Ants with Attitude: Australian Jack-jumpers of the *Myrmecia pilosula* species complex, with descriptions of four new species (Hymenoptera: Formicidae: Myrmeciinae)

ROBERT W. TAYLOR

Research School of Biology, Australian National University, Canberra, ACT 0200.

Honorary Fellow, Australian National Insect Collection, CSIRO Ecosystem Sciences, Canberra.

E-mail: bob.taylor@homemail.com.au

Abstract

The six known “Jack-jumper species *Myrmecia pilosula* Fr. Smith 1858, *M. croslandi* Taylor 1991, *M. banksi*, *M. haskinsorum*, *M. imaii* and *M. impaternalata* spp.n. are reviewed, illustrated and keyed. *Myrmecia imaii* is known only from southwest Western Australia, the others variously from southeastern Australia and Tasmania. These taxa were previously confused under the name *M. pilosula* (for which a lectotype is designated). Previous cytogenetical findings, which contributed importantly to current taxonomic understanding, are summarized for each species. Eastern and Western geographical races of the widespread *M. pilosula* are recognized. *Myrmecia croslandi* is one of only two eukaryote animals known to possess a single pair of chromosomes ($2n=2 \times 3$ or 4). *Myrmecia impaternalata* is evidentially an allodiploid ($n=5$ or 14 , $2n=19$) sperm-dependent gynogenetic hybrid between *M. banksi* and an element of the eastern race of *M. pilosula*, or their immediate ancestry. The sting-injected venom of these ants can induce sometimes fatal anaphylaxis in sensitive humans.

Key words: Ants, Formicidae, Myrmeciinae, *Myrmecia*, Jack-jumpers, Tasmania, Kangaroo Island, karyology, hybridization, thelytoky, allodiploidy

Introduction

The *Myrmecia pilosula* complex was defined by Ogata and Taylor (1991) as a section of the species group of *M. pilosula* Fr. Smith 1858. There are six component species, four of which are described here as new. In addition, *M. pilosula* comprises two newly recognized geographical races. These sometimes common ants are known to Australians variously as “Jack-jumpers”, “Jackie-Jumpers”, “Jumping Jacks”, “Jumper Ants”, “Black Jumpers” or “Hopper Ants. *Myrmecia imaii* is apparently endemic to southwest Western Australia (WA) and the other species are collectively distributed in a zone extending from extreme SE Queensland (QLD), south along the Great Dividing Range and its flanks in eastern New South Wales (NSW), the Australian Capital Territory (ACT), Victoria (VIC) and Tasmania (TAS), ranging from sea level to the high slopes of Mt Kosciuszko (2, 228m) and the Tasmanian mountains; thence from SE Victoria westwards to SE South Australia (SA) and Kangaroo Island. The nearest records of an eastern species to the distributional range of *M. imaii* are those for *M. pilosula* in SA east of Spencer Gulf, an overland distance of over 2, 000km.

Because of close interspecific similarity relevant museum specimens were previously often labeled or placed in collections as “*Myrmecia pilosula*”, as if representing a single biological species. Various authors (e.g. Wheeler, 1933; Clark, 1943, 1951; Haskins & Haskins, 1951; W. L. Brown, 1953; Taylor & D. R. Brown, 1985, Browning, 1987; Heterick, 2009) followed this portmanteau nomenclature, though sometimes aware that the action was not well supported (e.g. Browning, 1987). During this project specimens of all six species recognized here were found identified as *M. pilosula* in Australian public collections. Material in the Australian National Insect Collection (ANIC), Museum of Victoria (MVMA) and Queensland Museum (QMBA) labeled by Clark when compiling his revisions of *Myrmecia* and its erstwhile subgenus *Promyrmecia* (Clark, 1943, 1951), indicate that he identified as *M. pilosula* specimens assigned here to *M. haskinsorum*, *M. imaii* and both races of *M. pilosula*.

The view that “*M. pilosula*” was composite was eventually confirmed by the author’s discovery of two distinct

sympatric species widely present in urban and suburban Canberra, including the CSIRO/ANIC Black Mountain site and the adjacent National Botanic Gardens, and a third species at higher elevations in the nearby Brindabella Ranges (taxa now recognized as *M. croslandi*, *M. impaternalata* and the eastern race of *M. pilosula*), and by cytotaxonomic demonstration that there was diversity in “*pilosula*” chromosome numbers consistent with species differentiation: most notably that one species (*M. croslandi*) frequently possesses only a single pair of chromosomes (Imai, Crozier *et al.*, 1977; Crosland and Crozier, 1986; Crosland *et al.*, 1988; Taylor, 1991). In his unpublished PhD dissertation Browning (1987) separately concluded that “*M. pilosula sens.lat.* is a complex of sibling species with indistinguishable (sic!) workers”, basing this opinion on “the variety of nest structures”, his own cytotaxonomic studies, and the karyological work of Imai, Crozier *et al.* (1977) and Crosland and Crozier (1986).

Previous karyological and cytotaxonomic research has importantly illuminated this study (references below). *Myrmecia*, which comprises about 100 estimated species, is one of the most karyologically diverse of all investigated non-polyploid animal genera, with chromosome numbers ranging from $2n=2$ in *M. croslandi* to $2n=84$ in *M. brevinoda* Forel (Crosland and Crozier, 1986; Imai and Taylor, 1989)—a 42-fold difference, second only to the maximum known animal range of 48-fold in the scale insect genus *Apiomorpha* (Hemiptera: Coccoidea: Eriococcidae), which has $2n=4$ to about 192 (Cook, 2000). $2n=2$ is the lowest possible eukaryote value and in animals is unique to *Myrmecia croslandi* and the nematode *Diploscapter coronata* (Cobb), which also has $2n=2$ (Hechler, 1968). *Myrmecia* covers much of the chromosome number range known for the order Hymenoptera, which has $2n=2$ (*Myrmecia croslandi*) to $2n=94$ (in the related monotypic Australian myrmeciine ant *Nothomyrmecia macrops* Clark), and a large part of the range for class Insecta (polyploids excepted), which comprises the known range for all arthropods (Imai, Taylor *et al.*, 1990).

Some complexes of closely similar *Myrmecia* species are chromosomally very diverse. Four similar species of the *M. piliventris* F. Smith complex cover almost two thirds of the known hymenopteran chromosome number range, with $2n=4, 6, 34, 64$ (Imai and Taylor, 1986). It seems likely that most of the other putative *Myrmecia* “species” considered to be morphologically variable will be found actually to comprise sets of “good” biological species, as in the *pilosula* complex.

Australian ants, especially species of *Myrmecia*, have from 1976 until recently been subject to karyological research by Japanese and Australian myrmecologists and geneticists working in association with Dr Hirotami T. Imai, formerly of the Japanese National Institute of Genetics, Mishima, the late Professor Ross H. Crozier (University of New South Wales: later at La Trobe University, Melbourne and James Cook University, Townsville) and the author (initially at CSIRO Division of Entomology, Canberra). This program is informally designated the “Japan/Australia Cooperative Ant Karyology Program” (JACP). Attention focused increasingly on the *M. pilosula* complex. Relevant papers include: Imai, Crozier *et al.*, 1977; Imai, Taylor, Crosland *et al.*, 1988; Imai, Taylor, Crozier *et al.*, 1988; Crosland *et al.*, 1988, Imai, Taylor *et al.*, 1992, and others referred to below. The project continued with research on molecular genetics in which base sequences in *Myrmecia* ribosomal and mitochondrial DNA were compared (Hirai *et al.*, 1994; Crozier *et al.*, 1995), on the analysis of telomere sequences (Meyne *et al.*, 1995) and on molecular phylogenetic analysis (Hasegawa & Crozier, 2006).

The purpose of this study is to provide a new species-level revision of the *M. pilosula* species complex, and to integrate these results with existing karyological knowledge.

Methods

Sources of study material: Two major research programs with primary interest in Jack-jumper species’ distribution provided most of the specimens reviewed here:

(1) *The Japan/Australia Cooperative Ant Karyology Program* (JACP), introduced above, furnished a large proportion of subject specimens. Vouchers for all Jack-jumper and other ant records reviewed in JACP publications (e.g. Imai, Taylor *et al.*, 1994, which summarizes and maps all then current *pilosula*-complex collections) are deposited in the ANIC. They carry accession numbers in the form “HI87–144”, indicating the year of collection and the sample number. The field work was collaborative and the “HI” label should be understood to indicate “H.T. Imai *et al.*” as collectors. Twelve collecting expeditions were mounted between 1985 and 1999. Locality data for 221 karyological samples are given below in the discussions of individual species (see also Imai, Taylor *et al.*,

1994, appendix). They generally cite a place name or landmark close to the actual collection locality without further detail. Geographical coordinates were not originally recorded, but have been added here. JACP field work was usually conducted in November/December when pharate worker pupae ("prepupae") with actively dividing brain cells suitable for karyological preparation were predictable. Male pupae at that season are less well developed, so few male karyotypes are known and no adult males were collected. The JACP expeditions and their personnel (see full names under "collectors" below) were: (1) 30 Sep/26 Nov 1985: ACT: NSW (HTI, RWT); (2) 27 Nov/30 Dec 1985: NSW, QLD (HTI, RWT, MK); (3) 9 Nov/22 Dec 1987: ACT, NSW, SA, TAS, VIC (HTI, RWT, SK); (4) 5/10 Dec 1989: WA (HTI, MK, MYW); (5) 11/26 Dec 1989: ACT, NSW, SA, VIC (HTI, RWT, MK, KOG, MYW); (6) 2/9 Dec 1991: WA (HTI, RWT, KOG); (7) 10/14 Dec 1991: ACT, NSW (HTI, RWT, KOG); TAS (HTI, RWT, KOG, BBL); (8) 20/29 Nov 1994: WA (HTI, RWT, HH, MY); (9) 8/10 Dec 1994: TAS (HTI, RWT, HH, BBL); ACT, NSW (HTI, RWT); (10) 11 Dec/3 Jan 1996: ACT, NSW (HTI, RWT, MK, KOG, KY); (11) 1/4 Jan 1999: ACT, NSW, SA (HTI, YU, KOH); (12) 24 Nov /21 Dec 1999: ACT, NSW, SA, TAS, WA (HTI, RWT, MK, EH). The project is recalled by Imai (2010).

(2) *The Australian Ant Venom Allergy Study* (AAVAS): This program was funded by The Australian National Health and Medical Research Council for the term 2004/2008, with Principal Investigator Dr Simon Brown, a Perth-based allergist (S.G.A. Brown *et al.*, 2011). Over 400 Jack-jumper and other *Myrmecia* samples were gathered in southwest WA, SA, VIC, NSW, the ACT and QLD, and deep frozen for later dissection and concentration for analysis of their poison gland contents. All samples have voucher specimens in the ANIC. Collection localities for 213 AAVAS *pilosula-group* records are cited below under the individual species headings. The project sought to identify the stinging ant species responsible for human anaphylaxis in Australia, the geographical distribution of reactions, the feasibility of diagnostic venom-specific testing, and to extend previous studies on the chemical composition and human toxicology of *Myrmecia* venoms. All Jack-jumper taxa recognized here have been found to be allergenic to humans.

Repositories: Abbreviations for collections consulted, with the names of collaborating curators are: **AMSA** = Australian Museum, Sydney (Derek Smith); **ANIC** = Australian National Insect Collection, CSIRO, Canberra (Steve Shattuck); **BMNH** = Natural History Museum, London, UK (Barry Bolton); **CASC** = California Academy of Sciences, San Francisco, U.S.A. (Brian Fisher); **JDMC** = Jonathon D Majer collection, Curtin University (Jonathan Majer, Brian Heterick); **MCZC** = Museum of Comparative Zoology, Harvard University, Cambridge Ma, USA (Stefan Cover); **MVMA** = Museum of Victoria, Melbourne (Ken Walker); **QMBA** = Queensland Museum (Chris Burwell, Rudolf Kohout); **QVML** = Queen Victoria Museum, Launceston, Tasmania (Robert Mesibov); **SAMA** = South Australian Museum, Adelaide (Archie McArthur); **TMGH** = Tasmanian Museum and Art Gallery, Hobart (Catherine Byrne); **WAMA** = Western Australian Museum, Perth (Mark Harvey).

Distribution records: Localities are listed by State in alphabetical order. Field coordinates determined by the original collectors are cited only for the AAVAS records or the specimen labels of some other collectors. Many of the AAVAS records have the format (-37.07.408, 139.59.683), representing 36°31'27"S, 148°15'37" (note parentheses). Other coordinates from labels have the format (-36 31, 148 15) (representing 36°31'S, 148°15'E) (note parentheses). Records for which original coordinates are not available (mostly those of the JACP collectors and B.B. Lowery) have been interpreted here by estimation using the online official Australian Government Place-name Gazetteer (<http://www.ga.gov.au/place-names/>). They are formatted [-36 31, 148 15] (note brackets), with the addition of an error term (e.g. ±3km) when distances from a reference site are provided by the original labels or published data. Otherwise each is based directly on the indicated reference locality, with an implicit unknown degree of error between that site and the true collection site.

Collectors: Abbreviations for the names of collectors cited below (and above) are: BBL: Bede Lowery; EFR: Edgar Riek; EH: Eisuke Hasegawa; GKI: Geoffrey K Isbister; HH: H. Hirai; HTI: Hirotami T. Imai; KOG: Kazuo Ogata; KOH: K. Ohnishi; KY: K. Yamauchi; MK: Masao Kubota; MY: M. Yamamoto; MYW: Masayasu Y. Wada; PSW: Philip S. Ward; RH: Robert Heddle; RM: Raymond Mullins; RWT: Robert W. Taylor; SB: Simon Brown; SK: Satoshi Kuribayashi; SM: Sharon Marsden; TG: Tom Greaves; YG: Yuri Gilhotra; YU: Y. Ugawa.

