Quantitative Studies on Major Workers of the Ant Genus *Dorylus* (Hymenoptera: Formicidae: Dorylinae)

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ABSTRACT

Ann. Entomol. Soc. Am. 73: 231–238 (1980)

Quantitative studies of the major workers of the Old World army ant genus *Dorylus* were undertaken to elucidate the underlying taxonomic structure of the morphological data gathered. This taxonomic structure was then compared to the existing 6 subgenera in which the species of *Dorylus* are currently classified. Although the status of the subgenera *Dichthadia* and *Typhlopone* remains unclear, the subgenera *Alaopone* and *Rhogmus* are deserving of continued individual status. Members of the subgenera *Dorylus* and *Anomma* form a single, diverse, but continuous taxon with species of the *emeryi* group connecting the morphological extremes. A formal taxonomic decision regarding the status of the 6 subgenera is not offered, but future decisions must recognize that these quantitative studies yield only 4 integral species clusters among major workers of *Dorylus* species: these correspond to the subgenera *Rhogmus*, *Alaopone*, *Typhlopone*, and *Dorylus* (s.s.).

Old World army ants of the genera *Dorylus* and *Aenictus* comprise the subfamily Dorylinae, while the New World species of "true army ants" belong to the subfamily Ecitoninae (Snelling 1980). This arrangement constitutes a recent change in taxonomic status for the army ants, since the traditional view placed both groups in a single subfamily. The change reflects the conviction that the New and Old World species are separately derived and that army ant behavior patterns and morphologies were arrived at convergently at least twice. It is possible that even *Dorylus* and *Aenictus* arose from different ancestors and only recently became sympatric over parts of their ranges (Gotwald and Kupiec 1975; Gotwald 1980).

The Ecitoninae were revised by Borgmeier (1953, 1955), and his revision is likely to remain relevant for years to come. The Indo-Australian species of *Dorylus* and *Aenictus* were revised by Wilson (1964), and thus of those army ants once regarded as a monophyletic group, only the African forms of *Dorylus* and *Aenictus* remain to be revised. One of us (WHG) is currently involved in such a revision, and the research reported here is part of the revisionary study.

Species of *Dorylus* are grouped into 6 subgenera (*Alaopone, Anomma, Dichthadia, Dorylus, Rhogmus,* and *Typhlopone*) that have been defined by relatively distinctive states of few characters (Fig. 1). These groupings, however, are not without their complications, the most vexing of which centers on the relationship of *Dorylus* (s.s.) to *Anomma*. Within *Anomma* is a series of species, referred to as the *emeryi* group, that appears transitional between the 2 subgenera. Obviously, the status of the subgenera must be reviewed within the context of the generic revision, and adjustments made to reflect accurately the broader taxonomic and phylogenetic conclusions.

With these points in mind, a quantitative study of the major workers of *Dorylus* was undertaken. Although the genus *Dorylus* as presently constituted may contain 40 or more species, only 24 are known from the major

workers. Because the nomenclature for African *Dorylus* has still not been determined decisively, species included in this study are referred to by number only. Correspondence with named species will be recorded in the generic revision (Gotwald, unpubl.). The goal of the research was to provide insight into the grouping of *Dorylus* species relative to the present subgeneric designations.

Materials and Methods

A set of 50 characters was chosen to describe each of the 24 species used in the study. The character set included metric, meristic, and ordered multi-state characters as well as several standard myrmecological indices. The exemplar method (Sneath and Sokal 1973: 183) of characterizing species by a selected specimen of the major worker (relatively rare in collections) for each species was used. One complete analysis was done of the full 50-character data set. A subset of 33 characters was chosen from the 1st to include only metric and meristic characters, and exclude the ordered multi-state characters. A separate analysis of the reduced, 33-character data set was performed to estimate the influence of size which dominates these characters and has influenced earlier taxonomic decisions on this group of species. To eliminate the overwhelming influence of size common to many phenetic studies (Wood 1979), all metric characters were transformed to ratios of pro-femur length, and the transformed data then served as the basis for a third complete set of analyses. Those characters (Appendix I) retained in the reduced set are marked with an asterisk and those converted to ratios with a dagger. The complete 50-character raw data set of scores for the 24 species of this study is available from either author upon request.

