Evidence for prey preference partitioning in the middle Eocene high-diversity crocodylian assemblage of the Geiseltal-Fossillagerstätte, Germany utilizing skull shape analysis

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Abstract – The Geiseltal fossil collection from southern Sachsen-Anhalt Germany contains remarkably well-preserved fossils of middle Eocene age. These include several crocodylian skulls, representing at least four different genera with a fifth genus represented by two mandibular rami. As sites with this many crocodylian genera are unknown in modern ecosystems, it has been hypothesized that these crocodylians may have differences in habit as compared to living crocodylians. In order to test similarities between the Geiseltal crocodylians and extant species, an analysis was conducted using geometric morphometrics to quantify shape in crocodylian skulls of all living species ($n = 218$) and all well-preserved crocodylian skulls of the Geiseltal fauna ($n = 28$). A relative warps analysis was used to quantify and compare skull shape, revealing *Allognathosuchus* and *Boverisuchus* to be very distinct from each other as well as from *Asiatosuchus* and *Diplocynodon*. Overlap in shape alone exists between some *Diplocynodon* and some *Asiatosuchus*, but there was significant difference in adult size. When compared with extant crocodylians, three Geiseltal genera occupied distinctly non-modern morphospace in the first two relative warps axes. Comparison of the diets of living crocodylians with similarly shaped skulls was used to reconstruct the prey preferences of the Geiseltal crocodylians, revealing differences in specialization. During the middle Eocene high global temperatures, partitioning of prey preference may have allowed this group to attain its higher than usual diversity, reducing the amount of direct competition.

Keywords: geometric morphometrics, specialization, Crocodylia, *Boverisuchus*, Eocene.

1. Introduction

The Geisel Valley of central Germany (Fig. 1) is infilled with fossil-bearing coal layers of mostly middle Eocene age. These fossils have been exquisitely preserved, including many different animals from this extinct ecosystem such as fossil beetles still containing iridescent epicuticular interference reflectors (Krumbiegel, Rüffle & Haubold, 1983). The local climate at this time was very warm, and the presence of fossil crocodylians at the nearby Messel fossil locality led to a crocodylian-derived temperature estimate of 20 °C (Berg, 1964). A more recent study based on palaeobotanical evidence estimated a mean annual temperature of 22.9–25 °C for the Geiseltal fossil locality (Mosbrugger, Utescher & Dilcher, 2005). These values are both higher than the mean annual temperature estimate derived from fossil teeth and bones of the nearby Messel-Fossillagerstätte of similar age, *c.* 18 ± 2.5 °C (Tütken, 2014). However, the estimates are similar to lake surface water temperature of Messel estimated at *c.* 25 ± 3 °C (Tütken, 2014). Crocodylians were not only present at Geiseltal, but abundant. No less than five genera are recognized: *Diplocynodon*, *Asiatosuchus*, *Boverisuchus*

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(until recently called *Pristichampsus*; Brochu, 2013), *Allognathosuchus*, and *Bergisuchus* (Berg, 1966; Rauhe & Rossmann, 1995; Hellmund, 2007). All but *Bergisuchus* have well-preserved skulls within the impressive Geiseltal collection (Geiseltalsammlung), housed at Martin-Luther-Universität, Halle-Wittenberg in Halle (Saale), Germany.

Modern crocodylians typically have a single genus in a given area. Overlap between two genera is not uncommon, particularly with the globally widespread genus *Crocodylus* (Ross, 1989). The greatest amount of potential overlap between living genera of crocodylians is four. However, this is only reconstructed from geographic ranges and no observations of four genera in a single modern area have been published. This potential is between three different caimanine genera (*Caiman*, *Melanosuchus* and *Paleosuchus*) and potential overlap with the Orinoco Crocodile (*Crocodylus intermedius*; Ross, 1989). Crocodylian species within a given area are known to spatially separate, as observed in neighbouring populations of caimanines in the Amazon, living in different bodies of water within the forested environment (Magnusson, Vieira da Silva & Lima, 1987). Spatial separation has been hypothesized for large-bodied predatory non-avian theropod dinosaurs as explaining occurrence of multiple species

Figure 1. (Colour online) Map of Germany with the Geiseltal-Fossillagerstätte marked with a star. Fossils were recovered from the Geisel Valley of southern Sachsen-Anhalt.

in one geological formation (Farlow & Pianka, 2003). However, these fossils were distributed across a much larger area than Geiseltal and one of the large species was notably less common than the other (Farlow & Pianka, 2003). There is also typically a significant size difference between neighbouring crocodylian species, such as the Australian fresh- and saltwater crocodiles that occasionally overlap in territory (*Crocodylus johnstoni* and *C. porosus*, respectively; Webb, Manolis & Sack, 1983). In the case of the Geiseltal crocodylians, however, each was found to co-occur within a very limited geographic area, at times from a single pit located within a single stratigraphic horizon, severely limiting any potential spatial and temporal differences between genera.

In regions with significant overlap in habitat between two genera, it has been proposed that these crocodylians specialize by having different prey preferences (Brochu, 2001; Pearcy, 2011). In the case of Australian varanids, six species are known to co-occur within the Great Victoria Desert and differ in size, method of prey acquisition and microhabitat (Pianka, 1994; Farlow & Pianka, 2003). Sympatric ceratopsian species have exhibited key differences in skull structure, indicating differences in dietary preference (Henderson, 2010). With five crocodylian genera at Geiseltal, specialization may also have occurred between these crocodylians. Given the number of genera, they may even have exceeded the current range of morphospace seen in modern crocodylians.

Crocodylian skull shape has a strong connection to its range of preferred prey (Pierce, Angielczyk & Rayfield, 2008; Sadleir & Makovicky, 2008). A seminal study of skull structure investigated the benefits of different shapes in extant crocodylian skulls for different feeding methods and found 'adaptive measures that strengthened the skull, reflecting different feeding behaviors' (Busbey, 1994). A more recent study utilizing geometric morphometrics and finite element analysis came to the conclusion that '... it appears that ecological specializations, related to feeding and foraging strategies, are major controls on the morphological diversity within extant crocodilian skulls' (Pierce, Angielczyk & Rayfield, 2008). Phylogenetic studies have found similar correlation between function and skull shape in fossil and modern crocodylians (Brochu, 2001). Differences in skull shape between genera of crocodylians can therefore be informative of their prey preference and their role within the ecosystem.

Structural stability is largely controlled by shape: shorter snouts deliver force without incurring a large amount of torsional strain, and narrow snouts deliver greater speed but have greater hydrodynamic drag and less resistance to strain (McHenry *et al.* 2006; Pierce, Angielczyk & Rayfield, 2008; Cuff & Rayfield, 2013). Short-snouted species of living crocodylians are in turn able to take advantage of harder foods such as bivalves, crustaceans, gastropods and testudines (Delany & Abercrombie, 1986; McHenry *et al.* 2006; Borteiro *et al.* 2009). However, their snouts are less adapted for swift prey such as certain forms of fish. Long, narrow-snouted crocodylians, such as the Indian Gharial, *Gavialis gangeticus*, are very well adapted for catching swift, unarmored prey, mostly fish (Piras *et al.* 2010, 2014; Stevenson & Whitaker, 2010), but lack the structural stability to regularly consume hard prey items. Long-snouted crocodylians were found to have adapted different musculature along different evolutionary lines to adduct the jaws, implying the function of primary driver of adaptation (Endo *et al.* 2002). Species with intermediate snouts tend to be generalists, not adapted particularly towards one end of the spectrum or the other (Brochu, 2001). Crocodylians eating much larger prey, such as the Nile Crocodile (*Crocodylus niloticus*), have rather long snouts that are wide and wedge-shaped, well-suited for a very strong bite (McHenry *et al.* 2006). This is particularly useful in an animal incapable of true mastication. All crocodylian skull shapes are capable of delivering comparable levels of force, as measured in extant forms on land (Erickson *et al.* 2012, 2014). The only significant correlation with non-aquatic bite force has been body size, showing that in each skull shape bite force increases with size (Erickson *et al.* 2014).

A study of the relationship between crocodylian morphological disparity and functional performance was conducted by Piras *et al.* (2009) by comparing snout shape and structural stability in the form of beam mechanics. This study focused on differences between the crocodile lineage (Crocodyloidea) and the

alligator lineage (Alligatoroidea). Their results suggested 'that the geometry of skull rostra is tightly linked to performance in prey capture . . . in Crocodyloidea'. The researchers found more of a phylogenetic connection to structure in Alligatoroidea. The team suggested that the 'evolutionary history of the clade Alligatoroidea is marked by its tightness to the ecosystems' and that they are less likely to branch out from their preferred ecological role (Piras *et al*. 2009). Despite these differences in morphological adaptability, the animals still maintain a connection between morphology and mode of predation. This study and a more recent one addressing the issue of modularity within crocodylian skulls (Piras *et al.* 2014) used only recent alligatoroids, and did not include any fossil alligatoroid taxa, which represent potentially greater occupation of morphospace.

Shape can be quantified using geometric morphometrics that utilizes a series of landmarks (Bookstein, 1991; Zelditch, Swiderski & Sheets, 2012). Each landmark represents a point of morphology that can be found in each specimen of the dataset, and can be represented in either two or three dimensions (Bookstein, 1991; Zelditch, Swiderski & Sheets, 2012). One example of a landmark used in crocodylians is the anterior-most extension of the premaxillary suture (Landmark 9 of Piras *et al*. 2009). Following the principle of anatomical homology, digitizing these landmarks creates a simplified digital version of each specimen (Mitteroecker & Gunz, 2009). When many specimens have been digitized in this manner, they form a dataset of specimens that can be analysed together. Procrustes superimposition is the method by which these landmarks are centred, scaled and rotated to a single orientation (Mitteroecker & Gunz, 2009). The differences between the spatial relationships of each specimen's landmarks can be studied by means of a principal components analysis or PCA (Slice, 2007). This kind of analysis isolates different linear combinations of the original dataset that 'most efficiently reproduce sample variability' (Slice, 2007). In a PCA, a consensus configuration is generated from the dataset and deviation from this configuration is summarized as a series of axes, with the first summarizing more variation than any of the following axes (Bookstein, 1991; Mitteroecker & Gunz, 2009; Polly *et al*. 2013). The majority of variation within the dataset is often covered by the first and second axes, but not always (Polly *et al*. 2013). Plotting the PCA axes provides a visual method for evaluating similarities and differences between specimens (Polly *et al*. 2013).

This study focuses on the application of geometric morphometrics to fossil and modern crocodylians in order to address the question of prey partitioning within a high-crocodylian-diversity site. Geometric morphometric methods have been applied to other crocodylian groups in order to address other questions regarding evolution, ecology and taxonomy (e.g. Pierce, Angielczyk & Rayfield, 2008; J. Martin, unpub. Ph.D. thesis, Univ. Lyon, 2009; Piras *et al*. 2009, 2010, 2014; Young

et al. 2010). Similar methods were applied to the extinct crocodylomorphs, the thalattosuchians, in order to assess factors affecting morphological variation (Pierce, Angielczyk & Rayfield, 2008, 2009; Young *et al*. 2010; Young, Bell & Brusatte, 2011a; Wilberg, 2015). These studies found correlation between dietary preference and skull structure in thalattosuchians (Pierce, Angielczyk & Rayfield, 2009; Young *et al*. 2010; Young, Bell & Brusatte, 2011a). Other recent studies of thalattosuchians specifically addressed the coexistence of two related taxa and found adaptations for specialization towards different preferred prey (Young *et al*. 2012; Buchy, Young & de Andrade, 2013). A recent study showed some degree of cranial separation between sympatric crocodylian taxa using traditional morphometrics from a Miocene site in Peru (Salas-Gismondi *et al*. 2015).

Geiseltal is not the only site which has recovered high crocodylian diversity. A middle Miocene site in Peru and a late Miocene site in Venezuela have both recovered a high diversity, reaching up to seven sympatric species within six genera (Scheyer *et al*. 2013; Salas-Gismondi *et al*. 2015). However, the number of well-preserved crocodylian specimens is greater at the Geiseltal site than the number of well-figured specimens from either of the other sites. Although the Geiseltal crocodylian taxa also appear at the nearby Messel fossil site (Keller & Schaal, 1988; Morlo *et al.* 2004), we have included only material from Geiseltal since the main focus of the study is where these crocodylians would have lived together. As a result, all fossils were chosen only from the Geiseltal brown-coal (lignite) deposit. As species-level diversity in crocodylians typically involves subtle morphologic differences, we instead focus on the taxonomic level of genera for this study where differences in skull shape are greater between taxa.

2. Materials and methods

2.a. Crocodylian skulls

A total of 28 skulls representing four of the five crocodylian genera of Geiseltal were included in the analysis (see examples of each in Fig. 2). As *Bergisuchus* from Geiseltal only has mandibular rami preserved (Rauhe & Rossmann, 1995; Rossmann, Rauhe & Ortega, 2000), it could not be included in the present analysis. Even the holotype of this taxon from Messel only includes a single mandibular ramus and a partial rostrum (Rauhe & Rossmann, 1995; Rossmann, Rauhe & Ortega, 2000). Some taxa were better represented than others at Geiseltal, and as a result this dataset includes: 14 *Diplocynodon*; 7 *Asiatosuchus*; 5 *Boverisuchus*; and 2 *Allognathosuchus*. We note here that the *Asiatosuchus* specimens pertain to *A. germanicus*, although recent work has shown this genus is potentially non-monophyletic (Delfino & Smith, 2009). This could lead to a potential revision of the generic name (Delfino & Smith, 2009), but given that this is not the
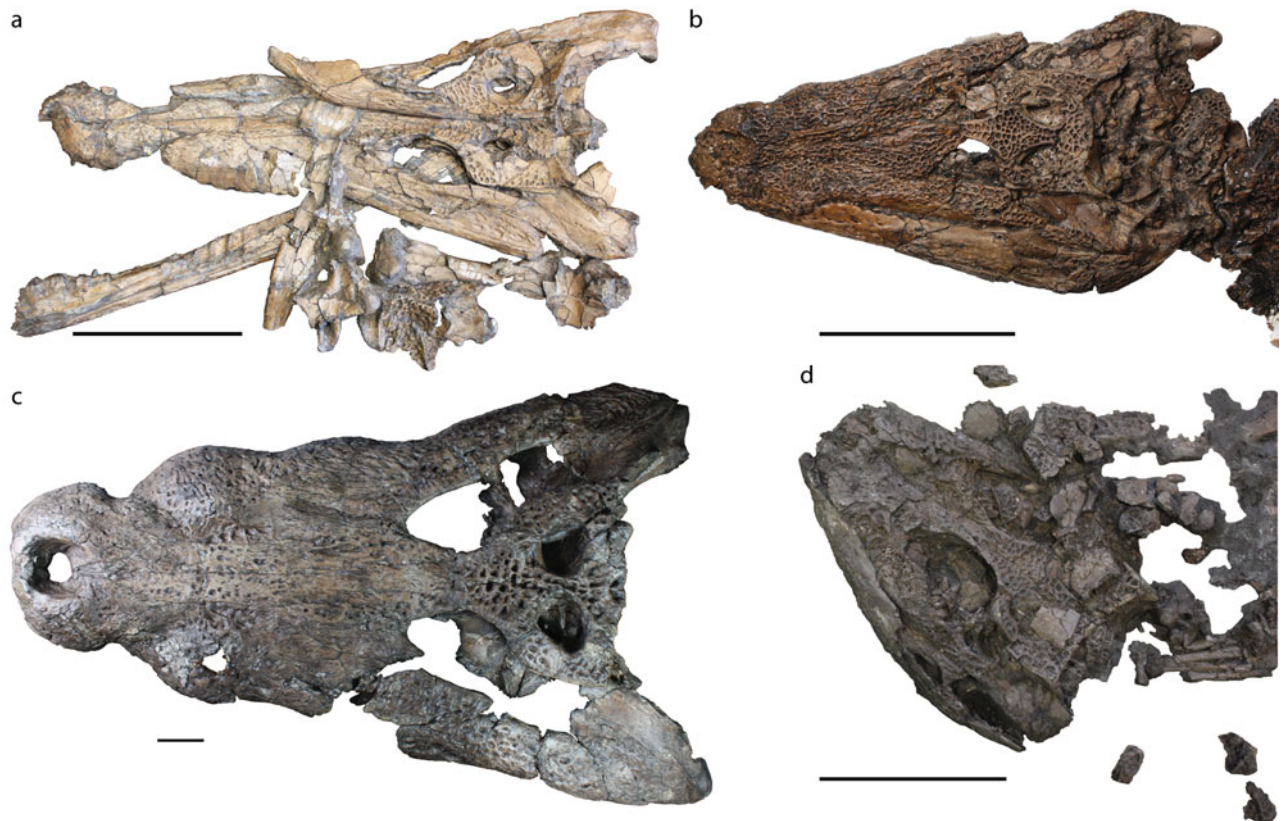
Figure 2. (Colour online) Examples of the skulls of the four fossil crocodylian genera included in the present study, all collected from Geiseltal, Germany. (a) *Boverisuchus*, GMH Ce II-5894-1930; scale bar 10 cm. (b) *Diplocynodon*, GMH Ce III-6075-1933; scale bar 10 cm. (c) *Asiatosuchus*, GMH XIV-420-1953; scale bar 4 cm. (d) *Allognathosuchus*, GMH Ce IV-5900-1932, scale bar 5 cm.

aim of the study, we refer to these specimens as *Asiatosuchus*. The skulls used in this analysis have at least one complete side preserved and are visible in dorsal view, resulting in the necessary exclusion of very-well-preserved material that was prepared in ventral view only. Only skulls of adults were used for this study. Very few well-preserved juveniles were collected from the locality and did not represent a large enough sample size for meaningful addition to the analysis. Furthermore, their morphology is consistently different enough that they would not be expected to place within the same morphospace as the adults. Adult status was determined based primarily on sutural closure of the vertebral column (sensu Brochu, 1996). Fossil specimens with noticeable taphonomic shear affecting both sides of the skull were not included in the analysis. A list of specimens used for the analysis can be found in Table 1.

