

# Diverging development of akinetic skulls in cryptodire and pleurodire turtles: an ontogenetic and phylogenetic study

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## Abstract

Extant turtles (Testudines) are characterized among others by an akinetic skull, whereas early turtles (Testudinata) still had kinetic skulls. By considering both ontogenetic and evolutionary adaptations, we analyze four character complexes related to the akinetic skull of turtles: (1) snout stiffening, (2) reduction of the basiptyergoid process, (3) formation of a secondary lateral braincase wall, and (4) the fusion of the palatoquadrate cartilage to the braincase. Through ontogeny, both major clades of modern turtles, Pleurodira and Cryptodira, show strikingly different modes how the akinetic constructions in the orbitotemporal and quadrate regions are developed. Whereas mainly the ascending process of the palatoquadrate (later ossified as epiptyergoid) contributes to the formation of the secondary braincase wall in Cryptodira, only the descending process of the parietal forms that wall in Pleurodira. This is related to the fact that the latter taxon does not develop an extended ascending process that could ossify as the epiptyergoid. Whereas the palatoquadrate directly fuses to the braincase in pleurodires by forming appositional bone of the quadrate (called Eßwein-fixation herein), both structures are ventrally bridged by the ptyergoid in cryptodires. Phylogenetic evidence, including fossil data, suggests that the cryptodiran type of skull fixation is plesiomorphic for crown turtles and that the pleurodire condition evolved secondarily within the crown. Embryonic neck muscle activity may be the cause of this shift of the palatoquadrate. Hidden-necked retraction in cryptodires pulls the palatoquadrate in a posterodorsal and -medial direction during ontogeny, whereas side-necked retraction in pleurodires redirects the palatoquadrate posterolaterally and -medially. These different muscle forces may result in differing positions of the palatoquadrate in relation to the braincase and eventually result in the two different attachment types. Moreover, the general construction of the jaw adductor chamber is affected by alternative fusion modes, which secondarily result in two different types of the trochlear system of the external jaw musculature. Related to that, changes in feeding habit through turtle evolution may have also triggered increasing stabilization of the skull. Palatoquadrate fixation, finally, was an important prerequisite for the reduction of the exocranial bones of the temporal skull region.

## Kurzfassung

Rezente Schildkröten (Testudines) sind neben vielen anderen Merkmalen durch einen akinetischen Schädel charakterisiert. Mehrere Stammgruppenvertreter (Testudinata) besitzen noch den plesiomorph kinetischen Schädel. An vier Merkmalskomplexen zeigen wir auf, wie sich der akinetische Schädel während der Ontogenie und der Evolution bei Schildkröten ausbildet. Wir analysieren (1) die Versteifung der Schnauze, (2) die Reduktion des Basiptyergoid-Fortsatzes, (3) die Bildung der sekundären lateralen Schädelseitenwand und (4) die Fusion des Palatoquadrat-Knorpels mit dem Hirnschädel. Beide Großgruppen der modernen Schildkröten, Pleurodira und Cryptodira, zeigen gravierend unterschiedliche Modalitäten in der ontogenetischen Ausbildung der akinetischen Konstruktionen ihrer Orbitotemporal- und Quadratumregionen. Während vor allem der Processus ascendens des Palatoquadratum, der später zum Epiptyergoid ossifiziert, zur Bildung der sekundären Schädelseitenwand der Cryptodiren beiträgt, wird diese bei Pleurodiren allein durch die absteigende Lamelle des Parietale gebildet. Damit steht im Zusammenhang, daß der Proc. ascendens bei letzteren nicht vorhanden ist. Während das Palatoquadratum bei den Pleurodiren direkt mit dem Hirnschädel durch die Bildung von Zuwachsknochen fusioniert (hier Eßwein-Fixierung genannt), werden beide Strukturen bei den Cryptodiren durch den Pterygoid-Knochen ventral abgestützt. Phylogenetische Hinweise, den Fossilbericht inbegriffen, legen nahe, daß die cryptodire Form der Schädelfixierung für die Kronengruppe der Schildkröten plesiomorph ist und die Bildung der pleurodiren Konstruktion sekundär evolviert ist. Die genannten Merkmale werden im Kontext der Muskelanatomie diskutiert. Embryonale Halsmuskulatur könnte für die beobachteten Verschiebungen des Palatoquadratum verantwortlich sein. Während der

Ontogenese zieht die vertikale Halsretraktion bei Cryptodiren das Palatoquadratum in eine posterodorsale und -mediale Richtung. Die Seitenretraktion bei Pleurodiren verlagert das Palatoquadratum in eine posterolaterale und -mediale Richtung. Diese Mechanismen könnten in unterschiedlichen Positionen des Palatoquadratus in Relation zum Hirnschädel resultieren und schließlich zu den unterschiedlichen Anlagerungen, die hier dokumentiert sind, führen. Zudem ist der generelle Aufbau der Kieferadduktorenkammer durch die differierenden Fusionierungsmodi beeinflusst, was sekundär mit zwei unterschiedlichen Arten des Trochlearsystems der äußeren Kiefermuskulatur einhergeht. Im Zusammenhang damit könnte auch ein verändertes Freßverhalten im Laufe der Schildkröten evolution die zunehmende Stabilisierung des Schädels beeinflusst haben. Die Fixierung des Palatoquadratus ist nicht zuletzt auch eine wichtige Voraussetzung für die Reduktion der exoskeletalen Knochen in der Schläfenregion des Schädels.

## Key words

Appositional bone; basiptyergoid articulation; Cryptodira; Eßwein-fixation; heterochrony; ontogeny; ossification; palatoquadrate; paleontology; Pleurodira; *Proganochelys*; secondary lateral braincase wall; secondary palate; stem-Testudines; Testudinata; Zuwachsknochen.

## Evolution of cranial kinesis

Intracranial mobility (Fig. 1) is a widespread phenomenon among vertebrates and helps manipulating food items. In early crossopterygians, splanchnokinesis, a kind of neurokinesis, was present. Early labyrinthodonts and possibly early reptilian clades show metakinesis (Fig. 1, blue arrowhead), in which the whole dermatocranium could move in relation to the endocranial braincase (IORDANSKY, 1990). Among amphibians, different types of rhinal mobility (ryncho- or prokinesis) are found (IORDANSKY, 2000) in which the ethmoid complex articulates with the palate (Fig. 1, green arrowhead). Also in amphibians, so-called pleurokinesis takes place between the palatoquadrate associated elements and the skull roof (Fig. 1, brown arrowhead). Within amphibians, cranial mobility is largely reduced during ontogeny (IORDANSKY, 1988; IORDANSKY, 2000, 2001), but may be retained as neotenic feature (IORDANSKY, 2001; NACHEV *et al.*, 2016). A combination of pleuro- and metakinesis (as pleurometakinesis) is found in early reptilian lineages and early archosaurs. A quadri-crank mechanism, which involves epiptyergoid mobility (Fig. 1, pink arrowhead; note, when ossified, the epiptyergoid can articulate also ventrally with the pterygoid), evolved within squamates (lizards and snakes) in order to flexibly handle fast arthropod prey (FRAZETTA, 1962; IORDANSKY, 1990; EVANS, 2008; WERNEBURG, 2019). For that, also a prominent mesokinetic articulation between parietal and frontal developed (Fig. 1, red arrowhead; together with metakinesis known as amphikinesis). Birds secondarily evolved a highly flexible prokinetic hinge (BOCK, 1964; ZUSI, 1984).

In fish-like vertebrates, a basipalatal articulation is formed, in which the visceral palatoquadrate, the dorsal part of the first pharyngeal arch (DE BEER, 1937), articulates with the basipalatal process of the basicranium (Fig. 1, orange arrowhead). This process is formed by the embryonic trabecles and is called basitrabecular process in the embryonic chondrocranium (YARYHIN & WERNEBURG, 2018). Only later in development does it become part of the ossified basisphenoid as the basipalatal process (MAIER & WERNEBURG, in prep.). In most sauropsids, the pterygoid bone secondarily braces the basipalatal process and the palatoquadrate, thus forming the so-called basi-

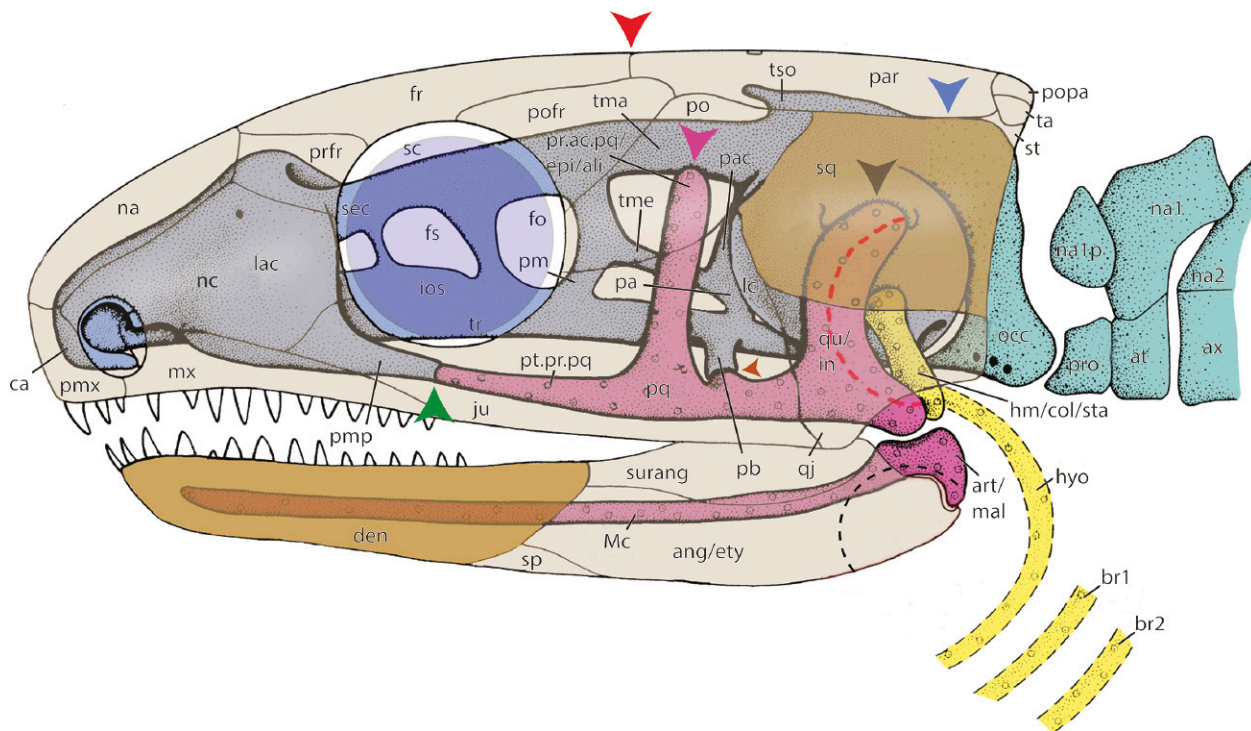
ptyergoid articulation. In this regard and for consistency with the existing turtle literature, we use the term basiptyergoid process and basiptyergoid articulation herein.

Compared to most other living tetrapods (BOCK, 1964; IORDANSKY, 1988, 2011; NACHEV *et al.*, 2016), mammals, crocodiles, and turtles have akinetic skulls with only the lower jaw articulating with the skull (IORDANSKY, 1964; BARGHUSEN, 1968; IORDANSKY, 1973; SCHUMACHER, 1973; WERNEBURG, 2011). These groups evolved strong interdigitating sutures between bones, i.e., in the rhino-, meso-, and metakinetic articulations. In mammals, the mobility of the quadrate, which is transformed into the incus, is partly preserved and serves for sound transmission; Maier (2017; Abb. 15-1) called this special case audiotyly. However, also more comprehensive morphological changes evolved, including the formation of robust snouts and secondary palates, secondary lateral braincase walls, and immobilized quadrates in order to stiffen the skulls (IORDANSKY, 1964; BARGE, 1967; IORDANSKY, 1973; SCHUMACHER, 1973; MAIER, 1989; ABRAMYAN *et al.*, 2014). The morphological details for the construction of these features are rather different among taxa. We will briefly summarize the conditions in mammals and crocodiles in the beginning and will analyze turtle morphology throughout the paper; we will only briefly discuss the snout- and palatal region but focus on the latter two modifications.

## Snout stiffening and secondary palate formation

Kinetic taxa have a primary palate built of bar-shaped elements, including pterygoids and palatines, among others (LAKJER, 1927; LAUTENSCHLAGER *et al.*, 2016). They are partly separated by vacuities making mobility possible. In akinetic taxa, however, the formation of a *secondary palate* and the closure of the vacuities resulted in the stiffening of the snout region.

Plesiomorphically, the internal nose opening (primary choana) connects the nasal (respiratory chamber) and mouth cavity directly. With that, breathing and feeding cannot occur at the same time. In mammals, it has been illustrated that suckling behavior in early newborns results in a strong force by the tongue pressing against the palate. Consequently, through evolution and in early



**Fig. 1.** Generalized skull of an early amniote at a hypothetical late embryonic stage illustrating the principal components of the cranium and the position of the intracranial joints (modified, mirrored, and expanded after MAIER (1993) and MAIER AND WERNEBURG (2014). Dermatocranium is light and dark brown, neurocranium is dark blue (ossifies in parts as endocranial neurocranium), 2nd to 4th pharyngeal arches (= 1st to 3rd branchial arches) are yellow. The first visceral arch, in purple, is composed of the ventral mandibular (Meckel's) cartilage and the dorsal palatoquadrate. The palatoquadrate is composed of a pars quadrata and a processus pterygoideus. The prospective position of the tympanic membrane in mammals is indicated by a black dashed line. The position of the tympanic membrane in sauropsids is indicated by a red dashed line (non-homologous to the membrane in mammals). Dorsal to the processus pterygoideus of the palatoquadrate, the ascending process is formed; it later ossifies as epipterygoid/alisphenoid. Medially, the palatoquadrate articulates with the basicranium at processus basitrabecularis, which is formed by the posterior section of the trabecle in embryogenesis. Intracranial joints are indicated by arrowheads: mesokinetik (red: fo/par), metakinetik (blue: skull roof/neurocranium), basipalatal (orange: pb/pq), ryncho- or prokinetik (green: ethmoid/palate), pleurokinetik (black: qu/neurocranium) articulations and articulation between epipterygoid (= ossified processus ascendens palatoquadrati) and the skull roof (pink). Articulation of quadrata and articular form the primary jaw joint. In mammals, the secondary jaw joint is formed between dentary and squamosal (both dermal bones are highlighted by darker rown) – quadrata (incus), hyomandibula (columella/stapes), and articular (malleus) become part of the middle ear in mammals.

ontogeny, medial outgrowths of the maxillary and palatine meet at the midline of the skull (MAIER, 1993; 2017; MAIER *et al.*, 1996, WERNEBURG & SPIEKMAN, 2018). They include the vomer(s) and, as hard secondary palate, they separate the mouth cavity from the nasal cavity. Thereby, the palatopharyngeal passage is formed. With that, the secondary choanal openings are displaced posteriorly; the primary choanae are retained as nasopalatine ducts (ducts of Steno). As such, in newborns and in adults, breathing and feeding (suckling, chewing) can occur in parallel at the same time; during swallowing, the air passage is interrupted. In addition to the hard palate, a muscular soft palate (velum) is formed posteriorly.

In crocodiles, a very similar formation of a hard secondary palate takes place. In this group, however, hard biting forces are considered as major reason for developing a secondary hard palate (PREUSCHOFT & WITZEL, 2002; ERICKSON *et al.*, 2003; PREUSCHOFT & WITZEL, 2005; WITZMANN & WERNEBURG, 2017). The pterygoids travel far posteriorly and serve as insertion sites for the exten-

sive pterygoid musculature (POGLAYEN-NEUWALL, 1953a; IORDANSKY, 1964; SCHUMACHER, 1973; HOLLIDAY & WITMER, 2007), a mechanism convergently developed in extinct temnospondyls with akinetic skulls (WITZMANN & WERNEBURG, 2017).

With the formation of secondary palates and the formation of a stiff snout, interpterygoid vacuities on both sides are closed and the basipterygoid articulations are obliterated.

## Secondary lateral braincase wall

The primary lateral braincase wall, covering the brain laterally, is formed by the primordial, embryonic skull, the chondrocranium, and consists of different pillars (pilae) and bridges (taeniae) of cartilaginous tissue and membranes (KUHN, 1971). During embryonic development, the palatoquadrate cartilage forms as the dorsal part of the first visceral (pharyngeal arch) element with the

lower part being Meckel's cartilage (Fig. 1). The major, posterior part of the palatoquadrate ossifies as the quadrate. Its elongated and bar-shaped anterior part becomes the cartilaginous pterygoid process, which supports the dermatocranial bones of the palate (pterygoid bone, palatine bone). Dorsally, however, the pterygoid process forms an ascending process (Fig. 1, pink), which ossifies as the epipterygoid in sauropsids and early synapsids (DE BEER, 1937; RIEPPEL, 1994; YARYHIN, 2010; YARYHIN & WERNEBURG, 2018).

