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Nanoa, an enigmatic new genus of pimoid spiders from western North America (Pimoidae, Araneae)

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The spider genus ***Nanoa* gen. nov.** (Araneae, Pimoidae) is described to place *Nanoa enana*, a new species of pimoids from Western North America. Parsimony analysis of morphological characters provides support for the monophyly of *Pimoa* plus *Nanoa* and corroborates the monophyly of Pimoidae and of the clade Linyphiidae plus Pimoidae.

ADDITIONAL KEYWORDS: cladistics – homology – Linyphiidae – morphology – phylogeny – systematics – taxonomy.

INTRODUCTION

The family Pimoidae is a small relictual group of araneoid spiders. The family currently includes 24 species classified in two genera. Pimoids are distributed in western North America (13 species, from California through to Alaska), southern Europe (two species) and Asia (seven described species from the Himalayas and adjacent areas and two species from Japan). Several new species of pimoids from western China remain to be described (C. E. Griswold & G. Hormiga, unpubl. data). Pimoidae was originally erected to include a single genus, *Pimoa*. The recent discovery of a second genus of pimoids, *Weintrauboa*, provided a modest increase in species richness but a dramatic increase in the diversity of the male genitalic morphology (Hormiga, 2003). The study of the genitalic morphology of *Weintrauboa* species required a re-evaluation of the synapomorphies supporting the monophyly of the 'Linyphioids' (Linyphiidae + Pimoidae), Pimoidae and *Pimoa*.

In this paper we describe a new species of Pimoidae from Oregon and California, USA. This enigmatic spider is in several aspects remarkably different from all known pimoids.

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The very few specimens available for study come from a pitfall trap faunal survey. During the sorting and identification of the spiders these specimens were singled out by James Cokendolpher (Lubbock, Texas, USA) because they did not easily fit in any of the known spider families. Detailed examination of these spiders shows that they belong to the family Pimoidae. We describe here the new species and explore its phylogenetic affinities using a cladistic approach. In light of this new evidence, Hormiga's (2003) diagnosis for Pimoidae is 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. A JEOL JSM840 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 in millimetres. Somatic morphology measurements were taken using a scale reticle in

the dissecting microscope. The position of the metatarsal trichobothrium is expressed as in Denis (1949). Female genitalia were excised using surgical blades or sharpened needles. Epigyna and palps were transferred to methyl salicylate (Holm, 1979) for examination under the microscope, temporarily mounted as described in Grandjean (1949) and Coddington (1983). The scarcity of specimens (only two adult males and three adult females of *Nanoa enana* are known) prevented a more in-depth study of the morphology using SEM. The spinnerets were first examined using epi-illumination at 200× with a Leica DMRM compound microscope. A female abdomen was prepared for SEM examination, but unfortunately the abdominal cuticle largely collapsed during preparation (due to poor preservation from the pitfall trap) allowing only limited access to the spinnerets (see Fig. 5D–E). We were not able to study the tracheal system anatomy or the male spinnerets and epiandrous fusules.

Anatomical abbreviations used in the text and figures

Male palp

A	alveolus
C	conductor
CP	cymbial process (CDP in Hormiga, 1994a)
E	embolus
MA	median apophysis
P	paracymbium
PCS	pimoid cymbial sclerite
T	tegulum

Epigynum

CD	copulatory duct
FD	fertilization duct
S	spermatheca

Somatic morphology

AG	aggregate gland spigot(s)
ALE	anterior lateral eye(s)
ALS	anterior lateral spinneret
AME	anterior median eye(s)
CY	cylindrical gland spigot(s)
FL	flagelliform gland spigot(s)
PLE	posterior lateral eye(s)
PLS	posterior lateral spinneret
PME	posterior median eye(s)
PMS	posterior median spinneret

Cladistic analysis

Taxa

The taxonomic sample used in the cladistic analysis was designed to infer the placement of *Nanoa* within the Pimoidae and is based on the most recent study on pimoid phylogenetics (Hormiga, 2003). We have added one taxon (*Nanoa enana*) and one character to the matrix of Hormiga (2003). *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 to reconstruct the placement of *Nanoa* within Pimoidae and to study how the inclusion of this latter genus affects the monophyly and diagnosis of 'linyphioids', Pimoidae and *Pimoa*. Outgroup selection followed the taxonomic sample of Hormiga (2000). The Linyphiidae sample attempts to represent morphological diversity at the subfamilial level. Representatives of three araneoid families (Tetragnathidae, Theridiosomatidae and Theridiidae) were used to root the 'linyphioids'.

Characters

A total of 76 characters was scored (see appendices 1 and 2 in Hormiga, 2003): Thirty-nine male and nine female genitalic characters, 25 somatic morphological characters, and three behavioural characters (see Appendix). The characters are those of Hormiga (2003), with the exception of Character 76 (taken from Miller & Hormiga, 2004), which is described here:

Character 76. Thoracic furrow: (0) nearly smooth, often recognizable only from pigment, not invagination (e.g. *Tapinocyba*, Hormiga, 2000: pl. 64C); (1) furrow a distinct invagination (e.g. *Pimoa*, Hormiga, 1994a: fig. 356).

Character 39 was modified with the inclusion of an additional state (state 4), an autapomorphy of *Nanoa*:

Character 39. Retrolateral trichobothria on male pedipalpal tibia: (0) two; (1) four; (2) three; (3) one; (4) zero.

A total of six 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 (Farris, 1988), NONA version 2.0 (Goloboff, 1993a), PAUP* 4.0 (Swofford, 2001) and Pee-Wee version 3.0 (Goloboff, 1993b). 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 nonadditive (unordered or Fitch minimum mutation model; Fitch, 1971). NONA (Goloboff, 1993a) was used to calculate Bremer support indices ('decay indices') (Bremer, 1988, 1995; Donoghue *et al.* 1992) using the following commands: hold2000; sub1; find*; hold4000; sub3; find*; hold8000; sub5; find*; bsupport.

