

The trapdoor-burrow: the success of a defense system

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1. INTRODUCTION

In this presentation I will not follow the subordinal classification of spiders worked out by PLATNICK and GERTSCH (1976). Instead I will use the terms Orthognatha and Labidognatha to indicate the suborders of spiders because I believe this is more correct.

An important task in biology is to unveil the course evolution has taken in the various groups of organisms. The cladistic approach currently plays a dominant role in spider taxonomy. This approach aims at constructing phylogenies from which the evolution of spiders can be read.

The information used is strictly morphological and ignores other arguments that may shed light on the evolutionary history of the group. Spiders however possess the uncommon quality of producing constructs (webs, eggsacs, retreats, nests, burrows etc.) that have a morphology of their own. As students of spiders, we are therefore in the favourable position to use the extra information contained in the morphology and functioning of spider constructs to reconstruct the evolution of spiders. Theoretically, if we knew enough about the morphology and functioning of spider constructs we could work out their probable phylogenetic relationships to test hypotheses of different origin.

This is of course nothing new. Starting with POCOCK (1895), arachnologists through time have built hypothetical evolutionary sequences of web types. In the work of POCOCK (1895), BRISTOWE (1958), SAVORY (1960) and KASTON (1964), to name a few of the most prominent, the effort was always aimed at explaining the evolution of the orb web. Araneomorph spiders and their constructs were the focus of attention; information on the constructs of mygalomorphs and liphistiomorphs was only marginally considered. What the web is for araneomorph spiders however, is the trapdoor burrow for mygalomorphs and liphistiomorphs (Orthognatha).

MOGGRIDGE (1873, 1874) already showed that various types of trapdoor burrows are as readily distinguishable as are the various types of webs.

The evolutionary sequencing of burrow types has to my knowledge, in contrast to that of web types, never been attempted. I am not going to make such an attempt now, because I believe too little is known at present of Orthognath spider constructs to do so. What I will do however is to point at a few remarkable differences between Labidognatha and Orthognatha that may be considered in future attempts to reconstruct the evolution of spiders.

2. THE TAXONOMICAL PERSPECTIVE

Looking at the taxonomical qualities of spider constructs, it becomes quickly apparent that the relationships that exist within the Labidognatha, do not exist within the Orthognatha. What I mean is that within the Labidognatha particular types of constructs are built by members of particular families. In other words, types of constructs within the Labidognatha are usually specific at the family level; or members of a particular family generally produce similar types of constructs. This is in contrast to the situation within the Orthognatha.

RAVEN (1985) in his reclassification of the Mygalomorphae, recognizes 15 families. Adding to this number the liphistiomorph families Liphistiidae and Heptathelidae, we obtain a total number of 17 orthognath spider families alive today. Members of no less than 11 out of these 17 families are known to construct trapdoor burrows. So if we consider the trapdoor burrow as one specific type of spider construct, it is rather typical for the whole suborder than it is specific to any one orthognath family.

A trapdoor is a hinged lid that closes off the entrance of the spider's nest. Usually this nest is a burrow, that is a hole the spider has actively dug out in the ground, or in some other substrate, to provide a living space. The construction of burrows is even more widely spread within the Orthognatha than is the construction of trapdoors. Members of 14 out of the 17 orthognath families are known to construct burrows. Only the micro-mygalomorphs of the families Microstigmatidae and Mecicobothriidae are not known to excavate burrows. The habits of the one remaining family, the Paratropidae, remain obscure in this respect. From the above though it may be safely concluded that burrowing in general and the construction of trapdoor burrows in particular is a dominant feature of the Orthognatha, if not to typify the suborder.

The lack of family-level specificity of spider constructs is not only apparent in the occurrence of particular types of constructs in several families, it is also apparent from the fact that within orthognath families different genera or species build different types of constructs. Theraphosidae for example may dig burrows in the ground or construct elaborate and complicated silken nests in elevated positions. Other members of this family appear to construct no nests at all. For the family Anthrodiaetidae, COYLE (1986)

describes 3 distinct burrow types that are partly genus-specific. *Antrodiaetus* species construct burrows with a collapsable collar entrance, *Atypoides* species either make a collapsable collar or a rigid turret entrance to the burrow and *Aliatypus* species construct a trapdoor. As already illustrated by the example of *Atypoides*, even at the level of the genus, Orthognatha may construct a diversity of burrow and nest types. COYLE (1986) provides a list of 12 orthognath genera of which member species build distinctly different types of constructs. From my own experience I may add the genera *Nemesia*, *Cyrtocarenum*, *Ancylotrippa* and *Ummidia* to this list and a search in the literature will undoubtedly produce many more.

I mentioned this to illustrate that the situation with respect to the existence of a relationship between taxonomical identity and construct type in the Orthognatha is very different from that in Labidognatha. It is impossible to rank orthognath families on grounds of the constructs they produce in a sequence that suggests a progressive evolutionary development, as has been done for Labidognatha in the earlier mentioned works of POCOCK, BRISTOWE, SAVORY and KASTON. Rather it seems that in the Orthognatha we observe a number of different more or less parallel evolutionary lines in different families or family-groups. Virtually all these lines include a burrowing stage and generally also a stage of trapdoor construction. The frequent occurrence of the burrow and the trapdoor throughout the families composing the suborder indicates that these structures are plesiomorphic within the Orthognatha.

