Zootaxa 5026 (1): 071–101
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5026.1.3
http://zoobank.org/urn:lsid:zoobank.org:pub:16F89211-2BD7-49AE-96FA-DFB02F6DC66F

Molecular phylogeny of pimoid spiders and the limits of Linyphiidae, with a reassessment of male palpal homologies (Araneae, Pimoidae)

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Abstract

We address the phylogenetic relationships of pimoid spiders (Pimoidae) using a standard target-gene approach with an extensive taxonomic sample, which includes representatives of the four currently recognized pimoid genera, 26 linyphiid genera, a sample of Physoglenidae, Cyatholipidae and one Tetragnathidae species. We test the monophyly of Pimoidae and Linyphiidae and explore the biogeographic history of the group. *Nanoa* Hormiga, Buckle and Scharff, 2005 and *Pimoa* Chamberlin & Ivie, 1943 form a clade which is the sister group of a lineage that includes all Linyphiidae, *Weintrauboa* Hormiga, 2003 and *Putaoa* Hormiga and Tu, 2008. *Weintrauboa, Putaoa*, *Pecado* and *Stemonyphantes* form a clade (Stemonyphantinae) sister to all remaining linyphiids. We use the resulting optimal molecular phylogenetic tree to assess hypotheses on the male palp sclerite homologies of pimoids and linyphiids. Pimoidae is redelimited to only include *Pimoa* and *Nanoa*. We formalize the transfer from Pimoidae of the genera *Weintrauboa* and *Putaoa* to Linyphiidae, re-circumscribe the linyphiid subfamily Stemonyphantinae, and offer revised morphological diagnoses for Pimoidae and Linyphiidae.

Key words: Systematics, Taxonomy, Morphology, Biogeography, Molecular Dating, Araneoidea

Introduction

The family Pimoidae comprises a relatively small lineage of araneoid spiders with a Holarctic distribution. As presently circumscribed the family includes the genera *Pimoa* Chamberlin & Ivie, 1943 (79 species), *Nanoa* Hormiga, Buckle and Scharff, 2005 (one species), *Weintrauboa* Hormiga, 2003 (eight species) and *Putaoa* Hormiga and Tu, 2008 (three species), for a total of 91 described species (WSC 2021; Fig. 1). Pimoids are found in Western North America (from California through Alaska), Southern Europe (Spain, France, and Italy) and Asia (the Himalayas and the Qinghai–Tibetan Plateau, other mountainous regions of China, Taiwan, Japan and the Sakhalin Island). Most species of pimoids are found in mountainous areas (often in caves, e.g., Mammola *et al.* 2017), where they build horizontal sheet webs close to the ground. Some pimoid species have broad geographic distribution ranges (e.g., *Pimoa altioculata* (Keyserling, 1886) can be found from northern California through Alaska) but most species seem to have a rather narrow distribution (e.g., *Pimoa graphitica* Mammola, Hormiga & Isaia, 2016 is restricted to the Piemonte region of northwestern Italy and the Hautes Alpes of southeastern France (Mammola *et al.* 2016)). Most of the Asian species have been described based on few specimens and localities. For example, Zhang *et al.* (2020) described eight new species from the Himalayas, six of them known only from the type locality (the other two from one additional nearby locality) and on average in that study each species is known by less than three specimens. Thus, the geographic distribution of Asian pimoids is poorly understood and the abundance of species in the Himalayas and adjacent areas point toward narrow distribution ranges and additional unknown species of *Pimoa*.

Accepted by A. Bonaldo: 12 Jul. 2021; published: 24 Aug. 2021

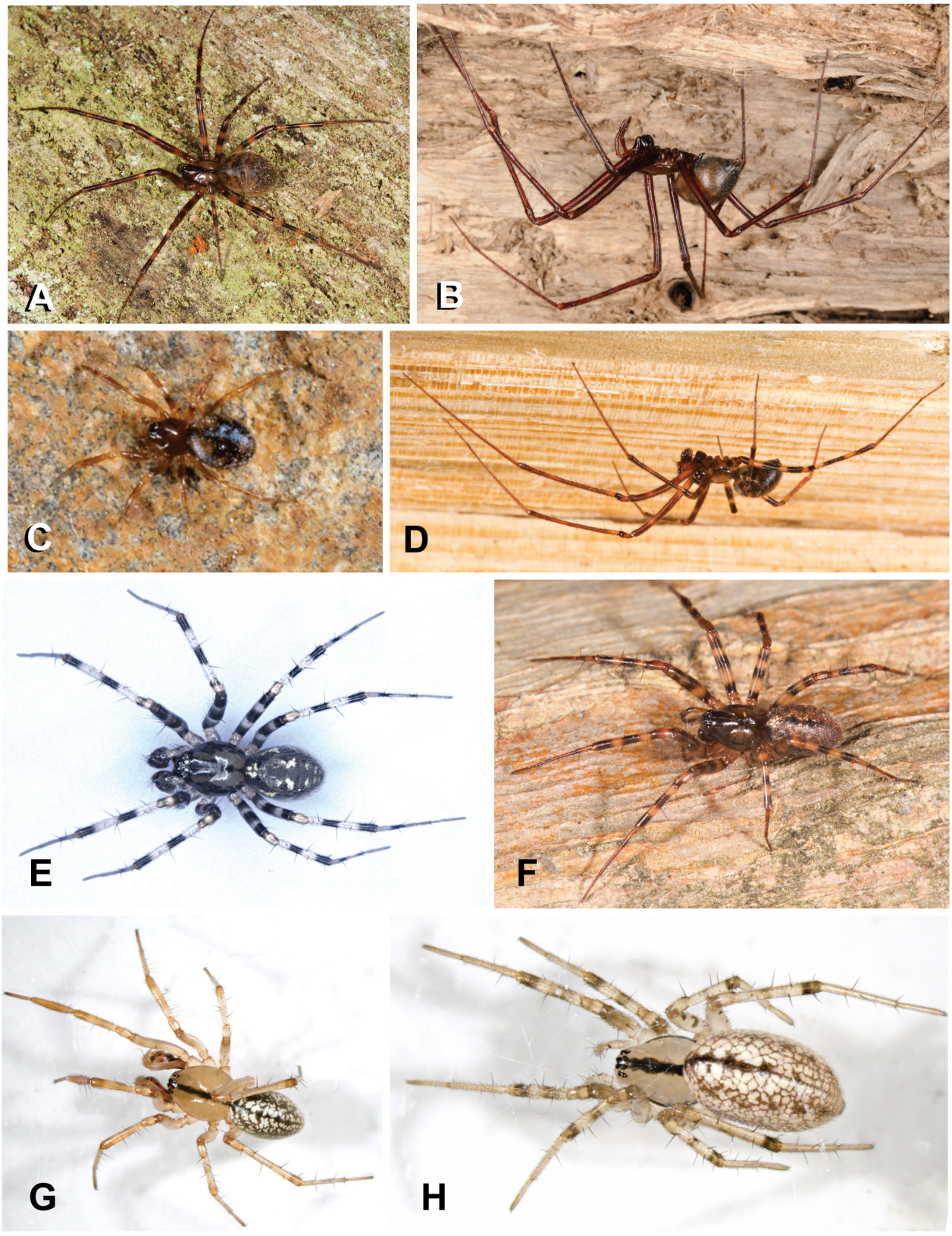

FIGURE 1. Pimoid and stemonyphantine habitus photographs. A, *Pimoa breviata* Chamberlin & Ivie, 1943, female from Oregon (DSC_5028). B, *Pimoa cthulhu* Hormiga, 1994, female from California (DSC_5065). C, *Nanoa enana* Hormiga, Buckle & Scharff, 2005, female from California (DSC_4865, GH0896). D, *Pimoa edenticulata* Hormiga, 1994, male from California (DSC_5023). E, *Putaoa seediq* Hormiga & Dimitrov, 2017, male from Taiwan. F, *Weintrauboa contortipes* (Karsch, 1881), female from Kanagawa Prefecture, Japan (DSC_0472). G, *Stemonyphantes lineatus* (Linnaeus, 1758), male from Zealand, Denmark. H, *S. lineatus*, female from Zealand, Denmark. Photos by GH.

Pimoidae is the sister group of the diverse family Linyphiidae (Wunderlich 1986, Hormiga 1993, 1994a, b), which includes 620 genera, grouping close to 4,700 described species (WSC 2021). Although some species of *Pimoa* had been originally described in the linyphiid genus *Labulla* in the late 1800s, Wunderlich (1986) was the first researcher to explicitly propose affinities between *Pimoa* (the only pimoid genus at the time) and Linyphiidae, based on two shared characters: the cheliceral stridulatory striae and the patella-tibia autospasy. Cladistic analyses corroborated these two shared traits as synapomorphies of the Pimoidae + Linyphiidae lineage (e.g., Hormiga 1993, 1994a, b, 2003), a clade that is informally known as the 'linyphioids.' Spinneret spigot morphology provided a third synapomorphy for linyphioids: the enlargement of the peripheral cylindrical spigot base on the posterior lateral spinnerets (PLS) (Hormiga 1993, 1994a, b). In the past, arachnologists found it difficult to reconcile the unusual morphology of *Pimoa*, particularly the male genitalia, with that of typical linyphiids (for example, as documented in Blauvelt 1936 and Merrett 1963), and perhaps not surprisingly, some of the species of *Pimoa* were thought to be tetragnathids (e.g., Thaler 1976). Wunderlich (1986: 106) suggested that pimoids were the sister group of the remaining linyphiids and erected the subfamily Pimoinae. Hormiga (1993) elevated Pimoinae to family rank. Pimoids were first monographed by Hormiga (1994a), with all species known at the time (21 species, 11 of them new) grouped under the genus *Pimoa*. Further systematic research on pimoids resulted in the addition of three new genera in the family: *Weintrauboa* (Hormiga 2003), *Nanoa* (Hormiga *et al.* 2005), and *Putaoa* (Hormiga & Tu 2008). Each of these studies empirically supported the placement and/or monophyly of the new taxa based on phylogenetic analyses of morphological characters. More recently, sperm ultrastructure has provided further evidence supporting the monophyly of linyphioids, based on the unusual 9+0 axonemal pattern found in *Pimoa* and in Linyphiidae (Michalik & Hormiga 2010). The advent of molecular systematics corroborated the monophyly of linyphioids with nucleotide sequence data, but with pimoids initially represented only by the genus *Pimoa* (e.g., Arnedo *et al.* 2009). The addition of representatives of other pimoid genera produced molecular phylogenies that were, in some cases, in conflict with morphological hypotheses. While linyphioids remained monophyletic, the *Weintrauboa* representatives clustered with the linyphiid genus *Stemonyphantes*, rendering pimoids paraphyletic (e.g., Dimitrov *et al.* 2012, Wang *et al.* 2015, Wheeler *et al.* 2017). On the other hand, targeted gene sequencing corroborated the placement of the enigmatic genus *Nanoa* as sister to *Pimoa* (Dimitrov *et al* 2012, 2017), a hypothesis originally proposed primarily based on male genitalic morphology (Hormiga *et al.* 2005). The addition of *Putaoa* to the Sanger sequencing-based phylogenetic analyses also refuted pimoid monophyly because this Asian genus clustered with the stemonyphantines, along with *Weintrauboa* (Dimitrov *et al.* 2017), rather than with *Pimoa* and *Nanoa*. More recent studies based on phylogenomic data have also refuted Pimoidae as circumscribed by morphological data. The transcriptomic analyses of Fernández *et al.* (2018) and Kallal *et al.* (2021) support the monophyly of linyphioids but place *Weintrauboa* as a sister group to the linyphiid clade, rather than to *Pimoa.* Analyses of ultraconserved elements (Kulkarni *et al.* 2020, 2021) have also supported the monophyly of linyphioids, based on representation of a single pimoid genus (*Pimoa*).

The goal of this paper is to address the phylogenetic relationships of pimoids using a standard target-gene approach with an extensive taxonomic sample of pimoids, which includes representatives of the four currently recognized pimoid genera. We aim to test the monophyly of Pimoidae and Linyphiidae. Morphological hypotheses of pimoid and linyphiid relationships rely extensively on the complex genitalic morphology of these groups. For example, the most recent morphological cladistic analysis of pimoid relationships (Hormiga 2008) was based on 83 characters, 45 of them coding for male genitalic features. We use the resulting molecular phylogenetic hypothesis to assess some of the hypotheses on the male palp sclerite homologies. Female genitalia provide a much smaller subset of characters (e.g., only nine characters in the aforementioned matrix of Hormiga 2008) and for the most part epigynal homologies are uncontroversial. For these reasons we focus our assessment of male palpal sclerites. Although the nucleotide data presented here are not particularly extensive (e.g., many *Pimoa* species are represented only by short COI sequences), it allows us to carry out some preliminary analyses of dating and biogeographic history.

Methods

Taxon sampling. To address pimoid phylogenetic relationships we assembled two different data matrices with focus on different hierarchical levels. The goal of data matrix 1 (M1) is to test the monophyly of linyphioids, Pimoidae, and Linyphiidae. It includes as outgroups eight physoglenid and seven cyatholipid terminals and uses *Leucauge*

(Tetragnathidae) as the root. The linyphioid outgroups were selected based on the phylogenomic hypothesis of Kulkarni *et al.* (2021). Pimoids are represented by nine terminals in the genera *Pimoa* (4), *Nanoa* (2 of the same species), *Weintrauboa* (2) and *Putaoa* (1). Linyphiidae are represented by 28 terminals and include species of the main lineages of the family. The data matrix 2 (M2) addresses relationships within *Pimoa* and is designed in part based on the results of the analysis of M1. Outgroups in M2 include three linyphiids, two physoglenids and the tree is rooted with two cyatholipids. Pimoids are represented by *Nanoa* (2 terminals) and *Pimoa* (90 terminals). See Table 1 for a complete list of taxa used in the study.

TABLE 1. List of taxa and the NCBI accession numbers for the DNA sequences used for phylogenetic analysis for the data sets M1 and M2. Distribution for pimoid species is provided in parentheses.

