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Author: Werneburg, Ingmar

Source: Zoological Science, 30(3) : 141-153

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.30.141>

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[REVIEW]

The Tendinous Framework in the Temporal Skull Region of Turtles and Considerations About Its Morphological Implications in Amniotes: A Review

Ingmar Werneburg*

*Geowissenschaftliches Institut der Eberhard-Karls-Universität,
Hölderlinstraße 12, 72074 Tübingen / Germany*

In 1926, Tage Lakjer hypothesized a replacement of the infratemporal bar in diapsids by a ligament spanning between quadrate and the upper jaw. As a similar ligament is also present in turtles, he argued for a diapsid origin of this group. Based on recent advances in the homologization of the tendinous framework in the reptile jaw adductor chamber – reviewed in this paper – one could argue for independent origins of the cheek ligaments in sauropsids. The quadratomaxillar ligament of turtles could, with reservation, be homologized with the quadrate aponeurosis of other sauropsids, as well as to the superficial tendon of *m. masseter* in mammals. These structures have a strong morphogenetic influence to cranial anatomy. Given such an identity, the hypothesis of a structural replacement of the lower temporal arcade in lizards would be refuted. Moreover, such a homology could be correlated to the evolution of the middle ear and to the origin of the chewing mechanism in mammals, which contributed to the evolutionary success of that group. The homologization presented herein is critically discussed and is open for revision. Nevertheless, the value of tendinous structures for fundamental homologisations in the vertebrate head is highlighted.

Key words: bone arches, ligaments, jaw musculature, reptiles, mammals, ligamentum quadratojugale, homology

Turtle origins and temporal bone arrangements

The phylogenetic origin of turtles is highly debated, particularly because of the unique arrangement of skull bones (Fig. 1). The basal most Testudinata lack any fenestration in the temporal region, which, in contrast, can be recognized in Synapsida (Fig. 1F), Diapsida (Fig. 1A, C), and among several fossil parareptilians (Fig. 1E). Plesiomorphically, the anapsid condition can be recognized in anamniotes (Fig. 1G), several parareptilian, and early eureptilian clades. The arrangement of the temporal bones in Testudinata (Figs. 1D, 2G–J), however, is barely comparable to the “typical” anapsid skull (Müller, 2003) and raises difficulties in reconstructing the position of turtles among amniotes in phylogenetic analyses (Werneburg, 2012) and resulted in a variety of hypotheses for turtle origin (Rieppel, 2008).

Cladistic analyses observing the phylogenetic position of turtles only detected few cranial characters supporting either hypothesis. The amount and quality of characters and the results are clearly dependent on the anatomical, taxonomic, and methodological focus of the respective authors.

Nevertheless, different cranial characters, exemplarily cited in Table 1, support either relationship. They should serve as an overview to this topic and should highlight the scant knowledge and understanding we currently have on the arrangement of temporal bones. Given the derived shape of dermatocranial bones in turtles (Müller, 2003) it is worth mentioning that several derived features are detected for a position of turtles among non-diapsid-clades (Table 1).

Definition of the spatial anatomy in the temporal region (Fig. 1A–B)

Several synonyms exist on the terminology of spatial structures in the temporal region of the tetrapod skull. To avoid confusion and for clarification, I define the terminology that I use herein.

1. *Temporal openings* are herein defined as reductions of the plesiomorphically complete dermatocranial temporal armour, which was present in early tetrapods. These openings involve temporal fenestrae and/or emarginations, the origins of which are not well understood and remain the subject of recent debates (reviews by Rieppel, 1993; Werneburg, 2012).

1a. *Emarginations* are marginal excavations of the temporal dermatocranial armor, which appear in several tetrapod groups. In turtles, ventrolateral and posterodor-

* Corresponding author. Tel. : +49-7071-29-78929;
Fax : +49-7071-29-5059;
E-mail: i.werneburg@gmail.com

doi:10.2108/zsj.30.141

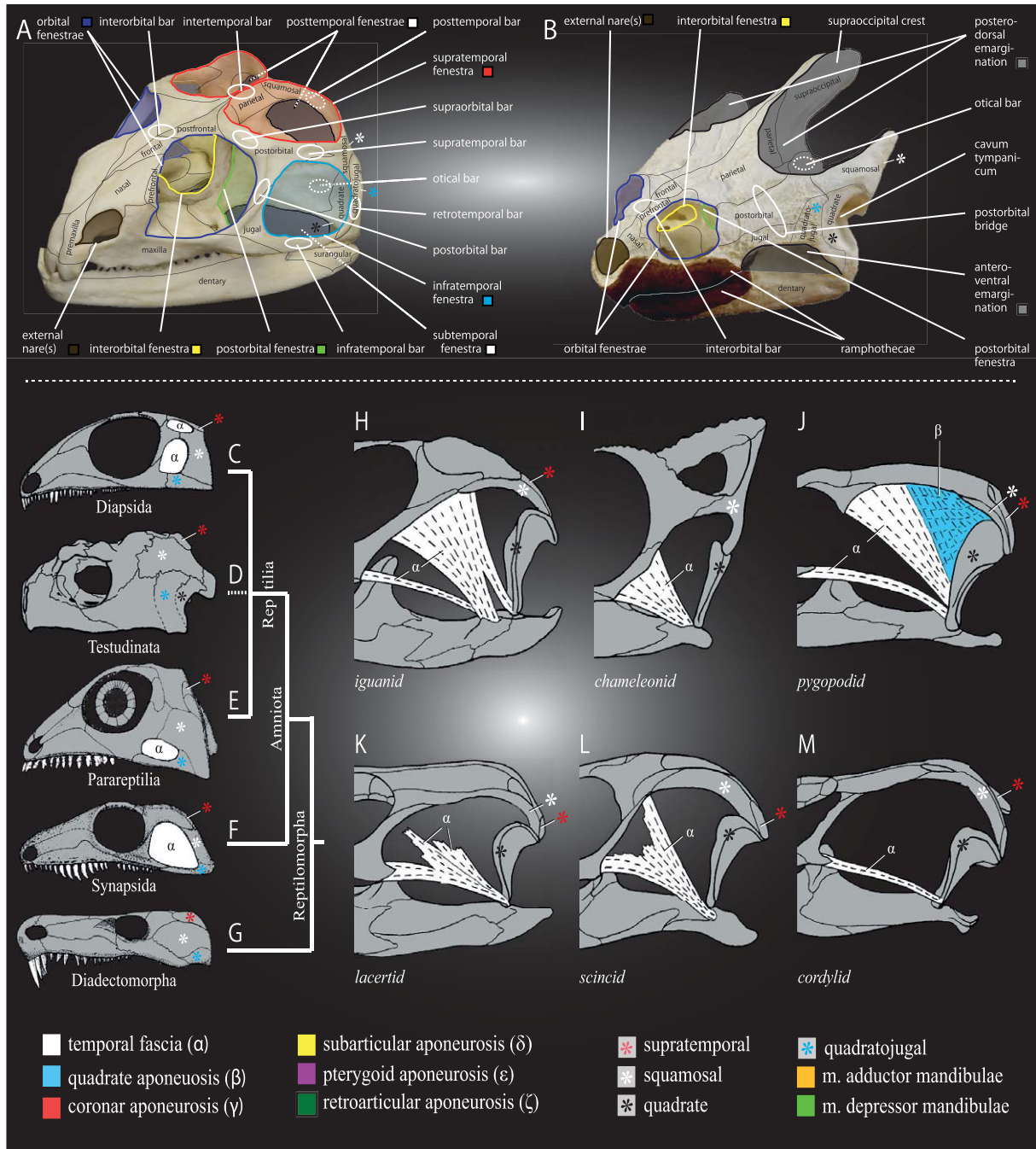


Fig. 1. The temporal region of amniotes. (A–B) Terminology used herein, modified from Jones et al. (2010) and Werneburg (2012). (A) *Sphenodon punctatus*, (B) Testudines: *Chelydra serpentina*. (C–M) The temporal region with the temporal fascia(ε) and below the legend for Figs. 1 (C–M) and 2. (C–G) major taxa of Reptilomorpha with an uncertain position of turtles. (H–M) Diversity of the temporal fascia in Squamata. (C) *Petroplacosaurus* (image modified from: Carroll, 1988); (D) *Proganochelys quenstedtii* (Gaffney, 1990); (E) Bolosauridae: *Bolosaurus* (Carroll, 1988); (F) Varanopidae: *Aerosaurus* (Benton, 2005); (G) *Limnoscelis* (Romer, 1956); (H) *Leiocephalus cubensis* (lordansky, 1996); (I) *Chamaeleo bitaeniatus* (lordansky, 1996); (J) *Pygopus lepidopodus* (lordansky, 1996): the temporal fascia is continuous with the quadrato aponeurosis; (K) *Lacerta trilineata media* (lordansky, 1996); (L) *Eumeces schneideri* (lordansky, 1996); (M) *Cordylus cordylus* (lordansky, 1996).

