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Notes on the Subgenera of the New World Carpenter Bees of the Genus *Xylocopa* (Hymenoptera, Apoidea)[1]

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The carpenter bees of the genus *Xylocopa* of the New World are neither so numerous in species nor so diverse morphologically as are those of the Old World. The majority of the New World forms occur in South America, with distributions of some species extending well into Central and North America. Three distinctive groups of these Neotropical species are each represented in the United States by one or two species. None of these groups is related, except remotely, with the Old World *Xylocopa,* in spite of the apparent superficial resemblance of some of the species. One additional group of New World species, the morphological affinities of which are closest to the Old World *Xylocopa,* especially its nominate subgenus, and of which the present distributions are clearly Nearctic, are quite apparently a relatively recent derivation of that fauna (see Hurd, 1955, p. 42, map 1). This interpretation is further strengthened by the fact that this group of species [*X. californica* Cresson and *X. virginica* (Linnaeus)] is closely associated with, and utilizes for nesting purposes some of the floral derivatives of, the Arcto-Tertiary Forest.

In a recent paper Michener (1954, p. 155) has divided the New World

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carpenter bees of the genus *Xylocopa* into three subgenera. Two of these, *Neoxylocopa* Michener proposed for the reception of *Xylocopa brasilianorum* (Linnaeus) and relatives, and *Schönherria* Lepeletier which includes such species as *X. micans* Lepeletier and *X. barbata* Fabricius, are most certainly Neotropical subgenera some of the species of which have extended their ranges subsequently into the Nearctic area.

The third New World subgenus, *Xylocopoides* Michener, as has been suggested earlier, includes two diverse groups (see Hurd, 1955, p. 42). One of these is composed of the two Nearctic species *Xylocopa virginica* (Linnaeus), the type of the subgenus, and *X. californica* Cresson. The other group contains the Neotropical species *X. tabaniformis* Smith, a number of closely related Central and South American species, and/or forms of *X. tabaniformis* (*alborufa* Friese, *azteca* Cresson, *chiriquiensis* Pérez, *illiota* Cockerell, *melanura* Cockerell, *4-maculata* Friese, *rufina* Maidl, and others), and some of the species assigned to Group II of the Maidl (1912) classification.

Because the subgenus *Xylocopoides* Michener, as now understood, is polyphyletic, one of the purposes of the present paper is to propose a new subgenus for the reception of the Neotropical elements at present included in that subgenus.

NOTOXYLOCOPA, NEW SUBGENUS

TYPE OF SUBGENUS: *Xylocopa tabaniformis* Smith, 1854.

Included in this subgenus are those New World species that have the following combination of characters.

Body of relatively small size, integument predominantly black, never metallic, males often with pale face markings and frequently with a pale spot near the base of each mandible; pubescence black, though often with variable amounts of pale pilosity, most noticeably on thorax and abdomen, especially in the male; mandibles of both sexes bidentate at apex, not expanded on outer margin near apex; inner orbits of male converging above, less so in the female; interantennal crest short, scarcely elevated, not produced into a high, prominent, laterally compressed tubercle; spines of anterior coxae and trochanters in the male present or virtually absent, not dorsoventrally compressed or expanded posteriorly; tarsal claws of both sexes with outer and inner teeth slender, nearly parallel, the inner ones shorter, approximately three-fourths as long as the outer ones; male with posterior margin of last metasomal tergum produced into a pair of well-separated acute teeth (penicilli); gonocoxite of male, viewed laterally, broad almost to apex, terminating rather abruptly medio-apically, forming a short, curved, hook-like process provided with

a brush of quite long, stiff bristles; posterior tibiae of females with scales simple, not or scarcely foveate; female with the two rows of spines on sixth metasomal tergum scarcely diverging anteriorly and thus forming a very acute angle with each other just before the posteriorly projecting flat-topped spine, the resulting groove so demarked is narrow and somewhat slit-like.

Key to the New World Subgenera of *Xylocopa*

1. Integument brightly metallic blue, green, or purple (weakly so in *X. virginica, sensu stricto*), sometimes with the under surface of the abdomen partly or largely testaceous 2
   Integument black or largely testaceous or yellowish, never metallic . . 3
2. Male gonocoxite, viewed laterally, broad throughout, apex nearly truncate, not divided; sixth metasomal tergum of female with the two rows of spines widely divergent anteriorly, nearly forming a right angle with each other just before posteriorly projecting flat-topped spine . . . . *Xylocopoides*
   Male gonocoxite, viewed laterally, attenuate apically, apex bifid as seen from above; sixth metasomal tergum of female with the two rows of spines scarcely diverging anteriorly, forming a very acute angle, the resulting groove so demarked is narrow and somewhat slit-like . *Schönherria*
3. Male gonocoxite, viewed laterally, attenuate apically, with apex somewhat expanded, the gonocoxite subapically produced ventrally into an acuminate prominence as well as inwardly towards the mid-genital region where it terminates as an acute process; integument of males often yellowish or testaceous; female with upper clypeal margin elevated and smooth; first metasomal sternum of female entire, never with a notch-like emargination . . . . . *Neoxylocopa*
   Male gonocoxite, viewed laterally, broad almost to apex, terminating rather abruptly, forming medio-apically a short, curved, hook-like process which is provided with a brush of quite long, stiff bristles; integument of both sexes black; female with upper clypeal margin not elevated and smooth; first metasomal sternum of female deeply emarginate medio-apically . . . . . *Notoxylocopa*

