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A Morphological and Molecular Revision of the *Camponotus nigriceps* Group (Hymenoptera: Formicidae) from Australia

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Abstract

The *nigriceps* group of the formicine genus *Camponotus* is revised using both morphological and allozyme techniques. Nine species from southern Australia are recognised. Four new species are described: *C. dryandrae, C. eastwoodi, C. loweryi* and *C. longideclivis*. Two subspecies are raised to specific status: *Camponotus nigriceps clarior* and *C. nigriceps pallidiceps*. Two new synonyms have been determined: *C. consobrinus* = *C. nigriceps obniger* and *C. nigriceps* = *C. nigriceps perthiana*. A key for separating species in the group and known distributions is presented.

Introduction

Ants of the formicine genus *Camponotus* are amongst the most common in Australia both in number of individuals and species, yet little is known of their taxonomy. The genus occurs on most continents in a wide range of habitats. Emery (1925) proposed 34 subgenera and many subsubgenera for the world. One of Emery's subgenera was '11me. Groupe *nigriceps*' which comprised eight named forms from Australia possessing a clypeus that was 'deeply notched in the middle of its anterior border'. The character is so distinctive that Emery's *nigriceps* group is generally accepted as a natural grouping within *Camponotus*, although this has yet to be confirmed by modern cladistic methods. Although species can be readily assigned to the *C. nigriceps* group, commonly called sugar ants in Australia (Froggatt 1905), it has not been possible to identify species within the group to any degree of certainty.

More than ever there is an urgent need for accurate knowledge of the taxonomy of members of the *C. nigriceps* group, which are amongst the most commonly encountered ants in survey work in southern Australia. Ants are often used as major biological indicators of the 'environmental health' of an area, an endeavour that requires a sound systematic framework and an accurate taxonomic key. Unfortunately, neither is currently available for this group, and, as a consequence, field biologists are often forced to classify ants as 'species A', 'species B' and so on (e.g. Andersen 1991). Such a system is unsatisfactory, particularly given that different castes in this group, even when taken from the same nest, display such wide differences in size, form and pilosity that they could conceivably be considered to be different species. However, the morphological complexity shown by members of the *C. nigriceps* group has itself dissuaded taxonomists from tackling a revision of the group.

The past 10–20 years have seen the emergence of a more holistic approach to systematics, involving the integration of both morphological and molecular analyses on the same sets of individuals. This integrated approach is more powerful than either component used alone, with the strengths of each technique complementing the relative weaknesses of the other. A variety of molecular techniques is now used routinely in systematics; some of these centre directly on the genetic material DNA, whilst others measure genetically determined variation in proteins (Hillis and Moritz 1990). Of the latter, the most widely used technique has been allozyme electrophoresis, a process in which the enzymatic products of different alleles at a single gene

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locus ('allozymes') are distinguished from one another by their mobility in an electric field (Harris and Hopkinson 1976). Allozyme electrophoresis is the molecular technique of first choice when assessing species boundaries within a group (Moritz and Hillis 1990; Richardson *et al.* 1986). It can be used to compare different life-history stages of the same organism, allows for a rapid assessment of genetic relatedness between individuals, populations and species, is particularly powerful in recognising the existence of morphologically 'cryptic' species in sympatry, and can provide an objective measure of the degree of genetic divergence between allopatric populations (Richardson *et al.* 1986; Adams *et al.* 1987).

This study uses a combined morphological and allozyme approach to clarify species boundaries and the nomenclature of the *C. nigriceps* group. The species-level revision presented here explicitly invokes the biological species concept (Mayr 1970). The two significant features of the biological species concept are (1) that individuals of the same species are capable of freely exchanging genetic material, and (2) that each species is reproductively isolated from all other species (i.e. it has a unique gene pool). Together these features emphasise the genetic cohesiveness of individual species to the exclusion of all others. In particular, the existence of two distinct gene pools in broad sympatry, whether diagnosed by morphological or electrophoretic markers, is conclusive evidence of the existence of reproductive isolation between the two species so defined. Where two taxa have disjunct distributions, no unequivocal yes/no answer can be given, regardless of the species concept used. The decision as to their specific status must of necessity be reduced to an assessment of the degree of divergence between them, with both morphological and allozyme data again being of use.

The authorship of all names should be attributed to A. J. McArthur.

Materials and Methods

Morphological Analyses

The first stage of morphological analysis was to examine all available specimens of the *C. nigriceps* group held in the South Australian, Western Australian, Victorian and Australian Museums, and in the Australian National Insect Collection. On the basis of this preliminary morphological study, an attempt was made to collect live specimens from nests representing all the recognised morphological forms, including intermediates, from as wide a geographic spread as possible.

Where possible, between 50 and 100 ants were collected from each nest. Attempts were made to select representatives of the three worker castes (major, medium and minor), and these were preserved in 75% alcohol. Alate castes were not taken. Obvious biological attributes such as the type of nest construction and habitat preference were noted. This material also formed the basis of the electrophoretic examination (see below).

Characters

A study of museum specimens and a review of the literature resulted in the development of a suite of characters that appeared to have potential in discriminating taxa. Specimens representing the three castes (major, medium and minor workers) from colonies used in the electrophoretic study were scored separately for these characters. Of the characters, 21 were found to be 'informative' (i.e. they were able to separate *C. nigriceps* group taxa more readily than the remainder, all of which displayed unacceptably high levels of within-nest variability). The informative characters were colour of coxae; colour of femora; colour of anterior gaster; colour of posterior gaster; length of gula setae; number of gula setae; form of head sides in top view; predominant colour of head; head width:length ratio (HW:HL); height of mesosoma; colour of mesosoma; sculpturing of mesosoma; average of midtibial lengths (TL); angle of inclination of setae of midtibia; form of node summit in rear view; curvature of propodeal setae < 0·25 mm; spacing of propodeal setae < 0·25 mm; number of propodeal setae > 0·25 mm; percentage of propodeal dorsum covered by setae > 0·25 mm; propodeal dorsum:declivity ratio (PD:D); and the ratio TL:log HL. A schematic drawing of a *C. nigriceps* group ant is shown in Fig. 1 in lateral view and defines many of the terms used above.

Using the above characters, museum specimens, including types, were sorted into a number of recognisable and consistent morphological groups. These morphological groups were then compared with the groupings obtained independently from the allozyme analyses. Nomenclature was then reconstructed and the distribution of the taxa plotted.

Under the microscope, pilosity was best observed using transmitted light (light source below the specimen), whereas reflected light was better for other observations.

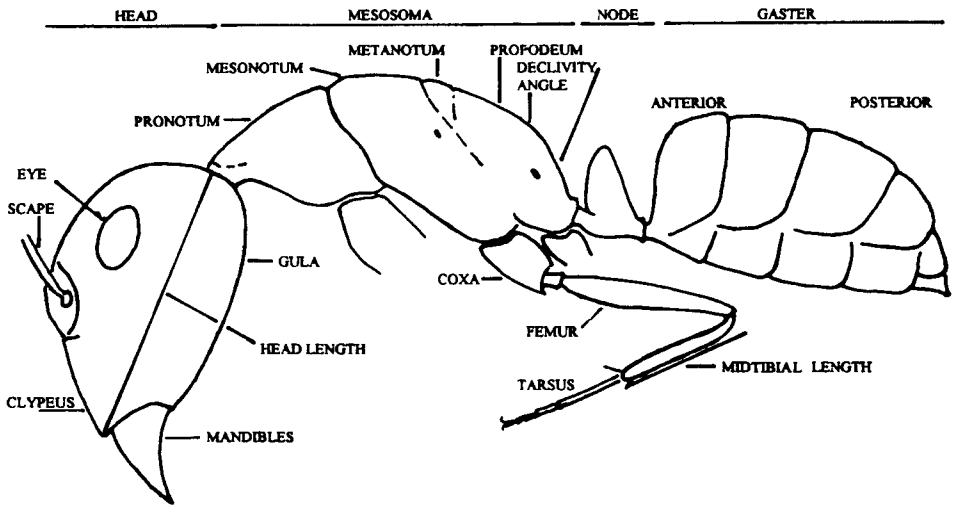

Fig. 1. A major worker of the *Camponotus nigriceps* group, indicating characters that are referred to in lateral view. Characters referred to in other views are indicated in subsequent figures.

Abbreviations

Location of material examined

ANIC, Australian National Insect Collection, Canberra, Australian Capital Territory; BMNH, Natural History Museum, London, United Kingdom; GMNH, Museum d'Histoire Naturelle, Geneve, Switzerland; MCG, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy; NVMA, Museum of Victoria, Abbotsford, Victoria; SAMA, South Australian Museum, Adelaide, South Australia; WAM, Western Australian Museum, Perth, Western Australia; ZMB, Museum fur Naturkunde an der Universitaet Humboldt zu Berlin, Germany.

Collectors of material examined

ALY, A. L. Yen; AMA, A. J. McArthur; BBL, B. B. Lowery; CHS, C. H. S. Watts; EGM, E. G. Matthews; FAC, F. A. Cudmore; GFG, G. F. Gross; GLH, G. L. Howie; JAF, J. A. Forrest; JC, John Clark; JDE, J. D. Erskine; JED, J. E. Dowse; JEF, J. E. Feehan; MAA, M. Adams; NBT, N. B. Tindale; PIT, Pitjantjatjara Lands Survey, South Australian National Parks & Wildlife Service; PJF, P. J. Fargher; PSW, P. S. Ward; RHF, R. H. Fisher; RHM, R. H. Mew; RSM, R. S. McInnes; RVS, R. V. Southcott; RWT, R. W. Taylor; SANP, South Australian National Parks & Wildlife Service; SOPS, South Olary Plains Survey, South Australian National Parks & Wildlife Service; TG, T. Greaves; VS, Vertebrate Survey, South Australian National Parks & Wildlife Service; W&F, South Australian Woods & Forests Department; WMA, W. M. McArthur; WMW, W. M. Wheeler; WWF, W. W. Froggatt.

Allozyme Analyses

Specimens for electrophoretic characterisation were taken at the same time that nests were sampled for morphological analysis. Ants were placed either individually or collectively inside small plastic 'Eppendorf' tubes and immediately snap-frozen in liquid nitrogen. Samples were stored frozen at -80°C until required for electrophoresis.

A pilot study was conducted to (1) select an appropriate method for the extraction of active soluble enzyme from each ant, and (2) determine those enzymes that displayed electrophoretic activity and resolution suitable for allozyme characterisation. In reference to (1) above, the gaster proved totally unsuitable as a source of soluble enzyme, whilst either head or mesosoma were equally suitable in this regard. Moreover, initial homogenisation trials clearly indicated that unbuffered homogenising solution was not appropriate, irrespective of the choice of tissue type. Even where a buffered homogenising solution was used, different samples exhibited considerable variability for the final pH of the homogenate, with poor enzyme activity resulting where the final pH was less than about 5.

The final protocol for sample preparation was as follows. Each ant was removed from –80°C and the field identification quickly confirmed under a dissecting microscope. After excising the gaster, the head/mesosoma was rinsed in deionised water and then dried on clean blotting paper. Samples were placed in the bottom of an 'Eppendorf' tube and homogenised by hand in an equal volume of buffered homogenising solution (0·05 M Tris-HCl pH 9·1, containing 1 μL of 2-mercaptoethanol and 0·1 mg NADP per mL), using the detached microtip from a sonicator. The pH of the resultant homogenate was quickly checked using narrow-range pH paper; where the pH had dropped below 6, a half quantity of homogenising solution was added to the homogenate, and the pH re-checked. Samples that continued to display unacceptably low pHs were discarded, and another animal from that nest selected. All samples were then placed on ice to await loading.

Allozyme electrophoresis was conducted on cellulose acetate gels (Chemetron, Milan) according to the methods and protocol outlined in Richardson *et al.* (1986). The following enzymes were successfully screened: aconitase hydratase (ACON, EC 4.2.1.3), aminoacylase (ACYC, EC 3.5.1.14), fructose-bisphosphate aldolase (ALD, EC 4.1.2.13), arginine kinase (ARGK, EC 2.7.3.3), diaphorase (DIA, EC 1.6.99.?), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1.?), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPD, EC 1.2.1.12), aspartate aminotransferase (GOT, EC 2.6.1.1), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), alanine aminotransferase (GPT, EC 2.6.1.2), hexokinase (HK, EC 2.7.1.1), isocitrate dehydrogenase (IDH, EC 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.37), 'malic' enzyme (ME, EC 1.1.1.40), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEPA, EC 3.4.13.?), tripeptide aminopeptidase (PEPB, EC 3.4.11.?), proline dipeptidase (PEPD, EC 3.4.13.?), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), and triose-phosphate isomerase (TPI, EC 5.3.1.1). The enzymes hexosaminidase (HEX, EC 3.2.1.30), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27) and phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44) displayed activity but were not scorable in all taxa. The conventions for referring to loci and allozymes follow Adams *et al.* (1987).

Samples were run over a 12-month period in three separate batches of 40–45 ants per batch. The first batch of ants was run after the 1992 round of field collections, and included ants from four other species of *Camponotus*: two *C. michaelseni* from separate nests in south-west Western Australia, one *C. testaceipes* from the same area, one *C. myoporus* from Danggali Conservation Park in South Australia, and one *Camponotus* sp. from the nearby Riverland area of South Australia. These species were included to gauge the extent of genetic diversity present in the genus, as well as to provide a simple test of the assumption of monophyly for members of the *C. nigriceps* group. The remaining two batches were run after all 1993 collections had been made, and included ants re-sampled from key nests that had been represented in the original batch.

For each batch, the ants were homogenised and screened for all enzymes on the one day. Prior to loading the full complement of gels for each batch, a test gel was run for 40 min at higher voltage (300 V DC) and stained for two of the most active enzymes in *Camponotus*, namely GPI and MDH. Samples that displayed no activity or poor activity at these two enzymes were excluded from the full batch. Homogenates were immediately frozen after being loaded onto the gels, and were subsequently thawed once more to conduct repeat or line-up gels as required. Controls consisting of ants taken from the same nest for key taxa were included in each of the three batches, to allow the results from the different batches to be integrated. In addition, numerous intra-gel repeats were used (generally between 5 and 8 samples were re-loaded in two different origin positions per gel).

Statistics

Genetic divergence between nests and between taxa was calculated as the percentage of fixed differences (%FD, see Richardson *et al.* 1986), Nei's unbiased genetic distance D (Nei 1978), or as Rogers' R (Rogers 1972). Dendrograms were constructed from the genetic distance matrices using the unweighted pair group method of analysis (UPGMA, Sneath and Sokal 1973).

The multivariate technique of Principal Co-ordinates Analysis (PCoA), as implemented via the statistical package PATN (Pattern Analysis Package; Belbin 1987), was used to give a more accurate representation of the genetic relationships amongst selected nests. PCoA (not to be confused with Principal Components Analysis) maps the distance between taxa in multi-dimensional space and then uses ordination to identify the minimum number of dimensions needed to account for most of the variability in the original data. This particular multivariate technique was chosen because unlike most others it uses the genetic distance matrix as the input data. We did not use principal component analysis as recommended by Crozier *et al.* (1986), as this technique requires that allozymes rather than loci be used as characters, a procedure that has been criticised on both theoretical and practical grounds (Richardson *et al.* 1986; Swofford and Olsen 1990). Rogers' R was used to generate the input matrix for PCoA since it is less likely to non-metric

than Nei's D or %FD (A. Georges, personal communication). As dendrograms are constrained to a single dimension, two-dimensional PCoA plots give a more realistic portrayal of the genetic relationships amongst taxa that show unequal rates of genetic divergence.

Results

Initial Morphological Analysis

Nine morphological forms were distinguishable in the initial survey of collections of the *C. nigriceps* group. Included in these were forms corresponding to the species or subspecies *pallidiceps*, *nigriceps*, *consobrinus*, *clarior*, *perthiana*, *obniger* and *prostans*, plus one unassignable form and a north-eastern form of *nigriceps*. In a few cases morphologically intermediate specimens existed but most could be placed unequivocally into one of the nine forms. At this stage the taxonomic status of these working complexes was not an issue, as the initial aim was that they could be recognised and that together they encompassed all the major morphological variation found within the *C. nigriceps* group. This initial categorisation formed the framework for all targeted collections of *C. nigriceps* group ants for both the detailed allozyme and morphological analyses that followed.

Allozyme Analyses

Generic relationships

The initial 1992 screen comprised ants representing the *C. nigriceps* group (individuals subsequently diagnosed as representing five species within the group), plus those ants representing the four other species of *Camponotus*. In total, 28 loci were successfully scored, with an additional four loci being identified as potential genetic markers but requiring modification of the electrophoretic conditions. Members of the *C. nigriceps* group showed low-to-moderate levels of genetic divergence from one another, with Nei's Ds ranging between 0·182 and 0·336 (14–27%FD). In contrast, the four other species of *Camponotus* all displayed greater levels of genetic divergence when compared with members of the *C. nigriceps* group, with Nei's Ds of between 0·481 and 0·982 (38–60%FD). The limited allozyme data therefore do not present any challenge to the concept that the taxa comprising the *C. nigriceps* group represent a monophyletic lineage within the genus as a whole.

Species boundaries within the C. nigriceps *group*

For the *C. nigriceps* group itself, 141 ants were examined over the three batches. These ants were screened for either 28 loci (first batch) or 32 loci (the remaining batches). Samples that displayed no activity at more than 25% of the 32 loci (including the four loci not scored in the first batch) were discarded from the final analysis. This approach was adopted to minimise the 'noise' generated by the inclusion of inaccurate genetic distances resulting from the presence of too many missing values. None of the excluded ants displayed novel allozymes at the other loci, indicating that no additional taxa were being jettisoned using this approach. The final data set then comprised 102 animals from 75 nests, genotyped at 32 loci. The location for each of the final 75 nests used in this study is shown in Fig. 2, whilst the allozyme profiles of the 102 individuals are presented in Table 1.

The majority of nests were represented by a single ant (57 of 75 nests). This left 18 nests where two or more ants were sampled, comprising 13 nests ($n = 2$), two nests ($n = 3$), two nests ($n = 4$) and one nest ($n = 5$). Most within-nest polymorphism involved the presence of two alleles, and only one case of a three-allele polymorphism was detected (*Est-2* locus, nest 36; $n = 4$). Moreover, comparisons of individual genotypes indicated a high degree of genetic similarity between ants taken from the same nest, with only 18 of 557 possible comparisons showing any genotypic dissimilarity. In particular, there was only a single case where ants from the same nest were homozygous for alternate alleles at a locus without a heterozygote for the two alleles also being present (nest 63 for locus *Idh*), and in this case both alleles were found in other nests subsequently shown to belong to that same species. These comparisons demonstrate the appropriateness of using a single ant to assess the genetic profile of a nest, and point to the need to screen as many nests as possible rather than simply screening a larger number of

individuals from a smaller number of nests. (This approach would not be suitable for a population genetic study, where it is important to precisely characterise nests for allele frequencies, not just determine the presence/absence of major alleles.)

Given the above, nests were chosen as the basic unit for an assessment of species boundaries within the *C. nigriceps* group. The advantage of this approach is that no assumptions need be made about the specific affinities of different nests, and thus the genetic analysis can proceed from first principles. However, as a consequence, it is possible for 'fixed' differences to be apparent between nests of the same taxon simply because the nests involved are homozygous for two different alleles that are present as a within-taxon polymorphism. Careful analysis is therefore required to distinguish within-taxon polymorphism from loci that are diagnostic for between-species differences. This problem of course is one shared by all types of systematic investigation, including morphological analysis.

Pairwise comparisons of the allozyme profiles displayed by each of the 75 nests were undertaken in order to generate a matrix of %FDs (the percentage of loci at which two nests have no alleles in common). For simplicity of presentation, the genetic relationships amongst nests are displayed diagrammatically in the form of a UPGMA dendrogram (Fig. 3). This dendrogram merely offers a convenient way to summarise the broad genetic affinities of

Fig. 2. Locations where nests were sampled for the allozyme study. Adelaide: nests 16, 19 and 25. Beachport: nests 18, 28, 32 and 33. Blue Mountains: nests 1–5, 12 and 13. Bulli Pass: nest 29. Canning Dam: nest 36. Cape Legrande: nests 34, 37, 38, 39, 40 and 41. Danggali CP: nests 15, 51–59. Dryandra State Forest: nests 42, 43, 50, 66, 67 and 71. Durokoppin NP: nests 44–49, 68–70. Eatonsville: nests 14, 74 and 75. Flinders Ranges: nests 8–11, 21, 22, 24 and 60–63. Gammon Ranges: nest 23. Grampians: nests 30, 31. Murray Lands: nests 17, 20, 26, 27, 64 and 65. Peak Charles NP: nest 35. Rankin's Springs: nest 6. Weethalle: nests 72 and 73. Nests are also cross-referenced in the *Other material examined* section of the species' descriptions.

individual nests, and is not intended to accurately depict the genetic or phylogenetic affinities of species within the group. As discussed above, the genetic-distance estimates between individual nests from different species will invariably be higher than the true values calculated when the nests are aggregated into species.

