

MORPHOSPACE OCCUPATION IN THALATTOSUCHIAN CROCODYLOMORPHS: SKULL SHAPE VARIATION, SPECIES DELINEATION AND TEMPORAL PATTERNS

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Abstract: Skull shape variation in thalattosuchians is examined using geometric morphometric techniques in order to delineate species, especially with respect to the classification of Callovian species, and to explore patterns of disparity during their evolutionary history. The pattern of morphological diversity in thalattosuchian skulls was found to be very similar to modern crocodylians: the main sources of variation are the length and the width of the snout, but these broad changes are correlated with size of supratemporal fenestra and frontal bone, length of the nasal bone, size of the orbit and premaxilla and position of the narial opening. Patterns of shape variation, in combination with discrete-state morphology and stratigraphic and geographic range data were used to distinguish nine species of teleosaurid and 14 species of metriorhynchid, with the four currently recognized Callovian species being split into eight. Metriorhynchids were found to be more disparate from the average shape of morphospace than teleosaurids. However, short-snouted metriorhynchids and long-snouted teleosaurids showed the greatest amount of

disparity with respect to snout morphotypes, indicating that each group tended to explore opposite areas of morphospace. Phylogeny was found to have a moderate influence on the pattern of morphospace occupation in metriorhynchids, but little effect in teleosaurids suggesting that other factors or constraints control the pattern of skull shape variation in thalattosuchians. A comparison of thalattosuchians with dyrosaur/pholidosaurids shows that thalattosuchians have a unique skull morphology, implying that there are multiple ways to construct a 'long snout'. Moreover, the skull geometry of the problematic species *Pelagosaurus typus* was found to converge on the teleosaurid area of morphospace. Finally, the temporal distribution of thalattosuchian species and morphotypes demonstrate a clear and highly correlated relationship with sea level curves and mass extinction events through the Jurassic and the Early Cretaceous.

Key words: disparity, Metriorhynchidae, morphometrics, phylogeny, Teleosauridae, shape, skull.

As with crown-group crocodylians (Pierce *et al.* 2006, 2008; Pierce 2007), there is a long tradition of separating thalattosuchians, a clade of marine-adapted Jurassic crocodylomorphs, into two broad groups based on the relative proportions of rostral length and width (e.g. Andrews 1913; Wenz 1968; Young 2006). Species have been considered either longirostrine (i.e. long, narrow-snouted forms) or brevirostrine (i.e. short, broad-snouted forms). This artificial assignment of species and specimens has resulted in a complex, unrealistic taxonomy and ambiguous notions about evolutionary relationships. Dozens of species have been described within a broad array of genera (see Steel 1973 for review).

Victorian taxonomic philosophies, which left little room for individual variation in species, are mainly to blame for this taxonomic confusion (e.g. Bronn 1841; Münster 1843; Wagner 1850). However, the lack of communication between early marine crocodile workers also compounded the problem. Although many subsequent authors recognized that far too many species were named, all previous efforts to unravel the alpha-level taxonomy (e.g. Vignaud 1995) failed to provide a comprehensive and convincing resolution. Thalattosuchian taxonomy, therefore, remains uncertain, leaving the nature and extent of this dramatic radiation unclear.

The classification of Callovian thalattosuchians exhibits the most confusion and has commanded the most attention (e.g. Andrews 1909, 1913; Deslongchamps 1863–1869). This Jurassic stage has been a primary focus of systematists as it provides abundant and well-preserved thalattosuchian remains (Bardet 1994). Past attempts to rework the classification system failed to provide convincing alternatives, and usually exacerbated the situation by adding new species to the already extensive taxonomic list (e.g. Phizackerley 1951; Wenz 1968). More recently, Adams-Tresman (1987*a, b*) endeavoured to quantify the number of Callovian thalattosuchian species by employing ‘traditional’ morphometric techniques. To assess species differences, she used a variety of linear measurements taken across the dorsal surface of the skull and analysed their interrelationships using bivariate plots and principal coordinate analyses. The cranial dimensions could only distinguish two species of teleosaurid and two species of metriorhynchid: *Steneosaurus leedsi* and *Metriorhynchus superciliosus* were considered longirostrine forms, whereas *Steneosaurus durobrivensis* and *Metriorhynchus brachyrhynchus* were considered brevirostrine forms. Consequently, Adams-Tresman was able to create a more manageable taxonomic system by reducing the total number of Callovian teleosaurid species from eight to two and metriorhynchid species from nine to two. However, linear measurement-based techniques are not without problems, which may lead to misleading or incomplete results.

‘Traditional’ morphometrics uses a set of linear dimensions (e.g. length, depth, width) to describe the form of an object, but such data are not ideal when trying to quantify shape differences. For instance, measurements may overlap or run in similar directions, which could over-represent shape changes in a particular region of the skull in the data set (Zelditch *et al.* 2004). An examination of Adams-Tresman’s (1987*a, b*) cranial characters shows that measurements do indeed overlap and, thus, her results could be underestimating or overestimating the relationship between length and width of the skull and its utility for delineating thalattosuchian species. In addition, the measurements used in linear morphometrics are frequently highly correlated with size and, therefore, rarely identify size-independent shape variation (Zelditch *et al.* 2004). As one of the most important shape changes in thalattosuchians is related to a shift from brevirostrine to longirostrine skull morphologies, failure to differentiate allometric shape differences from size-independent differences may potentially underestimate species numbers.

The present study re-examines thalattosuchian taxonomy using landmark-based geometric morphometrics, which allows one to capture and analyse morphological information in terms of size-independent shape variation (Bookstein 1991). In addition to dealing with the problem of size, geometric morphometrics also provides a much

more precise picture of shape differences amongst specimens than can be achieved using linear measurements. As thalattosuchian species have been spuriously diagnosed by proportional differences of the skull, applying the method of landmark-based geometric morphometrics will provide a unique look at thalattosuchian morphology. Species from all geological ages and geographical locations in which thalattosuchians occur will be analysed in order to quantify and explore the full extent of shape variation present within the Thalattosuchia and to evaluate Adams-Tresman’s (1987*a, b*) delineation of Callovian species.

The specific objectives of this study are to (1) characterize the main pattern of shape variation in the skull roof of the Teleosauridae and the Metriorhynchidae the two main clades of Thalattosuchia; (2) determine the number of valid teleosaurid and metriorhynchid species and examine their distribution within morphospace; (3) explore the relationship between skull shape and phylogeny; (4) compare morphospace occupation between the Teleosauridae, the Metriorhynchidae, and other longirostrine ‘mesosuchian’ fossils groups (i.e. dyrosaur/pholidosaurids); (5) determine how each family and skull shape contribute to total morphological disparity; and (6) evaluate changes in the occupation of morphospace through thalattosuchian history.

MATERIALS AND METHODS

Shape variation

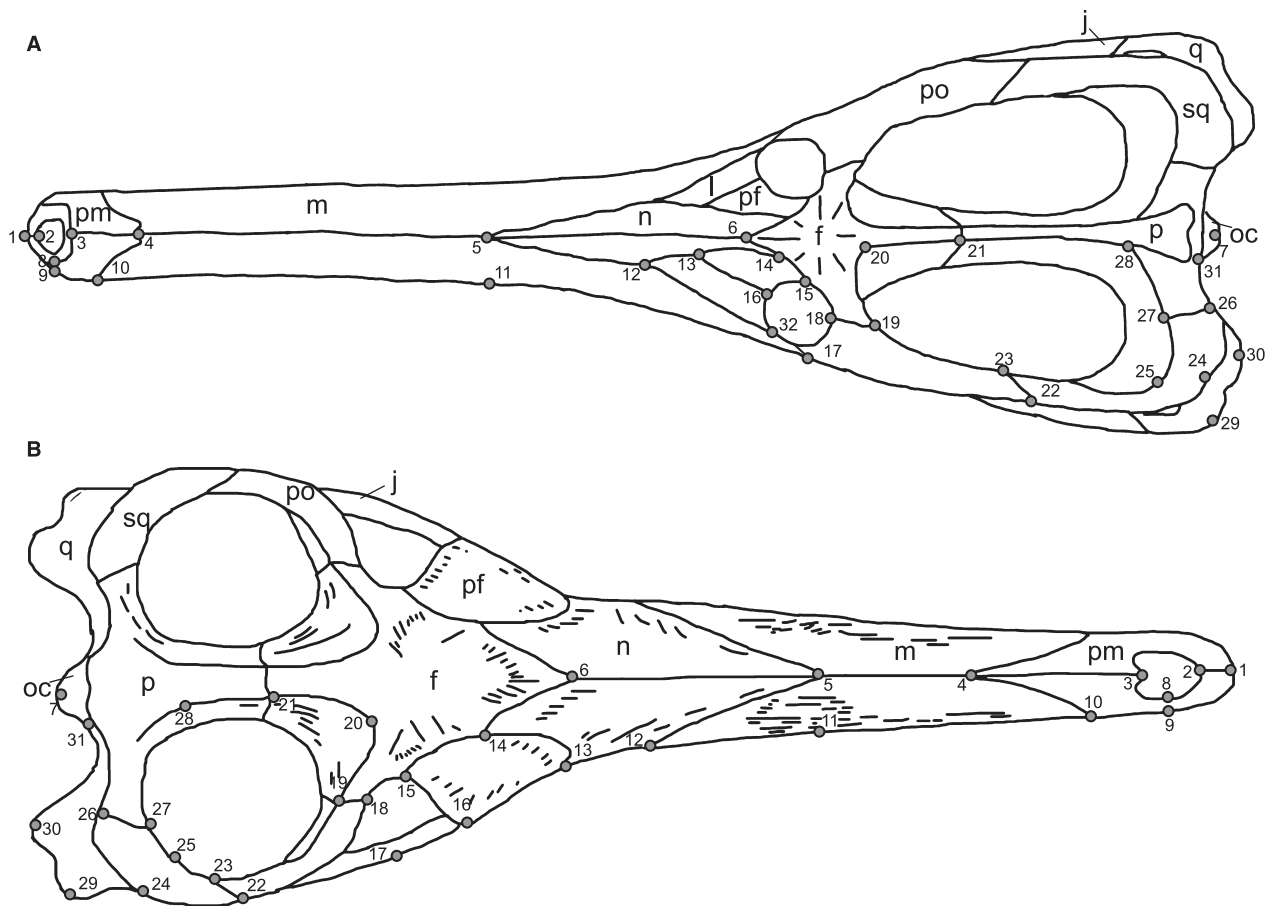
Specimens. A total of 31 teleosaurid (including *Pelagosaurus typus*), 35 metriorhynchid and five dyrosaur/pholidosaurid specimens were used in this study (Appendix). For ease of comparison amongst longirostrine species, dyrosaurs and pholidosaurids were united into one group even although this grouping is nonmonophyletic. The data set is composed of fossilized osteological specimens, as well as published photographs and drawings of reconstructed skulls. Reconstructions have been checked against original specimens when possible or compared to published photographs if available. Specimen selection was based on overall completeness of the skull and degree of taphonomic distortion, with the aim to maximize taxon sampling and to minimize missing data points and preservational artefacts. Skulls were photographed in dorsal aspect along the horizontal plane or scanned in dorsal aspect, and a scale was included to record the size of each specimen.

Landmarks. Shape variation in the dorsal surface of the skull was quantified using two-dimensional (2D) landmark-based geometric morphometrics. The total number of included landmarks varied with respect to three

separate analyses: (1) Teleosaurid Morphospace: 57 landmarks, with 52 bilaterally symmetrical landmarks and seven located along the midline of the skull; (2) Metriorhynchid Morphospace: 55 landmarks, with 48 bilaterally symmetrical landmarks and seven located along the midline of the skull; (3) Longirostrine Morphospace (including all thalattosuchians and dyrosaur/pholidosaurids): 55 landmarks, with 48 bilaterally symmetrical landmarks and seven located along the midline of the skull. The reduced set of landmarks for the Metriorhynchidae, when compared to the Teleosauridae, was necessary because of the vertical orientation of the lateral orbital margin in the former clade, which obscures the lacrimal and the jugal in dorsal aspect. To avoid inflating degrees of freedom in the statistical analyses and to reduce the amount of missing data, symmetric landmarks from one side of each specimen were reflected onto the other, and the average position for each pair of landmarks was calculated using BigFix6 (Sheets 2001a). Subsequent analyses were carried

out on these 'half' specimens. The anatomical relationships of landmarks and their descriptions can be seen in Text-fig. 1 and Table 1. All landmarks were digitized using TpsDig 2.04 (Rohlf 2005) and were of either Type 1 (e.g. intersection point of three bones) or Type 2 (e.g. extreme end point or curvature of bone) as stated by Bookstein (1991).

Superimposition. Landmark coordinates were superimposed using the generalized least squares, or Procrustes, method (Rohlf 1990) in the programme CoordGen 6f (Sheets 2001b) to remove the effects of position, orientation and scale from the data sets. A comparison of the Euclidean distances between all pairs of aligned and scaled specimens in the plane tangent to shape space and Procrustes distances between all pairs of specimens in Kendall shape space was conducted using TpsSmall 1.20 (Rohlf 2003a). The correlations were extremely high for all analyses ($r > 0.99999$), indicating that the area of shape space



TEXT-FIG. 1. Landmarks used in this analysis. A, Teleosauridae. B, Metriorhynchidae. For a description of landmarks see Table 1. Landmark coordinates for Longirostrine morphospace correspond to landmarks 1–31 in both teleosaurids and metriorhynchids. Abbreviations: f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, occipital; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate and sq, squamosal. Drawings modified from Adams-Tresman (1987a, b).

TABLE 1. Description of landmarks used in this study.

Landmark#	Anatomical position	Landmark#	Anatomical position
T1; M1	Anterior most position of snout at suture between left and right premaxilla	T17; (M17)	Suture between maxilla and jugal along lateral margin (or maximum width of orbit)
T2; M2	Anterior most position of external nares at suture between left and right premaxilla	T18; M18	Suture between frontal, postorbital and orbit
T3; M3	Posterior most position of external nares at suture between left and right premaxilla	T19; M19	Suture between frontal, postorbital and supratemporal fenestra
T4; M4	Suture between premaxilla and maxilla along dorsal surface	T20; M20	Extreme anteromedial edge of supratemporal fenestra along frontal
T5; M5	Suture between nasal and maxilla along midline	T21; M21	Suture between frontal and parietal along dorsal surface
T6; M6	Suture between nasal and frontal along midline	T22; M22	Suture between postorbital and squamosal along lateral margin
T7; M7	Posterior tip of occipital condyle in dorsal view	T23; M23	Suture between postorbital and squamosal along supratemporal fenestra
T8; M8	Maximum curvature of external naris along lateral edge	T24; M24	Extreme curvature of squamosal along posterior edge
T9; M9	Landmark #8 extended to the lateral margin of premaxilla	T25; M25	Extreme curvature of squamosal along medial edge
T10; M10	Suture between premaxilla and maxilla along lateral margin	T26; T26	Suture between squamosal and parietal along posterior edge
T11; M11	Landmark #5 extended to lateral margin of maxilla	T27; M27	Suture between squamosal and parietal along medial edge
T12; (M12)	Suture between nasal, lacrimal and maxilla (or nasal and maxilla on lateral margin)	T28; M28	Extreme posteromedial edge of supratemporal fenestra along parietal
T13; (M13)	Suture between nasal, prefrontal and lacrimal (or nasal and prefrontal along lateral margin)	T29; M29	Extreme curvature of lateral quadrate condyle
T14; M14	Suture between nasal, prefrontal and frontal	T30; M30	Extreme curvature of medial quadrate condyle
T15; M15	Suture between prefrontal, frontal and orbit	T31; M31	Contact between occipital condyle and parietal in dorsal view
T16; (M16)	Suture between prefrontal, lacrimal and orbit (or lateral tip of prefrontal)	T32	Suture between lacrimal and maxilla along orbit

T indicates landmark position in the teleosaurid skull and M indicates landmark position in the metriorhynchid skull. Landmarks for Longirostrine morphospace correspond to landmarks 1–31.

inhabited by the specimens is small enough that projection into the tangent plane for ease of statistical analysis does not introduce distortion.

Principal components analysis. To assess morphospace occupation and shape variation qualitatively, the data sets were subjected to a principal components analysis (PCA) using Morphologika (O'Higgins and Jones 2006). Axes that captured the most useful information about shape variation were selected by plotting eigenvalues, or percentages of total variance, against ordinal number of principal components (i.e. a scree plot) and finding the inflection point ('broken stick method'). This was further confirmed by performing a χ^2 statistic based on the likelihood-ratio criterion (see Zelditch *et al.* 2004).

Size. Because the data set includes specimens of different sizes, it is possible that allometric shape differences exist

amongst specimens of each species. The presence of such variation in the data could make comparisons between species more difficult. Therefore, it was necessary to investigate the relationship between size and shape in the data set to ensure that differences in size were not the primary factor controlling shape. The relationship was quantified for the teleosaurids and metriorhynchids by regressing Procrustes distances from the reference form (mean of the smallest three specimens in the data set) on the natural logarithm of centroid size. A multivariate regression of partial warp and uniform component scores vs. log centroid size was not possible because of low sample sizes relative to the number of landmarks. To assess the effects of size on longirostrine skull shapes, a multivariate regression of the partial warp and uniform component scores against log centroid size was conducted using the consensus form of all specimens as the reference specimen. In addition to this, the scores of the specimens

along significant PC axes, for all analyses, were regressed on log centroid size to check whether shape differences described by PC axes were correlated with size. The regressions were run in Regress6K (Sheets 2003b), Tps-Regr 1.28 (Rohlf 2003b) and Systat version 12.

Species delineation

To determine the number of morphologically distinct species, a variety of methods were employed. First, pair-wise significance tests using Goodall's F statistic were conducted on the morphometric data for species that are represented by two or more specimens in the data set to determine if their mean shapes were significantly different from each other, given the range of variation within each species. This initial step permits confirmation of currently recognized taxa and provides a basis to group or separate the remaining species. Second, a cluster analysis using Euclidean partial Procrustes distances was conducted on all specimens in order to recover groups of specimens, and pair-wise significance tests were then run on the mean shapes of all these broader groupings. These 'cluster' groups were also compared to the species defined in the first step, as well as geological age, geographical occurrence and anatomical descriptions. Finally, a new plot of species groupings was mapped onto morphospace to highlight synonyms and the total number of species delineated in the analysis. The pair-wise significance tests were conducted using TwoGroup 6h (Sheets 2000), and the cluster analysis was performed using Past version 1.59 (Hammer *et al.* 2001).

Phylogenetic correlation

In order to assess the correspondence between skull morphology and our current understanding of thalattosuchian phylogeny, a species-level cladogram was superimposed onto the PC plots using the following protocol (also see Pierce 2007; Pierce *et al.* 2008). First, the x and y coordinates of the average specimen for each species were calculated and plotted onto morphospace. Next, the x and y coordinates of each internal node within the preferred phylogeny were determined using the squared-change parsimony reconstruction method in Mesquite v 1.06 (Maddison and Maddison 2006), and the corresponding point was then plotted onto the same graph. The values of the internal nodes represent the maximum-likelihood estimate of the ancestral states under a Brownian motion model of evolution and provide a standardized method for drawing the phylogeny onto the morphospace plot. Finally, the internal nodes were connected to each other and their corresponding terminal points using straight

lines (for an alternative see O'Keefe 2002; Stayton 2005, 2006).

In addition, to statistically address the issue of association between skull shape and phylogeny, a comparison of morphological and phylogenetic distances amongst taxa was performed using the Mantel test (Mantel 1967). The morphological distance matrix consisted of partial Procrustes distances measured between the mean shapes of the taxa of interest. The phylogenetic distance was calculated using the character distance method, which takes into account of the lengths of the branches that link two nodes in a tree. The phylogenetic distance matrix is based on the morphological matrices of Mueller-Töwe (2006) for the Teleosauridae and Young (2006) for the Metriorhynchidae. The character matrices were adjusted (or pruned) to reflect the species used in the geometric morphometric analysis, and the synonyms created during species delineation. The correlation was subjected to 5000 random permutations in order to measure its significance. Partial Procrustes distances were calculated using TwoGroup 6h (Sheets 2000), and the Mantel tests were computed using Past version 1.59 (Hammer *et al.* 2001). A possible concern when using this approach is that it might overestimate the correlation between phylogeny and skull shape if the phylogenetic data matrix includes characters that capture some shape information, particularly if the phylogenetic analysis relies heavily on such characters. However, close inspection of the character matrices of Muller-Töwe and Young shows that their data are dominated by nonshape-related cranial and postcranial morphological features and, therefore, this concern should not be a fundamental problem in the current study.

Morphological disparity

In addition to the preceding analyses, it was also of interest to examine whether different taxonomic groups or shape categories within thalattosuchian morphospace display similar amounts of shape variation or disparity. For example, do the Teleosauridae display significantly more or less shape disparity than the Metriorhynchidae? Similarly, do long-snouted and/or short-snouted teleosaurid species display significantly more or less shape disparity than long-snouted and/or short-snouted metriorhynchid species? To answer these questions, specimens were grouped into families and snout morphotypes and then examined to see how each subgroup contributed to the total morphological disparity exhibited by the data set. Disparity was measured by summing the squared Procrustes distance between the mean shape of each subgroup and the grand mean shape of all subgroups in the data set (Zelditch *et al.* 2003, 2004). This technique is

used to assess how disparate the mean shape of each subgroup is from the grand mean shape of morphospace, rather than determining the degree of disparity or variation within a particular subgroup (Foote 1993). To assess whether the partial disparities of each subgroup were significantly different, a series of pair-wise comparisons were made using two-sample *t*-tests (Zelditch *et al.* 2004). Disparity calculations were carried out in DisparityBox 6h (Sheets 2006) and significance tests in TBox (Sheets 2003a).

Morphospace occupation through time

To evaluate temporal patterns of morphospace occupation, all 66 thalattosuchian specimens were grouped by age and plotted in morphospace. The following chronological groupings were used: (1) Lower Jurassic, which includes the Hettangian, the Sinemurian and the Pliensbachian, (2) Toarcian, (3) Aalenian/Bajocian, (4) Bathonian, (5) Callovian, (6) Oxfordian, (7) Kimmeridgian, (8) Tithonian and (9) Berriasian. The stages in the Lower Jurassic and the Aalenian/Bajocian were combined because of the lack of specimens from these time periods. In addition, the Berriasian was taken as the final stage as no specimens from this analysis are found in later stages of the Lower Cretaceous, despite the fact that some thalattosuchians persisted after this time. Because only species/specimens included in the geometric morphometric analysis were plotted, the total morphological variation at certain time periods might be underestimated. However, this is not a limitation for the purposes of investigating broad patterns of morphospace occupation through time, as the sample is representative of thalattosuchian diversity, and no taxa showing extreme morphologies were excluded from the analysis.

