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# An extraordinary new genus of spiders from Western Australia with an expanded hypothesis on the phylogeny of Tetragnathidae (Araneae)

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We describe ***Pinkfloydia*** Hormiga & Dimitrov **gen. nov.**, a new genus of tetragnathid spiders from Western Australia and study its phylogenetic placement. The taxon sampling from our previous cladistic studies was expanded, with the inclusion of representatives of additional tetragnathid genera and outgroup taxa. Sequences from six genetic markers, 12S, 16S, 18S, 28S, cytochrome *c* oxidase subunit 1, and histone 3, along with morphological and behavioural data were used to infer tetragnathid relationships. These data were analysed using parsimony (under both static homology and dynamic optimization) and Bayesian methods. Our results indicate that *Pinkfloydia* belongs to the '*Nanometa*' clade. We also propose a revised set of synapomorphies to define this lineage. Based on the new evidence presented here we propose a revised hypothesis for the intrafamilial relationships of Tetragnathidae and show that Mimetidae is most likely the sister group of Tetragnathidae. The single species in this genus so far, ***Pinkfloydia harveii*** Dimitrov& Hormiga **sp. nov.**, is described in detail and its web architecture documented and illustrated.


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## INTRODUCTION

Australia is well known for its highly diverse and distinctive biota. As a result of the long isolation of the continent an exceptionally high proportion of the native animals and plants are endemic to Australia and often represent lineages extinct in other continents. Probably the most popular examples of such taxa in the Australasian region are the monotremes, the platypus (*Ornythorhynchus anatinus*) and about a dozen species of echidnas (*Tachyglossus* and *Zaglossus* spp.). The same patterns of high endemicity and presence of ancestral lineages are observed in many other groups, including spiders. At present some 2700 spider species have been described in Australia, according to data made available on the Commonwealth Scientific and Industrial Research Organisation (CSIRO) web site and The World Spider Catalog (Platnick, 2009). This relatively small number in relation to the size of the continent and the diversity of habitats suggests that most of the Australian spider fauna remains largely unknown. Rough estimations predict that the actual number of spider species in Australia may be around 10 000 (Yeates, Harvey & Austin, 2003; CSIRO web page at: http://www.csiro.au/csiro/content/standard/ps27t.html) (see also Platnick, 1999). Recent taxonomic work on Australian groups certainly confirms this trend – for example, in Platnick's (2000) revision of the gnaphosoid family Lamponidae 171 species were new (90%), out of a total of 190 described. Similarly, Harvey (1995) described six new genera of Nicodamidae (previously only one) with numerous new species

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and Raven (1984a, b, 1985) described several mygalomorph genera and species.

Formerly 11 genera and 45 species of tetragnathids (Tetragnathidae + 'Nephilidae') spiders have been described from Australia. The recent change to family rank of the subfamily Nephilinae (Kuntner, 2006) further reduced these numbers, taking out the species from the three nephilid genera known from Australia (*Nephila* Leach, 1815, *Herennia* Thorell, 1877, and *Nephilengys* L. Koch, 1872). Additionally, the seven species in the genera *Phonognatha* Simon, 1894 and *Deliochus* Simon, 1894 have been transferred to Araneidae (Kuntner, Coddington & Hormiga, 2008), reducing the total number of Australian tetragnathid species to 29. The majority of the Australian tetragnathids (20) belong to the genus *Tetragnatha*. All other genera have fewer than five species and five genera are represented by just a single species.

Tetragnathids, commonly known as long jawed spiders, are members of the large superfamily Araneoidea. Tetragnathidae has a world-wide distribution with highest diversity in humid tropical and subtropical areas of the world. Many tetragnathid species are known to prefer to live near streams or other water bodies where they spin their orb webs. Some genera possess exceptional dispersal ability [e.g. *Tetragnatha* Latreille, 1804 (Gillespie, Palumbi & Croom, 1994; Gillespie, 2003a, b)] and their representatives can be found virtually world-wide. However, genera with limited distributions are also not exceptional (e.g. *Homalometa* Simon, 1897). Recently, tetragnathid relationships and diversity have attracted much attention and several generic revisions and family level phylogenetic hypotheses have been published (e.g. Tanikawa, 2001; Álvarez-Padilla, 2007; Dimitrov, Álvarez-Padilla & Hormiga, 2008, 2010; Levi, 2008; Álvarez-Padilla *et al*., 2009; Dimitrov & Hormiga, 2009). However, the phylogenetic affinities of several tetragnathid genera remain elusive. Most of these were not included in phylogenetic treatments except for *Azilia* Keyserling, 1881, *Diphya* Nicolet, 1849, and *Mollemeta* Álvarez-Padilla, 2007. Several hypotheses for the relationships of *Azilia* and *Diphya* have been proposed. Simon (1894) was the first to address tetragnathid relationships (as subfamilies of Argiopidae) and placed *Azilia* and *Diphya* in their own subfamilies, Azileae and Diphyeae, respectively. Levi (1980) treated *Azilia* as a member of the subfamily Tetragnathinae. Wunderlich (2004a) argued that Azileae and Diphyeae should be reinstated to subfamily rank. In more recent phylogenetic treatments *Azilia* was found to be either a member of Metainae (Álvarez-Padilla, 2007; Dimitrov & Hormiga, 2009) or the most basal member of Tetragnathidae (Álvarez-Padilla *et al*., 2009). The position of *Diphya* in these studies was even more unstable but two topologies were more commonly recovered: *Diphya* as the most basal Tetragnathinae (Álvarez-Padilla, 2007; Dimitrov & Hormiga, 2009; and some analyses in Álvarez-Padilla *et al*., 2009) or *Diphya* as sister group to *Azilia* (Álvarez-Padilla *et al*., 2009). Evidence against Tetragnathinae placement for *Diphya* has been presented (Dimitrov, Álvarez-Padilla & Hormiga, 2007; see also discussion in Álvarez-Padilla, 2007 and Dimitrov & Hormiga, 2009) but there were no data to support or reject any of the other alternatives. The position of *Mollemeta* is even more unstable and very sensitive to different analytical treatments (Álvarez-Padilla *et al*., 2009).

The present study is a continuation of our recent efforts to address unanswered questions about tetragnathid phylogenetic relationships and diversity. Hereby we describe a new genus of tetragnathid spiders from Western Australia. We also use both morphological and molecular characters to study its phylogenetic position within Tetragnathidae and its sister-group relationships. The spiders of this new genus present a unique combination of morphological characters that provide novel insights on tetragnathid morphology and character evolution. We also significantly expand the taxon sampling of tetragnathids and outgroups in comparison with published phylogenetic studies of Tetragnathidae and its relatives (Álvarez-Padilla *et al*., 2009). Based on these new results we propose a revised and expanded phylogenetic hypothesis for the generic relationships of Tetragnathidae.

## MATERIAL AND METHODS

Morphological methods of study were as previously described in Hormiga (2000, 2002) and Dimitrov & Hormiga (2009). Specimens were examined and illustrated using Leica MZ16 or Leica MZ16A stereoscopic microscopes with a camera lucida. Further details were examined and depicted under a Leica DMRM compound microscope with a drawing tube. All drawings were carried out with graphite pencils on acid-free cotton paper. Most of the hairs and macrosetae are usually not depicted in final drawings. For illustrations, left male palps were dissected and transferred to a methyl salicylate solution. Female genitalia were dissected and the nonchitinous abdominal tissues were digested with SIGMA Pancreatin LP 1750 enzyme complex (Álvarez-Padilla & Hormiga, 2008). After removing any remaining tissues with needles, the preparations were washed in distilled water and transferred to 75% ethanol or methyl salicylate for observation and illustration. All pencil drawings were scanned and additionally improved with the help of the computer program GIMP 2.6.4. Digital images of the specimens were taken using a Leica MZ16A stereoscopic microscope

with a Nikon DXM1200F digital camera attached. Series of partially focused images were processed using Auto-Montage 4.02.0014 software to produce a composite image with enhanced quality.

Scanning electron microscope (SEM) observations and photographs were taken with a LEO 1430VP scanning electron microscope. For SEM images, the abdomen, legs, cephalothorax, and left male palp were dissected and cleaned ultrasonically (less than 1 min). They were then transferred to 100% ethanol and left to dehydrate for 24 h. After this, preparations were critical point dried, mounted and Au-Pd coated for observation. The female internal genitalia and tracheal systems were cleaned and digested as described above before the critical point drying (no ultrasound cleaning needed).

All morphological measurements were taken with the help of scale reticle on the dissecting microscope. Morphological measurements in the text are in millimetres unless otherwise stated.

Molecular techniques followed the protocols described in (Álvarez-Padilla *et al*., 2009). DNA voucher specimens (Appendix) are deposited at the MCZ. DNA extractions are stored at The George Washington University.

### Abbreviations used in the text

ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; MPT, most parsimonious tree; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; PME, posterior median eyes; PMS, posterior median spinnerets.

*Museum collections*

MCZ (Museum of Comparative Zoology, Harvard University), AUSTMUS (Australian Museum, Sydney).

## PHYLOGENETIC ANALYSIS

### Taxon sampling

The only known species of *Pinkfloydia* was added to the matrix of the most recent study of tetragnathid relationships (Álvarez-Padilla *et al*., 2009). In this matrix, tetragnathids and outgroups are relatively well represented (23 out of 51 tetragnathid genera are included), allowing a rigorous test of the phylogenetic position of our newly described taxon. Tetragnathid taxon sampling was expanded by the inclusion of species in the genera *Antillognatha* Bryant, 1945, *Hispanognatha* Bryant, 1945, and *Mecynometa* Simon, 1894; all of them poorly studied and not present in previous phylogenetic treatments.

Representative species of two araneoid lineages not present in Álvarez-Padilla *et al*. (2009) were also added to the matrix: *Arkys* Walckenaer, 1837 (Araneidae) and *Mimetus* Hentz, 1832 (Mimetidae). The genus *Arkys* was originally placed in the family Mimetidae but Davies (1988) transferred it to Tetragnathidae from where it was subsequently transferred to Araneidae by Scharff & Coddington (1997).

Mimetids were traditionally placed in Araneoidea until Forster & Platnick (1984) suggested that they belonged in the distantly related Palpimanoidea on the basis of two putative cheliceral synapomorphies: the peg teeth on the promargin and the gland mounds on the retromargin. This latter conjecture has been one of the most controversial hypotheses in spider evolution. More recently, DNA sequence data (collected as part of the spider ATOL (Assembling the Tree of Life) project; see also Rix, Harvey & Roberts, 2008; Blackledge *et al*., 2009) and new morphological evidence (Schütt, 2003; Griswold *et al*., 2005) suggest that mimetids are indeed araneoids. An alternative higher classification for mimetids, Mimetidae *sensu lato* including Malkaridae and Pararchaeidae, was proposed by Wunderlich (2004b) but his hypothesis does not stem from a phylogenetic analysis and is not considered here.

In a recent phylogenetic study based mainly on molecular evidence Blackledge *et al*. (2009) found both *Arkys* and mimetids (*Mimetus*) to be more closely related to tetragnathids than to other araneoids or to palpimanoids; therefore, we have included representatives of these two taxa in our analyses.

Detailed specimen data about the species used in the analyses are given in the Appendix.

### Characters

Six gene fragments, three nuclear and three mitochondrial, including both fast and slowly evolving genes were targeted. Genes and approximate maximum size of the fragments sequenced were as follows: nuclear genes – most of the 18S rRNA (*c*. 1800 bp), the first portion of the 28S rRNA (*c*. 2500 bp), and histone 3 (H3; 327 bp); mitochondrial genes – 12SrRNA (*c*. 340 bp), 16S rRNA (*c*. 450 bp), and the cytochrome *c* oxidase subunit I (CO1; 657 bp). Primers and protocols for specimen collection, DNA extraction, amplification, and sequencing are described in Álvarez-Padilla *et al*. (2009). New DNA sequence data were gathered for representative species of the tetragnathid genera *Azilia*, *Diphya*, *Glenognatha* Simon, 1887, *Cyrtognatha* Keyserling, 1881, *Mollemeta*, *Allende* Álvarez-Padilla, 2007, *Mesida* Kulczynski, 1911, *Metleucauge* Levi, 1980, *Dolichognatha* O. P.-Cambridge, 1869, and a new Metainae genus from Australia. These were added to the DNA data matrix from Álvarez-Padilla *et al*. (2009). Summarized information about DNA fragments used in the analyses and Gen Bank accession numbers are given in Table 1.

**Table 1.** GenBank accession numbers. Numbers in bold indicate sequences generated during this study

| Species | Gene fragment | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 12S | 16S | 18S | | | 28S | | | H3 | CO1 |
| *Achaearanea tepidariorum* | AY425713.1 | AY230955.1 | EU003387 | | | | EU153157 | EU003395 | AY230989.1 | EU003277 |
| *Allende nigrohumeralis* | NA | EU003271 | EU003368 | EU003370 | | | EU003396 | | NA | NA |
| *Araneus marmoreus* | EU003230 | NA | EU003341 | | | | EU153158 | EU003397 | EU003312 | EU003278 |
| *Argiope savignyi* | EU003231 | NA | EU003388 | | | | EU153159 | EU003398 | NA | EU003279 |
| *Azilia guatemalensis* | EU003232 | EU003262 | EU003371 | EU003372 | EU003373 | | EU003399 | | EU003313 | EU003280 |
| *Chrysometa albogutata* | NA | NA | EU003389 | | | | EU153160 | EU003400 | EU003314 | NA |
| *Clitaetra* sp1. | NA | NA | NA | | | | NA | | EU003315 | EU003281 |
| *Cyclosa conica* | EU003233 | EU003254 | EU003343 | | | | EU153161 | EU003401 | EU003316 | EU003282 |
| *Cyrtognatha espaniola* | NA | NA | EU003344 | | | | EU153162 | EU003402 | NA | EU003283 |
| *Deinopis* sp1. | NA | EU003249 | EU003382 | EU003383 | | | EU153163 | EU003403 | NA | NA |
| *Deliochus* sp.E | EU003234 | EU003259 | EU003345 | | | | EU153164 | EU003404 | NA | EU003284 |
| *Dolichognatha* sp. | NA | NA | EU003346 | | | | EU153165 | EU003405 | EU003317 | EU003285 |
| *Epeirotypus brevipes* | NA | EU003273 | EU003347 | | | | EU153166 | EU003406 | EU003318 | EU003286 |
| *Gasteracantha cancriformis* | EU003235 | EU003256 | EU003348 | | | | EU153167 | EU003407 | EU003319 | EU003287 |
| *Herennia multipuncta* | EU003236 | EU003260 | EU003384 | EU003385 | EU003386 | | EU003432 | EU003433 | EU003320 | EU003288 |
| *Larinioides cornutus* | EU003237 | EU003250 | EU003349 | | | | EU153168 | EU003408 | EU003321 | EU003289 |
| *Leucauge argyra* | NA | EU003264 | EU003364 | | | | EU003427 | | EU003339 | EU003291 |
| *Leucauge venusta* | EU003238 | EU003263 | EU003350 | | | | EU153169 | EU003409 | EU003322 | EU003290 |
| *Linyphia triangularis* | EU003239 | AY078664.1 | EU003390 | | | | EU153170 | EU003410 | AY078702.1 | EU003292 |
| *Mangora maculata* | EU003240 | EU003258 | EU003351 | | | | EU153171 | EU003411 | EU003323 | EU003293 |
| *Mecynogea lemniscata* | EU003241 | EU003255 | EU003352 | | | | EU153172 | EU003412 | EU003324 | EU003294 |
| *Meta menardi* | NA | EU003268 | EU003353 | | | | EU153173 | EU003413 | EU003325 | EU003295 |
| *Metabus ebanoverde* | NA | EU003265 | EU003354 | | | | EU153174 | EU003414 | EU003326 | EU003296 |
| *Metellina merianae* | NA | EU003270 | EU003356 | | | | EU153176 | EU003416 | EU003328 | EU003298 |
| *Metepeira labyrinthea* | EU003242 | EU003253 | EU003355 | | | | EU153175 | EU003415 | EU003327 | EU003297 |
| *Metinae* sp. | NA | EU003272 | EU003357 | | | | EU153177 | EU003417 | NA | EU003299 |
| *Micrathena gracilis* | NA | EU003257 | EU003358 | | | | EU153178 | EU003418 | EU003329 | EU003300 |
| *Mollemeta edwardsi* | NA | EU003269 | EU003374 | EU003375 | EU003376 | | EU003419 | | EU003330 | NA |
| *Nanometa* sp. | NA | NA | EU003391 | | | | EU153179 | EU003420 | EU003331 | NA |
| *Neoscona arabesca* | EU003243 | EU003252 | EU003359 | | | | EU153180 | EU003421 | EU003332 | EU003301 |
| *Nephila pilipes* | NA | EU003276 | EU003377 | EU003378 | | | EU003422 | | NA | NA |
| *Nephila clavipes* | NA | NA | EU003392 | | | | EU003434 | | EU003333 | EU003302 |
| *Nephilengys malabarensis* | EU003244 | NA | AF005447 | | | | EU003435 | EU003435 | EU003334 | EU003303 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oncodamus bidens* | NA | EU003274 | EU003360 | | | | EU003436 | | | EU003335 | NA |
| *Opadometa* sp. | NA | EU003266 | EU003361 | | | | EU003423 | | | EU003336 | EU003304 |
| *Orsinome* cf. *vethi* | NA | EU003267 | EU003362 | | | | EU153181 | EU003424 | EU003337 | EU003305 | |
| *Pachygnatha degeeri* | NA | EU003261 | EU003363 | | | | EU153182 | EU003425 | EU003338 | EU003306 | |
| *Phonognatha graeffei* | EU003245 | EU003275 | EU003379 | EU003380 | EU003381 | | EU153183 | EU003426 | NA | NA | |
| *Steatoda borealis* | NA | NA | EU003393 | | | | EU153184 | EU003428 | NA | EU003307 | |
| *Tetragnatha versicolor* | EU003246 | NA | EU003394 | | | | EU153185 | EU003429 | NA | EU003308 | |
| *Tylorida striata* | NA | NA | EU003365 | | | | EU153186 | EU003430 | NA | EU003309 | |
| *Uloborus glomosus* | EU003247 | NA | EU003366 | | | | EU003437 | EU003438 | EU003340 | EU003310 | |
| *Zygiella x-notata* | EU003248 | EU003251 | EU003367 | | | | EU153187 | EU003431 | EU003341 | EU003311 | |
| *Arkys cornutus* | NA | FJ607448 | FJ607482 | | | | FJ607521 | | FJ607595 | FJ607556 | |
| *Mimetus sp.* | NA | FJ607463 | FJ607500 | | | | FJ607538 | | FJ607612 | FJ607574 | |
| *Allende* sp.* | NA | NA | **GU129574** | | | | NA | | **GU129649** | **GU129635** | |
| *Antillognatha lucida* | NA | NA | **GU129576** | **GU129577** | | | **GU129603** | | **GU129647** | **GU129631** | |
| *Azilia* sp. 834 | NA | **GU129570** | **GU129581** | | | | **GU129606** | | **GU129641** | **GU129624** | |
| *Azilia* sp. 838 | NA | NA | **GU129582** | | | | **GU129607** | | **GU129642** | **GU129625** | |
| *Cyrtognatha atopica* | NA | NA | **GU129583** | | | | **GU129608** | | NA | **GU129638** | |
| *Cyrtognatha* sp. 773 | NA | NA | NA | | | | **GU129609** | | **GU129645** | **GU129630** | |
| *Cyrtognatha* sp. 774 | NA | NA | NA | | | | **GU129610** | | **GU129646** | **GU129629** | |
| *Diphya spinifera* | NA | NA | **GU129584** | **GU129585** | | | **GU129611** | | **GU129643** | **GU129626** | |
| *Dolichognatha longiceps* | NA | NA | **GU129578** | **GU129579** | **GU129580** | | **GU129604** | **GU129605** | **GU129648** | **GU129632** | |
| *Glenognatha* sp.* | NA | NA | **GU129586** | | | | **GU129612** | | **GU129644** | **GU129627** | |
| *Hispanognatha guttata* | NA | NA | **GU129587** | **GU129588** | | | **GU129613** | | **GU129652** | **GU129633** | |
| *Mecynometa* sp. | NA | NA | NA | | | | **GU129614** | | NA | **GU129639** | |
| *Mesida* sp. | NA | NA | **GU129589** | **GU129590** | | | **GU129615** | | **GU129650** | **NA** | |
| Metainae sp. 123 | NA | NA | **GU129591** | | | | **GU129616** | | NA | NA | |
| Metainae sp. 124 | NA | NA | **GU129592** | **GU129593** | **GU129594** | | **GU129617** | **GU129618** | NA | NA | |
| Metainae sp. 128 | NA | NA | **GU129595** | **GU129596** | **GU129597** | **GU129598** | **GU129619** | **GU129620** | NA | NA | |
| *Metleucauge* sp. | NA | NA | **GU129599** | | | | **GU129621** | | NA | **GU129636** | |
| *Mimetus banksi* | NA | NA | **GU129600** | | | | **GU129622** | | **GU129651** | **GU129637** | |
| *Mollemeta edwardsi** | NA | NA | **GU129575** | | | | **GU129623** | | NA | **GU129634** | |
| *Pinkfloydia harveii* | NA | NA | **GU129571** | **GU129572** | **GU129573** | | **GU129601** | **GU129602** | **GU129640** | **GU129628** | |

