Weintrauboa, a new genus of pimoid spiders from Japan and adjacent islands, with comments on the monophyly and diagnosis of the family Pimoidae and the genus *Pimoa* (Araneoidea, Araneae)

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Received July 2002; accepted for publication February 2003

The spider genus Weintrauboa new genus (Araneae, Pimoidae) is described to place two species of pimoids from Japan and adjacent islands that were formerly classified in the linyphiid genus Labulla. Weintrauboa contortipes (Karsch) new comb., the type species, and W. chikunii (Oi) new comb. are redescribed. Parsimony analysis of morphological characters provides robust support for the monophyly of the genus Weintrauboa and corroborates the monophyly of Pimoa, Pimoidae, and the clade Linyphiidae plus Pimoidae. New diagnoses for Pimoa and Pimoidae are provided. © 2003 The Linnean Society of London, Zoological Journal of the Linnean Society, 2003, 139, 261–281

ADDITIONAL KEYWORDS: cladistics - Linyphiidae - morphology - phylogeny - systematics - taxonomy.

INTRODUCTION

'Linyphioid' spiders (Linyphiidae plus Pimoidae) are one of the largest lineages of the order Araneae and include the most speciose family-level clade of webweaving spiders, the family Linyphiidae (Platnick's (2003) on-line catalogue lists 559 valid linyphiid genera, grouping more than 4200 species). Pimoidae, the sister lineage of Linyphiidae, is a relictual group that contains a single genus and 22 described species. Understanding pimoid systematics is critical for the study of phylogenetic relationships within the Linyphiidae because of the role pimoids can potentially play in character polarization by outgroup comparison (Hormiga, 1993, 1994a). The discovery of a second genus of pimoids provides a modest increase in species richness (from 22 to 24 species) but a dramatic increase in the diversity of the male genital morphology. Because genital characters, especially those of the male, are an astonishingly rich source of phylogenetic data, it seems appropriate to study in close detail the morphology of these new pimoids. Although the species included in the new pimoid genus had already been described (one of them more than a century ago),

new descriptions are necessary to understand genital homologies and to reconstruct their phylogenetic placement.

Eugène Simon (1884) erected the linyphiid genus Labulla to accommodate the European species Linyphia thoracica Wider. Since then, Labulla has contained a diverse array of linyphiid and pimoid species, most of them not closely related to the type species (L. thoracica). As a result there have been numerous generic transfers, of which the most recent have been the two 'Labulla' species described by Simon (1900) from Hawaii, currently placed in the linyphiid genus Orsonwelles Hormiga (Hormiga, 2002; Hormiga, Arnedo & Gillespie, 2003). From a modern perspective, it looks as if the genus Labulla had been used as a dumping ground for morphologically deviant linyphioids. As presently delimited the genus Labulla is polyphyletic (Hormiga, 1994b, 2002). Labulla nepula Tikader, from India, is not congeneric with the type species. Only two species of the six currently classified in Labulla seem to be congeneric with L. thoracica, namely, L. flahaulti Simon (from France) and L. impudica Denis (from Algeria) (Hormiga, 2002). Detailed examination of the two 'Labulla' species from Japan and adjacent islands, L. contortipes (Karsch) and L. insularis (Saito) (= L. chikunii), shows

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that these taxa belong into the family Pimoidae. In this paper these Japanese species will be redescribed and its phylogenetic affinities explored using a cladistic approach. In light of this new evidence, Hormiga's (1994a) diagnoses for Pimoidae and *Pimoa* are also revised.

MATERIAL AND METHODS

Morphological methods are described in detail in Hormiga (2000, 2002). Taxonomic descriptions follow the format of Hormiga (1994a, 2002). Specimens were examined and illustrated using a Leica MZAPO stereoscopic microscope, with a camera lucida. Further details were studied using a Leica DMRM compound microscope with a drawing tube. Some microscope images were recorded using a Leica DC-200 digital camera and edited using the software package Auto-Montage. A LEO 1430VP scanning electron microscope was also used to study and photograph morphological features. Left structures (e.g. palps, legs, etc.) are depicted unless otherwise stated. Most hairs and macrosetae are usually not depicted in the final palp drawings. All morphological measurements are given in millimetres. Somatic morphology measurements were taken using a scale reticle in the dissecting microscope. Eye diameters are taken from the span of the lens. The cephalothorax length and height were measured in lateral view and its width was taken at the widest point. Similarly, the length and height of the abdomen were measured in lateral view and the width as the widest point as seen from a dorsal view. The measurements of the abdomen are only approximations because the abdomen size changes more easily in preserved specimens than do other more sclerotized parts (e.g. the chelicerae). The total length was measured in lateral view and is also an approximation because it involves the size of the abdomen and its relative position. Approximate leg article lengths were measured in lateral view, without detaching the legs from the animal, by positioning the article being measured perpendicularly. The position of the metatarsal trichobothrium is expressed as in Denis (1949) and Locket & Millidge (1953). Female genitalia were excised using surgical blades or sharpened needles. The specimen was then transferred to methyl salicylate (Holm, 1979) for examination under the microscope, temporarily mounted as described Coddington (1983). Male palps examined with the SEM were first excised and transferred to a vial with 70% ethanol and then cleaned ultrasonically for 1–3 min. The specimen was then transferred to absolute ethanol and left overnight. After critical point drying, the specimens were glued to rounded aluminium rivets using an acetone solution of polyvinyl resin and then Au/Pd coated for examination at the SEM.

ANATOMICAL ABBREVIATIONS USED IN THE TEXT AND FIGURES

Male palp

BH basal haematodocha

C conductor CB cymbium

CP cymbial process (CDP in Hormiga, 1994a)

E embolusEF embolic flap

m membrane (or membranous)

MA median apophysis P paracymbium

PCS pimoid cymbial sclerite PEP pimoid embolic process

ST subtegulum T tegulum

Epigynum

CD copulatory duct
CO copulatory opening
FD fertilization duct
S spermatheca

Somatic morphology

ACaciniform gland spigot(s) AG aggregate gland spigot(s) ALS anterior lateral spinneret **AME** anterior median eye(s) CYcylindrical gland spigot(s) FLflagelliform gland spigot(s) MAP major ampullate gland spigot(s) mAP minor ampullate gland spigot(s) PIpiriform gland spigot(s)

PLE posterior lateral eye(s)
PLS posterior lateral spinneret
PME posterior median eye(s)
PMS posterior median spinneret

Institutional abbreviations used in text are given in the 'Acknowledgements' section.

CLADISTIC ANALYSIS

Taxa

The taxonomic sample used in the cladistic analysis was designed to test the monophyly of *Weintrauboa* and *Pimoa* and builds on my previous phylogenetic work on the higher level phylogenetics of 'linyphioids' (Hormiga, 1994a, b, 2000, 2002; Hormiga *et al.*, 2003). The monophyly of *Pimoa* had been previously tested by Hormiga (1994a); in the present study *Pimoa* is represented by four species (out of 22 described species), including the two most basal taxa in Hormiga's (1994a: fig. 442) preferred cladogram, *P. rupicola*

(Simon) and P. breuili (Fage). The goal of this analysis was not to reconstruct intrageneric relationships in *Pimoa* but to test the monophyly of *Weintrauboa* and to study how the inclusion of this latter genus affects the monophyly and diagnosis of Pimoa. Outgroup taxon selection follows the taxonomic sample of Hormiga (2000). The Linyphiidae sample attempts to represent morphological diversity at the subfamilial level; a reduced sample of Erigoninae was used because identifying erigonine intergeneric relationships is not one of the goals of this analysis (nonetheless, 13 genera out of the 31 used by Hormiga, with emphasis on the basal erigonine lineages, follow Hormiga's preferred optimal cladogram (fig. 38)). Labulla thoracica was included in the analysis to test the conjecture that the Japanese taxa are only distantly related to the type species of Labulla. Representatives of three araneoid families (Tetragnathidae, Theridiosomatidae and Theridiidae) were used to root the 'linyphioids'.

