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Anonychomyrma inclinata sp. nov. (Hymenoptera: Formicidae): description, biology and interaction with the endangered bulloak jewel butterfly, *Hypochrysops piceatus* Kerr, Macqueen & Sands, 1969 (Lepidoptera: Lycaenidae)

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Abstract The ant *Anonychomyrma inclinata* **sp. nov.** is described. It is an arboreal species, nesting in hollows of living mature trees including *Allocasuarina luehmannii*, *Angophora leiocarpa* and various *Eucalyptus* species. *Anonychomyrma inclinata* can form colonies which are among the most populous recorded for an ant species in Australia, with over 10 000 workers and a total population of 170 000, including all castes. The ant forms extensive trails, forages for insects, collects nectar from a range of flowering plants including many mistletoes and collects honeydew from Hemiptera. The ant's distribution extends from northern inland New South Wales and south central inland Queensland, as far north-east as Home Hill, on the Burdekin River. The ant is an obligate attendant of the immature stages of the endangered bulloak jewel butterfly, *Hypochrysops piceatus* Kerr, Macqueen & Sands, 1969, and the southern population of the sapphire azure, *Ogyris aenone* Waterhouse, 1902. The distribution of *A. inclinata* is much wider than that currently known for *H. piceatus*, suggesting that suitable breeding sites may exist for this rare butterfly in areas not previously surveyed. While *A. inclinata* appears relatively widespread and is able to utilise a wide range of tree species, it is reliant, like *H. piceatus*, on mature live trees and so is subject to threats including vegetation clearance, timber-getting, grazing, and increased drought and fire frequency. Due to its critical importance in the life cycle of *H. piceatus*, any action taken to conserve the butterfly must also consider the importance of preserving healthy populations of *A. inclinata*.

Key words *Allocasuarina luehmannii*, *Anonychomyrma* sp. (*itinerans* group), bull oak, butterfly conservation, colony size, habitat, *Iridomyrmex* sp. (*itinerans* group), myrmecophily, *Ogyris aenone*.

INTRODUCTION

Many ant genera form associations with lycaenid butterflies. While no ant has been shown to be dependent on a butterfly, the level of dependence of butterflies on ants varies widely. For some, the association is obligate, defined as the butterfly being dependent on the ant for reproduction under field conditions (Pierce *et al*. 2002). These associations are typically highly specific, involving only a single genus or species of ant (Eastwood & Fraser 1999; Pierce *et al*. 2002; Orr & Kitching 2010). Of the 57 obligate associations observed between lycaenid butterflies and ants in Australia (Fiedler 2001), 67% (38 associations) are with dolichoderine ants, and a remarkable 28% (16 associations) are with the single genus *Anonychomyrma* Donisthorpe, 1947. Conversely, *Anonychomyrma* species only rarely form non-obligatory associations with butterflies. For example, 29 butterfly associations have been observed with *Iridomyrmex* Mayr, 1862, but only 10 (34%) are obligatory, while for *Anonychomyrma*, obligatory associations comprise 16 (89%) of the 18 associations observed (Fiedler 2001).

One such obligate association has been observed between the bulloak jewel butterfly, *Hypochrysops piceatus* Kerr, Macqueen & Sands, 1969, and a species of *Anonychomyrma* described here as *Anonychomyrma inclinata* sp. nov. The butterfly is a small 'blue', endemic to very limited areas of the southern Darling Downs in inland southern Queensland. The species is listed as endangered under the Queensland *Nature Conservation Act 1992* (Queensland Government 2006), was evaluated under the Queensland Government's species prioritisation framework as having high conservation status (Ponce Reyes *et al*. 2016) and has been assessed through an expert elicitation process as having a greater than one-in-three chance of extinction by 2040 (Geyle *et al*. 2021). The species is currently approved for assessment for listing under the Australian Government *Environment Protection and Biodiversity Conservation Act*

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1999 and the process is due to complete in April 2022 (Australian Government 2019).

Only two confirmed breeding locations for *H. piceatus* are currently known: one near Leyburn in New South Wales and the other in Queensland, north-east of Goondiwindi in Bendidee National Park, the adjacent Bendidee State Forest, and on nearby private land (Sands 2019). The sites are extremely limited in size and are exposed to the impacts of vegetation clearing, rubbish dumping, road widening, grazing, firewood collection, erosion, increased fire frequency, tree felling and removal of timber for turnery (Dunn & Kitching 1994; Sands & New 2002; Sands 2018a; Sands 2019).

The importance of the attendant ant in the life cycle of *H. piceatus* is well documented (Kerr *et al*. 1969; Common & Waterhouse 1981; Dunn & Kitching 1994; Eastwood & Fraser 1999; Braby 2000; Sands & New 2002; Orr & Kitching 2010; Sands 2018a; Sands 2019). The association of the ant with *H. piceatus* is obligatory – without attendance of the immature stages by the ant, the butterfly is unable to breed successfully (Fig. 1; Dunn & Kitching 1994; Eastwood & Fraser 1999; Sands 2018a). *Hypochrysops piceatus* larvae are monophagous, and breeding sites must contain stands of mature bulloak (*Allocasuarina luehmannii*) on which the larvae feed and shelter (Fig. 2; Dunn & Kitching 1994). However, some known breeding sites have become degraded over recent years (Fig. 3). In their extensive survey of the areas around known breeding sites, Dunn and Kitching (1994) noted that butterflies perched exclusively on trees occupied by the ant, and all known

Fig. 1. *Anonychomyrma inclinata* sp. nov. attending a laboratory-raised larva of *Hypochrysops piceatus*. (Larva, ants and image by Peter Sampson.)

Fig. 2. Mixed *Allocasuarina/Eucalyptus/Angophora* forest near Leyburn, Queensland, supporting *Anonychomyrma inclinata* sp. nov. and *Hypochrysops piceatus*.

