A taxonomic revision of the orb-weaving spider genus *Acusilas* Simon, 1895 (Araneae, Araneidae)

JESPER BIRKEDAL SCHMIDT & NIKOLAJ SCHARFF

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The spider genus *Acusilas* Simon, 1895 (Araneidae) is revised. It includes *Acusilas africanus* Simon, 1895; *Acusilas callidus* sp. n.; *Acusilas coccineus* Simon, 1895; *Acusilas dahoneus* Barrion & Litsinger, 1995; *Acusilas lepidus* (Thorell, 1898); *Acusilas malaccensis* Murphy & Murphy, 1983; *Acusilas spiralis* sp. n.; *Acusilas vei* sp. n.; *Acusilas vilei* sp. n., and one unassigned species of *Acusilas* from Sulawesi for which only females are available. The status of *Acusilas lepidus* (Thorell, 1898) is uncertain and the species is here considered incertae sedis. The unknown male of *Acusilas africanus* Simon, 1895 is described and illustrated for the first time and *Acusilas gentingensis* (Murphy & Murphy) is a synonym of *Acusilas coccineus* Simon, 1895. A phylogenetic analysis of the matrix of Scharff & Coddington (1997) with the addition of *Acusilas coccineus*, suggests sistergroup relationship between *Acusilas* and cyrthophorines (*Cyrthophora* and *Mecynogea*). This knowledge is used to select 6 outgroup taxa for a phylogenetic analysis based on 39 morphological characters scored for the 9 known species of *Acusilas.* The phylogenetic analysis supports the monophyly of *Acusilas*, but ingroup relationships are only weakly supported.

Jesper Birkedal Schmidt and Nikolaj Scharff, Natural History Museum of Denmark, Zoological Museum, University of Copenhagen Universitetsparken 15, DK-2100 Copenhagen, Denmark (golschmidt@gmail.com & nscharff@snm.ku.dk)

Introduction

Acusilas Simon, 1895 is a small orb-weaving spider genus in the family Araneidae. It is mainly distributed in Asia, but also includes a single species in Africa (Platnick 2008). Species are small to medium in size and for those species where the webs are known (Fig. 14) they build regular vertical orb-webs which incorporates a rolled leaf in the center.

Simon erected the genus to accommodate *Acusilas coccineus* and *Acusilas africanus* and placed it in his family Argiopidae (Simon, 1897) within his subfamily Argiopinae (more or less equivalent to the modern Araneidae). *Acusilas* was placed in the tribe Cycloseae (Simon, 1895) together with *Cyclosa* Menge, 1866, *Nemoscolus*, Simon, 1895 and *Salassina* Simon, 1895 (synonymized with *Witica* O. P.-Cambridge, 1895 by Levi 1986) and he later (Simon 1903) added *Deione* Thorell, 1898 and *Nemospiza* Simon, 1903. Simon defined Cycloseae on the basis of the shape of the female cephalothorax, which is divided into a narrow cephalon that is clearly set off from the thorax and clearly demarcated by a dark groove (Fig. 6A: arrow).

Since then one species was added to the genus by Levi (1983) when he excluded *Argiope lepida* Thorell, 1898 from the genus *Argiope* and suggested, that it could be the male of *Acusilas coccineus* (Levi 1983 p. 260). Levi did not formally synonymize the species, but *Argiope lepida* is currently listed as *Acusilas lepidus* (Thorell, 1898) in Platnick (2008). Finally, three new species have been added to the genus from Malaysia (*Acusilas gentingensis* Murphy & Murphy, 1983; *Acusilas malaccensis* Murphy & Murphy, 1983) and from the Philippines (*Acusilas dahoneus* Barrion & Litsinger, 1995) thereby expanding the genus from 3 to 6 species. All species except one (*A. africanus*) are distributed in South East Asia.

The aim of this study is to taxonomically revise the genus *Acusilas*, including descriptions of four new species, a key to all species, a species level phylogeny and phylogenetic placement of the genus within the family Araneidae.

Materials and methods

Measurements, drawings and observations were done with a WILD M3Z stereo microscope equipped with a scale reticule and a camera lucida. All morphological measurements are given in millimeters and measurements follow the format of Grasshoff (1968). Leg formulas (e.g. 1423) are given for the relative leg lengths (thus 1423 means, first pair of legs longest, followed by fourth pairs, followed by second pair, and third pair shortest). Photographs were taken with a Nikon DXM1200F camera attached to a Leica MZ16A stereomicroscope and edited with the software package Auto-Montage Pro. A JEOL JSM-840 scanning electron microscope (SEM) was used to study and photograph morphological structures. These structures were first excised and transferred to a vial with 70% ethanol and then cleaned ultrasonically for 1–2 min. The specimen was then transferred to absolute ethanol and left overnight. After critical point drying, the specimens were glued to rounded aluminum rivets or Cambridge stubs using an acetone solution of polyvinyl resin (Paraloid B72) or Carbon sticky tabs and then coated with a 120 nm layer of platinum/palladium for examination in the SEM. Expansions of male pedipalps were done by immersion in a KOH solution for five to ten minutes and subsequent transfer to distilled water. If expansion did not occur, or pedipalps only expanded partly, the treatment was repeated until the pedipalp was fully expanded. Expanded pedipalps were then transferred back to 70% ethanol for observation. Female genitalia were excised using surgical blades or sharpened needles. The detailed morphology of the female genitalia was subsequently studied in methyl salicylate, following the method of Holm (1979). The internal female genitalia were also studied, after excised genitalia had been placed in KOH or Subtilisin A (enzyme) to digest unsclerotized parts of the genitalia. The enzyme solution was prepared by dissolving eye lens cleaner tablets in distilled water (half a tablet to 1 ml distilled water). Terminology for the genitalia follows Levi (1983) for females and Scharff & Coddington (1997) for males. The following anatomical abbreviations are used in the text and figures.

Abbreviations

Somatic morphology

ACd	=	Anterior cheliceral condyle
ALE	=	Anterior lateral eyes
AME	=	Anterior median eyes
AME-AME	=	Distance between AME
AME-ALE	=	Distance between AME and ALE
ALE-PLE	=	Distance between ALE and PLE
AOQ	=	Width of anterior ocular quadrangle (sensu Grasshoff 1968, fig. 1)
Con	=	Concavity
MF	=	Median furrow
MR	=	Mesal rim
PCd	=	Posterior cheliceral condyle
PER	=	Width of posterior eye row
PLE	=	posterior lateral eyes
PLE-PME	=	Distance between PLE and PME
PME	=	Posterior median eyes
PME-PME	=	Distance between PME
POQ	=	Width of posterior ocular quadrangle (sensu Grasshoff 1968, fig. 1)
Sw	=	Swelling

Male genitalia

C	=	Conductor
Cym	=	Cymbium
DH	=	Distal haematodocha
Em	=	Embolus
EmT	=	Embolic tip
EmTh	=	Embolic thorn
MA	=	Median apophysis
Mz	=	Membraneous zone
pp	=	Pars pendula
p	=	Pedipalp
Ra	=	Radix
Sas	=	Small angular sclerite
SD	=	Sperm duct
St	=	Stipes
StO	=	Stipeal outgrowth
StE	=	Stipeal extension
Te	=	Tegulum
Th	=	Thorn
Tr	=	Truncus

Female genitalia

AB	=	Anterior bulge
AR	=	Anterior rim
Br	=	Brace shaped
CD	=	Copulatory duct
CDO	=	Copulatory duct opening
D	=	Depression
FD	=	Fertilization duct
PL	=	Posterior lip
PP	=	Posterior plate
Se	=	Septum
Sp	=	Spermathecae

Spinnerets

ALS	=	Anterior lateral spinnerets
PLS	=	Posterior lateral spinnerets

PMS = Posterior median spinnerets
Ac = Aciniform spigots
Ag = Aggregate spigots
Cy = Cylindriform spigots
Fl = Flagelliform spigots
MAP = Major ampullate spigot
mAP = Minor ampullate spigot
nub = Nubbin
Tr = Triad

Phylogenetic analysis

The mesal orientation of the male pedipalpal cymbium, the presence of a radix and the presence of a narrow tapetum in the posterior median eyes clearly place *Acusilas* in the family Araneidae, but the phylogenetic placement within the family is less obvious. In order to test the generic placement of *Acusilas* we used the published data matrix of Scharff & Coddington (1997), which included 57 araneid genera and 13 genera from 8 outgroup families, scored for 82 morphological and behavioral characters. To this matrix we added data for *Acusilas coccineus* Simon, 1895 (Appendix 1), the type species of the genus *Acusilas*. Thus the matrix we analyzed had 71 taxa and 82 characters. We decided to use the original data matrix of Scharff & Coddington (1997) instead of more recent versions of this matrix generated by authors who wanted to test the placement of other araneid genera (Tanikawa 2000 – *Zilla* C. L. Koch, 1834; Kuntner 2002 – *Perilla* Thorell, 1895; Kuntner & Hormiga 2002 – *Singafrotypa* Benoit, 1962; Smith 2005 – *Cyphalonotus* Simon, 1895, *Ideocaira* Simon, 1903, *Micropoltys* Kulczyński, 1911& *Poltys* C. L. Koch, 1843) and who also used the original data matrix of Scharff & Coddington, but without adding any extra characters. Scharff & Coddington (1997) had already shown that adding taxa to this particular dataset without additional characters would result in large numbers of trees with little or no resolution. Scharff & Coddington found 16 trees of length 282 for their 70 taxa whereas Smith (2005) found 948 trees and almost no resolution when she added 4 araneid genera to the matrix. Since we just wanted to test the generic placement of *Acusilas* in order to select an outgroup for a more detailed phylogenetic analysis, in which we also test the monophyly of *Acusilas*, we decided to add only the type species of *Acusilas* to the matrix of Scharff & Coddington. For the species phylogeny, we constructed a new matrix including 39 new and old characters (Appendix 3) and included all species of *Acusilas.* This phylogenetic analysis was designed to test the monophyly of *Acusilas* and to reconstruct the phylogeny of the nine species. Outgroup selection was guided by the result of the first analysis, where *Acusilas* was added to the data matrix of Scharff & Coddington (1997) but also included representatives of other major clades within Araneidae. See Appendix 4 for a complete list of specimens used for the species phylogeny.

The parsimony analyses were performed using the computer programs TNT version 1.1 (Goloboff, Farris & Nixon 2003) and PAUP*4.0 (Swofford 2001). Mesquite version 2.0 (Maddison & Maddison 2007) was used to build and edit the character matrix and MacClade 4 (Maddison & Maddison 2001) was used to study character optimizations on the cladograms. Ambiguous character optimizations were usually resolved so as to favour reversals or seconday loss over convergence (ACCTRAN optimization). If not, the optimization scheme is discussed in the text. Multistate characters (11 in the matrix of Scharff & Coddington and 4 in the current *Acusilas* matrix) were treated as non-additive (unordered). TNT was used to calculate branch support.

Results

Phylogenetic analysis. – Heuristic searches ("traditional search") in TNT under equal weights, using collapsing "rule 3" (tree collapsing = max. length 0; collapsing branches with no possible support), 700 replications and holding 700 trees during each replication (using TBR swapping algorithm), resulted in 16 minimal length trees of 284 steps for the large matrix with 71 taxa and 82 characters. Shortest length trees were only found in 163 times out of 700 replications, so we tried to broaden the search to include more replication and to hold more trees per replications. Various combinations from 20 replications holding 25.000 trees (where the same 16 shortest trees are found 15 out of 20 times) to 25.000 replications holding 20 trees per replication resulted in the same 16 trees of length 284. The strict concensus tree is shown in Fig. 1. The consensus is fully resolved for the argiopoid clade and rather unresolved for the araneine clade. All trees have *Acusilas* nested within the argiopoid clade and always as sister to cyrthophorines (*Cyrthophora* Simon, 1864 and *Mecynogea* Simon, 1903) (Fig. 1: arrow). Two characters were found to support this sistergroup rela-

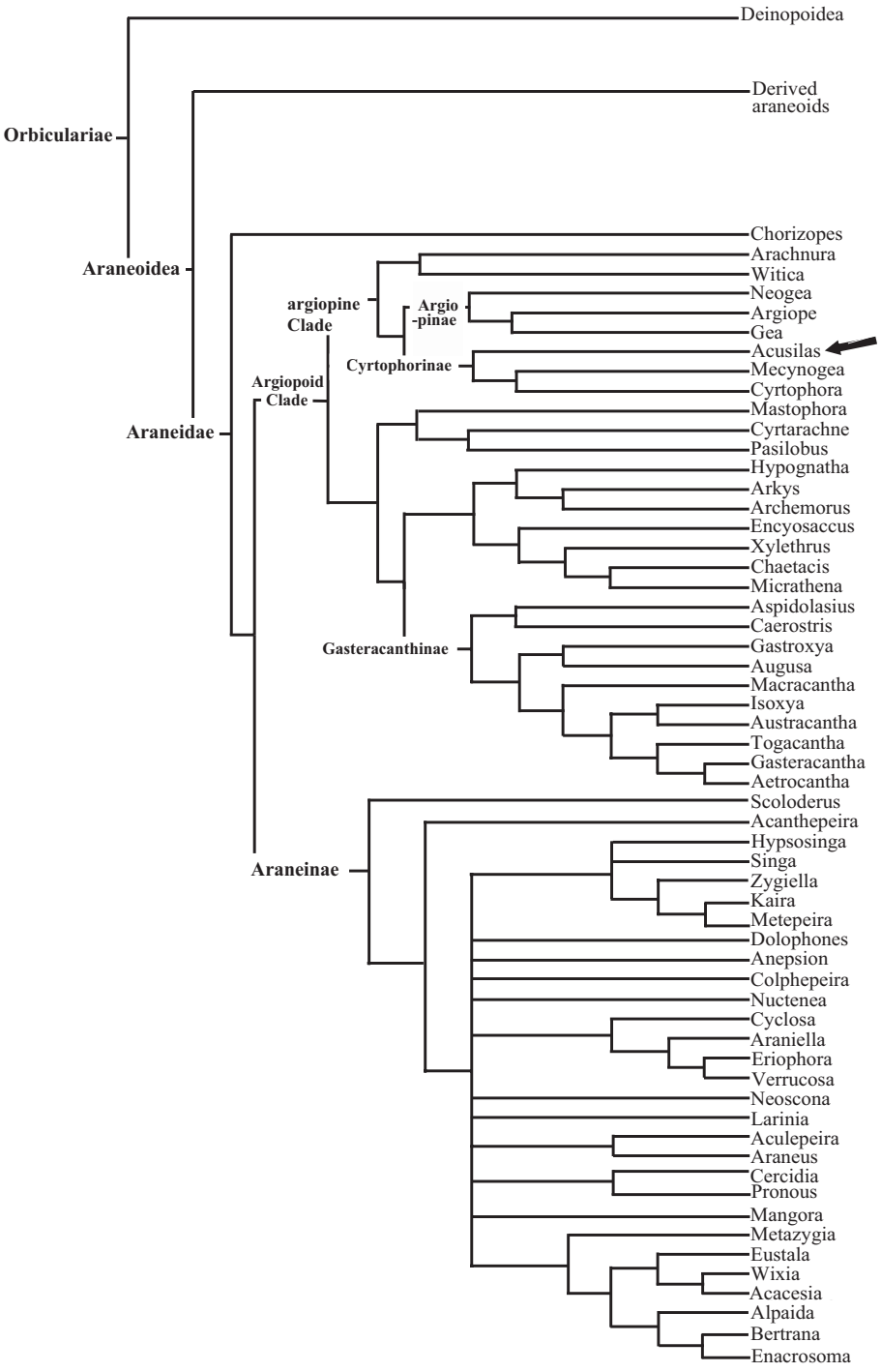

Fig. 1. Strict consensus cladogram of the 16 minimal length trees of 284 steps found by TNT when analyzing the datamatrix of Scharff and Coddington (1997) with the addition of *Acusilas coccineus*. Arrow points to *Acusilas*.

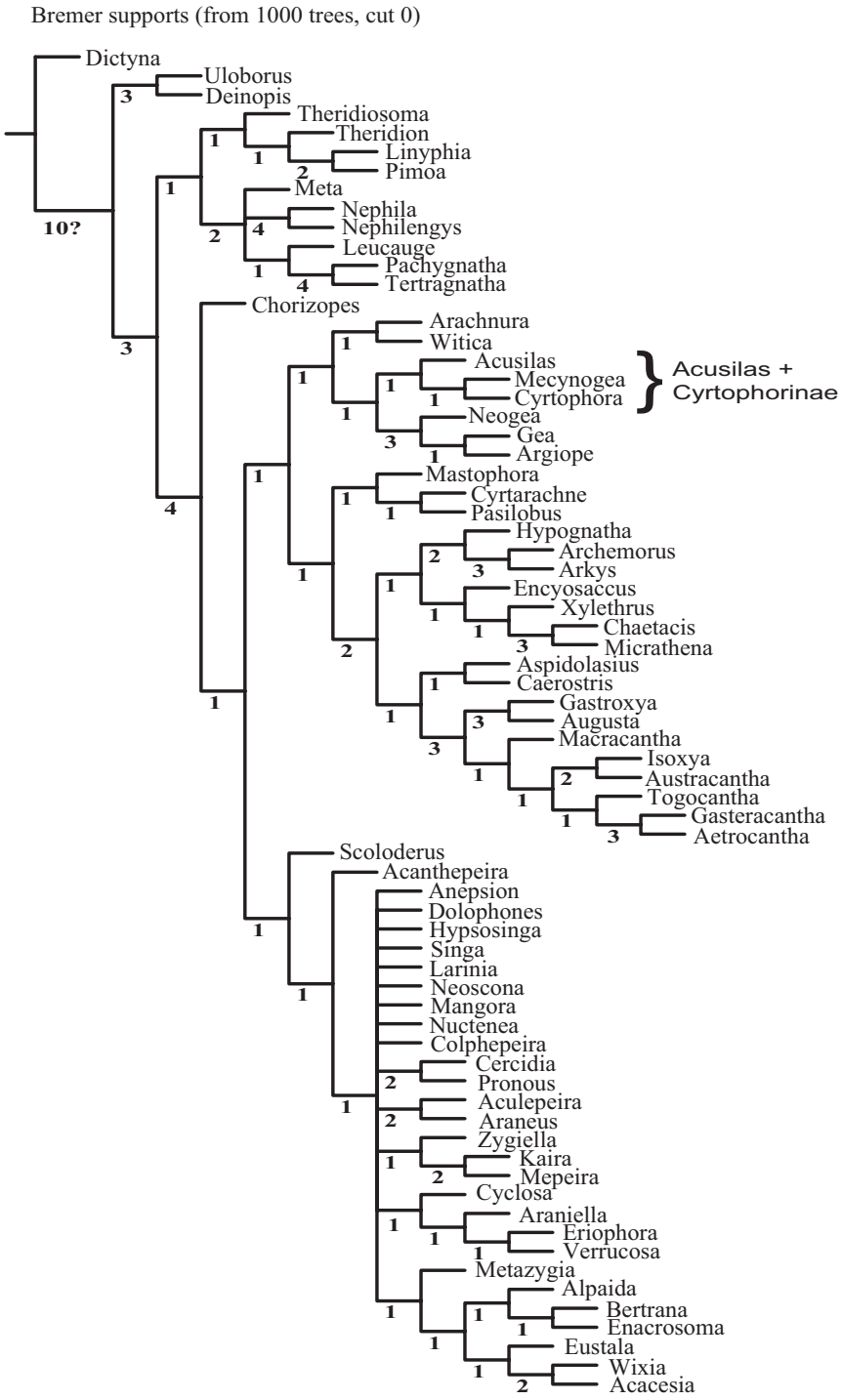

Fig. 2. Strict consensus cladogram with Bremer support values.

