

ORIGINAL ARTICLE OPEN ACCESS

Gross Anatomy of the Equine Masseter Muscle: Lamination and Intramuscular Course of the N. Massetericus

Franziska Süß¹ | Sinja Guth² | Hannes Müller-Ehrenberg³ | Michael Röcken⁴ | Carsten Staszky¹ 

¹Faculty of Veterinary Medicine, Institute of Veterinary-Anatomy, -Histology and -Embryology, Justus-Liebig-University Giessen, Giessen, Germany | ²Veterinary Practice Dr. Guth, Aschaffenburg, Germany | ³Orthopaedic Specialist, Münster, Germany | ⁴Clinic for Horses (Surgery, Orthopedics), Faculty of Veterinary Medicine, Justus-Liebig-University Giessen, Giessen, Germany

Correspondence: Carsten Staszky (carsten.staszky@vetmed.uni-giessen.de)

Received: 25 March 2024 | **Revised:** 9 October 2024 | **Accepted:** 11 October 2024

Keywords: anatomy | horses | masseter muscle | masseteric nerve

ABSTRACT

The masticatory muscles of the horse are arranged in an asymmetrical pattern. Four individual muscles on the medial side of the mandible are opposed by one muscle (M. masseter) on the lateral side. However, recent studies on various herbivorous mammals indicate that the masseter muscle features a complex stratigraphic structure that might account for a functional diversity resembling an arrangement of several individual muscles. The functional consideration of the multidirectional equine masticatory movements leads to a similar hypothesis. In order to elucidate the detailed anatomy of the equine masseter muscle, eight cadaveric equine heads were dissected. Additional 29 skull specimens were assessed with regard to the masseteric attachment within the Fossa masseterica. A constant arrangement of nine individual muscular layers within the masseteric muscle was determined. The individual layers were clearly separated by tendon plates and their attachment areas at the masseteric fossa of the mandible were arranged in a constant pattern of bony ridges. With similar consistency, the main trunk of the masseteric nerve was found to run from dorsocaudal to ventrorostral: On that course, the nerve penetrated between the muscular layers from medial to lateral at constant positions. The findings of this study serve as a basis for further studies with the aim of developing biomechanical concepts of equine masticatory movement.

1 | Introduction

The equine masticatory musculature exhibits an asymmetry in the arrangement of the individual muscles. Four muscles are located on the medial side of the mandible: the M. pterygoideus medialis, the M. pterygoideus lateralis and the M. digastricus, including its Pars occipitomandibularis (Liebich, König, and Maierl 2019; Seiferle and Frewein 2003). In horses, the Pars occipitomandibularis of the M. digastricus is also referred to as the M. occipitomandibularis due to its dimension and independent character (Seiferle and Frewein 2003; Wissdorf and Otto 2010). The belly of the M. temporalis is located in the Fossa temporalis, situated dorsomedially to the mandible. On the lateral side, however, there is only one masticatory muscle, the massive M. masseter, which is

considered the most important and strongest muscle of the masticatory apparatus (Kuryszko and Lyczewska-Mazurkiewicz 2004; Wally and Farag 2008). According to Liebich, König, and Maierl (2019) and Seiferle and Frewein (2003), the masseter muscle acts as an elevator and depressor of the mandible against the maxilla when contracted bilaterally and as a lateral mover of the mandible when contracted unilaterally, allowing for a grinding movement. The M. masseter is the only muscle that extends from the Crista facialis in the medial direction to reach the mandible. All other masticatory muscles (M. pterygoideus medialis, M. pterygoideus lateralis, M. digastricus, including its Pars occipitomandibularis) run from medially located cranial structures in a lateral direction to reach the mandible. However, it is now known that the horse's chewing and grinding movements involve many more

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Anatomia, Histologia, Embryologia* published by Wiley-VCH GmbH.

directional components than the previously described dorsoventral and laterolateral movements (Bonin et al. 2006; Sterkenburgh et al. 2021). As hindgut fermenters, horses are adapted to optimal comminution food in the mouth cavity, that is, disruption of the cell walls of the consumed plant materials. In order to fulfil these requirements, a very complex, lophodont dentition (Schultz et al. 2020) and a correspondingly adapted complex chewing movement have evolved. Accordingly, the equine chewing cycle is characterised by a highly constant as well as by a complex spatial and temporal movement pattern (Collinson 1994; Sterkenburgh et al. 2023), which is ensured by the masseter muscle, together with the other masticatory muscles. Hitherto, descriptions of the masseter muscle in veterinary anatomy textbooks often imply a simple morphology. In older textbooks, the masseter muscle was initially described as a two-layered muscle featuring a superficial and a deep layer (Leyh 1859; Ellenberger and Baum 1894; Martin 1914; Seiferle 1954; Seiferle and Frewein 1977). Some texts use different anatomical terms, referring to these layers as the Pars superficialis and Pars profunda (Popesko 2011; Nomina Anatomica Veterinaria 2017). This simple description has been further developed in more modern textbooks by further subdividing the superficial and profound portions. A total of either up to seven muscular layers (König et al. 2019) or even up to 15 layers have been mentioned (Seiferle and Frewein 2003; Liebich, König, and Maierl 2019). Specific studies on the detailed anatomy of the masseter muscle in various herbivorous mammals, including water deer, donkeys and giraffes suggest that the masseter muscle is more anatomically complex than previously thought, comprising up to five individual layers (Sasaki et al. 2001, 2013; Wally and Farag 2008).

The description of the innervation of the equine masseter muscle is limited to the observation that this muscle is innervated by the N. massetericus, a branch of the N. mandibularis which enters the masseter muscle at the Articulatio temporomandibularis (Böhme 2004). A more detailed description of the intramuscular course of the nerve and its branching pattern has not yet been provided in the literature.

To provide a detailed anatomical basis for further research in the flourishing field of equine dentistry, including the biomechanics of equine mastication and myofascial treatment techniques, we examined the lamination of the masseter muscle and the course of the masseteric nerve.

2 | Materials and Methods

Eight heads from horses without pathological changes in the head region were used for this study. The heads were obtained from slaughtered or euthanized horses (six warmbloods and two ponies). All horses had been slaughtered or euthanized for reasons unrelated to this study. The age of the horses was confirmed or estimated on the basis of dental shedding and the morphology of the incisor occlusal surfaces using the ageing guides by Muylle, Simoens, and Lauwers (1996, 1999) and Martin (2007). The youngest horse was 2 years old, and the oldest horse was > 20 years old.

The heads were frozen until dissection. After thawing, the skin and subcutaneous structures were removed to expose the masseter muscle. For the macroscopic examination, portions of the

masseter muscle were removed layer by layer and the orientation of their fibre course was recorded. Special attention was paid to the intramuscular course of the masseteric nerve.

Additionally, the bony structures in the Fossa masseterica were examined in 29 skulls. For this purpose, the skulls were first divided into two groups: one with a permanent dentition ($n = 22$) and one with an incomplete permanent dentition ($n = 7$). The bony attachment crests of the Fossa masseterica were assessed by macroscopic inspection and documented.

