

parasitized by other females. At the population level, parasitic eggs decrease the average value of the parental eggs laid by parasites, in turn favouring even greater allocation to parasitism (trade-off in Fig. 1): optimal clutch size depends on the frequency of parasitism, and vice versa. The dynamic nature of the problem is further enhanced in species where the success of parasitic eggs is also frequency-dependent²². These various game aspects do not alter the qualitative assumptions or predictions of the graphical model. It will be important, however, to incorporate these assumptions and predictions into a more quantitative, theoretical study and into some empirical tests. For example, in populations in which parasites are also hosts, the fitness estimates for a parasite's own clutch must reflect her risks and costs of being parasitized. I have accounted for these fitness estimates; egg survival estimates (Fig. 2) included parasitic females who were themselves parasitized (6 of the 23 parasitic females). Some of these females raised parasitic chicks and, consequently, sacrificed some of their own chicks in the process.

Here I have shown that, for some species, clutch size cannot be understood without considering conspecific brood parasitism. The opposite is also true, and this clutch-size model provides a new framework for understanding brood parasitism. Most studies of parasitism do not examine clutch-size constraints and cannot explain why parasites lay eggs in the nests of others rather than in their own nests; in some cases, the hypothesis that parasitism yields a direct increase in mean fitness has been prematurely rejected²³. Earlier studies of brood parasitism now need to be reassessed. By integrating two fields of research that are generally considered in isolation of each other—study of clutch size and conspecific brood parasitism—this new clutch-size model provides a framework for enriching our understanding of both fields. □

Methods

Comparing survival of parental and parasitic eggs. Brood parasites were identified using standard techniques¹². Eggs were considered successful (fledged) if the chicks survived to 30 d after hatching¹². As it is the fitness of parental eggs relative to the fitness of parasitic eggs that is important, survival to independence is a good measure of relative fitness, assuming that post-fledging mortality is similar for both egg types. Survival rates for eggs in parasitic females' own nests were calculated for successful nests (some eggs hatched) but then adjusted by the proportion of parental eggs that were laid in successful nests (82.1% of 731 eggs). Only nests where the fates of more than half the chicks were known were included in these analyses. Confidence limits for proportion of eggs surviving (Fig. 2) were based on sample size²⁴ for observed eggs and on 1,000 bootstrapped regression equations for predicted next eggs. For statistical comparisons of egg survival, a G-test compared last parental eggs with parasitic eggs, whereas 1,000 bootstrapped predictions of 'next'-egg survival were used to compare 'next' eggs with parasitic eggs.

I examined egg success in relation to an egg's position in the laying sequence (backwards from the last egg laid in the clutch), rather than on the basis of clutch size, to enable pooling of results despite large variations in clutch size¹² and to predict what parasites would gain if they were to add 'hypothetical' next eggs in the laying sequence to their clutches (Fig. 2). The survival value of eggs from a specific position in the laying sequence would not indicate the fitness increments from those eggs if later-laid eggs survive at the expense of earlier-laid eggs, because the survival of the eggs would need to be discounted by the fitness reduction they caused through the death of siblings. However, the two measures (survival and fitness increment) will be equivalent where there is strict laying-order-dependent survival within broods; in this study, few later-laid eggs survived at the expense of earlier-laid ones^{12,16}.

Clutch- and brood-size comparisons. For analysis of sizes of clutches of parasitic and non-parasitic females, host availability was determined on the basis of the observed spatial and temporal patterns of host use¹⁵. To reduce variance due to strong seasonal decline in clutch size, the effects of date were controlled by analysis of covariance (ANCOVA) ($F = 9.04$, $P = 0.002$); clutch sizes (Fig. 3) are therefore adjusted means. For chicks, the assumptions of ANCOVA are violated, so analysis of variance was used ($F = 0.64$, $P = 0.53$)

but, to avoid bias due to differences among groups in timing of nesting, only birds who initiated laying within 20 d of the first egg laid in the population are included.

