

CHAPTER ONE

A Cladistic Analysis of the Family Hersiliidae (Arachnida, Araneae) of the Afrotropical Region**Abstract**

The family Hersiliidae consists of six genera in the Afrotropical region, two of these taxa are newly discovered viz. *Tyrotama* gen. nov. and *Prima* gen. nov. *Murricia* Simon and *Neotama* Baehr & Baehr are newly recorded for the region. Of the three original genera, *Tama*, *Hersilia*, and *Hersiliola*, the latter two remain. A cladistic analysis based on 48 characters and 22 species, which included nine species that are not Afrotropical, inferred the following phylogeny: ((*Hersiliola Tyrotama*) (*Neotama* (*Prima* (*Murricia Hersilia*))))). Morphological data supports the monophyly of *Tyrotama* and the phylogeny suggests that the genus is closely related to *Hersiliola*. The new genus *Prima* is weakly supported as the sister taxon of *Neotama*. Support for the genus *Hersilia* is weak and synapomorphies that unite six identified species groups within the genus are much more consistent than those that unite *Hersilia*. However, the genus *Hersilia* is retained until a comprehensive generic level analysis for the world is conducted. A key to the genera of the Afrotropical Region is provided.

Key words: Hersiliidae, phylogeny, Afrotropical Region

Introduction

The Hersiliidae is a small spider family with 141 species and 10 genera excluding results from this study (Platnick 2004; Rheims & Brescovit 2004). The group is characterized by conspicuously long posterior lateral spinnerets, elongated legs and is limited to the tropical and subtropical regions of the world. All hersiliids are arboreal except for the representatives of *Hersiliola* Thorell, 1870 and *Tama* Simon, 1882. The latter two genera are ground active, inhabiting arid regions of Africa, the Mediterranean and the western parts of the Oriental Region.

The family has recently been the focus of extensive revisionary studies in the Australian (Baehr & Baehr 1987), Oriental (Baehr & Baehr 1993a), and Neotropical Regions (Rheims & Brescovit 2004). Baehr & Baehr's 1987 revision of Australian hersiliids resulted in the description of 29 species, of which 93% were new to science. Subsequent publications doubled the number of species known for the Australian Region to 55 in total (Baehr & Baehr 1988b, 1989, 1992, 1993b, 1995). In their revision of the Oriental Region, Baehr & Baehr (1993a) described 27 new species out of a total of 33 taxa and proposed a tentative phylogeny for the family. Rheims & Brescovit (2004) described six new species, redescribed five species, and proposed three new genera, *Yabisi*, *Iviraiva*, and *Ypypuera* for the Neotropical Region.

Members of the family Hersiliidae are found throughout the Afrotropical Region and include both arboreal and ground active genera. Before this study the Afrotropical Region had 30 species in three genera, *Hersilia* (22), *Hersiliola* (4), and *Tama* (4). Descriptive work was done between 1827 and 1976. Smithers (1945) revised the three genera of Hersiliidae of southern Africa and Benoit (1967) revised the genus *Hersilia* of the Afrotropical Region excluding Madagascar. None of these studies made an attempt to determine the phylogenetic relationships of hersiliid taxa.

Both *Tama* and *Hersiliola* occur in the warmer parts of the Afrotropical Regions where they are found under stones (Smithers 1945). *Hersiliola* construct a pholcid-like web and *Tama* construct a circular shaped retreat of closely woven webbing plastered with small pebbles, chips and vegetable debris. Anchor threads attached to the substratum warn the spider of approaching prey (Smithers 1945; Dippenaar-Schoeman *et al.* 1999).

They move at great speed overpowering their prey and dragging it back to their retreat where they are fed on (Lawrence 1964). Their egg sacs are attached to the underside of rocks and covered with stone chips (Dippenaar-Schoeman & Jocqué 1997).

Platnick (2004) catalogues the following ranges for *Hersilia*: Afrotropical, Oriental, and Australian Regions, although one species penetrates into the Palaeartic. All Afrotropical species of this genus live on the trunks of trees. When at rest they are well camouflaged with their flattened bodies, ad-pressed to the bark. They move at great speed when disturbed. Although specimens are very cryptic the reflection of sunlight on the guide threads they leave on trunks is a good indicator of their presence (Dippenaar-Schoeman & Jocqué 1997). Females cover their eggs with an oval shaped layer of silk camouflaged with bits of bark. She holds guard over the eggs in an upside down position above the silk patch until the young hatch (pers. obs.).

Petrunkevitch (1963), Schawaller (1981) and Wunderlich (2004) have described several fossil genera, whose relationship with extant Hersiliidae remains uncertain. Recent work on fossil spiders also suggests that the family is an ancient taxon, and predict the presence of Hersiliidae in the Cretaceous (Penney, 2002). Evidence point to a much wider distribution in Europe during the Oligocene and Miocene (Penney 1999). Lehtinen (1967) considered the Hersiliidae to be related to the Oecobiidae based on similarity of genital structures, modification of the carapace, eye pattern and spinnerets. Coddington & Levi (1991), in a cladistic analysis of all spider families, grouped the hersiliids with the oecobiids based on the similarity of the elongated posterior lateral spinnerets, and the distinct prey capture behaviour of the two families. Here the spider rapidly encircles the prey by facing away from it and ensathes it with silk from the spider's long posterior lateral spinnerets. Although Coddington & Levi (1991) placed the hersiliids in the Eresoidea (Hersiliidae, Oecobidae and Eresidae), basal within the Entelegenae, representative species of the Hersiliidae was not included in their analysis.

Baehr & Baehr (1993a) did not consider these relationships well supported and based their phylogenetic analysis on morphoclines. Baehr & Baehr's first attempt at inferring phylogenetic relationships for hersiliids in 1993, included representatives of the family from Australia, the Oriental Region and New Guinea. They subsequently also proposed a phylogeny for *Hersilia* from Australia and New Guinea (Baehr 1998). Their

hersiliid phylogeny has *Hersiliola* basal, based on the following plesiomorphic characters: short legs, shorter posterior lateral spinnerets, a convex abdomen and no flexible zone on the metatarsi of the legs. *Tama* is defined by longer legs, long posterior lateral spinnerets as well as the presence of a flexible zone on the metatarsi of legs I, II, and IV whereas *Hersilia* have a biarticulate metatarsus, very long I, II, and IV legs, and armed chelicerae. Rheims and Brescovit (2004) suggested the use of *Uroctea* as an outgroup based on the proposal by Lehtinen (1967) that Hersiliidae is a sister group of ecribellate Oecobiids belonging to the genus *Uroctea* and followed the principles set forth by Nixon & Carpenter (1993) for outgroup selection. In spite of the differences in approach, their proposed phylogeny correspond with that of Baehr & Baehr (1993a) except for placing *Neotama* and *Hersilia* as sister groups next to *Tamopsis*.

It is evident from these analyses, that Africa could be considered the place of origin of the family Hersiliidae. This could be based on the presence of the plesiomorphic hook-shaped median apophysis found on the male palp in some Afrotropical *Hersilia* species and the occurrence of the ground dwelling genera of Hersiliidae in Africa. Further questions include Baehr & Baehr's (1993a) suggestion that the southern African species presently listed in *Tama* might need to be transferred to *Neotama*. The taxonomic status of two Oriental genera, *Murricia* Baehr & Baehr and *Promurricia* Baehr & Baehr has also been brought into doubt (Rheims & Brescovit 2004). Only females are known for these two genera and both Baehr & Baehr (1993a) and Rheims & Brescovit (2004) suggested that *Murricia* is a junior synonym of *Hersilia* and *Promurricia* a morphological intermediate between these two genera.

However, clarification of these questions would only be possible after a worldwide revision of the Hersiliidae. The Afrotropical Region represents the last region for which no contemporary revision has been done. Such a revision will shed more light on generic delimitations in the family Hersiliidae (e.g. *Hersilia*, *Murricia* Simon and *Promurricia* Baehr & Baehr). This thesis will therefore (1) describe, differentially diagnose, illustrate, and characterise phylogenetically the genera and species of Afrotropical Hersiliidae, summarising their geography, and natural history (2) reconstruct the phylogeny of Afrotropical hersiliid species, using quantitative cladistic methods. In

this paper a phylogeny for the Hersiliidae from the Afrotropical Region is proposed based on 47 species after 920 specimens were examined.

Methods

A data matrix with 59 characters was constructed for 36 Afrotropical species and five non-Afrotropical hersiliid species viz. *Neotama cunhabebe* (Vellard) from the Neotropical Region, *Hersilia tibialis* Baehr & Baehr and *Hersilia jajaj* Rheims & Brescovit from the Oriental Region, *Tamopsis eucalypti* Baehr & Baehr and *Tama edwardsi* Lucas from the Mediterranean (Appendix A). *Murricia uva* is an artificial amalgamation of *M. emlynae* males and *M. uva* females. An outgroup consisting of one species of *Uroctea* sp. indet. from Namibia was included in the matrix based on Lehtinen (1967), Coddington & Levi (1991) and Rheims & Brescovit (2004).

All species with more than 10 ambiguities were excluded from the analysis as were all species with one of the sexes unknown. An exemplar was chosen from a set of species that were similar in terms of phylogenetically informative characters (Rheims & Brescovit 2004). Eleven characters became uninformative because of the exclusion of above taxa. The inclusion of these characters would lead to an artificial increase in the consistency and retention indices these eleven characters were also excluded from the analysis (Prendini 1999). These characters are, however, retained in the matrix published here, as they are informative of relationships with some of the species excluded from the analysis (Appendix). Excluded species are included in the summary cladogram (Fig. 2). The resulting matrix of 48 characters and 22 taxa was subjected to the analysis.

Analyses of the unweighted and unordered characters were subjected to heuristic searches in Nona (Goloboff 1997). Nona was done with h/1000, mult*1000, jump50. Successive weighting with the squared CI was also done in NONA entering the following command sequence: run swt.run h10000 h/1000 mult*1000 jump 50. Pee-Wee 2.6 (Goloboff 1997) was used to obtain trees that maximise implied weights across all characters (Goloboff 1993a), with all characters equally weighted (wt = 1) and for both ordered and unordered multi-states (h10000;h/1000;mult*1000;jump50;). Pee-Wee maximises total fit $F = \sum f_i$ where $f_i = k/(k + E S_i)$; k is a constant of concavity and can be varied between 1 and 6 with the “concN” command, allowing less (1) or more (6)

influence for homoplasious characters. Concavity constants 1, 3 and 6 were used in this analysis.

