

Pneumaticity in Vertebrae of Sauropods and other Saurischians

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with 19 illustrations in the text

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The question of whether the vertebrae of sauropods have a pneumatic character is answered in various ways; it mainly concerns the significance of the pleurocentral cavities (pleurocoels) which penetrate the bodies of the presacral vertebrae. Seeley (1870), who repeatedly occupied himself with the question of pneumaticity in fossil reptiles, already advocated the interpretation that these openings formed the inlet to air-filled cavities. Baron Nopcsa, in one of his papers on dinosaurs (1917), speaks of large pneumatic lacunae in the vertebral column of the sauropods, which occasionally extend to the dorsal rib ends. However, he later (1924) apparently altered his view, and saw no evidence for pneumaticity in the presence of pleurocoel cavities in the vertebrae of sauropods, because the stegosaur *Omosaurus* and *Baluchitherium* also had them in their cervical vertebrae, which were certainly not pneumatic. Nevertheless he reckons with the possibility that *Diplodocus* could inflate itself ... chameleon-like; "the lack of- small air sacs does not - allow this to be confirmed". "Intestinal" [interstitial] air sacs in sauropods seemed plausible to him to a degree. On the other hand, C. Wiman (1929) states that in the Chinese *Helopus* the pleurocoels in the anterior dorsal section lead to small air cavities. Most recently, A. S. Romer (1933) again articulated Seeley's interpretation, and W. E. Swinton (1934) also expressed the same opinion.

Ill. 1. 8th cervical vertebra of *Brachiosaurus brancai* Jan. 1 1/10 natural size.
ak=external cavern. pl=pleurocentral cavity.

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The treatment of the question, whether sauropod vertebrae are to be viewed as "pneumatized" can be preceded by a brief overview: in which groups of extant vertebrates and in which portion of the skeleton do these air-filled bones appear and in what manner does the air-filling occur. It appears to be confirmed as fact throughout, that all pneumatic spaces in skeletal bones are directly or indirectly connected with some branch of the respiratory passages. In living mammals numerous cranial elements can be "pneumatized", in general, admittedly rarely, in the nose and tympanic cavity as in *Hystrix*, and in the edentates *Tamandua* and *Choloepus* (L. Paulli 1900), even in the pharynx. The well-known example of the monkeys serves as an illustration that air sacs extending from the larynx can infiltrate the bones of mammals. In *Myctes*, a sac enters the hollow, expanded body of the hyoid, by which means sound is amplified. In birds as well the cranial bones of the nose and the larynx are "pneumatized"; above all, however, there are the highly developed air sacs which are connected with the lungs, -the bones of the axial skeleton, those of the associated girdles as well as the vertebral column. Among present day reptiles, only in the crocodylians are there cranial elements with air cavities which are connected with the nose and tympanic cavity.

Ill. 2. Cross section through a dorsal vertebra of *Brachiosaurus brancai*,
1/4 natural size
pl=pleurocentral cavity.

My originally quite skeptical impression of Seeley's interpretation gave way to a completely positive judgement in the course of 'the study; I even developed the conviction that the "pneumatization" of the presacral vertebrae, in connection with the development of a system of air sacs and air canals in the region of the vertebral column, presents a phenomenon which is important to the understanding of the organization of sauropods and their biology.

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**Indications of "pneumaticity" in vertebrae of sauropods.
The pleurocoel cavities.**

Morphological. The pleurocentral cavities ("pleurocoels") which are first and foremost to be considered as indications of "pneumaticization", are depressions in the lateral walls of the vertebrae; they are found in cervical and dorsal vertebrae (Ill. 1) but also in the vertebrae of the sacrum, more rarely in those of the tail. In the elongated cervical vertebrae they often occupy a large portion of the lateral surfaces, as in *Brachiosaurus*. In the posterior, shorter cervical vertebrae and in the dorsal vertebrae they possess a rounded, elliptical, oval, semicircular, occasionally even irregular outline, which furthermore can vary considerably from one side of the vertebra to the other. It must certainly be considered, that true pleurocoels with at least partially sharply-outlined borders, cut deeply into the outer wall of the vertebra, while shallow, uniform and gradually indenting depressions are not to be assessed in the same manner.

The volume of the vertebra is frequently reduced to an extraordinary degree by typically formed pleurocoels. In the dorsal vertebrae, only a very thin, more or less medially-located wall remains in the interior. This phenomenon of a high degree of cavitation is exhibited, for example, in *Brachiosaurus*, and is illustrated in my paper on the vertebral column of *B. brancai* (Ill. 2). In other genera, the condition has long been recognized, as in *Bothriospondylus*, *Ornithopsis*, *Camarasaurus* and in the very appropriately named juvenile sauropod *Pleurocoelus*. This median wall is also present in a lengthy middle section of the cervical vertebrae of *Brachiosaurus*. In *Barosaurus africanus* this apparently occurs only in the last shortened cervical vertebrae (Ill. 3), while in the anterior vertebrae the sidewalls are perforated in an irregular, variable manner.

Ill. 3. Cross section through centrum of a cervical vertebra of *Barosaurus africanus* (E. Fraas) close to posterior end. Tendaguru. 1/2 natural size.
Slightly reconstructed.
nk=neural canal
pl=pleurocentral cavity

Ill. 4. Sagittal section through the condyle of a cervical vertebra of *Brachiosaurus brancai*. 1/3 natural size.

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The pleurocoelous space in *Brachiosaurus* cervical vertebrae is bordered by very large-celled bone tissue which fills the condyle (Ill. 4). Apparently the inner space of the condyle was directly connected with the anterior portion of the pleurocoels. In a sagittal section cut near to the median wall of the larger anterior portion of a highly cavernous, long, mid-cervical vertebra belonging to a subadult *Barosaurus africanus*, there are visible, next to smaller bordering cells, only two main cells in the rear (Ill. 5). In the dorsal vertebrae as well, the vaulted anterior condyle can exhibit a very cancellous structure, as in *Brachiosaurus* (Ill. 6) or *Tornieria* (= *Gigantosaurus* E. Fraas). That the excavation [hollowing out] of the vertebra can in extreme cases reduce the wall to a thickness of a few millimeters and also almost entirely reduce the condyle is illustrated, in addition to the aforementioned *Barosaurus africanus* cervical vertebra, by the sagittal section through a dorsal vertebra of the same species.

Ill. 5. Sagittal section through the anterior end of a cervical vertebra of *Barosaurus africanus*. 1/2 natural size.

