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Notes

The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications

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Abstract: An acid- and transfer-prepared, juvenile *Rhamphorhynchus muensteri*, despite some fragmentation, is in an excellent state of three-dimensional preservation, exposing exquisite anatomical details hitherto unknown in other pterosaurs. Here we describe the axial pneumatizations of the cervical and anterior dorsal vertebrae and the sternum. The interior of the cervical centra is subdivided into a pair of large camerae, presumably by air sacs entering by large pleurocoels in the sides of the centra. This so-called 'camerate' type of pneumatization is hitherto unknown in pterosaurs. Another excavation enters from the ventral side into the base of the neural arch and stretches between the pre- and postzygapophyses. This type of cavity also penetrates from the ventral side into the base of the first few transverse processes of the dorsal vertebrae, although these lack central pleurocoels. The cristospine also has a complex pneumatic foramen.

Skeletal pneumaticity is most probably a result of a highly derived pulmonary system, as in extant birds. Morphologically similar pneumatic features are present in most saurischian dinosaurs and it is possible that they are the result of convergence. Because basal members of the various groups, including Triassic pterosaurs, appear to lack skeletal pneumaticity, convergence seems likely, although the stem-ornithodiran parsimoniously possessed a more bird-like than 'reptile'-like pulmonary system, albeit non-invasive. This points to possible tachymetabolism in these forms, which is in accord with the distribution of other factors such as integumentary structures and bone histology. It is concluded that evolution of this suite of advanced features, surprisingly, was among the earliest events in the ornithodiran lineage soon after it split off from its crocodylian sister-group.

For more than a century it has been recognized that pterosaurs possessed light skeletons, with thin and very compact bone walls and a meshwork of trabecular struts inside the hollow long bones for maintenance of mechanical strength (e.g. Wellnhofer 1991a; Ricqlès *et al.* 2000), as in extant birds (e.g. Rogers & LaBarbera 1993). Additionally, it has long been recognized that they also possessed distinct pneumatic fossae and foramina throughout the axial and appendicular skeleton (e.g. Seeley 1870, 1901; Marsh 1871, 1872; Eaton 1910; Wild 1971; Wellnhofer 1975a, b, 1978, 1980, 1991a, b; Kellner 1991; Bennett 1994, 2001a, b; Frey & Martill 1996; Viohl 2000). However, as Padian (1983a) pointed out, there is still no thorough systematic overview of the distribution of pneumaticity in pterosaurs and its possible systematic implications (but see Bennett 1994, Unwin 1995 and Unwin & Lü 1997 for discussion of pneumatic characters in pterodactyloid systematics). Despite the very common reference to pneumatopores when describing the osteology of pterosaurs, most references remain anecdotal, simply noting their presence with few if any comments on the detailed morphology and its systematic or soft-tissue implications. It appears, however, that the large pterodactyloids have more extensively pneumatized skeletons than the smaller 'rhamphorhynchoids', and

the cervical vertebral column in particular is often extensively pneumatized (see e.g. Eaton 1910, Kellner 1991, Bennett 1994, 2001a).

Pterosaurs, like theropod dinosaurs and mammals, have hollow longbones, but hollow bones do not in themselves imply the presence of pneumaticity. Wild (1971), for instance, notes that *Dorygnathus* has pneumatic bones and subsequently goes into some detail about why the pneumatic bones almost certainly lacked external pneumatopores! Wellnhofer (1975a, 23) claims that the forearm bones of *Rhamphorhynchus* are pneumatic but state that they lack pneumatopores. Both statements are contradictory, because pneumatization is defined as the process by which air diverticulae from the lungs resorb bony tissue, thus invading the bone from the exterior (Baer 1896; Bellairs & Jenkin 1960; King 1966). Accordingly, a very important parameter in the evaluation of the presence of pneumaticity is examination of the bone exterior for properly sized external foramina that communicate with the bone interior (Hogg 1980; Witmer 1990; Britt *et al.* 1998). Such features are indeed common in many pterosaurs, particularly in the cervicals of pterodactyloids, but the internal structure of these chambers is virtually unknown in most cases, unless the bones are very well preserved but fractured.

The 'rhamphorhynchoid' pterosaur *Rhamphorhynchus* from the Late Jurassic (Tithonian) Solnhofen limestone of southern Germany (Barthel 1978; Viohl 1985, 1998) is known from a large number of skeletal specimens (over 100), many of which are nearly complete (Wellnhofer 1975a–c), and some of the Solnhofen specimens are known with soft-tissue preservation, most notably the chiroptagia (Wellnhofer 1975b, 1991a; Viohl 2000). Accordingly, with the possible exception of the edentulous and considerably larger North American *Pteranodon* from the Late Cretaceous, which is also known from very abundant fossil material (e.g. Eaton 1903, 1910; Bennett 1994, 2001a, b), *Rhamphorhynchus* must be one of the most well-known and well-studied pterosaurs in the world. The specimens vary considerably in size, by more than a factor of four when comparing the length of the wings, and differ in skeletal ossification as well. Initially much of this variation was considered species specific, and as many as five species were recognized (e.g. Wellnhofer 1975b, c, 1991a). Subsequently, this variation has been attributed to differences in ontogeny within the same species, *Rhamphorhynchus muensteri* (Bennett 1995, 1996b). A wide size range within presumably adult specimens is also recognized in other species of pterosaurs and is attributed to prolonged, albeit slower rates of growth (Bennett 1993; Unwin 2001) succeeding the very rapid initial growth phases characteristic of endothermic vertebrates.

Rhamphorhynchus is the type genus of the family Rhamphorhynchidae, which is considered the sister-taxon to the monophyletic Pterydactyloidea (Unwin 1992, 1995), implying paraphyly of the 'Rhamphorhynchoidea'. Although *Rhamphorhynchus* is known from several hundred individuals a large number of detailed anatomical characters have remained relatively obscure, due to the state of preservation and particularly the method of preparation of virtually all the known specimens. Even complete and well-preserved specimens have nearly always been mechanically prepared, thus only exposing one face of the bones and obscuring from view the potentially very delicate details of the vertebral and cranial anatomy. The present specimen, housed at the Geological Museum in Copenhagen as MGUH 1891.738, differs substantially from this pattern. It is a disarticulated, partial skeleton that is very well preserved. The specimen was originally assigned to the type species *R. muensteri* by Wellnhofer (1975b) and, accordingly, has not been synonymized following the recognition that characters previously considered species-specific are probably ontogenetic (Bennett 1995). The specimen was figured and a few details were described by Wellnhofer (1975a, b), who based reconstructions of several anatomical details on this specimen (his specimen 71); but apart

from also noting the extraordinary nature of the specimen, he did not elaborate on many details of its anatomy. The mode of preparation, rather than the original state of preservation, appears, however, to be the primary agent responsible for the degree of details visible in the specimen. In this paper we consider the slab to be the part containing the major part of the skeleton, as opposed to Wellnhofer (1975a, b) who called this part the counterslab ('Gegenplatte').

