underestimates would be most significant in forested regions because wind-driven drops are captured more efficiently by trees than by short vegetation.

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A reinterpretation of the amphisbaenian orbitosphenoid

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The Amphisbaenia is a successful group of some 140 species of strange, specialized burrowing reptiles with reduced eyes and limbs, found mainly in parts of Africa and America. Their systematic position has been much debated[1]. They show many unique features, including a large orbitosphenoid bone which has previously been regarded as a cartilage ossification[2], like that of vertebrates in general[3]. However, appropriate embryonic material available for the first time shows that it is a membrane bone. This remarkable condition tends to emphasize the distinct status of the Amphisbaenia within the Squamata, as a sister-group equivalent to the lizards or the snakes[1,4,5].

In most lizards the orbital region of the chondrocranium consists of the interorbital septum which is partly derived from the fused trabeculae (trabecula communis): the planum supraseptale, a trough-like structure which supports the forebrain, and more posteriorly, a scaffolding of bars which like the planum belong to the orbital cartilage system. Some calcification of the orbital cartilages may occur in maturity, and parts of them may ossify to form small paired orbitosphenoids; in general, however, this region of the chondrocranium remains cartilaginous throughout life[2].

The orbitosphenoid (fused orbitosphenoids[6]) of adult amphisbaenians, however, is a substantial plate of bone which forms the floor of the anterior part of the cranial cavity. It lies dorsal to the rod-like trabecula communis (there is no proper interorbital septum) and to the palatines, ventral to the descending flanges of the frontals and parietals, and mainly anterior to the parasphenoid. In some forms, at least, it is pierced by foramina for the tiny optic nerves.

Comparison with lizards would suggest that this orbitosphenoid is a replacement ossification of the planum supraseptale and adjacent parts of the orbital cartilage system[2], and hence a relatively minor modification of the basic saurian pattern. However, all considerations of this region of the amphisbaenian chondrocranium have been based on postnatal material (and on one apparently very late embryo [7]). We have been able to obtain embryos of three stages of the South American species *Leposternon microcephalum*, and these strongly suggest that the nature of the orbitosphenoid has been misinterpreted.

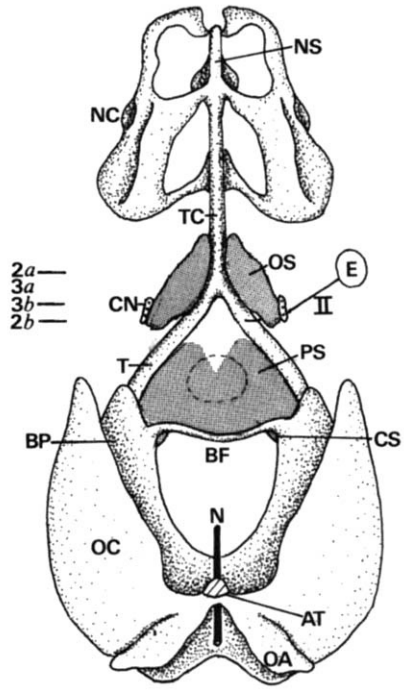

Fig. 1 *Leposternon microcephalum.* 5 mm head-length embryo. Simplified reconstruction of chondrocranium in dorsal view, also showing orbitosphenoid and membranous (parasphenoid) component of parabasisphenoid bone. Approximate levels of sections in Figs 2 and 3 shown on the left. AT, Anterior process of tectum (cut); BF, basicranial fenestra; BP, basal plate; CN, cartilaginous nodule associated with orbitosphenoid; CS, crista sellaris; E, eye (shown on right only); N, notochord (cut posteriorly); NC, nasal capsule; NS, nasal septum; OA, occipital arch; OC, otic capsule; OS, orbitosphenoid; PS, parasphenoid (outline of pituitary region in broken lines); T, trabecula; TC, trabecula communis; II, optic nerve.