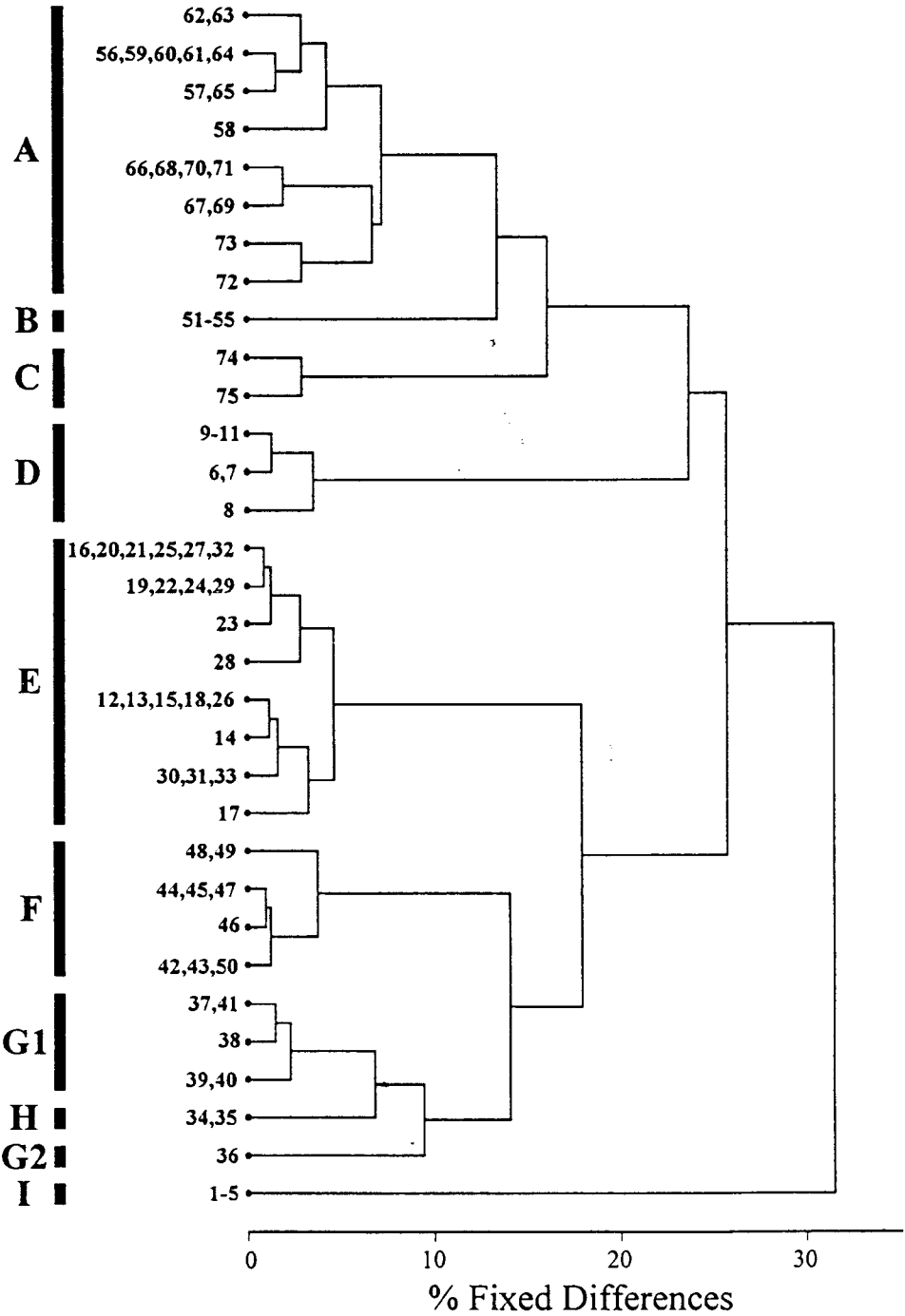

Fig. 3. Dendrogram depicting the genetic relationships amongst the 75 nests of *C. nigriceps* group ants. Nests have been arranged into the 10 genetic groups (A–F, G1, G2, H and I) as discussed in the text.

Table 1. Allozyme profiles for 102 ants of the *C. nigriceps* group at 32 loci

Ants are designated numerically by nest number (1–75), alphabetically where two or more ants were run from a single nest, and are also arranged according to genetic group A–I, as discussed in the text. Dashes (-) indicate no activity or that the locus was not scored for that sample. Code for loci: 1, *Acon;* 2, *Acyc*; 3, *Ald*; 4, *Argk*; 5, *Dia*; 6, *Enol*; 7, *Est-1*; 8, *Est-2*; 9, *Fdp-1*; 10, *Fdp-2*; 11, *Fum*; 12, *Gapd*; 13, *Got-1*; 14, *Got-2*; 15, *Gpi*; 16, *Gpt*; 17, *Hk-1*; 18, *Hk-2*; 19, *Idh*; 20, *Mdh-1*; 21, *Mdh-2*; 22, *Me*; 23, *Ndpk*; 24, *PepA*; 25, *PepB*; 26, *PepD-1*; 27, *PepD-2*; 28, *Pgam*; 29, *Pgk*; 30, *Pgm*; 31, *Pk*; and 32, *Tpi*

Ant	Group	Locus																													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	I	b	c	a	a	b	b	a	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
2a	I	b	c	a	a	b	b	a	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
2b	I	b	c	a	a	b	b	-	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
3	I	b	c	a	ab	b	b	a	g	b	a	a	a	b	a	b	b	a	b	b	a	ab	b	a	b	a	c	c	a	c	c	b	c
4a	I	b	c	a	a	b	b	a	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
4b	I	b	c	a	a	b	b	-	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
5	I	b	c	a	a	-	b	a	g	b	a	a	a	b	a	b	b	a	b	b	a	b	b	a	b	a	c	c	a	c	c	b	c
6	D	b	d	a	a	cd	b	d	b	b	a	a	a	e	d	b	b	a	b	b	a	a	b	a	b	a	d	f	a	c	b	b	b
7a	D	b	d	a	a	d	b	d	b	b	a	a	a	e	d	b	b	a	b	b	a	a	b	a	b	a	d	f	a	c	b	b	b
7b	D	b	d	a	a	cd	b	d	b	b	a	a	a	e	d	b	b	a	b	b	a	a	b	a	b	a	d	f	-	c	b	b	b
8	D	b	bd	a	a	d	b	d	b	b	a	a	a	e	d	b	b	a	b	c	a	a	b	a	-	a	d	f	a	c	b	b	b
9	D	b	bd	a	a	d	b	-	b	b	a	a	-	e	d	b	b	a	b	b	a	a	b	a	-	a	-	f	-	c	b	b	b
10	D	b	bd	a	a	d	b	-	b	b	a	a	-	e	d	b	-	a	b	b	a	a	b	a	-	a	-	f	-	c	b	b	b
11	D	b	b	a	a	d	b	d	b	b	a	a	-	e	d	b	b	a	b	b	a	a	b	a	-	a	-	f	-	c	b	b	b
12a	E	-	f	a	c	b	b	-	h	-	-	-	a	c	f	b	b	a	b	b	a	b	b	a	-	a	c	b	a	bc	b	b	b
12b	E	b	f	a	c	b	b	-	h	b	a	-	a	c	f	b	b	-	b	b	a	b	b	a	b	a	c	b	a	c	b	b	b
13	E	b	cf	a	-	b	b	d	h	b	a	-	a	c	f	-	b	a	b	-	a	b	bc	a	b	a	ce	b	a	bc	b	b	b
14	E	b	f	a	c	b	b	d	ch	b	a	a	a	c	f	b	b	a	b	b	a	b	b	a	b	a	e	ab	a	c	b	b	b
15	E	b	f	a	c	b	b	df	h	b	a	a	a	bc	f	b	b	a	b	b	a	b	b	a	b	a	c	b	a	c	b	b	b
16	E	b	f	a	c	b	b	-	h	b	a	a	-	f	f	b	b	a	b	b	a	b	b	a	-	a	-	bf	-	c	b	ab	b
17	E	b	f	a	c	b	b	d	h	b	a	a	-	c	f	b	b	a	b	b	a	b	b	a	-	a	-	fg	-	c	b	b	b
18	E	b	f	a	c	b	b	-	h	b	a	a	-	c	f	b	-	-	b	b	a	b	b	a	-	a	-	-	-	c	bc	b	b
19	E	b	f	a	c	b	b	-	h	b	a	a	-	cf	f	b	b	a	b	b	a	b	b	a	-	a	-	f	-	c	b	b	b
20	E	b	f	a	c	b	b	-	h	b	a	a	-	-	f	b	-	a	b	b	a	b	b	a	-	a	-	-	-	c	b	ab	b
21	E	b	f	a	c	b	b	-	hi	b	a	a	-	f	f	b	-	-	b	b	a	b	b	a	-	a	-	-	-	c	b	b	b
22	E	b	f	a	c	b	b	-	h	b	a	a	-	f	f	b	-	a	b	b	a	b	b	a	-	a	-	f	-	c	b	b	bd
23	E	b	f	a	c	b	b	d	hi	b	a	a	a	f	f	b	b	a	b	b	a	b	b	a	b	a	ce	f	ab	bc	b	b	b
24	E	b	f	a	c	b	b	f	h	b	a	a	a	f	f	b	b	a	b	b	a	b	b	a	b	a	ce	bf	a	bc	bc	b	b
25a	E	b	f	a	c	b	b	-	ch	b	a	a	-	cf	f	b	b	a	b	b	a	b	b	a	-	a	-	bf	-	c	b	b	b
25b	E	b	f	a	c	b	b	df	ch	b	a	a	a	cf	f	b	b	a	b	b	a	b	b	a	b	a	c	bf	a	c	b	b	b

25c	E	b	f	a	c	b	b	d	ch	b	a	a	a	f	f	b	b	a	b	b	a	b	b	a	b	a	c	bf	a	c	b	b	b
26	E	b	f	a	c	b	b	-	h	b	a	a	-	c	f	b	-	a	b	b	a	b	b	a	-	a	-	bf	-	bc b		b	b
27	E	b	f	a	c	b	b	-	h	b	a	a	-	bf	f	b	-	a	b	b	a	b	b	a	-	a	-	b	-	c	b	b	b
28	E	b	f	a	c	b	b	-	h	b	a	a	-	f	f	b	b	a	b	b	a	b	b	a	-	a	-	bf	-	c	b	a	b
29	E	b	f	a	c	b	b	f	h	b	a	-	a	f	f	b	b	a	b	-	a	b	b	a	b	a	ce	bf	a	bc	b	ab	b
30	E	b	f	a	c	b	b	-	h	b	a	a	-	c	f	b	b	a	b	b	a	b	b	a	-	a	-	b	-	ab	b	b	b
31	E	b	f	a	c	b	b	-	h	b	a	a	-	c	f	b	b	a	b	b	a	b	b	a	-	a	-	b	-	ab	b	b	b
32	E	-	f	a	c	b	b	d	h	b	a	a	a	f	f	b	b	a	b	b	a	b	b	a	b	a	c	b	a	c	b	b	b
33	E	b	f	a	c	b	b	d	h	b	a	a	a	c	f	b	b	a	b	b	a	b	bc	a	b	a	e	bf	a	bc	ab	b	b
34a	H	-	e	a	c	b	b	-	c	b	a	a	a	c	ef	b	b	a	b	b	a	b	b	a	b	a	b	f	-	c	b	b	b
34b	H	b	e	a	c	b	b	d	c	b	a	a	a	c	ef	b	b	a	b	ab	a	b	b	a	b	a	b	f	a	c	b	b	b
34c	H	b	e	a	c	b	b	d	c	b	a	a	a	c	ef	b	b	a	b	b	a	b	b	a	b	a	b	f	a	c	b	b	b
35a	H	b	e	a	c	b	b	d	c	b	a	a	a	c	f	b	b	a	b	b	a	b	b	ab	b	a	ab	f	a	c	b	b	b
35b	H	b	e	a	c	b	b	d	c	b	a	a	a	c	f	b	b	a	b	b	a	b	b	ab	b	c a	ab	f	a	c	b	b	b
36a	G2	-	e	a	c	b	b	d	b	-	-	-	a	-	e	b	-	-	a	b	a	b	b	a	b	a	c	c	-	c	b	ab	b
36b	G2	-	e	a	c	b	b	d	bd	b	a	a	a	c	e	b	b	a	a	b	a	b	b	a	b	a	c	c	a	c	b	b	b
36c	G2	-	e	a	c	b	b	d	d	b	a	a	-	c	e	b	b	a	a	b	a	b	b	a	-	a	-	c	-	c	b	b	b
36d	G2	b	e	a	c	b	b	d	ab	b	a	a	-	c	e	b	b	a	a	b	a	b	b	a	-	a	-	c	-	c	b	b	b
37a	G1	bc	eg	a	c	b	b	d	c	b	a	a	a	c	bf	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
37b	G1	bc	eg	a	c	b	b	d	c	b	a	a	a	c	bf	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
38a	G1	bc	eg	a	c	b	b	d	c	b	a	a	a	c	b	b	ab	a	a	b	a	b	b	a	ab	a	c	ef	a	c	b	b	b
38b	G1	b	eg	c	b	b	d	c	b	a	a	a	c	b	b	ab	a	a	b	a	b	b	a	ab	a	c	e	f	a	c	b	b	b
39a	G1	b	eg	a	c	b	b	d	c	b	a	a	a	c	e	b	ab	a	a	b	a	b	ab	a	ab	a	c	f	a	c	b	b	b
39b	G1	b	eg	a	c	b	b	d	c	b	a	a	a	c	e	b	ab	a	a	b	a	b	ab	a	b	a	c	f	a	c	b	b	b
40	G1	b	eg	a	c	b	b	-	c	b	a	a	a	c	e	ab	b	a	a	-	a	b	b	-	-	a	-	f	a	c	b	b	b
41	G1	b	e	a	c	b	b	d	c	b	a	a	a	c	ef	b	b	a	a	b	a	b	b	a	ab	a	c	f	a	c	b	b	b
42	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	e	b	b	a	b	b	a	b	b	a	bc	a	c	f	a	bc	ab	b	b
43	F	b	e	a	c	b	b	-	-	b	a	b	a	c	e	bc	b	-	b	b	a	b	b	a	b	a	c	f	a	b	ac	b	b
44	F	bc	e	a	c	b	b	-	b	b	a	b	a	c	e	c	b	a	b	b	a	b	b	a	b	a	c	f	a	b	b	b	b
45	F	-	e	a	c	b	b	cd	b	b	a	b	a	ac	e	bc	b	a	b	b	a	b	b	a	b	a	c	f	a	b	ab	b	b
46	F	b	e	a	c	b	b	d	b	b	a	b	a	c	ce	b	b	a	b	b	a	b	b	a	b	a	c	f	a	b	b	b	b
47	F	b	e	a	c	b	b	d	b	b	a	b	a	c	ce	bc	b	a	b	b	a	b	b	a	b	a	c	f	a	b	b	b	b
48	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	e	c	b	a	b	b	a	b	b	a	b	a	c	f	a	c	b	b	b
49	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	e	bc	b	a	b	b	a	b	b	a	b	a	c	f	a	c	b	b	b
50a	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	ce	b	b	a	b	b	a	b	b	a	b	a	-	fg	a	b	ab	b	b
50b	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	ce	b	b	a	b	b	a	b	b	ab	b	a	c	fg	a	b	b	b	b
50c	F	bc	e	a	c	b	b	d	b	b	a	b	a	c	ce	b	b	a	b	b	a	b	b	ab b		a	c	fg	a	b	b	b	b
50d	F	b	e	a	c	b	b	d	b	b	a	b	-	c	ce	b	b	a	b	b	a	b	b	a	-	a	-	fg	-	b	ab		b
50e	F	b	e	a	c	b	b	d	b	b	a	b	-	c	ce	b	b	a	b	b	a	b	b	a	-	a	-	fg	-	b	b	b	b

Table 1. continued

Ant	Group	Locus																													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
51	B	b	d	a	a	-	b	b	h	b	a	-	a	c	fg	b	b	a	a	b	a	b	b	a	c	a	c	d	a	c	b	b	b
52a	B	b	d	a	a	d	b	b	h	b	a	a	a	c	fg	b	b	a	a	b	a	b	b	a	c	a	c	d	a	c	b	b	b
52b	B	b	d	a	a	d	b	-	h	b	a	-	a	c	f	b	b	a	a	b	a	b	b	a	c	a	c	d	a	c	b	b	b
53a	B	b	d	a	a	d	b	b	h	b	a	a	a	c	f	b	b	a	a	b	a	b	ab	a	c	a	c	d	a	c	b	b	b
53b	B	b	d	a	a	d	b	b	h	b	a	a	a	c	f	b	b	a	a	b	a	b	ab	a	c	a	c	d	a	c	b	b	b
54	B	b	d	a	a	cd	b	b	h	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	c	a	c	d	a	c	b	b	b
55	B	-	d	a	a	-	b	b	h	b	a	a	a	c	f	b	-	a	a	b	a	b	-	a	c	a	c	d	a	c	b	b	b
56	A	b	d	a	a	d	b	b	ce	b	a	a	a	d	f	b	b	a	a	b	a	b	b	a	b	a	c	f	ac	c	b	b	ab
57	A	b	d	a	a	d	b	b	bc	ab	a	a	a	d	f	b	b	a	a	b	a	b	b	a	b	a	c	f	ab	c	b	b	b
58	A	b	d	a	a	d	b	b	f	b	a	a	-	d	f	b	b	a	a	b	a	b	b	a	-	a	-	f	-	c	b	b	b
59	A	b	d	a	a	d	b	b	e	b	a	a	-	d	f	b	b	a	a	bd	a	b	b	a	-	a	-	f	-	c	b	b	b
60	A	b	d	a	a	d	ab	b	be	b	a	a	-	d	f	b	b	a	a	b	a	b	ab	a	-	a	-	f	-	c	b	b	b
61	A	b	d	a	a	d	ab	b	be	b	a	a	-	d	f	b	b	a	a	b	a	b	ab	a	-	a	-	f	-	c	b	b	b
62	A	a	d	a	a	d	ab	b	e	b	a	a		d	f	b	-	a	a	b	a	b	b	a	-	a	-	f	-	c	b	b	b
63a	A	ab	d	a	a	d	b	b	e	b	a	a	-	d	f	b	b	a	a	b	a	b	b	a	-	a	-	f	-	c	b	b	b
63b	A	a	d	a	a	d	b	b	e	b	a	a	-	d	f	b	-	a	a	d	a	b	b	a	-	a	-	f	-	c	b	b	b
64	A	b	d	a	a	d	b	b	ce	b	a	a	-	d	f	b	b	a	a	b	a	b	b	a	-	a	-	f	-	c	b	b	b
65	A	b	d	a	a	d	b	b	c	ab	a	a	-	d	f	b	b	a	a	bd	a	b	b	a	-	a	-	f	-	c	b	b	b
66	A	b	d	a	a	b	b	b	be	b	a	a	a	d	f	b	b	a	a	ab	a	b	b	a	b	a	c	f	a	c	ab	b	b
67	A	b	d	a	a	b	b	-	b	b	a	a	a	d	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	ab	b	b
68a	A	b	d	a	a	b	b	b	be	b	a	a	a	d	f	b-	b	a	a	b	a	b	bd	a	b	a	c	f	a	c	a	b	b
68b	A	b	d	a	a	b	b	b	b	b	a	a	a	d	f	b	b	a	a	b	a	b	bd	a	b	a	c	f	a	c	a	b	b
69	A	b	d	a	a	b	b	-	b	b	a	a	a	d	f	b	b	-	a	b	a	b	bd	a	b	a	c	f	a	c	ab	b	b
70	A	b	d	a	a	b	b	b	ef	b	a	a	-	d	f	b	b	a	a	b	a	b	b	a	-	a	-	f	-	c	a	b	b
71	A	b	d	a	a	b	b	b	e	b	a	a	-	d	f	b	b	a	a	b	a	b	b	a	-	a	-	f	-	c	ab	b	b
72a	A	ab	d	a	a	b	b	b	e	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
72b	A	ab	d	a	a	b	b	b	e	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
72c	A	ab	d	a	a	b	b	b	e	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
72d	A	ab	d	a	a	b	b	b	e	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
73a	A	b	ad	a	a	b	b	b	f	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
73b	A	b	ad	a	a	b	b	b	f	b	a	a	a	c	f	b	b	a	a	b	a	b	b	a	b	a	c	f	a	c	b	b	b
74	C	a	d	a	a	ab	b	e	e	b	a	a	a	e	f	b	b	a	a	b	a	b	b	a	b	a	c	cf	a	c	b	b	b
75	C	a	d	a	a	b	b	de	e	b	a	a	a	ef	f	b	b	a	a	b	a	c	b	a	b	a	c	f	a	c	b	b	b

A comment on the presence of missing values in Table 1 is warranted at this point. Given the size of many of these ants and the technical difficulty associated with enzyme extraction, it is not surprising that a comprehensive characterisation of a large number of individuals and enzymes such as presented in Table 1 contains some missing values. Where missing values were present, genetic distances were calculated using only those loci defined in both nests under comparison. Whilst the genetic distance values obtained by comparing slightly different arrays of loci in this manner may not be strictly comparable, this approach can be justified on three grounds. First, %FDs, the most important statistic used in the allozyme analysis, are more likely to be significantly underestimated than significantly overestimated where a few of the loci are missing in a comparison and where values range from 0 to 30% (as they do in this study). For example, two nests differing at 1 of 30 loci, with two missing values, would be regarded as showing 3·3%FD genetic divergence. If both missing loci were available, this value could at best drop marginally to 3·1%FD (i.e. 1 of 32), but could conceivably increase dramatically to 9·4%FD (i.e. 3 of 32, if both missing values revealed additional fixed differences). Thus, our approach is a conservative one, designed to identify only the minimum number of taxa justifiable by the data. Secondly, an inspection of the data reveals that no loci displayed missing values once nests were aggregated into taxa, indicating that the genetic distances calculated between taxa are not subject to this slight anomaly. Thirdly, the existence of a parallel morphological examination of animals from the same nests allows an independent avenue for detecting the presence of additional taxa. None of the nests that displayed missing values was morphologically distinctive from those that were fully characterised.