Just as the pleurocoels open a path to the interior of the vertebra, dorsally-oriented cavities entering the walls of the neural arch can fill the majority of the interior of the neural arch, as illustrated by a dorsal vertebra of *Brachiosaurus*. A cross section through a cervical vertebra of *Barosaurus africanus* demonstrated the extremely cavernous character of the very thin-walled neural arch, in that the neural canal, bordered by a wall less than one millimeter thick in places, was surrounded by a very few spacious cells which were separated from one another by very thin bone lamellae (Ill. 8). That it is also possible for the condyle of a presacral vertebra to be entirely filled with spongiosa, is demonstrated by a sectioned cervical vertebra of *Dicraeosaurus sattleri* which also carries true external pleurocoels. The pleurocoels of this genus are always noticeably weakly developed and in the dorsal vertebrae they are even totally absent for the most part.

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Ill. 6. Sagittal section through the anterior end of a dorsal vertebra of *Brachiosaurus brancai*, 1/3 natural size.

Ill. 7. Sagittal section next to the median [wall] surface, through the anterior portion of a dorsal vertebra of *Barosaurus africanus*. 1/3 natural size. mw=median wall, whose lateral protrusion was cut during sectioning.

Ill. 8. Cross section through a cervical vertebra of *Barosaurus africanus*. 1/2 natural size.
nk=neural canal.

Pleurocoels also appear in the vertebrae of the sacrum, for example, in *Brachiosaurus*, and *Barosaurus*. In *Apatosaurus* the cavernous character of the sacrum is especially strongly developed, since Marsh (1896) could show that the body of the second sacral vertebra of *A. excelsus* was excavated down to a thin median wall, and that even the sacral ribs were hollow.

It appears important to me to examine whether the pleurocoels which also appear in the anterior portion of the caudal vertebral column, as particularly in *Diplodocus* and *Barosaurus*, are connected with hollow interior spaces or spaces filled with cancellous bone. These relationships are dealt with in somewhat greater detail here. A caudal vertebra of a small *Barosaurus* (Find St 677) from the middle dinosaur marl, whose relatively modest length (posterior width 100 mm, posterior height 96 mm, length 108 mm) indicates that it had a fairly anterior position in the tail, possesses well expanded, oval 30-mm-long pleurocoels 14 and 16 mm high respectively, which lead to roomy interior cavities. The cross section (Ill. 9) shows a picture common to the dorsal vertebrae of many sauropods; a 4-mm-thin median wall, and especially, cavities which are oriented downwards and whose lateral and ventral wall is certainly considerably stronger than in the dorsal vertebrae of *Brachiosaurus*. The lacunae in the sidewalls of the neural arch are oriented dorsally. In another, somewhat incomplete vertebra from the same site (Find St 31), which is of comparable length but significantly broader and taller, and which must be one of the most anterior caudal vertebrae, the empty interior exhibits a much larger lacuna, in which the middle wall is not preserved except for a small portion. The cavity, which extends towards the ends of the vertebra, exhibits the character of the pleurocoels of the dorsal vertebrae to an even greater degree than the previously described caudal vertebra. A large caudal vertebra from the upper dinosaur marl of Tendaguru depicts a similar internal construction to the initially described *Barosaurus africanus* caudal vertebra.

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Ill. 9. Transverse break through an anterior caudal vertebra of *Barosaurus africanus*. 1/2 natural size.
pl=pleurocoel cavity.

The centrum of this vertebra measured 27 cm long and 18 cm high and wide at the posterior end (Find C8). The interior, visible at broken surfaces, exposes more or less matrix-filled lacunae, separated from one another by a thin, approximately ½-cm-strong dividing wall which was slightly displaced from the median. A cavity extends forward from each pleurocoel - the right pleurocoel possesses an opening some 4 cm in length and 2 cm in height, the left pleurocoel possesses an opening some 5 cm long and 1 ¾ cm high. The right, its infilling prepared out, is irregularly segmented into vesicles, up to 5 cm wide and extends 4 cm up to the anterior end of the centrum. The left, not prepared, is likely somewhat wider. Only a single lacuna extends to the rear, and this from the right pleurocoel. It is only partially prepared, circa 4 cm wide; the exposed, unprepared cavity extends 6 cm up to the posterior portion of the centrum. An elongated, low, mid-caudal vertebra of *Barosaurus* from the middle dinosaur marl (Quarry dd) possesses no pleurocoels and, as shown by a transverse break, no lacuna, but rather fine spongy structure.

The study of caudal vertebrae of *Barosaurus*, consequently revealed that of the anterior vertebrae distinguished by pleurocoels, the anterior-most possess very voluminous lacunae, that these become smaller as the series moves to the rear, and that the middle pleurocoel-free vertebrae also no longer exhibit a lacuna.

On either side of the first five caudal vertebrae of *Apatosaurus*, E. S. Riggs (1903) found a pair of lateral cavities, one below and the other above the rib; certainly quite irregularly formed, in that they occasionally are present on one side but absent from the other. Further, he established that there were numerous small cavities in the interior of the first caudal vertebra. Therefore even this *Apatosaurus* demonstrated the connection between pleurocoels and interior cavernous structure in a caudal vertebra.

Pneumatic character of the pleurocentral cavities. To clarify the question of the significance of pleurocoels in sauropod vertebrae they are compared to similar structures in birds, where branches of air sacs enter at similar locations and continue further into the interior of the vertebrae.

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Ill. 10. Dorsal vertebra of a buzzard. Side view with large, round, pleurocentral cavity. 1/2 normal size.

In the sidewalls of dorsal vertebrae of the buzzard are found large roughly circular openings, which lead to voluminous interior lacunae, which possess no simple walls, but rather exhibit struts and perforations. These cavities may positively be compared with the pleurocoels in the dorsal or posterior vertebrae of sauropods.

Aepyornis is an additional good example, that avian cervical vertebrae possess large lateral pneumatic openings. Two *A. maximus* cervical vertebrae figured by Monnier (1913 table 5 Fig. 1 and 2) and regarded as the 8th and 15th, exhibit large, elliptical pleurocentral openings. Two cervical vertebrae of *A. hildebrandti* in the collection of the Geological-Palaeontological Institute and Museum in Berlin, among them one described by R. Burckhardt, possess large lateral cavities in the vertebra (cf Ill. 11); in one dorsal vertebra it is somewhat smaller (R. Burckhardt 1893). C. Wiman's (1935) lateral views of numerous cervical vertebrae, cervico-dorsal vertebrae and the two first dorsal vertebrae of *A. hildebrandti*, very nicely exhibit the pleurocoels on the lateral surfaces of the vertebrae, while in the following dorsal vertebrae this characteristic is altered insofar as the corresponding cavities are located more dorsally.

