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### The Endolymphatic Sacs in Embryos of *Amphisbaena darwini*

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Endolymphatic sacs of amphibians and reptiles are usually located inside the cranial cavity, posterior to the brain and dorsal to the foramen magnum (Wever, 1978, 1985). They are connected with the sacculus of

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TABLE 1. Specimens of *Amphisbaena darwini* used in this study staged according to Montero et al. (1999), except stages 0 and 12.

Specimen	Stage	Total length (mm)
I	stage 0	not taken
II	stage 4-5	27.35
III	stage 4-5	36.05
IV	stage 7	36.10
V	stage 11	47.10
VI	stage 11	49.05
VII	stage 12	not taken
Adult		not taken

the inner ear by means of endolymphatic ducts that pierce the internal bony wall of the otic capsules.

Endolymphatic sacs are better developed in some Iguania (Etheridge, 1959) and Gekkota (Kluge, 1967, 1987) than in Autarchoglossa (Bauer, 1989). The function of the endolymphatic sacs is dubious, and different theories have been proposed. Carus (1841 in Whiteside, 1922) related them to growth and calcification of embryonic bone in snakes (but see also Kästle, 1962; Packard et al., 1984; Kluge, 1987; Bauer, 1989). Other hypotheses relate them to calcium metabolism during development (Guardabassi, 1953; Yoshihara et al., 1992) or during the formation of the egg shell (Ruth, 1918; Bustard, 1968), with regulation of intrasacculus pressure (La Reau, 1926), or with the absorption of endolymph for pressure regulation of the inner ear (Hasse, 1881, in Dempster, 1930; Dieter Dellmann, 1993). It was also suggested that the endolymphatic sacs have an important role in inner ear immune defense (Wackym et al., 1987; Altermatt et al., 1990, 1992).

According to Wever and Gans (1970), there are no studies on reptiles that provide histological or cytological details of the endolymphatic sacs. For example, in the detailed studies of the adult amphisbaenian inner ear (Wever and Gans, 1970, 1972, 1973; Gans and Wever, 1972, 1974, 1975) the endolymphatic sacs were never described. Here we describe the morphology and development of the endolymphatic sacs both in an embryonic series and in an adult of *Amphisbaena darwini*, considering their function during development.

Eggs containing embryos of *Amphisbaena darwini heterozonata* Burmeister 1861 were collected on 16 December, 1997, at San Javier hills (altitude  $\pm$  1200 m a.s.l.); the adult specimen was collected in Yerba Buena city, both localities in Tucumán province (Argentina). The embryos were fixed in Baker's solution. Standard histological techniques (Pearse, 1960) were employed to obtain serial sections of 6-8  $\mu$ m in transverse, frontal, and sagittal planes. They were stained with hematoxylin-eosin or Gallego's trichrome stain (Vivoli, 1969). All the histological slides are housed in the Histological Collection of the Fundación Miguel Lillo, numbers 158-309.

Seven embryos and one adult were studied (see Table 1). They were classified by their external characteristics in the stages defined by Montero et al. (1999).

Comparative cleared-and-stained specimens (prepared according to Wassersug, 1976) of other squa-

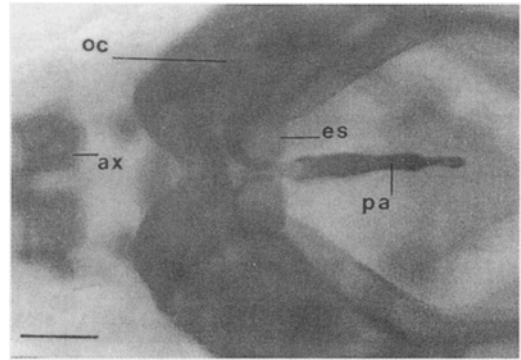


FIG. 1. Dorsal view of a cleared-and-stained stage 11 embryo. Anterior to the right. Bar = 0.5 mm. ax, axis; es, endolymphatic sac; pa, anterior process of tecti synotici; oc, otic capsule.

