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# The cranial musculature of turtles

Ingmar Werneburg

## ABSTRACT

Up to this date, no clear common reference system for muscle nomenclature in vertebrates exists due to 1. human medical anatomy dominated traditions, 2. typological, 'box-like' approaches, and 3. simplifications based on the taxonomic and topographical focus of the respective authors. Hence, a large terminological and homologisation confusion in the literature is recognisable, hindering evolutionary and developmental analyses. In this paper, a comprehensive study on the cranial musculature is presented, in which more than 100 references on cranium-associated musculature of turtles were critically reviewed. Following a new traceable approach to muscular terminology, a set of 88 adult 'muscular units' – the smallest parts of macroscopic muscular structures – were identified across turtle species, exemplarily demonstrated in a side-necked turtle. For example, the homology of jaw muscle portions and that of epaxial and hypaxial muscular structures are defined by a comprehensive consideration of criteria such as innervation, spatial characteristics, and ontogeny. Adult muscle arrangement variability among specimens, fusions of muscular units, and drop-like apoptosis are recorded. These phenomena are the result of a fluid pattern formation – first driven by neural crest stream patterning in ontogeny. Considering this fact of ontogeny, a new discussion of the evolutionary history of turtles and of particular cranial structures is possible.

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## INTRODUCTION

The synonyms and homologies of muscular structures in the vertebrate head over their evolutionary history are highly debated resulting in several terminological confusions and controversies (Hoyos and Dubois 2004; Diogo and Abdala 2010).

Dietrich Starck (1982, p. 7-8; own translation) stated on the terminology of muscles: "The nomenclature of singular muscles is not uniform and

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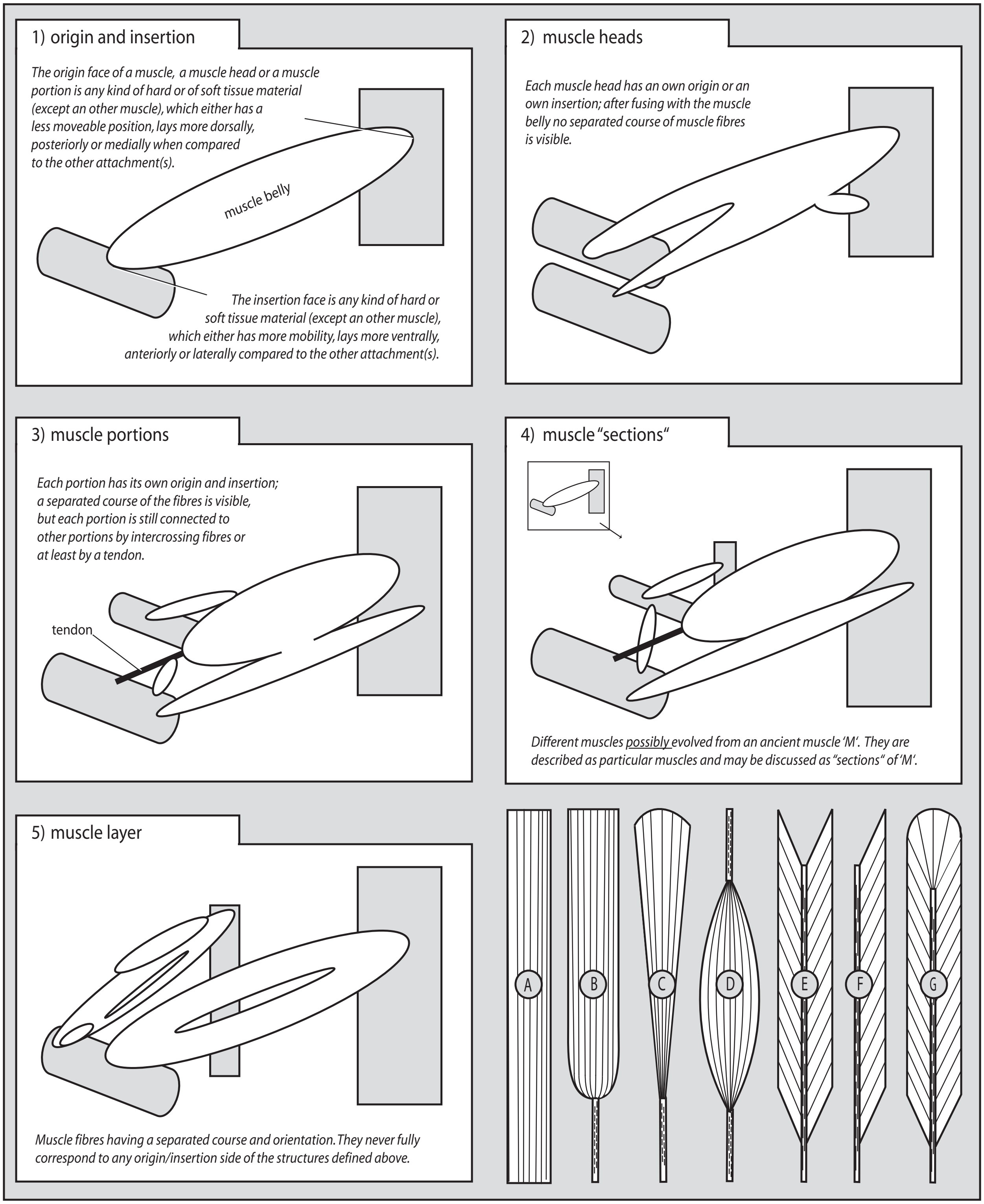
causes difficulties when comparing different vertebrate classes. Primarily adapted from human anatomy, non-comparable muscles are assigned with the same name. Additionally, many muscles were named by their function without referring to the fact that no muscle has only one function and that homologous muscles in different taxa may have different functions. To reach a more rational nomenclature in Comparative Anatomy, it was attempted to name muscles exclusively based on their origin and insertion [...]." At this point he generally refers to the works of Max Fürbringer and continues: "In addition, this approach had to fail, because origin and insertion are not unchangeably fixed in phylogeny. Hence considerable discrepancies occurred. Additionally, very unpractical sesquipedalians ['word monsters'] evolved, composed of up to six or more singular terms. Currently, following situation prevails […]. For particular muscles and muscles groups – especially valuable for primary musculature of the rump – homologies are clarified so far, hence, a consistent nomenclature is possible for all vertebrate classes. Easy and short designations are proved, derivable from topographical relationships and major courses. For mammals, the nomenclature is designed after human anatomy, particularly because homologies are widely verified. Apart from that, it is strongly recommended to transfer muscle names to other systematic taxa only if evolutionary derivations are assessable. Especially for musculature of the extremities of lower tetrapods an independent nomenclature should be used, because the adaptation of terms out of mammal-anatomy pretends homologies, which are not proved."

In the present contribution, I first set clear definitions of such basic and crucial terms as origin, insertion, muscle portion, and muscle section in cranium-associated muscular structures (Figure 1). For the cranial musculature of turtles, I then introduce both a simple numeration system of muscular units and – partly polysyllabic – muscle names. Although criticised by Starck (1982), the latter are unavoidable due to 1. nomenclatural traditions and 2. muscular units – the smallest part of macroscopic muscular structures (see below) – have a high anatomical resolution. As such, they require explicit terms.

Starck (1982, p. 8) stated that regarding the m. adductor mandibulae structures: "One stable terminology is exemplarily designed for the n. trigeminus supporting jaw musculature. Despite various differences in particular the homologies for all non-mammal taxa is widely resolved. A uniform nomenclature is possible." As shown below, this statement is correct regarding the superficial similarity of those muscles, but the homology of detailed differentiations of muscle portions and muscle heads are not understood in detail yet. Major structures such as m. adductor mandibulae posterior (No. 29-30; for the introduced numeration of muscular units see below) are the subject of various discussions due to uncertain homologisations.

The anatomy of the turtle head is of particular interest due to the uncertain position of turtles within amniotes (Rieppel 2008; Werneburg and Sánchez-Villagra 2009). Either turtles plesiomorphically show an anapsid skull or, when nested within diapsids, a secondary anapsid skull. In the latter case two temporal fenestra of the dermatocranium would have closed in evolution (Müller 2003). Jaw and cranium-associated neck musculature are assumed to have an important mechanical influence on the formation of dermatocranial bone arrangements in the temporal region of the skull (e.g., Frazetta 1968; Smith 1996; Rieppel 1993; Tarsitano et al. 2001). Several studies have proposed homologies and evolutionary transformations of this musculature across reptilian groups (Holliday 2006; Tvarožková 2006; Holliday and Witmer 2007; Diogo et al. 2008a, b).

Classic studies on the head muscle anatomy of single turtles species include those of Wiedemann (1803), Bojanus (1819-21), and Ogushi (1913b). More comprehensive studies between different turtle taxa were published by Hoffmann (1890), Lakjer (1926), Schumacher (1953-54, 1954, 1954-55a, 1954-55b, 1972), and Poglayen-Neuwall (1953a). Schumacher (1973) summarised the literature and set an often-cited standard when referring to head musculature in turtles (e.g., Wocheslánder et al. 1999; Wynecken 2003). From 313 known turtle species and 97 genera (sensu Fritz and Havaš 2007), the jaw musculature of more than 40 species and more than 30 genera are described (e.g., Figures 2–4). In contrast, the anatomy of neck musculature has been described only for a few species, with a focus on general differences of the neck muscles between side-necked (Pleurodira) and hidden-necked (Cryptodira) turtles (Vallois 1920, 1922; George and Shah 1955b; Shah 1963; Scanlon 1982; Herrel et al. 2008). Other muscle systems of the head – external and internal ocular, laryngeal, and hyobranchial muscles – are described only for a few species (von Bayern 1884; König 1934-35; Gräper 1932, 1932; Nishi 1916, 1938b; Gaunt and Gans 1969; Schumacher 1972).



*The origin face of a muscle, a muscle head or a muscle portion is any kind of hard or of soft tissue material (except an other muscle), which either has a less moveable position, lays more dorsally, posteriorly or medially when compared to the other attachment(s).*

*The insertion face is any kind of hard or soft tissue material (except an other muscle), which either has more mobility, lays more ventrally, anteriorly or laterally compared to the other attachment(s).*

*Each muscle head has an own origin or an own insertion; after fusing with the muscle belly no separated course of muscle fibres is visible.*

*Each portion has its own origin and insertion; a separated course of the fibres is visible, but each portion is still connected to other portions by intercrossing fibres or at least by a tendon.*

*Different muscles possibly evolved from an ancient muscle 'M'. They are described as particular muscles and may be discussed as "sections" of 'M'.*

*Muscle fibres having a separated course and orientation. They never fully correspond to any origin/insertion side of the structures defined above.*

**FIGURE 1.** Terminology of muscle anatomy as used in this study. **1 – 5)** Different degrees of evolutionary differentiation (for details see text). Left = anterior. **A – F)** Different muscle shapes and fibre courses. **A)** parallel fibred with two direct attachments, **B)** parallel fibred with one tendinous attachment, **C)** fan shaped, **D)** spindle shaped, **E)** bipinnated muscle including two portions, **F)** pinnated, **G)** bipinnated muscle not separated into two portions.

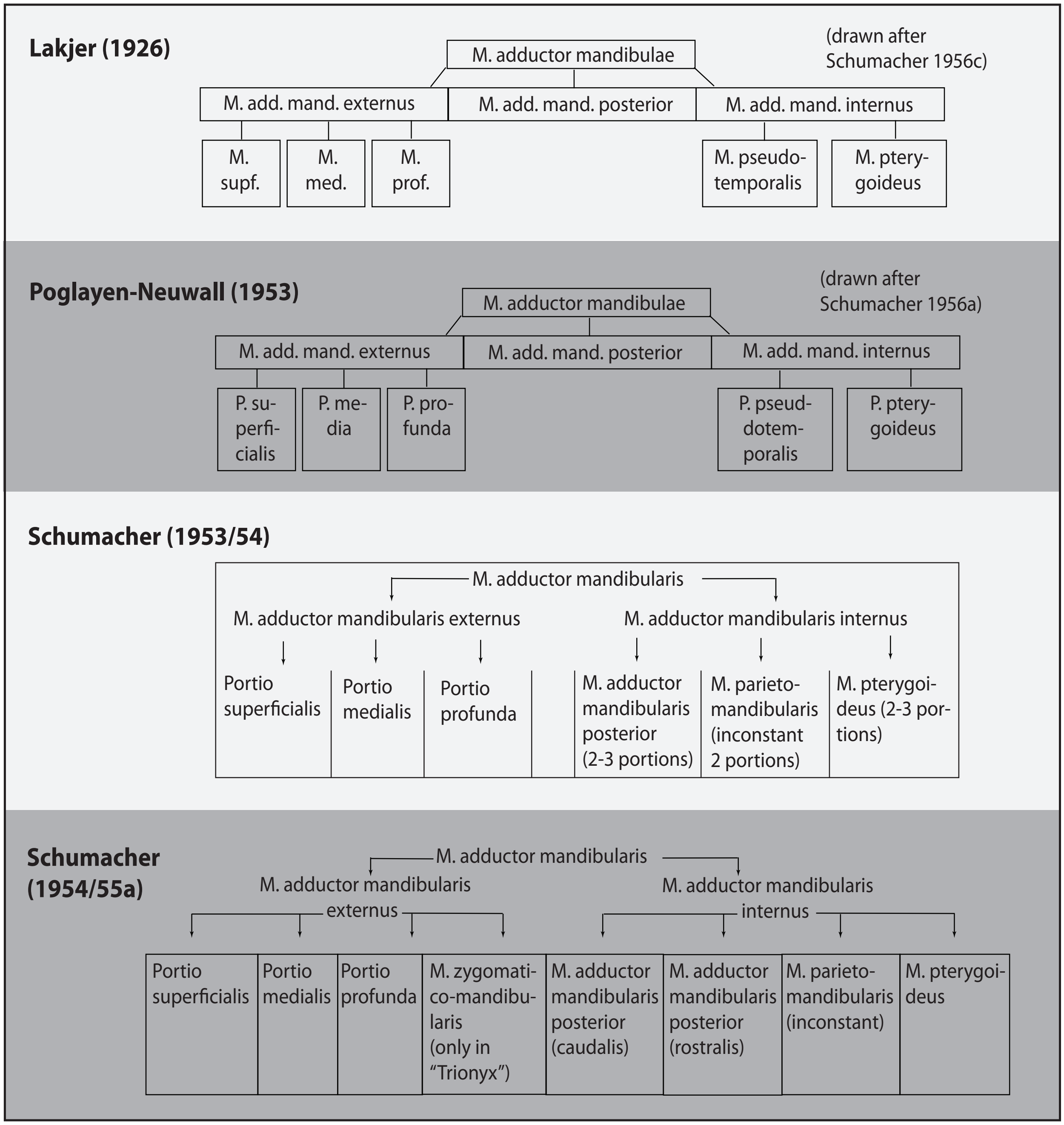


**FIGURE 2.** Scheme listing all arrangements proposed for turtle m. adductor mandibulae structures in the literature. The pictures are redrawn from Schumacher (1953-73). The appreviations, boxes, arrows, and breakups of words follow the style of Schumacher. German words are translated. Slight modifications are made in the scheme of Schumacher (1954-55a) to approximately correlate its muscle parts to those of other schemes. Note the "historically" shifting position of Pars porterior ("M. add. mand. posterior") in relation to the other muscular structures; also the parts of m. adductor mandibulae internus were categorised differently. Continued in Figures 3, 4.

In the present study, I review all cranium-associated muscular structures that – to my knowledge – were ever described for turtles in the literature (Appendix 1, Figures 5–16). The internal and external ocular muscles are innervated by n. oculomotorius (III) (No. 1-8), n. trochlearis (IV) (No. 9-10), and n. abducens (VI) (No. 34-38). The palatoquadrate, nose, and lower orbit region related musculature is innervated by n. trigeminus (V). The jaw depressor muscle, the superficial neck muscula-

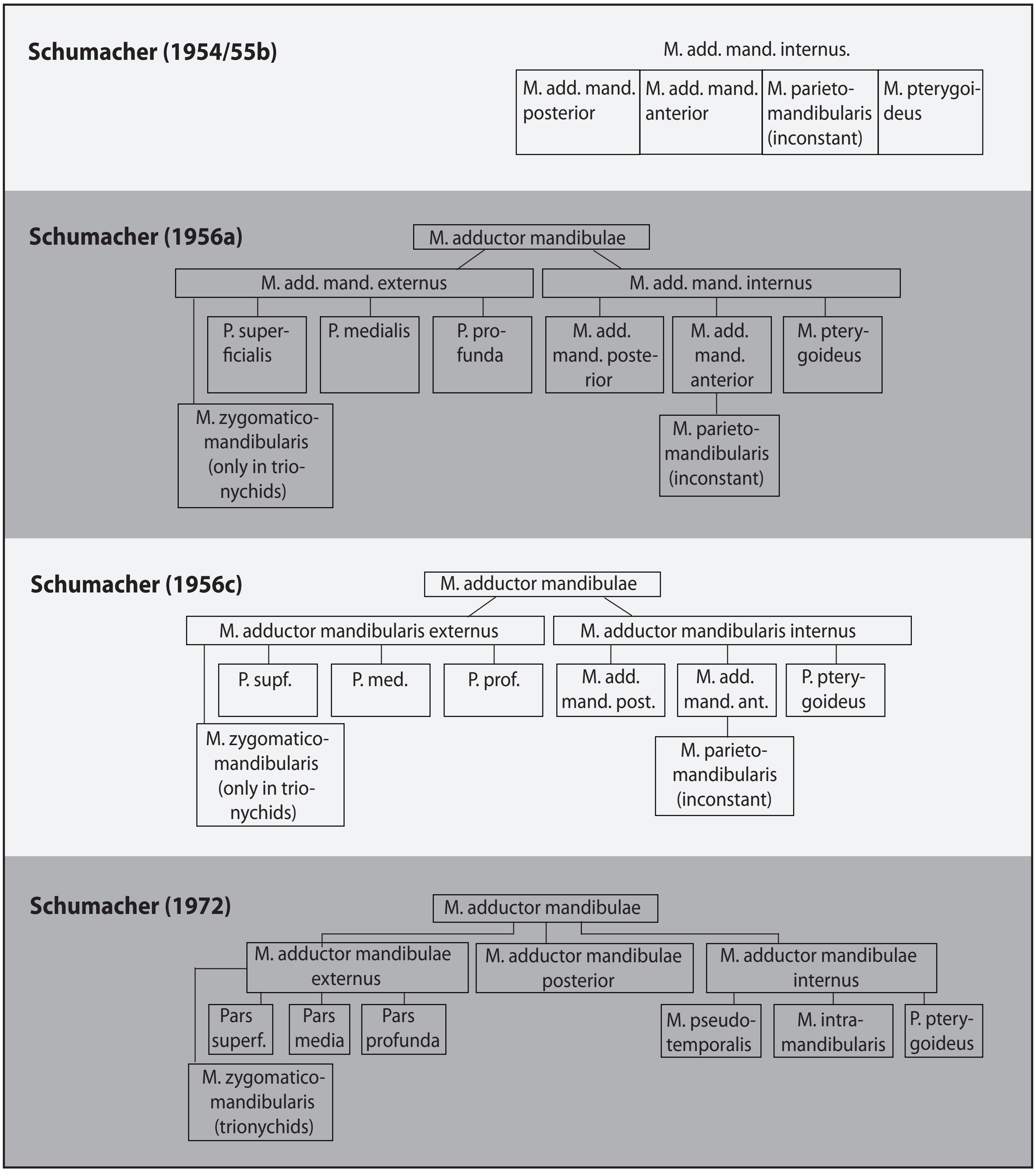


**FIGURE 3.** Continuation of Figure 2; continued in Figure 4.

ture and muscular structures medial to the ear capsule are innervated by n. facialis (VII) (No. 39-46). N. glossopharyngeus (IX) innervates branchiovisceral musculature (No. 47-48). N. vagus (X) and n. accessorius (XI) support laryngeal (No. 49-51), as well as one n. vagus (X) innervated shoulder muscle (No. 52) and its derivate (No. 53). The muscles of the tongue, the hyoid apparatus, and a few muscles of the neck region (No. 54-74) gain their innervation by n. hypoglossus (XII). Most neck-related muscles are exclusively innervated by spinal nerves, but depending on the anterior-posterior extend of the muscles as well as on their ontogenetic origin – e.g., from visceral mesoderm – they

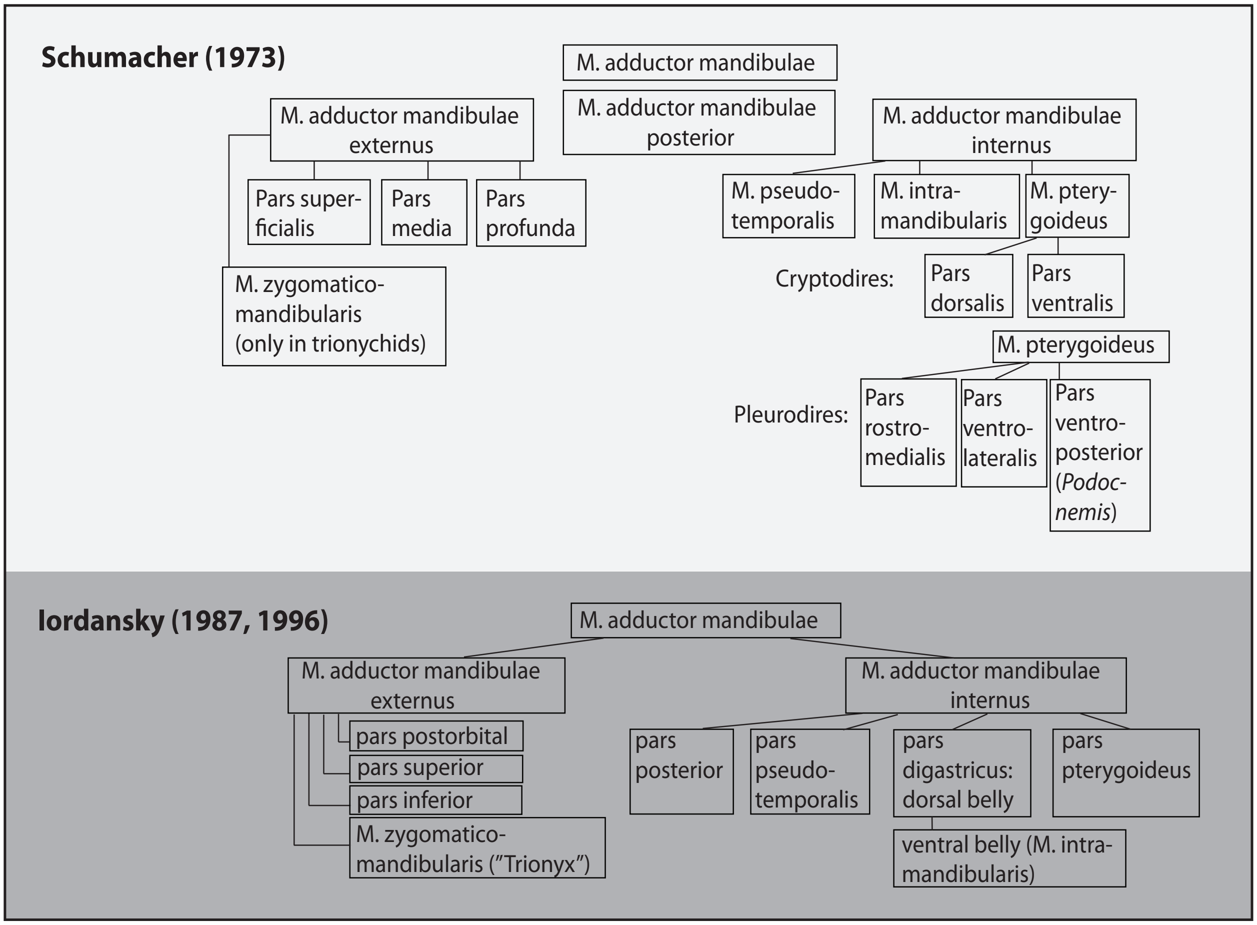


**FIGURE 4.** Continuation of Figure 2 and Figure 3.

may also be partly innervated by posterior cranial nerves; or – if originating from postcervical myotoms – also by nerves of the trunk and tail region (No. 75-88).

As a case study to demonstrate the presented standardisation of cranium-associated musculature in turtles, I studied the cranial anatomy of the red-bellied short-necked turtle *Emydura subglobosa* (Krefft 1876). It is a common carnivore species living in freshwater environments of Northern Australia and Papua New Guinea (Legler and Georges 1993). Due to its easy keeping and breeding requirements (Nicol 1993; Highfield 1996; Hennig 2001; Pawlowski 2001; Schwarz 2006), *E. subglobosa* was proposed to be a suitable pleurodiran "model" species for evolutionary developmental studies (Tzika and Milinkovitch 2008; Werneburg et al. 2009). By describing the adult head morphology of this species, I would like to expand knowledge of those structures in pleurodire turtles, which are underrepresented in most studies. Kesteven (1942-1945) and Schumacher (1954-55a) were the first to describe the cranial musculature of an *Emydura*-species, *E. macquarii kreftii* (Gray 1831), a species possibly opposing all remaining *Emydura*-species, and *E. subglobosa* is nested deep within the *Emydura*-clade (Georges and Thomson 2006; Iverson et al. 2007). The development of the external morphology and ossification patterns of *E. subglobosa* were recently described (Werneburg and Sánchez-Villagra 2009; Werneburg et al. 2009).

## MATERIAL AND TECHNIQUES

### CT-Scan

I used micro computed tomography (µ-CT) to document the cranial bones and cervical vertebrae of a subadult *Emydura subglobosa* specimen (PIMUZ labNo. 2009.37, CL: 63.58 mm, Figures 17, 18). The micro-CT method is commonly used in medical studies and allows non-destructive data acquisition of anatomical structures (Morton et al. 1990; Ritman 2004) with a high spatial resolution. In this study, the acquisition of digital three-dimensional data was performed with a medical Scanco® micro-CT 80 (www.scanco.ch) at the Anthropologi-

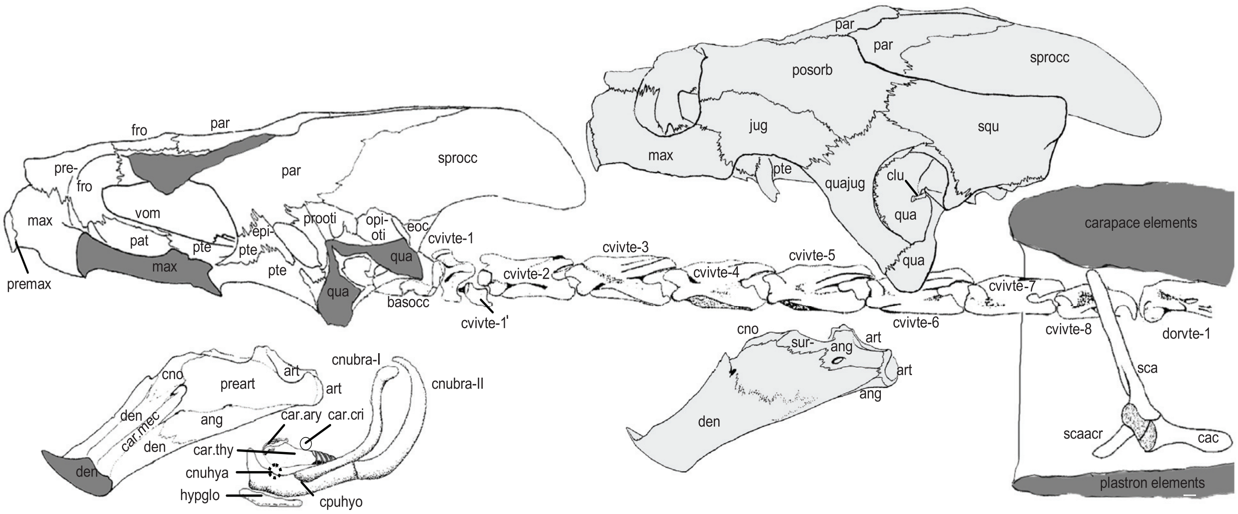


**FIGURE 5.** Illustration of the the skeleton in the cranial, cervical, and shoulder region of a turtle, modified from Gaffney (1972: *Chelydra serpentina*) and Herrel et al. (2008: *Apalone spinifera*). This Figure is used to illustrate the orientations of the muscular units in Figures 6-15. For abbreviations, see Appendix 4 and the abbreviation guide in the text.

cal Institute of the University of Zürich. The scanning process with an isotropic voxel resolution of 0.036 mm took about 3 hours and resulted in an isq-file size of about 2 Gigabytes with a standard resolution of 1024 × 1024 pixels per slide. The 3D-software Amira 4.1.2. (Visage Imaging Richmond, Australia) was used to create a surface rendering of the data (Appendix 2–4).

### Clearing and Staining

In order to study the spatial anatomy of cartilages in addition to ossified structures (Figures 19–21), one subadult specimen (PIMUZ labNo. 2009.9, CL: 79.2 mm) was cleared and double-stained following standard protocols (Taylor and Van Dyke 1985).

### Serial Sections and 3D-Reconstruction

I had access to a serial section series of a hatchling specimen (collection of Prof. Dr. Wolfgang Maier, Tübingen/Germany, CL: 28.5mm), which was stained with Heidenhain's Azan (Romeis 1989) and embedded with Euparal. Each slice had a thickness of 20 µm. Every second section was digitised with a Leica DFC420 C camera mounted to a Leica M165C stereo microscope. The colour images were saved in tif format at 2592 x 1944 pixel resolution including a micrometer scale. The software Amira 4.1.2. (Visage Imaging Richmond, Australia) was used to align the images (Figures 22–27). The technical limitations of the software and available computing power necessitated the conversion of images to greyscale mode and to 50% of the original size. Based on manually defined contour lines derived interactively from the digital images, surface renderings were provided by the software. Artefacts in the histological sections caused unevenness in the rendered surfaces of the anatomical structures. However, smoothing was avoided in order to reduce changes of the raw data, and re-drawings of the 3D reconstructions were prepared (Figures 22, 23).

### Manual Dissection

For manual dissection (Figures 28–31), four one-year-old subadult specimens (PIMUZ labNo. 2009.37-40, CL: ranging around 65 mm) and one adult specimen (PIMUZ labNo. 2009.10, CL: 96 mm) were studied. All these specimens were obtained from the pet trade, were intoxicated and mortified in chlorobutanol, fixed in a 4% formalin solution and preserved in 70% ethanol. In the hatchling (serial section), all muscles already reached attachment sites. Though all specimens studied in this study form a postembryonic ontogenetic series, the origin and insertion sites of the muscles, which eventually changed, were accurately recorded and discussed; variability was also documented. The branching pattern of cranial nerves was checked where possible to enable homologisations of the muscular structure in addition to other criteria such as origin, insertion or the tendinuous framework (Appendix 1). Before manual dissection, selected specimens were stained

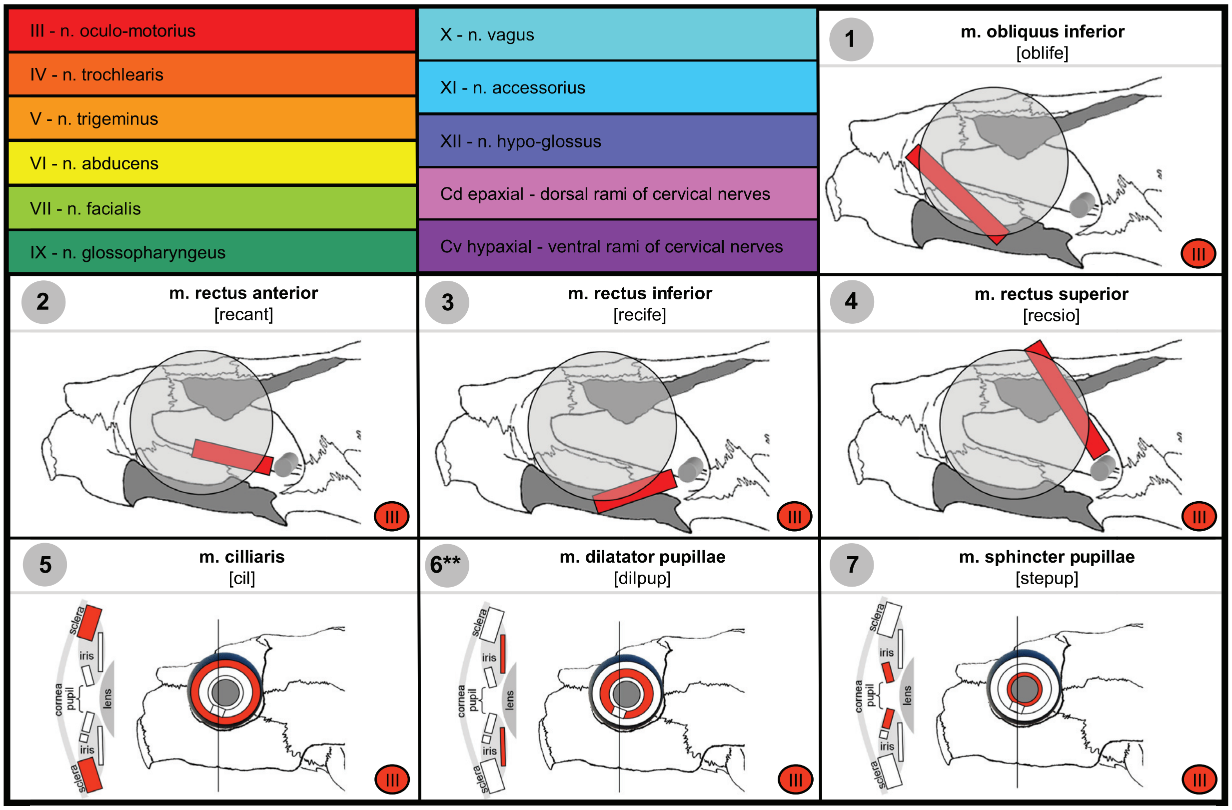


**FIGURE 6.** Schematic illustrations of all muscular units s. s. attaching the cranium in turtles. Muscular portions (coloured boxes) are represented in correlation to their related muscle (non coloured boxes). Illustrations of the skeleton are modified from Gaffney (1972: *Chelydra serpentina*) and Herrel et al. (2008: *Apalone spinifera*) (compare to Figure 5). The "rainbow colour code" represents the main innervation pattern of each muscular unit: innervated by n. oculomotorius (red, n. III), n. trochlearis (dark orange, IV), n. trigeminus (light orange, V), n. abducens (yellow, VI), n. facialis (light green, VII), n. glossopharyngeus (dark green, n. IX), n. vagus (light blue, n. X), n. accessorius (middle blue, n. XI), n. hypoglossus (dark blue, XII), dorsal branches of spinal nerves (pink, n. Sd), ventral branches of spinal nerves (purple, n. Sv). * = muscular unit only found in a few species/taxa, ** = only found in one species.

with alizarin-red in a diluted Borax solution (Borax 1:water 5) on an automated shaker for about 12–36 h, resulting in an irreversible staining of the bones in red, while muscles, nerves, and other soft tissue elements kept their whitish colouration. However, this procedure was not as successful as previously demonstrated for teleost fishes (Hertwig 2008; Werneburg and Hertwig 2009), due to the thick skin and very dense bones of turtles when compared to non-tetrapod vertebrates. As the specimens studied were relatively fresh, a good contrast was still visible between the whitish bones and the yellowish muscles; pigment cell sprinkled muscular structures.

## Nomenclature

The nomenclature of the neuro- and dermatocranial elements of turtles follows mainly Gaffney (1972, 1979). Splanchnocranial elements follow Fürbringer (1922) for the hyal apparatus and Siebenrock (1899) for the laryngeal apparatus. Cervical vertebrae nomenclature follows Herrel et al. (2008) (Figure 5). Shell element nomenclature follows Zangerl (1969). Nomenclature of the brain and cranial nerves is that of Shiino (1913).

Nomenclature of cranial musculature is newly defined, described, and depicted in Appendix 1 and Figures 6–15. Nomenclature and selected synonyms of remaining anatomical structures, such as tendinuous or overall spatial structures are listed in Appendix 5. To create the synonym-lists for 88 cranial muscular units (Appendix 1), more than 100 original references were compared, which discuss the cranial soft tissue elements of at least 70 turtle species following the taxonomic nomenclature of Fritz and Havaš (2007) (Appendix 6). An abbreviation guide can be found below; a list of abbreviations is presented in Appendix 7.

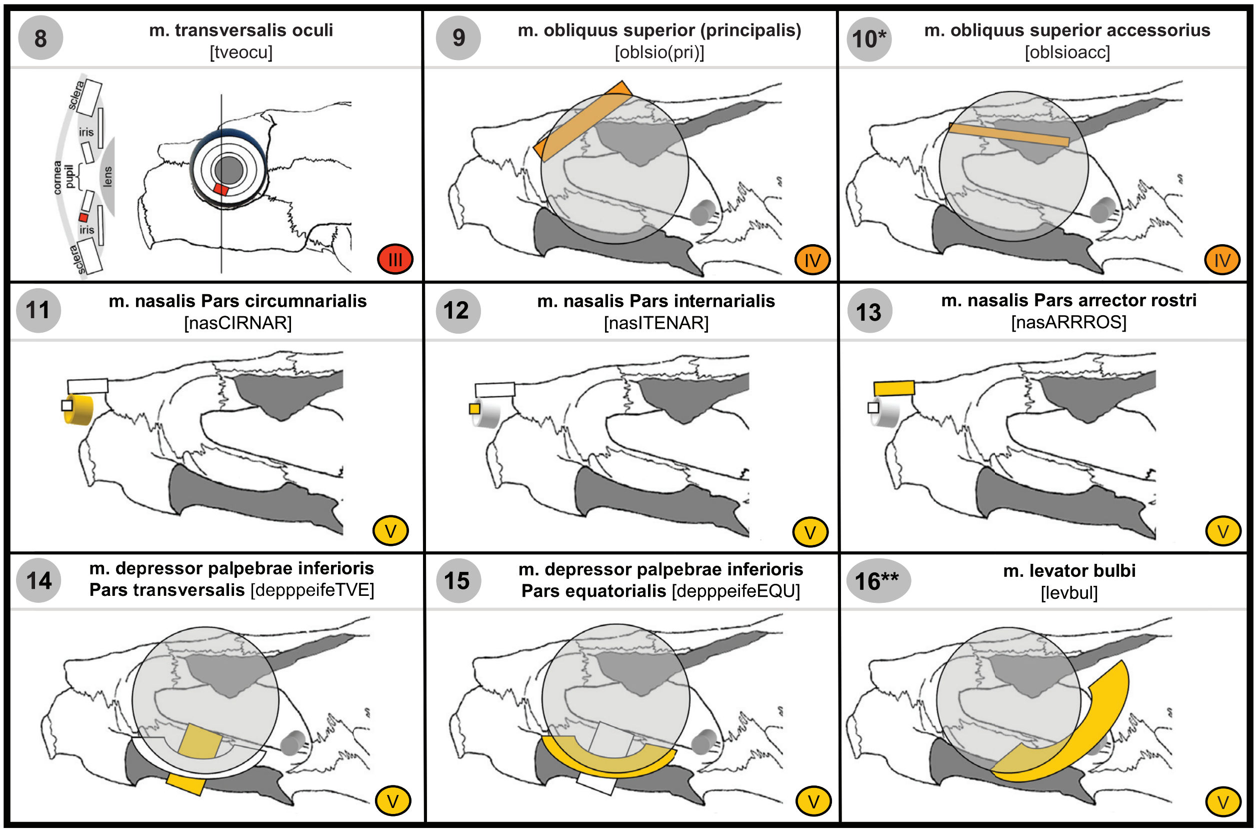


**FIGURE 7.** Continuation of Figure 6; continued in Figure 8. For caption, see Figure 6.

## NEW NOMENCLATURE AND THE SYNONYMY OF CRANIAL MUSCULATURE IN TURTLES

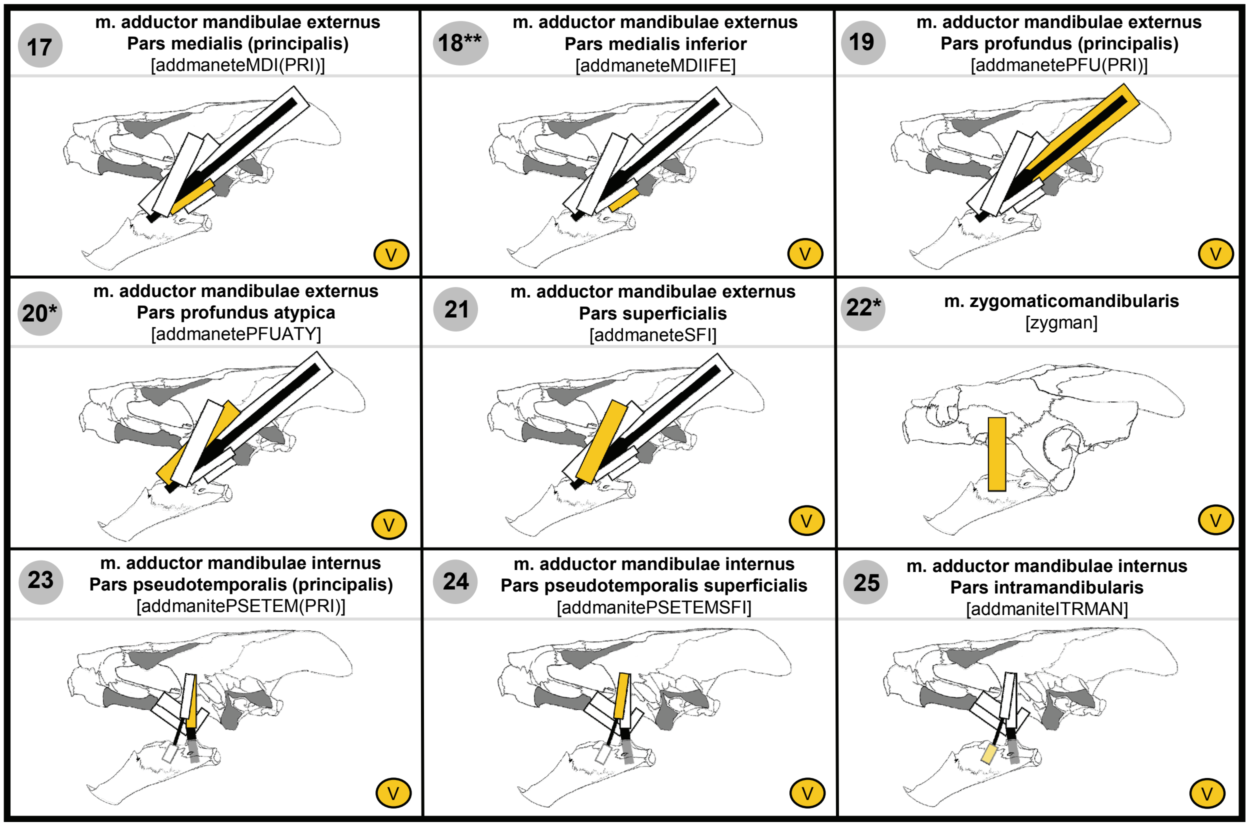
### Nomenclatural Traditions

In the literature, a large confusion about the terminology of muscular structures in vertebrates exists (Starck 1982). One reason is the anatomical, ontogenetic, and phylogenetic plasticity of muscular structures. If a muscle is separated into two prominent muscle heads – often performing particular functions – authors tend to name the parts of a single muscle as new "musculi" or "muscle portions". In older literature, authors introduced muscle names of mammals that they assumed to be "comparable" (homologous) to those of non-mammalian groups (e.g., Bojanus 1819-21; Cuvier 1935; Kesteven 1942-45; Starck 1982). In some cases, tables of synonyms are adopted from authors without checking the particular information that was previously presented by other authors cited within. In this study, I compared published tables of synonyms (e.g., Ogushi 1913b; Schumacher 1953-55, 1972, 1973; Poglayen-Neuwall 1953a) and re-checked all cited references by comparing the original anatomical descriptions in detail. All cranium-associated muscular structures that were ever described for turtle species are listed, including their related synonyms, proposed functions, and innervation patterns (Appendix 1). The criteria used to correlate synonyms in this study are based on the origin, insertion, spatial orientation, tendinuous framework, and innervation pattern of respective muscular structures. Homologies were also considered based on the pattern of muscle development known thus far (Edgeworth 1935; Rieppel 1990; Tvarožková 2006; personal observation). For the definition (Appendix 1) and discussion of particular structures of turtles see below.

### Definition of Nomenclature

The origin and insertion sites (Figure 1.1) of a muscular structure are any kind of hard or soft tissue material – except another muscular structure. Within the highly differentiated cranium, extended definitions of muscular structures – basically following proposals of fish anatomists Winterbottom (1974) with extensions by Hertwig (2005, 2008) and Werneburg (2007, 2009b) – are necessary as depicted in Figure 1 and described as follows.

In many cases, the definition of origin and insertion is very clear: the posterior, the dorsal, or



17 m. adductor mandibulae externus Pars medialis (principalis) [addmaneteMDI(PRI)]

18** m. adductor mandibulae externus Pars medialis inferior [addmaneteMDIIFE]

19 m. adductor mandibulae externus Pars profundus (principalis) [addmanetePFU(PRI)]

20* m. adductor mandibulae externus Pars profundus atypica [addmanetePFUATY]

21 m. adductor mandibulae externus Pars superficialis [addmaneteSFI]

22* m. zygomaticomandibularis [zygman]

23 m. adductor mandibulae internus Pars pseudotemporalis (principalis) [addmanitePSETEM(PRI)]

24 m. adductor mandibulae internus Pars pseudotemporalis superficialis [addmanitePSETEMSFI]

25 m. adductor mandibulae internus Pars intramandibularis [addmaniteITRMAN]

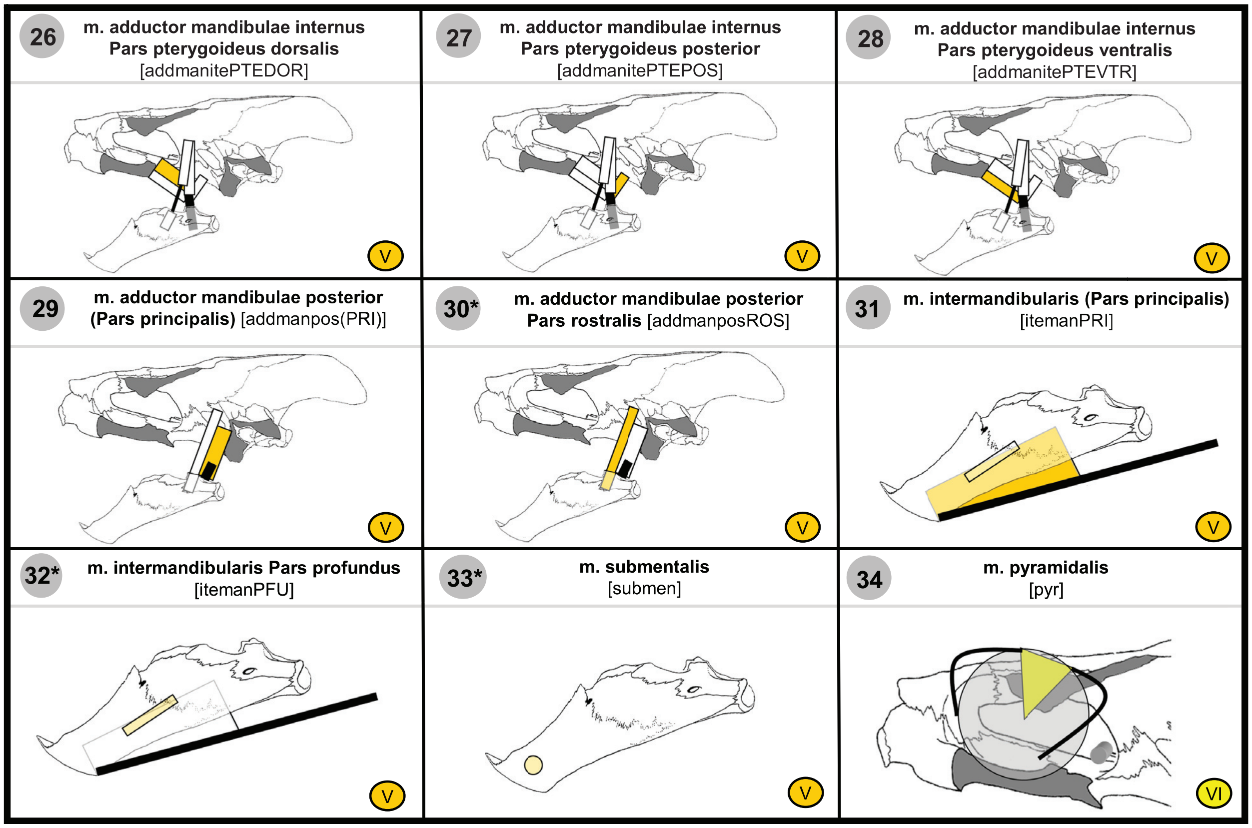
**FIGURE 8.** Continuation of Figure 6, Figure 7; continued in Figure 9. For caption, see Figure 6.

the less mobile structures (punctum stabile) provide the origin sites, while anterior or ventral structures or structures with a higher degree of mobility (punctum mobile) provide the insertion site (Starck 1982). There are more complicated examples, however, such as muscles of the tongue or the mouth floor. Concerning those, I define the following hierarchy of consideration for muscles only stretching between cranial structures: When defining an origin or insertion site, one should first consider the criterion of mobility to decide between both alternatives. If one cannot decide based on the mobility, one should consider the anterior-posterior axis next. If it is still not possible to decide between origin and insertion, one should consider the dorsoventral axis, with next option being the mediolateral axis. In that case, the origin would be medial, and the insertion would be lateral. One can summarise that hierarchy of consideration and define the related value of functional and spatial orientation as follows: mobility > anterior-posterior axis > dorsoventral axis > mediolateral axis. One example: A muscle spans between the symphysis of the dentaries and the dorsal integument of the tongue (m. genioglossus, No. 63). Although the lower jaw is situated more anteriorly and more ventrally, one has to consider the lower jaw to be the origin because it has less mobility when compared to the tongue.

In the nasal and the internal eye region, ring-shaped radiar muscular structures occur (No. 5-7, 11). I define the central attachment to be the origin and the outer attachment to be the insertion.

A muscle (Figure 1.1) is defined as having an own origin, course, and insertion site. It can be partly separated into muscle heads or muscle portions. Scanlon (1982) for example described one particular muscular structure (m. coracohyoideus Pars principalis, No. 58). During its course the muscle spatially splits into two muscle bellies, shortly after origin and shortly before insertion site those bellies are indistinguishably fused, hence the whole structure should be considered as a muscle sensu stricto (s. s.) (muscle layer, see below and Figure 1.5).

Muscles display different shapes. A parallel fibred muscle can have two direct (A in Figure 1.6) or one tendinuous attachment (B in Figure 1.6). A muscle with fan-shaped fibres generally attaches via a tendon (C in Figure 1.6). If the muscle has tendinuous attachments in the origin as well as in the insertion site it becomes spindle shaped (D in


26 **m. adductor mandibulae internus Pars pterygoideus dorsalis** [addmanitePTEDOR]

27 **m. adductor mandibulae internus Pars pterygoideus posterior** [addmanitePTEPOS]

28 **m. adductor mandibulae internus Pars pterygoideus ventralis** [addmanitePTEVTR]

29 **m. adductor mandibulae posterior (Pars principalis)** [addmanpos(PRI)]

30* **m. adductor mandibulae posterior Pars rostralis** [addmanposROS]

31 **m. intermandibularis (Pars principalis)** [itemanPRI]

32* **m. intermandibularis Pars profundus** [itemanPFU]

33* **m. submentalis** [submen]

34 **m. pyramidalis** [pyr]

**FIGURE 9.** Continuation of Figure 6, Figure 7, Figure 8, continued in Figure 10. For caption, see Figure 6.

Figure 1.6). In a bipinnated muscle, the fibres have direct attachments on the one hand and bilaterally attach to an internal tendon on the other hand (E in Figure 1.6). If fibres attach to such a tendon only on one side, a pinnated muscle is formed (Figure 1.6).

Muscle heads (Figure 1.2) – often confusingly described as singular muscles or muscle portions in the literature – are here defined as regional partitions of a muscle or a muscle portion. Muscle heads (singular: caput, plural: capitis) have either an own origin or an own insertion site. In their course, they fuse with other muscle heads into one inseparable muscle belly. Because of dependence to a particular muscle – or muscle portion – muscle heads are only considered in a descriptive way and in principle they do not gain a separated number (as a muscular unit) in Appendix 1 and Figures 6–16.