The secondary lateral braincase wall in modern mammals is mainly formed by the alisphenoid, which is homologous to the sauropsidian epipterygoid. As in sauropsids, it develops from the ascending process of the embryonic palatoquadrate as has been proven by morphological (MAIER, 1987) and molecular studies (JIANG *et al.*, 2002; GROSS & HANKEN, 2008) in developmental biology. At first, it develops as a cartilaginous ala temporalis and later ossifies endochondrally to form the proximal portion of the alisphenoid. In addition to endochondral ossification (within the cartilage), the ossification of a cartilage can appear at the surface and grows inwards. When this perichondrium hypertrophies beyond the borders of the cartilage, however, the bone outgrowth is called "Zuwachsknochen" in German (STARCK, 1955), translated as 'appositional bone' by MAIER (1993), and called membrane bone by PATTERSON (1977) [see RIEPPEL (1993) for further differentiations]. Such appositional bone forms the greater portion of the alisphenoid (HOPSON & ROUGIER, 1993). As a whole, the alisphenoid in mammals provides the lateral wall of the cavum epipterygium, a space, which encloses the trigeminal ganglion (MAIER, 1987, 1989, 2017).

In crocodiles, the lamina palatoquadrati anterior appears at and close to the anteromedial wall of the small ascending (epipterygoid) process of the palatoquadrate. It ossifies and sheathes the posterior part of the trigeminal ganglion laterally. As such, it is similar to the alisphenoid ossification of mammals although formed a bit differently. In addition, the lamina prootica anterior is formed and spreads above the trigeminal ganglion to contribute to the secondary braincase wall (KLEMBARA, 1991, 2004).

## Quadrate fixation

A third way to stiffen the skull is realized by the obliteration of the originally mobile quadrate in the jaw region. In synapsid evolution, along the mammalian stem line, the primary jaw joint between the quadrate and the articular of the lower jaw, both representing visceral elements, were displaced to the middle ear as the incus and malleus, respectively (MAIER & RUF, 2016) (still retaining audiostyly, see above). As a result, a secondary jaw joint developed between two dermal bones, the dentary and the squamosal (Fig. 1, dark brown). The squamosal sutures to the jugal anteriorly and to the braincase medially, eliminating intracranial mobility in that region.

In crocodiles, the quadrate is medially fused to the braincase and firmly fixed by a posterior extension of the pterygoid (IORDANSKY, 1973). Further developmental work is needed to fully understand quadrate fixation in crocodiles.

## Objectives and phylogenetic framework

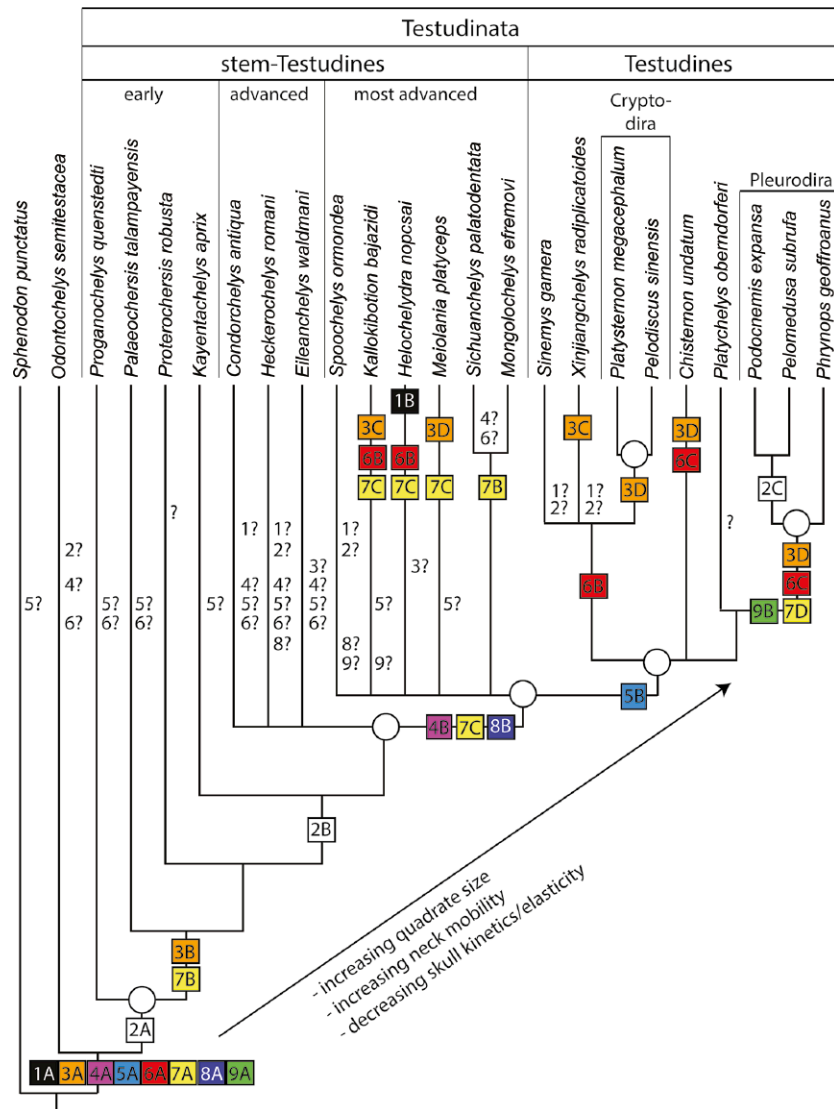
Early in turtle evolution, exemplified by the Triassic stem turtle *Proganochelys quenstedti*, a high degree of intracranial mobility was certainly present (GAFFNEY, 1990; RABI *et al.*, 2013) (Fig. 2). Fully akinetic skulls evolved in the two extant turtle clades: Pleurodira (side-necked turtles) and Cryptodira (hidden-necked turtles), which, however, show fundamental differences in their skull anatomy (GAFFNEY, 1975, 1979a) (Fig. 3). The emergence of diverging traits can only be interpreted properly on the basis of a comparative craniogenetic approach (e.g., RIEPPEL, 1976; ESSWEIN, 1992, 1993; PALUH & SHEIL, 2013; SHEIL & ZAHAREWICZ, 2014). Here we bring together available ontogenetic information and provide further details based on own observations of histological sections from several embryological collections. We then discuss the findings within the context of recent advances in the understanding of paleontological and morphofunctional patterns in chelonian evolution.

A phylogenetic consensus of early turtle evolution was recently provided by JOYCE *et al.* (2016). We present a reduced version of the consensus phylogeny in Fig. 2 in order to illustrate major evolutionary changes within early turtle evolution. Within Testudinata (true turtles with a fully formed shell *sensu* JOYCE *et al.* 2004), several fossil taxa are known. The 'early' stem-Testudines are *Pr. quenstedti* (GAFFNEY, 1990), *Palaeochersis talampayensis* (STERLI *et al.*, 2007), *Proterochersis robusta* (FRAAS, 1913), and *Kayentachelys aprix* (STERLI & JOYCE, 2007). The 'advanced' stem-Testudines (see Fig. 2) include *Condorchelys antiqua* (STERLI, 2008), *Heckerochelys romani* (SUKHANOV, 2006), and *Eileanchelys waldmani* (ANQUETIN *et al.*, 2009). The 'most advanced' stem-Testudines, close to crown turtles, include *Spoochelys ormondea* (SMITH & KAER, 2013), *Kallokibotion bajazidi* (GAFFNEY & MEYLAN, 1992), *Helochelydra nopcsai* (JOYCE *et al.*, 2011), *Meiolania platycephala* (GAFFNEY, 1983), *Sichuanichelys* spp. (YE & PI 1997), and *Mongolochelys efremovi* (KHOSATZKY, 1997). In addition to the extant forms (Pleurodira and Cryptodira) (GAFFNEY, 1975, 1979a), crown-group Testudines includes fossil taxa such as *Chisternon undatum*, *Sinemys* spp., *Platycheilus oberndorferi*, and *Xinjiangchelys* spp. (JOYCE *et al.*, 2016) (Fig. 2).

## Methods

We analyzed embryological serial sections of seven pleurodiran and nine cryptodiran species from different institutes: the collection of Zoologisches Institut der

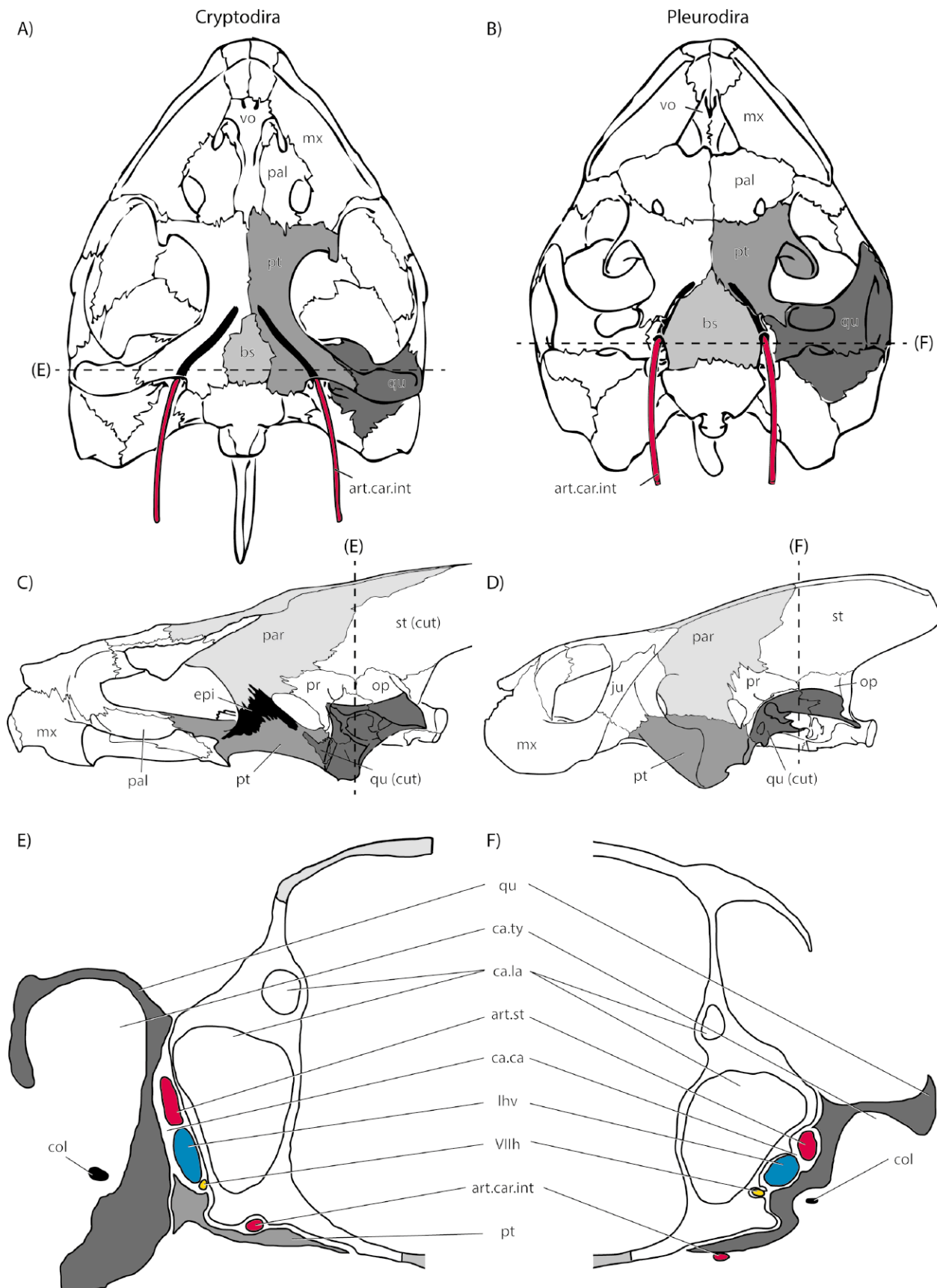




**Fig. 2.** Phylogeny of turtles (modified and simplified after Joyce et al. 2016). Stem-Testudines are separated in three informal groups: early, advanced, and most advanced stem turtles. Characters on the tree result from a character mapping as described in the text. **Character 1:** The appearance of the secondary palate. The secondary palate is formed by premaxilla, maxilla, and vomer, and the palatines are contacting in the midline (Fig. 2, character state: 1A) or palatines are not contacting in the midline (1B). **Character 2:** Vomer appearance. The vomer is paired (2A), single (2B), or is single and greatly reduced (2C). **Character 3:** Basipterygoid process. Present with moveable articulation (3A), present, facing ventrally, and sutured articulation with the pterygoid (3B), present, principally\* facing laterally, and sutured with the pterygoid (3C), or absent and sutured with pterygoid (3D). \* = the process orientation is not documented for *Spoochelys*, *Helochelydra*, and *Sichuanichelys*. **Character 4:** Ventral extension of the lateral secondary braincase wall. Contact of the parietal with pterygoid, epipterygoid, and/or palatine absent (4A) or present (4B). **Character 5:** Anterior extension of the lateral secondary braincase wall. Length of anterior extension of the lateral wall is short, the processus parietalis inferior only with narrow strut anterior to trigeminal foramen and no palatine contact (5A), anteriorly elongated, commonly with palatine contact (5B). **Character 6:** Epipterygoid. Present, rod-like (6A), present laminar (6B), absent (6C). **Character 7:** Flooring of the cranioquadrate passage. Absent (7A), by pterygoid, but pterygoid does not cover the prootic (7B), by pterygoid (7C), by quadrate and prootic (7D). **Character 8:** Processus trochlearis otici. Absent (8A), present (8B). **Character 9:** Processus trochlearis pterygoidei. Absent (9A), present (9B). – Question marks indicate that states of particular characters (e.g., “5?”) or all characters of a species (only “?”) are not known. Major discussed nodes in the tree are shown in white filled circles.

Universität Tübingen (ZIUT), the laboratory collection of Marcelo R. Sánchez-Villagra at Paläontologisches Institut und Museum der Universität Zürich, Switzerland (*Chelonia mydas*) (PIMUZ lab), Phyletisches Museum Jena (*Chelydra serpentina*) (PMJ), and the laboratory collection of Shigeru Kuratani (SK) at RIKEN Institute for Developmental Biology in Kobe, Japan (*Pelodiscus sinensis*,

*Caretta caretta*: see KURATANI, 1987, 1989, 1999 for further details). In the case of ZIUT, specimens do not have individual numbers, but the available information (specimen age, carapace length, etc.) is labelled on the section boxes and can be located there. In most cases, slice thickness was 10 µm but ranged between 7 and 60 µm depending on specimen size (see Figure legends for details).



**Fig. 3. Skull anatomy in extant turtles.** Ventral (A) and lateral (C) view of a cryptodire skull (*Chelydra serpentina*) and ventral (B) and lateral (D) view of a pleurodire skull (*Emydura* sp.). Transverse sections through the ear region of E) an adult cryptodire (*Chelydra serpentina*) and F) an adult pleurodire (*Podocnemis expansa*). Section levels indicated in A–D. Note the different positions of the internal carotid artery, the hyomandibular branch of n. facialis (VII), and the different orientation of the quadrate relative to the ear capsule. Redrawn and modified after (A,B,C,D) GAFFNEY (1979a) and (E–F) GAFFNEY (1975).

For an overview, the general anatomy of the turtle chondrocranium is briefly described for the pleurodire *Emydura subglobosa* (Fig. 4A). Chondrocranium and endocranial ossification of a hatchling of this species was already described by PALUH & SHEIL (2013) using cleared and double stained specimens. The anatomy of another hatchling (28.5 mm carapace length, ZIUT) and of sub-adult skulls was described by WERNEBURG (2011) based on histological sections, macerated skulls, and a computer tomography scan. A section-based 3d-reconstruction of a fully developed chondrocranium was provided by WERNEBURG & YARYHIN (2018). Here we present plate model reconstructions of the whole cranium of three pre-hatchlings with a carapace lengths of 8.3 mm, 16 mm, and 21 mm, which likely represent individuals of 13 to 37 days of age (WERNEBURG *et al.*, 2009). The borders of bones and cartilages were drawn for the models on Styrofoam plates with a thickness of 2 mm with the help of a camera lucida apparatus attached to a microscope, cut with a scalpel, and glued together. Using the (historical) airbrush technique, the resulting three-dimensional Styrofoam models were redrawn already back in the early 1990s (Fig. 4).

For anatomical comparisons with adult skulls, we had access to material of *Emydura subglobosa* (laboratory collection of Paläontologisches Institut der Universität Zürich, PIMUZ lab# 2009.38), *Chelonia mydas* (IW private), and a number of other turtle species as listed by WERNEBURG *et al.* (2015b).

