Pulmonary anatomy in the Trionychia and its bearing on cryptodiran evolution

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Background. The relationships among cryptodiran turtles often appear controversial depending on the approach followed (morphology vs. molecules). One controversy concerns the placement of the Trionychia (*Carettochelys insculpta* Ramsay, 1886 + Trionychidae), which usually is treated as sister taxon of Kinosternidae and thereby nested well within Cryptodira (morphology), or as sister taxon of all remaining cryptodirans (molecules). The aim of the present study is to introduce new data on the respiratory apparatus to this discussion.

Methods. Lungs and associated structures (extrapulmonary airways, coelomic integration, respiratory musculature), of *C. insculpta* and that of several Trionychidae were examined macroscopically. The excised lungs were dried, opened and photographed, or imaged using a µCT device.

Results. The lungs show a characteristic separation from the viscera by the post-pulmonary septum (PPS), which varies in its extent from highly incomplete to complete. The primary respiratory musculature is composed of the *musculus transversus thoracis*, *m. t. abdominis* and *m. obliquus abdominis*. The lungs of *C. insculpta* superficially resemble that of the Trionychidae, but differ markedly from them and all other turtles studied so far in that they exhibit a medially located, almost sac-like and elongated, huge additional chamber. The right extrapulmonary bronchi of all trionychians examined are shorter than the left ones, causing a dislocation of the trachea to the right side of the cervical region.

Discussion. The principal coelomic compartmentalization by the PPS agrees with previous studies on turtles, but indicates the convergent development of a completely separated pleural cavity in Trionychidae. The presence and anatomy of the respiratory musculature is in agreement with that recently inferred for turtles as a whole. Our data confirm the evolutionary distinctiveness of the taxon Carettochelyidae with its sole extant member *C. insculpta* based on their pulmonary autapomorphy. The monophyly of the Trionychia, as defined above, is

supported by several potential synapomorphies of the respiratory system. Most important, however, is that our data, especially on the extrapulmonary airways, provide morphological support for the predominantly molecular-based hypothesis of an early split of the Cryptodira into the Trionychia and the remaining lineages. The displacement of the trachea to the right side contrasts with the situation found in all remaining cryptodirans, in which the trachea lies to the left of the esophagus (or an extreme reduction of tracheal length as in Testudinidae). This anatomical dichotomy could be related to the evolution of the specialized mechanism of neck retraction in cryptodirans. Our study points up the importance of so-called soft-tissue characters in inferring the evolutionary relationships of organisms in general, and of turtles in particular.