

Chapter 6

Three Ways to Tackle the Turtle: Integrating Fossils, Comparative Embryology, and Microanatomy

Torsten M. Scheyer, Ingmar Werneburg, Christian Mitgutsch, Massimo Delfino, and Marcelo R. Sánchez-Villagra

Abstract Herein we review a series of case studies covering the evolution and phylogenesis of turtles, and the ontogenetic development of one of the most peculiar body plans within the Craniota. Comparative analyses of skeletal development, ontogenetic timing, and bone microstructure in both extant and extinct taxa are used to document patterns and make inferences about the origin of turtles, turtle ingroup relationships, and the evolution of turtle ontogenetic development. The need for a balanced sampling of both cryptodiran and pleurodiran turtle species for future comparative studies is highlighted.

Keywords Bone histology • Comparative anatomy • *Odontochelys* • Sequence heterochrony • Testudinata • Testudines • Turtle origins

Introduction

Hypotheses on the position of turtles within the amniote tree of life are contentious (Carroll 2012; Lyson et al. 2010), despite many efforts over the past century to solve this major problem in vertebrate evolution (Rieppel 2008). This situation is largely due to the peculiar morphology of the turtle body plan, especially the unique shell (Nagashima et al. 2009, 2012; Kuratani et al. 2011; Rieppel 2012) and the anapsid condition of the skull (Gaffney and Meylan 1988; Lee 1997a), which renders comparisons to other vertebrates difficult at best. In recent years, turtles have been treated either as a group of parareptiles or as diapsids; for the latter, relationships with Lepidosauromorpha, Archosauromorpha, or Sauria have been hypothesized.

The past two decades have brought refined techniques in molecular biology (Shaffer 2009) and evolutionary developmental biology, as well as in comparative anatomy, all of which have helped clarify interrelationships among living turtles (e.g., see summary by Werneburg and Sánchez-Villagra 2009). For ontogenetic approaches, several methods have been developed to analyze developmental timing data within a phylogenetic framework. One of those methods, Parsimov, has been extensively used to assess information from organogenesis or ossification patterns, for which an expanding body of data is being assembled (e.g., Sánchez-Villagra et al. 2009 and references therein). However, atomizing heterochronic data as performed in event-pair based algorithms, as well as the robustness and the value of its information content, have recently been reassessed and alternative approaches have been suggested (Ziermann 2008; Germain and Laurin 2009; Werneburg 2010; Werneburg and Sánchez-Villagra 2011).

In addition, new fossil discoveries continue to be important for documenting the evolution of turtles. Among the most important of these are fossils and taxa from Upper Triassic sediments on several continents, such as skeletons of

T. M. Scheyer (✉) · I. Werneburg · C. Mitgutsch · M. R. Sánchez-Villagra
Paläontologisches Institut und Museum, Universität Zürich,
Karl Schmid-Strasse 4, 8006 Zürich, Switzerland
e-mail: tscheyer@pim.uzh.ch; ingmar_werneburg@yahoo.de;
christian.mitgutsch@gmail.com; m.sanchez@pim.uzh.ch

M. Delfino
Dipartimento di Scienze della Terra, Università di Torino,
Via Valperga Caluso 35, 10125 Turin, Italy
and
Institut Català de Paleontologia Miquel Crusafont,
Universitat Autònoma de Barcelona. Edifici ICP,
Campus de la UAB s/n, 08193 Cerdanyola del Vallès,
Barcelona, Spain
e-mail: massimo.delfino@unito.it