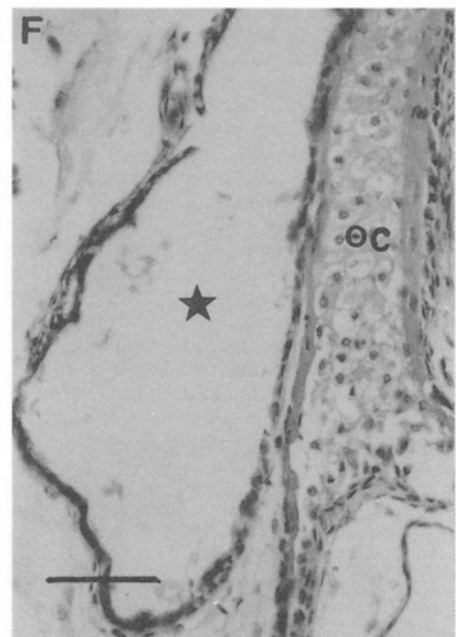
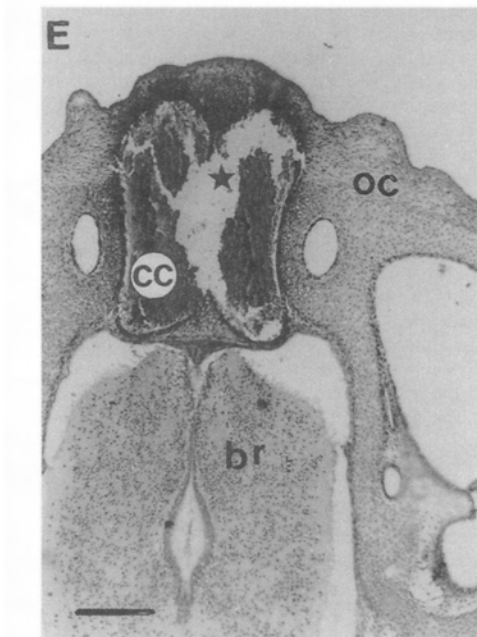
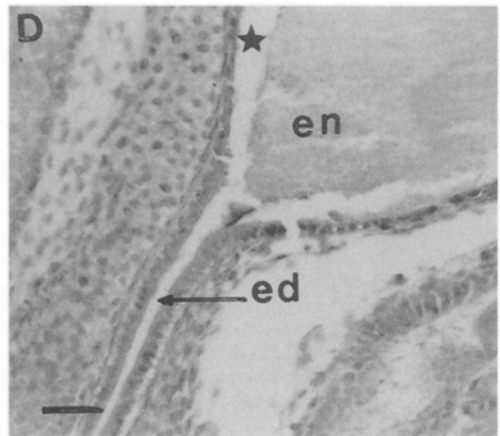
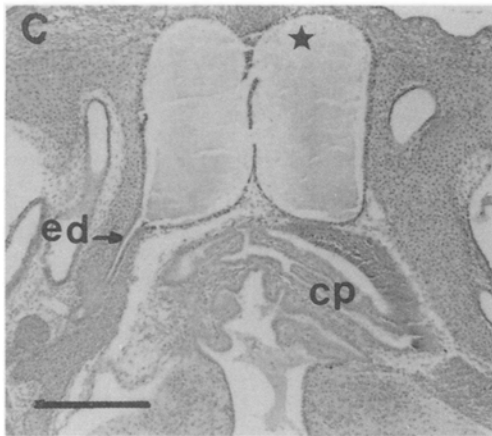
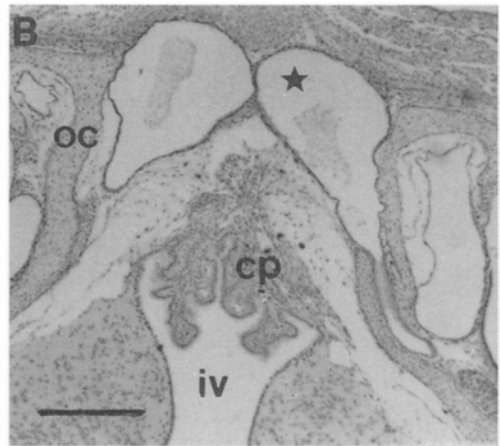
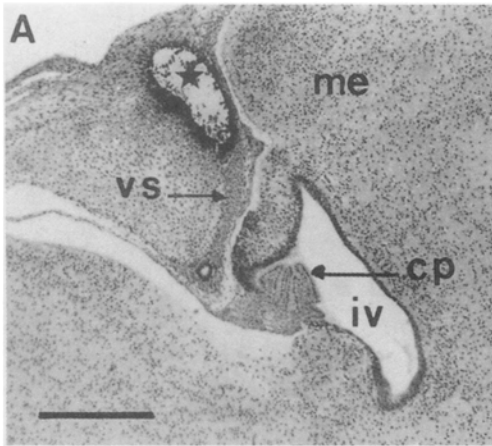
mate species come from the Herpetological Collection of the Fundación Miguel Lillo.