sal emarginations can appear to different extents (Kiliyas, 1957; Rieppel, 1993; reviewed by Werneburg, 2012). If in turtles both emarginations meet in the middle (e.g., *Terrapene*, Fig. 2J) or if one emargination is extremely expanded (e.g., *Chelodina*), the temporal dermatocranial armor is open laterally. Following my definition, emarginations can also be recognized among other tet-

rapod taxa.

1b. *Temporal fenestrae* are bony surrounded openings in the dermatocranial armor. The supratemporal fenestra appears to be apomorphic in adult Lepidosauromorpha, Archosauromorpha, and some early Diapsids. The presence of an infratemporal fenestra is either highly discussed as being apomorphic for Lepidosauromorpha.

Table 1. Cranial bone associated characters for Testudinata + its potential sister taxon summarized from selected cladistic analyses. Lower jaw or hyoid associated characters are not listed.

Testudinata + Pareiasauria (Lee, 1997)
a long lateral flange of exoccipital, opisthotic-squamosal suture, loss of ventral otic fissure, greatly thickened floor of brain cavity, blunt cultriform process, greatly inflected choana, large foramen palatinum posterius, reduced transverse flange of the pterygoid, palate raised above tooth row, supraoccipital with long sagittal suture along the skull roof, fusion of postparietals, frontal excluded from orbital margin, dorsal lump on distal end of retroarticular process, labio-lingually flattened teeth, seven or more cusps on teeth in upper jaw. Possible further diagnostic features are a fused basicranial articulation with a possible reversal in <i>Proganochelys</i> , a massive, curved paroccipital process, closed interpterygoid vacuities, lachrymal re-enters external naris (reversal, later 'unreverses' in turtles), pineal foramen near fronto-parietal suture, an enlarged quadratojugal, cranial dermal ornament composed of low bosses and regular radiating ridges
Testudinata + Procolophonia (Reisz and Laurin, 1991)
the cultriform process is greatly reduced in length; the teeth on the transverse glange of the pterygoid are lost and are replaced by a ventral ridge; a distinctly shaped anterodorsal expansion of the maxilla is formed directly posterior to the external naris; the prefrontal and palatine are massively buttressed against each other; the dorsal process of the quadrate is exposed laterally, but the edge of the well developed tympanic notch is formed by the squamosal and the enlarged quadratojugal (also present in <i>Proganochelys</i>); the slender stapes has lost both its dorsal process and foramen; the postparietale is greatly reduced or lost
Testudinata + Captorhinidae (Gauthier et al., 1988)
Tabular absent, ectopterygoid absent as discrete element in adult, suborbital fenestra small
Testudinata + Captorhinidae (Gaffney and Meylan, 1988)
Medial process of jugal present, ectopterygoid absent, area filled by jugal, pterygoid, and palatine with suborbital fenestra usually in jugal-palatine suture; tabular absent; foramen orbito-nasale present
Testudinata + Sauropterygia (deBraga and Rieppel, 1997)
the choana curve posteromedially so that the long axis would form an angle of about 45° with the medial surface of the maxilla; the parasphenoid is compressed into a nearly square element where its length is never more than 20% of its narrowest transverse width; transverse flange of the pterygoid is directed anteriorly at an angle of less than 45° to the parasagittal axis and the lateral and forward portions of the transverse flange merge smoothly forming a curved anterolateral margin
Testudinata + Lepidosauria (Müller, 2004)
Unequivocal: premaxillae are small; ACCTAN optimization: squamosal remains distinctly restricted to the dorsal region of the cheek; tooth implantation – teeth are superficially attached to bone; Müller (2004) mentioned that authors suggesting a close relationship of turtles to lepidosaurs refer to the common the semi-lunate embryonic shape of the jugal in squamates, <i>Sphenodon punctatus</i> , and turtles
Testudinata + Archosauromorpha (Bhullar and Bever, 2009: hypothesis A)
quadrate exposed laterally; crista prootica present; Unambiguous synapomorphies along the lineage leading to Archosauriformes, but lacking in <i>Proganochelys</i> (requiring reversal if <i>Proganochelys</i> is allied to Archosauriformes), are: snout greater than or equal to 50% of skull length; antorbital fenestra present; maxillary ramus of premaxilla extends as posterodorsal process to form caudal border of naris; ratio of lengths of nasal and frontal greater than 1.0; postparietal present; quadrate emargination present with conch; orientation of basiptyergoid processes lateral; internal carotid foramina on ventral surface of parasphenoid; post-temporal fenestra small
Testudinata + Archosauriformes (Bhullar and Bever, 2009: hypothesis B)
septomaxilla absent; laterosphenoid present

morpha or for early Diapsida, or as being not apomorphic at all (Evans, 2008). As shown by Müller (2003), multiple losses of the lower temporal arcade and reversals in the formation of the infratemporal fenestra can appear (e.g., *Sphenodon-punctatus*-lineage). This is related to the formation or reduction of the infratemporal arch. A supposed reduction of such a border can result in the formation of an emargination *sensu stricto* (s.s.). The closing of an emargination by a temporal arch can result in the bordering of a temporal fenestra s.s.

2. *Temporal bony bar* (= *arches*, *arcades*) border tem-

poral fenestrae. For nomenclature, I basically follow Jones et al. (2009). A full set of temporal bony arches is visible in *S. punctatus* (Fig. 1A). Temporal bony arches just describe bony bars in the skeletal architecture and do not necessarily indicate homologous bone elements. The posttemporal bar, for example, can be formed by different bones, and bones contribute to a different extent; some bones (e.g., supratemporal) can even be reduced during development of a species (Rieppel, 1992; Koyabu et al., 2012). The temporal openings, and consequently also the temporal bony arches, appeared several times independently in early amniote evolution (Tsuji and Müller, 2009; Piñeiro et al., 2012). As such,

