

The first pararchaeid spider (Araneae: Pararchaeidae) from New Caledonia, with a discussion on spinneret spigots and egg sac morphology in *Ozarchaea*

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Abstract

The first pararchaeid species to be recorded from outside Australia or New Zealand, *Flavarchaea humboldti* n. sp., is described from female specimens collected near the summit of Mont Humboldt, New Caledonia. Morphological and behavioural data are further described for Western Australian species of *Ozarchaea* Rix, with the spinneret spigot morphology of *O. harveyi* Rix imaged under a scanning electron microscope, and the egg sac of *O. westraliensis* Rix described for the first time. Pararchaeid spinnerets possess two major ampullate gland spigots on the anterior lateral spinnerets and no triad on the posterior lateral spinnerets; such a spinneret spigot arrangement does not support the placement of the Pararchaeidae in the superfamily Araneoidea, and further research is needed to test the phylogenetic position of this enigmatic family.

Key words: taxonomy, Nouvelle Calédonie, Western Australia, spinnerets, spigots, egg sac, Palpimanoidea, Entelegynae, Araneoidea

Introduction

The tiny, cryptic spiders of the family Pararchaeidae (Figs 32–34) have long been of interest to araneologists. Their rarity in collections (Rix 2006), combined with their remarkable morphology and unresolved phylogenetic placement, have helped make this family among the most enigmatic of all spider lineages – instantly recognisable and yet central to competing phylogenetic hypotheses within the Araneae. Previously known only from Australia and New Zealand (Rix 2006), the Pararchaeidae include seven genera and 34 described species (Platnick 2009), all characterised by strange ‘snap-jaw’ chelicerae armed with peg teeth and a comb of moveable setae (Figs 22, 25–29). Despite recent revisionary works and a clearer picture of pararchaeid taxonomy and phylogeny (Rix 2005, 2006), new species continue to be discovered, and much remains to be described for this unusual group. The recent discovery of the family on the Pacific island of New Caledonia highlights this problematic gap, and the need for a re-evaluation of the state of pararchaeid systematics.

Like Mecysmaucheniidae, Holarchaeidae and the ‘Assassin Spiders’ of the family Archaeidae (see Wood *et al.* 2007; Wood 2008), pararchaeid spiders possess a remarkable, elevated ocular region on the carapace bearing an unusual cheliceral foramen (Forster and Platnick 1984) (see Figs 5–6, 22–24, 29); a distinctive feature which has generated taxonomic interest and debate since Forster (1949), and which continues to influence the higher classification of this unusual group. While initially described and currently placed with the Archaeidae in the basal araneomorph superfamily Palpimanoidea (Forster and Platnick 1984), mounting phylogenetic evidence has questioned the affinities and phylogenetic placement of the family Pararchaeidae, and recent research suggests that these spiders may be nested within or near the superfamily Araneoidea (a megadiverse lineage including all of the orb-web building spiders and their kin) (see Schütt 2000; Griswold *et al.* 2005; Rix *et al.* 2008). Pararchaeids clearly possess an eclectic mix of features which suggest affinities

with several different higher taxa (e.g. Araneoidea, Palpimanoidea; see above), but no quantitative cladistic analysis has ever rigorously tested the phylogenetic position of this enigmatic group. Central to this problem has been the relatively poor understanding of several key pararchaeid character systems, and the scant inclusion of pararchaeid taxa in higher phylogenetic analyses. Exemplar data and a rigorous understanding of pararchaeid morphology will be critical to future hypothesis-testing within the Entelegynae, and the current study is thus an attempt to bridge some of these informational gaps.

Flavarchaea humboldti n. sp. is the first pararchaeid species to be described from New Caledonia, and the first species of *Flavarchaea* Rix, 2006 recorded from outside Australia. The spinneret spigots and egg sac morphology of species of *Ozarchaea* Rix, 2006 are further described for the first time, and discussed in relation to other entelegyne clades.

Material and methods

All species were described and illustrated from specimens that had been stored in 75% ethyl alcohol. Digital photographs were taken using a Leica MZ16A binocular microscope, and auto-montage images were captured using a Leica DFC500 mounted camera with Leica Application Suite version 2.5.0R1 software. Epigynes were dissected and cleared in a gently-heated solution of 10% potassium hydroxide, and illustrated under a Leica DM2500 compound microscope. For scanning electron microscopy, specimens were dehydrated in 95% ethyl alcohol, air-dried, mounted, and sputter-coated in gold, before being scanned with a Phillips XL30 environmental scanning electron microscope. ArcMap version 9.3.1 (ESRI Inc.) was used to create the map in Figure 11. All measurements are in millimetres, and descriptive terminology follows Rix (2006).

Specimens described in this study are lodged at the Queensland Museum, Brisbane (QMB), the Western Australian Museum, Perth (WAM) and the Muséum National d'Histoire Naturelle, Paris (MNHN).

Taxonomy

Family Pararchaeidae Forster & Platnick, 1984

Genus *Flavarchaea* Rix, 2006

Flavarchaea Rix, 2006: 212. Type species by original designation *Pararchaea lulu* Rix, 2005.

Flavarchaea humboldti n. sp.