Materials and methods

The specimen was recovered from the Solnhofen Lithographic Limestone (locality on the old label of 1891 states 'Solnhofen', without additional details). Initially not too much of the specimen was visible on the surface of the slabs, but it was apparent that soft tissues were probably not preserved, in which case the specimen would probably have had to be prepared mechanically. Accordingly, it was decided to attempt acid preparation. This was carried out by N.B. and other students during a student laboratory course in the early 1960s, under the supervision of E. Nielsen, at the time the only vertebrate palaeontologist in Denmark. The slabs were encased in a two-component artificial resin, which has subsequently turned yellow, although it retains much of its original transparency, and was prepared using the acetic acid (5–10%) transfer method of Toombs and Rixon (1959). Virtually all the original limestone matrix was dissolved; neither the slab nor counterslab sides have subsequently been filled with resin and, consequently, are fully open. Following acid preparation the specimen was carefully rinsed with water for an extended period.

Unexpectedly, the slabs proved to contain a completely uncrushed, disarticulated, partial skeleton (*contra* Wellnhofer [1975b, p. 155], who says that the wing phalanges appear crushed). The state of preservation and subsequent exposure by the acetic acid is such that the skeleton looks nearly extant and the apparent thinness and lightness of the bones belie the fact that they do not appear particularly fragile. In fact, several ribs were still somewhat elastic when the specimen was initially exposed, but most of this elasticity has subsequently diminished. The main slab has been on exhibit for almost three decades at the Geological Museum in Copenhagen, standing on one end and leaning against the back wall of a wooden showcase, without dampening tissue on the bottom edge. The specimen has deteriorated since Wellnhofer's (1975a–c) study. When the specimen was finally removed from the exhibit it was discovered to be slightly damaged, and that parts had come loose, probably as a result of slight, but nearly constant tremors from the subway that runs directly below the museum. The absence of

humidity and temperature control in the showcase has resulted in the bones losing their initial elasticity, and has perhaps also contributed to the slight damage of the specimen. In Wellnhofer (1975b, pls 23 (fig. 6) & 24) several ribs can be seen on the slab. The posterior-most of these ribs is now missing, and part of one lower jaw and some teeth and a few fragments of other skull bones were loose and displaced (now attached with glue to the resin).

The skeleton lacks parts of the braincase and skull, one wing and the caudal vertebral column (Fig. 1a, b), but most of the skull and braincase are preserved in undistorted, three-dimensional detail unprecedented in a rhamphorhynchoid pterosaur. The postcranium is also three-dimensional and displays intricate details of the axial and appendicular skeleton. The entire cervical vertebral column, consisting of nine vertebrae, is present and articulated, albeit disarticulated from the dorsal vertebral column, and the dorsal vertebral column, consisting of 14 vertebrae, is also present and articulated. The sacrum consists of three articulated sacra. In several vertebrae the lamella is absent or damaged, meaning that not only the external parts but also the internal parts of the vertebrae are exposed in great detail. Ironically, the excellent state of this specimen makes detailed comparisons with other *Rhamphorhynchus* specimens difficult. Compared, for instance, to the famous material in the collections of the Bayerische Staatssammlung in München, it is evident that many anatomical details of this specimen cannot be compared to those of most other specimens, even complete skeletons, as such details are simply not visible after mechanical preparation.

General description

The aim of this paper is to provide a detailed description of the pneumatic features, not the osteology of the specimen, but a few general remarks on other osteological characters seem appropriate. Wellnhofer's papers (1975a–c) remain the quintessential works on the anatomy of *Rhamphorhynchus*, but the descriptions of osteology (Wellnhofer 1975a) are often very brief, noting only a few details. The present specimen displays characters not featured in Wellnhofer (1975a–c) and, significantly, in some cases the observed characters in the present specimen differ from Wellnhofer's observations.

The slab (Fig. 1a) contains most of the preserved skeletal parts, and particularly the complete, articulated cervical vertebral column, exposed from the ventral side, is exquisitely preserved. The dorsal vertebral column is also present in articulation and is exposed from the dorsal side, although tilted to the left. In addition to the axial skeleton the slab contains the entire right wing, hindlimb, pelvic and

sternal elements, the disarticulated skull, and the three-dimensionally exposed, undistorted anterior end of the upper jaws. The counterslab (Fig. 1b) contains much less bone, but the wing is also clearly visible and a lower jaw ramus is fully exposed. Significantly, the counterslab contains the 14 articulated dorsal centra, exposed ventrally and up to about the level of the transverse processes. It also contains a three-dimensional prepubis, the entire cristospine and parts of the anterior face of the sternum, exposed dorsally and showing the articulating facets for the coracoids. Also visible on the counterslab is the three-dimensionally preserved row of cervical neural spines.

The humerus (Fig. 2) is medially exposed and shows a distinct, elongate sinusoid muscle scar on the medial face of the diaphysis, presumably the fleshy insertion of the *m. latissimus dorsi*. Such a morphology of this muscle scar is hitherto unknown in *Rhamphorhynchus*. Despite its size the humerus appears unpneumatized (Fig. 2). In the jaws replacement teeth can be seen in a few places and the slab and counterslab combined provide excellent exposures of nearly every aspect of the complicated carpus. The pelvis is dorsally exposed and undistorted (Fig. 2). It clearly demonstrates that the acetabulum was laterodorsally exposed, thus potentially contributing to the debate on pterosaur terrestrial locomotion (see e.g. Padian 1983a, b; Wellnhofer 1988, 1991b; Unwin 1996; Bennett 1997; Henderson & Unwin 2001a, b) by seemingly making bipedal running very awkward, if possible at all.

As noted by Wellnhofer (1975a) there are nine procoelous cervicals and the atlas is a small, short, ring-shaped element, about 1 mm long. Anteriorly the atlas is concave and, thus, resembles a 'normal' procoelous centrum. The neuropophyses of the atlas are slender, 3-mm long bones, paired and pointing backwards from the lateral sides of the atlantal centrum. Caudodorsally the neuropophyses touch the tall neural arch of the axis at a small distinct articular area. The two atlantal neuropophyses do not meet at all in the mid-line. Wellnhofer (1975a) states that there is a single triangular proatlas that extends anteriorly over the atlas. However, on the counterslab, adjacent to the characteristically tall and triangular neural spine of the axis, are exposed the paired neural arches of the proatlas (Fig. 1b, pa), lying at about a 50° angle to each other, each triangular in shape and most closely resembling an arrowhead. The proximal articulating facet of a proatlas is complex, sinusoid and irregular, indicating some mobility. In Wellnhofer (1975a, fig. 6a), the axis intercentrum is shown as a wedge-shaped bone with the sharp end directed ventrally. The present specimen, however, indicates that this is incorrect. In *Rhamphorhynchus*, as in other vertebrates, the sharp end of the wedge pointed dorsally. The ventral length of the axis intercentrum

