Systematic status of *Plectroctena mandibularis* Smith and *P. conjugata* Santschi (Hymenoptera: Formicidae: Ponerini)

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Plectroctena mandibularis Smith is the type species of *Plectroctena* F. Smith. Because there has been some doubt about its distinctness from *P. conjugata*, several techniques were used to assess the systematic status of the two species. Most crucially, several colony series contained workers of both phenotypes, and where these series included queens or males, the distinguishing feature of these specimens was not consistently related to those of the workers. Queens, males and workers did not manifest qualitative differences between the taxa, and morphological variation was continuous between the two. The putative morphological basis (funicular index) for distinguishing workers of the taxa arose from allometric variation. Putatively diagnostic colour variation in males was related to latitude, but no simple pattern of morphological variation could be correlated with geographical distribution. *Plectroctena conjugata* is therefore considered a junior synonym of *P. mandibularis*.

Key words: Ponerinae, systematics, morphometrics, biogeography, southern Africa.

INTRODUCTION

The genus *Plectroctena* F. Smith, 1858, was described to accommodate *P. mandibularis* Smith, 1858. This species has been difficult to distinguish from *P. conjugata* Santschi, 1914, the workers of which were distinguished from those of *P. mandibularis* by being smaller and having funicular segments 3–5 shorter than wide, rather than longer than wide (Table 1). Queens of *P. conjugata* apparently differ from *P. mandibularis* in being smaller, with proportionally shorter mandibles; males have a black gaster, while *P. mandibularis* males are yellow, orange-brown or reddish (Table 1).

Arnold (1926) synonymized *P. conjugata* with *P. mandibularis* on the basis that 'An examination of a specimen [of *conjugata*] sent to me by the author [Santschi] shows that it does not differ from the small variety of *mandibularis*, which is found in the coastal regions of the eastern part of the Cape Province. The species becomes progressively larger the further it is from the coast, and a complete transition series can be found from the smallest (Durban, etc.) to the largest or typical *mandibularis*, such as is found in Rhodesia'. Bolton (1974) treated the taxa as distinct, with the *caveat* that 'I am not convinced that the two actually represent distinct species ... the question of whether *conjugata* is a distinct species cannot be settled satisfactorily at present, and a decision must await the amassing of more specimens of all three castes'. In particular, only three males of *conjugata* were available to Bolton for examination.

Geographic variation and small samples have consequently confounded systematic assessment and, as the behaviour of these southern African taxa is attracting contemporary attention (Villet *et al.* 1984; Peeters & Crewe 1988; Villet 1989, 1991), clarification of their systematic status is essential.

MATERIAL AND METHODS

Material in the Albany Museum, Grahamstown (AMGS), Durban Museum (DMNH), National Collection of Insects, Pretoria (SANC), Transvaal Museum, Pretoria (TMSA), and South African Museum, Cape Town (SAMC), was examined. Specimens from the same nest (*i.e.* a nest series) were assumed to belong to the same species. Several nest series contained different castes and sexes. Caste was determined by the presence of ocellar vestiges in the form of two pits at the sites of the lateral ocelli in queens (Bolton 1974). Additional collections mentioned in the list of synonyms are the Natural History Museum, London (BMNH), Museum National d'Histoire Naturelle,

Table 1. Putative diagnostic features of *Plectroctena mandibularis* and *P. conjugata* (after Bolton 1974).

	P. conjugata	*P. mandibularis*
Worker head length	<3.0 mm	>3.0 mm
Worker eye length	0.32–0.38 mm	0.38–0.52 mm
Queen head length	<4.0 mm	>4.0 mm
Queen mandibular index	<83	>83
Queen scape length	<2.8 mm	>2.9 mm
Funicular segments 3–5	Annular, shorter than wide	As long or longer than wide
Striae on gula	Covering anterior half of gula	Covering whole gula
Male gaster	Black	Red-brown to orange

Paris (NHM), Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ), Musée Royal de l'Afrique Centrale, Tervuren (MRAC), and Naturhistorisches Museum, Basel (NMB).

