Introduction

Sea turtles (Cheloniaioidea) are adapted to a marine lifestyle in possessing flippers, hydrodynamic shells, lacrimal salt glands, and a specialised physiology for diving [1–18]. Their fossil record is considered by some to extends at least as far back as the Early Cretaceous, 110 million years ago (e.g. [9,19–23]), and the group contains seven living species: Caretta caretta, Chelonia mydas, Dermochelys coriacea, Eretmochelys imbricata, Lepidochelys kempii, Lepidochelys olivacea, and Natator depressus (Fig. 1) (sensu Fritz and Havas [24]). These turtles pursue a range of feeding strategies [2,23,25].

Extant sea turtles are of particular interest to comparative anatomists and evolutionary biologists because these turtles possess a temporal region largely enclosed by bone. There are no fenestrations, the emarginations are small, and the adductor chamber is almost entirely enclosed by dermocranial bones [26–29]. This contrasts with the condition found in many other turtles, whose skulls can show dramatic emarginations and are often more lightly built [29–32]. Historically, some authors considered the sea turtle phenotype to resemble or even represent the ancestral condition of Testudines [26,33–35]. However, early fossil turtle phenotype to resemble or even represent the ancestral condition of Testudines [26,33–35]. However, early fossil chelonoid?” taxon [25,26,36,37]” possesses skulls with an emarginated temporal region comparable to that of many extant non-chelonioid taxa. In addition, although the exact phylogenetic position of Chelonioida is still uncertain recent phylogenetic analyses nest chelonoidi within Cryptodira amongst clades of turtles with emarginated skulls [37–44]. Therefore, as proposed by Bouli [45], Goodrich ([46]: 273, [47]: 352–354), and others subsequently, the condition in sea turtles is secondary.
As the shapes of skull bones are highly influenced by loading from loads experienced during feeding (e.g. [48–56]), this raises questions as to whether the sea turtle skull with its enclosed temporal region is associated with a particular muscle architecture. Unfortunately, the cranial muscles of most sea turtles have not been fully surveyed, and previous descriptions are complicated by inconsistent homology or absence of detail (e.g. [57]).

Here, we describe the head and neck anatomy of Caretta caretta and Lepidochelys kempii. This will contribute to a better understanding of morphological diversity within the group, allow functional interpretation, and permit some evaluation of the muscle traits associated with an unfenestrated and almost non-emarginated skull.

Phylogenetic Background

The origin of turtles (total group Testudinata) and their phylogenetic relationship to other amniotes remains contentious (e.g. [42,58–60]). Although the detailed arrangement of individual bones differs, the enclosed temporal region of sea turtles is superficially comparable to that of many extinct non-amniotes and early reptiles. Consequently, turtles were commonly considered to represent a surviving lineage of early anapsids such as diadectids, captorhinids, Eutoiosaurus, pareiasaurs, or procolophonids (e.g. [61–69]). Although this interpretation is often labelled the “traditional” hypothesis (e.g. [59,70–74]), there are several examples of pre-cladistic and premolecular studies that instead argued in favour of a closer affinity between turtles and diapods based on morphological data (e.g. [45–47,75–79]).

Early cladistic studies placed turtles within anapsids close to or within captorhinids, pareiasaurs, or procolophonids (e.g. [80–82]). However, comparisons were largely restricted to Paleozoic taxa. Subsequent, more inclusive analyses recovered turtles within Diapsida, as a sister taxon of lepidosaurs (lizards, snakes, and tuatara) (e.g. [83–87]). Molecular analyses have also favoured an origin within Diapsida but repeatedly as the sister taxon of archosaurs (nDNA: [88,89]). Morphological evidence congruent with this hypothesis does exist but is rather meagre (e.g. [79,90–92]). Combined morphological-molecular studies to date, appear to mainly support an anapsid origin [70,73]. Evidence from embryological data suggests an origin from outside Sauria (Lepidosauria+Archosauria) [42]. Other recent morphological studies [58,93], which include a reexamination of the Palaeozoic reptile Eutoiosaurus [64,94], found renewed support for the anapsid origin of turtles. However, the most recent molecular analyses support an affinity with either lepidosaurs (mRNAs: [59]) or again archosaurs (nDNA: [60]).

As stated above, the precise phylogenetic position of Cheloniaidae within crown turtles (Testudines) remains uncertain [39–44]. A recent analysis by Joyce [40] based on morphological data found Cheloniaidae as the sister taxon to all other cryptodires (Fig. 1A), whereas Shaffer [41] using molecular evidence placed Cheloniaidae nested within cryptodires as the sister taxon to a clade that includes Chelidae and Kinosternidae (Fig. 1B).

Phylogenetic relationships within Cheloniaidae also remain unresolved [21,40,43,44,95–98]. For example, the results of recent phylogenetic analyses of Cheloniaidae disagree as to whether or not Chelonia mydas is the sister taxon of E. imbricata (Fig. 1 C, D) [23,40,43]. However, there is consensus that D. coriacea is the sister taxon to all remaining living sea turtles (Cheloniidae), as well as support for a grouping of C. caretta and L. kempii + L. olivacea [23,41,43,98,99] (Fig. 1 C, D), a clade referred to as Carettini [2,3,23]. Mitochondrial sequences suggest that C. caretta and L. kempii diverged from one another during the Miocene (10–20 Ma, [98,99]), a conclusion that agrees with previous inferences based on fossil data [3]. These two turtles are similar in their external morphology but the former tends to be much larger, possesses four inframarginal scales rather than three, lacks pores on these scales, and has maxillae that meet in the midline of the palate [7,29,40,100,101].

Ecological Background

The loggerhead turtle, C. caretta, is widely distributed and nests on a number of subtropical beaches along the coasts of the Mediterranean, eastern USA, Cape Verde Islands, Brazil, Africa, Oman, Japan, Australia, and various Caribbean islands [1,12,102–105]. It is a relatively large turtle with adults attaining carapace lengths of 85–124 cm and weights of 80–200 kg, although individuals described in historical reports greatly exceeded this [1,12]. Loggerheads mainly feed on sea pens, crabs, and mollusks, but there are proportional differences in diet according to ontogenetic age and the time of the year [1,25,106–110]. This is partly because juveniles tend to live in the open ocean whereas adults spend more time closer inshore where available food sources are different [25,104]. Bite force measurements are currently unavailable, but large adults clearly have powerful jaws [1,12], as, for example, Bystad [1] reports an individual biting through a clam shell 8 mm thick. Caretta caretta is important to marine-terrestrial food webs [1,12,102,111–114] as well as the tourist industry of both Greece and Florida [115]. Furthermore, it is of conservation concern [1,102,115].

The Kemp’s ridley, L. kempii, is less well known and is considered to be the rarest and most endangered sea turtle [1,6,12,116,117]. It nests on Atlantic beaches in Mexico and Texas but can be found far eastward into the Atlantic [12]. It is generally smaller than C. caretta, with adults having carapace lengths of 61–76 cm and weights of 36–46 kg [12]. As with C. caretta, juveniles of L. kempii tend to live in the open ocean whereas adults spend more time closer inshore [25,118]; they are thought to feed mainly on crustaceans (such as portunid crabs) and mollusks [12,25,100,107,119].

Institutional Abbreviations

LACM, Natural History Museum of Los Angeles County; LDUCZ, Grant Museum of Zoology, University College London, UK; UMZG, University Museum of Zoology, Cambridge, UK.

Results

General Head Anatomy and Osteology of the Cranium

The skull of Caretta caretta has been described by Carr [120], Gaffney [29], Kamezaki [101], and Arencibia et al. [57], whereas that of Lepidochelys kempii has been described by Hay [26], Carr [120], and Matzke [22]. A more general description of sea turtle skull morphology was provided by Wynken [8,100].

As in Chelonia mydas [121], both taxa show allometric variation in skull shape (particularly C. caretta, pers. obs. M.E.H.J.) but this
Sea Turtle Head and Neck Muscles
has yet to be fully surveyed. The variation makes it difficult to identify diagnostic skull shape differences between the two taxa that are size independent, especially because adult C. caretta are much larger than adult L. kempii, many published images lack scale bars or measurements (e.g. [8,101]), and geographic variation is not fully understood in these taxa. Nevertheless, the skull of an immature C. caretta does not entirely resemble a similar sized skull of L. kempii (Fig. 2A, B).

The skulls of both C. caretta and L. kempii are dome-shaped (Fig. 3), taper towards the rostrum and, compared to other Testudines, possess relatively small ventrolateral and posteroventral emarginations (Figs. 2A, B; [8,26,29,101,120,122]). In C. caretta, the temporal region (posterior portion of the cranium) is relatively large compared to the snout region (Figs. 2A, C, E) and the difference becomes greater with size (specimens LDUCZ x 11; UMZC R 4606; Video S1, S2; Table 1, [8,29]). In both taxa, the rostral tip of the skull is formed by a pair of premaxillae that lack any kind of dorso medial projection so that the nares are confluent (Figs. 2E, F). The maxilla has a well-defined facial process and a deep suborbital margin (Figs. 2A, B). As in all extant turtles, the lacrimal is absent [29]. The jugal lies at the posteroventral corner of the orbit and connects to the quadratojugal posteriorly and the postorbital dorsally (Figs. 2A, B). In both taxa, the posteroventral corner of the jugal occasionally bears a caudal spur (e.g. [8]: fig. 40), the size of which can vary between left and right sides (e.g. specimen M009/08, Table 2). In small specimens of C. caretta contact between the postorbital and quadratojugal in lateral view is almost excluded by the jugal and squamosal (e.g. XT757/07; LDUCZ x 1183; Figs. 2A). This is probably due to ontogenetic variation because contact is obvious in larger skulls (e.g. LDUCZ x 11; UMZC R 4606; [120]). The quadrate is located posterior to the quadratojugal, with its concave lateral surface forming the majority of the cavum tympanicum (Figs. 2B, E; [123]), which is associated with the auditory apparatus. Posteroventrally, the quadrate is rugose, particularly in large skulls (e.g. UMZC R 4606). The ventral end of the quadrate bears a relatively shallow condyle formed from cartilage. The two lobes are almost symmetrical but the slightly smaller lateral lobe projects more ventrally (Figs. 4A, B; XT161/08).

