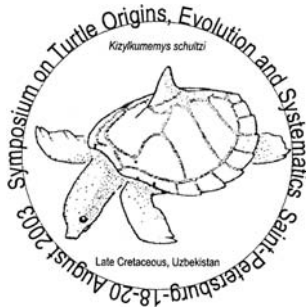# FOSSIL TURTLE RESEARCH

VOLUME 1

Proceedings of the Symposium
on Turtle Origins, Evolution and Systematics

August 18 – 20, 2003,
St. Petersburg, Russia

Edited by
Igor G. Danilov and James F. Parham

St. Petersburg, 2006

FOSSIL TURTLE RESEARCH

VOLUME 1

Editors: Igor G. Danilov and James F. Parham

Proceedings of the Symposium
on Turtle Origins, Evolution and Systematics
August 18 – 20, 2003,
St. Petersburg, Russia

Published in St. Petersburg, March 2006

**Cover photo: PIN 52-1a, holotype of *Yaxartemys longicauda* Riabinin, 1948,
Upper Jurassic of Kazakhstan, Karatau Ridge, vicinity of Mikhailovka village
Photograph: Igor Danilov**

THE PRESENCE OF CLEITHRA IN THE BASAL TURTLE *Kayentachelys aprix*

Walter G. Joyce[1], Farish A. Jenkins, Jr.[2] and Timothy Rowe[3]

A morphological review of all available *Kayentachelys aprix* material reveals the presence of cleithra, a primitive dermal component of the pectoral girdle. These structures are homologous with the equivalently placed «epiplastral processes» of other basal turtles, thus revealing the unambiguous retention of cleithra in the turtle stem lineage. The occurrence of cleithra in primitive turtles calls into question their placement within crown Sauria, as reacquisition and subsequent loss of cleithra within the turtle stem lineage is thereby implied. Fossil evidence reveals that cleithra were lost twice within the turtle crown group.

INTRODUCTION

The shoulder girdle of tetrapods is a composite structure consisting of dermal and endochondral elements. Paired anterior and posterior coracoids, scapulae, and suprascapulae represent the endochondral components of the girdle in basal tetrapods. The dermal components are comprised of a medial interclavicle, paired clavicles, and cleithra (Fig. 1). There is a general trend throughout the phylogeny of tetrapods towards a simplification of this pattern, particularly through the successive reduction of the dermal elements and the increased ossification of the endochondral components (Romer, 1956).

The history of the cleithrum is characterized by independent occurrences of reduction and loss in various groups of tetrapods. The earliest known stem tetrapods, exemplified by the Devonian taxon *Ichthyostega*, possessed an extremely large, strap-like cleithrum that overlapped numerous ribs (Jarvik, 1996; Coates et al., 2002; Clack, 2002), resembling in general shape and anatomical position the scapula of many modern tetrapods. Large cleithra are present in numerous stem representatives of crown Tetrapoda (Carroll, 1988). Among
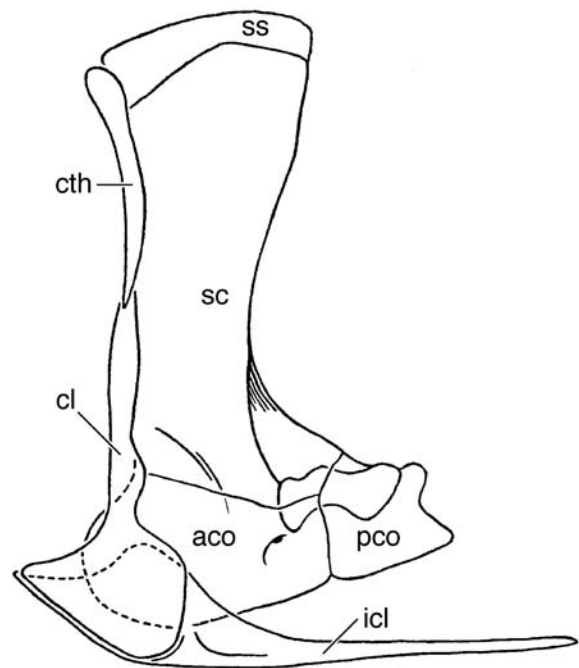

Fig. 1. The components of the shoulder girdle in primitive tetrapods (modified from Romer, 1956). Abbreviations: **aco**, anterior coracoid; **cl**, clavicle; **cth**, cleithrum; **icl**, interclavicle; **pco**, posterior coracoid; **sc**, scapula; **ss**, suprascapula.

[1] Peabody Museum of Natural History, Yale University, 170 Whitney Avenue, New Haven, Connecticut 06520, USA. E-mail: walter.joyce@yale.edu

[2] Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA

[3] The University of Texas at Austin, Department of Geological Sciences, 1 University Station C1100, Austin, Texas 78712, USA

extant amphibians with pectoral girdles, cleithra are absent in salamanders, but remain preserved as a narrow ossification along the anterior border of the scapula in some extant frogs (Duellman and Trueb, 1986), demonstrating another loss of cleithra within crown Amphibia.

