Comparative Morphology and Phylogeny of Liphistiomorph Spiders (Araneida : Mesothelae). III. Provisional diagram of relationships in Heptathelidae

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Summary. In recent years various propositions have been made concerning the classification of liphistiomorph spiders. In order to make the arguments more readily accessible to critical discussion, the present paper proposes a provisional diagram revealing the possible phylogenetic relationships of several species and/or subspecies of Heptathelidae described hitherto.
While the Japanese and Ryukyuan *Heptathela-kimurai*-group forms a distinct entity, continental *Heptathela* species are more diverse. Some species are even not well enough known to be included in this diagram. The problem of island populations of *Heptathela* and *Ryuthela* is discussed with reference to zoogeographical aspects.

Zusammenfassung: In den letzten Jahren sind verschiedene Ansichten zur Klassifikation liphistiomorpher Spinnen geäußert worden. Um die vorgetragenen Argumente einer kritischen Betrachtung besser zugänglich zu machen, wird hier der Entwurf eines Verwandtsschaftsschemas vorgelegt, der die möglichen phylogenetischen Beziehungen einiger der bisher beschriebenen Heptathelidenarten aufzeigt.
Während die japanisch-ryukyuanische *Heptathela-kimurai*-Gruppe sich als ziemlich homogen erweist, zeigen die kontinentalen Arten teilweise sehr auffällige Unterschiede. Einige Arten sind allerdings bisher noch völlig unzureichend bekannt, so daß sie nicht berücksichtigt werden konnten. Das Problem der Inselpopulationen von *Heptathela* und *Ryuthela* wird unter zoogeographischen Gesichtspunkten diskutiert.

In recent years the study of Mesothelae has attracted many arachnologists. As a consequence, there are diverging opinions concerning their classification (Raven, 1985, Ono & Nishikawa, 1989). Each opinion can be accepted as a contribution to the discussion, as there may be no immediate solution to some questions. Regarding these aspects, the diagram of relationships presented here (Fig. 1), is used to summarize and visualize the information available on the family Heptathelidae. In this way every argument is clearly laid open and can be subject to falsification, thus promoting the process of critical discussion.

In the approximative diagram of relationships, subspecies, species, and species groups have been scanned for joint characteristics which can be considered as derived from similar structures in outgroups. Such characteristics can be considered as apomorphic or synapomorphic for the groupings concerned. Generally, the palpal organs offer more convincing characteristics, but sometimes one has to refer to the female organs: In some cases (no. 17 and 20) it still proves difficult to detect sound synapomorphies, a problem which may be overcome by a more thorough study, once more material has been made available.
The following material has been studied from collections in Beijing (Zoological Institute, Academia Sinica), Cambridge, Mass. (Museum of Comparative Morphology), Changchun (Bethune Medical University), Changsha (Hunan Teachers' College), Hangzhou (Zhejiang Teachers' College), London (British Museum of Natural History), New York (American Museum of Natural History), Paris (Muséum national d' Histoire naturelle), and the author's own collection:

	♂♂	♀♀
Heptathela hangzhouensis CHEN, Zhang et Zhu, 1981	2	2
Heptathela kimurai amamiensis HAUPT, 1983[1]	7	7
Heptathela kimurai higoensis HAUPT, 1983	2	2
Heptathela kimurai kimurai (KISHIDA, 1920)	4	7
Heptathela kimurai yanbaruensis HAUPT, 1983	14	24
Heptathela schensiensis (SCHENKEL, 1953)	1	11
Heptathela sinensis BISHOP & CROSBY, 1932	1	5
Heptathela tonkinensis (BRISTOWE, 1933)	1	-
Ryuthela nishihirai nishihirai (HAUPT, 1979)	30	30
Ryuthela nishihirai ishigakiensis HAUPT, 1983	7	6

Not yet included are:

Heptathela bristowei GERTSCH, 1967	-	1
Liphistius heyangensis ZHU ET WANG, 1984	-	-
Heptathela hunanensis SONG & HAUPT, 1984	-	1
Heptathela jianganensis CHEN, GAO, ZHU ET LUO, 1988	-	-
Heptathela yunnanensis SONG & HAUPT, 1984	-	1
Heptathela sp. from Guangxi-province.	-	1

[1] The male of *H. k. amamiensis* has meanwhile been described by ONO & NISHIKAWA (1989). The males mentioned above were reared in Berlin from spiderlings collected in Amami-ôshima in 1980 and 1982.