Data for all analyses were first standardized by expressing each score as a deviation from the mean in standard deviation units. The standardized data set was then used to calculate average taxonomic distance from each species to every other species and the product-moment correlation coefficients between all species. Clustering on both of these similarity measures was then performed using the unweighted pair-group method on averages (UPGMA) which has been shown by a number
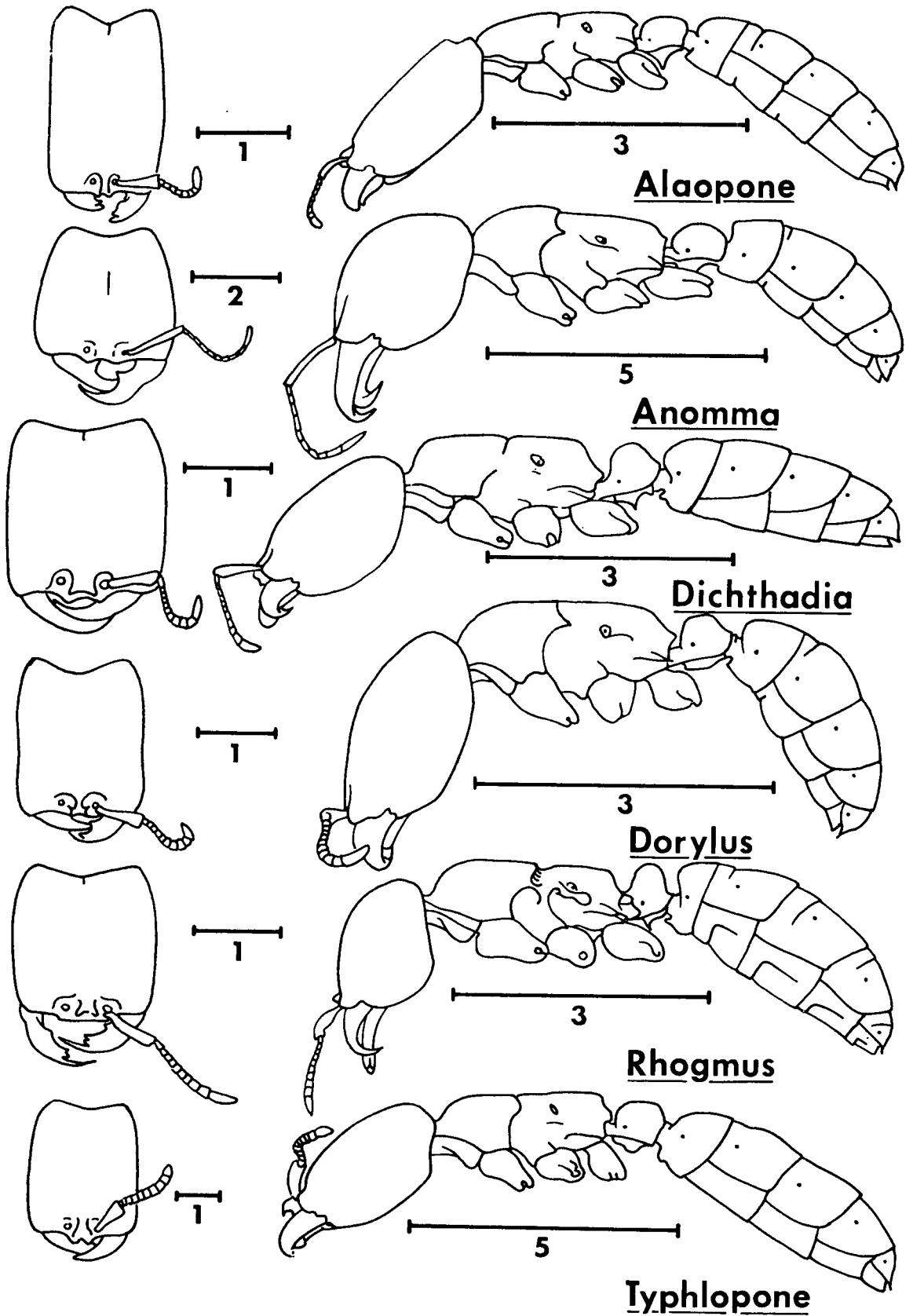
FIG. 1.—Major workers representing the 6 subgenera of the genus *Dorylus*. To the left of each habitus drawing (legs omitted) is the head in dorsal view. Scales in mm.

of authors (Sokal and Rohlf 1962, Sneath 1969) to yield highest correlations with the original similarity matrices. The results of clustering are displayed in the form of standard phenograms.

The standardized data also served as the basis for ordination procedures used to test the consistency of major groupings indicated by the clustering techniques. Principal components analysis (PCA) was used to array the 24 species in three-dimensional attribute (A) space. An ordination producing less distortion from the original distance matrices was produced by the technique of non-metric multi-dimensional scaling (MDS). The MDS ordination was subsequently rotated to alignment with the major axes of variation established by PCA. Areas of distortion of taxonomic relationships between the 24 taxa of the study were identified in both ordination techniques by fitting a minimum spanning tree based on distances or correlations as appropriate. Results were plotted as a three-dimensional diagram so that similarity of relationships could be more readily assessed visually. All procedures are discussed by Sneath and Sokal (1973).