Relative to the condition seen in basal stem tetrapods, the cleithrum of basal amniotes is reduced to a spoon-shaped bar that sits along the anterodorsal rim of the enlarged scapula and commonly overlaps the ascending process of the clavicle (Fig. 1) (Carroll, 1988). All living amniotes lack cleithra. However, the presence of cleithra in early stem synapsids taxa (Caseidae, Ophiacodontidae, Edaphosauridae, Sphenacodontidae, and Gorgonopsida; Carroll, 1988; Gauthier et al., 1988) and in stem reptilian taxa (captorhinids, milleretids, *Macroleter*, and *Paleothyris*; Laurin and Reisz, 1995; deBraga and Rieppel, 1997) indicates that cleithra were lost at least twice within Amniota.

The shoulder girdle of extant turtles is substantially modified relative to the condition in ancestral amniotes. Only the coracoid, scapulae, clavicles, and the interclavicle remain as distinct bones in the adult. The clavicles and the interclavicle are expanded, flat elements that form the solid anterior part of the plastron of the turtle shell (Romer, 1956; Fig. 2). They are more commonly referred to as the epiplastra and the entoplastron, respectively. The scapulae and coracoids, in contrast, retain their original identity and function of bearing the limbs, but their structure is unique among vertebrates by being able to move independently of the dermal component and by being situated within the ribcage. Cleithra were originally thought to be present (Jaekel, 1915) in the oldest unambiguous fossil «turtle,» *Proganochelys quenstedti* Baur, 1887, but the structures in question were later reinterpreted as simple outgrowths of the epiplastra and renamed epiplastral processes (Gaffney, 1990). Massive «epiplastral processes» that stretch from the plastron to the carapace have been reported for a number of other primitive tur-

tles, including *Proganochelys quenstedti*, *Proterochersis robusta* Fraas, 1913, and *Palaeochersis talampayensis* Rougier et al., 1995. Reduced processes are known for a series of others, including *Meiolania platyceps* Owen, 1886, *Mongolochelys efremovi* Khosatzky, 1997, *Glyptops plicatulus* (Cope, 1877), and *Xinjiangchelys latimarginalis* (Young and Chow, 1953) (see Joyce, In Press, for summary of distribution).

If the presence of cleithra can be demonstrated for a basal turtle taxon, then the homology of the equivalently placed epiplastral processes of other turtles must be reconsidered as indicating the presence of cleithra in basal turtles in general. As a consequence, the commonly hypothesized placement of turtles within crown Sauria (e.g., deBraga and Rieppel, 1997, Kumazawa and Nishida, 1999, Zardoya and Meyer, 2000), a clade that demonstrably lacks cleithra, would entail the unparsimonious conclusion that cleithra reappeared along the phylogenetic stem of turtles only to be subsequently lost again in crown turtles. The alternative placement of turtles outside of crown Sauria, in contrast, only requires the primitive retention of cleithra with its subsequent loss.

In view of the evidence that the newly described elements in *Kayentachelys aprix* are cleithra, they are referred to as such in this manuscript.

Institutional abbreviations – MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; TMM, Texas Memorial Museum, The University of Texas, Austin, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