The first step towards delineating biological species in the *C. nigriceps* group is to determine whether any significant genetic groups were present. It is clear (Fig. 3) that the 75 nests do not assort randomly with respect to one another. An assessment of the non-randomness of genetic relationships reveals that whilst nodes occur at genetic distances of 0–31%FD, 89% of these (66 of 74) involve nests clustering at distances of 0–10%FD. On the other hand, only 11% of nodes occur within 10–30%FD, despite this area of the dendrogram representing two-thirds of the total range encountered. Of course, recognition of the existence of genetic groups does not automatically enable the delineation of these groups, since it is possible to alter the number of groupings obtained by being more or less 'inclusive' of clusters as one proceeds along the scale. As such, the next step in the analysis is to determine what significant genetic groups are present in Fig. 3.

In addressing the genetic data revealed in Table 1 and Fig. 3, it is useful to focus specifically on the two major genetic criteria for species delineation under the biological species concept as outlined in the Introduction. First, the occurrence of two or more distinct genetic groups in broad sympatry is powerful evidence for the existence of discrete biological species, regardless of the level of divergence present (Richardson *et al.* 1986). To ensure that the groups so defined really are 'distinct', it is necessary to insist that fixed differences are found for at least two loci, and that the alleles involved do not occur as a polymorphism elsewhere in the range of the putative taxa. Secondly, where two genetic groups are not sympatric, one can nevertheless make an assessment of the extent of genetic divergence present and relate this to the maximum levels of divergence found over the full geographic range displayed within a taxon, for all taxa delineated within a study. Distinct species, the equivalent of so-called 'phylogenetic' species (Frost and Hillis 1990), can then often be delineated in allopatry by the existence of major discontinuities that are significantly greater than the maximum level of within-taxon divergence encountered in the lineage. The above two rationales have of course long been used in the application of morphological data to the delineation of species within a group, although the traditional style used to present taxonomic revisions does not involve the presentation of the data in such an overt manner.

Criterion 1 above provides the genetic framework needed to delineate the minimum number of significant genetic groups present in Fig. 3. Having identified these groups, an assessment can then be made as to their specific affinities using both criteria. Sympatric genetic groups by definition warrant full species rank regardless of the nature of any morphological characterisation, whereas groups with allopatric distributions require an assessment of the total available evidence.

The application of the first criterion to the allozyme data of Table 1 determines that there are a minimum of 10 genetic groups present within the *C. nigriceps* complex (Fig. 3). These genetic groups are henceforth referred to as A to F, G1, G2, H and I. Nests of group A are regionally sympatric with nests of group B (Danggali Conservation Park, South Australia), D (Flinders Ranges, South Australia; central New South Wales), E (Riverland region and Flinders Ranges, South Australia) and F (Dryandra Conservation Park, Western Australia). The recognition of groups A, B, D, E and F thus also defines group C, which itself co-occurred with nests of group E (Fig. 2). Nests of group I were collected from the same locality as those of group E. Regional sympatry also exists between groups F and G1 (south of Perth, Western Australia), and between G2 and H (Cape Legrande, Western Australia), thus defining all four of these groups.

An analysis of Table 1 indicates that the nests comprising a single genetic group show (1) little or no genetic divergence within broad geographic areas, and (2) with one exception, no significant genetic divergence across the entire range of that group. The single exception involves genetic group A, by far the most geographically widespread of all of the groups, where the two loci *Dia* and *Got-1* show fixed differences between regions across its range from Western Australia to New South Wales. By contrast, genetic groups D and E, widespread over the south-eastern half of the continent, show no fixed differences between nests from different regions. Thus, we feel confident that genetic groups that differ by significantly more than two diagnostic differences (e.g. 6%) in allopatry are likely to represent separate species. Given the comparatively low levels of divergence present between many of the sympatric groups, we have nominated four (e.g. 13%) as the minimum number of fixed differences necessary to fulfil the requirements of Criterion 2 above for nominating genetic groups as probable biological species. We stress here that the analysis of the systematic relationships amongst genetic groups is based at this point only on the allozyme data, and that the integration of the morphological and allozyme analyses will occur in a subsequent section.

The next step in the analysis is to determine the minimum number of biological species that are needed to accommodate the 10 genetic groups of Fig. 3. To facilitate this, a summary of the genetic relationships amongst groups has been presented in Table 2. For example, nests of group E are allozymically distinct in regional sympatry with those of group A (Riverland region and Flinders Ranges, South Australia), group B (Danggali Conservation Park, South Australia), group D (Flinders Ranges, South Australia and central New South Wales) and group I (Blue Mountains, New South Wales), thus confirming that none of these groups are conspecific with group E. Group I, on the other hand, whilst sympatric only with group E, differs from all other groups at 8–11 loci in allopatry, a result that strongly affirms its status as a full species.

There are only six cases out of 45 (Table 2) where the allozyme data do not suggest or indicate that a pairwise comparison of genetic groups involves the presence of two distinct

Table 2. Genetic divergence and its systematic implications amongst the 10 genetic groups A–F, G1, G2, H and I

Bottom left matrix: %FDs between groups (calculated from Table 1), based on comparing their most adjacent geographic regions (sympatric comparisons underlined). Top right matrix: an assessment of the taxonomic significance of each genetic divergence value. S, the groups show two or more fixed differences (6%) in regional sympatry; D, the groups show at least four fixed differences (13%) in allopatry

	A	B	C	D	E	F	G1	G2	H	I
A	–	S	S	S	S	D	S	D	D	
B	13	–	D	D	S	D	D	D	D	D
C	6	22	–	D	S	D	D	D	D	D
D	22	26	22	–	S	D	D	D	D	D
E	19	22	16	27	–	D	D	S		
F	22	28	25	26	13	–	S	D		
G1	16	22	16	29	9	9	–	S	D	
G2	19	25	22	29	16	9	6	–	D	D
H	22	25	22	26	9	9	6	13	–	D
I	25	34	31	31	25	31	31	28	31	–

biological species. Groups A and C show only 6% divergence in allopatry, indicating that the allozyme data alone cannot rule out the possibility that they belong to the same biological species. As both groups A and C are clearly distinct from all others, there is no point in undertaking additional analysis of the allozyme data. A final decision as to the taxonomic relationship between these two groups requires some input from the morphological data.

The five cases remaining all involve the groups E, F, G1, G2 or H (Table 2), which, with the exception of group E, have relatively restricted geographic distributions. It was decided to conduct a further analysis of the allozyme data from individual nests for these groups only, in order to properly assess how the generally lower levels of genetic divergence observed between these groups relate to patterns of within-group genetic diversity. Principal Co-ordinates Analysis (PCoA) was undertaken on the matrix of Rogers' R calculated between all pairwise comparisons of nests belonging to these five groups, and the PCoA scores for the first two dimensions plotted (Fig. 4).

Three distinct clusters emerge from this analysis: group F, group E, and a heterogeneous cluster consisting of groups G1, G2 and H (Fig. 4). As indicated in Table 2, group F is genetically distinct from and sympatric with group G2 and genetically divergent from Group E, confirming its rank as a full species when compared with these two groups. Groups G1 and G2 are allopatric populations of the same morphological form, with group G1 represented by only a single nest. Clearly, there is insufficient evidence from the allozyme data to place them in

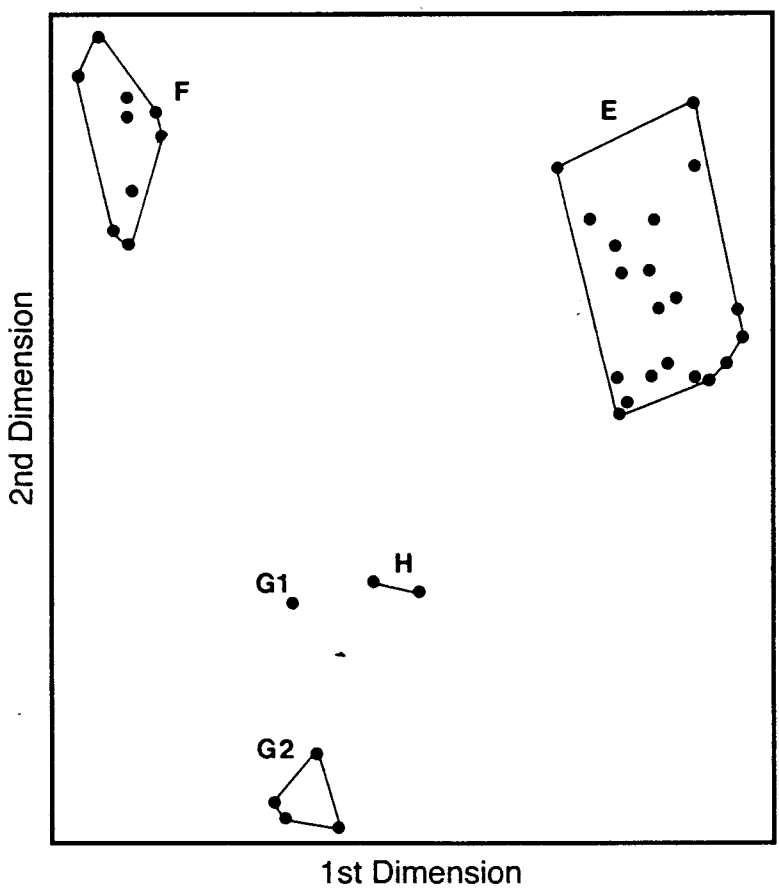

Fig. 4. Plot along the first two dimensions of the principal co-ordinates score for all nests comprising groups E, F, G1, G2 and H. Each point represents a single nest.

separate taxa. Group H displays two fixed differences from group G1 in regional sympatry (Table 2, Fig. 3), confirming that the two groups belong to separate biological species. However, the status of group H cannot be determined unambiguously using the allozyme data alone, since it is allopatric with groups E and F. Group F shows three fixed differences from group H (including a locus where group F is fixed for a unique allele at the *Fum* locus). Given the relatively close geographic arrangement of these two groups, it seems reasonable to propose that they are likely to represent separate species. On the other hand, the PCoA result for groups E and H supports but does not prove their specific distinctness. These two groups show fixed differences at 9% of their loci, but are found in quite different parts of the continent, over 1000 km apart. Nevertheless, the close genetic relationship of nests representing group E, some from as far apart as northern New South Wales and south-eastern South Australia, supports the notion that geographic separation need not automatically be accompanied by genetic divergence.

In summary then, the allozyme data combined with distribution data support the recognition of a minimum of seven distinct biological species, regardless of any considerations of morphology. These species correspond to genetic groups A, B, D, E, F, 'G' (G1 and G2 combined) and I. The status of groups C and H cannot fully be resolved by the allozyme data alone, since group C is genetically too similar in allopatry to species A, and group H is genetically too similar in allopatry to both species E and species F.

Heterozygosity

The allozyme profiles and direct count heterozygosity estimates (H) for each of the nine genetic groups A–I are presented in Table 3. Values for H range from 0·009 ± 0·006 to 0·084 ± 0·029, with an average across all groups of 0·056 ± 0·010. No obvious correlation is evident between heterozygosity and the geographic range occupied by a group, with the restricted group I and the wide-ranging group D displaying the two lowest levels of H and the regionally restricted groups F and G possessing the highest values.

Integration of the Morphological and Allozyme Analyses

Detailed morphological analysis of the material collected for joint allozyme and morphological characterisation confirmed the morphological distinctiveness of genetic groups A, B, D, E, F, G and I, and further indicated that groups C and H were both morphologically distinguishable from the other taxa (Table 4). In particular, group C animals were present in museum collections from areas that also housed nests of species A, confirming that these two taxa show morphological differentiation in sympatry. The allozyme profiles of the nine species A–I and their corresponding nomenclatural affinities are presented in Table 3.

Group H ants were clearly distinct from those of species F, and were morphologically similar to but distinct from those of species E, the nearest populations of which were from South Australia, over 1000 km away. Interestingly, there is a single specimen referrable to species E in the National Insect Collection, labelled as originating from Perth. However, as we have been unable to find other similar ants from Western Australia, we must consider the possibility that this specimen has been wrongly labelled, and hence cannot conclude unequivocally that species E is present in Western Australia. A clear demonstration that ants displaying the morphotype of species E are indeed present in the west would provide even stronger evidence for group H being a separate species.

The characters identified as informative and the taxonomic key devised were both tested extensively on other specimens (i.e. those not useable in the joint analyses), so as to confirm their utility on a wide range of individuals and locations. This process successfully demonstrated the existence and diagnosis of each of the designated nine species within the *C. nigriceps* group, corresponding to the genetic groups A–I. Of the nine morphotypic forms recognised initially, all were subsequently referable to valid species except for (1) *C. obniger* and *C. perthiana*, which proved to be morphological extremes of other, wide-ranging and morphologically variable taxa, (2) Western Australian '*nigriceps*', which was shown to include species A and F, and (3) Western Australian '*consobrinus*', which represented a unique taxon.

Table 3. Allozyme profiles for the nine species within the *C. nigriceps* group

Where a locus is polymorphic, the percentage frequency of the more common allele(s) is presented as a superscript. The frequency of the rarest allele can then be obtained by subtracting the sum of the frequencies of the other allele(s) from 100. The following loci were invariant: *Ald*, *Fdp-2*, *Gapd*, *Hk-1*, *Mdh-1* and *PepB*. The observed heterozygosity estimates (H) and standard errors (s.e.) for each species are also presented at the bottom of the table. Species are represented both by name and by genetic group A–I, with the sample size for each shown underneath in parentheses

Locus	*pallidiceps* I (7)	*loweryi* D (7)	*consobrinus* E (25)	*longideclivis* H (5)	*prostans* G (12)	*dryandrae* F (13)	*clarior* B (7)	*nigriceps* A (24)	*eastwoodi* C (2)
Acon	b	b	b	b	b^{83},c	b^{71},c	b	b^{81},a	a
Acyc	c	d^{64},b	f^{98},c	e	e^{71},g	e	d	d^{96},a	d
Argk	a^{93},b	a	c	c	c	c	a	a	a
Dia	b	d^{86},c	b	b	b	b	d^{90},c	b^{54},db^{75},a	
Enol	b	b	b	b	b	b	b	b^{94},a	b
Est-1	a	d	d^{73},f	d	d	d^{95},c	b	b	e^{75},d
Est-2	g	b	h^{88},c^{8},i	c	c^{67},b^{17},d^{12},a	b	h	e^{52},b^{23},f^{15},c	e
Fdp-1	b	b	b	b	b	b	b	b^{96},a	b
Fum	a	a	a	a	a	b	a	a	a
Got-1	b	e	c^{50},f^{46},b	c	c	c^{96},a	c	d^{75},c	e^{75},f
Got-2	a	d	f	f^{70},e	e^{63},b^{25},f	e^{73},c	f^{86},g	f	f
Gpi	b	b	b	b	b^{96},a	b^{69},c	b	b	b
Gpt	b	b	b	b	b^{82},a	b	b	b	b
Hk-2	b	b	b	b	a	b	a	a	a
Idh	b	b^{86},c	b	b^{90},a	b	b	b	b^{90},d^{8},a	b
Mdh-2	b^{93},a	a	b	b	b	b	b	b	b^{50},c
Me	b	b	b^{96},c	b	b^{92},a	b	b^{83},a	b^{90},d^{6},a	b
Ndpk	a	a	a	a^{80},b	a	a^{92},b	a	a	a
PepA	b	b	b	b^{90},	b^{78},	b^{95},c	c	b	b
PepD-1	c	d	c^{67},e	b^{80},a	c	c	c	c	c
PepD-2	c	f	b^{59},f^{36},g^{3},a	f	f^{59},c^{33},e	f^{81},g	d	f^{98},cf	
Pgam	a	a	a^{96},b	a	a	a	a	a^{92},b^{4},c	a
Pgk	c	c	c^{78},b^{18},a	c	c	b^{81},c	c	c	c
Pgm	c	b	b^{94},c^{4},a	b	b	b^{77},a^{19},c	b	b^{79},a	b
Pk	b	b	b^{90},a	b	b^{96},a	b	b	b	b
Tpi	c	b	b^{98},d	b	b	b	b	b^{98},a	b
H	0·009	0·022	0·072	0·056	0·083	0·084	0·026	0·049	0·047
s.e.	± 0·006	± 0·016	± 0·023	± 0·026	± 0·027	± 0·029	± 0·015	± 0·015	± 0·026

Table 4. Morphological profiles for each of the nine species at the most informative characters

Character states presented apply to the majority (>95%) of ants representing a species. Polymorphisms are shown as ab, abc and so on. Species are represented by abbreviated species name and by genetic group. pall, *C. pallidiceps*; lowe, *C. loweryi*, cons, *C. consobrinus*; long, *C. longideclivis*; pros, *C. prostans*; drya, *C. dryandrae*; clar, *C. clarior*; nigr, *C. nigriceps*; east, *C. eastwoodi*

Character	Species									Character states
	pall	*lowe*	*cons*	*long*	*pros*	*drya*	*clar*	*nigr*	*east*	
	I	D	E	H	G	F	B	A	C	
Coxae and femora, color relative to anterior gaster	b	b	a	b	b	a	ab	b	b	a, similar; b, lighter
Gaster color, anterior relative to posterior	b	b	a	a	b	a	b	b	b	a, distinct; b, not distinct
Gula setae (length > 0·25 mm), number	ab	a	a	a	b	c	c	c	b	a, absent; b, sparse; c, plentiful
Head sides, dorsal view, major worker	a	a	a	a	b	a	b	a	a	a, tapering to front; b, round
Head sides, dorsal view, minor worker	a	a	a	a	a	a	a	a	b	a, parallel; b, tapering to rear
Head, most of, color	b	a	a	a	a	a	b	a	a	a, area mostly dark; b, mostly light
HW:HL ratio, maximum (largest major worker)	a	b	a	a	b	a	a	a	a	a, ≤ 1; b, > 1
Mesosoma, color	b	b	a	b	a	ab	b	b	b	a, various; b, yellowish or brownish
Mesosoma, integument	a	a	a	a	b	a	a	a	a	a, glossy; b, very glossy
Node, summit, rear view	a	c	abc	bc	ac	ac	c	c	b	a, concave; b, flat; c, convex
Propodeum, setae < 0·25 mm, curvature	b	a	a	a	b	b	b	b	ab	a, adpressed; b, raised
Propodeum, setae < 0·25 mm, spacing	b	a	a	a	b	b	b	b	a	a, > length; b, < length
Propodeum, setae > 0·25 mm, number	a	a	a	a	a	a	ab	b	a	a, < 15; b, > 15
PD:D ratio, major workers	b	b	b	a	b	b	b	b	b	a, < 1·2; b, > 1·2
TL:log HL ratio	a	b	a	a	b	a	a	a	a	a, < 2·1; b, > 2·1
Maximum HW	a	c	a	b	a	b	b	c	b	a, < 3·7; b, 3·7–3·8; c, > 3·8

Systematics

Genus ***Camponotus*** Mayr

C. nigriceps Species-group Emery

Diagnosis of the Camponotus nigriceps *Group Workers*

In dorsal view, median anterior of clypeus projects forward; lateral margins never convex, varying from strongly concave in major workers to straight in minor workers; anterior corners always distinct (like teeth), varying from tapering outwards in major workers to tapering forward in minor workers; anterior margin of projection always concave, varying from V-shaped at centre in major workers to even and feebly concave in minor workers (e.g. clypei shown in Fig. 5*a*, *b*). (For comparison, clypei of three species from outside *C. nigriceps* group are shown in Fig. 6*a–d*.) Mandibles furnished with 6 teeth on masticating border (Fig. 7*a*, *b*), emargination occasionally lacking between proximal tooth and next shown dotted (never with a half tooth at proximal border as in Fig. 7*c*). Ventrum of pedicel pilose, convex (viewed from the side, see Fig. 8*a*, *b*). Head width always greater than pronotum. Head sides in dorsal view: medium workers rounded (Fig. 9*a*), minor workers parallel (Fig. 9*b*) except in smallest minors of *C. eastwoodi* (Fig. 9*c*). Antennae attached to head capsule at a distance from clypeus, distance being greater than diameter of antennal fossae. Tentorial pits distinctly depressed. Profile (viewed from the side) of that part of mesosoma, comprising pronotum, mesonotum, dorsum (= base) of propodeum and upper three-fourths of declivity of propodeum (proximal to dorsum) never concave except when metanotum is present; feeble concavity may occur between mesonotum and propodeum. Profile of the node (viewed from side), anterior face convex, summit sharp. Integument finely reticulate overall, never hidden by pubescence except sometimes on appendages. Midtibiae with a coat of short setae or pubescence, inclination varying from adpressed up to about 80°, length never exceeding 0·1 mm; with 2 rows of straight barbs on inner surface about 0·15 mm in length. Long setae on pronotum generally inclined forward; long setae on the gaster generally inclined backwards. Lacking 'J' shaped setae attached to the ventrum of head capsule (distinct from *C. testaceipes*, which possesses 5–10 setae). Polymorphic, head widths display dimorphism. Usually forage nocturnally, occasionally on overcast days. Nests in soil, frequently under logs, stumps or stones.