3 | Results

The masseter muscle was found to be composed of nine layers that were clearly demarcated from one another by the differing orientations of their muscle fibres (Figures 1–9). In all specimens, each layer was consistently present and arranged identically relative to the others. Each layer was characterised by a thin but clearly visible aponeurosis covering a fleshy part of varying thickness and extent. Each layer originated at the *Crista facialis/Arcus zygomaticus*. The layers either began with the fleshy part and attached with the aponeurotic part to the Fossa masseterica of the mandible or originated at the *Crista facialis/Arcus zygomaticus* with the aponeurotic part and inserted with the fleshy part at the Fossa masseterica of the mandible.

3.1 | Layer 1

Layer 1, the most superficial layer of the masseter muscle originated from the facial crest and zygomatic arch with an aponeurosis and inserted at the caudoventral border of the Ramus mandibulae from the Processus condylaris to the Incisura vasorum faciale by its fleshy portion. The aponeurosis extended over four-fifths of the total length of the facial crest and zygomatic arch with a fibre orientation of approximately 90° – 150° relative to the facial crest. The maximum thickness of layer 1 was 3 cm. Caudodorsally, layer 1 did not reach the temporomandibular joint, allowing deeper layers to become visible (Figure 1). This region was termed the ‘masseter window’.

3.2 | Layer 2

Layer 2 was completely covered by layer 1. It originated with its fleshy portion on the facial crest and inserted with an aponeurosis at the caudoventral border of the Ramus mandibulae. The fibres ran at an angle of 40° – 70° toward the facial crest. At the facial crest, the muscle fibres either merged with those of layer 1 or inserted directly at the facial crest. The maximum thickness of layer 2 was 5 mm (Figure 2).

3.3 | Layer 3

Large parts of layer 3 were located medial to layer 2, originating on the entire facial crest and inserting on the caudoventral margin of the mandible. Layer 3 was orientated at an angle of 90° – 140° relative to the facial crest. The maximum thickness of layer 3 was 1.5 cm (Figure 3).

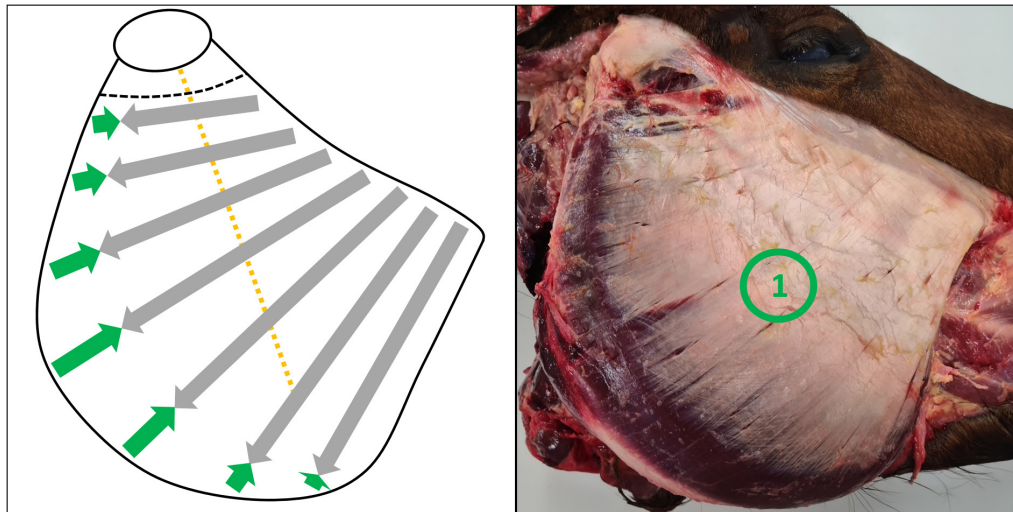


FIGURE 1 | Left: Schematic representation of layer 1. The circle represents the temporomandibular joint, the dorsal line represents the crista facialis, and the ventral curved line represents the extent of the masseter muscle. The dotted line indicates the caudodorsal edge of the masseter muscle. The arrows represent the direction of the muscle fibres, the colour of the arrows either the tendinous sheet (grey) or the fleshy portion (green). The orange line represents the course of the masseteric nerve. Right: Dissected specimen, right side of the head, lateral view of the layer 1.

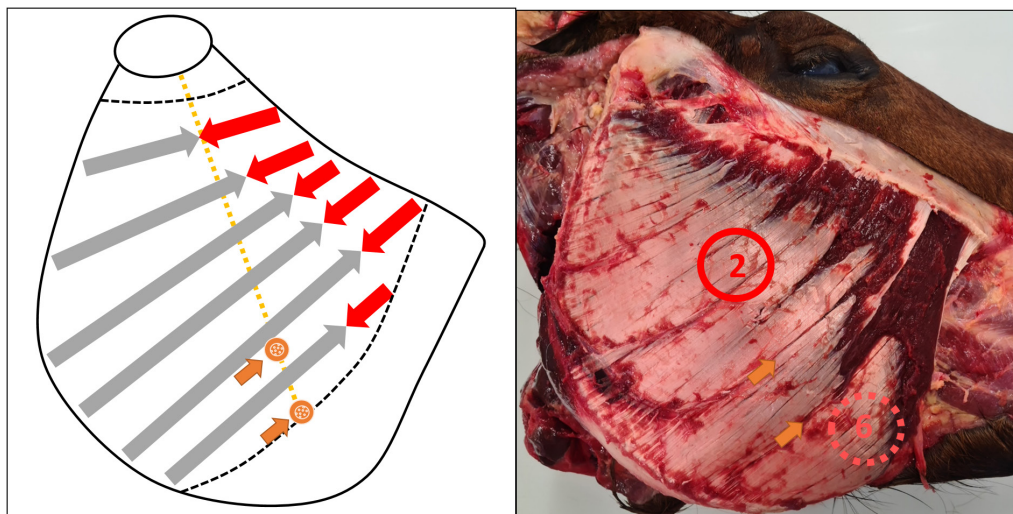


FIGURE 2 | Left: Schematic representation of layer 2. Same set of symbols as explained for Figure 1. Right: Lateral view of the layer 2. The dashed circle marks portions of layer 6. The orange arrows show the exits of the masseteric nerve from the muscle layers.

3.4 | Layer 4

Layer 4 was completely covered by layer 3. It originated with its fleshy part at the caudal aspect of the facial crest and inserted with an aponeurosis at a bony crest within the Fossa masseterica. The fibres were orientated vertically; that is, approximately 90° relative to the facial crest. The maximum thickness of layer 4 was 1 cm (Figure 4).

3.5 | Layer 5

Layer 5 was completely covered by layer 4. It originated with an aponeurosis at the caudal half of the facial crest and inserted with its fleshy part at the same bony crest as layer 4. Layer 5 was orientated at an angle of 80°–90° relative to

the facial crest. The maximum thickness of layer 5 was 1 cm (Figure 5).

3.6 | Layer 6

Layer 6 was divided into a rostral part and a caudal part separated by the passage of the masseteric nerve. The caudal part was completely covered by layer 5 and inserted with its aponeurosis at a bony crest within the Fossa masseterica. The rostral part had been visible since the removal of layer 1 and inserted with its aponeurosis at the rostroventral margin of the ramus mandibulae. Both parts exhibited a fleshy origin on the Crista facialis. The fibres were orientated caudally at an angle of 45°–90° relative to the facial crest. Layer 6 was 0.5–1.5 cm thick, becoming thicker as it advanced rostrally (Figure 6).

