Matters arising

Jaw roll and jaw yaw in early mammals

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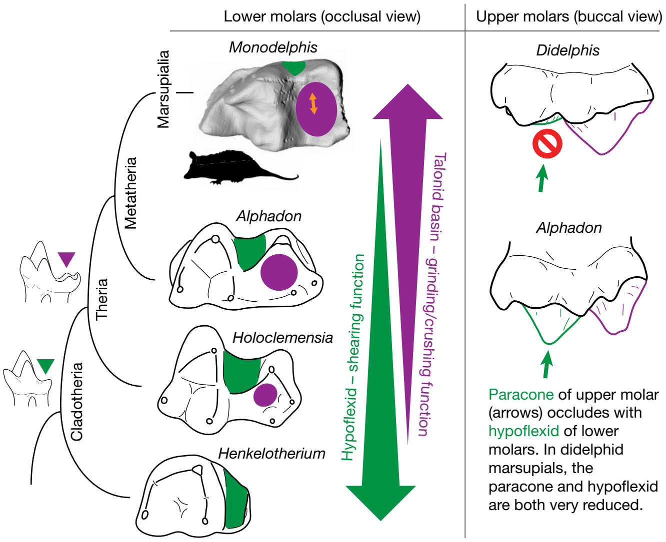
ARISING FROM B.-A. S. Bhullar et al. *Nature* https://doi.org/10.1038/s41586-019-0940-x (2019)

Recent fossil discoveries and methodological developments have triggered a renewed interest in the jaw mechanics of early mammals, and a study by Bhullar et al.[1] is a welcome contribution to this resurgence. They find that the chewing cycle in the grey short-tailed opossum (*Monodelphis domestica*) includes considerable jaw roll (rotation around the long axis of a hemimandible), which produces 'mortar-and-pestle'-like grinding by molars during occlusion. This is a fascinating result that contributes greatly to our understanding of the function of tribosphenic molars. However, I disagree with their hypothesis that the roll-dominated grinding in *Monodelphis* is an ancestral trait of therians (eutherians–placentals and metatherians–marsupials) that evolved in closely related early cladotherians (that is, non-therian cladotherians). Additional lines of evidence suggest that roll-dominated grinding is not a primitive trait in therians.

I have two primary concerns with the evolutionary hypothesis that roll-dominated grinding evolved with Cladotheria, proposed by Bhullar et al.[1]. First, didelphid marsupials such as *Monodelphis* possess derived morphological traits that are probably linked to increased roll of the jaw, which suggests that roll-dominated grinding evolved more recently than the cladotherian node (Figs. 1, 2). For instance, the 'mortar' (talonid basin) and 'pestle' (protocone) of didelphids are derived structures in therians that are absent in early cladotherians. Instead, in early cladotherians, the talonid 'shelf' (the hypoflexid) occludes with the paracone[2–6]. Although many therians maintain a paracone–hypoflexid occlusion, these two structures are considerably reduced in didelphids[7] (Fig. 1). Thus, the hypothesis put forward by Bhullar et al.[1] conflates the mortar-and-pestle action in the protocone–talonid occlusion of tribosphenic therians and the paracone–hypoflexid occlusion of non-tribosphenic cladotherians. Further, the hypoflexid in early cladotherians is simply a sloped shelf that is probably associated with extended shearing rather than grinding[3–6]. Therefore, early cladotherian molars lack the occlusal structure (the talonid basin) that is necessary for roll-dominated grinding (Fig. 1). More plausible evolutionary origins for the roll-dominated grinding of *M. domestica* are within crown therians (in concert with the appearance of the mortar-like talonid basin (Fig. 1)), or independently in several therian lineages that have increased grinding function of the molars[8]. For instance, didelphids possess adaptations for additional grinding that are not found in early therians, which suggests that the roll-dominated grinding of *M. domestica* evolved independently within Metatheria or Marsupialia. These adaptations include a broader talonid basin compared to ancestral metatherians[3,7] (Fig. 1) and an inflected angular process, which is an apomorphy of Metatheria that probably increases the mechanical advantage of the medial pterygoid muscle for roll (Fig. 2). Because roll-dominated grinding in *M. domestica* may be a derived trait in Metatheria, I question the claim made by Bhullar et al.[1] that they 'describe the ancestral tribosphenic therian chewing stroke'.