The squamosal is situated on top of the quadrate and quadratojugal and bears a lateral depression on its posterolateral corner (Figs. 2A, B; LDUCZ x 11); in similar-sized skulls of C. caretta and L. kempii, it is better defined in the latter species (Fig. 2B). The skull roof comprises paired parietals, frontals, and prefrontals of which the parietals form the largest component (Figs. 2E, F; [8,26,59,29]). In the smallest specimen of C. caretta the external junction between the frontals, prefrontal, and postorbital is very close to the orbital margin (XT757/07; Fig. 2E). In larger specimens the junction occurs more medially so that the frontals are fully excluded from the border of the orbit by the prefrontal and postfrontal (e.g. LDUCZ x 1183; LDUCZ x 11; UMZC R 4606; UMZC R 4609). This character does not generally occur in L. kempii, L. olivacea, Ch. mydas, or Eretmochelys imbricata (Fig. 2F; [8,22,26,120]) but it is present in one specimen thought to represent a species of Lepidochelys (LDUCZ x 34). Large specimens of C. caretta possess a prominent spine extending from the posterior edge of the squamosal (e.g. LDUCZ x 11; UMZC R 4606). In C. caretta and L. kempii, the squamosals meet the parietals and, medial to this, the supraoccipital projects posteriorly to form the crista supraoccipitale (Figs. 2A, B, E) but it is relatively larger in L. kempii (Figs. 2B, F). Within the adductor chamber the medial process of the quadrate and lateral process of the prootic meet to form the processus trochlearis otici.

The palatal arrangement is similar in both species, but in C. caretta the maxillae meet along the ventral midline, whereas in L. kempii and other chelonioids the vomers and premaxillae separate them (Figs. 2C, D; UMZC R 4606; [6,8,22,26,29,100,120,124,125]). In both taxa, the palate is reinforced by a central pillar between the

![Figure 2. The skulls of two sea turtles. (A, C, E, G, I, and J) Caretta caretta (XT757/07) and (B, D, F, H, K, and L) Lepidochelys kempii (M009/08). The cranium in (A and B) lateral, (C and D) palatal, and (E and F) dorsal views. The lower jaws and hyoid system in (G and H) in dorsal view. The left lower jaw in (I and K) lateral and (J and L) medial view. add. fos, adductor fossa, add.cha, adductor chamber, ANG, angular; ART, articular; ARY, arytaen; BO, basioccipital; BS, basioccipital or sphenoid; cav.tym, cavum tympanicum; CB1, cornu branchial-I; CB2, cornu branchial-II; CHL, cornu hyale; COH, corpus hyoidei; COR, coronal bone; cr.sup, crista suraopaccipitale; DEN, dentary; dep, depression; EX, exoccipital; Fon, fontanelle; FR, frontal; JUG, jugal; MX, maxilla; OP, opisthognathic; orb, orbit; PAR, parietal; pit, pits; PMX, premaxilla; PORB, postorbital; post.dors.em, postero dorsal emargination; PRA, prearticular; PRFR, prefrontal; PT, pterygoid; PAL, palatine; add.cha, adductor chamber; nar, narial opening; QJ, quadratojugal; QU, quadrate; se, suture seam; she, shelf; SQ, squamosal; ST, staples (columella); sul.mec, sulcus Meckeli; SUP, supraoccipital; SUR, surangular; sym, symphysis; tub, tubercle; vent.lat.em, ventrolateral emargination; VO, vomer. Scale bars = 10 mm. doi:10.1371/journal.pone.0047852.g002]

![Figure 3. Micro-CT slices of the sea turtle Lepidochelys kempii (M009/08) showing muscle structures. (A) coronal slice 520 of 980 and (B) parasagittal slice 193 of 675. apo.cno, coronar aponeurosis; CB1, cornu branchial-I; CB2, cornu branchial-II; MX, maxilla; mus, muscular structures; PAR, parietal; PORB, postorbital; PT, pterygoid; QJ, quadratojugal; QU, quadrate; SUR, surangular. Scale bars = 10 mm. doi:10.1371/journal.pone.0047852.g003]
The heads of both *C. caretta* and *L. kempii* are covered by scales composed of thickened epidermis and keratin [100,101]. Moreover, the upper jaw + palate and the lower jaw are covered by keratinous rhamphotheca which have narrow cutting edges and wider surfaces for crushing [8,100]. In both taxa, the shape of the upper rhamphotheca is related to the shape of underlying bones. Thus, in lateral view the ventral margin of the rhamphotheca is more sigmoid in *L. kempii* than it is in *C. caretta.*

The hyoid apparatus supports the tongue, pharynx, and floor of the mouth [126,127]. Its skeletal component comprises a somewhat pentagonal corpus ossis hyoidei located in the throat between the two lower jaws (Fig. 2H) [8]. Along the postero-lateral margins are three tubercles (or horns) and, anterior to posterior, these attach to the cornu hyale, cornu branchial-I, and cornu branchial-II (Figs. 2H, 3A). The latter are particularly well-developed and extend posterodorsally around the throat to a point level with the posterior tip of the quadrate.

**Osteology of the Neck**

Within living Testudines, two distinct mechanisms retract and move the neck/head region: the cryptodire condition, where the neck is moved and folded in a vertical plane, and the pleurodira condition, where the neck is moved and folded in a horizontal plane [128–130]. Sea turtles are cryptodires, but they have lost the ability to retract their necks [101,131]. Previous descriptions of cryptodire neck vertebrae include those by Williams [132], Hofstetter and Gasc [131], Gaffney [133], Meylan and Gaffney [134], and Herrel *et al.* [130]. Testudines have 18 presacral vertebrae of which eight are cervicals [128,131]. As in most cryptodire turtles, the atlas and axis of sea turtles are not fused and are connected by a ball and socket joint [128]. Vertebra 2 and 3 are opisthocoelous and 4 is biconvex, whereas 5 to 8 are procoelous [131,134]. The neural spines and transverse processes are relatively short but conspicuous keels project from the ventral surfaces of the centra (e.g. M009/08) [131,132].

The atlas is notably different from other neck vertebrae. That of *L. kempii* (M009/08) has a relatively wide neural arch from which two processes extend postero-laterally over the prezygapophyses of the axis. The atlas centrum and neural arch are anteroposteriorly short (M009/08; Fig. 5). The anterior cotyle appears almost hexagonal in its anterior aspect, whereas the posterior condyle is dorsoventrally compressed and about one third wider than tall. The atlas neural canal is triangular rather than ovoid, as it is in vertebrae 2–5 (Fig. 5). The associated first intercentrum is well-developed and possesses an obvious ventral keel. The axis, third and fourth vertebrae are similar in possessing pre- and postzygapophyses orientated almost parallel to the horizontal plane (M009/08). The third and fourth vertebrae are larger than the axis and have better developed ventral keels anteriorly (Fig. 5). The axis neural spine is not particularly tall but it projects anteriorly and is of equivalent build to the axis ventral keel (Fig. 5). The fourth vertebra is bicondylar (M009/08). The transverse processes are short and oval or sigmoid in cross-section. On the atlas, axis, and third vertebra, small paired processes can be seen to extend...
posterolaterally from the midline of the posteroventral edge of the centra (Fig. 5). These have previously been termed "intervertebral nodules" [131] and interpreted as the capitular part of vestigial ribs [135]. However, we suggest that their location is more congruent with them representing vestigial intercentra. The neck of *C. caretta* is

| Table 2. Specimens dissected or CT scanned. Measurements taken correspond to those listed in Wyneken [8] as far as possible. |
|---|
| Ref no. | Specimen no. | Taxon | Sex | Skull length | Neck Circumference | Straight overall length (SOL) | Linear shell length (SCL) | Straight carapace width (SCW) | Weight | Origin |
| T2007/06 | XT757/07 | *C. caretta* | ? | 50 | 165 | 270 | 190 | 190 | 1.426 | Tywyn, Gwynedd, Wales |
| T2008/10 | XT144/08 | *C. caretta* | M | 57 | 155 | 330 | 250 | 220 | 1.994 | Cae Du, Gwynedd, Wales |
| T2008/13 | XT162/08 | *C. caretta* | F | 110 | 260 | 590 | 440 | 400 | 11.4 | Black Rock Sands, Gwynedd, Wales |
| T2008/2 | XT043/08 | *L. kempii* | M | 48 | 150 | 255 | 195 | 180 | 1.185 | Porth Ceiriad, Gwynedd, Wales |
| T2008/17 | M009/08 | *L. kempii* | F? | 58 | 160 | 320 | 240 | 210 | 1.8 | Berbencula, Western Isles, Scotland |

All measurements except skull length were taken by the Cetacean Strandings Investigation Programme (CSIP), UK. The prefixes XT and M denote whether the postmortem was carried out by the Institute of Zoology, London, UK, or the Animal Health and Veterinary Laboratories Agency, Truro, UK, respectively. Skull length is measured along the midline from the rostrum parallel to a point level with the back of the quadrate condyle. Units in mm or kg. doi:10.1371/journal.pone.0047852.t002
very similar to that of *L. kempii*, but the neural spine of the axis is relatively more pronounced (XT757/07).

**Cranium-Associated Musculature and other Soft Tissue of the Head**

Previous descriptions of the feeding related musculature of sea turtles include those of *C. caretta* [136,137], *Ch. mydas* [138,139], *Demochelys coriacea* [140–142], and *E. imbricata* [76]. However, our understanding of turtle muscle homologies and nomenclature has progressed since this work was done [143]. Moreover, no jaw muscle descriptions of *Lepidochelys kempii* or *Natator depressus* are known to the authors, and only a few aspects of this anatomy in *L. olivacea* have been reported ([144]: 12). For a recent review of previous work, terminology, and muscle synonymies, see Werneburg [143].

