

A statistical study of the genus *Pterodactylus*

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In a recent revision of the genus *Pterodactylus*, a considerable synonymy was exposed. This was due to juvenile specimens being represented as separate species. The revision was largely by means of a thorough anatomical study. The present analysis uses a statistical approach to see if further information can be extracted. A total of 14 variables on 35 specimens are analysed by a components analysis and a principal coordinates analysis. The results agree closely with the previous study, except that a presumed juvenile of *P. micronyx* appears to be an adult. Doubt is raised about the specific difference between *P. antiquus* and *P. kochi*. Relationships of the different growth trends of *P. micronyx* and *P. kochi* are discussed.

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Introduction

In 1970, Dr. P. Wellnhofer published a comprehensive monograph revising the genus *Pterodactylus* (among others) with reference to material from the Upper Jurassic (Malm β) of the Schwabian Alps, southern Germany. This material was obtained from a narrow stratigraphic range, thus one infers that the species of this genus were probably near contemporaneous. They are distributed along what was the south coast of the basinal sea that covered most of central Germany during the Upper Jurassic; no great distances or geographical barriers are thus envisaged between where the species were found. In this work, Wellnhofer exposed a synonymy, which had earlier been erected for juvenile specimens, by detailed anatomical analysis and partly by an allometric study.

The present study was undertaken to see if a multivariate statistical analysis would further clarify any relationships not seen by the qualitative study; relationships not only between species, but within species — ontogenetic relationships. Sufficient data for the genus *Pterodactylus* only are supplied (encompassing *P. antiquus*, *P. micronyx*, *P. kochi* and *P. elegans*); a more complete study of the relationships with other species, and genera, was not possible.

Statistical analysis

The individuals from the genus *Pterodactylus* are regarded as a single sample in the following

analysis. The groupings that were discovered were then correlated with the species that Wellnhofer distinguished. Table 1 lists these species. The sample contained 35 specimens of both juveniles and adults, as distinguished by Wellnhofer. The following 14 measurements were taken from each individual (Wellnhofer 1970): X_1 = length of skull, X_2 = length of jaw, X_3 = length of neck, X_4 = length of backbone from the anterior dorsal vertebra to the sacral region, X_5 = length of humerus, X_6 = length of radius, X_7 = length of metacarpal IV, X_8 = length of phalange 1, X_9 = length of phalange 2, X_{10} = length of phalange 3, X_{11} = length of phalange 4, X_{12} = length of the flight finger, X_{13} = length of femur, X_{14} = length of tibia. (See fig. 1). Separately, a components analysis of the wings alone was made (X_{5-11}).

All calculations were performed on an IBM

Table 1. A list of species and their supposed ontogenetic growth stage of the genus *Pterodactylus* (after Wellnhofer 1970).

Specimen	Species	Ontogenetic stage
1	<i>P. antiquus</i>	Juvenile
2	<i>P. antiquus</i>	Adult
3—7	<i>P. kochi</i>	Juveniles
8—18	<i>P. kochi</i>	Adults
19—24, 26	<i>P. micronyx</i>	Juveniles
25, 27—29	<i>P. micronyx</i>	Adults
30—35	<i>P. elegans</i>	Adults