Specimen measurements and indices: Measurements are given for all holotypes and for the smallest and largest encountered specimens of each species. They have no special statistical significance except to indicate the general parameters of size and proportions for each taxon. They were prepared using a Zeiss stereomicroscope with hairline eyepiece and manual micrometer stage with digital electronic readout (read at mm/1000, rounded to mm/100). Conventions follow Ogata & Taylor (1991): **TL** = Aggregate total length of body tagmata and mandibles

measured as sections in side view and tallied. **HW** = Head Width (frontal view, maximum, across eyes). **HL** = maximum Head Length, from anterior clypeal border to a transverse line connecting the bilateral posteriormost extensions of the cranium (frontal view). **CI** = Cephalic Index ($HW \times 100 / HL$). **EL** = Maximum measurable length of compound eye in right oblique view. **SL** = Chord length of scape. **OI** = Ocular Index ($EL \times 100 / HW$). **SI** = Scape Index ($SL \times 100 / HW$). **PW** = Pronotum Width (dorsal view). **WL** = Weber's Length of mesosoma. **PetW** = Petiolar Node Width, dorsal view. **PpetW** = Postpetiole Width, dorsal view.

Illustrations are extended focus (Z stack) macro photographs prepared using an Olympus E330 digital camera; bellows mounted Zuiko OM 35mm 1:2.8 automacro lens; twin electronic flash heads with diffusers; camera stand; custom built electronically-controlled stepper stage; Combine Z software; with picture stacks of 20 to 40 images; the final image adjusted using Adobe Photoshop Elements 7 software). Scale is indicated in captions using standard dimensions of the illustrated specimens: HW, WL or PW.

Deposition of Types: Holotypes and most paratypes, including all queen and male specimens, are deposited in the ANIC. Paratypes or holotype-compared voucher specimens, wherever possible, are deposited in Australian State Museums (AMSA, MVMA, QMBA, SAMA, WAMA, TMHA) and in BMNH, CASC, MCZC, MHNG.

The *Myrmecia pilosula* species complex

Diagnosis. Workers of the *M. pilosula* complex are easily recognized within *Myrmecia* (Ogata and Taylor, 1991). Relatively small species: total length, including mandibles, ranging overall from about 10 to 14 mm; mean size only slightly different in the separate species. Body color essentially uniformly dark blackish brown to black; mandibles, antennae, and frequently tarsi and/or tibiae reddish-orange; clypeus pale yellowish to light brown. Tip of apical antennomere flushed dark brown. Foreleg tarsi and tibiae in all known species prominently reddish-orange; coxae, trochanters and femora always darkly colored, approximately matching body color; no transverse dorsal preoccipital carina; a ventral secondary tooth present near mandibular apex; mandibular dentition complete along length of jaw, all teeth essentially symmetrically erect, none inclined asymmetrically towards the mandibular base.

General morphology: General habitus as in the accompanying figures. Sculpturation generally similar among the species: mandibles smooth and shining, each dorsally with a few effaced apical longitudinal rugae. Head with longitudinal spaced striae separated by fine puncturation and effaced on the sides behind the eyes. Pronotum more strongly longitudinally striate than head, the nuchal collar smooth to very finely transversely striate. Mesonotum similarly or more finely longitudinally striate than pronotum, varying to almost smooth, with a “leathery” appearance in several species due to superficial sculpturing, notably in both races of *M. pilosula*. Propodeal dorsum generally with a short anterior section bearing essentially longitudinal, often posteriorly divergent striate rugosity; the remainder transversely more strongly striate rugose. Petiolar dorsum ranging from almost smooth to quite strongly rugose, the intensity of sculpturation varying, but in most specimens approximately matching that of the mesonotum. In both races of *M. pilosula* the sculptural intensity in these areas varies allometrically and in concert. Postpetiole and gaster very finely and densely micropunctate, only moderately shining. The exposed anterior sections of the second and third gastral tergites (true abdominal segments 5 and 6), which each insert beneath the preceding tergite, minutely transversely striate and reflective.

Pilosity generally abundant on body and appendages, with the notable exception of *M. haskinsorum* (see key couplet 1 below); the hairs generally short and erect to suberect, longer and more flexuous on the underside and apex of the gaster, beneath the postpetiole and on the propleurae.

Pubescence generally very fine, often dense, varying in density and color interspecifically (generally either silvery grey or yellowish gold) as specified below in the species descriptions.

Human exposure

Urban Jack-jumpers are common in Hobart (*M. pilosula* (Western Race)), Canberra (*M. croslandi*, *M. impaternalata*) and Adelaide (*M. pilosula* (Western Race)). They are less commonly represented in collections from Melbourne, with records of both races of *M. pilosula* and of *M. croslandi*, and poorly represented from Sydney, where there is

only a single current record of *M. banksi* from Leumeah in the southeast of the city. There have been relatively few reports of Jack-jumper sting allergy from Sydney (B. Baldo, *pers comm.*) unlike Melbourne and especially Hobart, Adelaide and Canberra, so Jack-jumpers might not be well represented there. This was also the view of long-time Sydney resident Rev B.B. Lowery (*pers comm.*), who collected many Jack-jumper samples elsewhere (including all species recognized here). I have located few Melbourne urban records, but this is a possible artifact of inadequate collecting. Brisbane and Perth are, as far as known, outside the range of any species, though *M. imaii* is likely present in Perth.

In recreational bushland areas “Western” *M. pilosula* is common in the Adelaide Hills, the Grampians (VIC) and widely in Tasmania. The eastern race of *M. pilosula* is widespread in the NSW Snowy Mountains and associated ranges including the Victorian Alps, the Brindabella Ranges (ACT) and in the Blue Mountains west of Sydney.

Taxonomy of the primary JACP report and other papers

Imai, Taylor *et al.* (1994) and Crozier *et al.* (1995) recognized the species *M. banksi*, *M. croslandi*, *M. haskinsorum* and *M. imaii* precisely as defined here. The “scientific” names of these taxa, apart from *M. croslandi*, were then used prematurely (and with explanation) without the sanction of formal taxonomic publication. Nomenclature of these neglected species is rectified here, and this is their place of formal taxonomic publication. The name “*M. pilosula* s. str.” of the JACP publications was applied to the Western Race of that species as defined here. Other entities deemed speculatively in 1994 to represent hybrids between *M. banksi* (B) and *M. pilosula* (P) are assigned here to the Eastern Race of *M. pilosula*. These and the other “PB hybrids” of the above papers are allocated below as follows: (1) The Tasmanian P/PB–1 Mix and P/PB–2 Mix entities are assigned to the Western Race of *M. pilosula*; (2) PBF₁–1 and PBF₁–2 are “synonymous” with *M. impaternata*; and (3) PB–1 and PB–2 are identified as the Eastern Race of *M. pilosula*. Details are discussed in the following section and under the relevant species headings.

Taxonomic synopsis

Myrmecia banksi sp. nov.

Myrmecia croslandi Taylor, 1991

Myrmecia haskinsorum sp. nov.

Myrmecia imaii sp. nov.

Myrmecia impaternata sp. nov.

Myrmecia pilosula Fr. Smith, 1858

= *Myrmecia ruginoda* (Fr. Smith 1858)

Key to species of the *M. pilosula* complex (workers)

Notes:

- (1) The use of characters involving pubescence is compromised if subject specimens are greasy.
- (2) *M. imaii* is currently the only *pilosula*-complex species known from WA.
- (3) Likewise the Western Race of *M. pilosula* is the only relevant taxon presently known from Western Victoria and SA, including Kangaroo Island.
- (4) All known Tasmanian specimens not identified as the easily recognized *M. haskinsorum* are referable to the Western Race of *M. pilosula*.
- (5) The eastern, hybrid-originated species *M. impaternata* is chromosomally very different from the WA *M. imaii* and the two could not possibly be considered conspecific. They are however morphologically similar, so the provenance of specimens can be important for their identification. The color of the brassy cephalic pubescence in *M. impaternata* can be hard to perceive in some lights. It is best seen in acute lateral diagonal view of the frons, across the near-side eye.

(6) The sculptural characters used in couplet 6 vary allometrically in both subject species, such that large specimens of eastern *M. pilosula* can be confused with *M. croslandi* by inexperienced identifiers. Small *M. pilosula* (Eastern Race) and large *croslandi* specimens are readily distinguished, so that the collection and consultation of specimens in size- ranged series is desirable.

- 1 Pilosity essentially lacking on all body surfaces except gastral apex, propleurae and undersides of head, postpetiole and gaster. Dorsal profile from mesonotum to first gastral tergite thus uninterrupted by standing hairs (a very few, very short minute bristles occasionally present) (Fig 2). Anterior femora more or less uniformly dark brown, without distinct reddish-orange apical sections matching the adjacent tibiae and tarsi (the femoral apices at most only very vaguely infuscated) (Fig 2). Middle and hind legs also generally dark brown, without reddish-orange segments, tarsi slightly less dark, lightest apically. (Fig 2). (Snowy Mountains, NSW Southern Tablelands, VIC Alps, TAS) *M. haskinsorum*.
- Relevant sections of dorsal body profile interrupted by numerous short standing bristles or longer hairs (Figs 5, 20). Anterior femora each with a distinct gradational reddish-orange apical section, colored like the adjacent tibia and contrasting with the dark brown femoral ground color (Fig 5). Middle and/or hind legs often with some reddish-orange segments beyond the femora 2.
- 2 Pubescence on clypeus and between frontal carinae and eyes distinctly brassy yellow (best observed in lateral oblique view), usually dense (Figs 4, 5, 16, 17, 19, 20) 3.
- Pubescence on clypeus and between frontal carinae and eyes silvery white (described as “ashy” by Smith, 1858) often dense, sometimes diffuse. (Figs 7, 8, 14) (See notes (4) and (6) above) 5.
- 3 Head, when viewed obliquely from above and behind, with a strong overall greenish-gold caste provided by the minute elements of dense brassy pubescence which crowd the surfaces between fine longitudinal sculptural costulae (Figs 4–6). (Coastal NSW, from just south of Sydney, south at least to Batemans Bay, currently unknown from elevations above ca 150m.) *M. banksi*.
- Cephalic pubescence and resulting color cast in oblique posterior view of head much less strongly developed. Species from much higher elevations on or around the New England and Southern Tablelands of NSW, the ACT or southwestern WA (Figs 19, 20) (See notes (2) and (4) above) 4.
- 4 Middle leg tibiae and tarsi reddish-orange, usually less bright than those of fore legs (the hind legs more or less uniformly dark brown, matching anterior and middle femora). Cephalic pubescence relatively prominent. (New England and Southern Tablelands of NSW and surrounding areas, including ACT) (Figs 16–18). *M. impaternalata*.
- Middle and hind legs more or less entirely dark brown, matching anterior femora. Cephalic pubescence less well developed (Figs 19–21). (extreme southwestern WA.) *M. imaii*.
- 5 Hind legs consistently almost entirely dark brown, the tarsi slightly lighter. Middle leg femora similarly colored but the tibiae and tarsi usually reddish-orange, though sometimes brown like the femora 6.
- Hind and middle tibiae and tarsi bright reddish-orange, matching those of the anterior legs. In Tasmania, where this is the only species additional to *M. haskinsorum* (eliminated in couplet 1 above), some individuals in nests which otherwise conform to this diagnosis may have the middle and hind tibiae brown, as in the alternative prescription. (Figs 13–15) (SA, including Kangaroo Island; VIC, generally west of longitude 145E and TAS). *M. pilosula* (Western Race).
- 6 Mesonotum usually obscurely shagreened and “leathery” in appearance; often with effaced or vestigial longitudinal striae, less strong than those of the pronotum (Fig 12). (Usually much less distinctly sculptured than in the opposed *M. croslandi*, except in large specimens). Petiolar dorsum less heavily sculptured than propodeal dorsum. The node at most bearing effaced coarse punctate rugosity, with the punctural elements clearly expressed, at least finely shagreened with a leathery appearance and almost smooth (especially medially) though not strongly reflective due to effaced traces of puncturation. (In intermediate individuals the rugosity appears to break down to coarse puncturation, which becomes peripheral and more spaced as the disk of the node becomes more nearly smooth). Pronotal and propodeal sculpture in general less strongly expressed than in *M. croslandi*. These features vary allometrically and are strongest in larger specimens. Petiole in dorsal view (Fig 12) generally smaller and less-bulky than in the alternative *M. croslandi* but less clearly distinguished in larger specimens (Figs 10–12) (eastern NSW, ACT and VIC, generally east of longitude 144E) *M. pilosula* (Eastern Race).
- Mesonotum distinctly longitudinally striate rugose, the elements clearly incised (Fig 9), generally a little less strongly developed than those of pronotal dorsum. Petiolar dorsum relatively heavily sculptured with medium, generally transverse rugosity; the elements almost as strong as those of the adjacent propodeal dorsum but relatively wavy, with clear radial and/or circular trends in some specimens and little trace of associated coarse puncturation. These features vary allometrically and are strongest in larger specimens. Petiole in dorsal view relatively large and bulky (Figs 11, 12) (eastern NSW, ACT; notably New England and Southern Tablelands, with scattered records south at least to Warrandyte, VIC). *M. croslandi*.

Descriptions and discussion of individual species

Myrmecia haskinsorum sp.n.