To avoid potential confounding effects of female quality in the analysis of host clutch-size responses, only host nests were included in these analyses. Residual clutch sizes from regressions of clutch size against laying data were used to control for strong seasonal declines in clutch size²¹.

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Exceptional soft-tissue preservation in a theropod dinosaur from Italy

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The Lower Cretaceous Pietraroia Plattenkalk (Benevento Province, southern Italy) has been known since the eighteenth century for its beautifully preserved fossil fishes. During Albian time (about 113 Myr ago¹), deposition of fine marly limestone in a shallow lagoonal environment, affected by cyclic periods of low oxygen levels², led to exceptional preservation of soft tissue in a



Figure 1 The holotype of *Scipionyx samniticus*, gen. et sp. nov., fossilized in a beige limestone from the Lower Cretaceous (Albian) of Pietraroia (Benevento, southern Italy). Scale bar, 2 cm. Courtesy of the Soprintendenza Archeologica, Salerno.

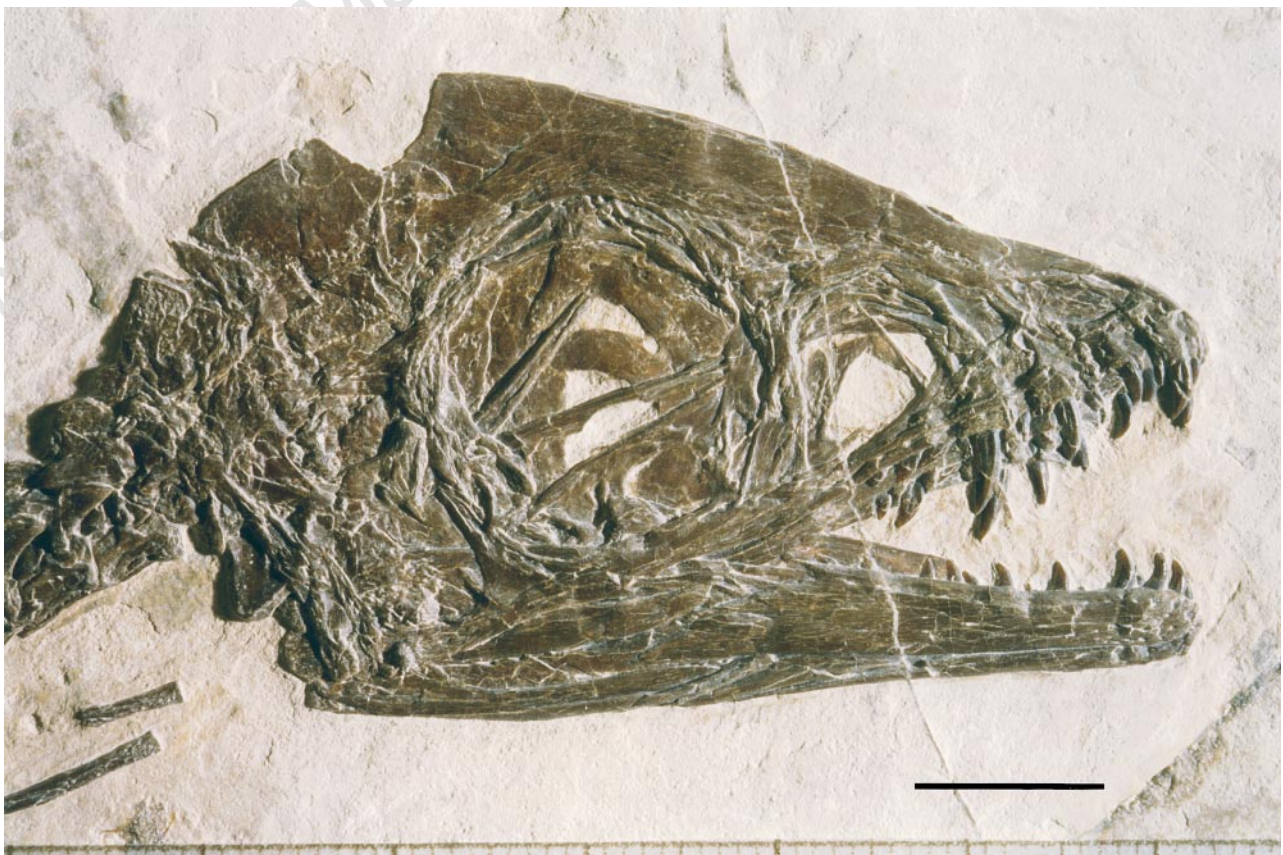


Figure 3 Close-up of the skull of *Scipionyx*. Scale bar, 1 cm. Courtesy of the Soprintendenza Archeologica, Salerno.

juvenile theropod. The specimen, diagnosed here as *Scipionyx samniticus* gen. et sp. nov., is the first dinosaur ever to be found in Italy. The fossil has been mentioned previously in two brief notes^{3,4} and generally examined in a doctoral thesis⁵. Here we report the full preparation of the specimen which shows details of soft anatomy never seen previously in any dinosaur. The preservation is better than in other *lagerstätten* (conservative deposits)⁶ where theropod soft tissue has been reported, such as the Santana Formation of Brazil⁷ and the Yixian Formation of

China⁸. Despite this, there is no evidence of feathers or any other integumentary remnants in the Italian specimen. *Scipionyx* represents a new maniraptoriform theropod. Its discovery is remarkable considering also the scarcity of juvenile theropod dinosaurs in the fossil record.

The skeleton of the Pietraraoia dinosaur, 237-mm long from the tip of premaxilla to the last (ninth) preserved caudal vertebra, lies on its left side (Figs 1, 2), in nearly perfect anatomical articulation. Although the head is upturned with respect to the position in life,