RESULTS

Teleosaurid morphospace

Shape variation. The PCA reveals that the majority of the variance in the data set is captured by the first two PC axes, with over 80 per cent of the variance explained (Text-fig. 2). PC1 is the dominant PC axis, describing 66.5 per cent of the total variance, whereas PC2 only describes 14.5 per cent. As PC1 and PC2 capture significantly more variance than any of the other axes, variation along these axes will be the focus of the remainder of the study. The regression of Procrustes distance on log centroid size shows a significant correlation between shape and size ($r = 0.4845$; $p = 0.002$). In addition, a regression of the first two PC scores on log centroid size reveals that

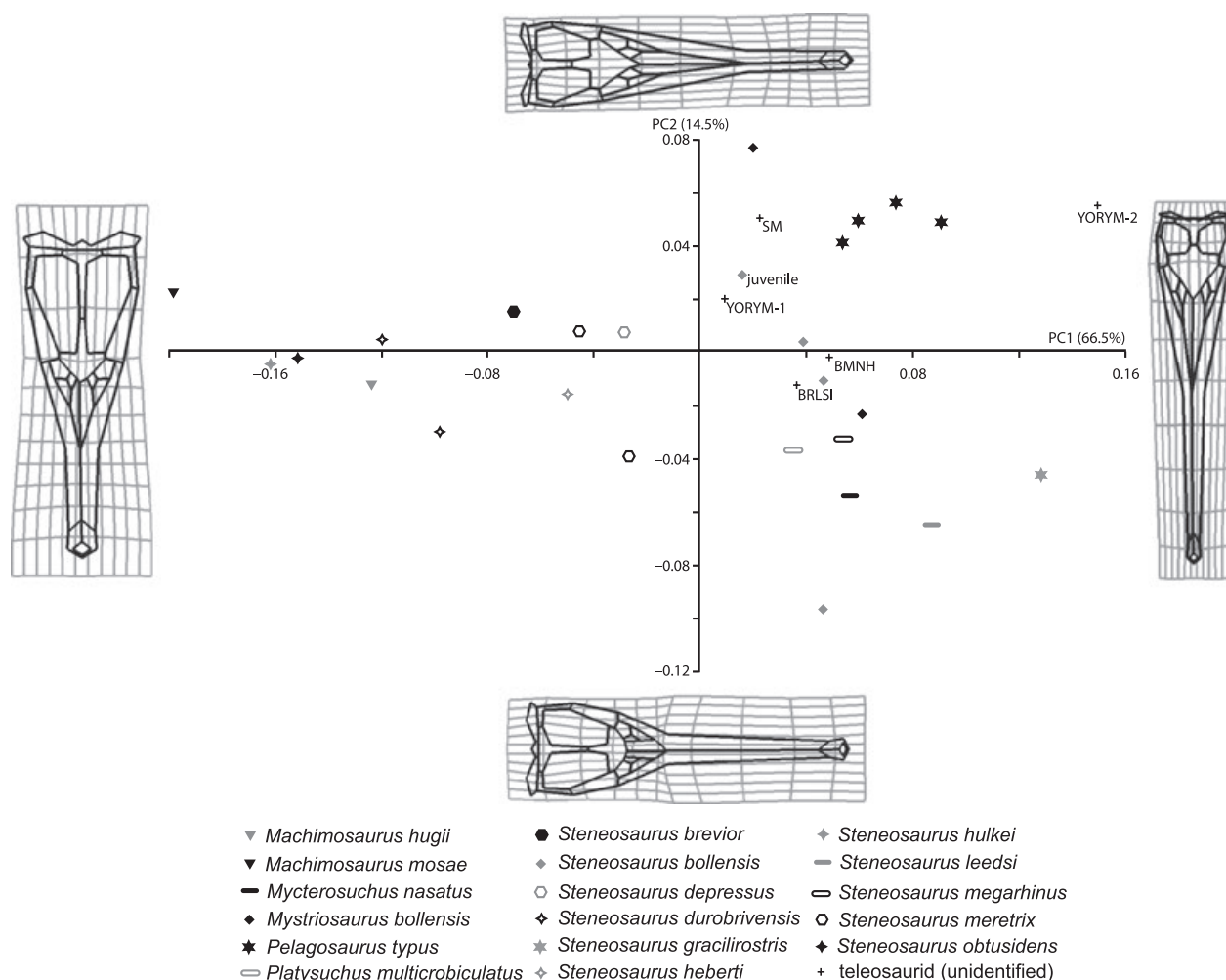
shape variation described by PC1 is not significantly related to size ($r^2 = 0.078$; $p = 0.127$), but that of PC2 is significantly related to size ($r^2 = 0.120$; $p = 0.038$). This implies that the patterns described by PC1 are not the result of differences in size amongst the specimens and, therefore, can be used to assess morphospace occupation. However, it also shows that much of the variation along PC2 is related to potential allometric differences. This is not surprising considering some 'species' in morphospace contain specimens of varying sizes, particularly *Steneosaurus bollensis* (see below).

The first PC axis describes variation in the length of the snout (especially the length of the maxillae), as well as the size of the supratemporal fenestrae, and the size of the frontal bone (Text-fig. 2). In contrast, the second PC describes variation in width of the snout, length of the nasal bones, width of the premaxilla lateral to the narial opening and size of the orbits (Text-fig. 2). As such, PC1 mainly discriminates short and long-snouted morphotypes, whereas PC2 discriminates broad and narrow-snouted morphotypes. The scatter plot demonstrates that teleosaurids fall within all four quadrants of morphospace, but that the morphospace is not uniformly occupied. For example, specimens along PC1 positive (long-snouted morphotypes) occupy the full range of PC2, whereas specimens along PC1 negative (short-snouted morphotypes) are much more restricted along PC2. Thus, not all possible morphospace is utilized.

Species delineation. Only four defined species were represented by two or more specimens: *Pelagosaurus typus*, *Steneosaurus bollensis*, *Steneosaurus durobrivensis* and *Steneosaurus meretrix*. Pair-wise significance tests conducted on the mean shape of each species (Table 2) found all four species to be significantly different from each other.

The cluster analysis (Text-fig. 3) and associated pair-wise significance tests (Table 3) recovered two broad groups within morphospace, Group A or short-snouted morphotypes and Group B or long-snouted morphotypes. The pattern of shape relationships within the short-snouted forms is more straightforward than within the long-snouted forms. Specimen clusters in Group A conform nicely to anatomical descriptions and geological occurrence, whereas specimen clusters in Group B show some discrepancies (see below).

Within Group A (Text-fig. 3) there are two main clusters, A.1 and A.2, which are significantly different from each other (Table 3). Cluster A.2 differs from A.1 in having specimens with shorter snouts and larger supratemporal fenestrae. These two clusters contain the species *Steneosaurus meretrix* (A.1) and *Steneosaurus durobrivensis* (A.2), which were found to have significantly different mean shapes (Table 3). Cluster A.1 is composed of *Steneosaurus brevior* from the Toarcian of England, *S. mere-*



TEXT-FIG. 2. Teleosaurid Morphospace. Principal components 1 and 2 with all 31 specimens. Extreme shapes for each axis are shown. Deformation grids indicate the shape change necessary to transform the mean shape into an extreme shape.

meretrix from the Bathonian of England and *Steneosaurus depressus* and *Steneosaurus heberti* from the Callovian of England and France, respectively. *Steneosaurus brevior* is here considered to be a separate taxon based on its Toarcian occurrence, its position in morphospace (i.e. shorter/broader snout and larger supratemporal fenestrae; Text-fig. 2) and unique anatomical characteristics including large, rectangular supratemporal fenestra, small rounded orbits, large mandibular fenestrae and large, well-defined antorbital fenestrae (Westphal 1961, 1962; Muller-Töwe, SEP, pers. obs.). As the remaining three species are interspersed, especially with respect to the shape range of *S. meretrix*, they are not considered distinct, and instead are referred to the species *S. heberti* (as this name holds priority).

The cluster of specimens composing the species *Steneosaurus heberti* (Text-fig. 4) to the exclusion of *Steneosaurus brevior* is supported by anatomical details of the teeth. As well as having a very similar skull geometry (Text-

figs 2, 4), Vignaud (1997) recognized a similar tooth structure (Type B1) in *S. heberti* and *Steneosaurus meretrix*. The teeth are more pointed relative to those of *Machimosaurus*, but have a similar arrangement of longitudinal canals. Unfortunately, the exact details of the teeth in *Steneosaurus depressus* could not be confirmed. In contrast, the tooth form of *S. brevior* is a stout version of that identified in *S. bollensis*: apically recurved with a pointed apex, very fine vertical striations and a single smooth carina running down the posterior edge. In addition to tooth form and overall shape, *S. brevior* differs from *S. heberti* in having a large, well-defined antorbital fenestra (Mueller-Töwe 2006).

In the past, similarities have been noted between *Steneosaurus brevior* and *Steneosaurus bollensis*. Westphal (1961), in his overview of Lias teleosaurids, found the absolute size of *S. brevior* corresponded to that of *S. bollensis* and suggested that the former species may be a transitional form of the latter. Steel (1973) synonymized

TABLE 2. Pair-wise comparisons of the mean shape of each teleosaurid species represented by more than two specimens in the data set.

Group pair	Goodall's F-value	p-value	Partial Procrustes distance between means
<i>P. typus</i> / <i>S. bollensis</i>	3.81	<0.0001	0.0636
<i>P. typus</i> / <i>S. durobrivensis</i>	31.96	<0.0001	0.1728
<i>P. typus</i> / <i>S. meretrix</i>	10.47	<0.0001	0.1126
<i>S. bollensis</i> / <i>S. durobrivensis</i>	10.04	<0.0001	0.1456
<i>S. bollensis</i> / <i>S. meretrix</i>	2.41	<0.0001	0.0779
<i>S. durobrivensis</i> / <i>S. meretrix</i>	2.28	<0.0001	0.0749

Significance judged using a Bonferroni-corrected α level of 0.008. Significant differences are indicated in bold. *P*, Pelagosaurus; *S*, Steneosaurus.

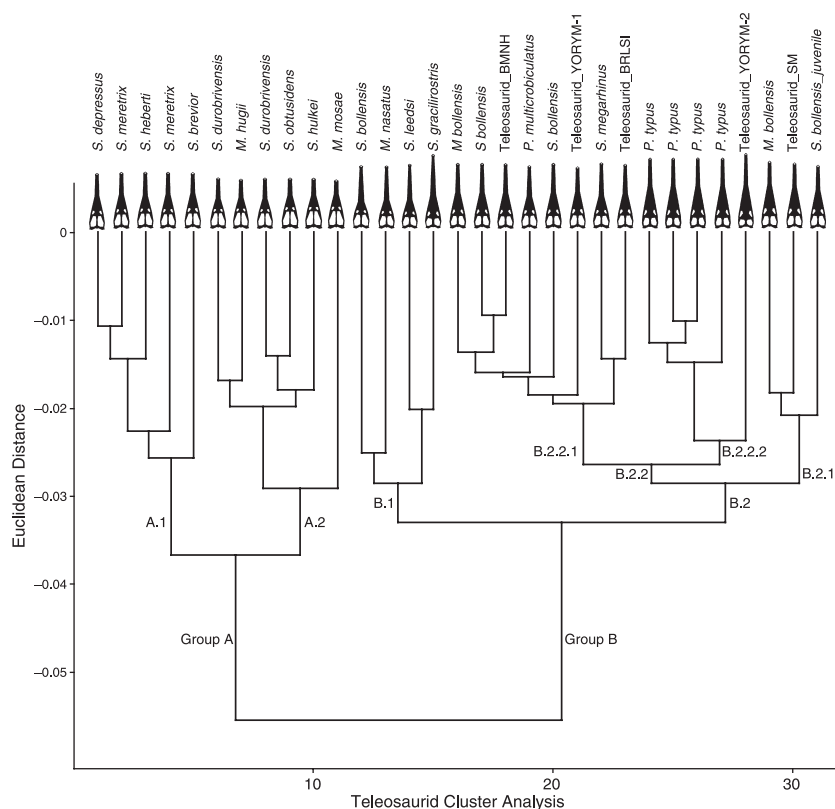
S. brevior, *S. bollensis* and *Steneosaurus gracilirostris* as well, presumably attributing all morphological differences (specifically length of snout) to phenotypic variation and variable preservation. However, the distribution of *S. brevior*, *S. bollensis* and *S. gracilirostris* in morphospace (Text-figs 2, 4) shows that all three species occupy very distinct regions. In a further account of Toarcian teleosaurids from the Yorkshire coast, Walkden *et al.* (1987) suggested that *S. brevior* was a possible synonym of *S. bollensis* as a new specimen showed a mixture of anatomical characteristics found in both species. The most recent description of Toarcian teleosaurids by Mueller-Töwe (2006) finds *S. brevior* to differ from *S. bollensis* by size of the mandibular fenestrae, size of the antorbital fenestrae and position of the external narial opening. In fact, the large antorbital fenestrae and anteriorly positioned external narial opening are more similar to *S. gracilirostris* than *S. bollensis*. Consequently, based on their positions in morphospace and differences in anatomical characteristics, *S. brevior* and *S. bollensis* can be considered distinct species, despite the attempts of previous authors to synonymize them.

Cluster A.2 (Text-fig. 3) is composed of *Machimosaurus mosae* from the Kimmeridgian (and possibly the Tithonian) of France and a smaller cluster of specimens composed of four species, *Steneosaurus durobrivensis*, *Steneosaurus hulkei* and *Steneosaurus obtusidens* from the Oxford Clay (Callovian) of England and *Machimosaurus hugii*, which ranges from the Oxfordian to Tithonian(?) of Western Europe. As the species in the smaller cluster appear to be interspersed, especially with respect to the shape range displayed by *S. durobrivensis*, they are not considered distinct and instead are referred to *M. hugii* (as this name holds priority). Although the geological range of *M. mosae* overlaps with *M. hugii*, it is considered

to be a separate taxon based on its position in morphospace (i.e. shorter/broader snout and larger supra-temporal fenestrae; Text-fig. 2).

The cluster of specimens composing the species *Machimosaurus hugii* in this study (Text-fig. 4) is also supported by anatomical details of the teeth. The genus *Machimosaurus* is defined by the presence of blunt, conical teeth with a series of longitudinal canals (Krebs 1967; Vignaud 1997). Andrews (1913) diagnosed *Steneosaurus obtusidens* and *Steneosaurus durobrivensis* mainly on the form of their teeth, which he stated were blunt and rounded at the tips in *S. obtusidens* and more pointed in *S. durobrivensis*. However, Andrews also noted that some of the replacement teeth in *S. durobrivensis* are similar in form to *S. obtusidens* and acknowledged the possibility that the former species was based on smaller individuals of the latter. Within this context, Adams-Tresman (1987b) highlighted a specimen (National Museum of Wales 1996 G12a) that appeared to show tooth crowns with an intermediate form between the two species. Hua *et al.* (1993, 1994) and Vignaud (1997) also recently acknowledged the similarity between the tooth morphology of *S. obtusidens* and *Machimosaurus*. In fact, Hua *et al.* (1993, 1994) found that the dental and anatomical differences between *S. obtusidens* and *M. hugii* can be interpreted in terms of ontogenetic variation and, therefore, proposed the synonymy of the two species. The tooth form in *Steneosaurus hulkei* could not be confirmed based on its fragmentary nature, but Vignaud (1997) noted similarities to both *S. obtusidens* and *S. durobrivensis*.

Although both *Machimosaurus mosae* and *M. hugii* are diagnosed by their characteristic blunt teeth and overlap stratigraphically, *M. mosae* has a rostrum that is shorter and more robust (Text-figs 2, 4). *Machimosaurus mosae* was described by Sauvage and Lienard (1879) on the basis of associated cranial and postcranial remains from the Kimmeridgian of France. Unfortunately, the type specimen disappeared during World War I and the paper's anatomical description and illustrations are ambiguous at the best. Krebs (1967, 1968) questioned the validity of *M. mosae* and proposed that the type specimen was based on heterogeneous material (some probably mosasaurian). Hua (1999) and Hua *et al.* (1993) reconsidered the taxonomy of the genus *Machimosaurus* based on a nearly complete skull from the Kimmeridgian of Boulonnais (France). Compared to *M. hugii*, the Boulonnais specimen has a shorter rostrum and fewer teeth. The robust nature of the snout, which had seemed suspicious to Krebs, confirmed the description presented by Sauvage and Lienard (1879) and allowed Hua (1999) and Hua *et al.* (1993) to resurrect the species *M. mosae*. As a result, two species can be distinguished within the genus *Machimosaurus*: *M. hugii*, with a long, slender rostrum and *M. mosae*, with a shorter, more robust rostrum (Text-fig. 4).

TEXT-FIG. 3. Results of cluster analysis of teleosaurid skull shapes.

Within Group B (Text-fig. 3) there are two main clusters, B.1 and B.2, which are significantly different from each other (Table 3). Cluster B.1 differs from B.2 in having specimens with narrower, more tubular snouts. B.1 is composed of four species: *Steneosaurus bollensis* (specimen described by Mateer 1974) and *Steneosaurus gracilirostris* from the Toarcian of England and Germany, and *Mycterosuchus nasutus* and *Steneosaurus leedsi* from the Oxford Clay (Callovian) of England. The *S. bollensis* specimen (number R161 in Appendix) in cluster B.1 falls outside the range of other *S. bollensis* specimens and, as such, its status as a member of this species is questionable. The reconstruction of this specimen is either incorrect (i.e. the nasal bones are considerably shorter than other *S. bollensis* specimens) or it is a representative of a distinct species. Until the anatomy of this specimen can be confirmed, it is not considered to belong to any species cluster. *Steneosaurus gracilirostris* is the longest snouted specimen in morphospace (Text-fig. 2) and occurs outside the stratigraphic range of *M. nasutus* and *S. leedsi*. As such, *S. gracilirostris* is considered to be a distinct taxon. The remaining two taxa *M. nasutus* and *S. leedsi*, which co-occur in the Oxford Clay, are considered to belong to the same species, *S. leedsi* (as this name holds priority).

The synonymy of *Steneosaurus leedsi* and *Mycterosuchus nasutus* (Text-fig. 4) has been suggested in the past. The

distinction of the genus *Mycterosuchus* from *Steneosaurus* by Andrews (1913) was based on three broad cranial characters possessed by *Mycterosuchus*: (1) greatly elongated snout, sharply marked off from the cranial region of the skull; (2) temporal fossae relatively smaller and shorter than in other steneosaurs and (3) slender teeth. However, Adams-Tresman (1987b) noted that all three of these characters are present in *S. leedsi*, and her morphometric analysis demonstrated that *M. nasutus* and *S. leedsi* have similar skull proportions. The positions of both species in the morphospace described in the current study (Text-figs 2, 4) confirm that the shape of the snouts and supra-temporal fenestrae have similar geometries. In addition, Adams-Tresman described both species as having teeth that are slender with sharply pointed crowns and enamel that is sculptured into a series of very fine longitudinal ridges. The similarity in tooth morphology was also highlighted by Vignaud (1997) who grouped both species into the same morphotype (Type A1).

Cluster B.2 (Text-fig. 3) is composed of two smaller clusters, B.2.1 and B.2.2, which are significantly different from each other (Table 3). Cluster B.2.1 consists of three Toarcian specimens, a juvenile *Steneosaurus bollensis*, an unidentified teleosaurid and *Mycterosaurus bollensis* (specimen described by Antunes 1967). In the past, the *M. bollensis* specimen has been regarded to have broad similarities with *Pelagosaurus typus* and has recently been

TABLE 3. Pair-wise comparisons of the mean shape of each teleosaurid group recovered in the cluster analysis.

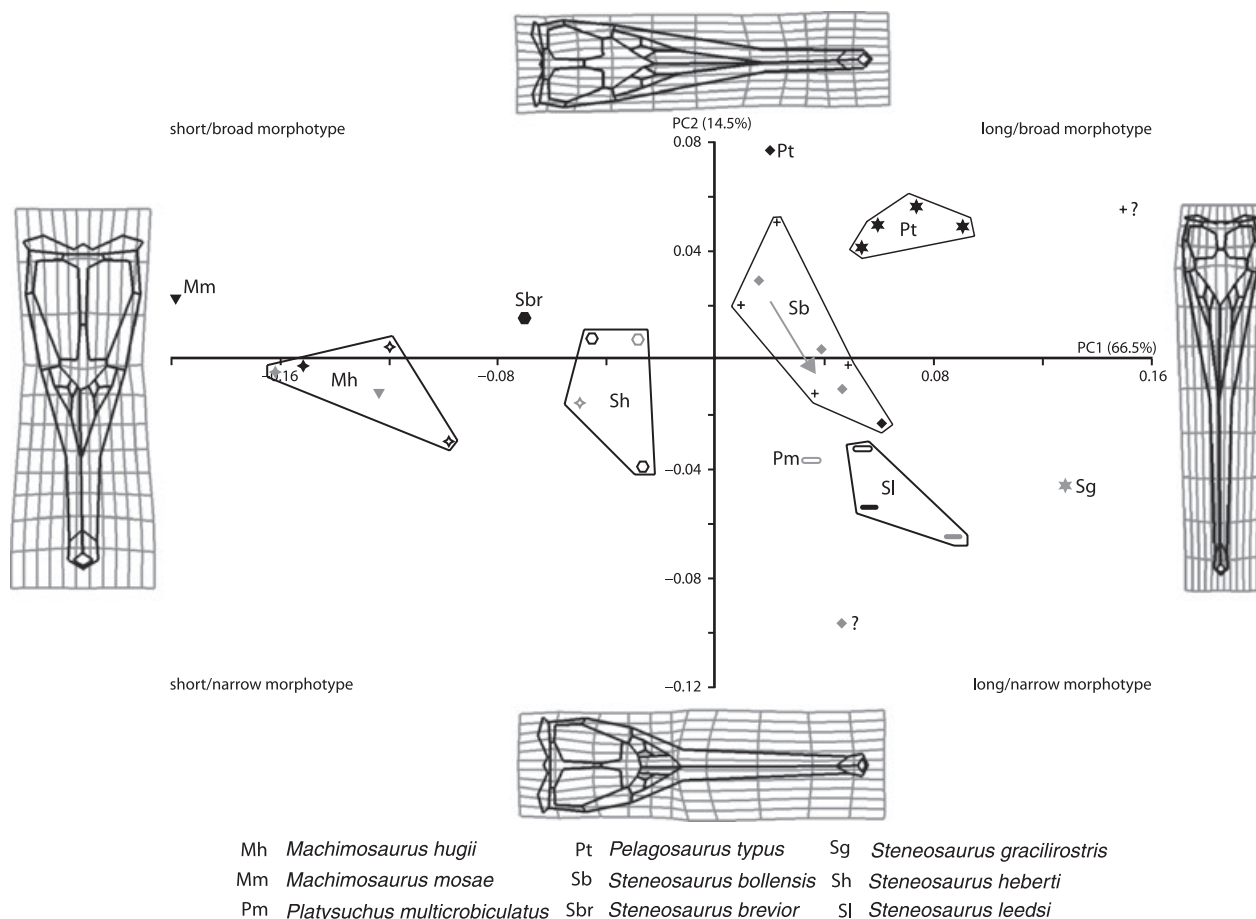
Group pair	Goodall's F-value	p-value	Partial Procrustes distance between means
Group A/Group B	29.34	<0.0001	0.1424
A.1/A.2	8.40	<0.0001	0.0990
B.1/B.2	8.21	<0.0001	0.0938
B.2.1/B.2.2	3.30	<0.0001	0.0687
B.2.1.1/B.2.1.2	7.91	<0.0001	0.0709

Significance judged using a Bonferroni-corrected α level of 0.01. Significant differences are indicated in bold.

reassigned to *P. typus* [Mueller-Töwe 2006; however, see Jouve (2009) for an alternate interpretation]. The specimen itself is missing the anterior tip of the snout, making the exact length of the snout unknown. If the specimen was reconstructed with a slightly longer snout, it would

sit within the range of other *P. typus* specimens in morphospace. Consequently, Antunes' specimen is cautiously assigned to *P. typus* until further anatomical work is conducted. The remaining two specimens in cluster B.2.1 are considered to be juvenile representatives of the species *S. bollensis*.

Cluster B.2.2 (Text-fig. 3) is composed of two smaller clusters, B.2.2.1 and B.2.2.2, which are significantly different from each other (Table 3). These two clusters contain the species *Steneosaurus bollensis* (B.2.2.1) and *Pelagosaurus typus* (B.2.2.2), which were found to have significantly different mean shapes (Table 2). B.2.2.1 contains a variety of specimens including *Mystriosaurus bollensis*, *S. bollensis*, *Platysuchus multicrobiculatus* and three unidentified teleosaurids from the Toarcian, along with *Steneosaurus megarhinus* from the Oxfordian–Kimmeridgian of England and Germany. *Platysuchus multicrobiculatus* differs from other Toarcian specimens in this cluster by occupying a somewhat divergent area of morphospace (i.e. a more negative score on PC2 negative) and in anatomical detail. In addition, *S. megarhinus* can be considered distinct from all



TEXT-FIG. 4. Teleosaurid species delineation with respect to specimen distribution along PC1 and PC2. Arrow indicates the ontogenetic trajectory of *Steneosaurus bollensis*.

other specimens in the cluster based on its geological occurrence (and its anatomical similarities with *S. leedsi*; see below). In fact, the skull shape, in association with its age, makes this species more reminiscent of *Steneosaurus leedsi* (Text-fig. 2). Consequently, *S. megarhinus* is here considered to be a synonym of *S. leedsi*. The remaining specimens in this cluster are grouped into the species *S. bollensis*.

Platysuchus multicubiculatus and *Steneosaurus bollensis* are both Toarcian species with a very similar skull shape; especially, with respect to snout length. However, the two species plot in somewhat divergent areas of morphospace (Text-figs 2, 4). The specimen attributed to *P. multicubiculatus* is similar in size to the adult *S. bollensis* specimens, but has a narrower snout, correspondingly smaller orbits and larger supratemporal fenestrae. In addition to skull geometry, *P. multicubiculatus* differs from *S. bollensis* in anatomical details of the postcranial skeleton. Westphal (1961) created the genus *Platysuchus* based on its possession of a short, heavily armoured body, small head to body ratio and extensive ornamentation of the cranial bones compared to *Steneosaurus*. The skull in *Platysuchus* comprises only 45 per cent of the trunk length, as opposed to almost 60 per cent in *S. bollensis*. The shortening of the body also is reflected in the tail, which is composed of fewer caudal vertebrae (i.e. 38 as opposed to 55 in *S. bollensis*). Moreover, the armour in *Platysuchus* is much more extensive, running almost the entire length of the body, and the individual osteoderms are rectangular in outline (c. 1.5 times wider than long). This contrasts with the genus *Steneosaurus*, which has armour extending two-thirds down the body and square osteoderms (Mueller-Töwe 2006; Westphal 1961).