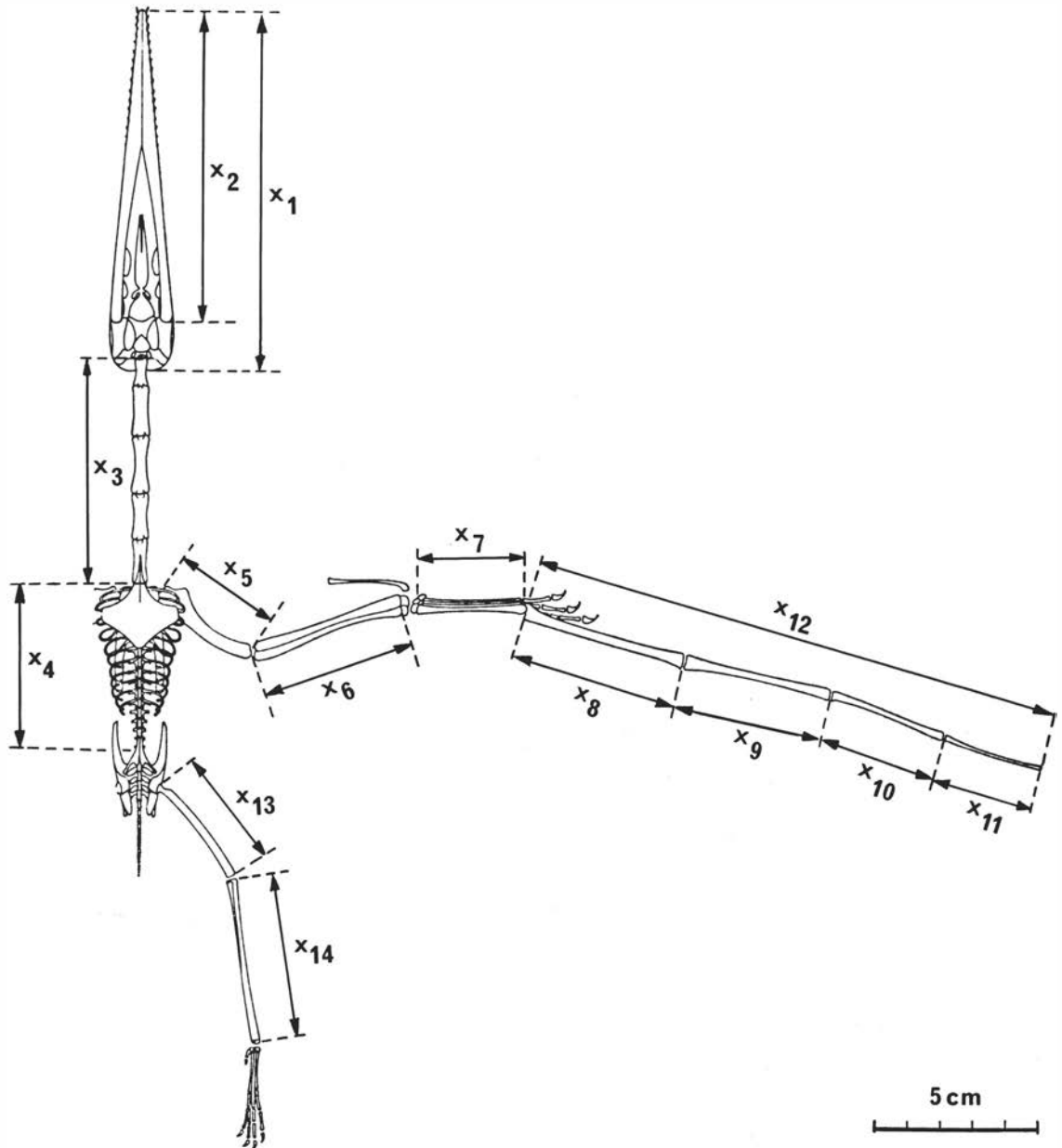


Fig. 1. Measurements taken from each of the 35 specimens in this study. A modified drawing of *P. kochi* after Wellnhofer (1970).

370/155 computer at the Uppsala University Computing Centre, using slightly modified versions of the PCOORD and PCA programmes (Blackith & Reyment 1971).

Components analysis

This multivariate technique has been used in biometrical research for many years now, and its

properties are well known. Details of this procedure may be found in most statistical texts including Davis (1973), and in Reyment (1966). Components analysis is used for studying the structure within either a multivariate covariance matrix or a correlation matrix, by reducing the many variables to relatively few linear transformations of the original variables. This gives a new set of variates, or components, each of which is

