Chapter 23
The Turtle Evolution: A Conundrum in Vertebrate Evo-Devo

Naoki Irie*, Hiroshi Nagashima*, and Shigeru Kuratani

Abstract Because of their unique morphology, turtles have raised profound questions as to their evolutionary origin. In striking contrast to the body plan of other tetrapods, the shoulder girdle of turtles sits inside the rib cage, which comprises the dorsal shell, or carapace. By this topological change of the skeletal elements, the carapace has been regarded as an example of evolutionary novelty that violates the ancestral body plan of tetrapods. In this chapter, we first overview the phylogenetic positioning of turtles, and then review how turtles evolved their unique body plan. In brief, three points have been clarified by recent studies. (1) Turtles have birds/crocodilians (or archosaurians) affinity of evolutionary origin. (2) During embryogenesis, the turtle also establishes the vertebrate basic body plan, as in other vertebrates, followed by the late developmental stages of generating turtle-specific structures, such as folding of the lateral body wall to make the apparent inside-out topology of shoulder girdle against ribs. (3) One of the causal factors of folding appears to be the concentric growth of carapacial margin, which involves an ancestral gene expression cascade in a new location. These reports allow us to hypothesize the

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stepwise, not necessarily saltatory, evolution of turtles, consistent with the recent finding of a transitional fossil animal, *Odontochelys*, that did not have the carapace but already possessed the plastron.

Keywords Development • Evolution • Phylogeny • Phylotype • Turtle

23.1 Introduction

Turtles have long been regarded not only as the most primitive extant amniotes but also as animals that evolved abruptly without any intermediate morphology. Their skull does not possess any temporal fenestrae (representing the anapsid state), a character that was once hypothesized to be a hallmark of basal amniotes and their ancestral amphibians (Romer 1956; reviewed by Tsuji and Müller 2009). The trunk of turtles, on the other hand, shows an extensively derived feature. The turtle shell is composed of dorsal and ventral moieties; the ventral moiety is referred to as a plastron, consisting of nine dermal elements corresponding to clavicle, interclavicle, and gastralia in other amniotes (Fig. 23.1b–d). The dorsal shell, termed the carapace, comprises the thoracic vertebrae, ribs, and dermal bones surrounding the axial skeleton (Fig. 23.1a). In many turtle species, these bony shells are covered by keratinous scutes, whereas in some species, such as the soft-shelled turtles, the scutes and the peripheral dermal bones are lost.

The outstanding feature in the turtle flank is not the shell itself, but the resultant body plan of turtles (Burke 2009). Turtle ribs, rather than growing ventrally, grow laterally to form the carapace, and the uniqueness of the turtles is that their shoulder girdle composed of scapula and coracoid is housed inside the ribcage. This inside-out morphology appears to have been established by violating the basic rules of the vertebrate body plan, thus regarded as a typical example of evolutionary novelties (Hall 1998; Rieppel 2001; Gilbert et al. 2001, 2008).

Lack of any transitional patterns to explain this turtle-specific topological change, as well as the absence of intermediate fossils, have led biologists to assume that turtles emerged by saltatory evolution (reviewed by Nagashima et al. 2012a). In this section, we overview the evolutionary origin of turtles by introducing studies aimed to clarify the phylogenetic position of turtles, followed by studies focused on the body plan evolution of turtles.

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Fig. 23.1 (continued) (*epi*) is homologized with clavicle, entplastron (*ent*) with interclavicle, and other dermal bones with gastralia. **c**, **d** Comparison of body plan between other amniotes (**c**) and turtles (juvenile of Chinese soft-shelled turtle, *Pelodiscus sinensis*) (**d**). Note that scapula (*sc*) and coracoid (*cor*) are outside of the ribs in other amniotes and inside the ribs in turtles. *ca* carapace, *c* clavicle, *cos* costal plate, *g* gastralia, *hyo* hyoplastron, *hypo* hypoplastron, *ic* interclavicle, *neu* neural plate, *nu* nuchal plate, *pe* peripheral plate, *pl* plastron, *py* pygal plate, *r* dorsal ribs, *spy* suprapygal plate, *v* dorsal vertebrae, *xiphi* xiphiplastron (figure modified from Nagashima et al. 2012a)

