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SPHEROID SENSE ORGANS ON THE CERCI OF POLYPHAGID COCKROACHES (BLATTARIA: POLYPHAGIDAE)

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Abstract—Conspicuous, bulbous, spheroid sensilla, of unknown function but apparently related to trichobothria, are found on the ventral surfaces of the cerci of some members of Polyphagidae [*Arenivaga* (*Arenivaga*) spp.; *Arenivaga* (*Psammoblatta*) spp.; *Eremoblatta* spp.; *Polyphaga* spp.; *Homoeogamia mexicana*; *Ergaula* spp.; *Therea petiveriana*].

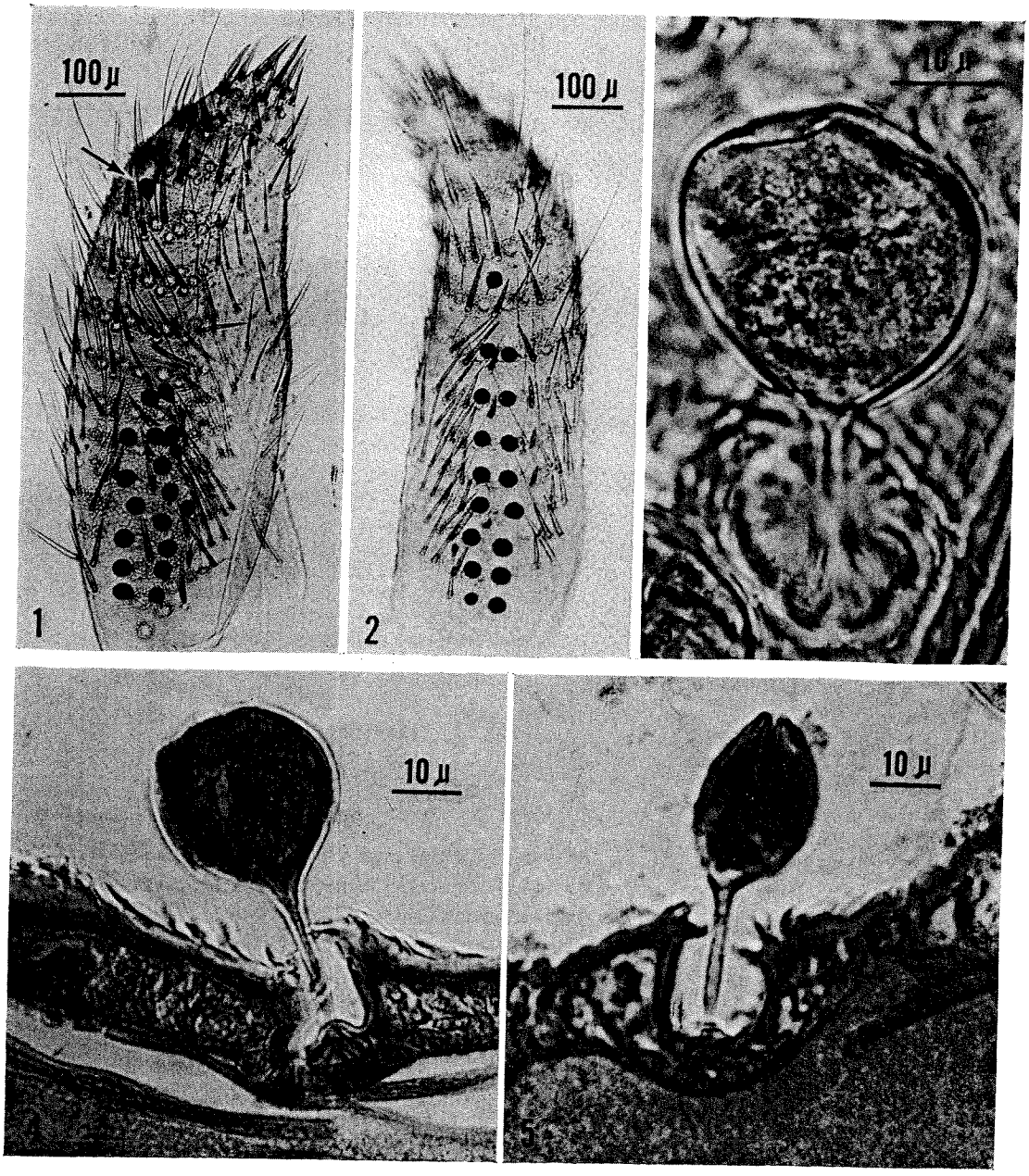
Spheroid sense organs were not found in 44 genera and 60 species representing the four other families (Cryptocercidae, Blattidae, Blattellidae, and Blaberidae) of Blattaria.

Index descriptors (in addition to those in title): Trichobothria, taxonomy.