Figs 1–11

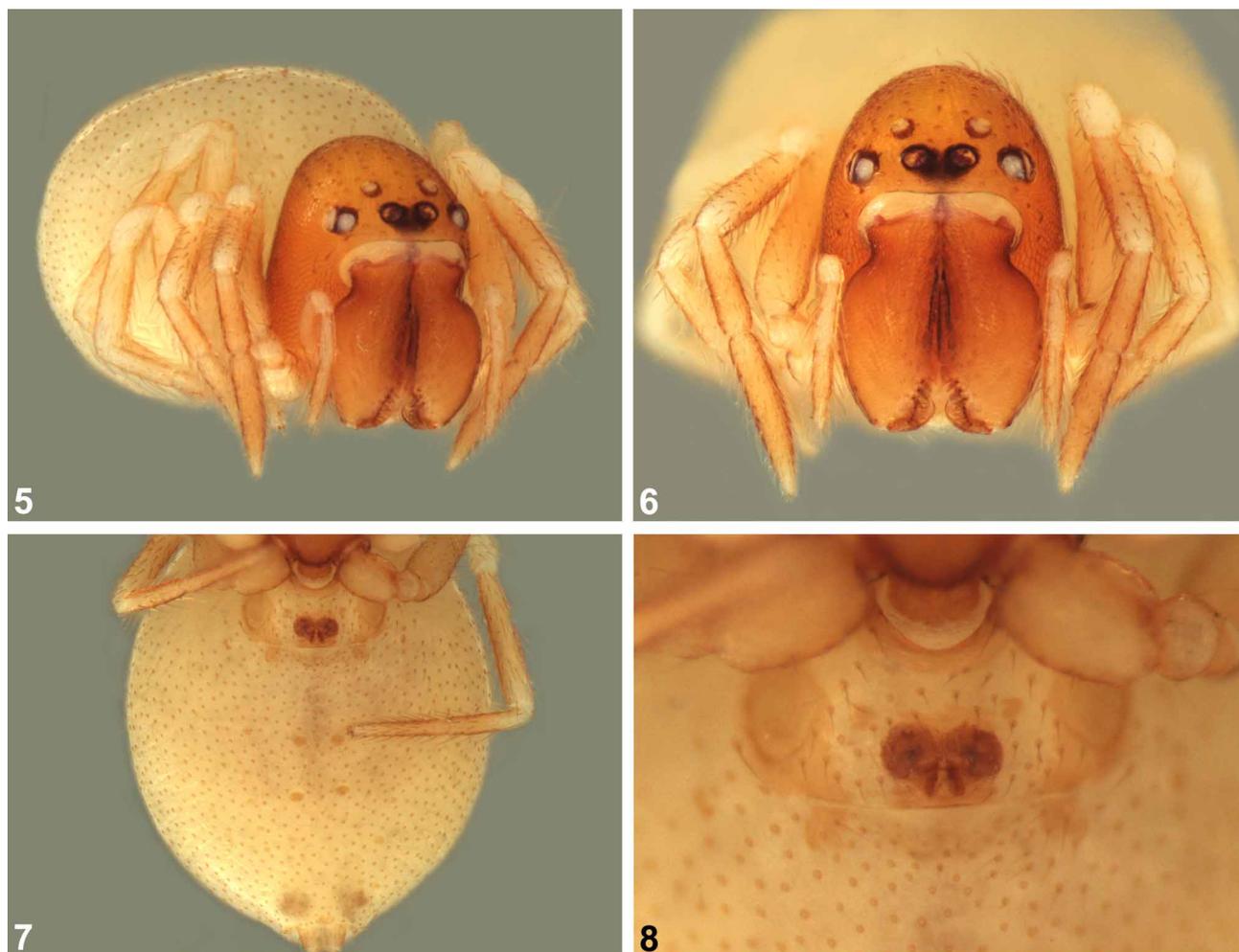
Type material. NOUVELLE CALÉDONIE: *Province Sud*: holotype female, Mont Humboldt, 21°53'S, 166°24'E, 1400 m, pyrethrum fogging trees and logs in moss forest, 6–7 November 2002, G. Monteith, C. Burwell (MNHN). Paratypes: 2 females, same data as holotype (QMB S88155); 1 female, same data as holotype (WAM T99064).

Etymology. The specific epithet is a patronym in honour of the German naturalist, geologist and explorer Alexander von Humboldt (1769–1859) – one of the founding figures of modern geography – after whom the type locality of 'Mont Humboldt' is named.

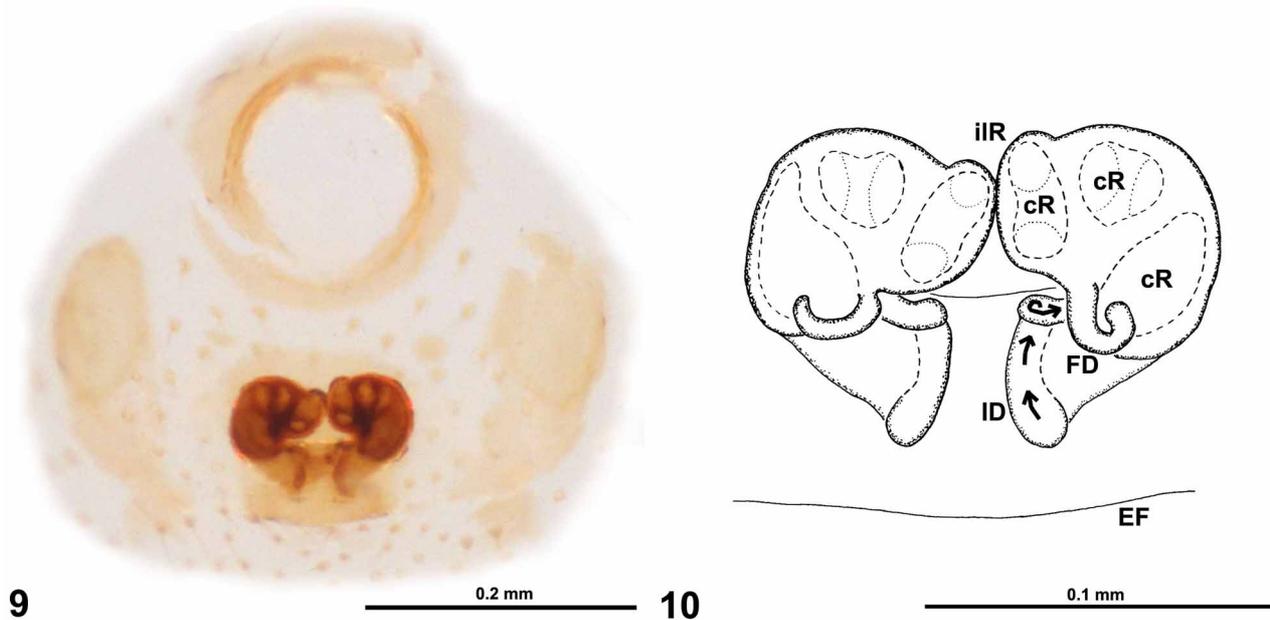
Phylogenetic affinities. Although male specimens are required to definitively diagnose the pararchaeid genera (Rix 2006), this species is extremely similar to Australian species of *Flavarchaea* (e.g. *F. anzac* Rix, 2006) in possessing numerous rows of setae on the dorsal pars cephalica (Figs 1, 3), receptacula with 'nose-like' inner lobes (Figs 9–10), a row of curved, peg-like setae on femur I (e.g. see Fig. 31), and a uniformly pale body colouration (Figs 1–8).



FIGURES 1–4. Holotype female *Flavarchaea humboldti* n. sp. from Mont Humboldt, New Caledonia: 1, habitus, dorsal view; 2, habitus, ventral view; 3, carapace, dorsal view; 4, sternum, ventral view, showing strongly reticulate cuticle.



FIGURES 5–8. Holotype female *Flavarchaea humboldti* n. sp. from Mont Humboldt, New Caledonia: 5, habitus, antero-lateral view; 6, cephalothorax, frontal view; 7, abdomen, ventral view; 8, epigyne, ventral view.



FIGURES 9–10. Cleared, dissected epigyne of paratype female *Flavarchaea humboldti* n. sp. from Mont Humboldt, New Caledonia: 9, receptacula, dorsal view; 10, detail of receptacula, showing ducts. Arrows denote the trajectory of insemination ducts. cR, internal chamber of receptaculum; EF, epigastric furrow; FD, fertilisation duct; ID, insemination duct; iIR, ‘nose-like’ inner lobe of receptaculum.

Diagnosis. Females of *Flavarchaea humboldti* n. sp. can be distinguished from all described Australian species of *Flavarchaea* by the profile of the external epigyne (Fig. 8) and the shape of the receptacula, which are strongly arched and bear oval, anteriorly-directed, ‘nose-like’ inner lobes (Figs 9–10) (see also Rix 2006, figs 58–64, for a comparison with other described species). Males are unknown.

