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A Systematic Revision of the *Rhytidoponera impressa* Group (Hymenoptera : Formicidae) in Australia and New Guinea

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Abstract

The *Rhytidoponera impressa* group is revised on the basis of worker ant morphology, supplemented by information from ecological and genetic studies. Five species are recognized, all of which occur in mesic habitats along the east coast of Australia: *chalybaea* Emery (New South Wales, southern Queensland), *confusa*, sp. nov. (Victoria, New South Wales, southern Queensland), *enigmatica*, sp. nov. (Sydney region, N.S.W.), *impressa* Mayr (Queensland), and *purpurea* Emery (north Queensland, New Guinea). *R. purpurea* is the most distinct morphologically. Of the remaining species, *chalybaea* and *confusa* are exceedingly similar and in some localities can be unequivocably distinguished only on the basis of electrophoretic (allozyme) differences. Biogeographical relationships of the *impressa* group are discussed in relation to past climatic and vegetational changes.

Introduction

The ponerine ant genus, *Rhytidoponera* Mayr (Ponerinae : Ectatommini), contains an impressive array of more than 100 species, which have collectively occupied almost every major terrestrial habitat in Australia. The genus is also represented by lesser numbers of species in New Guinea, the Moluccas, Timor, southern Philippines, Solomon Is and New Caledonia (Brown 1958; Wilson 1958).

The *Rhytidoponera impressa* group, as originally defined by Brown (1954), consists of several closely related species inhabiting the east coast of Australia (with one species occurring also in New Guinea). The present revision of this species-complex is based on worker morphology and distribution, supplemented by ecological, behavioural and electrophoretic studies. The latter technique (electrophoresis) supplies crucial evidence of reproductive isolation between several species-pairs which show very slight morphological differentiation. A detailed discussion of allozyme differences between species appears elsewhere (Ward 1978, 1980).

Material and Methods

Material for this revision is derived largely from extensive field collections made at more than 100 localities along the east coast of Australia, in the course of ecological and genetic studies on the group (Ward 1978). Voucher specimens from these studies have been deposited in the Australian National Insect Collection (ANIC), Canberra. Relevant material in the following collections was also studied:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
BMNH	British Museum (Natural History), London
DSIR	Entomology Division, DSIR, Auckland, N.Z.
MCSN	Museo Civico di Storia Naturale, Genoa, Italy

MCZ Museum of Comparative Zoology, Harvard University
NMV National Museum of Victoria, Melbourne

Other abbreviations used (collections not examined) are:

HNM Hungarian National Museum, Budapest
MHN Museum d'Histoire Naturelle, Geneva
NHMV Naturhistorisches Museum, Vienna

In the lists of material examined of each species, dates of collection and collector have been omitted, in the interests of brevity. The majority of material was collected by B. B. Lowery, R. W. Taylor, and P. S. Ward.

Scanning electron micrographs were prepared with a J.E.O.L. JSM-U3 scanning electron microscope, with gold–palladium coated specimens.

Measurements and Indices

Morphological measurements of workers were made at 32× magnification, on a Zeiss microscope with a Wild Heerbrugg 'Censor' Electronic Micro-length Measuring Attachment (to which an electronic digital readout had been wired).

The following 10 measurements were used (expressed in millimetres):

HL Head length: length of head proper, measured in full-face (dorsal) view, from the anterior clypeal margin to the midpoint of the occipital margin.
ML Mandible length: length of closed mandibles, from the anterior clypeal margin to the apices of the mandibles, measured in the *same plane as HL*.
SL Scape length: length of the first antennal segment, excluding the basal constriction.
ED Eye diameter: diameter of eye, measured longitudinally in lateral view.
HW Head width: maximum width of head, measured in full-face (dorsal) view, excluding the eyes.
WL Weber's length of the mesosoma (alitrunk): diagonal length, measured in lateral view, from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.
PW Pronotum width: maximum width of pronotum, measured in dorsal view.
DPW Dorsal petiolar width: maximum width of the petiolar node, measured in dorsal view.
PH Petiolar height: maximum measurable height of petiolar node, taken as a straight-line measurement in lateral view, from the summit of the node to the lowermost extremity of the subpetiolar process.
PNL Petiolar node length: length of the node, measured in lateral view, from the midpoints of maximum curvature where the anterior and posterior faces of the node meet the anterior and posterior peduncles.

Eleven indices (based on the previous measurements) were calculated:

ICI Inverse cephalic index: HL/HW.
MI Mandibular index: ML/HW.
MI2 Mandibular index, using HL: ML/HL.
SI Scape index: SL/HW.
SI2 Scape index, using HL: SL/HL.
OI Ocular index: ED/HW.
PI Pronotal index: PW/HW.
PNI Petiolar node width index: DPW/PW.
LPI Lateral petiolar index: PNL/PH.
PNI2 Petiolar node width index, using HW: DPW/HW.
DNI Dorsal petiolar node shape index: PNL/DPW.

CI (cephalic index) values (which are simply the reciprocal of ICI values) have been given in the species descriptions, to facilitate comparison with taxonomic literature.

Because some indices may take values greater than 1·00, the orthodox procedure of multiplying index values by 100 was not followed.

Morphological measurements were made on non-callow worker specimens from mature colonies. Most characters are approximately normally distributed (Table 1) with only six instances (out of 105) of highly significant ($P < 0{\cdot}01$) skewness, kurtosis, or both. This is the justification for giving standard deviations in the key and table. Ranges of some of the measurements are given in the species descriptions.

Synopsis

Workers of the *impressa* group may be diagnosed as follows: ponerine ants of the genus *Rhytidoponera*, with a distinctive saddle-shaped constriction of the dorsal surface of the mesosoma in the region of the posterior mesonotum and anterior propodeum (e.g. as in Figs 1, 3); relatively slender ants about 5 mm in length; most species with a characteristic metallic sheen, either of a blue, bluish purple, bluish green, or brassy hue. The range of variation in some morphological measurements and indices is indicated in Table 1. Differences between species are generally small and the group as a whole is rather homogeneous in habitus.

Table 1. Measurements (in millimetres) and indices, with standard deviations, for workers of the *Rhytidoponera impressa* group

Significant departures from normality due to skewness (*,**) and kurtosis (†,††) are also indicated. *, † $0{\cdot}01 < P < 0{\cdot}05$; **,†† $P < 0{\cdot}01$. All specimens of *chalybaea* and *confusa* come from nests whose specific identity was confirmed by electrophoretic evidence

Character	*confusa*	*chalybaea*	*impressa*	*enigmatica*	*purpurea*
HL	1·59±0·09	1·60±0·07	1·60±0·09	1·66±0·08	1·82±0·10
ML	0·59±0·04	0·62±0·04*	0·62±0·04	0·63±0·03	0·67±0·04*†
SL	1·52±0·08	1·57±0·07	1·55±0·06	1·62±0·07	1·83±0·10
ED	0·29±0·02	0·29±0·02	0·28±0·02	0·28±0·02	0·32±0·02
HW	1·32±0·08	1·36±0·08**	1·34±0·08	1·37±0·08	1·50±0·09
WL	2·21±0·12	2·24±0·12	2·25±0·12	2·37±0·11	2·54±0·14
PW	0·98±0·06	0·98±0·06*	0·98±0·07	1·04±0·06	1·10±0·07
DPW	0·51±0·04	0·50±0·04**††	0·49±0·04	0·54±0·04	0·52±0·04
PH	0·89±0·06	0·88±0·07**††	0·88±0·06	0·97±0·06	0·98±0·06
PNL	0·39±0·02	0·40±0·03	0·40±0·03	0·46±0·03	0·47±0·04*
ICI	1·20±0·02	1·18±0·02*	1·20±0·02	1·21±0·02	1·21±0·02
MI	0·45±0·02*	0·45±0·02	0·46±0·02	0·46±0·02	0·45±0·02
MI2	0·37±0·02	0·38±0·02	0·39±0·02	0·38±0·02	0·37±0·02*
SI	1·15±0·03	1·15±0·04**	1·16±0·04	1·18±0·03	1·22±0·03
SI2	0·96±0·02*	0·98±0·03	0·97±0·02	0·98±0·02	1·01±0·02
OI	0·22±0·01	0·21±0·01	0·21±0·01	0·21±0·01	0·21±0·01
PI	0·74±0·02*	0·72±0·02	0·73±0·02*††	0·76±0·02	0·73±0·01
PNI	0·52±0·02	0·51±0·02	0·50±0·02	0·52±0·02	0·47±0·02
LPI	0·44±0·02	0·45±0·02*	0·45±0·03	0·47±0·02	0·48±0·03
PNI2	0·39±0·01	0·37±0·02	0·37±0·02	0·40±0·02	0·35±0·01
DNI	0·77±0·04	0·80±0·04*	0·80±0·06	0·84±0·04*,††	0·90±0·04
No. of workers	151	80	31	28	30
No of nests	151	78	12	24	15
No. of popns	16	13	6	5	7

Functional winged queens occur commonly in most populations of *impressa*-group species, a situation found in no other *Rhytidoponera* except *croesus* Emery and possibly *aspera* Roger. (Queens occur infrequently in several other species including *victoriae* André, *inornata* Crawley, *metallica* F. Smith, and *clarki* Donisthorpe. In most species of *Rhytidoponera* winged queens are entirely unknown.)

Synonymic List of Species

1. *chalybaea* Emery, 1901, p. 51 (New South Wales, southern Queensland, New Zealand [introduced]) = *cyrus* (Forel) 1910, p. 13.

2. *confusa*, sp. nov. (Victoria, New South Wales, southern Queensland).
3. *enigmatica*, sp. nov. (Sydney region of New South Wales).
4. *impressa* (Mayr), 1876, p. 92 (Queensland).
5. *purpurea* (Emery), 1887, p. 444 (northern Queensland, New Guinea) = *splendida* (Forel) 1910, p. 12.

Key to Workers

The following key excludes electrophoretic characters, but allozyme analysis is sometimes necessary for positive identification of *chalybaea* and *confusa*. Furthermore, a preliminary study of electrophoretically detectable differences between populations of *impressa* (s.s.) suggests that *impressa* itself may be a complex of several reproductively isolated forms.