RESULTS

Heuristic searches in NONA under equal weights and 'amb-' using hold10000; hold/200; 1000 replicates of mult TBR + TBR (mult*1000) and jump*2 resulted in four minimal length trees of 188 steps in all 1000 replicates (the strict consensus cladogram is presented in Fig. 6), with a CI and RI of 0.53 and 0.73, respectively (the CI is 0.51 after exclusion of the uninformative characters). Successive character weighting in NONA, which weights characters by their consistency index, produces one tree of minimum length. This tree represents one of the four trees found by NONA under equal weights and includes one trichotomy in the distal erigonines. Using the command 'amb =' in NONA to interpret clade support (considering ambiguous change as support) produces eight topologies of minimal length in 1000 out of 1000 replicates, summarized by the same strict consensus cladogram that results from the analysis under 'amb-' (Fig. 6). Successive character weighting on these input trees resulted in two trees of minimum length. One is the same tree found with successive weighting under 'amb-' and the other is fully resolved (Fig. 7) and represents one of the eight topologies found under equal weights. Analysing the same data in PAUP with heuristic methods, equal weights and random addition sequence (1000 replications) resulted in ten minimal length trees of 188 steps. The PAUP trees include the eight trees found by NONA (amb =) and two additional fully resolved trees differing in the placement of *Stemonyphantes* and the clade that includes the genera *Drepanotylus*, *Sciastes* and a clade containing *Islandiana*, *Erigone* and *Walckenaeria*. The strict consensus tree is identical to the one generated with NONA on the eight topologies (Fig. 6). Successive character weighting in PAUP, using character weights according to the rescaled consistency index (default), produces the same two minimal length trees as found with NONA (amb =). Implied weighting in Pee-Wee, which weights the characters according to a concave function of homoplasy (Goloboff, 1993c), using 'k' values of 3 and 6 (and same search parameters as given for NONA), produces the same two maximum fit (and minimum length) trees as found by successive weighting in NONA and PAUP. Using a 'k' value of 1 (highest weights against homoplastic characters) produces 3 trees 195 steps long with basal topologies like those found with equal and successive weighting, but with different topologies in distal erigonines.

Topological conflict among the most parsimonious topologies resides in two areas. The first one is the resolution of the trichotomy *Stemonyphantes*, Mynoglenidae (*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 are particularly relevant for the problem at hand (pimoid higher level systematics) and have already been discussed in Hormiga (2000). One of the fully resolved minimal length trees found by Henning86, PAUP and NONA (under equal weights), successive weighting in NONA and PAUP, and implied weighting with Pee-Wee (using 'k' values of 3 and 6) has been selected as the preferred topology (Fig. 7). Bremer support values for the individual nodes are given in Figure 6.

DISCUSSION

The discussion of the enigmatic morphology of *Nanoa* is perhaps best illustrated by documenting the actual discovery process of its familial phylogenetic relationships.

The unusual combination of morphological features of *Nanoa* may, at first sight, conceal the familial affiliation of this spider. Its general appearance and habitus suggests membership in the superfamily Araneoidea (the ecribellate orbweavers and their relatives), although initially we could not easily place this taxon in any of the araneoid families. Detailed examination of *Nanoa* shows that this genus is in fact an araneoid, as it shares most of the superfamilial synapomorphies (Griswold *et al.*, 1998; but see Schütt, 2000, 2002), including the presence of juxtaposed lateral eyes, labium wider than long, high clypeus, paracymbium and the PLS triplet (the two aggregate and one flagelliform silk gland spigots). Based on the apparent presence of autospasy at the patella-tibia joint (uniquely exhibited by linyphioids among the members of Araneoidea), we initially suspected that this undescribed species would be either a linyphiid or a pimoid but it did not easily fit either of these families. The slightly larger diameter of the PLS mesal cylindrical gland spigot base of *Nanoa*, relative to the other PLS cylindrical base, is also consistent with linyphioids. Linyphioids typically build sheet webs, but nothing is known about the webs of *Nanoa*. Furthermore, *Nanoa* does not share the synapomorphies of any other araneoid families or groups of families (as documented by Griswold *et al*., 1998), so the linyphioid affinities seemed the best fitting hypothesis. The details of the male palp of *Nanoa* conclusively rule out inclusion in the Linyphiidae. The absence of an

embolic division and a suprategulum, combined with the presence of an integral paracymbium and two tegular sclerites (potential homologues of the araneoid conductor and median apophyses) would make *Nanoa* a pimoid. But the somatic morphology of the new species is in many respects unlike that of any known pimoid so far: they are very small, about 1.5 mm long (known pimoids vary in total length from *c*. 5–12 mm), almost devoid of macrosetae (unlike any other known pimoids, which have legs with numerous setae), and the chelicerae are relatively small and lack stridulatory striae (the latter present in most, but not all, pimoid species). Ultimately, the details of the male palp would confirm the placement of *Nanoa* in the family Pimoidae but also impose the need of a redefinition of the diagnosis of the family.

The main difference between the male palp of *Nanoa* and that of other pimoids is the absence of a pimoid embolic process and the bizarre morphology of the single cymbial cuspule. All other known pimoids have an embolic process of varying morphology which is absent in *Nanoa* (the cladogram in Fig. 7 suggests that this absence is secondary). All pimoids share the presence of modified macrosetae (cuspules) on the cymbium or on a cymbial process. The single 'cuspule' of *Nanoa* is unique among pimoids in being a conspicuously enlarged and bent macrosetae, located on the ectal cymbial process (as in *Pimoa*). *Nanoa* has a sclerotized area on the ectal margin of the alveolus (Figs 1B, 2B), in the same region where *Pimoa* has the alveolar sclerite. It seems logical to argue, on the basis of topological correspondence and similarity, that both structures are homologous.

The results of the cladistic analysis suggest that *Nanoa* is sister to *Pimoa* (Fig. 7), based on the following synapomorphies: alveolar sclerite, integral paracymbium, dorsal tibial process, and absence of PMS and PLS aciniform spigots. While the validity of monotypic genera is highly questionable (e.g. Platnick, 1976) we think that the large morphological gap between *Pimoa* and *Nanoa*, as shown by the cladistic analysis, justifies the proposal of a new genus.

SYSTEMATICS

PIMOIDAE WUNDERLICH, 1986

Pimoinae. – Wunderlich (1986: 16)
Pimoidae. – Hormiga (1993), type genus by monotypy *Pimoa* Chamberlin & Ivie. See also Hormiga (1994a, 2003).

Diagnosis: Male pimoids are distinguished form other araneoid spiders by the following combination of characters: palpus with integral paracymbium (intersegmental in *Weintrauboa*), a retrolateral cymbial sclerite, a dorsoectal cymbial process, and cuspules (modified macrosetae) on either the cymbial process (*Pimoa*; Hormiga, 1994a: figs 11 and 68; *Nanoa*, Fig. 1A–B, D) or the dorsal surface of the cymbium (*Weintrauboa*; Hormiga, 2003: figs 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 (absent in *Nanoa*). The epigynum is protruding (except in *Nanoa*), with a dorsal to lateral fold or groove with the copulatory opening at the distal end (Hormiga, 1994a: figs 14, 414; Figs 3C, 5A); fertilization ducts are anteriorly (*Pimoa*), posteriorly (*Nanoa*) or mesally (*Weintrauboa*) orientated. As in linyphiids, pimoids have stridulatory striae on the ectal side of the chelicerae (but the striae are absent in *Weintrauboa* and *Nanoa*), 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 (modified macrosetae); a retrolateral cymbial sclerite (pimoid cymbial sclerite, PCS); and the embolic process (pimoid embolic process, PEP, lost in *Nanoa*).

