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CERVICAL RIBS IN TURTLES

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The existence of cervical ribs in Recent turtles is frequently denied. In fact, however, cervical ribs in turtles have been discovered and rediscovered several times over. They are rudimentary in all post-Triassic forms and the nature of these highly peculiar rudiments is evident only in embryos or young specimens. The only description with any pretensions to fullness is that of C. K. Hoffman (1879, repeated in Bronn's *Thierreich* 1890). There is brief mention of their occurrence in embryos by Ruckes (1929), Naef (1929) and Emelianov (1937). None of these previous observations has been sufficiently detailed to make the nature and relationships of the rib elements quite clear, and, except for rather crude and incomplete sketches in Hoffman, no figures have been given.

I have myself seen cervical ribs and rib rudiments in both adults and embryos (Emydinae) or in adults only (Testudininae, Chelydridae, Dermochelyidae, Chelyidae and Pelomedusidae). Embryos of *Emys orbicularis* given me by Dr. B. W. Kunkel and of *Pseudemys* sp., loaned me by Dr. H. Ruckes, and of *Chrysemys marginata* and *Chelydra serpentina* in the Minot Collection, Harvard University, have provided me with the opportunity to study the embryonic condition and developmental history of the cervical rib rudiments, while I have been able to examine adult conditions from specimens in the osteological collections of the Museum of Comparative Zoology (MCZ), the American Museum of Natural History (AMNH), the United States National Museum (USNM), the British Museum (Natural History) (BM),

the Institut des Sciences Naturelles in Brussels, the Senckenberg Museum in Frankfurt, the Zoologische Staatssammlung in Munich and the Laboratoire d'Anatomie Comparée of the Museum National d'Histoire Naturelle de Paris (LAC).

In the course of the present study a wide variety of conditions has been observed, including (in adults) considerable intra-

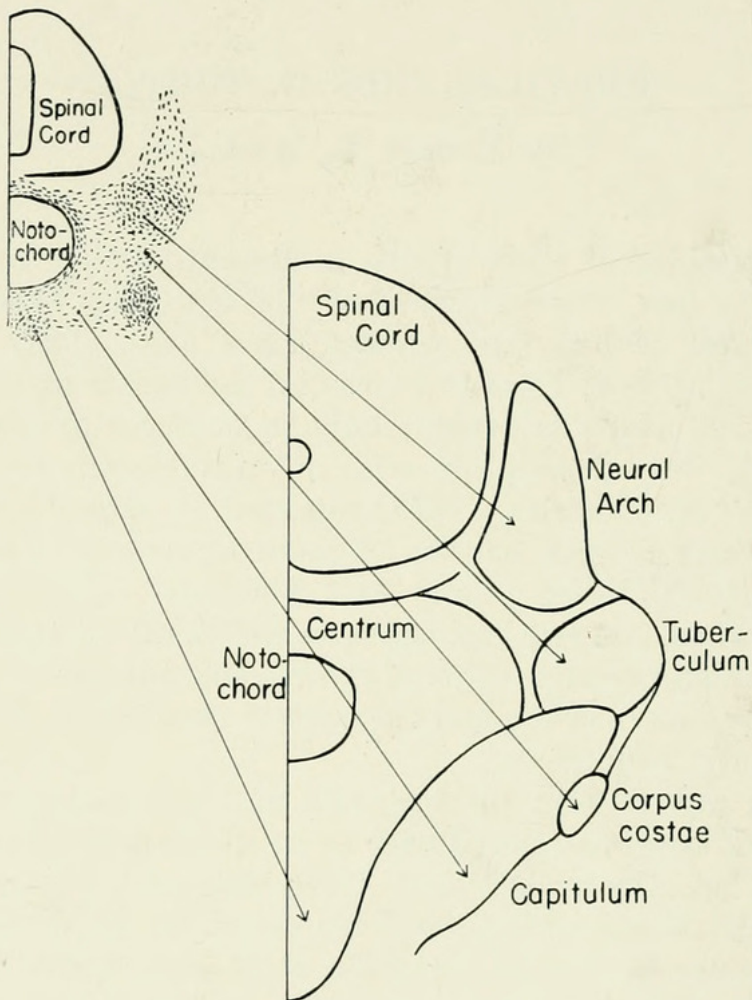


Fig. 1. Diagram to show the rib region in prechondral and cartilage stages of the cervical vertebrae of *Emys orbicularis*.

specific variation. In many instances the ribs are fragmented or broken into little ossicles, which have been many times reported but rarely correctly interpreted. In yet other instances

the ribs are still more rudimentary, represented in the adults only by cryptic fused elements. It would, in fact, be very difficult to understand the ribs of Recent adult forms if it were not for the evidence of embryos, and (as we shall see) of the Triassic fossils.