1. *a* Tooth of subpetiolar process consisting of a long thin spine (Fig. 24); lateral occipital lobes broadly rounded; head and mesosoma metallic purple-green with contrastingly duller greenish or brassy gaster (north Queensland, New Guinea) ..... *purpurea* Emery
   b Subpetiolar process with a shorter tooth, widening towards the base (Fig. 16); lateral occipital lobes narrowly rounded; head, mesosoma, and gaster brown or metallic blue, blue-purple, or grey-green 2
2(1). *a* Striation on 2nd gastric (4th abdominal) tergite usually longitudinal or transversely arched (Fig. 27); PNL 0·41–0·54 mm (mean 0·46 ± 0·03); head, mesosoma and gaster dull metallic blue with grey-green reflections; distribution: local, known only from Sydney region ..... *enigmatica*, sp. nov.
   b Striation of 2nd gastric tergite usually transverse (Fig. 26); PNL 0·33–0·48 mm (mean 0·39–0·40); head, mesosoma, and gaster brown or metallic blue-purple; distributions: widespread (Victoria to north Queensland) 3
3(2). *a* Head and mesosoma brown, with little or no hint of bluish purple iridescence (fresh, non-callow specimens) (Queensland) ..... *impressa* Mayr
   b Head and mesosoma iridescent blue-purple (fresh, non-callow specimens) 4
4(3). *a* Distribution: Victoria to Coffs Harbour, N.S.W. (on coast), farther inland north to Bunya Mts, Qld; tooth of subpetiolar process usually blunt, with a broad base (Fig. 16); striation on 2nd gastric tergite obsolete before the lateral margin (Fig. 17); head, mesosoma and gaster with deep bluish purple hue ..... *confusa*, sp. nov.
   b Distribution: Coffs Harbour, N.S.W. to southern Queensland, also localized further south (Sydney region, Wingham) in disturbed habitats; tooth of subpetiolar process pointed, with a shorter base (Fig. 18); striation on 2nd gastric tergite extending more completely to the lateral margin (Fig. 19); head, mesosoma, and gaster with less intense bluish iridescence ..... *chalybaea* Emery

Species Descriptions

Rhytidoponera chalybaea Emery

(Figs 4–6, 18, 19, 29)

Rhytidoponera impressa var. *chalybaea* Emery, 1901, p. 51. Holotype worker, New South Wales (Staudinger), in MCSN, Genoa (examined).

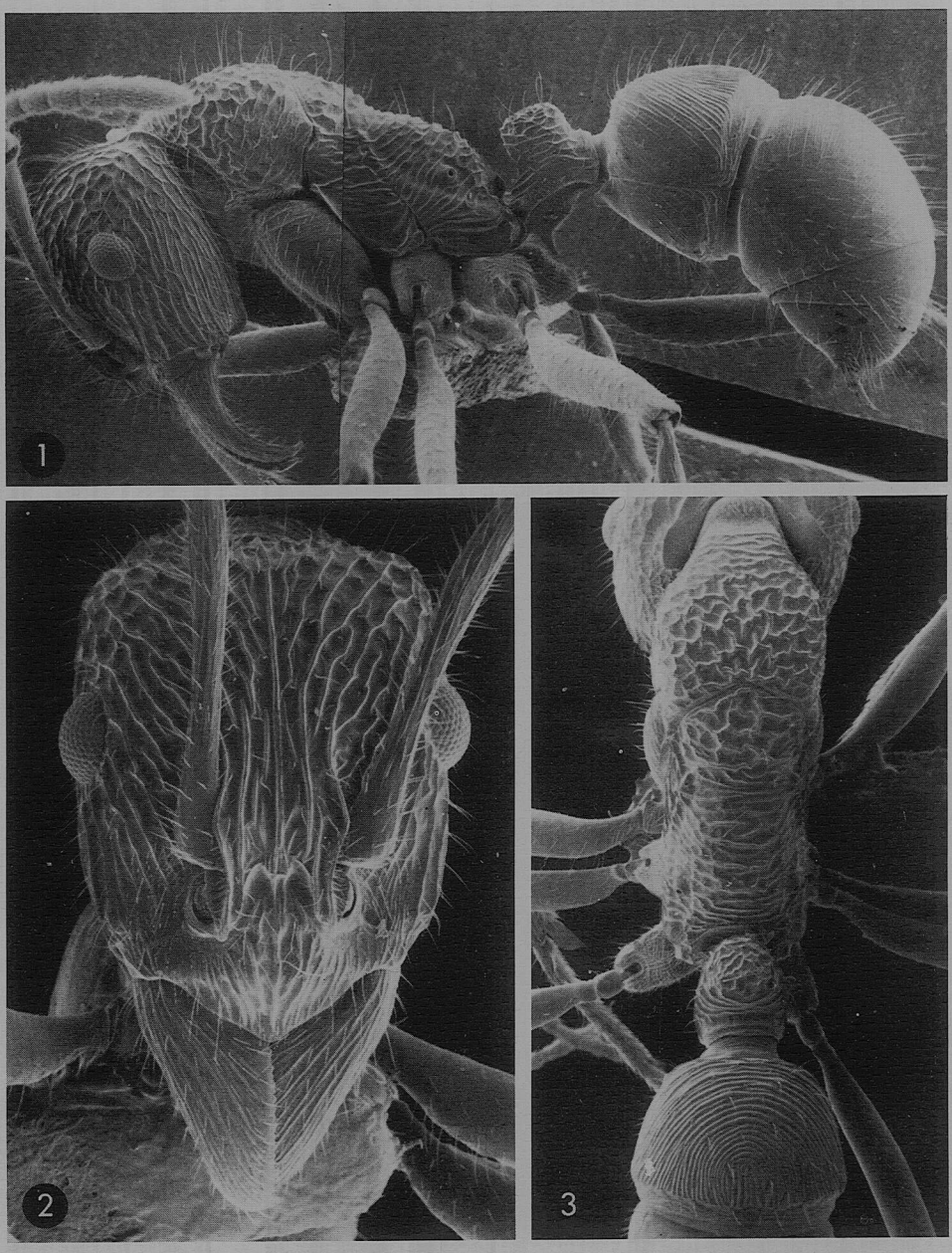
Ectatomma (*Rhytidoponera*) *cyrus* Forel, 1910, p. 13. Syntype workers, queen(s), Ballina, New South Wales, 1897 (W. W. Froggatt), in ANIC (seven workers examined) and presumably MHN (not examined). [Synonymy by Brown, 1954, p. 4.]

Rhytidoponera (*Chalcoponera*) *cyrus* (Forel); Emery, 1912, p. 81. [Discussion of relationship to var. *chalybaea* Emery.]

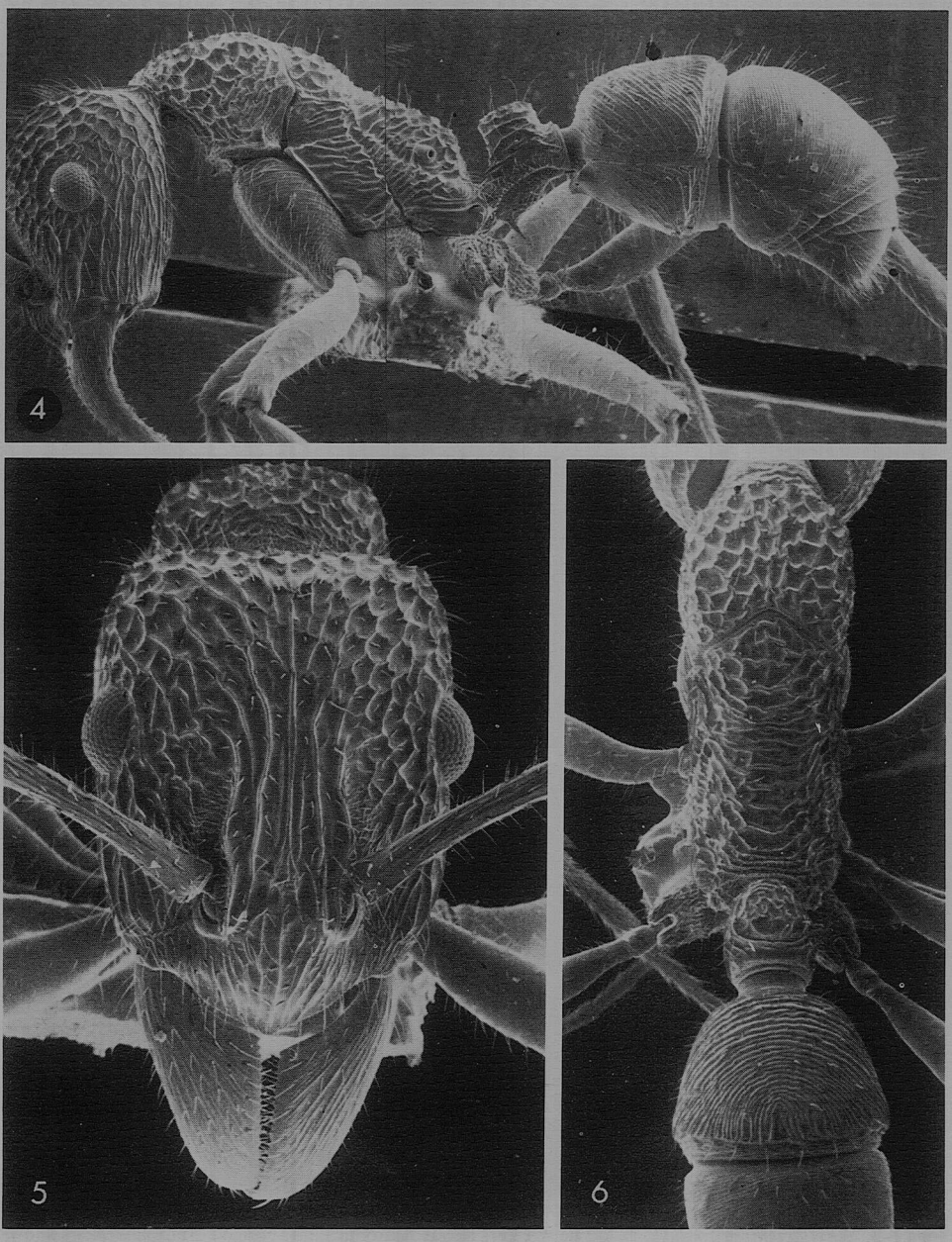
Rhytidoponera chalybaea Emery; Brown, 1954, p. 4. [Raised to species.]

Rhytidoponera chalybaea Emery; Taylor, 1961, p. 2. [Recorded from New Zealand.]

