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Australasian ants of the subfamily Heteroponerinae (Hymenoptera: Formicidae): (1) General introduction and review of the *Heteroponera leae* (WHEELER, 1923) species group, with descriptions of two new species

Robert W. TAYLOR

Abstract

The Australian species groups of *Heteroponera relicta* (WHEELER, 1915), *H. leae* (WHEELER, 1923) and *H. imbellis* (EMERY, 1895) are briefly discussed. The workers of *H. leae*, *H. crozieri* sp.n. (southeast Queensland) and *H. majeri* sp.n. (southwest Western Australia) and the dealate gyne of *H. crozieri* are reviewed, keyed and illustrated. *Heteroponera* is considered biogeographically to be a paleoaustral component of the Australian fauna.

Key words: Ants, *Heteroponera*, taxonomy, Australia, new species, biogeography, Gondwana.

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Introduction

Heteroponera MAYR, 1887 currently includes thirteen named Neotropical and four Australasian species (BOLTON 1995, PERRAULT 1998). Its Neotropical range extends from Costa Rica south to Uruguay and central Chile. The Australian taxa are assigned to the species groups of *H. imbellis* (EMERY, 1895), *H. leae* (WHEELER, 1923) and *H. relicta* (WHEELER, 1915), each with a single species (BROWN 1958). The New Zealand endemic *H. brounii* (FOREL, 1892) is a member of the *H. imbellis* group (DON 2007).

BROWN (1958) synonymized four previous taxa under *H. imbellis*, and subsumed under *Heteroponera* the genus-group names *Paranomopone* WHEELER, 1915 (see WHEELER 1915), and *Acanthoponera* (*Anacanthoponera*) WHEELER, 1923. *Heteroponera* was placed with eight other genera in subfamily Ponerinae, tribe Ectatommini. All were later assigned elsewhere in the classification of BOLTON (2003), in which *Heteroponera*, *Acanthoponera* MAYR, 1862 (Neotropical) and *Aulacopone* ARNOLDI, 1930 (Azerbaijan) comprise the subfamily Heteroponerinae (with *Aulacopone* deemed incertae sedis).

Heteroponera may be identified in Australia using the keys of SHATTUCK (1999, pp. 52-57), BOLTON (1994, pp. 159-160) or HÖLLDOBLER & WILSON (1990, pp. 55-56). The species groups are defined by characters specified in relevant couplets of the key to species given below.

With the addition here of two new taxa, the *Heteroponera leae* group now comprises three known species. *Heteroponera crozieri* sp.n. and *H. leae* are both reported from extreme northeast New South Wales (NSW). The range of *H. crozieri* extends northwards in eastern-central and southeast Queensland (Qld) to approximately the latitude of Mackay, and *H. leae* ranges southwards in northeastern and central-eastern New South Wales to the Royal National Park, just south of Sydney. *Heteroponera majeri* sp.n. is found a continent away in southwest Western Australia (WA).

Separate comprehensive reviews of the *Heteroponera relicta* and *H. imbellis* species group are planned following further study of material to hand. The *H. relicta* group is represented in the Australian National Insect Collection and elsewhere by at least seven undescribed species additional to *H. relicta*. All are known only from rainforest habitats in or near the Wet Tropics World Heritage Area of northeast Queensland, at localities ranging from just north of Cooktown south to near Proserpine (between 15° S and 20° 30' S). Relevant Australian specimens of the *H. imbellis* group are known from Iron Range in far northeast Queensland; from about the latitude of Cooktown, Queensland, south along the eastern continental coast and Great Dividing Range through New South Wales and the Australian Capital Territory to southern Victoria; from southern South Australia and from southwest Western Australia. An estimated six species are represented in collections, and some of the names synonymized under *H. imbellis* by BROWN (1958) will likely be reinstated.

Biogeography of *Heteroponera*

BROWN (1958), writing from the Harvard Museum of Comparative Zoology, discussed the distribution of *Heteroponera* and other "ectatommines" as "peripheral" to the "larger land masses of Eurasia, North America and Africa." He implied that current distribution of the genus was relictually derived from a more widespread northern distribution, ultimately with a holarctic link between the two modern faunas. This view was representative of its place and time, influenced by the book *Zoogeography*, then recently pub-

lished by Brown's MCZ colleague Philip J. DARLINGTON (1957). That volume is now recognized as the last hurrah of pre-continental drift, pre-gondwanic world biogeography. DARLINGTON (1965) and Brown (pers. comm.) later accepted continental drift and austral dispersal in southern-hemispheric biogeography, globally "upending" many of their previous perceptions.

