

A RECONSIDERATION OF THE *CYLINDRICUS* GROUP OF THE GENUS *ANOPLIUS* DUFOUR (HYMENOPTERA: POMPILIDAE)

HOWARD E. EVANS

Department of Entomology, Colorado State University, Fort Collins, Colorado 80523.

Abstract.—Three names are removed from the synonymy of *Anoplius* (*Pompilinus*) *cylindricus* (Cresson). These are *Arachnophila brevihirta* Banks, *Pompilinus subtruncatus* Dreisbach, and *P. truncatus* Dreisbach. *Pompilinus hispidus* Dreisbach is regarded as a synonym of *P. subtruncatus* Dreisbach, while *P. clavipes* Dreisbach continues to be considered a synonym of *A. (P.) cylindricus* (Cresson). *Anoplius* (*Pompilinus*) *cylindricus* is restricted to the southwestern United States and is clearly distinct from other members of this complex. The remaining three species are closely related and show some evidence of intergradation; two of them, *A. (P.) subtruncatus* and *A. (P.) truncatus*, occupy more limited ranges within that of the transcontinentally distributed species *A. (P.) brevihirta*. Some of the variation in *A. (P.) brevihirta* is analyzed. This species is restricted to broad areas of open sand, and populations in different sandy areas have in some cases diverged slightly in structure and color; there are also broadly geographic trends in structure and color.

Key Words: Spider wasps, Pompilidae, *Anoplius*, synonymy, distribution, variation

Retirement should provide time to re-think some of the problems in one's past research in which the solutions proposed seem naggingly unsatisfactory. Many years ago (Evans 1951) I placed four names in the synonymy of *Anoplius* (*Pompilinus*) *cylindricus* (Cresson); a fifth name was later added to the synonymy (Evans 1966). Evidence to support this lay in the apparent continuous variation in features of the male genitalia. Further collecting in the western half of the United States in recent years has convinced me that such a simplistic solution to this complex is not satisfactory. Here I propose that four species be recognized in this complex, with two other names being retained in synonymy.

Day (1974) placed the subgeneric name *Pompilinus* Ashmead (generotype *Pompilus cylindricus* Cresson) in the synonymy of the subgenus *Arachnophroctonus* Howard

(generotype *Psammochares marginalis* Banks). I regard *Pompilinus* as a probably monophyletic New World offshoot of the widely distributed *Arachnophroctonus*. In 1951 I erroneously placed the European *Anoplius viaticus* (L.), under the name *A. fuscus* (L.), in *Pompilinus*; more properly it belongs in *Arachnophroctonus*.

Whether *Pompilinus* deserves subgeneric status can be argued, but it is a large group divisible into at least three species-groups, so it is convenient to retain it as a subgenus. The most useful distinguishing features of this group are the fact that the transverse median vein of the fore wing meets the media beyond the origin of the basal vein, the third submarginal cell is petiolate, and the spines of the female tarsal comb rarely exceed the width of the basitarsus. The species of this group are difficult to separate in the female sex, and the males can be sep-

arated with assurance only by study of the genitalia. In 1951 I recognized two species-groups in *Pompilinus*, the *subcylindricus* and *cylindricus* groups. Here I restrict the *cylindricus* group to that species and three forms previously considered synonyms of it. The remaining members of the former *cylindricus* group of Evans (1951) may be considered to constitute the *marginatus* group.

The following are the distinguishing features of members of the *cylindricus* group as here defined. *Females*: eyes widely spaced, middle interocular distance 0.60 to 0.65 times transfacial distance; vertex passing straight across between tops of eyes; ocellar triangle broad and flat; propodeum convex, with a steep, oblique declivity, and bearing at least a few short hairs (may be quite hairy); femora usually hirsute; fore basitarsus with a comb of three or four spines, these spines one to two times as long as width of basitarsus; one or more basal tergites banded with orange. *Males*: subgenital plate slender, acute, hirsute (Figs. 5–8); genitalia with squamae at base of parameres prominent; digiti clothed with short setae, many of which are bent apically, except latero-apically with longer, straight setae; digiti broadly truncate apically (one exception) (Figs. 1–4); basal tergites with or without orange markings.

