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GEOGRAPHICAL DISTRIBUTION OF THE LOWER BRACHYCERA (DIPTERA)[1]

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Abstract. The geographical distribution of the genera and families of the lower Brachycera, excepting Stratiomyidae and Tabanidae, is presented in this paper. Continental drift is accepted as a fact, and all of the families and at least some of the genera in the lower Brachycera seem to be old in origin and might have already occurred during the Mesozoic on the continent Pangaea or at a later time in the Mesozoic on Laurasia and Gondwana. It must be recognized that "absent" in any 1 region may likely mean "extinct."

This paper presents the geographical distribution of the lower Brachycera except for the 2 largest families, Stratiomyidae and Tabanidae. For distribution of Tabanidae see Mackerras (1954, 1955, 1956, 1960, 1961) and his subsequent papers.

For a classification of the lower Brachycera see Nagatomi (1975a, 1977) and McAlpine et al. (1981) and for that of Rhagionidae see Nagatomi (1982). Female genitalia of the lower Brachycera were treated by Nagatomi & Iwata (1976, 1978) and Iwata & Nagatomi (1976). Male genitalia of the lower Brachycera will be shown by Nagatomi (in prep.). Hennig (1967) classified the lower Brachycera found in Baltic amber.

It should be noted that New Guinea and its adjacent islands are here treated conventionally as a part of the Australasian Region, but the fauna of the lower Brachycera in this area is apparently more similar to that found in the Oriental Region than to that in Australia.

Family Solvidae (=Xylomyidae)

Nagatomi & Tanaka (1971) recognized 3 genera: *Arthropeina* Lindner, 1949 (monotypic, Brazil); *Coenomyiodes* Brunetti, 1920 (monotypic, Assam); and *Solva* Walker, 1860 (s.l.).

Brunetti (1920) described *Coenomyiodes* as follows: "scutellum with two blunt apical spines .... Legs as noted previously" (under "*Coenomyiodes* gen. nov.") and "fore tibiae with one spur, posterior tibiae with two spurs" (under "subfamily Coenomyiinae").

I have reexamined the holotype female of *Coenomyiodes edwardsi* Brunetti, 1920, in the British Museum (Natural History) and have found that the scutellum has no spines and the fore tibia has no spur. *Coenomyiodes* may be a synonym of *Solva* (*Macroceromys*) Bigot, 1877.

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Although the family Solvidae could possibly be split into numerous genera based on characters of male and female genitalia (see Nagatomi & Tanaka 1971: 105), the 3 genera above are closely related to one another.

The distribution of Solvidae is as follows: the Palearctic Region, over 20 species (Lindner 1936–38, Nagatomi & Tanaka 1971, Krivosheina 1972, etc.); the Nearctic, 10 spp. (James 1965b, Vasey 1977); the Oriental, about 50 spp. (Adisoemarto 1973, Nagatomi 1975b); the Neotropical, 9 spp. from Central America, Brazil and Paraguay (James 1975); the Australasian, 9 spp. from the Moluccas, Halmahera, New Guinea and Solomons [of which *Solva laeta* Daniels, 1976 is distributed in Papua New Guinea and Australia (N Queensland)] (Kertész 1908, Daniels 1976); the Ethiopian, 5 spp. (Stuckenberg 1980).

Thus, solvids are absent from Chile and Argentina and practically nonexistent (their presence may be secondary or recent) in Australia.

Family Pantophthalmidae

Papavero (1967) listed 2 species of *Opetiops* Enderlein, 1921, 15 spp. of *Rhaphiorhynchus* Wiedemann, 1821, and 6 spp. of *Pantophthalmus* Thunberg, 1819, but Val (1976) accepted only 1 species of *Opetiops* as valid, listed 19 spp. of *Pantophthalmus,* and treated *Rhaphiorhynchus* as a synonym of *Pantophthalmus.*

The Pantophthalmidae is present in Central and South America, except for Chile and Argentina.

Family Rachiceridae

The Rachiceridae contains 3 living genera: *Gymnorhachicerus* Frey, 1954 (monotypic, Burma), *Paleorachicerus* Nagatomi, 1970 (n. n. for *Electra* Loew, 1850, only 1 living species from the Philippines), and *Rachicerus* Walker, 1854.

