Morphology of the temporal skull region in tetrapods: research history, functional explanations, and a new comprehensive classification scheme

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ABSTRACT

The morphology of the temporal region in the tetrapod skull traditionally has been a widely discussed feature of vertebrate anatomy. The evolution of different temporal openings in Amniota (mammals, birds, and reptiles), Lissamphibia (frogs, salamanders, and caecilians), and several extinct tetrapod groups has sparked debates on the phylogenetic, developmental, and functional background of this region in the tetrapod skull. This led most famously to the erection of different amniote taxa based on the number and position of temporal fenestrae in their skulls. However, most of these taxa are no longer recognised to represent natural groupings and the morphology of the temporal region is not necessarily an adequate trait for use in the reconstruction of amniote phylogenies. Yet, new fossil finds, most notably of parareptiles and stem-turtles, as well as modern embryological and biomechanical studies continue to provide new insights into the morphological diversity of the temporal region. Here, we introduce a novel comprehensive classification scheme for the various temporal morphotypes in all Tetrapoda that is independent of phylogeny and previous terminology and may facilitate morphological comparisons in future studies. We then review the history of research on the temporal region in the tetrapod skull. We document how, from the early 19th century with the first recognition of differences in the temporal region to the first proposals of phylogenetic relationships and their assessment over the centuries, the phylogenetic perspective on the temporal region has developed, and we highlight the controversies that still remain. We also compare the different functional and developmental drivers proposed for the observed morphological diversity and how the effects of internal and external factors on the structure of the tetrapod skull have been interpreted.

Key words: fenestration, macroevolution, functional morphology, Tetrapoda, Amniota, Lissamphibia, skull anatomy, biomechanics

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I. INTRODUCTION

The temporal region, the part of the dermocranium between the orbits and the occiput serves multiple purposes in the vertebrate skull: it incorporates the cranial origin sites of the jaw adductor musculature, the jaw hinge, and covers the ear and ultimately also the braincase. Accordingly, the temporal region exhibits a vast array of morphotypes, reflecting evolutionary differences in lifestyle and developmental patterns in the respective taxa. The high morphological diversity of the temporal region is most evident in the tetrapod crown-groups Lissamphibia and Amniota. While most, if not all, Paleozoic stem-tetrapods had a fully closed temporal dermatocranium (e.g. Clack, 1997, 2002; Blom, 2005; Daeeschler, Shubin & Jenkins, 2006), most lissamphibians and amniotes show either a greatly reduced temporal dermocranium or have developed a variety of temporal openings (e.g. Kleinsteich et al., 2012; Werneburg, 2019; Ford & Benson, 2020; Paluh, Stanley & Blackburn, 2020). Even in radiations of extinct crown-tetrapods, like Lepospondyli, a variety of temporal morphotypes, such as large ventral excavations or overall reductions of the dermocranium, can be observed (e.g. Bolt & Rieppel, 2009; Pardo & Anderson, 2016). The morphology of the temporal region in tetrapods has thus attracted much interest over the last 200 years, from palaeontologists and neontologists alike (e.g. Hallmann, 1837; Cope, 1892; Baur, 1894; Gaupp, 1895a,b; Williston, 1904; Fuchs, 1909; Jackel, 1913; Boas, 1915; Versluys, 1919; Broom, 1922; Fox, 1964; Frazzetta, 1968; Tarsitano et al., 2001; Werneburg, 2019). Apart from purely morphological comparisons (Hallmann, 1837), previous workers focussed on the functional (e.g. Dollo, 1884; Gaupp, 1895b; Gregory & Adams, 1915; Case, 1924; Frazzetta, 1968), developmental (e.g. Tarsitano et al., 2001; Schoch, 2014b; Ford, 2018; Werneburg, 2019), and phylogenetic background (e.g. Baur, 1894; Osborn, 1903; Williston, 1917; Broom, 1922; Kuhn-Schnyder, 1980; Müller, 2003; MacDougall & Reisz, 2014; Ford & Benson, 2020) of the structural diversity in the temporal skull region. Much emphasis has been put on the phylogenetic value of temporal morphology, inspiring the naming of several higher taxa, such as ‘Synapsida’, ‘Diaspida’, ‘Anapsida’, ‘Euryapsida’, ‘Stegokrotaphia’, and ‘Stegocephali’ (e.g. Cope, 1868; Osborn, 1903; Fuchs, 1909; Williston, 1917; Broom, 1922; Colbert, 1945; Boettger 1952; Cannatella & Hillis 1993), some of which remain in use to the present day — although often with a different definition.

Yet it has been demonstrated that some morphological traits, such as an infratemporal fenestra or a fully closed temporal dermocranium, appeared independently and repeatedly in distantly related taxa (Müller, 2003; MacDougall & Reisz, 2014; Ford & Benson, 2020), probably not always in response to the same selective pressure (Carroll, 1982; Werneburg, 2012, 2015, 2019). Additionally, the temporal region can vary distinctly in morphology among closely related taxa (Gow, 1972; Tsuji, Müller & Reisz, 2012), specimens of the same species (Cisneros, 2008; Ezcurra, Butler & Benson, 2015), or throughout ontogeny (Gow, 1972; Haridy et al., 2016). This highlights the complex evolution of the temporal region in tetrapods and casts doubt on a classification of various tetrapod clades that emphasizes their temporal morphology, especially within Amniota (e.g. ‘Synapsida’,...
‘Diapsida’, ‘Anapsida’, ‘Parapsida’, ‘Euryapsida’). It seems likely that similar temporal morphotypes evolved in different clades, either because of similar selective pressures or because different selective regimes favoured the convergent evolution of similar morphotypes. Thus, to establish an understanding of the diversity of the tetrapod temporal region, a holistic approach involving phylogenetic, functional, developmental, and ecological considerations is needed.

Here, we provide a completely new classification scheme for temporal morphology in both tetrapod groups (amphibians and reptiles), enabling us to discuss the diversity of the temporal skull region without adding confusion by expanding or modifying the vast number of previous perspectives. We then provide an overview of the research history of temporal morphology in Tetrapoda and their extinct relatives. We illustrate the different approaches used by previous, sometimes rarely cited, researchers to investigate the high disparity of the tetrapod temporal region, and we discuss which functional, developmental, and evolutionary factors they considered as fundamental to changes in temporal morphology.

(I) Morphological and taxonomic definitions

(a) Morphology

Morphological terms for the temporal region have been used differently by previous researchers. This applies especially to the question of whether excavations in the temporal region (e.g. ventrally in the ‘cheek’ of most squamates or the posterior or ventral excavations observed in most turtles) should be described as temporal fenestrae or not. For clarification on morphotypes as used herein, we provide definitions in Table 1 that are mostly based on Werneburg (2013b, 2019). [Correction added on 8 June 2021 after first publication: Werneburg (2013a) has been corrected to Werneburg (2013b) in the previous sentence]

Table 1. Morphological terms used in this review

| Term                     | Definition                                                                 |
|--------------------------|-----------------------------------------------------------------------------|
| Temporal opening         | Temporal openings are reductions of the temporal dermalcranium that are either formed within the suture of two or more bones (temporal fenestra) or by excavations in the dermal armour in a ventrolateral or posterodorsal direction. |
| Temporal fenestra        | Temporal fenestrae are temporal openings that are completely surrounded by bone. They always form within the sutureal contact of two or more temporal bones. An infratemporal fenestra forms in the ‘check’ region of the skull and is ventrally always bordered by a lower temporal bar (i.e. zygomatic arch). A supratemporal fenestra forms in the skull roof and is medially always bordered by the parietal. In some cases the temporal fenestra is confluent with the orbit (e.g. many Mammalia), or the orbit extends distinctly into the temporal region (e.g. Procolophonidae). Both conditions are referred to as an orbitotemporal opening, however, they have different developmental and evolutionary origins. |
| Temporal excavation      | Temporal excavations are ventrolateral or posterodorsal excavations of the dermal armour, formed either by the reduction of a temporal bar (squamates, birds), loss of bones (lissamphibians), or by an embayment of the dermal armour (mammals, turtles). The otic notch is not a temporal excavation. |
| Temporal bar             | Temporal bars are bony arches that border temporal fenestrae. The lower temporal bar (or zygomatic arch) is the bony arch that ventrally borders the infratemporal fenestra. The upper temporal bar borders the infratemporal fenestra dorsally, or the supratemporal fenestra laterally. The arch bordering the infratemporal fenestra anteriorly is the postorbital bar. The posterior equivalent is the posttemporal bar. |
| Temporal bridge          | Temporal bridges are remnants of the temporal dermal armour in-between two temporal excavations. They are mostly found in turtles but are also present in other taxa such as Recumibirostra (early Tetrapoda). |

(b) Taxonomy

In the works discussed herein, taxonomic names often were used in a non-cladistic sense or differed in their taxonomic content from their modern usage [e.g. ‘Synapsida’, which also incorporated ‘cotylosaurs’, placodonts, plesiosaurs, and turtles when Osborn (1903) first introduced the name]. Additionally, even in recent decades, the definitions of some commonly used taxa have been extensively discussed (e.g. Laurin & Anderson, 2004; Modesto & Anderson, 2004). Hence, to avoid confusion, we define how we use some of these names in Table 2.

As we show in this review, an apomorphy-based definition of clades using temporal morphology can be ambiguous, thus we avoid the application of such definitions here. This applies especially to Diapsida, which generally has been used as the amniote clade possessing both an infratemporal and a supratemporal fenestra; a presumed apomorphy inherited by the extant tuatara (Gauthier & de Queiroz, 2020). However, whether this trait appeared only once or arose several times independently in early reptiles is hard to determine (Ford & Benson, 2020; see Section III.1c). In fact, the morphotype of the tuatara may have evolved secondarily (e.g. Muller, 2003; Evans, 2008). We therefore use Diapsida herein with a node-based definition as has been applied in previous publications (e.g. Laurin, 1991; Laurin & Reisz, 1995).

II. AN UPDATED MORPHOLOGICAL CLASSIFICATION SCHEME

The history of research on the tetrapod temporal region involved the introduction of several classification schemes for the different temporal morphotypes and sometimes the
elevation of new taxa based on these morphotypes. While systems following Osborn (1903; see Section III.1c) and Gaupp (1895b; see Section III.1b) are in common use in comparative anatomy, we currently face two challenges.

First, amniote and amphibian researchers often apply two different classification schemes to describe the temporal morphology of their studied species. Amniote researchers usually prefer the scheme initiated by Osborn (1903) which uses ‘synapsid’, ‘anapsid’, ‘dipapsid’, ‘euryapsid’, and so forth, whereas in the amphibian literature the terms of Gaupp (1895b) (‘stegokrotaphic’, ‘zygokrotaphic’, ‘gymnokrotaphic’) prevail. It may be argued that this can be justified by the evolutionary distance and developmental/morphological differences between these groups. Yet, as demonstrated herein, developmental or functional reasons for temporal openings may even vary within amniotes and lissamphibians, and similar factors might invoke their convergent development.

Second, in the scheme used for amniotes, the commonly used terms are based on formally erected taxa. However, of these taxa only Synapsida and Diapsida are still considered to be monophyletic (e.g. Benton, 1985; Gauthier & de Queiroz, 2020; Laurin & Reisz, 2020), although with ongoing controversies on their actual taxonomic composition (e.g. Berman, 2013; Schoch & Sues, 2015; Laurin & Piñeiro, 2017, 2018; Ford & Benson, 2020). In fact, even the current consensus differs markedly from the point of view when these taxa were first introduced (Osborn, 1903; Williston, 1917) and the original terms are now often used to describe the morphology of species that were previously not considered to belong to one of these taxa (e.g. Nussbaum, 1983; Tarsitano, 1983; Carroll, 1988; Heckert, Lucas & Spielmann, 2012).

Hence, instead of further modifying one of the traditional schemes, especially by adding a new array of ‘apsid’ types, we introduce here a new and comprehensive classification scheme for the tetrapod temporal region that is neither based on phylogeny nor on assumed functional backgrounds or homology criteria (Fig. 1).

