Chapter 3
Was *Ophiacodon* (Synapsida, Eupelycosauria) a Swimmer? A Test Using Vertebral Dimensions

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Abstract *Ophiacodon,* a Permian synapsid, has been hypothesized to be semi-aquatic. This interpretation is based on a range of evidence, including observations of histology, phalangeal morphology, dentition, and taphonomy. However, many of these data are inconclusive or have been reinterpreted. Here we investigate whether the morphology of the axial skeleton in *Ophiacodon* displays specializations for aquatic locomotion. Qualitative and quantitative comparisons of *Ophiacodon* to extant terrestrial and semi-aquatic tetrapods demonstrate that the distribution of centrum lengths in its vertebral column is similar in some ways to those of extant semi-aquatic reptiles. However, other basal synapsids that are widely regarded as terrestrial show comparable patterns, and the correlation between swimming style and vertebral morphology in extant semi-aquatic tetrapods may be weaker than previously thought. Therefore, vertebral proportions provide little support for a semi-aquatic lifestyle in *Ophiacodon*. Given that most lines of evidence are equivocal at best, we suggest that future studies that consider the ecology of *Ophiacodon* use a terrestrial lifestyle as a null hypothesis.

Keywords Permian • Carboniferous • Centrum length • Limb length • Aquatic tetrapods • Ophiacodontidae

Introduction

The eupelycosaurian synapsid *Ophiacodon* (Fig. 3.1) is a common component of Late Carboniferous and Early Permian terrestrial ecosystems. Six species of *Ophiacodon* are currently recognized: the type species *Ophiacodon mirus* Marsh, 1878; *O. uniformis* (Cope, 1878) Romer and Price, 1940; *O. navajovicus* (Case, 1907) Romer and Price, 1940; *O. hilli* (Romer, 1925) Romer and Price, 1940; *O. retroversus* (Cope, 1878) Romer and Price, 1940; and *O. major* Romer and Price, 1940. All are found in North America (New Mexico, Texas, Utah, or Kansas) in terrestrial deposits (Marsh 1878; Reisz 1986; Eberth and Berman 1993; Eberth and Miall 1991), with the exception of *O. hilli*, which is known from marine limestones in Kansas (Romer 1925) and a fragmentary dentary from the Kenilworth Breccia in the United Kingdom that Paton (1974) referred to the genus. *Ophiacodon* was one of the larger animals in these communities, ranging from around 160 to 300 cm in total length (Reisz 1986) and between 26 and 230 kg in mass (Romer and Price 1940).

Ophiacodon has long been interpreted as a semi-aquatic piscivore (e.g., Case 1907; Romer and Price 1940; Kemp 1982; Reisz 1986; Germain and Laurin 2005) and several lines of evidence have been cited in support of this hypothesis. For example, Romer and Price (1940) suggested that the flattened unguals of *Ophiacodon* were indicative of aquatic habits, and its small, sharp teeth resemble those of extant crocodiles, perhaps indicating a piscivorous diet (Kemp 1982). Unique among Permian synapsids, the skeleton of *Ophiacodon* tends to be poorly ossified, particularly the limb bones (Reisz 1986). This morphology is thought to suggest a slowing of ossification in *Ophiacodon* relative to other taxa such as *Dimetrodon* (Brinkman 1988), and is reminiscent of the condition commonly seen in secondarily aquatic tetrapods (Romer 1948). The bone microanatomy of *Ophiacodon* also has been interpreted as consistent with a semi-aquatic lifestyle (Germain and Laurin 2005). Finally, a

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Fig. 3.1 Photograph of *Ophiacodon mirus* (FMNH UC 671) on display at the Field Museum of Natural History

single specimen, the holotype of *Ophiacodon hilli*, was found in a marine limestone (Romer 1925), although the majority of specimens occur in more terrestrial sediments that also produce other basal synapsids (Romer and Price 1940). Although these observations are consistent with an amphibious lifestyle, none are completely unequivocal and little detailed analysis of the semi-aquatic *Ophiacodon* hypothesis has been performed.

Here we test whether *Ophiacodon* was likely semi-aquatic by examining the morphology of the axial skeleton, specifically whether proportions of its vertebrae are comparable to other swimming tetrapods. The relationship between axial morphology and locomotor style in swimming tetrapods is well documented (Fish 1984, 1994; Ritter 1996; Buchholtz 1998, 2001a, b; Pierce et al. 2011), with the degree of adaptation for aquatic locomotion reflected in the flexibility of the vertebral column. Vertebral column flexibility depends in part on the proportions of the individual centra: long, thin, spool-shaped centra indicate greater flexibility, whereas short, wide, disc-shaped centra imply greater stiffness (Buchholtz 1998, 2001a, b). In addition, semi-aquatic and aquatic tetrapods have peaks or plateaus in centrum length corresponding to the point(s) of maximum undulation in the vertebral column, which are not found in terrestrial tetrapods (Buchholtz 1998, 2001a). We compared vertebral proportions in *Ophiacodon* to several extant and extinct tetrapods with known locomotor patterns to test whether its vertebral morphology was consistent with its hypothesized semi-aquatic lifestyle. In addition, we investigated the disparity in hind limb and fore limb lengths noted by Romer and Price (1940) and Kemp (1982) to test the hypothesis that the limb proportions of *Ophiacodon* were most similar to those of semi-aquatic tetrapods. A more decisive determination of the lifestyle of *Ophiacodon* will not only provide a better foundation for interpreting the distinctive features of its anatomy, but will also facilitate an improved understanding of the paleoecology of late Paleozoic Euramerican terrestrial communities.

Institutional abbreviations: FMNH, Field Museum of Natural History, Chicago, IL, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA.

Review of Evidence for a Semi-aquatic Lifestyle in *Ophiacodon*

The hypothesis that *Ophiacodon* was semi-aquatic has a long history, starting with Case's (1907) suggestion that ophiacodontids (Poliosauridae in Case 1907) were probably aquatic. However, Case provided no evidence in that monograph to support this assertion, and it seems to have received a mixed reaction. For example, Williston (1911, p. 80) stated that "the assumption that the animals were probably aquatic is evidently wrong," and did not include *Ophiacodon* among the taxa he discussed in his book on aquatic reptiles (Williston 1914). Likewise, Williston and Case (1913, p. 59) concluded that *Ophicaodon* was not a swimming animal, particularly noting that its slender tail "would have been of no use in the water in propulsion." Case (1915) himself is somewhat equivocal, commenting that ophiacodontids do not show aquatic adaptations of the feet or tail, but nevertheless proposing that they frequently took to the water to hunt and/or escape danger. Romer (1925) downplayed the significance of the discovery of the holotype of *Ophiacodon hilli* in a marine limestone, speculating that it was a terrestrial animal that had been washed out to sea after its death. In contrast, Romer and Price (1940) reasserted that *Ophiacodon* was likely semi-aquatic, and provided various lines of evidence from skeletal anatomy and taphonomy in support of the hypothesis. The assumption of a semi-aquatic ecology for *Ophiacodon* also played a key role in Romer's (1957, 1958) hypothesis that the amniotic egg evolved in the context of aquatic or semi-aquatic adults venturing onto land to reproduce. Most subsequent authors who have considered the subject cite Romer and Price's (1940) arguments directly, or use very similar lines of evidence.

Several morphological features of *Ophiacodon* have been used to infer that it was semi-aquatic. For example, *Ophiacodon* displays unusually poor ossification of the endochondral elements of the skull. The sutures between the elements of the braincase of other basal synapsids are normally indistinguishable, but they are all unfused and discernible in *Ophiacodon* (Reisz 1986). The joint surfaces of the long bones also appear to have remained cartilaginous throughout a longer period of ontogeny in *Ophiacodon* than in *Dimetrodon*, with the ulna and femur never reaching the degree of ossification seen in adult *Dimetrodon* specimens (Brinkman 1988). The sutures in the pelvis also remain poorly fused (Romer and Price 1940; Olson 1941). Romer and Price (1940) cited this poor ossification as evidence suggesting that *Ophiacodon* was semi-aquatic, and noted that this feature is well defined even in *O. major*, the largest species in the genus. Olson (1941) carried this argument further, using the lack of fusion of the pelvis in *O. major*, along with the species' expanded anterior ribs, tall caudal neural spines, and relatively late stratigraphic occurrence to propose that *Ophiacodon* became progressively more adapted to a semi-aquatic lifestyle over the course of its history. Whereas reduced ossification could be diagnostic of juvenile individuals with extremely rapid growth rates, specimens of *Ophiacodon* show little intraspecific size variation and are interpreted as adults (e.g., Romer and Price 1940; Ricqlès 1989). Reduced ossification of long bone articular surfaces and open sutures are widespread among secondarily aquatic tetrapods, and may be related to heterochronic changes in other aspects of gross morphology and microanatomy that frequently accompany secondary adaptation to semi-aquatic or aquatic habits in tetrapods (e.g., Ricqlès 1989; Ricqlès and Buffrénil 2001), so this evidence is consistent with a semi-aquatic lifestyle in *Ophiacodon*. At the same time some parts of the skeleton, such as the manus and pes, tend to be well ossified in *Ophiacodon* so the pattern is not perfect.

The skull and tooth morphology of *Ophiacodon* have been cited as evidence of a semi-aquatic lifestyle (Romer and Price 1940; Kemp 1982), primarily because they were interpreted as consistent with a piscivorous diet. Romer and Price (1940) noted that the skull of *Ophiacodon* is relatively tall and narrow compared to most other pelycosaur-grade synapsids, and that the jaws are relatively slender. They considered these features to translate into a mechanically weak skull that would be poorly suited to dealing with large terrestrial prey. This issue is difficult to address rigorously because the mechanical responses of "pelycosaur" skulls to loading have not received the same degree of attention as some therapsids (Jenkins et al. 2002; Jasinoski et al. 2009, 2010a, b, 2013; Jasinoski and Chinsamy-Turan 2012), and various lines of evidence suggest different conclusions about the mechanical properties of the skull of *Ophiacodon* compared to similarly-sized sphenacodontids such as *Dimetrodon*. For example, factor analysis indicates that its dimensions are generally similar to those of sphenacodontids (Gould 1965), primarily because of their proportionally longer snouts than herbivorous taxa such as *Edaphosaurus*. The large palatines of *Ophiacodon* also brace the maxillae in a manner similar to that described for *Dimetrodon* (Thomason and Russell 1986), which likely helped strengthen the snout against the bending and torsional loads expected when dealing with large prey. Additional evidence that the skull of *Ophiacodon* was likely resistant to such loads can be found in the fact that relatively tall, narrow skulls (i.e., oreinirostral skull morphologies) have been found to resist bending and torsion better than flatter (platyrostral) skulls in dinosaurs and crocodilians (McHenry et al. 2006; Rayfield et al. 2007; Rayfield and Milner 2008). However, the skull bones of *Ophiacodon* are relatively thin (Williston and Case 1913), which would weaken the skull even if it was similarly constructed.

The teeth of *Ophiacodon*, especially in the mandible, are smaller and more numerous than those of other large carnivorous pelycosaur-grade synapsids, and vary in shape from conical and relatively straight to slightly recurved. Serrations or distinct carinae are absent, although very weak ridges are sometimes present near the base of the crown. Strong wear features are not apparent, perhaps because of relatively frequent replacement (Reisz 1986). These features are not inconsistent with a piscivorous diet [e.g., the relative size and morphology of the teeth are similar to those in Massare's (1987) Pierce II and General guilds of marine reptiles, both of which were inferred to have a fish component in their diets], although the teeth of *Ophiacodon* are less numerous and more generalized than the slender, uniform, sharply pointed teeth of the closely related *Varanosaurus* (Berman et al. 1995). Indeed, Romer and Price's (1940) description of ophiacodontid teeth, which they use to argue for a piscivorous diet for members of the group, more closely resembles the dentition of *Varanosaurus* than *Ophiacodon*.

Romer and Price (1940) suggested that the relatively broad, flat unguals of *Ophiacodon* were indicative of a semi-aquatic lifestyle because they were unlike the laterally compressed, sharply pointed unguals of other basal synapsids. However, Maddin and Reisz (2007; also see Berman et al. 2004) recently examined changes in ungual morphology in basal synapsids and diadectids, and found evidence of an evolutionary trend from broad, flat unguals in the most basal synapsids and the outgroup to taller, more strongly curved, laterally compressed unguals in more crownward taxa, irrespective of inferred diet. In this context, the ungual morphology of *Ophiacodon* seems most likely a reflection of its relatively basal phylogenetic position than a proxy for its ecology.

Romer and Price (1940) and Kemp (1982) considered the disparity in limb lengths observed in *Ophiacodon* (hind limbs longer than fore limbs) as evidence of semi-aquatic habits. Little justification was provided for why this disparity would be consistent with such an ecology, aside from Romer and Price's statement that similar proportions are found in the aquatic mesosaurs. Differences in fore and hind limb proportions as adaptations to semi-aquatic or aquatic lifestyles have received attention in mammals, particularly in the context of whale evolution (e.g., Thewissen and Fish 1997; Gingerich 2003). Among mammals, limb proportions are useful in distinguishing hind limb- and fore limb-powered paddlers (Gingerich 2003). However, most of the changes in limb length occur in the manus or pes, particularly in the length of the metacarpals or metatarsals and the phalanges (Thewissen and Fish 1997; Gingerich 2003; Samuels and Van Valkenburgh 2008), reflecting the fact that the optimal shape for a drag-based propulsor is a tall triangle (Webb 1988; Thewissen and Fish 1997). The manus and pes of *Ophiacodon* do not show these sorts of proportional changes, however. Although the pes is larger than the manus (e.g., Romer and Price 1940), neither is especially triangular or elongate. Likewise, the length of the third and fourth metacarpals and metatarsals do not differ greatly from the lengths of the second and third metacarpals and metatarsals (e.g., Fig. 52 of Romer and Price 1940), similar to terrestrial mammals sampled by Thewissen and Fish (1997), but not semi-aquatic mammals with paddle-like feet.