Here we follow the system proposed by Werneburg [143] (Table 3), where all cranium-associated muscles of turtles are grouped based on a variety of homology criteria and are given a numerical label (between No. 1 and No. 88. As in Werneburg [143], for anatomical consistency, a ‘muscular unit’ (= a muscle *sensu stricto*, s.s., or a muscular portion s.s.) is defined according to possession of its own origin, course, and insertion site. In contrast to muscles s.s., however, muscular portions s.s. show some intercrossing fibres along their course. Muscular units may be partly subdivided into muscle heads. Muscle heads have their own origination or insertion site, but in their course they fuse with other muscle heads to form the discrete belly of a single muscular unit [143]. We do not describe the muscular units related to the nose or eyes (No. 1 to 16, 34–38), blood vessels (No. 48), larynx (No. 49–51), or anterior parts of the tongue (No. 63–74). The following muscular units are not present in either *C. caretta* or *L. kempii*: No. 18, 20, 22 (but see description of No. 21c), 24, 27 (but see description of No. 26), 30, 32–33, 39, 40, 44, 54, 56, 59, 61–62, 76, 79, and 84–85.

In the following account, the anatomy of *C. caretta* is usually described first followed by the differences found in *L. kempii* where present.

**Ligamentum Quadratomaxillare**

Although this structure in turtles is referred to as the “ligamentum quadratomaxillare” (e.g. [76,143]) it can involve contact with the jugal rather than the maxilla. After removal of the temporal scale, in both *C. caretta* and *L. kempii* this large ligament is visible between the jugal and the jaw joint (quadrotojugal/quadrate) below the shallow ventrolateral emargination (Figs. 6A–D). As in other turtles, a fascia is present (Fig. 6B; fascia temporalis carapacobasioccipitalis of Werneburg [143]) between the ventral margin of the skull and the medial surface of the ligament.

**The Coronar Aponeurosis**

The coronar aponeurosis (*sensu* Iordansky [145] = Bodenaponeurose *sensu* Lakjer [76] = bodenaponeurosis *sensu* Rieppel, [146] = external tendon e.g. *sensu* Schumacher [126]; see Werneburg [143] for further synonyms) a large aponeurosis to which some of the external adductor muscles insert. It has previously been described as attaching to the dorsal, medial, and/or lateral face of the coronoid, dentary, and surangular [136,137,143,145]. It attaches directly and broadly to the coronoid in *C. caretta* and extends posterodorsally into the adductor chamber passing over the processus trochlearis otici (Figs. 3B, 6E).

A cross-section through the left aponeurosis in specimen XT161/08 measured 13 mm wide by 9 mm tall. The aponeurosis in *L. kempii* follows a similar path (M009/08). Direct examination and

| Number | Muscular unit |
|--------|---------------|
| 17     | m. adductor mandibulæ externus Pars medialis |
| 19     | m. adductor mandibulæ externus Pars profundus |
| 21     | m. adductor mandibulæ externus Pars superficialis |
| 23     | m. adductor mandibulæ internus Pars pseudotemporalis principalis |
| 24     | m. adductor mandibulæ internus Pars pseudotemporalis superficialis |
| 25     | m. adductor mandibulæ internus Pars intramandibularis |
| 27     | m. adductor mandibulæ internus Pars pterygoideus posterior |
| 28     | m. adductor mandibulæ internus Pars pterygoideus ventralis |
| 29     | m. adductor mandibulæ posterior Pars principalis |
| 31     | m. intermandibularis |
| 41     | m. constrictor colli Pars spinalis |
| 42     | m. constrictor colli Pars intermandibularis |
| 43     | m. constrictor colli Pars oralis |
| 45     | m. depressor mandibulæ |
| 46     | m. dilatator tubae |
| 47     | m. branchiomanubialis visceralis |
| 52     | m. plastrocapitis |
| 53     | m. squamosobranchiale |
| 55     | m. branchiohyoideus |
| 57     | m. collosquamosus |
| 58+60  | m. coracohyoideus |
| 75     | m. atlantoeipistropheooccipitis |
| 77     | m. atlantoccipitis |
| 78     | m. atlantoepistropheooccipitis |
| 80     | m. collooccipitalis |
| 81     | m. testocapitis |
| 82     | m. testocapitis |
| 83     | m. transversalis cervicis |
| 86+87  | m. longus colli Partes capitis-I et Pars capitis-II/III |
| 88     | m. retrahens capiti collique Pars carapacobasioccipitalis |

doi:10.1371/journal.pone.0047852.t003

**Figure 5. The first four neck vertebrae of the sea turtle *Lepidochelys kempii* segmented from the micro-CT scan of specimen M009/08.** ant, anterior; AT, atlas; AX, axis; ce, centrum; cond, condyle; cot, cotyle; dors, dorsal view; ivn, intervertebral nodule; keel, keel; lat, lateral view; nu.arc, neural arch; nu.ca, neural canal; nu.sp, neural spine; post, posterior view; pozyg, postzygapophysis; prezyg, prezygapophysis; t.pr, transverse process; V3, third vertebra; V4, fourth vertebra; ven, ventral view. Scale bar = 10 mm. doi:10.1371/journal.pone.0047852.g005
removal of the surrounding muscles reveals the aponeurosis to be broadly trapezoidal in medial view with the anteroventral corner inserting onto the coronoid (Fig. 6E; XT161/08). In lateral view, a thin, strap-like sheet extends laterally from the posterolateral
surface and a triangular fold near the base. This fold is less obvious in *L. kempii*.

**M. Adductor Mandibulae Externus (No. 17–21)**

The m. adductor mandibulae externus (No. 17–21, see Table 3) is innervated by n. trigeminus (cranial nerve V) and is located between the maxillary (V2) and mandibular (V3) branches of n. trigeminus [76,126,143]. At its origin, it includes muscular units referred to as Pars medialis (No. 17), profundus (No. 19) et superficialis (No. 21).

The m. adductor mandibulae externus Pars medialis (No. 17), was previously figured by Schumacher [137]; table 7/2 as the “m. adductor mandibulae externus portio medialis” [for synonyms see [143]]. In accordance with this previous work, our specimens show that this muscular unit is relatively small and belt-shaped (Figs. 7A, B). It originates from the lateral half of the anteroventral face of the quadrate, exactly above the ventrolateral condyle of the quadrate, passes anteriorly, and inserts by a mixture of direct fibres and tendinous structures into the posterodorsal edge of the surangular. This muscular unit is similar in both *C. caretta* and *L. kempii* (Fig. 8A) but in the latter taxon Pars medialis (No. 17) is not as clearly separated from Pars superficialis (No.21) and some fibres also insert onto the medial face of the surangular.

According to Schumacher [126], the m. adductor mandibulae externus Pars profundus (No. 19) is usually the largest part of the m. adductor mandibulae externus complex (No. 17–19) in turtles. In *C. caretta*, Schumacher [137] described the Pars profundus as originating from the crista supraocipitalis, the lateral face of the supraocipital, and the lateral face of the processus descendens parietalis, and reaching caudally over the Pars medialis (No. 17) and the caudal end of the supraocipital. Similarly, Poglayen-Neuwall [136] reported that the Pars profundus originates from the lateral face and the dorsal edge of the parietal and supraocipital, and the edge of the temporal emargination. The Pars profundus (No. 19) reportedly inserts on the dorsal and ventral faces inside a groove formed by the main body of the coronar aponeurosis and a medial fold [136]. In our specimens, this muscular unit is the largest portion of the m. adductor mandibulae externus complex (No. 17–19) and dominates the medial half of the adductor chamber (Fig. 7). We found the Pars profundus (No. 19) to originate on the lateral face of the crista supraocipitalis and the posterior part of processus descendens parietalis. The muscle passes anteroventrally and inserts on the dorsal and ventral faces of the coronar aponeurosis involving two heads (19a and 19b) partially divided by a slip of soft tissue (XT161/08). The medial head (No. 19a) originates from the parietal and crista supraocipitalis and inserts on the ventromedial part of the coronar aponeurosis. The lateral head is smaller (No. 19b). It originates from the back of the adductor chamber (parietal and supraocipital) and inserts on the dorsomedial surface of the coronar aponeurosis. In *L. kempii* (Figs. 7 and 8) the muscular unit is undivided and insertion occurs on the medial surface of coronar aponeurosis.

The m. adductor mandibulae externus Pars superficialis (No. 21) represents the third unit of m. adductor mandibulae externus (No. 17–21). Pars superficialis lies in the lateral area of the postorbital adductor cavity, partially covering the Pars medialis (No. 17) caudally, but previous descriptions of its origin and insertion in *C. caretta* conflict.

As described by Schumacher [126], the fibres originate from the parietal in *C. caretta* and attach to the dorsal or lateral surface of the coronar aponeurosis. Other descriptions (e.g. Schumacher [137]) indicate the origin as being from the lateral temporal face of the parietal, the caudal end of the postorbital, the medial face of the squamosal, the dorsal face of the quadrate, and the dorsal part of quadrat jugal. A small part is also sometimes considered to originate from the dorsal area of the jugal (Schumacher [137]). Alternatively, Poglayen-Neuwall [136] documented that the origin comprised the rostromedial face of the quadrate, the temporal fascia, and the medial face of the quadrat jugal and the jugal. In addition, rostral fibres are said to originate from the posteroomedial face of the postorbital and rostral part of the squamosal. The insertion has been described as on the lateral edge of the coronar aponeurosis with more superficial fibres attaching directly to the dorsolateral surface of the surangular and the coronoid of the lower jaw (Schumacher [137]). Alternatively, the muscle is reported to insert directly on the dorsolateral surface of the mandible (surangular and coronoid) with some deep fibres inserting on the lateral face of the coronar aponeurosis (Poglayen-Neuwall [136]).