In 1951 I characterized *A. cylindricus* as a sand dune species, and various papers on behavior published under this name all apply to sand dune populations. All of these indicate that females prey on immature *Geolycosa* spiders occurring in sandy situations, using the spider's burrow in which to construct their own nest cells (Krombein 1953, Kurczewski and Kurczewski 1968, 1973, Gwynne 1979, Kurczewski 1981). The name *A. brevihirta* (Banks) is here applied to these populations.

Other elements in the species-group are by no means restricted to sandy places, but are often taken on plains or prairies. Unfortunately females cannot at present be associated with certainty with any of these

forms, so of course nothing can be said concerning their predatory or nesting behavior. Males taken away from sandy areas tend to be larger than *A. brevihirta* and are all black. These males can be sorted into groups equivalent to Dreisbach's species *Pompilinus subtruncatus* and *P. truncatus* and to Cresson's *Pompilus cylindricus*. On at least one occasion these three forms have been taken in one locality on the same date (Tornillo, El Paso Co., Texas). Two of them have been taken together on at least six occasions (localities in Texas, New Mexico, Colorado, Illinois, and Michigan). However, each of these forms (and *A. brevihirta*) is subject to variation in features of the male genitalia and subgenital plate, variation that in some cases blurs any lines that might be drawn between species.

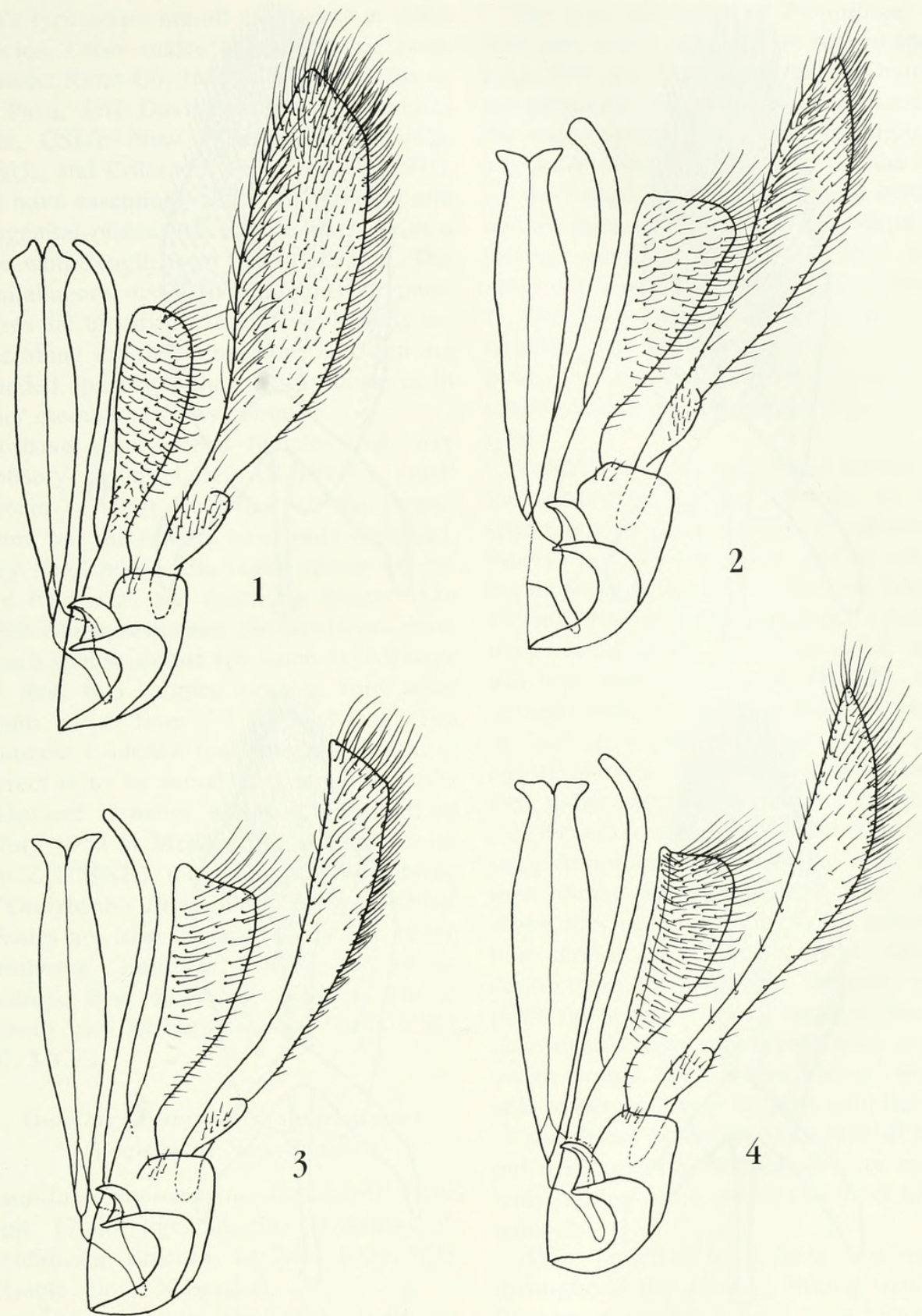
An exception is *A. cylindricus* itself. Study of the genitalia of the lectotype places this as a member of a population restricted to parts of the Southwest. The genitalia are quite distinctive, and I have seen no specimens intermediate with other members of this complex. These other members, *A. brevihirta*, *A. subtruncatus*, and *A. truncatus*, show evidence of intergradation, the latter two forming populations (not restricted to sand dunes) within the broad range of the dune-inhabiting *A. brevihirta*.

