ginate rim. Legs: simple; hind femora with only a few ventral spines. Wings: marginal cell open; apical cell petiolate, with long petiole; anterior crossvein distinctly before middle of discal cell.

Abdomen: elongate, with parallel sides.

Material examined: 3(3); *varipes* Shannon and Aubertin (PTs) *.

Discussion: In appearance, *Hemixylota* looks like a typical *Xylota* but with dichoptic eyes in the male and anterior crossvein distinctly before middle of the discal cell. *Xylota* is the only genus with which *Hemixylota* is likely to be confused, but besides the obvious differences mentioned above, *Hemixylota* differs from *Xylota* by its: 1) much smaller metathoracic spiracle, only about one-half as large as third antennal segment; 2) lack of trochanteral spurs in the male; and 3) lack of ventral spines on probasitarsi of male. *Chamaesphegina* might be confused with *Hemixylota* because of its concave face, orbicular third antennal segment and elongate abdomen but its lack of subscutellar fringe, scutellar bristles, and reduced alulae will clearly separate *Chamaesphegina* from *Hemixylota*.

Only three species of *Hemixylota* have been described. All species were described from the Chilean Subregion of South America by Shannon and Aubertin (1933) who have provided comparative notes for the identification of the various species.
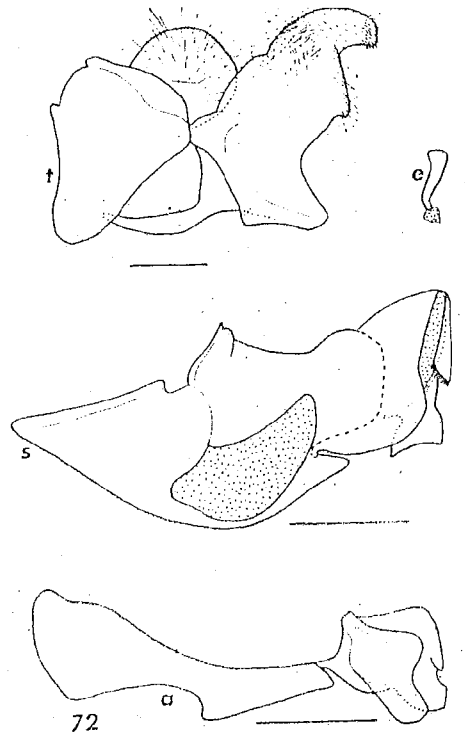
Genus Stilbosoma Philippi

(Fig. 25, 72)

Stilbosoma Philippi, 1865, Verh. Zool.-Bot. Ges. Wien 15:736. Type species, *Stilbosoma rubiceps* Philippi, 1865 (subsequent designation; Shannon 1926, Proc. U.S. Nat. Mus. 69(9):45).

Head: higher than long; face bare, thinly pollinose, concave; cheeks linear, more than twice as long as broad; facial grooves short, extending along lower fourth of eyes; facial stripes distinct, pilose; frontal prominence greatly produced forward, extending far beyond oral margin, above middle of head; front of male long, slightly longer than broad, as long as vertical triangle; vertical triangle slightly swollen, rectangular, broader than long, with sides straight; front of female broad, as broad as face, about as long as broad, about one-fourth longer than face, with parallel sides; ocellar triangle distinctly before posterior margin of eyes. Eyes bare, broadly dichoptic in male. Antennae short, about two-thirds as long as face; third segment large, orbicular; arista short, only about a third longer than antenna.

Thorax: as broad as long, with short pile; meso-katepisterna with separate dorsal and ventral pile patches; meso-anepimera with posterior portion bare; meropleurae bare; metathoracic pleurae bare; metasterna greatly developed, pilose; postmetacoxal bridge incomplete; metatho-

racic spiracle large, but not as large as third antennal segment; plumulae elongate; scutellum with ventral pile fringe and distinct apical emarginate rim. Legs: hind coxae with a blunt tubercle on inside; hind femora swollen, with apical ventral large notched plate on outside. Wings: marginal cell open; apical cell distinctly closed before reaching costa, but with very short petiole; anterior crossvein at outer fourth of discal cell, with anterior three-fourths strongly oblique and continuous with appendix, at junction of oblique and straight sections.

Abdomen: short and oval.

72, male genitalia of *Stilbosoma ruficeps* Philippi. a, aedeagus and apodeme; e, ejaculatory apodeme; s, sternum 9; t, tergum 9; all lateral view.

Material examined: 2 (2); *cyanea* Philippi *, *rubiceps* Philippi *.

Discussion: *Stilbosoma* is unique among syrphids for its long spur on the anterior crossvein and large notched ventral plate on hind femora. The spur, which Curran (1923) has called r5, to my knowledge is not only unique among syrphids but all cyclorrhaphous Diptera. Only two species of *Stilbosoma* are known. Both are restricted to the Chilean Subregion of South America and can be easily separated by the color of their heads: *cyanea* has a shiny black face and front; whereas *rubiceps* has an orange face and front.

Genus **Milesia** Latreille

(Fig. 73)

Milesia Latreille, 1804, Nouv. Dict. H. N. 24 (*Tab.*) :194. Type-species,
    Syrphus crabroniformis Fabricius, 1775, by designation of Willis-
    ton, 1887, Bull. U. S. nat. Mus. 31:254. To preserve the long and
    almost universal usage of *Milesia* in the sense of *Syrphus crabro-
    niformis* Fabricius, as type-species, the International Comission
    on Zoological Nomenclature should be asked to suspend the rules
    and suppress Rondani's (1844. Nuovi Ann. Sci. nat. Bologna
    (2)2:455) designation of *Musca diophthalma* Linnaeus (Type-spe-
    cies of *Spilomyia* Meigen) and to place *Milesia* Latreille on the
    Official list of Generic Names with *Syrphus crabroniformis* Fa-
    bricius as type-species (see Williston, 1887:254-255).