Evidence from historical biogeography implies that geographical isolation of the West Australian *H. majeri* stock from eastern Australian *Heteroponera* lineages occurred probably between 50 and 30 million years ago, when pluvial southwestern Western Australia became isolated from the east by the arid proto-Nullarbor plain (testé HOPPER & al. 1996, HOPPER & GIOIA 2004). The genus must therefore have been present on the Australian continental plate at least since Oligocene times, implying that *Heteroponera* is a paleoaustral element in the continental fauna, historically linked to the congeneric South American species through a southern (austral) connection. This view posits that the drifting Australian continent was too-far-distant from Southeast Asia during the Oligocene (or earlier) to have received possible *Heteroponera* stock from the north. It also implies that ancestral *Heteroponera* species were present on Gondwana prior to separation of the Australian and South American continental plates, or before intervening sea-ways were wide enough to prevent dispersal between the separating continents. The argument further supposes that *H. brounii*, like other endemic New Zealand ants, is either a paleoaustral relic, or a more recent neoaustral element derived from trans-Tasman immigrant Australian ancestry.

Gondwanic origination or ancestral trans-gondwanic dispersal between the Gondwana-incorporated or early separating South American and Australian continental plates have been previously argued for the ant subfamilies Dolichoderinae (WARD & al. 2010) and Myrmeciinae (WARD & BRADY 2003, TAYLOR 2007) (a position not compromised by a subsequent report of Eocene myrmeciines from British Columbia; ARCHIBALD & al. 2006), and for the genera *Rhopalothrix* and *Eurhopalothrix* (Myrmicinae: Basicerotini) (see TAYLOR 1990).

Heteroponera is unknown from Tasmania despite targeted search by the resident myrmecologist B.B. Lowery and my perusal of many Tasmanian soil and litter berlesates.

Materials and methods

Abbreviations: Collectors: GC – G. Cassis; AG – A. Graham; MG – M. Gray; GBM – G.B. Monteith, JDM – J.D. Majer; RWT – R.W. Taylor; TEW – T.E. Woodward. Other abbreviations are mostly copied from the original labels: km = kilometer(s); NP = National Park; SF or S.F. = State Forest.

Repositories: Abbreviations used for institutions are: AMSA – Australian Museum, Sydney; ANIC – Australian National Insect Collection, Canberra; MVIC – Museum of Victoria, Melbourne; QMBA or QM (as quoted from its labels) – Queensland Museum, Brisbane; WAMP – Western Australian Museum, Perth.

Distribution records: Localities are listed by state in numerical order of geographical coordinate values. Coordinates without brackets were copied from specimen labels; those enclosed in brackets were estimated (using Australian National Mapping Service sources) or copied from other labels of the same provenance. Some were recorded on labels in minutes (') and seconds ("). Several estimated citations use "short" 1-degree mapping coordinates without minutes (e.g., 21/148 indicates the grid cell 21° S × 148° E, and is cited for all samples collected in that grid cell).

Terminology: The conventional terms "gaster" and "gastral" refer to the large terminal section of the metasoma behind the petiole, with the (mesosomal) propodeum recognized properly as the first true abdominal segment and the petiole as the second (TAYLOR 1978). The first gastral segment in *Heteroponera* is true abdominal segment III, and the second true abdominal segment IV.

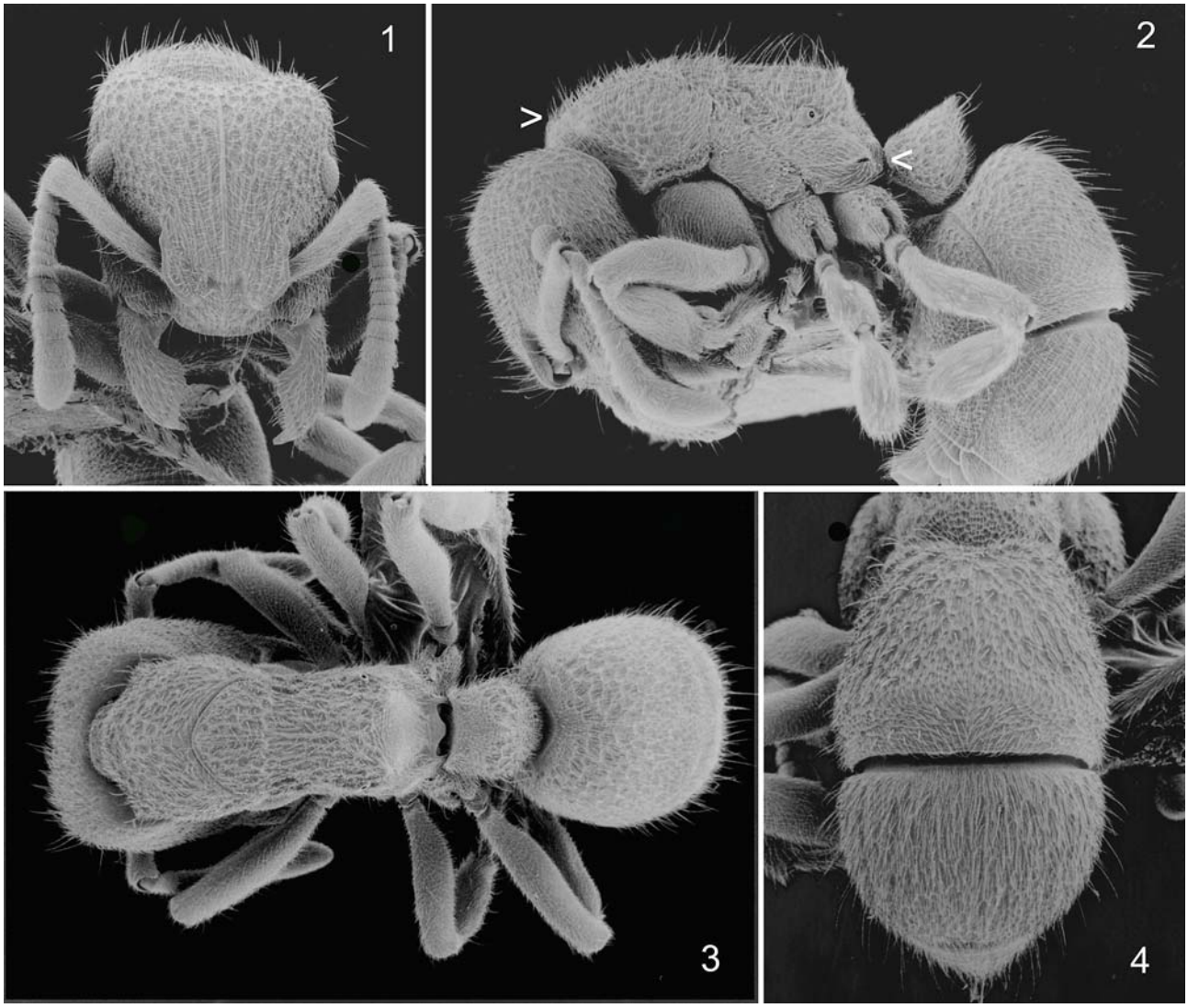
Measurements and indices: Measurements were prepared using a Zeiss stereomicroscope with hairline eyepiece and a manual micrometer stage with digital readout (read at mm / 1000, rounded to mm / 100). Details are given for each holotype and the smallest and largest available conspecific worker paratypes (their size ranking determined by initial survey of HW values), and for the *H. crozieri* gyne.