An asterisk indicates taxa for which sequences from this study were merged with data from Álvarez-Padilla *et al.* (2009)
COI, cytochrome *c* oxidase 1; H3, histone 3; NA, not applicable.

For the present study we used the morphological matrix from Álvarez-Padilla *et al*. (2009) to which only one character was added (character 214, PLS line of modified setae: 0, absent; 1, present; see character 169 in Dimitrov & Hormiga, 2009). The complete morphological character matrix is available as Supporting Information (see online Supporting Information file S1) or from the authors.

The genus *Mimetus* has several tegular projections that have not been unambiguously homologized to araneoid tegular structures, such as the conductor and the median apophysis. We coded the conductor and median apophysis as present in this genus based on our examination of the male palp of *Mimietus banksi* Chickering, 1947 and on information available in the literature (e.g. Griswold *et al*., 2005). The sclerotized ridge of the tegulum associated with the embolus, which forms a groove where the embolus lies, can be homologized to the conductor. However, it is difficult to assign the exact identity of the other tegular projections of *Mimetus*. We followed the decision of Griswold *et al*. (2005) to interpret one of them as the median apophysis and the other as the tegular apophysis without specifying which is which explicitly.

In addition to the composite taxa inherited from Álvarez-Padilla *et al*. (2009), the inclusion of DNA sequence data from *Glenognatha* sp. from Panama, which is not conspecific with *Glenognatha foxi* (McCook, 1894), resulted in an additional composite terminal in our analysis (see Table 1).

### Static homology analyses

Static alignments were built with MAFFT: multiple sequence alignment program v. 6. 626 (Katoh *et al*., 2002, 2005; Katoh & Toh, 2008). To build the alignments we used either the L-INS-i strategy (12S, 16S, CO1, and H3) or E-INS-i strategy when we had long gene fragments with several conserved regions spaced by various very variable and difficult to align sections (18S and 28S). The two protein coding genes were trivial to align as they did not show length variation at this level. To be consistent, however, we also used MAFFT to build the protein coding gene alignments rather than doing this by hand. Following the methodology of Álvarez-Padilla *et al*. (2009) gap information was transformed to binary characters with the program GapCoder (Young & Healy, 2002), in accordance to the method developed by Simmons & Ochoterena (2000). Gaps supplied an additional dataset with 483 characters, 171 of them informative. Static alignments were analysed under two optimality criteria, parsimony and Bayesian phylogenetics.

Parsimony analyses of the statically aligned data were performed with the software package TNT (Goloboff, Farris & Nixon, 2004, 2008). Driven and traditional searches were performed following the procedure described in Álvarez-Padilla *et al*. (2009): driven searches were run with the 'stabilize consensus' option until consensus was stabilized five times after finding trees of minimum length; traditional searches consisted of 1000 independent Wagner tree builds followed by subtree pruning and regrafting (SPR) and tree bisection-reconnection (TBR) swapping. In all TNT runs collapsing rule minimum length = 0 was used. Jackknife support values (Farris *et al*., 1996) were calculated in TNT performing 1000 iterations with probability of character removal set to 36%.

Bayesian analyses were performed with the parallel version of the program MrBayes 3.1.2 (Altekar *et al*., 2004) on the Biocluster at the University of Copenhagen (Copenhagen, Denmark) using the models of sequence evolution selected with MODELTEST v. 3.8 (Posada & Crandall, 1998; Posada, 2006) under the Akaike information criterion. DNA sequence data were partitioned by gene and models of sequence evolution were optimized for each partition independently. The general time reversible plus proportion of invariable sites plus gamma (GTR + I + G) model was selected for all gene fragments except 12S, where the GTR + G model was preferred. For the binary in/del dataset and the morphological data partition we used the 'standard discrete (morphology) model' of Lewis (2001). Two independent runs both with four independent chains (three heated and one cold) were run for either 15 000 000 generations (DNA dataset) or 7 000 000 generations (combined DNA and morphology dataset) saving one tree every 1000 generations. By this stage the standard deviation of the posterior probabilities was lower than 0.01%, which indicated convergence of the results. Posterior probabilities were calculated as the 51% majority-rule consensus of the saved trees after 'burnin'. To determine 'burnin' limits, trace files from the MrBayes runs were examined in the program TRACER v. 1.4.1 (Rambaut & Drummond, 2007).

### Direct optimization

Parsimony analyses under direct optimization were performed in the computer program POY 4.1.2 (Varón *et al*., 2009). Protein coding genes were treated as prealigned (alignments from MAFFT from the static homology analyses were used). Sensitivity of the results to different cost schemes was investigated using a set of different cost combinations for the gap opening, gap extension, and nucleotide substitution. To investigate the possible 'swamping' effect of the relatively more abundant molecular characters (Miyamoto, 1985; Swofford, 1991) we performed two sets of analysis: one with morphology character weight fixed to 1 (Álvarez-Padilla *et al*., 2009) and another with

morphological characters weighted equal to the highest of the molecular costs (e.g. Wheeler & Hayashi, 1998; Giribet & Wheeler, 1999; Wheeler *et al*., 2001). Incongruence length difference (ILD) scores were used to choose the combination of scores that maximized congruence amongst data partitions (Wheeler, 1995; Wheeler & Hayashi, 1998). The results from the analysis with the cost combination that resulted in the lowest ILD were chosen as our preferred topology. Statistics on the different cost combinations studied and the resulting ILD scores are given in Table 2. Two different approaches to the heuristic searches were explored. First we used a predetermined search routine through the *search* command in POY under specific time constraint. The *search* command executes tree building, TBR swapping, ratchet perturbation, and tree fusing. When time is constrained the program will repeat this pipeline for the maximum number of times possible given the constraint value. At the end the best tree was selected and kept in the memory; therefore, several consecutive time constrained runs of *search* are better than one long run for the same period of time. The other strategy consisted of importing starting trees into POY and then performing TBR swapping and ratchet and tree fusing on them. As starting trees we used the MPTs from time constrained searches in POY and the MPTs from TNT. Optimal trees resulting from these two search strategies were compared to ensure convergence of the results. Jackknife support was calculated using 1000 pseudoreplicates with character removal probability 36%. All direct optimization analyses were carried out on the Pyramid cluster at The George Washington University's High Performance Computing Laboratory.

## RESULTS

### Morphological analyses

*Equal weights*

Heuristic searches using a traditional search in TNT found six MPTs of length 1109 [consistency index (CI) = 0.246; retention index (RI) = 0.588]. The same trees were found using a driven search. Additional analyses using a parsimony ratchet (Nixon, 1999) as implemented in the new technology search in TNT produced the same optimal result. The strict consensus of these trees is shown in Figure 1. Tetragnathidae was found to be monophyletic but only weakly supported. Within Tetragnathidae several previously established subfamilies were recovered as monophyletic but only Tetragnathinae and Leucauginae (without *Azilia*) received robust support. *Dolichognatha* was found to be sister to *Diphya* and these were not closely related to Metainae and were placed

**Table 2.** Tree lengths and Incongruence Length Difference (ILD) score resulting from analyses under different cost combinations

| Cost (G, N, ext) | Combined | DNA only | 12S | 16S | 18S | 28S | CO1 | H3 | Morphology | ILDcomb | ILDdna |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1,1,0 | 21850 | 20610 | 898 | 1742 | 2905 | 6503 | 2982 | 959 | 1109 | 0.005995 | 0.224212 |
| 2,1,0 | 24420 | 23149 | 996 | 2000 | 3443 | 7941 | 2982 | 959 | 1109 | 0.006634 | 0.208562 |
| 3,1,0 | 26517 | 25260 | 1069 | 2204 | 3910 | 9081 | 2982 | 959 | 1109 | 0.005581 | 0.200119 |
| 3,2,0 | 36974 | 35695 | 1918 | 3775 | 6385 | 14595 | 5964 | 1918 | 1109 | 0.004598 | 0.031937 |
| 4,2,0 | 39287 | 38014 | 1992 | 4002 | 6886 | 15902 | 5964 | 1918 | 1109 | 0.004174 | 0.035513 |
| 3,1,1 | 24195 | 22962 | 1047 | 2017 | 3318 | 7999 | 2982 | 2982 | 1109 | 0.005125 | 0.113971 |
| 3,2,1 | 34747 | 33509 | 1903 | 3606 | 5792 | 13425 | 5964 | 1918 | 1109 | 0.003713 | 0.026888 |
| **4,2,1** | 35687 | 34476 | 1962 | 3703 | 5970 | 14070 | 5964 | 1918 | 1109 | **0.002858** | **0.025786** |
| 2,1,0* | 25642 | 23149 | 996 | 2000 | 3443 | 7941 | 2982 | 959 | 2218 | 0.010725 | 0.208562 |
| 3,1,0* | 28976 | 25260 | 1069 | 2204 | 3910 | 9081 | 2982 | 959 | 3327 | 0.013425 | 0.200119 |
| 3,2,0* | 39438 | 35695 | 1918 | 3775 | 6385 | 14595 | 5964 | 1918 | 3327 | 0.010548 | 0.031937 |
| 4,2,0* | 42976 | 38014 | 1992 | 4002 | 6886 | 15902 | 5964 | 1918 | 4436 | 0.012239 | 0.035513 |
| 3,1,1* | 26590 | 22962 | 1047 | 2017 | 3318 | 7999 | 2982 | 2982 | 3327 | 0.01132 | 0.113971 |
| 3,2,1* | 37139 | 33509 | 1903 | 3606 | 5792 | 13425 | 5964 | 1918 | 3327 | 0.008159 | 0.026888 |
| 4,2,1* | 39263 | 34476 | 1962 | 3703 | 5970 | 14070 | 5964 | 1918 | 4436 | 0.00894 | 0.025786 |

Costs are listed in the following format: G, gap opening; N, nucleotide substitution; ext, gap extension.
*Refers to analyses where morphology was weighted equally to the highest molecular cost (G). Lowest ILD values and corresponding cost combinations are in bold. ILDcomb, ILD that refers to the combined morphological and molecular partitions; ILDdna, refers to analyses of the DNA datasets only.

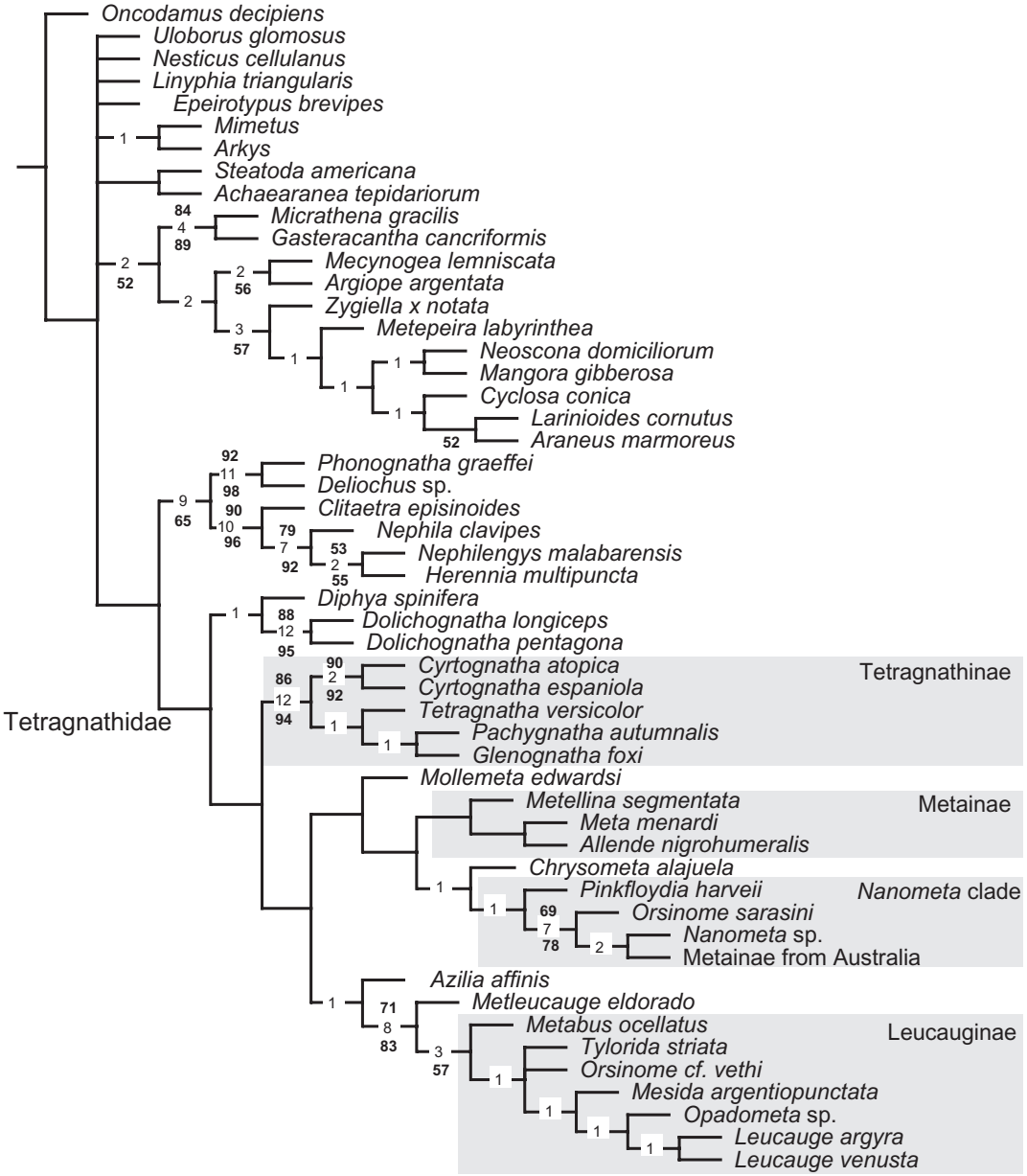


**Figure 1.** Strict consensus of the six most parsimonious trees found by the analysis of the morphological and behavioural dataset: length = 1172; consistency index = 0.233; retention index = 0.557. Bootstrap values > 50 are given above the branches; jackknife values > 50 are shown below the branches. Numbers cutting branches correspond to Bremer support. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

as the most basal tetragnathid lineage. *Pinkfloydia* is closely related to the genera in the *Nanometa* clade (*sensu* Álvarez-Padilla *et al*., 2009) but the latter was recovered as paraphyletic with respect to Metainae.

### Implied weights

Analyses under different values of $k$ (concavity constant) (3, 6, 10, 15, 20, 30, 50, 70, 100, 200, 300, and 500) always found a single most parsimonious cladogram. In all cases Tetragnathidae was monophyletic but different $k$-values resulted in topologies differing in relationships and composition of lineages within Tetragnathidae. Tetragnathinae and Leucauginae were recovered as monophyletic under all values of $k$ examined. In topologies from analyses with $k = 3$ and 6, Metainae was monophyletic including *Dolichognatha*, *Meta*, *Metellina*, and *Mollemeta*.

*Allende* and *Chrysometa* were placed in the *Nanometa* clade. When $k$ was greater than 6 and smaller than 200, *Allende*, *Chrysometa*, and *Mollemeta* were placed outside Metainae and the *Nanometa* clade was the sister group of Tetragnathinae. Values of $k = 200$ and greater suggested the same tetragnathid relationships as the analyses under equal weights. Independently of the $k$-value used *Pinkfloydia* was always closely related to the other Australian–New Zealand genera in the *Nanometa* clade; the only exception was when $k = 3$ where *Pinkfloydia* was the most basal member of the clade *Allende* and *Chrysometa* + Australian–New Zealand genera.

