

QUANTITATIVE STUDIES ON WORKERS OF THE OLD
WORLD ARMY ANT GENUS *AENICTUS*
(HYMENOPTERA : FORMICIDAE)

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SUMMARY

Multivariate analyses of workers of the Old World army ant genus *Aenictus* were used to investigate taxonomic structure inherent in the morphological data gathered. Results were compared to subgeneric and species groupings suggested in earlier taxonomic studies and to the known geographic ranges of the included species. African *Aenictus* form a distinct phenetic subgroup as do Asian species previously assigned to the subgenus *Typhlatta*. Other Asian species show an affinity for either the African species or the *Typhlatta* group. Of the five species groupings identified in an earlier taxonomic work, the "*currax*", "*laeviceps*", and "*wroughtoni*" groups are clearly revealed to be phenetically distinctive. How these results will affect the classification of the genus, especially at the subgeneric level, depends on further character analysis.

RESUME

**Etudes quantitatives sur des ouvrières des fourmis voyageuses
de l'ancien monde du genre *Aenictus* (Hymenoptera : Formicidae)**

Des analyses multivariées sur des ouvrières de la fourmi voyageuse de l'ancien monde du genre *Aenictus*, ont permis d'étudier la structure taxonomique ressortant des données morphologiques accumulées. Les résultats ont été comparés aux regroupements subgénériques et spécifiques suggérés par des études taxonomiques antérieures ainsi qu'aux appartenances géographiques connues des espèces étudiées. Les *Aenictus* d'Afrique forment un sous-groupe phénétique distinct comme le font des espèces asiatiques précédemment rangées dans le sous-genre *Typhlatta*. D'autres espèces asiatiques montrent une affinité soit pour les espèces africaines, soit pour le groupe *Typhlatta*. Parmi les cinq groupements d'espèces identifiés par une étude taxonomique antérieure, les groupements « *currax* », « *laeviceps* » et « *wroughtoni* » apparaissent clairement comme distincts. L'effet de ces résultats sur la classification sous-générique du genre dépendra d'autres analyses de caractères.

INTRODUCTION

Ants traditionally referred to as "true" army ants are currently placed in two distinct ant subfamilies. The New World species constitute the Ecitoninae, while the Old World forms comprise the Dorylinae. This placement reflects the belief among myrmecologists that the constellation of morphological and behavioral characteristics shared by the New and Old World forms and used to define the true army ants were arrived at convergently in the two groups (GOTWALD, 1982). This evolutionary scenario is further complicated by the fact that the Dorylinae consists of two genera, *Dorylus* and *Aenictus*, which may also have arisen independently of each other. GOTWALD (1979) hypothesized an early Tertiary origin for both genera: *Aenictus* arising in tropical Laurasia and *Dorylus* on the African continent. Thus, the true army ants may be triphyletic.

Because *Aenictus* is well represented throughout the Old World tropics, and *Dorylus* with only 4 species recorded from the Indo-Australian area is not, *Aenictus* is of special interest in terms of dispersal and speciation events. Although WILSON (1964) taxonomically revised the Indo-Australian dorylines, *Aenictus* species of the Middle East and Africa have received scant attention. EMERY (1910) conducted the last extensive taxonomic review of *Aenictus*, and WHEELER (1930) examined the subgeneric structure of the genus. In his revision, WILSON (1964) regarded Wheeler's subgeneric distinctions as "no longer tenable", but pointed out that phylogenetic analysis of the genus resulted in a "loose clustering of the species into 5 informal 'groups'".

Thirty-four species of *Aenictus*, known from the worker caste, are recorded from the Indo-Australian area, and approximately 15 from the African continent (WILSON, 1964). Although numerous species based solely on males have been described, it is not known how many of the independent worker and male descriptions represent synonymies (GOTWALD, 1982). One of us (WHG) is currently revising the African species of *Aenictus*, but a thorough revision is not possible without reexamination of the entire genus.

Because previous quantitative studies (GOTWALD and BARR, 1980; BARR and GOTWALD, 1982; BARR *et al.*, 1985) of the genus *Dorylus* have yielded results of both practical and heuristic value in the search for a practical subgeneric classification, it was decided to subject the workers of the genus *Aenictus* to an identical set of analyses. The objectives of the research were 1) to examine phenetically *Aenictus* workers from Africa and Asia as a unified group for the first time, 2) to determine the morphological affinities of the included species, 3) to ascertain if the species clusters that result from the analysis correspond to the previously identified taxonomic categories, and 4) to determine the degree to which the African and Asian populations differ from one another.