tionship ("embolus running in an anticlockwise direction" and "median ocular area narrower in front than behind"), but none of these characters are unique to this group of genera, since they also occur in genera that are not directly related to *Acusilas* or the cyrtophorines. The anticlockwise embolus is also found in *Witica* and *Zygiella* F. O. P.-Cambridge, 1902 (considered to belong to the subfamily Araneinae) and a "median ocular area narrower in front than behind" is also found in *Arachnura* Vinson, 1863, *Hypognatha* Guérin, 1839 and *Encyosaccus* Simon, 1895 and several araneines, such as *Singa* C. L. Koch, 1836, *Zygiella*, *Kaira* O. P.-Cambridge, 1889 and *Metepeira* F. O. P.-Cambridge, 1903 (Scharff and Coddington 1997). The bremer support value for the sistergroup relationship between *Acusilas* and cyrtophorines is only 1 (Fig. 2). The same 16 trees were found with PAUP using heuristic methods, equal weights and random addition sequence (1000 replications) holding 100 trees per replication. When the 16 tree solution set was filtered for compatible but polytomous topologies (using the "Do not retain a nonbinary tree if a more highly resolved but compatible tree exists" in the "Filter Trees/New Filter" menu of PAUP), 8 trees resulted (all of which had on trichotomy in the higher araneines). Implied weighting in TNT, which weights the characters according to a concave function of homoplasy (Goloboff 1993), using 'k' values of 1, 3 and 6, and the same search parameters as given above for the TNT analysis with equal weights, resulted in many more trees and less resolution (51.225 trees for k=6, 4.875 trees for k=1, and 7.800 trees for k=3), but *Acusilas* is still sister to cyrthophorines in all analyses. In the more resolved analysis based on equal weights, *Acusilas* is nested within the argiopine clade (Fig. 1) and we therefore decided to include several representatives from the argiopine clade as outgroups for a species level phylogeny of *Acusilas*. The genera *Gasteracantha* Sundevall, 1833 and *Araneus* Clerck, 1758 were also added as additional, more remote outgroups to *Acusilas*. The final species phylogeny matrix included nine species of *Acusilas* in the ingroup and representatives of six other araneid genera in the outgroup. The exemplars used for the species level phylogeny is given in Appendix 4 and the list of characters and their description is given in Appendix 3. The species phylogeny matrix was small enough to allow exact solutions via "implicit enumeration" in TNT, but other than that, search parameters were the same as for the larger dataset mentioned above. Analyses with equal weights resulted in 7 trees of length 77 and a strict consensus with a monophyletic *Acusilas* (Fig. 3A). Except for a polytomy involving *A. callidus*, *A. coccineus*, *A. dahoneus* and *A. spiralis*, the consensus tree is fully resolved. All trees have the unassigned *Acusilas* as the most basal species, sister to all other *Acusilas* species (Fig. 3A). Analyses with implied weights, using 'k' values of 1, 3 and 6, resulted in 40 trees, 7 trees and 7 trees respectively, all very similar to the trees found under equal weights. The 7 trees found under k=6 are exactly the same as those found with equal weights and the tree lengths is also 77. The 7 trees found under k=3 is one step longer (78), and except for a different placement of the unassigned *Acusilas* (here as sister to *Acusilas malaccensis* – Fig. 3B), it is identical to the 7 trees found under equal weights. The 40 trees found under k=1 agree with all the other analyses, but there is little resolution within *Acusilas* and the tree length is 81. Jackknife supports for the various clades found with implied weights (k=3) and equal weights are shown in Fig. 3C and D. Support values for most clades are very low.

Discussion

Phylogeny. – Using the data matrix of Scharff & Coddington (1997) we have been able to place the genus *Acusilas* within the family Araneidae. Unfortunately, the relationship suggested is only weakly supported (Fig. 2), so when we use this analysis to select possible outgroups for the species level phylogeny (Appendix 2), this obviously involve uncertainties. We see no other objective way to select outgroups for a species level phylogeny. *Acusilas* monophyly is supported by two male characters: the presence of two cheliceral condyles (character 2; Fig. 4) and endites provided with characteristic concavities (character 3; Fig. 5). No good female synapomorphies are known. As for the species level phylogeny, there is only little difference between the results of equal weighted analyses and those using implied weights (Fig. 3), but implied weights give higher support values for the various clades. We included representatives of the two different male size categories of *Acusilas coccineus*, in order to test species delimitations, but the results are inconclusive as both representatives (*A. coccineus*T and *A. coccineus*J) are placed in a polytomy.

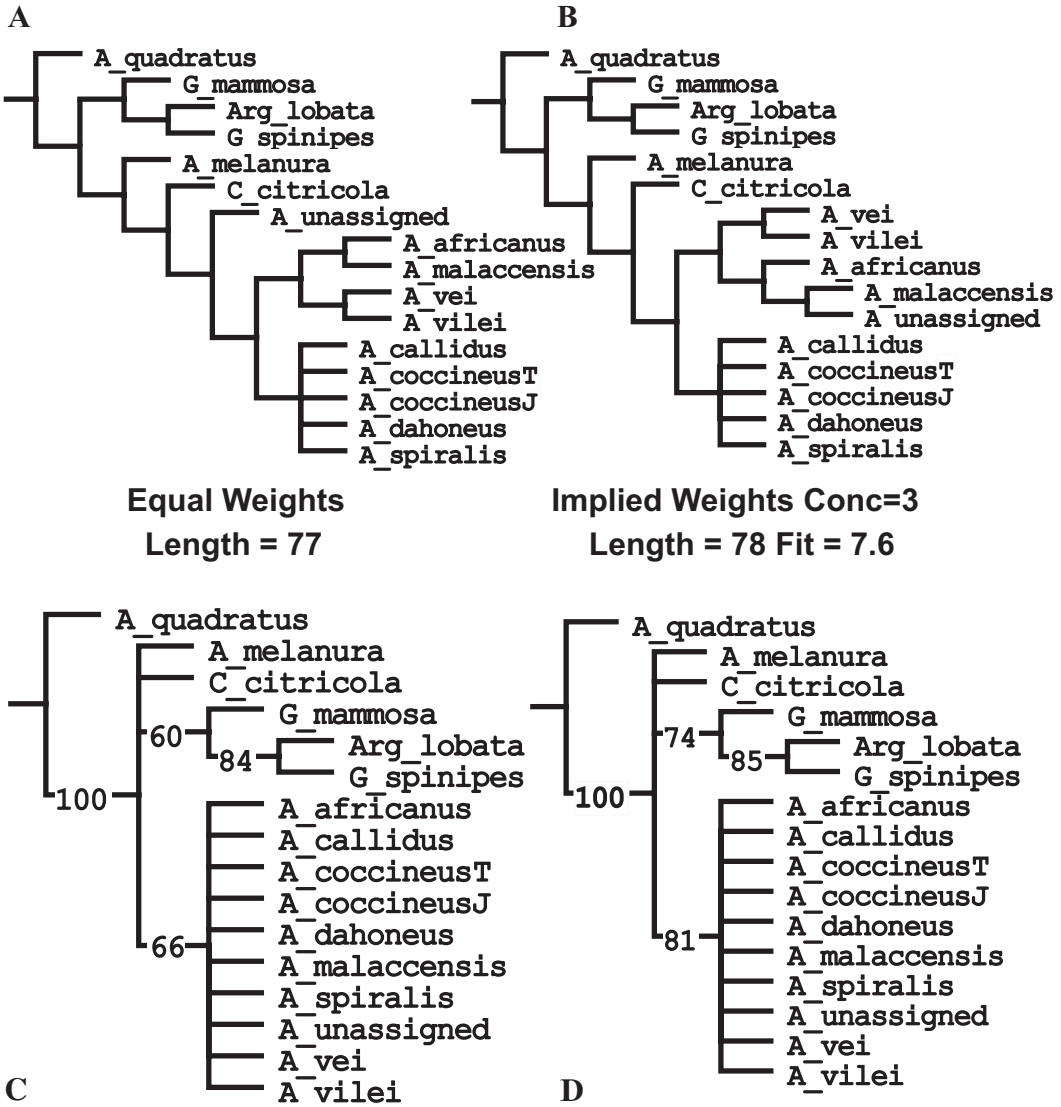

Fig. 3. A) Strict consensus cladogram of the 7 minimal length trees of 77 steps found by TNT (equal weights) when analyzing the data matrix presented in Appendix 2, B) Strict consensus cladogram of the 7 minimal length trees of 78 steps (fit=7.6) found by TNT (implied weights k=3) when analyzing the data matrix presented in Appendix 2, C) Jackknife support values (1000 replicates, cutoff=50, p=36) for the analysis presented in Fig 3A, D) Jackknife support values (1000 replicates, cutoff=50, p=36) for the analysis presented in Fig 3B.

Taxonomy

Genus *Acusilas* Simon, 1895

Acusilas Simon, 1895: 780-785, fig. 849; Murphy & Murphy, 1983: 115-116. Barrion & Litsinger 1995: 584.

Type species. – *Acusilas coccineus* Simon, 1895: 785 (by original designation).

Diagnosis. – *Acusilas* males differ from other araneid males by the presence of two condyles on the chelicerae (pro- and retrolateral)(Fig. 4) and by the presence of unique concavities on the endites

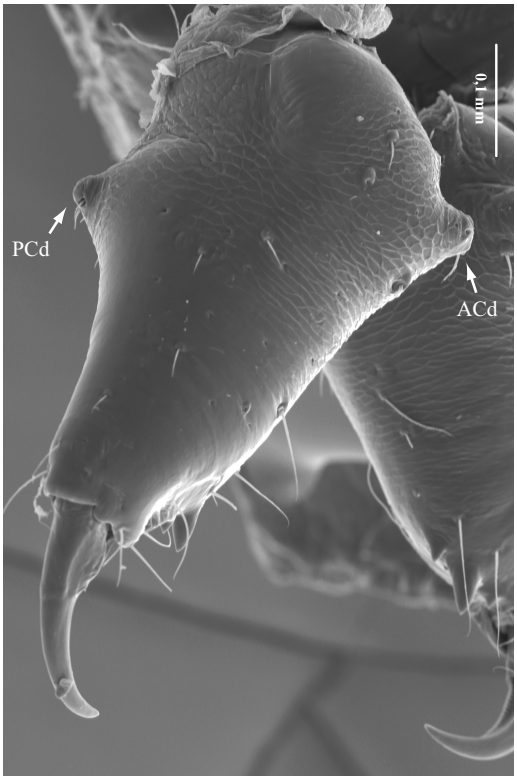

Fig. 4. Male chelicerae (*Acusilas malaccensis*, right chelicera, lateral view), (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP 2003). ACd, Anterior Condyle; PCd, Posterior Condyle.

(Fig. 5). Females with narrow "head" (cephalon), clearly demarcated by a prominent groove between thorax and cephalon, and AME closer to ALE than to each other (Fig. 6A). The narrow, clearly demarcated head is also found in *Cyclosa* and *Witica*, but none of these have AME close to ALE. The latter is also found in *Manogea* Levi, 1997 and *Mecynogea*, but none of these genera have narrow, clearly demarcated heads. Furthermore, the posterior eye row is procurved in *Manogea* and *Mecynogea* whereas it is strongly recurved in *Acusilas* (Fig. 6A).

Description. – Small to medium sized-spiders. Females 5.50-14.00, males 2.00-6.50. Female leg formula 1423, (except *A. callidus* sp. n. with 1243). Male leg formula 1243. Female cephalothorax with deep cephalic groove and narrow "head" (cephalon) (Fig. 6A). Chelicerae with 4 prolateral and 3 retrolateral teeth. Anterior and posterior eye rows recurved. Distance between ALE and AME shorter than distance between AME's. Female abdomen longer than wide, extending beyond spinnerets. Epigyne similar to that of *Argiope*, but weakly sclerotized, more or less transparent. Without scape and usually with small anterior bulge (Fig. 7A: AB) and a characteristic transverse rim (Fig. 7A-B: AR). Often with concavity/pocket between rim and bulge (Fig. 7A: Con) and septum (Figs 7A-B: Se) that separates two depressions (Fig. 7A: D) leading into the cop-

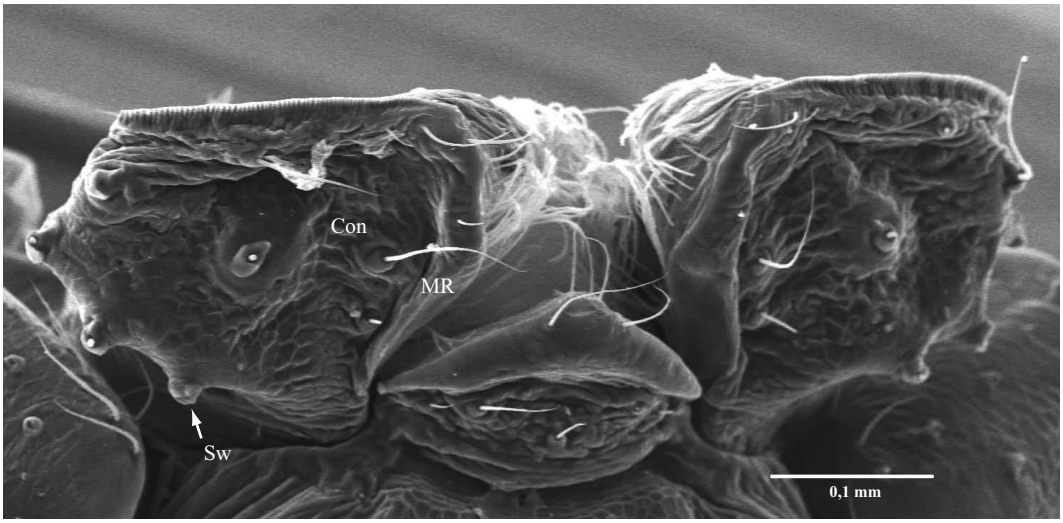

Fig. 5. Male endites (*Acusilas malaccensis*, ventral view), (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP 2003). Con, Concavity; MR, Mesal Rim; Sw, Swelling

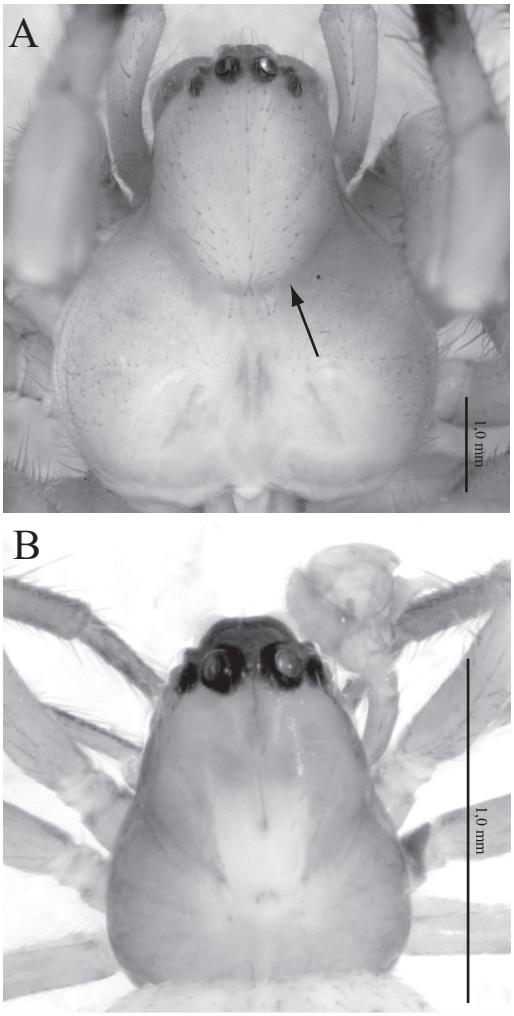

Fig. 6. Cephalothorax (*Acusilas malaccensis*) dorsal view. A) Female. Arrow points to cephalic groove. B) Male. (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP 2003 (ZMUC)).

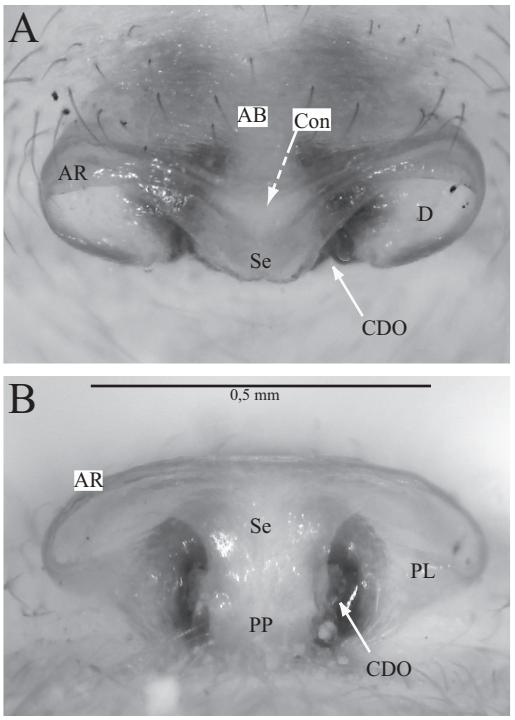

Fig. 7. Epigyne (*Acusilas coccineus*). A) Ventral view. B) Posterior view (Japan, Iriomotejima Is., Funaura 1992 (ZMUC)). AB, Anterior Bulge; AR, Anterior Rim; CDO, Copulatory Duct Opening; Con, Concavity; D, Depression; PL, Posterior Lip; PP, Posterior Plate; Se, Septum.

ulatory duct openings (Fig. 7A: CDO). Septum is connected to the rim anteriorly, and widens into a posterior plate posteriorly (Fig. 7B: PP). The copulatory duct openings are situated on each side of the posterior plate within the depressions. The ducts are broad at the openings, then narrows gradually towards the two oval spermathecae (Fig. 8A). The fertilization ducts leaves the spermathecae close to where the copulatory ducts enters the spermathecae (Fig. 8B: FD; Fig. 16C: FD) and the whole system is therefore a functional cul-de-sac type (Uhl 2002). The females of *A. africanus* (Fig. 9,17A) and *A. malaccensis* (Fig. 8) almost always carry broken-off emboli in their copulatory ducts. These could act as mating plugs, but they do not necessarily prevent a second male from trying to mate (Fig. 9), but only one set of emboli seems to reach the spermathecae. Embolic mating plugs may also be found in the in other *Acusilas* species, but so far, we have only observed them in *A. africanus* and *A. malaccensis*. The spinnerets of *Acusilas* females are typical for the family Araneidae (Scharff & Coddington 1997, Yu and Coddington 1990) (Fig. 10) and thus rather conservative and consistent with the araneiod groundplan. ALS with multiple piriform spigots (Pi) distributed uniformly across the tip and with a single major ampullate spigot (MAP) and a small nubbin at the mesal margin (Fig. 10B). PLS with multiple aciniform

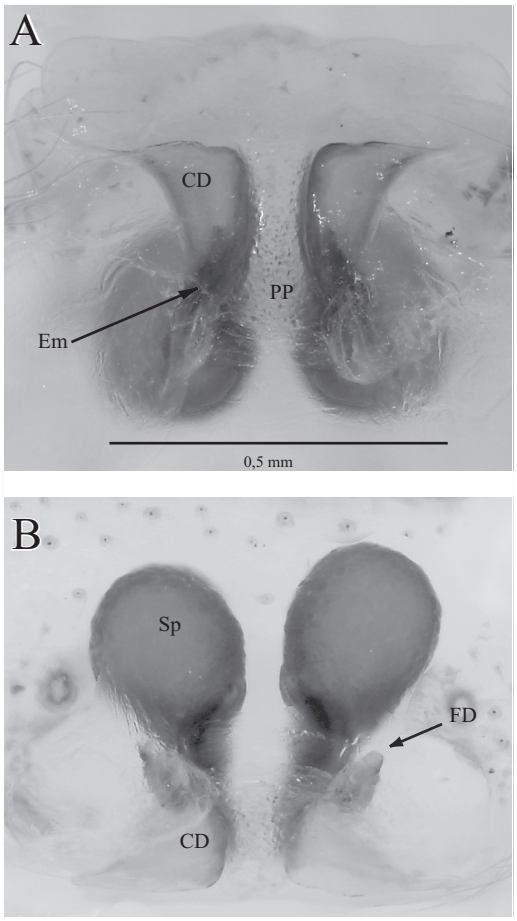

Fig. 8. Vulva (*Acusilas malaccensis*). A) Posterior view. B) Dorsal view (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP. 2003 (ZMUC)). CD, Copulatory Duct; FD, Fertilization Duct; Em, Embolus; PP, Posterior Plate; Sp, Spermatheca.