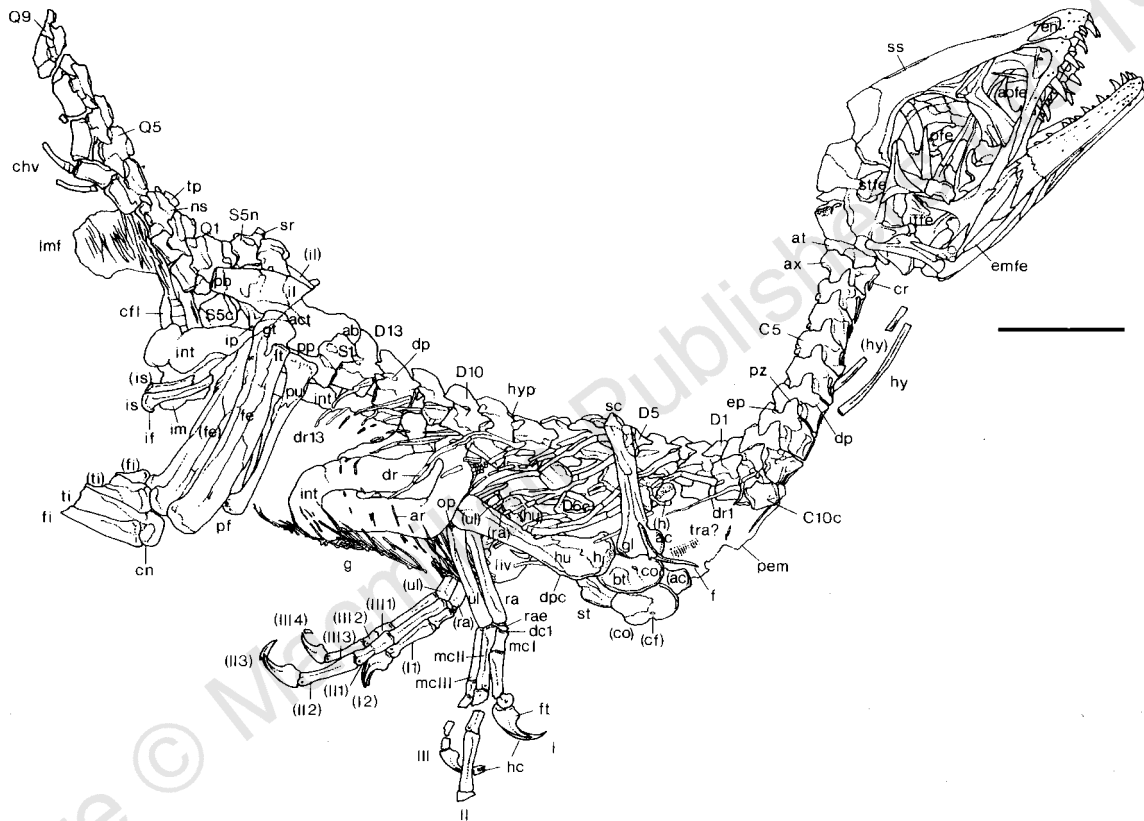


Figure 2 *Scipionyx samniticus* gen. et sp. nov. Sketch of the skeleton shown in Fig. 1. Abbreviations: ab, anterior blade of ilium; ac, acromion; act, acetabulum; aofe, antorbital fenestra; ar, abdominal rib; at, atlas; ax, axis; bt, biceps tubercle; C, cervical vertebra; Cc, cervical centrum; cf, coracoid foramen; cfl, *M. caudifemoralis longus*; chv, chevron bones; cn, cnemial crest; co, coracoid; cr, cervical rib; D, dorsal vertebra; Dc, dorsal centrum; dc, distal carpal; dp, diapophysis; dpc, deltopectoral crest; dr, dorsal rib; emfe, external mandibular fenestra; en, external naris; ep, epiphysis; f, furcula; fe, femur; fi, fibula; ft, flexor tubercle; g, gastralia; gl, glenoid fossa; gt, greater trochanter; h, head of humerus; hc, horny claw; hu, humerus; hy, hyoid; hyp, hyposphene-hypantrum; if, ischiadic foot; il, ilium; im,

ischadic musculature; int, intestine; ip, ischiadic peduncle; itfe, infratemporal fenestra; liv, liver; lmf, large muscular fibres; lt, lesser trochanter; mc, metacarpal; ns, neural spine; ofe, orbital fenestra; op, olecranon process; pb, posterior blade of ilium; pem, pectoral musculature; pf, pubic foot; pp, pubic peduncle; pu, pubis; pz, pre-postzygapophyses; Q, caudal vertebra; ra, radius; rae, radiale; sc, scapula; Sc, sacral centrum; Sn, sacral neural arch; sr, sacral rib; ss, sagittal suture; st, sternal plate; stfe, supratemporal fenestra; ti, tibia; tp, transverse process; tra, trachea; ul, ulna; I-III, first to third digits, 1-4, first to fourth phalanges. Left-side elements are in parentheses. Scale bar, 2 cm.