Composition: Three genera, *Pimoa* Chamberlin & Ivie, *Weintrauboa* Hormiga and *Nanoa* gen. nov.

NANOA GEN. NOV.

Type species: Nanoa enana.

Etymology: Derived from the Greek word *nanos* (dwarf), in reference to their small body size. The ending *-oa* follows that of *Pimoa*. Chamberlin & Ivie (1943) first used this ending for linyphioids with *Pimoa*. Although Chamberlin did not disclose the etymology of *Pimoa*, Prof. H. Don Cameron (University of Michigan) has deciphered its origin. *Pimoa* is a name derived from the language of the Gosiute people from Utah, and means 'big legs.' *Nanoa* matches the ending of the other two pimoid genera (*Pimoa* and *Weintrauboa*) and is feminine in gender.

Diagnosis: Nanoa differs from other pimoid genera by the following combination of characters: metatarsus–tarsus joint with a distinct constriction; male palpal tibia with dorsal process; dorsoectal cymbial process with a large and thick bent macroseta; alveolar sclerite on the ventral side of the cymbium, seen as a sclerotized spot on the ectal margin of the alveolus; pimoid embolic process absent (Figs 1A–D, 2A–B); cheliceral

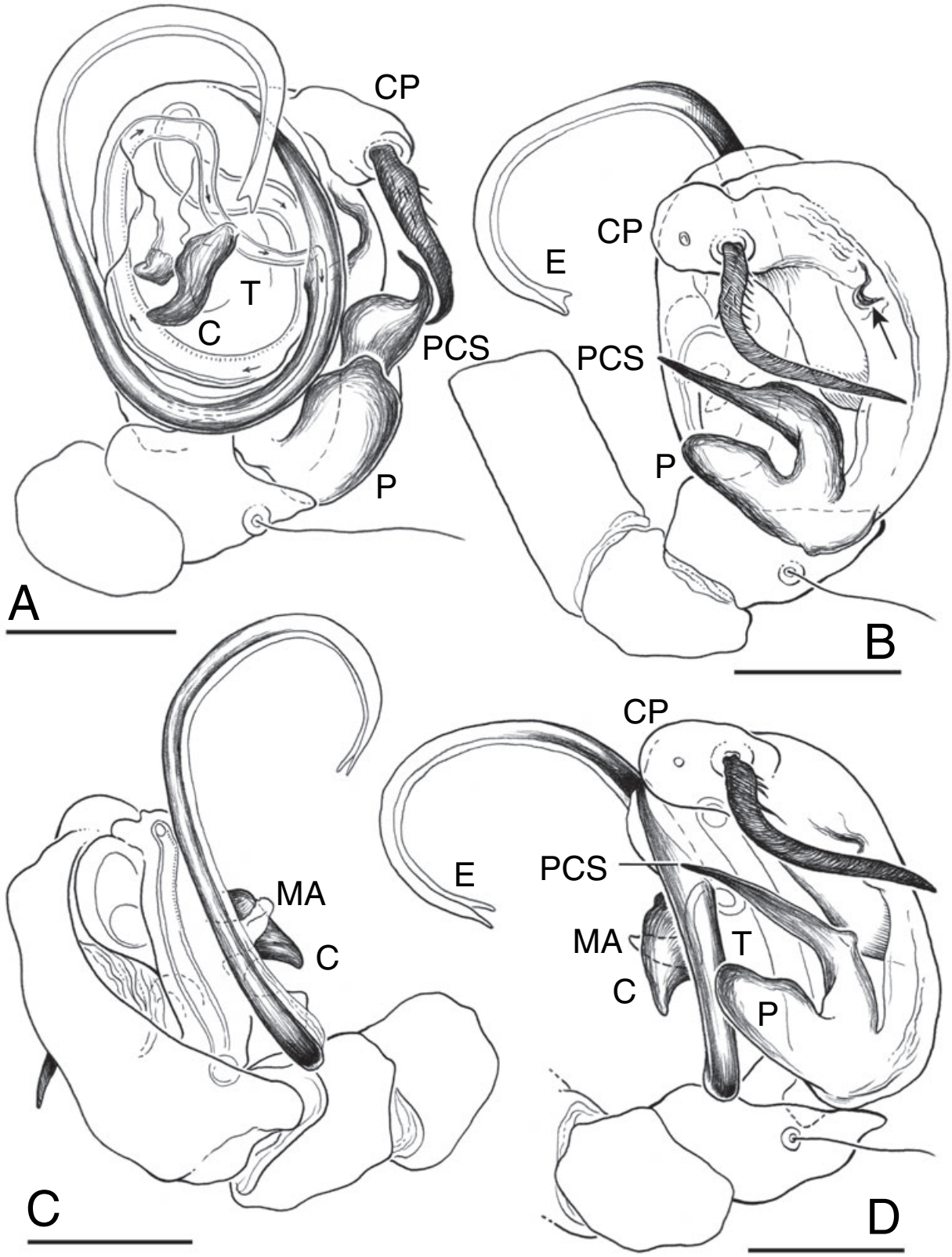

Figure 1. ***Nanoa enana*** **sp. nov.**, male palp (embolus in a slightly displaced position; normally its distal end rests tightly against the tegulum, next to the conductor). A, ventral; B, dorsoectal (arrow points out to homologue of alveolar sclerite); C, mesal; D, ectal. Scale bars = 0.1 mm. See main text for abbreviations.

