Journal of Anatomy

Original Articles

Information on this journal can be accessed at: http://www.journalofanatomy.com

Cover illustration: Embryo of *Pelusios subniger* (Pleurodira), CL = N.N., PIMUZlab 2012.IW10, serial section through right pes. See article by Joyce *et al.*, 'The hooked element in the pes of turtles (Testudines): a global approach to exploring primary and secondary homology', in this issue of *Journal of Anatomy* (2013) **223**, 421-441.

WILEY
Blackwell

Discover this journal online at
Wiley Online Library
wileyonlinelibrary.com

WILEY Blackwell

Journal of
Anatomy

ISSN 0021-8782

Volume 223, Issue 5, November 2013

Structure, Function, Development, Evolution

WILEY
Blackwell

ANATOMICAL SOCIETY

The hooked element in the pes of turtles (Testudines): a global approach to exploring primary and secondary homology

Walter G. Joyce,[1,2] Ingmar Werneburg[1,3] and Tyler R. Lyson[4,5]

[1]*Department of Geosciences, University of Tübingen, Tübingen, Germany*
[2]*Department of Geosciences, University of Fribourg, Fribourg, Switzerland*
[3]*Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland*
[4]*Department of Geology and Geophysics, Yale University, New Haven, CT, USA*
[5]*Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA*

Abstract

The hooked element in the pes of turtles was historically identified by most palaeontologists and embryologists as a modified fifth metatarsal, and often used as evidence to unite turtles with other reptiles with a hooked element. Some recent embryological studies, however, revealed that this element might represent an enlarged fifth distal tarsal. We herein provide extensive new myological and developmental observations on the hooked element of turtles, and re-evaluate its primary and secondary homology using all available lines of evidence. Digital count and timing of development are uninformative. However, extensive myological, embryological and topological data are consistent with the hypothesis that the hooked element of turtles represents a fusion of the fifth distal tarsal with the fifth metatarsal, but that the fifth distal tarsal dominates the hooked element in pleurodiran turtles, whereas the fifth metatarsal dominates the hooked element of cryptodiran turtles. The term 'ansulate bone' is proposed to refer to hooked elements that result from the fusion of these two bones. The available phylogenetic and fossil data are currently insufficient to clarify the secondary homology of hooked elements within Reptilia.

Key words: ansulate bone; chondrification; development; fossils; hooked fifth metatarsal; morphology; myology; ossification.

Introduction

The phylogenetic position of turtles within Tetrapoda remains one of the most controversial issues in vertebrate systematics. Although nearly every possible placement has been posited for turtles relative to the six primary crown clades of Tetrapoda within the last two centuries (i.e. a sister group relationship to Amphibia, Mammalia, *Sphenodon punctatus*, Squamata, Aves and Crocodylia, and many combinations thereof, see Joyce & Gauthier, 2004 for summary), the debate has focused on three primary hypotheses within the clade Reptilia in the last 20 years. Molecular data (e.g. Cao et al. 2000; Hugall et al. 2007; Shen et al. 2011; Tzika et al. 2011; Chiari et al. 2012; Crawford et al. 2012; Shaffer et al. 2013; Wang et al. 2013) typically favour a placement of turtles as sister to

Archosauria (= Aves + Crocodylia), but a recently compiled set of micro RNA data (Lyson et al. 2012) firmly place turtles as sister to Lepidosauria (= *S. punctatus* + Squamata). From a morphological perspective, there is an almost complete lack of support for a relationship of turtles with archosaurs (Rieppel, 2000), despite earnest attempts to find possible synapomorphies between the two groups (e.g. Bhullar & Bever, 2009). Instead, comprehensive, morphological studies regularly find evidence for placement of turtles either as sister to Lepidosauria (e.g. deBraga & Rieppel, 1997; Rieppel & Reisz, 1999; Müller, 2004; Li et al. 2008) or among basal reptiles as sister to Sauria (= Archosauria + Lepidosauria; e.g. Gauthier et al. 1988; Laurin & Reisz, 1995; Lee, 1997a; Werneburg & Sánchez-Villagra, 2009; Lyson et al. 2010). Most morphological data sets do not provide particularly strong support for either one of these two competing topologies, and the simple addition or omission of characters and/or taxa will often remove turtles from or return turtles to Diapsida (e.g. Rieppel & Reisz, 1999; Lyson et al. 2010). Given the lack of strong data that support either one of these two competing hypotheses, it is clear that every morphological character

is important in helping to resolve the origin of turtles, and much attention has therefore been given to identifying 'key characters' that might help resolve this issue (e.g. Lee, 1996; Rieppel & Reisz, 1999; Joyce et al. 2006; Müller et al. 2011; Lyson & Joyce, 2012; Werneburg, 2013a,b; Lyson et al. 2013; Lyson et al., in press).

The hind foot of all living groups of reptiles, with the exception of birds, is characterized by the absence of a fifth distal tarsal and the presence of an L-shape element called the 'hooked fifth metatarsal', which was utilized by Goodrich (1916) and Broom (1924) to unite the clade 'Sauropsida' relative to various extinct, mostly Palaeozoic, amniote lineages with a fifth distal tarsal and a straight fifth metatarsal. All recent phylogenetic analyses agree with the primary homology assessment of Goodrich (1916) and Broom (1924), although the resulting topologies either confirm that the hooked bone is a synapomorphy of crown Reptilia (e.g. Rieppel & Reisz, 1999) or that the hooked bone of turtles evolved independently from that of Sauria (= Lepidosauria + Archosauria; e.g. Gauthier et al. 1988; Laurin & Reisz, 1995; Lee, 1997a,b).

Embryologists have historically scrutinized the primary homology of the hooked fifth metatarsal by studying centres of chondrification and ossification (e.g. Rabl, 1910; Goodrich, 1916; Sewertzoff, 1929; ; Holmgren, 1933; Burke & Alberch, 1985; Rieppel, 1993a), but none of these traditional studies found any data that would contradict the primary homology of the hooked element ascertained by palaeontologists. However, two recent papers on the development of extant turtles (Sheil & Portik, 2008; Fabrezi et al. 2009) report observations that would indicate that the hooked element of turtles actually represents the extremely enlarged and hooked fifth distal tarsal. Earlier authors have historically referred to the hooked element as the fifth distal tarsal as well, particularly when describing fossil material (e.g. von Meyer, 1839a,b; Jourdan, 1862; Boulenger, 1889; Case, 1939), but these identifications appear to be casual mistakes and do not mirror primary or secondary homology hypotheses based on data or deep conviction. The ideas of Sheil & Portik (2008) and Fabrezi et al. (2009) can therefore be thought of as novel. This new hypothesis has gone uncontested to date (e.g. Werneburg et al. 2009; de la Fuente & Fernández, 2011; Vieira et al. 2011), although some authors prefer retaining traditional nomenclature by continuing to refer to this element as the hooked fifth metatarsal (e.g. Delfino et al. 2010). Nevertheless, a distal tarsal identity of the hooked element has important phylogenetic repercussions, because it favours placing turtles among early amniote groups with a fully developed fifth distal tarsal (e.g. various parareptilian or early diapsid groups). By contrast, if a distal tarsal identity is correct, most placements of turtles within crown Diapsida, as either sister to lepidosaurs or archosaurs, demand the unparsimonious and implausible straightening of the fifth metatarsal, regaining of the purported fifth distal tarsal, and the subsequent hooking of the fifth distal tarsal, as most lepidosauromorphs and all archosauromorphs reportedly have a hooked metatarsal and only four tarsals (see Discussion).

We identify five lines of evidence that have been used to assess the primary homology of the hooked element: myology; mode of ossification/recapitulation; timing of development; digital count; and the fossil record combined with general morphology and topology. The purpose of the present contribution is to report new data on myology and ossification patterns among extant turtles, and to systematically review the primary homology (Remane, 1952; Patterson, 1988; de Pinna, 1991) of the hooked element using all five lines of evidence. Although we believe that congruence is the ultimate arbiter of secondary homology (e.g. Nelson & Platnik, 1981; Rieppel, 1988; Joyce & Sterli, 2012), the controversial placement of turtles makes it impossible to fully resolve the secondary homology of the hooked element. Given that we ultimately conclude that the hooked element of turtles represents a composite element consisting of the fifth distal tarsal and the fifth metatarsal (though with unclear primary and secondary homology to the hooked element of other tetrapods), we herein use the term 'hooked element' when wishing to remain homology neutral, but otherwise suggest the new term 'ansulate bone' [= 'Knochen S' (bone S) of Ogushi, 1911] or 'ansulate' (from Latin ansula = hook) when wishing to express that this bone is the result of fusion.

Institutional abbreviations are as follows: AM = Albany Museum, Grahamstown, South Africa; BPI = Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; IVPP = Institut for Vertebrate Paleontology and Paleoanthropology; MCZ = Museum of Comparative Zoology, Cambridge, MA, USA; NHM = Natural History Museum, London, UK; PIMUZlab = Sánchez-Villagra Laboratory Collection, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SAM = South African Museum, Cape Town, South Africa; SKLK = Shigeru Kuratani Laboratory Collection, RIKEN Institute for Developmental Biology, Kobe, Japan; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany; YPM = Yale Peabody Museum, New Haven, USA.

Materials and methods

Neontological observations

To investigate the mode of ossification of the hooked element of extant turtles, we re-analysed the cleared and double-stained embryological series of *Emydura subglobosa* [PIMUZlab 2009.02 (crown rump length = 13.5 mm), 2009.06 (carapace length, CL = 22.93 mm), 2009.09 (CL = 79.2 mm), 2008.19 (CL = about 3.5 mm), 2008.23 (CL = about 9 mm), 2008.24 (CL = about 12 mm), 2008.25 (about 13.5 mm), 2008.28 (CL = 13.74 mm), 2008.29 (CL = 13.62 mm), 2008.73 (CL = 8.7 mm), 2008.74 (CL = 21.8 mm), 2008.75 (CL = 20.32 mm)] used by Werneburg et al. (2009), the

cleared and double-stained embryological series of *Pelodiscus sinensis* (PIMUZlab 2009.IW20-65, 71; SKLK uncat; see Fig. 3 for the CL measures of photographed specimens) used by Sánchez-Villagra et al. (2009), and the cleared and double-stained embryological series of *Caretta caretta* [SKLK B42 (CL = 27.8 mm), SKLK B46 (CL = 26.6 mm)] used by Kuratani (1987, 1989, 1999) and Sánchez-Villagra et al. (2007b). All of these specimens had previously been stained with Alizarin Red against calcified structures and with Alcian Blue against cartilaginous structures using standard protocols (Dingerkus & Uhler, 1977). In addition, we re-analysed the histological serial sections of single embryological specimens of *Chelodina longicollis* [PIMUZlab 2012.IW18 (CL = 11.8 mm)], *Emydura subglobosa* [PIMUZlab 2009.78 (CL = 28.5 mm, 46 days old, at about SES-stage 14–15 of Werneburg et al. 2009)], *Phrynops geoffroanus* [PIMUZlab 2012.IW15 (CL = 16.2 mm)] and *Podocnemis unifilis* [PIMUZlab 2012.IW19 (CL = 22 mm)] used by Sánchez-Villagra et al. (2007a). In addition we studied sections of the pleurodires *Pelusios subniger* [PIMUZlab 2012.IW10 (CL = N.N.)], *Po. unifilis* [PIMUZlab 2012.IW13 (CL = 27.5 mm)] and *C. longicollis* [PIMUZlab 2012.IW14 (CL = 18 mm)], and the cryptodires *Terrapene ornata* [PIMUZlab 2012.IW11, 'specimen A' (CL = 26.4 mm), PIMUZlab 2012.IW12, 'specimen C' (CL = 19.4 mm)] and *Chelonia mydas* [PIMUZlab 2009.71b, specimen XII, M25 (CL = 19.5 mm)].

Compared with the cleared and double-stained series, the histological specimens only represent a snapshot in ontogeny (i.e. one developmental stage) of each species. As such, the information gathered from them can only provide indications regarding global developmental patterns based on specific anatomical details. All anatomical compartments are nevertheless present in histological sections, which allows comparing points of muscle insertion and accurately assigning bone microstructure. We finally prepared, cleared and stained specimens of *Pelodiscus sinensis* [PIMUZlab 2012.IW25 (CL = 13.9 mm), 2012.IW26 (CL = 18.8 mm), 2012.IW27 (CL = 14.4 mm), 2012.IW28 (CL = 17.2 mm), 2012.IW29 (CL = 16.3 mm)], but only using Alizarin Red to avoid potentially dissolving minute ossifications by the acids in the Alcian Blue. The myological data were derived from a literature review on turtle and tetrapod hind limb musculature with a focus on classical studies such as Ribbing (1909, 1938) and Walker (1973). We herein follow the recommendations of Werneburg (2011) in regards to muscle terminology: (i) muscle origins are defined as being situated proximally/tibially; (ii) muscle insertions are defined as being placed distally/fibularly; and (iii) muscle numbers are assigned to the most differentiated muscular structures (see Appendix 1). For simplicity, however, we refrained from addressing muscular structures as muscular units *sensu stricto* (Werneburg, 2011), because this approach would demand a more comprehensive literature review. Hence, the term 'muscle' represents a nomenclatural simplification adjusted to the scope of the present study.

Palaeontological observations

To determine the number of tarsal bones and whether or not a hooked element was preserved in fossil stem members of various groups, we analysed the following specimens: stem Amniote – *Limnoscelis paludis* (YPMVP 811); Parareptilia – *Eunotosaurus africanus* (AM 5999), *Broomia perplexa* (NHM 4065), *Milleropsis pricei* (BPI 4203); stem Diapsida – *Araeoscelis casei* (MCZ 4380 and MCZ 8828), *Youngina capensis* (SAM K 7710); potential stem Lepidosauria – *Saurosternon bainii* (NHM 1234); stem Archosauria – *Mesosuchus browni* (SAM K 7416); and stem Testudines – *Odontochelys semitestacea* (IVPP V 13240), *Proganochelys quenstedti* (SMNS 17204

and SMNS 16980). The literature was consulted for a number of additional taxa. Relevant citations are provided in the text.

