

Parental care in an ornithischian dinosaur

A dramatic fossil may shed light on how modern archosaurs became devoted parents.

Crocodylians and birds show extensive parental care of their young^{1,2}, but whether this behaviour evolved independently in these two groups of living archosaurs is unknown — in part because features of parenting among related fossil groups such as dinosaurs³ are unclear. A dramatic specimen of the small ornithischian dinosaur *Psittacosaurus* sp. (Dalian Natural History Museum D2156) from Liaoning in China reveals a single adult clustered with 34 juveniles within an area of 0.5 square metres, providing strong evidence for post-hatching parental care in Dinosauria.

The Lower Cretaceous Yixian Formation, famous for its exceptionally well preserved feathered dinosaurs and birds, consists primarily of thinly layered lacustrine beds intercalated with volcanic deposits, as well as more massive units in the Lujiatun beds near its base⁴. The new specimen comes from a small outcrop of variegated mudstones, with root traces and gradational contacts, from the lowest portion of the formation near Shangyuan in western Liaoning.

The find consists of 34 articulated juvenile *Psittacosaurus* sp., closely associated with an adult (Fig. 1). The specimen is in red–grey mudstone, with clasts of volcanic rock fragments and minerals, feldspar and quartz. The unit is devoid of sedimentary structures apart from drab burrow mottling. Colour, composition, texture and sedimentary structures of this and adjacent units are consistent with the incipient development of almost neutral to slightly acidic soils on volcanically derived sediment.

There are no isolated bones or partial skeletons in the specimen, except those damaged by recent, pre-discovery erosion or excavation error. Juveniles show a consistent pattern of preservation: their skeletons have dorsal vertebrae, ribs and pelvis, with dorsal side up; the fore- and hindlimbs rest in lifelike poses, with humeri and femora splayed and the remaining portions folded below. The juveniles are all of similar size, with femora lengths ranging over 30–34 mm. Although postcrania commonly overlap one another, the skulls remain free of overlying skeletons.

The adult rests in a similarly articulated and upright pose. Visible elements include the skull, dorsal vertebrae, ribs and the dorsal portions of the scapula. The cervical series and posterior portion of the body are absent, probably lost to recent erosion. Portions of four juveniles overlies the rest of the skeleton but, like the juveniles, the adult head is slightly raised and uncovered.

In contrast to typical Yixian Formation skeletons such as *Sinosauropteryx*, which are

