

# Terrestrialisation and the cranial architecture of tetrapods

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## Abstract

Using four extinct land vertebrate species as examples, I discuss ontogenetic strategies as well as the potential influence of bite- and other external forces on the formation of the land vertebrate skull. In principle, areas under biomechanical stress are strongly ossified, whereas regions with little or no stress show only weak or no ossification. In this regard, all plates, arcades and openings of the skull – even in that of the multi-fenestrated dinosaurs – can be explained. I trace the changes in feeding mode and body posture at the transition from semi-aquatic to fully terrestrial tetrapods and discuss changes in the position of bite points. Through evolution, an increasing bite force is argued to have a crucial influence on the formation of new skull openings, such as the supratemporal and the antorbital fenestrae in archosaurs, by changing the direction of stress flows in the skull. The conquest of land was also associated with the appearance of novel types of behaviour such as inter- and intraspecific combats. Horns and other cranial weapons were formed repeatedly, which are shown to alter skull construction when receiving external forces. Changes in the skull biomechanics are associated with body posture and postcranial skeletal anatomy. Additionally, vice versa, the neck muscles are shown to have an important impact on the differentiation of the tetrapod skull. Finally, a new hypothesis is provided for the evolution of the temporal openings, based on biomechanical considerations. I argue that the synapsid (infracranial) morphotype was ancestral to amniotes related to a strong anterior bite in the mouth. Along the reptilian lineage – such as in many parareptiles, captorhinids and turtles – temporal fenestration was repeatedly closed by stiffening the temporal region in response to external forces. In addition, I argue that the upper temporal opening evolved first and that the diapsid (bifurcated) morphotype is secondary. The “triapsid” morphotype in ceratopsid dinosaurs is shown to be related to concentrated forces on the animal’s neck frill.

## Key Words

Bite performance, biomechanics, fenestration, stresses, ossification

## The story of the vertebrate land conquerors

The conquest of the terrestrial realm is considered to be one of the major “key innovations” in vertebrate evolution. Several physiological and anatomical adaptations were necessary for the animals outside the aquatic milieu (e.g. Laurin (2010); Clack (2012); Maier and Werneburg (2014); Schoch (2014a); Dial et al. (2015); Molnar et al. (2022a, 2022b)). These included, amongst others, the

development of specialised skins to avoid dehydration and the exclusive use of lungs to process atmospheric oxygen. Skeletal reorganisation evolved in response to gravity and limbs emerged, as documented by a well-resolved series of Devonian tetrapodomorph fossils (Clack 2012). Many early tetrapod groups (e.g. Temnospondyli) had a biphasic lifestyle with an early, larval stage in water and a later, adult stage on land – similar to their extant representatives, the lissamphibians (Gymnophiona, Caudata, Anura) (Schoch 2014a). Perhaps already some of the earliest reptiliomorphs (e.g. Diadectomorpha) (Berman 2013), as well

as the undisputed members of Amniota (Synapsida and Reptilia *sensu* Modesto and Anderson (2004)) completely skipped the aquatic phase of development and completed their early phase of ontogeny within the cleidoic (amniotic) egg. This prevents dehydration of the egg and embryo on land. The larval stage, as such, was transferred into a “test tube” environment, much more independent from the outside world with consequences also on skull development. This ontogenetic innovation permitted amniotes to conquer the most extreme regions on land, including deserts and mountains (Zhang et al. 2024).

Some of the most conspicuous structural remodelling at the water-to-land transition affected the skull. Ancestrally, it was a massive structure in aquatic fish-like vertebrates which both afforded protection for the brain and sensory organs against predation and hydrostatic pressure in the water column and during swimming (Liem et al. 2001). Sarcopterygian fishes adapted to near-shore environments (Werneburg et al. 2024a) with a tendency to flatten their skull, such as is evident in early tetrapodomorphs. Such a flattened skull enabled a faster sideways movement during hunting, because of less water resistance when compared to taller skulls (Hohn-Schulte et al. 2013; Preuschoft 2022). In addition to a lower water column, more terrestrial food was available. The feeding strategy has changed from the generalised fish-like suction feeding to a hunting behaviour (Bramble and Wake 1985; Schwenk 2000), in which the jaws were increasingly used as weapons (in the sense of Hülsmann and Wahlert (1972)) or as manipulating tools (see also Natchev et al. (2015)).

With the stepwise conquest of the terrestrial environment, shoulders separated from the skull (Preuschoft and Gudo 2005; Daeschler et al. 2006; Ahlberg 2018; Cloutier et al. 2020). Originally, shoulders and fins assisted in balancing the head during swimming and enabled updrift (Liem et al. 2001). In sarcopterygian fish, muscularised limbs pushed the heavy head forward in densely vegetated waters near the shore. When walking on land, force lines in the body were largely rearranged: shoulders and limbs now mainly had to handle the vertical weight force of the body stem (Preuschoft et al. 2022) and the connection to the skull became looser. A neck region evolved which enabled a more flexible head movement (Diogo et al. 2008; Diogo and Abdala 2010; Diogo and Abdala 2011; Clement 2019). The skull had to be lifted against gravity and the resulting strain had to be taken up by shoulders and limbs. As a consequence, the originally massive skull was lightened. This was enabled by reducing the number (Williston 1925; Gregory 1935) and thickness (Abel et al. 2022a, 2022b) of skull bones. In this context, the expansion and arrangement of skull bones experienced an enormous diversification in land vertebrates, particularly in the crown tetrapods: Lissamphibia (Schoch 2014b) and Amniota (Abel and Werneburg 2021, 2024). However, several skull reductions already and independently occurred amongst early tetrapod clades (Schoch 2014a; Abel and Werneburg 2021; see also the contribution of Kean et al. in this volume).

In this paper, I discuss potential factors that influenced the diversification of skull construction at the transition from early land vertebrates to well-established amniotes. I will, firstly, (A) discuss the ontogenetic preconditions for skull formation and, secondly, (B) the influence of external forces on skull construction. The latter will be separated into (B1) bite-related forces and (B2) forces resulting from body posture and, if present, from cranial armour. To explain the biomechanical principles, I selected four taxa:

- (1) The Early Triassic temnospondyl *Parotosuchus helgolandicus* (Schroeder 1913) has a rather ancestral tetrapodomorph skull anatomy (Lautenschlager et al. 2016; Witzmann and Werneburg 2017) (Fig. 1). It will be used to mainly discuss anterior perpendicular bite, i.e. the bite force that is vertically acting on the frontal teeth.
- (2) The Late Carboniferous, early reptiliomorph *Anthracosaurus russelli* (Huxley 1863; Panchen 1977; Clack 1987) has distinct temporal fenestration similar to the condition in the synapsid amniotes (Kemp 2005) and many parareptiles (Tsuji and Müller 2009) (Fig. 2). It will mainly serve as an example to illustrate the influence of strong anterior and low posterior perpendicular bite forces. Additionally, the influence of neck muscles will be discussed in this species, as they are considered relevant to stiffening the back of the skull.
- (3) The condition of a diapsid reptile with a strong posterior bite is exemplified by the Early Triassic archosauriform *Euparkeria capensis* (Broom 1913a; Broom 1913b; Sookias et al. 2020) (Fig. 3). Additionally, the influence of transversal bite forces will be briefly discussed in this species.
- (4) Finally, using the Late Cretaceous dinosaur *Protoceratops andrewsi* (Granger and Gregory 1923) (Fig. 4), I explore the implications of body posture and cranial armour (Section B2) on the skull construction of land vertebrates.

All species show very complex patterns of skull formation in evolution, which cannot be discussed in detail. In the chosen examples, only the biomechanical principles will be illustrated. These will be used as basis to reconstruct the evolution of temporal openings – an old topic in comparative anatomy (Abel and Werneburg 2021, 2024).

## A. Ontogenetic preconditions for skull formation

### A1. From larva to adult

The lungfishes (Dipnoi) are the closest living relatives of Tetrapodomorpha and a detailed observation of dipnoan development allows deep insights into the ancestral ontogeny of land vertebrates (Long 2011; Clack 2012;

Schoch 2014a). Adult lungfishes plesiomorphically have a head fully covered by dermal bones. The jaw adductor muscles close the mouth when feeding. They are inserted into the lower jaw, but arise from the lateral surface of the braincase and the interior surface of the temporal bones (Diogo and Abdala 2011). The “temple” is the area behind the eye (Werneburg 2019; Abel and Werneburg 2021; Werneburg and Abel 2022; Abel and Werneburg 2024).

The free-living and feeding larvae of lungfishes do not have a fully formed dermal skeleton yet and the temporal bones are loosely located on the head’s surface (Ziermann et al. 2018). To be able to feed, the larvae’s jaw musculature only originates from the braincase, which is already formed very early in development (de Beer 1937). Later in development, the dermal bones grow, become connected to each other and encompass the whole head externally. This can be interpreted as an adaptation to increased water pressure on the skull in the faster and deeper swimming adults (see above). With the formation of the full temporal skull cover, the jaw musculature expands laterally from the braincase to the internal surface of the temporal bones (Ziermann et al. 2018; Werneburg 2019). In that arrangement, which involves additional muscle fibres (i.e. a larger physiological cross-section), a greater bite force can be generated in the adult compared to the larva. This developmental process can be expected to have happened also in early tetrapods, including the temnospondyls, lepospondyls and most stem-amniote reptiliomorphs (e.g. Seymouriamorpha) with direct development from larva to adult.

Close to the origin of Lissamphibia, within dissorophoid temnospondyls, metamorphosis evolved, which includes remarkable reorganisations of the body (Schoch 2014a). The palate is largely reorganised at metamorphosis, whereas the skull roof undergoes changes related to other developmental processes (Schoch 2014b), as follows. The lissamphibian skulls are largely considered paedomorphic in relation to the original temnospondyl skulls. Several bones that appear late in the ontogeny of temnospondyls (postfrontal, postorbital, jugal, tabular) fail to form in the shortened ontogeny of lissamphibians (comparable to snakes in relation to lizards: Werneburg and Sánchez-Villagra (2015); cf. Fig. 5K). Bones that reach only a “half-way-development” compared to the ancestral dissorophoid (i.e. branchiosaurid) condition (parietal, prefrontal, squamosal, quadratojugal, parasphenoid, palatine, pterygoid), either remain small or fuse with each other (Schoch 1992). As a result, the skull of lissamphibians is extremely reduced in overall ossification and largely excavated in the cheek region (Schoch 2014b; Abel and Werneburg 2021). The large jaw adductor muscles fill the emarginated cheek region and can even expand – with more fibres (i.e. involving greater bite force) – on top of the skull roof bones (Schoch 2014b) because no temporal bones block them laterally.

