Savory, T. 1974. On the arachnid order Palpigradi. J. Arachnol. 2:43-45.

ON THE ARACHNID ORDER PALPIGRADI

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ABSTRACT

The opinion that the Palpigradi are a more primitive order of Arachnida that are the scorpions is taken as evidence that the Arachnida are a polyphyletic class. Their probably marine or littoral ancestors may have been of diverse character.

There has long been a habit, amounting almost to a tradition, of describing the scorpions as the most primitive order of Arachnida. This opinion, which dates back at least to 1902, when E. Ray Lankester wrote his long article on the class for the tenth edition of the Encyclopaedia Britannica, was based, no doubt soundly, on the resemblances between scorpions and some of the extinct Eurypterida. A relationship can hardly be gainsaid.

The primitive nature of the scorpions was assumed because of this resemblance. They were widely commended as being the first invertebrates to invade the land, and applauded for their success in establishing themselves in their new environment. But the uncritical acceptance of this must lead to the, perhaps unspoken, deduction that the arachnids of the other orders have arisen by evolution from this ambitious and pioneering stock. In other words, the implication is that the class Arachnida is monophyletic; and for this assumption there is, I believe, no evidence.

Two considerations arise. First, scorpions exhibit in their bodies many instances of elaborations. The large size and the chelate form of the pedipalpi, the existence of venom glands and sting in the telson, the presence of the mysterious pectines on the second abdominal sternite are external examples; the characteristic method of nourishing the young is internal and is associated with the birth of nymphs instead of the laying of eggs. This short list of specialisations is comparable to any similar list of the specialisations that help to characterise each and every one of the other orders, and recalls the important dictum that there are really no wholly primitive organisms but only primitive organs.

Secondly, there can be no justification for assuming that the exploring eurypterid which came ashore and lived to become the ancestor of *Protoscorpius* was the sole successful immigrant. The nature of the sea, from which the discontented creatures were compelled to escape, was no doubt unattractive to all; and it is only reasonable to suppose that several, perhaps many or very many, different types were similarly obliged to attempt the same landfall. It may well be true that "Animals are always attempting the impossible, and always achieving it," but side-by-side with their achievements there must have been many failures.

The successes may have been due to some form of pre-adaptation that unexpectedly became a vital attribute that made survival possible. Among the early terrestrial "Ur-arachnida" such pre-adaptation may have been the easy functioning of the gill-books of aquatic creatures as the lung-books of terrestrial animals, and perhaps also the presence of a layer of wax in the epidermis.

There is, however, another possibility, which should not be overlooked.

One obstacle to the exchange of the water for the land may have been the difficulty of using gills, adapted to take in oxygen from solution, as lungs adapted to the oxygen of the air. But if there were no respiratory organs the problem presents another aspect.

A very small animal has a surface large enough to admit by diffusion all the oxygen that it requires; and as long as the surface is wet its efficiency as a respiratory organ remains unimpaired. The small animals that live continuously under conditions of high relative humidity are known as the cryptozoa.

One of the chief general features of the cryptozoa as we know them is the high proportion of primitive types that are numbered among them. Indeed, it has been said that where a vetebrate palaeontologist looks for fossils an invertebrate palaeontologist looks for cryptozoa.

Our interpretation of the taxonomic position of the Palpigradi now becomes obvious. We may reasonably imagine a small marine 'proto-arachnid' leaving the almost uninhabitable sea and seeking asylum under the organic debris that littered the primaeval shore. Here, "in the dark and the damp" it was able to survive, its outer surface always sufficiently moist. Provided only that it could feed itself on whatever it may have been that its new home provided, continued life was reasonably assured.

Here, then, is a possible pedigree for the order that was discovered by P. Grassi in 1883 and placed at once in a new order which he called Microthelyphonidae. The order now contains about four dozen species and five genera, *Eukoenenia* Börner, 1901; *Prokoenenia*, Börner, 1901; *Allokoenenia* Silvestri, 1913; *Koeneniodes* Silvestri, 1913. *Leptokoenenia* was added by Condé in 1965 and is of special interest because its species live in the littoral zone, between the tide-marks.

The conclusion towards which we are now moving receives support from three different sources. The first of these is the high proportion of the organs of Palpigradi that have retained their primitive condition, and to make this plain one may follow the arachnid body from chelicerae to telson and note the state of the regions and organs one by one. This is conveniently demonstrated in Table 1, from which it may be seen that 80% of the attributes considered show no specialisations.

Table 1.—Comparison of primitive and advanced conditions in Palpigradi.

Part or Organ	Primitive State	Advanced State	State in Palpigradi
Carapace	Segmented	Uniform	Primitive
Opisthosoma	Segmented	Uniform	Primitive
Pedicel	Absent	Present	Primitive
Flagellum	Present	Absent	Primitive
Chelicerae	Three podomeres	Two podomeres	Primitive
Pedipalpi	Pediform	Chelate	Primitive
Sternum	Segmented	Uniform	Primitive
Legs I	Motor organs	Sensory organs	Advanced
Legs II-IV	Seven podomeres	Sub-segmentation	Advanced
Gnathobases	Absent	Present	Primitive

The second source is the somewhat unexpected quality of toughness in the animal as a whole, which contributed not a little to its ability to withstand the trauma of its original migration. This quality it has retained, as two striking examples confirm. In 1914 Lucien Berland reported the presence of a species acclimatised to life in the Museum de Paris; and in 1933 another was found living on Mount Osmound, near Adelaide. These occurrences are probably the results of chance transport in the baggage of man, and their existence supports the idea that Koenenia is both resistant and adaptable, as long as the precise milieu is tolerable.

Thirdly, there is geological evidence to be considered.

Unmistakable fossil Palpigradi have not been found, but the Jurassic *Sternarthron* from Germany demands some consideration. Its chief difference from recent Palpigradi is the existence of six distinct sternites in the prosoma, so that it has been placed in a family of its own, the Sternarthonidae. Millot has, however, stated that "il ne lui appartient vraisemblablement pas."

Whichever view is accepted, it is reasonable to see in *Sternarthron* either the ancestor of *Koenenia* or a type closely allied to it. Two features are significant. The size of *Sternarthron*, about 14 mm in length, is some six times the length of any living Palpigrade. So, too, was *Gigantoscorpius* at 36 mm, or nearly three times the size of the larger living species of scorpion.

Moreover, both *Gigantoscorpius* and *Sternarthron* are remarkable for their slender legs, which must have been too delicate to support their body weight. The deduction from this is that both lived in the shallows, where they were partly supported by the water, and where the opportunity for excursions ashore would be most favourable. The presence today of *Leptokoenenia* in just such a habitat gives welcome support to this speculation.

The general conclusion is, therefore, that the Palpigradi represent the earliest type of arachnid to have been evolved; and that they have brought from the sea, and have retained, a higher proportion of ancestral characteristics than has any other order. Thus they may properly occupy a subclass by themselves.

Other subclasses may well have had similar histories, as indeed have the scorpions, by general consent. These pedigrees may well go back to other adventurous kinds of Eurypterida, but since these were neither *Sternarthron* nor its relation, they represent distinct and parallel origins for the modern Arachnida.

The class Arachnida should therefore be regarded as a polyphyletic group, comprising several lines of descent from eurypterid-like ancestors. The temptation to describe and figure a single hypothetical archearachnid should be avoided.

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