Anoplius (Pompilinus)
cylindricus (Cresson)

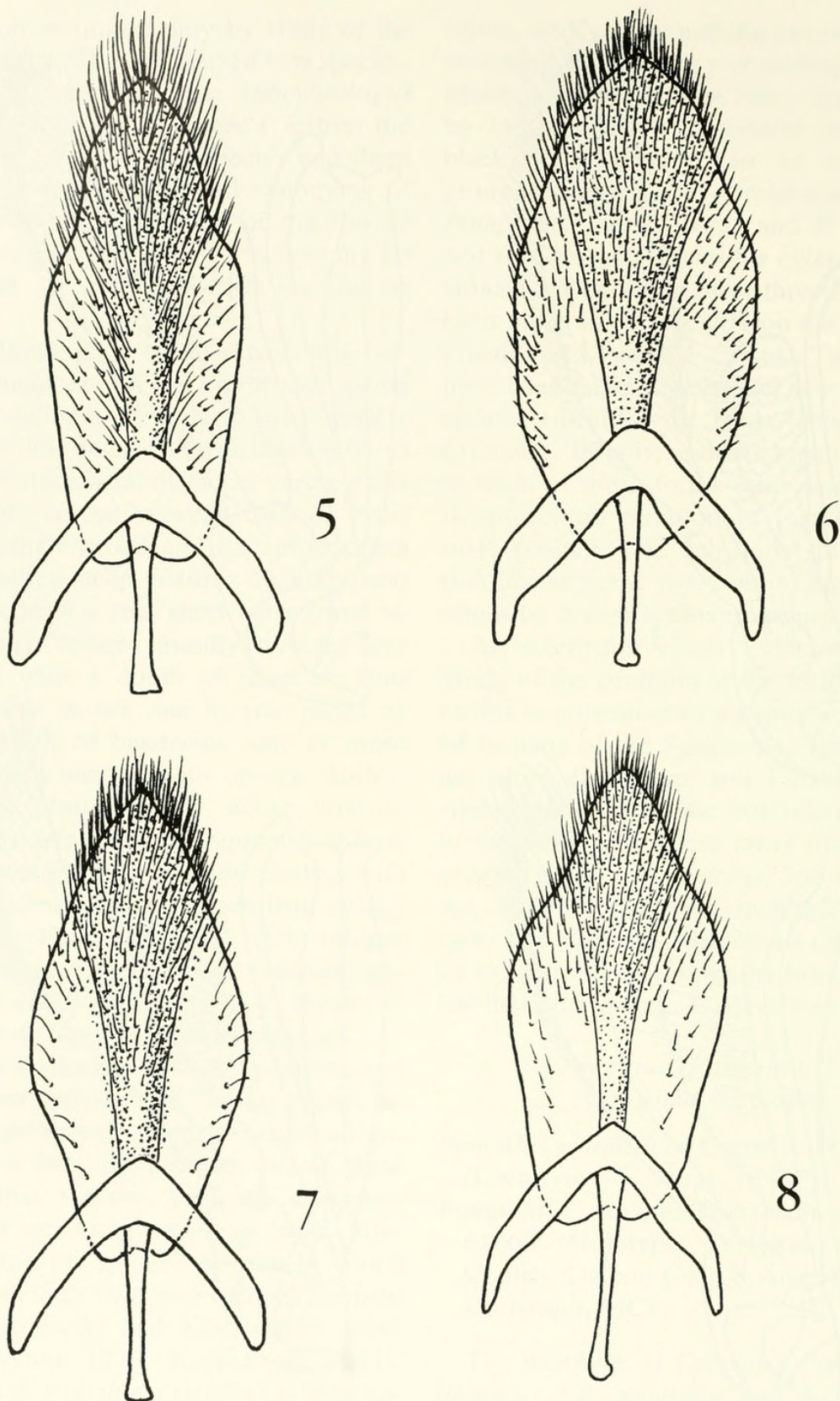
Pompilus cylindricus Cresson, 1867, p. 92.
(Lectotype: ♂, Texas, ANSP).