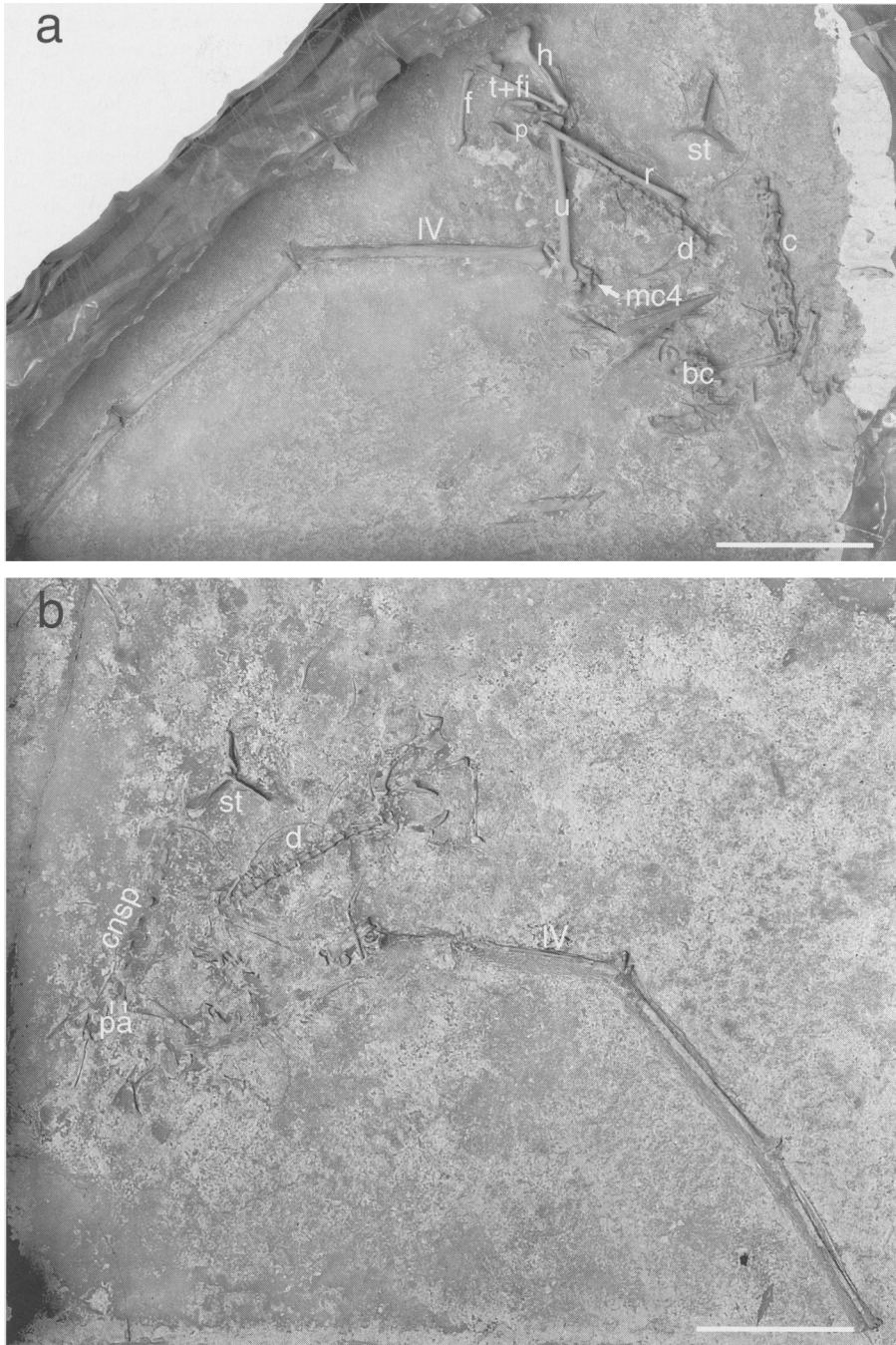


Fig. 1. *Rhamphorhynchus muensteri* MGUH 1891.738: (a) main slab and (b) counterslab. The specimen is encased in artificial resin and most bones are three-dimensionally exposed and virtually undistorted. bc, brain case; c, cervical vertebral column; cnsp, cervical neural spines; d, dorsal vertebral column; f, femur; h, humerus; IV, fourth digit; mc4, fourth metacarpal; p, pelvis; pa, proatlas (2); r, radius; st, sternum; t + fi, tibia and fibula; u, ulna. Scale bars 5 cm.



Fig. 2. Stereo close-up of right humerus, hindlimb and pelvis (viewed dorsally) from the main slab. Notice the elongate scar for *m. latissimus dorsi* on the humeral shaft (arrow), and the scar for *m. pectoralis* on the deltopectoral crest. The right metatarsals can be seen just below the humerus. Note also the position of the acetabula in the three-dimensionally preserved and undistorted pelvis. Scale bar 5 mm.

slightly exceeds that of the atlas. The intercentrum can be seen both anterior and posterior to the lower jaw on the slab (Fig. 7).

There is evidence of many hollow bones. The articulated dorsal centra on the counterslab have smaller pieces of lamella missing in several places around the distinctly procoelous articulating facets, revealing the trabeculated interior of the bones. Although the dorsal centra are fully uncrushed, very well preserved and expose their lateral sides on the counterslab there is no evidence of pleurocoels on any of the centra (but see below). The appendicular bones were also hollow. The articulating facets of the humerus and radius have pieces of the lamella missing in several places, exposing the spongy interior of the elements. Adjacent to the prepubis on the counterslab there is a pedal phalanx, also with slight damage to the lamella. Even this small bone has a spongy interior. At the anterior end of the dorsal series is a poorly preserved rib, missing part of the exterior and the upper part. This bone is distinctly hollow, but the absence of the proximal part precludes determination of pneumaticity, because this would seem a likely place for the air diverticulae to enter, as in birds and some non-avian dinosaurs (e.g. Janensch 1947, 1950; Britt 1993). Where small pieces of other ribs are missing it is evident that these were also hollow. Thus, the entire skeleton appears to have been very lightly constructed.

Pneumatic features

The counterslab has the entire cristospine and anterior part of the sternum three-dimensionally

exposed. Just posterior to the facets for the coracoids the sternum widens markedly and, in the transition from sternum to cristospine, there is a very large foramen, exposed laterally and posteriorly. The internal walls of the foramen are not smooth and level; rather, the internal structure is a complex meshwork of excavations and lamellar struts, probably for mechanical support (Fig. 3). This morphology is hitherto unknown for *Rhamphorhynchus*. Morphologically it bears a distinct resemblance to the interior of avian bones that have been excavated by air diverticulae. In extant birds the clavicular air sac is found in this area and pneumatizes the sternum, humerus and furcula among others (e.g. King 1957, 1966, 1979; Bellairs & Jenkin 1960). But it is uncertain, although not unlikely, whether a similar air diverticulum in pterosaurs produced this excavation. *Pteranodon* has a dorsal pneumatic foramen on the sternal plate penetrating into the cristospine (Bennett 2001a, pp. 65–66).