Results

Myology

The most comprehensive overview of the lower hind limb musculature of living tetrapods is presented in the monographs of Ribbing (1909, 1938). More detailed studies have since been undertaken for turtles (e.g. Zug, 1971; Walker, 1973), lepidosaurs (e.g. Robinson, 1975; Hoyos, 1990; Russel & Bauer, 2008), crocodilians (e.g. Brinkman, 1980; Carrano & Hutchinson, 2002) and birds (e.g. George & Berger, 1966; Hutchinson, 2002). We herein only intend to summarize general patterns that relate to the hooked element in all reptilian taxa with a fully developed fifth digit (i.e. turtles, lepidosaurs and crocodilians). However, given that it is beyond the scope of this paper to comprehensively review the pedal musculature of amniotes or to revise the primary homology of muscles among various groups, we follow the proposed primary homologies of Ribbing (1909, 1938) because he is the only author to employ an internally consistent set of homology criteria (i.e. origin, insertion, fibre course and innervation patterns) across Tetrapoda. To avoid confusing the reader with long lists of muscle names, we substitute muscle names with numbers in the text and the figures (*sensu*, Werneburg, 2011). The muscular structures of the turtle pes are schematically illustrated in Fig. 1B,C. A list of synonyms is provided in Appendix 1.

Following Zug (1971), who studied cryptodires, and Walker (1973), who summarized most of the then-available turtle literature, up to 10 muscular structures attach to the hooked element in turtles (i.e. muscles 1–3, 9, 11, 15–16, 22–23, 33). Although some variation is apparent among taxa, our revision of the literature reveals that a similar set of muscular structures (i.e. muscles 1–4, 9, 15–16, 22–23) inserts onto the hooked element of other reptiles (Ribbing, 1909).

Mode of ossification and recapitulation

Pleurodires
We observed small endochondral ossifications (i.e. replacement ossifications) in the hooked element of cleared and double-stained specimens of *Emydura subglobosa* (Fig. 2E, F). This corresponds to the observation of Fabrezi et al. (2009) for *Podocnemis unifilis*, and of Vieira et al. (2011) for *Podocnemis expansa*. In addition we also discovered a distinct perichondral ossification along the distal half of the hooked element in histological sections of an early specimen of *E. subglobosa* (Fig. 1K). This perichondral ossification, however, is almost invisible in cleared and stained *E. subglobosa* specimens (Fig. 2E,F). We suspect its putative absence is an artefact of using Alcian Blue to stain specimens, because this dye is slightly acidic and may therefore

Fig. 1 Histological sections and muscle anatomy. (A) Serial sections-based 3D-reconstructions of pedal anatomy, modified and mirrored from Sánchez-Villagra et al. (2007a: fig. 5), with kind permission of Marcelo R. Sánchez-Villagra: (A′) *Podocnemis unifilis,* carapace length (CL) = 22 mm; (A″) *Phrynops geoffroanus*, CL = 16.2 mm; (A‴) *Emydura subglobosa*, CL = 28.5 mm; (A″″) *Chelodina longicollis*, CL = 11.8 mm. (B) Dorsal (deep extensors) and (C) plantar view (deep flexors) of the pes musculature in *Trachemys scripta elegans*, modified after Walker (1973, fig. 30), see Appendix 1 for muscle numbers, dark grey coloured structures are not described herein. (D–M) Sections of the right pes in different turtle embryos. (D) *Pelusios subniger* (Pleurodira), CL = N.N., right pes. (E) *Po. unifilis*, CL = 27.5 mm. (F) Detail of (E), arrow in the figure indicates suture between embryonic metatarsal-V and embryonic distal tarsal 5; white arrows indicate the common tendon of mm. gastrocnemius (no. 1–2) et peroneus (no. 22/23) inserting onto the metatarsal V part of the ansulate bone. (G) *C. longicollis* (Pleurodira), CL = 18 mm. (H) *Terrapene ornata* (Cryptodira), CL = 26.4 mm. (I and J) *Chelonia mydas* (Cryptodira), specimen XII (M25), CL = 19.5 mm, with a more tibial (I) and a more fibial (J) section. (K) *Emydura subglobosa* (Pleurodira), CL = 28.5 mm. (L) *Phrynops geoffranus* (Pleurodira), CL = 16.2 mm, this section also used by Sánchez-Villagra et al. (2007a, fig. 7). (M) *Terrapene ornata* (Cryptodira), CL = 19.4 mm. (M1–8) Progressive, enlarged sections of the pes of *T. ornata* (M) illustrating the partial fusion of the endochondrally ossifying distal tarsal 5 to metatarsal V of the ansulate bone (an). Abbreviations: I–V = first to fifth pedal digit; 2nd = second element of toe-V, 2nd = second element of toe-V in the embryo of *Podocnemis unifilis* (E and F); 3rd = third element of toe-V; dt = distal tarsal; fi = fibula; i + f = fused intermedium (astragalus) and fibulare (calcaneum; 'astragalocalcaneum'; following Sánchez-Villagra et al. 2009); mt = metatarsal; f = fibulare; ph = phalange; ti = tibia. Arrows at the subfigure letters indicate tibial direction. Distal direction is top in A, D–F, K, L; left in B, C, G, I, J, M; right in H. All sections were stained with Azan-Domagk and embedded in paraffin, section thickness: 10 μm in E–H, K–M, 12 μm in D, 15 μm in I and J. Muscle names in the sections were only added where needed, as a comprehensive review would be necessary to evaluate every single structure (see text). White asterisk in F = common tendon of muscles 1–2 and 22/23 (mm. gastrocnemius/peroneus complex); black asterisk = perichondral ossification; red asterisk = endochondral ossification within the hooked element. Scale bars: no scales (A–C); 1 mm (D, E, H–J); 0.25 mm (F, M1–8); 0.5 mm (G, K–M).

dissolve small ossification centres. The perichondral portion of the hooked element starts to ossify in the serial sections at the same time as metatarsals I–IV (Fig. 1K). Later in development, the perichondral ossification expands and appears to overlap with the endochondral ossification (Fig. 2F). A dense cartilaginous epiphysis develops distally on the hooked element of *E. subglobosa,* which resembles the distal epiphyses of metatarsals I–IV (Figs 1F,K and 2F).

Our study of the available histological sections of *Phrynops geoffroanus* confirms the original findings of Sánchez-Villagra et al. (2007a) that the hooked element contains two separate anlagen (Fig. 1L). The proximal part of the hooked element ossifies endochondrally, whereas the distal part ossifies perichondrally.

Serial embryological sections of *Po. unifilis* (Fig. 1E–F), the same species studied by Fabrezi et al. (2009), show a fusion of two cartilaginous parts within the hooked element. Compared with *Ph. geoffroanus,* the proximal, endochondral portion is much larger relative to the distal, perichondral part (compare with Fig. 1A). The distal, perichondral part again forms a dense cartilaginous epiphysis similar to the distal epiphyses of metatarsals I–IV. The distal portion furthermore serves as the lone insertion point for the common tendon of muscles 1–2 and 22/23 (the mm. gastrocnemius/peroneus complex, Fig. 1F: indicated by an asterisk).

Cryptodires
We analysed two series of *Pelodiscus sinensis* embryos, of which one is double-stained with Alcian Blue and Alizarin Red, while the other is only stained with Alizarin Red. In one single-stained specimen (PIMUZlab 2012.IW25), we documented a weak ossification in the tarsal region in a stage of early ossification of metatarsal I–IV (Fig. 3D–F). At this stage, no ossifications are apparent in the tarsal region in double-stained specimens (Fig. 3B). An endochondral ossification (i.e. replacement ossification) is apparent within the

tibioproximal portion of the hooked element where the hooked element forms its articulation with an element formed by a fusion of distal tarsal 4 and a centrale (Sánchez-Villagra et al. 2009; Fig. 3A). We can exclude identifying this ossification as belonging to the fused distal tarsal 4/centrale element due to spatial relationships (compare Fig. 3F with Fig. 3A). A similar endochondral ossification cannot be found in any of the double-stained specimens of *Pe. sinensis*. As development proceeds, the hooked element appears to ossify perichondrally from the fibular side (Fig. 3L–P), just like metatarsals I–IV (Fig. 3K). The hooked element of *Pe. sinensis* shows evidence of rotation given that the cylindrical perichondral collar is arranged at an angle of approximately 90 ° relative to those of metatarsals I–IV (Fig. 3G–J). The fibular part of the distal epiphysis serves as the insertion site for muscles 1–2 and 22/23 (mm. gastrocnemius/peroneus complex), and thereby forms a prominent process that contributes to the hook shape of the bone (Fig. 1D–H, K–M). The tibial side of the distal epiphysis is expanded and serves as the articular surface for the remainder of digit V (Fig. 3K–P).

We also observed a distinct, lightly stained cartilaginous disk-like structure on the proximal side of the hooked element in double-stained embryos of *Pe. sinensis*, which had not yet ossified their hooked element (Fig. 3B). Complete removal of the hooked element from the foot revealed that it actually consists of two connected cartilages: a narrow proximal element that contacts distal tarsal 4 and metatarsal IV, and a broad distal element that does not contact any element of the fourth digit (Fig. 3C). The proximal element has the same topological position as the early endochondral ossification that was apparent in the specimens stained with Alizarin only, and we therefore interpret it as the same element. The large distal element, by contrast, appears to correspond to the part of the hooked element that ossifies perichondrally in other specimens. These two cartilages
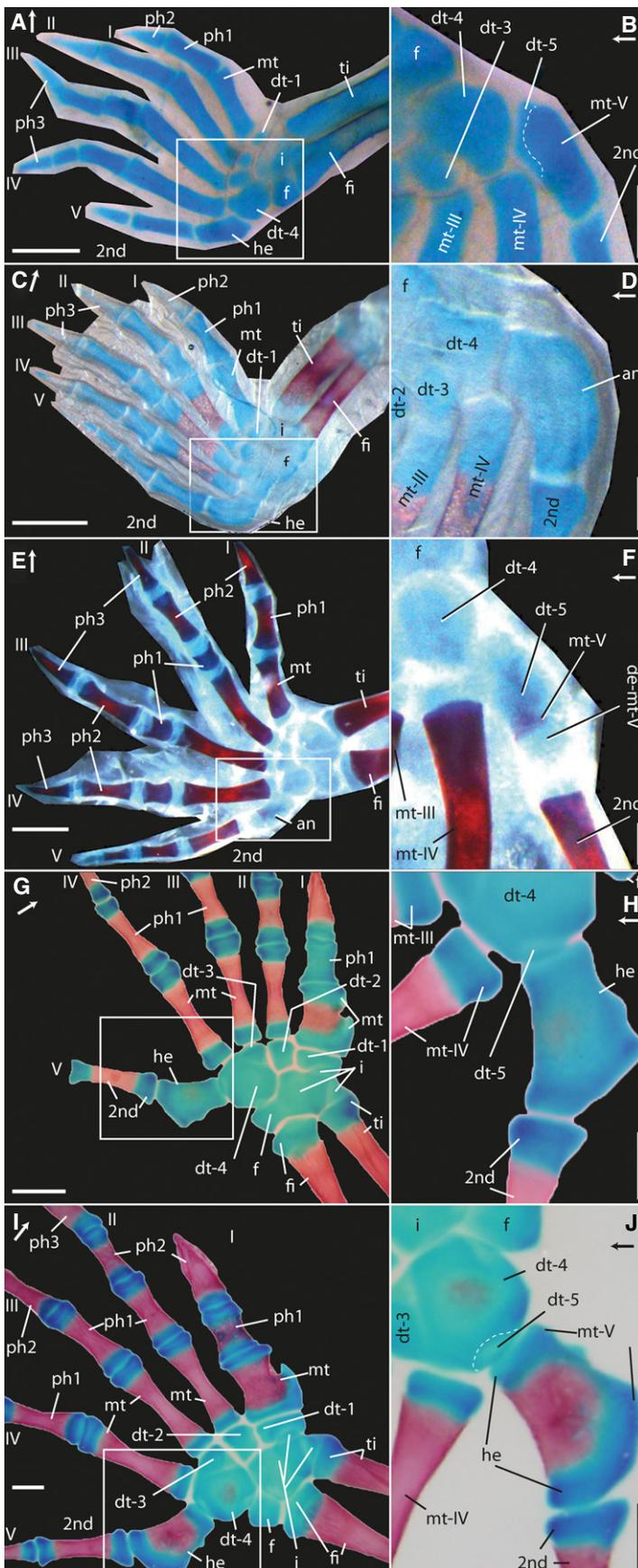
Fig. 2 Proposed primary homology of pedal elements during the embryological development of *Emydura subglobosa* (Pleurodira) and *Caretta caretta* (Cryptodira). All images were taken in dorsal view and all specimens represent right pes, with the exception of (G and H), which is a left pes that was mirrored for easier comparison. Stages are defined in Werneburg et al. (2009). (A and B) *E. subglobosa*, CL = 13.5 mm; (C and D) *E. subglobosa*, CL = 22.93 mm, SES-stage 13; (E and F) *E. subglobosa*, CL = 79.2 mm; (G and H) *C. caretta*, CL = 27.8 mm (mirrored); (I and J) *C. caretta*, CL = 26.6 mm. Abbreviations: I–V = first to fifth pedal digit; 2nd = second element of toe-V; an = ansulate bone (i.e. fused fifth distal tarsal and fifth metatarsal); de-mt-V = distal epiphysis of metatarsal-V; dt = distal tarsal; f = fibulare (calcaneum); fi = fibula; he = hooked element; i = intermedium (astragalus); mt = metatarsals; ph = phalanx; ti = tibia. Arrows indicate tibial direction. Scale bars: 0.5 mm (A, H); 0.25 mm (B, D, F); 1 mm (C, E, G, I, J).

cannot be distinguished from one another later in ontogeny (Fig. 3K).