Bhullar et al.[1] state that the jaw roll in *M. domestica* is muscle-controlled but do not address the possibility that roll during occlusion is also passively directed by molar morphology. Early cladotherian molars show three major wear facets (and no talonid basin), whereas tribosphenic therian molars have six or more[2,4,5]. Occlusion of these surfaces is asynchronous[5], and each is expected to deflect the path of the lower molar to some degree. Thus, the roll in *M. domestica* could be correlated in part with the complex molar occlusal patterns in derived tribosphenic therians, which once again suggests that didelphids are an imperfect model for the jaw kinematics of early cladotherians. Passive guidance of roll grinding by molar morphology does not diminish the functional importance of roll, but it suggests that necessary molar traits (such as a talonid basin) must be present for the roll to occur.

My second concern with the evolutionary hypothesis of Bhullar et al.[1] is that it relies on potential misconceptions concerning the functional link between roll-dominated grinding and the angular process of the jaw. They state that the development of the cladotherian angular process (Fig. 2) increases the mechanical advantage of attached muscles 'by dropping their insertions well below the central axis of the jaw'. This may be accurate for the angular processes of early mammaliaforms, which often do project ventrally[6]. However, in all known early



Paracone of upper molar (arrows) occludes with hypoflexid of lower molars. In didelphid marsupials, the paracone and hypoflexid are both very reduced.

Fig. 1 | Tribosphenic molar evolution and the lack of a grinding surface in pre-therian molars. Bhullar et al.[1] posit that the mortar-and-pestle action in *Monodelphis* evolved with cladotherians, but the mortar-and-pestle structures of *Monodelphis* (the talonid basin and protocone) are not present in early cladotherians. The occlusal surface formed by the hypoflexid (the talonid shelf) (green) is not homologous with that formed by the talonid basin (purple). The orange arrow on the image of the *Monodelphis* molar represents the occlusal contact of the protocone reported by Bhullar et al.[1]. The upper molar images are inspired by ref.[7], and the lower molars in medial view are from ref.[6]. The didelphid silhouette is from Sarah Werning (CC BY 3.0).

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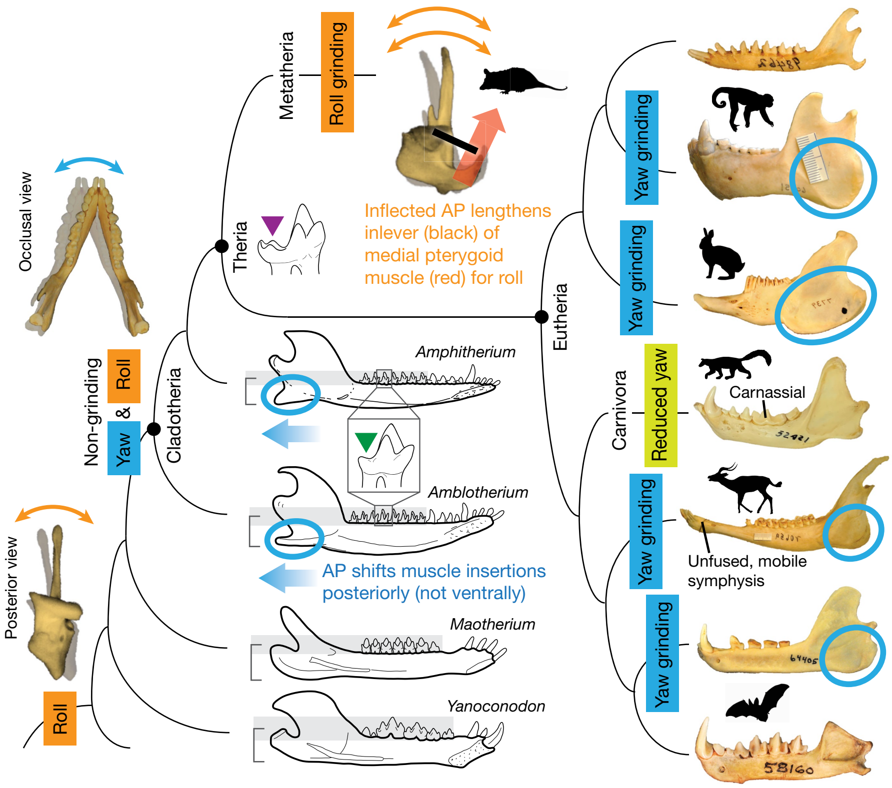