[2] *Liphistius heyangensis* clearly belongs to the genus *Heptathela,* as the number of spinnerets is not a character suitable for distinction on the level of genera (HAUPT, 1983).

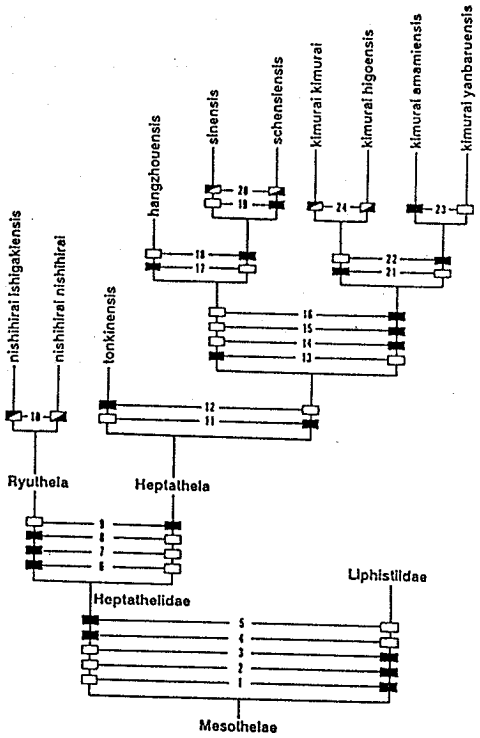

Fig. 1 Provisional diagram of relationships of Heptathelidae. synapomorphies (black mark), plesiomorphies (white mark), uncertain apomorphies (black and white), for explanation see text.

In the diagram of relationship (partly from HAUPT (1983)) the following characteristics have been used (synapomorphic form placed first):

1 male palpal organ with tibial apophysis
- male palpal organ without tibial apophysis
2 trichobothria partly with club-shaped hair-shafts
- trichobothrial hairshafts normal, slender
3 individuals spin stalked signal threads in front of the burrow
- no signal threads
4 palpal organ with conductor
- palpal organ without conductor
5 female receptacula in anterior position
- female receptacula in ventral position with ventral pore plate

6 embolus entirely sclerotized, opening oval
- embolus soft, with stiffening exocuticular bars, opening slit-like, spreadable
7 female receptacula monolobal, in median position
- female receptacula on each side bilobal
8 conductor and contrategulum fused
- conductor and contrategulum separated
9 tegulum tri-edged - tegulum bi-edged
10 conductor lengthened - conductor normal
11 conductor broadened - conductor slender
12 conductor awl-shaped, tip forked with three spikes
- conductor tip simple
13 conductor bispinal - conductor unispinal
14 female genital plate with lateroventral depressed contact area-
- without lateroventral depressed contact area
15 female receptacula in more lateral position, divided-
- female receptacula in more central position.
16 contrategulum with upright plate
- contrategulum a low, saw-toothed semicircle
17 female lateral receptacula reduced in size, in more ventral position
- lateral receptacula in normal position
18 conductor still broader, plate-like, trispinal
- conductor bispinal
19 median spine of conductor projecting
- median spine of conductor in line with surface
20 median spine of conductor smaller than lateral spines
- median spine of conductor of same size as lateral spines
(no decission on apomorphy possible)
21 conductor more or less oval with rounded apex
- conductor almost triangular, with curved acute apex
22 contrategulum with broad plate, slight depression at ridge
- contrategulum ax-shaped with broad depression at ridge
23 external part of embolus enlarged
- external part of embolus of normal size
24 apex of contrategulum rectangular, almost smooth
- apex of contrategulum rounded, but with spines

The present diagram represents two different levels of knowledge: While Japanese and Ryukyuan Heptathelids are fairly well known, much information on the continental species is still lacking. For this reason, some continental species could not be included in the diagram.

Either only one sex is known, or the necessary morphological details could not be elucidated from the decriptions and the type material was not yet accessible.
Nevertheless, once the necessary information becomes available, it can be introduced into the diagram and used to further elucidate relationships, and possibly to change the diagram .

Concerning the insular populations of Heptathelids on various islands in Southern Japan and the Ryukyuan archipelago (Fig. 2), it seems clear that the genus *Ryuthela* possibly has Southern connections hitherto unknown, while the *Heptathela*-group has evident connections to Zhejiang and other North-Eastern Chinese provinces.