The perichondral ossification of the diaphysis of the hooked element later covers the epiphyses, resulting in an almost completely ossified hooked element in the adult (Fig. 3A). The above-mentioned processus articularis of the distal epiphysis remains cartilaginous in adults (Ogushi, 1911) and articulates with the remainder of digit V. The opposite process (i.e. the 'hook') serves as the insertion site for muscles 1–2 and 22/23 (the gastrocnemius/peroneus muscle complex), and may ossify separately from the perichondral diaphysis expansion (Fig. 3N–P). All traces of the proximal element are later lost in ontogeny.

Similar results to what we observed in *Pe. sinensis* have been reported for all other studies of double-stained cryptodiran taxa: specimens are either fully unossified or they show a fully ossified hooked element (*Chelydra serpentina*: Sheil & Greenbaum, 2005; *Macrochelys temminckii*: Sheil, 2005; *Pelodiscus sinensis*: Sánchez-Villagra et al. 2009). If an unclear ossification centre is apparent, however, it may reasonably be interpreted as being perichondral (e.g. *Eretmochelys imbricate*: Sheil, 2003b; fig. 51e: *Apalone spinifera*: Sheil, 2003a; *Trachemys scripta*: Sheil & Portik, 2008).

The double-stained loggerhead embryos (*Ca. caretta*) studied herein show a tiny perichondral ossification in early development (Fig. 2G,H) that develops from the tibial side and appears to expand rapidly (Fig. 2I,J; see also Wyneken, 2001, fig. 90). An endochondral ossification was not found in the hooked element of *Ca. caretta*, but distal tarsal 4 shows a distinct fibulodistal chondrification area, which articulates with the hooked element and that may represent distal tarsal 5 (Fig. 2G–J). The available embryonic material of *Chelonia mydas*, by contrast, displays simultaneously occurring peri- and endochondral ossifications in the hooked element (Fig. 1I,J).

In an embryo of the dessert box turtle *Terrapene ornata*, we found the endochondrally ossifying proximal part of the hooked element in the process of fusing with the large unossified part of the hooked element (Fig. 1M,M1–M8). In an older embryo of the same species, only a perichondral ossification is visible covering the distal half and the proximal-most part of the hooked element (Fig. 1H). The subsequent presence of endochondral and perichondral ossifications further supports the double identity of the hooked element. Finally, and similar to *Pe. sinensis*, an approximate 90° rotation of the perichondral collar relative to those of metatarsals I–IV is visible in this specimen, as is the broad insertion of the gastrocnemius/peroneus muscle complex (no. 1–2, 22/23) along the fibular side of the hooked element (Fig. 3H).

Discussion

Our review of the available literature (Sheil & Portik, 2008; Fabrezi et al. 2009) allows us to identify five lines of evidence that can be used to assess the primary homology of the hooked element: myology, mode of ossification/recapitulation; timing of development; digital count; and the fossil record combined with general morphology and topology. We summarize each line of evidence, and discuss insights gained from taking a more global approach to primary and secondary homology (Fig. 4).

Myology

Of the 10 muscles that attach to the hooked element of turtles, all but two (muscles 11 and 33) also attach to the hooked element found in other reptiles. In addition, of the nine muscles that attach to the hooked element in other reptiles, all but one (muscle 4) attach to the hooked element of turtles as well. Similarity in muscle connectivity patterns therefore clearly supports the primary homology of the hooked element among reptiles. Fabrezi et al. (2009) nevertheless concluded using myological evidence derived from the pleurodire *Podocnemis unifilis* (i.e. our muscles 1–4, 22) that the hooked element of turtles is the fifth distal tarsal. Considering that we ultimately arrived at a conclusion contrary to that of Fabrezi et al. (2009), we felt obliged to review the primary data and rationales used by Fabrezi et al. (2009) to support the distal tarsal identity of the hooked element.

Fabrezi et al. (2009) first observed that muscle 22 (m. peroneus anterior) and muscle 1–2 (m. gastrocnemius complex), muscles of the crus, attach to the fibular and dorsal surface of the hooked element 'proximal' to the distal tarsal/metatarsal joint in the turtle *Po. unifilis*, but that the homologous muscles (i.e. mm. peroneus brevis, peroneus longus and gastrocnemius) of the lizard *Liolaemus multicolor* attach to a secondary ossification centre (plantar tubercle) on the hooked element 'distal' to the tarsal/metatarsal joint. Given that the same muscles purportedly insert proximally and distally to the tarsal/metatarsal joint, Fabrezi et al. (2009) argued that the hooked bones cannot be primary homology. We generally agree with the primary homology of the muscles involved in this argument, but question the rationale used to justify primary non-homology. The argument of Fabrezi et al. (2009) is elegantly formulated to pertain to topological differences in the insertion of muscles 1–2 and 22, but is false in assuming *a priori* that the hooked element is a distal tarsal in turtles but a metatarsal in lizards. This creates the illusion of topological differences in the insertion points of the relevant muscles relative to the presumptive tarsal/metatarsal joint. In fact, muscles 1–2 and 22 insert onto the same bone, the hooked element, in all reptiles and therefore actually support the primary homology of the hooked element among reptiles.

Fabrezi et al. (2009) next observed that a ligament of muscle 1–2 (m. gastrocnemius complex) fuses in *Po. unifilis* with the plantar aponeurosis of muscles 3–4 (the flexor
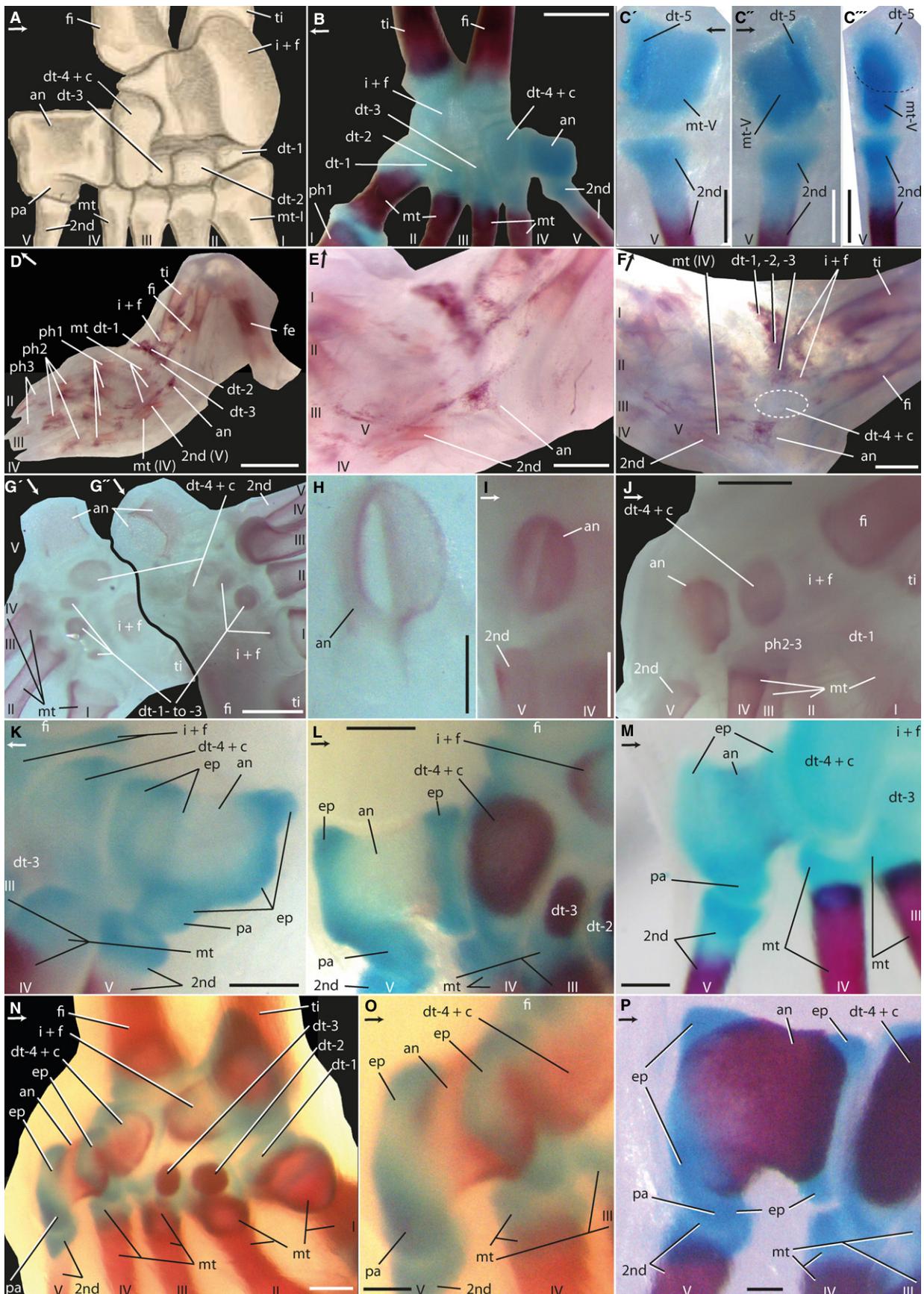
Fig. 3 Proposed primary homology of pedal elements during the development of *Pelodiscus sinensis* (Cryptodira). All specimens were double-stained with Alizerin Red (against calcified structures) and Alcian Blue (against cartilaginous structures), with the exception of (D–J), where only Alizerin Red was used. (A) Adult anatomy (modified after Ogushi, 1911). (B and C) left pes, PIMUZlab2011.IW41 (CL = 18.5 mm), in dorsal view with soft tissue removed (B), isolated ansulate and second element of toe-V in dorsal (C'), plantar (C'') and tibial (C''') view. (D–F) Left leg, specimen with CL = 13.9 mm; (D) leg in dorsofibular view; (E) magnification of (D) with a focus on the tarsal region; (F) focus on the tarsal region in a more dorsal view, non-ossified area of distal tarsal 4 and the central indicated by a circle. (G and H) Left pes of a specimen with CL = 17.2 mm; (G') dorsal view; (G'') plantar view with rotated ansulate element; (H) isolated ansulate bone in fibial view; (I) dorsofibial view of the ansulate bone of the right pes in a specimen of CL = 16.3 mm, ossification proceeded and only a cleft remains. (J) Dorsofibial view of the right pes, CL = 18.8 mm, ossification with no cleft remaining. (K) Ansulate bone of the left pes, PIMUZlab 2011.IW58 (CL = 17.7 mm), in dorsal view, epiphyses differentiated. (L–P) Variation and sequence of ossification in the elements of the pes. (L) PIMUZlab 2011.IW21 (CL = 19.7 mm), right pes, plantar view, beginning perichondral ossification. (M) Hatching specimen, SKLK uncat. (CL = about 19–20 mm), right pes, dorsal view, ossification proceeded in the diaphysis of the ansulate element. (N) PIMUZlab 2011.IW60 (CL = 22.4 mm), left pes, plantar view. (O) Detail of (N), whole diaphysis perichondrally ossified. (P) Specimen PIMUZlab 2011.IW64 (CL = 23.9 mm), left pes, plantar view, ossification of the epiphyses reaching the adult condition shown in (A). Abbreviations: I–V = first to fifth pedal digit; 2nd = second element of toe-V; an = ansulate bone; dt = distal tarsal; dt-4 + c = fused distal tarsal 4 and centrum (following Sánchez-Villagra et al. 2009); ep = epiphysis of the ansulate bone; fe = femur; fi = fibula; i + f = fused intermedium (astragalus) and fibulare (calcaneum; following Sánchez-Villagra et al. 2009); mt = metatarsal; ph = phalanges; pa = processus articularis of the ansulate bone; ti = tibia. Arrow indicates the tibial direction. Distal direction is below; except for D–F–H', where distal is left, and G'' where distal is right. Scale bars: no scale (A); 1 mm (B, G, J); 0.5 mm (C, D, H–I, K–L, N); 0.25 mm (E, F, M, O–P).

plate of Walker, 1973) and inserts onto the fibular side of the first phalanx of digit V. By contrast, the same ligament attaches to the hooked element in the lizard *L. multicolor*. If the insertion point of this ligament is thought to be primary homologous, one must therefore conclude that the first phalanx of digit V of turtles is primary homologous with the hooked element of lizards and actually represents a metatarsal.

This line of reasoning is correct in principle, but somewhat contradicted by the fact that the vast majority of the gastrocnemius muscle complex (muscle 1–2) actually attaches to the hooked element in turtles and lizards (see above). A more global approach reveals that the condition reported by Fabrezi et al. (2009) for *Po. unifilis* may not be representative for all turtles. A ligament of the gastrocnemius muscle complex that attaches to the first phalanx of digit V has never before been described for any other turtle in the extensive body of turtle hind limb literature (e.g. Hoffmann, 1890; Zug, 1971; Walker, 1973). Four possibilities exist that can explain this conflict in the primary data. It is firstly possible that Fabrezi et al. (2009) were simply confused and mis-identified the insertion site of muscle 5 (m. lumbricales), which inserts onto the penultimate phalanx of most reptiles (Ribbing, 1909; Walker, 1973). If this re-interpretation is correct, the observations of Fabrezi et al. (2009) actually support the metatarsal identity of the hooked element of turtles, given that the alternative unparsimoniously requires moving the insertion of muscle 5 onto the metatarsal.