Besides highlighting differences in the skull shapes of the sampled species, the ontogenetic trajectory of *Steneosaurus bollensis* through morphospace also can be traced (Text-fig. 4). Juveniles plot in the long/broad quadrant of morphospace, about half way up PC2 positive and very close to the mean shape along PC1. Conversely, adults plot in the long/narrow quadrant of morphospace, one-third along PC1 positive and PC2 negative. The morphological changes in the skull from juvenile to adult consist of shorter → longer snout; broader → narrower snout; longer/wider → shorter/narrower nasals; larger → smaller orbits; more laterally placed → more dorsally placed orbits; smaller → larger supratemporal fenestra and shorter → longer posterior aspect of skull. These ontogenetic changes in skull morphology contrast with those seen in the modern gharial, the only extant species with comparable skull morphology. Although *Gavialis gangeticus* experiences a decrease in size of the orbits and an increase in size of the supratemporal fenestrae during growth, the snout becomes shorter and broader instead of longer and narrower (Pierce 2007; Pierce et al. 2008).

The specific diagnosis of *Steneosaurus megarhinus* was expanded by Vignaud et al. (1993) who compared the species to long-snouted teleosaurids from the Upper Jurassic, mainly *Steneosaurus deslongchampsianus* and *Steneosaurus priscus*. The only differing character within these skulls is the number of teeth: 47/43 (=upper/lower dentitions) in *S. deslongchampsianus*, 35/? in *S. megarhinus* and 29/? in *S. priscus*. However, Vignaud et al. (1993) failed to compare the skull to long-snouted forms from the Middle Jurassic. This is curious as skeletal remains attributed to *S. megarhinus* have been recovered from Oxfordian sediments (Vignaud 1995). A comparison of the anatomical description of *S. megarhinus* to the Callovian teleosaurid *Steneosaurus leedsi* finds these two species to be almost identical. The only difference is in the number and shape of the teeth, which are fewer and more slender in *S. megarhinus* (Vignaud 1997). According to Adams-Tresman (1987b), however, tooth count cannot be used as the sole basis to recognize species. For instance, she noted an intra-specific variation of eight teeth in Callovian steneosaurs, and more recently, Mueller-Töwe (2006) identified a maximum difference of 15 teeth in the Toarcian teleosaurid *Steneosaurus gracilirostris*. As tooth count cannot be used to confidently designate species, only tooth form is considered to be a viable character. In this case, however, the differences in tooth form between the two species could be related to ontogeny or wear. Vignaud et al. (1993) suggested that *S. megarhinus* may be considered more juvenile as the bones are smooth and the frontal-postfrontal and frontal-nasal sutures are not totally closed. With this in mind, it cannot be ruled out that *S. leedsi* and *S. megarhinus* (and indeed other long-snouted Upper Jurassic teleosaurid species) represent an ontogenetic series of a single species or a chronocline (Text-fig. 4).

Finally, cluster B.2.2.2 (Text-fig. 3) is composed of the Toarcian species *Pelagosaurus typus* from Western Europe and an unidentified teleosaurid of uncertain relationships from the Toarcian of England. Although very similar to *P. typus*, the specimen has a longer snout, larger frontal bone and smaller supratemporal fenestrae than all other *P. typus* specimens. In addition, the specimen possesses an enlarged 'brow' ridge (SEP, pers. obs.). Whether this combination of cranial features is unique or an intra-specific variant of the condition seen in other *P. typus* specimens requires further investigation. As such, the unidentified teleosaurid in cluster B.2.2.2 is here considered to be independent of *P. typus*.

Pelagosaurus typus is a well-defined species (Pierce and Benton 2006). It occupies a distinct region of morphospace (i.e. the central area of the long/broad quadrant) as compared to all other teleosaurids (Text-figs 2, 4). The species is small and gracile, reaching a maximum length of only 2 m, and the skull is extensively sculptured. The snout is long and broad with large, laterally expanded

nasal and prefrontal bones. The orbits are large and laterally oriented (some specimens have been described with sclerotic rings), whereas the supratemporal fenestrae are relatively small and project dorsolaterally. All of these characteristics are in stark contrast to the anatomical features of other long-snouted teleosaurids, which display narrow snouts, dorsally placed orbits and expanded supratemporal fenestrae.

Text-figure 4 illustrates species groupings and synonyms recognized here based on the examination of morphospace occupation, pair-wise significance tests, cluster analysis, geological and geographical occurrence, as well as anatomical detail. The analysis delineated nine species: four short-snouted species and five long-snouted species. Within the short-snouted area of morphospace (PC1 negative), there are two machimosaur species and two steneosaur species. Both genera occupy distinct regions of morphospace. The machimosaur extend towards the extreme of PC1 negative, with *Machimosaurus mosae* plotting along the extreme limit of PC1 negative and within PC2 positive or the short/broad region of morphospace and *Machimosaurus hugii* sitting more centrally along PC1 negative and within PC2 negative or the short/narrow region of morphospace. The steneosaurs plot closer to the overall mean along PC1 negative, with *Steneosaurus brevior* plotting within PC2 positive or the short/broad region of morphospace and *Steneosaurus heberti* sitting within PC2 negative or the short/narrow region of morphospace. Conversely, within the long-snouted area of morphospace (PC1 positive), there are three steneosaur species, one pelagosaur species and one *Platysuchus* species. The steneosaurs and pelagosaur occupy distinct areas of morphospace, whereas *Platysuchus* occupies an area of morphospace similar to the steneosaurs. The steneosaurs extend along the entire length of PC1 positive and within PC2 negative (except juvenile *Steneosaurus bollensis*) or the long/narrow region of morphospace, with *S. bollensis* being closer to the average, followed by *Steneosaurus leedsi* and finally *Steneosaurus gracilirostris* that plots at the extreme of PC1 positive; the pelagosaur, *Pelagosaurus typus*, sits centrally along PC1 positive and towards the extreme of PC2 positive or the long/broad area of morphospace; and finally, *Platysuchus multicubiculatus* plots very close to both *S. bollensis* and *S. leedsi* in the long/narrow region of morphospace.

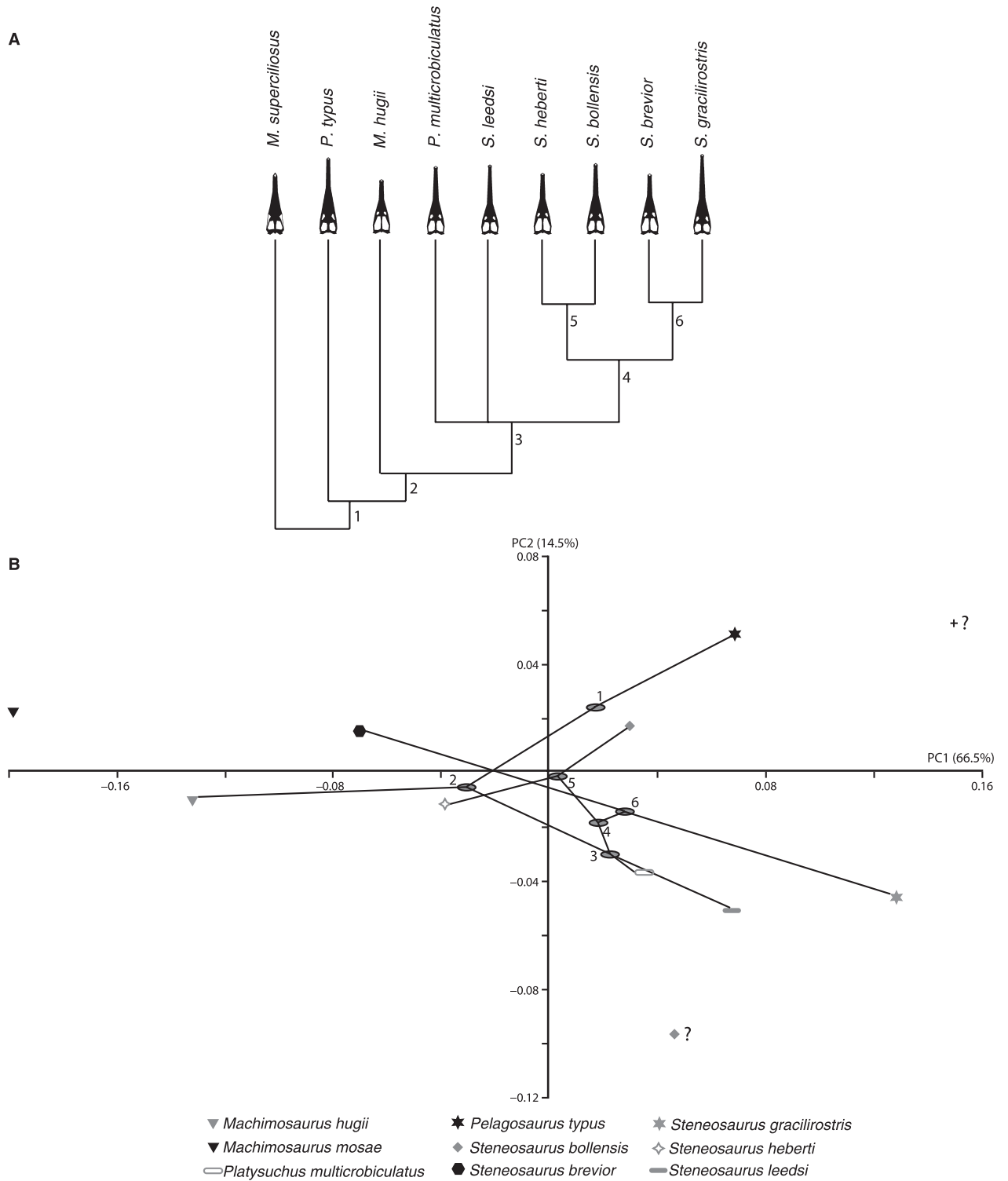
Phylogenetic correlation. The phylogeny was created by deleting unwanted taxa from the character matrix of Mueller-Töwe (2006), combining synonymous species and rooting the tree using *Metriorhynchus superciliosus*. The only species that needed to be combined in the analysis were *Steneosaurus leedsi* and *Steneosaurus megarhinus*. Out of 189 characters in the data set, these two species dif-

fered in the coding of three characters, which were treated as polymorphisms in the current analysis. One species in the present data set, *Machimosaurus mosae*, was not included in the analysis as it was not coded into the original character matrix. A branch-and-bound parsimony search found two equally parsimonious trees with 115 steps, and only 31 out of 189 characters were parsimony informative (C.I. excluding uninformative = 0.6207). The consensus tree is illustrated in Text-figure 5, and shows an interleaving of long-short-long-snouted species as successive outgroups. A clade consisting of the steneosaurs (to the exclusion of *S. leedsi*) was recovered. This steneosaur clade is separated into two smaller clades, each containing one long-snouted and one short-snouted species [(*Steneosaurus bollensis*, *Steneosaurus heberti*) (*Steneosaurus gracilirostris*, *Steneosaurus brevior*)]. *Pelagosaurus typus* was found to be the most basal teleosaurid and *Machimosaurus hugii*, an extreme short-snouted species that first appears in the Oxfordian, sits between the long-snouted Toarcian species *P. typus* and the clade formed by *Platysuchus* and steneosaurs.

This phylogeny is slightly inconsistent with that figured in Mueller-Töwe (2006). For example, she defined a clade composing *Steneosaurus leedsi* and *Steneosaurus heberti* to the exclusion of other teleosaurids and found *Platysuchus multicubiculatus* to sit in a more basal position. However, when the complete original character matrix of Mueller-Töwe (2006) was examined, her results could not be replicated. In fact, the analysis derived a fully unresolved consensus tree with a different number of equally parsimonious trees and a different tree length. As such, the phylogenetic relationships within the Teleosauridae remain uncertain, as does the monophyly of the clade, which was not explicitly tested by Mueller-Töwe (2006) or other authors [see Jouve (2009) who demonstrates that choice of outgroup affects the monophyly of teleosaurids]. Projecting the resolved species-level phylogeny of the Teleosauridae from this study onto morphospace (Text-fig. 5) shows multiple intersections of branches. This pattern stems from the fact that long and short-snouted morphotypes are interspersed within the cladogram – long and short-snouted species appear to be related in a complex way and do not form simple clades encompassing only one morphotype. The Mantel test using the character distance method found a very weak, nonsignificant correlation ($r = 0.05278$, $p = 0.38$). Therefore, it appears that within the Teleosauridae, skull shape is not strongly related to currently available phylogenies.

Metriorhynchid morphospace

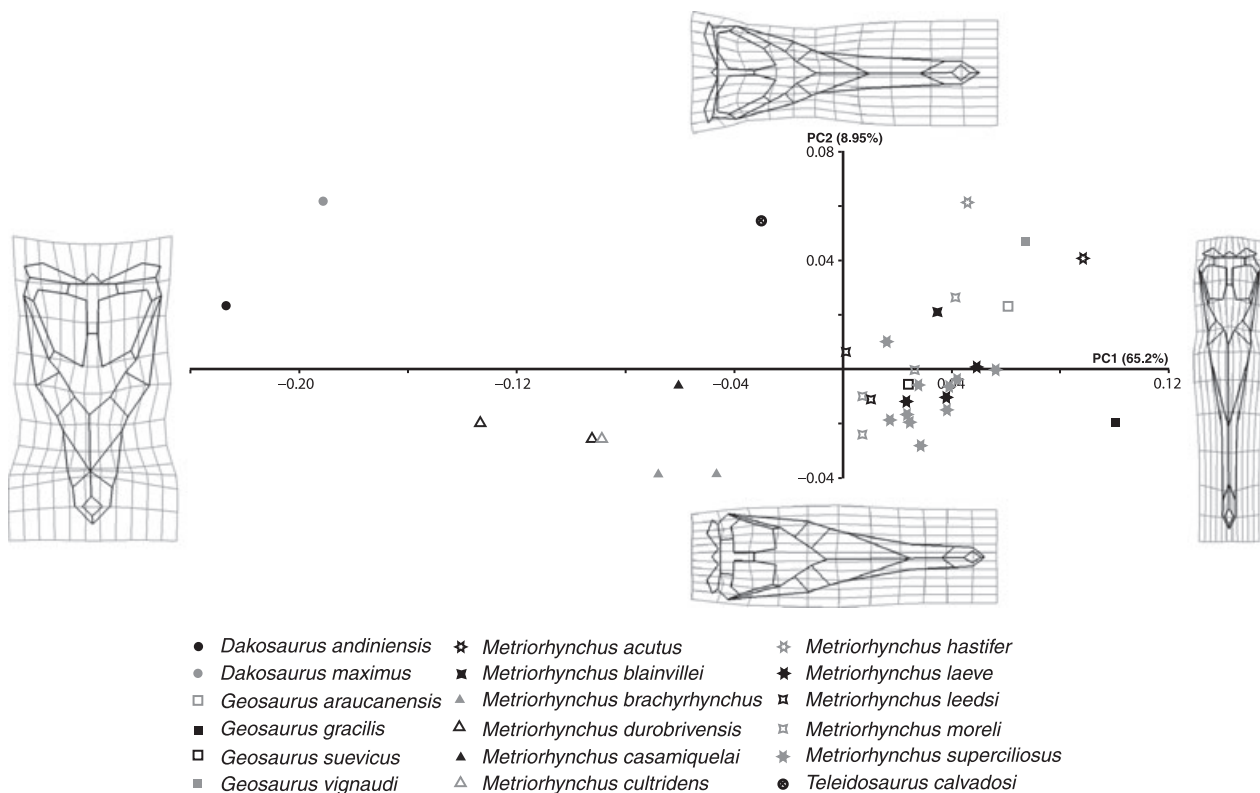
Shape variation. The PCA reveals that the majority of the variance in the data set is captured by the first two PC



TEXT-FIG. 5. Phylogenetic relationships of the Teleosauridae (A) superimposed on morphospace (B). Species that are not connected to the tree were not included in the phylogenetic analysis.

axes, with over 74 per cent of the variance explained (Text-fig. 6). PC1 is the dominant PC axis, describing 65.2 per cent of the total variance, whereas PC2 only describes 8.95 per cent. As PC1 and PC2 capture signifi-

cantly more variance than the other axes, variation along these axes will be the focus for the remainder of the study. The regression of Procrustes distance on log centroid size shows a poor correlation between shape



TEXT-FIG. 6. Metriorhynchid Morphospace. Principal components 1 and 2 with all 35 specimens. Extreme shapes for each axis are shown. Deformation grids indicate the shape change necessary to transform the mean shape into an extreme shape.

and size ($r = -0.2341$; $p = 0.91$). In addition, a regression of the first two PC scores on log centroid size reveals that the shape variation described by these axes is not significantly related to size ($0.75 < p < 0.89$). This implies that the patterns described by the first two significant PC axes are not merely the result of differences in size amongst the specimens and that these axes can be used with confidence to assess morphospace occupation.

The first PC axis describes variation in the length of the snout (especially the length of the maxillae), size of the supratemporal fenestrae and size of the frontal bone (Text-fig. 6). In contrast, the second PC describes variation in width of the snout (especially across the nasal bones), length of the nasal bones, size of the premaxillae and position of the narial opening (Text-fig. 6). As such, PC1 mainly discriminates short- and long-snouted morphotypes, whereas PC2 discriminates broad and narrow-snouted morphotypes. The scatter plot demonstrates that metriorhynchids fall within all four quadrants of morphospace, but that the morphospace is not uniformly occupied. For example, although specimens along PC1 negative (short-snouted morphotype) and PC1 positive (long-snouted morphotype) occupy the full range along PC2 (snout width), large gaps exist with respect to the

distribution of specimens along PC1 negative and, thus, not all morphospace is exploited.

Species delineation. Six defined metriorhynchid species (all from the Oxford Clay) are represented by two or more specimens: *Metriorhynchus brachyrhynchus*, *Metriorhynchus durobrivensis*, *Metriorhynchus laeve*, *Metriorhynchus leedsi*, *Metriorhynchus moreli* and *Metriorhynchus superciliosus*. Pair-wise significance tests conducted on the mean shape of each species (Table 4) find all species pairs to be significantly different from each other except *M. leedsi*/*M. laeve*, *M. laeve*/*M. moreli*, *M. leedsi*/*M. moreli* and *M. moreli*/*M. superciliosus*. Based on this result, as well as further comparisons made below, it appears that the long-snouted morphotypes *M. moreli* and *M. laeve* can be subsumed into the species *M. superciliosus* and *M. leedsi*, respectively (as the latter pair of names hold priority). The two short-snouted morphotypes, *M. brachyrhynchus* and *M. durobrivensis*, are considered independent species. Consequently, the Oxford Clay metriorhynchids are reduced from six species to four.

The cluster analysis (Text-fig. 7) and associated pair-wise significance tests (Table 5) recovered two broad groups within morphospace, Group A or extreme short/narrow-snouted morphotypes, and Group B, all

TABLE 4. Pair-wise comparisons of the mean shape of each metriorhynchid species represented by more than two specimens in the data set.

Group pair	Goodall's p-value	Partial F-value	Procrustes distance between means
<i>M. brachyrhynchus</i> / <i>M. durobrivensis</i>	1.83	0.003	0.0590
<i>M. brachyrhynchus</i> / <i>M. laeve</i>	8.88	< 0.0001	0.1054
<i>M. brachyrhynchus</i> / <i>M. leedsi</i>	6.54	< 0.0001	0.0883
<i>M. brachyrhynchus</i> / <i>M. moreli</i>	6.04	< 0.0001	0.0894
<i>M. brachyrhynchus</i> / <i>M. superciliosus</i>	10.77	< 0.0001	0.0911
<i>M. durobrivensis</i> / <i>M. laeve</i>	12.01	< 0.0001	0.1400
<i>M. durobrivensis</i> / <i>M. leedsi</i>	7.43	< 0.0001	0.1180
<i>M. durobrivensis</i> / <i>M. moreli</i>	9.76	< 0.0001	0.1242
<i>M. durobrivensis</i> / <i>M. superciliosus</i>	18.19	< 0.0001	0.1246
<i>M. laeve</i> / <i>M. leedsi</i>	1.08	0.348	0.0365
<i>M. laeve</i> / <i>M. moreli</i>	1.10	0.299	0.0342
<i>M. laeve</i> / <i>M. superciliosus</i>	2.26	< 0.0001	0.0364
<i>M. leedsi</i> / <i>M. moreli</i>	0.66	0.968	0.0294
<i>M. leedsi</i> / <i>M. superciliosus</i>	1.72	0.001	0.0363
<i>M. moreli</i> / <i>M. superciliosus</i>	1.24	0.117	0.0251

Significance judged using a Bonferroni-corrected α level of 0.003. Significant differences are indicated in bold. *M.*, Metriorhynchus.

other morphotypes. The pattern of shape relationships within the short/narrow-snouted forms is straightforward. There are two species *Dakosaurus maximus* from the Kimmeridgian–Tithonian of Europe and *D. andiniensis* from the Tithonian–Berriasian of South America.

The genus *Dakosaurus* (Text-fig. 8) is defined by the presence of several autapomorphic characters relative to other metriorhynchids: the rostrum is very short and high; a broad, deep sulcus runs down the lateral margin of the mandible; and the teeth are ziphodont, being large, robust, labiolingually compressed and ornamented with a serrated margin (Fraas 1902; Gasparini *et al.* 2006). This type of dental morphology is unique amongst marine reptiles, but more common amongst terrestrial carnivorous archosaurs, including some crocodylomorphs (e.g. *Sebecus*). Within this framework, the South American species *Dakosaurus andiniensis* contrasts with the European species *Dakosaurus maximus* in having a much shorter, more massive, skull (Text-figs 6, 8). In addition, *D. andiniensis* has maxillae and mandibles that are very stout, dorsoventrally high, and can only accommodate a maximum of 11 robust teeth. The premaxillae taper rapidly, producing an unusual, bullet-shaped skull outline (Gasparini *et al.* 2006).

Group B is composed of two main clusters (Text-fig. 7), B.1 and B.2, which are significantly different from

TEXT-FIG. 7. Results of cluster analysis of metriorhynchid skull shapes.

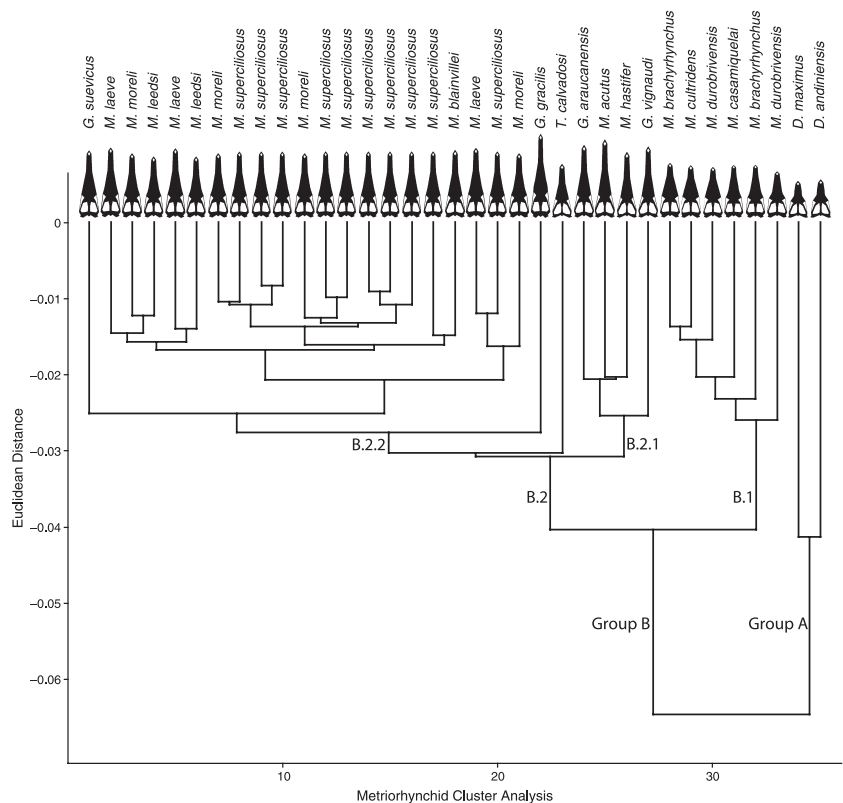


TABLE 5. Pair-wise comparisons of the mean shape of each metriorhynchid group recovered in the cluster analysis.

