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THE ECOLOGY OF SYMPHYLA*

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Introduction

The class Symphyla has held the interest of naturalists since about the middle of the eighteenth century. Most of the early studies were concerned with taxonomy, anatomy and phylogenetic relationships of the group. While these subjects still attract attention, important papers dealing with the economic and ecological aspects have appeared. However, the class is a small one and, generally speaking, its study has been neglected. Greatest interest in the group has been stimulated by the fact that many investigators believe Symphyla to be a type similar to that from which the insects have arisen. Comparative studies have shown that symphylans have many characters in common with the lower insects.

The ecology of the group is poorly known, and is difficult to study because of its soil-inhabiting nature, small size, and the fact the individuals are fragile and easily injured. The subject is one that challenges the imagination and because the field has been only lightly touched, it offers a fertile subject for investigation. In this discussion the present knowledge concerning the general ecological aspects of the group is considered. If emphasis of the large number of gaps in our knowledge of the group should stimulate further ecological studies, its purpose will have been served.

Description and Life History

Symphylans are small, white, soft-bodied, centipede-like organisms, with 12 pairs of legs, although in some the first pair is reduced to wart-like structures. They are regarded as having 15 body segments, and the genital opening is just anterior to the fourth pair of legs. They have prominent antennae and at the

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posterior end of the body there is a pair of functional spinnerets. Depending upon the species, they measure from about 2 to 9 mm in length.

Symphylans reproduce from eggs and the newly hatched individual has 6 pairs of legs although Tiegs (1945) reported *Hanseniella agilis* Tiegs as having 7 pairs. Molting occurs from time to time and an additional pair of legs is added with each subsequent molt until the full complement of legs is obtained. During this developmental period, body segments, scuta and antennal segments are added. At least with *Scutigerella immaculata* (Newport) molting continues at intervals during the entire life of the organism, and a single individual has been known to cast its skin as many as 52 times. To a certain point, at least, the individuals increase in size with each molt, and segments are added to the antennae. Members of the group are long lived and, in the laboratory, reared specimens have survived for more than four years. Reproduction is most active during the spring and summer. The population starts to increase in the early spring and under favorable conditions continues upward through the summer. As reproduction ceases, the population starts to decline, and usually reaches its lowest ebb in the late winter or just before reproduction gets well under way in the spring.

Distribution

Symphylans are widely distributed in nature. They are found under many climatic conditions, and are likely to be encountered everywhere except in the arctic regions. However, they appear to be most abundant in the warmer temperate and tropical regions. Some species are adapted to desert areas, others to humid regions. They occur in cultivated as well as uncultivated soils. Some prefer grassland, others forested or shrub-covered terrain. They are likely to be encountered from below sea level to at least an elevation of about 10,000 feet. At Point Reyes, *Symphylella essigi* Michelbacher has been collected in fair abundance at about high tide level. Actually there are species which occur in localities well below sea level, for *Scutigerella palmonii* Michelbacher was described from specimens collected in Palestine on the bank of the River Jordan near its emergence from the Sea of Galilee, which is more than 600 feet below sea level. *Scutigerella immaculata* (Newport) and *Symphylella subterranea* Michelbacher both occur sympatricly in the delta region of the Sacramento

River which ranges from less than 10 feet above to 15 feet below sea level. Symphylans are also found well distributed in the high mountains of California, and in Europe both Verhoeff (1933) and Friedel (1928) have reported collecting *Scutigerella immaculata* (Newport) at an elevation of 3000 meters.

Some species are found most abundantly in the surface soil, some appear to prefer the decaying forest litter and the soil just beneath it; still others are adapted to a wide range of movement in the soil, and some appear to prefer the subsoil. They are found in all soil types, which range from sands to clays and peats.

Symphylans apparently are unable to construct their own runways in the soil, therefore soil texture and structure greatly influence their distribution and abundance in localized areas. In general, they are to be found in greatest numbers where the soil structure is open. For this reason, uncultivated or undisturbed soils offer a more favorable environment for the development of most species than that encountered where cultivation is practiced. This is particularly true of those species which prefer the surface soil and it is possible that cultivation will so modify the environment of those species that inhabit the decaying forest litter and the soil just beneath it to a point where the species will no longer be able to survive.

Cultivation destroys the countless number of runways made by natural agencies such as decaying roots, and small soil-inhabiting organisms. Further, it alters the natural porousness and openness of the soil structure by producing changes in the crumb structure.

The changes produced by cultivation also probably exert an influence on those species of symphylans that range through the entire soil horizon and into the subsoil. However, most of these species are well adapted to living under conditions of soil cultivation and are often found present in cultivated fields in large numbers.

