



A multilocus phylogeny of Podoctidae (Arachnida, Opiliones, Laniatores) and parametric shape analysis reveal the disutility of subfamilial nomenclature in armored harvestman systematics



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ABSTRACT

The taxonomy and systematics of the armored harvestmen (suborder Laniatores) are based on various sets of morphological characters pertaining to shape, armature, pedipalpal setation, and the number of articles of the walking leg tarsi. Few studies have tested the validity of these historical character systems in a comprehensive way, with reference to an independent data class, i.e., molecular sequence data. We examined as a test case the systematics of Podoctidae, a family distributed throughout the Indo-Pacific. We tested the validity of the three subfamilies of Podoctidae using a five-locus phylogeny, and examined the evolution of dorsal shape as a proxy for taxonomic utility, using parametric shape analysis. Here we show that two of the three subfamilies, Ibaloniinae and Podoctinae, are non-monophyletic, with the third subfamily, Erecaninae, recovered as non-monophyletic in a subset of analyses. Various genera were also recovered as non-monophyletic. As first steps toward revision of Podoctidae, the subfamilies Erecaninae Roewer, 1912 and Ibaloniinae Roewer, 1912 are synonymized with Podoctinae Roewer, 1912 **new synonymies**, thereby abolishing unsubstantiated subfamilial divisions within Podoctidae. We once again synonymize the genus *Paralomanius* Goodnight & Goodnight, 1948 with *Lomanius* Roewer, 1923 **revalidated**. We additionally show that eggs carried on the legs of male Podoctidae are not conspecific to the males, falsifying the hypothesis of paternal care in this group.

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1. Introduction

In many taxonomic disciplines, and particularly entomology and arachnology, morphology continues to play a predominant role in both the systematics and phylogenetics of diverse arthropod groups. An apt example is provided by Laniatores, a suborder of harvestmen (order Opiliones) which contains ca. 4500 described species in approximately 30 families. Various families and hundreds of genera were historically established on the basis of questionable (and in some cases, polymorphic) character systems, such as shape, armature, and color of body or appendages (Roewer, 1949a, 1949b; Goodnight and Goodnight, 1953). More recently,

high-magnification microscopy has been deployed to identify new character systems and define attendant homologies (e.g., Gainett et al., 2014). In particular, characters derived from the male copulatory apparatus presently serve as the mainstay for new taxonomic descriptions and critically needed revisions (e.g., Martens, 1986; DaSilva and Gnaspini, 2009; Bragagnolo and Pinto-da-Rocha, 2012; Sharma, 2012; Sharma et al., 2012; Pinto-da-Rocha and Bragagnolo, 2013; Kury and Villarreal, 2015), but explicit consideration of phylogenetic structure and trait correlation, as inferred from an independent data class (namely, molecular sequence data), is uncommon for character systems in this group (Schwendinger and Martens, 2002; Sharma and Giribet, 2009; Gainett et al., 2014).

In order to quantify objectively the phylogenetic informativeness and degree of independence of character systems typically

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used in taxonomy and revisionary systematics of Laniatores, we selected as a case study the Indo-Pacific family Podoctidae.

Podoctids are small to mid-sized harvestmen (1–5 mm) that inhabit leaf litter and exhibit remarkable crypsis. Immediately recognizable by the spination of the first walking leg, this family is unusual among Opiliones due to its remarkable dispersal ability, being one of the three families of Laniatores that are found on remote Pacific islands (Goodnight and Goodnight, 1957; Sharma and Giribet, 2012). Podoctidae are further unique in that males of some species carry eggs attached to their walking legs (Martens, 1993). The eggs found attached to the males' legs are putatively conspecific, but mating behavior has never been observed in Podoctidae, and thus it is not known whether this observation corresponds to paternal care or to opportunistic egg-laying by heterospecific arthropods (e.g., Grosman et al., 2008; Cuthbertson et al., 2013). By contrast, mating behavior and parental care of conspecific eggs has been directly observed by behavioral ecologists in distantly related Neotropical species of Gonyleptoidea (e.g., Mora, 1990; Machado and Raimundo, 2001; Proud et al., 2011; Buzatto et al., 2014).

Previously considered part of Phalangodidae (Roewer, 1912), Podoctidae was elevated to family rank by Mello-Leitão (1938), who retained the subdivision of this group into three subfamilies defined by Roewer (1912). Ibaloniinae were diagnosed by the presence of a scopula on the tarsi of legs III and IV; Erecaninae were diagnosed by a single-segmented distitarsus in leg I; and Podoctinae were characterized by the absence of the previous characters. In addition, the subfamilies are loosely distinguishable by the shape of the body, with ibaloniines bearing an oval shape, and the remaining podoctids bearing an antero-posteriorly elongated shape (Kury and Machado, 2003), although numerous exceptions exist. Furthermore, the phylogenetic position of Podoctidae within Laniatores is not certain; various hypotheses of their relationships include placement in Samooidea (based on interpretation of male copulatory apparatus; Kury, 2007), a sister group relationship to Sandakanidae (five-locus phylogeny, one podoctid exemplar, no nodal support; Giribet et al., 2010), and a sister group relationship to Tithaeidae (ten-locus phylogeny; five podoctid exemplars; 59% bootstrap resampling frequency; Sharma and Giribet, 2011).

At present, the family contains approximately 150 species in 54 genera (Kury, 2011). Many of these genera are mono- or ditopic, holdovers from the system of Carl Friedrich Roewer, whose prolificacy was matched by the superficiality of his descriptive work (Roewer, 1912, 1923, 1949a, 1949b). As a result, various genera

and species in Laniatores were established on the basis of poorly defined and often highly variable characters (Roewer, 1912, 1949a, 1949b; Goodnight and Goodnight, 1957). The pitfalls of this method are exemplified by the taxonomic history of the Palauan species *Paralomanius longipalpus longipalpus*, whose sexually dimorphic male and female were once placed in separate genera (*Paralomanius longipalpus* and *Eulomanius brevipalpus*), subsequently synonymized as *Lomanius longipalpus* (Goodnight and Goodnight, 1957), and recently again placed in the ditopic genus *Paralomanius* (Zhang et al., 2013).