For extant crocodylia, complete osteological specimens were used from the Florida Museum of Natural History at the University of Florida (UF), the American Museum of Natural History (AMNH), the Herpetological Collections of the Universidad Nacional in Bogotá, Colombia (ICN), the Smithsonian United States Natural History Museum (USNM) and the Carnegie Museum of Natural History (CMNH). Again, only adult specimens were used. This sample represented all living species and individuals from all over the world to achieve a full-picture view of living crocodylians with a total sample size of 218.

Some species are represented better than others. A list of the extant specimens used in the analysis can be found in online supplementary Table S1 (available at http://journals.cambridge.org/geo).

2.b. Photography and landmark assignment

All specimens were photographed in dorsal view with a scale bar. Specimens were oriented so that the tip of the snout was raised up until the skull table was horizontal. For each specimen a camera was mounted directly above the skull, with the focus centred over the nasal-nasal suture as described by Pearcy and Wijtten (2010). By maintaining an appropriate distance between the specimen and the camera lens and by standardizing the method of photography, we endeavoured to minimize the potential effects of parallax. A past study recognized that even when slight parallax has affected a dataset, it affects all specimens very similarly as long as photography is standardized and therefore does not significantly affect the results of the analyses (Mullin & Taylor, 2002).

A total of 35 landmarks (Fig. 3) were used to encompass skull shape following the method of Pierce, Angielczyk & Rayfield (2008). This method focused on one half of the skull in order to take advantage of more of the fossil record. Had the procedure required complete skulls, the sample size would have been much smaller. The left side was

Table 1. List of Geiseltal fossil crocodylian specimens used for geometric morphometric analysis ($n = 28$). Ages are presented as mammal Palaeogene (MP) zones. Skull lengths were measured for this study. Estimated total body lengths (TBL) were calculated for *Allognathosuchus* and *Diplocynodon* using data from *Alligator mississippiensis* (Woodward, White & Linda, 1995; Young *et al.* 2011b). Estimates for *Asiatosuchus* were calculated using data from *Crocodylus porosus* (Sereno *et al.* 2001). Estimates for *Boverisuchus* were generated from this study. Taphonomy is based on compression as either having little to no compression (1) or having notable dorsoventral compression (2). Sheared specimens were not used in this study. GMH – Geiseltalsammlung, Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin-Luther-Universität Halle-Wittenberg, Halle (Saale), Germany.

Genus	Specimen	MP zone	Skull length (cm)	Estimated TBL (m)	Taphonomy
Allognathosuchus	GMH Ce IV-5900-1932	13	9.9	0.62	2
Allognathosuchus	GMH Ce IV-6042-1933	13	12.8	0.80	2
			Average: 11.3	**0.71**	
Boverisuchus	GMH II-10128-1949	11	26.7	1.51	1
Boverisuchus	GMH Ce II-5894-1930	13	30.8	1.74	2
Boverisuchus	GMH LVIII-1-1984	12	21.5	1.21	2
Boverisuchus	GMH XVIII-486-1960	12	22.9	1.29	2
Boverisuchus	GMH XXXVI-274-1962	13	22.7	1.28	1
			Average: 24.9	**1.41**	
Diplocynodon	GMH XXXVIII-9-1964	13	13.9	0.87	1
Diplocynodon	GMH Ce III-6043-1933	13	16.2	1.02	2
Diplocynodon	GMH XXXVIII-68-1964	13	16.1	1.01	1
Diplocynodon	GMH Ce IV-6040-1933	13	13.7	0.86	2
Diplocynodon	GMH Ce II-6073-1930	13	20.5	1.29	2
Diplocynodon	GMH Ce III-6074-1932	13	15.5	0.97	2
Diplocynodon	GMH Leo-3654-1932	13	15.0	0.94	2
Diplocynodon	GMH XXII-571-1965	12	9.3	0.58	2
Diplocynodon	GMH XXII-588-1965	12	9.1	0.57	2
Diplocynodon	GMH XXII-700-1965	12	10.0	0.63	2
Diplocynodon	GMH Ce III-6075-1933	13	14.7	0.92	2
Diplocynodon	GMH XXXVI-304-1963	13	12.4	0.78	1
Diplocynodon	GMH XXXVI-524-1963	13	19.6	1.23	1
Diplocynodon	GMH XXXVII-54-1964	13	17.2	1.08	2
			Average: 14.5	**0.91**	
Asiatosuchus	GMH XIV-420-1953	11	43.2	3.13	1
Asiatosuchus	GMH XIV-4757a-1956	11	42.7	3.09	1
Asiatosuchus	GMH XIV-573-1955	11	39.1	2.82	1
Asiatosuchus	GMH XXII-720-1965	12	34.1	2.43	1
Asiatosuchus	GMH XXXIII-42-1962	13	25.0	1.73	1
Asiatosuchus	GMH XXXV-220-1963	13	34.8	2.48	1
Asiatosuchus	GMH XXXV-477-1963	13	27.7	1.94	1
			Average: 35.2	**2.52**	

arbitrarily chosen for the analysis. In cases where fossils were better preserved on the right side, the images were digitally flipped so that it would not offset the analysis. Images were merged into a TPS file using the program tpsUtil (F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-utility.html). Landmarks were assigned using the program tpsDIG2 (F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-dataacq.html) from in-person comparison of the images to the specimens. Landmarks were chosen from the dorsal cranial surface (mostly on the snout and skull table) in order to minimize potential preservational effects of comparison between fossil and modern taxa. We used landmarks that were consistently applied in both fossil and modern crocodylian studies. The landmarks of this study are either similar or identical to those of other geometric morphometric fossil crocodylomorph studies (J. Martin, unpub. Ph.D. thesis, Univ. Lyon, 2009; Pierce, Angielczyk & Rayfield, 2009; Young *et al.* 2010).

2.c. Analysis

The TPS file from tpsDIG2 was loaded into tpsRelw (F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-tps.html) in order to generate relative warps, a process very similar to principal components analyses or PCA (Rohlf, 1993). The difference between these methods is whether or not a factor (alpha) is used to multiply partial warps before computing principal components, and therefore differentially weighting them in the analysis (Rohlf, 1993; Zelditch, Swiderski & Sheets, 2012). Since alpha in this study was left in the default position of 0, our study is effectively a PCA. Morphospace is represented in these analyses by XY scatter plots of the relative warps axes, referred to as the principal components of a PCA. The morphospace is identified by the relative warps analysis, showing distribution of variation relative to a consensus configuration, placed at the centre of the axes (Rohlf, 1993; F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-tps.html). The program tpsRelw can also generate deformation grids that are determined by calculating the deviation of landmarks from the consensus configuration at a given point in the relative warps (Bookstein, 1991; F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-tps.html). This method is based on the position of landmarks relative to each other, so that specimens group together due to similarity of shape and not similarity of size
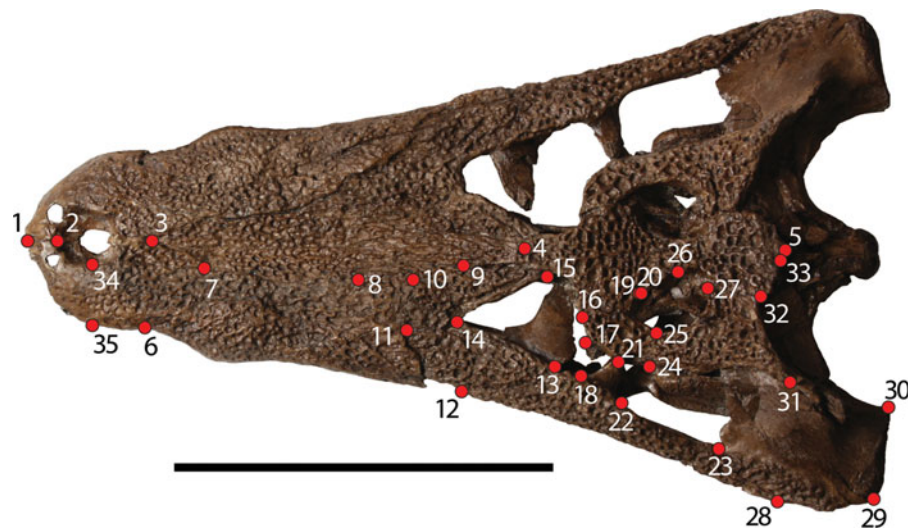
Figure 3. (Colour online) Landmarks used in the current study from Pierce, Angielczyk & Rayfield (2008). Specimen is an adult *Diplocynodon* (GMH XXXVI-524-1963). Scale bar 10 cm. All landmarks are assigned in dorsal view. (1) Anterior-most tip of the premaxillary suture. (2) Anterior point of the narial opening at the premaxillary suture. (3) Anterior-most point of the nasal. (4) Contact of the left and right nasal with the frontal. (5) Posterior-most extent of the supraoccipital, on the midline. (6) Contact of the premaxilla and maxilla along the lateral margin. (7) Contact of the premaxilla, nasal and maxilla. (8) Contact of the nasal, maxilla and prefrontal. (9) Contact of the nasal, frontal and prefrontal. (10) Contact of the maxilla, prefrontal and lacrimal. (11) Contact of the maxilla, lacrimal and jugal. (12) Contact of the maxilla and jugal along the lateral margin. (13) Contact of the jugal and lacrimal along the orbital margin. (14) Contact of the lacrimal and prefrontal along the orbital margin. (15) Contact of the prefrontal and frontal along the orbital margin. (16) Contact of the frontal and postorbital along the orbital margin. (17) Anterodorsal tip of the postorbital bar. (18) Anteroventral tip of the postorbital bar. (19) Contact of the frontal, parietal and postorbital. (20) Contact of the parietal and postorbital along the margin of the supratemporal fenestra. (21) Posterodorsal tip of the postorbital bar. (22) Posteroventral tip of the postorbital bar. (23) Contact of the jugal and quadratojugal along the infratemporal fenestra. (24) Contact of the postorbital, squamosal and quadratojugal. (25) Contact of the postorbital and squamosal along the margin of the supratemporal fenestra. (26) Midpoint of the supratemporal fenestra along the parietal. (27) Contact of the parietal and squamosal along the margin of the supratemporal fenestra. (28) Contact of the jugal and quadratojugal along the lateral skull margin. (29) Contact of the quadratojugal and quadrate along the lateral skull margin. (30) Medial condyle of the quadrate. (31) Posterolateral tip of the dorsal extension of the squamosal on the skull table. (32) Contact of the parietal and squamosal along the posterior margin of the skull table. (33) Lateral contact of the parietal and supraoccipital. (34) Mid-lateral point on the external narial opening. (35) Point on lateral margin of the premaxilla corresponding to Landmark 34, the mid-lateral point on the external narial opening.

(Bookstein, 1991; Rohlf, 1993, Zelditch, Swiderski & Sheets, 2012). By using two-dimensional (2D) methods of landmark assignment, we minimized the spatial difference between landmarks of compressed and uncompressed fossil specimens. This would have been more of a problem had our study used 3D methods of analysis. Dorsoventral compression of some specimens may have moved landmarks from their original location, but the resultant difference in position of landmarks as determined from 2D images is likely very small. Also, the study only used specimens where bones were still in their same relative positions (i.e. quadrate condyle ventral to skull table). In order to determine whether or not the compression of some specimens affected the geometric morphometric data, we conducted additional correlation statistics. Each fossil was assigned a '1' if it had little to no compression or '2' if it had notable compression. We then tested for correlation between these specimens across the entire dataset and within *Diplocynodon* and *Boverisuchus*. There was no variation of taphonomy within *Asiatosuchus* (all uncompressed, $n = 7$) or *Allognathosuchus* (all compressed, $n = 2$).

In order to evaluate relative variation within the dataset, disparity metrics were generated including sum of ranges, product of ranges, sum of variances and product of variances (Tables 2, 3) using Rare 1.2 (Wills, 1998). This program code was run using Chipmunk Basic version 3.6.6b0 (R Nicholson, unpub. program, 2012: http://www.nicholson.com/rhn/basic) and used to rarefy the data with 1000 replicates using bootstrapping, generating 95 % confidence intervals and utilizing all relative warps axes. Variance metrics are best suited for discerning between different forms and are comparatively less sensitive to differences in sample size, but are in turn more sensitive to inconsistent taxonomy (Wills, 1998). Range metrics are more sensitive to sample size, but are better suited for estimating the total extent of morphological differences within a group relative to another (Wills, 1998). Statistical differences in range and variance can be determined by overlap or non-overlap of 95 % confidence intervals.

2.d. Stratigraphic resolution of crocodylians and potential prey

Fossils from Geiseltal were collected over a series of decades and many different researchers have contributed their provenance data over this time (Haubold & Krumbiegel, 1984). In general, ages of the fossils

Table 2. Disparity metrics for the Geiseltal crocodylian geometric morphometric analysis using all 27 relative warps axes. Sample sizes are: *Boverisuchus* ($n = 5$), *Asiatosuchus* ($n = 7$) and *Diplocynodon* ($n = 14$). Due to the low sample size of *Allognathosuchus* ($n = 2$), this taxon could not be included in these metrics. Products were normalized by taking their 27th root.

Metric	Taxon	Value	Upper 95 % confidence interval	Lower 95 % confidence interval
Sum of ranges	*Boverisuchus*	0.832515	0.978577	0.491833
	Asiatosuchus	0.932532	1.066484	0.739543
	Diplocynodon	1.430245	1.546977	1.295868
Product of ranges	*Boverisuchus*	0.027675	0.027387	0.011043
	Asiatosuchus	0.031664	0.033535	0.021064
	Diplocynodon	0.041729	0.043759	0.036798
Sum of variances	*Boverisuchus*	0.008180	0.010004	0.004946
	Asiatosuchus	0.006997	0.008163	0.005350
	Diplocynodon	0.011127	0.013055	0.009118
Product of variances	*Boverisuchus*	0.000135	0.000135	0.000037
	Asiatosuchus	0.000146	0.000156	0.000080
	Diplocynodon	0.000167	0.000175	0.000146

Table 3. Disparity metrics from the geometric morphometric analysis of Geiseltal crocodylians in terms of mammal Palaeogene (MP) zone, using all 27 relative warps axes. Sample sizes are: MP 11 (n = 4), MP 12 (n = 6), MP 13 (n = 18). Products were normalized by taking their 27th root.