Quantitative variation in males, workers and queens was determined phenetically using morphometric measurements of 180 workers, 18 queens and 40 males. The morphometric variables were primarily those suggested and defined by Bolton (1974). In the case of workers and queens the measurements were head length (HL), mandibular length (ML), scape length (SL), maximum ocular diameter (OD), petiole length (PL), dorsal petiole width (DPW), length of funicular segment 4 (FSL) and width of funicular segment 4 (FSW); in males they were head length, head width, mandible length, eye length, mandible width, clypeus width and mesonotum length. The pigmentation of gasters of males was scored as orange/yellow (1), brown (2), brown-tipped (3) or black (4). Bolton (1974) also proposed and defined several ratios, the most important of which are the mandibulo-cephalic index (MI = ML/HL), for separating queens, and the funicular index (FI = FSL/FSW), for discriminating between workers (Table 1).

Measurements were log-transformed to linearize allometric variation, and analysed using principal component analysis and regression. Geographic patterns in quantitative variation and pigmentation were examined by canonical correlation analysis, using latitude and longitude as measures of geographical location.

RESULTS AND DISCUSSION

Colony membership

As specimens from the same nest series can be assumed to belong to the same species, an examination of intranidal variation was important in this study. Based on the distinguishing traits listed in Table 1, 13 (28 %) of the 47 nest series contained workers of both *P. mandibularis* and *P. conjugata*. Instances of this can be seen in Fig. 1, where the identity of specimens was decided on the basis of the mean funicular index of the colony series. Several worker specimens from *P. conjugata* colonies have funicular indices above 100, and even more specimens from *P. mandibularis* colonies have indices below 100. Revising the critical FI did not resolve the contradiction. Similar unresolvable contradictions arose from using head length or eye length to identify (presumably) related workers.

Regressing FI against head length as a measure of body size (Fig. 1) yielded a significant allometric relationship ($F = 394.6$; $P = 0.000$; $R^2 = 0.69$). The use of ratios such as funicular index to separate taxa is based on the implicit assumption that a ratio expressed shape independent of size. That this is not always true (Bookstein 1989) is evident in this case.

Four of the six queens associated with workers had morphological traits (mandibulo-cephalic indices, head length and/or scape length (Table 1)) that would place them in a different species from the workers. Similarly, five of the six males with black gasters (putative *P. conjugata*) were associated with *P. mandibularis* females. Colony membership therefore contradicted most putative distinguishing traits.

Morphometric variation: workers

Since other discriminatory traits could exist, it was also necessary to further test for the subdivision of the sample of ants using characters that have proved useful for other members of the genus (Bolton 1974).