Fig. 3. *Hypochrysops piceatus* breeding site degraded by cattle grazing, rubbing and trampling, damaging tree trunks and preventing recruitment of seedlings.

breeding colonies were associated with large bulloaks populated by the ant. Ant trails are always present on bulloaks chosen by female butterflies for oviposition (Dunn & Kitching 1994; Sands 2019), and no other ant species have been observed attending the immature stages of *H. piceatus* (Sands 2018a). The ants attending the larvae presumably offer protection from predators and parasites, receiving nutritious secretions in return (Pierce *et al*. 2002; Kaminski *et al*. 2010).

Despite the importance of the ant for the conservation of *H. piceatus* (as well as southern populations of another rare butterfly, *Ogyris aenone*, for which the ant's attendance is also obligatory; Braby 2000), the ant species has not been described previously. The ant was recognised earlier as an undescribed species of *Anonychomyrma* (Dunn & Kitching 1994) but not studied further. To date, authors have referred to the ant as '*Iridomyrmex* sp. (*itinerans* group)' (Common & Waterhouse 1981) or, following the revision of the genus *Iridomyrmex* (Shattuck 1992a), '*Anonychomyrma* sp. (?*itinerans* group)' (Dunn & Kitching 1994) or similar.

The genus *Anonychomyrma* has never been revised, and most species were described over a century ago, several on the basis of unassociated alates only. Many of the early descriptions are brief and three species (*Anonychomyrma myrmex* Donisthorpe, 1947, *Anonychomyrma procidua* Erichson, 1842 and *Anonychomyrma purpurescens* Lowne, 1865) have no extant specimens or images. In addition, recent work in the Queensland wet tropics using genetic and morphological data suggested that the genus includes significant unrecognised diversity; 20 undescribed species were identified (Leahy *et al*. 2020). Under these circumstances, a full revision of the genus prior to the description of a single new species would normally be warranted. However, the need for accurate identification of the ant which attends *H. piceatus* is urgent due to the butterfly's precarious conservation status. Currently, there is no published description of the ant and little information available on its biology and distribution; knowledge of both is fundamental for the development of effective action to conserve *H. piceatus*. The conservation status of the ant itself is uncertain due to the same lack of knowledge and its exposure to the same suite of processes that threaten *H. piceatus*. The ant may also be of reciprocal conservation significance due to its obligate association with *H. piceatus* (Sands 2018b). Under these circumstances, we believe that prioritising the description of the ant, its biology and its distribution is merited.

MATERIALS AND METHODS

Specimens

Ants were collected from known breeding sites of *Hypochrysops piceatus* as well as from areas with similar vegetation in the region. Specimens were mostly collected directly into 70%

ethanol and later dried and point-mounted for examination, imaging and measurement.

Existing mounted material was examined from collections in Australia and all relevant material brought to the Australian National Insect Collection for examination. The following abbreviations are for collections and institutions: ANIC, Australian National Insect Collection, Canberra, Australian Capital Territory; AM, Australian Museum, Sydney, New South Wales; QM, Queensland Museum, Brisbane, Queensland; NHM, Natural History Museum, London; MCZ, Museum of Comparative Zoology, Harvard University.

Imaging and measurements

Point-mounted specimens were imaged using a Leica M205A multifocus imaging system. Images were collated and measured using Leica Application Suite software to a precision of 0.001 mm, reported to 0.01 mm. Measured specimens were selected from the full range of the species distribution where available. The following measurements and derived indices were used after Heterick and Shattuck (2011):

HW – maximum head width measured in full-face view

HL – maximum head length in full-face view, measured from the anteriormost point of the clypeal margin to the midpoint of a line drawn across the posterior margin of the head

EW – maximum eye width

EL – maximum eye length

SL – length of scape (first antennal segment) excluding the basal neck and condyle

ML – mesosomal length measured from the anterior surface of the pronotum (excluding the collar) to the posterior extension of the propodeal lobes measured in lateral view

PpL – length of propodeum measured from the metanotal groove to the posterior extension of the propodeal lobes

PnW (workers) – maximum width of the pronotum measured in dorsal view

MssctmW (reproductives) – maximum width of the mesoscutum measured in dorsal view

MTL – maximum length of the tibia of the middle leg, excluding the proximal part of the articulation which is received into the distal end of the femur