3. THE HABITAT PERSPECTIVE

Mentioning the work of MOGGRIDGE (1873, 1874) I have already indicated that distinctly different types of orthognath spider burrows do exist. In its simplest form the burrow is a open hole of a few centimeters deep. The main variation in burrow types is produced by:

- 1) the variation in entrance structures (several types of trapdoors, silken collars, purse webs, sheet webs, etc.)
- 2) the variation in internal structures (internal doors, plugs, silken socks, etc.)
- 3) the variation in shaft morphology (side diggings, underground rooms, escape passages, etc.)
- 4) the variation in the degree of wall plastering and silk lining.

If the type of burrow a spider builds cannot be predicted from knowing its taxonomical status, what might dictate the particular burrow type a particular spider is going to construct?

Most specialists that have considered the question agree that the type of orthognath burrow found in a particular habitat is somehow related to the prevailing environmental conditions. Here again a conspicuous difference between the Labidognatha and the Orthognatha seems to exist. While orb webs, sheet webs, lattice webs, and other labido-

gnath web types may be found in a variety of habitat types without their constructive detail being very dissimilar, the type of orthognath burrow found in a particular habitat generally has particular characteristics. Discussing the Australian trapdoor spider genus *Aganippe* (family Idiopidae), MAIN (1976) states for example: "I discovered a whole array of related forms, each with its own distinctive type of burrow which occurred in a distinctive sort of habitat."

Drawing from my own experience, I found that burrows in open, exposed and dry habitats generally are deeper and have a simpler shaft form than burrows found in more shady, humid forest habitat. Moreover, burrows in open, exposed and dry habitats usually possess a relatively thick, tightly fitting trapdoor, whereas burrows in more shady, humid forest habitats tend to have thin, flexible trapdoors, collapsable collars or plain open entrances.

Understanding the habitat relations of particular types of burrows depends on understanding the functions of the various structures involved (trapdoors, silken collars, webs, underground rooms, etc.). Much still has to be learned in this respect. Broadly speaking however students of orthognath spiders agree that the burrowing habit essentially functions as an escape from adverse microclimatological surface conditions. Although the trapdoor burrow serves also as a defense against predators and even may have an offensive quality, providing a camouflaged ambush site, its primary function lies in the shelter it provides from hazardous climatological conditions.

It is remarkable though that a tribe of obligate predators such as the Orthognatha, should be characterized by a primarily defensive life strategy. The results of experiments by COYLE (1986), in which he showed that the presence of a trapdoor actually obstructs the spider's chances of capturing prey however supports this unlikely view. I also found this negative effect of the trapdoor on prey capture efficiency of Panamanian trapdoor spiders (DECAE, unpubl.).

4. LONGEVITY

A third conspicuous difference between Orthognatha and Labidognatha is the fact that orthognath females remain reproductively active for a number of years after reaching adulthood. In the literature this has also been seen as an adaptation to survive adverse environmental conditions. Because a population of orthognath spiders is typically composed of different yearclasses the population can survive consecutive years in which the conditions are never sufficiently favourable to even mate.

According to MAIN (1976) it will take at least 4 consecutive barren years to destroy a male population of trapdoor spiders. This quality would give the population the ability to survive long periods of hostile climatological conditions.

5. CONCLUSIONS

In summary, I have discussed three subjects that in my opinion illustrate important differences between the Orthognatha and the Labidognatha.

I believe these differences tell something about the different evolutionary histories of the two suborders of spiders.

Firstly the lack of family level specificity of construct types in Orthognatha indicates that this suborder much less than the Labidognatha represents an evolutionary unity exhibiting one or a few coherent lines of development.

Secondly, the strong habitat specificity of construct types in Orthognatha, when compared to the Labidognatha, indicates a lower degree of physiological adaptation to terrestrial environments in Orthognatha, that is compensated for by behavioural specialization, a behavioural specialization however that allows orthognath spiders to efficiently escape from even the most extreme surface conditions.

The longevity of Orthognatha finally reinforces their capabilities to endure long periods of harsh conditions. The habit of constructing strongly isolating trapdoor burrows, their longevity and the capability of remaining underground for prolonged periods classifies the Orthognatha as a race of spiders that is specilized to persist under circumstances of extreme physical environmental threat.

Departing from the point of view that the Orthognatha are ancestral to the Labidognatha, and taking into account the paleontological evidence that Orthognatha were among the early colonists of the land, it is suggestive to think that their qualities of endurance are linked to the dramatic changes of habitat the first terrestrial creatures had to withstand. The apparent plesiomorphy of the trapdoor burrow and its probable vital role in the survival strategy of this group, makes the burrow the most likely spider construct to have been present at the time the spiders originated.

I make this point because in recent publications (e.g. SHEAR 1986) it is still maintained that the initial spider construct may have been a silken cell spun in a crevice or some other sheltered position. I have argued before (DECAE 1984) that this sheltered position most probably was a burrow actively excavated by the spider.

The foremost distinguishing character to separate the Orthognatha from the Labidognatha, the orthognath chelicerae, in these early days of spiders functioned as they still function today, as specialized tools for digging holes in the ground.

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