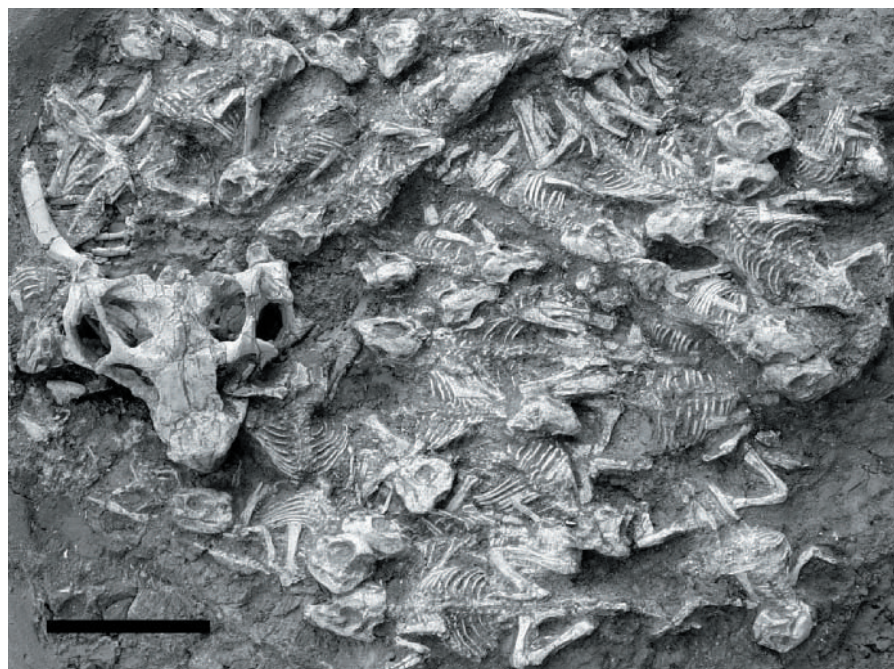


Figure 1 Adult and juvenile *Psittacosaurus* in plan view. Erosion has truncated several skeletons, including the adult, on the left and upper sides of the specimen. Skeletons in the centre sit topographically lower than those at the perimeter, suggesting an original basin-like feature. One skeleton at lower right appears to be draped over an edge of this structure. The absence of internal sedimentary structures makes it impossible to discern whether the basin topography is the result of sedimentary, biological or post-depositional deformational processes. Juveniles not adjacent to the adult generally lie subparallel to one another, showing no preferred orientation of the cranial end. Sediment texture and composition do not vary across the site, eliminating the possibility of a composite specimen. Scale bar, 10 cm.

flattened between thin lacustrine strata⁴, these *Psittacosaurus* retain a three-dimensional form and occur in more massive units. This posture is frequently seen in other vertebrate specimens from the lower Lujiatun beds⁴. The lack of disarticulation, weathering, scavenging or other disturbance indicates minimal subaerial exposure. The consistently lifelike postures and skulls free of overlapping skeletons rule out significant transport and suggest that the *Psittacosaurus* were rapidly entombed while still alive. Death scenarios might include burial by volcanic debris⁵, entrapment in a collapsed underground burrow⁶, or flooding of a nest or other surface excavation. The absence of glass and the poorly sorted nature of these sediments favour a rapid clastic deposition, rather than burial by a volcanic ash fall. The uniformity of the entombing sediments, perhaps a result of soil development, prevents identification of any definite event.

The close association of the adult and juvenile skeletons is consistent with a biological relationship and post-hatching parental care. The temporal extent of this care depends upon the age difference between hatchlings and these juveniles. Hatchling size is unknown for *Psittacosaurus*. Nevertheless, juvenile bones from this specimen are fully

ossified and well formed. This, combined with bone development, slow growth rates⁷, plus the overall size and number of young, indicates that post-hatching growth was substantial and parental care extensive.

Parental care has been inferred for various dinosaur lineages from nestlings with altricial bone tissues, assemblages of shed teeth and tooth-marked bone, and mixed-age bone beds^{3,8}, although these interpretations have been challenged on histological and taphonomic grounds^{9,10}. The *Psittacosaurus* aggregation provides compelling evidence for post-hatching care among dinosaurs³.

Modern archosaurs are conscientious parents, assisting their young in hatching, protecting them from predators, feeding them and providing warmth and shelter¹². But, given the disparity in ecology and physiology between crocodylians and birds, homology of their parental care is debatable^{11–13}. Discovery of similar aggregations for other dinosaurs would strengthen the idea that post-hatching parental care is the ancestral condition in Dinosauria and therefore a homologous character among crocodylians and birds.

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Bird song

Superfast muscles control dove's trill

Bird songs frequently contain trilling sounds that demand extremely fast vocalization control^{1,2}. Here we show that doves control their syrinx, a vocal organ that is unique to birds, by using superfast muscles. These muscles, which are similar to those that operate highly specialist acoustic organs such as the rattle of the rattlesnake, are among the fastest vertebrate muscles known and could be much more widespread than previously thought if they are the principal muscle type used to control bird songs.

The syrinx of ring doves (*Streptopelia risoria*) generates a relatively simple, highly stereotyped song — the familiar cooing sound. The coo contains a trill, whose elements are generated at repetition rates of up to 30 Hz (Fig. 1a). When doves coo, respiratory airflow excites membranes in the syrinx³, causing them to vibrate^{4,5}. The vibrations depend on the tension in the membranes^{3,6}, which is modified by activating two pairs of syringeal muscles^{5,7}. These muscle pairs act as antagonists⁵: the tracheolateralis muscles cause the membranes to move out of the tracheal lumen (abduct), whereas the sternotrachealis muscles cause the membranes to slacken and to adduct.

We made simultaneous *in vivo* recordings of muscle activity and sound in cooing doves and found that the electromyographic (EMG) activity of the tracheolateralis muscles correlated significantly more strongly with voiced, rather than silent, periods: activating these muscles switches the sound

on, and not off as previously thought⁵, by positioning the membrane in the airflow. We also found that modulation of the tracheolateralis muscles' EMG correlated strongly with changes in sound frequency: the muscles change the tension in the membranes, which changes the frequency of the sound. (For methods, see supplementary information.)