MATERIAL AND METHODS

Remains of *Kayentachelys aprix* are a common occurrence in the Lower Jurassic Kayenta Formation of Coconino County, Arizona. Specimens are typically found as isolated, broken elements, but almost complete skeletons are oc-
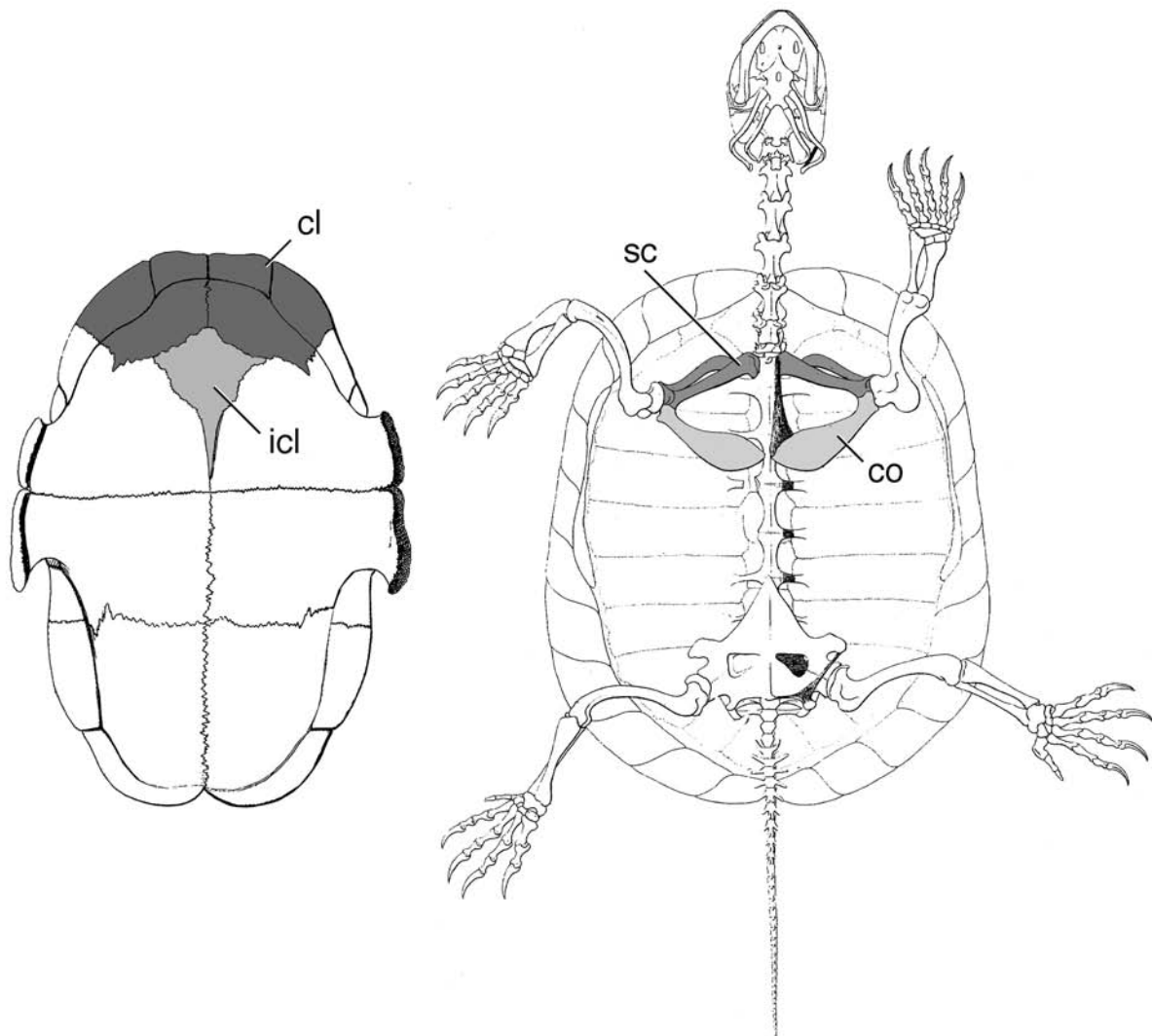
Fig. 2. The shoulder girdle of extant turtles as exemplified by *Emys orbicularis* (redrawn from Bojanus, 1819). Abbreviations: **co**, coracoid; **cl**, clavicle (= epiplastron); **icl**, interclavicle (= entoplastron); **sc**, scapula.

casionally found as well. Sediments in this region are dominated by variegated mudstones and silt-stones, ranging from red to purple to blue reflecting changing redox conditions during deposition and diagenesis. Fossils vary in their preservation from being heavily cracked, crushed, and thickly coated with iron oxides, to being preserved three-dimensionally and without an oxide coating (Clark and Fastovsky, 1986).

Numerous specimens are available with partially or fully preserved cleithra, epiplastra, and entoplastra. All material is diagnosable as *Kayentachelys aprix* based on the associated cranial or postcranial remains. Given that the visceral side of the epiplastra and entoplastron are not exposed in many specimens and that others are too heavily encrusted with iron oxides to display any detail, our analysis is restricted to the six best-preserved specimens: MCZ 8917, an almost complete,

partially disarticulated skeleton, including fused left epiplastron and cleithrum (Fig. 3A-B); MCZ 8986, a partial skeleton lightly encrusted with iron oxides, including disarticulated epiplastra and almost complete entoplastron; MNA V1563, a fragmentary skeleton, including articulated partial left hyoplastron, entoplastron, right and left epiplastra, and fused partial left cleithrum; TMM 43658-1, partial skeleton consisting of disarticulated shell and limb elements, including articulated fragment of anterior plastron lobe consisting of medial epiplastral parts, anterior half of entoplastron, and the bases of cleithra (Figs. 3C, 4); UCMP 150073, partial shell with almost complete, articulated anterior plastral lobe, no cleithra preserved; UCMP 150074, partial skeleton consisting of almost complete plastron, including entoplastron and left epiplastron, no cleithra preserved (Fig. 3D).

Specimens were prepared and examined using a binocular microscope. In addition, TMM 43658-1 was scanned using the University of Texas High Resolution x-ray CT Facility (Rowe et al., 1997; Ketcham and Carlson, 2001) to observe any sutural relationships between elements that may exist within the specimen.

DESCRIPTION

The cross-shaped entoplastron of *Kayentachelys aprix* is characteristic of basal turtles (Fig. 3D). An anterior process extends to the anterior rim of the plastron, thus blocking medial contact of the epiplastra. Pronounced lateral processes are present, but they do not reach the lateral margin of the anterior plastral lobe as in *Proganochelys quenstedti*. The posterior process of the entoplastron is not fully preserved in any specimen, but appears to have almost reached the hyoplastral–mesoplastron contact posteriorly.

The epiplastra of *K. aprix* are small elements that form the anterolateral margins of the plastron. Their sutures with the neighboring plastral elements are clearly visible in all specimens. Posterolaterally the epiplastra contact the hyoplastra along a simple, interdigitating suture. The remaining sutures with the entoplastron, in contrast, are complex. Medially the epiplastra contact the entoplastron along oblique sutures that render the visceral exposure of the anterior plastral process narrower relative to the external exposure. Posteromedially, the epiplastra envelop the entoplastron by means of a short, massive ridge extending below and an expansive, and notably thin flange overlapping above.

