



a large nest has approximately a twofold survival advantage if it is in its mother's nest rather than in another female's nest. In none of the few other communally-laying species<sup>8,12</sup> have birds been shown to be able to recognise their own eggs. The ability opens up new complexities in the evolution of 'cooperative' breeding systems.

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BRIAN C. R. BERTRAM

The Research Centre,  
King's College,  
Cambridge, UK

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## New look at the origin of birds and crocodiles

DURING the period 1926-73 most ornithologists and vertebrate palaeontologists supported Heilmann's theory of avian origins. Heilmann<sup>1</sup> argued that all dinosaurs and pterosaurs were too specialised to have been ancestral to birds. Instead he chose to derive birds directly from a primitive group of Triassic archosaurs, the Pseudosuchia. Heilmann's theory has recently been challenged by Walker<sup>2-4</sup>, who has suggested that birds evolved from an early crocodylian, and by Ostrom<sup>5-10</sup>, who argued that birds descended from theropod dinosaurs. We recently began a study of the otic region in archosaurs and birds, in search of advanced, homologous features which would give definitive support to one theory or the other. The results of this investigation, discussed below, strongly support a hypothesis of a common pseudosuchian origin for birds and crocodiles, independent of dinosaurs.

The otic region of the living rhynchocephalian, *Sphenodon*, is usually assumed to represent the primitive amniote condition<sup>11</sup>, although the middle ear is somewhat specialised. In all tetrapods the inner ear is composed of two distinct fluid-filled compartments, an endolymphatic compartment which contains the sensory apparatus for hearing and orientation, and an investing perilymphatic compartment (Fig. 1b). In the vestibular region the endolymphatic channel is drawn out into a short lobe, usually termed the lagena, which contains the sensory hair cells of the basilar membrane. Sound vibrations from the stapes are transmitted to the sensory membrane by a perilymphatic duct which is wrapped around the lagena. Compressional waves carried by the duct must be dissipated outside the otic capsule. In primitive reptiles, the perilymphatic duct leaves the otic capsule in the internal wall of the braincase, passes along a groove in the braincase wall and is exposed to supratharyngeal tissues after passing through the fissura metotica (vagus foramen). In addition to transmitting the perilymphatic duct, the metotic fissure of *Sphenodon* and primitive reptiles provides an exit for the ninth to eleventh cranial nerves. In birds and crocodiles, the perilymphatic duct leaves the otic capsule lateral to its primitive position

and is exposed as a secondary tympanic membrane in the middle ear cavity (Fig. 1c, d). De Beer<sup>12</sup> has called the new external exit of the duct the "fenestra pseudorotunda", by analogy with the round window of mammals.

It has been generally assumed<sup>13</sup> that the otic specialisations shared by birds and crocodiles were characteristic of all archosaurs and hence provided no further evidence of avian relationships. However, well preserved neurocrania or endocranial casts of dinosaurs and early thecodonts reveal a primitive, *Sphenodon*-like relationship between the perilymphatic duct and the braincase. In ankylosaurs, hadrosaurs, sauropods and the theropod *Allosaurus*, the perilymphatic duct entered the cranial cavity medially, passed posteriorly along a groove in the braincase wall and left the cranium by the metotic fissure (Fig. 2a-d). A primitive relationship is also indicated by the crania of *Tyrannosaurus*<sup>14</sup> and *Megalosaurus* (BMNH R 1946, 3129) in which there is a groove for the duct between the internal opening of the 'vestibule' and the vagus foramen. In the coelurosaur, *Dromaeosaurus*, the opening previously described as a 'foramen rotundum'<sup>15</sup> is a glossopharyngeal (ninth cranial nerve) canal minus its roof and the overlying otic capsule. The glossopharyngeal foramen, which occurred in a variety of dinosaurs, had little effect on the course of the perilymphatic duct, which maintained its passage through the internal wall of the braincase and out through the metotic fissure. Dinosaurs apparently lacked a fenestra pseudorotunda, as did the early thecodontians<sup>16-18</sup>, eosuchians<sup>19</sup> and captorhinomorphs<sup>13</sup>.

