

Article XXVI.— THE GEOGRAPHIC DISTRIBUTION OF BOMBIDÆ (HYMENOPTERA), WITH NOTES ON CERTAIN SPECIES OF BOREAL AMERICA.

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The fauna of boreal America is interesting not only because of its ability to withstand severe and prolonged cold but because of its bearing upon the problem of the origin of the entire American fauna. If it be true that the fauna of the warmer parts of America has been derived by successive waves of migration from the polar regions, the climate there having been, at times, milder than it is now and the path between Asia and Alaska fairly open, the present-day fauna of the boreal region may be considered to be one which has largely displaced its predecessors. Such of these predecessors as are now living are, for the most part, to be found in milder climates. Two reasons have been suggested for this movement: it may be that the older forms were adapted to the environmental complex which accompanies a milder climate and for this reason changed their range as the climate changed or it may be that there was an animate *vis a tergo*, the new forms actually driving the old out by competition. The effect would be much the same. Some of the species now found in the boreal region are doubtless remnants — representatives of groups which were formerly dominant there — and some are the result of eddies or tides in the southward-flowing stream of faunal migration — forms which have come in to help populate a region now more habitable than it was in the immediate past — so that the case is not so clearly defined as one might wish but it ought to be possible, by a study of distribution of the boreal and related species, to gather hints concerning the history of the faunal movements in America. Unfortunately, in the case of insects, sufficient direct paleontological evidence is not available for a definite decision.

The bumble bees (Bombidæ) have been selected in this case partly because we have a good monograph¹ of the American species and partly because it is generally believed that the family is of relatively recent origin. The first reason is of practical importance and the second is important to the discussion of theory. If a group is of recent origin we are fairly certain that it is nearly the culmination of its particular line. On the other hand

¹ Franklin, H. J. 1913. 'The Bombidæ of the New World.' Trans. Amer. Ent. Soc., XXXVIII, pp. 177-486; XXXIX, pp. 73-200.

a group which is of ancient origin may or may not be the latest that its line has produced.

For some reason, possibly because it is still actively evolving or possibly because the chips formed in the process of making species have not yet been cleared away, the Bombidæ are very difficult taxonomically. Many of the species were founded only on the color of the pilosity and, in fact, subgenera have also been proposed with color as the chief distinguishing characteristic. The only excuse for such subgenera is that they are of some help in identification. Variability in color is astonishingly great in certain species and is to be looked for in most of them. On the other hand, structural distinctions between species are usually slight and difficult to describe.

The Psithyridæ are Bombidæ which largely, or altogether, lack the habit of making nests and gathering pollen. In correlation with the lack of the pollen-gathering habit, the Psithyridæ do not have either corbiculæ or "pollen mills." Their eyes are smaller and their hind metatarsi narrower than those of their more industrious relatives. Further differences are the largely toothless mandibles, the lateral elevations on the female hypopygium, and the volsellæ of the male genitalia membranous (instead of corneous) with the apical projections absent. There is little doubt that the Psithyridæ are closely related to and have been derived from the Bombidæ by "degeneration." Giving a separate family name to them or classifying them with *Bombus* are merely matters of convenience and both plans are in good usage. They are not considered in this paper.

Two main divisions of American Bombidæ, in the narrow sense, are recognized: *Bombus* and *Bombias*. These are sometimes given generic rank but the distinctions are slight and they are more generally considered as subgenera of *Bombus* while Franklin (1913) believes that "the name *Bombias* should be entirely suppressed." This is not the time or place to discuss the relative advantages of the two arrangements and, furthermore, the Old World species have not been divided in this way so that we are, as yet, unable to bring them into line. In *Bombias* the ocelli are larger and placed lower, relative to the upper margins of the eyes, than in *Bombus*; the eyes of male *Bombias* are more bulging; the apices of the hind metatarsi of the female are usually not drawn out into so prominent and acute a projection, behind the insertion of the second tarsal segment; the malar space is usually shorter than its width at the apex; the volsellæ of the male genitalia are long and hind metatarsi of this sex are furnished with long hind fringes.

Franklin (1913) has divided the American species of *Bombus* into seven "groups": *Fraternus*, *Auricomus*, *Dumoucheli*, *Pratorum*, *Kirbyellus*, *Borealis* and *Terrestris*. The first two are divisions of *Bombias* and the rest

of *Bombus* in the narrow sense. The divisions follow, to a great extent, those of Radoszkowski¹ who was a pioneer in the application of a study of the genitalia to the taxonomy of these bees. Because of the relative inaccessibility of his paper, as well as because of the bearing of this grouping upon the present discussion, I list here the species as divided by Radoszkowski, not changing the synonymy.

1. The group of *B. pratorum* L.
B. pratorum L.
B. consobrinus D.
B. hypnorum L.
B. lapponicus F.
B. alticola K.
B. modestus E.
B. ussuriensis R.
B. pyrenaica P.
B. scrimshiranus K.
B. hæmaturus K.
2. The group of *B. lapidarius* L.
B. lapidarius L.
B. lefevrei Lep.
B. sicheli Rad.
B. niveatus Krich.
B. caucasicus Rad.
B. eriophorus Bib.
3. The group of *B. wurfleini* Rad.
B. wurfleini Rad.
B. mastrucatus Gerst.
B. vorticatus Gerst.
B. eximius Smit.
4. The group of *B. derhamellus* Kirb.
B. derhamellus Kir.
B. viduus Erich.
B. balteatus Dlb.
B. dagestanicus Rad.
B. baicalensis Rad.
B. muscorum L.
5. The group of *B. canus* Pall.
B. canus Pal.
B. pomorum Poz.
B. mesomelas Ger.
6. The group of *B. sylvarum* L.
B. sylvarum L.
B. equestris F.
B. mlokoscwitsi Rad.
7. The group of *B. tristis* Seidl.
B. tristis Seidl.
B. insipidus Rad.
8. The group of *B. fervidus* F.
B. fervidus F.
B. subterraneus L.
B. distinguendus M.
9. The group of *B. dumoucheli* Rad.
B. dumoucheli Rad.
B. chilensis Spil.
B. thoracicus Sich.
10. The group of *B. terrestris* L.
B. terrestris L.
B. fairmairi Sich.
B. portchinski R.
B. renardi Rad.
11. The group of *B. soræensis* F.
B. soræensis F.
B. perplexus Rad.