I argue that the ancestral ontogenetic condition described for lungfish larvae above (Ziermann et al. 2018) is, by paedomorphosis, retained in modern Batrachia (caudates and anurans). The flattened skulls of batrachians result in

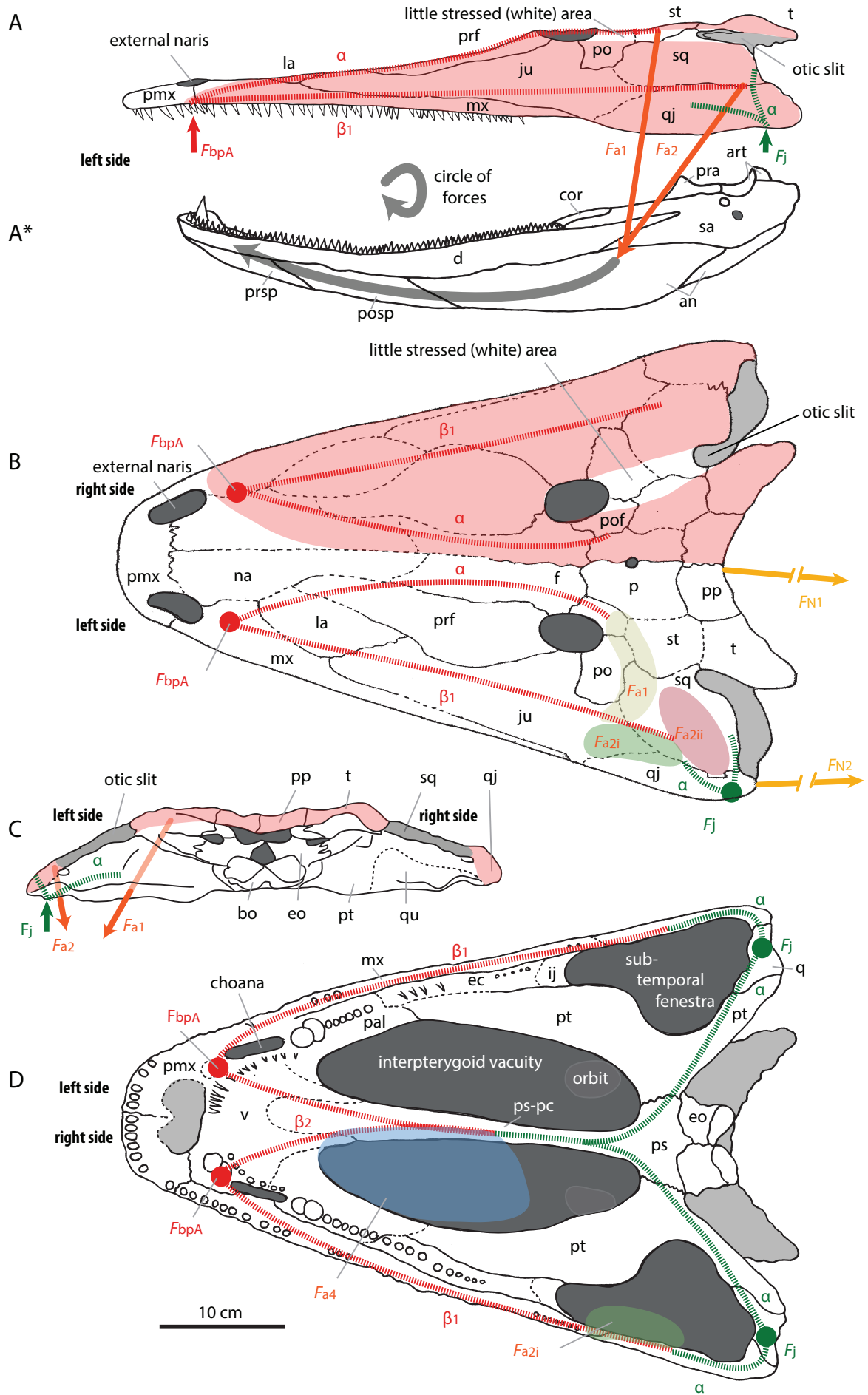
longer muscle fibres (Schoch 2014b), which allow a larger gape when compared to the shorter fibres in the fully encapsulated skull of ancestral tetrapods. The fossorial adaptation of caecilians resulted in the secondary stiffening of the skull (Schoch 2014a) and already the oldest known caecilian representatives had a typically stiffened skull (Evans and Sigogneau-Russell 2001). Developmental evidence suggests a similarity between early batrachian and caecilian skull development (Müller et al. 2005). Moreover, as in batrachians, their jaw musculature solely originates on the braincase in larvae (Edgeworth 1935; Kleinteich and Haas 2007; Kleinteich 2009) and adults (Lowie et al. 2023), representing the ancestral larval stage of the lungfish (Ziermann et al. 2018).

With the emergence of the cleidoic egg in amniotes, the free-living larval stage was skipped and the hatchling more closely resembles the adult. That means that the amniote embryo does not need to develop the functional muscle arrangement of a free-living larva that is otherwise seen in non-amniote vertebrates (Werneburg 2019). In particular, the jaw muscles do not attach to the braincase in the early development of amniotes (Edgeworth 1935). Similar to the temporal bones, the developing jaw musculature is not functional in the embryo yet and associates with the skull bones only late in development (Rieppel 1987). The late emerging association is related to the particular functional needs of the post-hatching animal (Werneburg 2019; also sensu Maier (1999)). This pre-adaptation must be understood as an evolutionary consequence of a genetically fixed ontogenetic penetration (Schlindwein et al. 2022).

There are two major routes of feeding behaviour with several modifications and combinations. These two feeding adaptations are typified in early amniotes. Synapsida concentrate on a bite anterior in the mouth with higher bite forces in this region; Diapsida (within Reptilia), in contrast, concentrate on a bite more posterior in the snout. Both conditions will be discussed below (Sections B1-3 and B1-4).

## A2. Sensory organs and skull bone arrangement

In early embryology, the brain and the sensory organs are amongst the first cranial structures to develop (Schoenwolf and Mathews 2007; Werneburg 2009). Cranial bones emerge only late in embryogenesis as small ossification centres (Rieppel 1994; Sánchez-Villagra et al. 2008; Werneburg et al. 2009; Weisbecker and Mitgutsch 2010; Mitgutsch et al. 2011; Spiekman and Werneburg 2017). Only later in development do the bones arrange into the typical skull architecture (Werneburg et al. 2015c; Werneburg 2019; Xing et al. 2022). Muscles become active and promote specific ossification modes and at hatching or birth, the feeding apparatus must be functional (Maier 1999; Schlindwein et al. 2022). In addition to the brain, skull bones developmentally arrange around the pre-existing sensory organs, including the nose, eyes and the





labyrinth organ (Sánchez-Villagra et al. 2008; Werneburg et al. 2009; Weisbecker and Mitgutsch 2010; Koyabu et al. 2014), which, therefore, provide a crucial spatial constraint to skull shape. When an animal bites, stress flows (i.e. resultants of the force) distribute in the head, which over evolutionary time, contributes to forming ossified areas around the brain and the sensory organs. This process can be traced in late-term embryos/foetuses, in which the specific jaw movements are already present (Werneburg and Maier 2019) and bones are arranged along the stress flows (Spiekman and Werneburg 2017; Werneburg 2019).

## B. The influence of external forces on skull construction

Recently, Werneburg and Preuschoft (2024) provided a basic biomechanical discussion on skull construction in land vertebrates. They showed that the point of attack, the amount of bite force in the mouth and the handling of the food items are important aspects to consider when interpreting temporal bone architecture. Feeding mode was discussed as an overwhelming driving factor in altering the shape of the temporal skull region in evolution and the phylogenetic value of this anatomical region must be regarded as informative only on selected taxonomic levels with similar trophic adaptations. Two principal considerations are important (e.g. sensu Preuschoft (2022)): 1. Only those areas of the head that are under biomechanical stress form bone, whereas unstressed areas result in openings in the skull. 2. Stresses are taken up by jaw musculature ( $F_a$ ), neck musculature ( $F_N$ ) and the scruff of the neck ( $F_s$ ) to guide the stresses back to the point of attack – i.e. in a “circle of forces” – via the lower jaw or via the postcranial skeleton and the soil that the animal and the food item (prey or plant) share.

In the present paper, I summarise the approach of Werneburg and Preuschoft (2024) and expand on their study. Here, I discuss the general skull construction of the four selected early tetrapods from the Paleozoic and Mesozoic eras in terms of their specific vacuities and ossified areas. These include their snout, palatal and occipital skull regions, as well as their lower jaw. This study aims to provide an overview of forces acting on the skull during feeding (Section B1) and enlighten the evolutionary “precondition” for the later success of taxa with the related cranial adaptations. However, I argue that not only bite-related forces,

but also further external forces (Section B2) – induced by neck posture and cranial weapons (e.g. horns) – need to be considered for a more comprehensive understanding of tetrapod skull construction. This paper can only touch upon the surface of the highly complex patterns of skull formation in land vertebrates. I developed stress flow diagrams as graphical reconstructions. This is an exclusive qualitative, not a quantitative approach. Such basic considerations, however, are largely under-represented in the literature and, in my opinion, need more attention. Providing experiments, such as finite element system syntheses (FESS) or -analyses (FESA) (Witzel and Preuschoft 2005; Rayfield 2007), was beyond the scope of this article, but they will be important in future work seeking to test and elaborate the arguments discussed herein.

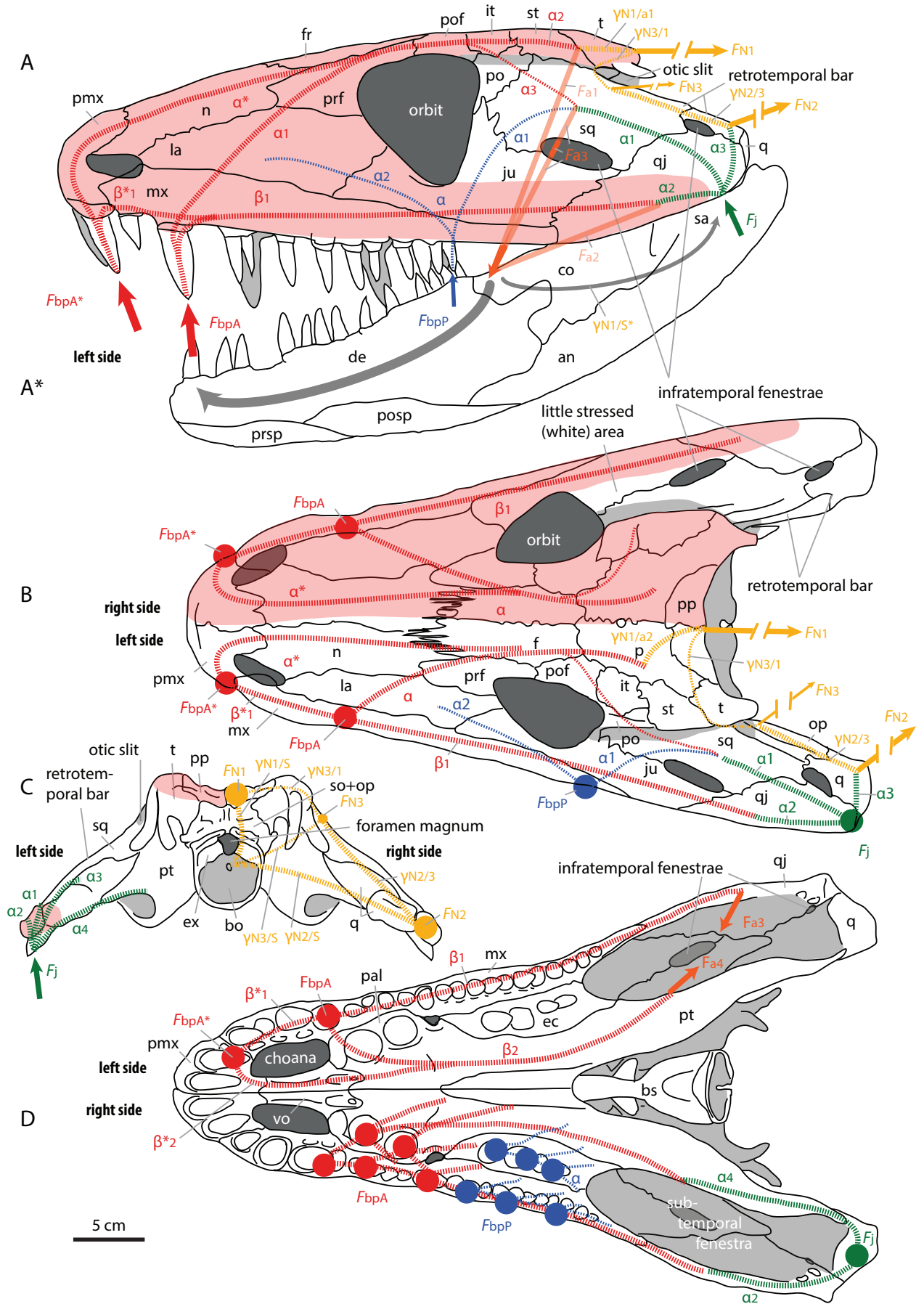
The major effects of each stress – compression or tension – is indicated as  $\alpha$  or  $\beta$ , respectively, although complex stress patterns are present in the actual skull as shown by finite element analyses, depending on the internal bone anatomy, architectural integration in the skull and stress flows from other forces. In particular, the stresses induced by the obliquely orientated neck muscles will result in a complex combination of tensional (backwards) and compressional (midwards) stress patterns. Those are indicated as  $\gamma$  in the figures. Stresses received also numbers, which are just descriptive to refer to them in the figures and texts and do not necessarily indicate ‘homologies’.