Partial cleithra are present in several specimens, but notably absent from others. When present, the cleithra are positioned over the posteromedial, overlapping contact of the epiplastra with the entoplastron. In the specimen in which the most complete cleithrum is preserved (MCZ 8917; Fig. 3A, B), this element is a slender rod that tapers dorsally and broadens ventrally at the articulation with the epiplastron and entoplastron. The cleithrum is oriented posterodorsally (at about 50 degrees from horizontal) and is inclined slightly laterally. The full extent of the cleithrum is unclear even in this specimen because the dorsal end is broken. However, based on the degree of tapering and the lack of articular facets on the carapace of

Fig. 3. Stereoscopic photographs of *Kayentachelys aprix* specimens. A, B – MCZ 8917, an almost completely preserved left cleithrum (cth) fused to an isolated left epiplastron (epi): A – ventral view; B – left lateral view. A crack along the base of the cleithrum (arrow) does not represent a suture, but rather a break to the fossil. C – Ventral view of TMM 43658-1, isolated fragment of the anterior plastral lobe, consisting of the partial left and right epiplastra, the anterior portion of the epiplastron, and the bases of both cleithra (arrows). D – Ventral view of UCMP 150074, an almost complete anterior plastral lobe, consisting of the left epiplastron (epi), the entoplastron (ent), and both hyoplastra (hyo). The overview image below was digitally enhanced to emphasize the location of the articular scar of the missing left cleithrum (arrows) and the suture between the left epiplastron and the entoplastron. All scale bars equal 0.5 cm.
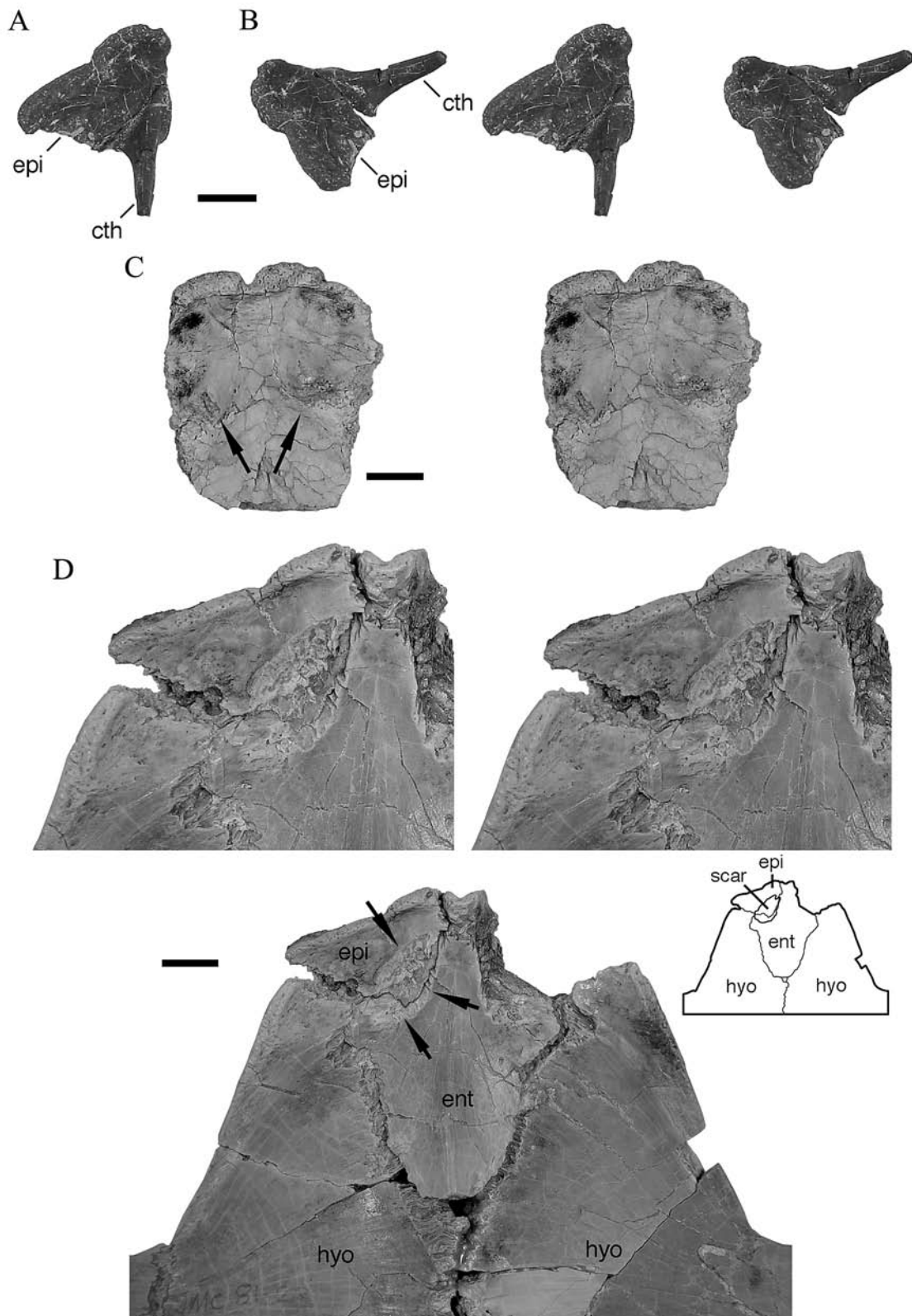
all known material of *Kayentachelys aprix* material, it appears certain that the cleithrum did not possess a bony contact with the carapace, as seen in *Proganochelys quenstedti*. In cross-section, the base of the cleithrum has the shape of an acute triangle, with its apex pointing anteriorly. The posterior, short side of the triangle bears a shallow groove of uncertain function. In all specimens in which the cleithra are preserved, the posterior overlapping contact of the cleithrum with the entoplastron is clearly visible, but an anterior suture with the epiplastra is absent, indicating that the cleithrum and epiplastra are fully fused with one another in this area. However, high resolution CT scans of TMM 43658-1 (Figs. 3C) reveal the persistence of a dense lamellar zone (arrows, Fig. 4), which represents the original cortical contact of the cleithrum with plastral elements. Furthermore, the denser cleithra are histologically distinct from the underlying elements.