Muscle portions (singular: pars, plural: partes) (Figure 1.3) are partitions of a muscle, in which separate origins, courses, and insertions are recognisable. The muscle portions are muscle fibre bundles that are still connected to each other by shared or intercrossing fibres, or at least by a common tendon. One example is the nomenclature of “m. pseudotemporalis” and “m. intramandibularis” (Figures 2–4, Schumacher 1953-54) that I define as two portions of m. adductor mandibulae internus. Both portions are only connected to each other by a tendon (“Zwischensehne” of Poglayen-Neuwall 1953a). Parts of the “pseudotemporalis” portions are still connected to the remaining parts of m. adductor mandibulae internus (Figure 16) and consequently “pseudotemporalis” and “intramandibularis” have to be defined as portions of adductor mandibulae internus (No. 23-25). Bipinnated muscles may have two muscle portions as shown as E in Figure 1.6, characterised by a separated origin or insertion. In contrast, if this attachment of the whole muscle would be inseparable and the fibre courses would still be bipinnate, the whole structure would be called a muscle s. s. with an internal tendon (G in Figure 1.6). In the literature, some cases exist where the identity of a “muscle bundle” is not entirely clear, due to lack of descriptions or insufficient depiction concerning the homologisation propositions here presented. One case is the “Nebenbündelchen” (“little bundle nearby”) of König (1934/35), who described internal eye musculature. For now, I incorporated such unclear structures as a muscle head to the related

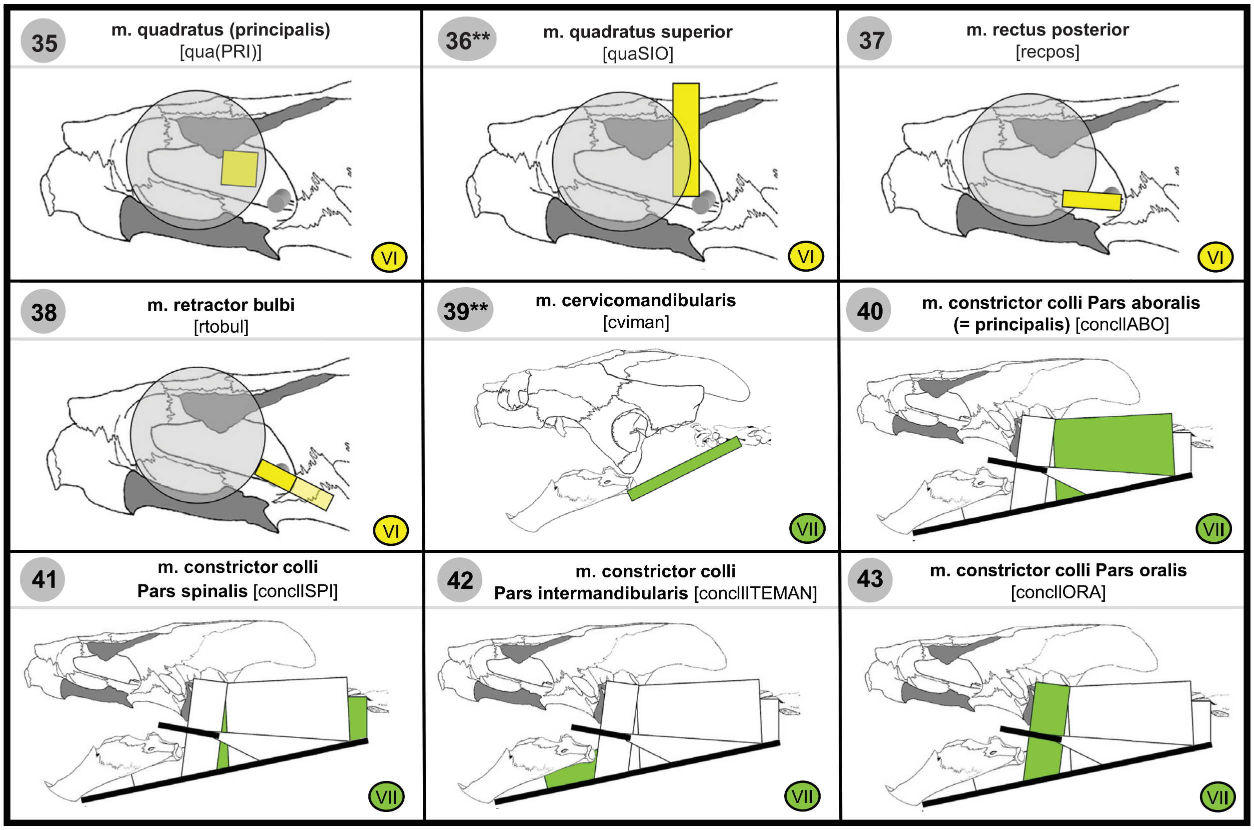


**FIGURE 10.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, continued in Figure 11. For caption, see Figure 6.

donor muscle or muscle portion; however, the identity of the "Nebenbündelchen" needs to be rechecked by specific studies of this region.

A muscle section (Figure 1.4) is defined as a completely separated muscle s. s. that clearly originates from another muscle in phylogeny. However – due to difficulties of prejudiced homologisations and developmental hierarchy – the term "section" is only used for discussion, but is not to name a particular muscle structure.

Finally, as an additional term one has to define the muscle layer. These are muscle fibres within one of the above defined muscular structures having a separated course and orientation. When compared to the surrounding or underlying muscle fibres, they never fully correspond to any origin or insertion site of a muscle, a muscle portion, or a muscle head (Figure 1.5).

In several cases, such as in trionychids (Ogushi 1913b; Lakjer 1926), little muscles (sections) or muscle portions obviously are separations of a donor muscle that one can see in related species as a consistent structure. If the bigger donor muscle retains its identifying (Appendix 1) general origin, course, insertion, and innervation, I only introduced a new term and number for the little muscle, but kept the nomenclature of the donor muscle as compared to the similar muscle of other species. Hence, by strict definition the synonyms (Appendix 1) do not necessarily represent homologous structures in the species as a whole structure, but instead only insertion/origin/innervation are comparable. An example is a set of species with an m. adductor mandibulae internus Pars pseudotemporalis (No. 23), which originates from the processus descendens of the parietal and inserts to the medial side of the lower jaw. Some of those species have an additional Pars pseudotemporalis superficialis (No. 24) – showing a different origin/insertion pattern – that most likely separated from Pars pseudotemporalis in evolution. The Pars pseudotemporalis (No. 23) does not show a major anatomical difference in those species, hence it should keep its name by the definition of Appendix 1. Following Sondhi (1958), I put an additional, informative term, "principalis", in brackets after the donor muscle name to differentiate it clearly, when a superficialis portion (No. 24) also exists. It would thus be Pars pseudotemporalis (principialis) (No. 23), while preserving its indicating number. Muscu-

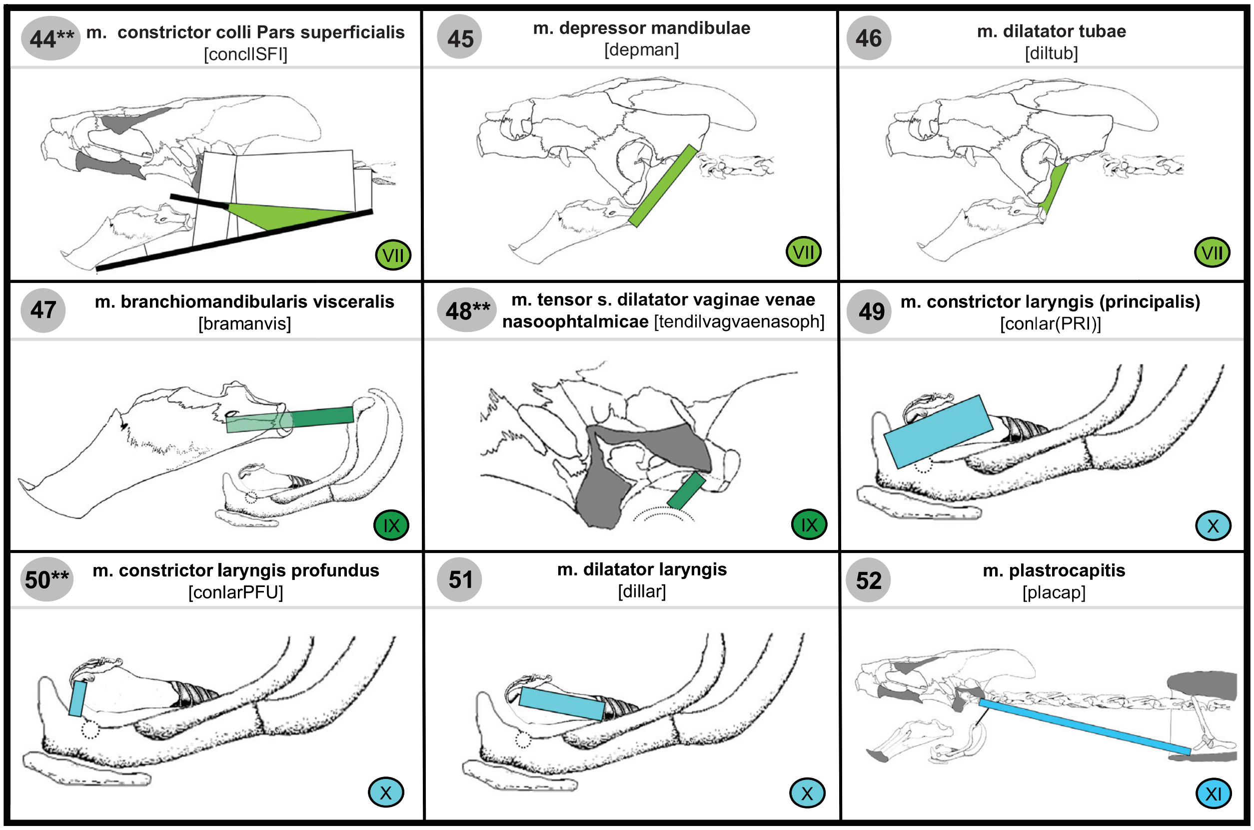


**FIGURE 11.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, Figure 10, continued in Figure 12. For caption, see Figure 6.

lar units as described in Appendix 1 should be considered as homologous at first glance (primary homology). If a small muscular structure turns out to be autapomorphically present in one group of species (secondary homology), one should consider the phylogenetic origin of that structure from a donor muscle/portion.

The terms anterior and posterior correspond to a defined region of a particular element, whereas rostral and caudal are used to indicate a spatial orientation of one element or a part of it when compared to others. Dorsal, ventral, lateral, and medial are used for both cases. Terms ending with -ad (e.g., mediad) indicate a direction. In combined terms, antero-/rostro- and postero-/caudo-form the first part, hierarchically followed by dorso- and ventro-. The terms –lateral/d and –medial/d always form the second part. Only two terms can be combined. As commonly found in recent literature, such constructions as “anterodorsomedial at element A” should be re-described as ‘anterodorsally on the medial face of element A’.

## Ordering

Following the approach of Bojanus (1819-21), Hoffmann (1890), and Ogushi (1913b), I created a numeration system for cranium-associated muscular structures. I introduce the term muscular units – which are, by definition, non-partitioned (non-portioned) muscles (s. s.) parri passu muscle portions (s. s.). Each muscular unit gains one number: listed and illustrated in Figures 6–15 and Appendix 1. There are several examples in which muscular units can occur as a muscle portion or as a separated muscle in different species. The assumption behind the statement of primary homology is based on spatial orientation (origin, course, insertion) and innervation pattern. The decision whether a muscular unit is named as a real muscle or as a muscle portion (Pars) in Appendix 1 is based on the most common behaviour of that muscular unit known in turtles. If a “regularly” occurring muscle portion “irregularly” occurs as a separated muscle in a particular species, it may gain a slightly modified name (musculus vs. Pars) (e.g., pterygoideus or pyramidalis muscular structures in *Emydura subglobosa*) – however, it should be discussed in regard to the

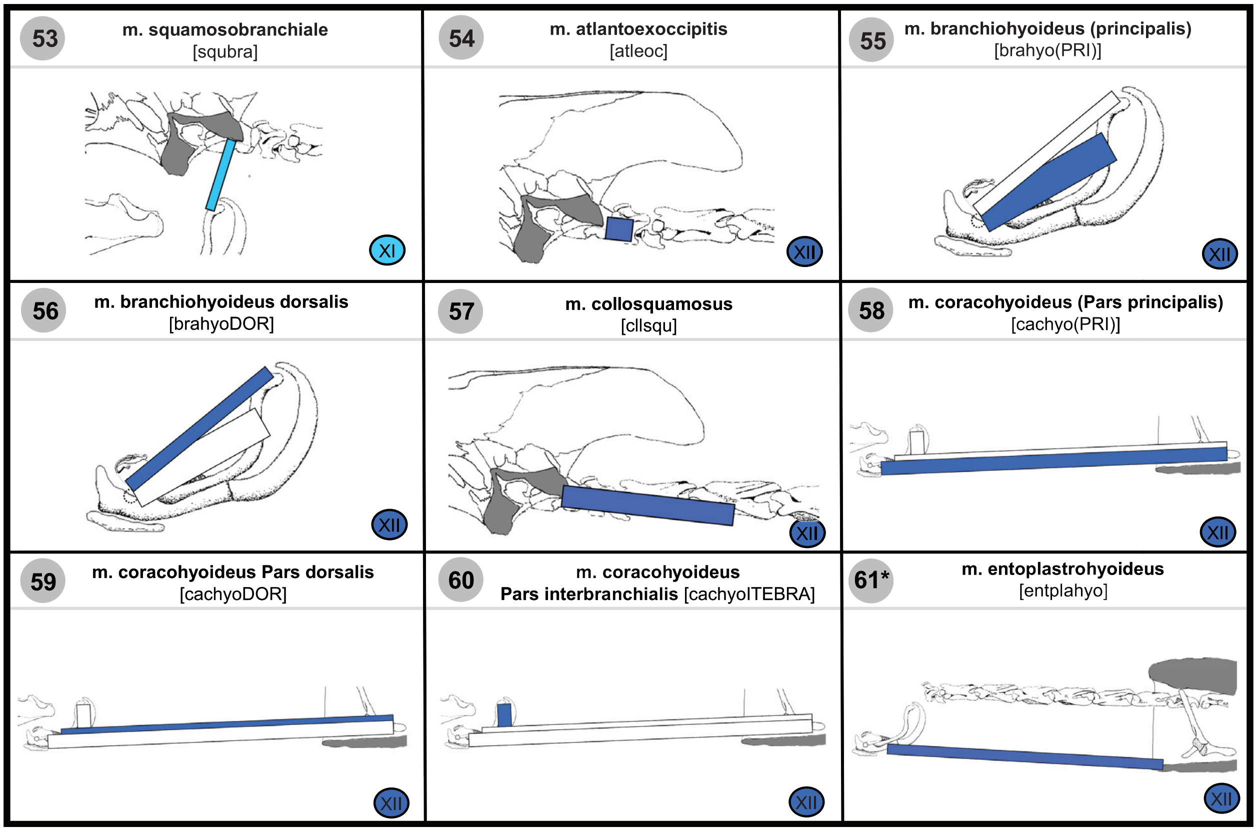


**FIGURE 12.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, Figure 10, Figure 11, continued in Figure 13. For caption, see Figure 6.

numbers as defined in Figures 6–15, and Appendix 1. Muscular units should be seen as numbered spatial, homologisable structures. In contrast, using only muscle names would lead to confusions and prepossessions in homology assumptions. Using the presented numbering system of muscular units, clear homologisation tables will be possible for comparing turtle data with those of other reptiles and other vertebrates. If muscles A and B are inferred to have fused in phylogeny, they may be discussed as a new muscle No. C (= A/B). The same is imaginable in ontogeny: if a muscle Anlage is known to separate into muscle D and E in development, it may be called Anlage No. D/E.

The muscular units presented in this study (Appendix 1, Figures 6–15) are grouped and ordered first according to their innervation (cranial nerves: n. III-XII, spinal nerves: n. S1, etc.) and separation pattern (muscle portions of a muscle) and – within those groups – in a regional and alphabetical order.

Neck muscles are often innervated by several spinal nerves at the same time, depending on the anterior-posterior extend, and the detailed anatomy of the muscle, hence a clear order of neck muscles – as done for the cranial nerves innervated muscles – was not possible. Gasc (1981) discussed the problem with allocating neck muscles of turtles to the epaxial and hypaxial system due to unclear ontogenetic and phylogenetic identities and innervation patterns. In the highly differentiated neck muscles, embryological rearrangements and integrations of several myotomes were also conceivable. After reviewing all available descriptions of cranium-associated neck musculature in turtles, I was able to assign each muscular unit to epaxial (dorsal branches of spinal nerves, nn. Sd) or hypaxial (ventral branches of spinal nerves, nn. Sv) musculature; within both groups muscular units are ordered in an alphabetical order. In some cases, the controversial identity of particular structures is discussed in this paper.

## Abbreviation Guide

Due to space restrictions, abbreviations are often necessary in journal figures. However, abbreviations are defined differently in the literature, mainly intuitively, and are based on the anatomical focus of the respective author – introducing difficulties when broadening the anatomical structures

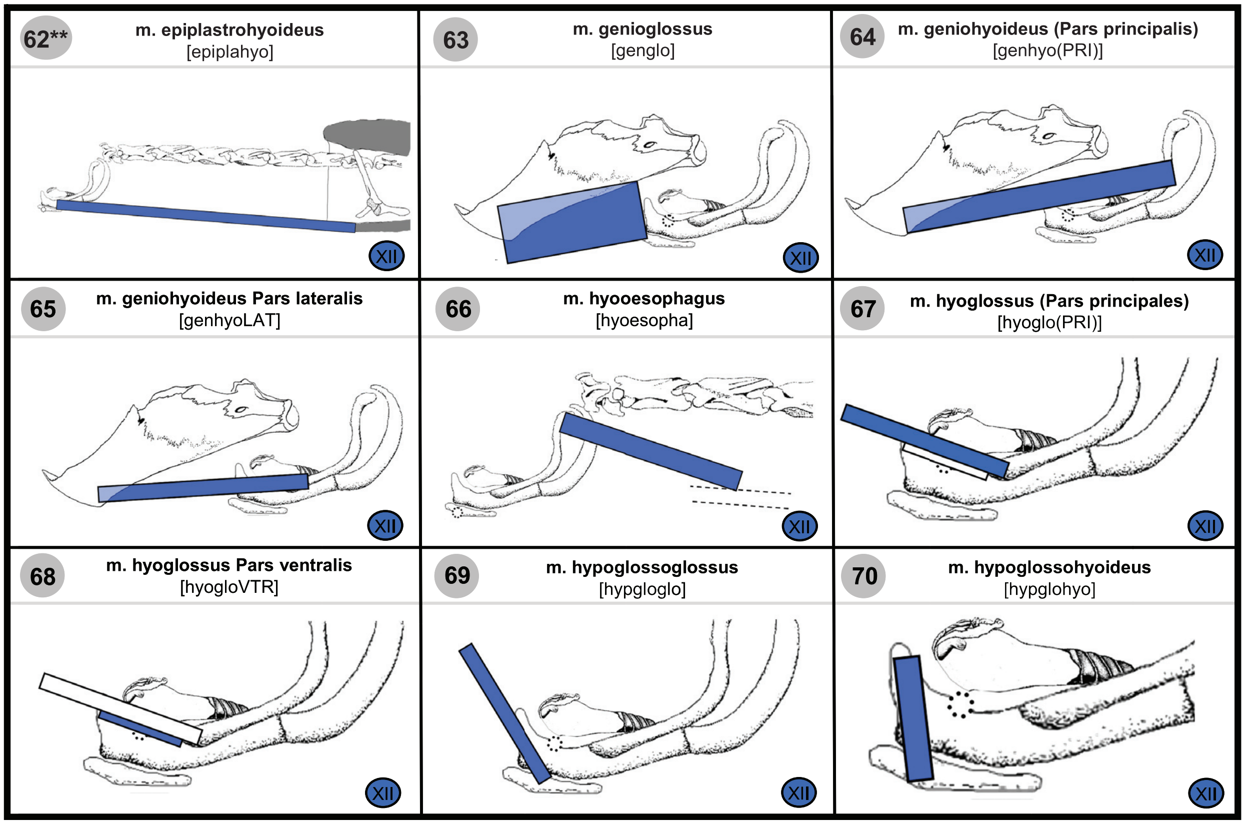


**FIGURE 13.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, Figure 10, Figure 11, Figure 12, continued in Figure 14. For caption, see Figure 6.

analysed (Rieppel 2007; Jones et al. 2009). I present a new and traceable abbreviation system that is primarily designed using the first three letters in the respective word parts (e.g., cil for "ciliaris"). If word parts contain less than three letters (e.g., "exoccipital") or begin with the same three letters (e.g., "sup…"), particular abbreviations are used – formed by the first letter of the word and the first letter(s) of the following syllable(s) (compare to "coronoid" or "corpus"; Appendix 7) – finally forming three letters (eoc for "exoccipital"). A few exceptions are of course unavoidable; however, this approach could be easily used to define abbreviations of additional anatomical elements.

The abbreviations of muscular units (Appendix 1) also follow the abbreviation guide (Appendix 7). Therein normal letters are used for the muscle (s. s.), and capital letters are used to indicate muscle portions of that muscle, e.g., the Pars medialis of an m. adductor mandibulae externus is abbreviated as m. addmaneteMED (No. 17). For easier reading, the muscle numbers as defined in Appendix 1 are added to the abbreviations. Muscle heads (s. s.) do not gain an anatomical term; however, they may gain an additional additive description in the text and can be labelled as regular letters added to the number of the muscular unit to which it belongs (e.g., caput "a" of muscular unit No. 40 = No. 40a).

Spatial structures expanding over several singular elements are labelled without abbreviation in the figures of this study (e.g., otic chamber, proc. trochlearis pterygoidei, or fascia); however, selected synonyms and suggestions for their abbreviation can be found in Appendix 5. Tendons – tendinuous attachments of muscular units with a +/- round cross section – do not gain a separate name and are handled in a descriptive way. The names of cartilages (car.), of strong connective tissue spanning between bones (ligaments, lig.), as well as flat tendinuous attachments of muscular units (aponeuroses, apo.), are abbreviated like bones and nerves (Appendix 7) or muscles (Appendix 1).

## THE CRANIO-CERVICAL SKELETON OF *EMYDURA SUBGLOBOSA*

The skull of *Emydura subglobosa* is twice as long as high. The maximum skull width is between

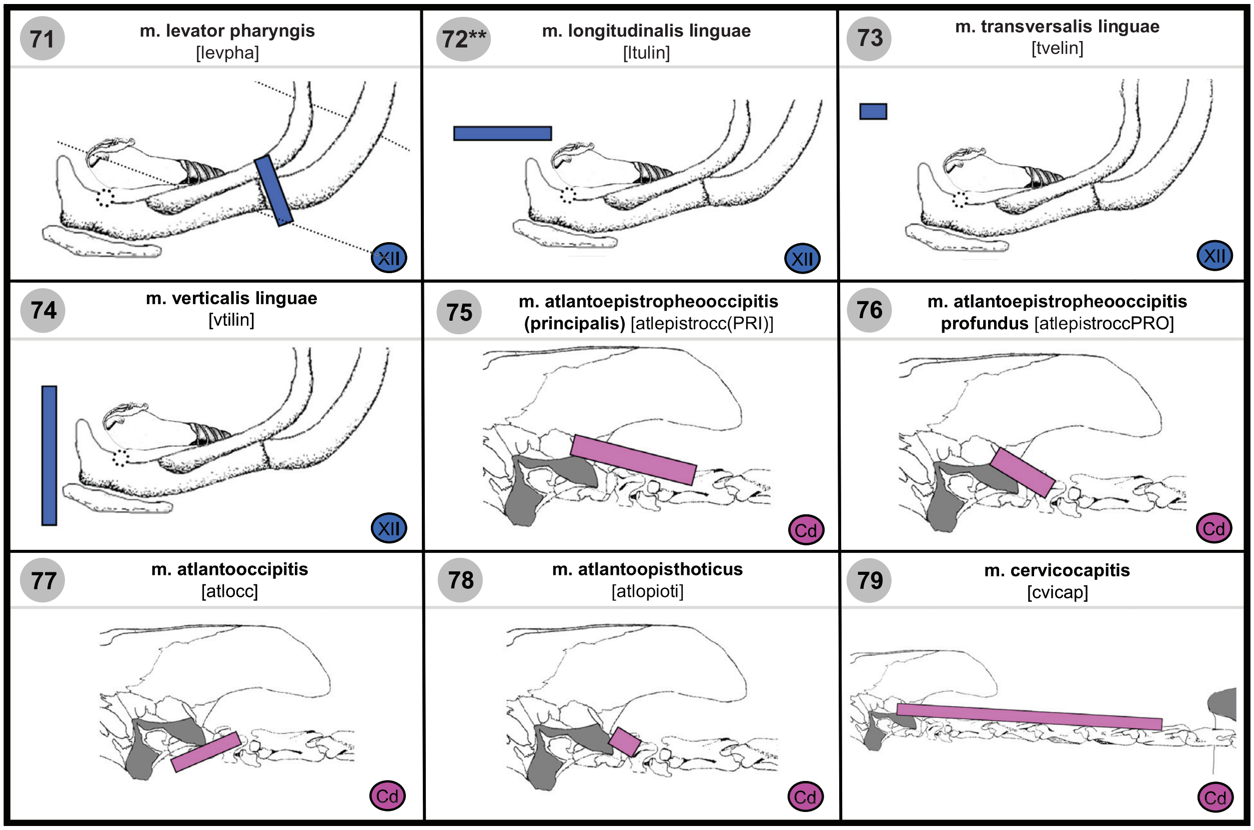


**FIGURE 14.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, Figure 10, Figure 11, Figure 12, Figure 13, continued in Figure 15. For caption, see Figure 6.

the squamosal wings, which participate in the formation of the otic capsule. The snout region is round in frontal view (Figure 17.2), and the posterior part of the skull is dorsoventrally flattened (Figure 17.4). The adductor (mandibulae) chamber is bordered by the orbital region anteriorly, the lower jaw and the pterygoid ventrally, by the otic capsule posteroventrally, and by a bony bridge – mainly formed by the squamosal – laterally in the temporal region. Separated by the otic capsule, the adductor chamber is formed by two regions, an anteroventral postorbital cavity, and a posterodorsal temporal cavity (Figure 18.3). In the fossa orbitalis, 13 scleral bones are present (Figure 17.1, Werneburg et al. 2009). As in all Testudines (Mickoleit 2004), eight cervical vertebrae exist (Figure 18.3). Posteroventral of the first cervical vertebra (atlas), a separated "processus odontoideus" (sensu Ogushi 1911, see also Kasper 1903) is visible. It represents the intercentrum of the atlas (C1' of Herrel et al. 2008; Hoffstetter and Gasc 1969).

## Neurocranial Elements

**Basisphenoid.** The unpaired and flat basisphenoid is situated posteroventrally to the eye region and has an oval shape that is broader than long. Anteriorly, it contacts the pterygoids; anterolaterally, it contacts the prootics, and posteriorly, it comes in contact to the basioccipital (Figure 18.1-2).

**Basioccipital.** The unpaired basioccipital has an oval shape that is broader than long. Anteriorly, it contacts the basisphenoid. Laterally, it has a narrow connection to the opisthotic and posteromedially, it contacts the exoccipitals each side. Posteromedially, it forms a broad processus that forms the lower part of the condylus occipitalis (Figures 18.1-2, 27.2). Dorsally, this processus meets the condylus processi of both exoccipitals.

**Prootic.** Together with the quadrate, the prootic forms the posteroventral margin of the whole adductor chamber. Anteriorly and anterodorsally, it sutures with the parietal. It sutures with the quadrate ventrolaterally. In its posterior region, it contacts the opisthotic, and posteromedially it contacts the supraoccipital. Posterolaterally, the prootic meets the squamosal and ventromedially, it meets the basisphenoid. Anteroventrally, it participates to the formation of the foramen nervi trigemini.

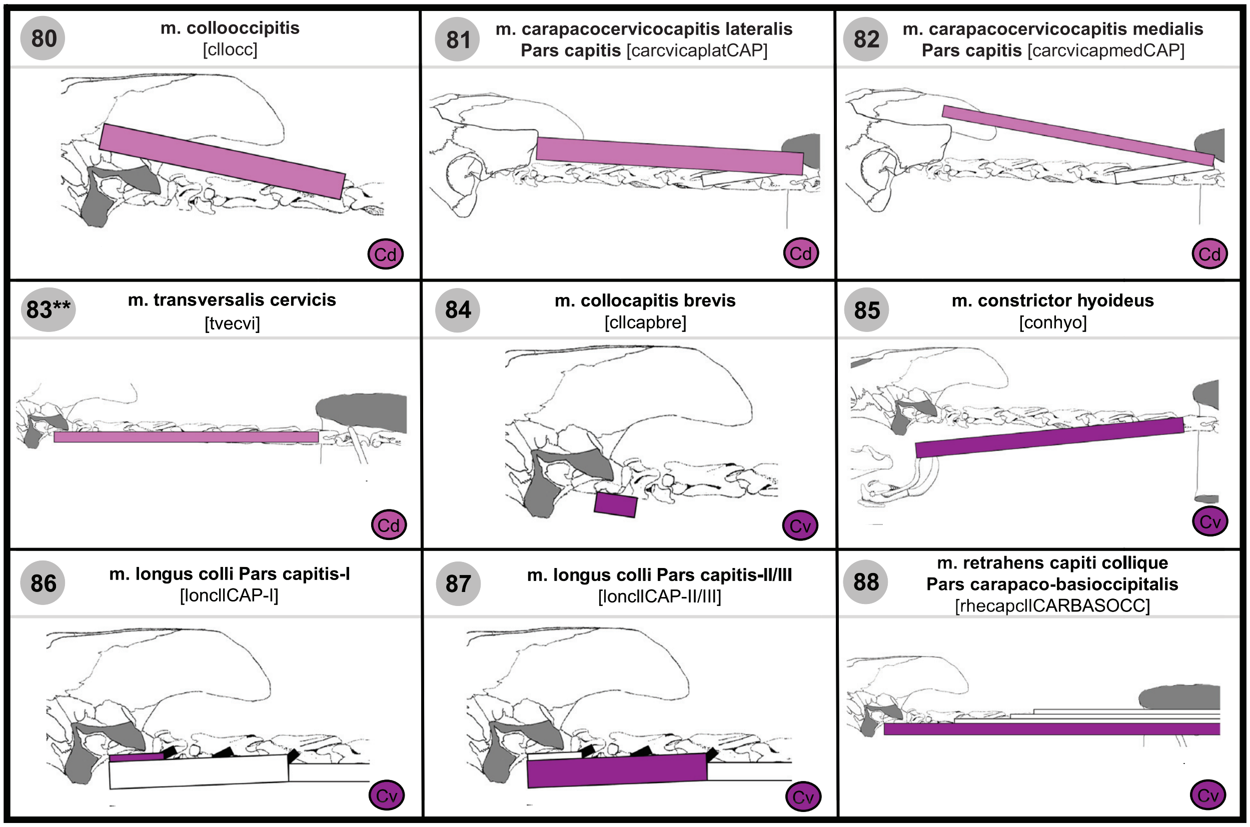


**FIGURE 15.** Continuation of Figure 6, Figure 7, Figure 8, Figure 9, Figure 10, Figure 11, Figure 12, Figure 13, Figure 14. For caption, see Figure 6.

**Opisthotic.** The opisthotic forms the posteroventral margin of the temporal cavity. Anteriorly, it contacts the prootic, laterally the squamosal, dorsomedially the supraoccipital, posteromedially the exoccipital, anteroventrally the basisphenoid, and posteroventrally the basioccipital.

**Exoccipital.** Except for the dorsalmost part – which is formed by the supraoccipitals – the exoccipitals form the surrounding margin of foramen magnum. Dorsally, the exoccipital contacts the supraoccipital, and laterally it contacts the opisthotic. Ventrally, it forms a posterior processus that forms the dorsolateral part of the condylus occipitalis. This processus meets the basioccipital ventrally (Figures 18.1-2, 27.2).

**Supraoccipital.** The unpaired supraoccipital posteroventrally forms the dorsal most margin of the foramen magnum. Anterodorsally, it contacts to the parietals in their posteromedial region, and in dorsal view, the supraoccipital is wedge-shaped. On both sides, the bone anteriorly contacts the vertical plates of the parietals and anteroventrally it contacts the prootics. Posteroventrally, it contacts the dorsal parts of the opisthotic and the exoccipitals. The crista supraoccipitalis is not elongated posteriorly and in lateral view, the supraoccipital and squamosal form a consistent curvature (Figure 17.1).

## Splanchnocranial Elements

### First Pharyngeal Arch: Palatoquadrate Element

**Quadrate.** The quadrate forms the dorsal, ventral, anterior, and medial wall of the otic capsule. Laterally, the quadrate forms an anterior and a ventral vaulting that results in a concave, chalice like shape of the otic capsule. In its posteroventral region, the quadrate is separated by a groove that continues mediad along the curvature of the quadrate and forms the incisura columellae auris; herein, the columella auris is situated. Posterodorsally, the quadrate has a broad circular contact area with the squamosal. Anteromedially and dorsomedially, it meets the prootic and posteromedially, it meets the opisthotic. Anteroventral of its medial face, it meets the posterolateral most edge of the pterygoid. Together with the prootic, the quadrate forms the posteroventral margin of the whole adductor chamber.

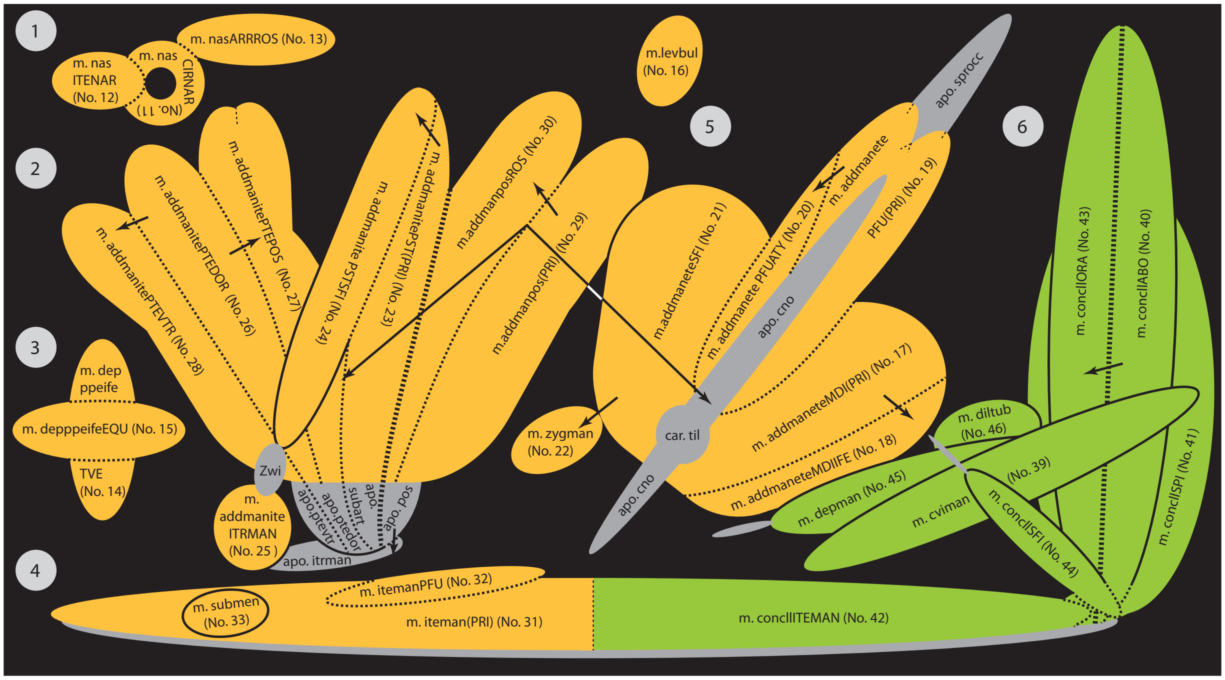


**FIGURE 16.** Scheme for the fluid pattern and plastic arrangement of n. trigeminus (V, orange) and n. facialis (VII, green) innervated musculature in turtles, including all potential muscular units as defined in the presented study; tendinuous structures are shown in grey. The scheme shows the maximum of partitions, which are observeable in turtles. There is no case, in which all muscular units are present. However, the arrows indicate potential phylogentic and ontogenetic origins of particular units. The thin dotted lines indicate different degrees of muscle separations, forming labelled muscle portions or non-labelled muscle heads. 1) Nasal musculature ((No. 11-13), 2) m. adductor mandibulae internus (No. 23-28) and posterior (No. 29-30), 3) lower eyelid muscle (No. 14-15), 4) intermandibular musculature: n. trigeminus (V) and n. facialis (VII) innervated muscular structures are fused (No. 31-33/42), 5) m. adductor mandibular externus (No. 17-21) and m. zygomaticomandibularis (No. 22), 6) n. facialis (VII) innervated musculature (No. 39-46). For abbreviations, see Appendices 1, 2, and 4.

### First Pharyngeal Arch: Mandibular Elements

**Cartilago meckeli.** The cartilago meckeli is situated in the primordial channel of the lower jaw, which is formed mainly by the medial face of the dentary, but also partly by prearticular and angular.

**Articular.** The articular forms the posterior most part of the lower jaw, and it articulates with the anteroventral curvature of the quadrate. Therefore, it forms a depression posterodorsally. Anteriorly, it contacts the dentary, anterodorsally, and laterally the surangular, ventrally the angular, and anteromedially and medially the prearticular.

### Second Pharyngeal Arch:Hyomandibular Elements

**Columella auris.** The columella auris extends into the cavum tympani of the otic capsule as a bar-shaped bone (Figure 30.4). It passes through the incisura columellae auris that is formed by the quadrate. Laterally, it connects with the extracolumella. Within the pericapsular recess of the inner ear (Wever 1978), the bar-shaped columella broadens as a disk that attaches the cochlear duct.

**Extracolumella.** The extracolumella (Wever 1978) is formed as an oval disk-shaped cartilage that connects laterally to the tympanic membrane (Figures 22.5, 23.3, 29.1, 29.3, 30.2-3). Medially, in the centre of the disk, it forms a process that connects to the columella auris.

### Second Pharyngeal Arch: Hyal Element

**Cornu hyale.** The short-bared cartilaginous cornu hyale is sitated below the suture of palatine and pterygoid in the closed mouth. Proximally, it articulates to the lateral process of anterior region of corpus hyoidei (Figures 22.4, 23.2).

### Second to Fourth Pharyngeal Arch: Basibranchial Elements

**Corpus hyoidei.** In the studied specimens, the flat unpaired corpus hyoidei is ossified only in its posterior region, and the ossification has a convex shape (Figures 18.1-2, 19). Together with the corni

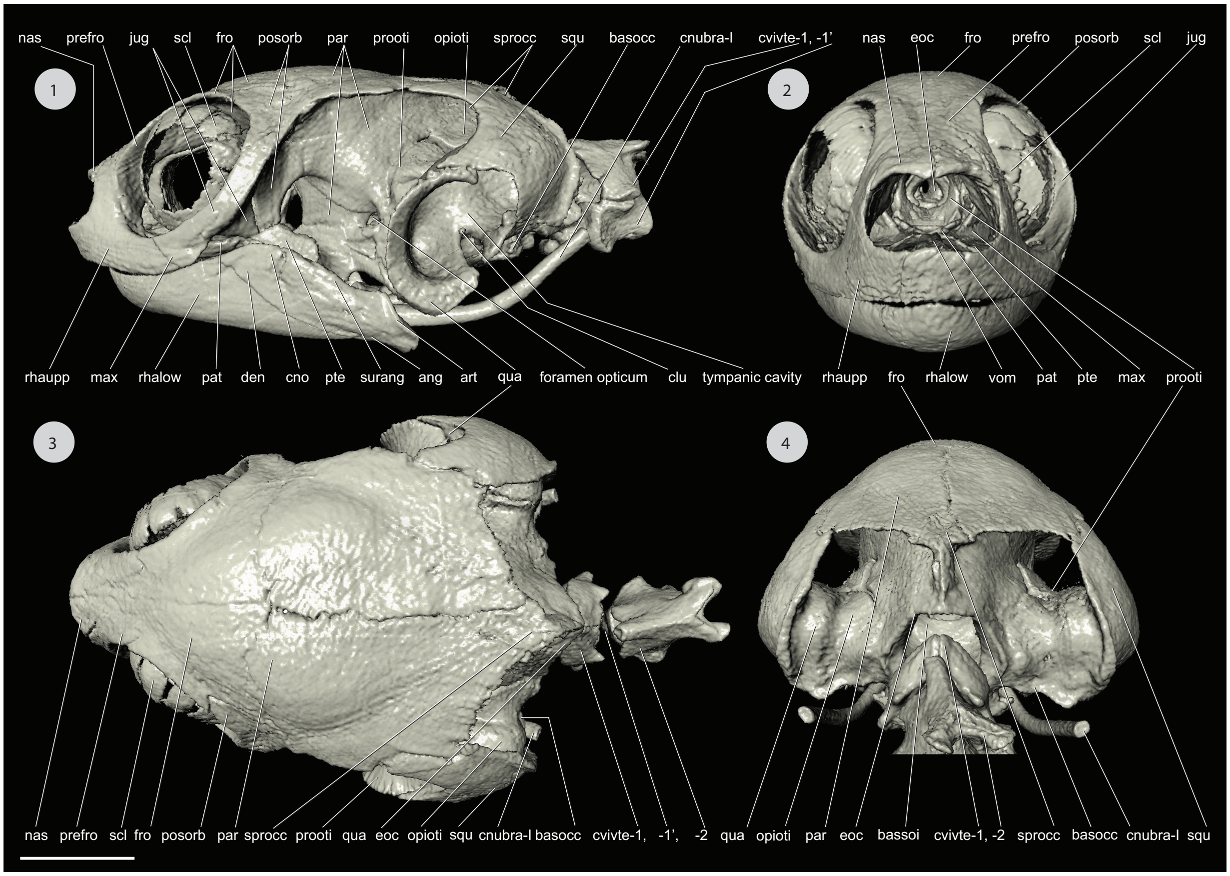


**FIGURE 17.** Subadult specimen of Emydura subglobosa (PIMUZ labNo 2009.37). Computer tomography based three-dimensional reconstruction of the skull in 1) left lateral, 2) frontal, 3) dorsal, 4) posterodorsal view. In the shown subadult specimen the cornu branchial-II and most of the corpus hyoidei is not yet ossified and not visible in CT-scan. Bar scale of 4 mm stands for 1-6. See also movies of Supplement S1-S3. Bar scale 4 mm. Continued in Figure 18.

hyale, the corni branchial, and the hypoglossum, it forms the hard tissue base of the mouth cavity. It is situated ventrally to the basisphenoid and pterygoid. Anteriorly, the cartilaginous region of corpus hyoidei forms the processi lateralis anterior that articulate to the corni hyale. Between those processi, the oval fenestra ossis hyoidis is formed, having an anterior-posterior extension. In the anterior cartilaginous region, posterior to the articulation with the corni hyale, the corpus hyoidei articulates directly with the cornu branchial-I; only a very small processus lateralis intermedius is suggestively recognisable. In the posterior region, lateral to the ossification centre, the corpus hyoidei laterally articulates with the corni branchial-II at the cartilaginous processus lateralis posterior. Anterodorsally, the corpus hyoidis forms an unpaired medial processus lingualis that is situated above the hypoglossum.

### Third and Fourth Pharyngeal Arch: Branchial Elements

**Cornu branchial-I.** The well ossified cornu branchial-I is situated below the pterygoid and the otic capsule. It articulates medially with the medial part of the corpus hyoidei. When the mouth is closed, its distal – corpus hyoidei opposing – part extends caudad beyond the skull up to the level of the first cervical vertebra. Here it is connected to the posteriormost edge of the squamosal via a short and strong tendon.

**Cornu branchial-II.** In subadult specimens, the cornu branchial-II is still partly cartilaginous (Figures 19–21). It is situated below the otic capsule and it reaches the anterior neck region ventromedially. Medially, it articulates with the posterior part of corpus hyoidei. As for cornu branchial-I, the distal part of the element extends caudad shortly beyond the posterior border of the skull.

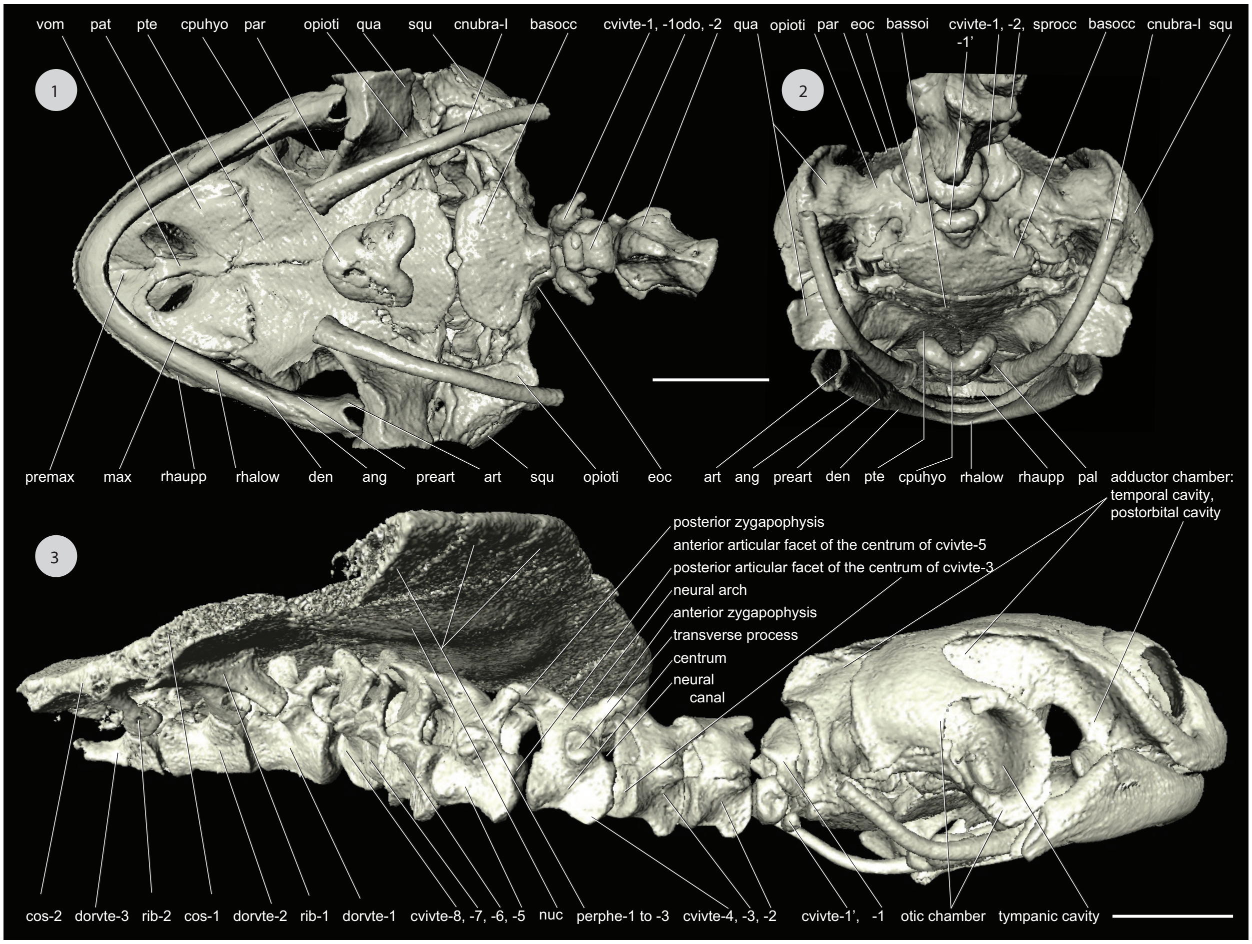


**FIGURE 18**. Continuation of Figure 17. Subadult specimen of *Emydura subglobosa* (PIMUZ labNo 2009.37). Computer tomography based three-dimensional reconstruction of the skull in **1)** ventral, **2)** posteroventral and **3)** the neck region in right lateral view. The carapace/trunk in 3) is cut in the anteromedial region. Bar scale: 1 and 2) 4 mm; 3) 2 mm.

## Skeletal Derivates of the Posterior Pharyngeal Arches

**Cartilago thyreoidea.** Dorsal to the fenestra ossis hyoidis of the corpus hyoidei, the tubular larynx is situated. It is formed by three cartilages that are very similar in shape when compared to those referred for *E. krefftii* (Siebenrock 1899). The short tube-like cartilago thyreoidea is the largest element of the laryngeal apparatus, and it is built of about five partly fused tracheal rings (Figure 19). Its dorsal region remains open, forming a longitudinal groove, the rima glottidis (Figure 25.1). It is closed in its posterior most part only. Posteriorly, it contacts the trachea. From its middle to anterior region, it is truncated from dorsal by the adjacent cartilagi arytaenoidea, resulting in an acuminated anteroventral tip. In the medial region of its dorsal groove, cartilago thyreoidea encloses the cartilago cricoidea and contacts it laterally.

**Cartilago arytaenoidea.** Dorsally to the cartilago thyreoidea, the paired triradiate cartilagi arytaenoidea are situated. Each of them has a short lateral processus muscularis in its anterior half. Ventrally, the cartilageproceed in a processus vocalis that directly contacts the anterior truncation of cartilago thyreoidea. The caudad-leading processi articularis of the contralateral cartilagi arytaenoidea do not contact each other, but their posterior tips contact the cartilago cricoidea.

**Cartilago cricoidea.** This very small oval and unpaired cartilage is situated within the medial part of rima glottitis. It contacts the cartilago thyreoidea laterally each side and the cartilagi arytaenoidea anterolaterally.

**Trachea**. In the subadult, at least four tracheal rings show ossifications that may be descendens of posterior pharyngeal ("gill") arches (Figure 19).

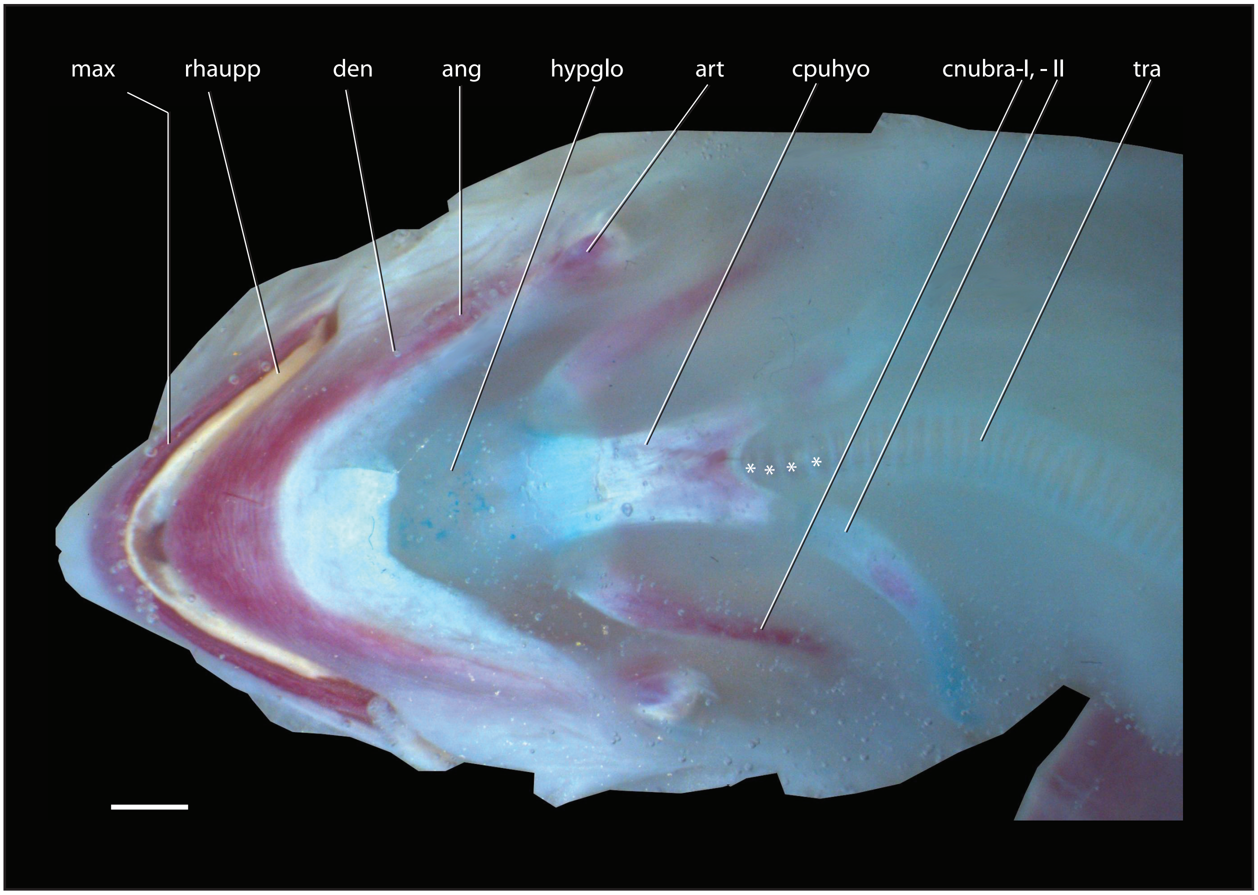


**FIGURE 19.** *Emydura subglobosa*. **1)** Ventral view of the head of a cleared and double stained subadult specimen (PIMUZ lab# 2009.9). Red = calcified tissue, blue = cartilaginous tissue, light blue = connective tissue, yellow = non stained keratin. Note the different degree of ossification of the bones of the hyoid apparatus; especially the cornu branchial-II has a very low amount of ossification. Asterisks indicate ossification centres in the tracheal rings.

## Dermatocranium

### Skull Roof

**Nasal.** The nasal is a rectangular element and about half the length of the prefrontal. Compared to all other *Emydura* species described or depicted (Schumacher 1954-55b; Gaffney 1975, 1979), the dorsoventral altitude is more flattened. The contralateral nasals meet each other anteriorly in a medial suture. Posteromedially, the nasal contacts a narrow anterior process of the frontal, and posteriorly it sutures the prefrontal.

**Prefrontal.** The dorsal plate of the prefrontal is small and rectangular. Its posterior most part forms a part of the dorsal margin of the orbit. The larger ventral plate of the bone extends ventrally and forms the anterior wall of the fossa orbitalis. Anteriorly and posteriorly, the prefrontal meets along transverse sutures with the nasal and frontal, respectively. Ventrally, it contacts the medial plate of the premaxilla. Dorsally, the prefrontals do not meet each other, and they are medially separated by anterior processi of the frontals.