Computations were carried out on the IBM system 370-165 computer at the Univ. of Toronto. Clustering and ordination procedures were performed with the NT-SYS package of programs (Rohlf et al. 1972). Representation of ordinations in three-dimensional perspective was accomplished by the program PHYSETER written by Ralph Gibson at the University of Toronto.

Results

The multivariate procedures used in this study have been employed in an exploratory rather than a confirmatory mode; no significance, therefore, is attached to precise similarity values. Rather, our attempt has been to discover the taxonomic structure inherent in the data and to draw preliminary conclusions as to the phenetic affinities of the *Dorylus* species included.

All phenograms produced by the UPGMA technique were similar, and those illustrated in Fig. 2 and 3 are representative. The UPGMA phenogram (Fig. 2) based upon average taxonomic distances from transformed data shows 6 distinct species clusters that reappear in one form or another in most analyses and resemble the subgeneric classification presently used (see Gotwald 1980) within the genus *Dorylus*. The 3 species of the subgenus *Typhlopone* cluster together and are joined at a lower level of similarity by the single *Dichthadia* species in the study. All species of the subgenus *Rhogmus* also cluster together as do the 5 members of *Dorylus* (s.s.). The 2 *Alaopone* species cluster together and are related at only a relatively low level of similarity to all of the aforementioned groups. Six species of the subgenus *Anomma* cluster together and are related at an extremely low level of similarity to the subgenera clustering with *Dorylus* (s.s.). The major difference between this phenogram and the existing classification is seen in the 3 *Anomma* species (20, 21, and 24) that cluster at a low level of similarity, not with the other 6 *Anomma* species, but with the remaining subgenera within the genus.

In the 2 other distance phenograms not reproduced here, the subgeneric groupings representing *Rhogmus* and *Alaopone* species are relatively well-integrated and

robust. The integrity of other groupings, however, is compromised by anomalous behaviour of several individual species and species groups. The small group of *Anomma* species, 20, 21, and 24, cluster in both instances with the other members of their subgenus, and *Typhlopone* species 2 and 3 are in one instance grouped with the *Anomma* species as well, as is *Dorylus* species 11. Even *Rhogmus* species 6 in one instance clusters more closely with the species of *Dorylus* (s.s.) than with its own group. All the distance phenograms agree with that illustrated in Fig. 2 in the detection of a major dichotomy between those species groups associated with the subgenus *Anomma* and those associated with the subgenus *Dorylus* (s.s.).

The correlation phenograms (e.g., Fig. 3) are also basically consistent with the currently accepted subgeneric classification of the *Dorylus* species in this study. Again, the groupings of *Typhlopone* species, *Rhogmus* species, *Alaopone* species, *Dorylus* (s.s.) species, and *Anomma* species show a high degree of integrity (Fig. 3). The single *Dichthadia* species is most closely related to *Typhlopone*, and *Rhogmus* and *Alaopone* have clustered together. Only *Dorylus* (s.s.) species 11 shows a degree of distinction from the other 4 species in the group. Most *Anomma* species show a relatively close, stepwise, relationship to one another except for the loose cluster of 3 species: 20, 21, and 24.

Only one major variation upon this pattern was seen in the correlation phenograms derived from the raw data of 50- and 33-characters. *Dorylus* (s.s.) species 11 clustered in one case loosely and in a second case more closely with species of the subgenus *Anomma*. When well integrated into the *Anomma* cluster, *Dorylus* species 11 showed greatest affinity with the already distinctive subgroup of species 20, 21, and 24 (33-character data set). All clustering analyses of this type preserved the clear dichotomy between species clustering with *Dorylus* (s.s.) and those species clustering with the subgenus *Anomma*. In all cases the 1st group included the major portion of the subgenera *Typhlopone, Rhogmus, Alaopone*, and the single *Dichthadia* species.

Ordination procedures in general can produce a more realistic picture of the affinities among included groups of OTU's in a numerical taxonomic study, because they preserve a continuous picture of degrees of similarity between closely related groups. Accordingly, an ordination procedure is not so readily adaptable to providing a classification (nor to matching existing classifications) as are the clustering procedures discussed above. Nevertheless, ordinations provide a healthy perspective on the results of clustering by indicating when clustering subdivisions represent artificial boundaries imposed on the true structure of the data.