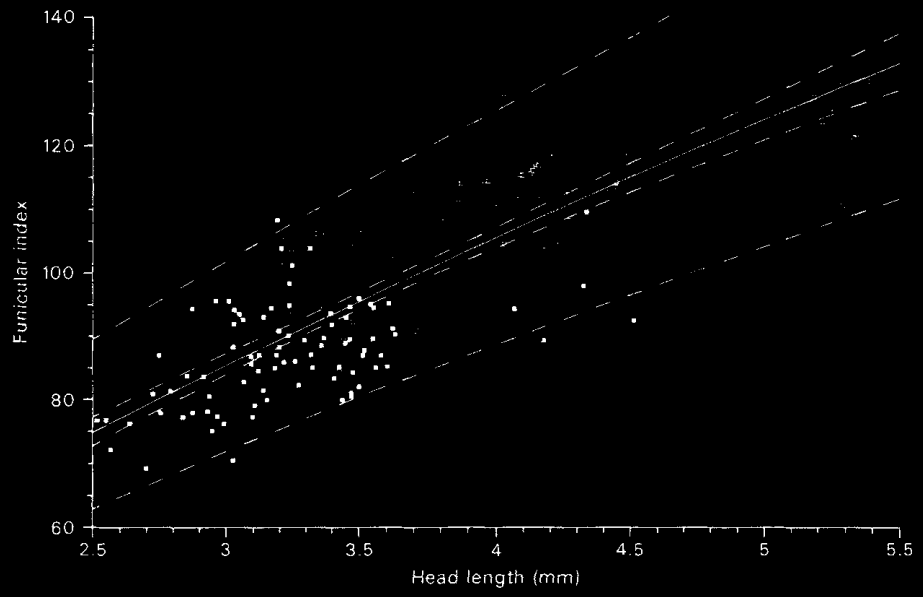

Fig. 1. Allometric regression of funicular index on head length for workers of *Plectroctena mandibularis* (⊐) and *P. conjugata* (■). $R^2 = 0.69$.

Table 2. Pearson's correlations of the first two components of a principal component analysis of worker morphology with each of the morphometric variables and with the funicular index for workers of *Plectroctena mandibularis* and *P. conjugata*.

Variable	PC1	r_1	$P(r_1 = 0)$	PC2	r_2	$P(r_2 = 0)$
Log_{10}(head length)	0.365	0.9863	0.0000	−0.048	−0.0227	0.7621
Log_{10}(mandible length)	0.358	0.9686	0.0000	−0.147	−0.0703	0.3484
Log_{10}(scape length)	0.360	0.9742	0.0000	−0.048	−0.0232	0.7575
Log_{10}(eye length)	0.333	0.9013	0.0000	0.891	0.4257	0.0000
Log_{10}(petiole length)	0.357	0.9638	0.0000	0.017	0.0082	0.9134
Log_{10}(dorsal petiole width)	0.360	0.9723	0.0000	−0.030	−0.0141	0.8505
Log_{10}(funicular segment length)	0.355	0.9605	0.0000	−0.348	−0.1664	0.0256
Log_{10}(funicular segment width)	0.338	0.9146	0.0000	−0.240	−0.1147	0.1254
Funicular index		0.8486	0.0000		−0.107	0.0435

Principal component analysis carried out on the measurements of 180 workers showed only one significant axis ($E_1 = 7.3$; $E_2 = 0.2$), which summarized 91.3 % of the variation. The second axis explained only a further 2.85 % of the variance and failed to separate the taxa (Fig. 2). The separation of the traditional taxa along the first axis was quite marked, although discrete groups were not formed (Fig. 2). The component weights of the first axis (Table 2) were all similar, and correlated highly and significantly with every original variable (Table 2). Only eye length and funicular segment length were significantly, but weakly, correlated with the second component (Table 2). Funicular index was significantly correlated with both components, although the degree of correlation with the second component was poor, and its correlation with the first component was weaker than that of the original variables.

In morphometric studies, the first axis of a principal component analysis of log-transformed data is generally an expression of size, and the second axis can be interpreted as a size-free expression of shape if all the original variables show similar, high correlations with the component scores (Bookstein 1989). Since they do so in this study (Table 2), the second axis suggests that workers of the two taxa are the same shape.