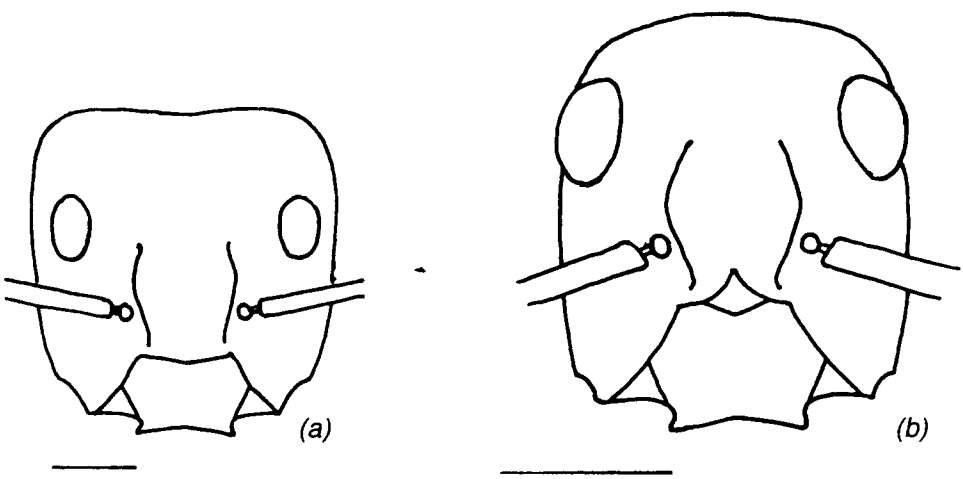

Fig. 5. Dorsal view of head, showing the projecting concave anterior margin of clypeus, diagnostic for the *C. nigriceps* group. *a*, *C. consobrinus* major worker; *b*, *C. nigriceps* minor worker. Scale lines = 1 mm.

Key To Species of the *Camponotus nigriceps* Group

The key is based on all worker castes (except where stated). Dorsal view of head is taken with anterior margin of clypeus and vertex in a horizontal plane.

1. Gula in lateral view without erect setae (Fig. 10*a*, *b*) 2
   Gula in lateral view, erect setae present (Fig. 10*c*, *d*) 4
2. Colour of anterior gaster distinctly lighter than posterior (e.g. yellow adjacent to dark brown or orange adjacent to black) 3
   Colour of gaster brown to yellow, anterior gaster only slightly lighter than posterior, often of uniform colour ..... *C. loweryi*
3. Major worker with PD:D in lateral view > 1·2 (Fig. 11*a*) ..... *C. consobrinus*
   Major worker with PD:D in lateral view < 1·2 (Fig. 11*b*) ..... *C. longideclivis*
4. Gula with erect setae (> 0·2 mm long) numbering > 20 or covering more than half the area of gula ... 5
   Gula with erect setae (> 0·2 mm long) numbering < 20 or covering more than half the area of gula ... 7
5. Dorsum of propodeum in lateral view with fewer than 10 erect setae concentrated near angle ..... *C. dryandrae*
   Dorsum of propodeum in lateral view with more than 10 erect setae distributed over most of dorsum ... 6
6. Colour of head, mesosoma, node and most of gaster, uniformly honey colour ..... *C. clarior*
   Colour of head, mesosoma, node and most of gaster not uniform, head black and/or brown, mesosoma yellow or red brown ..... *C. nigriceps*

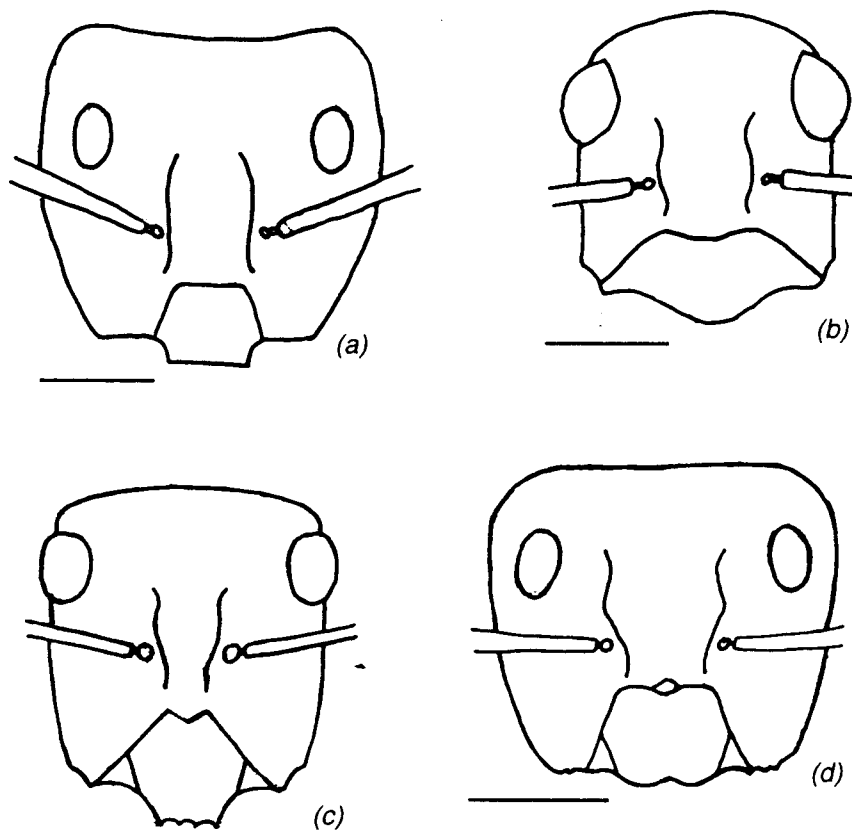

Fig. 6. Dorsal view of head of other *Camponotus* spp. with clypeus anterior margin dissimilar to *C. nigriceps* group, for comparison. *a*, *C. testaceipes* major worker; straight, projecting; *b*, *C. testaceipes* minor worker; convex, projecting; *c*, *C. ephippium* medium worker; tri-dented, projecting; *d*, *C. aeneopilosus* major worker, not projecting. Scale lines = 1 mm.

7. Maximum HW (minor workers only and in dorsal view) occurs anterior to a line through eye centres, head sides taper to the rear (Fig. 9*c*) ..... *C. eastwoodi*
   Maximum HW (minor workers only and in dorsal view) occurs near a line through eye centres, head sides parallel convex or parallel straight (Figs 5*b*, 9*a*, 9*b*) 8
8. Head reddish brown, never black; node summit concave (major workers only and viewed from rear, see Fig. 12*a*); HW:HL < 1 ..... *C. pallidiceps*
   Head black or very dark brown; node summit straight or convex (major workers only and viewed from rear); HW:HL > 1 in largest major workers ..... *C. prostans*

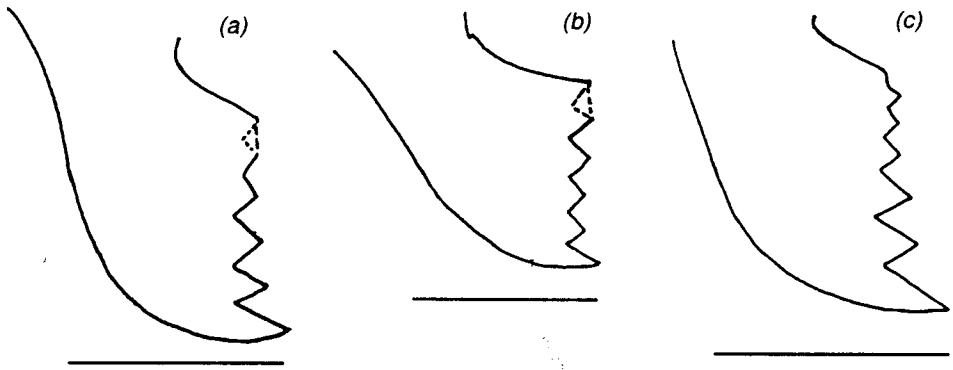

Fig. 7. Mandible, typical of *C. nigriceps* group showing distinct proximal tooth and valley between proximal and next tooth sometimes lacking. The margin between the two basal teeth (proximal) may vary within the dotted area. *a*, *C. loweryi* major worker; *b*, *C. loweryi* minor worker; *c*, mandible of *C. testaceipes* for comparison, showing off-set, basal half-tooth. Scale lines = 1 mm.

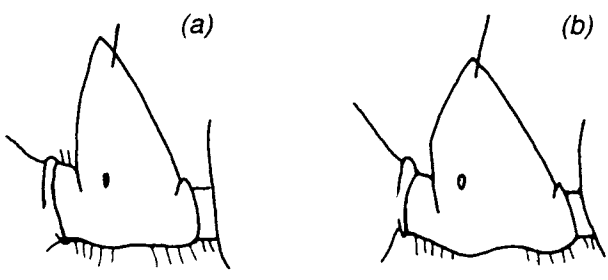

Fig. 8. Lateral view of pedicel ventrum. *a*, *C. consobrinus* major worker; *b*, *C. consobrinus* minor worker. Scale lines = 1 mm.

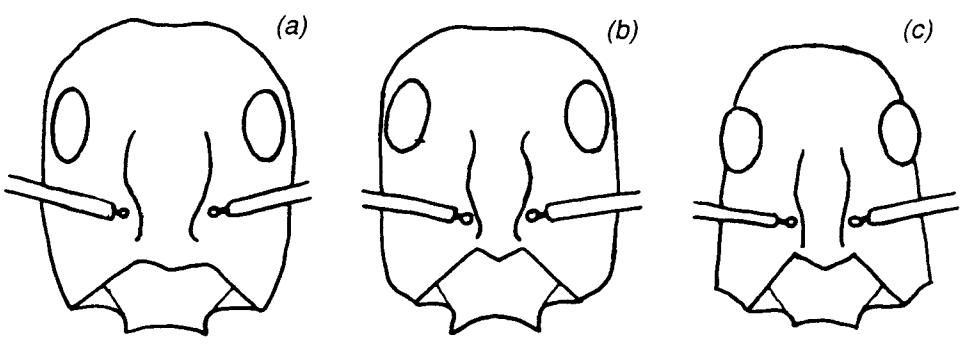

Fig. 9. Head in dorsal view. *a*, *C. consobrinus* medium worker, head sides parallel convex; *b*, *C. nigriceps* minor worker, head sides parallel; *c*, *C. eastwoodi* minor worker, head sides tapering to the rear. Scale lines = 1 mm.

Camponotus clarior Forel, stat. nov.

Camponotus nigriceps clarior Forel, 1902: 506.

Material Examined

Types. GMNH, Drawer 164, labelled 'typus', 1 major and 2 minor workers. Major worker: HW = 2·95 mm, HL = 3·2 mm, PW = 2·15 mm, HT = 2·1 mm, TL = 3·2 mm. Minor worker: HW = 2·1 mm, HL = 2·75 mm, PW = 1·7 mm, HT = 1·6 mm, TL = 2·75 mm. From Bendigo, Victoria.

Other material examined. **New South Wales:** Danggali, Mornington, 1993, AMA (SAMA). **South Australia:** Bakara, 8 km SE, 1991, VS (SAMA); Crystal Brook, 1957, FAC (ANIC); Crystal Brook, 1957, BBL (SAMA); Danggali CP, Morganvale, 1993, AMA (SAMA nests 51–54); Danggali CP, Mornington, 1993, AMA (SAMA); Danggali CP, Red Tank, 1993, AMA (SAMA nest 55); Illintjitja, 13 km SSE, 1993,

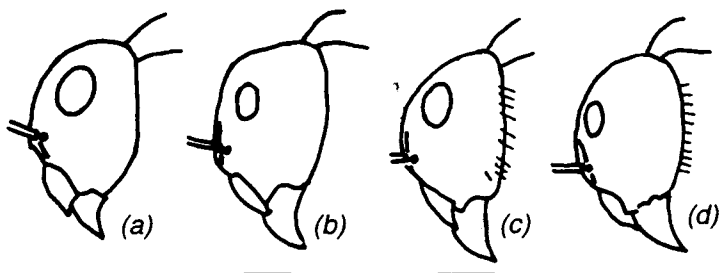

Fig. 10. Head, lateral view. *a*, *C. consobrinus* minor worker, showing absence of setae on gula; *b*, *C. consobrinus* major worker; *c*, *C. nigriceps* minor worker, showing plentiful setae on gula; *d*, *C. nigriceps* major worker. Scale lines = 1 mm.

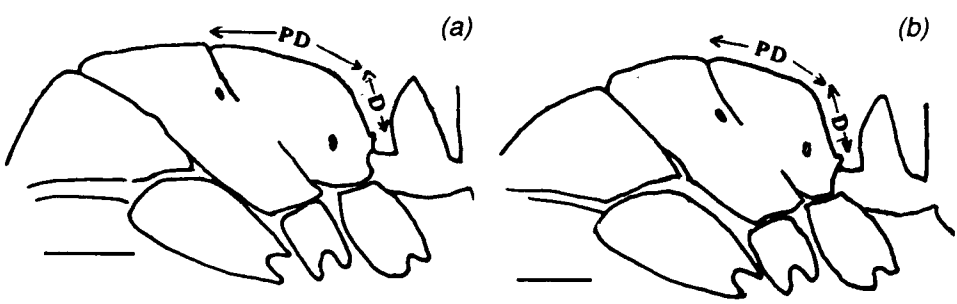

Fig. 11. Mesosoma in lateral view, showing the morphological characters PD and D. *a*, *C. consobrinus* major worker, with ratio PD:D = 1·8; *b*, *C. longideclivis* major worker, with PD:D = 1·2. Scale lines = 1 mm.

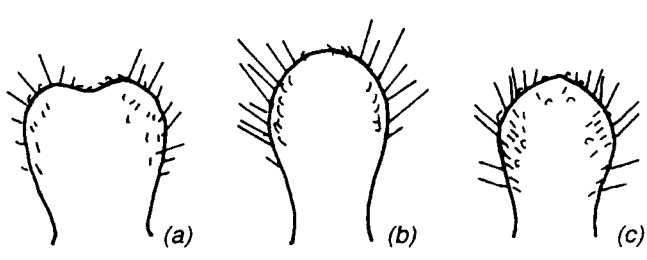

Fig. 12. Node, rear view. *a*, *C. pallidiceps* major worker, showing concavity; *b*, *C. consobrinus* major worker; *c*, *C. nigriceps* major worker. Scale lines = 1 mm.

PITJ (SAMA); Illintjitja, 28·5 km WSW, 1993, PITJ (SAMA); Kychering Soak, 1909, R. C. Chandler (NVMA); Middleback Range, Sinclairs Gap, 1986, P. Hudson (SAMA); Mt Cooperinna, Mann Range, 1994, PITJ (SAMA); Peebinga NP, 1992, GLH (SAMA); Serpentine Lake, 1994, JAF (SAMA); Waikerie, 20 km SW, 1969, FAC (NVMA). **Victoria:** Hattah, 1987, BBL (ANIC); Hattah, 18·9 km SW, 1985, ALY (NVMA); Hattah, 3 km NE, 1986, ALY (NVMA); Hattah, 5 km NE, 1987, ALY (NVMA); Lascelles, 13·3 km NW, 1986, ALY (NVMA); Meringur, 10·6 km ESE, 1986, ALY (NVMA); Milliwa Sth Bore, 1987, ALY (NVMA); Murrayville, 24·9 km SE, 1986, ALY (NVMA); Murray Valley Hwy, junction with Annuello Rd, 6 km SW, 1986, ALY (NVMA); Patchewollock, 20·9 km NE, 1985, ALY (NVMA).

Worker Description

Colour: honey colour with mandibles darker, legs lighter, posterior segments of gaster sometimes slightly darker. Pilosity: to 0·3 mm long plentiful on gula and sides of head, pronotum, mesonotum and present on propodeum (Fig. 13*a*, *b*), plentiful on gaster pointing backwards, short setae on scapes raised 30–40°, short setae on midtibiae 30–40°. Pubescence: a coat of curved raised setae about 0·1 mm long, spaced < length, is visible on the dorsum of mesosoma. Integument finely reticulate, glossy. Node summit viewed from rear: flatly convex, occasionally flat. Metanotum usually distinct in major workers.

Measurements

HW = 1·70–3·30 mm; TL = 2·70–3·50 mm; $n = 20$.
TL = 2·3 + 2·03 log HW ($n = 20$, $r = 0·90$, s.e.$_y = 0·16$, s.e.$_x = 0·08$).
PD:D = 1·5 in major workers increasing to 3·0 in minor workers.

Remarks

Camponotus clarior corresponds to genetic group B (Fig. 3, Table 3). It is easily distinguished by the strikingly uniform yellow colour of head and mesosoma. The gaster colour of specimens from central southern Australia is also yellowish or honey coloured whereas specimens from one population near the Western Australian border have a brownish gaster. This species is sympatric with *C. nigriceps* in mallee at Danggali Conservation Park, South Australia. Nest entrances of *C. nigriceps* and *C. clarior* in mallee habitats comprising *Eucalyptus dumosa*, *E. socialis*, *E. gracillis* or *E. cyanophilla* are distinct (G. L. Howie, personal communication). The entrance to the nest is a small hole in a hollow branch often 2 m above ground. Refuse from cleaning the galleries is deposited as a conspicuous cone sometimes 30 cm in height beneath this hole.

Distribution

The known distribution is confined to the Mallee areas of central southern Australia (Fig. 14).

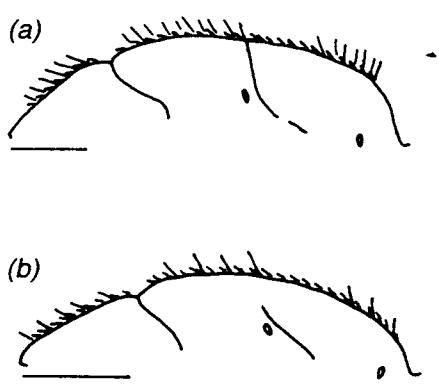

Fig. 13. *C. clarior*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

Etymology

Clarus (Latin: bright or shining), referring to its light overall colour.

Camponotus consobrinus Erichson

Formica consobrina Erichson, 1842: 258 (female). — Smith, 1858: 38 (worker); Lowne, 1865: 277 (biology).

Camponotus dimidiatus Roger, 1863: 4. — Roger, 1863: 44; Wheeler, 1933: 23 (syn); Clark, 1934: 70.

Camponotus consobrinus Roger, 1863: 4. — Roger, 1863: 44; Emery, 1925: 171 (genre incertain); Wheeler, 1933: 23; Greaves and Hughes, 1974: 337 (biology); Greenslade, 1979: 40; Burgman *et al.*, 1980: 28: Burgman *et al.*, 1980: 151 (biology); Hölldobler and Engel-Siegel, 1984: 219 (biology).