The symphylan that has received the most attention is *Scutigerella immaculata* (Newport). This species ranges from just under the surface of the soil to a depth of 4½ feet. It is well adapted to living in the subsoil, and in cultivated fields this zone furnishes a most favorable retreat. A large portion of its life is spent here, as is attested by the tremendous number of molted skins found in the runways. This species also ranges freely through the cultivated zone, and its movements are little hampered unless this soil horizon is thoroughly packed. It will move into the cultivated soil and destroy germinating seeds. However, if at planting time a tractor wheel passes over a row and thoroughly firms the soil, the germinating seed frequently escapes injury, due to the fact that the movement of the organism is greatly interfered with.

Symphylella subterranea Michelbacher is another species that is little affected by cultivation. Only rarely has it been taken in the first six inches of soil. It prefers the deeper soil and is likely to be found in most abundance below the 12 inch level, and therefore lives in a region seldom interfered with by cultivation.

Populations

The determination of symphylan populations is very difficult. Because they are so fragile and easily injured, it is difficult to recover them when a Berlese funnel is used. Because of this, a water flotation method of separation was developed (Michelbacher 1938). With this method it was determined that about 70 per cent of the individuals in a sandy silt soil could be recovered. On two occasions the efficiency of the above two means of separation were compared. In each survey 12 soil samples were run by each of the methods. In the first experiment a total of 157 symphylans were recovered by the water flotation method as compared to 17 for the Berlese funnel, and in the second, the ratio was 214 to 54. These tests definitely showed that the water flotation method was superior to the Berlese funnel. However, where a separation is desired from a sample containing considerable decaying forest litter or similar material, it is very possible that a Berlese funnel would give a more satisfactory separation because the debris contained in such samples would certainly interfere with the efficiency of the water flotation method.

Numerous population studies using the water flotation method have been conducted in the delta region of the Sacramento River and in greenhouses. In a field devoted to the production of field and truck crops the population of *Scutigerella immaculata* (Newport) was calculated to be 22,700,000 and that of *Symphylella subterranea* Michelbacher 2,705,000 per acre. In an adjacent field where the seasonal population trends were being followed, the peak population of *Scutigerella immaculata* (Newport) encountered was 8,000,000 while that for *Symphylella subterranea* Michelbacher was 4,915,000. These last populations were determined from samples taken on July 16.

Large populations of *Scutigerella immaculata* (Newport) are frequently found in greenhouses. In one where snapdragons were being seriously injured by this symphylan the population on an acre basis was found to be 90,300,000. All the above populations were calculated from the actual number of symphylans obtained from the samples, and no factor was applied for the probable number of individuals not recovered. Similar substantiating studies were conducted by the author where large populations of *Scutigerella immaculata* (Newport) were found to occur.

The populations reported above are larger than those encountered by most investigators who have considered symphylan populations. However, large populations were reported by Van Zwaluwenburg (1931) who carried out investigations in the Hawaiian Islands. The species involved were *Symphylella neotropica* (Hansen) and *S. simplex* (Hansen). These symphylans averaged about 90 per surface square foot in a growing cane field as against 150 in a fallow series. This on an acre basis is equivalent to 3,920,400 and 6,543,000 respectively.

Although found in lesser numbers, Symphylans have figured in many investigations that have involved population studies of the invertebrate soil fauna. Among those reporting their presence are Morris (1922, 1927), Thompson (1924), Edwards (1929), Sawa (1930), Starling (1944) and Pearse (1946). The investigations were conducted under several environments which included pasture, grass, arable and forested land. Thompson (1924) in his investigations found that Symphyla constituted 86 per cent of the total Myriapoda population. Edwards (1929) also found them to be much more abundant than all the other myriapods combined. Other workers have found them to be less abundant than some of the other myriapods. Among these Starling (1944) reported Symphyla as constituting 9.2 per cent of the population, while Pearse (1946) reported them as composing 32.9 per cent of the myriapod population.

Based on population studies and observations it appears that symphylans are not rare as stated by Ross (1948) but are probably the most abundant of all the myriapods as far as the number of individuals are concerned. Certainly they are found in large numbers wherever favorable environments are encountered.

Although individuals are found in abundance, the number of known species of Symphyla is not over 100. This paucity of species is due, at least in part, to the fact that the group has been badly neglected. In conducting surveys, undescribed material is frequently encountered, and it is but a matter of time before the number of named species will be greatly increased.

Some species have a rather wide geographical distribution. *Scutigerella immaculata* (Newport) probably has the widest known distribution, although some records that pertain to it apply to closely related forms. In my own experience this was true of certain specimens identified as *Scutigerella immaculata* (Newport) from various points in Europe which have proved to be new species.