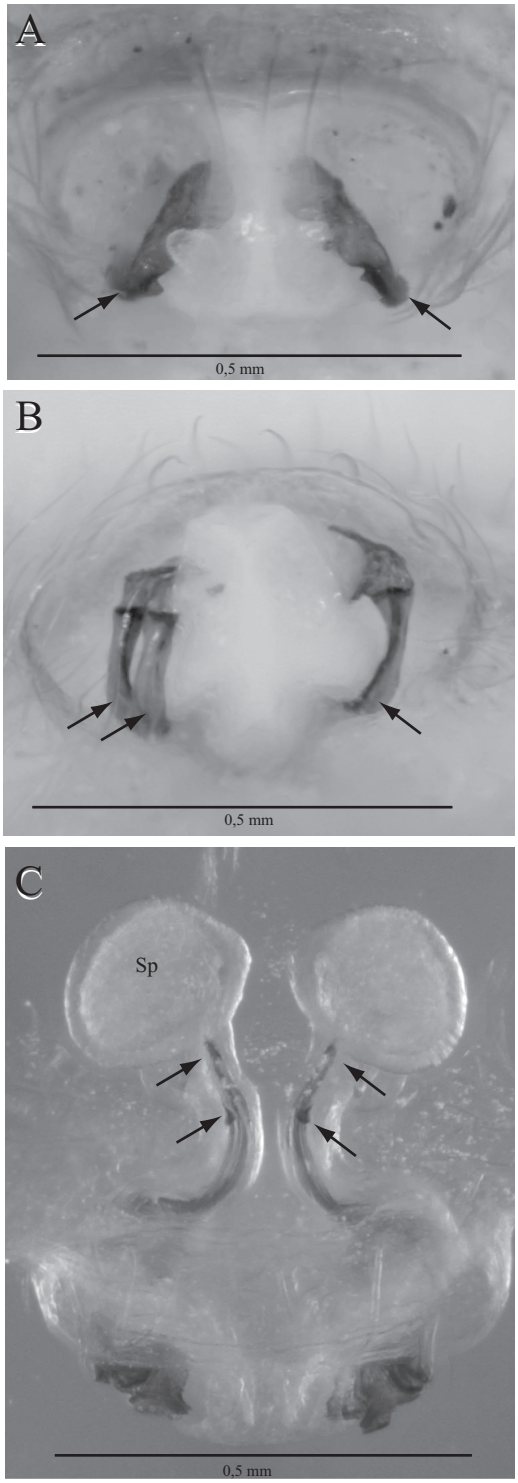

Fig. 9. Broken-off emboli (*Acusilas africanus*). A). Ventral view of epigyne with an embolus (arrow) in each copulatory duct (Cameroon 1891, Y. Sjöstedt leg., 6♀♀ (NHRS)). B). Posterior view of epigyne with two emboli (arrows) in the right copulatory duct and one embolus (arrow) in the left (Congo, Komi, 6. ii. 1930, J. Ghesquière leg. (MRAC)). C). Dorsal view of vulva with two emboli in each copulatory duct. Notice how the embolic tips (arrows) of only one of the emboli in each copulatory duct are able to reach the spermatheca (Congo, Komi, 27. i. 1930. J. Ghesquière leg. (MRAC)). Sp, Spermatheca.

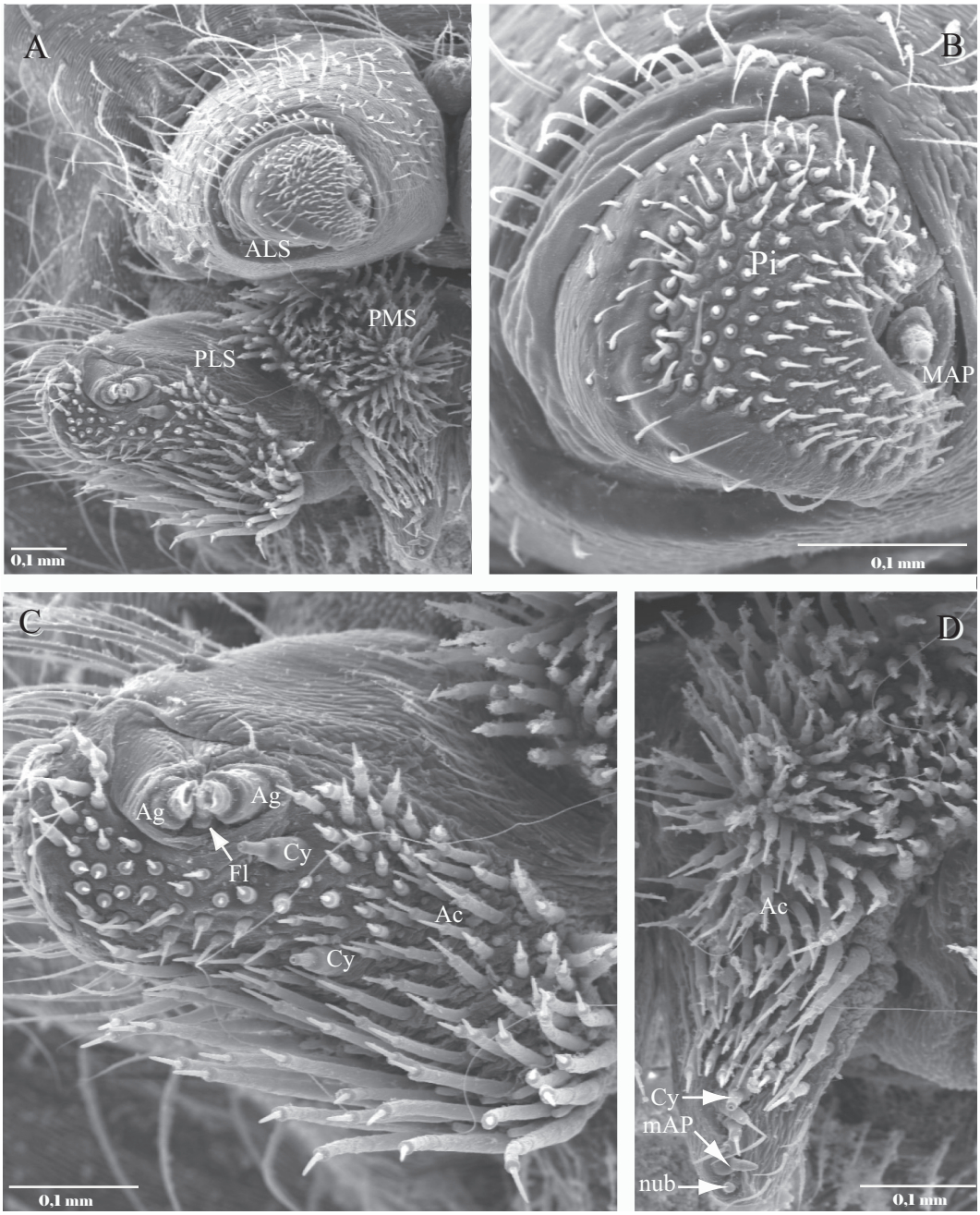

Fig. 10. Spinnerets of female, ventral view (*Acusilas coccineus*). A) Overview. B) ALS, Anterior Lateral Spinnerets, nubbin not visible in this view. C) PLS, Posterior Lateral Spinnerets. D). PMS, Posterior Median Spinnerets. (Singapore: Ubin Island, 1991 (ZMUC)). Ac, Aciniform spigots; Ag, Aggregate spigots; Cy, Cylindriform spigot; Fl, Flagelliform spigot; MAP, Major Ampullate spigot; mAP, minor Ampullate spigots; nub, nubbin; Pi, Piriform spigots.

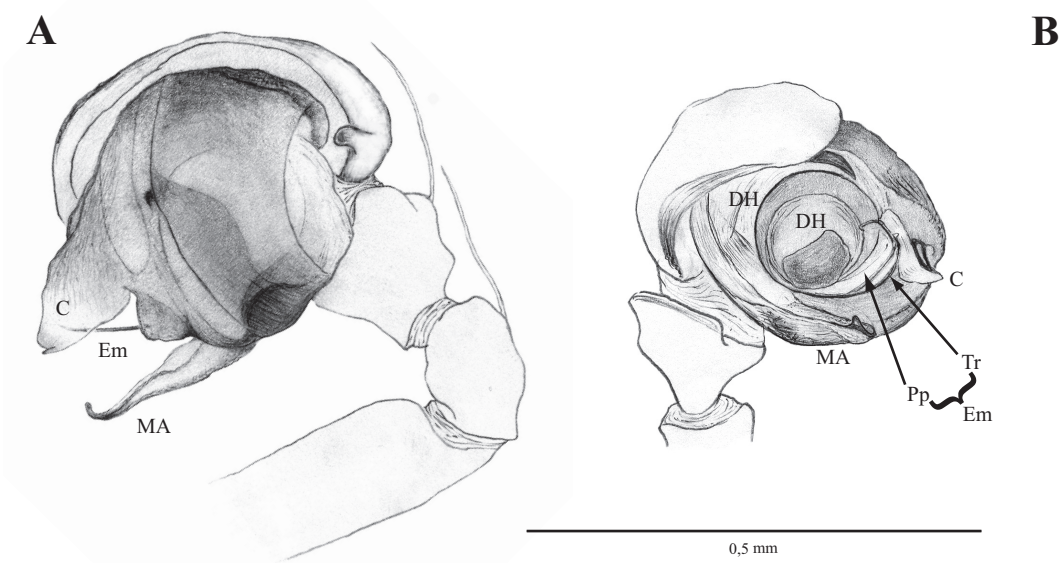

Fig. 11. Male pedipalp (*Acusilas coccineus*, left pedipalp). A) Lateral view. B) Postero-ventral view (Indonesia: Java, Cibodas NP 1986 (RMNH)). C, Conductor; DH, Distal Haematodocha; Em, Embolus; MA, Median Apophysis; PP, Pars Pendula; Tr, Truncus.

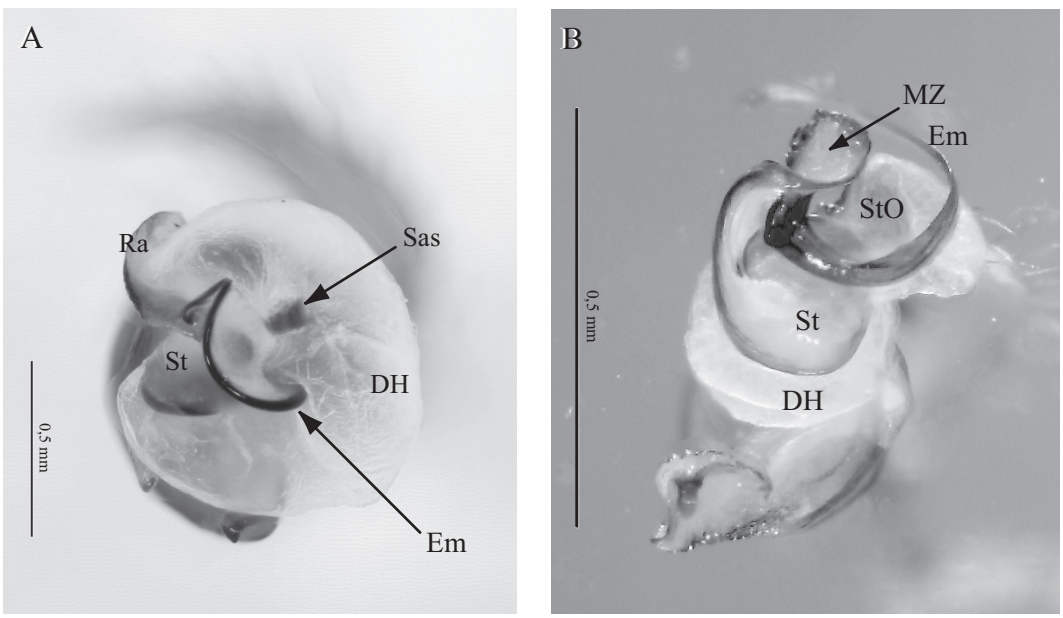

Fig. 12. Expanded pedipalps (dorsal view). A) *Acusilas coccineus* (Japan: Iriomotejima Is., Takana 2000 (ZMUC)). B) *Acusilas africanus* (Tanzania: Tanga, E. Usambara Mts. 1995 (ZMUC)). DH, Distal Haematodocha; Em, Embolus; MZ, Membranous Zone; Ra, Radix; Sas, Small angular sclerite; St, Stipes. StO, Stipeal Outgrowth.

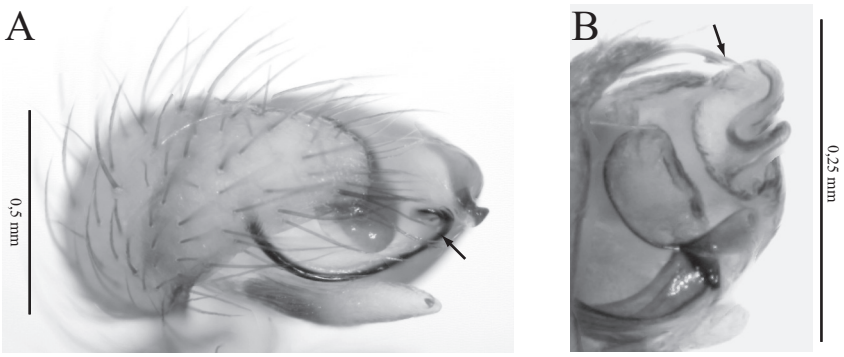

Fig.13. Curvature of embolus. A) Embolus (arrow) anti clock-wise (*Acusilas coccineus*, left pedipalp in postero-ventral view) (Japan: Iriomotejima Is., Takana 2000 (ZMUC)). B) Embolus (arrow) clock-wise in *Acusilas africanus* (left pedipalp in ventral view) (Tanzania: Tanga, E. Usambara Mts. 1995 (ZMUC)).

spigots (Ac), two cylindrical spigots (Cy) on the mesal margin and a triad consisting of a single flagelliform spigot (Fl) and two aggregate spigots (Ag) on the anterolateral margin (Fig. 10C). PMS with multiple aciniform spigots (Ac) covering the anterior surface of the spinnerets, one cylindrical spigot (Cy) protruding between the aciniforms, a minor ampullate gland spigot (mAP) and a nubbin at the tip of the PMS (Fig. 10D).

Males usually much smaller than females (approx. one fifth the length of the females), but males of *A. coccineus* from the northern part of its distribution range (China, Japan and Korea) are larger (Fig. 21). Cephalothorax of males without narrow head and cephalic groove. Eye pattern as in female (Fig. 6B). Chelicerae with two condyles (anterior and posterior; Fig. 4: PCd & ACd), 4 prolateral teeth and no retrolateral teeth, except in the large specimens of *A. coccineus*. Endites with characteristic ventral concavities (Fig. 5: Con). Concavities delimited by a mesal margin (Fig. 5: MR) and setae with swollen bases on the lateral margin of the endites (Fig. 5: Sw).

Tegulum of pedipalp carries a median apophysis (MA), a conductor (C) and an embolic division (ED). The latter consist of radix (R), stipes (S) and embolus (E) and a huge haematodocha (only visible in the expanded palp). The conductor is fused to the tegulum (t) and carries a small distal lobe or hook (Figs 11A, 16D, 19D, 20A, 25D, 26A). The median apophysis (MA) is slender, triangular and with distal hook or hood (Figs 11B, 13A, 19E, 20B, 30A, 34). Embolic division dominated by a huge haematodocha that reach from tegulum attachment point to embolus tip. Radix is attached to the tegulum via a membrane that seems to be part of the larger haematodocha and forms the wall of one side of the haematodocha (Fig 12A). It connects to a small inconspicuous sclerite distally, which itself is articulated with the embolus distally (Fig. 12A). Inside the haematodocha runs the sperm duct from the ED insertion point on the tegulum to the tip of the embolus. The small sclerite in between radix and embolus is homologized with the stipes. In *Acusilas*, stipes and radix are not tubes, in which the sperm duct runs (like in *Eriophora*) but rather a simple "brace" close to which the sperm duct runs, so that it has the brace-like stipes and radix on one side and the hematodocha on the other side. Some species, like *A. africanus,* has a distal outgrowth on the brace-like stipes (Fig. 12B: StO), whereas other species, like *A. coccineus* has a tiny separate sclerite in the same place Fig. 12A: Sas). This could be the distal outgrowth of the stipes that has become separate, or it could be a terminal apophysis of the distal hematodocha. Embolus (E) is of the spiral type (*sensu* Comstock 1910) (Figs 9, 11B, 17B, 19E, 25E, 30B) thus including a sclerotized truncus and a membraneous pars pendula. The latter is transparent in *A. coccineus* and *A. spiralis* sp. n., and pigmented in *A. malaccensis* and *A. africanus*. Pars pendula is absent from the apical part of the embolus in *A. vilei* and *A. vei* sp. nov. (Fig. 32 & 34A). The membrane separating embolus from stipes is easily seen in *A. malaccensis*, *A. africanus* and *A. vilei*. It constitutes a breaking point and broken off emboli have been found in

Fig. 14. Orb-web of *Acusilas coccineus*. A) The retreat in the free sector of the top half of the web. Notice the close proximity of the web to ground level. B) Close-up of hub, showing the opening of the retreat by the presence of the spider here. Arrows point to the attachment points of the capture spiral thread to the radii. (Photos: Fernando Alvarez, Thailand 2003).

the female copulatory ducts of *A. africanus* (Figs 9, 17A) and *A. malaccensis* (Fig. 8A). The embolus is running in an anti-clockwise direction (Fig. 13A), except in *A. africanus* where it is clockwise (Fig. 13B).

Composition. – *Acusilas* includes nine species: *Acusilas africanus* Simon, 1895 (Africa); *Acusilas callidus* sp. n. (type locality, Indonesia); *Acusilas coccineus* Simon, 1895 (Asia); *Acusilas dahoneus* Barrion & Litsinger, 1995 (type locality, Philippines); *Acusilas lepidus* (Thorell, 1898) (type locality, Burma); *Acusilas malaccensis* Murphy & Murphy, 1983 (Asia); *Acusilas spiralis* sp. n. (type locality, Indonesia); *Acusilas vei* sp. n. (type locality, Indonesia) and *Acusilas vilei* sp. n. (type locality, Indonesia).

Distribution. – All species, except *A. africanus* are Asian and most species are still only known from a single or few localities. Six of the nine species are from Indonesia and the most widespread species is *A. coccineus*, which can be found from India (M. Kuntner pers. comm) and Sri Lanka in the west to Papua New Guinea in the east (Murphy & Murphy 1983) and from Japan in the north (Yaginuma 1986) to Indonesia in the south.

