STUDIES ON THE NORTH AMERICAN REPRESENTATIVES OF *EPHEBOMYRMEX* (HYMENOPTERA: FORMICIDAE)

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Pogonomyrmex (*Ephebomyrmex*) *imberbiculus* was described by W. M. Wheeler in 1902 and seven years later he added the descriptions of *pima* and *townsendi*. Since that time there has been surprisingly little additional information published on these interesting ants. What has appeared has consisted largely of locality records, but few of these have added much to our knowledge of the ranges of these insects. It is gratifying to be able to present a more complete picture of the distribution of our representatives of *Ephebomyrmex*, particularly since this clears up certain questions related to the taxonomic status of *townsendi*. It has also been possible to expand Wheeler's account of the habits of *imberbiculus*, for it appears that these same habits are true of *pima* also. In past years the writer has been able to study 53 colonies of *Ephebomyrmex* at 40 stations. This study has shown that the ranges of both *imberbiculus* and *pima* are much more extensive than was formerly supposed. It has also shown that *townsendi* is a synonym of *imberbiculus*.

Wheeler described *townsendi* in 1909 (1) on the basis of a single specimen from Chihuahua. It is hard to avoid the suspicion that one of Wheeler's reasons for giving *townsendi* specific status is the fact that the type specimen came from Mexico. Certainly the structural features which distinguish *townsendi* from *imberbiculus* are not particularly impressive. They consist mainly of the sculpture of the postpetiole and the first gastric segment. Wheeler believed that in *imberbiculus* the postpetiole is

so feebly rugose as to be almost smooth and is marked only by scattered patches of punctures. In this same species the dorsum of the first gastric segment was said to be smooth and shining and without basal punctures. In *townsendi,* on the other hand, both the postpetiole and the dorsum of the first gastric segment were described as completely covered with fine, dense punctures and opaque. Wheeler also claimed that in general *townsendi* is more opaque than *imberbiculus.* Olsen accepted *townsendi* as a separate species in 1934 (2) but the writer in 1950 (3) treated it as a subspecies of *imberbiculus.* At that time there was little material of *townsendi* available but, since it was still the only member of the subgenus known from Mexico, it could be regarded as a southern race of *imberbiculus.* It is now clear that such a treatment is erroneous. As material began to accumulate it became apparent that *imberbiculus* occurs much further south in Mexico than does *townsendi* and that the latter form occurs at random, principally in the northwestern portion of the range of *imberbiculus.* The writer has taken colonies which agree well with the type of *townsendi* in northern Sonora and at three stations in southern Arizona. In these specimens both the postpetiole and the basal two-thirds of the dorsum of the first gastric segment are densely and evenly covered with small, close-set punctures which render the surface opaque or nearly so. These specimens can, without any diffculty, be assigned to *townsendi,* but this is not true of others which are intermediate in character. One nest from northwestern Chihuahua has the gastric punctuation limited to the anterior third of the segment. Another large colony from southeastern Arizona shows some individuals without gastric sculpture and others with only a small area of sculpture immediately adjacent to the postpetiole. In both these colonies the sculpture of the postpetiole is like that of *townsendi.* After it was appreciated that the supposedly definitive features of *townsendi* vary, a reexamination was made of all specimens previously assigned to *imberbiculus.* This established the

surprising fact that in most of the longer nest series there were a few workers which had a dull, densely punctate postpetiole like that of *townsendi.* In short, there is no constancy in the sculptural characteristics which were used as the basis for the recognition of *townsendi.* The case offers a close parallel to that of Olsen's *salinus,* a species which was also based on a single specimen which had a densely sculptured gaster. M. R. Smith has recently shown (4) that *salinus* is a synonym of *occidentalis,* being nothing more that an inconsequential variant which occurs in certain nests at the western end of the range of that wide-spread species. It appears that we must take the same stand with *townsendi.* Since *townsendi* is nothing more than a minor variation which occurs at random over a part of the range of *imberbiculus,* it is best treated as a synonym of *imberbiculus.*

Presented below is a list of the stations at which *imberbiculus* and *pima* have been taken. The previous records for *townsendi* are included with those for *imberbiculus.* Where possible elevational data for the older records have been supplied from topographic sheets. The writer is aware of the difficulties inherent in this method, but the stations so treated were in areas which left little doubt as to the elevation involved. The records for which no collector's name is given are those of the writer. Elevational data for these stations were secured from altimeter readings at the station, which were checked then or later against topographic sheets.

Pogonomyrmex (*Ephebomyrmex*) *imberbiculus* Wheeler:

CALIFORNIA: Yaqui Well, Anza Desert State Park (1400′).