## Molecular analyses

### *Static alignments*

Parsimony analyses of the statically aligned data found four MPTs of length 16 573 (CI = 0.357; RI = 0.423). The strict consensus of these trees is shown in Figure 2. Tetragnathidae is monophyletic but with poor support. The sister group of Tetragnathidae is a clade formed by *Arkys* + *Mimetus*; however, this relationship was not supported by bootstrap or jackknife values above 50%. Within Tetragnathidae there are several monophyletic groups. Most of these lineages coincide with previously defined groups: Leucauginae, Metainae, Tetragnathinae, and the *Nanometa* clade. In addition, two more clades, one formed by the genera *Allende* and *Chrysometa* and other by *Metleucauge*, *Diphya*, *Mollemeta*, and *Azilia*, are present. Leucauginae was found to be the most basal tetragnathid lineage; however, deeper nodes within Tetragnathidae did not receive support from resampling indices. *Pinkfloydia* is the most basal member of the *Nanometa* clade and this placement was relatively well supported by the bootstrap (80) and jackknife (85) indices.

Results from Bayesian analyses of the combined molecular datasets are presented in Figure 3. Tetragnathidae is monophyletic and its sister group is *Arkys*. The *Mimetus* clade is the sister group of *Arkys* + Tetragnathidae and this node was well supported. Within Tetragnathidae results mirrored those from parsimony, except for the basal position of Tetragnathinae and the placement of *Metleucauge* and the clade *Allende* + *Chrysometa*. *Metleucauge* was found to be closely related to leucaugines and *Allende* + *Chrysometa* are more closely related to *Diphya*, *Mollemeta*, and *Azilia* than to tetragnathines. *Cyrtognatha atopica* Dimitrov & Hormiga, 2009 was placed outside Tetragnathinae together with some leucaugines, which is most likely to be a result of missing data (see Discussion). All Australian–New Zealand genera form a well supported monophyletic group in which *Pinkfloydia* is the most basal member.

### *Direct optimization*

The cost combination that maximizes congruence amongst the molecular partitions is: gap opening 4, substitution 2, and gap extension 1 (Table 2). Analysis with this costs combination resulted in one optimal tree with length 34 476 (Fig. 4). Tetragnathids were found to be monophyletic and received a moderate jackknife support (69). *Arkys* is the closest relative of Tetragnathidae and *Mimetus* is the sister group of *Arkys* + Tetragnathidae. However, this topology did not receive jackknife support. Basal relationships within tetragnathids were also poorly supported. *Mollemeta* + *Diphya* are the most basal tetragnathids. *Pinkfloydia* is a member of the *Nanometa* clade which, excluding *Metleucauge*, is the only major tetragnathid lineage that received support higher than 50 (62). Tetragnathinae and Leucauginae are monophyletic as in the results from the analysis of the statically aligned data. Metainae lineages, however, do not form a monophyletic group: *Dolichognatha* was placed in a clade that contains *Chrysometa*, *Allende*, and *Azilia*. The Tetragnathinae species *Cyrtognatha epanola* (Bryant, 1945) appears as more closely related to *Meta* and *Metellina* than to other *Cyrtognatha* species.

Variations in the composition and relationships of Metainae were the only significant differences amongst the topologies found with different cost combinations.

## Combined analyses (morphology and DNA sequence data)

### *Static alignments*

Parsimony analyses of the combined static alignments and morphological matrix resulted in 58 trees. After collapsing unsupported nodes (using collapsing rule 4 in TNT) and removing suboptimal topologies 35 MPTs were left [length (L) = 17785; CI = 348; RI = 0.435]. Driven searches found somewhat fewer trees (29) of same length and converged on the same consensus. The strict consensus of the 35 MPTs from the traditional search is given in Figure 5. Tetragnathidae were found to be monophyletic and well supported with *Arkys* + *Mimetus* as its sister group. Metainae are the most basal tetragnathid lineage but again basal nodes within tetragnathids are unresolved or poorly supported. All other lineages except Metainae form an unresolved polytomy in the strict consensus, together with *Metleucauge*. This polytomy is caused by *Metleucauge* either being placed together with *Diphya*, *Mollemeta*, and *Azilia* or with the leucaugines. In some topologies where *Metleucauge* is the most basal leucaugine, the clade (*Mollemeta* (*Diphya*, *Azilia*)) changes its position from being a sister group to Tetragnathidae + (*Chrysometa*,

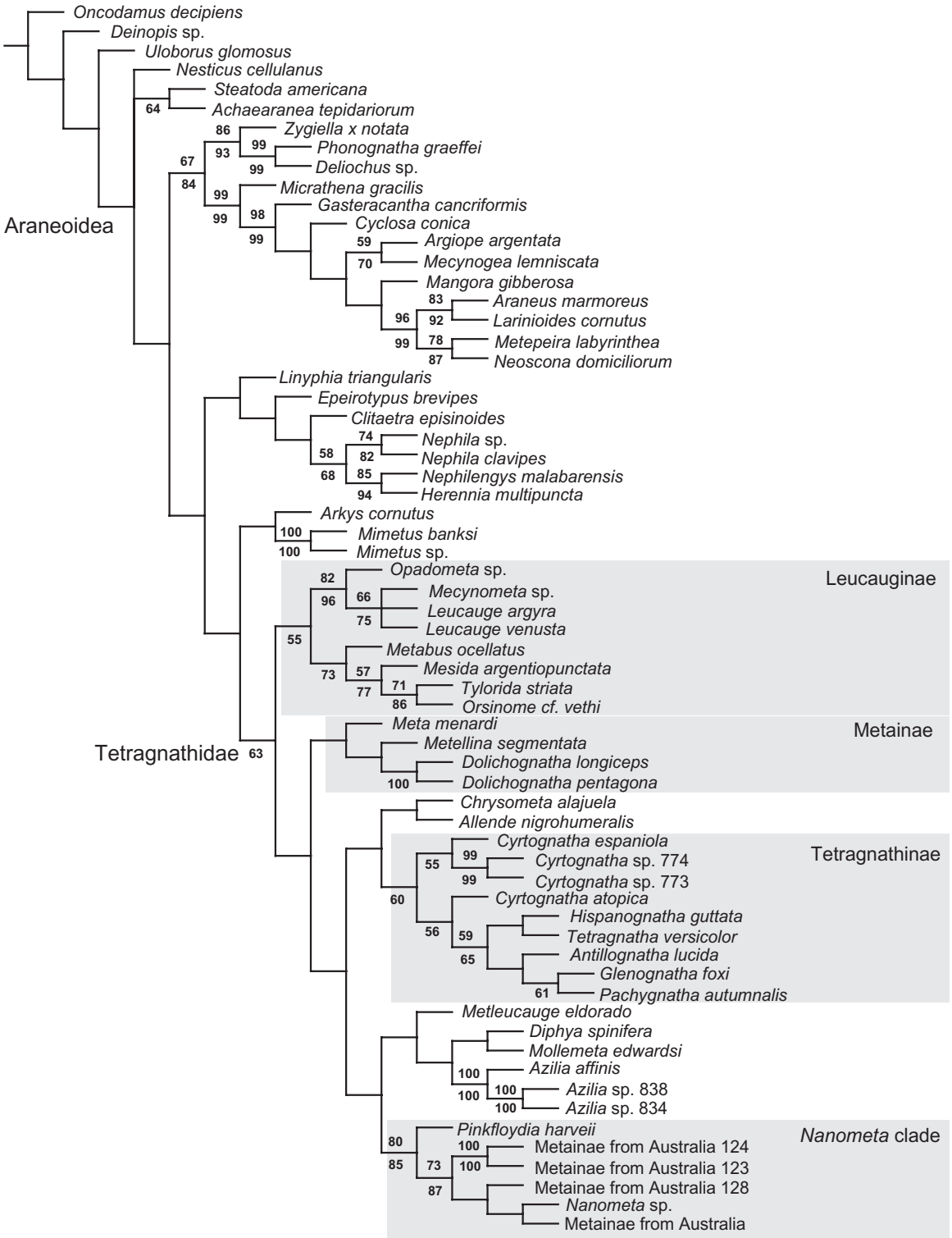


**Figure 2.** Strict consensus of the four most parsimonious trees found by the analysis of the molecular partition (static alignment; gaps treated as presence/absence): length = 16575; consistency index = 0.357; retention index = 0.423. Values above the branches represent bootstrap; values below the branches represent jackknife. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

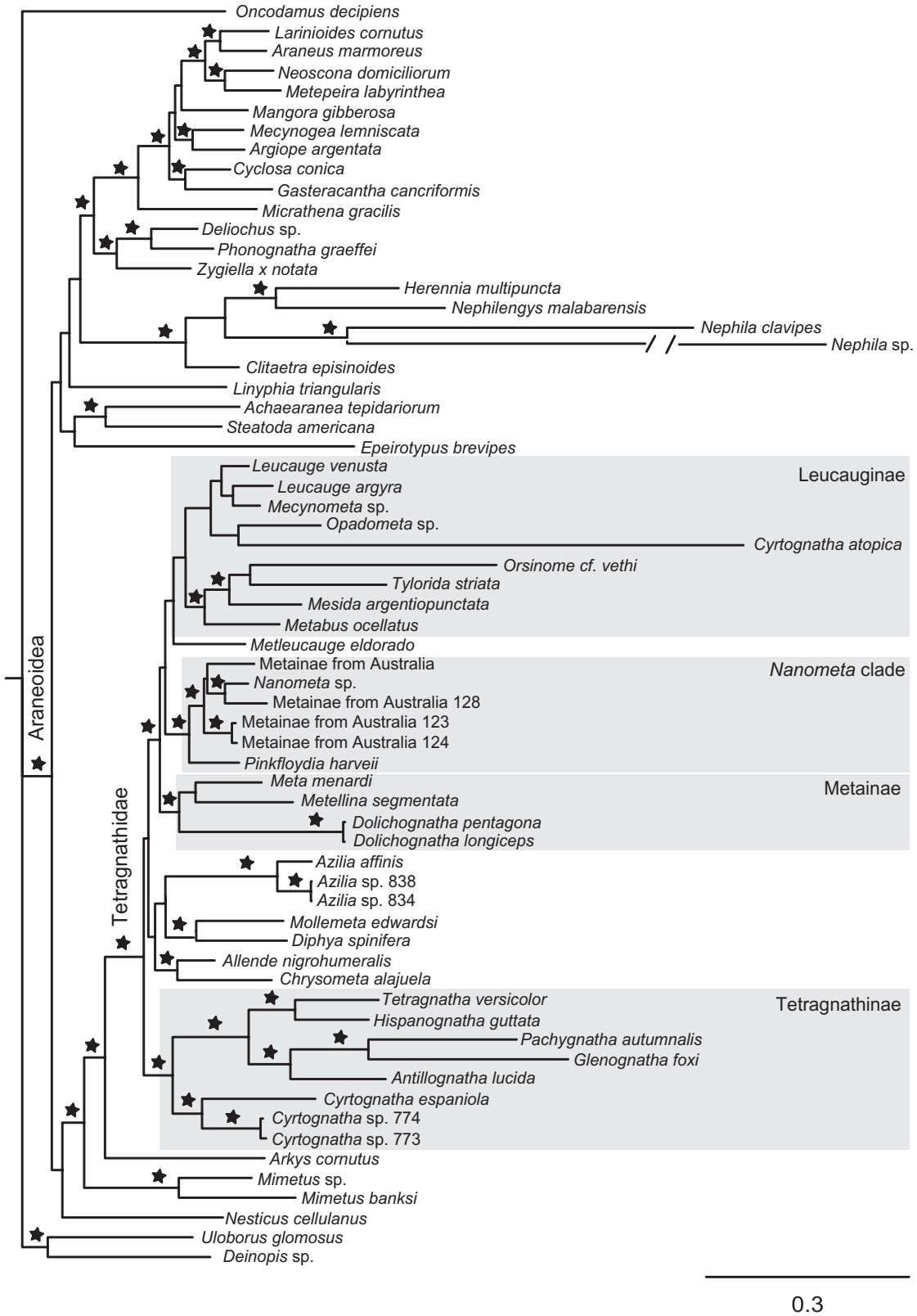


**Figure 3.** Result from Bayesian analyses of the molecular partition (gaps coded as presence/absence). Nodes with posterior probability > 95% are represented with stars. Branch length is proportional to the amount of divergence. The *Nephila* sp. branch is very long and was cut to fit in the figure. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

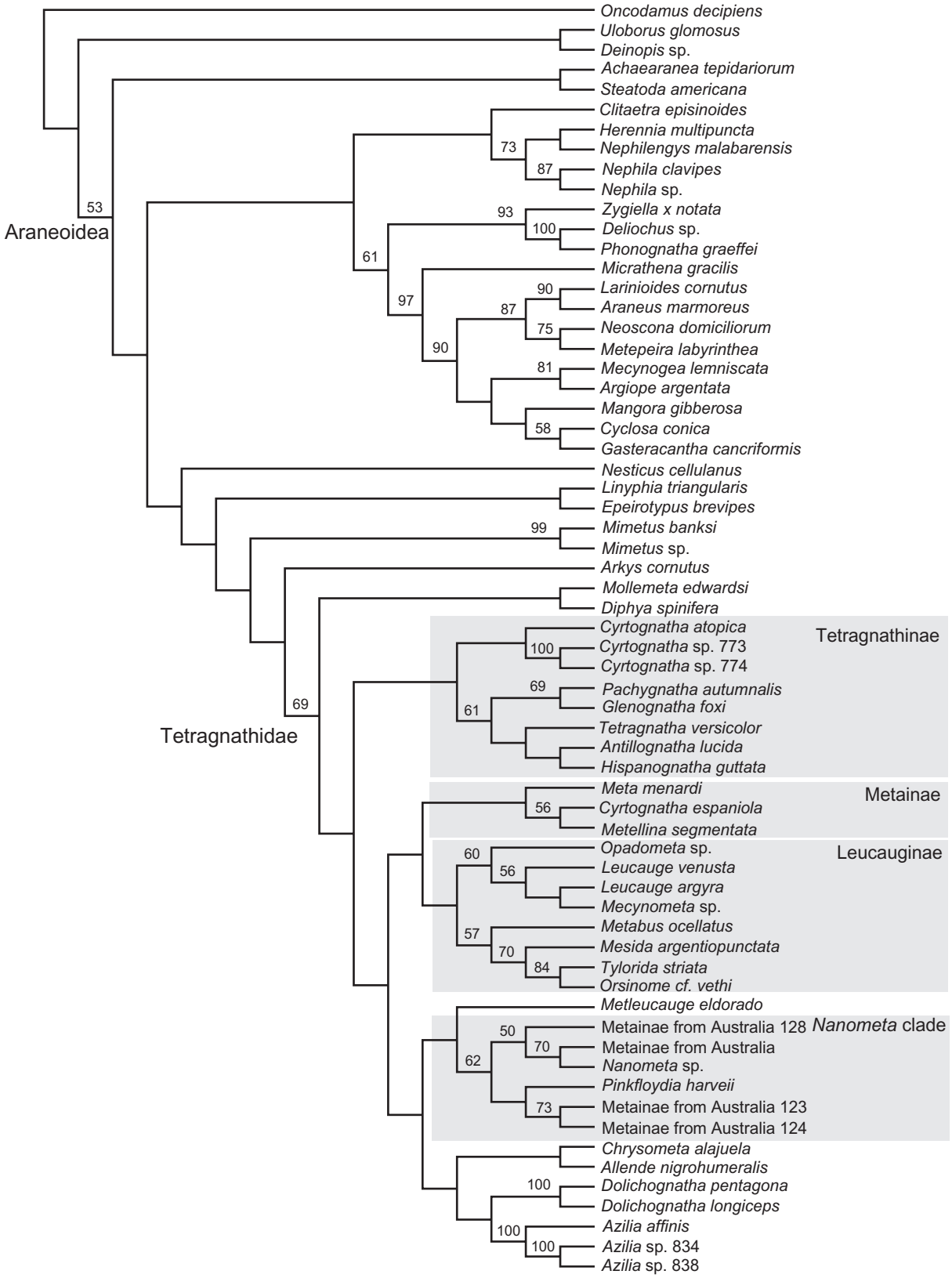


**Figure 4.** The optimal tree found by direct optimization analysis of the molecular dataset. Values above branches represent jackknife support. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

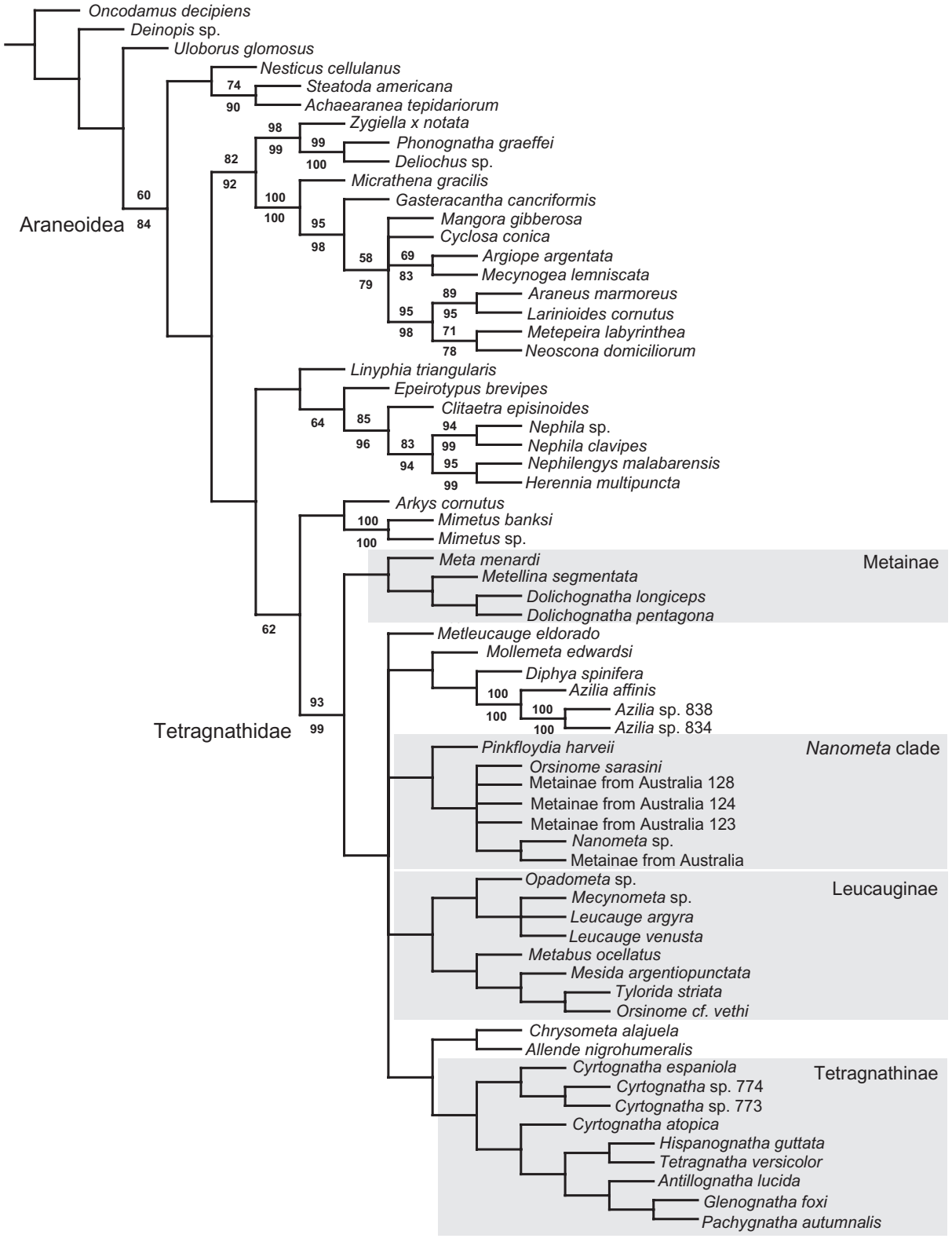


**Figure 5.** Strict consensus of the 35 most parsimonious trees found by the analysis of the combined data: length = 17941; consistency index = 0.345; retention index = 0.427. Values above the branches represent bootstrap; values below the branches represent jackknife. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

*Allende*) to a sister group of Tetragnathidae + (*Chrysometa*, *Allende*) + the *Nanometa* clade. *Pinkfloydia* is the most basal member of the *Nanometa* clade and this placement is supported by bootstrap and jackknife values of 86 and 95, respectively.

