

THE PSELAPHID AT HOME AND ABROAD

By ORLANDO PARK

Dr. Park (Ph.D., Chicago, 1929) is Professor of Zoology at Northwestern University. He is a noted ecologist with entomological leanings. He has two major research interests: the analysis of activity of animals and the study of beetles of the family Pselaphidae. In 1943 he was President of the Ecological Society of America.

IF ONE walks through a forest in the Chicago region in search of mushrooms, flowers, picturesque photographs, a glimpse of chipmunk or warbler, or to enjoy the quiet shade, more than a little of the unconscious relaxation is afforded by the yielding, leafy rug beneath each step.

It is with this moldering layer, the carpet of the forest floor, that we are concerned initially in our prying into the biology of a family of small beetles known as pselaphids. To appreciate these insects they must be fitted into the whole picture. We must begin with their habitat, this leaf-strewn carpet, not merely because it is important, but because it is vital to the forest.

Throughout the year the ground is the recipient of organic debris, of bits of bark, twigs, flower parts, fruits, seeds, leaves, and the excreta of animals or their dying or dead bodies. This diverse material accumulates, in season, from the largest tree or mammal to the smallest herb or invertebrate. As a tree dies from old age or disease, or is struck down by lightning or wind, it falls to the forest floor; in time it and its rooted stump add substance first to the carpet and then to the soil. Especially notable is the autumnal fall of leaves from the forest canopy. By weight of numbers, these leaves give a characteristic aspect to the floor and add materially to its thickness and potentiality.

These deposits must be maintained if any forest is to flourish; if they decline in quality or quantity beyond a subsistence level, the forest declines and eventually perishes. When these organic materials are properly broken down and combined they form humus and eventually mix with mineral soil to

form soil which provides a continual source of food for the forest plants. These plants are eaten by forest herbivores, such as aphids, white-footed mice, and, formerly, deer. In turn the herbivores are devoured by forest predators, such as the pilot black snake, weasel, and the now rare bobcat.

Furthermore, this organic carpet serves as an insulating layer against extremes of weather. It is relatively slow in cooling at night or in autumn, and relatively slow in warming in daytime or in spring. This means that the forest is cooler in summer and warmer in winter than adjacent external areas. Again, the spongy leaf mold holds water well, preventing rapid runoff and at the same time resisting erosion of the rich soil beneath. Many organisms find shelter here; some live in the leaf and log mold the year around; others enter this situation to hibernate.

The relation of the leafmold carpet to the forest as a whole is not so simple as it sounds. In order for the plants to obtain their food this biochemically complex layer must be separated and recombined into relatively simple mineral salts. In other words, the floor debris must decay. This is not possible without bacteria, and myriads of microbes labor ceaselessly at this essential and diversified task. This humus is at the same time the food of bacteria and fungi, but this food is formed, bit by bit, from the floor litter above, which in turn is derived from the forest flora and fauna.

Thus many organisms, from the tall trees, such as oak, elm, maple, and beech, to the short herbs, such as the violet and spring beauty, are engaged in production of plant

protoplasm. By means of the green chlorophyll of their leaves, they produce carbohydrate by photosynthesis. For this they need sunlight, water, and atmospheric carbon dioxide. Inorganic salts of many kinds, including those of nitrogen, sulphur, and phosphorus, are absorbed by their root systems from the forest soil and are synthesized into proteins.

Consequently, in this revolving cycle, inorganic salts are taken from the soil by plants; the plants synthesize protein and carbohydrate, die, and eventually are transformed by a complicated course of reactions into salts by bacteria and fungi. These parts of the cycle are more easily comprehended; they are important, but not independent of the rest of the food web. Plants must be fertilized by wind, or by animals, chiefly insects, and they must be dispersed, chiefly by insects, birds, and mammals. Still more vital, their falling leaves and other parts, which are to make up the bulk of the organic soil, must be first broken up, drained, dried, moistened, aerated and chewed up, swallowed, transported, and otherwise treated to allow the bacteria, fungi, and soil protozoans to produce the mature soil from which the plants can draw food. This latter phase is a multiplex industry in which imponderable numbers of animals cooperate—earthworms, mites, insects, millipeds, moles, and many others.

All this activity by forest animals and plants gives a concrete reality to the forest; it ceases to be a grove of trees and becomes a cooperating unit, a forest community. The community needs water and sunlight, and a place to grow, but beyond this minimum it is self-sustaining. That is, the component animals or plants cannot live in a vacuum, as it were, since each kind must have food. Bacteria die if their sources of supply are absent, just as readily as do trees without inorganic salts or aphids without plant sap. Food chains, then, are essential, and where food chains interlace and anasto-

mose a self-sustaining community is produced. This is life at its level of survival.

SINCE neither space nor time is at hand to study all the component organisms of such a community, it will be instructive to examine one group of soil-inhabiting arthropods, the Pselaphidae.

The pselaphids are minute beetles, composing one of the families of the vast beetle group—the Coleoptera. They articulate with the forest community at the point where the heterogeneous floor litter is being transformed into forest soil. These beetles perform no task that is exclusively their own, and in any one year or in any given community they are not a predominant influence. Despite this lack of drama, pselaphids share with numerous, similarly unsignalized, insects an essential role in the formation of humus: a strange, inverted role to be discussed presently.

Pselaphidae are a large family of small beetles. As with other beetles, they have chewing jaws, and have the first of two pairs of wings hardened into a pair of wing sheaths, or elytra. Most beetles have the elytra extended posteriorly to almost or quite cover the abdomen, but the pselaphids have short elytra, so that usually five abdominal segments are exposed (Fig. 1). This brachyelytrous condition is very uncommon in beetles, very few families having short elytra. Despite this fact, difficulty is to be expected in separating pselaphids from their close relatives, since the brachyelytrous rove beetles, or Staphylinidae, make up one of the largest families of beetles, in excess of 20,000 species, and resemble the pselaphids. These two families, the Pselaphidae and the Staphylinidae, probably evolved from a common ancestral stock. They have many structural features in common, but may be distinguished readily by a student who is familiar with a combination of characters. The staphylinids have a flexible abdomen with 7 or 8 segments usu-

ally exposed, and their 6 feet, or tarsi, have 3-5 segments. The pselaphids have a rigid abdomen, without dorsoventral movement and with usually 5-6 segments exposed; their tarsi always have 3 segments.