Ill. 11. Cervical vertebra of *Aepyornis hildebrandti*. Burck. 1/2 natural size.
pl=pleurocentral cavity. po=postzygapophysis. pr=prezygapophysis.

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There is no basis to consider the pleurocentral cavities in sauropod vertebrae as different from similar structures in the vertebrae of birds. As far as the studies in hand showed, the pleurocoels in sauropods always form the access to large interior cavities or interior spaces filled with large cells. One may conclude from this, that the pleurocoels signify not only a saving of bone mass in the flank of the vertebra and thus a weight reduction, but rather that they must also have yet another significance, and that, reversed, the lacunae in the interior and in the regions of large-celled structure obviously possessed a connection to the exterior.

The structure, particularly that of the condyles of the cervical vertebrae of *Brachiosaurus*, strongly calls to mind certain pneumatic skull elements of large ungulates. It is difficult to interpret these relationships differently - the pleurocoelous spaces, as well as the inner cavities and large cells to which the pleurocoels lead, were filled with air and were connected to the respiratory systems.

The character of the vertebral pleurocoels is often modified in such a way, that instead of a single perforation, numerous perforations are formed in the sidewall of the vertebrae. An example of this are the cervical vertebrae of *Apatosaurus louisae* in which three cavities can be found on one side, or a posterior cervical vertebra of *Tornieria robusta* with its four cavities (cf. Janensch 1929 Fig. 9), and several such caverns which appear in *Barosaurus africanus*. The significance of multiple pleurocoels appearing in various sizes can have been no different than that of a single pleurocoel.

When we attempt to produce a more exact conception of the type of "pneumaticization" of sauropod vertebrae, then again there remains no other method than to consider the relationships in the birds, which, among numerous other authors, M. Baer (1896) and B. Muller (1907) elucidated through studies of pigeons and other birds. The Canalis intertransversarius ramifies outwards on both sides from the cervical sacs which lie outside the thoracic cavity, in or before the thoracic passage. Accompanying the vertebral artery, the Canalis intertransversarius passes through the sequence [row] of the Foramina transversaria, throughout the complete cervical vertebral column. From these canals, branches infiltrate the cervical vertebrae and make them pneumatic. In a similar fashion, canals extend caudally from the cervical sacs along the dorsal vertebrae and also make these pneumatic. Furthermore it is known from the buzzards, that the lumbar vertebrae are not made pneumatic from the cervical sac, as are the anterior vertebrae, but rather from the abdominal sac.

One can likely assume in the sauropods, as in the birds, that canals passed along the cervical vertebral column through the Fo. transversaria, and air sacs entered the pleurocentral cavities. Since these foramina encompass a fairly large space which increases considerably as one moves through the series of cervical vertebrae in a caudal direction, there would certainly have been ample room in them for, in addition to the vessels, nerves and possible muscles, a spacious Canalis intertransversarius which presumably grew larger as one moved caudally. I would not like to presume, however, that it was the development of these air canals which lead to the Fo. transversarium becoming so wide, and, in the extreme case of *Apatosaurus*, induced the extraordinarily voluminous expansion of the foramen, particularly the enlargement of its width ventrally. Much more, it appears to me that the size and form of the cervical rib is determined by the particular type of function of the attached muscles, which, due to the significant width of the Fo. transversarium, acted at great distance from the fulcrum point located in the vertebral condyle, and therefore worked with a longer leverage than in the case of a narrow foramen.

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A lesser or greater development of the air sacs was possible, depending on the size of the foramen. Presumably this was made possible through the elimination of heavy "tissue filling" only once the foramen could become wide enough and the neck cross-section large enough that the weight of the neck did not become excessive.

What applies to the pleurocoels of the cervical vertebrae is also applicable to the dorsal vertebrae. In them, as well as in those of birds, an air canal can be reconstructed on either side of the vertebra, from which the pleurocoels can be made pneumatic via externally infiltrating diverticula.

If the presacral vertebrae supplied with pleurocoels are considered "pneumatized" then the same must also be valid for the sacral vertebrae of *Brachiosaurus*, *Barosaurus*, *Apatosaurus* and likely also other genera, as well as for the caudal vertebrae of *Barosaurus*, *Diplodocus* and *Apatosaurus*, which also exhibit the same characteristics. The manner in which and the position from which the vertebrae of the sacrum and tail were "pneumatized" is beyond this review.

In connection with this it is pointed out that highly pronounced pleurocoels appear in pterosaur cervical vertebrae, and *Fo. pneumatica* in axial elements, so one may assume that their thin walled bones were pneumatic (cf. the illustration of *Ornithocheirus* in R. Owen, 1859).

Pleurocoels in stegosaurs and *Baluchitherium*. The two examples, the pleurocoels in *Omosaurus* and *Baluchitherium*, which according to Baron Nopcsa (1924) argue against the pneumatic nature of the pleurocoels, definitely deserve careful attention. I was able to gain an opinion of the type of pleurocentral cavities in *Omosaurus* through an examination of the closely related *Kentrurosaurus* of Tendaguru, described by E. Hennig. Lateral cavities are found in certain vertebrae of this genus as well. A vertebra of approximately 61/2 centimeter length, which originates as a posterior cervical or one of the most anterior dorsal vertebrae, displays an oval, 12-mm-long clearly bordered cavity on the right side ; on the left, three cavities: an upper one and two below it, of varying size with partial sharp borders. A cross section demonstrated that the pits - the lower left is untouched by sectioning - do not open into an inner cavity, that is they simply represent external depressions. The unique external surface sculpturing on the flanks of the vertebra creates the impression that the growth in density or thickness did not occur evenly over the surface, but rather with strand like concentrations, between which lie areas where no such growth occurred. Because of this they became deepened and formed depressions similar to pleurocentral cavities. However, since they are not connected with interior cavities, they cannot be compared to the true pleurocoels of the sauropods, and permit no conclusions to be drawn on the nature of sauropod pleurocoels.

The cavities in the cervical vertebrae of *Baluchitherium*, about which C. Forster Cooper (1923) reported, are very unusual for a mammal. Lateral openings lead to lacunae, which occupy a large portion of the space of the centrum, and pierce each side so deeply that only a thin median wall of bone remains, exactly as we see it in the sauropods (see Ill. 12). The concept that these cavities were filled with air and somehow connected to the respiratory system at some location via air sacs will naturally be difficult to accept in a representative of the mammals, since this feature is unknown in the vertebrae of mammals. And yet I would not like to fundamentally reject the possibility of pneumaticity in cervical vertebrae of

Ill. 12. *Baluchitherium*, cross section through a cervical vertebra. 1/6 natural size (after Forster Cooper 1923).

pl=pleurocentral spaces

[12]

Baluchitherium in view of the following facts: pneumaticity occurs frequently in mammals, and certainly in the cranial bones. As previously mentioned, *Mycetes*, with its hollow, expanded, air sac supplied hyoid, serves as an example that an air sac extending from the larynx can also enter bones. Air sacs extending from the larynx are furthermore strongly defined in the orangutan, where the

branches even extend to, the armpit. But throat sacs which are located at the epiglottis are also reported in ungulates such as *R. tarandus*, antelope and *Dicotyles*.