Ordination by principal components analysis (PCA) in particular is generally considered to produce more accurate representation of the relationships between major subgroups of included taxa, but to be less reliable in representing the fine structure of phenetic affinities in subgroups (Rohlf 1972). All PCA ordinations computed in this study were fitted with a minimum spanning tree calculated from both distance and correlation matrix data, and all showed major distortions not only in the
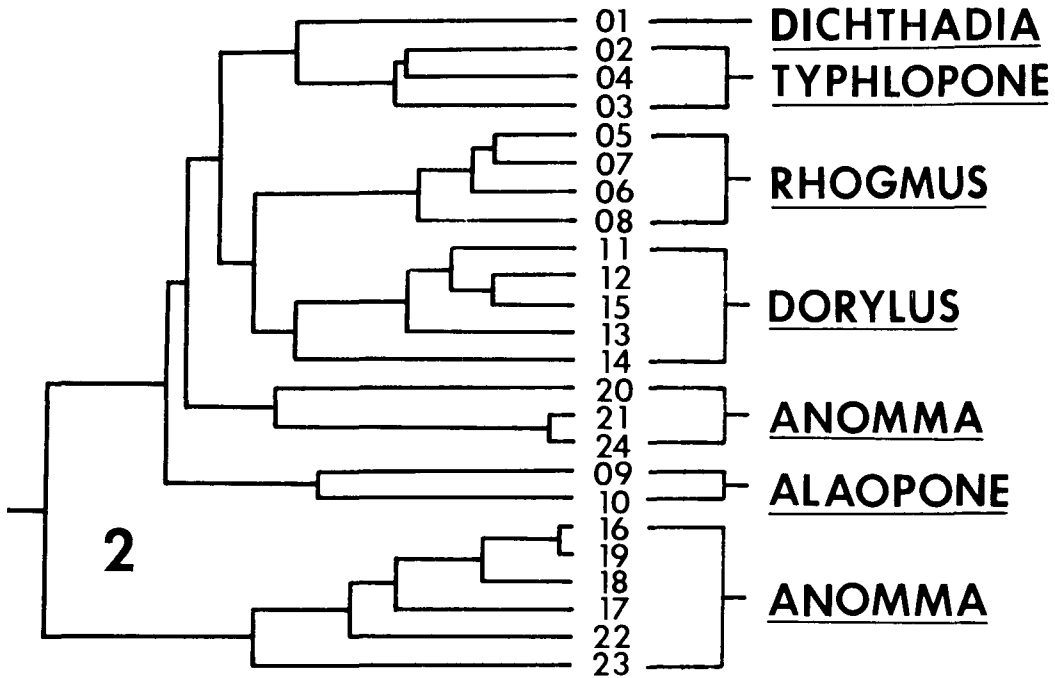
Fig. 2.—Phenogram produced by UPGMA clustering of average taxonomic distances calculated on the transformed data. Matrix correlation (cophenetic correlation) $r = 0.778$.
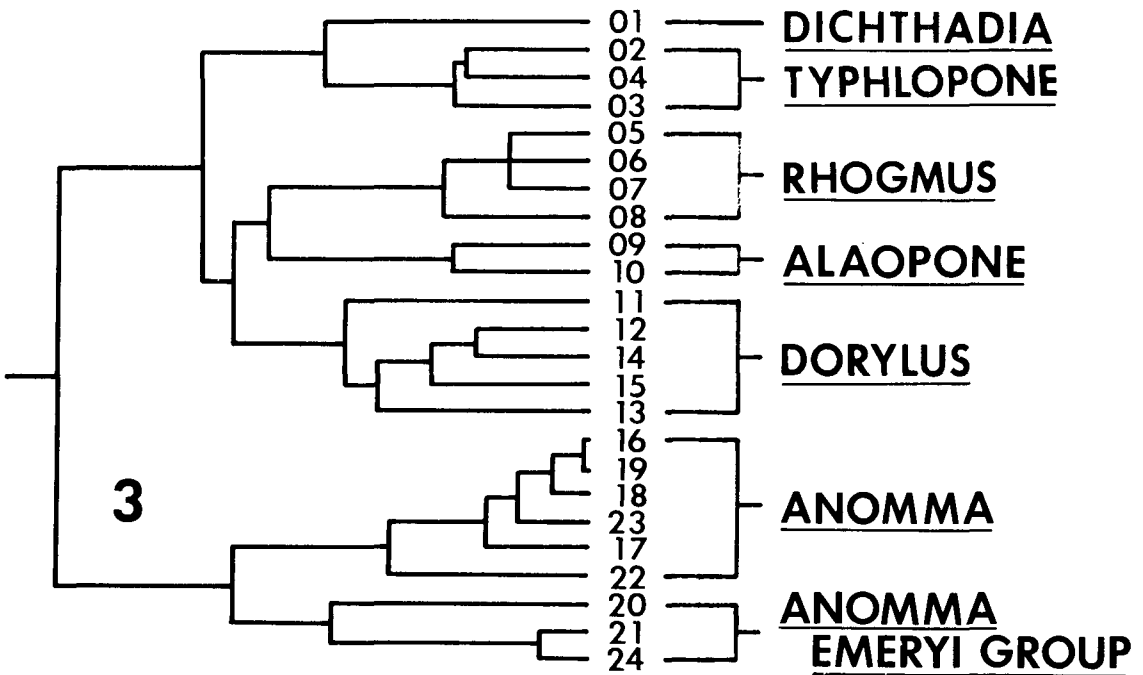

Fig. 3.—Phenogram produced by UPGMA clustering of product-moment correlation coefficients calculated on the transformed data. Matrix correlation $r = 0.887$.

position of specific taxa, but in the integrity of various species clusters. Because of this fact and also because the overall results of PCA ordination were fairly similar to those of multi-dimensional scaling (see Fig. 4,5), no diagrams of the results of the former technique are figured here.