It should be remembered that this was pioneer work, the author himself adding to the list in 1883² and making certain corrections, notably that the *viduus* of his 1884 paper was a misidentification. Furthermore it is, for the most part, concerned only with European species. However, *chilensis*

¹ Radoszkowski, O. 1884. 'Révision des armures copulatrices des mâles du genre *Bombus*.' Bull. Soc. Imp. Nat. Moscou, LIX, pp. 51-92.

² Radoszkowski, O. 1888. 'Études Hyménoptérologiques. I. Révision des armures copulatrices des mâles.' Horæ Soc. Ent. Rossicæ, XXII, pp. 315-323.

Table 1. Certain distinguishing characteristics of the various American groups of *Bombus*.

	<i>Dumoucheli</i>	<i>Pratorum</i>
♀ Head	elongate triangular	variable but usually distinctly triangular
♀ Malar space	of good length	usually of fully average length
♀ Mandibles	distinctly 3-toothed	as in <i>Dumoucheli</i>
♀ Hypopygium	without median carina	usually without median carina
♀ Pile	rather coarse and of medium length	medium to long, of variable texture
♂ Antennæ	long and slender	of not more than average length
♂ Corbiculæ	very slight or absent; little or no hair	more or less strong; long hairs
♂ Outer surface of Posterior tibiæ	distinctly convex	usually at least slightly convex
♂ Hind metatarsi	bearing no long hair	with posterior fringe variable, never very short and in most species rather long
♂ Claspers	thick and powerful, rather short; branches very wide at base and narrowing very rapidly toward the apical portion	rather slender and weak; apex of each branch broadly rounded, its inner side, in most cases, more or less pointed
♂ Volsella	very broad and thick with long triangular recurved apical projection	long and slender, usually of about the same width throughout except at the base where it is, in most cases, rather suddenly wider
♂ Squama	usually with a very prominent inner lobe, this usually being elongate in form and widened and rounded at the end	triangular in outline, the inner lobe being vestigial or absent

Table 1 (continued).

<i>Kirbyellus</i>	<i>Borealis</i>	<i>Terrestris</i>
very long triangular	triangular	broad and rounded
reaching its maximum length	long	short
as in <i>Dumoucheli</i>	as in <i>Dumoucheli</i>	strongly 4-toothed
without median carina	with median carina	without median carina
long and fine	short and fine	
moderately long and slender	very long and slender	of less than average length
very distinct; long hairs	not very distinct; for the most part, only short hair	very well developed; long hairs
very slightly convex	distinctly concaved	slightly convex
margins fringed with long hairs	bearing only short spines and pubescence, with no long fringes	with hind fringes short or very moderate, never very long
long and rather slender; branches with broadly rounded apices	long, rather thick and powerful; branches very broad at base but narrowing rapidly to a sharply rounded, almost pointed, apex	short, thick and stubby; branches wide at base but narrowing rapidly to an almost pointed apex
very long and slender, gradually tapering from the base and with a broadly rounded and irregularly serrate-margined apical projection	broad and heavy; narrowest toward apex, with broadly rounded and recurved apical projections, with very coarsely and irregularly serrate margins	considerably wider at the base than toward the apex, apex appearing very hairy and obliquely truncate and with a rather narrow recurved apical projection
oblong or irregularly triangular, the inner lobe vestigial or absent	large and prominent, with outer lobe vestigial, irregularly quadrate, with inner posterior part pointed or nearly so	almost divided by a deep notch on the inner side, inner lobe triangular and pointed on inner side

(now referred to *dahlbomii* Guér.) and *thoracicus* (*emiliae* D. T.) are South American and are placed by Franklin, following Radoszkowski, in the *Dumoucheli* group, together with numerous other species. Franklin has also placed a large number of American species in Radoszkowski's *Pratorum* group. *B. balteatus* Dlb., of the *Derhamellus* group, is probably a synonym of *B. kirbyellus* Curt. and was placed by Franklin in his *Kirbyellus* group together with other Old World species. The point, at present, is not what name should be given to the group but that the *Kirbyellus* group of America exists or has near relatives in the Old World. Franklin has renamed Radoszkowski's *Fervidus* group, calling it the *Borealis* group on the ground that the species which Radoszkowski identified as *fervidus* was really *borealis*, a not nearly related species. The *Terrestris* group of Radoszkowski is accepted by Franklin. It will thus be seen that all the groups of American *Bombus* are represented in the Old World.

Neither of the groups of *Bombias* have, as yet, had Old World species referred with certainty to them, although it seems probable that Franklin's *Fraternus* group is synonymous with Radoszkowski's *Wurfleini* group and Franklin suggests that *vorticossus* as described and figured by Schmiedeknecht, not the *vorticossus* of Radoszkowski's list, may belong to the *Auricomus* group.¹ As before, the main point here is that these groups, as well as the groups of *Bombus*, are represented in the Old World. According to the conclusions reached in this paper, I would expect the Old World species of *Bombias* to be most abundant in the western and southern parts of the range of the family.

Some of the more important distinguishing characteristics of the five American groups of *Bombus* are given in Table I. Franklin's key for separating the two groups of *Bombias* is as follows:

- "Females with the disc of the clypeus finely and evenly punctate all over; the males with the third antennal segment as long as the fourth and fifth taken together *Auricomus*.
 Females with at least the anterior part of the disc of the clypeus more or less smooth; the males with the third antennal segment at most not much longer than the fifth *Fraternus*."

There is little doubt that the Bombidæ were derived from the *Euglossa-Hemisia* complex, probably from an ancient *Euglossa*, as has been indicated by Friese² and others. At the present time, these bees are confined to the

¹ See pages 182 to 184 of the second part of Franklin's monograph. In Ent. News, 1915, XXVI, pp. 409-417, he refers additional Old World species to *Bombias*.

² Friese, H. 1900. Monographie der Bienengattung *Centris* (s. lat.). Annalen K. K. Naturhist. Hofmus., XV, p. 240.

Western Hemisphere and I know of no evidence which indicates that they ever were in the Eastern Hemisphere. Therefore, the Bombidæ probably originated in the New World, but this does not necessarily follow. At the present time the *Euglossa-Hemisia* complex is confined to the tropical and subtropical parts of America, but I do not consider this sufficient evidence to prove that the Bombidæ originated in the equatorial region. In fact I believe that quite the opposite is true.

