STEPHANODONTY IN FOSSIL MURIDS

A Landmark-Based Morphometric Approach

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ABSTRACT

Landmark based morphometric methods were used to study shape variation in fossil murid teeth. Nineteen landmarks were defined and recorded on the occlusal surfaces of first upper molars belonging to eight populations from Late Miocene and Pliocene localities in Spain. The study focused on an evolutionary sequence characterized by development towards a specialized crown structure known as stephanodonty. Population differences were investigated using Bookstein shape coordinates and analyzed using analysis of variance and Mahalanobis distances. Relative warp analysis was used to study the nature of the shape variation among the landmarks. The results are consistent with the accepted taxonomic classification, although the taxonomic position of one of the populations is problematic. The analyses show that the development towards stephanodonty (a feature defined by the presence of ridges) is correlated with changes in shape, which are themselves correlated with size in the evolutionary sequence studied. It is apparent that landmark-based approaches show promise for functional morphological and paleoenvironmental interpretations of fossil murid teeth.

INTRODUCTION

The number of applications of landmark-based morphometrics is growing, and more biological shapes are being described and analyzed with these new geometric methods (Bookstein, 1991). This study explores the potential of these methods for interpreting shape differences among lineages of fossil teeth from murid rodents during their Old World radiation evidenced in Late Miocene and Pliocene sediments of Spain (Misonne, 1969; Michaux, 1971; Van de Weerd, 1976). The study focuses on an extinct group of south-western European murids that show an evolutionary development towards stephanodonty (Schaub,

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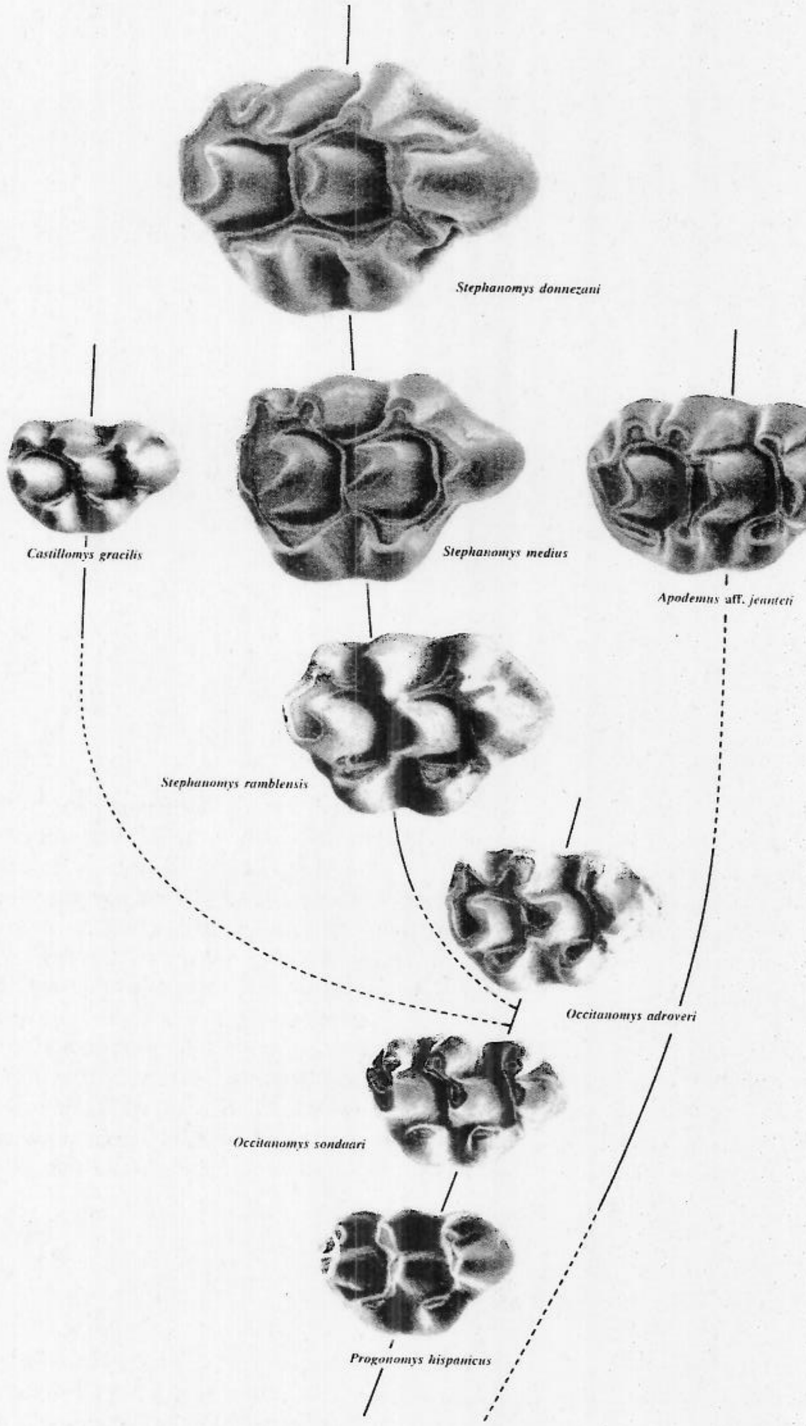

Figure 1. Evolutionary relationships among murid species used in this study, represented by their right upper molars. Dashed lines represent likely lineages. Enlargement approximately × 20.