The reference to this evidence is meant to show that even among the mammals, air sacs appear which branch from a cranial segment of the respiratory system, and that there are also examples that such air sacs enter available bones. Therefore it cannot in any way be viewed in advance as totally impossible that the cavernous cervical vertebrae of *Baluchitherium*, possessed air pockets. The presence of pleurocoels in this giant mammal can hardly be appropriate proof against the hypothesis of pneumaticity in sauropod presacral vertebrae, and equally inappropriate for Baron Nopcsa's other cited example, the stegosaur *Omosaurus*.

Cavernous Exterior Sculptures in the Neural Arch.

In individual genera of sauropods a cavernous external sculpture rather than interior lacunae is exhibited to various degrees in the walls of the neural arch, as well as in the apophyses, and in the frequently lamellar, thin ridges which, strongly oriented, are spread between the attachment points of the compression and tension forces which act on the processes. Recesses in the surface, or sharply bordered depressions with rounded, elliptical, egg-shaped outline or even more three and four sided form with rounded edges (Ill. 1) are found in such locations. Exact symmetry on both sides of the vertebra does usually not occur. These cavities differ fully from the deeply-contracted niches between the ridges of the external architecture, in the form and type of bordering. Such superficial, usually weakly sunken concavities which, in order to have a comfortable designation, I call "external cavities" because of their position on the external surfaces of the neural arch and its processes, are frequently located on the lateral sides of the bones of the neural arch which enclose the neural space.

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In *Diplodocus* cervical vertebrae they are found below the ridge which connects the prezygapophysis and diapophysis. In *Tornieria* and *Titanosaurus* they are in a somewhat more posterior location and below the postzygapophyses. In *Camarasaurus supremus* dorsal vertebrae they are found in the previously cited location. In *Dicraeosaurus hansemanni* and *Haplocanthosaurus* they are beneath the diapophyses. In *Apatosaurus louisae* they are found in the first dorsal vertebrae, lying somewhat further anteriorly in the "infraprezygapophysial niche"¹ which is located laterally below the prezygapophyses. They occupy the aforementioned position in the anterior dorsal vertebrae of *Camarasaurus supremus*. External caverns appear in the rear wall of the neural arch of *Apatosaurus excelsus* dorsal vertebrae. The same features appear on the parapophyses of the cervical vertebrae of *Brachiosaurus* which are particularly well supplied with cavernous structures, as well as on the ridge which ascends from prezygapophysis to neurapophysis. To a lesser extent they are also found on the ridge which in *Brachiosaurus* descends from the diapophysis to the rear of the centrum. In *Barosaurus africanus* cervical vertebrae and *Diplodocus* and *Camarasaurus* anterior dorsal vertebrae they are found on the dorsal side of the diapophysis. In a posterior cervical vertebra of *Tornieria* this type of external cavern is located more "cranially" on the upper surface of the ridge which runs to the prezygapophysis.

The neurapophysis of the cervical vertebra is an abundantly cavernous process; the sole branch in bifurcated vertebrae. In *Brachiosaurus*, *Camarasaurus*, *Apatosaurus* and *Helopus*, cavities appear on the base of the lateral side or over the neurapophyses. In *Diplodocus* and *Barosaurus* they appear right under the upper end of the neurapophyses. The expanded terminal end of the neurapophysis of *Brachiosaurus* dorsal vertebrae is tunnelled or undermined.

1) I call this niche infraprezygapophysial niches in reference to Osborn and Mook (1921) and Gilmore (1936), who designated it as infraprezygapophysial cavity.

Corresponding manifestations of "cavernosity" also appear in caudal vertebrae - as on the caudal side of the neural arch of (?) *Laplatasaurus araukariensis* (v. Huene 1929) and especially on the caudal side of the transverse process in *Apatosaurus* and *Diplodocus*. The caudal vertebrae in *D. excelsus* exhibit a pronounced degree of "cavernosity": in addition to that in the pleurocoels, there are caverns and perforations in the neurapophyses, which are even hollow in some vertebrae (Osborn 1899). Judging from the appearance of Osborn's illustrations the cavernous character of the neurapophyses extends back through the sequence of caudal vertebrae to the second last vertebra prior to the disappearance of pleurocoels.

It can be observed that these external cavities, especially those of larger dimensions and particularly in those of strongly pronounced overall cavernous character, are traversed and divided - by ridges of a second order which run in directions of structural stress. These ridges strengthen the thin base of the cavities and correspondingly produce small regions of bone substance which have resisted the dissolution process which created the depressions.

Cavernous Construction of Ribs.

The cavernous form of the vertebrae can also extend to ribs. The tubercular branch of the second dorsal rib of *Brachiosaurus brancai* exhibits invasive pockets (Ill. 13); in the upper portion of the shaft in *Brachiosaurus altithorax* there is even a large foramen which leads into an interior lacuna (Riggs 1904). In *Apatosaurus louisae* as well, according to C. W. Gilmore (1936, Table 29 Fig. 2.) the second dorsal rib possesses a round depression on the anterior surface under the tuberculum.

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According to an illustration of Marsh (1896, Fig. 9, 10) the tuberculum of an anterior dorsal rib on *A. excelsus* is hollowed out front and back through invasive caverns. Furthermore, according to Freiherr von Huene (1932), a deep pocket is located on the base of the tuberculum of the first dorsal rib of a titanosaur from Siebenburgen.

Ill. 13. Proximal portion of the second left dorsal rib of *Brachiosaurus brancai* with pneumatic cavity in the tuberculum. 1/10 natural size.

Air-Filled Spaces and Canals in the Sauropods and their Physiological Significance.