Worker measurements (n = 80). HL 1·46–1·80, HW 1·24–1·59, ML 0·55–0·72, SL 1·34–1·75, WL 2·00–2·55, CI 0·81–0·90, MI 0·41–0·50, SI 1·02–1·23.



Figs 1–3. *Rhytidoponera confusa*, holotype worker, Royal National Park, N.S.W. Standard views showing: *1*, lateral view of head, mesosoma, petiole and gaster; *2*, frontal view of head; *3*, dorsal view of mesosoma, petiole and first gastric tergite (third abdominal segment). HW = 1·26 mm, WL = 2·12 mm.



Figs 4–6. *R. chalybaea* worker, 6 km SW of Wardell, N.S.W. Standard views, as in Figs 1–3. HW = 1·27 mm, WL = 2·14 mm.

Diagnosis

Very similar to *confusa* (q.v.).· The following differences are most marked in areas of sympatry:

(1) Colour of head, mesosoma, and dorsum of gaster tends to be a less intense metallic blue in *chalybaea*; (2) mandibles, antennae, legs, and gaster underneath tend to be darker and less contrasting in *chalybaea*; (3) striae on 2nd gastric tergite usually extend completely to the lateral margin, and sides of the gaster are correspondingly less shiny, in *chalybaea*; (4) subpetiolar process in *chalybaea* with a sharper, more pointed tooth, arising from a shorter base.

Comments

The decisive evidence for reproductive isolation between *chalybaea* and *confusa* comes from an electrophoretic analysis of sympatric (as well as allopatric) populations. The allelic arrays at the esterase-4 locus show virtually no overlap; the common allele at the esterase-3 locus in *confusa* is completely absent in *chalybaea* and there exist large differences in gene frequencies at the amylase locus (Ward 1978, 1980).

The following characters (taken from Table 1), while not diagnostic, do have very significantly different means (t-test, $P < 0{\cdot}001$) in *chalybaea* and *confusa*: ML, SL, HW, ICI, MI2, SI2, PI, PNI, LPI, PNI2 and DNI.

R. chalybaea is a common and characteristic ant in the subtropical rain forests of northern New South Wales and southern Queensland, where it nests primarily in rotten logs and under stones. It is worth noting that south of Coffs Harbour, N.S.W., all records of *chalybaea* come from human-disturbed habitats, strongly suggesting a recent southward expansion of its range. In the Sydney region *chalybaea* occurs commonly in city parks and gardens, and only penetrates wet gullies (with wet sclerophyll and rain-forest vegetation) where these are floristicly highly disturbed (e.g. dominated by introduced weeds such as *Lantana*, *Ligustrum* and *Tradescantia*). In such locations the local rain-forest species, *confusa*, tends to be rare or absent. On the other hand, *chalybaea* and *confusa* do occur sympatrically in *undisturbed* mesic habitats in some parts of northern New South Wales and southern Queensland.

Material Examined

Sydney area: University of Sydney; Glebe; Pagewood; Hurstville; Cooper Park; Balls Head, Sydney Harbour; Greenacre; Mosman; Balgowlah; Manly; Castle Cove; Roseville Chase; West Ryde; Hunter's Hill; East Ryde; Lane Cove West; Grosvenor Rd, Lane Cove Park. **Other New South Wales localities:** Wingham; Sapphire Beach near Coffs Harbour; Camira Creek, Mt Marsh State Forest; Iluka; Wardell; Whian Whian State Forest; N. of Dunoon; Mt Warning; Tweed Range, Wiangarie State Forest; Cherry Tree State Forest; Boonoo Boonoo Falls; Murwillumbah; Lismore; Ballina. **Queensland:** Lamington Plateau; Coomera Gorge; Beechmont; Tamborine Mountain; Toowoomba; Mt Glorious; Mt D'Aguilar; Boombana National Park; Mt Nebo; Brisbane; Toowong; Mt Coot-tha; Blackall Range; near Kenilworth; Booroobin; Maleny; Mary Cairncross Park, near Maleny; Montville; Eungella Range, W. of Mackay; 16 km N. Eungella; Mt William, Eungella National Park.

The following material from New Zealand and from the geographical area of overlap between *confusa* and *chalybaea* in Australia is tentatively identified as *chalybaea* on the basis of coloration, gastric striation, and shape of the subpetiolar process, in the absence of electrophoretic data: **New Zealand:** Auckland; Waimauku, Auckland; Torbay, Auckland; Southdown, Auckland; Otara; Tauranga; Napier. **New South Wales:** 2 km E. The Gap, east of Mulbring; Coffs Harbour. **Queensland:**

Stanthorpe; Macpherson Range, (Lamington) National Park.
In AM, ANIC, DSIR, MCSN, MCZ and NMV.

Rhytidoponera confusa, sp. nov.

(Figs 1–3, 16, 17, 26, 28)

Rhytidoponera chalybaea; Brown (nec Emery), 1954, p. 4 (partim).
Rhytidoponera chalybaea; Imai, Crozier and Taylor (nec Emery), 1977, p. 373 [karyotype].
Rhytidoponera impressa; Imai, Crozier and Taylor (nec Mayr), 1977, p. 373 [karyotype].

Measurements

Holotype worker. HL 1·54, HW 1·26, ML 0·53, SL 1·45, WL 2·12, CI 0·82, MI 0·42, SI 1·15.
Worker measurements (paratypes and other material, n = 151). HL 1·38–1·85, HW 1·13–1·54, ML 0·48–0·69, SL 1·32–1·71, WL 2·00–2·59, CI 0·80–0·87, MI 0·39–0·50, SI 1·08–1·23.

Type Material

Holotype worker locality. Royal National Park, New South Wales, 34°09′S., 151°01′E., 50 m, 11.i.1977, P. Ward acc. No. 2129; from nest in rotten log, in rain-forest gully below waterfall.

Type series. Approximately 70 accessions (nest series) from the type locality (Royal National Park, New South Wales; leg. P. S. Ward; 1974–1978). Type series is hereby restricted to material from the type locality. Additional material believed to be conspecific is listed below (under *Material Examined*).

Holotype and series of paratypes in ANIC; other paratypes in MCZ, BMNH, MCSN and Australian State Museums.

Diagnosis

Measurements and proportions as given and illustrated. Head widest behind eyes, or slightly anterior to the eyes. Occipital margin (seen in frontal view) slightly convex. Occipital lobes or flanges (seen in lateral view) well developed. Inferior pronotal margin with conspicuous tooth. Dorsum of mesosoma with an obtuse V-shaped promesonotal suture, and a distinctive saddle-shaped mesoepinotal impression. Petiole subrectangular, the subpetiolar process consisting of a broad base with a relatively stout, blunt tooth.

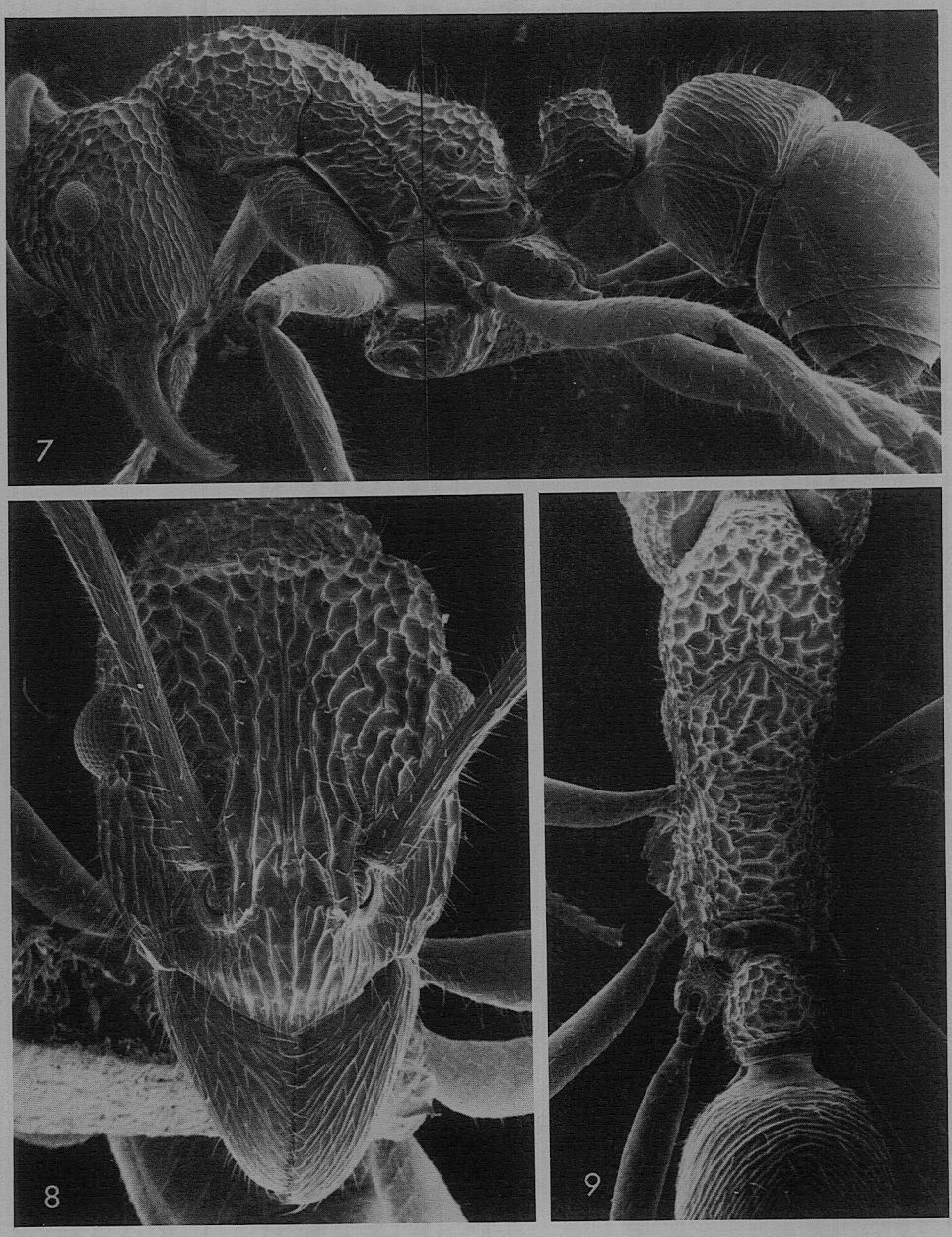
Mandibles and scapes with fine, longitudinal striation. Sculpturation of head, mesosoma, and petiole rugose, with coarse longitudinal striae on the head, and transverse striae on the propodeum, sides of mesosoma, and anterior face of petiole. 1st gastric (3rd abdominal) tergite with fine concentric striation, 2nd gastric tergite with very fine transverse striation, occasionally (4 specimens out of 200 examined for this trait) conspicuously arched transverse. Striation on 2nd gastric tergite tending to become obsolete towards the lateral margin, the gaster becoming correspondingly shiny.