1938; Cordy, 1976). In complete stephanodonty (Sensu Cordy, 1976) all cusps of the upper molars are connected by ridges, resulting in a garland-type dental pattern. Figure 1 shows this evolutionary trend in the first right upper molars of the sequence *Progonomys hispanicus-Occitanomys sondaari-Occitanomys adroveri-Stephanomys ramblensis-Stephanomys medius-Stephanomys donnezani*. This trend is accompanied by a size increase and the development of a special type of hypsodonty (elongation of the cusps in an oblique, posterior direction.)

The *P. hispanicus-O. sondaari-O. adroveri* lineage was described by Van de Weerd (1976) and represents an excellent example of anagenetic evolution (Chaline and Mein, 1979). The sequence *S. ramblensis-S. medius-S. donnezani* was interpreted as an evolutionary lineage by Cordy (1976, 1978) and Adrover (1986). The suggested relationship of these two lineages is shown in Fig. 1, with *S. ramblensis* descending from *Occitanomys* (Van de Weerd, 1976; Cordy, 1976).

A *Castillomys* species (*C. gracilis*) is included in this study because the genus shows stephanodonty, but the molars are small and brachiodont (Van de Weerd, 1976; Martín-Suárez and Mein, 1991). An *Apodemus* species is included as an outgroup. *Castillomys gracilis* and *A.* aff. *jeanteti* are shown in their respective phylogenetic positions in Fig. 1.

MATERIAL AND METHODS

In total, 250 first upper molars from eight populations were studied. Each population consisted of a different species. These eight species belong to five genera (Fig. 1; Table 1). The first upper molar was chosen because it represents the most diagnostic element of the murid dentition.

The oldest four populations come from the basin of Teruel in northeast central Spain (Van de Weerd, 1976). The most recent population comes from the Layna locality in central Spain (Cordy, 1976). The Caravaca locality of southwestern Spain is represented by three species: *Stephanomys medius* (Adrover, 1976), *Castillomys gracilis* (Van de Weerd, 1976) and *Apodemus* aff. *jeanteti* (de Bruijn et al, 1975). I included one locality for each MN biochronologic zone (Mein, 1990; de Bruijn et al., 1992) from MN 10 to MN 15. Absolute ages range from circa 9.5 to 3 million years before present (MYBP). All material examined is stored in the collection of the Institute of Earth Sciences of the Utrecht University. Nineteen landmarks were defined on the occlusal surface of the first upper molar (Fig. 2), 13 along

Table 1. Species used in this study and their collection data

Species	Locality	MN biozone[a]	Approx. age[b] (MA)	Sample size
Apodemus aff. *jeanteti*	Caravaca	14	5	57
Castillomys gracilis	Caravaca	14	5	9
Stephanomys donnezani	Layna	15	3	12
Stephanomys medius	Caravaca	14	5	32
Stephanomys ramblensis	Villalba Baja 1	13	5.5	3
Occitanomys adroveri	Masada de Valle 2	12	7.5	66
Occitanomys sondaari	Tortajada A	11	8.5	37
Progonomys hispanicus	Masia del Barbo 2B	10	9.5	34
Total				250

[a] MN biozones according to de Bruijn et al. (1992).

[b] Approximate ages estimated by the author on the basis of Pevzner and Vangenheim (1993) (magnetostratigraphy), Steininger et al. (1990) (correlation table), Van de Weerd (1976), and De Bruijn et al. (1992).

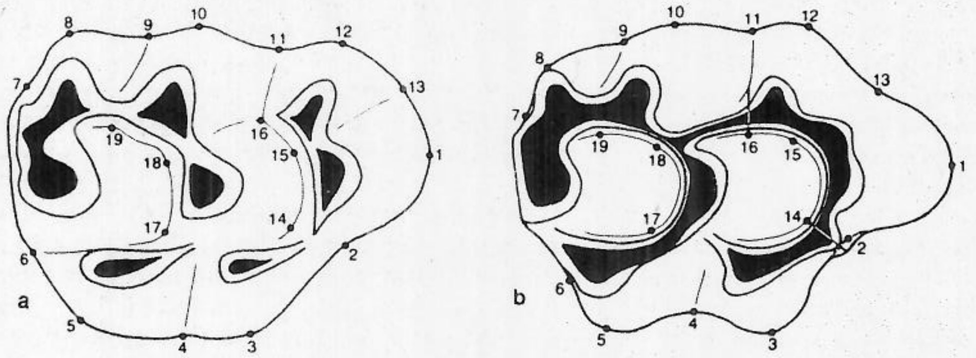

Figure 2. Location of landmarks on the occlusal surface of the right upper molar of (a) an *Occitanomys*-type molar and (b) an advanced *Stephanomys*-type molar. Orientation: right is anterior and bottom is lingual.

the outline and 6 on top, all in occlusal view. The 6 landmarks on top of the occlusal surface were defined in valleys between the cusps, rendering their location virtually independent of wear.