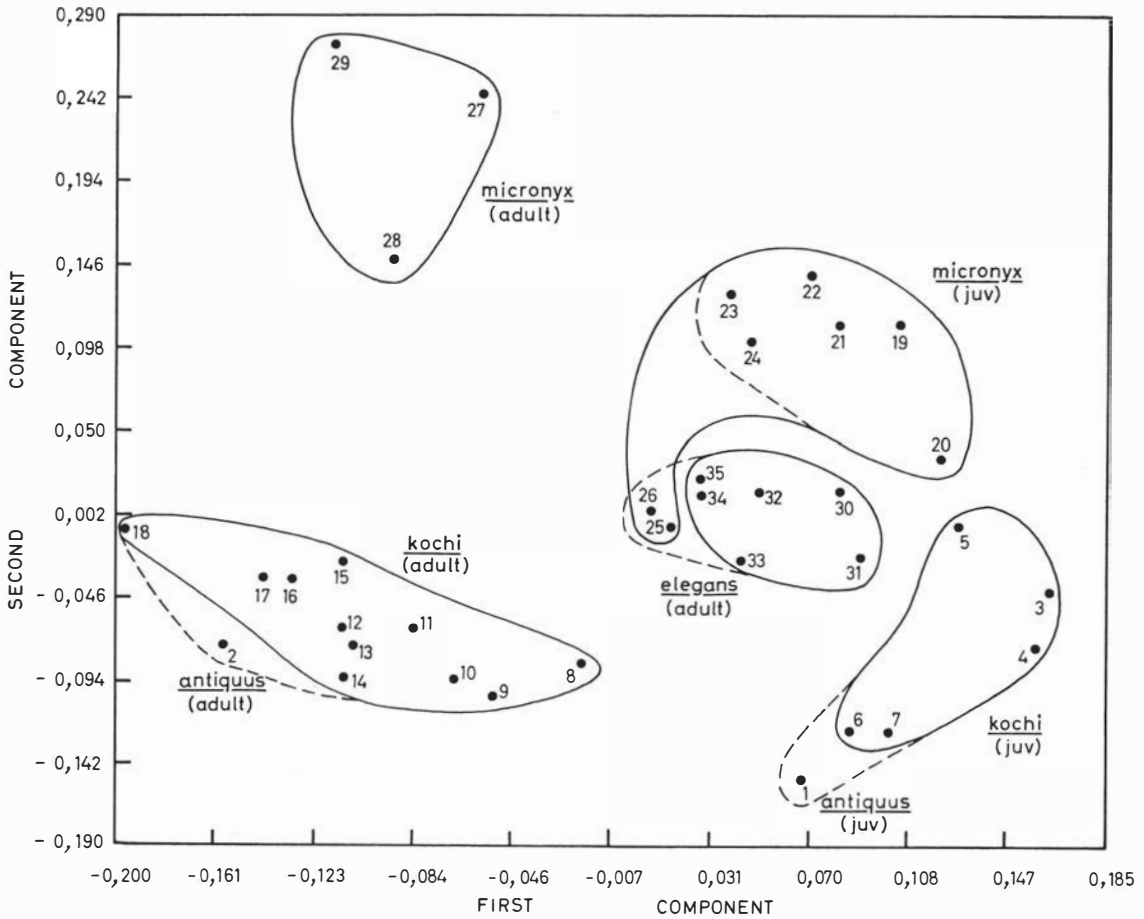


Fig. 2. The first and second components from the components analysis of *Pterodactylus*. The dotted lines indicate inclusion of specimens into specific groups proposed in this study.

uncorrelatable. These components are then associated with a proportion of the total variance; most of this variance is associated with a few, often three, principal components when the assumption of Hotelling's multivariate normality is taken. If multivariate normality is not present, then the variance is associated with components only (Jöreskog et al. 1976). The first of these components assumes maximum variance, and successive components assume a successively lesser part.

Most of the variance in the first component is frequently explained by size and size-correlated shape changes. That is, in biological terms, a growth trend (if the signs are equal for the first component coefficients), where a relatively homogeneous group is being analysed. The subsequent components reflect changes in proportions of the variables. Reyment (1966, 1969) dis-

cusses the details of associating size and shape with these components. The following analysis is based upon a covariance matrix which has been derived from the logarithms of the data.

First Component

Table 2 lists the coefficients for the first component. This first shows smaller values for the skull measurements (X_1, X_2, X_3) and larger values for the humerus and flight finger (X_5, X_{12}). All other coefficients are relatively uniform. This indicates that in the sample there is an overall size increase, with the skull increasing at a slightly slower rate than the other variables. Similarly, the humerus and flight finger appear to increase at a greater rate than the remaining variables. This may be seen from the data matrix on referring back.