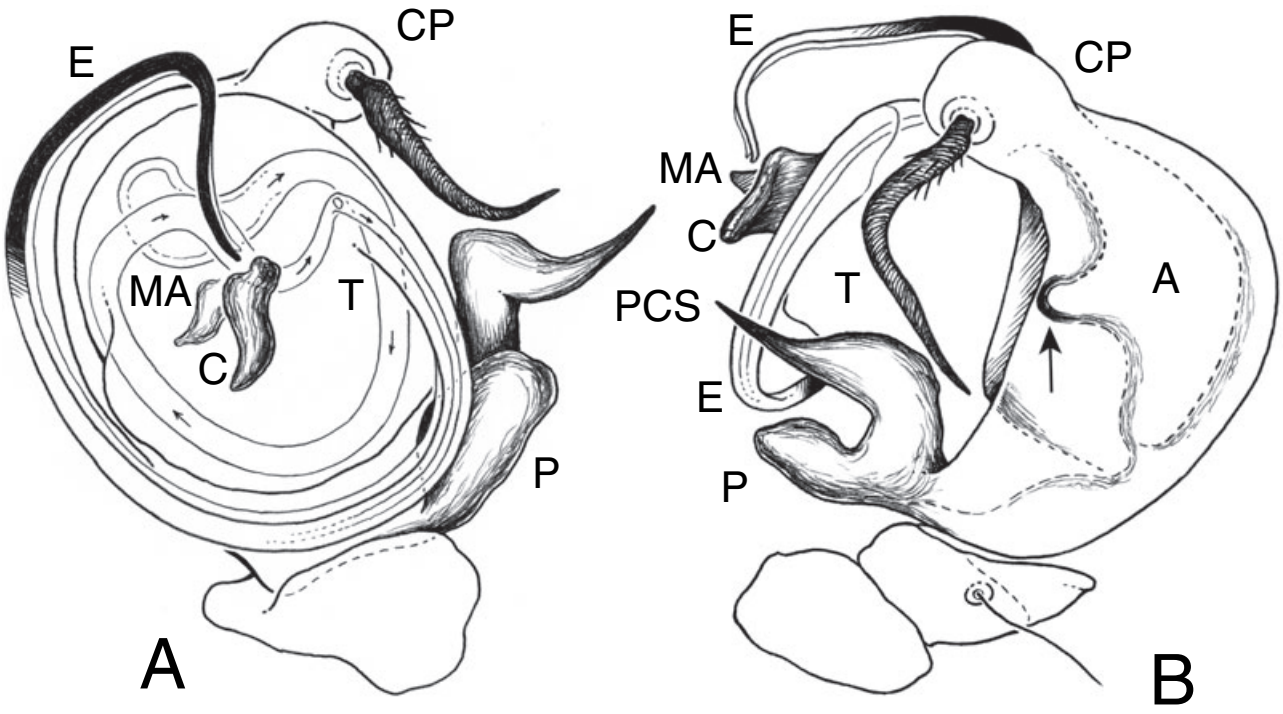

Figure 2. ***Nanoa enana*** **sp. nov.** A–B, male palp, schematic drawings. A, ventral; B, dorsoectal (arrow points out the homologue of alveolar sclerite, seen by transparency through the cymbial cuticle). See main text for abbreviations.

stridulatory striae absent; fourth coxae of male with two strong macrosetae, facing relatively large striated booklung covers (Fig. 3A); epigynum with a ventral scape-like septum and fertilization ducts posteriorly orientated (Fig. 3C–E). PMS and PLS without aciniform spigots; PMS minor ampullate spigot absent (Fig. 5D–E).

Description: Since the genus is monotypic, the description is given under *Nanoa enana*.

Phylogenetics: Nanoa is sister to *Pimoa*. In the present cladistic analysis the terminal branch leading to *Nanoa* is the longest one in the cladogram (Fig. 7) as a consequence of the highly modified morphology of this genus (despite the fact that many autapomorphic features were not coded in the matrix).

Natural history: Unknown.

Composition: One species, *Nanoa enana* sp. nov.

Distribution: California and Oregon, USA.

NANOA ENANA SP. NOV.
(FIGS 1–5)

Types: Male holotype from Siskiyou County, California and female paratype from Jackson County, Oregon (deposited at National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

Etymology: The species epithet means dwarf in Spanish. *Nanoa enana* is the smallest known pimoid species.

Diagnosis: See above, under genus description.

Description: Male holotype (from USA: California, Southern Cascade Mountains, Siskiyou County, Klamath National Forest, East facing slope of Ball Mountain, 25 km SSE of Dorris, 41°46′59.9′N–122°7′0.1′W, 1300 m elevation, 28 September 1999, pitfall trap plot 1B, collected N. Rappaport *et al*. – USDA Forest Service). Total length 1.42. Cephalothorax 0.60 long, 0.53 wide, 0.42 high. Sternum as long as wide (0.38). Abdomen 0.81 long, 0.56 wide. Cephalothorax, chelicerae, sternum, and legs yellowish brown. Ocular area black. Abdomen grey with lighter markings. AME diameter 0.036. Clypeus height 3 times one AME diameter. ALE, PME and PLE diameter 0.045. Chelicerae with two promarginal teeth and one retromarginal tooth (number of teeth difficult to determine with regular stereo microscope; it needs to be confirmed with SEM). Stridulatory striae absent. Femur I 0.50 long, 0.83 times the length of cephalothorax. Fourth coxae each with two strong macrosetae, facing relatively large striated booklung covers (Fig. 3A). Metatarsus-tarsus joints showing a distinct constriction (in both sexes). Metatarsi I-III with one dorsal trichobothrium (absent on metatarsus IV). Metatarsus I trichobothrium 0.43. Male pedipalp (Figs 1, 2): patella short