**Frontal.** The frontal is an elongated flat triangular bone that forms the major part of the dorsal margin of the fossa orbitalis, and it is three times as long as the prefrontal. The contralateral frontals are sutured medially. Posterolaterally, they are in contact with the postorbitals and posteriorly with the parietals. In its anterior region, the frontal forms a median processus that is laterally bordered by the prefrontal and anteriorly by the nasal. Laterally, the frontal forms the slightly vaulted dorsal rim of the orbit.

**Parietal.** The parietal consists of two plates. Dorsally, the flat horizontal plate is twice as long as the frontal, it has a rectangular shape and forms the major part of the skull roof. This dorsal plate contacts the frontal anteriorly, the postorbital anterolaterally, the supraoccipital posteromedially, and the squamosal posterolaterally. Ventrolateral of the horizontal plate, the vertical plate of the parietal

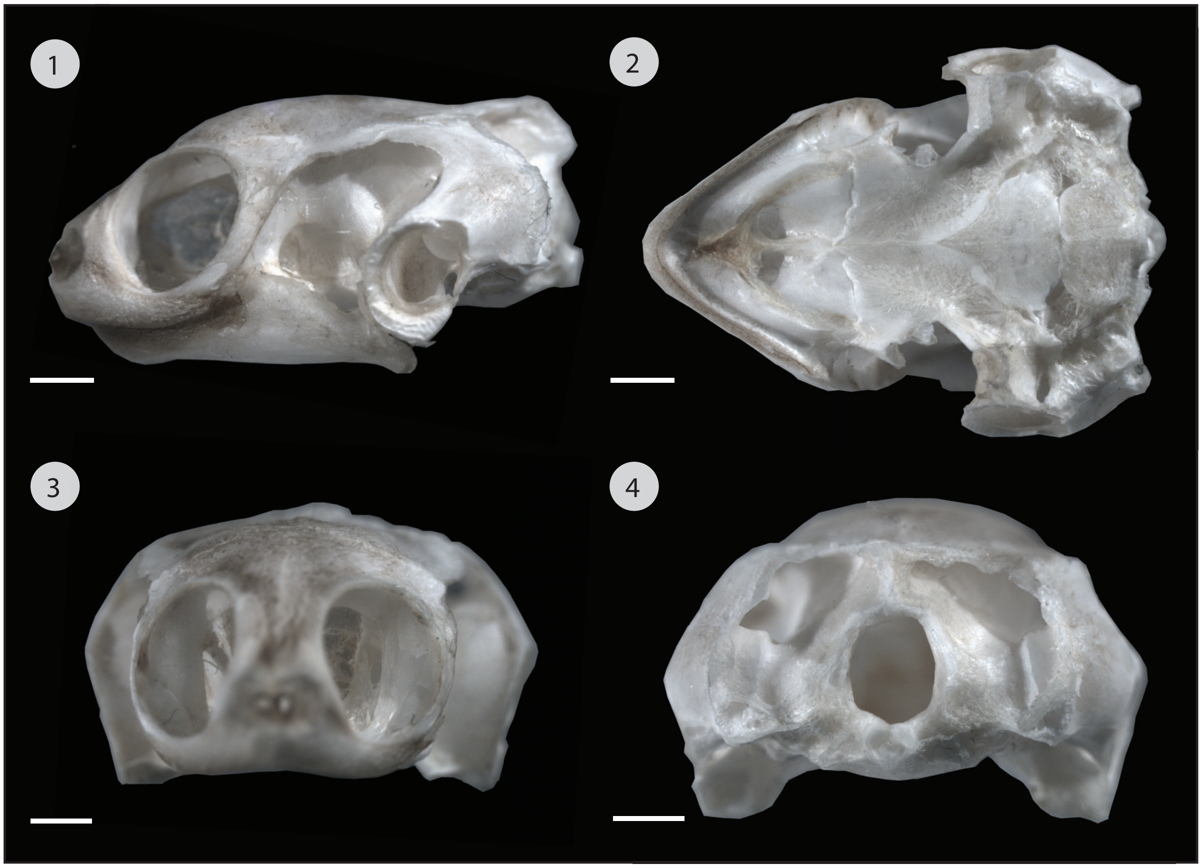


**FIGURE 20.** Skull of a subadult specimen (PIMUZ lab# 2009.38) (same specimen as in Figures 28-31): **1)** Left lateral view of the skull (focus lateral bones). Skull without lower jaw: **2)** Ventral, **3)** frontal (focus on postorbital wall), **4)** caudal view. Scale equals 2 mm. Continued in Figure 21.

forms the lateral wall of the braincase. Anteriorly, the vertical part of the parietal contacts the postorbital, posteriorly the supraoccipital, and posteroventrally the prootic. Ventrally, it continues as a concave, mediad leading bone lamella that contacts the pterygoid dorsally. Posterior to the suture with the pterygoid and ventral to the suture with the prootic, the vertical plate of the parietal contributes to the formation of the foramen nervi trigemini.

### Temporal Region

**Postorbital.** The postorbital contacts the parietal posterodorsally, the frontal anterodorsally, and the jugal ventrolaterally. It forms the posterodorsal wall of the fossa orbitalis and the anterodorsal border of the adductor chamber. A ventral-bar shaped part of the bone ventrally contacts the processus trochlearis of the pterygoid at its anterodorsal edge.

**Jugal.** In lateral view, the jugal is a bar-shaped bone with a lateral, convex curvature. It forms the major part of the posterior rim of the fossa orbitalis and the anterior border of the adductor chamber. Dorsally, it contacts the postorbital, ventrally the posterodorsal part of the maxilla. Ventromedially, the jugal forms a triangular processus, which dorsally contacts the postorbital and ventrally the maxilla. Ventrally of the postorbital, a tip of the jugal contacts the processus trochlearis pterygoidei. In *E. subglobosa*, as in other *Emydura* species, a quadratojugal is missing, and no zygomatic arch is formed.

**Squamosal.** As a vaulted posterodorsal part of the otic capsule, the anterior part of the squamosal contacts the quadrate at its posterodorsal region. Anteriorly, it contacts the prootic. Posteriorly and medially, it sutures the opisthotic. Dorsolaterally, a bone lamella is developed that extends dorsomediad in a convex course. The lamella narrows and contacts a short bone lamella formed by the posterolateral part of the parietal (horizontal plate).

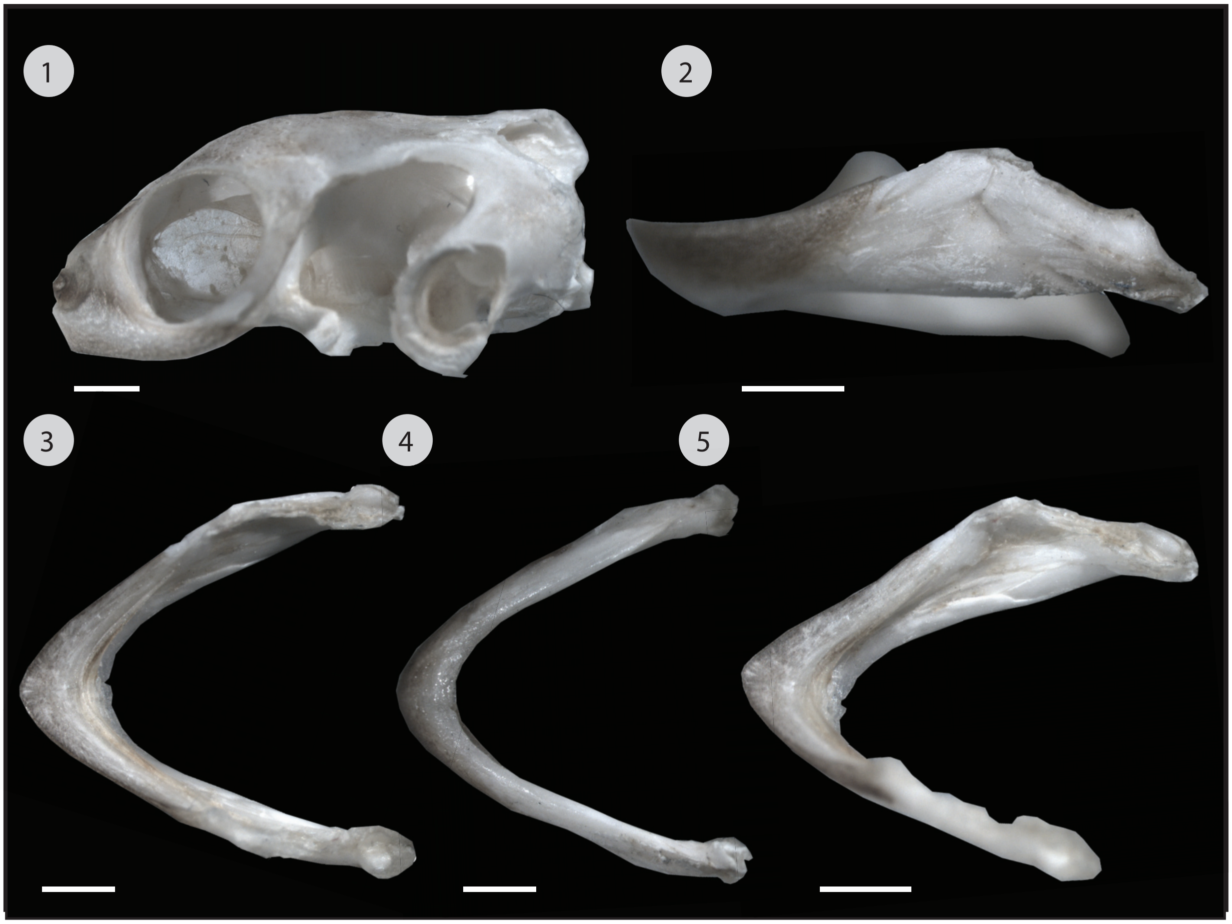


**FIGURE 21.** Continuation of Figure 20. **1)** Skull in left lateral (focus interorbital septum). Lower jaw in **2)** (mirrowed) right lateral, **3)** dorsal, **4)** ventral, **5)** dorsolateral view. Scale equals 2 mm.

### Palatal Elements

The unpaired upper ramphotheca forms the anterior most tip of the head and covers most parts of the premaxilla and the maxilla.

**Premaxilla.** The triangular premaxilla forms a part of the floor of the apertura narium externa (internal bony opening of the nares). Anteriorly, ventrally, and laterally, it is covered by the upper ramphotheca. Anteriorly, it forms a ventral ridge forming the anterior border of the mouth cavity. Laterally, it contacts the maxilla in a broad suture; medially, it sutures the contralateral premaxilla.

**Maxilla.** The maxilla has a lunate shape in lateral view, and it is laterally mostly covered by the upper ramphotheca. Its vertical arm contacts the nasal dorsally and the prefrontal posteriorly. The horizontal arm meets the jugal and the palatine posteriorly and forms a medial bone plate that anterolaterally contacts the premaxilla, the contralateral maxilla, and the vomer. Posterolaterally, this bone plate contacts the palatine, and in its medial region, it forms a part of the border of foramen orbito-nasale.

**Vomer.** The unpaired, bar-shaped vomer borders the foramen interorbitale ventrally. Anteriorly, it contacts the maxillae. Lateral to its anterior half, the foramen orbito-nasale is formed. In its posterior half, the vomer is thickened and laterally it contacts the palatines. Its posterior most tip reaches a point, where also the contralateral palatines and pterygoids meet.

**Palatine.** The triangular palatine forms the lateral border of the foramen orbito-nasale and the major part of the floor of fossa orbitalis. The palatine contacts the maxilla laterally, the vomer posteromedially and the pterygoid posteriorly. Posterolaterally, the palatine forms a short ascending process that contacts the jugal at its ventral tip.

**Pterygoid.** The flat and rectangular pterygoid builds the major part of the skull floor and is anteriorly connected to the palatine. At its anterolateral

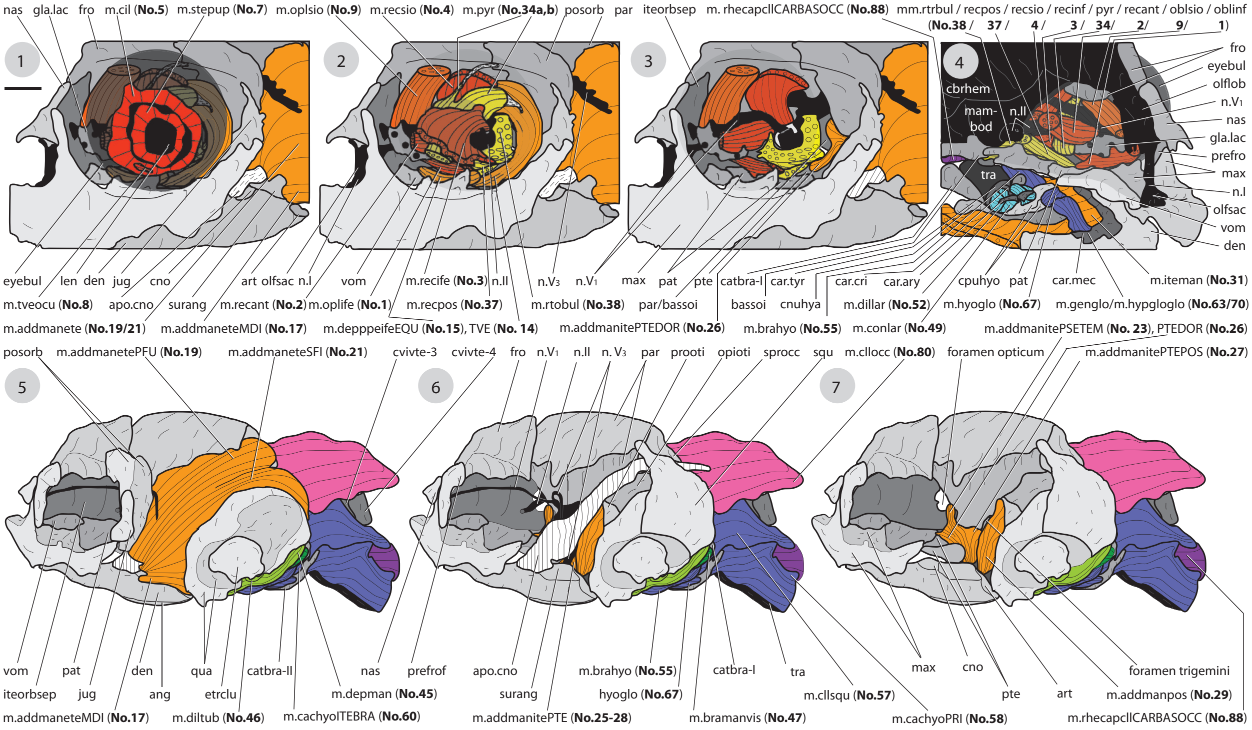


**FIGURE 22**. Hatchling specimen of *Emydura subglobosa* (collection of Prof. Dr. Wolfgang Maier / Tübingen). Different layers of cranial musculature mostly shown for the left body side. Drawings based on 3d reconstructions; superficial fibre courses based on manual dissections. **1-3)** frontolateral view to the eye region, prefrontal removed, **1)** internal eye muscles, **2)** external eye muscles, **3)** external eye muscles, deeper muscles, **4)** frontomedial view to the eye-, hyoid-, and lower jaw region, **5-7)** lateral view to the head/neck region, different layers of jaw adductor musculature (eye muscles and some neck muscles removed), **5)** portions of m. adductor mandibulae externus (No. 17, 19, 21), **6)** coronar aponeurosis (external adductor removed), **7)** mm. adductor mandibulae internus et posterior (No. 23, 25-28, 29). Bar scale (under "1"): for 1-4) ca. 0.25 mm, for 5-7) ca. 0.5 mm. Continued in Figure 23.

edge, it is connected to the prootic, jugal, and maxilla. Medially, it sutures with the contralateral pterygoid for a long distance. Posteriorly, it meets the oval basisphenoid. Posterolaterally, the bone is elongated and reaches the medial face of the quadrate at its anteroventral side. Together with the prootic, pterygoid, and parietal, it encloses the foramen nervi trigemini. The lateral part of the pterygoid vaults dorsolaterad and forms the processus trochlearis pterygoidei.

### Lower Jaw Elements

**Dentary.** The unpaired lower ramphotheca covers most of the dentary, and only the posterior and posterodorsal parts of the dentary are visible in lateral view. The dentary is the largest bone of the lower jaw and contacts the coronoid posterodorsally, the surangular posterolaterally, the angular posteroventrally, the prearticular posteromedially, and the articular posteriorly. The contralateral dentaries are fused in an anteromedial symphysis.

**Surangular.** The surangular forms a major part of the lower margin of the adductor chamber, and it is situated at the posterodorsal part of the lower jaw. Anterodorsally, it sutures with the coronoid, anteroventrally with the dentary, posteromedially with the articular, and ventromedially with the prearticular.

**Prearticular.** It is situated medially in the lower jaw and contacts the dentary anteriorly, the angular ventrally, the articular laterally and posterolaterally, the surangular dorsolaterally, and the coronoid posteroventrally.

**Coronoid.** The coronoid forms the dorsal most curvature of the lower jaw and contacts the dentary anteriorly and ventrally, the surangular posteroventrally, and in its posterior part the prearticular ventromedially.

**Angular.** Together with the dentary, the angular forms the ventral margin of the lower jaw. Anteriorly and laterally, it contacts the dentary, dorsally the

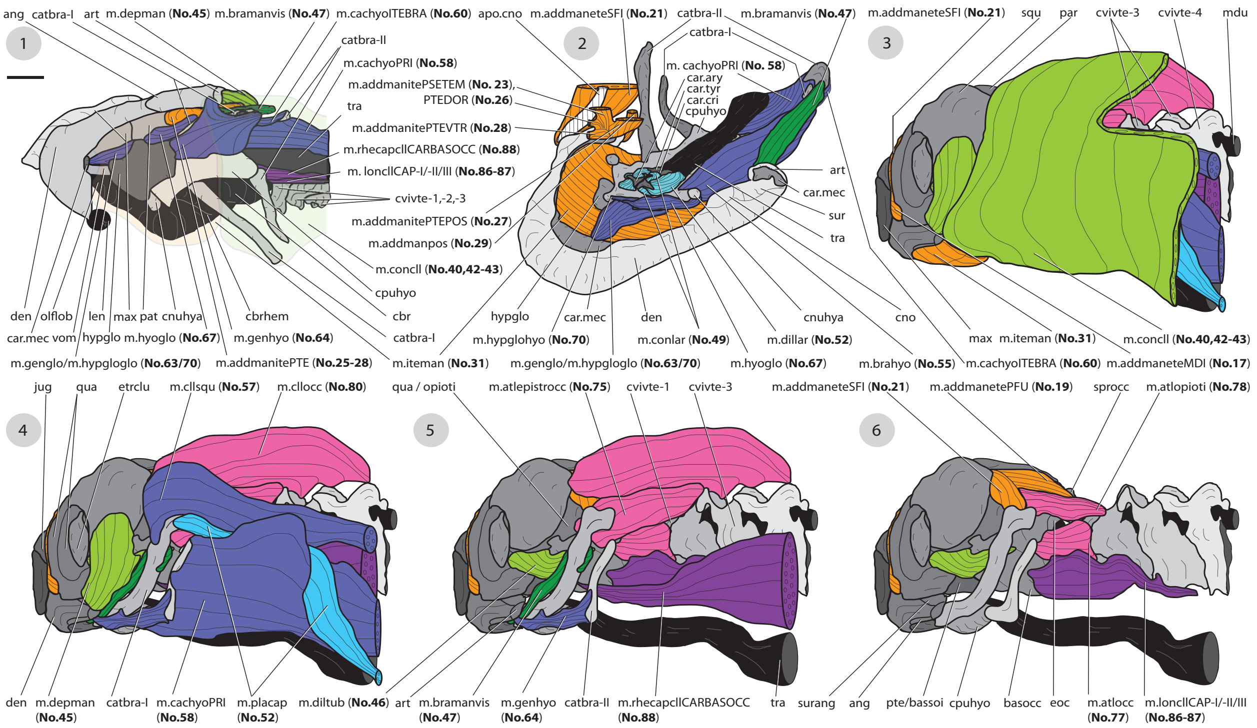


**FIGURE 23**. Continuation of Figure 22. **1)** ventral view to the lower jaw and hyoid region, mm. intermandibularis (No. 31) and constrictor colli (No. 40, 42-43) are transparent, **2)** dorsolateral and frontal view to the lower jaw and the hyoid region, **3-6)** different layers of neck and hyoid muscles, **3)** all neck muscles are shown, m. constrictor colli (No. 40, 42-43) is partly removed in in the posterodorsal region to enable a view to the dorsal aspects of the cervical vertebrae, **4)** m. constrictor colli (No. 40, 42-43) and m. intermandibularis (No. 31) removed, **5)** further neck muscles removed, **6)** most neck muscles removed highlighting the origin sites of m. adductor mandibulae externus (No. 17, 19, 21). Bar scale (under "1"): for 1, 3-6) ca. 0.5 mm; for 2) ca. 0.25 mm.

prearticular, and posteriorly and posterodorsally the articular.

### Additional Hard Tissue Elements in the Head

**Hypoglossum.** The flat, unpaired, and cartilaginous hypoglossum ("entoglossum" in several studies, e.g., Gräper 1932) is mainly situated below the anterior part of the corpus hyoidei, and it covers most of the fenestra ossis hyoidis ventrally. Only the anterior and anterolateral part extend below the corpus hyoidei. In ventral view, it has an anterior-posterior compressed, rectangular shape.

**Cartilago transiliens.** Short before its insertion to the lower jaw, the coronar aponeurosis forms the internal cartilago transiliens that articulates with the processus trochlearis pterygoidei ventrally.

### Cervical Vertebrae

*E. subglobosa* has eight cervical vertebrae (Figure 18.3). Dorsally of the centra, they proceed in a neural arch, that anterolaterally and posterolaterally forms zygophyses on each side (Herrel et al. 2008). Laterally, the vertebrae proceed in a transverse process each side. Among each other, the cervical vertebrae articulate over the anterior and posterior articular facet of the centrum. Posterior and anterior zygapophyses of two following vertebrae articulate over their articular facet. Anteriorly, the articular facet of the first vertebra centrum articulates with the cranium at the condylus occipitalis. Posteroventral of the first cervical vertebra, the intercentrum of the atlas is situated that is not fused with the remainder of the atlas. The eighth cervical vertebra articulates posteriorly with the first dorsal vertebra, which is connected to the carapace and the first rib.

## CRANIUM ASSOCIATED MUSCULATURE IN *EMYDURA SUBGLOBOSA*

Out of the 88 potential muscular units of turtles defined in this study (Appendix 1, Figures 6–15), the following structures were either not pres-

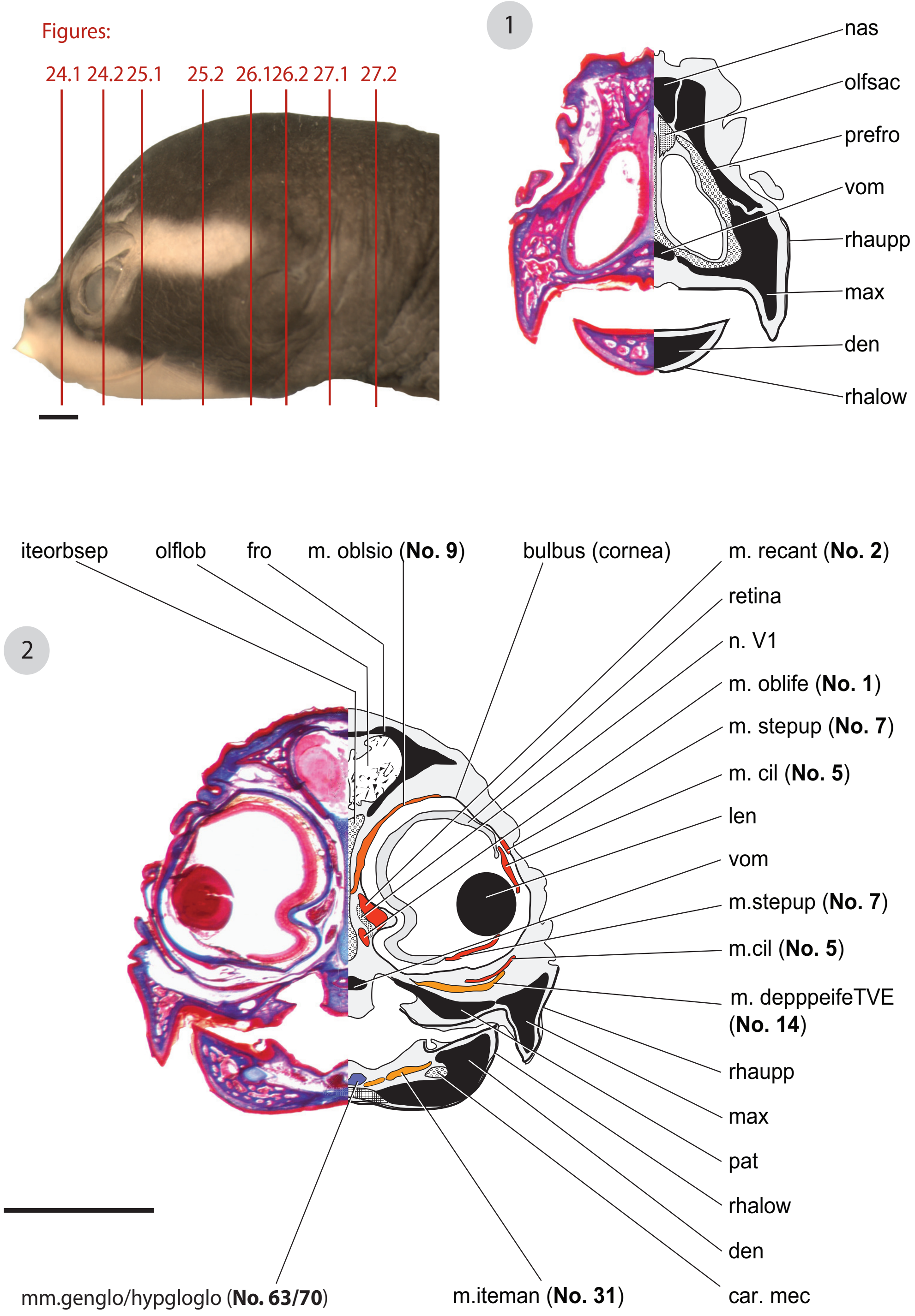


**FIGURE 24.** Hatching specimen of *Emydura subglobosa* (collection of Prof. Dr. Wolfgang Maier / Tübingen). Transverse section through the **1)** nasal region; **2)** medial part of the orbital region. For abbreviations see Appendices 1, 2 and 4. Thickness of slides: 20 µm. Bar scale under the embryo photograph: 1 mm; for all slices equal 1 mm. Continued in Figures 25, 26, 27.

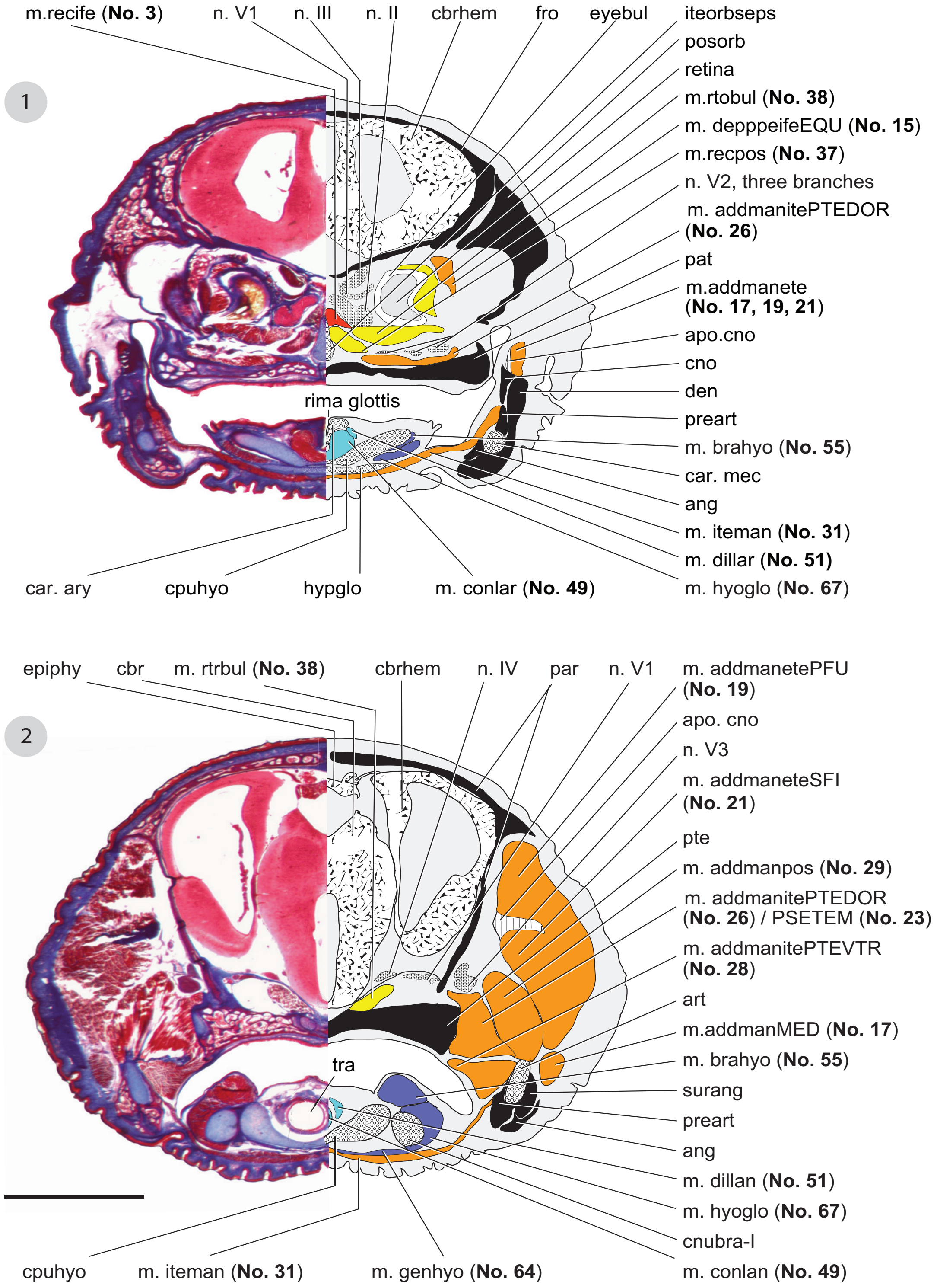


**FIGURE 25**. Continuation of Figure 24; continued in Figure 26. **1)** posterior part of orbital region; **2)** lower part of the adductor chamber.

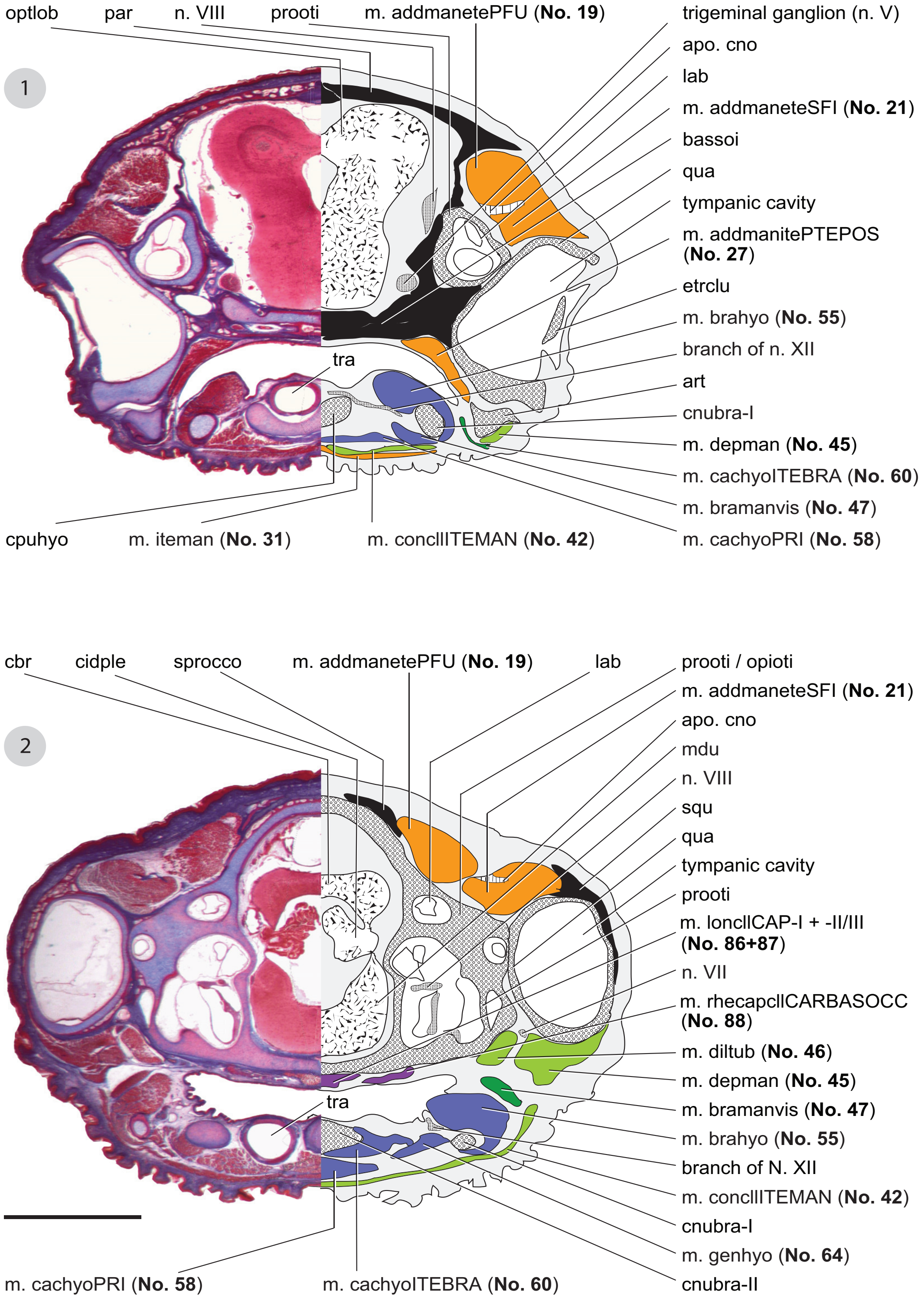


**FIGURE 26**. Continuation of Figures 24, 25; continued in Figure 27. **1)** medial part of the ear region; **2)** posterior part of the ear region.

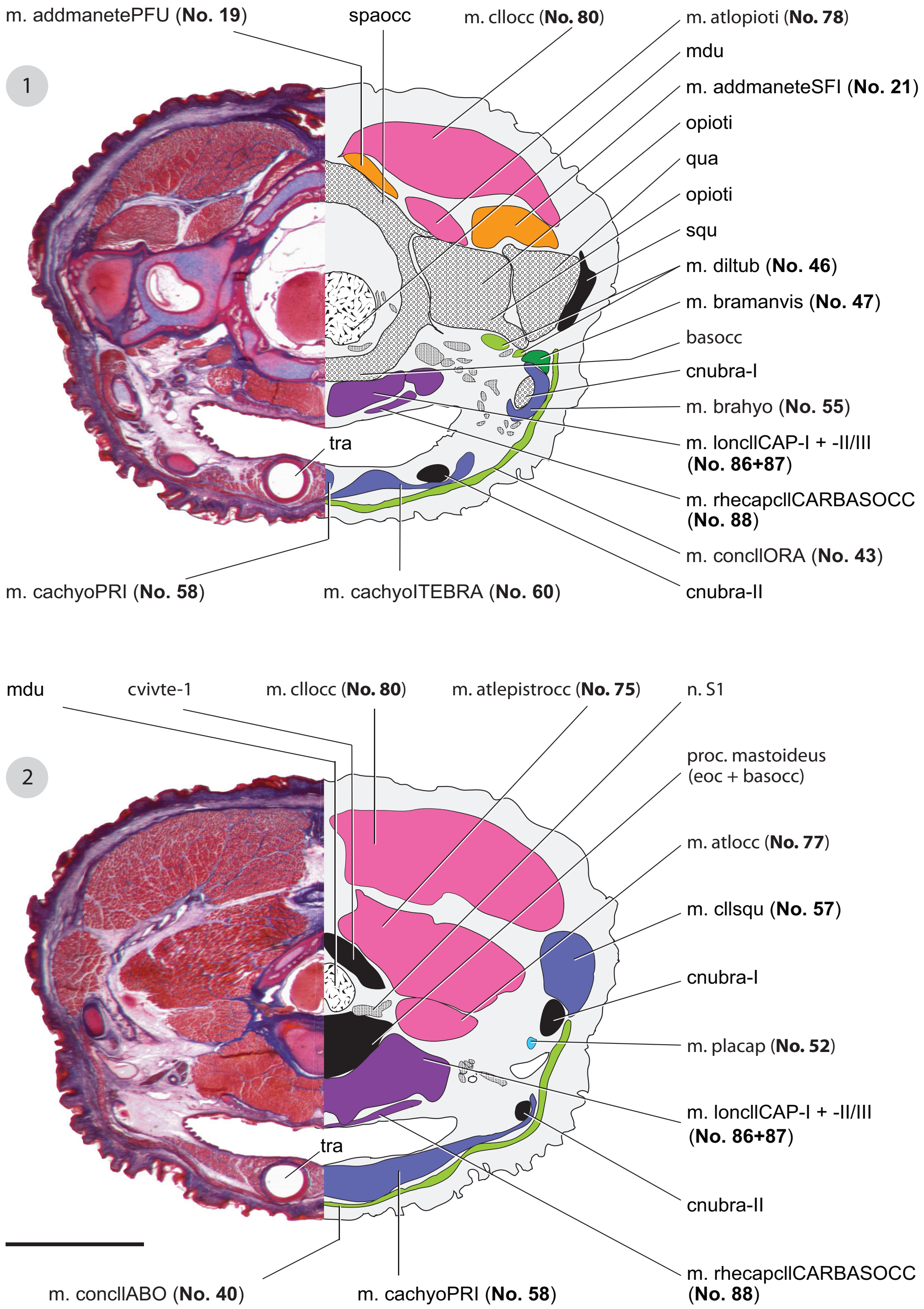


**FIGURE 27**. Continuation of Figures 24, 25, 26. **1)** occipital region; **2)** region of the first cervical vertebrae.

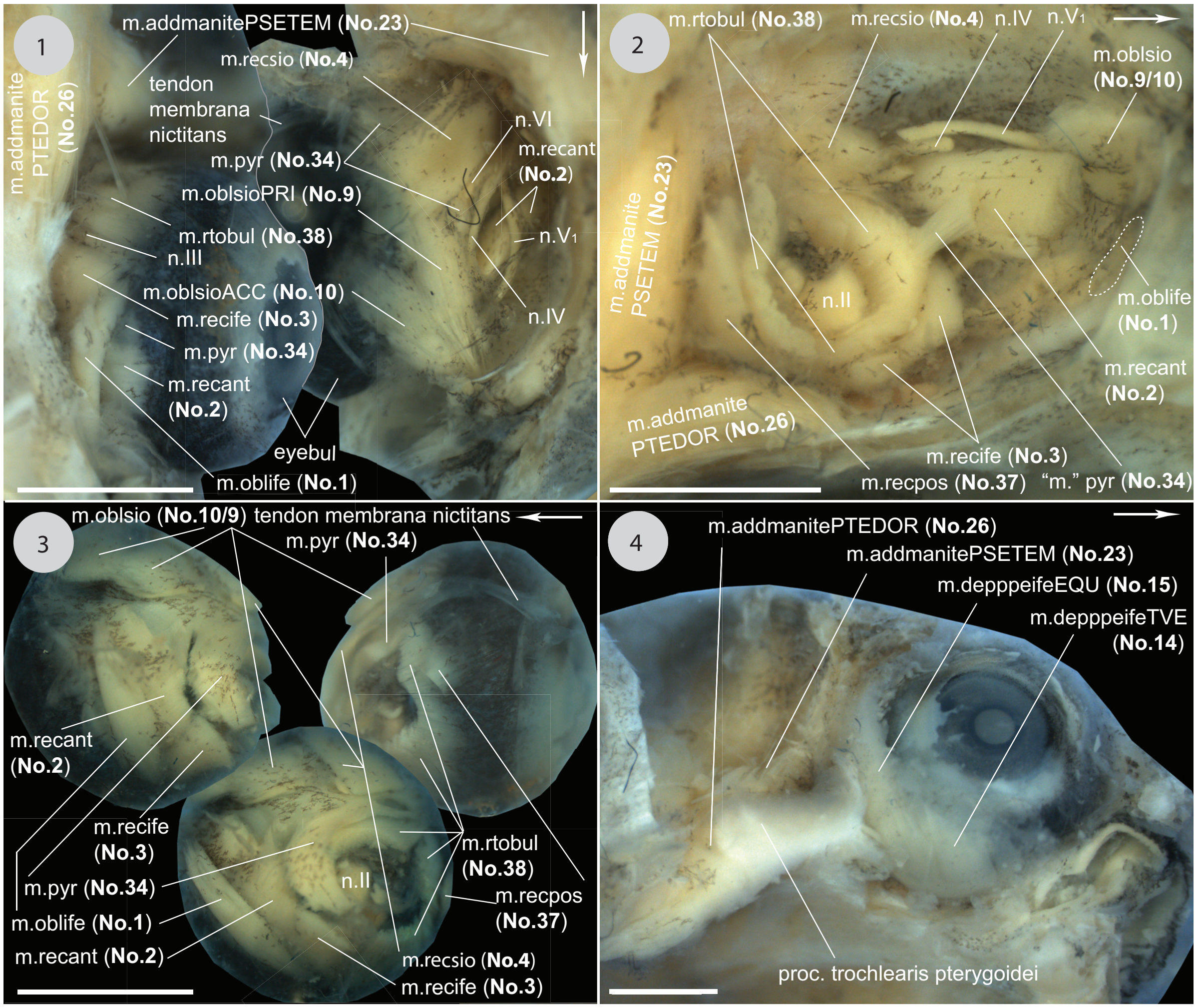


**FIGURE 28.** Dissection of a subadult specimen of *Emydura subglobosa* (PIMUZ lab# 2009.38) demonstrating selected regions of the head and the neck, to highlight anatomical structures, and to show differences to the hatchling specimen as depicted in Figures 22, 23, 24, 25, 26, 27. **1)** Eye muscles. Ventral (left) and dorsal view (right) to the eye bulbus: postorbital, premaxilla, maxilla, jugal, frontal, nasal removed. **2)** Eye muscles. Right lateral view into the optic chamber. Removed: bones removed as in 1, m. obliquus inferior (No. 1). **3)** Muscles attaching the eye bulbus. Left = anteroventral, right = posterorventral, bottom = medioventral view. **4)** Ventrolateral view to the anterior part of the head. Removed: Mm. adductor mandibulae externus (No. 17, 19, 21) et posterior (No. 29), dentary, hyoid apparatus, and the bones as in figure part 1. Continued in Figures 29, 30, 31. For Figures 28, 29, 30, 31: Fasciae and tympanon are removed. Right body side is shown in 28.14, 29.1-4, 31.1. Arrows in the dorsal right corners indicating the rostrad direction; in 28.3) the arrow is only valid for the lower view of the eye bulbus. White bar scale in the ventral left corner equal 2 mm.

ent or found in *Emydura subglobosa* or – in the case of some neck muscles – did not attach to the cranium: Muscular units No. 6, 11-13, 16, 22, 30, 32-33, 35-36, 39, 48, 50, 53-54, 56, 59, 61-62, 65-66, 68, 71, 76, 79, 81-85.

## N. Oculomotorius (III) Innervated Musculature

### Extraocular Eye Muscles

(Figures 22.2-4)

**M. obliquus inferior (No. 1).** The bent-shaped muscle originates laterally at half the height of the anterior region of the interorbital septum, medial to the insertion site of m. rectus anterior, (No. 2) and ventral to the course of n. ophthalmicus ($V_1$) (Figures 22.3-4, 28.2). The muscle runs caudoventrad (Figures 24.2, 28.3-4) and inserts to the posteroventral curvature of the eye bulbus (Figures 22.3,

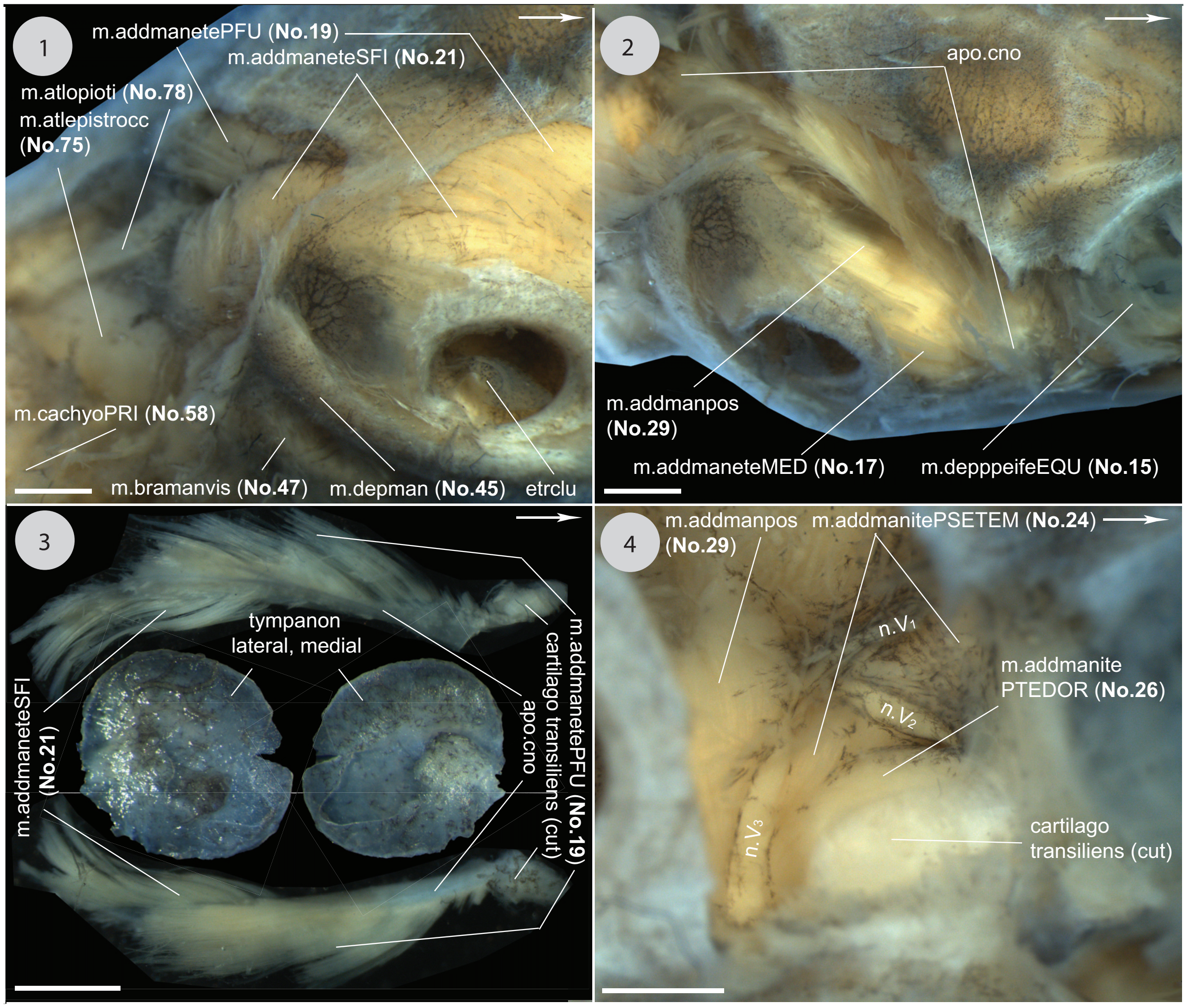


**FIGURE 29**. Continuation of Figure 28; continued in Figures 30, 31. **1)** Dorsolateral view to the posterior region of the head showing the origin sites of m. adductor mandibulae externus (No. 19, 21). Removed: mm. collooccipitis (No. 80) et plastrocapitis (No. 52), et collosquamosus (No. 57). **2)** Dorsal view to the adductor chamber demonstrating the course of the coronar aponeurosis, and the orientation of mm. adductor mandibulae externus Pars medialis (No. 17) et adductor mandibulae posterior (No. 29). Removed: jugal and postorbital, m. collooccipitis (No. 80), the bone bridge made of parts of squamosal and parietal, **3)** The coronar aponeurosis in lateral (top) and medial (bottom) view with most fibres of m. adductor mandibulae externus (No. 19, 21) removed, cut within cartilago transiliens. **4)** Dorsolateral view into the postorbital cavity of the adductor chamber. Removed: m. adductor mandibulae externus (No. 17, 19, 21) - cut within cartilago transiliens, postorbital, jugal. Scale equals 2 mm.

28.1, 28.3). The cross-section of the belly at insertion is twice that found at the point of origin.

**M. rectus anterior (No. 2).** The bent-shaped muscle originates at the anterodorsal border of the foramen opticum (Figures 22.4, 28.2). While passing n. ophthalmicus ($V_1$), ventrolaterally the muscle runs rostrad and keeps a consistent cross section in its course (Figures 22.3, 28.2). The muscle inserts to the anteromedial curvature of the eye bulbus (Figure 28.3).

**M. rectus inferior (No. 3).** The muscle originates at the anteroventral border of the foramen opticum (Figures 22.2, 22.4, 28.2), ventral to the origin of m. rectus anterior (No. 2). It runs anterodorsad, and instantly it becomes four times broader than its origin site (Figure 22.2). The muscle covers the tractus opticus from medial and spans over the insertion site of this nerve to the eye bulbus. The muscle has a broad insertion on the medial curvature of the eye bulbus (Figure 28.3).

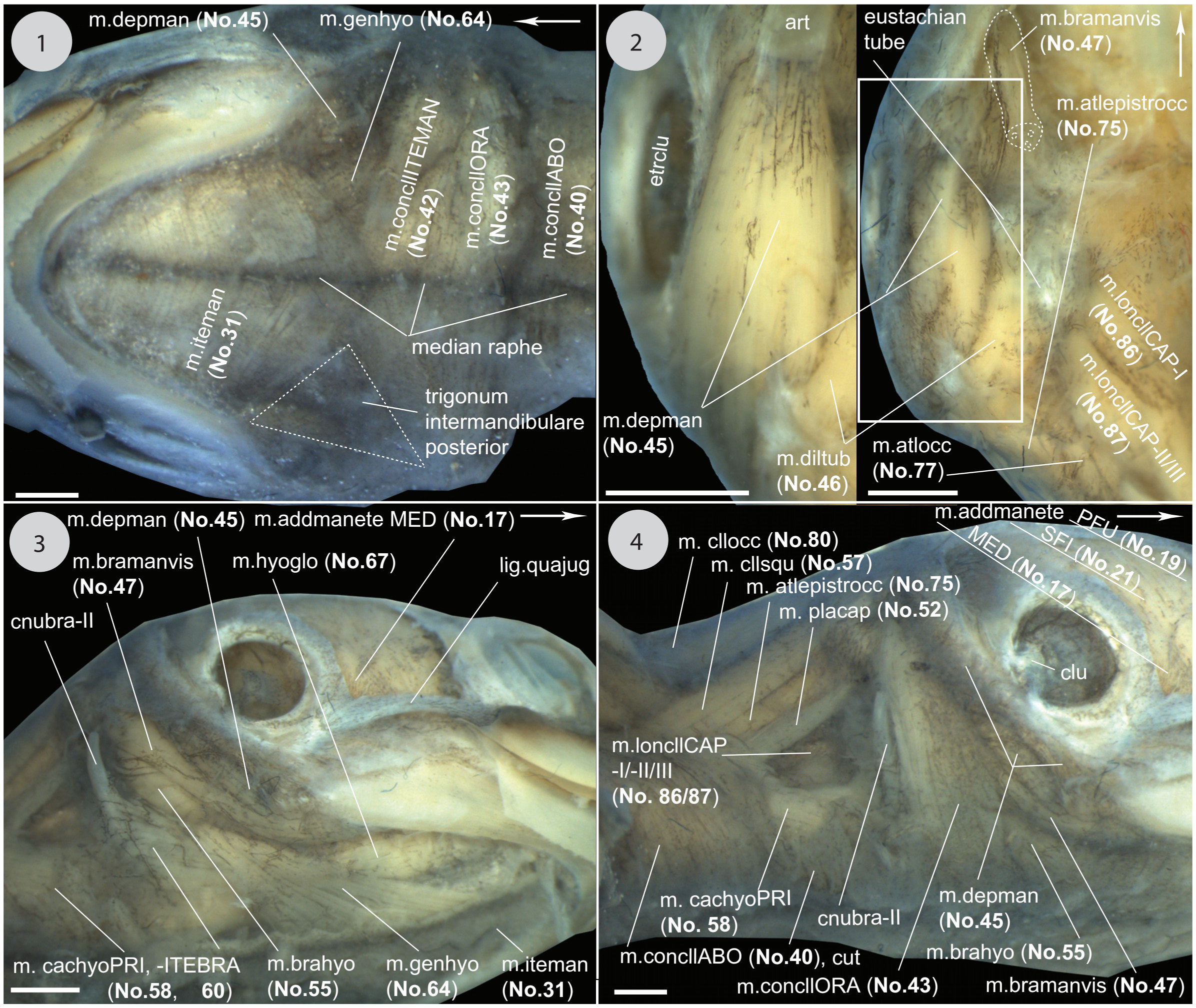


**FIGURE 30**. Continuation of Figures 28, 29; continued in Figure 31. **1)** ventral view to the head. **2)** Ventral view to the otic region. Removed: hyoid apparatus, mm. intermandibularis (No. 31) et retrahens capiti collique Pars carapacobasioccipitalis (No. 88). In the left picture a detail is shown and the superficial, ventralmost fibres of m. depressor mandibulae (No. 45) are removed. **3)** Ventrolateral view to the head/neck region. Removed (right side): mm. constrictor colli Pars intermandibularis (No. 42), m. intermandibularis (No. 31), and parts of m. constrictor colli Pars aboralis (No. 40). **4)** Ventrolateral view to the head/neck region on the left body side. The superficial neck constrictors (No. 40, 42, 43 / m. sphincter colli posterior), m. intermandibularis (No. 31), and m. geniohyoideus (No. 64) are removed. Scale equals 2 mm.