Head: higher than long; face bare in middle, distinctly pilose on
sides, extensively pollinose, concave; cheeks linear, more than twice as
long as broad; facial grooves short, extending along lower third of eyes;
facial stripes indistinct, pilose; frontal prominence low, slightly above
middle of head; front of male short, more than three times as long as
eye contiguity, two-thirds as long as vertical triangle; vertical triangle
long, about as long as face, more than twice as long as broad at occiput;
front of female narrow, about three-fifths as broad at antennae as
long, about one-fourth longer than face; ocellar triangle distinctly before
posterior margin of eyes. Eyes bare, narrowly holoptic in males. An-
tennae short, about half as long as face; third segment quadrate with
apical end slightly rounded; arista long, more than one-half longer
than antenna.
    Thorax: usually longer than broad, with short pile, usually with
bright color and pollinose markings; meso-katepisterna continuously
pilose from ventral to dorsal margins; meso-anepisterna with anterior
portion frequently with pile on upper half, with posterior apical edge
swollen ridge-like; meso-anepimera with posterior portion bare; mero-
pleurae bare; metathoracic pleurae bare; metasterna pilose, greatly
developed; postmetacoxal bridge incomplete; metathoracic spiracle
large, as large as third antennal segment; plumulae short, frequently
very short; scutellum with ventral pile fringe and distinct apical emar-
ginate rim. Legs: hind femora slightly swollen, with a small ventral
spur near apex. Wings: marginal cell petiolate, with a long petiole;
apical cell petiolate, with a long petiole; anterior crossvein at outer
fourth of discal cell, greatly oblique; apical and posterior crossvein
continuous, without spurs at their bases; anal cell with petiole meeting
wing margin perpendicularly.
    Abdomen: elongate and parallel-sided.

Material examined: 50(2); *brunetti* Hervé-Bazin, *scutellata* Hull
and *virginiensis* (Drury).
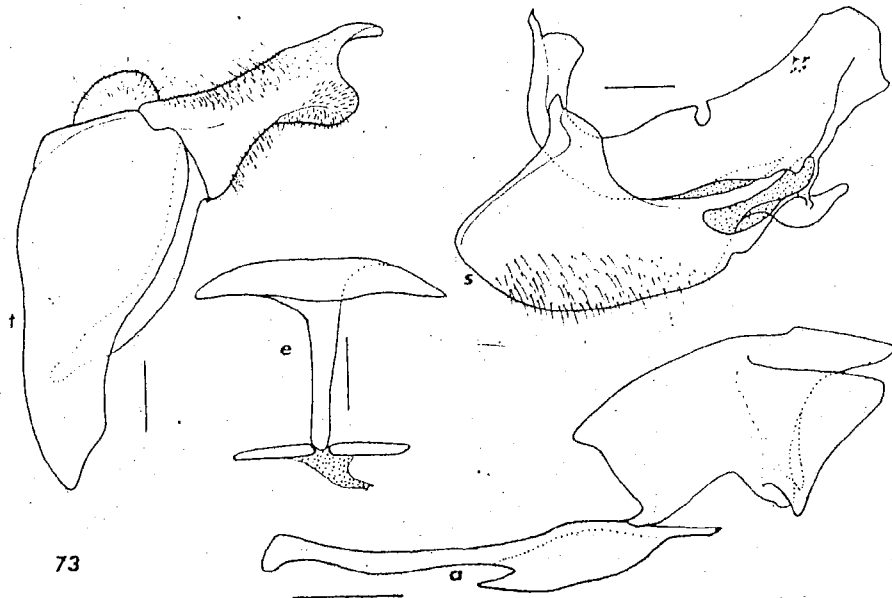
73, male genitalia of *Milesia virginiensis* (Drury). a, aedeagus and apodeme; e, ejaculatory apodeme; s, sternum 9; t, tergum 9; all lateral view.

Discussion: Milesia is readily recognized by its strongly concave face and petiolate marginal cell. The only other groups with petiolate marginal cells, the Eristalina and some volucellines, all have tuberculate faces. *Milesia* appears to be one of the most highly specialized syrphid genera as the following characteristics would seem to indicate: 1) petiolate marginal cell; 2) apical anterior crossvein, at outer fourth or more of discal cell; 3) greatly developed metasterna; and 4) concave face.

Milesia, which is a predominantly Oriental genus, is represented by only five New World species, of which two are found in the Neotropical Region. Both species are restricted to Central America. The comparative notes provided by Fluke (1939) in his description of *nigra* will separate this species from the rest of the New World species, to which Hull (1924) has provided a key.

Genus Spilomyia Meigen

(Fig. 74)

Spilomyia Meigen, 1803, Mag. Insektenkunde 2:273. Type-species, *Musca diophthalma* Linné, 1758 (subsequent designation; as *Syrphus diophthalmus* Fabricius, Coquillett, 1910, Proc. U.S. Nat. Mus. 37:607).

Head: higher than long; face bare in middle, pilose on sides above, straight with a slightly produced epistoma, in some species with a low medial tubercle; cheeks linear, more than twice as long as broad; facial grooves short, extending along lower third or eyes; facial stripes indisctint, pilose; frontal prominence low, on upper third of head; front of male short, about twice as long as eye contiguity, about three-fourths as long as vertical triangle; vertical triangle long, half as long as face, more than twice as long as broad at occiput; front of female broad, ranging from two-thirds to three-fourths as broad at antennae as long, about one-third to one-fourth shorter than face, with slightly convergent sides above; ocellar triangle distinctly before posterior margin of eyes. Eyes bare, holoptic in males. Antennae short, ranging from three-fourths to one-third as long as face; third segment subo-val, slightly longer than broad; arista short, shorter than or equal to antenna.

Thorax: about as broad as long, with short pile; meso-katepi-sterna with separate dorsal and ventral pile patches; meso-anepisterna with anterior portion pilose; meso-anepimera with posterior portion pilose on anterior basal half; meropleurae bare; metasterna pilose, greatly developed; meta-episterna with a distinct pile patch below and behind spiracles; postmetacoxal bridge incom-plete; metathoracic spiracle small; plumulae elongate; scutellum without a ventral pile fringe, usually with a distinct apical emarginate rim, without a rim in *gratiosa*. Legs: hind femora elongate, slightly swollen, with a ventral spur on outside near apex. Wings: marginal cell broadly open; apical cell distinctly closed before wing margin but with a very short petiole; anterior crossvein at outer fifth of discal cell, greatly oblique; anal cell with petiole greatly elongate and parallel to wing margin.