METHODS

Methods used in this study conform to a standard set of multivariate statistical procedures adopted by the authors for taxonomic analyses of three genera of the related genus, *Dorylus* (GOTWALD and BARR, 1980; BARR and GOTWALD, 1982; BARR *et al.*, 1985). In the earliest paper of the series, the analytical techniques chosen were discussed in more detail, and the rationale for their use demonstrated. The same set of procedures has been retained for our preliminary investigation of the phenetic relationships of species of *Aenictus* to ensure that results would be comparable with those of previous studies.

A set of fifty-three characters (see Appendix 1) was used to describe the workers of each of the forty-two species of *Aenictus* examined in the study reported here. Included were metric, meristic, and ordered multistate characters as well as several standard myrmecological indices. A complete set of raw data scores for all characters on each of the species included in this study is available from either author.

Aenictus workers are small, vary in color from a light yellow through orange, reddish brown and black, and do not display any pronounced size polymorphism (fig. 1). As is true with the army ants of the subfamilies Dorylinae and Ecitoninae,



Fig. 1. — Morphology of worker of *Aenictus* sp. (legs and pilosity omitted) showing major regions from which characters were drawn for this study.

Fig. 1. — Morphologie d'une ouvrière d'*Aenictus* sp. (omettant les pattes et la pilosité) montrant les régions majeures dont les caractères sont tirés pour cette étude.

Aenictus can be distinguished from other ants by the frontal carinae which are raised and which lack the lateral expansions typical of most other ants. Therefore, when the head is viewed dorsally, the antennal insertions are exposed. *Aenictus* possesses a two-segmented waist and thus cannot be confused with *Dorylus* and its single-segmented waist.

The exemplar method for characterizing species has proven serviceable in our taxonomic studies of army ants (BARR and GOTWALD, 1982), was essential for the work on *Dorylus* queens (BARR *et al.*, 1985) and has been continued here. The technique is always potentially indispensable when dealing with species which are poorly represented in collections.

All metric characters (those marked with an asterisk in the appendix) were first transformed to ratios of a standard size measure, because this method of reducing the influence of overall size on the resulting phenograms and ordinations was found most effective in our previous studies (e.g., GOTWALD and BARR, 1980). To maintain consistency with that earlier work on the genus *Dorylus*, profemur length was chosen as the general size indicator for metric transformations.

Next, all data in the transformed set were standardized to deviations from the character means in units of standard deviation. The standardized dataset was then used to calculate average taxonomic distance from each species to every other species, and also the product-moment correlation coefficients between all pairs of species. The unweighted pair group method on averages (UPGMA) was applied to the similarity measures generated by both techniques, resulting in standard phenogram plots demonstrating clustering of the species by phenetic similarity.

As a test of the accuracy of the artificial boundaries imposed by clustering methods, two ordination procedures, also based on the standardized data, were employed to provide a continuous representation of species relationships. The first three component axes indicated by principal components analysis (PCA) were used to define a three-dimensional attribute (A) space in which the species can be arrayed on the basis of their orthogonal character projections. Our experience with distortions in taxonomic data introduced by PCA, however, suggested that final results should be further adjusted by non-metric multidimensional scaling (MDS), with the MDS ordination further rotated to alignment with the first three PCA axes. The MDS ordination was plotted as a three-dimensional graph so that similarity relationships would appear as clusters of species in the A space. As a final objective test of the apparent clusters produced by MDS, a minimum spanning tree based on average taxonomic distances assisted in visualizing any distortion. All procedures were discussed by SNEATH and SOKAL (1973).

Computations were carried out on the IBM 3033 computer at the University of Toronto. All multivariate procedures were performed with the NTSYS program package (ROHLF *et al.*, 1972). The three-dimensional perspective plot of the MDS ordination was produced by the program PHYSETER, written by Ralph Gibson at the University of Toronto.

Some of the species included in this study are presently undescribed and others may change in status when the revision of African species is complete. In consequence, it is most convenient to refer to all species by number, although those forms which represent relatively well understood names are listed in Appendix 2. Appendix 3 records the subdivision of included species by i) geographic range, ii) WHEELER's (1930) subgeneric groupings and iii) WILSON's (1964) species groupings.

RESULTS

The methods employed here, of course, provide only an exploratory view of structure inherent in the taxonomic data. The relative phenetic affinities of the *Aenictus* species so disclosed may then provide the appropriate overview required as preparation for a revision of the African species, and a cladistic and zoogeographic analysis of the genus.