**M. rectus superior (No. 4).** The primarily bent-shaped muscle originates at the posterior border of foramen opticum (Figure 22.3-4). Medial of the eye bulbus, it runs anterodorsad and passes n. ophthalmicus ($V_1$) dorsolaterally (Figure 28.2). Below the suture of frontal and parietal, the muscle becomes broad and inserts to the dorsal curvature of the eye bulbus (Figures 22.3, 28.3).

### Intraocular Muscles

(Figures 22.1, 24.2)

**M. cilliaris (No. 5).** M. cilliaris (No. 5) originates with several radial and circumferential fibres in the connective tissue of the ciliar folds and abuts the m. sphincter pupillae (No. 7) internally. It is hard to distinguish both muscles in some regions, because here the former overlaps the latter laterally (Figure 24.2). The circular muscle inserts externally on the ora serrata, the border to the retina.

**M. sphincter pupillae (No. 7).** The circular muscle stretches around the pupil, and it forms the iris. It originates with several radial and circumferential fibres at the innermost connective tissue of the cil-

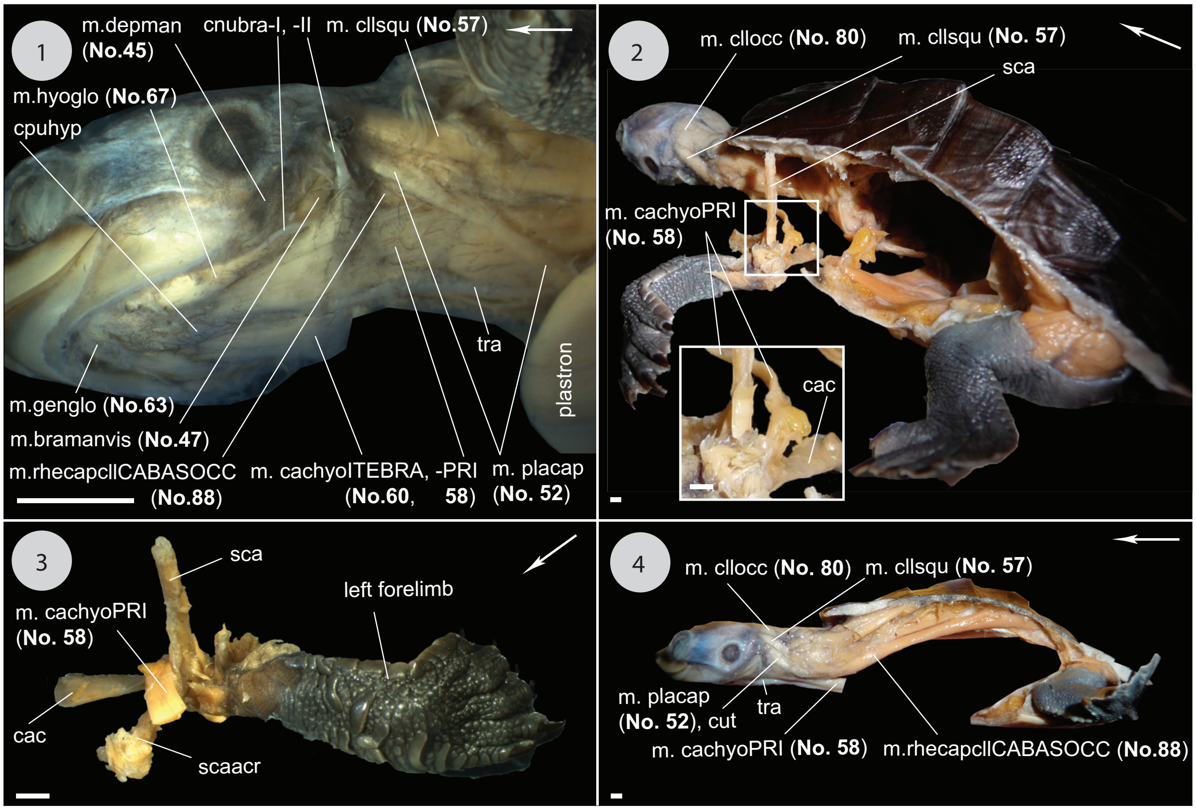


**FIGURE 31**. Continuation of Figures 28, 29, 30. **1)** Ventrolateral view to the head. Removed: mm. constrictor colli (No. 40, 42, 43) and the left half of m. intermandibularis (No. 31). **2)** Posterolateral and dorsal view to the body. Removed: parts of the carapace and the plastron, and the intestines. Focus on the insertion site of m. coracohyoideus (No. 58) on the shoulder girdle. **3)** Anterodorsal view to the left forelimb and shoulder girdle. All muscles except m. coracohyoideus (No. 58) removed. **4)** Lateral view to the whole animal: Removed: Forelimbs and shoulder girdles with the related muscles, most parts of the shell, intestines. Scale equals 2 mm.

iar folds (König 1934/35). These fibres run externally and insert inside the medial region of the ciliar folds; here they abut the m. cilliaris (No. 5).

**M. transversalis oculi (No. 8).** The short and narrow muscle (Figure 22.1) is situated anteroventral of the pupil and lateral of m. cilliaris (No. 5). Its origin and insertion are within connective tissue, and some fibres could be associated with fibres of m. ciliaris (No. 5).

### N. trochlearis (IV) innervated musculature

### Extraocular Eye Muscle

(Figure 22.4)

**M. obliquus superior Pars principalis (No. 9).** In the hatchling specimen, only an unseparated muscular structure is present (No. 9), which forms the Mutterboden for m. obliquus superior Pars accessorius (No. 10). It originates in the anterior most angle of the ocular cavity. The flat muscle originates laterally from the interorbital septum. The origin site lays medially to the course of n. ophthalmicus ($V_1$). The muscle runs dorsad and inserts to the anterodorsal curvature of the eye bulbus.

**M. obliquus superior Pars accessorius (No. 10).** This portion was only discovered in the subadult specimen; it originates laterally to Pars principalis (No. 9) on the prefrontal (Figure 28.2). It runs caudorostrad and dorsad and inserts dorsally onto the eye bulbus, laterally to the insertion of Pars principalis (Figure 28.1).

### N. Trigeminus (V) Innervated Musculature

### Eyelid Related Musculature

**M. depressor palpebrae inferioris Pars transversalis (No. 14).** The muscle originates anterior at the ventral border of septum interorbitale and dorsomedially at the vomer. It runs laterad and inserts into the lower eyelid. It is situated anteriorly to Pars equatorialis (No. 15) (Figure 22.1-2) and has crossing fibres with it at its posterior edge (Figure 28.4).

**M. depressor palpebrae inferioris Pars equatorialis (No. 15).** The flat muscle (Figures 22.2, 24.2, 24.4) originates posteriorly to the eye bulbus within connective tissue (Figure 24.3). It runs rostroventrad and covers the posterolateral curvature of the eye. Ventrally, the muscle continues as a very thin tendon and anteroventrally to the eye bulbus, it inserts within connective tissue. The muscle is not connected to any bone, neither to the postorbital or frontal dorsally nor ventrally at the palatine or pterygoid, which would identify it as m. levator bulbi (No. 16), moreover, in contrast to the latter, No. 15 contains smooth muscle fibres.

### Jaw Musculature (constrictor I lateralis)

**M. adductor mandibulae externus (No. 17-21).** This most prominent cranial muscle originates with three muscle portions from the cranium, these portions partly fuse together and insert to the coronar aponeurosis and the lower jaw in a complex pattern. In the hatchling, the medial most muscle portion, m. adductor mandibulae externus Pars profundus (No. 19), originates from the lateral face of the supraoccipital as a flat muscular structure (Figures 22.5, 23.6, 26.2, 27.1). In the subadult, the portion has extended its origin to the lateral face of the vertical plate and ventrally to the horizontal plate of the parietal (Figure 29.1). Shortly lateral to the parietal, some fibres also originate from the fascia temporalis (compare to Appendix 5), which is spanning above the postorbital cavity of the adductor chamber. Pars profundus (No. 19) runs rostrad and short after the origin site on the supraoccipital, it becomes a strong muscle portion. In the hatchling (Figures 22, 23), the m. adductor mandibulae externus Pars superficialis (No. 21) originates dorsally from the quadrate and from the opisthotic as well as from the dorsomedial face of the squamosal. In the subadult, fibres also originate from the fascia temporalis shortly anterior to the bony bridge formed by squamosal and parietal (Figure 29.1). Pars superficialis (No. 21) is stronger than Pars profundus (No. 19) and has a slightly flattened, roundish shape in cross-section (Figure 26.1). Following the dorsal curvature of the otic capsule, the portion runs anterodorsad shortly after its origin site (Figure 23.6). Dorsal of the quadrate, it runs rostrad (Figure 29.1). Shortly caudal of the bony bridge, the Pars profundus (No. 19) and Pars superficialis (No. 21) begin to partly fuse (Figures 22.5, 26.1). After passing the bony bridge anteriorly, the muscle portions are hard to distinguish in external view and finally they form a consistent muscle belly (Figures 22.1, 22.5, 25.2, 29.1). In serial sections, both muscle portions are still distinguishable (Figure 25.2) because of the strong horizontally orientated coronar aponeurosis (Figure 26.2), which partly separates No. 19 and No. 21 in their medial region. This coronar aponeurosis originates medially in the Pars superficialis portion (No. 21) (Figure 26.2) and becomes strong during its course through the whole muscle (Figures 29.2-3). The muscle fibres of Pars profundus (No. 19) and Pars superficialis (No. 21) by and by insert almost completely to this tendon, the former dorsally and medially, the latter laterally and ventrally (Figures 25.2, 26.1, 29.3). The coronar aponeurosis broadens near to the attachment site and forms the tendinous cartilago transiliens (Figures 22.6, 29.2-4). It continues as a broad and short tendon and inserts around the coronoid of the lower jaw (Figures 22.1, 22.5-6, 25.1, 29.2). Some fibres of the Pars profundus and Pars superficialis (No. 19, 21) do not insert to the coronar aponeurosis and insert posterolaterally from it to the coronoid process of the lower jaw (Figure 25.1). In the hatchling, the third portion of the muscle, m. adductor mandibulae externus Pars medialis (No. 17), originates as a narrow muscle portion ventrally at the anteroventral curvature of the quadrate (Figures 22.5, 23.3). In the subadult, it extended its origin site more dorsad to the anterior curvature of the quadrate (Figures 29.2, 30.3-4). The fibres of Pars medialis (No. 17) run rostrad and anterior to the quadrate, they fuse with the remaining m. adductor mandibulae externus. For a short distance, the whole muscle (No. 17, 19, 21) appears as a homogenous structure, still permeated by the coronar aponeurosis. Posterior to the coronoid, the fibres of Pars medialis separate ventrally from the rest of the muscle (Figure 25.2) – in the hatchling it has the same thickness and vertical altitude as before. It inserts laterally to the anterior part of surangular and the posterodorsal part of the dental (Figures 22.1, 22.5).

**M. adductor mandibulae internus (No. 23-28).** This muscle is separated into three to four muscle portions. This imprecise number has an ontogenetic reason. In the hatchling specimen (Figures 22, 23), following portions are identifiably: Ventral to the pterygoid bone, a distinct Pars pterygoideus ventralis (No. 28) is present (Figures 23.2, 25.2). Posteriorly to it, the Pars pterygoideus posterior (No. 27) is present (Figures 22.7, 23.2), originating as a flat structure ventrally from the posterior part of the pterygoid and medially to the optic capsule at the anterolateral part of the basisphenoid (Figure 26.1). Dorsally to those both very integrated portions, a muscular structure is present, including one head inserting dorsally to the pterygoid bone as well as to the posterior edge of the palatine. An additional dorsal head originates ventrally to the anteriormost edge of the vertical plate of the parietal as well as to the posteroventral tip of the postorbital and during its posteroventrad course a few fibres originating from the prootic are also incorporated. The former structure is homolog to the Pars pterygoideus dorsalis (No. 26). The latter structure, in contrast, represents the Anlage of Pars pseudotemporalis (No. 23) (Figures 22.3, 23.1-2, 25.2). A close relationship of both structures in turtle development was already reported by Rieppel (1990). In the hatchling, all three portions (No. 27, 28, 23/26) insert with their own distinct fibre course to the posteromedially edge of the lower jaw, namely to the border between angular and cartilago meckeli. In the subadult specimens, the following condition is recognisable: The Pars pterygoideus posterior (No. 27) is located in a more anterior position and originates from the pterygoid only. The Pars pterygoideus ventralis (No. 28) seems to be completely reduced or to be fused with the Pars pterygoideus posterior (No. 27), any anteroventral insertion of m. adductor mandibulae internus to the pterygoid bone is missing. The dorsal structure (No. 23/26) of the muscle is now separated into two distinct structures (Figures 28.1-2, 28.4, 29.4). Pars pterygoideus dorsalis (No. 26) is now clearly distinguished from the pseudotemporalis-structure (No. 23). Moreover, in some specimens, although keeping its origin site, the latter separated completely from the m. adductor mandibulae internus complex (No. 26, 27, 28) and became an independent muscle par definition. Compared to the hatchling, Pars pseudotemporalis (No. 23) extended its origin dorsad and now originates from the whole anterior border of processus descendens parietalis (Figures 28.2, 28.4). Via a short tendinuous structure, the subarticular aponeurosis, it inserts to the ventral edge of the articular, which is situated posteroventrally to the more or less direct attachment of the internus-complex (Figure 17.2). Hence, for some grown-up *Emydura subglobosa* specimens, one has to acknowledge an m. pseudotemporalis (No. 23) s. s.

**M. adductor mandibulae posterior (No. 29).** The muscle originates anterolaterally at the prootic and anteromedially at the quadrate (Figures 22.6-7, 29.4). A few fibres originate at the vertical plate of the parietal, where it contacts the prootic. The belly runs ventrad along the posterior margin of the postorbital cavity of the adductor chamber as a complanate sheet of muscle fibres (Figure 22.7). With a narrow insertion, the muscle attaches dorsally to the surangular and dorsomedially to the cartilago meckeli (Figure 25.2). M. adductor mandibulae posterior (No. 29) is clearly separated from the portions of m. adductor mandibulae internus Partes pterygoidei (No. 26-28) and to m. pseudotemporalis (No. 23) by ramus mandibularis nervi trigemini (V3) (Figure 28.4). In subadult *E. subglobosa* specimens, it more likely seems to be “related” to portions of m. adductor mandibulae externus (No. 17/19/21).

### Jaw Musculature (constrictor I ventralis)

**M. intermandibularis (No. 31).** The flat and thin muscle stretches transversely between the halves of the lower jaw and posteriorly transverses the symphysis of the dentaries. It originates medially at the cartilago meckeli, dentary, and angular. The contralateral parts are fused together in a thin medial raphe (= insertion site), which is ventrally covered by a high density of pigments. In the hatchling specimen, its anterior most part does not directly contact the symphysis of the dentaries (Figures 23.1, 24.2), whereas in subadult specimens this area is ventrally covered by the muscle (Figures 30.1, 30.3). Posteriorly, m. intermandibularis (No. 31) contacts the n. facialis (VII) innervated intermandibularis part of constrictor colli (No. 42) ventrally (Figures 23.1, 26.1). Laterally between both muscles, a trigonum intermandibulare posterior (Appendix 5) is visible enabling a view to the region around the jaw joint (Figures 23.1, 30.1).

### N. abducens (VI) Innervated Musculature Extraocular Eye Muscles

**M. pyramidalis (No. 34).** In the hatchling specimen, this flat muscle is the only extraocular eye muscle that does not originate from a bone or the interorbital septum (Figure 28.2). It originates on the ventromedial curvature of the eye bulbus, ventral to the insertion site of m. rectus inferior (No. 3). It runs caudodorsad without changing its thickness. During its course, the muscle is partly covered medially by m. rectus anterior (No. 2) (Figure 22.4) and laterally by m. rectus inferior (No. 3) (Figure 22.2). The muscle forms two short muscle heads. The stronger, posteromedial one develops a strong tendon leading to the lower eyelid in a posterolateral curve. The small, anterolateral head develops a thin tendon leading to the membrana nictitans also in a posterolateral curve. The muscle is dorsomedially innervated by n. abducens (No. VI). In one subadult specimen, I found a different origin pattern of the pyramidalis-structure (No. 34): Herein, its anterior part originates from the eye bulbus, comparable to the condition seen in the hatchling. Posteriorly, the structure is strongly integrated to m. retractor bulbi (No. 38) (Figure 28.2). Following the presented nomenclature of this paper (Figure 1), the pyramidalis-structure in this specimen should be mentioned as a portion of m. retractor bulbi (No. 38). After its “origin sites”, the pyramidalis structure itself becomes a continuous muscle with a similar shape as seen in the hatchling, hence no internal portions can be identified (Figure 28.3).

**M. rectus posterior (No. 37).** The flat muscle originates on the posteroventral border of foramen opticum (Figures 22.4, 25.1, 28.2). While extensively broadening, it runs anteroventrad and has a broad insertion to the posteroventral curvature of the eye bulbus (Figures 22.3, 28.3).

**M. retractor bulbi (No. 38).** The conical muscle originates in the posteriormost narrow angle of the optic cavity formed by pterygoid, prootic, basisphenoid, and parietal (Figure 25.2). It runs rostrad and has a broad insertion to the posterior curvature of the eye bulbus (Figures 22.3, 25.1, 28.2-3).

### N. Facialis (VII) Innervated Musculature

**M. constrictor colli (No. 40, 42-43).** The parts of m. constrictor colli are not distinctly separated from each other in the hatchling. The Pars aboralis (No. 40) homologue originates laterally on the lig. nuchae (Appendix 5); hence the fibres themselves seem to originate on the underlying m. collooccipitis (No. 80). In fact, both muscles are only connected to each other by connective tissue. The Pars oralis (No. 43) homologue originates from the posterior edge of the squamosal (Figure 27.1). Anteroventrally, it continues to the Pars intermandibularis (No. 42) homologue, which originates with some fibres from the posteroventral tip of the articular. Below the corpus hyoidei, it overlaps the m. intermandibularis (No. 31) dorsally. All three parts of m. constrictor colli indistinguishably insert into a thin medial raphe. Due to the unseparated condition of the muscle in *Emydura subglobosa*, one should declare all three parts of m. constrictor colli (No. 40-44) together to form only one muscle s. s. having three muscle heads in the origin. – Moreover, posteriorly, m. constrictor collis (No. 40-44) is indistinguishably fused with m. sphincter corticis (Ogushi 1913b: his No. 53) that gains spinal nerve support. By definition, both muscle parts, although having different ontogenetic and phylogenetic origin, should be named m. supracorticis. Thus the presented study concentrates on cranium-associated muscles only, and the innervation pattern of both parts are obviously different, I did not list m. supracorticis in Appendix 1 or Figures 6–15. Moreover, an extensive literature review would be necessary to get an impression of the “real” nature of this muscular structure in the trunk near region. Studies expanding the list of muscular units to non-cranium associated postcranial muscles should be aware of this problem and some modification of the here presented list may be necessary in the future.

In subadult specimens, I found a clear separation of the portions of m. constrictor colli (No. 40, 42-43) (Figures 30.1, 30.4). However, Pars aboralis (No. 40) was still indistinguishably connected to m. sphincter corticis (Ogushi 1913b).

**M. depressor mandibulae (No. 45).** In the hatchling specimen, the strong muscle originates laterally at the posterior curvature of the quadrate (Figures 20.4, 21.3-8, 21.2). Dorsally, only a few fibres come in contact with the ventral edge of the squamosal. In the subadult, the muscle origin expanded dorsad to the lateral face of the squamosal, and a few fibres attach to the posterodorsal border of that bone. As a parallel fibred muscle, it runs anteroventrad and covers the ventral curvature of the otic capsule laterally. Anteroventral of the quadrate, it extends its origin site to the ventral aspect of the quadrate, and the muscle belly broadens. Dorsomedially, the muscle contacts the m. dilatator tubae (No. 46) (Figure 26.2) and the m. constrictor colli (No. 43) posteriorly with connective tissue. Via a short tendon, the muscle inserts dorsolaterally to the posteriormost tip of the articular (Figure 26.1). In the subadult, m. depressor mandibulae (No. 45) seems to be separated into two muscle portions in ventrolateral view (Figure 30.3). However, after redissection of the superficial muscle fibres a homogenous muscle is recognisable (Figure 30.2). In the origin and in the insertion site, the muscle forms different muscle heads, either originating on different positions laterally on the squamosal or also posteroventrally on the opisthotic (Figure 30.2). Those muscle heads do not correspond to the portion-like superficial partition of the muscle; hence, no separation into portions, but a superficial muscle layer s. s. is present.

**M. dilatator tubae (No. 46).** Separated by the lateral head vein (Rieppel 1990), the muscle originates by two muscle bundles from the ventral face of the lateral lamella of the opisthotic (Figures 27.1, 30.2). Shortly after the origin, the muscle heads fuse and run rostrad. The muscle broadens extensively and surrounds the eustachian tube (Figures 30.2). This skinny element is situated posteroventrally to the groove formed by the incisura columellae auris. The muscle attaches the prootic and the quadrate ventrally (Figures 26.2, 30.2). The thin, anteriormost aspect of the muscle is still connected to the eustachian tube, where the tube opens into the mouth cavity.

### N. Glossopharyngeus (IX) Innervated Musculature

**M. branchiomandibularis visceralis (No. 47).** The long bent shaped muscle originates anteriorly at the distal most part of cornu branchial-I (Figures 22.5-7, 23.1-2, 30.1, 30.3-4, 31.1). Lateral to this bone, it runs anteroventrad (Figures 23.1-2, 27.1, 30.3-4, 31.1) and inserts medially to the angular and articular (Figures 26.1, 30.2-3).

### Nn. Vagus (X) et Accessorius (XI) Innervated Musculature

#### Larynx Musculature (ramus laryngeus sup. of N. vagus; Shiino, 1913)

**M. constrictor laryngis (No. 49).** The muscle (Figures 22.4, 23.2) originates dorsally in the anterior region of corpus hyoidei and reaches the basis of its processus lingualis (Figure 25.1). It runs caudodorsad and passes cartilago thyreoidea laterally and the m. dilatator laryngis (No. 52) medially (Figure 25.2). The muscle bends mediad around the curvature of cartilago thyroidea and inserts with the contralateral muscle in a median raphe, which is anterodorsal to cartilago cricoidea.

**M. dilatator laryngis (No. 51).** The bent shaped muscle originates on the lateral tip of the processus muscularis of cartilago arytaenoidea. It runs caudad and passes m. constrictor laryngis (No. 49) laterally. It inserts laterally in the posterior part of cartilago thyreoidea and a few fibres insert to the first tracheal ring.

**M. plastrocapitis (No. 52).** The muscle originates with a thin diameter medially on the dorsal face of the entoplastron (Figure 31.1). It runs rostrodorsad into the neck (Figures 30.4, 31.1, 31.4). In the posterior part of the neck, it lays ventrolaterally of the m. coracohyoideus Pars principalis (No. 58) (Figure 31.1). At the level of the third cervical vertebrae, it passes this muscle dorsally and lies medially of it in the anterior part of the neck (Figure 23.4: hatchling). In its whole course, m. plastrocapitis (No. 52) is strongly connected to m. coracohyoideus (No. 58) via connective tissue. After passing m. coracoideus Pars principalis (No. 58), the elongated m. plastrocapitis (No. 52) becomes a very thin muscle that attaches the cornu branchial-I medially with a few muscle fibres (Figures 23.4, 30.4, 31.1). Afterwards, the remaining muscle fibres run rostrad to insert into lig. hyosquamosal (Ogushi 1913b), which is stretched between cornu branchial-I and the posterior part of the otic. In the dissected specimens, the anterior part of the muscle appeared to be slightly brighter than all other muscles in the neck, possibly due to several internal tendinuous fibres (Figures 30.4, 31.1).

### N. Hypoglossus (XII) Innervated Musculature

#### Tongue Muscles and Rectus System

**M. branchiohyoideus (No. 55).** The massive, parallel fibred muscle originates at the medial third of cornu branchial-I (Figures 22.5-7, 30.1, 30.3). Here it originates from almost all sides of this bar-shaped bone. Only a narrow longitudinal, vertical area at the medial side of cornu branchial-I is not covered by the muscle in this region (Figure 27.1). The muscle fibres run rostrad (Figure 30.4). The dorsal fibres insert to the posteromedial face of cornu hyale (Figure 23.2). The ventral and medial fibres insert to the lateral and ventrolateral face of corpus hyoidei, around the articulations of cornu hyale and cornu branchial-I with corpus hyoidei (Figures 22.4, 23.2, 25.1).

**M. collosquamosus (No. 57).** By a tendon, the conical muscle originates ventrolaterally from the forth cervical vertebrae. In the hatchling, its origin site is not visible, possibly either because of the abrupt end to the serial sections or intraspecific variability with an appreciable origin from the fifth cervical vertebrae. The muscle runs rostrodorsad and laterad (Figures 30.4, 31.1-2, 31.4) and broadens extensively (Figure 23.4). In the hatchling specimen, the lateral muscle head inserts dorsolaterally to the distal third of cornu branchial-I and to the posterior edge of the squamosal (Figures 23.4, 27.2); a very short medial head inserts to connective tissue posterior to the skull. The insertion of collosquamosus (No. 57) to cornu branchial-I is not present in the subadult; however, it is connected via connective tissue.

**M. coracohyoideus (No. 58, 60).** The flat but strong muscular unit m. coracohyoideus Pars principales (No. 58) originates posteriorly from the proximal fifth of the coracoid bone of the pectoral girdle (Figures 31.2-3). It turns dorsad around the coracoid and runs rostrad. The portion forms the ventral margin of the neck region (Figures 23.4, 27.2, 31.1, 31.4), and it is only superficially covered by the inserting parts of the neck constrictors [No. 40, 42, 43, m sphincter corticis (Ogushi 1913b), Figures 30.2-3, 27.2, 30.4]. It inserts posteromedially to cornu branchial-I (Figures 23.4, 31.1), ventrolaterally to the proximal part of cornu branchial-II (Figures 23.1, 27.2), ventrally and laterally to the skull near the trachea (Figures 26.2, 27.1, 31.1), as well as ventrally to the posterior half of corpus hyoidei (Figure 26.1). In the area of the hyoid apparatus, it dorsolaterally shares fibres with m. coracohyoideus Pars interbranchialis (No. 60) (Figures 26.1-2, 27.1). The parallel fibred muscular unit M. coracohyoideus Pars interbranchialis (No. 60) originates from the dorso- and ventrolateral face of the medial third of cornu branchial-II (Figures 22.5, 23.1-2, 31.1). It runs rostrad (Figure 23.1) and inserts ventomedially to the proximal third of cornu branchial-I (Figures 26.1, 31.1). Postero- and ventromedially, this portion shares fibres with m. coracohyoideus Pars principalis (No. 58) (Figures 26.1-2, 27.1).

**Mm. genioglossus (No. 63) et hypoglossoglossus (No. 69).** Those muscular units are not clearly separated from each other in the hatchling stage of *Emydura subglobosa*. The structure originates dorsally at cartilago meckeli, laterally to the symphysis of the dentaries (Figures 23.1-2, 24.2). The fibres run caudolaterad and form two muscle heads dorsally to the anterior most part of hypoglossum (Figure 23.2). The longer, lateral head of the muscular complex inserts to the anterolateral edge of the hypoglossum, some fibres insert ventrally to the lateral aspect of hypoglossum (Figures 23.1-2). It is homologous to the posterior part of m. genioglossus (No. 63). Laterally to the anterior most tip of processus lingualis of corpus hyoidis, the short medial muscle head – the m. hypoglossoglossus homologue (No. 69) – runs caudad and inserts to the dorsal integument of the tongue. Here it anteriorly and directly opposes the insertion site of m. hyoglossus (No. 67). In subadult and adult specimens, the differentiation of both structures was much clearer, however, they still were not completely separated from each other (Figure 31.1).

**M. geniohyoideus (No. 64).** The flat and broad muscle (hatchling) covers the ventral surface of the hyoid apparatus, and it is situated dorsally to m. intermandibularis (No. 31). The major muscle head originates along the ventromedial surface of the proximal half of cornu branchial-I (Figures 23.1, 25.2). The muscle fibres run rostromediad. A small muscle head originates from the ventral face of articular and angular, and its muscle fibres incorporate into the whole muscle (Figure 23.1). The muscle inserts broadly to the thin medial raphe it shares with the contralateral geniohyoideus (Figure 25.2), as well as on the medial aspect of corpus hyoidei and at the posterior edge of hypoglossum (Figure 23.1). In the subadult/adult, no connection to the lower jaw is present (Figures 30.1, 30.3-4).

**M. hyoglossus (No. 67).** The major head of the muscle originates at the ventral aspect of the anterior most part of cornu branchial-I, lateral to the articulation of this bone to corpus hyoidei (Figures 23.1, 31.1). Some muscle fibres run rostromediad (Figure 30.3) and a few fibres, originating medially from the corpus hyoidei, between processus lateralis anterior and processus lateralis intermedius, incorporate into the muscle. A small muscle head originates ventrolaterally from cornu hyale. Anterior to the processus lateralis anterior and lateral to the processus lingualis of corpus hyoidei, the course of the muscle changes to dorsomediad (Figure 23.2). Dorsally to the hypoglossum and at the level the anterior most tip of processus lingualis, the muscle inserts to the dorsal integument of the tongue (Figures 22.4, 23.2).

**M. hypoglossohyoideus (No. 70).** The very small, thin, bent-shaped muscle originates laterally at the distal part of processus lingualis of corpus hyoidei. It runs caudad and has a ventrolateral course (Figure 23.2). It inserts dorsally to the hypoglossum.

**Linguae-muscles (No. 72-74).** I was able to identify several separated longitudinal and transverse as well as a few vertical muscle fibres in the tongue. Thus I only had access to a serial section series of a hatchling specimen, I am currently not able to state, whether the identified structures are linguae muscles (No. 72-74) or if they belong to the Anlagen of mm. genioglossus (No. 63) et hypoglossoglossus (No. 69) as described above. Sections of adult specimens as well as a comprehensive set of sections of other species are necessary to clearly identify such structures.

## Cranium Associated Musculature Innervated by Cervical Nerves (“neck muscles”) (nn. Sd/v)

### Epaxial Musculature (n. Sd)

**M. atlantoepistropheooccipitis (No. 75).** The muscle originates laterally at the neural arches up to the lateral processi of the first and second cervical vertebrae; some fibres also originate from the anterior zygapophysis of the third cervical vertebrae (Figure 23.5). The fibres run ventrolaterally (Figures 27.2, 30.4) and attach the exoccipital and opisthotic posteriorly (Figures 23.5, 29.1).

**M. atlantooccipitis (No. 77).** The conical muscle broadly originates from the whole transverse process of the first cervical vertebrae (atlas) (Figures 23.5-6). It runs anteroventrad and reduces its diameter (Figures 27.2, 30.2). With a small insertion area, it inserts posteromedially to the ventral face of the opisthotic (Figures 23.5-6), shortly next to the suture of the opisthotic to the basioccipital.

**M. atlantoopisthoticus (No. 78).** The parallel fibred muscle originates laterally from the neural arch of the atlas, runs rostrolaterad and slightly dorsad (Figure 29.1) and inserts posterodorsally to the opisthotic, directly between the origin sites of m. adductor mandibulae externus (No. 19, 21) (Figures 23.6, 27.1, 29.1).

**M. collooccipitis (No. 80).** The very massive, parallel fibred dorsal neck muscle originates with three muscle heads dorsally form the neural arches of cervical vertebrae-I to -IV (Figures 23.3-6). It runs rostrad (Figures 27.1-2, 30.4, 31.2, 31.4), completely covers m. atlantoopisthoticus (No. 78) dorsally, and inserts directly into the fascia temporalis posterostegalis, which is spanning between the posterior edge of squamosal, the parietal and the supraoccipital (Appendix 5).

### Hypaxial Musculature (n. Sv)

**M. longus colli Pars capitis-I et -II/III (86-87).** It is not possible to separate both muscle portions in the hatchling specimen via three muscle heads. The muscular structure originates directly at the ventral parts of the centra of cervical vertebrae-I to -III, a fourth head leads caudad to cervical vertebrae -IV (Figure 23.6), but connects to non-cranial portions of the whole m. longus colli complex. Shortly before the structure inserts to the basioccipital, it splits into a thin lateral head and a large medial (Figure 27.1), which reaches far more rostrad than the lateral one (Figure 26.2). The medial may be homologous to the anterior part of Pars capitis-I (No. 86), while the lateral one may be homologous to the inserting part of Pars capitis-II/III. In the subadult/adult specimens, a clearer separation of the portions is distinct (Figure 30.1).

**M. retrahens capiti collique Pars carapacobasioccipitale (No. 88).** This longest muscle in the turtle body originates medially from the ventral face of the 7th to 8th costal plate, ventrolaterally from the 7th to 8th dorsal vertebrae, and ventrally from the distal end of the related ribs. Some fibres also originate anteriorly from the 9th costal plate (Figure 31.4). The portion runs rostroventrad, and it is situated between m. longus colli (No. 86-87 + related portions) and the oesophagus (Figures 23.5, 27.2, 31.1). Via a long tendon, it inserts ventrally at the basioccipital, anteriorly to the cranial portions of m. longus colli (No. 86-87) (Figures 23.5, 26.2).

## NOMENCLATURE OF TURTLE CRANIAL MUSCULATURE

Appendix 1 and Figures 6–15 list all 88 cranium-associated muscular units ever described for turtles. I provide a list of synonyms, schematic illustrations, and descriptions for criteria of homology. When naming the muscular units, as far as possible I tried to keep the nomenclature of established literature and the traditional nomenclature to retain its historical background. For example, the m. pseudotemporalis (No. 23-24) was originally named referring to the temporalis muscle of humans. To differentiate its developmental and evolutionary identity, it received the somehow misguiding prefix “pseudo”. Alternatively proposed terms such as “m. anterior” or “m. adductor mandibulae posterior Pars rostralis” (Schumacher 1953-54, 1954-55a; Hacker 1954) are either of a rough topographical or a non-verified evolutionary identity of that structure (Figures 2–4; see below). Major differences to older nomenclature are on the handling of the terms Pars (portion) and musculus (muscle) and the descriptions of origin, insertion, and innervation are based on the broad scale analysis as presented herein. Some structures were either described or shown in literature, but not named or labelled at the same time. Those now gained names in the presented study.

In the following survey, I discuss the evolutionary identity of some critical structures and argue for the terminology as introduced within (Appendix 1). A word of caution: Currently no consensus exists about the developmental, evolutionary, or functionary identity of several cranium-associated muscles in turtles (Edgeworth 1935; Rieppel 1990; Eger 2006). Hence, the presented nomenclature of muscles are of a preliminary kind, and the identity and homology of several muscles still have to be tested in more comprehensive studies.

## HIERARCHY OF HOMOLOGY

In the presented study, I homologised muscular units mainly based on spatial characters in adult anatomy. In most cases, the origin and insertion patterns were used to decide between particular structures. However, Rieppel (1990, 2007), Mabee (2000), Haas (2001), and others have shown that there are different levels of homology to consider. A muscular structure such as the anterior head of m. adductor mandibulae posterior is to be mentioned (Rieppel 1990: ampa; homologue to No. 30), which develops as a part of the pseudotemporalis Anlage; ontogenetically it belongs to the m. adductor mandibulae internus complex, while in adult anatomy it has separated from that complex and shifted spatially. Finally, it has to be considered as a part of m. adductor mandibulae posterior (No. 29-30). Rieppel (1990) refers to the dynamics of developmental processes. That may involve spatial and temporal plasticity as well as intraspecific variability (Werneburg 2009a; see below).

Paraxial head mesoderm – the material source of the anterior parts of head musculature (No. 1-48) – is initially patterned by streams of cranial neural crest cells (cNCC) (Maier et al. 2004) and shows intermixtures with cNCC derivates (Grenier et al. 2009). Mitgutsch et al. (2009) have shown a high interspecific variability of very early cNCC migration in frogs. At later stages, their timing may contain a phylogenetic signal; and the pattern of tissue differentiation bears specific information for higher and lower taxonomic levels (Köntges and Lumsden 1996, 2000; Olsson et al. 2001). In different taxa different timing of the cNCC / mesoderm (muscle-Anlagen) interaction may result either in a different or comparable adult topology of cranial muscles.

In addition to origin / insertion of adult muscles, I propose also considering the innervation pattern and the pattern of the tendinuous framework (sensu Iordansky 1990, 1994) – both structures directly derived from NCC – to define homologies. As in every homology discussion, a consideration of several homology criteria has to be performed parallel due to heterotopic shifts of anatomical elements.

A comparable situation to paraxial mesoderm is recognisable in the postcranial region. The myotom parts of the somites form epaxial and hypaxial muscle Anlagen (Gilbert 2006). Steiner (1977) stated that there are several fusions and separations in developing muscles of tetrapods resulting in a shore leave adapted twisting of posthatching / postnatal muscle anatomy. Both cranial and postcranial musculature information on developmental patterns – as far as they are available – must not be disregarded, as they may expose homologies of structures that are intermixed or blurred in adult anatomy (e.g., the discussion on the homology of the parts of "m. cervico-hyo-capitis" of Ogushi 1913b).

## DYNAMIC MODEL OF MUSCLE EVOLUTION AND DEVELOPMENT

In previous studies, authors have categorised musculature into box-like schemes, an approach that was necessary to handle and to bring order to these elusive structures. As an example, I demonstrate the confusion that occurred for the categorisation of n. trigeminus (V) innervated jaw muscles in turtles (Figures 2–4). In every study, authors had different scientific approaches, and they were only aware of a certain taxonomic sample. That resulted in different assumptions of hierarchies and hence in divergent interpretations of homology and evolution.

To avoid this categorical approach I propose a novel approach to study muscular structures. Therefore, the above-defined idea of the muscular unit – the smallest macroscopic part of a muscular structure – forms the basic element. I noticed in the literature review as well as in my own observations, that muscular structures display a very "fluid" material. It develops and evolves very plastically. Parts of the muscular material separate from a Mutterboden at one point, but they may refuse to the same structure in other taxa or developmental stages. Elements of these parts may also fuse to a muscular structure of a different origin or innervation, such as m. intermandibularis (No. 31) and m. constrictor colli Pars intermandibularis (No. 42) in turtles (Figure 16.4). Lubosch (1933, p. 589) predicatively called this behaviour of muscular structures biomyotaxis. As many separations, refusions, and partial rearrangements occur in ontogeny and phylogeny, categorisations generally proposed as working tools by several authors are no longer tenable. In Figure 16, all possible arrangements of n. trigeminus (V) and n. facialis (VII) innervated muscular units that I detected in the presented study are represented. Every unit represents either a separated muscle (Figure 16.1) or a muscle portion that is still correlated to other muscle portions – a scheme that literary can be best described as a "lotus blossom shape". Every petal only represents a temporary (ontogenetic) or spatial (phylogenetic) potential that is seen e.g., in turtles. Some petals are connected to the "lotus stem" (tendon), some are "shed" (separated) and directly attach to the "soil" (bones, etc.). The size and mightiness of every "petal" (unit) may change, or the structure may be completely absent. Muscle heads may be "translated" as "leaf margins".

As exposed to the development of cNCC migration and possibly other factors too, cranial musculature may best fit to the lotus scheme. As I personally do not have detailed experiences with trunk muscle development and evolution, I can only assume a comparable pattern in that region. The somitogenic neck musculature here studied at least behaves like this.

The herein presented fluctuating system of appearing and dissolving muscular units expands to a fluid, somehow "irregularly" oscillating system of partitions, fusions, demerging "muscle drops", which themselves split, refuse with other parts, etc. (Figure 16). Any box-like thinking must be refused, and although the muscular units as illustrated in Figures 6–15 show some rectangles, they must be taken as pure descriptive simplifications, a tool kit for a more integrated discussion of fluid-lotus-like muscle evolution and development (Figure 16).

## HOMOLOGY OF PARTICULAR MUSCULAR STRUCTURES IN TURTLES

### Muscular Units Unique in Particular Species

Some muscular units are only known in singular species (indicated by two asterisks each in Appendix 1, Figures 6–15: No. 6, 16, 18, 30, 36, 39, 44, 48, 50, 62, 72) or are found in only a few often closely related species (indicated by one asterisk: No. 10, 20, 32, 33, 61, 83). These findings may be correlated to autapomorphic or plesiomorphic conditions seen in the respective taxa. Moreover, the breadth of the studied taxa and the differing accuracy of the authors, the different extent and the quality of manual dissections, and other techniques used such as serial sectioning (e.g., No. 6, 48), led to the identification of possibly unique structures. In addition, structures reduced during development may be observed as rudiments in subadult specimens (m. levator bulbi, No. 16). Guigova et al. (2009) discovered a contralateral variability in the number of eye muscles (retractor bulbi) in giraffes related to a unilateral combat behaviour in males. Intraspecific and contralateral variability in the number (No. 36) and extent (No. 66, Walter 1887) of cranial musculature also can be found in turtle species. This pattern could possibly be associated first to the phylogenetic identity (Pleurodira vs. Cryptodira) and second to the individual retracting behaviour of the head/neck region. However, if a muscular unit is only described for one species this does not mean that the muscle is absent in all other turtles. A detailed survey comparing several specimens of many species and focussing on all muscular units of the head is still lacking and would provide a more comprehensive understanding of cranial musculature in turtles. A first study tending toward this approach was performed by Jones et al. (unpublished work) on most of the feeding-related muscles of two marine turtle species. Appendix 1 and Figures 6–15 only represent the current state of knowledge. Once a broader set of taxa and specimens has been examined the scheme presented here can be expanded upon.

### External Eye Muscles (No. 1-4, 9-10, 34-38) (nn. III, IV, VI)

In the optic chamber of Tetrapoda four mm. recti (No. 2-4, 37), two mm. obliqui (No. 1, 9), and one m. retractor bulbi (No. 38) are present. The latter autapomorphically exists in this group and represents a separation of the m. rectus posterior of non-tetrapod vertebrates (Nishi 1938b). Within Sauropsida, additional muscles were described to attach the eye bulbus. Together with m. retractor bulbi (No. 38), they form an enormous diversity among sauropsids, and their homology is not completely understood (Nishi 1938b; Underwood 1970). Those differences may be explained by the extent of the membrana nictitans and an increase of its mobility. This "third eyelid" is a medial skin duplication of the lower eyelid and may have a cleaning and protecting function. It can be greatly reduced in some turtle taxa such as *Carettochelys insculpta* (Underwood 1970, p. 67).

The m. quadratus (No. 35) originates at the medial surface of the eye bulbus, runs caudally to insert into the posterior angle of the eyelids. Alternatively, it may develop two tendons, with the dorsal tendon inserts posteriorly into the upper lid, while the ventral tendon inserts posteriorly into the lower eyelid (Nishi 1938b). Anterior to m. quadratus (No. 35), m. pyramidalis (No. 34) originates at the medial surface of the eye bulbus. Via one tendon it runs to the membrana nictitans (*Pelodiscus sinensis*), in most species also via a second tendon to the lower eyelid. The muscle only occurs within Archosauria and Testudines and forms a potential synapomorphy of both taxa (Thomson 1932; Schumacher 1972; Rieppel 2004; Eger 2006). Edgeworth (1935) found the pyramidalis muscle in birds to be ontogenetically derived from the abducens primodium, and he identified an n. abducens (VI) innervation. For *Emydura subglobosa*, I also found an n. abducens (VI) innervation of m. pyramidalis (No. 34), which supports the homology of this muscular structure between birds and turtles. In *Chelonia mydas* (Edgeworth 1935), *Clemmys japanicus* (Nishi 1938b), *Pelodiscus sinensis* (Ogushi 1913b), or *Dermochelys coriacea* (Schumacher 1972), several modifications of m. pyramidalis (No. 34) are known. To clarify homologies among species, ontogenetic studies are necessary, and several new taxa must be studied because this structure seems to have an enormous diversity.

One may assume two new eye muscles in the ground pattern of Sauropsida (reptiles and birds). One membrana nictitans related muscular structure (~pyramidalis) and one muscle related to the angle of the upper and the lower eyelid (~quadratus). In *P. sinensis*, both muscles are still separated from each other. In *E. subglobosa* and other turtles (Eger 2006), only an m. pyramidalis (No. 34) is present inserting to the membrana nictitans, an m. quadratus (No. 35) is absent, but a second tendon of m. pyramidalis also inserts to the posterior part of the lower eyelid. Developmental studies should focus on the early development of this muscle in turtles such as *E. subglobosa*, which may be (at least partly) a fusion of the two above mentioned muscles in sauropsids. However, m. quadratus (No. 35) may be reduced in most turtles, and m. pyramidalis (No. 34) may have gained a new insertion to the lower eyelid. Though both muscles are innervated by n. abducens (VI), the detailed branching pattern of the nerve may give some information to the identity of the muscle. In *C. japanicus* the m. quadratus (No. 35), inserting to the upper lid, has one additional insertion to the tendon of membrana nictitans. M. pyramidalis (No. 34) is not present in this species as a separated muscle, but it may be homologous to the superficial part of m. retractor bulbi (No. 38) in *C. japanicus*, which inserts to the membrana nictitans (Nishi 1938) – an assumption supported by my own observation of *E. subglobosa*. This situation could indicate that the pyramidalis muscle (No. 34) phylogenetically/ontogenetically incorporates material from the quadratus (No. 35) as well as from the retractor bulbi (No. 38). With this hypothesis in mind, an insertion of m. pyramidalis (No. 35) to the lower eyelid in most turtles may also be explained.

In Squamata, the bursalis muscle (Underwood 1970) is clearly derived or still connected to the Mutterboden muscle, m. retractor bulbi (Nishi 1938b). One may assume m. bursalis of squamates to be homologous to the m. quadratus of birds and turtles (No. 35), because the m. quadratus (No. 35) is partly connected to retractor bulbi (No. 38) in *C. japonicus* and *D. coriacea*. In both species, it partly originates from the interorbital septum, a feature it shares with m. rectus posterior (No. 37), which is known to be the Mutterboden for retractor bulbi in tetrapods (Nishi 1938b). While in amphibians and most squamates the tendon to the membrana nictitans originates from the interorbital septum and is indirectly moved by eye activity, *Varanus salvator* shows an integration of this tendon to the bursalis muscles (Nishi 1938b). This character is an additional indication that the homology of bursalis is at least partly the Mutterboden of m. pyramidalis (No. 34) in turtles and archosaurs.

As a case of intraspecific variability, Ogushi (1913b) found one unique eye muscle in two adult specimens of *P. sinensis* inserting to the ventral face of the upper eyelid – m. quadratus superior (No. 36). Although discussed as a potential separation of m. quadratus principalis (No. 35) by Ogushi (1913b) himself, the muscle also may have been derived from rectus anterior (No. 2), which is partly connected to the posterior forth of lower eyelid in *D. coriacea*. The latter eyelid reaches relatively far into the dorsal region of the head due to the vertical orientation of the eyelids in this species; hence, spatial similarilarity to the insertion site found in *P. sinensis* exists. The innervation of m. quadratus superior (No. 36) is not clear but Ogushi (1913b) argued for an n. abducens (VI) innervation of the muscle and refutes an n. oculomotorius (n. III) innervation as gained by m. rectus anterior (No. 2).

Ogushi (1913b) described one additional external eye muscle (No. 10) in older specimens of the trionychid *P. sinensis* that may originate phylogenetically from m. obliquus superior (principalis) (No. 9). In my own observations on *Emydura subglobosa,* I found such onestructure in a subadult specimen. In contrast to the finding in *P. sinensis,* the structure was only present as a portion in *E. subglobosa* and consequently should be called m. obliquus superior Pars accessorius (No. 10) in that specimen (Figure 28.1) versus m. obliquus superior accessorius (No. 10) in the respective specimens of *P. sinensis*.

### Smooth Muscles of the Eye and the Nose (No. 5-8, 11-15) and M. Levator Bulbi (No. 16)(nn. III, V)

In contrast to former researchers, Lakjer (1926, p. 26) distinguished two muscles ventral to the eye bulbus. On the one hand, he defined the striped fibred m. levator bulbi (No. 16) as a homologue of Constrictor I dorsalis. On the other hand, he defined an m. depressor palpebrae inferioris (No. 14-15) composed of two muscle portions in turtles, which would have been consequently misinterpreted in the literature. He assumed that the "new" – smooth muscle fibred – m. depressor palpebrae inferioris "potentially" is "a particular transformation of connective tissue fibres of the periorbita." Different authors (Olsson et al. 2001; Ericsson et al. 2004) have shown that the contribution of cNCC to the patterning of the muscles of the mandibular and hyoid arch is mainly restricted to the formation of connective tissue material. Nevertheless, it has also been shown cardiac NCC form smooth muscles in the aortic vessels within visceral arches (see Hall 1999, p. 98); moreover, they contribute to all blood vessels of the face and forebrain with muscular material (Etchevers et al. 2001). In the eye region, Yamashita and Sohal (1987) have shown that the dorsal parts of iris muscles in birds also originate from cNCC. Bruner (1901) studied the smooth muscles in the facial region of Lissamphibia and refered to connective tissue and surrounding mesenchym to form nasal and eyelid muscles. Based on those considerations and the possibility of a smooth muscle origin out of NCC, I follow the opinion of Lakjer (1926) in discussing the m. depressor palpebrae inferioris (No. 14-15) to be of mesoderm-independent, cNCC-derived origin. M. levator bulbi (No. 16), in contrast, originates from n. trigeminus (V) innervated (jaw) muscle Anlagen. Pars transversalis of m. depressor palpebrae inferioris (No. 14) seems to be a novel (cNCC-derived) structure within turtles. It functionally replaces the dorsal head of m. levator bulbi (No. 16) and gains innervation from a branch of n. trigeminus ($V_2$) that innervates muscular structures ventral to the eye (Lubosch 1938b) – but never parts of m. levator bulbi (No. 16) (Lakjer 1926).

Except for birds, the Pars equatorialis of m. depressor palpebrae inferioris (No. 15) is known in all reptiles studied so far (Lakjer 1926). In addition to this muscle portion, those groups show well-developed – non-smoothed – derivates of Constrictor I dorsalis. The coexistence of both structures and their differing histology clearly speak for non-related muscles.

The smooth muscle fibres of m. depressor palpebrae inferioris Pars equatorialis (No. 15) and the striped fibres of m. levator bulbi (No. 16, dorsal head) have both an anterior-posterior orientation. Additionally, the fact that in *Dermochelys coriacea* a dorsal head of levator bulbi still exists and an equatorialis portion of m. depressor palpebrae inferioris (No. 15) is missing (Lakjer 1926) speaks for the hypothesis of a functional but no material replacement.

The Anlage of m. levator bulbi (No. 16) is visible in turtle embryos (Edgeworth 1907) and shows a different degree of postembryonic regeneration (Versluys 1912, p. 599; Fuchs 1915; Lakjer 1926). It may be remained as connective tissue (Nick 1912, p. 125) or be completely reduced (Schumacher 1973) in adults. A well-developed m. levator bulbi (No. 16), originating from the skull roof and reaching ventrally to the eye with two heads, was observed in a subadult *D. coriacea* (Lakjer 1926). In adult *D. coriacea* specimens, m. levator bulbi (No. 16) would be only visible as a thin fascia (Edgeworth 1935: cited after Poglayen-Neuwall 1953-54). Jones et al. (unpublished work: pers. obs. IW) possibly discovered an m. levator bulbi originating from the skull in a subadult *Caretta caretta*. Also in an adult non marine-turtle the muscle was found, in the trionychid *Apalone ferox* (Lubosch 1933), having only one insertion, which would be homologous to the ventral head found in *D. coriacea*. In most turtle species, such as *Terrapene carolina*, m. levator bulbi (No. 16) is completely reduced in adults – possibly related to the reduced mobility of the palatal region in turtles – and both portions of m. depressor palpebrae inferioris (No. 14-15) are well developed (Lakjer 1926).

Referring to Ogushi's (1913b) work, Edgeworth (1935) considered the "m. depressor palpebrae inferioris" (No. 14-15) and the "m. arrector rostri" (No. 13) as a single structure to be synonymised with his "Smooth (unstriped) ocular muscles of Chelonia." One should take his note with caution, because Ogushi (1913b) neither described the nose muscles having smooth muscle fibres, nor did he describe any innervation pattern. In contrast, he cautions against a homologisation to smooth muscles of other tetrapods as described by Bruner (1901).

Winokur (1982) studied the nasal muscles of turtles more in detail and found in sum three smooth muscle masses. Surprisingly not only in the proboscis of Trionychia, but also in the "flat" noses of some pleurodires the author found smooth nasal muscles (chelids: *Chelodina longicollis*, *Elseya latisternum*; pelomedusid: *Podocnemis unifilis*). The m. nasalis Pars arrector rostri (No.13) was not found in all pleurodires and only in Podocnemis unifilis a Pars internarialis (No. 12) is present. I define the three nasal muscles as portions s. s., because Winokur (1982) highlights the connectivity of the portions by fibres crossing in the anterior region of the muscular units. In species, where parasaggital cartilages are present (not *Chelodina longicollis*), a complete separation of the Pars arrector rostri (No. 13) and the circumnarial fibres (No. 11) occurs. One may hypothesise the Pars circumnarialis (No. 11) to be the phylogenetic Mutterboden of the nasal muscular units. However, in that case a sistergroup relationship of Trionychia (Carettochelys insculpta and trionychids, sensu Gaffney and Meylan 1988) to all remaining Cryptodira must be assumed. In the latter, consequently nasal muscles would have been reduced. Nasal muscles seem to be related to nasal closure in species living in the water. Winokur (1982) noted that marine turtles, such as *Caretta caretta*, have erectile non-muscular tissue in the nasal region, which enables a nasal closure.