Erect pale yellow hairs scattered on body surface.

Head, mesosoma, and gaster with a deep blue to bluish purple metallic sheen. Mandibles, antennae, and legs a contrasting rufous brown.

Comments

R. confusa (as presently conceived) is a very common species in rain forest and



Figs 7-9. *R. enigmatica*, holotype worker, Lane Cove West, N.S.W. Standard views as in Figs 1–3. HW = 1·42 mm, WL = 2·42 mm.

wet sclerophyll of eastern New South Wales. Further north it becomes progressively less abundant, and more restricted to higher elevations. The rather isolated populations from Ravensbourne and Bunya Mountains, Qld, are somewhat atypical, in the shape of the node and subpetiolar process. In some respects workers from these populations more closely resemble *chalybaea* than typical *confusa*. They are included with the latter on the basis of allozyme data.

Material Examined

Victoria: Queenstown near Hurstbridge; Seville; Ferntree Gully; Upwey; Belgrave; Woongalloe; Healesville; Millgrove; Fernshaw; Warburton; Baw Baw; Leongatha; Kinglake National Park. **New South Wales:** Naghi State Forest; Eden; Rosedale; Nelligen; Durras Lake; Upper Kangaroo Valley; Gerringong; 2 miles E. Berry; Gerroa, 6 miles S. Kiama; Foxground, 8 miles S. Kiama; Saddleback Mtn, near Kiama; 8 km SW. Jamberoo; 6 km W. Jamberoo; Macquarie Pass; Gooseberry I., Lake Illawarra; Mt Kembla; Mt Keira; Mt Pleasant, Wollongong; Mt Ousley near Wollongong; 3 km W. Bellambi; Corrimal; Royal National Park; Appin; Sutherland; Coxs River; Blackheath; Springwood; Bilpin; Manly; Forestville; Roseville Chase; Lane Cove West; Grosvenor Rd, Lane Cove Park; Gordon; Pymble West; Pymble; Kurrajong; Bola Creek National Park; Galston Gorge; Berowra; Hornsby; Jerusalem Bay; Cowan; McCarrs Creek; Dharug National Park; 5 km S. St Albans; Mangrove Mtn; Mooney Mooney Creek; Pearl Beach; Terrigal; Strickland State Forest; Ourimba State Forest, Wyong; Heaton State Forest; Fraser Park, 6 km S. Swansea; 15 km SW. Murrurundi; Salisbury; near Cobark; Upper Allyn River near Eccleston; Blue Gum Knob; Upper Chichester; Lagoon Pinch near Barrington Tops; Kings Head near Elands; Rawson near Comboyne West; Wingham; Bellangry Forest, NW. Wauchope; Hawks Nest; Myall Lakes (Boolambayte); Seal Rocks; Scotts Head; Manilla; New England National Park; Deer Vale; Dorrigo; Bruxner Park near Coffs Harbour; Sugarloaf Pt, Gibraltar Range Natonal Park; Point Lookout near Grafton; Girard State Forest; Boonoo Boonoo Falls; Beaury State Forest; Yabbra State Forest. **Queensland:** Coomera Gorge; Moran Falls; Christmas Creek, Lamington National Park; Spicers Gap; Ravensbourne; Bunya Mtns.

The following material from within the geographical range of both *confusa* and *chalybaea* is provisionally identified as *confusa*, on the basis of coloration, gastric striation, and shape of the subpetiolar process (in the absence of electrophoretic data): **New South Wales:** vic. Woodenbong; Tooloom Range. **Queensland:** Cunninghams Gap; Binna Burra; Gwongorella National Park.

In AM, ANIC, BMNH, MCZ.

Rhytidoponera enigmatica, sp. nov.

(Figs 7–9, 20, 21, 27, 30)

Measurements

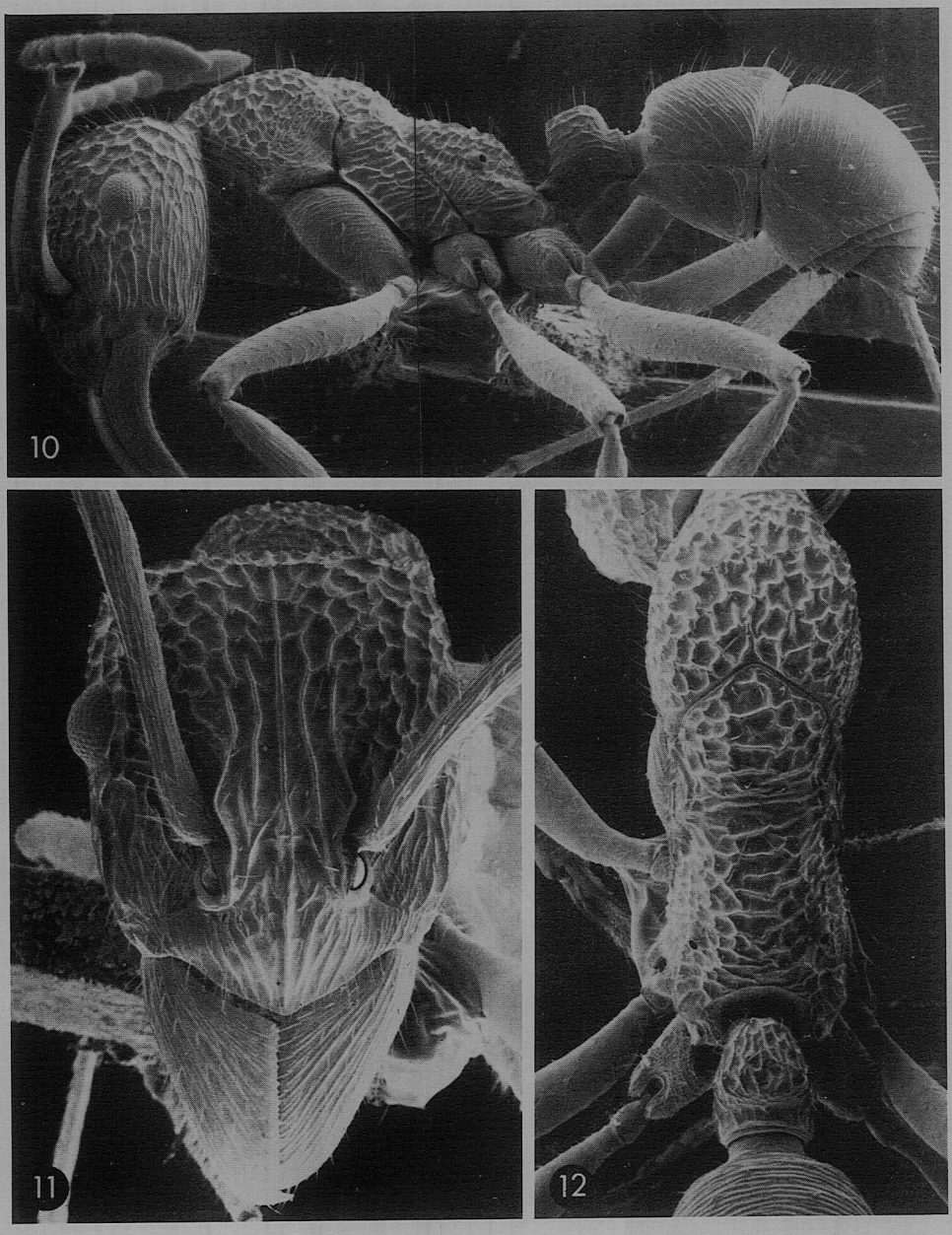
Holotype worker. HL 1·71, HW 1·42, ML 0·64, SL 1·66, WL 2·42, CI 0·83, MI 0·45, SI 1·17.

Paratype worker measurements (sample of 27). HL 1·54–1·81, HW 1·25–1·53, ML 0·57–0·68, SL 1·50–1·78, WL 2·20–2·62, CI 0·80–0·85, MI 0·42–0·49, SI 1·14–1·25.