Metric	MP zone	Value	Upper 95 % confidence interval	Lower 95 % confidence interval
Sum of ranges	11	0.64684	0.888904	0.394538
	12	0.978426	1.158069	0.776484
	13	1.593585	1.693242	1.468361
Product of ranges	11	0.024119	0.026317	0.007869
	12	0.028523	0.030316	0.018371
	13	0.044804	0.046857	0.040671
Sum of variances	11	0.006492	0.009187	0.002956
	12	0.010508	0.013001	0.007413
	13	0.014310	0.017338	0.011319
Product of variances	11	0.000127	0.000139	0.000021
	12	0.000134	0.000140	0.000066
	13	0.000174	0.000181	0.000158

have been determined based on their stratigraphic section and mammalian biostratigraphy. The crocodylian fossils of Geiseltal span the entire 'Geiseltalian' European land mammal age, falling into one of three mammal Palaeogene zones, MP 11 through MP 13 (Franzen & Haubold, 1987; Schmidt-Kittler, 1987; Haubold & Thomae, 1990; Aguilar, Legendre & Michaux, 1997; Hellmund, 2007). We determined the MP zone (MP 11, 12, or 13) for each of the 28 specimens in the study from original locality data (Table 1).

It should be mentioned that due to the sedimentary (non-volcanic) nature of the site, radiometric data are not directly available from the Geiseltal site. However, an approximation of the absolute age of Geiseltal can be made by comparison with two similar terrestrial fossil sites in central Germany. The beginning of the fossil record of Geiseltal during MP 11 is also identified for the Messel fossil site (Franzen, 2005). The Messel fossil deposit lies atop a basalt dated to 47.8 ± 0.2 Ma (Mertz & Renne, 2005). Younger fossils of Geiseltal were deposited during MP 13, the same stratigraphic zone as Eckfeld, a maar lake deposit from Eifel, Germany (Lutz & Kaulfuß, 2006). Basaltic ejecta from Eckfeld during a coeval eruption were dated to 44.3 ± 0.4 Ma (Mertz *et al.* 2000). This creates a roughly 3.5 Ma time span of fossilization at Geiseltal that can be divided into three stratigraphic zones (MP 11–13).

Interestingly, the four crocodylian taxa from Geiseltal discussed here are also reported from both the Messel fossil locality (MP 11; Morlo *et al.* 2004) and the Eckfeld fossil locality (MP 13; Neuffer *et al.* 1996). This shows that the interactions of these taxa likely occurred in central Germany throughout Geiseltalian time. Only at the Geiseltal site are all three MP zones recorded in a nearly continuous sequence at a single location, providing a more inclusive picture of interactions between these four different crocodylian genera. *Allognathosuchus* is relatively uncommon at all three localities, and only recorded from MP 13 at Geiseltal (Hellmund, 2007). The incomplete specimen of *Bergisuchus* was only recorded from MP 11 at Geiseltal and Messel (Rossmann, Rauhe & Ortega, 2000). *Asiatosuchus*, *Diplocynodon* and *Boverisuchus* can all be found in each MP zone at Geiseltal (Hellmund, 2007). As an example of their co-occurrence at Geiseltal, fossil teeth collected from one location within a single stratigraphic layer represent all four of these crocodylian species (XXXV within the 'Neumark-Süd' pit; MP 13). The dentition of these isolated teeth matches very well in terms of size and shape with teeth preserved in diagnostic jaws and skulls from other localities at Geiseltal. Furthermore, these teeth correspond to other teeth figured of *Boverisuchus* and *Asiatosuchus* (Prasad & de Lapparent de Broin, 2002) and

Diplocynodon (Delfino & Smith, 2012; Martin *et al.* 2014).

The fossils from the different-aged deposits of Geiseltal change throughout the Geiseltalian; certain taxa-like fish, amphibians, snakes and lizards do not appear at all during MP 11, are rare or absent in MP 12 and common during MP 13 (Hellmund, 2007). The reason for the absence of these taxa from the 'Unter-kohle' seam (MP 11) and their rarity or absence from the lower 'Mittelkohle' seam (MP 12) can only be reasonably explained as a geological or geochemical setting lacking suitable parameters such as hydrocarbon inflow for successful fossil preservation (Krumbiegel, 1977). Considering the lengthy and thorough means of collection over so many years, it is unlikely that fish and similar aquatic life were simply not collected; their lack of record from these layers more likely indicates a difference in fossilization and/or environment between the MP zones (G. Krumbiegel, pers. comm., 2013).

Ungulates are found at each MP zone at Geiseltal, and are the most common fossils discovered. Most notable of these are the relatively common primitive horses *Propalaeotherium* that include four valid species (the smallest now attributed to *Eurohippus*; Franzen, 2006). These early horses mainly differ in size, with some slight variation in tooth morphology (Hellmund, 2013a). The quantity of propalaeothere fossils in some locations is remarkably high, especially for site 'XIV' from MP 11 (Franzen & Haubold, 1986; Hellmund, 2013a).

3. Results

3.a. Geiseltal crocodylians

The relative warps analysis of Geiseltal crocodylians resulted in 27 axes (online supplementary material Table S2 and Fig. S1; available at http:// journals.cambridge.org/geo). The greatest amount of variation within the dataset was unsurprisingly composed of *Diplocynodon* specimens, which had the largest sample size (online supplementary Fig. S1). However, the largest portion of variation was within the first two axes for all taxa (online supplementary Fig. S1). Since the Procrustes analysis is generated within Kendall's shape space, a curved surface, data must be projected orthogonally onto a plane tangential to the consensus in order to be viewed in 2D space (Dryden & Mardia, 1998; Stayton & Ruta, 2006). We tested for potential distortion of this effect by regressing Procrustes distance against Euclidean distance using the program tpsSmall 1.28 (F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-tps.html). The resulting high correlation between these (0.999999) indicates that there is very strong agreement between the two projections (Stayton & Ruta, 2006).

The first relative warp axis (RW 1; Fig. 4) primarily summarizes the transition from the brevirostrine condition of *Allognathosuchus* (negative) and the more longirostrine condition of *Boverisuchus* (positive).

Landmarks of negative RW 1 configurations have: (1) more widely separated landmarks around the orbit, representing a relatively large orbit; (2) lateral margin landmarks that are relatively further from the midline, resulting in a 'bowed out' margin that creates a rounder, less straight lateral margin; (3) anterior landmarks that are relatively closer to other snout landmarks, resulting in a shorter snout; and (4) the landmark representing the anterior extent of the nasal is relatively closer to the anterior-most landmarks. Landmarks of positive RW 1 configurations have instead: (1) more constricted landmarks around the orbit, resulting in a relatively small orbit; (2) landmarks on the lateral skull margin that are relatively closer to the midline, resulting in a modestly 'bowed in' outline to the lateral margin; (3) anterior landmarks that are relatively further from the orbital landmarks, resulting in a longer snout; and (4) landmarks representing the anterior extent of the nasal bones and suture between the premaxilla and maxilla that are relatively closer to the orbital landmarks, resulting in a more elongated premaxilla.

The landmarks of the second relative warp axis (RW 2; Fig. 4) appear to encompass a transition in skull width, mostly between certain members of *Asiatosuchus* and *Diplocynodon*. The landmarks of negative RW 2 have: (1) orbital landmarks that are relatively closer to the lateral margin; (2) landmarks of the lateral margin that are relatively closer to those of the midline, resulting in a narrower snout; and (3) a slightly more posterior relative position of the landmark representing the posterior extent of the squamosal, resulting in a larger skull table in dorsal view. The landmarks of positive RW 2 have instead: (1) orbital landmarks placed relatively closer to the midline, resulting in an orbit that is more centrally placed; (2) landmarks of the lateral margin that are relatively further from the midline, resulting in a wider snout; and (3) a slightly more anterior position of the landmark representing the jugal-quadratojugal suture, resulting in a slightly reduced infratemporal fenestra in dorsal view.

Morphospace of the Geiseltal crocodylians shows fairly distinct and coherent grouping within each of the four genera included in the analysis, in terms of RW 1 v. RW 2 (Fig. 4). The most distinct of these are *Boverisuchus* and *Allognathosuchus* which both exhibited no overlap with any other genus. Although with a small sample size, *Allognathosuchus* plotted very distinctly from other taxa. The landmarks of this taxon are characterized by strongly negative RW 1 traits, and both specimens were very similar in relative landmark positions. The *Allognathosuchus* lateral skull margin landmarks were marginally farther from the midline, resulting in a slightly positive RW 2. On the other extreme of RW 1 is *Boverisuchus* with anterior landmarks more distant from orbital landmarks, resulting in a longer snout. Orbital landmarks of *Boverisuchus* are more closely set, also matching with a more positive RW 1 position. Specimens of *Boverisuchus* trended towards more negative RW 2 traits, with orbital landmarks still more closely set to each other but also more closely set to the landmarks
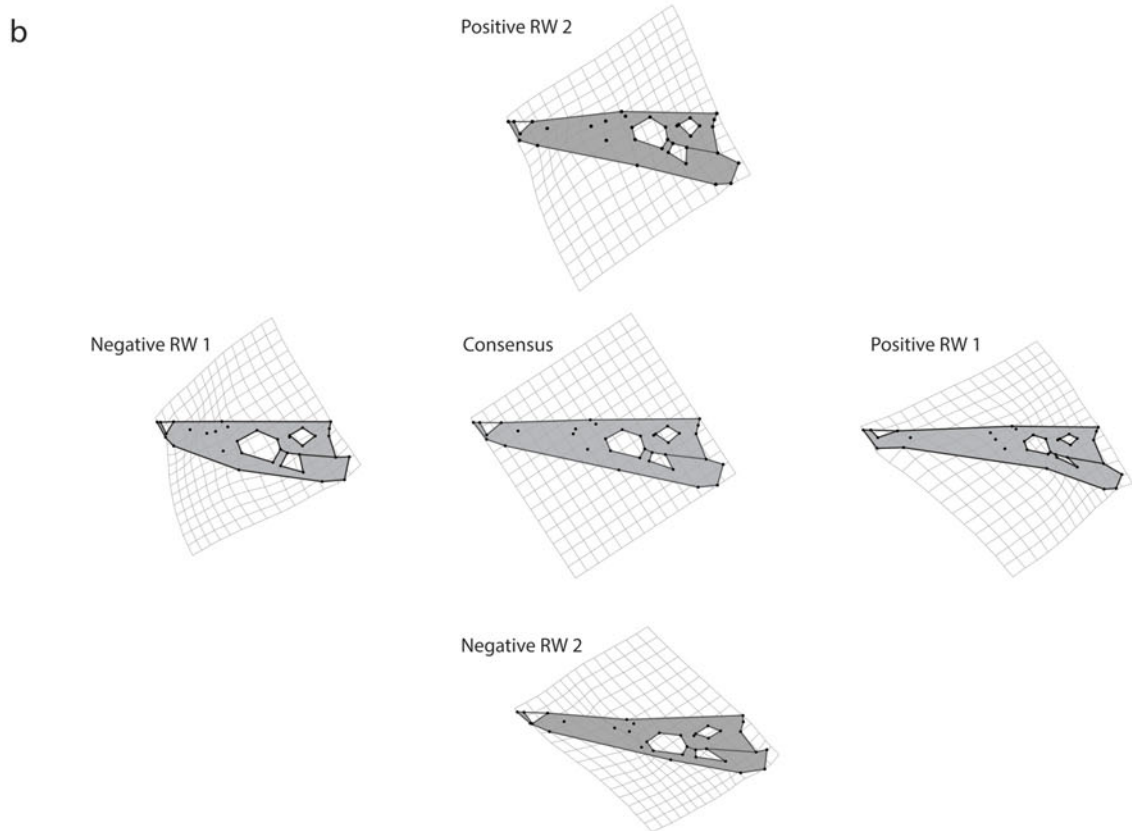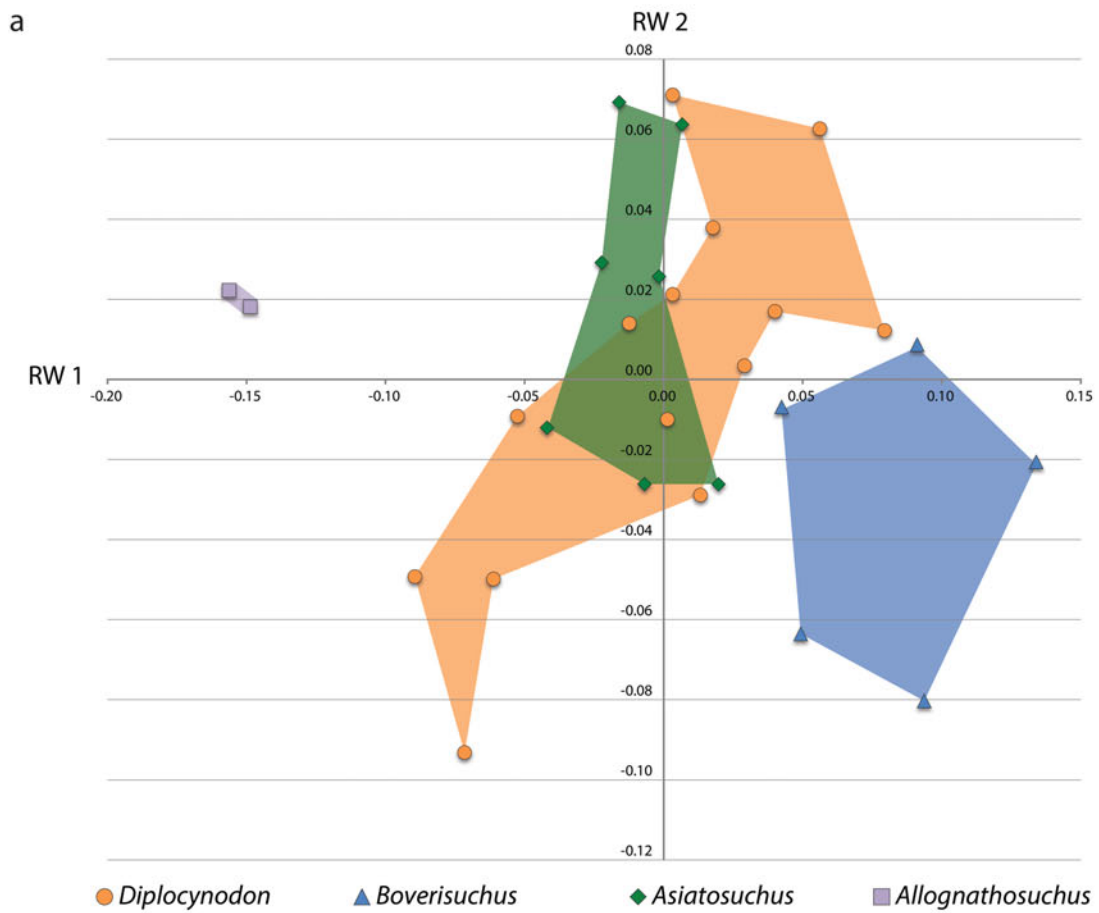
Figure 4. (Colour online) (a) Morphospace of 28 skulls representing four genera from Geiseltal, Germany. The horizontal axis is relative warp 1; the vertical axis is relative warp 2. (b) Deformation grids representing landmark placement centred on the consensus configuration and deviating in positive and negative directions for relative warps 1 and 2.
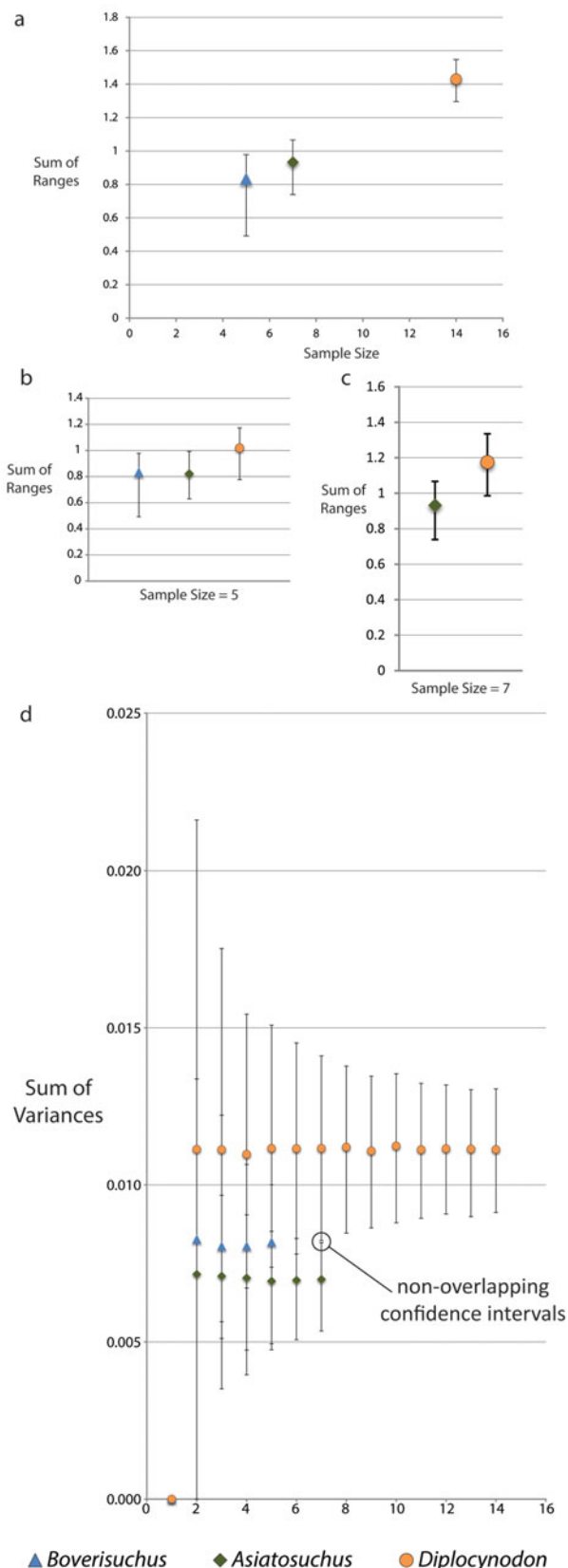
Figure 5. (Colour online) Disparity metrics with 95 % confidence intervals from the Geiseltal geometric morphometric analysis encompassing all 27 relative warps axes. Data were generated using Rare 1.2 (Wills, 1998). Key at bottom refers to all XY scatter plots. *Allognathosuchus* could not be included due to its small sample size (*n* = 2). (a) Sum of ranges for each taxon. (b) Sum of ranges data resampled by bootstrapping rarefaction to the smallest common sample size (*n* = 5). (c)