The distribution of Rachiceridae is as follows (Nagatomi 1970): the Palearctic Region, 3 species from Spain, China and Japan; the Nearctic, 5 spp.; the Oriental, 40 spp.; the Neotropical, 9 spp. from Central America and Brazil; the Australasian, 4 spp. from New Britain, New Guinea and the Moluccas.

Thus, representatives of the Rachiceridae are absent from Africa, Australia, Chile and Argentina.

Family Xylophagidae

This family is composed of only 1 genus (*Xylophagus* Meigen, 1803) (Nagatomi & Saigusa 1969), which contains 12 species in Europe, Siberia and Japan (Krivosheina & Mamaev 1972) and 7 spp. in North America (Webb 1979).

Family Coenomyiidae

The Coenomyiidae contains 5 genera whose species number and distribution are as follows (Nagatomi 1975a): *Anacanthaspis* Röder, 1889, 1 species and 1 subspecies from Siberia, Manchuria and Japan; *Arthropeas* Loew, 1850, 4 spp. and 2 subspp.

from Tibet, Manchuria, Korea, Siberia, Sakhalin and North America; *Coenomyia* Latreille, 1796, 3 spp. from Europe, Tibet, Nepal, Sikkim, Japan and N America; *Dialysis* Walker, 1850 (partly after Webb 1978), 12 spp. from Formosa, E China, Japan and N America; *Odontosabula* Matsumura, 1905 (=*Stratioleptis* Pleske, 1925), 3 spp. from Manchuria, Korea, E Siberia and Japan.

Family Heterostomidae

This family contains only 1 genus (*Heterostomus* Bigot, 1857), which is monotypic and present in South America (Chile).

Family Exeretoneuridae

The genus *Exeretoneura* Macquart, 1846, the only representative of this family, contains 4 species from Australia and Tasmania (Paramonov 1953).

Family Pelecorhynchidae

This family is composed of only 1 genus (*Pelecorhynchus* Macquart, 1850) (Mackerras & Fuller 1942), which contains 27 species from Australia and Tasmania (Mackerras & Fuller 1942) and 6 spp. from South America (Chile) (Philip 1968).

Family Rhagionidae

The data below are illustrated in Table 1 and Nagatomi (1982).

In number of species, the genera *Chrysopilus* Macquart, 1826, and *Rhagio* Fabricius, 1775, are large; *Atherimorpha* White, 1915, *Ptiolina* Zetterstedt, 1842, and *Symphoromyia* Frauenfeld, 1867, are much smaller, and the remainder of genera may be insignificant.

Only the genus *Chrysopilus* (Rhagioninae) is worldwide in distribution. *Litoleptis* Chillcott, 1963 (Spaniinae), a small genus, is widely distributed in the Nearctic, Neotropical (Chile), Palearctic (Japan) and Oriental (Nepal and Philippines) regions. *Rhagio* (Rhagioninae) is also widely distributed but is absent from Australia, South America and southern Africa. *Glutops* Burgess, 1878, and *Pseudoerinna* Shiraki, 1932 (=*Bequaertomyia* Brennan, 1935) (Glutopinae), *Ptiolina* and *Spania* Meigen, 1830 (Spaniinae), *Arthroceras* Williston, 1886, *Bolbomyia* Loew, 1850, and *Symphoromyia* (Rhagioninae) are limited to the Holarctic Region. *Arthroceras, Bolbomyia, Glutops* and *Pseudoerinna* are absent from Europe. *Atherimorpha* (Rhagioninae) lives in Australia, Tasmania, Chile, Argentina and S Africa, and *Austroleptis* Hardy, 1920 (Austroleptinae) in Australia, Tasmania and Chile. *Spaniopsis* White, 1914 (Spaniinae) is found in Australia and Tasmania only, *Neorhagio* Lindner, 1924 (Rhagioninae) in Mexico and Chile only, and *Arthroteles* Bezzi, 1926 (Rhagioninae) in S Africa only.