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M1, M2	Cyatholipidae	*Cyatholipus* sp. CG271	KY017644		KY015797	KY016374.1	KY016995.1
M1	Cyatholipidae	*Forstera* sp.	KM486437	KM486484	KM486296	KM486147	KM486363
M1	Cyatholipidae	*Matilda australis*	KM486452	KM486497	KM486309	KM486165	KM486377
M1, M2	Cyatholipidae	*Tekella* sp. CG205 ATOL	KY017648.1		KY015800	KY016377	KY016999
M1	Cyatholipidae	*Tekelloides* sp. CG242	KY017650			KY016380	KY017002
M1	Cyatholipidae	*Ulwembua* sp. CG31 ATOL	KY017651	KY018166	KY015801	KY016381	KY017003
M1	Cyatholipidae	*Wanzia fako*		KM486528	KM486337	KM486209	KM486419
M1	Linyphiidae	*Agyneta ramosa*	FJ838648.1	FJ838740.1	FJ838670.1	FJ838694.1	FJ838717.1
M1	Linyphiidae	*Australolinyphia remota* ATOL	KY017765	KY018270	KY015923	KY016499	KY017141
M1	Linyphiidae	*Centomerus trilobus*	GU338656.1	KT002817.1	GU338599.1	GU338468.1	GU338571.1
M1	Linyphiidae	*Diplocephalus cristatus* IZCL187	GU338696.1		GU338637.1	GU338490.1	
M1	Linyphiidae	*Dubiaranea distincta_ D.aysenensis*	GU338648.1	FJ838745	FJ838675	FJ838699	FJ838722
M1	Linyphiidae	*Erigone edentata*	GU338686.1			GU338486.1	GU338540.1
M1	Linyphiidae	*Floronia bucculenta*	FJ838654	FJ838746	FJ838676	FJ838700	FJ838723
M1	Linyphiidae	*Frontinella communis*	FJ838655.1	FJ838747.1	FJ838677.1	FJ838701.1	FJ838724.1
M1, M2	Linyphiidae	*Haplinis diloris*	FJ838657.1	KY018272.1	FJ838680.1	KY016502.1	KY017144.1
M1	Linyphiidae	*Labulla thoracica* ZZLi367	MG201052.1	MG201229.1	MG200517.1	MG200698.1	MG200875.1
M1	Linyphiidae	*Laetesia raveni*	KM486439	KM486486	KM486298	KM486149	KM486365
M1, M2	Linyphiidae	*Linyphia* sp. GH41	KY017771.1	KY018275.1	KY015929.1	KY016506.1	KY017148.1
M1	Linyphiidae	*Micrargus herbigradus*	KT002748.1	KT002848.1	KT003135.1	KT002947.1	KT003042.1
M1	Linyphiidae	*Microneta viaria*	GU338655	FJ838754	FJ838684	GU338502	GU338537
M1	Linyphiidae	*Neomaso patagonicus* IZCL158	GU338674.1		GU338626.1	GU338473.1	GU338578.1
M1	Linyphiidae	*Neriene radiata*	AY078696.1	AY078709.1	AY078710.1	AY078670.1	AY078684.1
M1	Linyphiidae	*Notholepthyphantes australis*	FJ838662	FJ838755	FJ838685	FJ838709	FJ838732
M1	Linyphiidae	*Novafroneta* sp. GH40	KY017772.1	KY018276.1		KY016508.1	KY017150.1
M1	Linyphiidae	*Oedothorax apicatus*	FJ838664.1	FJ838757.1	FJ838687.1	FJ838711.1	FJ838734.1
M1	Linyphiidae	*Orsonwelles polites*	AY078755	AY078701	AY078732	AY078671	AY078686

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TABLE 1. (continued)

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M1	Linyphiidae	*Ostearius melanopygius*	KX537231.1	FJ838758	FJ838688	FJ838758	FJ838758
M1	Linyphiidae	*Palaeohyphantes simplicipalpis*	KM486462	KM486510	KM486323	KM486183	KM486395
M1	Linyphiidae	*Pecado impudicus* TSM	MZ513612	MZ612027	MZ727963	MZ647991	MZ648025
M1	Linyphiidae	*Pocobletus* sp. LB2014a GH1173 Panama	KM486465.1	KM486516.1	KM486329.1	KM486191.1	KM486402.1
M1	Linyphiidae	*Solenysa partibilis*	KT002784.1	KT002885.1	KT003170.1	KT002983.1	KT003077.1
M1	Linyphiidae	*Stemonyphantes abantensis* GH1715		KM486519.1	KM486332.1	KM486195.1	KM486406.1
M1	Linyphiidae	*Stemonyphantes lineatus*	FJ838667.1	FJ838761.1	FJ838691.1	FJ838715.1	FJ838738.1
M1, M2	Linyphiidae	*Stemonyphantes* sp. GH32	KY017774.1	KY018278.1	KY015933.1	KY016511.1	KY017153.1
M1	Linyphiidae	*Tenuiphantes tenuis*	FJ838669.1	FJ838763.1	FJ838693.1	FJ838716.1	FJ838739.1
M1	Linyphiidae	*Weintrauboa yele*	GU338698.1		GU338641.1	GU338523.1	GU338588.1
M1	Linyphiidae	*Weintrauboa contortipes* SK	MZ513633		MZ727962	MZ647990	
M1	Physoglenidae	*Calcarsynotaxus* sp. CG298 ATOL	KY017853	KY018359	KY016041	KY016619	KY017273
M1	Physoglenidae	*Chileotaxus sans*	KM486433	KM486482	KM486288	KM486141	KM486357
M1	Physoglenidae	*Meringa borealis*	KM486454	KM486499	KM486312	KM486168	KM486380
M1	Physoglenidae	*Pahora* sp. CG241 ATOL	KY017858	KY018365	KY016047	KY016625	KY017279
M1	Physoglenidae	*Pahoroides* sp. CG244 ATOL	KY017860		KY016049	KY016627	KY017281
M1, M2	Physoglenidae	*Physoglenes* sp. LB-2014a		KM486514.1	KM486327	KM486189.1	KM486400.1
M1, M2	Physoglenidae	*Physoglenes* sp. SP.41	KY017861.1	KY018367	KY016050.1	KY016628	KY017282
M1	Physoglenidae	*Tupua* sp. CG299 ATOL	KY017862	KY018368	KY016051		KY017283
M1, M2	Pimoidae	*Nanoa enana* GH0895 (USA)	JN010202.1			JN010184.1	JN010189.1
M1, M2	Pimoidae	*Nanoa enana* GH0895_2 (USA)	JN010203.1			JN010183.1	JN010188.1
M2	Pimoidae	*Pimoa altioculata* 113921 (USA, Canada)	KU875900.1	KC849060.1			
M2	Pimoidae	*Pimoa altioculata* GH0779 (USA, Canada)	MZ513613		MZ727959	MZ647975	MZ648010
M2	Pimoidae	*Pimoa anatolica* GH0747 (China)	MZ513614		MZ727956		
M2	Pimoidae	*Pimoa anatolica* Yn1 (China)	EF128158.1				EF128114.1
M2	Pimoidae	*Pimoa binchuanensis* ZXQ0074 (China)	MK910743.1				
M2	Pimoidae	*Pimoa bomi* xq0252 (China)	MW727915.1				
M2	Pimoidae	*Pimoa breuili* MD834 (Spain)	MT607874.1				MT651647.1
M2	Pimoidae	*Pimoa breviata* GH0910 (USA)	MZ513615			MZ647981	MZ648016

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TABLE 1. (continued)

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M2	Pimoidae	*Pimoa breviata* USA1 (USA)	EF128151.1				EF128109.1
M2	Pimoidae	*Pimoa breviata* USA2 (USA)	EF128152.1				EF128110.1
M2	Pimoidae	*Pimoa cawarong* xq0260 (China)	MW727894.1				
M2	Pimoidae	*Pimoa clavata* B1 (China)	EF128123.1				EF128085.1
M2	Pimoidae	*Pimoa clavata* Ys1 (China)	EF128124.1				EF128090.1
M2	Pimoidae	*Pimoa cona* ZXQ0124 (China)	MT373707.1				
M2	Pimoidae	*Pimoa cthulhu* GH0905 (USA)	MZ513616			MZ647980	MZ648014
M2	Pimoidae	*Pimoa cthulhu* GH0933 (USA)	MZ513617			MZ647986	MZ648018
M2	Pimoidae	*Pimoa curvata* BIOUG07163-G01 (USA)	KP654400_1				
M2	Pimoidae	*Pimoa curvata* GH0916 (USA)	MZ513618			MZ647983	
M2	Pimoidae	*Pimoa daman* xq0088 (Nepal)	MW727922.1				
M2	Pimoidae	*Pimoa danba* xq0381 (China)	MW727903.1				
M2	Pimoidae	*Pimoa delphinica* GH0743 (Italy)	MZ513619			MZ647974	
M2	Pimoidae	*Pimoa deqen* xq0450 (China)	MW727899.1				
M2	Pimoidae	*Pimoa dongjiu* xq0481 (China)	MW727897.1				
M2	Pimoidae	*Pimoa duiba* ZXQ0162 (China)	MT373708.1				
M2	Pimoidae	*Pimoa edenticulata* GH0772 (USA)	MZ513620		MZ727961	MZ647976	MZ648011
M2	Pimoidae	*Pimoa edenticulata* Tilden (USA)	MZ513621			MZ647978	MZ648023
M2	Pimoidae	*Pimoa guiqing* xq0409 (China)	MW727927.1				
M2	Pimoidae	*Pimoa gyaca* xq0273 (China)	MW727920.1				
M2	Pimoidae	*Pimoa gyara* xq0242 (China)	MW727916.1				
M2	Pimoidae	*Pimoa gyirong* xq0230 (China)	MW727913.1				
M2	Pimoidae	*Pimoa haden* USA5 (USA)	EF128155.1		GU338640.1	GU338524.1	GU338587.1
M2	Pimoidae	*Pimoa heishui* xq0369 (China)	MW727923.1				
M2	Pimoidae	*Pimoa jellisoni* USA4 (USA)	EF128154.1				EF128111.1
M2	Pimoidae	*Pimoa jinchuan* xq0377 (China)	MW727901.1				

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TABLE 1. (continued)

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M2	Pimoidae	*Pimoa khaptad* XQ056 (Nepal)	MW727930.1				
M2	Pimoidae	*Pimoa koshi* xq0195 (Nepal)	MW727918.1				
M2	Pimoidae	*Pimoa laurae* GH0929 (USA)	MZ513622			MZ647985	MZ648023
M2	Pimoidae	*Pimoa lemenba* ZXQ0068 (China)	MT373706.1				
M2	Pimoidae	*Pimoa lhatog* xq0496 (China)	MW727925.1				
M2	Pimoidae	*Pimoa lihengae* Yn2 (China)	EF128157.1				
M2	Pimoidae	*Pimoa mainling* ZXQ0171 (China)	MT373710.1				
M2	Pimoidae	*Pimoa mechi* xq0198 (Nepal)	MW727919.1				
M2	Pimoidae	*Pimoa mephitis* GH0898 (USA)	MZ513623			MZ647982	MZ648015
M2	Pimoidae	*Pimoa mephitis* GH0904 (USA)	MZ513624			MZ647979	MZ648013
M2	Pimoidae	*Pimoa miandam* xq0227 (Pakistan)	MW727896.1				
M2	Pimoidae	*Pimoa miero* xq0373 (China)	MW727902.1				
M2	Pimoidae	*Pimoa mude* xq0192 (Nepal)	MW727929.1				
M2	Pimoidae	*Pimoa muli* xq0429 (China)	MW727924.1				
M2	Pimoidae	*Pimoa naran* xq0223 (Pakistan)	MW727898.1				
M2	Pimoidae	*Pimoa ninglang* xq0285 (China)	MW727893.1				
M2	Pimoidae	*Pimoa nyalam* xq0236 (China)	MW727912.1				
M2	Pimoidae	*Pimoa nyingchi* ZXQ0180 (China)	MT373713.1				
M2	Pimoidae	*Pimoa phaplu* xq0194 (Nepal)	MW727917.1				
M2	Pimoidae	*Pimoa putou* xq0375 (China)	MW727900.1				
M2	Pimoidae	*Pimoa rara* xq0201 (Nepal)	MW727907.1				
M2	Pimoidae	*Pimoa reniformis* GH0744 (China)	MZ513625		MZ727960		
M2	Pimoidae	*Pimoa reniformis* Sc9 (China)	EF128135.1				EF128094.1
M2	Pimoidae	*Pimoa rongxar* ZXQ0174 (China)	MT373712.1				
M2	Pimoidae	*Pimoa rupicola* SM182 22 (France, Italy)	KT832116.1				

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TABLE 1. (continued)

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M2	Pimoidae	*Pimoa rupicola* SM184 28 (France, Italy)	KT832115.1				
M2	Pimoidae	*Pimoa rupicola* ZZPi406 (France, Italy)	MG201051.1	MG201228.1	MG200518.1	MG200697.1	MG200876.1
M2	Pimoidae	*Pimoa samyai* ZXQ0173 (China)	MT373711.1				
M2	Pimoidae	*Pimoa sangri* xq0275 (China)	MW727911.1				
M2	Pimoidae	*Pimoa shigatse* xq0518 (China)	MW727921.1				
M2	Pimoidae	*Pimoa delphinica* SM-2016 PK719 (Italy)	KX018998.1				
M2	Pimoidae	*Pimoa delphinica* SM-2016 PK720 (Italy)	KX018999.1				
M2	Pimoidae	*Pimoa graphitica* SM-2016 PK717 (Italy, France)	KX018996.1				
M2	Pimoidae	*Pimoa graphitica* SM-2016 PK718 (Italy, France)	KX018997.1				
M2	Pimoidae	*Pimoa lihengae* ARACG73 (Yunnan, China)	KY017869.1	KY018371.1	KY016055.1	KY016636.1	KY017291.1
M2	Pimoidae	*Pimoa graphitica* SM-2015 SM068_21 (Italy cave)	KT832189.1				
M2	Pimoidae	*Pimoa* sp. n. XZ-2019 ZXQ0147 (China)	MK910745.1				
M2	Pimoidae	*Pimoa* sp. ARASP74 Gaoligong Shan (Yunnan, China)	KY017870.1	KY018373.1	KY016057.1	KY016638.1	KY017293.1
M2	Pimoidae	*Pimoa* sp. X131 (Arnedo et al. 2004) (China)	AY231025.1	AY230985.1	AY230940.1	AY230893.1	AY231072.1
M2	Pimoidae	*Pimoa* sp. ARACG81 (China)		KY018372.1	KY016056.1	KY016637.1	KY017292.1
M2	Pimoidae	*Pimoa jellisoni* GH0950 (Idaho, USA)	MZ513626			MZ647987	MZ648019
M2	Pimoidae	*Pimoa* sp. GH0951 Gaoligong Shan (Yunnan, China)	MZ513627			MZ647988	MZ648021
M2	Pimoidae	*Pimoa* sp. GH0952 (Jietou Township, China)				MZ647989	MZ648020
M2	Pimoidae	*Pimoa haden* GH1072 (USA)	MZ513628				MZ648022
M2	Pimoidae	*Pimoa tehama* BlackjackCamp1 (USA)	MZ513629		MZ727958	MZ647973	MZ648008
M2	Pimoidae	*Pimoa tehama* BlackjackCamp3 (USA)	MZ513630		MZ727957		MZ648009
M2	Pimoidae	*Pimoa tengchong* xq0358 (China)	MW727906.1				
M2	Pimoidae	*Pimoa trifurcata* GH0742 (China)	JN010205.1		JN010168.1	JN010186.1	JN010187.1

.....continued on the next page

TABLE 1. (continued)