If the 'round window' of birds and crocodiles is to be interpreted as a homologous feature originating in a unique common ancestor, then the most primitive birds and crocodiles in which the braincase is preserved should exhibit this feature as well. The Cretaceous toothed bird, *Hesperornis*, and the Triassic crocodylomorph, *Sphenosuchus*, should, therefore, provide critical tests of this hypothesis. Like their Recent counterparts, both

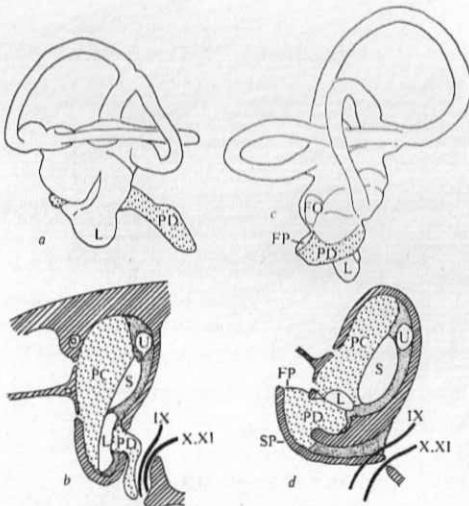


Fig. 1 Inner ear of the rhynchocephalian, *Sphenodon* (left), compared with that of birds and crocodiles (right). The perilymphatic compartment or its terminal portion is coarsely stippled. a, b Left ear of *Sphenodon* in lateral aspect (a) and transverse section (b), after Retzius<sup>23</sup>, de Burlet<sup>24</sup> and Baird<sup>11</sup>; c, the crow, *Corvus*, in lateral aspect, after Gray<sup>25</sup>; d, a crocodylid in transverse section, after Baird<sup>11</sup>. L, S, U, endolymphatic compartment; PD, perilymphatic duct; PC, perilymphatic cistern; FP, fenestra pseudorotunda ('round window'); FO, fenestra ovalis; SP, subcapsular process; IX-XI, cranial nerves.

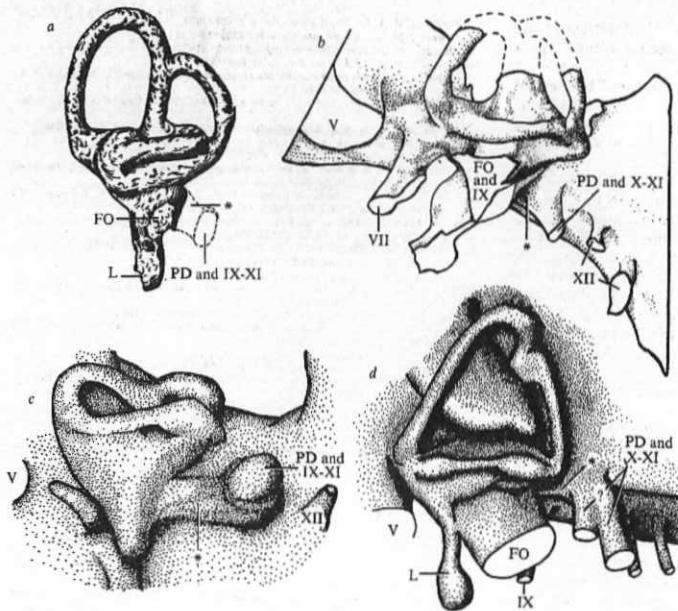


Fig. 2 Casts of the inner ear of saurischian and ornithischian dinosaurs. \* Indicate the cast of the groove in the braincase wall for the perilymphatic duct. a, The sauropod, *Brachiosaurus* after Janensch<sup>26</sup> and Lapparent and Lavocat<sup>27</sup>; b, the hadrosaur *Lophorotus*, after Langston<sup>28</sup>; c, *Ankylosaurus* (AMNH/American Museum 5214, right ear reversed to appear left); d, the theropod, *Allosaurus* (UUV/Univ. Utah 294, the cranioquadrate region is visually sectioned to allow view from this angle). V-XII, cranial nerves; other abbreviations as in Fig. 1.