The second possibility is that Fabrezi et al. (2009) correctly identified a split in the insertion points of muscle 1–2, but a more global context removes the significance of this observation. The muscle 1–2 complex of turtles usually has two muscle heads, one originating on the femur and the other on the tibia. According to Walker (1973), a complete separation of muscles 1 and 2 has so far only been documented for the trionychid *Pelodiscus sinensis* among a large sample of turtles (together as muscle no. 137 or 'm. flexor digito-

rum longus sublimes' of Ogushi, 1913, p. 130), although both heads nevertheless continue to insert distally onto the hooked element, which is the plesiomorphic condition. Given that no other turtle, including no other trionychid, has to date been shown to have separate insertion points for muscle 1–2 (e.g. Hoffmann, 1890; Zug, 1971), the separate insertion points identified by Fabrezi et al. (2009) for *Po. unifilis* are better interpreted as an autapomorphy of that taxon, perhaps in response to the need to further spread the webbing between the fourth and fifth toes (Walker, 1973, p. 88). If this interpretation is correct, then the muscle pattern observed by Fabrezi et al. (2009) must be viewed as an autapomorphy and has no bearing on the primary homology of the hooked element.

Fabrezi et al. (2009) finally utilized information from the interdigital muscles to support the distal tarsal identity of the hooked element in turtles. In particular, they stated that two muscles, 'mm. flexor digiti brevis et interosseum', span between metatarsal IV and the first phalanx of digit V in *Po. unifilis*, but that the same muscles (i.e. 'm. interosseum = m. intermetatarsale') span between metatarsal IV and the hooked element in the lizard *L. multicolor*. Assuming that these muscles attach to the same element in both animals, this observation implies that the second element of turtles is metatarsal V and that the hooked element of turtles is distal tarsal 5.

Walker (1973, p. 89) mentioned that there is "considerable confusion in the literature with respect to the intrinsic flexors of the foot." This confusion is perhaps a reason why Zug (1971) and Walker (1973) did not discuss any muscles spanning between adjacent toes in turtles. The relevant book page describing this muscle is unfortunately missing in Hoffmann (1890, p. 120/121), while Ogushi (1913) referred to similar, homotypic muscles in the manus in his description of these pes muscles of *Pe. sinensis*, which is not detailed enough for our anatomical focus here. Some information is nevertheless available from the literature for the European

pond turtle *Emys orbicularis*. Bojanus (1819–21, his muscle no. 122) and Ribbing (1909) separately described muscles 12–15 (mm. interossei plantares) for this turtle. These four serial muscles originate separately from the fibial side of the metatarsal and of the first phalanx and insert onto the tibial face of the adjacent metatarsal. Ribbing (1909) described for muscle 15 (m. interosseus plantaris-IV/V), which spans between the fourth and fifth toe, a broad insertion onto the hooked element and the first phalanx of toe-V (also see Bojanus, 1819–21, plate V). Based on outgroup comparison with other reptiles, a metatarsal/first phalanx to metatarsal course of muscles 12–15 is the plesiomorphic condition among reptiles (see Appendix 1). It therefore appears that the plesiomorphic condition is still present in turtles with relatively long hooked elements (Ribbing, 1909), such as in *E. orbicularis* (Bojanus, 1819–21, plate V), but that muscle 15 is forced to shift to a more distal element in turtles with a reduced hooked element, such as *Po. unifilis*. The unique position of muscle 15 in *Po. unifilis* must therefore be viewed as an autapomorphy of this species and has no bearing on the primary homology of the hooked element.

In contrast to the 'm. interosseum' (muscles 12–15, see above), we are uncertain what muscle Fabrezi et al. (2009, p. 859) might be referring to under the name 'm. flexor digiti brevis', a muscle that is purportedly fused to or runs parallel to muscle 15. Did they mean, by lingual similarity, a bundle of the serially arranged muscle 6 (mm. flexor digitorum communis sublimis), which usually arises from the plantar surface of muscles 3–4 (mm. flexores accessories) and attaches with four muscle heads to the proximal phalanges of the first four toes? Or did they mean muscles 29–32 (the extensor side muscles: mm. interossei dorsales), which are usually restricted to the first four toes and separately span between the distal tarsals and the adjacent metatarsals (e.g. from distal tarsal 4 to metatarsal-IV; Walker, 1973). A separate extensor side muscle of the fifth toe (muscle 33: m. interosseus dorsalis of toe-V) has to date been reported autapomorphically only for the trionychid *Lissemys punctata* (Zug, 1971). In either case (muscle 6 or muscle 33), the observations of Fabrezi et al. (2009) in *Po. unifilis* would have no bearing on the primary homology of the hooked element, because a global view using data from Zug (1971) and Walker (1973) revealed that a muscle 6 spanning between the fourth to fifth toe would be autapomorphically misplaced and that a muscle 33 spanning between the fourth and fifth toe would be a convergent development in *Po. unifilis*.

The third possibility is that Fabrezi et al. (2009) might have meant muscle 5 (m. lumbricales) when using the term 'm. digiti brevis'. Muscle 5 inserts with separate muscle heads onto the tibial sides of the penultimate phalanges of toes-II, -III, -IV and -V. However, according to Walker (1973), muscle 5 originates from the dorsal surface of the plantar aponeurosis, which in turn is formed by muscles 3–4 (m. flexor digitorum longus), and not from beneath the metatarsals as shown by Fabrezi et al. (2009). This third possibility therefore appears to be less likely.

The fourth and most plausible interpretation is that Fabrezi et al. (2009) identified muscle 9 (m. contrahentes digitorum of Ribbing, 1909), which tendinously originates on the hooked element and inserts on the first phalanges of toes-I to -IV.

Walker (1973) created some additional confusion in the literature by summarizing several of the interdigital muscles described above as 'mm. interossei planares' (no. 9–15; apparently he mostly referred to no. 9; see Appendix 1). However, Fabrezi et al. (2009) did not refer to that study, and the condition of the muscular structures in that region of the toe actually seems to be very diverse among species and would need a detailed revision with additional dissected material.

The study of the musculature of turtle hind limbs is still in its infancy, and many questions remain regarding primary homology and variation. Our review of the muscle data presented by Fabrezi et al. (2009) resulted in a complete refutation of their hypothesis that the hooked element represents the fifth distal tarsal, as their lines of reasoning either turn out to be faulty or because a more global approach reveals that the observations they made for a single turtle, the pleurodire *Po. unifilis*, are autapomorphic for that taxon. It is therefore clear that muscle data should only be viewed more globally (i.e. with broad sampling and detailed anatomical observations) when assessing primary and secondary homology. Given that all other, more detailed studies of turtle hind limb musculature have identified a number of autapomorphic muscles for other turtles (e.g. Ogushi, 1913; Walker, 1973), it is not surprising that *Po. unifilis* shows so many autapomorphic features. We therefore conclude that the available myological evidence favours the primary homology (Remane, 1952; Patterson, 1988; de Pinna, 1991) of the hooked elements found in extant crocodilian, lepidosaurs and turtles, and urge future authors to view muscle data in a global context.

Mode of ossification and recapitulation

Fabrezi et al. (2009) utilized mode of ossification as a criterion to resolve the identity of ossifications: distal tarsals are generally known to ossify endochondrally (i.e. through replacement ossification), whereas metatarsals ossify perichondrally. However, exceptions reveal that this is not universally true. For instance, the distal elements in the paddles of ichthyosaurs are known to ossify endochondrally (e.g. Caldwell, 1997). It is reasonable to postulate that the paddles of these animals are comprised of podials only, but a change in ossification mode for the metapodials and phalanges appears more likely (e.g. Woltering & Duboule, 2010). Genetic methods may provide useful insights into the problem of element identity. For example, *in situ* hybridizations of genes, which are expressed in early bone anlagen

(e.g. *Runx2*: Ducy et al. 1997) or in joints (e.g. collagen type II: Nalin et al. 1995), may be able to detect two skeletal elements in early development of the hooked element. However, under the absence of such external data and for the sake of simplicity, particularly among extant taxa, we utilize the identity criterion established by Fabrezi et al. (2009) for the moment to establish the primary homology of the hooked element of turtles.

Even though the body of literature pertaining to the embryological development of reptile limbs is extensive, surprisingly little detail has been accorded to the exact mode of ossification of the hooked elements, especially considering the possibility that this element may generally represent a fusion of a distal tarsal and metatarsal in all extant reptiles (Robinson, 1975). Fabrezi et al. (2009) were the first to explicitly note that the hooked element ossifies perichondrally in lizards (see Rieppel, 1992a,b; Shapiro, 2002; Fabrezi et al. 2007) like all other metatarsals, and that the hooked element of the pleurodire *Po. unifilis* ossifies endochondrally like a carpal or tarsal element (Fabrezi et al. 2009). The endochondral nature of the hooked element was confirmed for other pleurodires by Werneburg et al. (2009) and Vieira et al. (2011), respectively, and serves as the best line of evidence in favour of a distal tarsal identity of the hooked element.

Our observations on embryonic material indicate that the hooked element of most turtles (e.g. all but *Ca. caretta*) actually represent a composite bone consisting of the distal tarsal 5 and metatarsal V (*sensu*; Robinson, 1975 and after Sánchez-Villagra et al. 2007a). Our observations can be summarized as follows. First, we are able to observe in the early development of at least one cryptodire, *Pe. sinensis*, that the hooked element consists of two separate, tightly connected anlagen. The narrow proximal element and the broader distal element show the same connectivity to the surrounding tarsal and metatarsal elements as distal tarsal 5 and metatarsal V do in early reptilian lineages (e.g. *Araeoscelis casei*; Reisz et al. 1984). Second, we are able to confirm the observations of Fabrezi et al. (2009), Werneburg et al. (2009) and Vieira et al. (2011) that the hooked element of pleurodires exhibits endochondral ossification, and we are able to extend this observation for a number of cryptodires. The endochondral ossifications seen in pleurodires are relatively large compared with the full size of the hooked element, and endochondral ossification persists throughout ontogeny. On the other hand, the endochondral ossification seen in cryptodires is minute and only visible early in ontogeny. In both cases, however, the endochondral ossification is focused on the proximal part of the hooked element, an observation consistent with a distal tarsal origin of this part of the bone. However, epiphyses fail to develop in all pleurodires in the proximal part. Third, despite minor endochondral contributions, the hooked element of cryptodires predominately ossifies perichondrally from its fibular side and forms clear epiphyses, an observa-

tion consistent with a metatarsal origin of the fibular portion of this bone. However, a fine, fibular perichondral collar is also apparent in some pleurodire embryos (Fig. 1A). We speculate that the weak acids present in Alcian Blue are sufficiently strong to dissolve the fragile perichondral collar in most pleurodires and that this perichondral part is lost in most double-stained specimens. Finally, the perichondral collar of the hooked element of cryptodires is rotated 90° relative to the perichondral collars of metatarsals I–IV.

The available embryological evidence is consistent with the hooked bone of turtles phylogenetically originating from a fusion of the endochondrally ossifying distal tarsal 5 and the perichondrally ossifying metatarsal V. Distal tarsal 5 dominates the hooked element in pleurodires, and we cannot exclude the possibility that the metatarsal portion may perhaps be completely lost in some species (e.g. *Podocnemis unifilis*; Fabrezi et al. 2009; Vieira et al. 2011; but see Fig. 1E,F). Conversely, metatarsal V dominates the hooked element of cryptodires, and it is possible that the distal tarsal portion may be lost on occasion or, as in *Ca. caretta*, be fused with distal tarsal 4. The dominance of the perichondral ossification is likely the reason why the metatarsal identity for the hooked element had not been doubted for turtles in traditional studies, as these mostly focused on cryptodires. Only with the recent emergence of studies on pleurodire development did the conflicting signal apparent in this taxon become apparent. However, once again, much confusion could have been avoided by a more global approach.

Timing of development

The large body of recent literature pertaining to the development of extant turtles placed much effort into densely sampling ontogenetic stages to clarify sequences of chondrification and ossification (Rieppel, 1993a; Sheil, 2003a,b, 2005; Sheil & Greenbaum, 2005; Sánchez-Villagra et al. 2007a,b, 2008; Sheil & Portik, 2008; Bona & Alcalde, 2009; Werneburg et al. 2009; Vieira et al. 2011). Although much variation is apparent, all available developmental data from recent turtles agree in that the hooked element ossifies after metatarsals I–IV, but prior to all tarsals. A delayed ossification of the hooked element relative to metatarsals I–IV is also apparent in lizards (e.g. Rieppel, 1992a,b; Shapiro, 2002; Fabrezi et al. 2007) and crocodiles (e.g. Müller & Alberch, 1990; Rieppel, 1993b), and was argued by Rieppel & Reisz (1999) to be generally present in all extant reptiles. The delayed ossification of the tarsals relative to the hooked element, however, is unique to turtles.

In their discussion on the primary homology of the hooked element, Fabrezi et al. (2009) noted that metatarsals I–IV ossify in synchrony well in advance of the hooked element, and suggested that the developmental offset supports the non-metatarsal identity of the hooked element. We are unaware of other authors having used sequence of

ossification to justify primary homologies, but recognize the specious appeal of the argument.

The sequence of chondrification, ossification and other developmental events appears to have a genetic basis in amniotes, and changes to this sequence can therefore be used to explore phylogenetic patterns, as has been done in numerous studies (e.g. Sánchez-Villagra, 2002; Jeffery et al. 2005; Germain & Laurin, 2009; Werneburg & Sánchez-Villagra, 2009, 2011; Wilson & Sánchez-Villagra, 2009; Maxwell et al. 2010; Mitgutsch et al. 2011; Polachowski & Werneburg, 2013; Werneburg et al. 2013). It is apparent, however, that primary homology is not deduced from the absolute timing of chondrification or ossification, but rather from changes in this sequence relative to ancestral conditions, as inferred through outgroup analysis. A delayed onset of ossification of the hooked element relative to metatarsals I–IV is not only found in turtles, but is also generally found in all reptiles, which renders this line of evidence meaningless. As a consequence, delayed ossification of the hooked element relative to the remaining metatarsals appears to confirm the metatarsal identity of the hooked element in turtles, as had already been argued by Rieppel & Reisz (1999).