Landmarks 3, 5, 8, 10 and 12 are type 2 landmarks in the classification of Bookstein (1991): they are points of maximum curvature of the outline and are associated with cusps. Similarly, 4, 6, 7, 9, 11 and 13 are type 2 landmarks: they are points of maximum curvature and are associated with valleys. (Note that these last 6 landmarks could also be defined as intersections of a valley with the outline. Interpreted this way they become type 1 landmarks. However, the bottoms of these valleys usually do not form distinct lines but rather represent lines of maximum curvature between adjacent cusps). Landmarks 14, 15, 17, 18 and 19 come close to type 1 landmarks: they are defined as the 'intersections' of the central valleys (which do approach distinct lines) with lines perpendicular to these valleys running through the lowest part of the connections between the two adjacent cusps. In a number of specimens one or two additional cuspules have developed next to the central anterior cusp (i.e., *S. ramblensis* in Fig. 1): a cuspule called t1-bis at landmark 2 and a cuspule called t3-bis between landmarks 13 and 15. In these cases, landmarks 14 and 15 are defined by the intersections of the central valleys with lines perpendicular to these valleys running through the points of maximum curvature of the cuspules. Figure 2b shows the construction in the case of t1-bis. Landmark 16 is best classified as type 2. It is defined as the meeting point of three valleys in the *Progonomys*, *Occytanomys* and *Apodemus* species. For the *Stephanomys* and *Castillomys* specimens a construction had to be made for this landmark (Fig. 2b). Landmark 2 is a true type 2 landmark, being a point of maximum curvature of the outline. However, in some specimens the t1-bis was so large that it filled up the inner curve of the outline where landmark 2 was defined. When this was the case the position of this landmark was estimated as indicated in Fig. 2b. Landmark 1 is the anterior extreme of the molar in the orientation of Fig. 2. It is a type 3 landmark.

The *S. medius* and *S. donnezani* samples consist of specimens characterized by a moderate to high state of wear, because landmarks 14, 15, 17 and 18 would not have been visible in specimens with little wear.

Specimens were placed horizontally, and x and y coordinates of the landmarks were recorded using a Reflex three dimensional measuring microscope. Coordinates of left-side specimens were re-calculated as though they came from the right side.

Landmarks 4 and 11 were chosen as endpoints for the baseline (Bookstein, 1991). This baseline was chosen instead of one in the direction of the long axis of the tooth because landmarks such as 1, 13, 6 or 7 could be measured with relatively less precision.

Coordinates were rotated and scaled to the baseline with end points (0,0) and (1,0) to produce "size-free" Bookstein shape coordinates. Calculations were carried out using the program XY written by Baylac (1993), which was also used to calculate centroid sizes.

Uni-and multivariate analysis of variance were used to test for population differences. This was done with the SAS procedure CANDISC, which also produced Mahalanobis distances, *D*, between the populations. These distances were transformed into *F* values and were adjusted to compensate for bias according to Marcus (1993). An UPGMA cluster analysis was performed on the adjusted *D*.

Generalized Least Square (GLS) fitting was performed to find consensus specimens for each of the eight populations. Consensus specimens were fitted by Least Square fitting to the consensus specimen of the most primitive species, *Progonomys hispanicus*. The fits were calculated using the program GRF-ND written by Slice (1993).

The fitted consensus configurations were compared using relative warps (Bookstein, 1991; Rohlf, 1993a) with the TPSRW program of Rohlf (1993b).

Different options within the program were explored, such as the use of the parameter, α, whose value influences the scale of the nonlinear deformations, and the option to include the uniform component (the linear part of shape change) as estimated by the method of Bookstein ("Standard formula" article, this volume). When the latter option is used, the relative warps summarize non-linear as well as linear shape variation between the consensus specimens. The program TPSPLINE was used to visualize deformations of grids between different consensus specimens.

Partial warp scores (Bookstein, 1991, Rohlf, 1993a) and uniform components of the consensus specimen shapes were regressed on centroid size and geological time for the *P. hispanicus-S. donnezani* evolutionary sequence by means of TPSREGR (Rohlf, 1993 c). The consensus configuration of *P. hispanicus* was used as the reference. Deformation grids were produced for values of the independent variable. In each case, the initial condition was the average landmark pattern.