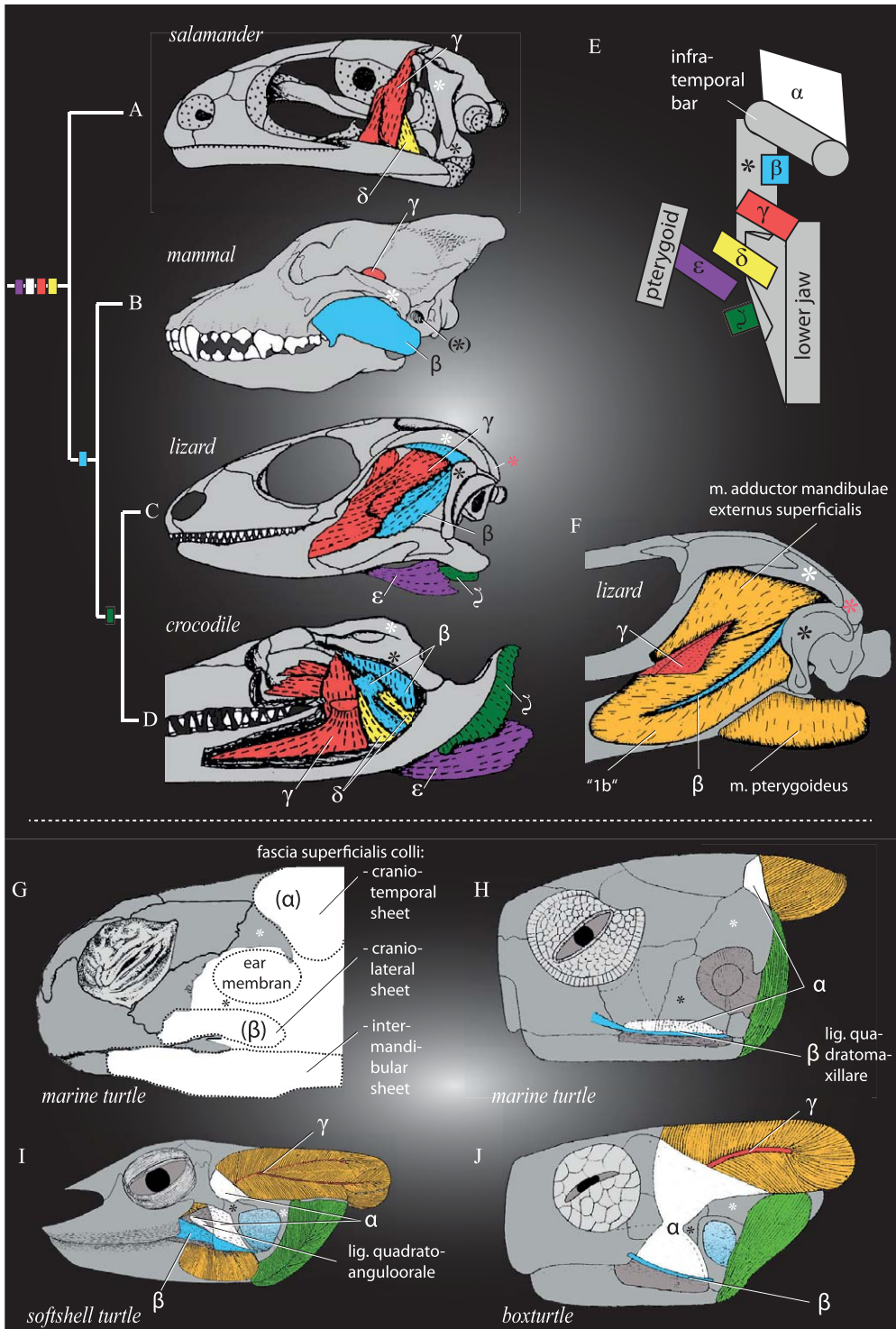


Fig. 2. Evolution and diversity of ligaments in the jaw adductor chamber region. **(A)** Lissamphibia: *Salamandra salamandra* (image modified from: Iordansky, 1994), temporal fascia not shown, subarticular aponeurosis partly covered laterally; **(B)** Mammalia: *Canis lupus* (Schumacher, 1961), the coronar aponeurosis (red) is ossified and integrated to the processus coronoideus; **(C)** Squamata: *Eumeces schneideri* (Iordansky, 1994), subarticular aponeurosis is covered laterally, temporal fasciae not shown; **(D)** Crocodylia: *Crocodylus siamensis* (Iordansky, 1994), lateral aspect of the temporal armour and lower jaw are removed, temporal fasciae not shown; **(E)** schematic illustration of the distribution of ligaments in the temporal and adductor region from anterolateral view; **(F)** Squamata: *Gerrhosaurus nigrolineatus* Rieppel (1980): m. levator anguli oris, ritual plate, lig. quadratojugal, and superficial muscle fibres of 1b (Rieppel, 1980: figure 8B) – muscle fibre courses are partly redrawn. In the tree the distribution of temporal ligaments is indicated. **(G–J)** Diversity of the temporal ligaments in Testudines. **(G)** Chelonioidae: *Chelonia mydas*, temporal sheet of the fascia superficialis colli larger drawn than in the original figure; **(H)** Chelonioidae: *Eretmochelys* (“*Chelone*”) *imbricata*, intermandibular fascia not visible, posterodorsal part of the temporal fascia partly indicated; **(I)** Trionychidae: *Amyda* (“*Trionyx*”) *cartilaginea*, intermandibular fascia not visible, posterodorsal part of the temporal fascia partly indicated; **(J)** Testudinidae: *Terrapene* (“*Cistudo*”) *carolina*, intermandibular fascia not visible, posterodorsal part of the temporal fascia partly indicated based on own comparative literature review, lig. quadratoanguloorale added based the description of Schumacher (1956) and personal observations. **(G)** modified from Schumacher (1956), **(H–J)** modified from Lakjer (1926). For legend see Fig. 1.

the infratemporal bars and fenestrae of synapsids, diapsids, and diverse parareptiles are mostly convergent developments in the lower temporal region.

3. *Bars vs. bridges* (Fig. 1B). The term *zygomatic bar* is usually used for the infratemporal bar s.s. of mammals (Greek Ζυγόμα = “yoke”). In turtles with a strong posterodorsal and weak anterolateral emargination, a similar structure forms in the temporal dermatocranial armour (e.g., Chelydridae,

Trionychia; Figs. 1B, 2I). As this structure does not border a temporal opening s.s. as it does in mammals, I use the term *zygomatic* or *postorbital bridge* to refer to the reduced temporal dermatocranial armor, to refer to a particular shape of emarginations in these turtles. In some turtle groups, the anteroventral emargination is widely expanded, resulting in a tiny remainder of the temporal dermatocranial armor posteriorly. I call this structure the *posttemporal bridge* (e.g.,

Werneburg, 2011: *Emydura subglobosa*), whereas the post-temporal bar in *S. punctatus* forms the posterior border of the supratemporal fenestra (Fig. 1A).

The ligament argument

To strengthen their hypotheses, studies suggesting a closer relationship of turtles to the subgroups of Diapsida (Müller, 2003; Rieppel and DeBraga, 1996) have referred to Tage Lakjer's (1926) 'studies on the trigeminus innervated jaw musculature of sauropsids'. This work represents one of the most influential, detailed, and comprehensive studies on reptilian jaw musculature; and fundamental considerations about homologies and distributions of cranial musculature among tetrapods are presented therein (Diogo and Abdala, 2010; Werneburg, 2011). Lakjer (1926) described the "ligamentum [lig.] quadrato-maxillare" as present in snakes, lizards, and some bird taxa, all of which would lack the quadratojugal bone. Consequently, Lakjer (1926: 27, 45) argued that this ligament structurally replaces the quadratojugal bone (his "quadrato-maxillare") in those diapsids to form the lower border of the infratemporal fenestra and to bridge the quadrate with the upper jaw. Lakjer (1926: 48) also found a quadrato-maxillar ligament in extant turtles, and consequently also hypothesized a replacement of the lower bony temporal arcade in this taxon. He argued hence for a "true lower fenestra" in turtles, surrounded by quadrate, jugal, squamosal, maxilla, and "lig. quadrato-maxillare."

