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Biometric study of some *Domasia* species (Acritarcha) from the Silurian of the Brabant Massif, Belgium

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ABSTRACT – Morphological variation within the genus *Domasia* hampers species determinations. As most species have a short stratigraphic range, it is important to differentiate them. The studied specimens belong to a morphon whose morphological end members are *D. elongata* (sensu Downie, 1960), *D. limaciformis* (sensu Cramer, 1971), *D. symmetrica* (sensu Cramer, 1971), and *D. trispinosa* (sensu Downie, 1960). A biometric study, based on 16 variables and a statistical analysis created four clusters. Cluster 2 and cluster 4 are close to *D. limaciformis* (sensu Cramer, 1971) and *D. symmetrica* (sensu Cramer, 1971) respectively. A discriminant analysis showed the validity of these clusters (98% of correct reallocation); and accordingly, these two species, which had been placed in synonymy, are considered to be differentiable. A classification law is presented to assist identification of specimens of the particular species. This study demonstrates the potential of multivariate statistical analysis for the solution of systematic problems.

RIASSUNTO – [Studio biometrico di alcune specie di *Domasia* (Acritarcha, Siluriano, Massiccio del Brabante, Belgio) – Variazioni morfologiche all'interno del genere *Domasia* rendono difficili le determinazioni specifiche. Dato che molte specie hanno una distribuzione stratigrafica ristretta, è importante differenziare queste specie. Gli esemplari studiati appartengono ad un morphon i cui estremi morfologici sono *D. elongata* (sensu Downie, 1960), *D. limaciformis* (sensu Cramer, 1971), *D. symmetrica* (sensu Cramer, 1971) e *D. trispinosa* (sensu Downie, 1960). Uno studio biometrico, basato su 16 variabili e su una analisi statistica ha prodotto 4 cluster. Il cluster 2 è vicino a *D. limaciformis* (sensu Cramer, 1971) ed il cluster 4 a *D. symmetrica* (sensu Cramer, 1971). Una analisi discriminante ha mostrato la validità di questi cluster (98% di allocazione corretta) e pertanto vengono distinte queste due specie che erano state prima messe in sinonimia. Viene inoltre proposta una legge di classificazione come un aiuto nella identificazione degli esemplari delle specie studiate. Questo studio illustra il potenziale della analisi statistica multivariata nella soluzione di problemi sistematici.

INTRODUCTION

The genus *Domasia* Downie, 1960 is composed of simple forms, but many transitional specimens hamper firm specific attributions. Since most of its species have short stratigraphic ranges it is important to establish new criteria to ease specific determinations. The goal of this study was to test the usefulness of biometric study coupled to multivariate statistical analysis in the solution of systematic problems.

The biometric measures were chosen after scanning the slides in which specimens were located and morphological variations noted. The statistical processing of the measurements began with a principal component analysis. This allowed us to reduce the number of variables to be taken into account. The grouping of specimens into clusters by K-mean cluster analysis led to various models with different numbers of clusters. We retained the model whose clusters presented the best consistency among the specimens displayed. This consistency was based on statistics and overall morphology rather than systematic criteria. The validity of the chosen model was tested with a discriminant analysis. This provided a classification law that allocates a specimen to one of the clusters according to its biometric measurements. Then we

gave a systematic attribution to each specimen in order to interpret and discuss the clusters. When transitional forms were encountered they were given two specific names. The first indicates the species to which the specimen is closest. The second indicates the species to which the specimen is transitional. The systematic attribution of specimens within the four clusters allowed us to compare some clusters with previously defined species. Consequently we are able to propose new biometric criteria to distinguish the studied species.

HISTORICAL REVIEW

Downie (1960) created the genus *Domasia* for "forms with ellipsoidal tests and unequal processes", and eleven species have been validly published so far (Fensome *et al.*, 1990). Cramer (1971), Thusu (1973), and Hill (1974) found that some *Domasia* species exhibited morphological variations that hampered specific determinations. The emended diagnosis of the genus (Hill, 1974) is as follows: "Vesicle hollow, subcircular to elongately ellipsoidal in outline. The long axis of the body is parallel with the axis of the vesicle. At one pole (the posterior) a single, often reduced process and at the opposite (anterior)

pole usually two single, sometimes three or one bifurcating process(es) are present. Vesicle wall smooth to microsculptured, unilayered. Vesicle symmetry axis longitudinal, hemimorphic."

Downie (1960) created three species with a material base of only four specimens (Downie, 1960, text-fig. 1). There were two specimens of *Domasia trispinosa*, one of *D. bispinosa* (not recorded herein), and one of *D. elongata*. *D. trispinosa* Downie, 1960 (type species) was originally described as follows: "The hollow ellipsoidal body is pale yellow-green with a smooth matte surface. In every specimen the interior is empty. The longer dimension of the body is about 17 µm. Two similar hollow spines of a length about equal to that of the body occur at one end (anterior). The spines bases are separate and merge with the test wall, distally they narrow steadily to a point. In some instances these spines are divided by internal septa. The single posterior spine is only a little shorter but is much narrower and it cannot be determined whether or not it is hollow". Specimens attributable to *D. trispinosa* are illustrated herein as Pl. 1, figs. 6, 7.

Domasia elongata was described by Downie (1960) as follows: "The hollow, elongate, more or less cylindrical test is pale yellow-green with a faintly granular surface. The interior is empty. The length of the body is about 20 µm. Two similar hollow spines without partitions occur at the anterior end, joined at their bases and about equal to the body in length. The posterior spine is hollow, less than half the length of the body and widens broadly at the base to merge with the test". Specimens 1 (Pl. 1, fig. 1) and 45 (Pl. 3, fig. 45) are here attributed to *D. elongata*. Downie (1963, text-fig. 2, p. 634) later noted possible morphological relationships among *D. trispinosa*, *D. elongata*, *Veryhachium elongatum* Downie, 1963, and other species.

Stockmans & Willière (1963) created two species of *Veryhachium*: *V. delmeri* and *V. limaciforme*. Martin (1969) placed *V. elongatum* in the synonymy of *V. limaciforme*. Concerning morphological series, Martin (1969, p. 147) noted that *V. limaciforme*, *V. delmeri*, *D. elongata*, *D. trispinosa*, *D. bispinosa*, and *D. amphora* were simple and closely similar forms: with the shape of more or less bulging isosceles triangles and with simple processes extending the angles of the central body in the same plane. Moreover, she stated that the species are easily distinguished since they do not vary greatly.

Cramer (1970, p. 68) considered *V. limaciforme* to be a synonym of *V. delmeri* and transferred *V. limaciforme* to *Domasia*, with the new combination *D. limaciformis* (Stockmans & Willière) Cramer, 1971. He provided a more detailed description of the species: "Central portion of the vesicle hollow, elongately triangular in outline. The long sides of the triangle are convex and grade into the broad based process. Apart from the basal portion, the processes

are long and slender. At the corner of the body there are simple processes present. The surface of the ectoderm is psilate and the vesicle wall is unilayered. The species tend to open by a straight to C-shaped split pylome which is just below the bases of one of the posterior processes and which is oriented parallel to the long axis of the body". Specimens 12 and 15 (Pl. 1, figs. 12, 15) are here attributed to *D. limaciformis*. Cramer's (1971, p. 68) arguments for merging *V. limaciforme* and *V. delmeri* together into *D. limaciformis* were: "it is practically impossible to tell one taxon apart from the other ... thousands of specimens occur which are all slightly different and are all attributable to either of Stockmans and Willière's species". Moreover, he noted that previously defined species of *Domasia* formed continuous groups. He distinguished two groups, one for *D. bispinosa* and *D. trispinosa*, and the other for *D. elongata*, *D. amphora*, *D. symmetrica*, and *D. limaciformis*. Concerning these last four species he stated that "transitional forms are quite abundant ... Consequently the limits of the above phenotypic centres are hazy".