(Figs 1–3)

Myrmecia haskinsorum is a species essentially of high elevations, known from the Snowy Mountains, Victorian Alps and upland Tasmania, with some Tasmanian records from lower elevations. In most localities of record nests

are regularly covered or brushed by winter snow (as also in sympatric populations of *M. pilosula* (Eastern Race) on mainland Australia and *M. pilosula* (Western Race) on Tasmania). This species was discussed as *M. haskinsorum* by Imai, Taylor *et al.* (1994).

Type locality. NEW SOUTH WALES: Dead Horse Gap (-36 31, 148 15), Snowy Mountains National Park, near Thredbo.

Type deposition. Holotype and paratypes in ANIC, paratypes or type-compared vouchers in AMSA, MVMA, QMBA, SAMA, WAMA, TMHA) and in BMNH, CASC, MCZC, MHNG.

Material examined, distribution. NEW SOUTH WALES: Alpine Creek [-35 55, 148 33], 4/xi/1935, G.F. Hill (QMBA, ANIC—some labeled “*Promyrmecia pilosula*” by John Clark); near Corang River Bridge (-35 12, 150 03) HI87–152, HI99–14; Dead Horse Gap [-36 31, 148 15], HI87–233, 234, HI91–046, 047, HI99–017; 27/i/2006, SB&SM, 7 samples (AAVAS); Eucumbene [-36 08, 148 36], 22/ii/1959, EFR; Jamberoo [-34 39, 150 46], 7 km W 600 m, 26/xi/77, PSW acc 2900, 2907 (PSW collection); Pipers Creek [-33 3, 149 55], 10/xi/1960, EFR; near Smiggins Holes [-33 59, 148 48], 1650 m, 27/i/75, PSW acc 607 (PSW collection). AUSTRALIAN CAPITAL TERRITORY: Mt Ginini, [-35 32, 148 46], HI99–016. VICTORIA: Benambra [-36 57, 147 42], 700 m, 25/i/2006 SB&SM (AAVAS); Ben Cairn [-37 43, 145 37], 14/v/1937, TG; Mt Buffalo, near The Chalet ski lodge [-36 43, 146 49], HI87–224, 225, TASMANIA: near Bothwell [-42 23, 147 00], HI87–197–199; Epping Forest [-41 46, 147 21], BBL; Great Lake [-41 53, 146 44], 28/x/1949, TG; Miena [-41 59, 146 43], HI91–027, 041, HI 99–022; Murderers Hill [-41 58, 146 40], HI87–200; Tunbridge [-42 08, 147 25], BBL. All ANIC unless indicated.

Worker diagnosis. General features as illustrated and in key couplet 1 above. The most easily recognized species of the *Myrmecia pilosula* complex. Distinguished by the almost total lack of pilosity interrupting the dorsal body profile, by the lack of reddish-orange apical color-marking on the dark brown anterior femora, and the absence of brightly differentiated reddish-orange tibiae and tarsi on the more or less uniformly dark brown, apically lightly infuscated, middle and hind legs. The body often has a distinctive and sometimes very noticeable diffuse bluish cast in live specimens, recalling the bloom of grape skin. This feature seems unique to *haskinsorum* in *Myrmecia* and is lost in dry or spirit-preserved specimens. It has been observed in the Snowy Mountains, Mt Buffalo and central Tasmania, and appears less prominent at lower elevations of record. Labrum yellowish in the center with bilateral dark brown markings. Terminal two or three antennomeres usually darkly infuscated. Mesonotum (longitudinally striate-rugose) and petiolar dorsum (more or less transversely rugose) distinctly and quite strongly sculptured, with little evidence of allometric reduction in smaller specimens. Pubescence silvery, without yellowish reflections; very fine, short and sparse except on the clypeus, coxae, femora, postpetiole and gaster. A very few short hairs may be visible in profile view of the head and pronotum, and a few minute bristles on the mesonotum, less often on the petiole.

Dimensions. (Holotype, smallest available specimen (Mt Buffalo), largest available specimen (Mt Buffalo) (mm): TL = 11.6, 11.4, 12.0; HW = 2.36, 2.34, 2.46; HL = 2.15, 2.13, 2.22; CI = 109, 110, 111; EL = 0.92, 0.87, 0.92; OI = 39, 37, 41; SL = 1.94, 1.90, 1.93; SI = 82, 81, 78; PW = 1.48, 1.45, 1.48; WL = 3.64, 3.60, 3.78; PetW = 0.86, 0.85, 0.88; PpetW = 1.36, 1.33, 1.41.

Elevational range. The AAVAS Dead Horse Gap sites were recorded by GPS at 1,553 to 1,608m, the highest confirmed for the *M. pilosula* complex, 620m short of Mt Kosciusko summit. Wheeler (1933) probably referred partly to *M. haskinsorum* when reporting “*M. pilosula*” from Mt Kosciusko (see below). Elevations for other key localities are: Corang River Bridge, ca 580m (GPS reading), the lowest mainland record for *haskinsorum*; Mt Buffalo, ca 1,300 m; and in Tasmania: Tunbridge, ca 200m (The lowest-elevation confirmed Tasmanian record) and Murderers Hill, ca 1,100 m (the highest-elevation Tasmanian record). Targeted search at the summit area of Mt William (= Mt Duwil – 1,167m), the highest peak in the Grampian Ranges, VIC, by four collectors including the author, failed to find *M. haskinsorum*, which perhaps does not range that far west.

Variation. The mainland and Tasmanian populations were presumably geographically isolated after dispersal of ancestral stock across intervening low elevation areas during a past cool climate episode prior to the separation of Tasmania (ca 14,000ybp) (since *haskinsorum* is present there). Diagnostic morphological characters are not significantly variable among available specimens. The Snowy Mountains and Mt Ginini populations are those most likely to have vestigial dorsal mesosomal pilosity. The body color is generally a little more blackish in *haskinsorum* than other *pilosula*-group species, and the brown sections of the legs darker in hue. Specimens from lower elevations tend to have the leg color lighter brown, as in Figs 1–3.

FIGURES 1–3. *Myrmecia haskinsorum*, Jamberoo, NSW. Standard views. HW 2.46 mm, WL 3.64 mm, PW 1.57 mm.

Etymology. Named for Caryl P. Haskins and his wife Edna Haskins in recognition of their important pioneering studies on the biology of *Myrmecia* and other Australian ants.

Karyology. Chromosome numbers vary between $2n=12$ and $2n=24$, the lower counts resulting mainly from centric fission, centric fusion and AM inversion (Imai, Taylor *et al.*, 1994: 147, Fig 6). The karyotypes of colonies from Corang River Bridge and Mt. Buffalo, respectively with $2n=23/24$ and $2n=20$, were considered by Imai, Taylor *et al.* to be closely related to those from Tasmania with $2n=18$. The Dead Horse Gap colonies have $2n=18/15/12$, and are karyotypically most similar to a Tasmanian colony with $2n=17$. Four fusions with different arm combinations were detected from colony HI87–234 (Dead Horse Gap).

Field associations. Sympatric with the Eastern Race of *M. pilosula* and *M. croslandi* near Corang River Bridge, with Eastern Race *pilosula* in the Snowy Mountains and on Mt Buffalo, and with the Western Race in Tasmania.

Discussion. Wheeler (1933: 56–57), who confused the two races of *M. pilosula* and *M. haskinsorum*, almost certainly referred to *haskinsorum* when describing “*pilosula*” workers and queens on Mount Kosciusko as “dull black, but when alive and in bright sunlight, with a distinct bluish tinge, probably due to a fugitive pigment”. Also, at least in part, when stating that on Kosciusko (“*M. pilosula*”) was “very abundant and the dominant species at elevations from 4000 to 6000 ft.” (c.a. 1220 to 1838 m).

Research prospects. Future potential research topics include (1) genetical and morphological comparison of the mainland and Tasmanian populations, which have a defined approximate time of geographical and phylogenetic separation; (2) investigation of the nature and role of the fugitive bluish flush in high alpine populations.

Myrmecia banksi sp.n.

(Figs 4–6)

Myrmecia banksi is known only from low elevations along a narrow coastal and sub-coastal strip in NSW south from Sydney to Batemans Bay.

This species was referred to in previous JACP publications as the “greenhead” form of *M. (pilosula)*, as “*M. (pilosula)* $2n=10$ ”, or informally as “*M. banksi*”.

Type locality. NEW SOUTH WALES: South Nowra, shortly north of the junction of Forest Road and Bulldog Avenue track (-34 56, 150 37), ca 800 meters west of the Forest Road/Princes Highway intersection. Forest Road marks the boundary between Currambene State Forest (to the North) and Nowra State Forest. The area is referred to locally as Comberton,

Type deposition. Holotype and paratypes in ANIC, paratypes or type-compared vouchers in AMSA, MVMA, QMBA, SAMA, WAMA, TMHA) and in BMNH, CASC, MCZC, MHNG.

Material examined, distribution. Known from coastal or sub-coastal NSW, from Leumeah, Sydney, south to Catalina, Batemans Bay. All collections are from elevations below 70 meters. Localities most distant from the coast are at Wandandian (ca 5km inland) and Leumeah (ca 24 km). *Myrmecia banksi* will almost certainly range further north and south, and could occur more widely in the Sydney area where records of Jack-jumpers are currently sparse.

JACP and AAVAS records. NEW SOUTH WALES: Leumeah, E of railway station [-34 03, 150 50], HI–AAGR13, AAGT11; Nowra [-34 53, 150 36], HI87–122–127, 91–057; South Nowra [-34 55, 150 36], HI99–013; AAVAS accessions 145, 147, 148, SB&SM; Wandandian [-35 5, 150 31], HI89–034, HI91–048, 100, 101; West of Nelligen [-35 39, 150 8], HI85–213, HI91–191; Sheep Station Creek near Nelligen [-35 39, 150 8], HI87–158; Batemans Bay [-35 42, 150 11], HI87–160; Catalina [-35 43, 150 11], AAVAS. The JACP “Nowra” samples were collected near HMAS *Albatross* Naval Air Station; the “South Nowra” records from the vicinity of the type locality; and the Batemans Bay sample from near the western end of Maloneys Beach.

Worker diagnosis. General features as illustrated and in key couplets 1, & 3 above. *Myrmecia banksi* is distinguished within the *pilosula* complex by its dense, brassy-green cephalic pubescence. This produces strong greenish-yellow reflections, readily visible in living specimens with hand lens magnification, and encouraged Imai’s field epithet “greenhead”. Anterior femora chocolate brown, each with a reddish-orange apical section up to 1/3 its length, matching the adjacent tibia. Middle tarsi and tibiae reddish-orange, matching those of fore legs. Hind

FIGURES 4–6. *Myrmecia banksi*, Holotype, South Nowra, NSW. Standard views. HW 2.66 mm, WL 3.86 mm, PW 1.72 mm.

femora and tibiae dark brown, like anterior femora; the tibiae sometimes a little lighter, with their apices and the tarsi progressively lighter in color towards the foot. *Myrmecia banksi* is otherwise morphologically similar to the eastern species *Myrmecia impaternalata* and the Western Australian *M. imaii*, which have similar but usually much-less dense brassy cephalic pilosity, and distinctive, very different karyology (see below). The provenance of specimens and their comparison with confidently identified vouchers is important in differentiating these taxa.

Dimensions. (Holotype, smallest paratype, largest paratype (mm): TL = 13.04, 11.81, 13.45; HW = 2.66, 2.26, 2.76; HL = 2.44, 2.48, 2.77; CI = 109, 109, 111; EL = 1.02, 0.87, 1.06; OI = 38, 38, 38; SL = 1.98, 1.75, 2.09; SI = 74, 77, 76; PW = 1.72, 1.70, 1.77; WL = 3.86, 3.33, 3.92; PetW = 0.94, 0.77, 1.01; PpetW = 1.50, 1.19, 1.60.

Etymology. Named for Joseph Banks (1743–1820) who with Daniel Solander in 1770 first scientifically collected Australian ants and other insects at Botany Bay, NSW, while exploring ashore from James Cook's HM Bark *Endeavour* in habitat similar to that at the *M. banksi* Type Locality. The *Endeavour* landing site is about 100km NNE of the *M. banksi* South Nowra site.

Karyology. Most examined specimens (sampled from all above localities except Catalina and Batemans Bay) had the monomorphic karyotype $2K=6M+2M^c+2A$ ($2n=10$) (Imai, Taylor *et al.*, 1994: 147, Fig. 5h). One putative mutant individual from Leumeah (sample HI–AAGH–11) had a complicated translocation producing $2n=9$ (Imai, Crozier *et al.*, 1977).

Notes. Sympatric associations with other *M. pilosula*-complex species are unknown. Convincing karyological evidence identifies *M. banksi* (or a close ancestor) as one of the parent species of the apparently parthenogenetic and hybrid-originated *M. impaternalata* (the other putative parental taxon is an element of the Eastern Race of *M. pilosula*: see below under *M. impaternalata*). Because of close similarity between *M. banksi* and *M. impaternalata* future studies, such as analysis of their distributional relationships between the NSW South Coast and Southern Tablelands, might require karyological or DNA analyses to authenticate identifications. A winged male is present in HI87–123. *Myrmecia pilosula* (Eastern Race) is considered likely to be found in future as a sympatric associate of *M. banksi*.

Research prospects. See below under *M. impaternalata*.

Myrmecia croslandi Taylor

(Figs 7–9)

Myrmecia croslandi Taylor, 1991: 288, worker, Type Locality: Immediately E to NE of Corang River Bridge (-35 12, 150 03), on the Nerriga Road, near Braidwood, NSW.

The type-locality is common to both *M. croslandi* and *M. impaternalata* (see below).