Fig. 2 | Evolutionary changes to the mammalian jaw that contradict the hypothesis that jaw roll grinding evolved in early cladotherians. The angular process (AP) of early cladotherians projects posteriorly and is unlikely to enhance the mechanical advantage of attached muscles for roll[6]. Rather than lacking angular processes[1], herbivorous eutherian clades with yaw-dominated grinding (right) have enlarged angular processes[10–12] (blue circles), and ruminant ungulates have unfused mandibular symphyses that permit roll[14,15]. Conversely, carnivorans such as the skunk (*Mephitis mephitis*) possess adaptations (for example, carnassial molars) for orthally directed shearing, which result in reduced yaw and a relatively small angular process[10,12,13]. The medially inflected angular process of metatherians lengthens the medial pterygoid inlever for roll, which suggests that the roll-dominated grinding of *M. domestica* may be a derived trait that evolved within Metatheria. All illustrations, except the *Amphitherium* jaw, are modified from ref. [6], and jaw photographs are specimens from the Field Museum of Natural History. Herbivore jaws are *Cebus apella*, *Sylvilagus floridanus*, *Aepyceros melampus* and *Pteropus alecto*; the omnivorous *Tupaia glis* (top) and carnivorous *Vampyrum spectrum* (bottom) are for comparison. The didelphid, lagomorph and primate silhouettes are unaltered images from Sarah Werning (CC BY 3.0); all other silhouettes are not copyrighted.

cladotherians, the angular process projects posteriorly—rather than ventrally—from the body of the jaw, parallel to the molar row[6] (Fig. 2). The depth of the angular region below the molar row (brackets in Fig. 2) represents the approximate distance of muscle insertions from the roll axis of rotation, and this depth decreases or remains unchanged with the evolution of the cladotherian angular process[6]. Therefore, the evolutionary appearance of the cladotherian angular process is unlikely to increase the mechanical advantage for roll.

To support their hypothesized link between the evolution of jaw roll and the angular process, Bhullar et al.[1] claim that the evolutionary loss of roll in 'various ungulate clades and primates' is associated with loss of the angular process, stating that the angular process disappeared as jaw roll was 'rendered impossible' by fusion of the mandibular symphysis. However, the opposite evolutionary pattern occurred: herbivores that lack roll have massively expanded angular processes[9–12] (Fig. 2) or functionally homologous angular regions. The enlarged angular processes of herbivores reflect their relatively large masseter and pterygoid muscles[10], which insert on the angular process. These muscles are key contributors to transverse jaw movement via yaw[6,13], and—as noted by Bhullar et al.[1]—the herbivore clades possess yaw-dominated grinding (in contrast to early cladotherians that use yaw for shearing[5,6]). Thus, rather than an increase in yaw being linked to the loss of the angular process[1], an increase in yaw is associated with an expanded angular process. Furthermore, many ruminant ungulates (such as goats and cows) have an unfused and flexible mandibular symphysis that permits roll[14,15], and ruminants possess yaw-dominated grinding and large angular processes[12,13] (Fig. 2). This contradicts the claim[1] that yaw-dominated grinding was 'necessitated by a secondarily fused jaw symphysis'.

I agree with the claim by Bhullar et al.[1] that jaw roll is a primitive trait of cladotherians (Fig. 2), but I disagree with their hypothesis that roll-dominated grinding evolved in concert with the evolutionary appearance of the angular process of the jaw and the molar hypoflexid (Figs. 1, 2). Instead, I suggest that the evolution of the angular process and hypoflexid are associated with increased transverse movement via yaw, enhancing shearing via extended paracone–hypoflexid occlusion[5,6] (Fig. 1). This posited link between yaw and the angular process is supported by the enlarged angular process of herbivores with yaw-grinding, as well as by the reduced angular process in carnivorans that lack yaw owing to their adaptations for carnivory (such as the carnassial molar and hinge-like jaw joints)[6,10,12,13] (Fig. 2). In many taxa with tribosphenic molars (including *M. domestica*), roll may be the dominant jaw movement during occlusion[1], but yaw generates considerable molar displacement during additional phases of the chewing cycle[6,8]. This includes during the fast-close phase, in which the molars align for occlusion (see figures 2c and 3d in ref. [1]).