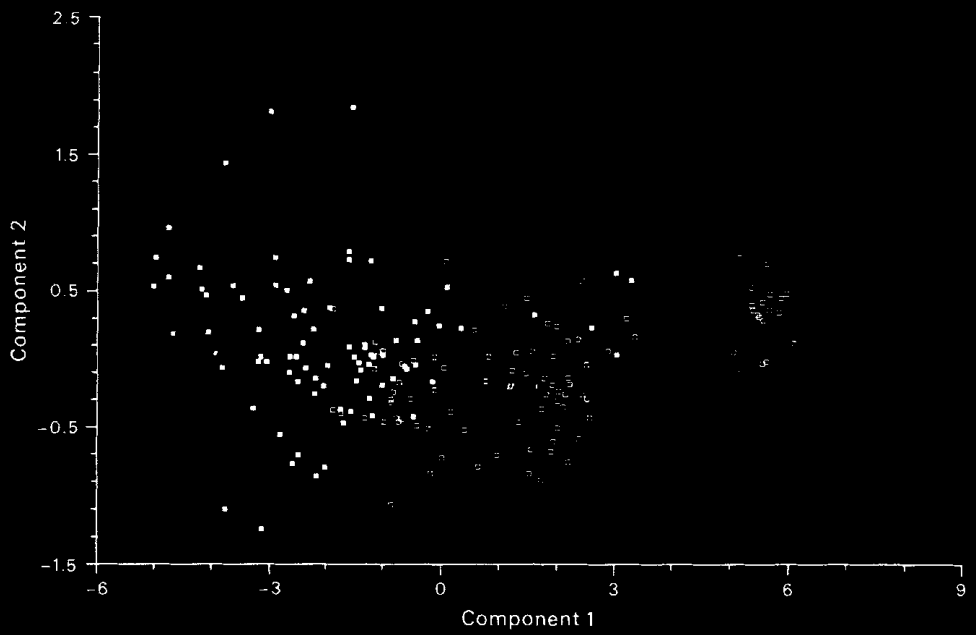

Fig. 2. Scatter diagram of the first two axes of a principal component analysis of the morphology of workers of *Plectroctena mandibularis* (□) and *P. conjugata* (■).

The geographical distribution of samples of workers covered most of the eastern half of southern Africa (Fig. 3), allowing an assessment of Arnold's (1926) hypothesis of geographical size variation. The first axes of a canonical correlation analysis showed strong positive loadings for both latitude and longitude, but a high score for petiole length only (Table 3); the loadings of the remaining measurements were of similar, small magnitude and of mixed sign (*i.e.* variously positive and negative). The morphological axis showed a separation of the taxa (Fig. 4) similar to that on the first axis of the principal component analysis (Fig. 2), with *P. mandibularis* generally scoring higher than *P. conjugata*. However, the canonical correlation was only 0.62, and no marked geographical trend emerged (Fig. 4). The second axes showed weaker correlation (Table 3), with a strong loading for latitude but not longitude, and emphasis on funicular segment length and eye length. This pattern parallels the results of the principal component analysis, indicating that the second principal component summarizes geographical variation, and implying that that variation is small relative to the overall variation in the sample.

Morphometric variation: queens

The 18 queens formed a single, diffuse cluster when the first two axes of the principal component analysis were plotted against one another. The first axis differentiated specimens on size, but characterized only 68.4 % of the total variation. The second axis had a high weighting (0.8) for eye length, but failed to distinguish the taxa. The remaining details of the analysis were similar to

Table 3. Results of canonical correlation analysis of morphology and sample location for workers of *Plectroctena mandibularis* and *P. conjugata*.

	CV1	CV2
Eigenvalue	0.3827	0.1974
Canonical correlation	0.6186	0.4442
Wilk's lambda	0.4955	0.8026
Chi-square	121.12	37.92
d.f.	16	7
P	0.0000	0.0000
Coefficients		
Log_{10}(head length)	−0.36162	0.67113
Log_{10}(mandible length)	0.24693	−0.98377
Log_{10}(scape length)	−0.34650	−0.09114
Log_{10}(eye length)	−0.38172	−1.48553
Log_{10}(petiole length)	2.34857	−0.66132
Log_{10}(dorsal petiole width)	−0.60227	0.99401
Log_{10}(funicular segment length)	−0.65837	1.70958
Log_{10}(funicular segment width)	0.50363	−0.13773
Latitude	1.20386	0.96842
Longitude	1.54448	−0.04097