The endolymphatic sacs of *Amphisbaena darwini* are paired, dorsoventrally and anteroposteriorly elongated structures. In living embryos, the sacs were observed through the semitransparent skin as white milky patches at the nape. In cleared-and-stained embryos the sacs appear as opaque structures lying under the chondral synotic tectum (Fig. 1) or, in more advanced embryos, under the cleared bones of the roof of the braincase. The sacs stain strongly with alizarine (Montero et al., 1999), revealing the calcium content (Fig. 1).

Histological examination reveals that the endolymphatic sacs of *A. darwini* embryos lie behind the mesencephalon and dorsal to the cerebellum of the developing brain (Fig. 2A-B). The sacs are intramembranous and are closely related to the dorsal longitudinal venous sinus and the choroid plexus of the fourth ventricle (Fig. 3B). The sacs are in close contact medially (Fig. 2B-C) but not fused. Laterally, they contact the cartilaginous otic capsule (Fig. 2B-C), except in stage 12 in which peri- and endochondral ossifications of the otic capsules have begun (Fig. 2F). Adult sacs show the same topology in relation to the fourth ventricle, choroid plexus, and dorsal venous sinus, being proportionally less developed and not so wide as those of embryos, resulting in a tubular structure.

Each sac is connected with the corresponding sacculus by means of an endolymphatic (otic) duct. The duct opens at the ventrolateral side of each sac, forming a small funnel. The duct has a low cylindrical epithelium that shows neither polarity nor peculiarities of the apical membrane of its cells (Fig. 2D).

The epithelium of the wall of the sacs is simple, mostly cuboidal; in some areas it is very thin and flat. The lamina propria is very thin. Until stage 7, the epithelium is strongly basophilic (Figs. 2A, 3A); in more advanced stages (stage 11 and up) the strong basophilic reaction disappears (Fig. 2F). An acidophilic cell type is intercalated in the basophilic epithelium, in the dorsal and ventral areas of the sac epithelium. The acidophilic cells are rounded, have an euchromatic nucleus, a high ratio of cytoplasm/nucleus and a dense patch of apical microvilli that projects into the sac lu-



men (Fig. 3B). They are bigger and more conspicuous than the basophilic cell type. There is a noteworthy vascularization on the external side of the sacs, corresponding to the areas in which the acidophilic cells appear (note the large venous sinus in Figs. 2A, 3A–B). The acidophilic cells are found from stage 4–5 and their number is greater in the more developed stages; in embryo V, they form a fold projecting over the sac lumen.

The wall between the sacs is formed by the epithelium of both contralateral sacs, which share a common lamina propria. Therefore, the wall is a delicate and fragile structure (mostly in the younger embryos in which it breaks very easily; Fig. 2C, E). In stage 12, the sac epithelium is very flat, with some areas exhibiting cellular lysis and very few acidophilic cells (Fig. 2F); therefore, it appears that it is nontrophic.

In the adult specimen, the epithelial cells have lost basophilia. In some places, they are vacuolated and their nuclei are apical. The acidophilic cells are smaller, fewer, and less evident than in embryos; they are intercalated with cuboidal cells. The funnel between the sac and the duct has a simple epithelium with highly vacuolated cells, being twice as tall as the sac epithelium. Those cells have apical nuclei.

The otic sacs contain endolymph, which appears in the histological preparations as acellular, dense, and basophilic (Fig. 2D). Crystallized calcium carbonate is suspended in the endolymph (Figs. 2E, 3A, C). The quantity and density of the crystals are inversely related with the age of the embryo. Crystals disappear with the onset of ossification processes. In the younger embryos (until stage 4–5), there are no ossification centers in the elements of the head, correlated with a large number of crystals. In stage 7, there are small ossification centers in the mandibles and the number of crystals is much lower than in the previous stages (Fig. 2B). In stage 11, there are several dermal ossifications in the cranium, whereas in the endolymphatic sacs only scattered and small crystals remain. In advanced embryos, with active osteogenesis, there are no crystals in the sacs, and only an amorphous and viscous content is observed (Fig. 2F), a condition also observed in adults.

The crystals are usually deposited over one side of the sac possibly because of postmortem sedimentation. The size and aspect of the crystals vary within and among specimens (e.g., Fig. 3C). Crystals were not observed within the sacculus in any embryo.

The general shape of the endolymphatic sacs changes with development. In young embryos (with numerous crystals), the sacs are distended (Fig. 2C). In older ones, without crystals, sacs are flaccid (Fig. 2F).