Characters

A total of 75 characters were scored (Appendices 1 and 2, Figs 1–10): 39 male and nine female genital characters, 24 somatic morphological characters, and three behavioural characters (see Appendix 1). These characters are those of Hormiga (2000), with some changes to accommodate increased representation of pimoids and the addition of *Labulla thoracica*. A total of seven characters are parsimony uninformative in this taxonomic context, but were kept in the analysis because they are potentially useful to reconstruct 'linyphioid' relationships.

Analyses

The parsimony analyses were performed using the computer programs Hennig86 version 1.5 (Farris, 1988), NONA version 2.0 (Goloboff, 1993). WinClada version 1.00.08 (Nixon, 1999) and Nexus Data Editor 0.4.9 (Page, 2001) were used to study character optimizations on the cladograms and to build and edit the character matrix, respectively. Ambiguous character optimizations were usually resolved so as to favour reversal or secondary loss over convergence (Farris optimization or ACCTRAN); if not, the optimization scheme is discussed in the text. The 14 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch, 1971). NONA (Goloboff, 1993) was used to calculate Bremer support indices (BS; 'decay indices') (Bremer, 1988, 1995; Donoghue *et al.*, 1992).

RESULTS

Heuristic searches under 'amb-' using 1000 replicates of mult TBR + TBR (mult*max*) resulted in four min-

imal length trees of 172 steps, with CI and RI of 0.56 and 0.74, respectively (the strict consensus cladogram is presented in Fig. 11). Exclusion of the seven parsimony uninformative characters reduces tree length to 164 steps and the CI to 0.54. Successive character weighting in Hennig86, which weights characters by their rescaled consistency index, produces stable results (eight trees) in the second iteration, with a strict consensus cladogram that is topologically identical to that of the consensus cladogram under equal weights. Using the command 'amb=' in NONA to interpret clade support produces eight topologies of minimal length, summarized by the same strict consensus cladogram than results from the analysis under 'amb-' (i.e. Fig. 11).

Topological conflict among the most parsimonious topologies resides in two areas. The first one is the resolution of the trichotomy *Stemonyphantes*, Mynogleninae (*Haplinis* plus *Novafroneta*) and Erigoninae. The second involves a distal erigonine clade that includes the genera *Drepanotylus*, *Sciastes* and a clade containing *Islandiana*, *Erigone* and *Walckenaeria*. None of these areas of conflict is particularly relevant for the problem at hand (pimoid higher level systematics) and they have already been discussed in Hormiga (2000). One of the four minimal length trees (under equal weight and 'amb-') has been arbitrarily selected to optimize character changes and to discuss character evolution (Fig. 12).

DISCUSSION

Detailed examination of the Japanese Labulla species shows that they are not linyphiids, but members of the family Pimoidae. In the absence of a generic circumscription to include these two species, a new genus is created to place them. The results of the cladistic analysis show that Weintrauboa contortipes and W. chikunii are sister species, and that Weintrauboa is the sister lineage of Pimoa. The addition of these two species to the family Pimoidae changes the diagnosis of both Pimoidae and Pimoa. Until now, Pimoa was the only member of Pimoidae, and thus the diagnosis and composition of the genus and the family were identical. Inclusion of Weintrauboa in the family indicates that the monophyly of Pimoidae is supported by the following unambiguous putative synapomorphies: a dorsoectal cymbial process, presence of cymbial cuspules, a retrolateral cymbial sclerite (PCS), and the embolic process (PEP). Under Farris optimization the cheliceral stridulatory striae are interpreted as secondarily absent (lost) in Weintrauboa.

The male genital morphology of Weintrauboa is rather different in the details from that of Pimoa,

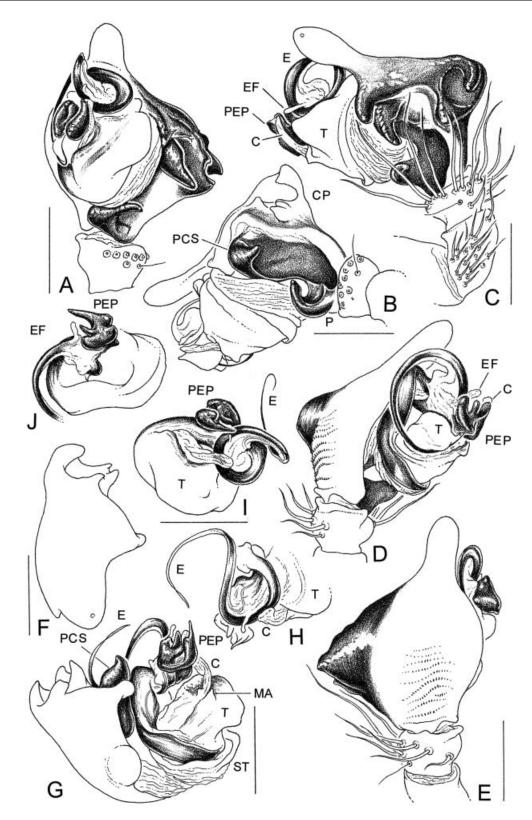


Figure 1. Weintrauboa contortipes (Karsch) n. comb., male palp. A–F, from Doi, Sakuto-Cho, Okayama Pref., Japan; E–J, from Japan (MNHN 3837), partially expanded. A, ventral; B, caudoectal; C, ectal; D, mesal; E, dorsal; F, cymbium, apical; G, apical; H–J, details of tegular division. Scale bars, 0.5 mm.

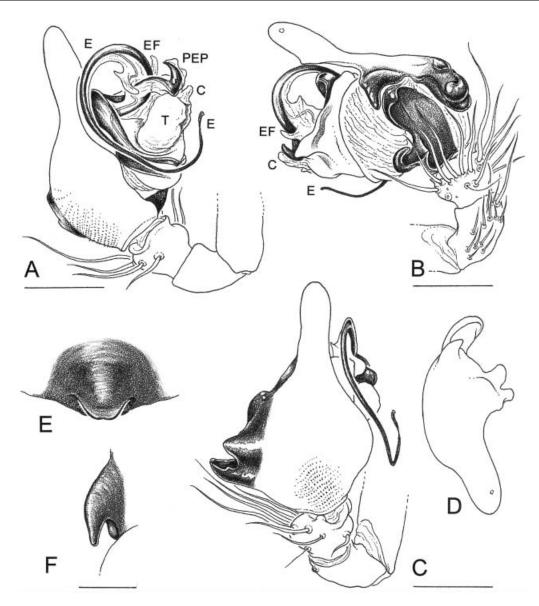


Figure 2. Weintrauboa chikunii (Oi) n. comb. (A–D), W. contortipes (Karsch) n. comb. (E–F). A–F, male palp, from Juzhno-Sakhalinsk, Sakhalin Island, Russia; E,F, epigynum, Mt Takiyama, Nagi-cho, Katsuta-gun, Okayama Pref., Japan. A, mesal; B, ectal; C, dorsal; D, cymbium, apical; E, ventral; F, lateral. Scale bars, 0.5 mm (A–D), 0.25 (E,F).

although it has the basic elements of pimoid palpal anatomy. The *Weintrauboa* palp has a large cymbial ectal process (with cuspules located at the base of the cymbium, not in the process itself as in the palp of *Pimoa*), a cymbial sclerite, continuous with the paracymbium (as in *Pimoa breuili* and *P. rupicola*), and an embolic process whose morphology is quite different from the homologous structure in *Pimoa*. The presence in *Weintrauboa* of a paracymbium attached to the cymbium by means of a membrane ('intersegmental paracymbium', Figs 1B,C, 2B, 5A, 6A) allows for the interpretation of this paracymbium condition as a symplesiomorphy in Linyphiidae. The intersegmental

paracymbium of linyphiids has been classically regarded as one of the synapomorphies of the family (e.g. Hormiga, 2000). In the sister lineage of 'linyphioids', the so-called 'Spineless femur clade' (sensu Griswold et al., 1998) which includes cyatholipoids plus theridioids, the paracymbium is continuous with the cymbium, without a membranous connection ('integral paracymbium'). The cladistic results suggest that the intersegmental paracymbium could have evolved in the common ancestor of pimoids and linyphiids, and that in *Pimoa* the paracymbium may be secondarily integral. In summary, the presence of an intersegmental paracymbium is now interpreted as