Our observations do not precisely match previous descriptions. In *C. caretta*, the m. adductor mandibulae externus Pars superficialis (No. 21) was found to originate by three distinct heads within the lateral part of the adductor chamber (Fig. 7A). One head (No. 21a) originates from the anterior face of the quadrate (Fig. 7B). A second head (No. 21b) originates from the posterior edge and the postero dorsal surface of the squamosal (Fig 7A), with some fibres arising laterally from the posterior face of the opisthonic (XT161/08). A third head (No. 21c) is lateral to the others and narrow in the parasagittal plane (Fig. 7A). The third head originates from the medial surface of four temporal bones: the anterior part of the quadrat jugal, the anterior part of the squamosal, the ventral part of the postorbital, and the posterior part of the jugal (XT161/08). The longest fibres originate slightly above the dorsalmost point of the cavum tympanicum (XT144/08). The first (No. 21a) and second (No. 21b) heads converge anteriorly beyond the processus troclearis otici. Dorsal fibres of No. 21a+b insert onto the dorsal surface of the coronar aponeurosis as well as dorsal to a lateral fold. Ventral fibres of No. 21a+b insert into the ventrolateral face of the coronar aponeurosis as well as the lateral fold (7A). Dorsolateral to the processus coronoides, the anterior half of the third muscle head (No. 21c) fuses medially with the other heads (No. 21a+b). These fibres insert into the coronar aponeurosis at the base of its attachment to the jaw. In *C. caretta* the remainder of the third muscle head (No. 21c) inserting into a broad aponeurosis that is closely apposed to the lateral surface of the lower jaw (surangular) but wraps ventrally to insert on the ventrolateral edge of the dentary and angular (Fig. 9E).

The arrangement in *L. kempii* (XT043/08) is slightly different. The medial portions (No. 21a, b) originate from the prootic and opisthonic, but not from the parietal, with the second head (No. 21b) having a relatively larger area of origin posteriorly. The lateral fold in the coronar aponeurosis (to which No. 21a+b insert) is also less obvious (Fig. 7E, F). Moreover, the lateral head (No. 21c) originates slightly higher on the postorbital and additionally from the squamosal (Fig. 2D, G, and 9C). Also the attachment does not reach as far ventrally as it does in *C. caretta*, so that its edge partly coincides with the prominent lateral shelf on the surangular (Fig. 8A, B; see also Video S3).

**M. Adductor Mandibulae Internus (No. 23–28)**

The m. adductor mandibularis internus (No. 23–28) is innervated by n. trigeminus (V) and is located between its ophthalmic (V1) and maxillary branches (V2). In the species described here, it includes the Pars pseudotemporalis principalis (No. 23), Pars intramandibularis (No. 25), and two Partes pterygoidei (No. 26, 28) [143].
Figure 7. The superficial adductor musculature in two sea turtles. (A and B) Caretta caretta (XT161/08) and (C to G) Lepidochelys kempii (XT043/08). (A) lateral view of the head following removal of the skull roof and lateral skull wall. The adductor chamber in (B) anterolateral view, (C) dorsolateral view, (D) posterolateral view, (E) dorsolateral view with external adductors folded forwards to show the processus trochlearis otici, (F) posterodorsal view, (G) anterior view. 17, m. adductor mandibulae externus Pars medialis; 19, m. adductor mandibulae externus Pars profundus; 21a,
According to Schumacher [126], the “pseudotemporalis muscle” is divided into two units in C. caretta, the Pars pseudotemporalis principalis (No. 23) and the Pars pseudotemporalis superficialis (No. 24). The former is said to arise from the ventrolateral surface of the parietal and to converge on a tendon which inserts onto the lower jaw postero-medial to the adductor chamber. Postero-dorsal to the origin site of Pars superficialis principalis (No. 23), the superficial unit (No. 24) arises from the dorsolateral surface of the processus descendens parietalis. The superficial unit converges on the Zwischensehne (sensa [136]), a tendon that connects it with the m. intramandibularis (No. 25). In our specimens of C. caretta, Pars pseudotemporalis (No. 23) is divided into two portions. Most fibres of this muscular unit originate from the lateral face of the processus descendens parietalis (Figs. 7B, and 8D), but some additional fibres arise from the roof of the adductor chamber (horizontal part of the parietal). All fibres converge into the Zwischensehne (Fig. 10A). In L. kempii, the anatomy of the Pars pseudotemporalis (No. 23) is similar (Figs. 7F, G, and 8D) but the more dorsally originating muscle fibres are apparently absent and the muscle inserts into a bifurcating Zwischensehne by two separate heads (Fig. 10 F, G).

As described by Poglayen-Neuwall [136] and Schumacher [137], the m. adductor mandibulae internus Pars intramandibularis (No. 25) in C. caretta originates from the ventral end of the Zwischensehne enters the adductor fossa and inserts into the sulcus Meckeli of the lower jaw. A section through the lower jaw confirms the presence of this muscle in C. caretta (XT144/08). The same muscle arrangement is also present in L. kempii (XT043/08) (Fig. 10 F, G).

In C. caretta, the m. adductor mandibulae internus Pars pterygoideus dorsalis (No. 26) originates from the dorsal surface of the palate (posterior half of the palate and the dorsal surface of the pterygoideal) and from the interorbital septum ventrolaterally, and some fibres may derive from the processus descendens parietalis. The posteriormost fibres may be homologous with the m. adductor mandibulae internus Pars pterygoideus posterior (No. 27). After it passes over the posterior edge of the palate, the muscular unit inserts on the medial face of the prearticular by a tendinous sheet that is continuous posteriorly with the tendinous sheet of the Pars pterygoideus ventralis (No. 28) (Fig. 10B). Some fibres also insert into the articular and jaw joint capsule. This is broadly similar to previous descriptions ([137]: table VII/3a; [126]). In L. kempii, the absence of the internus Pars pterygoideus posterior (No. 27) is more certain. The Pars pterygoideus dorsalis (No. 26) originates from a smaller area (not including the processus descendens parietalis) (Fig. 8E, and 9A) and inserts via the subarticular aponeurosis into the prearticular on the medial face of the lower jaw (Fig. 8). The Pars pterygoideus ventralis (No. 28) was described and figured by Schumacher ([137]: table VII/3b) as originating from the ventral and mediallymost edges of the pterygoideal so that the contralateral portions of No. 28 meet at the palatal midline, separated by a median raphe. In our specimen of C. caretta, this unit is composed of two muscle heads that are separated superficially but merge at their origin and insertion sites. The larger and more medial head (No. 28a) originates from the posteroventral edge of the palate and the complete ventral surface of the pterygoideal (Fig. 10A, B). As previously described, the contralateral muscle heads (No. 28a) are separated by a midline raphe (Fig. 10A, B). Each head passes ventrolaterally, becoming thinner and inserting into the same tendinous sheet as the Pars pterygoideus dorsalis (No. 26) (Fig. 10B), giving it (No. 28a) a superficially fan-shaped tendinous appearance in ventral view ("Schenspiegel" of Schumacher [137]). This tendinous sheet, as well as the deeper muscle fibres, inserts into the medial surface of the prearticular and articular. To reach this position, it passes posteriorly beneath a wide tendon associated with insertion of the m. depressor mandibulae (No. 45). As in the rhynchocephalian lepidosaur Sphenodon punctatus [147], some of the posteriormost fibres of the pterygoideal muscle complex insert behind the jaw joint (Fig. 10C; contra Schumacher [137]). The smaller muscle head (No. 28b) originates anteriorly from the lateral edge of the pterygoideal (Fig. 10A, B). Its fibres pass ventrally, along a fold extending from the tendinous sheet of No. 26 and No. 28a, and have an entirely fleshy insertion into the medial surface of the prearticular ventral to No. 26a and No. 28a (Fig. 9G and 10B).

In L. kempii (XT043/08), the Schenspiegel is not as clear and the fleshy insertion of the smaller head (28b) does not extend as ventrally (Fig. 9F and 10 E).

**M. Adductor Mandibulae Posterior Pars Principalis (No. 29)**

This muscular unit is innervated by n. trigeminus (V) and is located posterior to the mandibular branch (V₃). However, it may not be homologous with the m. adductor mandibulae posterior of some other reptiles because of apparently different developmental origins [143,146].

The adductor mandibulae posterior pars principalis (No. 29) has been described as having two heads of origin in C. caretta [126,137], with the site of origin of the anterior head reaching dorsally to the posterior border of the processus descendens parietalis [126,137]. In contrast, this unit (No. 29) originates directly from the anteromedial face of the quadrate in our specimens of C. caretta, below the processus trochlearis otici and from the complete anterior face of the prootic (Fig. 7B). It extends anteroventrally and inserts on the medial surface of the prearticular – anterior to the joint surface and dorsal to the insertion of the Partes pterygoidei (No. 26, 28) (Fig. 9G). According to Schumacher [126], some fibres would also attach to cartilago Meckeli in C. caretta, but we could not confirm this. In L. kempii, the origin is restricted to the anteromedial aspect of the quadrate, with insertion also taking place on the anterior edge of the articular. In medial view it has a tendinous appearance ventrally (Fig. 10G).

