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Notes on the Ant-mimic Genus *Anatea* Berland (Araneae: Theridiidae) and Two New Species from Tropical Australia

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ABSTRACT. The taxonomic history of the New Caledonian myrmecomorph spider, *Anatea formicaria* Berland (Hadrotarsinae: Theridiidae) is summarized, new records are presented and the female is figured for the first time. Two new species provisionally assigned to the genus are described from north-eastern Australia, *A. monteithi* Smith sp. nov. and *A. elongata* Smith sp. nov. Some undescribed *Anatea* species occurring on New Caledonia are shown, and aspects of hadrotarsine anatomy and ant specialization are discussed.

KEYWORDS. Anatea formicaria; myrmecomorphy; myrmecophagy; New Caledonia; Queensland; taxonomy

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The New Caledonian hadrotarsine spider, *Anatea formicaria* Berland, 1927, is thought to be a morphological ant mimic, or myrmecomorph (Berland, 1927; Reiskind & Levi, 1967; Cushing, 1997). Myrmecomorphs are especially prevalent in families such as Salticidae and Corinnidae (Cushing, 1997) but there are few in Theridiidae, with only five species in four genera listed by Cushing (1997; the sixth species listed appears to be a lapsus). Whilst most myrmecomorph spiders gain

the "extra" body section (a "petiole") as well as sometimes a postpetiole from constrictions in the cephalothorax or abdomen and / or colour (Reiskind, 1972), *A. formicaria* is unusual in that the primary modification is to the pedicel, which is not only elongated, but has an ant-like "node" (Figs 1, 5). Most hadrotarsines have not been thought of as particularly ant-like, although there are certain aspects of the anatomy of many species that could aid them hiding among

ant corpses—as recorded for a "Dipoena sp." regarded as a myrmecophile (Cushing, 1997). The adaptations of A. formicaria are therefore particularly striking. Associated behavioural traits that enhance an ant-like appearance, such as running on six legs and holding the front legs aloft like antennae, are common among better known myrmecomorph taxa, but we have found no field observations of the behaviour of A. formicaria in the literature.

Many spiders in the subfamily Hadrotarsinae have been noted to feed on ants. Cushing (2012) lists 10 hadrotarsine taxa as myrmecophages (plus "other *Euryopis* spp"). Indeed, Liu et al. (2016) based on a phylogenetic analysis, found that ant feeding is ancestral for the subfamily, though based on relatively sparse taxon sampling. They also found that: (a) subfamily Hadrotarsinae originates about the same time that ants become noticeably abundant in the fossil record (c. 55–45 Mya); (b) there is a strong correspondence between the abundance of ants and the diversity and abundance of hadrotarsines through evolutionary time; and (c) there is a similar correspondence in modern biodiversity inventories (Liu et al., 2016). Finally, the small, flexible chelicerae with sickle-shaped fangs, suggested by Reiskind & Levi (1967) to possibly indicate an ant-specialized diet, are found in most hadrotarsine taxa. Nevertheless, for the majority of species, like A. formicaria, we have no field observations. Our own observations of Australian hadrotarsines hunting, and with prey support the suggestion that many, if not all taxa are primarily myrmecophagous. Since species of Anatea possess similar cheliceral modifications to the known hadrotarsine myrmecophages, they may also feed on ants, or similar prev.

Berland came across the specimens he described as *Anatea* among ants along with some other ant-mimicking spider taxa in the collection of myrmecologist Ernest André (1838–1911). He surmised that although no doubt André knew these specimens were spiders, the original collector had probably mistaken them for ants whilst collecting. Then, as now, arachnologists recognized that ant mimicking spiders occur in several families (and are especially prevalent in Salticidae; Cushing, 1997). However, spiders of several genera that we now recognize as being unrelated were then commonly considered to belong together in the Clubionidae. Berland accordingly placed his monotypic genus *Anatea* there, in subfamily Micariinae, and suggested a relationship with *Micaria* Westring, 1851, a genus now included in the Gnaphosidae (World Spider Catalog, 2017).

Anatea remained in the Clubionidae until its affiliations with Euryopis Menge and Dipoena Thorell were recognized and it was transferred to Theridiidae (Reiskind & Levi, 1967). In this paper Reiskind & Levi described a male, which they attributed to A. formicaria, although we now realise this identification was incorrect (see below). However, no female Anatea has ever been figured despite being included in the original description by Berland (1927). The female of A. formicaria was erroneously characterized as being a

web-building non-mimic by McIver and Stonedahl (1993), and Cushing (1997) overlooked Berland's description and listed the female as unknown. But as described by Berland (1927), and shown here (Figs 5–7), it is similar to the male but with reduced scuta.

An ongoing review of Australian Hadrotarsinae has found two new species in northern Queensland that possess certain characters of *Anatea*, and in particular, they have an elongate pedicel that is currently diagnostic for the genus. The new species we describe are, however, somewhat tentatively placed here until further analyses are completed and, hopefully, the unknown male of one species is found. Here we figure the correct male of the New Caledonian *Anatea formicaria*, and also figure a female of that species for the first time. We describe the two new species from north-eastern Australia as *Anatea monteithi* sp. nov. and *Anatea elongata* sp. nov. We also provide a brief introduction to some of the New Caledonian *Anatea* diversity awaiting researchers.