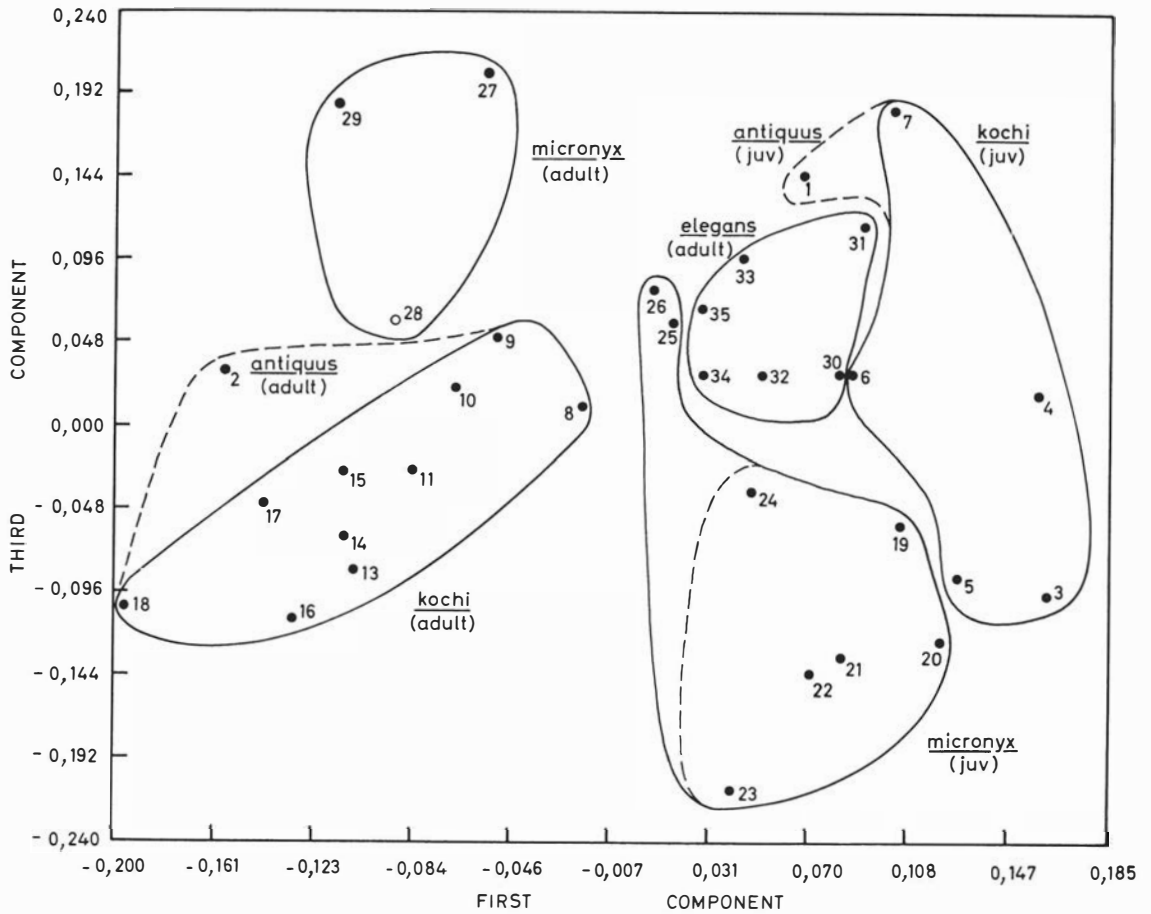


Fig. 3. The first and third components from the components analysis of *Pterodactylus*. The dotted lines indicate inclusion of specimens into specific groups proposed in this study.

Table 2. Component loadings from the first three components from the components analysis of the genus *Pterodactylus*.

	Component loadings		
	I	II	III
X ₁	0,3181	0,3501	-0,3218
X ₂	0,3487	0,3956	-0,4480
X ₃	0,3477	0,2793	-0,0340
X ₄	0,2466	-0,0038	0,1073
X ₅	0,2146	-0,0434	0,1798
X ₆	0,2389	-0,0338	0,1662
X ₇	0,2558	-0,5462	-0,2827
X ₈	0,2498	-0,4078	-0,0852
X ₉	0,2464	-0,0639	0,1207
X ₁₀	0,2253	0,2555	0,3883
X ₁₁	0,2039	0,0789	0,5912
X ₁₂	0,2420	-0,1844	0,0716
X ₁₃	0,2704	-0,1662	0,0984
X ₁₄	0,2827	-0,1948	-0,0795
Percent of total variance	94,87	2,94	0,94

Second component

The coefficients show large negative values for the skull, jaw and neck lengths (X₁, X₂, X₃) and for the phalanges 2 and 4 (X₁₀, X₁₁). On the other hand, large positive values are found for the radius and metacarpal 4 (X₇, X₈). From the original data, it was found that the radius and metacarpal 4 coefficients are associated with *P. micronyx*, and the skull measurements reflect variation in *P. kochi*. This may be more clearly seen in fig. 2. The first component, as already mentioned, accounts for most of the variance (94,87 %) which is interpreted as being size and size-correlated shape changes. The second component represents, primarily, the variance of the skull, metacarpal 4 and the phalange 3. The former (X₁, X₂, X₃) are polarized at the negative end of component 2, and the latter two (X₇, X₁₀) are at the positive end.

This is rather a simplistic concept of the variables forming poles to the second component