The embryonic cervical ribs of emydine turtles are *two-headed* with a dorsal tubercular attachment at the region of the neurocentral suture and a ventral attachment to the anterior intercentral ossicle, when that is present, or to the anterior centrum when the intercentrum is absent. These ribs may first be distinguished in precartilage stages (Fig. 1). They are then not very different from the precartilage cervical ribs of other reptiles.

With the onset of chondrification, however, these ribs undergo a partial degeneration. The dorsalmost portion chondrifies at its place of attachment to the neurocentral suture, but no joint forms here, and the separateness of the element is indicated at most by a suture line in cartilage (a line of small densely-packed, poorly-differentiated cartilage cells like those which constitute the cartilage neurocentral suture).

From the dorsal rib rudiment at the neurocentral suture a band of prechondral (later ligamentous) tissue extends ventro-anteriorly toward the anterior intervertebral region. In this band there is embedded at the middle of its length a separate small cartilage nodule. The prechondral or ligamentous band then continues forward to attach anteriorly to a separate antero-ventral nodule alongside a median intercentrum or to this element fused onto the intercentrum as a lateral parapophysial projection.

In the Emydinae, therefore, the bicipital rib of the membranous stage has fragmented into three distinct chondral elements. The morphological interpretation of these elements will be discussed a little later; for the present it will be well to have neutral terms for them, avoiding questions of homology. I suggest, therefore, calling the dorsalmost element the alpha rib element, the middle one the beta, and the ventralmost the gamma element.

I have seen this fragmented condition of the cartilage ribs in both *Emys* and *Pseudemys* embryos. I have not had the material to follow these structures into ossification stages, but the same elements are readily recognized in adult *Emys* and *Pseudemys* and in other Recent emydines.

In all living cryptodires the alpha element of the embryonic ribs is apparently represented by the low indistinct transverse processes found anteriorly at the junction of neural arch and centrum on each cervical. C. K. Hoffman (1890) has reported that this element ossifies separately in tortoises but remains cartilaginous in other forms. The second statement appears to be erroneous (except for *Dermochelys*); the first I cannot confirm from personal observation, but the statement has been repeated (whether copied or verified) by J. S. Thomson (1932).

I have three times observed separate ossification and hypertrophy of this element, in all cases as individual variations and always on the eighth vertebra — once asymmetrically (on the

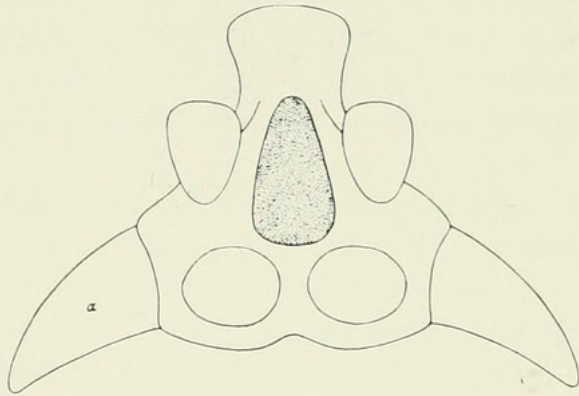


Fig. 2. *Pyxis arachnoides*. Anterior view of abnormal 8th vertebra. Symmetrical hypertrophied alpha elements.

left side only) in a specimen of *Pseudemys scripta elegans* (Lafayette College), once symmetrically in *Gopherus berlandieri* (A.M.N.H. 91916), and once symmetrically in *Pyxis arachnoides* (L.A.C. 1885-34) (Fig. 2). Siebenrock (1906) has reported the same condition in the last form. These conspicuous abnormal examples apart, the alpha element appears in all Recent adult types to be a cryptic fused element.

The ventral rib elements, when present, are less frequently cryptic, but extreme intraspecific variability makes their description somewhat difficult.