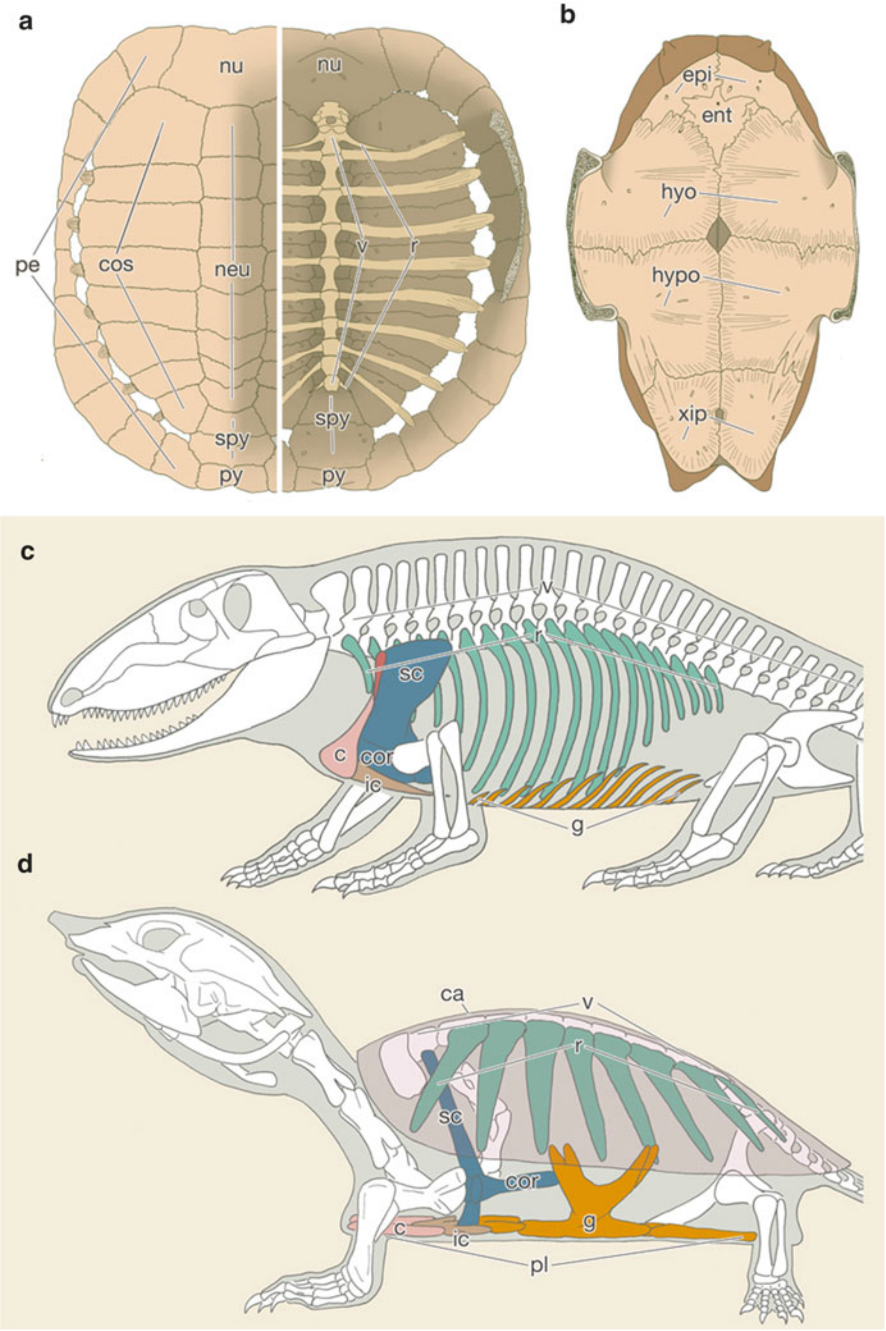

Fig. 23.1 The turtle shell and body plan of turtles. **a**, **b** Turtle shell. **a** Dorsal (*left*) and ventral (*right*) views of the carapacial skeleton of *Chinemys reevesii*. The carapace is formed by ribs (*r*), vertebrae (*v*), and dermal bones arranged peripherally. **b** Dorsal view of the plastron. Epiplastron