Pompilinus clavipes Dreisbach, 1958, pp. 61–63. (Holotype: ♂, Texas: Conlon [? Conlen, Dallam Co.], 8 Aug. 1952, R.R. Dreisbach, MCZ).

The lectotype of Cresson's *Pompilus cylindricus* has genitalia and a subgenital plate virtually identical to those figured for *Pompilinus clavipes* by Dreisbach, and as figured here (Figs. 1, 5). This lectotype was designated many years ago, prior to the studies of Dreisbach (1949) and Evans (1951). The other 12 specimens in Cres-



Figs. 1–4. Male genitalia (right half, ventral aspect) of *Anoplius* (*Pompilinus*) species. 1, *cylindricus* (Cresson). 2, *subtruncatus* (Dreisbach). 3, *truncatus* (Dreisbach). 4, *brevihirta* (Banks).



Figs. 5-8. Male subgenital plates (ventral aspect) of *Anoplius* (*Pompilinus*) species. 5, *cylindricus* (Cresson). 6, *subtruncatus* (Dreisbach). 7, *truncatus* (Dreisbach). 8, *brevihirta* (Banks).

son's type series are all assignable to other species. Other males before me are from Kansas: Reno Co. (MCZ, NMNH); Texas: El Paso, Jeff Davis, and Pecos counties (CU, CSU); New Mexico: Chaves Co. (CSU); and Colorado: Prowers Co. (CSU). All have essentially identical genitalia and subgenital plates. All are all black, with a fore wing length from 6.0 to 8.5 mm. The genitalia are distinctive in that the parameres are broadly spatulate and heavily setose along the mesal margin; the digiti are rounded apically, rather than truncate as in other members of this complex.

I have seen several females that very probably belong here. All have a small amount of short erect hair on the propodeum, but the femora have only scattered, very short hairs. The comb spines on the fore basitarsus are short, no longer than width of the basitarsus; the basitarsus bears 3 such spines (in one specimen 4). All have the first two tergites orange; fore wing length varies from 7.7 to 10.8 mm. The strongest evidence that this association is correct is to be found in a series of 3 females and 13 males, all taken by myself on 7 July 1953 at Medora, Reno Co., Kansas (MCZ, NMNH) (the males are all paratypes of Dreisbach's *Pompilinus clavipes*). Other females are from Kansas: Riley Co. (CU); Oklahoma: Grant Co. (MCZ); and Texas: Bastrop, Bee, Brewster, Dimmit, Travis, Kenedy, and Kleburg counties (BFL, CSU, CU, MCZ).