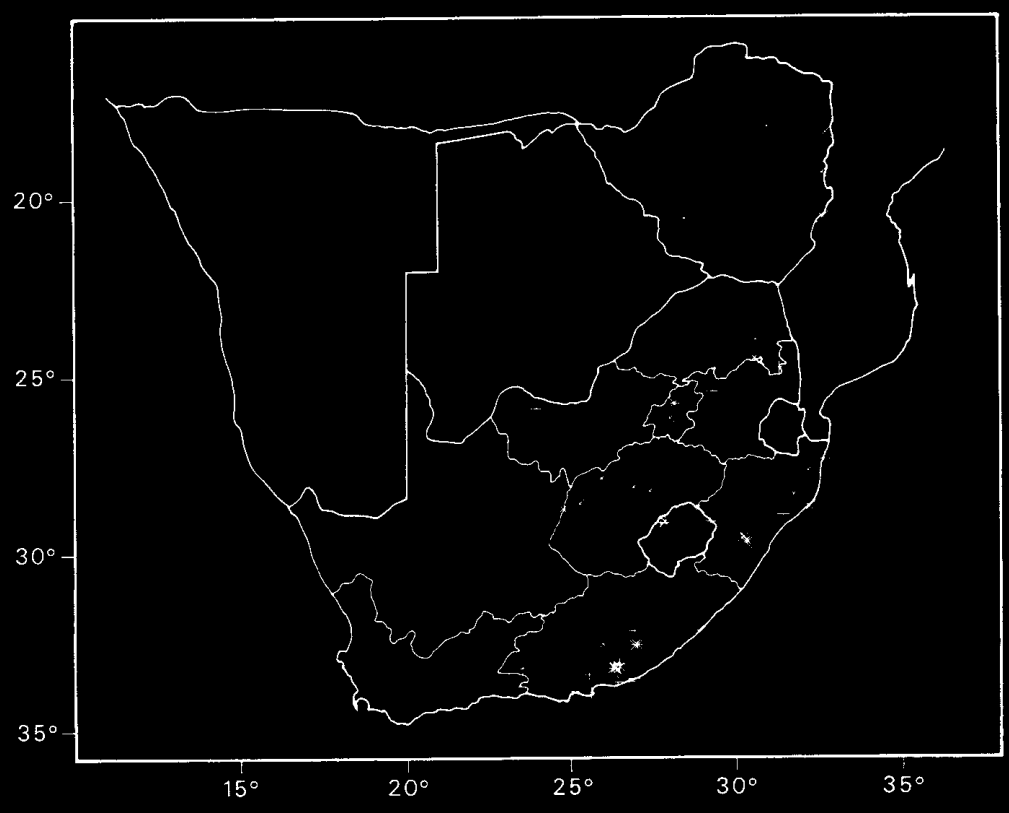

Fig. 3. Geographical distributions of samples workers of *Plectroctena mandibularis* (+) and *P. conjugata* (×).

those concerning the analysis of workers. FI and MI were significantly but weakly correlated with the first and second axes respectively ($r_{FI} = 0.65$; $r_{MI} = -0.51$), implying that they are poor indices of general morphology. For these reasons, no distinguishing features were identified.

Samples of queens were collected from most of southeastern Africa (Fig. 5). Canonical correlation analysis found no significant sets of axes relating morphology to distribution ($\Lambda_1 = 0.13$; $\Lambda_2 = 0.47$; $P > 0.10$ for both sets of axes).

Morphometric variation: males

A plot of the first two axes of a principal component analysis of the morphological measurements of 40 males showed only one spheroidal cluster, with the two taxa thoroughly mixed. The first axis had an eigenvalue of 2.9, accounting for 36.2 % of the variation. It was not uniformly or strongly correlated with the original variables. Abdominal pigmentation and clypeus width dominated the second axis with absolute weightings of 0.51, but did not correlate strongly with the associated component scores.