The confusion of cranial bone identity

Lakjer (1926) only studied anatomical features among extant turtles, and did not refer to stem Testudinata (e.g., *Proganochelys quenstedti*, Jaekel, 1915). This resulted in a misidentification of two cranial bones in turtles, which formed the basis of his hypothesis. Stem Testudinata show a plesiomorphic set of temporal bones forming a fully sutured, pure anapsid condition; namely the jugal, parietal, postorbital, quadrate, quadratojugal, squamosal, and supratemporal (Gaffney, 1990; Joyce, 2007; Li et al., 2008). Now, it is generally accepted that the supratemporal, a bone in the posterodorsal region of the skull, is lost in modern turtles (Joyce, 2007). However, by comparing to other extant sauropsids, Lakjer (1926) identified the quadratojugal of turtles to be his "squamosal" and the squamosal to be his "supratemporal;" consequently, he argued for a loss of the quadratojugal and its replacement by "lig. quadrato-maxillare," as he hypothesized for some diapsids. The actual presence of the quadratojugal in turtles, however, highlights that at least in turtles the "lig. quadrato-maxillare" is not a replacement of the quadratojugal bone. Referring to Lakjer's (1926) confidence of a "true lower fenestra" in turtles, Rieppel (1990) briefly indicated that, based on the development and architecture of the jaw musculature in the snapping turtle *Chelydra serpentina*, "...the arrangement of the jaw adductor musculature clearly refutes the homologies in the turtle skull as hypothesised by Lakjer [1926]." Rieppel (1990) did not focus on the homology of ligaments in detail; however, he stated that it "might indeed appear reasonable in view of developmental plasticity of precursor cells" that the lower temporal arcade could be replaced by a ligament.

Basic anatomical terms of tendinous structures in the cranium

As for the bony and spatial structures of the temporal region defined above, certain confusion exists about the terminology and identity of tendinous structures in that region. Following Schumacher (1956), Iordansky (1994), Hertwig (2005), and Werneburg (2007, 2011), herein, I distinguish tendinous structures as follows:

1. *Tendons* are elongated tendinous attachments of muscular structures.

2. *Aponeuroses* are flat tendinous attachments of muscular structures often forming a glossy surface (German "Sehnenspiegel:" 'tendon-mirror').

3. *Ligaments* are elongated, string-like tendinous structures spanning between bones.

4. *Fasciae* are flat tendinous structures spanning around muscles, muscle groups, or between bones. The term *membrane* is often used as synonym to fasciae; it refers more to a very thin fascia-appearance.

As derivatives of cranial neural crest cells (Hall, 2008), tendinous structures of the head/neck region are thought to structuralize the mesoderm, and hence the developing musculature during embryogenesis (Olsson et al., 2001; Ericsson et al., 2004; Schmidt et al., 2013). In accordance with this concept, Iordansky (1994) highlighted the importance of tendinous structures to homologize major separations of the jaw musculature among tetrapods above several other criteria of muscle homologisation [see that approach adopted by Werneburg (2011) for turtle musculature]. If a muscular structure is reduced, tendons and aponeuroses can turn into ligaments. Also, tendons can flatten and evolutionarily develop into aponeuroses in spite of this plasticity (see examples in Werneburg, 2013).

Tendons and aponeuroses are related to fasciae in a morphological sense. They are connected to each other in development and evolution, and can turn into each other respectively.

An even greater confusion exists about the terminology and homology of muscular structures. Herein, I refer to my previous definitions (Werneburg, 2011, 2013).

Tendinous framework of the jaw adductors musculature

Iordansky (1994) presented a thorough classification of the tendinous structures related to the jaw adductor musculature in Tetrapoda. He identified a coronar and a subarticular aponeurosis to bear and to structure the external and internal adductor muscles, respectively (Fig. 2A–E). Those and further tendinous structures found in the cranium are listed below and, where relevant, I list subdivisions.

Recently, I reviewed the literature on tendinous structures in the head of turtles and presented synonymizations (Werneburg, 2011: appendix 5). Homologous structures are only occasionally described for other tetrapods and did not experience a comparable categorization. As such, several tendinous structures listed in the following can only represent a preliminary list of potentially homologous structures among tetrapods (Fig. 2).

Jaw adductor muscle related aponeuroses (Fig. 2A–F)

1. *Coronar aponeurosis* ("y" and red in the Figures). The coronar aponeurosis attaches to/around the coronoid (pro-

cess) of the lower jaw. It serves as an insertion site for fibers of the external adductor mandibulae muscle in Reptilia and Lissamphibia (Iordansky, 1994). It is ossified in mammals (Gaffney, 1975; Frazetta, 1968) and in this group it serves as insertion site for the temporalis muscle, which is partly homologous to the external adductor muscle of Reptilia (Lubosch, 1938a, b; Schumacher, 1961; Diogo and Abdala, 2010; Kemp, 2005).

2. *Subarticular aponeurosis* (“δ” and yellow in the Figures). The subarticular aponeurosis represents a ventromedial separation from the coronar aponeurosis (Iordansky, 1994) and is partly still fused with it in Testudines (Werneburg, 2011). It attaches to the medial side of the lower jaw and serves as an insertion site for the internal adductor mandibulae structures in Reptilia and Lissamphibia (Iordansky, 1994).

In Mammalia, the musculus [m.] pterygoideus lateralis is generally considered as being at least partly homologous to the external adductor muscle in Reptilia (Diogo and Abdala, 2010). It is situated medially to m. temporalis and also inserts to the condylar region of the lower jaw (Schumacher, 1961; Turnbull, 1970); hence, its insertion tendon near the coronar region could be interpreted as an autapomorphic duplication of the coronar aponeurosis. However, given the preferential significance of the tendinous framework for the homologization of jaw musculature herein (Iordansky, 1994), the tendon of the external pterygoid muscle should be interpreted as subarticular aponeurosis and hence the muscle would need to be reconsidered as being only homologous to the internal adductor musculature of Sauropsida.

3. *Pterygoid aponeurosis* (“ε” and purple in the Figures). The pterygoid aponeurosis serves as an insertion site for the palate-related parts of the internal adductor structures (pterygoid muscle structures) to the pterygoid in Reptilia (Iordansky, 1994; Werneburg, 2011). In some turtle taxa the pterygoid aponeurosis is integrated to the subarticular aponeurosis (e.g., Poglayen-Neuwall, 1953), which could indicate a subsequential separation of the former in evolution and development.

As the medial most separation of the jaw adductor musculature in Mammalia (Diogo and Abdala, 2010; Schumacher, 1961), the m. pterygoideus medialis is usually considered as being homologous to parts of the internal adductor musculature in Reptilia (Diogo and Abdala, 2010). Bearing in mind the considerations on the homology of the lateral pterygoid muscle of mammals, the tendinous framework associated to the medial pterygoid muscle in mammals could be homologized to the pterygoid aponeurosis of Reptilia. Due to the separation of the posterior bone elements apart from the lower jaw in Mammalia (middle ear evolution) (Abdala and Damiani, 2004; Kemp, 2005), the positional relationship of coronar, subarticular, and pterygoid aponeuroses to each other differs from the spatial relationship found in Lissamphibia and Reptilia (Iordansky, 1994).

In Sauria, which represent the crown Diapsida, Iordansky (1994) additionally recognized the apomorphic presence of a quadrate and a retroarticular aponeurosis.

4. *Retroarticular aponeurosis* (ζ and green in the Figures). This aponeurosis represents a subsequential separation of the subarticular aponeurosis, which is attached to the retroarticular process. The aponeurosis is not found in tur-

tles, mammals, and lissamphibians.

5. *Quadrate aponeurosis* (“β” and blue in the Figures). The quadrate aponeurosis was named by Iordansky (1994) and identified to be present in lepidosaurs and archosaurs. It attaches to the anterior face of the bar-shaped quadrate in these groups and is associated to the lateral face of the external jaw adductor musculature. Rieppel (1980) found the quadrate aponeurosis to be associated to a distinct bundle of muscle fibres (redrawn in Fig. 2F). As such, that ligament appears to serve as a patterning structure in the external jaw musculature.

Further tendinous structures of the cranium

Besides other tendinous structures of the skull, which are not discussed herein (see Hacker and Schumacher, 1954; Iordansky, 1994; Werneburg, 2011), the following are relevant:

6. *Fascia temporalis* (“α” and white in the Figures). The temporal fascia spans above/between the temporal openings of amniotes, namely the emarginations of turtles (Werneburg, 2011) (Fig. 2G–J) and the temporal openings of saurians (Iordansky, 1996) and mammals (Fig. 1C, F, H–M).