Group pair	Goodall's F-value	p-value	Partial Procrustes distance between means
Group A/Group B	13.95	<0.0001	0.1838
B.1/B.2	19.51	<0.0001	0.1058
B.2.1/B.2.2	6.43	<0.0001	0.645

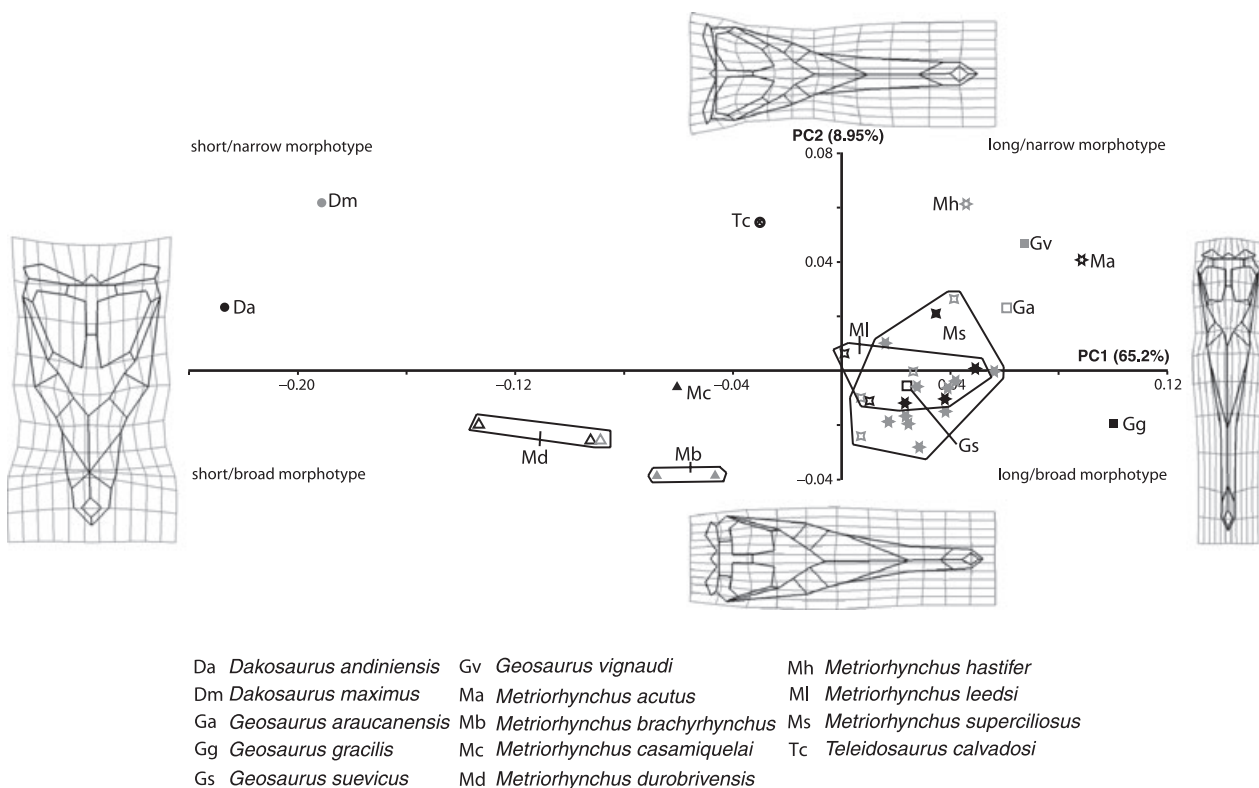
Significance judged using a Bonferroni-corrected α level of 0.016. Significant differences are indicated in bold.

each other (Table 5). B.1 is formed of specimens sitting in the short/broad area of morphospace. There are four species: *Metriorhynchus brachyrhynchus*, *M. cultridens* and *M. durobrivensis* from the Oxford Clay (Callovian) of England, and *M. casamiquelai* from the Callovian of Chile. Specimens of the four species are interspersed in the cluster. However, based on the pair-wise comparisons of mean shapes and their positions in morphospace (Table 4), *M. brachyrhynchus* and *M. durobrivensis* appear to be distinct species. As *M. cultridens* overlaps with *M. durobrivensis* in morphospace (Text-fig. 6), it is considered to belong to the species *M. durobrivensis*. Taking

the unique position in morphospace, geographic occurrence and limited number of discrete characters into account, *M. casamiquelai* is provisionally considered to be a valid taxon.

The taxonomy of short-snouted Callovian *Metriorhynchus* has been a contentious topic. Andrews (1913) subdivided the 'broad-skulled' metriorhynchids of the Oxford Clay, *M. brachyrhynchus*, *M. durobrivensis* and *M. cultridens*, based on five characters: (1) degree of separation of the nasals from the premaxillae; (2) number of teeth; (3) length of rostrum; (4) sutural relationship between the frontal and the prefrontal bones and (5) ornament of dorsal skull bones. Wenz (1968), working on Callovian specimens from France, noted a high degree of variability with respect to these characters, but he favoured the provisional retention of all three short-snouted species. The characters used by Andrews (1913) were subsequently used by Gasparini and Chong Díaz (1977) to define *M. casamiquelai*. Using traditional morphometrics and anatomical comparisons, however, Adams-Tresman (1987a) [and later on Vignaud (1995)] concluded that all five characters were too variable to be taxonomically useful and grouped the three species into one, *M. brachyrhynchus*.

An examination of the specimens finds the following distribution of characters: the snout of *M. cultridens* and *M. casamiquelai* are characterised by an extensive gap

**TEXT-FIG. 8.** Metriorhynchid species delineation with respect to specimen distribution along PC1 and PC2.

between the nasals and the premaxillae, whereas the nasals meet or nearly meet the premaxillae in *M. brachyrhynchus* and *M. durobrivensis*; all species have between 20 and 21 smooth, slightly recurved, maxillary teeth, except for *M. durobrivensis*, which has c. 16 teeth; *M. brachyrhynchus* and *M. casamiquelai* have longer snouts than *M. durobrivensis* and *M. cultridens* (contra Adams-Tresman, who found *M. cultridens* and *M. casamiquelai* to have longer snouts than the remaining two species); the prefrontal bones of *M. casamiquelai* and *M. brachyrhynchus* are smaller and more rounded, whereas *M. cultridens* and *M. durobrivensis* have larger, more triangular prefrontals (SEP, pers. obs.); the frontal-prefrontal suture is highly variable (see Adams-Tresman 1987a, fig. 8), but conforms to a broad 'V' shaped outline in all species; and finally, the degree of ornamentation of the dorsal skull bones appears to be continuous, with the ornament being poorly developed in *M. casamiquelai* and *M. cultridens*, and more extensively developed in *M. brachyrhynchus* and *M. durobrivensis*. An additional character used by Gasparini and Chong Díaz (1977) to distinguish *M. casamiquelai* from all other species is an 'M'-shaped suture separating the premaxillae and maxillae instead of the typical 'V' shape.

Consequently, it appears that patterns of variation in the detailed anatomical characteristics of the skull in short-snouted *Metriorhynchus* cannot be used to define species with much confidence. *Metriorhynchus cultridens* and *M. casamiquelai* are comparable with respect to the degree of separation between nasals and premaxillae, and reduction of dorsal ornamentation; however, the shape and size of their prefrontal bones and premaxillae/maxillae suture are clearly distinct. Similarly, *M. brachyrhynchus* and *M. durobrivensis* have nasals that meet or nearly meet the premaxillae, a 'V' shaped premaxillae/maxillae suture and more extensive dorsal ornamentation; yet, the shape and size of their prefrontal bones are noticeably different. Thus, based on these criteria Adams-Tresman's (1987a) proposed synonymy of all Callovian short-snouted metriorhynchids is logical. However, it appears overly simplistic when skull shape and patterns of morphospace occupation are taken into account (Text-figs 6, 8). The pair-wise significance tests (Table 4) found *M. brachyrhynchus* and *M. durobrivensis* to possess significantly different skull shapes. In contrast, *M. cultridens* converges on *M. durobrivensis* in morphospace, and the primary discrete characters that differentiate the species (tooth count and degree of skull ornamentation) are likely to stem from individual variation. Therefore, *M. cultridens* must be considered to belong to *M. durobrivensis* (Text-fig. 8). *Metriorhynchus casamiquelai* plots close to *M. brachyrhynchus* along PC1 negative, but it occupies a divergent area of morphospace along PC2 negative. The former species also occurs in a distinct geographic region and possesses

a unique 'M'-shaped suture between the premaxillae and the maxillae. Therefore, *M. casamiquelai* and *M. brachyrhynchus* can provisionally be considered separate taxa (Text-fig. 8). Nonetheless, because of low sample sizes, it is not possible to determine whether or not these results are statistically significant.

Cluster B.2 is composed of two smaller clusters (Text-fig. 7), B.2.1 and B.2.2, which are significantly different from each other (Table 5). Cluster B.2.1 differs from B.2.2 by including specimens with longer/narrower snouts. Cluster B.2.1 consist of four specimens belonging to four species including *Metriorhynchus acutus* and *Metriorhynchus hastifer* from the Kimmeridgian of France, *Geosaurus araucanensis* from the Tithonian of Argentina and *Geosaurus vignaudi* from the Tithonian of Mexico. Although both *M. acutus* and *M. hastifer* occur at the same geological time and in the same geographical area, they occupy divergent areas of morphospace along PC1 negative (i.e. *M. acutus* has a considerably longer snout than *M. hastifer*; Text-fig. 6) even though they are of similar size. As such, these two species are considered to be independent. Conversely, *G. araucanensis* and *G. vignaudi* occupy a similar area of morphospace with respect to snout length. Considering that these geosaur species come from disparate geographical regions and differ in their snout widths (i.e. their position along PC2), however, both are provisionally considered separate taxa.

Fraas (1902) considered *Metriorhynchus hastifer* to be a short-snouted metriorhynchid and subsequently Andrews (1913) and Wenz (1968) allied it with the Oxford Clay species *M. brachyrhynchus*, *M. durobrivensis* and *M. cultridens*. Alternatively, Buffetaut (1982) regarded both *M. hastifer* and *M. acutus* as distinct, long-snouted metriorhynchid species, with *M. hastifer* being robust and *M. acutus* being a gracile form. Unfortunately, during WWII the holotypes of *M. acutus* and *M. hastifer* were lost, making an in-depth anatomical comparison of the two species impossible. Based on their positions in morphospace, it is clear that both *M. hastifer* and *M. acutus* are long/narrow-snouted morphotypes, with *M. acutus* being one of the longest-snouted metriorhynchid species (Text-figs 6, 8). As such, the morphometric analysis supports Buffetaut's interpretation that *M. hastifer* is a long-snouted metriorhynchid (Text-fig. 8). Nonetheless, because there lacks evidence of discrete anatomical differences, the two species are only provisionally considered distinct taxa based on snout length (Text-fig. 8). Both species differ from all other long-snouted metriorhynchids by having shorter nasal bones and, by association, longer maxillae and a greater distance between the nasals and the premaxillae.

The genus *Geosaurus* is considered to be more highly adapted to a marine lifestyle than *Metriorhynchus*, and the

characters used to distinguish the two genera reflect this interpretation. *Geosaurus* has a posteriorly reflected external naris that is partially to wholly divided, presumably to restrict water from entering the nasal cavity; the ant-orbital fenestrae are greatly enlarged to house an expanded nasal salt-excretion gland; and the limbs are much more reduced, implying a complete reliance on an aquatic medium for locomotion (Gasparini and Dellapé 1976; Steel 1973). In addition to these marine adaptations, *Geosaurus* is also identified by a very conspicuous neck on the occipital condyle (also seen in dakosaurs), in association with the complete lack of skull ornamentation (Gasparini *et al.* 2005). Nonetheless, according to patterns of morphospace occupation, *Geosaurus* and *Metriorhynchus* show substantial shape overlap, perhaps reflecting the inheritance of these similarities from a common ancestor (Text-figs 6, 8).

The anatomical distinction between the two geosaur species, *Geosaurus araucanensis* and *G. vignaudi*, is not substantial. According to Frey *et al.* (2002), *G. vignaudi* differs from *G. araucanensis* in having subcircular supratemporal fenestrae (they are circular in *G. araucanensis*), 15–17 teeth in each mandibular ramus (opposed to 29 in *G. araucanensis*) and a snout that tapers more strongly rostrally. However, based on their positions in morphospace, the skull shapes of these geosaurs are generally similar, although *G. vignaudi* possesses a proportionally narrower snout (Text-figs 6, 8). The only discrete difference is the number of teeth, which is not considered to be a reliable character for species delineation (see above). Frey *et al.* (2002) suggested that *G. vignaudi* might be a juvenile animal based on the large size of its orbits, but the skull measurements imply that the specimen is of a similar size to *G. araucanensis*. Of course, the description, measurements and reconstruction of *G. vignaudi* are based on a single, disarticulated specimen and may not be totally accurate. Therefore, these two species are provisionally considered distinct taxa based primarily on their geographical occurrence (*G. vignaudi* is from Mexico and *G. araucanensis* is from Argentina) and slight difference in snout width until the anatomical characteristics of each species can be better substantiated (Text-fig. 8).

Teleidosaurus calvadosi from the Bathonian of France sits outside the final cluster of specimens, B.2.2 (Text-fig. 7). This species occupies a unique area of morphospace (Text-fig. 6): out of all the short-snouted forms, it is defined by having the longest and narrowest snout. The position of *T. calvadosi* in morphospace (Text-figs 6, 8) substantiates the fact that *Teleidosaurus* possesses a unique suite of characteristics when compared to dakosaurs, geosaurs and metriorhynchids proper. Although the postcranial anatomy of *Teleidosaurus* is unknown, features of the skull suggest that this genus was the least adapted to a marine lifestyle. Buffetaut (1982) noted that the pre-

frontals are less developed than in other metriorhynchid species and do not project laterally over the orbits, and that the orbits themselves are located in a more dorsal position. In addition, the lacrimals are large compared to the prefrontals, and the external naris is situated on the anterior tip of the snout.

Finally, B.2.2 is composed of a large cluster of specimens within a broad array of species (Text-fig. 7). Amongst these are the geosaurs *Geosaurus gracilis* and *Geosaurus suevicus* from the Kimmeridgian–Tithonian of Western Europe. These two species occupy highly divergent areas of morphospace, with *G. gracilis* being the longest-snouted metriorhynchid specimen in the analysis. As such, the geosaurs are considered to represent two independent species. Conversely, the remaining species include the Oxford Clay (Callovian) metriorhynchids *Metriorhynchus laeve*, *M. leedsi*, *M. moreli*, and *M. superciliosus*, as well as *M. blainvillei* from the Callovian of France. All specimens are interspersed; however, based primarily on the pair-wise comparisons of mean shapes (Table 4, also see below), both *M. superciliosus* and *M. moreli* and both *M. leedsi* and *M. laeve* can be united into the species *M. superciliosus* and *M. leedsi*, respectively. In addition, *M. blainvillei* can also be considered to belong to the species *M. superciliosus* as it clusters with all other *M. superciliosus* specimens.

The taxonomy of long-snouted Callovian *Metriorhynchus* species has been a highly debated subject. Andrews (1913) subdivided the ‘narrow-skulled’ *Metriorhynchus* species from the Oxford Clay into two broad groups based on cranial sculpturing: *Metriorhynchus laeve* and *Metriorhynchus leedsi* are forms without sculpturing, and *Metriorhynchus superciliosus* and *Metriorhynchus moreli* are forms with sculpturing. In addition to this feature, he delineated species based on three characters: (1) length and width of the frontal bone anterior to the supratemporal fenestra; (2) sutural relationship between the prefrontal and the frontal; and (3) number of teeth. Wenz (1968) also distinguished between ornamented forms and forms without ornament but found specific diagnoses beyond this unsatisfactory. Nonetheless, Wenz did illustrate that the French species *Metriorhynchus blainvillei* was actually synonymous with *M. superciliosus*. Subsequent to these studies, Adams-Tresman (1987a), using traditional morphometrics and anatomical comparisons, found all four characters too variable to be taxonomically useful and grouped all species into one, *M. superciliosus*. Most recently, Vignaud (1995) again reorganized the taxonomy of long-snouted Callovian *Metriorhynchus*, separating the specimens into two species, *M. superciliosus* and *M. leedsi*, based on the observation that *M. leedsi* has a higher tooth count.

An examination of long-snouted Callovian specimens supports Adams-Tresman’s (1987a) view of continuous variation in the characters defined by Andrews (1913).

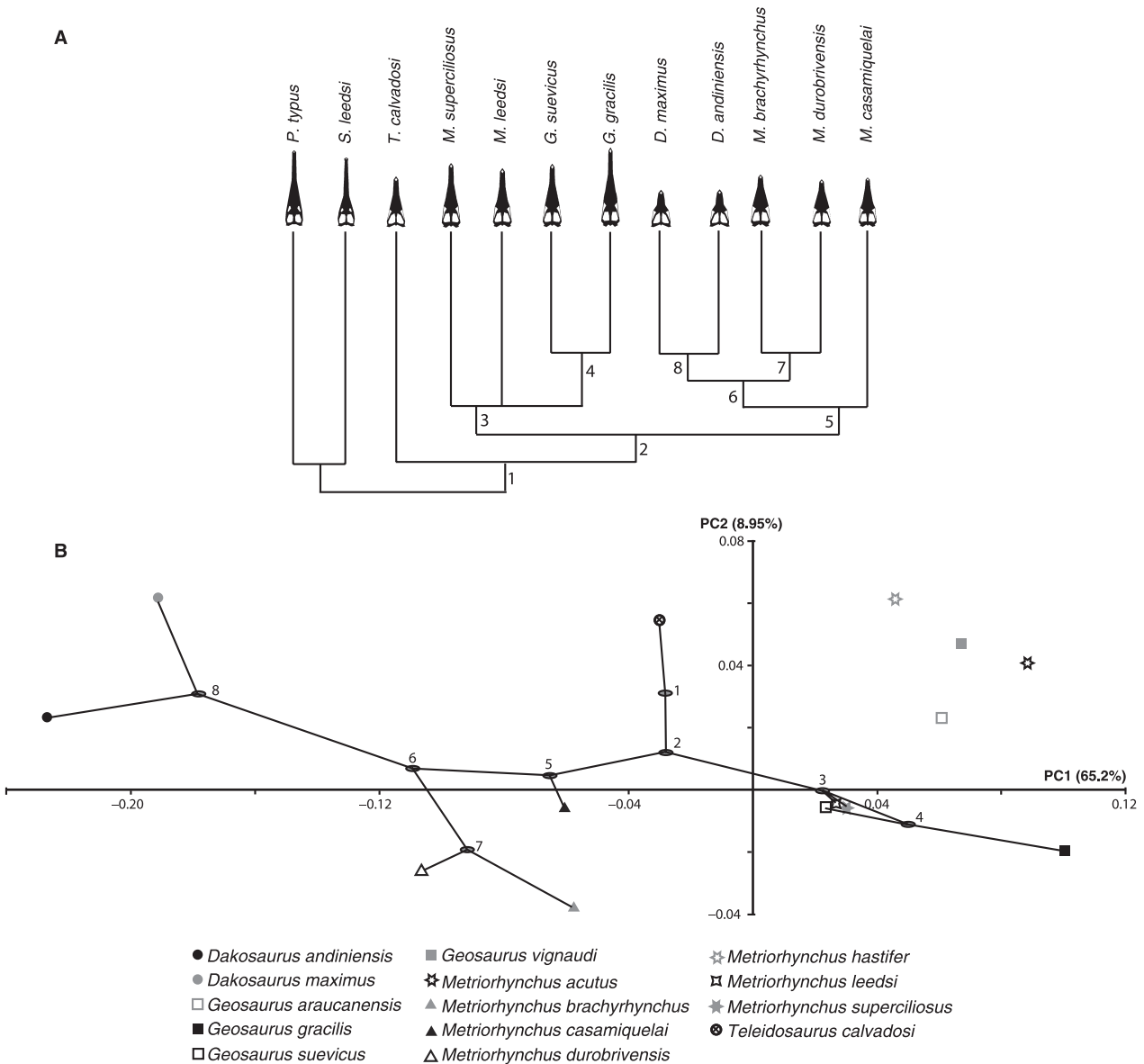
For instance, the length of the frontal bone is directly related to the shape of the prefrontal/frontal suture, a feature that shows considerable variation within specimens of the same 'species' (see Adams-Tresman 1987a, fig. 8). In addition, the number of teeth varies between 'species' (26–36) and within specimens of the same 'species' (by up to 10). Moreover, there appears to be a range of cranial sculpturing, from smooth to densely ornamented, but whether this represents variation within one species (e.g. Adams-Tresman 1987a) or a feature that can be used to differentiate species (e.g. Wenz 1968) is uncertain.

Looking primarily at patterns of morphospace occupation (Text-figs 6, 7), species separation is still impossible as all long-snouted specimens show extensive overlap with respect to overall skull shape. However, the pair-wise significance tests (Table 4) do demonstrate a significant difference in mean shape between *M. superciliosus*/*M. moreli* and *M. laeve*/*M. leedsi*. Therefore, the results of this study support the interpretation that there are two long-snouted Callovian *Metriorhynchus* species (Text-fig. 8), one with dense sculpturing and 'fewer teeth' (i.e. *M. superciliosus*) and one with faint sculpturing and 'more teeth' (i.e. *M. leedsi*). This delineation is further supported by the fact that there is no obvious difference in skull size between the two species. As such, the degree of sculpturing does not appear to be an ontogenetic characteristic; however, the possibility that sculpturing and tooth count is linked to sexual dimorphism or simply variable amongst individuals cannot be ruled out using available statistical methods.

Finally, the anatomical characteristics of the skull corroborate the geometric interpretation that *Geosaurus gracilis* and *Geosaurus suevicus* are separate species (Text-figs 6, 8). Frey *et al.* (2002) supplied a list of features that differed between the two species, but the specific characteristics were unknowingly mixed up (SEP, pers. obs. based on comparing skull reconstructions with original descriptions). Based on the description and illustrations produced by Fraas (1902) and Broili (1932), these two long/broad-snouted geosaurs can be distinguished by the following characteristics: *G. gracilis* has a more elongated rostrum, a sharply pointed snout tip, a partially separated external narial opening, enlarged antorbital fenestrae, an interorbital space that is only one-half the occipital width, a lateral process of frontal that is almost perpendicular to the medial plane of the skull and circular supratemporal fenestrae. Conversely, *G. suevicus* has a shorter rostrum, a rounded snout tip, a wholly separated external narial opening, slit-like antorbital fenestrae, an interorbital space that is almost as wide as the occiput and longitudinally oval supratemporal fenestrae. From patterns of morphospace occupation (Text-figs 6, 8) it is clear that *G. gracilis* has an extremely elongated rostrum compared to that of *G. suevicus* and all other metriorhynchid species.

Text-figure 8 illustrates species groupings and synonyms recognized here based on the examination of morphospace occupation, pair-wise significance tests, cluster analysis, geological and geographical occurrence, as well as discrete anatomical characters. The analysis delineated 14 species: six short-snouted species and eight long-snouted species. Within the short-snouted area of morphospace (PC1 negative), there are two dakosaur species, three *Metriorhynchus* species and one teleidosaur. All three genera occupy distinct regions of morphospace: the dakosaurs, *Dakosaurus andiniensis* and *D. maximus*, sit along the extreme limit of PC1 negative and within PC2 positive or the short/narrow region of morphospace; the *Metriorhynchus* species, *M. brachyrhynchus*, *M. casamiquelai* and *M. durobrivensis* extend along the central area of PC1 negative and within PC2 negative or the short/broad region of morphospace; and the teleidosaur, *Teleidosaurus calvadosi*, plots close to the average along PC1 negative and two-thirds up PC2 positive or in the short/narrow region of morphospace. Conversely, within the long-snouted area of morphospace (PC1 positive), there are four *Metriorhynchus* species and four *Geosaurus* species. Both genera occupy similar areas of morphospace: *M. leedsi*, *M. superciliosus* and *Geosaurus suevicus* extensively overlap and plot close to the average along PC1 positive and PC2, both in the positive and negative direction (i.e. long/broad and long/narrow region of morphospace); *M. acutus*, *M. hastifer*, *G. araucanensis* and *G. vignaudi* extend along the central area of PC1 positive and within PC2 positive or the long/narrow region of morphospace; and finally, *G. gracilis* plots along the extreme of PC1 positive and within PC2 negative or the long/broad area of morphospace.