A dove's trill cannot be achieved using typical vertebrate muscles, because they do not switch on and off fast enough to control the trill's brief sound elements (≥ 9 ms). The syringeal muscles must also contract aerobically to power cooing sessions that can last for many minutes. These extreme requirements can be met only by aerobic superfast muscles⁸. This muscle type is the fastest known in vertebrates: its twitch half-time is less than 10 ms, which is one to two orders of magnitude faster than that of typical locomotory muscles⁸.

Our measurements show that dove syringeal muscles attain superfast kinetics. The twitch half-times of the tracheolateralis and sternotrachealis muscles are 9.2 ± 0.8 ms and 10.3 ± 1.7 ms, respectively, and the stimulus repetition rates necessary to obtain tetanic contraction are 200–275 Hz for tracheolateralis and 200–400 Hz for sternotrachealis muscles. But, like all superfast muscles, the syringeal muscles trade force for speed⁹: they exert low twitch stresses (tracheolateralis: 8.0 ± 4.8 kilonewtons per m^2 ; sternotrachealis: 20.6 ± 15.7 kN m^{-2}).

We also subjected the syringeal muscles to a playback signal based on the *in vivo* EMG pattern. During the simulated trill, both types of muscle modulate force (Fig. 1b). As the silent intervals in the playback signal shorten from 12 to 3.5 ms, neither is able to relax completely between trill elements.

Our results indicate that both muscles exert control directly at the syringeal membranes by altering the membrane position, which in turn alters membrane tension. The tracheolateralis muscles pull the syringeal membranes apart, thereby allowing them to vibrate in the airflow, which supports indirect evidence that the syrinx is closed between trills¹⁰. This control mode implies that gating is determined by the membrane position and that membrane tension determines pitch.

Our *in vitro* experiments show that both syringeal muscles have the superfast properties necessary to control individual sound elements during the dove's trill. Co-activation of the antagonistic muscles affords the bird very fast and accurate position control of the syringeal membranes, akin to saccadic eye and rapid arm movements¹¹.

Birds modulate their songs extremely rapidly, with frequencies exceeding 100 Hz (ref. 2). Although the intrinsic nonlinear properties of the syrinx⁶ add complexity to the level of motor control, only muscle control can explain the fast but gradual modulations that underlie the extraordinary intraspecific variability and flexibility of

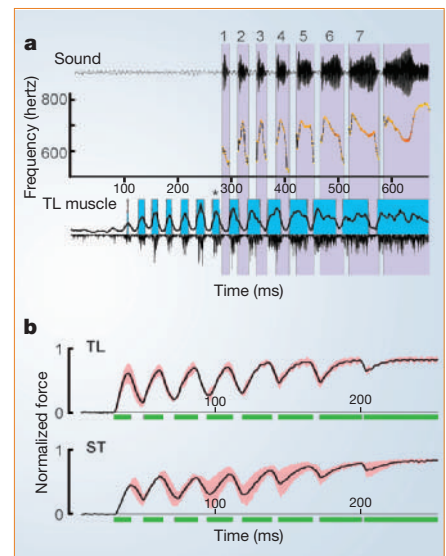


Figure 1 Superfast muscles control song sound in ring doves. **a**, Sound oscillogram, spectrogram and electromyographic activity of tracheolateralis (TL) muscles (upward, integrated; downward, rectified) during the trill. TL activation (blue boxes) precedes the corresponding trill elements (purple boxes). Asterisk indicates TL burst associated with the first trill pulse (trill 1). **b**, Normalized traces of *in vitro* force modulation of TL and sternotrachealis (ST) muscles during a stimulation pattern (green bars) based on an averaged trill (mean (black trace) \pm s.d. (pink trace); $n = 4$).

phonation¹. The stereotyped coos of doves are considered to be simple vocalizations among birds, but even doves use superfast muscles to control their song. Given their added vocal complexity¹², songbirds have probably evolved muscles that outperform the syringeal muscles of doves. Superfast muscle can no longer be considered a rare adaptation, found for example in the highly derived acoustic organs of the toadfish and rattlesnake⁸. We suspect that superfast vocal muscles are widespread among birds.

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