The remaining specimens of *Kayentachelys aprix*, particularly UCMP 150074, provide a further perspective on cleithral attachment. In these specimens, cleithra are completely missing and the plastron reveals a slightly depressed articular surface with no signs of breakage (Fig. 3D). Furthermore, those parts of underlying epiplastron that form much of this surface are fragile, but intact, indicating that the cleithra disarticulated easily.

DISCUSSION

The presence of cleithra in primitive turtles has not always been controversial. Jaekel (1915) was the first to report well-developed cleithra for the Upper Triassic turtle *Stegochelys dux*, a taxon currently recognized as a junior synonym of *Proganochelys quenstedti* (Gaffney, 1990). Although not specifically stated, Jaekel's identification appears to have been primarily driven by the topological position of these structures anterior to the scapulae and by comparisons with the pectoral
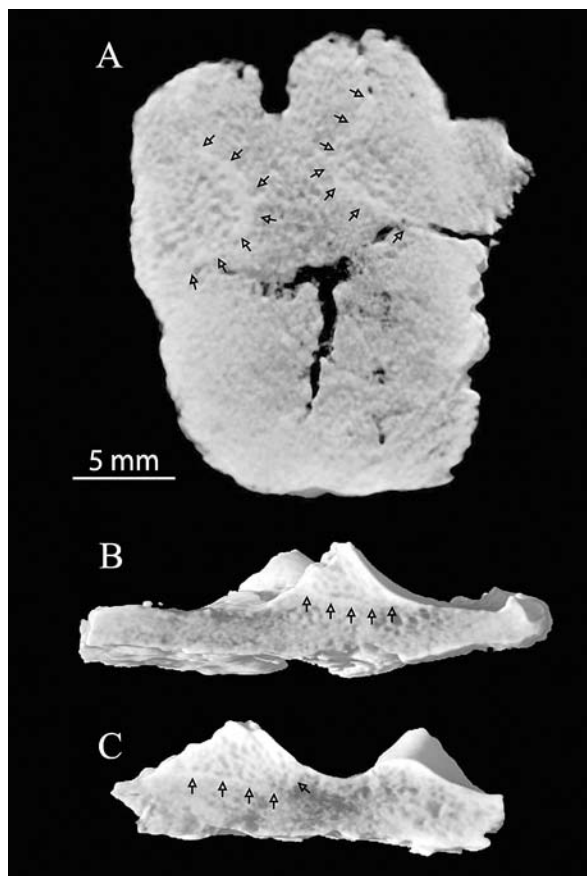

Fig. 4. Computer-generated volumetric renderings of the epiplastron and cleithra in *Kayentachelys aprix* (TMM 43658-1), based on high-resolution X-ray CT imagery consisting of 135 horizontal slices gathered at interslice spacings («slice thickness») of 0.0588 mm. A – horizontal slice, anterior toward top of image; B – parasagittal section; C – coronal section. The small arrows indicate the lamellar bone that separate the cleithra from the plastron.

girdle of the primitive tetrapod *Archegosaurus decheni* (Goldfuss, 1847). Unfortunately, the accompanying description is rather short, leaving unclear whether Jaekel (1915) was aware of the detailed morphology of these structures, and in particular the ventral contact of the cleithra with the dorsal surface of the plastron.

The presence of cleithra was not doubted in *Proganochelys quenstedti* for most of the following century until Gaffney (1990) carried out a comprehensive morphological review of this taxon.

Although Gaffney originally believed that cleithra were present in *P. quenstedti*, he ultimately concluded that the structures were instead outgrowths of the epiplastra. An explicit rational was not provided. However, given that well-developed ascending processes of the clavicle occur in many primitive tetrapods and that the clavicle is homologous with the epiplastron, an interpretation of these structures as processes of the epiplastron appears plausible.