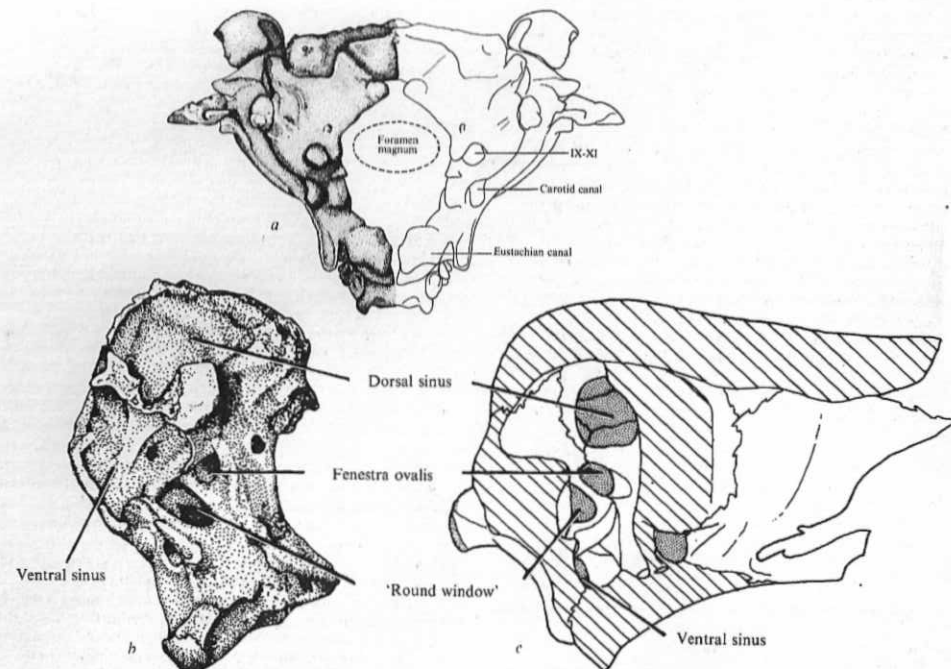


Fig. 3 Pneumatic spaces in the ear region of crocodiles and birds. a, Posterior view of a cast of the pneumatic spaces in the periotic bones of Recent *Alligator*, with associated structures indicated; b, lateral view of the middle ear region of *Hesperornis* (FMNH/Field Museum PA 219); c, ear region of a crocodylid in lateral aspect.

*Hesperornis* (Fig. 3b) and *Sphenosuchus*<sup>2,3</sup> had perilymphatic ducts which issued laterally from the lagenar recess into a fenestra pseudorotunda. The fenestra probably arose from a canal for the ninth cranial nerve which was 'captured' by a lateral shift of the perilymphatic duct. This eliminated the necessity for an ossified vestibular region in the braincase wall (as the duct no longer used this space to leave the otic capsule) and allowed the complete internal ossification of the adult otic capsule, a feature already present in *Hesperornis* and the Triassic crocodile, *Notochampsia* (BMNH R 8503). Although other living vertebrates (mammals and lizards) also have round windows, only in birds and crocodiles is this feature formed, embryologically, by a subcapsular process. This process is a cranial rib, ossified in the adult, which divides the metotic fissure and forms the floor and posterior wall of the fenestra<sup>12</sup>. In the adult it also forms a laterally directed flange, fused to the combined exoccipital/opisthotic bone at the back of the middle ear cavity, and supporting the secondary tympanic membrane (Fig. 1d). Such similarity in the developmental process would be unlikely if the fenestra pseudorotunda of birds and crocodiles was independently derived.

An additional feature shared by birds and crocodylians is a system of pneumatic spaces in the bones surrounding the middle ear (Fig. 3). An upper pneumatic chamber joins the middle ear cavity beneath the lateral shelf of the squamosal bone at its junction with the prootic and exoccipital/opisthotic bones. Lying just above the principal braincase articulation with the quadrate, this cavity extends medially and dorsally into the supraoccipital and parietal bones. A second chamber, below and behind the quadrate articulation, extends into the base of the paroccipital process. These periotic sinuses also occur in Mesozoic birds (*Hesperornis*) and Triassic crocodylians (*Notochampsia*), but are absent in theropod dinosaurs and other saurapsid reptiles. Functionally, periotic pneumatic cavities represent an enlargement of the air cushion which lies medial to the tympanic membrane. They are thus analogous to the enlarged auditory bullae or pneumatic petrosal bones of mammals. The dampening effect of the air cushion is such that a large middle ear cavity is better suited for low frequency sound, and a small cavity is better suited for high frequency<sup>20,21</sup>.