of the lateral skull margin. Variation in *Diplocynodon* was primarily along the RW 2 axis, with relatively less variation in the relative positions of anterior premaxillary landmarks and orbital landmarks. *Asiatosuchus* variation was closer to the consensus despite not having the largest representation within the dataset (7 of 28 specimens). Specimens of this taxon varied mostly in RW 2 values, but with less variation than *Diplocynodon*. *Asiatosuchus* and *Diplocynodon* overlapped in portions of their RW 1 v. RW 2 morphospace occupation. However, both genera had specimens outside the overlap zone.

Due to the small sample size of *Allognathosuchus*, disparity metrics could not be calculated for this taxon. Variance, which is less sensitive to sample size differences (Wills, 1998), was highest in *Diplocynodon* followed by *Boverisuchus* and *Asiatosuchus* (Table 2). However, these differences were not statistically different when the data were rarefied due to overlapping confidence intervals at the lowest common sample number of five individuals. However, comparison between the smallest common sample size of *Asiatosuchus* and *Diplocynodon* (seven individuals) did recover statistically significant, non-overlapping confidence intervals (Fig. 5). Range metrics indicate total extent of morphological differences, but are more sensitive to small sample size (Wills, 1998). On the whole, *Diplocynodon* had significantly higher disparity than *Boverisuchus* or *Asiatosuchus* (Table 2; Fig. 5) but this difference is no longer significant when the data are resampled at the lowest common sample number (both five and seven; Fig. 5).

We calculated Pearson's correlation coefficients and *p*-values for each of the 27 relative warps axes with respect to centroid size, stratigraphic age and taphonomy. These were conducted both as a whole for the Geiseltal dataset and within each taxon (except *Allognathosuchus*, which had too small of a sample size, *n* = 2), with the aim of determining statistically significant correlation (online supplementary Tables S2–S6, available at http://journals.cambridge.org/geo). There was a statistical correlation of centroid size for RW 3 and RW 10 in all Geiseltal specimens (online supplementary Table S2). When these data were subdivided into taxa, there was no significant correlation between size and the relative warps of *Diplocynodon* (online supplementary Table S3) or *Boverisuchus* (online supplementary Table S5). *Asiatosuchus* had statistically significant correlation in RW 6, 9, 13 and 15 (online supplementary Table S4). Centroid size had a significant inverse correlation with stratigraphic age for Geiseltal crocodylians as a whole and within *Diplocynodon* and *Asiatosuchus* (online supplementary

Sum of ranges data resampled by bootstrapping rarefaction to the next smallest common sample size (*n* = 7). (d) Sum of variances for Geiseltal taxa, with indication of statistically independent values between rarefied *Diplocynodon* and *Asiatosuchus* due to non-overlapping confidence intervals at equal sample size.
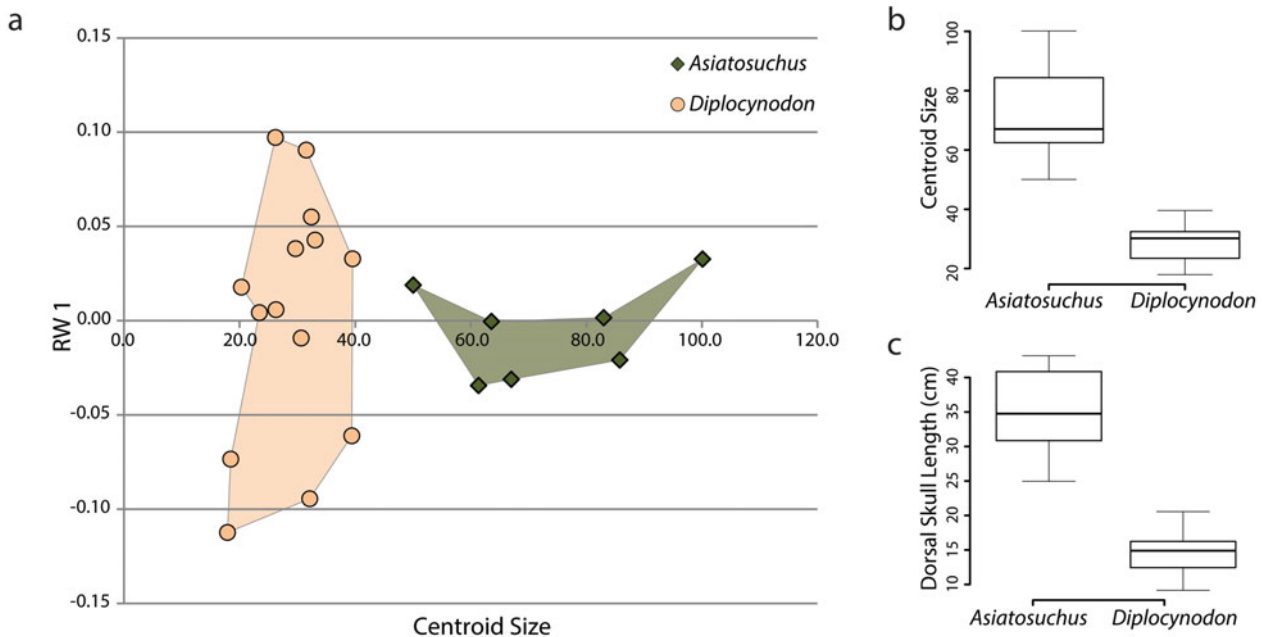
Figure 6. (Colour online) Data plots comparing *Asiatosuchus* and *Diplocynodon* from Geiseltal, Germany. (a) XY scatter plot incorporating the first order of variation from geometric morphometric analysis (relative warp 1, the vertical axis) with centroid size (horizontal axis). (b) Box plot of centroid sizes. (c) Box plot of dorsal skull lengths.

Table S6). In all three cases, size decreased with stratigraphic age. No such correlation was found in *Boverisuchus*.

In terms of taphonomic effect, we assessed whether compression had a statistical correspondence with any of the relative warps axes. When treated as a whole, the Geiseltal crocodylians only showed a statistically significant correlation between taphonomy and RW 6 and 7 (online supplementary Table S2). These two axes account for a total of 10.85 % of the variation within the dataset. When subdivided into taxa, taphonomy had a statistical correlation with RW 7 and 10 in *Diplocynodon*, accounting for a total of 8.51 % of the variation within the taxon (online supplementary Table S3). There was no correlation within *Boverisuchus* (online supplementary Table S5). Due to the lack of taphonomic variation within *Asiatosuchus* (all specimens were uncompressed), this correlation statistic could not be calculated. Taphonomy had a statistically significant correlation with centroid size for Geiseltal as a whole (online supplementary Table S6), which is not surprising given the lack of compression in the large *Asiatosuchus* and the presence of compression in the smaller *Diplocynodon* and *Allognathosuchus* (Table 1).

The most notable difference between skulls of *Diplocynodon* and *Asiatosuchus* is that those of adult *Asiatosuchus* are invariably much larger (Table 1). We conducted an independent analysis using only these two taxa and calculated centroid size. Centroid size was statistically independent between the two samples (p-value = 0.0003253) using a Welch Two Sample t-test in the statistics program *R* (see box plot Fig. 6; R Core Team, unpub. program, 2013: http://www.R-project.org). Dorsal skull length, meas-

ured from the tip of the snout to the posterior wall of the skull table, was entered into a second Welch Two Sample t-test and was also found to be statistically independent (p-value = 0.0001101; see box plot in Fig. 6). When centroid size was plotted against the first order of variation (relative warp 1), there was a distinct separation in size despite partial overlap in shape (Fig. 6). Pearson's correspondence analyses comparing each axis of the relative warps analysis to centroid size recovered only one (relative warp 2, comprising 10.75 % of total variance) with statistically significant correlation (Pearson's correlation: 0.6859, p-value: 0.0006). However, when the data from this same geometric morphometric analysis are separated into *Asiatosuchus* and *Diplocynodon*, statistical correspondence is significant in different axes (*Diplocynodon*: RW 2, 17; *Asiatosuchus*: RW 5). This may imply that the growth of the two species follows separate trajectories, with different parameters affecting shape with increasing size during ontogeny. Without a full ontogenetic series of these taxa, it is impossible to say whether or not young *Asiatosuchus* would overlap in shape and size with adult *Diplocynodon*. However, the sizes of these taxa are statistically distinct as adults.

The crocodylian fossil skulls of Geiseltal span the middle Eocene MP zones 11–13. We compared the data from the 27 relative warps axes against time, both for the Geiseltal crocodylians and for each taxon (online supplementary Tables S2–S6; available at http://journals.cambridge.org/geo). As a whole, only RW 3 had a statistically significant correlation when plotted against time (online supplementary Table S2), although the correlation is weak ($R^2 = 0.21731$; Fig. 7). Relative warps 1 and 2 had no statistical correlation,

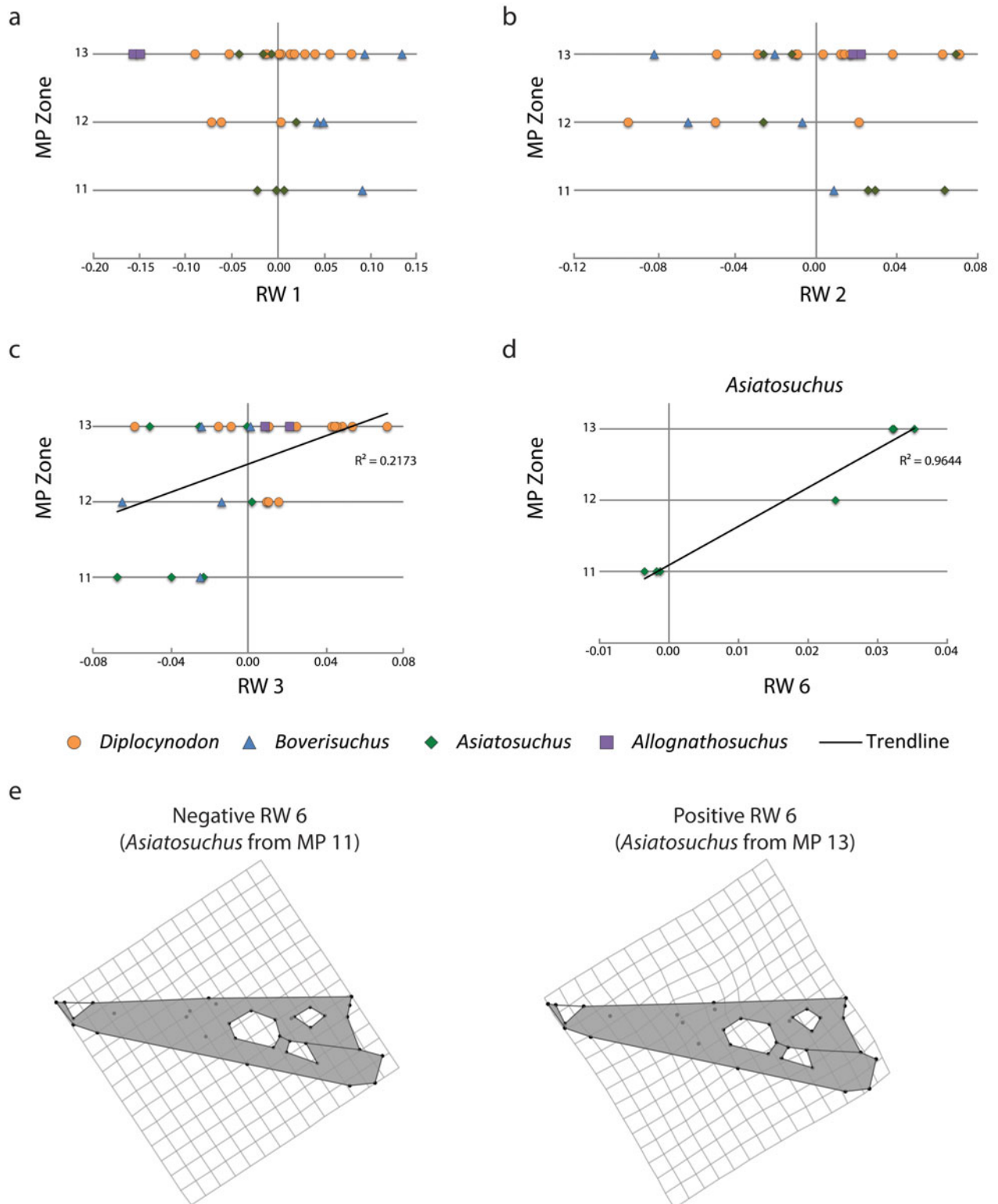Figure 7. (Colour online) Geiseltal crocodylian morphospace through the preserved mammal Palaeogene zones, MP 11–13, spanning the 'Geiseltalian' European land mammal age. These are limited to individuals with complete skulls and do not represent all genera occurring within each zone. (a) XY scatter plot, showing RW 1 of the Geiseltal dataset from MP 11 to 13, which showed no statistically correlated trend. (b) XY scatter plot, showing RW 2 of the Geiseltal dataset from MP 11 to 13, which showed no statistically correlated trend. (c) XY scatter plot, showing RW 3 of the Geiseltal dataset from MP 11 to 13, which showed only a weak statistical correlation; see online supplementary Table S2. (d) Strongest statistical correlation with time within the Geiseltal dataset, RW 6 v. MP zone in *Asiatosuchus*; see online supplementary Table S4. (e) Deformation grids showing negative to positive relationships of landmarks along the RW 6 axis, as generated from the consensus of the full Geiseltal dataset.

regardless of which taxa were included (Fig. 7). No statistical correlation was recovered from *Diplocynodon* and, with only two specimens, this analysis could not be conducted for *Allognathosuchus* independently of the rest of the data. *Asiatosuchus* showed strong correlation with relative warp 6 (Fig. 7) and weak correlation with relative warp 10 (online supplementary Table S4). Relative warp 6 appears to summarize only subtle differences in landmarks of the relative anterior extents and contacts between the prefrontal, nasal, frontal and lacrimal bones (Fig. 7). Trending with time, the frontal landmarks appear to reach slightly more anteriorly while the prefrontal landmarks do not reach as anteriorly in MP 13 *Asiatosuchus*. This trend is statistically significant, but is admittedly limited to the seven samples available. *Boverisuchus* only had statistical correlation with relative warp 27, which only summarized 0.79 % of taxon variation (online supplementary Table S5).