### B1. Bite related forces

#### B1-1. Otic notch

The early semi-aquatic tetrapods, including many temnospondyls and stem amniotes, were characterised by a rather flat skull with an otic notch at the posterior border of the temporal region (Figs 1, 2, 5A). It has been shown that this notch is spatially related to the ancestral vertebrate spiracle (i.e. 1<sup>st</sup> pharyngeal slit), which changed its functionality from breathing towards a hearing-related organ (Schoch 2014a; Fröbisch and Witzmann 2019; Gai et al. 2022). The exact position and extent of the spiracular openings in the dorsolateral parts of the skull vary amongst taxa (Figs 1, 2). Noteworthy, the spiracle does not have an elongated dorsoventral orientation in gnathostomes, which is different from the orientation of the adjacent gill openings. This can be partly explained by the original articulation of the hyomandibula and the

**Figure 1.** Skull (A, B–D) and lower jaw (A\*) of the temnospondyl *Proterosuchus helgolandicus* in left lateral (A, A\*), dorsal (B), posterior (C) and ventral (D) views; after Granger and Gregory (1923). Stress flows (i.e. resulting forces) are illustrated as dashed lines. Simplified scheme of anterior perpendicular bite ( $F_{bpA}$ ) with the resulting stress along the whole snout (red shaded area; Fig. 1A–C). This stress distribution, indicated by compressive (red  $\alpha$ ) and tensional (red  $\beta$ ) stress lines, passes the eye dorsally and ventrally. In the “shadow of the eye”, in the temporal region, less stress is present (not shaded). Here, the otic slit can form. The main stress lines are taken up by the jaw musculature ( $F_{a1-2i/i1}$ ). In addition to the anterior bite, compressive stress from the jaw joint ( $F_j$ ; green  $\alpha$ ) is indicated. The jaw muscles redirect the stresses to the lower jaw, where they distribute towards the point of attack. In this way, the circle of forces is closed (grey arrow in A). The stress lines from the anterior bite also travel along the palate (D) and are also taken up by jaw muscles ( $F_{a4+a2i}$ ). Neck muscles ( $F_{N1-2}$ ) are indicated, but do not have the same mechanical importance on the skull as in the reptiliomorphs (Figs 2–4) and, hence, no post-temporal bar is formed by them.



palatoquadrate leaving only the upper part of their intervening space (i.e. the spiracle) and no full gill slit open. In tetrapodomorphs, the hyomandibular of the hyoid apparatus and the upper jaw (palatoquadrate) became decoupled (Clack 2012; Schoch 2014a), which could have enabled a downward expansion of the external spiracle opening similar to the other pharyngeal slits in fish-like vertebrates – but it did not. Similar to the sensory organs described above, the skull bones are arranged around this developmentally pre-existing structure (i.e. pharyngeal opening). I argue that the specific architecture of bones around this opening depends on specific types of bite behaviour as outlined in the following.

A shift from the primarily fish-like suction to a primarily or exclusively prey-hunting feeding mode of tetrapods is obvious by the size reduction of the hyoid apparatus and by the large fangs in many temnospondyls (Fig. 1A\*) and other early tetrapod groups such as whatcheeriids, baphetids and colosteids. Fangs of the lower jaw may leave a recess or an opening in the upper jaw (light grey shade in Fig. 1D). When the animal bites anteriorly, the snout has to withstand the external bite force (red  $F_{bpA}$  in the figures) and ossified areas are formed. Stress distributes along the whole snout (reddish shade in Figs 1A, B, 2A, B). Dorsally in the snout, there is compressive stress (red  $\alpha$  in the Figures), whereas ventrally, tensional stress occurs (red  $\beta_1$ ). As mentioned above, the sensory organs are formed early in ontogeny. Hence, when biting, the stress flows have to travel around the eye as visible in *Parotosuchus* (Fig. 1A, B) and *Anthracosaurus* (Fig. 2A, B). As a consequence, the area behind the eye is under little stress (“in the shadow of the eye”) resulting in less potential to ossify (Figs 1A–C, 2A–C, 5A).

In *Anthracosaurus*, the cheek region is even spatially recessed from the skull table (Fig. 2A–C). This unstressed recess area corresponds to the skull hinge of early sarcopterygian fishes (Kemp 1980; Abel and Werneburg 2021; Abel et al. 2022a; Werneburg and Abel 2022); but see Panchen (1964)). To manipulate some food items, anterior bite was present in addition to suction feeding, but this was to a much smaller extent when compared to the more advanced tetrapods. Similar to early sarcopterygian fishes, the spiracle “finds its position” within the posterior part of the mechanically unstressed “hinge area”, i.e. inside the otic notch of early tetrapods. This notch is lost in all undisputed amniotes (Figs 3, 4, 5B/C).

Based on the considerations above, I suggest that, in *Protoceratops*, the anterior bite is primarily concentrated

on the animal’s beak ( $F_{bpA/A^*}$ ; Figs 4A, B, 5O). The associated compressive stress in the dorsal part of the skull (red  $\alpha_{1/2}$ ) will be very high and extended, resulting in a specialised occiput with a crest-bearing elongated parietal ossification. This is similar to the condition seen in other “beaked” amniotes, such as turtles and anomodont synapsids with their supraoccipital crests and/or their broad parietal- and squamosal expansions in the back of the skull (Kemp 1980; Werneburg 2011, 2012, 2013a; Kammerer et al. 2014). In birds, no crest develops because of the roundish and compact braincase of these animals, which distributed forces more evenly (similar to the tube-like nose in mammals: see Preuschoft and Witzel (2002)).

## B1-2. Circle of forces

Stresses increase along the skull (Werneburg and Preuschoft 2024) and, to avoid breakage, they are guided to close the “circle of forces”. In an animal exhibiting a perpendicular bite (shown on the left skull side in the Figures) without moving the head, the jaw adductor muscles ( $F_a$ ) assist in guiding the stresses ( $\alpha$ ,  $\beta$ ) from the temporal region back to the lower jaw and from there back to the point of attack (grey arrows in Figs 1A, A\*, 4B\*; only indicated in Fig. 3A\*). Related to the differentiation of the temporal and palatal region, the jaw musculature is separated into different portions and muscle heads (dark orange  $F_{a1-5}$  in Figs 1, 3, 4) (Holliday and Witmer 2007; Diogo and Abdala 2010; Daza et al. 2011; Werneburg 2011, 2013a; Ferreira and Werneburg 2019; Ziermann et al. 2019).

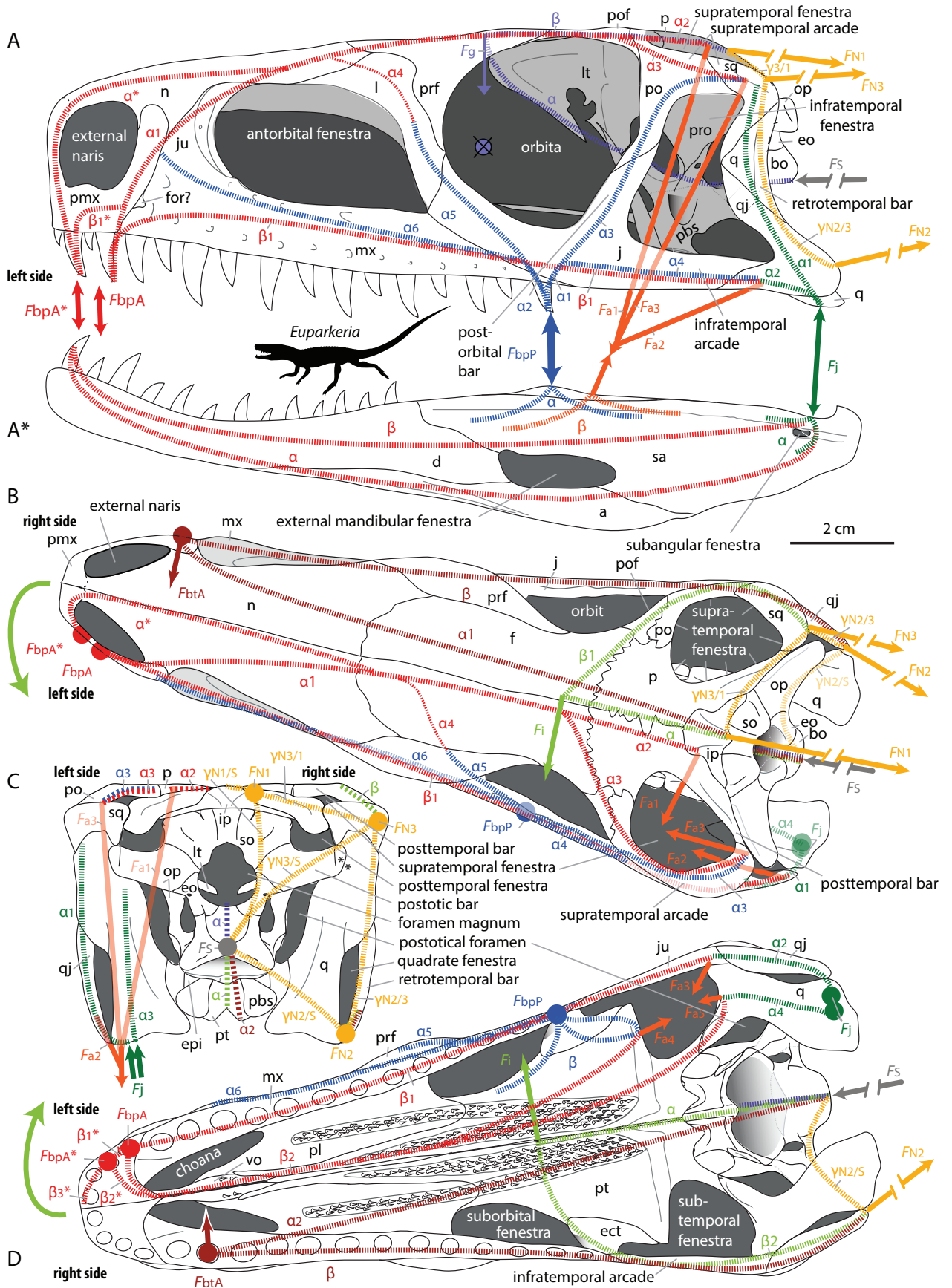
By correspondence with traces of muscle attachments on the bones, Witzmann and Werneburg (2017) reconstructed the jaw muscles of *Parotosuchus* (here simplified as  $F_{a1}$ ,  $F_{a2i}$ ,  $F_{a2ii}$ ). They aligned with the stress flows from the anterior bite (Fig. 1). In *Euparkeria* and *Protoceratops*, the jaw muscle heads originated on the temporal bars ( $F_{a2-3}$ ) and the skull roof ( $F_{a1}$ ; Figs 3A–C, 4A, B, D). Additionally, *Anthracosaurus* might have shown a similar complex differentiation of the jaw adductor musculature related to its differentiated temporal region (hinge and temporal opening; Fig. 2A).

## B1-3. Infratemporal opening

At the jaw joint, i.e. between articular (art) and quadrate (q), compressive stress develops (green  $\alpha$ ), because of the force generated here ( $F_j$ ) when biting. In early tetrapods, such as in *Parotosuchus* (Fig. 1), the force intensity at the

**Figure 2.** Skull (A–D) and lower jaw (A\*) of the early reptiliomorph *Anthracosaurus russelli* (Huxley 1863) in left lateral (A, A\*), dorsal (B), posterior (C) and ventral (D) views; after Panchen (1977) and Clack (1987). In addition to the processes shown in Fig. 1, strong anterior ( $F_{bpA}$ ) and most anterior ( $F_{bpA^*}$ ) perpendicular bites (red) as well as weak posterior perpendicular ( $F_{bpb}$ , blue) bites are illustrated. The latter influences, together with the compressive stresses (green  $\alpha_{1-3}$ ) from the jaw joint ( $F_j$ ), the shaping of the temporal region. The strong lateral neck muscle  $F_{N2}$  induces stress ( $\gamma_{N2/3}$ ) in the retrotemporal part of the temporal region. The stress induced by  $F_{N3}$  ( $\gamma_{N3/2}$ ) was not large enough to strongly shape the posttemporal region in the “shadow of the eye”, and a minute otic slit persisted. In the ventral view (D), the meaning of several teeth in the palate is indicated: Many bite points result in a mesh of stresses that result in the closure of palatal openings. A differentiation of three jaw adductor muscle portions ( $F_{a1-3}$ ) in the temple are hypothesised to correlate to the edges of the temporal opening and the upper temporal “hinge”-area (A, A\*).







jaw joint may have been low, because of the joint's long distance to the major, pterygoid-related jaw muscle ( $F_{a4}$ ) (Olson 1961). Stress from  $F_j$  (dark green  $\alpha_{1-2}$ ) contributed to an enforcement of the cheek region. Here it was taken up by the jaw musculature ( $F_{a2i/ii}$ ; Fig. 1B, D). The stress also travelled along the posterior border of the cheek, which is usually formed by quadratojugal (qj) and squamosal (sq) (dark green  $\alpha_1$ ; Fig. 1A).