Digital count

The digital count of the hands and feet varies widely among turtles, and variation is both apparent between species and within species (e.g. Minx, 1992; Joyce, 2000; Crumly & Sánchez-Villagra, 2004; Delfino et al. 2010). The most common digital formula among extant turtles is 2-3-3-3-3 in the hands and feet, and is optimized to be the basal condition for crown group Testudines (Hirayama et al. 2000; Joyce, 2007). The digital count is expanded relative to this ancestral condition in various groups of highly aquatic turtles (e.g. Trionychia; Delfino et al. 2010) or reduced in various terrestrial turtles (Crumly & Sánchez-Villagra, 2004; Joyce & Gauthier, 2004).

The digital count of both autopodia varies extensively among tetrapods in general, and it is apparent that digital count cannot be utilized to determine primary homology. Fabrezi et al. (2009) nevertheless utilize digital count to infer primary homology. Their line of reasoning can be paraphrased as follows: (A) the digital count in the pes of turtles is 2-3-3-3-3; (B) if the hooked element of some embryonic pleurodires is interpreted as a metatarsal, the digital count is rendered 2-3-3-3-4; (C) if the hooked element of the same embryonic pleurodires is interpreted as a distal tarsal, the digital count is rendered the more usual 2-3-3-3-3; (D) the hooked element is therefore best interpreted as a distal tarsal. This argument is incorrect for one primary reason: the premise that the digital formula of turtles is 2-3-3-3-3 is based on the assumption that the hooked element of all turtles is indeed the fifth metatarsal. If one reaches the conclusion that the hooked element actually represents the fifth distal tarsal, then the assumption upon which the premise is based is incorrect, the premise needs to be rephrased, and the basal digital formula of turtles is rendered 2-3-3-3-2. However, this new premise implies, using the material of Fabrezi et al. (2009), that the hooked element is a metatarsal, at which point the entire argument turns full circle. It is apparent that digital counts neither provide evidence for or against the primary homology of the hooked element, and that the extra phalanx seen in the fifth toe of some pleurodires is best interpreted as an autapomorphic acquisition relative to the basal turtle condition.

Fossil evidence, morphology and topology

Fabrezi et al. (2009) compared the morphology and topological position of the hooked elements of extant turtles, lizards and crocodilians, and found a number of similarities and differences that they felt to be of importance. We herein compare the morphology of the hooked element of extant reptilian taxa, and then attempt to trace changes in the morphology and topology of this element into the past using insights from the fossil record.

The hooked element of turtles is the most block-shaped among extant taxa, articulates medially with the fourth distal tarsal and fourth metatarsal along concavities, and articulates distally with the second element of toe-V along a ball-shaped condyle that is often offset from the main body of the element (Fig. 4). The hooked element is mostly in line with the tarsal elements, but the distal portions align with the metatarsals (Fabrezi et al. 2009). This morphology is already apparent among the earliest known crown turtles from the Late Jurassic of Europe and South America (e.g. Joyce, 2000; de la Fuente & Fernández, 2011).

The well-preserved foot of the unambiguous Late Triassic stem turtle *Proganochelys quenstedti* (Gaffney et al. 2007; Joyce, 2007) lacks a distal tarsal 5, but is otherwise significantly different from that of extant turtles in that the hooked element only exhibits modest hooking and mostly aligns with the metatarsals (Gaffney, 1990; figs 159 and 160). This morphology is generally consistent with the most derived, unambiguous stem turtle *Odontochelys semitestacea* (Li et al. 2008; fig. 1). The general morphology of the oldest known turtles is therefore more consistent with a metatarsal identity, and the placement of the hooked element near the distal tarsal row must be interpreted as a synapomorphy of crown Testudines (Joyce, 2007).

In the last 20 years, a number of fossil taxa have been hypothesized to be sister to turtles, but little resolution is in sight. Turtles have been hypothesized to be sister to various groups of Palaeozoic parareptiles (e.g. Laurin & Reisz, 1995; Lee, 1997a) or the enigmatic *Eunotosaurus africanus* from the Middle Permian of South Africa (Lyson et al. 2010a,b; 2013), all of which possess a straight metatarsal V and most of which possess a distal tarsal 5 (Fig. 4). Any sister group relationship to these taxa implies that the hooking seen in turtles and/or that the formation of an ansulate bone (i.e.
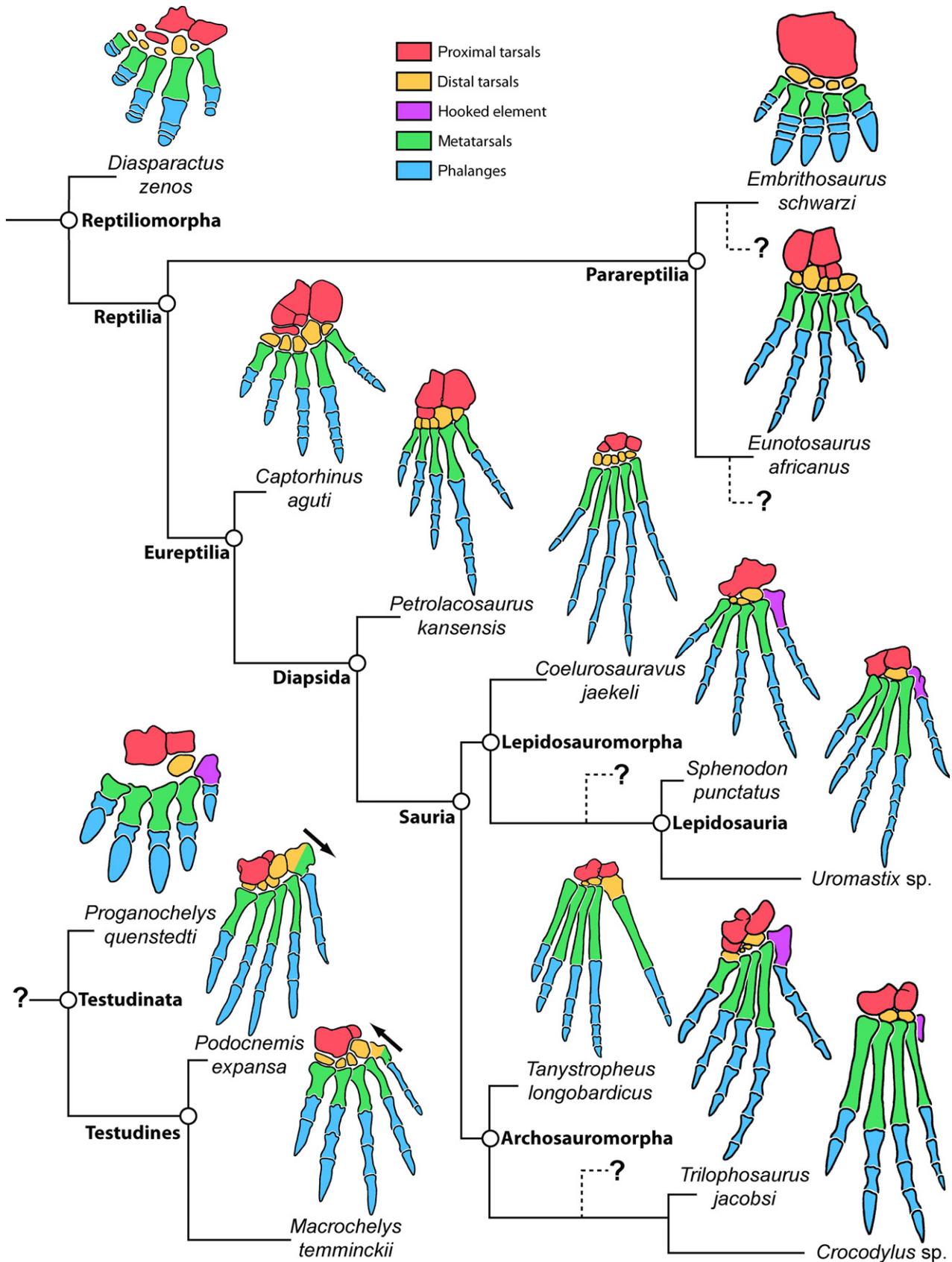
Fig. 4 The distribution of fifth distal tarsals, fifth metatarsals and hooked element of uncertain primary homology within Amniota. Question marks indicate commonly hypothesized phylogenetic positions of turtles.

the fusion of distal tarsal 5 and metatarsal V) occurred independently in turtles from other reptiles (Lee, 1997b). Turtles have also been posited to be sister to placodont sauropterygians along the stem of Lepidosauria, but the straight metatarsal seen in these taxa is typically interpreted as a reversal (deBraga & Rieppel, 1997; Rieppel & Reisz, 1999; Müller, 2004).

The hooked element of lepidosaurs is more elongated and cylindrical than that of turtles (Fig. 4). It also articulates with distal tarsal 4, metatarsal IV and the second element of toe-V, but the proximal contacts are convex instead of concave. Numerous processes, including the proximal hamate process, two plantar tubercles and a medial, mid-shaft insertion site for muscles, furthermore characterize the hooked element of lizards (see Myology above). Epiphyses adorn large muscle attachment sites, and the proximal and distal ends of the bone. The proximal portion of the element is in line with the distal tarsals, while the distal portion aligns with the metatarsals (Fabrezi et al. 2009). This morphology is consistent among all known lepidosaurs, including one of the earliest stem squamates, *Huehuecuetzpalli mixtecus*, from the Early Cretaceous of Mexico (Reynoso, 1998) and various Mesozoic stem sphenodontids, such as the Late Jurassic *Leptosaurus pulchellus* (e.g. Renesto & Viohl, 1997).

There is little agreement which taxa comprise the stem lineage of Lepidosauria (Evans, 2008; Evans & Jones, 2010). The earliest unequivocal stem lepidosaurs are kuehneosaurs (Evans & Jones, 2010), which have a straight metatarsal V. The Late Permian to Early Triassic *Saurosternon bainii* has been argued by some to be a stem lepidosaur based on a fused astragalus-calcaneum and overlapping scales (e.g. Gauthier et al. 1988), but others have not recovered this result (e.g. Müller, 2004). *Saurosternon bainii* has five tarsal bones and a straight metatarsal V. Together this implies the independent acquisition of the hooked element in lepidosaurs, or a reversal in kuehneosaurs and *S. bainii*.

The hooked element of crocodilians bridges the morphology seen in extant turtles and lizards, by being an intermediate elongate block-shaped element that lacks epiphyses, and contacts distal tarsal 4 and metatarsal IV along convexities (Fig. 4). The fifth digit is reduced in crocodilians, and the hooked element therefore does not have distal articulations. However, numerous muscles still attach to this structure (see Myology above). The hooked element mostly aligns with the metatarsals (Fabrezi et al. 2009).

A series of Permian to Triassic fossils form the stem lineage of crown Archosauria (Dilkes, 1998; Modesto & Sues, 2004). A hooked element is found in the pes of all but the basal-most stem archosaurs, the protorosaurs. These Triassic reptiles (e.g. *Dinocephalosaurus orientalis*; Rieppel et al. 2008) lack the hooked element. However, given that protorosaurs are mostly aquatic (Rieppel et al. 2008), it remains unclear if they preserve the basal amniote morphology (i.e. a large fifth distal tarsal and straight fifth metatarsal) or

developed a reversal similar to that seen in the aquatic sauropterygians (see above).

Parsimony and the primary homology of the hooked element

In contrast to all previous workers, Sheil & Portik (2008) employed an explicit numerical approach to select the most parsimonious primary homology assessment for the hooked element of turtles. For this purpose, Sheil & Portik (2008) evaluated five primary hypotheses that can be briefly summarized as follows: (1) the fifth distal tarsal condenses early in embryology, but is secondarily lost; (2) the fifth distal tarsal condenses early in embryology, but eventually fuses with the fourth distal tarsal; (3) the fifth distal tarsal condenses early in embryology, but eventually fuses with the fifth metatarsal; (4) the fifth distal tarsal never forms; and (5) the fifth distal tarsal develops and eventually enlarges to form the hooked element. According to Sheil & Portik (2008), these five hypothesis require three steps (loss of distal tarsal 5, hooking of metatarsal V, enlarging of distal tarsal 4), two steps (hooking of metatarsal V, fusion of distal tarsals IV and V), three steps (hooking of metatarsal V, enlarging of distal tarsal 4, fusion of distal tarsal 5 and metatarsal V), three steps (hooking of metatarsal V, enlarging of distal tarsal 4, non-development of distal tarsal 5) and two steps (hooking of metatarsal V, enlarging of distal tarsal 4), respectively. Although the fusion of the fourth and fifth distal tarsals (hypothesis 2) is equally parsimonious to the retention and eventual hooking of the fifth distal tarsal (hypothesis 5), Sheil & Portik (2008) favoured the latter hypothesis, as the former supposedly assumes rapid developmental change. We agree in principle with Sheil & Portik (2008) that parsimony should be employed when choosing among primary homology hypotheses, but given that all available evidence points towards a single hypothesis (see below), we see no need to utilize a numerical approach herein. In contrast to Sheil & Portik (2008), our primary homology analysis is informed by significantly more data and it is therefore not surprising that we arrive at a different result.