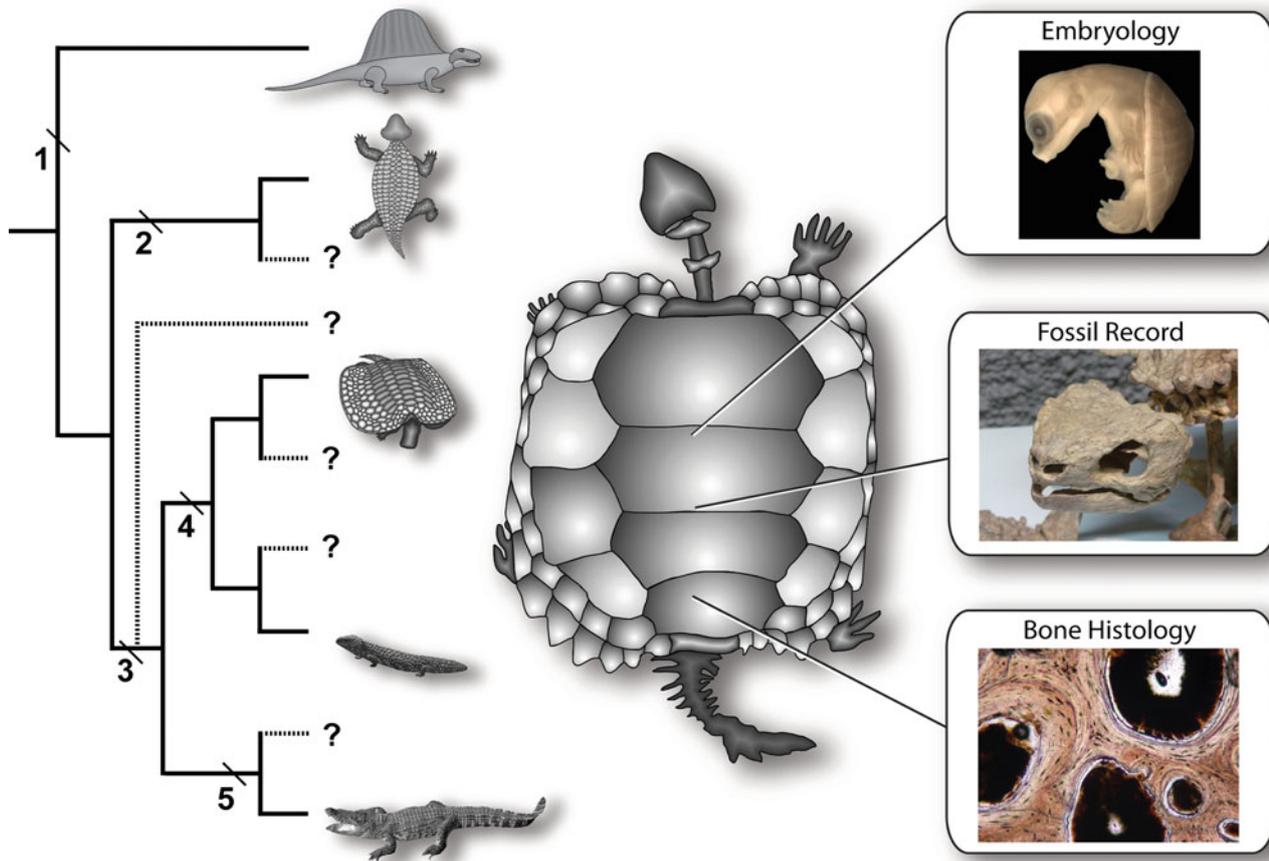


Fig. 6.1 Various hypotheses of the position of turtles within the amniote tree of life and applied methods of investigation. Numbers indicate proposed relationships between turtles and the following

groups: 1 Synapsida; 2 Parareptilia; 3 Diapsida; 4 Lepidosauromorpha; 5 Archosauromorpha

Odontochelys semitestacea from China (Li et al. 2008), which are providing new insights into the early evolution of turtles.

Lately, there has been an increasing trend to integrate ontogenetic aspects into paleontology-based studies and to interpret molecular data in the light of insights yielded from fossil taxa (Raff 2007; Shubin et al. 2009; Sánchez-Villagra 2010). Fossil developmental data, as is true for neontological data, can potentially reveal systematic relationships that are not apparent from adult morphology (e.g., Hall 2005; Schoch 2009; Sánchez-Villagra 2010). In a controversial clade like turtles, it is critical to consider as many developmental and evolutionary aspects as possible, in order to have a better understanding of the group's evolutionary history. Here we review a series of case studies that integrate evolutionary, developmental, and bone histological data from fossil and extant turtles (Fig. 6.1).