In addition to gross morphology, bone histology has been used to infer a semi-aquatic lifestyle for *Ophiacodon*. Enlow and Brown (1957) and Ricqlès (1974) both noted that the cortices of the *Ophiacodon* specimens they sectioned were unlike those of other pelycosaur-grade synapsids they sampled in being highly vascularized. Enlow and Brown (1957) interpreted this as evidence that *Ophiacodon* was fast growing, but Ricqlès (1974) interpreted this observation, along with the primarily longitudinal orientation of the vascular canals and the lack of a clear distinction between the cortex and spongiosa as indicating a semi-aquatic lifestyle. In their quantitative analysis of bone cross-sectional area, Germain and Laurin (2005) explored the link between the lifestyle of tetrapods (including *Ophiacodon*) and several parameters related to the compactness of the radius. The compactness (density) of limb bones of tetrapods generally relates to whether the organism is terrestrial, amphibious, or aquatic. Semi-aquatic tetrapods, as well as some aquatic forms, typically have more compact bone as an adaptation to reduce buoyancy, whereas highly pelagic taxa have reduced skeletal density to achieve near neutral buoyancy (e.g., Taylor 1994; Madar 1998; Ricqlès and Buffrénil 2001; Laurin et al. 2004; Germain and Laurin 2005; Houssaye 2009; Northover et al. 2010; although see Nakajima 2010). Germain and Laurin (2005) took cross-sections of the radii of 46 species of tetrapods whose lifestyles were known and three taxa (including *Ophiacodon*) whose lifestyles were unknown, and calculated several parameters for a model fit to the compactness profile of each taxon. The low overall compactness (C in their model; also see Girondot and Laurin 2003) they report for *Ophiacodon*, along with its high S and P values (implying a slow transition between the medullary cavity and cortex, with the transition point between the two zones being located relatively far from the center of the bone), are consistent with Enlow and Brown's (1957) and Ricqlès' (1974) observations, and are most similar to the parameters of extant aquatic tetrapods. However, *Ophiacodon* was an outlier in a linear discriminant analysis of the data, falling outside of the ranges occupied by extant terrestrial, semi-aquatic, and aquatic taxa, leading Germain and Laurin (2005) to tentatively conclude that *Ophiacodon* was likely semi-aquatic. Although they noted that additional sampling of basal synapsids and sauropsids would be necessary to provide context for understanding the bone histology of *Ophiacodon*, the taxon was not included in similar analyses of the humerus and tibia (Kriloff et al. 2008; Canoville and Laurin 2010), making it uncertain whether the taxon's bones consistently show compactness profiles expected for a semi-aquatic tetrapod, as well as how they compare to coeval taxa such as *Dimetrodon* or *Captorhinus*.

Finally, taphonomy has been used to argue that *Ophiacodon* was semi-aquatic. As noted above, Romer (1925) documented the occurrence of *Ophiacodon hilli* in a marine limestone, but speculated that the specimen had been washed into that depositional environment after its death. Romer and Price (1940) ascribed greater significance to this occurrence, and included it among the evidence they cited in support of a semi-aquatic lifestyle for the taxon. While it is true that *Ophiacodon* is not represented in the most terrestrial Lower Permian fossil localities (Sullivan and Reisz 1999; Martens et al. 2005; Voight et al. 2007; Evans et al. 2009; Berman et al. 2013), and that marine occurrences are very unusual for basal synapsids, it is not unheard of for terrestrial tetrapod fossils to be preserved in marine rocks. More importantly, the vast majority of *Ophiacodon* fossils have been collected in rocks that represent terrestrial lowland floodplain, lacustrine, and deltaic environments (Hentz 1988, 1989; Eberth and Miall 1991), so it seems unlikely that the marine record of *Ophiacodon* provides particular insight into its ecology.

Taken together, these observations paint an equivocal picture of potential aquatic adaptation in *Ophiacodon*. Although some data (e.g., bone histology, reduced ossification of limb elements) are certainly very suggestive of a semi- aquatic way of life, much of the other evidence (e.g., limb proportions, ungual morphology, taphonomy) are either contradicted by more recent studies or are anecdotal at best. Therefore, it is necessary to bring new data to bear on the semi-aquatic *Ophiacodon* hypothesis.

Vertebral Anatomy and Aquatic Locomotion in Tetrapods

Many semi-aquatic and aquatic tetrapods, such as whales and their ancestors, ichthyosaurs and their ancestors, crocodilians, and even semi-aquatic mammals like otters or minks, move with axial undulatory locomotion (Buchholtz 1998, 2001a, b). Undulatory swimming involves waves of motion passing repeatedly along a propulsor, in this case the vertebral column (Buchholtz 1998, 2001a, b). Various parts of the vertebral column are reinforced and stiffened in order to increase the wavelength and decrease the amplitude of undulations (Buchholtz 1998, 2001a), which may be laterally- or dorsoventrally-directed. The degree of undulatory flexibility is controlled by regional variation in the axial musculature, soft tissues, and skeleton (Buchholtz 2001a). If *Ophiacodon* was indeed semi-aquatic, it likely swam in an undulatory manner analogous to crocodilians and other semi-aquatic tetrapods, and thus may show similar modifications of the vertebral column.

Vertebral proportions serve as an osteological correlate for regional flexibility in the vertebral column, and the relationship between vertebral morphology and locomotor style in swimming tetrapods is well known (Fish 1984, 1994; Ritter 1996; Buchholtz 1998, 2001a, b; Pierce et al. 2011). Long, narrow, spool-shaped vertebrae are at the center of the undulatory wave (Buchholtz 2001a), with the elongated shape increasing the displacement of the intervertebral joints, and therefore axial flexibility. Conversely, short, disk-shaped vertebrae impart less flexibility (Buchholtz 2001a) because the disk shape increases the articular surface of the centrum, limiting angular displacement of the intervertebral joint (Buchholtz 1998, 2001a). These differences in individual vertebral proportions have been proposed to translate into functionally significant patterns that can be recognized across the vertebral column. For example, depending on speed, the trunks of lizards with robust limbs bend into either a standing or traveling lateral wave during terrestrial locomotion (Ritter 1992). The location of this undulation is reflected by a distinct peak in centrum length between the girdles, with the relatively longest vertebrae corresponding to the peak of the (standing) wave (Buchholtz 1998). The tails of extant semi-aquatic reptiles such as the marine iguana or gharial typically move in traveling waves of lateral undulation, and in these taxa a plateau of relatively long centra are present in the tail reflecting where series of vertebrae undergo similar patterns of displacement (Buchholtz 1998). Peaks in centrum length also are found in the locations of undulatory waves in extant and fossil semi-aquatic and aquatic mammals, with the position and size of the peaks depending on the details of swimming style (Buchholtz 1998).

These observations allow us to make predictions about the distribution of vertebral proportions across the column of *Ophiacodon* if it was indeed a swimmer. Given that *Ophiacodon*, like most basal synapsids, possessed limb and vertebral morphologies that would correspond to a sprawling posture and symmetrical gait (e.g., Romer and Price 1940; Kemp 1982, 2005; Carroll 1986; Panko 2001), we predict that *Ophiacodon* engaged in lateral undulation during terrestrial locomotion to increase its stride length and perhaps aid in force transmission, although the degree of undulation may be less than observed in modern reptiles (e.g., Kemp 1982, 2005; Hunt and Lucas 1998, although see Carpenter 2009) and may have included a larger rotary component (Sumida and Modesto 2001). A corollary of this prediction is that *Ophiacodon* should show a peak in centrum length in its trunk region corresponding to the peak of its undulatory wave, much like extant sprawling tetrapods. Similarly, because the locomotor style of *Ophiacodon* was most likely more similar to extant reptiles than extant mammals, we also predict that if *Ophiacodon* was a swimmer then it should show a plateau in centrum length in its caudal series that is comparable to that observed in extant swimming reptiles.

Materials and Methods

We examined a total of 50 specimens from the Field Museum of Natural History and two from the University of California Museum of Paleontology (Table 3.1), representing at least 28 fossil and extant species. Our fossil sample consisted of 19 specimens representing at least 12 species of pelycosaur-grade synapsids belonging to several synapsid taxa: Caseidae (*Angelosaurus, Casea, Cotylorhynchus*), Varanopidae (*Aerosaurus*, *Varanops*), Ophiacodontidae (*Ophiacodon*), and Sphenacodontidae (*Dimetrodon, Sphenacodon*). All of the specimens represent articulated or semi-articulated individuals for which vertebral positions were known or could be determined. In some cases the specimens were mounted for display and included reconstructed vertebrae, but we excluded the reconstructions from

Table 3.1 Values for range (R), polarization (C), irregularity (Cm), concentration ($E1$), and smoothness ($E2$) metrics, and fore and hind limb lengths, for measured specimens

Taxon	Specimen	R (length)	C (length)	Cm (length)	$E1$ (length)	$E2$ (length)	R (height)	C (height)	Cm (height)
Angelosaurus romeri	FMNH UR 827	0.491	0.196	0.004	0.294	0.193	–	–	–
Casea broilii	FMNH UC 656	0.488	0.191	0.001	0.297	0.191	–	–	–
Casea sp.	FMNH UC 960	0.432	0.204	0.002	0.228	0.202	0.372	0.154	0.001
Cotylorhynchus hancocki	FMNH UC 581	1.307	0.779	0.002	0.528	0.777	–	–	–
Cotylorhynchus hancocki	FMNH UR 272	1.441	0.634	0.002	0.808	0.631	–	–	–
Ophiacodon major	FMNH UC 1638	0.502	0.137	0.001	0.365	0.136	0.627	0.238	0.002
Ophiacodon mirus	FMNH UC 671	0.499	0.204	0.002	0.294	0.202	0.941	0.276	0.003
Ophiacodon retroversus	FMNH UC 458	0.649	0.178	0.002	0.471	0.176	0.576	0.278	0.001
Ophiacodon retroversus	FMNH UC 709	0.063	0.030	0.001	0.032	0.029	–	–	–
Ophiacodon uniformis	FMNH UC 690	0.358	0.136	0.004	0.222	0.132	–	–	–
Varanops brevirostris	FMNH UC 644	0.782	0.275	0.001	0.508	0.274	–	–	–
Varanops sp.	FMNH UR 607/UR 616	0.250	0.136	0.004	0.114	0.132	0.295	0.169	0.006
Varanops sp.	FMNH P 12841	0.264	0.124	0.003	0.140	0.121	0.311	0.131	0.004
Aerosaurus wellesi	UCMP V2814/40096	0.196	0.096	0.006	0.100	0.090	0.271	0.171	0.008
Dimetrodon giganhomogenes	FMNH UC 112	0.275	0.145	0.003	0.130	0.142	0.340	0.157	0.002
Dimetrodon loomisi	FMNH UC 1322	0.959	0.447	0.002	0.512	0.446	1.116	0.651	0.003
Dimetrodon sp.	FMNH UC 1758	0.861	0.336	0.003	0.525	0.333	–	–	–
Sphenacodon ferox	FMNH UC 35	0.634	0.248	0.002	0.386	0.246	1.048	0.431	0.002
Sphenacodon ferox	UCMP V3529/34226	0.442	0.218	0.002	0.224	0.216	0.884	0.422	0.003
Amblyrhychus cristatus	FMNH 22213	0.423	0.172	0.001	0.251	0.172	0.658	0.239	0.001
Iguana iguana	FMNH 22085	0.916	0.293	0.001	0.623	0.292	1.191	0.513	0.001
Varanus bengalensis nebulosus	FMNH 22495	0.626	0.352	0.001	0.273	0.352	0.796	0.383	0.002
Varanus bengalensis nebulosus	FMNH 211856	0.560	0.271	0.001	0.289	0.270	0.753	0.380	0.001
Varanus dumerili	FMNH 228151	0.473	0.283	0.001	0.190	0.282	0.588	0.314	0.001
Varanus exanthematicus	FMNH 228398	0.735	0.369	0.001	0.366	0.368	0.619	0.308	0.001
Varanus komodensis	FMNH 22197	0.936	0.460	0.000	0.476	0.459	1.437	0.753	0.001
Varanus rudicollis	FMNH 98947	0.606	0.299	0.000	0.307	0.299	0.851	0.441	0.001
Varanus salvator	FMNH 22204	1.251	0.481	0.000	0.770	0.481	1.552	0.771	0.001
Varanus salvator	FMNH 98866	0.536	0.194	0.001	0.341	0.194	0.557	0.243	0.001
Varanus salvator	FMNH 195576	1.019	0.338	0.001	0.681	0.337	1.210	0.505	0.001
Varanus salvator	FMNH 211938	0.707	0.404	0.001	0.303	0.403	0.661	0.381	0.001
Caiman crocodilus	FMNH 9150	0.265	0.082	0.001	0.183	0.081	1.240	0.449	0.001
Caiman crocodilus	FMNH 13062	0.505	0.136	0.001	0.369	0.135	0.862	0.331	0.001

(continued)

Table 3.1 (continued)