These advanced features in the ear region support a hypothesis of common ancestry for crocodylians and birds, independent of both saurapsid and ornithischian dinosaurs. A hypothetical common ancestor having a fenestra pseudorotunda and periotic pneumatization, but also having the primitive features retained by either birds or crocodylians (for example, cranial kinesis and 'semi-improved'<sup>22</sup> locomotion), would currently be classified within the paraphyletic grade, Pseudosuchia. A theory of a pseudosuchian origin for birds is, at the very least, a reasonable alternative to the dinosaur model proposed by Ostrom.

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K. N. WHETSTONE\*  
L. D. MARTIN

Museum of Natural History  
and Department of Systematics and Ecology,  
University of Kansas, Lawrence, Kansas 66045

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\* Present address: Dept of Palaeontology, British Museum of Natural History, Cromwell Road, London SW7 UK.

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## Transplantation of a circadian pacemaker in *Drosophila*

A MAJOR question in the physiology of activity rhythms is the nature of the coupling between the pacemaker and the motor system. There is good evidence for humoral coupling in several species. In the sparrow, pineal organs from donor birds maintained in a light-dark cycle different from that of the host were transplanted into the anterior chamber of the eye of recipient birds made arrhythmic by pinealectomy. In this case the activity rhythm of the host was restored and its phase was determined by a diffusible humoral factor from the implanted pineal<sup>1</sup>. In the mollusc *Aplysia* humoral coupling between the circadian pacemaker and the output cells is thought to control locomotor activity, although electrical coupling has not been ruled out<sup>2</sup>. In insects, however, experiments involving cockroaches and silkworms indicate that an intact electrical connection between the brain and thoracic ganglia is required for rhythmic activity. The pacemaker controlling the locomotor activity rhythm in the cockroach appears to reside in the optic lobes, and disruption of the electrical pathway between the optic lobes and thoracic ganglia results in arrhythmicity<sup>3-6</sup>. Initial transplant experiments with this insect indicated that activity could be hormonally controlled by the sub-oesophageal ganglion<sup>7</sup>. While these results have not been repeatable by other laboratories<sup>8-10</sup>, evidence from parabiosis experiments does suggest some humoral influence on the activity rhythm<sup>11</sup>. Surgical experiments using giant silkworms have also demonstrated the need for an intact neural connection between brain and thorax for expression of the flight activity rhythm<sup>12</sup>. Thus, until now, there has been no unambiguous evidence for humoral control of activity rhythms in insects. Here we show that a short-period mutant brain can produce a short-period activity rhythm when implanted into the abdomen of a genetically arrhythmic host. In this instance, there were no functional neural connections between the implanted brain and the locomotor system of the recipient, so the action of the brain must be mediated by humoral influences.

Adult brains from short-period mutant (*per<sup>s</sup>*) animals which normally exhibit 18- to 20-h activity rhythms in constant environmental conditions<sup>13</sup> were transplanted into the abdomens of arrhythmic mutant (*per<sup>0</sup>*) adults whose activity in these conditions is aperiodic. Of 55 individuals surviving the operation, 4 showed short-period activity rhythms for at least three consecutive cycles (four activity bursts) (Table 1). Figure 1a shows the activity of the A-21-24 arrhythmic host containing a