As to the phylogenetic relationship of *Bombus* and *Bombias*, Franklin says, "Certain of the *Bombias* species, which the writer has placed in the *Fraternus* group grade up so closely to certain species of the *Dumoucheli* group of the subgenus *Bombus* that they could almost be included in that group. It is found, furthermore, that the species which Robertson placed in the genus *Bombias*, fall naturally into two apparently distinct and widely different groups, as shown particularly by the differences in the genitalia of the males. The differences between these two groups (viz., *Auricomus* and *Fraternus*) seem to strongly indicate that they have had separate origins. Their geographical distributions, as far as they have been worked out, seem to greatly strengthen this supposition. . . . The writer regards the *Fraternus* group of the subgenus *Bombias* and the *Dumoucheli* group of the subgenus *Bombus* as being very closely related and as being the most primitive of all the groups of the genus *Bombus* present in the New World." Fig. 1 shows the American distribution of the *Fraternus* and *Dumoucheli* groups, the closeness of the shading roughly indicating the relative dominance, as estimated by the number of species, in various parts of the ranges of the groups. It will be noted that these primitive groups have a southern distribution.

Although Franklin expressed the opinion that the *Auricomus* group of *Bombias* originated independently of the *Fraternus* group, he does not seem to have indicated its nearest relatives. The outer surfaces of the posterior tibiæ of the males are "somewhat concaved." This is true of the *Borealis* group but not of the others. It is probably a recent character as it seems to be a transference of a female secondary sexual character to the male. On the other hand, the inner lobe of the squamæ is "a mere tooth at the base of the outer one." In *Borealis* the outer lobe is vestigial while the inner lobe is vestigial in the *Pratorum* and *Kirbyellus* groups. There are only two species at present placed in the *Auricomus* group so that it is scarcely worth while to discuss its phylogeny further. They are probably relatively recent species and they have a moderately northern distribution.

The relationships of the other groups of American Bombidæ are also not as clear as one might wish and their relationships to the Old World groups are less so. Of course, the American groups may not have been derived one

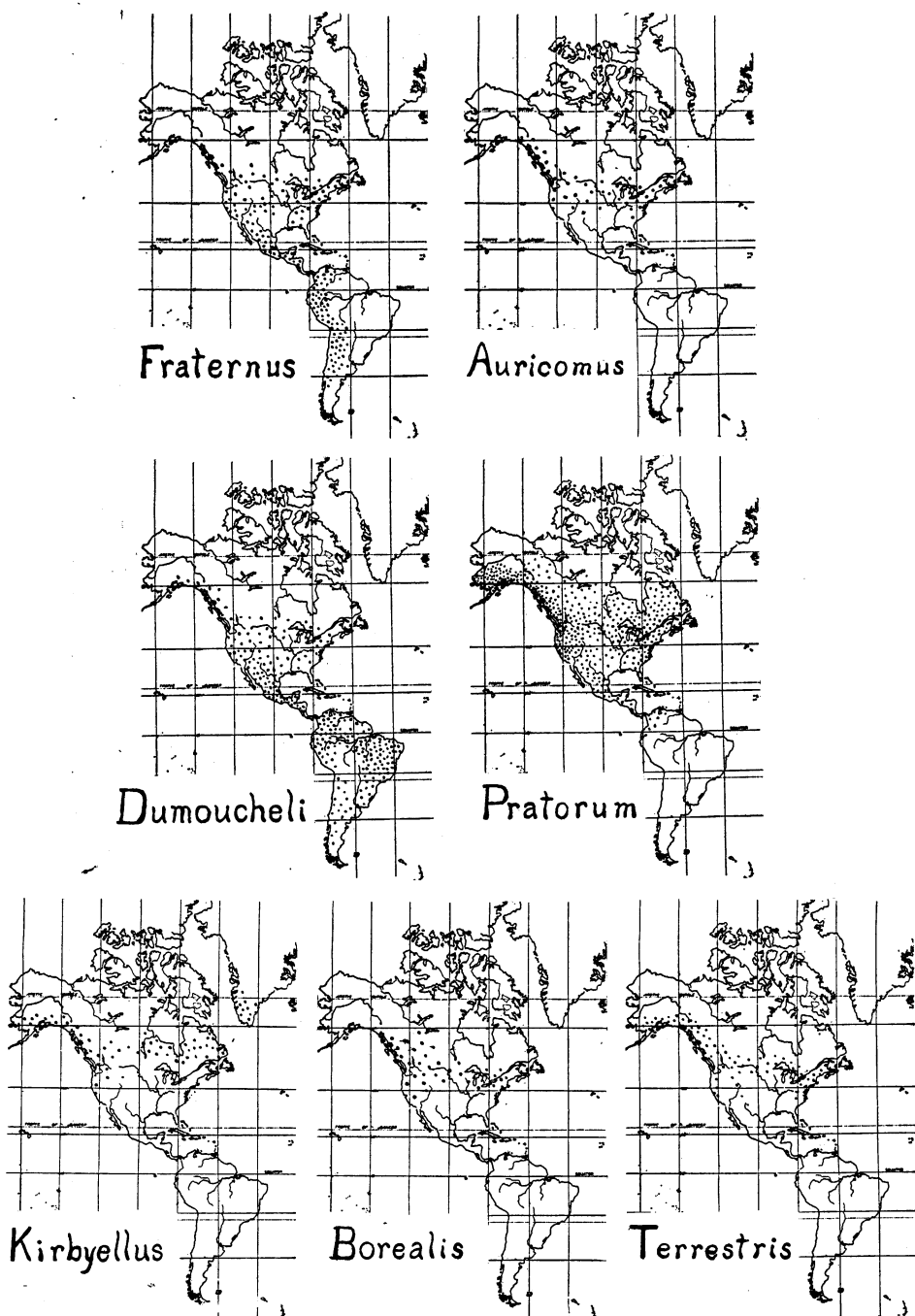


Fig. 1. The distribution, in America, of certain groups of *Bombus*. The relative number of dots in the various areas is roughly proportional to the number of species but the dots are not so placed as to indicate definite locality records.

from another but all, or a part of them, may have come from a group, or groups, which is now extinct or to be found only in the Old World. Furthermore, the groups may not be homogeneous, this being especially likely to be the case with *Pratorum*. However, some suggestions may be had from the table of characters given here. As a starting point we may follow Franklin in considering *Dumoucheli* to be the most primitive of the American groups.¹ On the other hand, "The sagittæ [of the male genitalia] attain their greatest complexity" in the *Terrestris* group (Franklin, p. 225) and the males of the *Terrestris* group have "very well developed corbiculæ" (p. 231). The latter character, like the concavity of the posterior tibiæ of *Auricomus* and *Borealis*, is a transference from the female to the male of a secondary sexual character and such a transference is usually considered to be a mark of relative lateness in phylogenetic history, so that we may start by putting *Dumoucheli* near one end of the series and *Terrestris* near the other.

