Received: 20 July 2022 | Accepted: 22 July 2022

DOI: 10.1111/ahe.12849

ORIGINAL ARTICLE

Anatomia Histologia Embryologia WILEY

The graviportal spine: Epaxial muscles of the African savanna elephant (*Loxodonta africana*)

Caroline Maria Victoria Birgfellner[1] | **John Thomson Soley**[2] | **Eva Polsterer**[1] | **Gerhard Forstenpointner**[1] | **Gerald Erwin Weissengruber**[1]

[1]Institute of Morphology, University of Veterinary Medicine, Vienna, Austria

[2]Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, South Africa

Correspondence
Caroline Maria Victoria Birgfellner, Institute of Morphology, University of Veterinary Medicine, Vienna, Austria.
Email: caroline@birgfellner.com

Funding information
International Relations Office of the University of Veterinary Medicine, Vienna, Austria

Abstract

In this study, we present not only a new and detailed anatomical description of the epaxial muscles and adjacent ligamentous and fascial structures in the African savanna elephant but also a structural and functional comparison with other Afrotherian mammals and some domestic quadrupeds. All structures were examined by means of standard anatomical techniques. The back of the largest land mammal is a crucial part of trunk construction according to the bow and string concept, which is applied also in other quadrupedal animals. The epaxial muscles of the African savanna elephant play an important role in the biomechanical properties of the entire back and in supporting and moving the heavy head. Situated in the short cervical region of the African savanna elephant is a large mass comprised of numerous muscle individuals together with a well-developed ligamentum nuchae. Parts of the mm. interansversarii ventralis cervicis form a strong muscle belly, which was named the m. intertransversarius longus. Whereas the head is held in a high or extended position most of the time during locomotion, the head and neck are highly mobile while the animal is foraging or socially interacting. Movements between the elements of the thoracic and lumbar spine are likely to be very limited due to the obvious rigidity of the bony vertebral column. Aponeuroses surrounding long epaxial muscles could contribute to an energy-saving mechanism, which is active during both stance and locomotion. The well-developed m. serratus dorsalis cranialis helps in facilitating effective breathing in an animal, which is equipped with an unusual pleural structure.

KEYWORDS
musculi dorsi, Proboscidea, vertebral column

1 | INTRODUCTION

Elephants belong to the taxonomic order Proboscidea within the clade Afrotheria and are closely related to the orders Sirenia (manatees and dugong) and Hyracoidea (hyraxes). The mammalian group Afrotheria encompasses other orders that differ morphologically (e.g., Tubulidentata or Afrosoricida) and for which anatomical data regarding soft tissues are not available (De Jong, 1998; Kuntner et al., 2011; Puttick & Thomas, 2015; Shoshani, 1986; Wilson & Reeder, 2005). The family Elephantidae within the order Proboscidea comprises one Asian and two African species. The existence of two species of African elephants has been disputed, but recent genetic investigations show that a distinction between the African forest (*Loxodonta cyclotis*) and the African savanna elephant (*Loxodonta africana*) is evident (Wittemyer, 2011). Although members of the elephant family have been represented artistically since the Stone Age, reliable scientific data regarding their anatomy are rare. One of the first detailed studies dealing with the locomotor apparatus dates back to the 17th century (Moulin, 1682). Most anatomical studies have focused on the Asian (Indian) elephant. Eales (1926, 1928, 1929) was the first author to describe anatomical structures in the African elephant followed by other groups of researchers (e.g., Shoshani & Marchant, 2001; Smuts & Bezuidenhout, 1993; Weissengruber et al., 2005). Predominantly, paleontological studies were not taken into consideration for this study. African savanna elephants are the largest terrestrial mammals. Since size is related to metabolic rate, a large body size is beneficial for elephants. Some reports state that male individuals can weigh up to 10,000 kg (Langman et al., 1995; Laws, 1966, Panagiotopoulou et al., 2016; Wittemyer, 2011). This enormous body size results in the manifestation of special features such as type of locomotion and structure of the limbs, which has been described in the literature (e.g., Hutchinson et al., 2006; Nagel et al., 2018). As it forms a central part of the bow and string concept of quadrupedal trunk construction, the vertebral column plays a distinctive role either in body support during the stance phase or in locomotion. In African and Asian elephants, anatomical data on this part of the active locomotor system are scarce. The main aim of the present study is to describe the major parts of the muscular system and associated fascial elements of the vertebral column of the African savanna elephant. The findings will not only complement our knowledge of the body structure of African elephants but will also allow relevant functional comparisons to be made between elephants, some species of closely related taxonomic orders and some domestic mammals.

2 | MATERIALS AND METHODS

Four juvenile African elephants were dissected using gross anatomical techniques. The heads, necks and trunks of three individuals and the head and neck of one individual were sourced from formalin-fixed animals in the collection of the Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, South Africa. Dissection of the preserved material was carried out using the facilities of the above institution. The elephants had been obtained from the Kruger National Park, South Africa, during the regular culling programme in the 1990s. Shortly after death, the animals were exsanguinated in the National Park and perfused with 10% formalin via the common carotid artery. The anatomical terminology used in the present study is based on that of Nomina Anatomica Veterinaria (2017).

3 | RESULTS

3.1 | Fascial elements of the back region

The epaxial muscles of the cervical, thoracic and the lumbar regions were covered by thick skin and branching layers of the fascia thoracolumbalis (Figure 1-1,8a). In the specimens dissected, this fascial structure was divided by layers of yellowish adipose tissue and muscles into superficial, deep and intermediate layers the latter of which varied in number. The fascia thoracolumbalis originated from the processus spinosi of the thoracic, lumbar and sacral vertebrae and via a tendon from the tuber sacrale. The superficial layer was situated close to the skin.

The cranial part of the fascia thoracolumbalis (caudal part of the neck to mid-thorax) consisted of a superficial, deep and several intermediate layers diverging between the mm. erector spinae, trapezius, latissimus dorsi and serratus dorsalis. The cranial part also attached to the medial surface of the scapula and to the funiculus nuchae.

The caudal part of the fascia thoracolumbalis (mid-thorax to os sacrum and tuber sacrale) showed only the three basic layers. A tendon-like band structure originating from the tuber sacrale and running between the mm. iliocostalis and longissimus (for abbreviated muscle names see below) formed the deep layer (Figures 1,2-8a) which fused at almost right angles with the overlying intermediate layer (Figure 2-8b). The latter covered the mm. spinalis et semispinalis, longissimus and iliocostalis laterally and attached on the procc. spinosi of the thoracic and lumbar vertebrae and the ribs. The horizontally oriented deep layer inserted via short tendinous strips ventral to the tubercula costae on the 5th to the last rib.

3.2 | Ligamentum nuchae, withers cap, ligamentum supraspinale

The well-developed ligamentum nuchae was composed of a paired tendon-like funiculus nuchae and a paired lamina nuchae.

The thick funiculus nuchae was circular in cross-section and had its origin on a dorsomedial area of the squama occipitalis (Figure 4-18,so). The widest diameter of the funiculus nuchae occurred at the level of the atlas and axis (Figure 3-18a). It was divided vertically along its length by a thin septum-like layer of loose connective tissue. The m. splenius capitis (Figure 1-4) originated via a fascial sheet on its dorsolateral surface and covered the funiculus laterally. The various other mm. capitis and the lamina nuchae were located ventral to the funiculus. The funiculus nuchae inserted at the dorsal tip of the processus spinosus of the 2nd to the 5th thoracic vertebra forming a withers cap (Figures 2,3-18b). Caudally, the withers cap fused with the ligamentum supraspinale (Figure 2-18c).

The paired lamina nuchae (Figure 3-18d) arose as several portions from the lateral surfaces of the processus spinosus of the 2nd to the 7th cervical vertebra and inserted on the ventral surface of the funiculus nuchae or the withers cap, respectively, and on the processus spinosus of the 1st thoracic vertebra.