### N. Trigeminus (V) Innervated Jaw Musculature (No. 17-30)

The mm. adductor mandibulae externus (No. 17-21), internus (No. 23-28), et posterior (No. 29, 30) are the most discussed muscles in chelonian literature, first because of the prominence and diversity of those muscles in turtles. Second, the unclear position of turtles within amniotes is particularly correlated to the anapsid skull condition, and several authors assumed especially the m. adductor mandibulae externus to have an important influence to the architecture of temporal bones in evolution (e.g., Fuchs 1909; Gregory and Adams 1915; Zdansky 1923-25; Kilias 1957; Frazetta 1968; Rieppel 2008) and development (Rieppel 1990). Recently, Tvarožková (2006) was able to show a prior influence of jaw muscle development to the formation of the emarginations of the skull, a process occurring relatively late in embryogenesis. However, jaw muscle development seems to be independent of the formation of temporal openings.

The differentiation of constrictor I lateralis musculature into three muscles represents a plesiomorphic condition that can be recognised in non-tetrapods, amphibians, and amniotes (e.g., Lubosch 1938b, c; Diogo et al. 2008a, b).

### The Portions of M. Adductor Mandibulae Externus (No. 17-21)

A partition of m. adductor mandibulae externus (No. 17, 19, 21) into three major portions, as proposed by Lakjer (1926) (Figure 2), is in some cases not clearly identifiable. Also in *Emydura subglobosa,* I was not able, to clearly distinguish between those in superficial view. When compared to other sauropsid taxa (Lakjer 1926; Lubosch 1933, 1938b), the interrelationship and proportions of these three portions are completely rearranged in turtles. This peculiar anatomy of m. adductor mandibulae externus architecture of turtles lead Iordansky (1987, 1996) to the confidence that the turtle's m. adductor mandibulae externus should be categorised in a completely different way than in other sauropsid groups. He proposed a postorbital, superior, and inferior part of this muscle (Figure 4). Concerning the above-defined nomenclature of muscular units (Appendix 1), the proposal of Iordansky (1987, 1996) represents a more functional categorisation rather than an evolutionary identity of these muscular structures. Nevertheless, thanks to the thorough considerations of this author a fundamental re-evaluation of jaw musculature is inspired.

My impression from the here presented study is that jaw musculature – at least m. adductor mandibulae externus – in turtles possibly experienced a completely different evolution than in Sauria. When compared to Lissamphibia, neither the saurian- nor the turtle-like m. adductor mandibulae externus condition has a comparable shape. Including mammalian jaw muscle architecture, one has to define four morphotypes of constrictor primus lateralis homologues in tetrapods. The herein proposed scheme of plastic jaw muscle behaviour (Figure 16) may be most convenient to interpret the evolutionary history of this structure among land living vertebrates. Comparative ontogenetic studies are needed to postulate homologies herein. Possibly those studies may result in the sobering corollary, that only m. adductor mandibulae externus as a whole structure is homologous among the tetrapod taxa, and the plastic paraxial mesoderm reorganises separately within the different clades: Lissamphibia, Mammalia, Testudines, and Sauria. When referring to the peculiar Crocodylian jaw muscle arrangement (Poglayen-Neuwall 1953b; Iordansky 1964; Tvarožková 2006; Holliday and Witmer 2007) for example also complete reorganisations of the head mesoderm are imaginable within those taxa.

As the homology of jaw muscle portions among Testudines is demonstrated in the presented study (Appendix 1), I discuss particular structures in the following.

Except for *Dermochelys coriacea* (Burne 1905; Lakjer 1926; Schumacher 1972) and *Chelus fimbriatus* (Poglayen-Neuwall 1966; in which it can be completely reduced: compare Lemel et al. 2010 and Appendix 1) m. adductor mandibulae externus Pars profundus (No. 19) is the most prominent muscle portion of the jaw apparatus in turtles. It is the dorsomedial most muscular unit originating mainly from the parietal and the supraoccipital crest and mainly inserts to the coronar aponeurosis (Appendix 1).

In trionychids and kinosternids the coronar aponeurosis develops multiple tendinuous differentiation (Appendix 5) resulting in a variety of muscle fibre courses and muscle heads (e.g., Dalrymple 1975). Lakjer (1926) defined five different partitions in *Amyda cartilaginea* that are also visible in related species such as *Pelodiscus sinensis* (Poglayen-Neuwall 1953a; Iordansky 1987) and in *Lissemys punctata* (Schumacher 1954-55a, 1954-55b). Except for his "portion D", Lakjer (1926) described a major region of the "portions" to originate from the parietal/supraoccipital crest, partly by the supraoccipital aponeurosis (Appendix 5, Figure 16, Lakjer's: "Sehnenband c"). His "portion D" is described to span between two branches of the coronar aponeurosis and hence should be described as a particular portion s. s. in the presented study. However, in Lakjer's figures (Lakjer 1926, fig. 152-153) a clearly unseparated origin of "D" (at least to "C") is visible. Finally, I defined the m. adductor mandibulae externus profundus (No. 19) to be only one muscle portion s. s. in trionychids. One could define Lakjer's (1926) "portions" as muscle heads because they all show different insertions to parts of the coronar aponeurosis, but a shared origin. Further investigations on the detailed anatomy of fibre courses and eventually separated origins may verify or change the nomenclature of those structures proposed herein.

An additional portion - m. adductor mandibulae externus Pars profundus atypica (No. 20) - is only known for *Mauremys caspica* and *Cuora amboinensis* (Poglayen-Neuwall 1953a). When compared to other sauropsid groups, this muscle cannot be homologised to any other known muscular structure. Both species having a Pars profundus atypica (No. 20) are characterised by several highly derived characters within cryptodire turtles. Within those, they are not closely related to each other. Consequently, one has to discuss the Pars profundus atypica (No. 20) as a novel structure that independently evolved within those species. Poglayen-Neuwall (1953a) did not refer to the innervation pattern of that muscular unit, however due to its insertion to the coronar aponeurosis one can assume, that it ontogenetically developed from the adductor externus Anlage and phylogenetically it is a separation of Pars profundus principalis (No. 23).

The m. adductor mandibulae externus Pars medialis portions (No. 17-18) originate at the quadrate in turtles and insert laterally to the lower jaw and/or the coronar aponeurosis (Appendix 1). M. adductor mandibulae externus Pars superficialis (No. 21) generally originates broadly medially on the lateral wall of the adductor chamber. In *Chelydra serpentina*, Rieppel (1990) clearly defined two strong muscle heads in the origin of Pars superficialis (No. 21), the postorbital and the squamosal related head. The former generally occurs in taxa with a strong zygomatic arch or in taxa with complete dermal armour in the postorbital/temporal region (e.g., Chelonioidea, Platysternidae). In the species studied herein, *Emydura subglobosa*, having only a posterior bony bridge, such a muscle head is not present. However, some fibres are known to attach the skin spanning above the adductor chamber in several turtles species (also *E. subglobosa*). To which extent those can be homologised to that muscle head should be investigated in the future.

In several species, the Pars medialis (No. 17) as here defined (Appendix 1) is not clearly distinguishable from the Pars superficialis (No. 21), which resulted in conflicting interpretations of the anatomy observed. Poglayen-Neuwall (1953a) for example declared the fused Pars medialis/Pars superficialis (No. 17/21) s. s. to be his "P. media" (compare to Figures 2–4, Appendix 1) and only the postorbital region related muscle head of Pars superficialis (No. 21) to be his "P. superficialis" (e.g., in *Mesoclemmys nasuta;* similarly to Poglayen-Neuwall 1966: *Chelus fimbriatus*).

As discussed above, the Pars profundus (No. 19) of kinosternids and trionychids is separated into several muscle heads in the origin site. In *Kinosternon scorpioides* Poglayen-Neuwall (1953a) defined one of the muscle heads of Pars profundus (No. 19) to be his "P. media" due to the fusion of No. 17/21. In *Pelodiscus sinensis*, Poglayen-Neuwall (1953a) named m. zygomaticomandibularis (No. 22) as his "P. superficialis" and Pars superficialis (No. 21) s. s. as his "P. media". All other authors who studied *P. sinensis* specimens have been able, to clearly distinguish the Pars medialis (No. 17) from the other portions. The proposal of Poglayen-Neuwall (1953a) to declare m. zygomaticomandibularis (No. 22) to be his "P. superficialis" may have lead him – if no case of variation – to overlook the separation of a Pars medialis (No. 17) that usually originates from the quadrate in *P. sinensis* separately.

In *Amyda cartilaginea*, Lakjer (1926) separated the "medialis region" of m. adductor mandibulae externus into three parts. Following the here presented definition of portions and the criteria of homology as summarised in Appendix 1, I define Lakjer's (1926) "dorsalis-portion" ("II dors") as the m. adductor mandibulae externus superficialis (No. 21): It has its own origin on the squamosal, its own course, and a unique insertion on the lateral face of the coronal aponeurosis. As mentioned above, a comparative arrangement of muscle bundles is also visible or described in other trionychids, *P. sinensis*, or *L. punctata*, and in kinosternids (Poglayen-Neuwall 1953a; Schumacher 1954-55a, b; Iordansky 1987).

All these considerations on Pars medialis (No. 17) and Pars superficialis (No. 21) highlight first the plasticity of cranial musculature not only between major taxonomic groups, and second the necessity to follow a clear nomenclature of muscular structures (Appendix 1).

Due to the particular posterior extension of the lower jaw in trionychids a clear Pars medialis principalis (No. 17) is visible; moreover, in *Amyda cartilaginea* (Lakjer 1926) it separates another portion, Pars medialis inferior (No. 18), to also enable an insertion to the posterior most extension of the lower jaw.

The m. levator anguli oris of lepidosaurs (e.g., Abdala and Moro 2003) stands in close relationship to the Pars superficialis of this group and may be convergent to the rictal plate attaching fibres of the superficialis portion (No. 21) that occurs in some turtles (Werneburg 2010), given that both are homologous among sauropsids.

### M. Zygomaticomandibularis (No. 22)

The m. zygomaticomandibularis (No. 22) is a particular muscular unit only existing in Carrettochelydae (pers. communication by Shigeru Kuratani) and Trionychidae. It has a convergent topology to the masseter muscle in mammals. However, it gains a different innervation and has to be declared as a "real adductor mandibulae muscle" (quote from Ogushi 1913b). Hence, most authors separate this zygomandibular structure as a real muscle s. s. apart from the three main portions (No. 17, 19, 21) of the adductor mandibulae externus complex (e.g., Schumacher 1973; Dalrymple 1975, 1977; Iordansky 1987). In contrast, Lakjer (1926) and Poglayen-Neuwall (1953a) described it as their "superficialis" (No. 21) in *A. cartilaginea* and *P. sinensis* based on its spatial relationships.

As mentioned above, Pars superficialis (No. 21) in several turtles exposes a postorbital region related muscle head that – in the origin face – is clearly separated from the squamosal-related muscle head of this portion. Together, both heads inseparabaly fuse and form one muscle belly, which inserts as one structure to the lateral face of the coronar aponeurosis as well as to the lateral face of the lower jaw. As such, Pars superficialis (No. 21) of the species showing this anatomy is partially comparable to m. zygomaticomandibularis (No. 22), which also originates around the postorbital region and inserts laterally to the lower jaw.

Jones et al. (unpublished work) have found a particular lateral head of the Pars superficialis (No. 21) in *Caretta caretta* and *Lepidochelys kempii* that is almost completely separated from the rest of the muscle portion. Next to the insertion to the anterolateral face of the coronar aponeurosis and the coronar process, Pars superficialis (No. 21) broadly inserts laterally to the lower jaw, and reaches ventrad almost to the ventrolateral edge of the lower jaw in these species. For *C. caretta,* such a separated head was not described by any other author before, and the insertion to the lower jaw does not show such extent. Intraspecific variability and/or a different focus of the authors may be the reasons for this difference. Also for other marine turtles, *Chelonia mydas* and *Eretmochelys imbricata*, such a comparable anatomy was never described or depicted. In *Dermochelys coriacea* (Schumacher 1972), the Pars superficialis (No. 21) does not insert to the lateral face of the lower jaw at all. – Marine turtles show almost complete dermal armour of the temporal region (Kilias 1957); Trionychia show a strong zygomatic arch. The lateral head of Pars superficialis (No. 21) in Chelonioidiae and the m. zygomaticomandibularis (No. 22) of Trionychia originate from homologous bones and, to a different extent, insert to the lateral face of the lower jaw. Based on this comparable anatomy, I hypothesise the lateral head or at least lateral parts of the Pars superficialis (No. 21) of Chelonioidae – depending on the underlying phylogenetic topology (Werneburg 2010, figure 7.11) – to represent either a homologous or a convergent structure to the m. zygomandibularis (No. 22) in Trionychia.

Developmental observations as well as more detailed comparative anatomical studies – particularly on the innervation pattern of the lateral region of the m. adductor mandibulae externus complex – will help to test the here proposed hypothesis.

### The Portions of M. Adductor Mandibulae Internus (No. 23-28)

The m. adductor mandibulae internus (No. 23-28) exposes a more comparable pattern among turtles (and tetrapods) than the external adductor muscular structures (No. 17-22) do. However, the identity of the 'pseudotemporalis', 'pterygoideus' and 'intramandibular' portions and their interrelationship to m. adductor mandibulae posterior (No. 29-30) were repeatedly discussed in the literature (Rieppel 1990, see below).

In several turtle species, a remarkable integration of m. adductor mandibulae posterior (No. 29-30) and m. adductor mandibulae internus Pars pseudotemporalis principalis (No. 23) may occur. This led Schumacher (1953-54, 1954-55a) and his student Hacker (1954) to name both units as "Pars caudalis" (No. 29) et "Pars rostralis" (No. 23) of the posterior adductor (Figures 2, 3). After observing a broader range of taxa, Schumacher (1954-55b) separated Pars pseudotemporalis principalis (No. 23) as "m. adductor mandibulae anterior." Later, Schumacher (1972, 1973) went back to the nomenclature and partitions of jaw musculature as proposed by Lakjer (1926) (Figure 2). Here I also follow the approach of the latter author. I separate Pars pseudotemporalis principalis (No. 23) as a portion of m. adductor mandibulae internus (Appendix 1). As reported by Poglayen-Neuwall (1953a, 1953-54, 1966), the innervation pattern of Pars pseudotemporalis (No. 23-24) is completely different to that of m. adductor mandibulae posterior (No. 29-30). In addition, the developmental and evolutionary identities of both structures differ as discussed below.

The Pars pseudotemporalis principalis (No. 23) has an abnormal horizontal orientation in *Chelus fimbriatus* due to its flat skull. In regard to the following considerations it is worth mentioning that Poglayen-Neuwall (1966) homologised this deep pseudotemporalis structure ("profundus") of *C. fimbriatus* to that of *Trachemys scripta* (Poglayen-Neuwall 1953a), although it has a different origin – I follow his proposal to homologise this structure in *C. fimbriatus* and other turtle species (Appendix 1).

In several species, an m. adductor mandibulae internus Pars pseudotemporalis superficialis (No. 24) may be developed. In contrast to the present study, Poglayen-Neuwall (1966) does not homologise the Pars pseudotemporalis superficialis (No. 24) of *T. scripta* and of *C. fimbriatus* because in those species that portion inserts differently. While in *T. scripta* the portion inserts to the Zwischensehne (Appendix 5, Figure 16), which is connected to m. intramandibularis (No. 25), the Pars superficialis (No. 24) of *C. fimbriatus* inserts to the subarticular aponeurosis. I do not follow the nomenclature of the author, because – as shown by himself – the innervation of Pars pseudotemporalis superficialis (No. 24) shows the same pattern in both species. As will be shown for the Partes pterygoidei (No. 26-28) below, the insertions of m. adductor mandibulae internus portions (23-28) can easily separate from or refuse to the subarticular aponeurosis and e.g., forming a pterygoideus- or a posterior aponeurosis (Appendix 5, Figure 16). The identity of the m. intramandibularis (No. 25) was previously discussed by Rieppel (1990) as well as by Iordansky (2008), and will also be discussed herein. The criterion of spatial orientation has to be preferred when discussing the identity of the Pars pseudotemporalis superficialis (No. 24). However, it is to be mentioned that a pseudotemporalis superficialis portion (No. 24) only occurs in a few turtle groups (Werneburg 2010: characters 110-113) that are not assumed to be closely related. Pars pseudotemporalis superficialis (No. 24) may have the same developmental origin in those taxa; however, it has to be declared as a convergent structure in the adult specimens of those groups.

The Pars pseudotemporalis (No. 23-24) structures in *T. scripta* provide a case study of the presented definition of muscular units (Poglayen-Neuwall 1953a; Iordansky 1987). Whereas *T. scripta* shows a common inseparable origin of Pars pseudotemporalis principalis (No. 23) and Pars pseudotemporalis superficialis (No. 24) – to be named as a portion No. 23/24 – *C. fimbriatus* shows two clearly separated portions s. s.

The m. adductor mandibulae internus Partes pterygoidei (No. 26-28) originate in the pterygoid region and insert directly, via an own (pterygoid) tendon and/or – together with the remaining m. adductor mandibulae internus portions – via the subarticular aponeurosis to the lower jaw (Appendix 1, 5). Schumacher (1973) mentioned a non-homologous arrangement of two Partes pterygoidei in Pleurodira and Cryptodira, a third portion would only occur in *Podocnemis* (Figure 4). After revising the original references and based on the above-defined terminology, I was able to define three homologous portions s. s. (Appendix 1) and the Pars pterygoideus posterior (No. 27) is present in several species. Partes pterygoidei dorsalis (No. 26) et ventralis (No. 28) are clearly separated in their attachment sides and by their fibre courses (Lakjer 1926: *Amyda cartilaginea*); however, in superficial view – also depending on the extend of the attachment of Pars pterygoideus ventralis (No. 28) – both may look like continuous structures (Lakjer 1926: *Eretmochelys imbricata*). Schumacher (1972) described two clearly separated portions in an adult specimen of *Dermochelys coriacea*, Lakjer (1926) did not find those in a young specimen. In the studied specimens of *Emydura subglobosa,* I recognised crucial heterotopic rearrangements in the Partes pterygoidei (No. 26-28). Intraspecific variability as well as ontogenetic differentiation must be taken into account when discussing those structures within a phylogenetic framework.

As mentioned above, m. adductor mandibulae internus Pars intramandibularis (No. 25) independently occurs in a few turtle species. Intramandibular, n. trigeminus (V) innervated muscles – attaching to the medial face of the lower jaw, mostly to cartilago meckeli – occur several times independently in vertebrate evolution (Albrecht 1876; Lubosch 1914; Rieppel 1990; Hertwig 2008; Iordansky 2008; Holliday and Witmer 2009; Werneburg 2009b). Iordansky (2008) functionally correlated their occurrence with strong dermal armour of the lower jaw ,in several reptiles. In Mammalia and Lissamphibia either a less armoured lower jaw or a modified arrangement of jaw bones is visible, hence an intramandibular muscle would be absent in those groups. According to Rieppel (1990), Iordansky (1990) defined two non-homologous kinds of intramandibular muscles in sauropsids that evolved from different parts of the ancestral jaw adductor musculature. The “crocodiloidan (respectively crocodilian)” type is an intramandibular muscle associated to the m. adductor mandibulae posterior (crocodiles, some birds). In contrast, the “lacertil[i]oidan” (several lepidosaurs) muscle type is associated to the m. adductor mandibulae internus muscular units. In Testudines, an intramandibular muscle (No. 25) associated to the n. adductor mandibulae internus portions was discovered in the marine turtle *C. caretta* (several authors, see Appendix 1), in the emydids *Chrysemys picta*, *Graptemys pseudogeographica, T. scripta* (Poglayen-Neuwall 1953a), *Trachemys terrapen* (Iordansky 1996), as well as in the chelydrids *Chelydra serpentina* (Rieppel 1990: embryologically), *Macrochelys temminckii*, as well as in the taxon *Platysternon megacephalum* (Schumacher 1953-54, 1954-55b). The marine turtle *Dermochelys coriacea* does not have an intramandibular muscle although through of oversight differently mentioned by Iordansky (2008) (compare to Burne 1905; Poglayen-Neuwall 1953a, 1953-54; Schumacher 1972, 1973). Although turtles obviously show the “lacertil(i)oidan” type, Iordansky (2008) mentioned an intermedial condition of the intramandibular musculature in turtles. In *Emys orbicularis,* he refers to an intramandibular aponeurosis (Figure 16, Appendix 5), which does not bear any muscular material and is connected to the posterior aponeurosis, that serves as insertion tissue of the m. adductor mandibulae posterior (No. 29-30) muscle. This muscle is completely separated from other muscular units in that species – a hint for the m. adductor mandibular posterior (No. 29-30) related origin of m. intramandibularis (No. 25), at least in emydids. Moreover, Rieppel (1990) has shown the intramandibular muscle in lacertilians and turtles to develop differently. In *C. serpentina*, a close relationship of intermandibular (No. 31-33) and intramandibular (No. 25) muscle Anlagen exists in early development. Later on, the intermandibularis (No. 31-33) Anlage separates, and a clear relation of m. intramandibularis (No. 25) Anlage to the m. adductor mandibulae internus (No. 23-28) Anlage is recognisable. Rieppel (1990) correlated this close development with similar innervation patterns of mm. intra-/intermandibularis (No. 25, 30-31) by posterior branches of n. alveolaris trigemini (V) (see also Poglayen-Neuwall 1953b).

Developmental studies in *Emys orbicularis* may show, if there are any muscular Anlagen within the intramandibular aponeurosis (Figure 16) that are reduced during embryogenesis or if the intramandibular aponeurosis is only a separation of the posterior aponeurosis allowing the m. adductor mandibulae posterior a broader area of activity. While the condition of m. adductor mandibulae posterior (No. 29-30) muscle indicates a closer relationship of turtles to archosaurs, the developmental program of intramandibularis formation out of m. adductor mandibulae internus Anlagen (Rieppel 1990) – with a potential muscle formation in adults – suggested a closer relationship of turtles to lepidosaurs. As mentioned for m. adductor mandibulae externus (No. 17-21/22), musculature the homology assumption of Lakjer (1926) and his followers is not entirely convincing. Particularly in crocodiles, the n. trigeminus (V) innervated jaw muscle portions more or less form a continuous muscle mass (e.g., Poglayen-Neuwall 1953b; Iordansky 1964; Schumacher 1973) – hence the topographical identity of m. intramandibularis may not necessarily reflect a different phylogenetic origin

(Iordansky 1996: 'they are perhaps homologous'; Holliday and Witmer 2007).

In this context, the term 'm. intramandibularis' may be misleading, because it would imply a homology to m. intramandibularis (Aω) of teleost fishes (Werneburg and Hertwig 2009). In that clade m. intramandibularis (Aω) evolved from the m. adductor mandibulae externus/posterior complex (A2 incl. A2-PVM sensu Diogo et al. 2008a), whereas the intramandibularis portion of turtles possibly separated from m. adductor mandibulae internus (A3 sensu Diogo et al. 2008a) (Schumacher 1953-54, 1954, see above).

### M. Adductor Mandibulae Posterior (No. 29-30)

I named the muscle originating at the ear capsule and inserting to the posteromedial aspect of the lower jaw as m. adductor mandibulae posterior (No. 29) (Appendix 1). In several turtles, this posterior part of adductor musculature inserts to the subarticular aponeurosis (e.g., *Chelonia mydas, Chelus fimbriatus, Dogania subplana, Podocnemis*). Consequently (s. s.) one should call it a Pars posterior of m. adductor mandibulae internus in those cases. In other cases (e.g., *Chrysemys*, *Geochelone*, *Pelodiscus*), the posterior muscle (No. 29) has a completely separated identity, exposing an own tendon (Figure 16.2: apo. pos) or/and exposing an own direct insertion to the lower jaw. In addition, intraspecific variability may occur such as in *Emys orbicularis* showing a separated or an integrated behaviour of those muscles (Hoffmann 1890; Poglayen-Neuwall 1953a). For *Testudo horsfieldi*, a contralateral variability of the course of $V_2$ was documented, which results in different conditions in the partition of the mandibular muscles (Iordansky 1987, 1990; see also Haas 2001).

Luther (1914) described a continuously increasing separation of externus, internus, and posterior adductor parts in the evolution of tetrapods – divers transitions are visible in several turtle species (*Pelodiscus sinensis*, *Terrapene carolina*, *Testudo graeca*). While Lepidosauria more likely show an integration of the posterior and the external muscle masses (Rieppel 1987) and their innervation patterns, Archosauria, some lepidosaurs (some lizards and chamaeleons), and turtles show an integration of the posterior and the interior muscle masses and their innervation patterns (Poglayen-Neuwall 1953a). In several turtle species (*Chelus fimbriatus*, *Hydromedusa tectifera*: Poglayen-Neuwall 1966), an integrated relationship of the posterior part to the internus part is recognisable. Within a phylogenetic framework, one may argue this condition to be a unifying character of a group consisting of Archosauria + Testudines. However, the particular patterns of innervation still have to be studied in several groups, and the ground pattern of lepidosaurian and turtle innervation has to be defined.

Following Diogo et al. (2008a), the mm. adductor mandibulae externus et posterior plesiomorphically form one single muscle within Osteichthyes, the A2. This close relationship is still recognisable in lepidosaurs and speaks for a derived condition uniting Archosauria and Testudines. Contrary to the hypothesis presented in Figure 16 – saying the posterior aponeurosis separates from the subarticular aponeurosis – Rieppel (1990) discussed the potential developmental origin of the pterygoideus/pseudotemporalis tendon from the posterior tendon. Moreover, Kesteven (1942-45) mentions Pars pterygoideus posterior (No. 27) of the internal adductor to possibly evolve from m. adductor mandibulae posterior (No. 29).

The close developmental relationship of m. adductor mandibulae internus Pars pseudotemporalis (No. 23) to the anterior head of m. adductor mandibulae posterior (No. 29) in *Chelydra serpentina* highlights the integration of those structures (see above; Rieppel 1990). However, Rieppel (1990) also mentioned that Lakjer's (1926) topological homologisation of this muscle head as a part of m. adductor mandibulae posterior would be correct – he adequately warns not to mix developmental plasticity and homology criteria of adult topology. The developmental variability of the structure was not studied by Rieppel (1990). It may explain the peculiar topographical condition of jaw musculature that the author observed (see Werneburg 2009b).

In a few species, an m. adductor mandibulae posterior Pars rostralis (No. 30) was found. Only more integrative studies can find a solution for the question, if this portion corresponds to the anterior head in the origin of m. adductor mandibulae posterior principalis (No. 29), which is found in several species (see Werneburg 2010).

Assuming the fluid pattern formation model as introduced above and reminding the examples presented in this chapter, I hypothetically assume the posterior Anlage (No. 29) (= m. adductor mandibulae Anlage) to represent the phylogenetic Mutterboden of both, m. adductor mandibulae externus (No. 17-22) et internus (No. 23-28) respectively (Figure 16; longest arrows). As a whole, the "pulsating" structure overridingly points either to the internal or to the external area in development. As evolution acts on organisms in the whole life span (Maier 1999), the differentiation of the three major jaw adductor muscles may be determined in this early time of development, running different paths of development and finally forming non-homologous muscle portions in adults.

### Mm. Intermandibularis et. Submentalis (No. 31-33)

The identity of the intermandibular structures in tetrapods were continuously discussed in the literature (Appendix 1), partly reviewed by Rieppel (1990). In sum, the anterior part of the intermandibular muscular structures is innervated by n. trigeminus (V) and is called m. intermandibularis (No. 31-32), an internal m. submentalis (No. 33) can occur (Appendix 1). The posterior part is innervated by n. facialis (VII). It is called m. constrictor colli Pars intermandibularis (No. 42) in this study (see below for details). Both can be very continuous – forming one muscle s. s. – or a large gap (posterior trigonum) may be present separating m. intermandibularis (No. 31-32) as a whole muscle (compare to Werneburg 2010: characters 178-182). As mentioned above, the most separated condition of muscular structures is defined in Appendix 1. However, in a comparative description, the integration of No. 31/42 should be reflected in the name of respective structures.

Sondhi (1958) depicts one remarkable muscle portion in *Asperideretes leithii* (Trionychia). This m. intermandibularis Pars profundus (No. 32) lies dorsally to m. intermandibularis Pars principalis (No. 31). Pars profundus and Pars principialis are innervated by two branches splitting from one branch that originates from n. alveolaris (V).

### N. Facialis (VII) Innervated Musculature (No. 39-46)

Ruge (1896) developed a detailed system for the evolutionary differentiation of n. facialis (VII) innervated musculature in vertebrates. In its plesiomorphic condition (Gnathostomata) the constrictor of the second pharyngeal arch (Constrictor secundus: $C_2$) has a dorsoventral (dv) orientation of muscle fibres ($C_2$dv). In evolution, this structure serves as Mutterboden for several n. facialis innervated muscles (Lubosch 1933). Anterodorsally it separates a mandibular part ($C_2$md). In turtles, three muscles corresponing to this $C_2$md are known: m. depressor mandibulae (No. 45), m. dilatator tubae (No. 46), and the m. cervicomandibularis (No. 39). The latter was only described for *Apalone ferox* [Lubosch 1933: note, although redrawn by Schumacher (1973) himself, he did state the muscle to be missing in turtles]. Lubosch (1933) referred to Gräper (1932) and Ogushi (1913b, by mistake he wrote "Osawa"), who would also have found this muscle in *A. ferox* and *Pelodiscus sinensis*. However, Ogushi (1913b) only referred to the "cervico-hyo-capitis" muscle complex that he mentioned to be a fusion of different homologous muscular units of other species (see below). This muscle does not attach to the lower jaw as the m. cervicomandibularis (No. 39) does (Lubosch 1933) and gains a different innervation. In addition, Gräper (1932) only mentioned an m. cervicocapitis [partly homologous to Ogushi's (1913) muscle], that among others, attaches the otic region in *A. ferox* and not to the lower jaw as described by Lubosch (1933b). In *P. sinensis*, the muscle is innervated by n. hypoglossus (XII). Developmental studies may observe if the n. facialis (VII) innervated m. cervicomandibularis (No. 39) of *Apalone ferox* (of Lubosch 1933) is incorporated into more medial neck muscles during ontogeny. In that case the muscle would have changed its innervation as well as its insertion pattern – or if m. cervicomandibularis (No. 39) develops the other way around.

M. dilatator tubae (No. 46), which attaches to the eustachian tube, is strongly associated to m. depressor mandibulae (No. 45) by connective tissue, hence Ogushi (1913b) decided to name it the internal depressor mandibulae muscle (Appendix 1). However, no overlapping fibres were ever described to declare both as portions of one muscle. Commonly described to be innervated by n. facialis (VII) (e.g., Ogushi 1913b; Schumacher 1973), McDowell (1963) second-guessed his former observations of 1961 and assumed an n. glossopharyngeus (n. IX) innervation of m. dilatator tubae (No. 46), a finding that would relate the muscle to cornu branchial-I (3rd pharyngeal arch) related musculature. The author focused on cranial arteries mainly and comparative muscle descriptions are absent in his studies that would more strongly justify his findings. In fact, he mainly based his observations on *Podocnemis expansa*, which has a unique orientation of cornu branchial-I distally ending between m. dilatator tubae (No. 46) and m. depressor mandibulae (No. 45). In this context the n. glossopharyngeus (n. IX) innervated m. branchiomandibularis visceralis (No. 47) is to be mentioned (see also below), which itself originates on the distal tip of cornu branchial-I. McDowell (1963) – who did not mention this commonly present muscle – could have intermixed the muscle masses and consequently their innervation pattern in the lower otic region. Alternatively, the strong integration of cornu branchial-I with the m. branchiomandibularis visceralis (No. 47) bearing n. glossopharyngeus (n. IX) in *Podocnemis expansa* may have resulted in a partial shift of some branches of the IXth cranial nerve. Serial section series would be able to detect the actual innervation pattern in this species. In *Caretta caretta*, Jones et al. (unpublished work) found a quiet short m. branchiomandibularis visceralis (No. 47) that runs parallel to the ventral face of m. dilatator tubae (No. 46). Both muscles attach the lower jaw in that species; however, no intercrossing fibres or nerves were detected.

Jones et al. (unpublished work) found the m. depressor mandibulae (No. 45) to include a complex tendinuous framework in *Caretta caretta* that almost separates it in two singular muscle portions. However, along the whole length of the muscle the two parts share a continuous muscle fibre distribution on the surface as well as in the insertion/origin areas. That defines both parts to form one muscle s. s. and not to form muscle portions. As a case of intraspecific variability, one may expect specimens, in which both parts are separated from each other and form two muscle portions. In that case a new muscle portion has to be added to the list (Appendix 1, Figures 6–15) as No. 89 after the last number in the list or – to be preferred – as a reference to the donor m. depressor mandibular (No. 45) as No. 45-1 (note: not as 45a, which would indicate a muscle head following the definition of this paper).

Anteroventrad the Mutterboden muscle $C_2$dv separates an intermandibular part in turtles, herein defined as m. constrictor colli Pars intermandibularis (No. 42). As discussed above, the dual ancestry of intermandibular muscles has been demonstrated by several authors (e.g., Poglayen-Neuwall 1953a), whereas the anterior, n. trigeminus (V) innervated part is Constrictor primus ventralis derived (m. intermandibularis, No. 31), the posterior part (No. 42) is n. facialis (VII) innervated. In my opinion, Lubosch (1933) misidentified all intermandibular muscle(s) to be of Constrictor secundus origin due to his focus on facialis innervated musculature. In *Chelodina longicollis*, the m. constrictor colli Pars intermandibularis (No. 42) may extend its general origin from the posteromedial aspect of the lower jaw to cornu branchial-I (Kesteven 1942-45).

$C_2$dv itself can be separated in two portions in turtles, the m. constrictor colli Pars oralis (No. 43) et Pars aboralis (No. 40). Whereas the former is attached to the cranium, the latter originates in a median raphe on the top of the neck/dorsal tip of the anterior cervical vertebrae. Pars aboralis (No. 43) may extend caudally and, fused with the posterior neck constrictor – m. sphincter corticis (Ogushi 1913: his No. 53; synonym: m. sphincter colli posterior sensu Fürbringer 1874 and Lubosch 1933) – it may cover the whole neck. Due to the diversity of m. constrictor colli (Lubosch 1933) and different degrees of fusion with other neck muscles in turtles a high confusion exists about the identity and synonymy of its muscular units (e.g., Schumacher 1973, p.163-166).

Mediad the $C_2$dv may separate two originally hyoid apparatus associated muscular parts in vertebrates, a dorsal $C_2$hd and a ventral $C_2$hv. The former only occurs in a very few cases within tetrapods and Lubosch (1933) mentions an m. stylohyoideus in birds and mammals and the m. strapedius in crocodiles to eventually be derivates of this dorsal hyoid constrictor ($C_2$hd). The n. XII innervated m. collosquamosus (No. 57) or the IX innervated m. branchiomandibularis visceralis (No. 47) – who may topographically correspond to the $C_2$hd – would have shifted their origins or insertions and gained a different innervation if they were descendents of $C_2$hd. However, based on current knowledge, it is most parsimonious to simply define the $C_2$hd to be absent in turtles. Ontogenetic studies as well as detailed anatomical observations in adults may detect the destiny of this structure.

The ventral $C_2$hv may be found in turtles. It is represented by a muscle portion of m. constrictor colli for which I introduce the name m. constrictor colli Pars spinalis (No. 41). It originates from the lateral aspect of the anterior cervical vertebrae, is present in several species, and seems to replace the m. constrictor colli Pars aboralis (No. 40) in most cases. Whereas the former originates laterally from the cervical vertebrae and lies ventrally to several epaxial muscles (such as No. 80, 81, 82), the latter originates dorsally to the anterior cervical vertebrae in a medial raphe or dorsally on the neural arches and lies superficially to all other muscles of the neck. Both portions (No. 40, 41) insert ventrally in a median raphe with the contralateral muscle. Surprisingly No. 40 ($C_2$dv Partim) and No. 41

($C_2$hv) never definitely occur at the same time. This could indicate a direct homology of both portions – in that case a radical shift of the origin site would have happened quite often in turtle evolution, perhaps enabled by extreme fluid developmental process of the constrictor colli Anlage (see discussion on Pars superficialis, No. 44, below). Nevertheless, after re-checking the very comprehensive study of Lubosch (1933) – who compared dissections of a broad range of sauropsid species and brought them in context with a large literature review on vertebrate taxa (e.g., Ruge 1896) – I follow his global interpretation where he discussed the condition seen in *Apalone ferox* (Lubosch 1933, figure 17). Here he found constrictor colli Pars oralis (No. 40) and Pars aboralis (No. 40), both of $C_2$dv origin, to be fused. Next to them, $C_2$hv (Pars spinalis, No. 41) is present, which valuates it to be an additional portion of m. constrictor colli. Again, only developmental studies can finally evaluate this opinion. – As trionychids are for Cryptodira, *Chelodina longicollis,* is characterised by several derived features within Pleurodira (as known so far). This may be possibly related to the high mobility and extention of necks in both taxa. Pars spinalis (No. 41) is commonly described to gain n. VII innervation (Gräper 1933). However, as an intraspecific variation of *C. longicollis* Kesteven (1942-45) described the portion to be innervated by spinal nerves nn. S1 et S2. One could argue the m. sphincter corticis of Ogushi (1913b: his No. 53) – the posterior constrictor of the neck, that is often indistinguishable fused with the n. facialis (VII) innervated m. constrictor colli (No. 40-44) – to have shifted rostrad and to suppress the facialis constrictor. Kesteven (1942-45) continued his description and first described three distinct heads in the origin of the Pars spinalis (No. 41), a character of this portion also found in other turtle species (e.g., *Dermochelys coriacea*, Schumacher 1972). Second, Kesteven (1942-45) described a different innervation pattern of the more posterior neck constrictor (m. sphincter corticis) by the ventral branch of spinal nerve n. S2. Ogushi (1913b) particularly mentioned a ventral spinal nerve innervation of m. sphincter corticis in turtles – but in *Pelodiscus sinensis,* it would come from spinal nerve n. S7. Hence, it is perhaps more reasonable, that Pars spinalis (No. 41) may have extended caudally as a whole in *C. longicollis*, suppressed m. sphincter corticis, and gained a new innervation. However, based on that differing innervation patterns, one cannot finally state the homology of this muscular unit in *C. longicollis*. I synonymised the muscle portion described by Kesteven (1942-45) to Pars spinalis (No. 41) due to similar origin and insertion when compared to other turtle species.

As demonstrated in the trionychid *Aspideretes leithii* (Sondhi 1958), the Mutterboden muscle $C_2$dv may also separate a lateral muscular unit, m. constrictor colli Pars superficialis (No. 44): a potential of this muscular Mutterboden that was never described in literature before. As its potential phylogenetical donor muscle ($C_2$dv), it gains innervation by n. VII (Sondhi 1958), inserts to the median raphe at the bottom of the neck, and is situated superficially to all other neck muscles. Surprisingly, the course of muscle fibres (= horizontally) is rotated by 90° to the fibre course of the remaining (common) constrictor colli portions (= vertically), that resembles an enormous positional change in evolution. Ontogenetically non-terminated myoblasts (No. 44 Anlage) that separate from the myoblast of the donor muscle Anlage ($C_2$dv) may have “simply” changed the program of their alignment, and the accumulated fibres may have consequently changed their orientation in the adult. An alternative, less parsimonious scenario is imaginable: It would be worth checking, if the constrictor colli Pars superficialis (No. 44) ontogenetically originates from the n. XII innervated coracohyoideus (No. 58) muscle Anlage. It also lies ventrally in the neck, has an anterior-posterior orientation of muscle fibres, and serves as a Mutterboden for several other muscles ventrally in the neck (see below). The ontogenetic muscle precursors of m. constrictor colli Pars superficialis (No. 44) may have been shifted from the coracohyoideus Anlage to a superficial position and may have been separated from its donor after the dorsoventrad expansion of constrictor colli Anlage ($C_2$dv). Here it may have gained the innervation of n. VII by positional reasons. In that case, the muscular portion should be named “coracohyoideus Pars superficialis”.

## N. Glossopharyngeus (IX) Innervated Musculature

Amniotes show a reduced number of splanchnocranial elements, and only two muscles are known in turtles that are exclusively innervated by n. glossopharyngeus (n. IX), which plesiomorphically is associated to the third pharyngeal arch. The partly very strong m. branchiomandibularis visceralis (No. 47) arises from the distal end of cornu branchial-I and it inserts medially to the posterior region of the lower jaw. Gräper (1932, 1933) considered a breathing correlated function while the lower jaw is closed. However, in several species, the cornu branchial-I is distally deeply imbedded between the neck muscles, and it is connected by connective tissue (Gräper 1932) or ligaments (Jones unpublished work: pers. obs. IW) to the occipital/squamosal region. A feeding mechanism does not include only snapping in turtles but there is some evidence for an anteroposterior movement (M. Jones, personal commun., 2009). The influence of this muscle should be tested in biomechanical analyses. The developmental origin of the muscle (No. 47) is not entirely clear. Instead of arising from the posterior most n. glossopharyngeus (IX) innervated part of the paraxial mesoderm, it may also develop from n. hypoglossus (XII) innervated myotom. A very strong connection/integration of m. branchiomandibularis visceralis (No. 47) to m. hyoglossus (No. 67) (Walter 1887) or also to m. genioglossus (No. 63) (von Bayern 1884, p. 63) was reported for some species (e.g., *Emys orbicularis*).

The second n. glossopharyngeus (IX) innervated muscle was only described for *Pelodiscus sinensis* based on serial section evaluations (Ogushi 1913b): m. tensor s. dilatator vaginae venae nasoophtalmicae (No. 48). The author argues that the muscle would pull the respective venae to the skull to avoid a constriction of the vessel, whilst the head/neck is retracted in the cryptodire style. Comparative studies should show if the muscle (No. 48) autapomorphically occurs in *P. sinensis* or soft-shelled turtles, or if the muscle is unique to all hidden-necked turtles. In the pleurodire turtle *Emydura subglobosa*, I was not able to identify such a muscle in serial sections, which would support Ogushi's (1913b) functional assumption for now.

### Nn. Vagus et Accessorius (X, XI) Innervated Musculature

The laryngeal muscles (No. 49, 50) show a relatively conserved count and shape among Testudines. Particularly the complete separation of cartilago cricoidea or its integration to cartilago thyreoidea (together as cartilago cricothyroidea: Schumacher 1972, 1973) has an influence to the insertion site of m. dilatator laryngis (No. 51). Only in *Caretta caretta* an additional muscle portion was found (No. 50) (Alessandrini 1834b), that apparently separated medially from m. constrictor laryngis principalis (No. 49).

In constrast, m. plastrocapitis (No. 52) develops a high degree of variability among turtle taxa and the muscle gained particular interest by some classic authors due to its phylogenetic relationship to sternocleidomastoideus muscle of Mammalia (e.g., Meckel 1828; Cuvier 1835; Fürbringer 1874). Nevertheless, it was often not recognised, because a confusing diversity of plastrocapitis (No. 52) evolved within turtle. This fact is realisable by the differing innervation pattern of the muscle among species. While it is innervated by n. accessorius (XI) in most species (sensu Ogushi 1913b; Shiino 1913), it may also be supported by branches of n. vagus (X) (Scanlon 1982: *Chrysemys picta*), and/or by the rami ventralis of the 3rd to the 4th spinal nerve (Fürbringer 1874; Ogushi 1913b: *Pelodiscus sinensis*, Schumacher 1972: *Dermochelys coriacea*). Finally, also the n. hypoglossus (XII) was described to contribute to the innervation of m. plastrosquamosus (No. 52) (Gräper 1932; Kesteven 1942-45).

Schumacher (1972) argued for the loss of m. plastrocapitis (No. 52) in *Chelodina longicollis*. He apparently based his knowledge on Gräper's study (1932); however, that author also discussed the muscle to be possibly integrated to other strong developed muscles (Gräper 1932, p. 185, his No. 4) of the neck region. In *C. longicollis* he discovered (page 186, his No. 10 N.N.) a new muscular structure spanning between the distal third of cornu branchial-I and the mastoid area (squamosal/quadrate). I call it the m. squamosobranchial (No. 53). Kesteven (1942-45, p. 264) found a comparable muscle to be present in the same species (his "cornu-hyoideus-capitis"). He also described an m. plastrocapitis (No. 52, his "sterno-thyroid"), which apparently shifted its origin from the plastron to the ventral area of the neck – possibly due to the exceptionally elongated neck of *C. longicollis*. In addition, the insertion seems to be replaced from the skull ventrad to the dorsal area of the hyoid apparatus – fibre attachments at the distal area of cornu brachiale-I and a few fibres at cornu branchial-II are reported. Although drawn in connection with plastrocapitis (No. 52), Ashley (1962) described his "sternomastoideus" to only connect one cornu branchial (by a tendon) with the base of the skull. Kesteven's (1942-45) and Ashley's (1962) observations show a strong relationship between both muscles (No. 52, 53). Schumacher (1972) and many others reported a tendinuous connection of m. plastrocapitis to cornu branchial-I in addition to its insertion to the mastoid area. One may finally argue for a phylogenetic origin of m. squamosobranchiale (No. 53) from the anterior part of m. plastrocapitis (No. 52).

Recently, Jones et al. (unpublished work) could show a so far unknown insertion of a thin m.

plastrocapitis (No. 52) to the lateral face of the atlas in *C. caretta*. In this species m. squamosobranchial (No. 53) is well developed. In *Lepidochelys kempii*, the authors did not find an m. squamosobranchial (No. 53); however, a thin tendon connecting cornu branchial-I and the squamosal may be homologous to the structure. Jones et al. (unpublished work) also did not find a separated m. plastrocapitis (No. 52) in *L. kempii*, but in this species, the muscle might be laterally fused with the superficially situated m. constrictor colli (No. 41-43). With this finding, one may perhaps argue for an origin of m. plastrocapitis (No. 52) from n. facialis (VII) innervated muscle Anlagen in turtles – that would strongly contradict its homology to the sternocleidomastoideus muscle of Mammalia. But Gräper (1933), who missed m. plastrocapitis (No. 52) in *Chelonia mydas* as a separated structure argues for an integration of the muscle into the n. hypoglossus (XII) innervated m. coracohyoideus (No. 58-60), which itself would be very complex in this species. In contrast, Hoffmann (1890) found the muscle to be completely separated in the same species – a case of intraspecific variability.

In sum, m. plastrocapitis (No. 52) is highly variable at all. It is reduced in size, replaced to other insertion sites, or integrated to other muscular structures of the neck. For this retractor muscle functional constrains – reduced retractibility (marine turtles), high mobility of long necks (*C. longicollis*), or also the distinguishing retraction mode of Cryptodira and Pleurodira – should be taken in account. Up to this date, m. plastrocapitis (No. 52) and m. squamosobranchiale (No. 53) are only described in detail for a few species, and one needs to check the correlations proposed above. Gräper (1932, p. 191) correlates the absence of n. accessorius (XI) with the very thin and reduced shape of m. plastrocapitis (No. 52) in trionychids (his *Apalone ferox* and Ogushi's 1913b: *P. sinensis*). Consequently, he later argues (Gräper 1933, p. 277) for a replacement of m. plastrocapitis (No. 32) by the colloplastralis muscle of Ogushi (1913b: his No. 32), spanning between the plastron and the neck. However, in *P. sinensis* both muscles (Ogushi 1913b: his No. 32, 33), m. colloplastralis and m. plastrocapitis (No. 52), are present as complete muscles (par definition: Appendix 1) at the same time, and one should not declare a replacement of both, neither functionally nor concerning homology.

### N. Hypoglossus (XII) Innervated Musculature

Sewertzoff (1929) discussed the developmental origin of several muscles in the hypoglossal region; Gräper (1932, 1933) very comprehensively demonstrated the immense interspecific diversity of muscular integration in tongue related muscles. Especially m. genioglossus (No. 63), which resembles the main developmental Mutterboden in this area, is partly connected to other muscular units (No. 64, 65, 69, 70, 72, 73, 74) in several species. As mentioned above, I named muscular units based on the most separated state of a muscular structure known from literature. However, particularly in the tongue region one could easily argue that a structure is only a muscle head of m. genioglossus (No. 63) s. s. when observing a few species. However, problems of homology will arise when making comparisons to species where this muscle "head" is separated as a muscle or a muscle portion.

One example for the consideration of synonymy, as it was accomplished for each cranial muscular unit separately (Appendix 1), should be demonstrated herein: One muscular structure (No. 65) was described by George and Shah (1955a) as belonging to m. genioglossus (No. 63) in *Lissemys punctata*, because as this muscle it originates from the symphysis of the dentaries. However, such as m. geniohyoideus principalis (No. 64), this muscular structure (No. 65) inserts to the cornu branchial-I. After rechecking the drawings, I realised – contra the description of the authors – the structure mainly originates from the medial aspect of the dentary (as No. 64), and only one part of the muscle has an anterior origin at the symphysis of the dentaries. In this example, intraspecific (or ontogenetic) variability finally shed light on the identity of the structure. In the *Lissemys punctata* specimen studied by Gnanamuthu (1937), m. geniohyoideus Pars lateralis (No. 65) is still connected to its Mutterboden m. geniohyoideus principalis (No. 64), while George and Shah (1955a) dissected a specimen of the same species in which those muscular units are completely separated. George and Shah (1955a) did not describe intercrossing fibres between their "Genio-glossus externus et internus" (No. 63 and 65), which would instead define them as portions of the same muscle. In their specimen, two separated muscles were described. George and Shah (1955a) and Schumacher (1973) mentioned the m. genioglossus (No. 63) to originate from the symphysis as well as from the medial side of the anterior third of the dentaries. Hence, it would be a correct synonymisation to call the "genioglossus externus" of George and Shah (1955a) the only homologous structure of m. genioglossus (No. 63) in the present study (No. 63). George and Shah (1955a) may have confused both muscles (No. 63 and 65) due to their strikingly similar orientation in the tongue and potentially similar functions – protraction and elevation of hyoid. Finally, I follow Gnanamuthu (1937) in naming the muscular structure mentioned as m. geniohyoideus Pars lateralis (No. 65), and hence to be in closer relationship to m. geniohyoideus Pars principalis (No. 64). Moreover, Kesteven (1942-45) described a structure in *Chelodina longicollis*, which should be named as m. geniohyoideus Pars lateralis (No. 65) par definition (Appendix 1). Apparently, the Pars principalis (No. 64) is lost in this species, probably due to changing anatomical conditions correlated to feeding behaviour. The "flexibility" of m. geniohyoideus (No. 64) can also be recognised by its innervation; while generally innervated by n. hypoglossus (XII) (Schumacher 1972), Shiino (1913) reported an additional support by n. glossopharyngeus (IX) in *Trachemys decussata*.

M. coracohyoideus (No. 58), spanning between the shoulder girdle and the hyoid apparatus, possibly resembles the ontogenetic and phylogenetic Mutterboden for several muscular units at the base of the neck (No. 59, 60, 61, 62, 66, 71). This is indicated by fibres that still intercross in some species (e.g., No. 60, No. 71; Gräper 1932: *Chelydra serpentina* and *Chelodina longicollis*) or a very similar complete course of those muscular units, which are unique in particular species (e.g., 61, 62 or 59: Gräper 1932). The potential origin of m. constrictor colli Pars superficialis (No. 44) out of m. coracohyoideus (No. 58) was already mentioned above. Myotomic material of (perhaps interspecifically) different myotom origin may be the ontogenetic precursor of m. coracohyoideus (No. 58). Myotomic material (perhaps interspecifically) originating from different myotomes may be the ontogenetic precursor of m. coracohyoideus (No. 58). This conclusion is supported by the muscle's innervation pattern. In addition to n. hypoglossus (XII) (Scanlon 1982), the muscle is supported by the rami ventralis of spinal nerves 2-3 in its anterior and of spinal nerves 4-5 in its posterior region (Gräper 1932; Schumacher 1972). In addition, the high anteroposterior extend of the muscle speaks for this multimyogen assumption, a condition comparable to the longest muscles of turtles, the m. retrahens capiti collique (including No. 88), which is also innervated by spinal nerves of the whole vertebral column (e.g., Ogushi 1913b; Scanlon 1982; Callister and Peterson 1992). The extension of only one myotom of the posterior head region (n. XII innervated) over the whole neck or body in early development is hardly conceivable.

The fluid character of cranial musculature as demonstrated for jaw muscles above is also exemplified in the "cornu hyoideus muscle," unique in *Aspideretes leithii* (Sondhi 1958). The structure originates from cornu branchial-II and runs to cornu branchial-I and corpus hyoidei. By the definition of origin and insertion (Appendix 1), m. coracohyoideus Pars interbranchialis (No. 60) and m. branchiohyoideus (No. 55) must have been fused in this species while loosing their origin/insertion on cornu branchial-I. In comparative studies, "cornu hyoideus" should be labelled as No. 55/60 following the above-mentioned proposal.

M. collosquamosus (No. 57) and m. atlantoexoccipitis (No. 54), two muscles arising from the cervical vertebrae, were described by Ogushi (1913b) as being innervated by n. hypoglossus (XII). However, an additional n. accessorius (XI) support was reported for the former, and a singular spinal nerve (n. S2) support was described for the latter in *Chryssemys picta* (Scanlon 1982). Ogushi (1913b) mentioned an autapomorphic loss of n. accessorius (XI) for *Pelodiscus sinensis*; hence, the double innervation of m. collosquamosus (No. 57) seems to be the more common situation. Myogenic material of n. accessorius (XI) innervated paraxial mesoderm as well as n. vagus (X) innervated myotomes is reduced to a large extent in tetrapods due to the loss of gill structures (Maier et al. 2004). For collosquamosus (No. 57), an integration of n. XI innervated muscular material to n. hypoglossus (XII) innervated material is still possible. However, n. accessorius (XI) may have changed the muscle to innervate in most species or it simply was reduced.