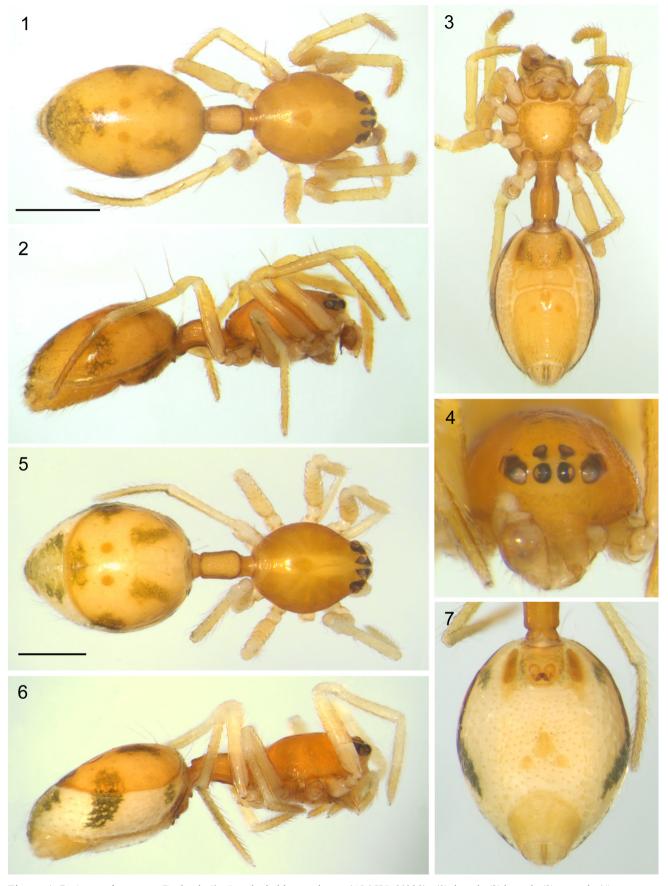
Methods

Specimen examinations, measurements and drawings were made using an Olympus SZ16 microscope, fitted with graticule and camera lucida. All measurements are in millimetres. Multiple photographs in different focal planes were taken using a Leica MZ16 microscope fitted with Spot Flex 15.2 Mp camera and layers combined using HeliconFocus 5.3 software. Plates were composed using Adobe Photoshop Elements. Maps were created using ArcGISt software by Esri (www.esri.com). Square brackets enclose notes added to original specimen record information. Specimen preparations for scanning electron microscopy were passed through an alcohol series (75–100 %), critical point dried and mounted on wire or pins before coating with gold and viewing using a Zeiss Evo LS15 SEM incorporating a Robinson backscatter detector. Details of female genitalia were usually drawn from an excised epigynum, briefly cleared in lactic acid if necessary.

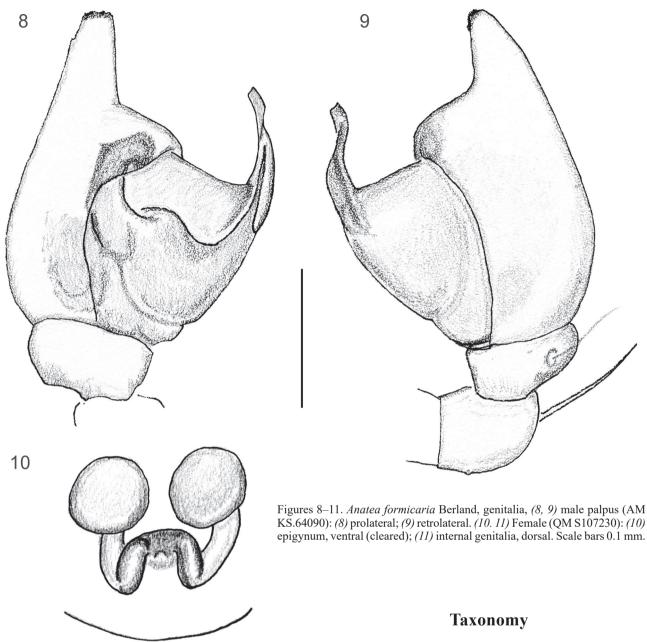
Abbreviations

All examined specimens are from Australian collections as indicated by the following: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth.

Morphological abbreviations: *AME* anterior median eye; *ALE* anterior lateral eye; *Co* conductor; *Cy* cymbium; *E* embolus; *ES* embolus spire; *FD* fertilisation duct; *ID* insemination duct; *MA* median apophysis; *PME* posterior median eye; *PLE* posterior lateral eye; *Sp* spermathecae; *ST* subtegulum; *T* tegulum; *TR* retrolateral tegulum rim; and *TTA* theridiid tegular apophysis.



Figures 1–7. *Anatea formicaria* Berland, (1–4) male, habitus and eyes (AM KS.64090): (1) dorsal; (2) lateral; (3) ventral; (4) prosoma, frontal. (5–7) Female, habitus and opisthosoma (QM S34107): (5) dorsal; (6) lateral; (7) ventral. Scale bars (1, 5) 0.5 mm.



Family Theridiidae Sundevall, 1833

Subfamily Hadrotarsinae Thorell, 1881

Anatea Berland, 1927

Anatea Berland, 1927: 53–55. Type species Anatea formicaria Berland by monotypy.

Diagnosis. Spiders of genus *Anatea* exhibit several typical hadrotarsine characters, e.g., sperm duct entering embolus counter-clockwise, cheliceral promargin without teeth, shortened cheliceral base, long slender cheliceral fang, palmate female palpal claw, grouped flat-tipped sensory setae on tarsus I (Agnarsson, 2004). They differ from many other hadrotarsine genera by having only one main pair of spermathecae and carapace not elevated, and differ from all known hadrotarsine genera by the extended and sometimes modified pedicel.