Phylogenetic correlation. The phylogeny was created by deleting unwanted taxa from the character matrix of Young (2006), combining synonymous species and rooting the tree using *Pelagosaurus typus* and *Steneosaurus leedsi*. The species that needed to be combined in this analysis were *Metriorhynchus leedsi* and *M. laeve*; *M. superciliosus* and *M. moreli*; and *M. cultridens* and *M. durobrivensis*. Out of 54 characters in the data set, only *M. cultridens* and *M. durobrivensis* differed in the coding of three characters, which were treated as polymorphisms in the current analysis. Four species in the present data set, *Geosaurus araucanensis*, *G. vignaudi*, *M. acutus* and *M. hastifer*, were not included in the analysis because they were not coded into the original character matrix. A branch-and-bound parsimony search found three equally parsimonious trees with 79 steps; 42 out of 54 characters were parsimony informative (C.I. excluding uninformative = 0.8611). The consensus tree is illustrated in Text-figure 9. The resolved phylogeny here corresponds directly to that figured by Young (2006) and includes two broad



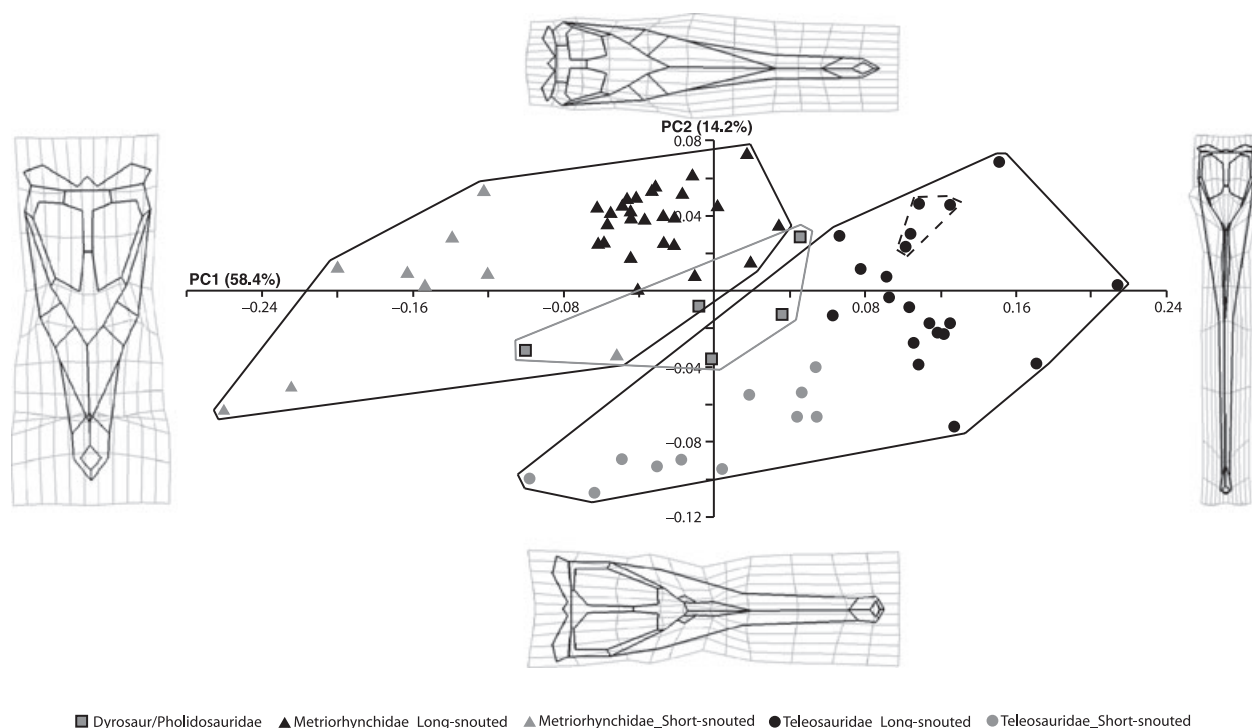
TEXT-FIG. 9. Phylogenetic relationships of the Metriorhynchidae (A) superimposed on morphospace (B). Species that are not connected to the tree were not included in the phylogenetic analysis.

clades, one composed of long-snouted species and one composed of short-snouted species. The long-snouted *Metriorhynchus* is the sister group of *Geosaurus*, and the short-snouted *Metriorhynchus* is the sister group of *Dakosaurus*. As such, it appears that Young’s phylogeny of the Metriorhynchidae is a stable and a good representation of the relationships within the group, even when operational taxonomic units are excluded or modified, and that *Metriorhynchus* is paraphyletic. Projecting the resolved species-level phylogeny of the Metriorhynchidae from this study onto morphospace (Text-fig. 9) finds no intersection of branches. This is the result of a clear distinction between long and short-snouted species within the

phylogeny and morphospace. The Mantel test using the character distance method found a significant relationship between morphospace occupation and phylogeny ($p = 0.01$), and the correlation was of moderate strength ($r = 0.4458$). Therefore, within the Metriorhynchidae skull shape and evolutionary history are related.

Longirostrine morphospace

Shape variation. The PCA reveals that the majority of the variance in the data set is captured by the first three PC axes, with over 79 per cent of the variance explained



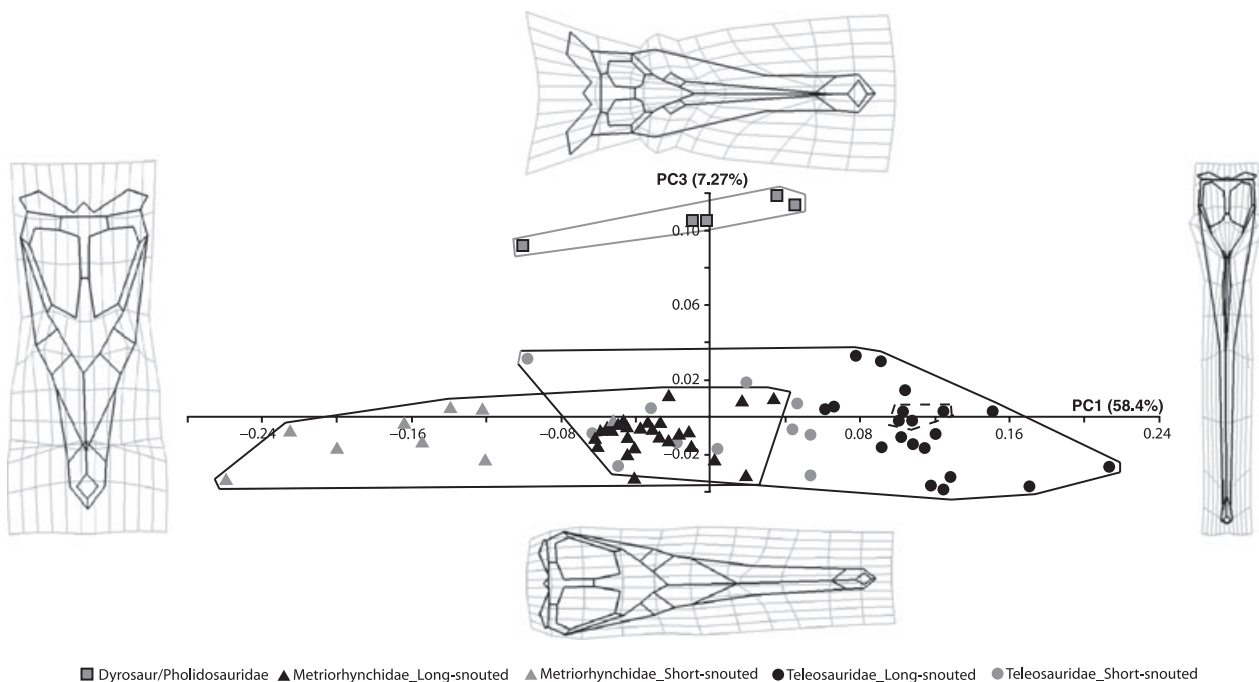
TEXT-FIG. 10. Longirostrine Morphospace (including all thalattosuchians and dyrosaur/pholidosaurids). Specimen distribution along principal components 1 and 2. Extreme shapes for each axis are shown. Deformation grids indicate the shape change necessary to transform the mean shape into an extreme shape. Dashed lines are encircling *Pelagosaurus*.

(Text-figs 10–11). PC1 is the dominant PC axis, describing 58.4 per cent of the total variance, whereas PC2 and PC3 describe 14.2 per cent and 7.27 per cent, respectively. As PC1, PC2, and PC3 are the only significant PC axes, they will be the focus for the remainder of the study. The multivariate regression reveals shape is not significantly correlated with log centroid size (Wilk's $\Lambda = 0.1252$, $p = 0.2476$). In fact the regression model only explains three per cent of the variance in the data set. This implies that the patterns described by the PC axes are not the result of differences in size amongst the specimens. With respect to specific morphological patterns, the first PC axis describes variation in the length of the snout, especially the length of the maxillae, the position of the narial opening and the width of the supratemporal fenestrae. The second PC axis describes variation in the width of the nasals and the prefrontals, the length of the premaxillae and the length of the supratemporal fenestrae. The third PC axis describes variation in the width of the snout, length of the nasal bones and overall size of the supratemporal fenestrae.

The scatter plots (Text-figs 10–11) demonstrate that teleosaurids and metriorhynchids occupy different but overlapping areas of morphospace. Metriorhynchids do not approach the quadrant of morphospace defined by PC1 positive and PC2 negative, and teleosaurids do not

approach the quadrant of morphospace defined by PC1 negative and PC2 positive. Thalattosuchians as a whole encompass a continuous range of snout lengths along PC1 (Text-fig. 10), with short-snouted metriorhynchids sitting at the extreme of PC1 negative (i.e. short maxillae, posteriorly placed narial opening and wide supratemporal fenestrae) and long-snouted teleosaurids at the extreme of PC1 positive (i.e. long maxillae, anteriorly placed narial opening and narrow supratemporal fenestrae). However, there is extensive overlap between short-snouted teleosaurids and long-snouted metriorhynchids near the mean shape of morphospace. This trend is particularly apparent in the PC1 and PC3 plot (Text-fig. 11). Differentiation of the thalattosuchian families occurs along PC2, where short-snouted teleosaurids tend towards PC2 negative (i.e. short premaxillae, narrow nasals and prefrontals and long supratemporal fenestrae) and long-snouted metriorhynchids tend towards PC2 positive (i.e. long premaxillae, wide nasals and prefrontals and short supratemporal fenestrae).

With respect to PC1 and PC2 (Text-fig. 10), dyrosaur/pholidosaurids occupy the area of morphospace between short-snouted teleosaurids and long-snouted metriorhynchids and sit within the same three quadrants as teleosaurids, not approaching the area of morphospace defined by PC1 negative and PC2 positive. Conversely,



TEXT-FIG. 11. Longirostrine Morphospace (including all thalattosuchians and dyrosaur/pholidosaurids). Specimen distribution along principal components 1 and 3. Extreme shapes for each axis are shown. Deformation grids indicate the shape change necessary to transform the mean shape into an extreme shape. Dashed lines are encircling *Pelagosaurus*.

the scatter plot along PC1 and PC3 (Text-fig. 11) demonstrates that PC3 separates thalattosuchians from dyrosaur/pholidosaurids. Dyrosaur/pholidosaurids occupy the extreme position along PC3 positive defined by a wide snout, long nasal bones that reach the premaxillae and small supratemporal fenestrae. Thalattosuchians occupy a position along PC3 that ranges from the extreme of PC3-negative to half way up PC3-positive area of morphospace defined by a narrow snout, short nasal bones that do not reach premaxillae and large supratemporal fenestrae.

Family delineation and disparity. Pair-wise comparisons of the mean shapes of each family within morphospace find all three longirostrine groups, Teleosauridae, Metriorhynchidae and dyrosaur/pholidosaurids, to be significantly different from each other (Table 6). Looking at the partial Procrustes distances between each family, we see that dyrosaur/pholidosaurids and metriorhynchids are closer to each other in shape space than either are to the teleosaurids. An analysis of shape disparity at the family level reveals that metriorhynchids display significantly more shape disparity than teleosaurids (Tables 7–8). With respect to snout morphotype, short-snouted metriorhynchids display the greatest amount of shape disparity within the Thalattosuchia, followed by long-snouted teleosaurids and finally short-snouted teleosaurids and long-snouted metriorhynchids (Table 7). Pair-wise *t*-tests

TABLE 6. Pair-wise comparisons of the mean shapes of the Teleosauridae, Metriorhynchidae and Dyrosaur/Pholidosaurids.

Group pair	Goodall's F-value	p-value	Partial Procrustes distance between means
Dyrosaur/ Pholidosaurids Metriorhynchidae	4.92	<0.0001	0.1295
Dyrosaur/ Pholidosaurids Teleosauridae	10.20	<0.0001	0.1569
Metriorhynchidae Teleosauridae	23.91	<0.0001	0.1393

Significance judged using a Bonferroni-corrected α level of 0.016. Significant differences are indicated in bold.

between the partial disparities of each snout morphotype (Table 8) show that all snout morphotypes display significantly different amounts of shape disparity, except for short-snouted teleosaurids and long-snouted metriorhynchids.

Temporal patterns. Thalattosuchian remains in the early Lower Jurassic are fragmentary, can rarely be identified to

TABLE 7. Partial disparity and percentage of total disparity for each thalattosuchian family and snout morphotype.

Taxon/Morphotype	Partial Disparity	Percentage
Teleosauridae	0.00572	42
Metriorhynchidae	0.00780	58
Total	0.01352	100
Teleosaurids Long-snouted	0.00483	36
Teleosaurids Short-snouted	0.00092	7
Metriorhynchids Long-snouted	0.00078	6
Metriorhynchids Short-snouted	0.00684	51
Total	0.01336	100

TABLE 8. Pair-wise comparisons of partial disparities of each thalattosuchian family and morphotype using two-sample *t*-tests.

Taxonomic/Morphotype pair	<i>t</i> -value	p-value
Teleosauridae/Metriorhynchidae	2.2019	0.028
Teleo_Long/Teleo_Short	7.0304	< 0.0001
Metrio_Long/Metrio_Short	11.1022	< 0.0001
Teleo_Long/Metrio_Long	9.3498	< 0.0001
Teleo_Short/Metrio_Short	9.1068	< 0.0001
Teleo_Long/Metrio_Short	2.8698	0.004
Teleo_Short/Metrio_Long	0.34804	0.73

Significance judged using an α level of 0.05 for family level and a Bonferroni-corrected α level of 0.008 for snout morphotype. Significant differences are indicated in bold.

the genus level, and none have been identified to species-level (e.g. Gasparini *et al.* 2000; Godefroit 1994). Consequently, although thalattosuchians are known from this stratigraphic interval, no specific morphotype can be identified and plotted in morphospace ('Lower Jurassic' in Text-fig. 12).

In the Toarcian (Lower Jurassic), thalattosuchian diversity is extensive, but restricted to specimens belonging to the Teleosauridae ('Toarcian' in Text-fig. 12). The plot demonstrates that teleosaurids had already diverged into long and short-snouted morphotypes by this time. However, morphospace occupation is largely characterized by an extensive radiation of long/broad- and long/narrow-snouted teleosaurids (*Pelagosaurus typus*, *Platysuchus multicrobicularis*, *Steneosaurus bollensis* and *Steneosaurus gracilirostris*), with only a single occurrence of a short-snouted teleosaurid (*Steneosaurus brevior*).

The Aalenian/Bajocian (Middle Jurassic) is, again, only represented by fragmentary remains. Remains of *Steneosaurus* are known, and we see the first appearance of the metriorhynchids during the Bajocian (e.g. Gasparini *et al.* 2000; Hua and Atrops 1995; Storrs and Efimov 2000). Nevertheless, species diagnoses are uncertain, and no

specific morphotype can be plotted in morphospace ('Aalenian/Bajocian' in Text-fig. 12).

In the Bathonian (Middle Jurassic), there is a complete disappearance of all long-snouted teleosaurids from morphospace. However, metriorhynchids appear for the first time ('Bathonian' in Text-fig. 12). Morphospace, although sparsely occupied, is characterized by the radiation of short-snouted taxa: short/narrow-snouted *Steneosaurus heberti* (Teleosauridae) and *Teleidosaurus calvadosi* (Metriorhynchidae), as well as short/broad-snouted *Metriorhynchus brachyrhynchus* (Metriorhynchidae).

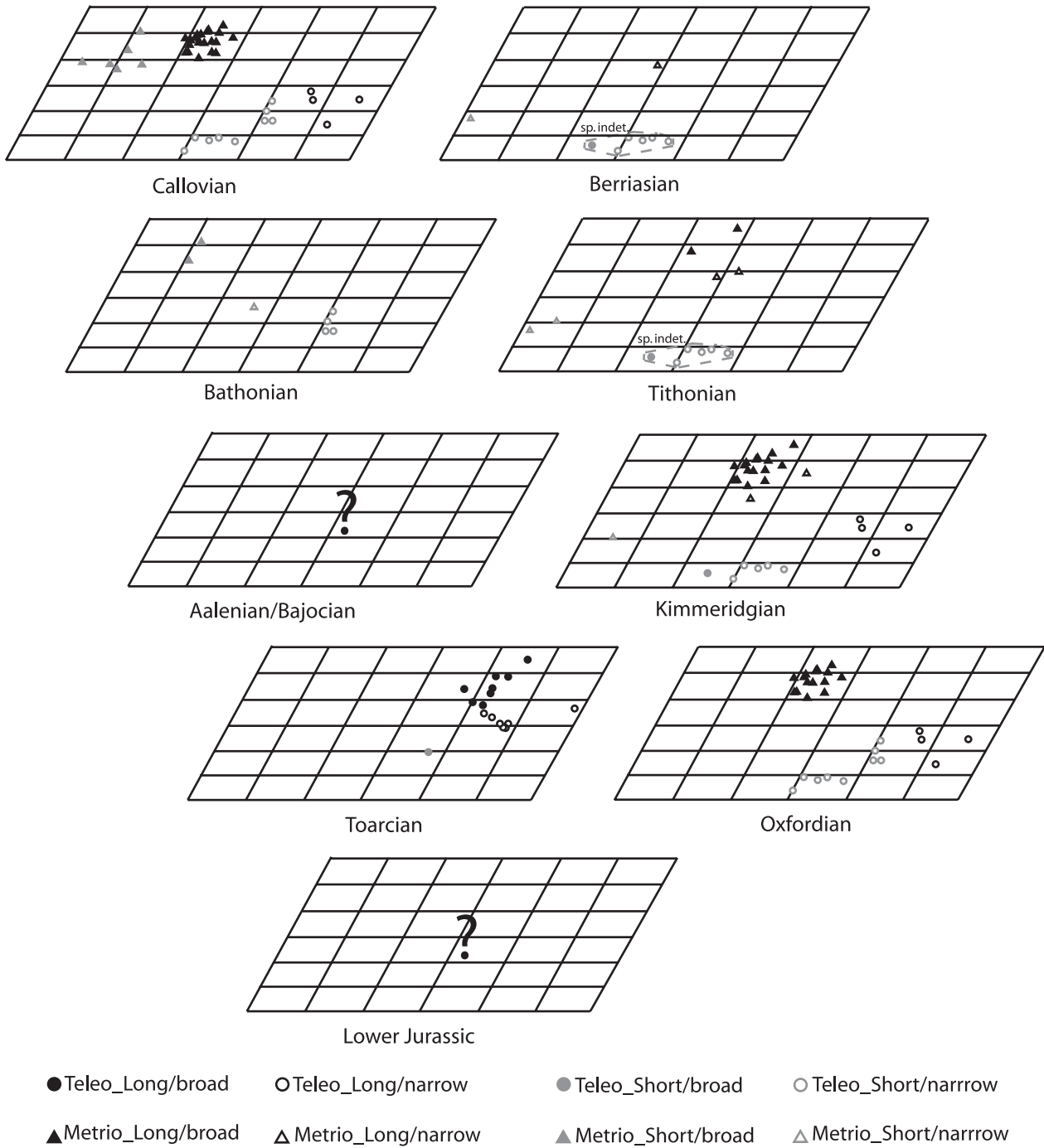
By the Callovian (Middle Jurassic) there is an explosion in diversity ('Callovian' in Text-fig. 12). Metriorhynchids diverge into long and short-snouted morphotypes for the first time. However, only long/broad (*Metriorhynchus brachyrhynchus*, *M. casamiquelai* and *M. durobrivensis*) and short/broad-snouted morphotypes are present (*M. superciliosus* and *M. leedsi*). Furthermore, short/narrow-snouted teleosaurids continue to radiate (*Steneosaurus heberti* and *Machimosaurus hugii*), and long/narrow-snouted teleosaurids emerge once again (*Steneosaurus leedsi*).

During the Oxfordian (Upper Jurassic), thalattosuchian diversity decreases with the complete disappearance of short/broad-snouted metriorhynchids from morphospace ('Oxfordian' in Text-fig. 12). Nonetheless, long/broad-snouted metriorhynchids maintain their diversity. Both long and short-snouted teleosaurids (*Steneosaurus leedsi* and *Machimosaurus hugii*) persist within morphospace.

The Kimmeridgian (Upper Jurassic) shows a small increase in diversity within the metriorhynchids ('Kimmeridgian' in Text-fig. 12). We see the radiation of extreme long/broad (*Geosaurus gracilis*), long/narrow (*Metriorhynchus acutus* and *M. hastifer*), and short/narrow-snouted forms (*Dakosaurus maximus*). Teleosaurids maintain their diversity but extend into the extreme short/broad-snouted portion of morphospace (*Machimosaurus mosae*).

During the Tithonian (Upper Jurassic), morphospace occupation becomes characterized by extreme morphologies ('Tithonian' in Text-fig. 12). Long/narrow and short/narrow-snouted metriorhynchids continue to radiate (*Geosaurus araucanensis*, *G. vignaudi* and *Dakosaurus andiniensis*), whilst other metriorhynchids (i.e. *Metriorhynchus*) disappear altogether. Teleosaurid diversity decreases, with a singular occurrence of an extreme short-snouted form [*Machimosaurus* (species indeterminate)] and the complete disappearance of long-snouted forms from morphospace.

Finally, by the Berriasian (Lower Cretaceous) thalattosuchian diversity is considerably restricted ('Berriasian' in Text-fig. 12). Although both metriorhynchids and teleosaurids persist into the Cretaceous, they are almost all



TEXT-FIG. 12. Thalattosuchian morphospace occupation through time. Based on the distribution of species within longirostrine morphospace. Triangles represent the metriorhynchids and circles represent the teleosauroids. Dashed lines in the Tithonian and the Berriasian are encircling both *Machimosaurus mosae* and *M. hugii* as the species identification during these intervals is indeterminate.

characterized by extreme short-snouted morphotypes. Within the metriorhynchids, the extreme short/narrow-snouted morphotype endures [*Dakosaurus andiniensis* (although there remains some evidence of the of the

long/narrow-snouted geosaur *Geosaurus araucanensis*)]. Likewise, within the teleosauroids, only the extreme short-snouted morphotype (*Machimosaurus* sp.) continues across the Jurassic–Cretaceous boundary.

DISCUSSION

Thalattosuchian alpha-taxonomy

The alpha-taxonomy of thalattosuchian crocodylomorphs has been an enduring source of confusion and debate. Repeated attempts to revise the clade's taxonomy using various kinds of data have produced inconsistent and sometimes unsatisfactory results. In this context, quantitative analyses of skull shape using geometric morphometrics have much to offer, but most likely do not represent a complete solution on their own. Instead, we argue that difficult taxonomic problems are best solved by integrating multiple lines of evidence, such as morphometrics, discrete-state anatomical characters and patterns of stratigraphic and geographic occurrence, and this is the approach we have attempted to apply in this paper [see Botha and Angielczyk (2007) for another example]. However, this also brings up the issue of what to do in situations where morphometric differences are the best or the only means of differentiating putative species. Thalattosuchians are a border-line case in this regard because some discrete-state differences exist amongst most species, although they are often not as obvious or unambiguous as would be believed. As a result, we have relied heavily on shape differences uncovered during the course of our morphometric analyses to diagnose the species we recognize as valid (see Systematic Palaeontology section below). Although this might make it more difficult to identify specimens in the field or in museum collections without incorporating them into a quantitative analysis, we believe the increase in precision (and hopefully accuracy!) is a reasonable trade-off in at least some cases. Furthermore, this situation parallels the growing recognition by neontologists that sophisticated quantitative techniques are often required to delineate morphologically cryptic species initially identified by genetic data (e.g. Dobigny *et al.* 2002; Baylac *et al.* 2003).

Morphological conservatism and integration

The PCA results show that the most variable aspects of shape in teleosaurid and metriorhynchid skulls are the length and the width of the snout (Text-figs 2, 4, 6, 8). Although this trend in skull proportions is well established (e.g. Westphal 1961, 1962; Adams-Tresman 1987a, b), geometric morphometrics discriminated more variation within the confines of these dimensions than analyses using linear measurements, as well as possible correlations between snout length and other aspects of skull morphology. For instance, PC1 describes not only the length of the snout but also the size of the supratemporal fenestrae and size the frontal bone. Similarly, width of the skull

(PC2) is correlated with length of the nasal bones, size of the orbits and premaxillae and position of the narial opening. Nevertheless, thalattosuchian skulls appear to be morphologically conservative as the majority of shape disparity was captured by only the first two axes of variance.

