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The significance of cave-living animals in the study of zoogeography

It may seem somewhat paradoxical to begin an account of animal distribution by a reference to cave animals, which have by far the most isolated and circumscribed habitat of all the ecological communities; nevertheless a comparison of the cave habitat with those of the open lands seems to me to have some bearing on the problems of animal distribution.

Professor Louis Fage (1931) in an important study devoted to cavernicolous spiders has developed some very interesting ideas as to the origin of cave faunas. These and further confirmatory researches have recently (1954) been ably summarized in a publication issued by that remarkable centre for research on cave and subterranean faunas, Le Laboratoire Souterrain de Moulis, situated on the Haute Garonne, France. I have taken leave to quote the relevant parts of this summary in the following paragraphs.

Professor Fage's ideas were based on the researches of Mayer and Plantefol (1925) which deal with the physiology of respiration in mosses; these biologists established the fact that the respiratory processes became more feeble as the water content of the mosses was raised. Applying this principle to cave faunas, Dr. Fage concluded that animals that live in an atmosphere with a saturated humidity show a very low rate of oxidation. The most striking characters of cave animals are blindness and absence of pigmentation, the latter having been previously ascribed to the fact of the cave animals living in darkness, but we now know that the formation of pigment is essentially the result of oxidation of organic matter (tyrosine, dopa) acted upon by oxidizing diastases (tyrosinases, dopaoxydase). It is now also understood that a lowering of the rate of respiratory exchange entails a diminution of melanin formation and, in extreme cases, its disappearance.

Work on both aquatic and terrestrial cave animals by W. D. and M. P. Burbanck and Edwards (1948) in the U.S.A. and L. Derouet (1949, 1950) in France has shown that though cavernicolous animals are as sensitive to the reduction of oxygen in either water or air media as those living in the open, their respiratory metabolism is about three times lower as measured by oxygen consumption; the respiratory exchange of cave dwellers is thus distinctly inferior to that of forms related to them but living outside of caves. This falling off in the respiratory activity of cave animals finds an echo in their general behaviour; their movements are slower than those of animals in the open, the males are not so pugnacious. In Professor Vandel's words "the cavernicolous species are old, not only from the phylogenetic but also from the physiological point of view". Of the three principal factors

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operating on cave animals, high humidity, darkness and a uniform temperature, humidity is by far the most powerful and is in the main responsible for the modifications so characteristic of cave species, viz: lack of pigment, partial or total disappearance of the eyes, reduction of chitinization and the elongation of their bodies and appendages; uniformity of temperature and darkness, it is thought, play a subsidiary part which may be the non-activation of the oxidizing ferments in the absence of light.

The members of the large ecological group of cryptozoa which are found chiefly among the Arachnida, Myriopoda, Onychophora and Apterygote insects are also greatly affected by these three factors which however do not play as fundamental a part as in the case of the cavernicolous faunas. The cryptozoa may be said to occupy an intermediate position in these respects between the animals of the open and the troglobionts, while sharing with the latter the limitations of a metabolism that is dictated by humidity more than by any other single factor. The microfaunas of forests are mainly found in the humus-covered substratum and therefore occupy a double habitat or rather one habitat, the forest humus, enclosed within a second habitat, the forest itself, both providing an atmospheric mantle with a high, constant humidity and uniform temperature. When occurring in more open regions the cryptozoa live under stones or in crevices of soil which provide microclimates with fairly high and uniform humidities.

The cryptozoa share the poverty of vision of the cave faunas. Many have small or feeble eyes while large numbers have none at all. Thus in a general population of cryptofauna, such as can be assembled in a sackful of humus from the forest floor, the majority of the total numbers of individuals are blind. In contrast no insects, Arachnids or Myriopoda which live in the open have produced an eyeless form.