Anatea formicaria Berland

Figs 1-12, 42

Anatea formicaria Berland, 1927: 55, figs 1–7. Not species figured by Reiskind & Levi, 1967: 21, figs 1–6 (misidentification, we refer this to sp. "J5", Fig. 41).

Diagnosis. **Male**: From other New Caledonian species shown in Figs 38–41, 43 by pedicel and carapace morphology and careful comparison of palp, particularly embolus length. From Australian species, leg I longer than leg III, pedicel with "node", cymbium with extended apex, ventral abdomen with ventral plates (but note male of *A. elongata* sp. nov. is unknown). Female: from undescribed New Caledonian species by general morphology (as male) and details of genitalia; from Australian species by leg I longer than leg III, pedicel with "node", dorsal scutum present.

Type material (not examined). $1 \circlearrowleft \text{type}$, $1 \hookrightarrow \text{cotype}$, New Caledonia. Found by Berland (dried) in the collection of ants of Ernest André. Berland does not state what he did with the specimens.

Other material examined. NEW CALEDONIA: 1♀ QM S34107, Rivière Bleu, Parc.6, 22°05'S 166°40'E, 160 m, 9–22. iv.1987, L. Bonnet de Larbogne, J. Chazeau & A. & S. Tillier, Malaise trap, rainforest sassafras; 1♂ QM S34113, Rivière Bleu, Parc.7, 22°05'S 166°40'E, 170 m, 25.xi–8.xii.1986, L. Bonnet de Larbogne, J. Chazeau & A. & S. Tillier, Malaise trap; 1♂ 1♀ QM S20728, Mt Koghis, 22°11'S 166°32'E, 500 m, 23–24.v.1987, R. Raven, rainforest, general and night collection; 1♀, QM S107230, Pic d'Amoa, N slopes, 20°58'S 165°17'E, 500 m, 27.xi.2003–30.1.2004, G. Monteith, with *Pheidole* sp. ant, flight intercept trap, SC11482; 1♂ KS.64090, Mt Panie, 20°38'S 164°46'E, 6.vi.1996, M. Moulds; 1♀ WAM T86527, Col de Rossettes, 21°27'S, 165°28'E, 11.ii.1993, Harvey, M.S., Platnick, N. I., Raven, R.J., rainforest litter.

Size range. Male (n = 3). Carapace range, 0.75-0.80. Total length 2.05-2.15. Female (n = 3). Carapace range, 0.83-0.92. Total length 2.40-2.55. Berland (1927) gives the total length as 2.2 mm for the species. See Berland (1927) for full male description.

Distribution. Recorded from mountainous rainforest sites across the main island of New Caledonia (Fig. 12).

Notes. The habitus and genitalia of *A. formicaria* male and female are figured for comparison with the Australian species. Figure 1 is repeated as Fig. 42 to compare with other New Caledonian species.

Whilst Berland (1927) admitted his hypothesis that A. formicaria was a myrmecomorph could not be verified, he pointed out that it was found in a collection of ants and that the original collector had probably mistaken it for an ant; unfortunately, he did not (apparently) record which species or genera of ants the spiders were placed with in the collection. However, he comments (p. 53) that the spiders would match species of either Pheidole or Monomorium, both genera being well-represented in the New Caledonian ant fauna: En étudiant les Fourmis de Nouvelle-Calédonie, on trouve même sans trop de peine que l'Araignée se rapprocherait beaucoup d'un Pheidole ou d'un Monomorium, genres qui y sont très bien représentés.

Reiskind & Levi (1967) suggest different candidates as a model for the species they identify as *Anatea formicaria*

(which we have re-identified as a closely related species, "J5", see Figs 41, 42), they write: "Anatea formicaria is an accurate mimic of the small myrmicine ant Chelaner croceiventre (Emery), 2.6 mm long, which has been collected at the same locality as the spider. The color pattern (dark brown anterior and light, yellow-brown posterior) of both is quite rare in ants and is also found in specimens of Xiphomyrma tenuierius Emery, 2.9 mm. long, and a species of *Lordomyrma*, 4.8 mm long, two myrmicine ants found in the same area of rain forest (E. O. Wilson, pers. comm.)." The colour description given above, does not match the specimens we have seen of either A. formicaria or "J5", in which the cephalothorax is only slightly darker than the yellow-amber ground colour of the abdominal scute (see Figs 41, 42). This difference may be due to time since preservation or could represent colour polymorphism within the species "J5", as is recorded in some other myrmecomorphs (see examples in Cushing, 1997). Berland's original description of A. formicaria (1927) gives colouration of cephalothorax, pedicel and abdominal scuta as "light reddish fawn" ("fauve rougeâtre clair") but this is of minimal help as these were dried specimens of uncertain age.

Three of the Anatea samples we have examined each contain a single ant, which we deduce may have been included by collector or sorter of the specimens as a putative model. All three ants are of similar appearance (but may not be conspecific) and are from the genus Pheidole. The Pheidole specimens are of pale golden colour, similar to A. formicaria or our species "J5" (and possibly similar to juveniles of species "J1"). All these three Anatea species occur together: QM S10730 and OM S10732 that now contain A. fomicaria and species "J5", respectively, were separated from QM S88025, which now contains species "J1"; QM S88026 contains adults and a juvenile of species "J1" and a subadult A. ?formicaria. Of note is the size of the ants, which at c. 1.6 mm total length are considerably smaller than adult *Anatea* of either similarly coloured species, and slightly smaller than the sub adult male *Anatea* spp. included in two of the samples.