For a phylogenetic analysis of the evolution of adult characters through turtle phylogeny, we used the above described simplified phylogeny (Fig. 2) and a reduced version of the data matrix of JOYCE *et al.* (2016). We mapped a selected number of nine (out of 244) characters relevant for our study onto the tree and traced their evolutionary history using parsimony reconstruction in MESQUITE 3.4 (MADDISON & MADDISON, 2018). Our characters (Fig. 2) include the presence and/or formation of 1) the secondary palate (character ‘Maxilla C’ of JOYCE *et al.* 2016), 2) the vomer (‘Vomer A’), 3) the basipterygoid process (‘Pterygoid B’, with specifications based on RABI *et al.* 2013), 4) the ventral extent of lateral secondary braincase wall (‘Parietal B’), 5) the anterior extent of the lateral secondary braincase wall (‘Parietal C’), 6) the epipterygoid (‘Epipterygoid A’), 7) the flooring of the cranioquadrate passage (‘Quadrate A’), 8) the processus trochlearis oticum (‘Quadrate G’), and 9) the processus trochlearis pterygoidei (‘Pterygoid E’). Character states can be found in the caption of Fig. 2.

## The embryonic turtle skull

In the late phase of embryonic development, fundamental changes appear in the craniogenesis of turtles at a time when the chondrocranium is almost fully formed and when first endochondral and dermal ossifications appear. In this developmental period, the major components of the skull, including viscerocranial, neurocranial, and

dermatocranial elements, fuse. Heterochronic and spatial changes can be observed through ontogeny, which eventually result in the different skull constructions (Fig. 3) seen in adult pleurodires and cryptodires.

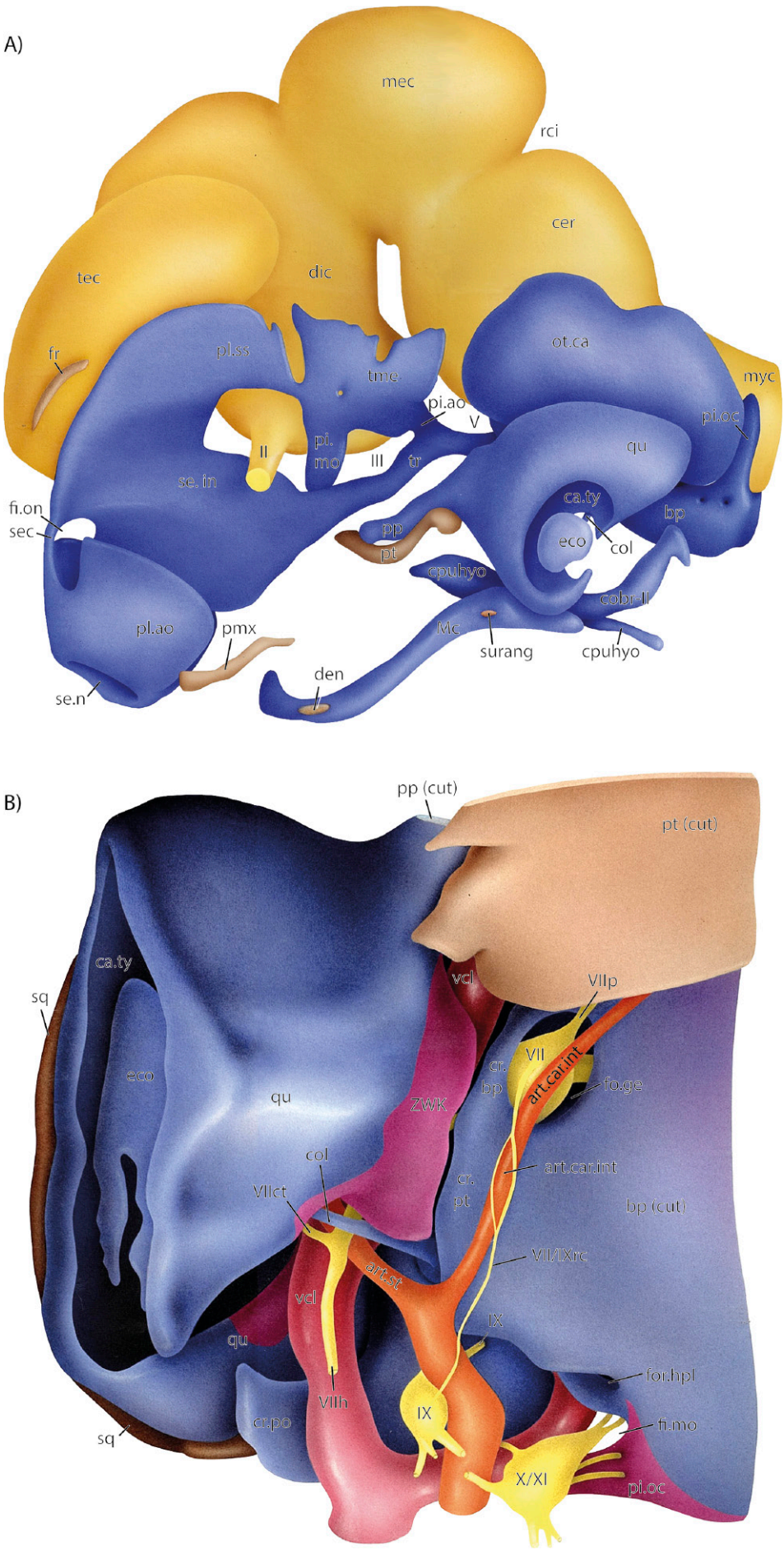
The general construction of a late turtle chondrocranium is here exemplified by the pleurodire *Emydura subglobosa* (Fig. 4A). The chondrocranium consists of an ethmoid (Fig. 5A, D), an orbitotemporal (Fig. 5B, E), an otic (Fig. 5C, F), and an occipital region. The ethmoid region is very broad and supports the broad upper jaw bones making rhinal mobility impossible (ESSWEIN, 1992). This might have served as the precondition for differentiating a ramphotheca. The orbitotemporal region of the chondrocranium is characterized by an extended interorbital septum between the eye balls anteriorly and by a largely reduced posterior part when compared to a more generalized reptilian chondrocranium (GAUPP, 1900; WERNEBURG & YARYHIN, 2018). Compared to the generalized reptilian chondrocranium, which usually consists of a number of vertical (pilae) and horizontal (taeniae) bars (BELLAIRES & KAMAL, 1981), only few structures are present in *E. subglobosa* (PALUH & SHEIL, 2013; WERNEBURG & YARYHIN, 2018). The otic region shows large otic capsules, which are medially fused with the braincase. A broad tectum synoticum can be distinguished dorsomedial to the otic capsules. In early ontogeny, cranial ribs can be found in the occipital region as mesenchymal condensations. They represent recapitulations of ribs belonging to the vertebral anlagen, which are fused to the skull (WERNEBURG *et al.*, 2013).

Stabilization of the skull towards an akinetic skull in turtles involves a number of anatomical structures. Mesokinetic movement along the frontal and parietal (NATCHEV *et al.*, 2016), for example, is prevented by interdigitating sutures. Metakinetic movement along the parietal and braincase bones such as the supraoccipital is prevented by strong suturing. In the following, we describe and discuss comprehensive anatomical transformations in turtle development and evolution. Those include snout stiffening and, most importantly, the reduction of the basipterygoid process, the formation of a secondary lateral braincase wall, and the quadrate fixation to the braincase. Extant turtle conditions remarkably differ from the plesiomorphic amniote anatomy, in which “the palatoquadrate is articulated to the braincase solely by means of the basipterygoid articulation, and the skull is usually considered to be kinetic” (GAFFNEY, 1975): 395). The comparison with stem-Testudines (Fig. 6–7) reveals the stepwise, often independent acquisition of the fully akinetic skull seen in crown turtles. The embryological and paleontological observations will finally be discussed in a biomechanical manner by considering neck and jaw muscle activity.

## Snout stiffening in turtles

**Ontogeny.** Extant turtles are typically characterized by robust upper jaws and snouts. The medial processes of the palatal bones contact in the midline and form a





primarily short secondary palate. The nasal capsule is large (Fig. 4A, 5A,D) compared to kinetic forms such as the lacertid squamates (GAUPP, 1900; YARYIN & WERNBURG, 2018) and broadly fuses to the upper jaw bones (Fig. 5A,D). Ventrally, the floor of the nasal capsule (solum nasi) is broad (FUCHS, 1907; LEUNG, 2011) and covered by a ramphotheca. It has been shown that nasal capsule and snout bone formation largely correspond to each other in amniote development (KAUCKA *et al.*, 2018), which supports our observation. No crucial differences could be detected between pleurodires and cryptodires, although it is hyperinflated in terrestrial taxa (PAULINA-CARABAJAL *et al.*, 2017; LAUTENSCHLAGER *et al.*, 2018).

**Evolution.** Already in early turtle evolution (Fig. 6-7), a partial stiffening of the skull can be recognized as the jaws and snouts of stem-turtles have a relatively similar robust appearance when compared to extant turtles.

Short secondary palates are present in all turtles (Fig. 2, character 1), although the extent is rather diverse among fossil and extant species (GÖPPERT, 1903; BARGE, 1967), which appears to be partly related to the hardness of food (FOTH *et al.*, 2017; HERMANSON *et al.*, 2018). Early stem-turtles had a relatively short secondary palate (Fig. 6A, 7B) and large interpterygoid vacuities were still present (Fig. 6A–C). Detailed observations on the diversity of the secondary palate among Testudinata are still missing. Noteworthy, however, is the modification of the vomer through turtle evolution (Fig. 2, character 2). Vomers are paired in *Proganochelys quenstedti* (GAFFNEY, 1990) and *Palaeochersis talampayensis* (STERLI *et al.*, 2007) (Fig. 6A–B), the earliest lineages in testudinate evolution (Fig. 2, character 2A). All other testudines have only a single fused vomer (Fig. 2, character 2B) (Fig. 6C,I–L). The vomer takes part in the formation of the secondary palate and a fused vomer largely reduces contralateral mobility of the upper jaws. The minute unpaired vomer is greatly reduced in pelomedusoids and trionychians (Fig. 2, character 2C), which might illustrate a greater robustness and extension of the palatines, possibly further increasing stability.

### Reduction of the basiptyergoid process in turtles

Adult extant turtles, pleurodires and cryptodires alike, do not have well-developed basiptyergoid processes (GAFFNEY, 1979a, RABI *et al.*, 2013) and the basisphenoid

shows interdigitating sutures with the pterygoids clearly preventing basiptyergoid articulation (Fig. 3A–B, 8–10) (STERLI & DE LA FUENTE, 2010).

**Ontogeny.** In our embryonic specimens, we never found a bar-shaped basitrabecular process (Fig. 8–12). Embryonic remnants of a process were described for a few cryptodire specimens only (KUNKEL, 1911; NICK, 1912; FUCHS, 1915). FUCHS (1915) speculated that the bar-shaped basitrabecular process could have shifted posteriorly in cryptodires and was modified to the elongated crista basiptyergoidea (Fig. 8) at the lateral margin of the embryonic basicranium (Fig. 5C, 8). The crista basiptyergoidea forms the anterior brace between the basicranium and the pterygoid in cryptodires (see below). Different spatial orientations of the basiptyergoid process were documented for a number of fossil turtles resulting in various homology discussions in the literature (GAFFNEY, 1979b; STERLI *et al.*, 2010; BRINKMAN *et al.*, 2013; RABI *et al.*, 2013). If the basiptyergoid process and crista basiptyergoidea are actually homologous, not only a spatial but also a functional shift, from mobility to fixation, must have occurred in the course of turtle evolution.

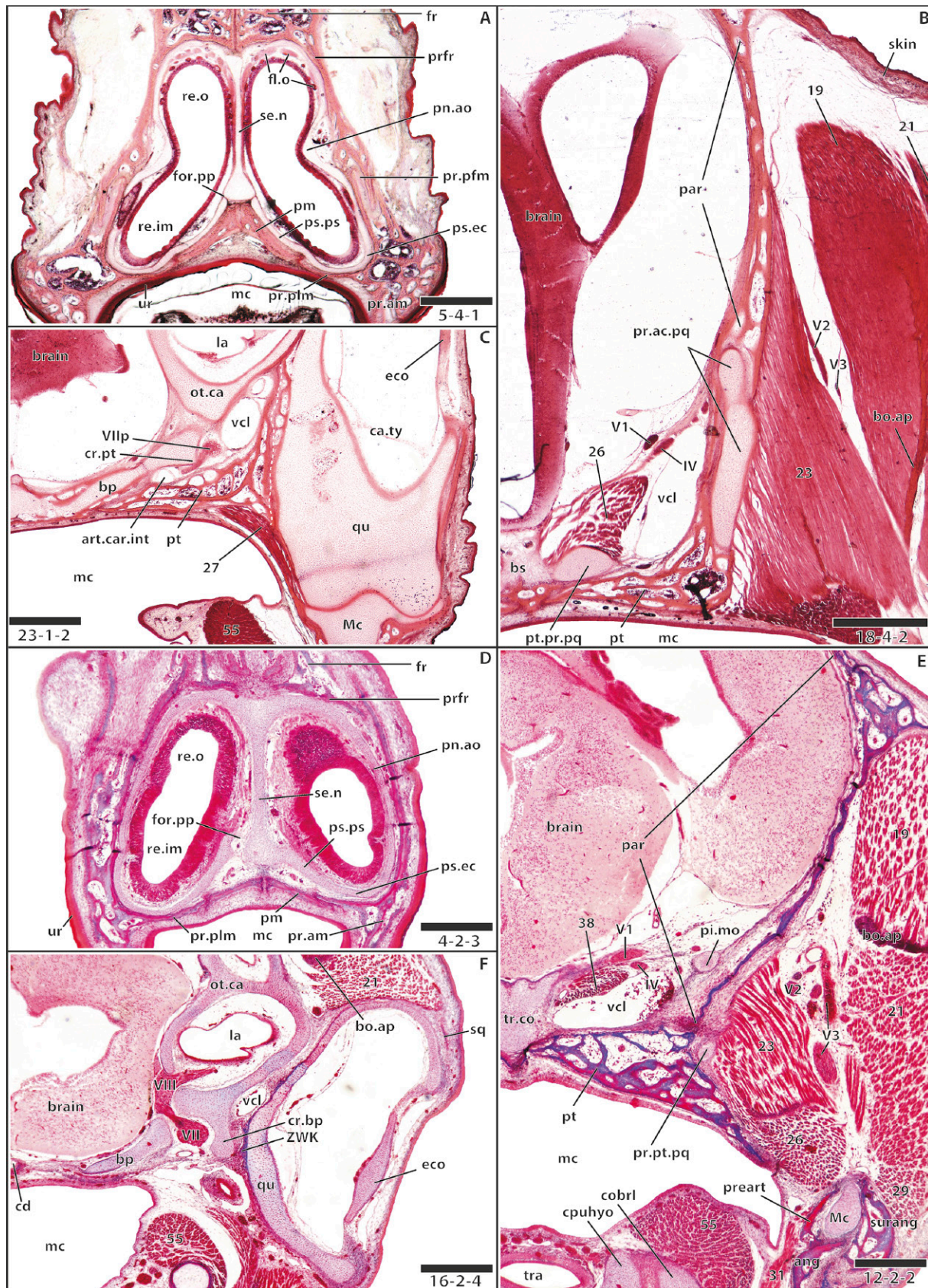
In addition to the crista basiptyergoidea, a crista pterygoidea is formed more posteriorly in cryptodires to connect the braincase with the pterygoid posteriorly (Fig. 5C, 12B). FUCHS (1915) found it separated from the anterior crista basiptyergoidea by the abducens nerve (VI) in *Eretmochelys imbricata*. We never found a clear separation into two distinct cristae and the foramen for the abducens nerve was always piercing the crest (Fig. 9A).

Among pleurodires, a remnant of a basitrabecular process was only described for an embryo of *Podocnemis expansa* (GAUPP, 1910). Early in development, a crista basiptyergoidea is formed lateral to the basal plate (Fig. 9A), comparable to cryptodires. Later in development, this crest appears to partly or fully attach ventrally to the otic capsule. In that way, the crest forms a lateral border of the genicular foramen (n. VII) as a genicular crest. Already GAUPP (1910) stated that the basitrabecular process is posteriorly ‘attached’ to the basal plate. Here, at the level of the basicranial fenestra, it borders the foramen genicularis laterally. The crest continues posteriorly as a substapedial crest (Fig. 4B), which appears to be homologous to the posterior crista pterygoidea in cryptodires.

Importantly, the crista genicularis is laterally connected to the palatoquadrate to make an akinetic connection (see below). As described for cryptodires above, the

← **Fig. 4. Three-dimensional reconstructions of chondrocrania of the pleurodire turtle *Emydura subglobosa*.** **A)** Plate reconstruction of the primordial cranium of an embryo with a carapace length of 8.3 mm (ZIUT) in right lateral view (mirrored). Different to Figure 1, the visceral elements – like the chondrocranium – are shown in blue. Developing dermal bones are brown, brain is yellow. **B)** Plate reconstruction of the right palatoquadrate, the otic, and the occipital region of an embryo with a carapace length of 21 mm (ZIUT) in ventral view (anterior is top, proc. pterygoideus palatoquadrati and the pterygoid are cut). The palatoquadrate is fixed to cartilaginous crest(s), lateral to ganglion geniculi (n. VII), via appositional bone. The cartilage is blue, ossifications are purple, blood vessels are red, nerve structures are yellow, bone is brown. Slice thickness of the underlying sections in A and B were 10 µm. Not to scale. The airbrush figures were drawn by Margret Roser; the underlying Styrofoam 3D-reconstructions were made by Stefan Eßwein.





modified processus basitrabecularis indicates a change of function. However, the mode(s) of processus basitrabecularis development require(s) further investigations with better-resolved embryonic series.