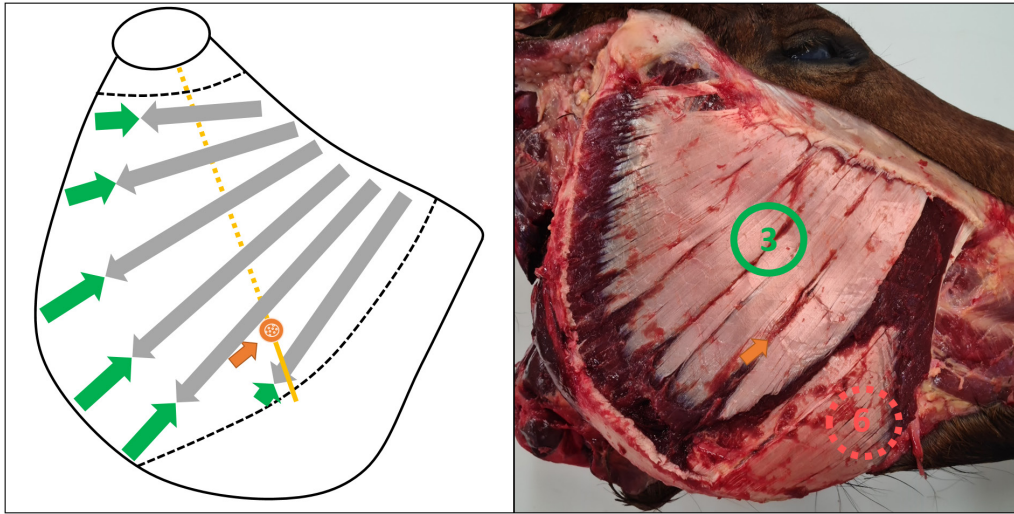


FIGURE 3 | Left: Schematic representation of layer 3. Right: Lateral view of the layer 3.

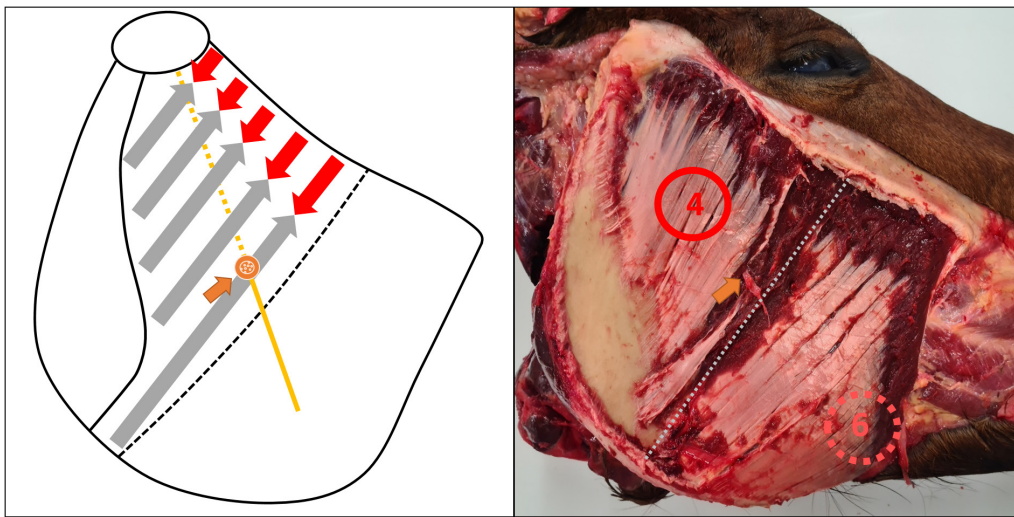


FIGURE 4 | Left: Schematic representation of layer 4. Right: Lateral view of the layer 4.

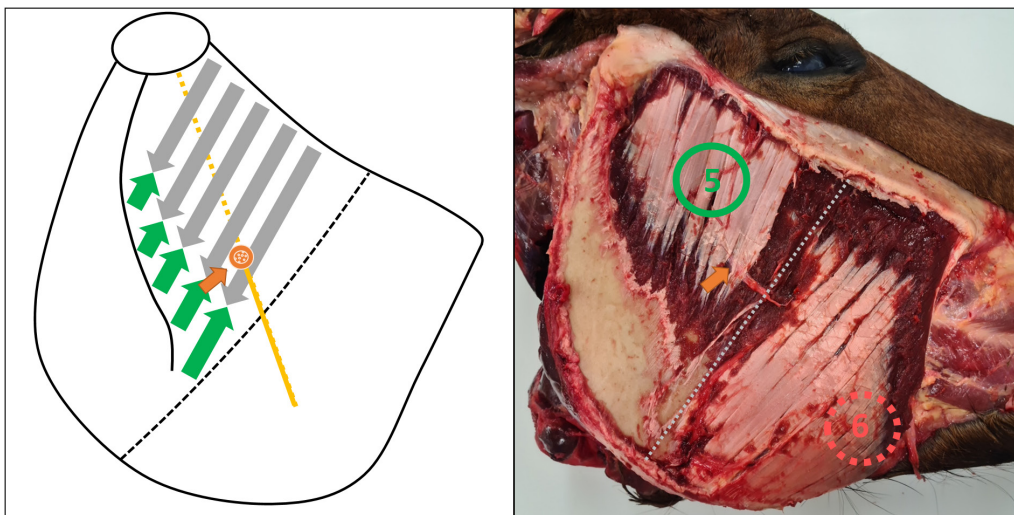


FIGURE 5 | Left: Schematic representation of layer 5. Right: Lateral view of the layer 5.

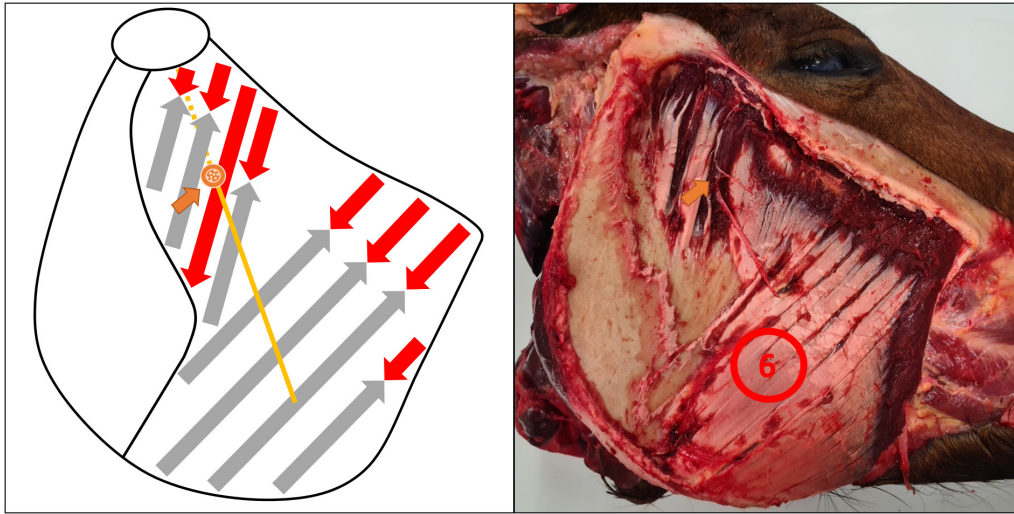


FIGURE 6 | Left: Schematic representation of layer 6. Right: Lateral view of the layer 6.