I believe I have made it plausible that true pleurocoels in sauropod vertebrae can be considered pneumatic and that they were filled with air along with the areas of open-celled bone structure which were connected to them. From this it was inferred that all pleurocoels were connected with the system of air canals which in most genera affected the entire cervical and dorsal vertebral column, frequently also the sacrum, and in genera with a particularly high degree of "cavernosity", such as *Diplodocus* and *Barosaurus*, extended far into the caudal region. But how are we to understand all of the described internal cavities in the neural arch and its apophyses as well as the caverns in the proximal portions of the dorsal ribs? Were they hollows in bone substance, the significance of which was purely to reduce body weight, or were they, like the pleurocoels, cavities in bones which originated through the pressure of expanding air sacs? That they do not lead to cavities or spaces filled with large cells does not decide against pneumatic character, since the elements in which they appear generally do not offer room for such lacunae. The neurapophyses of the anterior caudal vertebrae of *Diplodocus*, which on the contrary are sufficiently spacious for them, do possess interior lacunae.

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According to their nature, external cavities are totally different from the niches. These are bordered and formed by lamellae-like ridges whose orientation is determined by forces acting outside of the concave form of the niches. The form of these external cavities, which are delimited by curved

borders, or at least rounded edges, speaks against the form-building agency acting upon its own area, and indicates that the cavities must consequently have a different cause of origin than the niches. Since it can be made plausible that air sacs entered the pleurocoels, it is prudent to ask whether the external cavities were also air-filled and owe their development to the dissolving pressure of growing air sacs. It is easy to understand that this type of construction led to rounded borders. If all the external cavities on the apophyses of the neural arch were to have been of a pneumatic nature, one is certainly compelled to accept that a complexly-built system of air-filled sacs and tubes was evolved in the sauropods possessing highly cavernous vertebrae.

A more precise conception of how the air canals and sacs may have been able to develop in the vertebral column of sauropods can be deduced only from the relationships in the birds. In birds, diverticula from the *Canalis intertransversarii* pass through the intervertebral holes and unify into a canal, the *Canalis supramedullaris*, which runs over the spinal cord within the neural canal of the cervical vertebrae. A similar canal runs over the spinal cord in the dorsal region. Furthermore, *Diverticula supravertebralia* are found between the vertebrae of the pigeon. Ascending upwards and forwards, and somewhat club-shaped, they do not quite extend to the median surface. Now in the sauropods spacious intervertebral cavities are present above the centra, and enter the base of the neural arch from the front and rear, and particularly extend dorsally far over the neural canal, which I could present as abundantly developed in *Dicraeosaurus* (Janensch 1929a). These intervertebral spaces, only a fraction of which can be filled by the spinal cord and for which it is difficult to conceive a functionally important capacity, would certainly have provided little resistance to a tendency toward "pneumaticization". It does not appear to me to be in any way daring to assume that in some cases the "pneumaticization" of the vertebrae also altered such intervertebral lacunae, and that consequently air sacs, like the *Diverticula supravertebralia*, appeared in these spaces, possibly in connection with a *C. supramedullaris*.

The same question can be posed for the enlarged sacral spinal canal of sauropods which for the most part incorporates such intervertebral lacunae, and only a small portion of which could have been filled with sacral "pith", as I showed in a particular study (Janensch 1939). At that time I left undecided the question of what this sacral cavity contained in addition to the spinal cord, and only alluded to the fact that the similarly extraordinarily enlarged spinal cord canal of the cervical vertebral column of *Halicore* contained a network of vessels united by adipose tissue, and that the extensions of the sacral cavities of sauropods and stegosaurs could have had similar contents. I will now not exclude the possibility that they also enclosed air sacs. However, it seems somewhat unlikely to me that the laterally-expanded vesicular distensions of the sacral cavity are subject to air filling. In recent vertebrates the air sacs infiltrate the available spaces of bones and more or less fill them, but rarely lead to an expansion of the bone from the inside out as, for example, in the aforementioned exception of *Mycetes*, in which the air-filled body of the hyoid is expanded through the effects of sound amplification,

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as in *Coendu prechensiles* with lifted frontals (Lossen and Wegner 1936) or in the expanded pterygoids of some mammals. The lateral expansion of the sacral cavity of sauropods would more likely be connected with the deposition of particular contents. This is to be accepted in any case for the stegosaurs which exhibit no indications of "pneumaticization" in their skeleton.

In birds we observe that in extreme cases the air canals elongate themselves extraordinarily peripherally and can even enter the phalanges of the hand and foot. It therefore lies in the nature of the system of air sacs that it is capable in certain cases of becoming extraordinarily extended and complex. If one concedes a pneumatic character to the pleurocentral cavities, and I consider this totally justified, and it must follow that air sacs or canals emanating from the lungs of *Diplodocus* and *Barosaurus* extended far into the tail, then one does not demand too much from the deployment capability of the air canal system if one assumes that branches reached those locations of the neural arch upon which external cavities appear. Even such remote locations as the external cavities on the

neurapophyses and the caverns below their dorsal ends would not have been inaccessible to them. The same is valid for the lacunae in the neurapophyses of the anterior caudal vertebrae of *Diplodocus*. Raptors such as *Buteo* provide an example that air tubes can also appear in relatively high dorsal position in the vertebrae of recent birds. According to M. Baer (1896) an air-filled tube, tied like a string of pearls, extends on both sides of the neurapophyses as far as the occiput in *Buteo*.

However, there exist in the external architecture of sauropod vertebrae, spaces of various kinds, for which one can hardly conceive functionally important contents, particularly muscles. These are the deep niches between the lamellar structural ridges, the rill-like depressions between the median and lateral ridges which ascend the neurapophyses of the dorsal vertebrae, and finally, the spaces between the forks of the neurapophyses of bifurcated cervical and anterior dorsal vertebrae of some genera like *Diplodocus*, *Camarasaurus*, *Apatosaurus* and especially *Dicraeosaurus*. Connective tissue, particularly that with fat accumulation, could have been stored in these frequently quite capacious spaces. But a weight reduction would have occurred to the degree that diverticula of the air sac system filled these various spaces. Even if these spaces did not make a sculptural impression in these areas I still do not see a contradiction of this idea. In any case I believe one must reckon with the possibility of such a wide ranging extension of the air sacs.

This observation is also to be applied to the corresponding locations on the external architecture of the sacrum, especially also to the question of the contents of the spacious chambers which are located between the walls of the sacral ribs.

The question now arises, whether the "pneumaticization" of sauropod vertebrae was connected with an extensive air sac system in the trunk of the body or whether the air-filling was essentially restricted to particular spaces in and on the vertebrae. The indicators of "pneumaticization" in the proximal section of the anterior-most dorsal ribs of *Brachiosaurus* and *Apatosaurus* allows one to conclude that there was an extension of air spaces as far as this region. Beyond that, the presence of extensive air sacs in the trunk is not directly made plausible through morphological findings. Despite this one cannot declare the development of such a system as out of the question, when one considers that among the extant lacertilians

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air sac-like extensions to the lungs occur in quite distinct species in *Chamaeleo*, the iguanid *Polychrus* and in the geckonid *Uroplates* (cf. A. Milani 1894). The ability to inflate the dorsal body area through such internal air sacs like chameleons, which Baron Nopcsa once considered not totally impossible, would in any case require very voluminous air sacs. However, I would not like to ascribe this known defensive and protective behaviour of small reptiles against enemies to the gigantic sauropods as well, where the rib cage was certainly too tightly joined, and the inflation of the already extremely bulky trunk area could hardly have been conducive to the defense against or frightening of attacking enemies.