Nevertheless, the major consistent features of the 3 PCA analyses may be summarized. In all cases, *Dorylus* (s.s.) species formed one focus in the PCA ordination diagrams and the *Anomma* group of species a second. The 2 species groups *Alaopone* and *Rhogmus* showed a high degree of individual integrity and a consistent but narrow isolation from *Dorylus* (s.s.). The placement of the *Dichthadia* and *Typhlopone* species was unpredictable, some of them clustering on occasion with the *Dorylus* (s.s.) species, with a diffuse group of species in the region between *Dorylus* (s.s.) and *Anomma*, or by themselves as a satellite of *Dorylus* (s.s.). The integrity of the subgenus *Dorylus* (s.s.) was also unpredictable, especially because species 11 showed a tendency to move toward the *Anomma* group of species. On the other hand, *Anomma* species 20, 21, and 24 showed a strong tendency to move toward the centre of *Dorylus* (s.s.) and to a lesser degree, species 22 and 18 shared this tendency as well.

Aside from indicating in more detail the associations between some of the subgroups detected in clustering, the principal interest of the PCA analysis was in an examination of the loading of characters on the 1st 3 component axes chosen by the procedure. This type of analysis gives some appreciation of the character information which contributes most heavily to variation in the raw data and thus to the separation of species in both clustering and ordination procedures. For the 50-character data set, component axis I accounted for 53.38% of the total variation in the data and showed heavy loadings for all the major metric characters. Thus the 1st component axis proved here, as in a variety of other studies (e.g., Schnell 1970), to be representative of a general size factor among taxa. In the analysis of the 33-character set, the 1st component axis accounted for a much larger contribution towards total variation in the data (69.83%) and loaded even more heavily for characters expressive of overall size. Some of the spination characters also loaded heavily on axis I in this analysis, suggesting an allometric relation between size and spininess. Component axes II and III accounted for 6 to 10% each of the remaining variability explained by the 1st 3 component axes in the different analyses, and expressed the impact of characters of head and mouthpart morphology, as well as body sculpturing, color, and petiolar morphology.

After transformation of metric data to ratios of profemur length, PCA produced somewhat different results (all previous metric characters can now be interpreted as indicative of shape rather than size). The 1st 3 component axes accounted for only 60.86% of the total variation in the data, due primarily to the reduction in explanatory value of the 1st axis to 40.52%. The single character loading most heavily on the 1st principal component axis is still the only pure metric character left in the analysis, profemur length. Also important in separating species in

this dimension were shape characters related primarily to the thorax, petiole, gaster, and legs. Loading heavily for the 1st time in any of the PCA analyses were those shape indices originally scored as raw data relating to head characters such as the scape index, cephalic index, mandibulo-cephalic index, and 2 characters expressing the shape of mouthparts. Spination of the basisternum and the petiolar shape index also showed a significant relationship to the 1st axis. The 2nd component axis accounted for only 11.2% of total variation and was weighted most heavily for characters expressive of general morphology of head and mouthparts. Component axis III accounted for 9.31% of total variation and was again most heavily influenced by head morphology and sculptural features of the thorax and petiole. The 3 PCA procedures showed a strong relationship between the importance of component axis I in explaining variability and the extent of the influence of overall size on species separation.

At this point it was clear that size played an over-riding role in the data of the reduced, 33-character set, and was responsible for the anomalous placement of a number of taxa in previous analyses. Therefore, application of the multi-dimensional scaling technique was restricted to the 50-character set of raw data and this same data set after transformation of metric characters to ratios. This 2nd MDS ordination based on average taxonomic distances is illustrated in Fig. 4. Boundaries have been drawn around sets of species to define subgroups whose members have each other as nearest neighbors based on the minimum spanning tree also calculated from distances. Nearest neighbor distances from group to group are shown by dotted lines joining the particular species involved. While the perspective view shown in Fig. 4 is useful for identifying the major subgroupings, counterclockwise rotation of the diagram in the horizontal plane to yield the view shown in Fig. 5 provides additional visual information on certain relationships. The 3 axes of the ordination are those of the principal components analysis on transformed data described above.

