Available online at www.sciencedirect.com
ScienceDirect
Palaeoworld xxx (2017) xxx–xxx
Palaeoworld
www.elsevier.com/locate/palwor

A simple method for inferring habitats of extinct turtles

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Received 16 February 2016; received in revised form 15 February 2017; accepted 15 February 2017

Abstract

We present a simple method of inferring extinct turtle habitats based on four measurements of the shell (two ratios). These ratios are the maximum width of the carapace to the width of the abdominal-femoral sulcus of the plastron, and the ratio of the carapace length to the total height of the shell. Based on an extensive database, extant terrestrial turtles do not have a carapace-width-to-plastron-width ratio that exceeds 1.76. This carapace-width-to-plastron-width ratio in the Triassic turtle *Proganochelys* is ~2.1, and the length-to-height ratio of *Proganochelys* is ~2, which suggest an aquatic habitus. Triassic *Proterochersis* has a carapace-to-plastron-width ratio of 1.89, and a length-to-height ratio of 1.82, which are in the terrestrial range based on discriminant analysis. Inferences based on forelimb proportions and shell bone histology indicate a terrestrial paleoecology for *Proganochelys*. Conversely, femur morphology and shell cross sections indicate a semi-terrestrial to aquatic paleoecology of *Proganochelys*. The new method presented here indicates the early turtle *Proganochelys* was aquatic and *Proterochersis* was terrestrial in habitus.

Keywords: Testudines; Aquatic; Terrestrial; Paleoecology; *Proganochelys*; *Proterochersis*

1. Introduction

The phylogenetic affinities and ecology of the Triassic turtles *Proganochelys* (Fig. 1) and *Proterochersis* have long been in dispute. Both of these species are known from the Late Triassic (Norian) of Germany and were the first Triassic turtles described (Baur, 1887; Fraas, 1913; Gaffney, 1990). The ecology of *Proganochelys* has also been suggested to have a bearing on the identification of possible turtle ancestors (Joyce and Gauthier, 2004; Scheyer and Sander, 2007; Benson et al., 2011). We seek to use the shells of modern turtles to create a comparative basis to identify the likely habitus of *Proganochelys* and *Proterochersis*. To do so, we present a simple method of inferring extinct turtle habitats based on four measurements of the shell (two ratios).

2. Background

Modern turtle shell proportions are closely related to the environment in which the turtle lives (e.g., Rivera, 2008; Benson et al., 2011; Stayton, 2011; Rivera et al., 2014). Thus, phylogenetically closely-related turtles with a wide span of environmental preferences will often display great variation in shell shape and appearance that correlates with those preferences. In many cases, this results in an overall shell shape more similar to that of other turtles with similar environmental preferences than to close relatives that live in different environments. For example, taxonomically, aquatic painted turtles (*Chrysemys)* are much more closely related to terrestrial box turtles (*Terrapene)* than to terrestrial tortoises (Testudinidae), yet shell shape in box turtles more closely resembles that of tortoises than painted turtles (Crawford et al., 2014; Spinks et al., 2016). The particular mode of locomotion within the aquatic environment does not appear to impact shell shape significantly (Munteanu, 2014).

Recently, several methods have been used to infer fossil turtle habitats, specifically, the question of whether an extinct species was aquatic or terrestrial (Joyce and Gauthier, 2004; Scheyer and Sander, 2007; Benson et al., 2011). These methods have

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http://dx.doi.org/10.1016/j.palwor.2017.02.001
1871-174X/