Results from Bayesian analysis of the combined dataset are represented in Figure 6. The results generally agree with those obtained by the parsimony analyses with only a few differences: *Mimetus* was found to be the sister group to a clade formed by *Arkys* + Tetragnathidae; Tetragnathinae were found to be the most basal tetragnathid lineage and *Chrysometa* + *Allende* is the sister group of the clade [*Azilia*(*Diphya*, *Mollemeta*)]. As in some of the parsimony topologies, *Metleucauge* is the most basal leucaugine.

*Direct optimization*

The combination of costs that maximizes the congruence amongst partitions for the combined analyses is: gap opening 4, substitution 2, gap extension 1, morphology weight 1 (Table 2). The strict consensus of the five MPTs (35 687 steps) found with this cost combination is shown in Figure 7. Tetragnathids are monophyletic and well supported (jackknife of 82). *Mimetus* + *Arkys* is the sister group of Tetragnathidae but with fairly low support (62). The sister group relationships of *Mimetus* and *Arkys,* however, were not robustly supported.

Tetragnathinae is the most basal tetragnathid lineage. Five additional lineages within Tetragnathidae were found: Metainae, which, in addition to *Meta*, *Metellina*, and *Dolichognatha* includes as a basal member *Metleucauge*; the *Nanometa* clade including *Pinkfloydia*; Leucauginae; a clade including *Diphya*, *Azilia*, and *Mollemeta*; and the group *Chrysometa* + *Allende*. Only Leucauginae, the *Nanometa* clade, and *Chrysometa* + *Allende* received jackknife support values above 50 (56, 64, and 60, respectively).

## DISCUSSION

### Morphology

Initial examination of *P. harveii* specimens clearly singled them out from the other known tetragnathids based on their remarkable morphology. However, their unusual combination of characters (e.g., Figs 8A–H, 9A–D, 10A–E, 11A–D) associated with different tetragnathid lineages made assessment of *P. harveii*'s affinities, without the scrutiny of phylogenetic analysis, guesswork. Only after a thorough phylogenetic analysis did the placement of this genus in the *Nanometa* clade become apparent. Probably one of the most striking characters of *Pinkfloydia* is the very large PME placed on rounded projections and the elevated cephalic region, particularly pronounced in males (Figs 9A, B, 12A, B, D). The elevated cephalic region results in a high clypeus, which is not common in tetragnathids (but see *Diphya*). The elongated cephalic part of the prosoma and the posteriorly projecting and pointed abdomen of *Pinkfloydia* (e.g. Fig. 12A, F) are somewhat similar to the general appearance of *Dolichognatha*, but the male and female genitalia are very different. The male palp of *Pinkfloydia* has very well developed cymbial ectobasal and cymbial ecto-median processes (Figs 8A–C, 13A–E) and a paracymbium with large modified setae at the base (Fig. 13G). This combination of characters, together with the lack of macrosetae on the patella, is consistent with the morphology of the members of the *Nanometa* clade (Álvarez-Padilla *et al*., 2009), but *Pinkfloydia* lacks stridulatory files on the male booklung cuticle (Fig. 12H) and its median tracheal trunks are confined to the abdomen and not branched (Fig. 14F, I). *Pinkfloydia harveii* males have a conspicuous line of oval markings prolaterally on the leg femora (Fig. 12E, G). We observed such markings on the femurs of legs I and IV. On leg I the line of transversal markings extends over the tibia. The nature and origin of these structures is unclear and we do not know what their function might be. The ordered nature of the markings suggests that they are not of random occurrence. However, we did not find any external structure (e.g. gland secretory opening) that might explain their presence or function. It is possible that they indeed act as some kind of stridulatory device that does not interact with the booklung cuticle. *Pinkfloydia* epigynum morphology is highly autapomorphic but the spermathecae morphology and the enlarged membranous fertilization ducts are similar to the morphology of many Leucauginae (see diagnosis in Álvarez-Padilla *et al*., 2009).

Ultimately, phylogenetic analyses resolved this riddle of characters by placing *Pinkfloydia* in the *Nanometa* clade. These results also required a redefinition of the diagnosis of this lineage (see below), as *Pinkfloydia* lacks several of the diagnostic characters that have been used to circumscribe this latter group (Álvarez-Padilla *et al*., 2009).

### Tetragnathid sister group relationships and placement within Araneoidea

We have chosen as a working hypothesis of tetragnathid relationships the results from the combined analysis under direct optimization (with costs: gap opening 4, substitution 2, and gap extension 1 and morphology weighted as 1, see Fig. 7). The following discussion of relationships is based on this topology,

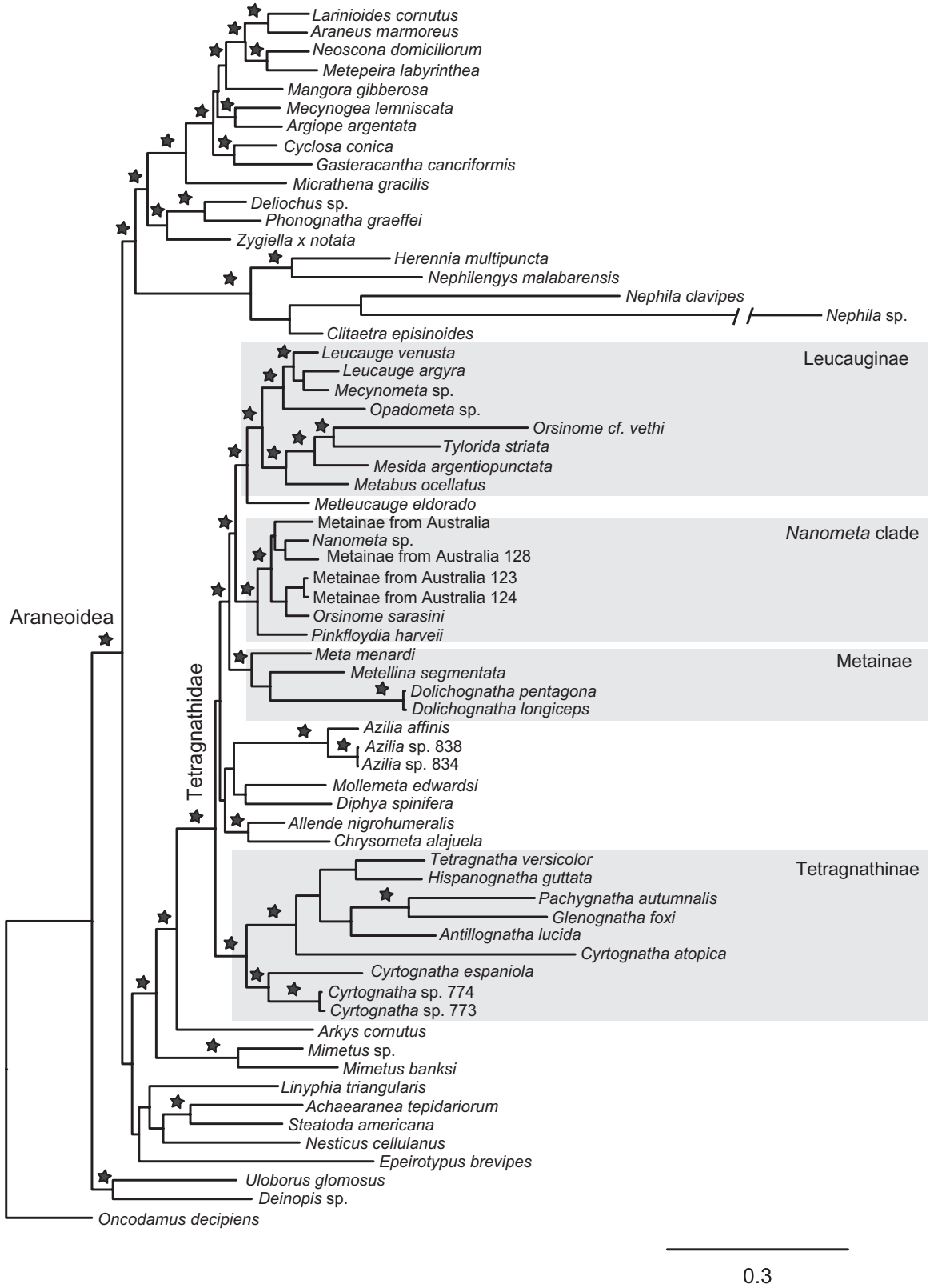


**Figure 6.** Result from Bayesian analyses of the combined dataset (gaps coded as presence/absence). Posterior probabilities > 95% are represented with stars. Branch length is proportional to the amount of divergence. The *Nephila* sp. branch is very long and was cut to fit in the figure. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

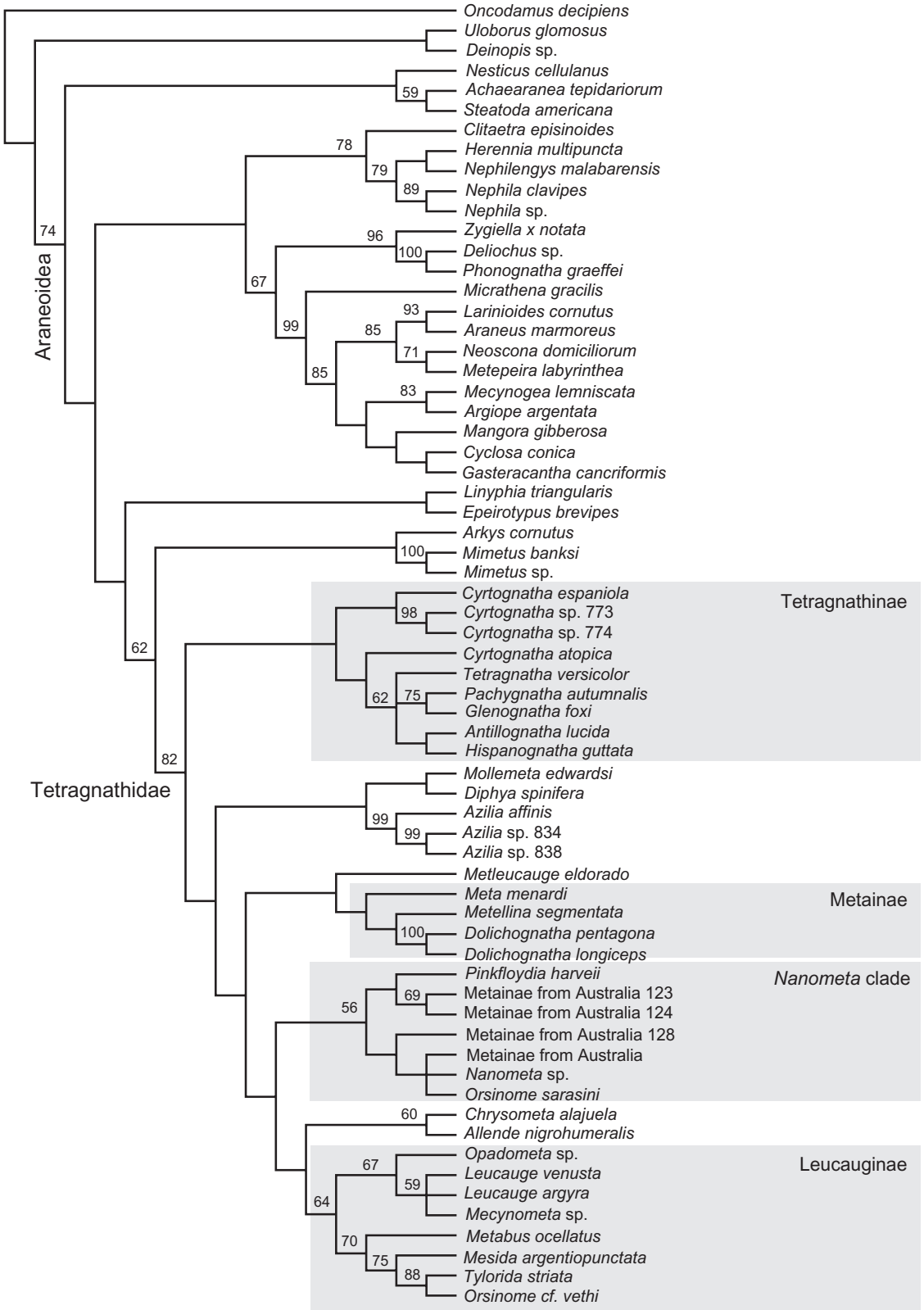


**Figure 7.** Strict consensus of the five most parsimonious trees found by direct optimization analysis of the combined dataset. Values above branches represent jackknife support. Suprageneric taxa of Tetragnathidae are circumscribed in grey boxes.

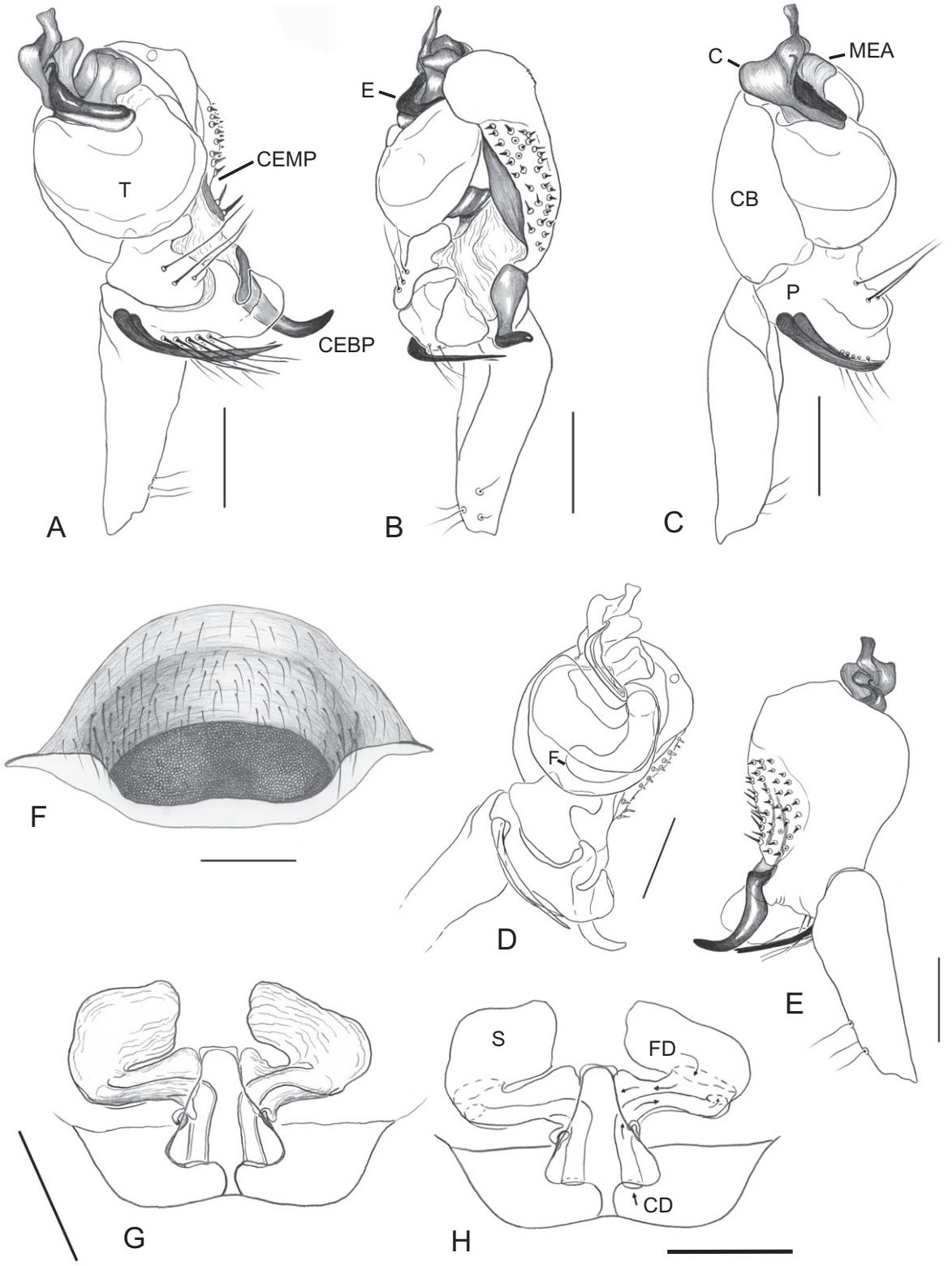


**Figure 8.** ***Pinkfloydia harveii*** **sp. nov.** Male palp (holotype): A, ventral; B, retrolateral; C, prolateral; D, schematic; E, dorsal. Female epigynum: F, ventral; G, dorsal; H, schematic. Abbreviations: C, conductor; CB, cymbium; CD, copulatory duct; CEBP, cymbial ecto-basal process; CEMP, cymbial ecto-median process; E, embolus; F, fundus; FD, fertilization duct; MEA, metine embolic apophysis; P, paracymbium; T, tegulum. Scale bars = 0.2 mm.