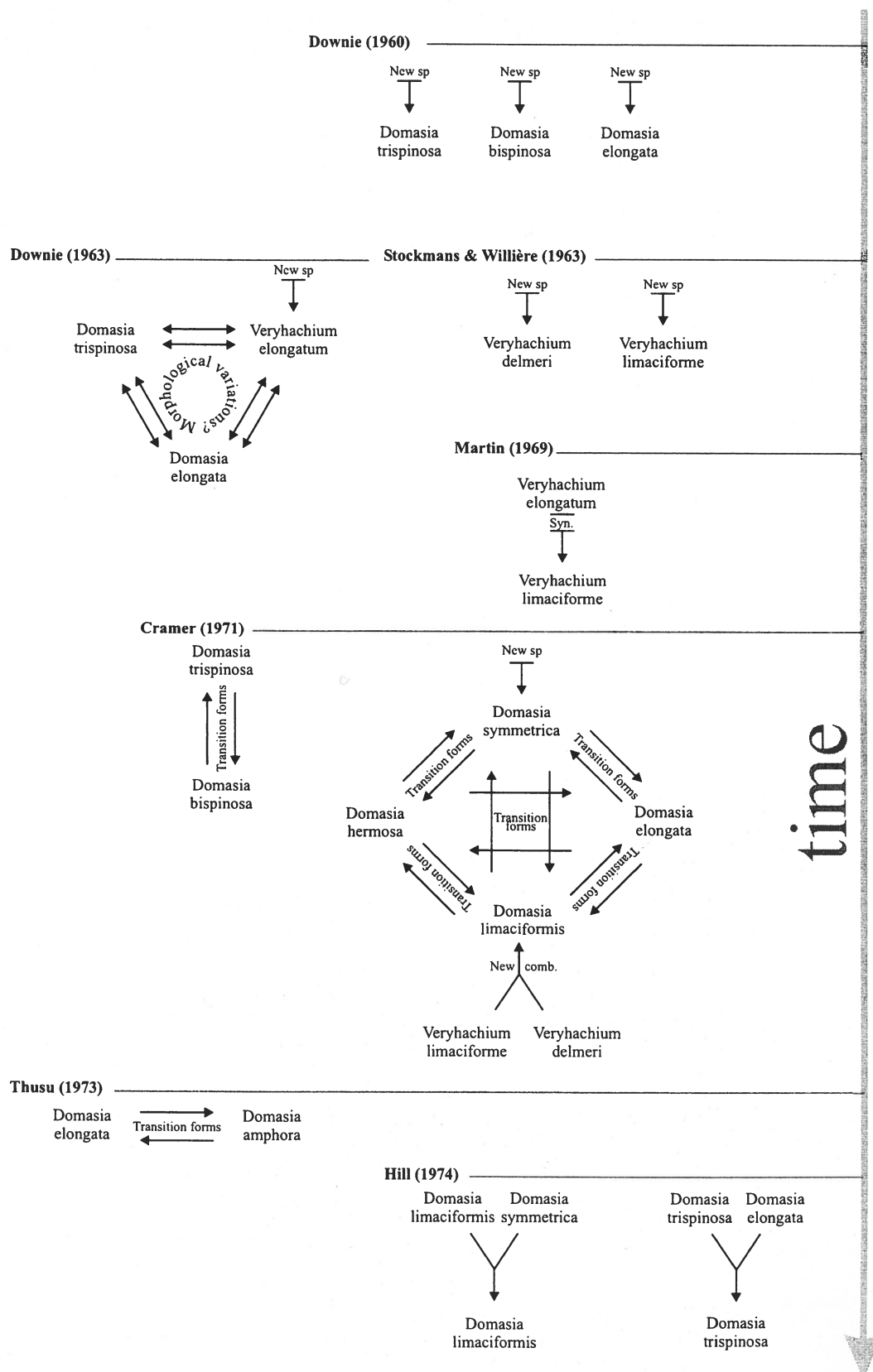
Domasia symmetrica was described by Cramer (1971) as follows: "The vesicle is hollow, elongately to equiradially triapsidate. The anterior and posterior processes are of approximate equal length and are relatively broad based, and - compared with other phenotypes of the *D. elongata/D. hermosa* group - are relatively blunt and stout. The body of the vesicle is formed by the fusion of the broad based processes. The vesicle wall is unilayered, and undifferentiated and uniform. Ectoderm surface psilate to granulate (elements less than 0.5 microns high). The species tends to open by a straight to C-shaped split pylome which is just below the bases of the posterior processes and which is oriented parallel to the long axis of the body". Specimens 50 and 60 (Pl. 4, figs. 50, 60) are here attributed to *D. symmetrica*.

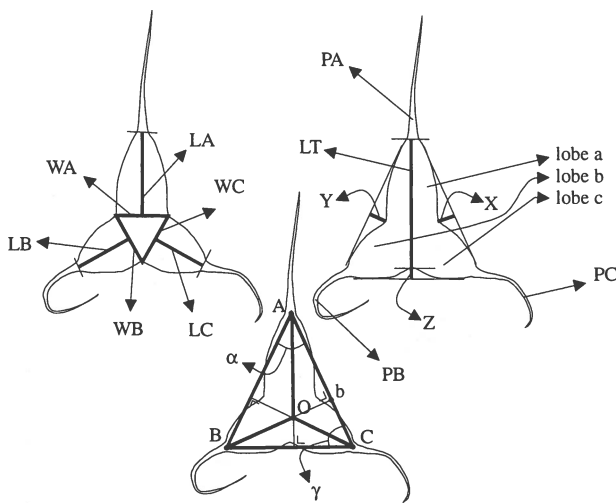
Thusu (1973, p. 808) observed transitional forms between *D. amphora* and *D. elongata* in Silurian material from New York state, U.S.A., and proposed hypothetical relationships (Thusu, 1973, text-fig. 2, p. 806). Hill (1974) emended the generic diagnosis and synonymized certain species, viz., *D. elongata* with *D. trispinosa*, and *D. symmetrica* with *D. limaciformis*.

MATERIAL AND METHODS

MATERIAL STUDIED

The studied material comes from the upper five samples of the 83 W-421 Kortrijk borehole (at 209.5 m, 216.2 m, 232.1 m, 240.1 m, and 244.1 m), Brabant Massif, Belgium, in the southern Flanders subsurface (Verniers & Van Grootel, 1991). Graptolites, chitinozoans, and acritarchs (Van Grootel *et al.*, 1998, and author's unpubl. data)

Text-fig. 1 - History of some *Domasia* spp.



Text-fig. 2 - Biometric and geometric measures.

enable correlation with the *sedgwickii* and *guerichi* graptolite biozones, of late Aeronian-lower Telychian (Silurian) age. Preservation is good, though many specimens are broken and/or folded and most bear broken processes. The colour of the acritarchs ranges from light to dark brown with a constant and often pronounced grey tint.

Temporal trends are not taken into consideration in the present analyses. This was motivated by three factors. First, *Dactylofusa estillis* Cramer & Diez 1972 occurs in all slides and is characteristic of zone 3a of Hill & Dorning (1984); the stratigraphic range of this species corresponds to the *guerichi* to *turriculatus* graptolite biozones (Molyneux *et al.*, 1996, Text-fig. 9, p. 509). Second, most specimens in the analyses (37 out of 62) are from the same sample, viz., 240.1 m. Third, the statistical tools we used are not designed to recognise temporal trends.

The studied specimens of *Domasia* spp. generally

have a trilobed outline. One lobe is longer than the others and is called the posterior lobe, following Downie (1960); the other lobes are termed anterior lobes. The outline of the lobes is generally convex. The separation between the lobes and the indentations is generally distinct (Pl. 2, fig. 17). Each lobe bears a single process which is generally slender and whip-like (Pl. 2, figs. 19, 29). The separation between lobe and process is generally marked by an inflexion point in the curved outline (Pl. 2, fig. 17). From present observations of complete processes, the posterior process seems shorter than the anterior processes as described by Hill (1974). When the outline of the anterior lobes grades to a concave curve, the separation between lobes, and between each lobe and its process, is less marked and is sometimes very hard to delimit (Pl. 2, fig. 29). Specimens close or attributable to *D. trispinosa* (*sensu* Downie, 1960) have no anterior lobes and the processes merge directly with the "posterior" lobe.