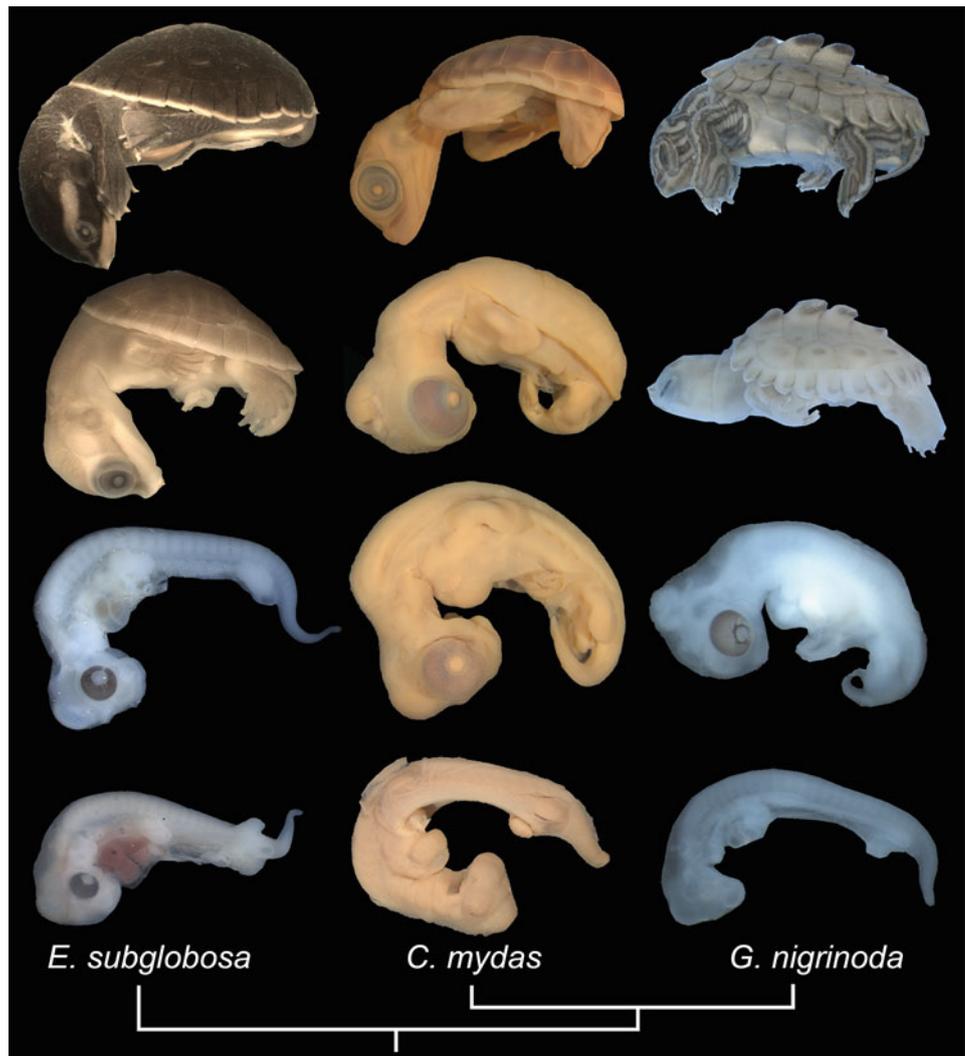
As discussed below, the existence and mode of reduction of shell features is a subject of particular relevance in current discussions of turtle origins (Lee 1997a, b; Li et al. 2008; Lyson and Gilbert 2009; Reisz and Head 2008; Burke

2009; Nagashima et al. 2009, 2012; Kuratani et al. 2011; Rieppel 2012). Because the turtle shell is such an enigmatic and key autapomorphy of turtles, many of the case studies summarized below focus on that part of the skeleton.

