

## MESSOR Forel

(Figs 25–32, 35–43)

- Messor* Forel, 1890a: lxviii [as subgenus of *Aphaenogaster* Mayr]. Type-species: *Formica barbara* L., 1767: 962, by subsequent designation of Bingham, 1903: 277.
- Messor* Forel; Bingham, 1903: 277. [Raised to genus.]
- Cratomyrmex* Emery, 1891: 572. Type-species: *Cratomyrmex regalis* Emery, 1891: 572, by monotypy. [Synonymy by Emery, 1922a: 357.]
- Veromessor* Forel, 1917: 235 [as subgenus of *Novomessor* Emery]. Type-species: *Aphaenogaster andrei* Mayr, 1886: 448, by subsequent designation of Emery, 1921: 67. **Syn. n.**
- Veromessor* Forel; Wheeler, 1922: 680. [Raised to genus.]
- Lobognathus* Enzmann, 1947: 152 [as subgenus of *Veromessor*]. [Erroneous entry for *Veromessor lobognathus* (Andrews); see Brown, 1949: 49.]

**DIAGNOSIS OF WORKER.** Granivorous myrmecine ants, mostly strongly polymorphic but a few monomorphic or only weakly polymorphic. Head massively constructed in larger workers. Mandibles large and powerful, multidentate in smaller workers (up to 15 teeth) but this number usually decreasing with increased body size until in largest workers only a few massive teeth or an edentate crushing edge remains. Sometimes also in small workers the teeth are worn down to an edentate margin. Palp formula predominantly 4,3 but in largest workers usually 5,3 (30 species dissected). Median portion of clypeus broad and shield-like, broadly inserted between the widely separated frontal lobes; both median and lateral portions of clypeus unmodified except for a central impression of the anterior margin in some species. Frontal lobes short but conspicuous, at least partially concealing the antennal insertions. Frontal carinae absent. Antennal scrobes absent. Antennae 12-segmented, either filiform and without an apical club (in which case the flagellar segments gradually increase in size apically), or with a feebly defined incipient club where the apical 3–4 segments are slightly enlarged. Eyes present, moderate to large in size, situated at or just behind the midlength of the sides in full-face view. Ventral surface of head with elongate ammochaete hairs which usually form a psammophore. This may be reduced and non-functional in some species but the hairs are still conspicuous and generally longer than those found elsewhere on the body; in a few species the psammophore is better developed in smaller than in larger workers. With the alitrunk in profile the promesonotum swollen and convex, frequently dome-like and sloping down steeply behind to the metanotal groove which is weakly to distinctly impressed. Propodeum rounded to strongly bispinose posteriorly and on a much lower level than the convex promesonotum. Promesonotal suture fused and inflexible but its track represented by a distinct arched impression across the dorsum. Mesonotum bounded by impressions on all sides, its boundary easily discernible except in the smallest workers of a few species. Metapleural lobes absent or at most represented by a pair of low broadly rounded ridges. Propodeal spiracle large and conspicuous, circular to subcircular and situated approximately at the midlength of the propodeum or sometimes slightly behind the midlength, but never shifted conspicuously back towards the declivity. Basal posterior portion of mesopleuron just above the middle coxa with a few hairs projecting downwards and backwards. (Whether these are guard-hairs indicating the exit site of a gland is not known, but the hairs remain even in species where other body pilosity is very reduced or absent.) Spurs on posterior tibiae varying from very feebly pectinate through partially barbate and minutely barbulate to simple. Alitrunk ventrally with a strong metasternal process which is usually large to very large (reduced but still conspicuous only in *rufotestaceus* (Foerster) and *vaucheri* Emery out of 45 species dissected). Petiole with a long anterior peduncle, the spiracle situated at about the midlength of the peduncle, well in front of the node. Petiole node in profile narrow and often bluntly triangular to conical in shape, but frequently a sloping differentiated dorsal surface is present where the anterodorsal angle is generally the highest point.

*Messor* is a moderately sized genus of granivorous ants occurring in grassland and savannah, and in arid to desert situations. The main base of the genus is in the Palaearctic region where about 70–80 species occupy a broad strip of territory reaching across the whole width of North Africa and the southern European countries, across the Near and Middle East and thence eastwards through the U.S.S.R. to China and Japan. Compared to this the faunas of other zoogeographical regions are relatively minor. The Afrotropical region has 12 species and Madagascar has 1; the Oriental region has 3–4 species and the Nearctic has 8, all distributed on the western side of the continent and formerly occupying a genus of their own, *Veromessor*, now synonymized. Species

of *Messor* are absent from the Neotropical region, the Indo-Australian region and Australasia, nor do they occur on any of the Pacific island systems.