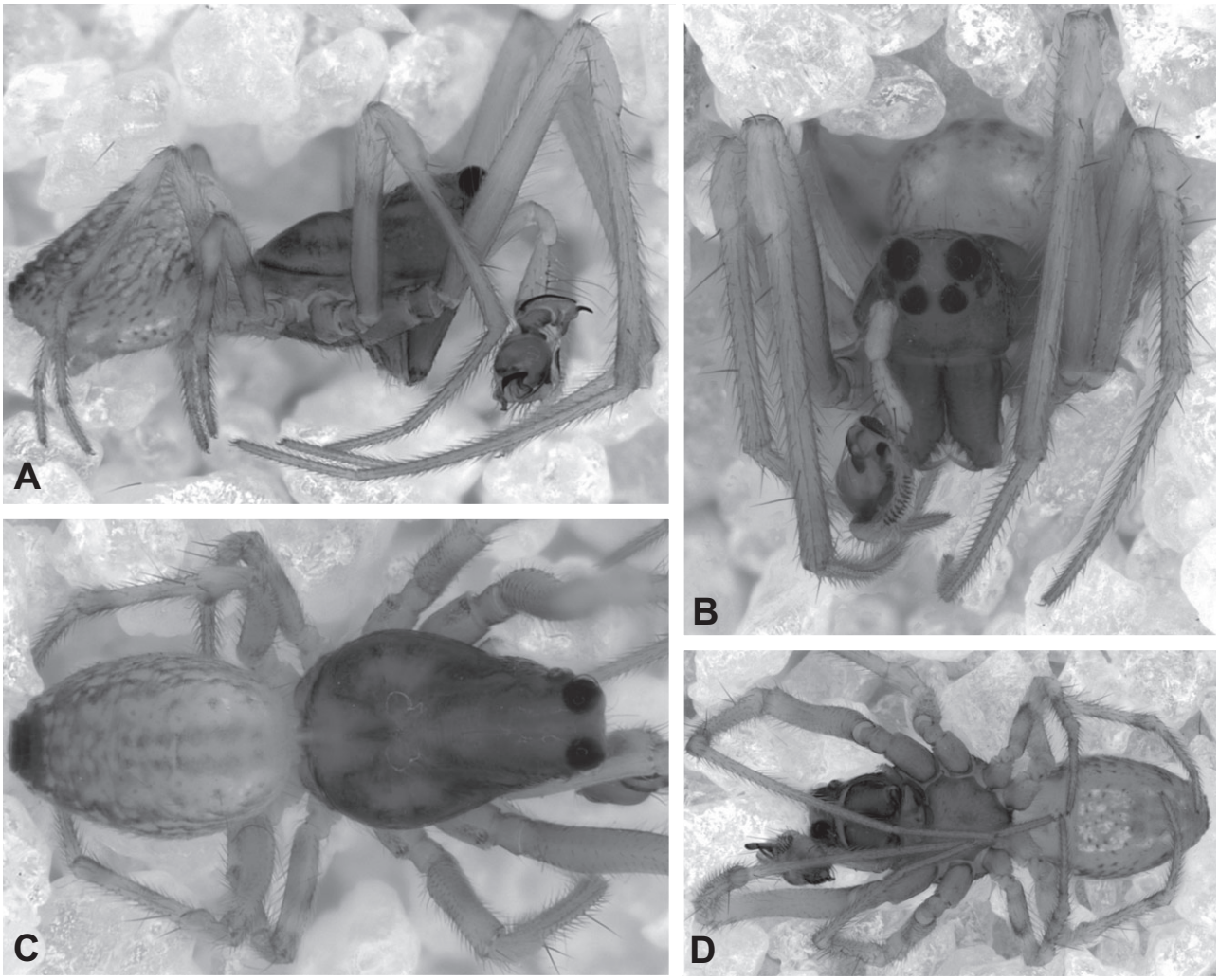


**Figure 9.** ***Pinkfloydia harveii*** **sp. nov.** Male (holotype): A, lateral; B, frontal; C, dorsal; D, ventral. Cephalothorax length is 1.36 mm (see species description for measurements).

except when stated otherwise. Presenting the rationale for the use of direct optimization is beyond the scope of the present paper and it has been discussed extensively elsewhere (Wheeler, 1996; Giribet & Wheeler, 1999, 2001; Wheeler *et al*., 2006; Lehtonen, 2008; Wheeler & Giribet, 2009).

In the most recent phylogenetic treatment of Tetragnathidae, Álvarez-Padilla *et al*. (2009) found some of the 'reduced piriform clade' (see Griswold *et al*., 1998) families included in their analyses to be the closest relatives of tetragnathids. However, this hypothesis of relationship proved to be very sensitive to different analytical treatments. They suggested that in order to palliate this issue, future studies should focus on expanding the sampling of araneoid families and adding several families that are allegedly misplaced in Palpimanoidea, such as mimetids (Schütt, 2000, 2003; Griswold *et al*., 2005; Rix, 2006; Harms, 2007; Rix *et al*., 2008; Harms & Harvey, 2009). The results of the analyses of ribosomal gene sequences (18S and 28S) of Rix *et al*. (2008) support the placement of their mimetid representative (*Australomimetus pseudomaculosus* Heimer, 1986). More recently, Blackledge *et al*. (2009) published an Araneoidea analysis that included a mimetid representative (*Mimetus* sp.). The results of their molecular analyses also confirmed the traditional mimetid placement within Araneoidea. Blackledge *et al*. (2009) also found that *Mimetus* and the araneid genus *Arkys* are the closest relatives of tetragnathids. All our results, except when morphological data were analysed separately, corroborate this finding. All evidence suggests that *Arkys* is not an araneid, but because of the limited taxonomic representation of mimetid diversity in our analysis (and the absence of representatives of Malkaridae), we cannot resolve unambiguously its

position. Some of the results suggest that *Arkys* should be treated as a basal tetragnathid (all Bayesian analyses; also Blackledge *et al*., 2009) whereas in other cases it appears to be a mimetid (dynamic and static homology parsimony analyses). In both cases mimetids seem to be the closest relatives of Tetragnathidae.

### Internal tetragnathid relationships

Our results mostly agree with recent phylogenetic analyses (Álvarez-Padilla *et al*., 2009). We recovered monophyletic Tetragnathinae, Metainae, Leucauginae, and the *Nanometa* clade, with group compositions very close to those discussed in Álvarez-Padilla *et al*. (2009). There are, however, several important differences that refer mainly to the position of taxa that lacked many of the molecular characters in previous analyses (e.g. the representative species of the genera *Azilia*, *Diphya*, and *Mollemeta*).

Our analyses show strong evidence for a monophyletic group that includes the genera *Azilia*, *Diphya*, and *Mollemeta*. In the only tetragnathid analysis that has included molecular data for some of these genera (Álvarez-Padilla *et al*., 2009), *Azilia* was found to be the most basal tetragnathid lineage, whereas the position of *Diphya* and *Mollemeta* was very unstable. Previous hypotheses for the relationships of these genera have not suggested a group with similar composition (Simon, 1894; Levi, 1980; Griswold *et al*., 1998; Wunderlich, 2004a; Álvarez-Padilla, 2007; Álvarez-Padilla *et al*., 2009; Dimitrov & Hormiga, 2009). This is not surprising, as this clade is supported only by molecular synapomorphies and previous studies were based only on morphological evidence or lacked sufficient molecular data (molecular data for *Diphya* was not available in Álvarez-Padilla *et al*., 2009). The lack of morphological synapomorphies and support (from both resampling indices and posterior probabilities) for this group requires that it be treated with caution as its composition may be affected by addition of data in the future. The sister group relationship of *Diphya* + *Mollemeta*, however, was supported by a posterior probability higher than 95% and the following morphological characters: presence of an epigynal mating plug of secretory nature, cymbial ectal margin sclerotized as cymbium and by the short median tracheal trunks.

The placement of *Pinkfloydia* in the *Nanometa* clade provides further support for the hypothesis of a monophyletic Australian–New Zealand tetragnathid group. All analyses support this placement. However, *Pinkfloydia* does not have some of the synapomorphies of this group (*sensu* Álvarez-Padilla *et al*., 2009, see above). In our analysis the morphological characters that support including *Pinkfloydia* in the *Nanometa* clade are: conductor originating from the centre of the tegulum, conductor–tegulum attachment solid, tubular embolus, presence of cheliceral denticles, epigynal mating plug from secretions, and absence of macrosetae in the male palpal patella.

None of our analyses recovered a monophyletic *Cyrtognatha*, which is probably a result of the high proportion of missing data for *Cyrtognatha atopica* (most of the molecular fragments did not amplify and the female is unknown). When *C. atopica* is excluded from the analyses (results not shown) *Cyrtognatha* is always found to be monophyletic. Furthermore, the genus *Cyrtognatha* was recently revised by Dimitrov & Hormiga (2009) and its monophyly is well supported by numerous synapomorphies. Several other genera (e.g. *Mecynometa*) present significant amounts of missing data but the information provided by the available gene fragments and morphological and behavioural data is often sufficient to infer their relationships. Missing data may also affect support values resulting in lower support indices for some of the basal nodes within Tetragnathidae.

This is the first phylogenetic analysis to include the genera *Antillognatha* and *Hispanognatha*. All analyses show strong support for the proposed Tetragnathinae placement for these two taxa (Álvarez-Padilla *et al*., 2009). The present work also represents the first attempt to address the position of *Mecynometa*. All analyses found *Leucauge* to be paraphyletic with respect to *Mecynometa* suggesting that these two genera should be synonymized. However, *Leucauge* itself is in need of a taxonomic revision (Dimitrov & Hormiga, in press). In light of this, making a formal taxonomic decision at this time might be premature.

In contrast to the relatively high agreement of different analyses on the number and composition of the main tetragnathid lineages, relationships amongst them remain largely unresolved. Virtually every different analytical treatment resulted in a different hypothesis of relationships amongst the main lineages of the family, none of them with significant clade support. Given the extensive taxon sampling it is very likely that we have reached the limits of resolution offered by these data and particularly by the molecular markers that we used. Therefore, collecting data from additional genes and developing new molecular markers is crucial in order to address higher level tetragnathid relationships.

### Female mating plugs in Tetragnathidae

Mating plugs have evolved in many spider lineages as a mechanism to prevent females from consecutive

mating by creating a physical barrier that blocks their copulatory openings. Mating plugs can be made of materials secreted by the male, the female or by both, or by diverse male body parts. Plugs are much more common in entelegyne spiders, although they also have been observed in several haplogynes (for review see Uhl, Nessler & Schneider, 2010). In tetragnathids, mating plugs have been studied in detail only in *Leucauge mariana* (Taczanowski, 1881), in which successful plug formation requires participation of both the male and female (Eberhard & Huber, 1998; Méndez, 2004; Aisenberg & Eberhard, 2009). If the female does not add a secretion to the material deposited by the male a functional plug cannot be formed. Aisenberg & Eberhard (2009) demonstrated that male copulatory courtship behaviour (Eberhard & Huber, 1998) can be directly related with female willingness to participate in plug construction. Resinous plugs are present also in *Leucauge argyra* (Walckenaer, 1841) but it is unknown how they are formed and if cryptic female choice plays a role in this process (Álvarez-Padilla *et al*., 2009; D. Dimitrov and G. Hormiga pers. observ.). In other species of *Leucauge* parts of the embolus have been found in the female genitalia (Wiehle, 1967; Kuntner, 2005; Kuntner *et al*., 2008). The only other known case in tetragnathids where parts of the male palp are left in the female genitalia is *Nanometa* sp. (Álvarez-Padilla, 2007; Álvarez-Padilla *et al*., 2009; D. Dimitrov and G. Hormiga pers. observ.).

Although best documented in *Leucauge*, mating plugs appear to be very common in tetragnathids. Secretory plugs are the more common type and are present in practically all entelegyne tetragnathid lineages (Álvarez-Padilla, 2007; Álvarez-Padilla *et al*., 2009; D. Dimitrov and G. Hormiga pers. observ.). Such mating plugs have been observed in *Diphya spinifera* Tullgren, 1902, an undescribed Metainae genus from Australia, *Orsinome sarasini* Berland, 1942, *Orsinome* sp., *Metleucauge eldorado* Levi, 1980, and *Mollemeta edwardsi* (Simon, 1904) (Álvarez-Padilla, 2007; Álvarez-Padilla *et al*., 2009; D. Dimitrov and G. Hormiga pers. observ.).

In most of the *P. harveii* females that we examined, we found 'resinous' female plugs (Fig. 10E). When in alcohol we were able to remove the material fairly easy using a fine insect pin. However, we received the spiders already in alcohol and we were unable to study the properties of the plug material when unaltered. It remains unclear how efficient a barrier for mating the plug in this species is. The epigynal plate in *P. harveii* has numerous pores (Figs 8F, 15D, G), which may be related to secretion of materials that take part in the plug formation. A histological study is needed to confirm this hypothesis. It is also unknown whether the male participates in some way, either by secreting materials or by emitting behavioural signals, in the construction of the mating plugs in *P. harveii*.

## TAXONOMY

### Family Tetragnathidae Menge, 1866

### *Pinkfloydia* Hormiga & Dimitrov gen. nov.

*Type species: Pinkfloydia harveii* Dimitrov & Hormiga sp. nov.

*Etymology:* The genus is named after the British psychedelic and progressive rock band Pink Floyd. In its heyday Pink Floyd was an innovative group that created music, which was an eclectic mixture of styles. The band also pioneered the use of very sophisticated lights and lasers in their live shows and often had highly innovative album covers. *Pinkfloydia* has very unusual morphological features and its name aims to reflect its uniqueness. *Pinkfloydia* is an undeclinable proper name and feminine in gender.

*Diagnosis: Pinkfloydia* can be easily distinguished from all other tetragnathid genera by the conspicuously enlarged PME placed on short ocular protrusions and by the conical and distinctively elevated cephalic area (Figs 9A, 10A, 12A, 14G). All other eyes are placed at the same level on the prominent cephalic region and are much smaller in size (Figs 9B, 10C, 12A, D, 14E). Males of *Pinkfloydia* differ from other tetragnathid males in having several conspicuously large macrosetae at the base of the paracymbium (Figs 8A–C, 13A–D, G) and an area of the cymbium covered with numerous modified short setae (cuspules) concentrated dorsally on the cymbial ecto-median process (Figs 8B, E, 13A, C, H, I). In addition, the *Pinkfloydia* male palp has a well developed metine embolic apophysis and an embolus that carries numerous short denticles (Figs 8A–C, 13B, E, F, 14A); the cymbium has a well developed cymbial ecto-basal and cymbial ecto-median processes (Figs 8A, 13A, D).

Females are diagnosed by the presence of a flat epigynal plate that has numerous pores opening on its ventral surface (Figs 8F, 15D–E, G; no similar plate has been described in any other member of Tetragnathidae). Copulatory openings are displaced caudally and hidden by the distal edge of the epigynum in a transversal groove (Figs 8G, H, 15F).