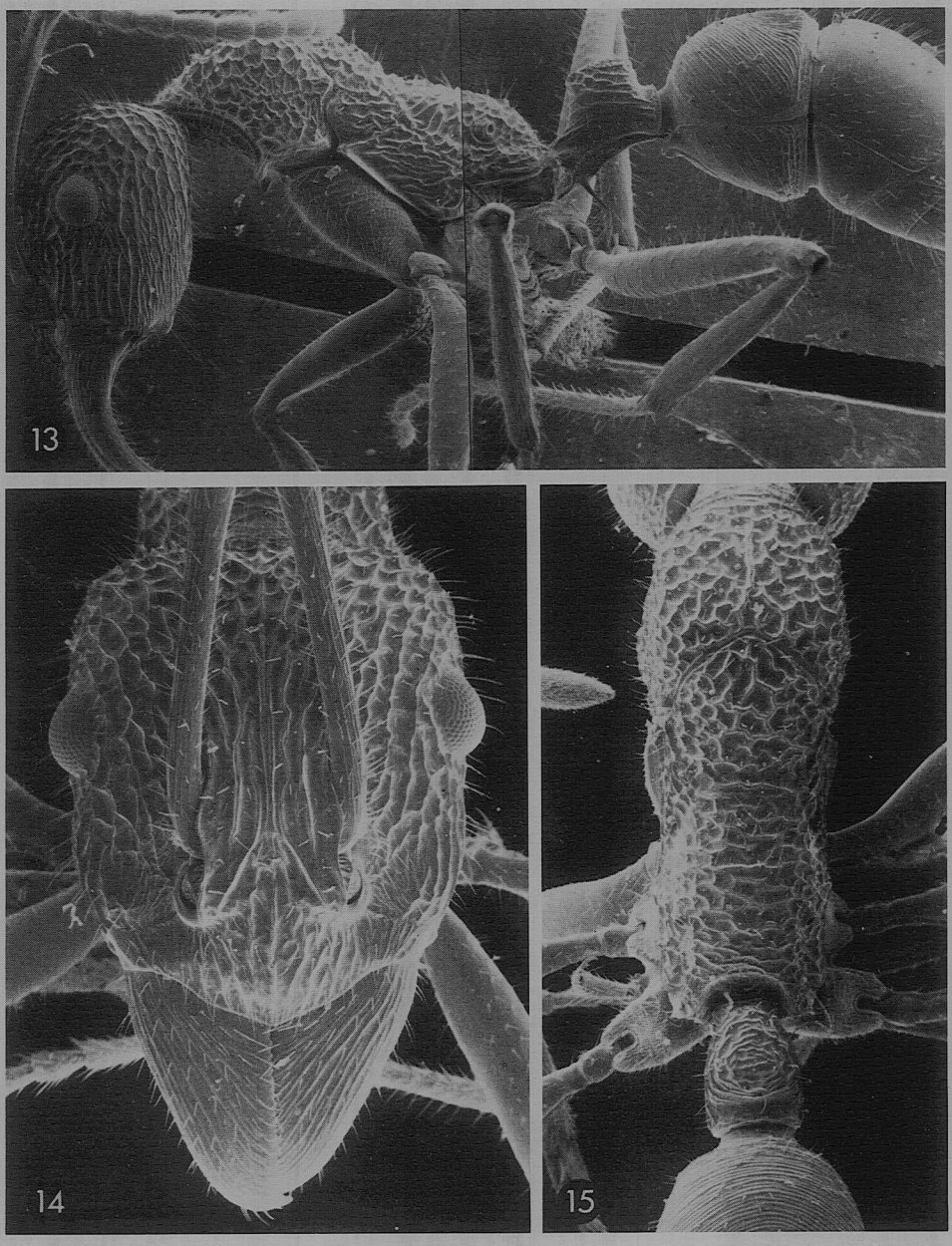
Type Material

Holotype worker locality. Stringy Bark Creek, Lane Cove West, New South Wales, 33°49′S., 151°09′E., 10 m, 30.iv.1977, P. S. Ward acc. No. 2442; nest under stone, in sandstone gully with disturbed wet sclerophyll vegetation, dominated by *Ligustrum* sp.

Type series. (1) A total of 179 workers from accession No. 2442 and 904 workers and 10 males from the following 11 additional accessions (nest series) from the type locality: P. Ward acc. Nos 2444, 2447, 2448, 2449, 2450, 2675, 2676, 2677, 2681, 2682, 2684. (2) Roseville Chase, N.S.W., 5.viii.1976, B. B. Lowery; under rock, beside dry rivulet on sandstone hillside; 27 workers. (3) Roseville Chase,



Figs 10–12. *R. impressa*, worker, Cooran Plateau, Qld. Standard views as in Figs 1–3. HW = 1·28 mm, WL = 2·14 mm.



Figs 13–15. *R. purpurea*, worker, Wau, PNG. Standard views as in Figs 1–3. HW = 1·58 mm, WL = 2·71 mm.

N.S.W., 33°46'S., 151°12'E., 80 m, 12.i.1977, P. Ward acc. No. 2143; nest under rock, disturbed vegetation (*Casuarina* dominant) on sandstone, near small intermittent stream; 121 workers. (4) Mosman, N.S.W., 33°50'S., 151°14'E., 20 m, 29.iii.1976, P. Ward acc. No. 1603; 1 worker foraging on mossy stone, disturbed vegetation, wet sandstone gully. (5) Manly Dam, N.S.W., 33°47'S., 151°15'E., 30 m, 12.i.1977, P. Ward acc. No. 2133; 1 worker, ground forager, on sandstone ledge above stream. (6) Coal and Candle Creek, Sydney, N.S.W., 1.xi.1970, B. B. Lowery; nest between rocks, exposed (sunny) location, sandstone gully; 6 workers examined. (7) Cowan, N.S.W., 3.vii.1970, B. B. Lowery; nest between sandstone rocks, open scrub hillside; 6 workers examined. (8) Appin, N.S.W., 34°12'S., 150°46'E., 180 m, 20.x.1974, P. Ward acc. No. 251; colony under rock, damp soil beside stream; wet sclerophyll. Also 7 additional accessions (P. Ward acc. Nos 254, 579, 943, 944, 1582, 1583, 1584) from this and a nearby stream gully at the same locality; total series of 1062 workers.

Holotype and series of paratypes in ANIC. Other paratypes in MCZ, BMNH, MCSN, and Australian State Museums.

Diagnosis

Head, mesosoma, and dorsum of gaster dull metallic blue, with grey-green reflections. Mandibles, antennae, legs, and gaster underneath a contrasting light ferrugineous brown.

Rugose sculpturation of head and messosoma similar to that of *confusa*; striae on sides of mesosoma more obscured.

Striation of 2nd gastric tergite predominantly longitudinal or strongly arched transverse (70 out of 82 workers examined for this trait); and such striation usually (72 out of 82 workers) obsolete before the lateral margin, the sides of the gaster thus being shiny.

Petiolar node averaging longer than in other *impressa* group species. Tooth of subpetiolar process similar to that of *chalybaea*, i.e. with a broad base.

Comments

R. enigmatica is a rather localized and obscure species, duller in colour than most others. It appears to be restricted to mesic habitats on sandstone in the Sydney region. At the type locality *enigmatica* occurs sympatrically with both *confusa* and *chalybaea*, from which it remains quite distinct (morphologically and genetically). It also departs from these other species in details of life cycle, colony structure, and nest site preferences.

Rhytidoponera impressa (Mayr)

(Figs 10–12, 22, 23, 29)

Ectatomma impressum Mayr, 1876, p. 92. Syntype workers, queens, Gayndah, Qld, in NHMV (not examined) and in MCSN (examined).

Rhytidoponera (Chalcoponera) impressa (Mayr); Emery, 1912, p. 77 [In key].

Rhytidoponera impressa (Mayr); Brown, 1954, p.5. [Discussion of relationships to *chalybaea* Emery and *purpurea* Emery.]

Worker measurements (n = 31). HL 1·47–1·78, HW 1·22–1·53, ML 0·54–0·69, SL 1·43–1·65, WL 2·05–2·47; CI 0·81–0·87, MI 0·42–0·50, SI 1·08–1·22.

Diagnosis

Similar to *confusa* and *chalybaea*, from which it is distinguished chiefly by colour. Head, mesosoma and gaster brown to dark brown with little or no hint of blue, purple or green iridescence. Mandibles, antennae, and legs a lighter ferrugineous brown. Considerable variation in the shape of the occipital lobe (but head not as broadly rounded as *purpurea*), in the shape of the subpetiolar tooth (from a sharp point to a broad blunt shape approaching that found in *confusa*), and in the amount of fine striation on the side of the 2nd gastric tergite.

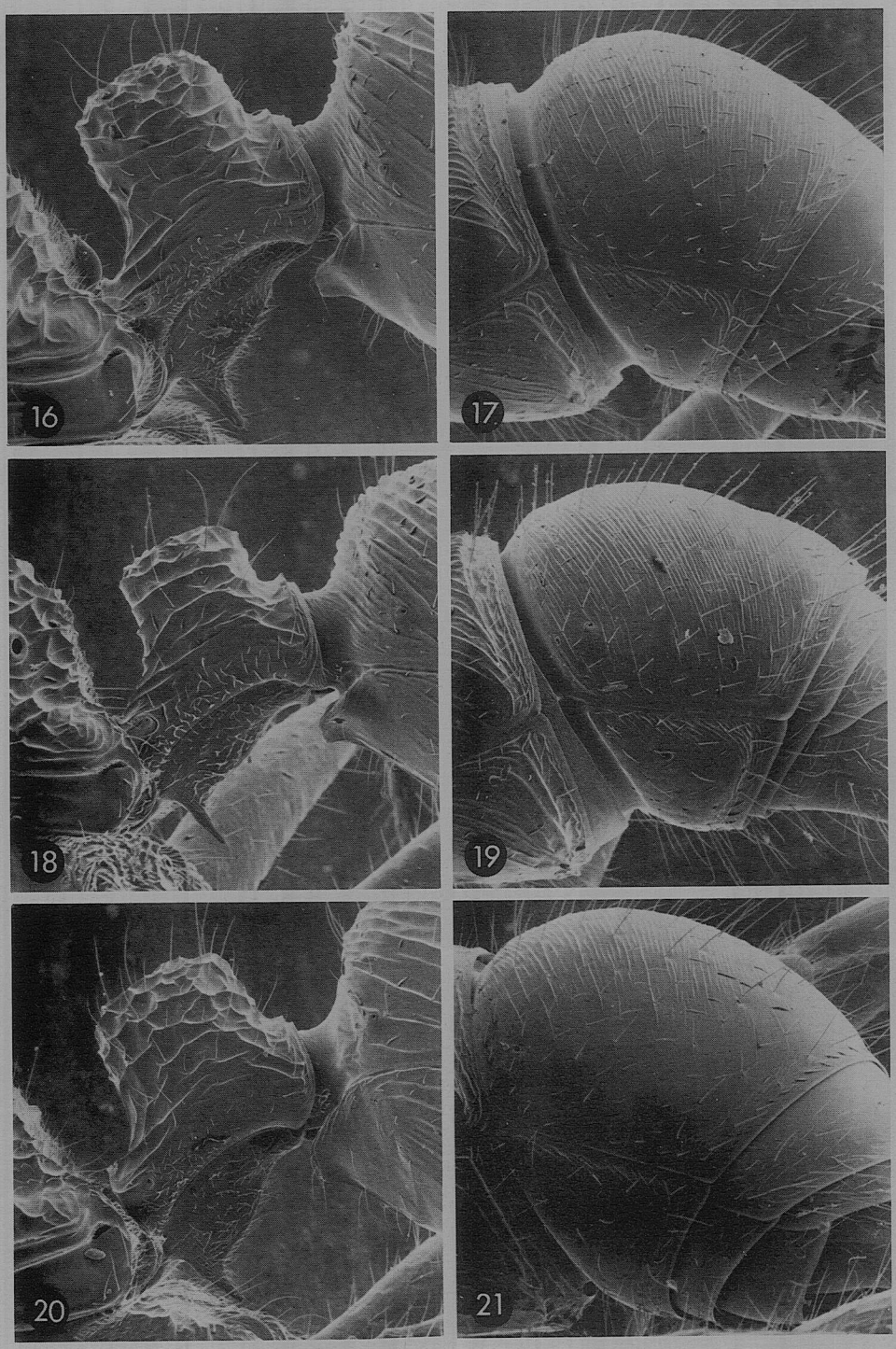
Comments

Specific distinctness of *impressa* is suggested by its sympatric associations with *purpurea* in northern Queensland, approximate sympatry with *chalybaea* in Eungella National Park, and sympatric association with *confusa* in southern Queensland (Ravensbourne). However, two factors complicate the issue: (1) there is considerable interpopulation variation in morphology; (2) *impressa* appears to intergrade with *chalybaea* in the Blackall Range, southern Queensland, over a distance of a few kilometres. An analysis of electrophoretically detectable genetic variation in several populations of *impressa* (detailed in Ward 1978) confirms that: (1) populations differ considerably in gene frequencies, and allelic substitutions occur between some populations suggesting reproductive isolation; (2) there is genic introgression between *impressa* and *chalybaea* in the Blackall Range.

