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THEROPOD BREATHING MECHANISM: THE OSTEOLOGICAL EVIDENCE

Recently, some authors have proposed, based on two small theropod dinosaurs preserving soft tissues (the Chinese *Sinosauropteryx* and the Italian *Scipionyx*), the hypothesis that theropods possessed a diaphragm assisted by a hepatic piston device as the mechanism to ventilate the lungs. Ruben *et al.* (1997, 1999) based this hypothesis on the idea that the theropod pelvic morphology is similar to that of crocodiles, on the absence of a completely closed thoracic box in theropods and on their interpretation of the soft tissue remains of both *Sinosauropteryx* and *Scipionyx*. This interpretation includes a complete abdominal-thoracic separation and a liver that extends from the ventral body wall to the vertebral column (both in *Sinosauropteryx* and *Scipionyx*), the position of both the trachea (ventral) and the posterior colon (dorsal) (in *Scipionyx*), and muscular fibers located cranially to the distal part of the pubis, identified as part of the diaphragmatic muscles (also in *Scipionyx*). Nevertheless, the identification of these soft structures has been just based on their visual aspect and position, assuming that they have been preserved undisplaced and undisturbed (which is dangerous to assume in a two-dimensional specimen), and no specific analyses have been made (as scanning electron microscopy and scanning microprobe analyses). The used methodology does not allow a reasonable guarantee in the identification of soft tissue, as can be exemplified by the misidentification of the soft tissues of *Pelecanimimus* (see Pérez-Moreno *et al.*, 1994, and Briggs *et al.*, 1997 for the correct identification). Moreover, alternative explanations can be suggested for the liver structure [staining of the matrix produced by the stomach acids or the decomposition of the soft tissues (Currie, 1998)] or for the diaphragmatic muscle fibers (muscles from the abdominal wall or wrinkled skin).

A detailed comparison of the pelvic morphology clearly shows that both pubic disposition and morphology are clearly different between theropods and crocodiles. While the crocodilian pelvis present a propubic disposition (the primitive condition for Archosauria), the non avian theropod pubis range from propubic and mesopubic to a opisthopubic disposition. The morphology of the pubic boot is also very different, being more cranially developed in crocodiles and more caudally developed in non avian theropods [the cranial part can even be completely absent, as in some dromaeosaurids and *Unenlagia* (Novas and Puerta, 1997)]. Moreover, the pubis in extant crocodiles and relatives is separated from the ilium by a cartilage (the pars acetabularis), not participating in the acetabulum but having a certain degree of mobility with respect to the other elements of the pelvis. On the contrary, the theropod (avian and non avian) pubis participate in the acetabulum and it is fixed to both the ilium and ischium, with no mobility among them. A hepatic piston breathing system requires a mobile pubis to avoid tilting movements of the pelvis when the diaphragmatic muscles are contracted, and this kind of pubis is absent in theropods. The original description of

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Pelecanimimus (from the Early Cretaceous Spanish Konservat-Lagerstätte of Las Hoyas) was just based on the slab, as the counterslab was still unprepared. After the preparation of the counterslab, new features have been discovered.

One of the more exciting traits is the presence of a completely closed thoracic box, with well ossified sternal ribs articulated to both the lateral margins of the large sternum and the thoracic ribs. All the joints present well developed articulation surfaces (which are slightly ginglymous) for the rib/sternum and thoracic rib/sternal rib relative movements. A completely closed thoracic box (or features suggesting its presence) has also been found in other theropods, as oviraptorosaurs (Clark, Norell and Chiappe, 1998) and dromaeosaurids (Norell and Makovicky, 1998). Thus, the thoraco-abdominal architecture (with the presence of a singular pattern of articulation of the gastral ribs) of some non avian theropods suggests a highly kinetic capability of the laterally flattened thoracic box, probably associated to a costal breathing mechanism. In fact, a costal breathing mechanism seems to be primitive for the tetrapod clade. Some groups, as mammals or derived crocodiles, have developed a singular, autopomorphic diaphragmatic lung ventilation. Theropod dinosaurs retain the primitive costal breathing mechanism. This primitive mechanism has been improved along the evolutionary history of Theropoda, reaching the sophisticated parabronchial and air sacs based mechanism present in extant birds.

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