Data set	Family	Taxon-list	CO1	H3	16S	18S	28S
M2	Pimoidae	*Pimoa trifurcata* Sc22 (China)	EF128142.1				EF128098.1
M2	Pimoidae	*Pimoa vera* GH0921 (USA)	MZ513631			MZ647984	MZ648017
M2	Pimoidae	*Pimoa xiahe* xq0405 (China)	MW727910.1				
M2	Pimoidae	*Pimoa xinjianensis* ZXQ0081 (China)	MK910744.1				
M2	Pimoidae	*Pimoa yadong* ZXQ0168 (China)	MT373709.1				
M2	Pimoidae	*Pimoa yejiei* xq0411 (China)	MW727928.1				
M2	Pimoidae	*Pimoa yele* xq0210 (China)	MW727905.1				
M2	Pimoidae	*Pimoa zayu* xq0257 (China)	MW727895.1				
M2	Pimoidae	*Pimoa zhigangi* xq0493 (China)	MW727914.1				
M1	Pimoidae	*Putaoa huaping* GH0780 (China)	MZ513632			MZ647977	MZ648012
M1	Tetragnathidae	*Leucauge venusta* (USA)	FJ607568	FJ607606	FJ607457	EU003350	EU153169

Morphological characters. We compiled a data matrix of male palp characters (data matrix 3, M3) scored for the taxa of M1 with the goal of reconstructing the history of those characters on the optimal molecular phylogenetic tree. M3 focuses on some of the characters often used to delimit the families Pimoidae and Linyphiidae (e.g., Arnedo *et al.* 2009, Hormiga & Tu 2008). It should be noted that this morphological matrix is not intended to infer linyphioid relationships as it only includes male palpal characters of linyphioids, and by design it lacks somatic or female characters. The matrix also does not have the morphological characters that could have been studied and scored to resolve the relationships of physoglenids and cyatholipids, which fall outside the scope of our study. Matrix M3 contains 38 characters scored for 50 taxa and it is taken in part from the matrices of Arnedo *et al.* (2009), Hormiga & Tu (2008) and Hormiga (2008). Cyatholipids and physoglenids have been scored primarily based on the works of Griswold (2001) and Forster *et al.* (1990). The character definitions and states are given in Results section. The program Mesquite version 3.61 (build 927) (Maddison & Maddison 2019) was used to produce and manage matrix M3, to calculate character statistics and to reconstruct ancestral states using parsimony.

Molecular datasets and phylogenetic analyses. Our M1 and M2 data sets included 53 and 109 terminals respectively generated by a concatenation of our newly generated sequences and publicly available sequences of five markers (Table 1) — two mitochondrial markers, the 16S mitochondrial ribosomal RNA (16S rDNA) and the cytochrome c oxidase subunit 1 (COI) genes, and three nuclear genes — the protein-coding histone H3 (H3), and small and large subunits of ribosomal RNA genes (18S and 28S, respectively). COI and H3 markers were aligned using MACSE (Ranwez *et al.* 2011) with the invertebrate mitochondrial code followed for COI. The remaining markers (16S, 18S and 28S) were aligned using MAFFT version 7 (Katoh & Standley 2013). Trimming was performed on all alignments using trimAL (Capella-Gutiérrez *et al.* 2009) with *-gappyout* setting. Phylogenetic analyses were performed on the gene-wise partitioned nucleotide data using IQ-TREE (Nguyen *et al.* 2015) version 2.1.1. Model selection was allowed for each data set using the TEST function (Kalyaanamoorthy *et al.* 2017). Nodal support was estimated via 1,000 ultrafast bootstrap (UFBoot) replicates (Hoang *et al.* 2018) and Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.* 2010). To reduce the risk of overestimating branch support with UFBoot due to model violations, the command -bnni was appended. With this command, the UFBoot optimizes each bootstrap tree using a hill-climbing nearest neighbor interchange (NNI) search based on the corresponding bootstrap alignment (Hoang *et al.* 2018). In the Results section, the nodal support values for each mentioned clade are indicated in parentheses as SH-aLRT/UFboot.

Molecular dating methods. We used fossil-based dating constraints based on data from the literature (see Table 2) to calibrate our phylogeny constructed with the M2 data set. Two dating methods were used: 1. treePL uses a tree with branch lengths and age constraints without prior parametric distributions to estimate divergence times using a penalized likelihood through identification of an optimal smoothing value (Smith & O'Meara 2012) and, 2. Least-squares dating version 2 (LSD2) which uses a least-squares approach based on a Gaussian model and is robust to uncorrelated violations of the molecular clock (To *et al.* 2016). Often it is not easy to place fossils in a particular lineage due to poor preservation or lack of close extant relatives. The two fossils we used to calibrate the phylogeny have been treated differently by different authors. The 'Linyphiinae' (Penney & Selden 2002) as crown Linyphiidae (e.g., Dimitrov *et al.* 2012, 2017) while other authors have argued that it may not be a linyphiid (e.g., Magalhaes *et al.* 2020). The *Pimoa* fossils described from Baltic amber (Wunderlich 2004) have clear *Pimoa* synapomorphies (e.g., cymbial denticulate process, cymbial sclerite and pimoid embolic process) and share some characteristics that are found in extant European species (namely, the cymbial sclerite continuous with the paracymbium and a large cymbial process with numerous cuspules in *Pimoa multicuspuli* Wunderlich, 2004). Thus, one could argue for using these fossils as a crown constraint for *Pimoa*, however the possibility that these similarities reflect an ancestral condition for *Pimoa* cannot be ruled out, which would suggest that these fossils should be used as a stem calibration instead. Given these uncertainties here we have explored the effect of the placement of these two fossils- the Baltic amber fossil *Pimoa multicuspuli* (Wunderlich 2004) as crown *Pimoa* versus stem *Pimoa* and, in presence and absence of the Lebanese amber fossil 'Linyphiinae' (Penney and Selden 2002) as crown Linyphiidae.

TABLE 2. List of fossils used to calibrate the phylogeny of Pimoidae.

Fossil	Minimum age	Maximum age
Linyphiinae Penney and Selden, 2002	125	135
Agyneta	15	NA
Pimoa multicuspuli Wunderlich, 2004	43	47.8

Biogeography methods. We reconstructed ancestral areas on internal nodes of the dated trees using the package BioGeoBEARS (Matzke 2013) implemented in RASP 4.0 (Yu *et al.* 2020). Each of the terminals was assigned to one of the following biogeographic regions: Nearctic, Eastern Himalayas, Western Himalayas, Tibetan Plateau-Sichuan region, Yunnan-Sichuan-Hunan, Gansu-Shaanxi, Beijing, Iberian Massif and Italian Peninsula. We retained only the Pimoidae terminals, and the other taxa were removed, following the recommendation to remove outgroup taxa by the authors of RASP (Yu *et al.* 2020). Maximum range size was constrained to four areas to reduce computation time. We evaluated the fit of our data to three distinct biogeographic models: DEC (Ree & Smith 2008), DIVALIKE (Matzke 2013) and BAYAREALIKE, using likelihood ratio tests based on Akaike information criterion corrected for small sample sizes (AICc). Our preliminary analyses indicated that the jump parameter (+j) was favored resulting in dispersal across most nodes, which is likely due to artificial inflation of likelihood values (Ree & Sanmartín 2018). Therefore, the +j parameter was not included in the final analysis.

Results

Morphological characters. The male palpal morphology characters discussed in the text and optimized in Fig. 11 are given here. Character definitions primarily follow Hormiga & Tu (2008), Hormiga (2008) and Arnedo *et al.* (2009). For each character, the number of steps, the consistency index and the retention index on the topology of Fig. 2 are provided in parentheses (the characters are treated as non-additive or unordered).

1. Alveolar sclerite: (0) absent; (1) present (1, 1, 1).
2. Ectal region of cymbium morphology: (0) smooth (no process); (1) with ectal cymbial process (6, 0.17, 0.64).
3. Cymbial macrosetae: (0) all about the same size; (1) at least some modified (larger, bigger socket/base)(2, 0.50, 0.8).
4. Larger cymbial macrosetae length: (0) long (many times its diameter); (1) short (cuspule type)(1, 1, 0).
5. Larger cymbial macrosetae location: (0) on cymbial process itself; (1) on dorsal surface of cymbium (not on process)(1, 1, 1).

6. Pimoid cymbial sclerite (PCS): (0) absent; (1) present (1, 1, 1).
7. Pimoid cymbial sclerite (PCS): (0) with membranous flap; (1) without membranous flap (1, 1, 0).
8. Pimoid cymbial sclerite (PCS): (0) attached/fused to paracymbium; (1) separate from paracymbium (1, 1, 1).
9. PCS-cymbium connection: (0) sclerotized and rigid; (1) membranous; (2) intermediate (1, 1, 1).
10. Distal end of cymbium: (0) rounded; (1) elongated; (2) conical (6, 0.33, 0.43).
11. Paracymbium attachment: (0) integral; (1) intersegmental; (2) intermediate, with both an intersegmental and an integral area (4, 0.50, 0.91).
12. Paracymbium morphology: (0) linguiform; (1) triangular; (2) *Stemonyphantes* type; (3) U or J; (4) hook; (5) straight and narrow; (6) cup (excavate); (7) knob; (8) *Weintrauboa* type (12, 0.88, 0.95).
13. Paracymbium apophyses: (0) present; (1) absent (6, 0.17, 0.28).
14. Tegular suture: (0) conspicuous; (1) subtle or absent (1, 1, 1).
15. Protegulum: (0) absent; (1) present (3, 0.33, 0.60).
16. Protegular papillae: (0) absent; (1) present (1, 1, 0).
17. Suprategulum: (0) absent; (1) present (1, 1, 1).
18. Suprategulum: (0) continuous with tegulum; (1) articulated (1, 1, 0).
19. Suprategular distal apophysis: (0) absent; (1) present (3, 0.33, 0).
20. Suprategular marginal apophysis: (0) absent; (1) present 5, 0.20, 0).
21. Median apophysis: (0) present; (1) absent (4, 0.25, 0.79).
22. Conductor: (0) present; (1) absent (2, 0.5, 0.96).
23. Conductor papillae: (0) absent; (1) present (2, 0.5, 0).
24. Conductor base: (0) narrowly connected to tegulum (tongue-like C); (1) broadly connected to tegulum (3, 0.33, 0.5).
25. Embolus length: (0) long; (1) short (8, 0.13, 0.53).
26. Embolic membrane: (0) absent; (1) present (3, 0.33, 0.67).
27. Embolic flap: (0) absent; (1) present (5, 0.20, 0.20).
28. Embolic process: (0) absent; (1) present (3, 0.33, 0.71).
29. Embolic process: (0) elongated; (1) compact (0.2, 0.50, 0.67).
30. Shape of elongated embolic process: (0) bifurcated; (1) simple (one branch)(2, 0.50, 0).
31. Radix: (0) absent; (1) present (2, 0.50, 0.95).
32. Radical tail piece: (0) absent; (1) present (5, 0.20, 0.20).
33. Radical tail piece morphology: (0) straight; (1) spiraled; (2) curved ectally; (3) curved mesally; (4) anteriorly directed (2, 0.10, 0).
34. Anterior radical process: (0) absent; (1) present (8, 0.13, 0.22).
35. Column: (0) absent; (1) present (3, 0.33, 0.90).
36. Fickert's gland: (0) absent; (1) present (3, 0.33, 0).
37. Terminal apophysis: (0) absent; (1) present (7, 0.14, 0.33).
38. Lamella characteristica: (0) absent; (1) present (7, 0.14, 0.63).

Matrix M1 (Fig 2). The outgroup families Cyatholipidae and Physoglenidae are monophyletic with high support (100/100). Physoglenidae is the sister group of the linyphioid clade (Linyphiidae + Pimoidae; 81.1/79). *Nanoa* and *Pimoa* form a clade (93.4/90) which is the sister group of a lineage that includes all Linyphiidae, *Weintrauboa* and *Putaoa* (73.5/73). *Weintrauboa, Putaoa*, *Pecado* and *Stemonyphantes* form a clade (Stemonyphantinae; 99.9/100) sister to all remaining linyphiids (89.1/83).

Matrix M2 (Fig. 3). The representatives of Linyphiidae and Physoglenidae were monophyletic and the physoglenid clade is the sister group of the linyphioid lineage (Cyatholipidae was used to root the tree, based on the results of the analysis of M1). Linyphiidae is the sister group of Pimoidae (68.1/58). The Pimoidae clade is composed of *Nanoa* and *Pimoa* (94.9/80); both genera were monophyletic (but note that *Nanoa*, although represented by two terminals, is monotypic). The *Pimoa* clade can be divided into three major sub-clades which correspond to their geographic distribution: the American *Pimoa* Clade (98.7/75), the Asian *Pimoa* Clade (98.1/75) and the European *Pimoa* Clade (98.8/99). The American *Pimoa* and the European *Pimoa* form a clade which is the sister group of the Asian *Pimoa* clade. Most of the Asian *Pimoa* representatives (46 of a total of 60 Asian species in M2) have only COI sequences, thus this part of the matrix is missing data from the other markers.