Phylogenetic signal was assessed with branch support indices (Bremer 1994). Branch support was calculated with NONA 1.8 (Goloboff 1993b) using the options h10000; bsupport 100. The Bremer Support for a given node in the shortest unconstrained tree is the number of additional steps required in the shortest trees for which that node collapses. A branch present in one of the most parsimonious trees is more strongly supported by the data if a large increase in length of additional trees is required before that branch is lost in the consensus. Branch support was truncated at values of 100 and Bremer support values reported range from 0 and or greater. The preferred tree must be the shortest, most resolved tree possible i.e. make the most predictions that can be tested given only unambiguous branch support (Griswold & Ledford 2001). Preference is, therefore, given to synapomorphic characters in the construction of a phylogeny as they have the largest predictive power (Farris 1985).

Character descriptions and interpretations

Character 1. — tibia/patella male palp (l=1; uninformative)

0 = short, close to one

1 = elongate, more than two

This character is a synapomorphy for *Neotama cunhabebe* and two other Neotropical species (Rheims & Brescovit 2004) but is uninformative in this cladogram and is an autapomorphy of *Neotama cunhabebe*.

Character 2. — Male palpal tibia form (l = 2; ci = 50; ri = 88).

0 = absent, palpal tibia cylindrical (Chap. 2, Fig. 9b).

1 = present, palpal tibia with angular dorsal projection, (Chap. 2, Fig. 15b).

Presence of such an angular dorsal projection arises as a synapomorphy for *Hersilia tibialis*, *H. incompta* and *H. nicolae* and an autapomorphy of *H. plara*.

Character 3. — Palpal tibia, dorsal spines (l = 5; ci = 20; ri = 75)

0 = absent (Chap. 2, Fig. 9b)

1 = present (Chap. 2, Fig. 15b)

Most Hersiliidae have no spines dorsally on their palps. The presence of these spines is very homoplasious and arises several times independently.

Character 4. — Cymbium and alveolus shape (l = 2; ci = 50; ri = 0).

0 = short cymbium with circular alveolus (Rheims & Brescovit 2004: fig. 32).

1 = elongate cymbium with oval alveolus (Chap. 2, Fig. 2a; Rheims & Brescovit 2004: fig. 34).

An elongate cymbium with oval alveolus arise independently in *Tamopsis* and *Prima*.

Character 5. — Cymbium (l = 2; ci = 50; ri = 0)

0 = narrows gradually (Rheims & Brescovit 2004: fig. 33).

1 = narrows abruptly (Chap. 5, Fig. 2a; Rheims & Brescovit 2004: fig. 31).

Rheims & Brescovit (2004) found that this character unites *Neotama cunhabebe* and two other *Neotama* species. It also is an autapomorphy for *Prima*.

Character 6. — Lamellar modification of the bulbus (l = 2; ci = 50; ri = 66)

0 = absent

1 = present (Chap. 2, Figs. 4b & 19a)

The bulbus form laminar projections that surround the median apophysis. The character is homoplasious and arises twice as a synapomorphy for the *Hersilia incompta* species group and an autapomorphy for *H. arborea*.

Character 7. — Sperm duct (l = 5; ci = 100; ri = 100).

0 = no basal modifications (Rheims & Brescovit 2004; fig. 35)

1 = with basal curvature (Chap. 1, Fig. 6a)

2 = with single basal loop (Chap. 1, Fig. 6b)

3 = with two basal loops (Rheims & Brescovit 2004; fig. 38)

4 = repeated curvature (Chap. 1, Fig. 6c)

5 = basal loop and medial curvature (Chap. 1, Fig. 6d)

This character is ambiguous at nodes A, B, C and E. A sperm duct with a basal curvature is synapomorphic at node H. A single basal loop is homoplasious, derived for *Hersiliola* and at node E. A meandering sperm duct is apomorphic for *Tyrotama* whereas a sperm duct with a basal loop and medial curvature unites *Hersilia jajaj* and *Murricia uva* at node P.

Character 8. — Bulbus with a basal swelling (l = 1; ci = 100; ri = 100).

0 = absent.

1 = present (Chap. 2, Fig. 26i).

The presence of a basally swollen bulbus unites all taxa in the *Hersilia baforti* species group.

Character 9. — Median apophysis (l = 4; ci = 25; ri = 40)

0 = present (Chap. 2, Fig. 2a).

1 = absent (Chap. 3, Fig. 5a).

Rheims and Brescovit (2004) suggested that the presence of a median apophysis is plesiomorphic based on Griswold *et al.* (1999) assessment of the secondary repeated loss of the median apophysis in several spider families e.g. Eresidae and Filistatidae. This character is ambiguous at node B and C, and is lost twice: as an autapomorphy for *Neotama corticola* and a synapomorphy for the *Hersilia baforti* species group.

Character 10. — Median apophysis, shape (l = 4; ci = 100; ri = 100).

0 = hooks-shaped (Chap. 2, Fig. 2a)

1 = bifid (Chap. 5, Fig. 2a)

2 = complex with two or more projections (Rheims & Brescovit 2004; fig. 48)

3 = concave and complex (Chap. 2, Fig. 19a).

A simple hook-shaped median apophysis is considered to be plesiomorphic (Baehr & Baehr 1993a). Although Rheims and Brescovit (2004) suggested that it might be derived based on their tree topology. A bifid median apophysis is an autapomorphy of *Prima ansiae*, while a complex median apophysis with two or more projections represents an

autapomorphy for the genus *Tamopsis*. The synapomorphy for *Hersilia incompta* species group is a concave and complex median apophysis.

Character 11. — Hook-shaped median apophysis, insertion (l = 3; ci = 100; ri = 100)

0 = basal (between five and seven o'clock) (Rheims & Brescovit 2004: fig. 103)

1 = medially (Chap. 2, Fig. 2a)

2 = retrolateral (between two o'clock and four o'clock) (Chap. 2, Fig. 17a & 26f; Rheims & Brescovit 2004: fig. 84)

3 = distally (between eleven and one o'clock) (Chap. 5, Fig. 2a)

This character is ambiguous at node A. A distally originating median apophysis is an autapomorphy for *Prima* and a retrolaterally originating median apophysis is synapomorphic at node K.

Character 12. — Conductor (l = 1; ci = 100; ri = 100).

0 = present (Chap. 2, Fig. 3b).

1 = absent (Chap. 2, Fig. 2a).

Griswold *et al.* (1999) and Rheims & Brescovit (2004: 198, character 19) suggested that the presence of a conductor is plesiomorphic. Rheims & Brescovit (2004) found that the loss of a conductor is apomorphic for the family Hersiliidae. However the character is ambiguous at node A and has been retained in the *Hersilia baforti* species.

Character 13. — Conductor size (l = 1; ci = 100; ri = 100).

0 = large, longer than width of bulbus (Chap. 2, Fig. 3a).

1 = small, shorter than width of bulbus (Chap. 2, Fig 5a)

As the loss of the conductor is considered derived (Character 7) the progressive reduction in size is also considered derived. The reduction in the size of the conductor varies considerably within the *Hersilia baforti* species group.

Character 14. Conductor with hyaline projection distally (uninformative).

0 = absent.

1 = present (Chap 2, Fig. 3a)

This character is synapomorphy for *Hersilia alluaudi* and *H. bubi*.

Character 15. — Conductor with ventral furrow distally (uninformative).

0 = absent.

1 = present (Chap. 2, Fig. 26i).

A ventral furrow arises as a synapomorphy of *Hersilia salda* and *H. dilumen*.

Character 16. — Sclerotized tegular projection (l = 1; ci = 100; ri = 100).

0 = absent.

1 = present (Chap 2, Fig. 21b).

This straight projection arises medially on the bulbus and is an autapomorphy of *H. plara*.

Character 17. — Slide-like tegular projection (l = 3; ci = 33; ri = 84).

0 = absent

1 = present (Chap. 2, Fig. 26a-e, g, h)

A slide-like tegular projection is homoplasious and unite all Afrotropical *Hersiliola* species as well as *Neotama* species and is a synapomorphy of *Hersilia caudata* and *H. sigillata* species groups.

Character 18. — Embolus, position from which embolus originate on bulbus (l = 7; ci = 42; ri = 77).

0 = prolateral (between eight and ten o'clock) (Chap. 2, Fig. 19a).

1 = apical (between eleven and one o'clock) (Chap. 3, Fig. 5a).

2 = basal (between five and seven o'clock)

3 = retrolateral (between two o'clock and four o'clock) (Chap. 2, Fig. 3a).

An embolus with an apical origin is very homoplastic. The retrolateral originating embolus is a synapomorphy for *Hersilia baforti*.

Character 19. — Embolus length (l = 5; ci = 40; ri = 50)

0 = short, not exceeding half the total length of the bulbus or do not complete circle around median apophysis (Chap. 2, Fig. 2a).

1 = long, equal or slightly longer than bulbus length or complete a circle around median apophysis (Chap. 2, Fig. 19a).

2 = very long, at least 1.5 times bulbus length or circles at least 1.5 times around median apophysis (Chap. 3, Fig. 2a).

Reihms and Brescovit (2004) suggested that short emboli are plesiomorphic and long emboli are a highly homoplasious character for four taxa: *T. eucalypti*, *N. cunhabebe*, and nodes M. Very long emboli are a synapomorphy for the genus *Hersiliola*.

Character 20. — Embolus shape (l = 3; ci = 100; ri = 100).

0 = filiform, round (Chap. 3, Fig. 5a; Chap. 2, Fig. 2a).

1 = laminar (Rheims & Brescovit 2004: figs. 19-22).

2 = three-cornered (Chap. 2, Fig. 19-22).

3 = cylindrical (Rheims & Brescovit 2004: figs. 47 & 48).

A cylindrical embolus is synapomorphic for all *Tamopsis* species and three-cornered emboli are derived character for the *Hersilia incompta* species group.

Character 21. — Embolus projection (l = 1; ci = 100; ri = 100).

0 = absent.

1 = present (Chap. 2, Fig. 26a-b)

Embolic projections are absent from most Afrotropical Hersiliidae except for *Hersilia caudata*, *H. occidentalis* and *H. albicomis*.

Character 22. — Embolus distally (l = 2; ci = 50; ri = 85).

0 = acute.

1 = furcated (Chap. 2, Fig. 13a).

