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Synchrotron scanning reveals the palaeoneurology of the head-butting *Moschops capensis* (Therapsida, Dinocephalia)

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Dinocephalian therapsids are renowned for their massive, pachyostotic and ornamented skulls adapted for head-to-head fighting during intraspecific combat. Synchrotron scanning of the tapinocephalid *Moschops capensis* reveals, for the first time, numerous anatomical adaptations of the central nervous system related to this combative behaviour. Many neural structures (such as the brain, inner ear and ophthalmic branch of the trigeminal nerve) were completely enclosed and protected by bones, which is unusual for non-mammaliaform therapsids. The nearly complete ossification, of the braincase enables precise determination of endocast volume and encephalization quotient, which are greater than expected for such a large herbivore. The presence of a correspondingly large brain would be consistent with the practice of complex social behaviours such as hierarchical ranking, ritualized display or intimidation, which are often observed in extant head-butting species. Additionally, the plane of the lateral (horizontal) semicircular canal of the bony labyrinth is oriented nearly vertically if the skull is held horizontal, which suggests that the natural position of the head was inclined about 60-65° to the horizontal. This is consistent with the fighting position inferred from osteology. Finally, the very large parietal tube must have been filled with thick conjunctive tissue to protect the delicate pineal eye from injury sustained during head butting.

Research Article

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Abstract

Dinocephalian therapsids are renowned for their massive, pachyostotic and ornamented skulls adapted for head-to-head fighting during intraspecific combat. Synchrotron scanning of the tapinocephalid *Moschops capensis* reveals, for the first time, numerous anatomical adaptations of the central nervous system related to this combative behaviour. Many neural structures (such as the brain, inner ear and ophthalmic branch of the trigeminal nerve) were completely enclosed and protected by bones, which is unusual for non-mammaliaform therapsids. The nearly complete ossification of the braincase enables precise determination of endocast volume and encephalization quotient, which are greater than expected for such a large herbivore. The presence of a correspondingly large brain would be consistent with the practice of complex social behaviours such as hierarchical ranking, ritualized display or intimidation, which are often observed in extant head-butting species. Additionally, the plane of the lateral (horizontal) semicircular canal of the bony labyrinth is oriented nearly vertically if the skull is held horizontal, which suggests that the natural position of the head was inclined about 60-65° to the horizontal. This is consistent with the fighting position inferred from osteology. Finally, the very large parietal tube must have been filled with thick conjunctive tissue to protect the delicate pineal eye from injury sustained during head butting.

Keywords: Endocast, Bony labyrinth, Trigeminal nerve, Head butting, *Moschops*, Dinocephalia

Introduction

Dinocephalia, are typically large-bodied non-mammaliaform therapsids (NMT) with interdigitating incisors and a pachyostotic and ornamented skull (Rubidge and Sidor, 2001; Kemp, 2005). The taxon name, Dinocephalia, which means 'terrible head', was coined by Seeley (Seeley, 1894) in reference to their thickened skull roof bones and pachyostosed cranial embellishments, such as the fronto-parietal shield (FPS) of tapinocephalids, the horns of *Struthiocephalus* and *Estemmenosuchus*, and supraorbital and angular bosses of anteosaurids (Boonstra, 1936; Brink, 1958; Olson, 1962; Rubidge and Sidor, 2001; Kemp, 2005; Kammerer, 2011). The impressive thickness of the cranial vault and the development of pachyosteosclerotic horn-like bosses in tapinocephalid dinocephalians highlight their morphological adaptation for direct and potentially ferocious head-to-head combat (Barghusen, 1975; Benoit et al., 2016a). To recognize the adaptation to head butting in these dinocephalians was not an easy task. Although head butting is a rather common practice among extant ungulates, comparisons with the fossil record are complicated as head butting encompasses a wide variety of behaviours, and because the horns, antlers and bosses that are used for fighting are mostly made of keratin which does not readily fossilize (Geist, 1966; Emlen, 2008; Benoit et al., 2016a). Moreover, unlike dinocephalians, the osseous correlates of ungulates are not made of compact bone, but rather filled with air sinuses (Geist, 1966; Emlen, 2008; Farke, 2008; Benoit et al., 2016a). Among extant species, only ziphiid whales, and more particularly the bottlenose whale (*Hyperoodon ampullatus*), are known to practice head butting using their densely mineralized rostrum and their compact maxillary crests, but this was discovered only recently (Gowan and Rendell, 1999; Lambert et al., 2011; Biannucci et al., 2013).

More than half a century passed after the name Dinocephalia was coined before Brink (1958) and Barghusen (1975) hypothesized that dinocephalian cranial features were adaptations for head-butting intraspecific contests. Barghusen (1975) pointed out that the robust architecture of the skull (with its thickened skull roof, post-orbital bar, and temporal arch) was an adaptation to accommodate direct impacts on the cranial vault. He also argued that the anteroventral position of the occipital condyle (and the resulting anterior position of the quadrate condyle) allowed the impact surface of the skull to be aligned with the neck during combat so that energy resulting from blows was transferred and dissipated from the dermatocranium to the vertebral column (Barghusen, 1975). Supraorbital thickening to absorb mechanical stress in super-carnivorous species as been invoked to explain pachyostosis of this region of the skull in anteosaurids (Kammerer, 2011), but for tapinocephalids, Barghusen's pioneering morpho-functional reconstruction has convinced most scholars, and the head-butting theory is now generally accepted (e.g. Geist, 1972; Rubidge and Sidor, 2001; Kemp, 2005; Benton, 2005; Benoit et al., 2016a).

Head butting profoundly altered the cranial osteology of tapinocephalids, allowing the cranium to not only physically resist violent impacts that could smash regular bone, but also to protect the delicate central nervous system (CNS) (Benoit et al., 2016a). Accordingly, the CNS must have also been modified to withstand these blows and maintain functionality under the same conditions. It may thus be expected that the endocast and other osseous structures which reflect CNS morphology, such as the bony labyrinth and cranial nerves, may be highly modified in tapinocephalids compared to the usually conservative CNS morphology in other non-mammalian therapsids (NMT) and Mesozoic mammals (Olson, 1944; Kemp, 1969, 1979, 2009; Sigogneau, 1970, 1974; Jerison, 1973; Hopson, 1979; Quiroga, 1980, 1984; Luo, 2001; Kielan-Jaworowska

et al., 2004; Rowe et al., 2011; Castanhinha et al., 2013; Rodrigues et al., 2013a, b; Laaß, 2015). In addition, since tapinocephalid dinocephalians underwent considerable cranial remodelling to accommodate the new posture of the head in order to transfer impact energy to the neck (Barghusen, 1975; Kemp, 2005), the new head posture might be reflected in the positioning of the endocast and bony labyrinth relative to the skull (Giffin, 1989 ; Witmer et al., 2003, 2008; Sereno et al., 2007; Araujo et al., 2016). Finally, head butting often involves ritualized display, intimidating ceremonies and other complex, social behaviours (Geist, 1966; Emlen, 2008) which would imply that tapinocephalids expressed significant behavioural complexity (Geist, 1972). If true, this should be reflected in the relative size of their brain (Jerison, 1973).

We analysed two new synchrotron scans performed on a sub-adult *Moschops capensis* (Fig. 1) to elucidate potential modifications of the CNS that may be adaptations allowing for combative behaviour.

Material and methods

Moschops capensis is a tapinocephalid dinocephalian from the *Tapinocephalus* Assemblage Zone (late Permian, Wordian, ~265 Ma) of the Beaufort Group of the South African Karoo. Specimen AM 4950 (Fig. 1) was found on the farm The Grant 39, north of Grahamstown, and is housed in the Albany Museum (Grahamstown, South Africa). It was preliminarily assigned to an anteosaurid prior to preparation (Modesto et al., 2001), but is now considered to be a sub-adult specimen of *Moschops capensis* (Benoit et al., 2016a) based on the lack of a developed canine tooth, presence of talons and heels on all the teeth, incomplete development of the supraorbital bosses and the unfused state of most cranial sutures, including the bones making up the fronto-parietal shield (FPS). The size of AM 4950 is close to adult size for *Moschops capensis* (basal

skull length: 34.02cm). This skull was scanned in two parts at the European Synchrotron Radiation Facility (Grenoble France), first the snout in 2007, and then the braincase in 2015. The temporary export of the material for scanning was allowed by the South African Heritage Resources Agency (cases 8090 and 8560). Details about scanning procedures, calculation of Encephalization Quotients (EQ; Jerison, 1973; Manger, 2006; Hurlburt et al., 2013) and estimation of body masses are provided in Text S1. Measurements of endocranial volume were taken using Avizo 8 (FEI VSG, Hillsboro OR, USA).