Heterochrony Analyses and Skeletal Development in Turtles

Several methods are now available to put sequence ontogenetic data into a phylogenetic context (Hall 2005; see also review by Maxwell and Harrison 2009; Germain and Laurin 2009), with the most widely used method currently being Parsimov (Jeffery et al. 2005). Patterns of chondrification and the onset of ossification were analyzed in several turtle taxa and a variety of outgroups in two recent studies by Sánchez-Villagra et al. (2009) and Werneburg et al. (2009). In the former study, a comprehensive developmental series of the Chinese soft-shelled turtle *Pelodiscus sinensis* demonstrated that in both the cranium and postcranium, dermal

Fig. 6.2 Developmental series of three extant turtle species, demonstrating the systematic value of embryological data. Taxa are: the pleurodire *Emydura subglobosa* (left) and the cryptodires *Chelonia mydas* (middle) and *Graptemys nigrinoda* (right). The selected specimens [all stored at the Paläontologisches Institut und Museum, Universität Zürich, Switzerland (PIMUZ)] illustrate major steps in development such as somitogenesis, limb bud formation, and development of the carapace. Specimens not to scale



elements ossify earlier than endochondral elements. Analysis of the ossification sequence of autopodial elements in *P. sinensis* also revealed high intraspecific variation, whereas the pattern of chondrification was consistent with Shubin and Alberch's (1986) concept of primary axis and digital arch. Finally, heterochronic shifts in chondrification patterns of fore- and hind limbs were minimal and there was no evidence for the anlage of a radiale or a tibiale in this taxon (Sánchez-Villagra et al. 2009), which confirmed the lack of those elements in turtles as had been independently suggested by Fabrezi et al. (2009).

The study by Werneburg et al. (2009) examined the timing of organogenesis in several turtle species, including for the first time a pleurodire species (Fig. 6.2). By analyzing a total of 15 turtle and seven other amniote species, and using the axolotl *Ambystoma mexicanum* as an out-group, the position of turtles as the sister group to the Archosauria/Lepidosauria clade was supported. That result was consistent with some previous, morphology-based

analyses of tetrapod relationships (e.g., Gauthier et al. 1988; Laurin and Reisz 1995), but stands in contrast to most, but not all, recent molecular studies that favored a turtle-archosaur relationship (e.g., Rest et al. 2003; Iwabe et al. 2004; Lee et al. 2004) and to some morphology-based studies that supported a turtle-lepidosaur relationship (e.g., Rieppel and deBraga 1996; deBraga and Rieppel 1997; Müller 2003; Hill 2005). A preliminary analysis of turtle shell bone microstructure also hinted at a potential turtle-archosaur relationship (Scheyer 2007).

One of us developed a new referencing system to study the timing of events in development with the goal of optimizing the acquisition of embryological data for vertebrates (Werneburg 2009). This new referencing system was applied by Werneburg et al. (2009) in a study on the embryogenesis and ossification patterns in the chelid *Emydura subglobosa*, which broadened the data base on the previously neglected pleurodiran branch of turtles. By comparing data from *E. subglobosa* with five other turtle