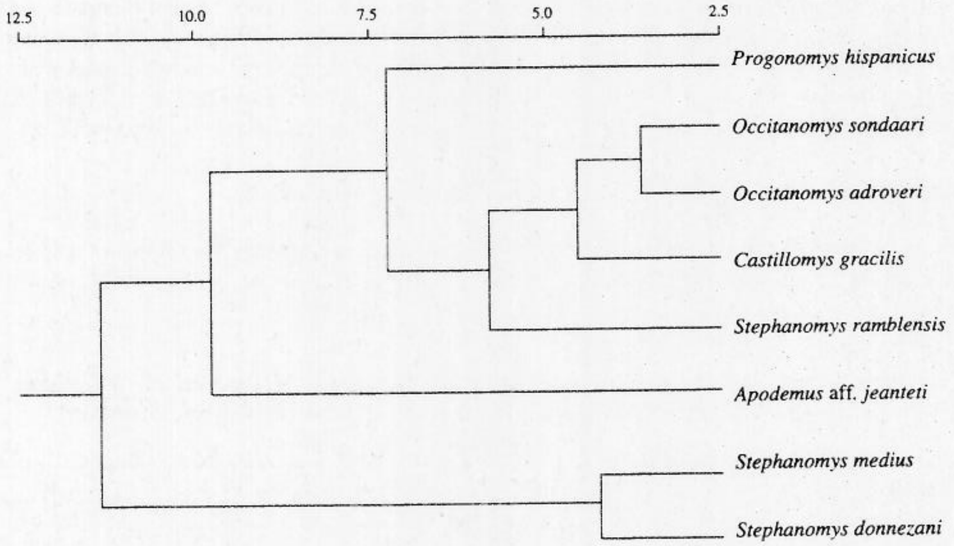

Figure 3. The UPGMA phenogram of populations based on adjusted Mahalanobis distances (see text) computed on 34 Bookstein shape coordinates.

Table 2. The *F* statistics and probability values (df 7, 242) from one-way ANOVA (SAS procedure CANDISC) testing population variation for the Bookstein shape coordinates

Variable	*F*	*p>F*	Variable	*F*	*p>F*
X1	36.37	0.0001	Y1	19.01	0.0001
X2	16.83	0.0001	Y2	7.62	0.0001
X3	23.09	0.0001	Y3	9.32	0.0001
X5	5.83	0.0001	Y5	22.07	0.0001
X6	112.34	0.0001	Y6	39.97	0.0001
X7	20.60	0.0001	X7	121.46	0.0001
X8	4.07	0.0003	Y8	60.62	0.0001
X9	3.45	0.0015	Y9	64.05	0.0001
X10	4.17	0.0002	Y10	54.81	0.0001
X12	6.52	0.0001	Y12	32.26	0.0001
X13	30.56	0.0001	Y13	13.31	0.0001
X14	7.68	0.0001	Y14	34.52	0.0001
X15	1.24	0.2802	Y15	32.30	0.0001
X16	15.37	0.0001	Y16	9.75	0.0001
X17	4.51	0.0001	Y17	120.16	0.0001
X18	25.86	0.0001	Y18	103.19	0.0001
X19	14.57	0.0001	Y19	48.78	0.0001

RESULTS

Statistical Differences between the Populations

Table 2 shows the univariate *F* ratios and probability values for the separate x and y Bookstein shape coordinates (except those of the baseline, which have fixed values of (0,0) and (1,0)) that resulted from a one way analysis of variance (ANOVA). Population differences were clearly significant for all the coordinates except for x_{15}, and for all coordinates together (Table 3). Table 4 shows the pairwise Mahalanobis *D* between the populations. The *D* are all significant with probability values less than 0.0001. Figure 3 shows the phenogram resulting from an UPGMA cluster analysis based on the adjusted Mahalanobis distances. It is interesting that *S. ramblensis* does not cluster with the other *Stephanomys* populations but with *Occitanomys* and *Castillomys*. That the *Apodemus* species does not form a tight cluster with the other species is consistent with its relatively more distant taxonomic position.

Landmark Shape Differences between the Populations

Figure 4a shows the GLS fitted consensus specimen for the *Progonomys hispanicus* population along with all the fitted specimens of this population. Figures 4b-h show the

Table 3. Multivariate statistics, *F* approximations and probability values (df 7,242) from multivariate analysis of variance (SAS procedure CANDISC) testing population variation for the Bookstein shape coordinates

Statistic	Value	*F*	Numerator df	Denominator df	*p*
Wilks' Lambda	0.00	15.00	238	1448.41	0.0001
Pillai's Trace	3.91	8.04	238	1505.00	0.0001
Hotelling-Lawley's Trace	35.96	31.32	238	1451.00	0.0001
Roy's Greatest Root	19.84	125.46	34	215.00	0.0001

Table 4. Mahalanobis distances between populations computed using Bookstein shape coordinates. Values below the diagonal are adjusted for bias