Force at the jaw joint ( $F_j$ ) is larger, when the jaw muscles are placed more posteriorly in the adductor chamber, because of the shorter lever arm to the joint (Olson 1961). A proportionally larger muscle mass posterior in the adductor chamber is associated with taller skulls to provide more area for muscle attachment. This is generally the case in Reptiliomorpha, including *Anthracosaurus* (Fig. 2) and amniotes (Figs 3, 4, 5C).

Please note that the here chosen species *Anthracosaurus russelli* is very special amongst Anthracosauridae (Embolomeri) in having a temporal fenestration similar to the amniote Synapsida and several parareptiles. It had a relatively high skull when compared to other early tetrapods and very large teeth on the jaws and on the palate (Fig. 1A, D), which distinguishes this animal as a specialised hunter with high bite forces (see also Porro et al. (2024)). This example also illustrates the large degree of convergences in the formation of temporal fenestrations amongst land vertebrates and strengthens the assessment that this character is not very informative in phylogenetic reconstructions (Abel and Werneburg 2021).

A retrotemporal bar is formed in fenestrated taxa. It is mainly established by the lateral neck musculature ( $F_{N2}$ ), which is – because of higher neck mobility – much more strongly developed in reptiliomorphs (Fig. 5B) compared to early tetrapods (Starck 1979–1982; Kardong 2008). It inserts into the posterolateral angle of the skull. Amongst early reptiliomorphs, *A. russelli* might be interpreted as a transitional taxon in regard to a stronger neck development. A movement of the head, enabled by contraction of  $F_{N2}$ , induced a resulting stress flow (yellow  $\gamma_{2/3}$ ) along the posterior border of the cheek region (Werneburg and Preuschoft 2024). The spatial relation of the insertion of  $F_{N2}$  to the jaw joint (Fig. 2) or even a transversal jaw movement may have resulted in different stress flows as in *A. russelli*, which, hence, developed two infratemporal openings (Fig. 2A, B, D). This, however, is a highly unusual case.

Recently, Werneburg and Bronzati (in press) have argued that, in crown diapsids, a great bite force would be correlated with the crescent- or crosier-shaped retrotemporal bar, which is unique to this clade and exemplified by *Euparkeria* herein

(Fig. 3). The dorsal part of the retrotemporal bar (upper section of squamosal) aligned with the (blue and red) stress flows in their supratemporal arcade (see Section B1–4), whereas the ventral part (lower part of quadratojugal) aligned with the tensional stress flow of the infratemporal arcade. The re-orientation of the retrotemporal bar was related to a separation of the columella, which ancestrally served as a mechanical brace of the skull flank, but became integrated into the hearing system. Embryonically, the re-orientation of the retrotemporal bar results in a tissue separation from the quadrate anlage to contribute to the extracolumella cartilage, which enhances the sound transmission in the middle ear of crown diapsids (Werneburg and Bronzati, in press).

In ceratopsid dinosaurs (Fig. 4), the presence of a specialised, laterally exposed and posteriorly decoupled cheek region, which can be interpreted as a kind of armour (see Section B2), likely resulted in a re-orientation of the tensional stress from the anterior bite ( $F_{bpA}$ ) away from the retrotemporal “edge” of the skull. In that configuration, the cheek-associated jaw musculature ( $F_{a2}$ ) was separated from the remaining jaw muscle portions ( $F_{a1+3}$ ) and inserted laterally into the dentary. The muscle ( $F_{a2}$ ) might have allowed transversal, chewing-like movements and might have served as a soft cheek to prevent food from falling off the mouth during feeding (Varriale 2016). As such, it is equivalent to the musculus (m.) masseter in mammals (Schumacher 1985) and the m. zygomaticomandibularis in trionychian turtles (Werneburg 2011, 2013a; Rollot et al. 2024). A reorganisation of the lower temporal part of the skull frequently results in the separation of a lateral muscle also known for parrots (Tokita 2004) and lizards (Rieppel 1980; Werneburg 2013b).

My interpretation is close to older interpretations regarding the insertion of the chewing muscle ( $F_{a2}$ ) to the lower jaw in ceratopsids (Haas 1955; Ostrom 1964, 1966; Holliday 2009). How far anterior or posterior the muscle originated at the skull flank can only be specified using muscle-associated riffling on the bones' surfaces (sensu Holliday (2009); Witzmann and Werneburg (2017)). Given the deep and long insertion groove in the dorsal face of the dentary (Ostrom 1964: fig. 5; see also Hatcher et al. (1907)), an origin at the upper jaw, also anterior to the tooth row, is quite plausible (Fig. 4A, B:  $F_{a2*}$ ). My reconstruction of the cheek muscle differs from that of Nabavizadeh (2020a, b, 2023) and Nabavizadeh and Weishampel (2023), who did not discuss particular stress distributions in the skulls. However, the other muscle reconstructions provided by these authors can be confirmed by the considerations of the present paper (i.e.  $F_{a1+3}$ ).

**Figure 3.** Skull (A–D) and lower jaw (A\*) of the early archosauriform diapsid *Euparkeria capensis* (Broom 1913a) in left lateral (A, A\*), dorsal (B), posterior (C) and ventral (D) views; after Sookias et al. (2020). In addition to the processes shown in Figs 1, 2, the influence of a very strong posterior perpendicular bite ( $F_{bPP}$ ) on the formation of the supratemporal, antorbital and mandibular fenestrae is indicated. With the establishment of an upper temporal bar, a clear separation of a new muscle portion is present ( $F_{a2}$ ) [but it might have been present in *Anthracosaurus russelli* already, Fig. 2]. In B–D, transversal anterior bite forces ( $F_{btA}$ ) as well as lateral movement of the head (large light green arrow) with the related inertia force ( $F_i$ ) are illustrated. Half of the resulting stress flows take diagonal courses (light green  $\beta_{1/2}$  + brown  $\alpha_{1/2}$ ), which contribute to the shaping of the skull, such as the orientation of the supratemporal bar. \*\* in C indicates the pleurokinetic articulation.



A high anterior bite force can also be found in crocodyles. The related stress flows can be related to a very strong ossification in the skull roof and on the skull side. As a result, the genetically fixed upper and temporal fenestrations are suppressed in a way that the postorbital bar is retracted to a more medial position in the head and that the upper temporal openings are almost or completely closed. In such a way, a “pseudosynapsid” (or pseudoinfracenestral) morphotype emerges “on top” of the diplapsid morphotype (Fig. 5L; Werneburg and Fernandez Blanco, in prep.).

#### B1-4. Supratemporal opening

As mentioned before, a greater bite force (blue  $F_{\text{bpP}}$ ) can be generated posteriorly in the snout because of the shorter lever arm to the jaw joint (Preuschoft and Witzel 2002). Whereas synapsid amniotes originally favoured anterior bites with large fangs to pierce the skin of their large prey (Kemp 1982), diapsid amniotes (Fig. 3) originally developed posterior bites to crack the chitinous exoskeletons of their arthropod prey (Gregory and Adams 1915; Evans 2008; Werneburg and Preuschoft 2024).

A posterior bite along the snout (blue  $F_{\text{bpP}}$ ) results in compressive stress below the eye (blue  $\alpha$ ). One part of this stress travels posterior to the eye (blue  $\alpha_1$ ), along the postorbital bar, which is built of jugal and postorbital (Fig. 2A). Here, this stress flow comes in contact with the compressive stress from the anterior perpendicular bite (red  $\alpha_1$ ) and both influence and redirect each other (Werneburg and Preuschoft 2024). The anterior stress flow (red  $\alpha_1$ ) separates into two sections above the eye (red  $\alpha_{2+3}$ ) and the lower part (red  $\alpha_2$ ) aligns with the re-orientated dorsal aspect of the postorbital part (blue  $\alpha_1$ ) of the posterior bite-related compression flow. In *Anthracosaurus*, it contributed to the stiffening of the upper cheek region (postorbital, squamosal) and the otic slit fell in between the separated stress flows of the anterior compressive stress (red  $\alpha_{2+3}$ ; Fig. 2A, B).

With increased neck mobility along the amniote stem, the otic slit was closed (Fig. 5B). This is because, between the original neck muscles ( $F_{\text{N1}}$  and  $F_{\text{N2}}$ ), a new muscle portion has been established related to the now taller skull ( $F_{\text{N3}}$ ; Figs 2–4). The contraction of this muscle portion results in a stress flow along the posterior part of the dorsal temporal region (yellow  $\gamma_{\text{N3/1}}$ ; Fig. 2A–C). When the posterior bite ( $F_{\text{bpP}}$ ) is large enough, as visible in *Euparkeria* (Fig. 3B), the separation of the dorsal anterior stress flow (red  $\alpha_1$ ) becomes very distinct. The area in between these two sub-flows (red  $\alpha_2 + \alpha_3$ ) and the  $F_{\text{N3}}$ -induced enforcement

of the skull (yellow  $\gamma_{\text{N3/1}}$ ) may then result in the formation of an upper temporal fenestra, posteriorly bordered by the post-temporal bar (Fig. 3A, B). This is a typical construction in almost all members of the Diapsida clade (Benton 2005). I refer to this group as ‘Suprafenestralia’ – not to replace the well-established name of the clade but: 1. to hint at its unique, non-diapsid (i.e. non-bifenestral sensu Abel and Werneburg (2021)) morphotype and 2. to also draw attention to the disputed interrelationship of the weakly-preserved earliest members of this group. Related to this, I introduce the terms “Fossafenestralia” (cf. sensu Maisch (2020)) and “Diplapsida” (cf. sensu Werneburg (2019)) to distinguish between the two major morphotypes in the advanced eureptiles (see Fig. 5).

In addition to the supratemporal fenestra, the early ceratopsian dinosaur *Protoceratops* had a parietal fenestra (Fig. 4A, B). Its medial border, the parietal, was much elongated to the frill. The bone still served, around its median crest, as the origin site of the medialmost jaw muscle portion ( $F_{\text{a1}}$ ; Figs 4A, 5O). The elongation of the parietal evolved in response to the medially concentrated anterior-most bite force ( $F_{\text{bpA}^*}$ ) at the peak of the rhamphotheca (r) and its related dorsal compressive stress (red  $\alpha_1/\alpha_2$ ) in the skull (Fig. 4A, B). The presence of the parietal fenestra (Fig. 5O) in addition to the supratemporal one is related to another external force, which will be discussed in Section B2–3.

As in other diapsid reptiles, the posterior extension of the dorsolateral muscle portion ( $F_{\text{a3}}$ ), which takes up the stress from the posterior (blue  $\alpha_3$ ) and anterior bite (red  $\alpha_3$ ) in the upper temporal arcade, does not go much beyond the articulation of the squamosal with the quadrate in *Protoceratops* (cf. Nabavizadeh (2023)). The more posterior extension of the supratemporal fenestra is associated with the external forces ( $F_{\text{F}}$ ,  $F_{\text{tLH}^*}$ ) discussed in Section B2. Holliday et al. (2020) comprehensively discussed the filling of the extended supratemporal fossa with typical soft tissue like fat or blood vessels (e.g. for changing colouration or temperature in the animal’s display).

#### B1-5. Orbita and naris

The naris and the orbit were already discussed as being related to the early presence of nose and eye organs in the embryo (Section A2). The dermal bones develop later and arrange around these organs (Rieppel 1993a, b). The orbit is originally surrounded by bones that are associated with the stress flows of anterior ( $F_{\text{bpA}}$ : red  $\alpha$ ,  $\beta_1$  in Fig. 1) and posterior bites ( $F_{\text{bpP}}$ : blue  $\alpha_{1/2}$  in Fig. 2, blue  $\alpha_{3/5}$  in Fig. 3).