Description. Female (holotype): *Dimensions:* total length 2.11; carapace 0.85 long, 0.52 wide; abdomen 1.31 long, 1.07 wide; leg I femur 0.52 long. *Colour:* carapace, chelicerae, sternum dark tan-yellow; legs dark tan-yellow with lighter cream patellae and distal tibiae; abdomen cream with light brown sigillae and setal sclerotic spots. *Carapace:* rhomboidal in lateral profile, with pars cephalica steeply elevated anterior to coxa III; dorsal surface of pars cephalica convex, sloping down to anterior median eyes from posterior margin (Fig. 5); numerous curved setae present on dorsal pars cephalica and around eyes and clypeus (Fig. 3). *Eyes:* eight present on antero-dorsal aspect of pars cephalica; AME, lateral eyes paired; PME separated by slightly more than twice their own diameter (Figs 1, 3). *Sternum:* longer than wide, posteriorly obtuse (Fig. 4); fused to lateral margins of carapace around petiole and anterior to coxa III, IV. *Labium:* wider than long, fused to anterior margin of sternum; not rebordered. *Maxillae:* directed across labium, distally convergent; serrula a single row of teeth. *Chelicerae:* rectangular, 2x longer than wide, constricted proximally (Fig. 6), protruding from oval foramen in cephalothorax, with pronounced keel extending along pro-ventral margin; peg tooth group A (PTA) with five peg teeth adjacent to fang; peg tooth group B (PTB) with three peg teeth near tip of fang; peg tooth group C (PTC) with three larger peg teeth on pro-dorsal margin adjacent to PTB; paturon also with numerous moveable setae on ventral surface. *Abdomen:* globose, broadly oval in dorsal profile, with two pairs of sigillae dorsally and ventrally (Figs 1–2); two, small, square post-epigastric sclerites situated slightly posterior to epigastric furrow (Figs 7–8). *Spinnerets:* six, posterior to colulus; surrounded dorsally and ventrally by separate, weakly sclerotised strips; posterior tracheal spiracle surrounded by small, oval sclerite. *Legs:* leg formula IV, I, II, III; short (leg I femur-carapace ratio 0.61), three-clawed, covered in short setae; retrolateral femur I with proximal, dorsally-curved row of five stout, peg-like setae; tibiae each with two long trichobothria; metatarsi each with single trichobothrium; tarsal organ capsulate. *Pedipalp:* five-segmented, without claw; tibia with single trichobothrium. *Epigyne:* entelegyne, relatively small, only slightly broader than petiole (Figs 8–10); receptacula ‘comma-shaped’, strongly arched, with complex internal chambers; each

receptaculum with bulbous distal portion bearing oval, anteriorly-directed, 'nose-like' inner lobe (Figs 9–10); fertilisation ducts short, strongly-curved (Fig. 10).

Male: Unknown.

Distribution and habitat. This species is known only from montane rainforest near the summit of Mont Humboldt, 46 km north of Nouméa, New Caledonia (Fig. 11). The type specimens were collected by pyrethrum fogging trees and logs in a moss forest at 1400 m altitude.

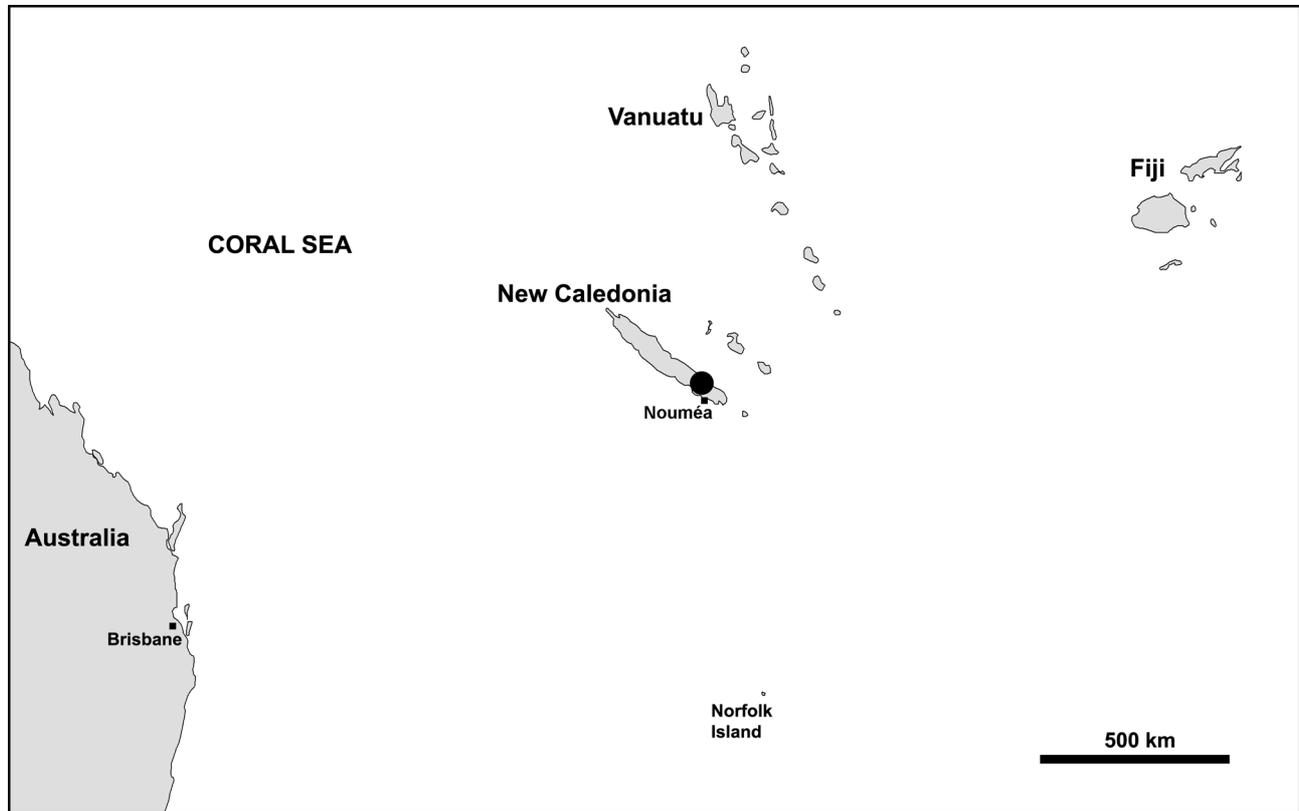


FIGURE 11. Distribution map showing the type locality of *Flavarchaea humboldti* n. sp. north of Nouméa, New Caledonia.

Genus *Ozarchaea* Rix, 2006

Ozarchaea Rix, 2006: 225. Type species by original designation *Pararchaea ornata* Hickman, 1969.