INTRODUCTION

FEW PAPERS have dealt with the sense organs on the cerci of cockroaches. Sihler's (1924) classical study of the cerci of insects included the sensilla found in *Blatta orientalis* L. and *Periplaneta americana* (L.). The ventral surfaces of the cerci are covered with hairs, thick bristles, and long thread-like setae. The last are now known as trichobothria. The dorsal surfaces of the cerci have campaniform sensilla, comparatively few bristles and no trichobothria. Sihler described the histology of the sensilla and indicated their numbers and distribution; he also noted that similar sense organs were present in *Blattella germanica* (L.) and *Ectobius lapponicus* (L.). Hsü (1938) described the histology of the sensilla chaetica and campaniform organs on the cerci of *B. orientalis*. More recent papers (Nicklaus, 1965, 1967; Nicklaus *et al.* 1967, 1968) have dealt with the fine structure of various sensilla on the cerci of *P. americana*.

The cerci of polyphagid cockroaches have sensilla chaetica and trichobothria characteristic of those found in the species mentioned above, and in addition a few small thick-walled hairs. However, they also have spherical sense organs unlike those previously mentioned. These are so unusual and readily seen that it is surprising that no one has described them in detail. Bey-Bienko (1950) apparently noted them in his descriptions of two polyphagids. He stated that the inner aspect of the base of the cerci of *Arenivaga* (*Psammoblatta*) *moris mortui* (Janson) had dark tubercles whereas *Arenivaga* (*Psammoblatta*) *livida* (Brunner) had black papillae in this region.



FIGS. 1–5. *Arenivaga investigata*. Photomicrographs.

FIGS. 1–2. Entire cerci of adult females; one spheroid sensillum (Fig. 1, arrow) broke off and floated above its normal position (KOH preparations).

FIG. 3. Spheroid sensillum on cercus of a recently-moulted adult male starting to darken. Eosin stained, whole mount.

FIGS. 4–5. Spheroid sensilla on cercus of a recently-moulted adult male. Sectioned at 7μ, stained with Mallory's triple.

The purpose of this paper is to bring to the attention of physiologists these interesting spheroid sense organs and to note their distribution in the Blattaria.

MATERIALS AND METHODS

Only cerci of *Arenivaga investigata* Friauf and Edney were used for histological and scanning electron microscope study. Some specimens were fixed in Bouin's fluid and others in 5 per cent formalin. Material to be sectioned was embedded in Paraplast. Sections were cut at 7μ and stained with Mallory's connective tissue stain.

Although the cerci of adults could be sectioned easily the spheroid sense organs, because of their hardness, proved to be extremely refractory. They were pushed aside by the microtome knife, instead of being cut, and usually dropped off the slide while the sections were being stained. The sense organs of newly-moulted individuals were sectioned successfully although many of the spheres were distorted in shape. It is probable that the embedding medium penetrated incompletely. These slides were coated with collodion before being stained to prevent loss of the spheroid bodies.

The cerci of *A. investigata* and 1 museum specimen of *Ergaula silphoides* (Walker) used for electron scanning were coated with palladium-gold *in vacuo*. Cerci from museum specimens, were treated with 10 per cent KOH, dehydrated, cleared, and mounted in Permount.

RESULTS AND DISCUSSION

We first noted the sensilla on the ventral surfaces of the cerci of nymphs and adults (both sexes) of *A. investigata*. They are black-ridged spheres on the ends of slender stalks arising from deep depressions in the cuticle (Figs. 1–10). The close association of the trichobothria with these unusual sense organs is shown in Figs. 19, 23 and 29–31, where the former appear as extremely slender hairs.

The spheres usually occur in 2 vertical rows and are present to about the middle or slightly beyond the middle of the cercus (Figs. 1, 2). Sometimes there may be a partial third row (Fig. 1). Counts made of the spheres remaining on the cerci of 10 nymphal skins ranged from 1 to 12. Low counts are due to the loss of some of the spheres. Rarely are there the same number of spheres in both rows. Adult females may have from 16 to 24 spheres. One male had 15 and 17 spheres, but these numbers probably vary somewhat.

The socket of the spheroid body, as well as that of the trichobothrium, consists of a cup-shaped cavity with a number of partitions on its inner surface that extend from top to bottom. When viewed from above, the partitions appear as irregular spines extending towards the center (Fig. 10). An extremely delicate membrane with a central opening forms the roof of the cup. The stalk of the spheroid body passes through the opening. Three or four of the partitions on the side of the cavity that faces the distal end of the cercus are composed of vertical rows of very fine spines.

The stalk of the sense organ decreases in diameter at its base, passes through a ring-shaped disc of cuticle in the floor of the cavity and then expands below the ring. The stalk with its expanded inner end appears to be freely movable within the ring through which it passes. Occasionally a socket was damaged in sectioning so that the stalk with its expanded inner end could be seen in its entirety separated from the floor of the cavity. The cuticular sheath that encloses the dendrite is attached near the center of the inner end of the stalk;

but the dendrite, itself, was not identified. Electron micrographs of sections would be helpful here.