In emydines, the gamma element may be present on all the cervicals, usually fused with the intercentra on the anterior

vertebrae, free on the middle vertebrae, and fused again but with the anterior end of the centrum on the last cervical. I have seen free gamma ossicles in: *Batagur baska*, *Kachuga tectum*, *Orlitia borneensis*, *Malaclemys terrapin*, *Pseudemys scripta*, *Pseudemys floridana*, *Pseudemys rubriventris*, *Pseudemys terrapen*, *Chrysemys picta*, *Graptemys geographica*, *Graptemys oculifera*, *Clemmys insculpta*, *Clemmys muhlenbergi*, *Clemmys guttata*, *Clemmys leprosa*, *Clemmys marmorata*, *Emys orbicularis*, *Emydoidea blandingi*, *Deirochelys reticularia*, *Terrapene carolina*, *Geoemyda trijuga*, *Geoemyda punctularia*, *Cuora amboinensis* and *Cyclemys dentata*. When it is considered that these are small elements which, if free, are readily lost by the usual methods of skeletal preparation, it becomes very probable that gamma ossicles are typically present in the Emydinae. Indeed, in one instance they are probably invariably present: the antero-

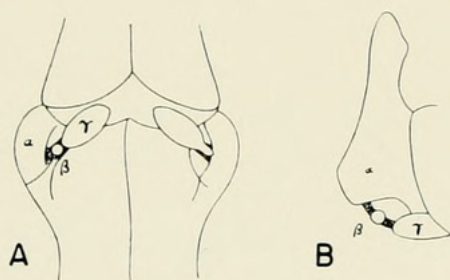


Fig. 3. *Terrapene carolina*. A. Ventral view of joint between 5th and 6th cervical centra showing separate beta and gamma rib elements. B. Anterior view of 6th vertebra in the same specimen. Compare Fig. 5.

ventrolateral processes lying alongside the hypapophysis of the eighth centrum in emydines are apparently fused gamma ossicles. Similar fusion of gamma ossicles occurs rather frequently at the anterior end of the seventh centrum.

The beta element, on the other hand, is unknown in adults except on the middle cervicals of a few individuals of certain emydine species. Here again, however, the probability of loss of these very small and loosely-attached elements must be taken into account as a possible explanation of the apparent rarity of these elements in adults.

An instance in which both ventral rib elements are well developed is seen in Figure 3A. The joint between centra 5 and 6 of a specimen of *Terrapene carolina* from my own collection is shown in ventral view. The gamma elements are relatively large flattened ossicles attached to the ventral side of the centrum (centrum 5) just below the paired, convex, posterior central articular surfaces. These ossicles extend posteriorly and somewhat laterally to lie partly underneath the anterolateral diminutive transverse processes (alpha rib elements) of the posterior vertebra (vertebra 6). Gamma and alpha rib elements are connected on each side by ligaments in which are embedded small rounded ossicles which are evidently the persisting beta elements. Figure 3B shows the same elements in anterolateral view. (Com-

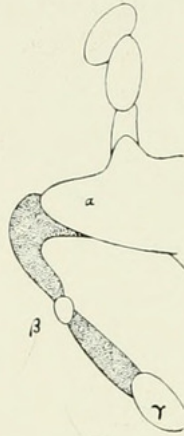


Fig. 4. *Pseudemys* sp. embryo. Section through right side of a middle cervical vertebra in early cartilage stages showing all three rib elements. Compare Fig. 3B.

pare Fig. 4.) The only element of the morphological chain which we saw in the embryo that is missing in this case is the median intercentrum; this is consistently absent on the posterior cervicals of turtles.

Museum specimens in which I have seen comparable conditions (i.e. both beta and gamma ossicles present) are: *Clemmys muhlenbergi* U.S.N.M. 29228, *Clemmys insculpta* U.S.N.M. 63089 and *Chrysemys picta* U.S.N.M. 29233, as well as *Emys orbicularis* B.M. 1920-1-20-2248 and other specimens of this

species at the British Museum. I should emphasize that these specimens are not the only ones by any means in which I have observed beta and gamma ossicles together; these are only certain readily accessible specimens upon which my observations may be confirmed. Museum specimens are not likely to have preserved these elements; careful preparation of specimens is required to reveal them.