Taxon	Specimen	*R* (length)	*C* (length)	*Cm* (length)	*E*1 (length)	*E*2 (length)	*R* (height)	*C* (height)	*Cm* (height)
Caiman crocodilus	FMNH 217159	0.240	0.087	0.001	0.153	0.087	1.012	0.410	0.001
Melanosuchus niger	FMNH 218507	0.331	0.128	0.000	0.204	0.127	1.002	0.373	0.001
Crocodylus rhombifer	FMNH 34677	0.653	0.202	0.001	0.451	0.202	1.575	0.689	0.001
Gavialis gangeticus	FMNH 82681	0.444	0.204	0.001	0.241	0.203	1.478	0.573	0.001
Chironectes minimus	FMNH 60576	1.705	0.971	0.001	0.734	0.970	0.993	0.443	0.002
Chironectes minimus	FMNH 60578	1.730	0.910	0.001	0.820	0.908	1.198	0.542	0.001
Castor canadensis	FMNH 18525	1.406	0.628	0.001	0.778	0.627	1.304	0.611	0.001
Castor canadensis	FMNH 134455	1.414	0.640	0.001	0.774	0.639	1.701	0.669	0.002
Castor canadensis	FMNH 141992	1.286	0.614	0.001	0.672	0.613	1.498	0.613	0.001
Lontra canadensis	FMNH 60655	0.585	0.310	0.001	0.274	0.309	0.906	0.274	0.001
Lontra canadensis	FMNH 160115	0.505	0.257	0.001	0.249	0.256	0.483	0.192	0.001
Lontra canadensis	FMNH 175293	0.514	0.229	0.001	0.285	0.228	0.912	0.285	0.001
Lontra canadensis	FMNH 180757	0.864	0.301	0.001	0.563	0.300	1.386	0.326	0.001
Neovison vison	FMNH 59739	1.047	0.392	0.002	0.655	0.390	0.762	0.228	0.001
Neovison vison	FMNH 59776	0.799	0.330	0.001	0.468	0.329	0.672	0.196	0.002
Neovison vison	FMNH 59793	0.817	0.402	0.002	0.415	0.401	1.061	0.269	0.001
Neovison vison	FMNH 112982	0.828	0.348	0.001	0.480	0.347	0.904	0.232	0.002

Taxon	Specimen	*E*1 (height)	*E*2 (height)	*R* (width)	*C* (width)	*Cm* (width)	*E*1 (width)	*E*2 (width)	Fore limb length	Hind limb length
Angelosaurus romeri	FMNH UR 827	–	–	–	–	–	–	–	–	–
Casea broilii	FMNH UC 656	–	–	0.862	0.297	0.001	0.565	0.296	15.10	12.61
Casea sp.	FMNH UC 960	0.219	0.152	0.648	0.279	0.002	0.369	0.277	–	–
Cotylorhynchus hancocki	FMNH UC 581	–	–	–	–	–	–	–	61.50	62.50
Cotylorhynchus hancocki	FMNH UR 272	–	–	–	–	–	–	–	46.50	43.50
Ophiacodon major	FMNH UC 1638	0.389	0.236	0.563	0.223	0.002	0.340	0.221	–	–
Ophiacodon mirus	FMNH UC 671	0.664	0.273	0.533	0.223	0.002	0.310	0.222	19.87	21.61
Ophiacodon retroversus	FMNH UC 458	0.298	0.277	0.284	0.103	0.003	0.181	0.100	–	–
Ophiacodon retroversus	FMNH UC 709	–	–	0.226	0.153	0.003	0.073	0.150	–	–
Ophiacodon uniformis	FMNH UC 690	–	–	0.262	0.144	0.009	0.119	0.135	–	–
Varanops brevirostris	FMNH UC 644	–	–	1.400	0.646	0.002	0.754	0.644	13.28	17.08
Varanops sp.	FMNH UR 607/UR 616	0.125	0.163	0.388	0.238	0.010	0.150	0.228	–	–
Varanops sp.	FMNH P 12841	0.181	0.127	0.155	0.061	0.003	0.094	0.058	–	–
Aerosaurus wellesi	UCMP V2814/40096	0.100	0.163	–	–	–	–	–	9.30	11.14
Dimetrodon giganhomogenes	FMNH UC 112	0.183	0.155	0.397	0.163	0.003	0.234	0.160	–	–
Dimetrodon loomisi	FMNH UC 1322	0.465	0.648	–	–	–	–	–	–	–

(continued)

Table 3.1 (continued)

Taxon	Specimen	$E1$ (height)	$E2$ (height)	R (width)	C (width)	Cm (width)	$E1$ (width)	$E2$ (width)	Fore limb length	Hind limb length
Dimetrodon sp.	FMNH UC 1758	–	–	–	–	–	–	–	–	–
Sphenacodon ferox	FMNH UC 35	0.617	0.429	0.790	0.389	0.002	0.400	0.387	25.50	27.87
Sphenacodon ferox	UCMP V3529/34226	0.462	0.419	–	–	–	–	–	19.10	22.40
Amblyrhychus cristatus	FMNH 22213	0.419	0.238	0.673	0.294	0.001	0.379	0.293	12.46	13.90
Iguana iguana	FMNH 22085	0.678	0.512	1.665	0.453	0.001	1.212	0.452	15.10	18.22
Varanus bengalensis nebulosus	FMNH 22495	0.412	0.382	0.719	0.383	0.001	0.336	0.382	9.11	10.91
Varanus bengalensis nebulosus	FMNH 211856	0.372	0.38	0.791	0.400	0.001	0.392	0.399	8.28	9.90
Varanus dumerili	FMNH 228151	0.274	0.313	0.505	0.292	0.001	0.212	0.292	7.92	8.97
Varanus exanthematicus	FMNH 228398	0.311	0.307	0.654	0.342	0.001	0.312	0.341	9.85	10.74
Varanus komodensis	FMNH 22197	0.685	0.752	1.189	0.677	0.001	0.513	0.676	28.97	31.99
Varanus rudicollis	FMNH 98947	0.411	0.440	1.031	0.393	0.001	0.638	0.391	14.97	16.53
Varanus salvator	FMNH 22204	0.781	0.771	1.355	0.764	0.000	0.590	0.764	19.18	19.77
Varanus salvator	FMNH 98866	0.314	0.242	0.562	0.329	0.001	0.233	0.328	15.96	17.82
Varanus salvator	FMNH 195576	0.704	0.504	1.080	0.432	0.001	0.649	0.431	21.50	21.17
Varanus salvator	FMNH 211938	0.280	0.380	0.672	0.403	0.001	0.269	0.402	11.16	12.74
Caiman crocodilus	FMNH 9150	0.791	0.448	1.672	0.670	0.001	1.002	0.669	–	–
Caiman crocodilus	FMNH 13062	0.531	0.330	1.128	0.475	0.001	0.653	0.474	14.51	17.54
Caiman crocodilus	FMNH 217159	0.602	0.409	1.304	0.471	0.001	0.833	0.470	–	–
Melanosuchus niger	FMNH 218507	0.629	0.372	1.175	0.485	0.001	0.690	0.484	–	–
Crocodylus rhombifer	FMNH 34677	0.885	0.688	2.298	0.883	0.001	1.416	0.881	18.10	26.95
Gavialis gangeticus	FMNH 82681	0.905	0.572	1.655	0.658	0.001	0.997	0.656	12.23	15.15
Chironectes minimus	FMNH 60576	0.550	0.442	1.025	0.378	0.002	0.647	0.376	10.33	11.57
Chironectes minimus	FMNH 60578	0.656	0.541	1.440	0.451	0.001	0.990	0.449	10.91	12.29
Castor canadensis	FMNH 18525	0.694	0.609	1.108	0.349	0.001	0.758	0.348	17.58	21.90
Castor canadensis	FMNH 134455	1.032	0.667	1.569	0.467	0.002	1.102	0.465	–	–
Castor canadensis	FMNH 141992	0.885	0.612	1.280	0.352	0.001	0.928	0.351	17.74	22.72
Lontra canadensis	FMNH 60655	0.632	0.273	1.233	0.400	0.002	0.833	0.398	15.00	17.14
Lontra canadensis	FMNH 160115	0.292	0.190	0.680	0.267	0.001	0.413	0.267	15.10	17.20
Lontra canadensis	FMNH 175293	0.627	0.283	1.563	0.500	0.001	1.062	0.499	16.35	18.27
Lontra canadensis	FMNH 180757	1.060	0.325	2.110	0.686	0.002	1.424	0.685	16.21	17.85
Neovison vison	FMNH 59739	0.534	0.227	1.371	0.679	0.001	0.693	0.677	8.27	9.58
Neovison vison	FMNH 59776	0.476	0.194	0.847	0.399	0.002	0.448	0.397	8.52	9.95
Neovison vison	FMNH 59793	0.792	0.268	1.622	0.710	0.001	0.912	0.709	10.42	11.81
Neovison vison	FMNH 112982	0.672	0.230	1.946	0.710	0.002	1.235	0.709	8.44	9.72

See text for details on calculation of the metrics. Fore limb length is calculated as the sum of humerus and radius length; hind limb length is calculated as the sum of femur and tibia length. Metrics for FMNH UC 581 are based on measurements from Olson (1962) our measurements. We only measured limb lengths (see below) for *Aerosaurus* because most of the vertebrae in the specimen are not exposed in a manner that allows centrum dimensions to be measured.

We also measured 31 specimens representing 16 species of extant semi-aquatic and terrestrial reptiles and semi-aquatic mammals. The extent reptile taxa measured were *Amblyrhynchus cristatus* (marine iguana), *Caiman crocodilius* (spectacled caiman), *Gavialis gangeticus* (gharial), *Iguana iguana* (green iguana), *Melanosuchus niger* (black caiman), *Varanus bengalensis* (Bengal monitor), *Varanus dumerilii* (Dumeril's monitor), *Varanus exanthematicus* (savannah monitor), *Varanus komodoensis* (Komodo dragon), *Varanus salvator* (water monitor), and *Varanus rudicollis* (roughneck monitor). The mammalian taxa were *Castor canadensis* (American beaver), *Chironectes minimus* (water opossum), *Lontra canadensis* (North American river otter), and *Neovison vison* (American mink). *Iguana iguana* and all of the *Varanus* species except for *V. salvator* were chosen as representatives of moderately-sized terrestrial reptiles that likely have a locomotor pattern comparable to that of basal synapsids; the other species were chosen because they are small- to medium-sized semi-aquatic reptiles and mammals that can provide insight into the range of variation in vertebral proportions found in semi-aquatic tetrapods with lifestyles that may be analogous to that of *Ophiacodon*. *Crocodylus rhombifer* is of interest because it spends more of its time on land than many other extant crocodiles and possesses specializations for terrestrial locomotion such as reduced webbing of the feet and powerful hind limbs (Braziatis 1973). Only specimens that had multiple centra in sequence were selected, and then only if the positions of the centra along the column could be determined.

We measured centrum length, width, and height for each available centrum except the atlas and axis, with all measurements made to the nearest 0.1 mm using either digital or dial calipers (Fig. 3.2). Measurements for FMNH UC 581 are taken from Olson (1962). To obtain a graphical overview of each specimen's vertebral profile that could be easily compared, we plotted centrum length against vertebral position (Figs. 3.3, 3.4, 3.5, 3.6, 3.7, 3.8, 3.9, 3.10). We also measured lengths of a femur, tibia, humerus, and radius for each specimen when these bones were available. Limb bone lengths represent the longest dimension of the bone.

In addition, we quantified the properties of the vertebral columns of the extant and fossil taxa using the series of metrics developed by McShea (1992; also see McShea 1993). Each metric (R, C, Cm, $E1$ and $E2$, see below) was calculated for each vertebral parameter (centrum length, width, and height) of each specimen. For each parameter for a given specimen, the series X_1 through X_N represents all the measurements along the vertebral column in order. The range, R, of that series is simply:

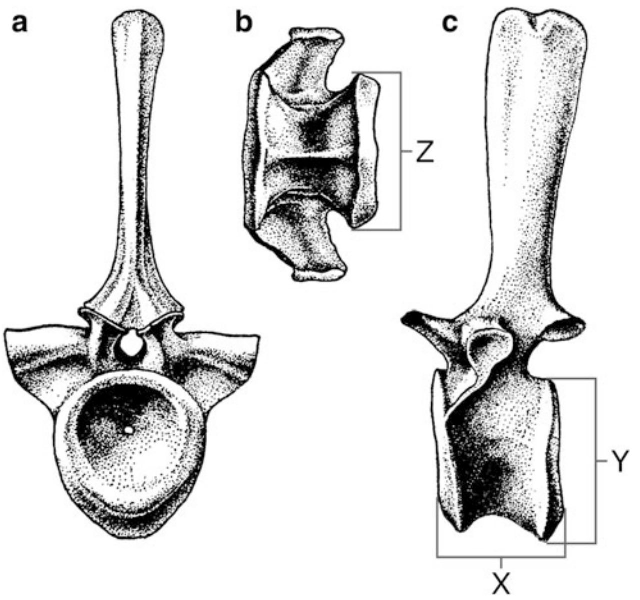

Fig. 3.2 Dorsal vertebrae of *Ophiacodon mirus* in anterior (**a**), inferior (**b**) and left lateral (**c**) view. Centrum width (X), centrum height (Y), and centrum width (Z) were evaluated as illustrated. Drawings from Romer and Price (1940)

$$R = \log(X_{max} - X_{min}).$$

Polarization, C, which considers the degree to which the vertebral column is divided into sections with dimensions clustered at high and low values, is calculated as:

$$C = \log\left(2\sum_{i=1}^{N}\left(X_i - \overline{X}\right)/N\right).$$

Irregularity, Cm, which quantifies the average difference in dimensions between successive vertebrae across the column, is calculated as:

$$Cm = \log\left(\left(\sum_{i=1}^{N-1}\left(X_{i+1} - X_i\right)\right)/(N-1)\right).$$