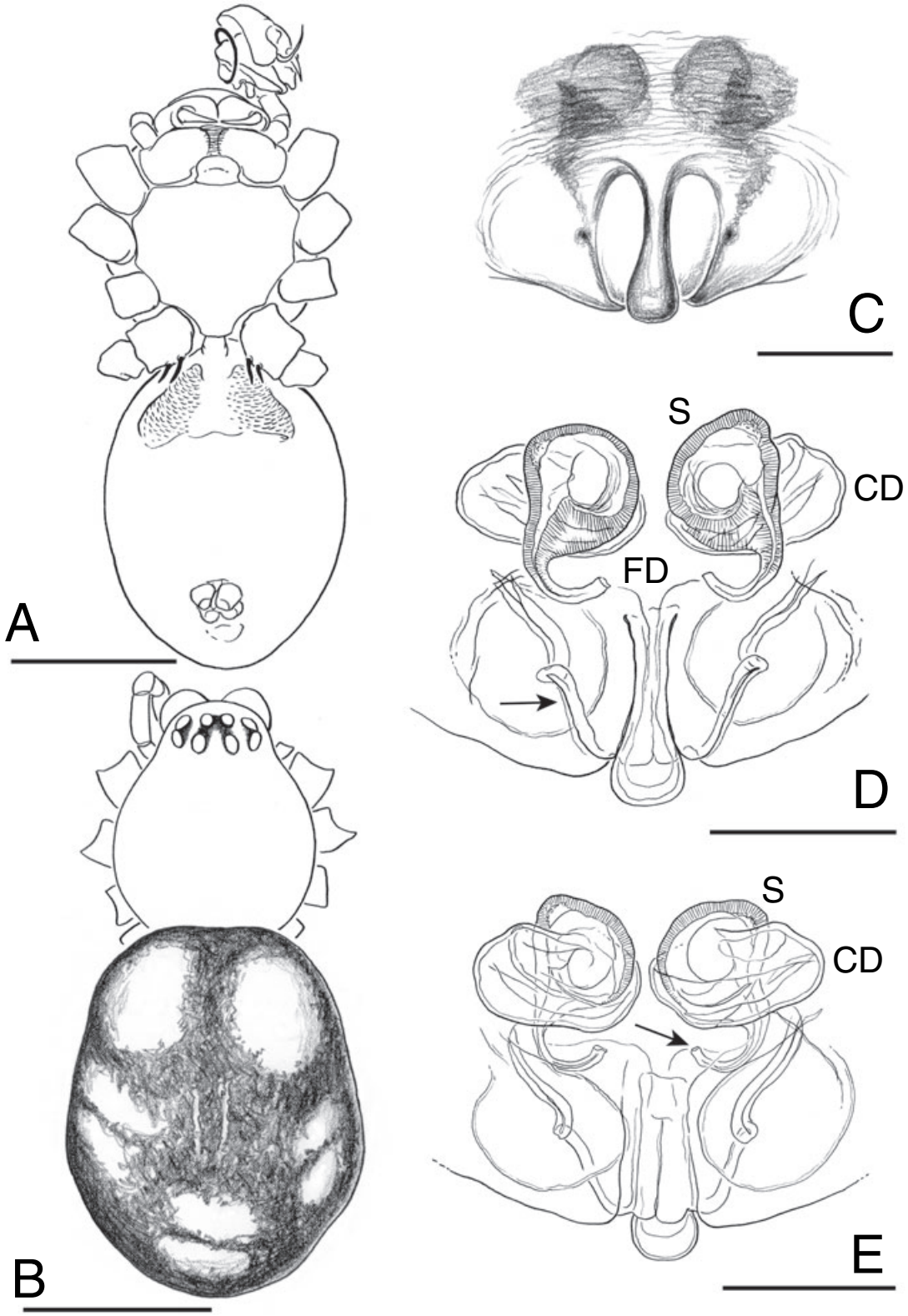

Figure 3. ***Nanoa enana*** **sp. nov.** A, male, ventral; B, female, dorsal; C, epigynum, ventral; D, cleared epigynum, ventral (arrow points out to possible location of copulatory opening); E, cleared epigynum, dorsal (arrow points out to distal end of fertilization duct). Scale bars: A, B = 0.5 mm; C–E = 0.1 mm. See main text for abbreviations.

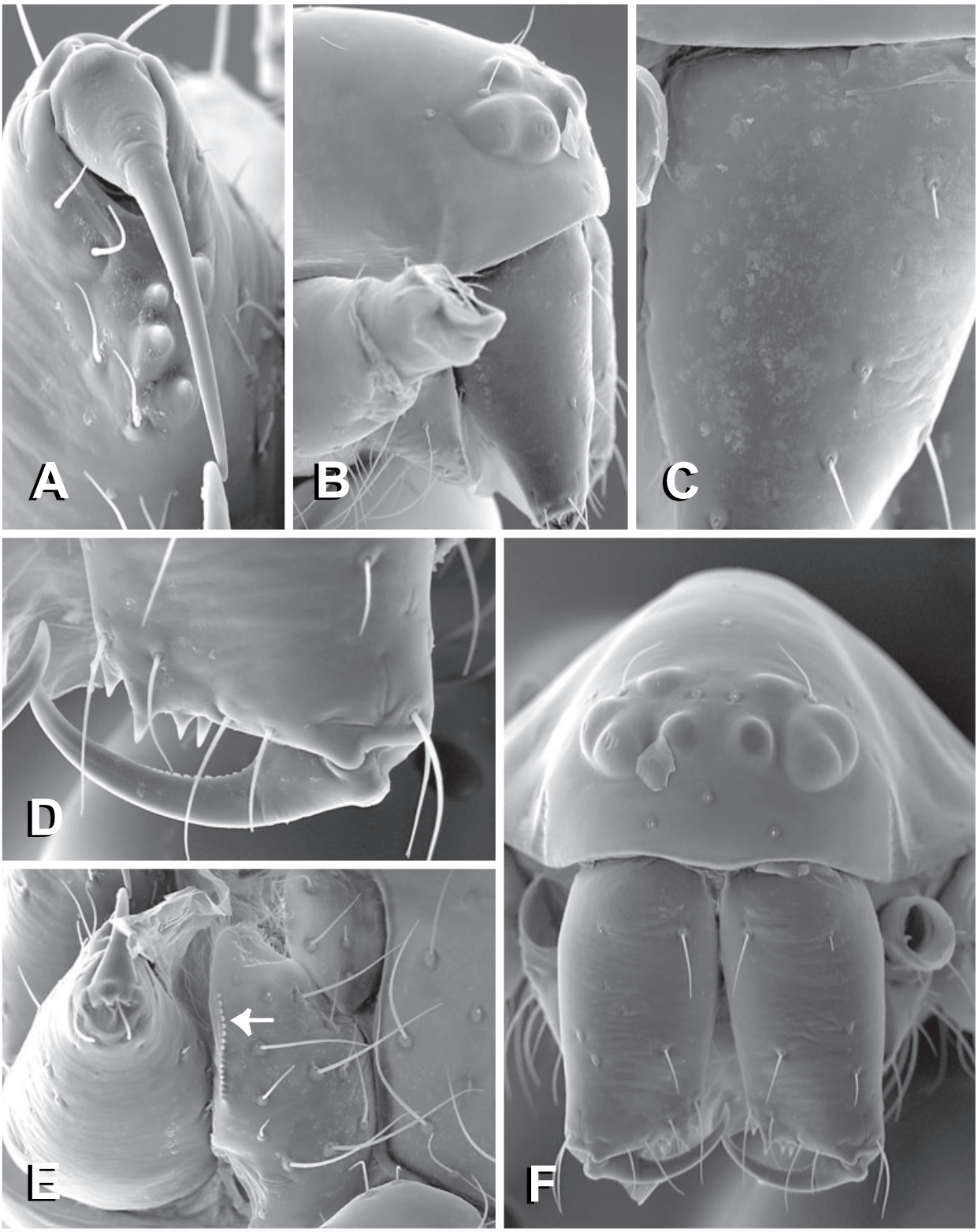

Figure 4. ***Nanoa enana*** **sp. nov.** Female. A, cheliceral teeth and fang, ventral; B, detail of cephalic region and prosoma, lateral; C, detail of ectal cheliceral side; D, cheliceral teeth, anterior; E, labium and maxillae (arrow points to serrula); F, prosoma, anterior.