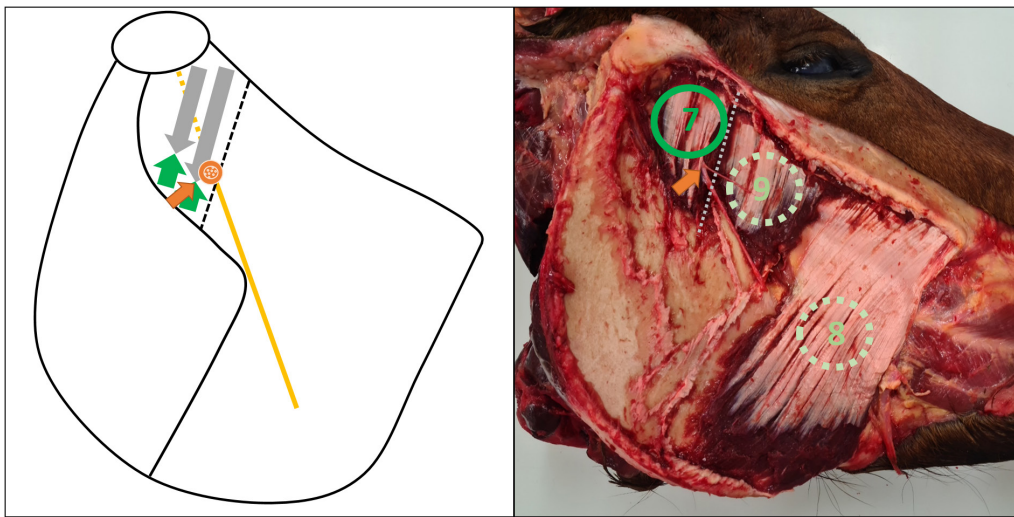


FIGURE 7 | Left: Schematic representation of layer 7. Right: Lateral view of the layer 7.

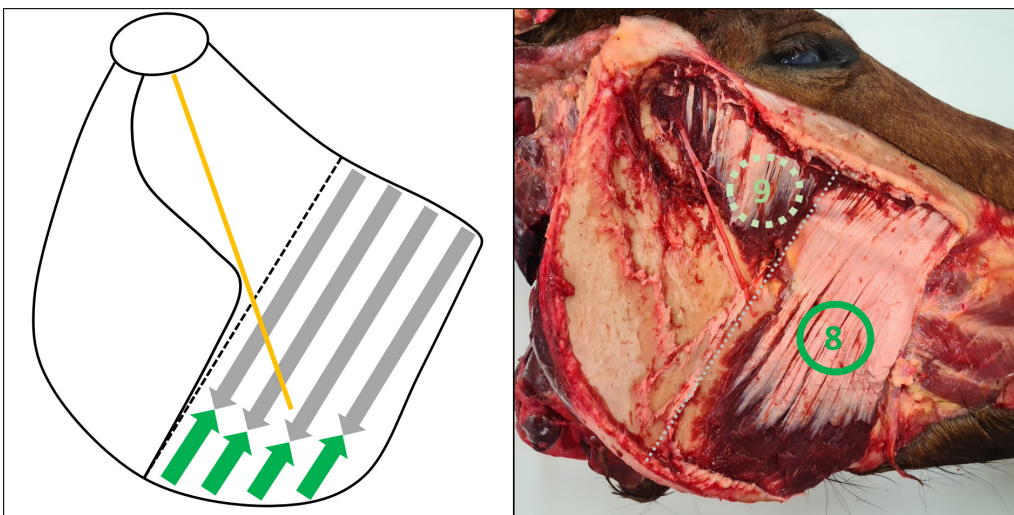


FIGURE 8 | Left: Schematic representation of layer 8. Right: Lateral view of the layer 8.

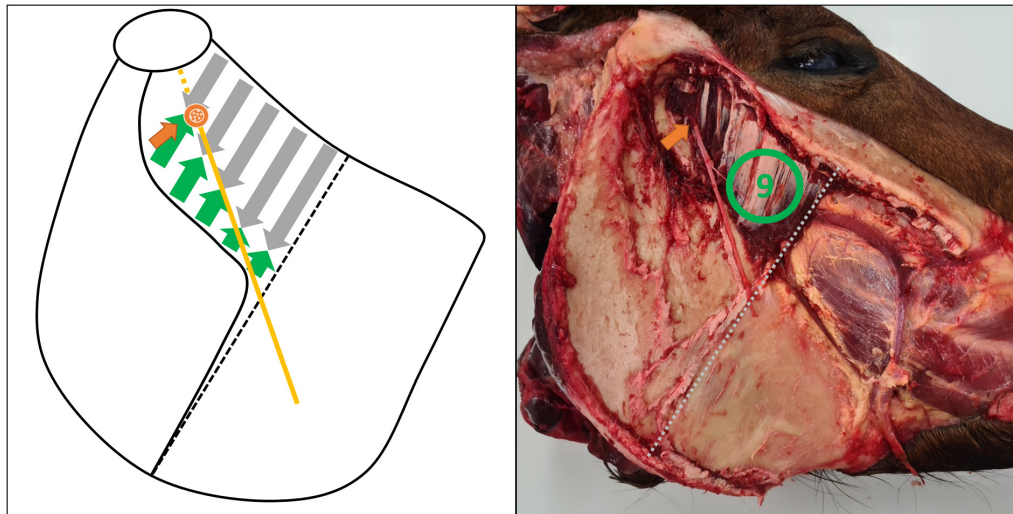


FIGURE 9 | Left: Schematic representation of layer 9. Right: Lateral view of the layer 9.

3.7 | Layer 7

Layer 7 was totally covered by layer 6 and was the smallest layer of the masseter muscle. It originated with its aponeurosis at the facial crest rostral to the temporomandibular joint and was orientated at an angle of 70° – 90° toward the ramus mandibulae. Layer 7 was approximately 0.5 cm thick (Figure 7).

3.8 | Layer 8

Layer 8 originated with its aponeurosis at the rostral part of the facial crest and diverged slightly toward the rostral end of the ramus mandibulae. The aponeurosis of layer 8 was tightly fused with the aponeurosis of layer 1. The thickness of layer 8 increased in the ventral direction, reaching a maximum of 2.5 cm. Layer 8 represented the medial demarcation of the masseter muscle and covered the following anatomical structures: the Pars molaris of the M. buccinator, the Sinus v. buccalis including its accompanying N. buccalis, and the Sinus v. profundae faciei (Figure 8).

3.9 | Layer 9

Layer 9 was almost completely covered by layer 7. It originated with its aponeurosis at the caudal half of the facial crest and ran at an angle of 80° – 90° relative to the facial crest to the most dorsal caudoventral border of the Ramus mandibulae. The tendinous sheet was not continuous, but consisted of individual strands. On the medial side, layer 9 also had an aponeurosis that represented the medial border of the masseter muscle in this area. Medial to layer 9, the Sinus v. profundae faciei, Sinus v. buccalis and extraperiorbital fat body became visible. Layer 9 was 2–4 cm thick (Figure 9).