Most of the species groups mentioned for previous analyses are distinguishable in the MDS diagram (Fig. 4) although divisions between them are not nearly so sharp. Even where the ordination does not show a group as clearly discrete, the nearest neighbor distances support the basic integrity of the *Rhogmus* species cluster (Fig. 4,5), the *Alaopone* species cluster (Fig. 5), the *Dorylus* (s.s.) (Fig. 4) species cluster, the *Dichthadia/Typhlopone* species cluster (Fig. 4), and the 5 *Anomma* species exclusive of the group 20, 21, and 24 (Fig. 5). *Alaopone* and *Rhogmus* species are clearly related to those of *Dorylus* but remain distinctive. The *Dichthadia/Typhlopone* species are also related to *Dorylus* (s.s.), and although they appear mixed in with them in Fig. 5, the view shown in Fig. 4 and results of nearest neighbor analysis support the distinctness of the former group of species.

Anomma species are very much strung out into a long, poorly coordinated species group (Fig. 5), and the 3 *Anomma* species 20, 21, and 24 are clearly shown in the view of Fig. 5 to be intermediate between *Anomma* and *Dorylus* (s.s.). In fact, this ordination shows what is
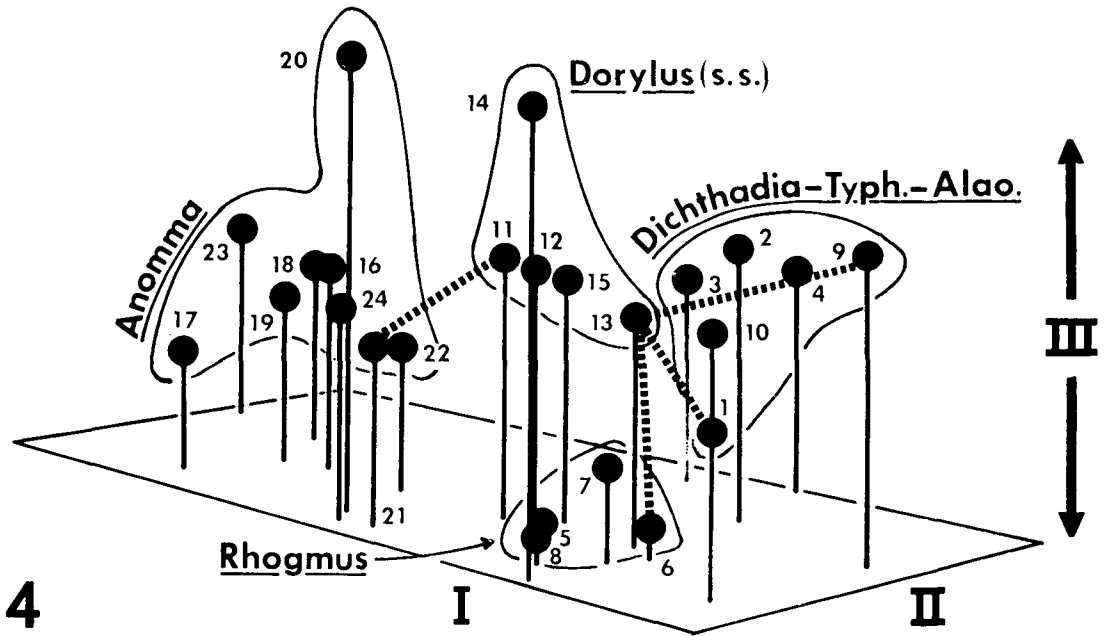
Fig. 4.—Non-metric multi-dimensional scaling (MDS) ordination of the 24 *Dorylus* species in the A-space defined by the 1st 3 component axes (I, II, III): based on average taxonomic distances calculated on the transformed data (stress = 0.168). Nearest neighbours in contiguous subgroups from the minimum spanning tree are joined by dotted lines; lengths of dotted lines in units of average taxonomic distance are: 21 to 22 = 0.997, 21 to 11 = 0.915, 13 to 6 = 0.911, 13 to 1 = 0.984, and 13 to 9 = 1.201. All other MST connections are within subgroups.
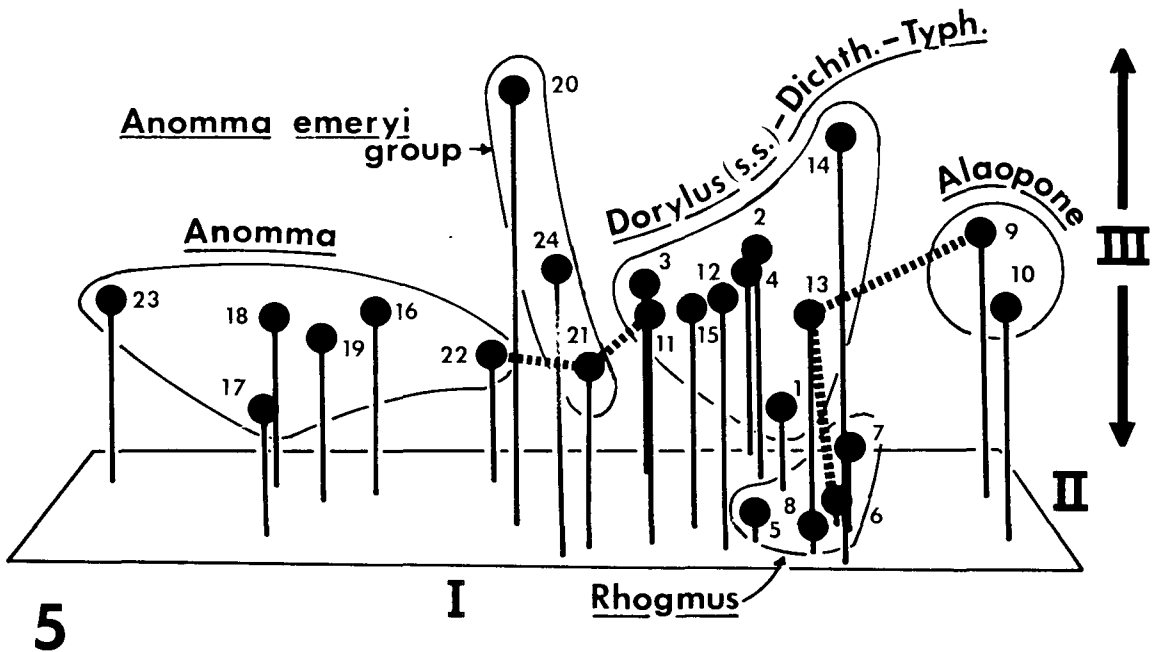