Anoplius (Pompilinus) subtruncatus
(Dreisbach) New Status

Pompilinus subtruncatus Dreisbach, 1949, pp. 17–18, figs. 58, 59. (Holotype: ♂, Nebraska, Lincoln, 14 June 1909, C.H. Gable, Univ. Nebraska).

Pompilinus hispidus Dreisbach, 1949, pp. 23–24, figs. 47, 48. (Holotype: ♂, Michigan, Tuscola Co., 20 Aug. 1940, R.R. Dreisbach, MCZ).

Anoplius hispidus, Evans, 1970, p. 482. (Teton Co., Wyoming).

The type specimens of *Pompilinus subtruncatus* and *P. hispidus* do indeed appear quite different. The former has the hairs on the subgenital plate short and depressed and the inner apical margins of the digiti not angularly extended. The latter has the hairs on the subgenital plate erect and bristling and the inner apical angles of the digiti projecting angularly. However, other specimens combine these two features differently. Dreisbach pointed out two small groups of setae near the midline of the subgenital plate of *P. hispidus*, but these are not present in specimens I have seen other than the type.

Variation in the condition of the hairs on the subgenital plate is striking. In some specimens they are wholly decumbent, in others only a few are erect, and in still others most are erect. In a male from Hialeah, Florida (NMNH), these hairs are especially long and bristling. A paratype of *P. hispidus* from Baldwin, Kansas (NMNH), has a strongly hirsute subgenital plate but the digiti lack an angulate process on the inner, apical margin. There are other examples that, to me, suggest that this is a single species subject to discordant variation in seemingly important features of the male abdomen. Some specimens have fewer setae along the mesal margin of the parameres than figured, suggesting possible intergradation with *A. brevihirta*. Smaller specimens fall within the size range of that species; overall size range (fore wing length) varies from 5.3 to 9.0 mm. I have been unable to associate any females with this species with any certainty. Males are all black, but it is probable that females are marked with orange as in other members of this complex.

This species is widely distributed throughout the United States from the Rockies eastward. I have seen specimens from the following localities: Florida: Hialeah (NMNH); Maryland: Bowie (NMNH); Louisiana (without further data) (NMNH); Michigan: Tuscola Co. (MCZ); Iowa: Sioux City (NMNH); Kansas: Baldwin (NMNH),

Clay Co. (NMNH); Nebraska: Chadron (Univ. Colorado, Boulder), Lincoln, Neligh (Univ. Nebraska); North Dakota: Beach (NMNH); Wyoming: Teton Co. (MCZ); Colorado: Bent, Elbert, Larimer, Otero, and Weld counties (CSU); Texas: Jeff Davis (CU), El Paso (MCZ), and Presidio (ANSP) counties.

Anoplius (Pompilinus) truncatus
(Dreisbach) New Status

Pompilinus truncatus Dreisbach, 1949, pp. 15, 16, figs. 40, 41. (Holotype: ♂, Michigan, Gratiot Co., 2 Aug. 1947, R.R. Dreisbach, MCZ).

As the species name implies, the parameres of the male genitalia are obliquely truncate apically (Fig. 3). An additional useful character is the absence of setae from the center of the disc of the digitus. The subgenital plate (Fig. 7) tends to be more slender and pointed than in the preceding species, but this is a subtle and not wholly dependable character; the sides of the plate are less sinuate than in *Anoplius cylindricus* (Fig. 5) and *A. brevihirta* (Fig. 8). The mesal margin of the paramere is relatively sparsely setose, much as in *A. brevihirta* but in contrast to *A. cylindricus* and *A. subtruncatus*.

In a series of 6 males from Tornillo, Texas (CSU), taken on the same day, some agree well with *A. truncatus* and others with *A. brevihirta*, while one has the left paramere truncate (as in *A. truncatus*), the right paramere acute (as in *A. brevihirta*). In a series of 4 males from Great Sand Dunes National Monument, Colorado (CSU), taken on the same day, three have genitalia typical of *A. brevihirta*, while the fourth has truncate parameres (although the digiti are fully clothed with setae and the subgenital plate is sinuate laterally). These specimens, and others, suggest that there is some interbreeding between these two species. Males of *A. truncatus* are all black and average larger than those of *A. brevihirta*, fore wing length varying from 5.5 to 7.2

mm. I have been unable to associate any females with this species.

