

# A pygostyle from a non-avian theropod

The independent evolution of a bird-like tail has been discovered in an oviraptorosaur.

In birds, vertebrae at the tail end of the backbone are fused into a structure called a pygostyle. We have found a pygostyle from a non-avian theropod, an oviraptorosaur from the Upper Cretaceous Nemegt Formation of Bugin Tsav, Mongolia. Although this taxon has similarities to birds, it is likely that the pygostyle evolved independently.

The specimen (Mongolian Geological Institute GIN 940824) includes most vertebrae, along with chevrons, ribs, gastralia, pelvis (Fig. 1), femora, tibiae, fibulae and proximal tarsals. It has a shorter tail (24 segments) than known oviraptorosaurs, and the last five caudals are co-ossified into a pygostyle.

GIN 940824 can be identified as an oviraptorosaur<sup>1</sup> on account of its pneumatic proximal caudal centra, short distal caudal centra, ilia that are close dorsally, and its vertical pubis. It is one of the largest oviraptorids known. Unlike *Ingenia*, recovered from the same site, the preacetabular blade of the ilium is higher than the postacetabular region, as in *Chirostenotes*<sup>2</sup>. It has a shorter tail than *Oviraptor* (GIN 100/42) and a lower preacetabular iliac blade with less pronounced dorsal curvature. The shaft of the pubis is straighter than in *Ingenia*. The ventrally directed pubis is 171% of the ischial length, compared with 148% in *Oviraptor*, 121% in *Ingenia*, and 221% in *Chirostenotes*<sup>3</sup>. The ischium curves strongly posteriorly, as in *Chirostenotes*<sup>2,3</sup>. Similarities of the ilium and ischium with North American caenagnathids, a family also known in Asia<sup>4</sup>, suggest it may be referable to that family.

Most non-avian theropods have long tails with elongate (relative length to width) caudal centra, whereas oviraptorosaurs have short tails with short, broad vertebral centra. The minimum caudal counts are 32 for *Conchoraptor* (GIN 110/19), 27 for *Ingenia* and 27 for "*Oviraptor*" *mongoliensis*. GIN 940824 has only 24 caudals, fewer than any non-avian theropod except *Caudipteryx*<sup>5</sup>, which has 22.

The pygostyle is a relatively straight, tapering co-ossified mass. The morphology of caudals 15 to 24 differs from their counterparts in other oviraptorosaurs. Fusion between the twentieth and twenty-first caudals is restricted to dorsal parts of the centra, leaving ventral margins separate. As in some modern birds<sup>6</sup>, the neural arches of the first centra in the pygostyle are not co-ossified. The remaining intervertebral articulations are completely co-ossified, although lines of fusion are still evident. At least two haemal

arches are fused. The number of fused vertebrae is the same as the number of caudals supporting tail feathers (rectrices) in *Caudipteryx*<sup>5</sup> and modern birds.

We can reject the possibility of pathology because the caudal vertebrae undergo a steady reduction in dimensions from the base to the end of the tail. None of the bones shows rough surface texture, asymmetry, growth interruption or any indication of trauma.

Birds generally have 18 (refs 7,8) to 23

(ref. 9) caudal vertebrae, although most are fused into the synsacrum and pygostyle, leaving between five and nine free caudals<sup>10</sup>. The avian pygostyle is composed of centra, neural arches and haemal arches<sup>9</sup>. Although most avian pygostyles have dorsally curved axes, some birds, including flightless ratites and penguins, have straight pygostyles like that of GIN 940824.

Phylogenetic analysis does not place oviraptorosaurs particularly close to bird origins, leaving no reason to assume that the short tail and fused caudals of GIN 940824 are homologous with avian tails. However, feathers are widespread in theropods<sup>5</sup>, possibly including oviraptorosaurs<sup>11</sup>, so GIN 940824 may have had rectrices similar to those of *Protarchaeopteryx* and *Caudipteryx*<sup>5</sup>. The latter is probably a basal oviraptorosaur, as it has an edentulous, beak-like dentary that is deeply invaded posteriorly by the enlarged external mandibular fenestra, a posteriorly concave ischium, short caudal centra, and a short tail.