METHODS OF MEASUREMENT

A letter is attributed to each lobe, "a" being the longest (posterior) lobe, "b" being the first lobe met when turning anticlockwise, and "c" being the final lobe ("b" and "c" are the anterior lobes, see Text-fig. 2). Indentations are similarly marked, "z" being the anterior indentation, "x" the first indentation met when turning anticlockwise, and "y" the final indentation ("x" and "y" are the lateral indentations).

Two types of measurements were made. Classical biometric measurements (see Text-fig. 2) and geometric measurements based on the supposed bilateral symmetry of the genus. The biometric measurements include lobe length (LA, LB, LC), lobe width (WA, WB, WC), indentation width (X, Y, Z), process length (PA, PB, PC), and the total vesicle length (LT), i.e., the distance between the contact of the

EXPLANATION OF PLATE 1

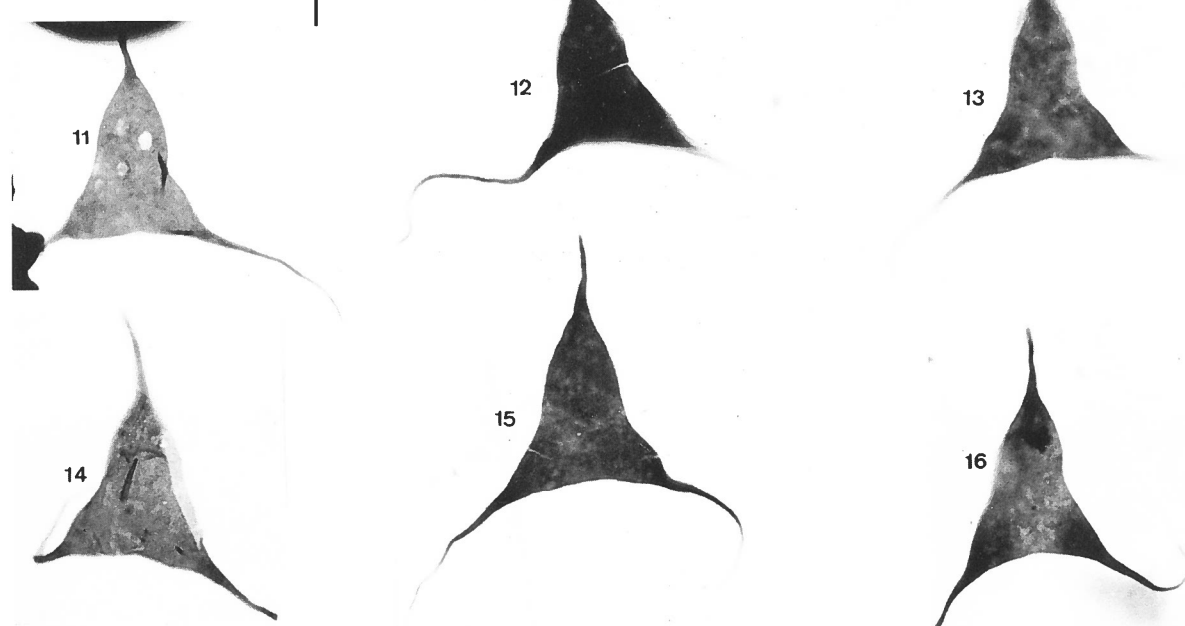
- Fig. 1 - *Domasia elongata* (*sensu* Downie, 1960), 240.1 m, P51/0, 67, cluster 1, 1.51.
 Figs. 2, 10 - *Domasia elongata* (*sensu* Downie, 1960)-*trispinosa* (*sensu* Downie, 1960). 2) 209.5 m, E50/2, 14, cluster 1, 1.95; 10) 209.5 m, T50/3, 12, cluster 1, 5.20.
 Fig. 3 - *Domasia trispinosa* (*sensu* Downie, 1960)-*elongata* (*sensu* Downie, 1960), 209.5 m, J52/0, 17, cluster 1, 2.33.
 Figs. 4, 8 - *Domasia elongata* (*sensu* Downie, 1960)-*symmetrica* (*sensu* Cramer, 1971). 4) 240.1 m, W48/0, 54, cluster 1, 2.41; 8) 209.5 m, V51/1, 16, cluster 1, 3.46.
 Fig. 5 - *Domasia symmetrica* (*sensu* Cramer, 1971)-*elongata* (*sensu* Downie, 1960), 209.5 m, V43/1, 3, cluster 1, 2.74.
 Figs. 6, 7 - *Domasia trispinosa* (*sensu* Downie, 1960). 6) 209.5 m, M45/0, 8, cluster 1, 3.23; 7) 209.5 m, D39/0, 1, cluster 1, 3.23.
 Fig. 9 - *Domasia trispinosa* (*sensu* Downie, 1960)-*limaciformis* (*sensu* Cramer, 1971), 232.1 m, J50/0, 26, cluster 1, 3.81.
 Figs. 11-16 - *Domasia limaciformis* (*sensu* Cramer, 1971). 11) 240.1 m, H38/0, 100, cluster 2, 0.67; 12) 209.5 m, H44/0, 5, cluster 2, 0.95; 13) 240.1 m, J37/0, 98, cluster 2, 0.96; 14) 240.1 m, J50/2, 66, cluster 2, 1.01; 15) 240.1 m, Q57/0, 90, cluster 2, 1.03; 16) 240.1 m, W42/0, 39, cluster 2, 1.07.

The following are cited for each figured specimen: sample depth, England Finder slide coordinates, photograph number, the cluster to which the specimen belongs, and the Mahalanobis distance from the centre of its cluster. If the specimen is morphologically transitional, two specific names are given, the first being the one considered more applicable. All magnifications $\times 1000$.

CLUSTER 1



CLUSTER 2



posterior lobe with its process and the anterior indentation. Unfortunately, there are only a few measurements of process length because of frequent process breakages. Hence this measurement could not be used in the statistical analyses. The biometric measurements were made using a light transmission microscope Axiolab (Zeiss) at 1000x magnification. The measurement error on the microscope is 0.5 μm .

The second set of measurements was taken on photomicrographs. It comprises the length ($\overline{AB}$, $\overline{AC}$ and $\overline{BC}$) of the sides of the triangle whose angles (A, B, and C corresponding to the previous notation, see Text-fig. 2) are situated at the contact of each process with its vesicle lobe. The distance from the orthocentre (O) of the triangle to these angles ($\overline{OA}$, $\overline{OB}$, and $\overline{OC}$) was also measured. In fact, $\overline{AB}$, $\overline{AC}$, and $\overline{BC}$ can be measured directly under the microscope. $\overline{OA}$, $\overline{OB}$, and $\overline{OC}$ can be calculated with the following equations:

$$\alpha = \arccos \left(\frac{\overline{AB}^2 + \overline{AC}^2 - \overline{BC}^2}{2 \cdot \overline{AB} \cdot \overline{AC}} \right)$$

$$\gamma = \arccos \left(\frac{\overline{BC}^2 + \overline{AC}^2 - \overline{AB}^2}{2 \cdot \overline{BC} \cdot \overline{AC}} \right)$$

$$\overline{Ab} = \overline{AB} \cos(\alpha)$$

$$\text{cal} \overline{OA} = \frac{\overline{Ab}}{\sin(\gamma)}$$

$$\text{cal} \overline{OB} = \frac{\text{cal} \overline{OA} \cos(\alpha + \gamma)}{\cos(\alpha)}$$

$$\text{cal} \overline{OC} = \frac{\text{cal} \overline{AC} \cos(\gamma)}{\cos(\alpha)}$$

The measurements errors on $\overline{AB}$, $\overline{AC}$, and $\overline{BC}$ (0.5 μm) generate errors on the evaluation of α , γ , $\overline{Ab}$, $\text{cal} \overline{OA}$, $\text{cal} \overline{OB}$, and $\text{cal} \overline{OC}$ given by the preceding formulas. Taylor's formula was used to estimate those errors. The errors on the angles α and γ amounted to <0.005 radian; and the errors on $\overline{Ab}$, $\text{cal} \overline{OA}$, $\text{cal} \overline{OB}$, and $\text{cal} \overline{OC}$ were <0.5 μm .