	*A.*aff *j.*	*C.g.*	*S.d.*	*S.m.*	*S.r.*	*O.a.*	*O.s.*	*P.h.*
Apodemus aff. *jeanteti*	0.0	10.0	14.2	13.0	12.5	9.6	9.5	7.5
Castillomys gracilis	9.8	0.0	10.8	8.8	6.2	4.3	4.7	7.0
Stephanomys donnezani	13.9	10.5	0.0	4.3	10.9	11.1	11.6	14.0
Stephanomys medius	12.8	8.6	4.1	0.0	9.5	9.5	10.0	12.3
Stephanomys ramblensis	12.2	5.9	10.6	9.2	0.0	5.0	6.9	10.3
Occitanomys adroveri	9.5	4.2	10.9	9.3	4.6	0.0	3.6	6.9
Occitanomys sondaari	9.4	4.5	11.4	9.8	6.6	3.5	0.0	5.8
Progonomys hispanicus	7.4	6.8	13.7	12.1	10.0	6.8	5.6	0.0

landmark shape differences of the consensus specimens of the other species relative to the *P. hispanicus* consensus specimen. The trends shown by Fig. 4a-f are the general broadening of the molars, the straightening of the posterior border, the relative broadening and the anterior shift of the central region and the sharpening of the anterior part in *Stephanomys medius* and *S. donnezani* by means of posterior-buccal movement of landmarks 10, 11 and,

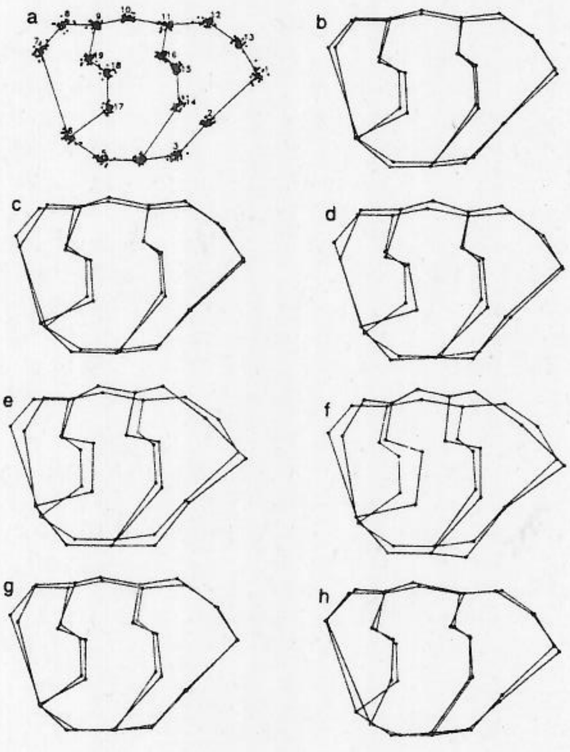

Figure 4. (a) Generalized Least Square fitted consensus specimen for the *Progonomys hispanicus* population together with the landmark points of all the fitted specimens. The landmark shape differences relative to the *P. hispanicus* consensus specimen (thin line) of the consensus specimens (thick line) of the populations of (b) *Occitanomys sondaari*, (c) *O. adroveri*, (d) *Stephanomys ramblensis*, (e) *S. medius*, (f) *S. donnezani*, (g) *Castillomys gracilis* and (h) *Apodemus* aff. *jeanteti*.

in particular 12. The shape of *Castillomys gracilis* (Fig. 4g) is very similar to that of the *Occitanomys* species. The largest difference between *A.* aff. *jeanteti* and the reference specimen is the position of landmark 6, which has moved in the antero-lingual direction. This shift is associated with the formation of a new cusp, the so-called t7 (see Fig. 1).

The results of relative warp analysis are presented in Fig. 5 and Table 5. Table 5 shows that in all three cases a large part of the variation is explained by the first relative warp (80.8, 77.6 and 78.9 %, respectively). Inspection of the relative warp loadings (not shown) indicate that the value of α, had little effect on the first relative warp. However, inclusion of the uniform component estimate resulted in significant differences between relative warp 2 and those higher, and yielded a meaningful second relative warp that did not reflect statistical error. The largest differences between the loadings of the first relative warp from analyses with and without the uniform component were localized in the posterior-lingual area of the teeth. Figure 5a shows the loadings as vectors for the first relative warp with estimation of the uniform component included. In the analysis excluding this uniform component, the vectors of landmarks 4, 5 and 6 point more to the posterior side of the teeth (not shown here). Figures 5a and b show that transverse deformation is mainly represented by relative warp 1 whereas longitudinal deformation is represented in relative warp 2. The unique morphology of *Apodemus* is reflected in relative warp 2 by the anteriorly directed vectors from landmarks 5 and especially 6 (compare with Fig. 4h). Figure 5c shows the first relative warp as a deformed grid (all eight populations included, $\alpha = 1$). The inflation and relative anterior movement of the central region and the generally symmetric shape (caused by the posterior movement of landmark 12 and the straightening of the posterior border) compared with the reference specimen were already observed in Fig. 4e and f. Figures 5d and e show a similar clustering of populations, indicating that the x and the y part of the uniform component contribute strongly to relative warp 2 and 1 respectively. Both plots are concordant with the phenogram in Fig. 3. It can be seen from the positions of the points in Fig. 5d that the order of the evolutionary sequence *P. hispanicus-S. donnezani* is reflected in the scores on relative warp 1, except for the relatively "advanced" position of *O. sondaari*. Relative warp separates the oldest four populations of the sequence (*Progonomys hispanicus*, the two *Occitanomys* species and *Stephanomys ramblensis*) from the two most recent populations (*S. medius* and *S. donnezani*), which like *Apodemus* aff. *jeanteti*, are characterized by stronger longitudinal shifts of landmarks. Both *A.* aff. *jeanteti* and *C. gracilis* remain relatively close to the primitive form, *P. hispanicus*.