The proximal part of the left lower jaw is exposed from its ventral side and overlies the atlas and second intercentrum. The medial surface of the jaw ventral to the articulation shows a large excavation at the posteromedial face (see Figs 6 & 7), which represents the mandibular foramen. At the dorsomedial internal edge is a small foramen that extends into the mandibular foramen, and this foramen may represent a pneumatic foramen (illustrated in figure 7 as a lightened area inside the mandibular foramen).

The illustration by Wellnhofer (1975a, p. 14, fig. 6a) of the ventral view of the cervical vertebral column of *Rhamphorhynchus* is based on the present specimen. Between the zygapophysial rami and the centra are distinct spaces that Wellnhofer (1975a)

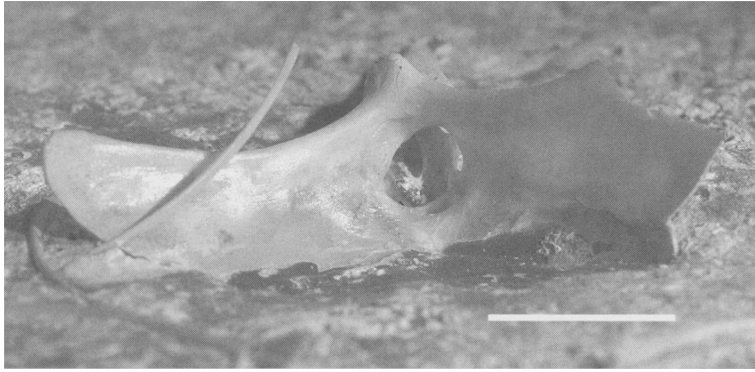


Fig. 3. Sternum (counterslab) viewed directly posteriorly. A large foramen is present on the anterior edge of the sternum and extends slightly into the posterior portion of the cristospine. The foramen opens laterally on both sides as well. The interior of the foramen is a complex meshwork of trabeculae which is partly visible on the right of the foramen in this figure. Scale bar 5 mm.

illustrated as cross-hatched. We can confirm that these spaces extend all the way into the interior of (but not through) the zygapophysial rami and thus are excavations not into the centra, but simply into the bases of the neural arches (cf. *Pteranodon*, Eaton 1910, pl. VI; Bennett 2001a, pp. 39–46, 52; further details below). Wellnhofer (1975a) also indicates spaces with cross-hatching on the ventral sides of the transverse processes of all the dorsal vertebrae (p. 14, fig. 6f, also based on this specimen). The counterslab exposes the articulated dorsal vertebral column in ventral aspect and, in a few places, also the transverse processes of the left side. On the slab the entire dorsal series is exposed dorsally, and here nearly all the transverse processes are present and rather well preserved, though most are broken. Wellnhofer does not describe these spaces but, because the cervical vertebrae have large distinct spaces, and because Wellnhofer illustrates the spaces on the cervical and dorsal vertebrae identically, this implies that all the dorsals also have holes/cavities, albeit up into the base of all the transverse processes. This implication does not correspond to the facts, as noted below.

On the slab the dorsals are exposed dorsally and laterally (Figs 4 & 5). Ventrally on the right transverse process of the first dorsal there is an elongate fossa in the anteromedial section of the process. Laterally the fossa is more narrow but as it approaches the centrum it expands anteroposteriorly and dorsoventrally into a distinct excavation. This bears resemblance to a pneumatic fossa. The following dorsal also displays a fossa, but it cannot be asserted whether or not they extend into the centrum. Evidence from the counterslab suggests that they do not. On dorsal 3 the parapophysis has migrated upwards and there is a slender pillar of bone that extends from the transverse process to the parapoph-

ysis, near the centrum. Just posterior to this pillar is a distinct excavation, probably similar to the preceding ones, but morphologically slightly different because of the position of the parapophysis. On dorsal 4 the parapophysis is situated at the anterior edge of the transverse process, and no fossa can be discerned on this vertebra on the slab.

On the counterslab, however, it is possible to view one of these foramina in detail, because the articulated row of dorsal centra have parts of the transverse processes preserved as well. Usually they are incomplete or nearly absent, but the most complete is from dorsal 4. The left transverse process of this vertebra is nearly fully preserved and displays a large foramen, although distinctly wider and more subcircular than indicated in Wellnhofer (1975a, p. 14, fig. 6f). These fossae are clearly not just holes, however, because none of the transverse processes of the slab and mainly the counterslab show any indication of a perforation on the dorsal faces of the transverse processes. Rather, close examination reveals that they are foramina that extend into the transverse processes from the ventral surface. The size and unusual location would indicate that they represent pneumatization of the dorsals, although not through pleurocoels, as is the case in saurischian dinosaurs (extant and extinct), but through the transverse processes. Several theropods and most birds pneumatize the vertebrae via the arch – not the centrum.

Examination of dorsal 5 and more posterior dorsals on the slab failed to indicate any fossae, and the preserved remains of the transverse processes on the counterslab corroborate this. Thus, the fossae probably did not extend posteriorly in the dorsal series, as indicated in Wellnhofer (1975a). On dorsal 5 the parapophysis has migrated to the anteroventral part of the transverse process, and it is possible that this simply precludes a fossa. Despite extensive

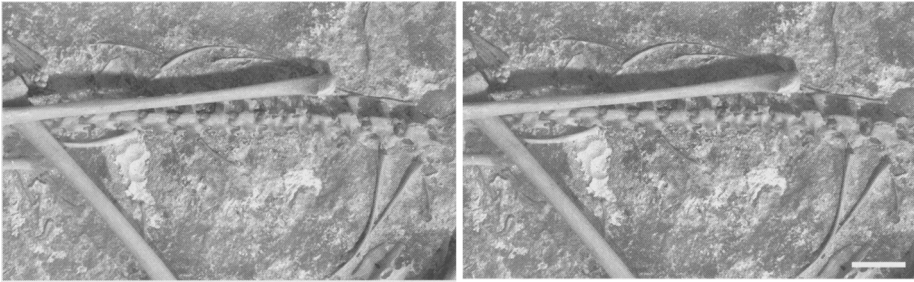


Fig. 4. Stereo close-up of dorsal vertebral column, viewed dorsally, from main slab. Scale bar 10 mm.