Description and comparisons

For clarity, the orientation of all endocranial structures described here are based on the assumption that the skull was held with an inclination of 60-65° from the horizontal to reflect the hypothesized natural alert posture of the animal (see discussion).

Braincase and endocast

In NMT the endocast is incomplete because ossification is limited to the dorsal aspect of the braincase, and the ventral part is ossified only posterior to the pituitary fossa (Olson, 1944; Kemp, 1969, 1979, 2009; Hopson, 1979; Gow, 1986; Kielan-Jaworowska et al., 2004; Rowe et al., 2011; Castanhinha et al., 2013; Rodrigues et al., 2013a; Laaß, 2015). In some taxa, the sphenethmoid complex (mostly the orbitosphenoid, in addition to the mesethmoid rostrally, the inter-orbital septum ventrally, and the epipterygoid caudally) forms a gutter that partially ossifies ventrally around the forebrain but still leaves the metopic fissure, a wide gap between the sphenethmoid complex and basicranium, unossified (Boonstra, 1968; Hopson, 1979; Ivakhnenko, 2008) (note that the metopic fissure can be reduced in some rubidgine

gorgonopsians and some biarmosuchians too [Sigogneau, 1970]). In contrast, the skull of *Moschops* is more robustly built than in other NMT (Boonstra, 1968; Benoit et al., 2016a). At the level of the braincase, the cranial vault comprises 50 to 60 mm thick bone divided into a 15 to 20 mm osteosclerotic surface forming the FPS and about 40 mm of internal cancellous bone (Fig. 2) (Benoit et al., 2016a). Unlike the condition in other NMT, in *Moschops* the sphenethmoid complex and basicranium share a suture, are pachyostotic and cancellous, and the braincase is also completely ossified ventrally (Fig. 2) (Benoit et al., 2016a). As a consequence, the endocranial cast of the braincase (endocast) is complete in *Moschops*, contrary to that of other NMT.

The endocast volume in this sub-adult specimen of *Moschops capensis* is 61 cm^3 (40 cm^3 excluding the pineal tube), which is close to the 65 cm^3 measured in an adult specimen of the more derived tapinocephalid *Struthiocephalus whaitsi* (Table 1). Unlike other NMT (Kemp, 1969, 1979, 2009; Hopson, 1979; Kielan-Jaworowska et al., 2004; Rowe et al., 2011; Castanhinha et al., 2013; Rodrigues et al., 2013a; Laaß, 2015), the main axis of the endocast is not aligned with that of the skull but appears nearly horizontal when the skull is inclined at about 60° from horizontal (Figs. 1B, 3A). This inclination of the braincase compared to the rostrum is present to various degrees in all dinocephalians in which the braincase has been studied (Barghusen, 1975; Boonstra, 1968; Ivakhnenko, 2008). The endocast is serially arranged in *Moschops* (Fig. 3B). The cerebral part of the endocast is short and the hemispheres are not distinct on its surface (Fig. 3B), which means that the brain was separated from the braincase by a thick layer of adnexa, most likely composed of meningeal tissue as well as arteries and venous sinuses (Bauchot and Stephan, 1967).

Concerning the olfactory bulbs, only the bony canals that house the olfactory tracts are ossified and are reconstructed here (Fig. 3B). Because of the ventral ossification of the braincase, the endocast of *Moschops* preserves canals for many nerves and other soft tissue structures that are not usually seen on the endocasts of other NMT. For instance, a discrete canal for the optic nerve is present, which is unique to dinocephalians (Fig. 3) (Boonstra, 1968). The metopic fissure is reduced to the passages of the middle cerebral vein and the root of the trigeminal nerve, as in other Dinocephalia (Boonstra, 1968). However, in AM4950 these passages are completely separate, resulting in two distinct canals, a dorsal one for the middle cerebral vein and a ventral one for the root of the trigeminal nerve (Fig. 3B).

A number of large canals, possibly for emissary veins, run from the surface of the FPS to the endocast (Fig. 1B). The pineal tube is prominent in *Moschops* and completely covers the midbrain in dorsal view (Fig. 3C). This tube is oriented slightly rostrally compared to the endocast and the parietal foramen opens right above the midbrain, as in other NMT (Olson, 1944; Kemp, 1969, 1979, 2005, 2009; Boonstra, 1968; Quay, 1979; Hopson, 1979; Kielan-Jaworowska et al., 2004; Castanhinha et al., 2013; Laaß, 2015), but compared to the skull it opens on the caudal margin of the cranial roof (Figs. 1B, 3A). *Moschops* and other dinocephalians are very distinctive because of their hypertrophied and deep hypophyseal fossa (Fig. 3B) (Boonstra, 1968). Unlike other NMT, in dinocephalians the hypophyseal fossa is completely ossified rostrally by the presphenoid, and its boundaries are well defined (Fig. 3B) (Boonstra, 1968). In this sub-adult *Moschops* the hypophyseal fossa is not bulbous, as in the adult *Moschops* and other tapinocephalids described by Boonstra (Boonstra, 1968), but it is long and slender, similar to the condition in *Jonkeria* and *Anteosaurus* (Fig. 3B) (Boonstra, 1968). The base of the hypophyseal fossa is pierced by the two foramina that transmitted the internal

carotid arteries (Fig. 3B). The stylomastoid canal for the facial nerve is long and located anterior to the bony labyrinth (Fig. 3B). A discrete jugular foramen, for the cochlear canaliculus and the glossopharyngeal and vagus nerves, is found immediately posterior to the bony labyrinth (Fig. 3B). There is a clear osseous separation between the vestibule of the bony labyrinth and the jugular foramen. This is a rare condition amongst NMT, but it has been observed in gorgonopsians previously (Sigogneau, 1974; Luo, 2001). The canals for the accessory and hypoglossal nerves are separate (Fig. 3B). There is a distinct pontine flexure of the endocast between the hindbrain and the foramen magnum (Fig. 3B). The floccular fossa is shallow in *Moschops* (Fig. 3B), as in other dinocephalians (Boonstra, 1968). It is encircled by the anterior semicircular canal of the bony labyrinth.

Bony labyrinth

The right side of the braincase is best preserved in AM4950, but the bony labyrinth is complete only on the left side (Fig. 1B, 3C). The vestibule in *Moschops* is long and conical (Fig. 3D) and a small and circular *fenestra vestibuli* opens on its distal extremity (Fig. 3D). There is no evidence for a cochlear recess. The medial ossification of the common crus, anterior ampulla and vestibule is not complete in AM4950, which results in a large area of fusion between the endocast and bony labyrinth (Fig. 2). In contrast, adult dinocephalian skulls studied by Boonstra (Boonstra, 1968) have only a small and discrete internal auditory meatus for the vestibulo-cochlear nerve, which shows that in adult specimens the bony labyrinth and the braincase are separated. The ampullae are inconspicuous in *Moschops* (Fig. 3D), the secondary common crus between the anterior and posterior semicircular canal is long (Fig. 3C), and the anterior semicircular canal appears to be the largest as it projects further dorso-caudally than the posterior canal (Fig. 3D). The lateral semicircular canal forms an angle of about 105-115° with the main axis of the skull

(Fig. 3A) which suggests that the actual natural position of the head was more vertical rather than horizontal (see discussion).