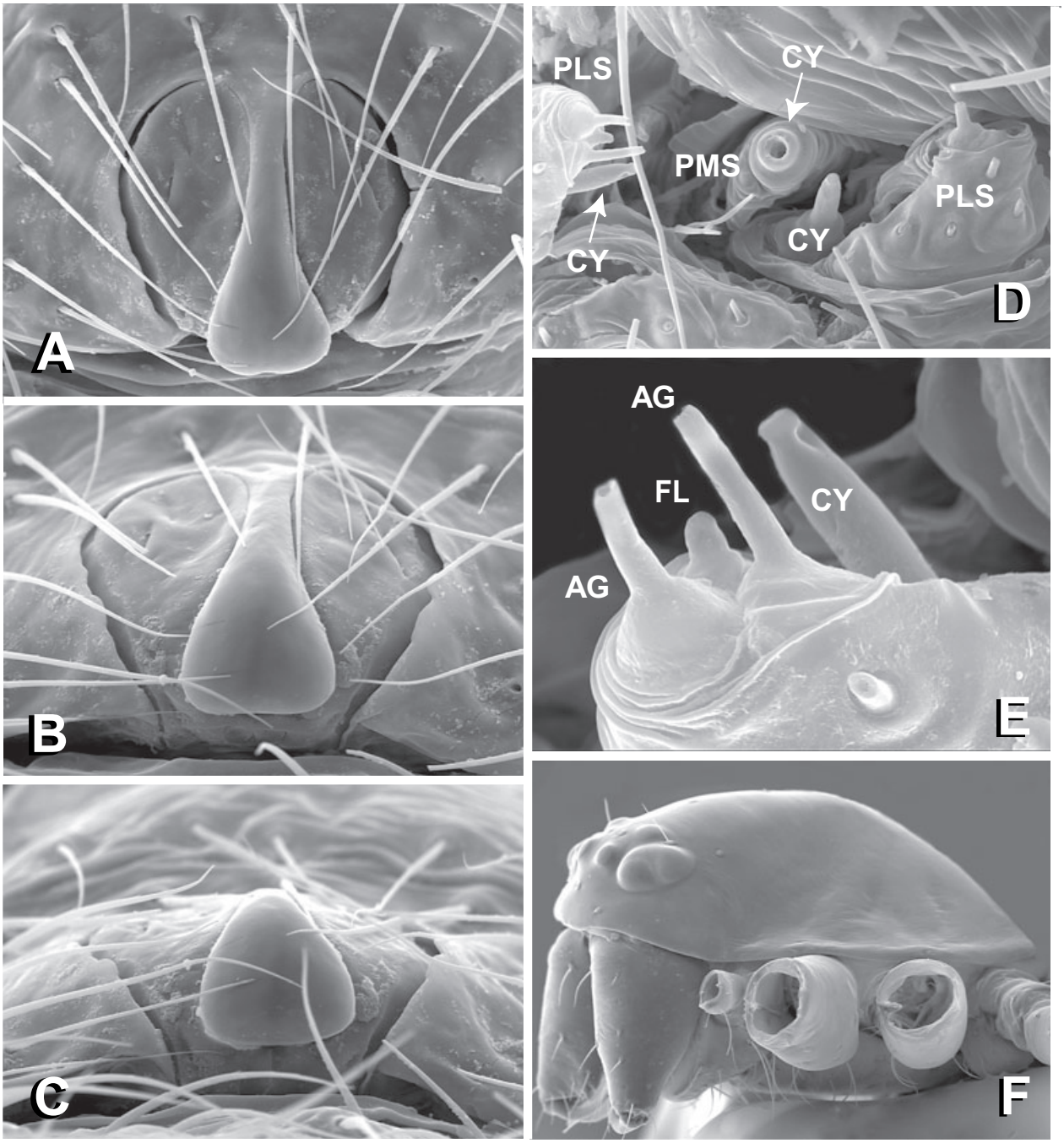

Figure 5. ***Nanoa enana*** **sp. nov.** Female. A, epigynum, ventral; B, epigynum, caudoventral; C, epigynum, caudal; D, partially damaged PLS and PMS (PMS cylindrical spigot has shaft broken off; left PLS, on right, has one cylindrical spigot and part of the triplet broken off); E, right PLS triplet with ectal cylindrical spigot; F, prosoma, lateral. See main text for abbreviations.

(Fig. 1A–D). Tibia approximately as short as wide, with a subtle tibial process; one prolateral and zero retrolateral trichobothria. Cymbium dorsal, with a sclerotized ectal process bearing a conspicuously large and thick macroseta, bent in the basal third towards the dorsal part of the cymbium (Figs 1A–B, D, 2A–B). This macroseta (cuspule) has near its base small hair-like processes (Fig. 1A–B, D). Alveolus with a dark sclerotized fold on its ectal region (Figs 1B, 2B, arrow). Paracymbium integral, linguiform, continuous with the cym-

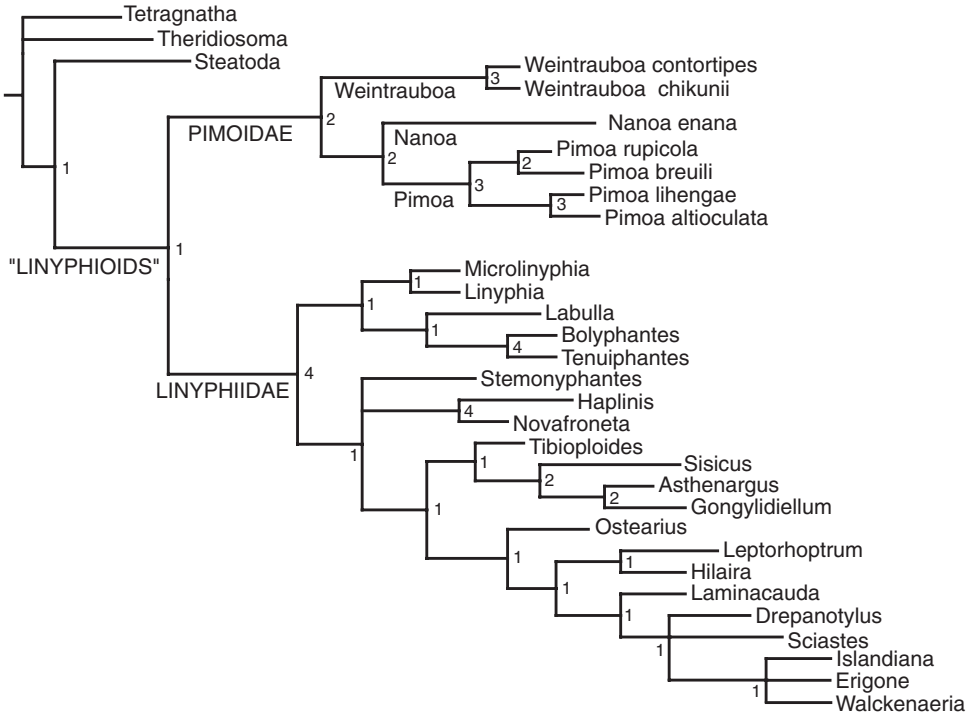

Figure 6. Strict consensus cladogram of the eight minimal length trees of 188 steps that result from the analysis of the data matrix presented in the Appendix. Numbers next to nodes denote Bremer support values (see text for details).

bium base, its proximal region continuous with the pimoid cymbial sclerite (Figs 1 A–B, D, 2B). Paracymbial apophyses absent. Pimoid cymbial sclerite connected to the cymbium without a less sclerotized region, continuous with the paracymbium (Figs 1B, D, 2B). Tegulum without a suture. Conductor longer than wide, blade-like slightly sclerotized process (Fig. 1A, C, D). Median apophysis a small process on tegulum, adjacent to the base of the conductor (Fig. 1A, C, D). Embolus, widest at its base, continuous with tegular margin (Fig. 1A, D), in ventral view arising from the ectal region of the tegulum (around three o'clock), curving clockwise (in left palp) around the tegular area to a full circle (Fig. 1A); distal end of embolus located near the conductor.