The hooked element of extant turtles is situated in the pes between the rows formed by the distal tarsals and the metatarsals, and only three hypotheses therefore need to be considered seriously when assessing the evolutionary identity of this element within Amniota. The hooked element either represents: (i) the fifth metatarsal; (ii) the fifth distal tarsal; or (iii) the fusion of the fifth metatarsal with the fifth distal tarsal. Palaeontologists had long noted that the loss of the fifth distal tarsal is correlated with the formation of the hooked element (e.g. Gauthier et al. 1988), but no living reptile had yet been convincingly shown to exhibit a fused hooked element (e.g. Müller & Alberch, 1990; Fabrezi et al. 2007, 2009) and discussion has focused on the other two hypotheses.

Our study demonstrates that the endochondral nature of the hooked element in pleurodiran turtles supports the distal tarsal 5 identity of this element (Fabrezi et al. 2009), but that the other lines of evidence that had previously been used to support the distal tarsal identity are either specious (i.e. digital count, timing of ossification) or actually support a metatarsal V identity of the hooked element (i.e. myology, fossils and ossification pattern seen in cryptodires). Under the absence of other data, we would have concluded that the hooked element of turtles phylogenetically originated from the fifth metatarsal, but that the element had rotated during the formation of a more effective heel into the distal tarsal row and started to ossify in pleurodires endochondrally like a distal tarsal. However, our study of embryological material reveals that pleurodires and cryptodires in general exhibit two anlagen in the hooked element. The proximal of these two anlagen has the topological position of the distal tarsal 5 of basal amniotes and ossifies endochondrally, whereas the distal of the two anlagen has the topological position of the distal metatarsal V and ossifies perichondrally. Interestingly, the proximal anlage dominates the hooked element in pleurodires, whereas the distal anlage dominates the hooked element in cryptodires. The conflicting observations made by previous research groups are therefore the result of taxonomic sampling. Given that the hooked element of turtles is neither the distal tarsal 5 nor the metatarsal V alone, we suggest naming this composite bone the ansulate bone (= bone S of Ogushi, 1911) to avoid accidental suggestions of primary or secondary homology through the incorrect use of homonyms.

The presence of an ansulate bone in the heel of turtles has direct implications for the primary homology of the hooked element among reptiles. There is only limited information regarding the development of the foot in crocodilians, but the available studies have not found any evidence for a fused hooked element in this taxon (Müller & Alberch, 1990; Rieppel, 1993b; Lima, 2010; Lima et al. 2011; Vieira, 2011). As a result, the element is best identified as metatarsal V. Similarly, even though only a few studies are available on the pedal embryology of lizards (Mathur & Goel, 1976; Rieppel, 1992a,b; Arias & Lobo, 2006; Fabrezi et al. 2007), all identified a single ossification in the hooked element and is universally interpreted as metatarsal V.

Although the presence of a metatarsal only in the hooked element of squamates and crocodilians speaks against their primary homology with the ansulate bone found in turtles, we are careful at the moment to advocate their primary non-homology based on these putative differences. In contrast to the limited number of studies that are available for the embryology of squamates and crocodilians, numerous studies that cover all primary regions of tree space exist on the development of turtle limbs (Burke & Alberch, 1985; Rieppel, 1993a; Sheil, 2003a,b; Sheil & Greenbaum, 2005; Sánchez-Villagra et al. 2007a,b, 2008,

2009; Santos & Vieira, 2007; Sheil & Portik, 2008; Vieira et al. 2009; Werneburg & Sánchez-Villagra, 2009). Yet, with the exception of a single study (i.e. Sánchez-Villagra et al. 2007a), none found any data that even hinted at the possibility that turtles possess a composite, ansulate bone [Ogushi (1913) suggested this identity but did not present any data]. We explain this issue with three interrelated observations. Firstly, in all extant turtles, one of the two anlagen in the ansulate bone is very poorly developed and therefore easily overlooked. Secondly, standard preparation methods can inadvertently destroy evidence of one of the two anlagen (i.e. dissolution of thin perichondral membranes by acidic staining solutions). And thirdly, all previous studies focused on general ossification patterns of the entire hind limb, instead of the identity of the hooked bone alone. Given that our focused efforts led to the discovery of the ansulate bone in turtles, we think it to be highly plausible that future studies may find evidence of an ansulate bone in lepidosaurs and crocodilians, and advise caution and more studies over premature conclusions.

The secondary homology of the hooked bones among reptiles

We concur that congruence should be the ultimate arbiter of secondary homology (e.g. Nelson & Platnik, 1981; Rieppel, 1988; Joyce & Sterli, 2012), and that the final story of evolution will ultimately be read directly from the tree of life. As a consequence, if turtles phylogenetically derived from an ancestral lineage well documented to lack an ansulate bone – perhaps either archosaurs or lepidosaurs – then we would ultimately have to conclude that the endochondral ossification found in turtles is a neomorph and not the phylogenetic vestige of distal tarsal 5. Given that the placement of turtles within amniote remains far from resolved (see Introduction for summary) and given that the pattern is fully clear within extant reptiles, it is apparent the data are not sufficient to reach final conclusions.

Our brief review of the fossil record does not provide any further data that might help resolve this situation, as all taxa of relevance also have controversial phylogenetic positions. The oldest unambiguous representatives of the turtle, lepidosaur and archosaur lineages display the morphology seen in their living relatives. By contrast, a number of candidate taxa with turtle, lepidosaur and archosaur affinities (i.e. *Eunotosaurus africanus*, *Saurosternon bainii* and protorosaurs, respectively) possess a full suite of distal tarsals and thereby hint at the possibility that the hooked element originated multiple times among amniotes. Multiple origins would perhaps explain differences that are apparent among various groups of descendants and the isolated presence of an ansulate bone in turtles, but the unclear identity of the hooked element in both lepidosaurs and archosaurs again prohibits any firm conclusion. We are therefore left to encourage biologists and palaeontologists to address this

issue together by clarifying the developmental identity of the hooked bones in lepidosaurs and crocodilians, and by fully resolving the phylogeny of amniotes.

Acknowledgements

References

Arias F, Lobo F (2006) Patrones de osificación en tupinambis merianae y tupinambis rufescens (Squamata: Teiidae) y patrones generales en Squamata. *Cuadernos de Herpetología* **20**, 3–23.

Bhullar B-AS, Bever GS (2009) An archosaur-like laterosphenoid in early turtles (Reptilia: Pantestudines). *Breviora* **518**, 1–11.

Bojanus LH (1819–1821) *Anatome testudines europaeae. Impensis auctoris*. Vilna: Josephi Zawazki.

Bona P, Alcalde L (2009) Chondrocranium and skeletal development of *Phrynops hilarii* (Pleurodira: Chelidae). *Acta Zool* **90**, 301–325.

Boulenger GA (1889) On the characters of the chelonian families Pelomedusidae and Chelydridae. *Annu Mag Nat Hist* **61**, 346–347.

deBraga M, Rieppel O (1997) Reptile phylogeny and the interrelationships of turtles. *Zool J Linn Soc* **120**, 281–354.

Brinkman D (1980) The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Can J Zool* **57**, 2187–2200.

Broom R (1924) On the classification of the reptiles. *Bull Am Mus Nat Hist* **51**, 39–65.

Burke AC, Alberch P (1985) The development and homology of the chelonian carpus and tarsus. *J Morphol* **186**, 119–131.

Caldwell MW (1997) Modified perichondral ossification and the evolution of paddle-like limbs in ichthyosaurs and plesiosaurs. *J Vertebr Paleontol* **17**, 534.

Cao Y, Sorenson MD, Kumazawa Y, et al. (2000) Phylogenetic position of turtles among amniotes: evidence from mitochondrial and nuclear genes. *Gene* **259**, 139–148.

Carrano MT, Hutchinson JR (2002) Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *J Morphol* **253**, 207–228.

Case EC (1939) A nearly complete turtle skeleton from the Upper Cretaceous of Montana. *Contrib Mus Paleontol Univ Mich* **6**, 1–19.

Chiari Y, Cahais V, Galtier N, et al. (2012) Phylogenomic analyses support the position of turtles as sister group of birds and crocodiles. *BMC Biol* **10**, 65.

Crawford NG, Faircloth BC, McCormack JE, et al. (2012) More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. *Biol Lett* **8**, 783–786.

Crumly CC, Sánchez-Villagra MR (2004) Patterns of variation in the phalangeal formulae of land tortoises (Testudinidae):

developmental constraint imposed by size and phylogenetic history. *J Exp Zool* **302B**, 134–146.

Delfino M, Fritz U, Sánchez-Villagra MR (2010) Evolutionary and developmental aspects of phalangeal formula variation in pig-nose and soft-shelled turtles (Carettochelyidae and Trionychidae). *Org Divers Evol* **10**, 69–79.

Dilkes DW (1998) The early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philos Trans R Soc B* **353**, 501–541.

Dingerkus G, Uhler L (1977) Differential staining of bone and cartilage in cleared and stained fish using alcian blue to stain cartilage and enzymes for clearing fish. *Stain Technol* **52**, 229–232.

Ducy P, Zhang R, Geoffroy V, et al. (1997) Osf2/Cbfa1: a transcriptional activator of osteoblast differentiation. *Cell* **89**, 747–754.

Evans SE (2008) The skull of lizards and tuatara. In: *Gans Morphology, H, The Skull of the Lepidosauria* (eds Gaunt AS, Adler K), pp. 1–247. Salt Lake City: Society for the Study of Amphibians and Reptiles.

Evans SE, Jones MEH (2010) The origin, early history and diversification of lepidosauromorph reptiles. In: *New Aspects of Mesozoic Biodiversity* (ed. Bandyopadhyay S), pp. 27–44. Berlin: Springer.

Fabrezi M, Abdala V, Martínez Oliver MI (2007) Developmental basis of limb homology in lizards. *Anat Rec* **290**, 900–912.

Fabrezi M, Manzano A, Abdala V, et al. (2009) Developmental basis of limb homology in pleurodiran turtles, and the identity of the hooked element in the chelonian tarsus. *Zool J Linn Soc* **155**, 845–866.

de la Fuente MS, Fernández MS (2011) An unusual pattern of limb morphology in the Tithonian marine turtle *Neusticemys neuquina* from the Vaca Muerta Formation, Neuquén Basin, Argentina. *Lethaia* **44**, 15–25.

Gaffney ES (1990) The comparative osteology of the Triassic turtle *Proganochelys*. *Bull Am Mus Nat Hist* **194**, 1–263.

Gaffney ES, Rich RH, Vickers-Rich P, et al. (2007) *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *Am Mus Novitates* **3599**, 1–35.

Gauthier J, Kluge AG, Rowe T (1988) Amniote phylogeny and the importance of fossils. *Cladistics* **4**, 105–209.

George JC, Berger AJ (1966) *Avian Myology*. New York: Academic Press.

Germain D, Laurin M (2009) Evolution of ossification sequences in salamanders and urodele origins assessed through event-pairing and new methods. *Evol Dev* **11**, 170–190.

Goodrich ES (1916) On the classification of the Reptilia. *Proc R Soc Lond B* **89**, 261–276.

Hirayama R, Brinkman DB, Danilov IG (2000) Distribution and biogeography of non-marine Cretaceous turtles. *Russ J Herpetol* **7**, 181–198.

Hoffmann CK (1890) *Schildkröten*. Leipzig: Winter'sche Verlagshandlung.

Holmgren N (1933) On the origin of the tetrapod limb. *Acta Zool* **14**, 185–295.

Hoyos JM (1990) Estudio cladístico en la familia Iguanidae (Sauria, Reptilia) con base en la musculatura del miembro posterior. *Rev Acad Colombiana Cienc Exact Fís Natur* **17**, 543–558.

Hugall AF, Foster R, Lee MSY (2007) Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. *Syst Biol* **56**, 543–563.

Hutchinson JR (2002) The evolution of hindlimb tendons and muscles on the line to crown-group birds. *Comp Biochem Physiol Part A Mol Integr Physiol* **133**, 1051–1086.

Jeffery JE, Bininda-Emonds ORP, Coates MI, et al. (2005) A new technique for identifying sequence heterochrony. *Syst Biol* **54**, 230–240.

Jourdan C (1862) Extraits des procès verbaux des séances de la Société impériale d'Agriculture et d'Industrie de Lyon, Séance du 21 mars. *Ann Sci Phys Nat Soc Agric Ind Lyon* 3rd Series 6, **3**, 2–33.

Joyce WG (2000) The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications. *J Paleontol* **74**, 684–700.

Joyce WG (2007) Phylogenetic relationships of Mesozoic turtles. *Bull Peabody Mus Nat Hist* **48**, 3–102.

Joyce WG, Gauthier JA (2004) Palaeoecology of Triassic stem turtles sheds new light on turtle origins. *Proc R Soc Lond B* **271**, 1–5.

Joyce WG, Sterli J (2012) Congruence, non-homology, and the phylogeny of basal turtles. *Acta Zool* **93**, 149–159.

Joyce WG, Jenkins FA, Rowe T (2006) The presence of cleithra in the primitive turtle *Kayentachelys aprix*. *Russ J Herpetol* **13**, Supplement (Fossil Turtle Research 1), 93–103.

Kuratani S (1987) The development of the orbital region of *Caretta caretta* (Chelonia, Reptilia). *J Anat* **154**, 187–200.

Kuratani S (1989) Development of the orbital region in the chondrocranium of *Caretta caretta*. Reconsideration of the vertebrate neurocranium configuration. *Anat Anz* **169**, 335–349.

Kuratani S (1999) Development of the chondrocranium of the loggerhead turtle, *Caretta caretta*. *Zool Sci* **16**, 803–818.

Laurin M, Reisz RR (1995) A reevaluation of early amniote phylogeny. *Zool J Linn Soc* **113**, 165–223.

Lee MSY (1996) The homologies and early evolution of the shoulder girdle in turtles. *Proc R Soc Lond B* **263**, 111–117.

Lee MSY (1997a) Pareiasaur phylogeny and the origin of turtles. *Zool J Linn Soc* **120**, 197–280.