The tribosphenic molar is a critical evolutionary innovation of therians[1–8], which comprise almost all extant mammals. Thus, elucidating the evolutionary history and functional morphology of this molar is critical to understanding the origins of modern mammal diversity; Bhullar et al.[1] make a substantial contribution to this effort. However, I urge caution in using the jaw kinematics of *M. domestica* as a basis for interpreting major evolutionary transitions in stem and early therians, especially without full consideration of the derived traits of this taxon.

Data availability

No new data were generated in this study.

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Author contributions D.M.G. performed all work in this study.

Competing interests The author declares no competing interests.

Additional information
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Reply to: Jaw roll and jaw yaw in early mammals

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REPLYING TO D. M. Grossnickle *Nature* (2020)

In the accompanying Comment[1], Grossnickle disputes our conclusion[2] that roll-dominated processing is ancestral for therian mammals on the basis of the following assertions: that the surface of the therian talonid basin (Fig. 1a–i) is not homologous to the ancestral cladotherian talonid heel; that the inflected angle in marsupials suggests secondarily increased jaw roll; that the rotational grinding stroke as we describe it might be a passive movement; that the cladotherian angular process (Fig. 1j–s) increases mechanical advantage for yaw instead of for roll; and that the angular process of yaw-processing mammals has expanded instead of vanished.

The principal objection raised by Grossnickle[1] to a cladotherian origin of roll-based processing is that the talonid 'heel' or 'shelf' of the ancestral cladotherian is not homologous to the talonid basin of therians because the inner or lingual cusp that bit into it (which is conventionally known as the paracone) is not homologous to the lingual cusp of therians (the protocone). We contend that the name assigned to the upper cusp is inconsequential, given the underlying structural and functional continuity between the cladotherian paracone and the therian protocone. Every species on the direct line from Cladotheria to Theria had triangular upper molars, the inner vertex of which bit into a shelf or basin attached to the back of the complementary triangle on the lowers[3] (Fig. 1a–i). The name paracone, as currently used, is tied to the identity of the cusp that shears along the posterior face of the trigonid to form the primary trigonid embrasure (Fig. 1a–i, in red; shearing surface 1 in ref. [4]). In early cladotherians, this was the upper lingual cusp[4–6] (Fig. 1c–e), which also contacted or closely approached the talonid. Nearer to Theria, in some early tribosphenidans the anterior labial cusp sheared broadly against the back of the trigonid and is therefore given the name paracone, whereas the lingual cusp—topologically continuous with the cladotherian paracone, but now termed the protocone—maintained its relation to the talonid (Fig. 1f). The embrasure in opossums is again formed by the side of the lingual cusp: surface 4 in ref. [5] and phase I surface of ref. [7] (in which it is shown in hot pink) (Fig. 1i). Therefore, in the topological sense and in the important functional sense of interacting with the talonid, the inner cusp of the ancestral cladotherian upper molar was the antecedent of the inner cusp of the therian molar. Indeed, a comparative survey reveals that the inner cusp is the most conserved feature of the upper molar, and that it is always located below the internal (and largest) of the three roots[8,9] (Fig. 1a–i). In sum, regardless of the name given to the internal cusp, there has been a fundamental continuity: always an inner cusp above and always a platform below (Fig. 1a–i). The talonid as a platform is homologous across cladotherians[10], which calls into question the identification[1,11] of the ancestral cladotherian talonid surface with the therian hypoflexid alone. It is true that the primitive talonid favoured shearing, whereas the therian basin allowed grinding. However, it has previously been observed that mediolateral motion from jaw roll would have increased the efficiency of both kinds of processing[4], which exist as points on a continuum rather than a dichotomy.

With regard to the so-called inflection of the marsupial angle, this phenomenon has previously been found[12] to be little more than an elaboration of a ventral bony lamina known as the pterygoid shelf in stem therians. Muscle attachments are largely the same as in placentals, with the pterygoid shelf extending beneath them, contrary to the accompanying Comment in which attachments are shown to have shifted onto the shelf[1]. Recent studies have found little evidence for a biomechanical explanation, and instead invoke the ontogeny of the middle ear—specifically, an especially intimate or protracted association of the dentary with the ectotympanic[12].