3.10 | Innervation of the Masseter Muscle

The N. massetericus entered the masseter muscle at its caudomedial border, slightly rostral to the temporomandibular joint. The

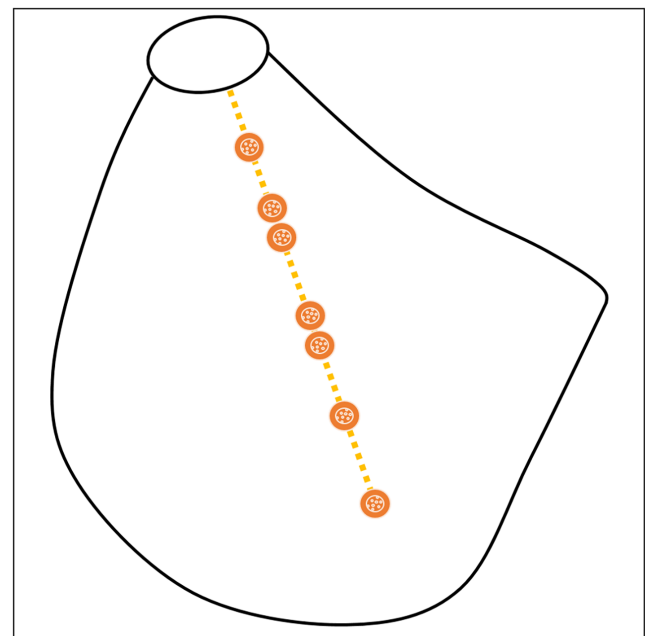


FIGURE 10 | Schematic representation of the path of the masseteric nerve. The circle represents the temporomandibular joint, the dorsal line represents the crista facialis, and the ventral line represents the extent of the masseter muscle. The dotted orange line represents the course of the masseteric nerve, the orange dots indicate the passage of the nerve through the muscle.

main trunk of the masseteric nerve travelled along a constant course from dorsocaudal to ventrorostral and showed a constant angulation of 30° – 40° relative to the facial crest (Figure 10). As it ran rostroventrally, the masseteric nerve moved from medial to lateral in a stepwise (not continuous) course. At six constant sites, the nerve either perforated the muscular layers (layers 6, 5 and 3) or travelled at the rostral border of layers 7, 4 and 2 in a lateral direction (Figure 11). The main trunk of the masseteric nerve showed a macroscopically perceptible thickness until it entered layer 1. During its course through the masseteric muscle, the masseteric nerve tapered only slightly and released

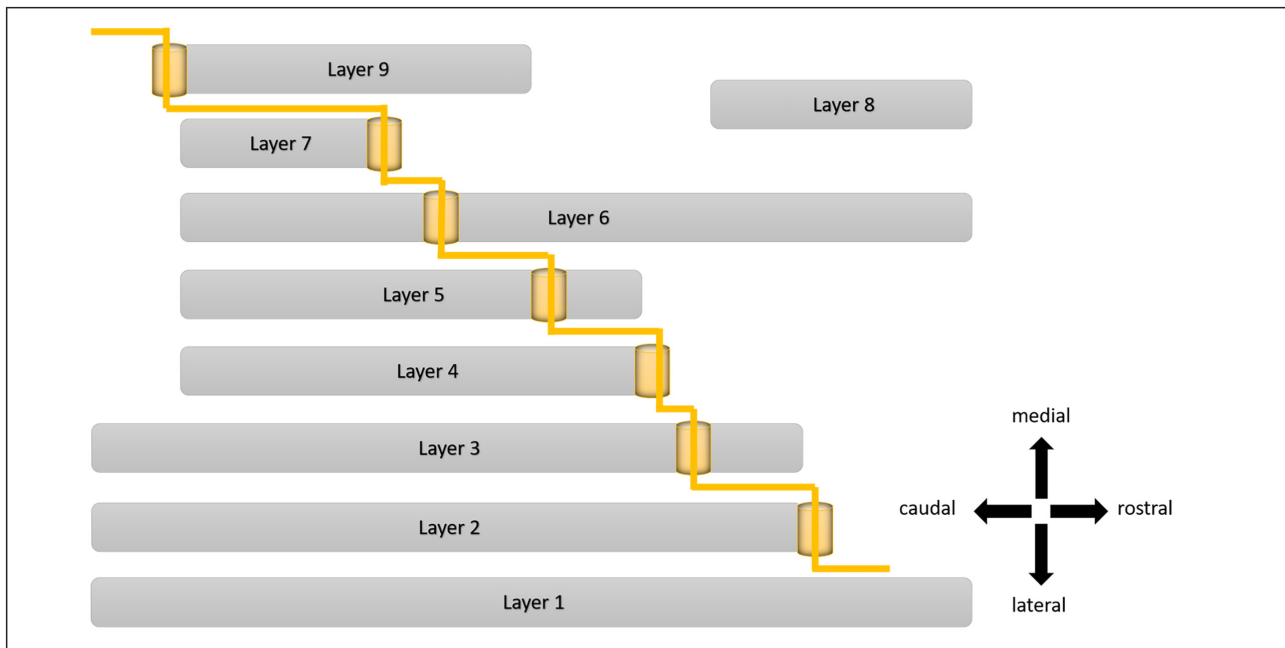


FIGURE 11 | Stepwise course of the N. massetericus through the layers of the M. masseter.

multiple branches that radiated into the adjacent muscular tissue (Figure 11).

3.11 | Vascularization of Masseter Muscle

The A. and V. masseterica entered the masseter muscle at the caudal edge of the mandible, between the dorsal second third and the ventral third of layer 1. Vascular branches also ran on the tendon plate in the ventral area of layer 2 and then branched out medially. Branches of the artery and vein were also seen on the aponeurotic portion of the rostral part of layer 6 (Figure 2).

The A. and V. transversa faciei were superficially located at the caudal edge of the masseter muscle, ventral to the temporomandibular joint. These blood vessels penetrated layer 3 in the caudal area of the Crista facialis. The V. transversa faciei widened in the fleshy part of layer 6 to form the Sinus v. transversae faciei.

3.12 | Bony Structures of the Fossa Masseterica

The consistent lamination of the masseter muscle, with fixed extensions and insertions of layers 1–9, was mirrored by a uniform pattern of bony attachment crests in the Fossa masseterica (Figure 12). This observation was confirmed in 22 equine skulls ($n = 44$ Fossae massetericae), all of which had permanent dentition. In seven skulls that did not yet have permanent dentition, the bony attachment crests were only very weakly pronounced or not yet visible.

To establish appropriate designation, it is proposed to refer to the bony crests as follows. The most pronounced crest runs along the ventral edge of the ramus mandibulae and is referred to as the Linea masseterica ventralis (Figure 12). It provides attachment for the muscular layer 2 and the fleshy portion of layer 1.