The cladogram suggest that a furcate embolus arise twice in some representatives of the *Hersilia baforti* species group and in *Hersilia madagascariensis*,

Character 23. — Epigynal plate (l = 5; ci = 20; ri = 75).

0 = entire (Chap. 2, Fig. 21f).

1 = median plate with pair of lateral borders (Chap. 2, Fig. 2f).

Rheims & Brescovit (2004) tree topology suggested that an entire epigynal plate is plesiomorphic whereas a divided epigynal plate is apomorphic.

Character 24. — Median plate (l = 3; ci = 33; ri = 50).

0 = partially covered by lateral borders (Chap. 2; Fig. 8f).

1 = free (Chap. 2, Fig. 15f).

This character was also proposed by Rheims & Brescovit (2004). Their optimization of this character were ambiguous at certain nodes but suggested that this character is an autapomorphy for *Hersiliola* and *N. corticola* and a synapomorphy for the *Hersilia incompta* species group.

Character 25. — Median plate (l = 2; ci = 100; ri = 100).

0 = smooth.

1 = with lateral sclerotizations or fixing structures (Chap. 2, Fig. 2f).

2 = rippled (Chap 2, Fig. 19e).

A rippled lateral border of the median plate is a synapomorphy of *H. incompta* species group. Fixing structures laterally on the median plate is a synapomorphy at node P for *Hersilia caudata* and *H. sigillata* species groups.

Character 26. — Epigynal plate with atrium surrounded by projecting rim (l = 1; ci = 1; ri = 1)

0 = absent.

1 = present (Chap. 3, Fig. 5f).

This character is synapomorphic for *Tyrotama*.

Character 27. — Epigynal plate medially with transverse unpigmented plate (l = 1; ci = 100; ri = 100).

0 = absent.

1 = present (Chap. 2, Fig. 21f).

A medially transverse unpigmented plate is derived for the *H. baforti* species group.

Character 28. — Copulatory openings.

0 = posterior (Chap. 2, Fig. 2g).

1 = median (Chap. 5, Fig. 2g)

2 = anterior (Chap. 3, Fig. 4g)

Copulatory openings open anteriorly of the spermathecae form a synapomorphy for *Tyrotama* and copulatory openings that open mesad are derived for *Prima*.

Character 29. — Copulatory openings (l = 2; ci = 100; ri = 100).

0 = inconspicuous.

1 = conspicuous as oval unsclerotized openings (Chap 2, Fig. 12f).

2 = conspicuous as circular sclerotizations (Chap. 2, Figs. 4f & 17f).

Conspicuous circular sclerotizations around the copulatory openings are derived at node O.

Character 30. — Length of copulatory duct (l = 2; ci = 100; ri = 100).

0 = very long, at least three times spermathecae length (Chap. 3, Fig. 2g).

1 = median, twice as long as spermathecae length (Chap. 4, Fig. 1b).

2 = short, equal (Chap 2, Fig. 8g).

A short copulatory duct is derived at node F, while a median copulatory duct is synapomorphic at node N and for *Hersilia incompta* species group.

Character 31. — Copulation ducts (l = 1; ci = 100; ri = 100).

0 = narrow.

1 = wide, exceed diameter of fertilization ducts (Chap. 5, Fig. 1g).

Wide copulation ducts are synapomorphic for the genus *Neotama*.

Character 32. — Number of spermathecae (l = 5; ci = 40; ri = 40).

0 = several spermathecae, more than 30 (Chap. 4, Fig. 1b).

1 = several small and one large (Chap. 2, Fig. 27g).

2 = one large spermathecae (Chap. 2, Fig. 2g).

Forster (1980) suggested a possible evolutionary sequence starting with *Grandungula sorenseni* where the invagination of bursal wall with several small spermathecae forms a stable bilobed arrangement of the spermathecae and a seminal receptacle. The possible loss of these secondary spermathecae would then give rise to the bilobed structure found in *Hersilia sigillata* group. The presence of multiple, more than 30, small spermathecae are most apparent in *Murricia uva* (Chap. 4, Fig. 2b). The tree topology suggests that that character is ambiguous at node A. several small spermathecae and one large spermathecae unites the *Hersilia sigillata* species group.

Character 33. — Spermathecae shape (l = 5; ci = 40; ri = 62).

0 = globose (Chap. 2, Fig. 2g).

1 = cylindrical (Chap. 2, Fig. 5g).

2 = kidney-shaped (Chap. 2, Fig. 27g).

Character 34. — Spermathecae stalk (l = 4; ci = 25; ri = 40).

0 = absent (Chap. 2, Fig. 5g).

1 = present (Chap. 2, Fig. 2g).

Rheims & Brescovit (2004) proposed stalked spermathecae as synapomorphies for *Hersilia* and *Hersiliola* respectively. The tree topology, however, suggests that this does not hold true for *Hersilia* where several taxa retained the plesiomorphic state.

Character 35. — Number of seminal receptacles (l = 3; ci = 100; ri = 100).

0 = more than two.

1 = two.

2 = one, large hyaline (Chap. 3, Fig. 5g).

3 = one, small sclerotized (Chap. 2, Fig. 2g).

4 = none.

This character is ambiguous at node A. The definition of a seminal receptacle here is taken from Rheims & Brescovit (2004) sensu (Sierwald 1999) as opening directly into the spermathecae and its stalk with no connection to the fertilisation duct or copulatory duct. Forster (1980) suggested that the presence of large unsclerotized, membranous hyaline

seminal receptacle is plesiomorphic (*Tyrotama australis* and *T. bicava*, Chap. 3, Figs. 6g & 6g). The reduction in number, size and sclerotization of the seminal receptacle is considered derived. The presence of a large hyaline seminal receptacle is synapomorphic for the genus *Tyrotama*.

Character 36. — Seminal receptacle shape (l = 7; ci = 28; ri = 44).

0 = globose (Chap. 2, Fig. 2a).

1 = cylindrical (Chap. 4, Fig. 1b).

2 = kidney-shaped (Chap. 2, Fig. 8g).

Character 37. — Position of seminal receptacle (l = 4; ci = 25; ri = 57).

0 = laterally of spermathecae (Chap. 2, Fig. 2g).

1 = medially of spermathecae (Chap. 2, Fig. 13g).

The cladogram suggests that a seminal receptacle laterally positioned in relation to the spermathecae is plesiomorphic.

Character 38. — Seminal receptacle borders (l = 2; ci = 50; ri = 90).

0 = smooth.

1 = with distal tubercle, often with glandular parts covered by threads.

Baehr & Baehr (1993a) referred to this character as glandular parts covered by threads.

This character is synapomorphic for all *Hersilia*. It reverses at node Q.

Character 39. — Clypeus length (l = 5; ci = 40; ri = 72).

0 = short, less than median ocular quadrangle length (Chap. 2, Fig 10d).

1 = long, less than twice median ocular quadrangle length (Chap. 2, Fig. 9d).

2 = very long, more than twice median ocular quadrangle length (Chap. 3, Fig. 5d).

A long clypeus unites all ground dwelling hersiliids.

Character 40. — ALE/AME (uninformative).

0 = <0.6.

1 = >0.7 (Chap. 2, Fig. 27g).

Rheims and Brescovit (2004: 194, character 2) identified the enlarged ALE, that is usually small and barely conspicuous, as an apomorphy of the genus *Yabisi*. In this tree topology it is autapomorphic for *H. sigillata*.

Character 41. — Interdistance AME-ALE (uninformative).

0 = equal or smaller than 1.5 AME diameter.

1 = more than twice AME diameter (Chap. 2, Fig. 27c).

Rheims and Brescovit (2004: 194, character 3) observed the projection of the AME anteriorly on the carapace and that it arised as a synapomorphy for all members of *Yabisi*. In this tree topology it is autapomorphic for *H. sigillata*.

Character 42. — Lateral eyes (l = 2; ci 50; ri = 0).

0 = on slightly conspicuous tubercles.

1 = on prominent tubercles (Chap. 4, Fig. 2d).

Baehr & Baehr (1993: 84, character 4) proposed that eyes on prominent tubercles are apomorphy for the genus *Murricia*. Rheims & Brescovit (2004: 194, character 1) cladogram suggests that it is a synapomorphy for *Yabisi*. In this analysis it is an autapomorphy of *H. sigillata* and *M. uva*.

Character 43. — cheliceral teeth on promargin (l = 1; ci =100; ri = 100).

0 = present (Fig. 5c).

1 = absent.

If present, there are usually three large cheliceral teeth on the promargin. The loss is derived for all groundliving hersiliids (node B).

Character 44. — cheliceral teeth on retromargin (l = 1; ci =100; ri = 100).

0 = present (Fig. 5c).

1 = absent.

According to Griswold et al. (1999) the presence of cheliceral teeth on the pro- and retromargin is plesiomorphic. Rheims and Brescovit (2004) interpreted a cheliceral groove as a reversal in Hersiliidae. In this analysis the cheliceral groove is retained as a plesiomorphic character.

Character 45. — Abdomen: pattern on dorsum (l = 2; ci = 100; ri = 100).

0 = lancet-shaped heart mark (Chap. 1, Fig 4a).

2 = rectangular (Chap. 4, Fig. 4b).

1 = heart mark heart mark broadens distally, form triangle (Chap 2. Fig. 5e).

Character 46. — Female abdomen with two pairs of tubercles laterally (l = 1; ci = 100; ri = 100).

0 = absent.

1 = present (Chap2, Fig. 19c).

The presence of two pairs of tubercles laterally on the abdomen is a synapomorphy for *Hersilia nicolae* and *H. incompta*. A smooth abdomen is considered plesiomorphic.

Character 47. — Dorsal muscular pit number (l = 3; ci = 66; ri = 50).

0 = <4 (Chap. 3, Fig. 6e).

1 = 4 (Chap. 2, Fig. 2e).

2 = 5 (Chap. 4, Fig. 5e).

The conspicuous dorsal muscular pits found in most hersiliids give rise to a dorso-ventrally flattened abdomen in all arboreal hersiliids uniting them as a group.

Character 48. — Relative length of leg III to leg I (l = 2; ci = 50; ri = 66).

0 = more than 0.6.

1 = less than 0.4.

The cladogram suggests that a long leg III is plesiomorphic and relative shortening of leg III is derived. There is, however, uncertainty whether it was due to a shortening of leg III or lengthening of leg I, II, and IV (Baehr & Baehr 1993a; Rheims & Brescovit 2004). The character is ambiguous at nodes A and B.