Ozarchaea harveyi Rix, 2006

Figs 12–31

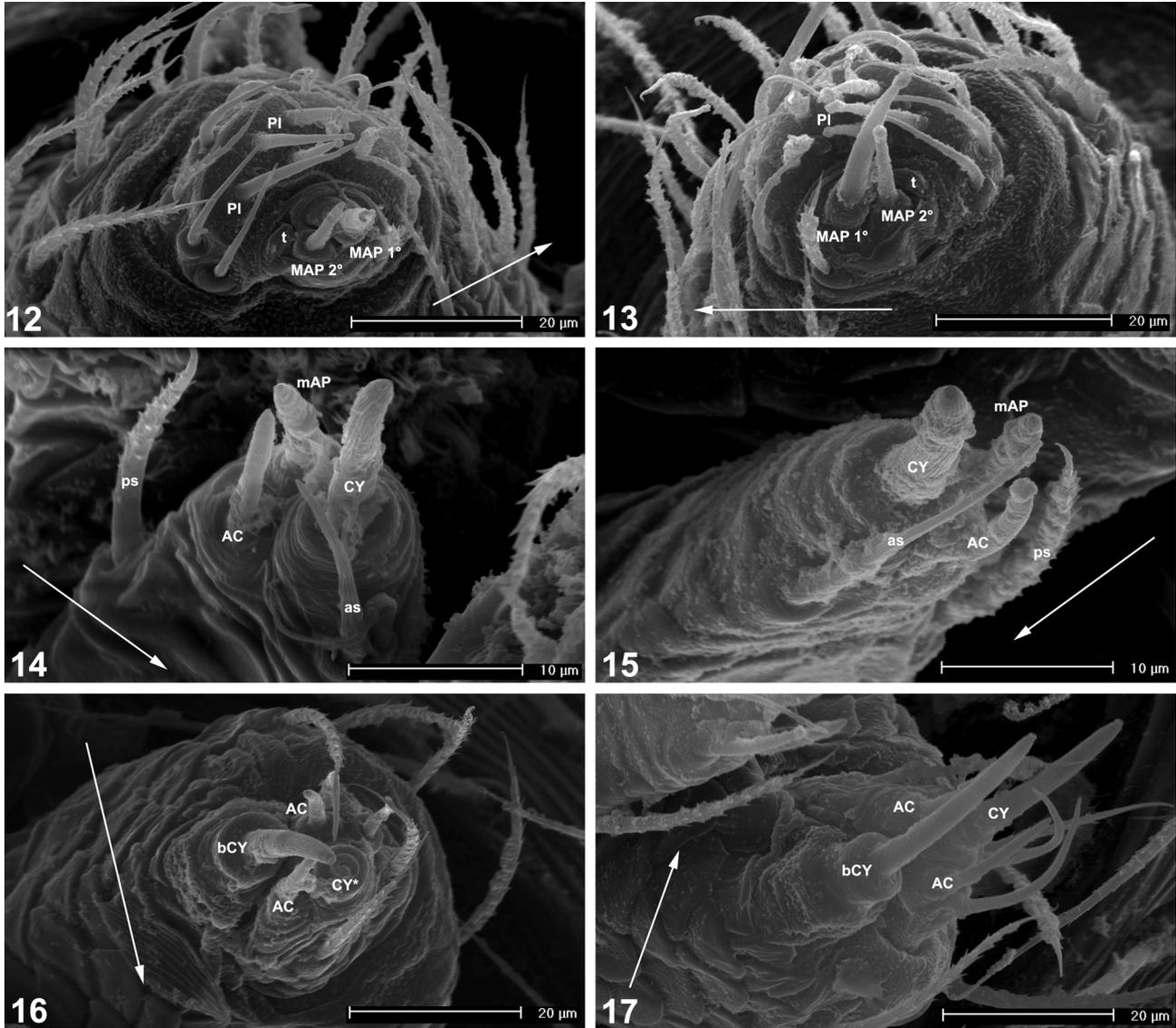
Ozarchaea harveyi Rix, 2006: 229, figs 10, 73–76, 115, 127.

Material examined. AUSTRALIA: Western Australia: 1 female, Huntly Mine, 5 km E. of Banksiadale Dam, 32°39'S, 116°05'E, tree trap on bark, 30 April–2 June 2005, A. Peck (WAM T63656); 1 female, same data except 13 July–24 August 2005 (WAM T64252); 1 female, same data except 25 August–6 October 2005 (WAM T66535); 1 male, same data except 2 June–14 July 2005 (WAM T64113); 1 male, same data (WAM T63897).

Description of spinnerets. Female (spinnerets): Anterior lateral spinnerets (ALS) with two major ampullate (MAP) gland spigots, tartipore and separate, weakly demarcated field of five piriform (PI) gland spigots with reduced bases (Figs 12–13). Posterior median spinnerets (PMS) with cylindrical (CY) gland

spigot and two adjacent, posterior spigots, coded here as an aciniform (AC) gland spigot and slightly larger minor ampullate (mAP) gland spigot (Figs 14–15); posterior mAP gland spigot nubbin and tartipore absent. Posterior lateral spinnerets (PLS) with two CY gland spigots separated by two AC gland spigots (Figs 16–17); basal CY gland spigot with enlarged base; triad absent.

Male (spinnerets): As for female except without CY gland spigots on PMS and PLS (Figs 18–21).



FIGURES 12–17. Scanning electron micrographs of spinnerets of female *Ozarchaea harveyi* Rix from near Banksiadale Dam, Western Australia: 12–13, anterior lateral spinnerets; 14–15, posterior median spinnerets; 16–17, posterior lateral spinnerets. Arrows denote the anterior, mesal direction. Note that the highlighted (*) CY gland spigot in Figure 16 has been broken off at the shaft. AC—aciniform gland spigot; as—anterior seta; bCY—basal cylindrical gland spigot; CY—cylindrical gland spigot; MAP 1°/2°—primary/secondary major ampullate gland spigot; mAP—minor ampullate gland spigot; PI—piriform gland spigot; ps—posterior seta; t—tartipore.