The temporal fascia in tuatara and crocodiles is separated in two parts, the infra- and supratemporal membranes (Fig. 1C). They are restricted within the borders of the temporal fenestrae. In 1996, Iordansky studied the diversity of the temporal fascia among squamates in detail.

In saurian taxa, in which either the ventral temporal arcade is absent or incomplete [squamates, some birds (Lakjer, 1926)], a ligament is present, which represents the remainder of the lower temporal fascia in this skull region (Iordansky, 1996). Whether a lower temporal arcade was actually present in the ground pattern of Squamata or even of Diapsida is highly debated (Müller, 2003; Evans, 2008). If not, the lower temporal opening of squamates could, with reservation, be called an emargination s.s. rather than an opened temporal fenestra s.s.

Schumacher (1956) stated that in turtles the temporal fascia would represent a non-separated structure. In taxa with a large posterodorsal emargination (type I of Kiliias, 1957; see Werneburg, 2012), including taxa with postorbital bridges and small anteroventral emarginations (Figs. 1B, 2), this would span within the borders of the posterodorsal opening. In taxa with a large anteroventral emargination (type II of Kiliias, 1957), it would span within the borders of the anteroventral opening only. In the latter case, it would be attached to a ventrolateral ligament (discussed below). Whereas in type I the epaxial neck musculature would attach to the temporal fascia posteriorly, the musculature would attach to the posttemporal bone bridge in type II. In taxa of type II, which have lost the posttemporal bridge (e.g., *Chelodina*), the musculature would attach to the temporal fascia (Schumacher, 1954/55). As reviewed by Werneburg (2011), and contra Schumacher (1954/55), actually two parts of the temporal fascia are present in turtles. This is supported by the observations by Lakjer (1926), Jones et al. (2012), and others. Poglayen-Neuwall (1953) described a ventral insertion of the temporal fascia to the rictal plate (German: “Mundplatte”) in turtle species, which lack a postorbital (zygomatid) bridge. However, *sensu* Schumacher (1954/55), he was not sure, if—in addition to a posterodorsal

fascia—an anteroventral fascia is actually present in taxa with a postorbital bridge. He found a separated lig. quadratomaxillare in all species.

One should be careful not to homologize a priori the anteroventral and the posterodorsal temporal fascia of turtles to the temporal fasciae spanning within the temporal fenestrae in diapsids, or even in mammals, as these soft tissue structures apparently only fill up empty spaces of the skull to border the adductor chamber laterally and appear to plastically follow the formation of the skull bones during ontogeny. Certainly one could homologize the temporal fascia(e) in general among species as being cranial neural crest cell [cNCC]-derived material in the lateral skull region, however, its actual separations seem to follow more robust anatomical structures, such as the cNCC-derived bones.

The so-called “temporal fascia” in mammals represents a “two-layer structure,” including a deep and a superficial layer (e.g., Wormald and Alun-Jones, 1991; Campiglio and Candiani, 1997). The deep layer is associated to the m. temporalis, and hence corresponds to the fascia(e) of the nervus trigeminus innervated jaw muscles (m. adductor mandibulae complex; see below). The external layer corresponds to the temporal fascia s.s. and spans above the temporal fenestration. Mammals have lost the posttemporal opening.

7. *Fasciae of the jaw muscles.* As summarized by Hacker and Schumacher (1954) and Werneburg (2011: appendix 5), there are several fasciae directly covering the subdivisions and aspects of mm. adductor mandibulae et intermandibularis separately.

8. *Fascia colli superficialis.* This fascia is spanned around the whole neck musculature and attaches to the posterior region of the skull (Hacker, 1954; Hacker and Schumacher, 1954; Schumacher, 1956c). Following the authors, it can form three tendinous sheets anteriorly, which I name Partes craniolateralis, craniotemporalis, et intermandibularis. The former attaches superficial to the ear region, Pars craniotemporalis lies superficial to fascia temporalis, and the latter represents an intermandibular continuation of the neck fascia and lies superficial to the fascia of m. intermandibularis. This differentiation is best developed in the marine turtle *Caretta caretta* (Fig. 2G), which cannot retract its head inside the shell. The cranial sheets of the superficial neck fascia seem to support the relatively stiffened head-neck-system.

Tendinous structures at the ventrolateral border of the adductor chamber

A ligament is spanning along the ventrolateral border of the adductor chamber—the “cheek”—in lizards, birds (those, which lack the quadratojugal bone), and turtles.

Lordansky (1996) studied the diversity of this ligament among lizards (*sensu* Evans and Jones, 2010) in detail. Lizards represent taxa, in which no or only an incomplete infratemporal bony bar is present. The author clearly identified and illustrated the ligament to represent the ventral aspect of the temporal fascia s.s. (Fig. 2F–K). Its anterior end attaches to the posterior tip of the maxilla/jugal and/or laterally to the rictal plate in lizards, while its posterior end attaches to the ventral tip of the quadrate or dorsolaterally to the lower jaw (Lordansky, 1996; Herrel et al., 1998). In lizards and birds, the cheek ligament lies ventrolaterally to the

quadrate aponeurosis (Lakjer, 1926; Lordansky, 1996).

In turtles, the structure at the ventrolateral border of the adductor chamber varies in consistence and expansion resulting either in a ligament or in a more fascia-like/membranous appearance attaching to the surrounding bones differently. Also the texture would vary from a rigid, to a fibrous, or to a softer consistence. As such, Schumacher (1953/54, 1954/55, 1956) did not allocate (“homologize”) those structures to each other and introduced different synonyms (i.e., ligamentum quadratomaxillare *sensu* Lakjer, 1926, squamoso-jugo-maxillaris, et ligamentum temporo-quadrato-mandibulare). However, due to obvious positional criteria (Remane, 1952), I define the structures to be homologous among all turtles (*sensu* Lakjer, 1926). Only in the big-headed turtle *Platysternon megacephalon* (Platysternidae), which, as a derived condition, has an extreme ventrolateral bone coverage of the temporal region, Schumacher (1954/55) did not find any ligament or membrane.

Medially to the lig. quadratomaxillare, Schumacher (1956) discovered a further, strong ligament to be present in several turtle species. It stretches between the quadrate and the angle of the mouth, and was named ‘lig. angulo-orale’. It is particularly well-developed in soft-shelled turtles (Trionychidae), which have a great lip-expansion and hence a mightily developed rictal (mouth-) plate. As such, two elongated tendinous structures are present at the ventrolateral border of the adductor chamber of turtles, the lateral lig. quadratomaxillare and the medial lig. quadratoangulo-orale.

On the homology of the cheek ligaments among sauripsids

Compared to the cheek ligament of lizards and birds, which represents an integrative part of the fascia temporalis (Lordansky, 1996), the lig. quadratomaxillare of turtles is separated from the temporal fascia (Poglayen-Neuwall, 1953; Schumacher, 1953/54, 1954/55, 1956; Werneburg, 2011) and although it can attach to the temporal fascia medially, it is easily separable from it in a preparation.

In my opinion, the cheek ligament of lizards and birds is unlikely to be homologous to lig. quadratomaxillare of turtles for the following reasons. First, the turtle ligament lies laterally to the whole temporal fascia and is only superficially attached to it. Only Schumacher (1954/55: 513) described the ligament as a ‘lateral and ventral thickening’ of the temporal fascia in the turtles *Emydura krefftii* and *Hydromedusa tectifera*. At this point of his text the author was not explicitly interested in the question of whether the ligament and the temporal fascia were actually fused. Later on, Schumacher (1954/55: 515–516) described *E. krefftii* in more detail and highlighted the distinctly separate nature of both structures. The tendon would be strongly fused with the skin laterally and medially to it would lie loosely over the bluish temporal fascia. Such a clear separation of both structures has been confirmed for *E. subglobosa* (Werneburg, 2011).