Although most of the stalked bodies on a cercus are spherical, or nearly spherical in shape, a few are elongated, or lens-shaped, and have a pointed tip (Fig. 5). The spheroid body of fully-hardened individuals, as noted earlier, resisted all efforts to section them. Attempts to crush the spheres between a cover glass and slide failed. It would be interesting to have more accurate data on the hardness of the structures and to compare them with other dense parts such as claws and the biting surface of mandibles.

In the newly-moulted nymph or adult the spheres are colorless. They then darken gradually, and after a few days become blackish and hard. How the newly-formed sphere is pulled out of the old one is a puzzle. The sphere in the moulting individual is soft and flexible and perhaps could be compressed. But to be pulled out of the old cuticle would require that the large bulb be compressed to the diameter of the stalk of the old sensillum. It is also possible that the sensillum is slender initially and it swells into its final spherical shape, by the time the insect is freed of the old cuticle.

The outer surface of the sphere is covered with a thin cuticular layer with many striae on its surface. Under favorable conditions these are visible with the light microscope and, in scanning electron micrographs, are conspicuous (Figs. 7–9). The interior of the sphere is filled with a dense reddish-brown or black material that is nearly, although not quite, homogeneous since a few irregular masses of different sizes and shapes are scattered through it.

In newly-moulted individuals where the spheres are still white, the surface of the sphere is the same as described above but the contents are quite different. The material appears as a finely granular coagulum (Fig. 3) and in slides prepared with Mallory's stain closely resembles the coagulated hemolymph in the lumen of the cercus. It also contains irregular masses, both large and small, of a denser material. These masses may be stained either red or blue. The contents of spheres from recently-moulted specimens that have begun to darken are intermediate in density between those that have just moulted and those that are fully developed. The contents of the spheroid bodies must originate as a secretion of the trichogen cell and, we may assume, consist of several substances that react to form the very dense material found in the bodies. They would thus be a special form of cuticle. A study of their fine structure before, during and after moulting should give interesting results.

The cup-like socket and the attachment of the inner end of both the trichobothrium and the spheroid bodies resemble very closely those of the trichobothria (*soies filiformes*) of *Gryllus domesticus* and the flask-shaped hairs (*soies en forme de bouteille*) of *Gryllotalpa vulgaris* studied by Hsü (1938, Figs. 31, 38). The trichobothria (*Fadenhaare*) and club hairs (*Keulenhaare*) of *Gryllus bimaculatus* examined by Gnatzy and Schmidt (1971, Fig. 3) are also very similar. The *keulenhaare* of *Gryllus* appear to be flat and strongly resemble the spheroid sensilla on the cerci of the polyphagids *Ergaula* and *Therea* (Figs. 29–33), when viewed under the light microscope.

FIGS. 6–10. *Arenivaga investigata*. Scanning electron micrographs.

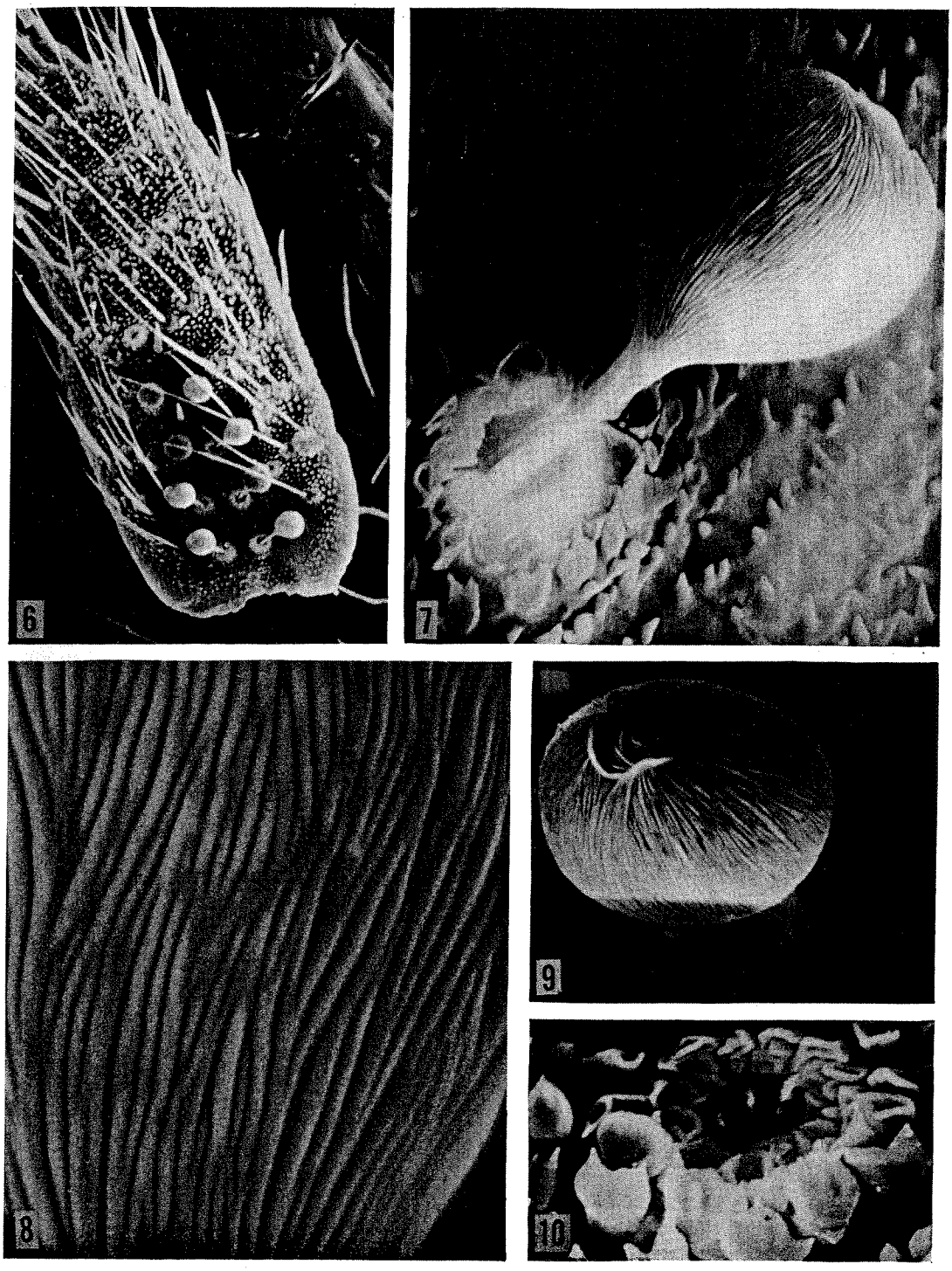
FIG. 6. Entire cercus (ventral) showing 9 spheroid sensilla arranged in 2 vertical rows, filiform trichobothria, and stout spines. × 200.