Pselaphids are quite small, even for insects. Their average size is about 1.5 mm. (.06 inch). Some species range down to 0.7 mm., as, for example, *Dalmosella tenuis* Casey and *Thesiastes pumilus* (LeConte), of North America. Others are relative giants; for example, *Hamotus ecitophilus* Raffray, which lives with the voracious army ants in Brazil, has a length of 5.5 mm.

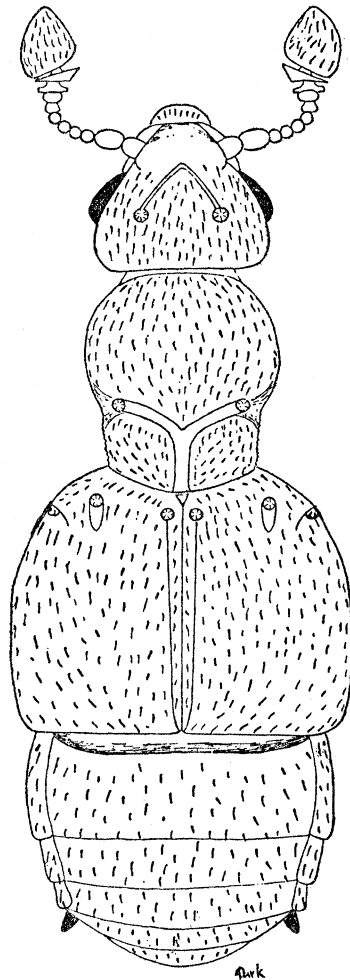
The pselaphids are entirely terrestrial beetles. Their geographic distribution is almost cosmopolitan. This aspect of their biology, the zoogeography of Pselaphidae, is a fascinating study within itself since it deals, not alone with the known distribution of species populations, but attempts to find solutions to questions having to do with past distribution, present trends in dispersal, and why certain dispersal patterns or pattern fragments exist and how they were formed. This involves a great deal of collateral information on the biogeography of plants and other animals, meteorology, oceanography, paleontology, geography, and many special aspects of zoology.

Although pselaphids are represented by numerous species, in many parts of the world, their zoogeography can be discussed only in the most general way. The reason for this is that most of the known species are represented by specimens from single localities. It will require much collecting, the analysis of many field records, and the description of many new species before our knowledge is sufficiently complete to warrant an adequate treatment of their distribution.

In general terms, biologists have divided the earth into six zoogeographical regions, each with its distinct assemblage of animals, its fauna. These regions and faunas are the Palearctic, Nearctic, Neotropical, Ethio-

pian, Oriental, and Australian. Although these regions were established primarily for birds and mammals, they represent six more or less well defined pselaphid beetle faunas.

The Palearctic region has been longest studied (since about the end of the eighteenth century) with respect to pselaphids, but with great irregularity and by only a few specialists. It is the best known of the six regions and includes all of Europe, Asia north of the Himalayas and east to the Pacific Ocean, and extends beyond the



After Park, 1945, *Chicago Acad. Sci.*
 FIG. 1. *CUPILA MEXICANA* PARK
 A NEOTROPICAL PSELAPHID BEETLE.

Mediterranean into northwestern Africa to include Morocco, Algeria, and Tunisia.

The Nearctic region is more closely related to the Palaearctic than to any other. It is less well known, having been studied by still fewer specialists and only since the middle of the nineteenth century. This region embraces almost all of North America. Its pselaphids extend southward, along each coast of Mexico about to the Tropic of Cancer, and in the interior of Mexico down the high Central Plateau to the Isthmus of Tehuantepec.

The Neotropical pselaphid fauna shows little affinity with that of other regions. Its large size as now known is but a small token of its real extent. This region extends from the Argentine pampas northward to include all of Central America and Mexico up to an irregular junction with the Nearctic fauna, all of the Antilles, and the tip of peninsular Florida. It has been studied only since the end of the nineteenth century.

The Ethiopian fauna is also little known. The pselaphids characteristic of this fauna are found in all of Africa, save for the northwestern area colonized by Palaearctic species. Provisionally, as concerns these beetles, it includes the large island of Madagascar. There are some indications of pselaphid affinity between the African fauna and that of adjacent Asiatic areas. Thus, several genera, or groups of allied species, have either the same, or related, species occupying Abyssinia on the one side and Palestine or the western border of Arabia, on the other.

Madagascar is usually included with the Ethiopian region. The French expert, Achille Raffray, who, before his death in 1923, did more for the study of pselaphids than any other person, believed that the Madagascan pselaphids were the most isolated of all of the world faunas. Certainly Madagascan pselaphids show little affinity with those of Africa, despite geographic

proximity. We shall return shortly to this matter.

The fifth region, the Oriental, is similarly poorly known in contrast, to Europe, say, but it contains a rich pselaphid fauna. This fauna extends from India on the west, south of the Himalayas, to the Pacific Ocean, up the Chinese coast and southward to include the Malay Peninsula, Sumatra, Java, Borneo, and the Philippine Islands. Many new kinds of pselaphids may be expected from this area. The separation of pselaphid faunas on the north, between the Palaearctic and Oriental regions, is not worked out, and the numerous islands have been little studied.

The last region, the Australian, includes New Zealand, the Moluccas, Australia, New Guinea, and New Caledonia and extends eastward to embrace the Fiji Islands. As noted above, future study must be relied on to draw more understandable boundaries between the Oriental and Australian faunas.

THE family Pselaphidae is divisible into two subfamilies, the Pselaphinae and the Clavigerinae. The two subfamilies vary greatly in size: the Pselaphinae in general are more primitive in structure, that is, more like staphylinids, and number about 4,800 known species; the Clavigerinae number some 200 species and live only in the nests of ants. This latter habit will be examined later in some detail. For the present we may study this small subfamily with respect to the forms found in the six zoogeographic regions outlined above, and especially the forms confined to these regions, i.e., "endemic" to them, as an example of pselaphid dispersal.

A study of this table brings out a number of interesting comparisons. With respect to general distribution, the Palaearctic and Nearctic regions contain about three-fifths of the land mass but only 5 genera and 49 species; the other four regions, with about two-fifths of the land mass, contain 52 genera and 151 species. The Palaearctic and

Nearctic are much better known than the other regions, so the conclusion drawn is that the tropical regions of the earth hold an overwhelming preponderance of clavigerids.