The nasal is surrounded by stress flows from anterior bites in the snout. Posteriorly, it is bordered by the

**Figure 4.** Skull (A–D, F) and lower jaw (B\*) of the early ceratopsid dinosaur *Protoceratops andrewsi* (Granger and Gregory 1923) in slightly rotated dorsal (A, C), in left lateral (B, B\*, D) and in posterior (F) views; after Weishampel et al. (2004). E. Whole skeleton of the species in left lateral view (after Scott Hartmann, Wikimedia Commons, license: CC BY 4.0). G, H. Schematic view on the posterior edge of the skull (G) with external forces acting on several osteoderms or (H) just on one osteoderm on each side with one concentrated external force each. Only in the latter, parietal fenestrae can form. Note that stress from the neck muscles can be taken up by the jaw musculature, which is then guided to the lower jaw and the scruff of the neck ( $F_{\text{S}}$ ). This is illustrated in D for  $F_{\text{N2}}$  only with its stress flow  $\gamma_{\text{N2/S}^*}$  (see also Fig. 2A:  $\gamma_{\text{N1/S}^*}$ ). Sutures in the basicranium in F are only tentatively drawn.



compressive stress (red  $\alpha$  / red  $\alpha_1$  in the Figures) that was discussed above concerning the anterior perpendicular bite ( $F_{bpA}$ ). This bite, however, only relates to the largest, the canine-like tooth. More anteriorly, at the incisor-like teeth, a further anterior bite force ( $F_{bpA^*}$ ) can develop. It introduces similar stress patterns as the canine-related bite ( $F_{bpA}$ ) with a dorsal compression (red  $\alpha^*/\alpha_1^*$ ) and a ventral tensional (red  $\beta^*/\beta_1^*$ ) stress flow, which relate to bone structures anterior, dorsal and ventral to the naris – i.e. the premaxilla (Higashiyama et al. 2021) (Figs 2A, B, 3A, B, D, 4A, B).

In birds, the orbits and visual cortex of the brain are largely expanded, which results in a roundish braincase and a compressed temporal region of an infra fossal morphotype (Abel and Werneburg 2021). Additionally, the unique jaw mechanisms induced comprehensive changes of this area (Fig. 5M) (Bock 1964).

### B1-6. Transversal bite

Pure perpendicular bite is rarely performed amongst tetrapods. Often the head is passively moved by fleeing prey or is actively moved to tear off food items. This results in transversal bite forces ( $F_{bt}$ ), which distribute differently in the skull when compared to the perpendicular bite ( $F_{bp}$ ). This typical condition is illustrated herein only for the anterior bite pointing to the mid-line of the skull (brown  $F_{btA}$  in Fig. 3B, D; i.e. on the right skull side). Further scenarios with other bite modalities were reconstructed by Werneburg and Preuschoft (2024) in detail.

The anterior transversal bite ( $F_{btA}$ ) results in two stress flows. Tensional stress (brown  $\beta_1$  in Fig. 3B, D) travels along the skull sides, along maxillary, jugal as well as quadrato-jugal and quadrate in *Euparkeria* – similar to the tensional stress of the perpendicular anterior bite (red  $\beta$ ). The tensional stress from transversal biting (brown  $\beta$ ) is then taken up by the lateral neck musculature (orange  $F_{N2}$ ). Dorsally in the skull, compressive stress (brown  $\alpha$ ) develops from the point of attack and travels along the nasal, frontal, parietal and interparietal in *Euparkeria* (Fig. 3B). This stress flow is taken up by the medialmost neck musculature (yellow  $F_{N1}$ ).

The medial and lateral neck muscles guided the stress along the neck, to the shoulder and the forelimbs, to finally close the “circle of forces” via the soil that *Euparkeria* and its prey shared (illustrated for the lateral direction of anterior and posterior transversal bite forces in fig. 4k of Werneburg and Bronzati, in press).

In situations where the head is passively swept to the side – a situation engendered by struggling prey (illustrated by the green bent arrow in front of the head in Fig. 3B, D) – inertia force ( $F_i$ ) is applied at the centre of mass of the skull. This transversal force ( $F_i$ ) also resulted in two stress flows (light green  $\alpha$  and  $\beta$  in Fig. 3). The compressive stress (light green  $\alpha$ ) was also taken up by the medialmost neck musculature ( $F_{N1}$ ). The tensional stress (light green  $\beta$ ) was taken up by a lateral neck muscle (e.g.  $F_{N2}$ ). Together with transversal bite forces in the back of the mouth ( $F_{btP}$ ; not illustrated here, but see Werneburg and Preuschoft (2024)), the inertia force ( $F_i$ ) contributed to shaping the orientation of the upper and lower temporal arcade.

When the head was actively pulled to the side, i.e. when tearing off food items, the resulting stresses from the inertia force ( $F_i$ ) took different courses, further altering the orientation and architecture of the temporal region (see Werneburg and Preuschoft (2024) for further scenarios).

In the remaining parts of Section B1, I will elaborate upon the above explanations on the influence of the feeding mode on skull formation. Anterior and posterior perpendicular and transversal bites, as well as inertia force, help explain much of the architecture of the snout, the palate and the occipital region, all of which were not discussed by Werneburg and Preuschoft (2024) before.

### B1-7. The antorbital fenestra

Most reptiles of the diapsid clade Archosauriformes (including birds, but excluding crocodiles) possess an antorbital fenestra anterior to the orbit (Sookias et al. 2020) and there has been a variety of hypotheses on how to explain the presence of this opening (Witmer 1997; Werneburg et al. 2019). Certainly, several factors are likely to have acted simultaneously, resulting in the origin and remodelling of this fenestra. Amongst them, feeding-related forces are most important to consider.

The early archosauriform *Euparkeria* established the first adaptations to very powerful biting “on its way” towards the hypercarnivorous dinosaurs. In a recent contribution, Sookias et al. (2020) studied all cranial material of *Euparkeria* to reconstruct its skull anatomy in great detail. In their article, the authors inferred, using Anatomical Network Analysis (AnNA) (Esteve-Altava et al. 2011; Rasskin-Gutman and Esteve-Altava 2014), on the modularity of the skull bones and provided functional interpretations. Compared to the skull integration of other land vertebrates, including a theropod dinosaur and a crocodile (Werneburg et al. 2019), *Euparkeria* was shown to have possessed a flexible skull “well adapted to feeding on swift preys, but with a clear tendency towards more carnivorous behaviour, placing the taxon at the interface between ancestral diapsid and crown archosaur ecomorphology, corresponding to increases in brain size, visual sensitivity, upright locomotion and metabolism around this point in archosauriform evolution” (Sookias et al. 2020: p. 2).

As I have shown above (Section B1-4, the compressive stress (dark blue  $\alpha$ ) of the posterior perpendicular bite force ( $F_{bpP}$ ) was distributed posterior to the orbit (dark blue  $\alpha_1$  in Fig. 2). With the formation of a distinct infratemporal arcade, as in *Euparkeria*, it was separated into two stress flows (dark blue  $\alpha_{3+4}$ ) to align with the major stress flows from the anterior bite (red  $\alpha_3$  and red  $\beta$  in Fig. 3).

Anterior to the eye, in the snout, the stress flow of the posterior bite (blue  $\alpha_2$  of Fig. 2A) took a steep course along the anterior border of the eye when an animal like *Euparkeria* bit hard (Fig. 3A). This process was further triggered by a strong anterior bite ( $F_{bpA}$ ), with the related compression (red  $\alpha_1$ ) and tension (red  $\beta_1$ ) stresses. They split and redirected the posterior perpendicular bite-related stress in front of the snout (blue  $\alpha_2$ ) into a dorsal (blue  $\alpha_5$ ) and a ventral (blue  $\alpha_6$ ) section, leaving the unstressed antorbital fenestra of the



snout in between (Figs 3A, 5G). A similar splitting process was discussed in connection with the formation of the supra-temporal fenestra above (Section B1-4).

The steep dorsal stress flow (blue  $\alpha_3$ ) was associated with the ossification in front of the orbit, i.e. the antero-dorsal wing of the jugal and the lacrimal in *Euparkeria* (Fig. 3A). Around the lacrimal, it deflected a part of the compressive stress from the anterior bite (red  $\alpha_4$ ). The ventral part of the posterior bite-related stress flow (blue  $\alpha_6$ ) aligned with the tensional stress from the anterior bite (red  $\beta_1$ ) along the maxillary.

The anterior and dorsal borders of the antorbital fenestra, formed by a dorsal wing of the maxilla and the nasal in *Euparkeria*, were associated with the compression flow of the anterior bite stress only (red  $\alpha_1$  in Fig. 3A).

The antorbital fenestra of the archosaur *Protoceratops* (Fig. 4) was narrower than in *Euparkeria* (Fig. 3) because of the influence of the beak, the height of the skull and fight-related forces (Section B2).

In general, the shape and size of the bars and fenestrae amongst taxa depend on the strengths and specific distributions of all the stresses discussed in this paper (Figs 1–5). Factors related to the general proportions, like brain and eye size or to other aspects of functional morphology, like chewing or suckling in mammals (Fig. 5J; Maier 1999; Herring et al. 2001), are worth considering. Specifying this further, however, goes beyond the scope of the present article.

## B1-8. Palate

The palate of the early tetrapods was plesiomorphically formed by elongated bones, inherited from fish-like ancestors. In most species, the bite forces were not strong enough to induce a full closure of the palate region yet. The interpterygoid vacuities (Fig. 1D; Witzmann and Werneburg 2017; Witzmann and Ruta 2018) were filled with membranes, which were spanned in between the bony bars surrounding these vacuities. The membranes were considered to be related to suction breathing in the past (Schoch 2014a). However, in a recent study on extant batrachians, it has been shown that their function is more likely to be related to the transport of food (Witzmann et al. 2019). In any case, a functional constraint might have hindered the closure of the palate. Moreover, the flattening of the skull resulted in the expansion of different skull areas, which also partly explains the wide palatal vacuities in the temnospondyls (Fig. 1).

The palate of early reptiliomorphs and amniotes shows remarkable diversity (Lakjer 1927). Some taxa have vacuities (Fig. 3D), partly inherited from their early tetrapod ancestors. Others have more or less closed palates (Fig. 2D). According to Lautenschlager et al. (2016), I argue that the position and shape of the palatal bones also largely relate to the stress flows when feeding (D-panels in Figs 1–3).

Within the palate, the lateral stress flow of the anterior bite ( $F_{bpA}$ , red  $\beta_1$  in Fig. 1) travelled along the maxillary, jugal and squamosal/quadratojugal in *Parotosuchus*. It

was passed to the lower jaw via the jaw adductor musculature (Fig. 1D;  $F_{azi/ii}$ ; see also Fig. 1B).

The medial stress (red  $\beta_2$ ) flow travelled medial to the choana in *Parotosuchus* (Fig. 1D). This skull opening was inherited from the fish-like precursors of tetrapods and corresponded to the internal (mouth) opening of the nasal organ. As with all sensory organs, it developed early in embryology and posed a spatial constraint for the skull architecture. The medial stress flow (red  $\beta_2$ ) was then distributed along the vomer (v) and the cultriform process of the parasphenoid (ps-pc) in *Parotosuchus* (Fig. 1D). Here the stress was taken up by the anterior jaw musculature ( $F_{a4}$ ). The compressive stress (dark green  $\alpha_4$ ) that developed from the jaw joint ( $F_j$ ) might have also travelled along the posterior part of the palate and been taken up by the same jaw musculature. The posterior jaw adductors ( $F_{a_{1,2+ii}}$ ) extended to the lower jaw through the subtemporal fenestra. In between both openings, the subtemporal fenestra and the interpterygoid vacuity, the pterygoid braced to the braincase. It could also transmit stresses from posterior perpendicular biting as illustrated for the right skull sides of *Anthracosaurus* (Fig. 2D) and *Euparkeria* (Fig. 3D; blue  $F_{bpP}$ ).

The tensional stress from the more anterior bite at the tip of the snout ( $F_{bpA^*}$ ) distributed laterally along the premaxillary (red  $\beta^*_1$ ) and medially along the vomer (red  $\beta^*_2$ ), surrounding the choana anteriorly as shown in *Anthracosaurus* (Fig. 3D).

The posterior bite force ( $F_{bpP}$ , dark blue  $\beta$ ) was not only distributed laterally along the skull flank (Figs 2A, B, 3A, B, 4A, B), but also medially to the palate, where it corresponded with particular ossifications such as the ectopterygoid (ec) (Figs 2D, 3D, left skull sides). Part of the posterior stress flow was taken up by the jaw adductor musculature ( $F_{a4}$ ; i.e. “pterygoideus muscle”; Fig. 3D).