In figure 2 of the accompanying Comment[1], Grossnickle suggests that yaw processing had its origins at Cladotheria and that it is retained in marsupials. He also suggests that roll processing is a marsupial autapomorphy. However, our data[2] show that, although yaw acts to position the teeth for occlusion on the working side of the jaw, yaw is the least important of the three rotational degrees of freedom at the temporomandibular joint. Grossnickle[1] is correct in observing that, in each half chew cycle, *Monodelphis* demonstrates a limited amount of yaw (approximately five degrees), for positioning. However, yaw nearly ceases (save for a highly variable number of small deviations) and roll continues when the jaws are sufficiently closed for food processing to occur (Fig. 2a).

There is a decades-old literature surrounding kinematic observations of mammalian chewing; however, it is often difficult to fully separate roll, yaw and joint translations. Fortunately, kinematic plots based on 'X-ray Reconstruction of Moving Morphology' (XROMM) have recently become available for skunks and raccoons[13]. These eutherians have some specializations for carnivory, but retain a fairly conservative feeding anatomy that includes unfused symphyses. Both taxa roll their jaws extensively, and both show indications of a rotational grinding stroke; this stroke is more erratic in raccoons, which also possess a more derived dentition (Fig. 2b). Neither raccoons nor skunks yaw their jaws during occlusion. During the rest of the chewing cycle, raccoons yaw the jaws by under one degree and skunks yaw the jaws even less (Fig. 2b). The fact that the pattern of chewing—prevalent roll, roll processing and little-to-no yaw—in these eutherians is similar to that in opossums (Fig. 2a, b) contradicts the prediction made by Grossnickle[1]

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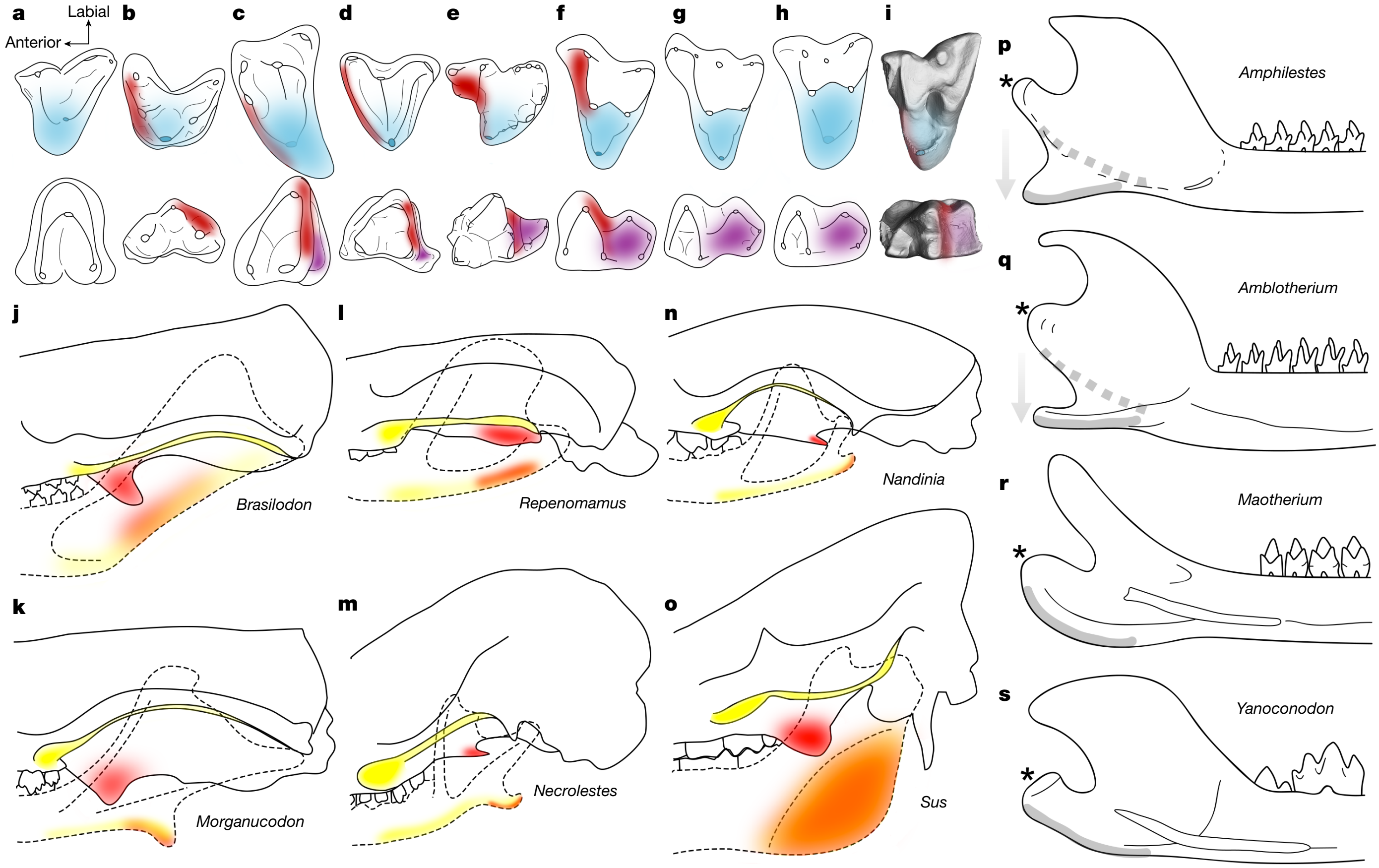