Of the 119 specimens located in the slides, only 83 present the complete set of biometric variables. Moreover, the geometric measurements were taken separately on 70 photomicrographs of the best-preserved specimens. A total of 62 specimens presented the complete sets of measurements and were processed in the statistical analysis.

STATISTICAL ANALYSIS

The statistical analysis was performed in three steps. The data were first submitted to a principal component analysis, to reduce the number of variables to be taken into account in further analyses. Subsequently, a cluster analysis was conducted to group the specimens together according to the variables selected in the first step. Finally, a discriminant analysis enabled the validity of the created clusters to be assessed and a classification law extracted.

Principal component analysis

Principal component analysis was conducted in two steps due to the high number of variables (16 measurements) against the number of cases (62 specimens). The first focused on the geometric set of variables and the second on the biometric set of measurements. The principal component analysis enabled reduction in the number of variables to be considered in further analyses, by grouping them and indicating redundant variables. We measured variables that were supposed to be symmetrical from the inferred bilateral symmetry, to test its statistical relevance.

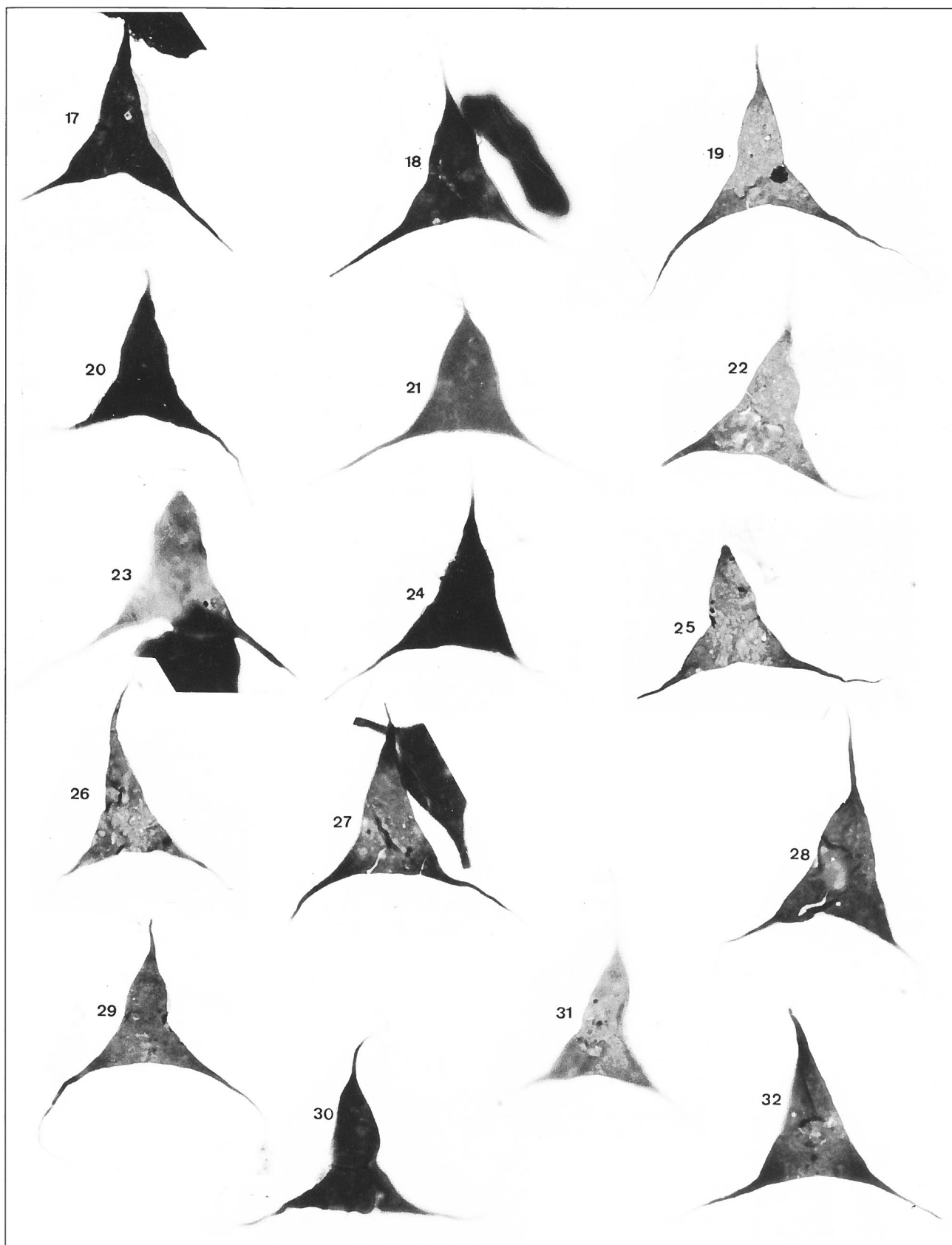
Principal component analysis of the geometrical set of variables – The six variables used in this analysis were $\overline{AB}$, $\overline{AC}$, $\overline{BC}$, $\text{cal} \overline{OA}$, $\text{cal} \overline{OB}$, and $\text{cal} \overline{OC}$. Four factors represent 98.8% of the total variation of the variance. Factor eigenvalues are respectively 2.85, 1.29, 0.93, and 0.86, explaining respectively 47.5%, 21.5%, 15.4%, and 14.4% of the variance.

Factor loadings allow the following interpretations. Factor 1 is best explained by $\overline{AB}$, $\overline{AC}$, and $\text{cal} \overline{OA}$, which is interpreted as the elongation of the

EXPLANATION OF PLATE 2

- Figs. 17, 18, 20-24, 27, 28 - *Domasia limaciformis* (sensu Cramer, 1971), 17) 240.1 m, H42/2, 40, cluster 2, 1.07, 18) 209.5 m, M53/2, 7, cluster 2, 1.13, 20) 240.1 m, S51/3, 69, cluster 2, 1.23, 21) 209.5 m, O49/0, 13, cluster 2, 1.27, 22) 40.1 m, M39/4, 30, cluster 2, 1.36, 23) 209.5 m, O47/3, 9, cluster 2, 1.36, 24) 209.5 m, U47/2, 11, cluster 2, 1.39, 27) 240.1 m, W58/1, 91, cluster 2, 1.55, 28) 244.1 m, D48/2, 107, cluster 2, 1.63.
- Figs. 19, 25, 26, 29-31 - *Domasia limaciformis* (sensu Cramer, 1971)-*symmetrica* (sensu Cramer, 1971), 19) 240.1 m, Z51/1, 70, cluster 2, 1.19; 25) 240.1 m, R53/4, 78, cluster 2, 1.46; 26) 244.1 m, L36/3, 110, cluster 2, 1.50; 29) 240.1 m, K51/4, 71, cluster 2, 1.70; 30) 240.1 m, U48/0, 53, cluster 2, 1.76; 31) 240.1 m, L39/2, 31, cluster 2, 1.82.
- Fig. 32 - *Domasia limaciformis* (sensu Cramer, 1971)-*Veryhachium* sp. (Deunff, 1954), 240.1 m, T53/3, 74, cluster 2, 1.85.

See Plate 1 explanation for information on specimen documentation given above for each figure. All magnifications $\times 1000$.

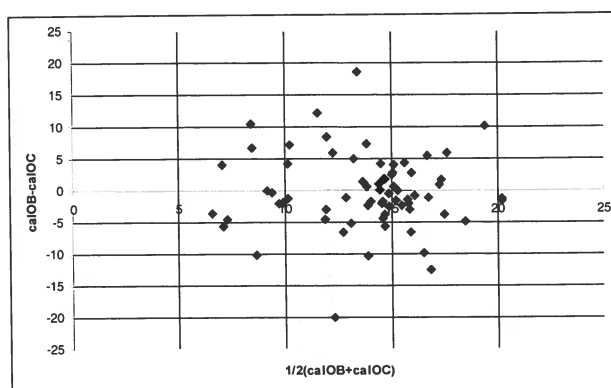


specimen. Important variables for factor 2 are $\overline{BC}$ and $\text{cal}\overline{OB}$; i.e., the width of the base of the triangle. Factors 3 and 4 are mainly explained by $\text{cal}\overline{OB}$ and $\text{cal}\overline{OC}$. They are positively correlated with factor 3 but negatively with factor 4. The inverse correlation of those two variables with factor 4 probably explains why $\text{cal}\overline{OC}$ is not among the important variables of factor 2. This result (discussed below) was unexpected, because specimens were supposed to be symmetrical. On the other hand, good correlation (>86%) exists between $\overline{AB}$ and $\overline{AC}$.