Kinetic taxa like *Lacerta agilis* have a well-developed meniscus between basitrabecular process and pterygoid (GAUPP, 1900) (Fig. 12A), which develops from the posterior tip of the trabecle (i.e., basitrabecular process

(YARYHIN & KLEMBARA, 2015; YARYHIN & WERNEBURG, 2018)) and facilitates kinesis between palatoquadrate and basicranium. Consistent with their akinetic skull, we never observed a meniscus in any turtle, although FUCHS (1915) reported one in an cryptodiran embryo (*Emys orbicularis*). In the same species, he also detected embryonic remnants of a levator pterygoideus muscle. Atavistic recapitulation supports the idea that extant turtles, at some point of their shared evolution, had kinetic ancestors. Adult *E. orbicularis* specimens, however, do not have a basipterygoid articulation nor a levator pterygoideus muscle preserved and have fully akinetic skulls (SCHUMACHER, 1954, 1954/55; WERNEBURG, 2011, 2013b).

**Evolution.** There has been some discussion on the evolution of the basipterygoid articulation in turtles (STERLI & DE LA FUENTE, 2010; RABI *et al.*, 2013). *Eorhynchochelys sinensis* (LI *et al.*, 2018), *Odontochelys semitestacea* (LI *et al.*, 2008), and *Proganochelys quenstedti* (GAFFNEY, 1990) (Fig. 6A), as earliest uncontested representatives of the turtle stem, have a characteristic joint between the basipterygoid process of the basisphenoid and the pterygoid (Fig. 2, character 3A). Further crownwards, the condition of this basipterygoid articulation is modified. Except for few meiolaniforms (e.g., *Meiolania platyceps* in our sample: Fig. 6I) (GAFFNEY, 1983), the basitrabecular process is always present in stem-Testudines, but is described as being sutured (RABI *et al.*, 2013) (Fig. 6). In most stem-turtles such as *Kayentachelys aprix* (Fig. 6C) (STERLI & JOYCE, 2007) and *Condorchelys antiqua* (Fig. 6D) (STERLI, 2008), the process points to a ventral direction (Fig. 2, character 3B). The closer turtles are related to the crown, the process tends to face laterally (Fig. 2, character 3C) and to become smaller and crest-like (M. Rabi, pers. communication). Except for very few stem-turtles (Fig. 6I), the basipterygoid process is fully reduced only in most crown turtles (Testudines) (Fig. 2, character 3D; Fig. 3A,B).

The common presence of the basipterygoid process in the turtle stem suggests that some basipterygoid movement was still possible. The described fusion between pterygoid and basipterygoid process in fact only means that no articular facets were present. However, in no stem turtle with basipterygoid process is an interdigitating

suture present between the bones (M. Rabi, pers. communication) indicating that movement was still possible to some degree (*sensu* JONES *et al.*, 2011). Obviously, however, this potential mobility was much reduced compared to the earliest turtles mentioned above. Late meiolaniforms such as *Meiolania platyceps* (Fig. 6I, 7F) lived contemporary with crown pleurodires and crown cryptodires (GAFFNEY, 1983, 1992, 1996; DE LA FUENTE *et al.*, 2014; STERLI, 2015). All three clades show interdigitating sutures between basisphenoid and pterygoid and a complete loss of the basipterygoid process. One could imagine that contemporary environment conditions could have had influence on skull stabilization. This becomes even more obvious when observing other convergent cranial adaptation of *M. platyceps* when compared to crown turtles (GAFFNEY, 1996). Feeding behavior may be ruled out as *M. platyceps* was herbivorous and the majority of Testudines is not.

## Secondary lateral braincase walls in turtles

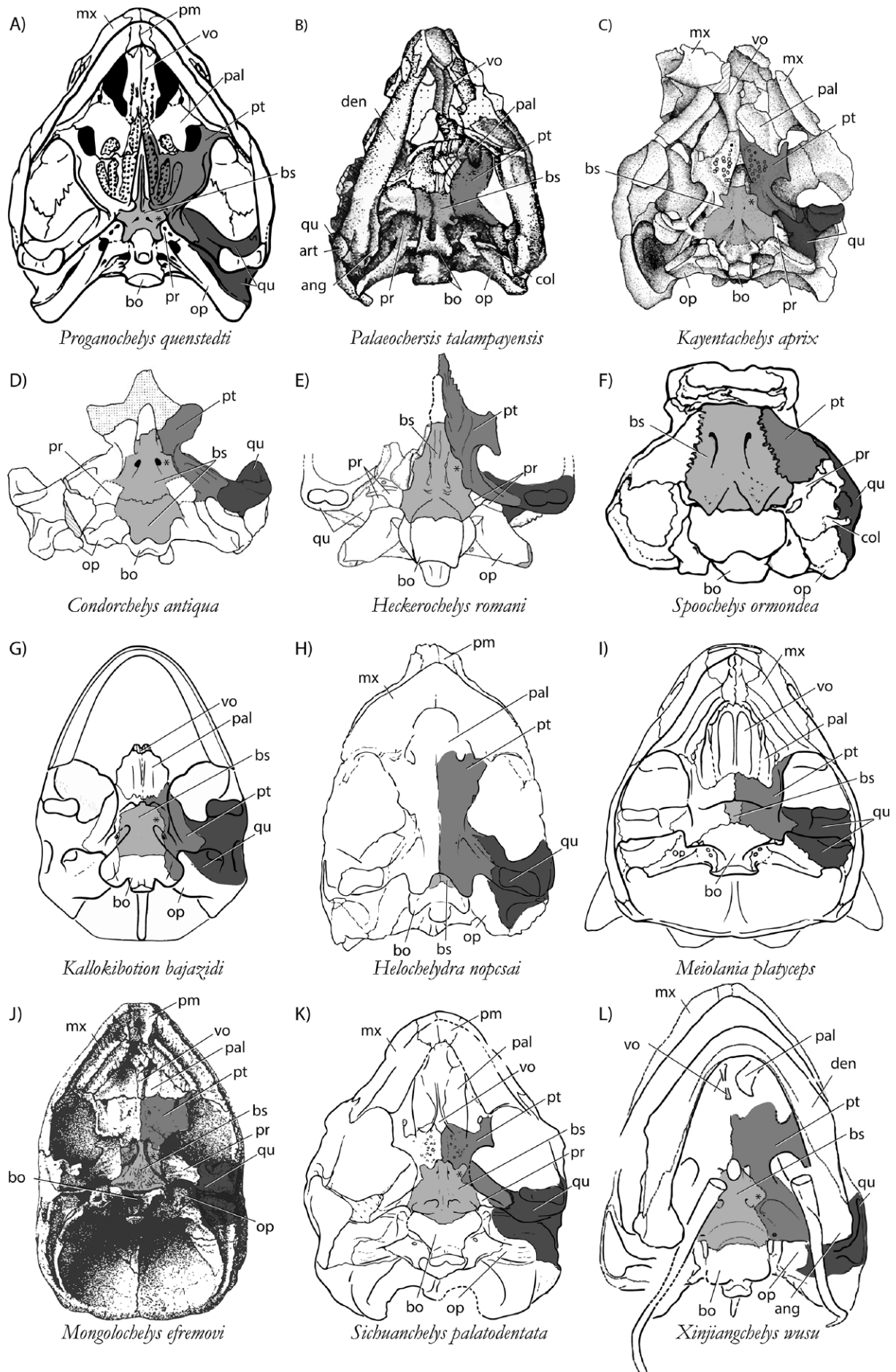
A secondary braincase wall laterally closes the cavum epiptericum in extant turtles (Fig. 3C–D). It is mainly formed by the vertical process of the parietal (processus inferior parietalis) (Fig. 5B,E, 11–12). Similar to the akinetic skull of mammals, cryptodire turtles possess an epipterygoid (Fig. 3C), which is firmly integrated within the bone mosaic of their secondary lateral braincase wall. In some cryptodire species (e.g., in trionychids, kinosternoids), also a direct contact between parietal and palatine is formed anterior to the epipterygoid and the palatine actually forms a large contribution to the secondary braincase wall.

All pleurodires lack an epipterygoid and the secondary lateral braincase wall is only formed by the direct contact of the pterygoid and the ventrally expanded parietal (Fig. 3D) (GAFFNEY, 1975, 1979a).

**Ontogeny.** In Cryptodira, visceral material, namely the processus ascendens of the palatoquadrate (together with its root in the processus pterygoideus palatoquadrati), is positioned between the dorsal surface of the pterygoid and the ventral edge of processus inferior parietalis

← **Fig. 5. Histological overview on the late embryonic skulls of a cryptodire and a pleurodire species.** A–C) Histological cross sections through the embryonic head of the cryptodire *Chelydra serpentina* (PMJ Rept. 1213, CRL=23 mm, hematoxylin & eosin staining, 30 µm slide thickness). A) Nose region in which the nasal capsule broadly aligns to the snout bones, B) lateral closure of cavum epiptericum by the descending process of the parietal and the ascendant process of the palatoquadrate [white dashed line indicates the border between pterygoid and the appositional bone (Zuwachsknochen, ZWK) of the quadrate], and C) fusion of the palatoquadrate to the braincase bridged by the pterygoid and appositional bone of the quadrate. Note that, different to pleurodires, the quadrate forms only little perichondral ossification that fuses with the pterygoid. A dashed line indicates the suture. D–F) Histological cross sections through the embryonic head of the pleurodire *Emydura sublobosa* (CL=19 mm, 37d, Azan staining after Heidenhain, 12 µm slide thickness, ZIUT). D) Nose region, comparable to cryptodires. E) Formation of the secondary lateral braincase wall. No visceral material is incorporated in the wall and the pterygoid process of the palatoquadrate lays lateral to the wall. Mirrored. F) Palatoquadrate fusion at the level of foramen genicularis. Ventrolateral to the otic capsule, the crista basipterygoidea is formed as a genicular crest. The quadrate forms appositional bone (ZWK) that will further grow and attach to the crista laterally. Bar scales equal 0.5 mm in A–C, 0.2 mm in D–E, and 0.1 mm in F. Numbers below bar scales refer to slide numbers.





(Fig. 5B). It ossifies as the epipterygoid (Fig. 10D–F) and builds about the lower third of the lateral braincase wall (Fig. 5B, 11D–F). The integration of the processus ascendens palatoquadrati as the epipterygoid into the sidewall in cryptodires was discussed repeatedly (NICK, 1912; FUCHS, 1915; RIEPPEL, 1976; ESSWEIN, 1992; SHEIL & ZAHAREWICZ, 2014).

Some variation in the formation of the secondary lateral braincase wall exists. In the marine turtle *Caretta caretta*, the processus ascendens is posteriorly supported by a dorsal outgrowth of the pterygoid (Fig. 10I–J). In the trionychid turtle *Pelodiscus sinensis*, an anterior outgrowth of the otic capsule also contributes to the formation of the secondary side wall (Fig. 10B): this possibly serves for further stabilization of the side wall during biting (DALRYMPLE, 1975; HERREL *et al.*, 2002) [side note: this unusual ‘deformation’ of the otic capsule results in the posteroventral expansion of processus inferior parietalis, which contributes to the formation of the trochlear process; compare to Joyce *et al.* (2016): their character “Parietal F”]. Unusual for cryptodires, the tortoise *Testudo hermanni*, shows a hypertrophied processus pterygoideus palatoquadrati and no ascending process is formed (see also BENDER, 1912). The massive pterygoid process, however, bridges the pterygoid bone and the processus inferior of the parietal (Fig. 10C). The marine turtle *Dermochelys coriacea*, also shows a reduction of the ascending process, but a small protuberance is left (“Epipterygoidhöcker”, NICK, 1912: fig. Q).

In general, the processus ascendens palatoquadrati does not develop appositional bone as in mammals. In most species, the cartilaginous process is bridging the pterygoid and the parietal before it ossifies. Only in *P. sinensis*, in which the sidewall closure appears relatively late, small bony outgrowths of the ascending process have started to form (Fig. 10B). Hence, formation of appositional bone might be related to developmental timing. In addition, the anterior process of the otic capsule contributing to the side wall formation, as mentioned above, also shows little outgrowth of perichondral ossification in the same, near hatching specimen (Fig. 10D).

In Pleurodira, the processus inferior parietalis grows far ventrally (Fig. 3B, 5E, 11A–E) and directly contacts the dorsal face of the pterygoid (Fig. 11F–I): no visceral material is incorporated. Gaffney (1975:400) suggested that the reduction of an epipterygoid in pleurodires “may be the result of the absence or extreme reduction of the cartilaginous precursor of the epipterygoid in that group”. In fact, the processus ascendens of the palatoquadrate does not develop as a distinct process in any of the studied pleurodire species (Fig. 11, 12C, 13C,F) (ESSWEIN,

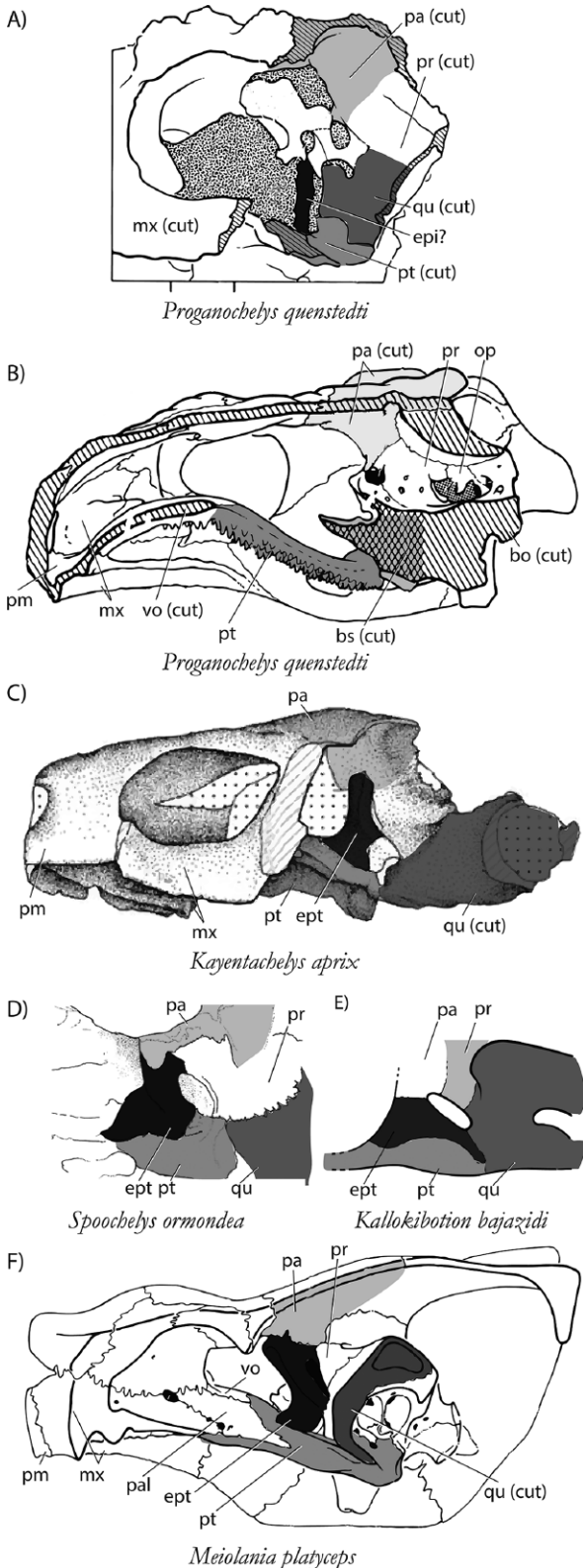
1992; BONA & ALCALDE, 2009; PALUH & SHEIL, 2013; WERNEBURG & YARYHIN, 2018). However, it is difficult to decide what is cause and effect. Only a potential rudiment of processus ascendens was reported for *Podocnemis unifilis* (SHEIL & ZAHAREWICZ, 2014), which does not contribute to the formation of the secondary lateral side wall. Based on the illustrations of the authors and our own observations, we assume that the process actually only represents the anterior tip of the pterygoid process of the palatoquadrate and that no ascending process is formed at all. We studied some developmental stages of pleurodires and can also confirm that there exists no processus ascendens during development (incl. *Po. unifilis*).

Compared to cryptodires, the pterygoid process of the palatoquadrate, from which the ascending process usually develops, is situated more laterally in pleurodires, it is enclosed in the developing pterygoid there (SHEIL & ZAHAREWICZ, 2014), and it never comes in contact with processus inferior parietalis (Fig. 11A–E). Therefore, an epipterygoid bracing of the parietal and pterygoid cannot develop. Among cryptodires, as mentioned above, only *Testudo* (this study, BENDER, 1912) does not develop an ascending process – like in pleurodires – however, the hypertrophied pterygoid process of the palatoquadrate is situated dorsally to the pterygoid – like in other cryptodires – and clearly contributes to the side wall formation.