Many early tetrapods showed extensive palatal dentition (Benton 2005; Clack 2012; Schoch and Milner 2014). The small denticles on the pterygoid and palatine bones served in the fixation and processing of food (Sues 2000), suggesting different points and magnitudes of the anterior and posterior bites ( $F_{bpA} + F_{bpP}$ ) and their related stresses resulting in different shapes of the palate. This becomes obvious in *Anthracosaurus* with its almost fully closed palate (Fig. 2D).

Additionally, the temporal arches can be shaped by palatal bite. The early synapsid *Edaphosaurus*, for example, was a herbivore with extended palatal dentition. The skull has a fossafenestral morphotype (different from the infrafenestral morphotype in its close relative *Dimetrodon*; Abel and Werneburg (2021, 2024); Werneburg and Preuschoft (2024)) and the suborbital fenestra is fully closed (Sues and Reisz 1998; Sues 2000), suggesting an extremely high posterior bite force on the palate.

As in the case of the temporal region (Werneburg and Preuschoft 2024), transversal stresses play a role in shaping the palate. A bite force directed to the mid-line of the skull ( $F_{btA}$ ) led to tensional stress along the maxillary, jugal and quadratojugal, as shown in *Euparkeria* (brown  $\beta$  in Fig. 3D, right skull side) and was taken up by the lateral neck muscle ( $F_{N2}$ ). Compressive stress was distributed more medially (brown  $\alpha_2$  in Fig. 3D) along the palatine, the pterygoid and

the basicranium to reach the occipital condyle ( $F_s$ ). In the described direction of the stress flow, mass inertia pointed to the direction of the opposite skull side ( $F_i$ ). The medial stress flow from the  $F_i$  (light green  $\alpha$  in Fig. 3D) reached the occipital condyle medially ( $F_s$ ) and the lateral stress flow (light green  $\beta_2$ ) travelled towards the lateral neck muscle ( $F_{N2}$ ), passing the pterygoid, ectopterygoid, jugal and quadratojugal. Taking it all together, the suborbital fenestra in *Euparkeria* was surrounded and internally built by different stress lines, which aligned along maxillary, palatine, pterygoid and ectopterygoid (Fig. 3D).

The chewing behaviour in *Protoceratops* (Varriale 2016) did not result in a closure of the palate. In mammals, chewing also does not influence the formation of the secondary palate – milk-sucking behaviour, in contrast, is most important for that (Maier 1999).

### B1-9. Fenestrae of the lower jaw

As in most Archosauriformes (Fig. 5G, L–N), a mandibular fenestra can be found in *Euparkeria capensis* (Fig. 3A\*). A mandibular fenestra is usually associated with a rather elongated lower jaw, which is exposed to high bending loads and strong symphyses (see Lessner et al. (2019)). Similar to the snout discussed above, the anterior bite resulted in compressive (red  $\alpha$ ) and tensile (red  $\beta$ ) stresses in *Euparkeria*, which flowed along the ventral and dorsal borders of the lower jaw. In between those stress flows, an unstressed area existed. As a result, a mandibular foramen could form along the sutures between dentary, surangular and angular.

More posteriorly, in *Euparkeria*, a subangular fenestra is present (Fig. 3A\*). As with the more posterior infratemporal opening in *Anthracosaurus russelli* (Fig. 2A, B), specific jaw movement abilities might have been responsible for the formation of this area without biomechanical stress. Modelling different amounts and directions of forces on the jaw joint will help understanding altering morphotypes.

The mandibular fenestra was secondarily closed in the archosaur *Protoceratops* (Fig. 5O), likely as a result of the influence of the jaw musculature ( $F_{a2}$ ) inserting into the dorsal and lateral face of the mandible (Fig. 4B\*).

### B1-10. Small openings in the skull

Whereas I discussed the major fenestrae of most tetrapods above, other cranial openings require brief comments. These include several foramina with little stresses, which permit the passage of nerves and vessels (e.g. Demes (1985)), particularly in the neurocranium, but also in other parts of the skull.

In *Euparkeria*, the median pineal foramen (Smith et al. 2018), below which the parietal organ usually receives information on light intensity in land vertebrates, was absent. It is, however, plesiomorphically present in reptiles (Evans 2008). Menaker et al. (1997) correlated the absence of the foramen with a potential nocturnality in *Euparkeria*. The foramen, however, is clearly visible in the extant mostly nocturnal tuatara (Jones et al. 2011; Cree 2014).

Feeding-related stresses in the skull would rather support the fusion of median openings in the skull; however, the physiological importance of the pineal organ requires the pineal foramen to stay open from the early beginning with bone formation in late embryonic development (Rieppel 1992; Zhang et al. 2022), similar to the other sensory organs discussed.

The tuatara also has a frontonasal fontanelle (Jones et al. 2011). It appears to be related to its unique functional feeding morphology. Werneburg et al. (2019) found a complex separation of anterior (incl. nasal and prefrontal) and posterior (incl. frontal) functional snout modules in tuatara, which might support a rather loose connection of the skull roof in this area (sensu Werneburg and Abel (2022)), perhaps also related to some degree of mesokinetic mobility (at least in the juveniles, see Rieppel (1992); Jones et al. (2011); Yaryhin and Werneburg (2019); Zhang et al. (2022)).

In turtles, the parietal foramen is closed, presumably due to the strong neck retraction-related forces exerted on the skull roof (Werneburg et al. 2021).

## B2. Further external forces acting on the skull

### B2-1. Cranial weapons

During the terrestrialisation process, not only feeding, but also inter- and intraspecific combat behaviour changed. In several land vertebrates, cranial weapons evolved for defence. At foremost, these include horns and exposed osteoderms, but also expansions of cranial regions, such as the frill of ceratopsian dinosaurs or the wide cheek expansions of the diplocaulid neotridians. In the latter, in particular, multiple functions of such structures are plausible including the use for swimming (e.g. Cruickshank and Skews (1980); Skews (2016)). Amongst temnospondyls, small horns are known for zatracheids (e.g. *Acanthostomatops*, *Zatrachys*; Schoch (1997); Witzmann and Schoch (2006)) and the dissorophoid *Stegops* (R. Werneburg et al. 2023). Amongst amniotes, taxa with cranial armour can be found amongst reptiles and mammals (e.g. Bovidae) with horns, antlers, osteoderms or just keratinised spines (Bubenik and Bubenik 1990; Hall 2015; Gates et al. 2016; Nabavizadeh 2023).

There are several studies on the evolution and function of the cranial armour of ceratopsians, comprehensively reviewed by Nabavizadeh (2023) and I already discussed some adaptations of the jaw musculature related to it (Section B1-3). Fig. 4 shows my interpretations of the biomechanics of the ceratopsian skull exemplified by *Protoceratops*. The initial cranial armour in ceratopsian evolution consisted of a vaulted beak, a nasal protuberance and a cheek extension as visible in *Psittacosaurus*, for example, followed by the frill, a medial nasal horn, large paired horns above the eye and, finally, large osteoderms at the edge of the frill (Nabavizadeh 2020b, 2023). *Protoceratops* already showed a well-developed frill and close relatives would evolve a nasal horn. Above the eyes,

small protuberances “foreshadowed” the lateral horns of more advanced species such as *Triceratops horridus* (Hatcher et al. 1907). True cranial horns were not present in *Protoceratops*, although its protuberances likely already had a similar functional meaning. As such, I modelled the horns as dashed lines in Fig. 4C, D ( $F_{NH}$ ,  $F_{PLH}$ ,  $F_{LH/ULH}$ ) to better illustrate my principle thoughts as outlined below.

## B2-2. Nasal horn

The unpaired nasal protuberance of *Protoceratops* received an external force ( $F_{NH}$ ), which resulted in a comprehensive distribution of compressive stresses. One of them (light green  $\alpha_1$ ) travelled along the anteroventral margin of the braincase [visible through the infratemporal fenestra in Fig. 4D] and was received by the scruff of the neck ( $F_S$ ). A second one (light green  $\alpha_2$ ) travelled along the skull roof and was received by the medial neck muscle ( $F_{N1}$ ; i.e. m. spinalis capitis, SC, sensu Tsuihiji (2010)); Fig. 4C, D). This pattern was similar to the stresses induced by the skull weight ( $F_g$ ) as reconstructed by Werneburg and Preuschoft (2024: fig. 2) and as illustrated for *Euparkeria* herein (Fig. 3A: purple  $\alpha+\beta$ ). A third stress (light green  $\alpha_3$ ) flow developed around the anterior curvature of the eye and found its way along the nasal, lacrimal, jugal and medial to the exposed cheek, along the pterygoid towards the occipital condyle ( $F_S$ ) (Fig. 4C, D, F).

Stress distributions within the skulls of rhinoceroses might be similar to that of *Protoceratops* with broad insertions of the nape muscles ( $F_{N1}$ ) on the skull. The pre-orbital stress flow (light green  $\alpha_3$ ) of rhinoceroses certainly distributed along the strong infratemporal bar to reach the occiput.

## B2-3. Parietal fenestra

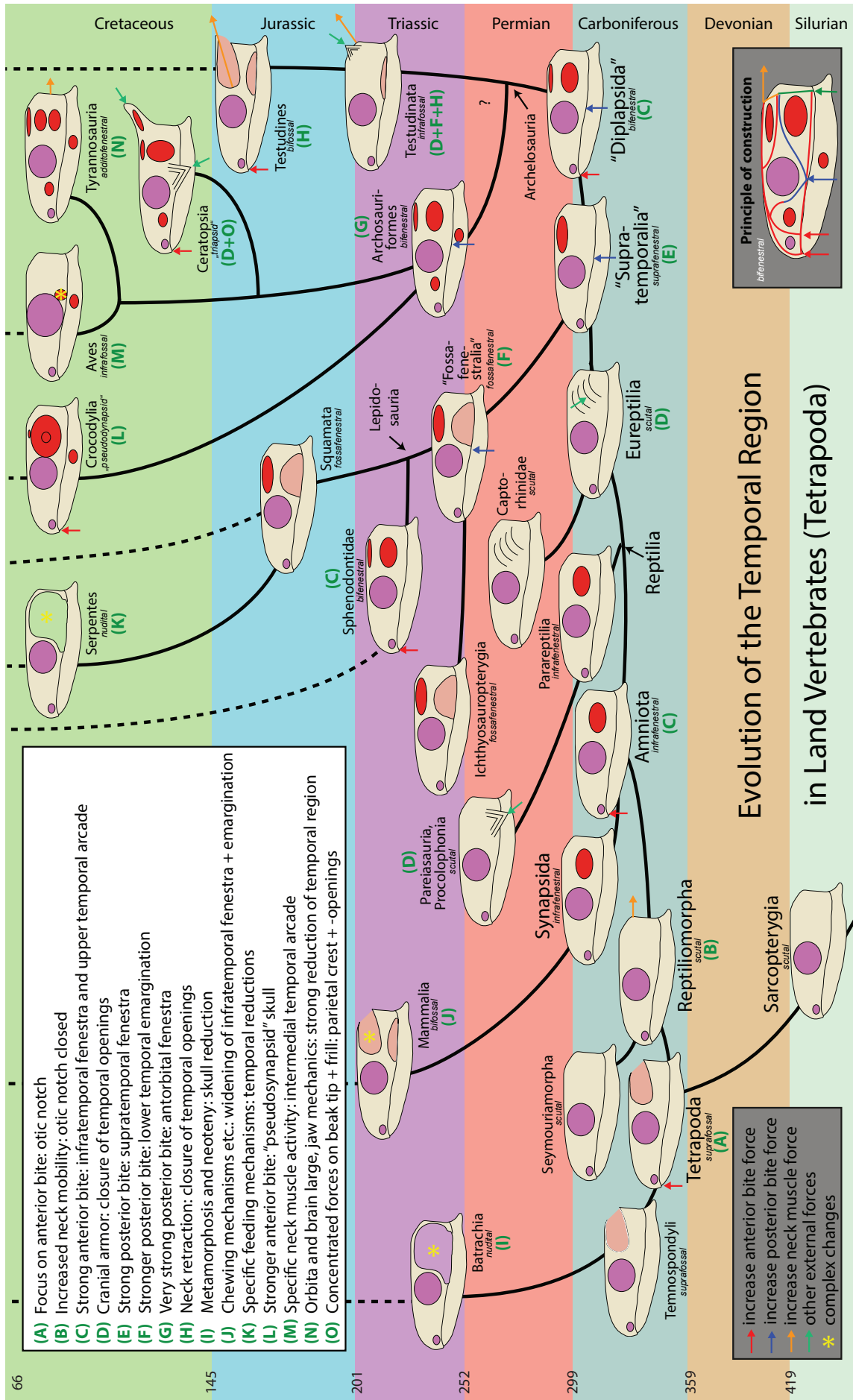
In case a force ( $FF$ ) acted on the posterolateral edge of the frill in *Protoceratops* (Fig. 4C, D, F, H), the resulting stresses travelled (as black  $\alpha_1$ ) toward the medial-most neck muscle ( $F_{N1}$ ) and (as black  $\alpha_2$ ) towards the neck muscle posterior to the posterodorsal corner of the infratemporal fenestra ( $F_{N3}$ ; i.e. m. longissimus capitis Pars articulo-parietalis, LCap, sensu Tsuihiji (2010)). In between them, the posterior half of the supratemporal fenestra was situated as an unstressed area. Posteriorly, the supratemporal fenestra corresponded to the external force related to combat ( $FF$ ). The anterior part of the fenestra, however, was related to the stress flows of anterior and posterior perpendicular bite (Section B1-4; dark blue  $\alpha_3$  and red  $\alpha_{2+3}$  in Fig. 4A, B). As discussed for *Anthracosaurus* and *Euparkeria* above (Section B1-3), the action of the lateral most muscle ( $F_{N3}$ ) resulted in the formation of the post-temporal bar (yellow  $\gamma_{N3/1}$ ), which mainly distributes along the posterior border of the broad parietal in *Protoceratops*. The parietal itself had its own fenestra, which spanned between the neck muscle-related stress flow (yellow  $\gamma_{N3/1}$ ) of the post-temporal bar and the stress flow from combat-/fight-related forces ( $F_P$ ,  $F_{LH}$  – see Section B2-5, for the latter).