The *Pratorum* group seems to be, in many ways, intermediate between *Dumoucheli* and *Terrestris* but certain characters, *e. g.*, the claspers, volsella and squama of the male genitalia, make it more probable that *Terrestris* is related more directly to *Dumoucheli* than through the intervention of *Pratorum*. However, the *Kirbyellus* group seems to have been derived directly from *Pratorum*, if from any of these, and *Borealis* may have been but it seems difficult to derive *Terrestris* from either *Borealis* or *Kirbyellus*. It will be noted that *Pratorum* is "variable" in many characters. This may be an indication of intermediateness or it may merely mean that the group, as now limited, is not homogeneous. Whatever the actual relationships, there are strong indications that the phylogenetic order is (1) *Dumoucheli*, (2) *Pratorum*, (3) *Borealis*, *Kirbyellus*, and *Terrestris*. From Fig. 1 it will be noted that this is also roughly the order, from south to north, of the centers of present-day distribution.

Table 2 gives a summary of the numbers of species in the various regions, taking the data given by Franklin in his monograph. The conclusions, drawn from this table and the discussion which has gone before, will doubtless differ. If these data were taken by themselves a very good case could be made out for the idea that the Bombidæ originated in South America from the *Euglossa-Hemisita* complex which is now and, as far as direct evidence goes, has always been confined to equatorial America. The *Sylvarum* group came first and spread to Asia and Europe but left no representatives behind. Then *Fraternus* and *Dumoucheli* originated either from

¹ Franklin suggests that the Old World *Sylvarum* group is more primitive but as we do not know what species belong to it we cannot discuss its distribution. It is interesting to note that its type species is found in Ireland and southern England.

Sylvarum or directly from *Euglossa* and spread northwards, both reaching the far north and continuing through Siberia westward. As these groups spread northward they left representatives behind and gave rise to other groups, *Pratorum* first and later to *Borealis*, *Kirbyellus* and *Terrestris*.

Table 2. The number of species in various regions.

	Boreal N. A.	Nonboreal U. S.	Mexico and C. A.	S. A.	Total
<i>Fraternus</i>	1	6	10	12	23
<i>Auricomus</i>	1	1	—	—	2
<i>Dumoucheli</i>	1	3	11	15	24
<i>Pratorum</i>	14	9	5	2	27
<i>Terrestris</i>					
<i>Borealis</i>	10	1 (or 2)	—	—	11
<i>Kirbyellus</i>					

Although such a history might be possible, as far as the direct data go, I doubt that it is correct for several reasons: (1) such does not seem to have been the history of groups concerning which we have fossil evidence; (2) changes of climate in geologic time; (3) there are no *Bombus* in the Antilles, and they are rarer in the south temperate than in the north temperate, and (4) it seems to me much like rolling up hill for a group to leave the tropics and not only enter but become dominant in the Arctic. These reasons are stated in what seems to me to be the order of their importance.

1. We probably never will have sufficient fossil evidence concerning the ancient insect faunas to use it decisively in a discussion of distribution. However, if the evidence furnished by fossils of other groups show that all, or even most, of them originated in polar regions and moved toward the equator, we should see if the distributions of the other groups could be similarly explained. If they can, without a distortion of fact, such an explanation should be favored. Dispersal from polar, especially north polar, regions has so recently been discussed¹ that the arguments need not be repeated here.

2. It is well established that, in addition to minor fluctuations, there

¹ Matthew, W. D. 1915. 'Climate and Evolution.' *Annals N. Y. Acad. Sci.*, XXIV, pp. 171-318; Lutz, F. E. 1915. 'List of Greater Antillean Spiders with notes on their distribution.' *Annals, N. Y. Acad. Sci.*, XXVI, pp. 71-148 and 1916. 'Faunal Dispersal.' *Amer. Nat., L.*, pp. 374-384.

have been several large alternations between a zonal climate, cold at the poles, and a uniform warm climate. The creatures now under consideration are of so recent origin that doubtless only the last swing from mild at the poles to the present climate need concern us. If the Bombidæ originated, say with the *Sylvarum*, *Fraternus* and *Dumoucheli* groups, in the then mild north it is easy to believe that, as the climate there became more rigorous, the primitive species, being adapted to a mild climate spread southwestward (*Sylvarum*) and southward (*Fraternus* and *Dumouchlei*), and their place was taken by new forms adapted to the new conditions. These in turn gave place to still newer forms adapted to still more rigorous climatic conditions and to the environmental complex brought about by the new climate.

3. The only record of Bombidæ in the Antilles is *Bombus antiquus* Fab., which was described from Antigua but it is not known whether the island or one of the other numerous Antiguas was meant and, furthermore, there is even no certainty that it was a *Bombus*. It has never been found since but the name still hangs in the lists. In addition to all the other collecting which has been done, entomological expeditions from this museum have been in most of the Antilles, including Antigua, and none of them has brought back a *Bombus*. Now it is probable that if the Bombidæ originated in or near the American tropics some of the species would have found their way into the West Indies because, even though the family is a relatively recent one, that would mean that they had been in the adjacent continental region for a long time. Furthermore the islands offer environments which seem to be perfectly suited to Bombidæ and *Hemisid* is fairly abundant in them. Also, if Bombidæ originated in equatorial regions and spread out from there, one would expect to find them almost, if not quite, as abundant in the south temperate regions as in the north temperate ones. They do not seem to be; a fact which accords with the idea that they are of boreal origin and that only the van has reached South America.