**M. Intermandibularis (No. 31)**

This muscle is innervated by n. trigeminus (V) and connects the ventral aspects of the lower jaws [143]. Together with m. constrictor colli (No. 41, 42, 43), m. intermandibularis represents a part of the throat musculature. Its anterior fibres reach the ventral edge of the symphysis. Posteriorly it is continuous with the anterior part of the m. constrictor colli Pars intermandibularis (No. 42, see below).
Figure 8. Jaw muscle arrangement in the sea turtle *Lepidochelys kempii* (M009/08) based on reconstructions from micro-CT data. Shown with (A) parts of the right side of the skull absent, (B) part of the m. adductor mandibulae externus Pars superficialis (No 21c) absent, (C) all of the m. adductor mandibulae externus Pars superficialis (No 21abc) and m. depressor mandibulae (No. 45) absent, (D) all of the m. adductor mandibulae externus and m. depressor mandibulae (No. 45) absent, (E) only the m. adductor mandibulae internus Partes pterygoidei (No. 26, 28) and (F) all muscle absent. 17, m. adductor mandibulae externus Pars medialis; 19, m. adductor mandibulae externus Pars profundus; 21a, m. adductor mandibulae externus Pars superficialis, medial head; 21b, m. adductor mandibulae externus Pars superficialis, posterior head; 21c, m. adductor mandibulae externus Pars superficialis, lateral head; 23, m. adductor mandibulae externus Pars pseudotemporalis; 26, m. adductor mandibulae internus Pars pterygoideus dorsalis; 29, m. adductor mandibulae posterior Pars principalis; 45, m. depressor mandibulae; apo.cno, coronar
Figure 9. The origin and insertions of jaw muscles in two sea turtles illustrated using computer models based on micro-CT data. (A–D and F) L. kempii (M009/08) and (E and G) C. caretta (XT757/07). (A) dorsolateral and (B) lateral view of the cranium with the temporal region removed. (C) medial view of the temporal region of the left cranium. (D) and (E): lateral views of the left lower jaw. (F) and (G) medial views of the left lower jaw. 17, m. adductor mandibulae externus Pars medialis; 19, m. adductor mandibulae externus Pars profundus; 21a, m. adductor mandibulae externus Pars superficialis medial head; 21b, m. adductor mandibulae externus Pars superficialis posterior head; 21c, m. adductor mandibulae externus Pars superficialis lateral head; 23, m. adductor mandibulae internus Pars pterygoideus dorsalis; 28a, m. adductor mandibulae internus Pars pterygoideus large medial head; 28b, m. adductor mandibulae internus Pars pterygoideus small lateral head; 29, m. adductor mandibulae posterior Pars principalis; 45a, m. depressor mandibulae lateral part; 45b, m. depressor mandibulae medial part; 46, m. dilator tubae; 47a, m. branchiomandibularis visceralis small posterior head; 47b, m. branchiomandibularis visceralis large medial head; 75, m. atlantoepistropheooccipitis. Scale bars = 10 mm.
Figure 10. The internal adductor musculature of two sea turtles. (A–D) Caretta caretta (XT161/08), and (E–G) Lepidochelys kempii (XT043/08). (A) ventrolateral view of the left side adductor mandibulae internus, (B) ventral view of the right side internal adductors, (C) close up of the right side m. adductor mandibulae internus Pars pterygoideus ventralis, (D) posterior view of the internal adductors and hypaxial muscles, (E) ventral view of the right side of the palate, (F) medial view of the right lower jaw, (G) medial view of the right lower jaw after further dissection of the m. adductor mandibulae internus Pars pterygoideus. 19, m. adductor mandibulae externus Pars profundus; 21, m. adductor mandibulae externus Pars superficialis lateral head; 25, m. intramandibularis; 26, m. adductor mandibulae internus Pars pterygoideus ventralis; 28a, m. adductor mandibulae internus Pars pterygoideus large medial head; 28b, m. adductor mandibulae internus Pars pterygoideus small lateral head; 45a, m. depressor mandibulae lateral part; 45b, m. depressormandibulae medial part; 46, m. dilator tubae; 86, m. longus colli Partes capitis-I et Pars capitis-III; 87, m. longus colli Partes capitis-I et Pars capitis-II; 88, m. retrahens capiti collique Pars carapaco-basioccipitalis. ANG, angular; apo.cno, coronar aponeurosis; DEN, dentary; low.jaw, lower jaw; PRA, prearticular; QU, quadrate; rha.low, lower rhamphotheca; rha.upp, upper rhamphotheca; raphe, raphe; eus.tub, eustachian tube; zwi, Zwischensehne. Scale bars = 10 mm.
doi:10.1371/journal.pone.0047852.g010
M. Constrictor Colli (No. 41–43)

In contrast to m. intermandibularis (No. 31), the m. constrictor colli complex (No. 41, 42, 43) is innervated by n. facialis (VII). The intermandibular unit of m. constrictor colli (No. 42) lies between the posteroverentral edges of the lower jaws and continues anteriorly to m. intermandibularis (No. 31) in both species. A median raphe is visible. The m. constrictor colli Pars spinalis (No. 41) originates from the lateral aspects of the anterior cervical vertebrae and wraps beneath the throat where it inserts into a median raphe. The m. constrictor colli Pars oralis (No. 43) originates from a midline raphe on the dorsal edge of the neck, passes ventral, and inserts into a ventral median raphe. In C. caretta, the Pars intermandibularis (No. 42) and Pars oralis (No. 43) are separated ventrally, whereas in L. kempis they are completely continuous (Fig. 11A). Below the hyoid apparatus, in both species, some fibres of Pars oralis (No. 43) appear to attach to the ventral side of cornubranchial-I. Posteriorly, Pars oralis (No. 43) forms a continuous structure with the Pars spinalis (No. 41) in L. kempis, whereas only a few fibres connect these structures (No. 41, 43) in C. caretta.

M. Depressor Mandibulae (No. 45)

The m. depressor mandibulae (No. 45) is a large fleshy muscle located at the posterolateral corner of the skull and is innervated by n. facialis (VII) ([126,143] and [141]; table II/1-2) described the muscle as originating on the posterolateral face of the squamosal and the posterior process of the quadrate with a tendinous insertion onto the retroarticular process, as well as onto the ventral and lateral faces of the articular and its posteroverentral tip.

The muscle is composed of lateral (No. 45a) and medial (No. 45b) parts divided by an internal tendinous division but both components merge prior to their insertion (Fig. 10D). The lateral part (No. 45a) originates from behind the cavum tympanicum on the posterolateral surface of the squamosal within a large ventrolateral depression, which has an obvious dorsal boundary, but shorter and deeper fibres also originate laterally from the posteroverentral surface of the quadrate (Figs. 7A, 12B). The medial part (No. 45b) originates primarily from a depression in the posterior surface of the squamosal (Fig. 7A, 12B). The muscle parts converge approximately two thirds along the length of the complete muscle. The whole muscle inserts on the posterolateral corner of the short retroarticular process. The most medial region has a superficial tenden at the point of insertion that is continuous with that of the m. dilator tubae (No. 46) (Fig. 10D). The shape of the muscle is similar in both species, but in L. kempsi the lateral part (No. 45a) also originates from the ventral and lateral faces of the squamosal (Video S3) and has a tendinous attachment in its lateralmost region.

M. dilatator Tubae (No. 46)

This muscle is innervated by n. facialis (VII) and has a close association with the m. depressor mandibulae (No. 45; [53,143,148]). The thin muscle originates by connective tissue from the edge of the quadrate just behind the eustachian tube and passes ventrally (Fig. 10D). Its mid point is connected anterolaterally to the posterior lining of the eustachian tube. Posterior to the articular, the muscle separates into two heads. The posterior head (No. 46a) inserts in the posteroventral tip of the prearticular, anterior to the medial part of the m. depressor mandibulae (No. 45). The anterior head (No. 46b) has a tendinous component and overlaps Pars pterygoideus ventralis (No. 28) of the internal adductor and inserts into the medial face of the prearticular, posteroverentral to the insertion of the Pars pterygoideus dorsalis (No. 26) (Fig. 9G).

M. branchiomandibularis Visceralis (No. 47)

This muscle is innervated by n. glossopharyngeus (IX) [143]. It originates from the dorsal ends of cornubranchial-I (Fig. 11B) and inserts with two heads. The first head (No. 47a) inserts onto the posteriormedial aspect of the articular, whereas the second larger head (No. 47b) inserts on the complete medial aspect of the articular with a superficially tendinous component. In L. kempsi, this muscle also originates from cornubranchial-I but via less substantial connective tissue. It inserts on the lower jaw around and beneath the m. depressor mandibulae (No. 45) and is partly fused with the m. constrictor colli complex (No. 41–43).

M. plastopectus (No. 52)

This muscle is innervated by n. accessorius (XI). As we only had access to head- and anterior neck material, the origin of this strap-like muscle could not be identified. However, in both species, the origin is caudal to the sixth cervical vertebrae and presumably on the plastron [143]. In C. caretta, the muscle extends rostrally and inserts laterally, via a tendon, on the atlas and directly into connective tissue around the m. depressor mandibulae (No. 45) and cornubranchial-I. In L. kempsi, the lateral aspect of the muscle is partly fused with the m. constrictor colli complex (No. 41–43) along its course and the insertion onto the atlas is not tendinous.

M. squamosobranchiale (No. 53)

This muscle is innervated by n. accessorius (XI) and originates from the posterior end of the squamosal above the origin of m. depressor mandibulae (No. 45) and the insertion of m. collosquamosus (No. 57). M. squamosobranchiale inserts onto the distal edge of cornubranchial-I (Fig. 11B). The muscular unit m. squamosobranchiale (No. 53) appears to be absent in L. kempsi, but in its place is a very thin tendinous structure between the cornubranchial-I and the squamosal.

M. brachiohyoideus (Principalis) (No. 55)

This muscle is innervated by n. hypoglossus (XII). In both taxa the muscles originates from the anterior edge of cornubranchial-I, ventral to the origin of m. branchiomandibularis visceralis (No. 47) and passes anteriorly to insert on the corpus hyoidei (Fig. 10A).

M. collosquamosus (No. 57)

This muscle is innervated by n. hypoglossus (XII). It originates from cervical vertebrae-3 and -4, and possibly also from -5. It passes rostrolaterad and fans out at the level of the atlas to insert on the posterior surface of the squamosal, ventromedial to the insertion of m. squamosobranchiale (No. 53), dorsomedial to m. depressor mandibulae (No. 45), and lateral to m. atlantoocipitopfoeocipitius (No. 75) (Fig. 11G and 12B, C). The ventral part of the insertional area of the m. collosquamosus (No. 57) includes the region where the posterior squamosal spine is found in large specimens of C. caretta (e.g. LDUCZ x11; UMZC R 4606). The insertion of the m. collosquamosus (No. 57) onto the back of the skull appears to be broader in L. kempsi (and no spine is present).

