Speciation Among Cave Opilionids of the United States[1]

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Introduction

The opilionids or phalangids are members of the Order Opiliones of the Class Arachnida. Other orders within this class include such abundant and well-known forms as the spiders, pseudoscorpions, scorpions, whip scorpions, mites, and a few lesser known groups. The opiliones are nearly world-wide in their distribution; they are found from the far North to southern areas such as Argentina and South Africa. Widespread and abundant as they are, they achieve their greatest variety and abundance in the tropical and subtropical regions of the world.

The opiliones are quite varied in appearance and size, but all have the following common characteristics:

1. An unsegmented cephalothorax which is broadly joined to the faintly segmented abdomen.
2. Three-segmented chelate chelicerae.
3. Six-segmented palpi.
4. A pair of simple eyes which are usually located on a tubercle on the anterior third of the cephalothorax.
5. A genital opening on the second abdominal segment, usually covered by a genital plate.
6. A pair of scent glands at the anterior part of the cephalothorax.
7. Respiration by means of tracheae with spiracles located on the second abdominal segment.

Within the order Opiliones, there are three suborders as follows:

I. Cyphophthalmi: mite-like forms. Species are known from the states of Washington and Florida, without known species between. No cave forms are known in the United States.

II. Laniatores: tropical and subtropical forms, with but a few exceptions. There are a number of Laniatores in the southeastern United States and a few in the West. Species occur along the west coast as far north as central British Columbia. Some of the Laniatores have brightly colored bodies with elaborate dorsal color patterns as well as spines and tubercles. Usually they are found in moist areas, living under rotten logs or under stones. In tropical rain forests, some

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are found in the bromeliad clumps high up in trees. Since many of the Laniatores are small and live in dark places, they often inhabit caves. It is among the members of this suborder that the largest number of cavernicoles are found. In the United States and Mexico, three families are represented: (1) Cosmetidae; (2) Phalangodidae; and (3) Triaenonychidae.

Another family, the Gonyleptidae, is found in Central and South America. Neither the cosmetids nor the gonyleptids have representatives that seem to be true cave forms. The family Phalangodidae has the greater number of cavernicoles, but in the New World only one true cave form is known among the Triaenonychidae.

III. Palpatores. These are the commonest opilionids of this country. Two subgroups are recognized:

1. Dyspnoi: small secretive forms found in leaf mold. Among this group, a few true cavernicoles have evolved.

2. Eupnoi: the common long-legged species found all over the world. Most belong to the family Phalangiidae. These include the long-legged daddy-long-legs with which everyone is familiar. They are particularly common in the late summer and early fall. While frequently encountered in caves, no true cavernicoles are known.

CAVE ADAPTATIONS

Opilionids have a number of structural adaptations to cave life, many of which are quite obvious. One of these adaptations is the reduction or even complete loss of the eyes. Among some cave forms, an eye tubercle is present, but no eyes are visible externally. Among others, the eyes are present but the retina does not have the characteristic black color and appears to be nonfunctional. All degrees of development in this direction can be found.

Another development is the increased length of legs. Cavernicolous species tend to have longer and less robust legs than their epigeic relatives (Table I). Color, too, is another adaptation. Among the phalangodids living outside caves, the body color is usually bright

TABLE I.—Comparative measurements of a cavernicolous and an epigeic form of *Crosbyella* sp.

Length of legs	Epigeic form	Cavernicolous form
I.	2.9 mm	6.6 mm
II.	4.2 mm	11.1 mm
III.	3.3 mm	9.1 mm
IV.	4.4 mm	10.6 mm
Length of palpus	2.1 mm	2.8 mm
Total length of body	1.9 mm	2.0 mm
Length of cephalothorax	0.6 mm	0.6 mm
Width of body	1.4 mm	1.6 mm

reddish brown. In partially adapted types, the color is lighter and in true cavernicoles the color may be absent and the animal white. Associated with color is the degree of sclerotization. The cave species are much more weakly sclerotized than their epigeic relatives.

The true cavernicoles that have been described from the United States show no tendency towards an increase in size (Table I). Among some species known from Mexican caves, however, there seems to be this tendency. Some species described from caves in Mexico are many times larger than any related epigeic species.

Little is known of the physiological adjustments of these cave animals, but from their structure and habits it appears that they are more susceptible to drying than epigeic species. They would undoubtedly be less tolerant of changing conditions in their environment than related species living outside the caves. Much research remains to be done on the ecology, physiology, and habits of these cave forms.

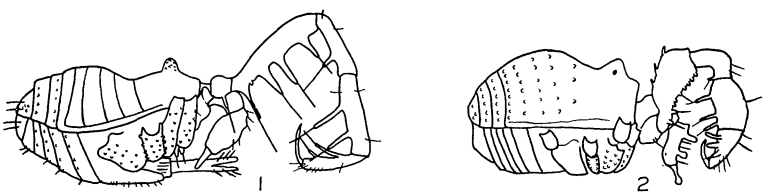
DISTRIBUTION OF THE CAVE SPECIES

By far, the largest number of cave species occur in the southeastern states.