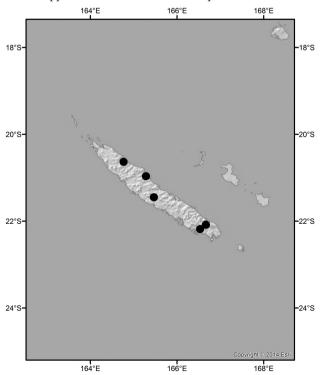


Figure 12. Recorded localities of *Anatea formicaria* Berland in New Caledonia.

Anatea monteithi Smith sp. nov.

Figures 13–24, 31, 35–37

Holotype ♀ QM S25842, Mt Formartine South, 10 km N Kuranda, [16°43'S 145°37'E, Queensland, Australia] 700 m, 23.xi.1990, G. Monteith, G. Thompson, pyrethrum trees & logs. Paratypes. 1♂, WAM T99420, Daintree NP, Alexandra Range lookout point, 16°14'15"S 145°26'10"E, 6.iv.2009, K. Edward, J. Waldock, sieved litter (WT 11); 1♂, AM KS.126452, Black Mountain Rd, start of track to Mt Formartine, 16°45'04"S 145°36'21"E, 425 m, 6.xii.2008, G. Milledge, H. Smith, beat, sweep; [right palp on SEM stub s/1049; right leg I on s/1050]; both Queensland, Australia.

Other material examined (Queensland, Australia): 1\$\varphi\$ AM KS.116502, Lake Barrine, E of Yungaburra, 17°15'S 145°38'E, 31.viii.2011, M. Zabka, B. Patoleta; [abdomen on SEM stub s/1048, legs I, IV on s/1047; epi cleared]. 1 juv. AM KS.7647, Thornton Peak, N of Daintree, 16°10'S 145°22'E, Nov. 1975, M. Gray, leaf litter sample (RF survey site 40). QM 1 juv. (unregistered), Bellenden Ker Ra, 0.5 km S Cable Tower 7, 17°16'S 145°51'E, 500 m, 25–31.x.1981, Earthwatch/Qld Museum, rainforest, pyrethrum logs, stones, tree trunks.

Etymology. The species is named for Geoff Monteith, in recognition of his enormous contributions to the study of Australian invertebrates through his collecting activities for the Queensland Museum.

Diagnosis. From New Caledonian species by leg III longer than legs I and II; pedicel without "node"; male without extended tip to cymbium; from *A. elongata* sp. nov. by pedicel shorter than carapace; female insemination ducts with short conjoined section, entering spermathecae posteriorly (Fig. 22).

Description

Colour (in alcohol) (Figs 13–19). Cephalothorax, mouthparts, sternum, pedicel and male scutum dark chestnut brown, glossy, except pedicel rugose, female abdomen and parts of male abdomen not covered by scutum dark charcoal grey, slightly paler ventrally, cuticle glossy between sparse but prominent setal bases; dorsal and ventral abdominal apodemes dark brown, obvious. Legs: (female) coxae and trochanters white on legs III, IV, suffused with brownish black on legs I, II; femora pale brown laterally, dark dorsally and ventrally (legs I, II) or vis. v. (legs III, IV), femora legs III, IV with distal white band extending onto proximal patella, traces of same legs I, II; tibiae-tarsi mid-brown proximally to amber brown distally, darkest coloration ventral on anterior legs to retrolateral on leg IV; male legs similar but darker, stronger coloration.

Carapace (Figs 13–15, 18) longer than wide, widest at coxae II, smooth transition to caput; fovea absent; in profile gently domed, highest at coxae I (male WAM T99420 rather flatter than female holotype, other male similar to female); eye group 3/5 carapace width; AME largest (Figs 14, 15) and prominent above slightly concave clypeus, clypeus > 2 × AME diameter in male, slightly lower in female. Labium bluntly triangular (Fig. 16), cheliceral bases shorter than maxillae, flexible with slender, curved fangs. Female palpal claw weakly palmate with three or four large teeth.

Legs: 4312 (holotype female missing both fourth legs but confirmed in female from other material). Legs with sparse dorsal macrosetae on patellae and tibiae (a few visible in Figs 13, 14), hadrotarsine flat-topped setae (see Agnarsson, 2004) present on distal tarsus I, few on II. Pedicel sclerotized, open "S" in lateral view, slightly expanded anterior to apex and constriction at abdominal articulation (Fig. 18). Abdomen egg-shaped, widest anterior to mid-point (Figs 17, 19), constricted by sclerotized band around spinnerets; male with dorsal scutum covering central abdomen but leaving bare small surround of cuticle in dorsal view (Fig. 13), sclerotized around pedicel and genital plate (Fig. 17); female without scutum (Fig. 18) and only small sclerotized band around pedicel insertion (Fig. 19). One pair of dorsal apodemes, prominent in female, embedded in scutum of male; three circular ventral plates/apodemes in both sexes (Figs 17, 19). Genitalia. Male: Cy blunt with two short, broad based tooth-like modified spines (Fig. 21). Palp with Co, TTA, MA (Fig. 35); TR extends ventrally to wrap over the ES, Co arises from apicodorsal T and apicolateral tegular rim (Figs 35, 37). TTA large, arising basally, extending beyond tip of Cy. ES tip resting between TTA and Co. MA base and basal E conjoined proventrally (Figs 35, 36). Female: externally with ridges and grooves in lateral profile (Fig. 23), projecting lip on posterior margin of ovoid fossa. Internally (Fig. 22), ID exit fossa posteriorly and almost immediately turn anterolaterally, entering spermathecae Sp at posterior end. Fertilisation ducts FD exit adjacent to ID, with terminal nodule (possibly degenerate second pair of Sp) before terminal part of FD.