The subgenus *Notoxylocopa* is not clearly related to any of the known New World subgenera, as is discussed above. Its nearest relatives are probably to be found in the Old World, but the indications are that such a relationship will be remote, indeed much more removed than the Nearctic subgenus *Xylocopoides*.

All the known species of *Notoxylocopa* are of relatively small size though of robust form and reminiscent of the larger *Anthophora*.

The type species of *Notoxylocopa, X. tabaniformis* Smith, ranges from northern South America well into the mountainous regions of western North America, where one of its subspecies, *X. tabaniformis orpifex*

Smith, has come in contact with *X. californica,* a member of the Nearctic subgenus *Xylocopoides,* in the redwood forests of the Pacific Coast.

It is of further interest that the association with the redwood flora by *Notoxylocopa* presumably occurred after that established by the Nearctic *Xylocopoides.*

Cockerell (1914, p. 102) also has considered that those species that I restrict to the subgenus *Xylocopoides* Michener are not related to the species of tropical Mexico and Central America. Cockerell (*ibid.*), in discussing the species *X. californica* Cresson (especially the currently regarded synonym, *X. libocedri* Cockerell) and *X. virginica* (*Linnaeus*), observed that the mandibles are bidentate in the female, rather than tridentate as in the Old World *X. violacea,* the type of the nominate subgenus. That author concluded that the association of *X. californica* (= *X. libocedri*) with the incense cedar, *Libocedrus decurrens,* might be accidental, but that it is interesting to find a member of what appears to be a rather old type of North American bee connected with a plant genus which we know to be an ancient and now waning member of the flora.

It now seems quite likely that the Nearctic subgenus *Xylocopoides* was derived during the Tertiary from an Old World stock that remained associated with the Arcto-Tertiary Forest in North America. The following sequence of events, though admittedly largely speculative but based on an interpretation of the present knowledge of the group, seems to elucidate certain evolutionary aspects not previously evident or, for that matter, even possible. As the forest moved southward the original immigrant stock divided, one branch coming down along the Pacific coast, while the other moved eastward and eventually southward along the Atlantic coast (see fig. 1). When the trans-northern connection of the Arcto-Tertiary Forest, which had provided in the form of suitable nesting softwoods, disappeared, the complete isolation of the Pacific coast and Atlantic coast stocks occurred. Each of these stocks continued to differentiate and ultimately became specifically distinct from each other. Subsequently each of these in turn differentiated, the Pacific Coast species (*Xylocopa californica*) into three currently recognized subspecies, and the eastern United States species (*X. virginica*) into two subspecies. These species through their respective subspecies are today in virtual geographic contact in Texas, though they are apparently ecologically separated and no integradation has been demonstrated (see Hurd, 1955, map 1). In the process of this later differentiation, which has presumably brought these terminal populations in near geographic contact, each of the subspecies of the two species (*X. californica* and *X. virginica*) is

now associated with different types of softwood than available formerly to the original immigrant stock, with the possible exception of the nominate subspecies of *X. californica* which utilizes incense cedar and redwood for nest construction. It is noteworthy (Hurd, 1954) that the Pacific coast stock moved from incense cedar and redwood (the sub-