A similar pattern of morphological conservatism and shape correlation, with respect to the length and the width of the snout, has been observed in modern crocodylians (Pierce *et al.* 2006, 2008; Pierce 2007). This similarity suggests that certain areas of the crocodylian skull may intrinsically be linked and that this integration may have been established early on in crocodylomorph evolution. Studies have shown that a complex relationship exists between morphological integration, phylogenetic relatedness and mechanical function (e.g. Goswami 2006; Marroig and Cheverud 2001). For instance, phylogeny may underpin similar patterns of gross morphological integration, whereas function may result in the assimilation of specific traits related to feeding and foraging strategies. This concept of modules, or semi-autonomous sets of highly correlated traits within larger units, has been applied to diverse biological systems (e.g. Ackermann and Cheverud 2004; Buchholtz 2007; Goswami 2007; Gould and Garwood 1969; Klingenberg and Zaklan 2000; Olson and Miller 1958; Pachut 1992; Sanchez and Lasker 2003; Smith 1997), but patterns of modularity have never been recognized or assessed in the crocodylian skull.

If we qualitatively compare patterns of morphological integration amongst modern crocodylians and thalattosuchians, we see that, in general, length of the snout varies with size of the supratemporal fenestrae and the width of the snout varies with length of the nasal bones (Text-figs 2, 4, 6, 8; Pierce *et al.* 2006, 2008; Pierce 2007). However, the direction of covariation is different. In modern crocodylians, as snout length increases, the supratemporal fenestrae enlarge (Endo *et al.* 2002; Pierce 2007; Pierce *et al.* 2008), and as the snout widens, the nasal bones shorten. In contrast, in thalattosuchians as a whole, as snout length increases, the size of the supratemporal fenestrae decrease, and in metriorhynchids as the snout widens, the nasal bones elongate. The fact that these regions of the skull consistently covary in comparatively distantly related clades of crocodylomorphs suggests that the crocodylian skull may be modularized, and that these modules were likely established early in the clade's evolutionary history. If this is the case, the observed difference in the direction of covariation could imply that the modules can be influenced by specific functional demands imposed on the skull through ecological factors (e.g. adoption of near-shore or off-shore predatory lifestyles) or by the phylogenetic histories of individual clades. Alternatively, the difference could imply that the hypothesized modularity evolved independently in thalattosuchians and extant crocodylians, or that the strength of the integration is weak. Further investigation of these possibili-

ties is clearly merited, but beyond the scope of the present analysis.

Phylogeny: functional implications for noncorrelation?

Plotting a species-level cladogram in morphospace found a general correspondence between phylogeny and morphology for metriorhynchids, with closely related species clustering in similar areas of morphospace (Text-fig. 9). Conversely, teleosaurids display multiple intersections of branches (Text-fig. 5), suggesting that phylogeny does not match morphological clustering well (Stayton 2006). The Mantel tests confirmed that there was a significant correlation between phylogeny and skull shape within the Metriorhynchidae but not in the Teleosauridae. Within the Metriorhynchidae, however, phylogeny accounts for only 20 per cent of the skull shape variation observed within morphospace. Therefore, the results of this study imply that there is a large amount of morphological convergence amongst thalattosuchian skulls, and that factors other than phylogeny may play important roles in determining skull shape.

One such factor that may affect skull shape within thalattosuchians is ecomorphological separation resulting from niche partitioning. For example, in the Middle Jurassic Oxford Clay Formation of Peterborough, England a diverse assemblage of similar sized thalattosuchian species, belonging to the genera *Steneosaurus* and *Metriorhynchus*, coexisted in a narrow seaway (Hudson and Martill 1994; Martill *et al.* 1994). The stability of this crocodile-rich ecosystem almost certainly depended on an intricate partitioning of available resources. It is known that competitive interactions of sympatric populations sometimes lead to morphological differentiation or character displacement (Adams and Rohlf 2000), and Pierce *et al.* (2008) demonstrated that these processes are active amongst extant crocodylians. As with modern crocodylians (Pierce 2007; Pierce *et al.* 2008), character displacement in thalattosuchians is presumably linked to feeding and foraging strategies, as the most obvious difference in head shape is related to rostral dimensions.

Evidence from modern crocodylians shows that slight differences in head shape and trophic morphology can have a dramatic effect on maximum bite force (Erickson *et al.* 2004), size and orientation of adductor musculature (Endo *et al.* 2002) and overall skull strength (Busbey 1995; McHenry *et al.* 2006). In fact, modern crocodylians show a high and significant correlation between peak stress in the snout and skull morphotype, with short-snouted morphologies experiencing far less stress than long-snouted morphologies under equivalent loads (Pierce 2007; Pierce *et al.* 2008). Considering that thalattosuchian skulls display a comparable pattern of shape variation to

modern crocodylians, a similar relationship between skull morphology and skull strength might exist. With this in mind, the distribution of thalattosuchian species in morphospace may be controlled by a similar combination of ecomorphological and functional pressures, and an analysis into this association could prove fruitful (Pierce 2007; Pierce *et al.* 2009).

Division of longirostrine morphospace

Combining all longirostrine fossil 'mesosuchian' crocodylomorphs into one morphospace (Text-figs 10–11) highlighted a significant difference in skull shape between the two thalattosuchian families (i.e. Teleosauridae and Metriorhynchidae), and between thalattosuchians and dyrosaur/pholidosaurids (Table 6). This pattern contrasts with Busbey's (1995) analysis of crocodylomorph rostral morphology, which found significant overlap in rostral shape between teleosaurids, metriorhynchids and dyrosaurids. Based on linear ratios of snout length and snout width, Busbey (1995) recovered two main clusters of longirostrine marine crocodylomorphs in morphospace. The first cluster was defined by teleosaurid and metriorhynchid species with narrow, medium-length snouts, whereas the second cluster was defined by teleosaurid, metriorhynchid, and dyrosaurid species with narrow, long snouts. In addition, there were two outlier species, *Metriorhynchus brachyrhynchus* and *Dakosaurus maximus*, which plotted in the narrow, short snout region of morphospace. However, *M. brachyrhynchus* plotted out as the shortest-snouted species, as opposed to this study, which found *D. maximus* to have a considerably shorter snout than *M. brachyrhynchus* (Text-figs 6, 8). Considering that it was possible to subdivide these clusters more finely in the present analysis, it appears that the consideration of the entire skull shape and the use of a more sensitive measurement technique (i.e. geometric morphometrics) are beneficial when investigating longirostrine crocodylomorph skull morphology.

Analysis of shape disparity within thalattosuchians discovered that metriorhynchids display significantly more morphological disparity than teleosaurids (Tables 7–8). This outcome demonstrates that the metriorhynchid skull design is more morphologically distinct from the mean shape of thalattosuchian morphospace than is the case for teleosaurids. In addition, it was found that short-snouted metriorhynchids and long-snouted teleosaurids exhibit the majority of shape disparity based on snout morphotype, and that long-snouted metriorhynchids and short-snouted teleosaurids have a similar degree of shape disparity (Tables 7–8). Consequently, the generation of morphological diversity in teleosaurids and metriorhynchids occurred in different directions, with teleosaurids

tending to explore the long-snouted region of morphospace and metriorhynchids tending to explore the short-snouted region of morphospace (see Pierce *et al.* 2009 for a functional interpretation of these disparity trends).

Finally, the analysis of thalattosuchian morphospace discovered that *Pelagosaurus typus* plotted with other long-snouted teleosaurids (Text-figs 10–11). This is significant considering the conflict that surrounds the systematic position of this taxon (for full review see Pierce and Benton 2006). Although Westphal (1961, 1962) maintained a teleosaurid classification after analysing the anatomy and the taxonomy of Upper Lias crocodylomorphs, Buffetaut (1980, 1982) argued for a metriorhynchid affinity of *Pelagosaurus* based on its broad nasals, large frontals, lateral orbits, sclerotic rings and a similar arrangement of the prefrontal and lacrimal when compared to the metriorhynchid *Teleidosaurus*. The results of this study, however, show that the skull shape of *Pelagosaurus* corresponds to the teleosaurid condition and is highly divergent from the pattern displayed by *Teleidosaurus*. This is consistent with recent cladistic analyses conducted by Mueller-Töwe (2006), Young (2006), and Gasparini *et al.* (2006), all of whom recovered *Pelagosaurus* as a teleosaurid. Thus, based on the analysis of skull shape and discrete morphological characters, *Pelagosaurus* appears to be a teleosaurid.

Fluctuating sea levels, mass extinctions and temporal patterns

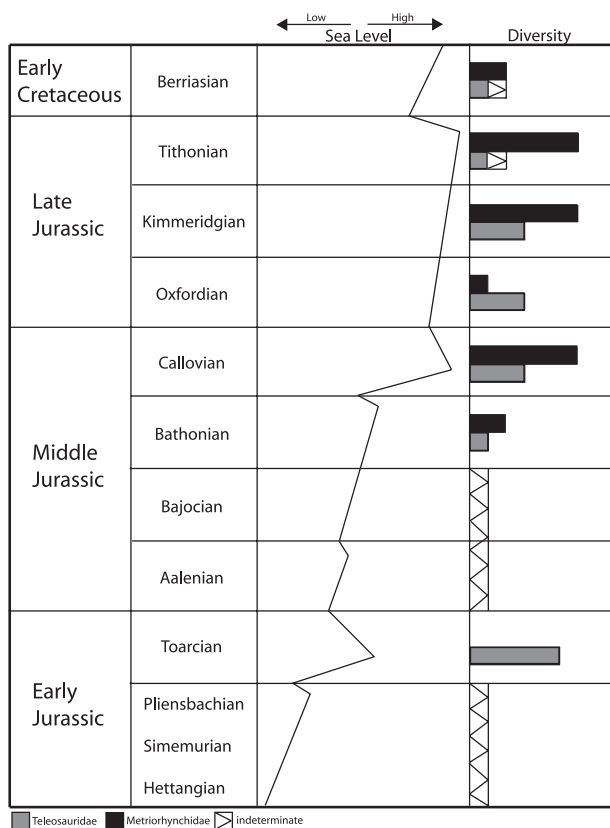
Changes in thalattosuchian diversity and disparity over time closely correspond to fluctuating sea levels and mass extinction events throughout the Jurassic and the Early Cretaceous (Text-fig. 13). Starting in the early Lower Jurassic, the oldest representatives of the Thalattosuchia are only known from fragmentary remains that show few diagnostic features (e.g. Gasparini *et al.* 2000; Godefroit 1994). The lowermost Jurassic, however, is known for its scanty fossil record in general. Bardet (1994) calculated the completeness of the fossil record (SCM) of marine reptiles during the Pliensbachian at 16 per cent. The exact reason for this poor sampling is uncertain, but it could be representative of multiple regression events throughout the Pliensbachian stage (Hallam and Cohen 1989). Therefore, although it can be stated that by the earliest Jurassic thalattosuchians had started to diversify, the extent of this diversification is uncertain ('Lower Jurassic' in Text-fig. 12).

The end Pliensbachian–early Toarcian is marked by a minor extinction event within the marine realm (Text-fig. 13). The boundary between these two stratigraphic stages is characterized by a regressive phase, which resulted in epicontinental habitat loss and heightened marine invertebrate extinction (Hallam and Cohen 1989). How-

ever, this regression was quickly followed by one of the most important Jurassic transgression events, the early Toarcian transgression (Hallam 1981). This extensive sea level rise (Text-fig. 13) provided new epicontinental habitat space for the origination and proliferation of marine invertebrates and vertebrates, with an associated rise in the SCM of marine reptiles to 87 per cent (Bardet 1994). The transgression peaked in the *Harpoceras serpentinum* zone (=former *H. falciferum* zone: Gradstein *et al.* 2004) and the *Hildoceras bifrons* zone, two major ammonite zones of the Toarcian where there is an explosion in teleosaurid diversity (Mueller-Töwe 2006; 'Toarcian' in Text-fig. 12). The more aquatically adapted teleosaurids, *Pelagosaurus typus* and *Steneosaurus bollensis*, became widespread during this time, whereas more 'robust' forms such as *Steneosaurus brevior* and *Platysuchus multicubiculatus* were palaeogeographically restricted. This relationship suggests that the 'robust' forms might have been more reliant on a terrestrial environment (Mueller-Töwe 2006).

Although the Toarcian transgression provided new habitat space, it also brought with it an oceanic anoxic event (OAE) (Jenkyns 1985). The OAE was accompanied by a biological crisis that affected both benthic and pelagic forms (Mueller-Töwe 2006). Continued extinction occurred in the Aalenian and the Bajocian because of sea level fall (Text-fig. 13) and loss of epicontinental habitat. The combined effect of the OAE and a regressive phase ultimately had an effect on the diversity of thalattosuchians during this time. This is evident from the change in morphospace occupation patterns across the Toarcian–Aalenian/Bajocian boundary ('Toarcian–Aalenian/Bajocian' in Text-fig. 12). However, because of the regression, the Aalenian and the Bajocian have an incomplete fossil record, with a calculated SCM for marine reptiles of only 20 and 0 per cent respectively (Bardet 1994). As such, the diversity of thalattosuchians during this time likely would be greater than what is preserved. Nonetheless, there is a distinct gap in the thalattosuchian fossil record during these stages, which results in prominent ghost lineages for these stratigraphic units (Mueller-Töwe 2006).

In spite of this, during the Bajocian we do see the first appearance of metriorhynchids in the fossil record. Both *Teleidosaurus* and *Metriorhynchus* remains have been found, but specific identifications for the specimens are uncertain (Gasparini *et al.* 2000; Hua and Atrops 1995). Whether or not this origination event was stimulated by loss of epicontinental habitat during the regressive phase, or if it corresponds to periodic transgressions throughout the Bajocian (Hallam and Cohen 1989), is unknown. As metriorhynchids are highly derived marine forms that lived in open ocean environments, loss of epicontinental shelf could have promoted the radiation of thalattosuchians from near-shore ancestors to off-shore ocean dwellers. Alternatively, the periodic transgressions would



TEXT-FIG. 13. Relative sea level curve and thalattosuchian diversity (based on species numbers from this study) through the Jurassic and the Early Cretaceous. Sea levels taken from Hallam (1981) and Hallam and Cohen (1989).

have supported the radiation of epicontinental faunas and permitted the development of new predator–prey associations.

In the Bathonian, sea level steadily increased, and with this came both an increase in the SCM of marine reptiles to 40 per cent (Bardet 1994) and the reappearance of well preserved thalattosuchians in the fossil record (Text-fig. 13). However, the ocean environment at this time appears to only support off-shore metriorhynchids and more terrestrially adapted ‘robust’ teleosaurids (‘Bathonian’ in Text-fig. 12). Sea levels continued to rise through the Middle Jurassic and eventually culminated in the most important sea level high stand of the Jurassic (Text-fig. 13), the Callovian transgression (Hallam and Cohen 1989). The Callovian is known for its excellent preservation and an SCM for marine reptiles of 100 per cent (Bardet 1994). In addition, the fossil record shows a strong origination peak for both marine invertebrates and vertebrates during this stage (Bardet 1994; Hallam 1986). As is evident from temporal patterns, thalattosuchian diversity significantly increases during the Callovian, with respect to both teleosaurids, including the more aquatically adapted forms, and metriorhynchids (‘Callovian’ in

Text-fig. 12). This spike may be linked to the availability of extensive epicontinental habitat space and the abundance of available prey items, but it also may stem in part from unusually high rates of preservation for thalattosuchians at the time.

Following the Callovian transgression, sea levels begin to fall again (Text-fig. 13) resulting in a regressive peak at the Callovian/Oxfordian boundary (Hallam 1981) and a significant reduction in the SCM of marine reptiles during the Oxfordian to 42 per cent (Bardet 1994). The restricted epicontinental habitat space during sea level fall could be responsible for the observed decrease in thalattosuchian species numbers and the lack of origination events during the Oxfordian (‘Oxfordian’ in Text-fig. 12). Nonetheless, the majority of the Oxfordian is defined by a slow increase in sea level (Hallam 1981) and, therefore, the apparent decrease in thalattosuchian diversity could also be influenced by collection bias.

The Kimmeridgian and the Tithonian are defined by diversification and good preservational conditions, which resulted in an increase in the SCM for marine reptiles to 77 per cent (Bardet 1994). During the Kimmeridgian sea levels continued to increase (Text-fig. 13), and thalattosuchians (and other marine reptiles; see Bardet 1994) show a strong origination spike that corresponds to the appearance of the genera *Geosaurus* and *Dakosaurus* and the species *Machimosaurus mosae* (‘Kimmeridgian’ in Text-fig. 12). These extreme morphologies continued to diversify throughout the Tithonian (Text-fig. 12 Tithonian), although the genus *Metriorhynchus* becomes extinct. The juxtaposition of radiation and extinction during the Tithonian might be influenced by fluctuating sea levels (Hallam 1981), or it could simply be the result of the long-snouted *Geosaurus* out-competing the long-snouted *Metriorhynchus* for habitat and food sources (which ultimately could have been related to fluctuating sea levels).

Finally, at the Tithonian/Berriasian boundary we see the second minor mass extinction of the Jurassic, the Tithonian extinction (Text-fig. 13). This event, however, was not global. During the end-Tithonian there was a major regression of shallow epicontinental seas in Europe, but at the same time, there was a widespread transgression in South America (Hallam 1986). The localized sea level fall in Europe led to restricted habitat space and high extinction rates, and ultimately culminated in almost a complete loss of thalattosuchians from the European realm. Conversely, marine reptiles in South America at the Tithonian/Berriasian boundary seem to flourish (Spalletti *et al.* 1999), with one of the most morphologically unique metriorhynchid species originating during this time, *Dakosaurus andiniensis* (Gasparini *et al.* 2006; ‘Tithonian and Berriasian’ in Text-fig. 12). Nonetheless, there is a decrease in thalattosuchian diversity in the South American realm, with the loss of most geosaurs in the Berriasian. The

decline of geosaurs at this time might be a consequence of competitive displacement by dakosaurs and other more successful marine reptiles (Spalletti *et al.* 1999).

SYSTEMATIC PALAEOLOGY

Remarks. The following species diagnoses are restricted to cranial anatomical characters and the proposed synonyms are limited to the data set used in the present study. For further information on the history of species synonyms please refer to the literature (e.g. Steel 1973). In addition, the diagnoses are a compilation of characters revealed from this study, examination of specimens (SEP, pers. obs.; see Appendix for specimen numbers), and descriptions from the literature (see Reference material below).

Institutional abbreviations. BHN, Museum d'Historire Naturelle de Boulogne-sur-Mer; BMNH, The Natural History Museum, London; MGHF, Museo Fuenzalida at the Universidad Católica del Norte, Antofagasta, Chile; MHNSR, Museo de Historia Natural de San Rafael, Mendoza, Argentina; MLP, Museo La Plata, Paleontología Vertebrados; MNHM, Museum National d'Histoire Naturelle, Paris; SMNS, Staatliches Museum für Naturkunde, Stuttgart; SMSS, Palaeontologische Sammlung im Museum der Stadt Solothurn; SNSD, Staatliche Naturhistorische Sammlungen Dresden; TMH, Teylers Museum, Haarlem; UANL-FCT, Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico.

Suborder THALATTOSUCHIA Fraas, 1901
Family TELEOSAURIDAE Geoffroy Saint-Hilaire, 1831

Genus MACHIMOSAURUS Meyer, 1837

Type species. *Machimosaurus hugii* Meyer, 1837.

Machimosaurus hugii Meyer, 1837

1967 *Machimosaurus hugii* Meyer; Krebs, p. 46, figs 1–4.

1909 *Steneosaurus durobrivensis* Andrews, p. 124, pl. 6, text-figs 31–35, 37–39, 41–42.

1909 *Steneosaurus obtusidens* Andrews, p. 130, pl. 7, text-fig. 50.

1913 *Steneosaurus hulkei* Andrews, p. 122.

Holotype. SMSS Nr. 96.

Reference material. Andrews (1909, 1913); Krebs (1967); Buffetaut (1982); Adams-Tresman (1987b); Hua *et al.* (1993).

Diagnosis. *Machimosaurus hugii* is a short-snouted teleosaurid characterized by massive skull; short and narrow

rostrum; anteriorly positioned external narial opening; very large, longitudinally expanded supratemporal fenestra; small and subcircular orbits; frontal that terminates just anterior to orbits; irregular pits on frontal and prefrontal; longitudinal grooves of varying lengths on rostrum; contact between the ectopterygoid and anterior two-thirds of the pterygoid; marked posterior concavity of the palatine fenestra on pterygoid; 21–34 teeth on maxilla; 24–31 teeth on mandible; teeth blunt and circular cross-section; tooth enamel ornamented with numerous irregular ridges and weak anteroposterior carina is visible; pit-like sockets on maxilla to receive dentary teeth and symphyseal region 40–44 per cent of length of dentary.

Stratigraphical range. Callovian–Berriasian(?). Upper Jurassic–Lower Cretaceous.

Geographical occurrence. France, Switzerland, Portugal.

Machimosaurus mosae Sauvage and Lienard, 1879

1879 *Machimosaurus mosae* Sauvage and Lienard, p. 1, pl. 1–4.

Neotype. BHN 2R 1100.

Reference material. Hua *et al.* (1993); Hua (1999).

Diagnosis. *Machimosaurus mosae* is a short-snouted teleosaurid that differs from *M. hugii* in having extremely short and broad rostrum; strongly developed pterygoid wings; contact between ectopterygoid and median third of pterygoid; reduced posterior concavity of the palatine fenestra of pterygoid; posterior edge of mandibular symphysis at the same level dorsally as ventrally and c. 17 maxillary and 19 dentary teeth.

Stratigraphical range. Kimmeridgian–Berriasian (?). Upper Jurassic–Lower Cretaceous.

Geographical occurrence. France.

Genus STENEOSAURUS Geoffroy Saint-Hilaire, 1825

Type species. *Steneosaurus megistorhynchus* Geoffroy Saint-Hilaire 1825.

Steneosaurus bollensis (Jaeger, 1828)

1824 *Mystriosaurus bollensis* Cuvier, p. 73, pl. 10–11.

1828 *Crocodylus bollensis* Jaeger, p. 6, figs 1–3.

Holotype. SNSD uncatalogued. Labeled SNSD 1 by Mueller-Töwe (2006).

Reference material. Westphal (1962); Mueller-Töwe (2006); Appendix.

Diagnosis. *Steneosaurus bollensis* is a long-snouted teleosaurid characterized by large, flat skull; long, narrow rostrum that gradually broadens posteriorly; lacrimal and postorbital separated by jugal; small, slit-like antorbital fenestra; small, elliptical orbit; large, longitudinally expanded supratemporal fenestra; ornamentation present on frontal, prefrontals, postorbitals, squamosals and parietal; diastema present between premaxillary and maxillary suture; 24–35 teeth on maxilla; 26–34 teeth on dentary; teeth apically recurved with pointed apex and tooth enamel with very fine vertical striations and a single smooth carina running down posterior edge.

Stratigraphical range. Toarcian (Lias), Lower Jurassic.

Geographical occurrence. England and Germany.

Steneosaurus brevior Blake, 1876

1876 *Steneosaurus brevior* Blake; Tate and Blake 1876, p. 244, pl. 1, figs 1–2.

Holotype. BMNH 1478.

Reference material. Westphal (1961, 1962); Mueller-Töwe (2006).

Diagnosis. *Steneosaurus brevior* is a short-snouted teleosaurid that differs from *S. bollensis* in having large, robust skull; relatively short, broad rostrum; large, rectangular supratemporal fenestrae; small rounded orbits; large mandibular fenestra and large, well-defined antorbital fenestra.

Stratigraphical range. Toarcian (Lias), Lower Jurassic.

Geographical occurrence. England and Germany.

Steneosaurus gracilirostris Westphal, 1961

1961 *Steneosaurus gracilirostris* Westphal, p. 211, fig. 2.

Holotype. BMNH 14792.

Reference material. Westphal (1961, 1962); Mueller-Töwe (2006).

Diagnosis. *Steneosaurus gracilirostris* is a long-snouted teleosaurid that differs from *S. bollensis* in having extremely

elongated, very slender rostrum; large antorbital fenestra; relatively large ellipsoid orbit; small, rounded supratemporal fenestra; canial ornamentation reduced, including a smooth squamosal; small suborbital fenestra; palate forming median ridge accompanied by a paired lateral groove and *c.* 60 teeth on each maxilla and dentary; tooth crowns very slender, conical, pointed, and apically recurved.

Stratigraphical range. Toarcian (Lias), Lower Jurassic.