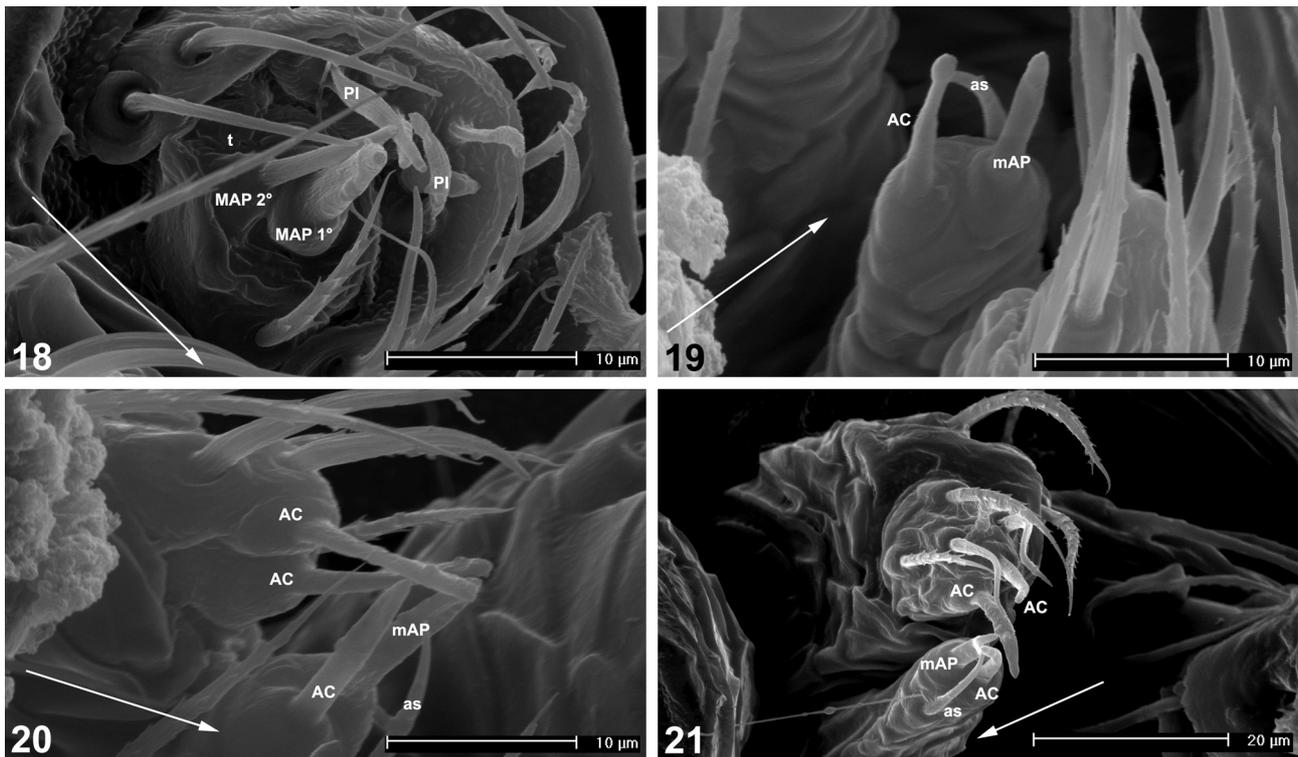
Ozarchaea westraliensis Rix, 2006

Figs 32–35

Ozarchaea westraliensis Rix, 2006: 243, figs 107–110, 119, 127.

Material examined. AUSTRALIA: Western Australia: 1 female, Mount Cooke, 32°25'26.9"S, 116°18'39.0"E, sifting wet leaf litter below 'saddle', 30 August 2009, M. Rix, D. Harms, S. Harms, J.

Waldock (WAM T99059); 1 egg sac, Cottonwood Crescent (formerly 'Tuart Hill') Bushland Reserve, Dianella, Perth, 31°52'S, 115°51'E, 20 August 2006, M. Rix.



FIGURES 18–21. Scanning electron micrographs of spinnerets of male *Ozarchaea harveyi* Rix from near Banksiadale Dam, Western Australia: 18, anterior lateral spinnerets; 19, posterior median spinnerets; 20–21, posterior median and posterior lateral spinnerets. Arrows denote the anterior, mesal direction. AC—aciniform gland spigot; as—anterior seta; MAP 1°/2°—primary/secondary major ampullate gland spigot; mAP—minor ampullate gland spigot; PI—piriform gland spigot; t—tartipore.

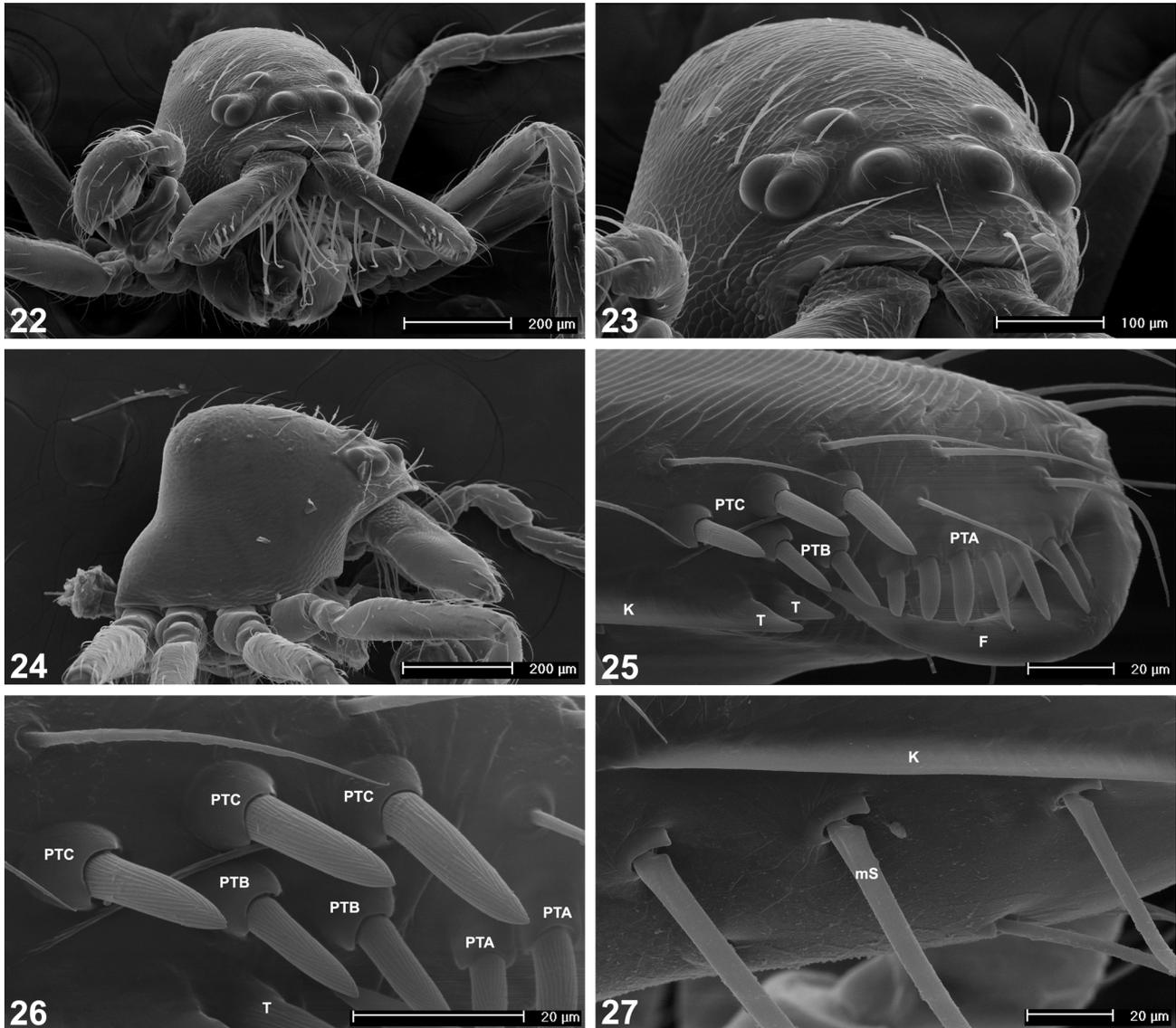
Description of egg sac. Similar in most respects to that described for *Anarchaea raveni* Rix, 2006 (see Rix, 2006, fig. 146), with two discrete protective layers comprising a remarkable silken complex (Fig. 35). Egg sac proper discoid, circular in dorsal profile, attached to substrate. Inner silken layer covering egg sac, attached to substrate around margins, comprised of fine, mesh-like silk. Outer silken layer complex, star-shaped, forming protective three-dimensional 'cap' over inner layer and egg sac.

Remarks. While a female spider was not collected with the described egg sac, *Ozarchaea westraliensis* is the only pararchaeid species recorded from Cottonwood Crescent Reserve, which is also the type locality of this species (Rix 2006).