Trigeminal canals

The trigeminal canals are divided into ophthalmic, maxillary and mandibular branches housing the corresponding branches of the trigeminal nerve and accompanying vessels (Fig. 4) (Benoit et al., 2016b). Although the path of the trigeminal nerve from its root (Fig. 3B) to the trigeminal canals (Fig. 4) is not preserved, the three ramifications are readily identifiable. The maxillary canal is more ramified than that of any other NMT in which it has been documented (Benoit et al., 2016b); however, it comprises essentially the same branches as in other taxa. As in most other NMT, three alveolar rami innervate the lip above the maxillary teeth (Fig. 4). These rami are oriented rostrally instead of ventrally, likely in response to the elaborated development of the rostral dentition in tapinocephalids. There is an important postero-dorsal extension of the external nasal ramus, which reaches the bone surface caudal to the external naris (Fig. 4). The internal nasal and superior labial rami reach the rostral-most margins of the maxilla (Fig. 4). The ophthalmic branch is exceptionally well preserved in *Moschops*, with clearly identifiable frontal and nasal rami, which is a rare condition amongst NMT (Benoit et al., 2016b). Indeed, with the noticeable exception of *Thrinaxodon liorhinus*, the route of the ophthalmic nerve is usually not ossified in NMT and only short and isolated bony channels that go through the nasal and frontal bones mark its presence (Benoit et al., 2016b). As in *Thrinaxodon*, both the frontal and nasal rami are ossified, but they do not innervate the same area. In *Moschops*, the nasal ramus ramifies inside, and opens on the surface of the premaxilla instead of the nasal bone as in *Thrinaxodon* (Fig. 4). In a similar manner, the frontal ramus ramifies more rostrally than in *Thrinaxodon* and opens on the surface of the nasal bone in *Moschops*, instead of the frontal bone (Fig. 4).

Nevertheless, it is possible than some of the canals identified for emissary veins in Figure 1 could also have carried some branches of the frontal ramus, though it is unlikely given they do not branch to the canal identified here as the frontal ramus. As for the maxillary canal, the mandibular canal has numerous branches that open into many mental foramina on the surface of the dentary (Fig. 4).

Discussion

Bony labyrinth and head posture

The bony labyrinth in *Moschops* is very unusual amongst NMT, firstly, because of the thickness and robust morphology of the semicircular canals and the lack of development of the ampullae (Fig. 3C). These two characteristics are not unique to *Moschops* as they are generally encountered in large-sized tetrapods such as sauropods, diprotodontians, and elephants (Clarke, 2005; Witmer et al., 2003, 2008; Sereno et al., 2007; Benoit et al., 2013; Alloing-Séguier et al., 2013). Secondly, compared to other NMT in which all semicircular canals look similar, the bony labyrinth of *Moschops* displays a distinctly larger anterior semicircular canal, a character also commonly encountered in mammals as well as in the sister taxon of Mammaliaforms *Brasilitherium* (Olson, 1944; Kemp, 1969, 1979, 2009; Hopson, 1979; Gow, 1986; Luo, 2001; Kielan-Jaworowska et al., 2004; Castanhinha et al., 2013; Rodrigues et al., 2013b; Laaß, 2015; Ekdale, 2015). Thirdly, *Moschops* differs from other NMT in the horizontal orientation of the vestibule when the skull is orientated with the tooth row parallel to the horizontal (as it is the case in most reconstructions, Fig. 5A). As a result, the plane of the lateral semicircular canal is oblique with respect to the horizontal whereas a more natural position for the head would be with the plane of the lateral canal closer to the horizontal, parallel to the substrate surface plane

±10° (Girard, 1929; Vidal et al., 1986; Sereno et al., 2007; Witmer et al., 2008; see Araujo et al. (2016) for a discussion in the context of NMT). The reconstructed natural alert position of the head is shown in Figure 5B. According to this new reconstruction, the skull would have been held with the rostrum pointing downward in *Moschops* and probably other tapinocephalids, because in this position, the occiput comfortably articulates with the cervical vertebrae (Barghusen, 1975; Kemp, 2005). This head posture also positions the FPS facing forward, which is consistent with the reconstructed head-butting combat habits of tapinocephalids (Barghusen, 1975) and would have facilitated ground-level browsing in these herbivorous animals (Sereno et al., 2007).

As early as 1958, Brink (1958) noted that in *Struthiocephalus*, the braincase is tilted posteriorly so that the FPS, the foramen magnum, and the vertebral column were aligned during fighting (Barghusen, 1975). This allowed for the transfer of energy to the vertebral column as a result of head-butting (Fig. 6) (Barghusen, 1975; Benoit et al., 2016a). This posterior re-orientation of the braincase is particularly pronounced among tapinocephalids (Boonstra, 1968; Ivakhnenko, 2008). The tilted condition of the braincase may thus be the by-product of the necessity to align the FPS, foramen magnum and vertebral column during fighting, and also to displace the parietal foramen away from the FPS (Barghusen, 1975; Benoit et al., 2016a). One may thus argue that the orientation of the bony labyrinth does not reflect the natural head posture, but rather results from this flexure of the basicranium and occiput. However, the re-orientation of the dinocephalian braincase leaves the pontine flexure of the endocast unaffected, meaning that the entire braincase underwent a re-orientation, not only the basicranium (Fig. 3A, B) (Boonstra, 1968). By comparison, in pachycephalosaurid dinosaurs, the only other group displaying a re-

organisation of the skull comparable to tapinocephalids, this alignment is achieved by the loss of the pontine flexure (Fig. 5C) which enables the foramen magnum to be positioned right at the base of the skull (Giffin, 1989; Bourke et al., 2014; extant ungulates don't show such reorganisation [Girard, 1929; Piveteau, 1958]). However, this leaves the braincase and bony labyrinth in the same orientation as the skull (Fig. 5D) (Giffin, 1989; Bourke et al., 2014). This indicates that a complete re-orientation of the braincase is not a necessity to align the FPS with the foramen magnum and the neck, thus supporting the hypothesis that the rotation of the bony labyrinth and braincase is an adaptation to head posture in *Moschops* and is not simply an epiphenomenon.

Protection of the CNS and modifications related to head butting

Dinocephalians are unique amongst NMT in having a complete endocast (Figs 2, 3) (Boonstra, 1968). Dorsally, the cranial roof is thickened and covered by a densely ossified FPS, and ventrally the bony complexes of the skull base (sphenethmoid complex and basicranium) are expanded dorsally and medially toward one another to enclose the braincase (Fig. 2) (Boonstra, 1968; Barghusen, 1975; Benoit et al., 2016a). Unlike other NMT, the endocast in *Moschops*, including the hypophyseal fossa, is fully enclosed by bone. The bony labyrinth is isolated from the braincase in adults, and the roots of many cranial nerves are preserved as discrete canals (Fig. 3B) (Boonstra, 1968). Only the ventral aspects of the olfactory bulbs are not ossified. Previous studies on head butting in *Moschops* have focused on morphological and histological adaptations such as the thickened bones of the FPS and post-orbital bar, the roughened surface of the FPS to support a cornified plate, the ventral position of the foramen magnum and inclined occiput to align the FPS with neck vertebrae, and the presence of cancellous bones under the dense FPS to

absorb energy and lighten the skull (Barghusen, 1975; Benoit et al., 2016a). These adaptations not only prevented bone breakage under physical forces exerted during head butting, but also protected the CNS by transferring and dissipating shock waves (Fig. 6). For instance, the presence of thickened and columnar bones surrounding the endocast (particularly the orbitosphenoid, prootic and epipterygoid) protected the brain and transferred shocks to the base of the skull (Figs. 2, 6). Moreover, since the brain was not in direct contact with the braincase in *Moschops*, as indicated by the absence of impressions of the nervous tissue on the endocast (Fig. 3), they must have been separated by a thick layer of soft tissue (adnexa), presumably meninges, blood vessels (such as the emissary veins), and other conjunctive and protective tissues that surrounded the brain and helped to absorb vibrations.