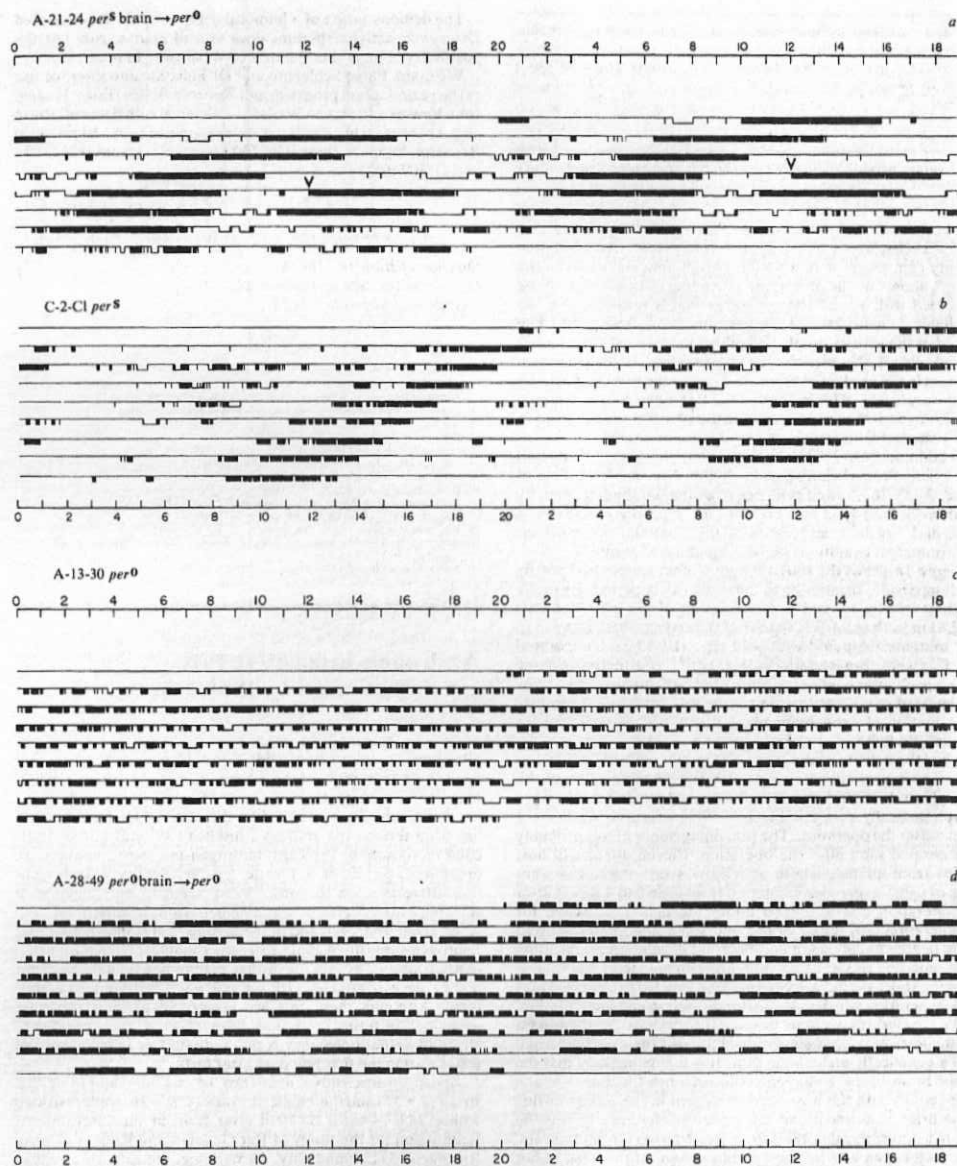


Fig. 1 Locomotor activity of individual adult *Drosophila melanogaster*. a, A *per<sup>s</sup>* fly implanted with a *per<sup>0</sup>* brain; b, an unoperated *per<sup>s</sup>* fly; c, an unoperated *per<sup>0</sup>* fly; d, a *per<sup>0</sup>* fly implanted with a *per<sup>s</sup>* brain. Event recorder data of activity monitored in IR light using a device similar to that described previously<sup>13</sup>. Data plotted modulo 20 h. Each line indicates the start of successive 20-h intervals. Successive intervals are also plotted to the right of the immediately preceding interval for visual continuity. Female flies bearing the *per<sup>0</sup>* or *per<sup>s</sup>* mutation were raised in identical 12 h white light-12 h dark cycles. One to two days after eclosion, brains from *per<sup>0</sup>* and *per<sup>s</sup>* donors were dissected in *Drosophila* Ringer's solution<sup>15</sup> and injected with Ringer's into the abdomens of *per<sup>0</sup>* hosts, using a glass micropipette with a small constriction. Host animals were kept in a moist environment for 1 d to facilitate wound healing. Two to four days later, surviving hosts and unoperated *per<sup>0</sup>* and *per<sup>s</sup>* controls which had been raised in the same light-dark cycle were inserted into the activity monitor. Locomotor activity was usually recorded for an initial 2-d entrainment period which continued the previous light-dark cycle, using long-wave UV light. Flies were then maintained in constant conditions (24 °C) for an additional 7 to 10 d during which locomotor activity was monitored in IR light. Events were also counted each hour and the digital data used for periodogram analysis.