Camponotus nigriceps obniger Forel, 1902: 506. — Forel, 1910: 73 (new syn.).

Material Examined

Types

Formica consobrina: ZMB (cabinet 165/3), one queen, from Van Diemansland, posterior tergites of gaster missing; bicoloured gaster, clypeus, pilosity, pubescence, integument and colour referable to *C. consobrinus* workers. HW = 2·55 mm, HL = 2·6 mm.

Formica dimidiatus: ZMB (cabinet 164/1), one queen, labelled 'coll Roger Van Diem', clypeus, pilosity, pubescence, integument and colour referable to *C. consobrinus* workers. HW = 1·7 mm, HL = 2·2 mm, PW = 1·4 mm, TL = 2·4 mm.

Camponotus nigriceps obniger: GMNH, 6 types and many cotypes. Major worker: HW = 3·35 mm, HL = 3·5 mm, PW = 2·2 mm, HT = 2·4 mm, TL = 3·2 mm. Minor worker: HW = 1·5 mm, HL = 2·1 mm, PW = 1·3 mm, HT = 1·35 mm, TL = 2·4 mm. From Australia.

Voucher specimens examined

Camponotus sp. no. 16 (ANIC) — Burgman *et al.*. 1980.

Fig. 14. *C. clarior*, known distribution.

Other material examined

Australian Capital Territory: Canberra, 1954, E. F. Riek (ANIC); Canberra, Carotel Caravan Park, 1966, RHM (SAMA); Kosciusko, 1946, M. Joyce (ANIC); Kowen, 1936 L. W. (ANIC); Paddy's Rv., 1934, TG (ANIC). **New South Wales:** Anabranch to Wentworth Road, 1969, RHM (SAMA); Armidale, 1969, RWT (ANIC); Berellan, 1979, BBL (ANIC); Blakehurst, 1977, R. Craig and M. Burgman (ANIC); Blue Mountains, Mt Victoria, 1993, AMA and MAA (SAMA nests 12, 13); Bogan River, J. Armstrong (ANIC); Bombala, 16 mi to Orbost, 1939, FAC (NVMA); Brindabella, 1953, E. F. Riek (ANIC); Broken Hill Lubra Mine, 1965, RHM (SAMA); Bulli Pass, 1993, CHS (SAMA nest 29); Calga, west of Coonamble, 1934, A. B. Comarius (ANIC); Cliefden, 1960, P. Aitken (SAMA); Como, 1914, WMW (SAMA); Duckshot Stn via Oxley, 1968, EGM (SAMA); Etonsville, 1993, R. Eastwood (SAMA nest 14); Finley, 12 km N, 1979, BBL (ANIC); Forbes, WWF (ANIC); Glen Innes, 14 mi S, 1937, FAC (NVMA); Gordon, 1974, PJW (ANIC); Grafton, 5 mi S, 1951, D. Ross (ANIC); Gunnedah, 31 mi SSW, 1949, TG (ANIC); Katoomba, 1993, AMA and MAA (SAMA); Kilcare, 1966, RHM (SAMA); L. Cawndilla, RHM (SAMA); L. Cowal, 1971, W. Vestjens (ANIC); Lane Cove, 1957, A. Dyee (ANIC); Legume, N of Tenderfield, 1937, FAC (NVMA); Londonderry, 1974, PJW (ANIC); Menindee, 1964, RHM (SAMA); Menindee, 22 km S, 1965, RHM (SAMA); L. Menindee, RHM (SAMA); Mootwingee, 1955, RHM (SAMA); Moulamein, 14 mi E, 1947, TG (ANIC); Mt Victoria, 1993, AMA and MAA (SAMA); Mt Victoria, 1976, BBL (ANIC); Mungindi, 10 mi NE, 1949, TG (ANIC); Mungindi, 10 mi SSW, 1949, TG (ANIC); Murrurundi, 2 mi N, 1937, FAC (NVMA); Nyngan, 14 mi NW, 1949, TG (ANIC); Pennant Hills, 1966, RHM (SAMA); Picton, 1980, R., Patterson (ANIC); Pymble, 1956, FAC (NVMA); Royal NP, Flat Rock Ck, 1977, M. Burgman (ANIC); Royal NP, Govt. Game Lookout, 1977, R. Craig and M. Burgman (ANIC); Shrimpton's Ck, North Ryde, 1977, R. Craig (ANIC); South Grafton, Leslie Dam, 1993, R. Eastwood (SAMA); Sutherland, 1914, WMW (SAMA); Sydney, 1939, K. H. L. Key (ANIC); Trundle, 1964, BBL (ANIC); Uralla, 1914, WMW (SAMA); Walgett, 10 mi SSW, 1949, TG (ANIC); Wallacia, 1927, H. M. Hale and NBT (SAMA); Wanda Stn, 1961, RHM (SAMA); Wentworth Falls, 1937, C. V. Motissel (ANIC); Werris Ck, 6 mi S, 1937, FAC (NVMA); Whallen, 25 mi NNE Collarenebri, 1949, TG (ANIC); Wilcannia, 3 mi SE, 1949, TG (ANIC); Wycott Stn, 1963, RHM (SAMA); Wyong, 3 mi NE, 1937, FAC (NVMA). **Queensland:** Bribie I., 1914, WMW (SAMA); Brisbane, 1936, TG (ANIC); Charters Towers, 30 km S, 1980, BBL (ANIC); Clermont, 1937, FAC (NVMA); Condamine, 8 mi N, 1962, JED (SAMA); Emerald, 1946, J. Hayes (SAMA); Frazer I., 1972, M. Dick and P. Hunt (ANIC); Gayndah, 1972, S. A. Harrington (ANIC); Gayndah, 10 mi E, 1937, FAC (ANIC); Goondiwindi, 24 mi N, 1962, JED (ANIC); Goondiwindi, 7 mi E, 1949, TG (ANIC); Greenmount, 6 mi S, 1949, TG (ANIC); Gympie, 9 mi N, 1951, TG (ANIC); Millmerran, 1942, J. Macqueen (SAMA); Mt Mort, 1933, S. H. Parlett (ANIC); St George, 1965, BBL (ANIC); Tara, 33 mi SSW, 1962, JED (SAMA); Tumoulin, 1938, TG (ANIC); Yelarbon, 4 mi WSW, 1949, TG (ANIC). **South Australia:** Adelaide, Sth Terrace Parklands, 1993, P. Magarey (SAMA); Adelaide, Brown Hill Ck, with *Ogyris* spp., 1993, RHF (SAMA nest 16); Adelaide, Athelstone, 1993, C. Horne (SAMA nest 19); Adelaide, Highbury, 1992, MAA (SAMA nest 25) Andamooka, 1947, GFG and R. J. Mitchell (SAMA); Andamooka, Exp. Tower Hill, 1947, R. J. Mitchell and GFG (SAMA); Angorichina, 5·9 km E, 1992, AMA and MAA (SAMA); Arkaroo Rock, Flinders Ra., 1992, AMA and MAA (SAMA); Avenue Ra., 1955, D. J. Barratt (SAMA); Bascombe Wells, Eyre Peninsula Kappawanta Basin, 1986 JAF (SAMA); Beachport, Picaninny Lane, 1993, AMA (SAMA nests 18, 28); Beachport, Field Nats Block, 1993, AMA (SAMA nests 32, 33); Beachport, Wooley's Lake, 1991, AMA and JDE (SAMA); Belair NP, 1956, B. Daily (SAMA); Belair NP, 1963, RHM (SAMA); Belair NP, 1992, AMA (SAMA); Belair, nuptual flight, 20.i.1991, S. A. Parker (SAMA); Blanchetown, 1979, G. P. Browning (SAMA); Blinman, 6·3 km NW, 1992, AMA and MAA (SAMA); Bordertown, 15 km W, 1992, RHF (SAMA); Buccleuch, 3 km S, 1991, VS (SAMA); Burnside, 1992, Georgia Verschoyle (SAMA); Burra, 1986, K. B. Ashby (SAMA); Canegrass, 1993, AMA (SAMA); Canunda, Woakwine Ra., 1985, C. K. Pawsey (SAMA); Carappee, Eyre Pen., 1964, GFG and R. J. Mitchell (SAMA); Chowilla, 1988, S. Lewer (SAMA); Coonalpyn, 1991, JAF (SAMA); Coulta, 15 km N, 1947, TG (ANIC); Cummins, 2 mi N, 1947, TG (ANIC); Danggali CP, NW entrance, chenopod, 1993, AMA (SAMA 15); Deep Creek NP, 1981, EGM and JAF (SAMA); Devon Downs, 1927, NBT (SAMA); Dutchmans Stern NP, 1993, AMA (SAMA); Elgin Drain M, 1993, AMA and JDE (SAMA); Elizabeth East, F. Miller (SAMA); Ettrick NP, 1993, GLH (SAMA); Flinders Ranges, Blinman, 1993, AMA and MAA (SAMA nests 21, 24); Flinders I., 1990, L. Mathews (SAMA); Gambak Park, 2 km NE, 1991, VS (SAMA); Gammon Ranges, Arkaroola, Wooldoonooldoona Water hole, 1993, AMA and MAA (SAMA nest 23); Gammon Ranges, Mainwater Ck, AMA (SAMA); Gawler, Heysen Trail, 1989, AMA and PJF (SAMA); Gawler Ra., Kolay Dam, 1989, JAF (SAMA); Gawler Ra., Rockwater, 1985, NPS (SAMA); Greenock, 2 km S, 1993, M. Kreig (SAMA); Hatherleigh, 1988, AMA (SAMA); Hatherleigh Hills, 1993, AMA (SAMA); Highbury, 1985, JAF (SAMA); Innes NP, Pondalowie Bay, 1990, AMA (SAMA); Jupiter Ck, 1991, AMA (SAMA); Kangaroo I., American R., 1990, EGM and JAF (SAMA); Kangaroo I., American R., 5 km WSE, 1990, NPS (SAMA); Kangaroo I., Cape Torrens CP, 1990, EGM and JAF (SAMA); Kangaroo I., Cape Willoughby, 8 km SW, 1990, VS (SAMA); Kangaroo I., Dudley CP, 1990, EGM and JAF (SAMA); Kangaroo I., Murray's Lagoon, NE shore,

1993, AMA (SAMA); Kangaroo I., Ravine Des Casoars, 1990, EGM and JAF (SAMA); Kangaroo I., Rocky River, 1990, EGM and JAF (SAMA); Kangaroo I., Salt Lagoon, 1990, EGM and JAF (SAMA); Kangaroo I., Seal Bay, 5 km N, 1990, VS (SAMA); Kangaroo I., Sth Coast Rd, 1990, EGM and JAF (SAMA); Kangaroo I., West Bay, 1991, VS (SAMA); Kangaroo I., Western Rd, 1990, EGM (SAMA); Kangaroo I., Wingara Hs., 1990, VS (SAMA); Keilira Stn, 13 km N, 1993, DH (SAMA); Kielira Stn, 1992, JAF and EGM (SAMA); Kingston, Bernarra Res., 1994, G. Medlin (SAMA); Lobethal, with *Ogyris* spp., 1992, M. Pickett (SAMA); Lucindale, Feuerheerdt (SAMA); Magill, 1992, EGM and JAF (SAMA); Magill, 1993, M. Kreig (SAMA); Maitland, 1925, NBT (SAMA); Mambray Ck, 1994, A. B. Dow (SAMA); Maynards Well, 1974, J. A. Herridge (SAMA); McGrath Flat, 9 km NW, 1991, VS (SAMA); McLaren Flat, Douglas Scrub, 1985, JAF (SAMA); Meningie, 10 km S, 1959, GFG (SAMA); Mitcham, 1975, RVS (SAMA); Mitcham, with *Ogyris* spp., 1992, RHF (SAMA); Mitcherie Rockhole, 1987, VS (SAMA); Monarto, 1985, W&F (SAMA); Monarto Zool. Pk, Bretag Scrub, 1993, T. P. Morley (SAMA); Morgan, in marina, 1991, P. M. Thomas (SAMA); Morgan, 1992, AMA and MAA (SAMA); Morialta Res., 1969, BBL (ANIC); Mt Barker, 1963, J. A. Heridge (SAMA); Mt Mary, 1992, AMA and MAA (SAMA); Mt Remarkable NP, Alligator Gorge, 1976, GFG and J. A. Herridge (SAMA); Mt Rescue NP, 1992, JAF and EGM (SAMA); Murray Lands, Morgan, 1992, P. M. Thomas (SAMA nest 17); Murray Lands, Renmark, 1992, I. Tolley (SAMA nest 20); Murray Lands, Pooginook, 1992, AMA and MAA (SAMA nests 26, 27); Naracoorte to Kingston Rd, 1958, GFG (SAMA); Naracoorte Stick Cave, 1993, R. G. Simms (SAMA); Narrung, 6 km SE, 1991, VS (SAMA); Ngarkat NP, Box Flat, 1991, JAF (SAMA); North Blinman Hotel, 1976, J. J. H. Szent-Ivany (SAMA); Norwood, 8 km E, 1969, BBL (ANIC); Peridinya, 5 km SE, 1991, VS (SAMA); Rabbit Island Dam, 1991, VS (SAMA); Red Stringy Bark NP, 1990, AMA (SAMA); Rendelsham, 1987, AMA (SAMA); Rendelsham PO, 1989, R. Stiles (SAMA); Rendelsham, in orchard, 1988, R. Todd (SAMA); Renmark, 1965, RHM (SAMA); Renmark, 5 mi upstream, 1991, AMA (SAMA); Renmark Caravan Pk, 1967, RHM (SAMA); Renmark, Tolley's Orchard, 1992, AMA and MAA (SAMA); Rhynie, 1 mi S, 1947, TG (ANIC); Roachdale, 1980, J. J. H. Szent-Ivany (SAMA); Rockhill HS., 1992, CHS (SAMA); Rockwater, Gawler Ra., 1985, SANP (SAMA); Salisbury, nuptual flight, 28.xii.1993, James Knight (SAMA); Sevenhill, 1957, FAC (NVMA); Swan Reach, 17 km NW, 1991, VS (SAMA); Thornlea, nr Beachport, 1993, AMA (SAMA); Thornlea, Picaninny Lane, 1992, AMA and JDE (SAMA); Tintinarra, Jimmys Well, 1965, P. Aitkin and NBT (SAMA); Upper Sturt, nuptual flight, 22.i.1992, Alfred Smith (SAMA); Victor Harbour, 10 km N, with *Ogyris* spp., 1990, RHF (SAMA); Wangary, 10 km N, 1985, JAF (SAMA); Weona HS., 10 km SE, 1991, VS (SAMA); West Gums Stn, nr Kingston, 1972, A. W. Forbes (SAMA); White Dam, 1992, AMA and MAA (SAMA); Whyalla, Munyaroo CP, 1991, W. Head (SAMA); Wilmington, Stony Ck, 1993, D. Hirst (SAMA); Wilpena Pound, 1956, GFG (SAMA); Woods Well, 1971, J. Herridge, GFG and M. Gross (SAMA); Worlds End, 5 km E, 1992, SOPS (SAMA); Yudnamutana, Flinders Ra., 1970, BBL (ANIC). **Tasmania:** Asbestos Ra., 1993, BBL (SAMA); Bothwell, 6 mi S, 1938, FAC (NVMA); Brown's River, C. Lord (ANIC); Cape Barren I., 1940, NBT (SAMA); Flinders I., H. H. Finlayson (SAMA); Frankford, 10 km W, State Forest, 1993, BBL (SAMA); George Town, 1914, A. M. Lea (SAMA); Hobart, 1938, FAC (NVMA); Hobart, 1980, A. Newton and M. Thayer (ANIC); Hobart, 1993, WMA (SAMA); Launceston, 1914, A. M. Lea (SAMA); Maria I., 1992, BBL (SAMA); Mole Ck, 1993, BBL (SAMA); Mt Rumney, RHM (SAMA); Mt William NP, 1993, BBL (SAMA); New Norfolk, 1940, H. M. Hale (SAMA); Turnbridge, 1992, BBL (SAMA). **Victoria:** Ararat, 1917, G. F. Hill (NVMA); Bairnsdale, Dargo High Plains, 1973, JEA (SAMA); Bendigo, F. E. Wilson (ANIC); Bendigo, Heathcote, 1961, BBL (ANIC); Billabong, 1969, RHM (SAMA); Bright, 1965, RHM (SAMA); Casterton, 10 km E, 1992, AMA and JDE (SAMA); Casterton, 1950, P. Denormam (NVMA); Chiltern, 1943, TG (ANIC); Derrimut, 1929, TG (ANIC); Eltham, 1928, TG (ANIC); Eltham North, 1992, GFG (SAMA); Fern Tree Gully, 1929, TG (ANIC); Grampians, 1985, nr Mt Zero, AMA (SAMA); Grampians, Halls Gap, 1992, AMA and JDE (SAMA nests 30, 31); Grampians, Wannan Divide, 1956, NBT (SAMA); Greensborough, J. McAreavey (ANIC); Kiata, 1928, C. H. B. (SAMA); Lake Tyers, 1940, FAC (NVMA); Lindsay R., junction with Mullaroo Ck, 6·3 km N, 1986, ALY (NVMA); Lorne, 1989, S. Morrison (SAMA); Mt Buffalo NP, Eurobin Creek, 1980, A. Newton (NVMA); Murray Valley Hwy/Annuello Rd., 10·4 km S, 1987, ALY (NVMA); Nelson, Glenelg R., 1958, NBT (SAMA); Nhill, 1908, J. Searle (ANIC); Sealake, J. C. Couldie (NVMA); Swan Hill, 1965, RHM (SAMA); Werribee, 1928, TG (ANIC); Werribee Gorge, 1958, FAC (NVMA); Wyperfeld, at mallee fowl mound, 1933, Professor Wood-Jones (SAMA); Wyperfield Park, 1929, E. S. Hanks (ANIC).

Worker Description

Colour: head black to red brown; mesosoma, node black to yellow including orange; anterior gaster lighter than posterior, posterior gaster usually near colour of head. Pilosity: always absent on gula; setae erect slightly forward pointing, 0·3–0·5 mm long on mesosoma dorsum, 3–10 on propodeum (Fig. 15*a*, *b*), 5–20 on mesonotum, 15–30 on pronotum, plentiful on gaster pointing

backward; on head and mandibles more erect and shorter, not plentiful. Short setae on scapes raised to an inclination of up to 20° when viewed from front. Short setae on midtibiae: inclination 5–40°. Pubescence (= short setae, length always < 0·2 mm) on head and mesosoma adpressed, spacing > setae length. Integument: glossy finely reticulate, front of head with shallow sparse punctation. Node summit viewed from the rear: straight or convex (Fig. 12*b*), occasionally slightly concave in largest majors.

Measurements

HW = 1·30–3·30 mm; HL = 1·75–3·40 mm; $n = 261$. TL = 2·95–3·00 mm; $n = 49$.
TL = 1·9 + 1·87 log HW ($n = 49$, $r = 0·93$, s.e.$_y = 0·07$, s.e.$_x = 0·07$) (Fig. 16).
PD:D = 1·3 in major workers increasing to 3·0 in minor workers.
Distinctly polymorphic. Maximum frequency of head widths in minor workers occurs at

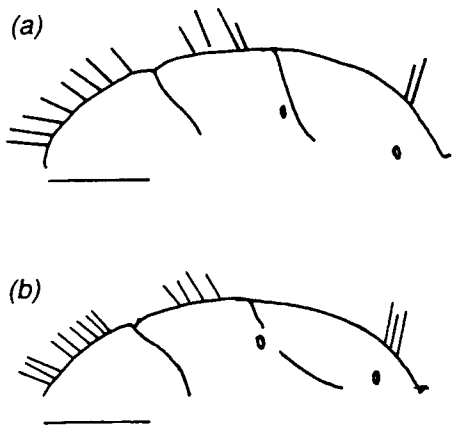

Fig. 15. *C. consobrinus*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

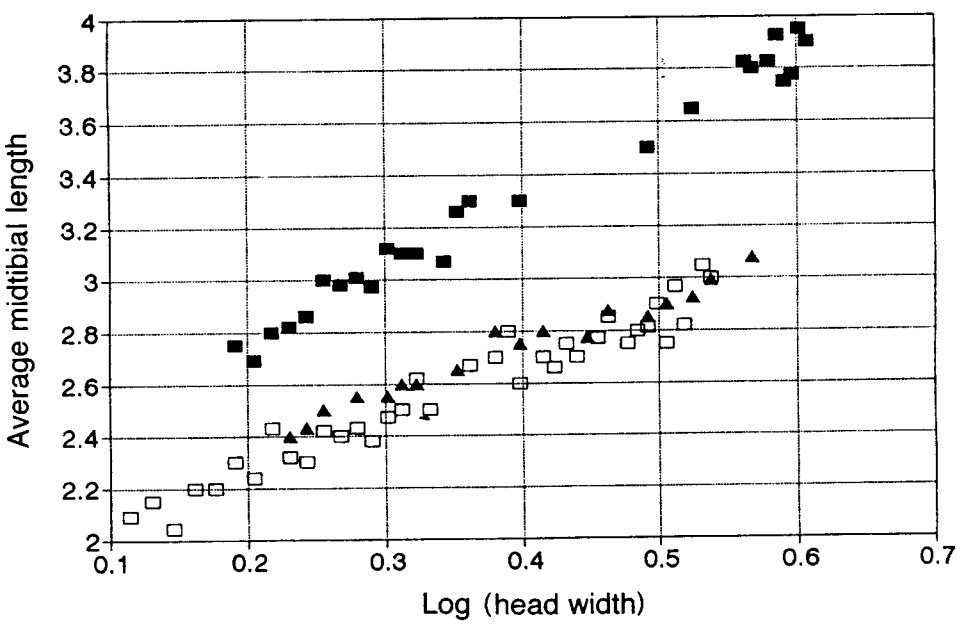

Fig. 16. Comparison of midtibial lengths: ants taken from two nests of *C. consobrinus*, one nest of *C. longideclivis*, and two nests of *C. loweryi*. ■, *C. loweryi*; □, *C. consobrinus*; ▲, *C. longideclivis*. No within-species differences were evident between ants from different nests.

about 1·75 mm, in medium workers at about 2·8 mm and in major workers at about 3·25 mm (Fig. 17*a*). The relationship between log HW and log HL is practically linear (Fig. 17*b*). Major workers, whose role is to defend the nest, have developed large muscles attached to their mandibles. Thus, major workers possess disproportionately wide heads (Huxley 1936).