One of the unsolved questions is the great disparity in number of species of clavigerids between the Palaearctic and Nearctic regions. The former has been better studied, but not so much so as to account for 75 per cent excess of species, especially since both regions have few genera. A more probable answer lies in the wide distribution and general adaptiveness of the Old World genus *Claviger*.

The 3 genera in the Palaearctic are *Claviger*, with 36 species in Europe and the Near East and 1 species in Algeria; *Diartiger*, with

TABLE 1
REGIONAL DISTRIBUTION OF CLAVIGERINE
PSELAPHIDS

	Palaearctic	Nearctic	Neotropical	Ethiopian	Oriental	Australian
Total Genera	3	2	3	30	11	8
Endemic Genera	2	1	2	28	8	6
Species	40	9	22	56	14	61

2 species in Japan; and *Articerodes* with a species in Mesopotamia. The 2 genera in the Nearctic are *Adranes*, with 6 species in the United States, and *Fustiger* with 3 species.

Thus no genus is found in the two regions, and *Claviger*, restricted to the Palaearctic, contains 37 out of 40 species known from this vast area.

When we extend this examination of geographic restriction, or endemism, to the six zoogeographic regions, it will be seen from Table 1 that all regions have a high proportion of restricted genera. This suggests, but does not prove, great isolation, involving geographic and ecological barriers. This is brought to light more vividly in Table 2.

In this second table it should be noted that out of 50 clavigerid genera, only 4 cover

more than one region. A single genus, *Fustiger*, may be thought of as widely distributed. This genus occurs in five of six regions. Strangely enough, it is absent from the Palaearctic, which may be a consequence of direct competition with *Claviger* for suitable ant hosts or an indirect effect involving the restriction of its usual host ants. Climatic barriers do not appear to be involved, since *Fustiger* is established in the Nearctic. *Fustiger* has a large predominance in the Neotropical region, a region, paradoxically, poorest in clavigerids. Such a dispersal pattern might suggest that *Fustiger* arose in the Neotropical region, spread through North America into the Palaearctic region, where

TABLE 2
CLAVIGERINE GENERA COMMON TO TWO OR MORE
REGIONS

Genus	Species per Region					
	Palaearctic	Nearctic	Neotropical	Ethiopian	Oriental	Australian
<i>Articerodes</i>	1	0	0	2	2	0
<i>Articeropsis</i>	0	0	0	1	1	0
<i>Clavigeropsis</i>	0	0	0	1	0	2
<i>Fustiger</i>	0	3	20	3	1	5

from extinct (or undiscovered) Asiatic stock it spread into the Oriental region and from here into Africa and Madagascar to the west and the discontinuous Australian region to the east.

This is one interpretation of *Fustiger* distribution. It assumes that the region of largest number of species is the ancestral home of the genus. Let us examine the pattern from another aspect and assume that *Fustiger* is a very old genus which may not withstand competition with more modern genera and hence is extinct or impoverished in its original home and able to flourish only at the periphery of its range. This type of dispersal may be called Matthewsian,

after W. D. Matthew, who set forth the importance of this type of distribution.

According to this view, *Fustiger* arose elsewhere and has been pushed into the Neotropical and Australian regions. In the former area it has flourished, and even probably given rise to the other two related neotropical genera (*Pseudofustiger* and *Neofustiger*). In the Australian region, it is not found in Australia itself, where the large genus *Articerus* is endemic with 49 species, but only in the remote Fiji Islands, where there are 5 species of *Fustiger*.

The case of *Fustiger* has been given as an example, and two of the possible interpretations have been suggested to emphasize how

In time a seventh zoogeographic region, the Malagasy region, may have to be added for the peculiar pselaphid fauna of Madagascar, as has been done for certain other groups.

LET us turn our attention from the distribution of the pselaphids in the zoogeographic regions to their habitat relations. These beetles are known from the fringes of the northern conifer forests of both hemispheres southward to the pampas of Argentina, the southern tip of Africa, and Australia. All continents and, where they have been looked for by entomologists, all major island groups have their pselaphid faunas with one exception. Despite repeated search, no pselaphids have been found on the Hawaiian Islands.¹

Their absence from these islands is not unusual. This distribution can be duplicated for many groups of plants and animals and, among diseases, human malaria. Pselaphids could not fly to the Hawaiian Islands from, say, the Fiji group or North America; the ocean currents are not advantageous for these beetles to effectively colonize these islands by natural floating rafts.

Pselaphids occur from sea level up to the Temperate Zone on mountains; for example, to at least 10,500 feet on Totonicapam in Guatemala. Present information shows an altitudinal distribution of species of pselaphids in the usual zonal pattern in Guatemala and Mexico, although the data are too few in a quantitative sense to do more than outline this problem of vertical distribution.

Other pselaphids descend into deep caves and are structurally adjusted for a cavernicolous life; for example, certain species of the genera *Macrobrythus*, *Glyphobythus*, *Apobythus*, *Linderia*, and *Loophobythus*.

¹ Personal communication of Dr. Eliot C. Williams states that he found no pselaphids in the Hawaiian Islands as late as April 1945. This lack was corroborated for Dr. Williams by Dr. Elwood C. Zimmerman, of the Bishop Museum, Honolulu, and serves to substantiate the older literature.

TABLE 3

CLAVIGERINE RELATION BETWEEN MADAGASCAR AND AFRICA

	Ethiopian Region	Africa	Madagascar
Total Genera.....	30	12	19
Endemic Genera...	29	11	18
Common Genera..	1	1	1 (<i>Fustiger</i>)
Extraregional Genera.....	2	2	1 (<i>Fustiger</i>)
Total Species.....	56	27	29
Endemic Species..	55	26	29
Extraregional Species.....	1	1	0

little we know about pselaphid distribution and evolution.

To return briefly to the Ethiopian region, this poorly explored area should be examined in the light of Raffray's view as to the distinctness of the pselaphids of Madagascar.

From this third table it will be seen that Madagascan clavigerids are as distinct from those of Africa as from those of any other region. They are more distinct than those of Africa are from the Palaearctic, since one species, *Articerodes syriacus* Saulcy, ranges from Syria and Mesopotamia into Abyssinia. The only common bond is the widely distributed genus *Fustiger* previously noted.