**Evolution.** Along the stem line of Testudines, a gradual fixation of the palatal shelf takes place. In ‘early stem-turtles’ (Fig. 2, character 4A), as in *Kayentachelys aprix* (Fig. 7C), the inferior process of the parietal is very short and just reaches the trigeminal foramen (STERLI & JOYCE, 2007). The most ‘advanced stem-turtles’ such as *Kallokibotion bajazidi* (Fig. 7E) (GAFFNEY & MEYLAN, 1992) and *Mongolochelys efremovi* (KHOSATZKY, 1997) show contact of the inferior process of the parietal with the pterygoid and epipterygoid (Fig. 2, character 4B). Only crown-group turtles (Testudines) also show an anterior extension of the inferior process, which can even reach the palatine (Fig. 2, character 5B). In all stem-Testudines, however, the processus parietalis inferior has only a narrow strut anterior to trigeminal foramen (Fig. 2, character 5A; Fig. 7). The formation of the secondary lateral braincase wall and the related fusion of parietal and pterygoid are obviously related to the reduced mobility of the basiptyergoid articulation discussed above.

A clear distinction between kinetic and akinetic skulls is problematic, because species with tight sutures between bones could actually be able to perform intracranial movement similar to species with articulations (WERNEBURG *et al.* 2019). This was recently demonstrated for two cau-

← **Fig. 6. Fossil stem- and crown turtle skulls in ventral view.** Pterygoid, basisphenoid, and quadrate are highlighted in different grey scales. Images modified after **A**) GAFFNEY (1990), **B**) STERLI *et al.* (2007), **C**) STERLI & JOYCE (2007), mirrored, **D**) STERLI (2008), **E**) SUKHANOV (2006), mirrored, **F**) SMITH & KAER (2013), **G**) GAFFNEY & MEYLAN (1992), **H**) JOYCE *et al.* (2011), **I**) GAFFNEY (1983), **J**) KHOSATZKY (1997), **K**) JOYCE *et al.* (2016), mirrored, **L**) RABI *et al.* (2013), mirrored. Images not to scale. For phylogenetic position of each species, see Figure 2. In some parts of the skull, the exact borders were difficult to distinguish. Anterior is top. \* indicates basiptyergoid process; not present (F, H–I) or visible (B) in some taxa; note the different orientations of the process.



**Fig. 7. Fossil stem turtle skulls in left lateral view.** Images modified after the original publications: **A–B**) GAFFNEY (1990), **C**) STERLI & JOYCE (2007), mirrored, **D**) SMITH & KAER (2013), **E**) GAFFNEY & MEYLAN (1992), mirrored, **F**) GAFFNEY (1983). Images not to scale. For phylogenetic position of each species, see Figure 2. In some parts of the skull, exact borders are difficult to distinguish; we highlighted the parietal, epipterygoid, quadrate, basisphenoid, and the pterygoid to illustrate the bone mosaic in the lateral braincase wall. Anterior is left.

date lissamphibians. Whereas a particular newt species has well flexible joints in the skull, the fire salamander has tightly sutured articulations. Both species, however, perform a similar amount of intracranial movement. In the “akinetic” fire salamander, this is possible by thin and elastic bones (Natchev et al. 2016).

The successive anterior extension of the inferior process of the parietal through turtle evolution (STERLI *et al.*, 2007) helps stabilizing the palatal shelf, but also reduced the elasticity of the skull roof. In crown turtles, the anterior extensions to the palatine bone finally resulted in a fully akinetic skull.

The presence of the epipterygoid in early stem-turtles is uncertain in the phylogenetic reconstruction, although highly plausible (Fig. 2, character 6A). A short bar-shaped element in the orbitotemporal region of *Proganochelys quenstedti* could possibly represents the epipterygoid (Fig. 7A) (GAFFNEY, 1990; WERNEBURG & YARYHIN, 2018). The no report of this structure in other early stem-turtles such as *Palaeochersis talampayensis* (STERLI *et al.*, 2007) could simply mean that this element was not preserved during the fossilization process. Certainly, the epipterygoid was still mobile and loosely attached to the surrounding skull bones in early stem-turtles and, as such, it could have been disarticulated easily after dead. The integration of the epipterygoid into the secondary lateral braincase wall is first visible in *Kayentachelys aprix* (STERLI & JOYCE, 2007) (Fig. 7C). Although bar-shaped dorsally, like in the outgroup (*Sphenodon punctatus*) (JONES *et al.*, 2011), the epipterygoid is relatively broad at its basis, where it fuses with the pterygoid. Dorsally, the epipterygoid already contacts the parietal and a reduced mobility can be assumed. The ‘advanced stem-turtles’ (Fig. 2) do not have their epipterygoid preserved and only within the ‘most advanced stem-’ (Fig. 2, 7D–F) and in crown turtles it is an integrated part of the secondary braincase wall. Except for *M. platyceps* (Fig. 7F) (GAFFNEY, 1983), the epipterygoid becomes laminar and completely loses its bar-shape (Fig. 2, character 6B). The laminar shape corresponds to the more expanded inferior process of the parietal. Within crown turtles, all pleurodires [and maybe for some baenids: *Chisternon undatum* (JOYCE *et al.*, 2016)], related to the absence of processus ascendens palatoquadrati in the embryos, do not have an epipterygoid (Fig. 2, character 6C).

### Closure of the cranio-quadrate space

The quadrate in crown turtles has a large cup-shaped expansion and surrounds the spherical cavum tympanicum (GAFFNEY, 1972) (Fig. 3–4). The extensive fusion of the quadrate to the braincase in turtles largely contributes to the establishment of an akinetic skull (GAFFNEY, 1975; GAFFNEY & MEYLAN, 1988; JOYCE, 2007). The fusion resulted in the restriction of the plesiomorphically wide-spanned cranioquadrate passage (GOODRICH, 1930) into a series of narrow nerve and blood vessel canals (Fig. 3E–F).



In cryptodires, the pterygoid expands far caudally and forms a main brace between the quadrate and the braincase (Fig. 3A). In pleurodires, however, the quadrate forms a shorter medial process, which forms the main brace to the braincase (Fig. 3B). Related to the broad pterygoid bracing, in cross section, the quadrate has a more lateral (vertical) orientation in cryptodires when compared to the more oblique one in pleurodires (Fig. 3E–F, 8–9, 13B, 13D).

Related to these differences of quadrate to braincase fixation in pleurodire and cryptodire turtles, soft tissue anatomy in this region also differs (GAFFNEY, 1975; GAFFNEY, 1979a; Fig. 3A, B).

**Ontogeny.** In contrast to Pleurodira (Fig. 3B), the pterygoid in Cryptodira is involved in the developmental fixation of the palatoquadrate to the braincase (Fig. 3A) (GAFFNEY, 1979a, JOYCE, 2007).

The pterygoid of cryptodires has a caudal process, the lateral edge of which is connected to the medial face of the palatoquadrate (Figure 8B). The medial edge of the pterygoid attaches to two or one continuous crest(s) of cartilage, oriented in ventrolateral direction. The posterior crest-part is formed by the lateral edge of the basal plate (“crista pterygoidea” of FUCHS, 1915) (Fig. 8C). The anterior part is formed by the trabecular base (“crista basipterygoidea”) (Fig. 8B). Only the crista basipterygoidea appears to be homologous to the primary process basitrabecularis (FUCHS, 1915) (see above).

In pleurodires, the fixation of the palatoquadrate to the braincase is realized by the formation of appositional bone (Zuwachsknochen) at the medial part of the quadrate. The appositional bone represents the hypertrophied outgrowth of the perichondral ossification (Fig. 4B, 5F, 9C, D–E, G). It fuses directly to the cartilaginous crista basipterygoidea anterior (Fig. 5F) and via crista pterygoidea (discussed above) to the ear capsule (Fig. 9D, G). This unique mode of palatoquadrate fixation was first discovered by ESSWEIN (1992). We had access to Eßwein’s unfinished PhD-thesis. In honor to Stephan T. Eßwein, we suggest to name the unique development of palatoquadrate fusion in pleurodires the “Eßwein-fixation”.

**Evolution.** As shown above, the gradual evolution of the fully akinetic skulls in extant turtles is well documented in the fossil record. Not only the fixation of the basipterygoid articulation (Fig. 6) and the formation of the secondary braincase wall (Fig. 7), but also the broad quadrate fixation (Fig. 6) was acquired gradually (Fig. 2). This is correlated with the gradual enlargement of the quadrate (Fig. 7), which surrounds a voluminous cavum tympanicum, and a broader attachment to the braincase.

The flooring of the cranioquadrate passage by the pterygoid and with that a ventral fixation of the quadrate already appeared in *Palaeochersis talampayensis* (Fig. 2, character 7B) (STERLI *et al.*, 2007). In ‘early-’ and in ‘advanced stem-turtles’, the pterygoid, however, did not cover the prootic yet. In most of the ‘most advanced

stem-turtles’ and in the last common ancestor of Testudines the pterygoid also covered the prootic ventrally (Fig. 2, character 7C). In all pleurodires, the pterygoid is again restricted to a more anterior position (like in the ancestral Testudinata condition) and only the quadrate forms the ventral brace of the cranioquadrate passage (Fig. 2, character 7D; Fig. 3B).

## Developmental timing

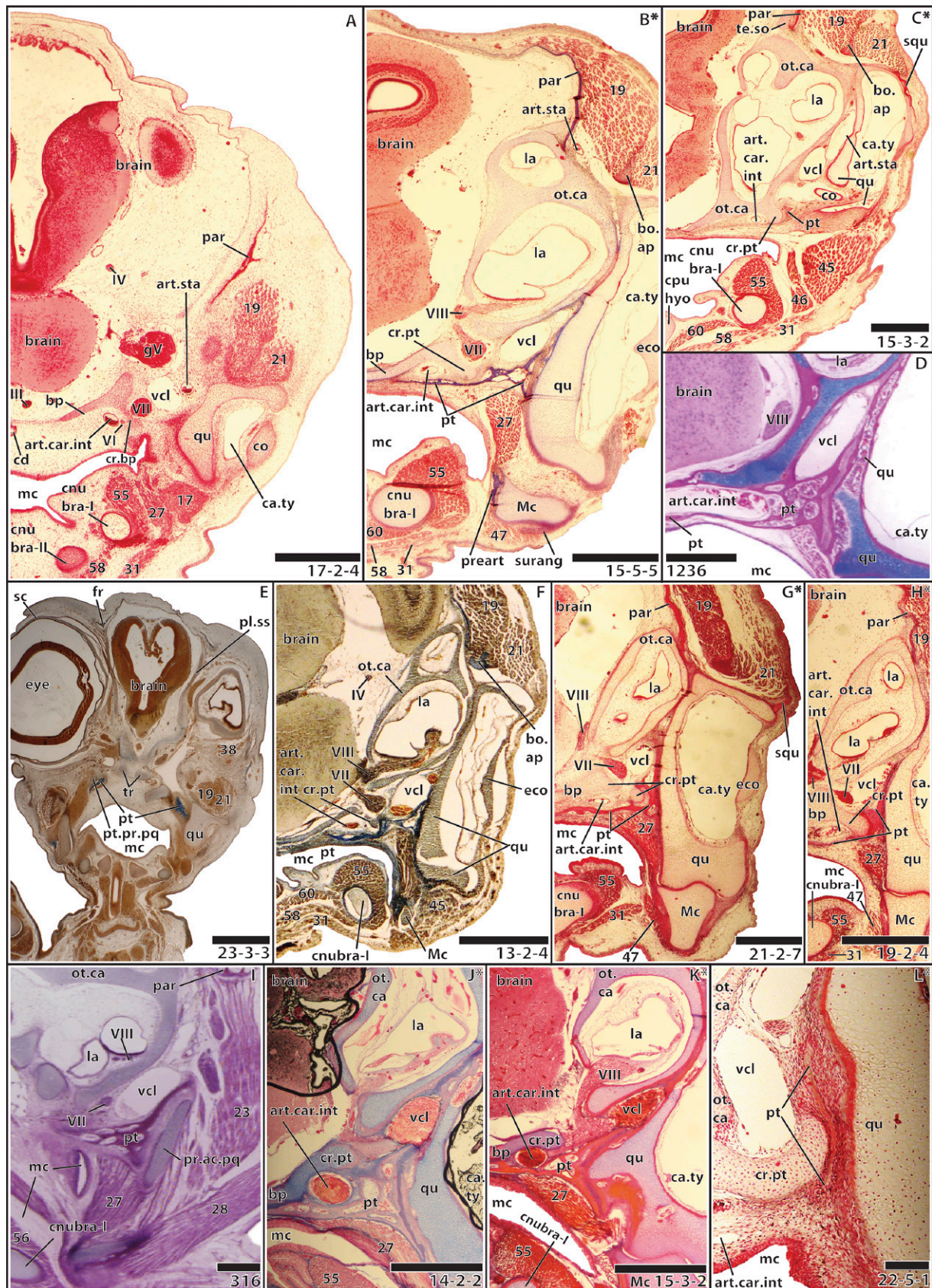
ESSWEIN (1992) recognized that in Pleurodira, the fixation of the palatoquadrate to the braincase appears later in ontogeny when compared to cryptodires. When the fixation takes place in pleurodires, dermal and endochondral ossifications are already further developed. At the time when the quadrate (pars quadrata palatoquadrati) attaches to the braincase, the processus inferior parietalis already extends far ventrally in pleurodires (Fig. 9B vs. 11C, 9C vs. 11I, 9D vs. 11D, 9E vs. 11H). As such, the bracing connection between pterygoid and skull roof is accomplished without the inclusion of any part of the palatoquadrate (i.e., without processus ascendens or the pterygoid process of the palatoquadrate). Nevertheless, we can show that the palatoquadrate is always in close association to the braincase through ontogeny and there is no spatial distance that would prevent an earlier fixation of pars quadrata in pleurodires. Due to its oblique orientation in cross section (Fig. 13D), the quadrate-part is always even closer to the braincase than in cryptodires and one would expect an earlier fixation in pleurodires. As is shown by the present study, the processus pterygoideus palatoquadrati is situated more lateral to the pterygoid in pleurodires (Fig. 11C) so that it cannot get involved in secondary lateral braincase formation between pterygoid and parietal – independent of the developmental timing of bone formation.

Whereas the ground pattern of Testudines was cryptodiran-like already (Fig. 2), the late evolutionary appearance of pleurodires within turtle evolution (i.e., Late Jurassic/Early Cretaceous, JOYCE *et al.* 2016) is probably correlated to their specific mode of late developmental palatoquadrate fixation and represents a ‘terminal addition to a developmental sequence’ in ontogenetic terminology (WÄGELE, 2005; SÁNCHEZ-VILLAGRA & WERNBURG, 2016).

## Neck-skull-interface

**Overview.** Cryptodires and pleurodires are at once distinguished by their different modes of head retraction. Cryptodires, the so-called hidden-necked turtles retract their neck in a vertical plane (Fig. 13A–B, E) inside the shell for protection (HERREL *et al.*, 2008). Pleurodires, the so-called side-necked turtles, in contrast, retract their head and neck in a horizontal plane under the anterior edge of the shell (Fig. 13C–D, F). To enable such movements, which also involves S-shaping of the neck during





retraction, the cervical vertebrae experienced comprehensive anatomical modifications compared to the ancestral condition. Most obviously, neck ribs were reduced through testudinate evolution in order to fold the neck

inside the shell (WILLIAMS, 1959; GAFFNEY, 1985; WERNEBURG *et al.*, 2013). The vertebrae became more slender, further anatomical specializations occurred (WILLIAMS, 1950; WERNEBURG *et al.*, 2015a; BÖHMER & WERNEBURG,



2017), and the articulation of the neck with the first shell-vertebra was largely modified in both extant clades independently to enable complete flexions of the neck (DALRYMPLE, 1979; WERNEBURG *et al.*, 2015a).

It has been shown that already in the egg pleurodires and cryptodires perform their clade-specific neck movements in late stages of development (WERNEBURG *et al.*, 2009; CORDERO, 2014; TELEMCO *et al.*, 2016; CORDERO, 2017; MAGALHÃES *et al.*, 2017). In this period, neck muscles are differentiated (WERNEBURG *et al.*, 2013) and the skull components fuse as described in this paper. We hypothesize a causal connection between neck muscle function and skull formation in turtle development. Neck muscles attach to the occipital region of the skull but they also directly and indirectly (via connective tissue) connect to the palatoquadrate cartilage in late term embryos (WERNEBURG, 2011). Muscle activity changes the relationships between different skull portions. Cryptodires pull their head in a posterodorsal and -medial direction (Fig. 13Aa, Ba, Ea), which results in posterodorsal and -medial tension on the palatoquadrate (Fig. 13Aa', Ea').