Female paratype (from USA: Jackson County, Southern Cascade Mountains, Medford Resource Area, Bureau of Land Management, south-east of Ashland, 42°8′58.0′N–122°24′45.7′W, about 1530 m elevation, pitfall trap #12, 7–21 June 1999, collected R. W. Peck, C. Niwa *et al*. – USDA Forest Service). Total length 1.65. Cephalothorax 0.60 long, 0.52 wide, 0.43 high (Fig. 5F). Sternum 0.44 long, 0.41 wide. Abdomen 1.14 long, 0.78 wide. Same colour pattern as male (Fig. 3B). AME diameter 0.041. Clypeus height 2.50 times one AME diameter (Fig. 4F). ALE, PME, and PLE diameter 0.054. Chelicerae with three promarginal and one retromarginal tooth (Fig. 4A, D). Stridulatory striae absent (Fig. 4B–C, E–F). Femur I 0.54 long, 0.90 times the length of cephalothorax. Metatarsi I–III with one dorsal trichobothrium (absent on metatarsus IV). Metatarsus I trichobothrium 0.43. Female pedipalp with tarsal claw. Spinnerets as in Figure 5D–E. Colulus large and fleshy, with setae. Spinnerets (studied in two females) typical of a 'linyphioid' (Hormiga, 1994a, b, 2003) but showing reduction (Fig. 5D, E). ALS with *c.* eight piriform spigots and a major ampullate spigot. PMS with a single spigot, the cylindrical gland spigot (thus lacking aciniform spigots and the minor ampullate spigot). PLS without aciniform spigots and two cylindrical gland spigots. Base of the peripheral cylindrical spigot slightly larger than the base of the distal one. Aggregate spigots well developed in the females (Fig. 5D, E), flagelliform spigot reduced to a nubbin (Fig. 5E). Tracheal system morphology unknown. Epigynum (Figs 3C–E, 5A–C) protruding less than its width, with a distinctive ventral plate longitudinal scape; copulatory ducts long, with a broad turn before reaching globular spermathecae; fertilization ducts posteriorly oriented (Fig. 3A–C). We could not resolve the exact location and details of the copulatory opening and the first section of the copulatory duct (Fig. 3D, E). SEM examination did not reveal the openings (Fig. 5A–C), which are probably concealed under cuticular lateral folds (on both sides of the scape).

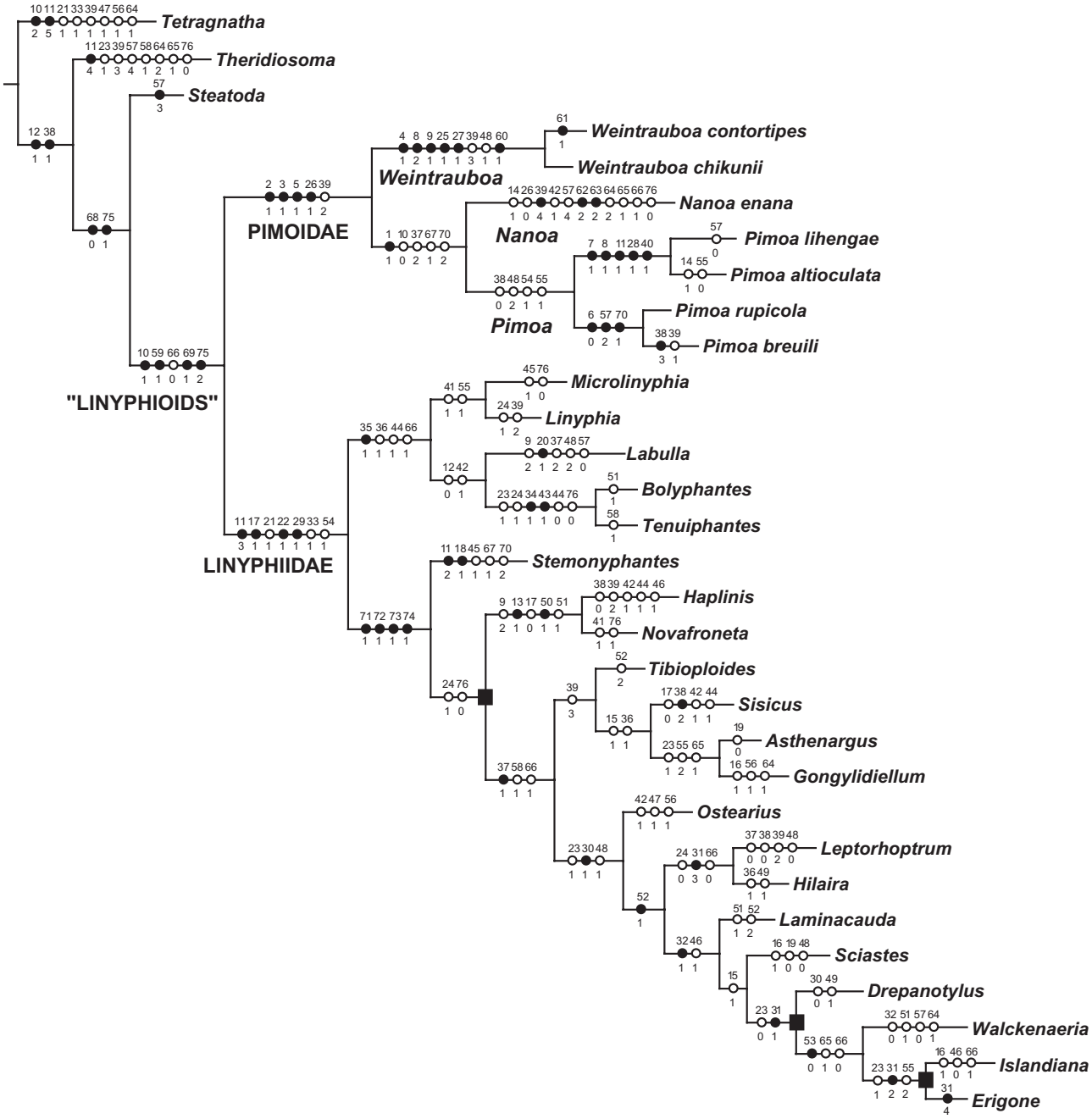

Figure 7. One of the eight minimal length trees of 188 steps that result from the analysis of the data matrix presented in the Appendix (CI = 0.53, RI = 0.73). Exclusion of the six parsimony uninformative characters decreases the tree length to 179 steps and the ensemble consistency index to 0.51. Most of the ambiguous character changes are resolved under 'Farris optimization.' Closed circles represent nonhomoplasious character changes. The three nodes that collapse in the strict consensus cladogram of the eight most parsimonious trees (Fig. 6) are marked with a closed rectangle. The basal trichotomy has been resolved according to the araneoid topology presented in Griswold *et al*. (1998) (see text for details).