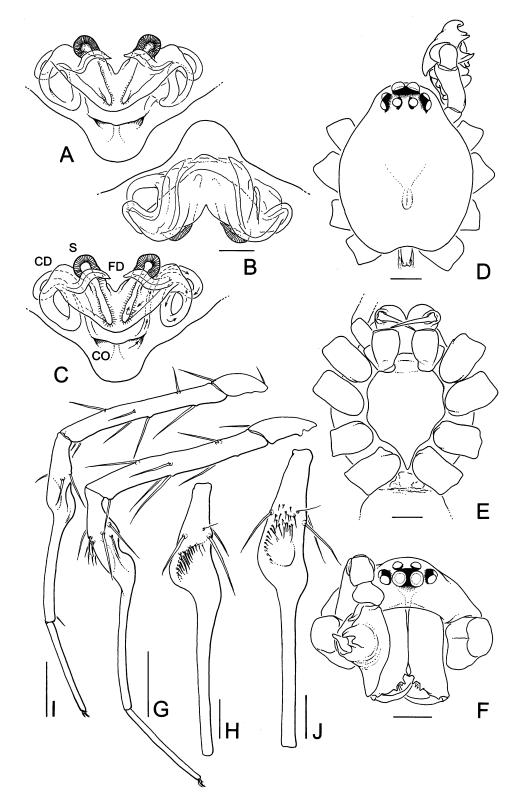


Figure 3. Weintrauboa contortipes (Karsch) n. comb. (A–H), W. chikunii (Oi) n. comb. (I,J). A, epigynum (cleared), dorsal; B, epigynum (cleared), ventral; C, epigynum (cleared), dorsal (schematic); D, prosoma, dorsal; E, prosoma, ventral; F, prosoma, anterior; G, male first leg, lateral; H, male first metatarsus, dorsal; I, male first leg, lateral; J, male first metatarsus, dorsal. Scale bars, 0.1 mm (A–C), 0.5 (D–F, H,J), 1.0 (G,I).



Figure 4. Weintrauboa contortipes (Karsch). Male (A) and female (B) from Doi, Sakuto-Cho, Okayama Pref. (Japan). Carapace width 2.15 (male), 2.25 (female).

a synapomorphy of 'linyphioids' (Pimoidae plus Linyphiidae), rather than as a synapomorphy of Linyphiidae. Analysis of these new data suggests that the monophyly of Linyphiidae is supported by the following six synapomorphies: the typical linyphiid paracymbium (usually U or J shaped), presence of a suprategulum, absence of a median apophysis and conductor, presence of a radix and presence a column membrane between the embolic and tegular division.

Little is known about the epiandrous fusules of pimoids and linyphiids. Hormiga (2002) documented these male fusules in eight species of Orsonwelles and discussed variation in the morphology of the fusules in Linyphiidae. In the few studied pimoid species the arrangement of the epiandrous fusules varies from singles (Pimoa altioculata (Keyserling), Fig. 9C,D) to clusters of 2–5 fusules (*P. breuili* (Fage), Fig. 9E,F; Weintrauboa contortipes, Figs 6E,F, 9A,B). P. breuili the epiandrous spigots are grouped, but they do not come out from a common pit as they do in Weintrauboa contortipes (e.g. Fig. 9B) and in some linyphiids (e.g. in Labulla thoracica). Although Marples (1967: 221) had reported substantial intraspecific variation in the number of fusules, we still lack a solid understanding of the levels of intraspecific variation, which is essential to assess the phylogenetic information content of this character system.

Pimoids are a relictual group, distributed in the western coast of North America, Europe (the Alps and the Apennines, and the Cantabrian Mountains of northern Spain), and the Himalayas. Their disjunct pattern suggests an ancestral widespread Holarctic distribution, with subsequent extinction in the inter-

vening areas (Hormiga, 1994a). Hormiga (1994a) had suggested that new species of pimoids probably existed in the Himalayas. The recently described new species from the Gaoligong Mountains of China (Griswold, Long & Hormiga, 1999) confirms that prediction. The Japanese species described in this paper significantly expand the geographical range of the family Pimoidae.

SYSTEMATICS

PIMOIDAE WUNDERLICH, 1986

Pimoinae. Wunderlich (1986: 16)

Pimoidae. Hormiga (1993), type genus by monotypy *Pimoa* Chamberlin and Ivie.

Diagnosis

Male palpus with a retrolateral cymbial sclerite, a dorsoectal cymbial process, and cuspules on either the cymbial process (*Pimoa*; Hormiga 1994a: figs 11, 68) or the dorsal surface of the cymbium (*Weintrauboa*; Fig. 1E, 5E). Conductor and median apophysis present in most species. Embolus continuous with the tegulum (the typical linyphiid embolic division is absent), with an embolic process of varying morphology. The epigynum is protruding, with a dorsal to lateral fold or groove with the copulatory opening at the distal end (Hormiga, 1994a: figs 14, 414; Fig. 3A); fertilization ducts are anteriorly (*Pimoa*) or mesally (*Weintrauboa*) orientated. As in linyphiids, pimoids have stridulatory striae on the ectal side of the chelicerae (but the striae

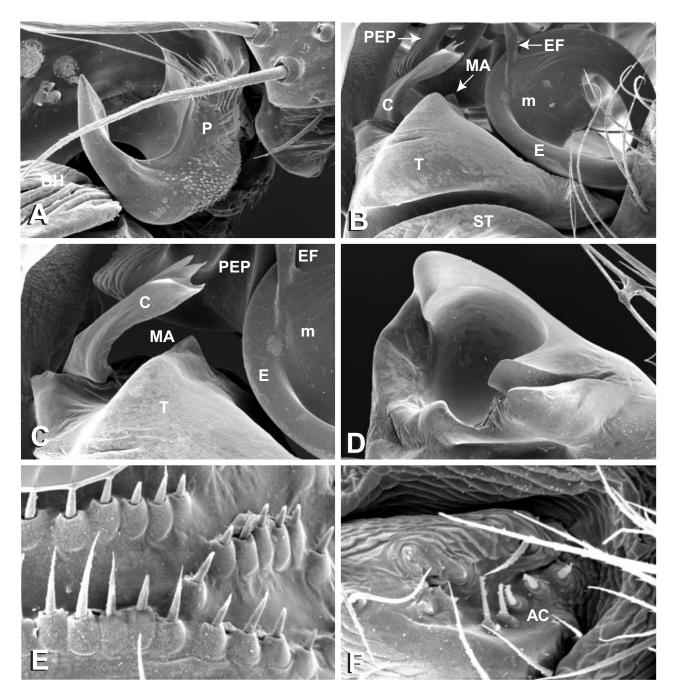


Figure 5. Weintrauboa contortipes (Karsch). A, paracymbium, ectal; B, tegular division, ectal; C, tegular division, detail; D, cymbial process; E, cymbial cuspules; F, male PLS.

are absent in *Weintrauboa*), build sheet-webs and exhibit autospasy at the patella-tibia junction.

Description

See Hormiga (1994a) for family description.

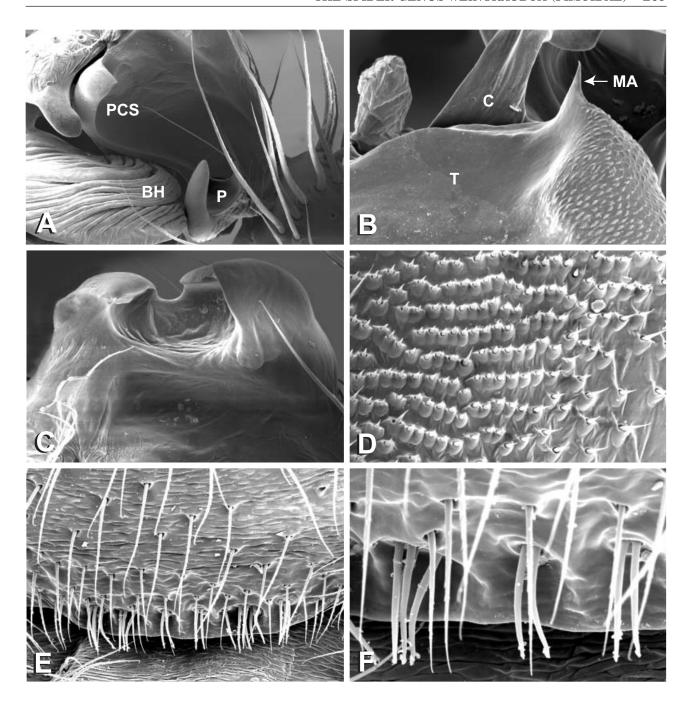
Phylogenetics

The monophyly of Pimoidae is supported by the

following four unambiguous putative synapomorphies: a dorsoectal cymbial process, cymbial cuspules, a retrolateral cymbial sclerite (PCS) and the embolic process (PEP).