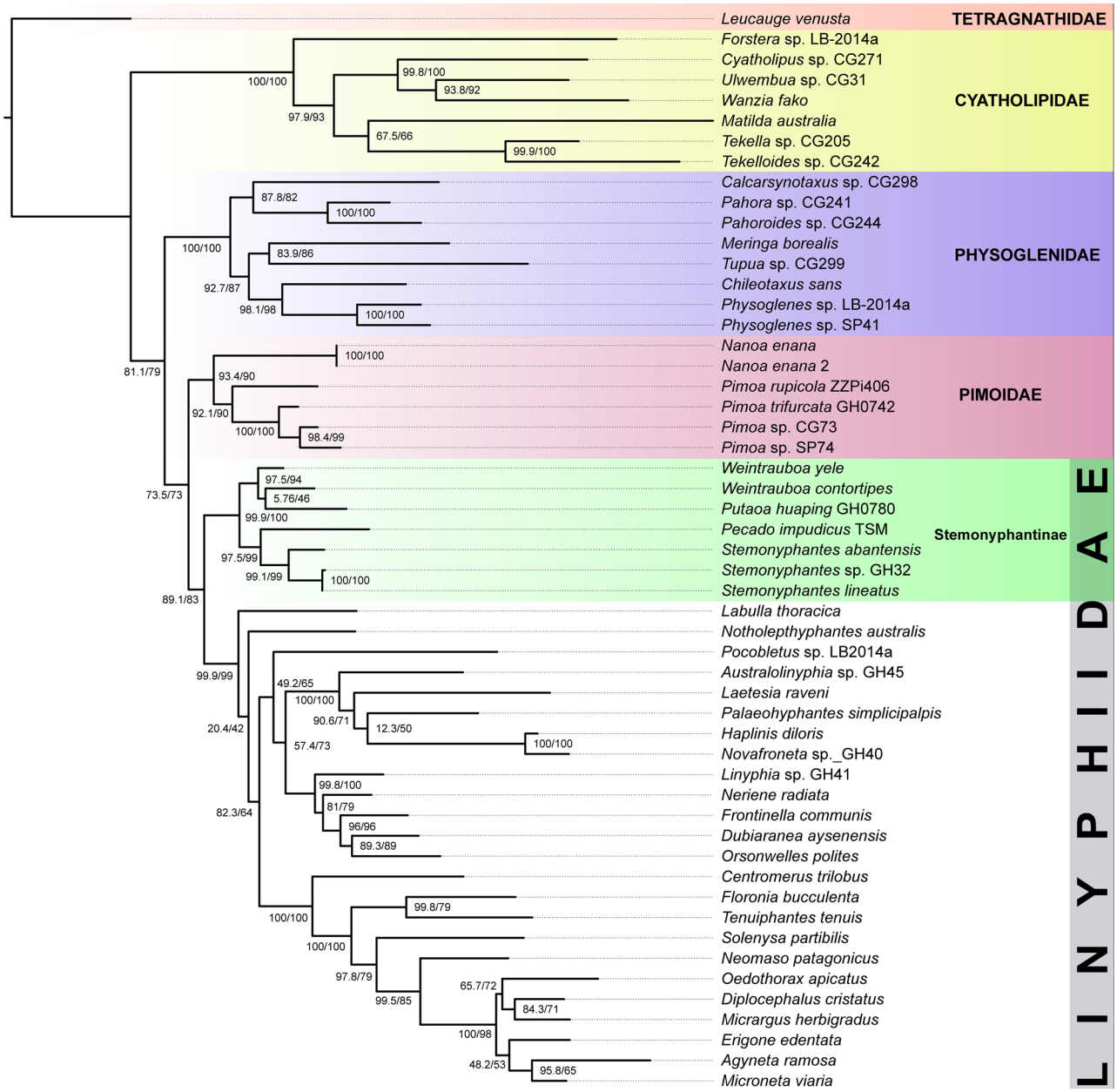

FIGURE 2. A maximum likelihood phylogeny of linyphioid families (Linyphiidae and Pimoidae) using five molecular markers (matrix M1). Support metrics at nodes indicate Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT)/ultrafast bootstrap (UFBoot).

Dating. TreePL and LSD2 inferred dates, optimized using fossil calibrations with the inclusion and exclusion of the Lebanese amber 'Linyphiinae' fossil as crown Linyphiidae and the *Pimoa* fossil as crown *Pimoa* versus stem *Pimoa*, recovered the dates as listed in Table 3 (See supplementary trees available at https://drive.google.com/drive/folders/1EgILXljZkaol_2kB6LxS5LR7m_bOePk3?usp=sharing). In summary, the dates for the occurrence of the last common ancestor of linyphioids (= Pimoidae + Linyphiidae) and Linyphiidae were 131.49 Ma and 125 Ma respectively (Table 3). However, the exclusion of the Linyphiinae fossil resulted in more recent age estimates of 68.62 Ma and 73.32 Ma for the same nodes (Table 3). The analysis where we placed *Pimoa multicuspuli* fossil at the crown node of *Pimoa* and the 'Linyphiinae' fossil at the crown node of Linyphiinae was 81.77 Ma, however, with the exclusion of the 'Linyphiinae' fossil it was recovered as 57.68 Ma (Table 3). The use of the *Pimoa multicuspuli* fossil as a stem calibration for *Pimoa* recovered a date of 47.8 Ma for the split of *Pimoa* and *Nanoa* and was unaffected by the 'Linyphiinae' fossil (Table 2).

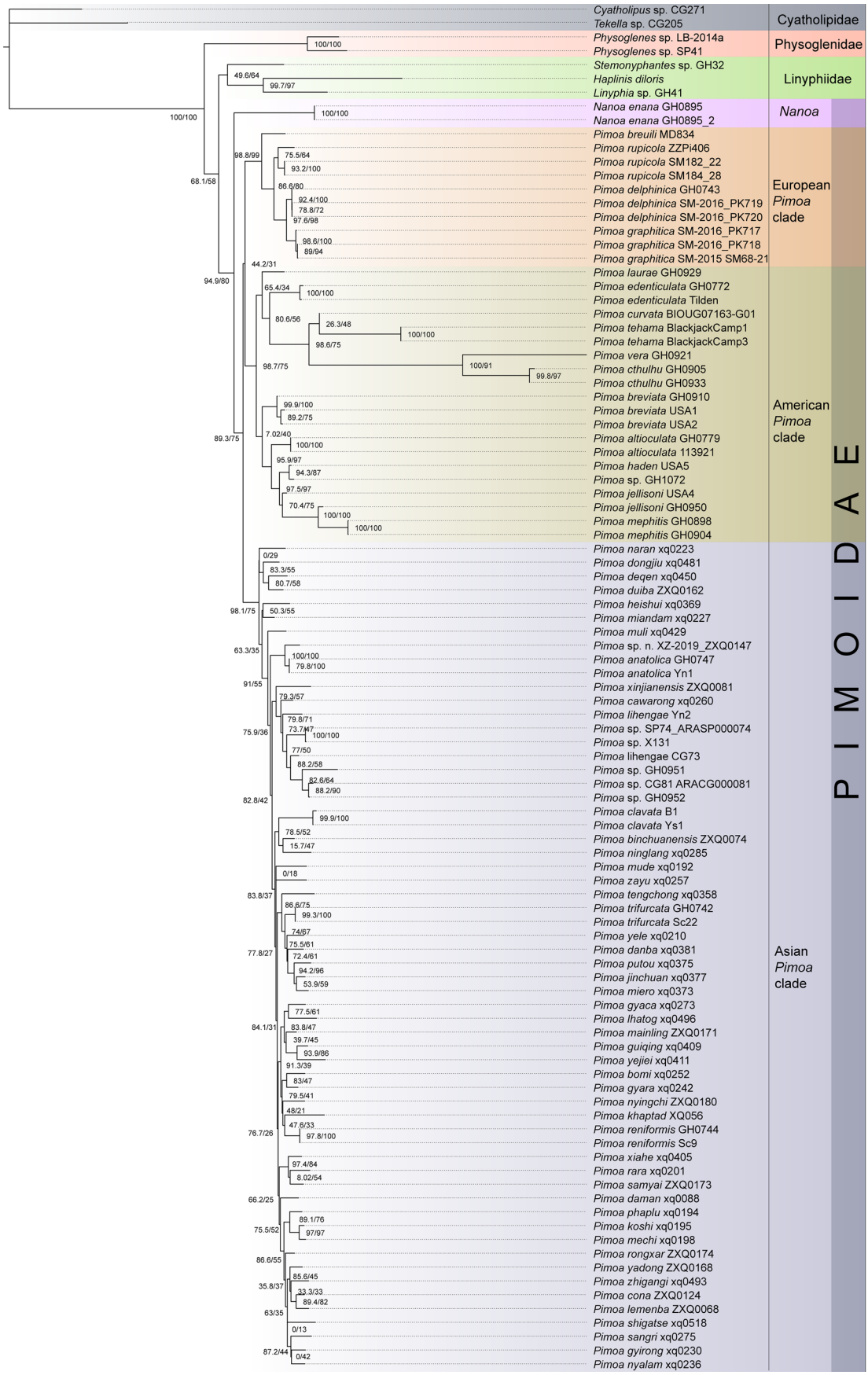

FIGURE 3. A maximum likelihood phylogeny of Pimoidae using five molecular markers (matrix M2). Support metrics at nodes indicate Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT)/ultrafast bootstrap (UFBoot).

TABLE 3. Dates (million years ago) recovered from the fossil calibrations using treePL and LSD2 (provided as range in parentheses) for the most recent common ancestor (MRCA) of Linyphiidae, linyphioids and Pimoidae.

Fossil treatment	Linyphiidae (MRCA)	Linyphiidae+Pimoidae (=Linyphioids) (MRCA)	Pimoidae (MRCA)
Linyphiinae fossil as crown Linyphiidae + *Pimoa multicuspuli* as crown *Pimoa*	125 (135-125)	131.49 (136.98-125)	81.77 (97.58-73.64)
Pimoa multicuspuli as crown *Pimoa* (Linyphiinae excluded)	68.62 (70.16-52.30)	73.32 (80.34-63.85)	57.68 (65.98-52.45)
Linyphiinae fossil as crown Linyphiidae + *Pimoa multicuspuli* as stem *Pimoa*	125 (135-125)	130.52 (136.93-125)	47.8 (47.8-43)
Pimoa multicuspuli as stem *Pimoa* (Linyphiinae excluded)	56.59 (63.48-43.61)	60.36 (70.56-53.68)	47.8 (47.8-43)

Biogeography. We conducted the biogeographic analysis using the dated phylogeny based on the M2 data set, including the Linyphiinae fossil at crown Linyphiidae and the *Pimoa* fossils as a crown constraint for *Pimoa*. The best fitting model for the reconstruction of ancestral areas was the DEC model (AICc=242.8, Table 4). As aforementioned, the phylogenetic tree of Pimoidae consists of four major clades: the *Nanoa* clade (represented by two terminals of the monotypic genus) and three clades within *Pimoa*, the American Clade, the European Clade and the Asian Clade. The RASP analysis with the DEC model recovered ambiguity (40%) followed by a widespread area for the ancestral area of Pimoidae at about 81.77 Ma (Fig. 4) including a combination of Nearctic, Yunnan, Sichuan and Hunnan (YSH), Iberian Massif and Italian Peninsula regions (29.18%) followed by the inclusion of Western Himalayas region (instead of YSH) (13.98 %), which diverged through dispersal. The preferred hypothesis for the ancestral area of the *Pimoa* Clade (Fig. 4) included a combination of Nearctic, YSH, Iberian Massif and Italian Peninsula regions (39.81%) followed by the replacement of YSH region by Western Himalayas region (18.92%) and diverged via dispersal. The ancestral area of the American Clade was the Nearctic region (99.58%), for the European Clade included a combination of Iberian Massif and Italian peninsula regions (75.55%) and for the Asian Clade included a combination of Western Himalayas, between Tibetan Plateau and Sichuan region and YSH regions (33.39%). For the Asian Clade, the second preferred hypothesis was the YSH region (26.29%). The divergence of the Asian Clade was supported by dispersal and that of the American + European and the European Clades was supported by vicariance events. Several dispersal and vicariance events were recovered in the Asian Clade (Fig. 4).

TABLE 4. Model parameters recovered from the biogeographic analysis of RASP for the M2 data set. The best fitting model was selected based on the Akaike information criterion (AIC) and is marked with an asterisk (*).

Model	LnL	numparams	d	e	j	AICc	AICc_wt
DEC*	-119.3	2	0.0008	0.0027	0	242.8	3.20E-13
DIVALIKE	-124.6	2	0.0013	0.0024	0	253.4	1.60E-15
BAYAREALIKE	-147.2	2	0.0011	0.019	0	298.5	2.60E-25

Discussion

The results of our phylogenetic analyses corroborate the monophyly of linyphioids and suggest that the genera *Weintrauboa* and *Putaoa* are part of a linyphiid lineage that includes *Stemonyphantes* and *Pecado*. As noted, the linyphiid affinities of *Weintrauboa* had already been pointed in molecular analyses using Sanger sequencing (Dimitrov *et al.* 2012, 2017, Wang *et al.* 2015, Wheeler *et al.* 2017) and corroborated with transcriptomic data (Fernández *et al.* 2018, Kallal *et al.* 2021). Thus, as presently delimited, the family Pimoidae is not monophyletic. To fulfill the requirement that all taxa must be monophyletic (e.g., Farris 1976), we circumscribe Pimoidae to only include *Pimoa* and *Nanoa* and transfer the genera *Weintrauboa* and *Putaoa* to Linyphiidae. Up to this date the linyphiid subfamily Stemonyphantinae has included only the genus *Stemonyphantes* (e.g., Gavish-Regev *et al.* 2013). Stemonyphantines are of key phylogenetic relevance because this clade is the sister group of the lineage that includes all other

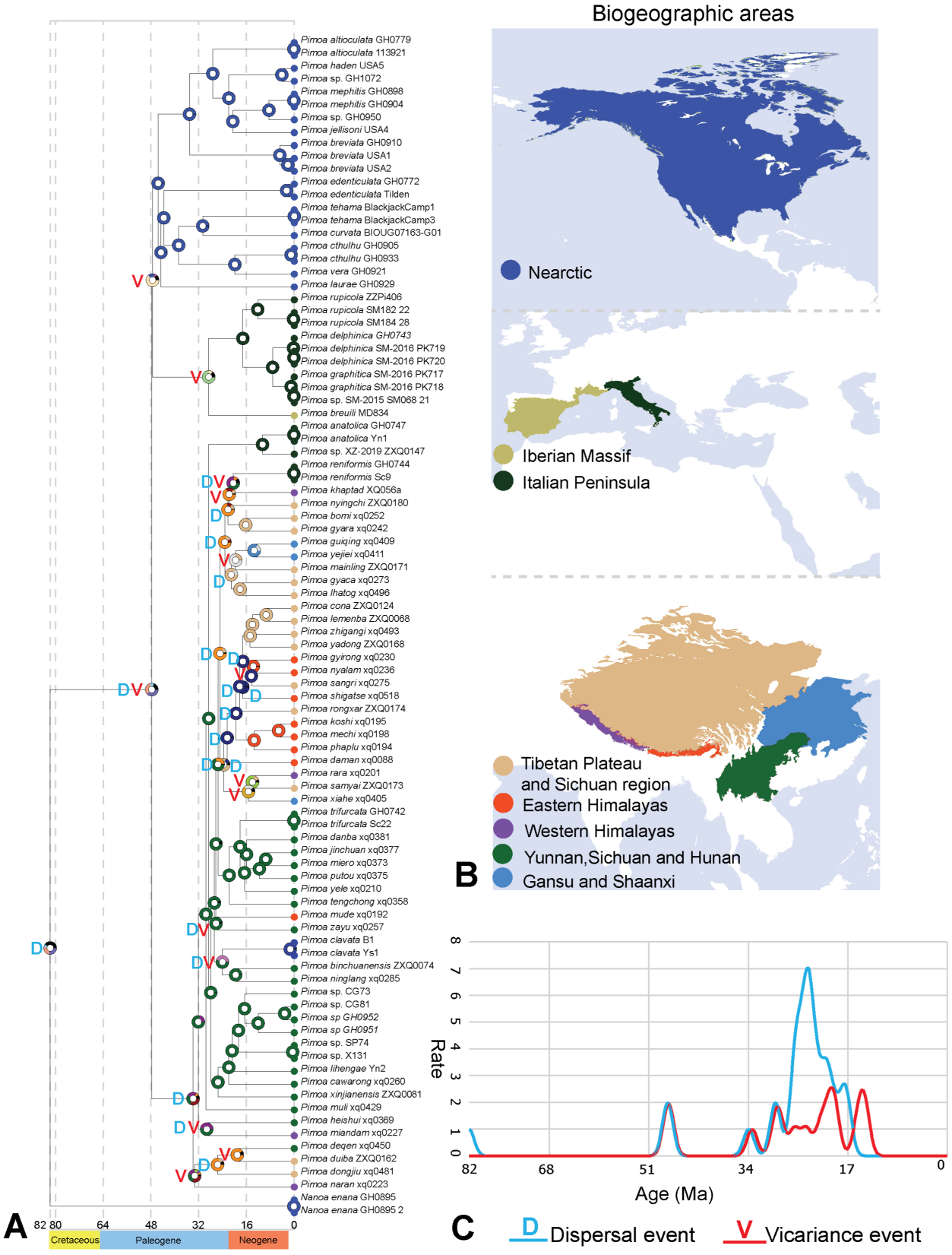

FIGURE 4. A, Biogeographic hypothesis obtained from the Dispersal-Extinction-Cladogenesis (DEC) model of RASP analysis on a dated phylogeny reconstructed with fossil calibrations using treePL. B, Biogeographic areas used as input in RASP (see Table 4 for details). Note that this is not a distribution map of pimoids, the range of any given pimoid species does not occupy all of the shaded biogeographic area (e.g., in North America pimoids are exclusively found in the west). C, Dispersal and vicariance rates optimized by the DEC model of RASP.

linyphiids, and thus are important to understand the evolution and diversification of the family. Our analyses place *Stemonyphantes* in a larger clade (with *Pecado*, *Weintrauboa* and *Putaoa*) that remains sister to all other linyphiids. Based on our results we now circumscribe the linyphiid subfamily Stemonyphantinae to also include the genera *Pecado*, *Weintrauboa* and *Putaoa*. These changes in the phylogenetic classification of pimoids and linyphiids also require revising the diagnosis of these two families (see the 'Systematics' section) and help us to better understand the homologies of some of their male palpal characters.