Our main goal for the new terms to be (i) short and coherent in their phrasing, and (ii) descriptively distinct but still generally applicable to a high number of clades. Our classification scheme introduces 10 distinct morphotypes applicable to Tetrapoda and other Stegocephali (Fig. 2). Some skulls may not be unambiguously assignable to a single one of these morphotypes. This is as expected: naturally occurring morphological variation may never fit an artificial scheme perfectly. Yet, we believe the majority of tetrapod skulls can be assigned to one of these types. Our scheme is not based on homology criteria, but rather on the presence, configuration, and number of temporal openings. Hence, it does not consider the exact suturing between the temporal bones, the presence or absence of a specific bone, the presence of a posttemporal fenestra, skull proportions, or muscle arrangements. The relative size of a temporal opening is only considered for temporal excavations, whereas the relative size of a temporal fenestra has no implications for morphological assignment herein. This approach thus carries the risk of integrating only superficially similar temporal skull conditions within the same morphotype. Nevertheless, this scheme also retains independence from taxonomic and functional interpretations. Ordering the tetrapod temporal region by a simple morphological scheme in our opinion ensures a better comprehension of the complexity and functional adaptations in this large area of the cranium and provides a basis for future quantitative studies that examine the underlying developmental patterns and structural homology of the temporal dermatocranium.

(1) Scutal

From Latin scutum = ‘shield’, scutal describes skulls with a fully roofed temporal region, i.e. a temporal dermatocranium lacking fenestrations or distinct temporal excavations (Fig. 1A). It corresponds, among others, to ‘anapsid’ (after Williston, 1917), ‘stegokrotaphic’ (after Gaupp, 1895b), and ‘stegal’ (Jaekel, 1909a; see also Fig. 1A for further synonyms). It is the ancestral condition in Tetrapodomorpha and is mostly retained, with a reduced number of dermal bones, in the stem-groups of Lissamphibia and Amniota, and likely as a symplesiomorphy in early Amniota and Gymnophiona (for further details of the taxa and literature mentioned in the skull type descriptions, see Section III.1d). It reappeared likely secondarily in Pareiasauromorpha, early Tetradontognath, and a number of Testudines, as well as in some hyperossified Anura. The skulls of some Mammalia may be referred to this type.

### Table 2. Definitions of taxonomic names used in this review

| Taxon         | Definition                                                                 |
|---------------|-----------------------------------------------------------------------------|
| Stegocephali  | Used mostly sensu Laurin (2020a) as the clade containing Tetrapoda, but not Panderichthys rhombolophtys and Tiktaalik roseae. |
| Tetrapoda     | Used sensu Laurin (2020b) as the most inclusive clade containing Amniota and Lissamphibia. |
| Amphibia      | Used sensu Laurin et al. (2020a) as the clade containing Lepidosauria and all taxa closer to Lissamphibia than to Amniota. |
| Lissamphibia  | Used sensu Laurin et al. (2020b) as the least-inclusive clade containing Anura (frogs), Caudata (salamanders), and Gymnophiona (caecilians). |
| Reptilia      | Used mostly sensu Modesto & Anderson (2004) as the clade containing Lepidosauria (squamates and tuataras), Archosauria (crocodiles and birds), Testudines (turtles), and all taxa closer to these than to Mammalia. |
| Diapsida      | Used mostly sensu Laurin (1991) and Laurin & Reisz (1995) as the least-inclusive clade containing Lepidosauria, Archosauria, Youngina capensis, and Araeoscelis gracilis. |
| Synapsida     | Used mostly sensu Laurin & Reisz (2020) as the clade containing Therapsida (mammals and their relatives) but not Reptilia after Modesto & Anderson (2004). |
Fig. 1. Novel comprehensive classification scheme for the arrangement of temporal openings in Tetrapoda. (A) Scutal, (B) nudital, (C) infrafenestral, (D) infrafossil, (E) suprafenestral, (F) suprafossil, (G) bifenestral, (H) bifossil, (I) additofenestral, (J) fossafenestral. Red = temporal fenestra; light pink = temporal excavation; dark pink = other skull openings. Skull outlines are generalized after the early reptile Captorhinus from Fox & Bowman (1966). Widely used synonyms are highlighted in blue.
Fig. 2. The ten morphotypes proposed by our novel classification scheme (see Fig. 1), with examples of taxa to show the potential variation. (I) Acanthostega gunnari (early Stegocephali; after Clack, 2002); (II) Casops morrisi (Temnospondyli; after Reisz et al., 2009); (III) Microcaecilia iwokramae (Gymnophiona; after Wake & Donnelly, 2012); (IV) Captorhinus aguti (early Reptilia; after Fox & Bowman, 1966); (V) Kapes bentoni (Parareptilia; after Zaher et al., 2019); (VI) Proganochelys quenstedti (early Testudinata; after Gaffney, 1990); (VII) Cryptobranchus alleganiensis (Caudata; after Carroll & Holmes, 1980); (VIII) Bombina orientalis (Anura; after AmphibiaTree, 2004); (IX) Aegyptodraco fasciolata (Squamata; after Das et al., 2019); (X) Terrapene ornata (Testudines; after Gaffney, 1979); (XI) Anthracosaurus russelli (Embolomorpha; after Panchen, 1977); (XII) Calyptocephalella gepi (Anura; after Boas, 1915); (XIII) Cylindrophorhynchus romeri (early Synapsida; after Romer & Price, 1940); (XIV) Ophiacodon uniformis (early Synapsida; after Romer & Price, 1940); (XV) Syodon bicornutum (Dinocephalia; after Kammerer, 2011); (XVI) Bolosaurus striatus (early Parareptilia; after (Figure legend continues on next page.)
(2) Nudital

From Latin *nuditas* = ‘barenness’, nudital describes skulls that lack temporal bars or bridges due to a heavily reduced temporal dermatocranium (Fig. 1B). Usually only the parietal region still retains dermal bones. This morphotype corresponds with ‘gymnokrotaphic’ (after Gaupp, 1895b). It is widespread in Batrachia and Ophidia, but occurs also in a number of other Squamata, as well as some Testudines.

(3) Infrafenstral

From Latin *infra* = ‘below’ and *fenestra* = ‘window’, infrafenstral describes skulls that possess an infratemporal fenestra as their only temporal opening (Fig. 1C). This morphotype corresponds mainly to ‘synapsid’ (after Osborn, 1903), but also partly to ‘zygokrotaphic’ (after Gaupp, 1895b) or ‘zygal’ (Jaekel, 1909a). It occurs most notably in the majority of non-neotherapsid Synapsida, Gorgonopsia, and many Parareptilia. It can be also found in the embolomere *Anthracosaurus russeli* and the caiman *Paleosuchus*, and a number of Anura. The size of the fenestra varies distinctly among taxa, ranging from miniscule to large openings that occupy most of the ‘check’. The infrafenstral type may have arisen independently in Synapsida and Parareptilia, or may represent a synapomorphy of Amniota (see Section III.1.e). In caimans, this morphotype emerged by secondary closure of the supratemporal fenestra.

(4) Infrafossil

From Latin *infra* = ‘below’ and *fossa* = ‘cavity’, infrafossil describes skulls with a large ventral excavation in the ‘check’ as the only temporal opening, with this excavation occupying more than 30% of the temporal height (Fig. 1D). Smaller excavations are not considered for classification. Skulls of this type have been sometimes referred to as ‘anapsid’, but the best historical analogues may be ‘hemi-stegokrotaph’ (Gaupp, 1895a, ‘second series’ (Fuchs, 1909), and ‘pleurokeiroid’ (Smith, Chiszar & Frey, 1983). The morphotype occurs most notably in Pleurodira, but also in *Euamosaurus africanus*, Scincoidea, some Parareptilia, and some Lepospondyli.

(5) Suprafenstral

From Latin *supra* = ‘above’ and *fenestra* = ‘window’, suprafenstral describes skulls that possess a supratemporal fenestra or lateromedial widened infratemporal fenestra as the only temporal opening (Fig. 1E). This morphotype corresponds mostly to ‘euryapsid’ (after Colbert, 1945), but also ‘parapsid’ (after Williston, 1917), and ‘metapsid’ (after Boettger, 1952). It occurs especially in various Sauropterygia and Ichthyosauromorphia, as well as in non-mammalian Eutheriodontia. It is also present in the early diapsid *Araeoscelis graciei*, a few Archosauromorpha, and some Choristodera. In all reptiles with a suprafenstral skull, this morphotype likely evolved due to closure of the infratemporal fenestra. In Eutheriodontia, however, the suprafenstral type evolved by a lateromedial widening of the infratemporal fenestra.

(6) Suprafossil

From Latin *supra* = ‘above’ and *fossa* = ‘cavity’, suprafossil describes skulls with a large posteroventral excavation in the skull roof as their only temporal opening, with this excavation occupying more than 30% of the temporal length (Fig. 1F). Skulls of this type have been sometimes referred to as ‘anapsid’. The best historic analogues may be ‘first series’ (Fuchs, 1909) and ‘opisthokeiroid’ (Smith et al., 1983). This morphotype occurs most notably in Cryptodira, but also in several Gymnophiona. Arguably may also be referred to various Mammalia.

(7) Bifenstral

From Latin *bis* = ‘two’ and *fenestra* = ‘window’, bifenstral describes skulls that possess an infratemporal and a supratemporal fenestra (Fig. 1G). This morphotype corresponds mainly to ‘diapsid’ (after Osborn, 1903). Occurs mostly in non-avialan Archosauromorpha, but also in some early Diapsida, several Lepidosauria, and late Rhynchosauria. Arguably also present in some Anura, but overall restricted to reptiles. May be the ancestral condition in Diapsida, however, the bifenstral morphotype in many Sauria is likely a secondary condition that emerged through the development.

(Figure legend continued from previous page.)

Broom, 1913; [XVII] *Listrostes friesi* (Lepospondyli; after Bolt & Rieppel, 2009); [XVIII] *Brachydectes newberryi* (Lepospondyli; after Pardo & Anderson, 2016); [XIX] *Millerops friesi* (Parareptilia; after Gow, 1972); [XX] *Criosaura typica* (Squamata; after Maisano, 2003); [XXI] *Enydrura marquini* (Testudines; after Gaffney, 1979); [XXII] *Galilus gallus* (Avialae; after Jollie, 1957); [XXIII] *Gymnagnostus platyops* (early Eutheriodontia; after Broom, 1911); [XXIV] *Temnodontosaurus trigonodon* (Ichthyosauria; after Maisch & Hungerbühler, 2001); [XXV] *Placodus gigas* (Placodontia; after Sues, 1987); [XXVI] *Pliosauros kerani* (Placosauria; after Benson et al., 2013); [XXVII] *Solecomorphus sp.* (Gymnophiona; after DigiMorphy Staff, 2002); [XXVIII] *Zelambdalestes lechei* (Mammalia; after Wible et al., 2004); [XXIX] *Pelodiscus sinensis* (Testudines; after Ogushi, 1911); [XXX] *Pelorosaurus kawensis* (early Diapsida; after Reisz, 1977); [XXXI] *Crocodaria bidenti* (Rhincocephalia; after Fraser, 1988); [XXXII] *Erythrosuchus africanus* (early Archosauromorphes; after Nesbitt, 2011); [XXXIII] *Thalattosaurus superciliosus* (Thalattosuchia; after Andrews, 1913); [XXXIV] *Testudo graeca* (Testudines; after Gaffney, 1979); [XXXV] *Delothyris eifelii* (Parareptilia; after Hershie et al., 2016); [XXXVI] *Postosuchus kirkpatricki* (early Pseudosuchia; after Weinbaum, 2011); [XXXVII] *Pleurodales urati* (Caudata; after AmphibiaTree & Goslinge-Jeldani, 2008); [XXXVIII] *Lystrosaurus murrayi* (Anomodontia; after Ray, 2005); [XXXIX] *Claudiosaurus germani* (early Diapsida; after Carroll, 1981); [XL] *Iguana iguana* (Squamata; after Conrad & Norell, 2010).
of a lower temporal bar in a fossafenestral ancestor. The shape and proportions of both fenestrae can vary drastically.

(8) Bifossal
From Latin *bis* = ‘two’ and *fossa* = ‘cavity’, bifossal describes skulls that possess a large posterodorsal and ventral excavation as temporal openings, occupying more than 30% of the temporal height or temporal length, respectively (Fig. 1H). There is no perfectly fitting historical analogue. Overall restricted to Testudines. Arguably, most mammal skulls fall under this type, however, in their case the posterodorsal excavation is a drastically widened infratemporal fenestra, and both excavations are separated by the former lower temporal bar (i.e. zygomatic arch), whereas in turtles the excavations are secondary reductions of a former subcutaneous skull and separated by a temporal bridge.

(9) Additofenestral
From Latin *additus* = ‘additional’ and *fenestra* = ‘window’, additofenestral describes skulls that possess two pairs of infratemporal fenestrae often in addition to a supratemporal fenestra (Fig. 1I). There is no perfectly fitting historical analogue, but skulls of this type are often referred to as ‘diapsid’. The second pair of infratemporal fenestrae can emerge by the subdivision of a large infratemporal fenestra by a bony process or within another suture of the temporal dermocranium. Occurs in Tyrranosauridae, several early Loricata, and some Pareocephalia. Infrafenestral types with an ‘auxiliary’ fenestra on one side of the skull (as in some early synapsids) may, arguably, be referred to this type.