3.3 | Epaxial musculature

3.3.1 | M. serratus dorsalis cranialis

The flattened fleshy bellies of this serratus muscle (Figures 1,2-2) arose from the superficial layer of the fascia thoracolumbalis, extending

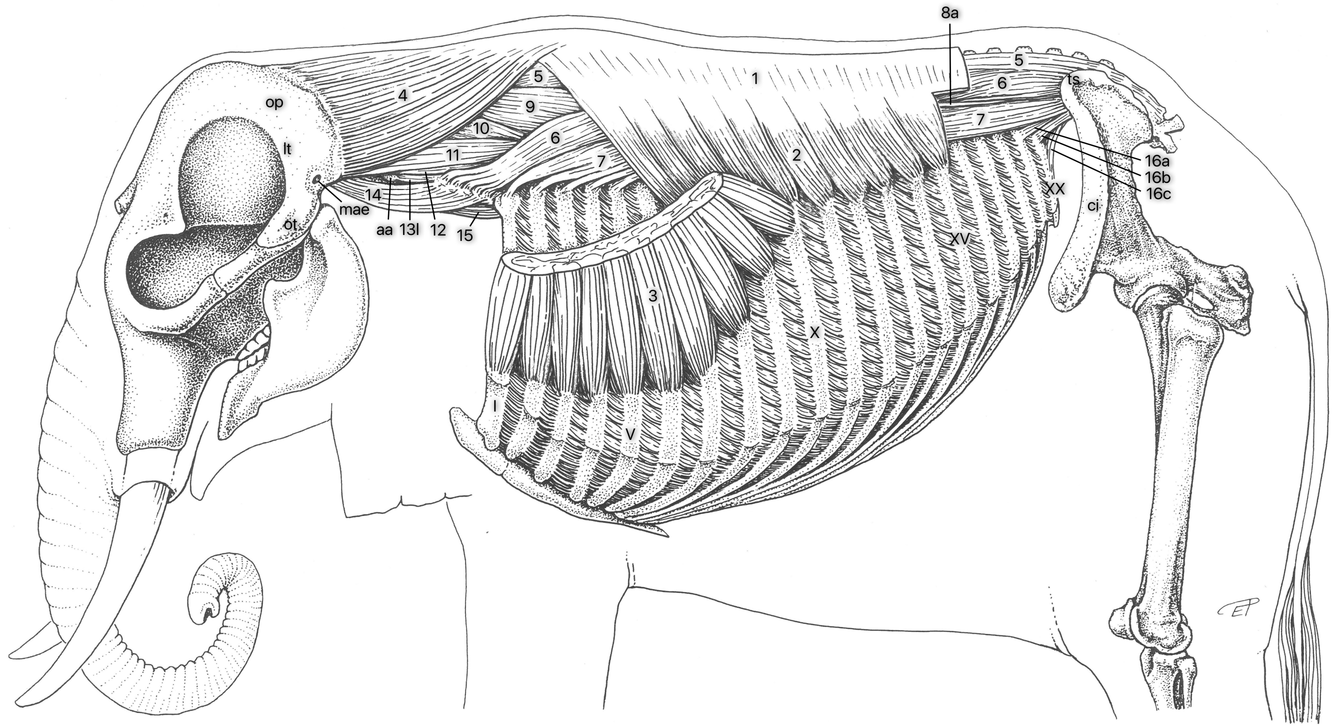

FIGURE 1 Superficial layer of epaxial muscles extending between the occiput and sacrum in the African savanna elephant. Left body side, lateral view. Skin, front limb including muscles, adipose tissue, superficial layer and parts of the deep layer of the fascia thoracolumbalis, mm. capitis, mm. olli (except m. longus colli), mm. hyoidei, m. trapezius, m. rhomboideus capitis, m. latissimus dorsi, parts of mm. serrati, mm. thoracis, abdominis, caudae and membri pelvini removed. 1: Superficial layer of the fascia thoracolumbalis (caudal aspect removed), 2: m. serratus dorsalis cranialis, 3: m. serratus ventralis thoracis (partially removed), 4: m. splenius capitis, 5: m. spinalis et semispinalis thoracis et cervicis, 6: m. longissimus lumborum, thoracis et cervicis, 7: m. iliocostalis lumborum et thoracis, 8a: deep layer of fascia thoracolumbalis, 9: m. biventer cervicis, 10: m. complexus, 11: m. longissimus capitis, 12: m. longissimus atlantis, 13 l: m. intertransversarius longus, 14: m. longus capitis, 15: m. longus colli, 16 a, b, c: m. retractores costae of the 19th and 20th rib. I, V, X, XV, XX: ribs numbered, ci: crista iliaca, lt: linea temporalis, mae: meatus acusticus externus, op: os parietale, ot: os temporale, ts: tuber sacrale.

from the 6th to the 16th thoracic vertebra. The bellies were covered medially by the intermediate fascial layer.

A thick ligamentum dorsoscapulare which was partly embedded in the so-called m. serratus profundus (Figure 2-17; Trenkwalder, 2013) was located at the cranial border of the m. serratus dorsalis cranialis. The ligamentum dorsoscapulare extended from the processus spinosus of the 2nd and 3rd thoracic vertebrae to the dorsomedial surface of the scapula.

The serratus dorsalis cranialis muscle revealed approximately ten bellies. Cranioventral parts of the muscle were covered by the m. serratus ventralis thoracis (Figure 1-3) and craniodorsally by the m. rhomboideus cervicis et thoracis.

The bellies of the m. serratus dorsalis cranialis inserted on the 8th to the 15th rib at the transition from the dorsal to the middle third. A short distance before their insertion on the ribs, numerous veins were situated between the bellies and embedded in subcutaneous tissue.

3.3.2 | M. iliocostalis lumborum et thoracis (abbreviated in text as M. iliocostalis)

This muscle revealed several origins. The m. iliocostalis displayed a thin and fleshy origin, together with the m. retractor costae of the 19th rib, from the dorsal quarter of the crista iliaca (Figures 1,2-7,16a). The m. iliocostalis was fused with the m. longissimus and also originated with the latter from the tuber sacrale. Furthermore, the m. iliocostalis displayed a fleshy origin from the caudal edge of the angulus costae of the 19th to the 5th thoracic rib.

Several cranioventrally directed tendinous strips from the deep layer of the fascia thoracolumbalis inserted dorsally on the iliocostalis muscle.

The m. iliocostalis covered parts of the ribs, the mm. intercostales externi, levatores costarum and retractores costae laterally. The m. longissimus was related to the dorsal surface of the iliocostalis muscle.

The iliocostalis muscle was composed of overlapping muscle fibre bundles that bridged the intercostal spaces in a craniolateroventral direction. The bundles inserted via tendinous slips ventral to the tubercula costae of the 14th to the 4th rib. The bundles were thickest in the cranial thoracic region. Bundles bridging three to four intercostal spaces were found cranial and caudal to the 8th rib. Thin tendinous strips originating on the medial surface of the iliocostalis muscle inserted on the caudal margin of the last to the 14th rib.

The cranial tendinous strips of the m. iliocostalis inserted on the caudal edge of the processus transversus of the 1st, 2nd and 3rd

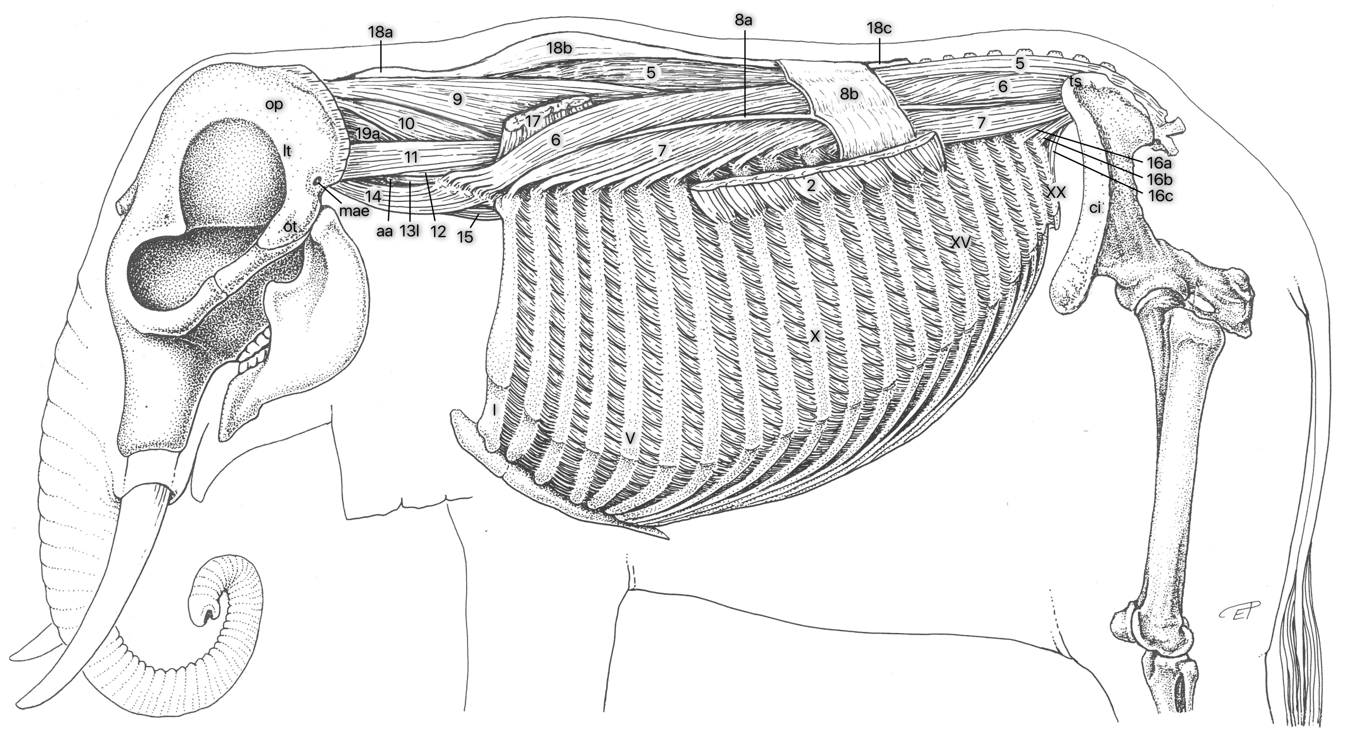

FIGURE 2 Mid-layer of epaxial muscles in the African savanna elephant. Left side of body, lateral view. Mm. splenius capitis and serratus ventralis thoracis removed. 2: m. serratus dorsalis cranialis (partially removed), 5: m. spinalis et semispinalis thoracis et cervicis, 6: m. longissimus lumborum, thoracis et cervicis, 7: m. iliocostalis lumborum et thoracis, 8a: deep layer of the fascia thoracolumbalis, 8 b: intermediate layer of the fascia thoracolumbalis (cranial and caudal aspects removed), 9: m. biventer cervicis, 10: m. complexus, 11: m. longissimus capitis, 12: m. longissimus atlantis, 13 l: m. intertransversarius longus, 14: m. longus capitis, 15 m. longus colli, 16 a, b, c: m. retractores costae of the 19th and 20th rib, 17: m. serratus profundus, 18 a: funiculus nuchae, 18 b: withers cap, 18 c: lig. supraspinale, 19 a: m. obliquus capitis cranialis. I, V, X, XV, XX: ribs numbered, ci: crista iliaca, lt: linea temporalis, mae: meatus acusticus externus, op: os parietale, ot: os temporale, ts: tuber sacrale.

thoracic vertebra and on the corresponding tubercula costae. The strip to the 1st thoracic vertebra fused with an additional one originating from the m. longissimus.