FIG. 7. Spheriod sensillum. ×2000.

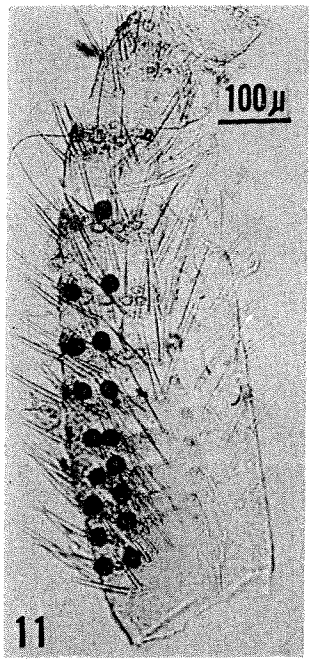
FIG. 8. Wall of bulbous portion of spheroid sensillum. × 10,000.

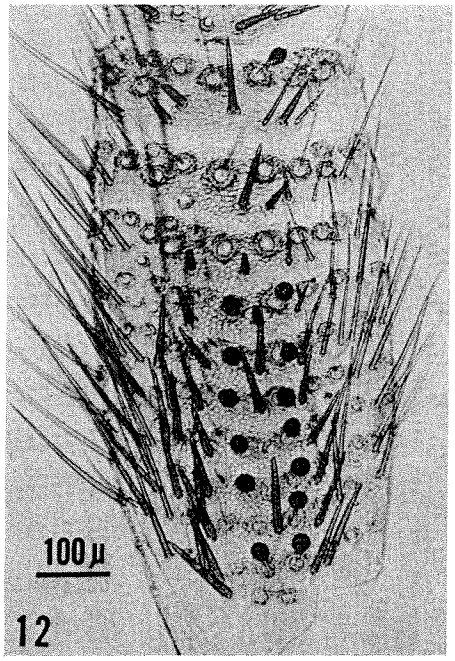
FIG. 9. Oblique dorsal view of spheroid sensillum. × 2000.

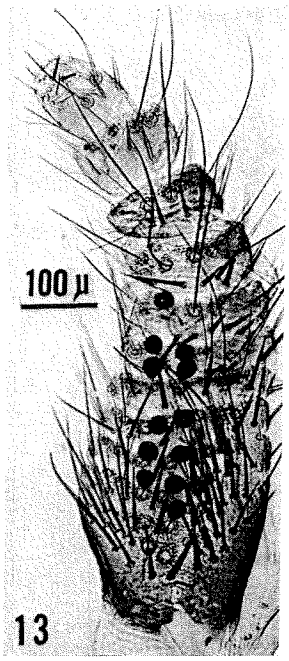
FIG. 10. Socket of a spheroid sensillum. × 2000.

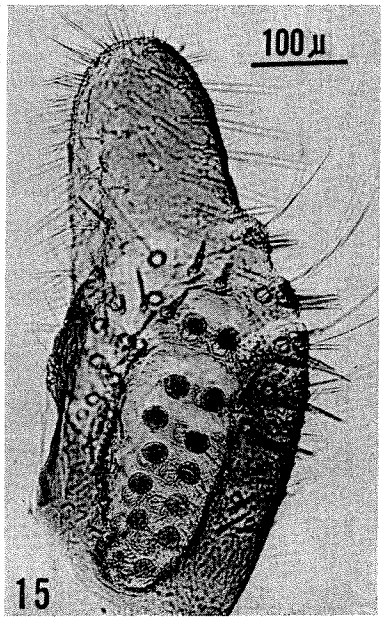


FIGS. 6–10. *Arenivaga investigata*. Scanning electron micrographs.