Distribution

The known distribution is confined to south-eastern and eastern Australia (Fig. 18).

Remarks

Camponotus consobrinus corresponds to genetic group E, (Fig. 3, Table 3). Emery's (1925) classification of *Camponotus* species was based on characters of the workers. However, Erichson (1842) had erected *consobrinus* on the description of a queen and made no reference to workers. Because of this, we presume Emery placed *C. consobrinus* as 'de sous-genre incertain'. *C. nigriceps obniger* was described by Forel as a dark-coloured form of *C. consobrinus* with adpressed pubescence on tibiae. As some populations of dark coloured *C. consobrinus* possess suberect pubescence on tibiae, we propose *C. consobrinus* = *C. nigriceps obniger. C. consobrinus*, *C. loweryi* and *C. longideclivis* always lack setae on the

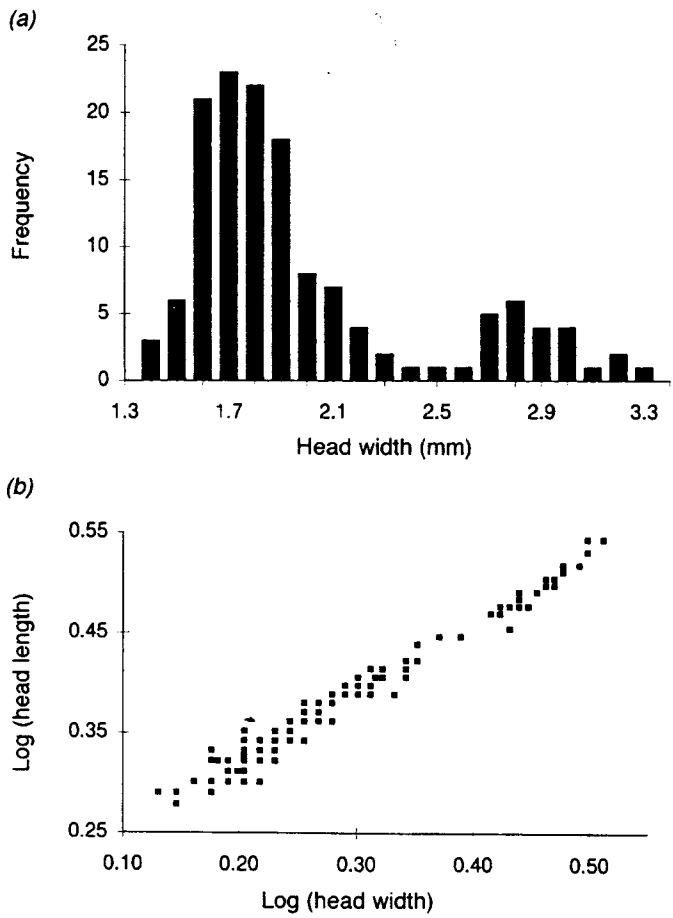

Fig. 17. *C. consobrinus*, a sample of ants from one nest at Hatherleigh near Beachport (n = 140). *a*, Frequency distribution of head width, showing three peaks corresponding to (left to right) the minor, medium and major workers; *b*, graph of head length against head width.

gula and they may be distinguished as follows. *C. loweryi* major workers (maximum HW = 4·3 mm) are larger than *C. consobrinus* (maximum HW = 3·6 mm) and *C. longideclivis* (maximum HW = 3·7 mm). Gaster colour in *C. loweryi* shows little variation from posterior to anterior whereas *C. consobrinus* is distinctly bicoloured. In Mallee areas, *C. consobrinus*, *C. loweryi*, *C. clarior* and *C. nigriceps* are sympatric. In the Blue Mountains of New South Wales, *C. consobrinus* and *C. pallidiceps* are sympatric. In the north-east of New South Wales, *C. consobrinus* and *C. eastwoodi* are sympatric. Alate specimens at SAMA indicate that nuptial flights occurred near Adelaide on 20 January 1991 and 21 January 1992. As discussed earlier, there is a single pinned specimen of *C. consobrinus* in ANIC labelled 'Perth. John Clark'. We await other finds before including it in our distribution map of this species.

Etymology

Consobrina (Latin: cousin). Erichson (1842) recognised some similarity of this species to *Formica herculaneus*.

Camponotus dryandrae, sp. nov.

Material Examined

Holotype. One major worker (pinned) SAMA plus paratypes in alcohol, SAMA, ANIC, WAM. Collected by M. Adams, Nov. 1992, from Dryandra State Forest, Western Australia.

Other material examined. **Western Australia:** Armadale, JC (WAM); Bungulla, 1929, TG (ANIC); Darlington, Greenmount, 1992, AMA and WMA (SAMA); Dryandra State Forest, 1992, AMA and WMA (SAMA); Dryandra State Forest, 1992, MAA (SAMA nest 50); Dryandra State Forest, NE entrance, 1993,

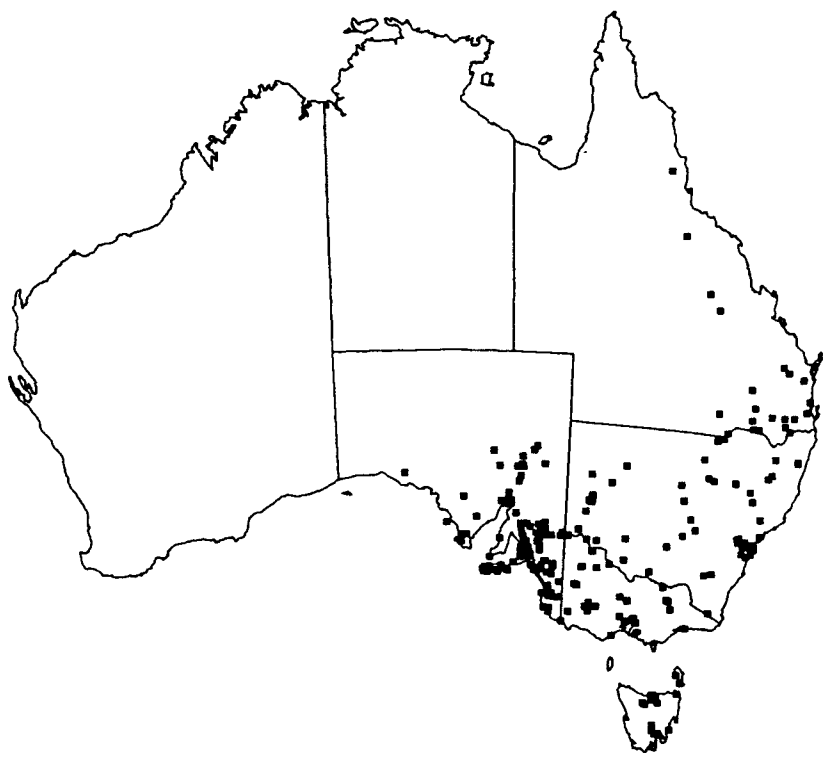

Fig. 18. *C. consobrinus*, known distribution.

AMA and WMA (SAMA nest 42, 43); Durokoppin NP, NE corner W block, 1993, AMA and WMA (SAMA nest 44); Durokoppin NP, NW corner, 1993, AMA and WMA (SAMA nests 45–49); Kalamunda, 1929, TG (ANIC); Laverton, 12 mi NNE, 1960, JED (ANIC); Mundaring, JC (ANIC); Mundaring Dam, 1965, P. Humphries (WAM); North Bannister, 2 km E, 1992, AMA (SAMA); North Bannister, 2 km NW, 1994, MAA (SAMA); Ongerup, 4 mi E, 1947, TG (ANIC); Warburton Mission, 1 mi N, 1960, JED (ANIC); Worsley, 1990, Curtin University (WAM).

Worker Description

Colour: head black, mesosoma, node, coxa and femur red brown, gaster black sometimes with a trace of red-brown proximal to the node, tarsi slightly darker than tibia. Pilosity: up to 0·4 mm long, plentiful on pronotum, less on mesonotum and 5–10 on propodeum, clustered near angle (Fig. 19*a*, *b*), plentiful but shorter on gula, plentiful on gaster pointing backwards, short setae on scapes raised to 20°, short setae on midtibiae raised to 30°. Pubescence: suberect setae about 0·1 mm long, spaced < length, visible on the dorsum of mesosoma, more adpressed on head. Integument finely reticulate, glossy. Node summit viewed from rear: flatly convex, in major workers sometimes slightly concave. Metanotum usually distinct in major workers.

Measurements

HW = 1·40–3·75 mm; TL = 2·60–3·53 mm; n = 10.
TL = 2·34 + 1·65 log HW (n = 10, r = 0·93, s.e.$_y$ = 0·16, s.e.$_x$ = 0·07).
PD:D = 1·5 in major workers increasing to 3·0 in minor workers.

Remarks

Camponotus dryandrae corresponds to genetic group F (Fig. 2, Table 3). Near *C. nigriceps* in colour and form but with distinct pilosity. *C. dryandrae* possesses < 10 setae (length > 0·3 mm) on the propodeum, all clustered at the propodeal angle and cover < 50% of propodeal dorsum. In *C. nigriceps* similar long setae are dense and cover > 50% propodeal dorsum. *C. dryandrae* can occur in sympatry with *C. nigriceps* over at least part of its range.

Distribution

The known distribution is confined to central and south-western Western Australia (Fig. 20).

Etymology

This species is named after Dryandra State Forest, Western Australia, from where it was first collected. Robert Brown of the Flinders Expedition named the genus of plants after Dryander, a contemporary botanist.

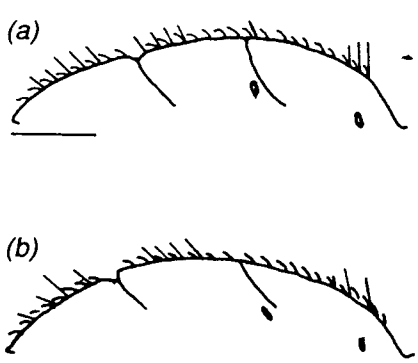

Fig. 19. *C. dryandrae*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

Fig. 20. *C. dryandrae*, known distribution.

Camponotus eastwoodi, sp. nov.

Material Examined

Holotype. One major worker (pinned) SAMA plus paratypes in alcohol, SAMA, ANIC. Collected by Mr Rod Eastwood, Nov. 1993, from Leslie Dam, Eatonsville, South Grafton, New South Wales.

Voucher specimens examined. *Camponotus* sp. no. 2 (ANIC) — Burgman *et al.*, 1980.

Other material examined. **Queensland:** Beaudesert, 1934, FAC (ANIC); Beaudesert, 3 mi N, 1912, H. Hacker (SAMA); Brisbane, S. H. Parlett (ANIC); Bundaberg, 1962, RWT (ANIC); Camp Mt, 1939, WWF (ANIC); Doongul State Forest, 1914, WMW (SAMA); Enoggera, 1914, WMW (SAMA); Enoggera, 1937, G. Ball (ANIC); Gladstone, 1937, FAC (NVMA); Mackay, 1973, R. Kohout (ANIC); Mt Coot-Tha, 1962, RWT (ANIC); Toowoomba, east of rifle range, 1977, RWT and A. Weir (ANIC); Mt Coot-Tha, 1976, RWT and A. Weir (ANIC); Mount Morgan, 5 km NE, 1977, BBL (ANIC). **New South Wales:** Eatonsville, with *Ogyris* spp., 1993, R. Eastwood (SAMA nests 74, 75); Ninbin Rocks, BBL (ANIC); Kyogle, 1968, RWT (ANIC); Roto R. Stn, 1965, RHM (SAMA); South Grafton, 1993, R. Atkins (SAMA); South Grafton, 1937, FAC (NVMA).

Worker Description

Colour: head black or very dark brown with lighter patches, mesosoma, node, coxa and femur honey coloured or light brown or yellow, gaster usually the same colour or slightly darker, tibia and tarsi red brown. Pilosity: up to 0·4 mm long plentiful on pronotum, less on mesonotum and 5–10 on propodeum (Fig. 21*a*, *b*), on gaster plentiful pointing backwards; on gula shorter, sparse in major workers sometimes absent, usually present but sparse in other workers, short setae on scapes raised to 10°, short setae on midtibiae raised to 10°. Pubescence: adpressed setae about 0·1 mm long, spaced < length, scarcely visible on the dorsum of mesosoma, sparse on head. Integument finely reticulate, glossy. Node summit viewed from rear: convex or flat in major workers, convex in other workers. Metanotum usually distinct in major workers.

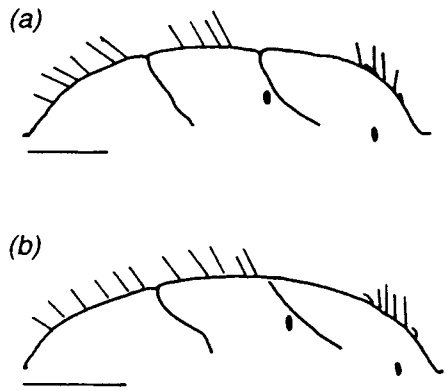

Fig. 21. *C. eastwoodi*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

Measurements

HW = 1·60–3·80 mm; TL = 2·65–3·40 mm; n = 17. In smallest minor workers where HW < 1·8 mm, the head sides taper to the rear; HW (at mandibles) minus HW (at vertex) is often > 0·1 mm.

TL = 2·46 + 1·70 log HW (n = 17, r = 0·95, s.e.$_y$ = 0·06, s.e.$_x$ = 0·10).

PD : D = 1·0 increasing to 3·0 in minor workers.

HW : HL in major workers often reaches 1·0 when HW exceeds 3·7 mm.

Remarks

Camponotus eastwoodi corresponds to genetic group C (Fig. 3, Table 3). It is similar in appearance to *C. loweryi* and *C. nigriceps*. Gula setae in *C. eastwoodi* sparse in major workers,

Fig. 22. *C. eastwoodi*, known distribution.

slightly more plentiful in minor workers; whereas in *C. nigriceps* dense in minor workers (Fig. 10*d*); in *C. loweryi* absent (similar to Fig. 10*a*, *b*). Head sides of smallest workers tapering to the rear (Fig. 9*c*). Mutual relationship with *Ogyris* spp. (Lepidoptera:Lycaenidae), (R. Eastwood, personal communication).

Distribution

The known distribution is confined to parts of eastern Australia (Fig. 22).

Etymology

This species is named after Mr Rod Eastwood who collected it at Eatonsville near South Grafton, New South Wales.

Camponotus longideclivis, sp. nov.

Material Examined

Holotype. One major worker (pinned) SAMA plus paratypes in alcohol, SAMA, ANIC, WAM. Collected by A. J. and W. M. McArthur, July 1993, from under a rock at eastern corner of Granite outcrop, Peak Charles, north of Esperance, Western Australia.

Other material examined. **Western Australia:** Balladonia, 1947, TG (ANIC); Cape Legrande NP, Thistle Cove, 1993, AMA and WMA (SAMA nest 34); Cape Legrande NP, Lucky Bay, 1977, R. P. Mcmillan (WAM); Esperance, 1971, BBL (ANIC); Peak Charles NP, 1983, G. P. Browning (WAM); Peak Charles NP, 1985, T. F. Houston (WAM); Peak Charles NP, 1993, AMA and WMA (SAMA nest 35).

Worker Description

Colour: head and scapes dark brown, funiculus, mesosoma and node lighter red brown, posterior gaster black, anterior gaster red brown; coxa and femurs and tibia lighter than mesosoma, more yellowish, tarsi darker, more brownish. PD:D in largest major workers about 1·2 (Fig. 11*b*), ratio greater in minor workers (Fig. 23*a*). Pilosity: absent on gula, 15–20 to 0·5 mm long on pronotum, less on mesonotum and 4–8 on propodeum, plentiful on gaster pointing backwards, short setae on scapes raised to 20°, short setae on midtibiae raised to 30°. Pubescence: on dorsum of mesosoma and head adpressed setae < 0·1 mm long, spaced >>

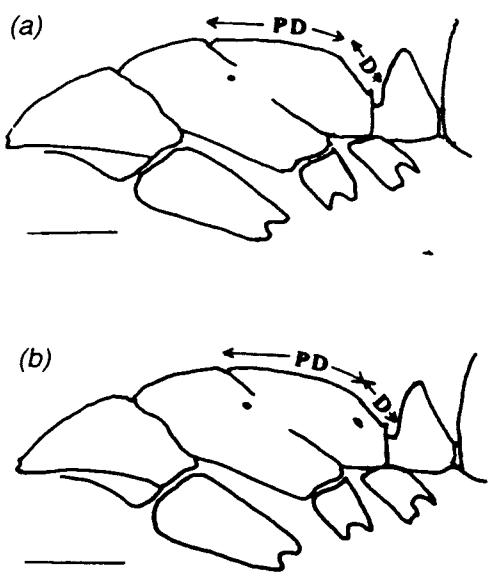

Fig. 23. Mesosoma dorsum lateral views, showing ratios PD:D are very similar (about 2·5) in minor workers of both *C. longideclivis* and *C. consobrinus*. *a*, *C. longideclivis*; *b*, *C. consobrinus*. The major workers of the two species show clear differences for the ratio PD:D (Fig. 11).

length. Integument finely reticulate, glossy. Node summit viewed from rear: flatly convex. Metanotum feeble or obsolete in major workers, obsolete in minor workers.

Measurements

HW = 1·70–3·70 mm; TL = 2·38–3·08 mm; $n = 23$.
TL = 2·03 + 1·78 log HW ($n = 23$, $r = 0{\cdot}94$, s.e.$_y = 0{\cdot}10$, s.e.$_x = 0{\cdot}05$) (Fig. 16).
PD:D = 1·2 in major workers increasing to 2·5 in minor workers.
HW:HL = < 1·0.

Remarks

Camponotus longideclivis corresponds to genetic group H (Fig. 3, Table 3). It is distinguished from *C. consobrinus* by the ratio PD:D of major workers where the mesosoma of *C longideclivis* is distinctly higher than *C. consobrinus* (Fig. 11*a*, *b* shows major workers and for comparison Fig. 23*a*, *b* shows minor workers).

Distribution

The known distribution is confined to south-western Western Australia (Fig. 24).

Etymology

The specific name is derived from longe (Latin: length) and declive (Latin: a slope or declivity) because the declining face of the propodeum is distinctly longer than that of its near relative, *C. consobrinus*.

Fig. 24. *C. longideclivis*, known distribution.

Camponotus loweryi, sp. nov.

Material Examined

Holotype. One major worker (pinned) SAMA plus paratypes in alcohol, SAMA, ANIC. Collected by A. J. McArthur, May 1993, at Tipperary Dam in Danggali Conservation Park, South Australia.