Lee MSY (1997b) The evolution of the reptilian hindfoot and the homology of the hooked fifth metatarsal. *J Evol Biol* **10**, 253–263.

Li C, Wu X-C, Rieppel O, et al. (2008) An ancestral turtle from the Late Triassic of southwestern China. *Nature* **456**, 497–501.

Lima FC (2010) Desenvolvimento do esqueleto em embriões de *Caiman yacare* (Daudin, 1802) (Crocodylia, Alligatoridae). Unpublished PhD Thesis, Universidade Federal de Uberlândia, Uberlândia.

Lima FC, Vieira LG, Santos ALQ, et al. (2011) Skeletogenesis of the pectoral girdle and forelimbs in embryos of *Caiman yacare* (Daudin, 1802) (Crocodylia, Alligatoridae). *J Morph Sci* **28**, 4–10.

Lyson TR, Joyce WG (2012) Evolution of the turtle bauplan: the topological relationship of the scapula relative to the ribcage. *Biol Lett* **8**, 1028–1031.

Lyson TR, Bever GS, Bhullar B-AS, et al. (2010) Transitional fossils and the origin of turtles. *Biol Lett* **6**, 830–833.

Lyson TR, Sperling EA, Heimberg AM, et al. (2012) MicroRNAs support a turtle + lizard clade. *Biol Lett* **8**, 104–107.

Lyson TR, Bever GS, Scheyer TM, et al. (2013) Evolutionary origin of the turtle shell. *Curr Biol*, **23**, 1113–1119.

Lyson TR, Bhullar B-AS, Bever GS, et al. (in press) Homology of the enigmatic nuchal bone reveals novel reorganization of the shoulder girdle in the evolution of the turtle shell. *Evol Dev*, in press.

Mathur JK, Goel SC (1976) Patterns of chondrogenesis and calcification in the developing limbs of the lizard *Calotes versicolor*. *J Morphol* **149**, 401–420.

Maxwell EE, Harrison LB, Larsson HCE (2010) Assessing the phylogenetic utility of sequence heterochrony: evolution of avian ossification sequences as a case study. *Zoology* **113**, 57–66.

von Meyer H (1839a) *Idiochelys Fitzingeri*. Eine Schildkröte aus dem Kalkschiefer von Kehlheim. *Beiträge zur Petrefacten-Kunde* **1**, 77–89.

von Meyer H (1839b) *Eurysternum Wagleri*. Eine Schildkröte aus dem Kalkschiefer von Solnhofen. *Beiträge zur Petrefacten-Kunde* **1**, 89–95.

Minx P (1992) Variation in phalangeal formulae in the turtle genus *Terrapene*. *J Herpetol* **26**, 238–241.

Mitgutsch C, Wimmer C, Sanchez-Villagra MR, et al. (2011) Timing of ossification in duck, quail, and zebra finch: intraspecific variation, heterochronies, and life history evolution. *Zool Sci* **28**, 491–500.

Modesto SP, Sues H-D (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. *Zool J Linn Soc* **140**, 335–351.

Müller J (2004) The relationships among diapsid reptiles and the influence of taxon selection. In: *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia G, Cloutier R, Wilson VH), pp. 379–408. München: Verlag F. Pfeil.

Müller GB, Alberch P (1990) Ontogeny of the limb skeleton in *Alligator mississippiensis*: developmental invariance and change in the evolution of archosaur limbs. *J Morphol* **203**, 151–164.

Müller J, Sterli J, Anquetin J (2011) Carotid circulation in amniotes and its implications for turtle relationships. *Neues Jb Geol Paläontol Abh* **261**, 289–297.

Nalin AM, Greenlee TK, Sandell LJ (1995) Collagen gene expression during development of avian synovial joints: transient expression of types II and XI collagen genes in the joint capsule. *Dev Dyn* **203**, 352–362.

Nelson G, Platnik N (1981) *Systematics and Biogeography*. New York: Columbia University Press.

Ogushi K (1911) Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japanicus*). I. Mitteilung. *Morphologisches Jahrbuch* **43**, 1–106.

Ogushi K (1913) Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japanicus*). II. Mitteilung: Muskel- und peripheres Nervensystem. *Morphologisches Jahrbuch* **46**, 299–562.

Patterson C (1988) Homology and classical and molecular biology. *Mol Biol Evol* **5**, 603–625.

de Pinna MGG (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**, 367–394.

Polachowski KM, Werneburg I (2013) Late embryos and bony skull development in *Bothropoides jararaca* (Serpentes, Viperidae). *Zoology* **116**, 36–63.

Rabl C (1910) *Bausteine zu einer Theorie der Extremitäten der Wirbeltiere*. Leipzig: Engelmann.

Reisz RR, Berman DS, Scott D (1984) The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. *J Vertebr Paleontol* **4**, 57–67.

Remane A (1952) *Die Grundlagen des natürlichen Systems der vergleichenden Anatomie und der Phylogenetik*. Leipzig: Akademische Verlagsgesellschaft Geest & Portig.

Renesto S, Viohl G (1997) A sphenodontid (Reptilia, Diapsida) from the late Kimmeridgian of Schamhaupten (Southern Franconian Alb, Bavaria, Germany). *Archaeopteryx* **15**, 27–46.

Reynoso V-H (1998) *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. *Philos Trans R Soc B Lond B* **353**, 477–500.

Ribbing L (1909) Die Unterschenkel- und Fussmuskulatur der Tetrapoden und ihr Verhalten zu der entsprechenden Arm- und Handmuskulatur. *Lund Univ Arssk Med Mat Nat* **5**, 1–158.

Ribbing L (1938) Die Muskeln und Nerven der Extremitäten. In: *Handbuch der vergleichenden Anatomie der Wirbeltiere* (eds Bolk L, Göppert E, Kallius E, Lubosch W), pp. 1025–1064. Berlin: Urban & Schwarzenberg.

Rieppel O (1988) *Fundamentals of Comparative Biology*. Basel: Birkhauser.

Rieppel O (1992a) Studies on skeleton formation in reptiles. I. The postembryonic development of the skeleton in *Cyrtodactylus pubisulcus* (Reptilia, Gekkonidae). *J Zool* **227**, 87–100.

Rieppel O (1992b) Studies on skeleton formation in reptiles. III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). *Fieldiana (Zool)* **68**, 1–25.

Rieppel O (1993a) Studies on skeleton formation in reptiles: patterns of ossification in the skeleton of *Chelydra serpentina*. *J Zool* **231**, 487–509.

Rieppel O (1993b) Studies on skeleton formation in reptiles.V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). *Zool J Linn Soc* **109**, 301–325.

Rieppel O (2000) Turtles as diapsid reptiles. *Zool Scripta* **29**, 199–212.

Rieppel O, Reisz RR (1999) The origin and early evolution of turtles. *Annu Rev Ecol Syst* **30**, 1–22.

Rieppel O, Li C, Fraser NC (2008) The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province southern China. *J Vertebr Paleontol* **28**, 95–110.

Robinson PL (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Colloq Natx Cent Natl Rech Sci* (Paris, 4–9 Juin) **218**, 461–483.

Russel AP, Bauer AM (2008) The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In *Biology of the Reptilia*, Vol. **21**. (eds Gans C, Gaunt AS, Adler K). New York: Society for the Study of Amphibians and Reptiles.

Sánchez-Villagra MR (2002) Comparative patterns of postcranial ontogeny in therian mammals: an analysis of relative timing of ossification events. *J Exp Zool* **294**, 264–273.

Sánchez-Villagra MR, Winkler JD, Wurst L (2007a) Autopodial skeleton evolution in side-necked turtles (Pleurodira). *Acta Zool* **88**, 199–209.

Sánchez-Villagra MR, Mitgutsch C, Nagashima H, et al. (2007b) Autopodial development in the sea turtles *Chelonia mydas* and *Caretta caretta*. *Zool Sci* **24**, 257–263.

Sánchez-Villagra MR, Ziermann JM, Olsson L (2008) Limb chondrogenesis in *Graptemys nigrinoda* (Emydidae), with comments on the primary axis and the digital arch in turtles. *Amphibia-Reptilia* **19**, 85–92.

Sánchez-Villagra MR, Müller H, Sheil CA, et al. (2009) Skeletal development in the Chinese soft-shelled turtle *Pelodiscus sinensis* (Reptilia: Testudines: Trionychidae). *J Morphol* **270**, 1381–1399.

Santos ALQ, Vieira LG (2007) Sequence of metatarsal and phalangeal bone formation in embryos of *Podocnemis expansa* Schweigger, 1812 (Testudines, Podocnemididae). *South Am J Herpetol* **2**, 11–16.

Sewertzoff SA (1929) Zur Entwicklungsgeschichte der Zunge bei den Reptilien. *Acta Zool* **10**, 231–341.

Shaffer HJ, Minx P, Warren DE, et al. (2013) The western painted turtle genome, a model for the evolution of extreme physiological adaptations in a slowly evolving lineage. *Genome Biol* **14**, R28.

Shapiro MD (2002) Developmental morphology of limb reduction in *Hemiergis* (Squamata: Scincidae): chondrogenesis, osteogenesis, and heterochrony. *J Morphol* **254**, 211–231.

Sheil CA (2003a) Osteology and skeletal development of *Apalone spinifera* (Reptilia: Testudines: Trionychidae). *J Morphol* **256**, 42–78.

Sheil CA (2003b) Skeletal development in turtles: patterns of ossification through ontogeny in *Apalone spinifera*, *Chelydra serpentina*, *Macrochelys temminckii*, and *Eretmochelys imbricata* (Reptilia: Chelonii). Unpublished PhD Thesis, University of Kansas, Lawrence.

Sheil CA (2005) Skeletal development of *Macrochelys temminckii* (Reptilia: Testudines: Chelydridae). *J Morphol* **263**, 71–106.

Sheil CA, Greenbaum E (2005) Reconsideration of skeletal development of *Chelydra serpentina* (Reptilia: Testudinata: Chelydridae): evidence for intraspecific variation. *J Zool (Lond)* **265**, 235–267.

Sheil CA, Portik D (2008) Formation and ossification of limb elements in *Trachemys scripta* and a discussion of autopodial elements in turtles. *Zool Sci* **25**, 622–641.

Shen X-X, Liang D, Wen J-Z, et al. (2011) Multiple genome alignments facilitate development of NPCL markers: a case study of tetrapod phylogeny focusing on the position of turtles. *Mol Biol Evol* **12**, 3237–3257.

Tzika AC, Helaers R, Schramm G, et al. (2011) Reptilian-transcriptome v1.0, a glimpse in the brain transcriptome of five divergent Sauropsida lineages and the phylogenetic position of turtles. *EvoDevo* **2**, 19.

Vieira LG (2011) Desenvolvimento embrionário de *Melanosuchus niger* (Crocodylia, Alligatoridae): descrição de estágios e ontogenia do esqueleto. Unpublished PhD Thesis, Universidade de Brasília, Brasília.

Vieira LG, Santos ALQ, Lima FC, et al. (2009) Ontogeny of the plastron of the giant amazon river turtle *Podocnemis expansa* (Schweigger, 1812) (Testudines, Podocnemididae). *Zool Sci* **26**, 51–54.

Vieira LG, Santos ALQ, Lima FC, et al. (2011) Chondrogenesis of the limbs and mesopodial ossification of *Podocnemis expansa* Schweigger, 1812 (Testudines: Podocnemidae). *J Morphol* **272**, 404–418.

Walker WFJ (1973) The locomotor apparatus of Testudines. In: *Biology of the Reptilia*, Vol **4**. (ed. Gans C), pp. 1–100. London: Academic Press.

Wang Z, Pascual-Anaya J, Zadissa A, et al. (2013) The draft genomes of soft-shell turtle and green sea turtle yield insights into the development and evolution of the turtle-specific body plan. *Nat Genet* **45**, 701–706.

Werneburg I (2011) The cranial musculature in turtles. *Palaeontol Electron* **14**, 15A.

Werneburg I (2013a) The tendinous framework in the temporal skull region of turtles and considerations about its morphological implications in amniotes: a review. *Zool Sci* **30**, 141–153.

Werneburg I (2013b) Jaw musculature during the dawn of turtle evolution. *Org Divers Evol* **13**, 225–254.

Werneburg I, Sánchez-Villagra MR (2009) Timing of organogenesis support basal position of turtles in the amniote tree of life. *BMC Evol Biol* **9**, 82.

Werneburg I, Sánchez-Villagra MR (2011) The early development of the echidna, *Tachyglossus aculeatus* (Mammalia: Monotremata) and patterns of mammalian development. *Acta Zool* **82**, 75–88.

Werneburg I, Hugi J, Müller J, et al. (2009) Embryogenesis and ossification of *Emydura subglobosa* (Testudines, Pleurodira, Chelidae) and patterns of turtle development. *Dev Dyn* **238**, 2770–2786.

Werneburg I, Tzika AC, Hautier L, et al. (2013) Development and embryonic staging in non-model organisms: the case of an afrotherian mammal. *J Anat* **222**, 2–18.

Wilson LAB, Sánchez-Villagra MR (2009) Heterochrony and patterns of ectocranial suture closure in hystricognath rodents. *J Anat* **214**, 339–354.

Woltering JM, Duboule D (2010) The origin of digits: expression patterns versus regulatory mechanisms. *Dev Cell* **18**, 526–532.

Wyneken J (2001) The anatomy of sea turtles. U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470, 1–172.

Zug GR (1971) Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. *Misc Publ Mus Zool Univ Mich* **142**, 1–98.