Principal component analysis of the biometric set of variables – The 10 variables used in this analysis are LT, LA, LB, LC, WA, WB, WC, X, Y, and Z. It releases five factors explaining 93.0% of the total variance of the 10 variables. Factors eigenvalues and percentages of the explained variance are respectively 3.77 (37.7%), 2.85 (28.5%), 1.75 (17.5%), 0.59 (5.9%), and 0.35 (3.5%). Factor 5 was omitted because it accounted for less than 5% of the total variance.

Factor 1 is best explained by LB, LC, WB, and WC; i.e., the anterior lobes' dimensions. The main variables in factor 2 are LA, X, and Y, showing the importance of the elongation of the posterior lobe and of the lateral indentations width. Factor 3 is mainly explained by LT, WA, and Z. Note that the correlation of LT and WA is positive with factor 3, while Z is negatively correlated. Factor 4 is mainly explained by a positive correlation with WA and Z. Furthermore, it is important to note a very good correlation between LB and LC (85%) and WB and WC (90%).

Discussion of the principal component analysis – The results of the analysis suggest that it is possible to reduce the number of variables to be taken into account, mainly by using means instead of two separated variables. This is clearly the case for $\overline{AB}$ and $\overline{AC}$, LB and LC, and WB and WC. The means of these variables are respectively $m\overline{ABAC}$, $m\overline{LBLC}$, and $m\overline{WBWC}$. These transformations emphasise the symmetry of the specimens. Therefore, the lack of correlation between $\text{cal}\overline{OB}$ and $\text{cal}\overline{OC}$ seems even more puzzling.



Text-fig. 3 - Scatterplot of specimens on $1/2(\text{cal}\overline{OB} + \text{cal}\overline{OC})$ vs. $(\text{cal}\overline{OB} - \text{cal}\overline{OC})$.

Looking at an isosceles triangle it is evident that a slight asymmetry (making it an ordinary triangle) will have more effect on $\overline{OB}$ and $\overline{OC}$ (and therefore $\text{cal}\overline{OB}$ and $\text{cal}\overline{OC}$) than on $\overline{AB}$ and $\overline{AC}$. This effect is clearly evident when inspecting $\overline{AB}-\overline{AC}$, and $\overline{OB}-\overline{OC}$. A slight increase in $\overline{AB}-\overline{AC}$, will be accompanied by a more marked increase in $\overline{OB}-\overline{OC}$. This asymmetry is due to slight folding and tearing, interpreted as a taphonomic phenomenon. The fact that no significant difference was observed between $1/2(\text{cal}\overline{OB} + \text{cal}\overline{OC})$ and $(\text{cal}\overline{OB} - \text{cal}\overline{OC})$ and also that a scatterplot of $1/2(\text{cal}\overline{OB} + \text{cal}\overline{OC})$ vs. $(\text{cal}\overline{OB} - \text{cal}\overline{OC})$ shows no trends (correlation coefficient $r = 0.03$, $p\text{-value} = 80\%$; Text-fig. 4) indicates that these two measurements have the same mean and the same variance. Therefore we can use the mean between $\text{cal}\overline{OB}$ and $\text{cal}\overline{OC}$ ($m\text{cal}\overline{OB}\overline{OC}$) to eliminate the taphonomic effect.

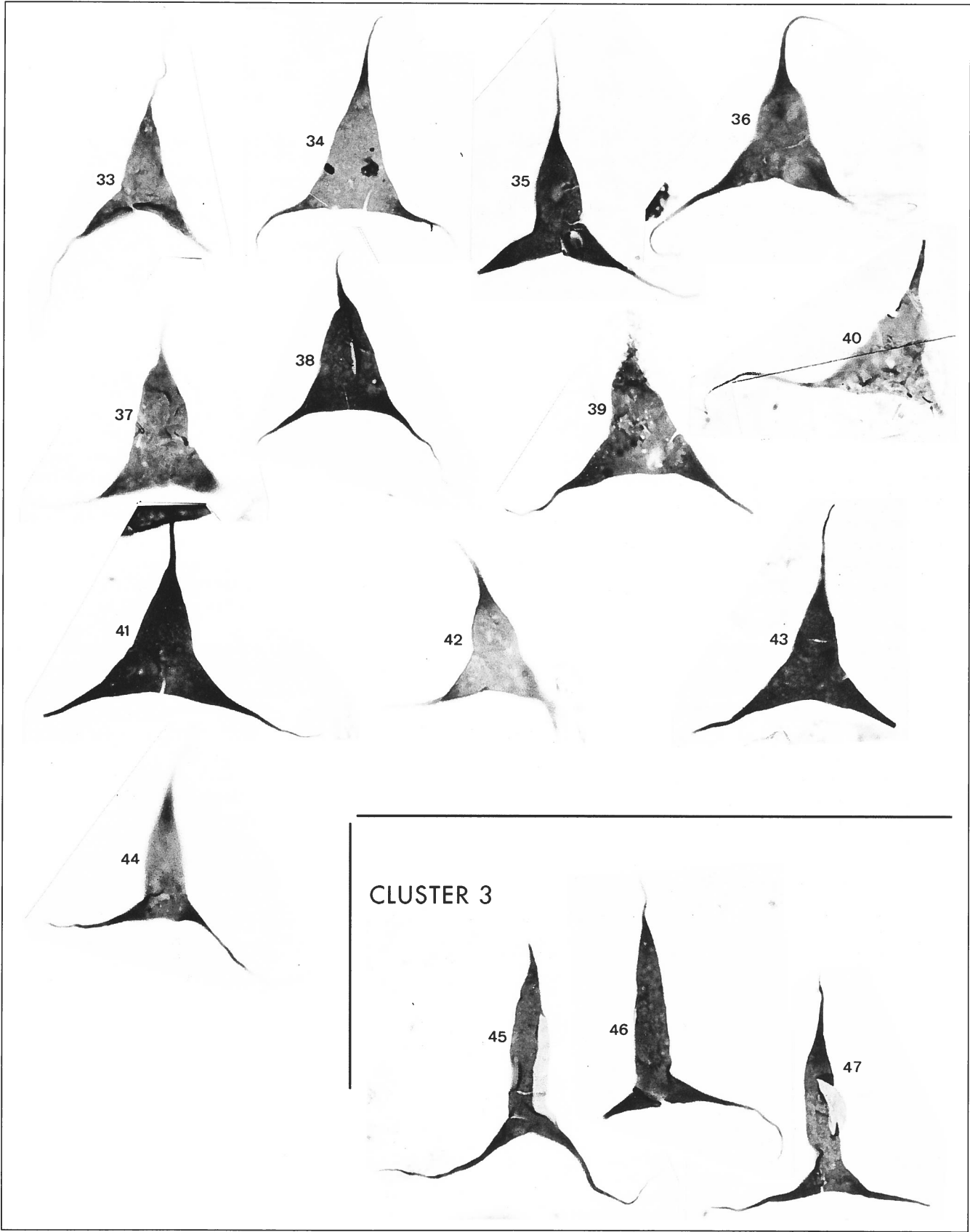
Cluster analysis

The cluster analysis is based on 10 variables ($m\overline{ABAC}$, $\overline{BC}$, $\text{cal}\overline{OA}$, LT, LA, WA, $m\overline{LBLC}$, $m\overline{WBWC}$, X, and Y). We use a K-mean clustering analysis designed to find the optimum partition of