23.2 Phylogenetic Position of Turtles

When and where did turtles come into being? Historically, three major hypotheses have been proposed for the phylogenetic origin of turtles. Largely based on the skull morphology, the earliest hypothesis relegated turtles to early-diverged reptiles, called anapsids, located basal to Diapsida (Tsuji and Müller 2009; Kuratani et al. 2011). Meanwhile, with almost every accessible element from egg, embryo, and adult morphology, Rieppel and de Braga (1996) proposed the turtle as a sister group with the lizard–snake–tuatara (Lepidosauria) clade (Fig. 23.2). As the third hypothesis, first by molecular phylogenetic analysis with rRNA (Hedges et al. 1990), and other molecular studies (Caspers et al. 1996; Crawford et al. 2012), it was alleged that turtles are closely related to a lineage including crocodilians and birds (Archosauria) (Fig. 23.2). What confused researchers was that controversy arose even among the molecular-based approaches. Based on the existence or absence of miRNAs,

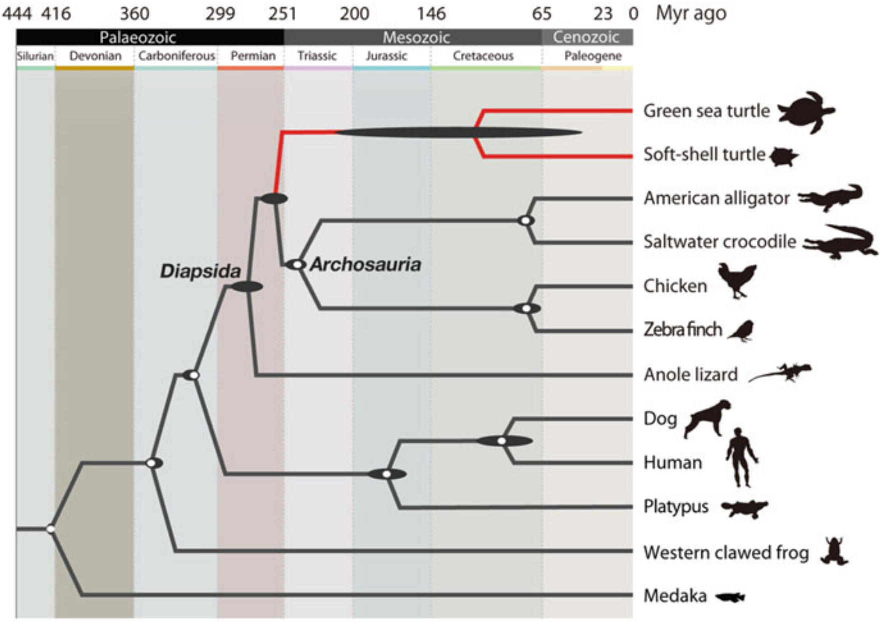

Fig. 23.2 The common ancestor of turtles arose around 267.9–248.3 million years ago, splitting from archosaurians. Molecular phylogenetic analysis based on genome-wide data (1,113 orthologous genes from 12 vertebrate species) supported that turtles are a sister group of archosaurians. Molecular clock analysis, calibrated with fossil records (*white dots* in each branching node) supported that the split occurred around 267.9–248.3 million years ago, the period that overlaps or followed shortly after the Permian extinction event (Chen and Benton 2012). The *black ellipses* on the nodes indicate the 95 % credibility intervals of the estimated posterior distributions of the divergence times (figure modified from Wang et al. 2013)

Lyson et al. (2012) reported that the turtles are a sister group of Lepidosauria. For this study, however, Hedges (2012) draws cautionary attention that the phylogenetic analysis using miRNA is yet to be established to obtain significant results. Finally, recent studies that reported the draft genome sequences of turtles (*Pelodiscus sinensis* and *Chelonia mydas*, by Wang et al. 2013; *Chelonia picta*, by Shaffer et al. 2013), robustly supported the archosaurian affinity of turtles (Fig. 23.2).

These molecular phylogenetic studies are already making some impact on paleontological study, and some paleontologists are reexamining the morphological characters to reconcile morphological data with molecular results (Rieppel 2000). For example, morphology of the vormer (Damiani and Modesto 2001), temporal region (Müller 2003), and carotid circulation (Müller et al. 2011) are suggested not to support a turtle–anapsids relationship. The presence of a laterosphenoid ossification in a basal turtle is proposed to unite turtles to Archosauria (Bhullar and Bever 2009). In the archosauromorph lineage, Merck (1997) found the Euryapsida (Helveticosaurus, Sauropterygia, and Ichthyosauria)–Thalattosauria clade, to which turtles are suggested to be a sister group (Rieppel and de Braga 1996).