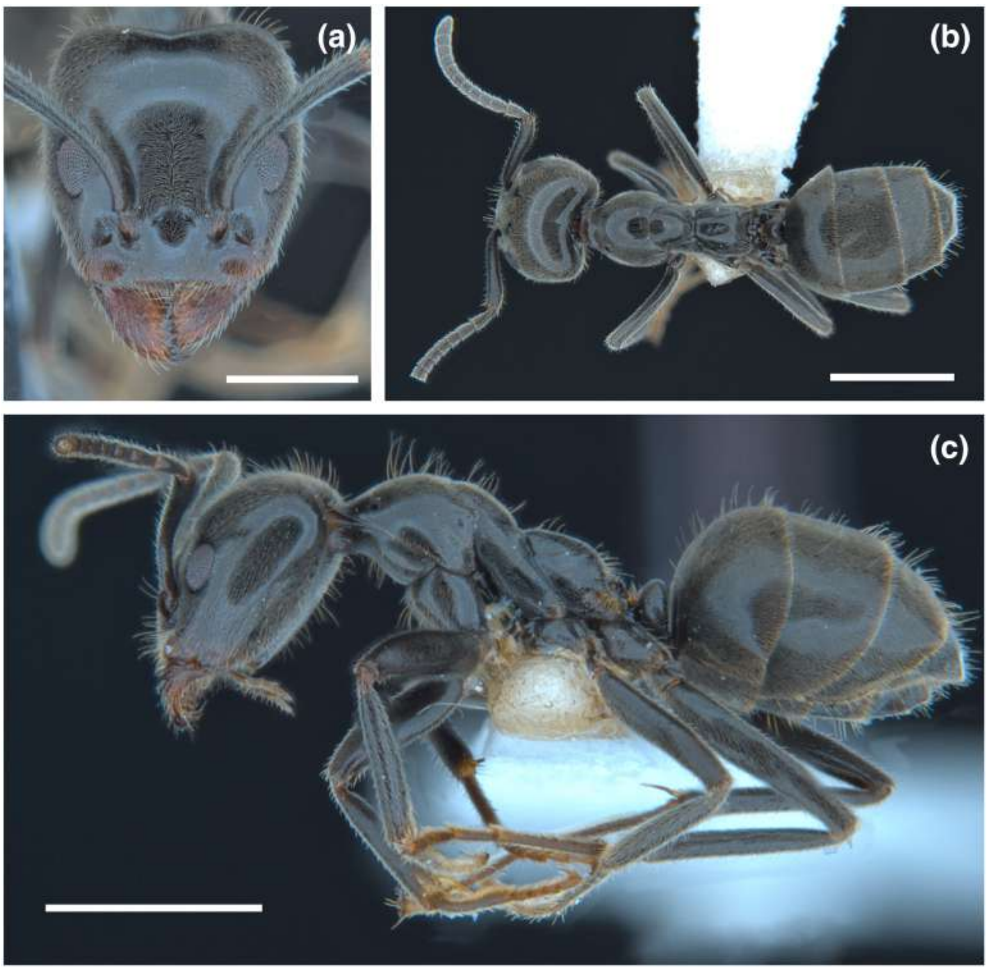

Fig. 4. *Anonychomyrma inclinata* sp. nov. (holotype worker): (a) head in full-face view, bar 0.5 mm; (b) body in dorsal view, bar 1 mm; and (c) body in lateral view, bar 1 mm.

HFL – maximum length of hind femur
PpH – maximum height of propodeum measured tangentially to the line measuring PpL
CI – cephalic index: HW/HL × 100
EI – eye index: EL/HW × 100
SI – scape index: SL/HW × 100

TAXONOMY

Genus *Anonychomyrma* Donisthorpe, 1947

Anonychomyrma Donisthorpe 1947: 588

Remarks

Established on the basis of a single male specimen from Papua New Guinea. The genus was redescribed by Shattuck (1992a,b) and expanded to comprise 26 species and five subspecies, incorporating a number of taxa previously assigned to *Iridomyrmex*. Members of the genus range geographically from southern Australia to Papua New Guinea, Malaysia and the Solomon Islands, typically in forested moist to semi-arid areas, and are generally arboreal (Shattuck 1992b).

Anonychomyrma inclinata sp. nov.

(Figs 4–6)
http://zoobank.org/lsid:zoobank.org:act:A3A3BAC0-E22A-45C5-B17C-8BC85311678A

Material examined

Holotype

☿AUSTRALIA: 'Queensland. Ellangowan Nature Refuge, Leyburn. 27.97986°S 151.622676°E. 439 m. 20 Nov 2018. From bulloak with *Hypochrysops piceatus*. Sands, D. (Coll A)' (ANIC 32-146018 (QM)).

Paratypes

Queensland: ☿1 '28°19′S 150°30′E. Bendidee Nat. Pk. Site 5. 21–22 Mar 2003. 51144. J. Haines. 235 m. Brigalow wilga.

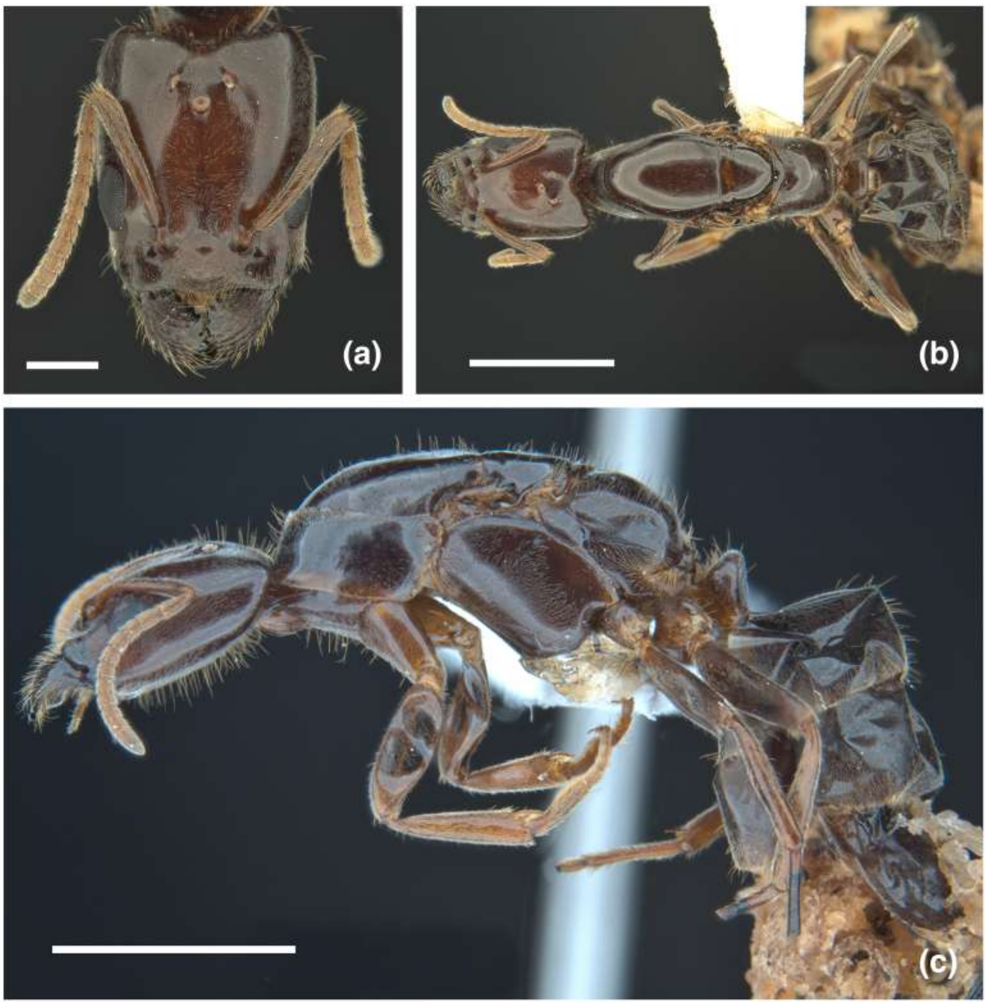

Fig. 5. *Anonychomyrma inclinata* sp. nov. (paratype queen): (a) head in full-face view, bar 0.5 mm; (b) body in dorsal view, bar 2 mm; and (c) body in lateral view, bar 2 mm.