In the central aspect of the Fossa masseterica, a system of two parallel bony crests is referred to as the Lineae massetericae centrales (Figure 12). These bony crests provide attachment for layer 4 (ventral) and the caudal portion of layer 6 (dorsal). A distinct bony crest near the dorsal border of the mandibular ramus is referred to as the Linea masseterica dorsalis (Figure 12) and provides attachment for layer 9. Rostral to the Lineae massetericae centrales, a perpendicular crest is referred to as the Linea masseterica perpendicularis (Figure 12) and provides attachment for the rostral part of layer 6 and for layer 8. Not all layers attach to distinct bony crests; some attach in the region between the defined Lineae massetericae. This includes the fleshy portions of layer 3, attaching between the Linea masseterica ventralis and the distal part of the Lineae massetericae centrales; layer 5, attaching between the two Lineae massetericae centrales and layer 7 attaching between the proximal part of the Lineae massetericae centrales and Linea masseterica dorsalis.

4 | Discussion

In this study, a distinct multipennate structure of the equine M. masseter was documented. This finding contradicts the commonly accepted descriptions of the equine masseter muscle in anatomical textbooks, which describe it as a muscle largely composed of a superficial layer and a deep layer (Nomina Anatomica Veterinaria 2017) with possible further subdivision in several muscular layers (Seiferle and Frewein 2003; König et al. 2019; Liebich, König, and Maierl 2019). Other authors either mention no pennation (Kölle, Reese, and Mülling 2014), report the presence of muscular layers without specifying the number or orientation (Salomon 2020), or even deny the presence of separate muscular layers altogether (Heinze 1963).

An unambiguous definition of the Pars superficialis and the Pars profunda of the masseter muscle is not provided in any textbook.

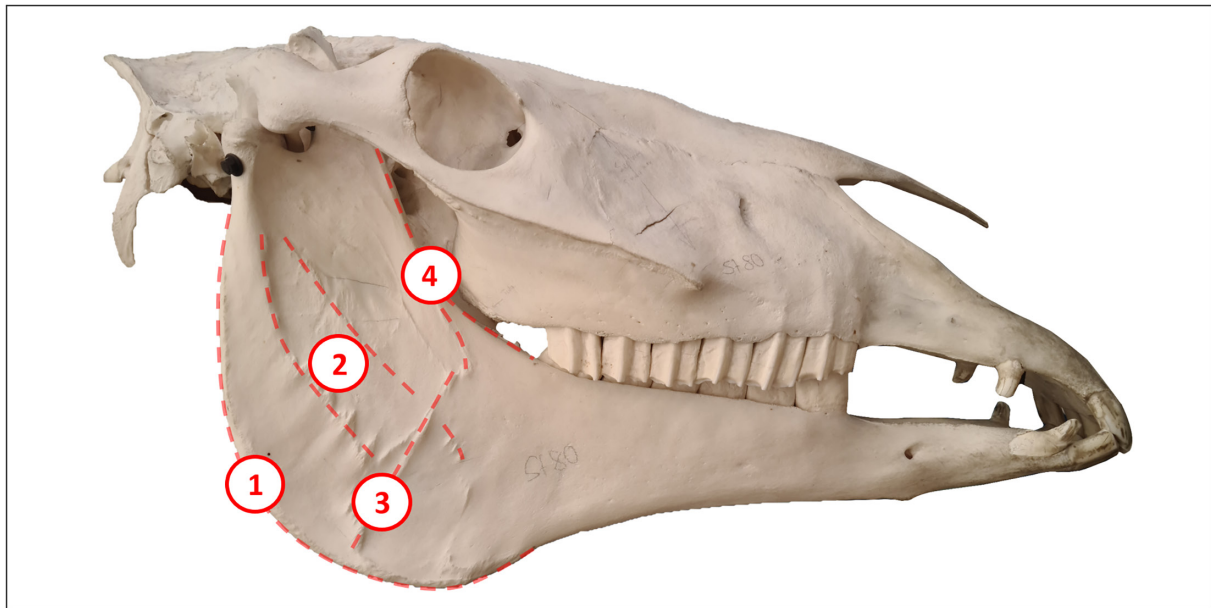


FIGURE 12 | Constant pattern of bony attachment crests within the Fossa masseterica. The red, dotted lines indicate bony attachment crests. (1) Linea masseterica ventralis, (2) Lineae massetericae centralis (dorsal and ventral crest), (3) Linea masseterica perpendicularis and (4) Linea masseterica dorsalis.

However, the fibre course of the Pars superficialis is described as either sagittal (Liebich, König, and Maierl 2019) or caudoventral and divergent (Seiferle and Frewein 2003), while that of the Pars profunda is described as horizontal (Liebich, König, and Maierl 2019) or vertical (Seiferle and Frewein 2003). According to Seiferle and Frewein (2003), the Pars superficialis and Pars profunda are clearly separated only near the temporomandibular joint, where the course of the Arteria and Vena transversa faciei indicates the border between these portions of the muscle. Based on this description, layers 1–3 as defined in our study might correspond to the so-called Pars superficialis, and layers 4–9 might reflect the Pars profunda.

In contrast to the heterogenous description of the equine masseter muscle in common anatomical textbooks, detailed investigations of the masseter musculature of a wide spectrum of different herbivores (including donkeys, horses, water deer, camels and giraffes) homogeneously report a multipennate muscular organisation (Khalifa and Daghsh 2010; Sasaki et al. 2001, 2013; Toldt 1905; Wally and Farag 2008). These authors reported their results using a terminology introduced by Yoshikawa et al. (1961, 1962), who conducted comparative morphological studies on the masseter musculature of different ungulates, including the horse, goat, sheep, cattle, sika deer, camel and nilgai. Aiming to establish a uniform terminology to describe the species-specific particularities of the masseter muscle, Yoshikawa et al. (1961) introduced the term ‘proper muscle’ and ‘improper muscle’. By definition, the proper muscle consists of five portions: the masseter superficialis muscle, which contains a lamina prima and a lamina secunda; the masseter intermedius muscle; and the masseter profundus muscle, which contains a pars anterior and a pars posterior. The improper muscle consists of two defined portions: the maxillomandibularis muscle and zygomaticomandibularis muscle (Yoshikawa et al. 1961). Altogether, Yoshikawa et al. (1961) reported the presence of seven muscular portions using a heterogenous nomenclature

without any delimiting definition of the terms ‘lamina’, ‘pars’ and ‘muscle’.

To describe the findings of our study, we propose the homogenous use of the term ‘layer’ for each individual portion of the masseter muscle. This appears to be justified by the generally homogenous structure of the individual layers, each of which was composed of a fleshy portion and a tendinous portion. Although the layers differed in size and thickness, no layer was separated by an all-embracing fascia or a distinct vascular or nerve supply that would justify the identification of a separate muscle.

Despite our proposal of a different terminology to distinguish specific portions of the masseter muscle, our study reveals general similarities with the findings of other authors concerning the structure of the masseter muscle in different herbivore species. Layers 1 and 8 in our study correspond to the lamina prima of the masseter superficialis muscle defined by Yoshikawa et al. (1961). Such observations were also made in the horse (Heinze 1963), donkey (Wally and Farag 2008), and giraffe (Sasaki et al. 2001). Layer 2 corresponds to the lamina secunda of the masseter superficialis muscle, and layer 3 corresponds to the masseter intermedius muscle described by Yoshikawa et al. (1961). Layer 6 exhibited distinct splitting into rostral and caudal parts, corresponding to the description of a division into the pars anterior and pars posterior of the masseter profundus by the masseteric nerve in several herbivore species (Wally and Farag 2008; Yoshikawa and Suzuki 1965). Layer 9 corresponds to the zygomaticomandibularis muscle described by Yoshikawa et al. (1961). However, layers 4, 5 and 7 cannot be clearly assigned to any of the muscular portions defined by Yoshikawa et al. (1961), and the maxillomandibularis muscle described by Yoshikawa et al. (1961) does not correspond to any layer identified in the present study. Therefore, the terminology suggested by Yoshikawa et al. (1961) does not consistently reflect the findings of the horses examined in our study.