M. coracohyoideus (Pars Principalis et Pars Interbranchialis) (No. 58-60)

This muscle is innervated by n. hypoglossus (XII) [143]. Problematically, some or all of it has previously been referred to as the “m. rectus cervicis” (e.g. [128,130] and see [143]). The main unit (No. 58) reportedly originates from the pectoral girdle [143] and inserts on the ventral surface of cornubranchial-II as well as on the posterior edge of the proximal half of cornubranchial-I (Figs. 11A, B). A small unit (No. 60) connects the
ventral surface of cornu branchial-II to the posterior edge of the proximal half of cornu branchial-I (Fig. 11B).

The Tongue

The tongue of turtles is composed of several small muscular units including, for example, the mm. genioglossus (No. 63) et hypoglossus (No. 69) [143]. We did not investigate the individual structure of these, only the gross morphology of the tongue as a whole. The tongue is located in front of the pharynx, supported by the hyoid apparatus, and occupies the space between the occlusal surfaces of the lower jaws. In both taxa it is fleshy with a slightly wrinkled dorsal surface (Figs. 11C–E).

**M. atlantoepistropheooccipitis (No. 75)**

This muscle is innervated by the dorsal branch of the cervical spinal nerve-1 and includes what has been referred to problematically as the rectus capitis superficialis (e.g. [128]; see [143]). The m. atlantoepistropheooccipitis (No. 75) is located above the m. constrictor colli (No. 41–43) and originates by two heads, one (No. 75a) from the dorsolateral surfaces of the first two cervical vertebrae and the other (No. 75b) as a small slip from the anterodorsal surface of the third cervical vertebrae (Figs. 11F, G and 12E, F). Both heads merge shortly after origin, and the muscle fans out towards the braincase inserting on the posterior surface of the squamosal, opisthotic, and exoccipital, above the insertion of m. atlantooccipitis (No. 78), and medial to the insertion of m. collosquamosus (No. 57) (Figs. 12B, C). In *Caretta*, the insertion may also involve the posterior edge of the supraoccipital (Figs. 11F, 12B), whereas in *L. kempii* the insertion is less extensive medially and ends at or near the suture between the opisthotic and the supraoccipital (Figs. 11F, 12C).

**M. atlantooccipitis (No. 77)**

This muscle is innervated by the dorsal branches of cervical nerves [143]. It originates from the lateral face of the atlas and inserts via a tendon on the medialmost part of the ventral surface of the basioccipital (Fig. 12B, C), posterior to the insertions of mm. longus colli (No. 86+87) et carapacobasiosoccipitales (No. 88).

**M. atlantoopisthoticus (Principalis) (No. 78)**

This muscle is innervated by the dorsal branches of cervical nerves [143]. It originates dorsolaterally from the atlas and axis (Fig. 12E), extends ventrad, and inserts on the posterior face of the opisthotic and the exoccipital (Fig. 12B, C).

**M. collosoccipitales (No. 80)**

This muscle is related to the “m. obliquis capitis” of *Shah* [129] (but see [143]), and originates by three separate strap-like muscle heads from the connective tissue over the neural spines of the neck vertebrae: two from above the fourth and the fifth cervical vertebrae and a more slender contribution from above the third (Figs. 11G and 12F). It inserts onto connective tissue dorsal to and between the m. adductor mandibulae externus Pars medialis (No. 17) et profundus (No. 19) and also into the posterior edge of the parietal and supraoccipital (Fig. 12B, C).

**M. transversalis Cervicis (No. 83)**

This muscle originates from the ventrolateral surfaces of the fifth to the seventh vertebrae and passes rostrad along the side of the neck before converging and inserting anteriorly in the region of the atlas and axis.

**M. longus Colli Partes Capitis-I et Pars Capitis-II/III (No. 86 et No. 87)**

The anterior unit (No. 86) has a mainly fleshy origin from the ventral surface of the atlas. The posterior unit (No. 87) is tendinous (Fig. 11H, and 12E, F) and arises from the ventral keels of the second to the fourth cervical vertebrae (Figs. 11C, and 12E, F). The two units fuse shortly after their origin, run rostrad and insert on the ventral surface of the basioccipital (Figs. 11I and 12B, C) with the anteriormost fibres (No. 86) inserting medial to the posterior fibres (No. 87), and anterior to the insertion of m. atlantooccipitis (No. 77).

**M. retrahens Capiti Collique Pars Carapacobasiosoccipitales (No. 88)**

As a part of the multiportioned m. retrahens collique, this unit (No. 88) originates from the ventral face of the carapace [143] and passes along the side of m. longus colli (No. 87). At the level of the third cervical vertebra it (No. 88) becomes entirely tendinous and inserts on the basioccipital tubercle posterolateral to the insertion of the m. longus colli (No. 86+87; Fig. 11G, H).

**Discussion**

**Sea Turtle Muscle Anatomy**

*Caretta caretta* and *Lepidochelys kempii* share a number of general features related to their musculature. However, available descrip-
tions of other taxa suggest that many of these similarities are more widely distributed within turtles [44,76,126,136,143,149–152]. An origin of the m. adductor mandibulae externus Pars medialis (No. 17) from the rostral face of the quadrate is also found in Eretmochelys imbricata [76], whereas an origin of the m. adductor mandibulae internus Pars pterygoideus dorsalis (No. 26) that includes the palatine appears to be present in all cheloniids, many other cryptodires and some chelids (e.g. [44,126,136]). There is one character that appears to be a synapomorphy of C. caretta and L. kempii: insertion of the m. adductor mandibulae internus Pars

Figure 12. Neck muscle origins and insertions of two sea turtles illustrated using computer models based on micro-CT data. (A and B) Caretta caretta (XT757/07) and (C, D, E and F) Lepidochelys kempii (M009/08). Posterior views of the cranium showing (A) the osteology and (B and C) sites of muscle insertion. Lateral views of the neck (D) with skull, (E) showing sites of origin for muscles 75, 80, 86 and 87, and (F) showing the structure of muscles 75, 80, 86 and 87. 19, m. adductor mandibulae externus Pars profundus; 21b, m. adductor mandibulae externus Pars superficialis posterior head; 28b, m. adductor mandibulae internus Pars pterygoideus small lateral head; 45a, m. depressor mandibulae lateral part; 45b, m. depressormandibulae medial part; 46, m. dilator tubea; 53, m. squamosobranchiale; 57, m. collosquamous; 75, m. atlantoepistropheooccipitis; 77, m. atlantooccipitis; 80, m. collooccipitis; 81, m. testocapitis; 82, m. testoooccipitis; 86, m. longus colli Partes capitis-I et Pars capitis-II; 87, m. longus colli Partes capitis-I et Pars capitis-III; 88, m. retrahens capiti collique Pars carapacobasiooccipitis; AT, atlas; AX, axis; BO, basioccipital; EX, exoccpital; OP, opisthotic; PAR, parietal; PR, prootic; QJ, quadratojugal; QU, quadrate; SQ, squamosal; ST, stapes; SUP, supraoccipital; ten, tendon; V3, third vertebra; V4, fourth vertebra; V5, fifth vertebra. Scale bars = 10 mm.

doi:10.1371/journal.pone.0047852.g012
muscle characters (see Table 4).

Despite a general similarity in the cranial muscle anatomy of C. caretta and L. kempii there are also several differences. These include the relative proportions of different muscle parts, the exact location of origins and insertions, and the relationship between muscles and particular aponeuroses. In L. kempii, for example, the second head of the m. adductor mandibulae externus Pars superficialis (No. 21b) has a relatively more extensive origin than in C. caretta (Fig. 7D, 12B), whereas in C. caretta, the lateralmost part of the muscle (No. 21c) has a more ventrally located insertion than in L. kempii (Fig. 12). In L. kempii the m. depressor mandibulae (No. 43) originates from more lateral and ventral locations on the squamosal, than in C. caretta. In general muscle organisation tends to be more complicated in C. caretta than in L. kempii where the m. adductor mandibulae externus (No. 17–21) and m. constrictor colli complex (No. 41–43) are less finely divided, the m. branchio-mandibularis visceralis (No. 47) is less distinct, and the m. squamosobranchiale (No. 53) appears to be entirely absent. Whether this is related to the greater adult size of C. caretta remains to be tested.

One feature apparently common to Chelonioida appears to be the presence of a large fleshy m. adductor mandibulae Pars superficialis (No. 21) with a broad origin inside the cheek and an insertion on the lateral side of the lower jaw [44,76,126,136]. Chelonioida all lack m. adductor mandibulae externus Pars medialis inferior (No. 18), m. zygomatico-mandibularis (No. 22), and m. adductor mandibulae externus Pars profundus atypica (No. 20) [76,126,136], and seem to share a number of other muscle characters (see Table 4).

Feeding Behaviour

Sea turtles generally begin life as pelagic carnivores (or at least omnivores) but as adults they demonstrate a range of feeding ecologies [2,12,23,25,97,100,118]. Dermochelys coriacea remains highly pelagic and forages throughout the water column for jellyfish and salps [25,133]. Caretta caretta moves to coastal waters and feeds opportunistically on a variety of benthic prey (sea pens, crabs, and molluscs) with seasonal variations [25,107–110]. Chelonia mydas also moves to near shore habitats but becomes herbivorous and feeds on sea grass and algae [25,133]. Lepidochelys kempii tends to move to coastal waters as an adult when it generally preys on crustaceans such as crabs [25,107,119] but L. olivacea is more oceanic [25]. Adult Natator depressus generally inhabit coastal waters and shallow bays where they feed on soft corals, sea grass, sea pens, and soft-bodied invertebrates [154], whereas E. imbricata usually lives in nearshore reefs and eats sponges [155]. Despite this diversity of foraging mode, the feeding kinematics of sea turtles have not specifically been examined, but some inferences can be made based on the observed anatomy and known feeding behaviour in other aquatic turtles.