Here, we constructed a multilocus phylogeny to test subfamilial relationships within this family and characterize the evolution of morphological characters in a quantitative framework. Specifically, we tested the phylogenetic utility of two character systems that have served as the mainstays of Roewerian taxonomy since the early 20th century: scutal shape and tarsal formula.

Separately, we discovered in our collections two male specimens, an ibaloniine and a podoctine, that were each carrying a single bundle of eggs attached to the third or fourth walking legs (Fig. 1B and C). To test the hypothesis that the egg carrying behavior is phylotypic in Podoctidae, we additionally sequenced a subset of the eggs, with the prediction of identical molecular sequence data of eggs and their carriers, consistent with conspecific paternal care.

2. Materials and methods

2.1. Species sampling

Specimens of Podoctidae were collected by several individuals over multiple expeditions (2006–2013) by sifting leaf litter in sites throughout the Indo-Pacific and in the Indian Ocean. Podoctidae was represented by 73 specimens (17 Erecaninae, 26 Ibaloniinae, and 30 Podoctinae), including four terminals previously sequenced by us (Sharma and Giribet, 2009, 2011). Outgroup taxa consisted of five Sandakanidae, three Epedanidae, four Tithaeidae, and seven Petrobunidae previously sequenced by us. All specimens included in the study and their locality data are provided in Supplementary File 1.

2.2. Imaging

Specimens of Podoctidae were imaged in dorsal, ventral, and/or lateral views, where possible; due to dorsal armature, ventral

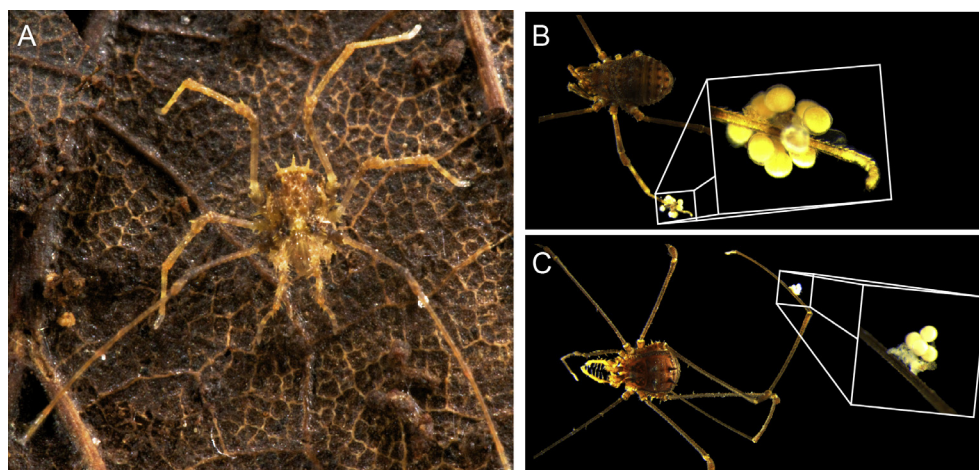


Fig. 1. *Lomanius longipalpus longipalpus* from Babeldaob, Palau (collected by RMC and PPS). Photo: G. Giribet. (B) Egg-carrying male of *Ibalonius* sp. 1 from Luzon, with magnification of egg clutch. (C) Egg-carrying male of *Japetus* cf. *longipes* from Borneo, with magnification of egg clutch.

views were not feasible without damage in some species, and were therefore omitted. Photographs were taken using a Leica MC120 HD camera mounted on a Leica M60 stereomicroscope. A series of images (from three to ten) was taken at different focal planes and assembled (focus-stacked) with the Helicon Focus Pro software package. Monochrome images of the dorsal profile of the scutum were generated from focus-stacked images using Adobe Photoshop CC2015. The tarsal formula was recorded for all terminals for which adult specimens were available, as juveniles of most Phalangida have reduced tarsal formulae relative to adult stages.

2.3. Molecular methods

Molecular markers consisted of two nuclear ribosomal genes (complete 18S rRNA and partial 28S rRNA), two mitochondrial genes (16S rRNA and cytochrome *c* oxidase subunit I), and one nuclear protein-encoding gene (histone H3). Genomic DNA was extracted from legs of animals using a Qiagen DNEasy Tissue Kit (Valencia, CA, USA) and used as template for PCR amplification. PCR and Sanger-sequencing protocols are described in detail in our previous works (Boyer et al., 2007; Sharma and Giribet, 2009). All primer sequences are provided in Sharma and Giribet (2011).

2.4. Phylogenetic reconstruction

Examination of previous data sequenced by PPS revealed a contamination of the COI sequence of *Dongmoa* sp. (Podoctidae) with an unpublished sequence of *Gnomulus* sp. (Sandokanidae) (GenBank accession number FJ475905.1; (Prashant Sharma and Giribet, 2009); PPS, *personal communication*). At the time, no other podoctids had been sequenced, and thus the contamination was not recognized. Similarly, we identified presumable contamination of the 16S rRNA sequences of *Pellobunus insularis* (Samoidae) and *Pyramidops* sp. (Pyramidopidae) (GenBank accession numbers JF786469.1 and JF786468.1, respectively; Sharma and Giribet, 2011); as the Pyramidopidae were once considered African “samoids”, the contamination previously went undetected.

We therefore removed all three of these sequences from the ten-locus phylogeny of Sharma and Giribet (2011) to examine how the placement of Podoctidae would be affected by the exclusion of the contaminated sequences, which have since been deaccessioned from GenBank. After alignment with MUSCLE v.3.8.31 (Edgar, 2004) and culling of ambiguously aligned regions with GBLOCKS v.0.91b (Castresana, 2000), the resulting alignment (henceforth, “Dataset 1”) consisted of 101 terminals, 6945 bp, and 29.0% missing/gap data.

To test the effect of broader taxonomic sampling on the placement of Podoctidae in the phylogeny of Laniatores, we added all of the new podoctid terminals to the ten-locus phylogeny of Sharma and Giribet (2011) and thereby constructed a second alignment (henceforth, “Dataset 2”), consisting of 168 terminals, 6653 bp, and 38.8% missing/gap data.

To establish the effect of missing data on placement of Podoctidae in the phylogeny of Laniatores, we further modified Dataset 2 by removing the five genes missing for the new terminals. The resulting alignment (henceforth, “Dataset 3”) consisted of 168 terminals, 5204 bp, and 27.0% missing/gap data.