A third possibility was put forward by Lee (1996) who suggested that the vertical anterior projections of the plastron of primitive turtles represent the clavicles and that the epiplastra are separate bones that must be considered neomorphs (see Table 1 for comparison with the other hypotheses). Although an explicit rationale was not provided, it is noteworthy that Lee's (1997) interpretation was formulated with explicit reference to Gaffney's (1990) conclusion that cleithra were absent.

An overwhelming amount of evidence indicates that the epiplastra of extant hard-shelled turtles derive partially or fully from embryological precursors that must be interpreted as clavicles (e.g., Zangerl, 1939, 1969; Walker, 1947; Williams and McDowell, 1952; Cherepanov, 1984, 1997, 2005; Rieppel, 1993; Gilbert et al., 2001; Sheil and Greenbaum, 2005). A crucial point is the developmental relationship of the processes to the epiplastra. If the processes are outgrowths of the epiplastra (i.e., the clavicles), the interpretation of Gaffney (1990) is validated. However, if the processes are proposed to be elements separate from the epiplastra (Lee, 1996, 1997) and the epiplastra are indeed formed by clavicular precursors, then

it is logically impossible for the projections to be clavicles as well. Lee's homology scheme can thus be rejected. The two primary competing hypotheses are therefore that these structures are either cleithra (following Jaekel, 1915) or the ascending processes of the epiplastra (following Gaffney, 1990).

The hypothesis that these elements are ascending clavicular processes would be supported by the following interpretations or features: 1) they are true outgrowths of the epiplastron, 2) they are inseparate from the epiplastron, 3) postmortem breakage would likely occur along the narrower part of the process, not between the broad base and the epiplastron, and 4) the character of the bone of the process and epiplastron are indistinguishable. None of these features or interpretations is confirmed by this study. In contrast, the hypothesis that these elements are cleithra is directly supported by the observations that 1) the structures are ontogenetically independent from the epiplastra (clavicles), 2) even when fused with the epiplastra, sutural evidence of their own identity is present during later ontogeny, 3) the structures separate along the ontogenetic sutural contacts under postmortem mechanical stress, and 4) the bone density differs from that of the bordering epiplastra, and an abrupt transition in bone density is seen at the cleithral-epiplastral contact. Inasmuch as both the cleithrum and the clavicle are dermal elements and positioned anterior to the scapula, no additional information can be gained from topological arguments.

Although not explicitly stated, Gaffney (1990) observed some of these features when assessing the identity of these structures in *Proganochelys quenst-*

TABLE 1. Comparison of primary homology assessments to the anterior plastral region of primitive turtles.

	Jaekel (1915)	Gaffney (1990)	Lee (1996)
epiplastral process	cleithrum	clavicle	clavicle
epiplastron	clavicle	clavicle	neomorph
entoplastron	interclavicle	interclavicle	interclavicle

edti (Gaffney, pers. comm. WGJ, 2003). Gaffney's careful external analysis of all available *P. quenstedti* material did not reveal any sutures along the base of the processes and he consequently concluded that they were part of the epiplastra. A similar observation can be made for about half of the available material for *Kayentachelys aprix*. In addition, in the same specimens of *K. aprix* and all available specimens of *P. quenstedti,* the process tends to break well above its base, indicating a firm connecting between the process and the epiplastron.

Although all of the material of *Proganochelys quenstedti* and some specimens of *Kayentachelys aprix* suggest that the processes represent outgrowths of the epiplastra, the remaining *K. aprix* material provides multiple lines of evidence that the processes should be regarded as independent structures. We conclude that the structures in question are cleithra that initially are independent but fuse with the epiplastra during later ontogeny. Unfortunately, the available *K. aprix* material does not allow an assessment of the proposed ontogenetic fusion, because all specimens in this study are approximately equal in size. Modest size differences do exist, but these cannot be quantified rigorously because no two specimens possess comparable landmarks for measurement.

Considering that equivalent structures can be found in other primitive turtles, such as *Proterochersis robusta* and *Palaeochersis talampayensis*, our finding firmly establishes the presence of cleithra in primitive turtles and indicates that cleithra were lost in the turtle lineage independently of the loss seen in the mammal stem lineage and in saurian reptiles (Matsuoka et al., 2005).

The presence of cleithra in primitive turtles has intriguing phylogenetic implications. Placement of turtles within crown Sauria, a clade that demonstrably lacks cleithra, requires the unparsimonious conclusion that cleithra reappeared along the phylogenetic stem of turtles, only to be subsequently lost again. An *ad hoc* hypothesis that

these structures should not be considered to have been derived from girdle elements at all, but rather are neomorphs, does not make a difference, because the acquisition of neomorphs would also add an additional step. Naturally, the presence of cleithra (or equivalent neomorphs) in turtles is a just a single character that may be rendered homoplastic by a comprehensive phylogenetic analysis.