The innervation pattern of m. atlantoexoccipitis (No. 54) was only described in the above-mentioned studies (n. XII or n.S2), and no consensus existed regarding evolutionary identity of this muscle. M. atlantoexoccipitis (No. 54) is innervated by ramus epistropheo-squamosi of n. hypoglossus (XII) in *Pelodiscus sinensis* (Ogushi 1913b). It originates from the ventrolateral aspect of cervical vertebrae-1 and inserts to the exoccipital. For *Chrysemys picta*, Scanlon (1982) described a muscular structure, the "m. collo-capitis longus," which is innervated by n. S2. It originates with a thin tendon from the ventrolateral surface of m. collo-squamosus (No. 57) and it inserts to the exoccipital. Due to its tendinuous connection to this muscle

(No. 57), the structure (No. 54) would be a portion of collosquamosus (No. 57) by definition, but as mentioned above, the most common condition of the muscle known in turtle literature should be mentioned when naming a structure. Scanlon (1982) homologised this structure with the cranium-associated part of m. longus colli (No. 86/87) of other authors, which is situated ventrally in the neck. However, he additionally described an m. longus colli Pars capitis (No. 87) to be present, which would be separated in two "portions" – his "longus colli of CV-2 / -3". He did not synonymise these two "portions" with muscles described by other authors. I homologise Scanlon's (1982) "m. collo-capitis longus" to m. atlantoexoccipitis (No. 54) due to the synopsis of following aspects: 1. a close relationship of atlantoexoccipitis (No. 54) and m. collosquamosus (No. 57) by a shared n. hypoglossum (XII) innervation in *Pelodiscus sinensis* (Ogushi 1913b). 2. the connection of Scanlon's (1982) "m. collo-capitis longus" to m. collosquamosus (No. 57). 3. a similar course, as well as 4. the same insertion of both structures to the exoccipital. Consequently, m. atlantoexoccipitis (No. 54) in *C. picta* must have changed both its origin site and its innervation pattern, possibly subsequent to a slightly changed spatial orientation.

### Neck Musculature (n. Cd/v)

Hypaxial and epaxial muscle layers – that are still distinct in fish – show a complicated morphology in tetrapods due to adaptations to land locomotion and holding the head in the air (Steiner 1977; Liem et al. 2001; Maier et al. 2004). Especially in turtles and birds, the musculature of the very mobile neck underwent a large number of modifications (Nishi 1916, 1938a; Gasc 1981) resulting in several fusions and partitions. The homologisation of muscle regions seems to be possible only based on innervation patterns. In addition, innervation patterns may change during evolution (Haas 2001, 2003a, b), especially in such a variable region as the neck. Hence, the most valuable source of homologisation would be comparative developmental studies of the neck region, but so far, those are missing for turtles. While discussing n. facialis (VII) innervated neck constrictors (No. 40-44), Lubosch (1933, p. 589) introduced the term *myobiotaxis* that adumbrates the ability of muscles to partly fuse, differentiate, re-fuse, etc. Keeping this in mind, the homologisations of the cranium-associated neck muscular units presented here (No. 54, 57, 75-88) are of a very premature nature in terms of research. Considering neck musculature, the lotus approach as presented for the adductor mandibulae above (Figure 16) reaches a new level of relevance.

In this regard, one example was extensively discussed by Ogushi (1913b) in which he defines a peculiar "m. cervico-hyo-capitis" (his No. 35; in this study at least parts of No. 71, 75, 78, 79: see below) in the trionychid turtle *Pelodiscus sinensis*. He described this muscle to originate from cervical vertebrae 3-6. The muscle belly forms four muscle heads (Ogushi 1913b: "caudae") anteriorly, attaching to the squamosal, the occipital region, the cornu branchial-II and finally the ventral aspect of corpus hyoidei. Ogushi (1913b) argued that this muscle does not find any corresponding homologue as a whole structure in *P. sinensis,* but most muscle fibres may be homologous to m. cervicocapitis (No. 79). Ventrally, the apparently epaxial muscle of Ogushi (1913b) could have been fused with hypaxonic musculature forming the anterior part of the muscle head which inserts to corpus hyoidei ("venter anterior" =anterior to the inscription of "cauda hyoidea" sensu Ogushi 1913b: No. 35a). However, I assume this muscle head to originate phylogenetically from the dorsal aspect of m. levator pharyngis (No. 71). The muscle head originates from cornu branchial-I and is innervated by ramus levator pharyngis branches of the n. hypoglossus (XII). The persistence of the innervation in addition to a somehow "major" shift of the muscle mass additionally supports this assumption. For another trionychid turtle, *Apalone ferox*, Gräper (1932, p. 190) described the m. levator pharyngis (No. 71) as still connected to m. coracohyoideus Pars principalis (No. 58), which highlights the "flexibility" of this structure among genera.

Ogushi (1913b) also argued that the m. atlantoopisthoticus (No. 78, his No. 47) and m. atlantoepistropheooccipitis (No. 75, his No. 46) are derived from the anterior heads of "m. cervico-hyo-capitis" namely from capita squamosi et occipitalis. Both muscles (No. 75, 78) exist next to the proposed donor muscle and are not connected to it, they may at most be partly homologous to those muscle heads. Hence, I list them as unrelated muscular units (no portions of one muscle s. s.) in Figures 6–15. Without the integrated approach of the lotus system at this point, a general question of homology would arise again. Could one homologise a muscle A in one species with a muscle A in an other species where "lotus spoken" unrelated "muscle drops" could have originated from B? Again, the lotus system does not list clear tables of homology, as it is simply a list of muscular units of a fluid material.

M. cervicocapitis (No. 79), the major part of Ogushi's (1913) "m. cervico-hyo-capitis" is well defined as a separated muscle by several authors and is innervated by the dorsal rami of the first four (Scanlon 1982) to five (Vallois 1922) spinal nerves.

Whether m. collosquamosus (No. 57) phylogenetically separates from the "cauda squamosi" part of Ogushi's (1913b: No. 35) "m. cervico-hyo-capitis" (~ m. cervicocapitis, No. 79) can only be tested ontogenetically. Both muscles (No. 57 and ~ No. 79) originate from different cervical vertebrae and gain a different innervation, arranging the former to hypoglossus (n. XII) and the latter to epaxial muscular regions.

For neck muscles, a large confusion exists about homology, nomenclature, and evolutionary identity (see synonyms in Appendix 1). Some further problematic structures are exemplarily mentioned next.

The identity of m. atlantoopisthoticus (No. 78) was discussed in literature. It is innervated by R. m. epistropheo-squamosi of n. XII in *P. sinensis* (Ogushi 1913b, p. 360) but spinal nerve n. S1 innervated in *Chrysemys picta* (Scanlon 1982). Ogushi (1913b) assumed the muscle – together with the S1d-innervated m. atlantoepistropheooccipitis (No. 75) – to originate phylogenetically from the anterior part of the S2d- to S5d-innervated m. cervicocapitis (~ No. 79, see above). In contrast, Scanlon (1982) assumed it being the spinal nerve-1 innervated atlas-part of the serially arranged intracervical m. interspinalis cervicis. Only developmental studies can solve this problem. However, both hypotheses assume an epaxial muscular origin of m. atlantoopisthoticus (No .78), which I also do. The shape of the posterior skull region, as well as the related retracting mechanism (Dalrymple 1979) differentiates trionychids such as *P. sinensis* (Ogushi 1913a; Dalrymple 1977) from the emydid *C. picta* (Jamninsky 2007) and all other turtle taxa. This may have resulted in a rostrad shift of m. atlantoopisthoticus (No. 78) insertion, correlated to a shift of innervation from spinal nerve-1 to n. hypoglossus (XII) in *P. sinensis*. The same scenario is also imaginable for the above-mentioned n. XII innervated m. atlantoexoccipitis (No. 54) from a spinal nerve innervated region, which would also give some further evidence for the presented identity of "m. collo-capitis longus."

The phylogenetic origin of m. atlantoepistropheooccipitis Pars profundus (No. 76) is not entirely clear. Topographically, it seems to be a separation of m. atlantoepistropheooccipitis Pars principalis (No. 75); and in *Chelonoidis denticulata*, it is still connected to No. 75 (Wiedemann 1803). However, George and Shah (1955a, figure 7) have drawn it as a cranium-attached continuation of the intercervical m. longissimus cervicis complex. As the authors did not draw any fibres crossing between those muscles, I correlated m. atlantoepistropheooccipitis Pars profundus (No. 76) to m. atlantoepistropheooccipitis Pars principalis (No. 75), and as the latter muscle (after Ogushi 1913b) I hypothesise it to be innervated by the dorsal branch of n. S1.

Vallois (1922) distinguished two muscles spanning between the anterior part of the carapace and the cervico-cranial region, one lateral, and one medial one. Each of them has one capitis- (No. 81, 82 and related portions) and one cervicis-portion. The observation of Vallois (1922) is supported by descriptions of Burne (1905) and Herrel et al. (2008). The diversity of m. carapacocervicocapitis lateralis Pars capitis (No. 81) was discussed by Vallois (1922), who distinguished two major types. It inserts to the basicranial region in Pleurodira (Shah 1963), whereas in marine turtles it attaches the posterodorsal edge of the skull (e.g., Rathke 1848; Hoffmann 1890; Vallois 1922; Schumacher 1972; Jones et al. unpublished work). In all remaining cryptodires, the muscle portion (No. 81) is missing (Meckel 1828; Rathke 1848; Hoffmann 1890; Ogushi 1913b; Shah 1963; Scanlon 1982). The shared condition with pleurodires may be evidence for a basal position of marine turtles within cryptodires; however, a functional explanation for the different insertions is difficult. A ventral insertion in Pleurodira may be explained by the laterad retracting mechanism of this group. Cryptodires retract their neck differently to pleurodires and may have lost the insertion of m. carapacocervicocapitis lateralis to the head (No. 81). Marine turtles lack the ability to retract their neck, and the presence of m. carapacocervicocapitis lateralis Pars capitis (No. 81) may represent a plesiomorphic relict of Testudines-ancestors. As with marine turtles, the stem taxa of Testudines apparently did not retract their neck, indicated by bony spines in the neck region (*Proganochelys quenstedtii*: Gaffney 1990), an absence of a carapace, or an absence of a domed rib cage (*Odontochelys semitestacea*: Li et al. 2008). Assuming a basal position of marine turtles (Werneburg and Sánchez-Villagra 2009) one may declare the non-retracting morphotype of No. 81 to plesiomorphically perform a stabilisation function, whereas in Pleurodira No. 81 – having a derived condition with a shifted insertion – acts as a lateral retractor. In cryptodires, able to retract their neck (non-marine turtle cryptodires), No. 81 may have been reduced because in this taxon the longest muscle of turtles – m. retrahens capiti collique (No. 88 with three related portions, Scanlon 1982) – acts as the main retractor of the head/neck (Callister et al. 1992).

With a very similar shape, m. carapacocervicocapitis medialis Pars capitis (No. 82) occurs dorsally in the neck of Cryptodira (excl. trionychids: e.g., Rathke 1848; Ogushi 1913b), but it is missing in Pleurodira (e.g., Gräper 1932: *Chelodina longicollis*). Due to the multidirectional flexibility of the neck in trionychids and the lateral flexure behaviour of pleurodires, No. 82 may have been reduced in those taxa.

M. carapacocervicocapitis lateralis Pars capitis (No. 81) was described for *Chelodina longicollis* as a muscular structure with two broad heads in the origin (Shah 1963). One may assue a fusion of No. 81 and No. 82 in this species or a phylogenetic / ontogenetic donor-derivate relationship of both muscular units at this point. In actual fact, the mm.testocervicocapitis lateralis et medialis may have been derived from one donor muscle (m. longissimus, Gasc 1981; Tsuihiji 2005, 2007); however, the comparative approach of this study speaks for a derived two-headed origin of No. 81 in *C. longicollis* and not for a fusion of No. 81 and No. 82. The integration of No. 81 to the cervicalis-portion of m. carapacocervicocapitis lateralis was not described or depicted by Shah (1963); further observations will help to understand the anatomy in this species.

The spinal nerves nn. S1v-S7v innervated (Ogushi 1913b) m. longus colli is a serially arranged muscle ventral to the cervical vertebrae. It forms two portions attaching via one tendon to the basioccipital region of the cranium. M. longus colli Pars capitis-II/III (No. 87) originates with two heads/tendons ventrally from the 2nd and the 3rd cervical vertebrae, m. longus colli Pars capitis-I (No. 86) originates ventrally from the 1st cervical vertebrae. The whole m. longus colli was described as the ventralmost muscle in the neck and not to be included into the n. XII innervated m. coracohyoideus complex (No. 58-60) (Shah 1963). Most authors recognised intercrossing fibres between the serially arranged portions; however, Bojanus (1819-21), Meckel (1828), or Hoffmann (1890) named No. 87 as a separated muscle (Appendix 1). Due to the inconsequence of muscle nomenclature and the diverse anatomy of the anteriormost muscular structures of the neck, a strange confusion is recognisable in literature (Appendix 1). For example, m. collocapitis brevis (No. 84) was assumed being part or a homologue to the anteriormost portion of m. longus colli (No. 87) or vice versa (Scanlon 1982). In addition to a separated m. collocapitis brevis (No. 84), Hoffmann (1890) still recognised three independent origins of the two cranium-attaching portions of m. longus colli (No. 86, 87), which converge in one tendon. Hence, I elaborated separated muscular units at this point. After accurate observations, Jones et al. (unpublished work) did not find No. 84 in *Caretta caretta* and *Lepidochelys kempii* (Chelonioidea). Where the muscle occurs, one may infer m. collocapitis brevis (No. 84) to originate phylogenetically from anterior portions of m. longus colli complex. Scanlon (1982) also described a close relation of No. 84 to both longus colli capitis-I (No. 86) and -II/III (No. 87) in insertion site.

## CONCLUSIONS

1. Associated to the cranium, 88 homologous muscular units can be distinguished in Testudines (Appendix 1).
2. The basis of the new nomenclatural system for cranial muscles in turtles takes into account the connections among muscular units and the plasticity and hierarchical nature of muscle development and evolution.
3. As in all vertebrates, the n. trigeminus (V) and the n. facialis (VII) innervated muscles are the best-studied muscular structures in turtles. Cranium-associated structures of the nose, the eye, the tongue, or the neck region are rarely described for particular species.
4. The crucially different arrangement of mm. adductor mandibulae externus among all major tetrapod groups – Lissamphibia, Mammalia, Sauria, Testudines – suggests an independent, non homologisable differentiation of those muscular structures in evolution. This could imply a position for turtles outside all remaining living Reptilia. I cannot test based on my exclusively neontological data whether Testudines evolved within one of the fossil “"Anapsida”-clades or on the stemline of Sauria within Diapsida.
5. A sister group relationship of Testudines + Archosauria could be supported by the presence of an n. abducens (VI) innervated m. pyramidalis (No. 35) and by a derived pattern of jaw muscle development: autapomorphic-

ally m. adductor mandibulae internus et posterior are closely related to each other.

6. A sister group relationship of Testudines + Lepidosauria on the other hand, could be supported by the shared tendency to derive intramandibular musculature from the m. adductor mandibulae internus Anlage.
7. Due to highly derived neck bending mechanisms, both Pleurodira and Cryptodira show a particular anatomy of the anterior neck muscles leading to confusions about the epaxial or hypaxial identity of the respective structures. Mainly based on considerations regarding the innervation pattern, I was able to asign each singular structure to either one or the other region.

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## APPENDIX 1.

Synonym list for muscular units. For abbreviations see Appendix 4. “Partim” added by IW. Asterisks used as in Figures 6–15. Functions as referred in the literature or hyothesised based on the orientation of the muscular structure and surrounding tissues (available online).