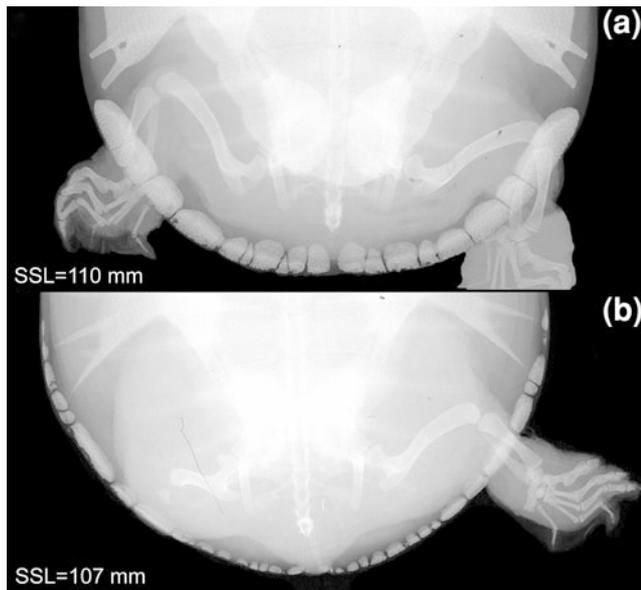


Fig. 6.3 Radiographs of the posterior portion of the body of extant *Lissemys* (Trionychidae), showing the different arrangements of peripheral ossicles around the posterior margin of the carapace that are unique to this genus within the family. **a** *Lissemys punctata* (MTD 32146) and **b** *Lissemys scutata* (MTD 40367). Pictures taken at the Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden, Germany (MTD), in collaboration with Uwe Fritz. Abbreviation: SSL, straight shell length

species and a number of other tetrapod taxa from the literature, Werneburg et al. (2009) showed that late development of the neck is autapomorphic for Testudines. Within turtles, the same study further showed that (1) timing in the development of the mandibular process differed between pleurodires and cryptodires and (2) the epiplastron developed earlier in pleurodires than in cryptodires.

Homology of Peripheral Ossicles in Soft-Shell Turtles

Most soft-shelled turtles are characterized by a complete lack of peripherals. The species of *Lissemys*, however, are an exception in having a series of peripheral ossicles posteriorly and a prenuchal anteriorly. Delfino et al. (2010) reassessed the nature of these ossicles using data generated from X-ray scans and macerated skeletons of *L. punctata* and *L. scutata* (Fig. 6.3), and by studying the microstructure of those bones histologically. All of Remane's (1952) classic criteria for homology assessment—the criteria of topology, structural equivalence, and presence of intermediate forms—were considered in testing the identity of the peripheral ossicles in *Lissemys*. Posterior peripheral ossicles were found to fulfill all of Remane's (1952) criteria.

Although *Lissemys* might not be the sister group of all remaining trionychids (Joyce and Lyson 2010; but see Head et al. 2009), their posterior peripheral ossicles can still be interpreted as homologues to the peripherals of non-trionychid turtles based on 'deeply homologous' (sensu Shubin et al. 2009) underlying developmental processes, despite a lack of one-to-one correlation between the ossicles and the dorsal ribs or costal plates. The prenuchal on the other hand, in not fulfilling any of Remane's (1952) criteria, is interpreted as a neomorphic dermal bone present only in species of *Lissemys* and *Cyclanorbis*.

Ontogeny of the Shell in Side-Necked Turtles

Scheyer et al. (2008) combined histological data from shell bones of fossil and extant post-hatching turtles with ontogenetic data of extant turtles to examine development of the shell in pleurodires. Their data set included a developmental series for the extant pleurodire *Emydura subglobosa* and revealed a bimodal development for the costals and neurals (see below). No distinct ossification centers were identified for the costals or neurals. Instead, these elements start as initial outgrowths of the periosteum of the ribs and vertebral arches, respectively, before the mode of ossification switches to metaplastic ossification (i.e., ossification and incorporation of surrounding preformed and differentiated dermal tissue into the bone [Scheyer et al. 2008]). Metaplastic ossification had already been identified as the main mode of ossification in trionychid turtle shells, where the incorporation and transformation of preformed dermal soft tissue structures into the mineralized bone tissue is most obvious (Scheyer et al. 2007). In contrast, in a recent review of integumentary structures by Vickaryous and Sire (2009), which was based on several other developmental studies (Gilbert et al. 2001, 2007; Cebra-Thomas et al. 2007; summarized by Rieppel 2012), intramembraneous ossification (i.e., growth of bone spiculae into the surrounding soft tissue) was proposed to be the main mode of costal and neural development. Given these conflicting data and interpretations, here we propose that both metaplastic and intramembraneous ossification, to various degrees and at different stages in ontogeny, play a role in costal and neural formation.