Adnexa may have occupied much of the pineal tube as well. This tube is comparatively large in *Moschops*, occupying 35% of the volume of the complete endocast (Fig. 3; Table 1). The parietal tube and foramen housed the membranous pineal nerve and pineal eye (or third eye) (Edinger, 1955; Quay, 1979; Roth et al., 1986; Benoit et al., 2016c). In extant reptiles, these delicate nervous structures monitor biological cycles and rhythms (Quay, 1979; Roth et al., 1986). Hopson (1979) argued that the enlarged parietal foramen and the correspondingly large diameter of the pineal tube in dinocephalians must have been for a large pineal eye and nerve. However, in the case of head-butting species, the enlarged parietal tube and foramen is more likely to have housed a thick sheath of soft tissue to isolate and protect the pineal eye and nerve from injury during combat. The complete ossification of a bony tube for the dorsal-most branch of the trigeminal nerve (the ophthalmic branch) may also reflect a protective adaptation related to this part of the CNS. Moreover, the ophthalmic branch appears to have shifted rostrally in *Moschops* (Fig. 4), maybe for distancing the ophthalmic nerve (particularly its frontal ramus) and

accompanying vessels from the FPS where they could have been injured and triggered pain and bleeding during combat. Therefore, instead of innervating and supplying the nasal bone, the nasal branch of the ophthalmic canal is located in the premaxilla, and instead of innervating and supplying the frontal bone (which belongs to the FPS), the frontal branch of the ophthalmic canal is located in the nasal bone (Fig. 4).

Endocast volume and behaviour

As dinocephalians display a unique degree of ossification of the braincase, endocast volume can be accurately measured in this taxon. Boonstra (1958) was the first to measure the size of the endocranial cavity in a dinocephalian, a specimen of *Struthiocephalus whaitsi*. Excluding the olfactory bulbs, the endocast of *Struthiocephalus whaitsi* is rather small, only 65 cm^3 (excluding the olfactory bulbs), which, given its body size (about 288kg, Table 1), makes its relative endocranial capacity the third smallest according to Jerison's EQ and the second smallest according to Manger's EQ (Table 1); however, according to Hurlburt et al's EQ, the *Struthiocephalus* endocast is among the largest for NMT (Table 1). With an endocast of about 62 cm^3 for a body mass estimated to be about 129 kg, the relative endocranial capacity of *Moschops* is comparatively larger than that of *Struthiocephalus* (Table 1). Depending on the EQ, the relative endocranial size of *Moschops* appears comparable to, or larger than, that of most NMT and early mammaliaforms, such as *Morganucodon* and *Hadrocodium* (according to Jerison's EQ and Hurlburt's EQ), or it is in the average for NMT (according to Manger's EQ) (Table 1). This result is quite unexpected for such a large herbivore, as mammalian herbivores usually have relatively smaller brains due to larger body mass and because of negative allometry of brain mass scaling with body mass (Jerison, 1973; Eisenberg, 1981; Manger, 2006). The high EQ of *Moschops* compared to that of the adult *Struthiocephalus* may reflect the young age of the

328 *Moschops* specimen analysed here. Alternatively, the practice of head butting is often associated
329 with ritual, social and display behaviours, and a hierarchical society in extant gregarious species
330 (Geist, 1966). Such complex behaviour,, though currently without evidence for Dinocephalia,
331 may have driven selection for the increased relative brain size (Geist, 1972; Pérez-Barbería and
332 Gordon, 2005). Complete ossification of the braincase protects the central nervous system from
333 injury and could be expected in: (i) species with a relatively enlarged brain and in which
334 behavioural complexity is a central requirement for survival, as in Mammaliaforms (Rowe et al.
335 2011); and/or (ii) species using their head as a weapon in intraspecific fights which could
336 endanger their central nervous system (Sues, 1978; Goodwin and Horner, 2004, 2009; Peterson
337 et al., 2013; Benoit et al., 2016a). The high EQs measured here suggest that CNS evolution in
338 dinocephalians may have been influenced by both factors.

339 Nevertheless, the endocast volume of dinocephalians must be interpreted with caution because,
340 as stated above, the brain did not fill the braincase and thus the endocast volume does not reflect
341 brain size as accurately as it does in mammals. Moreover, the large volume of the pineal tube
342 plays an important role increasing endocast volume as shown by the calculations of EQs where
343 the pineal tube is removed (Table 1). Finally, the hypertrophied hypophyseal fossa also
344 contributes to the volume of the endocast (2.54%, 3.89% when excluding the volume of the
345 pineal tube; Table 1). Boonstra (1958) argued that the large size of the hypophyseal fossa in
346 dinocephalians may reflect the degree of cranial pachyostosis. This would make this character
347 relevant for a discussion about neurological adaptations to head butting, but a similarly
348 hypertrophied hypophyseal fossa is present in many sauropod dinosaurs and other large extinct
349 species in which the skull is not pachyostotic (Edinger, 1942). As the hypophyseal fossa houses
350 the pituitary gland, which secretes growth hormones, and since an hypertrophied fossa is present

in mostly gigantic species, it is more likely that in dinocephalians the size of this fossa may be correlated with large body size rather than cranial pachyostosis (Edinger, 1942

Concluding remarks

The skulls of tapinocephalid dinocephalians exhibit extensive adaptations for head butting combat, to the extent that complete ossification and re-orientation of the braincase sets them apart from all other NMT. Intraspecific head butting combat is considered a sexually selected behaviour, but the effect of sexual selection and related behaviours are difficult to define and reconstruct from the fossil record. Therefore the recognition and identification of neural characters that facilitate head-butting behaviour in *Moschops* are crucial for future palaeobiological studies of NMT. These characters include the complete bony enclosure of the endocast, bony labyrinth and ophthalmic branch of the trigeminal nerve, a 105-110° inclination of the skull compared to the plan of the lateral semicircular canal, an anterior placement of the ophthalmic canal, and the enlargement of the parietal tube. Given the relatively large number of NMT taxa that manifest signs of head butting behaviour (Benoit et al., 2016a), recognition of such adaptations will certainly change the way the daily life of these long-extinct animals are imagined and also shed new light on the ancestry of mammalian behaviour and sociality.

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532 **Figure legends**

533

534 **Figure 1.** The skull of *Moschops capensis* AM4950 in lateral view. A, photograph of the skull.
535 B, reconstruction of the skull (bone transparent) to reveal the neural structures discussed in this
536 paper. Numbers indicate the position of the cross sections in the subsequent figures. EmV,
537 emissary veins; End, endocranial cast; Hyp, hypophyseal fossa; Lab, bony labyrinths; Pin, pineal
538 tube. Photo by LN.

539 **Figure 2.** CT sections of the skull of *Moschops capensis* AM4950 in positions 1 and 2 (see Fig.
540 1). Abbreviations: Bas, basisphenoid; BrC, braincase; Floc, floccular fossa; FMg, foramen
541 magnum; Hyp, hypophyseal fossa; Mes, mesethmoid; FPS, fronto-parietal shield; Fr, frontal
542 bone; Lab, bony labyrinth; Orbsp, orbitosphenoid; PostFr, postfrontal bone; PostOrb, postorbital
543 bone; PrOt, prootic.

544 **Figure 3.** Digital reconstruction of the brain endocast and bony labyrinth of *Moschops capensis*
545 AM4950 digitally reconstructed. A, transparent skull in left lateral view showing the endocast
546 and bony labyrinth; B, C, Endocranial cast in lateral and dorsal views (pineal tube removed in C
547 for clarity); D, Bony labyrinth in lateral view.Abbreviations: I, olfactory tract; II, optic nerve; V,
548 trigeminal nerve; VII, facial nerve; VIII, vestibulo-cochlear nerve; XI, accessory nerve; XII,
549 hypoglossal nerve; AntAMp, anterior ampulla; ASC, anterior semicircular canal; CC, common
550 crus; CCII, secondary common crus; FMg, foramen magnum; Floc, floccular fossa; Hyp,
551 hypophyseal fossa; IntCar, internal carotid artery; JugF, jugular foramen; Lab, bony labyrinth;
552 LatAmp, lateral ampulla; LSC, lateral (horizontal) semicircular canal; Mcv, middle cerebral
553 vein; ParF, parietal foramen; PinT, pineal tube; PSC, posterior semicircular canal; Vest,
554 vestibule; Fvest, fenestra vestibuli.