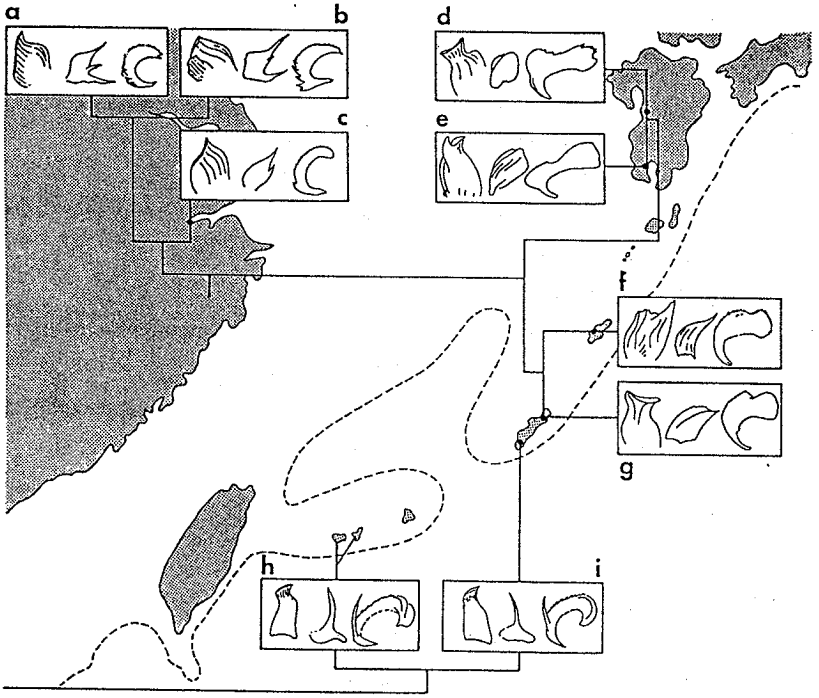

Fig. 2 The phylogenetic relationships of insular representatives of Heptathelidae (approximate coastal line during the pleistocene era streaked). From left to right embolus, conductor and contrategulum of each species/subspecies. a *Heptathela schensiensis*, b *H. sinensis*, c *H. hangzhouensis*, d *H. kimurai higoensis*, e *H. kimurai kimurai*, f *H. kimurai amamiensis*, g *H. kimurai yanbaruensis*, h *Ryuthela nishihirai ishigakiensis*, i *R. nishihirai nishihirai*.

Keeping in mind that all these islands had a direct connection to the continent during the pleistocene era, the island populations of today are the specialized descendants of a widespread *Ryuthela* species in the South, and a possibly even more widespread

representative of *Heptathela* in the North. The residual populations have been separated by the rising sealevel at the end of the ice-ages, and it is only natural that populations on small islands may have specialized further than those of large islands like Kyushu, as they originated from smaller separated populations in the beginning which may have represented only certain specialized aspects of the genepool since the origin of separation.
Some characteristics of *Heptathela kimurai amamiensis* which resemble Northern Chinese Heptathelids (rather broad embolus) (Ono & Nishikawa 1989) may be interpreted as symplesiomorphies. H. k. amamiensis forms a link between continental Heptathelids and the Japanese and Ryukyuan island populations, as the ventral contact area on the genital plate of the female is present, although narrow. This contact area is a clear synapomorphy of the whole kimurai-group, together with the upright contrategulum plate of the male palpal organ not present in any other Heptathelid species.

For the classical taxonomist it will be of interest to know which of these recent populations have to be considered as species. Formally, some taxonomist tended to describe a new species once some morphological difference was found. In an archipelago this view point would leed to an inflation of the number of new species to be described. For this reason the author has preferred to use the trinominal nomenclature for species and subspecies, when the populations dealt with are not sympatric on any of the islands concerned (Haupt, 1983). In populations from different islands, the criterion of existing fertile reproduction can only be tested experimentally. In Nature only another ice-age could bring these separated populations together and prove how far speciation has proceeded. In order to cope with these difficulties generally posed by island populations to the taxonomist, the terms *Artenkreis* (Rensch, 1929) or superspecies (Mayr, 1931) have been introduced . The genus Heptathela on East Asian islands is another typical example of this kind.

We have to accept that evolution is a process, of which we can only observe a very small part. If we reconstruct historical events in a diagram of relationships, it may be considered unimportant which rank a certain population is given, once its sister group is known (Ax, 1987).

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