(10) Fossafenestral
From Latin *fossa* = ‘cavity’ and *fenestra* = ‘window’, fossafenestral describes skulls that possess a supratemporal fenestra together with a large ventral excavation in the ‘cheek’ that occupies at least 30% of the temporal height (Fig. 1J). Corresponds mainly to ‘parapsid’ (after Williston, 1917) and ‘katapsid’ (after Boettger, 1952). Widespread in Diapsida, especially within Lepidosauria, in most Anomodontia and some Salamandridae. However, in Anomodontia the supratemporal fenestra is evolutionary derived from a widened infratemporal fenestra. The size of the suprafenestral fenestra can differ markedly. This morphotype is often associated with a streptostylic jaw.

III. RESEARCH HISTORY OF THE TEMPORAL SKULL REGION

(1) Temporal skull diversity as a classification tool
Comparative studies of the vertebrate skull, including differences in the temporal region, pre-date the Darwin revolution with a notable contribution by Cuvier (1829). The first detailed monograph on the temporal skull region was by Hallmann (1837). He described the osteology and myology of the temporal region as well as the associated neurobiology, and the auditory system mainly of extant vertebrates. Hallmann (1837) did not examine the skull under a phylogenetic perspective, but focussed particularly on embryological differences among vertebrates and how the various morphotypes formed during prehatching/prenatal ontogeny.

(a) Early phylogenetic inferences
Scientific interest in the morphology of the temporal skull region increased by the end of the 19th century (Fig. 3). Due to increasing attempts to understand evolutionary changes metaphorically as a ‘tree’ (Tassy, 2011), together with the growing acceptance of Darwinian theories of evolution (Darwin, 1859) and better availability of palaeontological data, morphological differences were increasingly viewed in terms of phylogenetic relationships. The early phylogenetic discussions were mostly focussed on the homology of particular temporal bones (mainly the squamosal and quadratojugal). To our knowledge, the first attempt explicitly to discuss phylogenetic aspects of temporal anatomy was Günther (1867), who highlighted similarities in the temporal region between tuatara (*Sphenodon punctatus*) and crocodiles, contrasting these with the morphology of squamates and turtles. Baur (1889) was probably the first to describe the evolution of the ‘temporal arches’ (i.e. temporal bars) in different tetrapods from early stegocephalians and their assumed gar-like ancestors with a complete dermal covering of the temporal region.

Cope (1892), who argued for homology of the temporal arches among reptiles, further distinguished between a ‘Series I’, ‘Series II’, and ‘Series III’ in the evolution of reptiles with respect to the formation of temporal bars (Fig. 3). Like Baur (1889), Cope (1892) considered a closed dermocranium as the ancestral condition from which the reduced dermocranium of turtles (Series I), the supratemporal fenestra [‘supramastoid foramen’ in Cope (1892)] of Ichthyopterygia (Series II), as well as different appearances and losses of temporal bars in various other amniotes (Series III) evolved.

Baur (1894) discussed the works of Cope (1892) and Gaupp (1895a,b, see Section III.1b) with regard to homologies of the temporal bones among different taxa. Case (1898) argued that the non-fenestrated Pareiasauria were the ancestral ‘reptilian’ group, of which, first, the ‘Proganosaurus’ with an infratemporal and supratemporal fenestra arose, followed by branches leading to extant reptiles (‘sauropsidal group’) and mammals (‘mastocephalous group’; Fig. 3).

Gegenbaur (1898) postulated that taxa with several ‘Spangen’ (‘claspers’, meaning temporal bars and bridges) like rhynchocephalians or crocodiles represent the condition that arose first from taxa with a fully roofed dermocranium, from which taxa with only one ‘clasp’ (turtles, ‘enaliosours’, and ‘theromeres’) and also the morphotypes of squamates evolved.
Fig. 3. Overview of previous descriptive classification schemes based on the morphology of the temporal skull region. Skulls are as listed in legend to Fig. 2 with the addition of ‘Holo-stegocrothaph’: Limnoscelis paludis after Romer (1946); ‘Anasynapsid’: Tachyglossus aculeatus after Macrini (2004); ‘Type 3’, ‘Type 8’; Edaphosaurus boanerges after Modesto (1995); ‘Type 6’, ‘Type 9’: Candelaria barbouri after Cisneros et al. (2004).
(b) Handling morphological diversity

Gaupp (1895a,b) was the first to introduce anatomical terms for different temporal morphotypes, coining the terms ‘stegocrotaph’, ‘zygocrotaph’, and ‘gymnocrotaph’ (Fig. 3). With reference to the taxon Stegocephali, he adopted the term ‘stegocrotaph’ [from Ancient Greek στῆγος (stågos) = ‘roof’ and κρόταφος (krotaphos) = ‘temple’] for species with a fully closed dermocranium in their temporal region, including early stegecephalians, marine turtles, and ‘Cotylosauria’. In fact, Stegocephali [from Ancient Greek στήγας (ståghas) see above] and κεφαλή (kephalē) = ‘skull’, which was introduced by Cope (1868) for a set of Paleozoic tetrapods, may be the first time a taxon was named based on its temporal morphotype.

Gaupp (1895a) proposed a further subdivision of ‘stegocrotaph’ skulls into ‘holo-stegocrotaph’ and ‘hemi-stegocrotaph’ types. He used ‘holo-stegocrotaph’ [from Ancient Greek ὅλος (hōlos) = ‘complete’] for skulls that possess a fully enclosed temporal region, whereas ‘hemi-stegocrotaph’ skulls [from Ancient Greek ἡμιος (hēmos) = ‘half’] have a completely ossified skull roof but a ventrally emarginated ‘cheek’ region like that found in scinoids. ‘Zygocrotaph’ [from Ancient Greek ζύγομα (zýgōma) = ‘bar’], which Gaupp (1895b) subdivided into ‘mono-zygocrotaph’ and ‘di-zygocrotaph’, was used for skulls with one or two fully formed temporal bars.

Gaupp (1895b) defined a ‘mono-zygocrotaph’ condition [from Ancient Greek μύος (mýos) = ‘single’] to be present in anurans, mammals, birds, the majority of turtles, and non-oophidian squamates, whereas a ‘di-zygocrotaph’ cranium [from Ancient Greek Δίς (dís) = ‘double’] is found in rhynchocephalians, crocodylids, and some fossil taxa like non-avian dinosaurs. ‘Gymnocrotaph’ [from Ancient Greek γυμνός (gymnos) = ‘naked’] referred to crania missing most of the dermal bones in the temporal region, which Gaupp (1895b) used for mosasauroids, snakes, gekkotans, and chelid turtles [Cheilodae in Gaupp (1895a,b)]. Gaupp (1895b) also postulated the ‘stegocrotaph’ skull to be the ancestral condition from which first the ‘zygocrotaph’ morphology, and from this the ‘gymnocrotaph’ morphology evolved. Fürbringer (1900) suggested an extension of Gaupp’s (1895a,b) scheme with the terms ‘anazygocrotaph’ [from Ancient Greek ανα (ánna) = ‘up’] and ‘katazygocrotaph’ [from Ancient Greek κάτα (kátā) = ‘downward’], depending on a ventral or dorsal position of the temporal bar, respectively (Fig. 3).

Jaeckel (1909a) criticized the terms introduced by Gaupp (1895b), not only because he considered them to be ‘almost unpronounceable’ (‘fast unaussprechlich’), but also because he emphasized the distinct osteological differences present, for example between early Stegocephali and turtles. Jaeckel (1909a) suggested as an alternative the similarly defined terms ‘stegal’ and ‘zygai’, with the latter also subdivided into ‘monozygal’ and ‘dizygal’ (Fig. 3). The ‘stegal’-like type in extant turtles, he considered to be a specialised condition derived from a ‘zygai’ skull, hence he referred to them as ‘tegal’ [from Ancient Greek τήγας (tēgas), also meaning ‘roof’], Jaeckel (1909a) also highlighted differences among the ‘stegal’ skulls of early stegecephalians, ‘placoderms’ and other ‘fishes’ with fully roofed dermal armour in their skull, arguing for a need for similar rigorous comparison as already performed for fenestrated skulls in reptiles.

Fuchs (1909) also described the development and evolution of the temporal region in tetrapods (‘Quadrapeda’). He demonstrated a trend for simplification of the temporal dermocranium during tetrapod evolution [see also ‘Williston’s law’, sensu Williston (1914)] and highlighted its unique position covering the large jaw adductor musculature. He ordered skulls with temporal openings using a new morphological classification system that partly considered phylogeny. He erected two ‘main groups’ (‘Hauptgruppen’), subdivided into ‘subgroups’ (‘Unterguppen’) or ‘series’ (‘Reihen’; Fig. 3). Fuchs’ (1909) first main group incorporated all skulls with temporal fenestrae (‘zentral gelegene Reduktion’), his second main group included skulls with temporal excavations (‘randständige Reduktion’). Fuchs (1909) adopted Jaeckel’s (1909a) terms ‘stegal’ and ‘zygai’, but ordered his first main group mostly in the sense of Osborn (1903; see Section III.1c). Accordingly, his ‘subgroup a’ of the ‘first main group’ contained all skulls with two temporal fenestrae, which he identified with Osborn’s (1903) ‘Diapsida’, and all skulls that Fuchs (1909) thought were derived from them (i.e. squamates, birds, ‘pelycosaurs’). ‘Subgroup b’ of this ‘first main group’ contained all skulls with only a dorsally open temporal fenestra, which the author described as present in most early Synapsida, Sauropterygia, and Ichthyopterygia. Fuchs (1909) restricted his ‘second main group’ to Testudinata: the ‘first series’ of this group contained turtle skulls predominantly with a large posterior excavation in the skull roof; his ‘second series’ incorporated skulls with a large ventral excavation in the ‘cheek’ region (Fig. 3).

Discussing the evolutionary origins of procolophonian reptiles, von Huene (1912; Fig. 3) described amniote skulls using a scheme derived from Gaupp (1895a,b) and Führinger (1900). He hypothesized that from the ‘stegocrotaph’- ‘cotylosauria’, five amniote radiations with convergent temporal openings emerged: ‘dizygocrotaph’ forms (he presumably meant forms like tuataras, although not named explicitly), ‘katazygocrotaph’ therapsids, ‘pseudozygocrotaph’ turtles [from Ancient Greek προς (prous) = ‘false’], ‘hypozygocrotaph’ ‘deuterosaurs’ [from Ancient Greek ὑπό (hypo) = ‘under’], as well as ichthyosaurs together with mesosaurids, which von Huene (1912) apparently also counted as ‘zygocrotaph’. von Huene (1912) interpreted procolophonians as late-surviving ‘cotylosauria’ and the only such taxon to evolve temporal openings. However, he distinguished them from ‘normal zygocrotaph’ taxa by their evolution of an orbitotemporal opening, suggesting the term ‘pseudoostegocrotaph’. Note that von Huene (1912) did not include the ‘stegocrotaph’ Pareiasaurormorpha inside Procolophonia, in contrast to more recent analyses (e.g. MacDougall & Reisz, 2014). The ‘deuterosaurs’ mentioned by von Huene (1912) as examples of the ‘hypozygocrotaph’ type are now nested within Dinoccephalia (Kammerer, 2011). As they had a large infratemporal fenestra in their ‘cheek’, it could be argued that von Huene (1912)
understood hypozygocrotaph as similar to Fürbringer’s (1900) term ‘katazygocrotaph’ (Fig. 3), although von Huene (1912) used katazygocrotaph to refer to taxa that he considered to be therapsids.

Williston (1912) modified the terms of Gaupp (1895b), referring to them as ‘stegocrotaphic’ and ‘zygocrotaphic’. Additionally, for the type found in ‘Theromorpha’ he coined the term ‘therocrotaphic’ [from Ancient Greek θέριον (théiron) = ‘beast’] and for the condition in Diapsida with two temporal bars he used ‘saurocrotaphic’ [from Ancient Greek σαῦρος (saurus) = ‘lizard’; Fig. 3].