In birds the most significant air sacs, in size and function, are the unusually very large sacs in and directly before the trunk. In contrast to these, the air sacs in and on the vertebrae as well as in the remaining skeletal elements are far less significant in volume. The air sacs play an important role in respiration in that they function like bellows: air is forced out of the air sacs located in the musculature and through the lung, as a result of muscle action during flight. In addition it is assumed that body temperature, as well as buoyancy in swimming birds is regulated by the air sacs (cf. E. Stresemann 1927). Whether and to what degree they filled various functions in pterosaurs, as in birds, is naturally not ascertainable but the impression certainly exists, that their physiological significance in both animal groups was analogous in certain respects - thus possibly in the reduction of body weight; possibly also in the modification of respiration. It is to be understood throughout that the swift carnivorous saurischians, particularly the lightly-built coelurosaurs, gained a weight saving through "pneumaticization" of vertebrae; the extremely thin-walled limb bones of several genera create the impression throughout, that they were also air-filled.

The findings and concepts concerning the physiological significance of pneumaticity in skeletal

elements of volant or cursorial birds, pterosaurs and bipedal saurischians cannot be transferred to the ponderous sauropods - on the contrary, their special collective character is to be taken into consideration. It is unlikely that air sacs, which also filled a special function in respiration as in birds, developed in these admittedly non-agile animals. If vertebrae in sauropods were pneumatic, this could have had corresponding special significance to the organization of these ponderous reptiles. The carriage and movement of the neck played a surpassing role in the entire area of bodily mobility in the sauropods, so that the structure of the presacral vertebral column was determined by this. The "cavernosity" of these vertebrae and their "pneumaticization" likely only had significance to lighten the vertebrae of the neck. Lightening through air-filling must have made itself strongly noticeable, due to the length of the neck and particularly the greatly burdensome weight resulting from the long leverage. However, the "pneumaticization" did not stop at the neck-trunk border, but rather also extended to the dorsal vertebrae, and in *Diplodocus* and *Barosaurus*, even carried through far into the anterior portion of the tail. The concept of a connection between significant neck length and "pneumaticization" of vertebrae, harmonizes with the fact that "pneumaticization" is noticeably weak in *Dicraeosaurus*, a very short-necked genus for a sauropod.

Referring to the other cavernous character of the presacral vertebrae, that is particularly to the formation of external cavities, it is unmistakable that these quite generally are much more strongly developed in the large sauropods

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Brachiosaurus, *Apatosaurus*, *Camarasaurus*², *Diplodocus*, *Barosaurus*, *Tornieria*, than in smaller sauropods such as *Dicraeosaurus* or *Haplocanthosaurus*. In the giant forms the requirements for reduction in neck weight must have been effected through heightened cavitation, from correspondingly greater mechanical stresses. In relation to the construction of external caverns, that is the external "pneumaticization" of the neural arch and its apophyses, this cavitation has reached an extreme in the particularly long-necked giant *Brachiosaurus*. In birds the factor of body size also plays a role in relation to "pneumaticization". In them, the skeleton of the larger forms of members of the same family was usually "pneumatized" to a greater degree than in the smaller ones, to which E. Stresemann (1927) alludes.

In at least certain genera of sauropods there may have been a relationship between the "pneumaticization" of the vertebral column and the residence in water. In *Diplodocus* and *Barosaurus* which are viewed as adapted to a water habitat due to the positioning of the nasal openings to the rear I would like to assume as I have already presented earlier (Janensch 1935/36) without accounting for the "pneumaticization" of the vertebrae, that they could let their necks, greatly lightened through the air spaces, float on the water, and especially assumed this position while resting or sleeping. But even for those genera which did not exhibit the specified adaptation, it is highly likely that considerable time was spent lingering in water, especially during rest, just as some large recent reptiles enjoy this. Allowing the neck to float could have been the resting position in other genera as well as those previously named. Whether dinosaurs stood with their feet on the bottom while resting, or floated freely on the surface would have been dependent on the water depth. The anterior portion of the tail of *Diplodocus* and *Barosaurus*, with its "pneumatized" vertebrae, may also have been buoyant. It would be in keeping that, in careful mounting, as in the *Diplodocus* skeleton in the Senckenberg Museum and that of the U.S. National Museum in Washington, the anterior portion of the tail proceeds backwards horizontally. This is connected with the upper concave sagging of the sacrum. While floating at rest the rear half of the tail could have laid on the bottom and the body could have ridden at anchor so to speak. Highly characteristic for *Diplodocus* and *Barosaurus*, the

² The species *Camarasaurus lentus* is excluded from consideration due to the juvenile character of the described skeleton (C. W. Gilmore 1925) and the resultant incompletely developed external sculpture.

ventral flattening of the posterior caudal vertebrae, and the haemapophyses, which are split into two separate rods and which, with their connected tendons stiffened the vertebral column against lateral flexing, likely made the posterior portion of the tail well suited to anchor the floating body by pressing against the bottom.

The aforementioned "cavernosity" of the cervical vertebrae of *Baluchitherium* is connected with gigantism and elongation of the neck, two characteristics which this mammal has in common with the sauropods. *Baluchitherium* is therefore a noteworthy parallel case in the mammals for the argument-that-the special stresses caused by gigantism and neck elongation went hand in hand with a weight reduction of cervical vertebrae through cavitation of the centra, and perhaps even their "pneumaticization".

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Indications of Pneumaticity in the Vertebrae of other Saurischians.

Apart from the sauropods, it is the coelurosaurs above all among the saurischians, which exhibit features which could with great probability be considered valid indications of pneumaticity. Thus H. G. Seeley (1888) surmised pneumatic features in the cervical vertebra of the coelurosaur *Thecocoelurus*, (= *Thescospondylus daviesi*) which he described. Seeley discovered foramina which he considers pneumatic in this extraordinarily thin-walled vertebra, the interior of which was divided into a few large chambers. One of these is located just behind the anterior end, on the side of the centrum and gives the impression of a small pleurocoel. In such a lightly-built reptile the assumption is obvious, that here, as in the birds, there had evolved air spaces connected with the lungs.