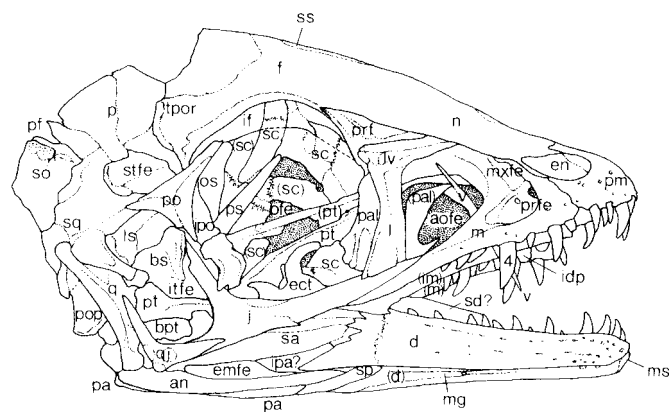


Figure 4 Sketch of the skull of *Scipionyx* shown in Fig. 3. Abbreviations: an, angular; aofe, antorbital fenestra; bpt, basiptyergoid; bs, basisphenoid; ect, ectopterygoid; emfe, external mandibular fenestra; en, external naris; f, frontal; idp, interdental plates; if, inner (orbital) wall of frontal; im, inner (lingual) wall of maxillary; ipa, inner prearticular; ipo, inner (orbital) wall of postorbital; itfe, infratemporal fenestra; j, jugal; l, lachrymal; ls, laterosphenoid; lv, lachrymal vacuity; m, maxillary; mg, meckelian groove; ms, mandibular symphysis; mxfe, maxillary fenestra; n, nasal; ofe, orbital fenestra; os, orbitosphenoid; p, parietal; pa, prearticular; pal, palatine; pf, parietal flange; pm, premaxillary; po, postorbital; pop, paroccipital process; prf, prefrontal; prfe, promaxillary fenestra; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sc, sclerotic plates; sd, supradentary; so, supraoccipital; sp, splenial; sq, squamosal; ss, sagittal suture; stfe, supratemporal fenestra; tpor, transverse postorbital ridge; v, vomer; 4, fourth maxillary tooth. Left-side elements are in parentheses. Scale bar, 1 cm.

there is no opisthotonic condition⁹ in the neck. The hindlimbs are missing distal to the proximal epipodials, as are most of the tail and most of the second right manual claw.

Theropoda

Tetanurae

Coelurosauria

Maniraptoriformes

Scipionyx samniticus gen. et sp. nov.

Etymology. Scipio (Latin male name): dedicated to Scipione Breislak, who first described the Pietraroia Plattenkalk, and Publius Cornelius Scipio (nicknamed Africanus), *consul militaris* of the Roman Army, who fought in the Mediterranean area; onyx (Greek): claw; samniticus (Latin): of the Samnium, ancient name of the region including the Benevento Province.

Holotype. Nearly complete, articulated skeleton, housed at the Soprintendenza Archeologica, Salerno.

Horizon and locality. Lower Cretaceous (Albian) of the Pietraroia Plattenkalk (Benevento Province, southern Italy).

Diagnosis. Referable to Theropoda^{10–12} for the synapomorphic presence of denticulate teeth, intramandibular joint, straplike scapular blade, distal carpal 1 clasping metacarpals I and II, manus with digits IV and V absent and with elongate penultimate phalanges, booted pubis. Referable to Coelurosauria^{11,12} on the basis of the

derived presence of jugal participation in the antorbital fenestra and metacarpal I being one-third the length of metacarpal II; more primitive than other coelurosaurians in retaining stout lachrymal and ischial foot. Referable to Maniraptoriformes^{12,13} on the basis of the derived presence of third antorbital fenestra, elongate cervical prezygapophyses, forelimb/presacral ratio of 0.75, ulna bowed posteriorly, semilunate carpal, and slender metacarpal III. Differs from all other Maniraptoriformes in the unique possession of an accessory transverse postorbital ridge at fronto–parietal contact, and by the compressed nature of the radiale and semilunate carpal; differs also in the primitive retention of large prefrontal, pronounced scapular acromion, and rounded coracoid caudal end.

The body proportions indicate that this animal is little more than a hatchling^{14–16}. The skull/presacral ratio (0.48) is higher than in any known adult theropod, including *Tyrannosaurus*¹⁷; moreover, the antorbital region is short, and the orbit is large and circular. Many skeletal elements (scapulo–coracoid, sternal plates, sacral vertebrae) are unfused¹⁸, and several neural arches are separate from their centra. The symmetry of tooth development in both maxillary rami suggests that the first tooth replacement had not occurred; furthermore, the low denticle count may be related to juvenile age^{14,19}.