The complete reduction (i.e., loss) of neurals frequently occurs among extant pleurodires (e.g., in Chelidae) and also in some fossil pleurodires, such as the pelomedusoid *Bairdemys* from the Caribbean Neogene (Wood and Díaz de Gamero 1971; Sánchez-Villagra and Scheyer 2010). The ontogenetic data assembled by Scheyer et al. (2008) revealed a heterochronic shift (i.e., postdisplacement), in neural arch and neural development in pleurodire species

that lack neurals. This heterochronic shift, together with a reduction or lack of interaction between integumentary and musculoskeletal structures, was proposed to be responsible for complete neural reduction in *Emydura subglobosa*.

Implications for the Origin of Turtles

As indicated above, the systematic position of turtles within amniotes is far from being resolved. Several extinct reptilian clades have been hypothesized to be close turtle relatives (Fig. 6.1; Carroll 2012), one of them being the anapsid pareiasaurs (e.g., Lee 1997a, b), which are large, herbivorous, parareptiles from the Permian (Tsuji and Müller 2009), whose bodies were, to varying amounts, usually covered with dermal armor plates (i.e., postcranial osteoderms). A recent histological study of osteoderms of three pareiasaur taxa from South Africa showed that intramembraneous ossification is likely to be the general mode of skeletogenesis for pareiasaur postcranial armor (Scheyer and Sander 2009). Those elements share only a few histological characters with turtle shell bones and osteoderms (or with other extant eureptilian osteoderms). That finding indicates that the armor structures of turtles and pareiasaurs are not homologous, which argues against a turtle-pareiasaur relationship.

Recently, another classical morphology-based sister group relationship has been revived. In Lyson et al.'s (2010) study, turtles were recovered as the sister group to *Eunotosaurus africanus*, an un-armored, terrestrial parareptile from the Middle Permian of South Africa (Rubidge et al. 1999), which has extremely broadened ribs.

Prior to the description of the now oldest and basal-most turtle, *Odontochelys semitestacea* from Upper Triassic, marine black shales in China (Li et al. 2008), all stem turtles of comparable age (i.e., *Paleochersis talampayensis*, *Proganochelys quenstedti*, and *Proterochersis robusta*) in recent years had been interpreted as terrestrial forms (Joyce and Gauthier 2004; Scheyer and Sander 2007; Sterli et al. 2007). At present, *Chinlechelys tenertesta* from the Upper Triassic Chinle Group of New Mexico, USA, remains problematic in this regard, due to its highly fragmentary nature (Joyce et al. 2009). *Odontochelys* combines a rudimentary carapace with a fully developed and well-ossified plastron; in that sense, it can be described as being 'half-shelled'. The shell structure and depositional setting of *Odontochelys* raised the question whether turtles had an aquatic or a terrestrial origin (Rieppel and Reisz 1999; Li et al. 2008; Reisz and Head 2008; Rieppel 2012). As summarized by Lyson and Gilbert (2009, p. 133), it is still unclear whether *Odontochelys* argues for a primary aquatic origin for turtles, as Li et al. (2008) proposed, or if

Odontochelys belongs to an early radiation of turtles into the water, as favored by Reisz and Head (2008).

Several years previously, the oldest purported fossil turtle shell fragment, belonging to *Priscochelys hegnabrunnensis* and recovered from deposits of the Germanic Muschelkalk (Middle Triassic) in southwestern Germany, had prompted Joyce and Karl (2006) to propose that turtles might have evolved in an aquatic environment. Using bone histology observation, Scheyer (2008) subsequently showed that material of *Priscochelys* represents a placodont armor fragment, instead of a turtle shell fragment and, therefore, is irrelevant to discussions on the origin of turtles.