- TL Total length measured in side view (aggregate of: head and mandibles + mesosoma (or mesosoma and petiole) + gaster (or petiole and gaster). The terminal measurement is taken at the point of maximum extension of the posterodorsal curvature of the reflexed second gastral segment.
- HW Head Width (frontal view, maximum, across eyes).
- HL Head Length at midline, maximum, excluding mandibles (frontal view).
- CI Cephalic Index (HW × 100 / HL).
- EL Maximum Eye Length.
- SL Chord length of scape, excluding articular condyle.
- SI Scape Index (SL × 100 / HW).
- PW Pronotum Width (dorsal view, maximum).
- WL Weber's Length of mesosoma, measured in lateral view, the end points as illustrated in Fig. 2.
- PetW Petiolar node width, dorsal view.
- PetH Petiolar height, lateral view.
- GW Gastral Width, dorsal view, across widest segment (abdominal segment III (gastral 1) in workers, IV (2) in gyne).

Illustrations: Most illustrations were prepared using a JEOL JSM4 scanning electron microscope (SEM) at the CSIRO Black Mountain Laboratories, Canberra. Those of the *H. crozieri* gyne are extended focus (Z stack) macrophotographs prepared using a stand-mounted Olympus E330 digital camera, Zuico OM 35mm 1:2.8 auto macro lens, with bellows extension, electronic flash illumination, a custom-built electronically controlled stepper-stage and Combine-Z software (www.microscopy.uk.org.uk). The illustrations vary in magnification. Scales are indicated in the plate captions using standard dimensions of the specimens illustrated. SEM illustration has been generally superseded in ant taxonomy by extended focus macrophotography. Comparison of the illustrations presented here demonstrates the sometimes superior quality of the SEM for clear depiction of sculpturation and pilosity.

Key to the Australasian species groups of *Heteroponera* and species of the *H. leae* group (workers, gynes)

The characters of all known species of the *H. imbellis* and *H. relicta* species groups have been considered in compiling this key. Knowledge of the *H. crozieri* gyne implies



Figs. 1 - 4: *Heteroponera leae*, worker, Cobcroft Camp, Werrikimbe NP (31° 15' S, 152° 14' E), NSW, standard views (HW = 1.11 mm, PW = 0.83 mm, WL = 1.69 mm, GW = 1.12 mm). The end-points for WL measurement are indicated in Figure 2.

that the key should be effective for identifying gynes of the other species.