Males were sampled from across their southern African range (Fig. 6). Only the first axes of a canonical correlation analysis of their morphology and coloration with geographical location was significant (Table 4). The first axes emphasized latitude and gaster coloration, with very small loadings of mixed sign for the other variables (Table 4), so that only a strong latitudinal trend in gaster colour was revealed. Such trends are not rare *within* species of southern African wasps and bees (Steele *et al.* 1998; C.D. Eardley 1983, pers. comm.; F.W. Gess, pers. comm.), which suggests a common underlying environmental effect.

TAXONOMIC CONCLUSION

Intranidal morphological variation contradicts the traditional means of distinguishing *P. mandibularis* from *P. conjugata*, since representatives of both taxa may occur in the same nest. This conclusion is supported by the lack of categorical distinction between them in the principal component analysis of males. Only in the workers and queens was there a degree of differentiation between the taxa, and this is attributable to body size and its effect on allometric variation. There was also no coherent geographical differentiation of the taxa besides latitudinal variation in the gaster colour of males. No categorical variation in the structure of

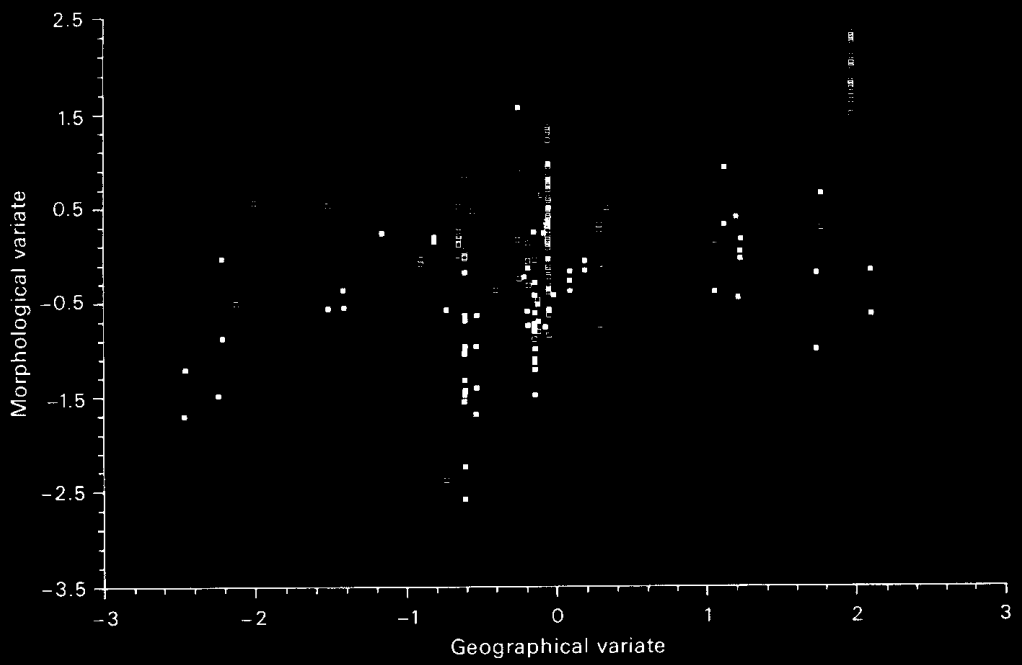

Fig. 4. Scatter diagram of the first canonical axes derived from canonical correlation analyses of the morphology and geographical location of samples of workers of *Plectroctena mandibularis* (❑) and *P. conjugata* (■).

the male genitalia could be found (Robertson, unpubl.). *Plectroctena conjugata* Santschi, 1914 is consequently relegated to synonymy of *P. mandibularis* F. Smith, 1858. The synonymy of *P. mandibularis* is therefore as follows.

Table 4. Results of canonical correlation analysis of morphology and sample location for males of *Plectroctena mandibularis* and *P. conjugata*.