Composition

Two genera, *Pimoa* Chamberlin & Ivie and *Weintrau-boa* new genus.



 $\textbf{Figure 6. Weintrauboa\ chikunii}\ (Oi)\ (A-D), \textbf{W.\ contortipes}\ (Karsch)\ (E,F).\ A,\ paracymbium\ and\ pimoid\ cymbial\ sclerite,\ ectal;\ B,\ detail\ tegular\ division,\ ectal;\ C,\ cymbial\ process;\ D,\ cymbial\ cuspules;\ E,\ male\ epiandrous\ fusules;\ F,\ male\ epiandrous\ fusules,\ detail.$

WEINTRAUBOA NEW GENUS

Type species: Linyphia contortipes Karsch, 1881

Etymology

Named after Professor Dr Robert L. Weintraub (1912–1996), benefactor of the systematics programme at

The George Washington University. *Weintrauboa* is an undeclinable proper name and masculine in gender.

Diagnosis

Weintrauboa differs from Pimoa by the following combination of characters: male palpal tibia lacking dorsal

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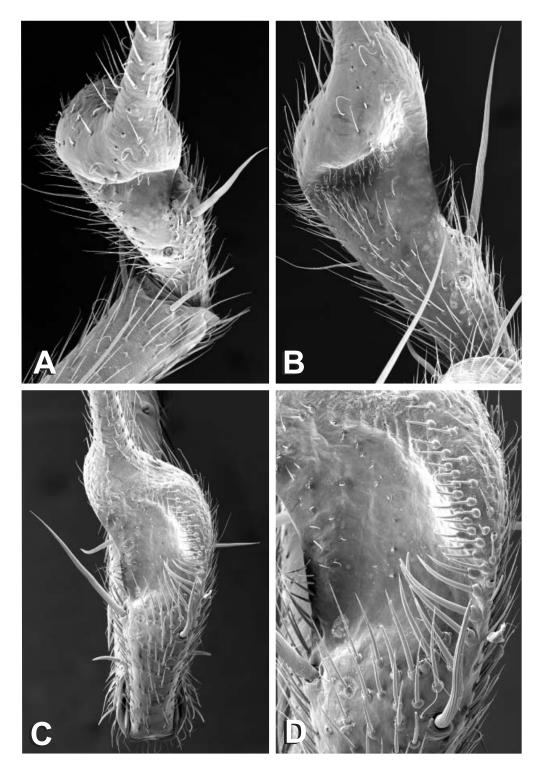


Figure 7. Weintrauboa contortipes (Karsch), male first metatarsus. A, ectoventral; B, ventral; C, dorsal; D, dorsal.

process; distal end of cymbium finger-like; dorsoectal cymbial process heavily sclerotized and without cuspules; cuspules arranged in rows, on dorsal surface of the cymbium; absence of an alveolar sclerite on the ventral side of the cymbium; a small elongated mem-

brane, the embolic flap, arising from the area where the embolic process (PEP) connects to the embolus; PEP embolic process compact (filiform or lamelliform in *Pimoa*), of varying morphology; enlarged and sinuous metatarsal I base in males; cheliceral stridulatory

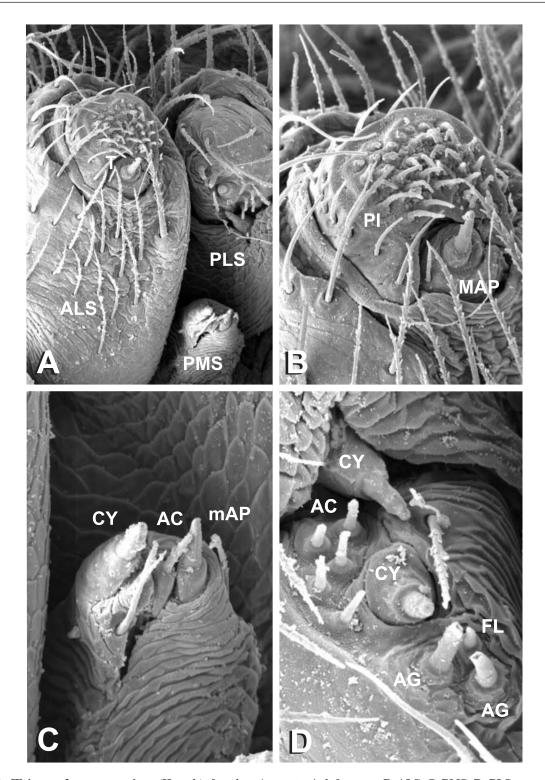


Figure 8. Weintrauboa contortipes (Karsch), female spinnerets. A, left group; B, ALS; C, PMS; D, PLS.

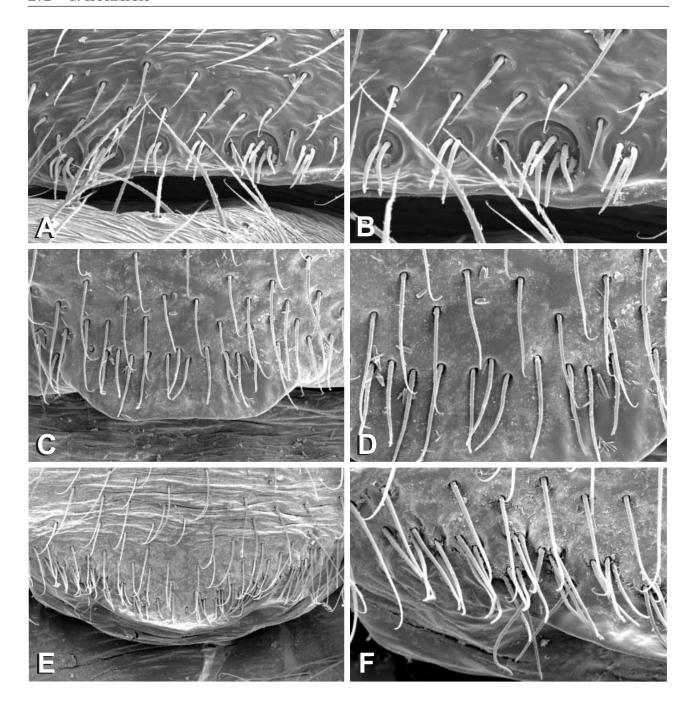


Figure 9. Pimoid epiandrous fusules. A,B, Weintrauboa contortipes; C,D, Pimoa altioculata; E,F, Pimoa breuili.

striae absent; fertilization ducts mesally orientated; and PMS with at least two and PLS with at least five aciniform spigots.

Description

Small- to medium-sized pimoid spiders, total length 4.9–6.0 in males and 4.7–8.0 in females. Carapace longer than wide, 2.2–2.9 long in males and 2.1–3.1 in

females, with a conspicuous thoracic fovea (Fig. 4). Colour photographs of $Weintrauboa\ contortipes$ (Karsch) and $W.\ chikunii$ (Oi) are published in Chikuni (1989: figs 11, 12) and Shinkai & Takano (1984: 27). Sternum longer than wide, pointed in the posterior region, slightly projecting between coxae IV (Fig. 3E). AME very close together (Fig. 3F), $c.\ 0.17$ –0.29 their diameter apart, larger than the rest, which are roughly of the same diameter; ALE and PLE juxta-

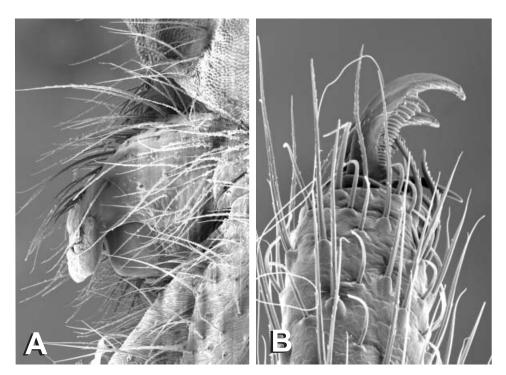


Figure 10. Weintrauboa contortipes (Karsch). A, epigynum, lateral; B, male, tarsal claws, first leg (mesal).