Recent studies of *Messor* include those of Arnoldi (1977) on the fauna of the U.S.S.R., and Collingwood (1978) on the species of the Iberian Peninsula. The only previous synthesis of sub-Saharan African species is that of Arnold (1920), for the then-recognized South African forms, but no key was given in that revue. Creighton (1950) has keyed the North American species formerly in *Veromessor*. Knowledge of the detailed biology of the species is sparse, but good basic work has been done on some African species by Lévieux & Diomande (1978), and Lévieux (1979).

The closest relatives of *Messor* are the genera *Aphaenogaster* and *Pheidole* Westwood. Members of the latter genus are easily separated from *Messor* as the palp formula is reduced to 2,2, its species are dimorphic, and the antennal funiculus ends in a strongly defined 3-segmented club. *Aphaenogaster*, which is absent from sub-Saharan Africa, is more difficult to differentiate as its species, apart from being uniformly monomorphic, are very close to *Messor* and share most of its diagnostic characters, including the filiform to feebly clavate funiculi and high palp formula (PF) count. Of 55 species of *Aphaenogaster* dissected 31 had PF 5,3, and 24 had PF 4,3. For some reason, although species with the higher PF apparently outnumber those with the lower count, the zoogeographical distribution of the latter is much wider than that of the former. *Aphaenogaster* species with PF 5,3 are found in the Nearctic, Palaearctic and Oriental regions; species with PF 4,3 are also found in these three regions and in the Neotropical, Malagasy, Indo-Australian and Australasian regions as well.

After a study of *Aphaenogaster* for genus-level characters, primarily a search for strong characters to separate it from *Messor*, it became apparent that Brown (1973) was correct in relegating the former subgenera of *Aphaenogaster* to the synonymy. These former subgenera (*Attomyrma* Emery, *Deromyrma* Forel, *Nystalomyrma* Wheeler and *Planimyрма* Viehmeyer) have no significance as they are founded upon minor, inconsistent or gradient character-states. Further, it is now clear that Brown (1974) was also correct in assigning *Novomessor* to the synonymy of *Aphaenogaster*. The only real character separating the two was the fore-wing venation, there being one closed cubital cell in the former and supposedly two in the latter. The same character was invoked to separate *Veromessor* from *Messor*, again the former having one, the latter two closed cubital cells. A survey of the venation of *Aphaenogaster* and *Messor* shows that in both genera the same finely graded series of changes in wing venation occurs (Figs 35–43), which obviates these supposed differences in number of closed cubital cells; it is instructive to consider both genera together.

The most complete, and therefore most primitive, venation pattern (Fig. 35, *M. galla*) shows two closed cubital cells and has  $R_s + M$  dividing well in front of the level of cross-vein  $m - cu$ , so that  $m - cu$  arises from  $M$  itself and there is a short free section of  $M$  between the point of division of  $R_s + M$  into its constituent parts and the point where  $m - cu$  meets  $M$ .

The free section of  $M$  then contracts (Fig. 36; *M. tropicorum*, *angularis*, *nigriceps* Santschi; *A. geei* Wheeler, *schurri* (Forel)) as the fusion of  $R_s + M$  lengthens outwards along the wing until the condition shown in Fig. 37 is seen (*M. rugosus* (André); *A. schurri*) where there is no free portion of  $M$  between  $R_s + M$  and the point of origin of  $m - cu$ , the veins  $R_s$ ,  $M$  and  $m - cu$  all appearing to arise from a point at the apex of  $R_s + M$ .