*Description:* Tiny spiders, total length 2.77–3.75 in males, 3.54–4.51 in females (but note that so far *P. harveii* is the only known species in this new genus). Cephalothorax brown, longer than wide – 1.36–1.61 long in males and 1.68–1.86 in females – with a well marked fovea (Figs 9C, 10B); cephalic area conical,

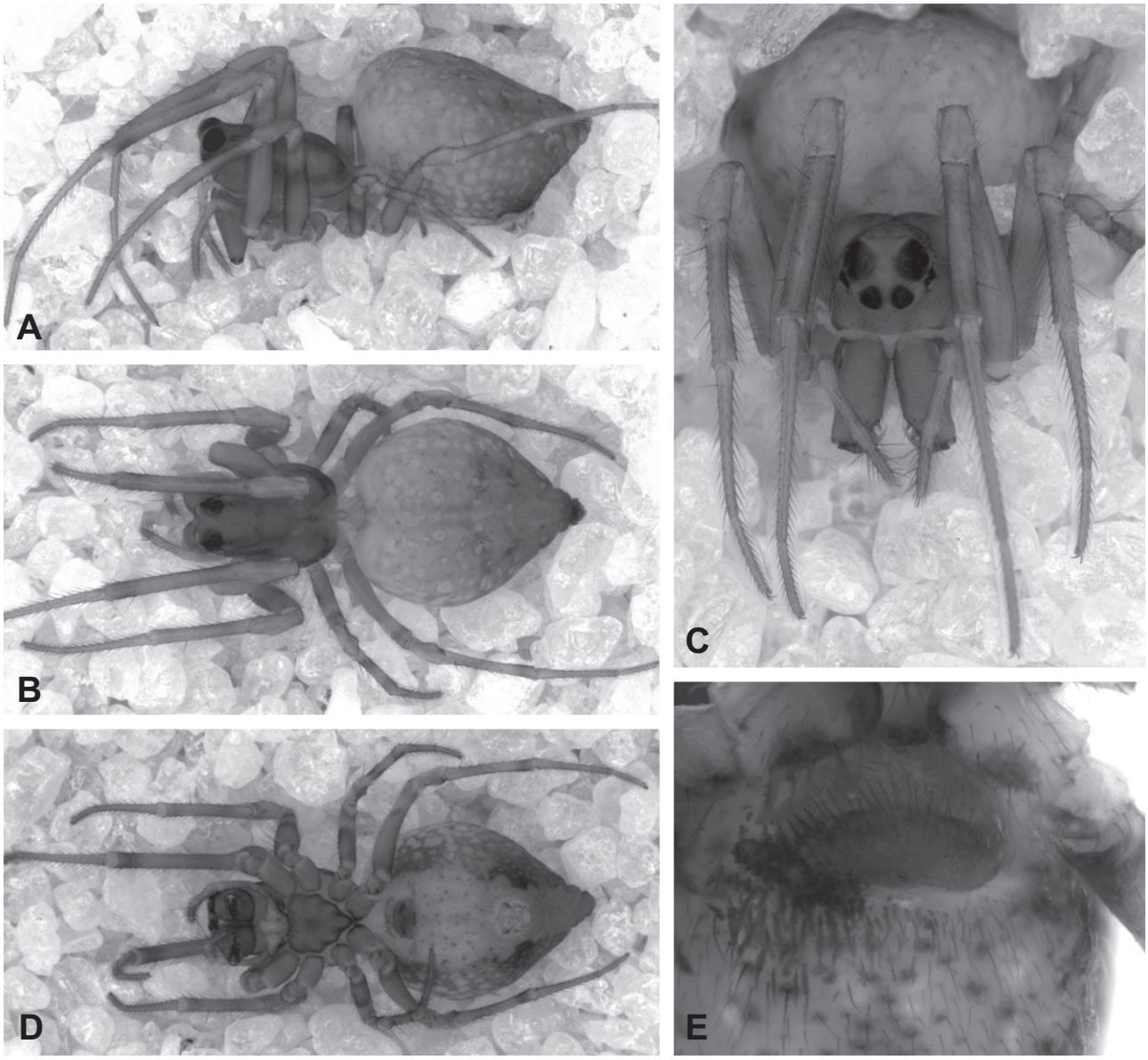


**Figure 10.** ***Pinkfloydia harveii*** **sp. nov.** (paratype). Female: A, lateral; B, dorsal; C, frontal; D, ventral; E, epigynum with mating plug. Cephalothorax length is 1.86 mm (see species description for measurements). Note that Figure 10E depicts a different specimen.

conspicuously elevated and slightly projected over the chelicerae (Figs 9A, 10A, 12A, 14G). Sternum slightly longer than wide; conspicuously narrower distally, and with a ridged cuticle (Figs 12C, 14J). AME slightly larger than ALE and PLE but much smaller than PME; PME much larger than the other eyes and placed over small rounded rises at the top of the elevated cephalic area; PLE and ALE juxtaposed over a slight elevation (Figs 12A, 14G). Clypeus height more than one AME diameter, slightly higher in males than in females. Chelicerae cylindrical, longer and slender in males, with three teeth on the anterior and two teeth on the posterior margin (Figs 12D, 14E). Chelicerae with two small denticles near the fang joint (Fig. 12I). Legs without dorsal femoral trichobothria in both sexes. Abdomen rounded with a prominent caudal tubercle, more elongated in males (Figs 12F, H, 15B, C). Spinneret morphology (studied in one male and two females) as in most other tetragnathid spiders: ALS with about 30 piriform gland spigots in females and about 20 in males, ordered roughly in four (females) or three (males) arched lines (Figs 14B, 16D). PMS with two aciniform gland spigots, between the cylindrical and the minor ampu-

tate gland spigots (Fig. 16E, F). PLS with six aciniform gland spigots ordered in a straight line between the cylindrical spigots and the 'araneoid triplet' (Fig. 16G). Flagelliform and aggregate gland spigots well developed in females (Fig. 16G) but reduced in adult males (Fig. 14C). Flagelliform spigot conical, apically pointed; aggregate spigots with wider bases and wide sockets (Fig. 16G). Epiandrous fusules placed in a shallow epigastric groove and arranged in three groups separated by low cuticular ridges (Fig. 14D). Tracheal spiracle placed very close to the spinnerets. Tracheal system consisting of two longer lateral tubes and two shorter medial ones (Fig. 14F, I). All tracheal tubes confined to abdomen (i.e. do not enter the prosoma). Male pedipalp with very large modified setae on paracymbium (Figs 8A–C, E, 13A, B, G). Cymbium carrying cymbial ecto-basal and cymbial ecto-median processes (Figs 8A, B, E, 13A, D). A field containing numerous short modified setae (cuspules) arranged in longitudinal lines is placed dorsally over the cymbial ecto-median process, which extends over the cymbium (Figs 8E, 13A, C, D, H, I). Tegulum well sclerotized, large and spherical in shape (Figs 8A–C, 13B). Conductor and embolus coiling together and arising apically from the centre of the tegulum (Figs 8A, C, 13E, F). Conductor well sclerotized, with a robust apical apophysis (Fig. 13F). Embolus with robust metine embolic apophysis, dorsoapically with numerous short denticles and a distinctively slender apex (Fig. 13F). Spermatic duct enters the tegulum (towards the fundus) through the embolus base, widening in diameter shortly after (Fig. 8D). Spermatic duct without switchbacks and one and a half spiral turns before reaching the fundus (Fig. 8D).

Female genitalia entelegyne, with a flat, well chitinized epigynum that has numerous pores dorsally (Figs 8F–H, 15D–H). These pores might be related to the secretions that form the epigynal plug observed in some of the specimens (Fig. 10E). Spermathecae oval with weakly sclerotized walls (Figs 8G, 15F, H).

*Phylogenetics: Pinkfloydia* is a member of the Australian–New Zealand tetragnathid lineage *Nanometa* clade.

*Natural history:* See under *P. harveii* sp. nov.

*Composition:* The only known member of this genus is *P. harveii* sp. nov.

*Distribution:* Western Australia (see under *P. harveii* sp. nov.).

### *PINKFLOYDIA HARVEII* DIMITROV & HORMIGA SP. NOV. (FIGS 8–16)

*Types: Holotype*: male from Australia, Western Australia, Stirling Range National Park, Wedge Hill; 34°23′17″S, 118°10′18″E; 02.v.1996, Harvey, M. S., Waldock, J. M., Main, B. Y. Legit (Leg). (AUSTMUS T66621).

*Paratypes:* 1 female, same data as holotype (in the same vial). Australia, Western Australia: 1 female, Walpole, Tinglewood Road, 35°00′S, 116°40′E, 13.vi.1987, Main, B. Y. Leg. (AUSTMUS 93/2124); 4 females, Mt Cooke, 32°25′S, 116°18′E, 27.iv.1992, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2080, 93/2081; 93/2082, 93/2083); 1 male, Boddington Bauxite Mine, site SSB02, 32°59′36″S, 116°28′23″E, vi.2003, Graby, G. Leg. (AUSTMUS T71617); 1 female, Stirling Range National Park, Toolbrunup Peak Track, 34°24′S, 118°04′E, 2.iv.1993, Harvey, M. S. Leg. (AUSTMUS T66619); 1 female, Bold Park, site BP1, 31°57′07″S, 115°45′30″E, 20.v.–20.vii.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2075); 1 female, Bold Park, site BP3, 31°56′33″S, 115°46′13″E, 20.v.–20.vii.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2076); 2 males, Bold Park, site BP4, 31°56′29″S, 115°46′01″E, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2077, 93/2078); 1 male, Perth Airport, site PA5, 31°58′03″S, 115°58′11″E, 24.vi.–28.vii.1993, Harvey, M. S., Waldock, J. M., Sampey, A. Leg. (AUSTMUS 93/2085); 1 male, 1 female, Talbot Road Reserve, site TR2, 31°52′24″S, 116°02′52″E, 24.vi.–28.vii.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2086, 93/2087).

*Etymology:* The species epithet is a patronym after the Australian arachnologist Mark S. Harvey, collector of this and many other new species of arachnids from Western Australia.

*Diagnosis:* As this genus is monotypic the diagnosis of *P. harveii* coincides with the diagnosis given for the genus (see above under Diagnosis).

*Description (male holotype):* Total body length 2.77. Cephalothorax 1.36 long, 0.93 wide, 1.11 high. Sternum almost as long as wide; 0.67 long, 0.65 wide. Abdomen 1.41 long, 0.90 wide, 0.98 high. Cephalothorax, chelicerae, and sternum brown; dorsally sternum with darker markings laterally. Fovea well marked, with darker coloration. Eyes placed on a conically elevated and slightly projected forward cephalic region; PME on short elevations, much larger than the rest of the eyes (Figs 9B, 12A, B, D). Lateral eyes juxtaposed. Distance between AME 1.5 times one AME diameter; between AME and ALE about one

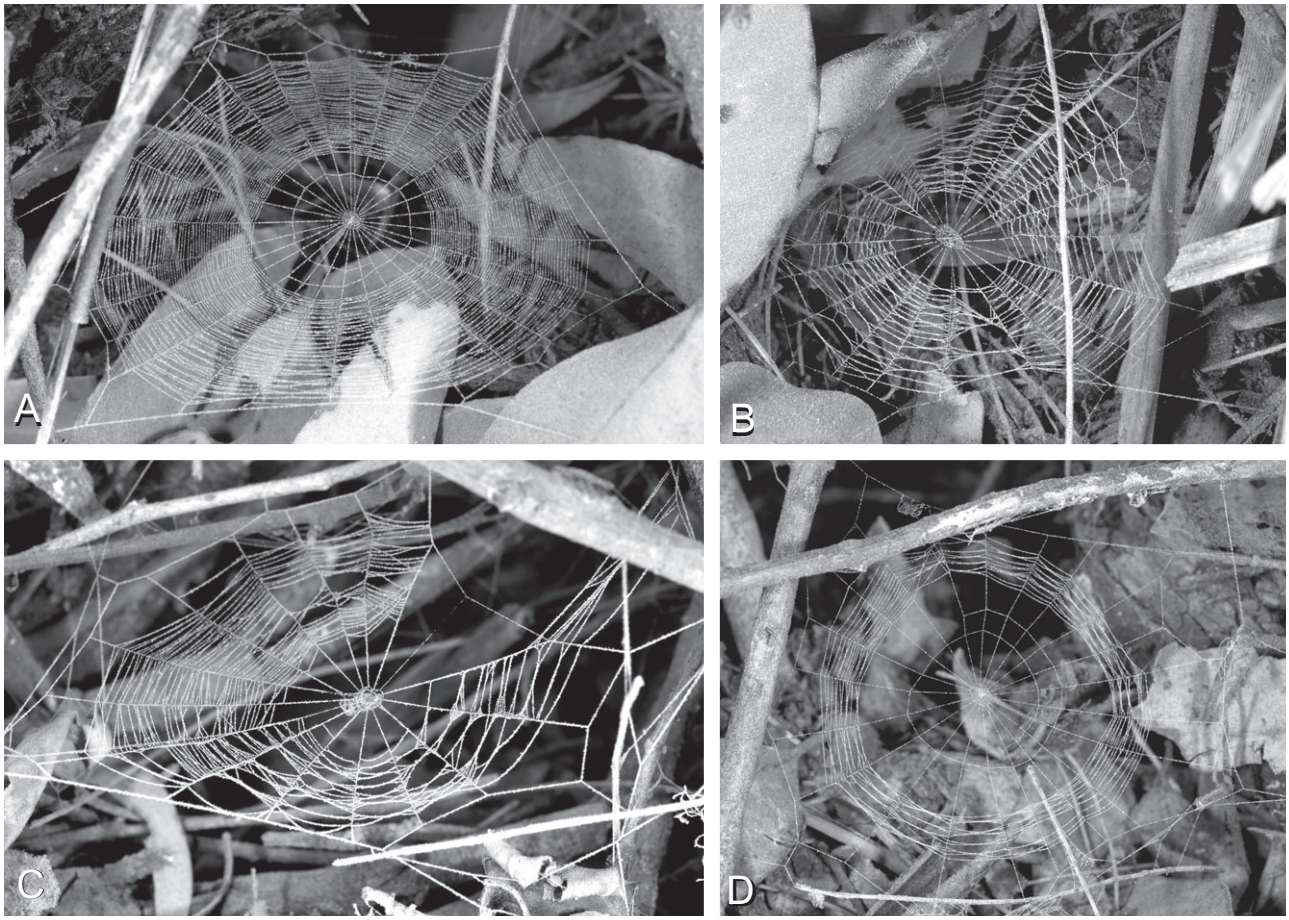


**Figure 11.** ***Pinkfloydia harveii*** **sp. nov.** Capture webs of four different juveniles photographed in the leaf litter at night, near Walpole. All webs have been dusted with cornstarch. A, recently spun orb, maximum horizontal web frame width is 67 mm (photo series 0209-0215/27ii06GH). B, maximum horizontal web frame width is 52 mm (photo series 0201-0202/27ii06GH). C, partially damaged web with spider at the hub; maximum horizontal web frame width is 92 mm (photo series 0206-0208/27ii06GH). D, unfinished web; the spider is on the upper left frame corner, maximum horizontal frame width is 62 mm (photo series 0203-02105/27ii06GH).

AME diameter. Distance between PME almost two PME diameters. Lateral eyes placed close to the PME. Clypeus height 1.85 times one AME diameter. Chelicerae slender, elongated, and cylindrical (Figs 9B, 12D), with three anterior and two posterior teeth, and two small denticles between the anterior and posterior margins, adjacent to the fang joint (Fig. 12I). Cheliceral cuticle rugose (Fig. 12D). Abdomen oval, longer than wide, with grey-brownish coloration and very few remains of guanine patches. Dorsally with a darker band medially delimited by two clearer dorsolateral bands. Caudal tubercle more darkly pigmented (Fig. 9A, C). Ventrally abdomen lighter in colour, with few small darker dots medially. Legs yellowish. Femur I 1.78 long; 1.30 times the length of the cephalothorax. Femur I with a conspicuous line of oval markings prolaterally (Fig. 12E, G) that extend over the tibia. Similar markings also present on femur IV (under the SEM these markings seem to be made of adhered particles). Palp (Figs 8A–E, 13A–C, E, 14A) with a very long tibia, as long as or slightly longer than the cymbium (Fig. 12A, B). Patella without macrosetae (Fig. 12A, B, D). Paracymbium large and ventrally displaced with two distinctive black, long, and thick macrosetae (Figs 8A, C, 13G, 14A). Cymbial ecto-basal process very long with pointed tip and strongly chitinized (Figs 8B, 13A, D). Cymbial ecto-median process with transparent rim and numerous cuspules dorsally (Figs 8B, E, 13D, H, I). Embolus with large metine embolic apophysis, rectangular, with a pointed and folded laminar distal edge (Figs 8A–C, 13B, F, 14A). Conductor with blunt tip narrower than its base (Fig. 13B, E, F). Epiandrous fusules as in Figure 14D.

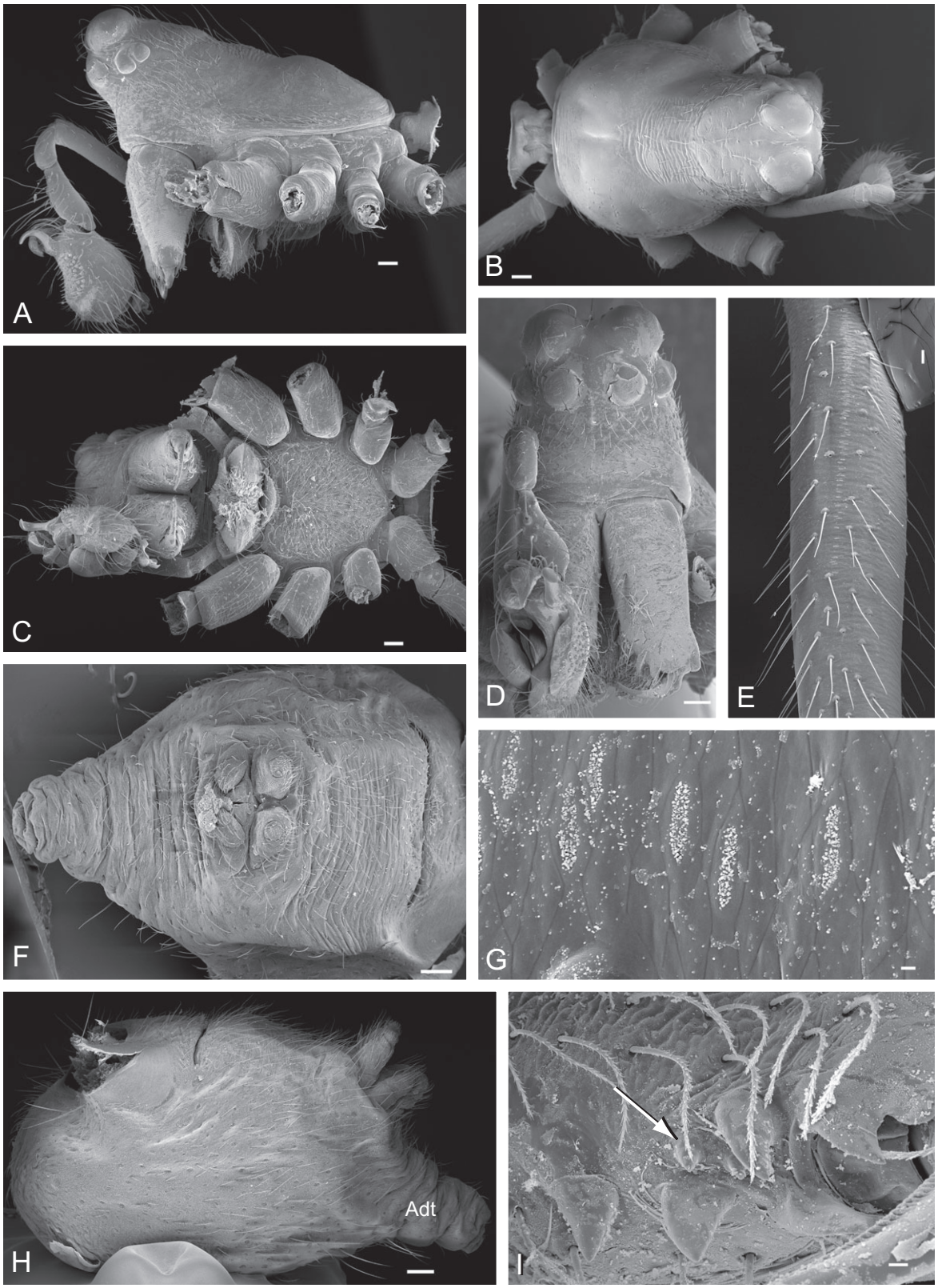


**Figure 12.** ***Pinkfloydia harveii*** **sp. nov.**, male. Cephalothorax: A, lateral; B, dorsal; C, ventral; D, frontal. Leg I femur: E, prolateral; G, detail. Abdomen: F, ventral; H, lateral. I, cheliceral denticles. Adt, distal tubercle of the abdomen. Scale bars: A, B, C, D, F, H = 100 μm; E = 30 μm; I = 10 μm; G = 2 μm.