FIG. 5.—Same MDS ordination as Fig. 4, rotated counterclockwise in the horizontal plane ca. 60°

hinted in preceding analyses, that there is almost a continuum between the species of the *Dorylus* (s.s.) subgroup and those of *Anomma*, with the 3 *Anomma* species of the *emeryi* group (20, 21, and 24) in a clearly intermediate position. The MDS ordination of distances calculated from raw data showed the same basic features as illustrated in Fig. 4 and 5, but the species-group clusters are considerably more distinct and compact, with only individual species 11 and 22 bridging the gap between the *Dorylus* (s.s.) cluster and the *Anomma* group.

Discussion

The underlying taxonomic structure inherent in phenetic data from major workers of 24 *Dorylus* species is similar to several features of the current subgeneric classification. Results of the different analyses have shown considerable consistency, indicating reality of the underlying structure, and have pointed out certain features of the data responsible for variation in the affinities of particular species or species groups.

Several pieces of information led us to the conclusion that overall size was a feature of the data causing serious distortion of analytic results. Most species of the subgenus *Anomma*, for instance, are distinctively larger than other *Dorylus* species, and *Anomma* species number 22 is the smallest of its subgenus. *Dichthadia* and *Typhlopone* species number 4 are also relatively large members of the genus *Dorylus*, as is *Dorylus* (s.s.) species number 11, which is distinctively larger than the rest of the species in that subgenus. It is precisely these species, which differ from their relatives in the existing classification primarily on the basis of size, that have shown the most variable behavior in the various procedures of this study. This fact, and the heavy loading of metric characters on the 1st principal component axis coupled with the importance of this axis in separating species groups, led us to identify size as a major confounding factor throughout the study. The impression was further strengthened by the analysis of the size-weighted, 33-character data set which simply increased the anomalies described above, exactly as would be expected if species placement was being influenced primarily by size rather than some other constellation of characters.

The analyses on the transformed data set are most free of bias introduced by overall size and show a good balance of the influence of characters expressive of shape, morphology of the head and mouthparts, and general body sculpturing. Opinions both critical (Atchley et al. 1976) and supportive (Hills 1978) of the use of ratios as characters in quantitative studies have been published. Our results, however, show that in practice, the use of ratios can eliminate a good portion of obvious size-related effects. Thus Fig. 2, 3, 4, and 5 represent the least biased and least distorted picture of basic taxonomic structure.

Based upon the studies reported here, it is possible to make a number of generalizations about the phenetic affinities of the *Dorylus* species included in this study. The 2 *Alaopone* species are consistently most closely related to one another and are never split up or transferred to other species groups. The closest affinities of the group are about equally with *Dorylus* (s.s.) and *Rhogmus*. The 4 species classified currently in the subgenus *Rhogmus*

also show a high degree of interspecific affinity throughout this study, and their affinities too are more or less equally with *Dorylus* (s.s.) and *Alaopone*.