FIGS. 11–16. Cerci of polyphagids (Photomicrographs of KOH preparations).
FIG. 11. *Arenivaga apacha* (adult ♂).
FIG. 12. *Arenivaga bolliana* (adult ♂).
FIG. 13. *Arenivaga* sp.
FIG. 14. *Eremoblatta subdiaphana* (adult ♂).
FIG. 15. *Eremoblatta hirsuta* (from ♂ type).
FIG. 16. Portion of cercus of *Homoeogamia mexicana* (adult ♀).

Apparently one of the functions of cockroach cerci (*Periplaneta americana*) is to perceive vibrations—either sound or air movement (Pumphrey and Rawdon-Smith, 1936a, b). Whether the spheroid sensilla on the cerci of polyphagids have a similar function remains to be seen. The facts (1) that the sockets of the spheroid sense organs so closely resemble the sockets of the trichobothria, (2) that they are innervated by a single neuron, and (3) that the 2 kinds of sense organs occur closely intermingled on the same area of the body suggest that the spheroid sense organ is a variant of the trichobothrium. The latter are present in many arthropods and experimental evidence supports the idea that they are sensitive to vibrations. Nicklaus (1969) concluded that the clubshaped sensilla on the cerci of *Gryllus* served as gravity receptors. The spheroid organs on the cerci of *Arenivaga* may be gravity receptors since the bulb is filled with a dense material; the weighted end of the sensillum could cause the stalk to move at its base, depending on the orientation of the cercus. References to the extensive literature on the structure and function of the trichobothria and related types of sense organs may be found in the papers of Sihler (1924), Hsü (1938), Slifer and Sekhon (1970) and Gnatzy and Schmidt (1971).

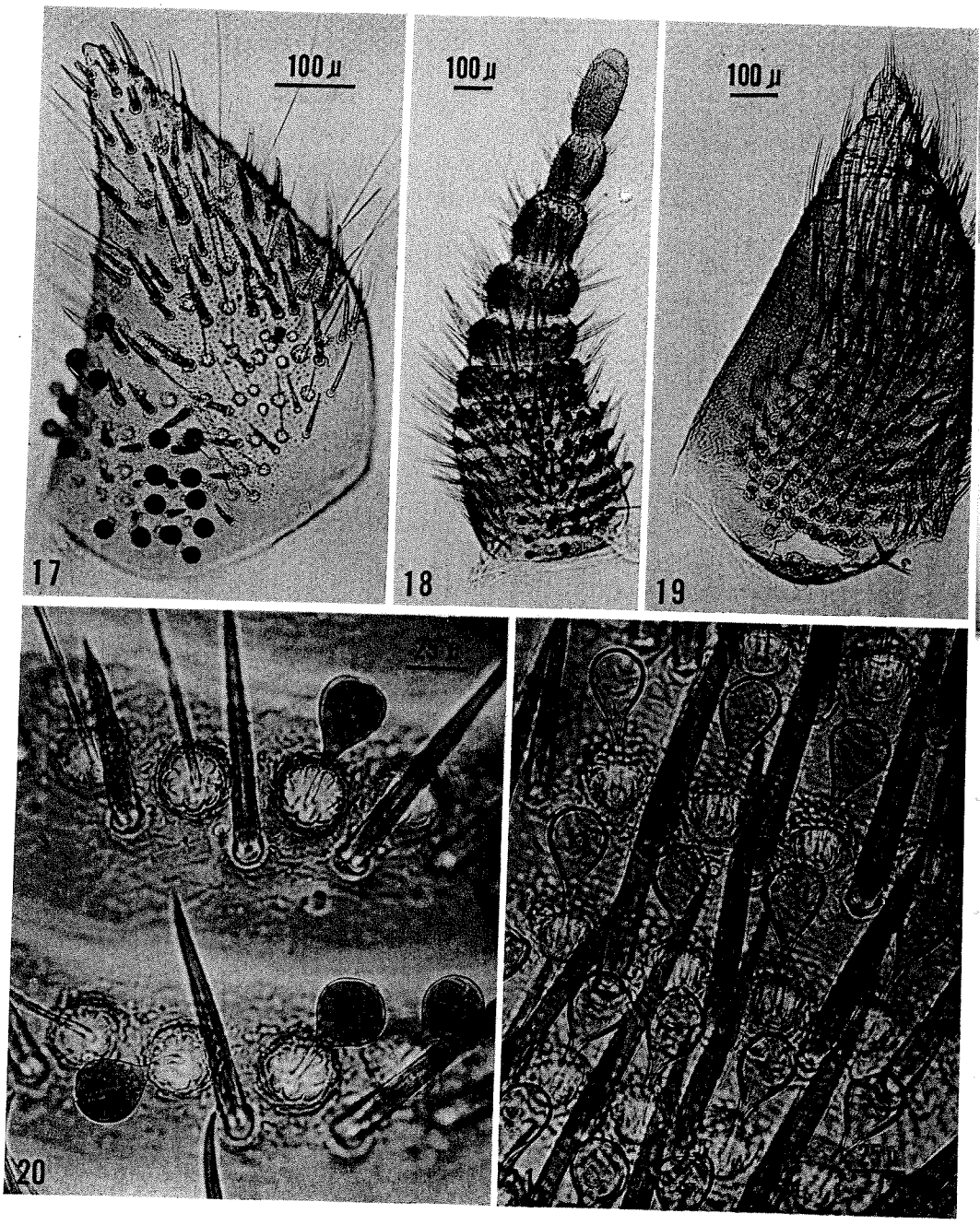
The distribution of the trichobothria and spheroid bodies only on the underside of the cercus in *Arenivaga* presents interesting problems. Many polyphagids in the United States and elsewhere are desert forms and often burrow in sand. Whether or not the spheroid sensilla are involved with behavior in this habitat is not known but should be invesitgated.