4. The fourth reason need not be given much space. It is a feeling more than anything else and probably is largely anthropic. We know that men of northern countries are more vigorous than those of the tropics and have repeatedly spread into equatorial regions, displacing the natives. We "feel" that conditions in the arctic must be more rigorous than in regions of milder climate and it is difficult to believe that creatures adapted to a mild climate could successfully invade the boreal region and become dominant there.

The history, then, of Bombidæ in America seems to me to be that they originated in the north from the *Euglossa-Hemisid* complex at a time, presumably just prior to the last oncoming of zonal climate, when climatic conditions in the north were at least mild. Of the American groups,

Fraternus and *Dumoucheli* were the first to appear and, as the climate became more rigorous, their immediate ancestors moved southward accompanied and followed by them. Certain species of these groups were, or became, adapted to the new conditions and lagged behind the others. Both groups sent representatives to the Old World and *Dumoucheli* probably gave rise to the *Pratorum* group. This in turn spread southward but it has only got half way, so to speak. The other groups came later but they contain so few species in America and they have spread so little, in the southern direction, although all of them have spread into the Old World, that the analysis is more difficult. The only reason for placing the area of origin in the northern New World rather than in the northern Old World is that the *Euglossa* complex, the presumed ancestors, seem to be confined to the New World.

Cockerell¹ has given us a short but interesting discussion of the phylogeny of *Bombus*, based upon his intimate knowledge of fossil insects. The following extracts show his views.

The Bombidæ thus appear to have originated in Europe, but to have reached America as early as the Miocene.

Although *Bombus* and *Psithyrus* are thus derived from *Calyptapis* in the diagram, this must not be taken too literally, as meaning that they are of American origin. *Calyptapis* very probably occurred in both hemispheres, as *Bombus* does to-day, or was represented in Europe and Asia by allied genera, from which *Bombus* might equally well be derived.

It would even be possible to use *Calyptapis* as an argument in favour of the Old-World origin of *Bombus*. It is recognized that nearly all modern insect-genera are older than the Miocene; hence if *Bombus* already existed it would probably be in the Old World, and *Calyptapis* would represent an earlier type segregated in America, to be exterminated later by the invasion of *Bombus*.

As was indicated above, it is immaterial to the point of this paper whether *Bombus* originated in America or in the Old World or both. Cockerell's discussion of what may have happened to *Calyptapis* is right in line with the present argument — the ancestral type overcome (in this case exterminated) by a newer type moving from the north.

Further study of the more remote phylogeny may favor Siberia as the area of origin but the point which it is desired to make here is that new forms appeared in the north and that when newer forms appeared the older ones, for the most part, moved before them. It is not meant to imply that there was an absolutely linear progression but that, roughly, this was the order, individual species, however, lagging behind and catching up while, what is

¹ Cockerell, T. D. A. 1908. Descriptions and records of bees. XX. Ann. Mag. Nat. Hist., Ser. 8. II, pp. 323-334.

very important, new species originated and old ones died out along the way. The metaphor of a stream has been used. Perhaps that of a certain sort of rocket might be suggested: the progress of the rocket is in a certain definite direction but in its course it shoots stars in all directions and these, in turn, break up into other sprays of stars.

NOTES ON BOREAL SPECIES.

Fraternus group.

In giving the distinctive characters of *Bombias*, Franklin says "The apices of the hind metatarsi usually not drawn out into so prominent and acute a projection, behind the insertion of the second tarsal segment, as is the case in the subgenus *Bombus*" and notes that *Bombias rufocinctus* and *mexicensis* are two of the more notable exceptions to this. *B. rufocinctus* is the most northern species of the *Fraternus* group, in fact, the only boreal or subboreal representative, while *mexicensis* is little more than a southern form of it. I fear we cannot say, at present, whether *Dumoucheli* came from *Fraternus* or the reverse but, if we should look to the north for recent forms, this northern *Bombus*-like *Bombias* would indicate that *Dumoucheli* came from *Fraternus*. In that case we would need to explain why *Fraternus*, in South America, has largely kept to the mountains while *Dumoucheli* has spread out over the lowlands. It might be because the lowlands were too swampy when *Fraternus* reached there (there being evidence that such might have been the case up to late Tertiary) and dry enough for Bombids when *Dumoucheli* arrived, but I think such an explanation is rather lame and the character noted is so slight that it needs support before much reliance can be placed upon it in tracing relationships. Considering the more fundamental differences between *Bombus* and *Bombias*, such as in the position of the ocelli and venation of the wings, it seems likely that the form of the metatarsus of *B. rufocinctus* is a reversion to the *Bombus* pattern or even that the two groups originated from the *Euglossa* complex independently. If *Fraternus* is a more recent group than *Dumoucheli* we can readily understand why it has not, as yet, established itself generally on the lowlands of South America.

B. rufocinctus is at home in the mountains of western United States and the following points outline its known range: British Columbia, Quebec, New York, Kansas, New Mexico.

Dumoucheli group.

In the far north this group is represented only by *californicus* Smith (*neglectulus* Ashmead). Like *Bombias rufocinctus*, this species is extremely variable. There may be nothing in it but one is tempted to wonder whether there is any relation between extreme variability — plasticity — of a species and recentness of origin. More likely the connection in these cases is between variability and distribution in regions of extreme isolation. The range of *californicus* is from southern Alaska to Saskatchewan and south to Lower California and New Mexico. There is no representative of the *Dumoucheli* group in the eastern boreal region, *fervidus*, a species closely related to *californicus* belonging rather to the Transition. *B. pennsylvanicus* is also close to these, especially to *fervidus*. It belongs to the austral fauna of the United States.

Franklin considers "*montezumæ* and *nigrodorsalis* the most primitive of all the New World species of *Bombus*." The former is now considered to be a variety of the latter. The species occurs from Mexico to Costa Rica, while *wilmattæ* Ckll., with its closest ally in *nigrodorsalis*, is recorded from Guatemala and Ecuador. Franklin does not give his reasons for believing these to be the most primitive but, even if they are so, the theory of dispersal from the north is not negated by the finding of the most primitive forms stranded along the way.

Pratorum group.