Pleurodires contract one neck muscle side and pull their head towards a posterolateral direction (Fig. 13Cb, Db, Fb). Thereby they pull the palatoquadrate in that direction. At the same time, the contralateral neck muscles are stretched and passively move the other palatoquadrate to a posteromedial direction at the same head side (Fig. 13Cc, Dc, Fc). As pleurodire specimens always retract their neck to both body sides (pers. obs. I.W.), both posterolateral (Fig. 13Cb', Fb') and posteromedial (Fig. 13Cc', Fc') rotations can be expected for both the left and right side palatoquadrates respectively. Already turtle embryos show various modes of movements inside the egg (CORDERO *et al.*, 2018), and neck retraction can be considered a developmental event by its own (WERNEBURG, 2009). Whether this is an active movement is yet unknown. Space limitation in the egg, nevertheless, at least result in the passive, taxon-specific relocation ("retraction") of the neck in late developmental stages (WERNEBURG *et al.*, 2009; CORDERO & JANZEN, 2014). Much earlier in development, neck

muscles are already differentiated and attach to the skull (WERNEBURG *et al.*, 2013). As such, either actively or passively, embryonic neck muscle related movements can be considered to result in a reorientation of the palatoquadrate as outlined in the following:

**Cryptodira.** We hypothesize that in cryptodires the anterior part of the palatoquadrate, namely the processus pterygoideus with its dorsal processus ascendens, is pushed mediad against the orbitotemporal region (Fig. 13Ad), just above the pterygoid and below the downwards growing parietal. As a result, the processus ascendens could become incorporated into the secondary braincase wall. To which degree neck retraction actually contributes to this formation cannot be judged because ancestrally the epipterygoid (proc. ascendens) is already an integrated part of the orbitotemporal region (e.g., in our outgroup species *Sphenodon punctatus*, JONES *et al.*, 2011) and could already be in the position where the secondary lateral braincase wall will form.

Neck musculature mainly inserts posterodorsally to the quadrate-part of the palatoquadrate (Fig. 13) and, as a result of the posterodorsal and -medial direction of movement (Fig. 13Aa, Ba, Ea), a rotation of the quadrate against the ear capsule and towards a more vertical orientation of the quadrate is the result (Fig. 13Bf). Dorsomedially, the quadrate stays in contact with the ear capsule, whereas ventromedially, the quadrate and braincase are separated. Consequently, the cranioquadrate passage becomes wider and the pterygoid can pass posteriorly to bridge the open space ventrally. This results in the architecture described for late embryos and adults (Fig. 3A, 13B).

**Pleurodira.** We hypothesize that in pleurodires, a posterolateral (Fig. 13Cb) respectively a posteromedial (Fig. 13Cc) direction of neck force results in a different orientation of the palatoquadrate when compared to cryptodires. The pterygoid process is rotated away from the orbitotemporal region (Fig. 13Ce) by posteromedial neck force direction (Fig. 13Cc, Dc, Fc), will lay more

← **Fig. 8. The fusion of the quadrate to the braincase in cryptodire turtles.** **A)** Early stage, in which the parietal still grows downwards. A crista basipterygoidea is formed laterally to the basal plate and flanked by the palatine branch of the facial nerve (n. VII) (*Trachemys terrapen*, CL=10.8, mm, HL=7.5 mm, CL=19mm, 33d, ZIUT), **B)** The pterygoid bridges the quadrate laterally with the braincase medially. It contacts the crista pterygoidea, here at the level of the facial ganglion (n. VII) (*Chrysemys picta elegans*, ZIUT, embryo with 67 slides), **C)** Crista pterygoidea is still present more posteriorly, attaching to the posteriormost tip of the pterygoid (*Chrysemys picta elegans*, CL=19mm, 33d, ZIUT), **D)** The pterygoid bridges quadrate and braincase (*Pelodiscus sinensis*; SK, TK-stage 27), **E)** Pterygoid braces quadrate and braincase (*Chelonia mydas*, CL=12 mm, PIMUZ lab# 2009.69), **F)** Section comparable to B (*Chrysemys picta elegans*, ZIUT, embryo with 67 slides), **G)** Crista pterygoidea shows a distal thickening and inserts as a small distal outgrow to a pocket formed by the pterygoid (*Testudo hermanni*, CL=23.4 mm, HL=12.1 mm, ZIUT), **H)** Similar to F, distal thickening is more obvious (*Testudo hermanni*, CL=15.6 mm, HL=8.9 mm, ZIUT), **I)** The pterygoid also braces the anterior part of the palatoquadrate and forms a dorsal process posteromedial to the ascending process (compare to Figure 10I, *Caretta caretta*; SK, specimen B36), **J)** The pterygoid closely aligns to the braincase and covers the internal caroid artery ventrally. Crista pterygoidea is small (*Sternotherus odoratus*, HL=17.6 mm, ZIUT), **K)** The pterygoid also closely aligns to the quadrate, which forms a medial crest in this species (*Sternotherus odoratus*, ZIUT), **L)** A very broad crista pterygoidea is formed in this species, reminding of a basitrabecular process in cross section. However only the most anterior part of the crest might be homologous to that process (*Testudo hermanni*, CL=23.4 mm, HL=12.1 mm, ZIUT). Bar scales equal 0.5mm except for D with 0.05mm and L with 0.1mm. Numbers below scale bars correspond to section numbers. Slice thickness: 10 µm, except for B, E–F, J–K) 15 µm, D) 6 µm, and I) 12 µm. \* = image mirrored.







The posteromedial force direction during pleurodiran neck retraction results in a very close association of pars quadrata palatoquadrati to the braincase (Fig. 13Dc). The alternating friction and pressure possibly results in the development of appositional bone on the medial side of pars quadrata (Fig. 12C) developing into the unique ‘Eßwein-fixation’ defined above. The close association of the quadrate and braincase results in the closure of the cranioquadrate passage ventrally. Consequently, we consider that compared to cryptodires, the pterygoid can not expand posteriorly in pleurodires, and although the dermal pterygoid is further developed in general (i.e., broader; Fig. 13F) (ESSWEIN, 1992), it is blocked posteriorly by the Eßwein-fixation.

**Evolution.** WERNEBURG *et al.* (2015b) postulated a simple diagonal neck tucking in the earliest stem turtle *Proganochelys quenstedti*, which was not comparable to both the modern pleurodiran and the modern cryptodiran modes of neck retraction. The latter are clearly associated with the extensive modifications of the neck vertebrae in the last common ancestor of Testudines and on the stem-line towards Pleurodira and Cryptodira (WERNEBURG *et al.*, 2015a). Nevertheless, WERNEBURG *et al.* (2015a) have shown that through the evolution of the stem-Testudines an increasing ability of diagonal movement took place. Still today, cryptodires not only move their necks in a strait vertical plane but can also show some diagonal neck orientation when retracting their necks.

The phylogenetic considerations of the present paper, however, possibly allow to draw a more refined picture to the evolution of neck retraction in turtles due to its supposedly secondary correlations to the skull. We discussed that the flooring of the cranioquadrate passage in cryptodires is likely related to the cryptodiran mode of retraction because the reorientation of the quadrate enables the pterygoid to expand posteriorly in development. Our phylogenetic reconstruction shows (Fig. 2) that already *Palaeochersis talampayensis* (STERLI *et al.*, 2007) and all other successive ‘early-’ and ‘advanced stem-turtles’ show an initial expansion of the pterygoid (Fig. 2, character 7B; Fig. 6B–L). As in *Pr. quenstedti* (GAFFNEY, 1990), cervical ribs, massive dorsal epiplastral processes

that connected the plastron and the ribcage/carapace, and the general architecture of the neck vertebrae clearly hindered a cryptodiran-like mode of neck retraction in *Pa. talampayensis* (STERLI *et al.*, 2007). Similarly, the most ‘advanced stem-turtles’ such as *Meiolania platyceph* (without epiplastral processes) (GAFFNEY, 1996) were not able to perform any neck retraction much beyond the diagonal neck tucking shown for *Pr. quenstedti* (WERNEBURG *et al.*, 2015b).

Nevertheless, in the most ‘advanced stem-turtles’ (Fig. 6F–L), the pterygoid travels even more posteriorly than in the earlier lineages (Fig. 2, character 7C). This observation indicates that the increasing ability to diagonally tuck the neck through turtle evolution (WERNEBURG *et al.*, 2015a, WERNEBURG *et al.*, 2015b) had some influence to palatoquadrate fixation. In the ancestral neck tuck, the neck is oriented diagonally and is, as such, quite similar to the vertical orientation seen in cryptodires; i.e., neck muscles in stem turtle must have retracted the palatoquadrate in a posterodorsal as well as – and even more than in cryptodires – in a posteromedial direction. This consequently must have resulted in a widening of the cranioquadrate passage and a posterior pterygoid expansion. The straighter vertical orientation of the neck in cryptodires during retraction, as such, did not change much the orientation of the palatoquadrate compared to stem-turtles. It was *still* influenced by posterodorsal and posteromedial neck retraction in the embryos.

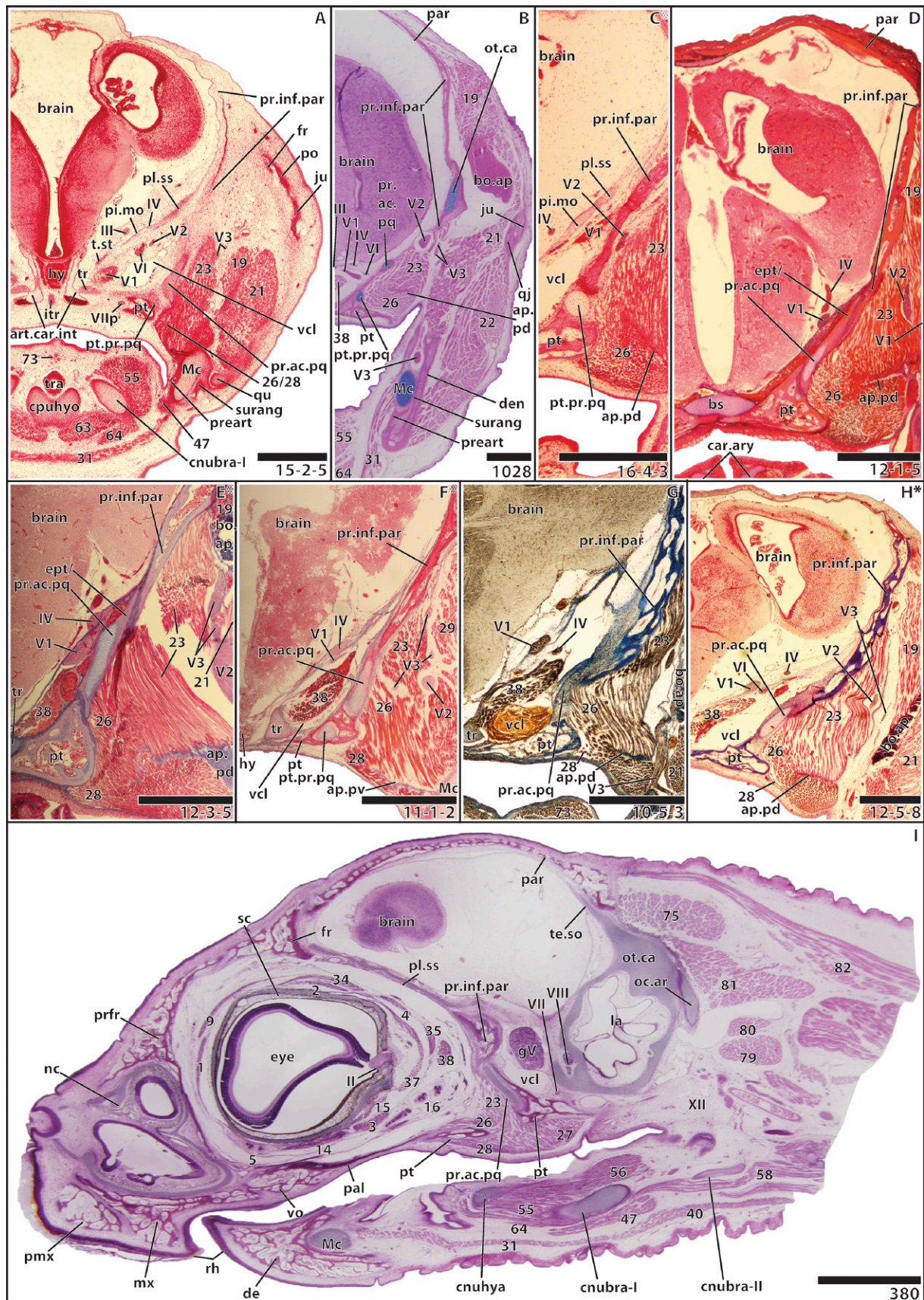
Pleurodires are unique in the mode of their neck retraction (for some cryptodiran xinjiangchelyids, see below). Admittedly, they also adopted the diagonal neck tucking from the stem-turtles in their own way, but the straight horizontal orientation of their neck is clearly derived. The associated Eßwein-mode of palatoquadrate-fixation (ESSWEIN, 1992), consequently, only applies to the unique mode of neck retraction evolved in Pleurodira.

### Evolutionary consequences of palatoquadrate fixation

The fusion of the palatoquadrate to the braincase in turtles resulted in two major evolutionary changes in the ar-

← **Fig. 9. The fusion of the quadrate to the braincase in pleurodire turtles.** **A)** In an early stage, without replacement bone, a short crista basiptygoidea is present. The pterygoid only reaches the foramen of ganglion genicularis (n. VII) (*Chelodina longicollis*, CL=14mm, 40d, ZIUT), **B)** Crista ptygoidea is formed (*Emydura subglobosa*, CL=16 mm, 31d, ZIUT), **C)** The quadrate has formed endochondral and perichondral ossifications. The perichondrium has developed appositional bone medially, surrounds the stapedial artery, and fuses with the otic capsule medially (*Podocnemis unifilis*, CL=33 mm, HL=27.5 mm, ZIUT), **D)** Initial formation of appositional bone (*Pelusios sinuatus*, CL=13 mm, HL=7mm, ZIUT), **E)** Appositional bone medial from the quadrate contacts the perichondrial ossification of the ventral part of the otic capsule (*Chelodina longicollis*, CL=18 mm, HL=11.7 mm, ZIUT), **F–G)** Sections through the anterior part of the quadrate, short before the otic trochlear (F) and section through the contact area between quadrate and braincase (G). Note the interdigitating sutures between the appositional bone (ZWK) of the quadrate and braincase (*Pelomedusa subrufa*, subadult, CL=96 mm, ZIUT), **H–K)** Section series through the otic capsule and the quadrate. Note that the pterygoid cannot expand further posterior because of the close association of quadrate and braincase and the progressing formation of appositional bone medial to the quadrate (ZWK). In this late stage embryo, a crista ptygoidea is visible (as a crista substapedialis) ventrolaterally at the otic capsule, which closely associates to the quadrate (*Emydura subglobosa*, CL=21 mm, ZIUT). Bar scales equal 0.5 mm except for F–G with 2 mm. Numbers below scale bars correspond to section numbers. Slice thickness: 10 µm, except for F–G) 40 µm. \* = image mirrored.





chitecture of the turtle skull related 1) to marginal bone reductions in the temporal dermal skull region and 2) to the shape of the jaw adductor chamber.

**Emarginations.** Stem-turtles had a more or less complete dermal bone coverage above the adductor chamber illustrating the pure anapsid nature of their skull (WER-

NEBURG, 2012). Turtles most likely had diapsid ancestors with temporal fenestrations as suggested by molecular (RIEPEL, 2008; WANG *et al.*, 2013) and paleontological findings (SCHOCH & SUES, 2015). Neck musculature attaches to the temporal region and introduces tension force. To resist this tension during neck retraction, turtles might have closed these fenestrations for better strength distribution resulting in a secondary anapsid skull (WERNEBURG, 2015; LI *et al.*, 2018; FERREIRA & WERNEBURG, 2019). Ancestrally, dermal bones in the temporal skull region (in anapsid as well as in fenestrated taxa) serve for stabilization of the quadrate against the lower jaw (jaw joint). With the fusion of the quadrate to the braincase in turtles, this stabilization function of the dermal armor was increasingly diminished (ZDANSKY, 1923) and was an important prerequisite to largely reduce the temporal bone coverage (KILIAS, 1957; WERNEBURG, 2015). In fact, crown turtles show comprehensive and diverse marginal reductions of the temporal skull armor known as emarginations (ZANGERL, 1948; WERNEBURG, 2012). It has been shown that these are significantly correlated to the way turtles retract and move their necks, because the high tension applied by the neck musculature needs to be buffered by broader insertion sites, i.e., deeper emarginations (WERNEBURG, 2015; FERREIRA & WERNEBURG, 2019). In cryptodires, related to the vertical plane of neck retraction, the posterodorsal area of the temporal region is generally more reduced, also to easier pass the narrow opening of the shell and to enable elastic space for the folded neck during retraction. Pleurodires (particularly Chelidae), in contrast, generally show large lateral emarginations, which correlate to the horizontal plane of the retracting neck, which is also a prerequisite for packing the head inside the shell. Nevertheless, also other factors, such as jaw muscle performance, skull dimensions, and the type of food, are considered to have shaped the temporal skull region in turtles (WERNEBURG, 2012, 2015).