The rest of the genera (all Rhagioninae) are limited to the following Oriental and Australasian areas: *Desmomyia* Brunetti, 1912, highlands of India; *Rhagina* Malloch, 1932, Java and Sumatra; *Schizella* Bezzi, 1917, and *Stylospania* Frey, 1954, Philippines; undescribed genus 1, Celebes; undescribed genus 2, Solomons.

TABLE 1. Geographical distribution of Rhagionidae (see Nagatomi 1982).

TAXA	No. NAMED SPECIES	DISTRIBUTION (NO. SPECIES)
Austroleptinae		
Austroleptis	5	Australia and Tasmania (3), Chile (2)
Glutopinae		
Glutops	11	Japan (3), Siberia (1), N America (7)
Pseudoerinna	2	Japan (1), N America (1)
Rhagioninae		
Arthroceras	8**	E China (1), Siberia (2), Japan (3), N America (4)
Arthroteles	3	S Africa
Atherimorpha	38	Chile and Argentina (14), Australia and Tasmania (20), S Africa (4)
Bolbomyia	5	Japan,* Kamchatka (1), N America (4)
Chrysopilus	ca. 270	Worldwide
Desmomyia	1	Highlands of India
Neorhagio	1	Mexico,* Chile (1)
Rhagina	3	Java (2), Sumatra (1)
Rhagio	ca. 100	Widely distributed but absent from S America, Australia, and S Africa
Schizella	2	Philippines
Stylospania	1	Philippines
Symphoromyia	32**	Europe (3), Central Asia (1), Japan (1), N America (29)
Undesc. genus 1	1*	Sulawesi*
Undesc. genus 2	1*	Solomons*
Spaniinae		
Litoleptis	3	Japan,* N America (1), Nepal,* Philippines (1), Chile (1)
Ptiolina	22	Europe (9), Siberia (2), Japan,* N America (11)
Spania	1**	Europe (1), Japan,* N America (1)
Spaniopsis	7	Australia and Tasmania

* Undescribed species on hand.

** Some species are widely distributed in Europe and Japan, Japan and N America, or Europe and N America.

Atherimorpha, Austroleptis and *Spaniopsis,* all of which are present in Australia, are not recorded in New Guinea and its adjacent islands. Rhagionidae has not been recorded from the Hawaiian Islands (Hardy 1960). One species of *Chrysopilus* is known in New Zealand (Miller 1950) and 27 spp. of the genus are found in Madagascar (Stuckenberg 1965a).

The number of species of *Chrysopilus* and their distribution is as follows: the Palearctic Region, 45–50 (of which 18 are recorded from Japan); the Nearctic, 32; the Oriental, 65 (or so); the Neotropical, 54 (of which 2 are recorded from Chile and 0 from Argentina); the Australasian (except Australia, Tasmania and New Zealand), 9–10 from the Moluccas, Misool, Waigeo, New Guinea and Fiji; Australia and Tasmania, 24; New Zealand, 1; the Ethiopian, 35 (of which 27 are recorded from Madagascar).

The number of species in *Rhagio* is as follows: the Palearctic, 60–70 (of which 14

are recorded from Japan); the Nearctic, 21 (Chillcott 1965, James 1965a, 1965b); the Oriental, 16; the Neotropical, 2 from Mexico (which may possibly belong to *Neorhagio*).

Family Athericidae

The genera *Atherix* Meigen, 1803, *Ibisia* Rondani, 1856 (whose type-species is *marginata* Fabricius, 1781, from Europe), *Pachybates* Bezzi, 1926 (2 species from South Africa), *Suragina* Walker, 1860, and *Xeritha* Stuckenberg, 1966 (1 species from Brazil) are here treated tentatively as *Atherix* s.l. which is distributed as follows: the Palearctic Region, about 15 species (Szilády 1934, Nagatomi 1958); the Nearctic, 4 spp. (Webb 1977); the Oriental, 17 (or so) spp. (Nagatomi 1975b, 1979a); the Neotropical, 6 spp., of which 3 are known from Central America and 3 from Peru, Bolivia, or Brazil (Stuckenberg 1966, James 1968); the Ethiopian, 20 spp. (Stuckenberg 1980); the Australasian, 1 sp. from Buru (Colless & McAlpine 1970 wrote, "[*Atherix* was] recently found in Queensland").