The phenogram generated by UPGMA clustering from average taxonomic distances (fig. 2) demonstrates five relatively isolated species (23, 26, 4 and the pair, 11 and 16) and two major clusters (lettered on the phenogram as A and B). The former group, consisting of twelve species, is relatively uniform, but the second group, of twenty-five species, consists of at least two major

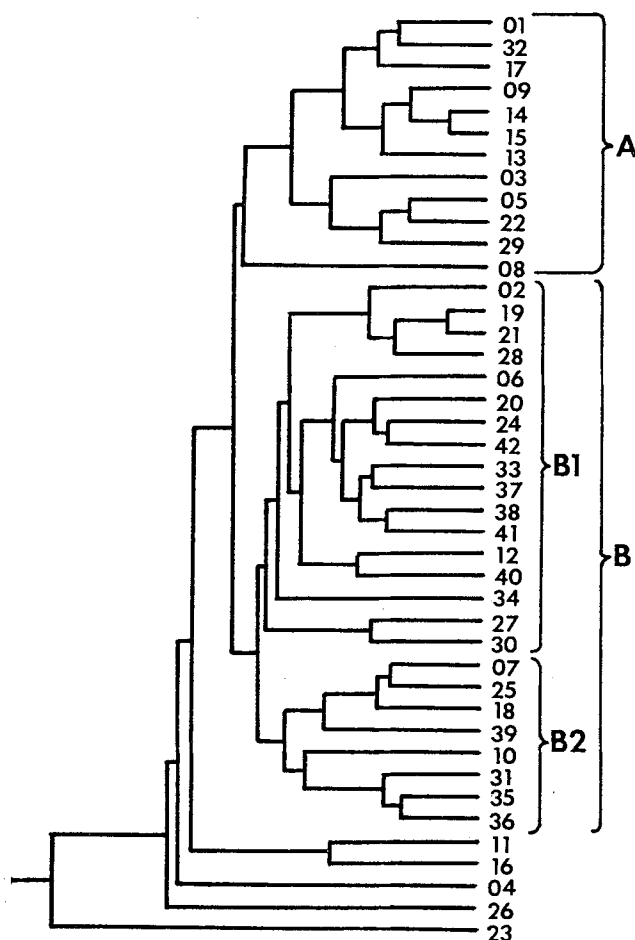


Fig. 2. — Phenogram produced by UPGMA clustering of average taxonomic distances calculated on the transformed data. Matrix correlation (cophenetic correlation) $r = .747$.

Fig. 2. — Dendrogramme résultant du regroupement UPGMA des distances taxonomiques moyennes, calculées sur les données transformées. Matrice corrélée (corrélation cophénétique) $r = .747$.

sub-clusters (B1 and B2) and a number of more or less identifiable subgroups within the first. When compared with information on geographic origin, this analysis places all African species within subgroup 'B', and all Asian species of Wheeler's subgenus *Typhlatta* (except for sp. 4) within subgroup 'A'. The remaining, non-*Typhlatta* Asian species are scattered across all the main subgroups, but species 26, which is the sole representative of Wheeler's subgenus *Paraenictus*, is well separated from the others.

Product moment correlation coefficients yield a more balanced hierarchical UPGMA phenogram (see fig. 3), with a nested structure of groups lettered in the phenogram as follows: A, B (U [W, X], V [Y, Z]). Again, the Asian *Typhlatta* all occur together in group 'A', but although all African species occur in group 'B', they are distributed among the three subgroups,