Although the terminal vertebrae of *Caudipteryx* are not fused, they seem to form a stiffened rod. The short tail and pygostyle of GIN 940824 maybe indicative of a fan of elongate tail feathers (rectrices) in oviraptorosaurs (Fig. 2) that is more derived than in *Caudipteryx*. Pygostyle-like structures could have evolved independently at least three times in theropods, although the presence of rectrices in two of these taxa suggests a functional association.

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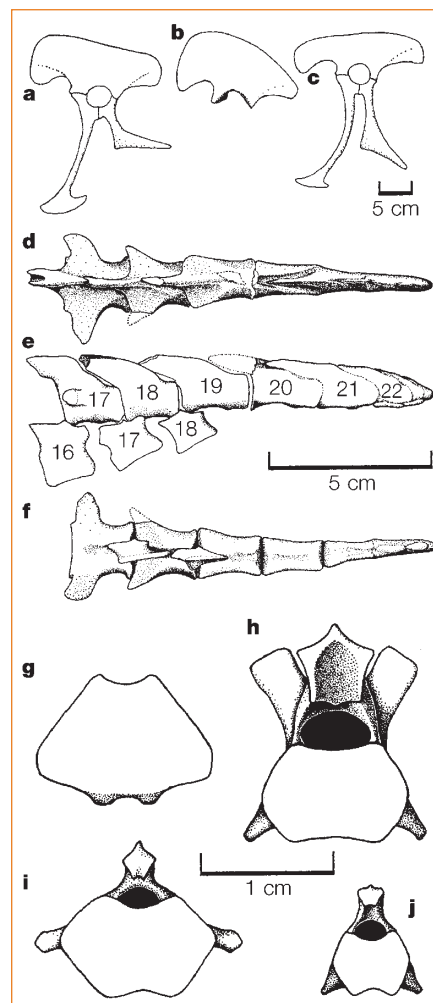
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**Figure 1** Pelvic girdles of oviraptorids. **a**, GIN 940824; **b**, ilium of "*Oviraptor*" *mongoliensis*, GIN 100/32A; **c**, ilium, pubis and ischium of *Ingenia*, GIN 100/33. **d-f**, Drawings of pygostyle of GIN 940824 in dorsal (**d**), left lateral (**e**) and ventral (**f**) aspects. **g-j**, Posterior views of oviraptorid caudal vertebrae: **g**, nineteenth caudal of GIN 940824; **h**, nineteenth caudal of *Ingenia*, GIN 100/33; **i**, twenty-seventh caudal of *Ingenia*, GIN (100/32); **j**, twenty-sixth caudal of "*Oviraptor*" *mongoliensis*, GIN 100/32A.

**Figure 2** (above right) The function of the pygostyle of the new oviraptorosaur interpreted as a support for a fan of tail feathers. Drawing by Michael Skrepnick.



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Evolutionary fitness

## Tall men have more reproductive success

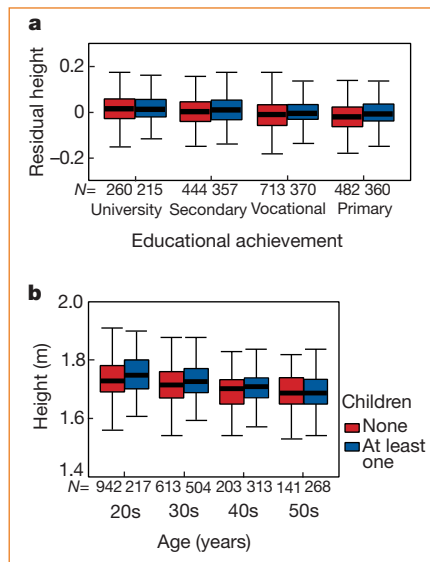
Sexual selection is a well established evolutionary process based on preferences for specific traits in one sex by members of the other sex. It is important in the evolution of morphological traits, and several sexually dimorphic traits in humans, such as facial hair and facial shape<sup>1</sup>, are assumed to be the outcome of such a process. Here we demonstrate that taller men are reproductively more successful than shorter men, indicating that there is active selection for stature in male partners by women.

There are well known academic<sup>2</sup>, social<sup>3,4</sup>, health<sup>5–9</sup> and economic<sup>10,11</sup> correlates of height, but we know of no studies that have examined its direct implications for evolutionary fitness. To examine the possible evolutionary consequences of stature, we have analysed data from the medical records for 4,419 healthy men aged 25–60 who received compulsory medical examinations between 1983 and 1989 at the Lower Silesian Medical Centre in Wrocław, Poland. Because the records were not anonymous and many bachelors admitted to having offspring, the risk of false declarations was probably small.