Finally, to infer relationships within Podoctidae with as much ingroup sequence data as possible upon culling with GBLOCKS v.0.91b, we constructed a final dataset with only the 73 ingroup and 19 closely related outgroup terminals indicated in the previous section (see Species Sampling). The resulting alignment (henceforth, “Dataset 4”) consisted of 92 terminals, 4897 bp, and 30.9% missing/gap data.

For all four datasets, maximum likelihood (ML) analyses were conducted in RAxML v.7.7.5 (Stamatakis, 2006) with 500 independent starts and 500 bootstrap resampling replicates (Stamatakis et al., 2008). For each data partition, a unique GTR model of sequence evolution with corrections for a discrete gamma distribution (GTR + Γ) was specified. For Dataset 4, Bayesian inference (BI) analysis was conducted using MrBayes v. 3.2.2 (Ronquist et al., 2012) with a unique GTR model of sequence evolution, and corrections for a discrete gamma distribution and a proportion of invariant sites (GTR + Γ + I) specified for each partition, as selected in jModeltest v. 0.1.1 (Guindon and Gascuel, 2003; Posada, 2008) under the Akaike information criterion (AIC) (Posada and Buckley, 2004). Default priors were used starting with random trees. Four runs, each with three hot and one cold Markov chains, were implemented for 4×10^7 generations. Convergence diagnostics were assessed using Tracer ver. 1.5 (Rambaut and Drummond, 2009). As a conservative measure, 1×10^7 generations were discarded as burnin.

A dated molecular phylogeny was generated using Dataset 3 in BEAST v.1.8.1. The backbone topology of Opiliones was constrained to match the result of a phylogenomic analysis of Opiliones (Fernández et al., in prep.). Following recent interpretations of fossil placements (Garwood et al., 2014) and phylogenomic dating of Opiliones (Sharma and Giribet, 2014), the ages of Eupnoi and Dyspnoi were constrained using normal priors with mean 350 Ma and standard deviations of 20 Ma. The root was constrained using a uniform prior between 420 and 450 Ma. We specified a unique GTR model of sequence evolution with corrections for a discrete gamma distribution and a proportion of invariant sites (GTR + Γ + I) for each partition; and we further separated site models for first and second (1 + 2) vs. third (3) codon positions for the protein-encoding genes. An uncorrelated lognormal clock model was assumed for each partition, and a birth-death process was assumed for the tree prior. Four runs of 5×10^7 generations were computed and convergence assessed using Tracer v.1.5. As a conservative measure, 1×10^7 generations were discarded as burnin.

2.5. Multivariate analysis of shape data

To obtain a continuous estimate of shape data, geometric morphometric analyses were conducted with the R package Momocs (Bonhomme et al., 2014). Outlines of the scutum (dorsal prosoma and fused tergites) of available adult males were extracted from image data using inbuilt tools in Adobe Photoshop CC2015 and converted into monochromatic jpeg files. We focused on dorsal scutal morphology because the dorsal view of the body is the most common illustration of Opiliones in the taxonomic literature.

Images were imported into R converting them into lists of coordinates that describe the closed outlines. Then, we checked for their proper alignment and conducted an Elliptical Fourier Analysis (EFA) using 32 harmonics (the default parameter setting), and including the normalization of coefficients, and a single smoothing iteration. Resulting coefficients were then summarized using Principal Component Analysis (PCA) to extract shape variables to match to the phylogeny. The dated molecular phylogeny from BEAST v.1.8.1 was culled to retain only the intersection of terminals with available shape data. Visualization of morphospace as well as the change of shape through time were conducted using functions from Momocs and phytools (Revell, 2012).

2.6. Quantification of phylogenetic signal

To quantify phylogenetic signal of continuous morphological characters, we used Pagel's λ (Pagel, 1999) and Blomberg et al.'s K (Blomberg et al., 2003). λ is a parameter used to scale traits correlations between terminals in order to test a null model

of Brownian evolution. $\lambda \approx 0$ corresponds to an unresolved dendrogram (i.e., no evidence of correlation between species), whereas $\lambda \approx 1$ indicates consistency with the Brownian expectation. K is a scaled ratio of variance between terminals to variance in contrasts; $K \approx 0$ indicates little phylogenetic signal, whereas $K \approx 1$ corresponds to the Brownian expectation. The dated molecular phylogeny from BEAST v.1.8.1 was culled to retain only terminals representing adult tarsomere count data ($N = 67$ terminals; data provided in [Supplementary File 1](#)), as juveniles hatch with a reduced number of tarsomeres (typically, a tarsal formula of 2:2:2:2 in the first instar of most Grassatores). In rare cases of left-right asymmetry, the higher of the two values was scored.

2.7. Tests of trait correlation

To test for character independence within the tarsomere dataset, we conducted pairwise tests for correlation for each leg's tarsomere count. To account for missing data due to inapplicable characters we identified the intersection of terminals bearing entries for both characters under consideration in each pairwise test, and culled all other terminals. Pairwise tests were conducted using BayesTraits v.2.0 ([Pagel and Meade, 2006](#)). Bayesian estimators were used to compare each of two models (dependent and independent evolution) under a random walk model, with 10,000 generations per run and a burnin of 1000 generations. Model evaluation was conducted via Bayes factor comparisons for competing models.

2.8. Test of paternal care

To test the hypothesis that male specimens of Podoctidae carry eggs of their own species, we sequenced a subset of the egg masses for the two specimens depicted in [Fig. 1C](#) and [F](#), using the methods described above. The 28S rRNA locus was chosen for this purpose due to its diagnostic power at higher taxonomic scales. Sequences obtained from eggs were identified using BLASTn searches and aligned to the complete podoctid 28S rRNA dataset.