Some species are widely distributed in California. Among these are *Scutigerella immaculata* (Newport), *Hanseniella vandykei* Michelbacher, *Symphylella essigi* Michelbacher, and *Geophilella americana* (Hilton), but present knowledge indicates that the distribution of many species is extremely limited. A number described from California are known only from the type locality. These include *Scutigerella linsleyi* Michelbacher, *Symphylellopsis alba* Michelbacher, *S. oviceps* Michelbacher and *S. longiseta* Michelbacher.

Some genera apparently have a wide geographical distribution, without being represented by many species. For example, *Geophilella* as known at present is represented by but two species. One of these was described from Europe and the other from California. Although widely separated the two species are extremely closely related, which would indicate that the genus is probably conservative. The same appears to be true of *Symphylellopsis* which contains but four species, three from Europe and the other from California. Here again the species are all very closely related, and show no marked divergence.

Food

The food habits of symphyla as a group are poorly known. On the whole they feed on a vegetable diet although some species, at least, will feed on animal matter. The subject is certainly in need of thorough investigation and a complete knowledge of the exact type of food preferred by the several groups of Symphyla must await these studies.

Food habits are best known in the case of *Scutigerella immaculata* (Newport). Newport (1845) and Latzel (1884) believed they fed upon the smaller soil-inhabiting arthropods. Williams (1907) thought that Protozoa which swarm over the decaying materials of a forest floor probably made up the major portion of their food. Later investigations have established that they are primarily vegetable feeders. They feed upon the roots of many of the higher plants, and even the foliage of some, if it is available. Michelbacher (1938) successfully reared them on the leaves of lettuce. There can be but little doubt that under moist conditions, and where the leaves of such plants as lettuce are in contact with the soil, *Scutigerella immaculata* (Newport) will come to the surface to feed. In such an environment they can sometimes be found just beneath the soil surface, or even beneath a leaf. Although *Scutigerella immaculata* (Newport) probably prefers succulent vegetation, they do feed on lower forms of plant life. Michelbacher (1938) noted that they fed heavily on compressed yeast, and believed that they fed on the unicellular green algae as well as fungi which grew on the substratum of the rearing dishes. He also noted that *Scutigerella immaculata* (Newport) ate any individuals that died and observed them feeding on injured specimens. The apparent ability of *Scutigerella immaculata* (Newport) to feed on the soil microflora probably accounts for their living in the absence of apparent food as has been observed by a number of investigators, including Wymore (1924) Friedel (1928) and Almeida (1930).

Higher plants certainly influence the distribution of *Scutigerella immaculata* (Newport) in the soil. They are attracted to growing vegetation, and population studies and other observations have shown them to be most abundant about growing plants. They will come up to just beneath the surface of the soil to feed on germinating seeds and young seedlings or recently transplanted plants, and occasionally, as already noted, they come to the soil surface to feed on leaves in contact with the soil. About growing plants they are found most abundantly within the top six inches of soil, while away from them they are found in greatest numbers in the deeper soil or subsoil.

Scutigerella immaculata (Newport) has feeding and non-feeding phases. These are associated with the molt and the non-feeding phase occurs during the critical premolting and molting period. Most food is consumed during the early period of each feeding phase.

Other Symphyla also feed on higher plants. Rand (1926) reported *Hanseniella unquiculata* (Hansen) as being injurious to sugar cane, and Takashima (1938) has also reported *Hanseniella* sp. as attacking this crop. However, there appears to be many symphylans that do not feed on living higher plants, and various investigators have believed their food to be decaying organic matter or humus. Although this may be the case, it seems more probable that they actually feed on the microflora and the saprophytic growth that arises from the humus and other organic material.

It has been shown that living higher plants exert no noticeable effect on certain species. This was clearly indicated in population studies that involved *Symphylella subterranea* Michelbacher (Michelbacher 1939). Samples of soil were taken along rows of growing plants and a similar set in the center of the space between rows. In the samples taken in the rows, 273 individuals were recovered as compared to 274 for the interspaces. Further, there was no evidence that the plants were attracting individuals to the surface layer of soil. From the above observations it appears certain that the principal food of this species must be something other than higher plants. In another laboratory conducted experiment it was found that *Symphylella essigi* Michelbacher did not appear to feed on lettuce, but fed heavily on compressed yeast.