Abdomen: suboval, with apical half of second segment and all of third and fourth segments emarginate.

Material examined: 22(1); *ephippium* (Osten Sacken) (HT), *fusca* Loew, *gratiosa* Wulp*, *haemifera* Loew, *interrupta* Williston, *longicornis* Loew, *pleuralis* Williston (HT) *quadrifasciata* (Say) and *terana* Johnson (HT).

Discussion: The presence of pile on both the anterior portion of the meso-anepisterna and meta-episterna as found in *Spilomyia* is a unique combination among the milesine syrphids. Other distinctive characteristics of *Spilomyia* are; 1) anterior crossvein strongly oblique and extending to outer fifth of discal cell; 2) hind femora with a small ventral spur near the apex; 3) scutellum with apical emarginate rim; and 4) eyes with metallic patterns. The very similar wing venation of *Spilomyia* and *Milesia* along with the common possession of character 2 and 3 above indicate a close relationship between the two genera. Only one species of *Spilomyia* has been described from the Neotropical Region. *Spilomyia gratiosa* Wulp was described from Argentina and I
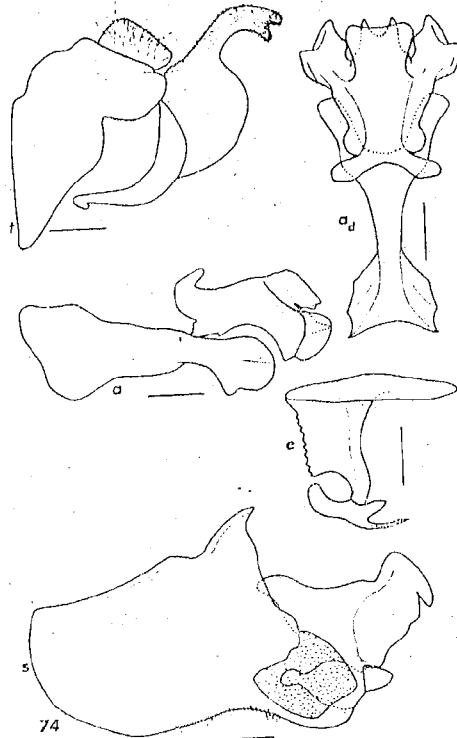
74, male genitalia of *Spilomyia gratiosa* Wulp. a, aedeagus
and apodeme; e, ejaculatory apodeme; s, sternum 9; t, tergum 9; all lateral view, except a_d dorsal view.

have figured the male genitalia of a specimen from the coastal mountains of Brazil. This species does not appear to have been recorded since it was originally described. *Gratiosa* has an extensively yellow pleuron and will key to *pallipes* Bigot in Curran's key to Nearctic species (1951). However, it should be readily recognized by its distinctive color pattern which was beautifully illustrated by Wulp (1888) in his original description.

Genus Cacoceria Hull

Cacomyia Hull, 1930, Trans. Amer. Ent. Soc. 56:147 (preoccupied, Coquillett 1906). Type-species, *Cacomyia cressoni* Hull, 1930 (original designation).
Cacoceria Hull, 1936, Ent. News 47:277 (new name for *Cacomyia* Hull).

Head: twice as high as long; face bare, pollinose, straight with a low medial tubercle, produced, downward; cheeks broad, as broad as long; facial grooves short, extending along lower third of

eyes; facial stripes indistinct; frontal prominence low, as high as facial tubercle, at upper third of head; front of male long, about one-third longer than eye contiguity; vertical triangle small, one-half as long as eye contiguity, about twice as long as broad; front of female short, only three-fourths as long as face, narrow, longer than broad at antennae; ocellar triangle slightly protuberant and distinctly before posterior margin of eyes. Eyes bare, holoptic in male. Antennae very long, more than one and one-half times as as long as face; first segment elongate, about four times as long as broad; second segment elongate, more than twice as long as broad; third segment elongate, in female more than twice as long as broad, in male with two long slender adjacent prongs of equal length; arista short, shorter than antenna.

Thorax: as long as broad, with short pile; meso-katepisterna with two widely separated dorsal and ventral pile patches; meso-anepimera with posterior portion bare; meropleurae bare; metathoracic pleurae bare; metasterna pilose, greatly developed; postmetacoxal bridge incomplete; metathoracic spiracle small; plumulae short; scutellum with a ventral pile fringe, without a distinct apical emarginate rim. Legs: hind femora greatly swollen medially, tapered at both ends, spindle shaped, with a row of distinct long ventral spines on apical third; hind tibiae strongly arcuate, ending in long ventral spur. Wings: marginal cell open; apical cell petiolate; anterior crossvein at or beyond middle of discal cell, straight.

Abdomen: constricted, with second segment forming petiole, with constriction only one-half of width of second segment.

Material examined; 2(2); one undetermined species.

Discussion: *Cacoceria* is a rather aberrant genus not closely related to any other milesine genus. The very long antennae, with deeply bifurcate third segment in the male, is unique among the syrphids. The pilose and well-developed metasterna, enlarged hind femora, tuberculate face in both sexes and subscutellar fringe places the genus in the Milesini but neither the male genitalia nor any other characteristic reveals any indication of the probable ancestral group. Thompson (1968) called *Cacoceria* a genus of Myoleptini but at that time I was not clear about the limits of either the Myoleptini or Milesini. Only two known species of *Cacoceria* are from Mexico and Peru, respectively.

ZOOGEOGRAPHY OF THE NEOTROPICAL MILESINAE

A REVIEW OF CONTINENTAL DRIFT AND ITS EFFECT ON THE NEOTROPICAL FAUNA

Ever since evolution replaced the biblical notion of special creation as an explanation of organic diversity, biologists have been left with the questions of when, from where, and how animals became distri-

buted. In fact, it was the observation of present and past distributions
of animals, particularly those of South America, that led Darwin to
doubt the idea of special creation and to suggest evolution instead. Thus,
modern zoogeography began with Darwin's *On the Origin of Species*,
1859. Since then, there have developed two main schools of thought
on animal and plant distribution.