	CV1	CV2
Eigenvalue	0.5801	0.1260
Canonical correlation	0.7617	0.3550
Wilk's lambda	0.3669	0.8740
Chi-square	33.586	4.513
d.f.	16	7
P	0.0062	0.7191
Coefficients		
Abdomen colour	0.93981	0.19334
Log_{10}(head length)	–0.30739	0.20642
Log_{10}(head width)	0.17712	–1.15098
Log_{10}(mandible length)	0.07094	0.07119
Log_{10}(eye length)	–0.13843	–0.18159
Log_{10}(mandible width)	0.15749	0.01367
Log_{10}(clypeus width)	–0.18025	0.20776
Log_{10}(mesonotum length)	–0.20999	–0.03976
Latitude	1.03211	0.46879
Longitude	0.07253	1.13126

Plectroctena mandibularis Smith

Plectroctena mandibularis F. Smith, 1858: 101, pl. 7, figs. 1–5. Syntype queen (ergatoid) and male, SOUTH AFRICA: Natal, Durban, Gueinzius (BMNH).

Ponera caffra Spinola, 1851: 53 (attributed to Klug). (*Nomen nudum;* material referred to *mandibularis* by Roger 1861: 41).

Plectroctena caffra st. *major* Forel, 1894: 74. Holotype queen (not worker as stated), MOZAMBIQUE: Delagoa, P. Berthoud (NHM). (Synonymy by Emery 1899: 469.)

Plectroctena minor st. *conjugata* Santschi, 1914: 8. Syntype workers and queen (ergatoid), SOUTH AFRICA: Natal, Stamford Hill, Charlestown, 30.iv.1905, and Zululand, I. Trägårdh (MCZ, MRAC, NMB). (Raised to species by Santschi 1924: 166; maintained as species by Bolton 1974: 326). Syn. n.

Plectroctena mandibularis var. *integra* Santschi, 1924: 161. Syntype worker, KENYA: Nairobi, Wa Kikongo et Masai, 1904, Ch. Alluaud; and syntype male, KENYA: Bura, Wa Taita, 1904, Ch. Alluaud (NMB). (Synonymy by Bolton 1974: 330.)

Plectroctena mandibularis st. *strigosa* var. *strialiventris* Stitz, in Santschi 1924: 162. (Unavailable name; material referred to *mandibularis* by Bolton 1974: 330).