The m. iliocostalis cervicis was absent.

3.3.3 | M. longissimus lumborum, thoracis et cervicis (abbreviated in the text as m. longissimus)

The major part of the longissimus complex extended from the os ilium to the skull in the form of caudocranially oriented fibre bundles (Figures 1,2-6). It consisted of the mm. longissimi lumborum, thoracis and cervicis. The mm. longissimi capitis and atlantis are described separately.

The m. longissimus can be described as a single muscle with a broad and fleshy origin from the medial aspect of the tuber sacrale together with the m. iliocostalis and the deep layer of the fascia thoracolumbalis. The m. gluteus medius originated partly from the m. longissimus. Other areas of origin were located on the processus transversi, mamillares and spinosi of all lumbar and caudal thoracic vertebrae as well as from the cranial part of the os sacrum where the m. longissimus (Figures 1,2-6) was fused with the m. spinalis et semispinalis (Figures 1,2-5). The extent of this fusion varied from individual to individual. The origins of the m. longissimus on all lumbar vertebrae were fleshy, those on the processus transversi of the last to the 12th thoracic vertebra tendinous. Fleshy strips of the muscle also originated from the processus spinosus of the 7th thoracic to the 4th cervical vertebra.

The m. longissimus was accompanied ventrolaterally by the m. iliocostalis. In the lumbar region, the m. longissimus and the m. spinalis et semispinalis were covered laterally by an aponeurosis. From the 7th to the 19th rib, several thin tendinous strips covered the m. longissimus medially. These strips bridged up to three segments and inserted tendinously on the processus mamillares of the 12th to the 1st thoracic vertebra. At the transition from thorax to collum, the main part of the muscle turned into a tendon and inserted on the tubercula dorsalia of the 7th to the 3rd cervical vertebra.

3.3.4 | M. longissimus capitis

This flattened muscle (Figures 1,2-11) was covered by a thin aponeurosis and arose via a tendon from the processus articularis cranialis of the 1st thoracic vertebra and from the processus articularis caudalis of the last cervical vertebra. Furthermore, it had fleshy origins

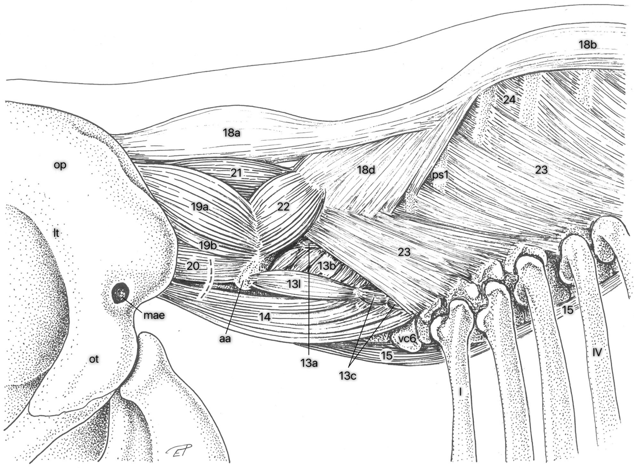

FIGURE 3 Deep muscles of the neck and cranial thoracic region in the African savanna elephant. Left side of body, lateral view. Fasciae, mm. iliocostalis, longissimi, spinalis et semispinalis, biventer cervicis, complexus removed. 13 a: mm. intertransversarii dorsales cervicis, 13 b: mm. intertransversarii medii cervicis, 13 c: mm. intertransversarii ventrales cervicis, 13 l: m. intertransversarius longus, 14: m. longus capitis, 15: m. longus colli, 18 a: funiculus nuchae, 18 b: withers cap, 18 d: lamina nuchae, 19 a: m. obliquus capitis cranialis, 19 b: m. rectus capitis lateralis, 20: m. rectus capitis ventralis, 21: m. rectus capitis dorsalis, 22: m. obliquus capitis caudalis, 23: mm. multifidi, 24: mm. interspinales. I, IV: ribs numbered, aa: ala atlantis, lt: linea temporalis, mae: meatus acusticus externus, op: os parietale, ot: os temporale, ps 1: processus spinosus of 1st vertebra thoracica, vc 6: Lamina ventralis of 6th vertebra cervicalis. Broken line indicates the articular space between the condylus occipitalis and the atlas.

from the ventral surface of the processus articularis cranialis of the 7th to the 2nd cervical vertebra.

The m. longissimus capitis inserted on the skull medial to the opisthokranion (Schopf, 2010). The area of insertion (Figure 4-11) was situated medially to that of the m. splenius capitis (Figure 4-4) and laterally to that of the fused mm. obliquus capitis cranialis, rectus capitis ventralis and rectus capitis lateralis (Figure 4-19a,b,20). In the smallest individual examined, the areas of insertion of the m. longissimus capitis and the mm. obliquus capitis cranialis, rectus capitis ventralis and rectus capitis lateralis were fused.

3.3.5 | M. longissimus atlantis

This small muscle arose from the processus articularis cranialis of the 7th cervical vertebra and ran ventromedially to the m. longissimus capitis (Figures 1,2-12). Caudally, both muscles were covered laterally by a common aponeurosis.

The m. longissimus atlantis inserted via a thin tendon on the ala atlantis. This tendon was situated ventral to the insertion of the m. obliquus capitis caudalis. The m. longissimus atlantis was fused medially with the mm. intertransversarii dorsalis cervicis (Figure 3-13a).

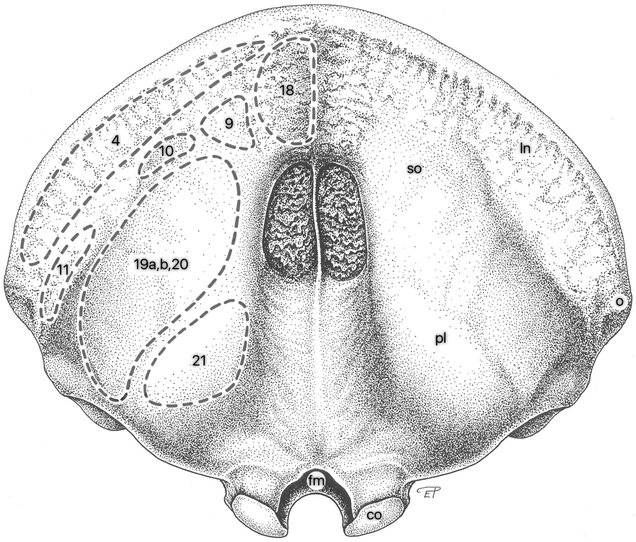

FIGURE 4 Attachments of epaxial muscles and the ligamentum nuchae on the cranium in the African savanna elephant. Caudal view. 4: m. splenius capitis, 9: m. biventer cervicis, 10: m. complexus, 11: m. longissimus capitis, 18: lig. nuchae (funiculus nuchae), 19 a, b, 20: common insertion of the mm. obliquus capitis cranialis, rectus capitis lateralis and rectus capitis ventralis, 21: m. rectus capitis dorsalis. co: condylus occipitalis, fm: foramen magnum, ln: linea nuchae, o: opisthokranion (Schopf, 2010), pl: pars lateralis, so: squama occipitalis.

3.3.6 | M. spinalis cervicis

The m. spinalis cervicis was situated medially to the mm. semispinales cervicis and capitis. It was divided noticeably into three parts bridging the spaces between the processus spinosi of the 2nd thoracic, the 1st thoracic and the 7th cervical vertebra. Variations in the number of clearly visible parts were observed. The m. spinalis cervicis was accompanied by the mm. multifidi (Figure 3-23) and parts of the muscle were attached laterally to the cervical part of the m. spinalis et semispinalis (abbreviation—see below).

3.3.7 | M. spinalis thoracis et semispinalis thoracis et cervicis (abbreviated in the text as m. spinalis et semispinalis)

The components of the m. spinals et semispinalis (Figures 1,2-5) formed a uniform muscle mass, which extended craniocaudally lateral to the processus spinosi of the sacral, lumbar and thoracic vertebrae. In the sacral area, the muscle merged with the tail muscles.