Measurements. Male. Carapace range, 0.81 to 0.88 (n = 2). WAM T99420. Total length, 2.35; carapace length, 0.88; width, 0.62; height, 0.37; abdomen length, 1.25; width, 0.91; pedicel length, 0.50; clypeus height, 0.22. Eyes: AME, 0.10; PME, 0.05; ALE, 0.06; PLE, 0.06; Limbs (femur + (patellatibia) + metatarsus + tarsus = total): leg I, 0.49 + 0.51 + 0.28 + 0.24 = 1.51; leg II, 0.44 + 0.54 + 0.25 + 0.29 = 1.51; leg III, 0.50 + 0.56 + 0.24 + 0.33 = 1.63; leg IV, 0.55 + 0.84 + 0.33 + 0.36 = 2.08.

Female. Carapace range, 0.86 (n = 2). Holotype QM S25842. Total length, 2.88; carapace length, 0.86; width, 0.69; height, 0.33; abdomen length, 1.68; width, 1.32; pedicel length, 0.56; clypeus height, 0.16. Eyes: AME, 0.10; PME, 0.06; ALE, 0.07; PLE, 0.06; Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): leg I, 0.49 + 0.60 + 0.31 + 0.26 = 1.66; leg II, 0.48 + 0.58 + 0.26 + 0.30 = 1.61; leg III, 0.50 + 0.61 + 0.26 + 0.34 = 1.71; leg IV, missing (but longest in female AM KS.116502).

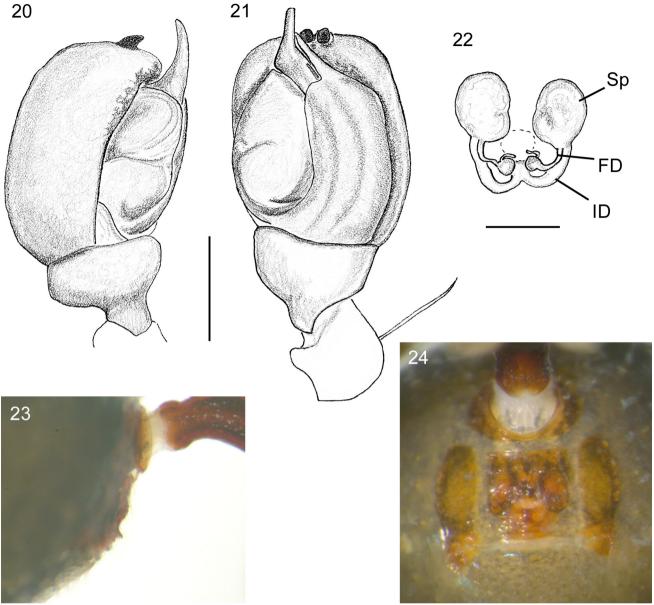
Distribution. Northeast Queensland. Recorded from rainforests, mainly at higher altitudes, between Thornton Peak and Bellenden Ker, and on the Atherton Tableland at Yungaburra (Fig. 31).

Notes. Without observations of behaviour, it is unclear exactly if, or how, ant mimicry is achieved in the Australian species, but as in New Caledonian species, the long pedicel and overall appearance are ant-like. Relative leg length, with both III and IV longer than I or II is unusual and may indicate behavioural modifications.

The tropical rainforests of northeastern Queensland occupied by *A. monteithi* hold an extremely high diversity of ants, with over 66 genera recorded in these areas (*Antwiki*,



Figures 13–19. *Anatea monteithi* sp. nov. (13–17) male, habitus and detail (WAM T99420): (13) dorsal; (14) lateral; (15) frontal; (16) prosoma, ventral; (17) opisthosoma, ventral. (18, 19) Holotype female (QM S25842): (18) habitus, lateral; (19) opisthosoma, ventral. Scale bars (13, 18) 0.5 mm.



Figures 20–24. Anatea monteithi sp. nov. genitalia, (20, 21) male palpus (AM KS.126452): (20) prolateral; (21) ventral. (22–24) Female: (22) internal, dorsal (AM KS.116502); (23, 24) external views (holotype QM S25842): (23) lateral; (24) ventral. Scale bars 0.1 mm. FD, fertilization duct; ID, insemination duct; Sp, spermatheca.

2017). If *A. monteithi* is indeed an ant mimic, candidate models are found in several myrmecine genera. Examples of genera with species in an appropriate size range for adult spiders include *Monomorium*, *Orectognathus*, *Pheidole*, *Pristomyrmex* and *Vombisidris*.

Anatea elongata Smith sp. nov.

Figures 25-31

Holotype ♀ ANIC 42 002257, 12 km SSE Heathlands, 11°51'S 142°38'E [Queensland, Australia], 25.iv–7.vi.1992, T. McLeod, FIT#2, F.I.T., ANIC 1248, closed forest.