It is one of the interesting features of the cryptofauna that in each class or subclass there is at least one large order or even suborder, which consists entirely of eyeless forms; thus the Chilopoda have the suborder Geophilomorpha, the Diplopoda the Polydesmoidea, while in the Arachnida there are several orders, the Ricinulei, the Palpigradi, and the Oribatoidea among the mites. These are large groups consisting usually of hundreds of species and confined in each case to a clearly differentiated order or suborder. In the cave faunas the case is very different, the blind species consisting of a few isolated forms, usually related to normal species living in the open or connected with these by various gradations of eve reduction.

This relationship between cavernicolous species and normal ones living in close proximity to them can be illustrated by three interesting South African examples belonging to three quite different groups of arthropods found on Table Mountain, Cape Town, where the well known Wynberg Caves occur in water eroded sandstone. The normal Cape Peripatus, *Peripatopsis balfouri* is closely related to the blind and unpigmented *P. alba*, the Pseudoscorpion *Chthoniella heterodonta* to the eyeless species *Ch. cavernicola*, the Opilionid *Purcellia illustrans* to *Speleosiro argasiformis*. In each of these orders the first named species can be found living just outside the openings of the cave in which the second species occurs. The troglobiont Peripatid and false-scorpion differ from their cryptic relatives in being eyeless, while the Opilionids belong to a suborder of predominantly blind forms, both being eyeless.

This pervading condition of eyelessness in large groups rather than in individual species points to the fact that the cryptozoa have a very ancient history during which the absence of eyes has had time to become stabilized and crystallized in major taxa. Their origins and ecology can probably be connected with the earliest forest associations in the Carboniferous and they provided the stocks from which the cave faunas have arisen as specializations on the one hand and on the other the more modern insects and the families of spiders which now live in the open. The change led to complete isolation on the one hand of the cave

faunas, to the reverse in the case of the insects and other modern classes.

From the viewpoint of their humidity requirements it might be useful to divide all terrestrial animals into two chief categories and attempt to summarize the differences which separate them. Such an attempt is understandably of a very general nature which must perforce ignore the many halfway or intermediate types which cannot be easily accommodated in either of them.

Animals of the open lands are those which can tolerate wide ranges and changes of humidity, temperature and light; they have the ability to adapt themselves to a wide range of these conditions and are equipped with balancing or regulatory mechanisms in their respiratory and vascular systems. They have developed some sort of dermal covering such as a thick waterproof exoskeleton or cuticula supplied with pigment which prevent undue loss of moisture and heat by evaporation. They are thus able to withstand the direct impact of sunlight and are active animals able to disperse themselves over long distances by their own bodily exertions. To this division belong the higher winged insects, and, among the terrestrial vertebrates, the more recently evolved mammals and birds with a high dispersal potentiality.

The cryptozoic animals lack almost every one of the features listed for the animals of the open lands or are negative in these respects. They require the highest categories of humidity and a reduction below saturation point is often fatal. Both temperatures and light intensities are extremely uniform in the microclimates of their habitat, and the range of all three factors is extremely narrow. Their respiratory systems are of a very simple nature and are deficient in lacking regulatory mechanisms; in particular there is an almost complete absence of the highly developed and complex occlusory mechanisms of the pterygote insects which, by means of an elaborate muscular system, regulate the closure of the spiracles and enable them to prevent water loss by evaporation. The most typical examples entirely lack a well chitinized protective cuticle which, as in cave animals, often contains no pigment at all. They are thus unable to withstand the direct impact of sunlight on their bodies or the dessicating effects of air movements in the open and are confined by the nature of their structural deficiencies to the micro-environment in which they live. From the point of view of distribution they have a low dispersal potential and are in general static animals.

In times of catastophe, such as the destruction of their habitat by a sudden lowering of humidity or a forest fire, annihilation is as complete as that caused by the eruption of Krakatoa; none can escape, no remnant is left to perpetuate the stock elsewhere in more favourable circumstances, as would be the case in vertebrates or insects. Those that have survived have been called by various names such as the relict faunas, archaic or palaeogenic elements, groups which must have persisted with little change over great periods of time.