The histology of the endolymphatic sacs and ducts of *A. darwini* is similar, in a broad sense, to that re-

ported in amphibians (Dempster, 1930; Guardabassi, 1953). Nevertheless, the acidophilic cells were not described previously. They seem to play a physiological role that becomes more important in more developed embryos: their number increases, and they become more closely related to the vascular system (although the vascularization is a generalized process, not only related to those structures). The acidophilic cells may be related to the transfer of calcium from the sacs. The diminution of the basophilic reaction of the cuboidal cells during ontogeny may be related to the lack of cellular secretory activity; this was observed also in amphibians (Kawamata, 1990). If this assumption is true, it is possible to interpret cuboidal cells as glands related to the concentration of calcium carbonate in the sacs. The glandular appearance was suggested previously (Guardabassi, 1953; Kluge, 1967).

The endolymphatic sacs seem to progressively decrease in size during the embryogenesis in *A. darwini*. There is an apparent relationship between the presence of the crystals and the onset of the ossification process. Therefore, the sacs may play an important role in the development of the skeletal system. The adult sacs are not well developed as the ossification processes have diminished. Nevertheless, it cannot be discounted that the sacs are involved in the adult calcium metabolism as they are in amphibians (Stiffler, 1993, 1996) and other vertebrates (Marmo, 1982).

The calcium content of the embryos may be derived from yolk or shell calcium (Bauer, 1989). We have no clues about the mechanism of concentration of calcium carbonate or about the formation of the crystals (but see Marmo, 1982). Kluge (1967) stated that the endolymph hardens upon exposure to air and certain preservatives; therefore the presence of crystals could be an artifact.

In a survey of cleared-and-stained specimens of different taxa, we observed the calcified endolymphatic sacs only in embryos and juvenile specimens. It seems that this technique is not useful to reveal the endolymphatic sacs of adults, because of the relatively smaller size and reduced calcium content. Nevertheless, it should be kept in mind that the survey was made using the specimens at hand in the FML herpetological collection, and we had no control over specimen preparation; therefore technical artifacts could not be discounted.

Endolymphatic sacs were detected in cleared-and-stained juveniles of *Pantodactylus schreibersi* (Gymnophthalmidae), *Eunectes notaeus* (Boidae), *Hydrodynastes gigas* (Colubridae), and late embryos of *Phymaturus punae* (Tropiduridae), *Tupinambis marianne* (Teiidae; F. Lobo, per. comm.), and *Amphisbaena darwini* (this paper). On the other hand, they could not be detected in cleared-and-stained adults of the following fami-

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FIG. 2. (A) Stage 7 embryo, sagittal section. Dorsal on top, anterior to the right. Bar = 225  $\mu$ m. (B) Stage 11 embryo, transverse section. Posterior on top. Bar = 202  $\mu$ m. (C) Stage 4–5 embryo, frontal section. Posterior on top. Bar = 225  $\mu$ m. (D) Stage 4–5 embryo, detail of the endolymphatic sac. Posterior on top. Bar = 30  $\mu$ m. (E) Stage 0 embryo, transverse section. Dorsal on top. Bar = 150  $\mu$ m. (F) Stage 12 embryo, transverse section. Dorsal on top. Bar = 56  $\mu$ m. All sections stained with Hematoxylin and Eosin. br, brain; cp, coroid plexus; ed, endolymphatic duct; en, endolymph; iv, IV ventricle; me, mesencephalum; oc, otic capsules; star, endolymphatic sac; vs, venous sinus.