One school, Wegenerians, has stressed the positions of and con-
nections between the land masses as being of major importance in the
dispersal of living things. The other school, Matthewites, feels that
the movement of the continents and the presence of land bridges other
than those present now are not necessary to explain the distribution
patterns of life. They maintain that the forces of competition and
climate working directly and through evolution are sufficient to account
for the distribution patterns of animals and plants.

As with all disputes, neither side is all right or all wrong and
both have valid points. As Darlington, a Matthewite, has clearly
stressed, favorable climate and large areas are related to the evolutions
of dominance among animals and there *is* a trend for the more com-
petitive organism to evolve and disperse from the tropics and to replace
the less efficient elsewhere. But it is also true that the continents
have not long been where they are and their migration *has* influenced
the distribution of past and present organisms. To deny either one
is to see only half of the true picture. Since Darlington (1957:chap.9;
1965:chaps.5&6) has done an excellent job in summarizing the inter-
relationships and effects of area, climate, and evolution on dispersal and
distribution patterns, I will not delve into these here. However, the
past history of land connections has been greatly neglected in the
biological literature due to the dominance of the Matthewite school of
thought. Therefore, I will briefly review these connections and their
biological implications for South America.

The following review of the geologic history of South America
and the southern continents is mainly based on King's *Morphology
of the Earth* (2nd Ed., revised 1967) but other sources such as Carey
(1958) and Runcorn (1962) have been reviewed. It is restricted to
describing the relative positions of the continents and the major geolo-
gic events that might have biological significance.

Fortunately, the history of the geographical relationhips of South
America to other land masses is fairly well known since South America
has been one of the key points of emphasis in proof of the Continental
Displacement. When animals first came out on land, sometime in the
Devonian Period or earlier, South America probably was part of a
large supercontinent called Gondwanaland. Gondwanaland consisted of
all the southern continents: South America, Africa, Antarctic, India,
Australia, and associated islands. It is not clear when this superconti-
nent was first formed since as one goes further back into time the
geological record becomes more fragmentary. There are some indica-
tions, such as strike direction in the basement rock of the southern
continents (King, 1967:84), that Gondwanaland has existed since

buted. In fact, it was the observation of present and past distributions of animals, particularly those of South America, that led Darwin to doubt the idea of special creation and to suggest evolution instead. Thus, modern zoogeography began with Darwin's *On the Origin of Species*, 1859. Since then, there have developed two main schools of thought on animal and plant distribution.

One school, Wegenerians, has stressed the positions of and connections between the land masses as being of major importance in the dispersal of living things. The other school, Matthewites, feels that the movement of the continents and the presence of land bridges other than those present now are not necessary to explain the distribution patterns of life. They maintain that the forces of competition and climate working directly and through evolution are sufficient to account for the distribution patterns of animals and plants.

As with all disputes, neither side is all right or all wrong and both have valid points. As Darlington, a Matthewite, has clearly stressed, favorable climate and large areas are related to the evolutions of dominance among animals and there *is* a trend for the more competitive organism to evolve and disperse from the tropics and to replace the less efficient elsewhere. But it is also true that the continents have not long been where they are and their migration *has* influenced the distribution of past and present organisms. To deny either one is to see only half of the true picture. Since Darlington (1957:chap.9; 1965:chaps.5&6) has done an excellent job in summarizing the interrelationships and effects of area, climate, and evolution on dispersal and distribution patterns, I will not delve into these here. However, the past history of land connections has been greatly neglected in the biological literature due to the dominance of the Matthewite school of thought. Therefore, I will briefly review these connections and their biological implications for South America.

The following review of the geologic history of South America and the southern continents is mainly based on King's *Morphology of the Earth* (2nd Ed., revised 1967) but other sources such as Carey (1958) and Runcorn (1962) have been reviewed. It is restricted to describing the relative positions of the continents and the major geologic events that might have biological significance.

Fortunately, the history of the geographical relationhips of South America to other land masses is fairly well known since South America has been one of the key points of emphasis in proof of the Continental Displacement. When animals first came out on land, sometime in the Devonian Period or earlier, South America probably was part of a large supercontinent called Gondwanaland. Gondwanaland consisted of all the southern continents: South America, Africa, Antarctic, India, Australia, and associated islands. It is not clear when this supercontinent was first formed since as one goes further back into time the geological record becomes more fragmentary. There are some indications, such as strike direction in the basement rock of the southern continents (King, 1967:84), that Gondwanaland has existed since

Pre-Cambrian times. By the time of the arrival of the first insects in the Carboniferous the evidence is overwhelmingly in favor of the existence of Gondwanaland.

Although the southern continents were united in a single unit throughout the Paleozoic Era, they were not stationary. They moved considerably as a unit before breaking up as the accompanying text maps illustrate. This displacement has been a critical determinant of climate since it has determined position relative to the poles and thus has affected the angle of incidence of sun's rays. Gondwanaland was tropical for most of its existence[1]. As Darlington (1957, 1965) has maintained, the tropics are the workshop of evolution and the main trend in animal distribution is for dominant groups to arise in the tropics and to move outward. Thus, the paleoclimate of South America, as determined by the relative continental position, is a major factor in the determination of the size and diversity of the Neotropical fauna.

Besides the paleoclimate of South America, the history of accessibility of South America to the influx of animals from other continents is also a major factor affecting faunal composition. During the Paleozoic Era there were a number of cordilleras stretching across the various areas of Gondwanaland that later brooke up into the present southern continents. These formerly continuous cordilleras provide an explanation for the present disjunctive distribution of various ancient cold-adapted groups of animals in the southern hemisphere, as has been shown by Brundin (1966) for the primitive austral chironomid midges. The question of whether there was a connection between the southern land mass, Gondwanaland, and its northern counterpart, Laurasia, during the late Paleozoic is still a moot point. Present geological evidence strongly suggests that if there was a connection between Laurasia and Gondwanaland, it *was not* through the South American area of Gondwanaland.