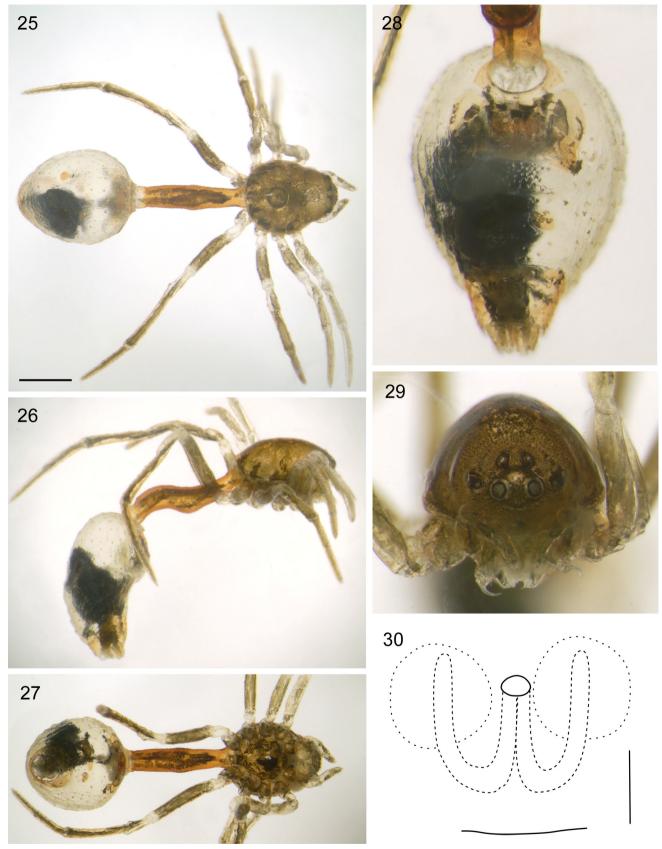
Etymology. The species is named in reference to the pedicel, the longest compared to carapace length so far observed in genus *Anatea*.

Diagnosis. From New Caledonian species by leg III longer than legs I and II; pedicel longer than carapace, without "node"; from *A. monteithi* sp. nov. by pedicel longer than carapace; insemination ducts with long conjoined section, crossing ventral spermathecae to entry point towards anterior (Fig. 30).

Description

Colour (in alcohol). Probably similar to *A. monteithi* but specimen extremely faded, pedicel appears rather reddishbrown; coxae brown, trochanters white on legs III and IV; otherwise apparently similar to *A. monteithi* except extent of abdominal colour cannot be established as only 1 patch remains.

Carapace (Figs 25, 26, 29) generally similar to female of *A. monteithi*; eye group slightly over half carapace width



Figures 25–30. *Anatea elongata* sp. nov. holotype female (ANIC 42 002257). (25–27) Habitus: (25) dorsal; (26) lateral; (27) ventral. (28) Opisthosoma, ventral. (29) Prosoma, frontal. (30) Epigynum and internal structure, ventral (uncleared). Scale bar (25) 0.5 mm, (30) 0.1 mm.

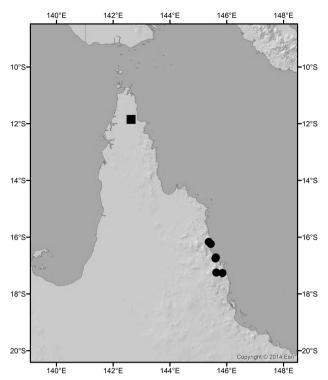


Figure 31. Recorded localities of *Anatea monteithi* sp. nov. (●) and *Anatea elongata* sp. nov. (■) in North East Queensland.

(Fig. 29); eyes and mouthparts similar to *A. monteithi*. Female palpal claw strongly palmate with at least 8 teeth. Legs: 43(12). Pedicel sclerotized, almost straight ventrally in anterior half then arching posteriorly, narrowest anteriorly and thickest, slightly ridged at mid-point, much longer than carapace (Figs 25–27). Abdomen as in *A. monteithi*. Legs missing any visible setae but setal bases suggest macrosetae probably present as in *A. monteithi*.

Genitalia. Externally with fine edge curving anterior to ovoid fossa, but otherwise apparently smooth in profile. Internal genitalia not dissected but visible through cuticle (Fig. 30), ID exit fossa to posterior, running together for 2/3 of distance to genital groove, then turning away from each other and simultaneously turning dorsally, crossing ventral Sp and entering anteroventrally. Sp lying to either side of fossa in ventral view. FD not visible.

Measurements. Female. Total length, 3.04; carapace length, 0.93; width, 0.72; height, 0.38; abdomen length, 1.32; width, 0.90; pedicel length, 1.06; clypeus height, 0.17. Eyes: AME, 0.09; PME, 0.06; ALE, 0.06; PLE, 0.06; Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): leg I, 0.52 + 0.60 + 0.30 + 0.26 = 1.68; leg II, 0.50 + 0.60 + 0.28 + 0.30 = 1.68; leg III, 0.58 + 0.68 + 0.32 + 0.38 = 1.96; leg IV, 0.70 + 0.98 + 0.42 + 0.42 = 2.52.

Male. Unknown

Distribution. Northeast Queensland. Recorded only from the type locality on the Cape York Peninsula (Fig. 31).

Notes. The single female has lost most of its colour and may not be robust enough to excise the genitalia without severely

damaging the specimen. Due to the lack of pigment, the external view is sufficient to see the route of the ducts and this is clearly different from *A. monteithi*.