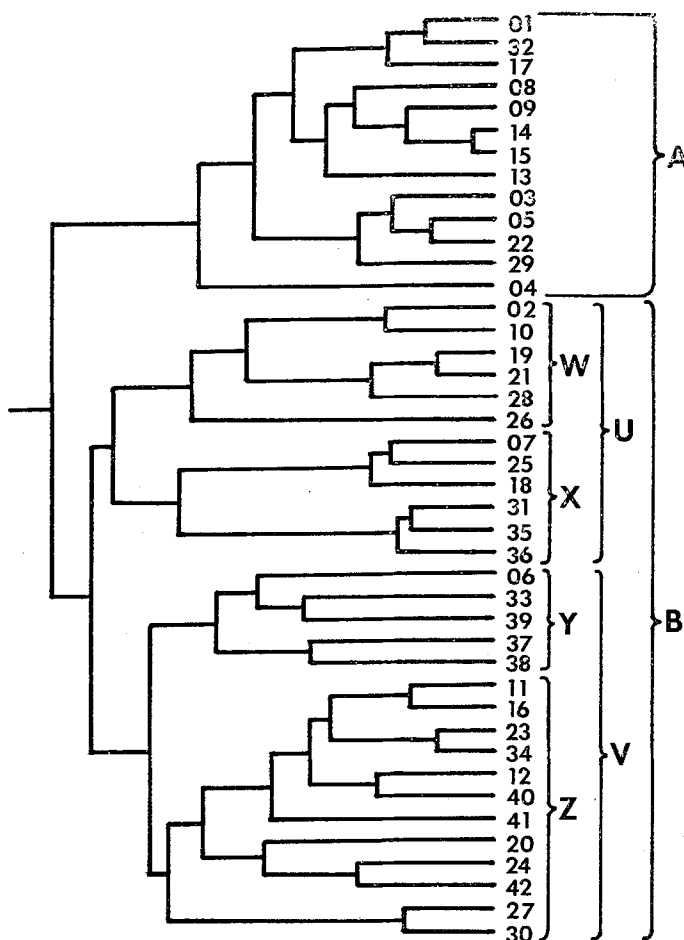


Fig. 3. — Phenogram produced by UPGMA clustering of product moment correlation coefficients calculated on the transformed data. Matrix correlation $r = .708$.

Fig. 3. — Dendrogramme résultant du regroupement UPGMA des coefficients de corrélation, calculés sur les données transformées. Matrice corrélée $r = .708$.

'X', 'Y' and 'Z'. Asian species from Wheeler's subgenus *Aenictus* (sensu strictu) occur in all major subgroups of this phenogram, and species 26 (*Paraenictus*) appears as an unremarkable member of the relatively uniform subgroup, 'U'.

The PCA analyses are not reported in detail here, and were used by us primarily to establish the three primary axes of variation (first three principal components) and as a seed for the MDS procedure. The first three principal components accounted for 50.9 % of total variation (a reduction from 60.4 % which was demonstrated in a parallel analysis of the raw dataset).

The transformation of all metric characters (apart from profemur length) to ratios, means that all three principal component axes now express variation in shape rather than primarily in size (GOTWALD and BARR, 1980). Component axis I accounted for 27.5 % of total variation and expressed primarily the influence of characters from the head (including antennae) and petiolar regions, with a few characters loading heavily (either positively or negatively) from trunk (thorax + propodeum) and legs. The second principal component axis summarizing 12.6 % of total variation expresses substantial influence from the trunk region as well as exoskeletal coloration, with lesser contribution from characters of the head, legs and petiole. Component axis III accounted for only 10.9 % of total variation and

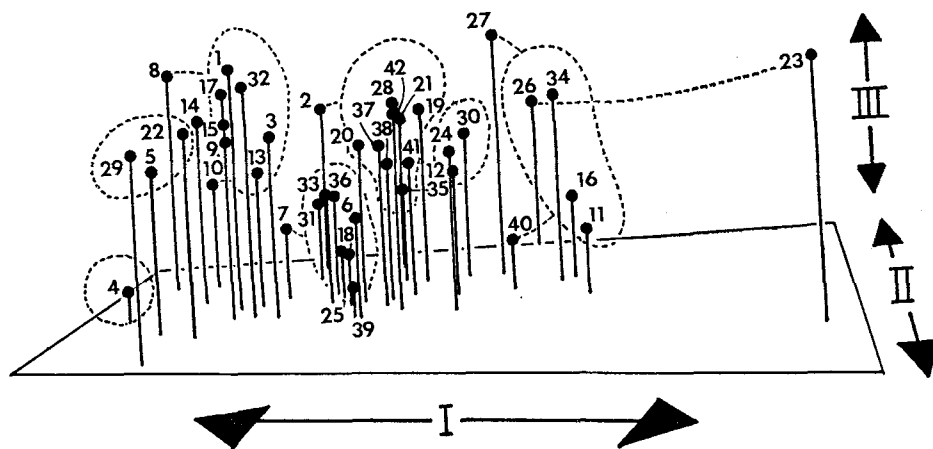


Fig. 4. — Nonmetric multidimensional scaling ordination of 42 *Aenictus* workers in the A space defined by the first three component axes (I, II, III), based on average taxonomic distances calculated on the transformed data (stress = .240). Matrix correlation $r = .962$.

Fig. 4. — Ordination non-métrique en échelle multidimensionnelle des 42 ouvrières du genre *Aenictus* dans l'espace « A », défini par les trois premiers axes des composantes (I, II, III), basés sur les distances taxonomiques moyennes calculées sur les données transformées (« force » = .240). Matrice de corrélation $r = .962$.

was influenced primarily by characters from the head and mouthparts and secondarily by legs, petiole and coloration.

