera *Orchesella* and *Tomocerus* in South America (old records for Chile are not reliable). The paucity of species of *Onychiurus*, seven in total, which represents less than 5% of the European forms, is also curious. This is especially conspicuous in flat areas such as pampas and llanos where they are practically absent, dwelling only in the neighborhood of human settlements.

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