A survey was made for the presence of these sense organs on the cerci of other museum specimens of polyphagids. Their shape, arrangement and occurrence is as follows:

1. Spherical, blackish bodies arranged principally in 2 vertical rows:
   Arenivaga (*Arenivaga*) *apacha* (Saussure) (Fig. 11)
   A. (*A.*) *bolliana* (Saussure) (Fig. 12)
   A. (*A.*) *erratica* Rehn
   A. (*A.*) *grata* Hebard
   A. (*A.*) *investigata* (Figs. 1, 2, 6)
   A. (*A.*) *rehni* Hebard
   A. (*A.*) *tonkawa* Hebard
   A. (*A.*) sp. (undescribed from Kelso dunes, Cal.) (Fig. 13)
   Eremoblatta hirsuta Hebard (Fig. 15)
   E. subdiaphana (Scudder) (Fig. 14)
   Homoeogamia mexicana (Burmeister) (Fig. 16)

In *Eremoblatta* spp. the ventro-basal half of the cercus is deeply concave (perhaps due to drying) and the spherical sensilla lie in this depression (Figs. 14–15). Princis (1960) placed *Homoeogamia* in the Homoeogamiidae and the other species in the Polyphagidae.

2. Spherical dark bodies arranged in many vertical rows:
   Arenivaga (*Psammoblatta*) *africana* (L.) (Figs. 18–21)
   A. (*P.*) *cerverae* (Bolivar) (Fig. 17)
   A. (*P.*) *rugosa* (Schulthess-Rechberg) (Figs. 22–23)
   Polyphaga aegyptiaca (L.) (Figs. 25–27)
   P. obscura Chopard (Fig. 24)
   P. plancyi Bolivar (Fig. 8)
   Ergaula capucina (Brunner) (Figs. 29–30)
   E. capensis (Saussure) (Figs. 32–33)
   E. silphoides
   Therea petiveriana (L.) (Fig. 31).