A combination of characters that usually identify different clades^{11,12} is present in the Italian theropod. The forelimb ratios and most elements of the skull (Figs 3, 4) resemble features of dromaeosaurids^{17,20,21}. Among them are the following derived characters: sloping postorbital region; quadrate with a single head

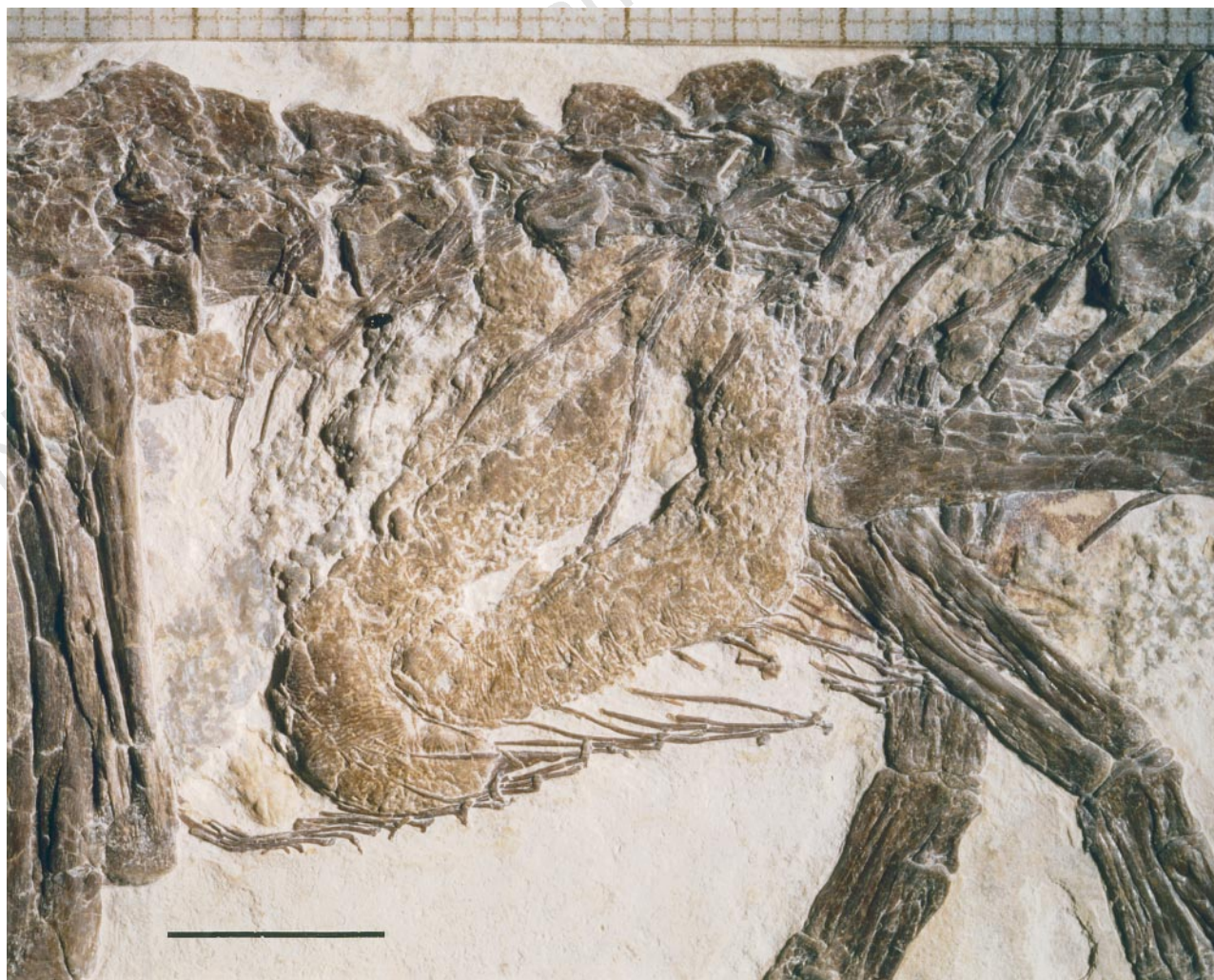


Figure 5 Close-up of the abdomen of *Scipionyx*, showing the perfectly fossilized intestine (left) and a reddish macula that might represent the remains of the liver (right). Scale bar, 1 cm. Courtesy of the Soprintendenza Archeologica, Salerno.