Fig. 1 | Evolution of mammalian molars and adductor muscles. a–i, Molars. The upper lingual or inner cusp (blue) and lower talonid basin (purple) are broadly conserved in a topological sense. The surface of the primary trigon or trigonid embrasure (red)—the presence of which defines the paracone—is also shown where it has been described as such in the literature; it has been omitted in cases in which occlusion is not explicitly described. Left upper (top) and right lower (bottom) molars in occlusal view redrawn from line art and electronic micrographs in primary descriptions, apart from *Monodelphis*, which is rendered from our computed tomography data. Sources are listed by taxon in Supplementary Information. **a**, *Spalacolestes cretulablatta* (Symmetrodonta: Spalacotheriidae). **b**, *Anebodon luoi* (Symmetrodonta: Zhangheotheriidae). **c**, *Laolestes eminens* (Cladotheria: Dryolestidae). **d**, *Brandonia intermedia* (Cladotheria: Meridiolestida). **e**, *Nanolestes drescherae* (Cladotheria:; Zatheria). **f**, *Pappotherium pattersoni* (Cladotheria: Tribosphenida). **g**, *Holoclemensia texana* (Cladotheria: Theria). **h**, *Alphadon marshi* (Cladotheria: Theria). **i**, *Monodelphis domestica* (Cladotheria: Theria). **j**–**s**, Adductor muscles. For **j**–**o**, taxa for which skulls and jaws are available, attachments of the superficial masseter are shown in yellow; attachments of the medial pterygoid are shown in red. Regions in which fibres of both muscles attach are indicated in orange. For **p**–**s** (taxa drawn after the accompanying Comment[1]), reconstructed actual muscle attachments (pterygoideus; masseter attachments are more difficult to estimate in the absence of a skull) are shown as solid grey lines, and hypothetical attachments in the absence of an angular process are shown as dashed lines. Condyles are marked with stars. Contrary to previous reconstructions[16], the superficial masseter originates broadly along its external contact with the zygomatic. Superficial fibres of the adductor externus in reptiles and the masseter in monotremes have their origin along the entire external surface of the zygomatic with no concentration at the anterior margin; therians show some anterior concentration, but fibres and connective tissue continue to attach along the length of the arch. Therefore, the major component of the muscle force vectors is vertical (for roll) and not horizontal (for yaw). The angular process projects both muscle insertions downward, which increases the mechanical advantage (inlever component) for jaw roll. The derived angular region of yaw-processing omnivores and herbivores (here exemplified by the pig (*Sus*)) represents a dorsal and posterior expansion of attachments, not a further development of the ancestral angular process; muscles attach only to the ventral border of this process. Sources are listed by taxon in Supplementary Information. **j**, The non-mammaliaform cynodont *Brasilodon*. **k**, The non-mammal mammaliaform *Morganucodon*. **l**, The eutriconodontan *Repenomamus*. **m**, The dryolestidan *Necrolestes*. **n**, The carnivoran *Nandinia*. **o**, The artiodactyl *Sus*. **p**, *Amphilestes*. **q**, *Amblotherium*. **r**, *Maotherium*. **s**, *Yanoconodon*.

that roll processing is a marsupial autapomorphy as well as his suggestion that conservative placentals should show less roll and more yaw than marsupials. Indeed, it would be reasonable to infer a lower magnitude of positioning yaw in the therian ancestor than is present in opossums, and no yaw processing.