Nevertheless, the family is preponderantly tropical. Of the 5,000 or more species, some three-fifths inhabit the Torrid Zone. The Western Hemisphere, for example, holds 1,348 known species. Of this number, 384 species are known north of the Tropic of Cancer and 964 south of this general limit between the 2 faunas.

Pselaphidae, then, are to be found over most of the earth. In this great expanse of territory they occupy two chief habitats, the leaf and log mold of forest floors, and the nests of ants and termites. Both deserve consideration.

About 85 percent of the species of Pselaphidae live in the leaf and log mold of the forest floor. Such preponderance should give to the family the common name "leafmold beetles," but several other families of beetles coinhabit the floor litter, and, early in the study of the pselaphids, the relatively few that live with ants were called "ant beetles." The common appellations "ant beetle," "antlike beetle," and "antloving beetle" have been applied to the family since that time.

The leafmold-inhabiting pselaphids are nocturnal or, more exactly, crepuscular. Most of the day is passed quietly in the moist, irregular, dimly illuminated mold passages. Near dusk they become relatively much more active and walk or fly in search of food, water, or mate. This activity is usually concentrated into the period from sunset up to 10:00 P.M.; some species continue their activity to midnight; a few are active in the early hours before dawn. They drink from the droplets of moisture on the mold. The pselaphids are predacious. They feed upon a variety of animals. These latter include any they can overpower with their forelegs and sharp jaws; for example, small insect larvae, injured earthworms, small flies (*Sciara*), and especially mites.

Their mite-devouring proclivity has been known for a long time. It was known to one of the earliest students of the pselaphids,

Henry Denny, who gave the food of British pselaphids in 1825 as "mites, in damp situations." My students and I have observed pselaphids eating mites, in laboratory nests, from numerous localities in the United States and in the American tropics.

The humus and floor debris swarm with free-living mites and free-living stages of parasitic mites belonging to many families, among which may be mentioned the Oribatidae, Hoplodermatidae, and Parasitidae. These mites are usually minute, between a fourth to a half the size of a pselaphid. The majority of such mites are herbivorous. They infest the floor in force. I have counted them in the coniferous forests of Wisconsin, the deciduous forests of Indiana, and the rain forest of Panama. They may occur in numbers, up to 7,000 mites per kg. of mold. Since their leafmold-eating is an important factor in litter reduction, mentioned in the opening paragraphs of this article, these mites are important in the well-being of the whole forest community.

Such mites are one of the chief foods of the leafmold pselaphids. A beetle overtakes a mite, holds it down with its foretarsi, and chews it with its jaws. Since the mites are important in humus production, this predation by pselaphid beetles might seem to have a negative value. Destruction of mites may appear to invalidate the view that their enemies are beneficial to the forest community as a whole. Consider, however, that if these mites and their numerous allies in litter reduction were not held in check, the litter would be too rapidly reduced.

Such a situation might lead to an initial period of increased bacterial activity and plant growth. Nevertheless, a time would come when the invaluable humus reserve would be depleted, when the floor would become exposed to erosion and would have less insulation. There would be the annual crop of debris and leaves, but no reserve. This would lead eventually to community disaster.

Consequently, in the over-all picture of the complex operations which I refer to as community metabolism, predators are as important as herbivores. The pselaphids and their allies in predation hold the mites of the leaf and log mold, and their allies in litter reduction, in a delicate biological balance.

The leafmold pselaphids are well adjusted for their life in the litter and mold of the forest floor. This adjustment is both structural and functional.

They react positively to a relatively high amount of atmospheric moisture. If pselaphids are placed in a gradient of relative humidity, from, say, 30-80 percent, they aggregate in the upper third of the gradient. If they are placed in a glass-covered dish, on a sheet of moistened filter paper, they walk about while the sheet is giving off its moisture into the confined space. But gradually through the day the filter paper dries out and the relative humidity of the enclosed air decreases. The beetles become more and more active, running about until, by trial and error, they find the last wet patch on the filter paper. They make short excursions to and from this oasis, gradually forming a place aggregation on the moist spot. Finally, the moisture evaporates and the pselaphids die at, or near, the moist area.

Such behavior is in keeping with their natural habitat in the moist floor mold and litter. It tends to keep them at, or near, the forest floor.

They react negatively to strong light. If pselaphids are placed in a gradient of light, from about 100 foot-candles intensity down to darkness, they wander about and, by trial and error, select the dark third of the gradient.

There are no experimental studies on the visual acuity of pselaphids. On the structural side, the pselaphid visual equipment is not so effective as that of the many insects that capture their food while flying, like dragonflies. Most of them have only 60-100 facets per eye. This is a very low number for

insects in general. Species of pselaphids that live in deep leaf mold, beneath boulders embedded in the soil, or in caves, have eye size and number of ocular facets reduced. Thus among the species of the *Rhinoscepsis* the eyes vary, from 8 facets per eye in a Mexican species to 30 facets per eye in a Brazilian species. *Bibrax* from Panama has eyes with only a single facet, and *Arianops* of Appalachian North America has no eyes at all.

In other genera, the eye development is correlated with sex. Thus 2 large American genera, *Jubus* (with 49 species), and *Arthmius* (with 104 species) have eyes with significantly fewer facets in the female sex. This is a not uncommon feature in the family, although by no means the general rule. In some genera, the eye reduction in the female sex is even more pronounced. Thus the species of *Glyphobythus*, *Apobythus*, *Lindera*, and others, of Europe, have females with vestigial eyes.

The relatively poor optical equipment of leafmold pselaphids is in harmony with the reduced light intensity of their habitat. In forests, when the foliage is at its maximum and the pselaphids are in their active period of the year, the floor is usually dimly illuminated (25-50 foot-candles) during the day. Under such conditions the beetles would tend to remain in areas of deep shade.

In those genera in which both sexes lack eyes, or the female sex has reduced eyes or no eyes at all, dispersal would be very slow. In the first case, both sexes would move into adjacent areas with difficulty; in the latter cases, the species could not be established by the male alone.

The general effect of these adjustments, that is, the tolerance for high relative humidity and low light intensity, coupled with a relatively poor ocular development, would be a natural tendency for the populations of these beetles to keep to the forest floor or to caves.