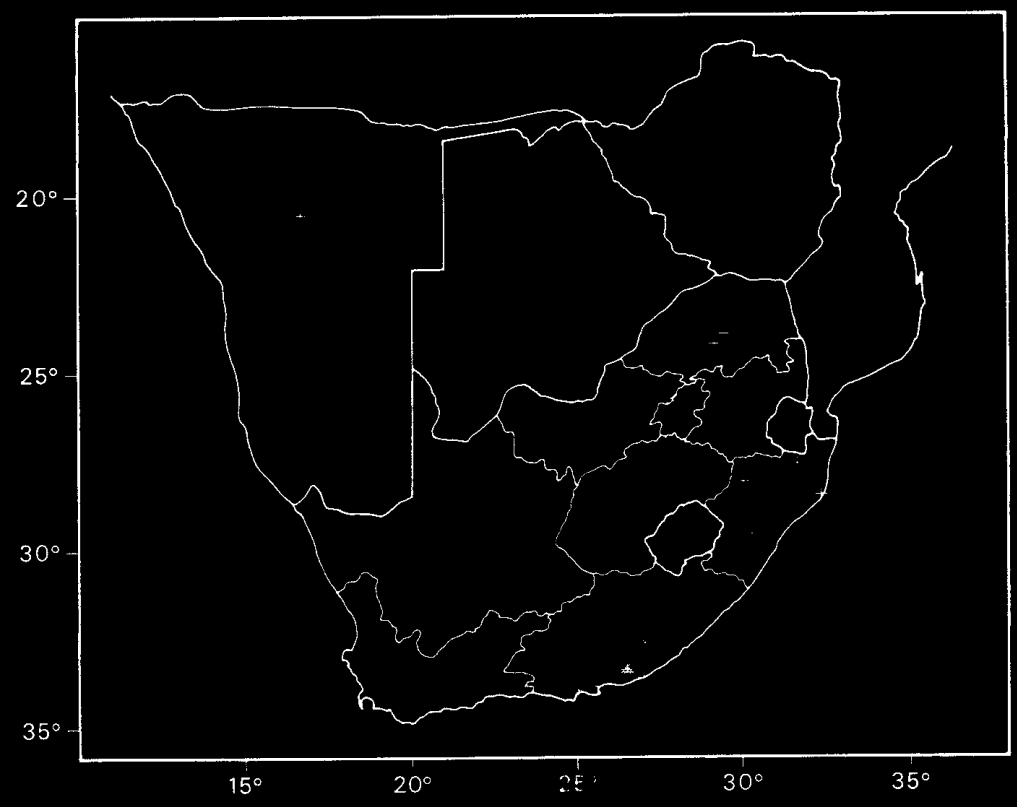

Fig. 5. Geographical distributions of samples queens of *Plectroctena mandibularis* (—) and *P. conjugata* (×).

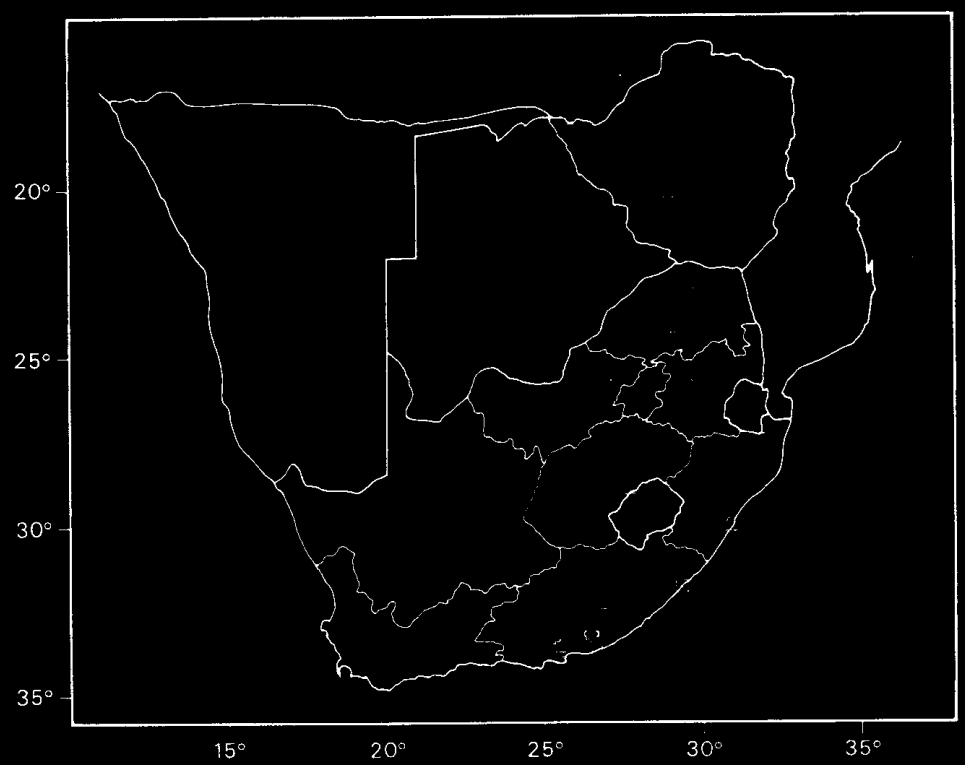

Fig. 6. Geographical distributions of samples of males with abdomens that were black ( ), brown-tipped (⊿), browr (×), and orange-yellow ( ).

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