Feeding within an aquatic medium is problematic because a predatory strike can deflect prey away from the mouth [32,127,156–159]. Observations of freshwater turtles show that this problem is overcome by rapid expansion of the esophagus as the jaws open and retraction of the relatively large and well-osssified hyoid apparatus by the m. branchiostegal hyoideus (No. 55). This creates a negative pressure within the buccopharyngeal cavity so that food is effectively sucked in [32,127,157,158]. Freshwater turtles also use the neck to move the head rapidly towards prey [160] and often have a dorsoventrally compressed and streamlined skull to reduce water displacement [32,161,162].

The relatively small tongue in C. caretta and L. kempii is consistent with some use of suction feeding [32,127,156], but the generally shorter neck limits head mobility and the hyoid apparatus is not as well-developed. Moreover, in contrast to many freshwater turtles [32,163], C. caretta and L. kempii possess a number of cranial features that suggest they are capable of forceful biting [23]. These include the wide trituratation surfaces, the reinforced palate, and a large fused symphysis (Fig. 3; [19,29]). They also possess a tall skull, a trait that is associated with a relatively greater biting performance [163], perhaps because its associated with muscles that are larger and have fibres with a more perpendicular orientation relative to the long axes of the jaws. A tall skull is also better shaped to resist the bending and torsional forces related to forceful biting [164–166]. Shape analysis of testudinid and emydid turtles found that small rather than large ventrolateral emarginations are associated with a durophagous diet [162]. Pitting on the bony surfaces that contact the rhamphothecae are probably related to nutrient supply but they may also serve to increase the surface area, and therefore the strength, of attachment. Both C. caretta and L. kempii tend to take rather slow moving but occasionally armoured prey such as sea pens, crabs, and molluscs [108,109,119]. Fish consumption is less common, and when recorded it probably represents feeding on the discarded by-catch of commercial fishing vessels [119,167,168]. Thus, for these turtles forceful biting once prey is caught may be more important than speed and suction feeding during prey acquisition.

The large jaw muscles are also consistent with forceful biting. Both C. caretta and L. kempii possess a coronar aponeurosis into

| No. | Character |
|-----|-----------|
| 1   | Origin of the m. adductor mandibulae externus Pars medialis (No. 17) includes the anterior surface of the quadrate but not the capsule of the jaw joint, postorbital, prootic, supraccipital, or parietal. |
| 2   | Origin of the m. adductor mandibulae externus Pars profundus (No. 19) extends more posteriorly than that of the Pars superficialis. |
| 3   | Origin of the m. adductor mandibulae externus Pars profundus (No. 19) includes the supraoccipital but not the postorbital, opisthotic, or prootic. |
| 4   | Origin of the m. adductor mandibulae Pars superficialis (No. 21) includes the quadrate, squamosal, postorbital, and jugal. |
| 5   | Insertion of the m. adductor mandibulae internus Pars pterygoideus dorsalis (No. 26) includes the prearticular. |
| 6   | Origin of the m. depressor mandibulae Pars pterygoideus ventralis (No. 28) includes the palatine. |
| 7   | Origin of the m. depressor mandibulae (No. 45) includes the posterior face but not the dorsal surface of the squamosal. |

Table 4. Muscle features common to Chelonioida. Compiled from Lakjer [76], Gnanamuthu [138]; Poglayen-Neuwall [136,141], Schumacher [126,141,142,149–151], Werneburg [44,143,152].

doi:10.1371/journal.pone.0047852.t004
which jaw muscles from the back of the adductor chamber insert (e.g. m. adductor mandibulae externus Pars profundus [No. 19]). Because this aponeurosis loops over the otic area (Fig. 2B) before inserting into the lower jaw its line of action is close to vertical regardless of how far back the origins of the most posterior jaw muscle portions lie. As a result of this pulley system and pennation, the volume of adductor muscle is large and has effective leverage [29,150,169–171]. The bony covering of the cheek is bowed outward, so there is nothing to suggest that the fully ossified temporal region restricts the volume of the large m. adductor mandibulae Pars superficialis which inserts on the lateral side of the lower jaw.

In both C. caretta and L. kempi, the articular surface on the lower jaw is at least twice the length of the quadrate condyle, and the articular surface bears two parallel troughs, one on either side of a median ridge (Fig. 4). This suggests some relative antero-posterior translation during jaw movement. The symmetrical shape of the articular surface is important in permitting such movement given that the lower jaw symphysis is immobile (see [172]). Based on muscle arrangements, this sort of "propalinal" movement has been considered to occur widely in turtles [126,170] but the relationships between the articular and quadrate are poorly known and essentially undescribed in most taxa.

The orientations of muscle paths can provide a good indication of their role during jaw movement. For example, Curtis et al. [173] showed that muscle activity predicted by a multibody dynamics computer model according to muscle orientation is very similar to that recorded in vivo. In the sea turtles described here, the posteriorly located m. depressor mandibulae opens the lower jaw, perhaps with some support from the most posterior fibres of the Pars pterygoideus ventralis (No. 20). Otherwise the orientation of the Pars pterygoidei (No. 26, 20) suggests their main function is to close the jaws and pull them forward, particularly when the jaws are wide open [51,174]. The large m. adductor mandibulae externus Pars profundus (No. 19) and the vertically orientated m. adductor mandibulae externus Pars superficialis (No. 21) would provide the greatest power during the final stages of jaw closure [51,174]. The origin and insertion of the m. adductor mandibulae externus Pars medialis (No. 17) are positioned so that the long axis of that portion is approximately parallel to that of the lower jaw when the jaws are closed. It should therefore be very effective at pulling the lower jaw posteriorly when the jaws are closed or almost closed. This suggests palinal rather than proal movement: the jaws moving posteriorly rather than anteriorly at jaw closure [169,174,175]. Whether this movement serves to enhance food prehension or food reduction remains uncertain. In addition to allowing palinal jaw movement, the counter orientation of the internal and external adductor portions may reduce reaction forces at the jaw joint [127,147].

The ligamentum quadratoprasillare [76,136,143,149,151] may represent a passive tension cord (cf. [176]) for resisting tensile strains that might arise along the ventrolateral edge of the dome-like cranial durante. This hypothesis may be tested using finite element modelling similar to that used in Curtis et al. [177].

The skull mechanics of Ch. mydas, E. imbricata, L. olivacea, and N. depressus are probably broadly comparable to those of C. caretta and L. kempi, but this requires further examination with appropriate consideration for ontogenetic and geographic variation [121,178]. Demochelys coriacea differs from other chelonoids [142] in both skull shape and muscle arrangement. The skull is relatively tall with a short crista supraoccipitalis [179], a carillogloss transiens is absent, and the main jaw adductor muscles do not loop over the ear region [76,140,142] but have a more direct path. The implications of this derived but apparently simpler arrangement require further investigation.

Muscles and Skull Emargination

Sea turtle skulls are of particular interest to comparative anatomists because, unlike those of most extant turtles, which have variably developed ventrolateral and posterostral emarginations, their temporal region is almost entirely covered by bone (Figs. 3, 14; [8,29,100,124]). The postorbital, jugal, quadrate, parietal, and squamosal all contribute to the temporal region and the parietal, squamosal, and postorbitals all meet one another. Ventrolateral and posterostral emarginations are present but small (reviewed by Zdansky [27], Killias [28], Gaffney [29], and Wernburg [122]). This means that, unlike the skulls of most reptiles which are composed of a rod-like framework of bone [177,180,181], the skulls of sea turtles have a shell- or dome-like shape. Although the detailed arrangement of individual bones differs, this condition is superficially comparable to that of stem turtles (e.g. Proganochelys quenstedti, [182]) and to the anapsid skull condition found in many extinct non-ornithischians, parareptiles, and basal eureptiles (e.g. Captorhinus sp., [183]).

Although skull emarginations are widespread in extant non-cheloniodid turtles, there is substantial variation as to their size and shape [29,30,122]. The posterostral emarginations are largest in most turtles (e.g. Fig. 13.1–3, 9–12, 21, 29, 31–33), but the ventrolateral ones are larger in chelids (e.g. Fig. 13.25, 27). Both emarginations tend to be large in trionychids and testudinids, resulting in a superficially diapsid-like skull lacking infra- and posttemporal arcades (e.g. Gopherus polyphemus, Figs. 13.1, 13–15), and this is taken one step further in some geoemydids (Hieremys annandali, Heosemys spinosa, Figs. 13.16), emydid (e.g. Terrapene carolina and T. ornata, Fig. 13.20), and chelids (e.g. Chelodina expansa, Chelodina nasoavagans, Figs. 13.26,28) where the emarginations are confluent. By contrast, Carettochelys insculpta (Fig. 13.3), Macrochelys temminckii (Fig. 13.3), kinosternids (e.g. Kinosternon subrubrum, Sternotherus odoratus Fig. 13.11,12), and some podocnemids (e.g. Peltocephalus dumerilii, Figs. 13.32) almost lack a ventrolateral emargination. The same is true for Platysternon megacephalum, arguably the least emarginated turtle outside Chelonioidea, but this species is unusual in having a small jugal (Fig. 13.24).

The near absence of emargination in extant sea turtles appears to be secondary, because they all have living or extinct relatives with moderate or large emarginations. Early fossil Chelonioidea such as Toxochelys latiremis (Fig. 13) and Allipleura hoffmanni, and early cryptodires (e.g. Orchosmyris sp., [39]) possess an emarginated temporal region comparable to that of many extant non-cheloniodid taxa [22,29,36]. Within pleurodirids, Peltocephalus dumerilii and Emydopus fasciatus or Emydopus fasciatus are nested amongst more emarginated extant members of Podocneminae and related fossil taxa [43,104,185]. Similarly, Pseudemydura umbina is phylogenetically nested amongst highly emarginated chelids [43] and, like other clade members, lacks a quadratodugal [29,31]. Therefore, secondary enclosure of the temporal region appears to have occurred within testudinines several times.