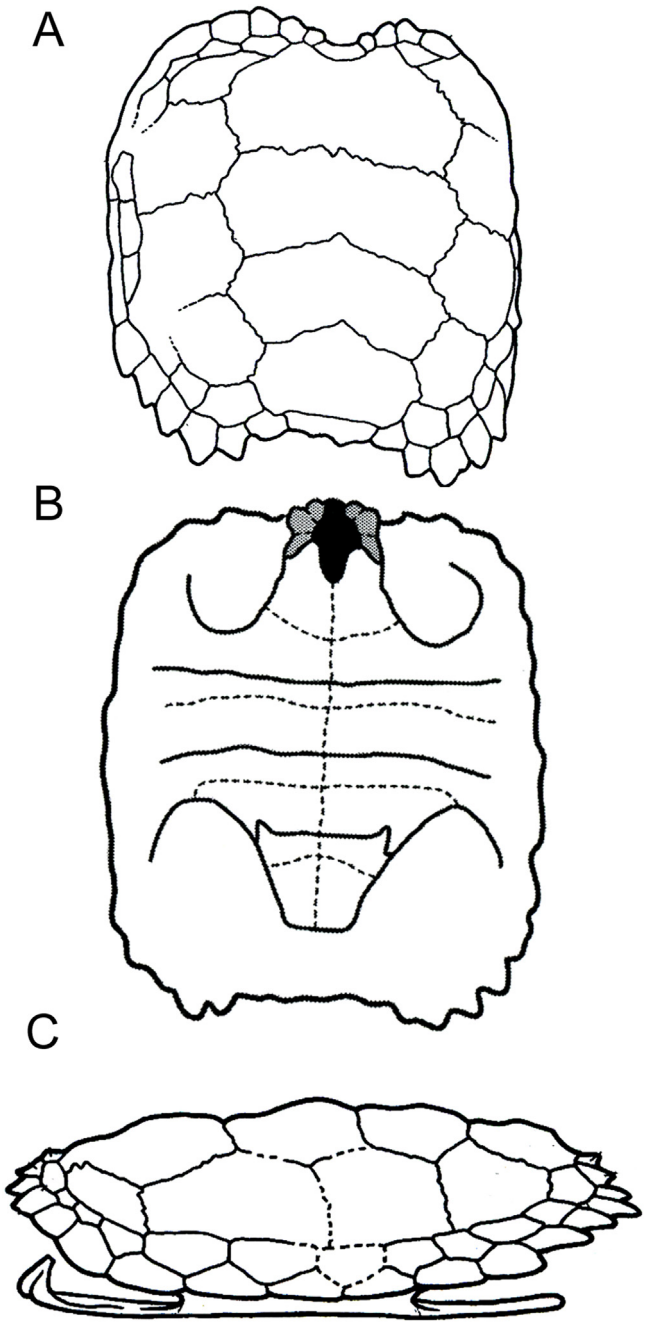

Fig. 1. Various images of *Proganochelys*. (A) SMNS 17204, line drawing of dorsal view from Gaffney (1990); (B) line drawing of the ventral view from Joyce (2007); (C) SMNS 16980, line drawing of reconstructed left lateral view from Gaffney (1990).

also been applied to the habitats of the earliest turtles, of Late Triassic age, to narrow the list of likely turtle ancestors to those with similar inferred ecologies (Joyce and Gauthier, 2004; Joyce, 2015). Here, we present a new, and relatively simple, method for inferring extinct turtle habitats and use it to infer the habitats of some of the oldest turtles.

All methods of inferring the paleoecology of Triassic fossil turtles based on morphological features, including ours, share a few key problems. These include: (1) The limited sample size available for Triassic turtle species. (2) Most of the fossils available are incomplete to varying degrees. (3) All modern species of terrestrial turtles are testudinoid, a relatively recent (Paleocene–Recent) and substantially derived taxonomic group that is being compared to their much more primitive, distant Late Triassic relatives.

In addition, it could be that the lack of a neck retraction mechanism in Triassic turtles may have impacted shell shapes. However, we believe that the effect of the addition of a neck retraction method, which took place by the Late Jurassic, has had a limited impact on shell shape selection. This hypothesis is based on the observations of Rivera (2008), Stayton (2011), Domokos and Varkonyi (2008), and Rivera et al. (2014), which suggest that the shape of modern aquatic turtle shells are highly influenced by hydrodynamics, which should remain constant through time. Further, the self-righting method of pushing over with a strong flexible neck should be achievable without the modern retraction method. In terrestrial turtles, there is a preference toward strong-domed shapes (Domokos and Varkonyi, 2008; Stayton, 2011). Stayton (2011) notes that these shapes diverge from the strongest shapes modeled, but this may be the result of the adaptation toward having no static points to self-right (Domokos and Varkonyi, 2008). This self-righting, in particular, is a uniquely difficult problem for land turtles. Furthermore, actualism suggests that it is likely the mechanical solutions to these issues have remained similar through geologic time.

Zug (1971) pointed out that terrestrial species of living turtles usually have a ventrally closed intertrochanteric fossa. We attempted to provide a more quantitative assessment of the degree of closure by measuring the depth of this fossa between the two tronchaters relative to the length of the femur (see Supplementary data S1). As a result we note a clear trend of more terrestrial turtles having this fossa reduced in size. Zug (1971) provided no functional explanation for this correlation, but we speculate it may be related to the change in walking gait between terrestrial and aquatic turtles addressed in his paper. This open intertrochanteric fossa is consistent with our observations of the limbs of modern turtles and appears to be present in closely related turtles (e.g., *Terrapene ornata* and *Terrapene coahuila*). The Triassic turtles *Proganochelys* and *Odontochelys* have a pronounced intertrochanteric fossa, which suggests an aquatic paleoecology based on Zug (1971).

The method of Joyce and Gauthier (2004) utilized measurements of the length of the manus, ulna, and humerus to infer turtle ecology/paleoecology. This study found that among living turtles, humerus-to-ulna length ratio is nearly constant, whereas ulna-to-manus-length ratios vary with environments. Joyce and Gauthier (2004) divided turtles into six ecological categories: primarily on land; primarily on land, seldom in water; primarily on land, often in water; living in stagnant or small bodies of water; living in all bodies of water; and living in moving or large bodies of water. However, the small sample sizes (generally one specimen) of Joyce and Gauthier's study precluded estimating intraspecific variation in the forelimb ratios, so it is unclear how much these may have varied within a species.

Benson et al. (2011) pointed out that the tortoise *Kinixys* is more aquatic in its ecology than Joyce and Gauthier (2004)

Please cite this article in press as: Lichtig, A.J., Lucas, S.G., A simple method for inferring habitats of extinct turtles. Palaeoworld (2017), http://dx.doi.org/10.1016/j.palwor.2017.02.001