ARIZONA: Kofa Mountains, Palm Canyon (1600′); Ajo Mountains, Alamo Canyon (2300′); Santa Rita Mountains, mouth of Madera Canyon (4800′); Tucson (2400′) W. M. Wheeler; Pinaleno Mountains, Fort Grant (4800′) Cornell Univ. Exped.; Whetstone Mountains, Dry Canyon (5000′); Huachuca Mountains, Garden Canyon (5800′); Safford (3000′).

SONORA: Divisadora de Leon, 23 miles north of Hermosillo (1200′).

NEW MEXICO: Aden (4300′) W. M. Wheeler; Animas Mountains, San Luis Pass (5400′); Lordsburg (4200′); Alamogordo (4300′) G. von Krockow. The ten records which follow are those of A. C. Cole: Dillia (5200′); 25 miles east of Bernardo (5950′); 18 miles southeast of Bayard (6000′) Malpais Lava Beds, near Carrizozo (5400′); 8 miles west of Alamogordo (5800′); 6 miles northwest of Deming (4550′); 20 miles north of Bernardo (6550′); 7 miles west of Socorro (7000′); 12 miles west of Hope (5200′); 23 miles north of Las Cruces (4500′).

CHIHUAHUA: Sierra de en Medio, Nogales Ranch (5000′); 6 miles south of Gallego (5100′); 7 miles north of Chihuahua City (4700′); 15 miles west of General Trias (5600′); Ojo del Cerro Chilicote, C. H. Townsend.

DURANGO: 17 miles south of Rodeo (5500′); 5 miles west of Durango (6300′).

COAHUILA: Sierra de la Muralla, 46 miles south of Monclova (4000′); 24 miles east of Ramos Arizpe (4600′).

TEXAS: 10 miles west of Sierra Blanca (4500′); Chinati Mountains, Arsarca Canyon (4800′); Chisos Mountains, Burnhams Ranch (4000′); Davis Mountains State Park (5000′); Ft. Davis (4700′) W. M. Wheeler; Alpine (4500′); San Angelo (1850′) W. M. Wheeler; Pyote 2600′); Langtry (1300′) W. M. Wheeler; Del Rio (950′) W. M. Wheeler; Juno, Cornell Univ. Exped.; Austin, Mt. Barker (640′) TYPE LOCALITY W. M. Wheeler.

OKLAHOMA: Wichita National Forest, W. Fisher; Harmon County, W. Fisher.

Pogonomyrmex (*Ephebomyrmex*) *pima* Wheeler:

ARIZONA: 5 miles south of Wickenberg (1800′); Tempe (1100′) W. M. Wheeler; Phoenix (1100′) W. M. Wheeler; Florence (1500′) W. M. Wheeler; Casa Grande (1500′)

W. M. Wheeler; 8 miles north of Casa Grande (1500′); 5 miles east of Aguila (2200′); 20 miles east of Gila Bend (2700′); Organpipe Cactus National Monument, Headquarters (1600′), Dripping Spring (1700′), Abra Wash (1300′), Quitobaquito (900′); Tucson (2400′) TYPE LOCALITY W. M. Wheeler; Bowie (3750′) W. M. Wheeler; Continental (2900′) no collector.

SONORA: 10 miles south of Sonoyta (1400′); 5 miles south of Santa Ana (2500′); Puerto Gonzalitos (2500′); 10 miles south of Hermosillo (700′); 33 miles north of Guaymas (500′); 15 miles north of Guaymas (100′); 5 miles south of Peon (sea level).

I have omitted from this list the extraordinary record for *pima* carried by Olsen (2) in his 1934 study of *Pogonomyrmex*. Among the Arizona stations Olsen gave "Mt. Lemmon, South Catalina Mts., 8000-9150 feet." Mt. Lemmon is the main peak in the Santa Catalina Mountains just north of Tucson and has a height of 9185 feet. The writer has collected there on several occasions and can state that there is scant likelihood that *pima* could occur above the 3000 foot level. That it could live above the 8000 foot level is out of the question. Above 8000 feet Mt. Lemmon supports a fairly heavy stand of conifers. At its higher levels Mt. Lemmon is certainly not the place where one would expect to find a strict xerophile such as *pima*. It is possible that the specimens on which Olsen's record was based were winged forms, carried by updrafts to the crest of Mt. Lemmon. But if they were workers it is evident that the specimens were incorrectly labelled as far as elevation is concerned. It also seems probable that the record from Bowie, attributed by Olsen to *pima*, is actually *imberbiculus*. As may be seen from the foregoing list, all other records for *pima* come from stations below 3000 feet and well to the west of the latitude of Bowie.