Discussion

New Caledonian Pararchaeidae. The discovery of a pararchaeid species on New Caledonia represents a significant range extension for the family, although the record is perhaps not surprising given the otherwise Australian and New Zealand distribution of the family (Rix 2006). Several typically 'southern-temperate' spider families (see Platnick 1991) from Australia and New Zealand are well-known from New Caledonia, including species of Anapidae (Platnick and Forster 1989), Migidae (Raven 1985) and Micropholcommatidae (Rix *et al.* 2008). Like the pararchaeid genus *Ozarchaea*, species of *Flavarchaea* are most diverse and widespread in Australia (Rix 2006), with only a single species recorded from outside mainland Australia or Tasmania. It is unknown whether the presence of *Flavarchaea* on New Caledonia is the result of Gondwanan vicariance or dispersal from Australia, but recent studies (see Grandcolas *et al.* 2008) suggest that the latter

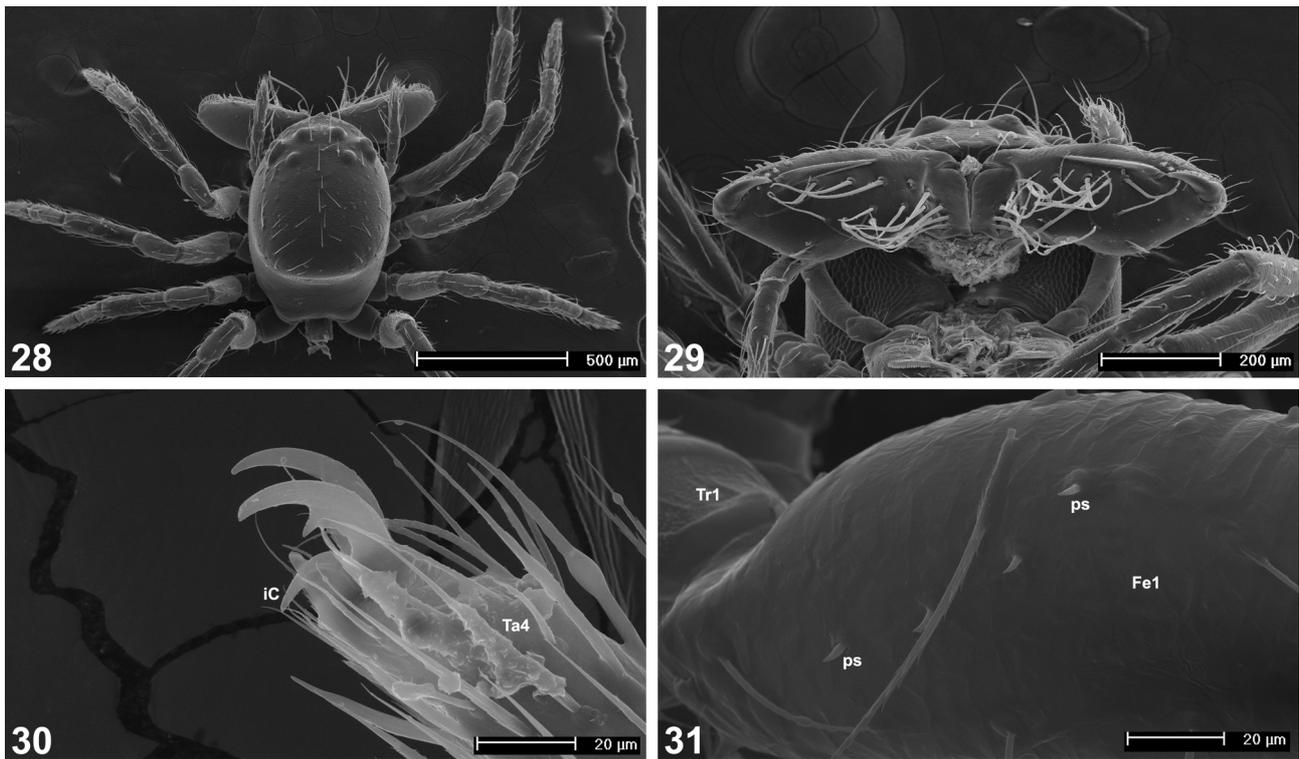
scenario is likely for all terrestrial taxa. Certainly, similar species of *Flavarchaea* are widespread in eastern Australia (Rix 2006, figs 65–66), and an ancestral dispersal event from Queensland or New South Wales seems plausible.



FIGURES 22–27. Scanning electron micrographs of male *Ozarchaea harveyi* Rix from near Banksiadale Dam, Western Australia: 22, cephalothorax, frontal view, showing splayed chelicerae and comb of moveable setae; 23, eyes and clypeus, frontal view; 24, cephalothorax, lateral view; 25, cheliceral dentition, proximal view, showing dorsal stridulatory file, peg teeth and ventral keel; 26, detail of (25), showing peg teeth; 27, left cheliceral paturon, proximal view, showing keel and base of moveable setae. F—fang; K—keel; mS—moveable seta; PTA/B/C—peg tooth group A/B/C; T—tooth.

What is unusual about the presence of *F. humboldti* **n. sp.** on the mountainous south of New Caledonia, is the apparent absence of additional populations or species in other montane habitats on the island. Numerous collecting expeditions over many decades have sampled the spider fauna of New Caledonia, including several visits by American Museum, Queensland Museum and Western Australian Museum staff largely designed to search for tiny spiders in moss and leaf litter microhabitats. These expeditions have revealed a diverse mygalomorph and araneomorph spider fauna, including several genera with species endemic to different mountainous regions (e.g. see Platnick and Forster 1989; Raven 1991; Raven and Churchill 1991; Platnick 1993). To the knowledge of the authors, the newly described specimens from Mont Humboldt are the first

Pararchaeidae ever recorded from New Caledonia, suggesting that the family may be highly restricted or at least extremely rare on the island.



FIGURES 28–31. Scanning electron micrographs of *Ozarchaea harveyi* Rix from near Banksiadale Dam, Western Australia: 28, female cephalothorax, dorsal view; 29, female splayed chelicerae, ventral view; 30, female leg IV claws; 31, male leg I femur, retrolateral view, showing curved row of peg-like setae. Fe1—femur I; iC—inferior claw; ps—peg-like seta; Ta4—tarsus IV; Tr1—trochanter I.

Pararchaeid egg sacs. Egg sacs of Pararchaeidae were first described by Rix (2006), and illustrated for *Anarchaea raveni* from south-eastern Queensland (see Rix 2006, fig. 146). The newly described egg sac of *Ozarchaea westraliensis*, collected from the type locality of that species in Perth, confirms that the remarkable morphology of pararchaeid egg sacs is not restricted to species of *Anarchaea*, and may be a synapomorphy of the family. Like that of *A. raveni*, the egg sac of *O. westraliensis* (Fig. 35) is composed of a remarkable, highly distinctive silken complex overlying the egg sac proper, representing a potentially huge silken investment by the female spider. A female specimen was not collected with the egg sac, suggesting further evidence for the absence of maternal care in Pararchaeidae.