The presence of cleithra in the primitive turtle *Kayentachelys aprix* has interesting implications regarding basal turtle evolution as well. When first described, this taxon was assessed to be the most basal known representative of the cryptodiran stem lineage (Gaffney et al., 1987). Considering the absence of cleithra in all living pleurodires and cryptodires, this would imply the loss of cleithra in both lineages. A recent, comprehensive analysis of basal turtles relationships, however, that used 136 osteological characters with 171 derived character states for 45 fossil and 22 living species of turtles (Joyce, In Press) placed *K. aprix* along the phylogenetic stem of crown turtles. Despite this reassessment of the placement of *K. aprix*, this analysis does not reveal the loss of cleithra to be an unambiguous synapomorphy of crown Testudines. Instead, the presence of remnant cleithra in the unambiguous stem cryptodire taxa Baenidae and *Xinjiangchelys latimarginalis* indicates that these structures were lost independently along the stem lineages of crown Pleurodira and Cryptodira. Cleithra were thus lost at least twice in turtles (Fig. 5).

CONCLUSIONS

A morphological review of all *Kayentachelys aprix* material reveals that this taxon possesses cleithra. In addition to topological arguments, this conclusion is primarily supported by observations that demonstrate this element to be developmentally independent from the epiplastron and hence not an outgrowth thereof. The equivalently placed «epiplastral processes» of other primitive
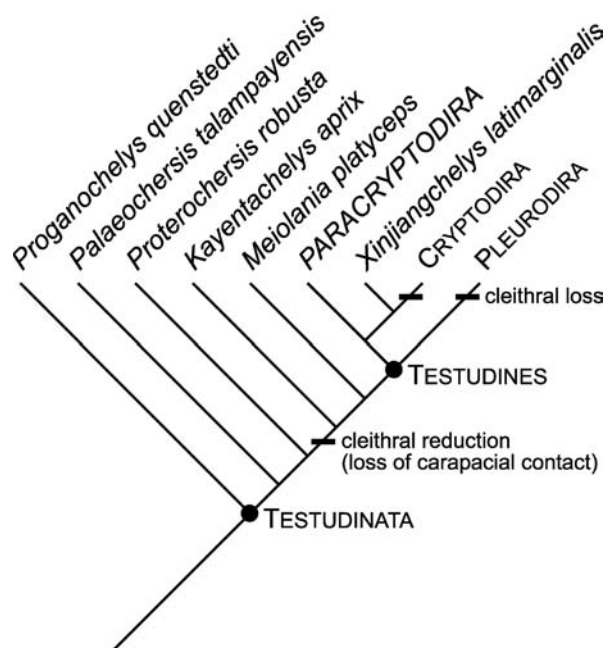
Fig. 5. A phylogenetic hypothesis of basal turtles revealing the independent loss of cleithra along the phylogenetic stem of both crown Pleurodira and Cryptodira.

turtles are reinterpreted as cleithra that are fused with the epiplastra during ontogeny. The presence of cleithra in primitive turtles is a character that supports a basal placement of turtles within Reptilia, rather than a placement within crown Sauria, a clade that demonstrably lacks cleithra, which would imply the reformation and subsequent loss of cleithra along their phylogenetic stem. Finally, regardless of the phylogenetic position of turtles within Amniota, fossil evidence reveals that cleithra were lost twice within the turtle crown group.

REFERENCES

Baur G. (1887), «Ueber den Ursprung der Extremitaeten der Ichthyopterygia,» *Ber. Versamml. Oberrhein. Geol. Ver.*, **20**,17-20.

Bojanus L. H. (1819), *Anatome* Testudinis europaeae, Josephus Zawadzkus, Vilna.

Carroll R. L. (1988), *Vertebrate Paleontology and Evolution*, Freeman and Company, New York.

Cherepanov G. O. (1984), «On the nature of the anterior elements of the plastron in turtles,» *Zoologicheskii Zhurnal*, **63**, 1529-1534. [in Russian with English abstract]

Cherepanov G. O. (1997), «The origin of the bony shell of turtles as a unique evolutionary model in reptiles,» *Russ. J. Herpetol.*, **4**, 155-162.

Cherepanov G. O. (2005), «Morphogenesis of the bony shell and a problem of Testudinata origin,» *Zoologicheskii Zhurnal*, **84**, 464-475. [in Russian with English abstract]

Clack J. E. (2002), *Gaining Ground: The Origin and Evolution of Tetrapods.* Indiana University Press, Bloomington.

Clark J. M. and Fastovsky D. E. (1986), «Vertebrate biostratigraphy of the Glen Canyon Group in northern Arizona,» in: Padian K. (ed.), *The Beginning of the Age of Dinosaurs*, Cambridge Univ. Press, Cambridge, pp. 285-301.

Coates M. I., Jeffery J. E. and Ruta M. (2002), «Fins to limbs: What the fossils say,» *Evol. Devel.*, **4**, 390-401.

Cope E. D. (1877), «On reptilian remains from the Dakota Beds of Colorado,» *Proc. Amer. Philos. Soc.*, **17**, 193-196.

deBraga M. and Rieppel O. (1997), «Reptile phylogeny and the interrelationships of turtles,» *Zool. J. Linn. Soc.*, **120**, 281-354.

Duellman W. E. and Trueb L. (1986), *Biology of Amphibians*, McGraw-Hill, New York.

Fraas E. (1913), «*Proterochersis*, eine pleurodire Schildkroete aus dem Keuper,» *Jahr. Ver. Vaterl. Naturkd. Württ.*, **69**, 13-90.

Gaffney E. S. (1990), «The comparative osteology of the Triassic turtle *Proganochelys*,» *Bull. Am. Mus. Nat. Hist.*, **194**, 1-263.