Other material examined. **New South Wales:** Cobar and Mt Hope, 1980, A. Atkins (SAMA); Cobar, 19 mi W, 1949, TG (ANIC); Hermidale, 4 mi E, 1949, TG (ANIC); Hillston, 27 mi S, large crater mound, 1978, BBL (ANIC); Lightning Ridge, 1961, FAC (NVMA); Mt Boppy, 3 mi E, 1949, TG (ANIC); Nyngan, 1966, J. Armstrong (SAMA); Nyngan, 1975, FAC (NVMA); Rankin's Springs, 1978, BBL (ANIC); Rankin's Springs, 1993, AMA and MAA (SAMA nests 6, 7); Silverton, 20 km SW, 1963, K. Dansie (SAMA); West Wyalong, 93 km W, 1993, AMA and MAA (SAMA). **Queensland:** Alpha, 1937, FAC (NVMA); Charters Towers, 1976, BBL (ANIC); Mackay to Marlborough, Lotus Ck, 1969, RWT (ANIC); Miles, 5 mi S, 1962, JED (ANIC); Mt Coot-Tha, Brisbane, 1956, FAC (ANIC); St George, 1965, BBL (ANIC); Taroom, Brigalow, 1975, BBL (ANIC); Tambo, airport, 1979, RHM (SAMA). **South Australia:** Angorichina, 1988, AMA (SAMA); Angorichina, 5 km E, 1988, AMA (SAMA); Arkaba Ck, Flinders Ra., 1973, EGM (SAMA); Beltana, 22 km N, 1972, J. E. Feehan (SAMA); Blinman, 1992, AMA and MAA (SAMA); Brachina Gorge, Flinders Ra., 1994, CHS (SAMA); Coffin Dams, 1992, SOPS (SAMA); Danggali CP, Hypurna, 1989, AMA (SAMA); Danggali CP, Morganvale, 1993, R. Ramsey (SAMA); Danggali, Tipperary Dam, 1992, AMA (SAMA); Flinders Ra., Angorichina, 5·9 km E, 1992, AMA and MAA (SAMA nests 10, 11); Flinders Ra., Blinman to Arkroola Rd, 1992, AMA and MAA (SAMA nests 8, 9); Gawler Ra., Rockwater, 1985, NPS (SAMA); Kingston, R. Murray, 1965, RHM (SAMA); Moolooloo, W. J. Kimber (SAMA); Morgan, 6 km W, on pipeline, 1980, JAF (SAMA), Wirrapowie Ck, Gammon Ra. NP, 1989, AMA and PJF (SAMA). **Victoria:** Meringur, 10·6 km ESE, 1985, ALY (NVMA); Meringur, J. C. Couldie (ANIC); Sealake, 1986, ALY (NVMA); Waloeup, 14·4 km SE, 1926, WWF (NVMA).

Worker Description

Colour: head black or brown with lighter patches, mesosoma, node and most of gaster honey colour or yellowish posterior gaster sometimes slightly darker, coxa and femur lighter often whitish, tibia and tarsus red brown. Pilosity: up to 0·5 mm long, plentiful on pronotum, less on mesonotum and 5–10 on propodeum (Fig. 25*a*, *b*), absent on gula, plentiful on gaster pointing backwards, short setae on scapes raised to 10°, short setae on midtibiae raised to 10°. Pubescence: adpressed setae about 0·1 mm long fine, spaced < length, scarcely visible on the dorsum of mesosoma, sparse on head. Integument finely reticulate, glossy. Node summit viewed from rear: convex or flat in major workers, convex in other workers. Metanotum usually distinct in major workers.

Measurements

HW = 1·60–4·05 mm; HL = 2·20–4·25 mm; TL = 2·70–4·00 mm; n = 40. HW:HL sometimes reaches 1·0 in major workers where HW > 4·0 mm.

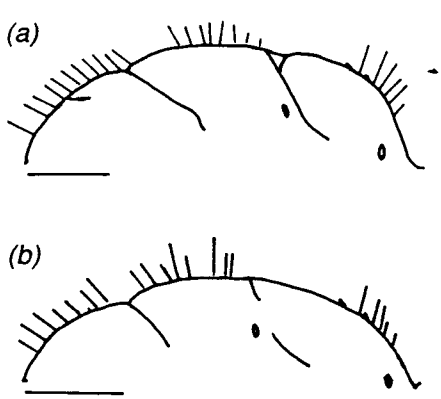

Fig. 25. *C. loweryi*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

TL = 2·26 + 2·73 log HW (n = 20, r = 0.96, s.e.$_y$ = 0.12, s.e.$_x$ = 0·08) (Fig. 16).
PD:D = 1·0 in major workers increasing to 3·0 in minor workers.

Remarks

Camponotus loweryi corresponds to genetic group D (Fig. 3, Table 3). It resembles *C. eastwoodi* and some light-coloured specimens of *C. consobrinus*, and *C. nigriceps* in colour and pilosity. *C. loweryi* can be distinguished thus: (1) gula setae absent in *C. loweryi* and *C. consobrinus*, dense in *C. nigriceps*, sparse in *C. eastwoodi*; and (2) gaster of *C. consobrinus* is distinctly bicoloured, gasters of *C. eastwoodi* and *C. loweryi* are for the most part uniform yellowish brown colour or vary only slightly in colour from posterior to anterior. Sympatric with *C. consobrinus*, *C. nigriceps* and *C. clarior*.

B. B. Lowery described the appearance of the nest above ground at Hillston, New South Wales, in 1978 in a collection that he donated to ANIC. A mound about 20–30 cm in diameter and 2–4 cm in height is generally constructed away from the tree canopy. The entrance near the centre of the mound is usually circular and decorated with small stones.

Distribution

The species is widespread in south-eastern and eastern Australia (Fig. 26), particularly in semi-arid habitats.

Etymology

This species is named after the Reverend B. B. Lowery SJ.

Fig. 26. *C. loweryi*, known distribution.

Camponotus nigriceps Smith

Formica nigriceps Smith, 1858: 38.
Camponotus nigriceps dimidiatus Roger, 1863: 4, 44.
Camponotus nigriceps Mayr, 1876: 63. — Emery, 1887: 211; Emery, 1925: 103; Burgman *et al.*, 1980: 152 (biology).
Camponotus nigriceps dimidiatus perthiana Forel, 1915: 97. — Crawley, 1922: 35 (male and female).
Camponotus consobrinus perthiana Wheeler, 1933: 33.
Camponotus perthiana Burgman *et al.*, 1980: 152 (biology). — Hölldobler and Engel-Siegel, 1984: 219 (biology); Haskins and Haskins, 1992: 31 (biology).

Material Examined

Types

C. nigriceps: BMNH, 1 worker labelled 'Holotype' from Entomology Club Australia (11.620 Series 11.485). HW = 2·0 mm, HL = 3·2 mm, HT = 2·1 mm, TL = 3·1 mm.

Camponotus nigriceps dimidiatus perthiana Forel: GMNH, Drawer 164, 4 types, 12 cotypes. Major worker: HW = 3·7 mm, HL = 4·0 mm, PW = 2·5 mm, HT = 2·3 mm, TL = 2·45 mm. Minor worker: HW = 1·45 mm, HL = 2·0 mm, PW = 1·1 mm, HT = 1·8 mm, TL = 2·2 mm. From Perth.

Voucher specimens examined

Camponotus sp. no. 1 (ANIC) — Imai *et al.*, 1977; Burgman *et al.*, 1980.
Camponotus sp. no. 2 (ANIC) — Hölldobler and Engel, 1978; Imai *et al.*, 1977.
Camponotus sp. JDMC 182 (ANIC) — Majer, 1983.

Other material examined

Australian Capital Territory: Black Mountain, 1966, I. F. B. Common (ANIC); Canberra, 1959, GFH (ANIC); Long Gully Lane, 1935, TG (ANIC); Red Hill, 1924, G. F. Hill (ANIC). **New South Wales:** Armidale, 1959, FAC (NVMA); Berowra, N Sydney, 1969, RWT (ANIC); Broken Hill, Wankeroo Hs., 1975, BBL (ANIC); Broken Hill, Wilcannia Rd, 1962, RHM (SAMA); Brooklyn, 1938, Little (SAMA); Bulla Bulla Tank, 2 mi E, 1949, TG (ANIC); Callubri Stn, 1949, TG (ANIC); Como, 1922, C. B. (ANIC); Condoblin, Mt Nobby, 1971, D. Andria (SAMA); Euston, 26 km E, 1973, R. J. Kohout (ANIC); Faulcon Bridge, Blue Mtns, 1971, A. Campon (SAMA); Fowlers Gap, 1975, PJW (ANIC); Girilambone, 4 mi SE, 1949, TG (ANIC); Gosford, 1946, J. McAreavey (ANIC); Heathcote, 1914, WMW (SAMA); Hornsby, 1914, WMW (SAMA); Hornsby, Galston Gorge, 1958, TG (ANIC); Ku Ring Gai Chase, 1983, J Gardener (SAMA); Mungindi, 10 mi NE, 1949, TG (ANIC); Narooma, 6 km W, 1939, FAC (NVMA); Narooma, 9 mi W, 1939, FAC (NVMA); Neath, 1990, D. Hirst (SAMA); Nyngan, 49 km W, 1949, J. Boyd (ANIC); Razorback, 1967, RHM (SAMA); Rankin's Springs, 1993, AMA and MAA (SAMA); Ryde, Caravan Pk, 1966, RHM (SAMA); Sutherland, 1914, WMW (SAMA); Sydney, A. M. Lea (SAMA); Trundle, 1964, BBL (ANIC); Weethalle, 1993, AMA and MAA (SAMA nests 72, 73); Wyong, 3 mi NE, 1937, FAC (NVMA). **Queensland:** Ballandean, 2 mi NNE, 1949, TG (ANIC); Beaudesert, S. H. Parlett (ANIC); Brisbane, A. M. Lea (SAMA); Crowsnest, 1966, J. B. Williams (SAMA); Gladstone, A. M. Lea (SAMA); Herberton, 1937, J. B. McAdan (ANIC); Jolly's Lookout, 1962, RWT (ANIC); Karara, 6 mi SW, 1949, TG (ANIC); Maryborough, 1951, TG (ANIC); Millmerran, 1941, J. McQueen (SAMA); Ravenshoe, Millstream NP, 1975, BBL (ANIC); St George, 1965, BBL (ANIC); Tara, 22 mi S, 1962, JED (ANIC); Tumoulin, 1937, TG (ANIC); Walkerston, 1975, BBL (ANIC). **South Australia:** Angorichina, 5·9 km E, 1992, AMA and MAA (SAMA); Arkaroo Rock, 1992, AMA and MAA (SAMA); Blanchetown, 10 km WNW, 1991, VS (SAMA); Blinman, 1992, AMA and MAA (SAMA); Blythe, 1957, BBL (ANIC); Border Village, 8 km SE, 1984, Nullabor Survey (SAMA); Brookfield NP, 1992, J. A. Barry (SAMA); Bullock Dam, 7·6 km NNE, 1992, SOPS (SAMA); Canegrass, 1992, AMA (SAMA); Chowilla Stn, 1994, T. Reardon (SAMA); Coultong, 1992, AMA and MAA (SAMA); Crystal Brook, 1957, BBL (ANIC); Danggali CP, Canopus, 1992, AMA (SAMA); Danggali CP, Jan's Camp, 1992, AMA (SAMA); Danggali CP, Morganvale, 1993, AMA (SAMA nests 56, 57); Danggali CP, Mornington, 1993, AMA (SAMA nests 58, 59); Danggali CP, SE corner, 1989, AMA (SAMA); Danggali CP, Tipperary Dam, 1993, AMA (SAMA); Danggali, Sth entrance, 1994, AMA and JDE (SAMA); Danggali, Mornington T-junction, 1992, AMA (SAMA); Emu, 30 mi WNW, 1960, JED (ANIC); Flinders Ranges, Angorichina, 1992, AMA and MAA (SAMA nests 60, 61); Flinders Ranges, Blinman, 1992, AMA and MAA (SAMA nests 62, 63); Ferries McDonald NP, 1979, EGM (SAMA); Gawler Ra., Scrubby Peak, 4 km SW, 1989, JAF (SAMA); Glossop, Woolmas, 1982, J. Szent-Ivany and M. Szent-Ivany (SAMA); Hartley, 1993, GLH (SAMA); Huon Downs, 5 km NE, 1991, VS (SAMA); Illintjitja, 28·5 km WSW, 1993, PITJ (SAMA); Karkoo, 5·9 km along Lock Rd, 1977, JEF (SAMA); Katarapko, Murray NP, 1991, AMA (SAMA); Kingoonya, 30 km W, 1975, BBL (ANIC); Kyancutta, 1954, NBT (SAMA); Lake Gilles, 1972, B. K. Head (SAMA);

Lamaroo, A. M. Lea (SAMA); Loxton, Paynes Farm, 1991, AMA (SAMA); Loxton, Snodgrass Farm, 1991, AMA (SAMA); Meningie, L. H. Mincham (SAMA); Middle Dam, 1·5 km SW, 1992, SOPS (SAMA); Monarto South, 1991, VS (SAMA); Monarto Zool. Pk, Bretag Scrub, 1993, T. P. Moorley (SAMA); Moonabie, 1992, GLH (SAMA); Moonabie NP, 1992, GLH (SAMA); Mootatunga, 4 km S, 1991, VS (SAMA); Mt Christie Siding, 1987, YS (SAMA); Murray Bridge, 2 km W, 1991, VS (SAMA); Murray Bridge, A. M. Lea (SAMA); Ngarkat NP, 1989, AMA (SAMA); Murray Lands, Coultong, 1992, AMA and MAA (SAMA 64, 65); Pandappa, 1992, SOPS (SAMA); Paney Stn, Kolay Dam, Gawler Ra., 1989, JAF (SAMA); Parachilna, 1909, F. M. Hale (SAMA); Paringa, 11 km NE, VS (SAMA); Peebinga NP, 1992, GLH (SAMA); Peridinya, 5 km SE, 1991, VS (SAMA); Pooginook, 1993, GLH (SAMA); Qualco, 1990, RHF (SAMA); Scrubby Peak, Gawler Ra., 1989, JAF (SAMA); Streaky Bay, 1957, BBL (ANIC); Sutherlands, 1992, AMA and MAA (SAMA); Tarcoola, 7 mi W, 1947, TG (ANIC); Windser, H. B. White (ANIC); Wingoona Hill, 23 km SW, 1992, SOPS (SAMA); Yumbarra NP, Sth boundary, 1988, JAF (SAMA). **Victoria:** Bendigo, 1961, BBL (ANIC); Bendigo, Heathcote, 1961, BBL (ANIC); Broadford, 1934, F. G. Holday (ANIC); Grampians, Halls Gap, Mt Zero Rd, 1989, AMA (SAMA); Hattah, 14·6 km S, 1985, ALY (NVMA); Hattah, 19·2 km SW, 1986, ALY (NVMA); Hattah, 5·4 km E, 1986, ALY (NVMA); Lascelles, 14·5 km NW, 1985, ALY (NVMA); Lascelles, 14·9 km NW, 1987, ALY (NVMA); Lindsay R., at junction with Mullaroo Ck, 1986, ALY (NVMA); Meringur, 1986, ALY (NVMA); Meringur, 10·6 km ESE, 1986, ALY (NVMA); Meringur, 23·5 km WSW, 1985, ALY (NVMA); Meringur, 3·2 km ESE, 1987, ALY (NVMA); Meringur, 9·4 km ESE, 1986, ALY (NVMA); Milewa Sth, Bore, 3·7 km N, 1987, ALY (NVMA); Millewa Sth Bore, 19·4 km N, 1986, ALY (NVMA); Millewa Sth Bore, 22·3 km N, 1985, ALY (NVMA); Milliwa Sth Bore, 3·7 km N, 1985, ALY (NVMA); Milliwa Sth Bore, 7·1 km N, 1987, ALY (NVMA); Murrayville, 13·6 km SSW, 1987, ALY (NVMA); Murrayville, 16·5 km SSW, 1986, ALY (NVMA); Murray Valley Hwy, junction with Annuello Rd, 1986, ALY (NVMA); Patchewollock, 15·8 km NE, 1987, ALY (NVMA); Patho, H. A. Potter (ANIC); Rostron, 1991, AMA (SAMA); Sealake, A. M. Lea (SAMA); St Arnaud, 1991, AMA (SAMA); Swan Hill, 20 mi NW, 1947, TG (ANIC); Underbool, 3 km W, 1959, GFG (SAMA); Walpeup, 12·6 km SE, 1986, ALY (NVMA); Wyperfeld Park, 1929, E. S. Haniks (ANIC). **Western Australia:** Abrakkurrie Cave, 1960, P. Aitken (SAMA); Armadale, JC (ANIC); Balladonia Stn, 1947, TG (ANIC); Bencubbin, 1979, R. P. Mcmillan (SAMA); Bluff Knoll, Stirling Range NP, 1985, PSW (ANIC); Brookton, 1975, A. M. Douglas and M. J. Douglas (WAM); Condinup, 1994, MAA (SAMA); Coolgardie, 53 mi SSW, 1969, RWT (ANIC); Curry, 1900 (Curtin University, Western Australia); Darlington, Greenmount, 1992, AMA and WMA (SAMA); Dryandra State Forest, 1992, MAA (SAMA nest 71); Dryandra State Forest, mallet, 1992, AMA and WMA (SAMA); Dryandra State Forest, NE. entrance, 1993, AMA and WMA (SAMA nests 66, 67); Dryandra State Forest, Wandoo, 1993, AMA and WMA (SAMA); Durakoppin NP, NW corner, 1993, AMA and WMA (SAMA nests 68, 69); Durakoppin NP, in unused meat ant nest, 1993, AMA and WMA (SAMA); Durakoppin NP, 1992, MAA (SAMA nest 70); Durokoppin, La Lobry De Bruyn 1987 (Curtin University, Western Australia); Fraser Range Hs., 34 mi N, 1969, RWT (ANIC); Frenchman Bay, nr Albany, 1973, L. P. Kelsey (ANIC); Kalamunda, 1939, TG (ANIC); Kalgoorlie, 1960, P. Aitken (SAMA); Kalgoorlie, 1976, C. A. M. D. (WAM); Kalgoorlie, 3 km N, 1994, MAA (SAMA); Kambalda, 10 km N, 1982, G. P. Browning (WAM); Karonie, 6 mi W, 1947, TG (ANIC); Kellerberrin NP, 1992, MAA (SAMA); Kurrawang Res., 1988, R. P. Mcmillan (WAM); Meekatharra Granites, in termite mound, 1967, C. Mercovitch (ANIC); Mekatharra, golf course, 1967, C. T. M. (WAM); Mt Ragged, 12 mi W, 1947, TG (ANIC); Nanambinia Stn, 1974, B. Dimer (ANIC); Narregin, 6 km S, 1983, G. P. Browning (WAM); Perth, 62 mi N, 1958, TG (ANIC); Perth, Mjoberg Expedition (ANIC); Pindar, 1963, C. Mercovitch (ANIC); Pingrup, 1958, TG (ANIC); Ravensthorpe, 1947, TG (ANIC); Salmon Gums, 1970, BBL (ANIC); Southern Cross, 70 km E, 1994, MAA (SAMA); Stirling Ra., 1983, G. P. Browning (WAM); Stirling Ra. NP, Nth Boundary, 1993, M. R. Williams (SAMA); Stirling Ranges, 1983, W. Craig (SAMA); Tammin, 1929, TG (ANIC); Tardun, 1963, CTM (SAMA); Weebubbie Cave, 1960, P. Aitken (SAMA); York, 1975, A. Douglas (WAM).

Worker Description

Colour: head black or dark brown sometimes with lighter patches, mandibles and anterior clypeus usually darker, sometimes lighter, mesosoma and node honey colour or light brown sometimes reddish, coxa and femur lighter, tibia and tarsi reddish brown, gaster black to light brown, sometimes posterior is slightly darker than the anterior. Most of head never lighter than most of gaster. Pilosity: to 0·3 mm long plentiful on gula, sometimes sparse on sides of head of major workers but always plentiful in minor workers, to 0·4 mm plentiful on pronotum and mesonotum and >20 on propodeum (Fig. 27*a–d*), plentiful on gaster pointing backwards. Short setae on scapes raised 10–50°, short setae on midtibiae 20–40°. Pubescence: a coat of curved

raised setae about 0·1 mm long, spaced < length, visible on the dorsum of mesosoma, sparse and more adpressed on head. Integument finely reticulate, head and gaster glossy. Node summit viewed from rear: convex or flat sometimes sharply convex in major workers (Fig. 12*c*), flat or weakly convex in other workers. Metanotum usually distinct in major workers.

Measurements

HW = 1·60–4·30 mm; HL = 2·25–4·40 mm; n = 145. TL = 2·70–3·80 mm; n = 21.
TL = 2·47 + 1·92 log HW (n = 21, r = 0·95, s.e.$_y$ = 0·10, s.e.$_x$ = 0·06).
PD:D = 1·5 in major workers increasing to 3·0 in minor workers.