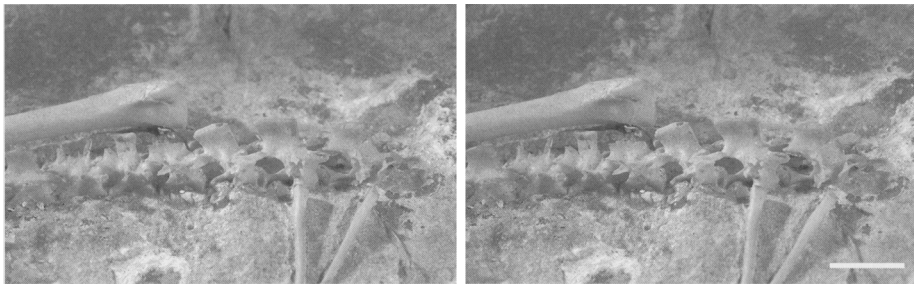


Fig. 5. Stereo close-up of anterior dorsals, viewed from right lateral side, from main slab. Notice the pneumatic foramina in the upper lateral part of the anterior two centra. Scale bar 5 mm.

pneumatization of the skeleton, even the carpals (Wellnhofer 1985), the posterior dorsals of pterodactyloids are frequently unpneumatized (e.g. Eaton 1910; Wellnhofer 1991a, b; Bennett 2001a, b), in the sense of lacking pleurocoels. They do, however, often have pneumatic notaria vertebrae (e.g. Bennett 2001a). However, if the dorsals without pleurocoels of this more basal pterosaur, a ‘rhamphorhynchoid’, in at least some instances appear to be pneumatized from the transverse processes, it would seem sensible to look for something similar in more advanced pterosaurs. Wellnhofer (1978) notes that *Rhamphorhynchus* has pneumatized dorsals, but it is uncertain whether he meant to implicate the centra. The counterslab offers ample opportunity to examine the entire ventral and most of the lateral faces of the dorsal centra, and none have pneumatic foramina or fossae. If the centra were pneumatic this would have to be via the transverse processes; the medial walls of these cavities, however, appear to be intact. In some instances bones are even pneumatized indirectly from other bones (particularly in the skull; Witmer 1990). At present it cannot be verified whether the centra of our fossil are pneumatized indirectly from the transverse processes.

The best evidence for pneumaticity stems, however, from the ventrally exposed cervical vertebral column of the slab (Figs 6–9). The tiny atlas described above does not show any evidence of pneumatization, but all of the succeeding eight cer-

vicals do. The ventral surface lamella of the second centrum is broken away and exposes the interior, which shows a slightly asymmetrical thin medial wall with some complicated perforations between left and right sides. Because of the breakage the entrances to these cavities in the lateral face of the centrum cannot be seen (Figs 6 & 7). However, these pleurocoels are very evident in the third centrum, which is almost intact, apart from an opening in the rear, convex articular surface. Through this hole the interior medial wall, perforated by large irregular holes, can be seen. The excavations are clearly of the camerate type (cf. Britt 1993, 1997). The lateral sides of this centrum are perfectly preserved and show three large perforations into cavities in the centrum and the base of the neural arch (Fig. 7). The neural arch is perforated by a large foramen on the ventral surface of the strong ridge between the pre- and postzygapophyses. This hole is oval and quite large, about 2 mm long. The cavity inside probably extends the entire length between the two zygapophyses. There is an equally large pleurocoel into the mid-dorsal part of the centrum that leads into the two large lateral chambers divided by the incomplete medial wall. Immediately anterior to this pleurocoel is another, and slightly smaller, one that excavates the anteroventral part of the centrum. Paired chambers are thus formed, separated from the two main air chambers by a thin subhorizontal wall. Thus there are at least three pairs of large excavations into



Fig. 6. Stereo close-up of the anterior cervicals and left posterior lower jaw ramus, viewed ventrally, from main slab. Notice the marked excavations along the central sides between the zygapophyses and the large mandibular fenestra in the posterior part of the lower jaw ramus. Scale bar 5 mm.

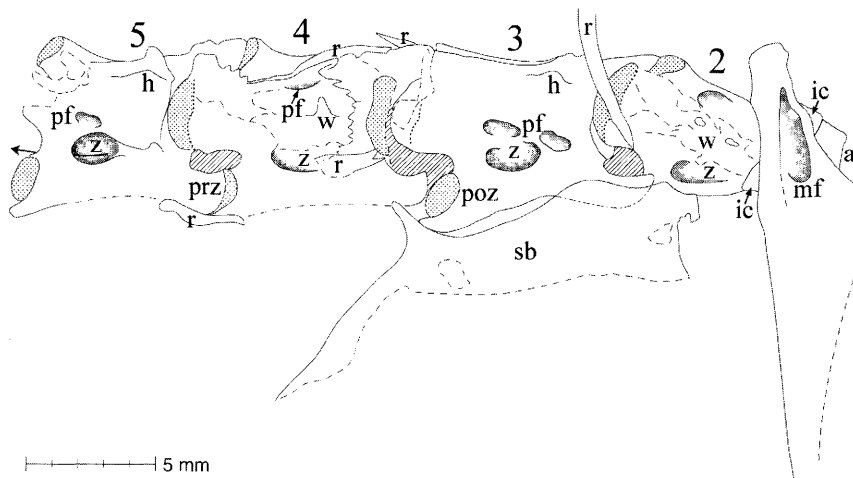


Fig. 7. The five anterior cervicals, including the atlas. ---, broken bone or limit to resin; - - - - -, outline hidden behind bone; ······, boundary between centra and articular surfaces; dotted areas, articulating surfaces; cross-hatched areas, spaces between bones. 2–5, second to fifth cervical vertebra; a, atlas; h, hypapophysis; ic, axis intercentrum; mf, mandibular fenestra; pf, pneumatic foramen; poz, postzygapophysis; prz, prezygapophysis; r, rib; sb, unidentified skull bone; w, wall of bone; z, zygapophysial foramen; long arrow through posterior wall of neural arch. (Camera lucida drawing by N.B.)

each vertebra. Also the neural spines appear hollow, as seen from a few that are broken, but if there are pneumatopores into these spines they must penetrate via the neural arches, because there are no more external perforations. The separate antero-ventrolateral cavities are actually also indicated, but less evident, in the second and fourth centrum, and so is the medial irregular wall, of which small remnants are seen in the broken fourth centrum (Figs 7–8).

On the right side of the fourth centrum a small, double-headed cervical rib, about 5 mm long, is articulated to the parapophysis, a small tubercle extending ventrolaterally near the anterior, concave articular surface of the centrum (Figs 7 & 8). Similar, but slightly broken tubercles are seen on the

third centrum, and between the two there is a medial low hypapophysis, also weakly indicated on the fifth centrum. The anterior head of the rib cannot be seen articulating with the vertebra. The second to sixth centra are all a little over 6 mm long, while the seventh is approximately 5 mm, the eighth c. 4½ mm, and the ninth c. 4 mm long. The fifth centrum has lost its posterior end, so the internal medial wall is also visible here, and one parapophysis is broken to show its hollow interior. The fourth and the fifth vertebrae are the only ones in which the posterior wall of the neural arches is well exposed, and they show a small perforation probably penetrating into the zygapophyseal chamber (Fig. 7). Whether there are foramina holes in the anterior walls of the neural



Fig. 8. Close up of cervical 4 from main slab, viewed ventrally. The cervical is missing the entire lamella along its ventral side, exposing the interior in great detail. Notice the two large, elongate chambers running anteroposteriorly inside the vertebra (arrows). These communicate to the exterior via narrow canals that open up on the upper, anterior surface of the centrum as large foramina, approximately 20% of centrum length. Scale bar 5 mm.

arches cannot be observed. Such pneumatic foramina are seen in *Pteranodon* (Eaton 1910, pl. VI, figs 13 & 14; Bennett 2001a, figs 35, 39–42) and azdarchids (Britt 1993).