To broaden our coverage, we mined data from as many kinematic studies of mammalian chewing as we could locate (Fig. 2c). Our survey revealed jaw roll in every mammal with a mobile symphysis, including monotremes[14]. Contrary to Grossnickle's[1] prediction, the wombat, which possesses a fused symphysis, does not roll its hemimandibles in the manner of ancestral therians[15]: its whole-mandible roll is a unique autapomorphy. Whereas positioning yaw occurs in most therians, extensive yaw processing occurs only in specialized herbivores and frugivores, most of which have immobile symphyses (Fig. 2c). The data indicate jaw roll, perhaps with no yaw, at the Mammalia node; roll processing and positioning yaw at the Theria node; and yaw processing only in specialized herbivores (Fig. 2c). Incidentally, we can set aside passive cusp–cusp effects as an explanation for the rotational grinding stroke because this stroke occurred consistently when the teeth were widely separated by large food items, and in symmetry on working and balancing sides[2].

Grossnickle[1] claims that the ancestral angle projected muscle attachments backward instead of downward and therefore increased

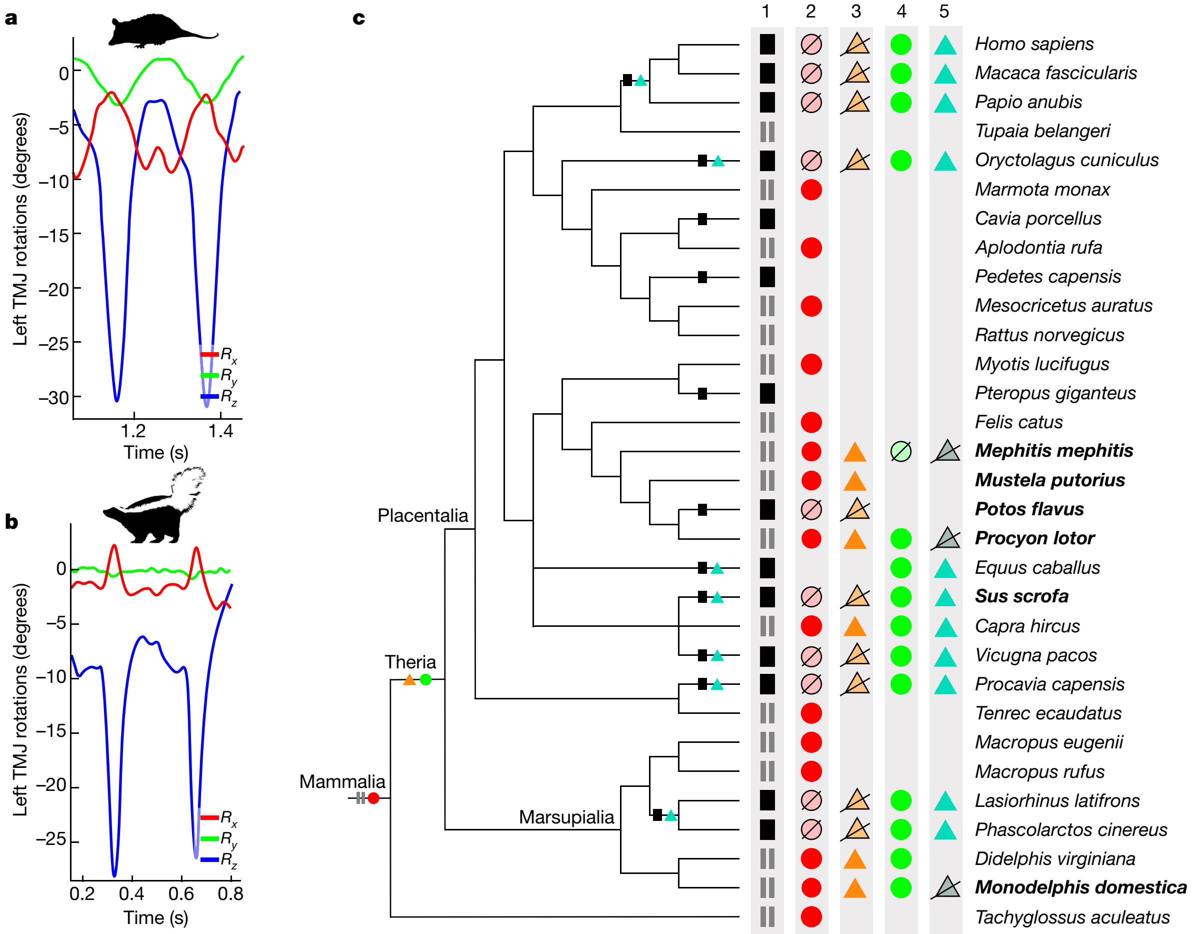

Fig. 2 | Evolution of jaw kinematics in Mammalia. a, Representative segment of chewing sequence for the opossum *M. domestica*. TMJ, temporomandibular joint. **b**, Representative segment of chewing sequence for the skunk *Mephitis mephitis*[13]. In the opossum, yaw (green) positions the jaw but largely halts during maximum jaw closure (blue); in the skunk, yaw is barely detectable at any time. At maximum closure, the opossum displays a single rotational grinding stroke and the skunk displays two such strokes. **c**, Distribution of symphysial mobility and chewing kinematics across Mammalia. Bold indicates taxa known from XROMM studies. Column 1, symphysial mobility: a single rectangle indicates an immobile symphysis, and two rectangles indicate a mobile symphysis. In columns 2–5, coloured shapes indicate the documented presence of an action; faded shapes with strikethroughs indicate an absence confirmed by an XROMM study; and no symbol indicates that presence or absence of the character could not be determined from the published literature. Column 2, independent hemimandibular roll; column 3, roll-based processing; column 4: mandibular yaw; column 5: yaw-based processing. The most parsimonious explanation of the data is that, minimally, the mammalian ancestor had a mobile symphysis and hemimandibular roll, and that the therian ancestor had roll-based processing and mandibular yaw for positioning but not processing. Sources are listed by taxon in Supplementary Information. Silhouettes from http://phylopic.org/; credit to Sarah Werning for opossum (CC-BY-3.0) and José Infante for skunk (CC-BY-3.0).