In speaking of this cleavage between cryptic and other terrestrial animals in respect to their humidity requirements there are naturally some groups which do not strictly fulfil the conditions set out in the definitions given above but fall between them, while all the large classes of arthropods have some members of both the divisions. In the insects for instance there is a vast physiological difference between the higher winged orders and the apterygote insects at the other end of the scale which in groups like the minute Protura and endotrophic Thysanura (*Campodea* and *Japyx*) have all the distinctive characters of the cryptozoa, absence of eyes, lack of pigment or a thick cuticle. Both are insects but in their respiratory physiology and ecology are fundamentally different and for purposes of distribution cannot be treated under the covering term of insect.

The dispersal potentialities of various orders and suborders within the same class may be very different, being dependent on basic dissimilarities of organization, often with respect to the structure of their respiratory systems; some of the large Diplopoda with their powerful body armour live largely in the open while the small, thin-skinned orders pass their whole

lives in the shelters afforded by wood debris and soil. Among the Arachnida many of the more familiar families of spiders live in the open like the insects, indirectly dependent on the vegetation on which they spin their snares; most families however are invisible to the collector and completely cryptic in habit.

The scorpion and the solpugid are both Arachnids which flourish in deserts. The scorpion is a slow-moving nocturnal cryptic animal existing in burrows or in the humid atmosphere prevalent under large stones, with a comparatively simple respiratory system based on four pairs of lung-books. The Solpuga on the other hand is an arachnid with habits and movements more like those of many roving predaceous beetles which run over the desert sands, but is capable of even more rapid movement. It excels all other Arachnida in the efficiency of its respiratory system, being equipped with a vast elaboration of very wide tracheae while the chitinous ring-like openings of the spiracles are controlled by occlusory muscles. It further differs from its sister orders in having adopted the abdominal breathing movements typical of insects. Although both scorpion and Solpuga are desert living arachnids, the respiratory exchange measured by the oxygen consumption of the latter is many times greater than in the former. According to the degree of activity of the various groups and the accessory means used, such as the ballooning habits of certain spiders, the means of dispersal is modified and their distribution influenced.

This division, based chiefly on the presence or absence of regulatory and balancing mechanisms in the respiratory systems of animals and on the humidity factor, provides a physiological rather than a physiographical basis for the great differences in the manner of distribution of animal groups and the actual pattern of distribution which they reveal at the present day.

That there are differences in the distribution of the older cryptic animals and the more modern classes, both vertebrate and invertebrate, is fairly obvious and many authors have noted them for different groups of animals and plants. When Richard Hesse in his book "Tiergeographie" says that the fauna of Africa south of the Sahara exhibits a striking uniformity, he could have been speaking only of the higher categories of vertebrates and insects or of some special members of other invertebrate classes. With regard to the cryptic invertebrates, the reverse of Hesse's statement would be nearer the truth as will be seen from the examples which follow.

In the homogeneous arachnid order of Opiliones all the members live in forests and are with a few exceptions cryptic in habit; about 80 per cent of all tropical African species belong to one family, the Assamiidae. But in South Africa 78 per cent of the fauna belongs to another quite different family, the Triaenonychidae. In the tropics of Africa therefore the Assamiidae are completely dominant, in temperate South Africa the Triaenonychidae; no species of the former occurs in South Africa, or of the latter in tropical Africa. The cleavage of the faunas is thus complete, the boundary between them being represented by the valley of the Limpopo River. In respect of these two families the fauna of Madagascar also differs completely from that of tropical and subtropical Africa lying in parallel latitudes but is in strong agreement with the fauna of temperate southern Africa.

In another suborder of Opiliones, the Cyphophthalmi, the contrast between the faunas is even more marked. Six species of this small primitive group of blind harvest-spiders live at the extreme southern end of Africa, divided between two or three genera in the subfamily Sironinae. The only other African forms are two species of *Ogovea* and one of *Paragovia* in French West Africa, completely isolated from the other members of the suborder, both geographically and phylogenetically, and belonging to another subfamily, the Stylocellinae. The similarity in the distribution of the African members of this suborder to that of the Onychophora is quite remarkable.