In the horse, the masseter muscle is regarded as the strongest and most important muscle of the masticatory system (Kuryszko and Lyczewska-Mazurkiewicz 2004; Wally and Farag 2008). The masseter muscle is evolutionarily adapted to exert large forces of up to 1758 N on the molars, enabling effective disruption of fibre-rich roughage (Sasaki et al. 2001; Staszuk et al. 2006). Together with enlargement of the masseter muscle, the horse developed an elongated crista facialis and a well-developed masseteric fossa, providing sufficient space for a pronounced masseter muscle (Heinze 1963; Sasaki et al. 2001).

Five muscles that comprise the masticatory apparatus (M. pterygoideus medialis, M. pterygoideus lateralis, M. temporalis and M. digastricus along with its Pars occipitomandibularis) connect the mandible with cranial structures medial to the mandible (Seiferle and Frewein 2003). By contrast, only one muscle (the masseter muscle) connects the mandible with a cranial structure (the facial crest) located lateral to the mandible. This suggests that the masseter muscle is predominantly involved in movements of the complex equine chewing cycle, which have a lateral movement component. This does not exclude the possibility that other muscles, for example the contralateral medial pterygoid muscle, can contribute to sideways movements. The orientation and dimensions of the masseter muscle also imply its simultaneous involvement with a dorsal movement component. These functional considerations might explain the complex layered structure of the masseter muscle found in the present study. Chewing is a unilateral process in which one side of the mandible performs the actual grinding of the roughage (chewing or working side) while the other side follows the movements of the chewing side with no tooth-to-tooth contact (balancing side) (Staszuk et al. 2006; Bonin et al. 2006; Sterkenburgh et al. 2021). Because the equine Sutura intermandibularis is ossified and correspondingly immobile, finely tuned movements that act on the left and right sides of the mandible are necessary. The herein-described layered organisation of the masseter muscle supports the hypothesis that multiple divergent movements must be guaranteed. Yoshikawa and Suzuki (1965), Kuryszko and Lyczewska-Mazurkiewicz (2004) and Salomon (2020) argued along similar lines when discussing their findings of several portions of the masseter muscle. The following hypotheses are possible alternative explanations for the observed multi-layered organisation of the masseter muscle. The masseter muscle might be optimised for strength generation while the muscles on the medial side are responsible for the adjustment of delicate movements. Or else, the multiple layers might represent a morphological correlate of fatigue resistance. However, the detailed functional explanation of the multi-layered organisation of the M. masseter cannot be clearly elucidate using the available data but requires further studies.

To date however, only vague data have showed the actual separate contraction of individual masticatory muscle portions and the resulting different jaw movements (Williams et al. 2007). Notably, the origin of the individual layers is heterogeneous (either aponeurotic or fleshy). Whether this observation also has functional or biomechanical significance cannot be determined at this point.

There is agreement on the fact that the masseter muscle is exclusively innervated by the masseteric nerve (e.g., Yoshikawa

and Suzuki 1965; Böhme 2004). However, the herein demonstrated remarkably straight and constant course of the nerve as well as its step-by-step passage through the muscular tissue at constant positions was unexpected and has not been previously described.

From a terminological perspective, the consistently occurring bony ridges in the masseteric fossa, which have not been previously mentioned, must be recognised. All identified layers of the masseter muscle attach to one of these bony ridges or between them. Accordingly, the bony ridges are collectively referred to as 'Lineae massetericae'. To distinguish the individual bony ridges, the following anatomical terms are proposed:

“Linea masseterica dorsalis”, “Lineae massetericae centralis”, “Linea masseterica ventralis” and “Linea masseterica perpendicularis.”

When assigning the individual muscle layers to the individual Lineae massetericae, a certain distribution pattern consisting of three muscular layer groups becomes apparent. The superficial layer group consists of the most superficial layers 1, 2 and 3, which extend from the facial crest and Arcus zygomaticus to the entire length of the ventral rim of the Ramus mandibulae (i.e. the Linea masseterica ventralis). The profound caudal layer group consists of layers 4 and 5, the caudal part of layer 6, and layers 7 and 9. All these layers attach to portions of the Lineae massetericae located caudal to the Linea masseterica perpendicularis. By contrast, the rostral part of layer 6 and layer 8 attach rostrally to the Linea masseterica perpendicularis, representing the profound rostral layer group. Further morphological analyses show that the superficial layer group as well as the profound rostral group are represented by muscular layers with a notably longer extension than the muscular layers of the profound caudal layer group.

5 | Conclusion

The equine masseter muscle features a remarkably constant layered organisation and likewise a constant and particular course of the masseteric nerve. The identification and evaluation of these morphological conditions provides a solid basis for further studies with the aim of developing biomechanical concepts of equine masticatory movement.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Böhme, G. 2004. “Nervus Trigemini.” In *Lehrbuch der Anatomie der Haustiere: Nervensystem, Sinnesorgane, Endokrine Drüsen*, edited by R. Nickel, A. Schummer, and E. Seiferle, vol. 4, 4th ed., 305–321. Stuttgart: Parey.