3. Results

3.1. Phylogenetic placement of Podoctidae within Laniatores

Removal of three potentially contaminated sequences from the ten-locus dataset of [Sharma and Giribet \(2011\)](#) resulted in an ML tree topology largely similar to the one previously reported (Dataset 1; [Fig. 2A](#)). The major topological change observed was the sister group relationship of Assamioidea and Gonyleptoidea, albeit without nodal support. The relative positions of Sandokanidae and the four other southeast Asian Laniatores families (Epedanoidea *sensu stricto*; = Epedanidae + Petrobunidae + Podoctidae + Tithaeidae) were unchanged, and the sister group relationship of Podoctidae and Tithaeidae received no nodal support (37% bootstrap resampling frequency [BS]). Similarly, the clustering of the non-sandokanid southeast Asian families was not supported, disfavoring the systematic validity of “Epedanoidea”, either including

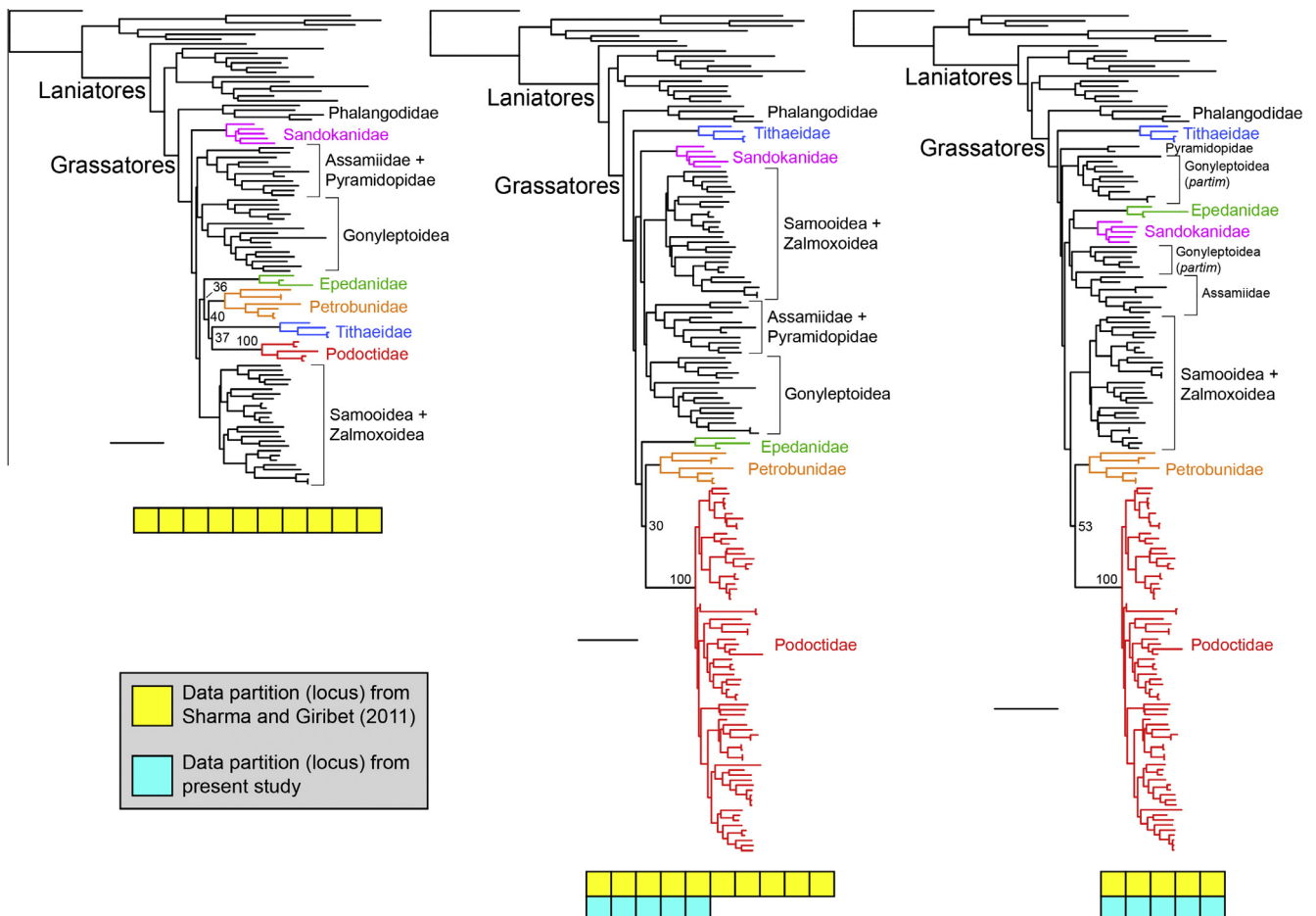


Fig. 2. Maximum likelihood tree topologies inferred from Dataset 1 (left; $\ln L = -75644.14$), Dataset 2 (middle; $\ln L = -94862.11$), and Dataset 3 (right; $\ln L = -82636.72$). Icons below depict data partitions (gene fragments) as squares.

(Kury, 2011) or excluding (Sharma and Giribet, 2011) Sandokanidae.

Addition of the new podoctid terminals to the data matrix resulted in the dissolution of Epedanoidea, due to the exclusion of Tithaeidae and its placement in a grade with Phalangodidae and Sandokanidae at the base of Grassatores (Dataset 2; Fig. 2B). Petrobunidae was recovered as the sister group of Podoctidae, but with no nodal support (BS = 30%). Removal of the five loci not sequenced for the new podoctid terminals marginally increased the nodal support for the clade Petrobunidae + Podoctidae (BS = 57%), albeit with polyphyly of “Epedanoidea” as well as Gonyleptoidea and Assamioidea (Dataset 3; Fig. 2C).

None of the analyses recovered a sister group relationship of Podoctidae with Sandokanidae or a placement of podoctids within Samooidea.

3.2. Internal phylogeny of Podoctidae

Both ML and BI analyses of Dataset 4 recovered the monophyly of Podoctidae with maximal nodal support (Fig. 3). In both tree topologies, the subfamily Ibaloniinae was recovered as a grade at the base of ingroup taxa, due to the placement of Seychellois species as sister group to the clade Podoctinae + Erecaninae (BS < 50%; posterior probability [PP] = 0.95). Podoctinae in turn was recovered as a grade with respect to Erecaninae, with support for some nodes (BS = 83%; PP = 1.00). Within “Ibaloniinae”, all genera represented by multiple terminals were recovered as para- or polyphyletic, save for *Metibalonius*. While taxonomic sampling of Erecaninae was limited to two of the four genera, *Paralomanus* was recovered as nested within *Lomanus* (BS = 87%; PP = 1.00).

The dated phylogeny of Podoctidae recovered a similar basal topology, albeit with the nested placement of *Baramia longipes* within Erecaninae (Fig. 4). Thus, all three subfamilies were recovered as non-monophyletic in the dated tree topology.