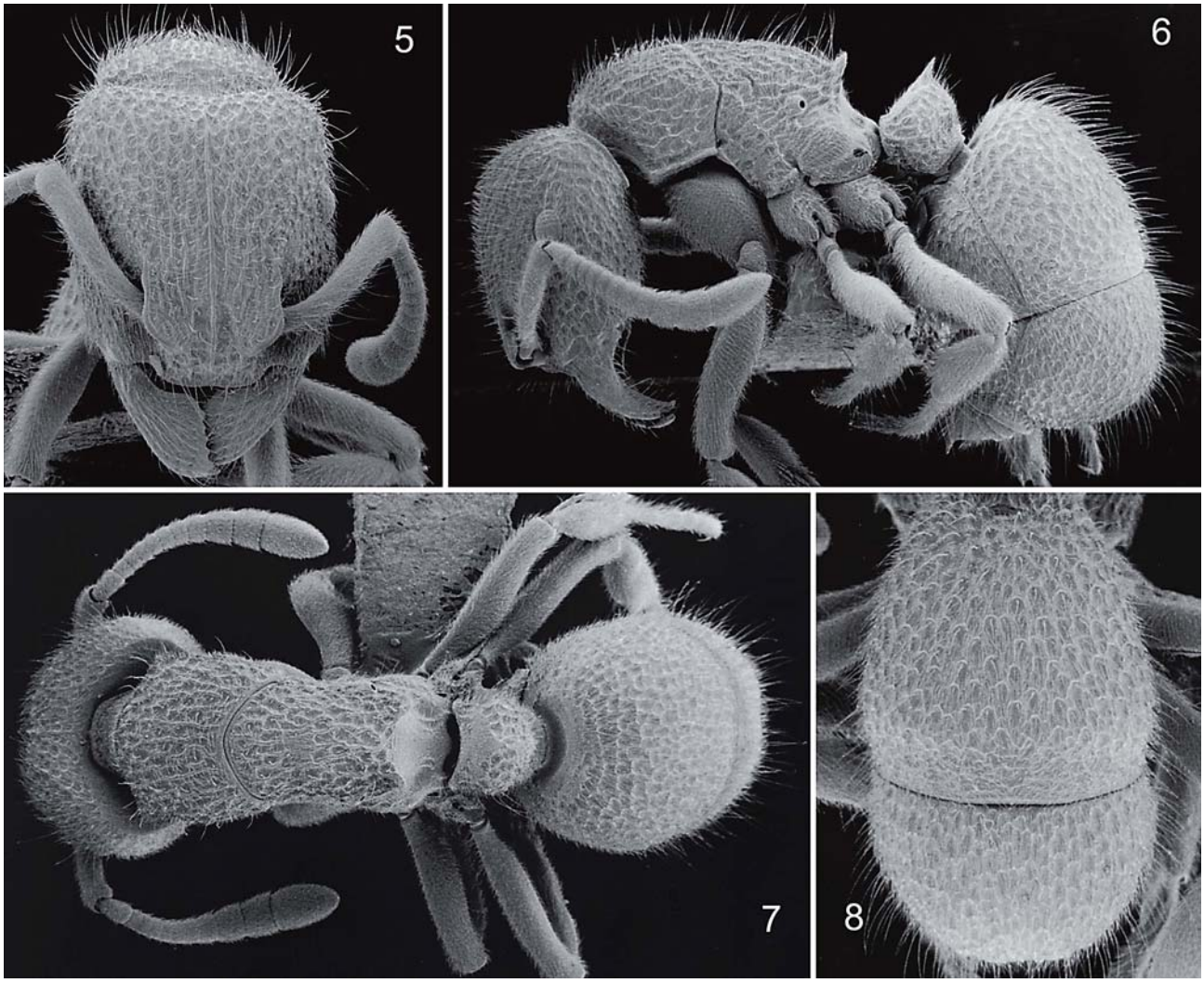
1 Petiole lacking a dorsomedial spine. Propodeum lacking slender erect spines, though sometimes with sculpturally jagged posterolateral edges. Reflexure of second gastral segment unexceptional. Antennal scrobes often (but not always) strongly developed. **2**

– Petiole armed dorsally with a small, erect median spine. Propodeum with a pair of similarly proportioned posterodorsolateral spines or homologous transversely lamellate spine-like processes. Second gastral segment in side view markedly reflexed, so that the gastral apex is directed anteroventrally. Antennal scrobes lacking (Figs. 2, 6, 13) (***H. leae* species group**). **3**

2(1) Generally larger species (HW seldom < 1 mm). Second gastral segment in dorsal view notably narrower than first; often tapered, narrowing posteriad. Antennal scrobes usually strongly developed, vestigial in one species. (The group known only from northeast coastal Queensland and adjacent highlands between 15° S and 20° 30' S – from just north of Cooktown, south to the approximate latitude of Proserpine). .... ***H. relicta* species group**

– Size generally smaller (HW seldom > 1 mm, and usually substantially smaller). Second gastral segment in dorsal view neither notably narrower than first nor markedly tapered posteriorly. Antennal scrobes lacking. (Widespread, all states except Tasmania). ..... ***H. imbellis* species group**

3(1) Head in square frontal view with the median vertexal (= "occipital") profile short, essentially straight, not broadly emarginate; the profile curving evenly towards the eye on each side (Fig. 13). Propodeal spines represented as small flattened transverse tabs. Second gastral segment very strongly reflexed; in lateral view its dorso-posteroventral profile enclosing slightly