Myrmecia croslandi was described initially from the ACT, nearby NSW and Warrandyte South, VIC. It is now known also from the New England Tablelands in northeastern NSW and upland localities on the Darling Downs of SE QLD, from Glen Innes in northeastern NSW, and from near Cobangra, VIC. It was discussed as “*M. pilosula*” by Crosland and Crozier (1986), and as “*M. (pilosula) n=1*” by Imai & Taylor (1989).

Material examined, distribution. QUEENSLAND: Dalby [-27 11, 151 16], 6/xii/35, N.Geary, 2 alate gynes (QMBA); Millmerran [-27 53, 151 16], 12/v/1941, J. Macqueen (QMBA); Stanthorpe [-28 39, 151 56], 21/ix/30, E. Sutton (MVMA, QMBA); Warwick [-28 13, 152 2], 480 m, 1 Jan 2006, P. McAllister (QMBA). NEW SOUTH WALES: Glen Innes [-29 44, 151 44], 6/ix/1937, F.A. Cudmore (MVMA); New England National Park [-30 30, 152 30], 900 m (-30 25, 152 30) D.S. Olson (PSW collection); near Corang River Bridge (-35 12, 150 03), (Type locality), HI87–136, –148, –151, –153, HI89–030–032, HI91–049–050, HI99–05; Mayfield [-35 12, 149 48], HI87–154. AUSTRALIAN CAPITAL TERRITORY: Bruce [-35 15, 149 6, 18/iii/2007, AAVAS; Curtin [-35 19, 149 5], 28/iii/2006, AAVAS; Canberra [-35 18, 149 8], HI87–135–165–236; National Botanic Gardens (35 16-766, 149.06-579), AAVAS. VICTORIA: Cobungra [-37 6, 147 25], 10 miles W (MVMA); Warrandyte South [-37.46, 145 15] HI87–213.

Myrmecia croslandi (along with the locally less frequent *M. impaternalata*) is common in Canberra parks, gardens, suburban grass lawn roadside “nature strips” and in grassy bushland. Nests of the two species are sometimes found only meters apart. *Croslandi* was found similarly common at localities near Armidale, NSW in Dec/Jan. 1995–96 and Nov. 1999 by JACP collectors. It is also sympatric there with *M. impaternalata*. Several records confirm the presence of this species in SE Queensland.

FIGURES 7–9. *Myrmecia croslandi*, Canberra, ACT. Standard views. HW 2.50 mm, WL 3.74 mm, PW 1.60 mm.

Worker diagnosis. General features as illustrated and in key couplets 1, 2, 5 & 6 above. Distinguished from other *pilosula*-complex species by its robust form, more massive petiolar node, especially *versus* representatives of the two races of *M. pilosula* (compare Figures) and other details, as specified in the key. Middle and hind tibiae medium brown, matching the femora, the tibial apices minutely lightly infuscated at the bases of the reddish-orange spurs. Larger workers of both races of *M. pilosula* often closely resemble those of *M. croslandi*. Western *M. pilosula* is then distinguishable by its reddish-orange hind tibiae (see below under that species), but *Eastern M. pilosula* and *M. croslandi* are essentially identical in leg coloration (see key couplet 6 above for their discrimination).

Dimensions. The holotype and smallest and largest available specimens have the following dimensions (mm): TL = 13.54, 12.46, 13.53; HW = 2.63, 2.54, 2.79; HL = 2.35, 2.37, 2.51; CI = 112, 107, 111; EL = 1.02, 1.02, 1.08; OI = 39, 40, 39; SL = 2.02, 1.99, 2.06; SI = 77, 78, 74; PW = 1.70, 1.60, 1.81; WL = 3.88, 3.73, 4.06; PetW = 1.06, 0.93, 1.14; PpetW = 1.59, 1.43, 1.69.

Etymology. Named for Michael W. J. Crosland, who as a student of R. H. Crozier at the University of New South Wales, Sydney, discovered the $2n=2$ chromosome count while experimenting with the Crozier/Imai air-drying technique of chromosome preparation for microscopy (to great initial consternation that the technique had failed, but later celebration). Crosland had collected the subject specimens shortly before at Tidbinbilla Nature Reserve near Canberra.

Karyology. Workers and queens in some colonies have the minimum possible eukaryote chromosome count of $2N=2$. *Myrmecia croslandi* is widely celebrated as the only animal other than the nematode *Diploscapter coronata* known to possess a single pair of chromosomes. Imai & Taylor (1989) reported that its chromosome numbers in fact vary, ranging $2n=2$, 3 or 4, and that *croslandi* demonstrates highly complicated chromosome polymorphisms, including telomere fusion, shift of centromeric activity by centromeric inactivation, salutatory growth of constitutive heterochromatin (C^+), and AM inversion. Typical *croslandi* karyotypes with $2n=2$ ($2K=2M^{cl}$), and $2n=3$ ($2K=1A^c+1M+1M^{cl}$) were illustrated by Imai, Taylor *et al.* (1994, figs 5a, 5b), and karyological details discussed by Imai, Hirae *et al.* (1992).

Field associations. Sympatric variously with *M. impaternalata* and Eastern *M. pilosula*, and with *M. haskinsorum* (and Eastern *pilosula*) at Corang River Bridge (-35 12, 150 03). Most known records of *M. impaternalata* were taken in sympatry with *M. croslandi*.

Research prospects. See below under *M. impaternalata*.

***Myrmecia pilosula* Fr. Smith (Western Race)**

(Figs 13–15)

Myrmecia pilosula Fr. Smith, 1858: 146. Lectotype worker (here designated), Australia; Tasmania (BMNH) (BMNH(E)1015843) (examined).

= *Ponera ruginoda* Fr. Smith, 1858: 93. Holotype male, Australia (BMNH) (BMNH(E) 1015844) (not examined). Synonymy by W.L. Brown; 1953: 6.

See W.L. Brown (1953) for further nomenclatural details regarding past spurious assignments of *ruginoda* to the genera *Rhytidoponera* and *Ectatomma*. Other combinations of *M. pilosula* have been *Myrmecia* (*Halnamyrmecia*) *pilosula* (Wheeler, 1922: 195); *Myrmecia* (*Promyrmecia*) *pilosula* (Wheeler, 1933: 56); and *Promyrmecia pilosula* (Clark; 1943: 109).

Myrmecia pilosula mediorubra Forel, 1910 is a junior synonym of *M. chasei* Forel, following Clark (1951). The Western Race of *M. pilosula* was cited as “*M. pilosula s. str.*” by Imai, Taylor *et al.* (1994).

The listing “*M. pilosula*” from Rockhampton, QLD, by Clark (1951: 204) was presumably an error.

Myrmecia pilosula is considered here to comprise two geographical races. *M. pilosula* (Western Race) includes all Jack-jumper specimens known from western Victoria, southeast mainland South Australia and Kangaroo Island. It occurs widely in Tasmania (from where *M. pilosula* was originally described) and is found there sympatric with *M. haskinsorum* at higher elevations. It is common in Tasmania from sea level to at least 1,000 meters.

Type material, lectotype designation: Extended-focus images of a damaged, headless Tasmanian syntype worker in the BMNH (specimen code BMNH(E)1015843), including its labels, are accessible on the CASC/Antweb website (<http://www.antweb.org>) (CASC specimen code ANTC22283). That specimen is here designated

Lectotype of *Myrmecia pilosula*, and will be so labeled. Any other syntypes are here designated paralectotypes. The legs of the lectotype, while faded, indicate reddish-orange hind tibiae matching those of the middle legs. It therefore represents the “red-hind-tibial” typical form of *M. pilosula* found on Tasmania, and elsewhere across the geographical range of Western-Race *M. pilosula* (see below under “variation”). Identification of other specimens discussed here is thus confirmed by indirect lectotype comparison (compare the Antweb illustration details with Figs 13–15).

Browning (1987) noted that Smith’s *M. pilosula* syntype male (BMNH) is “not the same species as the other syntypes” but “a species of the (*Myrmecia*) *mandibularis* group”.

The unique holotype male of the putative synonym *Ponera ruginoda* (BMNH(E)1015844) is comprehensively illustrated on the Antweb site (Casent0902800) where dissection of its terminalia by G.P. Browning in 1983 is noted. The metasoma is detached and not illustrated. Browning’s (1987) records of his “*M. pilosula sens.lat.*” included at least both races of *M. pilosula*, *M. imaii* and *M. impaternalata* (*pers obs.*, based on known distribution of the several taxa and details of ANIC specimens cited by Browning and re-examined here). His figure 91 illustrates the terminalia of “*Myrmecia pilosula*” males from Rocky River (Kangaroo Island) and Urailda (Adelaide Hills). In the apparent absence of indicated voucher specimens (ANIC) they are reasonably referable to *M. pilosula* (Western Race), since it is the only known South Australian Jack-jumper, and all available Browning SA specimens represent it (as do all other known SA collections). Browning’s figs 92a and 92b depict genitalic components of the dissected *Ponera ruginoda* holotype, which “appear to be very similar to *pilosula*.” Browning further states that “no variation has been observed in the male terminalia of *pilosula*”, presumably including the *ruginoda* holotype.

If the *M. pilosula* worker lectotype and the *ruginoda* male holotype were concluded to represent separate biological species the epithet “*ruginoda*” could be a potential senior synonym of one of the new species recognized here. A former attempt by the author to resolve this matter was inconclusive because of the condition of the *ruginoda* type and the limited species-representation of other Jack-jumper males for comparison. Final determination is considered at present not possible, but the above synonymy is nonetheless considered “safe”. For confident identification to species males must be collected with associated workers, preferably from parental nests, and the annual seasonal window for such opportunity is very limited.

Distribution: The Western Race of *M. pilosula* is the only Jack-jumper taxon known from southern VICTORIA west of Port Philip Bay and contiguously from southeast SOUTH AUSTRALIA east of Spencer Gulf, including KANGAROO ISLAND. It is very common in the central and southwest districts of Victoria; spectacularly so in and around Halls Gap in the Grampians. Elsewhere in Victoria it is known from the Mornington Peninsula and in west Gippsland, where its range contacts or intersects the putatively conspecific Eastern Race. It is the only Jack-jumper species known from South Australia. *Myrmecia pilosula* (Western Race) is widespread in TASMANIA, including King, Flinders and Bruny Islands. It appears to be absent from well surveyed Maria Island (*testé* B.B. Lowery). See below under “variation” for explanation of boldface citations for some Tasmanian localities listed here.

Material examined. JACP records have “HI” accession numbers. The “RWT” Victorian records were collected in March 2010. Unless otherwise indicated other accessions are AAVAS. Collectors are indicated by names or initials. Most South Australian AAVAS series were collected in 2005 or 2006 by SB&RH or RH&RWT (most in fact from the residential properties of known *M. pilosula*-allergic medical patients). KANGAROO ISLAND: Rocky River [-35 57, 136 44], HI87–166–169; Western River Conservation Park [-35 42, 136 56], HI87–171–176. MAINLAND SOUTH AUSTRALIA: Aldgate (-35.00.530, 138.44.300); Ashton [-34 56, 138 44]; Balhannah (-34 59.542, 138.49.933); Barooka (-37.07.408, 139.59.683); Belair [-35 0, 138 38], HI87–181–185; Belair (-35.00.411, 138.36.970); Boathouse Beach Track (-35.38.09, 138.16.00); Bridgewater (-35.00.305, 138.45.866); Carey Gully (-34 57.994, 138.45.724); Chandlers Hill; Charleston (-34 55.041, 138.55.791); Cherry Gardens (-35 04, 138 39); Coromandel Valley (-35.03.169, 138.38.188); Crafers (-34 59.408, 138.43.515); Crafers West, (-35.00.614, 138.41.571); Deep Creek Conservation Park (-35 36 03 138 1501); Echunga (-35.06.56, 138.45.05); Flaxley (-35.09.143, 138.47.516); Greenhill (-34.57.255, 138.44.066); Gumeracha (-34°52'28 138°56'28); Hahndorf (-35.03.326 138.48.310); Heathfield (-35.01.561, 138.43.362); Houghton (-34.50.437, 138.44.969); Inman Valley (-35°29'35 138°27'29); Ironbank (-35 02, 138 41); Kersbrook [-34 47, 138 51]; Little Hampton (-35.02.995, 138 51.851); Lobethal (-34.54.381, 138 52.579); Longwood; Lucindale (-36.58.379, 140.22.832); Millicent (-35.401, 140.19.789); Mount Barker [-33 36, 136 42]; Mount George (-35.00.148, 138.33.215); Mount Torrens (-34.52.128, 138.56.084); Mt Lofty [-35 0, 138 43], HI87–177, 178; Mylor (-