3.3. Multivariate analysis of shape data

The `import_jpeg` function of Momocs placed 1714 ± 462 coordinates around the outlines. The first three principal components derived from elliptical Fourier transformations of scutal outlines accounted for 82.2% of the variance. The first principal component (PC1; 40.6%) corresponded to length-to-width ratio; PC2 (24.4%) to the size of the lateral projections of the anterior scutal margin; and PC3 (17.2%) to the degree of anterior projection of the ocularium. Pairwise comparisons of principal components revealed broad overlap in values of PC1 and PC2 across the three nominal subfamilies, relative to PC3. Only PC3 demonstrated some differentiation, with lower values for Erecaninae than for Ibaloniinae, but with some overlap with Podoctinae (Fig. 4).

Observation of individual principal components as a function of phylogenetic relationships corroborated the distinction between Erecaninae and Ibaloniinae, and additionally revealed a pattern of convergence in PC3 for Erecaninae and Podoctinae (Fig. 4C). A second group of Podoctinae closely related to Erecaninae bore values of PC3 similar to erecanines, suggesting that both convergence and phylogenetic inertia have contributed to the similarity of ocularial projection in podoctids.

3.4. Quantification of phylogenetic signal and trait correlation in tarsomere counts

Numerous workers have critiqued Roewer's taxonomic works for the superficiality of his criteria for species and genus delimitation (e.g., Shear, 2001; Bragagnolo and Pinto-da-Rocha, 2012). However, the value of character systems central to Roewer's works

has not been tested in a quantitative framework. To characterize the evolution of tarsal formula, we measured λ and K for the number of tarsomeres in each individual walking leg.

Significantly high values of λ were obtained for walking leg I ($\lambda_{L1} = 0.784$, $p \ll 0.001$) and walking leg II ($\lambda_{L2} = 1.000$, $p \ll 0.001$), consistent with high phylogenetic structure (Table 1). This result was also reflected in their corresponding values of K ($K_{L1} = 0.567$, $p = 0.001$; $K_{L2} = 0.932$, $p = 0.002$). Non-significant values of λ and K were obtained for walking legs III and IV (at $\alpha = 0.001$), reflecting strong conservation of tarsomere counts in the posterior two pairs of legs within Podoctidae.

To test whether tarsal formula constitutes a one-character system, we conducted pairwise tests of trait correlation using BayesTraits v. 2.0 (Table 2). Strong evidence of trait correlation was obtained for the tarsomeres of walking legs III and IV (BF = 95.5). Weak evidence of correlation was also obtained for legs I and IV (BF = 3.4). All other comparisons did not differ significantly under dependent and independent models.

3.5. Sequence identity of egg masses

28S rRNA sequences obtained from both egg masses demonstrated non-identity with each of their carrier males, and incongruence with sequence regions conserved across Epedanoidea. The best BLASTn hits against the obtained sequences were those of araneoid spiders (eggs carried by *Japetus* cf. *longipes*) and of haplogyne spiders (eggs carried by *Ibalonius* sp. 1). Sequences are provided in Supplementary File 2.

4. Discussion

4.1. Topological sensitivity of Epedanoidea sensu stricto

Among the superfamilies of Grassatores, Epedanoidea *sensu stricto* (= Epedanidae + Petrobunidae + Podoctidae + Tithaeidae) has proven the most difficult to define, and the most sensitive to data partitioning and algorithmic treatment (Giribet et al., 2010; Sharma and Giribet, 2011). Few morphological characters unite this group of families, and various character subsets are frequently in conflict (Sharma et al., 2011). As examples, Podoctidae and Tithaeidae share a deeply cleft ventral plate in the male copulatory apparatus, though a spiniferous first walking leg occurs in both Podoctidae and Triaenonychidae (Sharma and Giribet, 2011). Petrobunidae and Phalangodidae have highly comparable male genitalic structures, though some petrobunids were once considered part of Zalmoxoidea due to convergence in scutal and appendicular morphology (Sharma and Giribet, 2011). Epedanidae was recovered as the sister group of Gonyleptoidea in morphological cladistic analyses (Kury, 1993), with some epedanid species once placed within Podoctidae (Roewer, 1923; Kury, 2008).

After screening previous sequence data for contaminations and analyzing different data partitions with tradeoffs for matrix size and completeness, we observed little support for the monophyly of Epedanoidea *sensu stricto* and for the sister group relationship of Podoctidae and Petrobunidae (Fig. 2). While support for the clade Podoctidae + Petrobunidae was obtained in a separate phylogenomic analysis of Opiliones (Fernández et al., in prep.), the family Tithaeidae was not included in that analysis. We therefore treat the identity of the podoctid sister group as unresolved.

The aforementioned phylogenomic analysis of Opiliones (Fernández et al., in prep.) recovered an identical basal topology within Grassatores to the ML and BI trees of Sharma and Giribet (2011), with high nodal support and analytical congruence in most parts of the basal topology (the only two cases of basal incongruence consisted of the monophyly of Insidiatores and