Figs. 5 - 8: *Heteroponera crozieri* sp.n., holotype worker, standard views (HW = 1.23 mm, PW = 0.84 mm, WL = 1.64 mm, GW = 1.14 mm).

less than a right-angle, with a relatively short, tightly curved median section (Fig. 14) (southwest Western Australia). ..... ***H. majeri* sp.n.**

– Vertexal margin more broadly transverse and concave in outline (Figs. 1, 5). Propodeal spines acutely pointed, not tabulate. Second gastral segment less-strongly reflexed (Figs. 2, 6) (eastern Australia). **4**

4(3) Dorsal profile of second gastral segment an even semicircular arc, its tergite moderately finely, longitudinally striate-reticulate with the longitudinal trend very distinct. (Figs. 5 - 8) (northeast and eastern central New South Wales, 29° - 34° S). ..... ***H. leae***

– Dorsal profile of second gastral segment not evenly semicircular, more strongly curved in the median section than elsewhere, its tergite moderately reticulate punctate-rugose with a less-well-developed longitudinal trend (Figs. 9 - 12) (southeast Queensland and far northeast New South Wales, 20° - 28° S). ..... ***H. crozieri* sp.n.**

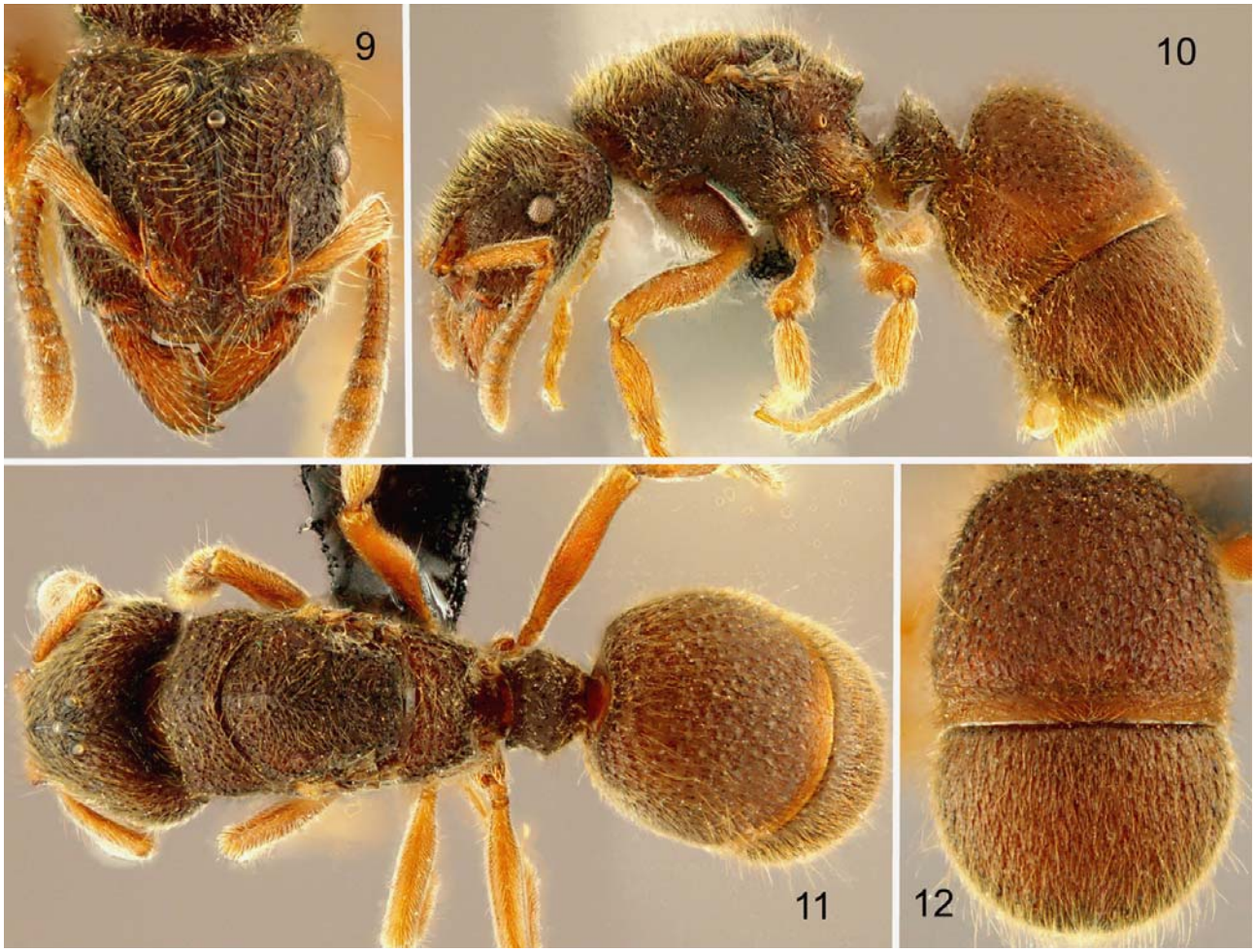
Discussion of individual species

***Heteroponera leae* (WHEELER, 1923)** (Figs. 1 - 4)

Acanthoponera (*Anacanthoponera*) *leae* WHEELER, 1923: 181; worker; type locality: National Park (= Royal National Park, 34/151), NSW (syntype examined).