Variation: Male cephalothorax is 0.60 long in the two known male specimens. Female cephalothorax ranges in length from 0.56 to 0.60 ($N = 2$; average 0.58). Male total length ranges from 1.42 to 1.50 ($N = 2$; average 1.46). Female total length ranges from 1.52 to 1.65 ($N = 2$; average 1.59). Female Tm I ranges from 0.43 to 0.46 ($N = 2$; average 0.45).

Natural history: Unknown. The study specimens were primarily collected using pitfall traps in mixed conifer forests (see notes).

Distribution: Northern California and Southern Oregon.

Other material examined (paratypes): USA: Oregon, Eastern Siskiyou Mountains, Jackson County, Ashland Ranger District, Rogue River National Forest, Ashland watershed, south of Ashland, 42°8′58.0′N–122°42′24.9′W, 978 m elevation, pitfall trap 174, 29 September – 13 October 1998, collected R. W. Peck, C. Niwa *et al*. – USDA Forest Service, 1 male (deposited at California Academy of Science); 42°9′50.2′N–122°42′24.9′W, 925 m elevation, pitfall trap #120, 17 June – 8 July 1998, collected R. W. Peck, C. Niwa *et al*. – USDA Forest Service, 1 female (deposited at California Academy of Science); Southern Cascade Mountains, Jackson County, Medford Resource Area, Bureau of Land Management, south-east of Ashland, within a 10 km radius of 42°07′N–122°26′W, elevation between 1000 and 1500 m, litter exclusion trap #3–1 C1, collected R. W. Peck, C. Niwa *et al*. – USDA Forest Service, 21 June 2000, 1 female (deposited at USDA–Western Forest Insect Collection, Corvallis), 2 immatures.

Notes: The seven known specimens are from southwestern Oregon and northern California; all within about 90 km of each other. The collection sites are in the Southern Cascade Mountains and Eastern Siskiyou Mountains at elevations of about 925–1530 m in late-successional old growth forest litter. The dominant overstory trees at the Oregon sites were primarily white fir [*Abies concolor* (Gord. & Glend) Lindl. ex Hildebr.] and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], but also included sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and incense-cedar (*Libocedrus decurrens* Torr.). The overstory of the California collection site was dominated by old growth *Pinus ponderosa* [Ecological unit M261De (Southern Cascades Section, Butte Valley)]. Although the site in California was relatively flat ground at the foot of Ball Mountain, the other sites were steeper. Two males and two females of this species were collected by pitfall traps from June to early October whereas the only known immatures and a female were collected from forest litter during June.

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APPENDIX

Character state matrix.

Tetragnatha	000-0---02	500-0-0---	100000--0-	--10000010	-----1-00	?0-0-11000	-001010100	00?201
Theridiosoma	000-0---00	410-0-0---	001000--0-	--00000130	00-0000000	?0-0-04100	-002110100	00?200
Steatoda	000-0---0-	--0-0-0---	000000--0-	--00000100	00-0000000	?0-0-03000	-000010000	00?211
Nanoa enana	1110110000	01010-0---	000000--0-	--00002140	0100000000	???0-04010	-222111012	?????0
Pimoa rupicola	1110100000	01000-0---	000-01000-	--00002020	00-0000200	00-1?02010	-000001011	00???1
Pimoa breuili	1110100000	01000-0---	000-01000-	--00002310	00-0000200	00-110?010	-000002011	00???1
Pimoa lihengae	1110111100	11000-0---	000-01010-	--00002021	00-0000200	???1100010	-000001012	????21
Pimoa altioculata	1110111100	11010-0---	000-01010-	--00002021	00-0000200	?0-100?010	-000001012	00?221
Weintrauboa contortipes	0111110211	01000-0---	000-111-0-	--00000130	00-0000100	???0-01011	1000000010	00?221
Weintrauboa chikunii	0111110211	01000-0---	000-111-0-	--00000130	??-????00	???0-0??11	00000?????	?????1
Labulla	000-0---21	300-0-1011	110000--10	-010112100	0101000200	?0-1000010	-000010010	00?221
Microlinyphia	000-0---01	310-0-1010	110000--10	-010110100	10-1100000	00-1101010	-000010010	000020
Linyphia	000-0---01	310-0-1010	110100--10	-010110120	10-1000000	00-1101010	-000010010	000021
Bolyphantes	000-0---01	300-0-1010	111100--10	-011110100	0110000000	10-1001010	-000010010	00???0
Tenuiphantes	000-0---01	300-0-1010	111100--10	-011110100	0110000000	00-1001110	-000010010	000020
Stemonyphantes	000-0---01	210-0-1110	110000--10	--10000100	00-0100000	00-100?010	-000001012	11???1
Haplinis	000-0---21	311-0-0---	110100--10	-010000020	0101010001	10-1001010	-000000010	1111?0
Novafroneta	000-0---21	311-0-0---	110100--10	-010000100	10-0000001	10-1001010	-000000010	11???1
Asthenargus	000-0---01	310-101000	111100--10	-010011130	00-0000000	?0-??01110	-00011??10	11???0
Gongylidiellum	000-0---01	310-111010	111100--10	-010011130	00-0000000	00-1211110	-001110010	11???0
Sisicus	000-0---01	310-100--?	110100--10	-010011230	01?1000000	00-1001110	-000010010	11???0
Tibioploides	000-0---01	310-0-1010	110100--10	-010001130	00-0000000	0211001110	-000010??0	11???0
Ostearius	000-0---01	310-0-1010	111100--11	0010001100	0100001100	00-1011110	-000010010	11???0
Leptorhoptrum	000-0---01	310-0-1010	111000--11	3010000020	00-0000000	?111?01110	-000000?10	11???0
Hilaira	000-0---01	310-0-1010	111000--1?	-010011100	00-0000110	0111001110	-000000010	11???0
Laminacauda	000-0---01	310-0-1010	111100--11	0110001100	00-0010100	1211001110	-000010010	11???0
Drepanotylus	000-0---01	310-101010	110100--10	-110001100	00-0010110	0111001110	-000010010	11???0
Sciastes	000-0---01	310-111000	111100--11	0110001100	00-0010000	0111001110	-000010010	11???0
Islandiana	000-0---01	310-111010	111100--11	2110001100	00-0000100	0101201110	-000110010	11???0
Erigone	000-0---01	310-101010	111100--11	4110001100	00-0010100	0101201110	-000100010	111120
Walckenaeria	000-0---01	310-101010	110100-?11	1010001100	00-0010100	1101000110	-001100010	11?220