Character 49. — Relative length of leg IV to leg I (l = 1; ci = 100; ri = 100)

0 = leg IV longer than both leg I and II

1 = leg IV shorter than both leg I and II

Elongate leg I and II is a synapomorphy for all arboreal hersiliids at node E.

Character 50. — Metatarsi articulation of leg I, II, and III (l = 4; ci = 75; ri = 83).

0 = uniarticulate.

1 = elongate flexible zone (Fig. 5f).

2 = narrow flexible zone.

3 = biarticulate (Fig. 5e).

Baehr (1998) suggested a possible evolutionary sequence in which an elongate flexible zone is reduced in length to form a narrow flexible zone and ultimately develop into a biarticulation. A biarticulate metatarsus is synapomorphic at node K whereas a narrow flexible zone is derived for *Neotama*. The uniarticulate legs of *Hersiliola* and *Tyrotama* is a reversal.

Character 51. — Metatarsus/tarsus (l = 2; ci = 50; ri = 60).

0 = Less than four.

1 = More than six.

This character is also ambiguous at nodes A and B.

Character 52. — Leg spine microstructure (l = 1; ci = 100; ri = 100).

0 = Scale-like projections (Fig. 3e,g & h).

1 = longitudinal grooves dorsally (Fig. 3f).

Electron microrgraphs of large spines on the legs of specimens suggest that scale-like projections on the surface of these spines are plesiomorphic as it is also found in *Uroctea*. The longitudinal grooves dorsally on the spines of *Hersiliola* and *Tyrotama* are derived.

Character 53. — Metatarsal trichobothria (uninformative).

0 = one to two.

1 = four.

Griswold (2004: 56, character 5) noted that the presence of more than two metatarsal trichobothria is derived for entelegyne spiders. The presence of four trichobothria distad on the metatarsi of hersiliids represents a synapomorphy for the family.

Character 54. — Claw tuft hairs (uninformative).

0 = absent.

1 = present (Fig. 3d).

Rheims & Brescovit (2004: 195, character 8) considered the thick claw tufts found in all hersiliids to be a synapomorphy for the family.

Character 55. — Legs spination, ventral surface (l = 2; ci = 100; ri = 100).

0 = pair of parallel rows of strong spines along the entire leg.

1 = pair of parallel rows of strong spines only along femora strong spines absent.

2 = strong spines absent.

Rheims & Brescovit (2004) noted the presence of two rows of strong spines ventrally along the entire length of *Uroctea* legs. In the ground active representatives of Hersiliidae these rows are restricted to the femora and they are absent in arboreal hersiliids (node E).

Character 56. — Feathery hairs (uninformative).

0 = absent.

1 = present (Fig. 3a).

Griswold et al. (1999: 56, character 18) considered the presence of feathery hairs as derived. This character is a synapomorphy for all hersiliids.

Character 57. — PLS: tS/bS

0 = Close to one.

1 = more than three times.

A synapomorphy for all arboreal hersiliids (node E) is the terminal segment of the posterior lateral spinnerets that are very elongate, at least three times the length of the basal segment (Baehr & Baehr 1993a: 84, character 21).

Character 58. — Anal tubercle (uninformative).

0 = large.

1 = small.

Griswold *et al.* (1999: 56, character 80) suggest that a small anal tubercle is plesiomorphic. However the polarity proposed by Rheims & Brescovit (2004) is accepted in this analysis where a large anal tubercle is plesiomorphic. The small anal tubercle of all hersiliids is therefore derived.

Character 59. — Habitat (I = 1; ci = 100; ri = 100).

0 = ground-dwelling.

1 = arboreal.

Both Baehr & Baehr (1993a) and Rheims & Brescovit (2004) suggested that ground active behaviour is plesiomorphic in Hersiliidae. The latter authors also noted that *Tama edwardsi* has elongated spinnerets and modified metatarsi, suggesting that this species were pre-adapted for an arboreal life style. An alternative could be that arboreal habits are plesiomorphic and ground-dwelling in the arid regions of the Afrotropical and Palearctic Regions are derived. A compelling argument for it is the absence of ground active representatives of Hersiliidae in the Neotropical, Australian and Oriental Regions.

Discussion

Heuristic searches of the matrix in NONA with characters unweighted resulted in two most parsimonious trees (L = 126; CI = 59; 71). Successive weighting of the unordered multi-state matrix in NONA, generated one most parsimonious tree of 126 steps that corresponds with results obtained with implied weights where k values were 1, 3, and 6 (Table 1). All four trees resemble one of the trees found in the unweighted search; this is the preferred tree (Fig. 1). The second tree differs only in the placement of the *Hersilia sigillata* species group.

The proposed phylogeny is largely congruent with that of Baehr & Baehr (1993a) and Rheims & Brescovit (2004) except that the groundliving hersiliids form a sister group to the arboreal hersiliids based on the absence of cheliceral teeth on the pro- and retromargin of the chelicerae and the longitudinal grooves dorsally on their spines. *Tama edwardsi* is basal in this sister group, not *Hersiliola* as is the case in the tree topologies of both Baehr & Baehr (1993a) and Rheims & Brescovit (2004). The Afrotropical species of *Tama* appear in a distinct clade, which is not closely related to the genus *Tama*. This excludes *Tama* from the Afrotropical region and confirms Baehr & Baehr's (1993)

suggestion. As such, the genus new *Tyrotama* is described to include *Hersiliola australis*, *H. fragilis*, *Tama arida*, *T. bicava*, *T. incerta* and the new species *T. gamkasiensis*, *T. makaliensis* and *T. taris*. The new genus is based on the following synapomorphies: epigynal plate with an atrium, copulatory openings that open anteriorly of the spermathecae and large hyaline seminal receptacles.

The Afrotropical species, *Hersilia corticola* is closely related to *Neotama* based on the presence of a narrow flexible zone on the metatarsi and a wide copulatory duct. Therefore *H. corticola* were transferred to *Neotama*. Two new species *Prima ansiae* and *P. syda* appear as a separate clade because the following synapomorphic characters: a bifid median apophysis that originate distally on the bulbus, median copulatory openings, an elongate cymbium with an oval alveolus, and a cymbium that narrows abruptly.

The remaining Afrotropical species were placed in a distinct clade based on the possession of a biarticulation on their metatarsi I, II, and IV. This clade appears subdivided into six species groups. *H. baforti* species group which consist of *H. alluaudi*, *H. bubu*, *H. clarki*, *H. dilumen*, *H. ferra*, *H. plara*, *H. salda*, *H. unca*, *H. vanmoli*, *H. woutrinae*. This taxon forms a monophyletic group based on the presence of a basal swelling on the bulbus, an embolus that originate retrolaterally on the bulbus, the presence of a transverse unpigmented area posteriorly on the median plate and a heart mark that broadens posteriorly to form a triangle. The new species *Murricia uva* and the Oriental species *Hersilia jajaj* appear as sister groups based on the sperm duct that has a basal loop and a medial curvature and the possession of smooth seminal receptacles. *Hersilia incompta*, *H. nicolae* and the Oriental species *H. tibialis* form a monophyletic unit due to the presence of a concave and complex median apophysis, a three cornered embolus, the median plate of the epigynum that has ripples laterally and the embolus that originate prolaterally on the bulbus. *H. madagascariensis* and *H. arborea* group together because of a concave median apophysis, the retrolateral origin of the median apophysis and the presence of conspicuous sclerotizations around the copulatory openings. The monophyletic unit consisting of *Hersilia caronae*, *H. insulana*, *H. sigillata* and *H. vinsoni* has the following synapomorphic character: The possession of several small spermathecae basally on a large spermathecae. The remaining species, *Hersilia albicomis*,

H. caudata, *H. occidentalis*, *H. pungwensis*, *H. sericea*, *H. setifons* and *H. tamatavensis* is monophyletic evidenced by the triangular projection distad on the embolus.

Synapomorphies that unite these species groups are more consistent than those that unite all these species it would be preferable to erect a genus for each of these. I do however feel that to erect these genera in the absence of other species groups within *Hersilia*, notably those from the Oriental Region, is premature. Cladistic support for the *Hersilia caudata* and *H. sigillata* species groups is also weak.

The paucity of hersiliid species with biarticulate metatarsi in the Neotropical and Australian Regions except for representatives of *Hersilia* in the far northern parts of Australia, suggest that the group had its origins before the break up of Gondwanaland. The distribution of *Hersilia incompta* and *Hersilia caudata* species groups as well as *Murricia* throughout the Oriental and Afrotropical Region point to the colonisation, presumably repeatedly, of hersiliid species from the Afrotropical Region after the closure of the Thetys sea (Sierwald 1997).

Although some of the species groups in *Hersilia* are supported by several synapomorphies, their basal relationships are uncertain. The monophyly of the genus *Hersilia* is questioned as it is based on weak evidence that includes the possession of glandular parts covered by threads on seminal receptacles. The current classification is, however, retained until a world-wide revision of the family is completed.

Taxonomy

Family Hersiliidae Thorell 1870 (Figs. 4,5)

Herséliensis Simon, 1864: 343 (Lycosiformes, in part)

Hersilioidea Thorell, 1870: 109, 114; Ausserer, 877: 110

Chalinuroidea Thorell, 1873: 605; Kaston, 1938: 640 (Chalinuroidea = Hersiliidae)

Hersilidae Simon, 1874: 14, 15 (*lapsus*)

Hersiliidae Simon, 1882: 255; Lucas, 1869: 1; Simon, 1893: 440; Smithers, 1945: 1;

Benoit, 1967: 1; Baehr & Baehr, 1987: 351; 1993a: 3; Dippenaar-Schoeman & Jocqué, 1997: 181; Levi, 2003: 1; Rheims & Brescovit, 2004: 202; Wunderlich 2004: 814.

Type genus: *Hersilia* Audouin, 1827.

Diagnosis

Three-clawed, ecribelate, entelegyne spiders; posterior lateral spinnerets long, terminal segment tapering, longer than basal segment; legs very long, longest leg at least 1.4× times total body length. Hersiliidae differs from Oecobiidae in the reduced anal tubercle; plumose setae that cover cephalothorax and abdomen; modified claw tufts surrounding tarsal claws (Fig. 3d); 3-5 trichobothria distad on metatarsi.

Description

Size: small to medium (3-13 mm).