Next, the fusion of  $R_s + M$  advances further out along the wing so that  $R_s$  and  $M$  now separate a short distance beyond the point of origin of  $m - cu$ , which now arises direct from  $R_s + M$  (Fig. 38; *M. intermedius* Forel, *angularis*, *himalayanus* Forel, *aciculatus* (Smith), *structor* (Latreille), *regalis*; *A. rudis* Emery, *treatae* Forel). Following this the fusion of  $R_s + M$  advances further out along the wing, drawing closer to cross-veins  $2r$  and  $r - m$ , as shown in Figs 39, 40, this stage constituting what may be considered as the normal pheidoline venation (*M. barbarus* (L.), *capitatus* (Latreille), *structor*, *galla*, *denticornis*, *capensis*, *leubberti*, *muticus* (Nylander), *aegyptiacus* (Emery), *nigriceps* Santschi, *semirufus* (André), *instabilis* (Smith), *meridionalis* (André); *A. geei*, *rudis*, *lamellidens* Mayr, *famelica* (Smith), *fulva* Roger, *japonica* Forel, *pallida* (Nylander), *huachucana* Creighton, *splendida* (Roger), *megommatus* Smith, *subterranea* (Latreille), *occidentalis* Emery, *crocea* André, *gemella* (Roger), *senilis* Mayr).

As the fusion of  $R_s + M$  progresses still further along the wing a critical point is reached at which cross-vein  $r - m$  vanishes. This occurs whilst the advancing fusion is still some little distance away from  $2r$ . A male of *A. spinosa* Emery in BMNH shows the critical point as the specimen has  $r - m$  present on the left wing but it has vanished from the right. The disappearance of  $r - m$  leaves the venation as in Fig. 41, which is present in a wide range of species (*M. pergandei* (Mayr), *lobognathus*, formerly of *Veromessor*; *A. albisetosus* Mayr, formerly of *Novomessor*; *A. dromedarius* (Emery), *longiceps* (Smith), *pythia* Forel, *phalangium* Emery, *beccarii* Emery, *araneoides* Emery, *sagei* Forel).

Eventually the stage seen in Fig. 42 is reached where  $R_s$  and  $M$  are fused to the point of intersection of  $2r$  (*M. andrei* (Mayr); *A. cockerelli* André), and finally in *A. ensifera* Forel the fusion of  $R_s + M$  has extended beyond the level of  $2r$  so that this cross-vein now arises from  $R_s + M$  (Fig. 43).

It should be pointed out that there is considerable variation present along this sequence within single species and that it is by no means rare to find specimens with different venation patterns on the left and right forewings, representing different stages in the sequence, and thus showing it to be a dynamic rather than a static system. Also, adventitious vein-stubs frequently arise at random from all the main veins, and from the cross-veins too on occasion.

Thus the loss of  $r - m$  cross-vein, reducing the two cubital cells to only one, rather than being the concise taxonomic character it was thought to be in the past, can now be seen as just one step in a long gradual sequence of venation development in both *Aphaenogaster* and *Messor*, and of no significance in genus-level discrimination among these ants. To draw a line at any point in the sequence and claim that it is more significant than a line drawn at any other point is thus purely arbitrary, and as a direct consequence of the establishment of this sequence the synonymy of *Novomessor* with *Aphaenogaster* is confirmed and the name *Veromessor* falls into the synonymy of *Messor*, there being no other consistent character to separate them.

A side development in the history of *Novomessor*, following Brown's (1974) synonymy, was the suggestion of Hölldobler, Stanton & Engel (1976) that the name might be resurrected for two of its former members (*albisetosus* and *cockerelli*) because of the presence of an exocrine gastral glandular system which was absent from other *Aphaenogaster* species examined, and incidentally absent also from the third former *Novomessor* species (*ensifera*), which was to be retained in *Aphaenogaster* despite the fact that it is otherwise very close to the first two. The obvious inference was that the presence of such a gland system merited genus-level consideration. This is reasonable logic as far as it goes, though many would argue (myself included) that basing genera on such features is grossly over-weighting a relatively weak single character. The discussion would probably have rested there but Kugler (1978) published a paper indicating that such glands occur widely in the Myrmicinae in a range of genera, including a member of *Aphaenogaster* (*phalangium*) whose placement in that genus has never been doubted, but which is not closely related to any of the three mentioned above. This gives rise to three possibilities.

Firstly, that the presence of such glands is highly significant and that, following the model of *Aphaenogaster*-*Novomessor*, every species showing such structures must be assigned to a genus separate from the parent genus, irrespective of any basic similarities they may otherwise show. The idea is ludicrous of course, and obviously not at all what Hölldobler *et al.* intended; the plethora of pointless generic names thus produced would be incredible and no more sensible than selecting genera from groups of closely related species on grounds of, say, presence or absence of hairs on the first gastral tergite. Hölldobler *et al.* in their study found a gastral exocrine system in one species of *Ocymyrmex* Emery but not in two others; they did not suggest the creation of a separate genus here.