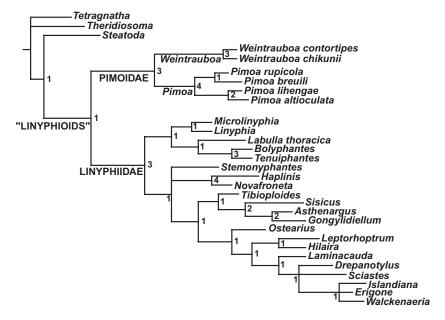


Figure 11. Strict consensus cladogram of the four minimal length trees of 172 steps that result from the analysis of the data matrix presented in Appendix 2 (L = 174, CI = 0.55, RI = 0.74). Numbers next to nodes denote Bremer support values.

posed. Clypeus height 1.38–1.5 times an AME diameter. Chelicerae large (Fig. 3F), with three prolateral and three or four retrolateral teeth; stridulatory striae absent. Legs slightly longer and slender in the adult male; femur through metatarsus usually with dark

annuli. Femur I 1.1 in males and 1.0 in females times the length of cephalothorax. Male metatarsus I proximal third enlarged and sinuous, with a row or enlarged macrosetae (Figs 3G–J, 7A–D). Tibia I–IV with two dorsal spines; prolateral and retrolateral tib-

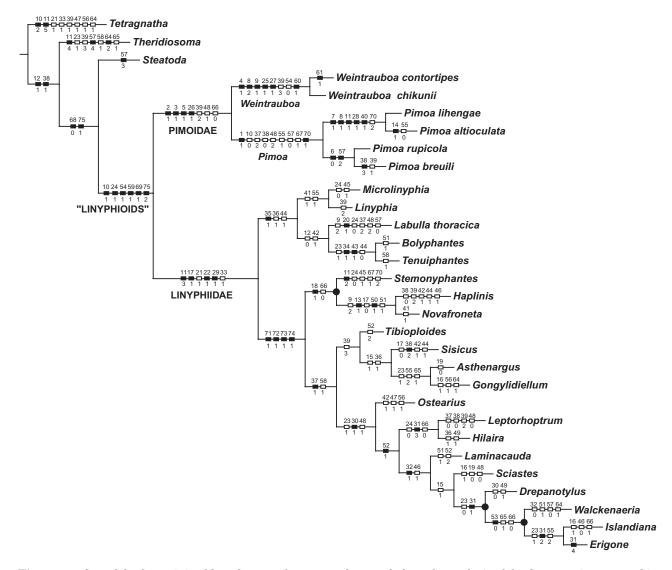


Figure 12. One of the four minimal length trees of 172 steps that result from the analysis of the data matrix presented in Appendix 2 (CI = 0.56, RI = 0.74). Exclusion of parsimony uninformative characters decreases the tree length to 164 steps and the ensemble consistency index to 0.54. Most of the ambiguous character changes are resolved under 'Farris optimization'. Closed rectangles represent non-homoplasious character changes. The three nodes that collapse in the strict consensus cladogram of the four most parsimonious trees are marked with a closed circle. The basal trichotomy has been resolved according to the araneoid topology presented in Griswold $et\ al.\ (1998)$ (see text for details).

ial spines present varying from one (male *W. chikunii*) to two (male and female *W. contortipes*); ventral tibial spines varying from four to six; femur I–IV with dorsal spines in variable numbers; femur I–IV with one dorsal spine, femur I–II with one prolateral spine, femur III–IV without prolateral spines. Metatarsal spines present in all legs. Trichobothrium metatarsus I c. 0.2; trichobothrium metatarsus IV present. Leg autospasy at the patella–tibia junction. Abdomen ovoid, longer than wide, dark brown/grey with lighter marks and some guanine spots (see photographs in Chikuni, 1989). Colulus large and fleshy, with setae. Spinnerets

(studied in one male and one female *W. contortipes*) typical of a 'linyphioid' (Hormiga, 1994a) (Fig. 8A–D). ALS with *c*. 25 piriform spigots. PMS have two aciniform spigots between the cylindrical and the minor ampullate spigot. PLS with 4–5 aciniform spigots between the two cylindrical spigots; base of the peripheral cylindrical spigot larger than the base of the distal one. The flagelliform and aggregate spigots (araneoid 'triplet') are well developed in the females (Fig. 8D), reduced to nubbins in the adult males (Fig. 5F). Epiandrous fusules (studied in one male *W. contortipes*; Figs 6E,F, 9A,B) arranged linearly

along the posterior margin of the epigastric furrow, most of them in groups of 2-5 fusules emerging from a common circular pit. The fusules have a long shaft and are somewhat shorter than the surrounding macrosetae. Tracheal system morphology unknown. Female pedipalp with tarsal claw. Male pedipalp: patella short, with several thick dorsal macrosetae (Fig. 1C). Tibia approximately as short as wide, its distal margin with a row of thick macrosetae (Fig. 1C); one prolateral and one retrolateral trichobothrium. On dorsal view, cymbium widest at it median region (Figs 1E, 2C), with a sclerotized ectal process of varying degrees of complexity that has a conspicuous concavity facing ventrally (Figs 1C, 2B); alveolus occupying the basal two-thirds of the cymbium, the distal third of the latter much narrower and finger-like (Figs 1E, 2C). Cuspules present in rows, on the proximal region of the dorsal part of the cymbium, but absent from the cymbial ectal process (Figs 1E, 2C). Paracymbium intersegmental and linguiform, broadly attached to the ectal margin of the cymbium base by means of a membrane, its proximal region continuous with the pimoid cymbial sclerite (Fig. 1B). Paracymbial apophyses absent; a sclerotized fold can be seen in the middle part of the paracymbium (Figs 1B, 2B). Pimoid cymbial sclerite connected to the cymbium by a relatively less sclerotized region (but not fully membranous), continuous with the paracymbium (Figs 1B,C, 2B). Tegulum with a conspicuous suture, delimiting an apical tegular region less sclerotized and lighter in colour than the rest of the tegulum. Conductor a small, longer than wide membrane without papillae (Fig. 5C). Median apophysis a small process on tegulum, adjacent to the base of the conductor (Fig. 5C). Embolus, widest at its base, continuous with tegular margin (Fig. 1D), in ventral view arising from the posterior region of the tegulum, curving clockwise (in left palp) around the anterior tegular area, and shortly after curving anticlockwise to an almost full circle (Fig. 1D); distal end of embolus located near the embolic process (PEP). PEP arises, in ventral view, from inner region of embolus (Fig. 1D,J); PEP compact (not filiform or lamelliform), with various processes (Fig. 1J); in the membranous area where the PEP connects to the embolus there is a small, elongated membranous flap (embolic flap, Figs 1C, 2B, 5B). Epigynum protruding less than its width (internal genitalia unknown for W. chikunii); copulatory ducts long, making several turns before reaching elongated spermathecae; fertilization ducts mesally orientated (Fig. 3A-C).

Phylogenetics

The monophyly of *Weintrauboa* is supported by at least the following putative synapomorphies: narrow

(finger-like) distal end of cymbium; embolic flap; a single retrolateral trichobothrium in male pedipalpal tibia; absence of cheliceral stridulatory striae; and the presence of an enlarged and sinuous metatarsal I base in males.

Natural history

The web of *W. contortipes* is illustrated in Shinkai & Takano (1984: 27).

Composition

Two species, Weintrauboa contortipes (Karsch) and W. chikunii (Oi).

Distribution

Japan and adjacent islands.

WEINTRAUBOA CONTORTIPES (KARSCH) NEW COMBINATION

Linyphia contortipes Karsch, 1881: 39.