The m. spinalis et semispinalis originated from the processus spinosus of the 1st and 2nd sacral vertebrae and together with the m. longissimus (Figures 1,2-6) from the processus transversi of the first sacral vertebra. In one, individual examined a single muscle strip originated from the m. gluteus medius.

Several tendinous strips had their origins on the ligamentum supraspinale and on the processus mamillares of all lumbar and the last to the 14th thoracic vertebrae. In two individuals, fusion with the m. longissimus was observed to start in the region of the 12th thoracic vertebra whereas in the other specimens it occurred further caudally. The middle and caudal parts of the m. spinals et semispinalis covered the m. longissimus medially, dorsally and to a lesser extent laterally. These parts were also fused with the medially situated mm. multifidi (Figure 3-23). The craniomedial part of the m. spinalis et semispinalis corresponded to the m. semispinalis cervicis (NAV, 2017). This flattened component originated tendinously from the remaining mass of the m. spinalis et semispinalis in the vicinity of the cranial thoracic vertebrae. Further cranially, it became fleshy and was covered laterally by a thin aponeurosis. The craniomedial part of the m. spinalis et semispinalis inserted with fleshy attachments on the processus spinosi of the 7th cervical to the 2nd thoracic vertebra.

The main muscle mass of the m. spinalis et semispinalis inserted tendinously on the dorsal aspect of the processus spinosi of the cranial thoracic vertebrae with the exception of the 1st, on the withers cap (Figures 2,3-18b) and on the cranial part of the lig. supraspinale (Figure 2-18c).

3.3.8 | M. semispinalis capitis

This broad muscle consisted of two parts, the dorsomedial m. biventer cervicis (Figures 1,2,4-9) and the ventrolateral m. complexus (Figures 1,2,4-10) both of which originated together. The two parts of the muscle were fused in the cranial part of the thorax.

3.3.9 | M. biventer cervicis

The mm. biventer cervicis and complexus (Figures 1,2,4-9,10) had a predominantly tendinous origin from the processus transversus of the 14th thoracic vertebra, whereas fleshy strips originated from the 1st to the 13th thoracic vertebra. Cranially, both muscles originated together from the processus articulares cranialis and caudalis of the last cervical vertebra. Caudoventrally, the m. biventer cervicis was covered by the m. longissimus (Figures 1,2-6). The m. spinalis et semispinalis (Figures 1,2-5) was situated medial to the m. biventer cervicis. The m. biventer cervicis covered the lateral surface of the ligamentum nuchae (Figures 2,3,4-18a,18c) and the mm. rectus capitis dorsalis (Figure 3-21), obliquus capitis caudalis (Figure 3-22) and multifidi (Figure 3-23).

The m. biventer cervicis revealed a lateral aponeurosis, which made contact with two thin tendons within the dorsal third of the muscle. These tendons were u-shaped in cross-section and extended craniocaudally.

The biventer muscle was broad at its origin and converged towards its fleshy insertion on the os occipitale between the median plane, the linea nuchae (Figure 4-ln) and the squama occipitalis (Figure 4-so). The point of insertion of the m. biventer (Figure 4-9) was located lateral to that of the lig. nuchae (Figure 4-18), ventral to the medial aspect of the m. splenius capitis (Figure 4-4), medial to the m. complexus (Figure 4-10) and dorsal to the fused mm. obliquus capitis cranialis, rectus capitis ventralis and rectus capitis lateralis (Figure 4-19a,b,20).

3.3.10 | M. complexus

This muscle (Figures 1,2-10) was partly fused with the m. biventer (Figures 1,2-9). The m. complexus displayed fleshy origins from the dorsolateral aspect of the processus articulares craniales and caudales of the 6th to the 4th cervical vertebra.

It inserted (Figure 4-10) rather tendinously on the os occipitale between m. splenius capitis (Figure 4-4) and the fused mm. obliquus capitis cranialis, rectus capitis ventralis and rectus capitis lateralis (Figure 4-19,a,b,20).

3.3.11 | Mm. multifidi

This group of small muscles (Figure 3-23) was located along the cervical, thoracic and lumbar vertebrae. The mm. multifidi were fused with the m. spinalis et semispinalis and the m. spinalis cervicis.

The mm. multifidi originated on the os sacrum and on the processus mamillares and articulares of the lumbar, thoracic and caudal cervical vertebrae, coursed in a dorsocranial direction over two (lumbar region) to five (cervical region) segments and terminated on the processus spinosi up to the axis.

3.3.12 | Mm. rotatores

These muscle bundles lay deep to the mm. multifidi and coursed from the processus transversi to the processus spinosi of the 7th cervical to the 12th thoracic vertebra.

3.3.13 | Mm. interspinales

These muscles coursed between the processus spinosi of the caudal cervical and all thoracic vertebrae (Figure 3-24).

3.3.14 | Mm. intertransversarii

In the specimens investigated for the present study, the mm. intertransversarii thoracis and lumborum were absent.

The mm. intertransversarii on the neck could be divided into three groups. The thin and longitudinally orientated mm. intertransversarii dorsales cervicis (Figure 3-13a) coursed between the processus articulares craniales of the 1st thoracic vertebra to the processus articulares caudales of the 3rd cervical vertebra. Laterally, they were fused with the m. longissimus atlantis (Figures 1,2-12).

The mm. intertransversarii medii cervicis (Figure 3-13b) originated at the processus articulares craniales of the 7th to the 3rd cervical vertebra and coursed in a cranioventral direction from segment to segment. The cranial muscle of this group inserted on the processus transversus of the axis.

The mm. intertransversarii ventrales cervicis (Figure 3-13c) coursed horizontally between the processus transversi of all cervical vertebrae. Lateral parts of the muscles between the processus transversus of the 4th cervical vertebra and the ventrocaudal edge of the ala atlantis (Figure 3-aa) formed a uniform muscle belly, which we named the m. intertransversarius longus (Figures 1,2,3-13l; see Seiferle & Frewein, 2004).

3.4 | Musculi capitis

3.4.1 | M. obliquus capitis cranialis

This thick muscle (Figures 2,3-19a) arose from the laterodorsal edge of the arcus dorsalis and the ala atlantis (Figure 3-aa) and coursed craniodorsally. It was fused lateroventrally with the smaller m. rectus capitis lateralis.

3.4.2 | M. rectus capitis lateralis

The small m. rectus capitis lateralis (Figure 3-19b) arose from the lateral edge of the ala atlantis and accompanied the m. obliquus capitis cranialis.

3.4.3 | M. rectus capitis ventralis

This muscle (Figure 3-20) had its own area of origin laterally on the ala atlantis and the arcus ventralis atlantis.

Cranially, all three muscles mentioned above were fused and inserted together on a large central area of the squama occipitalis (Figure 4-19a,b,20).

3.4.4 | M. rectus capitis dorsalis

The undivided m. rectus capitis dorsalis (Figure 3-21) had its origin on the processus spinosus of the axis and the tuberculum dorsale of the atlas. The muscle had a broad and fleshy insertion (Figure 4-21) caudoventrally on the occiput, at the squama occipitalis and the pars lateralis of the os occipitale (Figure 4-so,pl).

3.4.5 | M. obliquus capitis caudalis

This strong muscle (Figure 3-22) coursed obliquely from the processus spinosus and the lateral edge of the processus articularis caudalis of the axis to the dorsal surface of the ala atlantis.

3.4.6 | M. longus capitis

This muscle (Figures 1,2,3-14) arose from the processus transversus of the 3rd to the 6th cervical vertebra and inserted ventrally on the pars basilaris of the os occipitale. It was situated ventrolaterally to the m. longus colli (Figures 1,2,3-15).

3.5 | Musculi colli

3.5.1 | M. splenius capitis

This large and fan-shaped muscle (Figure 1-4) originated from a broad fascial sheet, which was longitudinally attached to the funiculus nuchae (Figures 2,3-18a). At a point corresponding to the position of the 2nd thoracic vertebra, this fascial sheet merged with the intermediate layer of the fascia thoracolumbalis (Figure 2-8b). Medially, the muscle was covered by an aponeurosis.

The m. splenius capitis inserted caudally on the linea nuchae (Figure 4-ln) between the planum medianum and the opisthokranion (Schopf, 2010; Figure 4-o).

A m. splenius cervicis was absent.

3.5.2 | M. longus colli

The m. longus colli (Figures 1,2,3-15) originated in bundles from the ventral surfaces of the cranial six thoracic vertebrae and the ventral surfaces of the corpora and processus transversi of the 3rd to the 6th cervical vertebra. The bundles coursed cranially and terminated ventrally on the 5th thoracic to the 1st cervical vertebra in a plait pattern. On the cranial half of the neck, the m. longus colli merged laterally with the m. longus capitis (Figures 1,2,3-14).

3.6 | M. retractor costae

In African elephants, 20 or 21 ribs are present. Depending on the number of ribs, either the 20th or the 21st rib was a costa fluctuans.