Correlated with this is their period of

activity during the dusk and night hours. When active, pselaphids all walk rather well, and many fly. They may be taken by net during the evening, often in great numbers. *Biblopectus*, for example, has been taken in Kentucky, from a moving automobile with attached nets, between 6:00 P.M. and 8:00 P.M., by Dr. H. E. McClure. This same method has been used by Dr. Alfonso Dampf to capture Mexican pselaphids in flight at sunset.

Most pselaphids have wings. These flying organs are delicate, membranous structures which, when extended, are about as long as the body; when at rest the wings are folded up into a square and tucked beneath the hard elytra. Some pselaphids have vestigial wings, too short and narrow for flight; in some cases poor flight is associated with vestigial eyes.

In common with many other nocturnal animals, pselaphids are attracted to lights at night, especially in the tropics. This is not a fully explained response.

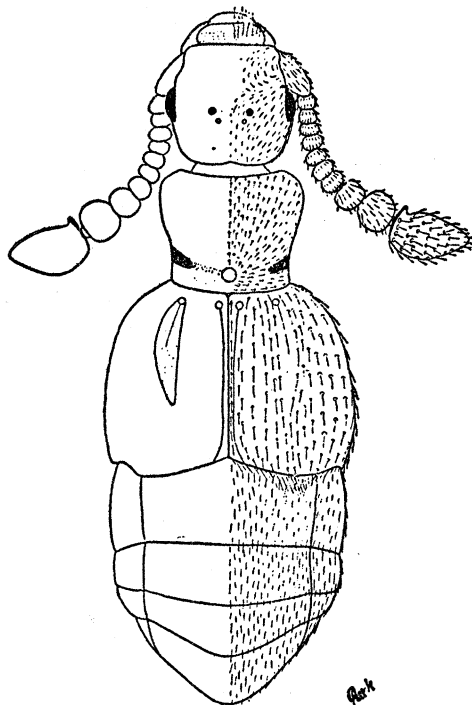
Another behavior of many leafmold pselaphids is their "feigning death," "playing possum," or "letisimulation." When they are uncovered in their native habitat, some genera (*Melba*, *Rhexidius*, *Tmesiphorus*) crouch close to the substratum, with their legs and antennae folded tightly beneath their bodies. Experimentally, this letisimulation may be induced by vibration of the laboratory habitat, or by touching the beetles. The usual period of such feigning is 30-70 seconds. On repeated stimulation the duration of the death-feigning response is gradually reduced.

What information or stimulus to orientation is unavailable to leafmold pselaphids as a consequence of their deficient optical equipment is probably obtained through the sense of touch and by chemoreceptors. Whether in their native litter or under the microscope in an artificial habitat, they are seen to be continually twirling their antennae or tapping these organs on the sub-

stratum. In addition to these appendages, pselaphids have a pair of maxillary palpi, which are segmented structures growing laterally from a second pair of jaws, the maxillae. When the insects are eating or drinking, these palpi are continually tapping the food or moisture.

Both antennae and maxillary palpi are highly developed in the family as a whole. The name of the family is taken from the genus *Pselaphus*, described by J. F. Herbst in 1792 and derived from the Greek, meaning "I feel my way," in allusion to the very long and peculiar palpi of this genus.

The antennae are usually clubbed, clavate or capitate, the last 2 to 3 segments being abruptly larger (Fig. 2). These organs vary within the family from 2 to 11 segments, and one or more segments may bear deep pits (foveae), or spines. These accessory



From Park, 1946, *Chicago Acad. Sci.*
 FIG. 2. *HAMOTOCCELLUS ARAUJOI* PARK
 A PSELAPHID ASSOCIATED WITH TERMITES IN BRAZIL.

structures are often found in the male sex only, and in many species reach fantastic proportions.

The maxillary palpi are similarly variable in the whole family. They are almost universally 4-segmented, often very long, and bear an almost infinite series of variations limited to species. One entire group of genera, centering around the Neotropical genus *Hamotus* (89 species), has the last segment longitudinally grooved. From this palpal sulcus a pearly liquid is secreted.

Most pselaphids are covered with "hair," or setae. This pubescence is usually very short, and the individual hairs are sharp-pointed and inconspicuous. There are numerous exceptions to this, and often the setae are so specialized that they may appear to be tactile in function, or to have some unknown sensory role. Obviously, we need much research upon this point before reaching conclusions. A few examples will give the range of variation in pselaphid pubescence.

One whole section of the family (the Ctenistini) is characterized by having the setae greatly flattened and widened, so that each seta is a spade-shaped wafer. In other genera certain special setae have greatly enlarged tips. These hairs may end in a relatively large sphere, or have the tip flattened to form an umbrella-shaped structure. Setae may be concentrated about glandular areas of the body. Finally some few, such as the Japanese *Batrishilbus* and the essentially Neotropical *Eupsenius*, are glabrous, that is, lack all pubescence.

What has been outlined in regard to pselaphid anatomy and behavior leads us to the conclusion that these beetles are well suited for a life in the forest floor litter and humus; that, through their predation, they assist in maintaining a balance of forces in litter reduction.

Not all pselaphids inhabit the forest floor. Other terrestrial niches may be sparingly

occupied. We have mentioned their residence beneath deeply embedded boulders, usually on the sides of hills or in rocky meadows. Similarly, the cavernicolous habit has been noted. Other species inhabit the unstable vegetation mat of quaking bogs.

Quite a few live in the relatively thin humus and floor of prairie communities and may be taken from bluegrass with a sweep net. An aspect of the predacious nature of meadow pselaphids may become economically important. In the past few years H. W. Stunkard, of New York University, has demonstrated that the oribatid mite genus *Galumna* is the intermediate host of the sheep tapeworm, *Moniezia expansa*. Since pselaphids feed upon mites, *Galumna* included, their predation in contaminated pastures is to be thought of as an ecological deterrent to the dispersal of the vector and its parasite.

All the nonforest habitats seem to be secondary. All are more or less adjusted to fit the living requirements of these beetles, and have some resemblance to the forest habitat niches.

There remains a remarkable habitat penetrated by about 15 percent of the species of Pselaphidae. This is the complex social environment of ant and termite nests. Pselaphids that live in these nests as guests (or "inquilines") are "ant beetles" in truth, and include some of the most highly specialized genera. The contact of ant beetles with social insects has elicited some of the most intricate patterns of insect behavior.