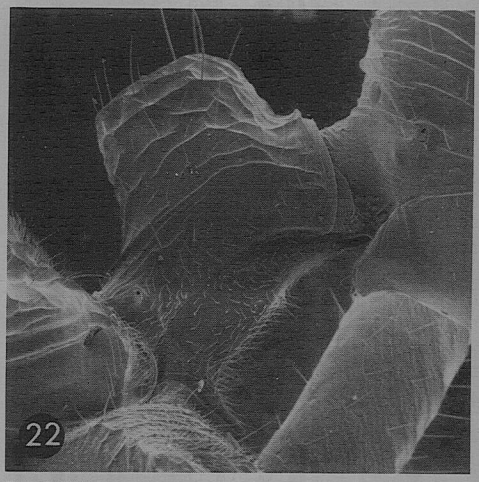
Given the fragmented nature of suitable mesic habitat (rain forest) in eastern Queensland, it is perhaps not surprising that populations have differentiated to the level of incipient speciation.

Regarding the occurrence of *impressa–chalybaea* intergrades in the Blackall Range, it would seem (on the basis of colour patterns in fresh material collected during the present study) that these are restricted to a narrow zone between Maleny and Mapleton. Fresh material collected from Mapleton Falls and Kondalilla National Park displayed no bluish purple iridescence, while conversely a large series of accessions from Mary Cairncross Park (near Maleny) contained uniformly metallic bluish purple specimens. The only freshly collected material which was intermediate between *impressa* and *chalybaea* (with feeble violaceous reflections) came from approximately 4 km south of Montville. Electrophoretic evidence, however, suggests that the hybrid zone is broader, with introgressed genes occurring throughout the Blackall Range.

It is unfortunate that the colour character separating these two forms cannot be reliably applied to old material which has faded. Discoloured *chalybaea* workers become indistinguishable from *impressa* and there is some evidence that cabinet specimens of *chalybaea* from the Blackall Range lose their purple iridescence rather rapidly. This may be the explanation for the records of '*impressa*' from Mary Cairncross Park in the ANIC (17.iii.1973, ex small rotten wood fragments, R. W. Taylor and R. Kohout acc. Nos 73.183, 73.185, 73.186 and 73.189). During the present study approximately 20 man-hours were spent at the same locality, resulting in the acquisition of more than 8300 workers (from 45 nests), *all* of which displayed a distinctive bluish purple iridescence. There may be some nest-site partitioning between *chalybaea* and *impressa*, since Brown (1954) records both forms from Montville, but in different habitats.



Figs 16–21. Lateral views of petiole and second gastric segment (fourth abdominal segment) of workers: *16, 17, R. confusa*; *18, 19, R. chalybaea*; *20, 21, R. enigmatica*. Petiolar heights (PH) 0·86, 0·83 and 1·01 mm, respectively. These are the same individuals depicted in Figs 1–9.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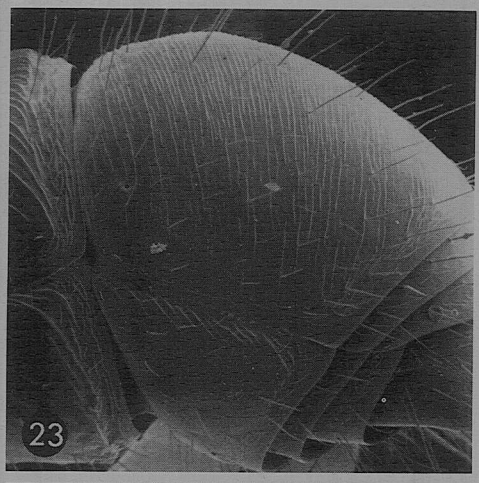
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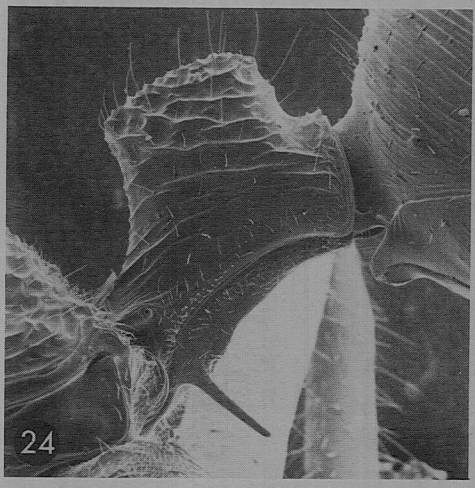
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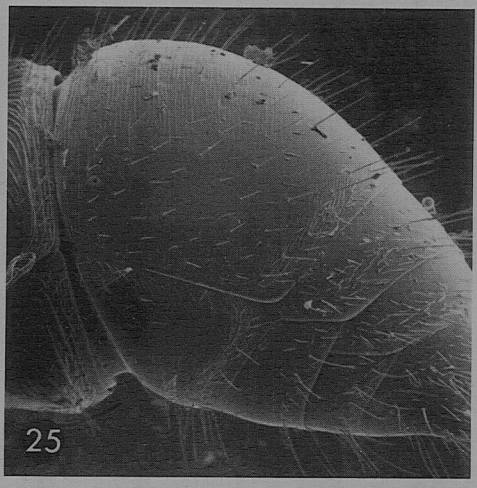
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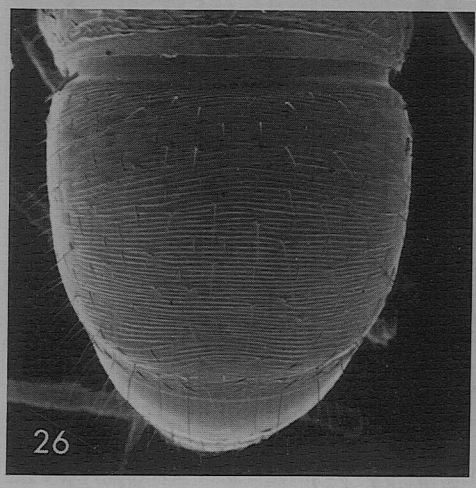
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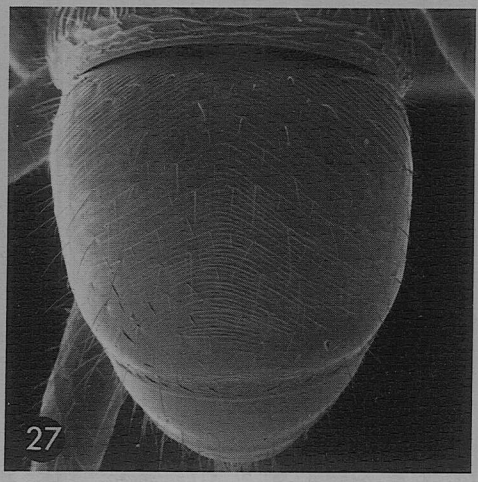
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There is little evidence of introgression between *impressa* and *chalybaea* in Eungella National Park, central coastal Queensland. However, one collection of *impressa* (3 km S. Eungella, 780 m, 2–3.v.1973, R. W. Taylor acc. No. 73.365) contains a single worker with faint purplish iridescence.

Material Examined

Queensland: Mapleton Falls National Park; Obi Obi Creek Track; Kondalilla National Park; Montville; Maleny; Benarkin; Ravensbourne National Park; 9 km S. Maidenwell; Kilcoy; Cooran Plateau, near Traveston; Gayndah; Mt Jacob; Jimna; 3 km S. Eungella; Broken River, Eungella National Park; 12 miles S. Calen; Mt Elliot; Mt Spec near Townsville; Crystal Creek National Park; Mt Helen Stn Rd, Paluma Range; Paluma; Paluma Range, 2 km W. Paluma; 5 km W. Paluma; 2 km S. Paluma Dam; Charmillan Creek, 16 km from Tully Falls; Kirrama Range, vic. Cardwell; Mt Fox Plateau near Ingham; 2 km E. Lake Barrine; Lake Eacham National Park; Malanda; Mtns above (SW.) Millaa Millaa; Crater National Park, Herberton; Atherton to Herberton; W. of Ravenshoe.

Provisionally identified as *impressa*: **New Zealand:** North Island Exped. (prob. north Taranaki, Nov.–Dec.1970, A. W. Don), 1 ☿, DSIR (this may well be a discoloured *chalybaea* worker).

In ANIC, DSIR, MCSN, MCZ and NMV.

Rhytidoponera purpurea (Emery)

(Figs 13–15, 24, 25, 30)

Ectatomma impressum var. *purpureum* Emery, 1887, p. 444. Syntype workers, Hatam, New Guinea, 1875 (Beccari), in MCSN (examined).

Ectatomma (*Rhytidoponera*) *impressum* var. *splendidum* Forel, 1910, p. 12. Syntype workers, Kuranda, Queensland (R. Turner) in MHN (not examined) and MCSN (one worker examined).

Rhytidoponera purpurea (Emery); Brown, 1954, p. 7. [*Splendida* synonymized.]

Rhytidoponera purpurea (Emery); Wilson, 1958, p. 315. [Ecology and distribution in PNG.]

Rhytidoponera purpurea (Emery); Haskins and Whelden, 1965, p. 92. [Colony structure.]

Rhytidoponera purpurea (Emery); Imai, Crozier and Taylor, 1977, p. 373. [Karyotype.]

Worker measurements (n = 30). HL 1·64–2·02, HW 1·31–1·70, ML 0·55–0·74, SL 1·63–2·04, WL 2·23–2·85, CI 0·79–0·86, MI 0·41–0·47, SI 1·15–1·30.

Diagnosis

Head and mesosoma metallic purple to purplish green; gaster a contrastingly duller greenish or brassy hue. Mandibles, antennae and legs a lighter shade of brown.