The single species of *Dichthadia* is always shown with closest affinity to one or more of the *Typhlopone* species, but this group of 4 species shows a very close relationship to the species of *Dorylus* (s.s.) and in some analyses breaks down, the individual *Typhlopone* species 2 and 3 becoming intermixed with species in the *Dorylus* (s.s.) group. There is a general distinction between a nodus of species currently assigned to *Dorylus* (s.s.) and a separate center of species currently assigned to *Anomma*, but it appears from the relationships between these 2 groups and the diffuse nature of the *Anomma* cluster that they represent opposite ends of a continuum rather than clearly distinct taxa. Thus, the dichotomy shown in the phenograms is an artificial classificatory device typical of clustering methods. Of particular interest is the *emeryi* group of species (20, 21, and 24) of the subgenus *Anomma*, which previous classical taxonomic analysis has identified as being rather *Dorylus*-like representatives of their subgenus. They would appear to lie in the A-space of the MDS diagram (and this is supported by most PCA analyses as well), in a position intermediate between the *Anomma* and *Dorylus* (s.s.) ends of the continuum.

Conclusions

It would be premature at this time to propose a revision of the taxonomic structure of the genus *Dorylus* based only on our studies of major workers. We intend in the future to include similar phenetic analyses of characters from the males and other characters of the genus, and final decisions on intrageneric classification must be reserved until that time. However, our preliminary study indicates several potentially unsatisfactory features of the current classification and suggests features of the taxonomic structure to be watched for in future analyses.

In particular it would seem that the subgenera *Rhogmus* and *Alaopone* are deserving of continued individual status, although the status of the subgenera *Dichthadia* and *Typhlopone* is much less clear. There would also seem to be considerable support for regarding the species currently assigned to *Dorylus* (s.s.) and *Anomma* as members of a diverse but continuous taxon encompassing the entire range of variation of the two original subgenera. The species of the *emeryi* group neatly fill the gap between the two extremes.

Thus the phenetic relationships among major workers of *Dorylus* suggest that one of the options available for the future would be to recognize only 4 integral species clusters among the species previously classified in the genus: *Rhogmus*, *Alaopone*, *Typhlopone*, and *Dorylus* (s.s.). Whether to regard these 4 groups at the generic or subgeneric level can only be determined by extension of the study to additional phena within the genus *Dorylus* and to other genera of the Dorylinae and Ecitoninae.

Acknowledgment

script. H. Sutton and N. Avruch assisted in processing the data, and funds for computer time were provided by the Royal Ontario Museum. The research was supported, in part, by National Science Foundation Grant DEB77-03356 (W. H. Gotwald, Jr., Principal Investigator). The junior author acknowledges receipt of operating grant No. A9725 from the Natural Sciences and Engineering Research Council (Canada).

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Appendix I

Character List

(All lengths measured in mm to nearest 0.01 mm)

*1. Number of antennal segments (including scape). †*2. Length of terminal flagellar segment. †*3. Scape length (excluding neck) (SL). *4. Scape index (SL × 100/HW). †*5. Head length (HL). *6. Cephalic index (HW × 100/HL). †*7. Maximum head width (HW). †*8. Anterior head width (AHW). †*9. Posterior head width (PHW). †*10. Degree of head taper (AHW–PHW). 11. Shape of occipital angles in dorsal view. 12. Shape of occipital angles in lateral view. †*13. Interantennal distance (between mesal margins of sockets). 14. Spination of frontal carinae. 15. Shape of frontal carinae in lateral view. 16. Texture of head exoskeleton. 17. Head color. †*18. Mandible length (ML). *19. Mandibulocephalic index (ML × 100/HL). *20. Number of subapical mandibular teeth. 21. Mandibular shape. 22. Shape of 1st subapical mandibular tooth. *23. Number of labral tubercles. *24. Number of segments in maxillary palpus. †*25. Length of terminal segment of maxillary palpus. †*26. Length of terminal segment of labial palpus. 27. Shape of galeal crown. 28. Shape of anterior clypeal margin. 29. Texture of pronotal exoskeleton. 30. Color of pronotum. †*31. Pronotal width in dorsal view. †*32. Length of mesosoma. 33. Promesonotal/promesopleural suture completion. †*34. Distance from propodeal spiracle to posterior mesosomal margin. 35. Spination of basisterna. †*36. Profemur length. †*37. Protibia length †*38. Mesofemur length. †*39. Mesotibia length. †*40. Metafemur length. †*41. Metatibia length. †*42. Length of petiolar node (PL). †*43. Minimum width of petiole (PNW). †*44. Maximum width of petiole (PWW). *45. Petiolar index A (PNW × 100/PL). *46. Petiolar index B (PWW × 100/PL). 47. Development of subpetiolar process. †*48. Length of gaster in lateral view. 49. Shape of pygidial impression margins. 50. Color of gaster.