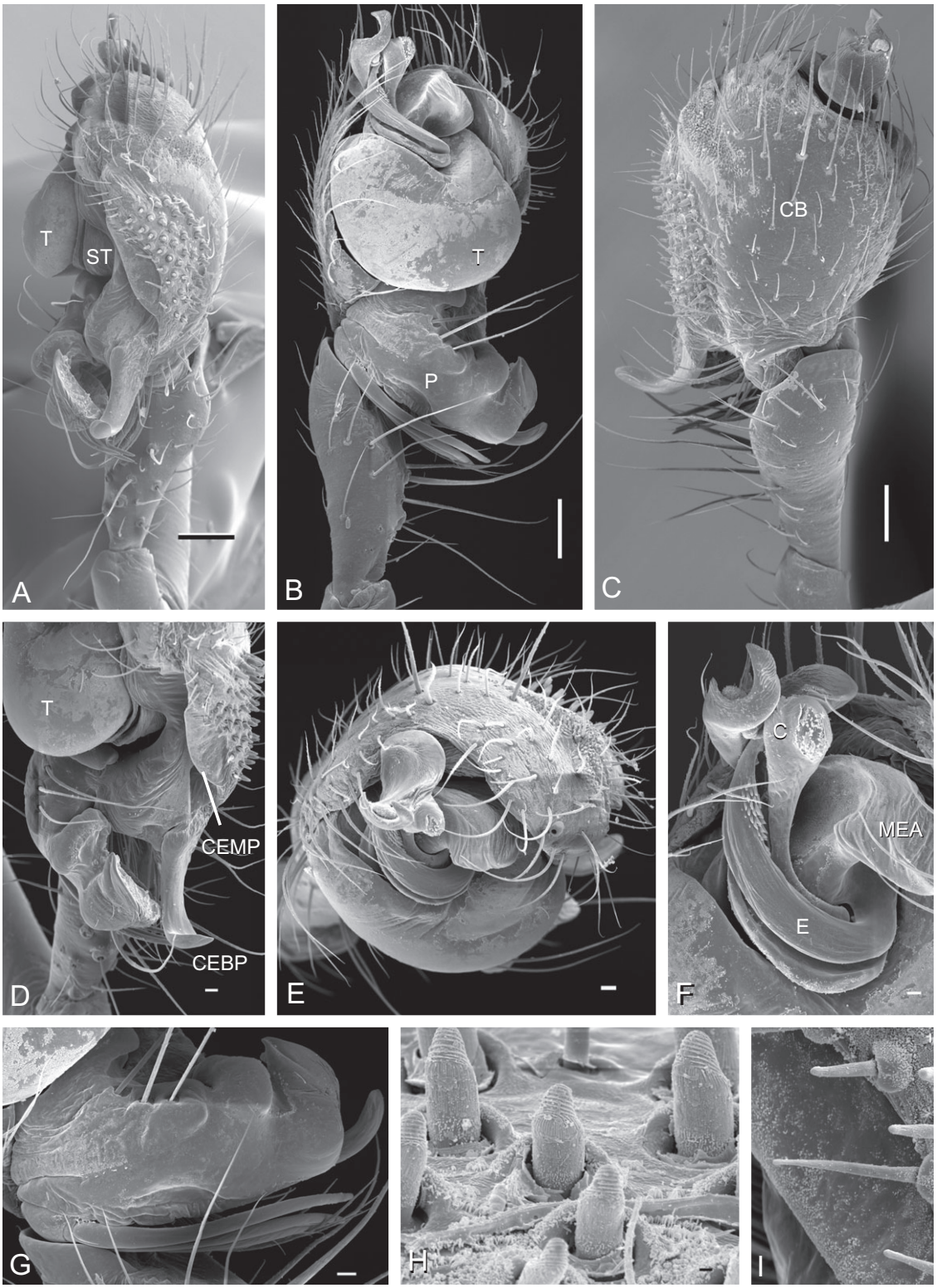


**Figure 13.** ***Pinkfloydia harveii*** **sp. nov.**, male. Palp: A, retrolateral; B, ventral; C, dorsal; D, retrolateral close up; E, apical; F, conductor and embolus detail; G, paracymbium; H, modified setae on the CEMP (type I); I, modified setae (cuspules) on the CEMP (type II). Abbreviations: C, conductor; CB, cymbium; CEBP, cymbial ecto-basal process; CEMP, cymbial ecto-median process; E, embolus; MEA, metine embolic apophysis; P, paracymbium; S, spermatheca; ST, subtegulum. Scale bars: A, B, C = 100 μm; D, E, G = 20 μm; F = 10 μm; H = 2 μm; I = 3 μm.

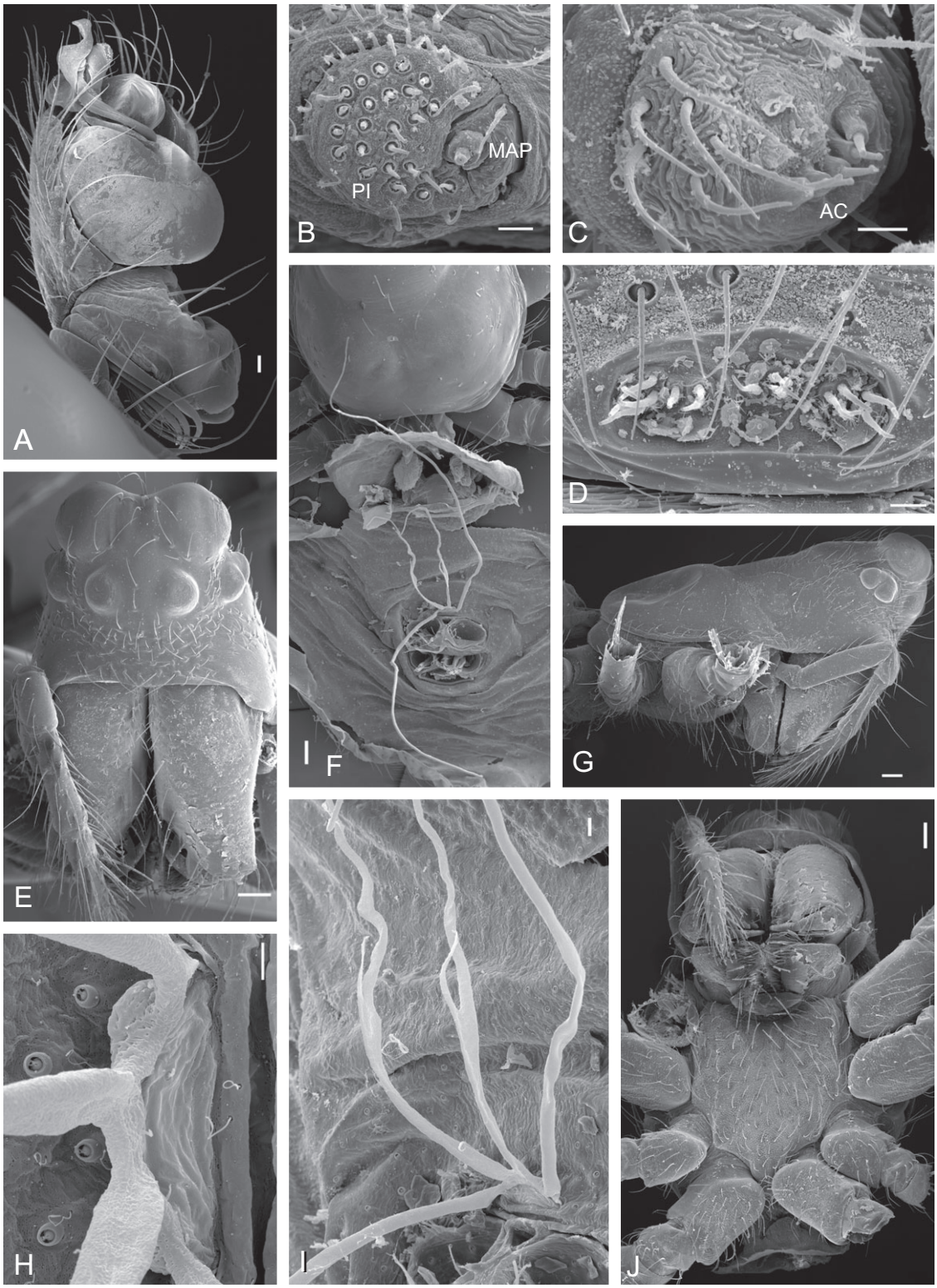


**Figure 14.** ***Pinkfloydia harveii*** **sp. nov.**, male. Palp: A, prolateral. B, ALS. C, PLS. D, epiandrous spigots. ***Pinkfloydia harveii*** **sp. nov.**, female. Cephalothorax: E, frontal; G, lateral; J, ventral. Tracheal system: F, dorsal overview; H, tracheal base detail; I, dorsal close up. Abbreviations: AC, aciniform gland spigots; ALS, anterior lateral spinnerets; MAP, major ampullate gland spigot; PI, piriform gland spigots; PLS, posterior lateral spinnerets. Scale bars: A, E, F, G, J = 100 μm; B, C, D, H = 10 μm; I = 20 μm.

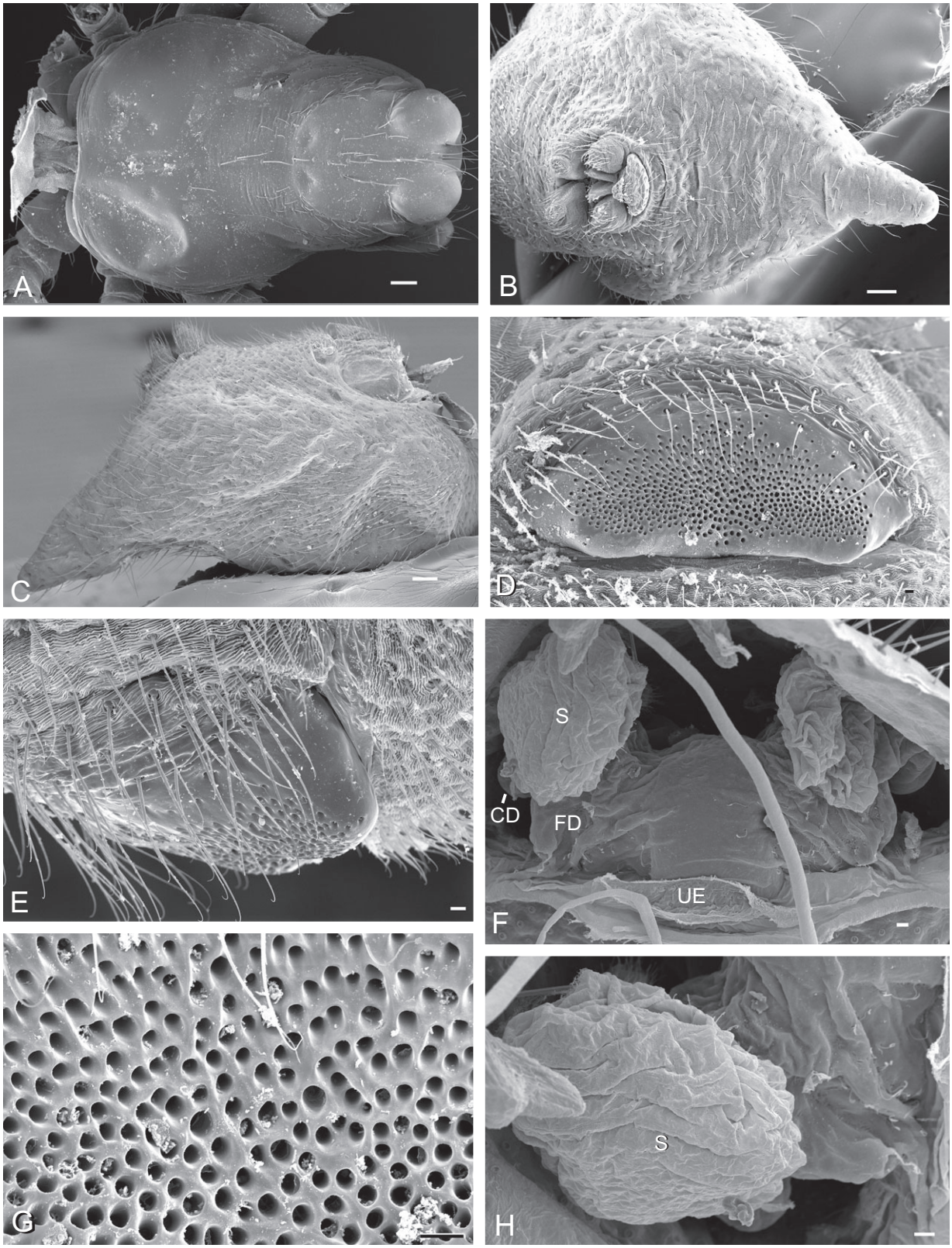


**Figure 15.** ***Pinkfloydia harveii*** **sp. nov.**, female. A, cephalothorax, dorsal. Abdomen: B, caudal; C, lateral. Epigynum: D, ventral; E, lateral; F, dorsal; G, epigynal plate detail. H, spermathecae. Abbreviations: CD, copulatory duct; FD, fertilization duct; S, spermatheca; UE, uterus externus. Scale bars: A, B, C = 100 μm; D, E, F, G, H = 10 μm.

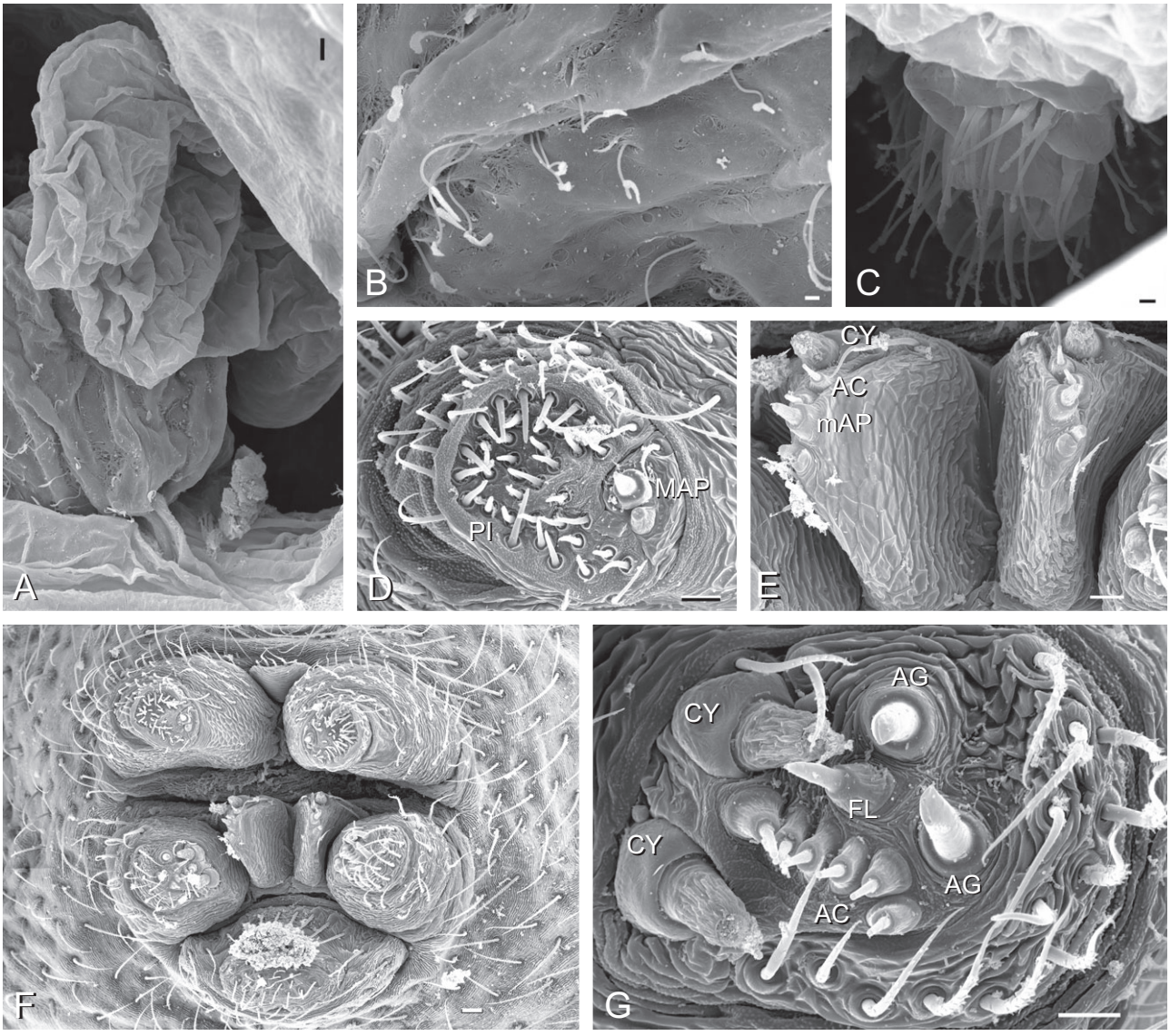


**Figure 16.** ***Pinkfloydia harveii*** **sp. nov.**, female. A, fertilization duct detail. B, epigynum dorsal, cuticular glands ductiles. C, copulatory duct detail. Spinnerets: D, ALS; E, PMS; F, spinnerets overview; G, PLS. Abbreviations: AC, aciniform gland spigots; AG, aggregate gland spigots; ALS, anterior lateral spinnerets; CY, cylindrical gland spigots; FL, flagelliform spigot; mAP, minor ampullate gland spigot; MAP, major ampullate gland spigot; PI, piriform gland spigots; PLS, posterior lateral spinnerets; PMS, posterior median spinnerets. Scale bars: A, D, E, G = 10 μm; B, C = 2 μm; F = 20 μm.