Gondwanaland was extensively glaciated towards the end of the Carboniferous Period and during the early part of the Permian Period. It was then much farther south than now and the land mass was moving through the South Pole area (Irving and Robertson, 1968). As Gondwanaland swung in an arc across the South Pole, the land mass was progressively glaciated slowly from west to east. The glaciation was followed by a cold-temperate climate period. Thus, for example, Australia was glaciated later than the other continents and remained cold throughout the Permian while the Congo and India were semi-tropical (King, 1967:55). The Permo-carboniferous glaciation was restricted to the southern continents, as one would expect if the phenomenon was due to the displacement of the continents and not a world-wide climate change.

---

(1) The tropics are by definition the areas of the earth where the sun's rays fall perpendicularly (Darlington, 1957:4). Thus, the tropics are bounded by the tropic of Cancer and Capricorn (23°27' north and south of Equator).

The disruption of Gondwanaland in the Mesozoic Era into its various component continents was the result of two major breaks (see text maps). The first divided Gondwanaland into a western and an eastern component. The eastern component consisted of Australia, India, and possibly Antarctica, whereas the western part contained South America and Africa. The questionable position of Antarctica in either the western or eastern component is due mainly to the lack of paleomagnetic data from this continent.The time of this first break is also somewhat uncertain at present. Opinions on the time of breakup of eastern Gondwanaland range from the beginning of the Mesozoic to the beginning of the Tertiary. Irving and Robertson (1968) have suggested that the fragmentation began between the Permian and Triassic Periods whereas King (1967) thinks it started in the middle of the Jurassic Period. These discrepancies need not worry the reader since the connections between South America and the continents of eastern Gondwanaland were always indirect, either though Africa or Antarctica. Thus, the important break is the second one, between South America and Africa (or the rest of Gondwanaland, if you please), and the time of occurrence of this break is well documented. In the mid-Cretaceous period the Atlantic basin began to open up in the south and gradually the two continents, Africa and South America, moved apart. The separation was complete by Upper Cretaceous times and South America drifted slowly westward to its present position, arriving there at the beginning of Tertiary times.

The rest of the geological story of South America is the same whether one be a Wegenerian or conventional geologist. As Darlington has defended and clearly stated, "*the Tertiary isolation of South America is a fact*" (Darlington, 1957:594). However, during the Tertiary the water gap between North America and South America fluctuated in size with changes in the geomorphism of Central America and the Antilles. There were two island arcs. Lesser Antilles and present Panama area, over which some animals could have "leap-frogged" their way into or out of South America. The Lesser Antilles form such a connection from South America through Trinidad and Tobago to Greater Antilles, the latter being simply an extension of the North American cordilleran structures. The Panama island arc connected Colombia with the south borders of Nicaragua. Both island arcs appear to have been present and above water since the late Cretaceous Period. During the late Pliocene and early Pleistocene the Panama island arc became a continuous land bridge.

In summary, there are three key geological time points in respect to the biogeography of south America. *First*, up to the mid-Cretaceous times South America was directly connected to Africa, and earlier still in the Paleozoic Era both of these continents were also attached to Antarctica, Australia, and India, forming a single land mass called Gondwanaland. *Second*, South America was an island from the time it separated from Africa until the time the present isthmus of Panama was formed, that is, from Upper Cretaceous to the end of Tertiary.

Third, throughout the Tertiary there was a fluctuating water gap between them. Therefore, there should be three corresponding faunal and floral strata in South America, reflecting the geologic history: old residents from Gondwanaland, island-hoppers crossing narrow water gaps from North America during the Tertiary, and recent arrivals coming by way of the isthmus of Panama during the Pleistocene.

GENERAL ANALYSIS OF THE ZOOGEOGRAPHY OF THE NEOTROPICAL MILESINE FAUNA

GROSS STATISTICAL ANALYSIS OF THE NEOTROPICAL MILESINE FAUNA IN COMPARISON TO THE OTHER REGIONAL FAUNAS.

The zoogeography of the Neotropical milesine syrphids will be examined from a general viewpoint; first, by comparison of the gross statistics (such as number of species and genera) of the Neotropical milesine fauna with the fauna of various other regions; and second, by plotting the distribution of the Neotropical genera on maps and studying the resulting patterns. The treatment of the individual genera has been included under the generic discussions.

Table III lists the number of milesine genera and their species endemic to each particular region, along with the total number of milesine genera and species for that region. The species counts are approximate for the number of species described as of 1965 exclusive of fossil species, and were compiled from the following sources: Wirth *et al.* (1965) for the Nearctic region, exclusive of Mexico; Fluke (1956) for the Neotropical region and Mexico; Hull and Fluke (1950) for the genus *Cheilosia, sensu lato;* Hull (1949) for the rest of the world; and the Zoological Record (1945-65). During the course of this study

Table III. Number of genera and species, total and endemic,

for each faunal region

Region	nº endemic genera-species	nº genera	nº species
Palearctic	16 -- 32	70	805
Nearctic	15 -- 35	66	738
Holarctic	17 -- 513	91	1523
North-Temperate	48 -- 579		
Ethiopian	5 -- 19	22	267
Neotropical	26 -- 137	42	570
Oriental	9 -- 20	47	652
Australian (includes Oceania)	13 -- 19	26	150

on Neotropical milesine genera I have critically reviewed about 80%
of the world milesine genera. The total number of genera and the
number of endemic genera listed for each particular region considerably
reflect my opinions of what are good genera (see Appendix II).