The entire centrum of the sixth vertebra is lost; only secondary calcite in the large neural canal and the neural arch is preserved. The seventh cervical vertebra is turned more ventrolaterally and exposes a 1 mm long pleurocoel rather low on the lateral surface of the centrum (Fig. 9). The eighth and ninth vertebrae lack pleurocoels, but have foramina into the ventral surface of the zygapophyseal region. A well-preserved double-headed cervical rib may belong to one of those two vertebrae. The seventh and eighth centra show small paired apophyses (traditionally called exapophyses, but see Bennett 2001a for discussion) lateroventrally near the intervertebral articular surfaces, which are in all vertebrae clearly procoelous. The eighth cervical and subsequent vertebrae seem to lack pleurocoels (Fig. 9). Only a few more dorsal vertebrae have lateral cavities excavated into the bases of the transverse processes (Fig. 5).

The neural spines of the third to eighth cervicals are triangular and slightly smaller and less pointed than that of the axis (visible on the counterslab), while the ninth and those further back are thinner and more laterally compressed; as mentioned some are broken and show a hollow interior. Their dorso-lateral faces are mainly preserved as imprints in the resin and, as mentioned above, they show no indications of external perforations.

In summary, cervical vertebrae from the second to the seventh are extensively pneumatized with three pairs of large pores, two leading into paired camerae

in the centrum, one into the base of the neural arch forming a cavity between pre- and postzygapophyses. These camerae and cavities take up most by far of the internal space of the vertebrae. Some or most of the cervicals also have pores through the posterior wall of the neural arch, perhaps into the zygapophysial cavity. Cervical 8 and backwards to dorsal 4 have large perforations into the ventral surface of the transverse processes, perhaps penetrating further into the centra, which are very hollow like the neural arches are. From the fifth dorsal and backwards no perforations or pleurocoels of the vertebrae can be observed, but they are very hollow anyway.

Physiological implications of pneumatic bones in pterosaurs

The presence of pneumatopores in much of the skeleton is strongly suggestive of a pulmonary system radically different from that of other 'reptiles', except most saurischian dinosaurs (including Neornithes). Pneumatopores indicate the presence of air diverticulae extending from the lungs proper into the bones and, presumably, into the body cavity as well, as in birds (Baer 1896; Salt & Zeuthen 1960; King 1966). The presence of external pneumatopores, communicating with internal chambers, and the internal resorption of bone tissue, results in an unusual and distinctive morphology that cannot be confused with any other process among extant vertebrates. This strongly indicates that one can extend such inferences to fossil taxa as well. Pneumatopores, and the inferred highly derived pulmonary system, have been taken as indicative of tachymetabolic endothermy (e.g. Seeley 1870; Viohl 2000), although this was doubted by Bakhurina & Unwin (1995a). However, it remains a fact that only animals that display many other distinct signs highly suggestive of tachymetabolic endothermy (extinct saurischian dinosaurs) or that are known to be tachymetabolic endotherms (extant saurischian dinosaurs) possess these features. Coupled with the evidence for pterosaur 'hair' (see Bakhurina & Unwin 1995a, b for discussion), along with the highly energy-demanding task of powered flight, which appears highly unlikely for non-tachymetabolic vertebrates (e.g. Maina 2000), this strongly points to tachymetabolic endothermy in pterosaurs, a conclusion also supported by their bone histology and inferred growth rates (e.g. Bennett 1993; Ricqlès *et al.* 2000; Unwin 2001).

It has been suggested that the function of the air diverticulae in pterosaurs was either to make the respiratory system more efficient, and perhaps also to cool the blood during powered flight (e.g. Viohl 2000; Bennett 2001b), or, to heat the inhaled air (Wellnhofer 1991a). However, the suggestion that pneumatic bones imply a greater surface area for gas

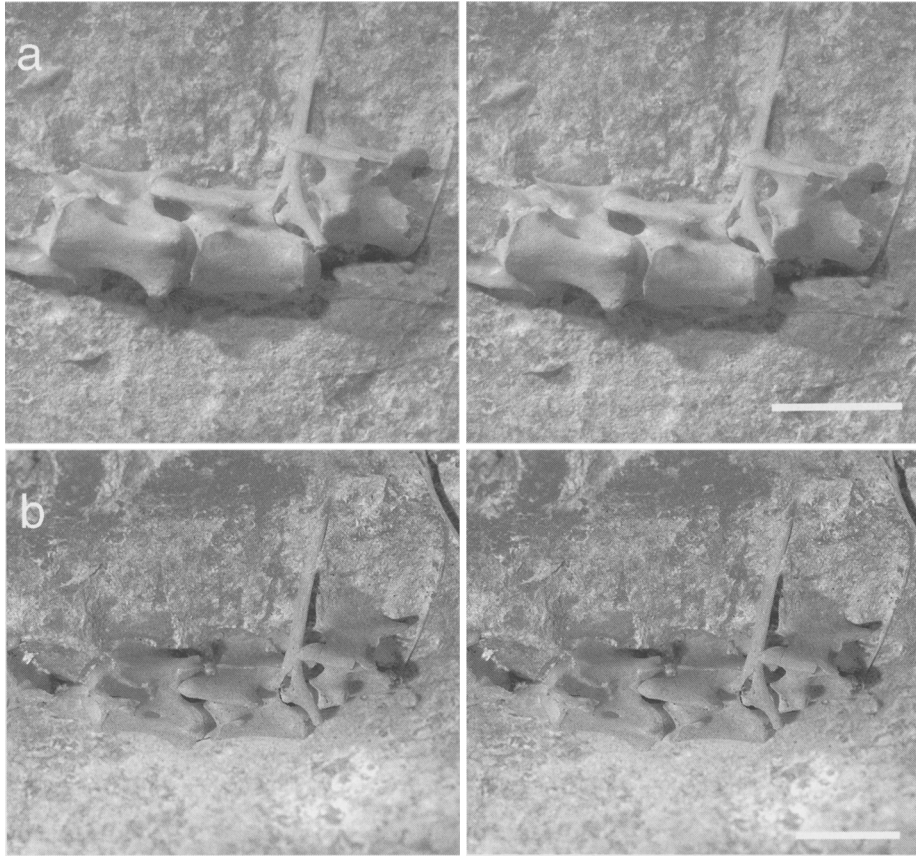


Fig. 9. Stereo close-up of three posterior cervicals (7–9) from main slab: (a) ventrolateral aspect, (b) lateral aspect. Notice the elongate pneumatic foramen on the centrum of cervical 7 and the short, blunt ‘exapophyses’. Scale bar 5 mm.

exchange is highly dubious, not just because the amount of ventilation that could pass through these rather narrow spaces is limited (Bennett 2001b), but also because the air diverticulae in the only extant analogues, neornithine birds, are nearly avascular and serve the unidirectional flow of air through the parabronchial lumen, not the uptake of oxygen (Salt & Zeuthen 1960; Schmidt-Nielsen 1975; Scheid 1979). The cooling or heating hypotheses are possible, but have not been demonstrated in birds. Lacking sweat glands, extant birds pant to combat hyperthermia, and a large part of the evaporation from the respiratory system takes place in the air sacs (Salt & Zeuthen 1960). However, the primary function of air sacs appears to be as participators in an advanced oxygen-uptake system. Although heating or cooling purposes as a selective driving force for the evolution of air sacs cannot be ruled out, it would seem excessive to develop such an advanced respiratory system merely to enhance capabilities already possible with normal tetrapod lungs. Hypothermia in pterosaurs could probably

also be prevented from heat loss through the flight membrane, as in bats but unlike birds.