Versluys (1919) summarized the temporal region in terms of the then-understood phylogeny of Reptilia. Like previous authors, he interpreted the fully roofed condition as the ancestral state. From this he derived four ‘types’ (Fig. 3): the first type (‘1. Typus’) referred to a skull with infra- and supratemporal fenestrae, as found in Diapsida; a second type (which he also called ‘type A’ when it appears in synapsid skulls) was used for skulls with only the infratemporal fenestra present; a third type (or ‘type B’ in the synapsid skull) had only the supratemporal fenestra present, as found in Sauropetrygia and Ichthyosaurus; and, lastly, a fourth type applied only the supratemporal fenestra present, as found in Sauropetrygia (which he also called ‘stegocrotaphic’ [from Ancient Greek στέγας (stegás) = ‘arch’] and ‘Diapsida’ (from Ancient Greek δί (dí) = ‘two’), mainly based on the osteology of their temporal region (Fig. 4). Osborn (1903) summarised under his ‘Synapsida’ species with skulls having “primarily […] single, or united temporal arches”, whereas the ‘Diapsida’ possess “primarily […] double, or separated temporal arches” (Osborn, 1903, p. 276). While still regarded as a monophyletic taxon (with a different delimitation) (e.g. Ford & Benson, 2020), Osborn’s (1903) original ‘Synapsida’ also incorporated Placodontia, Plesiosauria, Testudinata, and ‘Cotylosauria’.

Instead of using his own terms from Jaekel (1909a), Jaekel (1909b) referred to temporal morphotypes using the terms of Osborn (1903): ‘diapsid’ and ‘synapsid’. Due to his opinion that Sauropetrygia should be classified as Diapsida instead of Synapsida (as done by Osborn, 1903), he coined the term ‘pseudosynapsid’ with regard to their morphology.

Williston (1917) elaborated Osborn’s (1903) classification by coining the names ‘Anapsida’ [from Ancient Greek ἀνευ (anēu) = ‘without’] and ‘Parapsida’ (from Ancient Greek παρά (pará) = ‘near’]. Containing ‘cotylosaurs’ and turtles, Williston’s (1917) ‘Anapsida’ corresponded basically to ‘stegocrotaph/stegal’ reptiles. ‘Parapsida’ incorporated, among others, Ichthyosaurus and Squamata, with Williston (1917) arguing that their fenestrated morphotype evolved separately from this morphology in Synapsida and Diapsida (Fig. 4).

Contrary to Osborn (1903) but like Williston (1917), Fuchs (1909) considered turtles not to be assignable to Synapsida with confidence but also neither to Diapsida (Fig. 4). Hence, he erected the new taxon ‘Heterapsida’ [from Ancient Greek ἕτερος (hétēros) = ‘different’].

Broom (1922) raised doubts regarding homology of the temporal arches in Ichthyosauria, Plesiosauria, and Placodontia with those of ‘mammal-like reptiles’. Broom (1922) also highlighted similarities of turtles with plesiosaurs and placodonts, arguing that the turtle skull likely derived from an ancestor with a supratemporal fenestra. Subsequently, Broom (1922) distinguished between four taxa of Reptilia, partly defined by their temporal region: Anapsida, Diapsida, Synapsida, and a new taxon he named ‘Anomapsida’ [from Ancient Greek ἄνομαλος (ánomaλos) = ‘irregular’], which comprised ichthyosaurs, plesiosaurs, placodonts, and turtles (Fig. 4).

Colbert (1945) classified Sauropetrygia, Placodontia, and Protorosauria into ‘Euryapsida’ [from Ancient Greek εὐρός...
Euryapsida = ‘broad’], identifying them by the presence of a supratemporal fenestra only, laterally bounded by the post-orbital and squamosal bones (Fig. 4). In fact, the term ‘Euryapsida’ was originally suggested by Romer in a personal correspondence as indicated by a footnote in Colbert (1945).

**Fig. 4.** Overview of amniote systematics as proposed by different authors based on the temporal region. Skulls are as listed in legend to Fig. 2 with the addition of Pareiasauria: *Scutosaurus karpinskii* after Lee (2000); ‘Protorosauria’: *Prolacerta broomi* after Nesbitt (2011); Mesosauridae: *Mesosaurus tenuidens* after Modesto (2006).
Kilias (1957) argued for phylogenetic relevance of the temporal excavations ("Hiatus") in the turtle skull, at least regarding differentiation between Pleurodira and Cryptodira. Additionally, and contrasting with some previous studies (e.g. Jaekel, 1909a, Versluys, 1913; Zdansky, 1923–1925), he interpreted the fully roofed temporal region in sea turtles as the retention of an ancestral condition due to their highly aquatic lifestyle.

The final author to name new amniote taxa based on their temporal morphology was Boettger (1952), who coined the terms ‘Metapsida’ [from Ancient Greek μετά (meta) = ‘between’] and ‘Katapsida’ [from Ancient Greek κατά (kata) = ‘downward’]. He chose the name Katapsida to reflect his belief that there was a loss of (or at least a tendency to lose) the lower temporal bar in these taxa. ‘Katapsida’ comprises Rhynchocephalia (with choristoderes), Squamata, and Thalattosauria. ‘Metapsida’ incorporates only Ichthyosaurusia, justified by Boettger (1952) on the grounds that ichthyosaurs only possess a temporal fenestra on the top of their skull (Fig. 4).

Criticism of phylogenies based on temporal morphology was present long before large-scale cladistic analyses became possible. Fuchs (1909) had already highlighted that differences in temporal morphology may not necessarily be of high phylogenetic value as similar arrangements could be seen in distantly related taxa. Goodrich (1916), while accepting the existence of a ‘reptile’ branch leading to mammals (‘theropсидan’) and one leading to birds (‘sauropsidan’), cautioned against the use of temporal morphology as a phylogenetic trait, as an appearance of a temporal opening could not be distinguished properly from disappearance of the same in extinct taxa.

In the second half of the 20th century, Kuhn-Schnyder (1954, 1963, 1967, 1980) worked extensively on the phylogenetic implications of temporal openings, especially with regard to sauropterygians and squamates. Kuhn-Schnyder (1954) discussed the ancestry of lizards (‘Lacertilia’) mostly with respect to their temporal morphology, although he highlighted that similar structures may be the result of convergent evolution. Kuhn-Schnyder (1963) provided a literature review on reptile systematics, especially with regard to previous interpretations of temporal morphotypes. Regarding the ancestry of lizards, Kuhn-Schnyder (1963) reiterated his earlier arguments and highlighted the many routes for the formation of a supratemporal fenestra. He also explicitly used temporal anatomy as an argument against a close relationship between placodonts and other sauropterygians. He argued that the ancestors of placodonts never possessed an infratemporal fenestra, in contrast to the assumed ‘diapsid’ ancestors of Nothosauria and Plesiosauria. Consequently, Kuhn-Schnyder (1963, 1967) considered placodonts to be part of Synapsida and the only large taxon representing Colbert’s (1945) ‘Euryapsida’, with other sauropterygians classified as Diapsida. Kuhn-Schnyder (1980) again reviewed the association between temporal fenestration and reptilian phylogeny. While accepting there may be temporal morphotypes unique to the respective reptilian clades, he cautioned that the assumed biomechanical factors leading to temporal fenestration could argue against the use of temporal morphology as a reliable phylogenetic trait.

Nevertheless, new terms in the tradition of Osborn (1903) have been coined occasionally in recent decades. These were explicitly introduced as descriptive terms to order the vast diversity of temporal morphotypes, as originally done by Gaupp (1893a, b) and Jaekel (1909a), and not to describe novel taxa. Smith et al. (1983), for example (Fig. 3), introduced a large number of morphological terms applying to the amniote temporal region, partly based on what was interpreted to be a secondary or derived condition, such as ‘euryapsid’ [from Ancient Greek εὐ (eu) = ‘good’] for most mammal skulls and ‘hemidiapsid’ for the skulls of most squamates. Smith et al. (1983) introduced a novel ‘keiroid’ type [from Ancient Greek κειρεῖν (keirein) = ‘to cut’] based on the position of excavations in the turtle skull (‘episthekeiroid’, from Ancient Greek ὑπσιθεκείριοδός (hypisthekeiroidos) = ‘backwards’; ‘pleurokeiroid’, from Ancient Greek πλευροκείριο (pleurokeiroid) = ‘flank’) and how much space these occupy in the temporal region [e.g. ‘meiopisthokeiroid’, from Ancient Greek μείως (meios) = ‘less’; or ‘metapleurokeiroid’ from Ancient Greek μεταπλευροκείριο (metapleurokeiroid) = ‘in-between’].

Being aware of cranial plasticity during evolution, Wernburg (2019) took a simplified approach, subdividing the morphology of the amniote temporal region into ‘anapsid’ (no temporal openings), ‘monapsid’ [infratemporal fenestra present; from Ancient Greek μονάς (monas) = ‘single’], ‘diapsid’ [infratemporal and supratemporal fenestrae present; from Ancient Greek διπλά (diplos) = ‘double’], and ‘excavation’ types [all skulls with any kind of temporal emargination or embayment (Fig. 3)] and illustrated the diverse phylogenetic shifts among morphotypes.

The descriptive terminology introduced by Gaupp (1893b) occasionally inspired researchers to allocate names to new formal taxa. Based on their often ‘stegokrotaphic’ skulls, Cannatella & Hillis (1993) erected the clade ‘Stegokrotaphia’ for all non-rhinatrematid caecilians.

There are additional descriptive terms in the tradition of Osborn (1903), mostly used in educational material, that sometimes include the morphology of the preorbital skull. As we were unable to find scientific literature that officially introduced this terminology, we do not include a discussion of these terms herein.

(d) Modern phylogeny and morphological patterns

With the rise of cladistics and large-scale morphological and molecular phylogenetic analyses in the second half of the 20th century, as well as many new fossil finds, especially of parareptiles (e.g. DeBraga & Reisz, 1996; Tsuji, 2006; Modesto et al., 2009; Tsuji & Müller, 2009; MacDougall & Reisz, 2014) and potential stem-turtles (Bever et al., 2015; Schoch & Sues, 2015, 2018), phylogenies based on temporal fenestration fell out of favour. It can be demonstrated that various temporal morphotypes evolved convergently, repeatedly, and can vary intraspecifically (e.g. DeBraga & Rieppel,
bordered by the jugal, postorbital, quadratojugal, and squamosal (e.g. Romer & Price, 1940). The contribution of the quadratojugal declines in Metopophora (e.g. Ophiacodontidae, Edaphosauridae, Sphenacodontidae; Romer & Price, 1940). In many Therapsida, but also in some metopophorans, the parietal contributes to the infratemporal fenestra (e.g. Boonstra, 1936; Modesto, 1995; Kammerer, 2011).

In most Anomodontia (15 in Fig. 5), the infratemporal fenestra lateromedially expanded and a distinct ventral excavation formed in the cheek region, overall resulting in a fossafrenal morphotype (e.g. Ray, 2005; Sullivan & Reisz, 2005). Comparable to a ‘true’ supratemporal fenestra, the jugal no longer contributes to the temporal fenestra. Instead, it is only bordered by the postorbital, squamosal, and parietal (Sullivan & Reisz, 2005). The infratemporal fenestra in early Eutheriodontia (16 in Fig. 5) expanded in a similar manner (e.g. Kemp, 1984), leading to a suprafrenal morphotype. However, the non-expanded fenestra in early anomodontians (Angeleczyk, 2004; Cisneros et al., 2015), as well as in the possible Eutheriodontia sister-clade Gorgonopsia (Gebauer, 2007), argue for an independent evolution of the lateromedially expanded fenestra. Crownward, the temporal fenestra often became confluent with the orbit by loss of the postorbital (e.g. Kemp, 1984). Consequently, this orbitotemporal opening in most mammals and their nearest relatives is bordered by the jugal, squamosal, parietal, and frontal. Arguably, this orbitotemporal opening may be referred to as a temporal excavation, making this a suprafrenal morphotype (17 in Fig. 5), or even bifossal if the zygomatic arch is distinctly dorsally bended to form a ventral excavation that occupies more than 30% of the temporal height (see Section II.H). In some mammals, the zygomatic arch became confluent with the braincase (18 in Fig. 5), effectively forming a scutal morphology (Macrini, 2004), although functionally with little similarity to other scutal tetrapods (Murray, 1981).