O. C. Marsh (1896) considers the cervical vertebrae of the coelurosaur *Coelurus* to be pneumatic. He discovered relatively large pneumatic foramina which lead to interior lacunae, while he could confirm only very small openings in the no less lightly-built dorsal vertebrae. An illustrated caudal vertebra which due to its elongated, low form must have been positioned fairly far to the rear, exhibits an internally hollow centrum. Similarly, Baron Nopcsa (1923, p. 100) considers the skeleton of coelurosaurs to be "pneumaticized" to a high degree, and even A. S. Romer presumes that many coelurosaur vertebrae and even limb elements possessed air-filled lacunae. This interpretation certainly has plausibility. *Elaphrosaurus bambergi* from the Tendaguru Beds is another example that pleurocoels occur in coelurosaurs. Anterior-lying pleurocoels with sharply-defined borders occur in its cervical vertebrae, in addition to the wide posterior cavities of many vertebrae (Janensch 1925). Elongated pleurocoels are sunk deeply into the centrum of a posterior cervical vertebra, and plainly establish the entrance to an inner lacuna running lengthwise. A transverse break in the middle of the vertebra reveals a cross section of the centrum in the form of a regular square 13 mm long on the sides with a lime-filled 8-mm-wide lacuna. The neural arch, as far as can be recognized from the unclearly preserved structure, appears to exhibit coarse spongiosa which perhaps encloses some small lacunae in the region above the neural canal. In any case the vertebrae of *Elaphrosaurus* are not nearly as thin-walled in construction as in *Coelurus* or *Thecocoelurus*.

The Fo. pneumaticum which Seeley mentions below and lateral to the prezygapophysis of *Th. daviesi*, I believe to be able to confirm in the same location in a posterior dorsal vertebra of *Elaphrosaurus* illustrated by me (Janensch 1925, Fig. 16, Ill. 14). It occurs in the deep niche next to and below the prezygapophysis, and between the prezygapophysis and the ridge which runs down from the parapophysis. Careful preparation showed that this "infraprezygapophysial niche", sunken extraordinarily deep towards the rear, becomes constantly narrower. At the end of the left niche a three-millimeter-long elliptical foramen could be exposed, which enters the neural arch medially. The foramen could not lead to a cavity of any size worth mentioning, since the neural arch offers no room for such a cavity here.

Pleurocoels are confirmed in various genera among the large, short-necked carnivorous saurischians. Thus in *Antrodemus* C. W. Gilmore (1920) found them in all cervical vertebrae from the atlas onwards. He reports that they appear to lead to internal chambers, and that the cervical

vertebrae are pneumatic to a high degree. The third dorsal vertebra, as the last, contains a small pleurocoel.

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Pleurocoels also occur in the second and third cervical vertebrae of *Ceratosaurus nasicornus* Marsh, as shown by the illustrations in Gilmore. Pleurocoels occur in the entire row of dorsal vertebrae of *Gorgosaurus libratus* Lambe (1917) from the Belly River Formation of Alberta (Canada). Certainly the centra of the cervical vertebrae, which were not preserved, also had them. Similarly, the development of the pleurocoels in *Tyrannosaurus* (Osborn 1917) is extreme. They occur in the cervical vertebrae, in at least the majority of the dorsal vertebrae and even in the first two sacral vertebrae. Finally, the Hungarian Cretaceous genus *Magyarosaurus* (F. v. Huene 1932) can be cited as an example of the presence of pleurocoels in the sacral vertebrae, in which even caudal vertebrae exhibit pleurocoels, albeit not very deep ones.

Many generically indeterminate vertebrae of carnivorous saurischians from the material of the Tendaguru Expedition on which I had worked previously, offered the possibility of individual examination. The centrum of an anterior dorsal vertebra of a carnivorous saurischian from excavation TL at Tendaguru (Janensch 1925, Fig. 21) possesses a deeply-invasive pleurocoel on both sides behind the parapophysis.

Ill. 14. *Elaphrosaurus bambergi* Jan. with exposed infraprezygapophysial niche. 1/2 natural size. di=diapophysis. fo infpr=infraprezygapophysial foramen. if prn=infraprezygapophysial niche. n=neurapophysis pr=prezygapophysis.

Ill. 15. Transverse break through the centrum of the anterior dorsal vertebra of a carnivorous saurischian from Tendaguru. 2/3 natural size. nk=neural canal. ve=edge of the anterior end surface. pl=pleurocentral cavity.

A transverse break shows that the two pleurocoels are separated through a very thin, irregular and unsymmetrically-running median wall, and that a foramen leads down from the left pleurocoel into one of the large cells which fill the space of the centrum to the thin external wall and the even thinner cell walls (Ill. 15). Similarly, the right pleurocoel proceeds upwards in a canal into the upper large-celled space of the centrum (not presented in the illustration). According to this discovery there is nothing to oppose the assumption that the foramen is a *Fo. pneumaticum*, and that the cells in the vertebra were filled with air during life.

Features which argue for pneumaticity, or at least can be interpreted as such, are exhibited in several other vertebrae. The neural arch of a large carnivorous saurischian which I described from the Tendaguru Beds (Janensch 1925, Fig. 17, Find St 297) offered important information after further preparation.

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Broken surfaces on the diapophysis and postzygapophysis reveal matrix-filled lacunae. A transverse break through the basal region of the prezygapophysis exhibits extreme large-celled construction (Ill. 16). It is particularly important that, analogous to the coelurosaur *Elaphrosaurus*, two large, wide, elliptical, roughly 8-mm-long foramina are found at the base of the deeply-invasive infraprezygapophysial niche, from which one leads upwards, the other medially into the hollow interior of the neural arch (Ill. 17). These two openings have the character of a *Fo. pneumaticum* throughout. Furthermore, the large niche below the postzygapophysis opens into a large three-sided, 15-mm-wide aperture into the interior of the neural arch. This aperture also appears to have had the function of a *Fo. pneumaticum*.

Ill. 16. Transverse break through the right prezygapophysis of a cervical vertebra of a large carnivorous saurischian from Tendaguru, large-celled structure. 1/1 natural size. m=medial. v=ventral.

Ill. 17. Neural arch of the same cervical vertebra as Ill. 16, ventral view, insignificantly enhanced. 2/3 natural size. n=suture. line to centrum. ifprn=infraprezygapophysial niche. pr=prezygapophysis. d=diapophysis. fo ifpr=infraprezygapophysial foramen. nk=neural arch.