Among the two extant groups of flying vertebrates pterosaurs have more often been compared to bats than to birds, mainly because of their ‘leathery wings’ supported by a bony strut. However, it seems likely that the bat analogy is probably less justified with respect to the pulmonary and vascular systems. Birds and bats are both tachymetabolic endotherms, though many, particularly bats, are not homeothermic (e.g. Schmidt-Nielsen 1995), and both groups achieve high levels of oxygen consumption during powered flight. This, however, is facilitated by different means. Birds have smaller lungs than comparably sized mammals (Maina *et al.* 1989) and their lungs are nearly inexpandable (Jones *et al.* 1985), although some movement of the ribs does occur, thus contributing to ventilation (Salt & Zeuthen 1960). The very complex avian respiratory system, with its voluminous air sacs and associated, advanced venous blood flow perpendicular to the unidirectional air flow through the parabronchial lumen, makes the avian

respiratory system very efficient in terms of oxygen uptake (Schmidt-Nielsen 1975; Schied 1979). This seems to be the primary function and advantage of the air sacs.

Bats, on the other hand, do not possess this very efficient unifold respiratory system, and their lungs are basically typically mammalian, albeit proportionally much more capacious than in terrestrial mammals (Maina & King 1984). Additionally, they have proportionally much larger hearts and cardiac output (e.g. Snyder 1976) and substantially greater haematocrit values and blood–oxygen carrying capacity (Riedesel 1977). The net effect is that their effective oxygen uptake rivals that of birds (Thomas 1987). With respect to the pulmonary system, pterosaurs appear to have been more similar to their sauropsidan cousins than their synapsidan counterparts. Potentially, this could have influenced overall body size. It is well known that the giant azdarchids and pteranodontids particularly, but in effect all pterosaurs, possessed very compact and foreshortened bodies (see e.g. Viohl 2000, p. 25 for comparison between *Rhamphorhynchus* and a seagull). This would clearly not have been possible if they had mimicked the condition of bats with enlarged internal organs.

The compact bodies of giant pterosaurs compared to birds of similar wing span was perhaps one of the factors allowing certain forms to exploit giant size, simply allowing them to be lighter than a bird at any given wing span (see e.g. Paul 1990, 1991). However, the extent of the influence of pneumaticity on these factors is hard to evaluate, but the avian-style respiratory system would seem to be a prerequisite for reducing body volume to the extent attained in huge pterosaurs. Large birds also tend to have more compact bodies, but not to the same extent as in giant pterosaurs.

Homology of the air diverticulae in pterosaurs and birds

There are striking similarities between the excavations of the cervical and anterior dorsal vertebrae in *Rhamphorhynchus* and those that are correlated with pneumatization in modern birds. It is, however, not clear that the two are strictly homologous; they are much more likely to have been convergently derived in the two groups. The distribution of air sacs penetrating the axial skeleton in archosaurs is as follows (see Britt 1993). There are air sacs in the vertebrae, at least in the cervicals and some dorsals, in most modern birds, but there is a large variation in extent and distribution within the skeleton. There are pleurocoels in most theropods (also present in *Archaeopteryx* – see Britt *et al.* 1998 and Christiansen & Bonde 2000 – although we subsequently failed to

find good evidence for pneumatic foramina in the third species [Bonde 1996], *A. bavaria* Wellnhöfer 1993, in München) and advanced sauropods (see below), and similarly in many pterosaurs. But there is not a convincing overview of the distribution within this group (Padian 1983a), although Bennett (1994) and Unwin & Lü (1997) used pneumatic characters in discussions of pterodactyloid systematics. Crocodiles and more basal fossil archosaurs are generally supposed not to have had pneumatized skeletons (but see below). This also applies to the most primitive theropods (herrerasaurids) and prosauropods (Padian & Brit, pers. comm., report pneumaticity also in basal prosauropods) and probably to the more plesiomorphic sauropods(?), as well as all ornithischian dinosaurs. In fact, pneumatizations have not been described for basal pterosaurs either.

The Triassic pterosaurs of northern Italy were recently examined by one of us (N.B.) with equivocal results. In *Eudimorphodon ranzii* (Zambelli 1973) there may be a pneumatic foramen as a small slit or tiny hole in the middle of the broad proximal plate of the humerus in all three specimens – juveniles and an adult – figured by Wild (1978, fig. 13, indicated only in two of them as a rather shallow depression), but this is on the dorsal side of the humerus, and the foramina are too small to be convincing as pneumatic. The adult type further has a deep slit covered by a shelf in the distal end near the condyle, which might also be a pneumatic foramen. The juvenile No. 8950 in Bergamo (with skin and ‘hairy’ impressions, see Wild 1994) is also equivocal concerning the vertebrae. Although most vertebrae are exposed from the lateral face, the cervical transverse processes more or less obscure depressions in the centra which might be pleurocoels. Similar depressions lateral in the dorsal centra may also be pleurocoels, but they are not very convincing. Some holes in the ‘right place’ in a few of the crushed vertebrae of the ‘juvenile’ *Eudimorphodon* in Milano (MPUM 7309) seem artificial.

In the large *E. ranzii* holotype in Bergamo (No. 2888, Wild 1978) it is also not evident whether narrow depressions (filled with sediment) in the region between the centrum and the neural arch of the ‘lumbar’ vertebrae could be pneumatic or are simply an effect of the transverse process being pressed down towards the centrum during fossilization, because most of the vertebrae are exposed from the ventral side. Similarly there is no safe indication of pneumatics in the cervicals, mostly preserved in dorsal view (see Monastersky 2001, pp. 100–101). The wing bones are all hollow and crushed, but some of them show rather small but distinct depressions or pits, often near the ends of the bones. Some of these pits might be pneumatic, but are still not very convincing.