Natural History. – *Acusilas* has only been collected from primary and secondary rain forest habitats. Females of *Acusilas coccineus* make vertical orb webs approximately 30 by 30 cm. The retreat is a curled leaf placed in the middle of the upper part of the web and opening at the hub. The sectors are open on each side of the retreat, i.e. without the spiral capture thread (Fig. 14A). The webs are placed approximately 50 cm above ground level. Similar webs have been described for *A. malaccensis* and *A. dahoneus* (Murphy & Murphy 1983, Barrion & Litsinger 1995). The webs of other species are unknown. Similar extensions of the abdomen are found in *Hingstepeira* Levi, 1995, *Milonia* Thorell, 1890, and *Perilla* Thorell, 1895 and the abdominal shape could perhaps be a leaf-roller adaptation (Kuntner & Hormiga 2002). Like *Acusilas*, these genera create and use a rolled leaf or rolled grass stems as a retreat in the web.

Key to the species of the genus *Acusilas*

Females

1. Abdomen triangular-like; truncated anteriorly and pointed posteriorly (Fig. 15A)..... 2
Abdominal oval or round 3
2. Abdominal folium white w. black crossbars. Fresh specimens orange (Fig. 24A).. *A. malaccensis*
Abdominal folium w. four lobes anteriorly ..... *A. africanus*
3. Transverse rim of epigyne with finger-like projection (Fig. 28A)..... *A. callidus* sp. n.
Transverse rim of epigyne strait, without finger-like projection 4
4. Septum of epigyne wider anteriorly than posteriorly (Fig. 19A)..... *A. coccineus*
Septum of epigyne wider posteriorly than anteriorly, of equal width, or as wide as epigyne..... 5
5. Septum of epigyne as wide as epigyne (total width), and with posterior margin brace--shaped (Fig. 23)..... *A. dahoneus*
Epigyne with median furrow (Fig. 36A: MF). Septum bipartite and forming two lateral pockets (Fig. 36A: Se) ..... Unassigned *Acusilas* females

Males

1. Stipes-embolus fused 2
Stipes-embolus membranous 3
2. Stipes-embolus forming a spiral, describing approximately two turns (Fig. 30B) *spiralis* sp. nov. Embolic tip bent backwards at conductor interface. Stipes-embolus describing max. 1.5 turns (Fig. 19E)..... *coccineus*
3. Cymbium dark brown, bulb light brown and conductor bifid (Figs 15B and 16D) .... *A. africanus*
Stipes with distal thorn-like extension, embolus with proximal thorn and tip of embolus arrow-shaped (Figs 25D – F).
If embolus is absent, look for the distal thorn-like extension on stipes (Fig. 26: StE)..... ..... *A. malaccensis*
Embolus distally without pars pendula and tip bifid (Fig. 32)..... *A. vei* sp. nov.
Embolus distally without pars pendula and tip pointed (Fig. 34)..... *A. vilei* sp. nov.

Acusilas africanus Simon, 1895

(Figs 9 and 15-17)

Acusilas africanus Simon, 1895: 785, fig. 849; Murphy & Murphy 1983: 119, figs. 7-8; Dippenaar-Schoeman & Wassenaar 2006: 68 (Table 2).

Type material. – The female holotype is from Sierra Leone, Africa, and should be deposited in MNHN. However, the collection there only included a single specimen from Gabon (C. Rollard pers. com.). The type status of this specimens is therefore uncertain, but most probably not the type material.

Other material examined. – **Cameroon:** 1891, Y. Sjöstedt leg., 6♀♀ (NHRS); Olounou, N 02°49', E

Fig. 15. Habitus of *Acusilas africanus*. A) Female (Tanzania, Tanga region, E. Usambara 1995 (ZMUC)). B) Male (Tanzania, East Usambara Mts., Dodwe Stream, 1980, (ZMUC)).

12˚08', 11.-19. ix.1971, F. Puylaert leg., 2♀♀ (MRAC); Kitta, 1891, Y. Sjöstedt leg., 4♀♀ (NHRS); **Gabon:** 1♀ (MNHN); **Democratic Republic Congo:** Komi, S 03˚23', E 23˚46', i-iii.1930, J. Ghesquière leg., 10♀♀ (MRAC); Kasei, Sankury, Komi, 6.ii.1930, J. Ghesquière leg., 2♀♀ (SMF); Bambesa, N 03˚28', E 25˚43', xi.1933, J. Leroy leg., 1♀ (MRAC); Eala, N 00˚03', E 18˚19', iii.1936, J. Ghesquière leg., 1♀ (MRAC); Bendera Katanga, terr. d'Albertville, S 05˚03', E 28˚54', ix.1958, litter from gallery forest, 1000 m, N.

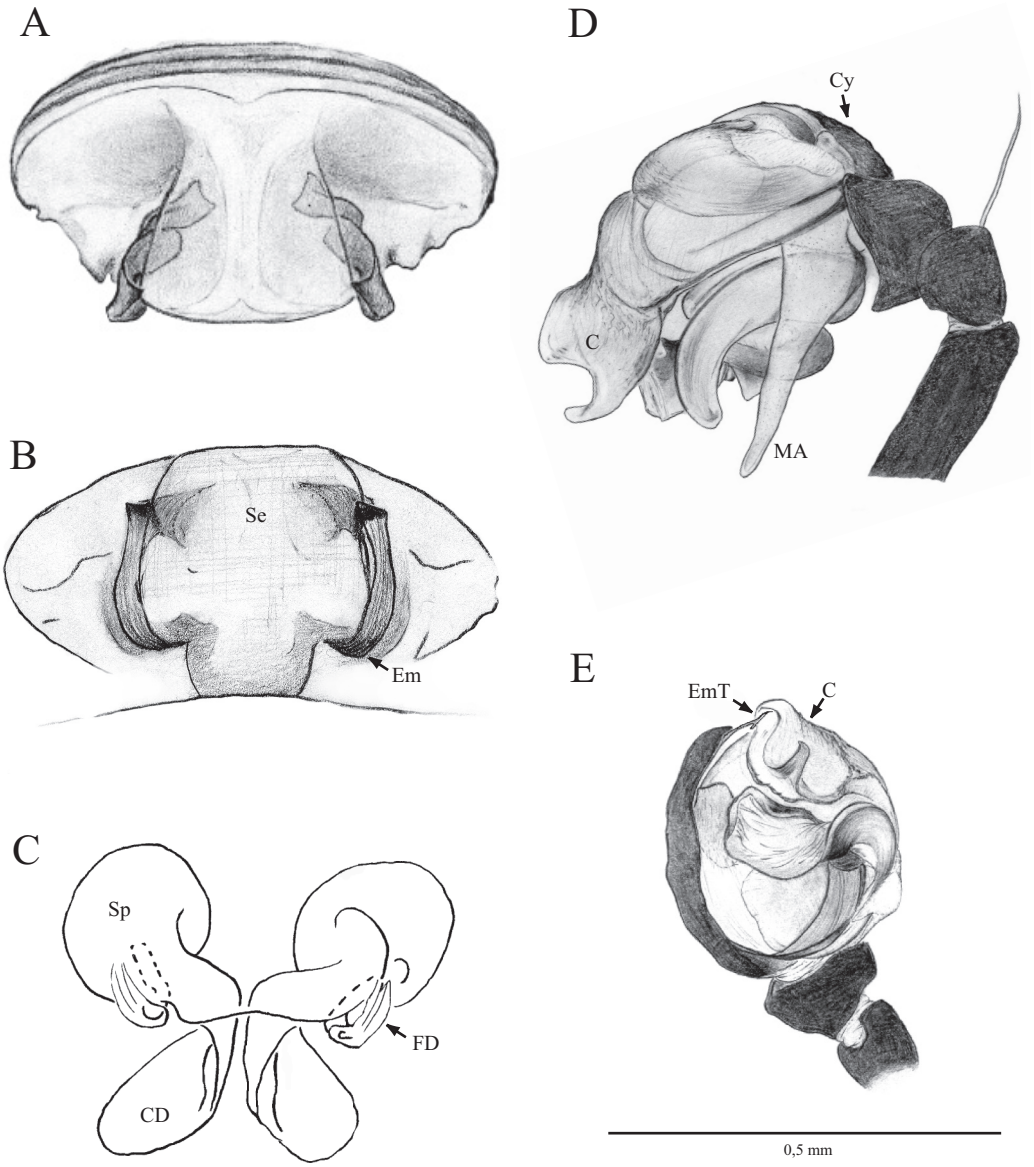

Fig. 16. Genitalia of *Acusilas africanus*. A) Epigyne, ventral view. B) Epigyne, posterior view. (MRAC 18815). C) Vulva, dorsal view (Cameroon: Kitta 1891 (NHRS)). D) Male pedipalp, lateral view. E) Male pedipalp, ventral view (Tanzania: E. Usambara Mts., Sigi River 1980 (ZMUC)). AR, Anterior Rim; C, Conductor; CD, Copulatory Duct; Cy, Cymbium; D, Depression; Em, Embolus; EmT, Embolic Tip; FD, Fertilization Duct; Se, Septum; Sp, Spermatheca.

Leleup leg., 1♀ (MRAC); Lumani, Kasongo, Riv., Maniema, S 04˚27', E 26˚40', iii.1960, Benoit leg., 1♀ (MRAC); **French Congo:** Benito River, Bates leg., 1♀ (BMNH); **Tanzania:** Morogoro Region, Uluguru Mts., Kimboza Forest, 18.vii.1981, 250 m., M. Stoltze & N. Scharff leg., 1♂ (ZMUC); East Usambara Mts., Dodwe Stream, 10.vii.1980, 1000 m., M. Stoltze & N. Scharff leg., 1♂ (ZMUC); Tanga Region, East Usambara Mts., Sigi River, 15.vii.1980, 750–500 m., M. Stoltze & N. Scharff leg., 1♂ (ZMUC); Tanga Region, East Usambara Mts., 12 km SE of Amani, Kihuhwi–Zigi, E 38˚40.6', S 5˚6.3', 2–4.xi.1995, 400 – 450 m., C.E. Griswold, N. Scharff & D. Ubick leg., 1 juv♀2♂♂ (ZMUC).

Note. – We have been able to examine a female from Gabon, identified by Simon (MNHN #17036). The male is described here for the first time. Males and females have not been found together, but they have been matched by the shape of the embolus tip found in the female copulatory ducts (Fig. 17).

Diagnosis. – The female of *Acusilas africanus* differ from other members of the genus in the four anterior lobes of the dorsal abdominal folium (Fig. 15A), the septum of the epigyne, which is longer than wide and widest posteriorly (Fig. 16A: Se). It shares the triangular-like shape of the abdomen with *A. malaccensis*, but the dorsal pattern of the abdomen is different in *A. africanus* (compare Figs 15A and 24A) and the colour of the abdomen is grey in *A. africanus* whereas it is orange in *A. malaccensis*. The males differs from other *Acusilas*-species in the bi-lobed conductor (16D), the dark brown cymbium (in contrast to light brown bulb), and the distinct embolic tip shaped like an arrow-head (17A-B).

Description. – Female (MNHN, #17 036): Total length 12.00. Cephalothorax 5.00 long, 3.53 wide, 1.48 high. Abdomen 6.79 long, 4.56 wide, 2.50 high. Sternum 1.98 long, 1.94 wide. Leg length: p) 1.46+0.74+0.98+1.48=4.66, 1) 3.97+1.86+3.04+2.94+1.23=13.04, 2) 3.66+1.84+2.65+2.65+1.18=11.98, 3) 2.54+1.36+1.67+1.52+0.93=8.02, 4) 3.77+1.89+2.91+2.98+0.96=12.51. AME 0.28, PME 0.28, ALE 0.14, PLE 0.25, AME-AME 0.18,

Fig. 17. Embolic tip of *Acusilas africanus*. A) Vulva of *Acusilas africanus* carrying one embolus in each copulatory duct, dorsal view (D. R. Congo: Comi 1930 (MRAC)). B) Expanded pedipalp, mesal view (Tanzania: Tanga, E. Usambara Mts. 1995 (ZMUC)). Circles enclose embolic tips. Notice how both the embolic tip of the mated female (A) and the embolic tip from the virgin male (B) matches in shape. The vulva (A) has collapsed a little because of prolonged methyl salicylate treatment.

AOQ 0.63, PME-PME 0.20, POQ 0.68, PER 1.40, AME-ALE 0.10.

Colour (based on females from Tanzania, Tanga region, E. Usambara 1995 (ZMUC)): Eye region black. Cephalothorax and sternum consistently light yellowish brown. Patura of chelicerae same color, fangs dark amber. Legs with weakly developed dark annulations. Abdomen light grey, with white folium provided with a dark rim. Anterior edge of folium drawn out into four lobes (Fig. 15A).

Epigyne (Figs 16A-C based on female MRAC #18815): Anterior bulge small, transverse rim narrow, without concavity/pocket. Septum longer than wide, and widest posteriorly. Copulatory ducts as in Fig. 16C.

Variation. – Females (n = 28): Total length 8.54-13.66. Cephalothorax 4.51-5.20 long, 3.3-3.7 wide, 1.4-1.52 high. Abdomen 4.88-8.17 long, 3.54-5.49 wide, 2.50-5.11 high. Sternum 1.72-2.01 long, 1.54-1.88 wide. Legs length: 1) 11.79-13.73, 2) 11.01-12.34, 3) 7.31-9.39, 4) 11.59-13.15.

Male (Tanzania, East Usambara Mts., Dodwe Stream, 10.vii.1980, 1000 m., (ZMUC)): Total length 2.06. Cephalothorax 1.11 long, 0.79 wide, 0.35 high. Abdomen 1.00 long, 0.80 wide, 0.68 high. Sternum 0.50 long, 0.46 wide. Leg length: p) 0.30+0.09, 1) 0.76+0.38+0.52+0.42+0.37= 2.45, 2) 0.70+0.34+0.44+0.38+0.34=2.20, 3) 0.48+0.24 +0.24+0.26+0.24=1.46, 4) 0.66+0.32+ 0.44+0.39 +0.31=2.12. AME 0.12, PME 0.09, ALE 0.06, PLE 0.08, AME-AME 0.08, AOQ 0.30, PME-PME 0.12, POQ 0.28, PER 0.48, AME-ALE 0.02.

Colour: Black rings around eyes. Cephalothorax, chelicerae and sternum dark brown. The latter with brokenmedian stripe and light spots between coxae. Abdomen light grey, mottled with black. Legs light brown, first and second pairs darker ventrally, third and fourth pairs with light annulations. Cymbium of pedipalp dark brown (Fig. 15B).

Pedipalp (Figs 16D-E): Conductor with two lobes distally, anterior one broadest, and supporting the embolic tip. Embolus long, curved clockwise. Embolus tip shaped like an arrow-head (Figs 17A-B).

Variation. – Males (n = 4): Total length 2.02-2.76. Cephalothorax 1.02-1.36 long, 0.65-0.90 wide, 0.29-0.44 high. Abdomen 1.15-1.52 long, 0.6-1.21 wide, 0.76-1.03 high. Sternum 0.49-0.56 long, 0.42-0.57 wide. Leg length: 1) 2.17-2.98, 2) 1.64-2.73, 3) 1.26-1.72, 4) 1.47-2.43.

Natural History. – *Acusilas africanus* has been collected in rain forest habitats up to 1000 m., above sea level. During copulation the embolus breaks off and stays in the copulatory ducts, thus acting like mating plugs (Fromhage & Schneider 2006). All females examined had broken emboli stocked in their epigynes (Fig 9).

Distribution. – Cameroon, Democratic Republic of the Congo, Gabon, Sierra Leone, South Africa and Tanzania.

Acusilas coccineus Simon, 1895

(Figs 18–21)

Acusilas coccineus Simon, E. (1895): 785. Petrunkevitch, 1928: 135. Uyemura, 1939: 142, figs. a-f (♀). Yaginuma, 1960: 59, fig. 58 (♀). Namkung, 1964: 37, fig. 23 (♀). Yaginuma, 1971: 59, fig. 58 (♀). Murphy & Murphy, 1983: 117, figs. 3-6 (♀, description). Hu, 1984: 88, figs. 78.1-2 (♀). Yaginuma, 1986: 116, fig. 61.2 (♂,♀). Chikuni, 1989: 75, fig. 40 (♂, ♀). Chen & Zhang, 1991: 112, figs. 106.1-3 (female). Yin et al., 1997: 109, figs. 35a-d (♂,♀). Song, Zhu & Chen, 1999: 230, figs. 133A-D, 145M (♂, ♀). Namkung, 2002: 256, figs. 19.18a-b (♂, ♀). Kim & Kim, 2002: 177, figs. 1, 70-71, 156-157 (♂, ♀). Namkung, 2003: 257, figs. 19.17a-b (♂, ♀).

Acusilas gentingensis Murphy & Murphy, 1983: 122, Figs 18-22. Murphy & Murphy, 2000: 92, Plate 15 figs 4-5. NEW SYNONYMY.

Type material. – *Acusilas coccineus* Simon, 1895: Indonesia, Java, 1♀ syntype (MNHN #16.823; examined). Moluccas, Halmahera Island, Edkor, Barfan, 4♀♀ syntypes (MNHN #8.861; examined).

Acusilas gentingensis Murphy & Murphy, 1983: Malaysia, Pahang, Genting, 1♀ holotype (BMNH; examined).