Second, the turtle ligament appears to be non-homologous to the lizard’s ligaments, as it usually attaches to the broad lateral surface of the maxilla/jugal, whereas in lizards the temporal fascia integrated ligament usually inserts to the posteroventral-most edge of the jugal, sometimes expands dorsally along the jugal and/or expands to the maxilla or rictal plate.

Table 2. Character definition based on the presented discussion on primary homology. X = not applicable.

Character	Character states	Lissamphibia	Mammalia	Testudines	Squamata	Sphenodon	Aves	Crocodylia
1	Coronar aponeurosis serves as attachment site for the external m. adductor mandibulae structures (0) or for m. temporalis (1).	0	1	0	0	0	0	0
2	A subarticular aponeurosis is not separated from the coronar aponeurosis (0) or is separated from it (1).	0	1	0, 1	1	1	1	1
3	The pterygoid aponeurosis forms a part of the subarticular aponeurosis (0) or is separated from it (1).	0	1	0, 1	1	1	1	1
4	A quadrate aponeurosis is not separated (0) or is separated (1) from fascia superficialis colli.	0	1	0, 1	1	1	1	1
5	Anteriorly, the quadrate aponeurosis attaches to the jugal/maxilla (0), or does not insert to the upper jaw (1).	X	0	0	1	1	1	1
6	Posteriorly, the quadrate aponeurosis has no attachment to the quadrate (0), attaches to the ventral part (1), or to the dorsal part (2) of the quadrate.	X	0	1	2	2	2	2
7	The quadrate aponeurosis lies ventrally/ventrolaterally (0), or medially (1) to the temporal fascia.	X	0	0	1	1	1	1
8	Ventrally, the temporal fascia does not form a quadrato-jugal ligament (0), or it forms such a ligament, which can be partly or fully separated from the remainder of the temporal fascia (1).	X	0	1	1	0	0	0
9	A retroarticular aponeurosis is absent (0) or present (1).	0	0	0	1	1	?	1

Third, the turtle's ligament attaches onto the anteroventral curvature of the quadrate only (Fig. 2G–J), whereas it has a very variable posterior attachment in squamates (quadrate or lower jaw: Lordansky, 1996; Herrel et al., 1998; Fig. 1H–M).

Schumacher (1956) has shown that several turtle taxa have a clear defined lig. quadratoanguloorale. It is situated medially to lig. quadratomaxillare (added to Fig. 2I) and was never described to be an integrated part of the temporal fascia in turtles.

From the current state of knowledge, the identity of lig. quadratoanguloorale cannot be clearly defined. Either it represents, as in lizards (Fig. 1H–M), the remainder of a lower temporal fascia. However, in lizards, the cheek ligament is, in most cases, at least partly associated to the remainder of the temporal fascia. In turtles, no fusion or integration, but a clear separation, to the lig. quadratoanguloorale was documented. More plausible is the hypothesis that lig. quadratoanguloorale, may represent a duplicate/medial separation of lig. quadratomaxillare in turtles.

One could, finally, homologize the lig. quadratomaxillare of turtles to the last "remaining" possible tendinous element of the jaw apparatus of reptiles described by Lordansky (1994), namely the quadrate aponeurosis. As this structure, lig. quadratomaxillare, in turtles exclusively attaches to the quadrate posteriorly and is situated laterally to the whole jaw musculature. As for the quadrate aponeurosis of diapsids, a tendency of the ligament to split into different sheets (Lordansky, 1994) may also be recognizable in turtles: lig. quadratomaxillare et quadratoanguloorale. As transitional (fossil, ontogenetic) conditions are unknown for ligaments, however, this hypothesis is correlated to several assumptions one needs to draw with a great caution in the following. These speculations are derived from indications, and need to be tested by experimental data (cNCC development). But questions will occur regarding the levels of homology. The ligament is, for example, a continuous structure, whereas

the lower temporal arcade is mostly made of a species-dependent contribution of two cranial bones. While the former may be derived from one cNCC population, the latter may be derived from two different ones. The identity and comparability of all these streams would need to be discussed in a high spatiotemporal resolution and in regard to developmental and taxonomic plasticity. Given these problems, an ultimate answer may never be presented. In the context of this review and the presented homologizations, I present a possible theoretical scenario, which is open to discussion and, as such, does not make

the attempt to be complete, or even to present the "truth."

Scenario for the evolution of the quadrate aponeurosis

One may hypothesize that plesiomorphically the quadrate aponeurosis spanned between the lateral face of the jugal/maxilla and the lateral face of the quadrate. It could have retained this general attachment pattern in Testudines (or be a reversal, depending on the phylogenetic position of turtles within amniotes). In correlation with the evolution of the extremely concave shape of the quadrate in Testudines (Joyce, 2007), the posterior attachment of the quadrate aponeurosis could have come to a relatively ventral position (Fig. 2G–J).

Compared to Testudines, the quadrate evolved to a relatively rodlike element in Sauria and has a vertical orientation (Carroll, 1982; Figs. 1A, C, H–M, 2C, D, F; quadrate is laterally covered by the squamosal in Fig. 1C, compare to Reisz, 1977: fig. 2 below). Possibly correlated to a different cranial kinesis, the quadrate aponeurosis lost its anterior attachment to the jugal/maxilla in this group and became a morphogenetic part of the external jaw adductor in that taxon (see above).

Plesiomorphically in Reptilia, the quadrate aponeurosis may have lain ventrally in relation to the temporal fascia(e). Due to the formation of a concave shape of the quadrate in advanced Testudinata, the aponeurosis would have been able to shift towards a slightly lateral position relative to the temporal fascia(e). In Sauria, the quadrate became rodlike and got a vertical orientation. With this, the quadrate aponeurosis may have shifted towards a dorsomedial position relative to the temporal fascia as visible in extant taxa. Moreover, with the apomorphically elongated quadrate in saurians, it is imaginable that the attachment site of the aponeurosis on this bone came to a relatively higher position within the skull. With this, a separation of the quadrate aponeurosis from its anterior attachment site, and an integration to the jaw musculature is imaginable leading to the

Table 3. Character optimizations for the topologies tested. For character names, compare to Table 2. For character history in topology 1, compare to Fig. 4.