By comparing the locality lists for *imberbiculus* and *pima* it is easy to appreciate that the former species is decidedly more adaptable. The lateral range of *imber-*

biculus exceeds that of *pima* both east to west and north to south. The vertical range of *imberbiculus* is almost twice as great as that of *pima,* for although *imberbiculus* does not descend to sea level, as *pima* does, it is capable of reaching levels above 6000 feet, while *pima* rarely reaches the 3000 foot level. The more restricted range of *pima* makes it easy to place that species in the Sonoran Desert biotic association as defined by Shreve (5) but no such single association is possible in the case of *imberbiculus.* Most of the middle of the range of *imberbiculus* lies in what Shreve calls the Chihuahuan Desert, a biotic association found on the Mexican plateau and adjacent portions of west Texas, New Mexico and Arizona. But it is scarcely possible to consider the stations in central Texas and Oklahoma in this category and those in western Arizona, Sonora and California are clearly in the Sonoran Desert association. It thus appears that the distribution of *imberbiculus* spans at least three different biotic areas.

It is interesting to contrast the distribution of *imberbiculus* and *pima* with that of *Novomessor cockerelli* and *albisetosus,* since the latter two xerophiles occur in many of the stations where *Ephebomyrmex* is present. The writer has attempted to show (6) that the distribution of our two species of *Novomessor* is largely determined by their response to elevation. There can be no doubt that elevation is also a highly important factor in the case of *imberbiculus* and *pima.* The response of *imberbiculus* to elevation is very similar to that of *N. cockerelli* hence it is not surprising to find that the two species occur together over a very large area from western Texas to western Arizona and south along the Mexican plateau as far as Durango. With certain restrictions this range is true of *N. albisetosus* also. But *pima* behaves in an entirely different fashion. Its distribution is limited to Arizona and Sonora and in those states it occurs only in stations of low to moderate elevation. It is hard to escape the conclusion that this behavior is a result of the different elevational range possessed by *pima.* Since the upper limit of this range appears to be in the neighborhood of 3000 feet it follows that *pima* would, on this

basis alone, be unable to utilize stations on the Mexican plateau or similar areas to the north of it. I do not for one moment maintain that elevational range is the only factor that restricts *pima* to the Sonoran Desert region but it would surely seem to be one of the more important factors which go to determine this range.

I wish now to consider the habits of *imberbiculus* and *pima*. It is much to be regretted that Wheeler did not content himself with the excellent account of the habits of *imberbiculus* which he published in 1902 (7). All the nests on which Wheeler's original account was based were found under stones and each nest contained very few workers. Beneath the stones Wheeler discovered small chambers containing unhulled seeds and others full of brood. When transferred to artificial nests the *imberbiculus* workers made no effort to utilize the seeds as long as they were supplied with insect food. But when the supply of insect food was cut off the workers hulled the seeds and not only ate them but also fed pieces of them to the larvae. Wheeler was soon aware (8) that his original nests of *imberbiculus* had been exceptional in that they were built under stones, for he discovered other colonies at San Angelo, Texas, where the nests were free in the soil and surmounted by small craters. But it may be said that at the start Wheeler presented a very accurate picture of the nesting habits of *imberbiculus*. It is, therefore, difficult to explain why he obscured this picture in 1910 (9) by grouping *imberbiculus* and *pima* with other species of *Pogonomyrmex* with which they have little or nothing in common. In his celebrated volume *Ants* (page 283) Wheeler makes the following observation:

"1. *P. subdentatus, apache, sancti-hyacinthi* and *desertorum* and *Ephebomyrmex imberbiculus, townsendi* and *pima*. These are small species confined to the deserts of Texas, New Mexico, Arizona, Californa and northern Mexico. Their colonies are always insignificant and widely scattered, comprising only a few individuals. The nests are small, obscure craters, 10-20 cm. in diameter and a

few centimeters high. The workers make no attempt to cut down the surrounding vegetation which often grows on the crater immediately around the entrance."