Related to polarization is $E1$, or concentration, which measures the degree to which centrum dimensions are concentrated at the mean or at the extremes, is calculated as:

$$E1 = R - C.$$

Related to irregularity is $E2$, or smoothness, which measures the degree to which successive vertebrae are constrained to have similar dimensions, is calculated as:

$$E2 = C - Cm.$$

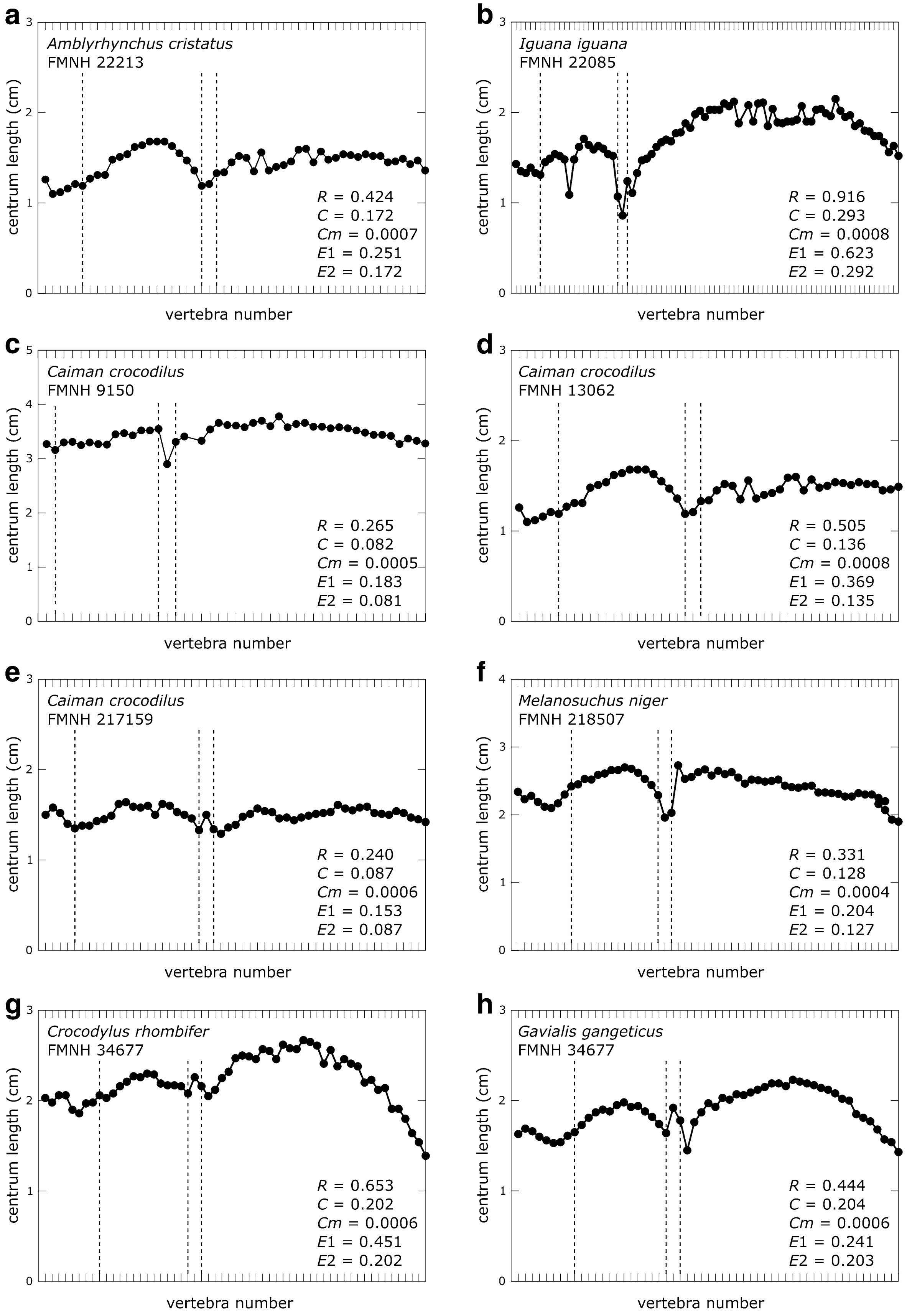

Fig. 3.3 Plots showing centrum length profiles for *Amblyrhynchus*, *Iguana*, *Caiman*, *Melanosuchus*, *Crocodylus*, and *Gavialis*. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae in each specimen

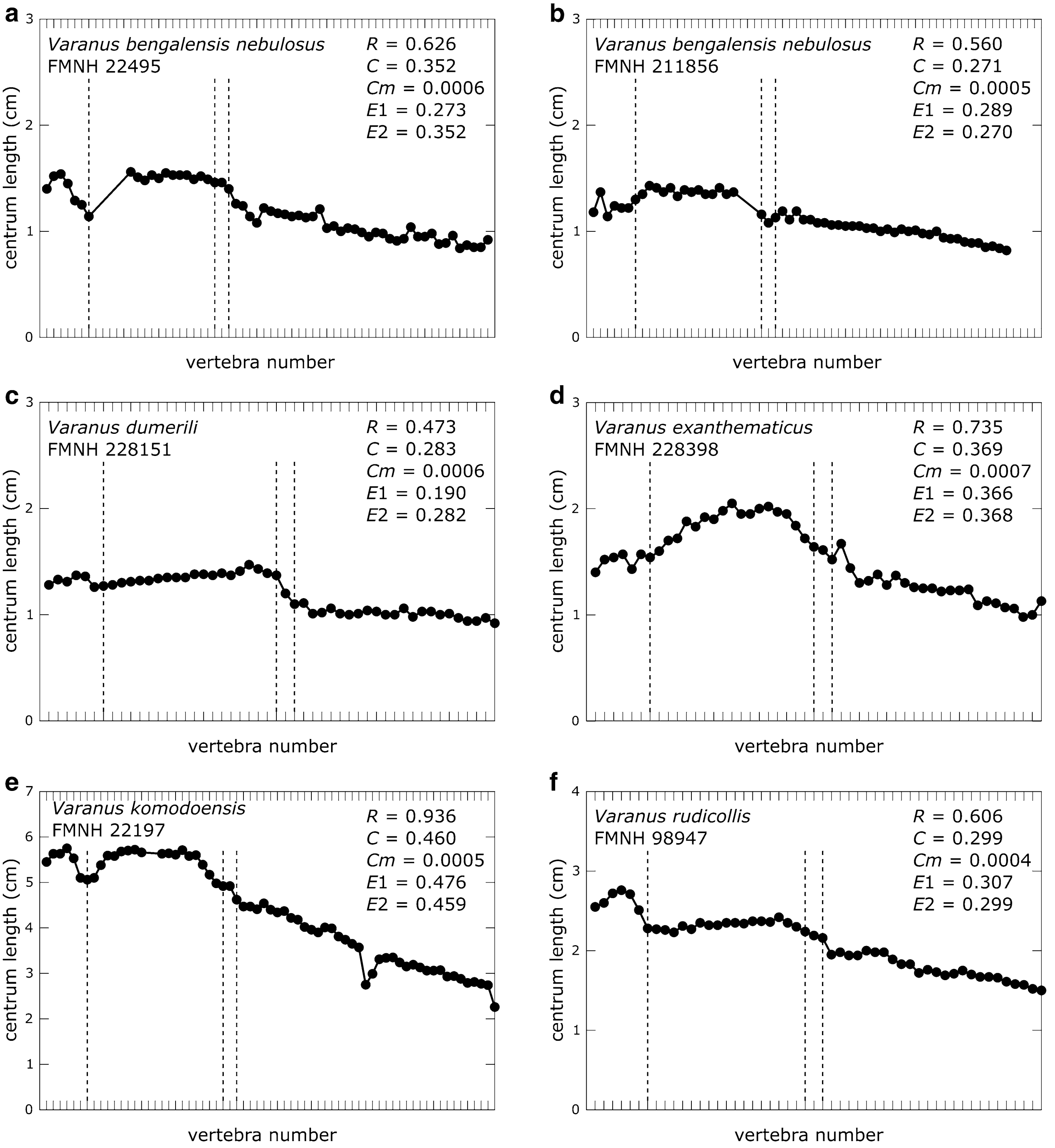

Fig. 3.4 Plots showing centrum length profiles for the terrestrial varanid specimens. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae in each specimen

Following McShea (1993), we removed size effects by log transforming all centrum measurements before computing the metrics, and then omitting the log operation from the above equations.

To visualize patterns captured by these metrics, we performed two principal components analyses (PCA) on variance-covariance matrices of the metrics. The first PCA used only the five metrics calculated for our centrum length

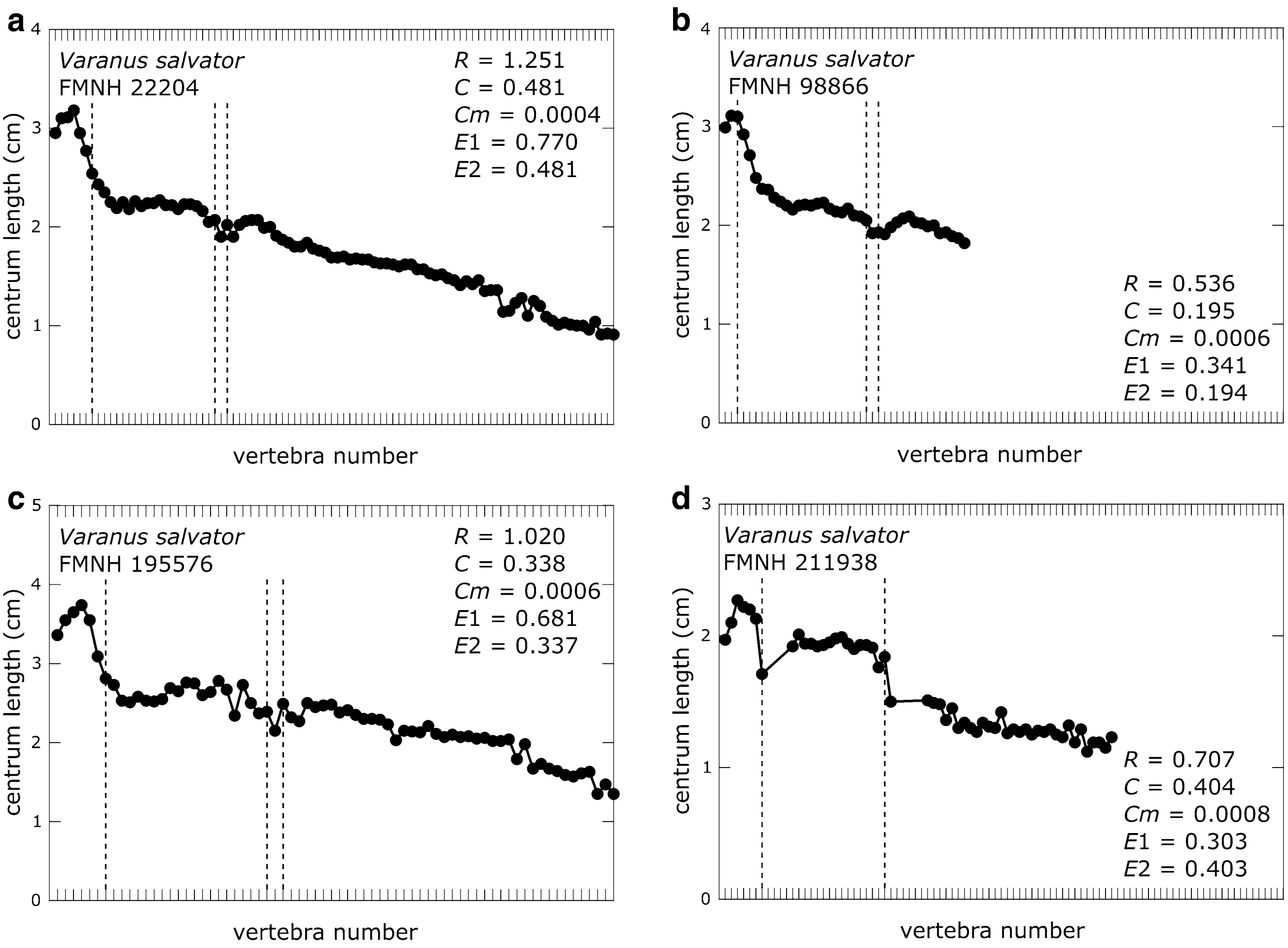

Fig. 3.5 Plots showing centrum length profiles for *Varanus salvator* specimens. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae in each specimen. The last sacral is missing in FMNH 211938

measurements because we were able to measure this dimension on nearly all specimens. To avoid spurious results, we excluded seven fossil specimens (FMNH P 12841, FMNH UC 112, FMNH UC 690, FMNH UC 709, FMNH UR 607/UR 616, FMNH UR 827, UCMP V2841/40096) because they preserve only limited sections of the vertebral column and therefore likely do not capture the full range of variation in centrum lengths originally displayed by the specimens. The second PCA was based on the metric values for centrum, length, width, and height (for a total of 15 variables). Although this analysis has the potential to provide a more nuanced view of variation in vertebral proportions, it has the drawback of including a smaller number of specimens because all three dimensions could not be accurately measured for all of the fossil specimens (Table 3.1). All specimens but one (FMNH UR607/UR616) that had length, height, and width metrics were included in this analysis. Note that two specimens, FMNH UC 112 (*Dimetrodon giganhomogenes*) and FMNH P 12841 (*Varanops* sp.), which we excluded from the length-only PCA were included in this analysis despite the relatively limited number of vertebrae available for each to ensure that these taxa had at least one representative in the data set.