As only reasonably complete skulls were included, these results are only representative of the specimens preserved well enough for the study. Each taxon, except *Allognathosuchus*, has representative fossils in each stratigraphic zone. The lack of *Diplocynodon* with complete skulls in MP 11 does not mean that *Diplocynodon* was not present at this time. The MP 11 zone only contained three *Asiatosuchus* and one *Boverisuchus* skull. More skulls were preserved within the MP 12 zone: three *Diplocynodon*, one *Asiatosuchus* and two *Boverisuchus*. The MP 13 zone contained the most specimens that could be used for this study ($n = 18$) with three *Asiatosuchus*, two *Allognathosuchus*, two *Boverisuchus* and eleven *Diplocynodon*.

Both range and variance metrics steadily increase with time across the MP zones (Table 3; Fig. 8). There is a statistically signficant difference between the sum of ranges during MP 13 compared to both MP 11 and 12, as well as the sum of variances between MP 11 and MP 13 (Table 3; Fig. 8). However, when the data were resampled by rarefaction, statistical significance is lost when sampling was limited to the smallest common sample size (for both four and six individuals), as indicated by overlapping 95 % confidence intervals (Fig. 8). It should however be noted that greater variation would be expected during MP 13 regardless of sample size due to *Allognathosuchus* only having been present during this particular MP zone.

In the interests of presenting alternative views, we split the landmark file into three seperate tps files and reran the relative warps analysis for each of the MP zones independently. Since these analyses were run using only the members present during each of the MP zones, the average skull shape was reset for each, meaning deviation from the centre is different for each zone. This analysis is not meant to identify trends with age, but to look at each zone as an independent collection of specimens. The MP 11 zone shows clear separation between the one specimen of *Boverisuchus* and the three *Asiatosuchus* in relative warps 1 and 2 (Fig. 9). The MP 12 specimens all plotted separately, but the
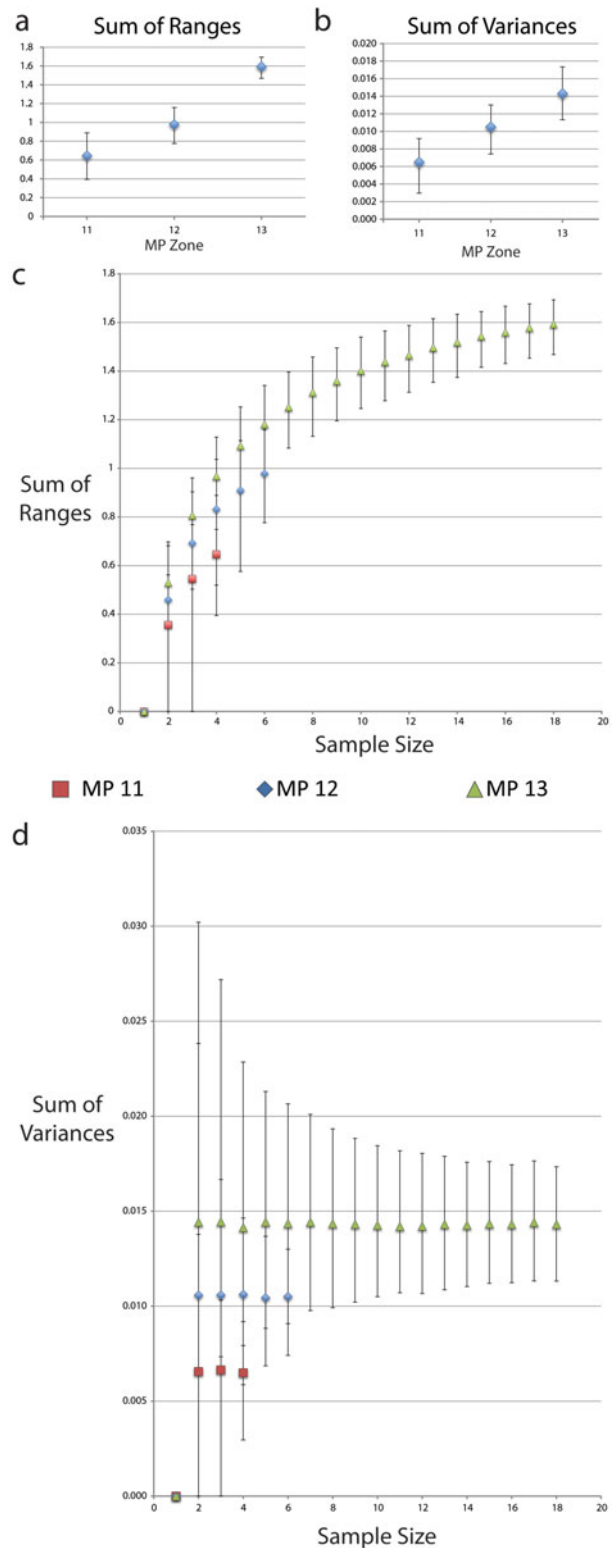

Figure 8. (Colour online) Disparity metrics with 95 % confidence intervals from the Geiseltal geometric morphometric analysis encompassing all 27 relative warps axes. Data were generated using Rare 1.2 (Wills, 1998). Key in middle refers to XY scatter plots of both (c) and (d). (a) Sum of ranges data from whole samples at each MP zone. (b) Sum of variances data from whole samples at each MP zone. (c) Sum of ranges data resampled using bootstrapping methods, creating rarefaction curves. (d) Sum of variances data resampled using bootstrapping methods, creating rarefaction curves.
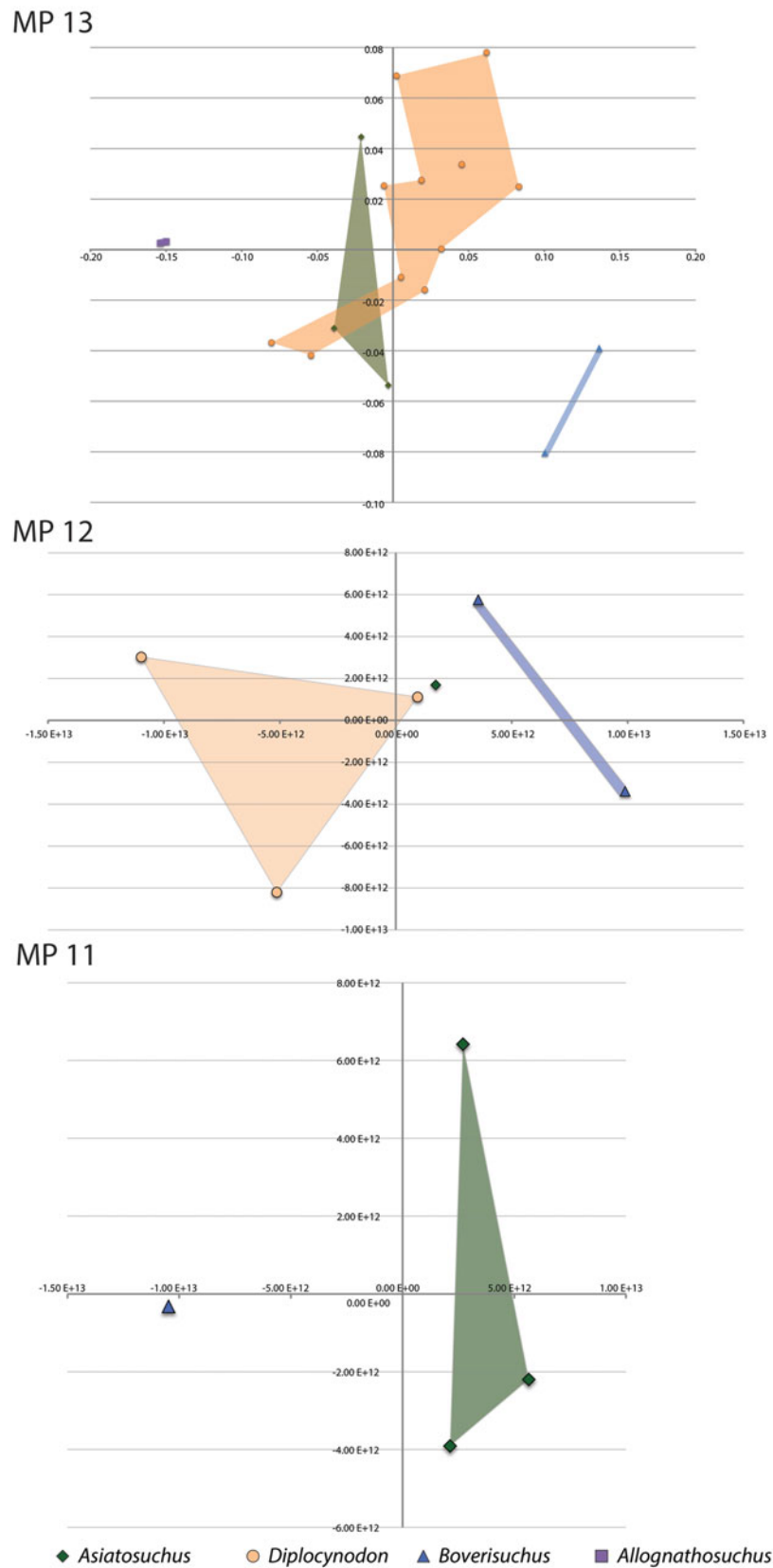
Figure 9. (Colour online) Geiseltal crocodylian morphospace separated by mammal Palaeogene zones, MP 11–13. Each plot represents a separate analysis using MP zone-specific subsets of the original landmark dataset. In each plot, the horizontal axis is relative warp 1; the vertical axis is relative warp 2.

one *Asiatosuchus* plotted very close to a *Diplocynodon* specimen. Not surprisingly, the same overlap between *Asiatosuchus* and *Diplocynodon* persisted in MP 13. During MP 13, *Boverisuchus* and *Allognathosuchus* again have very distinct separation in morphospace.

3.b. Comparison to extant crocodylians

The relative warps analysis including the Geiseltal specimens and modern crocodylians resulted in 66 axes. The first two axes (RW 1 and RW 2) summarize 19.66 % of the total variation within the combined analysis, which summarize more variation than any other axis (online supplementary Fig. S2; available at http://journals.cambridge.org/geo). We tested the combined analysis for correspondence between Kendall's shape space and Euclidean coordination by regressing Procrustes distance against Euclidean distance in tpsSmall 1.28 (F. J. Rohlf, unpub. program, 2013: http://life.bio.sunysb.edu/morph/soft-tps.html). The resulting high correlation (0.999996) indicates strong agreement between the two projections.

The primary axis of variation, RW 1, again involves mostly differences in landmarks reflecting brevirostrine versus longirostrine skulls (Fig. 10). The relationship of landmarks in this respect is the same as that found using only the Geiseltal specimens. The only notable difference is that negative RW 1 in the combined dataset also has a constriction of the landmarks of the supratemporal fenestra, resulting in a more bony skull table. Positive RW 1 landmarks share all the same traits found in the Geiseltal-only dataset, with a much stronger emphasis on premaxillary landmarks being relatively further from orbital landmarks, resulting in a longer snout in proportion to the rest of the head. This more extreme elongated skull shape is due to the inclusion of the longirostrine gharial (*Gavialis gangeticus*) and false gharial (*Tomistoma schlegeliii*). The positive RW 1 landmarks of the supratemporal fenestrae are also expanded, resulting in a less bony skull table. The second axis, RW 2, also mostly summarizes variation in width, but the direction of width is reversed. The other features describing differences in landmarks of RW 2 in Geiseltal are not comparable with the combined dataset. Instead, negative RW 2 is characterized by: (1) lateral margin landmarks that are further from the midline, resulting in a robust, wider snout; (2) landmarks that are more widely set between the quadratic condyle and quadrate-quadratojugal suture; and (3) more anterior extent of the jugal-quadratojugal suture along the infratemporal fenestra, resulting in a slightly different angle of the fenestra in dorsal view. Positive RW 2 is characterized by: (1) more close placement of landmarks from the lateral margin to the midline, particularly at the premaxilla, resulting in a more pointed, narrow skull shape; (2) slight difference in the quadratic condyle landmark, resulting in a slightly narrower condyle; and (3) more posterior position of the landmarks, representing the jugal-quadratojugal suture along the infratemporal fenestra, resulting in a more angled fenestra in dorsal view.

The RW 1 v. RW 2 morphospace plot, including both Geiseltal crocodylians and extant crocodylians, shows separation of *Boverisuchus*, *Allognathosuchus* and *Diplocynodon* from all living species of Crocodylia (Fig. 10). The only overlap with extant taxa was *Asiatosuchus*, which overlapped with members of both Alligatoridae and Crocodylidae. The overlap between *Asiatosuchus* and *Diplocynodon* is still present, although this overlap does not coincide with any extant crocodylian in the dataset. *Diplocynodon* are characterized by positive RW 2, with more specimens verging on negative RW 1. The range of *Diplocynodon* in RW 1 is very similar to that of extant Alligatoridae. There was only minimal overlap in RW 2 with extant Crocodylidae, but much more overlap with some members of living Alligatoridae. When these two factors are combined, however, *Diplocynodon* appears as a distinct group from the extant members. *Boverisuchus* is characterized by only positive RW 2 and all but one specimen had positive RW 1. In terms of RW 2, *Boverisuchus* overlaps with *Diplocynodon* and some of *Asiatosuchus*, but is more distinct in terms of its more positive RW 1 values. The extant population shows that modern alligatorids vary mostly in terms of RW 2, while crocodylids vary most in terms of RW 1 landmark positions. The RW 1 variation of Crocodylidae is likely due to the inclusion of the false gharial, *Tomistoma schlegelii*, but is also contributed to by the slender-snouted crocodile, *Mecistops cataphractus*.

4. Discussion

4.a. Correlations between size, taphonomy and stratigraphic age

Due to the manageable number of axes from the Geiseltal component of the analysis, we ran statistical correlation along all 27 relative warps axes. The correlation between centroid size and relative warps axes was strongest in *Asiatosuchus*, accounting for a total of 13.97 % of taxon variance (online supplementary Table S4; available at http://journals.cambridge.org/geo). This indicates a small but noteworthy allometric effect on skull shape. The fact that one of these axes (RW 6) also has statistically significant correlation with stratigraphic age (Fig. 7) is likely related. The other relative warps that correlated with size had no correlation with stratigraphic age in *Asiatosuchus* (online supplementary Table S4), indicating non-directional change in these allometric patterns through time.