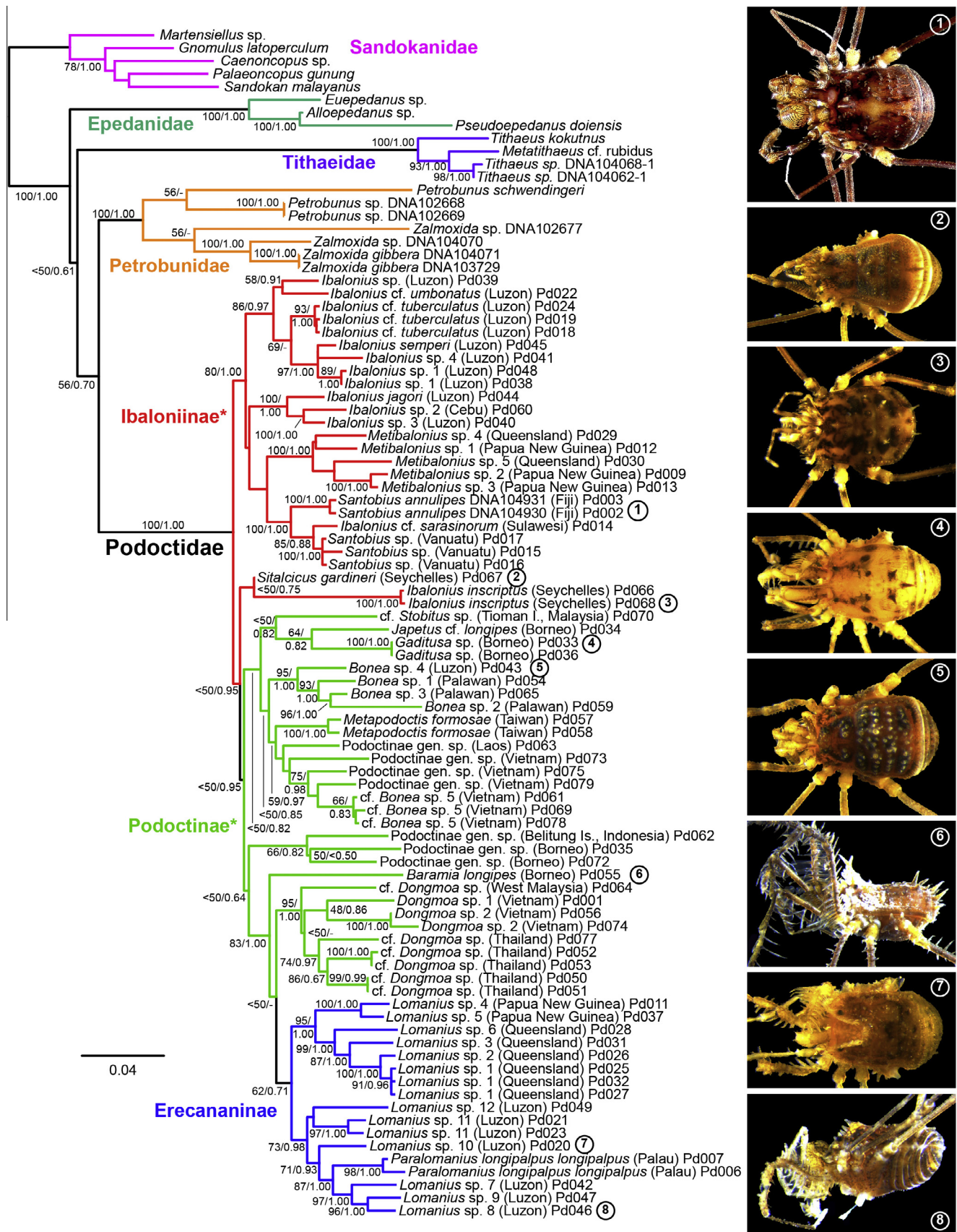


Fig. 3. Bayesian inference tree topology inferred from Dataset 4 (lnL = -34047.85). Colors in tree correspond to families or subfamilies, as indicated by corresponding text. Numbers on nodes indicate bootstrap resampling frequencies under maximum likelihood (integers) and posterior probabilities under Bayesian inference. Right: Representatives of podocid subfamilial diversity.