Other material examined. – **Indonesia:** Borneo, Kalimantan, Sepaku, 40 km N of Balipapan, primary forest, 2–5.viii.1980, C.L. & P.R. Deeleman leg., 1♀ (RMNH); Sumatra, Gunung Leuser National Park, Bohorok Rehabilitation Centre, 28.v.1983, Suh. Djosudharmo leg., 1♀ (RMNH); same locality, 15.ix.1983, Suh. Djosudharmo leg., 2♀♀ (RMNH); same locality, 2.-16.xi.1983, Suh. Djosudharmo leg., 3♀♀ (RMNH); same locality, 2.i.1984, Suh. Djosudharmo leg., 2♀♀ (RMNH); same locality, Mt. Singalang, Anai. 400-500 m., secondary forest, 16-20.vi.1994, Suh. Djosudharmo leg., 1♀ (RMNH); Java, Id., Mt. Gedeh, Cibodas National Park, 1500 m., 6-10.xii.1986, Suh. Djosudharmo leg., 1♂ (RMNH); Moluccas, Batjan, Mt. Sibella. 22.-26./8. 1954, A.H.G. Alston leg, 1♀ (NHM); **Malaysia:** Eastern Sabah, Borneo, Danum Valley Field Centre, 9.v.1991, C.L. & P.R. Deeleman leg., 1♂ (RMNH); **Singapore:** Bukit Timah Nature Reserve, 21-22.ii.1983, C.L. & P.R. Deeleman leg., 1♀ (RMNH); Pulau Ubin Island, 5.xi.1991, N. Scharff leg., 2♀♀ (ZMUC); **Sri Lanka:** Ratnapura, Sinharadj, 23.viii.1981, C.L. & P.R. Deeleman leg., 1♀ (RMNH); **Thailand:** Prov. Nakhon Ratchasima, Khao Yai National Park, 12.xi.1987, 1000

Fig. 18. Habitus of *Acusilas coccineus*. A) Female (Thailand: Khao Luang NP 2003 (ZMUC)). B) Male. (Malaysia: Eastern Sabah, Borneo, Danum Valley Field Centre, 1991, C.L. & P.R. Deeleman leg., (RMNH)).

m., seconday forest, C.L. & P.R. Deeleman leg., 1♂ (RMNH); same locality, 25-27.xii.1988, 1000 m., C.L. & P.R. Deeleman leg., 2♀♀ (RMNH); Chang Mai Province, Doi Suthep National Park, 15.ii.1992, 1600 m., M. Andersen leg., 2♀♀ (ZMUC); Surat Thani Province, Khao Sok National Park, Bang Hua Raed, N 8°55'0.4" E 98°31'40.9", 300 m, 19-20.x.2003, N. Scharff & J.B. Schmidt leg., 2♀♀ (ZMUC); Nakhon Si Thammarat Province, Khao Luang National Park, N 8°43'25.2'' E 99°40'7.7'', 355 m., 10-12.x.2003, N. Scharff & J.B. Schmidt leg., 1♂ (ZMUC); Chiang Mai, Queen Sirikit Botanical Garden, 98°51'E 18°53'N, around guesthouse,700-800 m., 1.x.2003, N. Scharff & J.B. Schmidt leg., 2♀♀ (ZMUC); **Japan:** "Hatsurigumo" Kami-Iwade, Naga-Grun, Ex. H. Yoneda S. Kobayashi leg., 25.vi.1951, #92, 1♀ (AMNH); Komi, Iriomotejima Island, Okinawa Pref., 3.v.1984, A. Tanikawa leg., 1♀ (ZMUC); same locality, 2.i.1990, A. Tanikawa leg., 1♀ (ZMUC); Hachiouji-jôshi, Motohachiouji.cho, Hachiouji-shi, Tokyo, 21.v.1989, Ken-ichi Kumada leg., Kumada det., Ar. 1947, 1♀ (NSMT); Omija, Iriomotejima Island, Okinawa Pref., 2.v.1990, A. Tanikawa leg., 1♀ (ZMUC); Shirahama, Iriomotejima Island, Okinawa Pref., 3.v.1990, A. Tanikawa leg., 1♀ (ZMUC); Urauchi, Iriomotejima Island, Okinawa Pref., 22.vii.1991, A. Tanikawa leg., 1♀ (ZMUC); Sonai, Iriomotejima Island, Okinawa Pref., 26.xii.1991, A. Tanikawa leg., 1♀ (ZMUC); Funaura, Iriomotejima Island, Okinawa Pref., 15.viii.1992, A. Tanikawa leg., 1♀1juv. (ZMUC); Takana, Iriomotejima Island, Okinawa Pref., 29.iii.2000, A. Tanikawa leg., 1♀1♂ (ZMUC);

Diagnosis. – Females of *Acusilas coccineus* differ from other members of the genus by the epigynal septum which is widest anteriorly (Fig. 19A). The copulatory ducts are often visible without clearing the epigyne. The copulatory ducts are also visible in *Acusilas dahoneus*, but this species has a completely different septum, which is wider than long and covers almost the entire depression of the epigyne (Fig. 23A). Males of *A. coccineus* differ from other species by the black and slender embolus with a truncated tip. At the point of contact with conductor the embolus makes a turn, pointing back towards the center of the bulb (Figs. 19E and 20B). It resembles the embolus of *Acusilas vilei*, but this species does not have pars pendula at the distal part of the embolus (Fig. 34).

Description. – Female syntype (MNHN 16 823): Total length 8.90; Cephalothorax 3.82 long, 3.14 wide, 1.13 high. Abdomen 5.20 long, 4.65 wide, 2.55 high; Sternum 1.67 long, 1.55 wide. Leg length: p) 1.12+0.60+0.74 +1.14=3.60, 1)3.13+ 1.47+2.33+2.26+1.07=10.26, 2) 2.85+1.41+2.05 +2.11+0.99=9.41, 3) 2.14+ 1.09+1.27+1.24+0.78 =6.52, 4) 3.10+1.46 +2.17+2.31+0.91=9.95. AME

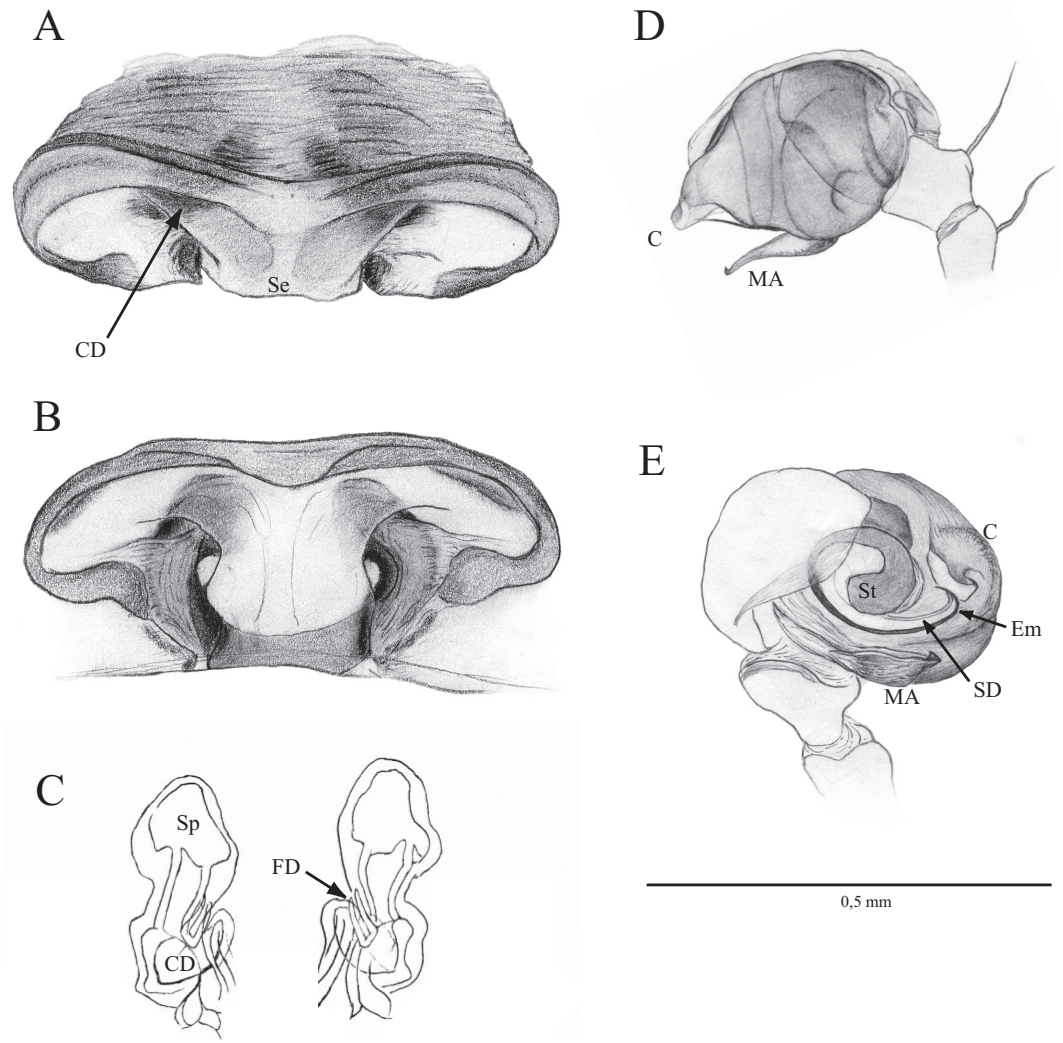

Fig. 19. Genitalia of *Acusilas coccineus*. A) Epigyne, ventral view. B) Epigyne, posterior view. C) Vulva, dorsal view (Japan: Iriomotejima Is, Funaura 1992 (ZMUC)). D) Male pedipalp, lateral view. E) Male pedipalp, postero-ventral view (Malaysia: Borneo, E. Sabah, danum Valley FC 1991 (RMNH)). C, Conductor; CD, Copulatory Duct; SD, Sperm Duct; Em, Embolus; MA, Median Apophysis; Se, Septum; Sp, Spermatheca; St, Stipes.

0.26, PME 0.24, ALE 0.17, PLE 0.20, AME-AME 0.18, AOQ 0.54, PME-PME 0.10, POQ 0.56, PER 1.17, AME-ALE 0.06.

Colour (The female syntype is very pale, due to long storage in alcohol, so the following description is based on additional more recent material): Eye region black. Cephalothorax, chelicerae, sternum and legs light brown to reddish brown. Abdomen brownish grey to reddish brown, dorsally with white folium and zigzag bands. These bands may be entirely absent, or broken and then forms oblique bars, or dark patches, or there may be only a dark marginal band dorsally (Fig. 18A). Epigyne (Figs 7A-B, 19A-C): Septum broadest anteriorly, eventually without pigment (white) or light brown. Copulatory ducts visible through septum and copulatory openings can be seen as dark markings posteriorly (Fig. 7A – arrow CDO).

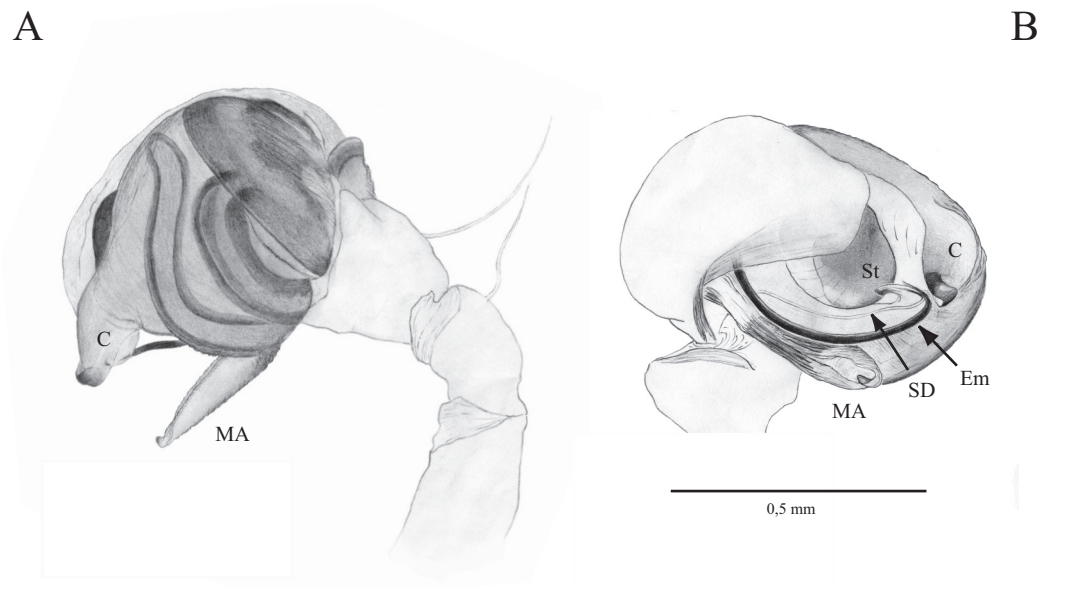

Fig. 20. Genitalia of *Acusilas coccineus* "Mega-male". A) Male pedipalp, lateral view. B) Male pedipalp, postero-ventral view (Japan: Iriomotejima Is, Funaura 1992 (ZMUC)). C, Conductor; SD, Sperm Duct; Em, Embolus; MA, Median Apophysis; St, Stipes.

Variation. – Females (n = 14): Total length 6.24-9.60; Cephalothorax 2.70-3.72 long, 2.05-2.76 wide, 0.69-1.25 high; Abdomen 3.92-6.98 long, 2.41-4.20 wide, 2.13-4.47 high; Sternum 1.18-1.51 long, 1.09-1.46 wide. Leg length: 1) 6.29-10.88, 2) 5.66-9.73, 3) 3.96-6.63, 4) 5.94-9.76.

Male (Malaysia, Eastern Sabah, Borneo, DanumValley Field Centre, 9.v.1991, C.L. & P.R. Deeleman leg. (RMNH)): Total length 2.42. Cephalothorax 1.33 long, 0.90 wide, 0.47 high. Abdomen 1.18 long, 0.93 wide, 0.93 high. Sternum 0.58 long, 0.54 wide. Leg length: p) 0.34+0.58+0.12=0.58, 1) 0.84+0.40+0.60+0.54+0.41=2.79, 2) 0.76+0.38+0.50+0.50+0.40=2.54, 3) 0.56+0.28+0.32+0.30+0.30=1.76, 4) 0.62+0.36+0.49+0.44+0.33=2.24. AME 0.14, PME 0.11, ALE 0.08, PLE 0.10, AME-AME 0.08, AOQ 0.32, PME-PME 0.08, POQ 0.27, PER 0.52, AME-ALE 0.02.

Colour: Eye region black. Cephalothorax and chelicerae reddish brown. Sternum and legs light brown. Legs with weak annulations, especially on legs III and IV. Abdomen light to dark grey, with light coloured rings around muscle attachment points (sigillae)(Fig. 18B).

Pedipalps (Figs 19D-E and 20): Embolus with black truncus and sperm duct visible in transparent pars pendula. Tip truncated, often transparent in small specimens, and bent backwards. Stipes and embolus fused (Fig 19E).

Variation. – Males (n = 6): Total length 2.06-6,32; Cephalothorax 1.02-3.68 long, 0.71-2.50 wide, 0.41-0.94 high; Abdomen 1.15-3.39 long, 0.93-2.30 wide, 0.81-2.11 high; Sternum 0.47 -1.32 long, 0.47-1.35 wide. Leg length: 1) 2.37-10.22, 2) 2.14-8.85, 3) 1.40-5.30, 4) 2.08 -7.05. Colour: Eye region black or reddish brown. Cephalothorax brown, reddish brown or yellowish brown. Legs often with annulations on tibiae, metatarsi and tarsi and often most pronounced on legs III and IV.

Natural History. – See description under genus. An egg sack laid inside the retreat has been observed in *Acusilas coccineus* (pers. observation).

Distribution. – *Acusilas coccineus* is found in China (Song et *al*. 1999), Malaysia, Indonesia, India (Kuntner pers. com.), Japan, Indonesia, Korea (Kim & Kim 2002, Nam Kung 2002, 2003),

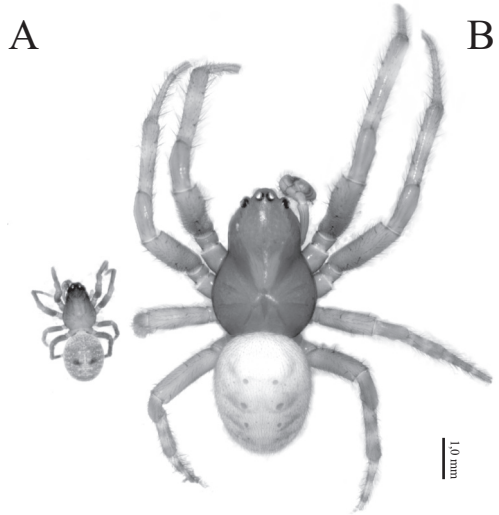

Fig. 21. Intrasexual size dimorphism of *Acusilas coccineus* males. A) "Small male" (Japan: Iriomotejima Is., Takana 2000 (ZMUC)). B) "Mega male" (Thailand: Nakhon Ratchasima Prov., Khao Yai NP 1987, C.L. & P.R. Deeleman leg. (RMNH))

Singapore, Sri Lanka , Taiwan (Song et *al*. 1999), and Thailand.

Notes. – We examined and compared the morphology of the type specimens of *Acusilas gentingensis* and *Acusilas coccineus* and conclude that they belong to the same species.

The size difference of males in this material is very pronounced. Males from the northern parts of the distribution range are much larger than males from southern areas (Fig. 21), but since genitalia of males and females from all areas are the same, we decided to treat all specimens as one species. In *Acusilas* males, the best diagnostic characters are found in the embolic division (embolus-stipes-radix), and the conformation of the embolic division in large and small males are the same. Only difference between the males seems to be body size and small differences in the shape of the median apophysis, but both body size and shape of median apophysis are well known to be unreliable for species separations in araneids (e.g., Grasshoff 1968, Levi 1991).When the sclerites of the embolic division are compared between the *Acusilas coccineus* males of the different size categories, they are alike in both shape and relative position. The relative length of the embolus/stipes complex is the same and it has the same number of turns, bends backwards at the same point of contact with the conductor and has the same truncated tip. The shape of the conductor is also the same in the males of all sizes. This is best seen in the postero-ventral view (Figs 19E, 20B).

Acusilas dahoneus Barrion & Litsinger, 1995

(Figs 22 & 23)

Acusilas dahoneus Barrion & Litsinger, 1995: 584, fig. 363a-e.

Type material. – Acusilas dahoneus Barrion & Litsinger, 1995: Philippines, Luzon Island, Cagayan Province, Solana, Banga village, 21.ix.1981, A.T. Barrion leg., 1♀ holotype (IRRI; examined).

Other material examined. – Two female paratypes together with the holotype.

Diagnosis. – Acusilas dahoneus differ from other species by its brown coloration and distinctive epigynal septum, which is transparent, wider than long, covering almost the epigynal depression and forming a characteristic brace-shaped lip posteriorly (Fig. 23A). As in *A. coccineus* the copulatory ducts are visible through the epigyne, but the septum is relatively smaller and does not cover the whole epigyne in *A. coccineus* (Fig. 19A).

Description. – Female holotype: Total length 5.43. Cephalothorax 2.40 long, 1.79 wide. Abdomen 3.42 long, 2.32 wide, 2.23 high. Sternum 1.03 long, 0.10 wide. Leg length: 1) 1.88+0.98+1.40+1.44+0.75=6.45, 2) 1.68+0.90+1.21+1.26+0.60=5.65, 3) 1.13+0.64+0.70+0.68+0.48=3.63, 4) 1.69+0.90+1.22+1.22+0.68=5.71. AME 0.18, PME 0.15, ALE 0.11, PLE 0.13, AME-AME 0.08, PME-PME 0.10, AME-ALE 0.02.

Colour: Eye region black. Cephalothorax and chelicerae brown, sternum and legs lighter brown. Legs with faint annulations. Abdomen greenish-brown with faint black markings posteriorly (Fig. 22).

Epigyne (Fig. 23): Anterior rim slender. Septum wider than long, almost covering entire depression of epigyne. Posterior part of septum forming pigmented brace-shaped lip. Septum and depression of epigyne transparent. Copulatory duct visible through tegument.

Variation. – Female paratypes (n = 2). – Total length 5.69-6.30. Cephalothorax 2.58-2.95 long, 1.95-2.01 wide, 0.72-0.74 high. Abdomen 3.17-3.42 long, 2.13-3.40 wide, 2.01-2.16 high.

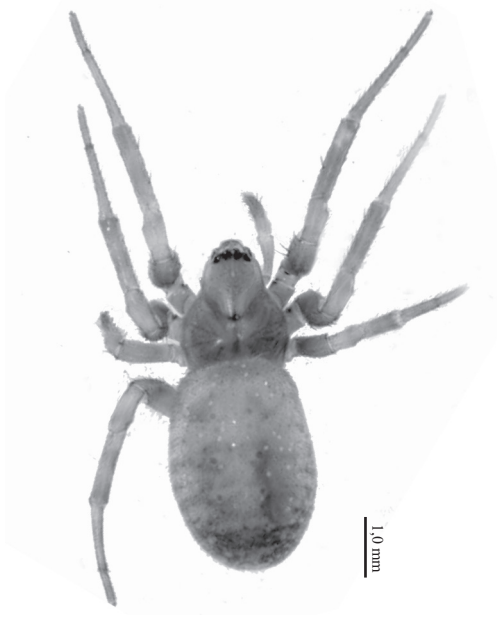

Fig. 22. Habitus of female *Acusilas dahoneus*. (Holotype. Philippines, Luzon Island, Cagayan Prov., 1981 (IRRI)).