It is hard to see what Wheeler had in mind here. Neither *subdentatus* nor *apache* (or its synonym *sancti-hyacinthi*) are small species. Indeed the major worker of *apache* is one of our largest species, being surpassed in this respect only by the major of *badius*. While the number of individuals in a nest of *apache* is small, there is ordinarily no crater nor disc around the nest entrance and this paucity of excavated material is, as Cole has recently shown (10), one of the characteristics of this species. The colonies of *subdentatus* ordinarily contain at least 500 individuals and this species usually constructs a ragged disc of gravel, not a crater, around the nest entrance. The nests of *desertorum,* while less populous than those of *subdentatus,* are far larger than those of *imberbiculus* and *pima,* and the coarse, flattened gravel mounds which *desertorum* customarily makes are wholly unlike the delicate craters constructed by our representatives of *Ephebomyrmex.* I mention these inconsistencies because it is certain that they have obscured Wheeler's original clear-cut presentation of the habits of *imberbiculus.*

As far as the writer has been able to determine the habits of *imberbiculus* and *pima* are so similar that a single account will cover both species. On rare occasions these ants will nest beneath stones but in most cases they build their nests without any covering object. The soil selected is always hard-packed and usually of a rather fine, sandy texture. There is a single, small nest entrance not more than 3 or 4 mm. in diameter, and the passages which lead from it are equally delicate. The storage chambers are small. Both the storage chambers and the passages collapse very easily if the nest is excavated and this makes it unusually difficult to trace them. The only practical method for doing so that the writer has found is to excavate the nest very gradually and allow time between excavations for the workers to reopen the caved-in passages. If three or four days can be devoted

to the process it is possible to follow the passages to their ends. There are usually not more than three or four of them and the length of any passage seldom exceeds five inches. The soil brought to the surface by the ants is usually very fine and the crater formed from it is easily dispersed by rain or wind, hence many nests are without a crater much of the time. Most of the craters measured by the writer were 2½ inches or less in diameter. There are seldom more than 75 workers in a nest. The average number seems to be about 50. The workers store both seeds and the remains of other insects, especially other ants. In view of the lack of pugnacity of our species of *Ephebomyrmex* it seems safe to assume that such stores of insect remains are secured by scavenging rather than by attacks on living victims. Seeds are stored unhulled and several sorts are accepted. One colony kept in an artificial nest preferred white clover seed to grass seed. The slow hulling of the seeds prevents the formation of a chaff pile for the hulls, which are discarded outside the nest entrance, are dispersed before they can accumulate into a chaff pile.

As Wheeler noted, it is unusually difficult to secure sexual forms. Since he observed a marriage flight of *imberbiculus* near Deming, New Mexico, on July 12th (13), and since the writer secured a colony of *imberbiculus* containing callow males and females in the Davis Mountains of Texas on May 25th, it might be expected that alates would ordinarily be present in the nests of this species during the month of June. Actually this is seldom the case and as *imberbiculus,* like many xerophilous ants in the southwest, apparently holds its marriage flight shortly after the onset of the summer rains in early July, the absence of alates in many nests during the month of June may mean that *imberbiculus* produces sexual brood only in especially favorable years. The pupal males and females show a surprising capacity for moving their appendages prior to transformation. The workers fail to remove all of the pupal exuviae from the alates when the latter transform, and the patches of pupal casing

which adhere to the newly emerged males and females give them the appearance of a person peeling after a bad case of sun burn. Wheeler calls these ants "timid" but perhaps it would be better to describe them as docile. They do not seem particularly frightened when they are disturbed and they make little effort to escape and none to sting. The writer has picked up hundreds of specimens and has yet to be stung by one of them. This seems rather curious, since these ants are provided with a powerful sting, despite their small size. The sting is fully two-thirds as long as that of the smaller workers of *barbatus*, a species which stings atrociously, and certainly the presumption would be that *imberbiculus* and *pima* could use their stings effectively if they chose to do so. These ants forage at least ten months a year and probably, in a mild winter, all year long. When foraging they move at a slow but steady gait. They usually forage singly.

There follows the description of the female of *imberbiculus*, which has not hitherto been described or figured: The features cited in this description are those which could not be shown in the figure:

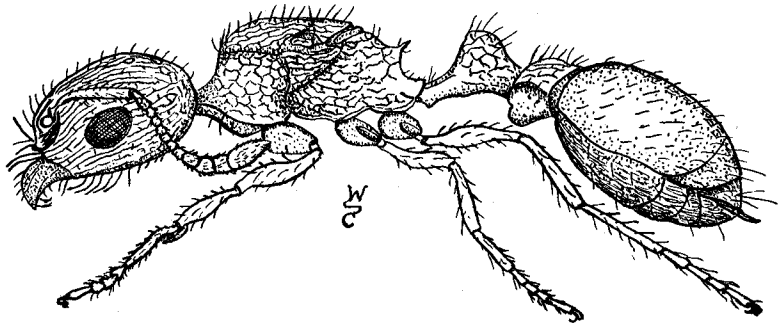

Fig. 1. Female of *Pogonomyrmex* (*Ephebomyrmex*) *imberbiculus* Wheeler.