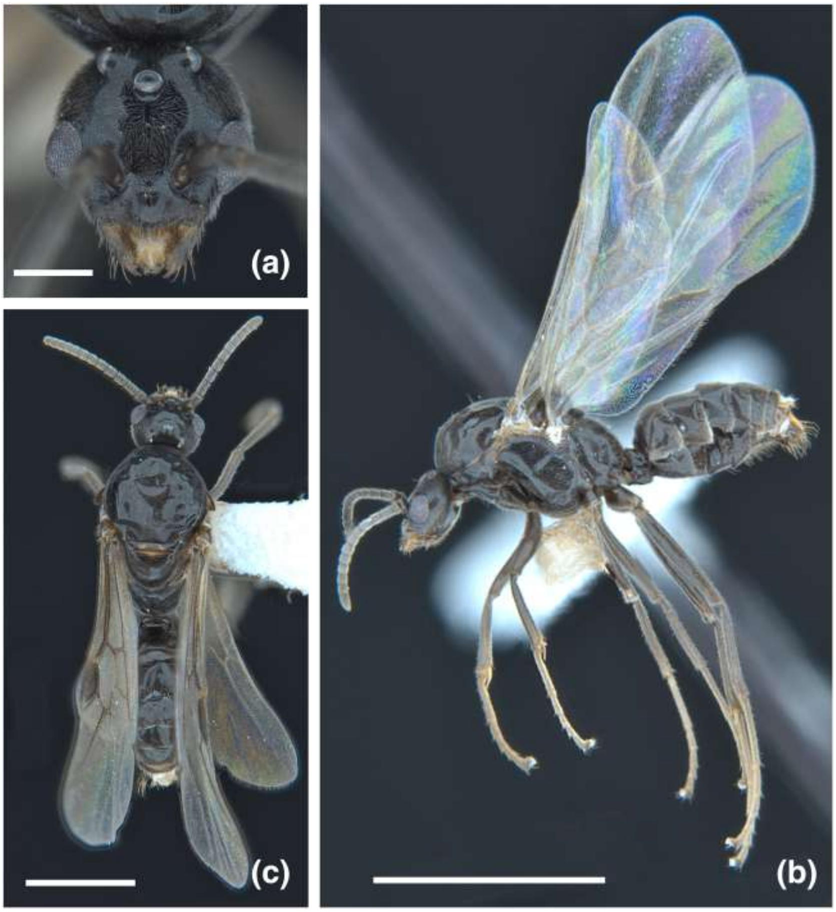

Fig. 6. *Anonychomyrma inclinata* sp. nov. (paratype male): (a) head in full-face view, bar 0.25 mm; (b) body in lateral view, bar 2 mm; and (c) body in dorsal view, bar 1 mm.

Mushroom trap' (QM). ☿1 '24.840°S 147.781°E. 8–14 Oct 2014. Carnarvon Stn Conglomerate Spring. *Eucalyptus crebra* woodland. 865 m. Pitfall. S. Wright, N. Starick. 37076' (QM T231707 (QM)). ☿3 'Ellangowan Nat. Ref. Leyburn. 27.957693°S 151.659129°E. 1 Sep 2019. Casuarina woodland. Trail on *Eucalyptus tereticornis*. J. Lewis & D. Sands Coll #764' (ANIC 32-146127 (ANIC, MCZ)). ☿1 'NE Goondiwindi. 28.308386°S 150.461702°E. 4–6 Nov 2020. Roadside. On Bulloak. Sands, D. WC1' (ANIC 32-158094 (ANIC)).

New South Wales: ☿1 'Dthinna Dthinnawan NP. 28.74203°S 150.86459°E. 1 Nov 2018. On bulloak with scar. Sands, D & Andren, M' (ANIC 32-146122 (AM)). ☿1 'Nth Yetman. 28.74920°S 150.78232°E. 30 Apr 2019. On bulloak and *Angophora*. Sands, D. RT7' (ANIC 32-146120 (NHM)). ☿1 'Nth Yetman. 28.74935°S 150.7820°E. 30 Apr 2019. On *E. crebra* 5 m from bulloak. Sands, D. RT5' (ANIC 32-146124 (ANIC)). ☿1 'Dthinna Dthinnawan Nat. Res. 28.770837°S 150.74524°E. 2 Sep 2019. Casuarina forest. Nest in *Allocasuarina luehmannii*. J. Lewis Coll #772' (ANIC 32-146133 (ANIC)). ♀1 ♂3 ☿3 'North Star Rd, SW Yetman. 28.946984°S 150.729708°E. 5 Feb 2021. J. Lewis Coll #824. Ant nest in termite tunnels in *Eucalyptus* 10 m above ground. Mixed woodland *Eucalypt*, *Allocasuarina*, *Cypress*' (♀1 ANIC 32-158095 (ANIC); ♂3 ANIC 32-159096, 32-159097, 32-159098 (ANIC); ☿3 ANIC 32-158103, 32-158104, 32-158105 (ANIC)).