Sternum 1.38-1.18 long, 0.73-1.18 wide. Leg length: 1) 7.63-8.25, 2) 6.43-7.06, 3) 4.45-4.79, 4) 6.51-7.21.

Natural History. – *Acusilas dahoneus* has been collected from webs with retreats made from dry rolled leafs of bamboo (*Bambusa* sp.; Barrion & Litsinger, 1995).

Distribution. – *Acusilas dahoneus* is only known from the type locality.

Acusilas lepidus (Thorell, 1898) incertae sedis

Argiope lepida Thorell, 1898: 337. Levi, 1983: 260 (listed as misplaced *Argiope*, "probably the male of *A. coccineus*").

Type material. – *Argiope lepida* Thorell, 1898: Burma, Mount Carin (Karen), Chebà, 1♂ holotype (MCSNG; not available).

Note. – We were not able to borrow the type material from Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy, but the holotype was examined by H.W. Levi in 1981 and he kindly forwarded a sketch of the male cephalothorax, abdomen and pedipalp. According to Levi it is probably the male of *Acusilas coccineus*, since "it has a very narrow head and a strongly recurved eye row" (Levi 1983). This description fits *Acusilas* very well, and the shape of the cephalothorax and the median apophysis is also very *Acusilas*-like, but unfortunately, the sketch does not reveal critical details of the embolic division, so exact identification is impossible. The folium of the abdomen is not typical for *Acusilas* males, and the embolus is curved in a clockwise direction, whereas all other known *Acusilas* species (except *A. africanus*) have emboli that curve in an anti-clockwise direction. Based on the details visible in the sketch of Levi we conclude that it is probably not a species of *Acusilas*, but only an inspection of the holotype can prove this right or wrong. We therefore decided to treat this species as incertae sedis.

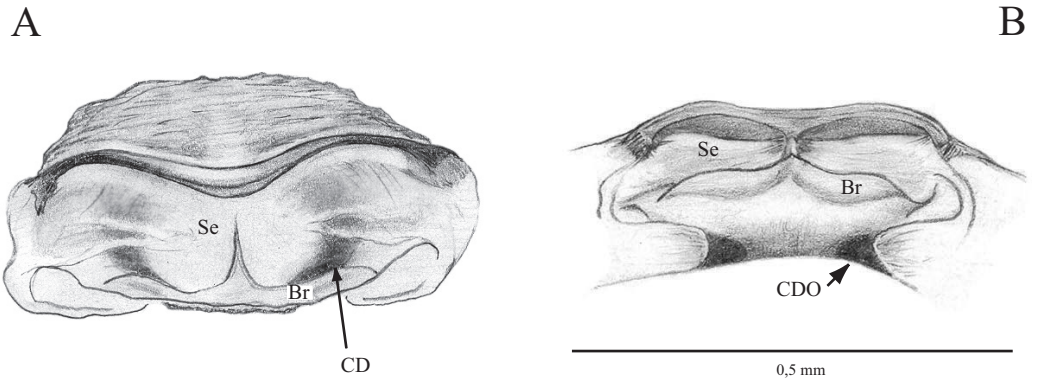

Fig. 23. Genitalia of female *Acusilas dahoneus*. A) Epigyne, ventral view. B) Epigyne, posterior view. (Female paratype. Philippines: Luzon Is., Cagayan Prov. ,1981(IRRI)). Br, Brace-shaped lip; CDO, Copulatory Duct Opening; Se, Septum.

Acusilas malaccensis Murphy & Murphy, 1983

(Figs 24–26)

Acusilas malaccensis Murphy & Murphy, 1983: 119, f. 9-17. Murphy & Murphy, 2000: Plate 15 figs 6-8.

Type material. – *Acusilas malaccensis* Murphy & Murphy, 1983: Malaysia, Phanag, Genting (near Kuala Lumpur), 16-22.viii.1979, J. & F. Murphy leg., 1♂ holotype (BMNH #8.404; examined).

Other material examined. – **Malaysia:** Borneo, Sarawak, Gunong Mulu National Park, around base camp 65, Alluvial forest, shrub layer, 29.x.1978, F. Wanless leg., Royal Geographic Society Mulu Expedition, 1977-1978, 1♂1♀ (MRAC); Phanag, Genting near Kuala Lumpur, 16–22.viii.1979, J. & F. Murphy leg., 1♀ (BMNH #8.404); Borneo, Western Sarawak, Matang Reserve, 1000 ft., C.L. & P.R. Deeleman leg., without date, 1♀ (RMNH); Borneo, Sarawak, Mulu National Park, night collecting, primary forest, 15.x.2003, C.L. & P.R. Deeleman leg., 1♀ (RMNH); **Indonesia:** Borneo (Kalimantan), Kaharian, S 2˚02', E 113˚40', swampy primary rainforest, leaf litter, 2-16.ix.1985, Suh. Djosudharmo leg., 1♂ (RMNH); Java, Mt. Gedeh, Cibodas National Park, 1450 m., 6.xii.1986, Suh. Djosudharmo leg., 1♀ (RMNH); Sumatra, 1974, W.S. Bristowe leg., 2 ♀♀ (BMNH); Sumatra, Mt. Singalang, Anai, 400-460 m., secondary forest, 10.vi.1983, B. Sink leg., 1♂ (RMNH); same locality, 10-22.vi.1994, Suh. Djosudharmo legit. 5♀♀1♂ (RMNH); Sumatra, Gunung Leuser National Park, Bohorok Rehabilitation Centre, 17.xi.1983, Suh. Djosudharmo leg., 1♀ (RMNH); **Thailand:** Yala Province, Bang Lang National Park, 6°04'N 101°11'E, lowland rainforest, below 400 m., 18.x.1991, M. Andersen, O. Martin & N. Scharff leg., 1♂ (ZMUC); same park, 6°11'47.5"N 101°9'50.9"E, 270 m., 15.x.2003, F. Alvarez leg., 1♀ (ZMUC); Satun Province, Thale Ban National Park, 6°42'N 100°10'E, lowland rainforest, below 400 m., M. Andersen, O. Martin & N. Scharff leg., 1♀ (ZMUC); Nakhon Si Thammarat Province, Khao Luang National Park, N 8˚43'25,2" E 99˚40'7,7", 355 m., 10-12.x.2003, N. Scharff & J. Birkedal Schmidt leg., 2♀♀1♂ (ZMUC); Surat Thani Province, Khao Sok National Park, Bang Hua Raed, N 8˚55'0,4" E 98˚31'40,9", 300 m., 19–20.x.2003, N. Scharff & J. Birkedal Schmidt leg., 1♂ (ZMUC). **Laos:** Louangnamtha, N 20˚58.702', E 101˚ 28.686', Luang Nam Tha, between ban Tavan 1 and Ban Tavan 2, 581-657 m, 9. xi. 2004, P. Jäger & V. Vedel leg., 1♀1♂ (SMF); Louangphabang, N 19˚40.963', E 102˚ 18.442', SE of Luang Prabang, Nam Khan, Ban Keng Koung, 372 m, 7. iii. 2006, P. Jäger & J. Altmann leg., 2♀♀1juv (SMF);

Diagnosis. – Females of *Acusilas malaccensis* differs from all other *Acusilas* species by their bright orange color (faded to yellowish white in alcohol preserved specimens) and transverse black stripes in a white folium (Fig. 24A). Like in *A. africanus* the abdomen is wide anteriorly and narrower posteriorly, thereby giving an impression of a more or less triangular-shaped abdomen, but *A. malaccensis* is easily distinguished by the black dorsal stripes. All other *Acusilas* species have females with cylindrical abdomens. Female with eggs may have more oval-shaped abdomens. Septum of epigynum with two lateral lobes (Fig. 25A), covering the depression and the copulatory openings. *A. dahoneus* also has a wide septum (Fig. 23A), but it is transparent, and the atrium and copulatory openings are clearly visible though the lobes. Males of *Acusilas malaccensis* can be distinguished by the arrow-shaped embolic tip, provided with a small cap, the proximal thorn of embolus (Fig. 25F-EmTh) and a distal extension on stipes (Fig. 25F-StE). Males of *A. malaccensis* is less dark than males of other species (Fig. 24B versus 15B, 18B, 21, 29, 31 & 33).

Description. – Female paratype (from Malaysia, Phanag, Genting near Kuala Lumpur, BMNH #8.404)**:** Total length 10.2. Cephalothorax 4.27 long, 3.35 wide, 1.21 high. Abdomen 5.62 long, 4.84 wide, 3.82 high. Sternum 1.96 long, 1.86 wide. Leg length: p) 1.44+0.71+0.93+?+? =3.08, 1) 4.19+ 1.77+3.28+3.14+1.36=13.74, 2) 4.02+ 1.71+2.89+ 2.92+1.22=12.76, 3) 2.76+1.30+1.61 +1.58+0.93= 8.18, 4) 4.09+1.81+2.84+3.04+1.64 =13.42. AME 0.26, PME 0.26, ALE 0.17, PLE 0.19, AME-AME 0.12, AOQ 0.59, PME-PME 0.14, POQ 0.58, PER 1.16, AME-ALE 0.09.

Colour (based on several specimens): Cephalothorax, sternum and legs bright orange, except tarsi, metatarsi and about 4/5 of tibiae, which are black. Occasionally, the black coloration does not cover entire leg segment and leg segments then appear annulated instead. Abdomen orange, dorsally with white folium, provided with five transverse black bars, decreasing in size towards the posterior end of abdomen. Anterior bar laterally connected to two black spots, but anterior bar may be entirely absent (Fig. 24A).

Epigyne (Figs 25A-B): White septum forming two lateral lobes, which open to the anterior like a couple of pockets. Septum covers almost entire concavity of epigyne.

Vulva (Fig. 25C): Copulatory ducts funnel-shaped.

Variation. – Females (n =16):Total length 8.91-12.69; Cephalothorax 4.15-5.00 long, 3.53-4.39 wide, 1.01-1.40 high; Abdomen 6.47-7.44 long, 4.88-7.81 wide, 3.05-6.10 high; Sternum 1.76-2.11,

Fig. 24. Habitus of *Acusilas malaccensis*. A) Female. B) Male. (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP. 2003 (ZMUC)).

long, 1.81-1.94 wide. Leg length: 1) 11.94-16.42, 2) 11.35-15.24, 3) 7.54-10.0, 4)11.31-15.38.

Male holotype: Total length 1.83. Cephalothorax 1.05 long, 1.26 wide, 0.44 high. Abdomen 0.87 long, 0.74 wide, 0.53 high. Sternum 0.48 long, 0.47 wide. Leg length: p) 0.20+0.02+0.11+?+?=0.33, 1) 0.71+0.33+0.50+0.44+0.34=2.32, 2) 0.66+0.32+0.44+0.40+0.32=2.14, 3) 0.45+0.22+0.24+0.22+0.24=1.37, 4) 0.60+0.28+0.38+0.34+0.30=1.90. AME 0.13, PME 0.11, ALE 0.06, PLE 0.08, AME-AME 0.07, AOQ 0.27, PME-PME 0.10, POQ 0.28, PER 0.46, AME-ALE 0.01.

Colour: Cephalothorax, chelicerae and legs light brown, with black markings on patellae, tibiae, metatarsi and tarsi. Sternum pale-yellowish white. Abdomen whitish grey with evenly distributed black dots, both dorsally and ventrally.

Pedipalp (Fig. 25). The holotype male has lost its embolus, but virgin males have intact emboli (Fig. 25). Tip of embolus arrow-shaped. Two protuberances at junction of stipes and embolus. One on the base of embolus and the other distally on stipes.

Variation. – Males (n = 8): Total length 1.86-2.33. Cephalothorax 0.93-1.26 long, 0.69-0.87 wide, 0.34-0.59 high. Abdomen 0.90-1.24 long, 0.87-1.21 wide, 0.68-0.93 high. Sternum 0.44-0.56 long, 0.40-0.52 wide. Leg length: 1) 2.14-2.80, 2) 1.95-2.52, 3) 1.29-1.71, 4) 1.80-2.21.

Colour: Some males darker than holotype. With black dots on posterior part of abdomen and sometimes with two white anterior markings. Tarsi, metatarsi, tibia and patellae of legs I & II darker prolaterally, legs III & IV darker retrolaterally. Pars pendula of embolus same colour as truncus (Figs 25D - F).

Natural History. – Male and female of *Acusilas malaccensis* were found together within a retreat (rolled leaf) (Thailand: Nakhon Si Thammarat Prov., Khao Luang NP. 10.-12. x. 2003. ZMUC). This indicates that mating may takes place there. During copulation embolus breaks off and stay in the female copulatory ducts.

Distribution. – Laos, Thailand, Malaysia and Indonesia.

Acusilas callidus sp. nov.

(Figs 27-28)

Type material. – Female holotype**.** Indonesia: Sulawesi, Togian Islands, Pulau Batu Daka, forest, 30.viii.1987, D. Bilbon leg., 1♀ (Deposited in RMNH).

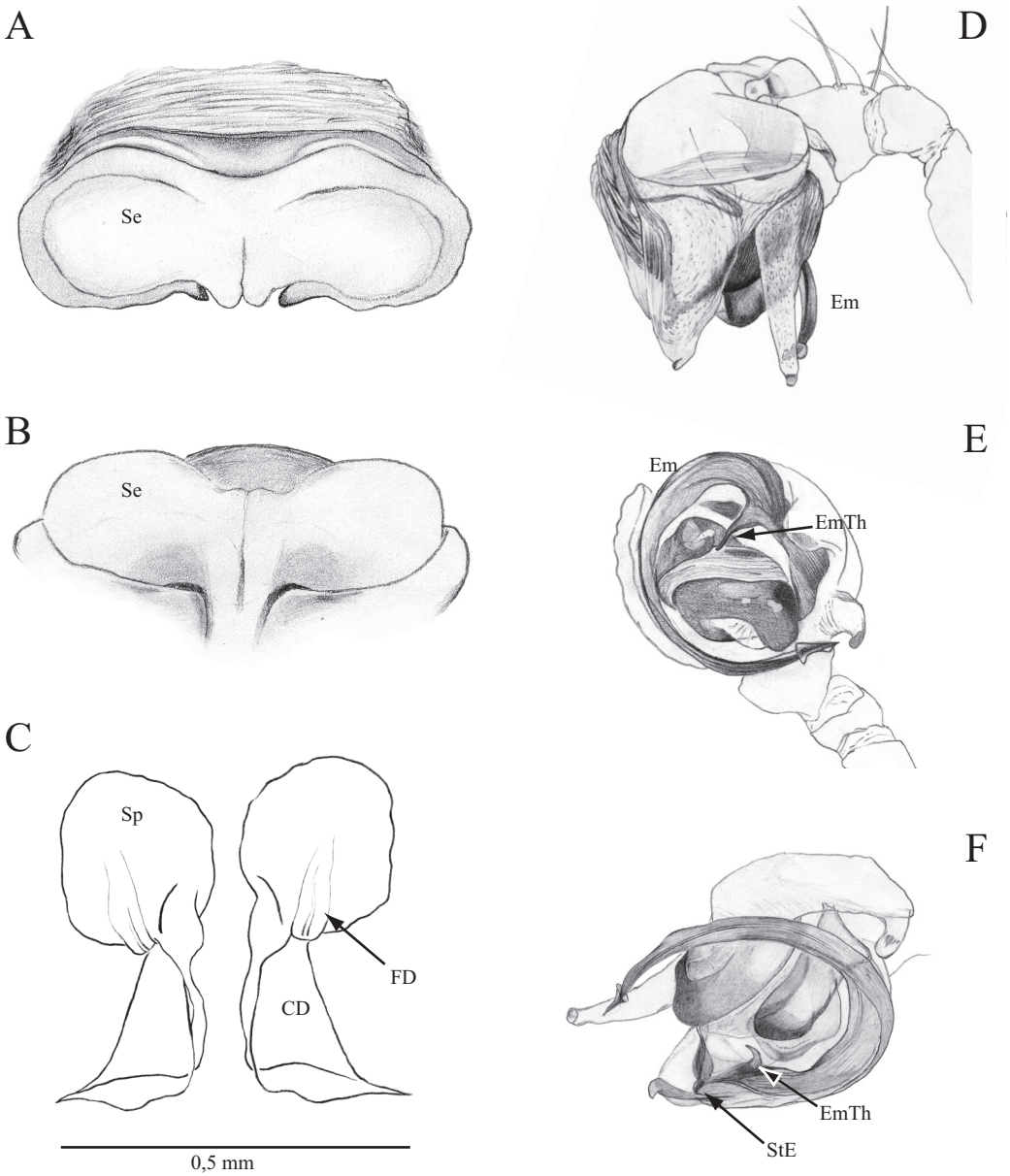

Fig. 25. Genitalia of *Acusilas malaccensis*. A) Epigyne, ventral view. B) Epigyne, posterior view (Indonesia: Sumatra, 1974 (BMNH)). C) Vulva, dorsal view (tilted slightly forwards) (Thailand: Khao Luang NP 2003 (ZMUC)). D) Male pedipalp, lateral view. E) Male pedipalp, ventral view. F) Fronto-mesal view (Thailand: Khao Sok NP 2003 (ZMUC)). CD, Copulatory Duct; FD, Fertilization Duct; Se, Septum; Sp, Spermatheca. Em, Embolus; EmTh, Embolic Thorn; StE, Stipeal Extension.

Etymology. – *Callidus* is a Latin adjective meaning cunning or shrewd. It refers to the rather subtle smile that the epigyne seems to portrait (Fig. 28B).

Diagnosis. – *Acusilas callidus* differs from other species by the projecting anterior rim of the epigyne, forming a ventral protrusion pointing posteri-

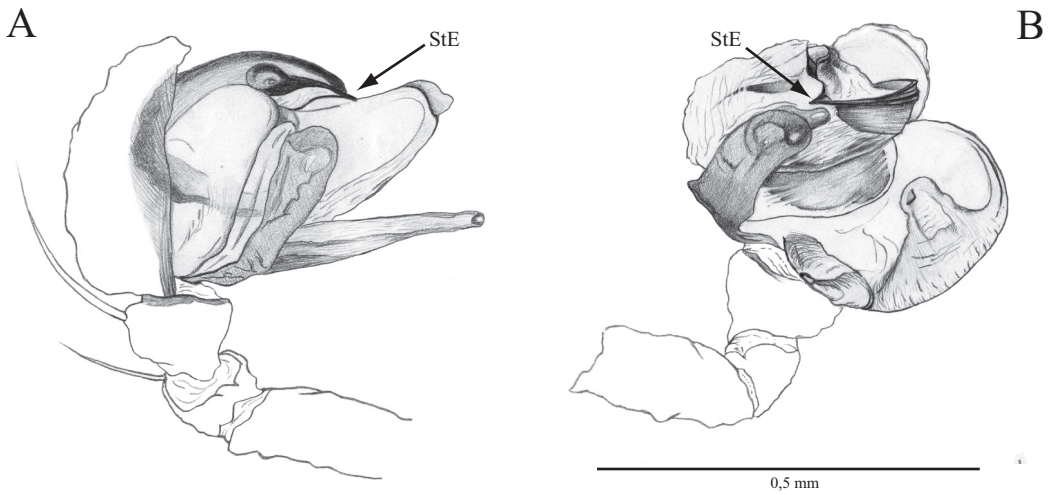

Fig. 26. Genitalia of mated male *Acusilas malaccensis*. A) Male pedipalp, mesal view. B) Male pedipalp, ventral view (Thailand: Khao Luang NP 2003 (ZMUC)). StE, Stipeal Extension.

orly (Fig. 28A). The septum is wider anteriorly than posteriorly as it is also seen in *Acusilas coccineus* (Fig. 19A). However, *Acusilas callidus* is easily recognizable from all the other species of *Acusilas* by the protruding rim of the epigyne.