The results of the MDS analysis are plotted in *figure 4*, with the three axes of the A space described above labelled I, II and III. The forty-two species are clustered densely, with species 4 and 23 the only conspicuous outliers. Based on geographic origin, only Asian "*Typhlatta*" species are moderately well clustered, with species 4 separated from the main group. The African species appear in at least three apparent clusters and the non-"*Typhlatta*" Asian species are scattered throughout. *Aenictus silvestrii* (26) occurs near the edge of the most densely populated area, but otherwise its position is not remarkable.

DISCUSSION

In examining the results of our analyses, we have concentrated on the degree of correlation with the early classification of WHEELER (1930) and the known geographic ranges of the included species. The agreement is not at all impressive, although the African species show modest coordination in the phenogram of average taxonomic distances (*fig. 2*) and the "*Typhlatta*" group of species shows substantial cohesiveness in all three analyses. Wheeler's subgenus *Paraenictus*, however, created for the single species, *A. silvestrii*, is not clearly distinguished from other subgroups.

The more recent classification of WILSON (1964), although it ignores the African species and stops short of a formal subgeneric classification, proposes some improvements over WHEELER'S (1930) revision. WILSON'S study included both phenetic and cladistic analyses, with a relatively close correspondence between the results of the two methods. As WILSON suggested, it proves instructive to compare the five informal species groupings proposed by WILSON (*wroughtoni*, *currax*, *pachycerus*, *laeviceps* and *ceylonicus*) with the taxonomic structure revealed by our more detailed analyses. WILSON'S "*currax*" and "*laeviceps*" groups contain all of the "*Typhlatta*" species and moreover explain the separation of species 4 and 13 (*laeviceps* group) from the other "*Typhlatta*" species. WILSON'S "*wroughtoni*" group appears to be an especially well-defined phenetic unit, clustering tightly in both phenograms and a little less so in the MDS ordination.

WILSON'S study (1964) seems to have been successful in identifying two other relatively uniform groups, "*pachycerus*" and "*ceylonicus*", but our results suggest that in considering formal subgeneric classification for the genus, these groups may require additional subdivision, in part along geographic lines. "*Pachycerus*" species 24, 10, 7, 27 and 30 are well separated from the rest of the group, and "*ceylonicus*" species 25 and 18 (as well, perhaps as 40, 16, 11, 34 and 23) are phenetically distinctive from the rest of that group.