Secondly, we can reassign such forms with gastral exocrine glands (or indeed any other individual specialization) when it suits us to do so, and ignore it otherwise. Thus we can utilize such a character to prop up an otherwise poorly defined or undefinable genus which looks like falling irrevocably into the synonymy. This idea does not hold much merit as it again leads unerringly to the creation of swarms of peripheral genera, each with only one or two species, which cannot be adequately separated from their closest relatives remaining embedded in the central mass of species.

Finally, we can consider that the development of such gland systems in some species of a genus but not in others, whilst uniformly stable genus-level characters span the entire range of species, reflects a specialization in the lifeway of the ants involved and is significant at species or species-group level but not beyond that, providing always that other genus-level characters remain uniform throughout. This is decidedly the alternative which I favour as in the long run it will produce strong, well-defined genera, and realistic species-groups within those genera.

To conclude the observations on the genus-level synonymy of *Aphaenogaster*, it is now apparent that the monotypic genus *Brunella* Forel sinks as a synonym. This Malagasy species has had a chequered career since its original description as *Aphoenogaster* [sic] *belti* Forel, 1895; 248. (Syntype workers, MADAGASCAR: Imerina, Moramanga (*M. Sikora*) (MHN, Geneva) [examined].) It was later shifted by Forel (1917) out of *Aphaenogaster* to form the type-species of his genus *Brunella*. Emery (1922a: 242) disagreed with this and synonymized *Brunella* under *Atopula* Emery, which for him was a catch-all genus to which a number of obscure species were relegated. During my study of the tetramorine genera (Bolton, 1976) it transpired that the type-species of *Atopula* was in fact a *Tetramorium*, so that the name *Atopula* fell into synonymy and the remaining former occupants of *Atopula* were transferred to other genera. At that time I had not examined the type-series of *belti* and so referred the species back to Forel's temporarily resurrected *Brunella*. Now, having at last examined the types of *belti*, it turns out to be a fairly unexceptional *Aphaenogaster* which seems to belong to the Oriental *sagei*-group as it has a broad occipital margin, relatively short antennal scapes, a moderately well-developed antennal club and distinct propodeal spines.

A summary of the current genus-level synonymy of *Aphaenogaster* is given in the appendix, p. 364.

Of the two names synonymized with *Messor* above, *Cratomyrmex* was recognized as a synonym by Emery as long ago as 1922. The separation of the two was based on the presence of pectinate hind tibial spurs in the latter and their supposed absence in the former. This was quickly spotted as a feeble and variable character and the status of the genus challenged (Santschi, 1920). The form of the hind tibial spurs is in fact very variable in *Messor*, showing all stages from feebly pectinate, through barbate and minutely barbulate to simple. Even in the same series there is sometimes variation in spur form between different-sized workers.

*Veromessor*, which began its existence as a subgenus of *Novomessor*, was given generic status by Wheeler (1922) who separated it from *Messor* on the venation character discussed above and now known to be spurious. The discussion in Wheeler & Creighton (1934: 356–360) indicated that *Messor* and *Veromessor* were extremely closely related, but no means of separating them was given. Presumably only the venation character invoked previously by Wheeler could be found. The present investigation has shown the two to be synonymous for, leaving aside the venation, all characters of *Messor* are duplicated in *Veromessor*, except for the species *relictus* Wheeler & Mann. This last was originally described as a member of *Aphaenogaster* but was transferred to *Veromessor* by Wheeler & Creighton (1934), for no apparent reason. In my opinion it is an ordinary member of *Aphaenogaster*, fitting the diagnostic characters of that genus and having all the criteria required to separate it from *Messor* which are tabulated below; it is herewith returned to *Aphaenogaster*. Finally, the fossil species *sculpturatus* Carpenter, originally described in *Messor* (where it is a junior secondary homonym of *sculpturatus* Stitz), later included in *Veromessor* but suggested as a possible *Pogonomyrmex* species by Wheeler & Creighton, is impossible to place at present and requires further study. The living North American species now included in *Messor* are *andrei* (Mayr) **comb. n.**, *chamberlini* Wheeler, *julianus* (Pergande) **comb. n.**, *lariversi* (Smith) **comb. n.**, *lobognathus* Andrews, *pergandei* (Mayr) **comb. n.**, *smithi* (Cole) **comb. n.**, *stoddardi* (Emery) **comb. n.**

*Aphaenogaster* and *Messor* are very closely related and certainly derive from a single parent stock. The characters tabulated below will separate them even though a few species show exceptions to one or another of the characters.