Heteroponera leae (WHEELER): W.L. BROWN 1958: 196.

Distribution, material examined: Known from the following collections (grid cells 29/152, 30/152, 31/151, 31/152, 32/151, 34/151), each record comprises a single worker unless indicated. **New South Wales:** Tooloom Scrub (28° 26' S; 152° 26' E), rainforest, berlesate, 720 m, 17.VIII. 2005 (C. Burwell, S. Wright), 4 workers (QMBA). Ewingar S.F., Ewingar Ck., Elkhorn Rd., 29° 06' 00" S, 152° 26' 20" E, 640 m, pitfall 12AG, 4.II.-9.IV.1993 (MG and GC, NSW NPWS Survey, AMSA). Dorrigo NP (30/152), rainforest leaf mould berlesate, 5.IV.1967 (E.B. Britton, ANIC). Killiekrankie Mtn., 30° 32.5' S, 152° 32.6' E, 880 m, human dung pitfall trap, 12.XI.1999 (C. Reid, AMSA). Mt Werrikimbe NP (31° 15' S; 152° 14' E), Cobcroft Camp, eucalypt forest litter berlesate, 12.X.1992 (J. Doyen, ANIC). Enfield State Forest, Mummei Forest Road, 31° 17' 00" S, 151° 51' 17" E, 1340 m, pitfall 37AG, 4.II.-9.IV.1993 (MG and GC,



Figs. 9 - 12: *Heteroponera crozieri* sp.n., paratype gyne, standard views (HW = 1.55 mm, PW = 1.24 mm, WL = 2.24 mm, GW = 1.71 mm).

NSW NPWS Survey, AMSA). Chichester SF, Allyn River Forest Rd., 32° 08' 14" S, 151° 28' 39" E, 378 m, pitfall 36CM, 4.II.-9.IV.1993 (MG and GC, NSW NPWS Survey, AMSA). Royal NP ["National Park"] (34/151), ex rotting leaves, (A.M. Lea), 1 syntype worker labeled "MCZ cotype 2/20390" and "Gift of W.M. Wheeler" (ANIC).

Worker diagnosis: General features as illustrated and in key couplets 1, 3, and 4. Similar to the more northerly distributed *H. crozieri* – see its entry below for comparative details. The first gastral tergite largely moderately punctate-rugose; the raised elements with a clear semicircular trend, and the posterior third of the dorsum forming a less-intensely punctate-reticulate transverse band. Second gastral tergite distinctly and somewhat reticulately longitudinally striate. Further characterization is unnecessary.

Measurements and indices: (mm – syntype worker; smallest available worker (Ewingar SF), largest available worker (Werrikimbe NP)): TL (ca.): 4.9; 4.77, 5.62. HW: 1.11; 1.12, 1.30. HL: 1.15; 1.17, 1.23. CI: 96; 95, 95. EL: 0.21; 0.19, 0.22. SL: 0.72; 0.72, 0.80. SI: 65; 64, 61. PW: 0.73; 0.74, 0.83. WL: 1.54; 1.57, 1.69. PetH: 0.62; 0.70, 0.71. PetW: 0.49; 0.48, 0.53. GW: 0.98; 1.02, 1.12.