Description. – Female holotype: Total length 7.70. Cephalothorax 2.89 long, 2.26 wide, 0.90 high. Abdomen 4.76 long, 2.15 wide, 3.59 high. Sternum 1.24 long, 1.18 wide. Leg length: p) 0.87+0.43+0.61+?+0.87=2.78, 1) 2.42+1.16+1.84 +1.77+0.84=8.03, 2) 2.20+1.08+1.60+1.58+0.81= 7.27, 3) 1.60+0.78+0.90+0.88+0.62=4.78, 4) 2.31+1.05+1.50+1.49+0.71=7.06. AME 0.22, PME 0.21, ALE 0.12, PLE 0.16, AME-AME 0.10, AOQ 0.48, PME-PME 0.14, POQ 0.48, PER 0.88, AME-ALE 0.06.

Colour: Cephalothorax, chelicerae, sternum and legs light brown. Eye region black. Abdomen grayish brown with white spots, faint patches and transverse stripes posteriorly (Fig. 27).

Epigyne (Fig. 28): Anterior rim drawn out ventrally and thus forming elongate structure. Septum connects to rim on posterior and lateral face.

Distribution. – Only known from the type locality.

Note. – Fourth leg shorter than second, which is unusual. Normally the fourth pair is longer than the second pair of legs in *Acusilas* females. However, the femur of leg four is still longer than

Fig. 27. Habitus of female *Acusilas callidus* (Holotype. Indonesia: Sulawesi, Togian Isl. 1987 (RMNH)).

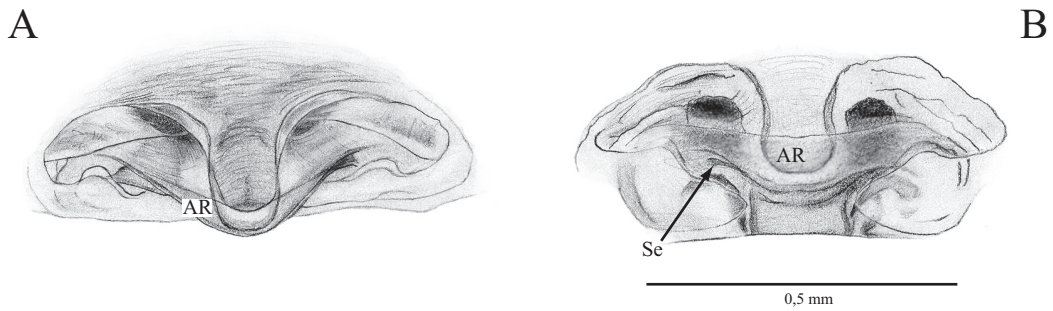

Fig. 28. Genitalia of *Acusilas callidus*. A) Epigyne, ventral view. B) Epigyne, posterior view. (Holotype. Indonesia: Sulawesi, Togian Isl. 1987 (RMNH)). AR. Anterior Rim; Se, Septum.

that of leg two. We do not attribute the difference any diagnostic value for this species, because sometimes leg segments of leg two are longer than those of leg four. See for instance the holotype of *Acusilas dahoneus* in which the metatarsus of leg two is longer than the metatarsus of leg four.

Acusilas spiralis sp. nov.

(Figs 29-30)

Type Material. – Male holotype. Indonesia: Sumatra, Gunung Leuser NP., Bohorok. 16.xii.1983. Suharto legit. (Deposited in RMNH).

Fig. 29. Habitus of male *Acusilas spiralis* (Holotype. Indonesia: Sumatra, Gunung NP 1983 (RMNH)).

Addition Material Examined. – **Indonesia:** Sumatra, Gunung Leuser NP., Bohorok Rehab. Centre. 15.ix.1983. Suh. Djosudharmo legit., 1♂ (RMNH).

Etymology. – The species epithet is a noun in apposition, derived from the Latin word for spiral, *spiralis*. It refers to the spiraling curvature of the embolus/stipes complex in the unexpanded state (Fig. 30B).

Diagnosis. – *Acusilas spiralis* males differ from males of other species by the embolus/stipes complex two-turn spiral run, following the circular outline of tegulum as seen in ventral view of unexpanded palp (Fig. 30B). The embolic tip is truncated as it also seen in *Acusilas coccineus*, but here the stipes/complex only do approximately 1.5 turn (Figs 19E, 20B).

Description. – Male Holotype**:** Total length 2.45. Cephalothorax 1.24 long, 0.87 wide, 0.49 high. Abdomen 1.27 long, 1.02 wide, 0.90 high. Sternum 0.54 long, 0.50 wide. Leg length: p) 0.32+0.12+ 0.14+0.48=1.06, 1) 0.87+0.40+0.62+ 0.53+0.39= 2.81, 2) 0.79+0.38+0.52+0.46+0.36 =2.51, 3) 0.56 +0.28+0.32+0.27+0.25=1.68, 4) 0.73+0.34+0.46+ 0.40+0.30=2.23. AME 0.16, PME 0.12, ALE 0.06, PLE 0.08, AME-AME 0.07, AOQ 0.34, PME-PME 0.08, POQ 0.28, PER 0.51, AME-ALE 0.02.

Colour: Eye region black. Cephalothorax and chelicerae amber brown. Sternum and legs light brown. Abdomen black with white rings around muscle attachments points (sigillae)(Fig. 29).

Pedipalp (Fig. 30): Embolus with kink (bends) at interface with conductor. At same point sperm duct goes from pars pendula into truncus. Embolic tip truncated. Embolus and stipes fused, spiral-shaped with two-turns.

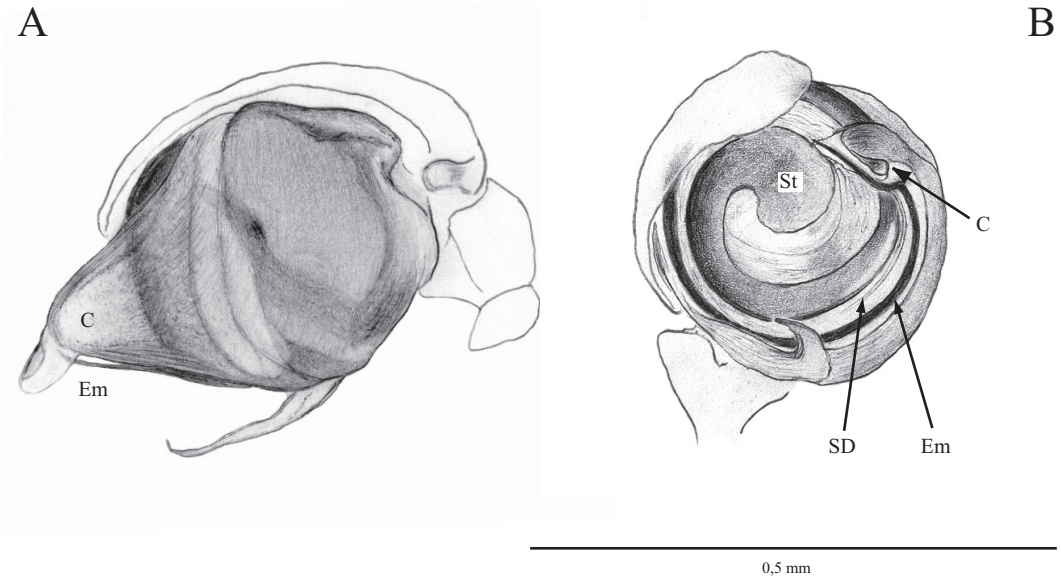

Fig. 30. Genitalia of male *Acusilas spiralis*. A) Male pedipalp, lateral view. B) Male pedipalp, ventral view (Holotype. Indonesia: Sumatra, Gunung National Park 1983 (RMNH)). C, Conductor; SD, Sperm Duct; Em, Embolus; St, Stipes.

Natural History . – This specimen was collected in primary rainforest (Deeleman-Reinhold 2001).

Fig. 31. Habitus of male *Acusilas vei* (Holotype. Indonesia: Sulawezi, Lore Lindu Reserve 1982 (RMNH)).

Acusilas vei sp. nov.

(Figs 31-32)

Type material. – Male holotype. Indonesia: Sulawesi, Lore Lindu Reserve, Marena Palu, 24.vii.1982, 1♂ (Deposited in RMNH).

Etymology. – Derived from the name Ve of the Norse mythology. Ve and his brother Vile temporarily married Frigg, the wife of their other brother Odin, king of the gods, while he was away. We have used this name to illustrate the problem of associating males and females.

Diagnosis. – *Acusilas vei* differ from other species of *Acusilas* by the long slender embolus with a bifid tip, which makes a loop alongside the conductor (Fig. 32A). As in *A. malaccensis* there is a proximal thorn on embolus (Fig. 32B). However, in *A. malaccensis* there is both a thorn proximally on embolus and a protuberance distally on stipes (Fig. 25F). *Acusilas vei* differs further by the small size of the subtegulum and tegulum in relation to the conductor as seen in lateral view (Fig. 32A). In other *Acusilas* species, conductor is equal to or smaller than the rest of the basal part of the bulb of the pedipalp.

Description. – Male holotype: Total length 2.11. Cephalothorax 1.15 long, 0.84 wide, 0.51 high.

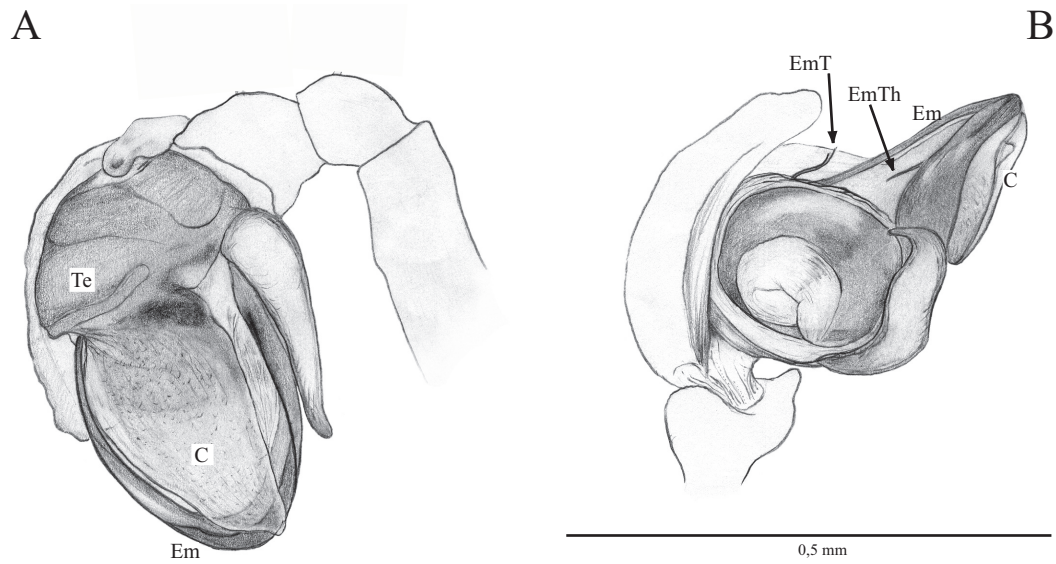

Fig. 32. Genitalia of male *Acusilas vei*. A) Male pedipalp, lateral view. B) Male pedipalp, ventral view (Holotype. Indonesia: Sulawezi, Lore Lindu Reserve 1982(RMNH)). C, Conductor; Em, Embolus; EmTh, Embolic Thorn; EmT, Embolic Tip; Te, Tegulum.

Abdomen 1.08 long, 0.99 wide, 0.83 high. Sternum 0.53 long, 0.51 wide. AME 0.13, PME 0.10, ALE 0.07, PLE 0.08, AME-AME 0.07, AOQ 0.30, PME-PME 0.09, POQ 0.27, PER 0.43, AME-ALE 0.02. Leg length: p) 0.30+0.12+0.12+ ?+?=0.54, 1) 0.86+0.39+0.77+0.51+0.38=2.91, 2) 0.78+0.38+0.50+0.44+0.34=2.44, 3) 0.52+0.25+ 0.30+0.24+0.28=1.59, 4) 0.70+0.30+0.42+0.36 +0.28=2.06.

Colour: Eye region black. Cephalothorax and chelicerae brown, mottled with black. Sternum and legs yellowish brown. Legs with faint annulations. Abdomen grey, mottled with black (Fig. 31).

Pedipalps (Fig. 32): Embolus runs in parallel with the large triangular conductor and continues past this structure (in the unexpanded palp). Tip of embolus bifid.

Natural History. – *Acusilas vei* was collected in primary forest.

Distribution. – Only known from the type locality.

Acusilas vilei sp. nov.

(Figs 33-34)

Type material. – Male holotype. Indonesia: Sulawesi, Utara, Dumogo-Bone National Park, xi.1985, Project Wallace leg., 1♂ (Deposited in BMNH).

Etymology. – Derived from the name Vile of the Norse mythology. For further explanation, see *A. vei.*

Diagnosis. – *Acusilas vilei* differ from other species of *Acusilas* by the characteristic proximal thorn on embolus (Fig. 34B: Th).

Description. – Male holotype: Total length 3.72. Cephalothorax 2.01 long, 1.37 wide, 0.64 high. Abdomen 2.01 long, 1.62 wide, 1.27 high. Sternum 0.83 long, 0.78 wide. Leg length: p) 0.62+0.19+0.25+?+?=1.06, 1) 1.36+0.62+1.10 +1.07+0.59=4.74, 2) 1.26+0.62+0.95+0.91+0.39 =4.13, 3) 0.88+0.43+.053+0.53+0.42=2.79, 4) 1.16+0.56+0.79+0.74+0.43=3.68. AME 0.17, PME 0.13, ALE 0.11, PLE 0.12, AME-AME 0.10, AOQ 0.40, PME-PME 0.10, POQ 0.35, PER 0.74, AME-ALE 0.03.

Colour: Eye region black. Cephalothorax reddish brown, with dark margin. Chelicerae same colour. Legs and sternum yellowish brown. Abdomen dark grey with white markings and white rings around muscle attachments points (sigillae) (Fig. 33).

Pedipalps (Fig. 34): Membraneous zone be-

Fig. 33. Habitus of male *Acusilas vilei* (Holotype. Indonesia: Sulawezi, Dumogo-Bone NP 1985 (BMNH)).

tween embolus and stipes clearly seen and sperm duct enters embolus at this point. Basal part of embolus bent and provided with long bend thorn (Fig. 34B: Th). Embolus without pars pendula.

Natural History. – Collected from rolled, silken leaf in centre of orb.

Distribution. – Only known from the type locality.

Acusilas sp.

(Figs 35-36)

Material examined. – Indonesia: Sulawesi, Marena Palu, Lore Lindu Reserve, 24.vii.1982, 1♀ (RMNH); Indonesia: Sulawesi, Utara, Dumogo-Bone National Park, xi.1985, P. Hillyard leg., 3♀♀ (BMNH).

Diagnosis. – These *Acusilas* females differ from other species of the genus by the pocket-like structures of the epigynal septum and by the median furrow in the posterior margin of the epigyne (Fig. 36A). *A. malaccensis* does also have an epigynal septum forming pocket-like structures, but this structure almost covers the entire depression of the epigyne (Fig. 25A).

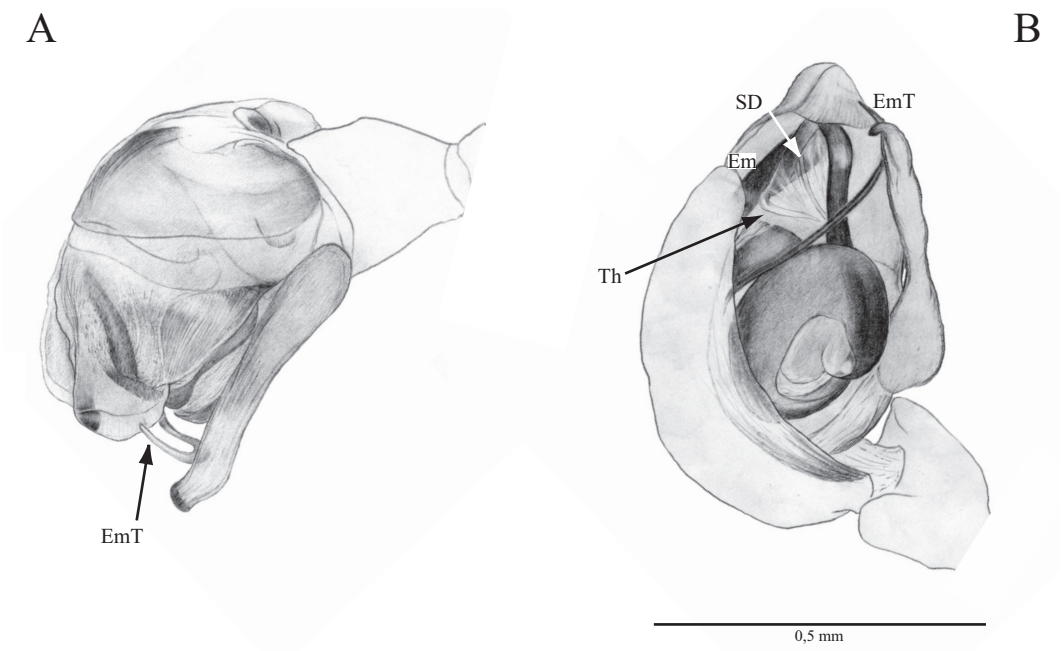

Fig. 34. Genitalia of male *Acusilas vilei*. A) Male pedipalp, lateral view. B) Male pedipalp, postero-ventral view (Holotype. Indonesia: Sulawezi, Dumogo-Bone National Park 1985 (BMNH)). SD, Sperm Duct; Em, Embolus; EmT, Embolic Tip; Th, Thorn.

Description. – Female from Marena Palu: Total length 9.00. Cephalothorax 4.12 long, 3.30 wide, 0.98 high. Abdomen 6.50 long, 4.00 wide, 3.50 high. Sternum 1.96 long, 1.67 wide. Leg length: p) 1.43+0.71+0.93+ 1.43=4.50, 1) 3.85+1.81+2.96+ 3.06+1.32=13.00, 2) 3.50+1.72+2.65+2.74+1.20 =11.81, 3) 2.50+ 1.30+1.57+1.52+0.98=7.87, 4) 3.58+1.81+2.65+ 2.84+1.15=12.03. AME 0.28, PME 0.24, ALE 0.17, PLE 0.20, AME-AME 0.13, AOQ 0.57, PME-PME 0.12, POQ 0.52, PER1.12, AME-ALE 0.10.

Colour: Eye region black. Cephalothorax, sternum and legs yellowish brown. Chelicerae reddish brown. Abdomen with white folium and black markings, as in *Acusilas coccineus* females (Fig. 18A). Rest of abdomen dark (Fig. 35).

Epigyne (Fig. 36A): Anterior rim broad, forming deep concavity. Septum forms two lateral pockets, posterior plate with median furrow.

Vulva (Fig. 36B): Entrance of copulatory ducts centrally, each opening placed just next to the median furrow. Copulatory ducts very short and broad.