Anoplius truncatus appears to have a more restricted range than *A. subtruncatus*, occurring from Texas and New Mexico to Illinois and Michigan. Dreisbach's paratypes are from Manistee and Midland counties, Michigan, Carlinville, Illinois, and Roswell, New Mexico. Other males I have seen are from Colorado: Bent, Larimer, Prowers, and Weld counties (CSU); New Mexico: Hidalgo Co. (CSU); and Texas: El Paso (CSU) and Jeff Davis (ANSP) counties.

Anoplius (Pompilinus) brevihirta
(Banks) New Status

Arachnophila brevihirta Banks, 1945, p. 105. (Holotype: ♀, Chicago, Illinois, July, C.T. Brues, MCZ).

Anoplius (Pompilinus) cylindricus, Evans, 1951, pp. 294–297, figs. 91, 123. (In part).

This is the most widely distributed member of this complex, ranging from coast to coast and from Canada deep into Mexico. It is the form most often identified as *A. cylindricus*, under which name there have been several reports on its biology (as discussed above). It is characteristic of areas of open sand, and virtually every system of dunes I have visited has a population of these wasps. Males average smaller than those of the preceding three species, fore wing length varying from 4.0 to 7.0 mm. The genitalia have the parameres acute, their mesal margins sparsely setose; the digiti are fully clothed with setae and the distal, mesal angle is prominent (Fig. 4). The subgenital plate is slender, with sinuate margins, and is clothed ventrally with subrecumbent setae (Fig. 8).

Even with the removal of the three preceding species from synonymy, this remains a very variable species. About 75% of the males I have seen have one or more basal tergites marked with orange. All-black males cannot always be distinguished

from those of other members of this complex without examining the genitalia. Even so, occasional specimens are puzzling. A male from Mt. Vernon, Missouri (CSU), has the parameres very slender, almost linear. A few males have the parameres somewhat truncate apically; two such specimens were cited under *A. truncatus*.

Females vary in fore wing length from 4.5 to 9.5 mm. Those from any one locality often differ greatly in size, suggesting that they have developed on spiders of different sizes. Females also differ in the number of spines on the fore basitarsus and in the amount of erect hair on the femora and the propodeum. Females have at least the second tergite banded with orange, sometimes part or all of the first and third tergites and some of the basal sternites. Since sand dune systems tend to be widely spaced in nature, it is possible that local populations have diverged slightly in structure and color.

Some of the variation also has a broadly geographic component (Table 1). Males from the eastern coastal states invariably have orange coloration on the abdomen, and this is true of males from Kansas, Texas, and eastern Colorado. Females from these same areas usually have only 3 comb spines on the fore basitarsus, while those from Michigan and from south central Colorado usually have 4 comb spines (in these two areas males are usually all black). Females from many western sites tend to have much more hair on the propodeum and femora than those from eastern localities, which may be almost devoid of such pilosity.

It is not clear why there are resemblances between the population at Great Sand Dunes in Colorado (represented by a series at CSU) and that at Warren Dunes, Michigan (represented by a series at MCZ) (Table 1). The latter site is subject to cooling winds from Lake Michigan, such that certain microclimatic conditions may approximate those at a much higher elevation (2440 m) in Colorado; however, the Colorado site has a much lower annual precipi-

Table 1. Geographic variation in male coloration and the number of comb spines on the fore basitarsus of females of *Anoplius (Pompilinus) brevihirta* (Banks).¹

Locality	No. of Males		No. of Females	
	Marked with Orange	All Black	3 Comb Spines	4 Comb Spines
MA and CT	7	0	17	0
NJ and MD	3	0	17	0
NC	17	0	64	0
FL	20	0	48	0
NY and PA ²	0	3	11	1
MI ³	5	15	3	16
KS	10	0	19	7
E. TX	1	0	6	0
W. TX	3	0	1	11
E. CO	8	0	14	7
S. CO ⁴	1	8	11	44
NM	1	0	4	9
Totals	76	26	215	95

¹ Includes only localities with a sample size of 5 or more. States are combined when records are consistent; states are divided when separate parts differ.
² Three localities on Lakes Erie and Ontario: Erie Co., PA, Oswego and Jefferson Co., NY.
³ Warren Sand Dunes State Park, Berrien Co.
⁴ Great Sand Dunes National Monument, Alamosa Co.

tation than the Michigan site. Specimens from Kansas, eastern Colorado, and a smattering of localities in the Great Plains, tend to approximate eastern specimens.