Figures 6 a, b and c show grid deformations from the primitive form to *O. adroveri*, *S. donnezani* and *A.* aff. *jeanteti*, respectively. The grids in Fig. 6a and b reflect the first

Table 5. Results of relative warp analysis on consensus specimens, based on the consensus configuration of the *Progonomys hispanicus* population as the reference. Reported for the first three relative warps are singular values (SV), proportion of explained variance (prop. var.) and probability values for equality of the remaining singular values (prob.). Results are given for three different combinations of program options. The , = 0 and , = 1 options give more weight to small-scale and large-scale variations, respectively. In the case of , = 1 singular values are adjusted (see TPSRW documentation; Rohlf 1993b)

	Relative warp analysis								
	$\alpha = 0$, uniform component not included			$\alpha = 0$, uniform component included			$\alpha = 1$, uniform component not included		
	Singular value	Proportion variance	p	Singular value	Proportion variance	p	Singular value	Proportion variance	p
1	0.158	0.808	0.000	0.078	0.776	0.000	0.269	0.789	0.000
2	0.066	0.141	0.001	0.029	0.104	0.384	0.101	0.110	0.164
3	0.030	0.030	0.234	0.023	0.067	0.528	0.067	0.049	0.411

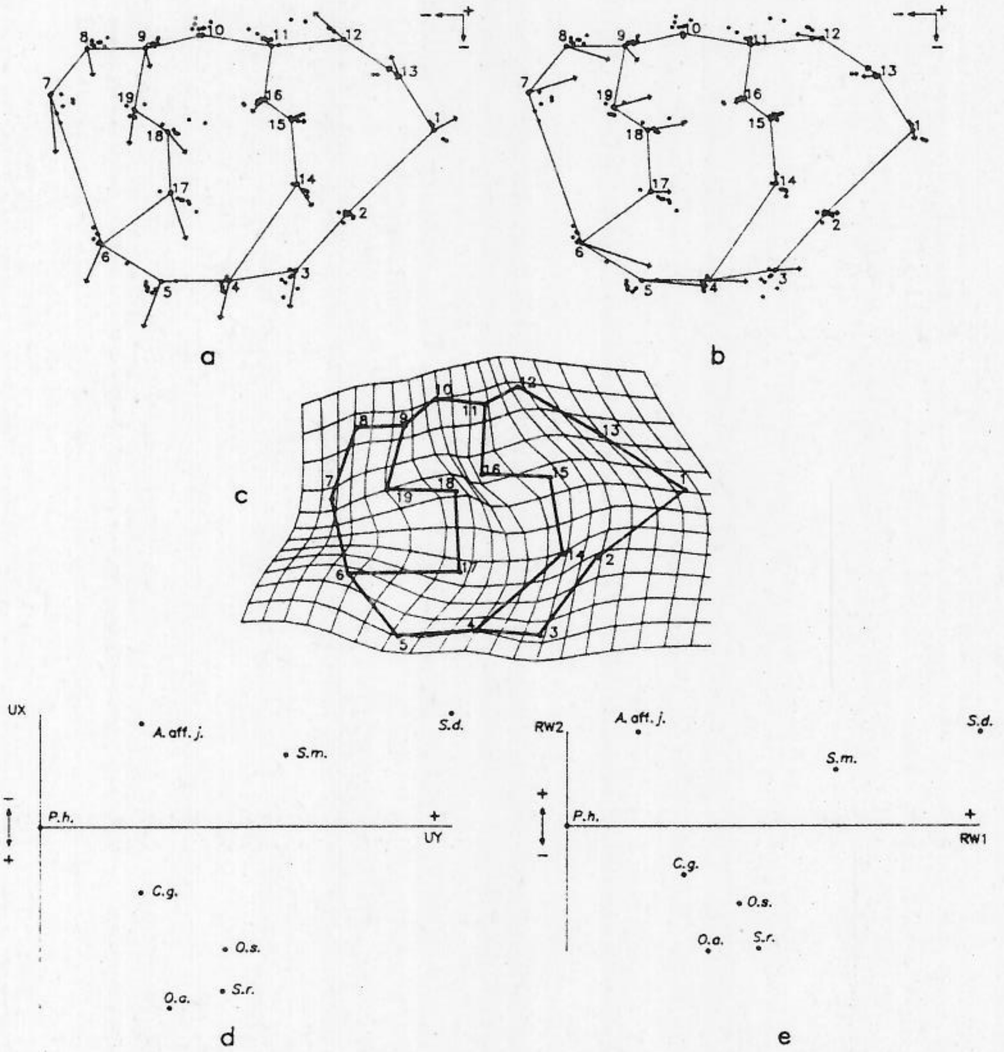

Figure 5. (a) Vectors of landmark changes for the first relative warp. Estimation of uniform component included, $\alpha = 0$, and all populations used. (b) Vectors of landmark changes for the second relative warp. Options as in (a). (c) Deformation grid for the first relative warp. Estimation of uniform component not included, $\alpha = 1$, and all populations used. (d) Plot of uniform x (Ux) and uniform Y (Uy). Options as in (a). (e) Plot of the first two relative warps. Options as in (a).

relative warp (compare Fig. 5c). The deformation seen in Fig. 6b appears essentially to be a magnification of the deformation seen in Fig. 6a, and corresponds to a more advanced evolutionary state. The deformation in Fig. 6c is of a different type, reflecting relative warp 2.