The ancestral condition in Reptilia may have been scutal (e.g. Muller & Reisz, 2006; Ford & Benson, 2020), however, this is highly dependent on the nesting and interrelationships of Parareptilia (Piñeiro et al., 2012; Cisneros et al., 2021). The earliest parareptiles were likely infrafenestral (20 in Fig. 5; Cisneros et al., 2021; but see the controversy surrounding Mesosauridae in Section III.1e). Later, also infrafenossal (19 in Fig. 5; Gow, 1972; Tsuji, Muller & Reisz, 2010), scutal (21 in Fig. 5; - Lee, 1997), and additofenossal (Haridy et al., 2016) forms appeared. In contrast to synapsids and later reptiles, the infratemporal fenestra in infrafenossal parareptiles often forms between the jugal, squamosal, and quadratojugal (Broom, 1913; DeBraga & Reisz, 1996; Tsuji, 2006), probably indicating independent evolution of this temporal opening. Procolophonoids have large orbitotemporal openings (Colbert, 1946; Zaher, Coram & Benton, 2019). In some procolophonoids, the infratemporal fenestra can co-occur with a ventral excavation in the ‘cheek’ (Cisneros et al., 2004).

Independent of the current hypotheses on parareptile interrelationships, Diapsida likely emerged from a scutal ancestor (22 in Fig. 5; Muller & Reisz, 2006; Ford & Benson, 2020). The ancestral condition of diapsids may have
been bifenestral (23 in Fig. 5; Reisz, 1977; Ford & Benson, 2020). However, the fossafenestral condition in several other early diapsids (Carroll, 1981; Bickelmann, Müller & Reisz, 2009), as well as the different bone configuration in later bifenestral taxa (Müller, 2003), could also argue for an ancestrally fossafenestral condition in Diapsida (Evans, 2008) or would at

**Fig. 5.** Composed and simplified phylogenetic tree of Tetrapoda, depicting the distribution of the temporal morphotypes proposed in this review. Relationships that are currently controversial (early Tetrapoda, early Amniota, Parareptilia, late Diapsida) are depicted as polytomies. Note that the colours depict the presence of one representative morphotype within a clade but do not indicate its relative abundance within the respective clade. Skulls are listed as in legend to Fig. 2, unless otherwise indicated below: (1) Acanthostega gunnari; (2) Eryops megacephalus (after Sawin, 1941); (3) Anthracosaurus russelli; (4) Lystrodon pricei; (5) Erythrosuchus macrourus (after Jenkins et al., 2007); (6) Microcoelus taylori; (7) Eocholeodactylus sp.; (8) Cryptobranchus alleganiensis; (9) Pleurodeles waltli; (10) Bombina orientalis; (11) Cynognathus platyceps; (12) Gastrotheca galeata (after Paluh et al., 2020); (13) Limnoscelis paludis; (14) Cynognathus romeri; (15) Lystrosaurus murrayi; (16) Coanastes platypterus; (17) Zalambdalestes lehli; (18) Tachyglossus aculeatus; (19) Milleropus pricei; (20) Bolosaurus striatus; (21) Scutosaurus karpinski; (22) Captorhinus aguti; (23) Petrolacosaurus kansensis; (24) Claudiosaurus germanicus; (25) Temnodontosaurus trigonodon; (26) Cleosaurus hudsoni; (27) Iguana iguana; (28) Argyrodes fasciolatus; (29) Henodus cheyops (after Rieppel, 2001); (30) Keichousaurus hui (after Holmes et al., 2008); (31) Phacosaurus kavanii; (32) Pseudobachytes quenstedti; (33) Emydura macquarii; (34) Pelodiscus sinensis; (35) Testudo graeca; (36) Erythrosuchus africanus; (37) Postosuchus kirkpatricki; (38) Thalattosuchus superciliosus; (39) Gallus gallus.
least imply secondary evolution of the bifenestral morphotype in these forms (26, 36, 38 in Fig. 5). In fact, Ichthyosauromorpha, Lepidosauromorpha, Sauropterygia, Archosauromorpha, and Pantestudines likely were all ancestrally fossafenestral (Waldman & Evans, 1994; Evans & Borsuk-Bialynicka, 2009; Nesbitt, 2011; Neenan, Klein & Scheyer, 2013; Motani et al., 2015; Zhou et al., 2017) or at least infrafenestral in the case of Pantestudines (Li et al., 2008; Bever et al., 2015). Nevertheless, the supratemporal fenestra would have been ancestrally present in either scenario (Müller, 2003; Evans, 2008; Ford & Benson, 2020), originally likely bordered by the postorbital, squamosal, parietal, and supratemporal (Reisz, 1977). Its size (e.g. Nicholls, 1999; Benson et al., 2013), as well as the contributions of the supratemporal, frontal, and postfrontal varied in later representatives (e.g. Müller, 2003). Additionally, the temporal opening in the ’cheek’ is closed in several extinct diapsids (Kuhn-Schnyder, 1967; Tarsitano, 1983; Reisz, Berman & Scott, 1984), most notably in Ichthyosaurus (25 in Fig. 5) and various Sauropod groups (51 in Fig. 5), leading to a suprafenestral morphotype.

The fossafenestral state was retained in most Lepidosauria (27 in Fig. 5; Evans, 2008), although in Rhynchocephalia (26 in Fig. 5; Whiteside, 1986; Jones, 2004), as well as a few Squamata (Mo, Xu & Evans, 2010), the bifenestral state reappeared. In Scincoida, the supratemporal fenestra is closed (infrafenestral; Gaupp, 1895a), whereas in Ophidia (28 in Fig. 5) and some other squamate clades, large portions of the temporal dermocranium have been reduced, forming a nudital morphotype (e.g. Das et al., 2019). Testudinata are ancestrally scutal (32 in Fig. 5), however with morphological differences from the scutal ancestors of diapsids (e.g. Jaekel, 1909a; Rieppel & de Braga, 1996; Müller, 2003; Werneburg, 2012). This condition formed likely by closure of the supratemporal fenestra, followed by closure of the ventral excavation (Werneburg, 2015; Schoch & Sues, 2018). In Testudines, distinct ventral and postero dorsal excavations formed in the temporal dermocranium (Gaffney, 1979; Werneburg, 2012). Pleurodira usually possess a large ventral opening (infrafenestral; 33 in Fig. 5), whereas in Cryptodira the postero dorsal opening is often dominant (suprafenestral; 34 in Fig. 5). Sometimes both the ventral and postero dorsal excavations can be enlarged, leaving only a narrow temporal bridge between them (bifenestral; Gaffney, 1979) or even become entirely confluent (nudital; Gaffney, 1979). The set of dermal bones that contribute to the testudine temporal bridges varies considerably (Werneburg, 2012). Notably, the scutal morphotype reappeared in Testudines, especially in Chelonioidea (Jones et al., 2012).

The ancestral fossafenestral state in Archosauromorpha evolved twice independently into a bifenestral condition by closure of the lower temporal bar: in late Rhynchosauria (Benton, 1983), as well as in Archosauromorpha (36 and 38 in Fig. 5), where it became the dominant morphotype in all non-avialan taxa (Nesbitt, 2011). In some early archosauriforms, the infratemporal fenestra was closed again (suprafenestral; Heckert et al., 2012), whereas in some Caimaninae the supratemporal fenestra is closed instead (infrafenestral; Mook, 1921). In some early Pseudosuchia (37 in Fig. 5), an additional pair of infratemporal fenestrae even appeared (additofenestral; Sulej, 2005; Weinbaum, 2011). A similar arrangement formed in Tyran nosauria by subdivision of the previous infratemporal fenestra by a bony process (e.g. Carr, 1999). Finally, within Ornithothoraces, the supratemporal fenestra was closed and the lower temporal bar disappeared (e.g. Jollie, 1957; O’Connor & Chiappe, 2011; Field et al., 2018), leading to the typical infrafenestral morphotype of birds (39 in Fig. 5). Within Neognathae, the upper temporal bar reformed several times independently (fossafenestral; Elzanowski & Mayr, 2017).

(c) Unresolved controversies

In spite of moving away from using temporal morphology as a major trait in phylogenies, ongoing debates remain regarding the temporal morphology of phylogenetically unstable taxa and on the ancestral condition for some radiations. As indicated in Section III.1d, such debates surround the ancestral condition in early amniotes, as well as the evolution of the turtle skull.

While there is mostly a consensus on the content of early Synapsida and early Reptilia (e.g. Müller & Reisz, 2006; Benson, 2012; MacDougall et al., 2018; Spindler et al., 2018; but see also Laurin & Piñeiro, 2017, 2018; Ford & Benson, 2020), the relationships of some Paleozoic tetrapod groups relative to Amniota are subject to debate. For example, the Diadectomorpha, traditionally seen as the sister taxon to Amniota (e.g. Laurin & Reisz, 1995, 1997; Lee & Spencer, 1997; Reisz, 1997; Laurin & Piñeiro, 2017; Ford & Benson, 2020), have also been repeatedly argued to nest within the amniote crown-group as sister to synapsids (e.g. Berman, Sumida & Lombard, 1992; Sumida, Lombard & Berman, 1992; Berman, 2000, 2013; Marjanovic & Laurin, 2019; Klembara et al., 2019). Similarly, Recumbirostra, a potential clade of ‘microsaurs’ and some other lepospondyls has been proposed actually to represent one of the earliest reptilian radiations (Pardo et al., 2017; Mann, Pardo & Maddin, 2019). In fact, the monophyly and phylogenetic position of lepospondyls within Tetrapoda is still controversial (e.g. Marjanovic & Laurin, 2019). The potential nesting of diadectomorphs and recumbirostrans within Amniota would have implications for the ancestral condition and early evolution of the temporal region in the amniote crown-group. Like many other Paleozoic tetrapods, diadectomorphs typically had a fully roofed dermocranium (Kissel, 2010). If they are indeed the sister-clade to synapsids, the infratemporal fenestra in synapsids could have evolved later, after the split of the synapsid-diadectomorph clade from Reptilia, or the fully roofed (scutal) morphotype in diadectomorphs could have been a derived condition from a fenestrated ancestor. Piñeiro et al. (2012) argued that the possession of an infratemporal fenestra could be the ancestral condition in
amniotes. However, this would be dependent on the phylogenetic position and temporal morphology in Mesosauridae (see below). Lastly, nesting recurvirostra within reptiles would add another set of temporal morphotypes to the early morphological diversity of Reptilia, including excavations and distinct reductions of the dermatocranium (e.g. Pardo & Anderson, 2016; Mann et al., 2019).

A second major discussion relates to the presence of an infratemporal fenestra in the Permian reptile taxon Mesosauridae. Despite an uncertain phylogenetic history [see Modesto (2006) and references therein], mesosaurids are usually seen as an early-diverging branch of parareptiles (e.g. Tsuji & Müller 2009; Ford & Benson 2020), or taking an even more stemward position within reptiles (e.g. Laurin & Piñeiro, 2017). Thus, they could be a key to reconstructing the ancestral temporal morphotype for Parareptilia, and potentially also for Reptilia or Amniota as a whole (Piñeiro et al., 2012). Previously interpreted to possess both an infratemporal and supratemporal fenestra (MacGregor, 1908), later work (von Huene, 1941) led to a new consensus that only the infratemporal fenestra was present. This changed with Modesto (2006), who redescribed the cranial anatomy of mesosaurids, interpreting them to possess a fully rooted temporal region. By contrast, Piñeiro et al. (2012) reported the infratemporal fenestra to be present in the specimens they described and even to be demonstrable in disarticulated remains due to the shape of the jugal and postorbital. Their interpretation has since been disputed [MacDougall & Reisz, 2014; MacDougall et al., 2018; but see Laurin & Piñeiro (2018) for a response]. It has been also suggested that the infratemporal fenestra may have been ontogenetically (MacDougall et al., 2018) or intraspecifically variable, given that both scenarios have been demonstrated for other parareptiles (Gow, 1972; Cisneros, 2008; Haridy et al., 2016). Despite being able to examine the mesosaurid material of the Senckenberg collections in Tübingen and Frankfurt am Main, Germany, we remain unable to agree confidently with either hypothesis. At present, there seems to be no consensus on mesosaurid phylogeny and temporal morphology. Their highly aquatic lifestyle (Silva et al., 2017) may also mean that their morphology is too derived to be able to draw conclusions regarding the ancestral cranial morphotype in amniotes.