The m. retractor costae could be divided longitudinally into three separate muscles, each of which arose dorsally from the os ilium and inserted on the caudal edges of the last ribs. The muscle to the 19th rib (Figures 1,2-16a) fused with the caudoventral aspect of the m. iliocostalis (Figures 1,2-7) and coursed in a cranioventral direction to its insertion on the proximal portion of the corresponding rib.

The m. retractor costae of the 20th rib (Figures 1,2-16b) was unclearly divided into three parts which arose from the crista iliaca and the tuber sacrale. This muscle contacted the deep layer of the fascia thoracolumbalis (Figures 1,2-8a) and coursed horizontally. In individuals with 20 ribs only, the third retractor muscle (designated as retractor of the costa fluctuans; Figures 1,2-16c) also inserted on the 20th rib. This m. retractor costae of the costa fluctuans arose ventral to the other retractors and coursed almost vertically along the last rib.

4 | DISCUSSION

As this study revealed only minor deviations in the structure of the epaxial musculature between the African and the Asian elephant, the discussion is confined to the relevant differences. In the literature, no relevant data are available on the Forest elephant (*Loxodonta cyclotis*). As far as could be ascertained the specimens dissected in the present study represented the Savanna elephant (*Loxodonta africana*). The muscles examined were compared with the findings of Mayer (1847), Miall and Greenwood (1878), Shindo and Mori (1956), Boas and Paulli (1908), Shoshani and Marchant (2001), Mariappa (2005) and Marchant and Shoshani (2007) in the Asian elephant, as well as with the findings of Eales (1926, 1928, 1929) and Marchant and Shoshani (2007) in the African Savanna species. Comparisons were made to closely related orders such as manatees, the dugong and Hyrax capensis where anatomical findings were available. Additionally, our findings were compared with domestic ruminants and the horse mainly for further clarification of functional aspects. As no relevant anatomical descriptions are presented in the literature on the fascia thoracolumbalis of the elephant, it was not possible to compare our findings in the specimens examined. The insertions of fascial elements on the ribs and tuber sacrale noted in the present study is also found in horses (Seiferle & Frewein, 2004), but the extraordinary thickness and the occurrence of more than two layers are not described in other mammals. It can be assumed that this large fascial structure supports the muscular system. It covers and encases some muscles of the back and the frontlimb, forms muscle compartments, functions as muscle attachments to bones and most probably helps in storing energy. Although in elephants diseases affecting the locomotor system occur (Richman et al., 2014; West, 2006; Wiedner & Schmitt, 2009), we could not detect any pathologic alterations in the specimens studied. In the Proboscidea, including the African savanna elephant, and other land mammals, individual components of the epaxial muscle system form a single muscle (Eales, 1926, 1928, 1929; Seiferle & Frewein, 2004; Shindo & Mori, 1956). In the aquatic Sirenia, most epaxial muscles are fused forming a continuous muscle mass between the occiput and the tail. The occurrence of this fusion could be explained by the shortening of the neck and the lack of hind limbs (Domning, 1977, 1978). In the elephants studied, the mass and number of epaxial muscle was greatest in the cervical region. This is a common finding in land mammals, because the number of discernible muscles and spinal mobility generally is increased towards the head (Schaller, 2007; Seiferle & Frewein, 2004).

It can be assumed that, in elephants, the strongly developed m. serratus dorsalis cranialis has an inspiratory function as in other mammals (Seiferle & Frewein, 2004) and would contribute to effective breathing. In elephants, according to our findings and those in the literature (Eales, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956), a m. serratus dorsalis caudalis is missing. During inspiration, the m. serratus dorsalis cranialis pulls the rib cage, the pleura and the attendant lungs in a dorsocraniolateral direction. In juvenile and adult elephants, the pleural space is obliterated (Short, 1962; West, 2002; personal observation) due to a massive thickening of the fascia endothoracica and the parietal pleura together with an increase in connective tissue within the pleural space (Brown et al., 1997; Eales, 1929; West et al., 2003). These structures would assist in holding the lungs in their anatomical position (personal assumption) and reduce the pressure on the lung during snorkelling or during filling the trunk with water (Brown et al., 1997; West, 2001, 2002; West et al., 2003).

In domestic mammals, the m. longissimus belongs to the m. erector spinae group and is subdivided into the mm. longissimi lumborum, thoracis, cervicis, atlantis and capitis (NAV, 2017; Schaller, 2007). In the orders Proboscidea, Sirenia and Hyracoidea the m. longissmus is strongly developed (Domning, 1977, 1978; Eales, 1928; Miall & Greenwood, 1878; Murie & Mivart, 1865; Shindo & Mori, 1956), as was the situation in the present study. According to our findings in the African savanna elephant, this muscle can be divided into the uniform m. longissimus lumborum, thoracis et cervicis and the two more or less separate mm. longissimi capitis and atlantis. In the literature dealing with the corresponding Afrotherian musculature (see above), the m. longissimus or parts thereof were named as follows: M. longissimus dorsi, m. longissimus cervodoris, m. transversalis cervicis, m. trachelomastoid and m. longissimus capitis. In the mentioned literature, a separate m. longissimus atlantis has not been described. In order to simplify the nomenclature, we applied only names listed in the NAV (2017). In the individual animal (a foetus) described by Eales (1928), the m. longissimus showed some differences to that seen in the present study. Eales (1928) specified the origins of the muscle from the os ilium, the sacral vertebrae and the processus transversi of all lumbar and thoracic vertebra. In our specimens, fleshy strips originated further cranially from the processus spinosi of the 7th to the 3rd cervical vertebra, whereas origins from the middle thoracic vertebrae were missing. A similar pattern to our observations was found by Shindo and Mori (1956) in the Asian elephant. In the aquatic Sirenia, the caudal origin of the m. longissimus was situated at the tip of the tail and a division into trunk and tail parts was not discernible (Domning 1977, 1978; Murie, 1872). According to some earlier studies (Eales, 1928; Miall & Greenwood, 1878) insertions of the m. longissimus were found on the processus transversi of each cervical vertebra. In the present study, insertions did not reach the atlas or the axis but ended cranially at the 3rd cervical vertebra. This pattern of insertion has also been described in the Asian elephant (Shindo & Mori, 1956) and in Hyrax capensis (Murie & Mivart, 1865). In ruminants and horses, the origins of the m. longissimus from the ossa sacrum and ilium were quite similar to our findings in the African savanna elephant although the cranial insertion of this muscle was restricted to the 7th or 6th cervical vertebrae only in these domestic species (Seiferle & Frewein, 2004). According to data in the literature, the m. longissimus capitis inserted on the occiput (processus mastoideus) in the Asian elephant (Miall & Greenwood, 1878; Shindo & Mori, 1956). This is a common pattern also found in ruminants and horses (Seiferle & Frewein, 2004). In the African elephant dissected by Eales (1926, 1928), it inserted on the cervical vertebrae whereas in the present study in inserted on the occiput medial to the opisthokranion (Figure 4-11). The occurrence of a m. longissimus capitis had also been mentioned in Sirenia (Domning, 1977; Murie, 1872).

According to the NAV (2017), the m. iliocostalis is subdivided into a m. iliocostalis lumborum, thoracis and cervicis and belongs to the m. erector spinae muscle group. In our findings, the m. iliocostalis thoracis resembled a simple cranial continuation of the m. iliocostalis lumborum and a m. iliocostalis cervicis was not observed. In African and Asian elephants, the main origin of the iliocostalis muscle was located on the os ilium (present study, Eales, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956). Additionally, in the savanna elephant, it originated from the caudal edge of the angulus costae of the 19th to the 5th rib (present study). Similarly, in the Asian elephant, Miall and Greenwood (1878) described origins from the 6th to the 19th rib. In the Sirenia, the m iliocostalis did not originate from the pelvis but solely from the ribs and it inserted on 6th or 7th cervical vertebra (Domning, 1977, 1978; Murie, 1872), whereas in elephants, it did not reach the neck (present study; Eales, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956). In domestic ruminants and horses, the origins and insertions of the m. iliocostalis cervicis et thoracis are quite similar with the exception that in horses, this muscle does not originate on the crista iliaca (Seiferle & Frewein, 2004). In the elephants dissected for the present study, the m. iliocostalis originated from the os ilium but contrary to the findings in ruminants and horses (Seiferle & Frewein, 2004) inserted on thoracic vertebrae only.

The m. spinalis et semispinalis belongs to both the transversospinalis and the erector spinae muscle group (NAV, 2017) and is subdivided into the mm. semispinales thoracis, cervicis, capitis and mm. spinales thoracis and cervicis. According to the findings in the present study, a continuous muscle mass could be identified as the m. spinalis thoracis et semispinalis thoracis et cervicis, whereas the m. semispinalis capitis was described as separate muscle. In the study by Eales (1928), the so-called spinalis muscle originated from the ilium which was not observed in our specimens. In contrast, this muscle originated from the processus spinosi of the first two sacral vertebrae and the Ala ossis sacri. In Asian elephants, the muscle had origins from the os sacrum (Miall & Greenwood, 1878; Shindo & Mori, 1956), the os ilium (Miall & Greenwood, 1878), the processus spinosi of the lumbar and caudal thoracic vertebrae, and the processus articulares or the processus transversi of the caudal thoracic vertebrae (Miall & Greenwood, 1878; Shindo & Mori, 1956). Similar to our findings, Miall and Greenwood (1878) described a fusion of the m. spinalis et semispinalis with the mm. multifidi in the Asian elephant. Insertions of the spinalis and semispinalis muscle group on ligamentous structures, that is ligamentum nuchae or supraspinale, have been described in both African and Asian elephants (present study; Eales, 1928; Miall & Greenwood, 1878). In our specimens, the cranial insertion of the m. semispinalis cervicis reached the 7th cervical vertebra only and, therefore, did not correlate with older findings in the Asian or the African elephant in which the muscle inserted cranially on the atlas or axis respectively (Eales, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956). Contrary to the findings in elephants, the cervical part of the m. spinalis et semispinalis of horses and ruminants inserted cranially on the 3rd cervical vertebra, which may be due to the differing length of the cervical vertebral column. In the Sirenia, the m. spinalis et semispinalis extends between the axis and the end of tail forming a compact muscle mass with the mm. multifidi and partially with the m. longissimus (Domning, 1977, 1978; Murie, 1872).