Regressions of Landmark Shape on Size and Geological Age

Least-square-regressions of the partial warp scores and uniform components of the consensus specimens for the populations of the *P. hispanicus-S. donnezani* sequence were

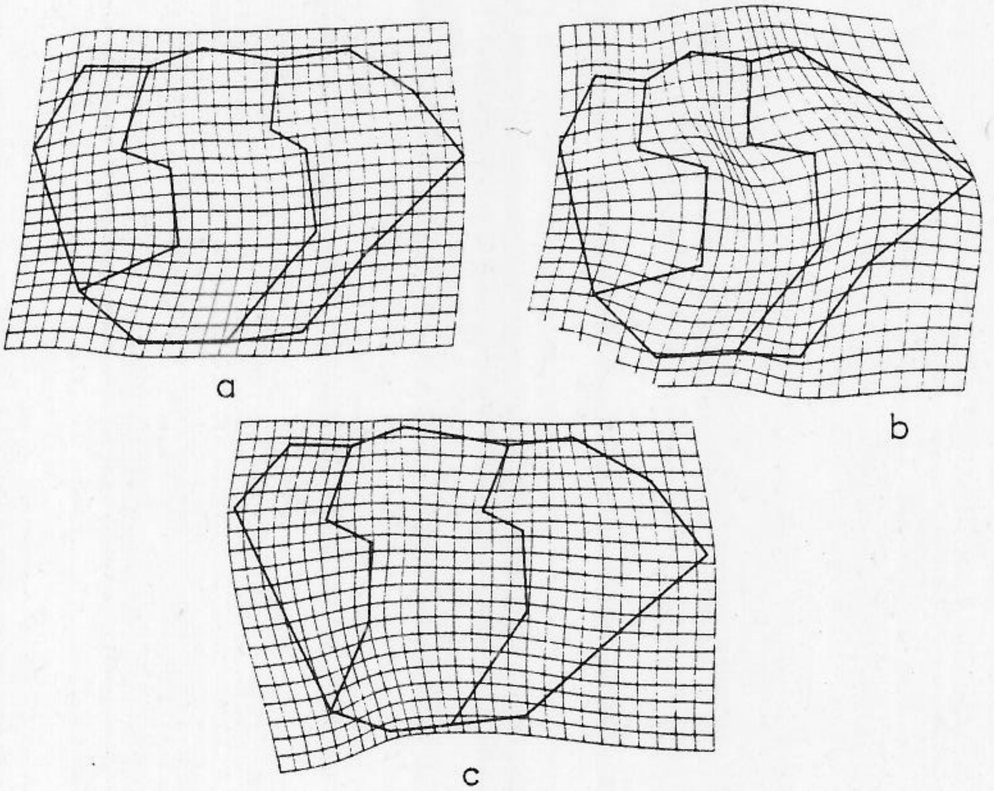

Figure 6. Thin-plate spline grid deformations from the *P. hispanicus* consensus specimen into consensus specimens for (a) *Occitanomys adroveri*, (b) *Stephanomys donnezani*, (c) *Apodemus* aff. *jeanteti.*

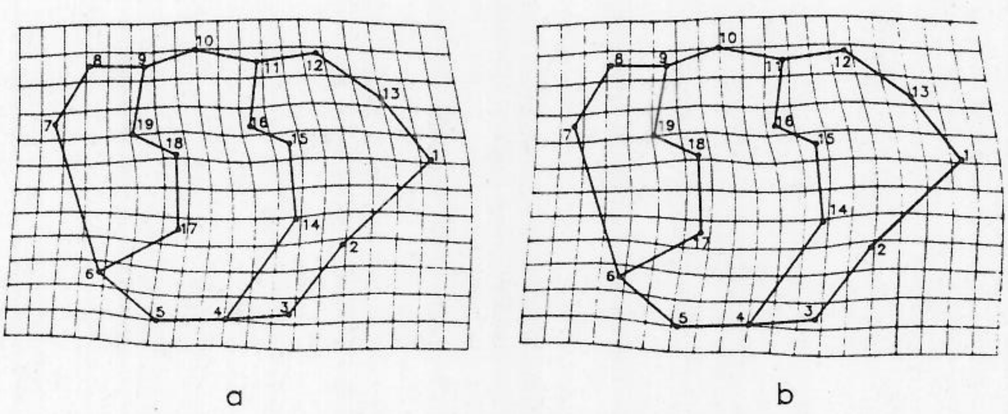

Figure 7. (a) Deformation grid resulting from a least-square regression of the partial warp scores and uniform component for consensus specimens of the *P. hispanicus-S. donnezani* sequence on centroid size (centroid size = 4.483). The *P. hispanicus* consensus configuration was used as the reference. (b) Deformation grid resulting from a regression as in (a) but with absolute age as independent variable (absolute age = 3.25 MYBP).