The family includes 3 additional genera with species number and distribution as follows: *Atrichops* Verrall, 1909, 7 (or 8) species from Europe, Japan, Vietnam, Thailand, the Philippines and Central Africa (1 undescribed species on hand) (Nagatomi 1979b); *Trichacantha* Stuckenberg, 1955, 1 sp. from South Africa; *Dasyomma* Macquart, 1840, 11 spp. from Australia and Tasmania (Paramonov 1962) and 17 spp. from South America (Argentina and Chile) (James 1968).

Atherix s.l. is absent from Argentina and Chile and may be practically so (the presence may be secondary or recent) in Australia, where a number of species of *Dasyomma* are recorded.

Stuckenberg (1973: 671) erected a new subfamily Dasyomminae, monotypic for *Dasyomma,* and wrote, "The genus appears to have a sister-group relationship with all the other athericids, so a separate subfamily is required."

Family Vermileonidae

The genera and distribution of Vermileonidae are given below.

Lampromyia Macquart, 1835 (Szilády 1934; Stuckenberg 1960, 1961, 1965b, 1971, 1980): the Palearctic Region, 7 species from southern Europe and North Africa (Canary I, Morocco, etc.); the Ethiopian, 14 spp. from southern Africa. *Vermileo* Macquart, 1834 (Szilády 1934, Edwards 1935, James 1965b, 1968): the Palearctic Region, 2 species from southern Europe and North Africa (Sudan); the Nearctic, 2 spp. from California, Nevada, Utah and New Mexico; the Neotropical, 4 spp. from Mexico, Jamaica and Cuba. *Vermitigris* Wheeler, 1930 (Nagatomi 1975b): the Oriental Region, 3 species from India, W Malaysia, Borneo and Sumatra. Recently Yang (1979) described a new genus and species from China (Shaanxi), *Vermiophis ganquanensis.*

Vermileonidae is absent from Australia and South America.

DISCUSSION

General considerations

Every organism has its ancestor. The origin of the genus is earlier than that of the species but later than that of the family. In any taxon, one line declines or dies out when another comes into being and succeeds. Attention must be paid to extinction in tracing geographical distribution.

Recent advances in geology show that the continental drift discussed by Wegener is not a mere theory but a fact. The following arguments are based on this fact.

The hypothetical routes of geographical dispersal in various groups of organisms are presented diagrammatically in Fig. 1, and explanatory notes follow below. Roman numerals and numbers are assigned to different regions and stages.

I and II, only 1 (Pangaea) or 2 (Laurasia and Gondwana) continents on earth; III and IV, land divided into 5 continents or 6 main regions (besides Antarctica).

IB, IIA, and IVB (shaded), distributed throughout the world; IC and IID (unshaded), not yet occurring in the world; IIB and IIC (½ shaded), distributed in the Northern Hemisphere or the Southern Hemisphere; IIIB and IIIC, distributed in Eurasia and North America or Australia and South America (expressed as an example in which the distribution is limited to some regions).

IIB from IB, and IIC from IB: extinct in the Southern Hemisphere or in the Northern Hemisphere.

IIB from IC, and IIC from IC: having arisen in and distributed in the Northern Hemisphere or in the Southern Hemisphere.

IIIB from IIB or IVB, and IIIC from IIC or IVB: extinct except for Eurasia and North America or except for Australia and South America.

IIIB from IID, and IIIC from IID: having arisen in and distributed in Eurasia and North America or in Australia and South America.

IVB from IIA: distributed throughout the world both in the past (at period of Pangaea or Laurasia and Gondwana) and in the present (5 continents or 6 main regions).

IVB from IIIB and IID: having arisen in Eurasia or North America and distributed throughout the world.

IVB from IIIC and IID: having arisen in Australia or South America and distributed throughout the world.