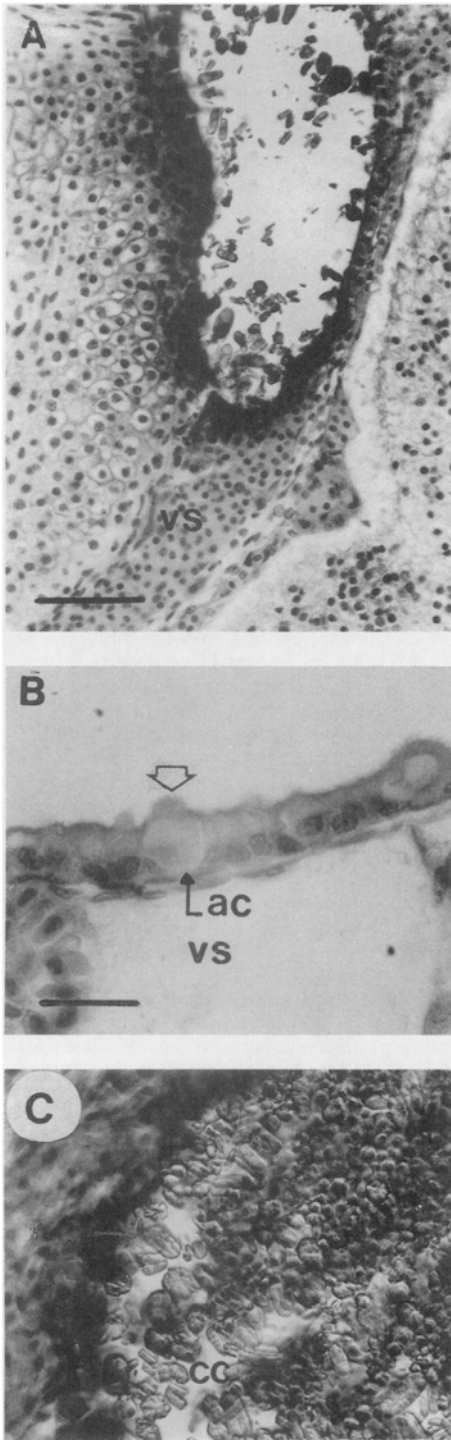


FIG. 3. (A) Stage 7 embryo, sagittal section. Dorsal on top, anterior to the left. Bar = 49  $\mu\text{m}$ . (B) Stage 11 embryo, acidophilic cells. Bar = 19  $\mu\text{m}$ . (C) Stage 4-5 embryo, aragonite crystals. Illumination method, phase contrast (Ph 3). Bar = 19  $\mu\text{m}$ . All sections stained with Hematoxylin and Eosin coloration. ac,

lies: Tropicoduridae (five species of *Liolaemus*), Teiidae (two species of *Kentropyx* and one of *Cnemidophorus*), Scincidae (one species of *Mabuya*), Anguidae (one species of *Ophiodes*), Amphisbaenia (one species of *Amphisbaena* and one of *Anops*), Leptotyphlopidae (two species of *Leptotyphlops*) and Colubridae (one species of *Clelia*, two of *Liophis*, one of *Waglerophis*, and two of *Philodryas*). In two species of the gekkonid genus *Homonota*, the extracranial extension of the sacs was observed in adult specimens. The position, shape, and size of the sacs are similar in the case of *Amphisbaena*, *Phymaturus*, *Pantodactylus*, and *Tupinambis*. In the case of the juvenile snakes surveyed (*Eunectes* and *Hydrodynastes*), the position is similar, but the sacs are much more reduced and elongated in shape. The sacs are hypertrophied, extending even extracranially, in adults of some Iguania and Gekkota, but they are poorly developed in adults of other Squamata (Autarchoglossa). Our observations indicate that, in that sense, *Amphisbaena* is similar to Autarchoglossa. However, it is uncertain whether this similarity is a result of common ancestry.

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acidophilic cell; arrow, microvilli of acidophilic cell; cc, calcium carbonate crystals; star, endolymphatic sac; vs, venous sinus.

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### A Fossil Leaf-Toed Gecko from the Oppenheim/Nierstein Quarry (Lower Miocene, Germany)

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Although the lizard family Gekkonidae is diverse and cosmopolitan, its fossil record is poor. Other than a few finds from Palaeogene and Neogene deposits, most gekkonid fossils are no older than the Pleistocene and can be easily referred to extant genera (Estes, 1983). Of the Miocene European and North African gekkonid remains, Hoffstetter (1946) described two species in the genus *Gerandogekko* from the French sites St.-Gérard-le-Puy (Lower Miocene; MN 2) and La Grive-Saint-Alban (Middle Miocene; MN 7–8), and Estes (1969) described material from Devínska Nová Ves, Slovakia (Middle Miocene), that he referred to cf. *Phyllodactylus* sp. Rage (1976) reported unidentified remains of gekkonids from the Lower Miocene of Beni Mellal (Morocco), and Schleich (1987) described *Palaeogekko risgoviensis* from the Middle Miocene (MN 6) of Bavaria (Germany). Schleich (1985) also listed several additional Miocene localities from southern Germany that yielded indeterminate remains of gekkonids. In the present work, we describe gekkonid remains from the Lower Miocene of the Mainz Basin, Germany, assigning it to the modern genus *Euleptes* (European leaf-toed geckos).

GPIM: Institut für Geowissenschaften der Johannes-Gutenberg-Universität Mainz, Germany; NHMB: Naturkundemuseum Basel, Switzerland; ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig Bonn, Germany.

*Materials and Methods*.—Referred fossil material is

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