The Onychophora have a long geological history going back in time to perhaps the

Middle Cambrian with little change of organization or appearance. The homogeneous structure of its members in different parts of the world at the present day points to a very wide former distribution. At the present there are less than 60 living species accommodated in two families, all of them very similar in structure and organization.

The dozen species found in South Africa are isolated at the extreme south of the Continent, no others being found between the East Transvaal and the northern coasts of Africa. The one exception is a West African species of *Mesoperipatus* which belongs to a different family and has no relationship with the South African fauna. According to Brinck, there are two centres of distribution for the South African Onychophora, one for *Peripatopsis* in the south west Cape where the largest number of species occur (four in the Cape Peninsula itself), the other for *Opisthopatus* in Natal where there are two species. *Peripatopsis* extends from the Cape Peninsula to Natal, *Opisthopatus* from Port Elizabeth eastwards, fading out towards the north-east, only one species being found in the Southern half of the Transvaal and that rarely, while none occurs north of the Limpopo. The relationships of the South African fauna are not with the rest of Africa but with Australasia and the southern parts of South America.

These are homogeneous groups but in a larger and more heterogeneous class of Arthropoda such as the Diplopoda there are enormous differences within the groups themselves with respect to size, thickness of the cuticle and activity, so that distributional relationships between the central and southern faunas may be quite different in two given families or two suborders of this class. In the Polydesmoidea for instance, an order of small blind millipedes, the cryptozoic family Spaerotrichopidae is strictly limited to rain forests. This predominantly African family is represented by 15 genera in South Africa, one of them, *Gnomeskelus*, greatly exceeding all the others in range and number of species. There is one genus in Madagascar while five occur in Australia and Chile each, but not a single species in the whole of Africa north of the Limpopo River.

The situation is however quite different in another suborder of Diplopoda, the Odontopygidea, which are larger, well chitinized, more active millipedes, well able to live outside of forests in grasslands and thornveld. The recent work of Kraus (1960) has shown that in this suborder only six of the 34 African genera live in southern Africa, the remainder in tropical Africa, all being different from the South African ones. Seventy species, or three-fourths of the whole South African fauna, is confined to a single genus *Spinotarsus* while all the tropical genera are on the other hand quite small, with an average of four species per genus. This seems to indicate that the north-south migration route of these millipedes is the normal one followed by active self-dispersing animals living in the open. The central African fauna with its numerous clearly separated genera but with comparatively few species in each is thus obviously older than that of southern Africa, the numerous species of the one genus *Spinotarsus* representing the end product of an evolutionary line which commenced in or passed through the tropics and has ended in South Africa.

In summing up, the position with regard to the dispersal of animals in Africa seems to be as follows: the more active groups which are able to disperse by means of their own bodily activities and which can easily endure wide ranges of humidity and temperature, of which the mammals among the vertebrates, the insects among the invertebrates are the most typical, have migrated through Africa along a north-south route, following for the most part the eastern side of the continent.

The more sluggish cryptozoic invertebrates can only exist in an atmosphere of high humidity and with uniform temperatures. Being unable to withstand the direct impact of sunlight they are confined to their micro-habitats and are static as regards dispersal. These are so-called relict forms, much older than the animals of the open lands and do not appear to have migrated in a longtitudinal direction but to have had local centres of distribution

at the extreme end of the continent. They have no particular relationships with the tropical African faunas or only distant ones and differ further in having distinct affinities with those of Australia, New Zealand, South America or Madagascar in approximately the same latitudes.

It might not be so difficult to explain the fact that various families of cryptozoa living at the extreme apex of Africa are more closely related to those of Australia, South America and Madagascar than to any African families of the same groups living north of the Limpopo. What seems more difficult to explain is why these families do not occur in Africa at all north of the South African limits while being well represented in southern continents separated from Africa by thousands of miles of ocean. If only these relict forms were to be taken into consideration, southern Africa would have to be redefined as a new zoological province or subregion outside the Ethiopian one and differing from it as much as the Mediterranean subregion at its northern extremity differs faunistically from the rest of the continent.

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