*Female (paratype, AUSTMUS 93/2124):* Total body length 4.51. Cephalothorax 1.86 long, 1.16 wide, 1.15 high. Sternum almost as long as wide; 0.77 long, 0.70 wide. Abdomen 2.65 long, 2.15 wide, 1.86 high. Coloration pattern and eyes distribution as in males. Sternum slightly more elongated than in males; 0.77 long, 0.70 wide. Abdomen wider than in males, which gives it more rounded appearance (Fig. 10A, B, D). Chelicerae shorter and more robust than in male, with smooth cuticle (Figs 10C, 14E). Clypeus height 1.40 times one AME diameter. Legs brown-yellowish; femur I 1.83, 0.98 times the length of the cephalothorax. Epigynum well sclerotized, dark brown (Figs 8F, 10D, 15D–E). Epigynal plate flattened, with numerous cuticular pores (Fig. 15D, E, G). Remains of a 'resinous' secretion forming a genital plug are visible around the edges of the epigynum (Fig. 10E). Copulatory ducts well chitinized, opening on the ventral side of the epigynum and entering the spermathecae at their base (Figs 8G, H, 15F, 16C). Fertilization ducts membranous, originating very close to the copulatory duct entrance in the spermathecae but much

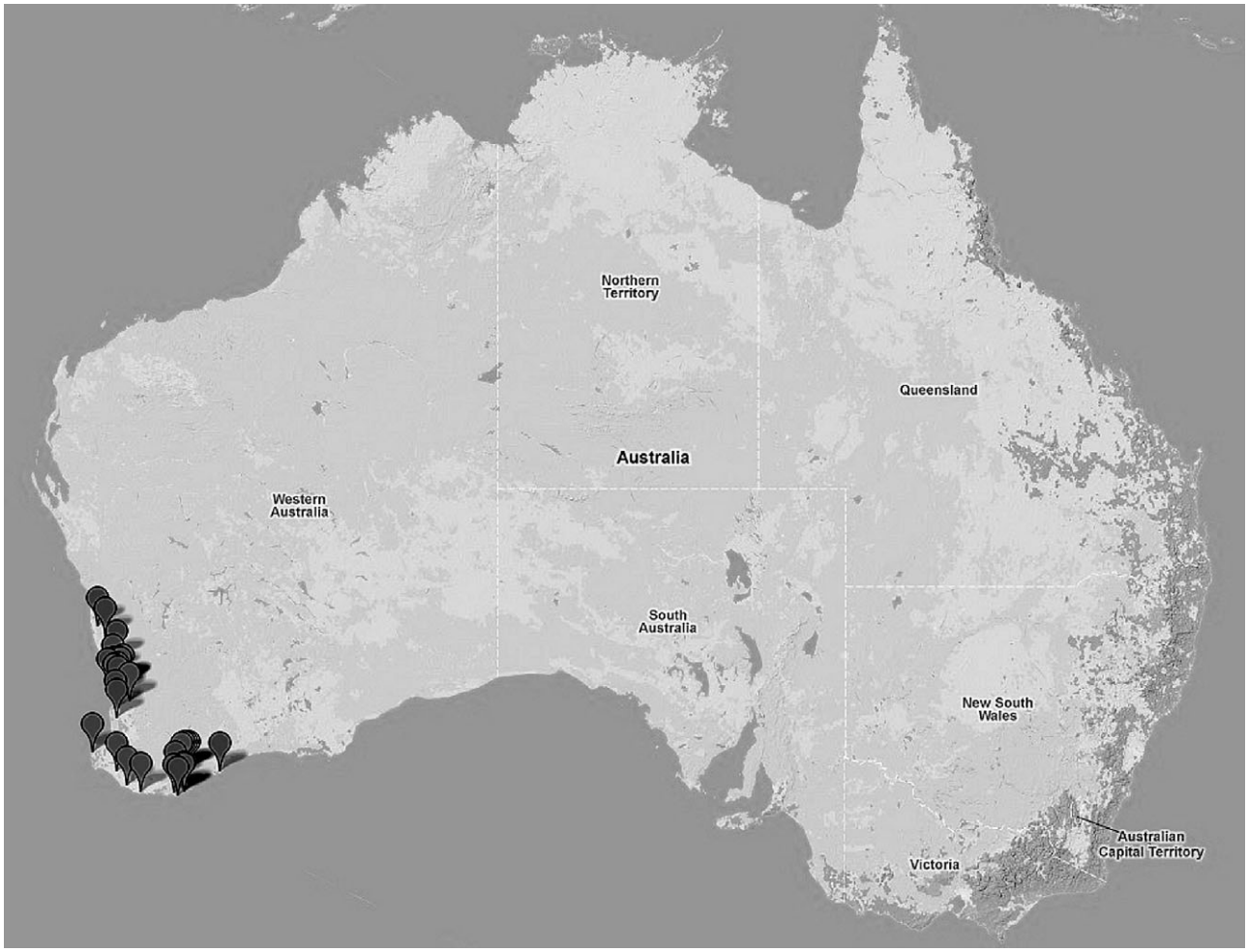


**Figure 17.** Map of the collection records of ***Pinkfloydia harveii*** **sp. nov.**

wider than it (Figs 8G, H, 15F, H, 16A). Spermathecae oval, weakly sclerotized, and sack like (Fig. 15F, H).

*Variation:* Male cephalothorax ranges in length from 1.36 to 1.61 ($N = 7$). Female cephalothorax length varies from 1.68–186 ($N = 14$). Male total body length ranges from 2.77 to 3.75 ($N = 7$). Female total body length ranges from 3.54 to 4.51 ($N = 14$). The male abdominal tubercle varies in height and length, in some specimens being very short, which gives the distal edge of the abdomen a more rounded appearance.

*Natural history:* Very poorly known. Many of the specimens that we studied were collected by pitfall traps. We photographed the webs of four juvenile specimens of *P. harveii* in the Walpole area (Darling Range). Their horizontal webs were built on the leaf litter in a disturbed area and had a maximum frame width between 52 and 92 mm. These orbs were relatively densely spun, as they had many radii (17–28, mean 22, $N = 4$), lack split radii, and have numerous spiral turns (Fig. 11). The hub is closed and the temporary spiral is removed in the final web (see Fig. 11D). We observed one of the webs being built at night time.

*Distribution:* Southern Western Australia (see map in Fig. 17).

*Additional specimens studied:* Australia, Western Australia: 1 female, Chesapeake Road at Gardner River, 34°48′S, 116°11′E, 1.v.1990, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2079); 1 juvenile (juv.), Perth Airport, site PA5, 31°58′03″S, 115°58′11″E, 10.v.–20.vi.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2084); 1 juv., Talbot Road Reserve, site TR2, 31°52′24″S, 116°02′52″E, 24.vi.–28.vii.1993, Harvey, M. S.,

Waldock, J. M. Leg. (AUSTMUS 93/2088); 1 male, Talbot Road Reserve, site TR3, 31°52′25″S, 116°03′03″E, 24.vi.–28.vii.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS 93/2089); 1 juv., Kings Park, site J(E1), 31°58′S, 115°50′E, 26.iii.1981, UWA Zoology students, and B. Y. Main Leg. (AUSTMUS T66615); 1 female, Mt Cooke, 32°25′S, 116°18′E, 24.iv.1992, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS T66616, used for SEM); 1 male, Carabooda area, A. Lombardo's property, un-named cave, YN-515, twilight zone, 31°35′S, 115°42′E, 22.v.1999, Foulds, R. Leg. (AUSTMUS T66617 used for SEM); 1 juv, Stirling Range National Park, Toolbrunup Peak Track, scree slope, 34°24′S, 118°04′E, 31.iii.1993, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS T66618); 1 female, Stirling Range National Park, S. of Bluff Knoll, 34°23′S, 118°15′E, 1.v.1996, Harvey, M. S., Waldock, J. M., Main, B. Y. Leg. (AUSTMUS T66620 used for dissection and SEM); 1 juv., Glenbourne, S. of Gracetown, site 5, 33°53′S, 115°00′E, 18.iv.–20.iv.1998, Marsh, L. *et al*. Leg. (AUSTMUS T66622); 1 juv., Karri Valley Resort, 34°26′S, 115°51′E, 21.x.1997, Waldock, J. M. Leg. (AUSTMUS T66623). 3 juv., forest near Tinglewood Cabins, 34°54′51.0″S, 116°43′50.9″E, elevation 185 m, G. Hormiga Leg. (GH0111, one of the specimens sequenced); 1 female, Talbot Road Nature Reserve, 31°52′24″S, 116°03′04″E, 29.viii.2006, Waldock, J. M., Edward, K. Leg. (AUSTMUS T79005); 2 juv., Jandakot Airport, site JK1, 32°05′36″S, 115°52′39″E, 4.v.–6.vii.1995, Waldock, J. M., Harvey, M. S. Leg. (AUSTMUS T98587); 1 juv., Jandakot Airport, site JK1, 32°05′36″S, 115°52′39″E, 21.ii.–4.v.1995, Waldock, J. M., Harvey, M. S. Leg. (AUSTMUS T98588); 1 juv., Perth Airport, site PA6, 31°58′05″S, 115°58′05″E, 6.i.–18.iii.1994, Harvey, M. S., Waldock J. M. Leg. (AUSTMUS T98589); 1 juv., Woodman Point, site WO2, 32°07′50″S, 115°45′28″E, 04.xi.1994–19.i.1995, Waldock, J. M., Harvey, M. S. Leg. (AUSTMUS T98590); 1 juv., Woodman Point, site WO1, 32°07′47″S, 115°45′23″E, 19.i.–21.iii.1995, Harvey, M. S., Waldock, J. M. Leg. (AUSTMUS T98591); 1 female, Rottnest Island, near Lake Timperley, 32°00′23″S, 115°31′11″E, 13.vi.2007, Rix, M. G. Leg. (AUSTMUS T98592); 1 male, 1 female, Porongurup National Park, deep gully west of Waddy's Hut, 34°40′55″S, 117°50′55″E, 29.iv.2008, Rix, M. G., Harvey, M. S. Leg. (AUSTMUS T98593); 1 male, Boonarring Nature Reserve, off Wannamel West Road, 31°10′27″S, 115°50′57″E, 15.vi.2007, Rix, M. G.Leg. (AUSTMUS T98594); 2 males, 1 female, Austin Bay Nature Reserve, E. of Peel Inlet, end of Beacham Road, 32°36′42″S, 115°47′11″E, 12.vi.2007, Rix, M. G.Leg. (AUSTMUS T98595); 1 female, Sand Patch Beach Reserve, Cuthbert, W of Roberts Road, 35°01′59″S, 117°47′47″E, 18.iii.2008, Rix, M., Harvey, M. S. Leg. (AUSTMUS T98596); 2 males, 1 female, S. of Bremer Bay, near Yate Road, 34°24′10″S, 119°22′43″E, 02.v.2008, Rix, M. G., Harvey, M. S., Newell, J. Leg. (AUSTMUS T98597); 1 male, Two Peoples Bay Nature Reserve, Sinker Reef Road, 34°59′12″S, 118°08′56″E, 01.v.2008, Rix, M., Harvey, M. S. Leg. (AUSTMUS T98598); 1 male, Stirling Range National Park, base of Pyongurup Peak, 34°21′54″S, 118°19′44″E, 05.viii.2008, Rix, M., Harvey, M. S. Leg. (AUSTMUS T98599); 1 female, Lesueur National Park, north of Mt Lesueur, 30°09′59″S, 115°12′06″E, 19.vi.2007, Rix, M. G. Leg. (AUSTMUS T98600); 1 female, 1 juv., Torndirrup National Park, Salmon Hole Road, 35°06′07″S, 117°58′03″E, 30.iv.2008, Rix, M. G., Harvey, M. S. Leg. (AUSTMUS T98601); 1 female, Badgingarra National Park, off Bibby Road, 4.4 km W of Brand Highway, 30°29′14″S, Lon; 115°26′05″E, 19.vi.2007, Rix, M. G. Leg. (AUSTMUS T98602); 1 male, Two Peoples Bay Nature Reserve, near Picnic Area, 34°58′27″S, 118°10′42″E, 01.v.2008, Rix, M., Harvey, M. S. Leg. (AUSTMUS T98603); 1 male, Buller Nature Reserve, 9.5 km SW of Waroona, 32°52′04″S, 115°49′43″E, 22.vii.2007, Rix, M. G. Leg. (AUSTMUS T98604); 1 male, Modong Nature Reserve. 1.5 km NE of Rockingham, 32°13′10″S, 115°54′09″E, 5.vi.2007, Rix, M. G. Leg. (AUSTMUS T98605).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

**Figure S1.** The file Pinkfloydia_morphological_dataset.ss provides the morphological matrix for Description of *Pinkfloydia*, a remarkable new genus of tetragnathid spiders from Western Australia, with an expanded hypothesis on the phylogeny of Tetragnathidae by D. Dimitrov and G. Hormiga.

The file is in NONA format and therefore readable by a variety of programs (NONA, TNT, Winclada, Mesquite). The file is provided in this format to optimize portability and can easily be converted with Mesquite if needed.

Characters 1 to 213 are from Álvarez-Padilla *et al.* (2009) and detailed descriptions can be found there.

Character 214 was added to the matrix of Álvarez-Padilla *et al.* (2009) and its definition is as follows: PLS line of modified setae: 0, absent; 1, present; (see character 169 in Dimitrov & Hormiga, 2009).

## APPENDIX

Additional material used for DNA extraction and/or morphological studies

| Species | Locality | DNA voucher code |
|---|---|---|
| *Allende* sp. | Chile, Region X de los lagos, P. N. Puyehue, near Termas Aguas Callientes, 26.2 km E Entre Lagos. 40°44.130′S, 72°18.427′W, elevation *c.* 460 m. 9–12.iii.2008, C. Griswold | GH0889 |
| *Antillognatha lucida* | Dominican Republic, Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth. 18°05′54.8″N, 71°11′22.0″W, 1220 m, 6–9.iv.2005. G. Hormiga, F. Alvarez & S. Benjamin. | GH0240 |
| *Azilia* sp. 834 | Mexico, Chiapas, Ocosingo, Hidalgo Cortés orillas de la Reserva Montes Azules. 16°42′19.1″N, 90°53′08.2″W, EPE 07 145 m. 31.x.2005. L. Lopardo, J. Castelo, F. Alvarez. | GH0834 |
| *Azilia* sp. 838 | Mexico, Chiapas, Ocosingo, Hidalgo Cortés orillas de la Reserva Montes Azules. 16°42′19.1″N, 90°53′08.2″W, EPE 07 145 m. 31.x.2005. L. Lopardo, J. Castelo, F. Alvarez. | GH0838 |
| *Cyrtognatha atopica* | Argentina, Misiones, Cruce Caballero, San Pedro. 26°28′0.012″S, 53°58′0.012″W. 13–16.i.2005, Grismado, Lopardo, Piacentini, Quaglino, and Rubio | GH1075 |
| *Cyrtognatha* sp. 773 | Panama, Prov. Chiriquí: Reserva Forestal Fortuna, Quebrada Honda, 1 ha. PANCODING inventory, 8°45′00.3″N, 82°14′20.7″W, 1135 m, 7–12.vi.2007 | GH0773 |
| *Cyrtognatha* sp. 774 | Panama, Prov. Chiriquí: Reserva Forestal Fortuna, Quebrada Honda, 1 ha. PANCODING inventory, 8°45′00.3″N, 82°14′20.7″W, 1135 m, 7–12.vi.2007 | GH0774 |
| *Diphya spinifera* | Argentina, Tierra del Fuego, Parque nacional Tierra del Fuego, area Lapatalia. 9.i.2003. Col. M. Ramirez and C. D. Haese | GH0837 |
| *Dolichognatha longiceps* | Thailand, Nakhon Si Thammarat Prov., Khao Luang NP, 8°43′25.2″N, 99°40′7.7″E, 355 m, 10–12.x.2003, ATOL Expedition 2003 | GH0544 |
| *Glenognatha* sp. | Panama, Prov. Panamá: P. Nac. Altos de Campana, 8°41′00.4″N, 79°55′47.4″W, 895 m.16.vi.2007 Col. G. Hormiga | GH0759 |
| *Hispanognatha guttata* | Dominican Republic, La Vega Prov., Constanza, Reserva Científica Valle Nuevo, fern forest, 18°41′49.4″N, 70°35′23.7″W, 2274 m, 12–14.iv.2005. F. Alvarez & S. Benjamin. | GH0518 |
| *Mecynometa* sp. | Panama, Campana, 14–19.vi.2007, G. Hormiga | GH0850 |
| *Mesida* sp. | Thailand, Chiang Mai Prov., Doi Chiang Dao, Amphen Chiangdao, below guest house along road, 19°19′13.2″N; 98°49′47.0″E, *c.* 1500 m, 2.x.2003, ATOL Expedition 2003 | GH0535 |
| Metainae sp. 123 | Australia, Tasmania, Cradle Mnt. National Park, Waldheim Cabins, 41°38′20.5″S, 145°56′26.5″E, 3–4.iii.2006, elevation *c.* 926m, G. Hormiga | GH0123 |
| Metainae sp. 124 | Australia, Tasmania, Cradle Mnt. National Park, Waldheim Cabins, 41°38′20.5″S, 145°56′26.5″E, 3–4.iii.2006, elevation *c*. 926m, G. Hormiga | GH0124 |
| Metainae sp. 128 | Australia, Tasmania, Cradle Mnt. National Park, Waldheim Cabins, 41°38′20.5″S, 145°56′26.5″E, 3–4.iii.2006, elevation *c.* 926m, G. Hormiga | GH0128 |
| *Metleucauge* sp. | USA, CA: Siskiyou Co., Marble Mountains, Deep lake Creek off road. 22.68 km W. Fort Jones, 41°36′43.2″N, 123°06′54.8″W, elevation 1140 m. Large, shaded stream in forest, 12–13.vii.2008, G. Hormiga | GH0897 |
| *Mimetus banksi* | Costa Rica, Heredia, near Puerto Viejo, Finca La Selva, elevation 50 m, i.1978, W. Eberhard Leg. (MCZ 77187) | NA |
| *Mimetus banksi* | Costa Rica, San Jose, Bajo La Hondura, 3.v.1995, B. A. Huber Leg. (MCZ 771671) | NA |
| *Mimetus banksi* | Panama, Parque Fortuna, Sendero Km 63, PANCODING inventory 2008 | GH0881 |
| *Mollemeta edwardsi* | Chile, Region X de los lagos, P. N. Puyehue, near Termas Aguas Callientes, 26.2 km E Entre Lagos. 40°44.130′S, 72°18.427′W, elevation *c.* 460 m. 9–12.iii.2008, C. Griswold | GH0888 |
| *Arkys* sp. | New Guinea, McAdam Memorial Park near Wau. 1.iv.1966, G. Bush Leg. (MCZ 77274) | NA |

NA, not applicable.