As noted above, Romer and Price (1940) and Kemp (1982) also cited the disparity in limb lengths (hind limbs longer than fore limbs) observed in *Ophiacodon* as evidence for a semi-aquatic lifestyle. To determine whether such a difference should be expected, we measured fore and hind limb lengths (measured as the summed length of the humerus and radius or femur and tibia) in all of the examined specimens in which these elements were preserved. We excluded the manus and pes from these measurements because they were infrequently preserved in the fossil specimens. We then carried out two Kolmogorov-Smirnov two-sample tests on the ratios of fore limb length to hind limb length. In the first test, we included only the extant specimens, whereas we included the extant and fossil specimens (excluding *Ophiacodon*) in the second test. To test whether *Ophiacodon* is indeed more similar to semi-aquatic taxa in this regard, we calculated whether the

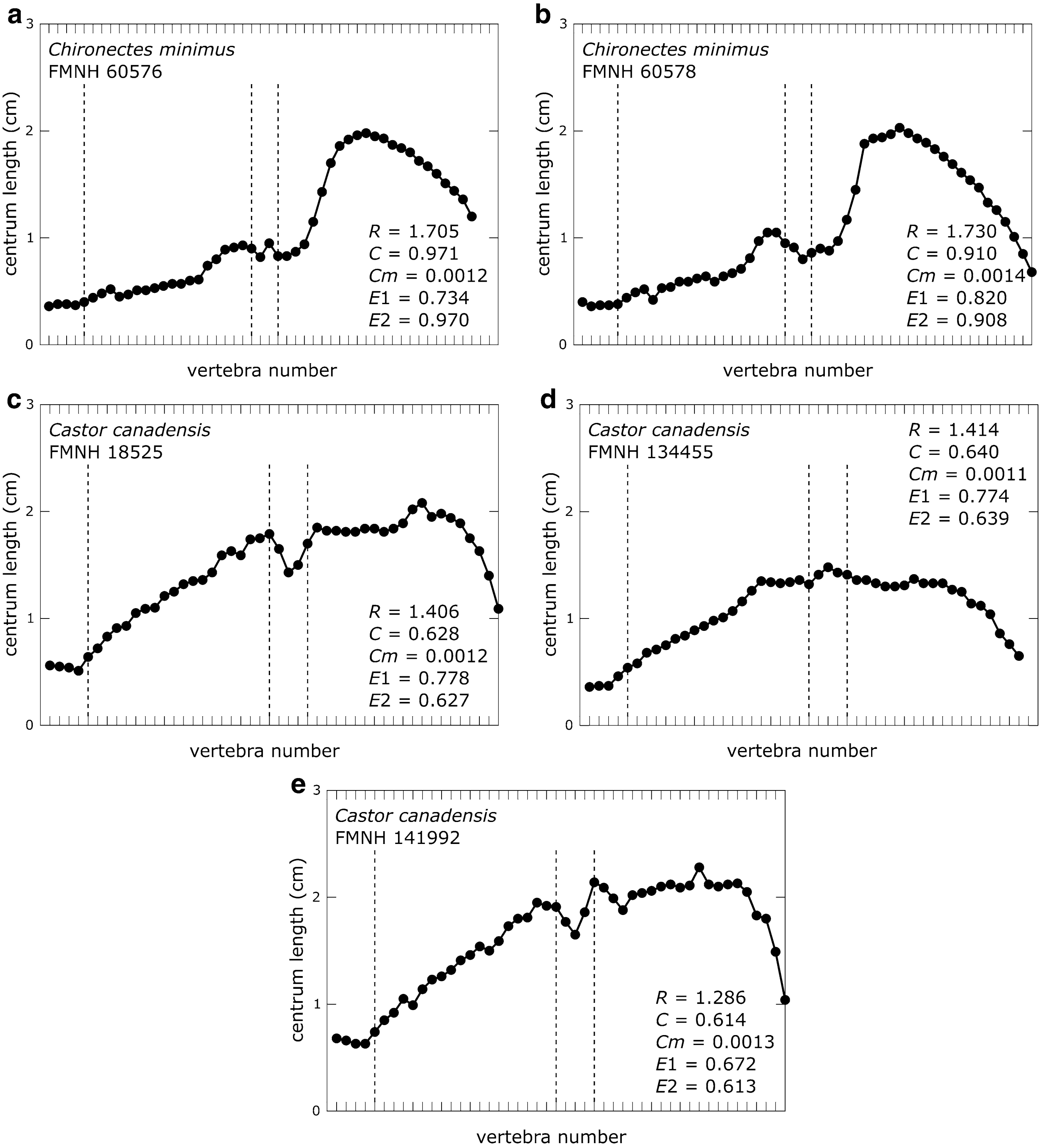

Fig. 3.6 Plots showing centrum length profiles for *Chironectes* and *Castor*. *Dashed lines* mark the last cervical, lumbar, and sacral vertebrae in each specimen

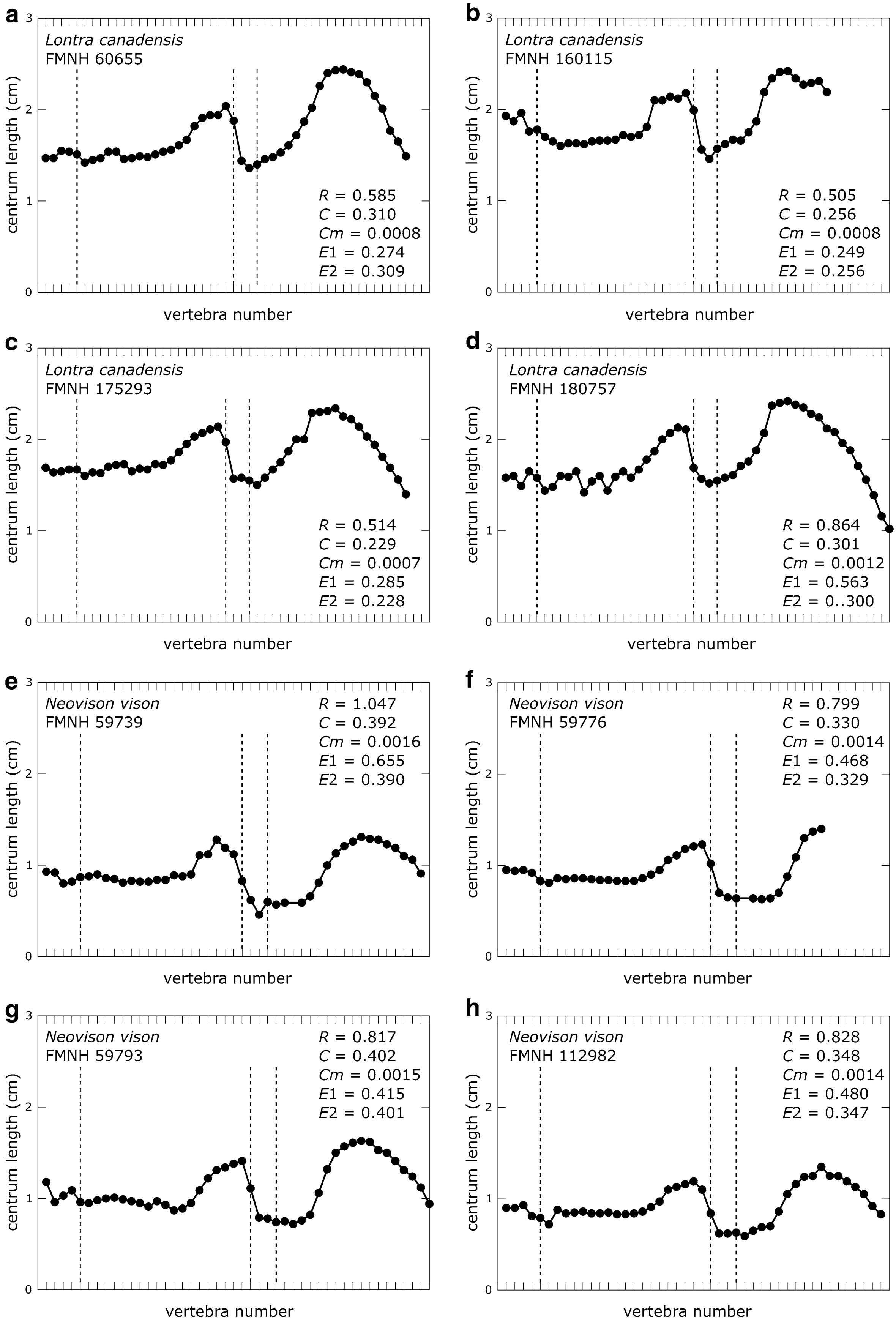

Fig. 3.7 Plots showing centrum length profiles for *Lontra* and *Neovison*. *Dashed lines* mark the last cervical, lumbar, and sacral vertebrae in each specimen

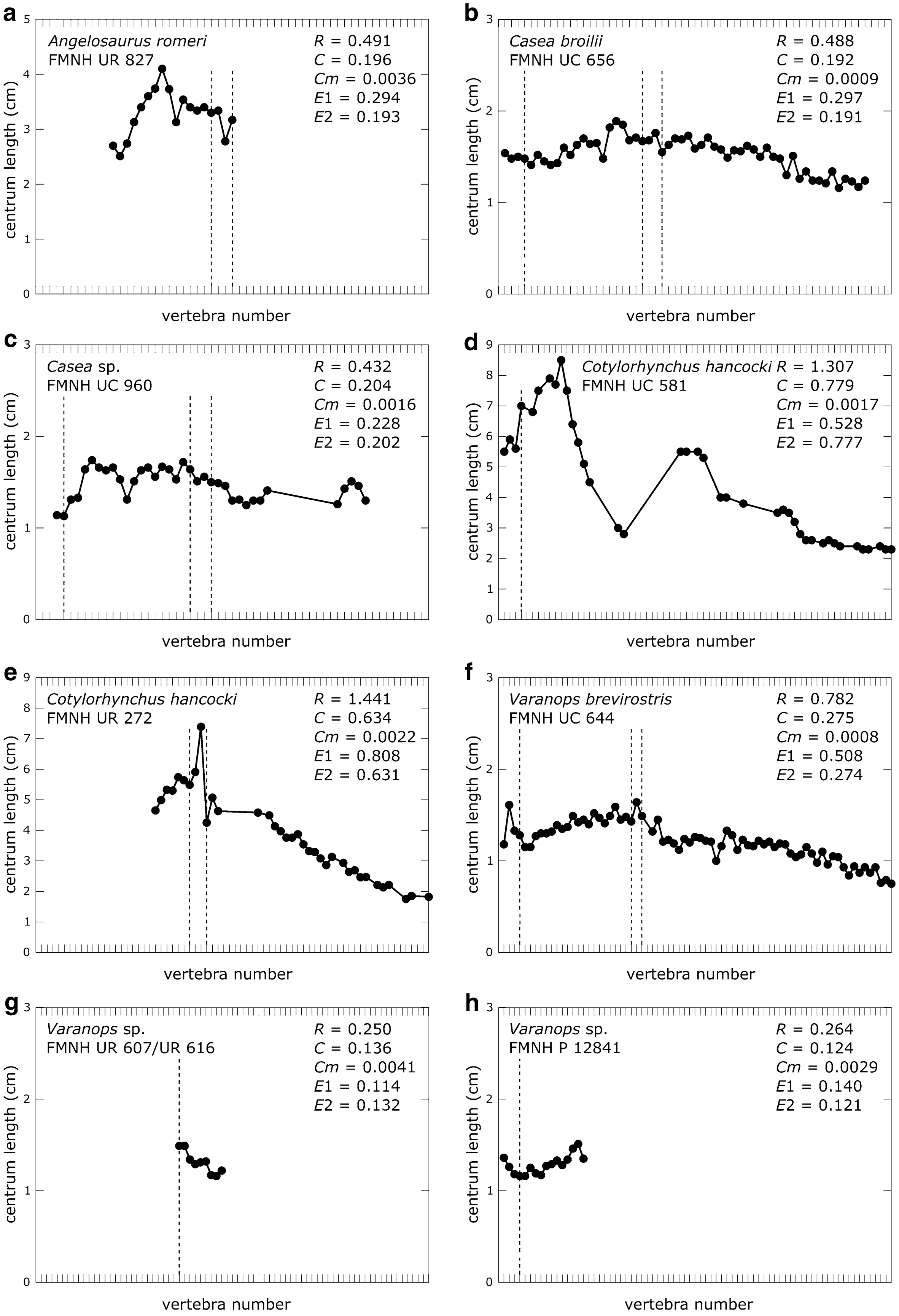

Fig. 3.8 Plots showing centrum length profiles for the caseid and varanopid specimens. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae in each specimen. The last cervical is not preserved in FMNH UR 827 and FMNH UR 607/UR 616. The last sacral is not preserved in FMNH UR 607/UR 616, and no sacrals are preserved in FMNH UC 581 and FMNH P12841