Remarks

Camponotus nigriceps corresponds to genetic group A (Fig. 3, Table 3). In populations of *C. nigriceps* the gaster colour varies from black through browns to yellowish brown and the mesosoma varies from red-browns to yellow. The number of long setae on the propodeum varies from 20 to 100 (Fig. 27*a–d*). Populations resembling *C. nigriceps perthiana* have black gaster and reddish mesosoma with about 40–100 long setae on propodeum. Other populations possess similar pilosity but because of their lighter colour do not fit Forel's description of *perthiana*.

Because some populations of *C. nigriceps* resemble *C. loweryi* and *C. eastwoodi* in colour and pilosity, identification in these cases is only possible by examining minor workers thus: (i) erect setae on gula cover > 50% gula area in *C. nigriceps* (Fig. 10*d*); < 50% in *C. eastwoodi*;

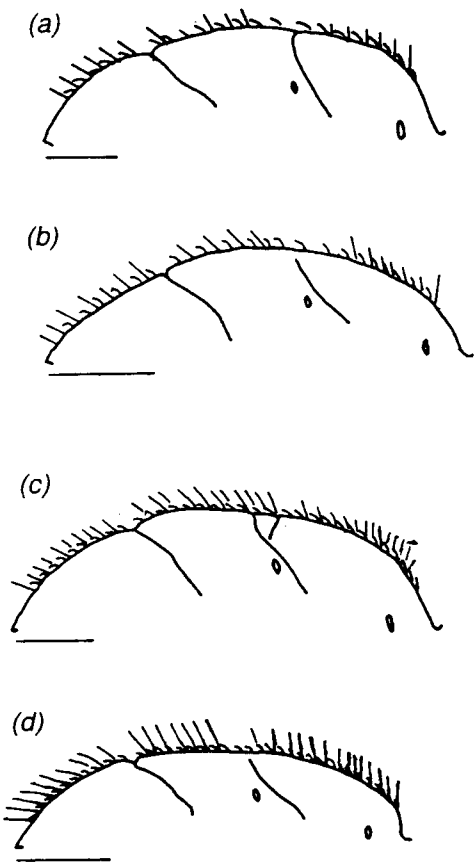

Fig. 27. *C. nigriceps*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker; *c*, major worker, hirsute form; *d*, minor worker, hirsute form. Scale lines = 1 mm.

Fig. 28. *C. nigriceps*, known distribution.

gula setae absent in all castes of *C. loweryi* (similar to Fig. 10*a–b*) and (ii) head sides of smallest minors in dorsal view taper to the rear in *C. eastwoodi* (Fig. 9*c*); *C. loweryi* and *C. nigriceps* parallel (Fig. 9*b*), and rounded in larger minor and medium workers (Fig. 9*a*).

Distribution

The known distribution covers most of Australia excluding the Northern Territory and north Western Australia (Fig. 28). It extends into north Queensland but the paucity of specimens available for examination points to the need for more collection and study.

Etymology

Nigra (Latin: black), cephal (Greek: head). Smith described a specimen possessing a distinctive black head.

Camponotus pallidiceps Emery, stat. nov.

Camponotus nigriceps pallidiceps Emery, 1887: 211. — Wheeler, 1933: 23.

Material Examined

Types. MCG, Drawers 39 and 113, 1 major worker and 1 medium worker each labelled 'typus', many cotypes. Major worker: HW = 3·3 mm, HL = 3·45 mm, PW = 2·0 mm, HT = 2·5 mm, TL = 2·9 mm. Medium worker: HW = 1·5 mm, HL = 2·85 mm, PW = 1·3 mm, HT = 1·2 mm, TL = 2·4 mm. D'Albertis collection, 1873, from Mount Victoria, New South Wales.

Other material examined. **New South Wales:** Blackheath, 1966, BBL (ANIC); Blue Mtns, H. J. Carter (ANIC); Cowan, 1959, BBL (ANIC); Hazelbrook, 1935, TG (ANIC); Lawson, 1977, BBL (ANIC); Leura, 1914, WMW (SAMA); Mt Duval, Armidale, 1973, FAC (ANIC); Mt Victoria, 1970, BBL (ANIC); Mt Victoria, 1993, AMA and MAA (SAMA nests 1–5); Mt Wilson, 1959, FAC (NVMA); Nowra, Mt Camberwarra, 1969, BBL (ANIC); Wentworth Falls, 1976, BBL (ANIC).

Worker Description

Colour: brown with lighter patches on head and mesosoma, mandibles and anterior clypeus darker, legs and node lighter, gaster black or dark brown. Pilosity: up to 0·35 mm long, plentiful on pronotum and mesonotum and 8–15 on propodeum (Fig. 29*a–b*), on gula sparse sometimes obsolete, plentiful on gaster pointing backwards, short setae on scapes raised < 10°, short setae on midtibiae 20–40°. Pubescence: a coat of curved raised setae about 0·1 mm long, spaced < length, visible on the dorsum of mesosoma, sparse on head. Integument finely reticulate, head and gaster glossy, reflectivity from mesosoma reduced by pubescence. Node summit viewed from rear: usually concave in major workers (Fig. 15*a*) but sometimes flat, flat or slightly convex in other workers. Metanotum usually distinct in major workers.

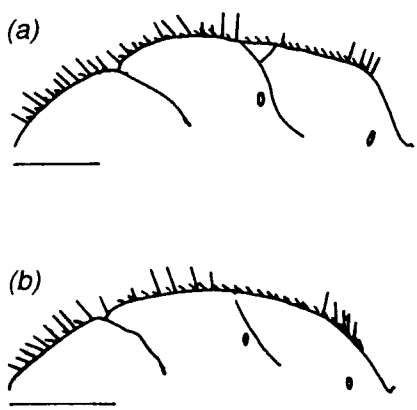

Fig. 29. *C. pallidiceps*, lateral view mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

Measurements

HW = 1·60–3·20 mm; HL = 2·15–3·15 mm; TL = 2·30–2·90; $n = 20$.
TL = 2·06 + 1·77 log HW ($n = 19$, $r = 0·87$, s.e.$_y = 0·16$, s.e.$_x = 0·07$).
PD:D = 1·5 increasing to 3·0 in minor workers.

Remarks

Camponotus pallidiceps corresponds to genetic group I (Fig. 3, Table 3). Most of the largest major workers possess a distinctive scalloped summit of the node when viewed from the rear (Fig. 12a). As worker size decreases this scallop fades with the summit becoming flat or slightly convex. Sometimes *C. consobrinus* displays a feeble scallop at the node summit. It can be separated from *C. consobrinus* by gula setae which are sparse in *C. pallidiceps* particularly in minor workers and absent in *C. consobrinus*.

Distribution

The known distribution is centred on the Blue Mountains of New South Wales, with a single collection from the Armidale region (Fig. 30).

Etymology

Pallidus (Latin: pale or pallid) and cephal (Greek: head). Presumably, Emery considered this species to be a pale headed subspecies of Smith's black-headed *C. nigriceps*.

Fig. 30. *C. pallidiceps*, known distribution.

Camponotus prostans Forel, new status

Camponotus nigriceps obniger prostans Forel, 1907: 301 (unavailable infra-subspecific name).
Camponotus nigriceps prostans Forel, 1910: 72 (first available usage).
Camponotus prostans Taylor, 1986: 14.

Material Examined

Types. GMNH, 1 major worker, 1 minor worker, many cotypes. Major worker: HW = 3·1 mm, HL = 3·1 mm, PW = 2·0 mm, HT = 2·1 mm, TL = 2·6 mm. Minor worker: HW = 1·65 mm, HL = 2·1 mm, PW = 1·3 mm, HT = 1·3 mm, TL = 2·1 mm.

Other material examined. **Western Australia:** Albany, TG (ANIC); Albany, 15 mi NE, 1947, TG (ANIC); Albany, 30 mi NE, 1947, TG (ANIC); Bridgetown, 1938, M. F. Day (ANIC); Bridgetown, 5 km S, 1994, MAA (SAMA); Canning Dam, 11 km NW, 1992, MAA (SAMA nest 36); Canning Dam turnoff, 1994, MAA (SAMA); Cape Legrande NP, 1993, AMA and WMA (SAMA nests 37–41); Denmark, 1938, M. F. Day (ANIC); Denmark, 11 mi N, 1969, RWT (ANIC); Dryandra State Forest, wandoo woodland, 1993, AMA and WMA (SAMA); Esperance, 1970, BBL (ANIC); Esperance, 1969, BBL (ANIC); Esperance, 40 mi W, Coonalbridgup Swamp, 1969, BBL (ANIC); Grass Patch, 25 km W, 1989, AMA (SAMA); Midland, Perth, 1969, FAC (NVMA); Mt, Burdette, 1988, AMA (SAMA); Mt Clare, 4 mi W, Walpole, 1969, RWT (ANIC); Mundaring, JC (ANIC); Nannup, 5 km W, 1982, W. Craig (ANIC); North Bannister, in termite mound, 1992, AMA and WMA (SAMA); Ongerup, 5 km E, 1994, MAA (SAMA); Perth, JC (ANIC); Pingrup, TG (ANIC); Porongurup, 40 km NE, 1994, MAA (SAMA); Ravensthorpe, 49 mi WSW, 1947, TG (ANIC); Stirling Ra., Mt Trio, 1969, RWT (ANIC); Stirling Ra. NP, Moingup Spring, 1985, PSW (ANIC); Torbay, 1905, Hamburg Expedition (ANIC); Yornup, 8 km S, 1994, MAA (SAMA).

Worker Description

Colour: head black to dark brown; mesosoma colour ranges from black all over to reddish brown all over, some specimens with combinations of above colours; legs lighter, often yellowish; posterior gaster black or dark brown, anterior gaster colour similar to posterior gaster

or like most of mesosoma. Pilosity: up to 0·5 mm long plentiful on pronotum and mesonotum with 2–8 on propodeum (Fig. 31*a*, *b*), sparse and shorter on gula sometimes obsolete, plentiful on gaster pointing backwards, short setae on scapes raised to 30°, short setae on midtibiae 20–40°. Pubescence: a coat of suberect setae about 0·1 mm long, spaced < length, usually whitish, visible with transmitted light on the dorsum of mesosoma; adpressed and sparse on head. Integument finely reticulate, glossy. Node summit viewed from rear: convex or flat in major workers, convex in other workers. Metanotum usually distinct in major workers.

Measurements

HW = 1·80–3·5 mm; HL = 2·30–3·45 mm; TL = 2·60–3·00 mm; $n = 20$.
TL = 1·89 + 2·22 log HW ($n = 11$, $r = 0{\cdot}95$, $s.e._y = 0{\cdot}17$, $s.e._x = 0{\cdot}04$).
PD:D = 2·0 in major workers increasing to 3·0 in minor workers.
HW:HL = often reaches 1·05 in major workers where HW > 3·4 mm.

Remarks

Camponotus prostans corresponds to genetic group G (Fig. 3, Table 3). It possesses a few setae on gula, and is distinguished from Western Australian *C. longideclivis* and eastern Australian *C. consobrinus* by the absence of setae on the gula in the latter two species. In dorsal view, the heads of the largest major workers in *C. prostans* appear circular, as a consequence of HW being greater than HL.

Distribution

The known distribution is confined to the south-west of Western Australia (Fig. 32).

Etymology

Presumed from prosto (Latin: outstanding) as the colour of the subspecies type is much darker than that of the type, *C. nigriceps*.

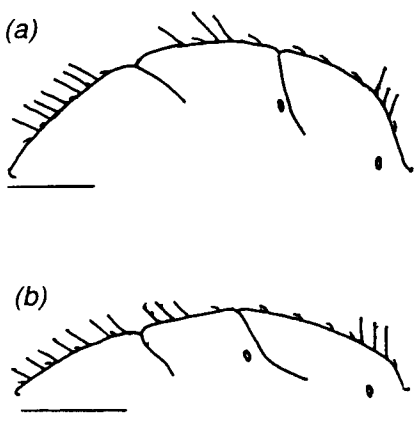

Fig. 31. *C. prostans*, lateral view of mesosoma dorsum. *a*, Major worker; *b*, minor worker. Scale lines = 1 mm.

Species Excluded from the *C. nigriceps* Species-group

Camponotus nigriceps lividipes Emery

Camponotus nigriceps lividipes Emery, 1887: 211. — Forel, 1907: 302 (species incerta sedis).

Material Examined

Type. MCG, Drawer 113, 1 major worker from Australia, 1 medium worker, damaged. Major worker: HW = 2·45 mm, HL = 2·5 mm, PW = 1·5 mm, HT = 2·5 mm, TL = 2·0 mm. From Adelaide, D'Albertis collection, 1873, New South Wales.

Fig. 32. *C. prostans*, known distribution.

Remarks

The clypeus of *C. nigriceps lividipes* resembles *C. testaceipes*, where the anterior margin is more straight and dissimilar to the concave anterior margin of the *C. nigriceps* group. *C. nigriceps lividipes* is therefore not included in this revision.

Discussion

Prior to this study, the *C. nigriceps* group within the genus *Camponotus* was in a state of some disarray, with the existence of several named species plus a number of subspecies and 'races'. This paper presents morphological and electrophoretic evidence for the existence of nine species within the *C. nigriceps* group, and provides a detailed description of each species, including its known geographic distribution. A number of significant taxonomic changes has resulted, most notably the recognition of four new species, *C. eastwoodi, C. dryandrae, C. longideclivis* and *C. loweryi.* In addition, the subspecies *clarior* and *pallidiceps* have been elevated to full species whilst two others *obniger* and *perthiana* have been included within the wide-ranging species *C. consobrinus* and *C. nigriceps* respectively. As a result, the taxonomy of the group is now underpinned by a solid systematic framework, and includes a simple key that will assist field biologists in obtaining reliable identification. The morphological data for the key characters used to diagnose the nine species in the *C. nigriceps* group are summarised in Table 4.

It is necessary to emphasise that for accurate identification of these species, the key requires that both major workers as well as minor workers be available for examination. Although both major and minor workers may be taken with certainty from nests, the probability of taking major workers at a distance from the nest is low. Thus, this key may not be completely satisfactory to the field biologist attempting to identify a catch from pitfall traps installed outside the range of major workers. Nevertheless, the use of the characters listed in Table 4 in conjunction with the key should allow researchers to identify workers from all castes in most circumstances.

Ants formerly ascribed to the subspecies *C. n. lividipes* have been shown to not belong to the *C. nigriceps* group, as the deeply notched clypeus (which is diagnostic for the group) is lacking in the type specimen (also observed by Forel 1907). Unfortunately, we were unable to recognise any specimens referable to this form in museum collections nor collect any material for allozyme analysis. As such it was not possible to independently assess whether the original placement of *C. n. lividipes* within the *C. nigriceps* group was simply an error or indicates that the character state identifying the group is not totally diagnostic.

Indirect support for the monophyly of the nine species within the *C. nigriceps* group comes from the estimates of genetic divergence obtained in this study. Species differ from one another at 6–31% of their loci (comparable to a Nei D range of 0·10–0·38), a result consistent with the expectations for a recently evolved lineage (Thorpe 1983; Richardson *et al.* 1986). Indeed, some of the species are genetically and morphologically so similar to others in the group that interspecies hybridisation should be considered a possibility. Nevertheless, there is no indication of such happenings in those areas where two or more species co-exist, with up to four species being found in some regions (e.g. *C. nigriceps*, *C. loweryi*, *C. consobrinus* and *C. clarior* in Danggali Conservation Park, South Australia). An earlier allozyme study of 12 loci by Burgman *et al.* (1980) on nine taxa of *Camponotus* (including the following representatives of the *C. nigriceps* group: *C. consobrinus*, 'sp. no. 16'; 'sp. no. 1', identified herein as *C. nigriceps*; and 'sp. no. 2, identified herein as *C. eastwoodi*), also provides support for the monophyly of the *C. nigriceps* group. Nothing more can be made of comparisons between the results of Burgman *et al.* (1980) and this study, as only 5 of the loci are common to both data sets.

The concordance between the morphological and allozyme analyses presented here is considerable. Seven of the nine species are diagnosable using the allozyme data alone, whilst the remaining two species are genetically divergent in allopatry. All nine species are morphologically distinct, although the differences are sometimes subtle, again reflecting a probable recent origin for the group. A coordinated morphological and molecular approach to systematic revisions has been used successfully for ants in the past (e.g. Ward 1980; Greenslade and Halliday 1982; Ross and Trager 1990). Such an approach represents a sensible first step when undertaking a revision of any group that may consist of a species complex, regardless of the organism involved (Richardson *et al.* 1986; Donnellan *et al.* 1993).

One of the often unstated but critical factors in undertaking a proper systematic revision of a group is the comprehensiveness of the analysis being undertaken. Many systematic assessments are much too superficial in terms of the numbers of independent characters employed to be able to detect anything other than the most obvious within-group dichotomies. With respect to allozyme electrophoresis, studies on ants have often not been able to extend the range of characters examined much beyond 18 loci (Packer and Owen 1992). This study demonstrates that considerable resolution can be obtained within recently evolved groups, provided that the technical difficulties associated with scoring sufficient numbers of enzyme loci can be overcome. To illustrate this, the sympatric species *C. longideclivis* and *C. prostans* show diagnostic allozyme differences at only 2 loci out of the 32 characterised; their genetic distinctiveness may not have been apparent if say only 16 loci had been assessed. In a similar light, the disparity between early revisions of the *C. nigriceps* group (e.g. Wheeler 1933) and the revision presented here reflects in part the greater number of morphological characters surveyed in this study.

Whilst the primary purpose of the allozyme data has been to assist in the delineation of species boundaries in this study, two within-species genetic trends emerge that are worthy of comment. Firstly, the values for within-population genetic variability, as assessed by heterozygosity estimates, can readily be compared with those obtained in other studies. The observed heterozygosity (H) estimate averaged over all species in the *C. nigriceps* group is 0·056 ± 0·010, with values ranging from 0·009 to 0·084. This range of values is typical of that encountered for the Hymenoptera. For example, Crespi (1991), in summarising H values for 58 species, provides an average H for the Hymenoptera of 0·048 ± 0·035 (range 0·000–0·167), whereas Halliday (1981) calculated an average H for 50 species of Hymenoptera as 0·036 (range 0·000–0·084). Species of Hymenoptera are, however, typically less variable than the insects as a whole, where H values average about 0·100 ± 0·09 (Nevo *et al.* 1984). This

outcome, whilst suggesting that it may be difficult to find enough variable loci to conduct detailed studies of the population genetics of individual species of ant, does at least indicate the utility of allozyme data to systematics, where the existence of within-species genetic variation can complicate matters considerably. Haplodiploidy and eusociality have been suggested on theoretical grounds to lead to lower levels of variability (Pamilo and Crozier 1981) although other factors have been implicated (Crespi 1991). Any detailed assessment of our data in this area is beyond the scope of this revision, particularly since the numbers of animals sampled per nest are inadequate to facilitate population genetic analysis.

The second within-species phenomenon of note is the generally high level of genetic similarity between nests across the range of individual taxa. With the single exception of *C. nigriceps*, species with significant geographic distributions exhibited little or no genetic divergence over their ranges. *C. nigriceps* displayed both genetic and morphological heterogeneity between Western Australian, South Australian and eastern populations, although this heterogeneity did not correlate with the existence of a 'perthiana' form. The finding that most species show little genetic divergence across their geographic range may be a reflection of recent extensions in the range of these species, perhaps as the rangelands have become more arid in the Quaternary (Cranston and Naumann 1991). Certainly, species such as *C. consobrinus* are adept at colonising city habitats such as gardens and parks, places that could be considered 'disturbed' habitats.

This study has presented comprehensive molecular and morphological evidence for the existence of nine biological species within the *Camponotus nigriceps* group. As such it represents a useful baseline study that will facilitate the future documentation of any ecological and behavioural differences which may exist between species. In time any such differences will help field biologists to further identify species within the group, and allow a natural history profile to be built up for each species. Whilst we hesitate to put too many superficial observations of behaviour and ecology into the literature at this early stage, nevertheless a few comments may assist others to further explore the significance of the practices involved. With regard to nest structure, Lowery described (on a label in ANIC) the mound-like form of the construction above ground and the small stones used to decorate the entrances in *C. loweryi*. Whilst our observations on this species support Lowery's notes, we have yet to see this phenomenon for the nests of any other species in the group. In addition, colonies of *C. nigriceps* and *C. clarior* at Danggali Conservation Park practice soil transport and the construction of cones of soil as part of their nesting behaviour. This practice has not been observed elsewhere. With regard to another behavioural trait found within the *C. nigriceps* group, larvae of the butterfly *Ogyris* spp. (Lepidoptera: Lycaenidae) are known to have a mutualistic relationship with at least three of the nine species namely *C. consobrinus* (Fisher 1978), *C. nigriceps* (R. Fisher, personal communication) and *C. eastwoodi* (R. Eastwood, personal communication). Whether this reflects a species-specific character within the *C. nigriceps* group, or simply the distribution of the butterfly, remains to be determined. These and other observations may be able to be included in an expanded key in the future.

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