Recent histological and embryonic studies (e.g., Scheyer et al. 2008; Sánchez-Villagra et al. 2009 and references therein) of extant turtles are potentially relevant for assessing the nature of the neurals and costals in *Odontochelys*. The broadened or expanded ribs (Li et al. 2008) of *Odontochelys* look like paedomorphic ribs of extant turtles in being slightly reduced in length, to the extent that their distal ends do not reach the lateral extensions of the hyo- and hypoplastral lateral processes of the plastron. Although the ribs of *Odontochelys* resemble turtle costals in shape and topology, they differ in lacking anterior and posterior sutural margins. A similar lack of sutures, at least in the distal part of the costals, occurs in some extant turtles; e.g., in 'geodesic' tortoises (sensu Pritchard 2008) *Manouria emys* and *Malacochersus tornieri* (Fig. 6.4). In the former species, the fontanelles in the carapace (which separate the distal ends of the costals) and plastron eventually close in adults, whereas these openings are permanent in the latter (Procter 1922). In all species of *Manouria* and *Malacochersus*, sutural contact of the carapace and the plastron remains via the bridge peripherals, to maintain the structural integrity of the shell (Procter 1922; Pritchard 2008).

Li et al. (2008, p. 499) stated that, based on the broad shape of its dorsal ribs, *Odontochelys* resembled an embryonic, extant turtle at the stage "... before marginal, nuchal and pygal elements start ossification." However, whereas peripherals and pygal elements appear relatively late in comparison to the neurals and costals (e.g., Sheil and Greenbaum 2005), the nuchal is amongst the first bones to ossify during postcranial development in extant turtles, shortly after the onset of ossification of plastral elements (contra Li et al. 2008). Even in taxa in which the peripheral shell elements are lost by developmental truncation, such as in most trionychids (e.g., Sánchez-Villagra et al. 2009) and in the leatherback *Dermochelys coriacea*, the nuchal is always consistently present and a prominent element of the thecal shell (e.g., Scheyer 2007). Furthermore, the statement that the "neural plates are not fused with broadened neural spines of dorsal vertebrae but were displaced laterally during fossilization" (Li et al. 2008, p. 498) raises the