555 **Figure 4.** Digital reconstruction of the trigeminal canals, presumably for branches of the
556 trigeminal nerve, of *Moschops capensis* AM4950. Abbreviations: CaudAl, caudal alveolar ramus
557 of the maxillary canal; ExtNas, external nasal ramus of the maxillary canal; IntNas, internal nasal
558 ramus of the maxillary canal; Mand, mandibular ramus; MedAl, medium alveolar ramus of the
559 maxillary canal; MxAnt, maxillary antrum; OphFr, frontal ramus of the ophthalmic branch;
560 OphNas, nasal ramus of the ophthalmic branch; RostAl, rostral alveolar ramus of the maxillary
561 canal; SupLab, superior labial ramus of the maxillary canal.

562 **Figure 5.** Hypothesized reconstructions of the natural head posture in *Moschops capensis*. A,
563 Redrawn after the mounted skeleton at the American Museum of Natural History (Gregory,
564 1926). B, Based on the position of the plane of the lateral (horizontal) canal. C, comparison of
565 the pontine flexure (indicated by the arrow) in *Moschops* and its absence in the
566 pachycephalosaurid *Stegoceras* (redrawn after Bourke et al., 2014). D, the skull of *Moschops* and

567 *Stegoceras* (redrawn after Bourke et al., 2014) aligned according to the plan of their lateral
568 semicircular canals. Artwork by JB.

569 **Figure 6.** Hypothesized dissipation of the energy during head butting in the skull of *Moschops*
570 *capensis*. Arrows indicate the direction of energy transfer. A, CT section of the skull of
571 *Moschops capensis* AM4950 in position 3 (see Fig. 1). B, The proposed route of the dissipation
572 of energy through the dermatocranium (left) and the braincase (right) in two fighting *Moschops*.
573 Abbreviations: Bas, basicranium; BrC, braincase; CR, cranial roof; Ept, epipterygoid; FMg,
574 foramen magnum; FPS, fronto-parietal shield; Occ, occipital condyles; PrOt; prootic. Artworks
575 by JB.

Table 1(on next page)

Measurements of the endocranial cast and calculations of body mass and encehalization quotients in Therapsida.

Abbreviations: BM, body mass; EQ, encephalization quotient; EV, endocast volume.

Table 1. Measurements of the endocranial cast and calculations of body mass and ~~encephalization~~ quotients in Therapsida. Abbreviations: BM, body mass; EQ, encephalization quotient; EV, endocast volume. [Raw data]

		Skull length (mm)	Pineal volume (cm^3)	Hypophysis fossa volume (cm3)	BM1 (g)	BM2 (g)	BM3 (g)
Morganucodon	Mammaliaformes	-	-	-	-	-	-
Hadrocodium	Mammaliaformes	-	-	-	-	-	-
Brasilitherium	Cynodontia	-	-	-	-	-	-
Therioherpeton	Cynodontia	-	-	-	-	-	-
Probainognathus	Cynodontia	-	-	-	-	-	-
cf. *Probelesodon*	Cynodontia	-	-	-	-	-	-
Exaeretodon	Cynodontia	-	-	-	-	-	-
Massetognathus	Cynodontia	-	-	-	-	-	-
Diademodon	Cynodontia	-	-	-	-	-	-
Diademodon	Cynodontia	-	-	-	-	-	-
Thrinaxodon	Cynodontia	-	-	-	-	-	-
Pristerodon	Dicynodontia	-	-	-	-	-	-
Niassodon	Dicynodontia	-	-	-	-	-	-
Lystrosaurus	Dicynodontia	180	-	-	15746	29444	10342
Moschops	Dinocephalia	340	21,28	1,55	106299	215918	63748
Moschops (no pineal tube)	Dinocephalia	-	-	-	-	-	-
Strutiocephalus	Dinocephalia	443	-	-	234686	493346	136495
Tetracynodon	Therocephalia	75	-	-	1139	1901	910

		Average BM (g)	EV (g)	Jerison's EQ	Manger's EQ	Hurlburt et al's EQ	Source
Morganucodon	Mammaliaformes	51	0,33	0,20	0,35	2,38	Rowe et al. 2011
Hadrocodium	Mammaliaformes	2	0,05	0,24	0,51	1,99	Rowe et al. 2011
Brasilitherium	Cynodontia	99	0,38	0,15	0,25	1,93	Ruf et al. 2014
Therioherpeton	Cynodontia	64	0,36	0,19	0,32	2,33	Quiroga 1984
Probainognathus	Cynodontia	590	1,20	0,14	0,21	2,27	Quiroga 1980
cf. *Probelesodon*	Cynodontia	3807	4,33	0,15	0,20	2,92	Quiroga 1980
Exaeretodon	Cynodontia	46877	19,19	0,12	0,14	3,23	Quiroga 1980
Massetognathus	Cynodontia	1865	3,33	0,18	0,26	3,34	Quiroga 1980
Diademodon	Cynodontia	50000	26,97	0,17	0,19	4,39	Rowe et al. 2011
Diademodon	Cynodontia	7000	8,00	0,18	0,23	3,86	Jerison 1973
Thrinaxodon	Cynodontia	700	1,46	0,15	0,23	2,52	Rowe et al. 2011
Pristerodon	Dicynodontia	1358	2,18	0,15	0,21	2,61	Laaß 2015
Niassodon	Dicynodontia	491	1,06	0,14	0,22	2,23	Castanhinha et al. 2013
Lystrosaurus	Dicynodontia	18511	8,00	0,10	0,12	2,25	Jerison 1973
Moschops	Dinocephalia	128655	61,12	0,20	0,21	5,89	This study
Moschops (no pineal tube)	Dinocephalia	128655	39,85	0,13	0,14	3,84	This study
Strutiocephalus	Dinocephalia	288176	65,00	0,12	0,13	4,01	Bounstra 1968
Tetracynodon	Therocephalia	1317	2,28	0,16	0,23	2,77	Sigurdsen et al. 2012 (using graphic double integration)

7

Figure 1

The skull of *Moschops capensis* AM4950 in lateral view.

A, photograph of the skull. B, reconstruction of the skull (bone transparent) to reveal the neural structures discussed in this paper. Numbers indicate the position of the cross sections in the subsequent figures. EmV, emissary veins; End, endocranial cast; Hyp, hypophyseal fossa; Lab, bony labyrinths; Pin, pineal tube. Photo by LN.