*Messor*

Mostly polymorphic species (a very few feebly polymorphic and monomorphic species known).  
 Mostly with ammochaete hairs present (reduced in a few species).  
 Head massive and broad, in medium to large workers CI > 90 (range 95–125 in 64 species measured).  
 Metasternal process large to very large, always very conspicuous (45 species dissected).  
 Outer margins of mandibles strongly curved towards midline, the mandibles massive and heavy.

*Aphaenogaster*

Entirely monomorphic.  
 Mostly without ammochaete hairs (present in a very few species).  
 Head usually slender, CI 90 at maximum, generally much less (range 49–90 in 75 species measured).  
 Metasternal process small to absent, approaching size seen in *Messor* only in *A. subterranea* (55 species dissected).  
 Outer margins of mandibles not strongly curved towards midline, the mandibles triangular in shape and not massive.

**Synonymic list of Afrotropical *Messor* species*****angularis* Santschi stat. n.*****capensis* (Mayr)***pseudoaegyptiaca* Emery **syn. n.***barbarus* subsp. *capensis* var. *schencki* Forel (unavailable)*braunsi* Forel **syn. n.***donisthorpei* Santschi **syn. n.*****cephalotes* (Emery)***plinii* Santschi **syn. n.*****collingwoodi* sp. n.*****decipiens* Santschi stat. n.***barbarum* r. *capense* var. *decipiens* Forel (unavailable)*barbarus* subsp. *capensis* var. *proba* Forel (unavailable)*arcistriatus* Santschi **syn. n.*****denticornis* Forel***denticornis* var. *parvidens* Forel **syn. n.***denticornis* var. *brunni* Forel **syn. n.*****galla* (Mayr)***barbarum* subsp. *caduca* var. *galla* Emery (unavailable)*barbarus* subsp. *semirufus* var. *rufa* Forel (unavailable)*barbarus* st. *galla* var. *triempresa* Santschi (unavailable)*barbarus* st. *latinodis* Santschi **syn. n.***barbarus* r. *semirufus* var. *rufula* Forel (unavailable)*barbarus* subsp. *galla* var. *armata* Emery (unavailable)*galla* st. *nobilis* Santschi **syn. n.***galla* var. *airensis* Bernard **syn. n.*****incisus* Stitz (nomen dubium)*****luebberti* Forel stat. n.*****piceus* Stitz*****regalis* (Emery)***regalis* var. *rubea* Santschi **syn. n.***sculpturatus* Stitz **syn. n.*****ruginodis* Stitz stat. n. (nomen dubium)*****striatifrons* Stitz stat. n.*****tropicorum* Wheeler stat. n.***denticornis* var. *laevifrons* Stitz **syn. n.***braunsi* var. *nigriventris* Stitz **syn. n.****Key to species (medium to large workers)**Note. The nomina dubia *incisus* Stitz and *ruginodis* Stitz are omitted from the key.

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|---|--|---|
| 1 | Hairs absent from first gastral tergite or at most with a single sparse transverse row at the extreme apex of the sclerite | 2 |
| – | Hairs present on first gastral tergite, more or less evenly distributed over the whole surface of the sclerite             | 5 |