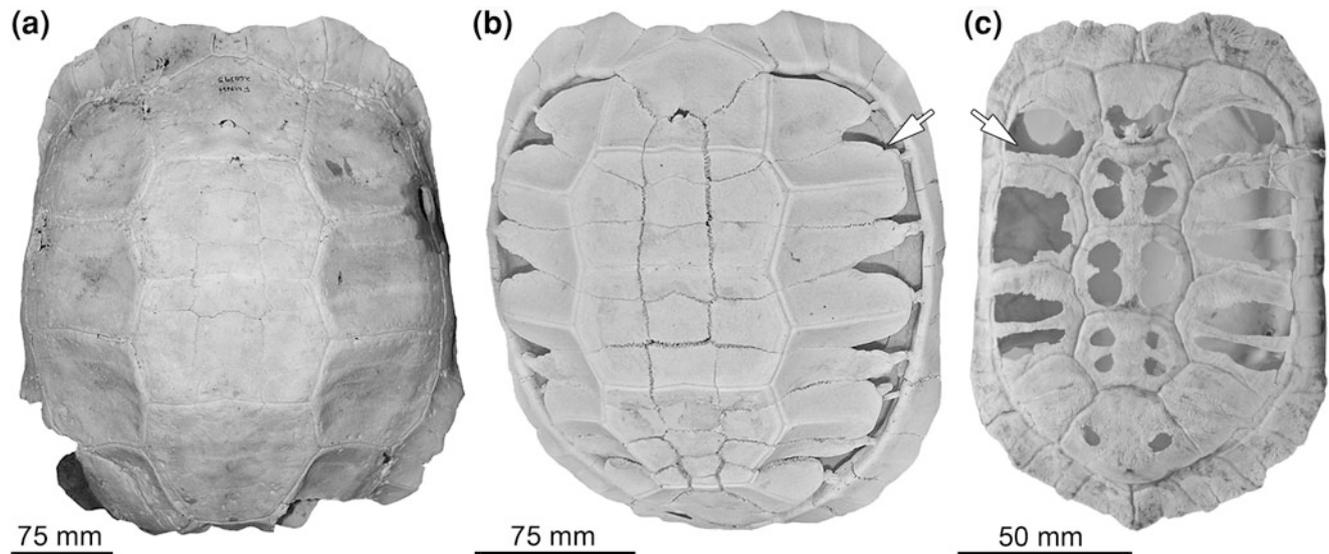


Fig. 6.4 Carapaces of the tortoises *Manouria emys* and *Malacochersus tornieri*, as examples of extant turtles in which the carapace bones may not be sutured together. **a–b** Sub-adult specimens of *Manouria emys*: **a** example of carapace already completely ossified (FMNH 260395; note that shell is damaged posteriorly); **b** ‘geodesic’ shell condition (MTD D 19981) in which the costals are still paper-thin bones that largely lack sutures distally. Fontanelles (arrow in **b**) may

close later during ontogeny. **c** Adult specimen of *Malacochersus tornieri* (MTD D 010) showing the extremely reduced condition of shell bone formation and the persisting fontanelles (arrow) between the costals and neurals typical for this species. Institutional abbreviations: FMNH: The Field Museum, Chicago, Illinois, USA; MTD: Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden, Germany

possibility that separation of the neural plates from the corresponding neural arches could be a taphonomic effect.

The question remains whether the lack of a nuchal in the holotype skeleton of *Odontochelys* is because that bone was absent in life (i.e., not developed) or if it was present but lost postmortem, perhaps due to the same taphonomic processes that may have been responsible for shifting the neurals (see also discussion in Rieppel 2012). Based on the pictures and drawings provided by Li et al. (2008), the presence or absence of a nuchal bone also remains ambiguous in the paratype and only other published, relatively complete specimen of *Odontochelys*. Considering that in many living turtles the nuchal is an integral part of the neck muscular system (e.g., Herrel et al. 2008), if the nuchal was indeed absent in *Odontochelys* that could have significant implications for the structure and function of its neck.

Conclusions

In summary, it is essential that in a group with a peculiar body plan like turtles all sources of data are exploited by integrating paleontological and neontological data. Detailed anatomical studies can expose hidden homologies that were previously not recognized.

The timing of organogenesis as revealed by heterochrony studies using both cryptodires and pleurodires indicates a possible turtle-Sauria sister-group relationship. Turtle autopodial

development, as studied for example in the trionychid *Pelodiscus sinensis*, is in accordance with the concept of a primary axis and digital arch. In addition, the posterior peripheral ossicles in the trionychid *Lissemys* were found to fulfill all of Remane’s (1952) criteria of homology and, thus, were interpreted to be homologous with the peripherals in non-trionychid turtles based on ‘deeply homologous’ underlying developmental processes. The nature of the neural and costal bones in the turtle shell remains poorly understood; however, metaplastic and intramembraneous modes of ossification appear to contribute to their formation at different stages during ontogeny. A heterochronic shift involving post-displacement in neural arch and neural development, together with reduction or lack of interaction between the integument and underlying musculoskeleton was presented as a cause for the complete reduction (i.e., loss) of neurals in fossil and extant pleurodires. Furthermore, new fossil finds, especially of Mesozoic stem-turtles such as *Odontochelys semitestacea*, have revealed new and exciting aspects of anatomy that shed light on the early evolution of the group and the development of one of its key features, the shell.

Acknowledgments We thank Shigeru Kuratani (Kobe), Johannes Müller (Berlin), Uwe Fritz (Dresden), Alan Resetar (Chicago), and Janine M. Ziermann (Jena/Leiden), as well as all of their colleagues, for various help in accessing and studying specimens. Nadia Fröbisch (Chicago), James Gardner (Drumheller), Olivier Rieppel (Chicago), and Matt Vickaryous (Guelph) are thanked for their constructive

comments on the manuscript. We also thank all of our collaborators and the SNSF, grant 31003A_127053/1 (to TMS), for supporting this research.

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