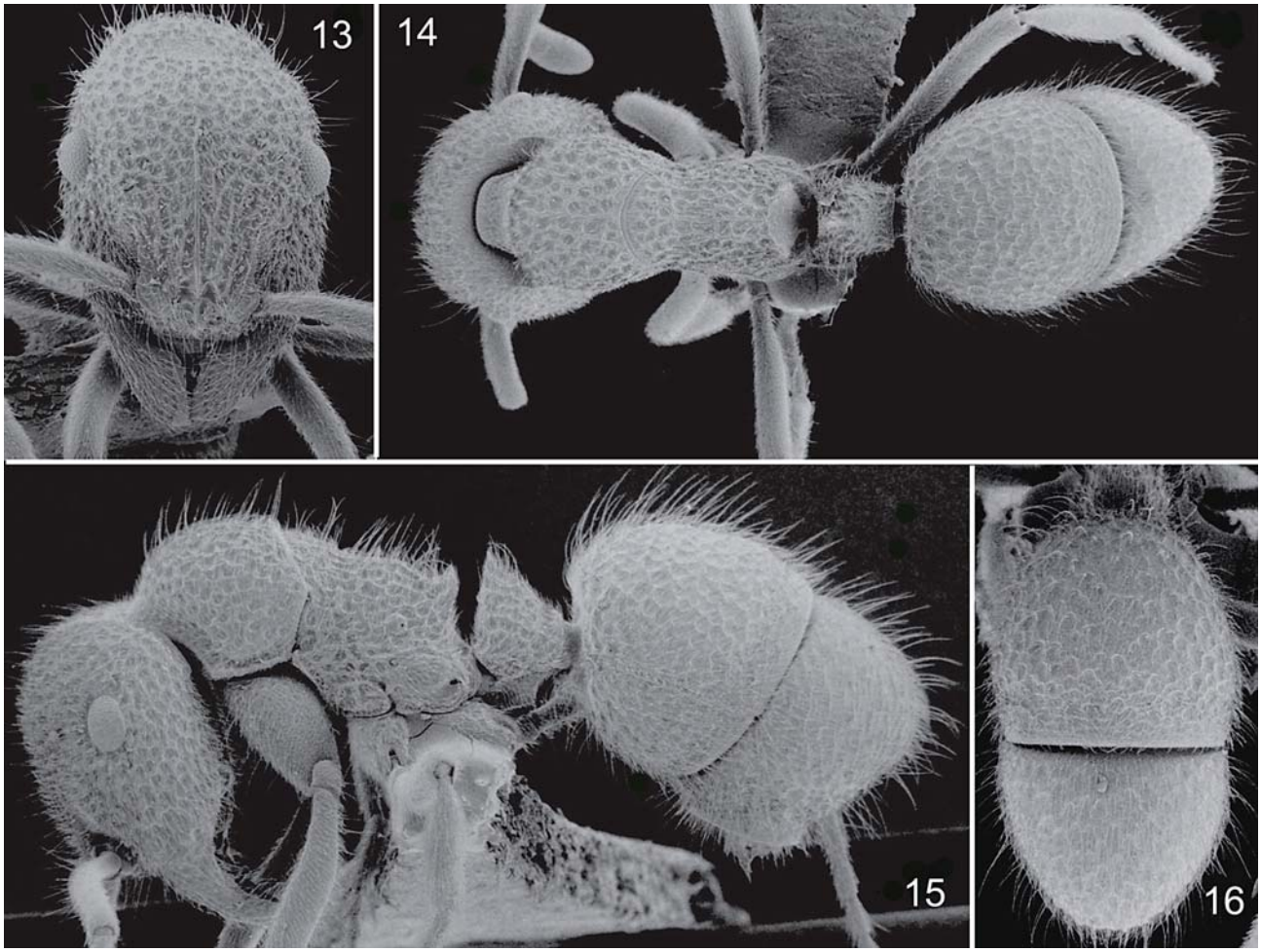
Remarks: A holotype-matched, gold-palladium coated worker from the Cobcroft Camp, Mt Werrikimbe NP series was used to prepare the illustrations of this species.

***Heteroponera crozieri* sp.n.** (Figs. 5 - 8, 9 - 12)

Type locality: 3 km S of Eungella (= Dalrymple Heights), Queensland.

Type deposition: Holotype, paratypes (from most localities), in ANIC; paratypes in QMBA, AMSA (including gyne), MVIC. Holotype gold coated for SEM study.

Distribution, material examined: Known only from the following eastern Queensland and far northeast New South Wales records (Grid cells 20/148, 21/148, 24/150, 24/151, 28/152, 28/153). Unless noted each comprises a single worker collected by Berlese funnel from rainforest leafmould or litter. All specimens additional to the holotype have been designated paratypes and are so labeled: **Queensland:** Mt. Macartney, Cathu State Forest, 20° 51' S, 148° 33' E, stick brushings, QM berlesate 54, 750 m, 22.IV.1979 (GBM); 3 km S of Eungella (21° 09' S, 148° 29' E), 780 m, 21.IX.1975 (RWT), holotype worker; same locality at 21° 08' S, 148° 30' E, 780 m, under stone, 23.-24.X.1982 (RWT & P. Pamilo), 2 workers; Kroombit Tops SSW of Caliope – Beauty Spot, 98, 24° 22' S, 150° 59' E, QM berlesate 679, 860 m, 29.-30.IX.1985 (GBM), 9 workers; Three Moon Scrub, 24° 25' S, 151° 03' E, QM berlesate 681, 940 m, 29.-30. IX.1985 (GBM), 2 workers (QMBA). Mt. Clunie foothills (28/152), 5.IV.1953 (TEW); Beechmont (28/153), 1.VIII.1954 (TEW), 2 workers; Binna Burra (Guest House



Figs. 13 - 16: *Heteroponera majeri* sp.n., holotype worker, standard views (HW = 1.37 mm, PW = 0.90 mm, WL = 1.79 mm, GW = 1.24 mm).

area, 28/153), 10.VII.1952, 2 workers (TEW); Canungra – Glen Witherin (labeled "Curtis Farm") (28/153), stick brushings, QM berlesate 207, 9.IX.1979 (GBM). **New South Wales:** Richmond Range SF 47A, Goanna Creek Rd., 28° 36' S, 152° 41' E, 545 m, 4.II.-9.IV.1993 (MG & GC, NSW NPWS Survey), dealate gyne (AMSA). The habitat is not specified for Mt. Clunie, Beechmont and Binna Burra specimens. They were probably taken in rainforest like the other samples, all of which are so labeled.