The published records of *B. ternarius* Say place it rather definitely in the boreal fauna, the most northern being central Alberta on the west and Prince Edward Island on the east, while the most southern records are South Dakota and West Virginia. In the southern part of its range, its distribution is "spotty." The following localities, extending its known range, may be added from our collection: Battle Harbor, Labrador (C. W. Leng); and Lake Marcia, Sussex Co., New Jersey (F. E. Lutz).

B. edwardsii Cresson shares with *rufocinctus* (and *californicus*) the honor of having "probably caused the workers on the Bombidæ of North America more trouble than most others" because of its variability. It also is of our western mountains, ranging from southern Alaska to Alberta and south to Beulah, New Mexico. Franklin suggests that "sufficient collecting is likely to show that those color variants with the second and third dorsal abdominal segments largely covered with ferruginous-red pile are much more numerous in the southern part of its range (Colorado, Utah, Nevada, California and New Mexico) while those color variants which have these

segments mostly black are much more numerous in the northern part (Alaska, British Columbia, Alberta, Montana, etc.) — this is evidently the case in Montana and Colorado and only the *nearcticus* form has been taken in Alaska. As will be seen, this apparent characteristic is closely paralleled in the case of *flavifrons* and *rufocinctus*." We have specimens from Vancouver which have the pile on the second and third segments reddish, but in many other ways the fauna of Vancouver Island is more southern than its geographic position. This may be because it is an island, a refuge for the older, more southern, forms. Our specimens from Banff, Alberta, have these segments black or black and yellow.

Bombus melanopygus Nylander belongs to the western boreal fauna, ranging from southern Alaska to Baffin Land south to Colorado but not east of Saskatchewan and Colorado in the southern part of its territory. We have a male from above 6000 feet altitude near Colorado Springs, Colorado (H. F. Wickham).

Bombus sylvicola Kirby is purely boreal — Point Barrow, the northern extremity of Alaska, to Ungava Bay and Labrador. It does not appear to have reached southern Canada. We have it from Langton Bay, Northwest Territory (R. M. Anderson).

Bombus gelidus Cresson. After giving Aleutian Islands, Popoff Island, Koyukuk River, Kukak Bay and Nualaska as the distribution of this species, Franklin adds "one worker before me, which seems to be a little aberrant in coloration, from Signuia, Baffin Land (Schuchert and White), appears to belong to this species." We have five specimens collected by Mr. C. W. Leng at Battle Harbor, Labrador, which certainly seem to be *gelidus* so that the species is to be looked for throughout northern Canada.

Bombus perplexus Cresson is recorded from the Hudson Bay Country, Manitoba to Quebec and in the mountains to Tennessee and North Carolina; also from North Dakota to Michigan. Mr. Wm. T. Davis has a specimen from the mountains of Georgia which seems to be this species.

Bombus bolsteri Franklin was described from four queens and five workers from Newfoundland. We have numerous workers from Spruce Brook (C. W. Leng) and Codroy (L. P. Gratacap), Newfoundland, as well as three specimens from Spruce Brook which appear to be the undescribed male of this species. They have

Face, including the clypeus, densely covered with pile to above the bases of the antennæ, yellow but with a strong sprinkling of black especially around the antennæ; pile of the occiput yellow (a few black hairs on one specimen), above the eyes black. Malar space somewhat longer than its width at the apex. Fifth antennal segment very slightly longer than the third, the third somewhat longer than the fourth. Pile

of the thorax and scutellum yellow except for a very broad black interalar band which starts, in one of the specimens, with scattered black hairs among the yellow of the anterior dorsal part and, in two of the specimens, has a projection on the median portion of the scutellum. The pile of the dorsum of the abdomen is yellow on the first and second segments and black on the third and fourth; in two of the specimens the pile on the fifth and sixth segments is largely yellow but in the other specimens this pile is largely black except for the posterior angles of the fifth segment; seventh segment dark. Hind tibiae with the outer surface largely bare; the median area broadest near the apex, smooth and shining; long lateral hairs black. Short hairs on the hind metatarsi reddish, the long hairs on the basal portion of the posterior border black. Genitalia much like those of *vagans*.

It will be noted that one of Franklin's distinctions between this species and *vagans*, the yellow fifth dorsal abdominal segment, does not apply strongly to one of the males. One of our females also has no yellow back of the second segment, and in another the yellow on the fifth segment is strongly mixed with black.

Bombus couperi Cresson belongs to the eastern boreal fauna, being known from Labrador, the region of Newfoundland, Ontario and Isle Royale, Lake Superior.

Bombus frigidus F. Smith reaches from Alaska to Labrador and Newfoundland. In more southern regions it seems to be confined to the west where its distribution is spotty and high in the mountains, *e. g.* "Truchas Peak, above timber line" and "top of Las Vegas Range," both from New Mexico by T. D. A. Cockerell. We have a male from the Athabasca River, Alberta (R. M. Anderson) and a worker from Collins, Idaho.

Bombus pleuralis Nylander, appears to be confined, in America, to the Alaskan region but it has been reported also from Siberia.

Bombus flavifrons Cresson ranges from Alaska to Alberta and, in the mountains, south to Beulah, New Mexico. More eastern records have been given but Franklin doubts them. We have a specimen from Truches Peak, New Mexico (W. P. Cockerell). Franklin notes that this species may not be distinct from *pleuralis*.

Bombus sitkensis Nylander appears to be common in Alaska and British Columbia. It occurs at least as far south as California and Idaho but apparently has not extended its range eastward.

Bombus mixtus Cresson occurs from Alaska to Labrador and south, in the mountains, to California and Colorado. It is most abundant in the northwestern part of its range.

Bombus alboanalis Franklin includes a number of records for *hortorum* in America and some of those for *sitkensis*. In America it seems to be confined to Alaska but it is reported from northeastern Asia and may not be distinct from the European *hortorum* (Linné).