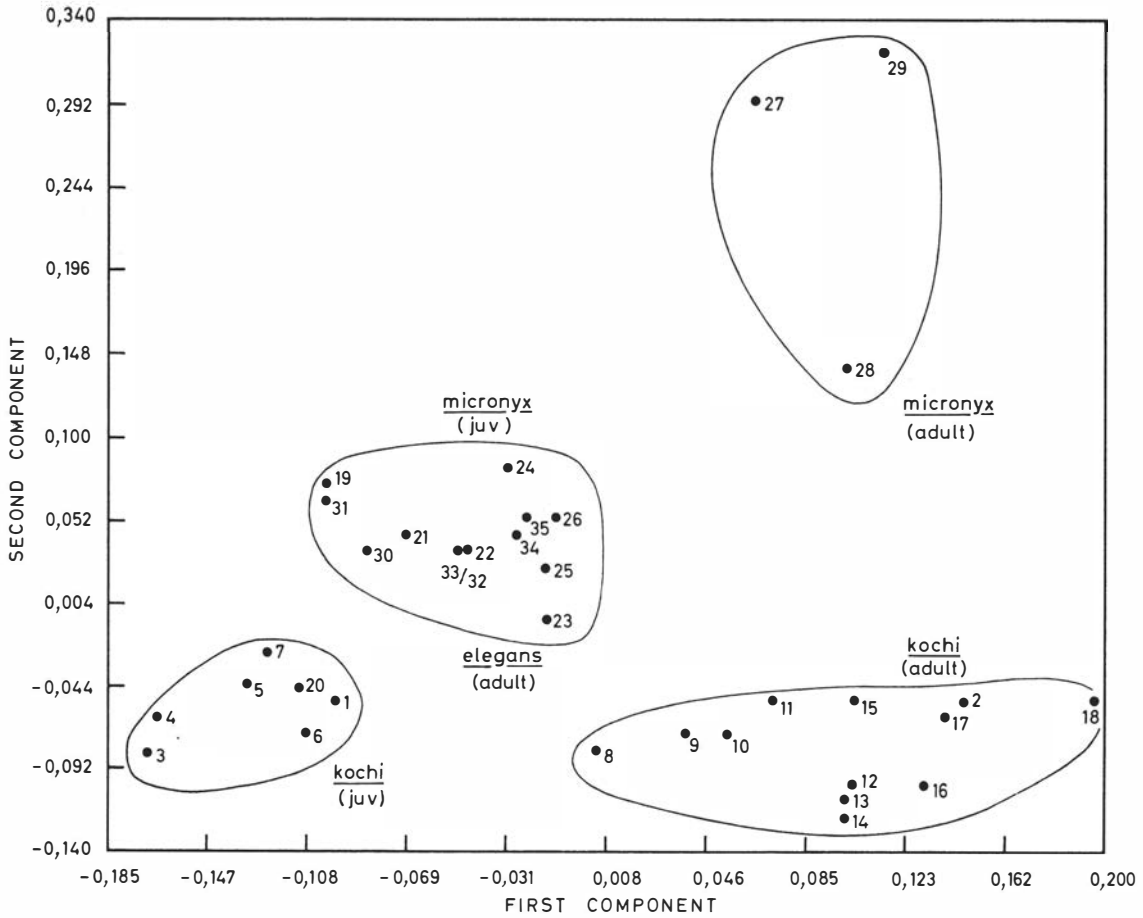


Fig. 4. The first and second components from the components analysis of the wing of *Pterodactylus*.

along which the specimens are distributed, in that it ignores other variables showing less of the total variance. However, the *P. kochi* shows very little variance with regard to component 2 (fig. 2), thus indicating ontogenetic allometry. In *P. micronyx*, the metacarpal 4—phalange 1 fraction has a stronger, more positive effect than the skull fraction, thus “pulling” the growth trend up slightly. Simply, the skull grows faster in relation to the wing in *P. kochi* than in *P. micronyx*. *P. antiquus* follows a similar trend to that of *P. kochi*.

Third component

This constitutes less than 1 % of the total variance. This component shows large negative coefficients for the skull and jaw lengths and the metacarpal 4 length. At the other extreme, there are large negative coefficients for the phalanges 3 and 4. When plotted against the first component (fig. 3), the

growth trends of *P. kochi* (and *P. antiquus*) diametrically oppose that of *P. micronyx* except for specimens 5 and 3 which have a neutral trend. This would appear to be for the same reasons as discussed under the second component: a different allometric relationship exists between these two species on the basis of variables X_1 , X_2 , X_6 , X_7 , X_{10} , X_{11} .

Components analysis of the wings

The plot of the first and second components (fig. 4) show the same trend of growth as seen in the components analysis of the whole body (fig. 2). *P. kochi* shows a horizontal trend indicating allometry with regard to the major influencing factors of component 2: metacarpal 4 (phalange 1) positive, and phalange 2 (phalange 3) negative. These two sets of factors have a very high positive and negative loading on eigenvalue 2.