Another controversial topic in terms of the evolution of the temporal region remains the ancestry and phylogenetic position of turtles. Traditionally depicted as possessing an ancestral fully rooted temporal region (e.g. Cope, 1892; Williston, 1917; Boettiger, 1952; Kilias, 1957), many early researchers highlighted the derived morphology of the turtle skull relative to the condition in early tetrapods (e.g. Baur, 1889; Fuchs, 1909; Jaekel, 1909a; Zelansky, 1923–1925). Different phylogenetic analyses have nested turtles deep within Diapsida and, hence, implied their descent from ancestors with a fenestrated temporal region (e.g. Rieppel & de Braga, 1996; DeBraga & Rieppel, 1997; Bhullar & Bever, 2009; Schoch & Sues, 2015). An example of a fenestrated stem-turtle possibly has been found: the description of the Triassic diapsid *Pappochelys rosinae* suggests that it had a supratemporal fenestra and distinct ventral excavation in the ‘cheek’ region (Schoch & Sues, 2015, 2018). An even more stemward stem-turtle may be the Permian *Eumolops africanus* (Lyson et al., 2010; Bever et al., 2015; Schoch & Sues, 2015). Bever et al. (2015) argued that in juvenile specimens of *E. africanus*, in addition to the distinct ventral excavation observed for assumed adults, a supratemporal fenestra was present. The supratemporal fenestra would have been closed during ontogeny by the extreme anterior, autapomorphic expansion of the supratemporal and hence may perhaps represent an early stage of the condition in turtles. However, we consider this scenario as unlikely, because such an extraordinary bone growth in post-hatching ontogeny is extremely rare among amniotes, and when present usually concerns multiple bones aligning to each other (e.g. Hall, 2014). For closure, even separate ossification inside the upper temporal opening may occur (Klembara et al., 2017). However, we argue that the juvenile presented by Bever et al. (2015) rather shows a taphonomic disruption than a preservation of an early ontogenetic state of fenestral development. Compared to the adult condition, the jugal is broken off the postorbital and unnaturally reaches into the ventral temporal excavation in the juvenile suggesting that some pressure on the snout travelled along the maxilla to break the jugal. Before breakage, the force was likely further transmitted via the postorbital towards the dorsal temporal region and the scute-like supra-temporal (Bever et al., 2015) was likely spilled off. A precise description and reconstruction of the juvenile bones, by which a premature and unbroken supratemporal could be discovered would, however, support the hypothesis of Bever et al. (2015). It is worth noting that *E. africanus* could also represent a species of parareptile or synapsid, not closely related to turtles (Lee, 1995, 2013; Tsuji & Müller, 2009; MacDougall & Reisz, 2014; Lichtig & Lucas, 2021); correspondingly, *P. rosinae* has been also argued by some to nest outside of the turtle stem-group (Lichtig & Lucas, 2021).

Ford & Benson (2020) provided the most recent assessment of the phylogenetic implications of temporal fenestrae on the relationships of early amniotes. In contrast to most previous workers (although see Laurin & Piñeiro, 2017), they found parareptiles as well as the traditional synapsid group Varanopidae to nest within Diapsida. This would have major implications for the ancestral condition in diapsids as, if varanopids and parareptiles are early-branching diapsids, the infrafenestral morphotype could either have been the ancestral state of all diapsids (similar to synapsids) or evolved secondarily by closure of the supratemporal fenestra. This would mean there could have been diverse temporal morphotypes around the base of Diapsida with taxa possessing both temporal fenestrae (Reisz, 1977; Müller, 2003; Ford & Benson, 2019), with a secondarily closed infratemporal fenestra (Reisz et al., 1984), with a secondarily closed or never evolved supratemporal fenestra (Tsuji & Müller, 2009; Piñeiro et al., 2012; MacDougall & Reisz, 2014), with a supratemporal fenestra and distinct ventral excavation (Carroll, 1981; Modesto & Reisz, 2003), or...
with a ventral excavation alone (Tsuji et al., 2010; MacDougall & Reisz, 2014).

(2) Understanding the functional origins of temporal openings

Early in the research history of the temporal region, investigators not only described the morphological patterns they observed, but also attempted to explain how the vast structural diversity in lissamphibian and especially in amniote skulls had arisen. For example, Hallmann (1837) already emphasized the functional background to the observed temporal anatomy.

(a) Comprehending diversity (1880s–1900s)

Dollo (1884) compared the temporal anatomy of non-avian dinosaurs and other extinct taxa with extant groups to predict the size of different jaw adductor muscles. He argued that dominance of either the internal or external jaw musculature would affect the feeding mode of a taxon. Dollo (1884) also argued that dominance of internal jaw adductors in crocodylians and sauropods was related to the posterior movement of the choanae or external nares, respectively, enabling more space for these muscles in the anterior palate. Dollo (1884) saw this as the reason for the small size of the supratemporal fenestra in crocodylians compared with the enlarged fenestra in extinct marine crocodiles, with the latter having their choanae positioned more anteriorly.

Gaupp (1895b) related the transition of a closed, ‘zygocrotaph’ dermatocranium to a fenestrated, ‘zygocrotaph’ appearance to the presence of hydrostatic forces acting on the skull. According to Gaupp (1895b), the lack of external hydrostatic forces in terrestrial vertebrates as well as the increased need to counter gravitational forces, favoured a reduction of skull mass. The remaining temporal bars in the ‘zygocrotaph’ skull would then be aligned and strengthened or weakened depending on the forces applied by the jaw musculature. Gaupp (1895b) interpreted the ‘gymnocrotaph’ morphology (i.e. a temporal region, in which the temporal bars are reduced) as the result of limited forces acting on the temporal bones.

Gegenbaur (1898) also provided an in-depth discussion of the relationships between jaw musculature and temporal morphology. He was probably the first explicitly to interpret the evolution of temporal openings as an adaptation to provide attachment sites for the jaw muscles. Particularly with reference to mammals, Gegenbaur (1898) made a connection between a more ‘massive’ dentition and stronger jaw musculature, which would influence the morphology of the zygomatic arch and parietal crests relative to the feeding strategy of any taxon. By contrast, a reduction of the dentition in insectivorous taxa like Tachyglossus would allow a corresponding reduction of the zygomatic arch and parietal crest.

Fuchs (1909) argued that simplification of the dental covering of the temporal region would not inevitably lead to the evolution of temporal openings. Fuchs (1909) postulated that the relative proportions of the braincase and otic capsules as well as the evolution of a streptostylic jaw (i.e. with a mobile quadrate) were major factors explaining the observed variations in the temporal region. Fuchs (1909) described how the dermal bones of the temporal region can extend internally to the jaw adductor musculature (internal lamella) with the potential to replace the primary cartilaginous braincase of the embryonic skull (as seen in mammals and turtles; Werneburg & Maier, 2019). With changes in the size of the braincase, the size of the internal lamellae and hence temporal anatomy would also have been affected. Also affecting the size of the internal lamellae would be the size of the otic capsules, which Fuchs (1909) argued would ancestrally have been large but occupied less space in the interior cranium in later taxa. Lastly, Fuchs (1909) correlated the presence of ‘monimostyly’ versus ‘streptostyly’ with the extent of the temporal dermatocranium. A fully closed temporal region or rigidly sutured temporal bars would create a fixed quadrate and, hence, monimostylic jaw, whereas a reduction of a rigid temporal coverage would have enabled the evolution of a streptostylic jaw.

(b) The interplay between muscle and bone (1910s–1950s)

Gregory & Adams (1915) considered the relationship between temporal morphology and jaw musculature. They observed that in extant taxa like Sphenodon and turtles the jaw adductor musculature is attached to the sagittal crest and/or to temporal bars. Gregory & Adams (1915) argued that the temporal openings provide more space for action of the temporal musculature and concluded that in extinct taxa with a closed dermatocranium the temporal musculature had to be positioned medially to the dermal bones. Stresses induced by the jaw and neck musculature were thus partly responsible for modifications of temporal osteology in later taxa. Adams (1919) extended these ideas to the relationships between osteology, diet, and myology, using evidence from numerous extant taxa and embryology.

Versluys (1919) discussed in detail how different actions of the internal and external jaw adductor musculature could be related to the evolution of different temporal morphotypes. Versluys (1919) argued that in early aquatic vertebrates with a fully closed temporal region, greater muscle movement could be achieved by simply enlarging the jaw adductor chamber. Further evolution of the neck and increased mobility of the tetrapod skull would have favoured the evolution of a lighter and narrower skull. This would have restricted the possible action of the jaw adductor musculature, which could have been offset by opening the temporal dermatocranium. Versluys (1919) argued that the best way to create temporal fenestrae would have been the loss of the intertemporal bone in amniotes or degeneration between the sutures of the jugal, squamosal, and quadratojugal. Depending on the taxon, the temporal fenestrae also could have developed at other sites in the temporal region. Versluys (1919) interpreted the selection pressure involved to be differences in feeding mode, which would require different proportions of internal and external
adductor musculature, depending on whether a high biting force or rapid closure of the jaw was required.

Zdansky (1923–1925) was interested in the temporal morphology of turtles, which he considered to be more diverse than in other vertebrates. Similar to Jaekel (1909a, 1916), Zdansky (1923–1925) interpreted the fully roofed temporal dermalcranium of modern turtles to have evolved secondarily in forms that could not, or could only partly, retract their head under the shell (e.g. in the sea turtles, *Platysternon, Macrochelys,* and *Podocnemis*). A similar conclusion had been drawn by Hay (1908), Zdansky (1923–1925) interpreted the return to a fully roofed dermalcranium in these taxa as a defensive adaptation to compensate for the lack of a retractable neck.

Inspired by observations on postcranial bones, Case (1924) investigated the role of muscle action on the formation of temporal openings. In the postcranial bones of humans, such as the scapula or ilium, the associated muscles are attached to thickened margins of the respective bones, whereas the centres of the bones, which experience little direct loading, are distinctly thinned. According to Case (1924), this pattern represented an adaptation to greater muscle force acting on the marginal regions of the bones, triggering the development of additional trabecular bone in these areas. Applying this logic to the temporal region, Case (1924) argued that in forms with a closed dermaticranium, the load would have been concentrated on marginal sections of the temporal bones, which would thicken in response, whereas sections subject to less loading could be thinner and subsequently reduced, forming a skull with temporal fenestrae and thickened temporal bars.

Lakjer (1926) considered in depth the functional differences in the jaw muscles, the associated bones, and skull kinesis of reptiles (‘Sauropsida’) and other vertebrates. Lakjer (1926) particularly highlighted the relationship between muscle size and bite force for non-ophidian squamates [‘Sauria’ in Lakjer (1926)], including taxa that were herbivores, omnivores, or predators of large prey. He also observed a relationship between muscle size and temporal dermal armour in lissamphibians, as demonstrated in the differentiation of fenestrated morphotypes. Fox (1964) also interpreted this to have led to rearrangement of the posterior skull region, Olson (1961) did not find evidence for major changes in the jaw musculature in these forms; however, Olson (1961) postulated that with the rise of Tetrapoda, the evolution of several modifications of the K–I and S–P systems took place. While early Amphibia and predominantly aquatic Amniota evolved only a derived K–I system, Olson (1961) associated the evolution of the S–P system in amniotes with doming of the skull and a tendency to develop temporal openings as well as other osteological adaptations for muscle attachments. Comparable to the conclusions of Versluys (1919) and Case (1924), Olson (1961) argued that the terrestrial lifestyle of early amniotes would have been accompanied by higher mobility of the head and changes in feeding habits, which influenced the origin sites of the jaw musculature: dermaticranium strengthening was concentrated on the few functional attachment sites for muscles, whereas the regions of the dermal roof without a function in muscle attachment were reduced. This morphology, Olson (1961) described as a ‘network of lines of stress’.

The notion of ‘lines of stress’ to explain the evolution of temporal openings was developed further by Fox (1964), who observed that in the early Permian reptile *Capitosaurus,* the centre of the fully covered ‘cheek’ region was thinned. Similar observations had been made by Jaekel (1902) for the possible reptiliomorph *Gephyrostegus bohemicus,* who proposed that they represented an early stage in the evolution of fenestrated morphotypes. Fox (1964) also interpreted this morphology to result from lower levels of stress in the cheek centre. As these areas apparently did not function as muscle attachment sites, and additionally were not needed as sources of calcium for attached muscles, there would be no selection against reduction of the bone. Fox (1964) considered all
possible stresses affecting the ‘check’ region, including forces arising from the weight of the anterior part of the cranium, jaw articulation, and muscle action. Fox (1964) also highlighted that selective pressures leading to the development and enlargement of temporal openings were likely to be multidimensional and to differ among various clades. For the further enlargement of temporal openings in later amniotes, Fox (1964) proposed that additional space for the jaw adductor muscles and a reduction in weight of the skull were likely to be the main factors involved.