The holotype of *Peteinosaurus* has no vertebrae preserved, but the alleged *Peteinosaurus* (Bergamo

no. 3359 without skull, but with a long 'rhamphorhynchoid' tail, see Wild 1978) shows the two posterior cervicals from the dorsal side rather than laterally (as indicated by Wild 1978), while the succeeding dorsals are exposed laterally but show no depressions to indicate pleurocoels. The last dorsals and one 'lumbar' are seen ventrolaterally and show only very weak depressions, if any at all, and one has a tiny foramen; however, there are no real indications for pneumaticity. Neither do the limb bones show signs of pneumatic foramina, unless a hole most proximal in the humerus (Wild 1978, fig. 35) is taken as such indication. (*Preondactylus* [Wild 1984] is preserved only as an imprint [see also Dalla Vecchia 1998], and it is unlikely to indicate anything about pneumatization).

In conclusion there appears to be no reliable evidence of skeletal pneumatization in the more well-preserved specimens of *Eudimorphodon* and *Peteinosaurus*, although it cannot be entirely excluded.

The problem therefore is that advanced pterosaurs, advanced (perhaps all) sauropodomorphs, and advanced theropods, including extant forms (birds), all appear to develop pneumatic air sacs, invading the axial and appendicular skeleton, but basal members of the three groups apparently did not possess such features. Accordingly, the pneumatic foramina in the vertebrae of these groups are presently best interpreted as the results of convergent (or parallel) evolution. We suggest that this raises some interesting questions about the soft-tissue morphology of the last common ancestor of the above groups.

Reconstructing primitive (morphotypic), ancestral dinosaur features from skeletal evidence alone might conceivably indicate a form without air sacs and with a crocodile-like respiratory system (implied e.g. by Ruben *et al.* 1997, 1999). But the evidence from the nearest sister-group, the Pterosauria, which has advanced air-sac systems in the axial skeleton of semi-advanced members such as *Rhamphorhynchus*, indicates an additional possibility: The last common ancestor of all ornithodirans (*sensu* Gauthier 1986 and Benton 1990) at least had air-sac systems, although they did not penetrate the skeleton. This again implies that, quite early after the split from the crocodylian sister-group, the ornithodiran line evolved an advanced respiratory system and presumably an advanced physiology (*contra* Ruben *et al.* 1997, 1999). Major, non-invasive air diverticulae are present in crown-clade Saurischia (Salt & Zeuthen 1960; King 1966, 1979).

Discussion

Other character distributions might support this non-traditional conclusion. Indeed there are other

'exotic' features with a similar distribution, namely integumental structures, feathers and 'protofeathers' (or cryptoptiles, Bonde & Christiansen 2002a, b; Christiansen & Bonde 2003), which are classically found in birds and avialans, including *Archaeopteryx*. With the recent discovery of several Lower Cretaceous (Swisher *et al.* 1999; Smith *et al.* 2001) small and medium-sized theropod dinosaurs with pennaceous or plumulaceous feathers and hair-like 'protofeathers' (Currie 1998; Ji *et al.* 1998; Xu *et al.* 1999a; Xu *et al.* 1999b) it is most likely that true pennaceous feathers had already evolved in basal Maniraptora, including the oviraptorosaurs (represented by feathered *Caudipteryx*) as well as dromaeosaurs (Norell *et al.* 2002) and avialans (Padian 1998; Holtz 2000; Padian *et al.* 2001). Additionally, the much more primitive compsognathid coelurosaurs have hair-like protofeathers covering most of the body and neck (Ackerman 1998; Chen *et al.* 1998; Currie & Chen 2001). Such cryptoptiles seem preserved in many more advanced theropods including early 'birds'. In primitive theropods the evidence is more indirect: the impressions of 'feather-like' structures at some footprints of the Early Jurassic (Gierlinski 1997). Ornithischian dinosaurs apparently do not have similar integumental structures. Some mummified hadrosaurs show rather 'scale-like' skin impressions, – but as-yet unverified reports of the little '*Psittacosaurus*', from the same Early Cretaceous deposits as the above feathered theropods, have found very odd, long, thin and curved appendices attached to the dorsal side of the tail, and some apparently have 'hair-like' structures on the body. If so, potentially, ornithischian dinosaurs also possessed some sort of proto-feathers.

Several pterosaurs show 'hair-like' integumentary structures, most notable the famous *Sordes pilosus* (Bakhurina & Unwin 1995a, b; Viohl 2000), but so does one of the Triassic forms, *Eudimorphodon* (Wild 1994, specimen studied by N.B.), and it is now generally agreed that pterosaurs were probably all covered in a 'hairy' coat (Wellnhofer 1991a; Cherkas & Ji 2002), most likely some sort of 'proto-feathers'. Thus, the possible distribution of air sacs and of an insulating coat of 'feathers' or proto-feathers is roughly similar to the distribution of skeletal pneumatization (a possible difference in the pattern of these features concerns ornithischians(?) and sauropods). This may indicate that the basal ornithodirans were already endothermic with isolating proto-feathers and an advanced respiratory 'flow-through' system with air sacs distributed between the internal organs (but not yet penetrating the skeleton). This is in accordance with the advanced physiology, probably tachymetabolic endothermy, that is also indicated by bone histology and inferred growth rates (Bennett 1993, Padian & Rayner 1993, Ricqlès *et al.* 2000).

We are well aware that the ornithodiran hypothesis is not necessarily correct. Some analyses indicate pterosaurs to be an earlier, stem-archosaurian lineage, split off from basal archosaurs before the crocodylian lineage (Wild 1978, Unwin 1995, 1999; Bennett 1996a; Peters 2000). The most radically different opinion is the hypothesis of Peters (2000), who concludes a cladistic study by indicating that pterosaurs belong with the Prolacertiformes, quite close to such former 'thecodonts' as *Longisquama* and *Sharovipteryx*, i.e. a very basal stem-archosaur lineage. We will not enter detailed discussion of this model here, but only note that, if correct, our conclusion that the last common ancestor of pterosaurs and birds already had this advanced physiology and air sacs becomes much less probable. This is because one would then have to assume that crocodiles secondarily lost these advanced features, which is not a very likely event. If Peters (2000) is correct, and the advanced features of pterosaurs are moved to a phylogenetic position far from the origin of dinosaurs, then it is also less likely that early dinosaurs, including the entire lineage of ornithischians (in the lack of some of the 'direct' evidence), possessed this advanced physiology. However, there are some dubious traces of possible pneumatics in some advanced 'thecodonts' with crocodylian affinities, such as rauisuchians, according to Gower (2001); although not particularly convincing, this might save the hypothesis of crocodiles reversing to secondarily primitive physiology.

Here we accept the traditional and well-discussed hypothesis of ornithodirans as an (advanced) sister-group of the crocodylian lineage. This prompts us to conclude, surprising as it may seem, that the evolution of advanced physiology and anatomy may have been one of the earliest events in the ornithodiran lineage, shortly after the split from the crocodylian lineage. In fact, both pterosaurs and dinosaurs were quite likely much more bird-like than is generally assumed. Cuvier after all was not right (1801, 1809): The famous 'Ptero-Dactyle' should not be called a 'reptile' (in the traditional sense), but was rather like a bird.

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