EXPLANATION OF PLATE 3

- Figs. 33, 35, 37, 39 - *Domasia limaciformis* (sensu Cramer, 1971)-*symmetrica* (sensu Cramer, 1971). 33) 240.1 m, T50/1, 63, cluster 2, 1.91; 35) 240.1 m, Z49/0, 57, cluster 2, 1.97; 37) 244.1 m, K41/0, 105, cluster 2, 2.19; 39) 244.1 m, R50/0, 103, cluster 2, 2.42.
- Fig. 34 - *Domasia limaciformis* (sensu Cramer, 1971)-*Veryhachium* sp. (Deunff, 1954), 240.1 m, U58/1, 92, cluster 2, 1.93.
- Figs. 36, 38, 40, 42 - *Domasia limaciformis* (sensu Cramer, 1971). 36) 240.1 m, R36/2, 97, cluster 2, 2.15; 38) 240.1 m, G47/4, 46, cluster 2, 2.39; 40) 209.5 m, V53/0, 18, cluster 2, 2.47; 42) 209.5 m, Q41/2, 2, cluster 2, 2.86.
- Fig. 41 - *Domasia symmetrica* (sensu Cramer, 1971)-*limaciformis* (sensu Cramer, 1971), 240.1 m, G38/3, 50, cluster 2, 2.54.
- Fig. 43 - *Domasia symmetrica* (sensu Cramer, 1971), 240.1 m, N54/0, 81, cluster 2, 3.01.
- Fig. 44 - *Domasia elongata* (sensu Downie, 1960)-*symmetrica* (sensu Cramer, 1971), 232.1 m, Z43/2, 23, cluster 2, 3.09.
- Figs. 45 - 47 - *Domasia elongata* (sensu Downie, 1960). 45) 244.1 m, H45/3, 101, cluster 3, 1.25; 46) 240.1 m, U48/3, 48, cluster 3, 1.51; 47) 240.1 m, W47/4, 47, cluster 3, 1.90.

See Plate 1 explanation for information on specimen documentation given above for each figure. All magnifications $\times 1000$.



Variables	2 cluster model	3 cluster model	4 cluster model	5 cluster model
$m\overline{AB\ AC}$	.0000	.0000	.0000	.0000
$\overline{BC}$	.0481	.0000	.0000	.0000
$cal\overline{OA}$	.0000	.0000	.0000	.0000
LT	.0000	.0000	.0000	.0000
LA	.0000	.0000	.0000	.0000
WA	.3265	.0000	.0000	.0145
mLbLC	.2296	.0000	.0000	.0000
mWBWC	.0054	.0000	.0000	.0000
X	.0194	.0621	.0114	.0088
Y	.0002	.0002	.0000	.0013

Tab. 1 - P-value of each variable in the different clustering models.

the set of data with the goal of minimising within-cluster variance and maximising between-cluster variance. The data were tested with 2, 3, 4, and 5 clusters. A one-way Anova led to omission of Z due to its low relevance ($p = 90.2\%$); but this shows the relevance ($p < 2\%$) of the created clusters for the other variables.

The 4 cluster model provides the optimum grouping. Anova on the different models (from 2 to 5 clusters) revealed that this cluster model provides the smallest p-value for each variable (Tab. 1). The 5 cluster model presents a lower p-value for X but higher p-values for WA and Y. This indicates that the 4 cluster model provides clusters with the best consistency and the most discriminant variables. Moreover, the groups were consistent with the overall morphology of the specimens but not necessarily with any other systematic criteria.

Description of the clusters – Cluster 1 is composed of 10 specimens displaying different overall morphologies (specimens 1-10, Pl. 1), but each characterised by short anterior lobes ($\mu(mcalLbLC) = 4.7\ \mu m$). Cluster 2 (specimens 11-44, Pls. 1-3) contains 34 specimens with a posterior lobe ($\mu(LA) = 14.7\ \mu m$)

roughly 1.5 times longer than the anterior lobes ($\mu(mcalLbLC) = 10.0\ \mu m$). Cluster 3 (specimens 45 to 47, plate 3) contains 3 specimens with a very elongated and narrow posterior lobe ($\mu(LA) = 28.3\ \mu m$ and $\mu(WA) = 7.3\ \mu m$). Cluster 4 (specimens 48 to 62, plate 4) is composed of 15 broad-based specimens with large lobes ($\mu(BC) = 29.2\ \mu m$, $\mu(WA) = 12.2\ \mu m$ and $\mu(mWBWC) = 9.7\ \mu m$). The means and standard deviations of the ten variables for each cluster are shown in Tab. 2.

Discriminant analysis

In order to assess the validity of the clusters and to extract a classification law that would enable allocation of a given specimen to one of them, we submitted our data to a discriminant analysis. A first analysis was performed with all the variables used in the cluster analysis (standard analysis). For a second analysis, a backward selection of the variables was used to simplify the classification functions of the classification law (backward analysis). Each specimen was then reallocated using the classification law to evaluate the latter's performance. It is evident that the percentage of correct reallocation will be high because the test applies to specimens used to extract the classification law in the first place. Testing the classification law on another population would give a better test of its validity and usefulness.

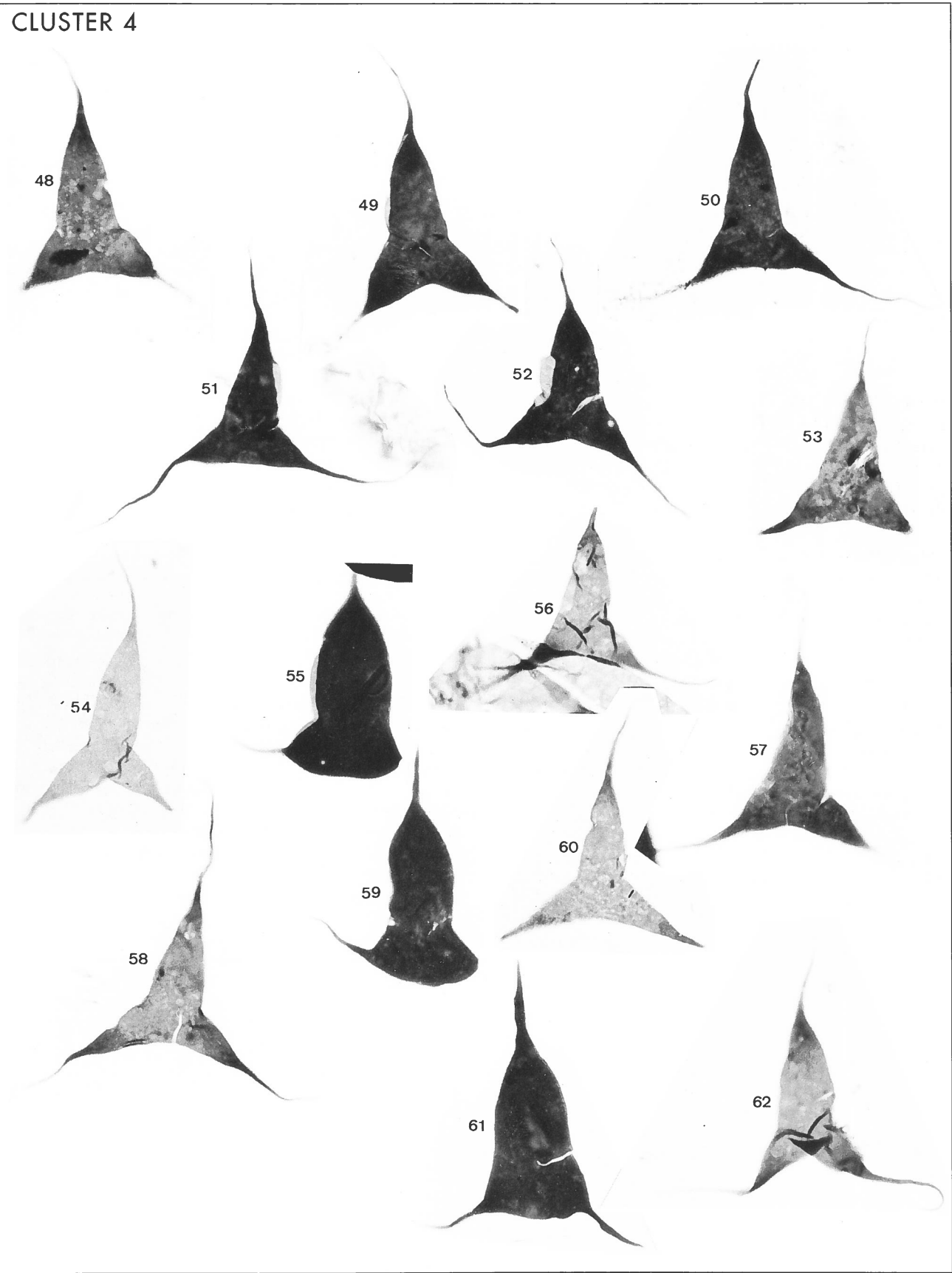
Standard analysis – Every cluster is significantly different from the others as the p-values are $< 0.4\%$ (see Tab. 3, p-values above the diagonal). The only p-value that reaches 0.4% is between clusters 1 and 3. Reallocation of specimens according to the classification law reaches a correct percentage of 96.8%. Only two specimens (53 and 56, Pl. 4) from cluster 4 were wrongly reallocated to cluster 2. The correct reallocation percentage for cluster 4 is 87%.