A comparison of the females from two widely separated areas of extensive sand is especially interesting (Fig. 9). In coastal North Carolina there is evidently a spring generation in which females are larger and have only 1–1.5 tergites orange. This is followed by a summer generation of females that are smaller and have 2 or 3 basal tergites orange. (These data are based on a long series of specimens from Nags Head and Kill Devil Hills in NMNH.) Presumably the large females of the spring generation result from the fact that females of the preceding summer took more mature *Geolycosa* spiders, while the small females of the summer generation developed on less mature spiders. At Great Sand Dunes National Monument the season is much short-

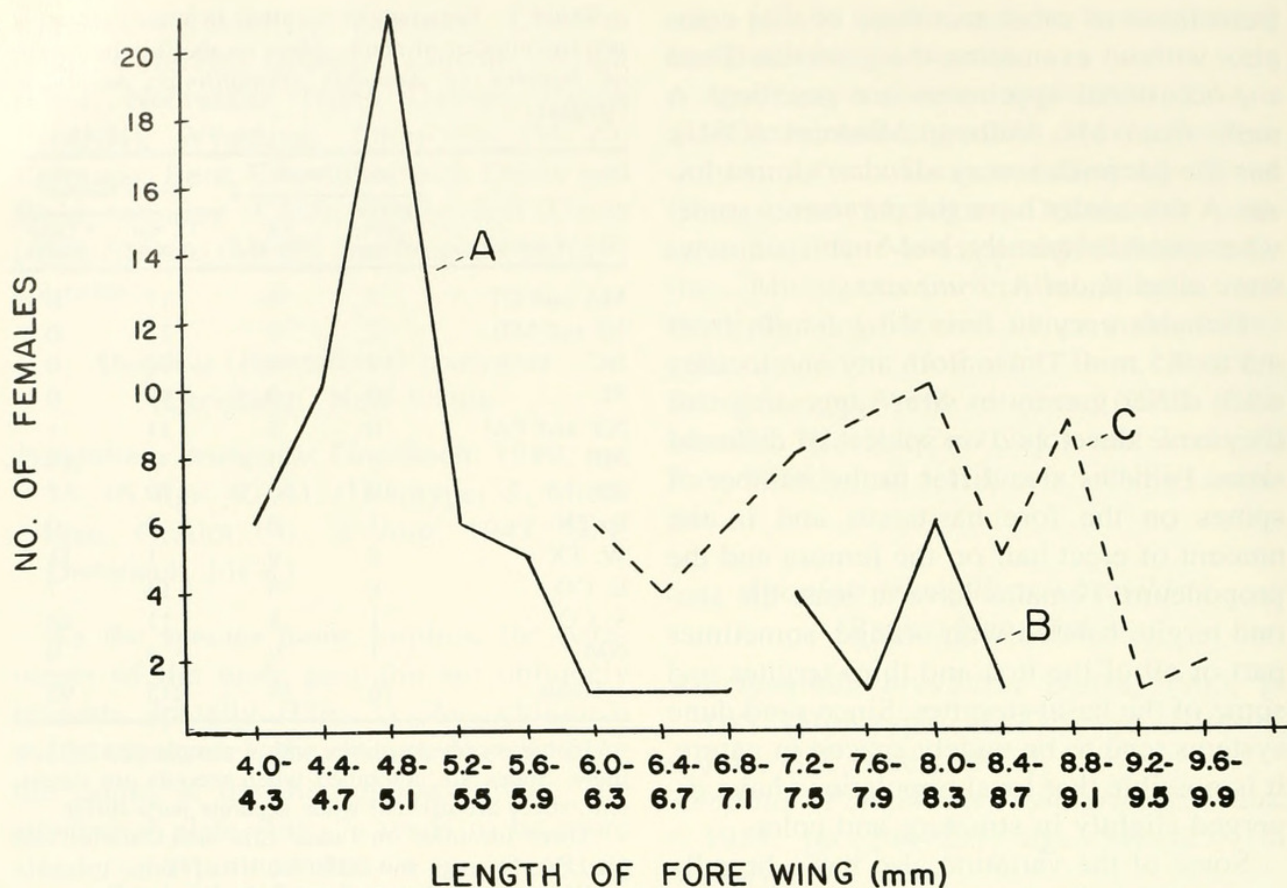


Fig. 9. A size and color comparison of two generations of *Anoplius (Pompilinus) brevihirta* (Banks) from coastal North Carolina and the single generation from southern Colorado at 2440 m elevation. A, Kill Devil Hills, NC, 23 June to 14 Sept.: 2-3 tergites orange. B, Kill Devil Hills, NC, 24 May to 22 June: 1-1.5 tergites orange. C, Great Sand Dunes National Monument, CO, July-August: 1-1.5 tergites orange.

er; here the females approximate in size and coloration members of the spring generation in coastal North Carolina. However, these females have much more body hair and a stronger tarsal comb. It is possible that the more extensive orange coloration of the second generation in North Carolina is the result of summer heat on the pupal stage, as occurs in other Hymenoptera. Males from Texas, New Mexico, and eastern Colorado are almost invariably marked with orange, and there is a corresponding tendency for females from these areas to be more extensively marked with orange. Clearly we are far from explaining the observed variation in this species, but it must be recognized when one attempts to circumscribe this species as distinct from others.

KEY TO MALES OF THE A. CYLINDRICUS GROUP

1. Digiti rounded apically; parameres broadly spatulate (Fig. 1) *cylindricus* (Cresson)
- Digiti broadly truncate apically; parameres less broadly expanded apically 2
2. Parameres obliquely truncate apically; center of disc of digiti devoid of setae (Fig. 3) *truncatus* (Dreisbach)
- Parameres more or less acute apically; center of digiti covered with short setae 3