Frazzetta (1968) also argued that selection for the initial development of a temporal opening could differ from selection for retaining or enlarging it in later forms. Nevertheless, Frazzetta (1968) considered it likely that there was a common adaptive reason for the development of temporal openings in all clades. Frazzetta (1968) suggested that the lack of temporal openings in early tetrapods and their ancestors could be explained by their plesiomorphically flat skull. The main jaw action in these skulls would involve the pterygoid musculature, which would create a predominantly tangential force affecting the temporal region (i.e. the K–F system Olson (1961)). In most amniotes and other tetrapods with a more domed skull, the main jaw action instead would arise from the jaw adductor musculature attached to the skull roof, creating predominantly perpendicular forces. Frazzetta (1968) emphasized the restricted attachment site of these muscles, which correlated with the development of medial bony ridges as described by Fox (1964) for Captorhinus. These ridges, representing the previously described ‘network of lines of stress’, thus functioned to strengthen the skull at the muscle attachment sites. Another factor affecting the restricted attachment area of the jaw musculature within the adductor chamber might be the pennate structure of the jaw adductors, which is related to more efficient adduction of the mandible. Frazzetta (1968) saw the restricted attachment of the jaw adductors as a reason for the development of fenestrae in less-loaded areas of the skull. Frazzetta (1968) supported this argument with skulls of the early synapsid Ophiacodon retroversus, in which some specimens have a second pair of infratemporal fenestrae between the jugal, squamosal, and quadratojugal (i.e. additofenestral). When this ‘accessory temporal opening’ was not present, or was present on only one site of the cranium, the area between the three bones was still ‘paper thin’. Romer & Price (1940) had argued there would have been no disadvantage to leaving this suture open, indeed jaw adductor action may even have benefited from the additional free space, and that the development of large fenestrae with thickened margins (i.e. bony ridges) would provide sites for a more concentrated attachment of the jaw adductor musculature. Frazzetta (1968) further suggested that the meeting points of three dermal bones would favour the development of fenestrae where they were not subjected to loading. Finally, Frazzetta (1968) argued that, in flat-skulled tetrapods like temnospondyls, the low vertical resistance and muscle attachment without the development of bony ridges would oppose the formation of temporal fenestrae. Even in more domed tetrapods without temporal fenestration, the skull roof was only connected to the cheek region by the remnant of an intracranial joint. Development of fenestrae in these taxa, according to Frazzetta (1968), would have significantly weakened the skull.

Yet, Frazzetta (1968) did acknowledge that this condition may be present in some fenestrated amniotes such as the early synapsid Varanosaurus. In contrast with both Gregory & Adams (1915) and Fox (1964), Frazzetta (1968) disagreed that bulging of the jaw musculature or conservation of structural materials could explain the formation of temporal openings, as the earliest temporal fenestrae would have been too small to function in this way. [Correction added on 8 June 2021 after first publication: in the fourth sentence of the preceding paragraph, the citation to Fox (1964) has been corrected to Olson (1961)]

Like previous authors (Fuchs, 1909; Kuhn-Schnyder, 1954, 1963), Gow (1972) noted that similar traits may have evolved independently in distantly related taxa, even though for similar reasons. He disagreed with Fox (1964) that the weak zone in the ‘check’ of Captorhinus could be the predecessor of a temporal fenestra. Instead, he argued that the Permian parareptilian group Milleretidae may be key to understanding the evolution of temporal fenestration in reptiles. Gow (1972) demonstrated that in juveniles of Milleretta rubidgei a small infratemporal fenestra was present that disappeared completely in adults, mostly due to an anterior extension of the squamosal. He explained this by contraction/expansion in the ‘check’ induced by expansion of the palate at the basicranial articulation (i.e. the articulation between the pterygoid and braincase). According to Gow (1972), this could represent a condition derived from the intracranial kinetics of anthracosaurs, which could likely move their braincase and skull roof relative to their palate and ‘check’ (Thomson, 1967). In contrast to the typical saccopterygian intracranial joint between ‘check’ and skull roof found in the putatively reptilomorph anthracosaurs, the squamosal of M. rubidgei was firmly attached to the skull roof. This would result in a ‘line of weakness’ between the jugal, squamosal, and quadratojugal on whose dorsal termination the temporal fenestra was formed. Gow (1972) noted that widening of the temporal region would have been a significant precondition to allow such a development in M. rubidgei. Further reductions of the temporal dermatocranium (i.e. the formation of a ventral excavation) in other milleretids, especially Milleretops, would have resulted in even greater intracranial mobility.

Notably, Gow (1972) highlighted that temporal fenestrae in the Permian Tongina and later diapsids were likely to have different causes.

Over the course of the 20th century, a growing consensus on the relationship between temporal openings and jaw adductor musculature inspired several studies on jaw biomechanics in extinct and extant taxa (e.g. Crompton, 1963; Barghusen, 1973; Kemp, 1969, 1980, 1984; Rieppel & Gronowski, 1981). The notion that temporal fenestrae functioned as an adaptation to allow bulging of the jaw musculature (see Gregory & Adams, 1915) fell out of favour.

Kemp (1980) proposed that the infratemporal fenestra in early synapsids did not evolve from a skull similar to that of...
early Eureptilia (‘Romeriidae’), but instead from a type more similar to the diadectomorph Limnoscelis. Kemp (1980) highlighted that the appearance of supratemporal and tabular bones in synapsids is comparable to the condition in Limnoscelidae. Like other early tetrapods, Limnoscelis retained a loose connection between ‘cheek’ and skull roof as a remnant of the saccopterygian skull with its intracranial joint. According to Kemp (1980), the synapsid infratemporal fenestra could have formed by the adductor musculature attaching to the bony margins of the intracranial joint, which was then strengthened by the processes described above. The fenestra would subsequently form in the connecting area between the ‘cheek’ bones and skull roof.

Kühn-Schnyder (1980), agreeing with Frazzetta (1968) that temporal fenestrae predominantly form in the sutures between three bones, identified the jugal–squamosal–quadrate-jugal and postorbital–squamosal–parietal contacts as key regions. While apparently considering muscle action as the main selective force underlying fenestration, Kühn-Schnyder (1980) also argued for a role of the atlanto-occipital joint (see also Versluys, 1919). Elongation of the neck and higher mobility of the head would require a lighter skull and hence favour the formation of fenestrae. He cautioned that such biomechanical causes would make taxonomic classifications based on temporal morphology less reliable, but he considered temporal morphotypes to be mostly constant within single reptilian groups.

Carroll (1982) interpreted early synapsids predominantly as macropredators with the relatively short jaw adductor chamber enabling a wider jaw gap, whereas early diapsids were insectivores in which the presence of temporal fenestrae would have created a lighter skull and the temporal bars formed as areas of maximal resistance against forces generated during feeding (see also Evans, 2008). Similar ideas had been proposed by Versluys (1919), who interpreted temporal differences between early Synapsida and Diapsida in terms of their different feeding ecology requiring a different arrangement of the jaw musculature. Despite the presence of two pairs of temporal fenestrae in early diapsids, Carroll (1982) argued that their jaw mechanics and muscle distribution would have been similar to their non-fenestrated reptilian ancestors.

The loss of the lower temporal bar in Lepidosauria and a variety of other fossil taxa was discussed by several researchers (Robinson, 1973; Evans, 1980; Rieppel & Gronowski, 1981; Whiteside, 1986). They generally disagreed that this loss had a functional relationship with the evolution of streptostyly as proposed by previous researchers (Fuchs, 1909; Romer, 1956). Based on an incomplete lower temporal bar and fixed quadrates in the early rhynchocephalian Cleosaurus hudsoni, Robinson (1973) argued that this may be an auditory adaptation, separating the quadrates from the lower temporal bar to reduce interference with the ears during feeding. Evans (1980) disagreed with this interpretation, because action of the dentulous palatine and stretching of the post-quadrato tympanic membrane by the mandible would still affect hearing ability during feeding, making any effect of a jugal–quadrate separation negligible.

She also suggested that this and similar excavations of the ‘cheek’ bones were not related to quadrate movement and that skulls with a mobile quadrate represented a derived condition relative to skulls lacking the lower temporal bar (in squamates) or in which the lower temporal bar was present (in birds). Evans (1980) favoured a relationship with the location and attachment sites of the jaw adductor musculature, probably making the lower temporal bar unnecessary for muscle attachment. Rieppel & Gronowski (1981) also did not support a relationship with streptostyly, instead postulating that loss of the lower temporal bar was a consequence of differentiation of the external jaw adductor musculature: a newly developed muscle unit extended posterovertrally from the posterior temporal region to the lateral mandible. Whiteside (1986) drew connections between the weak but rapid bite that would have accompanied the punctuating dentition in these taxa, and interpreted the reappearance of the lower temporal bar in the extant tuatara as an adaptation to ensure precise occlusion of the jaws in taxa with a more powerful bite.

In a study on turtles, Lakjer (1926) interpreted a ligament between the quadrate and jugal as the retention of a lower temporal arch from diapsid ancestors. Werneburg (2013b), however, demonstrated that this ligament was derived from a superficial craniocephalic aponeurosis and argued that adjacent bones could not develop histologically into one consistent ligament. The quadrate-jugal ligament would serve in turtles as tension cord (sensu Klenner et al., 2015) to buffer bite forces (Werneburg, 2013b; see also Jones et al., 2012). In other amniotes, this ligament is either detached from the quadrate in mammals (i.e. as the external masseter fascia) or from the jugal in non-turtle reptiles (i.e. as the quadrate ligament; cf. Iordansky, 1996) and serves as a morphogenetic element to differentiate the external jaw musculature in these taxa (Werneburg, 2013b).

(d) Quantitative modelling and other recent approaches (1990s–present)

The recent increase in computational power has enabled researchers to perform quantitative analyses on the functional morphology of tetrapod skulls. In addition to large-scale statistical analyses of diversity patterns (e.g. Jones, 2008; Young et al., 2010; Ferreira et al., 2020; Paluh et al., 2020), these include muscle reconstructions and finite element analyses of the skull, and modelling of strain distributions along the temporal bones (e.g. Hylander & Johnson, 1997; Hollday & Witmer, 2007; Lautenschlager, 2015; Lautenschlager et al., 2017; Ferreira et al., 2020; Nabavizadeh, 2020). An in-depth discussion of this literature is outside the scope of this review, but these studies provide a valuable basis for future large-scale studies on the comparative functional morphology of the tetrapod temporal region.

Of particular interest are the functional causes underlying the temporal morphology of caecilians (Gymnophiona). Extant caecilians either possess a distinct posterooral excavation between the parietal and squamosal (‘zygokrotaphic’) or a fully roofed dermatocranium (‘stegokrotaphic’; e.g. Kleinteich et al., 2012; Sherratt et al., 2014). In contrast
to earlier interpretations (Nussbaum, 1983), the ancestral morphology of caecilians was likely ‘stegokrotaphic’ (i.e. scutal) and probably sympleisomorph with the condition in dissorophid temnospondyls, the putative sister-clade to lissamphibians (Madlin et al., 2012; see Section III.1d) with ‘zygokrotaphic’ (i.e. suprafossil in caecilians) forms having evolved several times independently in the crown-group (Kleinicheh et al., 2012). ‘Stegokrotaphy’, together with eyes covered by bone and a subterminal mouth, has been interpreted as an adaptation to a fossorial lifestyle including head-first burrowing (Sherratt et al., 2014; Bardua et al., 2019). ‘Stegokrotaphic’ forms differ in their fossorial behaviour from ‘zygokrotaphic’ taxa, as they are apparently better adapted to burrow in more compact soil (Gower et al., 2004). However, Kleinicheh et al. (2012) demonstrated that the temporal bones are relatively unaffected by forces assumed to act during head-first burrowing. They postulated instead that ‘zygokrotaphy’ evolved in caecilians to provide more space for the jaw adductor musculature. Nevertheless, even among ‘zygokrotaphic’ caecilians, the alignment of the jaw adductors can vary (Nussbaum, 1983). We propose that an influence of the neck musculature might be relevant if head mobility varies among taxa (sensu Werneburg, 2015).

In another group of lissamphibians, namely anurans, Paluh et al. (2020) inferred a relationship between a hyperossified cranium and dietary or defence adaptations. In anurans, the temporal region is usually reduced to the frontoparietal, squamosal, and quadratojugal (e.g. Schoch, 2014b). In several lineages, hyperossification of the frontoparietal, squamosal, as well as the maxilla led independently to secondary closure of the temporal region, sometimes with formation of an infratemporal fenestra in the ‘cheek’ (e.g. Ceratophrys, Calyptocephalella) or a casque-like cranium (e.g. Hemisus, Myobatrachus) (Paluh et al., 2020). In a large-scale quantitative analysis, the authors reported that such hyperossification occurs in hypercarnivorous taxa adapted to feed on other large vertebrates and is correlated with high and wide skulls that are also anteroposteriorly short. Paluh et al. (2020) further argued that this may represent an adaptation to the high forces acting on the skull during feeding. The casque-like cranium was found in taxa capable of phragmatic behaviour, i.e. the ability to retract the eyes within the orbital cavity, which is likely a defensive strategy, protects the eyes during feeding, or prevents water loss through evaporation.