Geographical occurrence. England.

Steneosaurus heberti Morel De Glasville, 1876

1876 *Steneosaurus heberti* Morel De Glasville, p. 342, pl. 8–9.

1951 *Steneosaurus depressus* Phizackerley, p. 1189, fig. 10.

1951 *Steneosaurus meretrix* Phizackerley, p. 1185, figs 8–9.

Holotype. Unknown catalogue number.

Reference material. Morel De Glasville (1876); Phizackerley (1951); Vignaud (1997).

Diagnosis. *Steneosaurus heberti* is a short-snouted teleosaurid that differs from *S. bollensis* in having relatively short, narrow rostrum; dorsoventrally flattened skull; larger, more longitudinally expanded supratemporal fenestra; large, dorsolaterally oriented orbits; unexpanded premaxilla; preorbital region only slightly wider than rostrum; mandibular symphysis extending almost half the length of mandible; 32–40 teeth on maxilla; 31–36 teeth on mandible and tooth crown slender, conical, striated and generally vertical.

Stratigraphical range. Bathonian–Oxfordian, Middle–Upper Jurassic.

Geographical occurrence. England and France.

Steneosaurus leedsii Andrews, 1909

1871 *Steneosaurus megarhinus* Hulke, p. 442; Vignaud *et al.* 1993, p. 1509, fig. 2.

1909 *Steneosaurus leedsii* Andrews, p. 300, pl. 8, fig. 1.

1913 *Mycterosuchus nasutus* Andrews, p. 136, pl. 8, text-figs 51–54.

Holotype. BMNH R3320.

Reference material. Andrews (1909; 1913); Adam-Tresman (1987b); Vignaud *et al.* (1993); Vignaud (1997); Appendix.

Diagnosis. *Steneosaurus leedsi* is a long-snouted teleosaurid that differs from *S. bollensis* in having greatly elongated, narrow rostrum that is sharply marked off from the cranial region of the skull; rectangular supratemporal fenestra; broad, downwardly deflected premaxilla; long distance between nasal and premaxilla; dorsally and slightly laterally directed orbits; long, posteriorly extended mandibular symphysis; mandible mediolaterally compressed; 28–46 teeth on maxilla; 42–44 teeth on mandible; and teeth slender with sharply pointed crowns and enamel that is sculptured into a series of very fine longitudinal ridges.

Stratigraphical range. Callovian–Kimmeridgian, Middle–Upper Jurassic.

Geographical occurrence. England and France.

Genus PELAGOSAURUS Bronn, 1841

Type species. *Pelagosaurus typus* Bronn, 1841.

Pelagosaurus typus Bronn, 1841

1841 *Pelagosaurus typus* Bronn; Bronn 1841, p. 28, pl. 3, figs 1–6.

Holotype. TMH Nr. 2744.

Reference material. Pierce et al. (2006); Appendix.

Diagnosis. *Pelagosaurus typus* is a long-snouted teleosaurid characterized by long, broad rostrum; small prefrontal and lacrimal visible in dorsal aspect; sagittal crest made up of equal portions of the frontal and parietal; supraorbital constriction on the frontal absent; small, shallow, oval antorbital fenestra present within the lacrimal and maxilla; supratemporal fenestra short anteroposteriorly; paired, large frontal; broad nasals; laterally oriented orbit; sagittal crest broad and sculpted; jugal oriented vertically; anterior margin of internal choanae tapers anteriorly between the paired palatines; presence of a choanal septum on the palatine and pterygoid; sculpturing on almost the entire skull and mandible, with extensive sculpturing on the prefrontal, lacrimal, frontal, parietal, temporal arcade and the posterior extent of the mandible; presence of mandibular fenestrae; 30 piercing teeth on each side of the upper and lower jaws and four premaxillary teeth.

Stratigraphical range. Toarcian (Lias), Lower Jurassic.

Geographical occurrence. England, France, Germany, and Portugal.

Genus PLATYSUCHUS Westphal, 1961

Type species. *Platysuchus multicrobiculatus* (Berckhemer, 1929).

Platysuchus multicrobiculatus (Berckhemer, 1929)

1929 *Mystriosaurus multicrobiculatus* Berckhemer, p. 20, pl. 4.

Holotype. SMNS 9930.

Reference material. Westphal (1961); Mueller-Töwe (2006).

Diagnosis. *Platysuchus multicrobiculatus* is a long-snouted teleosaurid characterized by relatively small skull (45 per cent of trunk length); long, thin rostrum with broadly enlarged premaxilla; sub-circular, dorsally directed orbit; jugal excluded from orbital rim; supratemporal fenestra relatively small and slightly longer than wide; extensive ornamentation on cranial bones including prefrontal, nasal, lacrimal, jugal, postorbital, squamosal, frontal and parietal; *c.* 30–30 maxillary teeth and 37–40 mandibular teeth; and teeth slender, conical, pointed, apically recurved and covered with fine longitudinal striations.

Stratigraphical range. Toarcian (Lias). Lower Jurassic.

Geographical occurrence. Germany.

Family METRIORHYNCHIDAE Fitzinger, 1843

Genus DAKOSAURUS Quenstedt, 1856

Type species. *Dakosaurus maximus* (Plieninger, 1846).

Dakosaurus andiniensis Vignaud and Gasparini, 1996

1996 *Dakosaurus andiniensis* Vignaud and Gasparini, p. 245, pl. 1, figs 1–4.

Holotype. MHNSR PV 344.

Reference material. Vignaud and Gasparini (1996); Gasparini et al. (2006).

Diagnosis. *Dakosaurus andiniensis* is a short-snouted metriorhynchid characterized by robust skull; exceedingly short, high rostrum; dorsal surface of rostrum at same level as skull roof; ‘M’ shaped premaxilla-maxilla contact; anteroposteriorly expanded prefrontal; large, ovoid supratemporal fenestra; deep, elongate antorbital

fenestra; nasal participates in antorbital fenestra; neurovascular foramina aligned obliquely below antorbital fenestra; anterior end of jugal sigmoidal; tooth row composed of 13–14 teeth; and teeth buccolingually compressed with large denticles on mesial and distal margins.

Stratigraphical range. Tithonian–Berriasian, Upper Jurassic–Lower Cretaceous.

Geographical occurrence. Argentina.

Dakosaurus maximus (Plieninger, 1846)

1846 *Geosaurus maximus* Plieninger, p. 150, pl. 3, fig. 2.

Holotype. Unknown catalogue number.

Reference material. Fraas (1902).

Diagnosis. *Dakosaurus maximus* is a short-snouted metriorhynchid that differs from *D. andiniensis* by having shorter, more narrow rostrum; large teardrop-shaped prefrontals; rounded anterior tip of snout; large, round, dorsally positioned narial opening; large, mediolaterally compressed, serrated teeth; 13 maxillary teeth.

Stratigraphical range. Kimmeridgian–Tithonian, Upper Jurassic.

Geographical occurrence. England, France, Germany and Switzerland.

Genus GEOSAURUS Cuvier, 1824

Type species. *Geosaurus giganteus* (Soemmering, 1816).

Geosaurus araucanensis Gasparini and Dellapè, 1976

1976 *Geosaurus araucanensis* Gasparini and Dellapè, p. C3, figs 1–2.

Holotype. MLP 72-IV-7-1.

Reference material. Gasparini and Dellapè (1976); Fernández and Gasparini (2008).

Diagnosis. *Geosaurus araucanensis* is a long-snouted metriorhynchid characterized by long, narrow rostrum; proportionally small skull; large, circular supratemporal fenestra; small infratemporal fenestra; large, laterally oriented orbits with a strongly developed sclerotic ring; dorsally positioned external nares separated completely by a

bony partition; enlarged antorbital fenestra; ‘salt-gland’ situated within prefrontal; smooth cranial surface; small interalveolar space; 27–28 maxillary teeth and 29 mandibular teeth; sharp, smooth teeth.

Stratigraphical range. Tithonian–Berriasian, Upper Jurassic.

Geographical occurrence. Argentina.

Geosaurus gracilis (Meyer, 1831)

1831 *Rhacheosaurus gracilis* Meyer, p. 173, pl. 15, fig. 2.

Holotype. Unknown catalogue number.

Reference material. Fraas (1902); Broili (1932); Frey *et al.* (2002).

Diagnosis. *Geosaurus gracilis* is a long-snouted metriorhynchid that differs from *G. araucanensis* in having extremely elongated, broad rostrum; sharply pointed snout tip; partially separated external narial opening; interorbital space only one-half the occipital width; lateral process of frontal almost perpendicular to medial plane of skull.

Stratigraphical range. Kimmeridgian–Tithonian, Upper Jurassic.

Geographic occurrence. Germany.

Geosaurus suevicus Fraas, 1902

1902 *Geosaurus suevicus* Fraas, p. 41, pl. 5–8.

Holotype. SMNS 9808.

Reference material. Fraas (1902); Buchy *et al.* (2006).

Diagnosis. *Geosaurus suevicus* is a long-snouted metriorhynchid that differs from *G. araucanensis* in having shorter, broader rostrum; oval supratemporal fenestra; anteroposteriorly elongated external narial opening; smooth cranial surface; mandible slightly longer than upper jaw, creating an ‘over-bite’; 23 maxillary teeth and 26 mandibular teeth.

Stratigraphical range. Kimmeridgian–Tithonian, Upper Jurassic.

Geographical occurrence. Switzerland.

Geosaurus vignaudi Frey *et al.*, 2002

2002 *Geosaurus vignaudi* Frey *et al.*, p. 1468, figs 1–3, 6.

Holotype. UANL-FCT-R1.

Reference material. Frey et al. (2002)

Diagnosis. *Geosaurus vignaudi* is a long-snouted metriorhynchid that differs from *G. araucanensis* in having longer, narrower rostrum; shallow supraorbital notch; subcircular supratemporal fenestra; anterior tip of dentary curved ventrally; long interalveolar space on mandible; 15–17 mandibular teeth and teeth subcircular in cross-section, lacking carina and possessing faint longitudinal ridges.

Stratigraphical range. Tithonian, Upper Jurassic.

Geographical occurrence. Mexico.

Genus METRIORHYNCHUS Meyer, 1830

Type species. *Metriorhynchus geoffroyii* Meyer, 1832.

Metriorhynchus acutus Lennier, 1887

1887 *Metriorhynchus acutus* Lennier, p. 84, pl. 20, figs 1–2.

Holotype. Destroyed/lost during the Second War World (complete skull).

Reference material. Lennier (1887).

Diagnosis. *Metriorhynchus acutus* is a long-snouted metriorhynchid characterized by very long, narrow rostrum; premaxilla slightly broader than anterior portion of maxilla; maxilla gradually broadens towards orbits; external nares dorsally positioned; narial opening circular-shaped; supratemporal fenestra square-circular in outline; narrow sagittal crest with posterior portion forming a triangular table with occipital region; 25–26 maxillary teeth and teeth long and thin with fine striations.

Stratigraphic range. Kimmeridgian, Upper Jurassic.

Geographical occurrence. France.

Metriorhynchus brachyrhynchus Deslongchamps, 1867

1867 *Metriorhynchus brachyrhynchus* Deslongchamps, p. 333, pl. 23, fig. 1.

Holotype. Destroyed/lost during the Second World War (complete skull).

Reference material. Deslongchamps (1863–1869); Andrews (1913); Adams-Tresman (1987a); Appendix.

Diagnosis. *Metriorhynchus brachyrhynchus* is a short-snouted metriorhynchid characterized by comparatively short, broad snout; nasal meets or nearly meets premaxilla; small, rounded prefrontals; outer angle of prefrontal almost a right angle; supraorbital notch forms acute angle; ornamentation developed on frontal and extensive on prefrontal; 20–21 teeth on maxilla and teeth stout, moderately compressed, nearly smooth, with posterior carina more marked than anterior carina.

Stratigraphical range. Callovian–Oxfordian, Middle–Upper Jurassic.

Geographical occurrence. England and France.

Metriorhynchus casamiquelai Gasparini and Chong Díaz, 1977

1977 *Metriorhynchus casamiquelai* Gasparini and Chong Díaz, p. 343, figs 3–5.

Holotype. MGHF 1-08573.

Reference material. Gasparini and Chong Díaz (1977); Gasparini et al. (2000).

Diagnosis. *Metriorhynchus casamiquelai* is a short-snouted metriorhynchid that differs from *M. brachyrhynchus* in having slightly narrower skull; distance between nasal and premaxilla proportionally long; no ornamentation on frontal or prefrontal; quadrangular supratemporal fenestra; massive postorbital; frontal very wide between orbits; posterior edge of frontal perpendicular to longitudinal axis of skull; circular orbits; well developed lacrimal and antorbital foramen; internal nares closed posteriorly; long, wide pterygoid fossa and 20–23 dentary teeth.

Stratigraphical range. Callovian, Middle Jurassic.

Geographical occurrence. Chile.

Metriorhynchus durobrivensis (Lydekker, 1890)

1890 *Suchodus durobrivensis* Lydekker, p. 285, figs 2–3.

1913 *Metriorhynchus cultridens* Andrews, p. 196, pl. 11, figs 2–4, text-figs 60–61, 66, 73E.

Holotype. BMNH R1994.

Reference material. Andrews (1913); Adams-Tresman (1987a); Appendix.

Diagnosis. *Metriorhynchus durobrivensis* is a short-snouted metriorhynchid that differs from *M. brachyrhynchus* and *M. casamiquelai* in having shorter rostrum; supraorbital notch ranging from angulated to a more open, continuous curve; narrow intertemporal bar; 16–21 teeth in the premaxilla and maxilla; 12–17 dentary teeth and tooth crowns strongly compressed, long and relatively slender, almost completely smooth and with sharp carinae.

Stratigraphical range. Callovian, Middle Jurassic.

Geographical occurrence. England.

***Metriorhynchus hastifer* (Deslongchamps, 1866)**

1866 *Teleosaurus hastifer* Deslongchamps; Deslongchamps 1867, p. 146, pl. 23, fig. 2, pl. 24, figs 1–5.

Holotype. Destroyed/lost during the Second War World (complete skull).

Reference material. Deslongchamps (1863–1869).

Diagnosis. *Metriorhynchus hastifer* is a long-snouted metriorhynchid that differs from *M. acutus* in having shorter, more narrow rostrum; rostrum width constant, slightly broadening at orbits; shape of supratemporal fenestra verging on a parallelogram; heavily ornamented frontal; pits on maxilla, nasal, and prefrontal; notches present on the dorsal edge of prefrontal; naris positioned on anterior tip of snout, opening dorsally and large, horseshoe-shaped narial opening.

Stratigraphic range. Kimmeridgian, Upper Jurassic.

Geographic occurrence. France.

***Metriorhynchus leedsi* Andrews, 1913**

1913 *Metriorhynchus leedsi* Andrews, p. 195, p. 11, fig. 1; text-fig. 73B.

1913 *Metriorhynchus laeve* Andrews, p. 192, pl. 10; text-figs 65, 69B, 73A.

Holotype. BMNH R3540.

Reference material. Andrews (1913); Adams-Tresman (1987a); Appendix.

Diagnosis. *Metriorhynchus leedsi* is a long-snouted metriorhynchid that differs from *M. acutus* in having relatively

long rostrum that gradually increases in width towards orbits; nasal and premaxilla separated to variable degrees, but never in contact; smooth frontal and prefrontal; prefrontal with small irregular notches around edge; broad intertemporal bar; 30–36 maxillary teeth; tooth crowns sharp, somewhat compressed and pointed with fine discontinuous ridges and carina present on anterior and posterior edge.

Stratigraphical range. Callovian, Middle Jurassic.

Geographical occurrence. England.

***Metriorhynchus superciliosus* (Blainville, 1853)**

1853 *Crocodylus superciliosus* Blainville; Deslongchamps 1867, p. 118, pl. 20.

1868 *Metriorhynchus blainvillei* Deslongchamps, pl. 20.

1869 *Metriorhynchus moreli* Deslongchamps, p. 320, pl. 21, figs 4–5, pl. 22, figs 1–2.

Neotype. MNHN 8903.

Reference material. Deslongchamps (1863–1869); Andrews (1913); Adams-Tresman (1987a); Appendix.

Diagnosis. *Metriorhynchus superciliosus* is a long-snouted metriorhynchid that differs from *M. acutus* (and *M. leedsi*) in having snout convex from side to side; extensive pitting or ornamentation on frontal and prefrontal; narrow intertemporal bar and 25–26 maxillary teeth.

Stratigraphical range. Callovian–Kimmeridgian, Middle–Upper Jurassic.

Geographical occurrence. England and France.

Genus TELEIDOSAURUS Deslongchamps, 1869

Type species. *Teleidosaurus calvadosi* (Deslongchamps, 1866).

***Teleidosaurus calvadosi* (Deslongchamps, 1866)**

1866 *Teleosaurus calvadosi* Deslongchamps, p. 193, pl. 1.

Holotype. BMNH 3353 (cast; original destroyed during Second World War).

Reference material. Buffetaut (1982); Appendix.

Diagnosis. *Teleidosaurus calvadosi* is a short-snouted metriorhynchid characterized by short, narrow rostrum; pre-

frontals less developed than other metriorhynchids and not projecting laterally over orbits; prefrontal does not penetrate narial opening; lacrimal large as compared to prefrontal; lacrimal/nasal suture dorsal and linear (not sigmoidal); orbits more dorsally positioned; external naris on anterior tip of snout; heavily ornamented frontal and supratemporal fenestra ‘tear-drop’ shaped.

Stratigraphic range. Bathonian, Middle Jurassic.

Geographical occurrence. France.

CONCLUSIONS

This study aimed to quantify shape variation and morphospace occupation in thalattosuchian skulls using landmark-based geometric morphometrics in order to delineate species and characterize morphological trends through time. The pattern of morphological diversity in thalattosuchian skulls was found to be more complex than previously thought. The main source of variation is the length and the width of the skull, but a considerable amount of disparity exists within these boundaries and patterns of morphological integration are apparent. For example, length of snout is correlated with size of supratemporal fenestrae and size of frontal bone, whereas width of the skull is correlated with length of the nasal bones, size of the orbits and premaxillae and position of the narial opening. Comparable patterns of shape variation and morphological correlation have been observed in modern crocodylians, although they differ in some details.

Delineating species using geometric morphometric techniques, in combination with discrete-state morphology and the consideration of geographic and stratigraphic range data, proved to be more successful than species diagnoses based primarily on linear measurements. By analysing the full geometry of the skull, this study was able to distinguish eight Callovian species as opposed to Adams-Tresman’s (1987a, b) four. Within the Teleosauridae, *Steneosaurus durobrivensis* (*sensu* Adams-Tresman) was separated into *Machimosaurus hugii* and *Steneosaurus heberti*, whereas *Steneosaurus leedsi* (*sensu* Adams-Tresman) was regarded as valid. Conversely, within the Metriorhynchidae, *Metriorhynchus superciliosus* (*sensu* Adams-Tresman) was separated into *M. superciliosus* and *M. leedsi*, and *M. brachyrhynchus* (*sensu* Adams-Tresman) was separated into *M. brachyrhynchus*, *M. casamiquelai*, and *M. durobrivensis*.

In addition to species delineation, geometric morphometrics provided the necessary tools to explore patterns of disparity within the Thalattosuchia. In terms of overall morphology, metriorhynchids were found to be more

disparate from the average shape of longirostrine morphospace than teleosaurids. However, short-snouted metriorhynchids and long-snouted teleosaurids showed the greatest amount of disparity with respect to snout morphotypes. This suggests that teleosaurids and metriorhynchids tended to explore opposite areas of morphospace. Phylogeny was found to have a moderate influence on the pattern of morphospace occupation in metriorhynchids, but not in teleosaurids. Therefore, other factors such as ecomorphological or functional constraints, likely control the pattern of shape variation in thalattosuchian skulls. A comparison of all longirostrine fossil crocodylomorphs showed that thalattosuchians possess a unique skull morphology, implying that there is more than one way to construct a ‘long snout’. Finally, the temporal distribution of thalattosuchian species and morphotypes show a clear and highly correlated relationship with sea level curves and mass extinction events through the Jurassic and the Early Cretaceous.

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REFERENCES

- ACKERMANN, R. R. and CHEVERUD, J. M. 2004. Morphological integration in primate evolution. 302–319. In PIGLIUCCI, M. and PRESTON, K. (eds). *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford University Press, Oxford, 443 pp.
- ADAMS-TRESMAN, S. M. 1987a. The Callovian (Middle Jurassic) marine crocodile *Metriorhynchus* from central England. *Palaeontology*, **30**, 179–194.
- 1987b. The Callovian (Middle Jurassic) teleosaurid marine crocodiles from central England. *Palaeontology*, **30**, 195–206.
- ADAMS, D. C. and ROHLF, F. J. 2000. Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. *Proceedings of the National Academy of Science*, **97**, 4106–4111.
- ANDREWS, C. W. 1909. On some new steneosaurs from the Oxford Clay of Peterborough. *Annals and Magazine of Natural History*, **3**, 299–308.

- 1913. *A descriptive catalogue of the marine reptiles of the Oxford Clay*, 2. British Museum (Natural History), London, 206 pp.
- ANTUNES, M. T. 1967. Um mesosuquiano do Liásico de Tomar (Portugal). Considerações sobre a origem dos crocodilos. *Mémoria Servicos Géologicos de Portugal*, **13**, 7–66.
- BARDET, N. 1994. Extinction events among Mesozoic marine reptiles. *Historical Biology*, **7**, 313–324.
- BAYLAC, M., VILLEMANT, C. and SIMBOLOTTI, G. 2003. Combining geometric morphometrics with pattern recognition for the investigation of species complexes. *Biological Journal of the Linnean Society*, **80**, 89–98.
- BOOKSTEIN, F. L. 1991. *Morphometric tools for landmark data*. Cambridge University Press, Cambridge, MA, 435 pp.
- BOTHA, J. and ANGIELCZYK, K. D. 2007. An integrative approach to distinguishing the Late Permian dicynodont species *Oudenodon bainii* and *Tropidostoma microtremata* (Therapsida: Anomodontia). *Palaeontology*, **50**, 1175–1209.
- BERCKHEMER, F. 1929. Beitrag zur Kenntnis der Krokodilier des schwäbischen oberen Lias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B*, **64**, 1–60.
- BLAINVILLE, H. M. D. DE 1853. Lettre sur les Crocodiliens vivants et fossiles. *Mémoires de la Société linnéenne de Normandie*, **9**, 109–120.
- BROILI, F. 1932. Weitere Beobachtungen an *Geosaurus*. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **68**, 127–148.
- BRONN, H. G. 1841. Untersuchung zweier Gavial-Skelette und der Gaumen zweier andern aus dem Boller Lias-Schiefern. 5–30. In BRONN, H. G. and KAUP, J. J. (eds). *Abhandlungen über die Gavialartigen Reptilien der Las-Formaton*. Schweizerbart, Stuttgart, 47 pp.
- BUCHHOLTZ, E. A. 2007. Modular evolution of the cetacean vertebral column. *Evolution and Development*, **9**, 278–289.
- BUCHY, M.-C., VIGNAUD, P., FREY, E., STINNESBECK, W. and GONZÁLEZ, A. H. G. 2006. A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of northeastern Mexico. *Comptes Rendus Palevol*, **5**, 785–794.
- BUFFETAUT, E. 1980. Position systématique et phylogénétique du genre *Pelagosaurus* Bronn, 1841 (Crocodylia, Mesosuchia), du Toarcien d'Europe. *Geobios*, **13**, 783–786.
- 1982. Radiation évolutive, paléoécologie et biogéographie des crocodiliens mésosuchiens. *Mémoires de la Société Géologique de France*, **42**, 1–88.
- BUSBY, A. B. 1995. The structural consequences of skull flattening in crocodilians. 173–192. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge, MA, 293 pp.
- CUVIER, G. 1824. Sur les ossements fossiles de Crocodiles, 5. 143–160. In DUFOUR, G. and D'OCAGNE, E. (eds). *Recherches sur les ossements fossiles* (Second édition), Paris. 548 pp.
- DESLONGCHAMPS, E. E. 1863–1869. *Notes Paléontologiques*. Le Blanc-Hardel and Savy, Caen and Paris, 392 pp.
- DOBIGNY, G., BAYLAC, M. and DENYS, C. 2002. Geometric morphometrics, neural networks and diagnosis of sibling *Taterillus* species (Rodentia, Gerbillinae). *Biological Journal of the Linnean Society*, **77**, 319–327.
- ENDO, H., AOKI, R., TARU, H., KIMURA, J., SASAKI, M., YAMAMOTO, M., ARISHIMA, K. and HAYASHI, Y. 2002. Comparative functional morphology of the masticatory apparatus in the long-snouted crocodiles. *Anatomia, Histologia, Embryologia*, **31**, 206–213.
- ERICKSON, G. M., LAPPIN, A. K. and VLIET, K. A. 2004. Comparison of bite-force performance between long-term captive and wild American alligators (*Alligator mississippiensis*). *Journal of Zoology*, **262**, 21–28.
- FERNÁNDEZ, M. and GASPARINI, Z. 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. *Naturwissenschaften*, **95**, 79–84.
- FITZINGER, L. J. F. J. 1843. *Systema Reptilium*. Braumüller and Seidel Eds., Wien, 106 pp.
- FOOTE, M. 1993. Contributions of individual taxa to overall morphological disparity. *Paleobiology*, **19**, 403–419.
- FRAAS, E. 1901. Die Meerkrokodile (Thalattosuchia) eine Sauriergruppe der Juraformation. *Jahreshefte des Vereins für vaterländische Naturkunde Württemberg*, **57**, 409–418.
- 1902. Die Meer-Crocodilier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Palaeontographica*, **49**, 1–71.
- FREY, E., BUCHY, M.-C., STINNESBECK, W. and JOSE GUADALUPE, L.-O. 2002. *Geosaurus vignaudi* n.sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico. *Canadian Journal of Earth Sciences*, **39**, 1467–1483.
- GASPARINI, Z. and DELLAPÉ, D. 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Jurásico, Tithoniano) de la Provincia de Neuquén (República Argentina). *Congreso Geológico (Chileno, Santiago) Actas*, **1**, C1–C21.
- and CHONG DÍAZ, G. 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodyliformes: Thalattosuchia), a marine crocodile from the Jurassic (Callovian) of Chile, South America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **153**, 341–360.
- VIGNAUD, P. and CHONG, G. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: a paleobiogeographic approach. *Bulletin de la Société Géologique de France*, **171**, 657–664.
- CICHOWOLSKI, M. and LAZO, D. G. 2005. First record of *Metriorhynchus* (Reptilia: Crocodyliformes) in the Bathonian (Middle Jurassic) of the Eastern Pacific. *Journal of Paleontology*, **79**, 801–805.
- POL, D. and SPALLETTI, L. A. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous boundary of Patagonia. *Science*, **311**, 70–73.
- GEOFFROY SAINT-HILAIRE, E. 1825. Recherches sur l'organisation des gavailes. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, **12**, 97–155.
- 1831. Recherches sur de grands sauriens trouvés à l'état fossile aux confins maritimes de la Basse-Normandie, attribués d'abord au Crocodile, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*. *Mémoires de l'Académie des sciences*, **12**, 1–138.