The degree of possibility for these routes may be indicated as follows. IIA → IVB: strong (in higher taxa), less strong (in genus), or very weak (in species); IIA → IVB → IIIB: strong; IIA → IVB → IIIC: strong; IB → IIB → IIIB: strong; IB → IIB → IIIB → IVB: weak; IB → IIC → IIIC: strong; IB → IIC → IIIC → IVB: weak; IC → IIB → IIIB: strong; IC → IIB → IIIB → IVB: strong; IC → IIC → IIIC: strong; IC → IIC → IIIC → IVB: weak; IID → IIIB: strong; IID → IIIB → IVB: strong; IID → IIIC: strong (arose in Australia or South America) or weak (arose in Australia and moved to South America, or arose in South America and moved to Australia); IID → IIIC → IVB: weak.

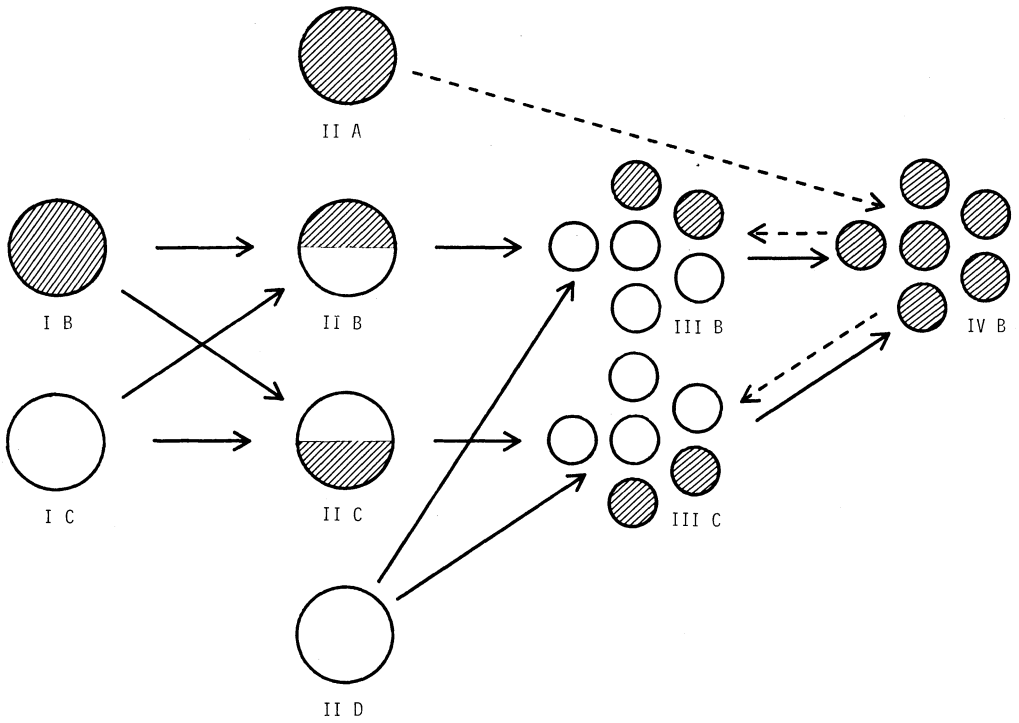

FIG. 1. A model showing the hypothetical routes of geographical distribution in various groups of organisms (in III and IV, Africa is at left, Eurasia, the Oriental Region and Australia are in center, and North America and South America are at right). See text for explanation of Roman numerals and numbers.

It may be accepted that various groups of organisms in Australia, South America or South Africa are generally less advanced. If so, it is probably due to the fact that each of these lands is smaller and isolated from the northern larger continents where evolution may take place more rapidly and taxa may disperse more easily.

Distribution at the family level

The Rhagionidae and Athericidae, as with the Stratiomyidae and Tabanidae, are worldwide in distribution. Solvidae is absent from Chile and Argentina and practically so (the presence may be secondary or recent) from Australia; Pantophthalmidae is present in Central and South America (except Chile and Argentina); Rachiceridae is absent from Chile and Argentina, Australia, and Africa; Xylophagidae and Coenomyiidae are present in Eurasia and North America; Heterostomidae is present in South America (Chile) only; Exeretoneuridae is present in Australia only; Pelecorhynchidae is present in Australia and South America (Chile) and Vermileonidae is absent in Australia and South America.