On the other hand, a foramen (Ill. 18) is located on both sides of the infraprezygapophysial niche in the posterior cervical vertebra of a mid-sized carnivorous saurischian from Tendaguru (EH 103), as reported by me (1925, Table 8, Fig. 10-c). The left foramen is 8 mm long and 4 mm high; the right leads into a low, approximately 1 1/2-cm-long lacuna, as can be seen on the broken surface. I have not investigated whether these foramina are connected with cavities in the base of the neural arch because I did not want to damage the valuable original specimen. In any case it was only a question of very weak "pneumaticization" in the posterior dorsal vertebra, because the interior of its centrum is completely filled with dense spongiosa.

It is also noteworthy that in a half vertebra of a *Plateosaurus* from Halberstadt out of Slg. Jaekel (Find IX), which must be the tenth or a neighbouring one, a medially-invasive foramen could be exposed, entering the well developed infraprezygapophysial niche on the left. This foramen is constricted on both sides and is approximately 11 mm long and 4 mm high (Ill. 19).

One could object to the concept of the infrazygapophysial foramen as a Fo. pneumaticum - that its obviously widely-distributed appearance in saurischians and indeed even its presence in vertebrae without any distinctive indication of "pneumaticization" indicates that it can be considered the inlet for an important blood vessel.

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Ill. 18. Dorsal vertebra of a carnivorous saurischian; cross section through the root of the diapophysis. Tendaguru. 1/2 natural size. di=diapophysis. fo ifpr=infraprezygapophysial foramen. n=neurapophysis. pa=parapophysis pr=prezygapophysis. wk=centrum.

Ill. 19. *Plateosaurus* M. Middle Keuper of Halberstadt ; view of the left side. 2/3 natural size. di=diapophysis. fo ifpr=infraprezygapophysial foramen. pr=prezygapophysis.

As a vessel foramen it would however, in any case be unusually wide, aside from the fact that its outline in the *Plateosaurus* vertebra is a poor match to this interpretation, especially in the neural arch of the cervical vertebra examined here. Even though two large openings are present in this case, and moreover, that they appear along with the noticeable broad-celled inner bone structure, this cannot be explained with reference to vessels. In any case, I have never found a larger vessel foramen at the location in question in other reptiles of various orders. Therefore the pneumatic nature of the foramen seems more plausible to me. The infraprezygapophysial niche appears to be a location which is somehow preferred for the onset of "pneumaticization" in *Thecocoelurus* according to Seeley's statement and according to my observations in *Elaphrosaurus*, and in the aforementioned large neural arch. This impression is strengthened still more by the fact that a very large Fo. pneumaticum appears in the same location on a dorsal vertebra of *Aepyornis hildebrandti* described by Burckhardt. If in contrast to these examples, sauropods have only displayed pneumatic foramen in this niche in a few species, it may be accounted for by the fact that in sauropods the surroundings of the niche and especially the entire dorsal portion of the neural arch which carries the various apophyses is built in such a finely-lamellar fashion that a space for interior lacunae is hardly present.

Finally, it must be mentioned here that H. G. Seeley (1904) described a large Fo. pneumaticum in the unusual vertebra recently interpreted by F. Frh. v. Huene (1942) as the atlas of a theropcephalian *Tamboeria maraisi*, Seeley from the *Tapinocephalus* Zone, that is the Upper Permian of the Cape Province. This foramen, the actual presence of which F. v. Huene questions, is visible, according to Seeley, on the underside of one of the lamellae which extend out laterally on the underside of the side wall of the centrum, and carry a facet for a rib. The foramen sits deeper than the previously described cases of the Fo. infraprezygapophysiale so that its existence in no way appears implausible to me.

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That ribs in carnivorous saurischians can be "pneumaticized" as in certain sauropods, is demonstrated in *Antrodemus valens* in which the first short dorsal rib (?last cervical rib) exhibits deep cavities in the inner side. (C. W. Gilmore 1920). As a result the presence of air sacs off the vertebrae may certainly also be inferred in this genus, which we may in general assume in the carnivores with well-developed "pneumaticization" of the vertebrae.

If the interpretation that the infraprezygapophysial foramen is pneumatic is correct, then one can further conclude that in the saurischians as well, which exhibit only this foramen as an indication of "pneumaticization", air-filled tubes or sacs were present which extended from the lung or another portion of the respiratory system as in the chameleons today, in the skeleton of which there are absolutely no indications of such tubes or sacs. If therefore, this characteristic can even be ascribed to the plateosaurs, which in contrast to the majority of the saurischians are even more primitive in many respects, then it were likely conceivable that such a modification of the respiratory system was already spread amongst older reptiles than one could previously assume. It is desirable that possible indications of "pneumaticity" were also observed in pseudosuchians for example. It does not appear out of the question that "pneumaticity" of skeletal elements wasn't initially acquired together with the power of flight in the highly pneumatically-constructed flying sauropsida, birds and pterosaurs, but rather was already developed to a lesser degree in their presumably quite agile, lightly-built but not yet flighted ancestors.

Conclusions.

The interpretation that air sacs infiltrated the centra of presacral vertebrae in sauropods via the pleurocentral cavities is supported by a comparison with corresponding structures in birds and by the evidence that such cavities are connected with interior structures of pneumatic character. In *Brachiosaurus* and *Barosaurus* as well as in other genera, they consist of the hollowing-out of the vertebrae to a median wall; in the cervical and dorsal vertebrae of *Brachiosaurus*, in the dorsal vertebrae of *Barosaurus*, and in the very large-celled structure of the condyles. The latter is absent in the only partially "pneumaticized" vertebrae of *Dicraeosaurus*. In contrast a connection can even be demonstrated between pleurocentral cavities and interior lacunae in the anterior caudal vertebrae of *Barosaurus*.

A pneumatic character is also assumed for the cavities ("external caverns") which appear in the neural arch and its apophyses, and also for the caverns in the proximal portion of the dorsal ribs of certain genera.

The nature of the evolution of air sacs and canals in and on the vertebrae of birds is utilized to obtain a concept of the corresponding structure in sauropods.

The pleurocentral cavities are also interpreted in the same manner in carnivorous saurischians, and a connection with large inner cells is demonstrated in a vertebra from the Tendaguru Beds.

A presumably pneumatic foramen was repeatedly confirmed in the "infraprezygapophysial niche" ; also in Plateosaurus, and in another case in connection with inner large-celled structure. [24]

The "pneumaticization" of the vertebral column was of physiological significance for the swift running carnivorous saurischians, as for the volant pterosaurs, in the reduction of body weight. In

the ponderous sauropods the weight reduction made the movement of the long neck easier and enabled relief during rest, in that the neck could float on the water through its own buoyancy.