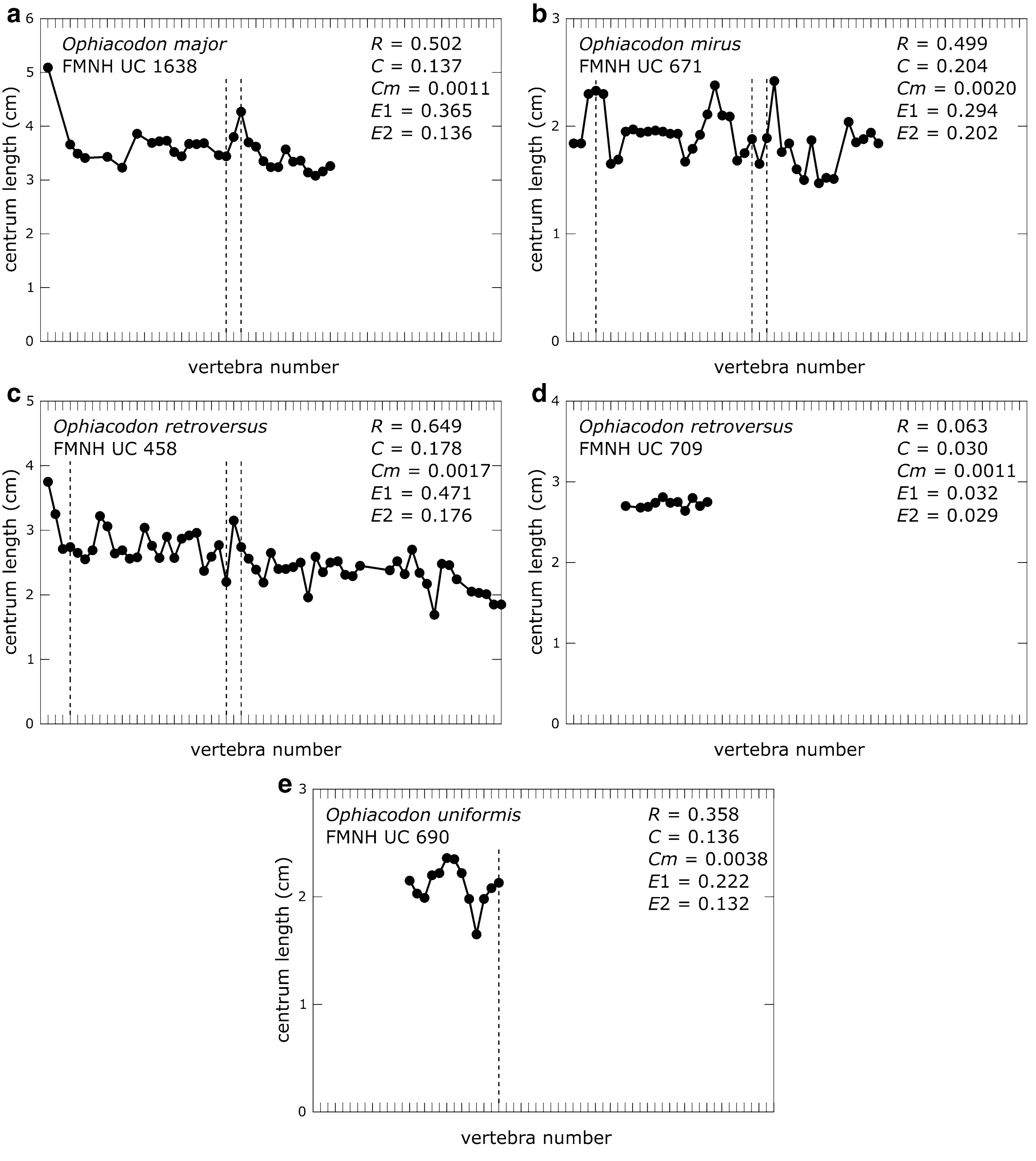

Fig. 3.9 Plots showing centrum length profiles for *Ophiacodon* specimens. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae in each specimen. The last cervical is not preserved in FMNH UC 1683, FMNH UC 709, and FMNH UC 690. The last sacral is not preserved in FMNH UC 690, and the last dorsal and the last sacral are not preserved in FMNH UC 709

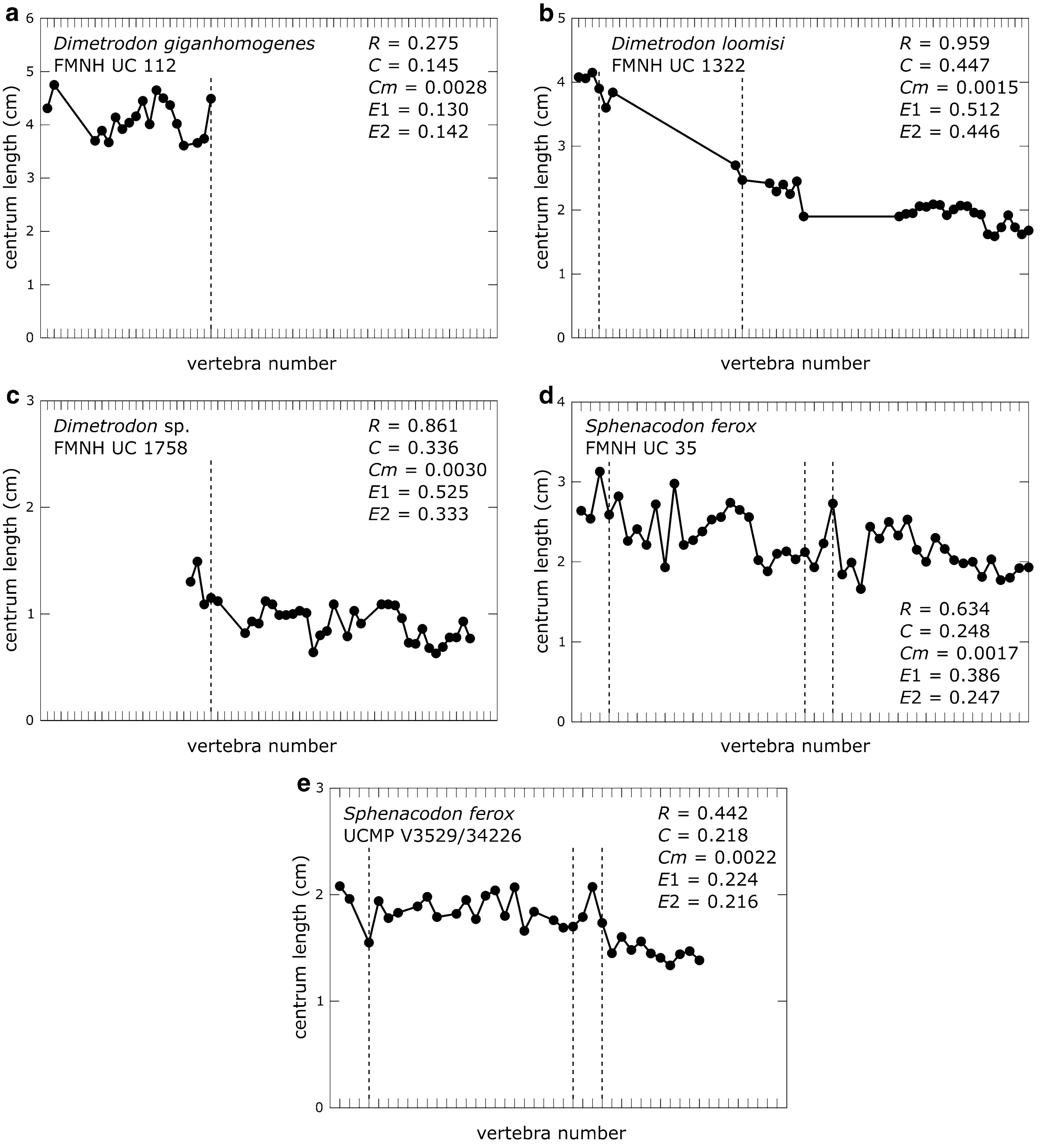

Fig. 3.10 Plots showing centrum length profiles for the sphenacodontid specimens. *Dashed lines* mark the last cervical, dorsal, and sacral vertebrae. The last cervical and last sacral are not preserved in FMNH UC 112 and FMNH UC 1758. The last sacral is not preserved in FMNH UC 1322

Ophiacodon specimen we measured (FMNH UC 671) was closer to the mean value for the terrestrial or aquatic groups.

Results

The extant taxa show several distinct patterns of vertebral morphology. Although many of these are congruent with previous observations (e.g., there is a great deal of similarity between our plots and those of Buchholtz (1998) for those taxa sampled in both studies), some unexpected patterns emerged, especially among the reptiles. Because of the importance centrum length has played in previous works on swimming style, we focus on these results.

The *Amblyrhynchus*, *Iguana*, *Caiman*, *Crocodylus*, and *Gavialis* specimens we measured all show a peak in centrum length between the pectoral and pelvic girdles, corresponding to the area of lateral undulation during terrestrial locomotion (Buchholtz 1998), although the shape of the peak (sharp vs. more plateau-like) varied from taxon to taxon (Fig. 3.3). These taxa also all show a peak or plateau in vertebral length in the caudal vertebrae, which Buchholtz (1998) stated represents the region where traveling undulatory waves pass along the tail during swimming (in semi-aquatic taxa) or terrestrial locomotion (in taxa with reduced limbs). In general, these taxa tended to have relatively low to moderate values for the metrics we calculated (Table 3.1) for length, indicating that they have comparatively uniform vertebral columns. Interestingly, among these taxa, the terrestrial *Iguana iguana* had the highest scores for all metrics.

The six *Varanus* species we measured show several vertebral length profiles, all of which are unlike those of the other reptiles (Figs. 3.3, 3.4). *Varanus exanthematicus*, *V. bengalensis nebulosus,* and *V. komodoensis* possess a peak or plateau in centrum length between the pectoral and pelvic girdles, much like the other reptiles, but then show a steady decline that starts near the pelvic girdle and continues throughout the tail. A distinct peak between the pectoral girdles is absent in *V. dumerilii* and *V. rudicollis*. Instead, after a decrease in length near the pectoral girdle, there is a gradual increase in centrum length to just before the sacrum. Centrum length then declines and either continues a gradual decrease (*V. rudicollis*) or is relatively constant for the remainder of the tail (*V. dumerilii*). Finally, *V. salvator* shows a sharp drop in length in the first few dorsal vertebrae followed by very slowly decreasing centrum lengths for the rest of the vertebral column. In general, the varanids were characterized by moderate ranges of centrum length (R), moderate to high polarization (C), low to moderate irregularity (Cm), a wide range of $E1$ values, and moderate to high $E2$ values (Table 3.1). These patterns reflect the fact that the varanids tend to be characterized by small changes in length between successive vertebrae (i.e., low amounts of noise), but often have relatively polarized columns, with longer presacrals and shorter caudals.

The plots of vertebral length in extant mammals (Figs. 3.6, 3.7) also fall into several categories. The two mustelids measured, *Lontra canadensis* and *Neovison vison*, display distinctly bimodal patterns of centrum length. Both show uniform centrum length in the thorax, a peak in centrum length in the lumbar region, and a second peak in centrum length in the distal caudal region. *Chironectes minimus* also displays a bimodal centrum length profile, but the lumbar peak in centrum length is less well defined than in the mustelid genera. Unlike the other extant mammal taxa examined, *Castor canadensis* does not display a bimodal pattern in centrum length. Rather, it shows a uniform increase in centrum length, width, and height through the trunk, followed by a plateau in the dimensions of the caudal vertebrae. The mammals tended to be characterized by moderate to high ranges of centrum length (R) and polarization (C), low to moderate irregularity (Cm), and moderate to high $E1$ and $E2$ values (Table 3.1). This reflects the fact that most of the mammals have vertebral columns characterized by relatively great peaks of centrum length, as well as relatively close correspondence in centrum length in successive vertebrae (i.e., low amounts of noise).

The synapsid specimens measured also display several centrum length profiles, but many do not show an exact correspondence with the extant taxa (Figs. 3.8, 3.9, 3.10). The caseid specimens (Fig. 3.8) are the most basal, and perhaps among the most terrestrial, synapsids we measured. Most show evidence of a plateau or peak in centrum length between the pectoral and pelvic girdles, although its exact placement along the column seems to vary. In contrast, FMNH UC 656 (*Casea broilii*) and perhaps FMNH UC 272 (*Cotylorhynchus hancocki*) show a weak pattern of increase in centrum length to the pelvic girdle. However, FMNH UC 656 includes vertebrae from three individuals (Williston 1911), and FMNH UC 272 preserved a limited number of presacrals, so they may provide a biased picture of the vertebral proportions of the presacral column. All caseids with well-preserved tails show a gradual decline in centrum length in the caudal series. Taken together, the centrum length profile that emerges for caseids includes a weak plateau in length between the girdles, followed by gradually decreasing centrum lengths in the tail, a pattern resembling some of the *Varanus* species we measured (e.g., Fig. 3.4). Although it occupies a more crownward position in synapsid phylogeny than the caseids, the varanopid *Varanops* also displays a centrum length profile resembling that of the extant varanids, particularly *V. dumerilii* (Fig. 3.4). Most of the caseid and *Varanops* specimens show low to moderate ranges of centrum length (R), and polarization (C) (Table 3.1), although

Cotylorhynchus hancocki is characterized by higher *R* and *C* values, likely reflecting its large size (McShea 1993). Like all of the fossil specimens, the caseids and *Varanops* have relatively high irregularity values (*Cm*), perhaps because of minor amounts of deformation (McShea 1993). Finally, these specimens show a wide range of *E*1 and *E*2 values. Although this likely reflects genuine differences in some cases (e.g., centrum lengths for *Casea broilii* cluster more closely around their mean value than is the case for *Cotylorhynchus hancocki*), some of the values may be artifacts reflecting the fact that certain of the measured columns represent only small sections of the original vertebral series of those specimens.