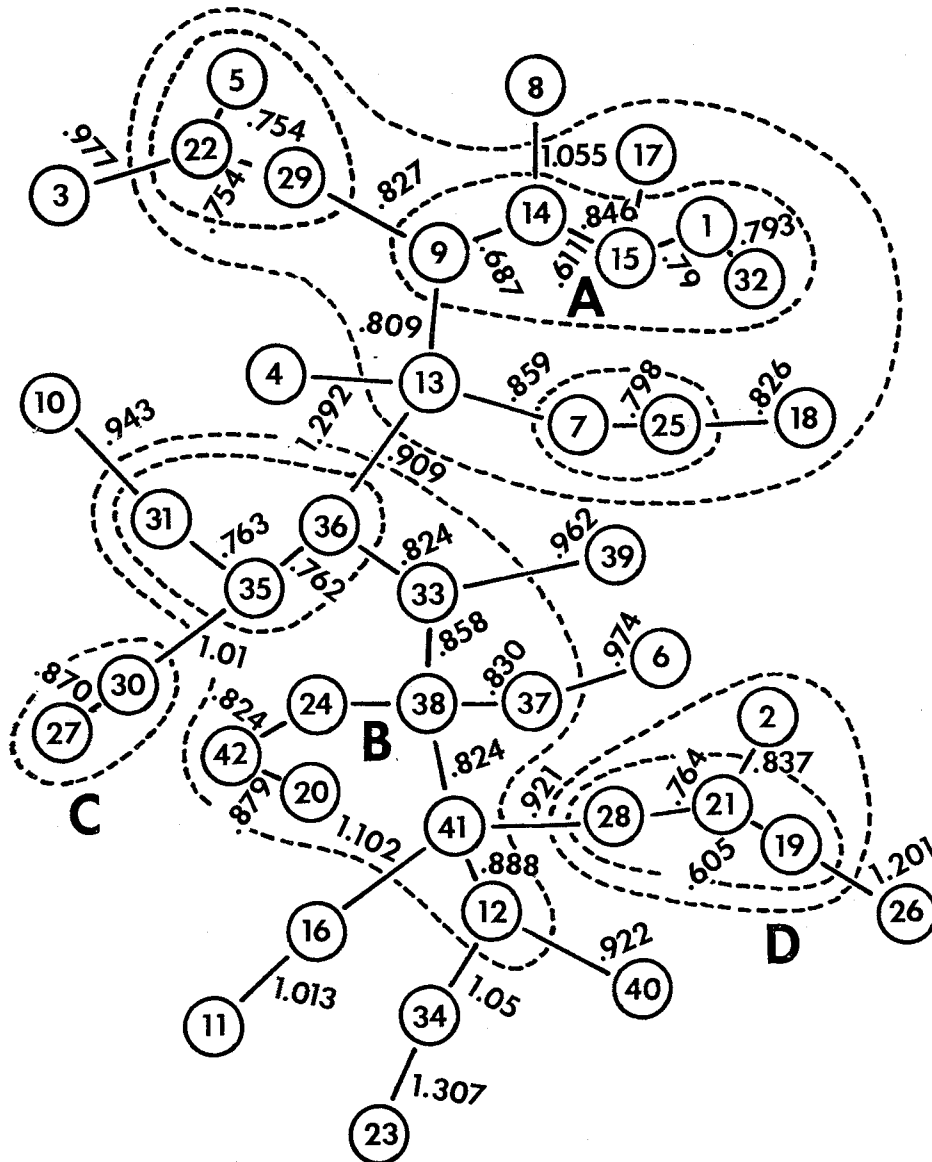


Fig. 5. — Schematic representation of phenetic affinities of *Aenictus* spp. determined in the present study with the minimum spanning tree superimposed. Line lengths are in units of average taxonomic distance. Broken lines define species groups such that all exgroup nearest neighbour distances exceed those within groups (see text).

Fig. 5. — Représentation schématique, pour cette étude, des affinités phénétiques des espèces du genre *Aenictus*, avec l'arbre embrassant minimum superposé. Les longueurs des lignes sont exprimées en unités de distance taxonomique moyenne. Les lignes discontinues définissent des groupes d'espèces tel que toute distance avec le groupe le plus proche est supérieure aux distances intra-groupes (voir texte).

Figure 5 represents a type of diagrammatic representation of all of our results which we have found useful in summarizing logical conclusions from the less than precise findings of a suite of analyses. It is based upon the MDS ordination (reduced to two dimensions) and the results of clustering, with the minimum spanning tree of nearest neighbour distances (based on average taxonomic distance) superimposed. Broken lines have been used to define species groups, each group consisting of those species with inter-species nearest neighbour distances shorter than inter-species distances outside the groups. With this large and complex genus, two levels of grouping have been used, based on three inter-species ATD ranges ($< .800$, $.801 - .899$, and $> .899$).

When the zoogeographic considerations and the WHEELER and WILSON subgeneric groupings are compared with figure 5, it is clear that our analyses explain a good deal of the range of variation found in this genus. African *Aenictus* are all associated with a distinguishable phenetic sub-group (labelled 'B' in fig. 5) which is distinct from the even more compact sub-group (A) with which all of the "*Typhlatta*" group of Asian species are associated. The remaining Asian species appear to have two major affinities, either with the *Typhlatta* subgroup or with the African subgroup. WHEELER's *Paraenictus* (26) is indeed a relatively distinctive species, but not sufficiently so to warrant sub-generic ranking.

Several of WILSON's supra-specific groupings are substantiated by our results. "*Currax*" and "*laeviceps*", which together correspond to WHEELER's *Typhlatta*, are clearly referable to a phenetically distinctive species group, and our results support, as well, the distinction between the two. The "*wroughtoni*" group is also a tightly knit unit, demonstrating most direct phenetic affinities with the *Typhlatta* species.

Our results do not, however, support the phenetic uniformity of either of WILSON's "*ceylonicus*" or "*pachycerus*" groups. A large portion of the "*ceylonicus*" group is consistent with subgroup B of figure 5, but species 25 and 18 are dissociated. WILSON's "*pachycerus*" group (apparently a catch-all for species of uncertain affinities) displays a heterogeneous composition in our analyses, with species falling not only in two compact and distinct subgroups (C and D), each of which shows rather different affinities to subgroup B, but also within both subgroups A and B. A reappraisal of the mandibular and thoracic characters found by WILSON (1964) to characterize these two species groups is apparently indicated.