Pimoid male palpal characters under a new phylogenetic light

The new hypothesis of pimoid and linyphiid relationships (Fig. 2) has implications for the interpretation and optimization of some of the morphological characters of linyphioids, particularly the male palpal sclerites. Some of the male palpal structures of araneoids are notoriously difficult to homologize across families (e.g., Coddington 1990, Griswold *et al.* 1998) but nonetheless have played a major role in reconstructing pimoid and linyphiid relationships (e.g., Hormiga 1994a, b, Miller & Hormiga 2004, Hormiga & Tu 2008, Frick & Scharff 2013). We discuss here some of the characters that require a revised interpretation under the light shed by the results of our molecular phylogeny (Figs 2, 11).

Cymbial processes and sclerites. Pimoids have a dorsoectal cymbial process with modified macrosetae (cymbial cuspules, characters 2—5, Fig. 5). In *Nanoa* the cymbial process, which bears a large modified macroseta, is in a more anterior position (Fig. 5 C, D). Stemonyphantines also have an ectal cymbial process. In *Stemonyphantes* the process can be less pronounced (e.g., *S. lineatus* Linnaeus, 1758 and *S. blauveltae* Gertsch, 1951; Fig. 8) but in some species the ectal process is large and conspicuous (e.g., *S. abantensis* Wunderlich, 1978 and *S. agnatus* Tanasevitch, 1990; Figs 8, 9). *Pecado* (Fig. 9), *Weintrauboa* (Fig. 6) and *Putaoa* (Fig. 7) have a basal cymbial process which we consider homologous to that in pimoids and *Stemonyphantes*. Ectal cymbial processes can be found in other linyphiids (e.g., *Floronia* O. Pickard-Cambridge, 1896 or *Agyneta* Hull, 1911). Pimoids have a retrolateral cymbial sclerite (pimoid cymbial sclerite, PCS, character 6) which is unique to this family (Fig. 5). In *Nanoa* and the European species of *Pimoa* the PCS is continuous with the ectal cymbial margin and thus connected to the paracymbium (character 8). American and Asian species of *Pimoa* have the PCS connecting to the cymbium by means of a membrane. *Weintrauboa* and *Putaoa* had been interpreted as having a PCS continuous (attached) with the paracymbium by means of an area of intermediate degree of sclerotization (Hormiga & Tu 2008). The placement of *Weintrauboa* and *Putaoa* in the linyphiids suggests that the PCS is absent, and that their large structure is the anterior (proximal) arm of the paracymbium, rather than a PCS homolog, which is joined to the ectal margin by a band of semi-membranous tissue (Figs 6,7). *Pimoa* and *Nanoa* have an additional sclerite (absent in linyphiids) on the margin of the alveolus (the alveolar sclerite, character 1), although in the latter genus it is less developed (Fig. 5).

Paracymbium. *Pimoa* and *Nanoa* (Fig. 5) have a paracymbium (characters 11—13) that is an extension of the basal cymbial margin (integral paracymbium), lacking the typical articulated, membranous connection of most linyphiids (but not all, for example, *Intecymbium antarcticum* (Simon, 1895), Miller & Hormiga 2004). *Weintrauboa* and *Putaoa* have an intersegmental paracymbium (Figs 6, 7), broadly attached to the ectal margin of the cymbium base by a membrane (Hormiga & Tu 2008). In *Stemonyphantes,* although the paracymbium is integral in some species (e.g., *S. agnatus* and *S. altaicus* Tanasevitch, 2000; Fig. 9), in most it has both a ventral membranous connection and an integral connection on the dorsomesal side (e.g., *S. lineatus*, *S. blauveltae*, *S. conspersus* (L. Koch, 1879) and *S. abantensis*; van Helsdingen 1968, Wunderlich 1978, Gavish-Regev *et al.* 2013; Fig. 8). The paracymbium of *Pecado* has a similar intermediate condition (Fig. 9): it is dorsally connected to the cymbium by means of a membranous area, but its proximal branch ventral margin is sclerotized and continuous with the ectal cymbial margin (Hormiga & Scharff 2005). In sum, pimoids retain the plesiomorphic condition of araneoids (integral paracymbium), stemonyphantines have an integral or intermediate state and the remaining linyphiids have an intersegmental paracymbium (with occasional exceptions), attached by means of a membrane.

Suprategulum. Linyphiids have an anterior extension of the tegulum (character 17) that carries the membranous stalk (or column, character 35) that connects to the embolic division (the radix and various radical sclerites). Saaristo (1977) coined the term suprategulum for this structure through which the sperm duct passes. Although *Weintrauboa* and *Putaoa* had been interpreted as lacking a suprategulum (e.g., Hormiga 2008), Hormiga & Tu (2008) pointed out that in *Putaoa* the ectal region of the tegulum that is prolonged into the base of the pimoid embolic

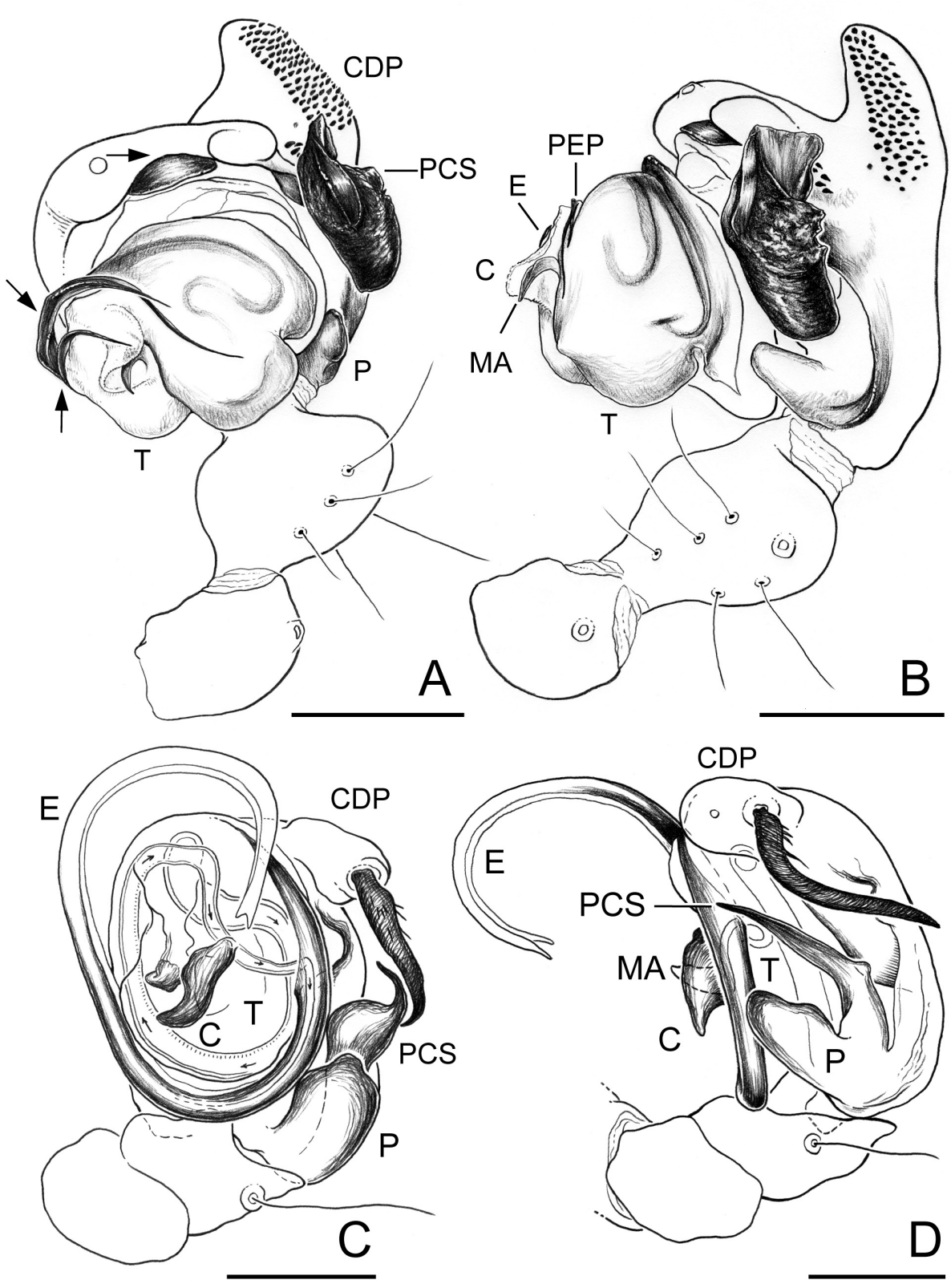

FIGURE 5. Pimoid male genitalic morphology: *Pimoa graphitica* Mammola, Hormiga & Isaia, 2016 (A-B), *Nanoa enana* Hormiga, Buckle & Scharff, 2005 (C-D). A, Palp ventral (arrow up points to embolus; arrow down points to pimoid embolic process; arrow right points to alveolar sclerite). B, Palp, ectal. C, Palp ventral (the embolus is in a slightly displaced position; normally its distal end rests tightly against the tegulum, next to the conductor). D, Palp dorsoectal. Scale bars: A-B, 0.5 mm; C-D, 0.1 mm. Modified from Hormiga *et al.* (2005). Abbreviations: C= conductor; CDP = cymbial denticulate process; E = embolus; MA= median apophysis; P = paracymbium; PCS = pimoid cymbial sclerite; PEP = pimoid embolic process; T = tegulum.

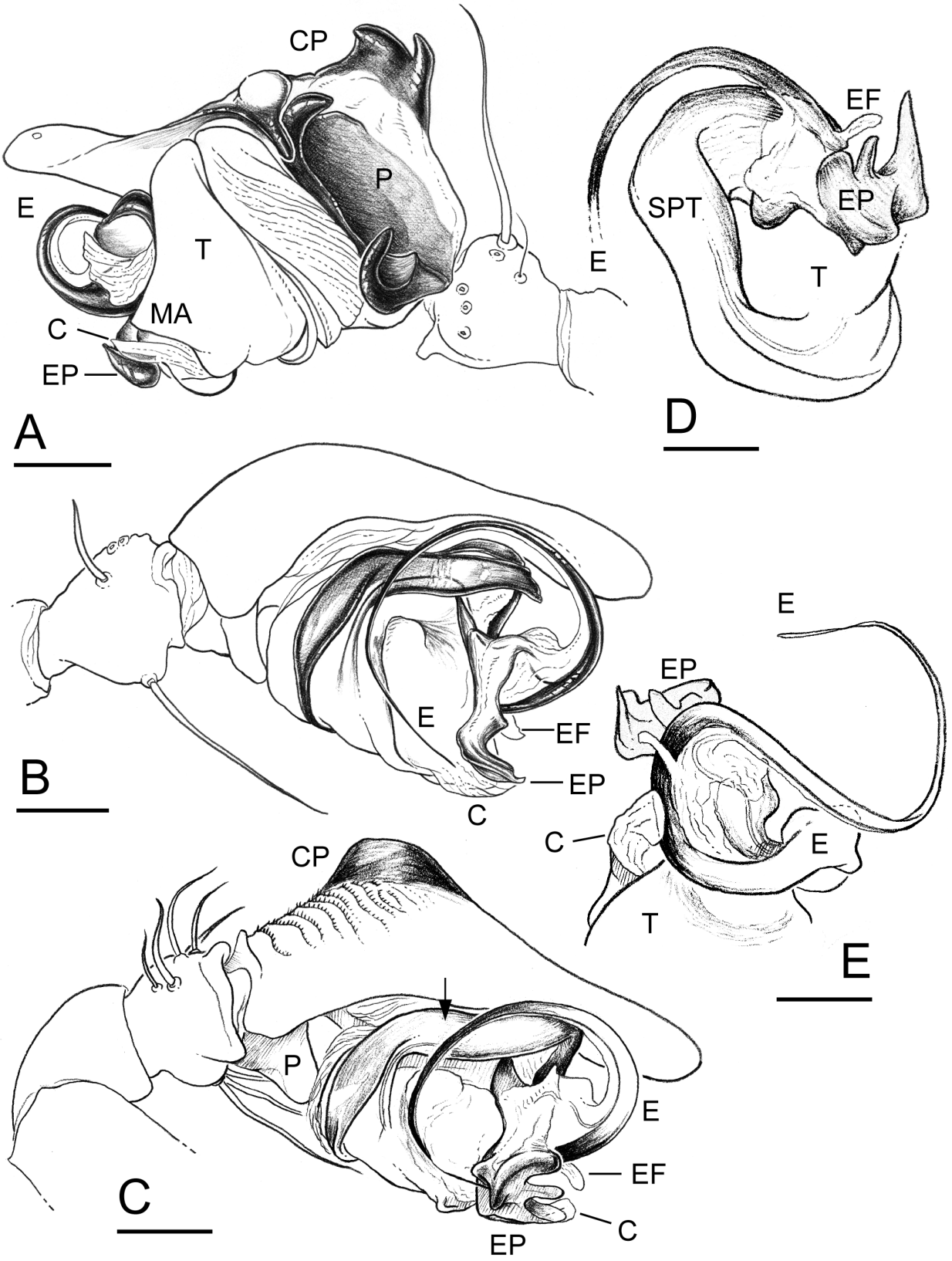

FIGURE 6. *Weintrauboa* male genitalic morphology: *Weintrauboa yele* Hormiga, 2008 (A-B), *W. contortipes* (Karsch, 1881)(C-E). A, Palp, ectal. B, Palp, mesal. C, Palp, mesal (arrow points to suprategulum). D, E, Tegulum, suprategulum and embolus base. Modified from Hormiga (2003, 2008). Scale bars: A-B, 0.2 mm. Abbreviations: C= conductor; CP = cymbial process; E = embolus; EF = embolic flap; EP = embolic process; MA= median apophysis; P = paracymbium; SPT= suprategulum; T = tegulum.