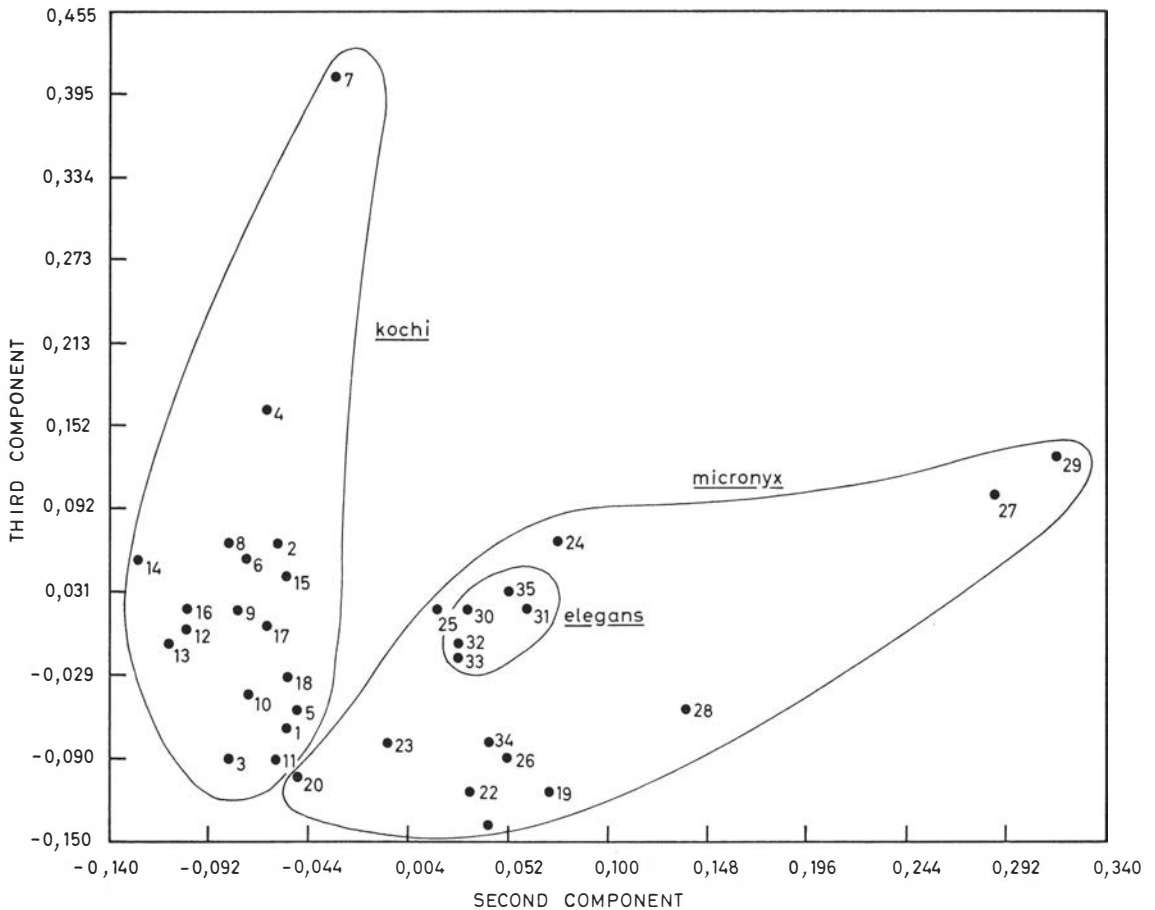


Fig. 5. The second and third components from the components analysis of the wing of *Pterodactylus*.

In fig. 4, *P. micronyx* is clearly directed during ontogeny to having a decreased wing-tip (phalanges 3, 4) length, but an increased metacarpal 4 length. It may be assumed from the apparent allometry of *P. kochi* that wing proportions stay very much the same as the body proportions. Again, *P. antiquus* follows the trend of *P. kochi* closely.

When components 2 and 3 are compared (fig. 5), we see an increase of the phalange 3 against phalange 4 which has dispersed the specimens of *P. kochi*. The allometric relationship within *P. kochi* is again represented by all these specimens lying in a cluster. Specimens 4 and 7, both of which are juveniles of *P. kochi*, are separated greatly from the main cluster of the species. *P. antiquus* closely follows *P. kochi* once again; *P. micronyx* and *P. kochi* are morphologically quite similar during their juvenile stages.

Principal coordinates analysis

A second type of analysis was carried out on the same data as with the components analysis (for the complete body). This technique developed from the need of a sound mathematical treatment of data being analysed for taxonomic similarity. In this analysis, the interrelationships of the individuals are given in a matrix of distance similarity (using the city block distance in this case) in which the row elements, or individuals, are plotted in Euclidean space as coordinates for point T. A three-dimensional diagram of these plots is given in fig. 6. For a more detailed treatment of this method, see Blackith & Reyment (1971).

The first point to note in fig. 6 is that the plots of the specimens lie within a very narrow band and not in clusters as in the components analysis. For this reason, lines could be drawn