Colour: varies from golden brown to white to almost black with mottled appearance

Carapace: ovoid and flattened, as wide as long; narrow longitudinal fovea with three pairs of radiating striae; densely covered with plumose setae. Cephalic region moderately elevated, thoracic region inclined (Chap. 3, Fig. 8c) or raised, higher than thoracic region and thoracic region flattened. Eyes: eight in two strongly recurved rows (Fig. 4); anterior median eyes often largest; lateral eyes on inconspicuous (Chap. 2, Fig. 31c,d) or conspicuous tubercle (Chap. 4, Fig. 2d). Clypeus length variable, short (Chap. 5, Fig. 1d) or very elongate (Chap. 3, Fig. 6d) Chelicerae: unarmed (*Tyrotama Tama*, and *Hersiliola*); armed with three large teeth on promargin and 5-11 minute teeth on retromargin (*Hersilia*, *Murricia*, *Neotama*, and *Prima*); labium free with rounded tip; endites oblique often touching each other. Sternum: heart-shaped, anterior edge straight or slightly convex.

Abdomen: dorsoventrally flattened, with 4-5 distinct dorsal muscular pits (*Hersilia*, *Murricia*, *Neotama*, *Prima*, and *Tama*) (Fig. 4a) or convex with four or less indistinct dorsal muscular pits (*Tyrotama*, *Hersiliola*) (Fig. 4b); abdomen oval to triangular in shape; densely covered with plumose setae (Fig. 3a); respiratory system: two booklungs; tracheal spiracle opening close to spinnerets; anal tubercle small, reduced. Spinnerets: six spinnerets; posterior lateral spinnerets longer than cephalothorax width

(*Hersilia*, *Murricia*, *Neotama*, and *Prima*), shorter than cephalothorax width (*Tyrotama*, *Tama*, and *Hersiliola*); cylindrical with elongated and tapering terminal segment; inner surface with series of long spinules producing the thin silk threads (Figs. 5b,c).

Legs: three claws with modified claw tufts surrounding claws (Fig. 3d); unpaired claw simple with two teeth; paired claws with 5-12 minute teeth, legs very long; leg III shortest; All legs, except leg III with metatarsi uniarticulate (*Tyrotama*, *Hersiliola*, and *Yabisi*), elongate flexible zone distad (*Prima*, *Tama*, *Tamposis* and *Iviraiva*), narrow flexible zone (*Neotama*), biarticulate (*Hersilia* and *Murricia*); 3-5 trichobothria distad on metatarsi; legs with few spines of which scale-like projections covering spine surface (Fig. 3e,g) (*Hersilia*, *Murricia*, *Neotama*, *Prima*), or spines dense, longitudinal grooves dorsally (Fig. 3f) (*Tyrotama*, *Tama*, and *Hersiliola*); autospasy occurs at patella-tibia joint.

Epigyne: Epigynal plate entire (Chap. 2, Fig. 13f) or longitudinally divided into three parts, a median plate and two lateral borders (Chap. 2, Fig. 2f); median plate free (Chap. 2, Fig. 14a) or slightly covered by lateral borders (Chap. 3, Fig. 2f); median plate smooth (Chap. 3, Fig. 2f) with sub-triangular (Chap.2, Fig. 24f), sickle-shaped fixing structures laterally (Chap. 2, Fig. 8f), atrium surrounded by a sclerotized rim (Chap. 3, Fig. 5f) or semicircular pockets (Chap. 2, Fig. 19f). Copulation openings posterior (Chap. 2, Fig. 2g), medial (Chap. 5, Fig. 2g) or anterior (Chap. 3, Fig. 5g); copulatory ducts simple short (Chap. 2, Fig. 2g), simple, elongate, as long as epigynal plate (Chap. 2, Fig. 19e) or coiled (Chap. 3, Fig. 2g). Spermathecae large, hyaline (Chap. 3, Fig. 5g), small sclerotized (Chap. 2, Fig. 2g); spermathecae shape varies from globose (Chap. 2, Fig. 2f), cylindrical (Chap. 2, Fig. 5g; Chap. 4, Fig. 1b) to subtriangular (Chap. 2, Fig. 27g). Seminal receptacles, absent (Chap. 3, Fig. 5g), unique (Chap. 2, Fig. 2g), several and small (Chap. 2, Fig. 8g) several and large (Chap. 4, Fig. 1b); fertilization ducts short, curved (Chap. 2, Fig. 2g) elongate, straight (Chap. 2, Fig. 19e), elongate with medial curve (Chap. 2, Fig. 13g)

Palps: tibiae short as long as patellae, apophysis and modified structures absent; cylindrical (Chap. 2; Fig. 2a,b) or with dorsal projection (Chap. 2, Fig. 19a,b) spines absent (Chap. 2, Fig. 2a,b) or two to seven strong spines present on promargin (Chap. 2, Figs. 19a,b & Fig. 24b); Ventrally with several setae that extends in front of bulbus

(Chap. 2, Fig. 2a). Cymbium covered with short setae; elongate setae laterally extends in front of bulbus (Chap. 2, Fig. 24b; Chap. 5, Fig. 1a); 2-7 strong spines apically; cymbium compact, not projecting much beyond bulbus (Chap. 3, Fig. 5a); apex narrowing abruptly beyond bulbus (Chap. 4, Fig. 1a), digitate, (Chap. 3, Fig. 2a); bulbus, globose (Chap. 3, Fig. 5a), flattened (Chap. 3, Fig. 2a), round (Chap. 2, Fig. 2a) or basally swollen (Chap. 2, Fig. 3a); subtegulum semicircular, sclerotized and entire; tegulum with tegular projection (Chap. 2, Fig. 3a) or basal embolar process that accompanies the embolus (Chap. 2, Fig. 3a & 6a) or slide like tegular projection of varying sizes that accompany embolus often forming a fulcrum in which the embolus lies (Chap. 2, Fig. 26h); embolus stout, hook-shaped (Chap. 3, Fig. 5a), filiform (Chap. 2, Fig. 2a); angular (Chap. 2, Fig. 19a); embolic projections usually absent, when present subapical (Chap. 2, Fig. 26a,c); origin apical (Chap. 2, Fig. 2a), basal (Chap. 3, Fig. 2a), or prolateral (Chap. 2, Fig. 19a); sperm duct regularly curved (Chap. 2, Fig. 2a); repeated curvature (Chap. 3, Fig. 6a); incurved (Chap. 2, Fig. 3a,b); complexly coiled (Chap. 4, Fig. 2a). Median apophysis, if present, hook-shaped, sclerotized, convex, apex acute (Chap. 2, Fig. 2a) (Chap. 2, Fig. 2a), hook-shaped, sclerotized, concave, apex acute with (Chap. 2, Fig. 8a) or without basal projection (Chap. 2, Fig. 16a); or apex truncate (Chap. 2, Fig. 28a,b), complex, sclerotized (Chap. 2, Fig. 19a), bifid (Chap. 5, Fig. 2a); insertion medial (Chap. 2, Fig. 2a) or distal (Chap. 5, Fig. 3a; Chap. 4, Fig. 2a).

Composition. *Hersilia* Audouin, 1826 – 73 species; *Hersiliola* Thorell, 1870 – seven species; *Murricia* Simon, 1882 – 5 species; *Tama* Simon, 1882 – 1 species; *Tamopsis* Baehr & Baehr, 1987 – 49 species; *Neotama* Baehr & Baehr, 1993 – 1 species; *Ypypuera* Rheims & Brescovit, 2004 – three species; *Ivivraiva* Rheims & Brescovit, 2004 – two species; *Yabisi* Rheims & Brescovit, 2004 – two species; *Tyrotama* – nine species; *Prima* – two species.

Distribution. Tropical and subtropical zones worldwide. The genus *Hersilia* from the Palearctic, Afrotropical, Oriental and Australian Regions; *Hersiliola* from the Palearctic and Afrotropical Regions; *Murricia* from the Oriental and Afrotropical Regions; *Prima* from the Afrotropical Region; *Promurricia* from the Oriental Region; *Neotama* from the Oriental and Afrotropical Regions; *Tama* from the Palearctic region;

Tyrotama from the Afrotropical Region; *Ypypuera* and *Iviraiva* from the Neotropical Region; *Yabisi* from the Nearctic and Neotropical Regions.

Phylogenetics. The family Hersiliidae forms a monophyletic unit based on the elongate cylindrical terminal segment of the posterior lateral spinnerets. The presence of tarsal claw tufts, a small anal tubercle, four trichobothria distad on the metatarsi and the presence of feathery hairs that cover most of the body.

Key to the genera of Hersiliidae from the Afrotropical Region

1. Chelicerae unarmed; posterior lateral spinnerets < carapace width; leg IV longest; thoracic region of carapace sloping (Chap.3; Fig. 4c).....2
 - Chelicerae armed; posterior lateral spinnerets > carapace width; leg I or II longest; thoracic region of carapace dorso-ventrally flattened (Chap.3; Fig. 3c).....4

2. Metatarsi with elongate flexible zone in distal third; leg III < 0.4× leg I.....
 -*Tama* (Simon)
 - Metatarsi uniarticulate, leg III > 0.5 times leg I.....3

3. Seminal receptacle, small and sclerotized; bulbus flattened with regularly curved sperm duct; embolus coiled, elongate, filiform; median apophysis hook-shaped (Chap. 3; Fig. 2a,b).....*Hersiliola* (Thorell)
 - Seminal receptacle large, unsclerotized; bulbus globose, sperm duct meandering; embolus short, stout, originate distally on bulbus; tegular apophysis, if present, , short stout distad on bulbus (Chap. 3; Fig. 5a).....*Tyrotama* gen. nov.

4. Metatarsi distally with flexible zone on legs I, II, and IV.....5
 - Metatarsi biarticulate in legs I, II, and IV.....6

5. Distal third of metatarsus I,II, IV flexible.....*Prima* gen. nov.
 - Narrow flexible zone in distal third of metatarsi I, II, and III.....
 -*Neotama* Baehr & Baehr

6. Five pairs of dorsal muscular pits, second pair small, postero-mesad of first pair (Chap. 4; Fig. 2e); abdomen sub-triangular to sub-quadrate; dorsal surface of eye area concave; segment.....*Murricia* Simon
 - Four pairs of dorsal muscular pits; abdomen ovoid to obovate; dorsal surface of eye area convex; distal segment of metatarsi variable in >0.3 and <0.8 times proximal segment.....*Hersilia* Audouin

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Table 1. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by analysis with equal weights (EW), Successive weights (SW and Implied weights (IW) with three values for the Concavity Constant (k).