Labulla contortipes Bösenberg & Strand, 1906: 170, pl. 5, figure 49, pl. 11, figures 234, 237. Yaginuma, 1971: 43, figure 41.4. Shinkai & Takano, 1984: 27. Yaginuma, 1986: 72, figure 38.2. Chikuni, 1989: 48, figure 11.

Types

Male and female syntypes from Saga, Japan (Dönitz leg.), at Institut für Systematische Zoologie, Universität zu Berlin (ZMB3545); examined. Although the syntype label states 'Saga, Japan, leg. Dönitz' this locality seems incorrect, as the Japanese spiders that Karsch described between 1879 and 1881 were collected by Dönitz around Tokyo, where he was living at the time before moving to Saga (H. Ono, unpubl. data).

Diagnosis

Males of *W. contortipes* differ from those of *W. chikunii* in the shape of the ectal cymbial process and paracymbium, the number of cymbial cuspules (more numerous in the latter species), the morphology of the PEP (larger and more complex in the former species) and in the degree of sinuosity of the metatarsus I base (less sinuous in *W. chikunii*). The female genital morphology of the two *Weintrauboa* species differs significantly in ventral view; in *W. contortipes* the epigynum appears as a protrusion of the abdomen, a subtle bulge, whereas in *W. chikunii* it has a strongly marked cordiform appearance, darker in the medial region.

Description

Male (from Doi, Sakuto-Cho, Okayama Pref.; Fig. 4A). Total length 5.43. Cephalothorax 2.54 long, 2.17 wide, 1.61 high. Sternum 1.55 long, 1.27 wide. Abdomen 2.64 long, 1.83 wide. AME diameter 0.19. Clypeus height 1.43 times one AME diameter. Chelicerae with three prolateral and three retrolateral teeth (Fig. 3F). Femur I 2.82 long, 1.11 times the length of cephalothorax. Metatarsus proximal third enlarged and sinuous, with a row of enlarged macrosetae (Fig. 3G,H). Metatarsus I trichobothrium 0.19. Pedipalp as in Figures 1A–J, 5A–E. Pedipalpal tibia with one prolateral and one retrolateral trichobothria.

Female (same locality as male; Fig. 4B). Total length 6.88. Cephalothorax 2.95 long, 2.17 wide, 1.46 high. Sternum 1.55 long, 1.40 wide. Abdomen 4.22 long, 3.22 wide. AME diameter 0.21. Clypeus height 1.38 times one AME diameter. Chelicerae with three prolateral and four retrolateral teeth. Femur I 2.81 long, 0.95 times the length of cephalothorax. Metatarsus I trichobothrium 0.22. Epigynum as in Figures 2E,F, 3A–C, 10A.

Variation

Male cephalothorax ranges in length from 2.26 to 2.81 (n=4). Female cephalothorax ranges in length from 2.14 to 3.12 (n=8). Male total length ranges from 4.88 to 5.77 (n=3). Female total length ranges from 4.65 to 8.00 (n=8).

Natural history

Sheet web illustrated in Shinkai & Takano (1984: 27); the photograph shows an inclined (c. 45°) sheet web built against a substrate, with little if any scaffolding above or below the web. Epigynal plugs are common.

Distribution

Kyūshū and Honshū islands (Japan).

Material examined

Japan: Okayama Pref., Doi, Sakuto-cho, Aida-gun, 26.i.1990, Kōichi Nojima, 1 male, 1 female (YIPC); Okayama Pref., Mt Takiyama, Nagi-cho, Katsuta-gun, 14.iii.1992, Kôichi Nojima, 1 male (YIPC); Hiroshima Pref., Mt Gokurakuji, Hatsukaichi-shi, 3.v.1991, 1 female, Yoh Ihara (YIPC); Hiroshima Pref., Taishaku-kyo Gorge, Tojo-cho, Hiba-gun, 19.vi.1996, 1 female, Yoh Ihara (YIPC); Okayama Pref., Mt Takiyama, Nagi-cho, Katsuta-gun, 4.vi.1989, Kōichi Nojima, 2 female (YIPC); Hiroshima Pref., Mt Gokurakuji, Hatsukaichi-shi, 26.i.1992, Yoh Ihara, 1 female (YIPC);

Japan: Rakusan, Shimane, 24.iv.1965, S. Kageyama, 1 female (ZMUT); Mie Pref., R. Hashimoto, no. 6, 1 male (ZMUT); 'Japan', 3837 c. St., 1 male, 1 female (MNHN).

WEINTRAUBOA CHIKUNII (OI) NEW COMBINATION

Labulla contortipes chikunii Oi, 1979: 330, figures 9–12. Chikuni, 1989: 48, figure 12.

Labula chikunii Eskov, 1992: 53 (lapsus calami; elevated from subspecies of Labulla contortipes).

N.B. Marusik et al. (1993: 75) synonymized Labulla chikunii Oi, 1979 with Lepthyphantes insularis Saito. This synonymy is rejected here. Tanasevitch & Eskov (1987: 194) had stated that Lepthyphantes insularis Saito, described after a single female specimen from the Sakhalin Island, did not belong in Lepthyphantes, based on Saito's (1935: fig. 1b) epigynum illustration (Tanasevitch & Eskov did not provide any new illustrations or redescription of insularis, nor did they examine the type). In their view, Lepthyphantes insularis should probably be transferred to Labulla, and it could be a (junior) synonym of L. thoracica, though they did not formalize any transfer or new synonymy. Oi (1979) described and illustrated both sexes of Labulla contortipes chikunii. Saito's type material, formerly at the University of Hokkaido, is presumably lost (H. Ono, unpubl. data). I have not been able to study any female specimens of chikunii (none was available for study), but Oi's illustration of the chikunii epigynum, as well as Chikuni's (1989: fig. 12) excellent colour photograph, shows substantial differences with Saito's (1935) epigynum illustration. In Lepthyphantes insularis the ventral scape is very short and wide, and the posterior edges of the ventral epigynal wall curve posteriorly. The comparable structure in *chikunii* is much longer and thinner and the posterior edges of the ventral epigynal wall curve first anteriorly before descending towards the epigastric furrow. In addition, the leg formula in insularis is 4123, whereas in chikunii it is 1243. As Marusik et al. (1993) did not base their synonymy on examination of types, and the descriptions of these two species are quite different, on the basis of the available evidence it is unjustified to synonymize Labulla chikunii with Lepthyphantes insularis.

Types

Oi's types (male holotype and one female paratype) are apparently lost (H. Ono, unpubl. data).

Diagnosis

See diagnosis of W. contortipes.

Description

Male (from Juzhno-Sakhalinsk, Sakhalin Island). Cephalothorax 2.93 long, 1.99 wide, 1.95 high. Sternum 1.64 long, 1.33 wide. Abdomen (poorly preserved, no accurate width measurement possible) 3.74 long. AME diameter 0.20. Clypeus height 1.50 times one AME diameter. Chelicerae with three prolateral and four retrolateral teeth. Femur I 3.08 long, 1.05 times the length of cephalothorax. Metatarsus proximal third enlarged and sinuous, with a row of enlarged macrosetae (Fig. 3I,J). Metatarsus I trichobothrium 0.20. Pedipalp as in Figures 2A–D, 6A–D. Pedipalpal tibia with one prolateral and one retrolateral trichobothria.

Female. No specimens were available for study. The epigynum has been illustrated by Oi (1979: fig. 12) and photographed by Chikuni (1989: fig. 12).

Variation

Male cephalothorax ranges in length from 2.22 to 2.93 (n=2). An additional male specimen measured 4.91 in total length. The male in illustrated in Chikuni (1989: fig. 12) shows a metatarsus I with a more subtle basal process than the specimens studied here and a conspicuous dark median band (very subtle in the specimens I examined). The Sakhalin Island specimens that I have studied have shorter legs than those described in Oi (1979; Femur I is 1.48 times the length of cephalothorax) and Chikuni (1989; Femur I is 1.8 times the length of cephalothorax).

Distribution

Recorded from Horigane (Nagano-ken Pref.) (Oi, 1979) and Sakhalin island (Marusik *et al.*, 1993).

Material examined

Russia, Sakhalin Island, Juzhno-Sakhalinsk, Tourist valley, 18.x.1985, A.M. Basarukin, 2 males (handwritten label in Russian; KEPC).