Other material

Queensland: ☿1 Darling Downs, near Cecil Plains, Dunmore Forest. 17 May 1966. Lee, K.E. (ANIC 32-146135). ☿4 Home Hill, Groper Creek. 22 Jun 1981. Lowery, B.B. (ANIC 32-146136). ☿2 Carnarvon Station, Mt Lyon Rd, 24.845°S 147.763°E. 9 Oct 2014. Wright, S. (QM T231721). ☿3 Carnarvon Station, Mailman Spring, 24.847°S 147.698°E. 16 Oct 2014. Wright, S. (QM T231713). ☿3 Ellangowan Nature Refuge, Leyburn, 27.9812°S 151.62055°E. 22 Aug 2018. Sands, D. (ANIC 32-146118). ☿4 Leyburn, 27.99518°S 151.64802°E. 13 Sep 2018. Sands, D. (ANIC 32-146019). ☿4 Inglewood, 28.14079°S 151.38049°E. 2 Jul 2019. Sands, D. (ANIC 32-146123). ☿8 Leyburn, 27.995019°S 151.647708°E. 1 Sep 2019. Lewis, J. & Sands, D. (ANIC 32-146131). ☿6 Leyburn. 27.995086°S 151.648246°E. 1 Sep 2019. Lewis, J. & Sands, D. (ANIC 32-146132). ☿6 Ellangowan Nature Refuge, Leyburn. 27.959836°S 151.656102°E. 1 Sep 2019. Lewis, J. & Sands, D. (ANIC 32-146129). ☿5 Ellangowan Nature Refuge, Leyburn, 27.982651°S 151.61848°E. 1 Sep 2019. Lewis, J. & Sands, D.

(ANIC 32-146130). ☿5 Isaac River crossing, 80 km SE Nebo, 22.42038°S 148.69691°E. 20 Mar 2021. Braby, M.F. & Beaver, E.P. (ANIC 32-158113).

New South Wales: ☿3 Dthinna Dthinnawan NP, 28.77089°S 150.74553°E. 30 Oct 2018. Andren, M. (ANIC 32-146036). ☿6 Yetman, 28.94635°S 150.73009°E. 31 Oct 2018. Sands, D. & Andren, M. (ANIC 32-146035). ☿4 Dthinna Dthinnawan NP, 28.78603°S 150.73971°E. 24 Apr 2019. Sands, D. (ANIC 32-146121). ☿3 Dthinna Dthinnawan NP, 28.77010°S 150.74552°E. 29 Apr 2019. Sands, D. (ANIC 32-146125). ☿4 Nth Yetman, 28.74958°S 150.78235°E. 30 Apr 2019. Sands, D. (ANIC 32-146117). ☿3 Holdfast Nature Reserve, 28.78295°S 150.76753°E. 30 Aug 2019. Andren, M. (ANIC 32-146126). ☿6 Dthinna Dthinnawan Nature Reserve, 28.770109°S 150.745583°E. 2 Sep 2019. Lewis, J. (ANIC 32-146134). A further 40 specimens were examined from holotype and paratype sites.

Diagnosis

Based on workers, *A. inclinata* can be differentiated from most Australian species by its low, sloping propodeum, which has moderately prominent spiracles and an obtuse angle between the dorsal and declivitous faces, combined with the moderate hairiness of the body. *Anonychomyrma itinerans* Lowne, 1865 (including all subspecies), *Anonychomyrma fornicata* Emery, 1914, *Anonychomyrma malandana* Forel, 1915 and *Anonychomyrma nitidiceps* Andre, 1896 have strongly rounded, domed or protuberant propodea with the dorsal surface relatively short. The more similar *Anonychomyrma gilberti* Forel, 1902 is readily recognised by its longer legs, scapes exceeding the posterior margin of the head by at least their maximum diameter, abundant hairiness and dense downy yellow pubescence, giving a shaggy appearance. *Anonychomyrma biconvexa* Santschi, 1928 has shorter scapes that do not reach the posterior margin of the head; the occipital border is more deeply concave; and the propodeum is evenly rounded, not planar, and less hairy.

From those species for which only queens are described and images are available, *A. inclinata* can be differentiated on the basis of head morphology. *Anonychomyrma longiceps* Forel, 1907 is readily differentiated by its extremely elongate head. The sides of the head of *Anonychomyrma froggatti* Forel, 1902 are straight and very nearly parallel, the eyes smaller, scapes shorter, the centre of the clypeus projects further and the posterior ocelli are more closely set than *A. inclinata*. In *Anonychomyrma arcadia* Forel, 1915, the eyes are smaller and the scapes clearly exceed the upper margin of the posterior ocelli. In addition, the rear margin of the head of *A. inclinata* curves sinuously before reaching the centre of the concavity, a feature not present in any of the other three species.

For two other Australian species, no extant specimens or images exist, and the descriptions are brief. The workers of *Anonychomyrma purpurescens* are described as having purplish iridescence and nesting in the ground (Lowne 1865), neither of which are characteristic of *A. inclinata*. *Anonychomyrma procidua* is based on a queen collected in Tasmania (Erichson 1842) and is described as a black ant with a nearly square head.

Although morphology and distribution made *A. inclinata* unlikely to be among the undescribed Wet Tropics species identified in Leahy *et al*. (2020), this was confirmed by generating standard cytochrome *c* oxidase subunit 1 (COI) barcode data for two individuals of *A. inclinata* for comparison with those of the undescribed Wet Tropics species. Both sequences were identical, and no match was found with the Leahy *et al*. (2020) species, *A. inclinata* having a COI sequence 11.9% divergent from the most similar Wet Tropics species. The COI data for the specimens (ANIC 32-146120) are available on GenBank (accession number MZ313336).

Description

Worker

Head. Posterior margin of head moderately concave in smooth curve or with indistinct central angle; moderately abundant erect to suberect setae on posterior margin in full-face view, setae curved and tapering, length approximately 1× maximum scape diameter. Sides of head convex, curved evenly, with many short suberect setae; pubescence on frons scant to moderate; underlying integument smooth and finely puncticulate. Ocelli absent. In full-face view, eyes set slightly below midpoint of head capsule; eyes shallowly convex, asymmetrical, inner curve stronger than outer; in lateral view, eyes set anteriad of head capsule. Antennae 12-segmented, frontal carinae concave, terminating at about midpoint of eye; scapes slightly clavate, equal to or surpassing the posterior margin of head by less than their maximum diameter. Suberect setae on scape less than half maximum scape diameter, moderately abundant, with underlying pubescence. Anterior clypeal margin flat, with slight undulation and indistinct central concavity. Long, erect setae present on venter of head. Mandibles striate-punctate, orange–brown to dark brown, generally lighter than head; basal margin dentate; masticatory margin with four or five teeth and several denticles; apical tooth approximately twice length of the subapical tooth.