A definitive subgeneric classification of the genus *Aenictus*, if indeed one is deemed necessary, must await completion of the revision of the African species; nevertheless, certain preliminary conclusions are suggested by our results. The groups labelled A and B in figure 5 could correspond to two major subgenera. Because the substructure of Group A ("*Typhlatta*" group) is not regularly hierarchical, it is suggested as a single subgenus,

which should probably include the miscellaneous outliers 8, 3 and 4. Group "B" (the african or "*ceylonicus*" group) is equally lacking in a regular substructure and is prime candidate for a single subgenus, to include the numerous outliers 10, 39, 6, 11, 16, 23, 34 and 40. Two portions of WILSON's "*pachycerus*" group, "C" and "D" in *fig. 5*, are reasonable candidates for equivalent subgeneric status.

Whether these indications from phenetic analysis can eventually serve as a formal guide to practical taxonomic structure will be dependent on further character analysis, to determine whether usable diagnostic characters are available, and a revised cladistic analysis to trace the course of character evolution and the derivative relationships of the phenetic groups identified here.

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APPENDIX 1: CHARACTER LIST

(All lengths measured in millimetres to nearest 0.01 mm. Those characters transformed to ratios of profemur length for the analysis described in detail in the text are marked with an asterisk). 1. Number of antennal segments (including scape). *2. Scape length (LS) (excluding neck). 3. Scape index (SI), $SL \times 100/HW$. *4. Length of terminal flagellar segment. *5. Interantennal distance (shortest distance between mesal margins of antennal sockets). 6. Mandible shape. 7. Clypeal-mandibular gap (absent, moderate, wide). *8. Mandible length (ML). 9. Mandibulocephalic index (MCI), $ML \times 100/HL$. *10. Head length (HL). *11. Head width (HW). *12. Head depth (HD) in lateral view. 13. Cephalic index (CI), $HW \times 100/HL$. 14. Clypeal border shape. 15. Clypeal teeth (absent, 2 teeth, 4 or more teeth). 16. Condition of parafrontal ridge. 17. Condition of occipital collar. 18. *Typhlatta* spots (absent, muted, bright). 19. Occipital angles, in dorsal view (rounded, subquadrate, quadrate). 20. Head surface sculpturing. *21. Pronotum width (PW). 22. Pronotal armature (present or absent). 23. Pronotal sculpturing. 24. Condition of promesonotal depression. *25. Trunk (mesosoma) length (TL). 26. Mesonotal-mesopleural suture (present or absent). 27. Condition of mesosomal rugae. 28. Condition of propodeal junction. 29. Condition of propodeal collar. 30. Propodeal sculpturing. 31. Profemur length. *32. Mesofemur length. *33. Metafemur length. *34. Protibia length. *35. Mesotibia length. *36. Metatibia length. *37. Protarsal segment I length. *38. Mesotarsal segment I length. *39. Metatarsal segment I length. 40. Metatibio-tarsal index (MTI), $\text{metatarsal segment I length} \times 100/\text{metatibia length}$. 41. Condition of subpetiolar process. *42. Petiole length (PEL). *43. Petiole width (PEW). 44. Petiolar index (PI), $PEW \times 100/PEL$. 45. Postpetiolar length (PPL), measured in dorsal view. *46. Postpetiole width (PPW), measured in dorsal view. 47. Postpetiolar index (PPI), $PPW \times 100/PPL$. 48. Dorsal petiolar sculpturing. *49. Gaster length (GL), maximum straight-line length in lateral view. 50. Head color. 51. Trunk color. 52. Waist color. 53. Gaster color.

APPENDIX 2 : SPECIES LIST

(Type specimens or specimens compared with types were used in the study whenever possible. Field numbers are given for those specimens collected by WHG). 1. *alticolus* WHEELER and CHAPMAN (cotype). 2. *aratus* FOREL (MC-005). 3. *artipus* WILSON (holotype). 4. *binghami* FOREL (cotype). 5. *camposi* WHEELER and CHAPMAN. 6. *ceylonicus* MAYR (cotype of var. *latro*). 7. *chapmani* WILSON (paratype). 8. *cornutus* FOREL (MC-004). 9. *currax* EMERY. 10. *dentatus* FOREL (MC-001). 11. *doryloides* WILSON (holotype). 12. *exilis* WILSON (holotype). 13. *fergusoni* FOREL (compared to type by WILSON). 14. *gracilis* EMERY (MC-007). 15. *huonicus* WILSON (compared to type). 16. *javanus* EMERY. 17. *luzoni* WHEELER and CHAPMAN (cotype). 18. *nganduensis* WILSON (holotype). 19. *pachycerus* FR. SMITH (compared to type by WILSON). 20. *peguensis* EMERY. 21. *philiporum* WILSON (holotype). 22. *wroughtoni* FOREL. 23. *pierci* WHEELER and CHAPMAN. 24. *powersi* WHEELER and CHAPMAN (cotype). 25. *schneirali* WILSON (paratype). 26. *silvestri* WHEELER (cotype). 27. *rabori* CHAPMAN (cotype). 28. *reyesi* CHAPMAN (cotype). 29. *sagei* FOREL (compared to type by WILSON). 30. *philippinensis* CHAPMAN. 31. n. sp. (col. MASCHWITZ). 32. n. sp. (col. GOTWALD, MC-003). 33. *asantei* CAMPIONE, NOVAK and GOTWALD (paratype). 34. African sp. B (GC-071). 35. African sp. C (GAC-044). 36. African sp. D (GAC-047). 37. African sp. E (GAC-054). 38. African sp. I (GAC-034). 41. African sp. G (GAC-076). 42. African sp. J.