Topology-No.	1	2	3	4	5
		Lepidosauria +	Lepidosauria +	Lepidosauria +	Archosauria +
Sauropsidian topology	Sauria + Testudines	(Archosauria + Testudines)	((Crocodylia + (Aves + Testudines))	((Aves + (Crocodylia + Testudines))	(Lepidosauria + Testudines)
Amniota --> Lissamphibia					
2: 1 ==> 0	C	C	C	C	C
3: 1 ==> 0	C	C	C	C	C
4: 1 ==> 0	C	C	C	C	C
Amniota --> Mammalia					
1: 0 ==> 1	C	C	C	C	C
Amniota --> Sauropsida					
5: 0 --> 1	-	A	C	C	-
6: 0 --> 1	C	-	-	-	-
7: 0 --> 1	-	A	C	C	-
9: 0 --> 1	-	A	A	A	A
Sauropsida --> Testudines					
8: 0 ==> 1	C	-	-	-	-
Sauropsida --> Sauria					
5: 0 ==> 1	C	-	-	-	-
6: 1 --> 2	C	-	-	-	-
7: 0 ==> 1	C	-	-	-	-
9: 0 ==> 1	C	-	-	-	-
Sauropsida --> Lepidosauria					
5: 0 --> 1	-	D	-	-	-
7: 0 --> 1	-	D	-	-	-
9: 0 --> 1	-	C	D	D	-
Sauropsida --> Archosauria					
5: 0 --> 1	-	-	-	-	D
7: 0 --> 1	-	-	-	-	D
Sauropsida --> (Lepidosauria + Testudines)					
8: 0 --> 1	-	-	-	-	A
(Archosauria + Testudines) --> Testudines					
5: 1 --> 0	-	A	-	-	-
6: 2 ==> 1	-	C	-	-	-
7: 1 --> 0	-	A	-	-	-
8: 0 ==> 1	-	C	-	-	-
9: 1 --> 0	-	A	-	-	-
(Archosauria + Testudines) --> Archosauria					
5: 0 --> 1	-	D	-	-	-
7: 0 --> 1	-	D	-	-	-
Archosauria --> Crocodylia					
9: 0 --> 1	-	D	-	-	D
(Testudines + Aves) + Crocodylia --> (Testudines + Aves)					
9: 0 --> 1	-	-	A	-	-
(Testudines + Aves) + Crocodylia --> Crocodylia					
9: 0 --> 1	-	-	D	-	-
(Aves + Testudines) --> Testudines					
5: 1 ==> 0	-	-	C	-	-
6: 2 ==> 1	-	-	C	-	-
7: 1 ==> 0	-	-	C	-	-
8: 0 ==> 1	-	-	C	-	-
(Crocodylia + Testudines) --> Testudines					
5: 1 ==> 0	-	-	-	C	-
6: 2 ==> 1	-	-	-	C	-
7: 1 ==> 0	-	-	-	C	-
8: 0 ==> 1	-	-	-	C	-
9: 1 --> 0	-	-	-	A	-
(Crocodylia + Testudines) --> Crocodylia					
9: 0 --> 1	-	-	-	D	-
(Lepidosauria + Testudines) --> Testudines					
5: 1 --> 0	-	-	-	-	A
6: 2 ==> 1	-	-	-	-	C
7: 1 --> 0	-	-	-	-	A
8: 0 --> 1	-	-	-	-	D
9: 1 --> 0	-	-	-	-	A
(Lepidosauria + Testudines) --> Lepidosauria					
5: 0 --> 1	-	-	-	-	D
7: 0 --> 1	-	-	-	-	D
9: 0 --> 1	-	-	-	-	D
Lepidosauria --> Squamata					
8: 0 ==> 1	C	C	C	C	-
8: 0 --> 1	-	-	-	-	D
Lepidosauria --> Sphenodon					
8: 1 --> 0	-	-	-	-	A

condition visible today (Fig. 2C–D, F). Comparable anatomical changes are common in vertebrate evolution, and were found in the evolution of the feeding apparatus in teleosts, for example (Hertwig, 2008; Werneburg, 2009). A rotation of the maxillary of particular taxa resulted in different insertion sites of a tendinous structure, tendon duplications, and even an associated rearrangement of jaw muscle portions appeared.

Given the plesiomorphic condition of the quadrate aponeurosis to be preserved in Testudines, one may further hypothesize also a similar condition in the ground pattern of Amniota (in which, as in stem turtles, the cheek was covered by dermatocranial bones). And with this, during synapsid evolution, a differentiation of the quadrate aponeurosis is also conceivable.

Correlated to the differentiation of the zygomatic bar in the synapsidian Cynodontia (Abdala and Damiani, 2004; Kemp, 2005), the lateral part of m. adductor mandibulae differentiated resulting in the formation of mm. temporalis, zygomaticomandibularis, et masseter (Diogo and Abdala, 2010); the latter of which spans between the zygomatic bar and the lateral face of the dentary [Schumacher, 1961; side note: Trionychid turtles (Schumacher, 1973) and parrots (Tokita, 2007), all of which have a very similar zygomatic appearance. This results in the formation of muscular structures similar in shape to m. masseter.] In Cynodontia as well, the quadrate became the incus of the middle ear and lost its primary function for jaw articulation.

I hypothesize that, correlated to the driftage of the quadrate (= incus), the quadrate aponeurosis of early Synapsida lost its attachment to the quadrate/incus but, as in turtles, kept its plesiomorphic attachment to the postorbital region (jugal/maxilla; Tables 2–3: character 6 infers a different evolution because only extant taxa could be analyzed) forming the

Tendinous structure	Amphibia / early Tetrapoda	Amniota (hypothetic condition)	Mammalia	Testudines	Squamata	Aves	Crocodylia, <i>Sphenodon</i>
temporal fascia [α]	absent ?	medial separation of cranio-temporal sheet of fascia superficialis colli ?	“superficial temporalis fascia”	fascia(e) temporalis	fascia temporalis	fascia temporalis	fascia(e) temporalis
quadrato-jugal ligament (as part or separation of α)	absent	absent	absent as a lower temporal bar is present	ligamentum quadratoanguloorale	ligamentum quadratojugale	ligamentum quadratojugale or absent, if a quadratojugal bone is present	absent as a lower temporal bar is present
quadrate aponeurosis [β]	absent	absent	fascia masseterica	ligamentum quadratomaxillare; = cranio-lateral sheet of fascia superficialis colli (<i>Chelonia mydas</i>)	quadrate aponeurosis	quadrate aponeurosis	quadrate aponeurosis
coronar aponeurosis [γ]	coronar aponeurosis	coronar aponeurosis	part of proc. coronoideus	coronar aponeurosis	coronar aponeurosis	coronar aponeurosis	coronar aponeurosis
subarticular aponeurosis [δ]	subarticular aponeurosis	subarticular aponeurosis	part of tendinous framework of pterygoideus lateralis	subarticular aponeurosis	subarticular aponeurosis	subarticular aponeurosis	subarticular aponeurosis
pterygoid aponeurosis [ε]	pterygoid aponeurosis	pterygoid aponeurosis	part of tendinous framework of pterygoideus medialis	pterygoid aponeurosis	pterygoid aponeurosis	pterygoid aponeurosis	pterygoid aponeurosis
retroarticular aponeurosis [ζ]	absent	absent	absent	absent	retroarticular aponeurosis	retroarticular aponeurosis ?	retroarticular aponeurosis

Fig. 3. Hypothesized potential identities of the tendinous structures in the temporal region of tetrapods. Greek letters as used in the Figures.

fascia masseterica. As in Sauria (Hofer, 1950; Rieppel, 1980; Lordansky, 1994, see above), the quadrate aponeurosis homolog of mammals (“fascia masseterica”) apparently has a strong morphogenetic influence to the differentiation of the external jaw adductor musculature: This may explain the 90° rotation of their external-most fibers in the jaw adductor complex, namely the *superficial* layer of *m. masseter* (Schumacher, 1961). The latter assumption is strengthened by the fact that the evolution of the masseter muscle is directly correlated to the evolution of the middle ear within Cynodontia (Kemp, 2005). Depressions in the proposed attachment areas of *m. masseter* on the lateral face of the dentaries and on suborbital bones were identified by Abdala and Damiani (2004). Correlated with this is the origin of the mammalian chewing mechanism that potentially contributed to the ecological diversity and evolutionary success of that group (Schumacher, 1961; Turnbull, 1970; Abdala and Damiani, 2004; Kemp, 2005; Diogo and Abdala, 2010). With a detachment of the quadrate-aponeurosis-“anchor” from the quadrate, the infratemporal fenestra could have easily shifted dorsad on the branch leading to mammals due to changed functional requirements (*sensu* Werneburg, 2012).

Evolution of the tendinous framework

Based on the suggested possible homology of the tendinous framework (Fig. 3), I defined eight (certainly biased) cladistic characters (Table 2) and mapped them onto alternative topologies of tetrapod interrelationship (topologies based on Werneburg and Sánchez-Villagra, 2009: table S6,

Table 4. Results of the character mapping on five different topologies (see Fig. 3). See text for details. Consistency index (CI), homoplasy index (HI), CI excluding uninformative characters (CIE), HI excluding uninformative characters (HIE), retention index (RI), rescaled consistency index (RC).