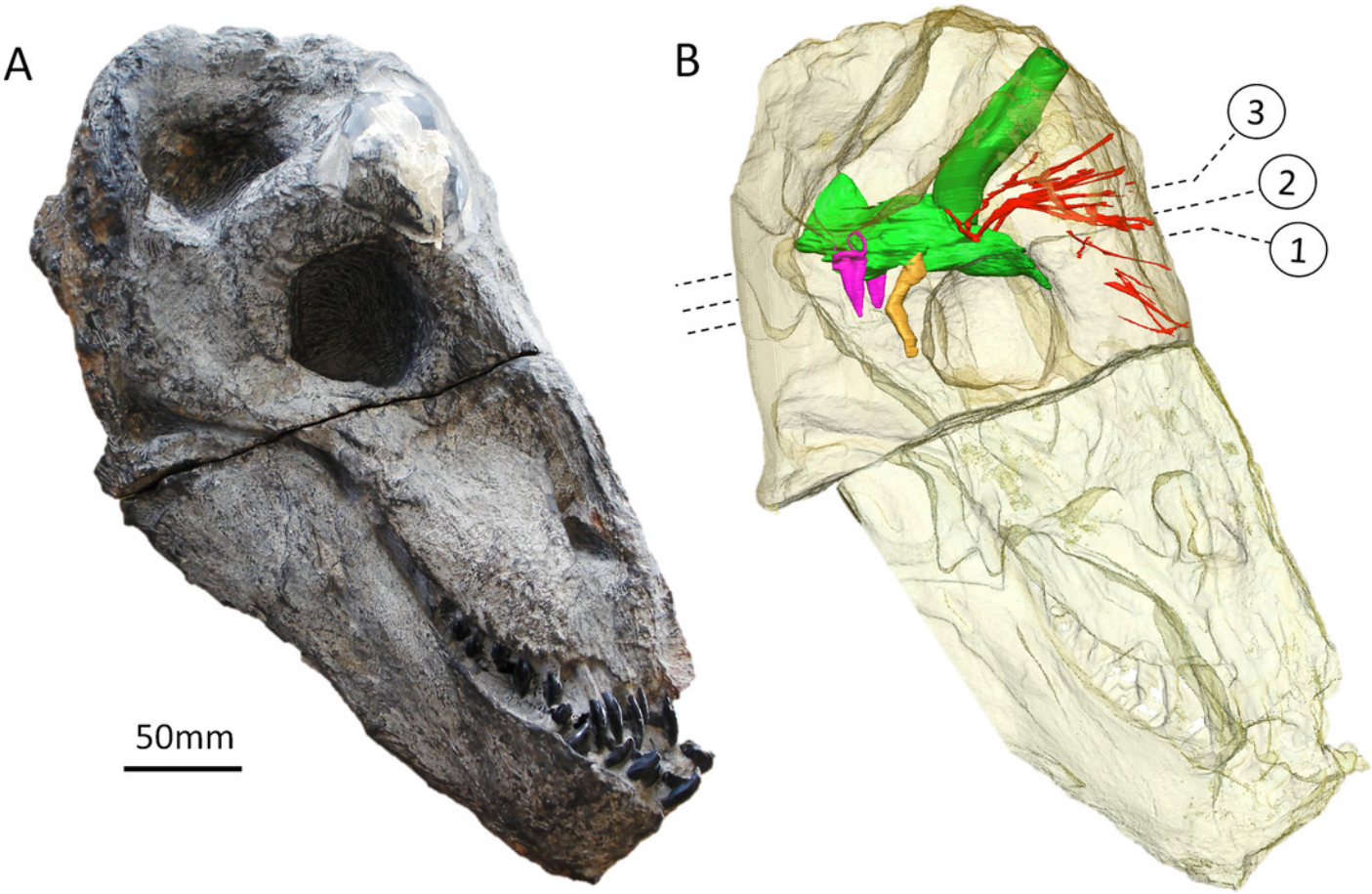


Figure 2

CT sections of the skull of *Moschops capensis* AM4950 in positions 1 and 2 (see Fig. 1).

Abbreviations: Bas, basisphenoid; BrC, braincase; Floc, floccular fossa; FMg, foramen magnum; Hyp, hypophyseal fossa; Mes, mesethmoid; FPS, fronto-parietal shield; Fr, frontal bone; Lab, bony labyrinth; Orbsp, orbitosphenoid; PostFr, postfrontal bone; PostOrb, postorbital bone; PrOt, prootic.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

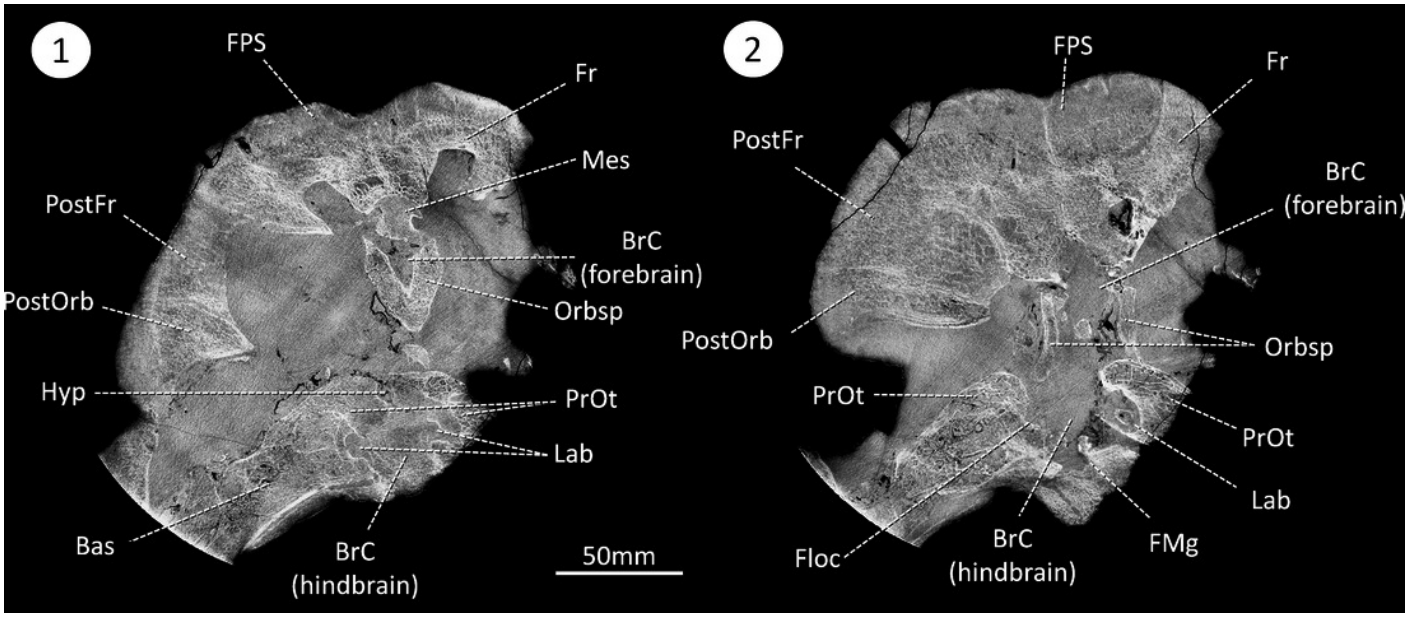


Figure 3

Digital reconstruction of the brain endocast and bony labyrinth of *Moschops capensis* AM4950.

A, transparent skull in left lateral view showing the endocast and bony labyrinth; B, C, Endocranial cast in lateral and dorsal views (pineal tube removed in C for clarity); D, Bony labyrinth in lateral view.Abbreviations: I, olfactory tract; II, optic nerve; V, trigeminal nerve; VII, facial nerve; VIII, vestibulo-cochlear nerve; XI, accessory nerve; XII, hypoglossal nerve; AntAMp, anterior ampulla; ASC, anterior semicircular canal; CC, common crus; CCII, secondary common crus; FMg, foramen magnum; Floc, floccular fossa; Hyp, hypophyseal fossa; IntCar, internal carotid artery; JugF, jugular foramen; Lab, bony labyrinth; LatAmp, lateral ampulla; LSC, lateral (horizontal) semicircular canal; Mcv, middle cerebral vein; ParF, parietal foramen; PinT, pineal tube; PSC, posterior semicircular canal; Vest, vestibule; Fvest, fenestra vestibuli.