APPENDIX 3 : ZOOGEOGRAPHICAL AND CURRENT TAXONOMIC AFFILIATIONS OF SPECIES IN THE STUDY

Zoogeography of *Aenictus* species.

ASIAN SPECIES : 1. *alticolus*. 2. *aratus*. 3. *artipus*. 4. *binghami*. 5. *camposi*. 6. *ceylonicus*. 7. *chapmani*. 8. *cornutus*. 9. *currax*. 10. *dentatus*. 11. *doryloides*. 12. *exilis*. 13. *fergusoni*. 14. *gracilis*. 15. *huonicus*. 16. *javanus*. 17. *luzoni*. 18. *nganduensis*. 19. *pachycerus*. 20. *peguensis*. 21. *philiporum*. 22. *wroughtoni*. 23. *pierci*. 24. *powersi*. 25. *schneirlai*. 26. *silvestrii*. 27. *rabori*. 28. *reyesi*. 29. *sagei*. 30. *philippinensis*. 31. n. sp. (col. MASCHWITZ). 32. n. sp. (col. GOTWALD, MC-003).

AFRICAN SPECIES : 33. *asantei*. 34. sp. B. 35. sp. C. 36. sp. D. 37. sp. E. 38. sp. F. 39. sp. H. 40. sp. I. 41. sp. G. 42. sp. J.

WHEELER'S (1930) subgenera.

(Only those species included in the present study are listed; species described since 1930 are presumed to be placed in their appropriate subgenera).

SUBGENUS *AENICTUS* : 2. *aratus*. 3. *artipus*. 5. *camposi*. 6. *ceylonicus*. 7. *chapmani*. 10. *dentatus*. 11. *doryloides*. 12. *exilis*. 16. *javanus*. 18. *nganduensis*. 19. *pachycerus*. 20. *peguensis*. 21. *philiporum*. 22. *wroughtoni*. 23. *pierci*. 24. *powersi*. 25. *schneirlai*. 27. *rabori*. 28. *reyesi*. 29. *sagei*. 30. *philippinensis*. 31. n. sp. (col. MASCHWITZ). 33. *asantei*. 34. African sp. B. 35. African sp. C. 36. African sp. D. 37. African sp. E. 38. African sp. F. 39. African sp. H. 40. African sp. I. 41. African sp. G. 42. African sp. J.

SUBGENUS *TYPHLATTA* : 1. *alticolus*. 4. *binghami*. 8. *cornutus*. 9. *currax*. 13. *fergusoni*. 14. *gracilis*. 15. *huonicus*. 17. *luzoni*. 32. n. sp. (MC-003).

SUBGENUS *PARAENICTUS* : 26. *silvestrii*.

WILSON'S (1964) species groups.

(The following lists include species not examined in this study; all African species are presumed here to belong to WILSON'S *ceylonicus* group).

WROUGHTONI GROUP : 3. *artipus*. 5. *camposi*. 29. *sagei*. 22. *wroughtoni*.

CURRAX GROUP : 8. *cornutus*. 9. *currax*. 14. *gracilis* 15. *huonicus*.

PACHYCERUS GROUP : 2. *aratus*. 7. *chapmani*. 10. *dentatus*. 19. *pachycerus*. 30. *philippinensis*. 21. *philiporum*. 24. *powersi*. *punensis*. 27. *rabori*. 28. *reyesi*. 26. *silvestrii*.

LAEVICEPS GROUP : 1. *alticolus*. 4. *binghami*. 13. *fergusoni*. *laeviceps*. 17. *luzoni*.

CEYLONICUS GROUP : *biroi*. *brevicornis*. 6. *ceylonicus*. 11. *doryloides*. 12. *exilis*. 16. *javanus*. 18. *nganduensis*. 23. *piercei*. 25. *schneirlai*. 33-42. African species.

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