It is not strange that pselaphids should be able to live with ants and termites; many animals do. The relatively uniform air temperature and relative humidity of the host nest, its darkness, and the abundant food supply are ecological conditions that fit the requirements of leafmold inhabitants. There are two apparent objections from the pselaphid standpoint. The first of these is that the food might differ qualitatively from that of the leafmold carpet. The second is

that the generalized leafmold pselaphid must become adjusted to the host; that is, the beetle must be either tolerated by the ants or termites or able to avoid them successfully in the nest.

As to the first of these points, the pselaphid diet is so varied as to kind and condition of the animal eaten that the first problem does not apply to most ant hosts. The majority of ants assemble in their nests a great variety of foodstuffs. Pselaphids inhabiting such nests feed upon the food brought in by the worker ants, and also upon injured ants, ant larvae and pupae, and upon the mites which live in the ant nest and on the ant integument. The food factor presents a more serious problem with respect to the establishment of the pselaphid-host relationship in termites, for termites, miscalled "white ants," have a restricted diet of woody fiber, or cellulose, and this is not a food of the predatory pselaphids.

One may postulate a sudden genetic mutation of a leafmold pselaphid that would endow the beetle with such an array of adaptive features that the species population would fit into the termite society without difficulty, would be unmolested by the host, and could feed on termite exudates, feces, or on sick or immature inmates.

Such a postulate is not the most probable explanation. We may rather imagine that there has been a gradual evolution of guest pselaphids. Each pselaphid species population so involved would be subjected to environmental selection, the selection in this case being made by the social matrix of ant or termite. From this point of view, the primitive mold pselaphids would pass through a stage in which they were facultative, could live in the humus or in the nest at the dictate of circumstance. Gradually, over great periods of time, positive selection for the nest habitat would operate on pselaphid mutants. There would be a tendency for the dark, stable nest climate and the

abundance of assorted food stores and immature hosts to produce beetles that had become more and more adjusted to the life of a social parasite, and less adjusted to the mold habitat.

If this general view is tenable, then the ant society, with its more varied and abundant food, should be colonized more often than the termite society, which has its food base in wood fiber and offers fewer feeding possibilities to the invading beetles. The fact is that there are a great many more pselaphids found with ants than with termites. For example, in the American tropics there are 964 known kinds of pselaphids. Of this number, there are 54 species known from the nests of social insects, or 5.7 percent of the fauna. This is lower than in the better known Nearctic fauna and reflects our ignorance of the tropics. Of the 54 pselaphid inquilines, 42 species, or 78 percent, live with ants as "myrmecocoles," and 12, or 22 percent, with termites as "termitocoles."

As to the second objection, the difficulty of adjustment to the host by the pselaphid is met by the fact that a great number of these beetles do live with social insects, thus proving that these beetles have adjusted, and are continuing to adjust themselves, to ant and termite societies. This inquilinous adjustment has arisen in many different tribes within the Pselaphidae, and 2 tribes, the Attapseniini and the Clavigerini, are restricted to this way of life.

Apparently, the role of the pampered guest is neither the result of a sudden genetic change nor the exclusive property of a particular stock.

As expected, some pselaphids are at home either in the forest floor or the ant nest. In the United States we may mention 2 species as examples of this category, *Batrisodes globosus* and *Tmesiphorus costalis*. These species are "leafmold beetles" most of the time but are frequently recorded as "ant beetles" with a variety of different kinds of ants. As species become more adjusted to

ant societies they tend to inhabit the nests of fewer species of hosts, until they become more or less restricted to a single kind of ant, or to a few closely related kinds. The genuine guest (myrmecophile) is not taken at liberty in the humus; the more specialized forms have rudimentary mouth parts and appear to be unable to live outside the host circle.

Many entomologists have worked on ant-beetle ecology; the list of their names is a cosmopolitan one. Such men include Erich Wasmann (Belgium), Alfred Hetschko and Erich Krueger (Germany), H. J. K. Donisthorpe (England), Filippo Silvestri (Italy), E. A. Schwarz, W. M. Wheeler, and H. F. Wickham (United States), Carlos Bruch and Angel Gallardo (Argentina).

Erich Wasmann, a pioneer in this phase of investigation, gave a classification of the guests of social insects in general, and Wheeler modified this classification in 1910. This modified version, with strict application to the pselaphids, includes two categories, the synoeketes and the symphiles.

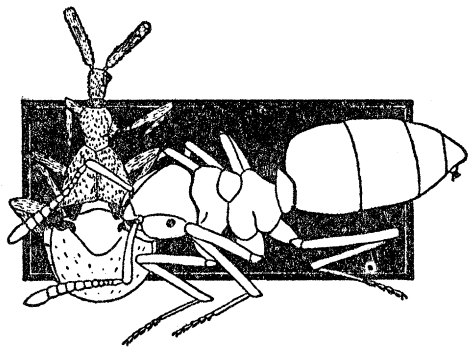
The synoeketes are pselaphids that live within the nests of ants and termites without being actively persecuted by the host. Usually such species are indifferently tolerated. Within this category there are many subdivisions, from the facultative forms to those approaching the symphile condition. There are many pselaphids in this general group, including species of *Batrisodes*, *Rybaxis*, *Cedius*, *Tmesiphorus*, *Ceophyllus*, and *Cercocerus* living with ants, and *Phategnomus* with termites.

The symphiles, or true guests, are the elite among ant beetles. They include the entire subfamily Clavigerinae, and possibly the remarkable new tribe, Attapseniini, known so far by 2 species living with the leaf-cutting ants (*Atta*) in Brazil and Argentina. The attapseniines have been described by Carlos Bruch and August Reichenperger, but we lack ecological information about them as yet. They are noted here since they are structurally intermediate in

many ways between the subfamily Pselaphidae and the subfamily Clavigerinae.

The symphiles exhibit a number of characteristic responses, or "symphiloid characteristics." Their behavior pattern and structural aspect include:

1. A more or less shining, light-colored integument, often resembling the "oily yellowish sheen" of their hosts.
2. Special tufts of long, golden setae (trichomes) that convey a special secretion. This secretion is produced by gland cells at the base of the trichome and is very stimulating to the host, the worker ants frequently stopping their



From Park, 1932, *Ann. Ent. Soc. Amer.*

FIG. 3. HOST AND GUEST

A HOST ANT (*Lasius aphidicola* WALSH) LICKING AND SUCKING THE TRICHOMES OF THE PSELAPHID *Adranes lecontei* BRENDDEL.

communal activities to lick and suck these golden bundles (Fig. 3).