	MPTs	Steps	CI	RI
EW _u	2	126	59	71
SW _{Nu}	1	126	59	71
IW _u = 1	1	126	59	71
IW _u = 3	1	126	59	71
IW _u = 6	1	126	59	71

<i>Hersilia salda</i>	0 0 1 0 0 0 1 1 1 - - 0 0 0 1 1 0 3 0 0 0 1 0 - - 0 0 0 1 1 0 2 0 1 3 0 1 1 1 0 0 0 0 0 2 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia scopulae</i>	0 0 1 0 0 0 1 0 0 1 1 1 - - - 0 1 1 0 0 0 0 - - - - - - - - - - - - - - - - 1 0 0 0 0 0 0 - 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia sericea</i>	0 0 1 0 0 0 1 0 0 0 1 1 - - - 0 1 1 0 0 0 0 1 0 1 0 0 0 0 2 0 2 0 1 3 0 0 1 1 0 0 0 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia setifrons</i>	0 0 0 0 0 0 1 0 0 0 1 1 - - - 0 1 1 0 0 0 0 1 0 1 0 0 0 0 2 0 2 0 1 3 0 0 1 1 0 0 0 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia sigillata</i>	0 0 0 0 0 0 1 0 0 0 1 1 - - - 0 1 1 0 0 0 0 1 0 1 0 0 0 0 2 0 1 2 0 3 2 0 1 0 1 1 1 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia tamatavensis</i>	0 - - 0 0 0 1 0 0 0 1 1 - - - 0 1 1 0 0 0 0 - - - - - - - - - - - - - - - - 0 0 0 0 0 0 0 - 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia unca</i>	0 - - 0 0 - 0 - - 0 1 0 1 2 0 2 1 0 3 1 1 1 1 0 0 0 0 0 2 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia vanmoli</i>	0 1 0 0 0 0 1 1 1 - - 0 1 0 0 0 0 3 0 0 0 0 0 - - 0 1 0 0 1 0 2 1 0 3 1 1 0 0 0 0 0 0 0 2 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia vinsoni</i>	0 - - 0 0 - 1 0 1 0 0 0 0 2 0 1 1 0 3 2 0 1 1 0 0 0 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>Hersilia woutrinae</i>	0 0 0 0 0 0 1 1 1 - - 0 1 0 0 0 0 3 0 0 0 0 0 - - 0 1 0 0 2 0 2 1 0 3 1 1 1 0 0 0 0 0 0 2 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>(Hersilia tibialis)</i>	0 1 1 0 0 1 1 0 0 4 1 1 - - - 0 0 0 1 2 0 0 1 1 2 0 0 0 0 1 0 2 0 1 3 0 - 1 1 0 0 0 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>(Neotama cunhabebe)</i>	1 0 0 0 1 0 2 0 0 0 1 1 - - - 0 1 2 1 0 0 0 1 0 0 0 0 0 0 2 1 2 1 0 1 1 - 0 0 0 0 0 0 0 0 0 1 1 1 2 1 0 1 1 2 1 1 1 1
<i>(Tamopsis eucalypti)</i>	0 0 0 1 0 0 2 0 0 3 1 1 - - - 0 0 2 1 3 0 0 0 - - 0 0 0 0 0 0 2 1 0 3 0 - 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 1 2 1 1 1 1
<i>(Hersilia jajaj)</i>	0 0 0 0 0 0 5 0 0 - - 1 - - - 0 0 1 1 1 0 0 1 0 0 0 0 0 0 1 0 2 0 0 3 1 1 0 0 0 0 0 0 0 0 0 1 1 1 3 1 0 1 1 2 1 1 1 1
<i>(Tama edwardsi)</i>	0 0 0 0 0 0 0 1 - - 1 - - - 0 0 0 0 0 0 0 0 - - 0 0 0 0 0 0 2 0 0 3 1 - 0 2 0 0 0 1 1 0 0 1 1 0 1 1 1 1 1 1 1 1 0 1 0

List of characters

- 1 tibia/patella male palp
- 2 Palpal tibia: angulate dorsal projection
- 3 Palpal tibia: dorsal spines
- 4 Cymbium and alveolus shape
- 5 Cymbium narrows
- 6 Lamellar modifications
- 7 Sperm duct form
- 8 bulbus: basal swelling
- 9 Median apophysis
- 10 Median apophysis shape
- 11 Median apophysis origin
- 12 Conductor
- 13 Conductor: size
- 14 Conductor, hyaline projection distally
- 15 Conductor with ventral furrow distally
- 16 Sclerotized tegular projection
- 17 lateral tegular projection

- 18 Embolus, position from which embolus originate
- 19 Embolus length
- 20 Embolus shape
- 21 embolus with a triangular projection distally
- 22 Embolus apex
- 23 Epigyne plate
- 24 Median plate: lateral lobes partially covered by lateral borders free;
- 25 median plate form
- 26 Epigynal plate: atrium
- 27 Epigynum medially transverse unpigmented plate
- 28 Copulatory openings position relative to spermathecae
- 29 Copulatory openings sclerotizations
- 30 Length of copulatory duct
- 31 Copulation ducts shape
- 32 Number of spermathecae
- 33 Spermathecae shape
- 34 Spermathecae stalk
- 35 Seminal receptacle number
- 36 seminal receptacle shape
- 37 Position of seminal receptacle relative to spermathecae
- 38 Seminal receptacle borders
- 39 Clypeus length
- 40 ALE/AME
- 41 Interdistance AME-ALE
- 42 Lateral eyes on tubercles
- 43 cheliceral teeth on retromargin
- 44 cheliceral teeth on promargin
- 45 Abdomen: patten on dorsum
- 46 Female abdomen with two pairs of tubercles laterally
- 47 Dorsal muscular pit number
- 48 Relative length of leg III to leg I
- 49 Relative length of leg IV to leg I $>1 <1$
- 50 Metatarsi articulation of leg I, II, and III
- 51 Metatarsus/tarsus
- 52 Leg spine microstructure

- 53 Claw tuft
- 54 Metatarsal trichobothria
- 55 Legs spination, ventral surface
- 56 Feathery hairs
- 57 PLS: tS/bS
- 58 Anal tubercle
- 59 Habit

Appendix 2 Index of species

Chapter 2

Hersilia Audouin, 1826

1. *Hersilia albicomis* Simon, 1887 (Figs. 2, 26a & 33)
2. *Hersilia alluaudi* Berland, 1919 (Figs. 3 & 34)
3. [*Hersilia arborea* Lawrence, 1928](#) (Figs. 4 & 38)
4. [*Hersilia baforti* Benoit, 1967](#) (Figs. 5 & 34)
5. *Hersilia beva* sp. nov. (Figs. 6 & 34)
6. *Hersilia bubi* sp. nov. (Figs. 7 & 34)
7. *Hersilia caudata* Audouin, 1826 (Figs. 9, 26b & 33)
8. [*Hersilia caronae* sp. nov.](#) (Figs. 8, 26g & 35)
9. [*Hersilia clarki* Benoit, 1967](#) (Figs. 10 & 34)
10. *Hersilia dilumen* sp. nov. (Figs. 11 & 34)
11. *Hersilia eloetsensis* sp. nov. (Figs. 12 & 36)
12. *Hersilia ferra* sp. nov. (Figs. 13 & 34)
13. *Hersilia hildebrandti* Karsch, 1878 (Figs. 14 & 38)
14. *Hersilia incompta* Benoit, 1971 (Figs. 15 & 37)
15. *Hersilia insulana* Strand, 1907 (Figs. 16 & 35)
16. [*Hersilia madagascariensis* \(Wunderlich 2004\)](#) (Figs. 17, 26a & 36)
17. *Hersilia moheliensis* sp. nov. (Figs. 18 & 36)
18. *Hersilia nicolae* sp. nov. (Figs. 19 & 38)
19. *Hersilia occidentalis* Simon, 1907 (Figs. 20, 26c & 33)
20. *Hersilia plara* sp. nov. (Figs. 21 & 34)
21. *Hersilia pungwensis* Tucker, 1920 (Figs. 22 & 33)
22. *Hersilia salda* sp. nov. (Figs. 23, 26i & 34)
23. *Hersilia sericea* Pocock, 1898 (Figs. 24, 26d & 33)
24. *Hersilia setifrons* Lawrence, 1928 (Figs. 25, 26e & 33)
25. *Hersilia sigillata* Benoit, 1967 (Figs. 27, 26h & 36)
26. *Hersilia taita* sp. nov. (Figs. 28 & 36)
27. *Hersilia tamatavensis* sp. nov. (Figs. 29a-d & 33)

28. *Hersilia unca* sp. nov. (Figs. 29e-i & 34)
29. *Hersilia vanmoli* Benoit, 1971 (Figs. 30 & 34)
30. *Hersilia vinsonii* Lucas, 1869 (Figs. 31 & 35)
31. *Hersilia woutrinae* sp. nov. (Figs. 32 & 34)

Chapter 3

Hersiliola Thorell, 1870

1. *Hersiliola macullulata* (Dufour, 1831) (Figs 2 & 11)
2. *Hersiliola simonii* (O.P.-Cambridge, 1872) (Figs. 3 & 11)
3. *Hersiliola versicolor* Blackwall, 1865 (Figs. 4 & 11)

Tyrotama gen. nov.

1. *Tyrotama arida* (Smithers, 1945) comb. nov. (Figs. 5 & 12)
2. *Tyrotama australis* (Simon, 1893) comb. nov. (Figs 6 & 12)
3. *Tyrotama bicava* (Smithers 1945) comb. nov. (Figs. 7 & 12)
4. *Tyrotama fragilis* (Lawrence, 1928) comb. nov. (Figs. 8 & 12)
5. *Tyrotama gamkasiensis* sp. nov. (Figs. 9a-e & 12)
6. *Tyrotama incerta* (Tucker, 1920) comb. nov. (Figs. 9f-j & 12)
7. *Tyrotama makalaliensis* sp. nov. (Figs. 10a,b & 12)
8. *Tyrotama taris* sp. nov. (Figs. 10c-g & 12)

Chapter 4

Murricia Simon, 1882

1. *Murricia uva* sp. nov. (Figs. 1 & 3)
2. *Murricia emlynae* sp. nov. (Figs. 2 & 3)

Chapter 5

Neotama Baehr & Baehr, 1993.