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| | | | |
| 1 | m. obliquus inferior | m. oblife | III |
| origin | anteriodorsal corner of optic cavity, partly on septum interorbitalis, ventral to obliquus superior (No. 9) | | |
| insertion | ventrally at eye bulbus | | |
| function | movement of the eye bulbus (rotation to anterodorsal direction) | | |
| synonyms | *inferior oblique* (Underwood 1970), *obliquus inferior* (Filatoff 1907, Johnson 1913, Ogushi 1913b: No.7, Hoffmann 1890: No. 6, Shiino 1913, Thomson 1932, Nishi 1938b, Schumacher 1972, Kuratani 1989), *obliquus oculi inferior* (Bojanus 1819-21: No. 10, Stannius 1854, Owen 1866), *ventral oblique* (Brudenall et al. 2008) | | |
| 2 | m. rectus anterior | m. recant | III |
| origin | by 1-2 heads anteriorly from foramen opticum | | |
| insertion | by 1-2 heads anteromedial face of eye bulbus, the possible second head into lower eyelid or membrana nictitans | | |
| function | movement of the eye bulbus (rotation to anteromedial direction) | | |
| synonyms | *rectus anterior* (Underwood 1970), *internal rectus* (Martin and Moale 1881), *medial rectus* (Brudenall et al. 2008), *rectus anterior* (Eger 2006), *rectus interior* (Kuratani 1987), *rectus internus* (Hoffmann 1890: No. 2, Filatoff 1907, Thomson 1932), *rectus internus oculi* (Bojanus 1819-21: No. 7, Owen 1849, Stannius 1854), *rectus nasalis* (Nishi 1938b), *rectus medialis* (Johnson 1913, Ogushi 1913b: No. 4, Shiino 1913, Schumacher 1972) | | |
| 3 | m. rectus inferior | m. recife | III |
| origin | ventrally to foramen opticum | | |
| insertion | ventrally at eye bulbus | | |
| function | movement of the eye bulbus (rotation to posterodorsal direction) | | |
| synonyms | *inferior rectus* (Martin and Moale 1881, Underwood 1970), *rectus inferior* (Filatoff 1907, Ogushi 1913b: No. 2, Johnson 1913, Shiino 1913, Thomson 1932, Nishi 1938b, Schumacher 1972, Kuratani 1987), *rectus oculi inferior* (Bojanus 1819-21: No. 6, Owen 1849, Stannius 1854, Hoffmann 1890: No. 4), *ventral rectus* (Brudenall et al. 2008) | | |
| 4 | m. rectus superior | m. recsup | III |
| origin | dorsally to foramen opticum | | |
| insertion | dorsally at eye bulbus | | |
| function | movement of the eye bulbus (rotation to dorsomedial direction) | | |
| synonyms | *dorsal rectus* (Brudenall et al. 2008), *rectus oculi superior* (Bojanus 1819-21: No. 5, Owen, 1849, Stannius 1854, Hoffmann 1890: No. 3), *rectus superior* (Filatoff 1907, Johnson 1913, Thomson 1932, Ogushi 1913b: No. 1, Shiino 1913, Nishi 1938b, Schumacher 1972, Kuratani 1989), *superior rectus* (Martin and Moale 1881, Underwood 1970) | | |
| 5 | m. cilliaris | m. cil | III |
| origin | ciliar connective tissue or basal membrane of epithelium | | |
| insertion | at medial most scleral lamellae, ring shaped as a whole, most fibres are radial | | |
| function | ciliar body pulled to outside (König 1934/35), accomodation | | |
| synonyms | *ciliary body musculature* ( Brudenall et al. 2008), *ciliary muscle* (Thomson 1932: with meridonal and circular fibres), Crampton’s muscle (Underwood 1970: Cm), *medionale + zirkuläre Zilliarmuskulatur* (König 1934/35: M.m.+M.z. or Z.-M., Franz 1934: cm) | | |
| 6* | m. dilatator pupillae | m. dilpup | III |
| origin | inner third of the iris (Brudenall et al. 2008) | | |
| insertion | to the iris root, adjacent to the posterior iris epithelium (Brudenall et al. 2008) | | |
| function | accomodation | | |
| synonyms | *dilator muscle* (Brudenall et al. 2008) | | |
| comments | only described for *Dermochelys coriacea* (Brudenall et al. 2008) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 7 | m. sphincter pupillae | m. stepup | III |
| origin | ring shaped, peripherally from the pupil margin (Brudenall et al. 2008) | | |
| insertion | | | |
| function | constriction of pupil by circular fibres, widening of pupil by the few radial fibres (König 1934/35), accomodation | | |
| synonyms | *iris sphincter* (Brudenall et al. 2008), *muscles of the iris* (Thomson 1932), *sphincter muscle + dilatator fibres* (Underwood 1970: df), *zirkuläre + radiäre Irismuskulatur* (König 1934/35: mz + mr I.-M.) | | |
| 8 | m. transversalis oculi | m. tveocu | III |
| origin | within the cleft formed by the rest of the embryonal ocular vesicle | | |
| insertion | indirect connection to lens by zonula fibres | | |
| function | small rostrad movement of the lens (König 1934/35) | | |
| synonyms | *bisher unbekannter Muskel im Reptilienauge* (Hess 1912: M), *lens or transversal muscle* (Thomson 1932), *transversalis* (Walls 1967, Underwood 1970, Brudenall et al. 2008), *Transversalmuskel* (König 1934/35: T.-M., Franz 1934: TM) | | |
| 9 | m. obliquus superior (principalis) | m. oblsio(pri) | IV |
| origin | anterodorsal corner of optic cavity, partly on septum interorbitalis, from the border of frontal/nasal, dorsally to obliquus inferior | | |
| insertion | dorsally on eye bulbus | | |
| function | movement of the eye bulbus (rotation to anteroventral direction) | | |
| synonyms | *dorsal oblique* (Brudenall et al. 2008), *obliquus superior* (Hoffmann 1890: No. 5, Johnson 1913, Shiino 1913, Nishi 1938b, Schumacher 1972, Kuratani 1987), *obliquus oculi superior* (Bojanus 1819-21: No. 9, Stannius 1854, Owen 1866), *obliquus superior proprius* (Ogushi 1913b: No. 5), *superior oblique* (Martin and Moale 1881, Thomson 1932, Underwood 1970) | | |
| 10* | m. obliquus superior accessorius | m. oblsioacc | IV |
| origin | posterodorsal of m. obliquus superior (after Ogushi 1913b: TextFig. 7) | | |
| insertion | posterior curvature of eye bulbus, mostly covered by accessory head of m. retractor bulbi (Ogushi 1913b) | | |
| function | movement of the eye bulbus (rotation to posteromedial direction) | | |
| synonyms | *obliquus superior accessorius* (Ogushi 1913b: No. 6) | | |
| comments | only described for *Pelodiscus sinensis* (Ogushi 1913b) | | |
| 11 | m. nasalis<br>Pars circumnarialis | nasCIRNAR | IV |
| origin | consists of radial fibres, from medial walls of paranasal cartilages or connective tissue (Winokur 1982) | | |
| insertion | lateral parts of the lamina propria mucosa, a few fibres connected to Pars arrector rostri in anterior regions of snouts where paranasal cartilages are absent (Winokur 1982) | | |
| function | nasal vestibula pulled laterally or dorsolaterally and thus also dilating the nasal openings (Winokur 1982) | | |
| synonyms | *circumnarial muscle* (Winokur 1982) | | |
| 12* | m. nasalis<br>Pars internarialis | m. nasITENAR | V |
| origin | complex array of fibres forming a trabecular network, from medial sides of narial vestibulae (Winokur 1982) | | |
| insertion | to the midline of the internarial region or between to the medial vestibular wall of the contralateral body side (Winokur 1982) | | |
| function | at least transverse oriented fibres act as nasal dilator, pulling the medial walls of the nasal vestibula medially (Winokur 1982) | | |
| synonyms | *internarial muscle* (Winokur 1982) | | |
| comments | only described for *Podocnemis unifilis* (Winokur 1982) | | |
| 13 | m. nasalis<br>Pars arrector rostri | m. nasARRROS | V |
| origin | ventrally at the anterior border of nasal and medially at maxilla (George & Shah 1955a) / by aponeurosis from apertura narium externa and parts of nasal capsule (Ogushi 1913b) / prefrontal bone and nasal cartilages (Winokur 1982) | | |
| insertion | skin bordering the nostrils (George and Shah 1955a) / nasal capsule (around fenestra superior) and neighbouring submucosa (Ogushi 1913b) / by flat tendon between mediql and lateral cartilagenous anterior extension of nasal capsule (Winokur 1982) | | |
| function | lifting the nose out of water for breathing (Ogushi 1913b), contraction acts as dilatator of external nares (George & Shah 1955a) / elevates anterior part of snout (Winokur 1982) | | |
| synonyms | *arrector rostri* (Ogushi 1913b: No. 12, Winnokur 1982), *tensor nasalis* (George and Shah 1955a) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 14 | m. depressor palpebrae inferioris Pars transversalis | m. depppeifeTVE | V |
| origin | at ligamentum flavum (connection between periorbita and septum interorbitale) (Lakjer 1926), basisphenoid (?) (Hoffmann 1890) | | |
| insertion | periphery of lower eye lid (Lakjer 1926), sometimes upper eye lid (Hoffmann 1890) | | |
| function | lowers the lower eye lid (Ogushi 1913b, Lakjer 1926) | | |
| synonyms | *depressor palpebrae inferior* partim (Edgeworth 1935: smooth (unstriped) ocular muscle of Chelonia, Stannius 1854), *depressor palpebrae inferioris* partim (Ogushi 1913b: No. 11 frontale glatte Fasern ), *depressor palpebrae inferioris et superioris* (Hoffmann 1890: No. 8: this is only one muscle, Thomson 1932), *glatte Lidmuskulatur Pars transversale* (Lakjer 1926: Trans.), *glatter Augenmuskel* partim (Poglayen-Neuwall 1953a), *glatte Muskeln der Periorbita* partim? (Burkard 1902: partim?: he only described equatorial fibres), *palpebralis* partim (Bojanus 1819-21: No. 12), *reichliche glatte Lidmuskulatur* partim (Lubosch 1933), *smooth (unstriped ocular muscle of Chelonia* partim (Edgeworth 1935), *transversale, ventrale Schicht glatter Musekelzellen* (Lubosch 1938) | | |
| comments | Tiedemann (1819): p. 355, „... beiden ?ehr beweglichen Augenlider einen gro?sen gemein?chaftlichen Muskel enthalten.“: indicates a relationship of m. pyramidalis, No. 34, with m. depressor palpeprae inferioris (No. 14-15); innervation: $V_2$ (Ogushi 1913b, Lubosch 1933) | | |
| 15 | m. depressor palpebrae inferioris Pars equatorialis | m. depppeifeEQU | V |
| origin | praefrontal (anterior wall of orbita) (Lakjer 1926) | | |
| insertion | parietal (posterior wall of orbita) (Lakjer 1926) | | |
| function | lifts up the eye bulbus (Lakjer 1926), empties lacrimal gland (Burkard 1902:90) | | |
| synonyms | *depressor palpebrae inferioris* partim (Edgeworth 1935: smooth (unstriped) ocular muscle of Chelonia, Stannius 1854), *depressor palpebrae inferioris* partim (Ogushi 1913b: No. 11), *dorsale, longitudinale Schicht glatter Musekelzellen* (Lubosch 1938), *glatte Lidmuskulatur* Pars äquatoriale (Lakjer 1926: Long.), *glatter Augenmuskel* partim (Poglayen-Neuwall 1953a), *glatte Muskeln der Periorbita* partim (Burkard 1902: partim?: he only described equatorial fibres), *palpebralis* partim (Bojanus 1819-21: No. 12), *reichliche glatte Lidmuskulatur* partim (Lubosch 1933), *smooth (unstriped ocular muscle of Chelonia* partim (Edgeworth 1935) | | |
| comments | not in *Dermochelys* (who still has the m. levator bulbi) and *Pelodiscus,* but in *Terrapene carolina* (where no m. levator bulbi is visible) (Lakjer 1926) | | |
| 16* | m. levator bulbi | m. levbul | V |
| origin | ventral of the processus descendens parietalis, short before prootic, anterior cartilaginous border of brain case/septum interorbitale | | |
| insertion | head 1 (ventral head): Pars palatina palatoquadrati (cartilages along a rim on the dorsal face of pterygoid);<br>head 2 (dorsal head): ventrally to periorbita | | |
| function | dorsal head without function (Lakjer 1926) / dorsal head lifting of the eye bulbus | | |
| synonyms | *adductor maxillae superioris* (Fischer 1852: Sauria)*, levator bulbi* (Lakjer 1926, Lubosch 1933, 1938), *palpebralis* (Schumacher 1973: II-B1'''/'), *depressor palpebrae* (Versluys 1912), *Depressor palpebrae inferioris* (Weber 1877: in Lacertidae, Edgeworth 1935: Sauropsida), *Schädelpterygoidmuskulatur* (Fuchs 1915)<br>anterior head only: *m. levator bulbi Pars dorsalis* (*Levator bulbi dorsalis*) (Lakjer 1926), posterior head only: *m. levator bulbi Pars ventralis* (*Levator bulbi ventralis*) (Lakjer 1926) | | |
| comments | mostly or completely reduced in the adults of most species, described for *Dermochelys coriacea* (Lakjer 1926) | | |
| 17-21 | m. adductor mandibulae externus complex | - | V |
| synonyms | adductor mandibulae externus (including all portions): *adductor mandibulae A2* (Diogo and Abdala 2010), *adductor mandibulae externus* (Lakjer 1926, Lubosch 1933, Edgeworth 1935, Poglayen-Neuwall 1953a, 1953/54, 1966, Kilias 1957, Shah 1963, Schumacher 1972, 1973: II-B2b(i-iii), Barghusen 1973, Weisgram 1985, Lemmell and Weisgram 1997, Sato et al. 1997: MAME, Van Damme and Aerts 1997, Wocheslânder et al. 1999, Lemell et al. 2000, Tvaročková 2006, Natchev and Weisgram 2007, Natchev et al. 2008), *adductor mandibularis externus* (Schumacher 1953/54, 1954/55a, b, 1956a, b, c), *adductor mandibulae externus medialis (II mit.)* (Lakjer 1926), *capiti-mandibularis* (Gregory and Adams 1915, Adams 1919), *external adductor* (Lemell et al. 2010: figure 4C), *Kaumuskulatur* (Fuchs 1915), *occipito-squamoso-maxillaris* partim (Hoffmann 1890: No. 9), *laterale Kaumuskulatur* (Fuschs 1931, 1933), *Schlaefenmuskel (temporalis)* (Wiedemann 1802: No. 1, p. 79), *temporal (muscle)* (Parker 1878-1879, Martina and Moale 1881, Ashley 1962, Arenciba et al. 2006), *temporalis* (Bojanus 1819-21: No. 1, Owen 1866, Stannius 1854, Edgeworth 1907: Temporal, Ogushi 1913b: No. 14, Shiino 1913, Fuchs 1915, Gregory and Adams 1915, Versluys 1919, Zdansky 1923-25, Thomson 1932: also occipito-squamoso-maxillary, Kilias 1957: also *adductor mandibulae externus*), *occipito-squamoso-maxillary* (Thomson 1932: also *temporalis*) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 17 | m. adductor mandibulae externus Pars medialis (principalis) | m. addmaneteMDI(PRI) | V |
| origin | anterior face of quadrate (Lakjer 1926) | | |
| insertion | lateral face of coronar aponeurosis coronoid, dentary, articular and dorsally to surangular (Schumacher 1973, Iodansky 1987) | | |
| function | adduction of lower jaw (caudad) | | |
| synonyms | *adductor mandibulae A2 medialis* (Diogo and Abdala 2010), *adductor mandibulae (quadrate part)* (Wyneken 2003), *adductor mandibulae externus Pars/Portio media* [Poglayen-Neuwall 1953, 1966 (exceptions for some species such as *Chelus fimbriatus* or *Mesoclemmys nasuta*: Pars medialis and the squamosal-related head of Pars superficialis are fused and the "Pars superficialis" of the author represents the postorbital region related head of Pars superficialis; see text for discussion), Schumacher 1972, 1973, Tvarožková 2006, Natchev and Weisgram 2007, Natchev et al. 2009, 2010], *adductor mandibulae externus medialis* (Lakjer 1926: *II/II mit.*, Schumacher 1956a, c, Hacker 1954, Kilias 1957, Dalrymple 1975, Lemell et al. 2010: possibly "Med" of figure 4D), *adductor mandibulae externus medius* (Lubosch 1933, 1938), *adductor mandibulae externus med. part* (Wyneken 2003: figure 2.20), *adductor mandibulae externus inferior* (Iordansky 1996: maei/mali, 2010), *adductor mandibularis externus medialis* (Schumacher 1953/54, 1954/55a, b, 1956a, c) | | |
| comments | fused with the squamosal head of the Pars superficialis (No. 21) in some species, see comments there | | |
| 18* | m. adductor mandibulae externus Pars medialis inferior | m. addmaneteMDIIFE | V |
| origin | anteroventral face of quadrate | | |
| insertion | dorsal edge of supraangular | | |
| function | adduction of lower jaw (caudad) | | |
| synonyms | *adductor mandibulae externus medialis (II vent.)* (Lakjer 1926) | | |
| comments | only described for *Amyda cartilaginea* (Lakjer 1926) | | |
| 19 | m. adductor mandibulae externus Pars profundus (principalis) | m. addmanetePFU(PRI) | V |
| origin | supraoccipital, parietal, occipital, opisthotic, prootic, fascia temporalis (Schumacher 1972) | | |
| insertion | medial surface of coronar aponeurosis and medially to surangular (Lakjer 1926) | | |
| function | adduction of lower jaw (mediad and caudodorsad) | | |
| synonyms | *adductor mandibulae A2 profundus* (Diogo and Abdala 2010), *adductor mandibulae (parietal, supraoccipital and opisthotic part)* (Wyneken 2003), *adductor mandibulae externus(:) Pars/Portio profunda* (Poglayen-Neuwall 1953, 1966; Schumacher 1972, 1973, Kilias 1957, Hacker 1954, Dalrymple 1975, 1977, Lemell et al. 2000, Wyneken 2003: figure 2.20, Tvarožková 2006, Natchev and Weisgram 2007, Natchev et al. 2009, 2010, Singer 2009), *adductor mandibulae externus profundus* (Lakjer 1926: III with five possible portions A-E, Lubosch 1933, 1938, Rieppel 1990), *adductor mandibulae externus superior* (Iordansky 1996: maes, 2010), *adductor mandibularis externus profunda* (Schumacher 1953/54, 1954/55a, b, 1956a, c), *splenius capitis* (Arencibia et al. 2006) | | |
| comments | can be reduced in *Chelus fimbriatus* (see Lemell et al. 2010, but see also Poglayen-Neuwall 1966) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 20** | m. adductor mandibulae externus Pars profundus atypica | m. addmanetePFUATY | V |
| origin | anteroventral part of parietal [exactly dorsally to m. adductor mandibulae internus Pars pseudotemporalis (No. 23-24)] | | |
| insertion | ventral most part of medial face of coronar aponeurosis (short before its insertion) to lower jaw and/or rictal plate | | |
| function | adduction of lower jaw (mediad and caudodorsad) | | |
| synonyms | *adductor mandibulae externus Portio profunda atypica* (Poglayen-Neuwall 1953: *P.pro.atypica*) | | |
| comments | only described for *Mauremys caspica, Cuora amboinensis* | | |
| 21 | m. adductor mandibulae externus Pars superficialis | m. addmaneteSFI | V |
| origin | postorbital, parietal, dorsally from quadrate, squamosal, prootic, opisthotic, fascia temporalis, (Schumacher 1973: basisphenoid: = possibly he meant basioccipital) | | |
| insertion | dorsally or ventrally to coronar aponeurosis, few fibres coronoid, dentary, surangular, rhamphotheca (Schumacher 1973), lateral face of mandible (Lakjer 1926), rostral head: posteriorly to rictal plate (*Pelusios niger*) | | |
| function | adduction of lower jaw (dorsad and posterodorsad) | | |
| synonyms | *adductor mandibulae A2 superficialis* (Diogo and Abdala 2010), *adductor mandibulae (prootic part)* (Wyneken 2003), *adductor mandibulae externus medialis* (Poglayen-Neuwall 1953: *Pelodiscus sinensis*), *adductor mandibulae externus medialis (II dors)* (Lakjer 1926), *adductor mandibulae externus(:) Pars/Portio superficialis* (Lakjer 1926: *II dors.*, Poglayen-Neuwall 1953, Hacker 1954, Schumacher 1972, 1973, Kilias 1957, Dalrymple 1975, 1977, Lemell et al. 2000, Wyneken 2003: figure 2.20, Tvarožková 2006, Natchev and Weisgram 2007, Natchev et al. 2009, 2010, Singer 2009, Lemell et al. 2010: squamosal head of Pars superficialis may be “Prof” of figure 4A, the postorbital head fursed with Pars medialis, No. 17, may be “Ext” of figure 4C and “Sup” of figure 4A; see comment below), *adductor mandibulae externus postorbitalis* (Iordansky 1996: maep/maepo, 2010), *adductor mandibularis externus superficialis* (Lubosch 1933, 1938: partim for trionychids, Schumacher 1953/54, 1954/55a, b, 1956a, c), *transversus cervicalis* (Arencibia et al. 2006) | | |
| comments | in some species the portion is clearly separated into a squamosal- and a postorbital region related head, the former can fuse with the Pars medialis (No. 17) (Poglayen-Neuwall 1966); the latter is possily homologous to the m. zygomaticomandibularis (No. 22) (see text for details) | | |
| 22** | m. zygomaticomandibularis | m. zygman | V |
| origin | by tendon or directly from the medial and/or ventral aspect of the zygomatic arch (jugal, quadratojugal), partly from ventromedial part of temporal fascia, lateral face of quadrate | | |
| insertion | partly tendinuously at the lateral aspects of the dentary and surangular area, almost reaching their ventral edges | | |
| function | adduction of lower jaw (dorsad) | | |
| synonyms | *adductor mandibularis externus* partim (Lakjer 1926: *I*, Lubosch 1933, Poglayen-Neuwall 1953), *adductor mandibularis externus* partim (Schumacher 1953-56), *adductor mandibulae externus* partim (Shah 1963: Ad.M.E.), *adductor mandibulae externus superficialis* partim (Poglayen-Neuwall 1953), *adductor mandibulae externus zygomaticomandibularis* (Schumacher 1972, 1973: II-B2b(iv), Iordansky 1987: maez, Diogo and Abdala 2010), *masseter* (Ogushi 1913b: No. 13, *occipito-squamoso-maxillaris* partim *(?)* (Gräper 1932), adductor mandibulae internus pterygoideus (Lubosch 1933: as drawn in figure 21), George and Shah 1955a), *zygomatico(-)mandibularis* (Dalrymple 1975, 1977) | | |
| comments | only known for Trionychia | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 23-28 | m. adductor mandibulae internus complex | - | V |
| synonyms | adductor mandibulae internus as whole structure (incl. Partes pteryggoidei, No. 26-28 et pseudotemporales, No. 23-24: if not separately discussed): *M. adductor mandibulae internus* (Weisgram 1985, Van Damme and Aerts 1997, Wocheländer et al. 1999), *adductor mandibulae internus pars pterygoideus* (Natchev et al. 2009: with a note that Partes pseudotemporalis and "pterygoideus" were not separable from each other), *adductor mandibulae medius* partim (George and Shah 1955a, Shah 1963: Ad.MM), *adductor mandibularis medius* partim (Edgeworth 1935, Shah 1963: Ad.M.M.), *Flügelmuskel* (Wiedemann 1803: No, 2, p. 79), *internus* (Tvarožková 2006), *internal adductor* (Lemell et al. 2000) *mediale Kaumuskulatur* (Fuchs 1931, 1933), *pterygoides* (Thomson 1932: also *pterygo-maxillary*), *pterygoideus internus* partim (Stannius 1854), *pterygoideus* (Bojanus 1819-21: No. 2, Owen 1866, Ogushi 1913b: No. 16, Fuchs 1915, Versluys 1919, Zdansky 1923-25), *pterygo-maxillaris* partim (Hoffmann 1890: No. 10), *pterygo-maxillary* (Thomson 1932: also *pterygoides*), *pterygoid* (Edgeworth 1907), *Pterygoidmuskulatur (Kaumuskulatur) (Fuchs 1915), pterygoideus anterior* partim (Adams 1919), *pterygomandibularis* (Versluys 1919: also pterygoideus)<br>Pars pseudotemporalis (if Pars pseudotemporalis superficialis and Pars intramandibularis are present but were not separately discussed): *adductor mandibularis anterior* (Schumacher 1953-56: unclear nomenclature), *adductor mandibulae medius* partim (Shah 1963: Ad.M.M.), *Flügelmuskel* partim (Wiedemann 1803), *pterygoideus anterior* partim (Adams 1919), *pterygoideus* partim (Bojanus 1819-21: No. 2), *pterygoid* partim (Edgeworth 1907), *adductor mandibularis medius* partim (Edgeworth 1935), *posterior adductor* (Lemell 2010: figure 4A, D) *pterygo-maxillaris* partim (Hoffmann 1873-78, 1890: No. 10), *pseudotemporalis* partim (Lakjer 1926, Poglayen-Neuwall 1953a), *pseudotemporalis* (Dalrymple 1975, Wyneken 2003), *pterygoideus* partim (Ogushi 1913b: No. 16), *pterygoideus* partim (Owen 1866), *pterygoideus internus* partim (Stannius 1854)<br>pterygoideus as a whole (incl. dorso-, ventro-, posteropterygoideus if not separately discussed or if not separated): *adductor internus pterygoideus* (Iordansky 2010), *adductor mandibulae internus* (Edgeworth 1935, Shah 1963: Ad.M.I), *adductor mandibulae internus Pars pterygoideus* (Iordansky 1987, 1996, Natchev and Weisgram 2007: also *... pterigoideus*), *adductor mandibularis internus Portio pterygoidea* (Poglayen-Neuwall 1966), *adductor mandibularis internus (= pterygoideus)* (Kilias 1957), *adductor mandibulae internus pterygoideus = Pterygoideus* (Lubosch 1933), Flügelmuskel partim (Wiedemann 1803), *pterygoideus* (Arencibia et al. 2006), *pterygoideus* partim (Bojanus 1819-21: No. 2), *pterygoideus anterior* (Adams 1919), *pterygoid muscles* (Gregory and Adams), *pterygoid muscle* (Lemell 2010), *pterygoid* partim (Edgeworth 1907), *pterygoideus* (Shiino 1913, Tvarožková 2006), *pterygo-maxillaris* partim *(Pterygoideus)* (Hoffmann 1873-78, 1890: No. 10), *pterygoideus* (No. 16) + *pterygo-mandibularis* (Ogushi 1913b: No. 17), *pterygoideus* partim (Owen 1866), *pterygoideus Pars dorsalis* (Cryptodira) (Schumacher 1973: II-B2d(iii)'), *pterygoideus internus* partim (Stannius 1854)<br>Pars superficialis + Pars intramandibularis together as a whole: *adductor internus digastricus* (Iordansky 2010), *adductor mandibulae internus digastricus* (Iordansky 1996: maid), *flat superficial bundle of pseudotemporalis* (Iordansky 1996), *parietomandibularis* (Schumacher 1955b, 1956c), *pesudotemporalis Pars digastrica* (Iordansky 1996)<br>posterior and pseudotemporalis together: *adductor mandibulae medius* (Edgeworth 1935) | | |
| 23 | m. adductor mandibulae internus Pars pseudotemporalis (principalis) | m. addmanitePSETEM(PRI) | V |
| origin | processus descendens parietalis, parietal; partly posterior region of the orbital cavity (interorbital septum), prootic and frontal; medially to Pars pseudotemporalis superficialis (No. 24) | | |
| insertion | together or without the pterygoideus portions (No. 26-28) via the subarticular aponeurosis or directly to the medial aspect of the lower jaw (processus coronoideus dentalis, prearticulare, surangulare, into fossa primordialis, cartilago meckeli); if Pars intramandibularis (No. 25) exists it inserts to the Zwischensehne | | |
| function | multidirectional arrangement of lower jaw (mainly orsomediad) | | |
| synonyms | *adductor internus pseudotemporalis* (Iordansky 2010), *adductor mandibulae internus pseudotemporalis* (Lubosch 1938: also temporalis, Barghusen 1973), *adductor mandibulae internus pars pseudotemporalis* (Natchev and Weisgram 2007), *adductor mandibulae internus temporalis* (Lubosch 1938: also pseudotemporalis), *adductor mandibulae posterior Portio medialis* (Schumacher 1953/54: *Podocnemis, Pelusios*), *adductor mandibulae posterior* (? Sato et al. 1997: MAMP), *adductor mandibulae posterior Portio rostralis* (Schumacher 1953/54: *Chelone, Caretta*, Hacker 1954), *pseudotemporalis* (Schumacher 1973, Tvarožková 2006, Diogo and Abdala 2010), *pseudotemporalis (mediale Portion)* (Poglayen-Neuwall 1953), *pseudotemporalis Pars profunda* (Poglayen-Neuwall 1953, 1966), *pseudotemporalis* (Iordansky 1987, 1996), *pterygoideus externus* (Kesteven 1942-45) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 24 | m. adductor mandibulae internus Pars pseudotemporalis superficialis | m. addmanitePSETEMSFI | V |
| origin | dorsal area of processus descendens parietalis, partly postorbital | | |
| insertion | directly on surangular part of proc. coronoideus or on internal tendon; if intramandibularis present to Zwischensehne | | |
| function | multidirectional arrangement of lower jaw (mainly dorsomediad) / stabilisation of Pars intramandibularis (No. 25) (if present) | | |
| synonyms | *adductor mandibulae internus digastricus, dorsal belly* (Iordansky 1996: maid), *pseudotemporalis (Wyneken 2001), pseudotemporalis (laterale Portion)* (Poglayen-Neuwall 1953), *parietomandibularis caput dorsale* (Schumacher 1954/55b), *pseudotemporalis Pars superficialis* (Poglayen-Neuwall 1953, 1966), *pseudotemporalis Portio dorsalis* (Schumacher 1953/54: *Chelone, Caretta*) | | |
| 25 | m. adductor mandibulae internus Pars intramandibularis | m. addmaniteITRMAN | V |
| origin | Zwischensehne | | |
| insertion | lateral to cartilago meckeli, in fossa primordialis | | |
| function | possibly together with Pars pseudotemporalis superficialis (No. 24), multidirectional arrangement of lower jaw | | |
| synonyms | *adductor mandibular A?* (Diogo and Abdala 2010), *adductor mandibulae internus digastricus, ventral belly (intramandibularis)* (Iordansky 1996: maid), *inframandibularis* (Wyneken 2003: only as depiction in figure 2.21), *intermandibularis* partim (Wyneken 2001: discussed as a part of intermandibularis which ends in a tendon that is connected to „pseudotemporalis“), *intramandibularis* (Poglayen-Neuwall 1953, Schumacher 1973: II-B2d(ii), Dalrymple 1975, Rieppel 1990, Tvarožková 2006), *parietomandibularis caput ventrale* (Schumacher 1954/55b), *pseudotemporalis Portio ventralis (M. intramandibularis)* (Schumacher 1953/54: *Chelone, Caretta*) | | |
| 26 | m. adductor mandibulae internus Pars pterygoideus dorsalis | m. addmanitePTEDOR | V |
| origin | caudally and dorsally at pterygoid: partly posterior to the dorsal face of palatine, processus descendens parietalis, caudally at septum interorbitalis, postorbitalis, jugal, maxillare | | |
| insertion | by tendon together or without Pars pseudotemporalis (No. 23) to prearticulare or directly to jaw joint, processus coronoideus, prearticulare or surangulare | | |
| function | adduction of lower jaw (rostrodorsad in mediad direction), multidirectional arrangement of lower jaw | | |
| synonyms | *anterior component adductor mandibulae internus pterygoideus* (Barghusen 1973), *adductor mandibulae internus Pterygoideus dorsalis* (Lubosch 1938), *dorsale Abteilung des pterygoideus* (Lakjer 1926: *Amyda cartilaginea*), *pterigoideus dorsal part* (Wyneken 2003: figure 2.21), *pterygoideus* (Lakjer 1926), *pterygoideus anterior* (Sato et al. 1997: MPta), *pterygoideus internus* (Kesteven 1942-45), *pterygoideus Pars dorsalis* (Hacker 1954, Schumacher 1973: Cryptodira, Dalrymple 1975), *pterygoideus Pars rostromedialis* (Schumacher: Pleurodira), *pterygoideus Port. dors.* (Ogushi 1913b: No. 16), *pterygoideus Portio dorsalis (Schumacher 1953/54: Chelone, Caretta)*, *pterygomandibularis dorsalis* (Diogo and Abdala 2010) | | |
| 27 | m. adductor mandibulae internus Pars pterygoideus posterior | m. addmanitePTEPOS | V |
| origin | caudally at processus of palatine, dorsally and ventrally at pterygoid, medially at quadrate, at prootic, in a medial raphe with contralateral muscle | | |
| insertion | tendinuously and directly to processus retroarticularis of articulare, partly to surangulare | | |
| function | multidirectional arrangement of lower jaw (mainly dorsomediad) | | |
| synonyms | *pterygoideus Pars ventro-posterior* (Schumacher 1973, text: *Podocnemis*), *pterygo-mandibularis* (Ogushi 1913b: No. 17, Hacker 1954), *pterygoideus (Part)* (Hacker 1954), *pterygoideus Portio ventralis bzw. M. intramandibularis* (Schumacher 1953/54: *Chelone*, *Caretta*), *posterior component adductor mandibulae internus pterygoideus* (Barghusen 1973), *posterior Part of the pterygoideus* (Mc Dowell 1963), *posterior portion of pars ventralis* (Dalrymple 1975), *pterygoideus medius* partim (Kesteven 1942-45) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 28 | m. adductor mandibulae internus Pars pterygoideus ventralis | m. addmanitePTEVTR | V |
| origin | ventrolaterally at pterygoid, posterolaterally at palatine | | |
| insertion | by tendon without (own pterygoid tendon) or with Pars pterygoideus dorsalis (No. 26) (via internal tendon) or directly to processus coronoideus, prearticular; directly by some fibres to connective tissue of upper ramphotheca, jugal, maxilla, surangular | | |
| function | multidirectional arrangement of lower jaw (mainly rostromediad) | | |
| synonyms | *adductor mandibulae internus Pterygoideus ventralis* (Lubosch 1938), *pterygoideus Pars ventralis* (Hacker 1954, Schumacher 1973: Cryptodira, Dalrymple 1975), *pterygoideus Pars ventro-lateralis* (Schumacher 1973: Pleurodira), pterygoideus Port. ventr. *(Ogushi 1913b: No. 16), pterygoideus Portio medialis (Schumacher 1953/54: Chelone, Caretta), Ventralschicht des pterygoideus* (Lakjer 1926: *Amyda cartilaginea*), *pterygomandibularis ventralis* (Diogo and Abdala 2010) | | |
| 29 | m. adductor mandibulae posterior (Pars principalis) | m. addmanpos(PRI) | V |
| origin | 1-2 heads, anteromedially at quadrate, postorbital, parietal, medial to adductor mandibulae externus medialis (No. 17) | | |
| insertion | some fibres directly, the major part with an own tendon or with the internal tendon of the adductor mandibulae internus portions (23-28) to the articular, prearticular, surarticular; some fibres to cartilago meckeli and into the fossa primordialis | | |
| function | multidirectional arrangement of lower jaw (mainly caudodorsad) | | |
| synonyms | *adductor internus posterior* (Iordansky 2010), *adductor mandibulae A2-PVM* (Diogo and Abdala 2010), *adductor mandibulae internus Pars posterior* (Iordansky 1987, 1996), *pars medialis of external adductor* (Lemell 2010: figure 4A, possibly also figure 4D), *adductor mandibulae posterior* ( Poglayen-Neuwall 1953, 1966, in most species: Schumacher 1953/54-56, Schumacher 1972, 1973: II-B2c, Barghusen 1973, Dalrymple 1975, Weisgram 1985, Wochesländer et al. 1999, Wyneken 2003: ‘adductor mandibulae post.’ in figure 2.21, Tvarožková 2006, Natchev and Weisgram 2007, Natchev et al. 2009), *adductor mandibulae posterior Portio caudalis* (Schumacher 1953/54: *Chelone, Caretta*, Hacker 1954), *adductor mandibulae posterior Portio intermedia et lateralis* (Schumacher 1953/54: *Podocnemis*), *adductor posterior* (Lubosch 1933), *hintere innere Abteilung des adductor posterior* (Lakjer 1926: kaud/caud), *pterygoideus medius* partim (Kesteven 1942-45), *posterior adductor* (Lemell et al. 2000), *quadrato-mandibularis* (Ogushi 1913b: No. 15) | | |
| comments | innervation: n. trigeminus (n. V), changing origins from externus or internus branches of V3 or directly from V3 | | |
| 30** | m. adductor mandibulae posterior Pars rostralis | m. addmanposROS | V |
| origin | prootic (Lakjer 1926) | | |
| insertion | dorsal face of cartilago meckeli, laterally to insertion of Pars anterior (Lakjer 1926) | | |
| function | multidirectional arrangement of lower jaw (mainly caudad) | | |
| synonyms | *vordere äußere Abteilung des adductor posterior* (Lakjer 1926: rost./rostr.) | | |
| comments | only found in *Dermochelys coriacea* (Lakjer 1926) and *Lissemys punctata* (Schumacher 1955a, b), *Pelusios sinuatus et subniger* (Schumacher 1953/54) | | |
| 31-33/42 | “m. inter-mandibularis” complex | - | V / VII |
| synonyms | intermandibular musculature as a whole, if portions of m. intermandibularis (No. 31) or a separation to of constrictor colli Pars intermandibularis (No. 42) are not separately discussed: *intermandibularis* (Lakjer 1926, Fuchs 1933, Lubosch 1933, Edgeworth 1935, Shah 1963: Im., Schumacher 1973: II-B3'/'', Wyneken 2003, Diogo and Abdala 2010), *intermaxillary* (Thomson 1932: also *mylohyoid*, *mylo(-)hyoideus*, Bojanus 1819-21: No. 13, Alessandrini 1834a, Stannius 1854, Owen 1866, von Bayern 1884, Walter 1885, Hoffmann 1890: No. 19a synonym, Burne 1905: No. 19a, Gräper 1932: mh, Gräper 1933), *mylohyoid* (Thomson 1932: also *intermaxillary*), *intermaxillaris* (Hoffmann 1890a: No. 19a, Ogushi 1913b: No. 22, Hacker 1954) | | |
| 31 | m. intermandibularis (Pars principalis) | m. iteman(PRI) | V |
| origin | medially at lower jaw, mostly dentary, dorsally of cartilago meckeli, partly reaching the symphysis of the dentaries | | |
| insertion | medial raphe with contralateral muscle, partly continuing with the constrictor colli Pars oralis posteriorly | | |
| function | regulation of the volume of the mouth cavity, breathing, lifts the tongue | | |
| synonyms | *C2mv* partim (Lubosch 1933), *anterior mylohyoid* (Edgeworth 1907, 1935), *anterior part of intermandibularis* (Fuchs 1931), *intermandibularis* (Kesteven 1942-45: Scv. 1, Weisgram 1985, Spindel et al. 1987, Van Damme and Aerts 1997, Wochesländer et al. 1999, Wyneken 2001, Arencibia et al. 2006, Natchev and Weisgram 2007, Natchev et al. 2008, 2009, 2010, Singer 2009), *intermandibularis anterior* (Lubosch 1938), *intermandibularis Pars oralis* (Poglayen-Neuwall 1953: M.C$_1$v), *intermaxillaris,* synonym: *mylohyoideus* (Shiino 1913: based on described innervation), intermaxillaire (Rouvière 1906: No. 1), *mylohyoideus anterior* (Gnanamuthu 1937), *mylohyoideus anterior principalis* (Sondhi 1958), *mylo-hyoïdien* (Chaine 1900), *vorderer Teil des M. intermandibularis* (Fuchs 1931) | | |
| comments | innervation: n. trigeminus (V) (Sondhi 1958: “Ramus ad musculum mylohyoideus”, at least anterior part) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 32** | m. intermandibularis<br>Pars profundus | m. itemanPFU | V |
| origin | dorsal to Pars oralis principalis at medial border of mandible Sondhi (1958) | | |
| insertion | runs transversely medianwards, inserts to gular septum Sondhi (1958) | | |
| function | curves the tongue (Gräper 1932) | | |
| synonyms | *mylohyoideus anterior profundus* (Sondhi 1958), mylohyoidus Portio mucosae (Gräper 1932: mhm) | | |
| comments | only described for the trionychids *Asperideretes leithii* (Sondhi 1958) and *Apalone ferox* (Gräper 1932) | | |
| 33** | m. submentalis | m. submen | V |
| origin | dorsal to anterior end of intermandibularis (from dentals) (Kesteven 1942-45) | | |
| insertion | fibres run transversally without a raphe (Kesteven 1942-45) | | |
| function | mediad movement of the dentaries | | |
| synonyms | *submentalis* (Kesteven 1942-45) | | |
| comments | only described for *Emydura macquariae* and in embryos of *Chelodina longicollis* (Kesteven 1942-45) | | |
| 34 | m. pyramidalis | m. pyr | VI |
| origin | medially at eye ball | | |
| insertion | to membrana nictitans and potentially to the lower eye lid | | |
| function | pulls the membrana nictitans dorsocaudally over the eye | | |
| synonyms | *der ungemein gro?se Augenmuskel des dritten Augenlids* (Tiedemann 1819: p. 355, „... beiden ?ehr beweglichen Augenlider einen gro?sen gemein?chaftlichen Muskel enthalten.“: indicates a relationship with m. depressor palpeprae inferioris, No. 14-15), *levator membranae nictitantis* (Ogushi 1913b: No. 10 – only to Membr.nict., Schumacher 1972: 5.3.9), *membranae nictitantis + palpraebrae inferioris in commune* (Tiedemann: cited after Ogushi 1913b), N.N. (Albers 1808:82), *palpebrae musculum pyramidalem* (Bojanus 1819-21: Fig. 129 BB), *palpaebrae pyramidalis* (Cuvier 1835), *pyramidalis* (Leuckard 1876, Martin and Moale 1881, Thomson 1932, Underwood 1970, Eger 2006, Brudenall et al. 2008), *pyramidalis + M. bursalis in commune* partim (Albers: cited after Ogushi 1913b), *pyramidalis nictitans* (to Membr. nict. and lower lid) (Edgeworth 1907), *retractor membranae nictitantis* (*Clemmys*: not yet distinguished from Retractor bulbi/Retr.bursalis) (Nishi 1938b) | | |
| 35 | m. quadratus (principalis) | m. qua(pri) | VI |
| origin | medial at eye bulbus, a possible second head from the edge of foramen opticus; between the origin of pyramidalis (No. 34) and the insertion of retractor bulbi (No. 38) | | |
| insertion | to the posterior angle of both eye lids or if two heads exist 1. to the lower eye lid by a thin tendon and 2. posterovantrally into the upper eye lid | | |
| function | elongates way of nictitans tendon pyramidalis and prevents a contact of this tendon to tractus opticus (Leuckard 1876) | | |
| synonyms | *depressor palpebrae inferioris et superioris* (Hoffmann 1890: No. 8), *levator palpebrae superior* (Ogushi 1913b: No. 9 – to both lids), *palpebralis* (Bojanus 1819-21: No. 12), *pyramidalis + M. bursalis in commune* partim (Albers: cited after Ogushi 1913b), *quadratus* (into slerotic) (Leuckard 1876, Edgeworth 1907, 1935), *retractor palpebrae* (Schumacher 1972: 5.3.8), *retractor palpebrae superioris* (Clemmys: to upper lid and Membr. nict.) (Nishi 1938b) | | |
| 36* | m. quadratus superior | m. quasio | VI |
| origin | with one head from anterior face of tractus opticus (n. II) and possibly also a second head from sclera of eye bulbus, next to the origin of m. pyramidalis (Ogushi 1913b) | | |
| insertion | tendinuous to the ventral face of the upper eyelid (Ogushi 1913b) | | |
| function | movement (lifting) of upper eye lid | | |
| synonyms | *levator palpebrae superioris* (Ogushi 1913b: No. 9-Anhang) | | |
| comments | only found in 2 adult specimens of *Pelodiscus sinensis* | | |
| 37 | m. rectus posterior | m. recpos | VI |
| origin | by 1-2 heads from basisphenoid and also from an area caudoventrally of foramen opticum, caudally to the origin of rectus inferior (No. 3) | | |
| insertion | posteromedially or posteriorly ar eye bulbus; intercrossing fibres with retractor bulbi in insertion | | |
| function | movement of the eye bulbus (rotation to posteromedial direction) | | |
| synonyms | *abducens* partim (Filatoff 1907), *lateral rectus* (Brudenall et al. 2008), *rectus externus* (Hoffmann 1890: No. 1), *rectus lateralis* (Johnson 1913, Ogushi 1913b: No. 3, Shiino 1913, Schumacher 1972), *rectus oculi externus* (Bojanus 1819-21: No. 8, Owen 1849, Stannius 1854), *rectus posterior* (Underwood 1970, Kuratani 1987, Eger 2006), *rectus temporalis* (Nishi 1938b) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 38 | m. retractor bulbi | m. rtobul | VI |
| origin | by 1-2 heads from basisphenoid, deep inside the posterior edge of the eye cavity | | |
| insertion | by 1-2 heads and partly via connective tissue posteroventrally at the eye bulbus, anteroventrally or around the insertion of the tractus opticus (n. II) into the eye bulbus | | |
| function | retraction of the eye bulbus | | |
| synonyms | *abducens* partim (Filatoff 1907), *external rectus* (Martina and Moale 1881), *suspensor oculi* (Bojanus 1819-21 No. 11), *retractor bulbi* (Brudenall et al. 2008), *re(c)tractor oculi* (Hoffmann 1873-78, Johnson 1913, Ogushi 1913b: No. 8, Shiino 1913, Thomson 1932, Nishi 1938b, Underwood 1970, Schumacher 1972, Kuratani 1987, Eger 2006) | | |
| 39* | m. cervicomandibularis | m. cviman | VII |
| origin | anterior cervical vertebrae (no details known) | | |
| insertion | at least to posterior region of the squamosal | | |
| function | lateral bending of the head | | |
| synonyms | *cervico(-)mandibularis* (Lubosch 1933: C.m.) | | |
| comments | only described for *Apalone ferox* (Lubosch 1933) | | |
| 40-44 | m. constrictor colli complex | - | VII |
| synonyms | constrictor colli as a whole (also when unclear distinction to pars oralis or m. intermandibularis): *$C_2dv$* (Ruge 1896), *constrictor colli* (Natchev and Weisgram 2007, Natchev et al. 2008, 2010, Singer 2009), *constrictor colli* (Lubosch 1933, Edgeworth 1935, George and Shah 1955a, b, Shah 1963, Schumacher 1972, Schumacher 1973: V-C1, Scanlon 1982: COL, Weisgram 1985, Spindel et al. 1987, Wyneken 2001, 2003, Herrel et al. 2008), *interhyoideus* (Diogo and Abdala 2010), *longissimus colli* (Ruge 1897, Hacker 1954), *peaucier* (Rouvière 1906: No. 2), *sphincter colli* partim (Fürbringer 1874, 1897, Hoffmann 1890a: No. 19, Burne 1905 : No. 19 partim, Ogushi 1913: No. 31, Shiino 1913), *mylohyoideus posterior* partim (Fürbringer 1874, Burne 1905, Gnanamuthu 1937, Sondhi 1958), *sphincter colli b/B* (Gräper 1933), *sphincter colli posterior* (Lubosch 1933), *sphincter (latissimus) colli* (Gräper 1932: sph), *subcuteanus cervicis* (Walter 1885), *Un peucier (which is in the position of) trapèze* (Cuvier 1835), *Stellvertreter mehrerer Halsmuskeln der Säugetiere* (Meckel 1818), *transverse jugulaire* (Chaine 1900)<br>constrictor colli as a whole together with sphincter corticis of Ogushi (1913b): *latissimus colli (Partes anterior et posterior)* (Bojanus 1819-21: No. 21a, b), *sphincter colli* (Burne 1905 : No. 19, Van Damme and Aerts 1997), constrictor colli (forth region) (Scanlon 1982),<br>constrictor colli as a whole together with m. intermandibularis (No. 31): *N.N.* (Ahley 1962: not described as such, but drawn as one muscle, m. intermandibularis in nor described), *mylohyoideus* partim (Gräper 1932, 1933) | | |
| 40 | m. constrictor colli<br>Pars aboralis (= principalis) | m. concllABO | VII |
| origin | dorsally at neck in a median raphe | | |
| insertion | ventral medial raphe, partly continuing with posterior neck constrictor (sphincter corticis of Ogushi 1913b) | | |
| function | compresses throat as in swallowing (Ashley 1962), in Lissemys punctata two heads in insertion: “contraction, therefore, would not only elevate but broaden the sheet and diffuse the pressure over a larger area” (Gnanamuthu 1937) | | |
| synonyms | *$C_2$ dv aboralis* (Lubosch 1933), *constrictor colli aboralis* (Lubosch 1938), *latissimus colli* (Ashley 1962), *latissimus colli (pars anterior)* partim (Bojanus 1819-21: No. 21b, Stannius 1854, Owen 1866 : part), *sphincter colli mittlere (b) und hintere (c) Portion* (Gräper 1932: *Chelonia mydas*), *sphincter colli Portio posterior* (Ogushi 1913: No. 31b) | | |
| comments | innervation: n. facialis (n. VII), posterior fibres also by cervical nerves | | |
| 41 | m. constrictor colli<br>Pars spinalis | m. concllSPI | VII |
| origin | laterally at cervical vertebrae or tendon (“Zwischensehne”) to *coracohyoideus* (No. 58-60) | | |
| insertion | medial raphe, contact to trachea, pharynx (Lubosch 1933), contact to cervicocapitis via Zwischensehne (Gräper 1933) | | |
| function | general constrictor colli: constrictor of neck, pharynx (sensu Schumacher 1973) and levator (Gräper 1932) | | |
| synonyms | *$C_2$ hv* (Lubosch 1933), *cervicohyoideus* (Gräper 1933), *coracohyoideus / omohyoideus cauda cervicohyoidea* (Gräper 1932, compare to Gräper 1933), *Hautmuskel des Halses (jugularis)* partim (Wiedemann 1803: No. 13), *hyoid superficial constrictor sheet Pars posterior (constrictor colli spinalis)* (Kesteven 1942-45: Csv.2´´), *interhyoideus* (Lubosch 1938: C2hv), *sphincter colli c/C/(C)* (Gräper 1933),<br>*vordere Constrictorportion* (Ogushi 1913b: following Lubosch 1933: figure 13) | | |
| comments | n. facialis (n. VII) (Gräper 1933) / or completely changes innervation by C1-2 (Kesteven 1942-45: *Chelodina longicollis*) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 42 | m. constrictor colli<br>Pars intermandibularis | m. concllITEMAN | VII |
| origin | medially at posterior part of the lower jaw / from median border of cbI (Kesteven 1942-45) | | |
| insertion | ventral medial raphe, partly continuing with the m. intermandibularis anteriorly and the caudally situated Pars oralis (No. 43) | | |
| function | regulation of the volume of the mouth cavity, breathing | | |
| synonyms | *C2mv* partim (Ruge 1897, Lubosch 1933), *interhyoideus* (Kesteven 1942-45), *m. intermandibularis Pars caudalis* (Poglayen-Neuwall 1953: M.$C_2$v, 1966), *intermandibularis Pars caudalis: m. interhyoideus* (Iordansky 1996), *intermandibularis posterior* (Lubosch 1938), *latissimus colli (pars anterior)* partim (Bojanus 1819-21: No. 21b, Rathke 1848, Stannius 1854, Owen 1866: part), *mylohyoideus posterior* (Sondhi 1958), *constrictor colli Pars oralis (intermandibularis Pars caudalis)* (Schumacher 1973), *sphincter colli Pars anterior* (Ogushi 1913b: No. 31a), *Hautmuskel des Halses (jugularis)* partim (Wiedemann 1803: No. 13) | | |
| 43 | m. constrictor colli<br>Pars oralis | m. concllORA | VII |
| origin | squamosal, up to ligamentum nuchae/supraoccipital | | |
| insertion | ventral medial raphe, partly continuing with the m. constrictor colli Pars intermandibularis (No. 42) | | |
| function | constriction of the posterior mouth cavity | | |
| synonyms | *$C_2$ dv oralis* (Lubosch 1933), *constrictor colli oralis* (Lubosch 1938), *Hautmuskel des Halses (jugularis)* partim (Wiedemann 1803: No. 13), *hyoid superficial constrictor sheet Pars anterior* (Kesteven 1942-45: Csv.2´), *latissimus colli (pars anterior)* partim (Bojanus 1819-21: No. 21b), *sphincter colli a* (Gräper 1933), *sphincter colli Portio anterior* (Ogushi 1913: No. 31a) | | |
| 44** | m. constrictor colli<br>Pars superficialis | m. concllSFI | VII |
| origin | ventrolaterally of the anterior part of the neck and laterally in the head skin by a thin origin/tendon, anterior-posterior course | | |
| insertion | ventral median raphe (together with m. constrictor colli aboralis) | | |
| function | possibly lateral movement of the head against the neck, pulls mouth angle caudad and helps mouth closure | | |
| synonyms | *constrictor colli* (Sondhi 1958) | | |
| comments | only known for *Aspideretes leithii* (Sondhi 1958) | | |
| 45 | m. depressor mandibulae | m. depman | VII |
| origin | with 1-2 heads caudally, laterally and dorsally from squamosal: seldom from quadrate, quadratojugal, opisthotic, cornu branchial-II, partly in contact with dorsal neck muscles, and with constrictor colli Pars oralis (No. 34) via a raphe | | |
| insertion | partly tendinuously from posterior and ventral aspect of articular and processus retroarticularis, laterally and medially from angular, caudally at jaw joint (capsule) | | |
| function | lowers lower jaw | | |
| synonyms | *apertores oris* partim (Rathke 1848), *apertor oris s. digastricus* (Owen 1849), *digastric* (Ashley 1962), *digastricus maxillae* (Bojanus 1819-21: No. 3), *depressor maxillae externus* (Ogushi 1913b: No. 19: separated in a lateral and medial part, medial part ostensibly descriped as depressor medialis internus following Schumacher 1972), *depressor mandibulae pars superficialis* ? (Scanlon 1982), *depressor mandibulae* (Ruge 1896: $C_2$md, Shiino 1913, Lubosch 1933: in figure 20 depicted as "Pterygoideus", 1938, Edgeworth 1935, Kesteven 1942-45: d.m.n, Hacker 1954, Mc Dowell 1961, 1963, Shah 1963, Barghusen 1973, Schumacher 1973: V-C1a, Weisgram 1985, Lemmell and Weisgram 1997, Sato et al. 1997: MDM, Van Damme and Aerts 1997, Wocheslânder et al. 1999, Lemell et al. 2000, Aerts et al. 2001, Diogo and Abdala 2010, Natchev and Weisgram 2007, Natchev et al. 2008, 2009, 2010, Singer 2009), *depressor mandibulae (complex)* partim ? (Wyneken 2001, 2003: *Dermochelys coriacea*), *digastric* (Martin and Moale 1881), *Maulöffner (aperto oris)* (Wiedemann 1803: No. 2, p.79), *Senker des Unterkiefers* (Stannius 1854), *squamoso-maxillaris* (Hoffmann 1890: No. 11, Gräper 1932, 1933), *squamoso-maxillaris (depressor maxillae)* (Burne 1905: No. 11) | | |
| 46 | m. dilatator tubae | m. diltub | VII |
| origin | processus squamosis quadrati, ventral face of the posterior wall of the quadrate, squamosal | | |
| insertion | skinny wall of the eustachian tube, partly at cavitas muscularis of articular (Ogushi 1913b) | | |
| function | stabilisation of eustachian tube | | |
| synonyms | *apertores oris* partim (Rathke 1848, sensu Ogushi 1913b), *depressor mandibulae internus* (Ogushi 1913b: No. 20), *dilatator tubae* (Bojanus 1819-21: No. 4, Hoffmann 1890a: No. 12, Ruge 1896, Burne 1905: No. 12, McDowell 1961, 1963, Schumacher 1973: V-C1b, Scanlon 1982), *dilatator tubae Eustachii* (Edgeworth 1935), *depressor mandibulae complex* partim ? (Wyneken 2003: *Dermochelys coriacea*) | | |
| comments | innervation: n. facialis (n. VII), n. glossopharyngeus (McDowell 1963) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 47 | m. branchiomandibularis visceralis | m. bramanvis | IX |
| origin | distally at cbI and encompasing other muscles originating at cbI (Gräper 1932) | | |
| insertion | posteromedially at lower jaw | | |
| function | pulls cornu branchial-I (and whole hyoid apparatus) ventrad, lowers mouth floor (breathing when jaw is closed) (Gräper 1932), indirect movement of cornu branchial I ventrad, air suction inside mouth cavity and pressing inside lung in a second step (Gräper 1932) | | |
| synonyms | *branchiomandibular muscle* (Lemell et al. 2010), *branchio(-)mandibularis* (Edgeworth 1935, Shah 1963: B.M., Weisgram 1985, Lemmell and Weisgram 1997, Van Damme and Aerts 1997, Wocheslӓnder et al. 1999, Lemell et al. 2000, Aerts et al. 2001, Natchev and Weisgram 2007, Natchev et al. 2008, 2009, 2010, Singer 2009), *branchiomandibularis visceralis* (Lubosch 1933: C3, 1938, Luther & Lubosch 1938, Schumacher 1972, 1973: V-C2a, Spindel et al. 1987), *cornu (-)maxillaris* (Hoffmann 1890a: No. 23, Burne 1905: No. 23), *digastrigue* (Chaine 1900), *geniohyoideus* (Arencibia et al. 2006), *geniohyoideus lateralis* (Walter 1885: gh'), *hyobranchialis* Partim (Diogo and Abdala 2010), *hyomandibularis* (von Bayern 1884, Ogushi 1913b: No. 18, Gräper 1932: hm, also *hyomaxillaris,* Gräper 1933, Kesteven 1942-45: M. hy., Hacker 1954), *hyo-maxillaire superficiel* (Rouvière 1906: No. 3), *hyo(-)maxillaris* (Bojanus 1819-21: No. 16, Owen 1866, Shiino 1913, Gräper 1932: also *hyomandibularis*, Gräper 1933), *hyo-maxillary* (Thomson 1932), *mandibulohyoideus* (Sondhi 1958), *pterygoideus posterior* (? Sato et al. 1997: MPtp), *stilomaxillaris* (Alessandrini 1834a) | | |
| 48* | m. tensor s. dilatator vaginae venae nasoophtalmicae | m. tendilvagvaenasoph | IX |
| origin | anteriorly and ventrally from processus mastoideus of squamosal | | |
| insertion | wall of the venae nasoophtalmicae | | |
| function | flexure of the venae during lateral flexure of the head/neck | | |
| synonyms | *tensor (s.) dilatator vaginae venae nasoophtalmicae* (Ogushi 1913b: No. 21, Edgeworth 1935) | | |
| comments | only described for *Pelodiscus sinensis* | | |
| 49 | m. constrictor laryngis (principalis) | m. conlar(pri) | X |
| origin | hyoid (processus lingualis) (Gaunt and Gans 1969) (medial to dilatator laryngis) | | |
| insertion | cricoid cartilage (Gaunt and Gans 1969) / rima glottis and proc. ascendens of cartilago arytaenoidea Schumacher 1972), cartilago thyreocricoidea, cartilago thyroidea | | |
| function | acts as a sphincter (Gaunt and Gans 1969), opens the rima glossis (Gräper 1932) | | |
| synonyms | *constrictor glottidis* (Bojanus 1819-21: No. 20), *constrictor largyngis* sic (Thomson 1932), *constrictor laryngis* (Edgeworth 1935, Schumacher 1973: V-D2b, Ogushi 1913b: No. 30, Diogo and Abdala 2010), *crico-hyoid* (Mitchell and Morehouse 1863), *crico-hyoideus* (Gaunt & Gans 1969), *hyolaryngeus* (von Bayern 1884), *hyo-thyreo-cricoideus* (Alessandrini 1834b), *sphincter glottitis* (Gräper 1932), *sphincter laryngis* (Schumacher 1972), *genioglossus* (Kesteven 1942-45: Th.v.: *sic: very unclear description but depiction is identifying*) | | |
| 50* | m. constrictor laryngis profundus | m. conlarpfu | X |
| origin | anterior margin and fascia of fossa of copus hyoideus (medial to constrictor laryngis principalis) | | |
| insertion | ventrolaterally to processus musculi of cartilago arytaenoideus | | |
| function | pulls laryngeal apparatus venrad into fossa of corpus hyoideus | | |
| synonyms | *hyo-arytaenoideus (dexter)* (Alessandrini 1834b) | | |
| comments | only described for *Caretta caretta* (Alessandrini 1834b) | | |
| 51 | m. dilatator laryngis | m. dillar | X |
| origin | hyoid (Gaunt and Gans 1969) or / and trachea/ cartilago thyreocricoidea (Schumacher 1972) or connective tissue of rima glottis (Gräper 1932) | | |
| insertion | body and processus muscularis of arytaenoidea ("Stellknorpel") (Gaunt and Gans 1969) | | |
| function | pulls laryngeal apparatus inside groove of corpus hyoidis and by pushing cartilago arytaenoidea ("Stellknorpel") median it clodes rima glottis (Gräper 1932) | | |
| synonyms | *crico-arytenoid* (Mitchell and Morehouse 1863), *crico-arytenoideus* (Gaunt & Gans 1969), *dilatator glottidis* (Bojanus 1819-21: No. 19), *dilatator laryngis* (Gräper 1932, Thomson 1932, Schumacher 1972, 1973: V-D2a, Ogushi 1913b: No. 29, Diogo and Abdala 2010), *thyreo-arytaenoideus* (Alessandri 1834b); drawn but not described or labelled (von Bayern 1884:64) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 52 | m. plastrocapitis | m. placap | X / XI |
| origin | dorsal face of plastron (anterior to middle area) (Schumacher 1972) | | |
| insertion | squamosal, quadratum, by tendon cornu branchial-I (Ogushi 1913b, Gräper 1932) (Schumacher 1972 wrote by mistake cornu branchial-II instead of I), also possible: lateral to the atlas (*Caretta caretta*) or by two heads to the squamosal and laterally to the atlas (*Lepidochelys kempi*) | | |
| function | indirect movement of cornu branchial-I (Gräper 1932), retraction of the head | | |
| synonyms | *capiti(-)plastralis* (Edgeworth 1935, Lubosch 1938), *capiti-plastralis (Sternocleidomastoideus)* (Fürbringer 1874: No. 1, Hoffmann 1890a: No. 38, Burne 1905: No. 38), *capitis cervico-plastralis* (George and Shah 1955a), *cucullaris s. capiti-plastralis* (Edgeworth 1935), *Kopfnicker, oberflächlicher Kopfbeuger, Brustbein- und Zitzenmuskel (sternomastoideus)* (Meckel 1828: §69, No, 1), *L'analogue du sterno-mastoidien* (Cuvier 1835), *plastro(-)squamosus* (Ogushi 1913b: No. 33, Schumacher 1972: 7.2.5.2., 1973: V-C4b, Scanlon 1982: PS), *rectus capitis cervico-plastralis* (George and Shah 1955b, Shah 1963), (Walter 1885: only in plate III, Fig. 21) *sternomastoid* (Ashley 1962: draw complete muscle and described only the head attaching cornu brachiale I), *sterno(-)mastoideus* (Bojanus 1819-21: No. 22, Stannius 1854: §114, No. 2, Owen 1866, Rüdiger 1868, von Bayern 1884, Shiino 1913, Gräper 1932: sm, also *omo-capitis*, Gräper 1933), *sterno-thyroid* (Kesteven 1942-45: s. thy), *omo-capitis* (Gräper 1932: sc (not depicted) for *Chelonia mydas*, also *sterno(-)mastoideus*), *trapezius* (Diogo and Abdala 2010) | | |
| comments | innervation: n. vagus (X) et accessorius (XI) (Scanlon 1982), also R. ventralis n. cervicalis III (Ogushi 1913, Shiino 1913, Schumacher 1972), hypoglossum (XII) (Gräper 1932), R. accessorius n. vadi and possible C3-4 (Fürbringer 1874), X/XI/XII (indistinguishable) (Kesteven 1942-45); most turtles: XI (Ogushi), CIII in *Pelodiscus sinensis* (Ogushi): in this species XI is reduced, also CIV in *Apalone ferox* (Gräper 1932) | | |
| 53 | m. squamosobranchiale | m. squbra | X / XI |
| origin | squamosal (Kesteven 1943-45) | | |
| insertion | distally at cornu branchial-I | | |
| function | pulls cornu branchial-I to skull (Gräper 1932) | | |
| synonyms | *branchiosquamosum* (Van Damme and Aerts 1997),cornu –*hyoideus-capitis* (Kesteven 1942-45: C.hy.c.), *n.n.*(Gräper 1932: muscle No. 10 in *Chelodina longicollis*), *sternomastoideus* (Ashley 1962: draw in connection with plastrocapitis, but described only as squamosobranchiale) | | |
| 54 | m. atlantoexoccipitis | m. atleoc | XII |
| origin | ventrolaterally from CV1 or by tendon from collosquamosal | | |
| insertion | posteroventrally/lateral to exoccipital | | |
| function | ventrolateral movement of the cranium | | |
| synonyms | *atlanto-exoccipitis* (Ogushi 1913b: No. 45, Herrel et al. 2008), *collo-capitis longus* (Scanlon 1982) | | |
| comments | innervation: R. epistropheo-squamosi of n. XII (Ogushi 1913b), in *Chryssemys picta* by CII (Scanlon 1982) | | |
| 55 | m. branchiohyoideus (principalis) | m. brahyo(pri) | XII |
| origin | cornu branchial-I | | |
| insertion | cornu hyale and surrounding area of corpus hyoideus | | |
| function | cbI is rotated forwards and outwards, thus the buccopharyngeal cavity is widened (Gnanamuthu 1937), important for breathing (Gräper 1932)/ dilatator of laryngeal apparatus / pharyngeal area (Ogushi 1913) | | |
| synonyms | *branchiohyalis* (Lubosch 1933: Brhy), *branchiohyoideus* (Schumacher 1972, 1973: V-C2b, Weisgram 1985: also misspelling as *branhiohyoideus*, Spindel et al. 1987, Van Damme and Aerts 1997, Natchev and Weisgram 2007, Natchev et al. 2010), *cornu hyoideus* (Gnanamuthu 1937, Sondhi 1958), *dorsal part of M. hyoglossus* (Gräper 1932: hgd, except for *Apalone ferox*), *dorsal part of M. hyoglossus* partim (Gräper 1932: hgd, for *Apalone ferox*), *hyobranchialis* Partim (Diogo and Abdala 2010), *hyoideus* (Rüdiger 1868), *hyohyoideus* (Natchev et al. 2009),*intercornuatus* partim (Ogushi 1913b: No. 25b, Edgeworth 1935, Shah 1963), *stilohyoideus* (Alessandrini 1834b), *thyro-hyoideus* (Kesteven 1942-45: Th.hy.) | | |
| comments | innervation: XII (Ogushi 1913b, Sondhi 1958), n. glossopharyngeus (IX) (Schumacher 1973: but he does not explain why it should not be XII innervated and does not cite anyone saying the muscle would be IX innervated) | | |
| 56 | m. branchiohyoideus dorsalis | m. brahyodor | XII |
| origin | tip of cornu branchial-I | | |
| insertion | cornu hyale and surrounding area of corpus hyoideus | | |
| function | dilatator of laryngeal apparatus / pharyngeal area (Ogushi 1913) | | |
| synonyms | *first part of geniohyoid muscle* (Lemell et al. 2010: GhI), *intercornuatus* partim(Ogushi 1913b: No. 25a), *dorsal part of M. hyoglossus* partim (Gräper 1932: hgd: *Apalone ferox*) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 57 | m. collosquamosus | m. cllsqu | XII |
| origin | basis of second to third cervical vertebrae | | |
| insertion | tendon to squamosal (prootic) | | |
| function | laterad movement of the head | | |
| synonyms | *collo-squamosus* (Hoffmann 1890: No. 28, Burne 1905: No. 28, Nishi 1916, Schumacher 1972: No. 4.4, Scanlon 1982: CSQ), *epistropheo-squamosus ventralis* (Ogushi 1913b: No. 41, Herrel et al. 2008), *Le trachelomastoidien* (Cuvier 1935), *second part of geniohyoid muscle* (Lemell et al. 2010: GhII), *Seitenmuskel des Kopfes (rectus-lateralis)*, (Wiedemann 1803: No. 9), *Seitlicher gerader Kopfmuskel* (Meckel 1828: No. 7, p. 122), testo-occipitis (Van Damme and Aerts 1997), *trachelo(-)mastoideus* (Bojanus 1819-21: No. 26, Owen 1849, Shah 1963: T.M.), *trachilo-mastoideus* (George & Shah 1955 a, b) | | |
| comments | innervation: n. hypoglossus (XII) (Ogushi 1913b), also n. accessorius (XI) (Scanlon 1982) | | |
| 58-60 | m. coracohyoideus complex | - | XII + C |
| synonyms | <u>as a whole or not separated:</u> *coracobranchialis medialis et lateralis etcoracopharyngeus* (Lubosch 1933: different muscle heads s.s.), *coracohyoid muscle* (Lemell et al. 2010), *coraco(-)hyoideus* (Stannius 1854, Rüdiger 1868, Fürbringer 1874, Ogushi 1913b: No. 34 incl. „M. constrictor tracheae", Schumacher 1973: V-C4a, Scanlon 1982: CHY, Weisgram 1985, Spindel et al. 1987, Wyneken 2001, 2003, Natchev and Weisgram 2007, Natchev et al. 2008, Singer 2009), *coraco(-)hyo(-)stiloideus* (Alessandrini 1834a: also *omohyoideus et scapulohyoideus*), *omohyoid* (Ashley 1962), *omo(-)hyoideus* (Bojanus 1819-21: No. 14, Alessandrini 1834a: also *coraco(-)hyo(-)stiloideus* and *scapulohyoideus*, von Bayern 1884, Shiino 1913, Gräper 1932: oh, Hacker 1954), *omohyoideus et omo-oesophagus* (Walter 1885: also *sternohyoideus* partim), *omohyoïdiens* (Cuvier 1835), *rectus cervicis* (Edgeworth 1935, George and Shah 1955a, Shah 1963: RC, Herrel et al. 2008), *scapulohyoideus* (Alessandrini 1934a: also *omohyoideus* and *coraco(-)hyo(-)stiloideus*), *Schulterzungenbeinmuskel* (Meckel 1828: p. 169, No. 3), *sternohyoideus* (Diogo and Abdala 2010), *sternohyoideus* partim (Walter 1885: also *omohyoideus et omo-oesophagus*) | | |
| 58 | m. coracohyoideus (Pars principalis) | m. cachyo(PRI) | XII |
| origin | coracoid, runs below esophagus | | |
| insertion | some fibres to esophagus, cb I and II and/or corpus hyoidei; head: *omooesophagus (Walter 1885)* | | |
| function | draw the hyoid apparatus backwards and upwards – helps depress jaw, retract head, and lower oral florr (Ashely 1962; *omooesophagus head:* together with hypesophagus (No.) it leads the esophagus when the neck shows a saggital flexure (Walter 1885) | | |
| synonyms | *coraco(-)hyoideus* (Hoffmann 1890: No. 20, Burne 1905: No. 20, Lemmell and Weisgram 1997, Van Damme and Aerts 1997, Wocheslãnder et al. 1999, Lemell et al. 2000, Aerts et al. 2001, Arencibia et al. 2006, Natchev et al. 2009, 2010) | | |
| comments | only described for *Chelonia mydas* (Hoffmann) and *Dermochelys coriacea* (Burne 1905) to be separated from the atlas; innervation: n. XII (Scanlon 1982), anterior part: n. S2-3, posterior part: n. S4-5, Caput cervicale in addition to n. S3 also n. hypoglossus (XII) (Gräper 1932, Schumacher 1972), ramus ventralis of Nn. cervicali 4-5 | | |
| 59 | m. coracohyoideus Pars dorsalis | m. cachyoDOR | XII |
| origin | coracoid | | |
| insertion | hyal apparatus | | |
| function | see No. 58 | | |
| synonyms | *coraco-cornu (-)hyoideus* (Hoffmann 1890: No 21, Burne 1905: No. 21), *am weitesten dorsal gelegene Fasern bilden ein selbständiges, kräftiges Bündel* (Gräper 1932: *Chelodina longicollis*) | | |
| comemnts | only described for *Dermochelys coriacea* (Burne 1905), *Chelonia mydas* (Hoffmann 1890), also *Chelodina longicollis* (Gräper 1932) | | |
| 60 | m. coracohyoideus Pars interbranchialis | m. cachyoITEBRA | XII |
| origin | cornu branchial-II | | |
| insertion | cornu branchial-I | | |
| function | nears cornu branchial-I and cornu branchial-II | | |
| synonyms | *coracohyoideus Pars interbranchialis* (Schumacher 1972, Weisgram 1985, Natchev and Weisgram 2007), probably: *depressor mandibulae* (Arencibia et al. 2006), *hyo-glossus* (Kesteven 1942-45 : Hy.gl.), *intercornuatus* (Gräper 1932 : *Chelodina longicollis*, p.192, Van Damme and Aerts 1997, Aerts et al. 2001, Natchev et al. 2010) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 61** | m. entoplastrohyoideus | m. entplahyo | XII |
| origin | anterior part of entoplaston (Sondhi 1958) | | |
| insertion | posterior part of basihyoid (Sondhi 1958) | | |
| function | draws the hyoid back (Gnanamuthu 1937) | | |
| synonyms | *sternohyoideus* (Gnanamuthu 1937), *sternothyroideus* (Sondhi 1958: “sternum” = entoplastron, see Vickaryous & Hall 2006) | | |
| 62* | m. epiplastrohyoideus | m. epiplahyo | XII |
| origin | dorsally from epiplastron (Sondhi 1958) | | |
| insertion | proximal part of cbI and middle component of corpus hyoideus (Sondhi 1958) | | |
| function | similar to No. 61 | | |
| synonyms | *sternohyoideus* (Sondhi 1958: “clavicle” = epiplastron, see Vickaryous & Hall 2006) | | |
| comments | only descriped for *Asperideres leithii* (Sondhi 1958) | | |
| 63 | m. genioglossus | m. genglo | XII |
| origin | symphysis of dentaries and anterior third of medial side of dental (Schumacher 1972) | | |
| insertion | tongue, ventral face of hypoglossum, partly cornu hyale or fascia intermaxillaris medialis (Schumacher 1972), anterior border of corpus hyoideus (“basihyoid”) | | |
| function | pulls the hyoid apparatus to anterior and the tongue outside (Gräper 1932) | | |
| synonyms | *génio-glosse* (Chaine 1900), *genio(-)glossus* (Bojanus 1819-21: No. 17, Alessandrini 1834a, Owen 1866, Walter 1885, Ogushi 1913b: No. 26, Gräper 1932: gg, Gräper 1933, Lubosch 1933, Edgeworth 1935, Gnanamuthu 1937, Hacker 1954, Shah 1963: G.G., Schumacher 1972: 7.2.4.3., 1973: V-C3d, Spindel et al. 1987, Van Damme and Aerts 1997, Wochesländer et al. 1999, Lemell et al. 2000, Natchev and Weisgram 2007, Natchev et al. 2008, 2009, 2010, Diogo and Abdala 2010), *genioglossus et hyoglossus inferior* (von Bayern 1884: the “hyoglossus inferior” head is the one inserting to the hypoglossum), *genioglossus externus* (Sewertzoff 1929), *maxillo(-)glossus* (Hoffmann 1890a: No. 25, Thomson 1932), *genioglossus* partim (Gräper 1932: in *Chelonia mydas*, lateral part) *genioglossus externus* (George and Shah 1955a) | | |
| 64 | m. geniohyoideus<br>(Pars principalis) | m. genhyo(PRI) | XII |
| origin | symphysis of dentaries, medial at lower jaw!, median raphe of M. intermandibularis, tongue (ventral of corpus hyoidis) | | |
| insertion | cornu branchial-I (= “posterior cornua” of Gnanamuthu 1937), in *Emydura subglobosa* also cornu branchial-II | | |
| function | draws whole hyoid apparatus forward, in co-operation with the posterior hyoid muscles it serves to fix the hyoid apparatus Gnanamuthu (1937), bringst cbI to median level (Gräper 1932) | | |
| synonyms | *genio(-)hyoideus* (Bojanus 1819-21: No. 15, Alessandrini 1834a, Hoffmann 1890a: No. 22, Burne 1905: No. 22, Ogushi 1913b: No. 23, Shiino 1913, Gräper 1932: gh, Gräper 1933, Lubosch 1933, Edgeworth 1935, Gnanamuth 1937, Hacker 1954, George and Shah 1955a, Sondhi 1958, Shah 1963: G.H.,, Schumacher 1973: V-C3b, Spindel et al. 1987, Lemmell and Weisgram 1997, Van Damme and Aerts 1997, Wocheslӓnder et al. 1999, Lemell et al. 2000, Wyneken 2001, 2003, probably: Arencibia et al. 2006, Diogo and Abdala 2010, Natchev and Weisgram 2007, Natchev et al. 2008, 2009, 2010, Singer 2009), *geniohyoideus medialis* (Walter1885: gh), *geniohyoideus profundus s. lateralis* (von Bayern 1884), *génio-hyoïdien* (Chaine 1900), *hyo-maxillaire profond* (Rouvière 1906: No. 4) | | |
| comments | innervation: n. hypoglossus (XII) (Schumacher 1972), in *Trachemys decussata* also by n. glossopharyngeus (IX) (Shiino 1913) | | |
| 65 | m. geniohyoideus<br>Pars lateralis | m. genhyoLAT | XII |
| origin | lower and anterior border of dentary (George and Shah 1955a), possibly by tendon (von Bayern 1884) | | |
| insertion | laterally to the proximal end of cornu branchial-I (George and Shah 1955a), also thyroid cartilage and around hypoglossus | | |
| function | protractor and elevator of hyoid (George and Shah 1955a: together with m. genioglossus) | | |
| synonyms | *genio(-)glossus internus* (George and Shah 1955a), *geniohyoideus* (Kesteven 1942-45: G.gl. sic), *geniohyoideus* partim (Gnanamuthu 1937: one of the described “bundles”), *geniohyoideus superficialis s. lateralis* (von Bayern 1884) | | |
| 66 | m. hyooesophagus | m. hyoesopha | XII |
| origin | distal end of cornu branchial-I | | |
| insertion | dorsally on esophagus (near insertion of omooesophagus head of m. coracohyoideus (Pars principalis) (Walter 1885) | | |
| function | together with m. omooesophagus head of m. coracohyoideus (Pars principalis) (No.) it leads the esophagus when the neck shows a saggital flexure (Walter 1885) | | |
| synonyms | *hyo(-)oesophagus* (von Bayern 1884, Walter 1885), after Walter (1885) also described by Cuvier (tome III, p 270) | | |
| comments | in *Emys orbicularis* it is stronger on the right side than the left side (Walter 1885) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 67 | m. hyoglossus<br>(Pars principales) | m. hyoglo(PRI) | XII |
| origin | proximal end of cornu branchial-I and medially from cornu hyale (Schumacher 1972) | | |
| insertion | into tongue (Schumacher 1972), or dorsal median raphe of tongue (Ogushi 1913b), cornu hyale (George and Shah 1955a) | | |
| function | retractor and depressor of hyoid (George and Shah 1955a, with caution due to derived anatomy of the muscle in *Lissemys punctata*) | | |
| synonyms | *cornu(-)glossus* (Hoffmann 1890a: No. 24, Burne 1905: No. 24, Thomson 1932: also *hyoglossus*), *hyo(-)glossus* (Bojanus 1819-21: No. 18, Cuvier 1835, Owen 1866, Stannius 1854, Walter 1885: hgl, Ogushi 1913b: No. 24, Thomson 1932: also *cornu –glossus*, Lubosch 1933, Edgeworth 1935, Gnanamuth 1937: with upper and lower devisions, Hacker 1954, Shah 1963: H.G., Schumacher 1972, 1973: V-C3c, Spindel et al. 1987, Van Damme and Aerts 1997, Diogo and Abdala 2010, Natchev and Weisgram 2007, Natchev et al. 2010), *hypo(-)glossus* (George and Shah 1955a, b), *stiloglossus* (Alessandrini 1834a), *hyoglossus, Teil, der wirklich in die Zunge einstrahlt* (Gräper 1932: *Apalone ferox*), *hyoglossus posterior* (von bayern 1884), *ventral part of M. hyoglossus* (Gräper 1932: hgd, except for *Apalone ferox*) | | |
| 68 | m. hyoglossus<br>Pars ventralis | m. hyogloVTR | XII |
| origin | more anterior and median than hyoglossus Pars principales from proximal end of cbI (Gnanamuthu 1937), muscle fibres originating from dorsal face of corpus hyoideus and proc. linguae (von Bayern 1884) | | |
| insertion | processus lingualis of corpus hyoideus (Gnanamuthu 1937: “processus entoglossus”) or directly into tongue | | |
| function | retractor and depressor of hyoid (George and Shah 1955a, with caution due to derived anatomy of the muscle in *Lissemys punctata*) | | |
| synonyms | *hyoglossus partim* (Gnanamuthu 1937: one of the two bundles), *Muskelzüge […] radiär in die Zunge ausstrahlen[d]* (von Bayern 1884: part of “dritte Gruppe der Zungenmuskeln”) | | |
| 69 | m. hypoglossoglossus | m. hypgloglo | XII |
| origin | dorsolaterally at hypoglossum | | |
| insertion | anteroventrally into tongue (close relation to Mm. hyoglossus and especially genioglossus, Gräper 1932) | | |
| function | hypoglossum against proc. lateralis and endoglossum and whole tongue rostrad (Gräper 1932: *Apalone ferox*), posterior tongue rostrad (Ogushi 1913: *Pelodiscus sinensis*) | | |
| synonyms | *entoglosso* partim (Edgeworth 1935), *entoglosso-glossus* (Ogushi 1913b: No. 27, Schumacher 1973: V-C3a and *N.N.* in C3e second part), *entoglosso(-)glossus* partim (Schumacher 1972: 7.2.4.4), *genioglossus* partim (Gräper 1932: in *Chelonia mydas*, medial part), *hypoglosso(-)glossus* (George and Shah 1955a, Schumacher 1973: V-C3e, Spindel et al. 1987, Natchev and Weisgram 2007, Natchev et al. 2009: g.g., 2010: hpg, Diogo and Abdala 2010), *hypoglosso-lateralis* (Sondhi 1958), transversalis (Sewertzoff 1929: in *Emys orbicularis*, separated from *m. genioglossus*), *lingual musculature ?* (Natchev et al. 2008), *transversalis linguae* (Sewertzoff 1929: in *Testudo graeca*, still connected to *m. genioglossus* – develops from an muscle Anlage called *genioglossus internus*), *verticalis linguae* (Gräper 1932), *lingualis* (Alessandrini 1834a: Fig. 4h), *Zahl der Muskelfasern, welche von der unteren Knorpelplatte entspringt und […] zum Zungenknorpel […] selbst gelangt* (von Bayern 1884: part of “dritte Gruppe der Zungenmuskeln”) | | |
| 70 | m. hypoglossohyoideus | m. hypglohyo | XII |
| origin | processus lingualis of corpus hyoidei | | |
| insertion | dorsal at hypoglossum (very short), in *Chelonia mydas* still connected with genioglossus (Gräper 1932) | | |
| function | saggital movement of corpus hyoideus backwards and hypoglossum forwards: elongates tip of the tongue (Gräper 1932), moves tongue rostrad (Gräper 1933) | | |
| synonyms | *entoglosso* partim (Edgeworth 1935), *entoglosso(-)glossus* partim (Schumacher 1972: 7.2.4.4, Diogo and Abdala 2010), *entoglosso-hyoglossalis* (Sondhi 1958), *entoglosso-hyoideus* (Ogushi 1913b: No. 28 with nomenclature as used in Textfigur 11, wrongly described as a second *entoglosso-glossus*: see also comment by Gräper 1932, p. 192), *hyoentoglossus* (Gräper 1932: also *protrusor linguae*), *hyoglossus* (Alessandrini 1834a: Fig. 4g), *hypoglosso(-)hyoideus* (George and Shah 1955a, Shah 1963, Spindel et al. 1987, Van Damme and Aerts 1997), *protrusor linguae* (Gräper 1932: p, also *hyo(-)entoglossus,* Gräper 1933), *Zahl der Muskelfasern, welche von der unteren Knorpelplatte entspringt und […] [zur] Zunge selbst gelangt* (von Bayern 1884: part of “dritte Gruppe der Zungenmuskeln”) | | |
| 71 | m. levator pharyngis | m. levpha | XII |
| origin | cornu branchial-I | | |
| insertion | ventral to oesophagus | | |
| function | dorsad movement, and possibly constriction of the pharynx | | |
| synonyms | *levator pharyngis* (Ogushi 1913b: No. 36), *omohyoideus Portio hyopharyngea* (Gräper 1932), *stilo-pharyngeus* (Alessandrini 1834a) | | |
| comments | in *Chelydra serpentina* and *Chelodina longicollis* still connected with coracohyoideus (Gräper 1932);<br>innervation: n. hypoglossus (XII) (Ogushi 1913b: usually two branches of its posterior root) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 72* | m. longitudinalis linguae | m. ltulin | XII |
| origin | median fibrous tissues in front of glottideal region – about the middle of the length of the tongue | | |
| insertion | fibrious tissues at the tip of the tongue | | |
| function | curling upwards of the tongue tip (Gnanamuthu 1937) | | |
| synonyms | *longitudinalis linguæ* (Gnanamuthu 1937) | | |
| comments | only described for *Lissemys punctata* (Gnanamuthu 1937: p. 40) | | |
| 73 | m. transversalis linguae | m. tvelin | XII |
| origin | median raphe dorsally at the anterior tip of the tongue (Gnanamuthu 1937) | | |
| insertion | dorsolateral border of tongue | | |
| function | movement of the dorsolateral border of tongue | | |
| synonyms | *transversalis linguae* (von Bayern 1884), *transversalis linguæ* (Gnanamuthu 1937) | | |
| 74 | m. verticalis linguae | m. vtilin | XII |
| origin | ventrolateral part of tongue | | |
| insertion | dorsolateral edge of tongue | | |
| function | vertical contraction of the lateral part of the tongue | | |
| synonyms | *annulares hyoglossi* (Sewertzoff 1929 – develops from an muscle Anlage called *genioglossus internus*), *verticalis linguae* (Schumacher 1972, 1973: described as a potential lateral part of *genioglossus*) | | |
| 75 | m. atlantoepistropheo-occipitis (principalis) | m. atlepistrocc(pri) | CId |
| origin | dorsally at first and second cervical vertebrae | | |
| insertion | opisthotic, exoccipital, squamosal | | |
| function | movement of the head in posterodorsad direction | | |
| synonyms | *atlanto-epistropheo-occipitis* (Hoffmann 1890: No. 32, Schumacher 1972: No. 4.7, Scanlon 1982: AE), *epistropheo-squamosal dorsalis* (Ogushi 1913b: No. 46: on page 330 wrong as "M. episterno-squamosus ventralis", Herrel et al 2008), *epistropheo-squamosus* (Gräper 1932), *Großer hinterer gerader Kopfmuskel (Rectus capitis posticus major)* (Wiedemann 1802: No. 5, p. 80; 1803), *No. 6* (Cuvier 1835: page 316), *rectus capitis posticus major* (Owen 1849, 1866), *rectus capitis posterior major* (Bojanus 1819-21: No. 31), *rectus capitis posterior maior* (Nishi 1916), *rectus capitis superficialis* (George and Shah 1955a, b, Shah 1963: R.C.S.), *suboccipitales (atlanto-epistropheo capitis)* (Vallois 1922) | | |
| comments | only in Cryptodira (Shah 1963); innervation: n. S1d (Ogushi 1913b, Scanlon 1982) | | |
| 76 | m. atlantoepistropheo-occipitis profundus | m. atlepistroccpro | Cd |
| origin | lateral aspect atlas or from ventrolateral aspect of collosquamosus | | |
| insertion | prootic, opisthotic | | |
| function | posterolaterad movement of the head | | |
| synonyms | *kleiner hinterer gerader Kopfmuskel* (rectus capitis posticus minor) (Wiedemann 1803: No. 6, could also be atlantooccipitis (No. 77), but described as not oblique and to situate directly under atlantoepistropheooccipitis principalis (No. 75) with no differing insertion than this muscle), *rectus profundus* (George and Shah 1955a), *rectus capitis profundus* (George and Shah 1955b, Shah 1963: R.C.P.)<br>comment(s): | | |
| comments | in pleurodires (*Chelodina longicollis*) only atlantoepistropheooccipitis profundus;<br>innervation: possibly n.S1d (after Ogushi 1913b, when the muscle is a ventral partition of muscle above) | | |
| 77 | m. atlantooccipitis | m. atlocc | Cd |
| origin | dorsal or lateral face of first cervical vertebrae (Ogushi 1913b) | | |
| insertion | exoccipital, basioccipital | | |
| function | rotation movements of the head (posterodorsad and laterad) | | |
| synonyms | *atlanto-occipitis* (Hoffmann 1980: No. 33, Scanlon 1982: AO), collo-capitis brevis (Scanlon 1982: CCB), *rectus capitis posterior minor* (Bojanus 1819-21: No. 32, Nishi 1916, Lubosch 1933: No. 32), *rectus capitis posticus minor* (Owen 1866), *(suboccipitales) atlanto capitis* (Vallois 1922), *atlanto-basioccipitalis medialis* partim (Ogushi 1913b: No. 44, "laterale Portion, deren Fasern viel steiler verlaufen", Herrel et al. 2008) | | |
| comments | innervation : n. S1 (Scanlon 1982), n. S1d (Vallois 1922) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 78 | m. atlantoopisthoticus | m. atlopioti | Cd |
| origin | anterodorsally at cervical vertebrae 1 | | |
| insertion | opisthotic | | |
| function | posterolaterad movement of the head | | |
| synonyms | *atlanto-opisthhoticus* (Ogushi 1913b: No. 47, Herrel et al. 2008), cervico-capitis (Ashley 1955), *intertransversalis* partim (Gasc 1981, with *epistropheo-atlantis dorsalis* of Ogushi 1913b: No. 43: cvivte-1to -2), *m. interspinalis cervicis of the first cervical vertebrae* (Scanlon 1982) | | |
| comments | innervation: such as m. atlantoexoccipitis by R. m. epistropheo-squamosi of n. XII, when partition of m. cervicocapitis: nn. S2d-5d (Ogushi 1913b, see comments to m. cervicocapitis), as m. interspinalis cervicis of cvivte-1 by n. S1 (Scanlon 1982) | | |
| 79 | m. cervicocapitis | m. cvicap | Cd |
| origin | dorsally to 3rd-6th cervical vertebrae (Ogushi 1913b) | | |
| insertion | tendon to squamosal, supraoccipital, fascia of m. adductor mandibulae externus (II), with 2-4 heads, Sehnenplatte also to cb II (Gräper 1932) | | |
| function | posterodorsad movement of the head | | |
| synonyms | *biventer cervical* (Ashley 1962), *biventer cervicis* (Bojanus 1819-21: No. 24, Owen 1849, 1866), *cervico-capitis* (Hoffmann 1890: No. 15, Burne 1905: No. 15, Schumacher 1972: No. 4.3, Scanlon 1982: CCA), *cervico-capitis medialis* (Vallois 1922), *cervico capitalis* (Nishi 1916), *cervicocapitis* partim (Gräper 1932: x, also *omohyoideus (coracohyoideus) Caput cervicale*: except "*cauda hyoidea*"), *cervico-hyo-capitis* partim (Ogushi 1913b: No. 35: except "*cauda hyoidea*"), *cervico-squamosal* (Thomson 1932), *dorsale Längsmuskulatur* (Lubosch 1933: figure 17: D.l.m.), *Kopfbauschmuskel* (splenius capitis) (Wiedemann 1803: No. 4, p. 80), *L'analogue du splenius de la tête* ( Cuvier 1835), *omohyoideus (coracohyoideus) Caput cervicale* (Gräper 1932: also *cervicocapitis* partim: except "*cauda hyoidea*"), *spinalis capitis* (Nishi 1938a, Gasc 1981), *spinalis(-)cervico(-)capitis* (George and Shah 1955a, b, Shah 1963: S.C.C., Herrel et al. 2008), *Zweibäuchiger Nackenmuskel* (analog) (Meckel 1828: No. 3, p. 116-117) | | |
| comments | innervation: nn.S2d-5d, nn. S1d-4d (Scanlon 1982), nn.S1d/2d-5d (Vallois 1922) | | |
| 80 | m. collooccipitis | m. cllocc | CId |
| origin | lateral cervical vertebrae 1-3 (Hoffmann), cervical vertebrae 3 (Scanlon), dorsal first and second cervical vertebrae | | |
| insertion | opisthotic, prootic | | |
| function | posterodorsad movement of the head | | |
| synonyms | *collo-occipitis* (Hoffmann 1890: No 27, Scanlon 1982: COC), *complexus* (Bojanus 1819-21: No. 25, Cuvier 1835, Owen 1866), *obliquus capitis* (George and Shah 1955a, b, Shah 1963: O.C., Van Damme and Aerts 1997) | | |
| 81 | m. carapacocervico-capitis lateralis Pars capitis | m. carcvicaplatCAP | Cd |
| origin | 1st costal plate | | |
| insertion | Pleurodira: skull base, prootic, opisthotic (Vallois 1922, Shah 1963); Chelonioidea: parietal, by aponeurosis to squamosal (Hoffmann 1890, Schumacher 1972), more lateral than No. 82 | | |
| function | lateral flexion and rotation of head (Vallois 1922) | | |
| synonyms | *Kopfbauschmuskel* (Meckel 1828: No. 2, p. 116), (Hoffmann 1890: No. 14, Burne 1905: No. 14, Schumacher 1972: No. 4.2), *testo(-)capitis lateralis* (Vallois 1922), *testo(-)capitis* partim (Shah 1963, Herrel et al. 2008), *testo-parietali-squamosal* (Hoffmann 1890: No. 14 synonym), *N.N.* (Cuvier 1835: No. 2, p. 316), *splenius capitis* (Rathke 1848: a, p. 160) | | |
| comments | not in non-marine turtle cryptodires; innervation: nn.S1d-6d | | |
| 82 | m. carapacocervico-capitis medialis Pars capitis | m. carcvicapmedCAP | CIII-VId |
| origin | ventrally in anteriomedian region of carapace, nuchale | | |
| insertion | temporal fascie, more medial than No. 81 | | |
| function | posterodorsad movement of the head | | |
| synonyms | *cucullaris* (Rathke 1848: a, p. 160), *Kappenmuskel der höheren Thiere analog* (Meckel 1828: No. 1, p. 115), *Muscle de la tête #2* (Cuvier 1835: No. 1, p. 316), *splenius capitis* (Bojanus 1819-21: No. 23, Stannius 1854, Gräper 1932: also *testooccipitis*, Lubosch 1933: No. 23), *tecto-occipitalis* (Schumacher 1973), *testocapitis* partim (Shah 1963: T.C., Herrel et al. 2008), *testo-capitis medialis* (Vallois 1922), *testo-occipitis* (Hoffmann 1890: No. 13, Burne 1905: No. 13, Gräper 1932, Schumacher 1972: No. 4.1, 1973, Scanlon 1982: TO), *testo(-)occipitalis* (Nishi 1916, Gräper 1932: also splenius capitis, Lubosch 1933: No. 23), *testospinalis capitis* (Nishi 1938a, Gasc 1981), *Zweibäuchiger Nackenmuskel (biventer cervicis)* (Wiedemann 1803: No. 3, p. 79-80) | | |
| comments | only in Cryptodira (Gasc 1981), not in trionychids (Rathke 1848, Ogushi 1913b), not in *Chelodina longicollis* (Gräper 1932) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 83* | m. transversalis cervicis | m. tvecvi | Cd |
| origin | cervical vertebrae 3-5/ cervical vertebrae 4-7 | | |
| insertion | cervical vertebrae 1-3, basioccipital | | |
| function | lateroventral movements of the cervical vertebrae | | |
| synonyms | *M. transversalis cervicis (TRC)* (Bojanus 1819-21, Owen 1866, Hoffmann 1890: No. 17, Burne 1905: No. 17, Callister 2005, Scanlon 1982), *Nackenzitzenmuskel, den hintern geraden und schiefen Kopfmuskel der höhern Thiere* partim (Meckel 1828), *articulo-transversalis longus* (Ogushi 1913b: No. 39a), *articulotransversarii 1ongi* (Nishi 1916). *transversarii obliqui cervicis et M. transversarius cervicis* (Vallois 1922), *transverse cervical* (Ashley 1962), *interarticularis superior* (Gasc 1981), *transversalis cervicis und capitis* (Nishi 1938a) | | |
| comments | generally present in turtles but only in *Dermochelys coriacea* (juvenile) extending to the skull (Burne 1905) | | |
| 84 | m. collocapitis brevis | m. cllcapbre | CIv |
| origin | ventrally from cervical vertebrae 1, most medial muscle of cervical vertebrae 1 | | |
| insertion | basioccipital | | |
| function | posteroventrad movement of the head | | |
| synonyms | *atlanto-basioccipitalis medialis* partim (Ogushi 1913b: No. 44, “mediale Portion”, Herrel et al. 2008), *collo-capitis brevis* (Hoffmann 1890: No. 31, Scanlon 1982: CCB), *interarticularis inferior* (Gasc 1981), *rectus capitis anterior minor* (Bojanus 1819-21: No. 30), *rectus capitis anticus brevis* (Owen 1866), *rectus capitis brevis* (George and Shah 1955a: R.C.B.), *rectus capitis ventralis brevis* (George and Shah 1955b: R.C.V.B.) | | |
| 85 | m. constrictor hyoideus | m. conhyo | Cv |
| origin | around cervical vertebrae 5-7 | | |
| insertion | at least posteriorly at cornu branchial-I | | |
| function | primary function presumably related to the abduction and retraction of cornu branchial-I, it presumably plays a role during lateral bending of the neck (Herrel et al. 2008), depressor and elevator of the floor of buccal cavity and other movements of hyoid apparatus (George and Shah 1955a), retractor of head/neck under shell (Shah 1963) | | |
| synonyms | *constrictor hyoideus* (George and Shah 1955a, b, Shah 1963: C.H., Herrel et al. 2008) | | |
| 86-87 | m. longus colli<br>Pars capitis with 2 portions | - | Cv |
| synonyms | longus colli muscle complex as a whole or only having a non cranial part: *cervico-spinalis medialis* (Ogushi 1913b: No. 38, Herrel et al. 2008), probably: *longus capitis* (Arenciba et al. 2006: also *longus colli*), *longus colli* (Bojanus 1819-21: No. 28, Cuvier 1835, Owen 1866, Hoffmann 1890: 29, Burne 1905: No. 29, George and Shah 1955a, b, Ashley, 1955, Shah 1963, Scanlon 1982: LC)<br>longus colli Partes capitis-I and –II/III fused: (only cranium related part): *collo-capitis longus* (Hoffmann 1890: No. 30: as the “oberstes Bündel” of No. 29, Schumacher 1972: No. 4.6 = wrong as dorso-capitis longus in Tabula III), *L’analogue du grand droit anterieur* partim (Cuvier 1835), *rectus capitis anterior longus* (Bojanus 1819-21: No 29, Owen 1866), *rectus capitis anticus longus* (Owen 1849), *Vorderer gerader Kopfmuskel oder Beuger* (Wiedemann 1803), *rectus capitis ventralis longus et major et ventralis minor* (George and Shah 1955b, Shah 1963: RCVL et RCVMaj et RCVMin), probably: *rectus ventralis* (Arenciba et al. 2006: also *longus colli*) | | |
| 86 | m. longus colli<br>Pars capitis-I | m. lonclICAP-I | Cv |
| origin | by a tendon ventrally from 1st cervical vertebrae | | |
| insertion | basioccipital | | |
| function | posteroventrad movement of the head | | |
| synonyms | *longus colli of CV-1* (Scanlon 1982), *rectus capitis ventralis minor* (George and Shah 1955b, Shah 1963: RCVMin) | | |
| comments | innervation: for m. longus colli as a whole: nn. S1v-7v (Ogushi 1913b) | | |
| 87 | m. longus colli<br>Pars capitis-II/III | m. lonclICAP-II/III | Cv |
| origin | by a tendon ventrally from 2nd + 3rd cervical vertebrae (+4th) | | |
| insertion | basioccipital | | |
| function | flexure of the head (Wiedemann 1803) | | |
| synonyms | head from cervical vertebrae 2 only: *longus colli of CV-2* (Scanlon 1982), *rectus capitis ventralis major* (George and Shah 1955b, Shah 1963: RCVMaj)<br>head from cervical vertebrae 3 only: *longus colli of CV-3* (Scanlon 1982), *rectus capitis ventralis longus* (George and Shah 1955b, Shah 1963: RCVL)<br>head from cervical vertebrae 2/3(4) together: *vorderer gerader Kopfmuskel / rectus capitis anticus* (Wiedemann 1803: No. 8), *longus colli profundus* (Gasc 1981), *scalenus anticus* (Rathke 1848), *vorderer Rippenhalter (scalenus)* (Meckel 1828) | | |
| comments | innervation: for m. longus colli as a whole: nn. S1v-7v (Ogushi 1913b) | | |