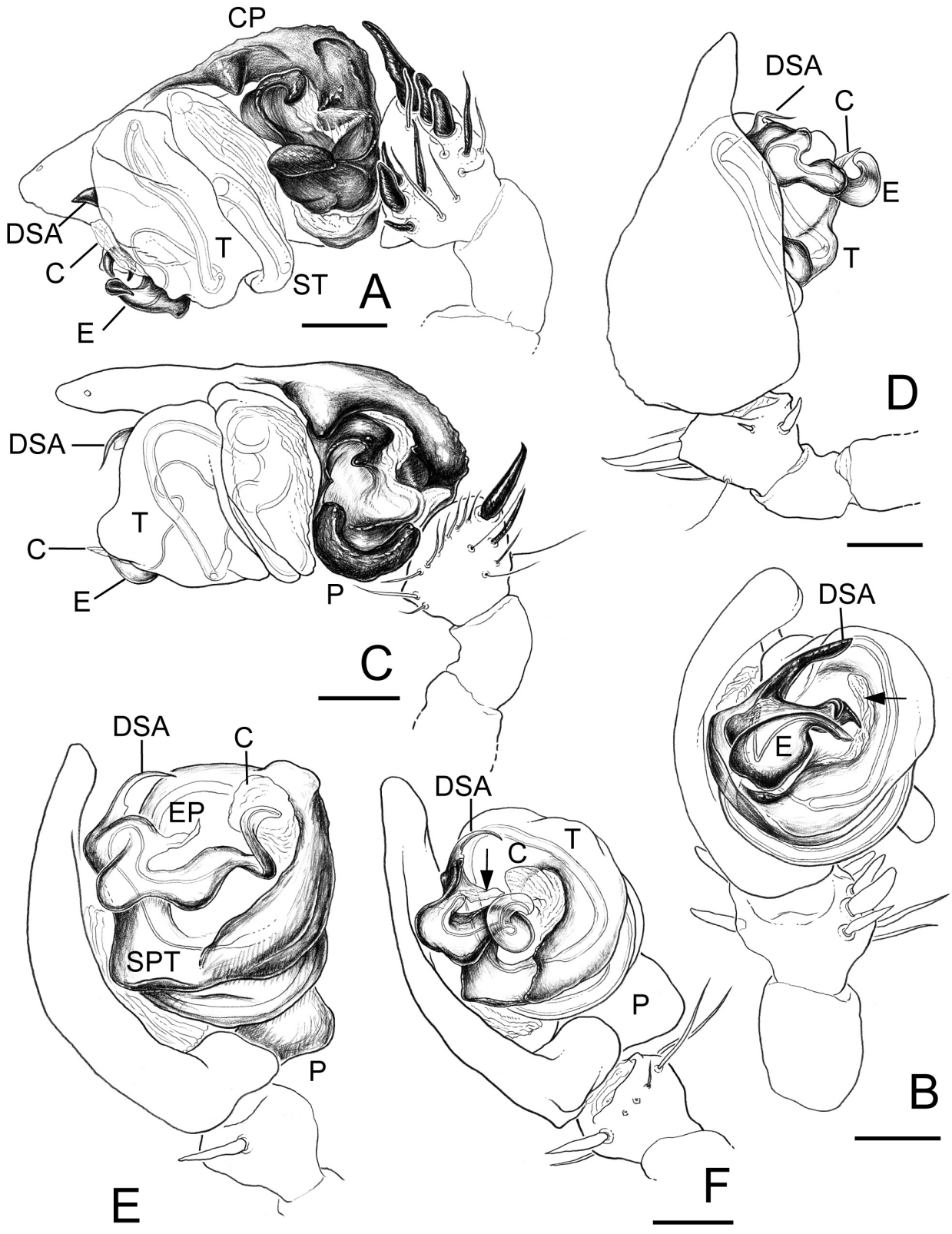

FIGURE 7. *Putaoa* male genitalic morphology: *Putaoa huaping* Hormiga & Tu, 2008 (A-B), *P. seediq* Hormiga & Dimitrov, 2017 (C-F). A, Palp, ectal. B, Palp, mesal (arrow points to conductor). C, Palp, ectal. D, palp, dorsomesal (modified from Hormiga 2003, 2008). E, Palp, mesal (schematic). F, Palp, mesal (arrow points to embolic process). Modified from Hormiga & Tu (2008), Hormiga & Dimitrov (2017). Scale bars: A-B, 0.2 mm. Abbreviations: C= conductor; CP = cymbial process; DSA = distal suprategular apophysis; E = embolus; EP = embolic process; P = paracymbium; SPT= suprategulum; ST = subtegulum; T = tegulum.

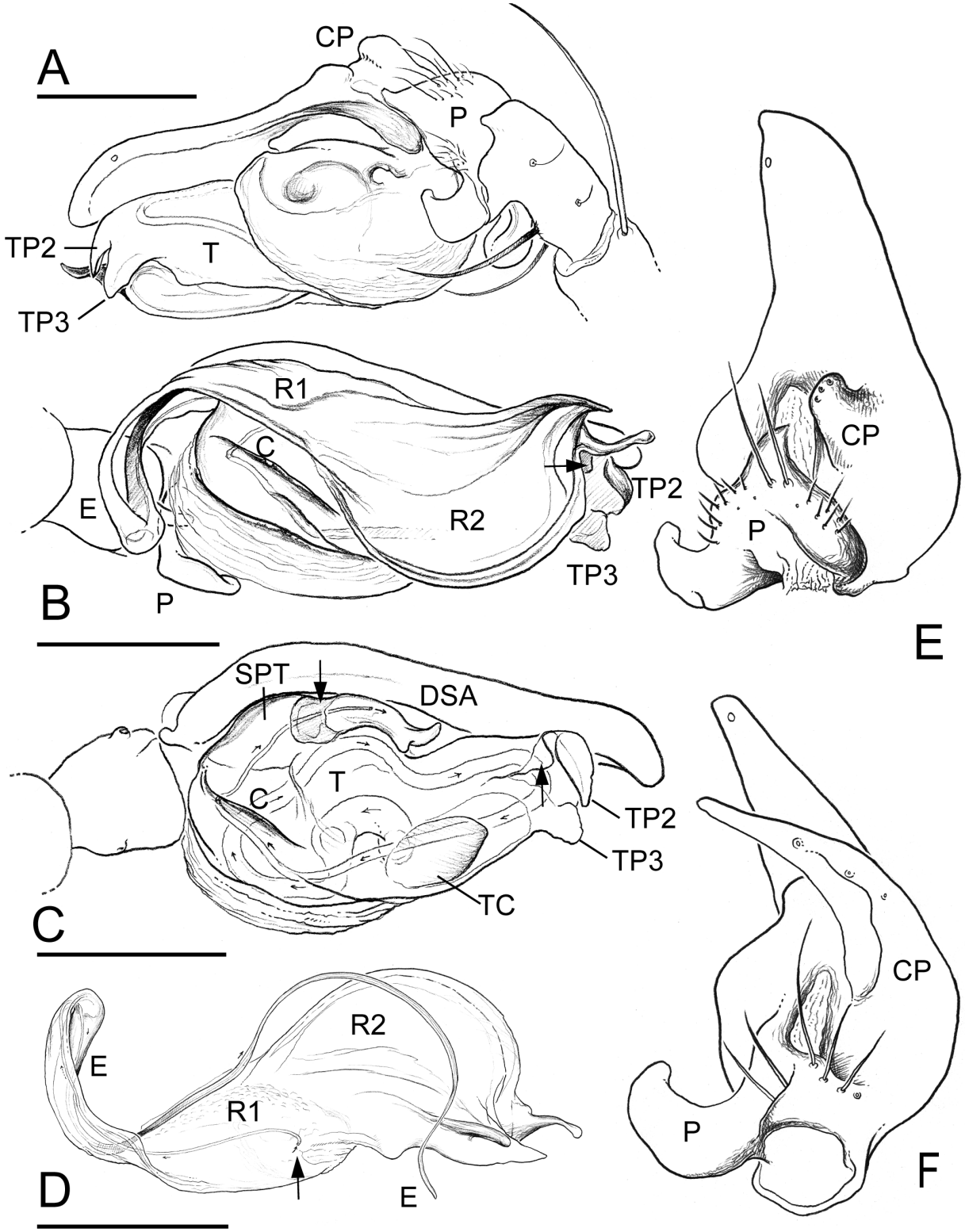

FIGURE 8. *Stemonyphantes* male genitalic morphology: *Stemonyphantes lineatus* Linnaeus, 1758 (A-E), *S. agnatus* Tanasevitch, 1990 (F). A, Palp, ectal. B, Palp, ventral (arrow points to median apophysis). C, Palp, mesoventral (embolic division removed; arrow up points to median apophysis, arrow down points to suprategular ring). D, Embolic division (arrow points to the membranous area connecting to the column). E, Palp, dorsoectal (schematic; the paracymbium is partially connected to the cymbium by a membrane). F, Palp, dorsoectal (schematic; the paracymbium is integral, an extension of the cymbium lacking a membranous attachment). Scale bars: A-D, 0.5 mm. Abbreviations: C= conductor;; CP = cymbial process; DSA = distal suprategular apophysis; E = embolus; P = paracymbium; R1 = radix (proximal region); R2 = radix (distal region); SPT= suprategulum; ST = subtegulum; T = tegulum; TP = tegular processes.

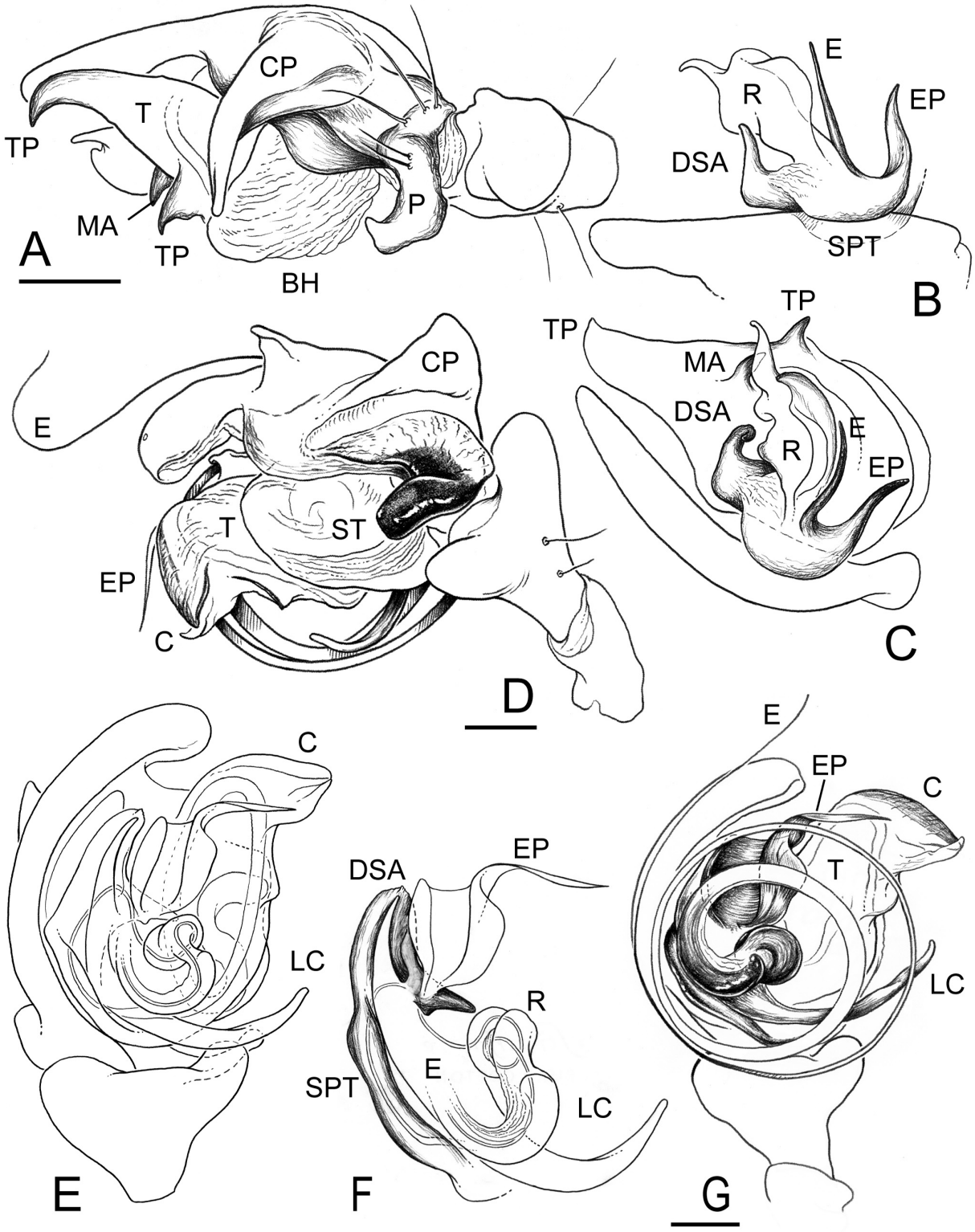

FIGURE 9. Stemonyphantine male genitalic morphology: *Stemonyphantes abantensis* Wunderlich, 1978, paratype (A-C), *Pecado impudicus* (Denis, 1945) (D-G). A, Palp, ectal. B, C, Palp, embolic division partially expanded (schematic). D, Palp, ectal. E, Meso ventral (schematic view of cleared palp with embolus rendered only in its basal region). F, Palp, dorsoectal, embolic division and suprategulum, schematic view of cleared palp with embolus rendered only in its basal region; the column and inter-sclerite membranes are not rendered and the radix has been displaced to right for clarity. Modified in part from Hormiga & Scharff (2005). Scale bars: A, D, G, 0.2 mm. Abbreviations: C= conductor; CP = cymbial process; DSA = distal suprategular apophysis; E = embolus; EP = embolic process; LC = lamella characteristica; P = paracymbium; R = radix; SPT= suprategulum; ST = subtegulum; T = tegulum; TP = tegular processes.

process (PEP, character 29) resembles the suprategular region of linyphiids and that topological correspondence and morphological similarity suggested that the base of the PEP may be homologous to the linyphiid suprategulum (Fig. 7). The corresponding tegular region in *Weintrauboa* is quite similar to that of *Putaoa*, and thus we now interpret these two genera as having a suprategulum (Figs 6, 7). *Putaoa* has an extension of the distal end of the suprategulum (homologous to the distal suprategular apophysis of linyphiids, character 19) but this apophysis is absent in *Weintrauboa*. *Pecado* has an ectal marginal apophysis in the suprategulum (character 20, Fig. 9), which lacks a homolog in the other stemonyphantines. The suprategulum of *Stemonyphantes* is unique in that it is articulated to the tegulum by means of a membrane (character 18; van Helsdingen 1968, Hormiga 1994b, Gavish-Regev *et al.* 2013; Fig. 8). *Stemonyphantes* and *Pecado* have a column, which is absent in *Weintrauboa* and *Putaoa*, although the corresponding suprategular area in the latter two genera is lightly sclerotized ventrally. In these latter two genera the embolus is an extension of the suprategulum (Figs 6, 7).