1. *Neotama corticola* (Lawrence, 1937) comb. nov. (Figs. 1 & 4)

Prima gen. nov.

1. *Prima ansieae* sp. nov. (Figs. 2 & 4)

2. *Prima syda* sp. nov. (Figs. 3 & 4)

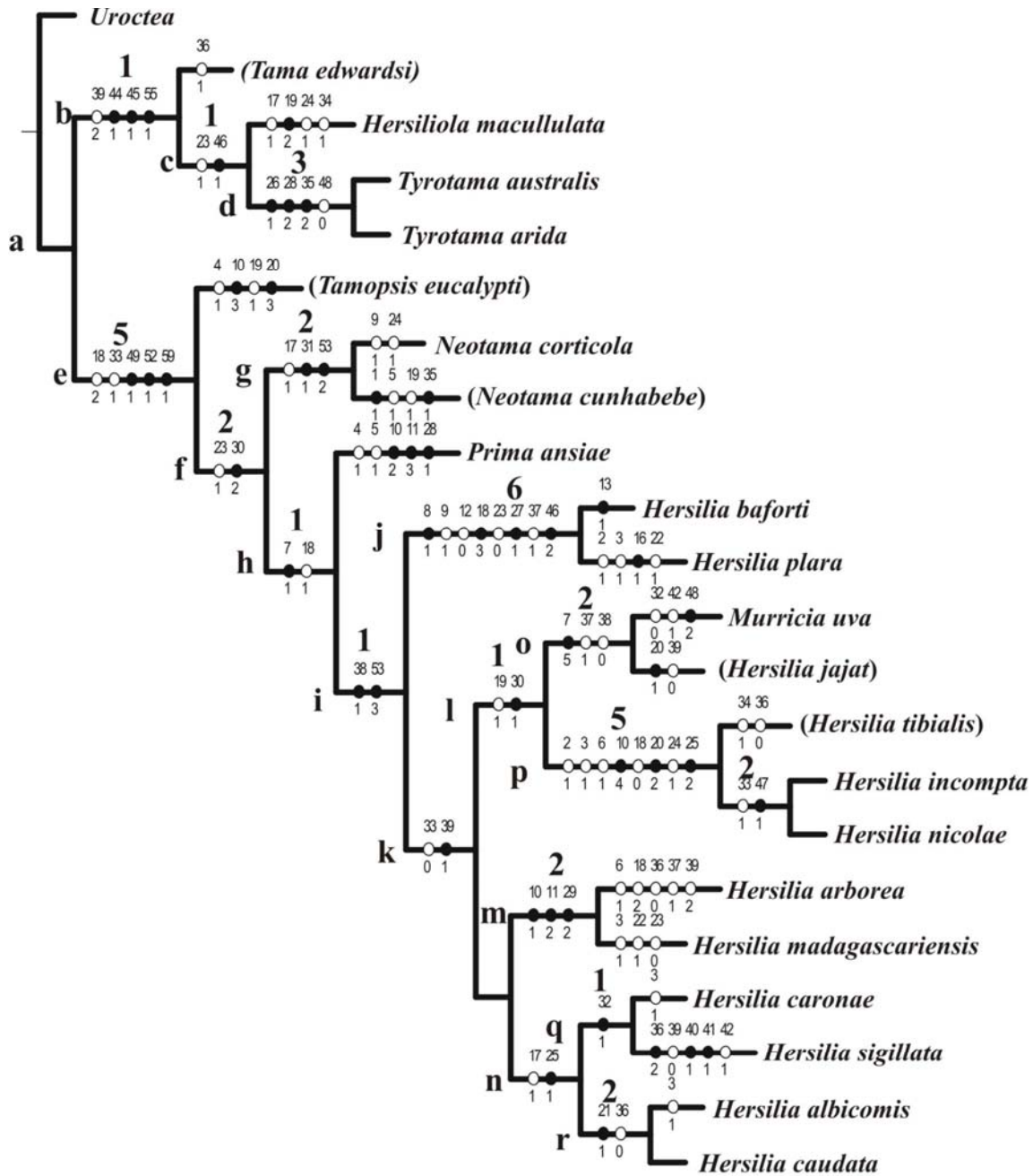


Figure 1. The preferred tree (length 126; CI 55; RI 78) with unambiguous character changes, Bremer support values are above the nodes. Species in parenthesis are not Afrotropical; ● = non-homoplasious characters; ○ = homoplasious characters.

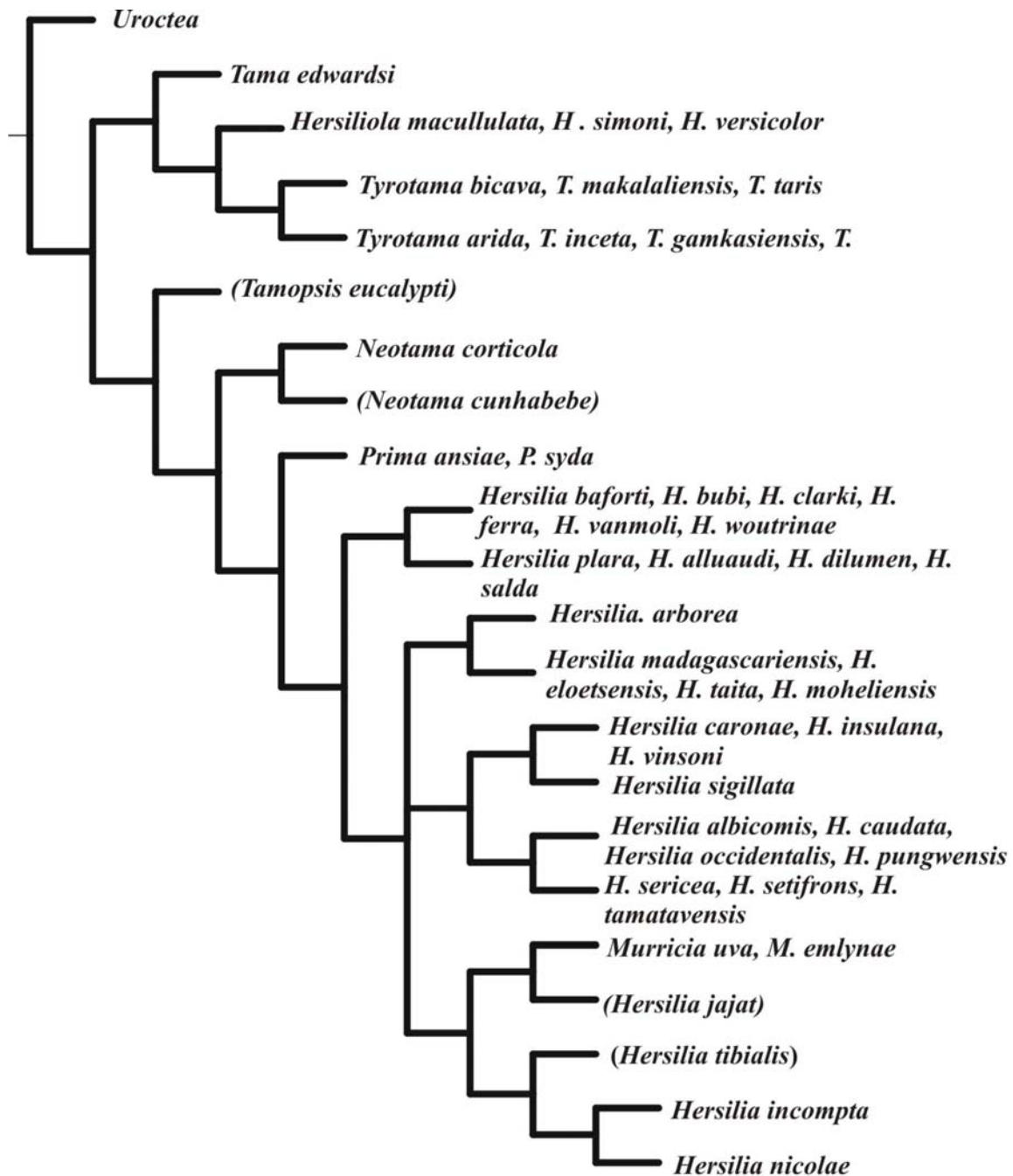


Figure 2. Summary cladogram for all Hersiliidae examined in this study (structure derived from preferred tree, Fig. 1).