Gaffney E. S., Hutchison J. H. Jenkins F. A. and Meeker L. J. (1987), «Modern turtle origins: The oldest known cryptodire,» *Science*, **237**, 289-291.

Gaffney E. S., Meylan P. A. and Wyss A. R. (1991), «A computer assisted analysis of the relationships of the higher categories of turtles,» *Cladistics*, **7**, 313-335.

Gauthier J., Kluge A. G. and Rowe T. (1988), «Amniote phylogeny and the importance of fossils,» *Cladistics*, **4**, 105-209.

Gilbert S. F., Loredo G. A., Brukman A. and Burke A. C. (2001), «Morphogenesis of the turtle shell: the development of a novel structure in tetrapod evolution, » *Evol. Devel.*, **3**, 47-58.

Goldfuss G. A. (1847), «Über das älteste der mit Bestimmtheit erkannten Reptilien, einen Krokodilier, und einige neue fossile Fische aus der Steinkohlen-Formation,» *N. Jb. Mineral. Geognos. Geol.*, **1847**, 400-404.

Jaekel O. (1915), «Die Wirbeltierfunde aus dem Keuper von Halberstadt. Serie II. Testudinata. Teil 1. *Stegochelys dux* n. g. n. sp.,» *Palaeontol. Zeitsch.*, **2**, 88-214.

Jarvik E. (1996), «The Devonian tetrapod Ichthyostega,» *Fossils and Strata*, **40**, 1 – 213.

Joyce W. G. (In Press), «Phylogenetic Relationships of Basal Turtles,» *Bull. Peabody Mus. Nat. Hist.*

Ketcham R. A. and Carlson W. D. (2001), «Acquisition, optimization and interpretation of X-ray computed tomographic imagery: applications to the geosciences.» *Comput. Geosci.*, **27**, 381-400.

Laurin M. and Reisz R. R. (1995), «A reevaluation of early amniote phylogeny,» *Zool. J. Linn. Soc.*, **113**, 165-223.

Lee M. S. Y. (1996), «The homologies and early evolution of the shoulder girdle in turtles,» *Proc. R. Soc. Lond. B*, **263**, 111-117.

Lee M. S. Y. (1997), «Pareiasaur phylogeny and the origin of turtles,» *Zool. J. Linn. Soc.*, **120**, 197–280.

Khosatzky L. I. (1997), «Big turtle of the late Cretaceous of Mongolia,» *Russ. J. Herpetol.*, **4**, 148-154.

Kumazawa Y. and Nishida M. (1999), «Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: Statistical evidence for archosaurian affinity of turtles,» *Mol. Biol. Evol.*, **16**, 784-792.

Matsuoka T., Ahlberg P. E., Kessaris N., Iannarelli P., Dennehy U., Richardson W. D., McMahon A. P. and Koentges G. (2005), «Neural crest origins of the neck and shoulder,» *Nature*, **436**, 347-355.

Owen R. (1886), «Description of fossil remains of two species of *Megalania* genus (*Meiolania*, Ow) from Howe's Island,» *Proc. R. Soc. Lond.*, **40**, 315.

Rieppel O. (1993), «Studies on skeleton formation in reptiles: Patterns of ossification in the skeleton of *Chelydra serpentina* (Reptilia, Testudines),» *J. Zool.*, **231**, 487-509.

Romer A. S. (1956), *Osteology of the Reptiles.* Univ. of Chicago Press, Chicago.

Rowe T., Kappelman J., Carlson W. D., Ketcham R. A. and Denison, C. (1997), «High-Resolution Computed Tomography: a breakthrough technology for Earth scientists,» *Geotimes*, **42**, 23-27.

Rougier G. W., Fuente M. S. de la and Arcucci A. B. (1995), «Late Triassic turtles from South America,» *Science*, **268**, 855-858.

Sheil C. A. and Greenbaum E. (2005), «Reconsideration of skeletal development of Chelydra serpentina (Reptilia: Testudinata: Chelydridae): Evidence for intraspecific variation, » *J. Zool.*, **265**, 235-267.

Walker W. F. (1947), «The development of the shoulder region of the turtle, *Chrysemys picta marginata*, with special reference to the primary musculature,» *J. Morphol.*, **80**, 195-249.

Williams E. E. and McDowell S. B. (1952), «The plastron of soft-shelled turtles (Testudinata, Trionychidae): A new interpretation,» *J. Morphol.*, **90**, 263-279.

Young C.-C. and Chow M.-C. (1953), «New fossil reptiles from Szechuan China,» *Acta Sci. Sinica*, **2**, 216-243.

Zangerl R. (1939), «The homology of the shell elements in turtles,» *J. Morph.*, **65**, 383-409.

Zangerl R. (1969), «The turtle shell,» in: Gans C., Bellairs A. and Parsons T. S. (eds.), *The Biology of the Reptilia, Volume 1,* Academic Press, London, pp. 311-339

Zardoya R. and Meyer A. (2000), «Mitochondrial evidence on the phylogenetic position of caecilians (Amphibia: Gymnophiona),» *Genetics*, **155**, 765-775.