This list included fourteen species, or alleged species, of the *Pratorum* group which may be considered boreal although *ternarius* and *perplexus* are doubtfully so; neither have been recorded from Alaska, Labrador or Newfoundland. Of the remaining twelve, ten are recorded from Alaska and six from either Labrador or Newfoundland or both. Six of these Alaskan species have not been found on the east coast and only two of the eastern species are not found in the west. Furthermore the species which do not extend from coast to coast seem to be more common in the western part of their range. Finally there are only twenty-seven described American species in the group, as listed by Franklin, so that about half of the group is included here. The impression one gets is that the center of the group, as far as America is concerned, is in northwestern Canada with a gradually diminishing representation east and, especially in the mountains, south. It would be interesting to trace relationships of the species in order to determine whether the more recent ones are in the Northwest or near the edges of the range but that seems almost impossible at present. However, if the reader will kindly remember that the following suggestions are purely tentative and made largely in the dark no great harm will be done. The statements of relationships are based largely on scattered remarks by Franklin. See Fig. 2.

B. pulcher and *ephippiatus* are closely related to each other but as we are following Franklin and as he does not state their relationships to the other members of the group they will not be considered further except to say that they are the only *Pratorum* species reported from South America. *B. impatiens* is the only species of the group recorded from Florida and from it all the other species may be derived. Let us suppose that *B. impatiens* was the first member to originate in the northwest. From it came *bimaculatus* and *vagans*, each starting a line. To anticipate, these moved south and east with *impatiens* in the van and finally reaching Florida. Now let us follow the *vagans* line because it is simpler; however it probably developed later than the *bimaculatus* line. It gave off *perplexus*, *cockerelli* and *bolsteri*; the first is now found throughout much of the range of its parent, the second in mountains of New Mexico, where its parent does not seem to be and the last in the extreme northeast, Newfoundland. From *bolsteri* came *couperi*, now found just back of it, *i. e.* Labrador to Newfoundland and Lake Superior; then *frigidus*, Labrador, Newfoundland, Hudson Bay, Mackenzie and Alaska. *B. frigidus* is also closely related to the Old World *rajellus*, and from near *frigidus* we got a set of species which went southward rather than eastward: *mixtus*, first, which reached Labrador on the east but California and Colorado on the south; *sitkensis* and *alboanalis* from it, the former now ranging from Alaska to California and Idaho, the latter

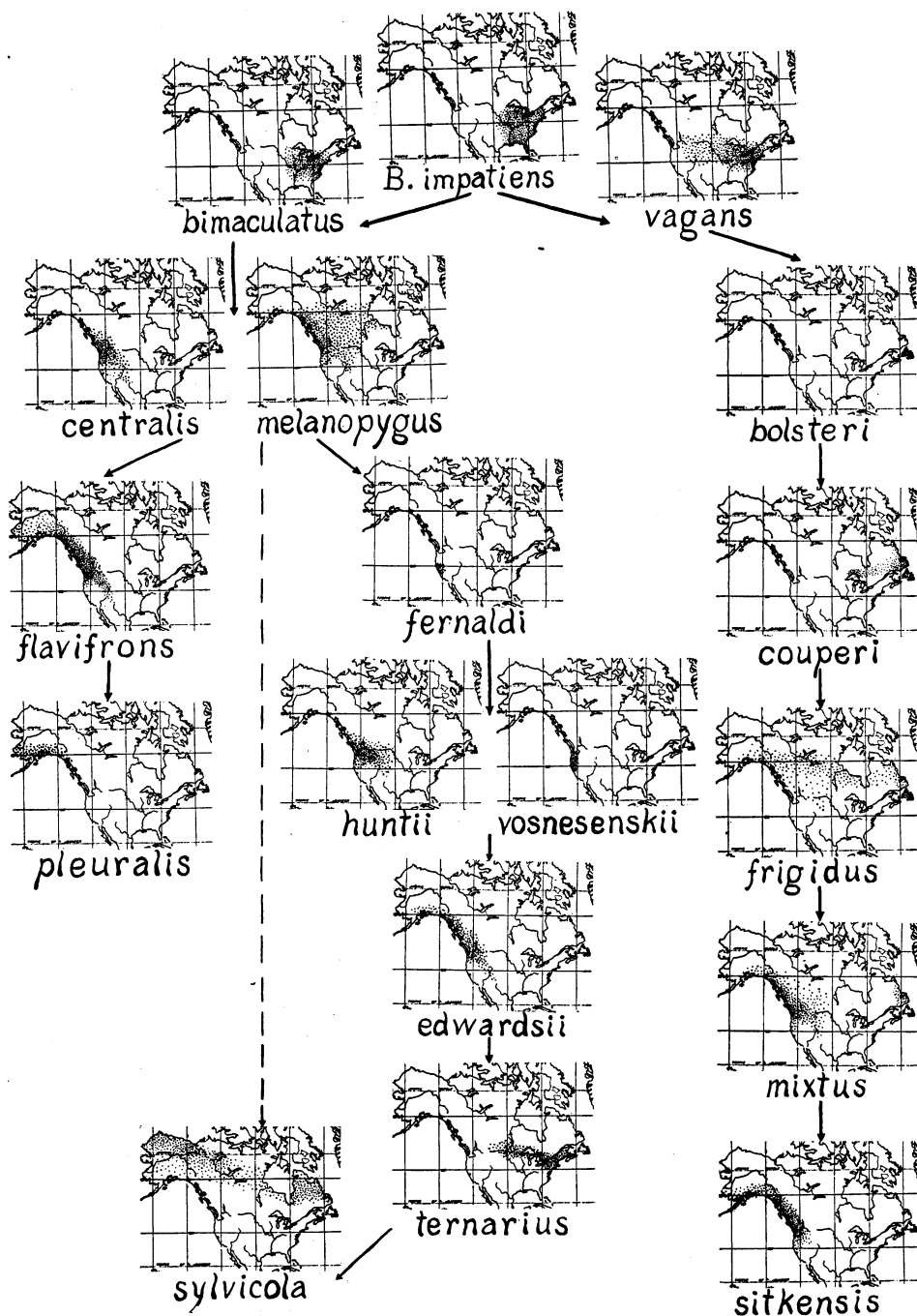


Fig. 2. The suggested phylogeny of a portion of the *Pratorum* group and the distribution of the species. The shading indicates general areas but the individual dots do not refer to definite locality records.

only in Alaska but related to the Old World *montanus*. Finally, the Pacific Coast *ambiguus* is probably only a form of *sitkensis*.