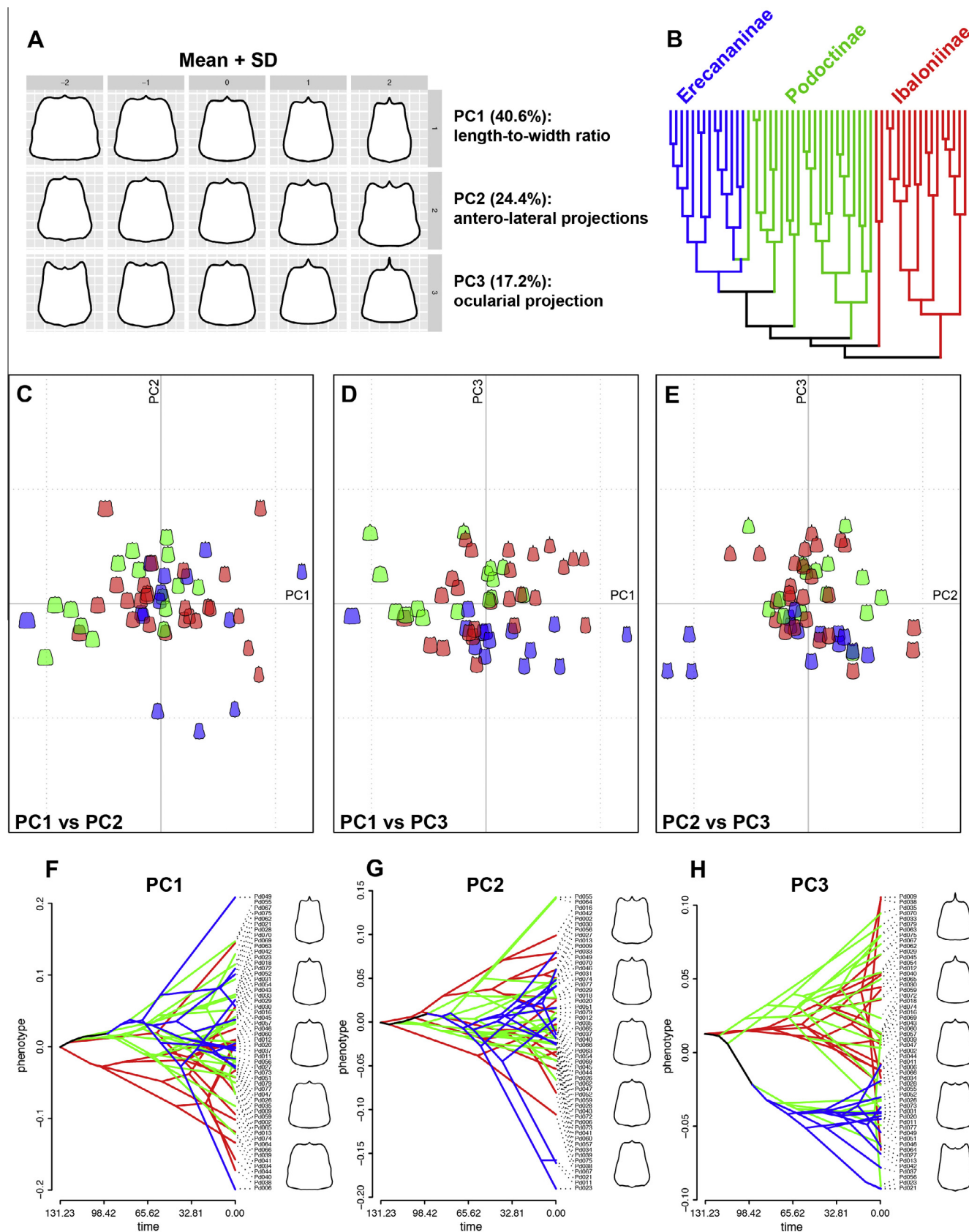


Fig. 4. (A) Major principal components identified upon elliptical Fourier transformation and parameterization of dorsal scutal shape data. (B) Dated phylogeny from BEAST, with colored branches corresponding to subfamilies. (C–E) Visualization of morphospaces demonstrates broad overlap in principal component values; PC1 vs PC2 (C), PC1 vs PC3 (D), PC2 vs PC3 (E). (F–H) Visualization of individual principal components' values as a function of phylogenetic relationship. Horizontal axis indicates time since basal divergence. Colors in (C–H) as in (B). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Correspondence of tarsomere counts and phylogeny.

<i>Walking leg I</i>			
λ	0.7835186	<i>K</i>	0.5659446
$\log L$	–42.90711	<i>p</i>	0.001
$\log L_0$	–68.45351		
<i>p</i>	8.81E–13		
<i>Walking leg II</i>			
λ	0.9999248	<i>K</i>	0.9321064
$\log L$	–133.0724	<i>p</i>	0.002
$\log L_0$	–151.8906		
<i>p</i>	8.52E–10		
<i>Walking leg III</i>			
λ	0.3110376	<i>K</i>	0.3613055
$\log L$	–26.67809	<i>p</i>	0.05137
$\log L_0$	–28.42224		
<i>p</i>	6.18E–02		
<i>Walking leg IV</i>			
λ	0.4904253	<i>K</i>	0.4031406
$\log L$	–24.70293	<i>p</i>	0.043
$\log L_0$	–26.64625		
<i>p</i>	4.87E–02		

Table 2
Bayes factor comparisons for tarsomere number in each pair of walking legs. Boldface text indicates significant (>2) values).

	Leg I	Leg II	Leg III	Leg IV
Leg I		–0.059102	–2.002808	3.403168
Leg II			–3.166656	–0.235676
Leg III				95.456378

non-monophyly of Samooidea recovered by the phylogenomic analysis). The monophyly of Epedanoidae *sensu stricto* (not including Tithaeidae) was supported in the phylogenomic analysis as well, but is not validated by surveys of morphological characters across the suborder (Sharma et al., 2011; Gainett et al., 2014). Barring a clear center of diversity in southeast Asia, little unites this group of harvestmen.

4.2. Internal phylogeny and shape analysis of Podoctidae demonstrate incongruence with traditional systematics

For diverse groups of understudied Laniatores (e.g., Assamiidae, Epedanidae), the degree of subdivision into superficial subfamilies, genera, or species established by Roewer can prove prohibitive to revision by present day systematists. One extreme example is Assamiidae, whose 474 species are divided into ca. 12 subfamilies and 264 genera (Kury, 2011)—a classification system that is so commonly held to be invalid that no taxonomic key has been proposed even at the subfamily level (Shear, 2001; Kury, 2007). Numerous untested subfamilies are scattered across Laniatores. In the present study, we began by examining the validity of subfamilial ranks in Podoctidae.

None of the tree topologies obtained supported the monophyly of Ibaloniinae or Podoctinae, and the tree topology recovered by BEAST additionally failed to recover the monophyly of Erecaninae (Figs. 3 and 4B). The non-monophyly of Ibaloniinae was supported only in BI analyses (PP = 0.95), whereas the nested placement of Erecaninae within a paraphyletic Podoctinae was supported by all analyses. These results suggest that subfamilial ranks are not meaningful entities in podoctid systematics.

These results are generally congruous with a previous morphological cladistic analysis of Podoctidae. In an unpublished analysis, Kury and Machado (2003) constructed an 80-character dataset that supported a polyphyletic Erecaninae nested within Podoctinae,

but also the monophyly of Ibaloniinae. However, that analysis did not include the Seychellois ibaloniine species that render the subfamily paraphyletic in this study. Furthermore, an important character in the dataset of Kury and Machado (2003) was the shape of the body and the degree of antero-posterior elongation (i.e., length-to-width ratio). Body shape is an important (if not always informative) character in harvestman taxonomy, because it is one of the most frequently illustrated views in the historical taxonomic literature.

As shown by our analyses of parametric shape data, the length-to-width ratio of the scutum certainly accounts for the greatest proportion of variance (40.6%), as measured by principal components analysis. However, this aspect of morphological variation is also prone to broad overlap across nominal subfamilies of Podoctidae (Fig. 4). For none of the first three principal components identified did we observe clustering in morphospace, regardless of phylogenetic relationships. Upon considering phylogenetic relationships of sampled terminals, we additionally observed a pattern corresponding to convergence in PC3 (degree of ocularial projection), with derived lineages of all three subfamilies attaining overlap in morphospace, in spite of initially disparate reconstructed ancestral states (Fig. 4). Taken together with the phylogenetic tree, parametric analysis of dorsal shape data disfavors the notion that the subfamilies of Podoctidae are meaningful for taxonomists or conventionally useful to field biologists. We therefore synonymize Erecaninae and Ibaloniinae with Podoctinae **new synonymies**.

The genus *Paralomanius* was recently resurrected by Zhang et al. (2013), on the basis that Goodnight and Goodnight (1957) did not provide sufficient justification when they synonymized the two genera, although Zhang et al. did not describe any characters that justify the distinction of the two genera either. To us, the absence of characters distinguishing two taxa is sufficient justification only for a synonymy, not for the establishment of a separate taxon. We therefore validate the synonymy of *Paralomanius* with *Lomanus* **revalidated**. We strongly discourage the further splitting of Laniatores genera in the absence of validation and/or demonstrable need, in order to circumvent the entrenchment of a Roewerian system of untenably high numbers of superficial mono- and ditypic genera.