Although the ancestor did not possess the complete dorsal shell such as that in existing turtles, the oldest known fossil turtle, *Odontochelys* (Li et al. 2008), showed that the turtle ancestor already existed 220 million years ago. Consistent with this oldest fossil record, Wang et al. (2013), based on their genome-wide dataset including two turtle species (Chinese soft-shelled turtle and green sea turtle), estimated that the common ancestor of turtles already existed before the emergence of *Odontochelys*. According to the estimate based on genome-wide analysis, turtles split from the lineage of archosaurians at around 267.9–248.3 million years ago. Interestingly, the period coincides with the one of the largest mass extinction events on this planet, called the Permian-Triassic extinction event (Chen and Benton 2012). However, whether this extinction event has a certain role in the evolution of the turtle ancestor awaits further investigation.

23.3 Body Plan Development and Evolution of Turtles

How did turtles evolve their unique body plan after splitting from the archosaurians (the group consisting of birds/crocodilians)? Substantial contribution has been made to this question by recent comparative embryonic studies.

Despite the uniqueness of the turtle body plan, recent studies clarified that turtles also follow the general rule for embryonic evolution of vertebrates, or the developmental hourglass model (Fig. 23.3) (Duboule 1994; Irie and Kuratani 2011; Wang et al. 2013), to produce their unique body. The model explains that vertebrate embryos pass through the conserved bottleneck-like period, the period that shows the basic vertebrate body plan (called the phylotypic period), and then specialize afterward. Meanwhile, earlier to, or later than, this phylotypic period, divergent characteristics appear among different species. Actually, the midembryonic stages

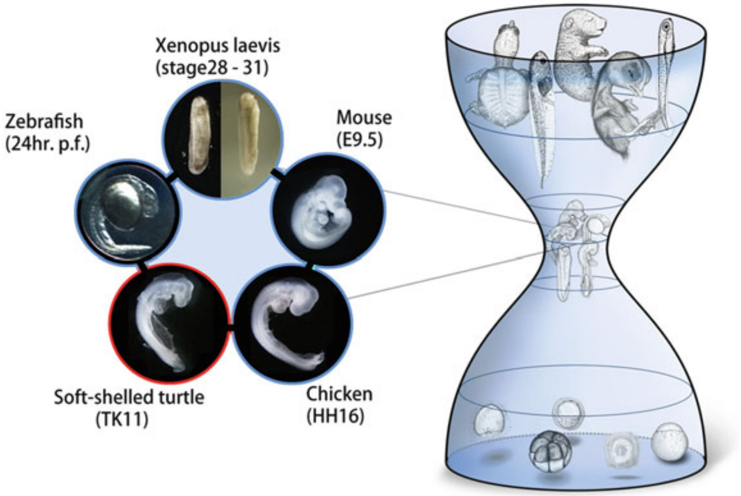

Fig. 23.3 Turtles also follow the developmental hourglass model during embryogenesis. The hourglass model (*right*), first proposed by Duboule (1994), explains that vertebrate embryogenesis is rather divergent during early and late stages whereas midembryonic stages show maximum similarity both in morphology and in whole embryonic gene expression profile. The bottleneck period, called the vertebrate phylotypic period, becomes the source of the vertebrate basic body plan found among adult vertebrates. The horizontal width of the hourglass model represents the evolutionary divergence among vertebrate embryos, and embryogenesis flows upward in this drawing. Recent molecular studies (Irie and Kuratani 2011; Wang et al. 2013) identified that pharyngular embryos are the stages that show most conservation among vertebrates

of turtles and chicken (e.g., stage TK11 of turtle and stage HH16 of chicken) appear somewhat more similar to each other than the earlier and later embryonic stages (Fig. 23.4). Furthermore, quantitative evidence was obtained from the study that took advantage of whole embryonic gene expression profiles (Wang et al. 2013), showing that maximal similarity between turtle and chicken embryos appears in the pharyngula stages (Fig. 23.4; red dashed circles). Direct inference of this observation suggests that turtles, similar to other vertebrates, develop their body first by establishing the vertebrate basic body plan, and then modify the developmental trajectory to obtain the turtle-specific morphological patterns. Actually, the first sign of a turtle-specific character, the carapacial ridge (CR; Figs. 23.4 and 23.5) (Burke 1989), appears after this phylotypic period (see following section). These studies as a whole tell us that the turtle body plan evolved by adding major changes to the embryonic stages after the vertebrate phylotypic period during evolution. Actually, Wang et al. reported that genes that potentially explain the turtle-specific features, such as genes involved in ossification, extracellular matrix reorganization, and collagen, show increasing expression only in the later phase of turtle embryogenesis (Wang et al. 2013).