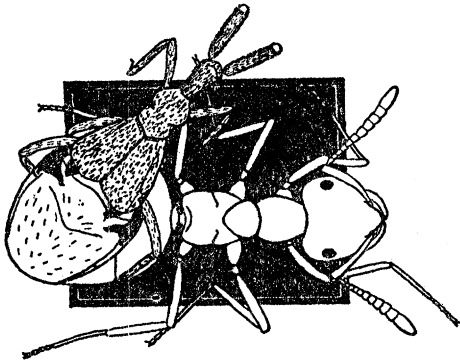
3. The inconspicuous, highly modified mouth parts: these are fitted for licking, scraping, and sucking, rather than chewing, a struggling leafmold mite.
4. The unusually modified antennae.
5. The deliberate, clocklike precision of their unhurried walk within the hurry of the nest.
6. The habit of twirling the antennae when approached by a host ant.

These features, in combination, are equivalent to a hallmark of the true guest. Some items, such as the elaborate antennae or shining integument, taken alone, are frequently seen in free-living pselaphids.

Of the 200 odd species of clavigerid sym-

philes, 3 are rather well-known, *Claviger testaceus* and *longicornis*, of Europe, and *Adranes lecontei*, of the United States. The day-to-day life of these 3 may be summarized as an example of symphilism.

The beetles are wholly immune from host attack, a condition hard to attain in the Amazon society of most ants. They stalk about the moist, dark galleries, especially the ant brood chambers. When approached by an ant, the pselaphids do not letisimulate or hurry away; rather they pass slowly by, or pause and twirl their antennae, or stop so that the ant must pass over or around. The ants suck assiduously at their trichomes, lick the beetle's integument and scrape at it. This sucking and licking goes on at all hours of the day or night, the ant society being arrhythmic. The beetles may be so attended by several ants simultaneously for several minutes at a time. Furthermore, they ride about the nest on the ant's body. This behavior (phoresy) may last for



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FIG. 4. A HITCHHIKER

A PSELAPHID, (*Adranes lecontei* BRENDDEL) BEING CARRIED ABOUT THE NEST OF THE HOST ANT (*Lasius aphidicola* WALSH) BY A HOST WORKER.

long periods. Thus an *Adranes* has been seen to climb on the abdomen of an ant and ride her about the nest for ninety minutes (Fig. 4). In addition to licking and sucking the beetle integument and trichomes, the ant workers feed the beetles directly. The ant

approaches a clavigerid and, after they have tapped each other with their antenna, regurgitates a drop of liquid food into the mouth of the beetle, just as she would for a sister ant. In return for such treatment, the beetle may strike at the nest society, just



From Park, 1932, *Ann. Ent. Soc. Amer.*

FIG. 5. TAKING CANDY FROM A BABY

A PSELAPHID (*Adranes lecontei* BRENDDEL) HOLDING, LICKING, AND SCRAPING A LARVA OF THE HOST ANT (*Lasius aphidicola* WALSH).

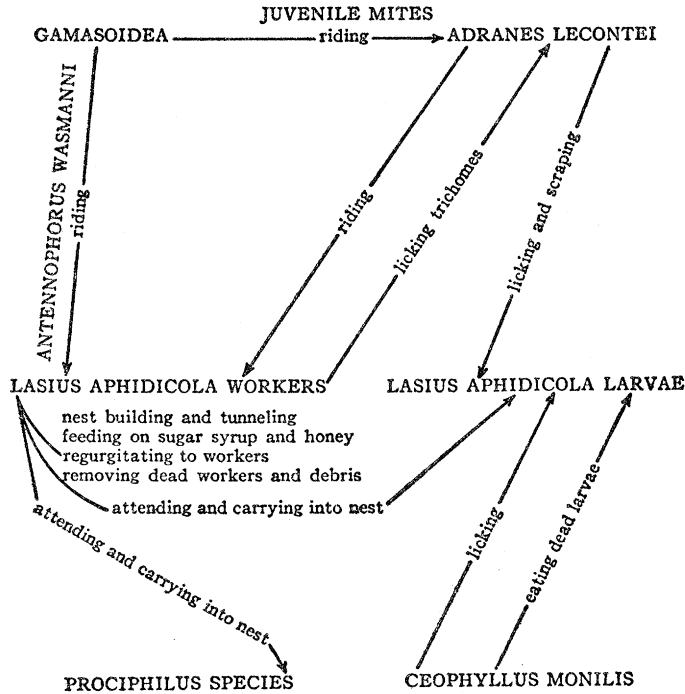
as gangsters and racketeers strike at the human society. Thus, some species haunt the brood chambers and occasionally scrape, puncture, and suck the eggs, larvae, and pupae of the host, or a badly injured worker ant (Fig. 5). This is a very complex pattern of behavior (Fig. 6). The common host *Adranes lecontei* is the pale yellow *Lasius aphidicola* or its close allies. With this ant live other guests besides the clavigerid, each guest having a separate pattern with every other guest and the host. Thus there is a large mite, *Antennophorus wasmanni*, which rides about on the ants. These mites also ride on the beetles; I have seen mites on a beetle and the beetle in turn perched on a burdened ant.

The species of *Claviger* and *Adranes* have no eyes. As a rule, they are not found beyond the confines of their host's nest. An exception may be noted in their probable method of dispersal. On at least three separate occa-

sions an individual of *Claviger testaceus* has been taken while clinging to a winged male or female ant. It will be remembered that the virgin queen ants and their male consorts compose the reproductive group. Such ants are usually winged. At the mating season these ants leave the parent nests, mate, and the fertilized queen ants found

tended by males, at the future nesting spot, breaks off her wings, and begins to lay eggs.

Thus it is difficult to imagine how clavigerids are dispersed without clinging to queen ants, at least for most ant species. It is nearly as difficult to understand how they can be established in a new nest by this method.