The *bimaculatus* strain is not so "simple," partly because of the uncertain relationships of the Rocky Mountain forms. *B. melanopygus* seems to have come from *bimaculatus* and to have been the starting point for a number of species. Franklin says it is "apparently a common species throughout western Canada and in southern Alaska, but for the most part rare in Canada east of the Rocky Mountains and, in the western United States, rare (very rare in Wyoming and Colorado) and confined mostly to the mountain chains, being a strictly Boreal form." It is closely related to the European *lapponicus* on the one hand and on the other hand *centralis* seems to be its southern offshoot. Perhaps *centralis* and *melanopygus* originated separately and in that case distribution would indicate that *centralis* is the earlier species, being now found from British Columbia to Nebraska, New Mexico and California. From the *centralis-melanopygus* combination, and perhaps directly from *centralis*, came *flavifrons*, Alaska to Alberta and New Mexico; and from it *pleuralis*, Alaska and (?) Siberia. From *melanopygus*, *sylvicola*, Alaska to Labrador, and *gelidus*, Alaska to Baffin Land may have been derived, but see below. Finally, there is a group which seems to have been derived from *melanopygus* through something close to the recently described *fernaldi*, California and Nevada. There is *vosnesenskii*, Washington to Nevada and southern California and *huntii*, Washington to Colorado, New Mexico and California, except the Lower Austral portions. *B. trinominatus* extends the distribution of *vosnesenskii* to Mexico and *laticinctus* does the same for *huntii*. From the *huntii-vosnesenskii* combination, but from nearer *huntii*, we got *edwardsi*, Alaska, to New Mexico and California. It seems to have given off *ternarius* which moved eastward and southward, Alberta to Prince Edward Island, South Dakota and West Virginia, in front of its offshoot, *sylvicola*, Alaska and Saskatchewan to Labrador, if we derive *sylvicola* from *ternarius* rather than directly from *melanopygus*.

In any discussion such as has just been indulged in there is danger of unconsciously twisting the data to fit the theory. A reference to Franklin's paper will, I think, show that such twists have been largely avoided in the present instance. The case of *centralis* would have fitted in more smoothly if that species had been indicated as closely related to *bimaculatus* but the irregularity is not serious and furthermore it may really have been derived from *bimaculatus* and yet now appear to be more closely related to *melanopygus*, another derivative, than to its parent species. My only fear is that I have proved too much. I do not expect that every group of animals would work out with such regularity and the danger is that the student, finding

that they did not, will discard the whole idea. Among the many sources of confusion, polyphyletic origins, backward movements of faunas and incorrect interpretations of phylogeny may be mentioned as the most likely to occur. I have not attempted a similar analysis of the other groups of *Bombus* since, with the exception of the *Dumoucheli* group there are too few species to make it interesting and Franklin does not give enough data to make the task of connecting up the various parts of the *Dumoucheli* group easy.

Kirbyellus group.

All of the *Kirbyellus* groups in America are boreal.

Bombus kirbyellus Curtis ranges from Siberia to Labrador and Greenland, southward through British Columbia and Alberta to Colorado and Truchas Peak, New Mexico, but not, as yet reported, from California. Through the courtesy of Mr. B. Preston Clark we have a number of specimens from Kadiak, Alaska, which Mr. Franklin says are probably aberrant males of this species.

Bombus kincaidii Cockerell is known only from the Pribilof Islands.

Bombus strenuus Cresson; Fort Yukon and Fort Cosmos, Alaska; Hudson Bay Country.

Bombus polaris Curtis is recorded from Labrador and Greenland but Franklin discredits Ashmead's report of this species in Alaska. We have a number of workers collected by V. Stefansson at Barrow, Alaska, and a queen collected by R. M. Anderson at Tupkak in the delta of the Mackenzie which certainly seem to be *polaris* although they have been in alcohol and identification is difficult.

Bombus arcticus Kirby: "Greenland and Arctic Canada. It seems not improbable that this is the same species which is present in the northern regions of Europe and Asia and is known as *B. hyperboreus* Schönherr."

It should be noted that the only species of *Bombus* recorded from Greenland belong to the *Kirbyellus* group, that three of the five American species of this group occur in Greenland and that two of these three are probably specifically identical with Siberian species.

Borealis group.

There are only two American species of the *Borealis* group given in Franklin's monograph.

Bombus borealis Kirby is not so boreal as many other species of *Bombus*. Its recorded northwestern limit is Alberta (Beaver Lake) and its north-

eastern, Newfoundland; its recorded southern limits are North Dakota and Massachusetts. We have specimens from Boisedale, Cape Breton Island (C. W. Leng); Codroy, Newfoundland (L. P. Gratacap) and Campo Bello Island, southern New Brunswick.

Bombus appositus Cresson. The only Canadian records are from British Columbia (Kelowna, the most northern) and it reaches its greatest abundance in northwestern United States, extending however to Colorado and New Mexico. It should probably, but not certainly, be classed as boreal.

Terrestris group.

The final American group is *Terrestris*. One of the species, *occidentalis*, joins *edwardsii*, *californicus* and *rufocinctus* in being extremely variable and as they all have much the same range the difficulty of identification is greatly increased and the supposition strengthened that there is something in the environment which is responsible for the variability.

B. occidentalis Greene is found throughout a great part of Alaska, British Columbia and western Alberta; extending south to California and New Mexico. The geographic extremes in our collection are Banff, Alberta (*ex* J. L. Zabriskie collection) and Beulah, New Mexico (T. D. A. and W. P. Cockerell). Franklin states that *occidentalis* is related to *terrestris* on the one side and *terricola* on the other.

Bombus terrestris (Linné) is mainly a palearctic species but what is probably a variety of it, *moderatus* Cresson occurs in Alaska and probably Yukon. We have a fine series of this species from Kadiak, Alaska, given us by Mr. B. Preston Clark. There is a tendency in both males and females (including workers) for the yellow on the thorax and second segment of the abdomen to be white; in fact, it is quite white in some specimens.

Bombus terricola Kirby belongs to the lower and eastern Boreal: Alberta to Newfoundland and south to North Dakota and Rhode Island according to the records, but we have a male from Ramsey, N. J. (F. E. Lutz) and a worker from the Black Mountains, North Carolina (Wm. Buetenmuller). Our most northern specimens are from Boisedale, Cape Breton Island and Codroy and Spruce Brook, Newfoundland.

The only other American species of the *Terrestris* group is *affinis* Cresson and it can scarcely be considered as boreal.