**Adductor chamber.** The broadly fused and expanded quadrate limits the space for the jaw muscles in the adductor chamber in extant turtles resulting in short lever arms for the muscle. To compensate for the related loss of muscle power, turtles evolved posteriorly elongated supraoccipital and squamosal crests, which provide long and broad attachment sites for the external jaw musculature (POGLAYEN-NEUWALL, 1953b; SCHUMACHER, 1973; WERNEBURG, 2011, 2013b) and complex tendinous structures evolved to concentrate muscle forces (OGUSHI, 1913; WERNEBURG, 2013a). As a result, turtles show a bite per-

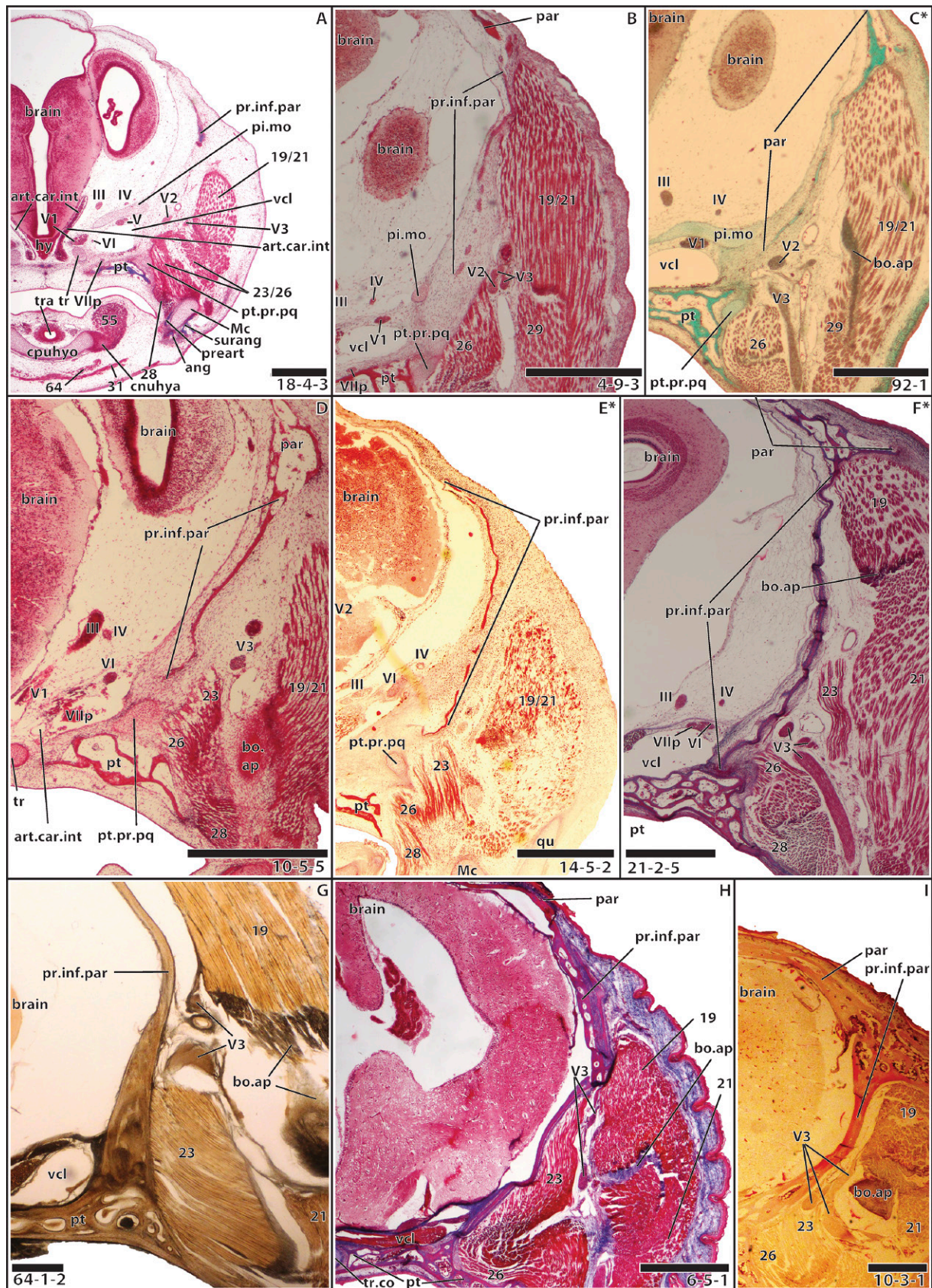
formance similar to other reptiles (HERREL *et al.*, 2002). Nevertheless, the jaw musculature of turtles is complex, as it has to bend around the large quadrate. For that, in Cryptodira, the jaw musculature bends around a processus trochlearis oticum (Fig. 13A\*), which is formed by a process provided by quadrate and prootic (plus parietal in trionychids). In Pleurodira, an anterior processus trochlearis is formed at the pterygoid bone (Fig. 12C\*, 13C\*) and the external jaw adductor muscle bends around this process before it inserts to the lower jaw (SCHUMACHER, 1956). As such, the processes, which enable the bending of the jaw musculature around the large quadrate, are not homologous in both turtle taxa; i.e., they must have evolved independently (JOYCE, 2007; WERNEBURG, 2011, 2013b; JOYCE & STERLI, 2012; FERREIRA & WERNEBURG, 2019). For articulation with the process, the coronar aponeurosis (synonyms: external jaw adductor tendon, bodenaponeurosis) generally forms a sesamoid structure, the cartilago (or os) transiliens. This sesamoid appears late in ontogeny (posthatching) and is the consequence of mechanical load during feeding (SCHUMACHER, 1956; RAY, 1959; WERNEBURG, 2011, 2013a).

The different anatomy of the jaw adductor chamber in pleurodires and cryptodires is influenced by the way the large quadrates are fused to the braincase during embryonic development. As explained for cryptodires above, posterodorsal neck retraction rotates the quadrate in a more vertical orientation being dorsally higher in relation to the braincase when compared to pleurodires, in which the quadrate is pulled towards a more vertical orientation. Consequently, cryptodires have to bend the jaw muscles around the elevated quadrate at the proc. trochlearis otici, whereas pleurodires developed a lever point in a more ventral position, at the pterygoid (proc. trochlearis pterygoidei). Early in turtle evolution, no trochlear process was present at all (Fig. 2, character 8A) and the quadrate appears to have started to restrict the adductor chamber only within the ‘most advanced’ stem-turtles (Fig. 7F) – related also to increased neck tucking and posterior pterygoid expansion (see above) – and an otic trochlear process was formed (Fig. 2, character 8B). The different positions of the process on the quadrate and prootic are quite variable among species, ranging from a minute roughness among stem-turtles to a prominent crest within cryptodires, and might be related to species-specific characteristics of neck retraction and related quadrate orientation in the adductor chamber and the skull height.

A trochlear process on the pterygoid is a unique feature of pleurodires (Fig. 2, character 9B) and likely de-

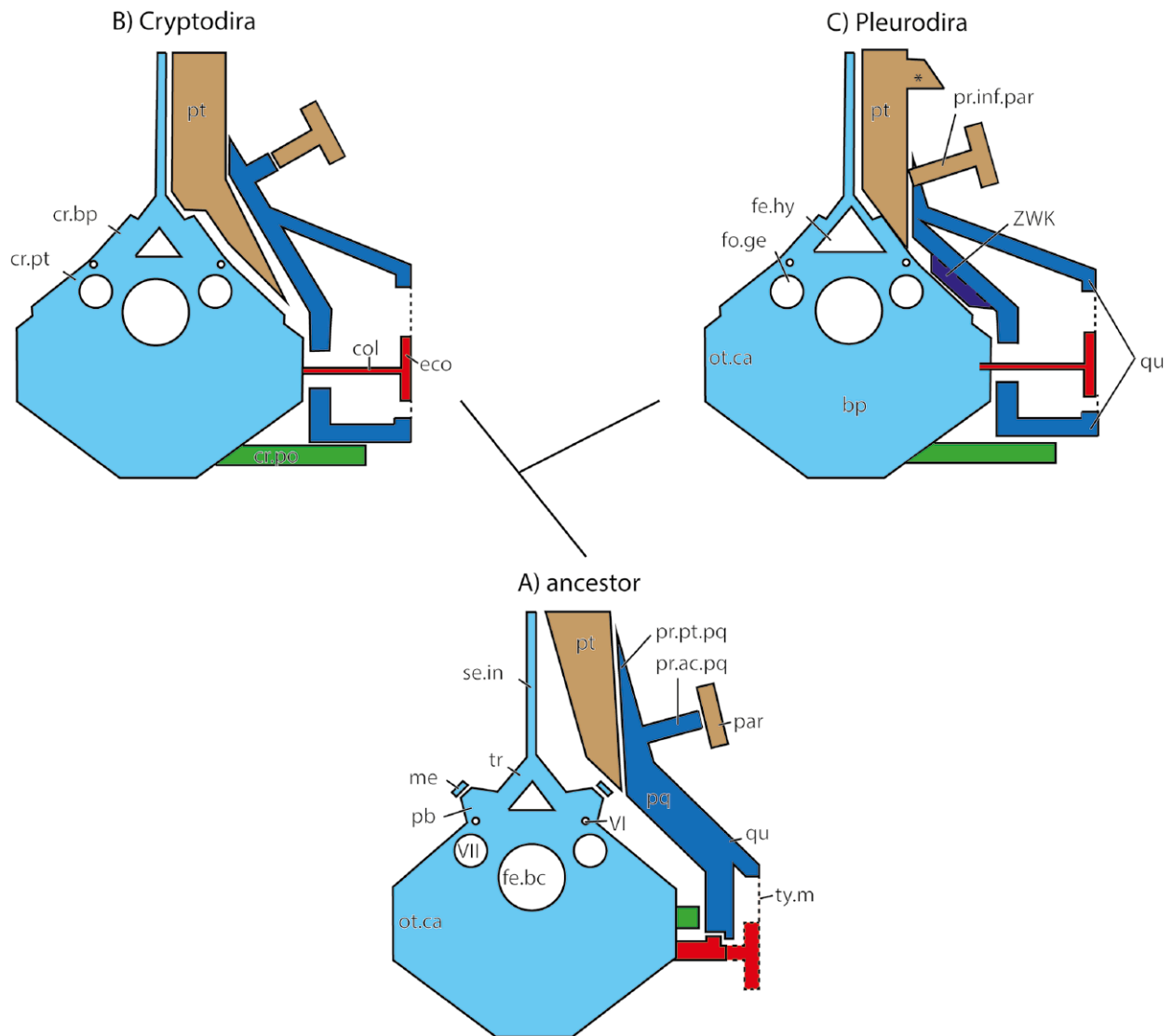
← **Fig. 10. The secondary lateral braincase wall in cryptodire turtles.** Processus ascendens palatoquadrati (ossified as epipterygoid) (with its root in proc. pterygoideus palatoquadrati) bridges the parietal and the pterygoid. **A)** *Trachemys terrapen* (CL=10.8 mm, HL=7.5 mm, ZIUT), **B)** *Pelodiscus sinensis* (SK, TK-stage 27), **C)** *Testudo hermanni*; note: a proc. ascendens is not developed, but only the proc. pterygoideus forms the bridging epipterygoid (CL=15.6 mm, HL=8.9 mm, ZIUT), **D)** *Sternotherus odoratus* (ZIUT), **E)** *Sternotherus odoratus* (HL=17.6 mm, ZIUT), **F)** *Graptemys kohnii* (CL=11.7 mm, HL=7.5 mm, ZIUT), **G)** *Chrysemys picta elegans* (ZIUT, embryo with 67 slides), **H)** *Chrysemys picta elegans* (CL=19 mm, 33d, ZIUT), **I)** *Caretta caretta* (SK, specimen B36). A–H) cross sections, I) sagittal section. Bar scales equal 0.5 mm except for I with 2 mm. Numbers below scale bars correspond to section numbers. Slice thickness: 10 µm except for B) 6 µm, D–E, G) 15 µm, I) 12 µm. \* = image mirrored.





**Fig. 11. The secondary lateral braincase wall in pleurodire turtles.** The wall is formed by a contact between parietal and the pterygoid. **A)** *Emydura subglobosa* (CL=12.3 mm, HL=7.4 mm, ZIUT), **B)** *Phrynops geoffroanus* (CL=16.7 mm, HL=12.3 mm, 60d, ZIUT), **C)** *Emydura subglobosa* (CL=16mm, 31d, ZIUT), **D)** *Pelusios sinuatus* (CL=13 mm, KL=7 mm, ZIUT), **E)** *Pelusios williamsi* (CL=13 mm, HL=7.9 mm, ZIUT), **F)** *Emydura subglobosa* (CL=21 mm, ZIUT), **G)** *Pelomedusa subrufa*, subadult (CL=96 mm, ZIUT), **H)** *Chelodina longicollis* (CL=18 mm, HL=11.7 mm, ZIUT), **I)** *Podocnemis unifilis* (CL=33 mm, HL=27.5 mm, ZIUT). Bar scales equal 0.5 mm. Numbers below scale bars correspond to section numbers. Slice thickness: 10 µm, except for G) 40 µm. \* = image mirrored.



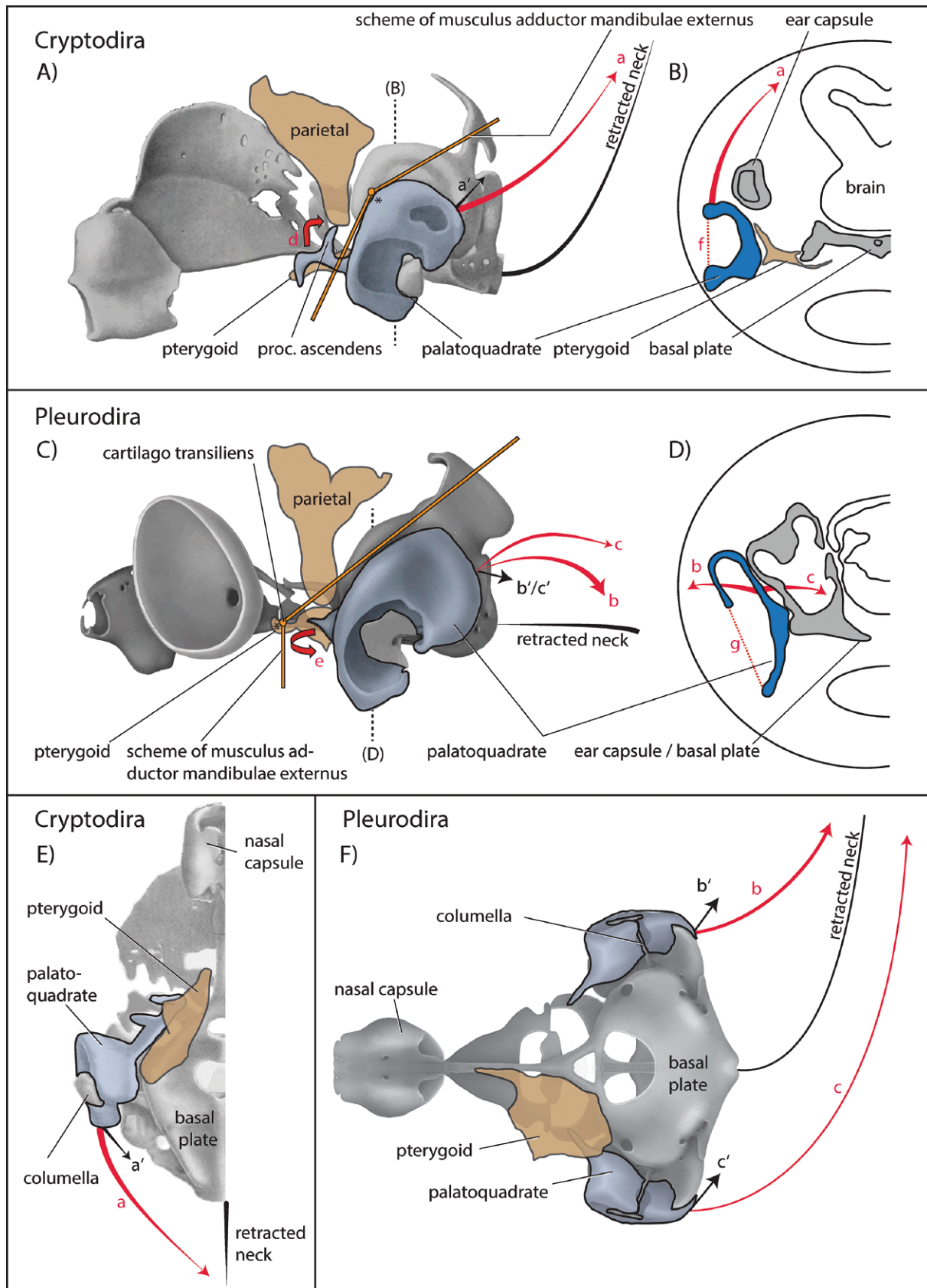


**Fig. 12. Palatoquadrate fixations.** Schematic illustration of the relations of the palatoquadrate (dark blue) to the neurocranium (light blue) in the hypothetical ancestral morphotype (A), in Cryptodira (B), and in Pleurodira (C) in dorsal view. Ancestrally, the palatoquadrate articulates with processus basipterygoideus and a meniscus is formed in between. The ascending process later ossifies as epipterygoid and is a mobile element (A). The stabilization of the jaw apparatus is achieved differently in Cryptodira and Pleurodira. The posteriorly expanded pterygoid (brown) bridges the palatoquadrate and the braincase in cryptodires (B). In pleurodires, the palatoquadrate is anteriorly fixed to the braincase via appositional bone (Zuwachsknochen) (purple) (C). In cryptodires, the processus inferior of the parietal attaches to the ascending process of the palatoquadrate to form a secondary braincase wall (B). In Pleurodires, no ascending process is formed and the parietal directly attaches to the pterygoid to form the secondary braincase wall (C).

veloped from the proc. pterygoideus externus (FERREIRA *et al.*, 2018b), which is well visible in stem-turtles such as *Heckerochelys romani* (Fig. 6E) (SUKHANOV, 2006) and in cryptodires (Fig. 3A).