Backward analysis – The backward analysis was performed on five variables in the model ($m\overline{AB\ AC}$,

EXPLANATION OF PLATE 4

- Figs. 48-51, 53-54, 58, 60 - *Domasia symmetrica* (sensu Cramer, 1971). 48) 240.1 m, R54/1, 83, cluster 4, 0.93; 49) 240.1 m, Q45/4, 106, cluster 4, 1.10; 50) 240.1 m, T54/2, 82, cluster 4, 1.24; 51) 240.1 m, P45/1, 108, cluster 4, 1.60; 53) 240.1 m, P44/4, 41, cluster 4, 1.95; 54) 240.1 m, Z41/4, 35, cluster 4, 2.18; 58) 240.1 m, P45/1, 42, cluster 4, 2.59; 60) 240.1 m, M53/1, 77, cluster 4, 2.96.
- Figs. 52, 56 - *Domasia symmetrica* (sensu Cramer, 1971)-*limaciformis* (sensu Cramer, 1971). 52) 240.1 m, E41/4, 38, cluster 4, 1.69; 56) 244.1 m, J56/2, 109, cluster 4, 2.43.
- Figs. 55, 59 - *Domasia symmetrica* (sensu Cramer, 1971)-*trispinosa* (sensu Downie, 1960). 55) 240.1 m, F50/3, 58, cluster 4, 2.27; 59) 240.1 m, V57/0, 88, cluster 4, 2.73.
- Figs. 57, 62 - *Domasia symmetrica* (sensu Cramer, 1971)-*elongata* (sensu Downie, 1960). 57) 240.1 m, O52/0, 72, cluster 4, 2.48; 62) 240.1 m, T40/0, 33, cluster 4, 3.00.
- Fig. 61 - *Domasia trispinosa* (sensu Downie, 1960)-*elongata* (sensu Downie, 1960), 232.1 m, X49/0, 25, cluster 4, 3.02.

See Plate 1 explanation for information on specimen documentation given above for each figure. All magnifications $\times 1000$.



	Cluster 1		Cluster 2		Cluster 3		Cluster 4	
Number of cases	10		34		3		15	
Variables	mean/sd (μm)		mean/sd (μm)		mean/sd (μm)		mean/sd (μm)	
$m\overline{AB\overline{AC}}$	35.0	2.4	33.0	2.3	43.9	3.0	40.5	2.5
$\overline{BC}$	16.6	3.0	27.1	3.0	20.5	1.9	29.2	3.7
$cal\overline{OA}$	32.0	3.4	23.9	2.3	40.4	2.9	32.2	3.2
LT	26.4	3.2	23.4	2.2	34.0	2.6	30.2	3.3
LA	19.7	6.3	14.7	1.8	28.3	2.1	21.1	1.6
WA	9.1	3.1	11.0	1.3	7.3	0.6	12.2	1.7
mLBLC	4.7	3.0	10.0	1.6	7.5	1.7	10.9	2.3
mWBWC	4.0	2.9	9.6	0.9	5.5	0.5	9.7	1.2
X	1.6	1.5	1.8	0.6	3.2	0.3	2.3	0.9
Y	1.4	1.0	1.6	0.8	3.7	1.2	2.8	0.9

Tab. 2 - Mean and screw deviation of each variable in the 4 clusters.

$\overline{BC}$, $cal\overline{OA}$, WA, and mWBWC) with p-values <0.8%. The last variable removed is LT (p-value = 12.5%).

Each cluster is significantly different from the others with p-levels <0.05% (see Tab. 3, p-values below the diagonal). Correct reallocation percentage reaches 98.4% and only one specimen (53, Pl. 4) was wrongly attributed to cluster 2 instead of cluster 4. The correct reallocation percentage for cluster 4 is 93%.

Classification law –The classification law is composed of one classification function for each cluster. The classification function of a cluster is a linear function of the variables. It determines the posterior probability for a given specimen to belong to the corresponding cluster, though the score of the classification function is not a probability in itself. Consequently, the higher the score, the more likely the specimen belongs to the cluster.

If we write the classification function corresponding to the cluster i as:

$$A_{0,i} + A_{m\overline{AB\overline{AC}},i} (m\overline{AB\overline{AC}})_i + A_{\overline{BC},i} (\overline{BC})_i + A_{cal\overline{OA},i} (cal\overline{OA})_i + A_{WA,i} (WA)_i + A_{mWBWC,i} (mWBWC)_i$$

or in a general form as:

$$A_{0,i} + \sum_{d=1}^r A_{j,i} x_i$$

or in a matricial form as:

$$A_{0,i} + A_i^T x$$

then the coefficients (A_i) and the independent term ($A_{0,i}$) are estimated using the following formulas:

$$A_{0,i} = -\frac{1}{2} (\overline{X}_i S^{-1} \overline{X}_i)$$

$$A_i^T = \overline{X}_i^T S^{-1}$$

Cluster	1	2	3	4
1	-	.0000	.0036	.0000
2	.0000	-	.0000	.0000
3	.0005	.0000	-	.0000
4	.0000	.0000	.0000	-

Tab. 3 - Between cluster p-values for the standard discriminant analysis (above diagonal) and for the backward discriminant analysis (below diagonal).

where $\overline{X}_i$ is the mean of X in cluster i , and S is the pooled covariance matrix.

The results of the four functions are necessarily calculated for each cluster on the basis of the five variables measured on the specimen. The specimen is attributed to the cluster whose classification function scores the highest result. Table 4 gives the coefficient for each variable and the independent term.

Coefficient	Cluster 1	Cluster 2	Cluster 3	Cluster 4
$A_{m\overline{AB\overline{AC}}}$	+8.373	+1.496	+10.194	-0.906
$A_{\overline{BC}}$	-1.346	+3.044	-1.667	+4.743
$A_{cal\overline{OA}}$	-2.009	+2.127	-2.062	+5.349
A_{WA}	+2.204	+4.155	+1.353	+4.227
A_{mWBWC}	+1.025	+4.297	+1.182	+3.836
$A_{0,i}$	-117.223	-135.536	-176.101	-182.822

Tab. 4 - Coefficients and independent term of the classification functions.

RESULTS AND DISCUSSION

DISCUSSION OF THE CLUSTERS

Prior to the interpretation of the clusters, a specific attribution (following Downie, 1960 and Cramer, 1971) was given to each studied specimen. Most of the specimens are transitional forms that were given two specific names. These two names correspond to the poles of which the specimen shows criteria.

Cluster 1 is the less consistent cluster because it is composed of specimens whose forms correspond to different poles of the morphon. It contains one specimen attributable to the *D. elongata* (sensu Downie, 1960) pole and two specimens attributable to the *D. trispinosa* (sensu Downie, 1960) pole. The others are transitional forms. Cluster 2 is mainly composed of specimens attributable to the *D. limaciformis* (sensu Cramer, 1971) pole, with some transitional forms to the *D. symmetrica* (sensu Cramer, 1971) pole and two specimens assignable to *D. symmetrica* (sensu Cramer, 1971). Cluster 3 is composed of three specimens attributable to the *D. elongata* (sensu Downie, 1960) pole. Finally, cluster 4 is composed of specimens assignable to the *D. symmetrica* (sensu Cramer, 1971) pole, with some transitional forms close to this pole, and one specimen intermediate between the *D. trispinosa* (sensu Downie, 1960) and the *D. elongata* (sensu Downie, 1960) poles. This cluster is consistent but for specimens 55, 59, and 61 (Pl. 4) which have less well-developed anterior lobes. These specimens are biometrically well-integrated in the cluster, though systematic criteria would exclude them.