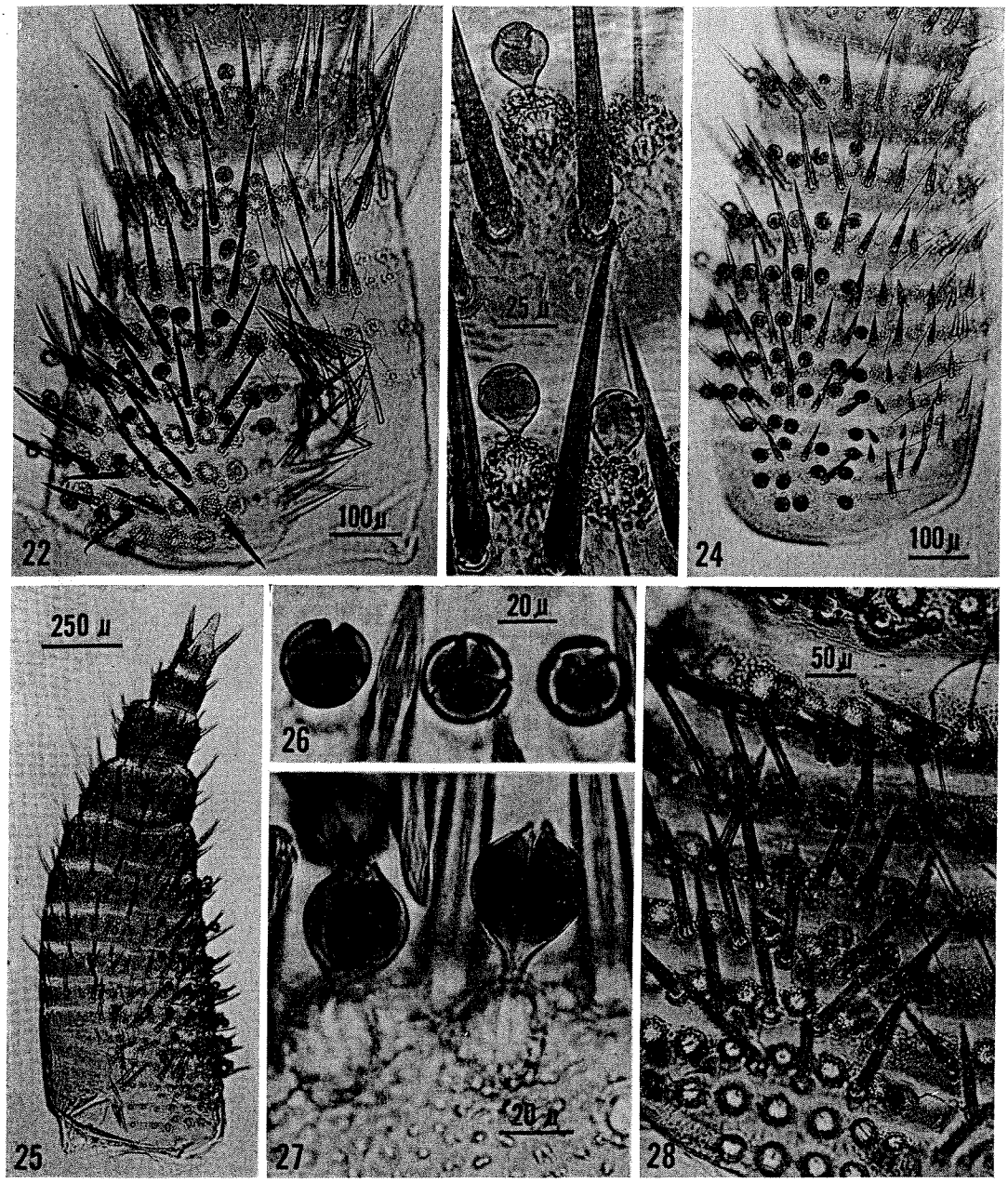


FIGS. 17–21. Entire, or parts of cerci of *Arenivaga* (*Psammoblatta*) spp. (Photomicrographs of KOH preparations).

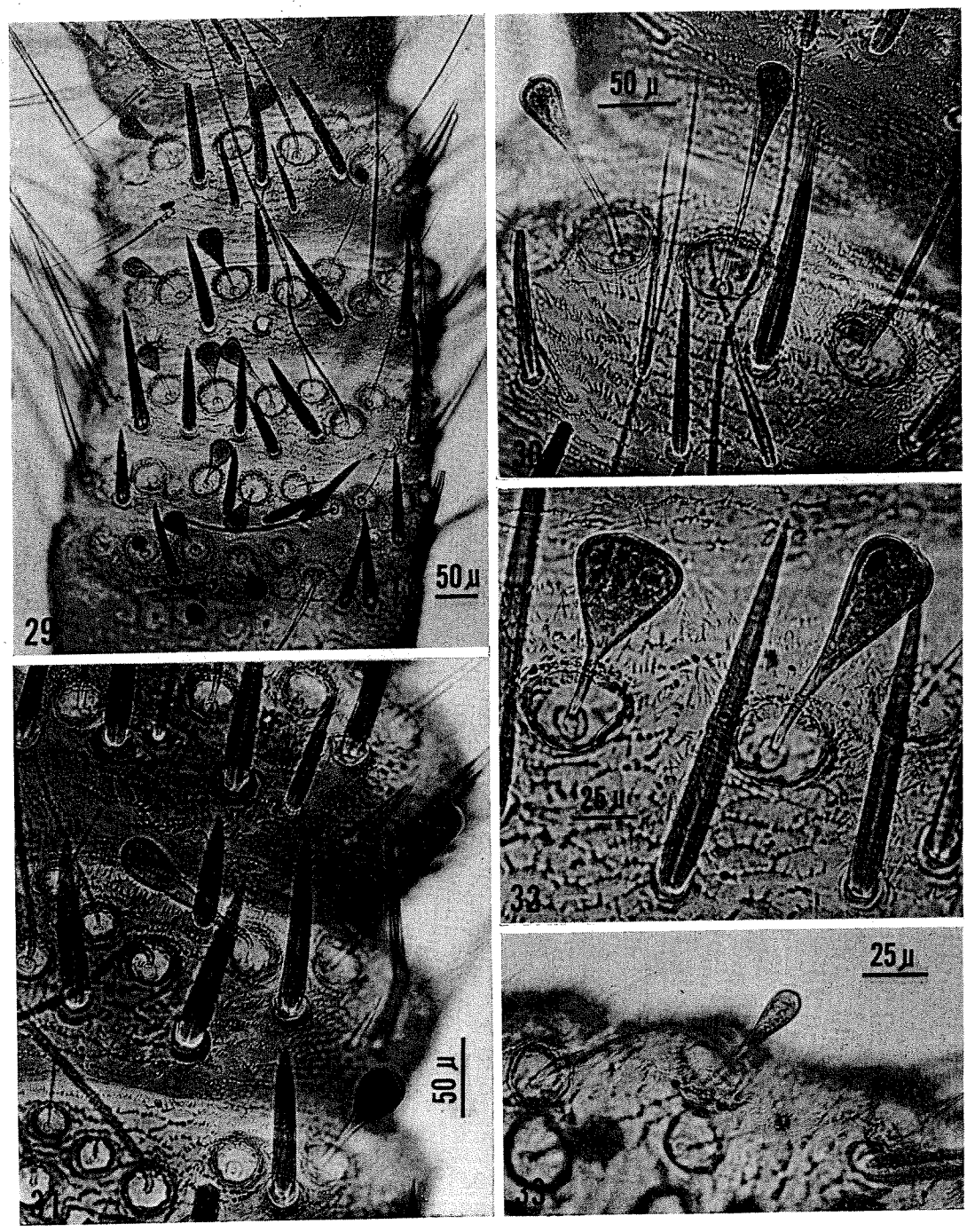
FIG. 17. *A.* (*P.*) *cerverae* (nymph).