35.02.533, 138.45.433); Nora Creina (-37.19.306, 139.51.059); North Little Hampton (-35°03'03, 138°51'38; One Tree Hill [-34 48, 137 34]; Reedy Creek (-36.53.749, 140.01.735); Scott Creek (-35.04.167, 138.41.709); Stirling [-35 1, 138 44]; Stonyfell [-34 56, 138 41]; Summertown [-34 58, 138 44]; Teringie (-34.54.841, 138.42.389); Upper Sturt (-35.01.600, 138.39.200); Woodside (-34.57.323, 138.52.849). VICTORIA: Allestree (-38.16.725, 141.39.528); Anglesea [-38.24, 144 11], RWT; Apollo Bay [-38 46, 143 40], RWT; Bayswater [-37 51, 145 16], (MVMA); Benloch [-37 12, 144 40]; Blairgowrie [-38 22, 144 46], RWT; Bolwarra [-38 17, 141 37]; Bridgewater Lakes (-38.19.139, 141.24.093); Cape Otway [-38 48, 143 34], RWT; Carrum North [-38 6, 145 10], (MVMA); Colerain [-37 36, 141 41], RWT; Corranderk Reserve, Healesville [-37 39, 145 31], (MVMA); Cowes [-38 27, 145 14], RWT; Dartmoor [-37 55, 141 16]; Dunkeld [-37 39, 142 21], RWT; Emerald [-37 56, 145 26]; Fern Tree Gully [-37 18, 143 14], (MVMA); Flowerdale (-37.18.200, 145.19.471); Geelong [-38 9, 144 21], RWT; Grampians [-37 16, 142 27], RWT; Grampians [-37 16, 142 27], (MVMA); Grantville [-38 24, 145 32], RWT; Halls Gap (-37.08.935, 142.30.047); Halls Gap, RWT; Hamilton [-37 45, 142 2], RWT; Hernes Oak [-38 14, 146 17], RWT; Inverloch, RWT; Inverloch [-38 38, 145 43], (MVMA); Johanna (-38.42.543, 143.22.933); Lavers Hill [-38 40, 143 22], RWT; Lorne [-38 32, 143 59], RWT; Marengo [-38 47, 143 40]; Marysville [-37.31, 145 45]; McCrae [-38 21, 144 56], RWT; Mitta Mitta [-36 47, 147 32]; Montrose (-37.48.721, 145.20.452); Mount Arapiles [-36 45, 141 50], (MVMA); Narrawong [-38 14, 141 42]; Painkalac Reservoir (-38.26.500, 144.04.142); Peterborough [-36 36, 142 52], RWT; Port Campbell [-38 37, 142 59], RWT; Port Fairy [-38 23, 142 14], RWT; Portland [-38 21, 141 36], RWT; Portland [-38 21, 141 36], (MVMA); Riddells Creek [-37 28, 144 41]; S of Colac [-38 20, 143 35], HI89-020, 021; Tarrington [-37 46, 142 7], RWT; Tarwin Lower [-38 42, 145 52], (MVMA); Tidal River [-39 02, 146 19]; Torquay [-38 0, 144 20], RWT; Twelve Apostles visitors center [-38 40, 143 6], RWT; Warnambool [-38 22, 142 28], RWT; Wilsons Promontory [-36 44, 144 5], HI87-214-218; Yarra Junction [-37 47, 145 37], (MVMA). TASMANIA: Arthur Plains [-43 8, 146 23], (MNVA); Browns River [-42 58, 147 19], (MNVA); **Bothwell 25k N** [-42 23, 147 0], HI91-032; Derwent Bridge [-42 8, 146 13], HI87-207-210, HI91-035-037; **Dodges Ferry** [-42 51, 147 37], HI87-189, 190; Flinders Island [-39 52, 147 55], (MNVA); Granton [-42 45, 147 13], HI87-203, 204; Hobart [-42 53, 147 20], (MNVA); King William Saddle [-42 13, 146 6], HI87-205, 206; Lake Dobson [-42 41, 146 35]; Launceston [-41 26, 147 8], (MNVA); Mt Nelson [-42 55, 147 20], HI87-186-188; Mt Weld [-43 0, 146 34], HI91-018; Mt Wellington [-42 53, 147 14], HI91-019, 020; **Murderers Hill** [-41 58, 146 40], HI87-201, 202, HI91-025, 026, 028, 034; **Conical Hill** [-42 58, 147 49], HI87-191-192, HI91-016, 017; N of Bothwell [-42 23, 147 0], HI-91-021-022, HI91-032 -034; N of Latrobe [-41 14, 146 25], HI91-039-040, HI 91-042-045; Orford [-42 34, 147 52], (MNVA); S of Starvegut Hill [-41 52, 146 50], HI91-029, 072; South Coast (MNVA); Southeast Coast (MNVA); Strathgordon [-42 46, 146 3], HI87-193-196. Trevallyn [-41 26, 147 7], (MNVA).

B.B. Lowery Tasmanian Accessions (ANIC): Other Tasmanian records are listed immediately above. KING ISLAND [-39 53, 144 3]: Cape Wickham; Currie, 10k S; Currie, 5k E; Currie, 8k S; Currie; Grassy Point; Martha Lavinia Scrub; Pennys Lagoon; Sea Elephant Rd; Yarra Creek Gorge. FLINDERS ISLAND [-39 52, 147 55], : Airport; Badger Corner; Emita, 5k N; Emita; Five Mile Rd; Furneaux Lookout; Holloway Point; Mt Bramich; Mt Strzelecki; Settlement Point; Vinegar Hill, Walkers Lookout, 2k E; Walkers Lookout. MAINLAND TASMANIA: Alum Cliffs [-41 32, 146 25]; Alum Cliffs Walk; Apsley Douglas NP – ; Apsley Gorge [-41 52, 148 10]; Archers Knob [-41 8, 146 37]; Asbestos Range NP [-41 8, 146 41]; **Bakers Beach** [-41 8, 146 35]; Beauty Point [-41 9, 146 49]; Bellbuoy Beach [-41 2, 146 50]; Ben Lomond NP [-41 34, 147 40]; Black Bluff [-42 37, 146 58]; Breona [-41 47, 146 42]; Bridport [-41 0, 147 34]; **Bust Me Gal Hill** [-42 37, 147 37]; Canopy Walk – ; Derwent Bridge (vicinity) [-42 8, 146 13]; **Devonport, 26k SE** [-41 11, 146 21±26km]; Devonport [-41 11, 146 21]; Dover [-43 19, 147 1]; 3k SE of Ulverstone [-41 10, 146 11]; East Springfield [-41 16, 147 30]; Frankford SF – ; Freycinet Gorge – ; Freycinet NP [-42 5, 148 17]; **Geeveston, 10k W** [-43 10, 146 56±10km]; Geeveston [-43 10, 146 56]; Gowrie Park [-41 28, 146 13]; **Great Lake** [-41 53, 146 44]; Hampshire, 10k SW [-41 16, 145 47±10km]; Hartz Mountains NP [-43 14, 146 46]; Hellyer Gorge [-41 16, 145 37]; Holwell Gorge [-41 16, 146 46]; **Humbug Point** [-41 16, 148 17]; Kimberly Rd [-41 24, 146 29]; King William Saddle [-42 13, 146 6]; Lake Dove [-41 40, 145 58]; Lake Rowallan [-41 44, 146 13]; Latrobe, 10k SE [-41 14, 146 25±10km]; Latrobe, 12k SE [-41 14, 146 25±12]; Launceston, 10k E [-41 26, 147 8±10km]; Lemonthyme turnoff – ; **Liawenee** [-41 53, 146 40]; Liffey Falls [-41 41, 147 53]; Liffey Falls, 10k W [-41 41, 147 53; 41 14, 146 25±10]; Mathinna, 15k W [-41 29, 147 53]; Mathinna, 30k W [-41 29, 147 53±30km]; McPartlan Pass [-42 51, 146 11]; **Miena** [-41 59, 146 43]; **Mt Roland** [-41 28 14x.16]; **Mt Wellington** [-42 53, 147 14]; Mt William NP [-40 57, 148 13]; **N on Lakes Highway**; Navarre River

[-42 9, 146 8]; Nunamara [-41 23, 147 19]; Oldina Forest Reserve [-41 1, 145 40]; **Palmer Rd, E of Devonport** [-41 11, 146 21]; Poatina [-41 48, 146 58]; Poatina, 15 km S [-41 48, 146 58±15km]; **Poatina, 6 km SW** [-41 48, 146 58±6km]; **Port Sorell** [-41 10, 146 33]; Port Sorell, 4k w [-41 10, 146 33±4km]; River Rd – ; **Rocky Cape NP** [-40 52, 145 29]; Rossarden, 12 k NE [-41 40, 147 44]; Rossarden, 7k W [-41 40, 147 44±7km]; Rowallan Dam [-41 44, 146 13]; Sandy Point – ; **Sisters Beach** [-40 55, 145 34]; Smiths Plains Rd – ; Southport, 4k N [-43.26, 146 58±4km]; **Strahan** [-42 9, 145 20]; **Swansea, 6–10k N** [-42 7, 148 4±10km]; Tahune Forest Reserve [-43 5, 146 43]; Taroona [-42 56, 147 20]; Tullah, 6k W [-41 45, 145 37±6km]; Waratah [-41 27, 145 32]; Wedge Forest Reserve [-42 51, 146 14]; West Frankford [-41 19, 146 43]; **Westerway** [-42 40, 16 47]; BRUNY ISLAND [-43 17, 147 17], : Adventure Bay; Adventure Bay, 6km S; Alonnah; Barnes Bay; Bruny Airfield; Game Reserve; Great Bay; Isthmus Bay; Labillardiere Reserve; Lunawanna.

Worker diagnosis. General features as illustrated and in key couplet 1, 2 & 5 above. Morphologically distinguished from the Eastern Race of *M. pilosula* largely by leg coloration, and otherwise by convincing karyological differences. Here all coxae and trochanters are typically dark brown, slightly paler but almost matching the body tagmata. The femoral apices are briefly flushed reddish-orange, slightly more so on the forelegs, and all tibiae and tarsi are similarly colored reddish-orange. That color is brightly clear in life, and usually somewhat faded in cabinet specimens. The recognition of faded museum specimens like the *M. pilosula* lectotype (see above) *versus* those of *M. pilosula* (Eastern Race), which has brown tibiae and tarsi, is however not usually compromised.

Sculpturation is more intense in large individuals than in small specimens, with intermediate gradation. In this regard large workers can resemble those of *M. croslandi*. The leg coloration in *croslandi* however resembles that of the Eastern Race of *M. pilosula* (with brown hind tibiae – see above) enabling distinction of *pilosula*. Specimens of large workers of both races of *M. pilosula* can most confidently be discriminated from *M. croslandi* if accompanied by smaller nest mates or conspecific field associates. Single large workers can be problematic.

Dimensions. dimensions of the smallest and largest available Tasmanian workers are (mm: TL = 10.31, 13.97; HW = 2.04, 2.63; HL = 1.81, 2.36; CI = 89, 90; EL = 0.80, 0.97; OI = 39, 37; SL = 1.65, 2.12; SI = 81, 81; PW = 1.22, 1.70; WL = 3.06, 3.99; PetW = 0.69, 1.04; PpetW = 1.11, 1.55. These dimensional ranges also apply to mainland specimens examined.

Variation. Some investigated Tasmanian *M. pilosula* nests predominately including workers with “normal” reddish-orange hind tibiae (RHT) also contain low numbers of individuals with leg coloration resembling the Eastern Race of *M. pilosula* (with brown hind tibiae – BHT). Imai, Taylor *et al.* (1994) suggested that this might evidence past crossing with gene introgression between western *M. pilosula* and Imai’s “PB” entities (the latter discriminated here as the Eastern Race of *M. pilosula*). That proposition is accepted here. Most Tasmanian nests are not mixed and comprise only RHT workers. Localities from which mixed colonies are known are identified above in the lists of sites for specimens examined by **bold** type. Note that these localities are widely scattered across Tasmania, and that there is no evidence of a tension zone boundary (in the sense of Key, 1974 or White, 1974), between cross-mating parapatric taxa, given the apparent present-day absence of the Eastern Race of *M. pilosula* from Tasmania.

If the introgression hypothesis is accepted it would follow that *either* (1) that the Eastern Race of *M. pilosula* has become extinct on Tasmania since the island separated from mainland Australia, arguably at that time complete with populations of both races of *pilosula*, with the hypothesized extinction event leaving introgressed eastern *pilosula* genes in the modern Tasmanian *M. pilosula* genome, *or* (2) that previously-introgressed *M. pilosula* populations including “mixed” colonies were present on the proto-Tasmanian landmass at the time of geographical separation.

These considerations imply that the two races of *M. pilosula* were (or had been) both present in southeast Victoria/Tasmania and probably already introgressing before the time of Tasmanian separation, which occurred about 14,000 years ago (*testé* Lambeck and Chappell, 2001). If the Eastern Race is genuinely no longer present on Tasmania and was not there at the time of Tasmanian separation, the purported BHT genes (in the absence of subsequent introgressive “topping up”) must have survived in the Tasmanian *M. pilosula* genome for the last 14,000 years (or less, from the time of local extinction, if the Eastern Race was initially present on insular Tasmania and later became extinct).

Karyology. Chromosome numbers determined by Imai for *M. pilosula* (Western Race) (cited as “*M. pilosula* s. str.”) are given in Imai, Taylor *et al.*, 1994, appendix, and illustrated in their fig. 7 (p. 149). The overall range is

2N=21 to 2N=30, with known haploid numbers N=10 to N=15. Both ranges have all intermediate values represented. Note that N=10 presumably indicates a likely minimum of at least 2N=20. *Myrmecia pilosula* (Western Race) exhibits less-prominent C banding than described above for *M. pilosula* (Eastern Race). It is also characterized by centric fission polymorphism (fission burst), *versus* fusion burst in the Eastern Race (Imai, *pers comm.* and in Imai, Taylor *et al.*, 1994). This distinction is considered by Imai (*pers comm.*) and the author to provide adequate evidence that the two taxa could be separate biological (and thus nomenclatural) species. That conclusion was also supported by Crozier (*pes comm.*).

Field associations. Sympatric with *M. haskinsorum* on Tasmania and with the Western Race of *M. pilosula* southeast of Melbourne.

Research prospects. See below under *M. pilosula* (Eastern Race).

***Myrmecia pilosula* Fr. Smith (Eastern Race)**

(Figs 10–12)

The Eastern Race of *Myrmecia pilosula* is abundant at moderate to high elevations in components of the Great Dividing Range in eastern Victoria, eastern NSW and the ACT. Its most northern records are in the high ranges east of the New England Tableland in northern central-eastern NSW, including mile-high Point Lookout and nearby Cathedral Rock National Park. It has not been collected at lower elevations westward on the Tableland proper towards Armidale, where *M. croslandi* and *M. impaternalata* are sympatrically common. In the southwest of its range *M. pilosula* (Eastern Race) is found in the vicinity of Melbourne, west to Ballarat across central Victoria and southeast to Mornington Peninsula, where its distributional range encounters that of the putatively conspecific Western Race.