performed on centroid size and on geological age by means of the TPSREGR program (Rohlf, 1993c). (See Table 1 for ages. Average centroid sizes are 2.62 (*P. hispanicus*), 2.75 (*O. sondaari*), 2.99 (*O. adroveri*), 3.59 (*S. ramblensis*), 3.79 (*S. medius*) and 4.75 (*S. donnezani*)). The initial average conditions of the deformations in both Fig. 7a and b correspond to stages between *O. adroveri* and *S. ramblensis*, whereas in both cases the resulting conditions were chosen so that they were close to those of *S. donnezani*. Both grids cannot be distinguished from each other by eye. This is not at all surprising because these two variables, centroid size and geological age, are highly correlated for this sequence ($r = 0.98$).

Figures 7a and b strongly resemble Fig. 6a, which represents the older part of the studied sequence. It is evident that the results of this regression analysis express, in another way, the effects of the first relative warp described above. However, as the shape changes are now explicitly related to size and time, we are justified in saying that allometry has played a major role in this evolutionary sequence.

DISCUSSION

Taxonomy

The taxonomy of the murid species studied is largely confirmed, except for *S. ramblensis* Van de Weerd, 1976, which clusters not so much with the other *S.* species as with the *Occitanomys* species. In this respect it is interesting that this author considers this species to be intermediate between *Occitanomys* and *Stephanomys* on the basis of size and stage of stephanodonty. He classifies it as *Stephanomys* because it fits in with the supposed evolutionary lineage toward the type species of this genus, *S. donnezani*. The sample size of the *S. ramblensis* population examined was very small ($n = 3$), but this does not account for the observed clustering. New material of this species will be available soon for further work. The results presented here suggest a shape of *S. ramblensis* that is much closer to *Occitanomys* than it is to *Stephanomys*. The shape of *C. gracilis* as defined by the landmarks is also similar to that of *Occitanomys*. This is in agreement with Van de Weerd's (1976) observation that the molars of the two genera closely resemble one another in shape but not in size.

Evolutionary Trends

The data presented above show that the degree of stephanodonty is correlated with changes in the pattern of landmarks as defined along the outline and on the surface of the molars. For instance, the anterior shift of the central landmarks allow an increase of oblique hypsodonty. Similarly, the lingual-buccal symmetry of the garland-like dental pattern in the true stephanodont forms corresponds to the lingual-buccal symmetry in the landmark patterns. Trends towards broadening of the molars and straightening of the posterior border, associated with increasing stephanodonty, have been mentioned in the literature. Results presented here show that the evolution towards a stephanodont pattern, is adequately described by the first relative warp.

Functional Morphology

Increase in stephanodonty has been interpreted as adaptation to grass eating (Michaux, 1982). This interpretation is based on comparison of the dental morphology and the diet of certain living African murids showing similar specializations (Misonne, 1969) and on the observation that the *Occitanomys-Stephanomys* cladogenesis occurs concurrently with the expansion of the steppe dwellers among the large mammals. In addition to their increase in stephanodonty, the molars of the *P. hispanicus-S. donnezani* evolutionary sequence also show a general increase in hypsodonty. The association of hypsodonty in herbivores with the bulk consumption of calorie-poor and relatively abrasive food (such as grasses) is well established for rodents (Rensberger, 1975) and mammals in general (Janis and Fortelius, 1988).

An interesting finding revealed by this study is the trend towards alignment of the "valley" landmarks 7, 19, 18, 16 and 15 on the one hand and 6, 17, and 14 on the other (Fig. 5c). Presumably, such a configuration allows a longer and more efficient power stroke, with increased guidance of movement by longitudinal ridges (see also Weijs and Dantuma, 1975 on mastication in *Rattus norvegicus*). During the power stroke the cusp rows of the lower molars move anteriorly and longitudinally across the upper molars. The two anterior cuspules, the t1-bis and the t3-bis of stephanodont forms, allow an even longer power stroke. In order to test such correlations and to make inferences about diet and paleoenvironment, more information concerning the function of the masticatory apparatus and wear patterns in recent murids is needed.

GENERAL CONCLUSIONS

This study shows that complex three-dimensional shapes like those of teeth can be described by landmark patterns. The example of stephanodonty makes it clear that landmark-based morphometrics are a very useful tool to describe and analyze shape in fossil murid molars. Population differences, evolutionary trends and allometry can be adequately described. The results are promising for taxonomic, evolutionary and functional morphological studies. This publication is no. 960402 of the Netherlands Research School of Sedimentary Geology (NSG).

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