Spinneret spigot morphology of Pararchaeidae. The comparative analysis of spinneret spigot morphology has become a central focus of spider phylogenetics, with many morphological studies highlighting the importance and utility of spinneret data (e.g. Coddington 1989; Platnick 1990; Platnick *et al.* 1991; Hormiga 1994; Scharff and Coddington 1997; Griswold *et al.* 1998; Ramírez 2003; Griswold *et al.* 2005; Lopardo *et al.* 2007; Townley and Tillinghast 2009). Several lineages (e.g. Araneoidea) can be largely defined on the basis of their spinneret morphology (Griswold *et al.* 1998), and thanks to modern studies using scanning electron microscopy, the arrangement of the spinneret spigots is now known for at least one representative of most araneomorph spider families. Pararchaeid spinnerets had been only partially (and very inadequately) illustrated in previous studies (see Schütt 2000, fig. 10C; Rix 2006, figs 36–37), and as a result the cladistic analysis of Griswold *et al.* (2005) could not accurately score some spinneret character states for *Pararchaea* Forster, 1955. With the complete illustration of the spinnerets of *Ozarchaea harveyi* in the current paper (Figs 12–21), these data are available for the first time.



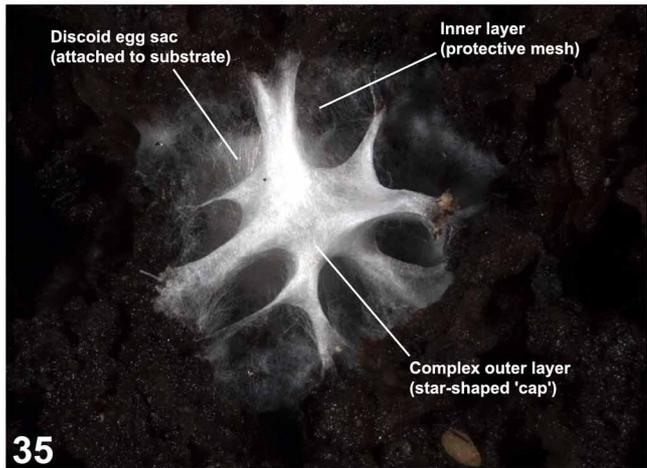
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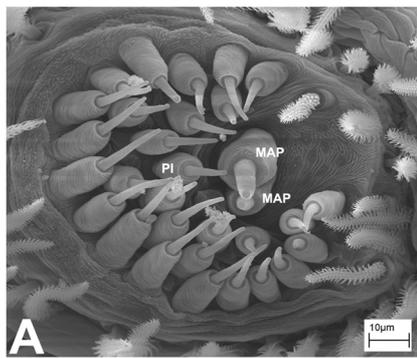
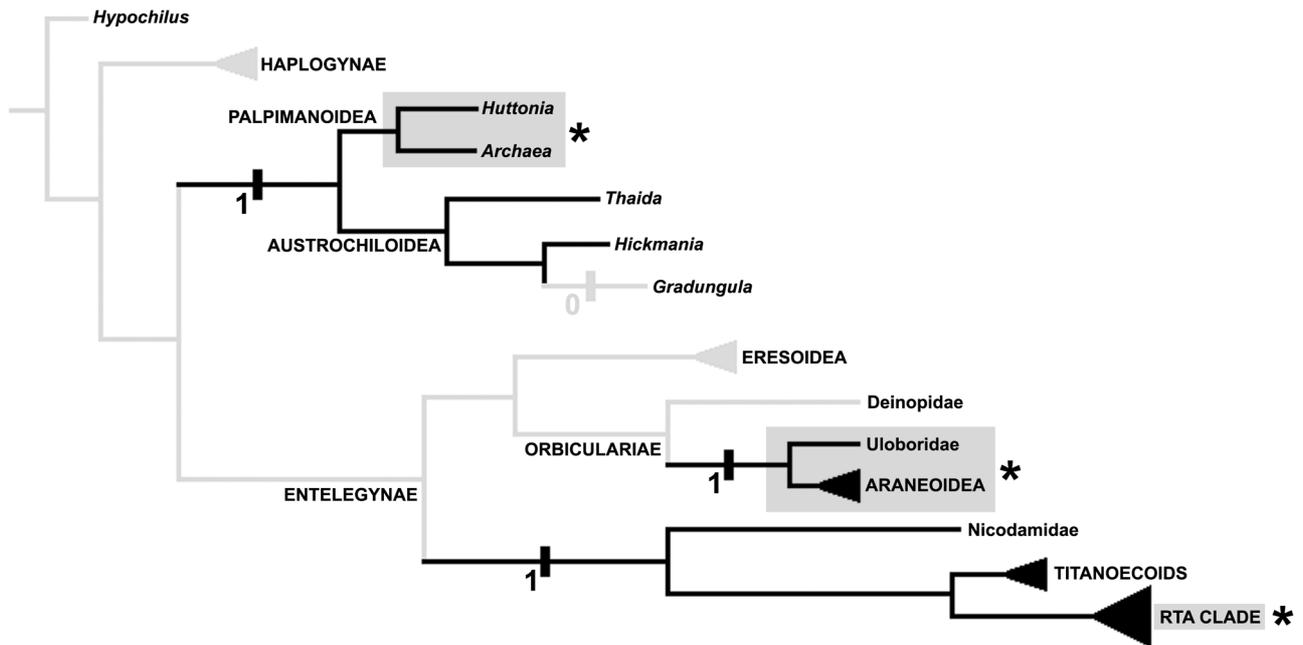
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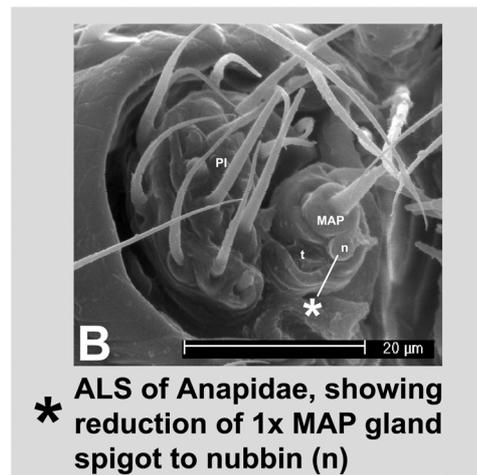
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FIGURES 32–35. Live images of *Ozarchaea westraliensis* Rix: 32–34, female from Mount Cooke, Western Australia, photographed in captivity; 35, egg sac from Cottonwood Crescent Reserve, Perth, Western Australia, showing complex outer layer and star-shaped 'cap'.