Finally, the reason why turtles still adhere to the conservation of the vertebrate phylotypic period is not clear; however, some researchers attribute this to a particularly complex signaling network working in this embryonic period (e.g., Hox colineality, interdependent molecular signals: Duboule 1994; Raff 1996).

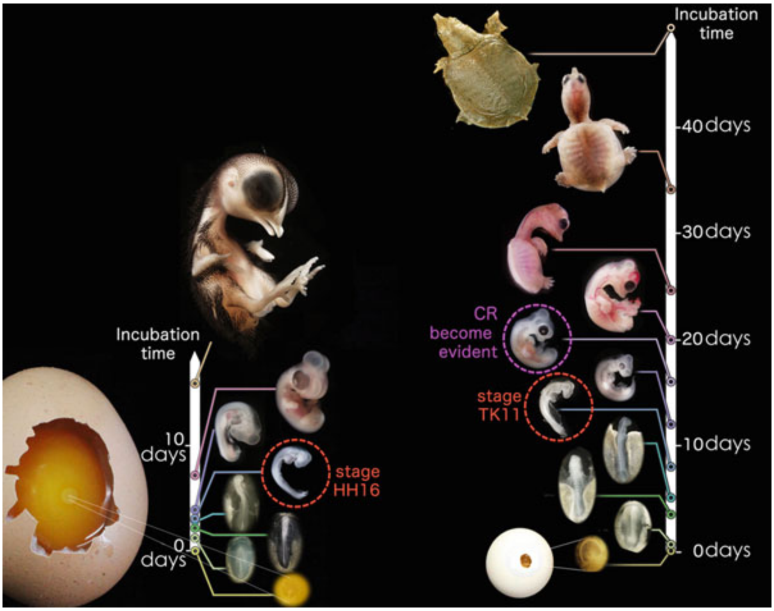

Fig. 23.4 External appearances of chicken and Chinese soft-shelled turtle embryos. Soft-shelled turtle embryogenesis shows a rather different morphology of the gastrula but soon converges to show similar morphology with the chicken at around the pharyngula stage. Actually, chicken stage HH 16 (Hamburger and Hamilton 1951) and turtle stage TK 11 (Tokita and Kuratani 2001) show the most similar gene expression profile compared to other developmental stages (*dashed circles*). These embryos show striking similarity in morphology as well, despite the fact that these two species split more than 250 million years ago, with almost twice the time for embryogenesis. *White arrows* show the direction and relative length of time needed for embryogenesis. Size of embryos not to scale

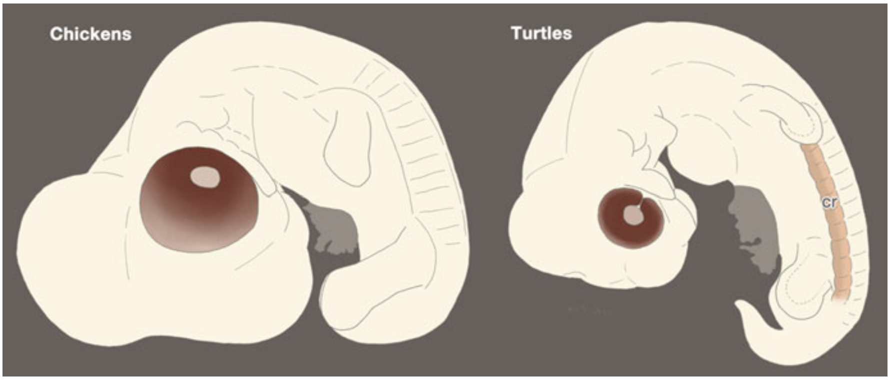

Fig. 23.5 Development of the carapacial ridge in turtle embryos. Comparison of the external morphology of embryos of stage 26 chicken and stage 14 *Pelodiscus sinensis*. In turtle embryos, the most ventral part of the axial part swells and makes a longitudinal ridge, which represents the carapacial ridge (*cr*)

23.4 Carapacial Ridge

As mentioned earlier, the CR appears after the phylotypic period as a longitudinal ridge on the lateral aspect of the flank of turtle embryos (Fig. 23.5). The CR forms the leading edge of the developing carapace, and functions to make the turtle-specific rostrocaudally expanded pattern of ribs through accelerated growth of the carapacial margin (Figs. 23.5 and 23.6) (Burke 1989, 1991; Nagashima et al. 2007).