| No. | muscle name | muscle abbreviation | general innervation |
|---|---|---|---|
| 88 etc. | m. retrahens capiti collique with four portions all together and one portion inserting to the cranium | - | Cv |
| synonyms | m. retrahens capiti collique as a whole:<br>*carapaco-basioccipitalis* (Ogushi 1913b: No. 37, Herrel et al. 2008), *dorso-occipitis* (Hoffmann 1890: No. 26, Burne 1905: No. 26, Thomson 1932, Schumacher 1972: No. 4.5), *Großer, vorderer, gerader Kopfmuskel, tiefer Beuger oder Niederzieher des Kopfes* (Meckel 1828: No. 2, p. 120), *langer Halsmuskel (longus colli)* (Wiedemann 1803: No. 7), *longus colli superficialis* (Gasc 1981), *muscle repondant aux fonctions du sacro-lumbaire, du transversaire grêle et à celles du long dorsal* (Cuvier 1935), *retractor colli et capitis* (Rathke 1848), *retractor muscles of the neck and* head (Martin and Moale 1881), *retrahens capitis* (Noble and Peterson 1931), *retrahens/retrachens capitis et colli / (et) collique* (Bojanus 1819-21: No. 27, Owen 1849, 1866, Stannius 1854, Shiino 1913, Ashley 1962, George and Shah 1955a, b, Shah 1963: RCC, Scanlon 1982: RC-, Callister 2005, Van Damme et al. 1995, Herrel et al. 2008), *(Corresponds in function to) sacro-lombaire et … transversaire grêle et … 1e long dorsal* (Cuvier (1835) | | |
| 88 | m. retrahens capiti collique<br>Pars carapacobasioccipitis | m. rhecapcllCARBASOCC | Cv I-VII |
| origin | basioccipital (anterior part) | | |
| insertion | dorsal vertebrae 7-8 and surrounded area, ribs | | |
| function | major retractor of the head/neck | | |
| synonyms | bundle 1 of retrahens capitis collique (Van Damme et al. 1995), retrahens capitis et colli (pars anterior) (Scanlon 1982) | | |
| comments | innervation: retrahens capiti collique as a whole: nn. S1v-7v (Ogushi 1913b), n.S3-4 (Scanlon 1982, Callister and Peterson 1992), n.S3v after Thomson 1932 | | |

## APPENDIX 2.

Quicktime-Video based on the CT-scan of the cranium of *Emydura subglobosa* (MPEG-4 compression), yaw- rotation, compare to Figures 17, 18 (available online).
palaeo-electronica.org/2011_2/254/appendix2.htm

## APPENDIX 3.

Quicktime-Video based on the CT-scan of the cranium of *Emydura subglobosa* (MPEG-4 compression), pitch- rotation, compare to Figures 17, 18 (available online).
palaeo-electronica.org/2011_2/254/appendix3.htm

## APPENDIX 4.

Quicktime-Video based on the CT-scan of the cranium of *Emydura subglobosa* (MPEG-4 compression), roll-rotation, compare to Figures 17, 18 (available online).
palaeo-electronica.org/2011_2/254/appendix4.htm

# APPENDIX 5.

Synonym list of spatial elements. For abbreviations see Appendix 7. Donor structures are highlighted. For simplification, not all abbreviations are used in the figures of that article (available online).

| Structure | Abbreviation | Selected synonyms | Comments / definition |
|---|---|---|---|
| aponeuroses | | | |
| I – coronar aponeurosis | apo. cno | *Adduktorensehne* (Schumacher 1953/54), *basal aponeurosis* (Haas 1973), *Binnensehne* (Poglayen-Neuwall 1953: bs), *Bodenaponeurose* (Lakjer 1926, Rieppel 1990), *central tendon* (Rieppel 1990: embryonally), *coronar aponeurosis* (Iordansky 1994, 1996), *external tendon* (Schumacher 1973), *Externussehne* (Schumacher 1972), *Sehne des m. adductor mandibulae externus* (Schumacher 1953/54, 1954/55a) | three sheets, lateral and medial sheet are connected by a bend (Iordansky 1994) |
| coronar aponeurosis, lateral sheet | apo. cnoLAT | *lateral sheet* (Iordansky (1994), *laterale Lamelle der Adduktorsehne / inferiore Sehnenplatte / unteres Sehnenblatt* (Schumacher 1953/54), *lateraler Zipfel der Adduktorsehne* (Schumacher 1954/55b, 1956b), *Sehne a* (Poglayen-Neuwall 1953) | anteriortly and laterally at coronoid, within m. adductor mandibulae externus (Iordansky 1994), with several terminal branches (Poglayen-Neuwall 1953: *with two terminal branches, a dorsal, saggital "a1" and a ventrocaudal, horizontal* "a2") |
| coronar aponeurosis, medial sheet | apo. cnoMDI | *medial sheet* (Iordansky (1994), *dorsale Lamelle der Adduktorsehne / superiore Sehnenplatte / oberes Sehnenblatt* (Schumacher 1953/54), *medialer Zipfel der Adduktorsehne* (Schumacher 1954/55b, 1956b), *Sehne b* (Poglayen-Neuwall 1953) | posteriorly to coronoid, within m. adductor mandibulae externus, largest sheet in turtles with an insertion anteriorly, dorsally and posteriorly to the coronoid (process) (Iordansky 1994) |
| coronar aponeurosis, anteromedial sheet | apo. cnoANTMDI | *anterio-medial sheet* (Iodansky 1994), ventraler Zipfel der Adduktorsehne (Schumacher 1954/55b, 1956b), *mediale Lamelle der Adduktorsehne / mediale Sehnenplatte / mittleres Sehnenblatt* (Schumacher 1953/54) | on the posterior edge of the coronoid or connected to the medial sheet (Iordansky 1994) – insertion face for m. adductor mandibulae internus Pars pseudotemporalis superficialis (No. 24) (if existing) |
| Zwischensehne | Zwi | *Insertionssehne des M. adductor mandibulae internus pseudotemporalis und Ursprungssehne des M. intramandibularis* (Poglayen-Neuwall 1953: T), *intramandibular tendon* (Schumacher 1973), *tensverse tendinuous inscription* (Iordansky 1994) | possibly homologous to the anteromedial sheet of the coronar aponeurosis (Ic), which shifts its attachment from the coronoid to the intramandibularis (if present) |
| coronar aponeurosis, dentary sheet | apo. cnoDEN | *additional lateral sheet* in *Malayemys* (Iordansky 1994) | additional lateral sheet in *Malayemys*, originating laterally from the dentary (Iordansky 1994), possibly a separation of the lateral sheet of the coronar aponeurosis |
| II – subarticular aponeurosis | apo. subart | subarticular aponeurosis (Iordansky 1994), *internal tendon (superficial aponeurosis)* (Schumacher 1973), *Sehne des m. adductor mandibulae internus* (Schumacher 1954/55b) | medially to the lower jaw, near the jaw joint (cartilago meckeli, prearticular, surangular, articular), possibly on a particular crest or process of the articular (Iordansky 1994), in Platysternon, trionychids and *Pelomedusa* from the coronoid (Schumacher 1973) |
| retroarticular aponeurosis | apo. rroart | *retroarticular aponeurosis* (Iordansky 1994) | separated from subarticular aponeurosis, inserting to the retroarticular process (Iordansky 1994) |

| Structure | Abbreviation | Selected synonyms | Comments / definition |
|---|---|---|---|
| supraangular aponeurosis | apo. sprang | *supraangular tendon* (Iordansky 1994) | fibres of m. adductor mandibulae internus Pars pseudotemporalis (No. 23) and m. adductor mandibulae posterior (No. 29) (Iordansky 1994) |
| supraangular aponeurosis intramandibular sheet | apo. sprangITRMAN | *branch of supraangular tendon to the intramandibularis muscle / intramandibularis aponeurosis* (Iordansky 1987, 1994) | rostrad leading sheet of the supraangular aponeurosis, inserting to the primordial channel of the lower jaw and bearing m. adductor mandibulae internus Pars intramandibularis (No. 25) (Iordansky 1994) |
| III – pterygoidal poneurosis | apo. pte | *pterygoidal aponeurosis* (Iordansky 1994), *Lamina anterior (of internal tendon)* (Schumacher 1973) | from the posterior process and the posteroventral edge of the pterygoid, embraces the m. adductor mandibulae internus Partes pterygoideus (No. 26-28) ventally, possibly laterally or medially; enters to the lower jaw as an internal sheet of the muscular structures (Iordansky 1994), partly separated in 2 tendons (Poglayen-Neuwall 1953) |
| pterygoidal aponeurosis, dorsal sheet | apo. pteDOR | *pterygoideus tendon a* (Poglayen-Neuwall 1953) | still a part of internal tendon such as in *Testudo graeca*: m. adductor mandibulae internus Pars dorsalis (No. 26) (Poglayen-Neuwall 1953) |
| pterygoidal aponeurosis, ventral sheet | apo. pteVTR | *pterygoideus tendon b* (Poglayen-Neuwall 1953) | in relation to m. adductor mandibulae internus Pars ventralis (No. 28) (Poglayen-Neuwall 1953: *Caretta caretta*, *Testudo graeca)* |
| IV – quadrate aponeurosis | apo. qua | *quadrate aponeurosis* (Iordansky 1994) | would not be present in turtles, has two sheets, that are dorsally connected to each other, originate dorsally from the anterior face of the quadrate and run rostroventrad in archosaurs and lepidosaurs (sensu Iordansky 1994) |
| quadrate aponeurosis, lateral sheet | apo. quaLAT | lateral sheet of quadrate aponeurosis (Iordansky 1994) | may be laterally connected to the fascia temporalis (Iordansky 1994), runs and inserts between the lateral and medial sheet of coronar aponeurosis at the lower jaw (Iordansky 1994) |
| quadrate aponeurosis, medial sheet | apo. quaMDI | *medial sheet of quadrate aponeurosis* (Iordansky 1994) | |
| lig. quadrato-maxillare | lig. quamax | *lig. quadrato-maxillare* (Lakjer 1926), Membrana quadrato-squamoso-jugo-maxillare (Schumacher 1956c), lig. quadrato-jugo-maxillare (Schumacher 1956c) | this structure is only found in turtles and is spanning between the quadrate and the lateral face of the posterior part of the maxilla/jugal; it may be homologous to the quadrate aponeurosis in archosaurs and lepidosaurs but not to the lig. quadratojugal of birds and squamates, which is derived from the temporal fascia (Werneburg, unpublished work; note modifications made to Werneburg 2010) |
| V – supraoccipital aponeurosis | apo. sprocc | *Supraoccipitales Sehnenblatt* (Schumacher 1955b), *Sehne b* and *Sehne, die den Muskelbauch medio-ventral umgibt* (Poglayen-Neuwall 1953: in *Kinosternon* and *Sternotherus*) (origin of Pars profundus=“profunda” and Pars medialis=“media”), *Sehnenband c* (Lakjer 1926), *supraoccipital tendon (lobe)* (Schumacher 1973) (origin of Pars profundus=“profunda”) | several splits possible, origin area for m. adductor mandibulae externus Pars profundus (No.) in trionychids and *Podocnemis*, who have a very extended supraoccipital crest (Schumacher 1973) |
| | | | |
| fasciae and membranae | | | |
| I – fascia colli superficialis | fas. cllsfi | *Fascia colli superficialis* (Hacker 1954, Hacker and Schumacher 1954, Schumacher 1956c) | around muscles of the neck; depending on the degree of rostrad expansion to the ear and buccal region following pars are defined (Schumacher 1956c): |

| Structure | Abbreviation | Selected synonyms | Comments / definition |
|---|---|---|---|
| fascia colli superficialis Pars craniolateralis | fas. cllsfiCRALAT | *Fascia colli superficialis … Pars auriculo(-)temporalis* (Schumacher 1953/54, Schumacher 1956c: found in *Chelonia mydas, Caretta caretta, Podocnemis expansa* or *Platysternon megacephalon*), *… Pars auriculo-supratemporalis* or *… Pars auricularis* (Schumacher 1956c: latter both found in *Pelomedusa subrufa, Mauremys rivulata, Graptemys geographica, Macrochelys temmincki* or *Hydromedusa tectifera*) | possibly homologous expansions of the fascia colli superficialis to the ear and buccal region: depending on the extend Schumacher (1956c) named the structure differently in the respective species |
| fascia colli superficialis Pars craniotemporalis | fas. cllsfiCRATEM | *Fascia colli superficialis Pars temporalis* (Schumacher 1956c: found in trionychids, *Hydromedusa tectifera* or *Chelodina longicollis*) | is an extension of the fascia colli superficialis to the temporal region of the head, lies superficially to the fascia temporalis (Schumacher 1956c) |
| fascia colli superficialis Pars intermandibularis | fas. cllsfiITEMAN | *Fascia intermaxillaris superficialis* (Hacker 1954: A1, Fortsetzung der Fascia colli superficialis, Hacker and Schumacher 1954) | intermandibular continuation of fascia colli superficialis, attached to ventromedial edge of lower jaw, ventrally to fascia intermandibularis and extend caudally over the area of m. intermandibularis and its fascia (Hacker 1954) |
| II – fascia temporalis | fas. tem | *fascia temporalis* (Hacker and Schumacher 1954, Schumacher 1956c), *Temporalfascie* (Lakjer 1926, Poglayen-Neuwall 1953: Tp.), *quadrato-temporal aponeurosis* (Iordansky 1994), *temporal fascia* (Rieppel 1980a) | lies directly in the temporal region and attaches to the periost of supraoccipital, parietal, postorbital, jugal, quadratojugal and/or squamosal; caudally it is an insertion side for the dorsal neck muscles; in taxa without lateral temporal armour (*Chelodina longicollis, Hydromedusa tectifera, Emydura kreffti*) it extends rostroventrad and attaches to the lig. quadratomaxillare medially; in taxa with a zygomatic arch it does not split or form a subzygomatic part (no lower temporal fascie; in taxa with a stegal morphotype (*Emydura*) or transition forms between zygal and stegal morphotype (Podocnemis, Schumacher 1956c:50) the temporal fascie can split into an anterior and posterior part (Schumacher 1956c) |
| fascia temporalis posterostegalis | fas. tempossga | *obere Temporalfascie* (Lakjer 1926) | “temporal fascie can split into an anterior and posterior part“ (Schumacher 1956c) |
| fascia temporalis anterostegalis | fas. temantsga | *untere Temporalfascie* (Lakjer 1926) | “temporal fascie can split into an anterior and posterior part (Schumacher 1956c)” |
| lig. quadratoanguloorale | lig. quaangora | *lig. quadrato-angulo-orale* (Schumacher 1956c) | This structure, especially found in trionychid turtles. It spans between the quadrate and attaches to the external edge of the mouth (mostly reduced, but visible in trionychids) (Schumacher 1956c). It may be developmentally homologous to the lig. quadratojugale of birds and squamates (Werneburg, unpublished work; note modifications made to Werneburg 2010) |
| III – fascia adductor mandibulae externus | fas. addmanete | *Fascie des M. adductor mandibulae externus* (Hacker and Schumacher 1954, Schumacher 1956c) | around the whole m. adductor mandibular externus (No. 17-21), and in addition m. zygomaticomandibularis (No. 22) in trionychids (Schumacher 1956c); nothing is known about inclusion of m. levator bulbi (No. 16) |
| IV – fascia adductor mandibulae internus | fas. addmanite | *Fascie des M. adductor mandibulae internus* (Hacker and Schumacher 1954, Schumacher 1956c) | includes all portions of m. adductor mandibulae internus and m. adductor mandibulae posterior (sensu Schumacher 1956c) |
| V – fascia intermandibularis | fas. iteman | *Fascia intermaxillaris superficialis* (Hacker 1954: A2, Fascie des M. intermaxillaris) | lies directly on the ventral surface of m. intermandibularis and is ventrally covered by fascia superficialis colli Pars intermandibularis (Hacker 1954) |

| Structure | Abbreviation | Selected synonyms | Comments / definition |
|---|---|---|---|
| VI – fascia intermandibularis medialis | fas. itemanmed | *Fascia intermaxillaris medialis* (Hacker 1954: B, Hacker and Schumacher 1954) | supports the lateral part of the mouth floor, which does not have many muscles (Hacker 1954) |
| fascia intermandibularis medialis, ventral sheet | fas. itemanmedVEN | *ventrales Blatt der Fascia intermaxillaris medialis* (Hacker 1954: B) | lateral to m. genioglossus (which inserts also to this fascia) , over Glandulae sublinguales, attached to medial face of lower jaw (Hacker 1954) |
| fascia intermandibularis medialis, dorsal sheet | fas. itemanmedDOR | *dorsales Blatt der Fascia intermaxillaris medialis* (Hacker 1954: B) | attached to hypoglossum; fused with the anterior parts of m. genioglossus; covers tongue ventrolaterally; attached to medial face of lower jaw; ventrally to glandula sublingualis (Hacker 1954) |
| VII – fascia intermandibularis profundus | fas. itemanpfu | *Fascia intermaxillaris profunda* (Hacker 1954: C, Hacker and Schumacher 1954) | caudal and dorsal to glandulae sublingualis; covers whole lateral part of the tongue; some fibres of m. hyoglossus insert to it; laterally attached to lower jaw (Hacker 1954) |
| VIII – membrana obturatoria orbitae | mem. otuorb | *Membrana obturatoria orbitae* (Schumacher 1956c) | between bones, that form the transition between orbital and adductor chamber |
| IX – membrana tympanica | mem. tym | *Membrana tympanica* (Schumacher 1953/54, 1956c), Tympanon (Poglayen-Neuwall 1953: Tymp., Schumacher 1954/55a) | spans over the otic cavity |
| X – ligamentum nuchae | lig. nuc | *Lig. nuchae* (Gräper 1932) | nape area |
| XI – ligamentum hyosquamosal | lig. hyosqu | *Lig. hyosquamosal* (Ogushi 1913b) | between the distal tip of cornu brachiale-I and the posteroventral area of the squamosal |
| | | | |
| Additional elements and spatial terms | | | |
| cartilago / os transiliens | car./os tsl | *cartilago transiliens* (Schumacher 1972, 1973), *os transiliens* (Ray 1959, Bramble 1974: only in Gopheridae ossified), *Sesamknorpel* (Lakjer 1926), a sesamoid cartilage or bone (Iordansky 1994) | formed within the coronar aponeurosis between its insertion side and the split into lateral and medial sheets; it forms a joint (possibly with a joint capsule) together with the processus trochlearis oticum in Cryptodira or the process trochlearis pterygoidei in Pleurodira; in Cryptodira a fascies articularis prootica articulates with the tuberculum osseus prootic and a facies articularis quadrata articulating with tuberculum osseus quadrati may occur at the articulation face of the cartilago transiliens – on the opposite face the inner mouth plate of the cartilago transiliens contacts the external mouth plate (Schumacher 1956b) |
| processus trochlearis oticum | proc. trooti | *processus trochlearis otico-quadratus* (Iordansky 1996: pto), *Proc. trochlearis oticum* (Gaffney), *Proc. trochlearis quadrati et prootici* (Schumacher1956b) | see cartilago / os transiliens |
| processus trochlearis pterygoidei | proc. tropte | *processus trochlearis pterygoidei* (Schumacher 1953/54), *processus trochlearis pterygoideus* (Schumacher 1956bm Iordansky 1996: ptp) | see cartilago / os transiliens |
| glandula lacrimalis | gla. lac | *Glandula lacrimalis* (Schumacher 1956c), *Tränendrüse* (Poglayen-Neuwall 1953: Tr.Dr.) | - |
| otic cavity | cav. oti | otic chamber | area, which is bounded by quadrate, prootic, opisthotic and squamosal |
| otic capsule | scu. oti | | area of the skull enclosing the otic cavity; it is made of quadrate, prootic, opisthotic and squamosal |

| Structure | Abbreviation | Selected synonyms | Comments / definition |
|---|---|---|---|
| orbital cavity | cav. orb | *Orbita* (Schumacher 1953/54) | area of the skull enclosing the eye bulbus, eye muscles and nerves |
| trigonum intermandibulare anterior | trig. itemanant | trigonum intermaxillaris rostralis (Hacker 1954) | a trigonal area posterior to the symphysis of the dentaries which is present of m. intermandibularis (No. 31) does not reach the anteromedial corner of the lower jaw |
| trigonum intermandibulare posterior | trig. itemanpos | trigonum intermaxillaris caudalis (Hacker 1954) | a trigonal area, which is present if the posterolateral extend of m. intermandibularis (No. 31) and the anteromedial extent of m. constrictor colli Pars intermandibularis (No. 42) do not fuse together |
| adductor chamber | cham. add | | roughly the area dorsal to the otic capsule and lateral to the brain case; it can be covered laterally by dermal bones and contains the trigeminus innervated jaw musculature |
| postorbital cavity of the adductor chamber | cham. addposorbcav | *untere Schläfenöffnung* (Lakjer 1926), *untere Temporalgrube* (Poglayen-Neuwall 1953) | roughly anterior to the otic capsule; area m. adductor mandibulae internus (No. 23-28), m. adductor mandibulae posterior (No. 29-30), m. zygomaticomandibularis (No. 22), and the insertion area of m. adductor mandibulae externus (17-21) |
| temporal cavity of the adductor chamber | cham. addtemcav | *obere Schläfenöffnung* (Lakjer 1926), *fossa temporalis superior (Schumacher 1954/55aobere Temporalgrube* (Poglayen-Neuwall 1953) | origin area of m. adductor mandibulae externus Partes profundus et superficialis (No. 19, 21) |

## APPENDIX 6.

Species and the related references compared in this study (available online)..

| Reference | Species or genera sensu Fritz and Havaš (2007) and invalid species or genera name used by the authors |
|---|---|
| Adams (1919) | *Chelydra serpentina and summary* |
| Aerts et al. (2001) | *Chelodina longicollis* |
| Albers (1808) | *Chelonia mydas (“Testudo Mydas”)* |
| Alessandrini (1834a) | *Caretta caretta (“Chelonia caouana“), Dermochelys coriacea (“test. coriaceae“)* |
| Alessandrini (1834b) | *Caretta caretta (“Chelonia caouana“)* |
| Arenciba et al. (2006) | *Caretta caretta* |
| Ashley (1962) | *Chelydra serpentina (?), Chrysemys picta* (drawn and possibly described) |
| Barghusen (1973) | *Chelonia mydas* |
| Bojanus (1819-1821) | *Emys orbicularis (“Testudo europaea“)* |
| Bramble (1974) | *Gopherus agassizii, flavomarginatus, polyphemus* |
| Brudenall et al. (2008) | *Dermochelys coriacea* |
| Burkard (1902) | *Testudo graeca* |
| Burne (1905) | *Dermochelys coriacea* |
| Callister et al. (1992, 2005) | *Trachemys scripta elegans (“Pseudemys“)* |
| Callister and Peterson (1992) | *Trachemys scripta elegans (“Pseudemys“)* |
| Chaine (1900) | *Astrochelys (“Testudo”) radiata* |
| Cuvier (1835) | *Caretta caretta (“caret“ / “caouanne“) Chelus fimbriatus (“matamata“), Pyxis, Terrapene, Trionyx (?), Lyssemis punctata (“Testudo scabra“), Malaclemys terrapin („Emys centrata“)* |
| Dalrymple (1975) | *Amyda cartilaginea (”Trionyx cartilagineus“), Apalone ferox (“Trionyx”), Apalone mutica (“Trionyx muticus”), Apalone spinifera (“Trionyx spiniferus”)* |
| Dalymple (1977) | *Apalone ferox* (and other *“Trionyx”)* |
| Diogo and Abdala (2010) | *Trachemys scripta* |
| Edgeworth (1907) | *Chelonia mydas* (*“Chelone”*, after Parker 1880) |
| Edgeworth (1911) | *Chrysemys picta marginata* (*Chrysemys “marginata”*) |
| Edgeworth (1935) | *Emys orbicularis “lutaria”* (partly after Filatoff 1907), *Chelonia mydas* (*“Chelone viridis”*), *Chelydra serpentina* (partly after Johnson 1913), *Chrysemys picta marginata* (*Chrysemys “marginata”*), *Emys orbicularis* (*“Testudo europaeus”*, after Bojanus 1819-1821), *Eretmochelys imbricata* (*“Chelone”*), *Chelonoidis denticulata* (*“Testudo tabulata”*), *Chelonoidis nigra* (*“Testudo elephantopus”*), *Dermochelys coriacea* (*“Sphargis”*), *Podocnemis, Cycloderma frenatum* (after Fürbringer 1922), *Pelodiscus sinensis* (*“Trionyx japonicus”*: after Ogushi 1913b) |
| Eger (2006, 2007) | *Emydura subglobosa, Testudo hermanni, Trachemys spec.* |
| Filatoff (1907) | *Emys orbicularis (“lutaria”)* |
| Fuchs (1915) | *Eretmochelys imbricata (“Chelone”), Chelonia mydas (“Chelone midas”), Emys orbicularis (“lutaria”)* |
| Fuchs (1931) | *Podocnemis expansa* |
| Fuchs (1933) | *Eretmochelys imbricata (“Chelone”), Emys orbicularis (“europaea”), Podocnemis expansa* |
| Fürbringer (1874) | *Chelonoidis denticulata (“Testudo tesselata”), Clemmys guttata (“Emys punctata”), Dermochelys coriacea (“Sphargis” juvenil), Emys orbicularis (“europaea”,* partly after Bojanus*), Testudo graeca, Trachemys scripta (“Emys serrata“), Pelodiscus sinensis (“Trionyx japonicus“)* |
| Gaunt and Gans (1969) | *Chelydra serpentina* |
| Gasc (1981) | *Chelonia mydas, Dermochelys coriacea, Emys orbicularis, Geochelone radiata, Mauremys leprosa, Testudo graeca, Trionyx triunguis* |
| George and Shah (1955a) | *Lissemys punctata* |
| George and Shah (1955b) | *Geochelone (“Testudo”) elegans* |
| George and Shah (1955c) | *Aspideretes (“Trionyx”) gangeticus, Geochelone (“Testudo”) elegans Lissemys puctata, Melanochelys (“Geomyda”) trijuga* |
| Gnanamuthu (1937) | *Chelonia mydas, Emyda vittata* |
| Gräper (1932, 1933) | *Apalone ferox (“Trionyx“), Chelodina longicollis, Chelonia mydas, Chelydra serpentina, Clemmys caspica, Testudo tabulata* |
| Gregory and Adams (1915) | *“Chelone”, Chelydra serpentina* |

| | |
|---|---|
| Hacker (1954) | *Testudo graeca* |
| Hacker and Schumacher (1954) | *Testudo graeca* |
| Herrel et al. (2008) | *Apalone ferox, Apalone spinifera (“spiniferus“), Chelodina longicollis, Chelodina reimanni (“reimani”)* |
| Hoffmann (1890) | partly after Bojanus, Fürbringer: *Chelonoidis denticulata (“Testudo tabulata”), Chersina angulata, Testudo graeca, Testudo graeca (“mauritana”), Emys orbicularia (“europaea”)* |
| Iordansky (1987, 1996, 2008) | *Chelonia mydas, Clemmys (“Mauremys“) caspica, Emys orbicularis, Graptemys pseudogeographica* (juvenil), *Malayemys subtrijuga, Pelodiscus (“Trionyx“) sinensis, Pelomedusa subrufa, Pseudemys terrapen, Testudo (“Agrionemys“) horsfieldii* |
| Johnson (1913) | *Chelydra serpentina, Chrysemys picta marginata (“marginata”)* |
| Kesteven (1942-45) | *Chelodina longicollis, Emydura macquarii („macquariae“)* |
| König (1934/35) | *Caretta (“Thalassochelys“) caretta, Emys orbicularis, Testudo graeca* |
| Kuratani (1987) | *Caretta caratta* |
| Lakjer (1926) | *Amyda cartilaginea (“Trionyx cartilagineus”), Chelonoidis denticulata (“Testudo tabulata“), Dermochelys („Sphargis“) coriacea, Eretmochelys (“Chelone“) imbricata, Terrapene (“Cistudo“) carolina* |
| Lemmell and Weisgram (1997) | *Pelusios castaneus* |
| Lemell et al. (2000) | *Pelusios castaneus* |
| Lemmel et al. (2002, 2010) | *Chelus fimbriatus* |
| Leuckard (1876) | *Chelonia mydas (“Mydas“)* |
| Lubosch (1933) | *Apalone ferox (“Trionyx“), Clemmys leprosa, Testudo graeca, Testudo horsfieldi* |
| Lubosch (1938) | review on Hoffmann 1890, Ogushi 1913b, Lakjer 1926, Lubosch 1933 |
| Martin and Moale (1881) | *Trachemys decussata (“Pseudemys rugosa”)* |
| McDowell (1961, 1963) | *Podecnemis expansa* (in regard to musculature) |
| Meckel (1828) | *Caretta caretta (“Chelone“), Chelonia mydas (“Chelone“), Chelonoidis denticulata (“Testudo tabulata“), Emys orbicularis, Eretmochelys imbricata (“Chelone“), Testudo graeca (“Testudo“), Trachemys scripta (“Emys serrata“),* |
| Mitchell and Morehouse (1863) | *Chelydra serpentina* |
| Natchev and Weisgram (2007) | *Cuora flavomarginata* |
| Natchev et al. (2008) | *Cuora amboinensis* |
| Natchev et al. (2009) | *Cuora amboinensis, Cuora flavomarginata* |
| Natchev et al. (2010) | *Cuora galbinifrons* |
| Nishi (1916) | *Chelydra serpentina* |
| Nishi (1938a, b) | review on Hoffmann 1890, Ogushi 1913b, Vallois 1920, 1922 |
| Noble & Peterson (1931) | *Emys orbicularis* |
| Ogushi (1913b) | *Chelonia mydas (“Chelone”), Malayemys (“Damonia”) subtrijuga, Testudo graeca (“iberica”), Pelodiscus sinensis (”Trionyx japonicus“), Psammobates geometricus (”Testudo geometrica”), Rhinoclemmys (“Nicoria”) punctularia* |
| Owen (1866) | review : *Emys orbicularis (”europaea“)* (after Bojanus 1819-21, Cuvier 1835) |
| Poglayen-Neuwall (1953) | *Batrachemys nasuta (”Rhinemys“), Caretta caretta, Chelodina longicollis, Chelydra serpentina, Chrysemys picta, Clemmys caspica et autata, Cuora amboinensis (“Cyclemys“), Dermochelys coriacea, Graptemys pseudogeographica (“Malaclemys lesueurii“), Kinosternum scorpioides et leucosternum, Malaclemys pileata littoralis, Pelodiscus (“Trionyx“, “Amyda“), sinensis, Pelusios niger, Pseudemys scripta troostii, Sternotherus odoratus (“Cinosternum odoratum“), Terrapene triunguis (“cinosternoides“)* |
| Poglayen-Neuwall (1953/54) | *Dermochelys coriacea* |
| Poglayen-Neuwall (1966) | *Chelus fimbriatus* |
| von Bayern, L.F. (1884) | *Emys orbicularis (lutaria), Testudo graeca (“Festudo“)* |

| | |
|---|---|
| Rathke (1848) | *Acanthochelys spixii (“Platemys Spixii”), Apalone ferox (“Trionyx ocellatus“, also “Trionyx ferox”), Aspideretes (“Trionyx“) gangeticus, Chelonia mydas (“Midas”,* also *“virgata”), Chelonoidis denticulata (“Testudo elephantina”), Dogania subplana (“Trionyx subplanus“), Emys orbicularia (“europaea“,* also *“lutaria”), Eretmochelys (“Chelonia”) imbricata, Kinosternum scorpioides (“Terrapene tricarinata“), Kinosternon subrubrum (“Terrapene pensylvanica”), Lissemys punctata (“Trionyx granulosus“), Pelomedusa subrufa (“Pentonyx capiensis“), Rhinoclemmys (“Emys“) punctularia, Dermochelys (“Sphargis”) coriacea, Testudo graeca* (also: *“mauritanica”*), *Trionyx truinguis (“aegyptiacus”)* |
| Ray (1959) | *Astrochelys yniphora (“Geochelone“), Chelonoides carbonaria (“Geochelone“), Chelonoides denticulata (“Geochelone“), Geochelone sulcata, Gopherus agassizii, Gopherus berlandieri, Gopherus polyphemus, Kinixys belliana* |
| Rieppel (1990) | *Chelydra serpentina* |
| Rouvière (1906) | *Testudo graeca* |
| Ruge (1896) | review on Fürbringer, Bojanus, Owen, Stannius, Hoffmann, Rathke |
| Rüdinger (1868) | *Caretta caretta (“Testudo“ / “Chelonia”), Chelonia mydas (“Testudo”), Emys orbicularia (“europaea”), Testudo graeca* |
| Sato et al. (1997) | *Mauremys japonica (“Clemmys”)* |
| Scanlon (1981) | *Chrysemys picta belli* (and a review of almost all neck muscle literature) |
| Schumacher (1953/54) | *Chelonia mydas, Caretta caretta, Podocnemis expansa, Podocnemis unifilis, Pelusios sinuatus (“Sternothaerus”), Chelonoidis nigra (“Testudo elephantopus”)* |
| Schumacher (1954) | *Chelonia mydas, Podocnemis expansa, Podocnemis unifilis, Pelusios sinuatus (“Sternothaerus”), Chelonoidis nigra (“Testudo elephantopus”)* |
| Schumacher (1954/55a, b) | *Platysternon megacephalon, Emys orbicularis, Testudo graeca, Pelomedusa subrufa, Mauremys rivulata (“Clemmys caspica rivulata”), Graptemys geographica, Hardella thurjii, Macrochelys temmincki (“Makrochelys”), Emydura krefftii, Hydromedusa tectifera, Chelodina longicollis, Lissemys (“Trionyx”) punctatus, Pelodiscus (“Amyda”) sinensis, Dogania subplana* |
| Schumacher (1956a-c) | summaries on jaw muscles in turtles |
| Schumacher (1972) | *Dermochelys coriacea* |
| Schumacher (1973, 1980, 1985) | review on cranial musculature in turtles (n. trigeminus, V, to n. hypglossus, XII, innervated muscles) |
| Sewertzoff (1929) | *Emys orbicularis (“europea“, “lutaria”), Testudo graeca* (*“græca”*: following von Bayern 1884) |
| Shah (1963) | *Chelodina longicollis, Deirochelys reticularia – compared to Lissemys, Testudo, “Trionyx“ “Geoemyda“* |
| Shiino (1913) | *Amyda cartilaginea (“Trionyx cartilagineus“), Clemmys guttata (“Nanemys“), Trachemys decussata (“Clemmys“)* |
| Singer (2009) | *Emys orbicularis, Sternotherus odoratus* |
| Sondhi (1958) | *Aspideretes (“Amyda“) leithii* |
| Spindel et al. (1987) | *Macrochelys temminckii (“temmincki“)* |
| Stannius (1854) | *Chrysemys picta (“Emys”), Chelonoidis denticulata (“Testudo tabulata”), Chelonoidis nigra (“Testudo”), Chelydra serpentina, Sternotherus (“Staurotypus”) odoratus* |
| Thomson (1932) | *Testudo graeca (also “ibera”)* |
| Tiedemann (1819) | *Chelonia (“Te?tudo”) mydas* |
| Tvarožková (2006) | *Chelydra serpentina, Podocnemis expansa, Terrapene carolina triunguis* |
| Underwood (1970) | *Chelonia mydas, Carettochelys insculpta, Caretta caretta* |
| Van Damme et al. (1995) | *Chelodina longicollis* |
| Van Damme and Aerts (1997) | *Chelodina longicollis, Trachemys scripta* |
| Vallois (1920, 1922) | *Pelomedusa subrufa (“galeata“), Pelusios spec. (*Pleurodires: *“Sternothaerus sp.“), Testudo marginata, Trionyx triunguis* |
| Walter (1887) | *Emys orbicularis (“europaea“)* |
| Wiedemann (1803) | *Chelonoides (“Testudo“) denticulata* |
| Winokur (1982) | *Apalone ferox (“Trionyx“), Apalone spinifera (“Trionyx spiniferous“), Carettochelys insculpta, Chelodina longicollis, Dogania subplana, Elseya latisternum, Lissemys punctata, Podocnemis unifilis* |
| Wocheslӓnder et al. (1999) | *Testudo hermanni* |
| Wynneken (2001, 2003) | *Caretta caretta, Chelonia mydas, Eretmochelys imbricata, Lepidochelys kempii et olivacea, Natator depressus* |

# APPENDIX 7.

Abbreviation list. See text for abbreviation guide (available online).

| | |
|---|---|
| abo | aboralis |
| acc | accessorius |
| acr | acromion |
| add | adductor |
| ang | angular |
| ant | anterior |
| apo. | aponeurosis |
| apo. cno | coronar aponeurosis |
| apo. itrman | intramandibular aponeurosis |
| apo. pte | pterygoidal aponeurosis |
| apo. ptevtr | ventral pterygoidal aponeurosis |
| apo. ptedor | dorsal pterygoidal aponeurosis |
| apo. qua | quadrate aponeurosis |
| apo. subart | subarticular aponeurosis |
| apo. spraocc | supraoccipital aponeurosis |
| apo. pos | posterior aponeurosis |
| arr | arrector |
| art | articular |
| ary | arytaen- |
| atl | atlant- |
| aty | atypica |
| bas | básis |
| basocc | basioccipital |
| bassoi | basisphenoid |
| bod | body |
| bra | branch |
| bre | brevis |
| bul | bulbus |
| cac | coraco-, coracoid |
| cap | caput |
| car | carapaco- |
| car. ary | cartilago arytaenoidea |
| car. cri | cartilago cricoidea |
| car. mec | cartilago meckeli |
| car. thy | cartilago thyreoidea |
| car. thycri | cartilago thyreocricoidea |
| car. til | cartilago/os transiliens |
| cav. | cavity |
| cnuhya | cornu hyal |
| cnubra-I | cornu branchial-I |
| cnubra-II | cornu branchial-II |
| cav. | cavity |
| cbr | cerebralis, cerebrum |
| cbrhem | cerebral hemisphere |
| cham. | chamber |
| cid | coroid |
| cidple | coroid plexus |
| cil | ciliaris |

| | |
|---|---|
| cir | circum |
| CL | carapace length |
| cll | coll- |
| clu | columella |
| cNCC | crania neural crest cells |
| cno | coronoid |
| cnu | cornu |
| cnuhya | cornu hyale |
| con | constrictor |
| cos-1, … | costal 1, … |
| cpu | corpus |
| cpuhyo | corpus hyoidei |
| csu. | capsule |
| cra | crani- |
| cri | cricoidea |
| cvi | cervico- |
| cvivte-1 | cervical vertebrae 1 |
| cvivte-1’ | intercentrum of cvivte-1 |
| den | dentary |
| dep | depressor |
| dil | dilatator |
| dor | dorsal |
| dorvte1 | dorsal vertebrae 1 |
| end | endo |
| ent | ento |
| entpla | entoplastron |
| eoc | exoccipital, exoxipital- |
| epi | epi |
| epiphy | epiphysis (pineal body) |
| epipla | epiplastron |
| epipte | epipterygoid |
| equ | equatorialis |
| ete | externus |
| etr | extra |
| etrclu | extracolumella |
| eye | eye |
| fac. | fascia |
| fro | frontal |
| gen | genio- |
| gla | glandula |
| gla. lac | Glandula lacrimalis |
| glo | glosso-, glossum |
| hem | hemisphere |
| hya | hyal |
| hyo | hyo- |
| hyopla | hyoplastron |
| hyp | hypo- |
| hypglo | hypoglossum |

| | |
|---|---|
| hyppla | hypoplastron |
| ifa | infra |
| ife | inferior |
| ite | inter- |
| iteorbsep | interorbital septum |
| itr | intra- |
| jug | jugal |
| lab | labyrinth |
| lac | lacrimal, lacrimalis |
| lar | laryng- |
| lat | lateral |
| len | lens |
| lev | levator |
| lgu | longus |
| lin | linguae |
| lob | lobus |
| low | lower |
| ltu | longitudinal |
| m. | musculus |
| mam | mammary |
| mambod | mammilary body |
| man | mandibula |
| max | maxilla |
| mdi | medial |
| mdu | medulla |
| mec | meckeli |
| mem. | membrana |
| men | mentalis |
| mes | meso |
| mespla | mesoplastron |
| mm. | musculi |
| n. | nervus |
| n. I | n. (Bulbus) olfactorius |
| n. II | n. (Tractus) opticus |
| n. III | n. oculomotorius |
| n. IV | n. trochlearis |
| n. IX | n. glossopharyngeus |
| n. V | n. trigeminus |
| n. $V_1$ | Ramus ophthalmicus n. trigemini |
| n. $V_2$ | Ramus maxillaris n. trigemini |
| n. $V_3$ | Ramus mandibularis n. trigemini |
| n. VI | n. abducens |
| n. VII | n. facialis |
| n. VIII | n. statoacusticus |
| n. X | n. vagus, |
| n. XI | n. accessorius |
| n. XII | n. hypoglossus |
| n. S1, etc. | spinal nerve 1n etc. |
| n. S1d | dorsal branch of spinal nerve 1 |
| n. S1v | ventral branch of spinal nerve 1 |
| nar | narial- |
| nas | nasal-, nasal |

| | |
|---|---|
| NCC | neural crest cells |
| neu | neural |
| nn. | nervi |
| nuc | nuchal |
| obl | obliq- |
| occ | occipit - |
| ocu | oculi |
| odo | odontoid- |
| oes | oesophagus |
| olf | olfactory |
| olflob | olfactory lobe |
| olfsac | olfactory sac |
| oph | ophthalmicus |
| opi | opis- |
| opioti | opisthotic |
| opt | optic |
| optlob | optic lobe |
| ora | oral, oralis |
| orb | orbita, orbital- |
| oti | otic |
| otu | obturatoria |
| par | parietal |
| pat | palatine, palato- |
| per | peri- |
| perphe | peripheral |
| pfu | profundus |
| pha | pharyngis |
| phe | pheral |
| phy | physis |
| pla | plastrum, plasto- |
| ple | plexus |
| pos | post, postero- |
| posorb | postorbital |
| ppe | palpebr- |
| preart | prearticular |
| prefro | prefrontal |
| premax | premaxilla |
| pri | principalis |
| pro | pro- |
| proc. | processus |
| prooti | prootic |
| pse | pseudo- |
| pte | pterygo- |
| pte | pterygoid |
| pup | pupill |
| pyg | pygal |
| pyr | pyramid- |
| qua | quadrate, quadrato- |
| quajug | quadratojugal |
| rec | rectus |
| rha | rhamphotheca |
| rhalow | lower rhamphotheca |

| | |
|---|---|
| rhaupp | upper rhamphotheca |
| rhe | retrahens |
| rro | retro- |
| rib | rib |
| rib-1, … | rib 1, … |
| ros | rostral |
| rto | retractor |
| sac | sac |
| sca | scapula |
| scaacr | acromion process of scapula |
| scl | sclerotical bones |
| sep | septum |
| sfi | superficialis |
| sga | stegalis |
| sio | superior |
| sis | superioris |
| soi | sphenoid |
| spi | spinal |
| spr | supra- |
| sprocc | supraoccipital |
| sprpyg | suprapygal |
| squ | squamosal, squamos- |
| ste | sphincter |
| str | strophe |
| sub | sub- |
| sur | sur- |
| surang | surangular |
| tem | temporal |
| ten | tensor |
| thy | thyreo- |
| til | transiliens |
| tra | trachea |
| trig. | trigonum |
| tub | tubae |
| tve | transvers |
| tym | tympanic |
| upp | upper |
| vae | venae |
| vag | vaginae |
| vis | visceralis |
| vom | vomer |
| vte | vertebrae |
| vti | verticalis |
| vtr | ventral |
| xip | xiphi, xipho |
| xippla | xiphiplastron |
| Zwi | Zwischensehne |
| zyg | zygomatico |