An embryo of 5 mm head-length provides the most critical stage for interpretation (Fig. 1). The floor of the orbital region of the cranial cavity is formed by two thin sheets of bone, one on either side of the midline. Their medial edges overlap the trabecula communis (Figs 2*a*, 3*a*) and the anterior parts of the paired trabeculae (Fig. 3*b*). The optic nerves pass ventral, and then medial to these bones to reach the brain (Figs 1, 2*b*). The position of these bones relative to the surrounding cranial elements and to the optic nerves leaves little doubt about their identities. Later fusion in the midline would give rise to the unpaired orbitosphenoid of the adult, and such fusion has partly occurred in an older, 6.5 mm head-length embryo. Owing to this fusion the optic nerves come to pass through discrete foramina in the definitive bone.

The histological appearance of the orbitosphenoids in the 5 mm embryo, stained with Masson's trichrome, strongly suggests that they are essentially membrane bones. They appear as thin plates of ossification within mesenchyme (Fig. 3*a*) and (except at one site; see below) do not resemble perichondral or endochondral ossifications replacing preexisting orbital cartilages. Indeed, these cartilages appear to be virtually absent in amphisbaenians, both in our embryonic material and in adults; as in snakes, the orbital region of the chondrocranium is represented entirely or almost entirely by trabecular derivatives.

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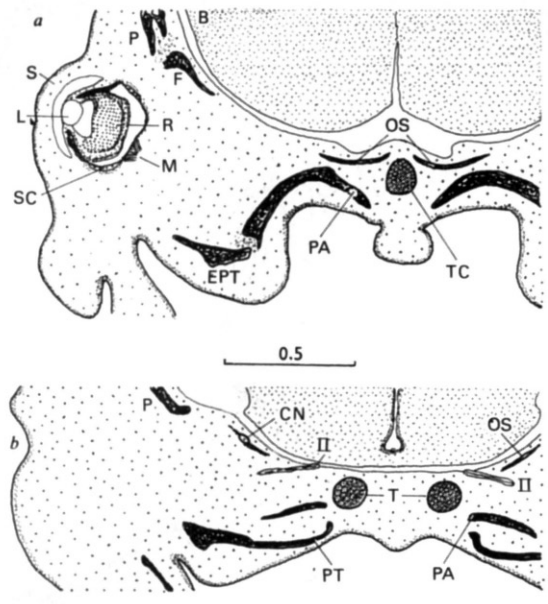

Fig. 2 *Leposternon*, 5 mm head-length embryo. *a*, Transverse section through left side of head at level of eye. *b*, Section at more posterior level showing optic nerves approaching brain. B, Brain; N, posterior extremity of cartilaginous nodule, associated with orbitosphenoid; EPT, ectopterygoid; F, frontal; L, lens; M, eye muscles; OS, orbitosphenoid; P, parietal; PA, palatine; PT, pterygoid; R, retina; S, spectacle; SC, scleral cartilage; T, trabecula; TC, trabecula communis; II, optic nerve. Other nerves and muscles not shown. Scale in mm.