As mentioned above, on anterior cervicals the gamma ossicles may be fused with the true median intercentra (or with the anterior of the two centra between which they lie), but occasional specimens show them separate from and lying alongside the intercentra, presenting in such cases the appearance of tripartite intercentra. I have seen this condition in *Chrysemys picta* U.S.N.M. 29233, *Pseudemys floridana* U.S.N.M. 60492, and *Orlitia borneensis* U.S.N.M. 37788 — in the first case only at the odontoid-second centrum articulation, in the two latter also at the joint between centra 2 and 3. I have seen such apparent triple intercentra also in *Chelydra serpentina* (a specimen at Lafayette College, A.M.N.H. 28942, and specimens 18308 and 18361 in the Natural History Museum of the University of Kansas).

Siebenrock (1907) mentions gamma ossicles in *Platysternon megacephalum*, regarding them, however, as rudimentary ventral arches. He says: "Rudimentäre unteren Bogen, Hypapophysen, kommen so wie bei *Macrocllemmys* Gray and bei vielen Emydidae am ersten bis fünften Halswirbel vor; sie fehlen dagegen bei *Chelydra* Schw., wie ich mich an drei darauf untersuchten Skeletten überzeugen konnte."

As Siebenrock states, gamma ossicles appear to be usually absent in *Chelydra* except at the odontoid-second centrum articulation, but one specimen of this genus at the Senckenberg Museum has gamma ossicles on centra 3 to 5, as does another specimen in the Staatssammlung at Munich. I have not myself seen any gamma ossicles in *Macrocllemmys*, though Siebenrock mentions them above, nor in *Staurotypus* or in *Kinosternon*. Beta ossicles have not been seen in any of the Chelydridae *sensu lato*.

I have seen neither of the ventral rib ossicles in *Dermatemys*, and I have seen gamma ossicles only rarely in the Testudininae (e.g. at the odontoid-second centrum joint in *Gopherus berlandieri* A.M.N.H. 91916), but Siebenrock (1906) records a series

of gamma ossicles in *Acinixys planicauda*, and Thomson (1932) reports them on the fourth, fifth and sixth vertebrae of *Testudo ibera* and *T. graeca*.

In the Cheloniidae and Dermochelyidae one ventral rib element is usually present on most or all the cervicals. It is cartilaginous in *Dermochelys* (e.g. U.S.N.M. 29492, see also the figure in Völker 1913), bony in *Caretta caretta* (e.g. U.S.N.M. 29372) (Fig. 5) and *Eretmochelys imbricata* (e.g. U.S.N.M. 59866). A special

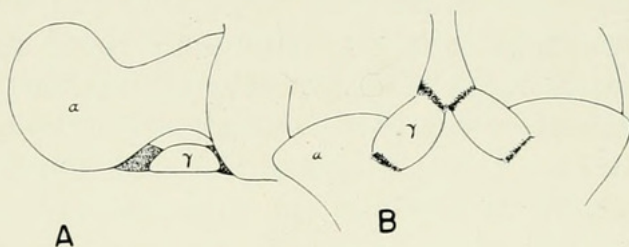


Fig. 5. *Caretta caretta*. A. Anterior view of 6th vertebra. B. Ventral view of joint between 6th and 7th centra in the same specimen.

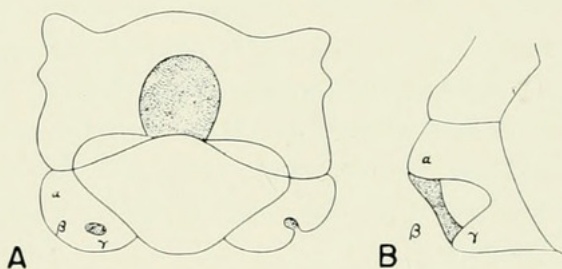


Fig. 6. *Chelonia mydas*. A. Anterior view of 7th cervical vertebra. B. Anterior view of right side of the 7th vertebra of another specimen.

condition is seen in *Chelonia mydas* (A.M.N.H. 46837) (Fig. 6A) in which on vertebra 7 the rib rudiment is seen to be fused to the right anterior side of the vertebra in such a way as to enclose a small "vertebrararterial" canal. The "vertebrararterial" canal is incomplete laterally on the left side of the same vertebra. In another specimen of the same species (A.M.N.H. 5912) (Fig. 6B) the "vertebrararterial" canal is completed laterally by cartilage on both sides of the seventh vertebra.