Taphonomic compression affected the fossils of Geiseltal differently. Only *Diplocynodon* and *Boverisuchus* had representative specimens of both preservation states (notable compression or little to no compression). Both of these taxa are intermediate in size while *Asiatosuchus*, the largest taxon, had only uncompressed specimens ($n = 7$) and *Allognathosuchus*, the smallest taxon, had only compressed specimens ($n = 2$). This differential preservation is most likely caused by the
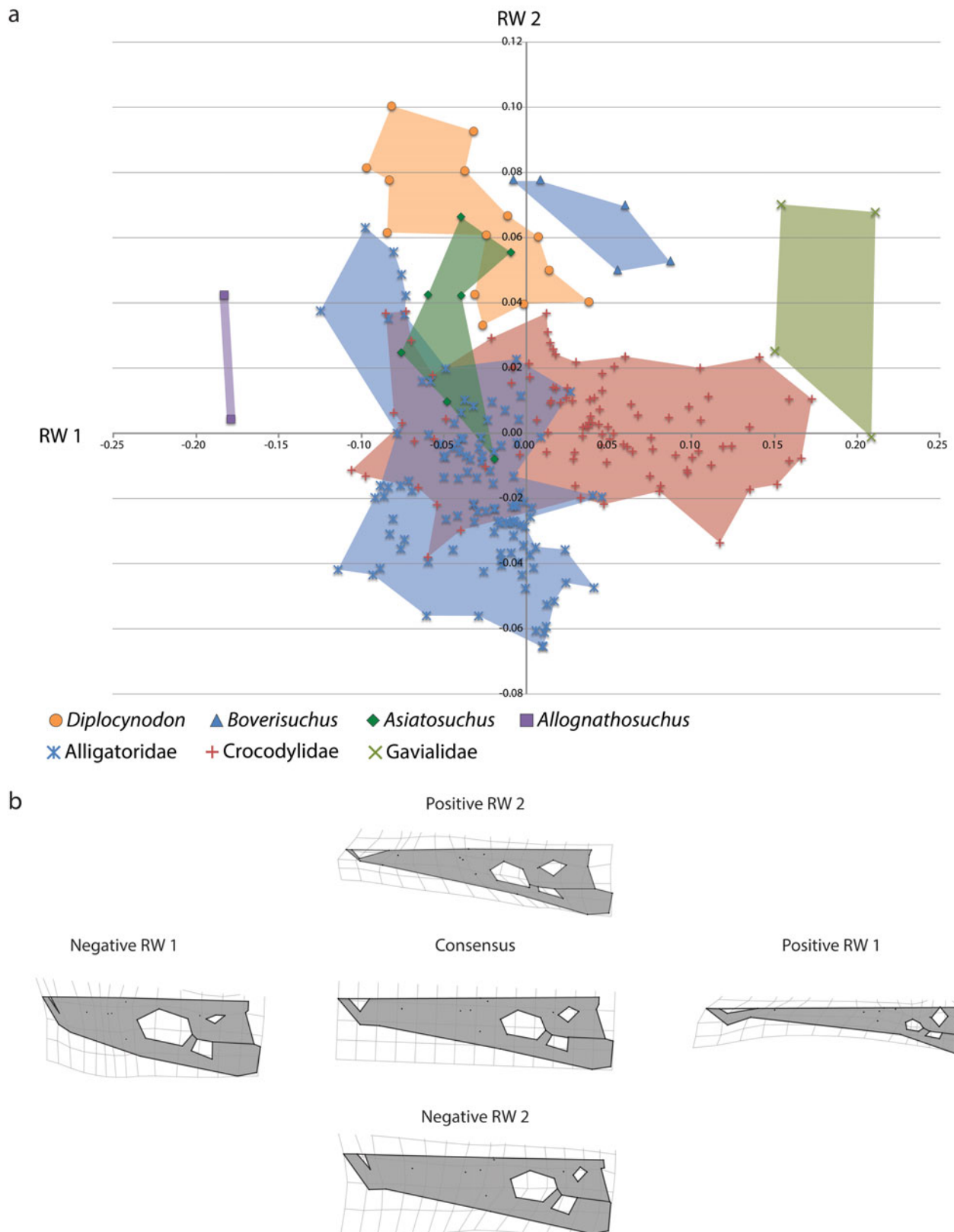
Figure 10. (Colour online) (a) Morphospace of Geiseltal crocodylian skulls ($n = 28$) and extant crocodylian skulls ($n = 218$) utilizing geometric morphometric analysis. The horizontal axis is relative warp 1; the vertical axis is relative warp 2. (b) Deformation grids representing landmark placement centred on the consensus configuration and deviating in positive and negative directions for relative warps 1 and 2.

difference in size, supported by the strong correlation between the centroid size and taphonomy within the full Geiseltal dataset (*p*-value = 0.0020; online supplementary Table S6). However, taphonomy appears to have had at most a minor effect on the geometric morphometric data. None of the first five relative warps axes (accounting for a total of 42 % of variation) had a statistically significant correlation with taphonomy (online supplementary Table S2). Within the full Geiseltal dataset, correlation was recovered with only RW 6 and 7 (accounting for a total of 10.85 % of variation). Even though RW 6 had statistically significant correlation with taphonomy in the full Geiseltal dataset, there was no such correlation within the taxon with the greatest sampling, *Diplocynodon* (online supplementary Table S3). This may indicate a more taxonomic bias to taphonomy in RW 6 than strictly shape altering, particularly considering *Allognathosuchus* were compressed and *Asiatosuchus* were not. Probably as a result of the taxonomic bias of taphonomy, centroid size had a statistical correlation with taphonomy but only when the entire dataset was considered. No such correlation existed within *Diplocynodon* or *Boverisuchus* (online supplementary Table S6). Correlation between taphonomy and shape was statistically significant within *Diplocynodon* for only relative warps 7 and 10 (accounting for a total of 8.51 % of taxon variance; online supplementary Table S3). No statistical correlation was found between taphonomy and the relative warps of *Boverisuchus* (online supplementary Table S5). Most of the discussion of these data is focused on the first and second axes, which summarize more of the variation than any of the other axes and lack a significant correlation with taphonomy, both as a whole and within each taxon (online supplementary Tables S2–S6).

Although *Boverisuchus*, *Asiatosuchus* and *Diplocynodon* are all found at each MP zone (11–13), reasonably complete skulls were not recovered at each level. The graphics of Figures 7 and 9 should therefore be interpreted with some reservation. The general lack of statistically significant correlation between relative warp axes and stratigraphic age show only minor directional change through time (Fig. 7). The strongest correlation between age and relative warps (RW 6 of *Asiatosuchus*; online supplementary Table S4) is the only clear example of directional change within the skull structure of Geiseltal crocodylians, towards subtle differences in the relative anterior extent of the frontal and prefrontal landmarks. By looking at each MP zone independently (Fig. 9) we can see how each system existed on its own, even though it does not identify statistical trends through time.

4.b. Reconstructing prey preference in Geiseltal crocodylians

4.b.1. Total body length of Geiseltal crocodylians

Datasets have been generated in the past from extant crocodylians in order to estimate total body length in fossil taxa using the living crocodylian species *Crocodylus porosus*, *Crocodylus moreletii*, *Gavialis gangeticus* and *Alligator mississippiensis* (Woodward, White & Linda, 1995; Sereno *et al*. 2001; Farlow *et al*. 2005; Platt *et al*. 2009; Young *et al*. 2011b). Given the presence of both crocodyloids and alligatoroids at Geiseltal, it seemed appropriate for this study to use multiple methods for total length estimation. We have provided the dorsal skull length measurements of each of the Geiseltal fossil specimens in Table 1.

There is a large difference in skull morphology between the Geiseltal crocodylians and *G. gangeticus* and, as a result, we decided not to use these data. Femoral dimensions from *A. mississippiensis* were published by Farlow *et al*. (2005) in order to calculate total body length but, given the lack of preserved femora with most Geiseltal crocodylians, this would also be impractical. This method was tested with *Diplocynodon*, *Asiatosuchus* and *Boverisuchus* from Geiseltal, and every specimen but one resulted in over-prediction of total body length (Farlow *et al*. 2005). Regressions for determining total body length from cranial length of modern *A. mississippiensis* were presented by Woodward, White & Linda (1995) and converted to a cranial length: total length ratio by Young *et al*. (2011b). As *Allognathosuchus* and *Diplocynodon* are both alligatoroids (Brochu, 2004; J. Martin, unpub. Ph.D. thesis, Univ. Lyon, 2009; Martin, 2010; Martin & Gross, 2011; Delfino & Smith, 2012; Martin *et al*. 2014), we have applied the calculation methods derived from *A. mississippiensis* (Woodward, White & Linda, 1995; Young *et al*. 2011b; Table 1). As *Asiatosuchus* belongs to crocodyloidea (Vasse, 1992; Delfino & Smith, 2009; Brochu, 2013) and is more similar in size and morphology to *C. porosus* than to *C. moreletii*, we chose to use the data derived from *C. porosus* (Sereno *et al*. 2001). These total body length estimates are also provided in Table 1.

As *Boverisuchus* is neither a crocodyloid nor an alligatoroid (Brochu 2013), the method of total body length calculation was more problematic. Only one complete skeleton of *Boverisuchus* is known (GMH Leo X-8001-1938). Unfortunately, the skull of this specimen is preserved in ventral view only, and a dorsal skull length can only be approximated. Best estimation of the dorsal skull length from the ventral surface is 36.5 cm, and we measured 2.06 m for the total length of the skeleton. This measurement is nearly identical to that recorded by Farlow *et al*. (2005). This creates a cranial length to total length ratio of 0.17727, higher than reported for *C. porosus* or *A. mississippiensis* (Woodward, White & Linda, 1995; Sereno *et al*. 2001; Young *et al*. 2011b). These are instead more similar to low values of *G. gangeticus*, but still much lower than for metriorhynchids (Sereno *et al*. 2001; Young *et al*. 2011b). Farlow *et al*. (2005) attempted to use femoral data from *A. mississippiensis* to predict the size of this same *Boverisuchus* specimen from Geiseltal. The calculation they generated from the specimen's femur was much higher than the measured total length of the specimen (Farlow *et al*. 2005). The researchers suggested that an
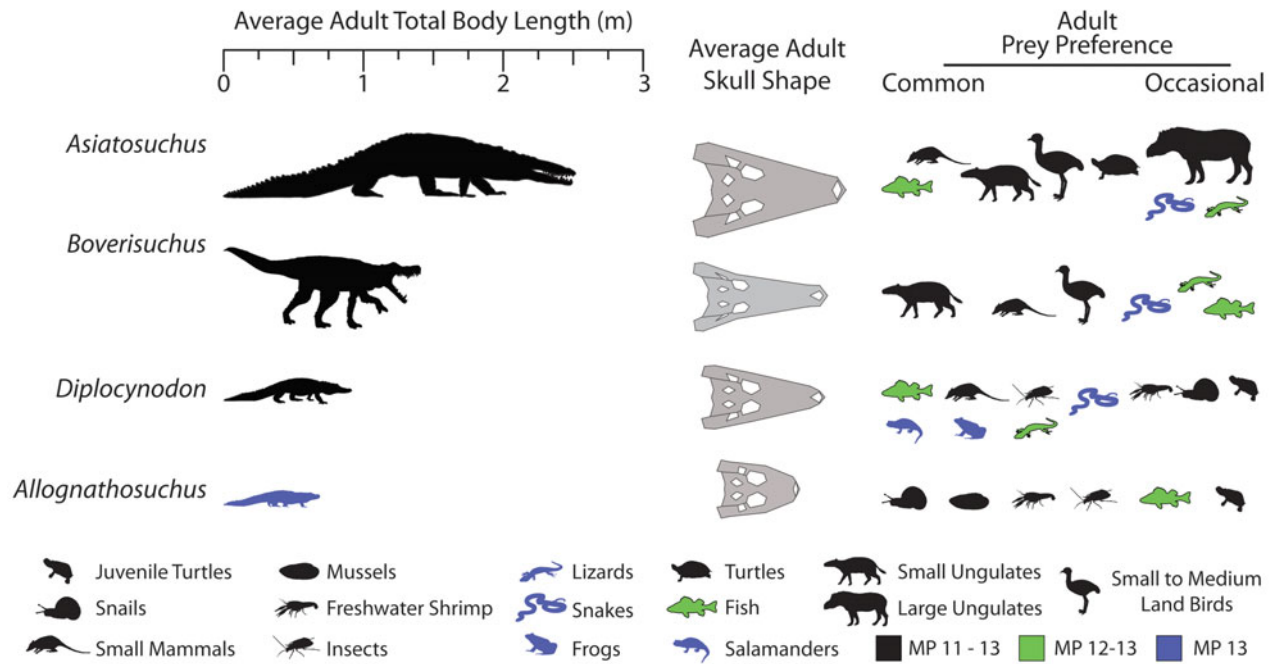
Figure 11. (Colour online) Reconstructed total body length estimated from fossil measurements (Table 1) and known relationships between head and body length in crocodylians (see Discussion 4.b.1 for details). Average adult skull shapes were formed from consensus plots of morphospace exclusive to the taxon. Reconstructed diet determined from similarity to extant morphospace and known fossil taxonomic occurrences at the Geiseltal-Fossillagerstätte, as well as other information; see Discussion 4.b.2–5 for details. MP stands for mammal Palaeogene zone.

unusually large femur length: total length ratio could have caused this problem (Farlow *et al*. 2005). The study also returned higher-than-measured estimates calculated from cranial lengths derived from *Alligator* and *C. porosus* (Farlow *et al*. 2005). In the absence of a larger dataset for a more closely related taxon, we elected to use this single ratio to estimate body sizes of the other fossil *Boverisuchus* of Geiseltal (Table 1). The average from the *Boverisuchus* specimens of this study (1.41 m) is smaller than the estimates from either *A. mississippiensis* (1.56 m) or *C. porosus* (1.72 m).

The averages of these values are presented in Figure 11, showing the relative sizes of the Geiseltal crocodylians. *Asiatosuchus* represents the largest Geiseltal crocodylian by far with an average length of 2.52 m, and is the largest predator from the fossil site, being much larger even than the mammalian carnivores. *Boverisuchus* was still quite large at an average adult length of 1.41 m. *Diplocynodon* averaged around 0.91 m, being consistently smaller than *Asiatosuchus* and *Boverisuchus*. The smallest are the *Allognathosuchus* at only 0.71 m average adult length. These small crocodylians are adults despite their small stature. At least three other individuals are known from Geiseltal that also represent small adults, although their skulls were not complete enough to be included in this study.

4.b.2. *Estimating potential prey preference of* Allognathosuchus

From comparison of skull shape and body size data for each Geiseltal taxon to the extant dataset, we can estimate the likely diet of these extinct crocodylians. The closest similarities within the extant geometric morphometric dataset to *Allognathosuchus* were the dwarf caiman, *Paleosuchus palpebrosus* and the dwarf crocodile, *Osteolaemus tetraspis* (Fig. 12). The size of these living crocodylians rarely exceeds 2 m (Eaton, 2010; Magnusson & Campos, 2010), making them the smallest species of living crocodylians. Body size estimates for *Allognathosuchus* are even smaller, less than 1 m (Table 1).