The m. semispinalis capitis belongs to the transversospinalis muscle group. It consists in our specimens, and contrary to the findings in the Sirenia (Domning, 1977, 1978; Murie, 1872), domestic ruminants and horses (Seiferle & Frewein, 2004), of two individual muscles the m. biventer cervicis and m. complexus. In the literature dealing with elephants, the m. semispinalis capitis was designated on the one hand as a uniform muscle (Eales, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956) and on the other as two separate muscles (Mayer, 1847). In Hyrax capensis, Murie and Mivart (1865) described a m. complexus major, a complexus minor and a tertius. In elephants (present study; Miall & Greenwood, 1878; Shindo & Mori, 1956) and the Sirenia (Domning, 1977, 1978), this muscle originated from the cervical and thoracic vertebrae (cranial/middle cervical to middle/caudal thoracic; Murie (1872): thoracic only). In an African elephant foetus, Eales (1926, 1928) described origins only at the cervical vertebrae. The insertion of the m. semispinalis capitis on the occiput did not show major differences between elephant species (present study; Eales, 1926, 1928; Miall & Greenwood, 1878; Shindo & Mori, 1956) and the Sirenia (Domning, 1977,1978; Murie, 1872).

Following the nomenclature of NAV (2017), the mm. intertransversarii in the present study were subdivided into the mm. intertransversarii dorsalis cervicis, medii cervicis and ventrales cervicis. The mm. intertransversarii thoracis and lumborum were absent. However, an additional muscle, the m. intertransversarius longus was described in the African savanna elephant following the description of Seiferle and Frewein (2004) in domestic ruminants and pigs.

The m. splenius capitis is categorized as a neck muscle (NAV, 2017). The uniform structure of the m. splenius capitis described by Eales (1926) and Trenkwalder (2013) correlated best with the findings in the present study. In some studies dealing with the Asian elephant (Boas & Paulli, 1908; Marchant & Shoshani, 2007; Miall & Greenwood, 1878; Shindo & Mori 1956; for varying nomenclature see also Birgfellner (2022), this muscle appears to be divided into a superficial dorsal and a deeper ventral part. Both muscle parts coursed between the ligamentum nuchae and the occiput. The occurrence of an additional muscle portion in Asian elephants may be explained by the larger height (dorsoventral) of the skull and the resulting increased leverage (Marchant & Shoshani, 2007). In the drawing shown in Shoshani and Marchant (2001), the muscle designated as the caudal part of the m. splenius capitis is most probably the m. rhomboideus cervicis. In horses, the m. splenius stabilizes the head and neck (Zsoldos, 2011; Zsoldos et al., 2010). Although the neck is much shorter in elephants, it can be assumed that this strong muscle together with the mm. capitis plays a major role in elevating the head and keeping it in an extended position. Among the Afrotherian species mentioned in the anatomical literature (Domning 1977, 1978; Murie, 1872; Murie & Mivart, 1865), a m. splenius capitis similar to that in the African savanna elephant occurred in Hyrax capensis (Rock hyrax), Dugong dugon (Dugong), Trichechus inunguis (Amazonian manatee) and, seemingly, in Trichechus manatus (West Indian manatee).

4.1 | Functional anatomy

It may be assumed that the back of elephants also functions according to the bow and string concept of Slijper (1946). The bow-like structure is formed mainly by the thoracic and abdominal parts of the vertebral column, which are held under tension by the ventral thoracic and abdominal wall. In the African savanna elephant, the dorsal flexion of the bow formed by the caudal thoracic and lumbar vertebrae seems to be quite flat as it is the case in ungulates such as the horse (Jeffcott, 1979; Windsteig, 2018). It should be stated here that in the African elephant, the outer contour of the back does not correspond to the shape of the vertebral column (Figure 5). Functions of epaxial muscles can be described as extension or erecting, flexion, lateral bending, rotating and stabilizing as well as for increasing the weight-bearing capacity of the spine (Seiferle & Frewein, 2004). In quadrupedal ungulates, the thoracic vertebral column is stabilized by the musculature, the lig. supraspinale, the rib cage and by the long processus spinosi of the vertebrae (Denoix, 1999; Von Scheven, 2010). In the lumbar region, the m. longissimus stabilizes the spine. Extension, that is ventral flexion, of the back is caused by certain limb movements and the weight of the contents of the thorax and abdomen (Seiferle & Frewein, 2004; Van Weeren, 2004). The highest range in dorsoventral and laterolateral motion of the equine vertebral column occurs within the cervical part with the exception of dorsoventral movements in the caudal lumbar region (Stubbs et al., 2006; Townsend et al., 1983; Von Scheven, 2010). According to video footage (Hutchinson et al., 2003), the back of elephants is maximally flexed when the hind limb is moved forward during locomotion. In the horse, a remarkable amount of axial rotation and lateral bending was measured at a level with the 11th or 12th thoracic intervertebral joints (Townsend et al., 1983). In elephants, neither rotation nor bending within the thoracic spine seems to play a decisive role. The widest range of movements within the entire axial skeleton of elephants seems to take place in the cranial part of the vertebral column. In ungulates, the ligamentum nuchae passively carries the head and is connected to the bow mechanism by the cranial thoracic vertebrae. Therefore, neck movements have an impact on the bow and string concept (Seiferle & Frewein, 2004; Slijper, 1946; Windsteig, 2018). The African elephant reveals a thick ligamentum nuchae, a well-developed withers cap and a taut ligamentum supraspinale. The weight of an elephant's head is caused by the massive trunk and the anatomical prerequisites of its finely tuned movements but also due to the weight of the teeth. It should be kept in mind that tusks can reach a weight up to 100 kg (Laws, 1966; Rijkelijkhuizen, 2011). Head and trunk movements are important for social display and foraging. The occurrence of massively developed mm. capitis in the African elephant underlines their importance. It is proven that in horses a lowered position of the head leads to extended forces of the ligamentum nuchae and the ligamentum supraspinale (Windsteig, 2018). On the contrary, a high position causes a lumbar back extension (Rhodin et al., 2009). In elephants, the length of the neck is shorter than that in other ungulates and the head is kept in a high position throughout all phases of locomotion. In other quadrupeds, movements of

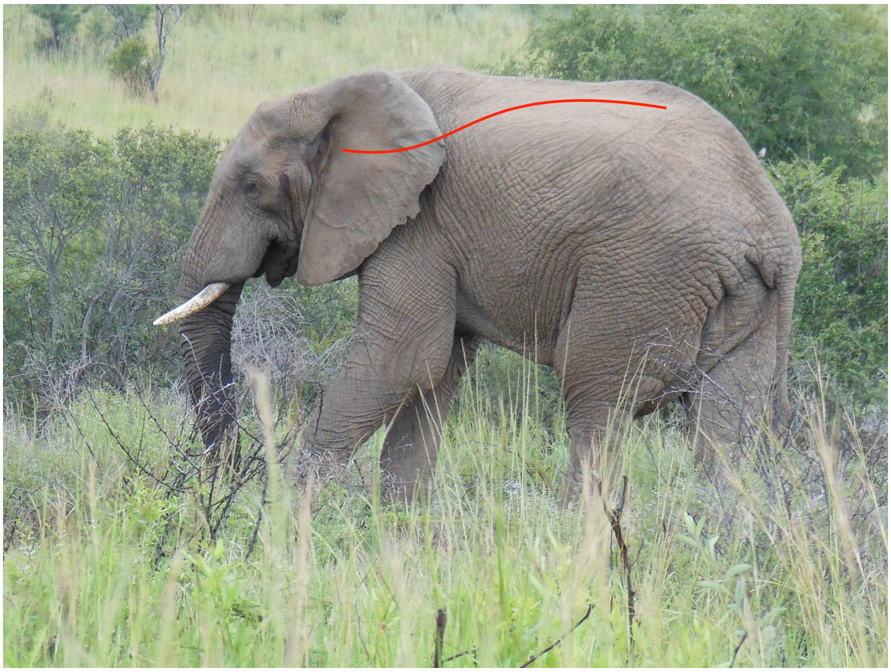

FIGURE 5 African savanna elephant in left lateral profile. The line indicates the position of the vertebral canal.