PIMOA CHAMBERLIN & IVIE, 1943

Type species (by original designation): Labulla hespera Gertsch & Ivie, 1936

Diagnosis

See *Weintrauboa* diagnosis. Male palpus (Hormiga, 1994a: figs 9–11) with a retrolateral cymbial sclerite with denticles or cuspules (Hormiga, 1994a: figs 11, 68; absent in *P. edenticulata* Hormiga) and an alveolar sclerite (Hormiga, 1994a: figs 54, 46, 156, 190, 233–

234, 257, 370). *Pimoa* males differ from those of *Weintrauboa* in having a dorsal palpal tibial process (usually round, but conical in some species), the paracymbium continuous with the base of the cymbium (in *Weintrauboa* the paracymbium is connected to the cymbium by means of a membrane), having an elongated filiform or lamelliform embolic process and lacking an embolic flap. Stridulatory striae present on the ectal side of the chelicerae.

Description

See Hormiga (1994a).

Phylogenetics

The monophyly of *Pimoa* is supported by at least the following putative synapomorphies: alveolar sclerite, integral paracymbium, presence of a dorsal tibial process on the male palp, two prolateral trichobothria on male pedipalpal tibia, epigynum with anteriorly orientated fertilization ducts, and aciniform spigots reduced to one or absent in the female PMS and PLS.

Composition

Twenty-two species; 21 are monographed in Hormiga (1994a), an additional species is described in Griswold *et al.* (1999). Additional new species have been recently discovered in China (C.E. Griswold and G. Hormiga, unpubl. data).

ACKNOWLEDGEMENTS

I would like to thank the following individuals and institutions for making specimens available for study (collection abbreviations used in text are given in parentheses): Jonathan Coddington (Smithsonian Institution, Washington, DC; USNM), Jason Dunlop (Institut für Systematische Zoologie, Universität zu Berlin; ISZ); Kirill Eskov (Moscow, private collection; KEPC), Charles Griswold (California Academy of Sciences, San Francisco; CAS), Yoh Ihara (Hiroshima, private collection; YIPC), Norman Platnick (American Museum of Natural History, New York; AMNH), Carles Ribera (Departament de Biologia Animal, Universitat de Barcelona; UB), Christine Rollard (Museum National d'Histoire Naturelle, Paris; MNHN), Michael Saaristo (Zoological Museum, University of Turku; ZMUT), and Nikolaj Scharff (Zoological Museum, University of Copenhagen; ZMUC). Dr Hirotsugu Ono (National Science Museum, Tokyo) provided valuable information on specimens and collections, sent me a copy of an obscure but important reference, and put me in contact with Mr Yoh Ihara, whose private collection was instrumental in carrying out this research. Yura Marusik (Magadan) helped me in obtaining specimens of *W. chikunii* deposited in Kirill Eskov's personal collection. Nikolaj Scharff helped with references from the ZMUC library. H. Don Cameron (University of Michigan, Ann Arbor) provided expert etymological advice. Svetlana Maslakova helped with Russian translations. Nikolaj Scharff, Charles Griswold, Hirotsugu Ono and an anonymous reviewer provided very helpful comments on an earlier version of this paper. Funding for this research has been provided by grants from the US National Science Foundation (DEB-9712353 and EAR-0228699) and the Research Enhancement Fund from The George Washington University.

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APPENDIX 1

Most of the characters presented here are discussed in detail and illustrated in Hormiga (2000). The majority of characters relevant to pimoids are taken from Hormiga (1994a). Only those characters that are new or that have been recoded are discussed in this section.

MALE PALP

- 1. Alveolar sclerite: (0) absent; (1) present (Hormiga, 1994a, fig. 54, the sclerite between the paracymbium and the pimoid cymbial sclerite). This is a small sclerite located on the ventral side of the cymbium, anteroectal to the distal margin of the alveolus. This sclerite appears as a dark sclerotized plate that lies between the distal end of the alveolus and the attachment of the pimoid cymbial sclerite (Hormiga, 1994a, p. 6). The presence of the alveolar sclerite is a synapomorphy of *Pimoa*.
- 2. Cymbium morphology (ectal region): (0) smooth (no process); (1) with ectal cymbial process. Hormiga (1994a) suggested that the presence of a dorsal denticulate process was a synapomorphy of pimoids. The study of *Weintrauboa* required redefining this character, because only in the genus *Pimoa* are the denticles (cuspules) located on the cymbial process.
- 3. Cymbial cuspules: (0) absent; (1) present.
- 4. Cymbial cuspules: (0) on cymbial process itself; (1) on dorsal surface of cymbium (but not on process; Figs 1E, 5E).
- 5. Pimoid cymbial sclerite (PCS): (0) absent; (1) present.
- 6. Pimoid cymbial sclerite: (0) with membranous flap; (1) without membranous flap.
- 7. PCS: (0) continuous with paracymbium; (1) separate from paracymbium. The plesiomorphic condition in pimoids is to have the PCS continuous with the paracymbium, as found in *Weintrauboa* (Fig. 1B) and in *Pimoa breuili* and *P. rupicola* (Hormiga, 1994a, figs 17 and 45).
- 8. PCS-cymbium connection: (0) sclerotized and rigid; (1) membranous; (2) intermediate. Most *Pimoa* species (e.g. *P. hespera*) have the PCS connected to the cymbium by means of a membrane. In *P. breuili* and *P. rupicola* the connection is sclerotized and rigid (Hormiga, 1994a: figs 17 and 45). *Weintrauboa* species have an intermediate condition, with the PCS connected by means of a rigid membranous area to the cymbium but at the same

- time continuous with the paracymbium, both being heavily sclerotized.
- 9. Distal end of cymbium: (0) rounded; (1) elongated; (2) conical. In Weintrauboa the distal end of the cymbium is distinctly narrowed, finger-like (Fig. 1E). In the mynoglenine genera Haplinis and Novafroneta and in the linyphiine genus Labulla the distal end of the cymbium is also somewhat elongated, but not as distinctly narrowed as in Weintrauboa.
- 10. Paracymbium attachment: (0) integral; (1) intersegmental; (2) articulated.
- 11. Paracymbium morphology: (0) linguiform; (1) triangular; (2) *Stemonyphantes* type; (3) U or J; (4) hook; (5) straight and narrow.
- 12. Paracymbium apophyses: (0) present; (1) absent.
- 13. Mynoglenine tegular apophyses: (0) absent; (1) present.
- 14. Tegular suture: (0) conspicuous; (1) subtle or absent.
- 15. Protegulum: (0) absent; (1) present.
- 16. Protegular papillae: (0) absent; (1) present.
- 17. Suprategulum: (0) absent; (1) present.
- 18. Suprategulum: (0) continuous with tegulum; (1) articulated.
- 19. Suprategular distal apophysis: (0) absent; (1) present.
- 20. Suprategular marginal apophysis: (0) absent; (1) present.
- 21. Median apophysis (MA): (0) present; (1) absent. *Weintrauboa* species have on their tegulum, near the base of the conductor, a small pointed protuberance (Figs 5C, 6B) that I have interpreted as a homologue of the MA.
- 22. Conductor: (0) present; (1) absent.
- 23. Embolus length: (0) long; (1) short.
- 24. Embolic membrane: (0) absent; (1) present.
- 25. Embolic flap: (0) absent; (1) present. *Weintrauboa* species have a small membranous flap that arises from the area where the embolic process connects to the embolus (Figs 1C, 5B).
- 26. Pimoid embolic process (PEP): (0) absent; (1) present.
- 27. PEP: (0) elongated; (1) compact. The PEP of Weintrauboa species is a complex sclerotized structure with several processes, connected to a membranous area of the embolus (Fig. 1D,J). The homologous structure in *Pimoa* is either filiform or lamelliform and located ectally in reference to the embolus.
- 28. Shape of elongated PEP: (0) bifurcated; (1) simple.
- 29. Radix: (0) absent; (1) present.
- 30. Radical tail piece: (0) absent; (1) present.
- 31. Radical tail piece: (0) straight; (1) spiralled; (2) curved ectally; (3) curved mesally; (4) anteriorly directed.