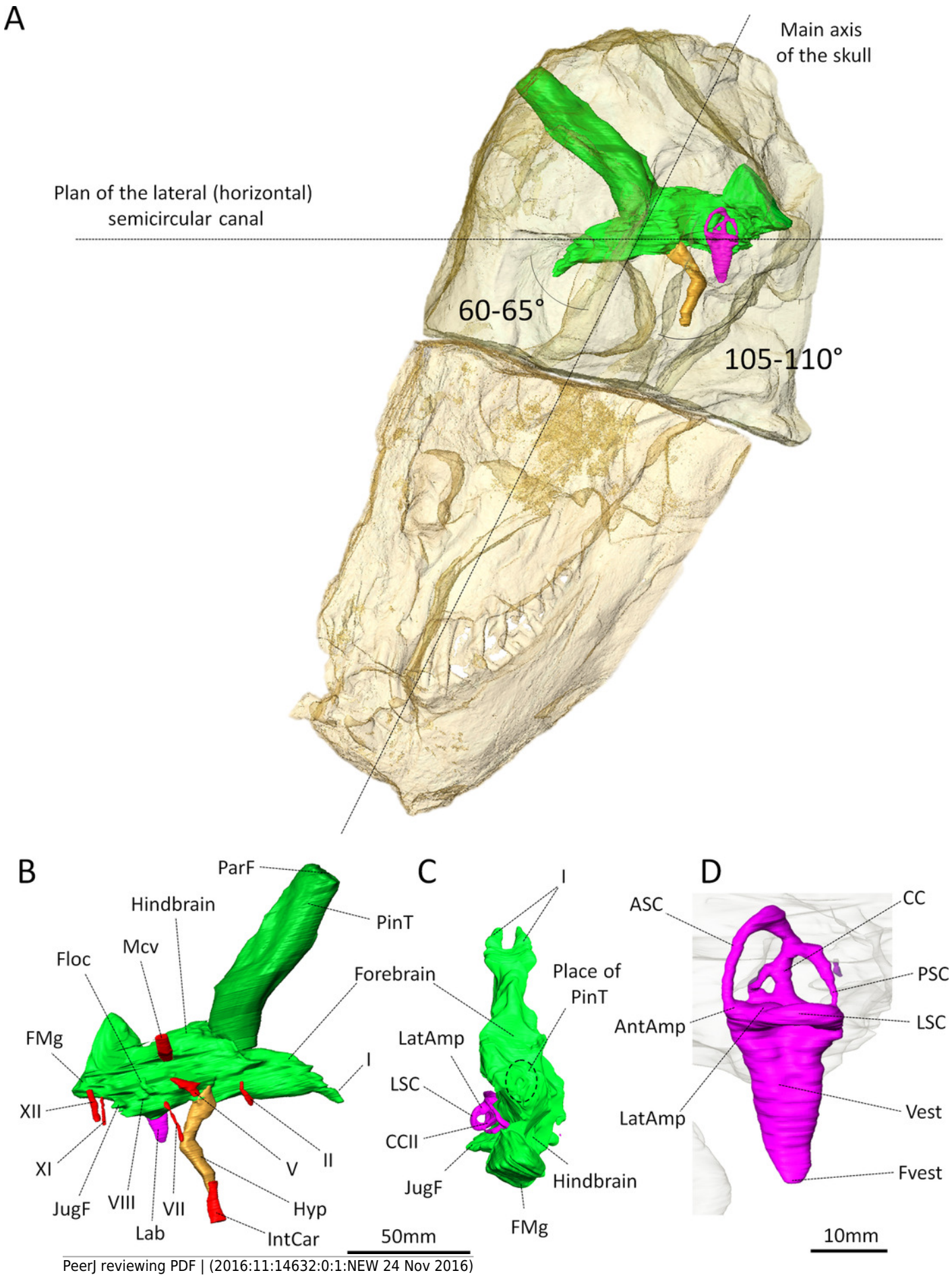

A
Main axis
of the skull
Plan of the lateral (horizontal)
semicircular canal
60-65°
105-110°
B
ParF
Hindbrain
PinT
Mcv
Floc
Forebrain
FMg
I
XII
XI
V
II
JugF
VIII
VII
Hyp
Lab
IntCar
50mm
C
I
Place of
PinT
Forebrain
LatAmp
LSC
CCII
JugF
Hindbrain
FMg
D
ASC
CC
PSC
AntAmp
LSC
LatAmp
Vest
Fvest
10mm

Figure 4

Digital reconstruction of the trigeminal canals, presumably for branches of the trigeminal nerve, of *Moschops capensis* AM4950.

Abbreviations: CaudAl, caudal alveolar ramus of the maxillary canal; ExtNas, external nasal ramus of the maxillary canal; IntNas, internal nasal ramus of the maxillary canal; Mand, mandibular ramus; MedAl, medium alveolar ramus of the maxillary canal; MxAnt, maxillary antrum; OphFr, frontal ramus of the ophthalmic branch; OphNas, nasal ramus of the ophthalmic branch; RostAl, rostral alveolar ramus of the maxillary canal; SupLab, superior labial ramus of the maxillary canal.

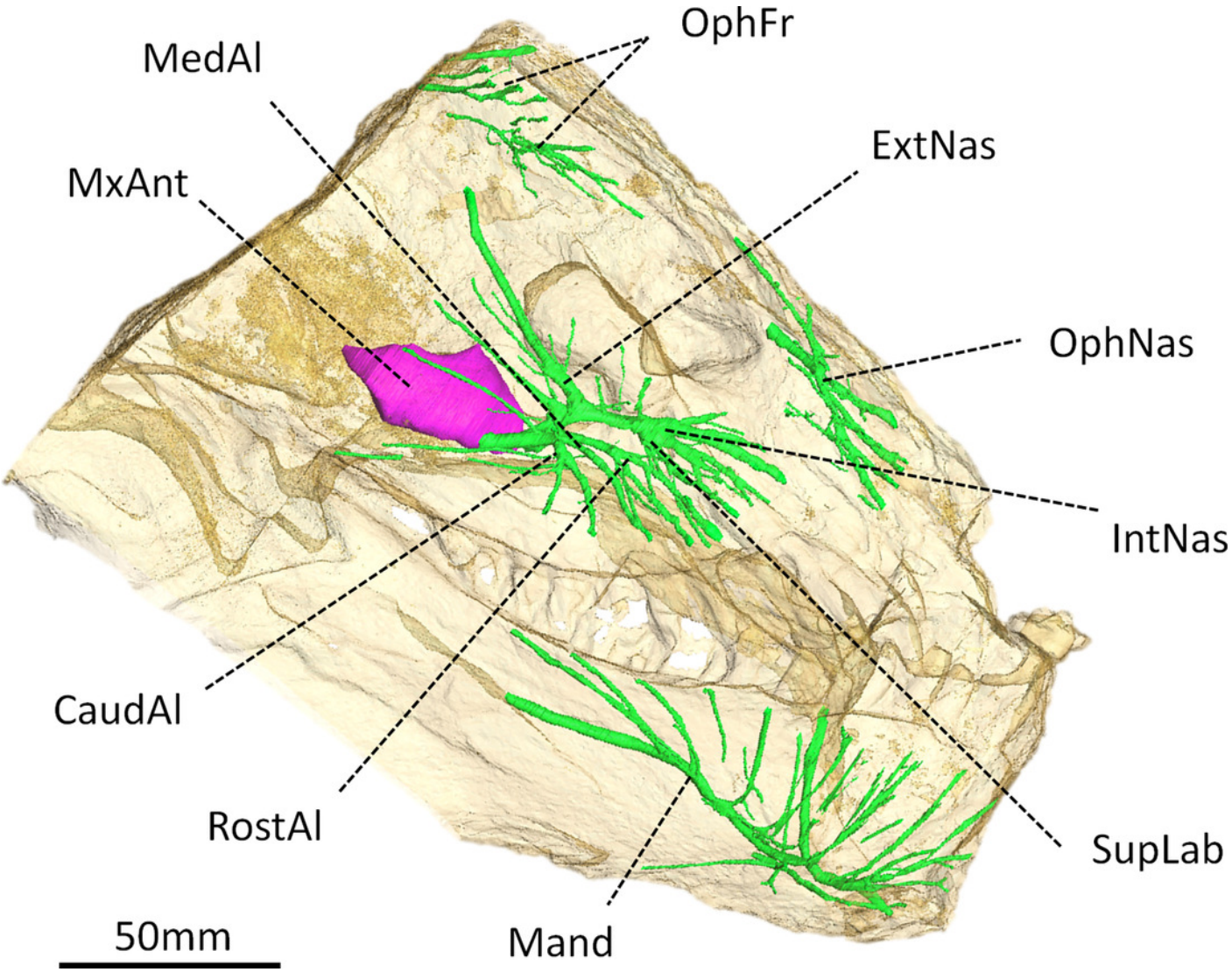


Figure 5

Hypothesized reconstructions of the natural head posture in *Moschops capensis*.

A, Redrawn after the mounted skeleton at the American Museum of Natural History (Gregory, 1926). B, Based on the position of the plane of the lateral (horizontal) canal. C, comparison of the pontine flexure (indicated by the arrow) in *Moschops* and its absence in the pachycephalosaurid *Stegoceras* (redrawn after Bourke et al., 2014). D, the skull of *Moschops* and *Stegoceras* (redrawn after Bourke et al., 2014) aligned according to the plan of their lateral semicircular canals. Artwork by JB.