FIGS. 18–20. *A.* (*P.*) *africana* (adult ♂).

FIGS. 19–21. *A.* (*P.*) *africana* (adult ♀).



FIGS. 22–28. Sense organs on cerci of polyphagids. (Photomicrographs of KOH preparations).
FIGS. 22–23. *Arenivaga* (*Psammoblatta*) *rugosa* (adult ♂).
FIG. 24. *Polyphaga obscura* (adult ♂).
FIGS. 25–27. *Polyphaga aegyptiaca* (♀ nymph); spheroids are split in 26 (end view) and 27 (lateral view).
FIG. 28. *Polyphaga plancyi* (adult ♂).



FIGS. 29–33. Sense organs on cerci of polyphagids (Photomicrographs of KOH preparations).
FIGS. 29–30. *Ergaula capucina* (adult ♂).
FIG. 31. *Therea petiveriana* (adult ♂).
FIGS. 32–33. *Ergaula capensis* (adult ♂).

Arenivaga and *Polyphaga* belong to the Polyphagidae and *Ergaula* and *Therea* are in the Homoeogamiidae (Princis, 1960).

In some specimens the spheres are split and have an apical beak-like projection (Figs. 26–27). The split spheres could be due to drying of pinned specimens.

Although the sensilla of *Ergaula* and *Therea* (Figs. 29–33) appear flat under the light microscope, a scanning electron micrograph of the sense organs on the cerci of *Ergaula silphoides* showed them to be round and ridged similar to those of *Arenivaga* (*Arenivaga*) spp.

Princis (1960) lists 7 families under his suborder Polyphagoidea. All of the above polyphagids belong to his Polyphagidae and Homoeogamiidae. Of his other polyphagoid families, the Attaphilidae is a member of the Blattellidae (Blattellinae) based on male genitalia, oöthecae, and ovaries (Roth, 1971); the cerci of *Attaphila fungicola* Wheeler lack the spheroid sense organs. *Latindia* sp. and *Compsodes schwarzi* (Caudell) also lack spheroid sense organs. Both of these genera were placed in the Latindiidae (Polyphagoidea) by Princis. *Eucorydia plagiata* (Walker) is a member of Princis' Homoeogamiidae. Its cerci (1 male) lack spherical sensilla but have long slender trichobothria arising from wide depressed sockets whose rims are not as uneven as those in other polyphagids. Many of the sockets lacked hairs which probably were broken off and it is possible that spheroid sensilla are present in this genus. *Holocompsa nitidula* is in Princis' sub-family Holocompsinae (Polyphagoidea: Euthyrrhaphidae) and it does not have spheroid sensilla. McKittrick (1964) suggested 2 subfamilies (Polyphaginae and Holocompsinae) for the Polyphagidae, but she studied only 2 genera (*Arenivaga* and *Hypercompsa*). Although we follow McKittrick's system of classification (Roth, 1970), Roth (1969, Table 4, footnote a) has pointed out that the taxonomy of the Polyphagidae is badly in need of revision. *Latindia* has an oötheca and oviposition behavior characteristic of Polyphagidae (Roth, 1971). However, its male genitalia differ markedly from other polyphagids such as *Arenivaga*. *Latindia* and *Compsodes* probably belong to a third subfamily (Latindiinae?) not covered by McKittrick.

A survey of various genera and species, other than polyphagids, was made for the presence or absence of the spheroid sensilla. Members of the following families did not have these sense organs:

1. Cryptocercidae (1 genus and species).
2. Blattidae (6 genera, 10 species).
3. Blattellidae (22 genera, 32 species).
4. Blaberidae (15 genera, 17 species).

The hair sensilla on the cerci of species belonging to the above families are principally stout, tapering, pointed bristles and long trichobothria. So far as we know at present spheroid sense organs occur only on the cerci of certain Polyphagidae.

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