JOYCE (2007) and JOYCE & STERLI (2012) postulated a transitional form in the pleurodiran ancestor with both an otic and a pterygoid trochlear. This scenario appears plausible as ancestrally an otic process and the anatomical prerequisite of the pterygoid process were already present. Whether such a bitrochlear construction of the jaw adductor chamber is biomechanically possible, however, would require reasonable tests as recently proposed by FERREIRA *et al.* (2018b). Nevertheless, having two trochlear processes with two lever

points and three related lever arms in the jaw adductor musculature, would clearly deteriorate jaw muscle performance. From an anatomical point of view, the trochlear processes in both pleurodires and cryptodires are always associated with one sesamoid structure inside the coronar aponeurosis. Forming two sesamoids as articulation facets with two trochlears inside the coronar aponeurosis seems unlikely; the tendon would become very elongated and a very complex arrangement of the consequently shorter and less powerful muscle fibers inserting to this structuralized tendon would be necessary. Anatomically, jaw muscle fiber insertions at the adductor tendon do not differ much between pleurodires and cryptodires and through ontogeny never two sesamoids



are developed. Actually, cartilago transiliens is formed in a very complex manner (SCHUMACHER, 1956; WERNEBURG, 2013a). A functional bitrochlear system therefore does not appear to be likely.

In pleurodires and cryptodires, the fusion of the palatoquadrate to the braincase is realized differently and in a different time window. The late Eßwein-fixation to the quadrate in pleurodires could imply that the ancestral



more-cryptodiran-like mode of neck retraction is recapitulated through ontogeny with an embryonic neck retraction shifting from a diagonal towards a horizontal position. Stem pleurodires are rarely preserved in the fossil record (FERREIRA *et al.*, 2018a), but gradual change from a more cryptodiran-like (i.e., *Platycheilus oberndorferi*, ANQUETIN *et al.*, 2017) towards a pleurodiran-like mode of neck retraction is expected (WERNBURG *et al.*, 2015a). It is possible, that in the pleurodiran ancestor a gradual reduction of the otic trochlear process (through a surface roughness state as seen in the ‘most advanced stem-turtles’) occurred in parallel with the incorporation of processus pterygoideus externus to the jaw trolley system. In the case a transitional pleurodire ancestor had both trochlear processes, likely one of them was non-functional. To avoid the biomechanical disadvantage of a bitrochlear system – already in the developing embryonic skull – compensating rearrangements of the palatoquadrate and the attachment sites of the jaw musculature can be expected in order to create a functional jaw mechanism – with only one trochlear system – at hatching.

Most likely, stem-turtles were terrestrial vertebrates (JOYCE & GAUTHIER, 2004; JOYCE, 2015; LAUTENSCHLAGER *et al.*, 2018). The shell protected them against predators, and fast predatory behavior was certainly not possible on land (comparable to the extant cryptodiran tortoises) (NATCHEV *et al.*, 2015). Therefore, it is assumed that evolution of keratinous ramphothecae covering the jaws and the subsequent loss of marginal and palatal teeth were adaptations to herbivory (WEISHAMPEL & NORMAN, 1989; KING, 1996; HOTTON *et al.*, 1997; WEISHAMPEL, 1997; SUES & REISZ, 1998; SUES, 2000; WERNBURG, 2014; JOYCE *et al.*, 2016). Compared to stem-Testudines, crown turtles (Testudines) became aquatic animals and changed their feeding to aquatic omnivory and piscivory. As a reversal, only the cryptodiran tortoises (Testudinidae), *Terapene* (Emydidae), and a number of geoemydids (incl. *Geoemyda*, *Cuora*, *Rhinoclemmys*) went fully ashore and partly became herbivorous again with correlated adaptation of the jaw apparatus (VON BAYERN, 1884; ERNST

& BARBOUR, 1992; NATCHEV *et al.*, 2015), which could be useful for inferring feeding behavior in stem-turtles to some degrees. For feeding in water, suction feeding evolved, whereas tortoises evolved elongated tongues for food transport on land (NATCHEV *et al.*, 2015). The change of feeding behavior certainly had important influence on the functional morphology of the jaw musculature (WERNBURG, 2013b). It is difficult to estimate jaw muscle forces in stem-turtles and extrapolating the relatively low bite force in the herbivorous extant tortoises (HERREL *et al.*, 2002) to herbivorous stem-Testudines is not unproblematic. Nevertheless, an increase of jaw muscle forces can be assumed, which could have been correlated with skull stiffening (similar to crocodiles, temnospondyls, and mammals). We have shown that neck retraction behavior has influenced palatoquadrate fixation already in the still herbivorous ‘advanced stem-turtles’ (Fig. 2, character 7C), whereas a drastic change in feeding probably first appeared in the crown-group. Nevertheless, a reciprocal influence on skull fixation, at least through late turtle evolution, can be expected.

## Conclusion

1. Modern turtles, cryptodires and pleurodires, show distinctly different ways in developing their akinetic skulls, resulting in remarkable differences in adult skull architecture.
2. Whereas the anatomy of the stiffened snout is very similar in turtles since the appearance of Testudinata in the Triassic, the stabilization of the skull through a palatoquadrate to braincase fixation already occurred on the lineage towards the turtle crown though the ventral bracing of the cranioquadrate passage by the pterygoid.
3. Whereas cryptodires show the ancestral, late turtle-mode of palatoquadrate fixation, the Eßwein-mode of palatoquadrate fixation of pleurodires by appositional

← **Fig. 13. Biomechanics of palatoquadrate fixation in pleurodire and cryptodire turtles.** Chondrocranium (grey), palatoquadrate (blue), pterygoid, and parietal (brown) of a cryptodire (*Emys orbicularis*, Kunkel 1912; A–B, E) and of a pleurodire turtle (*Emydura subglobosa*, compare to Figure 3; C–D, F) with A, C) lateral view, B, D) cross section (frontal view), and E–F) in ventral view. Forces transmitted by neck muscles, skin, and connective tissue are indicated by red arrows running into the picture plane. In cryptodires, hidden-necked retraction in the embryo results in a posterodorsal and -medial force direction, whereas side-necked retraction results in a posteromedial force direction in pleurodires. As a consequence, the palatoquadrate rotates more lateral in cryptodires enabling the pterygoid to expand between basal plate and palatoquadrate (E). Anteriorly, the pterygoid process and the ascending process are pushed towards the future lateral braincase wall and the ascending process contributes to its formation (but see note in the text) (D). In pleurodires, posteromedial force direction results in a close association to the ear capsule hindering the pterygoid to expand caudally (F–G). The lateral rotation of the palatoquadrate keeps the pterygoid process in a certain distance from the secondary braincase wall and, as such, it cannot contribute to its formation. \* indicates the area of processus trochlearis otici in adult Cryptodira (D) and the processus trochlearis pterygoidei in adult Pleurodira (F). (a) Posterodorsal and posteromedial pull of the neck musculature. (b) Posterolateral pull of neck musculature. (c) Posteromedial pull of neck musculature. (d) Integration of the anterior part of the palatoquadrate to the secondary lateral braincase wall. (e) Rotation of the anterior part of the palatoquadrate apart from the secondary lateral braincase wall. Dashed lines in (D) and (F) indicate section levels of (E) and (G). Red dotted lines in (E) and (G) indicate the tympanic membrane, which highlights the vertical (f) respectively diagonal (g) orientation of the quadrate in both taxa.

bone from the quadrate evolved with the relatively recent evolutionary origin of this group.

4. The mode of palatoquadrate fixation is correlated with the taxon-specific mode of neck retraction, which is already performed in the embryos. Whether an actual causal link is present cannot be stated and can only be tested in life experiments. A posterodorsal and posteromedial retraction in late stem-turtles and in cryptodires, as well as a posterolateral and posteromedial direction of neck movement in pleurodires might have resulted in the specific rotations of the palatoquadrate in each taxon. To proof our hypothesis, the so far unknown skull of the stem pleurodire *Platychelys oberndorferi* should retain cryptodiran skull features, as this turtle likely had a cryptodiran mode of neck retraction (ANQUETIN *et al.*, 2017). Similarly, xinjiangchelyids with pleurodiran neck retraction (WERNEBURG *et al.*, 2015b) should show pleurodiran skull features, even though they are stem cryptodires.

5. In cryptodires, the processus ascendens of the palatoquadrate is incorporated in the secondary sidewall of the braincase and ossifies as a small epipterygoid. In pleurodires, a rotation of the anterior part of the palatoquadrate away from the secondary braincase wall prevents its inclusion to this wall and no epipterygoid is formed anymore.

6. The firm attachment of the posterior part of the palatoquadrate (i.e., quadrate) to the otic region of the braincase has important evolutionary consequences for the skull architecture of turtles. The primary temporal skull roof, which served to stabilize the quadrate in early turtle evolution, could be reduced and secondarily be transformed by neck retraction in a taxon-specific mode. The alternative fusions in pleurodires and cryptodires result in different orientations of the quadrate, and the jaw musculature bends around the hypertrophied turtle quadrate in different ways. Although anatomically possible, a *functional* intermediate stage between pleurodiran and cryptodiran trochlear systems seems unlikely from a biomechanical perspective.

7. A change in feeding habits and correlated jaw muscle force distribution may have supported the stabilization of the skull in crown turtles in addition to the forces introduced by neck retraction.

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## Appendix

**Abbreviation:** **ang**, angular; **ali**, alisphenoid (in mammals); **ap.pd** = dorsal sheet of pterygoidal aponeurosis; **ap.pv** = ventral sheet of pterygoidal aponeurosis; **art**, articular; **art.car.int**, arteria carotis interna; **art.st**, arteria stapediale; **at**, pleurocentrum of atlas (1st cervical vertebra); **ax**, centrum of axis (2nd cervical vertebra); **bo**, basioccipital; **bo.ap**, bodenaponeurose (coronar tendon); **bp**, basal plate; **br1**, -2, 1<sup>st</sup> and 2<sup>nd</sup> branchial arches (together with hyo, br1 contributes to the tongue bone in mammals; br2 and br3 form cartilago thyroidea, whereas br4 forms cartilage crocoidea; see also **cobrII**); **bs**, basisphenoid; **ca**, cupola anterior; **ca.ca.**, canalis cavernosum; **ca.la**, cavum labyrinthum; **ca.ty**, cavum tympanicum; **car.ary** = cartilago arytanoidea; **cd**, chorda dorsalis; **cer**, cerebellum; **CL**, carapace length; **cnuhya**, cornu hyale; **cobrI**, cornu branchial-I; **cobrII**, cornu branchial-II; **col**, columella (in non-mammalian tetrapods); **cpuhyo**, corpus hyoideus; **CRL**, crown-rump-length; **cr.bp**, crista basipterygoidea (can be developed as a genicular crest in pleurodires); **cr.pt**, crista pterygoidea (developed as a sub-stapedial crest in pleurodires); **cr.po**, crista parotica; **d**, days of incubation; **den**, dentary; **dic**, diencephalon; **eco**, extracolumella; **epi**, epipterygoid; **ety**, ectotympanic in mammals; **fe.bc**, fenestra basicranialis; **fe.hy**, fenestra hypophyseus; **fi.mo**, fissura metotica; **fi.on**, fissura orbitonasale; **fl.o**, fila olfactoria; **fo**, fenestra orbitale; **fo.ge**, foramen genicularis; **for.hpl**, foramen hypoperilymphaticum; **for.pp**, foramen prepalatinum; **fr**, frontal; **fs**, fenestra septale; **HL**, head length; **hm**, hyomandibula (see **col/sta**); **hyo**, hyoid (= hyal in non-tetrapods; its dorsal part forms proc. styloideus/mastoideus in mammals); **hy**, hypophysis; **in**, incus (in mammals); **ios**, inter-orbital septum; **ju**, jugal; **la**, labyrinth; **lac**, lacrimal; **lc**, labyrinth capsule; **vcl**, vena capitis lateralis; **lta**, lamina transversalis anterior; **mal**, malleus (in mammals, note: the dermal prearticular/gonial bone medial to the lower jaw forms the anterior process of the malleus in mammals); **mc**, mouth cavity; **Mc**, Meckel's cartilage; **me**, meniscus; **mec**, mesencephalon; **mx**, maxilla; **myc**, myelencephalon; **na**, nasal; **na1**, -2, neural arch of 1st and 2nd cervicals; **na1p**, proatlas (belongs to neural arch of the atlas); **nc**, nasal capsule; **occ**, occipital; **op**, opisthotic; **ot.ca**, otic capsule; **pa**, pila antotica; **pac**, processus accessorius; **pal**, palatine; **par**, parietal; **pb**, processus basitrabecularis (~ basipalatinus, ~ basipterygoideus - see text for nomenclature); **pf**, prefrontal; **pi.ao**, pila antotica; **pi.mo**, pila metoptica; **pi.oc**, pila occipitalis; **pl.ao**, planum antorbitale; **pl.ss**, planum suprasetale; **pmp**, processus maxillaris posterior;

**pm**, pila metotica; **pmx**, premaxilla; **pn.ao**, planum antorbitale; **po**, postorbital; **po.fr**, postfrontal; **popa**, postparietal; **pp**, processus pterygoideus palatoquadrati; **pr**, prootic; **preart**, prearticular; **pr.fr**, prefrontal; **pr.ac.pq**, processus ascendens palatoquadrati; **pr.am**, processus alveolaris maxillaris; **pr.inf.par**, processus inferior parietalis; **pr.pfm**, processus prefrontalis maxillaris; **pr.plm**, processus palatinus maxillaris; **pq**, palatoquadrate; **pro**, processus odontoideus (intercentrum of atlas); **ps.ec**, pars entochonialis; **ps.ps**, pars parasetale; **pt**, pterygoid; **pr.pt.pq**, pterygoid process of the palatoquadrate; **qj**, quadratojugal; **qu**, quadrate, respectively pars quadrata palatoquadrati in embryos (see in); **rci**, rhomencephalic isthmus; **re.im**, region intermedialis; **re.o**, region olfactoria; **sc**, sclera (can be cartilaginous, belongs to the chondrocranium, (GAUPP, 1906)); **sec**, sphenethmoid commissure; **se.n**, septum nasi; **se.in**, septum interorbitale; **sp**, splenial; **sq**, squamosal; **st**, supratemporal; **sta**, stapes (in mammals); **surang**, surangulare; **ta**, tabular; **tma**, taenia marginalis; **tme**, taenia medialis; **tec**, telencephalon; TK, stage of TOKITA & KURATANI (2001); **tr**, trabecle; **tra**, trachea; **tr**, trabecle; **tr.co**, trabecula communis; **tso**, tectum synoticum; **ty.m**, tympanic membrane; **t.st** = taenia supratrabecularis (FUCHS); **ur**, upper ramphotheca; **ven.cap.lat**, vena capitis lateralis; **vo**, vomer; **II**, tractus opticus; **III**, (foramen for) nervus (n.) oculomotorius; **IV**, nervus trochlearis; **V**, (foramen for/ganglion of) n. trigeminus (ganglion Gasseri); **V1**, nervus ophthalmicus trigemini; **V2**, nervus maxillaris trigemini; **V3**, nervus mandibularis trigemini; **VI**, n. abducens; **VII**, ganglion of nervus facialis (ganglion genicularis); **VIIct**, chorda tympani; **VIIh**, ramus hyomandibularis n. facialis; **VIIp**, ramus palatinus n. facialis; **VIII**, n. statoacusticus; **IX**, ganglion of n. glossopharyngeus; **VII/IXrc**, ramus communicans n. IX – n. VII for n. IX externus; **X/XI**, ganglion of n. vagus (X) and accessories (XI); **ZWK**, Zuwachsknochen (appositional bone ventromedial to the quadrate in pleurodires); **19**, musculus (m.) adductor mandibulae externus Pars profundus; **21**, m. adductor mandibulae externus Pars superficialis; **22** = m. zygomaticomandibularis; **23**, m. adductor mandibulae internus Pars pseudotemporalis; **26**, m. adductor mandibulae internus Pars pterygoideus dorsalis; **27**, m. adductor mandibulae internus Pars pterygoideus posterior; **28**, m. adductor mandibulae internus Pars pterygoideus ventralis; **29**, m. adductor mandibulae posterior; **31**, m. intermandibularis; **38**, m. retractor bulbi; **55**, m. branchiohyoideus; **64**, m. geniohyoideus. Muscle numbers refer to Werneburg (2011).