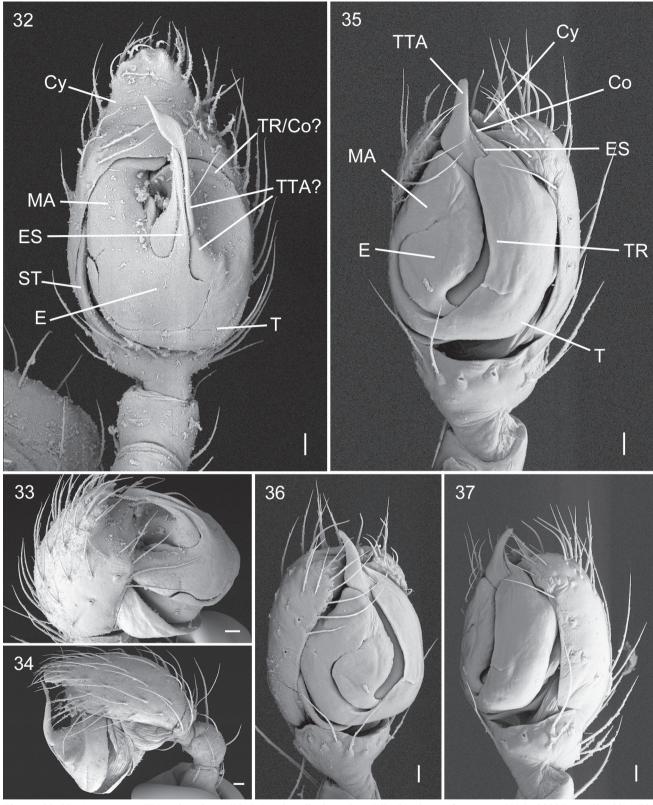
The habitat around the type locality is generally savannah woodland, or "closed forest" on the label, a contrast to the rainforest habitat of *A. monteithi*. The condition of the specimen is not good enough to determine gloss (except carapace) or be sure of colour. However, if the species is an ant mimic the extreme extension of the pedicel, should facilitate the identification of the model in ant samples taken from the area.

Discussion

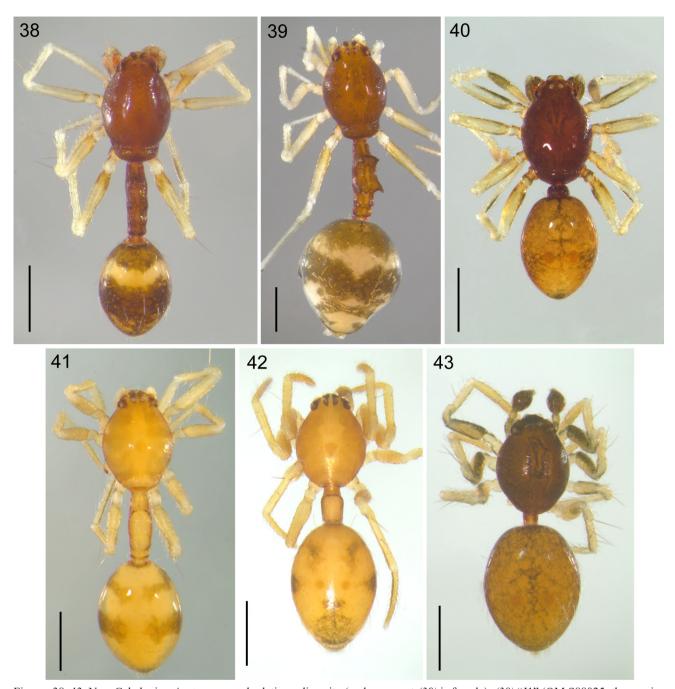
We here describe two new hadrotarsine species (Theridiidae) in the previously monotypic genus *Anatea*. Species of this genus are remarkable in showing what appears to be detailed ant mimicry that, unlike in most other ant mimics, is achieved by the modification of the pedicel that connects the cephalothorax to the abdomen. Similarities of *Anatea* fang morphology to Hadrotarsinae that are known to prey on ants may indicate another example of myrmecophagy in the subfamily, and lends support to a potential coevolutionary history of hadrotarsine and ant lineages (Liu *et al.*, 2016).

The New Caledonian specimens of A. formicaria figured here have been extracted from mixed Anatea material deposited in the Queensland Museum (see Appendix for details). Many of these samples were collected by Geoff Monteith, as was at least one of the Australian specimens. These few samples alone suggest that many more Anatea species, or relatives, await discovery in New Caledonia, including species without elongate pedicels and sometimes with other pedicular modifications that could mimic ants in subfamilies other than Myrmicinae (Figs 38–41, 43). It has also become apparent that the male of Reiskind & Levi (1967) was not in fact A. formicaria, but a rather similar species with a slightly shorter embolus and longer, more stepped pedicel—both species were found among these samples (Fig. 41). New Caledonia is not the focus of the present Australian study, so we merely flag the potential of this fascinating genus for further work there. However, it is noteworthy how abundant and diverse Anatea would appear to be in New Caledonia in comparison to Australia. One mixed New Caledonia sample in the QM collection was found to contain three different species; another included 8 males of one species. Our Australian material, by contrast, is all singletons and it has proven difficult to find more. As well as the unique female of A. elongata, A. monteithi is represented by only four adults and two juveniles. Considering the collecting effort put in by Geoff Monteith over many years in Queensland compared to a few visits to New Caledonia and use of similar collecting techniques, the difference is astounding. Perhaps the species we are describing tentatively as *Anatea* in Australia might be utilising a quite different niche and / or behaviour to their New Caledonian relatives.