Mesosoma. Pronotum evenly curved in profile. Erect pronotal setae moderate in number, length up to 2× maximum scape diameter. In profile, top of mesonotum level with or slightly raised above pronotum, evenly convex throughout length or slightly sinuous, being more strongly curved anteriorly and flattening towards metanotal groove. Erect mesonotal setae moderate in number, length approximately 1× maximum scape diameter. Metanotal groove shallow. Propodeum sloped; dorsum flat or gently convex; erect setae sparse. Propodeal spiracle moderately prominent, placed near angle between dorsal and declivitous faces; angle is rounded, obtuse. Moderate number of erect setae present on declivitous face. Whole mesosoma finely pubescent.

Legs. Femur and tibia with short suberect setae with moderate underlying pubescence.

Petiole. Petiole anteriorly inclined, posterior face flat; anterior face short and convex with numerous short setae extending anteriorly and laterally.

Gaster. Non-marginal erect to suberect setae present on all segments. Entire gaster clothed in moderately heavy, yellowish pubescence.

Measurements. (Average and range, mm, n = 14) HW 0.92 (0.82–1.04); HL 0.95 (0.83–1.07); EW 0.16 (0.14–0.18); EL 0.21 (0.18–0.23); SL 0.77 (0.68–0.84); ML 1.26 (1.01–1.44); PpL 0.55 (0.44–0.60); PnW 0.56 (0.51–0.62); MTL 0.76 (0.66–0.83); HFL 1.01 (0.84–1.14); PpH 0.15 (0.11–0.17); CI 97 (93.3–99.0); EI 23 (21.6–25.0); SI 83 (80.2–88.0).

General characters. Colour typically black, but can vary within a nest series from brown through to black, presumably darkening with age or exposure to sunlight. Some individuals may have reduced pilosity, possibly due to abrasion. The species has a strong and distinctive odour, characteristic of the genus.

Queen

Based on the paratype, which is the only known specimen of a queen of this species. The specimen was collected directly from the nest (details below). The specimen is dealate, and the gaster was damaged during collection.

Head. In full-face view, posterior margin with shallowly V-shaped concavity, each side sloping sinuously to distinct central angle; moderate abundance of yellowish, curved, tapering, suberect setae on apex and upper sides of head, length less than maximum scape diameter; anterior angles of head distinct. Sides of head shallowly convex, tapered slightly anteriorly; few setae present at mandibular insertions; scant pale grey pubescence on frons, underlying integument smooth, glossy and finely puncticulate. Ocelli present, weakly turreted, posterior pair widely set. Compound eyes elliptical, shallowly convex, set slightly below midpoint of head capsule; in lateral view, eyes set anteriad. Antennae 12-segmented; frontal carinae concave, terminating at about midpoint of eye; scapes slightly clavate, reaching upper margin of posterior ocelli. Scape with moderate yellowish pubescence, suberect setae confined to tip. Anterior clypeal margin broadly convex, centre equal to line drawn between lateral lobes. Long erect setae present on venter of head. Mandibles striate-punctate, dark brown, darker than head; basal margin edentate; masticatory margin with six teeth and three denticles; apical tooth approximately twice the length of subapical tooth.

Mesosoma. Mesosoma surface smooth, glossy and finely puncticulate with scant to moderate fine pubescence, moderate numbers of erect setae, length up to 2× maximum scape diameter. In dorsal view, mesoscutum narrower than head. In lateral view, anterior mesoscutum smoothly rounded, then flattening to form smooth, even curve with dorsal surfaces of mesoscutellar disc and propodeum.

Legs, petiole and gaster. As for worker.

Measurements. (Paratype, mm) HW 1.54; HL 1.89; EW 0.36; EL 0.48; SL 1.05; ML 3.50; PpL 1.32; MssctmW 1.27; MTL 1.20; HFL 1.62; PpH 0.34; CI 81; EI 31; SI 70.

Colour. Colour of live specimen pale brown, darkening to medium brown when dried and pinned.

Male

Head. In full-face view, posterior margin shallowly convex, broadly curving to form sides of head; whole head with moderately abundant short grey pubescence with occasional longer setae less than maximum scape diameter; underlying integument shiny, imbricate. Ocelli turreted, posterior pair widely set. Compound eyes large, elliptical, convex, set below midpoint of head capsule; in lateral view, eyes set anteriad. Antennae 13-segmented; scape about same length as second funicular segment; scape and first funicular segment with sparse setae and pubescence, remaining funicular segments with abundant suberect setae less than half maximum scape diameter with underlying pubescence. Anterior clypeal margin broadly convex, centre projecting past lateral lobes. Mandibles pale brown, lighter than head; subapical tooth less than half length of apical tooth, remaining masticatory surface denticulate.

Mesosoma. Mesosoma surface shiny, imbricate with moderate fine pubescence and scant erect setae, length up to 2× maximum scape diameter. In dorsal view, mesoscutum approximately 1.5× head width and projecting anteriorly to cover rear margin of head. In lateral view, mesoscutum projecting forward to partly cover apex of head before curving strongly to form dorsal surface. Mesoscutellar disc raised slightly above mesoscutum; propodeum depressed. Wings with pale iridescence, veins depigmented or pale brown, pterostigma dark brown.

Legs. Femur and tibia with short suberect setae and moderate underlying pubescence.

Petiole. Petiole short, anteriorly inclined with very short posterior face and broad joint to gaster.

Gaster. Shiny, imbricate with moderate fine pubescence and non-marginal erect to suberect setae present on all segments.