Morphologically, the embryonic body is composed of the dorsomedially located axial part and the ventrolaterally lateral body wall. The dermal mesenchyme of the former is derived from somites and that of the latter from the somatic mesoderm. The CR develops at the ventrolateral edge of the axial domain and delineates a boundary between the two kinds of dermal mesenchyme with its ventral edge through its development, which indicates the uniqueness of the structure among amniote embryos, because such a structure does not appear in other amniote embryos (Figs. 23.5 and 23.6) (reviewed by Kuratani et al. 2011).

Although the precise molecular mechanism involved in CR development is yet to be clarified, some studies have provided intriguing insights. Through a subtractive

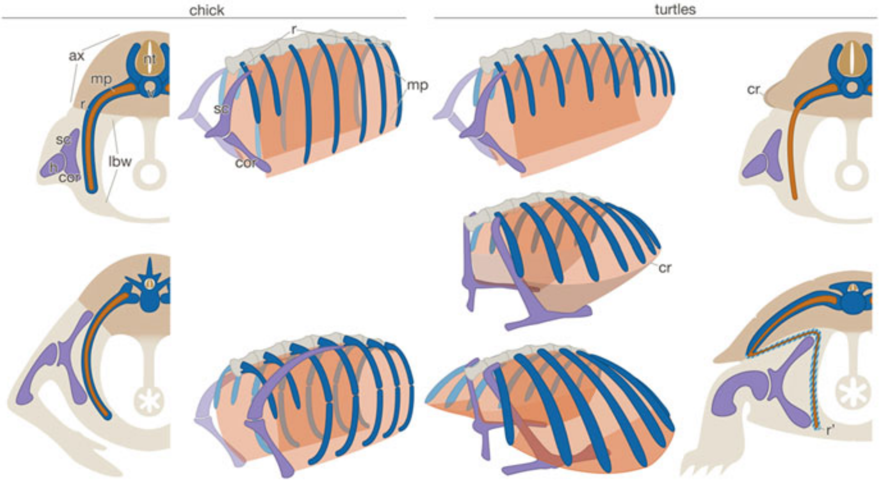

Fig. 23.6 A scheme representing trunk development in the chicken (*left*) and turtle (*right*). Plates at both *lateral ends* are transverse views; those in the *middle columns* are lateral view. From top to bottom, development proceeds as follows. *Top:* Both animals have nearly identical morphology at an early developmental stage. Note that turtle ribs (*r*) are morphologically shorter than those of chicken but grow along the the muscle plate (*mp*) as do chicken ribs. *Middle* and *bottom:* Chicken development proceeds without a major change in morphology from the initial state. The folding process occurring in the late developmental stage of turtles does not change the topological relationship between the ribs, muscle plate, and shoulder girdle from that at the beginning of development. Note that only the body folding is different between the animals. *Shaded domain* (*r′*) in transverse view of turtles (*bottom*) represents undeveloped ribs in the lateral body wall, which are expected to be found along the muscle plate as are those in chicken. *ax* axial domain, *h* humerus, *lbw* lateral body wall, *nt* neural tube, *v* vertebrae (figure modified from Nagashima et al. 2012a)

cDNA screening method, Kuraku et al. (2005) identified four genes specifically expressed in the CR, which include *cellular retinoic acid-binding protein* (*Crabp*)-*I*, *Sp-5*, *lymphocyte enhancer factor* (*Lef*)-*1*, and *Apcdd-1*. All these genes are components of, or are related to, the canonical Wnt signaling pathway (Kuratani et al. 2011). Actually, localization of β-catenin in nuclei of the CR epidermis (Kuraku et al. 2005) and arrest of CR formation after the inhibition of Lef-1 activity suggest that the Lef-1/β-catenin complex is involved in CR development as a transcriptional activator of the signal cascade (Nagashima et al. 2007).