In addition to similar landmark configuration, the dwarf crocodile and dwarf caiman both have heterodont dentition with sharpened teeth anteriorly and molariform teeth posteriorly (Frey & Monninger, 2010; Fig. 12). The posterior dentition of *Allognathosuchus* is remarkably molariform, being very flat without an apical point, and would likely have served well for a durophagous diet (Fig. 12). Furthermore, these teeth are often heavily worn (Fig. 12), showing strong similarity to teeth of fossil and modern crocodylians previously interpreted as crushing hard food items including molluscs, crustaceans and turtles (Ösi & Barrett, 2011). The dwarf crocodile and dwarf caiman commonly eat insects, snails, crabs, shrimp and fish (Magnusson, Vieira da Silva & Lima, 1987; Pauwels *et al.* 2007). Based on the diet, dentition and shape similarity of *Paleosuchus* and *Osteolaemus*, and the small size of *Allognathosuchus*, it was likely restricted to similar small, armored prey. Possible prey items that lived at the same MP 13 zone of Geiseltal included crustaceans (Beurlen, 1938), bivalves (Krumbiegel, 1990) and gastropods (Krumbiegel, 1963). Also available were insects
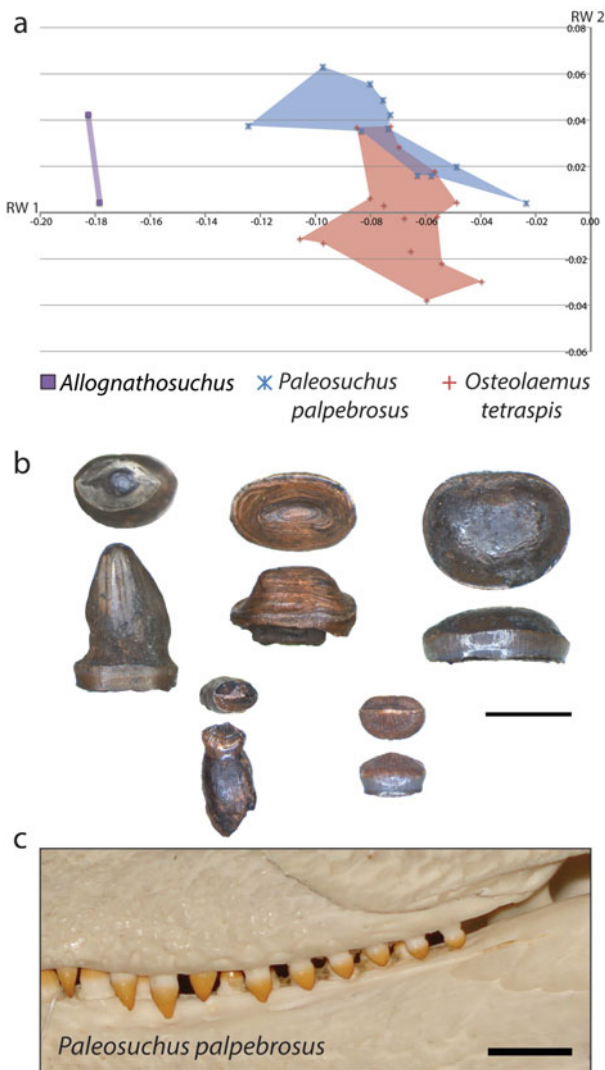
Figure 12. (Colour online) (a) XY scatter plot of relative warps 1 and 2 from the combined analysis showing only *Allognathosuchus* and extant species with closest similarity. (b) Examples of dentition from *Allognathosuchus* in worn condition (top three specimens) and unworn (bottom two specimens); each tooth is shown in occlusal and lateral view; GMH III-10173-1949; scale bar 5 mm. (c) Comparable dentition in *Paleosuchus palpebrosus* in left lateral view (ICN 1818); scale bar 1 cm.

(Weidlich, 1987) and fish (Voigt, 1934; Gaudant, 1988), which likely rounded out the diet based on the modern diet of both *Paleosuchus* and *Osteolaemus* (Magnusson, Vieira da Silva & Lima, 1987; Pauwels *et al.* 2007). Turtles were suggested as a probable prey item of *Allognathosuchus* (Carpenter & Lindsey, 1980) due to their very blunt teeth and stout jaw. Turtles were present at this time at Geiseltal (Hummel, 1935) but, due to the small size of *Allognathosuchus*, adult turtles were likely too large. However, juvenile turtles may have been an occasional prey item.

It should be noted that, being an alligatoroid (Brochu, 2004), *Allognathosuchus* would be predicted to be more similar to living forms due to the stronger phylogenetic effect on rostral morphology found in a 3D study of

modern crocodylian skulls (Piras *et al.* 2009, 2014). However, the more severely negative RW 1 traits of *Allognathosuchus*, combined with its highly flattened rear teeth, appear to represent adaptation towards a strongly durophagous diet to a greater degree than other Geiseltal genera.

4.b.3. *Estimating potential prey preference of* Boverisuchus

Within the combined Geiseltal and extant RW 1 v. RW 2 morphospace plots, *Boverisuchus* occupied a wholly different morphospace from all modern crocodylians and the other members of the Geiseltal fauna (Fig. 10). The positive but low RW 1 and positive RW 2 placement of *Boverisuchus* landmarks indicated a narrow, triangular snout. This shape was similar in terms of RW 2 to certain specimens of *Diplocynodon*. The landmark configurations of *Boverisuchus* specimens did not reflect nearly as extreme values of RW 1 as *Gavialis* skulls (Fig. 13) but were still longirostrine, and the general triangular shape of the skull is consistent in some ways with *Gavialis*. Furthermore, the shape analysis placed *Boverisuchus* from Geiseltal nearest to one member of the Cuban Crocodile (*Crocodylus rhombifer*; Fig. 13). The Cuban Crocodile has been noted for having a more terrestrial behaviour, having been seen far from water sources and even jumping on land for semi-arboreal hutias (Morgan & Albury, 2013). The Indian Gharial (*Gavialis gangeticus*) is however strictly fluvial in habitat (Stevenson & Whitaker, 2010). The dietary preferences of these two taxa reflect their preference of habitat. The Cuban Crocodile has a diet consisting mostly of small terrestrial mammals (Soberón, Ramos & Barr, 2001), while the gharial consumes almost exclusively fish (Stevenson & Whitaker, 2010). RW 1 values of *Boverisuchus* are more consistent with *C. rhombifer*, while RW 2 values are more consistent with *Gavialis*. *Boverisuchus* landmarks with respect to these two relative warps axes do not match either taxon, indicating a potentially different purpose but with at least some similarity to both.

To interpret the potential diet for *Boverisuchus*, it helps to also incorporate other known features of its morphology. For example the teeth have true serrations (Fig. 13), an unusual trait not seen in modern crocodylians and only seen in a small number of fossil crocodyliforms. Serrated teeth are typically seen in either fully terrestrial predators, such as theropod dinosaurs and Komodo dragons (D'Amore & Blumenschine, 2009), or in fully marine predators such as some sharks (Frazzetta, 1988). Truly serrated teeth (excluding falseziphodonty, *sensu* Young *et al.* 2013) are known to have evolved independently in multiple lineages of Crocodyliformes, typically from taxa interpreted as being either terrestrial (e.g. sebecids, baurusuchids or mekosuchines; Montefeltro, Larsson & Langer, 2011; Sobbe, Price & Knezour, 2013; Kellner, Pinheiro & Campos, 2014) or marine (e.g. certain metriorhynchids; Young *et al.* 2013). Given that the Geiseltal site is quite far from a marine habitat, even during middle Eocene
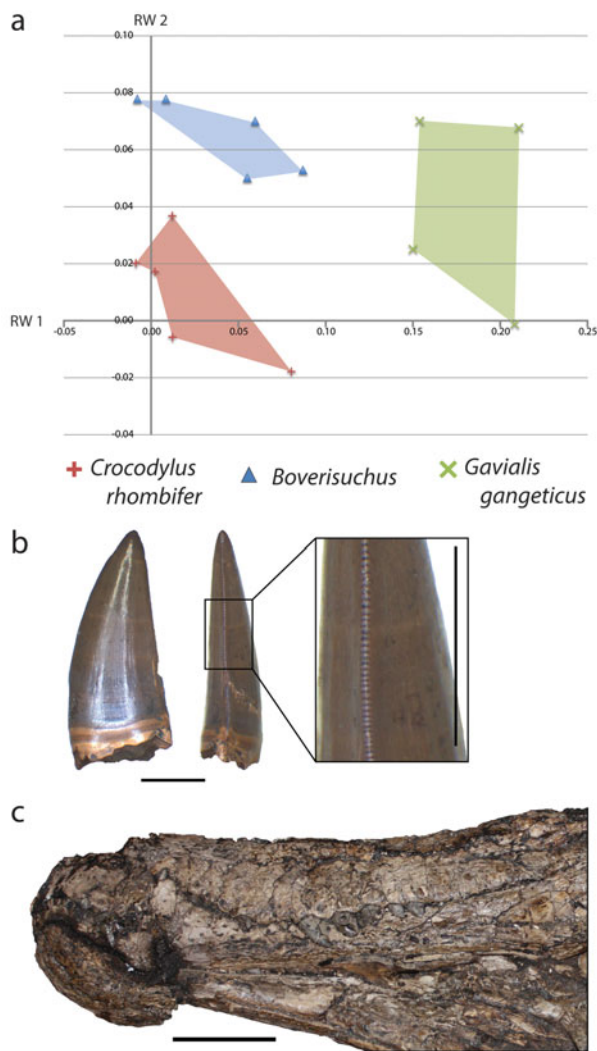
Figure 13. (Colour online) (a) XY scatter plot of relative warps 1 and 2 from the combined analysis showing only *Boverisuchus* and extant species with closest similarity. (b) Example of a serrated tooth from *Boverisuchus* in lateral and posterior views; GMH VI-1500-1952; both scale bars 5 mm. (c) Lateral view of exposed dentition of *Boverisuchus*; GMH Leo X-8001-1938; scale bar 10 cm.

time, the terrestrial preference seems more likely. In each case, serrations are useful for cutting prey that cannot be swallowed whole. This enables land predators to consume prey that is much larger than their jaws. For terrestrial predators that do not chew their food, this is necessary for defleshing the prey when force alone is not sufficient (D'Amore & Blumenschine, 2009). The teeth of *Boverisuchus* bow ventrally with elongated upper teeth exposed when the jaws are shut (Fig. 13), which is much more similar to the morphology of *C. rhombifer* than to *Gavialis*. Furthermore, *Boverisuchus* has longer limbs in relation to its body (Farlow *et al*. 2005) as well as hoof-like phalanges (Brochu, 2013), both of which have been interpreted as reflecting a more terrestrial habitat. Combining the evidence for different skull shape, tooth morphology, limb length and phalangeal morphology, *Boverisuchus* appears to have been

adapted for a very different method of prey acquisition from living crocodylians as well as from other Geiseltal crocodylians. Given the skull shape similarity, greater dentition similarity and connections to terrestrial (not fluvial) habitat (Soberón, Ramos & Barr, 2001), the Cuban Crocodile seems to be a better analogue than the Gharial for *Boverisuchus*.

There are some clues as to crocodylian predation of terrestrial prey within the middle Eocene fossil records of Germany. The Geiseltal fossil site is well-known for horses that were comparatively small in size, for example, *Propalaeotherium* (Hellmund & Koehn, 2000; Hellmund, 2013*a*). A small publication made during the ongoing excavations stated: 'Krokodilzähne in Kieferknochen von Paläohippiden deuten darauf hin, daß diese von Krokodilen angefallen und gebissen wurden' (original quote in German by Krumbiegel, 1959, p. 119), which translates as 'Crocodile teeth in the jawbones of primitive horses [formerly called palaeohippids] suggest that these were attacked and bitten by crocodiles'.

No crocodile teeth preserved within a horse jaw have yet been found within the Geiseltal Collection; however, they may have become disassociated during the last 56 years. An observation from the German fossil site Eckfeld (MP 13) states, regarding a fossil primate jaw, that 'bite marks in the front of the mandible and the [dis]solution of tooth enamel point in the case of the *Periconodon* specimen to crocodile digestion' (Franzen, 2004). Crocodylian predation of non-aquatic prey such as small horses and primates would be consistent with *Boverisuchus* as a terrestrial predator, although it does not mean that these animals were necessarily attacked by *Boverisuchus* specifically.

Crocodylus rhombifer is known to eat small mammals such as hutia (Soberón, Ramos & Barr, 2001). Similarly sized mammals were also present at Geiseltal, including insectivorans, marsupials and primates (Hellmund, 2007). These animals may have provided an appropriate prey source for *Boverisuchus*. Other prey of similar size at Geiseltal could have included occasional large snakes and/or lizards (Hellmund, 2007). Given the similarity in RW 2 between *Boverisuchus* and *Gavialis*, fish may also have been at least a component of its prey preference. It should be noted that snakes, lizards and fish grow far more common at Geiseltal up to MP 13 and have yet to be recovered from MP 11 (Hellmund, 2007; Table 1). Although it would represent a different kind of prey, Geiseltal fossils of terrestrial non-volant birds such as *Palaeotis* have been recovered that could have fallen prey to a terrestrial predator even at adult size (Houde & Haubold, 1987). Additionally, juveniles of the larger bird *Gastornis* may also have been a source of prey (Fischer, 1962; Hellmund, 2013*b*). The only mammalian cursorial carnivore of comparable size from Geiseltal was the creodont *Oxyaenoides bicupsidens*, but this taxon was only present during MP 11 (Morlo, 1999; Hellmund, 2007; Table 1); competition from other large-bodied land predators
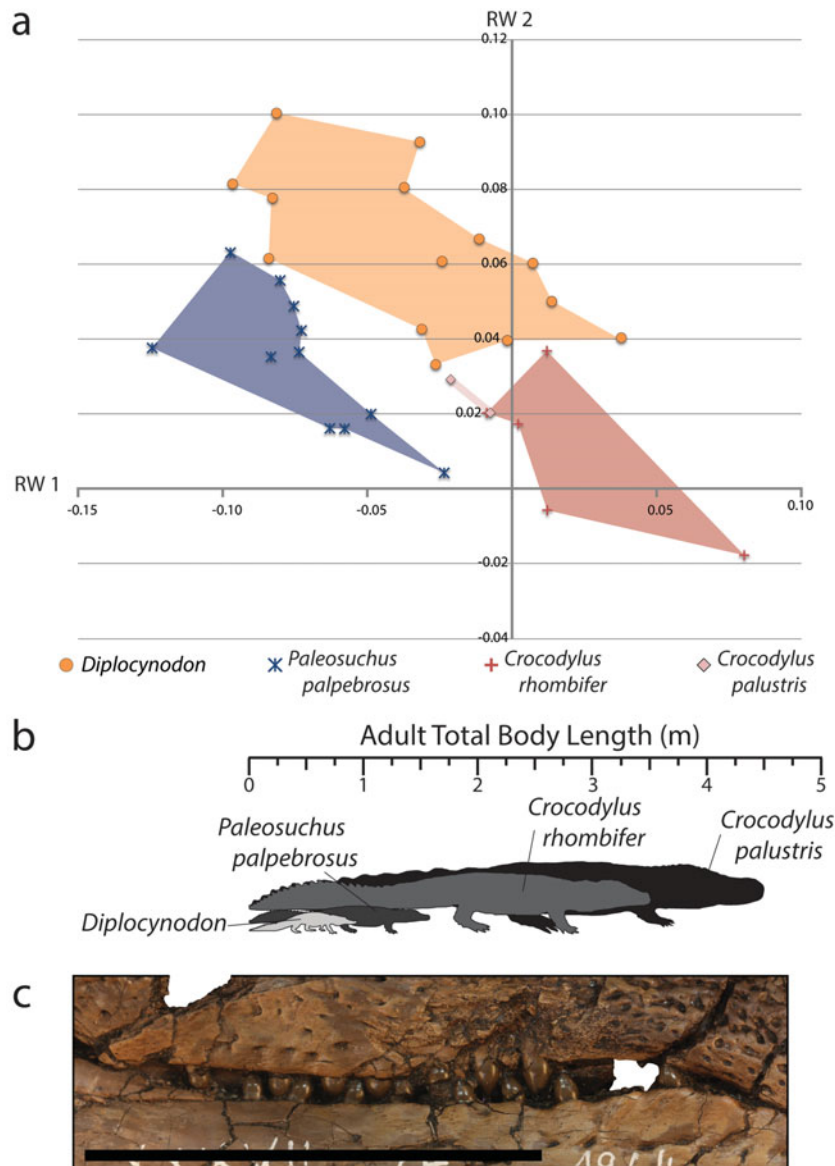
Figure 14. (Colour online) (a) XY scatter plot of relative warps 1 and 2 from the combined analysis showing only *Diplocynodon* and extant species with closest similarity. (b) Size comparison between *Diplocynodon* and the three extant taxa identified in the combined geometric morphometric analysis as having similar RW 1 v. RW 2 morphospace above; total body length values for extant taxa are: 1.6 m for *Paleosuchus palpebrosus* (Medem, 1981), 3.5 m for *Crocodylus rhombifer* (Varona, 1966) and 4.5 m for *Crocodylus palustris* (Chang *et al*. 2012); *Diplocynodon* estimate from this study. (c) Right lateral view of rear dentition of *Diplocynodon* from Geiseltal; GMH XXXVII-54-1964; scale bar 5 cm; anterior is to the right.

would therefore have been low to non-existent at Geiseltal.