Measurements. (Average, mm, n = 3) HW 0.63; HL 0.60; EW 0.20; EL 0.25; SL 0.14; ML 1.54; PpL 0.66; MssctmW 0.92; MTL 0.72; HFL 1.01; PpH 0.14; CI 105; EI 39; SI 23.

Colour. Colour of live and pinned specimens dark brown.

Etymology

Latin: *inclina*, meaning inclined, referring to slope of the propodeal dorsum of the worker.

Distribution

Examination of collections at the ANIC, the AM and QM revealed very few specimens corresponding to *A. inclinata*. Collection records show its distribution extending from northern New South Wales, near Yetman and Dthinna Dthinnawan National Park, through southern inland Queensland between Goondiwindi and Toowoomba, to central Queensland around Carnarvon Station and Isaac River north-west of Rockhampton, and as far north-east as Home Hill (Fig. 7). All sites are in the Brigalow Belt South or Brigalow Belt North bioregions (Thackway & Cresswell 1995) and range climatically from temperate subhumid in New South Wales, through subtropical moist in southern and central Queensland, to tropical moist around Home Hill (Hobbs & McIntyre 2005).

Vegetation at the known sites of occurrence of *A. inclinata* in northern New South Wales and southern Queensland is mostly mixed open forest and casuarina woodlands. Common tree species include *Allocasuarina luehmannii*, *Callitris endlicheri*, *Callitris glaucophylla*, *Angophora leiocarpa*, *Eucalyptus tereticornis*, *Eucalyptus crebra* and *Eucalyptus melanophloia*, with an understory including *Lomandra*, tussock grasses including *Triodia*, and scattered *Acacia*. The ground layer is generally open and grassy, or heavily littered, often with extensive areas of *A. luehmannii* needles, logs and woody debris. The single collection of *A. inclinata* from Home Hill was taken from 'paperbark', presumably a species of *Melaleuca*.

Biology

Nesting and foraging behaviour. *Anonychomyrma inclinata* is arboreal, making its colonies almost exclusively in mature live trees with access to internal hollows through fissures and cracks, lightning scars or broken limbs. Rarely nests are found in fallen trees. No colonies have been observed in the ground or under logs. The ant will occupy any of the tree species noted above if they are old enough to have suitable nest sites (Sands 2018a, 2019), and at the sites examined in northern New South Wales and southern Queensland, almost all trees populated with *A. inclinata* carried mistletoes. *Anonychomyrma inclinata* has been observed harvesting nectar from flowering mistletoes, particularly *Lysiana exocarpi* subsp. *tenuis* and *Amyema linophylla* subsp. *orientalis*, as well as nectar from flowering eucalypts, shrubs including *Jacksonia scoparia* and *Kunzea opposita*, and the epiphytic orchid *Cymbidium canaliculatum*. Honeydew from psyllids and scale insects also appears to be an important part of

Fig. 7. Distribution of *Anonychomyrma inclinata* sp. nov.

the ant's diet (Sands 2018a) along with insect prey gleaned from trees and the ground surface.

As well as providing suitable nest cavities and ready access to nectar and honeydew, large live trees probably offer the colonies greater protection from fire and extremes of heat and cold compared with dead or fallen timber due to their greater thermal buffering capacity (Shelton *et al*. 2020). The ants are active throughout the year, but foraging is strongly reduced once the temperature reaches 30–35 °C and only resumes once the temperature declines (D. Sands unpubl. data). The ants forage in the nest tree and adjacent trees, and on the surrounding ground. Strong trails have been observed up to 20–25 m between trees and up into the canopy, and the ants preferentially use fallen logs and branches to move across the ground between trees.

Colony structure. A queen and male specimens were collected from a nest in a recently fallen silver-leaved ironbark, *Eucalyptus melanophloia* subsp. *melanophloia*, approximately 15 m tall, with diameter at breast height of 25 cm. The tree was sectioned into 30 cm lengths and examined for queens, alates, workers and brood by vigorously shaking and hammering each section to dislodge ants from the nest into containers. For each section, a subsample of workers and males was counted, and then the number of remaining ants was estimated proportionately. Brood from each section were subsampled and later counted in the laboratory. The colony occupied abandoned termite tunnels accessed via a damaged area of the trunk approximately 10 m above ground. An estimated 13 000 workers were present in this nest, along with a single queen, no female alates, approximately 40 male alates and 160 000 brood at various stages, a total population in excess of 170 000. It was not possible to estimate the number of workers foraging outside the nest, but long, active trails were present. The total length of trunk and branches occupied by the colony was approximately 10 m and had a volume estimated at 12.5 L. The queen and bulk of the adults and brood were in the lower section of the nest, immediately above the nest entrance. Termite tunnels extended below the nest entrance but were partially water filled, which precluded their use for nesting but afforded the colony ready access to moisture. Several silverfish were also present in the nest, probably an undescribed species of *Acrotelsella* Silvestri, 1935. This genus of silverfish has been found previously in abandoned termite galleries in Australia but not in an active ant nest before (G. Smith pers. comm.).

Interaction with *Hypochrysops piceatus* and other butterflies. Freshly eclosed *H. piceatus* larvae have been observed being carried by the ant to protection in hollows and shelters and at dusk are carried or guided by the ants to the soft terminal leaves of the bulloak to feed (D. Sands, unpubl. data). Overwintering *H. piceatus* larvae shelter in hollows or under bark and pupae are found in similar locations, always attended by *A. inclinata*. At the Leyburn site, *A. inclinata* has also been observed attending immatures of other lycaenid butterflies, including those of *Hypochrysops cyane* Waterhouse & Lyell, 1914 and *Ogyris amaryllis meridionalis* Bethune-Baker, 1905 (Sands 2019).

DISCUSSION

The size of the *Anonychomyrma inclinata* colony examined in this work is large by Australian and international standards. Drawing on earlier studies which compiled global data on ant colony size, Burchill and Moreau (2016) found reliable records for 416 species, of which only 50 species had records of colony populations of 10 000 or more. The large majority of these were from the Dorylinae (18 species) and Myrmicinae (16 species). Only five were dolichoderines, and *Iridomyrmex purpureus* Smith, 1858 was the only Australian species in this group.