JACP vouchers recognized here as the Eastern Race of *M. pilosula* were discussed by Imai, Taylor *et al.* (1994) as possible representatives of an unnamed species which they speculated might have originated as a hybrid between *M. pilosula* and *M. banksi*, identified by the codes PB–1 (= *pilosula banksi*–1) and PB–2 (see following paragraph). Appropriate species-characteristic karyological differences between *M. banksi* and “*M. pilosula* s. str.” were reviewed, but they were not cited in support of the hybridization hypothesis, which was based entirely on morphotaxonomic characters involving leg coloration discussed above under *M. pilosula* (Western Race) (see Imai, Taylor *et al.*, 1994, Fig 10).

The Imai, Taylor *et al.* (1994) proposition posited that the similarities in leg color between the PB variants (PB1, PB2) and *M. banksi* (all with brown hind tibiae), and the differences between them and the Western Race of *M. pilosula* (cited as “*M. pilosula* s. str.”) (with reddish-orange hind tibiae), indicated that the PB entities had originated through hybridization between *M. banksi* and *M. pilosula* (Western Race). PB entities were shown (as here) to occupy a (very large) territory situated geographically between the current ranges of *banksi* and *pilosula*. I have consistently demurred from this interpretation (e.g. see Imai, Taylor *et al.*, 1994, p 152). In my opinion the leg coloration characters shared by *banksi* and *M. pilosula* (Eastern Race) are more likely derived synapomorphically from a common ancestor, or the character “brown tibiae” might be a homoplasy and not homologous at all in these species.

The 1994 geographical argument, while based on confirmed contemporary distribution patterns, failed to acknowledge that the purported hybridization event likely occurred at least hundreds of thousands, or more probably more than a million years ago; that very different distribution patterns on a geographically and environmentally different terrestrial substrate would have prevailed and that chromosomal rearrangements could have occurred subsequently. Nor did it acknowledge that the Eastern Race of *M. pilosula* has an extensive distributional range which widely separates the current ranges of its implied hybridic parent species *M. banksi* and western *M. pilosula*. The argument also failed to consider that a species originally derived as a hybrid between *M. banksi* (2n=9–10) and *M. pilosula* (Western Race) (2n=22–30) would likely be allodiploid, with unmatched haploid chromosome sets, as exemplified here by *M. impaternalata*, an evidentially well supported putative hybrid between *M. banksi* and a component of the Eastern Race of *M. pilosula* (see elsewhere in these pages).

The reported karyological differences contrasting the Eastern and Western Races of *M. pilosula* are discussed above.

FIGURES 10–12. *Myrmecia pilosula*, Eastern Race, Mongarlowe, NSW. Standard views. HW 2.12 mm, WL 3.11 mm, PW 1.26 mm.

FIGURES 13–15. *Myrmecia pilosula*, Western Race, Mt Wellington, Tasmania. Standard views. HW 2.45 mm, WL 3.63 mm, PW 1.49 mm.

Imai, Taylor *et al.* (1994) also recognized hybrid “back-cross” variants “P/PB–1, Mix” and “P/PB–2 Mix” known only from Tasmania. These were hypothesized to have originated as crosses between *M. pilosula* s.str with PB-1 and/or PB-2. They were recognised as discordant worker individuals collected from otherwise normal “*M. pilosula* s. str.” colonies, and identified only by features of leg coloration. They are assigned here to *M. pilosula* (see above).

Deposition of voucher specimens. AMSA, ANIC, MVMA, QMBA, SAMA, WAMA, TMHA, BMNH, CASC, MCZC, MHNG.

Distribution. *M. pilosula* (Eastern Race) is known to range southwards in NEW SOUTH WALES from the mountains east of the New England Tableland, along the Great Dividing Range and its flanks, including the Snowy Mountains, the Blue Mountains, and the Brindabella Ranges in the AUSTRALIAN CAPITAL TERRITORY, to the Victorian Alps and their slopes and the Gippsland coast in eastern VICTORIA. The known Victorian distribution carries westwards at least as far as Ballarat in the elevated country which extends the Great Dividing Range westwards across central Victoria north of Melbourne. This distribution evidently fails to carry approximately 120 km further west to the Grampians Range, SA, which is generally considered the western terminus of the East Australian Cordillera, because there the western putative race, *M. pilosula* (W), is exceptionally common at Halls Gap, its surrounds and elsewhere (as also southwards in the Hamilton district), and the Eastern Race of *M. pilosula* is unreported. Two damaged specimens from Ararat, VIC (MVMA), not far northeast of The Grampians, are identified as *M. pilosula* (Eastern Race). There are records of the Eastern Race from the SE corner of Victoria near Mallacoota, westwards to the Mornington Peninsula.

Colonies of the two races of *M. pilosula* appear to intersperse in Victoria SE of Melbourne, on or immediately east of the Mornington Peninsula, which they enter from the east and west respectively. There is no sound current morphological evidence of gene introgression between these taxa in Victoria, or evidence that they hybridize in the area of range overlap, and on these grounds it could be concluded that they represent separate, related, reproductively isolated, apparently parapatrically distributed, but previously allopatrically evolved, sister species. Their separate distinctive karyologies could support this conclusion. However, several known series of specimens from the Melbourne area are believed to evidence colonies containing workers representative of both forms (though the specimen labels do not specify the defining collection circumstances). Such “mixed” colonies are frequent and well confirmed in collections from Tasmania, where their presence was considered by Imai, Taylor *et al.* (1994) to evidence introgression of genes from the eastern *pilosula* race to its western counterpart, even though “pure” colonies of eastern habitus are unknown from Tasmania (see above). This evidence of interbreeding with gene introgression is the reason why the two designated forms are recognized here as geographical races of *M. pilosula*, rather than separate, putatively reproductively-isolated species. The present argument would presumably apply even if mixed colonies are not present in Victoria, in light of the Tasmanian evidence for crossing with introgression—though it is entirely plausible that two parapatrically distributed species/semispecies could experience introgression in some populations but not in others.

Material examined. The extreme northern record is from Cathedral Rock National Park [-30 25, 152.15], near Ebor, NSW, Imai, Kubota & Taylor, 27–11–1999 (HI 99–08) (Chromosomes: N=14). JACP records cited here have HI– accession numbers. Unless indicated other accessions are AAVAS: AUSTRALIAN CAPITAL TERRITORY: Condor Creek [-35 19, 148 50], HI85–376; Gudgenby [-35 46, 148 55], -Naas Creek HI87–134; Brindabella [-35 34, 148 57], 4/xii/2005; Picadilly Circus [-35 22, 148 48], HI85–373, 374, 378, 379, 89–003, 033, 91–051; Tidbinbilla [-35 28, 148 55], HI87–146, 147; Uriarra [-35 15, 148 55], 2/xii/2005. NEW SOUTH WALES: Blackheath [-35 38, 150 17], 950m (-33 38, 150 20) PSW; Braidwood [-35 26, 149 48], 5/xi/2006; Bredbo (-35, 57, 149 09), PSW; Captains Flat [-35 35, 149 57], HI87–141–145; Cathedral Range [-30 25, 152 15], HI87–222, 223; Corang River Bridge (35 12, 150 03), 3/xii/2005; Corang River Bridge [-35 12, 150 03], HI87–137–140; Cudgewa Bluff [-30 10, 149 25], HI87–227–229; Geehi River (-36 23, 48 10), 28/xi/2006; Island Bend, 1350m (-36 20, 148 28) PSW; Jindabyne (-36 23, 148 42), 1/x/2006; Kanangra Boyd Nat. Pk. [-33 59, 150 5], 1200m PSW; Kanangra Walls Road [-33 59, 150 8], 30/xi/2006; Lawson [-33 43, 150 26], HI87–111–115; Leather Barrel Creek (-36 31, 148 11) 28/xi/2006; Lochinvar [-32 42, 151 27], 23/vii/2006; Londonderry, 50m (-33 40, 150 46) PSW; Medlow Bath [-33 41, 150 17], HI87–116; Mongarlowe [-35 21, 150 0], HI85–192, 193–195, 85–227–233; Murray 1 Power Station [-36 24, 148 19], HI87–231–232; Murrumbidgee River, 29/xi/2006; Northangera [-35 28, 149 55], 3/xii/2005; Shannons Flat [-35 56, 148 57], HI87–131–133, HI91–077–079; Shoalhaven River nr Larbert [-35 18, 149 46], HI91–081; South Bowenfels [-33 31, 150 7], 1/ii/2007; Tumbarumba [-35 47, 148.1], 14/viii/2006; Wadbilliga

[-33 43, 15023], HI87–163, 164; Wambrook Creek [-36 11, 148 56], HI87–128–130; Wentworth Falls [-33 43, 150 23], HI87–117–121; Wyndham [-35 57, 147 7], 5/vii/2007. VICTORIA: Ballarat (-37.32.647, 143.54.984); Ballarat [-37 34, 143 52], (MVMA); Baxter [-38 12, 145 19], (MVMA); Buchan [-37 25, 148 10], RWT; Daylesford [-37 20, 144 9], (MVMA); Christmas Hills [-37 39, 145 18], RWT; Dartmouth [-36 45, 147 39], (MVMA); Dry Diggings (-37.16.982, 44.09.598); Eltham [-32 43, 145 8], (MVMA); Genoa [-37 29, 149 32], RWT; Gisborne [-37 29, 144 36], (MVMA); Harrietville (-36.53.562, 147.03.662); Healesville [-37 39, 145 31], (MVMA); Heathmont [-37 50, 145 15], (MVMA); Jericho [-36 55, 147 3], (MVMA); Langwarrin [-38 9, 145 12], (MVMA); Maldon [-36 59, 144 4], (MVMA); Mansfield [-37 3, 146 5], (MVMA); Marysville [-37 31, 145 45], HI87–220, 221; Merrijig, 12km SE [-37 39, 147 27±12k], (MVMA); Mt Buffalo [-36 44, 16 47], HI87–226; Mt Donna Buang [-37 42, 145 41], (MVMA); Mt Donna Buang [-37 42, 145 41], HI87–219; Mount Martha, N of Heywood [-38 16, 145 2], HI89–015, 016; Orbost [-37 42, 148 27], RWT; Powers Lookout [-36 51, 146 22], (MVMA); Riddell [-37 28, 148 27], (MVMA); Sarsfield [-37 45, 147 44], HI89–022–225; Warrandyte South [-37 46, 145 15], HI87–211, 212; Tawonga South (-36.44.925, 147 09.493); Wandiligong [-36 48, 146 58], 16/xii/2006; W of Genoa [-37 29, 149 32], HI89–026–028; Wesburn [-37 46, 145 39], (MVMA).

Worker diagnosis. General features as illustrated and in key couplets 1, 2, 5 & 6 above. Distinguished morphologically from the Western Race of *M. pilosula* largely by leg coloration (see key). Expression of this character-set in *pilosula* (Eastern Race) is generally similar to that of *M. pilosula* (Western Race) (see below), but the tibiae and tarsi are dull medium brown in color, lighter than the proximal leg segments, where those of *M. pilosula* (Western Race) are brightly reddish-brown, much like the fore-tarsi. The color difference between these forms is clearly distinguishable even in old, dry cabinet specimens. They correlate exactly with the karyological differences distinguishing the two taxa.

Sculpturation of large individuals is more intensely developed than in small specimens, with gradation in intermediate series. Large workers can be similar to those of *M. croslandi* (including details of leg coloration) and readily misidentified (see couplet 6 in the key to species above). Such specimens can most confidently be identified if associated with smaller nest mates or field associates. Single, unassociated large workers can be problematic.

Dimensions. (Holotype, smallest paratype, largest paratype (mm): TL = 1 27, 10.27, 12.26; HW = 2.28, 2.04, 2.37; HL = 2.07, 1.81, 2.14; CI = 110, 112, 111; EL = 0.86, 0.79, 0.92; OI = 38, 39, 38; SL = 1.91, 1.65, 1.93; SI = 84, 81, 81; PW = 1.42, 1.18, 1.53; WL = 3.28, 3.02, 3.47; PetW = 0.86, 0.68, 0.87; PpetW = 1.38, 1.10, 1.38.

Karyology. Chromosome numbers determined by Imai are given in Imai, Taylor *et al.*, 1994, appendix. The overall range is slightly greater than in *M. pilosula* (Western Race), with 2N=18 to 2N=32 (with all intermediate values represented except 2N=27 and 2N=31), and with a single recorded haploid count of N=15. Karyologically *M. pilosula* (Eastern Race) is distinguished from *M. pilosula* (Western Race) by remarkably elongated C-band polymorphisms and chromosome arrangements involving centric fusion (fusion burst) (Imai, Taylor *et al.*, 1994, fig. 11). Alternatively, ‘Fission burst’ characterizes the karyology of *M. pilosula* (Western Race).

Field associations. Sympatric with *M. haskinsorum* at most mainland sites from which the latter is known, variously with *M. croslandi* and with *M. pilosula* (Western Race) east and southeast of Melbourne. *Myrmecia pilosula* (Eastern Race) is not known from suburban Canberra where *M. croslandi* and *M. impaternalata* are common, but it is common at higher elevations in the nearby Brindabella Ranges and other local elevated areas, and in the Snowy Mountains.