Worker diagnosis: General features as illustrated and in key couplets 1, 3, and 4. Similar to the generally more southerly distributed *H. leae*. Salient differences are: (1) propodeal and petiolar denticles larger and more sharply acute; (2) reflexure of second gastral segment more pronounced – in side view (Fig. 6) the profile is less evenly arched than in *H. leae*, with a tightly curved median section; (3) first gastral tergite more-or-less evenly sculptured with coarse semi-foveate punctate-rugosity, the raised elements forming a somewhat longitudinally biased reticulum; (4) second gastral tergite similarly, but more-finely punctate-rugose, the longitudinal component clearly evident, but much less well-developed than in *H. leae*; the whole more reticulate than in *H. leae*.

Gyne: General features as illustrated. Appropriate characters consistent with those of the workers. Propodeal and petiolar spines a little-less prominent. Gastral reflexure and sculpturation as in worker.

Measurements and indices: (mm – holotype; smallest available worker specimen (Kroombit ops), largest available worker specimen (Beechmont); gyne): TL (ca.): 5.5; 4.8, 5.6; 7.6. HW: 1.23; 1.08, 1.32; 1.55. HL: 1.24; 1.15, 1.30; 1.50. CI: 99; 94, 98; 103. EL: 0.17; 0.13, 0.20; 0.25. SL: 0.80; 0.68, 0.82; 0.87. SI: 65; 63, 62; 56. PW: 0.84; 0.71, 0.90; 1.24. WL: 1.64; 1.42, 1.72; 2.24. PetH: –; 0.62, 0.76; 0.93. PetW: 0.48; 0.42, 0.51; 0.71. GW: 1.14; 0.97, 1.26; 1.71.

Dedication: Named for my late friend, colleague and frequent co-author Prof. R.H. (Ross) Crozier, formerly of James Cook University, Townsville, Queensland.

Remarks: The gyne was formerly alate, as evidenced by the presence of torn wing stubs. She thus resembles those described for the Neotropical species *H. dentinodis* (MAYR, 1887) and *H. inermis* (EMERY, 1894) = *H. schwebeli* (LUEDERWALDT, 1918) (see BROWN 1958). Some other species, like *H. relicta* and *H. brounii*, have wingless ergatoid queens with reduced mesosomal structure. Gamergate reproductives (mated workers) have not been reported for any *Heteroponera* species.

***Heteroponera majeri* sp.n.** (Figs. 13 - 16)

Type locality: Dwellingup (32° 43' S; 116° 04' E), ca. 85 km S of Perth, southwest Western Australia.

Type deposition: Holotype in ANIC, gold coated for SEM study; paratypes in J.D. Majer collection for future deposit in WAMP.

Distribution, material examined: Known only from the holotype and two paratypes, all workers from pitfall-trap collections at the following localities: **Western Australia:** Dwellingup (32/116), 7.VII.1975 (JDM, acc. 049, 17238), holotype worker; Worsley (33/116), Alcoa survey site, Pit trap AL 31 A1018, 15.X.1976 (J. Wallace, JDM acc. 92, JDM database No. 32 003034), paratype worker; same locality, Pitfall trap AL 31 A731, 25.VI.1976 (J. Wallace, JDM 92, JDM database No. 32 003035), paratype worker. The two Worsley specimens are labeled "Alcoa WA". The locality "Worsley" identified from JDM records by B.J. Heterick. Coordinates for Worsley are 33° 20' S, 115° 56' E.

Worker diagnosis: General features as illustrated and in the accompanying key. *Heteroponera majeri* is one of the most highly distinctive of all *Heteroponera* species. The major features distinguishing it from *H. leae* and *H. crozieri* include the very differently structured head, mesosoma and metasoma, as evidenced in the accompanying illustrations.

Measurements and indices: (mm – holotype; smallest paratype, largest paratype): TL (ca.): 6.0; 5.4, 6.4. HW: 1.37; 1.26, 1.49. HL: 1.47; 1.28, 1.48. CI: 93; 98, 100. EL: 0.29; 0.26, 0.30. SL: 1.04; 0.94, 1.07. SI: 76; 75, 72. PW: 0.90; 0.81, 0.98. WL: 1.79; 1.56, 1.94. PetH: 0.78; 0.71, not measurable. PetW: 0.44; 0.39, 0.48; GW: 1.24; 1.05, 1.29.

Dedication: Named for Prof. J.D. Majer of Curtin University, Perth, Western Australia.

Remarks: The species-group association of this somewhat aberrant taxon with *H. leae* and *H. crozieri* is based on the reasonable assumption that the propodeal and petiolar spines, vestigial antennal scrobes and strongly reflexed gaster in these species are synapomorphies. The biogeographic implications of the presence of *H. majeri* in southwestern Australia are discussed above under "biogeography".

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