To avoid any confounding pathological effects, we discarded the data from men whose height was more than three standard deviations from the sample mean ( $172 \pm 6.6$  cm). Locality of residence had a significant effect on stature (analysis of variance (ANOVA):  $F_{3,4409} = 11.02$ ,  $P < 0.001$ , with city-dwellers being taller than rural men), so we selected only individuals resident in either rural villages or in cities with more than 100,000 inhabitants (the extreme sub-populations). This yielded a final sample size of 3,201.

Stature is also confounded by a secular trend (linear regression against age:  $b = -0.00157$ ,  $F_{1,3199} = 184.5$ ,  $P < 0.0001$ ), so we calculated a residual from the common regression line against age for each subject and standardized this against the overall mean for the subject's residence. Stature is also confounded by educational achievement, probably because this correlates with family wealth and status, so we controlled for education.

Figure 1a shows means and variances in stature residuals for men with and without children. When all other variables are held constant, childless men are significantly



**Figure 1** Height (mean  $\pm$  s.d. and 95% range) of men with and without children. **a**, Residual height for men with different educational experience (removing effects due to both location of residence and a secular trend over time). **b**, Absolute height for men of different age cohorts, as a function of whether or not they had any children.

shorter than those who have at least one child (ANOVA: childedness,  $F_{1,3198} = 25.5$ ,  $P < 0.001$ ; education,  $F_{1,3198} = 93.1$ ,  $P < 0.001$ ). Multiple regression with number of children as the dependent variable, with height and age as independent variables, provides quantitative confirmation of these results (one-tailed tests: city,  $r^2 = 0.136$ ,  $n = 1,826$ ; height,  $P < 0.001$ ; age,  $P < 0.001$ ; rural,  $r^2 = 0.208$ ,  $n = 1297$ ; height,  $P = 0.041$ ; age,  $P < 0.0001$ ).

Comparisons of means for individual age cohorts (Fig. 1b) reveals that men with children are significantly taller than childless men in each case (twenties,  $t_{1157} = -2.97$ ,  $P = 0.005$ ; thirties,  $t_{1115} = -3.49$ ,  $P = 0.001$ ; forties,  $t_{514} = -3.06$ ,  $P = 0.002$ ), except for men in their fifties ( $t_{409} = 0.17$ ,  $P = 0.863$ ). Because these men were born during the 1930s, they entered the marriage market shortly after the Second World War when the population sex ratio was highly skewed in favour of women and sexual selection on males would have been greatly reduced as a result: the sex ratio for adults of working age (18–64 for men, 18–60 for women) in Wrocław was 114.3 women to 100 men in the post-war decade, but fell to 104–105:100 in subsequent decades<sup>12</sup>.

These results indicate that the effect of height on reproductive output might be due to shorter men being disadvantaged in

the search for a mate. This idea is supported by the fact that bachelors were significantly shorter than married men (ANOVA with residual height as the dependent variable, childedness as the covariate, and marital status as the independent variable:  $F_{1,3198} = 7.82$ ,  $P = 0.005$ ).

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Physiology

## Eel fat stores are enough to reach the Sargasso

It has long been assumed that the European eel (*Anguilla anguilla*) migrates to the Sargasso Sea — a region of the Atlantic Ocean between the Azores and the West Indies — to spawn<sup>1–3</sup>. During the past decade, however, the number of glass eels has inexplicably dropped<sup>4</sup>, and it has been suggested that a shortage of fat stores in adults, resulting from diminished food resources for juveniles in inland waters, may prevent the starving silver eels from reaching the spawning grounds<sup>4–6</sup>. But we find that the energetic cost of the 6,000-km migration is actually quite low, with 60% of the fat store remaining available for the developing gonads.

Silver eels leaving the coasts of Europe between September and November are likely to reach the Sargasso Sea from February to June<sup>3</sup>, so the average swimming speed for a female silver eel 1 metre long is about half a body-length per second. The estimated energy required is around 30% of the total energy at the start<sup>7</sup>. The fat reserves of migrating silver eels range from