Sculpturation similar to that described for *confusa*. Striation on 2nd gastric tergite usually obsolete well before the lateral margin, and sides of gaster correspondingly shiny.

Head (viewed laterally) broadly rounded, and occipital lobes little developed or protruded.

Subpetiolar process with distinctive tooth: a simple thin spine below the anterior peduncle.

Figs 22–25. Lateral views of petiole and second gastric segment (fourth abdominal segment): *22*, *23*, *R. impressa*; *24*, *25*, *R. purpurea*. Petiolar heights (PH) 0·81 and 1·05 mm, respectively. These are the same individuals as in Figs 10–15.

Figs 26, 27. Dorsal views of the second gastric tergite (fourth abdominal segment): *26*, *R. confusa*; *27*, *R. enigmatica*, showing the arched transverse striation typical of this species. These are the same individuals shown in Figs 1 and 7, respectively.

Comments

This is the most distinctive species in the *impressa* group, and the only one known to occur in both Australia and New Guinea. Workers from the latter tend to be larger in size, with a longer petiolar node, more greenish reflections on the head and mesosoma, and less well developed striae on the sides of the mesosoma. Brown (1954) and Wilson (1958) did not consider *purpurea* and *splendida* sufficiently different to be recognized as separate species. The finding (Ward 1978) of no electrophoretically detectable genetic differences between New Guinea and north Queensland *purpurea* adds support to this view.

Material Examined

Irian Jaya: Hatam [near Manokwari, Vogelkop Peninsula]. **Papua New Guinea:** Sattelberg, Huon Gulf; Ngandua, Mongi-Mape Watershed; Zingzingu, Mongi Watershed; Gemeng, Mongi Watershed; Boana, Bunbok Valley; Bulolo; Bulolo R. valley, 6 km NE. Wau; Wau Ecology Institute, Wau; McAdam Park, Wau. **Queensland:** Mt Finnegan, S. of Cooktown; Shipton's Flat, S. of Cooktown; Thornton Range; Gold Hill, McDowall Range; Mt Windsor Tableland; Mt Alexander, NW. of Daintree; Mossman Gorge, 3 miles E. Mossman; 1 mile E. Crawford's Lookout; Mt Sturgeon; Mt Lewis near Julatten; Danbulla; Black Mtn 25 miles N. Kuranda; Mt Tiptree, near Mareeba; near Kuranda; Barron Falls National Park; Crystal Cascade near Cairns; Black Mtn Rd, Kuranda; Yarrabah Mission near Cairns; Upper Mulgrave River; Codfish Creek, near Babinda; near Babinda Boulders National Park; Mt Bellenden Ker; Kamerunga; West McNamee Creek; 3 km E. Lake Barrine; Lake Barrine; Lake Eacham National Park; 4 km S. Mt Haig, Atherton Tableland; near Mt Haig; Atherton-Herberton; Herberton Shire Scrub; Crater National Park, Herberton; 5 miles NNE. Herberton; Malanda; Mts above (SW.) Millaa Millaa; Millaa Lookout; Mt Fisher, Atherton Tableland; Davies Creek Rd, Atherton Tableland; Longlands Gap, Atherton Tableland; Ravenshoe; 1 mile E. Palmerston School; Palmerston National Park; Topaz; Tully Lakes; Tully Falls National Park; Koombooloomba; 15 km SW. Innisfail; Mt Fox Plateau, near Ingham; Downie Creek; Kirrama Range; Mt Helen Stn Rd, Paluma Range; 10 km W. Mt Spec; Crystal Creek National Park; Townsville.

In AM, ANIC, BMNH, MCSN, MCZ and NMV.

Species Excluded from the *Rhytidoponera impressa* Group

Rhytidoponera aenescens Emery

Rhytidoponera aenescens Emery, 1900, p. 32. Syntype worker(s), Lemien near Berlinhafen [=Aitape, Papua New Guinea] (L. Biró) presumably in HNM (not examined); one syntype worker in MCSN (examined).

Rhytidoponera aenescens Emery; Emery, 1912, p. 77. [In key.]

Rhytidoponera aenescens Emery; Wilson, 1958, p. 306.

Apparently known only from type material, *aenescens* was previously considered likely to be allied to *purpurea* (Emery 1912; Brown 1954; Wilson 1958). Examination of a syntype worker in MCSN reveals that *aenescens* does not belong to the *impressa* group. It is slightly larger than *purpurea*, and rather like *strigosa* Emery in general habitus. Characteristic features include: pronotum with very slight dorsolateral tuberosities and with a lateral, longitudinal impression containing fine transverse striation; mesonotum raised relative to propodeum (in lateral view), but not forming a saddle-shaped constriction as in the *impressa* group; anterior face of petiolar node longer and more gently sloping than posterior face, the anterior peduncle of node thus being better developed than in the *impressa* group; subpetiolar process consisting of a very short blunt tooth; 1st gastric tergite (3rd abdominal segment) with concentric striation; 2nd gastric tergite with finer longitudinal striae.

Rhytidoponera scabrior Crawley, stat. nov.

Rhytidoponera (*Chalcoponera*) *aspera* var. *scabrior* Crawley, 1925, p. 590. Syntype worker(s), Lismore, New South Wales, (C. F. Deuquet), possibly in Hope Collection, Oxford (not examined); three 'cotype' workers in NMV (examined).

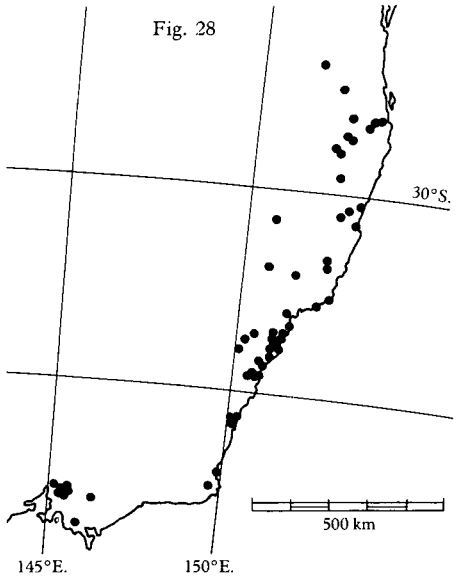
Brown (1954, p. 4) synonymized *scabrior* with *chalybaea* on the basis of a single *chalybaea* worker in the MCZ collection labelled 'Lsimore [sic]/N.S.Wales/C. F. Deuquet', 'Gift of /W. M. Wheeler', and '*Chalcoponera aspera* Roger/var. *scabrior* Craw./Det. J. Clark/after Crawley'. This specimen also bears two red type labels ('Type Series' and 'MCZ/Cotype/1/20403'). However, it does not agree with the original type description. On the other hand, there are topotypical worker specimens (leg. Deuquet) in the ANIC and NMV which *do* agree with Crawley's original description, and the three workers from the Melbourne collection (NMV) are clearly labelled as *scabrior* 'cotypes' (examined by Dr R. W. Taylor). In addition, the ANIC contains other conspecific material from north-eastern New South Wales and south-eastern Queensland. Dr Taylor and I have concluded that the name *scabrior* should be applied to this species, and that the MCZ specimen must be considered doubtfully a genuine type of *scabrior*. We hesitate to designate a lectotype from the Melbourne series because a holotype might exist elsewhere, although Crawley seems to have routinely labelled all members of his type series as 'cotypes'. If a lectotype is ever designated it clearly should be a specimen agreeing with Crawley's description and this would exclude the MCZ specimen from consideration, removing the need for concern about its validity as a type.

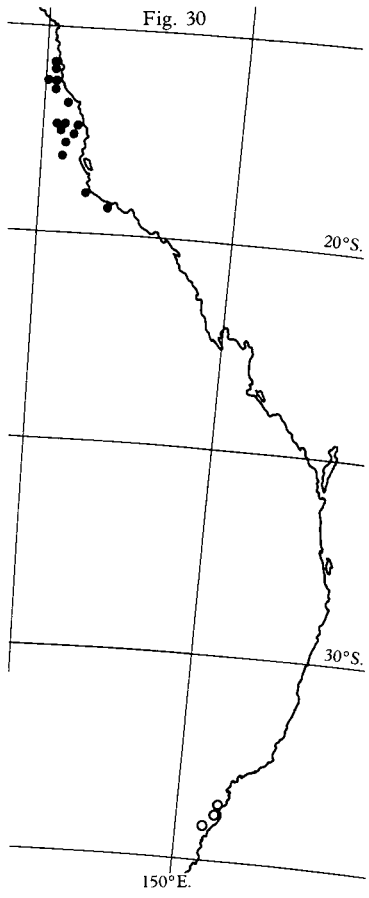
Taylor and I consider *scabrior* to be specifically distinct but closely related to *Rhytidoponera aspera* Roger, from which it is distinguished by the coarser striation of the first and second gastric tergites. The mesosoma is evenly convex in profile, clearly excluding the species from the *impressa* group.

Distribution Patterns and Species Relationships

The distribution pattern of the *Rhytidoponera impressa* group is typical of many taxa restricted to mesic habitats in Australia (see, e.g., Darlington 1961; Keast 1961; Mackerras 1970), in that it consists of a series of partially overlapping, quasi-isolated populations along the wet eastern coastal strip (Figs 28–30). Such a pattern is likely to be a result of successive contraction and expansion of wet forest, associated with previous climatic variation (see Crocker (1959), Nix and Kalma (1972), Kershaw (1976), Shaw (1976) and Beard (1977) for a discussion of past climatic fluctuations).