Conductor and median apophysis. In cladistic analyses linyphiids have been traditionally interpreted as lacking the araneoid conductor (character 22) and median apophysis (character 21)(e.g., Griswold *et al.* 1998, Hormiga 1994b, Miller & Hormiga 2004). Hormiga (1993, 1994a) interpreted two small tegular structures in *Pimoa* (one membranous, the other hook-like) as homologs of the araneoid conductor and median apophysis, respectively. More recently, Gavish-Regev *et al.* (2013) studied the male palp sclerite homologies in *Stemonyphantes* and concluded that this genus, unlike any other linyphiids, does have homologs of the araneoid conductor and median apophysis. Their morphological analyses also recovered *Stemonyphantes* as the sister group of the clade with remaining Linyphiidae and thus loss of the conductor and the median apophysis were hypothesized as synapomorphies of this latter lineage. Our results indicate that *Weintrauboa* and *Putaoa* are members of a clade that also includes *Stemonyphantes* and *Pecado*. *Weintrauboa* and *Putaoa* do have a conductor, but only the former genus has a median apophysis, albeit of very small size (Hormiga 2003, 2008, Hormiga & Tu, 2008; Figs 6, 7). Our analysis is the first to place the monotypic genus *Pecado* with nucleotide sequence data. Hormiga & Scharff (2005) studied the palpal homologies of *Pecado impudicus* (Denis, 1945) and concluded that it lacked a conductor and a median apophysis. The tegulum of *Pecado* has a sclerotized crest adjacent to a membrane on its apical region. We have interpreted this apical tegular membrane as a conductor and scored the median apophysis as absent in *Pecado* (Fig. 9). Alternatively, the pointed sclerotized crest could be homologized to the median apophysis (which is present in *Stemonyphantes* and some *Weintrauboa* species).

Embolus, embolic process and embolic division. The main difference in male palpal morphology between pimoids and linyphiids is in the structure of the embolic division. In pimoids the embolus is continuous with the tegulum, while in linyphiids there is a membranous stalk (the column, character 35) that connects the suprategulum to a radix (character 31), which carries the embolus and other sclerites, forming an embolic division of varying degrees of complexity. Thus, the linyphiid embolus is connected to the radix and not to the tegulum like in pimoids. In *Pimoa* there is an embolic process that runs parallel to the embolus (the pimoid embolic process, PEP, character 28) which is absent in *Nanoa* (Fig. 5). *Weintrauboa* (Fig. 6), *Putaoa* (Fig. 7) and some *Stemonyphantes* species (e.g., *S. agnatus S. serratus* Tanasevitch, 2011, and *S. abantenis*; Fig. 9) have a well differentiated basal embolic process which in the first two genera had been homologized with the process of *Pimoa* (e.g., Hormiga 2003, Hormiga & Tu 2008). *Pecado* has in a very similar position a sclerite that connects to the embolus base, which was considered a terminal apophysis by Hormiga & Scharff (2005). We now interpret the embolic process of *Pimoa* as a primary homolog of the embolic process of stemonyphantines (including *Pecado*); this process when optimized on the molecular phylogeny (Fig. 11, character 28) implies two independent origins of the embolic process in pimoids and stemonyphantines (absent in some *Stemonyphantes*). The linyphiid radix can be optimized as a synapomorphy of the family with a secondary absence in *Weintrauboa* and *Putaoa*, or alternatively as a synapomorphy of the non-stemonyphantine linyphiid clade, convergently present in the *Stemonyphantes* plus *Pecado* lineage.

The embolic division of *Stemonyphantes* is rather unusual (Blauvelt 1936, Merrett 1963, van Helsdingen 1968, Gavish-Regev *et al.* 2013), and given the possible homoplasy in the radix it is worth discussing it in more detail. In his study of linyphiid palpal morphology, Merrett (1963: 382) noted that the parts of the "radix" (his quotation marks) of *Stemonyphantes lineatus* "cannot be homologized accurately" and that "the genera *Stemonyphantes* and *Allomengea* are both so aberrant in palp structure that it is impossible to comment on their affinities…" (p. 457). Almost three decades before Merrett expressed his frustration on homologizing the structures of the embolic division of *Stemonyphantes*, Helen Blauvelt (1936) had published a detailed and beautifully illustrated comparative analysis of linyphiid palpal morphology, including that of *Stemonyphantes blauveltae* Gertsch, 1951. Her careful description

of the embolic division of the only American species in the genus was silent about anatomical correspondences to potentially homologous structures in other linyphiids (unlike the treatment of many other species in her monograph in which the embolic division sclerites were homologized and labeled across species). Van Helsdingen (1968: 135) distinguished in the flattened embolic division of *Stemonyphantes* a strongly chitinized distal part from a proximal part, which was connected to the column (his "connecting membranes") and extended into the embolus. He considered the proximal half to be derived (that is, homologous in our terminology) from the radix, and the distal half to be a remnant of the lamella or terminal apophysis. Wunderlich (1978) referred to the distal part of the embolic division as a "functional conductor" and Gavish-Regev *et al.* (2013) labeled the distal region as the "radical part (RP)" and the proximal part of the embolic division as "embolic part (EP)." The *Stemonyphantes* species with a well differentiated basal embolic process (e.g., *S. abantenis*, Fig. 9) also have a well differentiated distal region, and thus conjunction argues against homology between this anterior region and the basal embolic process. *Pecado,* the sister group of *Stemonyphantes*, has a complex embolic division with a column, a small radix, an embolic process and a lamella characteristica (Fig. 9). The radix of *Pecado*, is also unusual, small and very different from that in the latter genus, and interconnected to a sclerite that we have tentatively homologized with the embolic process (Fig. 9E–G). Alternatively, this sclerite in *Pecado* could be a homolog of the distal region of the embolic division of *Stemonyphantes*. Hormiga & Scharff (2005: fig. 15D) interpreted a small semi-membranous area between the distal apex of the lamella characteristica and the distal suprategular apophysis of *Pecado* as an embolic membrane. Access to additional (and more recently collected) specimens has allowed us to revise the original interpretation and it is now clear that the alleged embolic membrane of *Pecado* is in fact a small membranous fold that connects the posterior margin of the distal suprategular apophysis with the membranous region that connects the column to the lamella characteristica. *Pecado*, like all other stemonyphantines, does lack an embolic membrane. The embolic membrane is also absent in *Labulla,* and the presence of this membrane is a synapomorphy of the clade that includes all linyphiids except the stemonyphantines and *Labulla* (Figs 2, 11).

Biogeography of Pimoidae

Our biogeographic reconstructions suggest that ancestrally pimoids and *Pimoa* were widely distributed across the Palearctic, the Nearctic and the Sino-Japanese regions (see Holt *et al.* 2013 for definitions of zoogeographic regions). It has been suggested that during that time (80–48 Ma) a large continuous boreotropical forest was present at higher latitudes in the northern hemisphere (Tiffney 1985a, b; Lavin & Luckow 1993). *Pimoa* fossils from Baltic amber suggest pimoids have been associated with this forest. Gradual cooling, particularly pronounced after the late-Eocene, led to the retreat and fragmentation of the boreotropical forest and this has likely led to the vicariance events leading to the Nearctic, the Spanish Massif and the Italian peninsula lineages.

The biogeographical history of the Asian Clade, which is also the most speciose group of *Pimoa*, is more complex and dynamic. The dating of the common ancestor of this clade (with varying combinations of fossil placements) ranges between 47.8 Ma (mid-Eocene) and 23.07 Ma (Late Oligocene). Our biogeographic analyses indicate a widespread ancestral area for the Asian pimoids, which spans from the Western Himalayas to Hunan mostly within the Oriental region and with limited presence in the Sino-Japanese region.

The collision of the Indian raft with Eurasia is hypothesized to have begun during the early Eocene at about 50 Ma, with the Indian plate and mainland Asia contacting between 45-35 Ma and leading to the rise of the Himalayas by 23 Ma (Ali & Aitchison 2008, Clift *et al.* 2008, Metcalfe 2013). Some studies on rosefinches (Tietze *et al.* 2013), geckos (Agarwal *et al.* 2014), spiders (Zhao *et al.* 2020) and crabs (Klaus *et al.* 2010) have shown that the India-Asia collision along with the formation of the Himalayas has profoundly affected the biogeography of several organisms.

The timing of origin of the Asian *Pimoa* Clade and its known distribution (see Fig. 4 distribution map) coincides with the India-Eurasia collision. It can be conjectured that the connectivity of two biotas (of insular India and mainland Asia) and the rise of mountain barriers together with global cooling and increase of aridity in large parts of central Asia (to a large extent also due to the rise of the Himalayas) may be a driving force behind the diversification of this most speciose clade in the family. Our biogeographic analyses suggest multiple dispersal and vicariance events between the different Oriental and Sino-Japanese subregions that we considered here. However interesting, these biogeographical hypotheses cannot be tested here due to the limitations of our data set, since the majority

of Asian *Pimoa* have only COI sequence data. It is possible that the missing data may have influenced the branch lengths and relationships of taxa within this clade. In addition, many Asian *Pimoa* species are known only from the type material (providing a single point for the species distribution). It is therefore necessary to further study whether the known narrow ranges represent the actual distribution or are an undersampling artifact. Given these limitations we abstain from discussing in further details the inferred biogeographical history of the Asian Clade of *Pimoa*.

Conclusions

The sequence data and the analyses presented here help to clarify the limits of the families Pimoidae and Linyphiidae. Based on our results we now circumscribe Pimoidae to include only two genera (*Pimoa* and *Nanoa*). The Asian genera *Weintrauboa* and *Putaoa* are members of the expanded linyphiid subfamily Stemonyphantinae, along with *Stemonyphantes* and *Pecado*. Stemonyphantines are the sister lineage of the clade that includes all other Linyphiidae. The species in the genus *Pimoa* comprise three lineages which also carry a clear biogeographic signal: the American Clade, the European Clade and the Asian Clade. Pimoids were distributed in the ancestral boreotropical forests of the northern latitudes. Post-Eocene gradual cooling and aridification has led to the retreat of those ancestral forests resulting in fragmentation of pimoid distribution with the concomitant vicariance events that resulted in the Nearctic and southern Europe lineages. The biogeography of *Pimoa* is complex and the available data are still insufficient for a robust historical reconstruction. The new phylogenetic hypothesis (Figs 2, 11) allows for a reinterpretation of the complex male genitalic morphology of pimoids and stemonyphantines (Figs 5–10).

SYSTEMATICS

Family Pimoidae Wunderlich, 1986

Pimoinae Wunderlich, 1986: 119.
Pimoidae; Hormiga 1993: 534.

Diagnosis: Male pimoids are distinguished from other araneoid spiders by the following combination of characters: palp with integral paracymbium, a retrolateral cymbial sclerite, a dorsoectal cymbial process with modified macrosetae (cuspules in *Pimoa* and a large macroseta in *Nanoa*) (Fig. 5; see also figures in Hormiga (1994a) and Hormiga *et al.* (2005)). Conductor and median apophysis present in *Nanoa* and in most species of *Pimoa*. Embolus continuous with the tegulum (the typical linyphiid embolic division is absent), with an embolic process (absent in *Nanoa*) of varying morphology that runs parallel and external to the embolus. The epigynum is protruding in *Pimoa*, with a dorsal to lateral fold or groove with the copulatory opening at the distal end; fertilization ducts are oriented anteriorly (*Pimoa*) or posteriorly (*Nanoa*). As in linyphiids, most pimoids have stridulatory striae on the ectal side of the chelicerae (absent in *Nanoa*) and exhibit autospasy at the patella tibia junction. *Pimoa* species build sheet-webs (the natural history of *Nanoa* remains unknown).

Phylogenetics: The monophyly of Pimoidae is supported by the following putative synapomorphies: modified macrosetae on a dorsoectal cymbial process; a retrolateral cymbial sclerite (pimoid cymbial sclerite, PCS), an alveolar sclerite and the absence of aciniform silk gland spigots in the female PMS and PLS (Hormiga *et al.* 2005, Hormiga & Tu 2008, Hormiga 2008).

Distribution: *Pimoa* species are found in Western North America (from California through Alaska), Southern Europe (Spain, France and Italy) and Asia (the Himalayas area, China). *Nanoa enana* is found in northern California and southern Oregon.

Composition: Two genera, *Pimoa* (79 species) and *Nanoa* (monotypic).

Family Linyphiidae Blackwall, 1859

Linyphiidae Blackwall, 1859: 261.

Diagnosis: Araneoids with ectal cheliceral stridulatory striae and patella-tibia autospasy, both characters also

present in Pimoidae, but distinguished from the latter family by the presence in the male palp of an intersegmental paracymbium (partially intersegmental or integral in some stemonyphantines), a suprategulum, a distal suprategular apophysis and an embolic division that connects to the suprategulum by means of a membranous stalk (the column) (e.g., see figures in Blauvelt (1936), Merrett (1963), Millidge (1977) and Hormiga (1994b, 2000)). A membranous outgrowth of the column (the embolic membrane) is present in most linyphiids but absent in stemonyphantines. Unlike pimoids, the base of the embolus is differentiated in most linyphiids into a sclerite (radix).

Phylogenetics: Linyphiid synapomorphies include the intersegmental paracymbium, suprategulum, a distal suprategular apophysis, column and radix.

Distribution: Worldwide.

Composition: 625 genera, including *Weintrauboa* and *Putaoa* (transferred to Linyphiidae in the present work).