the head and the neck influence the kinematics of the thoracic and abdominal parts of the vertebral column (Rhodin et al., 2009; Windsteig, 2018). Eales (1928) stated that the weight of the elephant's head causes a reduction in spinal flexibility. It is very likely that in elephants effects on movements between elements of the thoracic and lumbar spine are very limited. This is probably also due to the obvious rigidity of the main parts of the vertebral column. The rather limited lumbosacral mobility in the African elephant compared with horses (e.g., Stubbs et al., 2006) could be caused by the low number (three) of lumbar vertebrae (Bezuidenhout & Seegers, 1996), the short distance between the last rib and the pelvis and the narrow lumbosacral space. The aquatic Sirenia reveal a reduced number of lumbar vertebra (one to three), which plays a distinct role in precaudal stability of the axial skeleton during movements (Buchholtz et al., 2007; Domning, 1977). On the contrary, the main position of flexion and extension during locomotion is located close to the base of the tail, whereas the rest of the trunk is more inflexible (Domning, 1977; Hartman, 1979). In the horse and African elephant, the m. longissimus lumborum et thoracis and the m. spinalis et semispinalis are fused in the lumbar region and covered by a strong aponeurosis and layers of the fascia thoracolumbalis. At least in walking horses, activity of the m. longissimus dorsi assists in stabilizing the vertebral column (Licka et al., 2009). In heavy mammals, skeletal muscles consist mainly of slow fibres (Type I), which are able to produce continuous strong tension (Goto, Itamoto, et al., 2013; Goto, Kawai, et al., 2013). It can be assumed that this ability is an important factor for stabilization also in elephants. Furthermore, the elastic aponeurosis helps in stabilization and may function as an energy-saving mechanism (Alexander, 1991; Alexander et al., 1985; Von Scheven, 2010). In African elephants, in which the energetic cost of locomotion is very low compared with other land mammals (Langman et al., 1995), the aponeurosis could therefore contribute to stabilization and reduction in muscular work during stance and locomotion.

ACKNOWLEDGEMENTS

We gratefully acknowledge the supply of manpower, equipment and facilities necessary for anatomical preparation by the Faculty of Veterinary Science of the University of Pretoria (Onderstepoort, Gauteng, South Africa). We highly appreciate the assistance and cooperation given by Prof. Herman B. Groenewald over many years and the technical assistance of the staff members of the Faculty. The International Relations Office of the University of Veterinary Medicine, Vienna (Austria) partly funded this study.

CONFLICT OF INTEREST

All involved authors declare neither a financial interest nor any other possible conflict of interest with regard to this publication.

DATA AVAILABILITY STATEMENT

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

ORCID

Caroline Maria Victoria Birgfellner https://orcid.org/0000-0002-0292-6494

REFERENCES

Alexander, R. M. (1991). Energy-saving mechanisms in walking and running. *Journal of Experimental Biology*, *160*, 55–69. https://doi.org/10.1242/jeb.160.1.55

Alexander, R. M., Dimery, N. J., & Ker, R. F. (1985). Elastic structures in the back and their role in galloping in some mammals. *Journal of Zoology*, *207*(4), 467–482. https://doi.org/10.1111/j.1469-7998.1985.tb04944.x

Bezuidenhout, A. J., & Seegers, C. D. (1996). Osteology of the African elephant (*Loxodonta africana*): Vertebral column, ribs and sternum. *Onderstepoort Journal of Veterinary Research*, *63*(2), 131–147. http://hdl.handle.net/2263/22045

Boas, J. E. V., & Paulli, S. (1908). *The elephants's head: Studies in the comparative anatomy of the organs of the head of the Indian elephant and other mammals*. Gustav Fischer. https://doi.org/10.5962/bhl.title.151091

Brown, R. E., Butler, J. P., Godleski, J. J., & Loring, S. H. (1997). The elephant's respiratory system: Adaptations to gravitational stress. *Respiration Physiololgy*, *109*(2), 177–194. https://doi.org/10.1016/S0034-5687(97)00038-8

Birgfellner, C. M. V. (2022). *Anatomische Untersuchungen der epaxialen Muskulatur des Afrikanischen Elefanten (Loxodonta africana)* [Doctoral dissertation]. University of Veterinary Medicine Vienna, Austria.

Buchholtz, E. A., Booth, A. C., & Webbink, K. E. (2007). Vertebral anatomy in the Florida manatee, *Trichechus manatus latirostris*: A developmental and evolutionary analysis. *The Anatomical Record*, *290*, 624–637. https://doi.org/10.1002/ar.20534

De Jong, W. W. (1998). Molecules remodel the mammalian tree. *Trends in Ecology & Evolution*, *13*(7), 270–275. https://doi.org/10.1016/S0169-5347(98)01335-4

Denoix, J. M. (1999). Spinal biomechanics and functional anatomy. *Veterinary Clinics of North America: Equine Practice*, *15*(1), 27–60. https://doi.org/10.1016/s0749-0739(17)30162-1

Domning, D. P. (1977). Observations on the myology of Dugong dugon (Müller). *Smithsonian Contributions to Zoology*, *226*, 1–57. https://doi.org/10.5479/si.00810282.226

Domning, D. P. (1978). The myology of the Amazonian manatee, *Trichechus inunguis* (natterer) (Mammalia: Sirenia). *Acta Amazonica*, *82*(Suppl. 1), 1–81. https://doi.org/10.1590/1809-43921978082 1s005

Eales, N. B. (1926). The anatomy of a Foetal African elephant, *Elephas africanus* (*Loxodonta africana*). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *54*(3), 491–551. https://doi.org/10.1017/S0080456800016082

Eales, N. B. (1928). The anatomy of a Foetal African elephant, *Elephas africanus* (*Loxodonta africana*). Part II. The body muscles. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *55*(3), 609–642. https://doi.org/10.1017/S0080456800013338

Eales, N. B. (1929). XI.-the anatomy of a Fœtal African elephant, *Elephas africanus* (*Loxodonta africana*). Part III. The contents of the thorax and abdomen, and the skeleton. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *56*(1), 203–246. https://doi.org/10.1017/S0080456800027800

Goto, M., Itamoto, K., Tani, Y., Miyata, H., Kihara, I., Mori, F., Tajima, T., & Wada, N. (2013). Distribution of muscle fibers in skeletal muscles of the African elephant (*Loxodonta africana*). *Mammal Study*, *38*(2), 135–140. https://doi.org/10.3106/041.038.0210

Goto, M., Kawai, M., Nakata, M., Itamoto, K., Miyata, H., Ikebe, Y., Tajima, T., & Wada, N. (2013). Distribution of muscle fibers in skeletal muscles of the cheetah (*Acinonyx jubatus*). *Mammalian Biology*, *78*(2), 127–133. https://doi.org/10.1016/j.mambio.2012.07.001

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. *The American Society of Mammologists, Special Publication*, *5*, 1–53. https://doi.org/10.5962/bhl.title.39474

Hutchinson, J. R., Famini, D., Lair, R., & Kram, R. (2003). Are fast-moving elephants really running? *Nature*, *422*, 493–494. https://doi.org/10.1038/422493a

Hutchinson, J. R., Schwerda, D., Famini, D. J., Dale, R. H., Fischer, M. S., & Kram, R. (2006). The locomotor kinematics of Asian and African elephants: Changes with speed and size. *Journal of Experimental Biology*, *209*, 3812–3827. https://doi.org/10.1242/jeb.02443

Jeffcott, L. B. (1979). Back problems in the horse—A look at past, present and future progress. *Equine Veterinary Journal*, *11*(3), 129–136. https://doi.org/10.1111/j.2042-3306.1979.tb01324.x

Kuntner, M., May-Collado, L. J., & Agnarsson, I. (2011). Phylogeny and conservation priorities of afrotherian mammals (Afrotheria, Mammalia). *Zoologica Scripta*, *40*(1), 1–15. https://doi.org/10.1111/j.1463-6409.2010.00452.x

Langman, V. A., Roberts, T. J., Black, J., Maloiy, G. M., Heglund, N. C., Weber, J. M., Kram, R., & Taylor, C. R. (1995). Moving cheaply: Energetics of walking in the African elephant. *Journal of Experimental Biology*, *198*, 629–632. https://doi.org/10.1242/jeb.198.3.629

Laws, R. M. (1966). Age criteria for the African elephant Loxodonta a. africana. *African Journal of Ecology*, *4*(1), 1–37. https://doi.org/10.1111/j.1365-2028.1966.tb00878.x

Licka, T., Frey, A., & Peham, C. (2009). Electromyographic activity of the longissimus dorsi muscles in horses when walking on a treadmill. *The Veterinary Journal*, *180*(1), 71–76. https://doi.org/10.1016/j.tvjl.2007.11.001

Marchant, G. H., & Shoshani, J. (2007). Head muscles of *Loxodonta africana* and *Elephas maximus* with comments on *Mammuthus primigenius* muscles. *Quaternary International*, *169–170*, 186–191. https://doi.org/10.1016/j.quaint.2007.02.004

Mariappa, D. (2005). *Anatomy and histology of the Indian elephant*. Indira Publishing House.

Mayer, C. (1847). *Beiträge zur Anatomie des Elephanten. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher. Vierzehnter Band*. Eduard Weber's Buchhandlung.