3. Mesal margin of parameres heavily setose (Fig. 2); subgenital plate somewhat broader, sides gradually tapered, often bearing erect setae (Fig. 6); all black *subtruncatus* (Dreisbach)
- Mesal margin of parameres more sparsely setose (Fig. 4); subgenital plate more slender, with sinuate lateral margins (Fig. 8); basal tergites with or without orange coloration *brevihirta* (Banks)

CONCLUSIONS

Members of the *A. cylindricus* species-group occur throughout much of North America and have commonly been considered to constitute a single variable species. However, four populations can be distinguished on the basis of the male genitalia. While the differences between them are slight, they seem sufficiently discrete to suggest that to a considerable degree they breed independently of one another. This is especially true of *A. cylindricus* itself, which is restricted to the southwestern states. Two others, *A. subtruncatus* and *A. truncatus* (both known from males only), occupy limited ranges within that of the very widely distributed *A. brevihirta*. The last is characteristic of broad areas of open sand, where females prey on *Geolycosa* spiders. While two or three of these species have sometimes been taken at the same time and place and remain recognizable, occasional specimens are somewhat intermediate in characters of the genitalia. Both *A. subtruncatus* and *A. truncatus* occur primarily on plains and prairies and may intergrade with *A. brevihirta* on the periphery of the sand dune habitats of the latter. Further collecting and data on nesting behavior are needed to fully clarify the components of this complex. Molecular studies might be useful both for associating the sexes and for better understanding the degree to which interbreeding occurs.

A. brevihirta, even as restricted here, is a very variable species. Populations in widely spaced sand dune systems have diverged slightly in features of structure and color, and there are also broadly geographic tendencies relating to the length and number of comb spines on the fore basitarsus of the females, the length and abundance of body pilosity, and the amount of orange coloration on the abdomen. Further collecting of larger series from more sand dune areas may serve to fill out details in the spatial distribution of these variable characters.

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