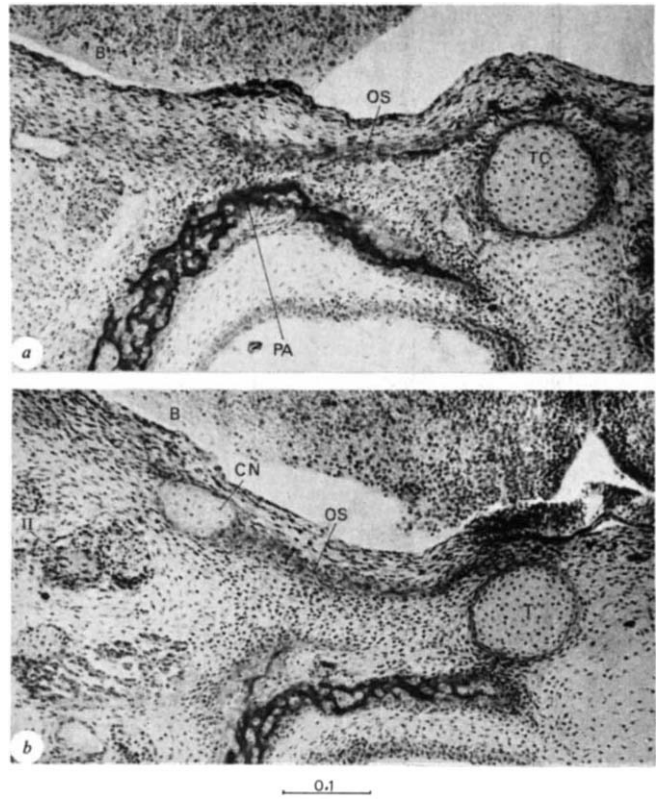

Fig. 3 *Leposternon*, 5 mm head-length embryo. *a*, Transverse section through left orbitosphenoid at similar level to Fig. 2*a*. *b*, Section between levels of Fig. 2*a* and *b* showing orbitosphenoid and associated cartilaginous nodule, and the left trabecula. Scale in mm. Lettering as in Fig. 2.

However, in the 5 mm head-length embryo there is a pair of small cartilaginous nodules, one on the posterolateral aspect of each orbitosphenoid (Figs 1, 3*b*). Each nodule seems to be undergoing perichondral ossification in continuity with the much more extensive ossification of the membrane bone. The nodules cannot make more than a small contribution to the definitive orbitosphenoid; it seems likely that they represent vestiges of the orbital cartilages of *Sphenodon* or lizards, such as are sometimes seen in the embryos of certain snakes[2].

It would therefore appear that the orbitosphenoid of *Leposternon*, and probably of other amphisbaenians (since the adult bone shows relatively minor variation) is largely or entirely a true membrane bone in the illuminating but as yet somewhat unfamiliar sense of Patterson[8]. Such bones ossify in membrane deep in connective tissue, away from the skin. Despite their ontogeny they may be phylogenetically homologous with cartilage bones in other forms. Patterson regards them as distinct from elements such as the frontals and parietals, which have traditionally been called membrane bones[3], but for which the term dermal bone is more appropriate because they are phylogenetically associated with the skin. He writes that while true membrane bones are not uncommon in bony fishes, their occurrence in tetrapods is doubtful and still a subject for investigation. The orbitosphenoid of *Leposternon* seems to conform with Patterson's definition of a membrane bone. Possibly a new term might be used, but we have retained the name 'orbitosphenoid' here.

We conclude that the amphisbaenian orbitosphenoid is of paired origin[6], but, contrary to some previous accounts[2], is usually, if not always, unpaired in the adult. It is important in reinforcing the floor of the anterior braincase and hence in giving the skull the box-like rigidity which, in amphisbaenians at least, is a feature of burrowing adaptation. A parallel enclosure of the cranial cavity is found in snakes, which may also be of burrowing origin[9], but here the bony floor of the cranium between the eyes is formed entirely by the descending flanges of the frontals and parietals, and mid-ventrally by the rostrum of the parasphenoid; there are no orbitosphenoid bones.

Among many lizards examined we have observed comparable ossification of the floor of the anterior braincase only in microteiids of the genus *Bachia*. Serial sections of adult *Bachia* (formerly *Ophiognomon*[10]) *trisanale* show this bone attached to the posterior edge of the cartilaginous planum supraseptale on each side; possibly it arises as an intramembranous extension from the planum. To some extent the bone resembles the paired orbitosphenoid of embryonic *Leposternon*. This finding is of interest since a relationship between microteiids and amphisbaenians has been postulated[11]. In other respects, however, the cranial anatomy of microteiids differs considerably from the amphisbaenian condition. The orbitosphenoids of *Bachia* are at present best interpreted as parallel developments, though their discovery supports the view that the morphology of the microteiids and of other fossorial squamates deserves further attention[1].

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