A single, clear pattern of region variation is not apparent in the *Ophiacodon* specimens that we measured (Fig. 3.9). FMNH UC 671 shows a weak plateau in centrum length in the anterior part of the thoracic column, but such a plateau is not apparent in FMNH UC 1638 or FMNH UC 709, and this section of the column is very "noisy" in FMNH UC 458. A narrow peak in centrum length is present five to seven vertebrae anterior to the sacrum in most of the *Ophiacodon* specimens in which this region is preserved, although the noisiness of FMNH UC 458 makes the pattern less distinct than in the other specimens. None of the specimens preserves a complete caudal series, but although some variation in centrum length among the caudals of the two most complete specimens exists (FMNH UC 458 and FMNH UC 1638), there is no evidence of a distinct peak or plateau comparable to that observed in the extant crocodilians, iguanas, or mammals. Taken together, these observations suggest that while some undulation may have occurred between the girdles of *Ophiacodon*, there was no obvious specialization in the tail for the propagation of undulatory waves used in swimming. The *Ophiacodon* specimens typically displayed low to moderate ranges of centrum length (*R*) and polarization (*C*), high irregularity (*Cm*), a wide range of *E*1 values and low *E*2 values (Table 3.1). These patterns reflect the fact that the specimens displayed relatively few distinct peaks or plateaus in centrum length, but had comparatively noisy vertebral columns.

A consistent pattern of regional variation also was not apparent for the sphenacodontids we measured (Fig. 3.10). The two *Sphenacodon* specimens present very different centrum length profiles: the presacral, sacral and anterior caudal centra of UCMP V3529/34226 are very uniform in length, with no apparent peaks or plateaus. The centra of FMNH UC 35 are much more variable, with an extremely noisy region in the cervicals and anterior dorsals, a peak in the mid-dorsal region, and a weakly developed peak in the anterior caudals. None of the *Dimetrodon* specimens available for this study preserve a complete vertebral column, but a relatively complete composite picture can be assembled from FMNH UC 112, FMNH UC 1322, and FMNH UC 1758. A peak in centrum length is present in the mid-to-posterior dorsal series of FMNH UC 112, as well as an increase in length towards the sacrum. The caudal series of FMNH UC 1758 is relatively noisy, but shows some evidence of a plateau or multiple peaks. The caudals of FMNH UC 1322 are much more uniform, but show a weak plateau in length near the distal end of the tail. However, the caudal peaks and plateaus in these specimens differ from those observed in the iguanas, crocodilians, and mammals because the centrum lengths in the peak/plateau are less than those in the presacral series, whereas they are as long or longer in the extant taxa. The sphenacodontids spanned a wide range of centrum length (*R*), polarization (*C*), *E*1 and *E*2 values, and possessed high irregularity (*Cm*) values (Table 3.1). These patterns likely reflect several causes, both real (e.g., wide range of lengths in FMNH UC 1322) and artifactual (e.g., only portions of the total column preserved in FMNH UC 112; noise in the measurements from minor deformation).

In the analysis based only on length metrics, the first two PC axes captured approximately 94.9 and 5.1 % of the variance, respectively, so we focus our interpretation on these two axes. The metric *R* had a high positive loading on axis 1, and *C*, *E*1, and *E*2 had moderate positive loading on this axis. The metrics *R* and *E*2 had moderate and high negative loadings on PC 2, respectively, whereas *C* and *E*2 had moderate positive loading. The metric *Cm* had a loading very close to zero on both axes. On a plot of axes 1 and 2, most of the extant semi-aquatic species fall together in an area near the origin, although *Iguana iguana* also falls within this region (Fig. 3.11). The terrestrial varanid species also are located near the origin on axis 1, but extend higher on axis 2 than the semi-aquatic reptiles (except one outlier in *V. salvator*, FMNH 211938, which is a captive specimen). *Castor canadensis* and *Chironectes minimus* have higher scores on axis 1 than the reptiles, but much like them *Castor* falls mostly on the negative side of axis 2. *Chironectes* has positive scores on axis 2. All of the basal synapsids were included in the PCA but two fall in the region occupied primarily by the extant semi-aquatic reptiles, with the three *Ophiacodon* specimens falling closest to the range of the extant crocodilians. The basal synapsid specimens that do not fall among the extant semi-aquatic reptiles are two specimens of *Cotylorhynchus*, one of which falls near *Castor canadensis* whereas the other is located in a unique position in quadrant 1. The greater noisiness of the basal synapsid vertebral columns is reflected by the fact the variable *Cm* has high positive loadings on PC axis 3 and the extant specimens (aside from *Neovison vison*) and fossil specimens segregate relatively well this axis. However, this axis accounts for a trivial proportion (approximately 0.02 %) of the variance in the data set.

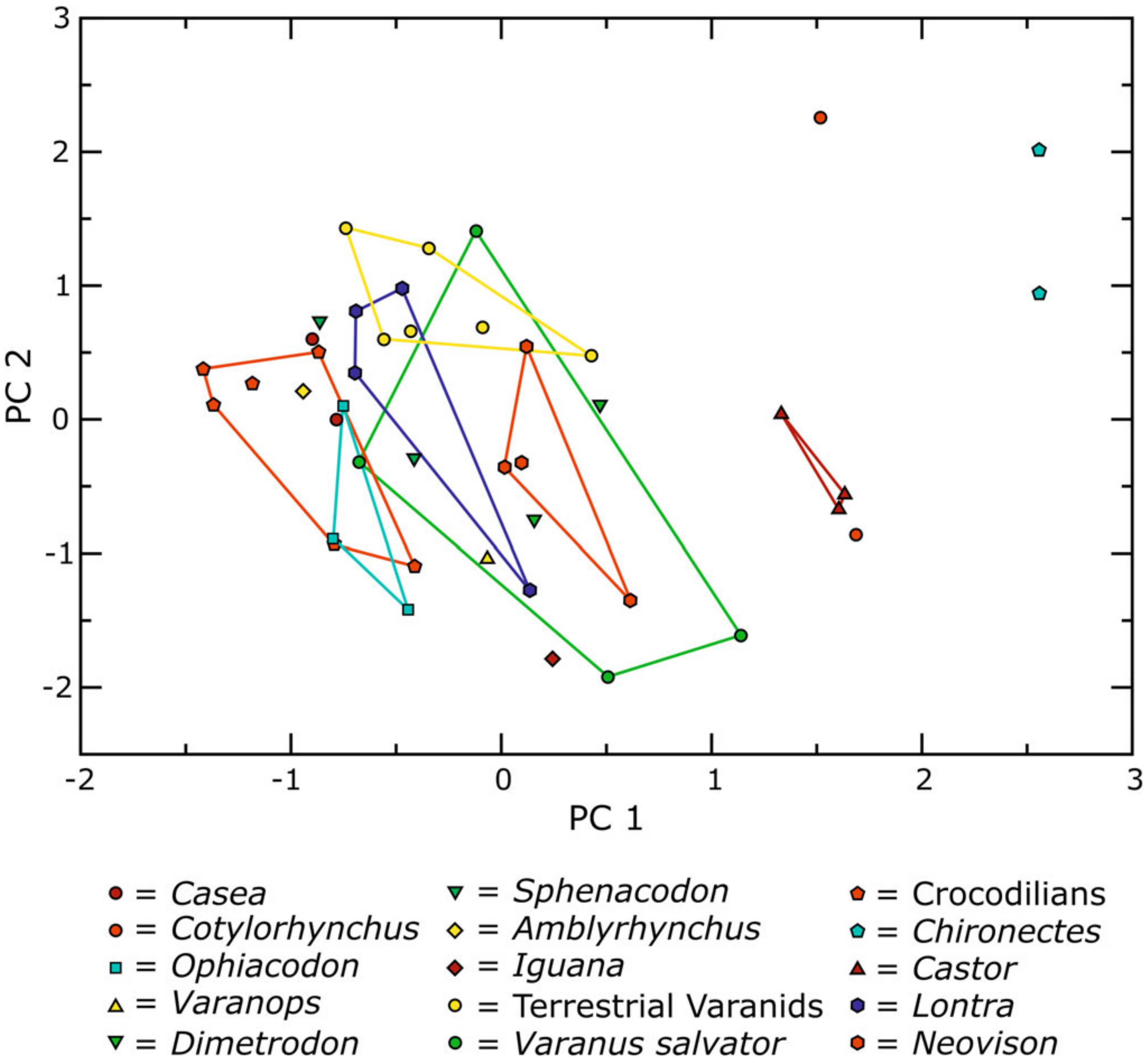

Fig. 3.11 Plot showing the distribution of specimens on principal components one and two of the PC analysis of centrum length metrics. Convex hulls have been drawn for taxa represented by three or more specimens

In the analysis based on all of the length, width, and height metrics, the first three PC axes captured approximately 66.9, 22.2, and 6.3 % of the variance respectively. The remaining axes captured 2.5 % of the variance or less, so our interpretation focuses on the first three axes. All of the length, width, and height metrics except the *Cm* metrics had positive loadings on PC 1. Most of these loadings were low to moderate, but R_{width} was noteworthy for having the highest positive loading of all of the metrics. The metrics *R*, *C*, *E*1, and *E*2 for length all had moderate to high positive loadings on PC 2. *R*, *C*, and *E*2 for height had low positive loading on PC 2, but *E1* had a low negative loading. Loadings for *R*, *C*, *E*1, and *E*2 for width were weakly to moderately negative on PC2. The *Cm* metrics had slightly positive loadings on PC 2 in all cases. The metrics *R*, *C*, *E*1, and *E*2 for length had low to moderate negative loadings on PC 3. *R* and *E1* for width also had moderate negative loadings on PC 3, but *C* and *E*2 for width had slightly positive loadings. All four of these metrics for height had moderate to strong positive loadings on PC 3. The *Cm* metrics had slightly negative loadings on PC 3 in all cases. The basal synapsids were differentiated from most of the extant specimens along PC 1 in this analysis (Fig. 3.12), and the area occupied by the synapsids was closest on

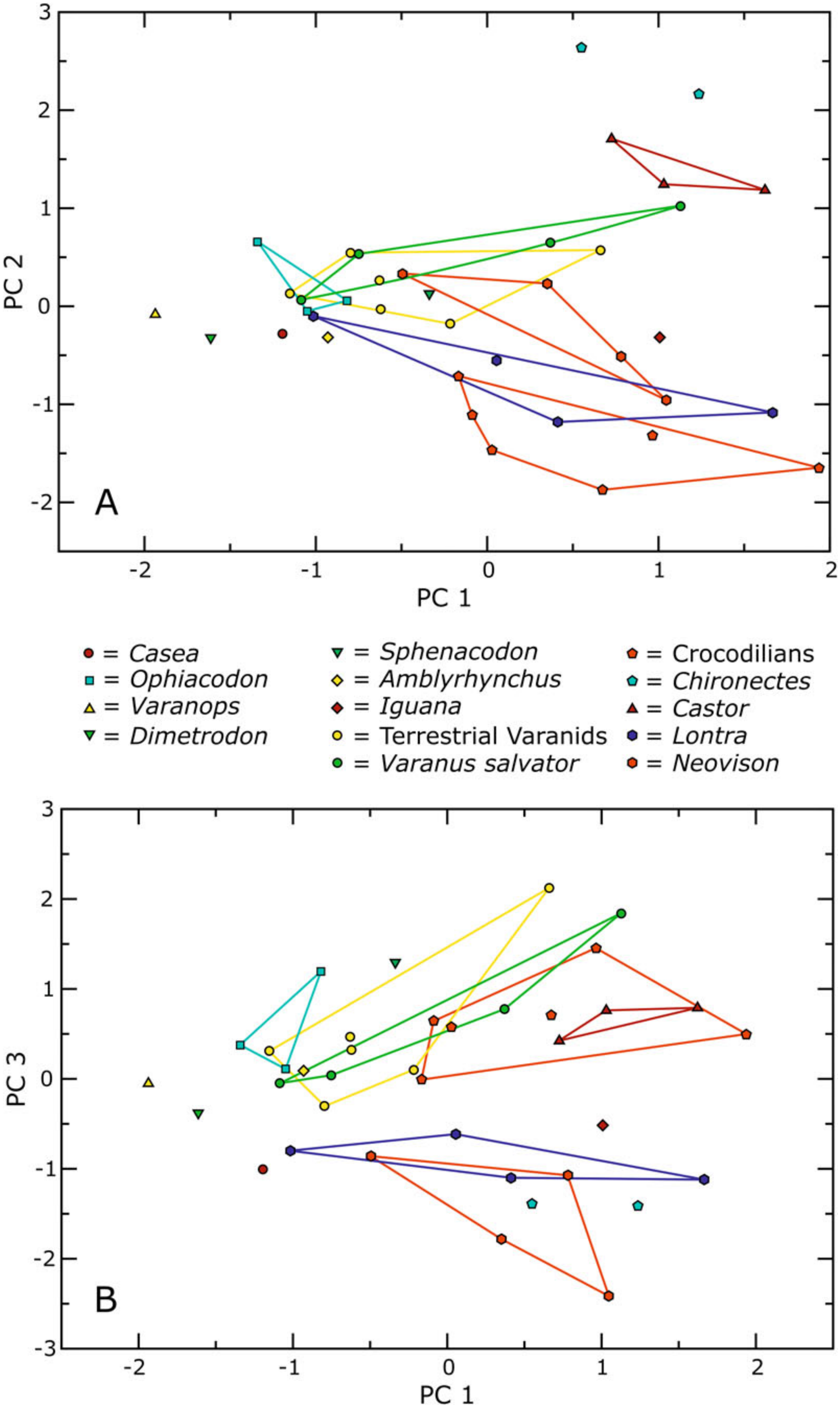

Fig. 3.12 Plots showing the distribution of specimens on principal components one, two, and three of the PC analysis of length, width, and height metrics. **a** PCs 1 and 2. **b** PCs 1 and 3. Convex hulls have been drawn for taxa represented by three or more specimens

average to the area occupied by the terrestrial varanid specimens. Among the basal synapsids, the three *Ophiacodon* specimens and one *Sphenacodon* specimen were located especially close to or within the area occupied by the terrestrial varanids. Surprisingly, the specimen of *Amblyrhynchus cristatus* fell close to the basal synapsids and terrestrial varanids, especially on PCs 1 and 3, whereas the *I. iguana* specimen was closer to the crocodiles and semi-aquatic mammals.