Noteworthy, the parietal fenestra was formed within one single bone, whereas all other openings of the skull are formed at least in between two bones.

The frill in Ceratopsida experienced a great diversification, with some taxa having parietal openings and some not (Nabavizadeh 2023). I hypothesise that this was largely related to the appearance of the frill as a weapon. A weaponry with many spines, such as in *Triceratops horribilis* (Hatcher et al. 1907), evenly distributed several external forces at the frill and the many resulting stress flows hindered the formation of a parietal foramen (Fig. 4G). This is mechanically similar to the use of many palatal teeth in taxa with closed palatines (Fig. 2D). Single salient osteoderms (i.e. “epiossifications” after Loewen et al. (2024)) or frill edges as in *Protoceratops* (Fig. 4C, D, F), concentrated the stress of a single external force ( $FF$ ) and resulted in clear-cut borders of a frill foramen (Fig. 4H).

In this context, I wish to mention the origin of turtles. Recently, a series of cranial “horn cores” (cf. Fig. 4G) have been discovered in the Late Triassic *Proganochelys* (Scheyer et al. 2022), one of the earliest representatives of the anapsid (labelled as ‘infra fossal’ in Fig. 5) Testudinata (Joyce 2007). This does not come as a surprise given the spiny osteoderms of this species on the dorsal side of the neck and it fits into the general picture of early turtle defensive behaviour, which includes the formation of a fully formed shell (Gaffney 1990; Werneburg et al. 2015a). Cranial armour is known from other stem turtles (e.g. *Meiolania*; Gaffney (1983)) and was likely used in intraspecific combats (Jannel 2015).

Turtles are currently considered to have derived from diapsid ancestors, based on molecular and morphological data (Rieppel 2008; Wang et al. 2013; Simões et al. 2022; Werneburg et al. 2024b) and, hence, must have closed their temporal openings in one way or another. In previous works, I developed an evolutionary scenario whereby the influence of neck retraction resulted in the reorganisation and secondary closure of the temporal region in turtle ancestors (Werneburg 2015; Werneburg et al. 2015a; Werneburg et al. 2015b; Böhmer and Werneburg 2017; Cordero and Werneburg 2018; Ferreira and Werneburg 2019; Werneburg 2019; Werneburg and Maier 2019; Ferreira et al. 2020; Werneburg 2020; Abel and Werneburg 2021; Werneburg et al. 2021; Werneburg and Abel 2022; Werneburg and Preuschoft 2023; Werneburg et al. 2024b). Given the discovery of osteoderms in *Proganochelys* (Scheyer et al. 2022), I would expand these thoughts (Fig. 5: “D+F+H”). When external forces were taken up by the osteoderms, broad compressive stresses were added to the posterior edge of the skull. To withstand, the temporal opening(s) might have closed. As such, the stresses from the horns were more evenly distributed into the skull (cf. Fig. 4G). A hypothesis of early turtles showing a fossorial lifestyle and stiffening the temporal opening by digging (similar to caecilians), can be excluded because a slender rather than a roundish, shell-related trunk would be required for such behaviour (discussed by Werneburg et al. (2024b)).





## B2-4. Cheek weapons

External force ( $F_e$ ) on the lateral cheek extensions (cheek wings) of *Protoceratops* was guided, firstly (light blue  $\alpha_1$ ), at the skull's surface along quadratojugal, jugal, postorbital and frontal/parietal towards the central nape muscle ( $F_{N1}$ ; Fig. 4D, F). A second major stress flow (light blue  $\alpha_2$ ) extended medially along the jugal/quadratojugal and the pterygoid and was taken up by the scruff of the neck at the occipital condyle ( $F_S$ ; Fig. 4D, F). The orientation of the cheek weapon, which could have been equipped with a distinct horn, resulted in changed directions of the stress flows and, hence, different patterns of skull ossifications (Fig. 5D). This is well visible in the skull of the therapsid *Estemmenosuchus* as well as in most parareptilian Procolophonida (incl. Pareiasauromorpha and Procolophonida). In the latter, distinct horns developed on the cheekbones (Fig. 5) and a “deformation” of the whole temporal region is visible (e.g. MacDougall and Reisz (2014)). Likely this led to the closure of the infratemporal fenestration that is otherwise visible in other parareptiles and other early amniotes, such as *Mesosaurus*, *Eumotosaurus*, Millerosauria and Bolosauridae, as well as many procolophonids without cheek armour. The influence of the cheek armour may even help explain the peculiar extension of the orbit above the cheek-wing and into the temporal region of many procolophonids.

In this regard, the evolutionary origin of temporal fenestration in amniotes might be briefly discussed (see also Abel and Werneburg (2021, 2024); Werneburg (2024)). Except for very few species (e.g. *Anthracosaurus russelli*, Fig. 2), most non-amniotic Reptiliomorpha had an anapsid skull condition, which is often considered ancestral for early Reptilia (Fig. 5B). In contrast, all undisputed synapsids have an infratemporal opening (Fig. 5). Reconstructions of early amniote phylogeny often result in contradicting scenarios for the origin of temporal openings (Ford and Benson 2020; Simões et al. 2022). In this regard, I wish to mention the contested monophyly and ingroup relationships of the early reptilian parareptiles, many of which have fenestrated temporal regions (Cisneros et al. 2004; Modesto et al. 2009; Piñeiro et al. 2012; MacDougall and Reisz 2014); see also this debate: (Laurin and Piñeiro 2017; Laurin and Piñeiro 2018; MacDougall et al. 2018).

Throughout all of their life, most early amniotes faced a completely different, i.e. harder food supply outside the aquatic milieu when compared to non-amniotic tetrapods. It is well imaginable that the earliest amniotes primarily made use of their ancestral focus on anterior bite (see Figs 1, 2),

which resulted – in association with the formation of the neck muscle-related retrotemporal bar (yellow  $\alpha_{N3}$ ; Section B1-3) – in the formation of an infratemporal opening (Fig. 5C). External forces acting on the head – resulting from combat or fossorial behaviour – might have resulted in the closure of the infratemporal opening in Eureptilia (Fig. 5D), as also discussed for Procolophonida above. In this regard, the heavily sculptured skull ossification of the eureptilian captorhinids (Fig. 5); (Abel et al. 2022b) and *Brouffia* (Fox and Bowman 1966; Abel et al. 2022a; Klembara et al. 2024) is worth mentioning. With more gracile skulls – related to a less exposed lifestyle (maybe in an arboreal habitat) – early diapsids might have re-evolved the infratemporal fenestration (Fig. 5) – in addition to their posterior bite-related supratemporal opening (cf. Fig. 5E) to feed on (tree-dwelling) arthropods (see Section B1-4; Fig. 5).

## B2-5. Lateral horns

*Protoceratops* already had distinct “brow” protuberances above the eye (Fig. 4A). As mentioned in the Introduction, I use the *Protoceratops* model to discuss a condition as if it would have had well-exposed lateral horns above the eye (dotted horn in Fig. 4C, D) that otherwise many ceratopsids had. When an external force ( $F_{PLH}$ ) directly acted on such a horn (Fig. 4D), the compressive stress flows (pink  $\alpha_{1+2}$ ) were transmitted toward the medial neck muscle ( $F_{N1}$ ) and the scruff of the neck ( $F_S$ ).

In case the horn was pulled to the side (e.g. inside the belly of a tyrannosaur), transversal forces acted on the skull. The principle is similar as explained with different scenarios by Werneburg and Preuschoft (2024) for transversal bite force and briefly discussed for *Euparkeria* above (Section B1-6). Here, in Fig. 4C, I illustrate only two cases in which the external force on the lateral horn is directed away from the skull ( $F_{LLH/LH*}$ ; cf. Werneburg and Preuschoft (2024): fig. 8b, d, f). If the force was large ( $F_{LLH}$ ), then one tensional stress flow (pink  $\beta_1$ ) travelled along the parietal and was taken up by the medial neck muscle ( $F_{N1}$ ). A second major stress flow (pink  $\beta_2$ ) travelled to the other side of the skull, along the parietals, the postorbital and the squamosal to the lateralmost neck muscle ( $F_{N2}$ ). If the transversal force on the lateral horn was small ( $F_{LLH*}$ ), then the angle between the major stress flows was smaller. The first stress flow (pink  $\beta_1^*$ ) was taken up by the medial neck muscle ( $F_{N1}$ ) again, whereas the second one (pink  $\beta_2^*$ ) took a different course, along the parietals, towards the muscle in between  $F_{N1}$  and  $F_{N2}$ ,

**Figure 5.** Hypothesis on land vertebrate interrelationships and skull evolution, based on biomechanical considerations, with a focus on the temporal region. Morphotypes (mainly sensu Abel and Werneburg (2021)) are indicated below the taxon names. Apomorphic and convergent traits are listed in the figure. Specific discussion of these traits can be found in the text of (A) Section B1-1, (B) Section B1-3, (C) Sections B1-3 and B2-4, (D) Sections B2-3 and -4, (E) Section B1-4, (F) Werneburg and Preuschoft (2024) and Section B1-3, (G) Section B1-7, (H) Sections B2-7 and B2-3, (I) Section A1, (J) Werneburg and Preuschoft (2024) and Preuschoft et al. (in press), (K) Section A1, (L) Section B1-3, (M) Section B1-5, (N) Section B2-7, (O) Section B2-3. See also Werneburg (2024). The idiosyncratic names for advanced eureptile groups are based on the hypothesised evolution of the temporal region and do not necessarily represent phylogenetic relationships (sensu Werneburg (2019)). However, please note the uncertainties of the interrelationship of early eureptilian taxa in the literature. By spatial restriction, the Late Cretaceous Ceratopsia had to be placed to the lower part of green field.

namely  $F_{N3}$  (Fig. 4C), which then transferred the stress into the body (see Section B1-6). The strength, the preferred transversal direction (e.g. medial or lateral) of the external force, as well as the size and the orientation of the lateral horns contributed to an altering shape of the lateral border of the parietal. In that way, also the shapes of the supra-temporal, as well as the parietal fenestrae, were defined.

## B2-6. Body posture

For all forces not related to perpendicular bites ( $F_{bpA/A*P}$ ), namely the transversal bites ( $F_{blA/A*P}$ ) and the cranial armour-related forces ( $F_P, F_C, F_{plH}, F_{llH}$ ), the resulting stresses ( $\alpha/\beta$ ) were taken up by the vertebral column (scruff of the neck,  $F_S$ ), as well as by the neck muscles ( $F_{N1-3}$ ). The postcranial skeleton assisted in closing the circle of forces (Section B1-6).