The amount and nature of the taxonomic work on a particular
region can greatly affect the number of taxa being recorded for the
area. In the analysis of any quantitative zoogeographic data the taxo-
nomic bias should be nearly the same from region to region. The only
area of the world on which there has been significantly more syste-
matic work done relative to the rest of the world is Europe. Thus the
greater amount of taxonomic work on the Palearctic region may bias
the figures. Whether taxonomists split or lump taxa in their work can
also affect the number of taxa. Thus it is essential that degree of
clustering of taxa be nearly the same for the faunal regions being
compared. On the species level, the problem of the "splitters and
lumpers" is not significant in syrphids since there has been very
little use of the infraspecific categories, such as variety, form, subspe-
cies, *etc.*, and most workers have used the same operational definition
of a species. On the generic level, when I critically reviewed the world
milesine genera I tried to apply criteria (see Introduction, definition
of genus) uniformly so that figures for the numbers of genera for
each region would have a uniform base. Only in some of the eristaline
groups do I feel that I may have had a tendency to lump more than
I did elsewhere. I have not recognized a number of subgroups in the
Eristalini, such as the subgenera of *Mallota, Mesembrius,* and *Eristalis.*
There undoubtedly has been a large eristaline radiation in the Old
World tropics and some of the groups that I have not recognized are
possibly valid; a thorough study is needed. When the cristaline radiation
is worked out, it is doubtful that more than a dozen genera will be
added to the syrphid faunas of the Old World tropics (Ethiopian and
Oriental). Such an eventuality would not upset my conclusions on zoo-
geographic relationships between the Neotropical fauna and the rest
of the world. Thus the numbers in Table III should allow for reliable
zoogeographical interpretations.

The regional milesine faunas are either quite large or small; none
are intermediate in size. Interestingly, the range of variation in the
number of species amongst the small faunas is the same as for the
large faunas, about 150 (except for the intensively worked Palearctic
fauna). Even the minimum gap between the numbers of species in the
large and small faunas is more than twice the above figure, over 300.
The Neotropical region, along with the Palearctic, Nearctic, and Orien-
tal regions, has as relatively large, rich milesine fauna, whereas
Australian and Ethiopian regions have rather depauperate faunas.

The various faunal regions are not of uniform land size (Table
IV) and because large areas tend to have larger numbers of taxa
than smaller areas, dividing the number of taxa by a unit of area
produces more meaningful comparative figures. The effects of area
on number of taxa are not arithmetic but geometric. However, within

Table IV. Land area for each faunal region, from Lane (1949) .

Region	Area of region in square miles	Rank
Palearctic	17,421,000	1
Nearctic	7,335,000	4
Holarctic	24,756,000	-
Ethiopian	10,762,000	2
Oriental	4,120,000	5
Neotropical	7,721,000	3
Australian	3,610,000	6

the range of values for the areas used in the present analysis, an arithmetic interpretation is sufficient to compensate for the area factor and thus to help evaluate the other influences affecting faunal size (see Williams, 1964, for details on the mathematical interpretation of species and area problems).

The numerical relationships between land area and number of taxa is not the same for all categories: as area becomes smaller, there is a greater effect on the lower categories like species than on higher categories like genus. Thus, a very small area may have many genera but only one species per genus, whereas a large area may have a few more genera but many more species per genus. For example, the milesine fauna of the Juan Fernandez Islands consists of two tribes representing two broad ecological niches, the terrestrial short-tailed maggots and the aquatic long-tailed maggots, but only one genus and species for each of the two broad niches as opposed to Chile with five tribes, twenty-three genera, and about fifty species representing the same two broad niches

The relationships indicated for the different milesine faunas based on the diverty per unit area (Table V) are quite different from those based on the unadjusted numbers of taxa (Table III) per faunal area. Although Africa, even based on diversity per unit area, has a depauperate milesine fauna, the small Australian fauna is as rich in species per unit area as is the Palearctic fauna and about twice as rich in genera. The Neotropical and Nearctic milesine faunas are intermediate in terms of diversity per unit area and the Oriental region has significantly more milesines than all others.

The differences between the figures of diversity per unit area for the various milesine faunas reflect mainly variation in climate and to some extent the history of accessibility of each faunal region to animals from other regions. Tropical climates produce much larger faunas than temperate climates when the land areas and other factors

Table V. Milesine diversity per unit area (100,000 sq.miles)

for each faunal region

Region	Generic	Specific
Palearctic	.42	4.6
Nearctic	.90	10.0
Holarctic	.37	6.1
Ethiopian	.20	2.5
Neotropical	.55	7.4
Oriental	1.14	15.8
Australian	.72	4.2

are equal. Islands and isolated continents generally have smaller faunas than connected areas when climate, area, etc. are equal[1] (see Darlington 1957&1965, and also MacArthur and Wilson 1966, for detailed discussion of the area, accessibility, and climate factors). Unfortunately, there is no numerical method or index for working with the climate or accessibility factors of a faunal region for the study of the taxonomic diversity of that region as there is for the area factor. Thus the best way to study the effects of the climate and accessibility variables is to designate a "standard" faunal region and compare the others with it. The Oriental region has the optimal conditions of both climate and accessibility and therefore provides a good reference point or "standard" for comparsion.

As Darlington (1957) has pointed out, the tropics are the workshop of evolution and for the workshop to be most efficient in producing species variety, it must be readily accessible for the inflow of new types.The Oriental region is almost completely within the tropical belt of the world with mostly tropical rain forest type of habitat, and has been readily accessible to the Palearctic and other faunal regions throughout the Cenozoic Era. As would be expected of a region with such ideal conditions, the Oriental region has a significantly greater milesine generic and species diversity per unit area than all other faunal regions. The Neotropical region and Australian region to a lesser extent also have extensive tropical areas, but both of these regions have been isolated from the rest of the world for long periods

---

(1) The above are general statements applying to taxonomic units occupying a wide variety of habitats and niches (sensu Elton). The milesine syrphids are such a large, diverse group that these general statements do have applicability to them. However, it would be absurd to apply, for example, the statement about tropical climate to a group like the Capniidae, a strictly cold adapted group of stoneflies.

of time and this isolation probably accounts for their smaller unit-area faunas of milesines relative to the Oriental region.

If isolation has indeed been a major factor in determining the diversity of a fauna, then one would expect a high percentage of endemic genera and a high endemic quotient (EQ). Endemic quotient is defined as the percentage of the *total number of species* represented by the *species in the endemic genera*. The endemic quotient and percentage of endemic genera are about the same for all faunal regions except for the Australian and Neotropical[1] regions (see Table VI).