- 2 Dorsum of propodeum with one or more pairs of standing hairs . . . . . 3  
 – Dorsum of propodeum without standing hairs . . . . . 4
- 3 Dorsum of head coarsely and densely reticulate-punctate everywhere, the mid-dorsal strip also rugulose. (Niger, Mali) . . . . . *collingwoodi* (p. 346)  
 – Dorsum of head smooth everywhere except for the rugulose mid-dorsal strip; without coarse dense reticulate-punctate sculpture. (Throughout Sahelian zone and northern East Africa, also occurring coastally in West Africa). . . . . *galla* (p. 349)
- 4 Head sculptured everywhere with close-packed longitudinal rugulae between which is reticulate-punctate ground-sculpture. Eyes slightly smaller,  $0.15-0.18 \times HW$  in HW range of 2.00–3.12. (Tanzania, Zimbabwe, Angola, Botswana, South West Africa, South Africa) . . . . . *leubberti* (p. 351)  
 – Head smooth except usually for a short central rugular area behind the frontal lobes. Eyes slightly larger,  $0.18-0.21 \times HW$ , in HW range of 2.00–2.76. (Kenya) . . . . . *angularis* (p. 344)
- 5 Basal third or more of first gastral tergite strongly and conspicuously sculptured with rugulae, costulae, coarse reticulate-punctation, or a combination of these. . . . . 6  
 – Basal third of first gastral tergite unsculptured except for hair pits and very faint superficial patterning. In some very large workers a few short basigastral costulae may develop but these are restricted to the area immediately behind the postpetiole . . . . . 7
- 6 With the head in full-face view the sides with projecting hairs. Petiole and postpetiole coarsely closely and deeply rugose. (Nigeria, Benin Republic, Congo) . . . . . *regalis* (p. 352)  
 – With the head in full-face view the sides without projecting hairs. Petiole and postpetiole finely sculptured with feeble rugulae, dense punctation or a combination of both. (Ethiopia, Kenya, Tanzania) . . . . . *cephalotes* (p. 346)
- 7 Posterior half of clypeus between frontal lobes with a distinct, strongly raised central step or welt. (Angola, South West Africa) . . . . . *tropicorum* (p. 354)  
 – Posterior half of clypeus between frontal lobes without a raised central step or welt, usually more or less flat or even slightly concave . . . . . 8
- 8 Eyes relatively large, the maximum eye diameter  $0.21-0.25 \times HW$ , in HW range of 2.50– > 4.00. (Botswana, South West Africa, South Africa) . . . . . *denticornis* (p. 349)  
 – Eyes smaller, the maximum eye diameter  $0.14-0.19 \times HW$ , in HW range of 2.50– > 4.00 . . . . . 9
- 9 In HW range 2.80– > 4.00 the sides of the head conspicuously evenly convex in full-face view (Fig. 27). Propodeum in profile relatively long and low (Fig. 32). (South West Africa, South Africa) . . . . . *striatifrons* (p. 353)  
 – In HW range 2.80– > 4.00 the sides of the head approximately straight in full-face view, the sides parallel or divergent anteriorly (Fig. 28). Propodeum in profile relatively short and high (Fig. 31) . . . . . 10
- 10 Body pilosity very dark in colour, deep red-brown to blackish. (Botswana, South Africa) . . . . . *piceus* (p. 352)  
 – Body pilosity pale, white or silvery to yellowish . . . . . 11
- 11 Head red in major workers, contrasting in colour with the much darker alitrunk and gaster. (Zimbabwe, Botswana, Lesotho, South Africa) . . . . . *decipiens* (p. 348)  
 – Head brown to black in major worker, about the same colour as the alitrunk and gaster. (South West Africa, Botswana, South Africa) . . . . . *capensis* (p. 345)

Among strongly polymorphic species such as these, where there is an enormous worker size-range, the standard measurements which I have otherwise used consistently for the Myrmicinae become meaningless and cannot be utilized. A few standard ratios have, however, proved to be of value in some cases and these are included in the relevant descriptions. The keys and descriptions are based on medium to large workers as these show the best discriminating characters, the minor workers of closely related species being sometimes indistinguishable. Size ranges covered by the descriptions are given for each species in terms of HW range.

The presence or absence of propodeal teeth or spines, which appears to be a functional diagnostic character in other parts of the range of *Messor*, is not of much use in the Ethiopian region species for, although some always have the propodeum armed (*regularis*, *collingwoodi*) and some always have it unarmed and rounded (*angularis*, *leubberti*), the rest show a disconcerting variability in this character, sometimes differing even in individuals from the same nest sample.

The 12 recognizable species are distributed roughly as follows in the Afrotropical region.

Northern (Sahelian) species: *collingwoodi*, *galla*, *cephalotes* (in extreme east).

Western species: *regalis*, *galla* (coastally).

Eastern species: *cephalotes*, *angularis*, *luebberti* (in south), *galla* (in north).

Southern species: *denticornis*, *luebberti*, *striatifrons*, *tropicorum*, *piceus*, *decipiens*, *capensis*.

The species fall into two groups in terms of pilosity. The first group, characterized generally by reduced pilosity and virtual absence of hairs on the first gastral tergite, contains the species *angularis*, *collingwoodi*, *galla*, and *luebberti*. In the second group pilosity is generally dense and is evenly distributed over the first gastral tergite. Included here are the remaining eight species noted above. Of them *regalis* is very conspicuous and not obviously close to any of the others. Of the remainder the southern complex of *piceus*, *decipiens* and *capensis* may represent a single species, and *denticornis*, *striatifrons* and *tropicorum* are closely related.