Pararchaeid spinnerets are unusual for a number of reasons, and raise yet more questions about the affinities and phylogenetic position of this enigmatic family. The anterior lateral spinnerets (ALS) of *Ozarchaea* and *Flavarchaea* bear two major ampullate (MAP) gland spigots (Figs 12–13, 18; see also Rix 2006, fig. 37), clustered along the inner margin of the ampullate spinning field; the secondary MAP gland spigot is not reduced to a nubbin, and the piriform spinning field is not obviously separated by a deep furrow. A similar reduction in the number of ALS MAP spigots – from three or more to two – is characteristic of most entelegyne taxa, including Palpimanoidea, Austrochilidae, Araneoidea and all higher (i.e. non-eresoid/non-orbicularian) Entelegynae (Griswold *et al.* 2005) (see Fig. 36). Among these four clades, the paired MAP gland spigots of the ALS are further modified in adult Palpimanoidea, Uloboridae, Araneoidea and some RTA clade lineages by the reduction of one MAP gland spigot to a non-functional nubbin (Griswold *et al.* 2005) (Fig. 36). That Pararchaeidae lack this modified ALS nubbin is evidence against their inclusion in the superfamily Araneoidea, and an observation which demands phylogenetic explanation. If members of the Araneoidea, the Pararchaeidae would be the only known lineage that possessed two ALS MAP gland spigots, either by plesiomorphic retention or by secondary reversal. Alternatively, the Pararchaeidae may actually be more closely related to other basal entelegyne taxa, for which the presence of two or more MAP gland spigots on the ALS is plesiomorphic (Fig. 36). Interestingly, the absence of a deep furrow on the ALS of Pararchaeidae, between the ampullate and piriform spinning fields (Figs 12–13, 18), is also extremely unusual for the Araneoidea, although Lopardo *et al.* (2007) noted a similar morphology in Synsphyridae.



A ALS of Titanoecidae, showing 2x MAP gland spigots (State 1)



B * ALS of Anapidae, showing reduction of 1x MAP gland spigot to nubbin (n) *

FIGURE 36. Summary cladogram from the phylogenetic analysis of Griswold *et al.* (2005, fig. 217), showing the optimal tree inferred in that study under implied weights parsimony. Black-coloured branches denote distal lineages which possess only two major ampullate (MAP) gland spigots on the anterior lateral spinnerets (State 1) (illustrated in Titanoecidae, inset A), as opposed to three or more MAP gland spigots (State 0). Shaded, highlighted (*) clades show State 1 taxa that possess a secondarily-reduced MAP nubbin (illustrated in Anapidae, inset B). Note the presence of this ALS MAP nubbin (*) in Palpimanoidea, Araneoidea, Uloboridae and some RTA clade genera. n—nubbin; PI—piriform gland spigot; t—tartipore. Image for inset A courtesy of Charles Griswold and Hannah Wood, used with permission.

The posterior median (PMS) and posterior lateral (PLS) spinnerets are significantly reduced in Pararchaeidae, and unusual in their complement of spigots. The PMS possess an anterior cylindrical (CY) gland spigot in females, and two adjacent posterior spigots in both sexes (Figs 14–15, 19); these posterior PMS spigots are coded here as aciniform (AC) and minor ampullate (mAP) gland spigots, respectively, although determining homology from external appearance alone is difficult (Lopardo *et al.* 2007). A posterior mAP gland nubbin and adjacent tartipore on the PMS – putatively synapomorphic for the Araneoidea but lost in many distal lineages (Griswold *et al.* 1998) – is clearly absent in *Ozarchaea* and *Flavarchaea*. The PLS of Pararchaeidae have only four spigots in females and two spigots in males (Figs 16–17, 20–21; see also Rix 2006, fig. 36; Schütt 2000, fig. 10C), including two CY gland spigots in females and two AC gland spigots in

both sexes. The classical araneoid PLS ‘triad’ – consisting of one flagelliform (FL) and two aggregate (AG) gland spigots – is absent.

As stated by Griswold *et al.* (1998: 7), the absence of the PLS triad could usually be taken as “strong evidence against araneoid affinity”. Unfortunately, however, the cursorial ecology of pararchaeid spiders makes even this interpretation problematic, given that several non web-building araneoid taxa (e.g. kleptoparasitic Mysmenidae, Mimetidae) have lost the PLS triad completely (Griswold *et al.* 1998; Schütt 2000; Townley and Tillinghast 2009). Like Pararchaeidae, the Malkaridae are one of only a few putatively araneoid spider families which are cursorial and no longer dependent on capture webs of any form (although their biology is very poorly known); while lacking AC gland spigots on both the PMS and PLS, species of Malkaridae have perhaps the most similar PLS morphology to species of Pararchaeidae (see Schütt 2000, fig. 10D), and lack any indication of a triad. Clearly, the morphology of a spider’s PLS is at least partly dependent on its ecology, and secondary absence of the PLS triad in Pararchaeidae must therefore be considered as a likely possibility.

Phylogenetic position of Pararchaeidae. What, then, can be said about the likely phylogenetic position of Pararchaeidae, given what is now known about their morphology? What evidence is there to suggest a phylogenetic placement within the Palpimanoidea, or the Araneoidea or the broader Entelegynae?

At a deep phylogenetic level, the family Pararchaeidae is almost certainly a member of the Entelegynae, and not a member of the otherwise basal, haplogyne superfamily Palpimanoidea. Griswold *et al.* (2005) provided morphological evidence to this end, in a preliminary cladistic analysis of basal and cribellate entelegyne spiders (see Griswold *et al.* 2005, fig. 217). Rix *et al.* (2008) also provided molecular evidence for the placement of Pararchaeidae within a diverse entelegyne (araneoid) clade, separate to otherwise basal taxa in the Palpimanidae and Mecysmaucheniidae (see Rix *et al.* 2008, fig. 5). While the cheliceral foramen and peg teeth of Pararchaeidae are very similar to those of Arachnidae and Mecysmaucheniidae, this morphology may represent one of the more striking examples of convergent evolution within the Araneae.

For a relationship *within* the Araneoidea, pararchaeids clearly possess a tantalising mix of distinctly araneoid-like features, including a paracymbium on the male pedipalp, squamate cuticle on the spinnerets (Figs 13, 16–17) and serrate setae on the legs. The reduced piriform spigot bases on the ALS (Fig. 12) may be evidence of an affinity with the araneoid ‘reduced piriform clade’ (see Griswold *et al.* 1998), and the enlarged basal cylindrical (bCY) gland spigot bases on the PLS (Figs 16–17) are clearly similar to those of certain Tetragnathidae, Linyphiidae, Pimoidae, Anapidae and Symphytognathidae (see Griswold *et al.* 1998). Lopardo and Hormiga (2008) proposed a ‘clawless female clade’ for distal araneoids lacking a claw on the female pedipalp, and female pararchaeids are similar to Cyatholipidae, Synsphyridae and the ‘symphytognathidan’ families in this respect (but lack the elongate leg IV inferior claw which is characteristic of many symphytognathidan taxa; Fig. 30). The overall reduction in the number of PMS and PLS spigots is also reminiscent of Malkaridae and Synsphyridae (see Schütt 2000; Lopardo *et al.* 2007), although in both cases the exact spigot complements are not easily comparable. For a relationship *outside* the Araneoidea, possibly within the higher Entelegynae, pararchaeids possess a number of otherwise plesiomorphic spinneret features with two MAP gland spigots on the ALS (Figs 12–13, 36), a weakly-demarcated groove between the ALS ampullate and piriform spinning fields, and the absence of a PLS triad (Figs 16–17).

Conclusions. The Pararchaeidae are clearly enigmatic spiders which are central to resolving the phylogeny of the Araneomorphae. With the ‘relimitation’ of the Palpimanoidea, and the recognition of a concomitantly ‘expanded’ Araneoidea, pararchaeid species must be included in future phylogenetic analyses of araneoid or basal entelegyne taxa. Additional research is needed to explore the phylogenetic position of this unusual family, and the conflicting character systems so typical of Pararchaeidae must be tested using a cladistic approach.

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