Holliday et al. (2020) showed that, at least in archosaurs, only part of the supratemporal fenestra serves as an attachment site for the jaw adductor musculature. Small excavations adjacent to the supratemporal fenestra, which they referred to as the ‘frontoparietal fossa’, may instead have contained vascular and adipose structures. Holliday et al. (2020) argued that these structures could have functioned in thermoregulation, especially of the eyes and/or brain, or they may have supplied integumentary structures used in display [see Carr (2020) for a discussion on Holliday et al.’s (2020) interpretation of the frontoparietal fossa].

Werneburg (2012, 2013a, 2015, 2019) and Werneburg et al. (2015a,b) reported a series of studies focussing on the temporal region of turtles. Werneburg (2012) reviewed the morphological, evolutionary, and ecological factors potentially influencing temporal morphology in turtles and other amniotes. Werneburg (2015) identified a correlation between neck retraction in cryptodiran turtles and the formation of posterior excavations in their temporal region. He postulated that the tensile forces generated during neck retraction would require the skull to form deep postero dorsal emarginations for better stress distribution. If the ancestral state in the turtle stem-group was indeed a fenestrated skull, this would have also resulted in closing of the temporal fenestrae to produce the non-fenestrated condition seen in Testudinata. Indeed, the turtle skull may have evolved in response to a complex set of adaptations initiated by an increase in neck mobility and the evolution of the turtle shell (Ferreira et al., 2020; Werneburg, 2020). The loss, reduction, or absence of the ability to retract the neck could also explain the distinct reduction in temporal excavations in many extant taxa like sea turtles, Platysiren, or the recently extinct meiolanids, a conclusion also drawn in some previous publications (Zdansky, 1923–1925; Gaffney, 1983; Jones et al., 2012).

(c) Developmental studies

The field of evodevo has grown considerably in recent decades (Olsson, Höfleld & Breidbach, 2006), offering a perspective on macroevolutionary patterns often not feasible using anatomy alone. Considering embryology, ontogenetic changes, and the genetic mechanisms behind skull development may be key to understanding the evolution of temporal openings in tetrapods.

Tarsitano et al. (2001) considered mineralization of the jaw muscle tendons as a main driver behind the evolution of temporal fenestrae in amniotes. They proposed that the evolution of temporal fenestrae allowed a size increase in jaw musculature while ensuring a low angle of bone attachment. For muscles originally attaching to the sutures of temporal bones, incomplete closure of these sutures would enlarge the available attachment area for the jaw muscles (as already argued by previous authors) while maintaining a low angle of attachment. Over time, the developmental relationship between bone and jaw muscles would select for a more circular shape of the fenestrae as this would maximize the available surface for muscle attachment. A low angle of attachment between muscle and bone is not only optimal for biomechanical reasons but also would be beneficial during prenatal ontogeny due to the physiological need to maintain a large attachment area for the transport of biomolecules from bone to tendon.

Tokita, Chaeychomsri & Siruntawinieti (2013) identified a possible relationship between temporal morphology in reptiles and the distribution of mesenchymal cells expressing Runx2 and Msx2 genes. They reported a higher distribution of Runx2 and Msx2 expression in the lateral skull of turtle embryos relative to a focal distribution on regions forming the temporal bars in a crocodile embryo, and a distribution restricted to the precursor of the braincase in a snake.
embryo. Tokita et al. (2013) interpreted these distribution patterns of Runx2 and Msx2 expression as a key element in the diversity of the temporal region of amniotes.

Schoch (2014a) provided a hypothesis for the origin of emarginated ‘gymnokrotaphic’ (i.e. nudital) skulls in batrachians (frogs and salamanders). He argued that the cranial osteeology of adult batrachians can be compared to the larvae of branchiosaurid temnospondyls but with a trend for successive flattening of the skull that led to the ‘gymnokrotaphic’ morphotype. According to Schoch (2014a), this skull flattening made it necessary for the jaw musculature to increase in length [see also Frazzetta (1968); Section III.2], which would require a reduction of the ancestrally fully rooded dermal armour. This was achieved both by a lack of ossification in some of the dermal bones present in their presumed temnospondyl ancestors and by early fusion of primordial bones. The latter enabled the jaw adductors to attach dor-sally to the frontal and parietal primordia before other dermal bones were formed. A dorsal attachment of the jaw adductors has been also reported for supratrofosal caecilians (Nussbaun, 1983; Kleinteich et al., 2012). However, note that the content of the lissamphibian stem-group, as well as their temnospondylan affinities are still debated [Schoch (2014a) and references therein; Laurin, Lapauze & Marjanović (2019; Marjanović & Laurin (2019)], and the ossification sequences of branchiosaurids may be different to those of extant amphibians (Laurin et al., 2019).

Werneburg (2019) postulated ontogenetic plasticity as an underlying cause for the high diversity in amniote temporal anatomy. He argued that the absence of a larval stage in amniotes enabled the jaw musculature to attach directly to the developing temporal dermacranium. Whereas in larvae the dermal bones are not fully differentiated and jaw musculature has to attach to the primordial skull to be functional (Ziermann et al., 2018), in the direct development of amniotes, the jaw musculature is not restricted to an insertion onto the chondro-respectively neurocranium, and has more freedom to respond to the functional requirements of the hatchling/newborn.

The scenarios proposed by Schoch (2014b) and Werneburg (2019) may explain how both tetrapod crown-groups could reduce their temporal dermacranium despite different developmental strategies. Yet, these developmental strategies are derived relative to those of extinct tetrapod groups (e.g. Packard & Seymour, 1997; Schoch, 2014a; Laurin et al., 2019). The lack of temporal openings in most other Paleozoic tetrapods must be explained by selective forces that prevented the development of temporal openings in these taxa. While the developmental strategies of several Paleozoic tetrapod groups were strikingly diverse [Schoch (2014a) and references therein], especially in groups that possessed temporal openings such as the embolomere Anthracosaurus russelli (Panchen, 1977; Clack, 1987) or some lepospondyls (e.g. Bolt & Rieppel, 2009; Pardo & Anderson, 2016), their ontogenetic trajectories are not understood in detail (Schoch, 2014a; Laurin et al., 2019). Nevertheless, many lepospondyls apparently had an unphasic life cycle, possibly comparable to amniotes or terrestrial salamanders (Schoch, 2014a). Hence, the development of temporal openings in some lepospondyls may be explained in the same way (Werneburg, 2019). In fact, several lepospondyls with distinctly reduced regions of the dermatocranium recently have been proposed to nest within Amniota (Mann et al., 2019; see Section III.1e). However, the proposed absence of larvae in lepospondyls could be also explained by a preservation bias (Michel Laurin, personal communication) and the absence of a consensus on early tetrapod interrelationships complicates any attempt to make developmental inferences regarding this essential period of skull evolution.

(3) Summary on the origins of temporal openings
The majority of researchers have made a connection between jaw muscular arrangement and the presence and morphology of temporal openings. Yet, the evolution of the temporal region is likely to be multidimensional (e.g. Fox, 1964; Kuhn-Schnyder, 1980; Ferreira et al., 2020). Temporal openings seem predominantly to form in weak areas of the dermacranium, characterized by relatively thin bone (Jaekel, 1902; Romer & Price, 1940; Fox, 1964) and along the sutures of three or more bones (Frazzetta, 1968; Kuhn-Schnyder, 1980) or at intracranial joints (Kemp, 1980). These ‘weak’ areas may be more likely to form temporal openings due to a lack of ossification (Romer & Price, 1940; Cisneros, 2008), as an adaptation to reduce skull weight (Gaupp, 1895b; Fox, 1964), or to reduce bone volume in functionally less important areas (Case, 1924; Olson, 1961; Fox, 1964; Frazzetta, 1968) to provide more space for the jaw adductors (Dollo, 1884; Gregory & Adams, 1915; Versluys, 1919; Lakjer, 1926; Kleinteich et al., 2012). The arrangement of the latter determines the force distribution on the temporal dermacranium, thereby favouring the development of bony ridges along ‘networks of lines of stress’ for attachment of the musculature. This could subsequently facilitate reduction of areas subject to lower applied forces and the formation of strong temporal bars in high-stress regions (Gaupp, 1895b; Gegenbaur, 1898; Case, 1924; Kilias, 1957; Olson, 1961; Fox, 1964; Frazzetta, 1968; Carroll, 1982; Tarsitano et al., 2001). The arrangement of the jaw adductors is then dependent on the shape of the skull (Olson, 1961; Frazzetta, 1968; Tarsitano et al., 2001; Schoch, 2014b), the relative dimensions and positions of different skull regions like the choanae, otic capsules, braincase, and orbits (Dollo, 1884; Fuchs, 1909; Lakjer, 1926), and on the ontogenetic strategy (Schoch, 2014b; Werneburg, 2019). Temporal morphology will be further related to aspects of feeding mechanics like jaw movement (Dollo, 1884; Versluys, 1919; Olson, 1961; Whiteside, 1986), jaw articulation, and cranial kinesis (Fuchs, 1909; Romer, 1956; Kilias, 1957). Temporal morphology may be also dependent on neck anatomy, including the mobility of the head–neck joint (Versluys, 1919; Olson, 1961; Kuhn-Schnyder, 1980; Werneburg 2015) and the ability to retract the head (Zdansky, 1923–1925; Kilias, 1957; Werneburg, 2012, 2015; Ferreira et al., 2020). Finally, external mechanical stresses during an aquatic or fossorial lifestyle may also be related to a reduction in the temporal

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region (Gaupp, 1895b; Olson, 1961; Sherratt et al., 2014; Bardua et al., 2019).

There is obviously no universal answer explaining the formation of temporal openings in Tetrapoda, with selective regimes varying according to taxon (Fig. 6). For example, the ability to retract the head arguably plays an important role for the turtle skull, but is unlikely to be able to explain the presence of temporal openings in lepidosaurs or lissamphibians. Temporal morphology will be a compromise of the various factors that act on the skull, including potential phylogenetic constraints. Nevertheless, examples of independent evolution of similar temporal morphotypes (e.g. MacDougall & Reisz, 2014; Ford & Benson, 2020) suggest that in some cases we will be able to uncover general patterns of selection leading to a particular temporal morphology.

IV. CONCLUSIONS

(1) We introduced a novel morphological classification scheme that subdivides tetrapod temporal morphology into 10 morphotypes: scutal, infrafenestral, suprafenestral, bifenestral, additofenestral, fossafenestral, infrafossil, suprafossil, bifossil, and nudital. This scheme represents an alternative to traditional classification schemes in being independent of phylogeny, homology criteria, and functional interpretations. Plotting these 10 morphotypes onto a phylogenetic tree illustrates the broad range of character distributions among taxa. The ancestral condition of major clades remains uncertain—including those of Amniota, Reptilia, and Synapsida—because many morphotypes evolved in parallel in the early members of these groups. Future research should focus on obtaining a detailed and homology-based character definition of the temporal region, including bone-to-bone contacts, suture anatomy, and suitable metrics to enable us to understand the detailed pathways of evolution of the temporal region. This will allow us to clarify how similar morphotypes evolved in different taxa in response to (potentially different) selective forces.

(2) Research on the tetrapod temporal region has a long history, extending back to the early 19th century.
The morphological differences observed comparatively early in this field of research were placed into an evolutionary context by the late 19th and early 20th century. Within this period, several authors independently devised naming conventions for the different temporal configurations, and for taxa based on the latter, with several of these terms still in common use.

(3) A relationship between jaw musculature and the formation of temporal openings was proposed early on and was generally accepted during the last century. Temporal openings appear to form predominantly in relatively weak areas of the dermal armour, such as in the contact zone of three or more bones or at the intracraniar joint between the parietal and ‘cheek’.

Many researchers interpreted the formation of temporal openings, or more precisely the associated temporal bars and thickened bony margins, as an adaptation to force distribution and muscle size. The development of temporal openings has been considered in the context of tetrapod terrestrialisation and postulated to be favoured by the absence of external hydrostatic pressure, weight reduction, evolution of the head–neck joint, doming of the skull, but also skull flattening (in batrachians), changes in the jaw hinge and cranial kinesis, evolution of the otic capsules and auditory apparatus, or by the absence of a larval stage in early ontogeny. Postulated selective pressures include changes in feeding mechanics, enlargement of the braincase, evolution of neck retraction, fossoriality, and differentiation of the jaw adductor musculature.

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[Correction added on 8 June 2021 after first publication: publisher name and location have been added to the reference Hay (1906)]

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