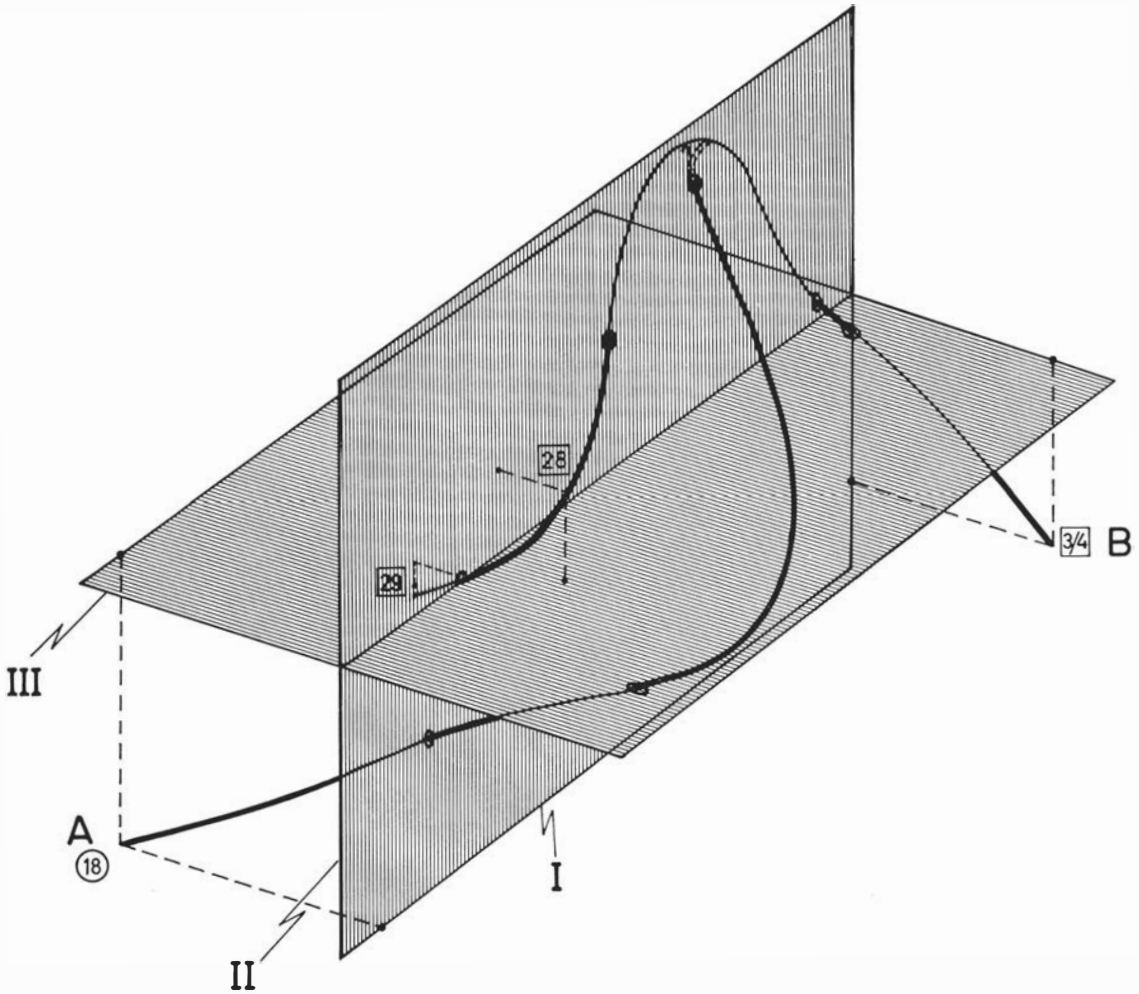


Fig. 6. A block diagram of the three-dimensional distribution of specimens of the genus *Pterodactylus* from the principal coordinates analysis.

(fig. 4, 5) to indicate the relationships of the species. The shape of the lines, or trends, is an artifact of this method: a quadratic relationship existing within the values of similarity; this is sometimes referred to as Kendall's horseshoe. This relationship has little significance in the results of this analysis. What is significant in fig. 6, 7, is the grouping of all juveniles together and the separation of the adults of *P. kochi* and *P. micronyx*. When regarded in relation with the components analysis, it would seem that this divergence during growth represents the different growth patterns of the two species. That is, during the juvenile stage, growth patterns are quite similar, but as they become adults, growth in *P. kochi* is dominant in the skull; in *P. micronyx*, growth in the wing is of greater importance (X_7 , X_8 , X_{10} ,

X_{11}). Again, *P. antiquus* follows the same trend to that of *P. kochi*.

Discussion

There is little in terms of the taxonomy that can be added to the work of Wellnhofer, although there is a discrepancy with regard to his juvenile specimen of *P. micronyx* (28). It is associated with the adults of this species and not with the juveniles (fig. 2, 3, 4, 5, 6, 7). The one juvenile and one adult of *P. antiquus* follow the trend of *P. kochi* so very closely that a separate specific allocation appears suspicious. This close relationship is quite significant because specimen 2 is the type for the species. Wellnhofer mentioned (per-