articulating exclusively with the squamosal; paroccipital processes distally slightly twisted postero–dorsally; maxillary fenestra dorsally displaced; palatine pneumatization; alignment of dentary foramina into two rows, not in grooves; and splenial emerging externally on the lateral surface of the mandible. Other characters, such as the small, L-shaped quadratojugal with equal rami, low cervical neural spines, and the barely propubic pelvis, are not dromaeosaurid, but appear synapomorphic with the Troodontidae²². There are also ornithomimid-like, plesiomorphic features, clearly differentiating the pelvis of *Scipionyx* from both the dromaeosaurid and the troodontid pattern (for example, the ilium is posteriorly truncated, and the ischium is three-quarters of the pubic length, with a forward-pointing foot^{12,23}). Moreover, characters such as the L-shaped lachrymal, fan-like coracoid, feeble development of the fourth trochanter, and slender and slightly curved chevrons, resemble a more generalized coelurosaurian bauplan^{9,11,24}.

The mosaic of characters does not allow attribution of this new genus to any known theropod family. But the phylogenetic relationships of *Scipionyx* must undoubtedly be searched for within the Maniraptoriformes, as it shares at least six unambiguous synapomorphies with that clade^{12,13} (see Diagnosis).

A unique, striking feature of the specimen is the preservation of soft parts (Figs 1, 5). Muscles are present in the pectoral area, with scattered acicular fibres clearly visible under $\times 50$ magnification. At the tail base, a fascium with at least three different arrangements of fibrae longae possibly represents part of the M. caudifemoralis longus^{25,26}. Most of the intestine (tenuis²⁷), 5.22-mm average diameter) is positioned further forwards than it is generally thought to be^{25,28}, whereas the colon²⁷ passes through the pelvic canal, close to the vertebral column, and ends just above the ischiadic foot. The gut is surprisingly short and deep in section, suggesting a high absorption rate. Its muscular wall has transverse folds, which are sometimes anastomized. Immediately above the furcula, there appear to be some tracheal rings. A large, reddish, well delimited haematitic halo is tentatively interpreted as liver traces, mainly because of its post-sternal location.

The gastralia, still in life position, allow estimation of the abdominal depth and reveal their contribution to an effective support for the posterior intestinal tract. The presence of a furcula in this articulated specimen eliminates every doubt about the interpretation of similar structures in other theropods^{29,30}. □

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Somatosensory discrimination based on cortical microstimulation

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The sensation of flutter is produced when mechanical vibrations in the range of 5–50 Hz are applied to the skin^{1–3}. A flutter stimulus activates neurons in the primary somatosensory cortex (S1) that somatotopically map to the site of stimulation^{4,5}. A subset of these neurons—those with quickly adapting properties, associated with Meissner's corpuscles—are strongly entrained by periodic flutter vibrations, firing with a probability that oscillates at the input frequency^{1,6}. Hence, quickly adapting neurons provide a dynamic representation of such flutter stimuli. However, are these neurons directly involved in the perception of flutter? Here we investigate this in monkeys trained to discriminate the difference in frequency between two flutter stimuli delivered sequentially on the fingertips^{1,7}. Microelectrodes were inserted into area 3b of S1 and the second stimulus was substituted with a train of injected current pulses. Animals reliably indicated whether the frequency of the second (electrical) signal was higher or lower than that of the first (mechanical) signal, even though both frequencies changed from trial to trial. Almost identical results were obtained with periodic and aperiodic stimuli of equal average frequencies. Thus, the quickly adapting neurons in area 3b activate the circuit leading to the perception of flutter. Furthermore, as far as can be psychophysically quantified during discrimination, the neural code underlying the sensation of flutter can be finely manipulated, to the extent that the behavioural responses produced by natural and artificial stimuli are indistinguishable.

Two monkeys (*Macaca mulatta*) were trained in a standard discrimination task⁷ in which two mechanical vibrations, termed base and comparison, are delivered in each trial (Fig. 1). The monkeys learned to indicate whether the comparison stimulus