From Park, 1932, *Ann. Ent. Soc. Amer.*

FIG. 6. SOME INTERRELATIONS WITHIN THE SOCIETY OF A HOST ANT
 RELATIONSHIPS BETWEEN HOST ANT WORKERS AND LARVAE (*Lasius aphidicola* WALSH), GAMASID MITES (*Antennophorus*), AND TWO SPECIES OF PSELAPHIDS (*Adranes* AND *Ceophyllus*).

new colonies. Consequently, *Claviger testaceus*, and other clavigerines as well, may become dispersed by this phoresy. The dispersal would be slowly achieved since at least 2 beetles, of opposite sexes, or a previously fertilized female clavigerid would have to be present. This raises certain objections. Two beetles have not been reported on the same winged female ant, and the fertilized queen ant usually arrives, unat-

One final point should be noted about ant beetles in general. There is an apparent correlation between the rate of locomotion of a myrmecocole and its ecological role in the host society. That is, symphilism is more or less inversely proportional to speed of movement. A single example must suffice. Five worker ants of *Lasius aphidicola* were clocked for 10 trials, each trial lasting one minute. These 50 trials averaged 52.5 inches

moved per minute. Their synoekete guests (*Batrisodes scabriceps*, *Batrisodes schauimi*, and *Ceophyllus monilis*) averaged 36.3 inches per minute. The symphile, *Adranes lecontei*, averaged 20 inches per minute when undisturbed.

Obviously, a beetle that is subject to host attack cannot perpetuate itself unless it (1) has a prodigious reproductive rate, or (2) can defend itself by physical means, or (3) can run faster than the host, or (4) hides in unfrequented parts of the host nest.

When we have found ant beetles relatively unmolested by the host ants and moving more slowly than their hosts, we have assumed that natural selection is operating upon changes in the heredity of the population. Consequently, natural selection must be regarded as acting as an ecological influence within the complex nest society of social insects.

This may partially explain why the category of persecuted guests (synechthrans) is rare or absent among pselaphids. The pselaphid beetle, with its rigid abdomen and generally slow locomotion, could hardly exist in an ant nest if the beetle were constantly pursued and attacked.

In such a general account, intended to present a group of insects to scientific colleagues, it seems fitting to emphasize the lack of information that is available on the life history of Pselaphidae.

If one brings back for leisurely study an entire ant nest, or a large quantity of forest floor mold, many kinds of adult insects are to be found, including pselaphids, and many insect larvae. These larvae can be identified or reared, in many cases, but one does not find the larvae of Pselaphidae. Why?

Eggs, larvae, and pupae of the related rove beetles, or Staphylinidae, have been described for a respectable number of species. The immature stages are known in many families of beetles with fewer species than the Pselaphidae. The pselaphids, with

about 5,000 species, are almost unknown with respect to their life history. Here is a strange thing indeed.

Since 1818, when P. W. J. Mueller began the study of pselaphid beetles in relation to host ants, there has been a paucity of information on the immature stages of these insects. Wasmann, Janet, Hetschko, Schmitz, Peyerimhoff, and Donisthorpe have discussed this problem and have studied *Claviger* carefully, but the larval stages remain unknown. Between 1930 and 1931 the American experts on beetle larvae, Adam Böving and F. C. Craighead, published a critical study on the larvae of beetles, but could identify and illustrate only the larvae of 2 species of pselaphids, *Batrisodes monstrosus* and *Euplectus confluens*.

Whereas there are many species of pselaphids, with the exception of a very few, they are known only from the mature adult stage (the imago). These beetles are widely distributed. In the tropics they can be taken in numbers around lights at night. They can be driven from humus by a gradient of heat, in what is called a "Berlese" or a "Silvestri" funnel. They can be picked out of an ant or termite nest. They are not easily collected and are not common in the usual sense of the term, but the adults can be accumulated with patience and persistence.

Since each adult pselaphid must have hatched from an egg as a minute, six-legged, wormlike stage known as a larva; and since each larva must pass through several periods of growth, with a molting of the larval integument at the end of each growth and differentiation period; and since the final larval stage must pass into a quiescent stage known as a pupa, before the adult emerges from the pupal skin, we should expect to find these several immature stages in the forest log and leaf mold, and in the nests of ants and termites.

At least there should be as many larvae as adults. Theoretically, there must be many more eggs, larvae, and pupae than adult beetles since these immature stages would be subject to destruction by carnivorous insects, bacterial and fungoid disease, and accident. If each species population is to maintain its size, or increase its size, there must be enough immature stages to furnish a margin of safety against such loss, a superabundance of immature animals.

The fact that the immature stages of pselaphids as a whole are almost unknown is thus a mystery. There must be some explanation. Perhaps it is quite simple; for example, some ecological factor operating upon their immature life in a peculiar way, or a physiological requirement, that causes their eggs, larvae, and pupae to be hidden in the humus or in the host nest so securely that we have not discovered them. This would be discoverable in time, by chance or deliberate search of unlikely places. Again, these immature stages may be parasitic for at least some of the species of pselaphids.²

Oddly enough, we have both ends of the chain: the mating act of the mature pselaphids, and the just-emerged adult.

I have seen pselaphids mate on several occasions at localities in widely separated

² This is not my view alone. My friend, H. S. Barber, of the U. S. National Museum, expressed this belief in a conversation several years ago.

parts of the Western Hemisphere, and in such free-living genera as *Batrisodes* and *Dalmosella*, and in the symphilic, blind *Adranes*. I have never seen the females lay their eggs.

The just-emerged adults are not at all uncommon in large collections. When a beetle breaks out of the pupal integument it is soft and light-colored. In the pselaphids, these "callows" are thin-skinned, delicate creatures of an almost uniform light-yellow color. If they are killed and pinned in this condition, they remain light in weight and color, although they become more or less shrunken with time.

The free-living leafmold pselaphids probably live at least a year. In temperate regions mating occurs most frequently in the late spring, between April 15 and May 15. The species probably hibernate as adults in the floor mold. The ant beetles such as *Adranes* and *Claviger* live a long time in captivity. I have kept *Adranes* alive with the host ants for fourteen months; *Claviger* has been kept for as long as three years by Donisthorpe in England and for four years by Janet in Europe.

We must await more information before an over-all view can be held regarding the life history of the Pselaphidae. But these beetles remain with us, a large, diversified assemblage, performing a useful function in the forest community, and generally unknown by biologists.