In those cases where a medial force ( $F_{NH}$ ) acted on the beak or the medial horn (Fig. 4C, D), the resulting stresses (light green  $\alpha_{1-3}$ ) were transferred to the vertebral column and further along the skeleton to the hind limbs (Fig. 4E, green arrow), which supported the body against the ground and guided back the forces – via the soil (Fig. 4E, grey arrow) – towards the origin of the initial force ( $F_{NH}$ ) that acted on the skull.

In those cases where external forces acted transversally to the skull ( $F_{blA/A*P}, F_P, F_C, F_{plH}, F_{llH}$ ), transversal stress flows reached the postcranium. First, they were taken up by the transversal processes/ribs of the neck vertebrae (Preuschoft et al. 2022). Then the stresses continued in the transversal direction towards the shoulder and to the sprawled forelimbs in reptiles and early synapsids or to the splayed-out forelimbs in horned and antlered mammals. After that, the stresses reached the ground to eventually close the circle of forces (Preuschoft and Gudo 2005; Werneburg and Bronzati, in press).

In summary, the postcranial bones were structured and arranged not only in relation to locomotion, but also in response to the forces acting on the skull. This is particularly clear in ceratopsids, which have more or less upright hind limbs to support a pushed-back body and the forelimbs could be sprawled in the lateral direction to prevent the body from falling over to the side when fighting (Preuschoft and Gudo 2006: fig. 9). Animals with less transversal forces on the head, namely without cranial armour and a rather perpendicular bite, tend to have less transversal processes/ribs and less sprawled forelimbs (Preuschoft et al. 2022; Preuschoft et al., in press). This is the case for mammals with their modified teeth, which reduced transversal bite behaviour (Preuschoft et al., in press). Additionally, shoulder anatomy depends on head posture and movements as outlined in all the cited works of Holger Preuschoft.

Three major neck muscles ( $F_{N1-3}$ ) have been discussed in this paper (Fig. 4E). Of course, in reality, there are more to take up specific stresses from the skull (see right side of Fig. 4F). The second major function of the dorsal neck muscles is to lift the skull above the ground. Partly stiff

tendons and ligaments can develop to save energy (e.g. in horses). The weight of the head, therefore, plays a crucial role also for the reshaping of the dorsal vertebrae with some taxa having very high and bent neural processes in their vertebrae and shoulder humps may develop (e.g. bison).

## B2-7. Occipital region

Posterior views of the skulls are shown in the C-panels of Figs 1–3 and in Fig. 4F. Pulling neck muscles also directly influence the shape of the occipital region and the adjacent skull parts. Werneburg and Preuschoft (2024: fig. 13b, c) have shown that some of the stresses are taken up by parts of the jaw musculature, which transmit them towards the lower jaw. These stresses are then transferred to the jaw joint ( $F_j$ ) and from there to the occipital condyle ( $F_s$ ) to close the circle of forces (Fig. 2A:  $\gamma_{N1/S*}$ ; 4D:  $\gamma_{N2/S*}$ ).

As explained above, the compressive stress induced by  $F_{N3}$  is associated with the formation of the posttemporal arcade ( $\gamma_{N3/1}$ ), which not only borders the supratemporal fenestra posteriorly, but also the posttemporal fenestra at its dorsal side (Fig. 3C). The ventral border of the post-temporal fenestra, in contrast, is formed by the ancestral pleurokinetic joint (\*\* in Fig. 3C) between palatoquadrate (i.e. via its quadrate part) and neurocranium (Natchev et al. 2016; Werneburg and Maier 2019).

The stress flow resulting from  $F_{N2}$  and with that the posteroventral margin of the skull in most species, pointed towards the middle of the skull ( $\gamma_{N2/S}$ ) and connected the quadrate and the pterygoid with the braincase in *Euparkeria* (Fig. 3C), leaving an unstressed area below the pleurokinetic joint, the foramen postoticum. With the structural reorganisations related to the frill, the stresses of the neck muscles were reorientated in *Protoceratops* (Fig. 4F).

A quadrate fenestra was formed between quadrate medially and quadratojugal laterally in *Euparkeria* and was associated with the compressive stress flows (dark green  $\alpha$ ) from the force acting in the jaw joint ( $F_j$ ; Fig. 3C). If such a quadrate fenestra has formed, a complex jaw movement can be expected (indicated by two dark green arrows in Fig. 3C).

The stress flows from the bite points and the cranial weapons reached the occiput dorsomedially, ventrolaterally and dorsolaterally and were transmitted by the respective neck muscle ( $F_{N1}, F_{N2}$  and  $F_{N3}$ ). It is apparent in the palatal and occipital views of the skull (Figs 2C, 3C, D, 4F) that several stress flows culminated in the occipital condyle. They were already mentioned in the previous Sections and should be kept in mind when interpreting occiput architecture. In this context, it is worth noting that reptiles only have one condyle, whereas therapsid synapsids and advanced temnospondyls have two. This condition can be explained by the high transverse forces in carnivorous taxa associated with different transversal stress directions that reach the occiput at different places. Towards Mammalia, i.e. amongst synapsids, the condyles shift more dorsally to assume a more lateral place in relation to the foramen magnum. This prohibits or at least makes difficult the lateral

rotation of the head and so facilitates the formation of an atlas-axis system (pers. comm. Holger Preuschoft in 2023).

Although mainly receiving stresses from external forces on the skull, neck muscles (as well as the jaw muscle) will also induce some stresses into the skull, beyond the occipital region. Great pulling of the dorsal neck muscles ( $F_{N1/2}$ ) has been discussed for the neck retraction mode of turtles, which influences the shaping of the temporal region and might even have contributed to the closure of the temporal openings in turtle ancestors (see Section B2-3) (Werneburg 2015). The movement and the posture of the neck contribute to the strengthening of the temporal arches, behind which the major neck muscles insert.

In this regard, the additofenestral condition of tyrannosaurids may be mentioned (Fig. 5N) (Plateau and Foth 2020). They have a temporal bar within the infratemporal fenestra which develops from the occipital regions. I discussed the unique functional morphology of *Tyrannosaurus* feeding elsewhere (Werneburg et al. 2019), and here I suggest that specific neck movements during feeding resulted in a stress flow that is taken up – via this unique temporal bar – to a separate muscle portion in these dinosaurs.

This final Section on the occipital region illustrates, again, that skull architecture needs to be analysed in a holistic manner, whereby distinct biomechanical conditions need to be considered in the context of the animal's behaviour as well as its life history mode. The four species exemplarily discussed herein may serve as a starting point for future more sophisticated technical assessments of skull biomechanics, such as the use of finite element analyses.

## Conclusions

The present contribution is a novel approach to understanding the enormous cranial diversity of land vertebrates. It takes both comparative anatomy as well as biomechanical considerations into account to provide a comprehensive picture of skull formation in time and space. Moreover, developmental and behavioural aspects of extant and extinct animals are incorporated to draw a comprehensive picture of skull evolution.

The evolution of cranial openings in tetrapods is, firstly, largely related to ontogenetic strategies with differences in directly developing and metamorphosing animals on one hand and larval and non-larval life histories on the other hand. Secondly, modulations of anterior and posterior bite points, the bite intensity, as well as the presence of cranial armour, such as horns and cheek wings (e.g. pareiasaurs, procolophonids, turtles, ceratopsids, bovids) or just bone thickenings (e.g. early eureptiles) correspond to the presence or closure of cranial openings. A scenario for the evolution of temporal skull openings is provided (Fig. 5).

It is shown that a strong bite anterior in the snout, as well as breathing behaviour, originally influenced the formation of the otic slit and the interpterygoid foramen in the earliest tetrapods. With increased terrestriation in the

amniote stem group, neck muscles became very important for skull formation and their tension resulted in the formation of a straight border at the posterior edge of the skull. An infratemporal fenestra appears to be ancestral to amniotes (Fig. 5C) – at least from a biomechanical point of view.

A preference for biting posteriorly in the jaw resulted in the formation of an upper temporal fenestra (and a ventral temporal excavation). Increased posterior bite force triggered the formation of an antorbital and a mandibular fenestra in Archosauriformes (Fig. 5G). The lower temporal bar of diapsid reptiles corresponds with a strengthened anterior bite.

Jaw muscles mainly relate to perpendicular bites. Neck muscles, in contrast, take up the stresses from transversal bite as well as from all other external forces acting on the skull. This leads to comprehensive responses in the postcranial skeleton to close the circle of forces. However, skeletal responses to neck muscle tension also appear in the occiput and other regions of the skull. This is most obvious in turtle evolution with neck retraction largely altering the skull anatomy.

The present paper may serve as a framework for future quantitative biomechanics that take a holistic view of the skull, in which ontogenetic, evolutionary, as well as comprehensive morphological aspects of skull architecture, will be considered.

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## Appendix 1

### Abbreviations:

**an**, angular; **bo**, basioccipital; **bs**, basisphenoid; **co**, coronoid; **de**, dentary; **ec**, ectopterygoid; **eo**, exoccipital; **ECM**, m. episternocleidomastoideus; **f**, frontal; **F**, force; **F<sub>a1</sub>**, force of the medial most jaw adductor muscle portion; **F<sub>a2</sub>**, force of the lateral most jaw adductor muscle portion; **F<sub>a2</sub>\***, possible anterior insertion of the “chewing” muscle in *Protoceratops*; **F<sub>a3</sub>**, force of the jaw adductor muscle portion in between **F<sub>a1</sub>** and **F<sub>a2</sub>**; **F<sub>bpA</sub>**, anterior perpendicular bite force (at the “caninus”-position); **F<sub>bpA\*</sub>**, most anterior perpendicular bite force (at the “incisivus”-position); **F<sub>bpp</sub>**, posterior perpendicular bite force (at the “caninus”-position); **F<sub>bTA</sub>**, anterior transversal bite force in the back of the mouth; **F<sub>C</sub>**, force acting laterally on the cheek extension; **F<sub>i</sub>**, inertia force; **F<sub>f</sub>**, force acting laterally on the frill; **F<sub>N1</sub>**, force of the medial most dorsal neck muscle; **F<sub>N2</sub>**, force of the neck muscle that inserts lateral most to the skull; **F<sub>N3</sub>**, force of the neck muscle placed between **F<sub>N1</sub>** and **F<sub>N2</sub>**; **F<sub>NH</sub>**, force acting on the nasal horn; **F<sub>pLH</sub>**, force acting perpendicularly on the lateral horn; **F<sub>pLH</sub>**, large pulling force acting transversally away from the lateral horn; **F<sub>pLH\*</sub>**, small pulling force acting transversally away from the lateral horn; **F<sub>s</sub>**, force at the scruff of the neck (neck vertebra vs. occipital condyle); **ij**, insula jugalis; **ip**, interparietal; **it**, intertabular; **ju**, jugal; **la**, lacrimal; **LCap**,

m. longissimus capitis Pars articulo-parietalis; **It**, latero-sphenoid; **mx**, maxilla; **n**, nasal; **oc**, occipital; **OCM**, m. obliquus capitis magnus; **op**, opisthotic; **p**, parietal; **pbs**, parabasisphenoid; **pc**, parietal crest; **pd**, prefrontal; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **pmx**, premaxilla; **po**, paroccipital; **posp**, postsplenial; **pp**, postparietal; **prsp**, presplenial; **ps**, parasphenoid; **ps-pc**, cultriform process of parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, rhamphoteca; **RCA**, m. rectus capitis anterior; **sa**, surangular; **SC**, m. spinalis captitis; **so**, supraoccipital; **sq**, squamosal; **t**, tabular; **v**, vomer, **α**, compressive stress; **β**, tensional stress.

### Colour code for forces (*F*) and related stresses (dashed lines):

**blue (dark)**, posterior bite; **blue (light)**, external force on the cheek; **brown**, transversal anterior bite; **green (dark)**, jaw joint; **green (light) in Fig. 3B–D**, inertia force and direction of skull move to the left side; **green (light) in Fig. 4D–F**, nasal horn; **orange (dark)**, jaw adductor muscles; **orange (light)**, neck muscles; **pink**, transversal force(s) on the lateral horn; **red**, anterior bite(s); **black**, external force(s) on the frill/posterior edge of the skull table; **yellow**, neck muscle related. Dashed lines indicate stress flows of merely compressive ( $\alpha$ ), tensional ( $\beta$ ), or mixed ( $\gamma$ ) stress.