- GODEFROIT, P. 1994. Les reptiles marins du Toarcien (Jurassique Inférieur) Belgo-Luxembourgeois. *Mémoires pour servir à l'explication des cartes géologiques et minières de la Belgique*, **39**, 1–98.
- GOSWAMI, A. 2006. Morphological integration in the carnivorous skull. *Evolution*, **60**, 169–183.
- 2007. Cranial modularity and sequence heterochrony in mammals. *Evolution and Development*, **9**, 290–298.
- GOULD, S. J. and GARWOOD, R. A. 1969. Levels of integration in mammalian dentition: an analysis of correlations in the *Nesophontes micrus* (Insectivora) and *Oryzomys couesi* (Rodentia). *Evolution*, **23**, 276–300.
- GRADSTEIN, F., OGG, J. and SMITH, A. 2004. *A geologic time scale 2004*. Cambridge University Press, Cambridge, MA, 589 pp.
- HALLAM, A. 1981. A revised sea-level curve for the early Jurassic. *Journal of the Geological Society*, **138**, 735–743.
- 1986. The Pliensbachian and Tithonian extinction events. *Nature*, **319**, 765–768.
- and COHEN, J. M. 1989. The case for sea-level change as a dominant causal factor in mass extinction of marine invertebrates [and discussion]. *Philosophical Transactions of the Royal Society of London, B*, **325**, 437–455.
- HAMMER, Ø., HARPER, D. A. T. and RAYN, P. D. 2001. PAST: palaeontological statistics software package for education and data analysis. *Palaeontologica Electronica*, **4**, 1–9.
- HUA, S. 1999. Le Crocodylien *Machimosaurus mosae* (Thalattosuchia, Teleosauridae) du Kimmeridgien du Boulonnais (Pas de Calais, France). *Palaeontographica Abteilung*, **252**, 141–170.
- and ATROPS, F. 1995. Un crâne de *Teleidosaurus* cf. *gaudryi* (Crocodylia, Metriorhynchidae) dans le Bajocien supérieur des environs de Castellane (Sud-Est de la France). *Bulletin de la Société Géologique de France*, **166**, 643–648.
- VIGNAUD, P., PENNETIER, E. and PENNETIER, G. 1994. Un squelette de *Steneosaurus obtusidens* Andrews 1909 dans le callovien de Villers-sur-Mer (Calvados, France) et le problème de la définition des Teleosauridae à dents obtuses. *Comptes Rendus de l'Académie des Sciences Paris*, **318**, 1557–1562.
- VASSE, D., BUFFETAUT, E., MARTIN, M., MAZIN, J.-M. and VADET, A. 1993. Un squelette de *Machimosaurus mosae* Sauvage et Lienard, 1879 (Crocodylia, Thalattosuchia) dans le Kimméridgien du Boulonnais. *Comptes Rendus de l'Académie des Sciences Paris*, **317**, 851–856.
- HUDSON, J. D. and MARTILL, D. M. 1994. The Peterborough Member (Callovian, Middle Jurassic) of the Oxford Clay Formation at Peterborough, UK. *Journal of the Geological Society*, **151**, 113–124.
- HULKE, J. W. 1871. Note on a fragment of a teleosaurian snout from Kimmeridge Bay, Dorset. *Quarterly Journal of the Geological Society of London*, **17**, 442–443.
- JAEGER, G. F. 1828. Über die Fossile Reptilien, welche in Württemberg aufgefunden worden sind. Metzler, Stuttgart, 48 pp.
- JENKYN, H. C. 1985. The early Toarcian and Cenomanian-Turonian anoxic events in Europe: comparisons and contrasts. *Geologische Rundschau*, **74**, 505–518.
- JOUVE, S. 2005. A new description of the skull of *Dyrosaurus phosphaticus* (Thomas, 1893) (Mesoeucrocodylia: Dyrosauridae) from the Lower Eocene of North Africa. *Canadian Journal of Earth Sciences*, **42**, 323–337.
- 2009. Redescription of the skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and phylogenetic analysis of Thalattosuchia. *Journal of Vertebrate Paleontology*, **29**, 88–102.
- BOUYA, B. and AMAGHZAZ, M. 2005a. A short-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia) from the Palaeocene of Morocco. *Palaeontology*, **48**, 359–369.
- IAROCHÈNE, M., BOUYA, B. and AMACHZAZ, M. 2005b. A new dyrosaurid crocodyliform from the Palaeocene of Morocco and a phylogenetic analysis of Dyrosauridae. *Acta Palaeontologica Polonica*, **50**, 581–594.
- KLINGENBERG, C. P. and ZAKLAN, S. D. 2000. Morphological integration between developmental compartments in the *Drosophila* wing. *Evolution*, **54**, 1273–1285.
- KREBS, B. 1967. Der Jura-Krokodilier *Machimosaurus* H. v. Meyer. *Paläontologische Zeitschrift*, **41**, 46–59.
- 1968. Le crocodylien *Machimosaurus*. *Memorias Servicos de Geologia Portugal*, **14**, 1–53.
- LENNIER, G. 1887. Description des fossiles du cap de la Hève. *Bulletin de la Société Géologique de Normandie, Le Havre*, **12**, 17–98.
- LYDEKKER, R. 1890. On a crocodylian jaw from the Oxford Clay of Peterborough. *Quarterly Journal of the Geological Society, London*, **46**, 284–288.
- MADDISON, W. P. and MADDISON, D. R. 2006. Mesquite: a modular system for evolutionary analysis: <http://mesquiteproject.org/mesquite/mesquite.html>
- MANTEL, N. A. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–222.
- MARROIG, G. and CHEVERUD, J. M. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of New World monkeys. *Evolution*, **55**, 2576–2600.
- MARTILL, D. M., TAYLOR, M. A. and DUFF, K. L. 1994. The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK. *Journal of the Geological Society*, **151**, 173–194.
- MATEER, N. J. 1974. Three Mesozoic crocodiles in the collections of the Palaeontological Museum, Uppsala. *Bulletin of the Geological Institutions of the University of Uppsala*, **4**, 53–72.
- McHENRY, C. R., CLAUSEN, P. D., DANIEL, W. J. T., MEERS, M. B. and PENDHARKAR, A. 2006. Biomechanics of the rostrum in crocodylians: a comparative analysis using finite element modeling. *Anatomical Record*, **288A**, 827–849.
- MEYER, H. VON 1830. Achte Versammlung der Naturforscher und Aerzte zu Heidelberg im September 1829. *Isis von Oken*, **1830**, 517–519.
- 1831. IV Neue Fossile Reptilien, aus der Ordnung der Saurier. *Nova Acta Academiae Leopoldino-Carolinae, Curios*, **15**, 173–184

- 1832. *Paleologica zur Geschichte der Erde*. Frankfurt am Main, 560 pp.
- 1837. Mitteilungen, an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, **4**, 413–418.
- MOREL DE GLASVILLE, M. 1876. Sur la cavité crânienne et la position du trou optique dans le *Steneosaurus herberti*. *Bulletin de la société géologiques de France*, **3**, 342–348.
- MUELLER-TÖWE, I. J. 2006. *Anatomy, phylogeny, and palaeoecology of the basal thalattosuchians (Mesoeucrocodylia) from the Liassic of Central Europe*. Unpublished PhD thesis, Universität Mainz, 422 pp.
- MÜNSTER, G. V. 1843. Über süddeutsche Lias-Reptilien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1843**, 127–136.
- O'HIGGINS, P. and JONES, N. 2006. Tools for statistical shape analysis. Hull York Medical School: <http://www.york.ac.uk/res/fme/resources/software.htm>
- O'KEEFE, F. R. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Paleobiology*, **28**, 101–112.
- OLSON, E. C. and MILLER, R. L. 1958. *Morphological integration*. University of Chicago Press, Chicago, IL, 376 pp.
- PACHUT, J. F. 1992. Morphological integration and covariance during astogeny of an Ordovician trepostome bryozoan from communities of different diversities. *Journal of Paleontology*, **66**, 750–757.
- PHIZACKERLEY, P. H. 1951. A revision of the Teleosauridae in the Oxford University Museum, and the British Museum (Natural History). *Annals and Magazine of Natural History*, **4**, 1169–1192.
- PLIENINGER, T. 1846. Ueber ein neues Sauriergenus und die Einreihung der Saurier mit flachen, schneidenden Zähnen in eine Familie. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **2**, 148–154.
- PIERCE, S. E. 2007. Morphospace occupation and mechanical performance in extant and extinct crocodile skulls: a combined geometric morphometric and finite element modelling approach. Unpublished PhD thesis, University of Bristol, 283 pp.
- and BENTON, M. J. 2006. *Pelagosaurus typus* Bronn, 1841 (Mesoeucrocodylia, Thalattosuchia) from the upper Lias (Toarcian, Lower Jurassic) of Somerset, England. *Journal of Vertebrate Paleontology*, **26**, 621–635.
- RAYFIELD, E. J. and ANGIELCZYK, K. D. 2006. Morphospace occupation in extant and extinct crocodiles. *Journal of Vertebrate Paleontology*, **26** (Suppl. 3), 110A.
- ANGIELCZYK, K. D. and RAYFIELD, E. J. 2008. Patterns of morphospace occupation and mechanical performance in extant crocodylian skulls: a combined geometric morphometric and finite element modeling approach. *Journal of Morphology*, **269**, 840–864.
- — 2009. Shape and mechanics in thalattosuchian (Crocodylomorpha) skulls: implications for feeding behaviour and niche partitioning. *Journal of Anatomy*, doi: 10.1111/j.1469-7580.2009.01137.x.
- QUENSTEDT, F. A. 1856. *Der Jura*. H. Laupp Verlag, Tübingen, 567 pp.
- ROHLF, F. J. 1990. Rotational fit (Procrustes) method. 227–236. In ROHLF, F. J. and BOOKSTEIN, F. R. (eds). *Proceedings of the Michigan morphometrics workshop*. University of Michigan Museum of Zoology Special Publication, MI, USA, 380 pp.
- 2003a. TpsSmall 1.20. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- 2003b. TpsRegr 1.28. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- 2005. TpsDig 2.04. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- SANCHEZ, J. A. and LASKER, H. R. 2003. Patterns of morphological integration in marine modular organisms: supra-module organization in branching octocoral colonies. *Proceedings of the Royal Society of London B*, **270**, 2039–2044.
- SAUVAGE, H. E. and LIENARD, F. 1879. Mémoire sur le genre *Machimosaurus*. *Mémoires de la Société géologique de France*, **3**, 1–31.
- SERENO, P. C., LARSSON, H. C. E., SIDOR, C. A. and GADO, B. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, **294**, 1516–1519.
- SHEETS, H. D. 2000. TwoGroup 6h: <http://www2.canisius.edu/~sheets/morphsoft.html>
- 2001a. BigFix6: <http://www2.canisius.edu/~sheets/morphsoft.html>
- 2001b. CoordGen 6f: <http://www2.canisius.edu/~sheets/morphsoft.html>
- 2003a. TBox 6: <http://www2.canisius.edu/~sheets/morphsoft.html>
- 2003b. Regress 6K: <http://www2.canisius.edu/~sheets/morphsoft.html>
- 2006. DisparityBox 6i: <http://www2.canisius.edu/~sheets/morphsoft.html>
- SMITH, K. K. 1997. Comparative patterns of craniofacial development in eutherian and metatherian mammals. *Evolution*, **51**, 1663–1678.
- SOEMMERING, S. T. 1816. Über den *Crocodylus priscus* oder über ein in Baiern versteint gefundenes Krokodil, Gavial der Vorwelt. *Denkschriften der Königlichen Akademie der Wissenschaften zu München*, **5**, 9–82.
- SPALLETTI, L. A., GASPARINI, Z., VEIGA, G., SCHWARZ, E., FERNÁNDEZ, M. and MATHEOS, S. 1999. Facies anóxicas, procesos deposicionales y herpetofauna de la rampa marina titoniano-berriasiana en la Cuenca Neuquina (Yesera del Tromen), Neuquén, Argentina. *Revista Geológica de Chile*, **26**, 109–123.
- STAYTON, T. C. 2005. Morphological evolution of the lizard skull: a geometric morphometric survey. *Journal of Morphology*, **263**, 47–59.
- 2006. Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution*, **60**, 824–841.
- STEEL, R. 1973. Crocodylia. In KUHN, O. (ed.). *Encyclopedia of palaeoherpetology*. Teil 16. Gustav Fischer Verlag, Stuttgart, 116 pp.
- STORRS, G. W. and EFIMOV, M. B. 2000. Mesozoic crocodyliformes of north-central Eurasia. 402–419. In BENTON,

- M., SHISHKIN, M. A., UNWIN, D. M. and KUROCHKIN, E. N. (eds). *The age of dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, MA, 736 pp.
- TATE, R. and BLAKE, J. F. 1876. *The Yorkshire Lias*. Van Voorst, London, 474 pp.
- VIGNAUD, P. 1995. Les Thalattosuchia, crocodiles marins du Mésozoïque: Systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. Unpublished PhD thesis, Université de Poitiers, 410 pp.
- 1997. La morphologie dentaire des Thalattosuchia (Crocodylia, Mesosuchia). *Palaeovertebrata*, **26**, 35–59.
- and GASPARINI, Z. B. 1996. New Dakosaurus (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences, Paris*, **332**, 245–250.
- LANGE-BADRE, B., HANTZPERGUE, P., DUTRIEUX, M. and MAURY, G. 1993. Découverte d'un crâne de Teleosauridae dans la Zone à *Eudoxus* du Kimméridgien supérieur quercynois (France). *Comptes Rendus de l'Académie des Sciences, Paris*, **317**, 1509–1514.
- WAGNER, A. 1850. Die fossilen Überreste gacialartiger Saurier aus der Liasformation in der k. paläontologischen Sammlung zu München. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse*, **5**, 511–606.
- WALKDEN, G. M., FRASER, N. C. and MUIR, J. 1987. A new specimen of *Steneosaurus* (Mesosuchia, Crocodylia) from the Toarcian of the Yorkshire Coast. *Proceedings of the Yorkshire Geological Society*, **46**, 279–287.
- WENZ, S. 1968. Contribution à l'étude du genre *Metriorhynchus* Crâne et moulage endocrânien de *Metriorhynchus superciliosus*. *Annales de Paléontologie (Vertébrés)*, **54**, 149–183.
- WESTPHAL, F. 1961. Zur systematik der deutschen und englischen lias-krokodilier. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **113**, 207–218.
- 1962. Die Krokodilen des deutschen und englischen oberen Lias. *Paleontographica A*, **118**, 1–96.
- WU, X.-C., RUSSEL, A. P. and CUMBA, S. L. 2001. *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *Journal of Vertebrate Paleontology*, **21**, 492–514.
- YOUNG, M. T. 2006. Evolution and taxonomic revision of the Mesozoic marine crocodyliforms Metriorhynchidae, a phylogenetic and morphometric approach. Unpublished MSc thesis, University of London and Imperial College, 140 pp.
- ZELDITCH, M. L., SHEETS, H. D. and FINK, W. L. 2003. The ontogenetic dynamics of shape disparity. *Paleobiology*, **29**, 139–156.
- SWIDERSKI, D. L., SHEETS, H. D. and FINK, W. L. 2004. *Geometric morphometrics for biologists: a primer*. Elsevier Academic Press, San Diego, CA, 443 pp.

APPENDIX

List of all specimens used in the geometric morphometric analysis.

Institutional abbreviations. BMNH, The Natural History Museum, London; BRLSI, Bath Royal Literary and Scientific Institute, Bath; MNHM, Museum National d'Histoire Naturelle, Paris; OUM, Oxford University Museum, Oxford; SM, Sedgwick Museum, Cambridge; YORYM, York Museum, York.

Taxon	Stage	Specimen Number	Reference
Teleosauridae			
<i>Machimosaurus</i>			
<i>M. hugii</i>	Oxfordian–Berriasian (?)	Reconstruction	Krebs (1967)
<i>M. mosae</i>	Kimmeridgian–Berriasian (?)	Drawing	Hua (1999)
<i>Mycterosuchus</i>			
<i>M. nasutus</i>	Callovian	Photograph of R2617	BMNH
<i>Mystriosaurus</i>			
<i>M. bollensis</i>	Toarcian	Photograph of 409–415	Antunes (1967)
<i>M. bollensis</i>	Toarcian	photograph of R3937	BMNH
<i>Pelagosaurus</i>			
<i>P. typus</i>	Toarcian	Photograph of M1412	BRLSI
<i>P. typus</i>	Toarcian	Photograph of M1413	BRLSI
<i>P. typus</i>	Toarcian	Photograph of M1418	BRLSI
<i>P. typus</i>	Toarcian	Photograph of 1883–914	MNHN
<i>Steneosaurus</i>			
<i>S. bollensis</i>	Toarcian	Photograph of R161	Mateer (1974)
<i>S. bollensis</i>	Toarcian	Photograph of J47094	SM

Appendix *Continued*

Taxon	Stage	Specimen Number	Reference
<i>S. bollensis</i>	Toarcian	Reconstruction of adult	Mueller-Töwe (2006)
<i>S. bollensis</i>	Toarcian	Reconstruction of juvenile	Mueller-Töwe (2006)
<i>S. brevior</i>	Toarcian	Reconstruction	Mueller-Töwe (2006)
<i>S. depressus</i>	Callovian	Photograph of J1420	OUM
<i>S. durobrivensis</i>	Callovian	Photograph of R2865	BMNH
<i>S. durobrivensis</i>	Callovian	Photograph of R3701	BMNH
<i>S. gracilirostris</i>	Toarcian	Reconstruction	Mueller-Töwe (2006)
<i>S. heberti</i>	Callovian–Oxfordian	Reconstruction	Morel De Glasville (1876)
<i>S. hulkei</i>	Callovian	Photograph of R2074	BMNH
<i>S. leedsi</i>	Callovian	Photograph of R3320	BMNH
<i>S. megarhinus</i>	Oxfordian–Kimmeridgian	Reconstruction	Vignaud <i>et al.</i> (1993)
<i>S. meretrix</i>	Bathonian	Photograph of J29850	OUM
<i>S. meretrix</i>	Bathonian	Photograph of J29851	OUM
<i>S. obtusidens</i>	Callovian	Photograph of R3168	BMNH
Platysuchus			
<i>P. multicubiculatus</i>	Toarcian	Reconstruction	Mueller-Töwe (2006)
Teleosaurid			
Teleosaurid	Toarcian	Photograph (no specimen # available)	BMNH
Teleosaurid	Toarcian?	Photograph (no specimen # available)	BRLSI
Teleosaurid	Toarcian	Photograph of J4709	SM
Teleosaurid	Toarcian	Photograph (no specimen # available)	YORYM-1
Teleosaurid	Toarcian	Photograph (no specimen # available)	YORYM-2
Metriorhynchidae			
Dakosaurus			
<i>D. andiniensis</i>	Tithonian–Berriasian	Reconstruction	Gasparini <i>et al.</i> (2006)
<i>D. maximus</i>	Kimmeridgian–Tithonian	Drawing of holotype	Fraas (1902)
GEOSAURUS			
<i>G. araucanensis</i>	Tithonian–Berriasian	Photograph of holotype	Gasparini and Dellapé (1976)
<i>G. gracilis</i>	Kimmeridgian–Tithonian	Drawing	Broili (1932)
<i>G. suevicus</i>	Kimmeridgian–Tithonian	Drawing of holotype	Fraas (1902)
<i>G. vignaudi</i>	Tithonian	Reconstruction of holotype	Frey <i>et al.</i> (2002)
Metriorhynchus			
<i>M. acutus</i>	Kimmeridgian	Drawing of holotype	Lennier (1887)
<i>M. blainvillei</i>	Oxfordian	Drawing of holotype	Deslongchamps (1869)
<i>M. brachyrhynchus</i>	Bathonian–Callovian	Photograph of R3699	BMNH
<i>M. brachyrhynchus</i>	Bathonian–Callovian	Photograph of R3700	BMNH
<i>M. casamiquelai</i>	Callovian	Photograph of holotype	Gasparini and Chong Díaz (1977)
<i>M. cultridens</i>	Callovian	Photograph of R3804	BMNH
<i>M. durobrivensis</i>	Callovian	Photograph of R2618	BMNH
<i>M. durobrivensis</i>	Callovian	Photograph of R4763	BMNH
<i>M. hastifer</i>	Kimmeridgian	Drawing of holotype	Deslongchamps (1863–1869)
<i>M. laeve</i>	Callovian	Photograph of R2031	BMNH
<i>M. laeve</i>	Callovian	Photograph of R2042	BMNH
<i>M. laeve</i>	Callovian	Photograph of R3015	BMNH
<i>M. leedsi</i>	Callovian	Photograph of R3540	BMNH
<i>M. leedsi</i>	Callovian	Photograph of R3899	BMNH
<i>M. moreli</i>	Callovian	Photograph of R2044	BMNH
<i>M. moreli</i>	Callovian	Photograph of R2054	BMNH
<i>M. moreli</i>	Callovian	Photograph of R6860	BMNH
<i>M. moreli</i>	Callovian	Drawing of holotype	Deslongchamps (1863–1869)
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of 19.96.G21.2	NMW
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2041	BMNH

Appendix Continued

Taxon	Stage	Specimen Number	Reference
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2051	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2053	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2055	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2058	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R2067	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R6859	BMNH
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R.165	Mateer (1974)
<i>M. superciliosus</i>	Callovian–Kimmeridgian	Photograph of R.170	Mateer (1974)
Teleidosaurus			
<i>T. calvadosi</i>	Bathonian	Drawing of holotype	Deslongchamps (1866)
Dyrosaurid/Pholidosaurids			
Arambourgisuchus			
<i>A. khouribgaensis</i>	Palaeocene	Reconstruction	Jouve <i>et al.</i> (2005a)
Chenaniisuchus			
<i>C. lateroculi</i>	Palaeocene	Reconstruction	Jouve <i>et al.</i> (2005b)
Dyrosaurus			
<i>D. phosphaticus</i>	Eocene	Reconstruction	Jouve (2005)
Sarcosuchus			
<i>S. imperator</i>	Aptian–Albian	Drawing	Sereno <i>et al.</i> (2001)
Terminonaris			
<i>T. robusta</i>	Turonian	Drawing	Wu <i>et al.</i> (2001)