Research prospects. Prospective research topics involving the Eastern and Western Races of *M. pilosula* include (1) genetical investigation of both races, to challenge the Tasmanian introgression hypothesis discussed above, and to clarify whether these taxa are genuinely parapatric in distribution in Victoria; (2) investigation of the several implied Victorian areas of geographical range contact or intersection, with search for possible genetical introgression between the two taxa, notably in West Gippsland and areas between Ballarat and the Grampians, possibly also at other localities on the eastern flanks of Melbourne; (3) investigation of comparative bionomics of both taxa in contact *versus* non-contact zones; and (4) locating the distributions of these two races and other Jack-jumper species in the Melbourne area and greater Victoria, and of the Eastern Race in the ACT and surrounding NSW.

***Myrmecia impaternata* sp.n.**

(Figs 16–18)

Myrmecia impaternata is broadly sympatric with *M. croslandi*, a matter of possible biological significance (see below). Both species are common in and around Canberra and on the New England Tableland around Armidale. There are confirmed Queensland records of *M. croslandi* from the Darling Downs in extreme SE Queensland, and of *M. impaternata* from Tamborine Mountain south of Brisbane. JACP voucher specimens of this taxon were discussed by Imai, Taylor *et al.* (1994) as “PBF1 hybrids”, with 2 types: PBF₁-1 and PBF₁-2 (PB = *pilosula* x *banksi*).

Type locality. Immediately E to NE of Corang River Bridge (-35 12, 150 03) on the Nerriga Road, near Braidwood, NSW. This type-locality is common also to *M. croslandi* (see above). The site, also supports *M. impaternata*, *M. croslandi* and *M. pilosula* (Eastern Race).

Type deposition. Holotype and paratypes in ANIC, paratypes or type-compared vouchers in AMSA, MVMA, QMBA, SAMA, WAMA, TMHA) and in BMNH, CASC, MCZC, MHNG.

Material examined, distribution. QUEENSLAND: Mt Tamborine [-27 55, 153 10], O. Deane (MVMA); Mt Tamborine Village [-27 53, 153 8], 15/i/57, BBL. NEW SOUTH WALES: *M. impaternata* was found common at localities near Armidale [-30 30, 151 40], NSW, in Dec/Jan. 1995–96 and Nov. 1999 by JACP collectors. It is sympatric there with *M. croslandi*. Localities elsewhere include: Corang River Bridge [-35 12, 150 03]; Charleyong [-35 15, 149 55], HI87–156; Yowrie [-36 19, 149 44], HI87–161, HI87–162. AUSTRALIAN CAPITAL TERRITORY: Canberra [-35 18, 149 8], HI85–372, 373, HI87–237. AAVAS collections are from the Australian National Botanic Gardens site [-35 17, 149 7], and the suburbs of Cook [-35 16, 149 4] and Hawker [-35 15, 149 2], VICTORIA: Mayfield [-35 12, 149.48], HI87–155.

Myrmecia impaternata (along with the locally more frequent *M. croslandi*) is common in urban and suburban Canberra (see below).

Worker diagnosis. General features as illustrated and in key couplets 1 – 4 above, which cover leg-coloration. The brassy color of the cephalic pubescence can be hard to discern stereomicroscopically using some types of illumination lamp, and color temperatures of the light provided. It is best observed beyond the near-side eye in acute diagonal lateral view of the head. This pubescence is arguably a legacy of the *M. banksi* hybrid parentage. Otherwise *M. impaternata* is similar in physiognomy and sculpturation to small/medium-sized workers of the second parental species, *M. pilosula* (Eastern Race). There is some size-related graded variation in cephalic and dorsal mesosomal sculpturation between small and large specimens, somewhat as in both races of *M. pilosula* but less extreme, especially at the high, more intensively-sculptured end of the range.

For significant scientific reasons discussed below investigation of the comparative biology of, and possible reproductive relationships between, *M. impaternata* and *M. croslandi* is a prime scientific subject. The two species may be readily differentiated using the characters of couplet 2 of the key to species above.

Dimensions. (Holotype, smallest paratype, largest paratype (mm): TL = 13.01, 10.87, 13.04; HW = 2.47, 2.22, 2.49; HL = 2.27, 2.06, 2.27; CI = 108, 107, 109; EL = 0.96, 0.88, 0.97; OI = 39, 39, 39; SL = 1.87, 1.84, 1.94; SI = 76, 82, 78; PW = 1.58, 1.42, 1.59; WL = 3.52, 3.34, 3.75; PetW = 0.97, 0.83, 0.96; PpetW = 1.39, 1.22, 1.33.

Etymology. The name *impaternata* is based on the Latinate (not truly Latin) biological term “impaternate” (= fatherless as a result of parthenogenesis). For explanation see the section on reproductive biology below.

Karyology. Details are provided by Imai, Taylor *et al.* (1994), and by Taylor, Imai and Hasegawa (in preparation). *Myrmecia impaternata* has an allodiploid karyotype: n=5 or 14, 2n=19. The 5-chromosome set closely matches one of the haploid sets of *M. banksi*, while the 14-chromosome haploid set is generally matched in the Eastern Race of *M. pilosula* – most closely resembling chromosomes from a colony (HI87–130) collected at Wambrook Creek (36°11'S, 148°56'), near Cooma, NSW. On these grounds *M. banksi* and *M. pilosula* (Eastern Race) (or close ancestral stocks) are identified here as the parental species which hybridized to originate *M. impaternata*. See also Imai, Taylor *et al.* (1994) appendix and fig. 8 (p. 150).

Field associations. All *M. impaternata* sympatric associations throughout its known distribution are with *M. croslandi*. Nests of both species are frequently encountered interspersed in Canberra parks and gardens, suburban roadside grass lawn “nature strips” and in local grassy bushland. Colonies of the two have often been encountered by the author and other researchers only a few meters apart.

FIGURES 16–18. *Myrmecia impaternata*, National Botanic Gardens, Canberra, ACT. Standard views. HW 2.29 mm, WL 3.35 mm, PW 1.42 mm.

Reproductive biology. There has been persistent historical failure by JACP researchers, and the author subsequently, to discover males in *M. impaternata* nests, despite targeted excavation of field colonies at appropriate seasons over many years. Only two male-right colonies have ever been located and collected. Both were closely adjacent at the Canberra Botanic Gardens

Research on males and queens from these nests by Taylor, Imai and Hasegawa (to be published elsewhere) has investigated the reproductive biology of *M. impaternata*. It convincingly demonstrates that *M. impaternata* is a sperm-dependent gynogenetic taxon in which unreduced eggs require contact with sperm or spermatid fluid (specifically without the occurrence of fertilization) in order to develop parthenogenetically, and thus to produce diploid workers and gynes (see Kokko *et al.* (2008) for theoretical background). The necessary spermatid material is evidentially obtained by gynes through copulation with nominally conspecific donor males bred in *impaternata* nests. In this example the sperm cells dissected from male testes and gyne spermathecae were identically and characteristically structurally degenerate and putatively incapable of actually effecting fertilization. Their presence in both sexes importantly attests previous mating between relevant males and gynes. The where's and when's of copulation are not known.

In other known sperm-dependent gynogenetic animals (all of which are hybrid-originated allodiploid entities, including various fish and amphibian species, none of which are known to possess a male sex) sperm is obtained for this unusual purpose by the females through parasitic copulation with males of other separate, sympatric, congeneric and usually closely related donor species. The distribution, stable presence and long-term population survival of such gynogenetic taxa is totally dependent on sympatric associations with sperm-donor host species, a factor which critically restrains their distributional ranges and dispersability, but ultimately ensures their survival as species in nature.

Because males in ants are genetically haploid, it is suggested that those produced by *impaternata* females will likely be of two types, genetically, karyologically and perhaps morphologically equivalent to males of the putative parental species *M. banksi* and *M. pilosula* (Eastern Race). Remarkably, males produced in *impaternata* colonies would technically therefore not be conspecific with their *impaternata* mothers. Taylor, Imai and Hasegawa conclude that: “*M. impaternata* thus has no need to maintain risky, restrictive parasitic affiliation or sympatry with other free-living, closely-related sperm-donor host species. It is apparently able to produce the necessary allospecific males by accessing its own genome!” The authors also suggest that *M. impaternata* queens might at times more usually operate as sperm parasites of *M. croslandi* by obtaining sperm allospecifically from *croslandi* males. This hypothesis is encouraged by the persistent historical failure to discover males in *M. impaternata* nests.

Status as a taxonomic species. Despite its apparent hybrid origin and reproduction by theletokous parthenogenesis, *M. impaternata* functions in nature as a biological species. It is accorded specific taxonomic status here following the precepts of Maslin (1968) and Cole (1985), on the grounds that it is a genetically and historically unique, self perpetuating, separately evolving entity, reproductively isolated from its ancestors and sympatrically-associated related species.

Taylor, Imai & Hasegawa raise the possibility that several *M. impaternata*-related hybrid clones with separately evolved alternative reproductive arrangements could be present in nature, each derived from a different foundation hybridization event between *M. banksi* and *M. pilosula* (Eastern Race). Note that Imai, Taylor *et al.* (1994) recognized two forms of *M. impaternata* (PBF1-1 and PBF1-2) differing in details of leg coloration (see their fig 10). These could arguably represent separately originated *banksi* x *pilosula* hybrid entities. Alternative hybrid lineages, if demonstrated, could not be considered formally conspecific with one another following the precepts of Maslin (1968) and Cole (1985) discussed above, nor would they be. *Myrmecia impaternata* and its kind could well have an interesting scientific future!

Research prospects. Further understanding of the reproductive biology of *M. impaternata* is greatly desirable. Of particular interest are: (1) determining whether sperm or spermatid materials actually enter the egg cytoplasm or not; (2) investigation of the possibility that two classes of males (comparable respectively to those found in colonies of *M. banksi* and *M. pilosula* [Eastern Race]) are developed from haploid *impaternata* queen-laid eggs; (3) testing the possibility that production of “*impaternata*” males and their presence in nests might in this case be unusual; (4) finding whether *impaternata* might also (more usually?) maintain a parasitic copulatory relationship with *M. croslandi*, considering their frequent, very proximate, and wide-ranging sympatric co-presence; and (5) determining when and where copulation occurs in either of these scenarios.

Myrmecia imaii sp.n.

(Figs 19–21)

Myrmecia imaii is known only from extreme southwest WA: south and SE of Perth, east to Esperance, seldom more than a few km from the coast.

Type locality. North of Denmark, Western Australia (-34 8, 117 21).

Type deposition. Holotype and paratypes in ANIC, paratypes or type-compared vouchers in AMSA, MVMA, QMBA, SAMA, WAMA, TMHA) and in BMNH, CASC, MCZC, MHNG.

Material examined, distribution. Known only from extreme southwest WESTERN AUSTRALIA: Albany (-34.59.290, 117.42.246) SB, Oct 2006; TG, 7/ii/1947; Denmark (-34.50.032, 117.24.430) SB, Oct 2006; TG, 7/xi/1947; N. Solomon, 23/i/1935 (MVMA); 11 mi. N of Denmark [-34 50, 117 24±11km], 24/x/1969, RWT; N of Denmark (Type Locality) HI89-005 -007, HI89-009, HI91-001-003, 005, 008; W of Denmark HI91-008; Esperance (-33.51.540 121.51.025) SB, Oct 2006; Esperance Airport, near Gibson [-33 39, 121 49], HTI&RWT; Jakkawilla (-34.38.256 118.2243), SB Oct 2006; Keynton, near Mount Mehniup [-34 58, 117 1], 28/ix/1969, RWT; 10mi. E of Nornalup, (-34 59, 116 49), 17/ii/1958, EFR; Porongurup National Park (-34.40.32, 117.52.164) 24/x/1969, 60m, RWT (accs 69/403, 407, 408); Porongurup Range [-34 41, 117 53], HI91-005; Telegraph Hill/Dempster Head [-33 53, 121 54], HTI&RWT; N of Walpole [-34 59, 116 44], 350m, 25/x/1969, RWT. JACP records may be identified above by their HI codes.

This is the species recorded as *Promyrmecia pilosula* by Clark (1951) from Albany (confirmed by MVMA voucher specimens), Denmark and Mundaring [-31 54, 116 10], the last locality extends the range indicated by the above records, and was a prime collecting site to Clark (who collected ants widely in the south-west, where he resided for many years). He commented that this species “is quite common in Albany and surrounding district, but it is rare further north” (1951: 204).

Worker diagnosis. General features as illustrated and in key couplets 1–4 above. The brassy cephalic pubescence is more diffuse and less evident than in *M. banksi*, and the middle and hind tibiae are consistently medium to dark brown, with the tarsi a shade lighter. Local identification remains straightforward as long as *M. imaii* remains the only species of the *M. pilosula* complex found in WA.

Dimensions. (Holotype, smallest paratype, largest paratype (mm): TL = ca 13.40, 12.00, 14.46; HW = 2.68, 2.32, 2.79; HL = 2.49, 2.16, 2.59; CI = 107, 107, 107; EL = 0.99, 0.88, 1.01; OI = 37, 38, 36; SL = 2.15, 1.93, 2.17; SI = 80, 83, 77; PW = 1.63, 1.43, 1.70; WL = 3.90, 3.33, 4.06; PetW = 1.07, 0.85, 1.08; PpetW = 1.64, 1.27, 1.65.

Etymology. Named for Hirotami T. Imai celebrating long friendship; to commend his leadership of the JACP project, his distinguished research on the karyology of *Myrmecia* species and other ants, his important “Minimum Interaction Hypothesis” for the evolution of chromosome numbers in animals and his productive stewardship of the Japanese Ant Database Group (2003).