- 32. Anterior radical process: (0) absent; (1) present.
- 33. Column: (0) absent; (1) present.
- 34. Fickert's gland: (0) absent; (1) present.
- 35. Terminal apophysis (TA): (0) absent; (1) present. Pimoids and the non-linyphild outgroup taxa have been coded as lacking a TA. One could argue that these taxa need to be coded as inapplicable (because they lack the radix, to which the TA connects; see comments for next character).
- 36. Lamella characteristica (LC): (0) absent; (1) present. Pimoids and the non-linyphiid outgroup taxa have been coded as lacking a LC. Again, one could argue that these taxa need to be coded as inapplicable (because they lack the radix, to which the LC connects). Coding characters 34 and 35 as inapplicable for pimoids produces the same topological results than coding those cells as 'absent.'
- 37. Male pedipalp tibial apophysis: (0) absent; (1) retrolateral (erigonine); (2) dorsal.
- 38. Prolateral trichobothria on male pedipalpal tibia: (0) two; (1) one; (2) zero; (3) three.
- 39. Retrolateral trichobothria on male pedipalpal tibia: (0) two; (1) four; (2) three; (3) one. Steatoda grossa (Theridiidae) has one prolateral and two retrolateral trichobothria on male pedipalpal tibia (I. Agnarsson, pers. comm.) and had been coded in error in Griswold et al. (1998) and Hormiga (2000).

EPIGYNUM

- 40. Degree of epigynal protrusion: (0) protruding less than its width; (1) protruding more than its width. External epigynal morphology for *Weintrauboa chikunii* has been coded after the illustration of Oi (1979: fig. 12) and the photographs of Chikuni (1989: fig. 12). No information is available about the internal epigynal morphology of *W. chikunii* and no female specimens were available for study.
- 41. Dorsal plate scape: (0) absent; (1) present.
- 42. Ventral plate scape: (0) absent; (1) present.
- 43. Ventral plate scape: (0) straight; (1) sigmoid.
- 44. Atrium: (0) absent; (1) present.
- 45. Copulatory duct: (0) separate from fertilization duct; (1) spirals fertilization duct.
- 46. Copulatory duct encapsulation: (0) absent; (1) present.
- 47. Spermathecae: (0) two; (1) four.
- 48. Fertilization duct orientation: (0) posterior; (1) mesal; (2) anterior.

SOMATIC MORPHOLOGY

- 49. Male post-PME lobe: (0) absent; (1) present.
- 50. Subocular clypeal sulci: (0) absent; (1) present.

- 51. Male cephalothoracic cuticular pores: (0) absent; (1) present.
- 52. Tracheal system: (0) haplotracheate; (1) desmitracheate; (2) intermediate. This character (and the next one) could not be coded for *Weintrauboa* because insufficient material was available for dissection.
- 53. Taenidia in tracheoles: (0) absent; (1) present.
- 54. Ectal side of male chelicerae: (0) smooth; (1) with stridulatory striae. *Weintrauboa* lacks the cheliceral striae typical of *Pimoa* and most linyphiids. This is interpreted as secondary absence.
- Cheliceral stridulatory striae: (0) ridged; (1) scaly;
 imbricated.
- 56. Dorsal spur on male chelicerae: (0) absent; (1) present.
- 57. Retrolateral teeth on female chelicera: (0) three; (1) four or more; (2) two; (3) zero; (4) one.
- 58. Female pedipalpal tarsus: (0) with claw; (1) without claw.
- 59. Patella-tibia leg autospasy: (0) absent; (1) present.
- 60. Male Metatarsus I base diameter (proximal third, in dorsal view): (0) approximately the same diameter as the base or less; (1) increasing in diameter, up to twice or more the diameter of the proximal end (Fig. 7C).
- 61. Male Metatarsus I proximal enlargement: (0) subtle sinuosity (Fig. 3I); (1) more sinuous (Fig. 3G).
- 62. Dorsal spines on tibia I: (0) two or more; (1) one; (2) zero.
- 63. Dorsal spines on tibia II: (0) two or more; (1) one; (2) zero.
- 64. Dorsal spines on tibia III: (0) two or more; (1) one; (2) zero.
- 65. Dorsal spines on tibia IV: (0) two or more; (1) one; (2) zero.
- 66. Trichobothrium on metatarsus IV: (0) present; (1) absent.
- 67. Aciniform spigots in female PMS: (0) one or more; (1) absent.
- 68. PMS mAP nubbins: (0) absent; (1) one.
- 69. PLS mesal CY base: (0) same size as other CY; (1) enlarged.
- 70. Aciniform spigots in female PLS: (0) two or more; (1) one; (2) absent.
- 71. PLS aggregate in male: (0) absent; (1) present.
- 72. PLS flagelliform in male: (0) absent; (1) present.
- 73. Male position during construction of sperm web: (0) above sperm web; (1) below sperm web.
- 74. Male position during ejaculation: (0) above sperm web; (1) below sperm web.
- 75. Web architecture: (0) orb; (1) tangle; (2) sheet. See comments in Griswold *et al.* (1998) for difficulties in coding this behavioural suite (note that in fig. 5D of Griswold *et al.* (1998) the web of *Bathyphantes pallidus* was incorrectly labelled as

'Frontinella pyramitela'). Weintrauboa contortipes has been coded as building a sheet web based on the web photograph of Shinkai & Takano (1984: 27). No information is available on *W. chikunii*'s web. *Pimoa lihengae* also builds sheet webs (Griswold *et al.*, 1999).

APPENDIX 2

CHARACTER STATE MATRIX

Tetragnatha	000-002500-0-01000000100000101-00?0-0-11000-00101010000??0
The ridiosoma	000-000410-0-000100000000013000?0000000?0-0-04100-00211010000??0
Steatoda	000-000-0-0-0-0-0-0-0-0-0-0-000010000?0000000?0-0-03000-00001000000??1
Pimoa rupicola	111010000001000-0000-010000000202000?000020000-1?02010-00000101100???
Pimoa breuili	111010000001000-0000-010000000231000-000020000-110?010-00000?01100???
Pimoa lihengae	111011110011000-0000-010100000202100-0000200???1100010-000001012????2
$Pimoa\ altioculata$	111011110011010-0000-010100000202100-0000200?0-100?010-00000101200??2
Weintrauboa contortipes	011111021101000-0000-111-00000013000-0000100???0-0101110000001000??2
Weintrauboa chikunii	011111021101000-0000-111-000000130??-?????00???0-0??1100000?????????
$Labulla\ thoracica$	000-021300-0-101111000010-0101121000101000200?0-1000010-00001001000??2
Microlinyphia	000-001310-0-101011000010-01011010010-11000000
Linyphia	000-001310-0-101011010010-01011012010-100000000
Bolyphantes	000-001300-0-101011110010-011110100011000000010-1001010-00001001
Tenuiphantes	000-001300-0-101011110010-01111010001100000000
Stemonyphantes	000-001210-0-1110110000101000010000-01000000
Haplinis	000-021311-0-011010010-010000020010101000110-1001010-0000000101111?
Nov a fronet a	000-021311-0-011010010-01000010010-000000110-1001010-000000
As the nargus	000-001310-10100011110010-01001113000-0000000?0-??01110-00011??1011???
Gongylidiellum	000-001310-11101011110010-01001113000-00000000
Sisicus	000-001310-100?11010010-01001123001?100000000-1001110-00001001011????
Tibioploides	000-001310-0-101011010010-01000113000-00000000
Ostearius	000-001310-0-101011110011001000110001000
Leptorhoptrum	000-001310-0-101011100011301000002000-0000000?111?01110-000000?1011???
Hilaira	000-001310-0-10101110001?-01001110000-0000110011
Laminacauda	000-001310-0-101011110011011000110000-00101001211001110-00001001011??2
Drepanotylus	000-001310-10101011010010-11000110000-00101100111001110-00001001
Sciastes	000-001310-11100011110011011000110000-00100000111001110-00001001
Islandiana	000-001310-1110101111001121100011000
Erigone	000-001310-1010101111001141100011000
Walckenaeria	000-001310-1010110110100-?11101000110000-00101001101000110-00110001011??2