Table VI. Endemic levels for each milesine syrphid fauna

Region	Per cent of Endemic Genera	Endemic Quotient
Palearctic	23	04
Nearctic	23	05
Holarctic	53	38
Ethiopian	23	07
Neotropical	62	24
Oriental	19	03
Australian	50	13

$$\text{Endemic Quotient} = \frac{\text{n? species belonging to endemic genera}}{\text{n? species belonging to all genera}} \times 100$$

The high endemic levels (EQ and percentage of endemic genera) for the Neotropical and Australian milesine syrphid faunas confirm the geological evidence that these faunas have long been isolated. The difference in endemic levels between Neotropical and Australian milesine syrphid faunas are probably due mainly to differences in accessibility and secondarily to differences in sizes of the regions. Table VI can be modified to show, by dividing by units of area (million square miles, 8 and 4, for example), that the endemic diversity per unit area is slightly higher for the Australian fauna than the Neotropical. Thus it can be safely stated that the slightly higher endemic levels per unit

(1)   The endemic quotient of the Neotropical region is rather conservative because of the arbitrary boundary of the Neotropical region which excludes the consideration of *Copestylum* and *Palpada* as endemic Neotropical genera. These two large genera account for about 70% of the total South American milesine fauna but about 10% of species of *Copestylum* and *Palpada* have extended their ranges across the Neotropical Nearctic boundary into Mexico and southern United States (see below under Transition between Neotropical and Nearctic fauna). If these two Neotropical radiations were scored as endemic, since they certainly had a recent origin in South America, the endemic quotient would be about 98% instead of 62%.

area for the Australian region are due to its slightly longer period of isolation than that of South America.

The Holarctic or North Temperate region has been physically joined to the Ethiopian and Oriental regions throughout the Cenozoic Era (also intermittently connected to South America). Therefore, the only plausible isolating mechanism to explain the high endemicity of the Holarctic milesine fauna is climate. The southern limits of the Holarctic region are, by definition, the tropics. Thus any northern group of animals that is strictly cold adapted will be limited to the Holarctic region.

The Nearctic milesine syrphid fauna is numerically significantly larger than the Neotropical one. Since the areas of both regions are roughly the same, the difference is probably due to the greater accessibility of the Nearctic region. This greater accessibility in comparison to the Neotropical region is due to North America's intermediate position between the Old World and South America. Thus the Nearctic region can receive taxa from both the Old World and the Neotropical region, whereas the Neotropical region can receive taxa from the Nearctic region only. The Neotropical milesine contribution (8 genera and 157 species) to the Nearctic fauna alone is sufficient to compensate for the difference between the two regions. And considering that the Nearctic fauna also receives a large number of taxa from the Old World too, it is clear how the Nearctic region with less extensive tropical area can have a larger milesine fauna than South America with its extensive tropical areas.

The reasons for the apparently depauperate milesine fauna of the Ethiopian region are not clear. The relatively small African tropical rain forest area, in conjunction with the Sahara Desert acting as a barrier, could help account for the reduced faunal variety of Africa. However, the low percentage of endemic genera and low endemic quotient for the Ethiopian region tend to suggest that geographic isolation has not been a significant factor. Similarly the reasons for the significant differences between the Nearctic and Palearctic milesine faunas when adjusted for area factor are not apparent unless one assumes an upper limit for the area factor beyond which it does not affect faunal size. Both regions have a similar climate and history of accessibility.

In summary, from a gross analysis of numbers of endemic genera and their species, along with total numbers of genera and species of the milesine syrphids of the major world faunal regions, several conclusions have been reached about the Neotropical milesine fauna: 1) Neotropical milesine fauna is relatively large in terms of absolute numbers of species and genera; 2) Neotropical fauna in diversity per unit area is only intermediate; 3) South America's relatively low milesine diversity for such a large area with extensive tropical climate is probably related to long isolation from the rest of the world; and 4) South America's unusually large number of endemic genera and
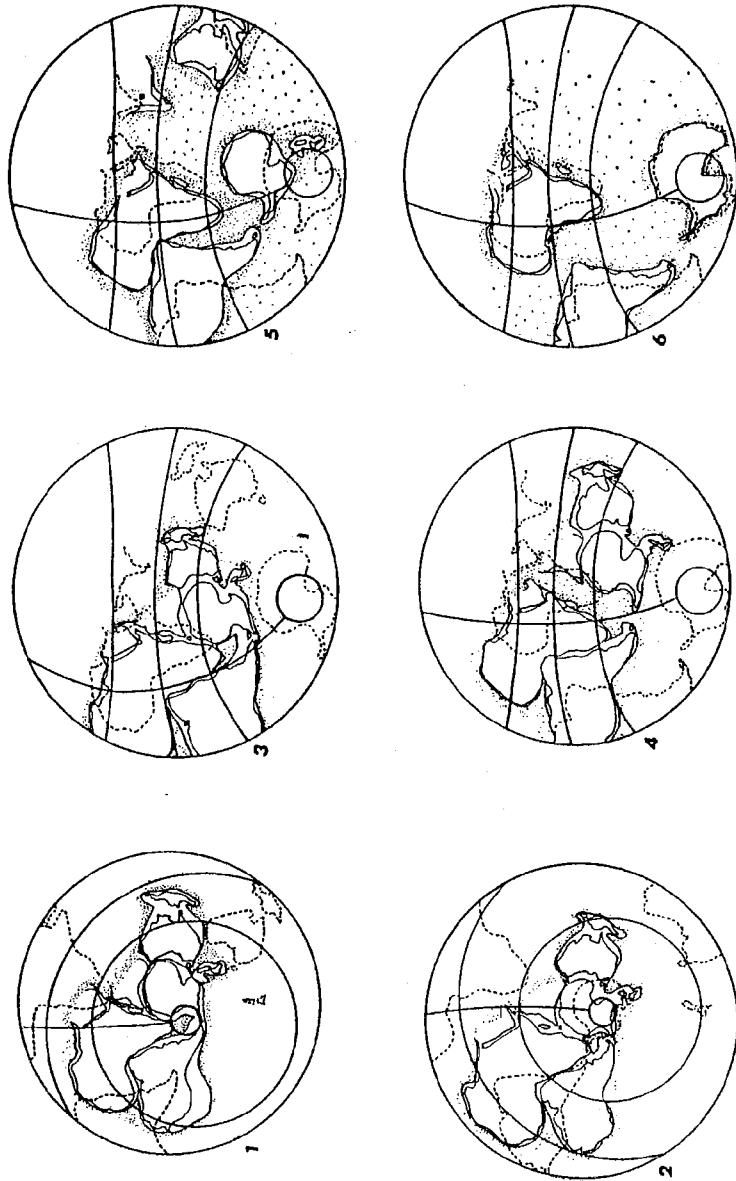
Maps 1-3, Gondwanaland. 1, late Carboniferous Period; 2, early Permian Period; 3, late Triassic Period. 4, separation of Eastern Gondwanaland during late Jurassic - early Cretaceous Period. 5, Beginning of separation of South America and Africa during mid to upper Cretaceous Period. 6, South America and Africa during the beginning of the Tertiary Period.

high endemic quotient strongly supports the idea of a long isolated South American milesine fauna.