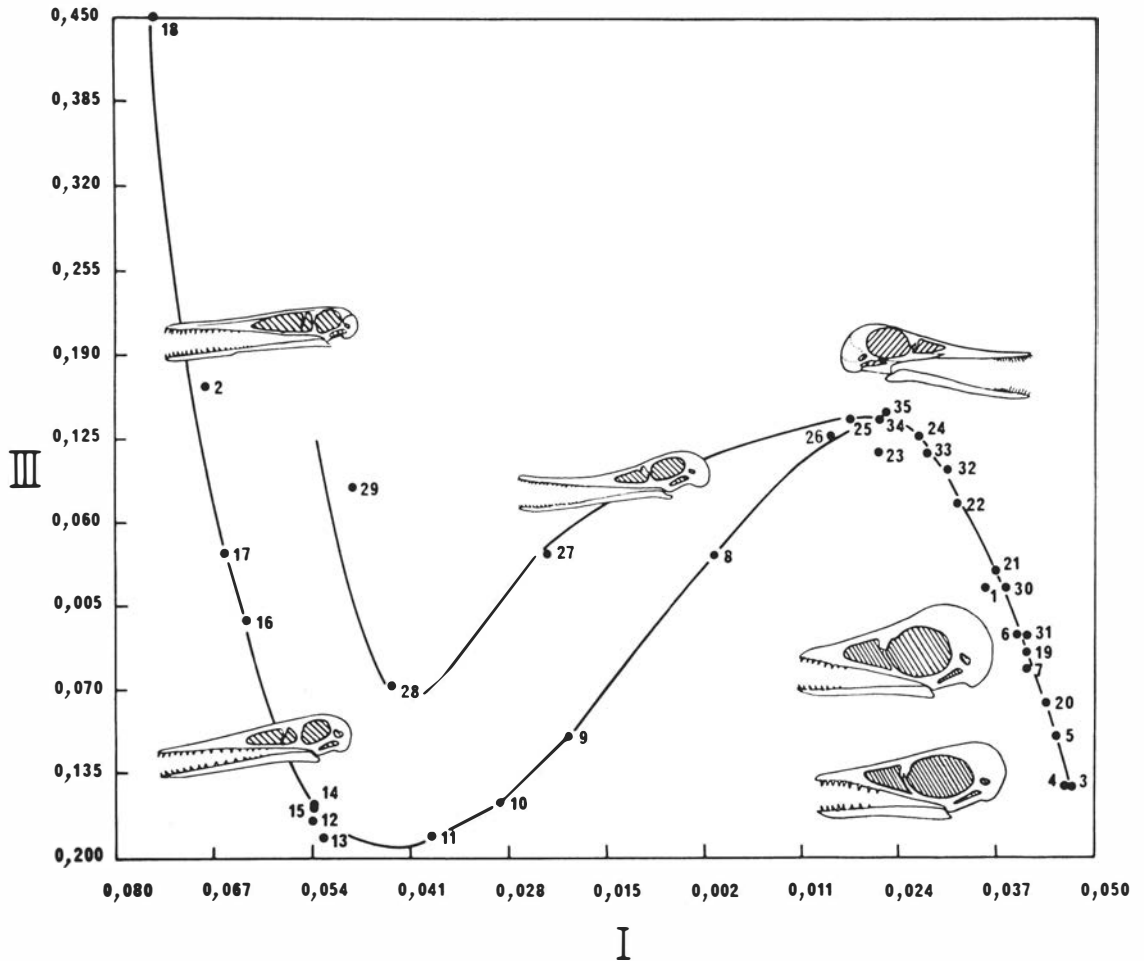


Fig. 7. The first and third principal coordinates from the principal coordinates analysis showing the divergence of specific differences during growth. The drawings are after Wellnhofer (1970).

sonal communication) that other variables, particularly the arrangement of the teeth, may also be of specific importance in this case. However, he published diagrams of the teeth of the species (p. 97, 1970); *P. kochi* and *P. antiquus* appear to be not too different. The specimens of *P. elegans* are adults only, forming a distinct cluster of their own. It is thus difficult to relate them to the other three species in terms of an ontogenetic growth series. It would appear that specimens 25 and 26 are too isolated from *P. micronyx* to be members of this species. Wellnhofer remarked (personal communication) that he was uncertain about these specimens; specimen 2 was denoted *P. micronyx* on the basis of its dentition, although the skull was thought to be too large. Specimen 26 was originally named *P. elegans*, but again the skull was thought to be too large, and Wellnhofer

allocated it under *P. micronyx*. From the forgoing analysis, I should prefer to call both these specimens *P. cf. elegans*. Generally, all specimens of *P. elegans* are similar to the juveniles of *P. micronyx*.

In this particular study, the components analysis has been of most use: it has produced a large dispersion of individuals giving a more distinct clustering of the species. In the principal coordinates analysis, back reference to the data matrix is very difficult and little dispersion is present, except for size and size-correlated shape changes. Differences in the growth rate are clearly seen however.

The conclusions from this study may be summarized as follows:

- 1). The skull generally grows at a slower rate

than the wings, much as one would expect. This is truer in *P. micronyx* than in *P. kochi*, the latter having almost an allometric growth trend.

- 2). From the components analysis of the wings, *P. kochi* again shows a near allometric increase during growth. In *P. micronyx*, the wing tip tends to grow faster than the more proximal parts of the wing.
- 3). The divergence in growth trends between *P. kochi* and *P. micronyx* is more clearly exemplified in the principal coordinates analysis. That this growth trend cannot be inferred from this analysis, and only from the components analysis, indicates that it must be used in conjunction with another analysis.

From these conclusions, it should be possible to infer the proportions of incomplete specimens with reasonable accuracy. A need for this sort of estimation has recently come with the discovery of very large, though incomplete, pterosaurs from Texas (Lawson 1975). Somewhat irrisorogous estimations have been made as to the wing span of these specimens, although small sample sizes are involved. The unique size of these specimens makes it impossible to estimate the wing span directly from the forgoing results: a separate regression analysis would be required.

A further comment may be added for which no definite proof can be given. In trying to explain the similarity of all species (here excluding *P. elegans*) in their juvenile stages, it is revealing to look at their geographical distribution. Within a relatively small area (Bavaria, S. Germany), *all* species occur; that is, there is no regionalization of different species. It is quite difficult to believe that, in the light of present knowledge of recent species, different species could inhabit such a small area of an apparently uniform environment. Two exceptions to this apply. First, that these four species occupied different ecological niches, and second, that they are not separate species. The only evidence to support the former exception is slight differences in tooth size and arrangements; perhaps soft-part

differences may have existed. In support of the second exception, sexual dimorphism may be put forward. It is well known that juveniles are more similar than adults of the same species in vertebrates. Unfortunately, no osteological evidence can support this fact, thus no taxonomical alteration may be made. However, I feel that from this reasoning, it is more likely that *P. kochi* and *P. micronyx* are sexual dimorphs (*P. kochi* tends to be larger, thus possibly it may be male), and that *P. antiquus* is more closely related to this *P. kochi-micronyx* than at the species level. *P. elegans* has the most different tooth arrangement (Wellnhofer 1970, fig. 28: teeth being concentrated towards the tip of the rostrum), this may be a separate species utilizing another ecological niche.

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