mechanical advantage (by lengthening the inlever) for yaw instead of roll. On the contrary, the cladotherian angular process does lower the position of muscle insertion, especially in cladotherians with conservative posterior dentaries (Fig. 1j–o). Moreover, the reconstructed force vectors (from muscle attachments) in ref. [16] and the reconstructed axis of rotation in the accompanying Comment[1] differ from those that we determined (Fig. 1j–o). With regard to force vectors, we found that the origins of the superficial masseter and medial pterygoid lie, at least in part, almost directly above the angular process in stem therians, not well in front of it as reconstructed in ref. [16] (Fig. 1l–m). The vertical (for roll) component of muscle force near occlusion is therefore much larger than reconstructed[16] and the horizontal (for yaw) component much smaller. With regard to mechanical advantage, we note that the author, in ref. [16], defined the jaw roll axis as passing through the jaw joint and the symphysis (as we also defined that axis[2]). It seems obvious that the jaw joint is the primary fulcrum for roll, and therefore that roll inlever should be approximated as the distance between the jaw joint and the location of muscle insertion on the jaw. The brackets in figure 2 of the accompanying Comment[1] should extend to the fulcrum if they are meant to depict inlevers. Regardless, the lowering of the muscle insertion permitted by the angular process clearly increases roll inlevers in all taxa, including those depicted in the accompanying Comment (Fig. 1j–s). As a final argument, we note that the first appearance of an angular process occurred before the reduction of the pterygoid transverse process made jaw yaw possible (Fig. 1j, k).

Grossnickle[1] observes that the jaw angle of yaw-processing herbivores is thickened and expanded; he interprets the thickening as an exaggerated angular process. We agree that herbivores have an expanded angular region. However, we maintain that the angular process, as a distinct structure and the primary site for superficial masseter and medial pterygoideus insertion, has vanished. Both muscles have become greatly enlarged and their insertions have migrated dorsally as a whole, in a reversal of the cladotherian ventral shift, to occupy large surfaces on the angle and ramus (Fig. 1n, o). Yaw processing requires much larger movements and greater forces than roll processing, and we posit that the expanded angular region of herbivore jaws accommodates the requisite muscle mass. In support of our hypothesis, we note that wombats, which anomalously roll the jaw despite symphysial immobility, have in fact retained the angular process.

Data availability

All referenced data are freely available as described in ref. [2].

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