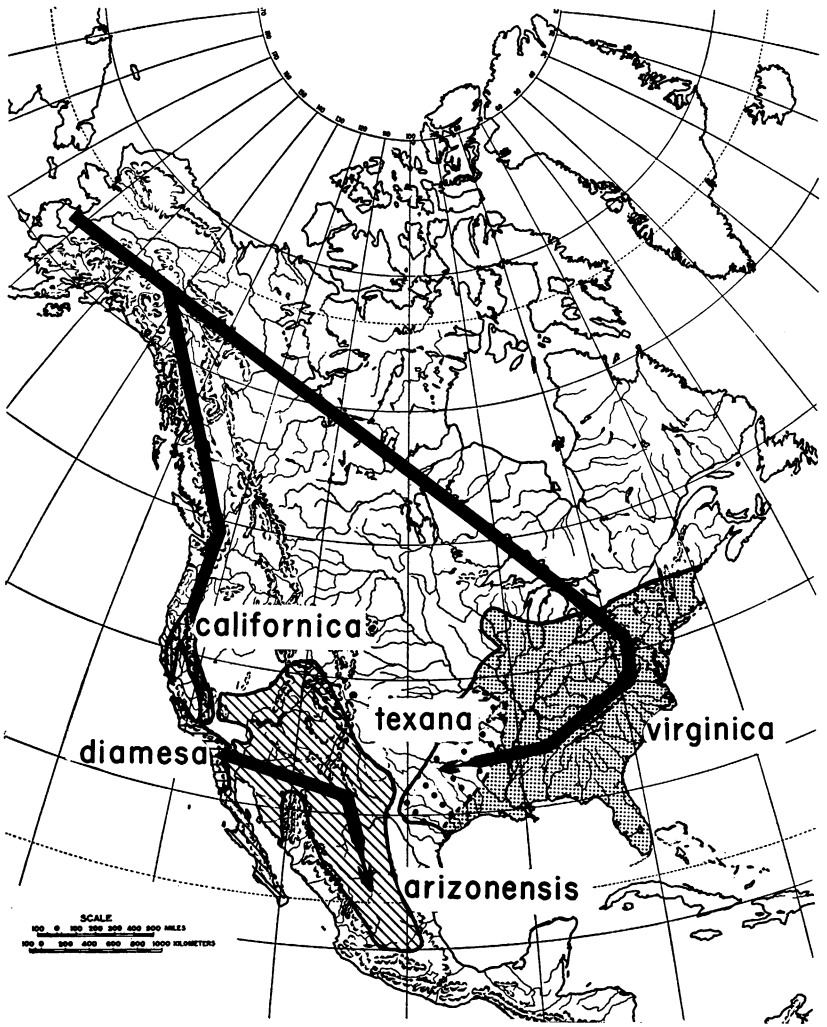

FIG. 1. Distribution (various overlays) and probable history (heavy black lines) of Nearctic *Xylocopa*, subgenus *Xylocopoides*. Distribution of *Xylocopa californica* Cresson and its subspecies (*arizonensis*, *californica*, and *diamesa*) indicated by parallel lines; that of *X. virginica* (Linnaeus) and its subspecies (*texana* and *virginica*), by dots.

species *californica*), to a Pacific slope group of the genus *Yucca* (the subspecies *diamesa*) which in all likelihood came in contact with the redwood flora at a later date, and thence to various interior yuccas and agaves (the subspecies *arizonensis*) eastward to Texas and southward onto the Mexican Plateau. In a similar fashion the species of the eastern United States (*X. virginica*) extended its geographic range southwestward into Texas where it apparently has reached the limits of its distribution in the region of the Edwards Plateau (*X. virginica texana*). That this type of range extension can occur in the genus has been suggested by the ability of *X. tabaniformis orpifex* to extend its nesting activities into areas of lower elevation than those formerly occupied by that subspecies. Such local range extensions are probably attributable to the creation of suitable nesting sites in the form of structural timbers placed by man in these areas previously unavailable to the bee (Hurd, 1955).

Of additional significance is the fact that the subspecies *X. californica arizonensis,* which as noted above normally nests in interior yuccas and agaves, will accept and nest in timbers of coast redwood which, except for the intervention of man, would never be available to the bee. Such activities have been personally observed in the Panamint Mountains of eastern California by E. G. Linsley and Ray F. Smith and attested to by specimens from Tucson, Arizona, which are labeled as "Ex nests in redwood plank." Both of these localities are well removed from the normal distribution of the redwood.

It is my interpretation therefore that the subgenus *Xylocopoides* Michener is the most recent addition to the New World *Xylocopa* fauna, that its two included species (*X. virginica* and *X. californica*) have evolved from a single stock which was derived from the Old World fauna, and that the subsequent evolutionary events are closely associated with the history of the Arcto-Tertiary Forest.

The newly proposed subgenus *Notoxylocopa,* as well as the other Neotropical subgenera (*Schönherria* and *Neoxylocopa*), was at this time already present in the New World and well differentiated, a conclusion that seems inescapable in view of the their relatively remote relationships today with the *Xylocopa* of the Old World.

It further seems likely that the contact between the Nearctic subgenus *Xylocopoides* and the Neotropical subgenus *Notoxylocopa* did not occur until those floral elements that provided suitable nesting softwoods (such as *Yucca* and *Agave*) became intermingled at least marginally with the softwoods (incense cedar and redwood) being utilized by the Pacific coast species of the subgenus *Xylocopoides*. This then provided the avenues of the respective southward and northward geographic range exten-

sions by species of these subgenera. It is a matter of speculation, of course, but, because the interpretation of the subspecies formation discussed above favors this idea, it seems the most likely explanation.

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