4.b.4. *Estimating potential prey preference of* Diplocynodon

The *Diplocynodon* of Geiseltal placed in RW 1 v. RW 2 morphospace not occupied by any modern crocodylian, although it did overlap with some specimens of *Asiatosuchus*. As an alligatoroid (Delfino & Smith, 2012) this is somewhat surprising, given the known phylogenetic effect on morphological disparity in Alligatoroidea (Piras *et al*. 2009). However, *Diplocynodon* of Geiseltal plotted close to another alligatoroid, the dwarf caiman (*Paleosuchus palpebrosus*), as well as two crocodyloids, the Indian Mugger (*Crocodylus palus-*

tris) and the Cuban Crocodile (*Crocodylus rhombifer*). Skull shape in these crocodylians seems to be characterized by positive RW 1 and RW 2 values near the consensus (Fig. 14). The *Diplocynodon* specimens closest to *P. palpebrosus* had more pointed snouts, with positive RW 2 and negative RW 1 traits. In turn, the *Diplocynodon* closest to *C. rhombifer* and *C. palustris* have less pointed snouts with low positive RW 2 and near-consensus RW 1 traits.

The diets of these three extant crocodylians are rather different from each other. The dwarf caiman regularly consumes insects, crustaceans, molluscs and fish (Magnusson, Vieira da Silva & Lima, 1987). The Indian Mugger, quite a bit larger than *Diplocynodon*, regularly consumes insects (as juveniles), crustaceans, fish,
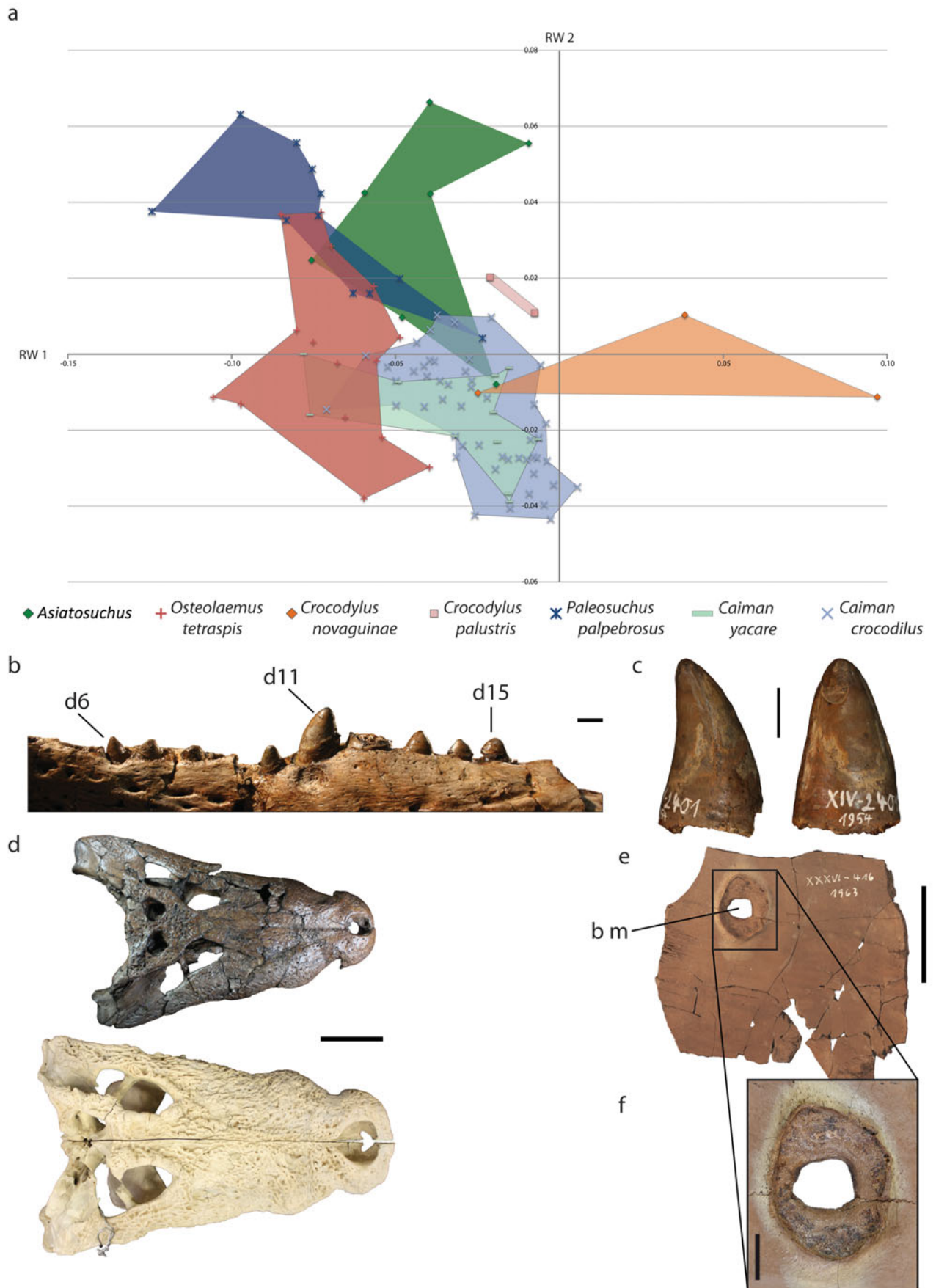
Figure 15. (Colour online) (a) XY scatter plot of relative warps 1 and 2 from the combined analysis showing only *Asiatosuchus* and extant species with closest similarity. (b) Left lower dentition of *Asiatosuchus* in left lateral view; GMH XIV-4757b-1956; scale bar 1 cm. (c) Enlarged view of *Asiatosuchus* tooth in anterior and labial views; GMH XIV 2401 1954; scale bar 1 cm. (d) Comparison of

frogs, reptiles, small mammals and occasional large mammals as adults (De Silva *et al.* 2011). As stated, the Cuban Crocodile is known for a diet consisting mostly of small terrestrial mammals (Soberón, Ramos & Barr, 2001).

Considering the shape similarity in RW 1 v. RW 2 morphospace with these three crocodylians and their widely variable dietary information, it appears *Diplocynodon* was a small generalist. Of the three extant forms, the size of adult *Diplocynodon* is most similar to *P. palpebrosus* (Fig. 14). Comparing the diet of the dwarf caiman to prey available at Geiseltal, *Diplocynodon* would likely have eaten from a variety of small prey, including those with armor. Studies of modern crocodylians found that bite force scales with body size in all living species (as measured on land; Erickson *et al.* 2012, 2014), so this difference of size likely translates to a difference in potential prey, both in terms of prey hardness and prey size. The small stature of *Diplocynodon* likely precluded large prey that similarly shaped *C. palustris* can consume, meaning that prey such as ungulates, adult land birds and adult turtles would not be likely food sources. The dentition of *Diplocynodon* (Fig. 14) is not nearly as flat or bulbous as *Allognathosuchus* (Fig. 12), but more similar to anterior teeth of *P. palpebrosus* (Fig. 12) than to the round, peg-like teeth of *C. palustris* or the more compressed teeth of *C. rhombifer*.

However, given the RW 1 v. RW 2 morphospace similarity to both *C. palustris* and *C. rhombifer*, *Diplocynodon* may have regularly consumed small mammals (Soberón, Ramos & Barr, 2001; De Silva *et al.* 2011). The lack of features associated with terrestriality in *Diplocynodon* indicates that, like most crocodylians, *Diplocynodon* was adapted to an aquatic habitat as in extant *P. palpebrosus* and *C. palustris* (Magnusson, Vieira da Silva & Lima, 1987; De Silva *et al.* 2011). Given their presence in the diet of *P. palpebrosus* and young *C. palustris*, small prey such as insects, fish, frogs and reptiles were a likely part of the diet of *Diplocynodon*. Fossils of insects, fish, frogs, salamanders, lizards and snakes have been recovered from the same levels as *Diplocynodon* at Geiseltal (Fig. 11). However, fish, amphibians, snakes and lizards are much more common during MP 13 at Geiseltal and are unknown so far from MP 11 (Hellmund, 2007; Table 1).

4.b.5. *Estimating potential prey preference of* Asiatosuchus

In the combined morphospace of RW 1 v. RW 2, *Asiatosuchus* specimens were characterized by negative RW 1 and mostly positive RW 2 traits (Fig. 10). Perhaps as a result of the high morphological disparity of crocodyloids (Piras *et al.* 2009), the morphospace of *Asiatosuchus* overlapped with three different genera of extant crocodylians (Fig. 15): *Osteolaemus tetraspis* (Dwarf Crocodile); *Paleosuchus palpebrosus* (Dwarf Caiman); and *Caiman* (*C. crocodilus* and *C. yacare*). The *Asiatosuchus* morphospace is also very close to that of *Crocodylus palustris* and *Crocodylus novaeguineae* (Fig. 15). These six species in four genera have fairly similar skull landmark configurations, with the specimens closest to *Asiatosuchus* being characterized by positive RW 1 traits but near the consensus. The *Asiatosuchus* with lower RW 2 traits were most similar to the caimans (*Caiman* and *Paleosuchus*) and the two true crocodiles (*C. palustris* and *C. novaguinae*). The *Asiatosuchus* with the highest RW 1 were nearest *Osteolaemus*, with similarly robust snouts.

The skull shape of these extant crocodylians is somewhat varied as in *Asiatosuchus*, and their diet is also fairly diverse. As mentioned above, the dwarf crocodiles and dwarf caimans commonly eat insects, snails, crabs, shrimp and fish (Magnusson, Vieira da Silva & Lima, 1987; Pauwels *et al.* 2007); however, their adult size is much smaller than that of *Asiatosuchus*. The spectacled caiman, *Caiman crocodilus*, typically consumes much of the same food, but with a greater portion of its diet coming from fish as individuals approach adulthood (Magnusson, Vieira da Silva & Lima, 1987). Adult *Crocodylus palustris*, the Indian Mugger, tend to eat crustaceans, fish, reptiles, small mammals and occasional large mammals (De Silva *et al.* 2011). Unfortunately, there is little to nothing published regarding the natural diet of the New Guinea crocodile, *Crocodylus novaeguineae*. *Asiatosuchus* does not appear to have any of the terrestrial adaptations described above for *Boverisuchus*.

Of the six most similar skull shapes within the extant dataset the specimens of *Asiatosuchus* seem most similar to *C. palustris* (Fig. 15), a large-bodied generalist ambush predator (De Silva *et al.* 2011). The similarity between the taxa is in terms of the body size, an overall flattened skull, a robust and wide snout and rounded, peg-like dentition in the rear of the jaw (Fig. 15). The only difference in diet between *C. palustris* and the others described above is a lack of insect consumption as adults (De Silva *et al.* 2011). For the diet of *Asiatosuchus*, small prey items such as insects, snails and crustaceans only appear to have been a regular part of the diet at young ages when body size was most similar to adults of *P. palpebrosus* and *O. tetraspis* (rarely exceeding 2 m; Eaton, 2010; Magnusson & Campos, 2010). However, without well-preserved juveniles of *Asiatosuchus*, it is unknown if skull shape at a young age was also similar to these crocodylians.

Asiatosuchus skull from Geiseltal (GMH XIV 4757a-1956) and modern specimen of *Crocodylus palustris* (ZMB 37193, Zoological Collection of the Museum für Naturkunde, Berlin); scale bar 5 cm. (e) Internal view of a costal section of the carapace of the freshwater turtle *Geochelone eocaenica* (GMH XXXVI-416-1963) with crocodylian bite mark preserved, including surrounding impact scar; scale bar 5 cm. (f) Enlarged view of the bite mark of the same specimen in (e); scale bar 1 cm. bm – bite mark; d6 – sixth dentary tooth; d11 – eleventh dentary tooth; d15 – fifteenth dentary tooth.

Given that there was some landmark similarity to *Caiman* in RW 1 v. RW 2 morphospace, the fact that *Caiman* gain a greater portion of their diet from fish as they grow larger (Magnusson, Vieira da Silva & Lima, 1987) may indicate that fish played a significant role in the diet of *Asiatosuchus*. Fish is also a regularly consumed item in *C. palustris* (De Silva *et al.* 2011). Again, it should be noted that fish are unknown from MP 11 at Geiseltal and are only common during MP 13 (Hellmund, 2007; Table 1). A single record of a lepisosteid is known from MP 12, but numerous fish have been recovered from MP 13 (Gaudant, 1988; Gaudant & Haubold, 1995). In earlier stratigraphic ages, fish and other aquatic animals were either not fossilized or the crocodylians relied more on their other prey preferences. The consumption of reptiles by *C. palustris* (De Silva *et al.* 2011) may indicate that occasional large snakes and lizards were also consumed by *Asiatosuchus*, but again these are more common during MP 13 and unknown for MP 11 (Hellmund, 2007; Table 1). The large size of *Asiatosuchus* and its similarity in RW 1 v. RW 2 morphospace to *C. palustris* suggests larger prey was viable in adulthood. By comparing this sort of prey of the Indian Mugger (deer, sambars, buffaloes; De Silva *et al.* 2011) to that found at Geiseltal, the most likely candidates are large and small ungulates such as *Lophiodon* and *Propalaeotherium*, present during all three MP zones discussed. Also present at Geiseltal are condylarths and several other groups of small mammals that represent sizes similar to prey of these extant crocodylians (Hellmund, 2007).

Based on studies of living crocodylians (Erickson *et al.* 2012, 2014), the larger size of *Asiatosuchus* (Table 1) would likely mean a proportionally greater bite force than *Diplocynodon*. As mentioned above, this has been used in *C. palustris* for consuming large ungulates (De Silva *et al.* 2011). Furthermore, the similarly sized and shaped *C. palustris* have been documented eating multiple kinds of testudines (De Silva *et al.* 2011). A fossilized predation attempt on the middle Eocene turtle *Neochelys* of Spain has been described previously as having been caused by *Asiatosuchus* (Jiménez-Fuentes, 2003). A partial carapace of the adult freshwater turtle *Geochelone eocaenica* (GMH XXXVI-416-1963) was recovered from Geiseltal (MP 13) with a clear crocodylian tooth puncture mark, consistent with teeth of *Asiatosuchus* (Fig. 15). The blunt, round teeth and robust jaws of *Asiatosuchus* likely assisted in managing armored prey. Given the similarity of shape between *Asiatosuchus* and *Diplocynodon*, but notable difference in size (Fig. 6), these taxa seem to have similar differentiation as sympatric *Crocodylus porosus* and *C. johnstoni* (Webb, Manolis & Sack, 1983). Interestingly, a study by Martin (J. Martin, unpub. Ph.D. thesis, Univ. Lyon, 2009) also found similarity in geometric morphometric morphospace between *Asiatosuchus* ($n = 4$) and *Diplocynodon* ($n = 7$), although these were from multiple sites and geological ages.

5. Concluding remarks

The fossil crocodylians of the Geiseltal fauna represent a situation of high diversity and provide a good framework for studying partitioning of prey preference within related taxa. As crocodylians are typically thought of as 'opportunistic feeders', there will be overlap among certain occasional prey items (Fig. 11). It is however clear from the present analysis that, within a community of opportunistic feeders, there are still adaptations and specializations that likely enabled these taxa to cohabitate. Also, the time when all four crocodylian genera are found together (MP 13) is also when far more aquatic prey species are recovered as fossils at Geiseltal. Considering these fauna are also present from MP 11 at Messel (Morlo *et al.* 2004) and MP 13 at Eckfeld (Neuffer *et al.* 1996), this interaction evidently persisted in central Germany for the entire Geiseltalian period (MP 11–13) but may have reached its peak at Geiseltal during MP 13. Studies have previously linked crocodylian diversity to changes in climatic conditions, primarily temperature (Markwick 1998*a*, *b*; Martin, 2010; Martin *et al.* 2014; Mannion *et al.* 2015). This high crocodylian diversity occurs during the middle Eocene period characterized by warm temperatures (Mosbrugger, Utescher & Dilcher, 2005; Tütken 2014), which likely played a large part in the ability of these ectotherms to diversify.

Declaration of interest

None.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0016756815001041.

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