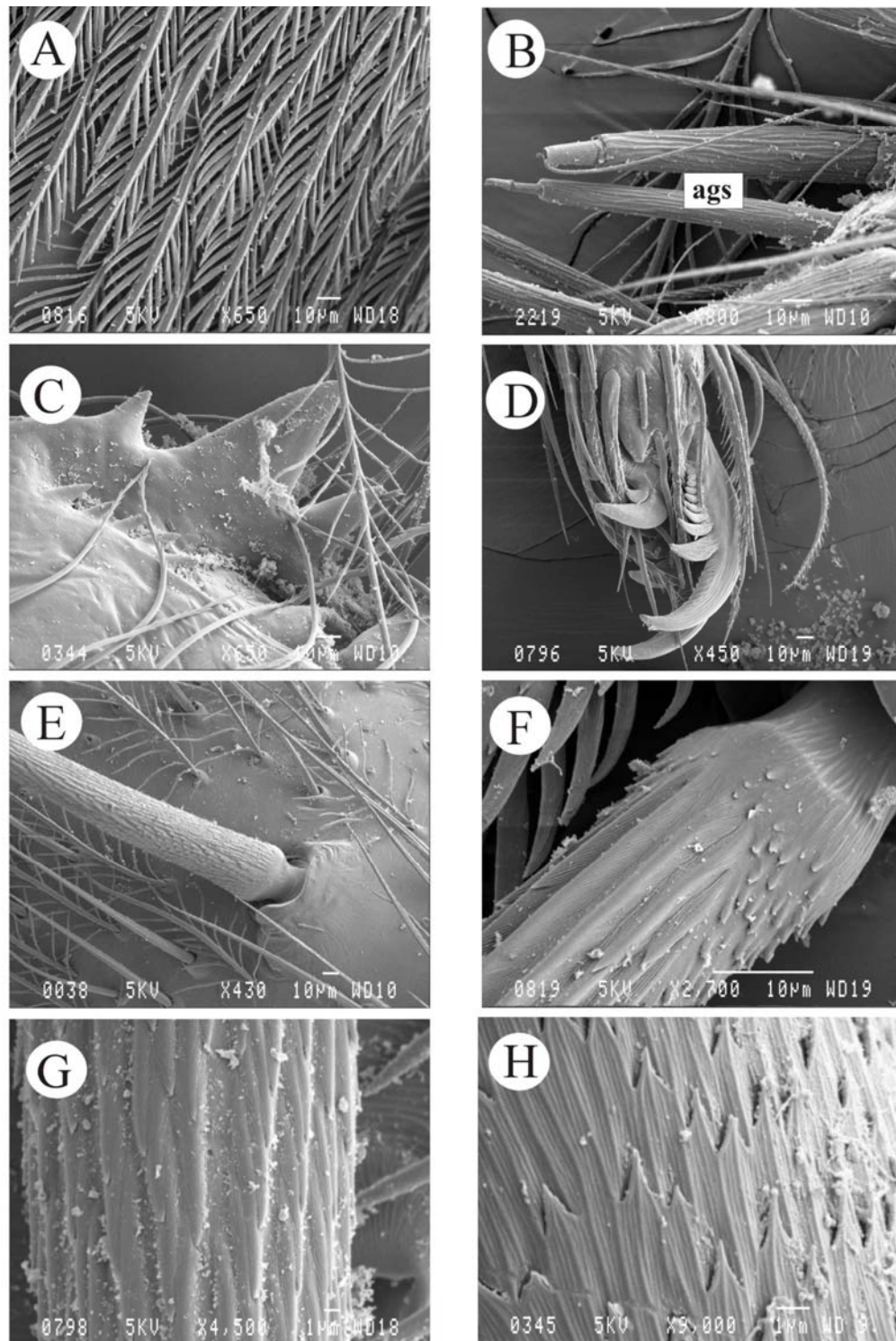


Figure 3. Scanning electron micrographs. *Hersilia sericea* Pocock, **A.** Plumose setae, **B.** posterior lateral spinnerets, ags = aciniform gland spigots, **C.** Cheliceral teeth, **D.** Tarsal claw, **E.** Microstructure on surface of leg spines; *Tyrotama gamkasiensis* sp. n., **F.** Microstructure on surface of leg spines; *Prima ansiae* sp. n., **G.** Microstructure on surface of leg spines; *Uroctea* sp., **H.** Microstructure on surface of leg spines.

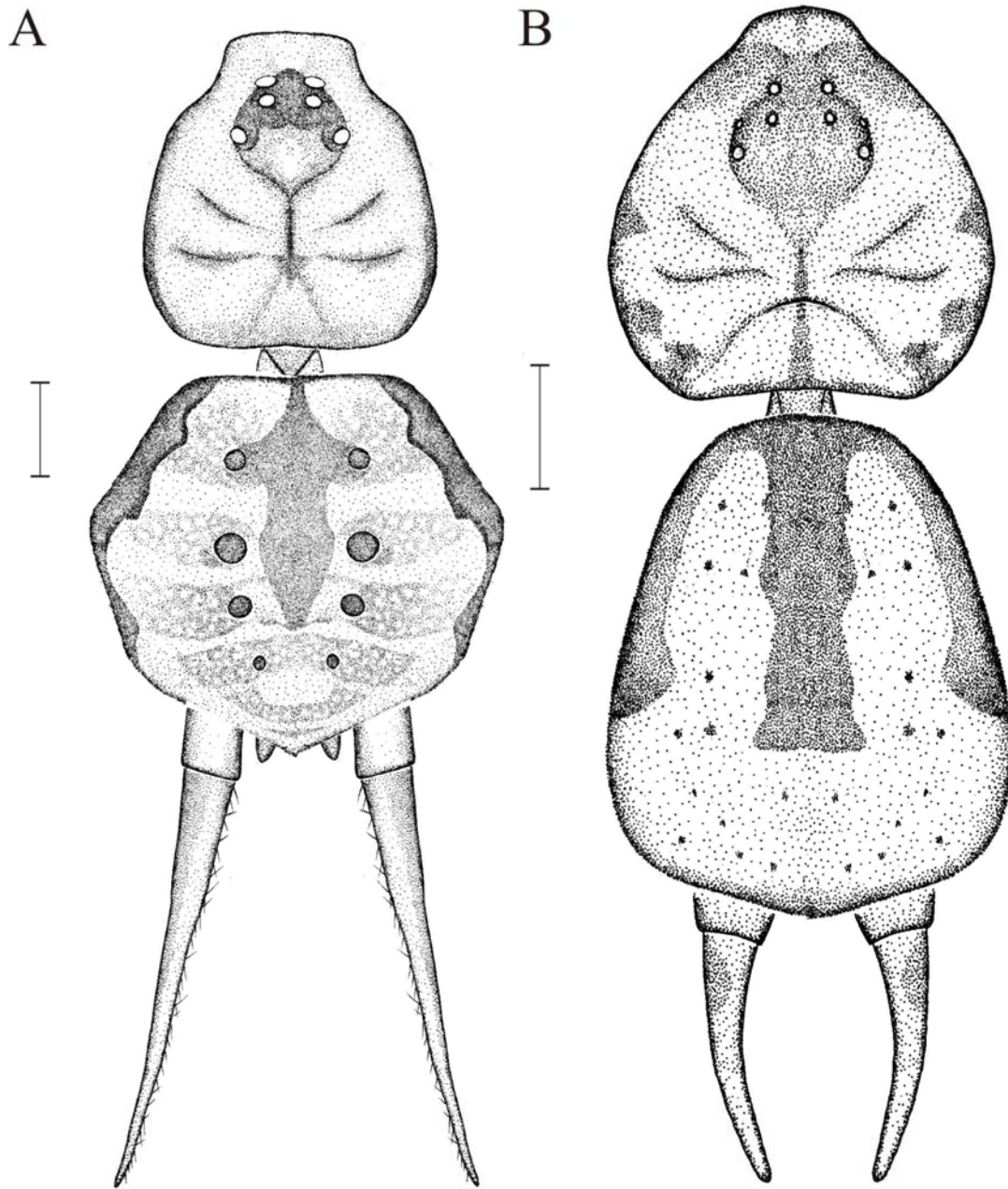


Figure 4. Dorsal view. **A.** *Hersilia caudata* Audouin. **B.** *Tyrotama gamkasiensis* sp. nov.

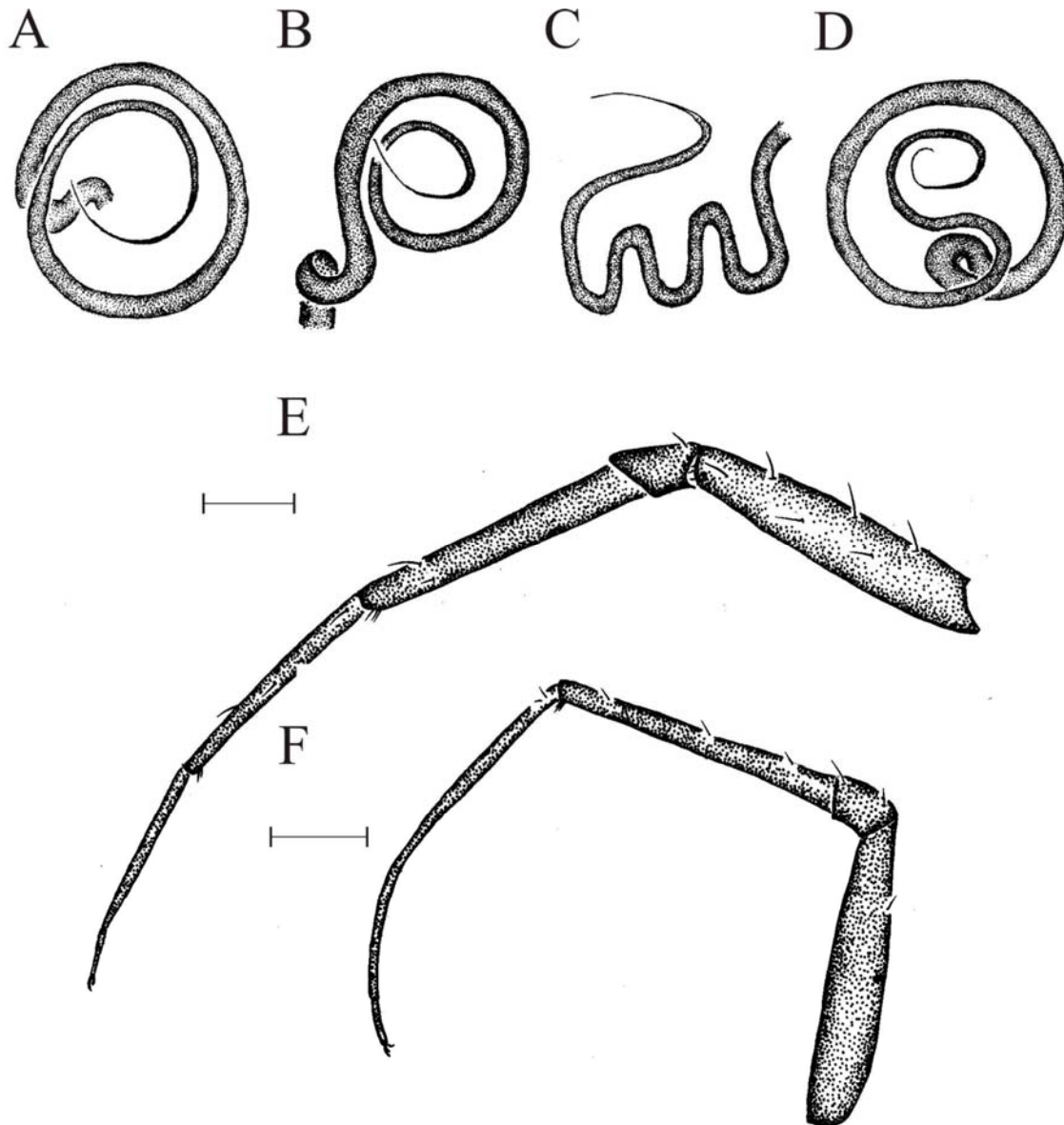


Figure 5. *Hersilia sericea* Pocock, **A.** sperm duct; *Neotama corticola* (Lawrence), **B.** sperm duct; *Tyrotama australis* (Simon), **C.** sperm duct; *Murricia emlynae* sp. nov., **D.** sperm duct; *Hersilia sericea* Pocock, **E.** leg I, lateral view; *Prima ansieae* sp. nov., **F.** leg I, lateral view.