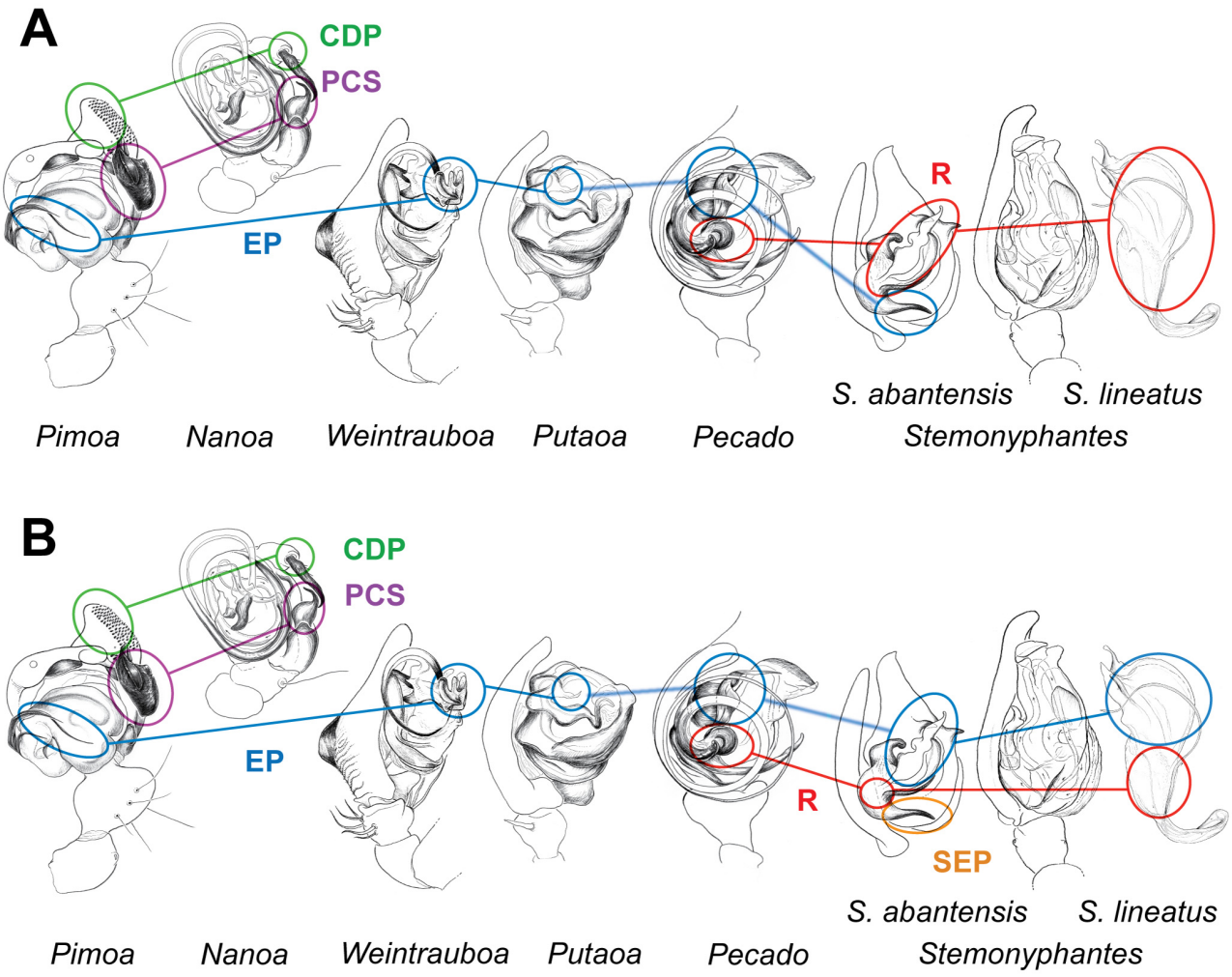

FIGURE 10. Graphic representation of some of the hypotheses of homology of the male palpal sclerites (indicated by circles) in pimoids (*Pimoa*, *Nanoa*) and stemonyphantines (*Weintrauboa*, *Putaoa*, *Pecado*, *Stemonyphantes*); homologous structures are connected by lines of the same color and blurred connecting lines denote that alternative primary hypotheses of homology are considered in the discussion. A, Embolic process (EP, in blue) homologous across all taxa (absent in *S. lineatus*); radix (R, red) present only in *Pecado* and *Stemonyphantes.* The cymbial process with cuspules (CDP, green) and the pimoid cymbial sclerite (PCS, purple) are unique to pimoids although a homologous cymbial process (without cuspules) is found in stemonyphantines and other linyphiids. B, Embolic process (EP, in blue) homologous across all taxa, including *S. lineatus* (the distal area of the embolic division, while the proximal is a homolog of the radix, in red). The Embolic process of *S. abantensis* (SEP, orange) is autapomorphic. See text for details.

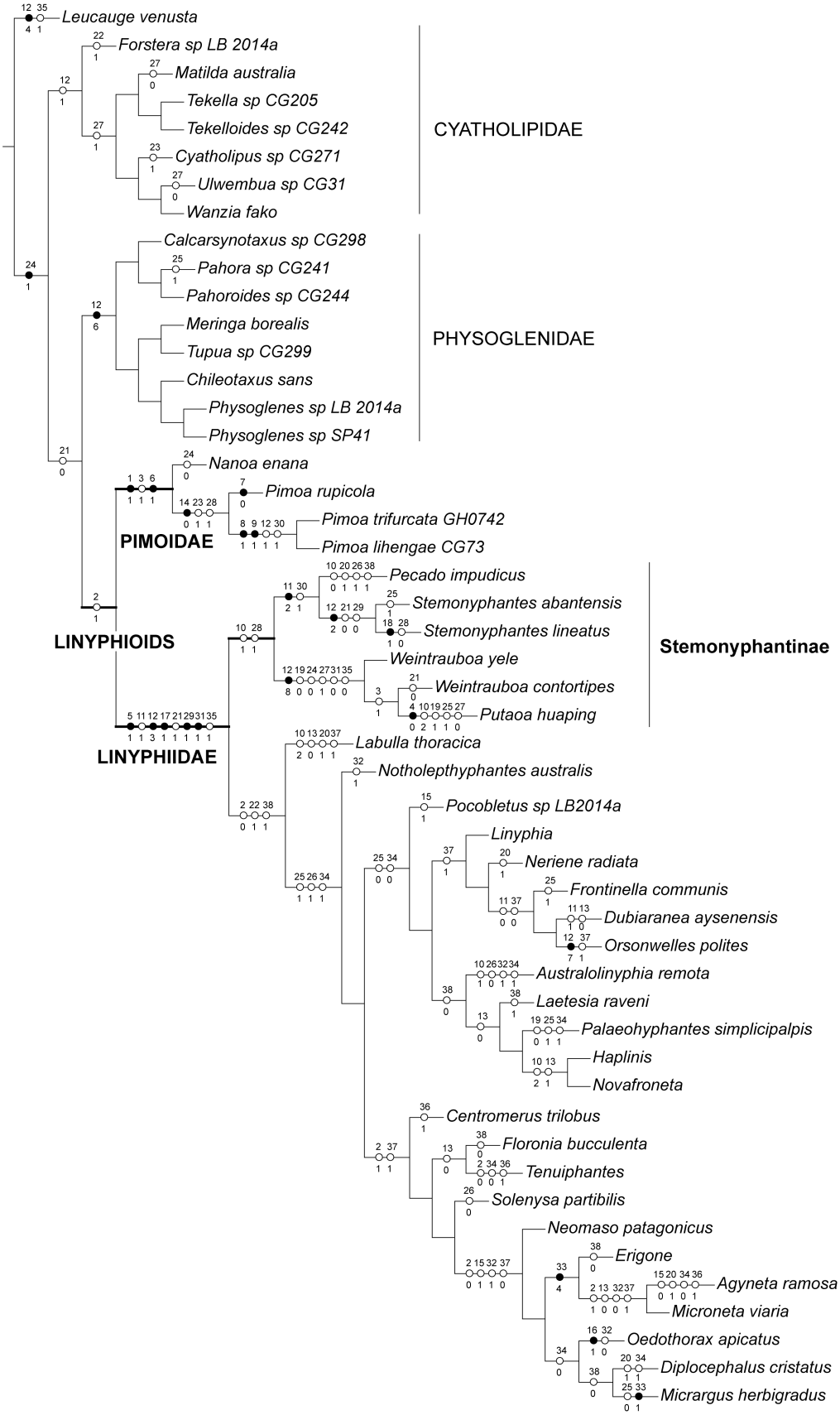

FIGURE 11. Optimization of 38 male palpal characters (matrix M3) on the optimal tree resulting from the maximum likelihood analysis of the molecular dataset M1. Ambiguous character changes are resolved under "Farris optimization" (ACCTRAN or Fast Optimization). Closed circles represent non-homoplasious character changes. The tree is 125 steps long and the consistency and retention indices are 0.38 and 0.72, respectively.

TABLE 5. Morphological character matrix (M3).

Leucauge_venusta	000--0---004110-0---10000000--0---1000
Forstera_sp_LB_2014a	000--0---001110-0---11--0-00--0---0000
Cyatholipus_sp_CG271	000--0---001110-0---10110-10--0---0000
Ulwembua_sp_CG31	000--0---001110-0---10010-00--0---0000
Wanzia_fako	000--0---001110-0---10010-10--0---0000
Matilda_australia	000--0---001110-0---10010-00--0---0000
Tekella_sp_CG205	000--0---001110-0---10010-10--0---0000
Tekelloides_sp_CG242	000--0---001110-0---10010-10--0---0000
Calcarsynotaxus_sp_CG298	000--0---006110-0---00?10-00--0---0000
Pahora_sp_CG241	000--0---006110-0---00011-00--0---0000
Pahoroides_sp_CG244	000--0---006110-0---00010-00--0---0000
Meringa_borealis	000--0---006110-0---00?10-00--0---0000
Tupua_sp_CG299	000--0---006110-0---00?10-00--0---0000
Chileotaxus_sans	000--0---006110-0---00?10-00--0---0000
Physoglenes_sp_LB_2014a	000--0---006110-0---00?10-00--0---0000
Physoglenes_sp_SP41	000--0---006110-0---00?10-00--0---0000
Nanoa_enana	111101100000110-0---00000-00--0---0000
Pimoa_rupicola	111101000000100-0---00?10-01000---0000
Pimoa trifurcata_GH0742	111101111001100-0---00?10-01010---0000
Pimoa lihengae_CG73	111101111001100-0---00110-01010---0000
Weintrauboa_yele	010--0---118110-100010?00-111-0---0000
Weintrauboa_contortipes	011110---118110-100000000-111-0---0000
Putaoa_huaping	011010---218110-101010001-01100---0000
Pecado_impudicus	010--0---023110-101110?100011110-01001
Stemonyphantes_abantensis	010--0---122110-101000?110010110-?1000
Stemonyphantes_lineatus	010--0---122110-111000010000--10--1000
Labulla_thoracica	000--0---213010-101111--0000--10-01011
Notholepthyphantes_australis	000--0---013110-101011--1100--11011001
Pocobletus_sp_LB2014a	000--0---013111?101011--0100--10-01001
Australolinyphia_remota	000--0---113110-101011--0000--11011000
Laetesia_raveni	000--0---013010-101011--0100--10-01001
Palaeohyphantes_simplicipalpis	000--0---013010-100011--1100--10-11000
Haplinis sp.	000--0---213110-101011--0100--10-01000
Novafroneta sp.	000--0---213110-101011--0100--10-01000
Linyphia sp.	000--0---013110-101011--0100--10-01011
Neriene_radiata	000--0---013110-101111--0100--10-01011
Frontinella_communis	000--0---003110-101011--1100--10-01001
Dubiaranea_aysenensis	000--0---013010-101011--0100--10-01001
Orsonwelles_polites	000--0---007110-101011--0100--10-01011
Centromerus_trilobus	010--0---013110-101011--1100--10-11111
Floronia_bucculenta	010--0---013010-101011--1100--10-11010
Tenuiphantes	000--0---013010-101011--1100--10-01111
Solenysa_partibilis	010--0---013110-101011--1000--10-11011
Neomaso_patagonicus	000--0---013111?101011--1100--11011001
Oedothorax_apicatus	000--0---0131111101011--1100--10-01001
Diplocephalus_cristatus	000--0---0131110101111--1100--11011000
Micrargus_herbigradus	000--0---01311??101011--0100--11101000
Erigone sp.	000--0---0131110101011--1100--11411000
Agyneta_ramosa	010--0---013010-101111--1100--10-01111
Microneta_viaria	010--0---0130110101011--1100--10-11011

Subfamily Stemonyphantinae Wunderlich, 1986

Stemonyphantinae Wunderlich, 1986: 120.

Diagnosis: Male stemonyphantines are distinguished from other linyphiids by the presence on the tegulum of a conductor (absent in all other linyphiids), and sometimes a median apophysis (also absent in all other linyphiids), and an integral or partially integral paracymbium. The apical region of the cymbium of most stemonyphantines is either narrow and elongated (*Stemonyphantes*) or conical (*Weintrauboa*, *Putaoa*) (e.g., see figures in Blauvelt (1936), Merrett (1963), van Helsdingen (1968) and Gavish-Regev *et al.* (2013)).

Phylogenetics: Putative morphological synapomorphies include the basal embolic process and elongated distal region of the cymbium.

Distribution: Holarctic (*Stemonyphantes*, 18 Palearctic and one Nearctic species), southern Iberian Peninsula and northern Africa (*Pecado impudicus*) and Asia (*Weintrauboa*, *Putaoa*).

Composition: Four genera, *Stemonyphantes* Menge, 1866 (19 species), *Pecado* Hormiga & Scharff, 2005 (monotypic), *Weintrauboa* Hormiga, 2003 (eight species) and *Putaoa* Hormiga & Tu, 2008 (three species).

Acknowledgments

Fieldwork in the Pacific Northwest was done in collaboration with Charles Griswold, Fernando Alvarez-Padilla, Andrea Carmichael and Alma Saucedo. The help of Man Miao Yang and her colleagues was instrumental for our fieldwork in Taiwan. We are grateful to Luis Crespo for the loan of specimens of *Pecado*. We are also grateful to Akio Tanikawa for sending study specimens. Nicolas Hazzi helped in preparing the figure of biogeographic areas. All analyses were conducted on the Colonial One High Performance Computing Facility at The George Washington University. GH's work in Denmark was supported by Nikolaj Scharff and ZMUC. We are grateful to Alexandre B. Bonaldo, Stefano Mammola and an anonymous reviewer for their comments and helpful suggestions on an earlier version of this manuscript. This study was supported by the US National Science Foundation (Grant Nos. Division of Environmental Biology 1457300 and 1457539 to G.H. and Gonzalo Giribet). Additional support was provided by the US National Science Foundation (Grant Nos. Division of Environmental Biology 1754289, 1754278, and Division of Environmental Biology 1754262 to G.H., Gonzalo Giribet, and Sarah Boyer).

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