However, all of the families in the lower Brachycera seem to be old in origin and

might already have arisen at the time of Pangaea or of Laurasia and Gondwana; it should be assumed that "absent" in any 1 region means "extinct."

Genera common to Australia, South America and sometimes southern Africa

The genera *Pelecorhynchus* (Pelecorhynchidae), *Austroleptis* (Rhagionidae), and *Dasyomma* (Athericidae) are present both in Australia and South America (Chile and Argentina), and *Atherimorpha* (Rhagionidae) is in Australia, South America (Chile and Argentina), and southern Africa. It is almost certain that these genera originated from the time of Pangaea or Gondwana, i.e., their routes are not IID → IIIC, but are IIC → IIIC or IIA → IVB → IIIC (see Fig. 1).

The number of genera extending over Australia and southern Africa is smaller than that common to Australia and South America, at least in Diptera. This may suggest that southern Africa was affected more profoundly by the invasion of the northern elements or it was separated from Australia and South America earlier.

Genera distributed both in Eurasia and North America

A number of genera are limited to Eurasia (especially the Far East) and North America. They are *Xylophagus* (Xylophagidae), *Anacanthaspis, Arthropeas, Coenomyia, Dialysis* and *Odontosabula* (Coenomyiidae), *Arthroceras, Bolbomyia, Glutops, Pseudoerinna, Ptiolina, Spania* and *Symphoromyia* (Rhagionidae). All or most of these seem to be primitive and may belong to IIB → IIIB or IIA → IVB → IIIB (Fig. 1), i.e., might have originated from the time of Pangaea or Laurasia.

Presence of sister-groups in both hemispheres

The Coenomyiidae (consisting of 5 genera, Eurasia and North America), Heterostomidae (1 genus, South America) and Exeretoneuridae (1 genus, Australia) are closely related and their relationships are either *A* or *B* in Fig. 2. The latter 2 families seem to be more primitive than the former (based on hair condition on metapleura, structure of male genitalia, etc.). If Heterostomidae and Exeretoneuridae were extinct, Coenomyiidae would have no relative in the Southern Hemisphere.

The genera of Spaniinae (Rhagionidae) are interesting in their distribution (bracketed localities refer to undescribed species on hand): *Litoleptis,* North America (1 species), [Japan], [Nepal], the Philippines (1) and Chile (1); *Spania,* Europe (1), [Japan] and North America (1); *Spaniopsis,* Australia and Tasmania (7); *Ptiolina,* Europe, Siberia, [Japan] and North America (a total of 22). The relationships among them are shown in Fig. 3. If *Litoleptis* and *Spania* were extinct, the nearest relative of *Spaniopsis* would be *Ptiolina* and if *Spaniopsis* ceased to exist, *Ptiolina* would have no relative in the Southern Hemisphere.

Origin of Rhagio (Rhagionidae) and Atherix s.l. (Athericidae), and distributional patterns of Solvidae, Rachiceridae and Vermileonidae

Rhagio has numerous species and is widely distributed, but it is absent from Australia, South America and southern Africa, where *Atherimorpha,* which is apparently a sister-group of *Rhagio,* is present.