PATTERNS OF DISTRIBUTION OF THE NEOTROPICAL MILESINE GENERA

When the geographic distributions of the Neotropical milesine syrphid genera are plotted on maps of the world the results can be grouped into four distinct patterns (see text maps 7 - 10). The first pattern represents the Holarctic endemic genera extending into the transitional zone between the Neotropical and Nearctic regions and marking the southern limits of the Nearctic fauna (see section below on transition between Nearctic and Neotropical faunas).

The second pattern also represents predominantly northern groups, but these extend into the Neotropical region along the Andean cordillera. The genera of the second pattern, like the above ones, are restricted to the temperate climate except for two genera, *Rhingia* and *Spilomyia*, extending across South America from the Andes to the semitropical coastal mountains of Brazil. I have called the genera of the second pattern, "recent invaders", due to the fact that these genera have not yet: 1) evolved new generic distinctions, nor 2) adapted to the true tropical climate. The older resident groups, Pattern III, have envolved generic distinctiveness in South America and can be divided into two groups depending on whether or not some of their species have had time to adapt to tropical climates. The two groups of endemic milesine genera are reflected by their different distributional patterns; Pattern IIIa representing endemic genera which have become adapted to the tropics, whereas Pattern IIIb represents endemic genera restricted to the temperate Chilean subregion.

It is quite apparent where the non-endemic Neotropical milesine genera (Pattern II) came from since their restricted distribution in South America along the Andean cordillera, but widespread distribution in the northern hemisphere strongly suggests that these genera have recently moved into South America by way of the Panama isthmus from the north. However, the question of where the endemic Neotropical genera came from is not quite as obvious. Some Neotropical endemic genera could possibly have come also from more distant places, like Australia or Africa. To decide which was or were the source or sources of the endemic Neotropical genera, two types of approaches will be used: one, by working out the phylogenetic relationships of the endemic genera and relating this to geographic origins; and two, by comparision with the history of the land connection of South America to see which routes of introduction were most plausible.

The history of the land connections between the Neotropical region and the rest of the world has already been discussed, so it will be sufficient just to point out where the milesine syrphids fit into the time table of that history. The first fossil syrphids known are from the Eocene period and they are representative of both present day
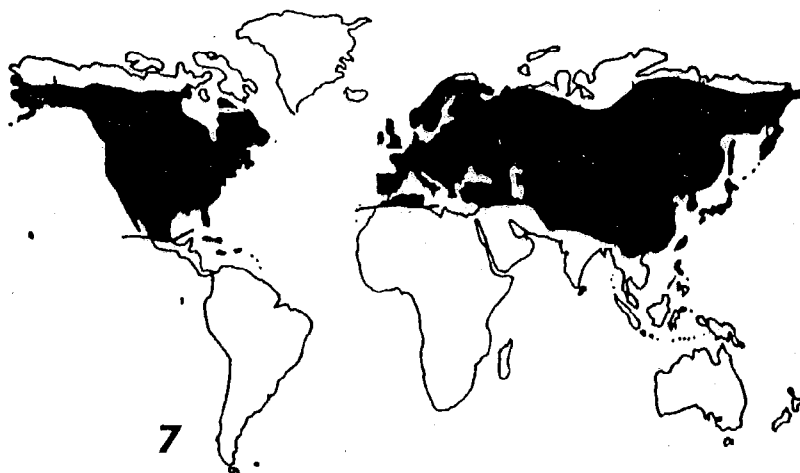
7
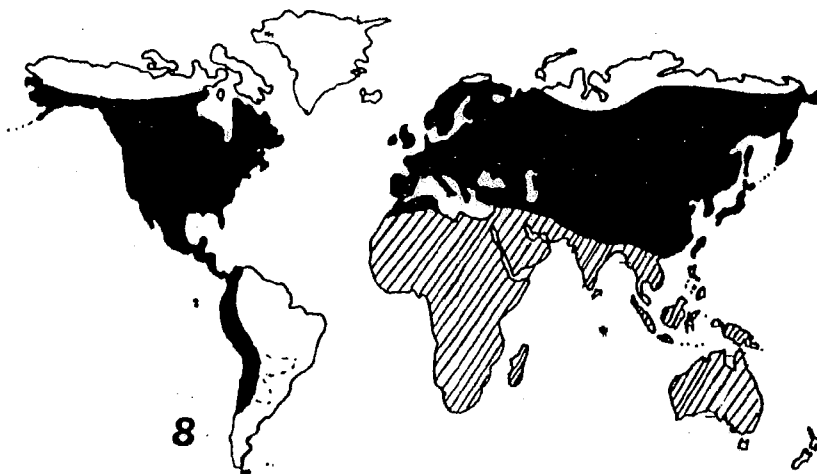
8

Map 7, Pattern I, Northern Groups; map 8, Pattern II, Recent Invaders.

subfamilies. Thus, the origin of the family and divergence into two subfamilies must have been before Eocene times. The two subfamilies probably arose in the Paleocene and the family itself probably in the late Cretaceous Period (Hull, 1945; also see Hennig, 1954). The relatively young age of the family Syrphidae and the subfamily Milesinae places their origin at a period in time when South America was an island. Thus either 1) the family arose in the Neotropical region and spread out to the rest of the world, or 2) the first syrphids must