Phalangodes armata Tellkampf is a true cave species, fully differentiated from its epigeic relatives (Fig. 1). It was first described from Mammoth Cave, Kentucky, and is now known from many caves in Kentucky and Tennessee. The specimens from Tennessee have a greater number of tarsal segments and were first thought to be a distinct species. Further collections have shown that transitional forms exist.

Phalangodes brunnea Banks is a strictly epigeic species which is known from a wide area encompassing Tennessee, the Great Smoky Mountain country, Georgia and Alabama (Fig. 2). It has been known to enter caves, but no strictly cave-adapted forms have been discovered.

Bishopella laciniosa (Crosby and Bishop) is widely distributed in and out of caves of the southern part of the Ohio River Valley region. It is frequently encountered in caves. Many show no cave adaptations, others show varying degrees. One specimen from a cave in Mt. Eagle, Tennessee, has long legs, a lighter color, and reduced eyes.



Figs. 1 and 2.—A comparison of two related species. 1. *Phalangodes armata,* a cavernicolous form; 2. *Phalangodes brunnea,* an epigeic form.

While it is not considered a true troglodyte, it certainly has some of the characteristics of such forms.

Phalangodes flavescens (Cope) is also found in a number of localities north of the Ohio River. It is primarily an epigeic form. In those caves where it has been found, such as in Virginia and the type locality, Wyandotte Cave in southern Indiana, it is lighter in color, has reduced eyes, and possesses somewhat longer legs. The individuals of a large population were once observed in Wyandotte Cave. They were feeding upon fungi which were growing on wood and the specimens showed many adaptations for cave living.

The southern portion of the Ohio River region is dominated by *Bishopella laciniosa;* north of the Ohio River, only the cave-adapted *Phalangodes flavescens* is found.

Phalangodes armata (Cope) is found south of the Ohio River, but occupies the middle portion of central Kentucky and Tennessee.

All the cavernicolous species are presumably derived from modern epigeic forms which can be found in localities both inside and outside the caves.

Other species, such as *Crosbyella* sp. in Arkansas, also have populations and races that are adapted to the cave environment.

Among the Palpatores, there are also cavernicolous forms. *Nemastoma inops* Packard has been reported from Kentucky caves and *Nemastoma pallidimaculosa* Goodnight and Goodnight was described from Rock House Cave near Oleander, Alabama. These are true cave species. Other epigeic species of this same genus live in leaf mold.

In the western states, only a few cavernicoles have been discovered. As the types of opilionids that readily differentiate into cave forms are not abundant in the dry areas that are found throughout the West, that is quite understandable. One member of the genus *Nemastoma* (*N. packardi* Roewer) is reported from a cave in Utah. Three widely scattered species of Laniatores are known from caves, and further exploration may yield more. These are:

Texella mulaiki Goodnight and Goodnight from Hays County, Texas.

Phalangodes californica (Banks) from Alabaster Cave, California.

Sclerobunus cavicolens (Banks) from Morrison's Cave near Bozeman, Montana.

DISCUSSION

The reasons for the development of some species of opilionids into cavernicolous forms can be speculated upon, but certainly at this time not determined. There must be some genetic factor which determines the direction of mutations. The long-legged leiobunums often congregate in large numbers in dark, moist places, so they are encountered in caves, usually not far from the entrance. They cluster in great clumps from the ceiling or walls of the cave. In spite of this predilection for caves, no true cavernicoles have evolved among the leiobunums and they are seldom, if ever, found deep within the

caves. Cosmetids too, for the same reason, often inhabit the favorable environment found in caves. In Mexico where this group is abundant, large numbers of cosmetids may be collected in moist caves, but they too seem generally unable to develop into true cavernicoles.

It is among the phalangodids that the greatest plasticity in the direction of mutations leading to a true cave existence are found. It is within this group that species that are truly cavernicoles exist. Some live deeply within caves and are so well adjusted to it that they could not survive outside such a constant environment. In this group are species closely related to epigeic forms that are outside the cave in the damp leaf mold of surrounding areas. In fact, among some groups of species, it is possible to observe the transition from the epigeic species to the cavernicolous species. These often have intermediate forms near the cave entrance with the true cavernicolous forms deep within the cave.

CONCLUSION

In conclusion, it can be said that in those groups that are genetically plastic, many cave forms have evolved. Usually their relationship with an epigeic species can be demonstrated. A review such as this points up how much remains to be learned concerning cave forms. Many caves, especially in the West, remain to be explored. Practically nothing is known of the embryology, life history, ecology, or physiology of cave opilionids.

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