Length of head (mandibles excluded) 1.2 mm.; length of thorax 1.75 mm.; overall length 4.5- 5 mm. The sides of the head behind the eyes slightly narrowing toward the occiput. Occipital border slightly concave in the middle. Middle of the clypeus scarcely projecting beyond the two prominent teeth which stand in front of the

antennal fossae. Mandibles armed with five prominent teeth which decrease in size from the apical tooth inward, and a single much smaller tooth at the angle between the masticatory margin and the inner margin. The antennal scape in repose reaches the level of the lateral ocellus. Base of the scape with a conspicuous flange. Frontal lobes rather narrow in front, only slightly divergent behind and not projecting much above the antennal fossae. Frontal area large and crossed by a single median ruga. Clypeus with five longitudinal rugae. Color, when alive, a deep, ferrugineous red which fades to an orange red as the specimen dries.

Gynetype: a female from Arsarca Canyon, Chinati Mountains, Texas, in the writer's collection. A second female from the Davis Mountains, Texas, agrees well with the type in the characters cited above.

It seems worth commenting here on Wheeler's original concept of the diagnostic features of the subgenus *Ephebomyrmex*. As his principal criterion for establishing the group Wheeler cited the absence of a beard or psammophore on the under surface of the head. In the figure of *imberbiculus* which accompanied the original description of the worker of that species, (7) Wheeler made no attempt to depict the pilosity, either on the gula or elsewhere. But in the description he noted the presence of a group of erect hairs on the gula which did not form a "conspicuous" beard. In this stand Wheeler seems to have been influenced by Forel, who had set up a subgenus to receive the beardless species *mayri* (11). But the gular hairs of *P. mayri* are uniformly short and even those at the anterior edge of the gula do not project much beyond it. They cannot by any stretch of imagination be said to form a psammophore. Unfortunately this is not the case with all the species of *Ephebomyrmex*. Oddly enough Wheeler's two species *imberbiculus* and *pima* are the worst offenders in this respect. Each has a small, median psammophore on the anterior half of the gula which runs diagonally inward toward the midline of the head. It may be admitted that these groups

of hairs are less regular in arrangement and much less conspicuous than the linearly-arranged lateral psammophores of some of the other species, but it certainly cannot be said that the gular pilosity of *imberbiculus* or *pima* is as scant as that of *mayri*. While our species of *Ephebomyrmex* do not have full beards, they certainly do have goatees, hence Wheeler's distinction is one of degree, not of kind. There can be little question that when Emery stated in 1921 (12) that the subgenus *Ephebomyrmex* is an artificial group, he had the above facts in mind. Emery pointed out that neither the absence of a psammophore nor the presence of a toothed epinotal flange at the insertion of the petiole distinguish the members of *Ephebomyrmex* from certain intermediate species ordinarily assigned to the subgenus *Pogonomyrmex*. Emery cited the South American species *silvestrii* and *brevibarbis* in this connection but he could have mentioned the North American species *huachucanus* with equal propriety. The psammophore in both worker and female of *huachucanus* is transitional both in degree of development and position. The hairs which form it are fairly long and, for the most part, linearly arranged, but this line of hairs runs diagonally inward from the insertion of the mandible to a point at the middle of the head which is a little in advance of the rear border of the gula. This gives a V-shaped median psammophore which is quite unlike that of most species in the subgenus *Pogonomyrmex*, where the hairs of the psammophore are arranged in a line along the outer edge of the gula and turn in toward the center of the head at its rear edge.

One can agree with Emery that the criteria which Wheeler used for the recognition of *Ephebomyrmex* are not well-chosen and one can further agree with him that substantial improvement in the situation will necessitate a better acquaintance with the sexual forms of this group. In this connection the writer would like to call attention to one interesting feature in the thoracic structure of the female of *imberbiculus*. The scutellum of the female of *imberbiculus* does not rise abruptly above the metano-

tum. Instead its rather thin rear edge forms, with the metanotum and the basal face of the epinotum, a single, sloping declivity which is broken only by the sutures at either side of the metanotum (see figure). In all species belonging to the subgenus *Pogonomyrmex* where the writer has been able to examine the female (*apache, badius, barbatus, californicus, huachucanus, occidentalis* and *subdentatus*), the scutellum rises well above the metanotum. This rise is usually abrupt and sometimes the rear face of the scutellum overhangs the metanotum. There is thus a break in the outline of the thorax at the metanotum and the dorsum of the scutellum is always at a level well above that of the metanotum or the anterior edge of the epinotum. As to whether these distinctions will hold uniformly through both subgenera remains to be seen, but if they do there should be less difficulty in defending the status of *Ephebomyrmex* as a valid subgenus.

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