Many stem turtles essentially lack posterostral emarginations (e.g. Olotosteocheles semistacea, Late Triassic, China: [186]; Pseudochelys quenstedti, Late Triassic, Germany; [182]; Kayentachelys aprix, Early Jurassic, USA: [187]; Condochelys antiqua, Middle Jurassic, Argentina: [188]), and ventrolateral emarginations, if present, are small (e.g. O. semistacea, [186]: 497; P. quenstedti [pers. obs. MEVH] and IV); E. aprix, [187]). Therefore, the pleiosomic condition for Testudinata (Testudines+stem group taxa) it is not necessarily the same as for the less inclusive Testudines.

Sea Turtle Head and Neck Muscles
Figure 13. Turtle skulls plotted against the topology of Shaffer (2009) with the addition of Proganochelys and Toxochelys. Major phylogenetic groupings include (A) Testudinata, (B) Testudines, (C) Pleurodira, (D) Cryptodira, and (E) Chelonioida. Euchelonioidae is used in the sense of Gaffney and Meylan [202]. Individual skulls represent (1) Lissemys punctata, (2) Chitra indica, (3) Carrettochelys insculpta, (4) Dermochelys coracea, (5) Chelonia mydas, (6) Lepidochelys kempii, (7) Eretmochelys imbricata, (8) Careta caretta, (9) Chelydra serpentia, (10) Macrochelys temmincki.
With a computer model of the extant rhynchocephalian Sphenodon as an example taxon, Curtis et al. [177] recently used Finite Element Modelling to show that when all loading conditions are taken into account, all of the bone in a reptile skull contributes to its structural integrity. This is consistent with the theory that skull shape is strongly linked to mechanical loading or strain [e.g. [48–52,54,56,122,176,181]]: from birth, as the skull grows around the sensory organs, loading from the muscles and feeding apparatus iteratively modify the shape of the skull via remodelling [189,190]. Correspondingly, it is known that aberrant loading conditions lead to aberrant skull shapes [e.g. (33,55,191)].

Given the apparent association between loading, muscles, and skull shape, the relationship between the m. adductor mandibulae externus Pars superficialis (No. 21) and the medial wall of the temporal region in turtles warrants consideration. In chelonioids, the muscle’s fleshy origin should mean that resulting loading is evenly spread rather than locally concentrated at a tendinous origin, a condition that may promote the deposition of bone [54]. A similar muscle arrangement is found in the non-cheloniod cryptodire Kinosternon subrubrum [29,136], which has a large jugal and a small ventrolateral emargination, but is absent in several turtles with large ventrolateral emarginations (e.g. Lissismys punctata, Terrapene carolina, Testudo graeca, Pelusios subniger, and chelids such as Emydura macquarii and Chelodina novegauineae) [29,32,136,149–151,192]. However, in the non-cheloniods Sternommys odoratus and Platysternon megacephalum [136,149–151] that lack ventrolateral emarginations, a broad fleshy origin of the m. adductor mandibulae externus Pars superficialis (No. 21) (including the jugal surface) is apparently not present. Thus, although some aspects of the pattern are suggestive of a correspondence between muscle anatomy and skull morphology, the relationship is not clearcut, and the presence or absence of emarginations probably involves a combination of factors [44,51,52,122,189]. The rhynchocephalian lepidosaur Sphenodon also has a large superficial adductor muscle, but it arises from the fascia that attaches to the edges of the large lower temporal fenestra so that loading is concentrated at the margins with bone deposition limited to this edge [147,177].

The relatively small posterodorsal emargination in chelonioids may be associated with the more posterior origin of m. depressor mandibulae from the squamosal [76,126,138,142]. Only in L. kempi does the m. depressor mandibulae encroach on the lateral surface of the squamosal, and this taxon has wider posterodorsal emarginations and a more dorsolateral origin of the m. adductor mandibulae externus Pars superficialis from the squamosal. Non-cheloniod turtles with a more posterior origin of m. depressor mandibulae include Chelydra serpentina, Emyx orbicularis, Malaclemys terrapin litoralis, and Podocnemis expansa [136,137,146,193,194]. Whereas the posterodorsal emarginations in P. expansa are small [29], those in Chely. serpentina, Emy. orbicularis and M. terrapin litoralis are relatively large [29,123]. Also, although most turtles with extensive posterodorsal emarginations (e.g. Terrapene carolina, Pseudemys scripta, Lissismys punctata [136,148,192]) have a laterally located origin of m. depressor mandibulae (No. 45) [44,143], some turtles with little or no posterodorsal emargination (e.g. chelids such as Emydura macquarii [193,194]).

Of all chelonioids, D. coriacea arguably shows the least emargination (Fig. 13.4), but this taxon is also unusual in lacking the troclearis system of the adductor musculature and in having a more linear orientation of the external adductor portions [137,142]. In addition, the internal adductor musculature does not originate from the processus descendens parietalis, an arrangement secondarily in this taxon lost after it appeared on the stem line of Testudines [171]. The absence of both a pulley system and a posterodorsal emargination in D. coriacea supports the hypothesis that these two characters are functionally correlated [171,122].

Further anatomical and modelling work on these and other reptiles may shed light on the relationship between soft and hard tissues in the generation of skull form. However, detailed anatomical surveys are an essential foundation for this work.

Methods

Materials

Between 2007 and 2008 three Caretta caretta and two Lepidochelys kempi specimens were recovered post mortem by the UK Cetacean Strandings Investigation Programme from beaches in Wales and Scotland (United Kingdom) (Table 2). They were identified by external examination and measured. All the specimens in our study represent immature animals [195] and thus individuals at the oceanic feeding stage of their life history [118]. Prior to our dissections, specimens XT161/08 and XT045/08 had their skull roofing bones cut open and brains removed for pathological examination.

Osteological material was also examined from collections at and the Natural History Museum of Los Angeles County, USA (LACM); Grant Museum of Zoology, University College London, UK (LDUCZ); and University Museum of Zoology Cambridge, UK (UMZC) (Table 1).

Dissections

Material was received and stored as frozen, but prior to dissection it was soaked overnight in diluted commercially available fabric softener. This made the tissues much easier to dissection it was soaked overnight in diluted commercially available fabric softener. This made the tissues much easier to dissection. Innervations were largely determined from the literature and previous dissections [143].

Micro-Computed Tomography

One specimen each of L. kempi (M009/08) and C. caretta (XT757/07) were subjected to micro-computed tomography (micro-CT) at the University of Hull, UK using a X-Tek HMX 160 scanner using a Beryllium target and aperture of 75%. To reduce beam hardening, the X-rays were filtered through a 0.1 copper plate. M009/08 was scanned using 1149 projections averaging 64 frames per projection, whereas XT757/07 was scanned using 1113 projections averaging 32 frames per projection. Anatomical structures were segmented using the software
Amira 4.1 (Konrad-Zuse-Zentrum für Informationstechnik Berlin), voxel resolution was 0.121 mm$^3$ for M009/08 and 0.001 mm$^3$ for XT757/07. The scan of L. kempii (M009/08) was particularly successful and included details of the muscle arrangement (Fig. 3) despite the absence of isotope staining as described by Metscher [197] and Jeffery et al. [198] (but see also [199]).

**Terminology**

The names used for neuro- and dermocranial elements of turtles mainly correspond to those of Gaffney [29,123], whereas the names used for splanchocranial elements follow Furringer [200]: lyal apparatus. Anatomical terms for the cervical vertebrae are similar to those used by Herrell et al. [130] and the nomenclature of cranial musculature and other soft tissues follows Werneburg [143] (Table 3). Taxonomic nomenclature follows Fritz and Havaš [24] and Joyce et al. [211].

**Note Added Post- Acceptance**

A recent publication on the ontogenetic scaling of bite force in Caretta caretta confirms that these turtles are durophagus as adults [203].

**Supporting Information**

**Video S1 Cranium of of a young Caretta caretta (XT757/07) based on reconstructions from micro-CT data.** The surface model has been simplified to 410000 faces. Also see figure 2. (MPEG)

**Video S2 Cranium of of a young Lepidochelys kempii (M009/08) based on reconstructions from micro-CT data.** The surface model has been simplified to 500000 faces. Also see figure 2. (MPEG)

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**Video S3 Skull of a young Lepidochelys kempii (M009/08) with parts of the right temporal region absent and jaw muscles shown.** The model is based on reconstructions from micro-CT data. Also see figures 3 and 8. (MPEG)

**Acknowledgments**

The sea turtle specimens, three Caretta caretta and two Lepidochelys kempii, were provided by the UK Cetacean Strandings Investigation Programme (CSIP) which is funded by Defra and the Devolved Administrations in Scotland and Wales. The animals were found on beaches around the UK between 2007 and 2010, recovered by the CSIP, and given postmortem examinations. Transfer of the material (which represent Annex IV listed species) to SEE and MEHJ was carried out by R. Deaville (UK Cetacean Strandings Investigation Programme, Institute of Zoology, Zoological Society of London) under licences issued by Countryside Council for Wales (CCW) and Natural England (NE) (WML-CL01 (01/12)). We thank S. Taflı (University of Hull, UK) for helping us to micro-CT scan the turtle specimens and L. Clarke for dissecting specimen XT043/08. For access to skeletal material, we thank M. Lowe (University Museum of Zoology Cambridge), N. Camacho (Los Angeles County Natural History Museum), and J. D. Nicholls (Grant Museum of Zoology, UCL). MEHJ thanks Kris A. Lappin (Cal Poly Pomona) for hosting a visit to California which provided the opportunity to visit the Los Angeles County Natural History Museum and also to Johannes Müller for hosting a visit to Museum für Naturkunde to examine Proganochelys specimen MB 1910.45.2. We also thank Juan Daza, Andrew Farke, and Casey Holiday for their constructive feedback on an earlier version of this manuscript.

**Author Contributions**

Conceived and designed the experiments: MEHJ IW SEE PO MJF NC. Performed the experiments: MEHJ IW SEE. Analyzed the data: MEHJ IW. Contributed reagents/materials/analysis tools: RP. Wrote the paper: MEHJ IW. Created the computed tomography model: MEHJ. Contributed significantly to editing/revision of the submitted manuscript: SEE PO MF NC.
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