New data on the oldest turtles: revision and reconsideration of Proterochersidae

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Background. The origin of turtles, their earliest evolution and the homologies of the elements building their shell are still enigmatic and remain an object of ongoing discussion and research. Although the oldest fully shelled turtle – *Proterochersis robusta* from the Lower Stubensandstein (Norian) of Germany – was described more than a century ago, until recently it was mostly ignored by researchers. This is surprising, not only because of its notable stratigraphic position, but also due to the critical significance of this taxon in two competing hypotheses of turtle interrelationships. The divergence time of two main branches of Testudines crown group depends on whether *Proterochersis* is a basal pleurodire or a stem turtle.

Methods. A detailed study of the German material of *Proterochersis* and *Murrhardtia* was performed by the author and the available specimens were compared with still growing collection of proterochersid remains from the Norian location in Poręba (Poland).

Results. Two controversial taxa from Germany, *Proterochersis intermedia* and *Murrhardtia staeschei* are proved to be the synonyms of *P. robusta*. Establishment of another two proterochersid taxa is proposed and new primitive postcranial characters are recognized, supporting the stem position of Proterochersidae on the turtle phylogenetic tree.

Discussion. Two general hypotheses concerning the split time of Cryptodira and Pleurodira are functioning in the literature, and *Proterochersis* plays a crucial role in these considerations. According to traditional view, this taxon is the oldest side-necked turtle, based on the sutural connection between its pelvis and shell. Numerous recent analyses tended to allocate the Pleurodira much higher on the tree, resulting in stem position of *Proterochersis*, though such placement usually lacked a strong support. This was caused by an incompletness of *Proterochersis* material (only shells) and errors in interpretation of some characters. New data, gathered mostly from the Polish – much more complete and well

preserved – specimens, supports the basal position of Proterochersidae and provides new insights in the ancestral structure of the turtle shell.