Recently, based on comprehensive in situ hybridization screening that took advantages of turtle genomes, one of the upstream factors, *Wnt 5a* expression, was discovered in the CR mesenchyme (Wang et al. 2013). The reason why the subtractive cDNA method between the CR and the lateral body wall failed to detect this gene is that the gene was also expressed in the body wall. As another upstream molecule, hepatocyte growth factor (HGF) expressed at the vicinity of the CR is suggested; inactivation of HGF function leads to degradation of the CR (Kawashima-Ohya et al. 2011). Consistent with this, carcinoma studies have found regulation of the canonical Wnt pathway by HGF (Nelson and Nusse 2004). In chicken and mouse embryos, expressions of the orthologous genes are not observed at the corresponding site, reconfirming the novel nature of the CR. Many of the genes are commonly expressed in the limb bud of the amniote embryos including turtles, indicating that some of the gene cascade functioning in limb development would be secondarily recruited to invent the CR (Kuratani et al. 2011; also see Gilbert et al. 2001, 2008).

23.5 Positional Change of Ribs and Scapula

One of the differences between turtle ribs and those of other amniotes is the relative lengths of the ribs: the turtle ribs are morphologically shorter than those of other amniotes, because turtle ribs are arrested in the axial domain, never penetrating into the lateral body wall as in many other amniotes (axial arrest of the ribs; Fig. 23.6) (Burke 1989; Nagashima et al. 2007; Kuratani et al. 2011).

As the cause for the truncation of turtle ribs, a turtle-specific expression pattern of *Hox* genes and unique features of Myf5 have been proposed (Ohya et al. 2005, 2006; Nagashima et al. 2012a, b). Especially, transcriptional factor Myf5 is involved not only in myogenic activity but also in inductive activity of ribs (Nagashima et al. 2012b), which would explain both rib truncation and the characteristic meager development of muscle plates, elongated myotomes, in turtles (Nagashima et al. 2005).

At first glance, turtle ribs appear to take different trajectories from those in other amniotes because they grow laterally and superficially. The turtle ribs, however, are along the muscle plate as are chicken and mouse ribs (Fig. 23.6), reflecting that the ribs are induced by the muscle plate. Hence, it is convincing to suppose that if turtles would have long ribs, they would be found along the muscle plate in the lateral body wall, indicating that the muscle plate can be regarded as “the latent ribcage.”

The shoulder girdle of turtles initially develops rostral to the ribs and outside the muscle plate or “the latent ribcage” as that in other amniotes (Fig. 23.6). Although chicken and mouse development proceed without much modification of this pattern, in turtles, the CR renders some of the rostral ribs fanned out rostrally to cover the scapula caudodorsally (Fig. 23.6). During this process, the shoulder girdle remains outside the muscle plate, which is now severely folded inward in the lateral body wall (Fig. 23.6). Thus, turtles change the spatial relationship between the ribs and shoulder girdle by folding the lateral body wall inward after skeletal development, and this process does not alter the body plan of amniotes (Nagashima et al. 2009).

These developmental findings highlight and fill the saltatory evolutionary gap once believed to be present in turtle evolution; namely, axial arrest, fanned-out expansion of ribs, and encapsulation of the scapula would have occurred in the ancestral animals of turtles successively. Illustrating this, a previously unknown fossil, *Odontochelys*, has intermediate morphology linking turtles and the ancestral animals (Li et al. 2008). This animal did not have a complete carapace but did have the plastron. The ribs were already arrested axially but did not show a flabellate pattern, so the scapula was still situated rostral to the ribs. This pattern is reminiscent of the morphological pattern of turtle embryos before the folding process. Thus, morphogenesis of *Odontochelys* would have been completed at this developmental stage and would not have acquired developmental programs to expand the ribs and to encase the shoulder girdle. Turtle evolution would have been achieved by secondarily adding the folding process in the late developmental phase of *Odontochelys-like* ancestral animals (Nagashima et al. 2009).

23.6 Perspective

Our studies have suggested that stepwise changes of the developmental program have caused the evolution of turtles. By comparative genomics as well as analyses of gene regulations, it could become possible in the near future to ascertain the net elements that are truly relevant to the modification of the animal body plan, especially through construction of a turtle-like developmental phenocopy by means of functional assays on model animals. By understanding the creation of animals such as turtles, which apparently violate the developmental constraints specific to vertebrates, we will be able eventually to correlate the DNA sequence and evolving morphology of animals. For this reason, turtles potentially provide very intriguing and promising aspects for the study of evolutionary developmental biology.

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