I have seen ossified gamma ossicles also in the Eocene sea turtle *Eosphargis gigas* in the magnificently preserved specimen in the Brussels Museum.

Beta ossicles are unknown in the Cheloniidae, and they may in fact be merged with the rather larger apparent equivalents of the gamma ossicles of emydines.

I have seen no trace of rib rudiments except the transverse processes in adult trionychids or in *Carettochelys*, but gamma ossicle equivalents exist in at least *Chelus* and *Erymnochelys* of the Pleurodira.

These peculiar conditions of the rib elements in modern turtles are fortunately traceable to a more primitive condition in Triassic turtles. Jaekel (1916) has described and figured the situation in *Triassochelys dux* (= *Proganochelys quenstedti*), and I can confirm his description in all essentials, having examined the magnificent skeletons of *Proganochelys* in the possession of the Stuttgart Museum, which are to be described by Dr. K. Staesche.

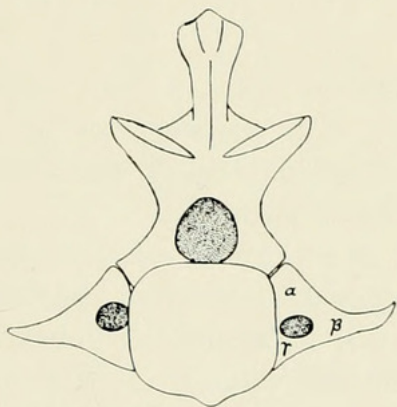


Fig. 7. *Proganochelys quenstedti* (= *Triassochelys dux*). Anterior view of 7th cervical vertebra showing bicapital rib. (After Jaekel.)

Figure 7 presents an anterior view of the seventh cervical vertebra in *Proganochelys* (after Jaekel). It will be seen that these are ribs of a normal bicapital type, the tuberculum lying across the neurocentral suture, the capitulum articulating more ventrally with the side of the centrum. Ribs of this type were present on cervicals 2 to 7. The eighth rib much resembled the abnormal vertebrae of *Pseudemys*, *Pyxis*, etc. described above. It is single-headed rather than bicapital, elongate rather than

short. It curves downward distally to a degree appropriate to its length. Its single head lies across the neurocentral suture in the position of the tuberculum. Probably the eighth and the ribs behind it retain only the tuberculum of the two original rib heads.

The congruence of the bicipital ribs in *Proganochelys* with the ribs that would be expected if the embryonic rib elements of Recent turtles were fully developed is very complete. With this evidence before us, the interpretation of the otherwise very singular, even anomalous rudimental rib ossicles of Recent turtles can hardly be questioned.

I have seen similar small ossicles that are apparently rib rudiments in large lizards, e.g. *Iguana iguana* A.M.N.H. 1269 (Comparative Anatomy collection). The phenomenon of rib fragmentation is thus not confined to the neck of turtles. Indeed, there is a considerable literature on anomalous rib conditions in Amniota (Baur 1886, Howes and Swinnerton 1901 — *Sphenodon*; Noble 1921 — *Sphaerodactylus*; Schinz and Zangerl 1937b — *Gallus*; Virchow 1929 — *Ornithorhynchus*; Albrecht 1882, Hayek 1928, de Burlet 1917, Federow 1910, Abel 1909 — various mammals.)

These special conditions have, I feel, implications of greater morphological moment than appears on the surface. They may require a careful re-examination of the origin and morphology of ribs throughout the Amniota.

Rib fragmentation in tetrapods occurs typically in regions of the column in which special movements are taking place (neck of turtles, lizards, etc., tail of amniotes generally), and in which, therefore, the thoracic rib pattern is not useful, or in aquatic forms in which the thoracic pattern itself may prove unstable. It is a phenomenon, therefore, of degeneration — of breakdown of the two-headed ribs primitively present in tetrapods, presumably throughout the column. However, it is precisely the origin and evolution of the two-headed ribs of tetrapods that is still a puzzle — a puzzle to which, I believe, these special conditions along with the ontogeny of less modified ribs have something to contribute. Specifically, the question of the possible origin of two-headed tetrapod ribs from a *union* of the dorsal and ventral ribs of fishes still needs a definitive yes or no answer.

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