No.	Topology of sauropsidian interrelationship	Tree length	CI	HI	CIE
1	Sauria + Testudines	11	0.9091	0.0909	0.8000
2	Lepidosauria + (Archosauria + Testudines)	14	0.7143	0.2857	0.5000
3	Lepidosauria + ((Crocodylia + (Aves + Testudines))	14	0.7143	0.2857	0.5000
4	Lepidosauria + ((Aves + (Crocodylia + Testudines))	14	0.7143	0.2857	0.5000
5	Archosauria + (Lepidosauria + Testudines)	14	0.7143	0.2857	0.5000

trees C–G, see there for references) (Tables 3–4, Fig. 4). In taxa with variable character states, multiple character states are listed. Lissamphibia were defined as the sister taxon to Amniota. The alternative topologies were drawn in Mesquite (Maddison and Maddison, 2007), character mappings were performed using PAUP* (Swofford, 2003). Gaps were treated as “missing” (coded as “?”) in PAUP*, multistate characters were interpreted as uncertainty. All characters were treated as unordered and equally weighted; five characters are parsimony-uninformative, three characters are parsimony-informative. The distribution of characters is

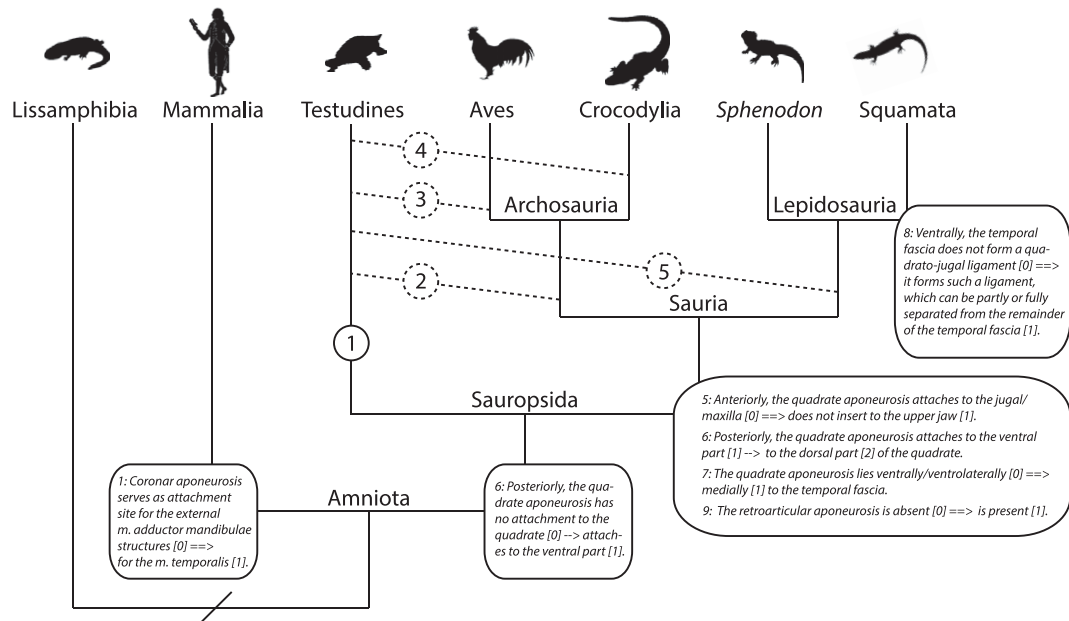


Fig. 4. Results of the character mapping with the five topologies tested. The consensus characters of shared branches are listed. Compare to Tables 2–4. Only extant taxa were coded. As such, the character changes leading to Mammalia and Sauropsida need to be understood in this context and do not reflect the palaeontological interpretation as presented in the text.

described by my scenario on ligament evolution. In the character mappings the tree length of the relationship Testudines + Sauria is the shortest with a count of 11. All other topologies, with a count of 14, have higher tree lengths. These numbers should not be used to decide for one preferred amniote phylogeny as the characters were only plotted and not used to build the tree (Assis and Rieppel, 2010; Werneburg, 2013). However, the comparison of tree lengths shows that the characters defined herein best fit into a phylogenetic framework with a turtle position outside of Sauria.

Consideration on the origin of the quadrate aponeurosis

The superficial fascia of the neck spreads above the posterior skull region of the marine turtle *Chelonia mydas*, forming a lateral sheet, the fascia colli superficialis Pars cranio-lateralis [Pars auriculo temporalis of Schumacher (1956)] (Fig. 2G). It laterally leads over the ventral border of the temporal bones and is strongly attached to the ventrolateral face of the quadrate posteriorly and the lateral face of the jugal and maxilla anteriorly. As such, the lig. quadratomaxillare may represent the homolog or a medial separation of the cranio-lateral sheet of the superficial fascia in *C. mydas* (Schumacher, 1956; Fig. 1H–J, Table 2). One may assume that the quadrate aponeurosis of all amniotes may have evolved from a plesiomorphic condition where it was (as tendinous sheet: Fig. 1G) an integrated part/sheet of the superficial neck fascia, which served to stabilize the head and the neck region against the trunk and spanning laterally to the cheek. A similar condition found in the *C. mydas* may be interpreted as a reversal in this marine turtle. Compared to other turtles, and as a reversal, the head and neck are relatively stiffened. In this context, the fascia temporalis and the intermandibular fascia could phylogenetically represent homologs or medial separations of supposedly cranial

sheets of the superficial neck fascia in early amniotes.

Conclusions

The interpretation on the identity of lig. quadratomaxillare in turtles as the quadrate aponeurosis of other sauropsids is highly speculative and certainly preliminary. Further research on the diversity, development, and histology of the cheek ligaments of amniotes are urgently needed to confirm or revise my cautious speculations. Nevertheless, the initial interpretation of Lakjer (1926) of a modified lower temporal arcade in the ancestor of turtles appears to be overcome. The same holds true for squamates, in which the cheek ligament represents a highly variable ventral thickening or separation of the lower temporal fascia and not a replacement of a lower temporal arcade. Certainly, an apparent positional similarity exists between cheek ligament and lower temporal bar; however, the material properties of a soft tissue ligament and a bony bar are obviously different and as such, the functional properties may also differ (*sensu* Herrel et al., 1998). Discussion of that, however, was beyond the focus of the present paper. Recently, Jones et al. (2012) mentioned that “the ligamentum quadratomaxillare [...] may represent a passive tension cord [Sverdlova and Witzel, 2010] for resisting tensile strains that might arise along the ventrolateral edge of the dome-like cranium during biting. This hypothesis may be tested using finite element modeling similar to that used in Curtis et al. [2011].” Poglajen-Neuwall (1953) hypothesized that the ligament serves to protect the rictal plate from tearing and in this context he mentioned that it is medially connected to the rictal plate by connective tissue.

The value of cranial tendinous structures for the homologization of cranial musculature was first highlighted by Lordansky (1994). This is conceptually confirmed by recent experimental studies on the development of cranial neural crest cells (cNCC), which form tendinous structures and

most cranial bones. And also there may be some degree of a twofold developmental influence, the cNCC-derived structures lead the way and muscular mesoderm is extradited. To understand the evolution of the temporal region in amniotes one needs to further explore developmental patterns of cNCC among several species. Here lies the starting point to test my hypothesis – but again, questions on the level of homology will arise.

The origin of turtles within amniotes will certainly never be solved, neither morphologically nor on a molecular basis. Arguments on either side are traceable but are highly dependent on the subjective sampling of taxa, the method, and techniques to be performed and subjective character choice and definition and conceptual background of data treatment. Nevertheless, case studies on particular anatomical structures as the one presented herein will help exploring different character complexes in detail in order to get a better understanding on morphological diversity and evolution and to view the same subjects from different points of view.

ACKNOWLEDGMENTS

I thank Walter G. Joyce, Daisuke B. Koyabu, Shigeru Kuratani, Wolfgang Maier, Marcelo R. Sánchez-Villagra, Laura A. B. Wilson, and anonymous reviewers for suggestions and for supporting my research. In particular, I am very grateful to Johannes Müller and Nikolai N. Iordansky for controversial discussions and for suggestions on previous versions of the manuscript. Support: SNF-No.31003A_133032/1 (to MRS-V), JSPS-No.11027 (to IW), DFG-No.928/1-1 (to WGJ).

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(Received September 24, 2012 / Accepted October 19, 2012)