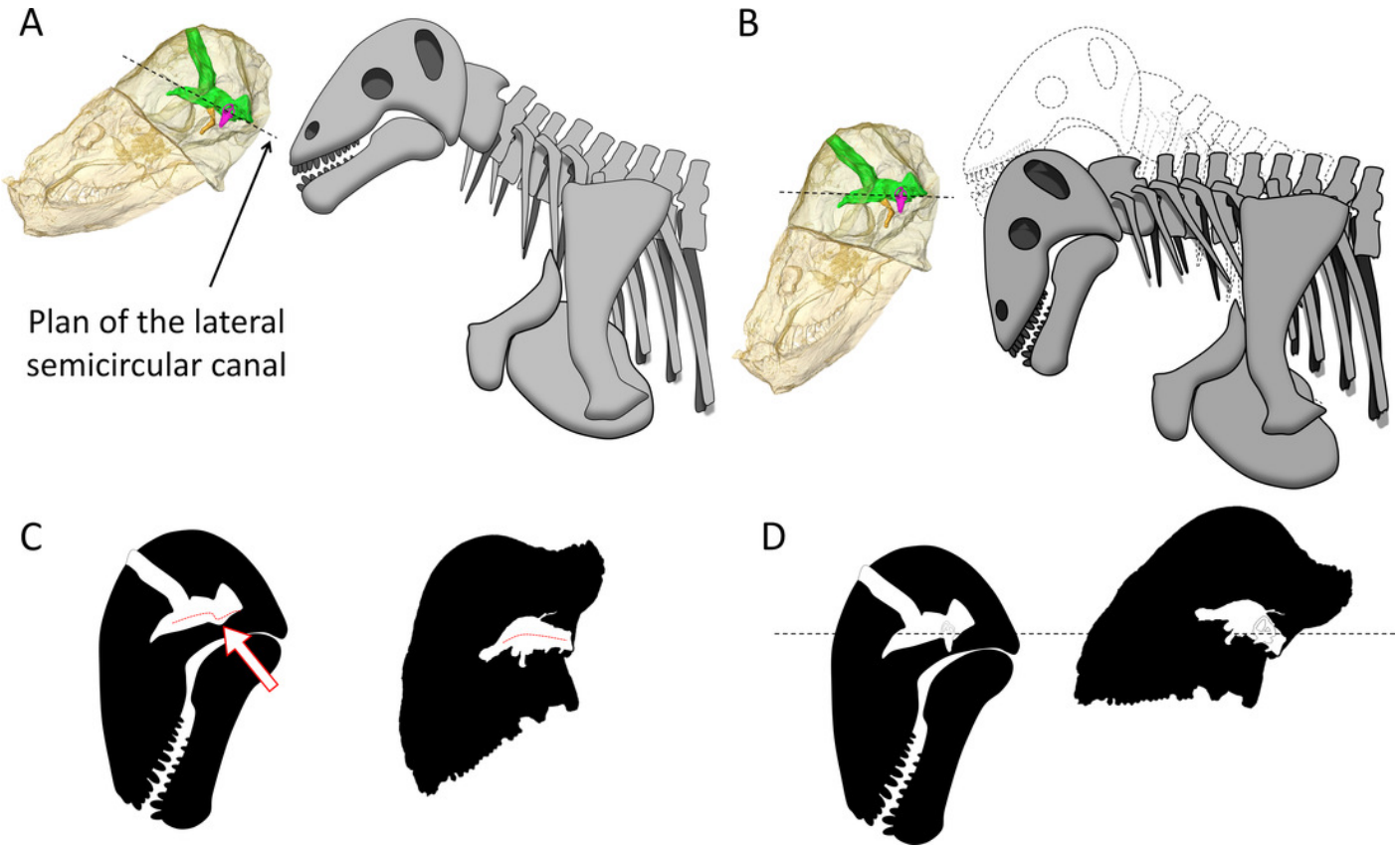
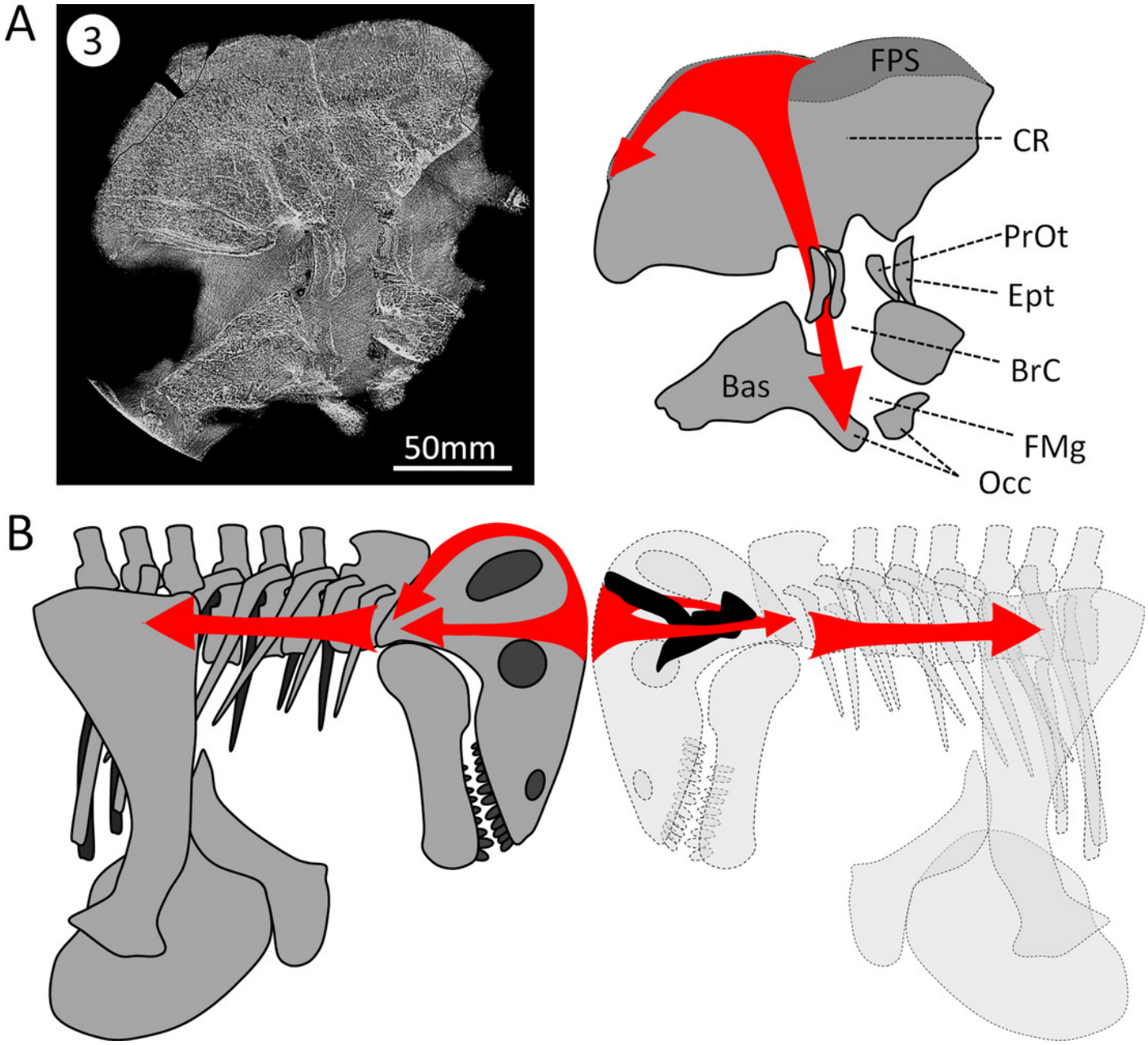


Figure 6

Hypothesized dissipation of the energy during head butting in the skull of *Moschops capensis*.

Arrows indicate the direction of energy transfer. A, CT section of the skull of *Moschops capensis* AM4950 in position 3 (see Fig. 1B). B, The proposed route of the dissipation of energy through the dermatocranium (left) and the braincase (right) in two fighting *Moschops*. Abbreviations: Bas, basicranium; BrC, braincase; CR, cranial roof; Ept, epipterygoid; FMg, foramen magnum; FPS, fronto-parietal shield; Occ, occipital condyles; PrOt; prootic. Artworks by JB.


A
3
50mm
FPS
CR
PrOt
Ept
BrC
Bas
FMg
Occ
B