There are several differences between the New Caledonian and Australian species that make us question whether *Anatea* is the correct placement for these new species. First, the unusually long rear legs of the Australian species give a leg length pattern of 4312. The typical hadrotarsine leg pattern is 4123, which is also found in the New Caledonian *Anatea* species. The long leg III is therefore highly unusual and



Figures 32–37. Anatea spp. SEM male palpus. (32–34) undescribed species "J1" related to A. formicaria (QM S88025; see Fig. 38): (32) ventral (unexpanded right palp, image reversed); (33) left palp expanded, prolateral; (34) ditto, retrolateral. (35–37) Anatea monteithi sp. nov. right palp, image reversed (AM KS.126452): (35) ventral; (36) prolateral; (37) retrolateral. Scale bars 20 μm. Co conductor; Cy cymbium; E embolus; ES embolus spire; MA median apophysis; ST subtegulum; T tegulum; TR retrolateral tegulum rim; TTA theridiid tegular apophysis.



Figures 38–43. New Caledonian *Anatea* spp. and relatives, diversity (males, except (39) is female). (38) "J1" (QM S88025; the species in Figs 32–34). (39) "J2" (QM S34185; note spines on pedicel). (40) "J4" (QM S37719; with "node" but not greatly elongated pedicel). (41) "J5" (QM S107231; Reiskind & Levi's species). (42) *Anatea formicaria* (AM KS.64090). (43) "J8" (QM S88024; another short-pedicel species with only a slight step, no "node"). "J3" and "J6" missing from sequence are the Queensland species. Scale bars 0.5 mm.

is evident in specimens of both known Australian species. The pedicel, whilst elongate, is simple, lacking the "node" seen in most New Caledonian species; the sclerites of the attachment zone between cephalothorax and pedicel are also subtly different. Finally, the male palp of all the examined New Caledonian *Anatea* species is apparently rather conservative and similar to that of Australian relatives of the New Zealand species "Euryopis" nana (O. Pickard-Cambridge, 1880), such as "Euryopis" petricola (Hickman, 1951). Both of these species were described in the genus *Atkinsonia* O. Pickard-Cambridge, 1879 (replacement name *Atkinia* Strand, 1929). Indeed, *Anatea*, as circumscribed here, is the sister group to these "Atkinia" taxa in a draft phylogeny (unpublished notes). A comparison of Figs 8, 9, 21

and Hickman (1951: figs 27, 33) illustrates the considerable differences in superficial morphology of the Australian *Anatea* species, but also shows significant similarities. With only two male specimens of *A. monteithi* in our possession, it was not deemed desirable to further investigate palpal structure. The usual theridiid sclerites of *A. monteithi* are all identifiable in the definitions used by Agnarsson (2004), whilst those of *A. formicaria*, like "*Euryopis*" petricola, have one of either theridiid tegular apophysis or conductor missing, or the two are fused (see Figs 32, 35). Despite the differences, *A. monteithi* is currently the sister taxon of the representative New Caledonian species "J1" in our draft phylogeny and, although as yet incomplete, this guides our tentative placement here.

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Appendix. List of specimens examined representing species shown in Figs 38–41, 43 (all localities in New Caledonia).

- "J1": QM S37930, 1, Mt Aoupinié, 21°01'S 165°18'E, May–Oct. 1992, R. Raven, E. Guilbert, pitfalls.
- "J1": QM S88025, 8 3, 1 , Pic d'Amoa, N slopes, 20°58'S 165°17'E, 500 m, 27.xi.2003—30.1.2004, G. Monteith, flight intercept trap, SC11482. (1 3 on SEM stub).
- "J1": QM S88026, 1 juv. ♂, 2♀♀, Mt Aoupinié, top camp, 21°11'S 165°18'E, 850 m, 23.xi.2001, G.B. Monteith, sieved litter, QM Berlesate 1045. Sample includes a *Pheidole* sp. ant, and a juv. ♂ *A. formicaria*. (Abdomen except epigyne, and some legs of 1♀ on SEM stub).
- "J2": QM S34185, 12, Rivière Bleu, Parc.5, 150 m, 25.xi-8.xii.1986, L. Bonnet de Larbogne, J. Chazeau & A. & S. Tillier, Malaise trap, rainforest.
- "J4": QM S37719, 1&, Mandjélia, 20°24'S 164°32'E, 13 May–Oct. 1992, R. Raven, E. Guilbert, G. Ingram, pitfalls.
- "J4": QM S60485, 12, Ningua Res. camp, 21°45'S 166°09'E, 1100 m, 12–13.xi.2001, G.B. Monteith, rainforest, sieved litter, QM Berlesate 1039.
- "J4": QM S55109, 1, Mt Do summit, 21°45'S 166°00'E, 1000 m, 21.xi.2000, G.B. Monteith, pyrethrum, trunks and logs, SC9919.
- "J5": QM S107231, 1&, Mandjelia summit, 20°24'S 164°32'E, 750 m, 29.xi.2003–31.1.2004, G. Monteith, flight int. trap. SC11486.
- "J5": QM S107232, 1♀, 1 juv., Pic d'Amoa, N slopes, 20°58'S 165°17'E, 500 m, 27.xi.2003–30.1.2004, G. Monteith, with a juvenile *A. formicaria* and a *Pheidole* sp. ant, flight intercept trap, SC11482.
- "J8": QM S88024, 3&&, Mandjelia summit, 20°24'S 164°32'E, 750 m, 29.xi.2003–31.1.2004, G. Monteith, flight int. trap. SC11486.