Miall, L. C., & Greenwood, F. (1878). Anatomy of the Indian elephant. In *Studies in comparative anatomy, no. 2*. Macmillan. https://doi.org/10.5962/bhl.title.48665

Moulin (Mullen), A. (1682). *An anatomical account of the elephant accidentally burnt in Dublin*. Sam. Smith.

Murie, J. (1872). On the form and structure of the manatee (*Manatus americanus*). *The Transactions of the Zoological Society of London*, *81*(3), 127–220. https://doi.org/10.1111/j.1469-7998.1872.tb08571.x

Murie, J., & Mivart, S. J. (1865). On the myology of hyrax Capensis. *Proceedings of the Zoological Society of London*, *33*, 329–352. https://doi.org/10.1111/j.1469-7998.1865.tb02348.x

Nagel, R. M., Forstenpointner, G., Soley, J. T., & Weissengruber, G. E. (2018). Muscles and fascial elements of the antebrachium and Manus of the African elephant (*Loxodonta africana*, Blumenbach 1797): Starring comparative and functional considerations. *Anatomia Histolologia Embryologia*, *47*(3), 195–205. https://doi.org/10.1111/ahe.12340

NAV (Nomina Anatomica Veterinaria), 6th edition. (2017). International Committee on Veterinary Gross Anatomical Nomenclature (I.C.V.G.A.N.). http://www.wava-amav.org/downloads/nav_6_2017.zip

Panagiotopoulou, O., Pataky, T. C., Day, M., Hensman, M. C., Hensman, S., Hutchinson, J. R., & Clemente, C. J. (2016). Foot pressure distributions during walking in African elephants (*Loxodonta africana*). *Royal Society Open Science*, *3*(10), 160203. https://doi.org/10.1098/rsos.160203

Puttick, M. N., & Thomas, G. H. (2015). Fossils and living taxa agree on patterns of body mass evolution: A case study with Afrotheria. *Proceedings of the Royal Society B*, *282*(1821), 20152023. https://doi.org/10.1098/rspb.2015.2023

Rhodin, M., Álvarez, C. G., Byström, A., Johnston, C., Van Weeren, P. R., Roepstorff, L., & Weishaupt, M. A. (2009). The effect of different head and neck positions on the caudal back and hindlimb kinematics in the elite dressage horse at trot. *Equine Veterinary Journal*, *41*(3), 274–279. https://doi.org/10.2746/042516409X394436

Richman, L. K., Zong, J. C., Latimer, E. M., Lock, J., Fleischer, R. C., Heaggans, S. Y., & Hayward, G. S. (2014). Elephant endotheliotropic herpesviruses EEHV1A, EEHV1B, and EEHV2 from cases of hemorrhagic disease are highly diverged from other mammalian herpesviruses and may form a new subfamily. *Journal of Virology*, *88*(23), 13523–13546. https://doi.org/10.1128/JVI.01673-14

Rijkelijkhuizen, M. (2011). Large or small? African elephant tusk sizes and the Dutch ivory trade and craft. In J. Baron & B. Kufel-Diakowska (Eds.), *Written in bones. Studies on technological and social context of past faunal skeletal remains*. Wrocławska Drukarnia naukowa PAN im. Stanisława Kulczyńskiego sp. z o.o.

Schaller, O. (2007). *Illustrated veterinary anatomical nomenclature*. Enke.

Schopf, B. (2010). *Beiträge zur Osteologie und Osteometrie des Schädels des Afrikanischen Elefanten* [Diploma thesis]. University of Veterinary Medicine Vienna.

Seiferle, E., & Frewein, S. (2004). Aktiver Bewegungsapparat, Muskelsystem, Myologia. In Nickel, R., Schummer, A., Seiferle, E., Frewein, J., Wille, K. H., Wilkens H. (Eds.): *Lehrbuch der Anatomie der Haustiere, Bewegungsapparat* (Vol. *1*). Paul Parey.

Shindo, T., & Mori, M. (1956). Musculature of the Indian elephant. Part III. Musculature of the trunk, neck, and head. *Okajimas Folia Anatomica Japonica*, *29*(1–2), 17–40. https://doi.org/10.2535/ofaj1936.29.1-2_17

Short, R. V. (1962). The peculiar lungs of the elephant. *New Scientist*, *316*, 570–572.

Shoshani, J. (1986). *On the phylogenetic relationships among Paenungulata and within Elephantidae as demonstrated by molecular and osteological evidence* [Doctoral dissertation]. Wayne State University.

Shoshani, J., & Marchant, G. H. (2001). Hyoid apparatus: A little known complex of bones and its contribution to proboscidean evolution. In *The World of Elephants, Proceedings of the First International Congress, Rome* (pp. 668–675). Consiglio Nazionale delle Ricerche.

Slijper, E. J. (1946). Comparative biologic anatomical investigations on the vertebral column and spinal musculature of mammals. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde*, *42*, 1–128.

Smuts, M., & Bezuidenhout, A. J. (1993). Osteology of the thoracic limb of the African elephant (*Loxodonta africana*). *Onderstepoort Journal of Veterinary Research*, *60*, 1–14. http://hdl.handle.net/2263/33019

Stubbs, N. C., Hodges, P. W., Jeffcott, L. B., Cowin, G., Hodgson, D. R., & McGowan, C. M. (2006). Functional anatomy of the caudal thoracolumbar and lumbosacral spine in the horse. *Equine Veterinary Journal*, *38*(s36), 393–399.

Townsend, H. G., Leach, D. H., & Fretz, P. B. (1983). Kinematics of the equine thoracolumbar spine. *Equine Veterinary Journal*, *15*(2), 117–122. https://doi.org/10.1111/j.2042-3306.1983.tb01732.x

Trenkwalder, H. (2013). *Über die Muskulatur des Schultergürtels und der proximalen Vorderextremität des Afrikanischen Elefanten* [Doctoral dissertation]. University of Veterinary Medicine Vienna, Austria.

Van Weeren, P. (2004). Structure and biomechanical concept of the equine back. *Pferdeheilkunde*, *20*(4), 341–348. https://doi.org/10.21836/PEM20040404

Von Scheven, C. C. A. (2010). *The anatomy and function of the equine thoracolumbar longissimus dorsi muscle* [Doctoral dissertation].

Ludwig Maximilians University Munich. https://doi.org/10.5282/edoc.12178

Weissengruber, G. E., Egger, G., Stanek, G., Forstenpointner, G., & Janach, K. (2005). Something different: The Articulatio genus of African elephants (*Loxodonta africana*). *Anatomia, Histologia, Embryologia*, *34*, 56–57. https://doi.org/10.1111/j.1439-0264.2005.00669_129.x

West, G. (2006). Musculoskeletal system. In *Biology, medicine, and surgery of elephants* (pp. 263–207). Blackwell Publishing. https://doi.org/10.1002/9780470344484.ch19

West, J. B. (2001). Snorkel breathing in the elephant explains the unique anatomy of its pleura. *Respiration Physiology*, *126*(1), 1–8. https://doi.org/10.1016/S0034-5687(01)00203-1

West, J. B. (2002). Why doesn't the elephant have a pleural space? *News in Physiological Sciences*, *17*(2), 47–50. https://doi.org/10.1152/nips.01374.2001

West, J. B., Fu, Z., Gaeth, A. P., & Short, R. V. (2003). Fetal lung development in the elephant reflects the adaptations required for snorkeling in adult life. *Respiratory Physiology & Neurobiology*, *138*(2–3), 325–333. https://doi.org/10.1016/S1569-9048(03)00199-X

Wiedner, E., & Schmitt, D. L. (2009). Captive elephant medicine: Recent developments. *Gajah*, *31*, 25–28.

Wilson, D., & Reeder, M. (2005). *Mammals species of the world: A taxonomic and geographic reference* (Vol. *1*). The Johns Hopkins University Press.

Windsteig, V. (2018). *Electromyographic activity of the equine longissimus dorsi muscle during induced back movements at stance* [Diploma thesis]. University of Veterinary Medicine Austria.

Wittemyer, G. (2011). Family elephantidae. In D. E. Wilson & R. A. Mittermeier (Eds.), *Handbook of the mammals of the world* (Vol. *2*). Hoofed Mammals. Lynx edicions.

Zsoldos, R. R. (2011). *Biomechanics of the equine cervical vertebral column* [Doctoral dissertation]. Movement Science Group Vienna, Clinical Department of Small Animals and Horses, University of Veterinary Medicine.

Zsoldos, R. R., Kotschwar, A. B., Kotschwar, A., Groesel, M., Licka, T., & Peham, C. (2010). Electromyography activity of the equine splenius muscle and neck kinematics during walk and trot on the treadmill. *Equine Veterinary Journal*, *42*, 455–461. https://doi.org/10.1111/j.2042-3306.2010.00263.x

How to cite this article: Birgfellner, C. M. V., Soley, J. T., Polsterer, E., Forstenpointner, G., & Weissengruber, G. E. (2023). The graviportal spine: Epaxial muscles of the African savanna elephant (*Loxodonta africana*). *Anatomia, Histologia, Embryologia*, *52*, 135–147. https://doi.org/10.1111/ahe.12849