1 Appendix: Overview of the muscles of the reptilian pes

The list below provides a generalized and simplified overview of all muscles attaching to the pes of turtles following Walker (1973) and for other tetrapods following Ribbing (1909). Synonymizations are mainly based on the proposals of Walker (1973). Note the major differences in assigning 'mm. interossei planares' by Walker (1973), and that Ogushi (1913) listed possibly autapomorphic muscular structures for *Pelodiscus sinensis* that are associated with the hooked element but that were not considered by Walker (1973; e.g. Ogushi's no. 148, 166). Summarizing those muscles in more detail is beyond the scope of this study and they are therefore not considered in our list.

(A) Flexores (plantar flexion)

1 Gastrocnemius pars gastrocnemius externus
Synonyms: flexor primordialis communis pars gastrocnemius externus (Ribbing, 1909). Gastrocnemius, external or femoral head (deeper layer; somewhat reduced in sea turtles; Walker, 1973).
Origin: by a tendon from condylus externus femoris (Ribbing, 1909). By a narrow tendon from the ventral side of fibular condyle of the femur (Walker, 1973).
Insertion: to metatarsal-V and together with the tendon of flexor primordialis communis pars gastrocnemius internus uniting with rest of m. flexor profundus (Ribbing, 1909).

2 Gastrocnemius pars gastrocnemius internus
Synonyms: flexor primordialis communis pars gastrocnemius internus (Ribbing, 1909). Gastrocnemius, internal or tibial head (superficial layer) (Walker, 1973).
Origin: one part from proximal part of tibia diaphysis, one part from 'proximal (von oben)' (Ribbing, 1909). Tibia (can be subdivided into two heads: anterior border and flexor side of proximal half of tibia; Walker, 1973).

Insertion: broad tendon to 'rudiment of toe-V' (metatarsal V?!), a flexor accessories-head is present (Ribbing, 1909).

1+2 Gastrocnemius (as a whole)
Insertion: at level of ankle become tendinous and form a extensive plantar aponeurosis (with two layers), covers sole of foot – inserts to anterior margin of toe-I, near bases of toes-II–IV (together with m. flexor digitorum communis sublimes; for plantar flexion) – aponeurosis and m. gastrocnemius together attach to the posterior edge of metatarsal V (for web spreading between toes-IV–V).

3+4 Flexor accessories (et flexor accessories medialis)
Synonyms: flexor accessories et flexor accessories medialis [in comm. unis] (not separated in turtles; but in other tetrapods a separation into mm. flexor accessories lateralis, no. 3, et medialis, no. 4, may occur; Ribbing, 1909); flexor digitorum longus (= the main flexor; Walker, 1973). Following Walker (1973), the 'major part of m. flexor primordialis communis' and m. flexor accessories would together be discussed as m. flexor profundus by Ribbing (1909, p. 14). But actually they are discussed separately.
Origin: first head: distal end of femur (proximal to condyles; Ribbing, 1909); second head: whole fibula and metatarsal V (Ribbing, 1909); one head (*Pseudemys*): fibula (epicondyle) until the femur (anterior to origin of external head of m. gastrocnemius); second head: fibula (entire length) and adjacent parts of tarsus (muscle as a whole deep to m. gastrocnemius, no. 1–2; Walker, 1973).
Insertion: tendon to distal phalanges of toe-I–IV (Ribbing, 1909). Two heads converge at the mesotarsal joint and form very tough flexor plate (= plantar aponeurosis), from which four flexor tendons run to the plantar side of toes-I–IV (terminal phalanges), in *Staurotypus* and Cheloniidae also a tendon to toe-V (Walker, 1973).

5 Lumbricales
Synonyms: flexores breves superficialis Partim (Ribbing, 1909). Lumbricales (as a side note, it appears to us as if the 'a' part of Ogushi's (1913) muscle (his no. 137) has to be associated with the m. lumbricales; Walker, 1973).
Origin: dorsally from flexor plate; note: apparently as a superficial head of this muscle part a third muscle 'layer' is described inserting to the first phalanges of toe-II–IV (Ribbing, 1909). Arises from dorsal surface of flexor plate of flexor digitorum longus (Walker, 1973).
Insertion: tibial face of phalanx II of toes-II–IV (Ribbing, 1909). Tibial side of toe-II–V, penultimate phalanx (in testudinids with lost fifth toe not to fifth toe; in cheloniids only to toe-II–IV) – some fibres to the web of the foot (trionychids; Walker, 1973).

6 Flexor digitorum communis sublimes
Synonyms: flexores breves superficialis Partim (Ribbing, 1909). Flexor digitorum communis sublimes (Walker, 1973).
Origin: ventrally from flexor plate (Ribbing, 1909). Arises from planar face of flexor plate of m. flexor digitorum longus (Walker, 1973).
Insertion: first bundle: phalanx I of toe-I; other three bundles: with two tendons each to base of phalanx II of toes-II, -III, -IV (Ribbing, 1909). Splits into four bundles attaching to proximal phalanges of toe-I–IV (mostly tibial side; Walker, 1973).

7 Pronator profundus

Synonyms: pronator profundus (Ribbing, 1909; Walker, 1973).
Origin: whole diaphysis of fibula (Ribbing, 1909).
Insertion: direct on distal part of tibia, and with a tendon the three internal tarsals and to the bases of metatarsals I and II (Ribbing, 1909).
General: spans between fibula (flexor face, deep to flexor digitorum longus), and adjacent proximal tarsals and base of metatarsal I (Walker, 1973).

8 Popliteus

Synonyms: interosseus (cruris; Ribbing, 1909). Popliteus (Walker, 1973).
General: fills spatium interosseus (between tibia and fibula; no such synonymization by Walker, 1973; Ribbing, 1909). Fills interosseus space between fibula and tibia (Walker, 1973).

9–15 Summarized as 'interossei plantares'

Synonyms: interossei plantares [Walker, 1973; apparently mostly referring to m. contrahentes digitorum (no. 9) in communis to mm. interossei (12–15) of Ribbing, 1909], Walker (1973) illustrated but did not describe one part of m. interossei plantares in fig. 30A ('*Pseudemys*' = *Trachemys scripta*), which apparently corresponds to m. interosseus plantaris IV/V (no. 15) herein.
Origin: distal tarsals and metatarsals I–IV (Walker, 1973).
Insertion: fibular side of proximal phalanges of those toes; in *Lissemys* also to fifth toe (Walker, 1973).

10 Contrahentes digitorum

Synonyms: contrahentes digitorum (Ribbing, 1909).
Origin: tendinuous from metatarsal V (Ribbing, 1909).
Insertion: bases of first phalanges of toes-I–IV (Ribbing, 1909).

11 Contrahentes digitorum-I

Synonyms: N.N. (Ribbing, 1909).
General: this additional muscle separated from m. contrahens digitorum (no. 9) with an origin on the tendon of m. pronator profundus (no. 7) inserting to first phalanx of toe-I (Ribbing, 1909).

12 Flexores breves profundi

Synonyms: flexores breves profundi (Ribbing, 1909).
General: apparently a superficial layer of m. contrahentes digitorum (no. 9) with similar origin and insertion (Ribbing, 1909).

12–15 Interossei, with (12) interosseus plantaris I/II; (13) interosseus plantaris II/III; (14) interosseus plantaris III/IV; (15) interosseus plantaris IV/V

Synonyms: interossei (Ribbing, 1909).
Origin: fibial face of metatarsals I–IV and fibial side of first phalanges of toes-I–IV (Ribbing, 1909).
Insertion: tibial faces of metatarsals II–V and phalanx I of toe-V (Ribbing, 1909).

16 Flexor metatarsi V

Synonyms: flexor metatarsi V (Ribbing, 1909).
Origin: distal end of fibula (Ribbing, 1909).
Insertion: metatarsal V (Ribbing, 1909).

17+18 Flexores digitorum minimi et interphalangei II and IV

Synonyms: flexores digitorum minimi et interphalangei II and IV (Ribbing, 1909).
General: not in turtles (Ribbing, 1909).

(B) Extensores (dorsal extension)

19 Extensor digitorum communis

Synonyms: extensor digitorum communis (Ribbing, 1909). Extensor digitorum communis, in Trionychidae with an additional muscle head 'm.' extensor hallucis longus (Walker, 1973).
Origin: condylus digitorum communis (Ribbing, 1909). Femur (dorsal surfaces and distal end; Walker, 1973).
Insertion: base of terminal phalanx of toe-I and at tibial side of first phalanx of toe-I, fibular side of metatarso-phalangeal joint of toe-I, fibular face of metatarsal II and III, and at both sides of metatarsal IV (Ribbing, 1909). Metatarsals I–IV (fibular side), in Trionychidae with an additional muscle head 'm.' extensor hallucis longus: a slip of extensor digitorum communis to the dorsum of the first toe (Walker, 1973).

20 Extensor tarsi tibialis

Synonyms: extensor tarsi tibialis (Ribbing, 1909). Tibialis anterior (Walker, 1973)
Origin: on whole tibia (Ribbing, 1909). Tibia (anterior border), in general: deep to extensor digitorum communis (Walker, 1973).
Insertion: to metatarsal I and to tendon of pronator and fascia of tarsus at its flexor (planar) face (Ribbing, 1909). Metatarsal I (anterior border + planar surface; Walker, 1973).

21 Extensor cruris tibialis

Synonyms: extensor cruris tibialis (Ribbing, 1909).
General: not present in turtles due to the tibial expansion of m. extensor tarsi tibialis (no. 20; Ribbing, 1909).

22 Peroneus anterior

Synonyms: peroneus anterior (Walker, 1973).
Origin: fibula (distal half, dorsal surface, in trionychids also a head from tibia, tendinous in sea turtles); in general: covered by extensor digitorum communis (Walker, 1973).
Insertion: metatarsal V (dorsum, some form a small tendon that extends distally to top of fifth toe), base of 5th toe but can spread to metatarsal IV or just insert there in those testudinoids in which the fifth toe is missing (Walker, 1973).

23 Peroneus posterior

Synonyms: peroneus posterior (missing in kinosternids and testudinoids; Walker, 1973).
Origin: fibula (distal end; Walker, 1973).
Insertion: metatarsal V (Walker, 1973).

22–23 Peroneus anterior et posterior

Synonyms: extensor tarsi fibularis (Ribbing, 1909).
Origin: distal two-thirds of fibula diaphysis (Ribbing, 1909).
Insertion: metatarsals IV and V, the part inserting to metatarsal V sends a thin tendon along the dorsal line of the rudimentary phalanges of toe-V (Ribbing, 1909).

24 Extensor cruris fibialis

Synonyms: extensor cruris fibialis (Ribbing, 1909).
General: only described for Urodela in communis with extensor tarsi fibularis (Ribbing, 1909).

25 Abductor hallucis

Synonyms: abductor hallucis (Walker, 1973).
Origin: distal tarsal 1 and adjacent parts of metatarsal I (Walker, 1973).

Insertion: penultimate phalanx of toe-I (Walker, 1973).

General: absent in *Emys orbicularis* (Ribbing, 1909); Ribbing (1909) mentioned the primary homologous tarsi digitus I of Hoffmann (1890), which was homologized to it by Walker (1973).

26 Extensor hallucis proprius
Synonyms: extensor breves superficialis, superficial layer, muscle 1 (Ribbing, 1909). Extensor hallucis proprius (Walker, 1973).
Origin: distal end of fibula (Ribbing, 1909). Fibula (distal end; Walker, 1973).
Insertion: both sides of fist phalanx of toe-I and in communis with the deep extensor to toe-I (Ribbing, 1909). Proximal phalanx toe-I (Walker, 1973).

27 Extensors digitorum brevis-2
Synonyms: extensor breves superficialis, superficial layer, muscle 2 (Ribbing, 1909).
Origin: from 'cuboid' (distal tarsal 4; Ribbing, 1909).
Insertion: together with the deep extensors to toe-III (Ribbing, 1909).

28 Extensors digitorum brevis-3
Synonyms: extensor breves superficialis, superficial layer, muscle 3 (Ribbing, 1909).
Origin: from 'cuboid' (distal tarsal 4; Ribbing, 1909; Walker, 1973).
Insertion: together with the deep extensors to toe-IV (Ribbing, 1909; Walker, 1973).

27–28 Extensors digitorum brevis-2 and -3 together
Synonyms: extensors digitorum brevis Partim (not separated from interosseus dorsales in sea turtles; Walker, 1973).
Origin: 3rd to 4th distal tarsal (Walker, 1973).

Insertion: distal segments of toes-II–IV (Walker, 1973).

28 Interosseus dorsales-I
Synonyms: extensor brevis profundus 1 (Ribbing, 1909).
Origin: metatarsal I (Ribbing, 1909).
Insertion: first phalanx of toe-I (Ribbing, 1909).

29 Interosseus dorsales-II
Synonyms: extensor brevis profundus 2 (Ribbing, 1909).
Origin: metatarsal II and basis of metatarsal I (Ribbing, 1909).
Insertion: first phalanx of toe-II (Ribbing, 1909).

30 Interosseus dorsales-III
Synonyms: extensor brevis profundus 3 (Ribbing, 1909).
Origin: metatarsal III and basis of metatarsal III (Ribbing, 1909).
Insertion: first phalanx of toe-III (Ribbing, 1909).

31 Interosseus dorsales-IV
Synonyms: extensor brevis profundus 4 (Ribbing, 1909).
Origin: metatarsal IV (Ribbing, 1909).
Insertion: first phalanx of toe-IV (Ribbing, 1909).

32 Interosseus dorsales-V
General: described as not present in *Emys orbicularis* (Ribbing, 1909).

29–33 Interosseus dorsales-I to -V together
Synonyms: interosseus dorsales (not separated from Extensors digitorum brevis in sea turtles; Walker, 1973).
Origin: metatarsals I–IV and adjacent distal tarsals 1–4, in *Lissemys* also fifth toe (Walker, 1973).
Insertion: periosteum of terminal parts (perhaps Walker, 1973 meant first phalanx) of the toes, in *Lissemys* also fifth toe (Walker, 1973).