Finally, only two of the specimens we measured that preserved fore and hind limb elements (FMNH UC 656, *Casea broilii*; FMNH UR 272, *Cotylorhynchus hancocki*) possessed fore limbs that were longer than hind limbs (Table 3.1). The remaining specimens all possessed longer hind limbs, regardless of ecology and phylogenetic position. The Kolmogorov-Smirnov tests showed that terrestrial and aquatic taxa did not differ significantly in limb length regardless of whether fossil taxa were included ($p = 0.295$) or not ($p = 0.809$). The fore limb to hind limb ratio of the measured *Ophiacodon* specimen was closer to the mean for terrestrial taxa regardless of whether fossil taxa were included or excluded.

Discussion

Centrum Length Profile and Swimming Style in the Extant Taxa Sampled

The centrum length profiles of several extant and extinct taxa have received attention in the literature (e.g., Buchholtz 1998, 2001a, b; Gingerich 1998; Buchholtz and Shur 2004; Buchholtz et al. 2005, 2007; Pierce et al. 2011), but most of this work has focused on mammals, particularly whales, and highly pelagic reptiles (i.e., ichthyosaurs). Our results for the extant taxa we examined suggest that there is likely more diversity in centrum length profile than has been appreciated previously, even intraspecifically, and that the correlation between centrum length profile and aquatic locomotion in semi-aquatic taxa may be less exact than in highly aquatic tetrapods.

Among the extant reptiles we sampled, the majority possess a peak in centrum length between the pelvic and pectoral girdles, corresponding to the area of lateral undulation during terrestrial locomotion (Buchholtz 1998). However, three of the varanid species we measured (*Varanus dumerilii*, *V. rudicollis*, and *V. salvator*) lack this peak, despite having sprawling limbs and laterally undulating during terrestrial locomotion, as do some specimens of *Caiman crocodilus*. The semi-aquatic reptiles *Caiman*, *Crocodylus, Gavialis*, *Melanosuchus*, and *Amblyrhynchus* also all possess a peak or plateau in centrum length in their tails, corresponding to the region where traveling waves pass along the vertebral column during swimming (Buchholtz 1998). The presence of this peak or plateau does not seem to be a foolproof indicator of a semi-aquatic lifestyle, though, because a similar plateau is present in the vertebral profile of the terrestrial *Iguana iguana* but is lacking in *Varanus salvator*, which is an adept swimmer.

A similarly inexact relationship between centrum length profile and swimming style is apparent when the extant mammalian results are considered. *Lontra canadensis*, *Neovison vison*, and *Chironectes minimus* all display a bimodal centrum length profile, with peaks in the lumbar and distal caudal regions of the vertebral column. Buchholtz (1998) documented a comparable pattern in *Enhydra lutra*, which she noted was consistent with the fact that dorsoventral undulation occurs in the lumbar and caudal regions of the body in swimming sea otters (also see Kenyon 1981). Therefore, similarity in centrum length profile to *E. lutra* is expected for *L. canadensis*, given that similar undulatory swimming is a component of its aquatic locomotor regime (Fish 1994), but it is surprising for *N. vison* considering that quadrupedal paddling is the main swimming style of the species (Williams 1983). Likewise, this profile likely has little to do with undulation during swimming in *C. minimus* because this species uses bipedal paddling of the hind limbs (alternate pelvic paddling) for aquatic propulsion and keeps the back horizontal while swimming (Fish 1993). Instead of corresponding only to swimming style, these bimodal centrum length profiles may represent retention or slight modification of an ancestral mammalian organization of the vertebral column, considering that a comparable bimodal pattern can also be found in fully terrestrial, cursorial taxa such as *Pachyaena* and *Canis* (Buchholtz 1998; Gingerich 1998). *Castor canadensis* differs from the other mammals we measured in showing a steady increase in centrum length in the presacral column, followed by a plateau in the proximal caudals. The unique pattern observed in *C. canadensis* likely reflects its derived caudal morphology, but the relationship between this morphology and swimming style is somewhat obscure. Much like *Chironectes*, alternate pelvic paddling is the primary source of propulsion in *Castor* (Fish 1996, 2001), with the tail playing at best a supporting role (Fish 2001).

Despite these qualitative differences, the length metric scores of the extant semi-aquatic taxa do differ on average from those of the terrestrial taxa. The extant semi-aquatic taxa have higher range (R), higher polarization (C), higher irregularity (Cm), higher $E1$, and higher $E2$ values on average for length than the terrestrial taxa, and a MANOVA on the metrics indicates that there is a significant difference between the two groups (Wilk's $\lambda = 0.0941$, d.f. = 5, 25, $F = 48.14$, $p \ll 0.001$).

Does Centrum Length Profile Support a Semi-aquatic Lifestyle in Ophiacodon?

Our observations of extant semi-aquatic taxa suggest that there is an inexact correlation between centrum length profile and swimming style, but that the length metrics can discriminate terrestrial and aquatic taxa effectively. Although the former observation adds complexity to the interpretation of our results for *Ophiacodon*, the available data largely refute the semi-aquatic *Ophiacodon* hypothesis.

The centrum length profiles of the *Ophiacodon* specimens do not show strong qualitative similarities to those of the extant semi-aquatic mammals or reptiles. In particular, *Ophiacodon* lacks the peak or plateau in caudal centrum length observed in *Amblyrhynchus* and the crocodilians that may be associated with undulatory swimming. The three *Ophiacodon* specimens included in the PC analysis of length metrics do fall within the area of morphospace occupied by most of the extant semi-aquatic taxa. Specifically, they largely overlap the area occupied by extant crocodiles. These results for *Ophiacodon* might suggest a semi-aquatic lifestyle, but they would be more convincing as evidence if the other basal synapsids fell in a different area of morphospace. However, nearly all of the basal synapsids fall in the area of morphospace occupied by most of the extant semi-aquatic taxa. Even the two *Cotylorhynchus* specimens, which fall outside of this area, are still closer in morphospace to the *Castor* and *Chironectes* specimens than to the terrestrial varanids or *Iguana*. Although this might imply that all of the basal synapsid taxa, including *Ophiacodon*, were semi-aquatic, such an interpretation would contradict almost all previous interpretations of their ecologies (e.g., Romer and Price 1940). This is particularly true of the caseids and *Varanops*, since caseids and varanopids often have been considered to be components of highly terrestrial, upland faunas (e.g., Olson 1952, 1962, 1968; Reisz 2005; Maddin et al. 2006; Evans et al. 2009; Berman et al. 2013). Instead, it seems more likely that the basal synapsid vertebral columns were organized in a different manner than those of the extant taxa, given that all of the basal synapsids also tend to cluster away from the extant taxa in the PC analysis based on the length, width, and height metrics.

The length metric results are somewhat more equivocal. The length metrics for *Ophiacodon* tend to be notably lower than either the extant terrestrial or semi-aquatic taxa (regardless of whether the three relatively incomplete specimens are included), although they are (slightly) closer to the values of the extant terrestrial taxa. In contrast, the length metrics for the other basal synapsids are closer on average to those of the extant semi-aquatic and terrestrial taxa, and their average values are intermediate between the two extant groups if only relatively complete specimens are considered. These differences imply that in terms of length, the vertebral column of *Ophiacodon* tends to be less polarized on average than those of the other basal synapsids and the extant tetrapods, as well as somewhat noisier. However, the relationship between this variation and lifestyle for basal synapsids is uncertain: *Ophiacodon* is different from the other basal synapsids, but not in the way we would predict if it was aquatic based on the extant specimens. Inclusion of a greater sample of terrestrial taxa, particularly extant terrestrial reptiles, in analyses such as those we present here may be useful for identifying a suitable modern analogue for *Ophiacodon* and the other basal synapsids. Nevertheless, when combined with the other observations on centrum length profile, we do not consider the length metrics for *Ophiacodon* to provide strong support for its hypothesized semi-aquatic lifestyle.

Is the Disparity in Limb Lengths in Ophiacodon Indicative of a Semi-aquatic Lifestyle?

Romer and Price (1940) and Kemp (1982) cited the fact that the hind limbs of *Ophiacodon* are longer than its fore limbs as evidence in support of a semi-aquatic lifestyle, but our results suggest that there is little importance to this observation. There was no significant difference in the ratio of limb lengths between aquatic and terrestrial taxa we sampled, with only two of the specimens we measured, FMNH UC 656 (*Casea broilii*) and FMNH UR 272 (*Cotylorhynchus hancocki*) possessing longer fore limbs than hind limbs. Although this is unlikely to be an artifact because the limb material in FMNH UC 656 represents only one individual (in contrast to its vertebral column; Williston 1911), it does emphasize that *Ophiacodon* is not unusual in its relative limb lengths. Furthermore, inclusion of manus and pes lengths most likely would not alter these conclusions. All of the basal synapsid taxa we examined possess relatively conservative manus and pes morphologies, and if anything show trends towards the development of short, broad feet rather than the long, triangular feet of paddling swimmers (Reisz 1986). Likewise, extant semi-aquatic reptiles do not show modification of the feet for swimming (Romer 1956), and only three extant lizards have been documented to use the feet for propulsion when swimming (Russell and Bels 2001). Among the semi-aquatic mammals we sampled, the hind limbs play a major role in aquatic locomotion in three of the four species, and they possess larger feet than hands. Taken together, these data indicate that limb length disparity should be eliminated from the evidence cited in support of the semi-aquatic *Ophiacodon* hypothesis.

Were Basal Synapsid Vertebral Columns Less Regulated than Those of Extant Taxa?

On average, the irregularity (*Cm*) of the basal synapsids are higher than those of the extant taxa, and their *E*2 (the metric quantifying the tendency of adjacent measurements to have similar values; McShea 1993) values are lower for height, length, and width. These statistics imply that a given vertebra in a basal synapsid column is less constrained to resemble the preceding vertebra than is the case for the extant taxa. McShea (1993) noted that the fossil taxa included in his analysis also tended to have more irregular columns than extant taxa, and attributed this to taphonomic artifacts such as deformation and rough bone preservation. Similar processes may be responsible for the greater noise in the basal synapsids, given that some show evidence of deformation (e.g., FMNH UC 112, FMNH UR 272), but others seem to be close to pristinely preserved (e.g., FMNH UC 1638). Alternatively, the greater noisiness of the basal synapsid columns may reflect a genuine difference because the centra of these taxa essentially are hour glass-shaped tubes that surrounded the notochord, which in turn widened in the intervertebral spaces (Romer and Price 1940). Given this mode of connection, centrum dimensions may have been less of a constraint on the function of the column, and therefore may have been less tightly regulated. This is a potentially important consideration because if the vertebral columns of the basal synapsids were operating under a different set of constraints than the extant taxa, then extant taxa may make poor predictors of expected morphologies for particular locomotor patterns and ecologies. A full test of this hypothesis is beyond the scope of this paper, but would be possible given a more systematic exploration of vertebral dimensions across a wider range of non-mammalian synapsids. It would also be interesting to determine whether an increase in regularity of vertebral dimensions accompanied the evolution of more regionalized vertebral columns in advanced non-mammalian synapsids.

Paleoecological Implications

The paleoecology of Early Permian terrestrial communities has been of interest for some time, especially in the context of the evolution of terrestrial communities with diverse, abundant tetrapod herbivores (e.g., Olson 1952, 1961, 1966, 1977, 1983, 1985a, b; Sullivan and Reisz 1999; Eberth et al. 2000; Berman et al. 2000, 2004, 2013; Reisz 2005; Evans et al. 2009). *Ophiacodon* has not figured prominently in these discussions, but when included it has been hypothesized to have fed primarily on aquatic food sources and perhaps to have been a food source for larger terrestrial carnivores like *Dimetrodon* (Olson 1977, 1983, 1985a, b). If *Ophiacodon* had a more terrestrial lifestyle, these hypotheses will need to be revised to include more terrestrial animals as potential prey items. The degree to which these communities were dependent on aquatic producers and primary consumers may also need to be reassessed. Nevertheless, the fact that *Ophiacodon* is not found in the most upland communities of the time, unlike some carnivorous basal synapsids (Berman et al. 2001, 2013), and became extinct as environments became drier (e.g., Olson 1983), implies that it did have some important connection to wetter, lowland environments. Further exploration of the functional morphology and paleoecology of *Ophiacodon* will be needed to determine whether this connection was related to its diet or other aspects of its physiology.

Conclusions

The hypothesis that *Ophiacodon* was semi-aquatic has a long history in the paleontological literature, and many lines of evidence have been advanced to support it. However, much of this evidence is inconclusive or has been reinterpreted. The unusually slow skeletal ossification of *Ophiacodon* and its bone histology may represent the data most suggestive of a semi-aquatic lifestyle that has been presented to date, but more extensive investigation of the bone histology of pelycosaur-grade synapsids is necessary before its true significance can be understood. Unfortunately, centrum length patterns across the vertebral column do not provide an unambiguous answer to the question of whether *Ophiacodon* was semi-aquatic. Although *Ophiacodon* does show centrum length patterns that are similar to some extant semi-aquatic tetrapods, these properties are also present in most of the other basal synapsids we examined, including taxa such as caseids and varanopids that are widely regarded as highly terrestrial. Therefore, we propose that the vertebral organization of *Ophiacodon* is more a function of its phylogenetic position than its ecology. The limb proportions of *Ophiacodon* also do not provide support for a semi-aquatic lifestyle. Given that there is almost no unequivocal evidence for an aquatic lifestyle in *Ophiacodon*, we do not think that such an ecology should be assumed. Instead, a more suitable null hypothesis is that it was terrestrial, and future studies should focus on falsifying that conjecture.

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