Karyology. The basic karyotype, $2K=6A+2A^m(2n=8)$ differs strongly from those of other species reviewed above. Two independent AM inversions on chromosomes 1 and 2 were described in detail by Imai, Taylor *et al.* (1994: 146, Fig 5c–g). Complicated chromosome polymorphisms accompanying chromosome number reduction ($2n=8 > 7 > 6$) by AM inversion, centric fission and centric fusion were also observed between chromosomes 1L and 4 and between chromosomes IS and 3. Despite this complexity the authors considered all examined specimens to be conspecific.

Discussion. All records of *M. imaii* are from the “High Rainfall” and “SE Coastal Provinces” of the “South Western Australian Floristic Region” defined by Hopper and Gioia (2004) and Hopper *et al.* (1996). Heterick (2009) reported the species from the recognized Botanical Districts of Esperance Plains, Jarrah Forest, Mallee and Warren. The fact that its relatives at species-complex level are of eastern Australian provenance implies that Jack-jumpers must previously have ranged or dispersed across southern Australia. The *M. imaii* progenitors were likely first geographically isolated in the west by incursion of inhospitable arid habitat across the early Nullarbor Plain, which is variously estimated to have occurred between 50 and 30 million years ago (Frakes, 1999; Nelson, 1996). The *M. pilosula* clade must therefore have originated no later than early Oligocene. This argument precludes the (unlikely?) possibility that Jack-jumper stock reached Southwest WA from the east since Oligocene times by a later dispersal event across increasingly-extending unsupportive Nullarbor habitat, and fully accords with well-accepted current hypotheses regarding the origins and isolation of the exceptional, highly endemic southwestern WA flora (see Hopper and Gioia, 2004; Hopper *et al.* 1996). The closest contemporary geographical records of a related eastern species are those of *M. pilosula* in South Australia east of Spencer Gulf.

FIGURES 19–21. *Myrmecia imaii*, Holotype, N of Denmark, WA. Standard views. HW 2.68 mm, WL 3.90 mm, PW 1.63 mm.

Research prospects. Sociobiological and genetical investigation of this long-time geographically-isolated species, *versus* its eastern relatives, is desirable.

Acknowledgments

The collegiality of JACP and AAVAS researchers listed above is commended, as are Steve Shattuck, Phil Ward, Robyn Meier, †Renate Saddler, Beth Mantle, David Yeates, Joachim Ziel, Ajay Narendra, Piyankarie Jayatilaka, Chloe Radershall, Sam Reid, Hugh and Marina Tyndale-Biscoe and Colin Beaton, John Longino and an appreciated anonymous referee. Wendy Taylor, Jan Robertson and David Somerfield participated in a 2010 Jack-jumper-focused collecting expedition covering much of Victoria. Masao Kubota mounted scores of JACP voucher specimens for the ANIC. Taxonomic work was partly funded by The Australian Biological Resources Study Participatory Program; AAVAS participation by the Australian National Health and Medical Research Council. JACP participation was funded by the Japanese Ministry of Education through Hirokami Imai's grant support, and facilitated by †Division of Entomology, CSIRO, and its former Chiefs †Douglas Waterhouse and Max Whitten. Special thanks to the South Australian mother of a dangerously *pilosula*-venom-sensitive child, who provided the title words "Ants with Attitude" when discussing the ants banefully common in her garden.

References

- Brown, S.G.A., van Eeden, P., Wiese, M.D., Mullins, R.J., Solley, G.O., Puy, R., Bleasel, K., Taylor, R.W. & Heddle, R.J. (2011) Ant sting anaphylaxis in Australia – The Australian Ant Venom Allergy Study. *Medical Journal of Australia*, 195, 69–73.
- Brown, W.L. Jr. (1953) Revisionary notes on the ant genus *Myrmecia* of Australia. *Bulletin of the Museum of Comparative Zoology Harvard University*, 111, 1–35.
- Browning, G.P. (1987) *Taxonomy of Myrmecia Fabricius (Hymenoptera: Formicidae)*. Ph.D. thesis, University of Adelaide, Adelaide, 431 pp.
- Clark, J. (1943) A revision of the genus *Promyrmecia* Emery (Formicidae). *Memoirs of the National Museum of Victoria*, 13, 83–149.
- Clark, J. (1951) *The Formicidae of Australia. Vol. I. Subfamily Myrmeciinae*. CSIRO, Melbourne, 230 pp.
- Cole, C.J. (1985) Taxonomy of parthenogenetic species of hybrid origin. *Systematic Zoology*, 34, 359–363.
<http://dx.doi.org/10.2307/2413153>
- Cook, L.G. (2000) Extraordinary and extensive karyotypic variation: A 48-fold range in chromosome number in the gall-inducing scale insect *Apiomorpha* (Hemiptera: Coccoidea: Eriococcidae). *Genome*, 43, 255–263.
<http://dx.doi.org/10.1139/gen-43-2-255>
- Crosland, M.W.J. & Crozier, R.H. (1986) *Myrmecia pilosula*, an ant with only one pair of chromosomes. *Science*, 231, 1278.
<http://dx.doi.org/10.1126/science.231.4743.1278>
- Crosland, M.W.J., Crozier, R.H. & Imai, H.T. (1988) Evidence for several sibling biological species centered on *Myrmecia pilosula* (F. Smith) (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society*, 27, 13–14.
- Crozier, R.H., Dobric, N., Imai, H.T., Graur, D., Cornuet, J.M. & Taylor, R.W. (1995) Mitochondrial DNA sequence evidence on the phylogeny of Australian jack-jumper ants of the *Myrmecia pilosula* complex. *Molecular Phylogenetics and Evolution*, 4, 20–30.
<http://dx.doi.org/10.1006/mpev.1995.1003>
- Forel, A. (1910) Formicides australiens reçus de MM. Froggatt et Rowland Turner. *Revue suisse de Zoologie*, 18, 1–94.
- Frakes, L.A. (1999) Evolution of Australian environments. *Flora of Australia*, 1, 163–203.
- Hasegawa, E. & Crozier, R.H. (2006) Phylogenetic relationships among species groups of the ant genus *Myrmecia*. *Molecular Phylogenetics and Evolution*, 38, 575–582.
<http://dx.doi.org/10.1016/j.ympev.2005.09.021>
- Haskins, C.P. & Haskins, E.F. (1951) Notes on the biology and social behavior of the archaic ponerine ants of the genera *Myrmecia* and *Promyrmecia*. *Annals of the Entomological Society of America*, 43, 461–491.
- Hechler, H.C. (1968) Postembryonic development and reproduction in *Diploscapter coronata* Nematoda: Rhabditidae. *Proceedings of the Helminthological Society of Washington*, 35, 24–30.
- Heterick, B.E. (2009) A guide to the ants of south-western Western Australia. *Records of the Western Australian Museum*, No 26 (Supplement), 1–207.
- Hirai, H., Yamamoto, M.T., Ogura, K., Satta, Y., Yamada, M., Taylor, R.W. & Imai, H.T. (1994) Multiplication of 28S rDNA and NOR activity in chromosome evolution among ants of the *Myrmecia pilosula* species complex (Hymenoptera: Formicidae: Myrmeciinae). *Chromosoma*, 103, 171–178. [Berlin]
<http://dx.doi.org/10.1007/BF00368009>
- Hopper, S.D. & Gioia, P. (2004) The southwest Australian floristic region: evolution and conservation of a global hot spot of

- biodiversity. *Annual Review of Ecology and Systematics*, 35, 623–650.
<http://dx.doi.org/10.1146/annurev.ecolsys.35.112202.130201>
- Hopper, S.D., Harvey, M.S., Chappill, J.A., Main, A.R. & Main, B.Y. (1996) The western Australian biota as Gondwanan heritage – a review. In: Hopper, S.D., Chappill, J.A., Harvey, M.S. & George, A.S. (Eds.), *Gondwanan Heritage: past, present, and future of the western Australian biota*. Surrey Beatty & Sons, Chipping Norton, pp. 1–46. [Australia]
- Imai, H.T. (2010) A productive friendship – my work in ant cytogenetics with Ross H. Crozier. *Myrmecological News*, 15, 1–5.
- Imai, H.T., Crozier, R.H. & Taylor, R.W. (1977) Karyotype evolution in Australian ants. *Chromosoma*, 59, 341–393. [Berlin]
<http://dx.doi.org/10.1007/BF00327974>
- Imai, H.T., Hirai, H., Satta, Y., Shiroishi, T., Yamada, M. & Taylor, R.W. (1992) Phase specific Ag-staining of nucleolar organizer regions (NORs) and kinetochores in the Australian Ant *Myrmecia croslandi*. *Japanese Journal of Genetics*, 67, 437–447.
<http://dx.doi.org/10.1266/jjg.67.437>
- Imai, H.T. & Taylor, R.W. (1989) Chromosomal polymorphisms involving telomere fusion, centromeric inactivation and centromere shift in the ant *Myrmecia (pilosula) n=1*. *Chromosoma*, 98, 456–460. [Berlin]
<http://dx.doi.org/10.1007/BF00292792>
- Imai, H.T., Taylor, R.W., Crosland, M.W.J. & Crozier, R.H. (1988) Modes of spontaneous chromosomal mutation and karyotype evolution in ants with reference to the minimum interaction hypothesis. *Japanese Journal of Genetics*, 63, 159–185.
<http://dx.doi.org/10.1266/jjg.63.159>
- Imai, H.T., Taylor, R.W., Crozier, R.H., Crosland, M.W.L. & Browning, G.P. (1988) Chromosomal polymorphism in the ant *Myrmecia (pilosula) n=1*. *Annual Report of the National Institute of Genetics*, 38, 82–84. [Japan]
- Imai, H.T., Taylor, R.W., Kubota, M., Ogata, K. & Wada, M.Y. (1990) Notes on the remarkable karyology of the primitive ant *Nothomyrmecia macrops* Clark, and on the related genus *Myrmecia* Fabricius (Hymenoptera: Formicidae). *Psyche*, Cambridge, 97, 133–140.
<http://dx.doi.org/10.1155/1990/91237>
- Imai, H.T. Taylor, R.W. & Crozier, R.H. (1994) Experimental bases for the minimum interaction hypothesis: 1. chromosome evolution in ants of the *Myrmecia pilosula* species complex (Hymenoptera: Formicidae: Myrmeciinae). *Japanese journal of Genetics*, 69, 137–182.
<http://dx.doi.org/10.1266/jjg.69.137>
- Imai, H.T., Taylor, R.W., Ogata K. & Crozier, R.H. (1992) Karyotypic divergence and speciation in the Australian *Myrmecia (pilosula)* species complex (Hymenoptera: Formicidae), with reference to modern cytological techniques. *Proceedings of the 19th International Congress of Entomology*, Abstracts, 7.
- Japanese Ant Database Group (2003) *Ants of Japan*, Gakken Press, Tokyo, 221 pp. [English Language Edition, Book and CD]
- Key, K.H.L. (1974) Speciation in Australian morabine grasshoppers – taxonomy and ecology. In: White, M.J.D. (Ed.), *Genetic Mechanisms of Speciation in Insects*. Australia and New Zealand Book Company, Sydney, pp. 43–56.
- Kokko, H., Heubel, K.U. & Rankin, D.J. (2008) How populations persist when asexuality requires sex: the spatial dynamics of coping with sperm parasites. *Philosophical Transactions of the Royal Society B*, 275, 817–825.
<http://dx.doi.org/10.1098/rspb.2007.1199>
- Lambeck, K. & Chappell, J. (2001) Sea level changes in the last glacial epoch. *Science*, 292, 679–686.
<http://dx.doi.org/10.1126/science.1059549>
- Maslin, T.P. (1968) Taxonomic problems in parthenogenetic vertebrates. *Systematic Zoology*, 17, 219–231.
<http://dx.doi.org/10.2307/2412001>
- Meyne, J., Hirai, H. & Imai, H.T. (1995) FISH analysis of the telomere sequences of bulldog ants (*Myrmecia*: Formicidae). *Chromosoma*, 104, 14–18. [Berlin]
- Nelson, E.C. (1981) Phytogeography of Southern Australia. In: Keast, A. (Ed.), *Ecological Biogeography of Australia*. W. Jung, the Hague, pp. 733–759.
- Ogata, K. & Taylor, R.W. (1991) Ants of the genus *Myrmecia* Fabricius: a preliminary review and key to the named species. (Hymenoptera: Formicidae: Myrmeciinae). *Journal of Natural History*, 25, 1623–1673.
<http://dx.doi.org/10.1080/00222939100771021>
- Smith, F. (1858) *Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae*. British Museum, London, 216 pp.
- Taylor, R.W. (1991) *Myrmecia croslandi* sp.n., A karyologically remarkable new Australian jack-jumper ant (Hymenoptera: Formicidae: Myrmeciinae). *Journal of the Australian Entomological Society*, 30, 288.
<http://dx.doi.org/10.1111/j.1440-6055.1991.tb00438.x>
- Taylor, R.W. & Brown, D.R. (1985) Hymenoptera: Formicoidea. *Zoological Catalogue of Australia*, 2, 1–149, 306–348.
- Wheeler, W.M. (1922) Observations on *Gigantiops destructor* Fabricius and other leaping ants. *Biological Bulletin (Woods Hole)*, 42, 185–201.
<http://dx.doi.org/10.2307/1536521>
- Wheeler, W.M. (1933) *Colony-founding among Ants with an account of some primitive Australian species*. Cambridge, Massachusetts, Harvard University Press, 179 pp.
- White, M.J.D. (1974) Speciation in the Australian morabine grasshoppers – the cytogenetic evidence. In: White, M.J.D. (Ed.), *Genetic Mechanisms of Speciation in Insects*. Australia and New Zealand Book Company, Sydney, pp 57–70.
<http://dx.doi.org/10.1007/978-94-010-2248-4>