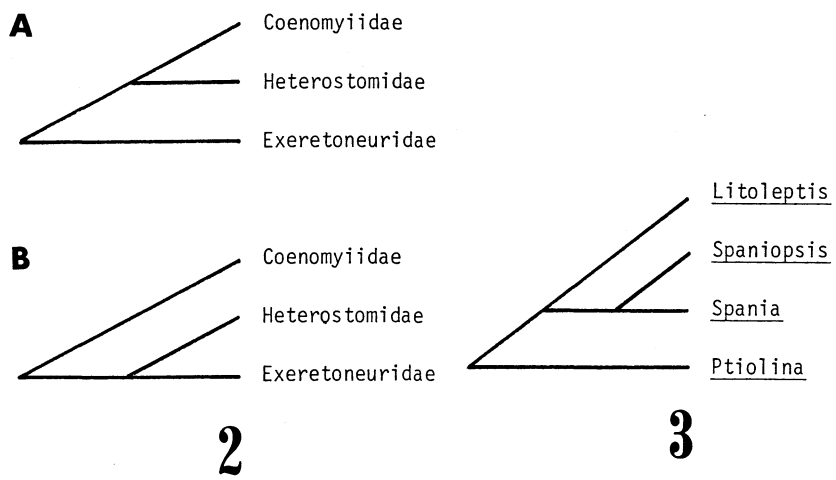

FIG. 2–3. **2.** Supposed phylogeny of Coenomyiidae, Heterostomidae, and Exeretoneuridae: **A,** Heterostomidae is more similar to Coenomyiidae than to Exeretoneuridae; **B,** vice versa. **3.** Supposed phylogeny of Spaniinae (Rhagionidae).

Atherix s.l. (including *Ibisia, Pachybates, Suragina* and *Xeritha*) is also widely distributed but it is absent from Argentina and Chile and practically so (the presence may be secondary or recent) from Australia, while a number of species of *Dasyomma,* a sister-group, is present in these 2 regions.

It is certain that *Rhagio* and *Atherix* s.l. are not representative of IB → IIB → IIIB or IIA → IVB → IIIB but of IC → IIB → IIIB or IID → IIIB (see Fig. 1).

If *Atherimorpha* and *Dasyomma* were extinct, *Rhagio* and its relatives (Nagatomi 1982) (although 1 species of *Neorhagio* is recorded from Chile) and the family Athericidae would be similar in distribution to Solvidae (absent from Chile and Argentina and practically so from Australia), Rachiceridae (absent from Chile and Argentina, Australia and Africa), and Vermileonidae (absent from Australia and South America). This implies the possibility of the past presence of ancestral or less advanced forms in Australia, South America, or southern Africa in the latter 3 families.

Origin of Chrysopilus (Rhagionidae)

Apart from Stratiomyidae and Tabanidae, there are over 40 genera of the lower Brachycera, of which only *Chrysopilus* is worldwide in distribution. The route in question in this genus would be either IID → IIIB → IVB (or less probably IID → IIIC → IVB) or IIA → IVB, although the possibility of IC → IIB → IIIB → IVB or IC → IIC → IIIC → IVB is present (see Fig. 1).

Among Rhagionidae, *Chrysopilus* seems to be one of the most advanced genera, as is *Rhagio.* Nevertheless, *Chrysopilus* might have originated at the time of Laurasia and Gondwana (i.e., IIA → IVB), granting that transoceanic dispersal is difficult for such a fragile fly; the possibility is weak if the age of this genus is young.

Habitat of Vermileonidae and Bolbomyia (Rhagionidae)

The Vermileonidae is scattered in distribution (see under family Vermileonidae and see Hennig 1967) and their larvae live in sand, making a pitfall as do antlions. It is naturally thought that this family had a golden day in the past, when the distribution was continuous and there were a number of genera, most of which lived in soil in the larval stage, but that, except for the genera specializing in sand and having no significant competitors, they were completely displaced by more advanced creatures.

Bolbomyia (Rhagionidae) is found in the zone of creeping pine near the top of high mountains. It may easily be imagined that this genus is compelled to live in such a hostile environment where it has no strong rival.

It seems to me that Vermileonidae and *Bolbomyia* are archaic and that the histories for these 2 groups suggested above are quite within the realm of probability.

Relationship of Diptera to the breakup of Pangaea

The earliest geological record of Diptera is at the boundary of the Triassic and Jurassic in coal deposits of central Asia (Rohdendorf 1964).

If "the breaking-up of Pangaea did not begin until the early Cenozoic," as suggested by Wegener (quoted from Kummel 1970), it is easy to understand the geographical distribution of the lower Brachycera discussed in this paper. But if Pangaea "split up as early as the Triassic period," as asserted by recent workers (Kurtén 1972), the time of origin of the lower Brachycera, which would be earlier than was thought, becomes a problem.

It is concluded that all of the families and at least some of the genera in the lower Brachycera are old in origin and might have already occurred during the Mesozoic on Pangaea or at a later time in the Mesozoic on Laurasia and Gondwana.

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