Variation. – Females (n = 3): Total length 10.25-10.49. Cephalothorax 4.03-4.58 long, 3.28-3.60 wide, 0.98-1.10 high. Abdomen 6.10-7.20 long, 4.27-5.73 wide, 3.40-5.86 high. Sternum 1.91-2.03, long, 1.72-1.89 wide. Leg length: 1) 11.97-13.00, 2)11.41-12.29, 3) 7.23-8.06, 4) 11.28-

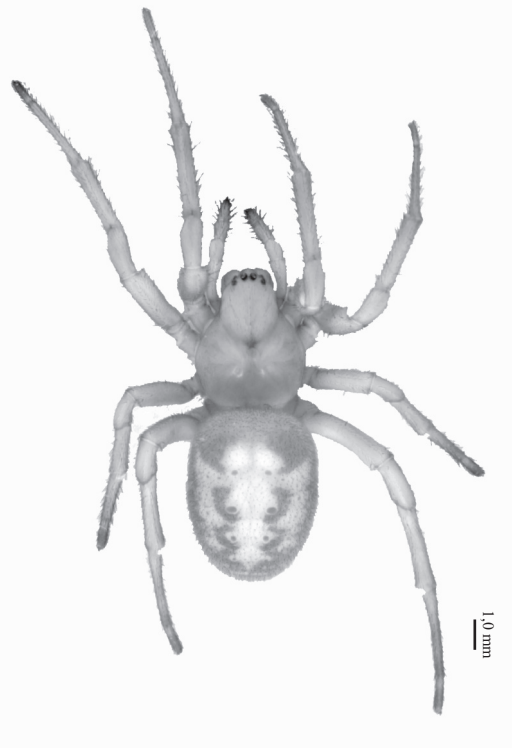

Fig. 35. Habitus of unassigned female *Acusilas* (Indonesia: Sulawezi, Dumogo-Bone NP 1985 (BMNH)).

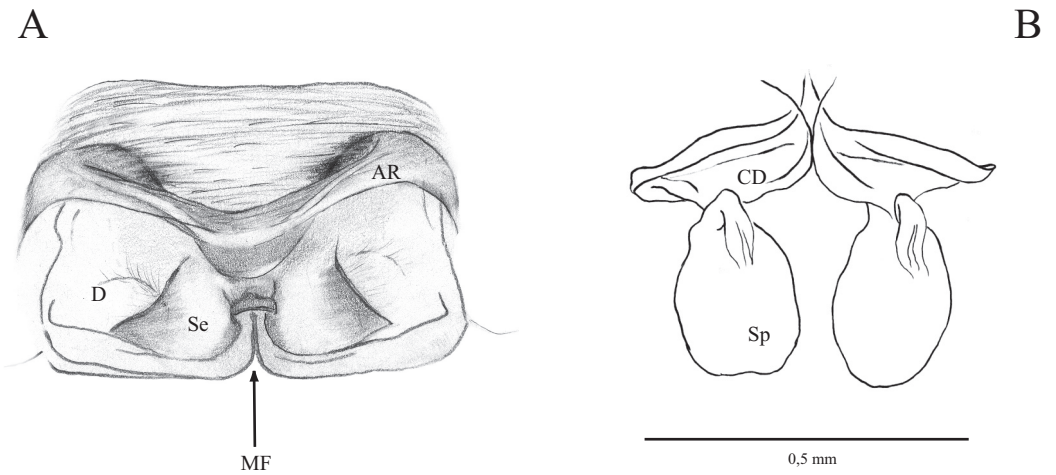

Fig. 36. Genitalia of unassigned *Acusilas* female. A) Epigyne, ventral view. (Indonesia: Sulawesi, Lore Lindu Reserve 1982 (RMNH)). B) Vulva, posterior view (Indonesia: Sulawezi, Dumogo-Bone NP 1985 (BMNH)). AR, Anterior Rim; CD, Copulatory Duct; D, Depression; MF, Median Furrow; Se, Septum; Sp, Spermatheca.

12.35. Carapace may have dark reticulate pattern in cephalic region.

Natural History. – The specimens from both localities were collected in primary forest and all specimens have been collected from rolled leafs placed at the centre of the orb web.

Note. – These females are not assigned to particular species, since all 4 females look exactly the same. However, they have been collected with different males. The specimen from Marena Palu was collected with the holotype male of *Acusilas vei* and the other three females from Utara with the holotype male of *Acusilas vilei*. Unfortunately, there are no broken-off embolus tips in the female copulatory ducts that could help associate males and females, so we do not feel confident about the associations of these females. Even though females from the two different localities were collected with different males, it does not automatically mean that the females represent different species. Their epigynes are clearly the same and there is no somatic character that makes it possible to differentiate the females. Males of araneid species are known to be attracted to closely related females (Foelix 1996) so even if specimens are found in the same web, they may not belong to the same species. Furthermore, specimens from 'same locality' could easily have been collected hours apart within different sites of the locality.

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Appendix 1. Coding of morphological and behavioral characters of Scharff & Coddington (1997) for *Acusilas coccineus* Simon, 1895.

Acusilas coccineus
0001110000000001000?0110000???0000000110000000010110000?0001001000100
21010?0?00?0.

Appendix 2. Character state matrix for species phylogeny.

Araneus quadratus	0000000001300000011-0001000000111110---0
Gasteracantha mammosa	1000001 1------00011-2021000100100000---0
Arachnura melanura	1000100000310010000000111100000111110---0
Argiope lobata	1000010 01--00101110010121011111100000-010
Gea spinipes	0000010 1------0001001010011111100001?110
Cyrtophora citricola	1001100 01--0??1000001001010000100111110
Acusilas africanus	1111101000201100110001000100100111110100
Acusilas callidus	???????????????????????1100010010011110100
Acusilas coccineusT	1111100001010010000111000100100111111110
Acusilas coccineusJ	0111100001010010000111000100101111111100
Acusilas dahoneus	???????????????????????1100010010011110100
Acusilas malaccensis	1111100001001111111000100010010011111111
Acusilas spiralis	?1111000011110100001??????????????????????
Acusilas 'unassigned'	???????????????????????1100010010111111111
Acusilas vei	?1111010 0?001111001-??????????????????????
Acusilas vilei	?1111000012011110 01-??????????????????????

Appendix 3. Character descriptions.

1. Male size: (0) normal, (1) small. Spider males are in some cases considerable smaller than the females. We use the definition male small, if the male is equal to or smaller than 50% of the female total size (Hormiga et *al* 2000).
2. Male cheliceral condyles: (0) absent, (1) present. Unlike most araneids, *Acusilas* and *Arachnura melanura* males have modifications of the chelicera in the form of two condyles provided with setae (Fig. 4).
3. Male endite concavity: (0) absent, (1) present. Endites with a shrunken and wrinkled surface. Endites appear concave, as the inner (mesal) side and the anterior margin with serula retain their normal appearance (Fig. 5).
4. Male endite swellings: (0) absent, (1) present. The surface around the setae is not shrunken, as is otherwise the case for the rest of the endite. Instead it has small cylindrical swellings at the base of the setae (Fig. 5).
5. Male MA distal hook: (0) absent, (1) present. The median apophysis may be equipped with a small distal hook (Fig. 11, MA).
6. Male MA filiform spur: (0) absent, (1) present. The median apophysis may be equipped with a thread-like spur (Levi 1983, fig. 13). Potential synapomorphy for argiopines (Levi 1983). Confirmed by Scharff and Coddington (1997).
7. Male radix distal shape: (0) parallel (1) wedge-shaped. In most of the species included in this analysis, the radix has parallel sides, but in few, like *Gasteracantha mammosa* and *Acusilas africanus* the edges are diverging distally, giving radix a wedge-shaped appearance.
8. Male stipes: (0) present, (1) absent.
9. Male stipes proximal apophysis: (0) present, (1) absent.
10. Male stipes proximal apophysis attachment: (0) attached, (1) detached. The stipes of *Acusilas africanus* has a large outgrowth basally (Fig. 12B, Sto). It is not attached to stipes in the other species of *Acusilas*, but is found as a separate sclerite placed between stipes and radix (Fig. 12A, Sas).
11. Male stipes proximal apophysis shape: (0) rectangular, (1) curved, (2) triangular, (3) bifid. Stipes proximal apophysis comes in various shapes.
12. Male stipes-embolus junction: (0) membranous, (1) fused. The connection between stipes and embolus may be either fused or membranous. There is no visible transition between the sclerites in the fused connection, embolus just continues as a smooth extension of the stipes (Fig. 19E). In the membranous type there is a large unpigmented and weakly sclerotized area between stipes and embolus (Fig. 12B, MZ). Embolus is recognized in both types by the entrance of the sperm duct from the distal haematodocha into the embolus (Fig. 34B, SD).
13. Male stipes-embolus turns: (0) less than1.5 turns, (1) more than 1.5 turns. Stipes and embolus, taken together, are spiral-shaped and makes a number of turns. In *Acusilas coccineus* stipes-embolus makes less than 1.5 turns (Fig. 19E), while there are more turns in other species (Fig. 30B).
14. Male stipes-embolus plane: (0) one plane, (1) more than one plane. In the unexpanded palp, the stipes-embolus complex may be lying in one plane (Fig. 30B), or the embolus may be turned several degrees relative to the plane of stipes (Fig 32B).
15. Male embolus direction: (0) clockwise, (1) anti-clockwise. The direction of embolus is determined by a lateral view of the left palp in the unexpanded palp (Levi 1986 figs 9 and 14, Scharff and Coddington 1997). Most species of *Acusilas* have emboli that run in an anti-clockwise direction, but in *Acusilas africanus* (Fig. 16E) it is clock-wise.
16. Male embolic basal thorn: (0) absent, (1) present. Some of the species with a membranous zone between embolus and stipes (character 12, state 0) have a proximal thorn on the embolus just next to the membranous zone (Figs 25E, F).
17. Male embolic distal head: (0) absent, (1) present. The embolus of some species have characteristic distal modifications (Fig.17), while others have a pointy and unelaborated apex (Fig. 34, EmT).
18. Embolic truncus: (0) present, (1) absent. The truncus is the densely chitinized outer (convex) side of the embolus (Comstock 1910). The embolus is without a truncus in some *Acusilas* species (Fig. 25F), while it is found in others. It is especially easy recognizable in *Acusilas coccineus* (Figs 11B, 19E, 20B).
19. Male embolic pars pendula: (0) present, (1) absent. The pars pendula is formed on the inside (concave) side of the truncus. It is a membranous flap containing the sperm duct (Comstock 1910). *Acusilas vei* and *vilei* are missing the pars pendula. The embolus of each of these two species consists of truncus only (Figs 32, 34).
20. Male pars pendula pigmentation: (0) present, (1) absent. The sperm duct is easy to see in the unpigmented pars pendula (Fig. 20B), while it may be a little harder to see in the pigmented pars pendula (Fig. 25F).

21. Female abdominal shape: (0) triangular-like, (1) oval, (2) angular. In dorsal view, the female abdomen may have various shapes. The triangular-like abdomen is truncated anteriorly and pointed posteriorly (Fig. 15A) – when not filled with eggs – otherwise more rounded. We use the term oval to cover the shape of an abdomen, which is oblong and have rounded corners (Fig. 18A). The angular abdomen is defined here as being more or less square in outline.

22. Female carapace furrow: (0) absent, (1) present. This furrow delimits the head region from the thoracic region. It is diagnostic for *Acusilas* females, but is also found outside the genus (Fig. 6A).

23. Female carapace shape (in a lateral view). (0) normal, (1) flat, (2) raised. The cephalic and thoracic parts are both equally high in the normal carapace. A flat carapace is seen in e.g. *Argiope* and a raised carapace has the cephalic part raised relative to the thoracic part.

24. Female cephalon hairiness: (0) scattered, (1) normal, (2) dense. This character describes the hairiness of the cephalic region. This is of course rather arbitrary, but we include it here because there is a clear difference between the dense covering in e.g. *Argiope* (2) and the few scattered setae in *Acusilas* (0) (Fig. 6A). *Araneus* among others is seen as an intermediate (1).

25. Female ocular quadrangle: (0) wider than long, (1) longer than wide. The anterior and posterior median eyes delimit the ocular quadrangle. If AOQ is greater than AOQ-POQ, the ocular quadrangle is wider than long (0). If AOQ is smaller than AOQ-POQ, the ocular area is longer than wide (1).

26. Female AME placement: (0) closest to AME, (1) closest to ALE. AME are placed distinctly closer to one another, than to ALE in most araneid species, but in few species like *Acusilas* and *Gea* there is an atypical eye pattern, where AME are placed closer to ALE than to each other.

27. Female ALE size: (0) normal, (1) reduced. ALE are normally a little smaller than PLE. But ALE of argiopines are even further reduced in size compared to the normal condition (Levi 1983).

28. Female ALE direction: (0) lateral, (1) ventral. While ALE turns laterally in most spiders, they turns downwards in argiopines (Levi 1983).

29. Female LE separation: (0) less than 0.5 diameter, (1) more than 0.5 diameter. LE are often placed so close, that they almost touch each other. However, in others eyes are clearly separated, and the distance is more than half the eye diameter (Levi 1983).

30. Female PE row: (0) recurved, (1) procurved. A procurved PE row is an argiopine autapomorphy (Levi 1983, Scharff and Coddington 1997).

31. Female PE spacing: (0) almost equal, (1) PME closest to PME. The eyes of the posterior eye row may all be approximately equally spaced or the PME may be placed closer to one another than to PLE.

32. Female femur III length versus patella+tibia III length: (0) longer, (1) shorter. Levi (1997) found that the genera *Mecynogea*, *Manogea*, *Kapogea*, *Cyrtophora, Argiope* and *Gea* shared a femur III length longer than the sum of patella and tibia.

33. Female femur IV length versus patella+tibia IV length: (0) longer, (1) shorter. Levi (1997) found that the genera *Mecynogea*, *Manogea*, *Kapogea*, *Cyrtophora, Argiope* and *Gea* shared a femur IV length longer than the sum of patella and tibia.

34. Female metatarsus+tarsus IV length versus patella+tibia IV length: (0) longer, (1) shorter. Levi (1997) found that the genera *Mecynogea*, *Manogea*, *Kapogea*, *Cyrtophora, Argiope* and *Gea* shared relatively shorter patellae and tibiae than in all other araneid genera. Characters 32 and 33 test the femora relative to patella and tibia and this character tests metatarsi and tarsi relative to patellae and tibiae. Levi (1997) states that these measurements apply to all the legs, but for the sake of simplicity, we have chosen only to use leg four.

35. Female epigyne anterior rim: (0) absent, (1) present. The epigyne may have a shiny sclerotized transverse rim (Levi, 1983) (Fig. 7A, AR).

36. Female anterior rim lateral extension: (0) absent, (1) present. The anterior rim may constitute both anterior and lateral edges of the epigynum (Fig. 7A, B), or it may form the anterior edge only (Fig. 23A).

37. Female septum shape: (0) longer than broad, (1) broader than long. Septum of epigyne (Levi 1983) is longer than broad, when the sagittal axis of the septum is longer than the transverse axis (Fig 16A). Accordingly, the septum is broader than long, when the transverse axis of the septum is longer than the sagittal axis (Fig. 25A, B).

38. Female septum transparency: (0) transparent, (1) opaque. Some species have a transparent septum, which make it possible to see the underlying copulatory ducts (Fig. 19A). The septum of other species may have a whitish pigmentation obscuring any structures lying behind (Fig. 25A).

39. Female septum pockets: (0) absent, (1) present. The septum has two lateral openings (Fig. 36A).

Appendix 4. Exemplar taxa used in the species level phylogeny.

Araneus quadratus Clerck, 1758: Male and female. Denmark, Dragør Golfklub 7.viii.2003, J. B. Schmidt leg. (ZMUC).

Gasteracantha mammosa (C.L. Koch, 1844): Female. Philippines, Bagnio 1929, G. G. Haslam. W. Robinson bequest (ZMUC). Male. Japan, Okinawa Pref., Iriomotejima Is., Otomi, 1.iv.1987, A. Tanikawa leg. (ZMUC).

Arachnura melanura Simon, 1867: Female. Singapore, Seletar Reservoir, N 1°24', E 103°48', forest, 7.xi.1991, < 100 m, M. Andersen, O. Martin, & N. Scharff leg. (ZMUC). Male. Japan, Iriomotejima Is., Urauchi, 28. xii. 1989, A. Tanikawa leg. (ZMUC)

Argiope lobata (Pallas, 1772): Female. Morocco. El Araish (Larache) (no date), William Sørensen det. (ZMUC). Male. Maltese Isl., Malta, Melleiha Bay; Ghadira. 19.–31.viii.1992. B. Petersen leg. (ZMUC).

Gea spinipes C.L. Koch, 1843: Female. Thailand, Yala Prov., Bang Lang NP, 6° 04' N, 101°11' E, lowland rainforest. 20.x.1991, M. Andersen, O. Martin & N. Scharff leg. (ZMUC). Male. Thailand, Satun Prov., Thale Ban NP. Forest at Yaroi Waterfall, 6°45' N, 100°10' E, < 400 m., 24.x.1991, M. Andersen, O. Martin & N. Scharff leg. (ZMUC)

Cyrtophora citricola (Forsskål, 1775): Female. W. Africa, Isle San Tome, Dec.–Febr.1950–51. Galathea Exp. (ZMUC). Male. Spain. Tenerife, Arafo, Casa Alemana. Dec 1956. A. M. Hemmingsen (ZMUC).

Acusilas africanus Simon, 1895: Female. French Congo: Benito River, Bates leg. (BMNH). Males. Tanzania, Tanga Region, East Usambara Mts., 12 km SE of Amani, Kihuhwi–Zigi, E 38°40.6', S 5°6.3', 2–4.xi.1995, 400–450 m., C.E. Griswold, N. Scharff & D. Ubick leg. (ZMUC).

Acusilas callidus sp. nov.: Female holotype. Indonesia: Sulawesi, Togian Islands, Pulau Batu Daka, forest, 30.viii.1987, D. Bilbon leg. (RMNH).

Acusilas coccineus Simon, 1895: Male and female. Japan. Okinawa Pref., Iriomotejima Is. Takana, 29.iii.2000, A. Tanikawa leg. (ZMUC).

Acusilas coccineus Simon, 1895: Female. Thailand, Prov. Nakhon Ratchasima, Khao Yai National Park, 27.xii.1988, 1000 m., C.L. & P.R. Deeleman leg. (RMNH). Male. Thailand Prov. Nakhon Ratchasima, Khao Yai National Park, 12.xi.1987, 1000 m., seconday forest, C.L. & P.R. Deeleman leg. (RMNH).

Acusilas dahoneus Barrion & Litsinger, 1995: Female holotype. Philippines, Luzon Island, Cagayan Province, Solana, Banga village, 21.ix.1981, A.T. Barrion leg. (IRRI).

Acusilas malaccensis Murphy & Murphy, 1983: Female. Thailand, Nakhon Si Thammarat Province, Khao Luang National Park, N 8º43'25,2'' E 99°40'7,7'', 355 m., 10-12.x.2003, N. Scharff & J. Birkedal Schmidt leg. (ZMUC). Male. Thailand Surat Thani Province, Khao Sok National Park, Bang Hua Raed, N 8°55'0,4'' E 98°31'40,9'', 300 m., 19–20.x.2003, N. Scharff & J. Birkedal Schmidt leg. (ZMUC).

Acusilas spiralis sp. nov.: Male holotype. Indonesia. Sumatra, Gunung Leuser NP., Bohorok Rehab. Centre. 15.ix.1983. Suh. Djosudharmo leg. (RMNH).

Acusilas vei sp. nov: Male holotype. Indonesia: Sulawesi, Lore Lindu Reserve, Marena Palu, 24.vii.1982 (RMNH).

Acusilas vilei sp. nov.: Male holotype. Indonesia: Sulawesi, Utara, Dumogo-Bone National Park, xi.1985, Project Wallace leg. (BMNH)

Acusilas sp.: Females. Indonesia: Sulawesi, Marena Palu, Lore Lindu Reserve, 24.vii.1982 (RMNH); Indonesia: Sulawesi, Utara, Dumogo-Bone National Park, xi.1985, P. Hillyard leg. (BMNH).