Estimates of colony population size for *I. purpureus* vary considerably and are complicated by factors including method of estimation, seasonal variation, whether the cited number refers to adult workers or all castes and brood, and whether the reference is to a single colony (i.e. a single discrete nest) or to the sum of a polydomous population. The most definitive data have come from colony excavations. Of the nine colonies examined by Greaves and Hughes (1974), four were found to have a total population of more than 100 000 including all castes and immatures. The largest was 132 000, comprising 52 000 workers, 69 000 larvae, 10 000 male alates and almost 1000 female alates. An estimated colony size of 300 000 (Ettershank 1971) is a derived figure based on whole colony respiration data and relies on uncited 'in press' oxygen consumption data for *I. purpureus*, which we are unable to trace. A claim that 'a large colony' can host over a million ants (Greaves 1973) is not supported by data, although may be plausible for a large polydomous colony.

While it is quite possible that some species of *Iridomyrmex* may have even greater nest populations, at over 170 000 the population of the single colony of *A. inclinata* examined in this study represents one of the largest monodomous colonies of any ant recorded in Australia. Given the extensive trail systems developed by this species, it is also possible that *A. inclinata* is facultatively polydomous like *I. purpureus*. The number of adult workers in the examined colony does not rival that of *I. purpureus*, but the number of brood appears far higher. These differences may be attributable to seasonal variation in colony population demographics: Greaves and Hughes (1974) excavated colonies in winter, while the *A. inclinata* colony reported here was examined in late summer. Similar large seasonal swings in population demographics have been reported for another highly populous, polydomous ant, *Dolichoderus mariae* (Laskis & Tschinkel 2008).

Colony data are available for only one other *Anonychomyrma* species: *Anonychomyrma scrutator* Smith, 1859, with nest sizes reported as 500 to 3000 adult workers (Wilson 1959). No data are available for the three other Australian genera which form obligate associations with butterflies, *Froggattella* Forel, 1902, *Philidris* Shattuck, 1992 and *Papyrius* Shattuck, 1992. In terms of nest volume, the estimated 12.5 L of the colony examined in this study is also large – by comparison, the volume of a 'typical' *I. purpureus* nest is 5 L (Ettershank 1968). However, as noted for colony population, larger nest volumes may well be possible for *I. purpureus*, although no published data are available.

The large colony size of *A. inclinata* is consistent with observations by other authors of the species being numerically dominant in the areas of occurrence (e.g. Dunn & Kitching 1994), and this is likely to be of direct relevance to its association with *Hypochrysops piceatus*. It has been demonstrated in other myrmecophilous butterflies that high ant abundance provides a signal for butterfly tree selection and oviposition and ensures sufficiently high attendance of ants to protect eggs, larvae and pupae (Pierce & Elgar 1985; Jordano *et al*. 1992; Wynhoff *et al*. 2008; Carleial *et al*. 2018). However, while Dunn and Kitching (1994) reported high and sometimes extreme abundance of *A. inclinata* in many of the areas they surveyed, this was not observed at Queensland and New South Wales sites visited in September 2019 following 5 years of severe regional drought (Queensland Government 2019) nor at New South Wales sites visited February 2021 after moderate rain.

As *A. inclinata* is critical for the conservation of *H. piceatus*, there is need to ensure that populations of the ant do not decline in known butterfly breeding areas. The relatively wide distribution of the ant and broad range of tree species used for nesting may suggest that *A. inclinata* is not itself currently of conservation concern, but management of land where both *A. inclinata* and *H. piceatus* are present should seek to optimise the conditions required for healthy populations of the ant. This approach has been proposed for the conservation of two other ant-dependent butterflies, prioritising management of the attendant ant populations as a key component of the butterflies' conservation plans (Wynhoff *et al*. 2011).

Fortunately, many of the requirements for strong populations of *A. inclinata* coincide with those of *H. piceatus*. Preservation or remediation of areas supporting mature trees including *A. luehmannii* and good populations of mistletoe will ensure nesting sites and food plants suitable for *A. inclinata* and *H. piceatus*. Sites with good populations of Hemiptera such as scale and psyllids would be of particular benefit to *A. inclinata* and other ants (Pierce & Elgar 1985): increased total ant abundance may reduce the number of predators and parasites of butterfly larvae and result in greater butterfly reproductive success (Kaminski *et al*. 2010). In addition, long-term casual observations around Leyburn suggest that *I. purpureus* colonies may be increasing in some areas as the ant responds to increased open space caused by clearing and vehicle tracks (Gibb & Hochuli 2003). As an increase in *I. purpureus* may pose a competitive threat to *A. inclinata*, protection of land from these disturbances should be prioritised.

In 1999 a narrow roadside strip comprising 11.8 ha of mixed forest including mature bulloaks supporting *H. piceatus* and good populations of *A. inclinata* was designated as the *Ellangowan Nature Refuge* (Queensland Government 1999; New *et al*. 2021), although no physical protection was provided for the site until late 2019 when the Queensland Department of Transport & Main Roads fenced part of the area (P. Sparshott, pers. comm.). A species recovery plan for *H. piceatus* was developed by the Queensland Environmental Protection Agency (Lundie-Jenkins & Payne 2000), but few of the recommended recovery actions have been implemented. While the plan's timeline lapsed in 2003, the proposed actions would still be of direct benefit to both *H. piceatus* and *A. inclinata* and may be a good blueprint for future action to preserve populations of both species.

In addition, distribution data for *A. inclinata* suggest that other breeding sites for *H. piceatus* could exist in areas not previously surveyed, particularly in the northern areas of the distribution where mature bulloak is present. Survey of these areas may be warranted to determine the extent of both *H. piceatus* and *A. inclinata* and to assist in better determining the conservation status of both species.

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