The lack of consistency in cluster 1 may result from two factors. First, the biometric variables and statistical analyses cannot discriminate between the specimens, whatever the population and/or measurements taken. Second, it may reflect an unbalanced population. Unbalanced populations lead to loosely defined groups and a mixed classification. This could be the case here because cluster 1 is composed of poorly represented forms in the studied population

[*D. trispinosa* (sensu Downie, 1960) and *D. elongata* (sensu Downie, 1960) poles]. On the other hand, cluster 3 contains only three specimens that were probably distinguished because they have very well-developed anterior lobes and consistent dimensions. This shows that the analysis can distinguish poorly represented specimens if they have characteristic features or dimensions.

These problems show that the classification function will probably not recognise specimens belonging to species other than *D. limaciformis* (sensu Cramer, 1971) and *D. symmetrica* (sensu Cramer, 1971). This can be resolved by repeating the analysis on a larger population in which each species or form reaches a confident level of representation and/or by examining a better balanced population.

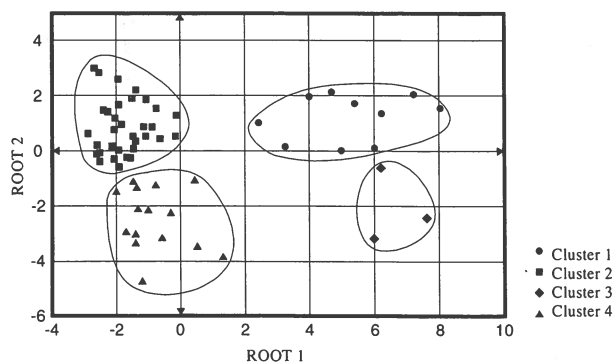
Text-figure 4 displays the specimens according to the first two canonical roots. It is evident that all clusters are well-separated. There are two broad groups: specimens close to the *D. limaciformis* (sensu Cramer, 1971)-*D. symmetrica* (sensu Cramer, 1971) poles on the left, and specimens close to the *D. trispinosa* (sensu Downie, 1960)-*D. elongata* (sensu Downie, 1960) poles on the right. According to the studied population, biometric variables, and statistical analysis, the two groups are unrelated, though some transitional forms are evident.

The significant separation (p-level <0.001%) between clusters 2 and 4 show them to be different species in the studied population. Because cluster 2 can be related to *D. limaciformis* (sensu Cramer, 1971) and cluster 4 to *D. symmetrica* (sensu Cramer, 1971), those two species are informally adopted here, contrary to Hill (1974).

THE *DOMASIA* MORPHON

The *Domasia limaciformis* (sensu Cramer, 1971) pole is characterised by lobes only slightly longer than wide. Indentations are present but not well-marked. The isosceles triangle ABC tends to be equilateral. Cluster 2 illustrates this form well. Its biometric values (summarised in Tab. 2) can be adopted for this pole. As specimen 11 has the smallest within-cluster Mahalanobis distance and because it shows most of the group's attributes, it is the most characteristic of this pole in our population.

The *Domasia symmetrica* (sensu Cramer, 1971) pole exhibits a larger posterior lobe and marked indentations. Generally, the lobes are appreciably longer than wide. The posterior lobe is wider and ca. twice the length of the anterior lobes. ABC is clearly isosceles with long sides and a wide base. Specimens grouped in cluster 4 provide consistent examples of this form. Therefore, the biometric values of cluster 4 (Tab. 2) can be adopted for this pole. Specimen 48 has the lowest within-cluster Mahalanobis distance but specimens 49 and 50 are more characteristic because they display at least one complete process.



Text-fig. 4 - Scatterplot of the specimens according to the first two canonical roots.

Because the classification functions are able to distinguish *Domasia limaciformis* (*sensu* Cramer, 1971) from *D. symmetrica* (*sensu* Cramer, 1971), they are useful in the specific assignment of transitional forms. Palynologists are cautioned not to use these classification functions blindly because the studied population was unbalanced. Systematic criteria should remain more conclusive for *D. elongata* and *D. trispinosa*.

Starting from the *Domasia limaciformis* (*sensu* Cramer, 1971) pole of the morphon, the other poles and the transitional forms can be explained by two morphological trends. The first is elongation of the posterior process (specimen 30, Pl. 2), leading to the *D. symmetrica* (*sensu* Cramer, 1971) pole. The second trend is reduction of the anterior lobes (specimen 9, Pl. 1), leading to the *D. trispinosa* (*sensu* Downie, 1960) pole. Specimens may also show both trends, leading to the *D. elongata* (*sensu* Downie, 1960) pole.

The results show that statistics can assist in clarifying systematics when transitional forms are present. In particular, the procedure helps to define species in an apparent continuum of forms, and to identify subsequently obtained specimens by means of a classification law. It is stressed that systematic criteria should be considered in conjunction with the classification law for confirmation of specific attribution.

Statistical analysis can aid selection of a type specimen by identifying those closest to the centre of the group according to their within-cluster Mahalanobis distance. The smaller this distance the closer to the centre. Subsequently, the type specimen selected should display the characteristic features of the species and should have a within-cluster Mahalanobis distance as small as possible. This will ensure that the specimen is biometrically average for its species and hence appropriately representative. In this study, the need to select type specimens did not arise, because all the species discussed herein had previously been described and typified.

SUMMARY AND CONCLUSIONS

This study is based on specimens from the upper part of the Kortrijk 83 W-421 borehole which is dated as late Aeronian-lower Telychian. A population of 119 specimens of *Domasia* spp. was measured, but only 62 were retained in the analysis due to missing values in some of the measurements. The study included 16 variables, 6 geometrical and 10 biometric. Process lengths were measured but could not be included in the study because of their insufficiency.

A principal component analysis reduced the number of variables taken into account to 10 ($m\overline{AB}$, $\overline{AC}$, $\overline{BC}$, $\text{cal } \overline{OA}$, LT, LA, $m\overline{LBLC}$, WA, $m\overline{WBWC}$, X, and Y). The specimens were grouped by a K-mean clustering analysis and the 4 cluster model was retained. From an assessment of the relevance of the clusters, a classification law with 5 variables ($m\overline{AB}$, $\overline{AC}$, $\overline{BC}$, $\text{cal } \overline{OA}$,

WA, and $m\overline{WBWC}$) was extracted by a discriminant analysis. The classification law reallocated correctly 98% of the studied specimens.

Systematic analysis of the specimens in the clusters revealed some inconsistencies mainly in cluster 1 (mixed classification and loosely defined cluster). It could be due to the low number of specimens and/or to an unbalanced population. This points to the need to work with a balanced population and/or a large population where each species or form is sufficiently represented. On the other hand, the analysis did facilitate recognition of three specimens of *Domasia elongata* (*sensu* Downie, 1960), putting them in a separate cluster. This shows that the analysis can distinguish very typical specimens even if poorly represented in the population.

A scatterplot of the specimens identified two broad groups: (a) *D. limaciformis* (*sensu* Cramer, 1971)-*D. symmetrica* (*sensu* Cramer, 1971) group; and (b) *D. elongata* (*sensu* Downie, 1960), *D. trispinosa* (*sensu* Downie, 1960), and some transitional forms. Because cluster 2, associated with *D. limaciformis* (*sensu* Cramer, 1971) and cluster 4, associated with *D. symmetrica* (*sensu* Cramer, 1971), are significantly different ($p\text{-value} < 0.001\%$), it is proposed to informally adopt the two species. Biometric criteria and two classification functions are utilised for attribution of specimens to one or other of the two species.

It is clear that biometric studies and multivariate statistical treatment of the data can help clarify problematical systematics: different clusters are distinguishable in a continuum of transitional forms. When these clusters can confidently be associated with previously defined species, the classification functions provide a useful tool to confirm specimen identification. Moreover, statistical analysis facilitates choice of a type specimen by the mean of the Mahalanobis distance.

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