Moisture

Moisture is one of the most important environmental factors affecting symphylans. They have relatively soft bodies, and are unable to withstand dessication. They apparently do best in moist soils, where the humidity is close to 100 per cent. Their distribution in the soil is largely influenced by the moisture content of the soil. Members of the class are most easily found when the surface soil is moist. Searching for them usually becomes more difficult as the soil dries out, and becomes discouraging when it has dried to a point where it is hard to work. Unless the soil can be easily handled and broken up for examination, the presence of symphylans is hard to detect. Due to their small size and fragile bodies, they are easily crushed or killed and difficult to find especially when searching for them under adverse conditions.

Of the symphylans studied, the moisture relationships of *Scuti-*

gerella immaculata (Newport) are best known. To a large extent this species moves up and down with the soil moisture, although some individuals are always likely to be encountered in the subsoil. They are, however, likely to be most abundant in the soil level which has a moisture content most favorable for the growth of plants. They will move into drier soil and have been encountered in such situations feeding on fleshy roots. They probably visit these locations just long enough to feed, after which they retreat to the deeper soil where moisture conditions are more ideal. The ability of *Scutigerella immaculata* (Newport) to live over a wide range in soil depths enables it to meet easily, changes in the soil moisture content. From its base in the deep subsoil *Scutigerella immaculata* (Newport) can move with ease to any horizon necessary to meet its need. An interesting vertical distribution of *Scutigerella immaculata* (Newport) was encountered in a field in late spring where a recent rain had wet the surface soil to a depth of four or five inches. The soil below this was dry for a depth of about 12 to 18 inches, beyond which it was moist. Symphylans were found in abundance in the surface and deeper moist soil, but none were encountered in the dry layer between.

Scutigerella immaculata (Newport) as well as other symphylans is not easily wet with water. Water is repelled and if trapped in the soil, they are enclosed in a tiny air bubble which affords them considerable protection from flooding. In these small air pockets the symphylans remain dry and can withstand submergence for a day or two to several weeks or longer. The length of time that they can survive depends largely upon the depth of water and temperature. In general, the period of survival decreases as the temperature rises. At low temperatures the survival period decreases as the depth of water is increased.

One point of interest is that if an air pocket containing a symphylan comes to the surface of the water it can be broken leaving the creature in a perfectly dry condition.

When land is flooded, *Scutigerella immaculata* (Newport) will, if possible, move up through the soil ahead of the rising water table, but will stop and be trapped by the rising water just under the surface of the soil. Where the soil is uneven they may congregate in large numbers just under the soil surface on the high spots. If these high spots are disturbed just before or after being flooded, symphylans will come floating to the surface of the water by the thousands. From limited observations it appears that most species of symphyla are unable to move up ahead of a rising water table with the same ease as does *Scutigerella immaculata* (Newport). This is certainly true of *Symphylella subterranea* Michelbacher and is probably the case within all the genera where the individuals are not capable of rapid movement.

It is doubtful whether all symphylans are capable of moving as deep into the soil as does *Scutigerella immaculata* (Newport). If they are greatly restricted in their movement, the question arises as to how they survive when the soil dries out. This can not be answered at present but to speculate, it is possible that some may encyst as do certain of the millipedes. Certain habits and actions of *Hanseniella vandykei* Michelbacher lead to the belief that this might be the case.

Reaction to Light

Symphylans are eyeless and although negatively phototropic they tolerate light of low intensity. In laboratory breeding cultures of *Scutigerella immaculata* (Newport), which were stored on a shelf where the light intensity was low, individuals would come to the surface of the soil section and lie there perfectly motionless. They also did not hesitate to come to the soil surface to feed on lettuce placed there for food. However, they do try to avoid light of high intensity. This response is probably one of the main reasons that accounts for their stopping just beneath the surface of the soil when a field is flooded. Apparently they would rather face submergence than light of high intensity.

In the absence of eyes, symphylans apparently rely upon the sensory organs of their antennae to guide them through the soil.

The function of the spinnerets is not known. Some investigators, including Williams (1907b), Riley (1929), and Filinger (1931) believed that *Scutigerella immaculata* (Newport) lined their runways with silken threads,. but this hardly appears to be the case. It is possible that some of the workers mistook fungus mycelia for silken threads.

Temperature

Symphylans are markedly affected by temperature. It influences their development and every phase of activity. Because of the insulating effect of their soil habitat they can tolerate a wide range in air temperature.

Investigations which have been conducted indicate that for normal activity the optimum temperature of their environment is betaween 12 and 20° C.

Conclusion

Only a brief review has been presented concerning the ecology of symphyla. The picture is still very incomplete and there are many gaps to be filled. Although there are many obstacles to be overcome in attacking the problem, it appears that these are not insumountable. Advances in rearing technique should go far in paving the way for additional studies. Because the field has been so poorly investigated, it offers a fertile opportunity for further study. Initiative and a well planned program should reap a rich reward.

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