In the case of the *R. impressa* group, the time scale involved is uncertain; given the near genetic identity (based on electrophoretic studies) of *purpurea* populations from north Queensland and the *north* side of the main dividing range in Papua New Guinea (all the more remarkable because of the absence of this species from lowland rain forest in Cape York Peninsula and Papua), it would seem that population differentiation is sufficiently slow for the origin of most *impressa* group species to predate the most recent Pleistocene climatic fluctuations (10,000–40,000 BP). Certainly *purpurea* and the remainder of the complex must have diverged earlier. On the other hand it may be that an early bottleneck reduced genetic variability in *purpurea* to such a low level (observed level of heterozygosity, $\hat{H}$, from electrophoretic data: 0·5%) as to preclude population differentiation in *pur-*





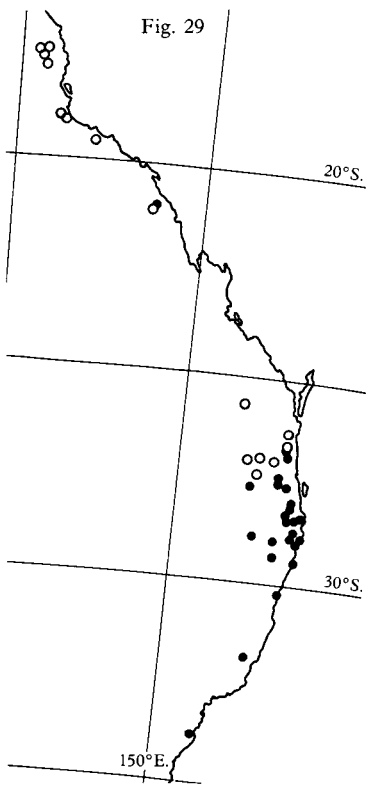


Fig. 28. Distribution of *Rhytidoponera confusa.*
Fig. 29. Distribution of *Rhytidoponera chalybaea* (●) and *R. impressa* (○).
Fig. 30. Distribution of *Rhytidoponera purpurea* (●) (excluding New Guinea) and *R. enigmatica* (○).

purea to the extent possible in the remainder of the species-complex, where observed levels of genetic variability ($\hat{H}$ = 0·8–7·2%; 33 populations) are considerably higher.

In any event, species and genetic diversity is currently highest in southern Queensland and northern New South Wales, where three species (*chalybaea*, *confusa* and *impressa*) may be found. This area is likely to have been an important rain-forest refuge during periods of much drier climate.

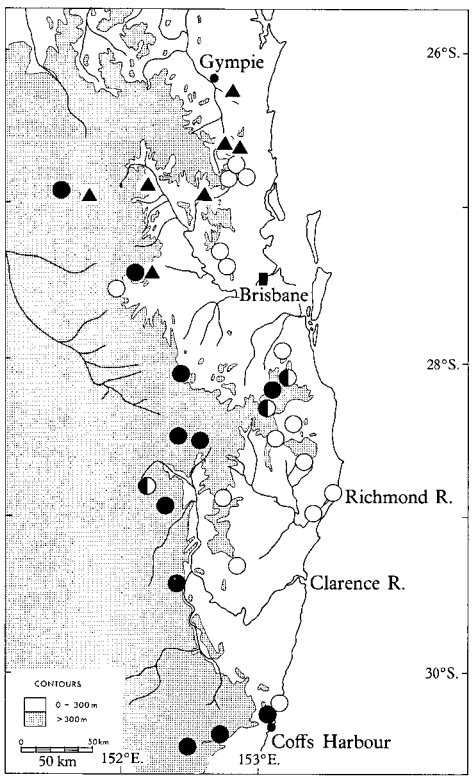


Fig. 31. Detailed distribution of *Rhytidoponera chalybaea*, (○), *R. confusa* (●) and *R. impressa* (▲) in southern Queensland and northern New South Wales. ◐ *R. chalybaea* and *R. confusa* together. Land over 300 m altitude is stippled.

The replacement of *confusa* by a sibling species (*chalybaea*) in coastal northern New South Wales is paralleled by many other examples (among insects and plants), and the region in question has been termed the Macleay–Macpherson Overlap Zone (Burbidge 1960). The detailed distribution of *chalybaea* and *confusa* in this area is shown in Fig. 31. The most likely historical barrier between the two species is the Clarence River valley, a region of non-volcanic rock producing rather nutrient-poor soils, which even today contains little in the way of suitable rain-forest habitat.

The *chalybaea–confusa* distribution pattern is shown by several other pairs of closely related species of rain-forest ants. These include *Leptogenys hackeri* Clark and *L. intricata* Viehmeyer, and *Pristomyrmex quadridentatus* André and *P. queenslandicus* Forel (Figs 32, 33). It may be noted parenthetically that, although Taylor (1965) synonymized *Pristomyrmex queenslandicus* with *P. quadridentatus*, field collections made during the present study have established their sympatric

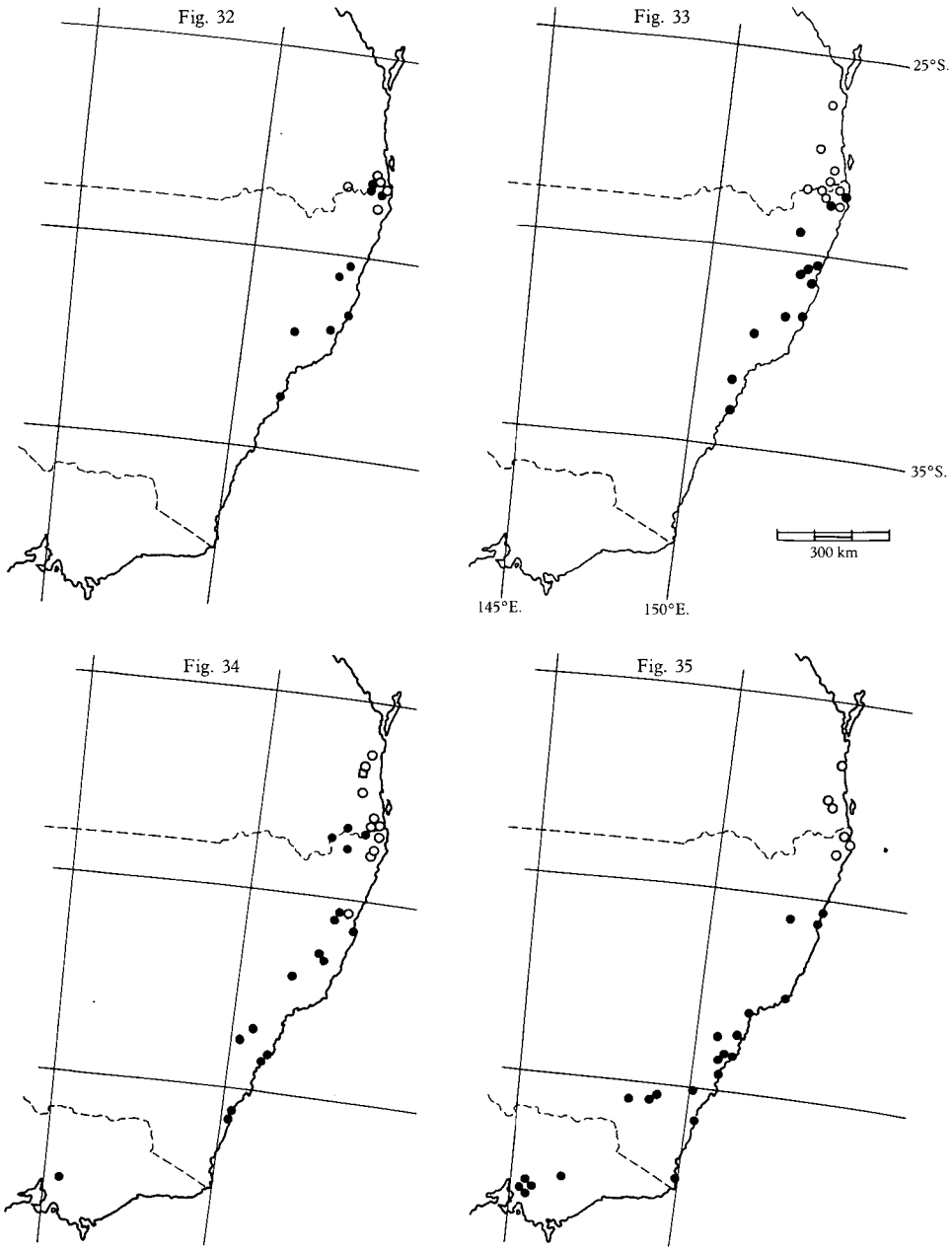


Fig. 32. Distribution of *Leptogenys hackeri* (●) and *L. intricata* (○) in northern New South Wales and southern Queensland. Based on records in ANIC.

Fig. 33. Distribution of *Pristomyrmex quadridentatus* (●) and *P. queenslandicus* (○) in northern New South Wales and southern Queensland. Based on records in ANIC.

Fig. 34. Distribution of *Rhytidoponera croesus*, s.l., in northern New South Wales and southern Queensland. ● *R. croesus* var. *fastuosa*. ○ *R. croesus*, s.s. □ Undescribed form. Based on records in ANIC.

Fig. 35. Distribution of *Rhytidoponera aspera* (●) and *R. scabrior* (○) in northern New South Wales and southern Queensland. Based on records in ANIC.

occurrence and probable specific distinctness. *Rhytidoponera croesus* Emery, s.l., consists of two 'colour forms' [bicoloured *croesus* and unicoloured blue-purple *fastuosa* Santschi; see Brown (1954)], which are quite likely sibling species, and whose distributions abut in northern New South Wales (Fig. 34). A third, undescribed, *croesus*-like form (unicoloured ferrugineous brown) occurs in the Blackall Range. Finally, *Rhytidoponera aspera* Roger and *R. scabrior* Crawley (of mesic habitats but not rain forest) show a distribution pattern comparable to that of *chalybaea* and *confusa* (Fig. 35).

A possible scenario for the origin of *confusa* from *chalybaea* involves the isolation (during a dry climate regime) of ancestral populations in lowland coastal rain forest (e.g. area of the recent Big Scrub, now largely destroyed) and a daughter population (proto-*confusa*) in upland rain forest either in the Dorrigo region (south of the Clarence River) or in the Macpherson Range. This might have occurred during the xerothermic period of approximately 30,000–10,000 BP (cf. Kershaw 1976), at the same time as populations were being isolated along the eastern Queensland coast. A subsequent period of climatic amelioration would have allowed *confusa* to spread south (and to a lesser extent north in upland areas towards the Bunya Mountains), concomitant with the expansion of range by *chalybaea.* That *chalybaea* was divided into several population isolates, one of which produced *confusa*, is consistent with the observation of considerable genetic heterogeneity between present-day *chalybaea* populations, contrasted with greater genetic homogeneity in *confusa* (Ward 1978).

The divergence of *impressa* and *chalybaea* along the east coast of Queensland is more difficult to explain, given their co-occurrence in the Eungella Range, and the parapatric distribution (with genic introgression) of these two forms in southern Queensland. A series of several dry and wet periods could be responsible for present-day patterns.

The apparent recent southward expansion of *chalybaea* in historical times, into environments disturbed by man, suggests that range expansion is potentially a rapid process. In this connection, *enigmatica* may be interpreted as an isolate from a previous southward expansion of a *chalybaea*-like form.

Acknowledgments

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