- Bonin, S. J., H. M. Clayton, J. L. Lanovaz, and T. J. Johnson. 2006. "Kinematics of the Equine Temporomandibular Joint." *American Journal of Veterinary Research* 67, no. 3: 423–428. <https://doi.org/10.2460/ajvr.67.3.423>.
- Collinson, M. 1994. "Food Processing and Digestibility in Horses (*Equus caballus*)." MD thesis, Clayton, Monash University.
- Ellenberger, W., and H. Baum. 1894. "Kaumuskelgegend." In *Topographische Anatomie des Pferdes Kopf und Hals*, edited by Ellenberger and Baum, 110. Berlin: Parey.
- Heinze, W. 1963. "Die Morphologie der Kaumuskulatur des Pferdes." *Anatomischer Anzeiger* 113: 119–130.
- Khalifa, E. F., and S. M. Daghsh. 2010. "The Lamination and Arterial Blood Supply of the Masseter Muscle of Camel (*Camelus dromedarius*)." *Journal of Veterinary Anatomy* 3, no. 1: 92–93.
- Kölle, S., S. Reese, and C. Mülling. 2014. "Kopf." In *Atlas der Anatomie des Pferdes*, edited by K. D. Budras, C. Mülling, C. Pfarrer, S. Reese, and S. Kölle, 7th ed., 164–205. Hannover: Schlüter.
- König, H. E., P. Sotonyi, H. Schöpfer, and H. G. Liebich. 2019. "Verdauungsapparat." In *Anatomie der Haussäugetiere: Lehrbuch und Farbatlas für Studium und Praxis*, edited by H. E. König and H. G. Liebich, 7th ed., 329–394. Stuttgart: Thieme.
- Kuryszko, J. K., and S. Lyczewska-Mazurkiewicz. 2004. "Equine Masticatory Organ. Part III." *Acta of Bioengineering and Biomechanics* 6, no. 1: 25–30.
- Leyh, F. A. 1859. "Jochmuskel des Hinterkiefers." In *Handbuch der Anatomie der Haustiere*, edited by F. A. Leyh, 2nd ed., 246. Stuttgart: Ebner & Seubert.
- Liebich, H. G., H. E. König, and J. Maierl. 2019. "Faszien und Muskeln des Kopfes und Stammes." In *Anatomie der Haussäugetiere: Lehrbuch und Farbatlas für Studium und Praxis*, edited by H. E. König and H. G. Liebich, 7th ed., 135–166. Stuttgart: Thieme.
- Martin, M. T. 2007. *Guide for Determining the Age of the Horse*. 8th ed. Lexington: American Association of Equine Practitioners.
- Martin, P. 1914. "Unterkiefermuskeln." In *Lehrbuch der Anatomie der Haustiere*, edited by Leyh, 2nd ed., 163. Stuttgart: Schickhardt & Ebner.
- Muyllé, S., P. Simoens, and H. Lauwers. 1996. "Ageing Horses by an Examination of Their Incisor Teeth: An (Im)possible Task?" *Veterinary Record* 138, no. 13: 295–301. <https://doi.org/10.1136/vr.138.13.295>.
- Muyllé, S., P. Simoens, and H. Lauwers. 1999. "Age-Related Morphometry of Equine Incisors." *Journal of Veterinary Medicine Series A* 46, no. 10: 633–643. <https://doi.org/10.1046/j.1439-0442.1999.00261.x>.
- Nomina Anatomica Veterinaria. 2017. *International Committee on Veterinary Gross Anatomical Nomenclature (I.C.V.G.A.N.)*. 6th ed. Hanover, Ghent, Columbia, Rio de Janeiro: Nomina Anatomica Veterinaria. <https://www.wava-amav.org/wava-documents.html>.
- Popesko, P. 2011. "Pferd." In *Atlas der topographischen Anatomie der Haustiere*, edited by P. Popesko, 7th ed., 111–177. Stuttgart: Enke.
- Salomon, F. V. 2020. "Muskeln des Kopfes." In *Anatomie für die Tiermedizin*, edited by F. V. Salomon, H. Geyer, and U. Gille, 4th ed., 172–176. Stuttgart: Thieme.
- Sasaki, M., H. Endo, H. Kogiku, et al. 2001. "The Structure of the Masseter Muscle in the Giraffe (*Giraffa camelopardalis*)." *Anatomia, Histologia, Embryologia* 30, no. 5: 313–319. <https://doi.org/10.1046/j.1439-0264.2001.00342.x>.
- Sasaki, M., J. Kimura, J. Sohn, T. Nasu, N. Kitamura, and M. Yasuda. 2013. "The Lamination of the Masseter Muscle in the Water Deer (*Hydropotes inermis*)." *Mammal Study* 38, no. 2: 91–95. <https://doi.org/10.3106/041.038.0204>.
- Schultz, J. A., S. Engels, L. C. Schwermann, and W. von Koenigswald. 2020. "Evolutionary Trends in the Mastication Patterns in Some Perissodactyls, Cetartiodactyls, and Proboscideans." In *Mammalian Teeth—Form and Function*, edited by T. Martin and W. von Koenigswald, 1st ed., 215–230. München: T. Martin & W. v. Koenigswald.
- Seiferle, E. 1954. "Aktiver Bewegungsapparat, Muskelsystem, Myologia." In *Lehrbuch der Anatomie der Haustiere*, edited by R. Nickel, A. Schummer, and E. Seiferle, vol. 1. Bewegungsapparat, 1st ed., 269. Berlin, Hamburg: Parey.
- Seiferle, E., and J. Frewein. 1977. "Aktiver Bewegungsapparat, Muskelsystem, Myologia." In *Lehrbuch der Anatomie der Haustiere*, edited by R. Nickel, A. Schummer, and E. Seiferle, vol. 1, 4th ed., 280. Berlin, Hamburg: Parey.
- Seiferle, E., and J. Frewein. 2003. "Aktiver Bewegungsapparat, Muskelsystem, Myologia." In *Lehrbuch der Anatomie der Haustiere*, edited by R. Nickel, A. Schummer, and E. Seiferle, vol. 1, 8th ed., 323–332. Stuttgart: Parey.
- Staszuk, C., F. Lehmann, A. Bienert, K. Ludwig, and H. Gasse. 2006. "Measurements of Masticatory Forces in the Horse." *Pferdeheilkunde* 22, no. 1: 12–16. <https://doi.org/10.21836/PEM20060102>.
- Sterkenburgh, T., E. Schulz-Kornas, M. Nowak, and C. Staszuk. 2021. "A Computerized Simulation of the Occlusal Surface in Equine Cheek Teeth: A Simplified Model." *Frontiers in Veterinary Science* 8: 789133. <https://doi.org/10.3389/fvets.2021.789133>.
- Sterkenburgh, T. R., B. Hartl, C. Peham, M. Nowak, M. Kyllar, and S. Kau. 2023. "Temporomandibular Joint Biomechanics and Equine Incisor Occlusal Plane Maintenance." *Frontiers in Bioengineering and Biotechnology* 11: 1249316. <https://doi.org/10.3389/fbioe.2023.1249316>.
- Toldt, C. 1905. "Der Winkelfortsatz des Unterkiefers beim Menschen und bei den Säugetieren und die Beziehung der Kaumuskulatur zu demselben." *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe K1*, no. 114: 315–476.
- Wally, Y., and F. Farag. 2008. "The Lamination and Arterial Blood Supply of the Masseter Muscle in the Donkey." *Journal of Veterinary Anatomy* 1, no. 1: 38–47. <https://doi.org/10.21608/jva.2008.45453>.
- Williams, S. H., C. J. Vinyard, C. E. Wall, and W. L. Hylander. 2007. "Masticatory Motor Patterns in Ungulates: A Quantitative Assessment of Jaw-Muscle Coordination in Goats, Alpacas and Horses." *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology* 307, no. 4: 226–240. <https://doi.org/10.1002/jez.362>.
- Wissdorf, H., and B. Otto. 2010. "Kopf-Hals-Bereich." In *Praxisorientierte Anatomie und Propädeutik des Pferdes*, edited by H. Wissdorf, H. Gerhards, B. Huskamp, and E. Deegen, 3th ed., 73. Hannover: Schaper.
- Yoshikawa, T., and T. Suzuki. 1965. "The Comparative Anatomical Study of the Masseter of the Mammal (II)." *Okajimas Folia Anatomica Japonica* 40: 339–363. https://doi.org/10.2535/ofaj1936.40.4-6_339.
- Yoshikawa, T., T. Suzuki, R. Kiuchi, and H. Matsuura. 1961. "The Comparative Anatomy of the Musculus Masseter of the Mammals." *Acta Anatomica Nippon* 36: 53–71.
- Yoshikawa, T., T. Suzuki, R. Kiuchi, and H. Matsuura. 1962. "The Lamination of the Masseter of the Ruminantia." *Acta Anatomica Nippon* 37: 430–442.