4.3. Phylogenetic signal is inherent to tarsal formula

Tarsal formula is a mainstay of Laniatores systematics, and especially of the Roewerian classification system, but has been criticized as one of Roewer's superficial characters. However, the utility of tarsal formulae as an arbiter of systematic relationships has remained unexplored. Anecdotaly, tarsal formula has been shown to be somewhat consistent with molecular phylogenies in some ground-dwelling lineages with few tarsomeres. In Sandokanidae, it is a reliable indicator of generic placement, is sexually monomorphic, and accords with the group's molecular phylogeny (Sharma and Giribet, 2009). In Cyphophthalmi, a handful of species display a partially or completely segmented tarsus IV in males, a condition that may have been secondarily evolved up to six times (five times in Pettalidae; once in Sironidae). However, species with this condition tend to be closely related, and a segmented tarsus is therefore an integral element of some generic diagnoses (Giribet and Boyer, 2002; Boyer and Giribet, 2007).

Our parametric analyses of phylogenetic signal demonstrate that tarsomeres of some walking legs do indeed retain phylogenetic signal, specifically in legs I and II, which are variable in Podoctidae. Due to the scale of this analysis (a single Laniatores family), tarsomeres of legs III and IV were not shown to retain phylogenetic signal, as their numbers are highly conserved within Podoctidae (either four or five tarsomeres on tarsi III and IV for the majority of species). Tarsi III and IV are nevertheless important

variables in higher-level Laniatores systematics due to their conservation within families more broadly. For example, tarsal formula was recently used as part of the justification of the familial placement of the oldest known Laniatores fossil (Selden et al., 2016).

These results partly rescue tarsal formula, an element of Roewer's system, from the criticism of superficiality. We note, however, that tarsal formula does not constitute a set of four independent characters. The strong correlation observed between tarsomere numbers of legs III and IV, and the somewhat weaker correlation in tarsomeres of legs I and IV, suggest that tarsal formula is likely evolutionarily constrained in Opiliones, and should be parametrically investigated on a case-by-case basis, after controlling for phylogenetic distances. This is especially the case for species-rich lineages like Sclerosomatidae, the largest family of Opiliones, and also one with high numbers of tarsomeres. A broader examination of tarsomere evolution should emphasize taxonomic sampling across all Opiliones, and in particular, the correlation between overall tarsomere count and lineage diversity.

4.4. Falsification of the paternal care hypothesis in Podoctidae

Among arthropods, Laniatores are renowned for an atypically high incidence of parental care. Various species of Gonyleptoidea display behaviors such as guarding eggs, establishing harems, and combating conspecific males over females or oviposition sites (reviewed by Machado and Macías-Ordóñez, 2007; Buzatto et al., 2014). A subset of these species engages in exclusively paternal care, the second-rarest type of parental care in arthropods after biparental care (Buzatto et al., 2014). While most cases of paternal care are concentrated in the Neotropical gonyleptoids, two unusual cases occur in the Paleotropics: the podoctids *Leytpodoctis oviger* and a second undescribed species (whose males carry eggs attached to their legs in a manner reminiscent of Pycnogonida); and the assamiid *Lepchana spinipalpis*, (wherein both males and females have been observed accompanying egg clutches and early juvenile instars; Martens, 1993; Kury and Machado, 2003). In the case of the podoctid males, the discovery of egg-carrying males in multiple species has led to the contention that parental care may be phylotypic (synapomorphic) of Podoctidae (Kury and Machado, 2003).

However, whereas parental care has been established by direct observation in various Neotropical gonyleptoid species, as well as in the assamiid *L. spinipalpis*, the assignment of paternal care in Podoctidae is inferential. The relationship between the egg-carrying male and the unhatched offspring has never been established, because females have never been observed depositing eggs on conspecific males, and eggs have never been developed to hatching from egg-carrying male specimens (Martens, 1993). Establishing this ontogenetic relationship by observation is particularly difficult in Podoctidae because many species are cryptic and dwell in leaf-litter; the method employed by us to collect these specimens (i.e., sifting litter) is highly disruptive and not conducive to observation of natural behavior (*contra* the large climbing species of Gonyleptoidea with polygynous mating systems; Buzatto et al., 2014). To test the hypothesis that egg-carrying behavior is a phylotypic trait in Podoctidae, we sequenced the eggs of the specimens shown in Fig. 1B and C, with the prediction that the male specimens imaged were carrying conspecific eggs. Contrary to this prediction, we established that sequences of both egg clusters are demonstrably not conspecific to the males that carry them. The closest matching sequences recovered by BLAST in GenBank were those of spiders.

While we are presumably unable to sequence the eggs borne by *Leytpodoctis oviger* and the second undescribed species, due to the specimens' age and incompatibility of preservation technique with

our sequencing protocols (Kury and Machado, 2003), our result strongly disfavors the notion that the discovery of eggs attached to adult individuals can be construed as evidence of parental care. The eggs attached to the specimens shown in Fig. 1 may alternatively be attributable to accidental attachment of debris (e.g., during disruptive bouts of sifting), or may represent a strategy among ground-dwelling spider females to lay eggs on a group of mobile, spined harvestman species that are equipped with repugnatorial glands. Examples of such strategies are common among marine arthropods (e.g., crabs of the genus *Loxorhynchus*), which sometimes bear micro-communities composed of multiple animal phyla on the dorsum of their cephalothorax. Regardless of interpretation or ensuing hypotheses, our result falsifies the hypothesis of paternal care in Podoctidae, until *bona fide* evidence of parental care can be established in this lineage. Future investigations of podoctid reproduction should emphasize observations of podoctid mating behavior, or integrate molecular tools for hypothesis-testing when behavioral data cannot be generated by direct observation.

5. Conclusion

Here we presented the first multilocus phylogeny of Podoctidae, an enigmatic group of armored harvestmen, to test the validity of subfamilial nomenclature and the phylogenetic utility of historically implemented character systems. We showed that the subfamilies of Podoctidae were not mutually monophyletic, and cannot be reliably distinguished using male scutal shape, the most heavily reported datum in the taxonomic literature of Opiliones. Nevertheless, we were able to show that tarsal formula may retain phylogenetic signal at various taxonomic levels. Finally, we demonstrated that male specimens in our collection with eggs attached to their legs are not carrying conspecific eggs, and thus cannot be interpreted as cases of paternal care.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2016.09.019>.

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