

bone can thus not be interpreted with confidence as a "residuum of the primitive torsion between humeral head and elbow condyle"⁸.

Rougier *et al.* remark that we excluded other relevant fossil taxa from our analysis, such as *Gobiconodon*⁹ and *Prokennaletherium*¹⁰. Regarding the former, a recent study¹¹ showed that inclusion of the pectoral girdle in the analysis has no effect on our results. Regarding the latter, which was published after our final analysis, only a single, partial, pectoral girdle is available. Finally, the small fossa on the distal end of the scapular blade in tritylodonts (absent in known multituberculates) may be homologous with some part of the broad crescentic fossa of therians, as Rougier *et al.* suggest. The presence of this distal fossa is, nevertheless, highly variable among therian outgroups (present in distant forms such as *Megacynodon*¹², but absent in forms undeniably closer to mammals such as *Probainognathus* and *Probolesodon*¹³). In our comparative figure, we failed to note that the distal end of the scapular blade of *Morganucodon* is based on a complete scapula of a close relative, the tritheledontid *Pachygenelus*, which is remarkably similar to the former where these bones overlap.

We join Rougier *et al.* in encouraging future attempts to re-evaluate multituberculate relationships on a broader sampling of taxa and characters. Indeed, this is the only means available to test whether the structural changes we outlined in the pectoral girdle in multituberculates and therians actually constitute key evidence for their common ancestry.

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MENG AND WYSS REPLY — Rougier *et al.*'s underlying objection stems from a misperception that our paper² and its comments concerning the placement of multituberculates was intended as an

exhaustive phylogenetic analysis of the major groups of mammals. The aim of our presentation of new anatomical information for the auditory apparatus in *Lambdopsalis*, in relation to several currently competing hypotheses of multituberculate relationships, was of necessarily limited scope. Attention was given to major taxa for which ear ossicles are currently known.

Moreover, their criticisms of 3 of the 16 anatomical features we presented are unsubstantiated and self-contradictory. First, the previously described fragmentary incus and malleus¹² are displaced (as noted in our Fig. 3 legend²). Thus, there is no basis for regarding the incus as having had a posterior position in *Lambdopsalis*. That the incus lies dorsal to the malleus (given the position of the fossa for the incudal articulation) is no more in doubt than the possession of a brain by mammals — a supposition that has "yet to be documented" directly.

Second, Rougier *et al.* assert that the horizontal ectotympanic shared by *Lambdopsalis* and monotremes is primitive for placentals (and therefore Mammalia) as well. This contradicts not only a recent analysis arguing against the homology of this feature in therians¹⁴ and monotremes, but also their own polarity assessment of this feature², in which an inclined ectotympanic was considered to characterize Theria ancestrally. Their assumption that orientation of the oval window predicts ectotympanic inclination has been contradicted repeatedly — not just by our specimen (V10777.3), in which the oval window inclines more than 30°, but also in other studies (for example, a ventromedially facing oval window in *Lambdopsalis*²⁰, a vertical ectotympanic coexisting with an inclined oval window in *Morganucodon*⁴, and a horizontal ectotympanic occurring with an anteroventrolateral oval window in *Scutisorex* (AMNH 48474)).

Third, the statement that the pterygoid is a broken piece (V10777.1) is incorrect. The widely appreciated problematic homology of the monotreme-multituberculate 'pterygoid' bone was signified in our paper by its placement in inverted commas in the figure legend. The claim that the monotreme 'pterygoid' is neo-

morphic is supported neither by phylogenetic studies¹⁴ nor by ontogenetic studies of the platypus skull^{21,22}. Even if one assumes this structure to be a neomorph in monotremes, this alone would not rule out its homology in multituberculates.

Finally, we would be the last to question the desirability of bringing to bear all available data in evaluating this, or any, phylogenetic question.

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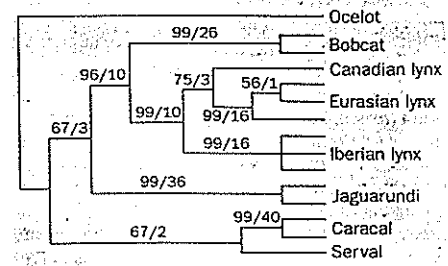
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Taxonomy of the Iberian lynx

SIR — The Iberian lynx, *Lynx pardinus*, is considered the most vulnerable cat in the world, yet its taxonomic status and relationship to other lynx species are controversial^{1,2}. Given that the Iberian lynx is listed as endangered and its populations are highly fragmented³, an understanding of its relationship to other taxa of *Lynx* is important for the development of an effective conservation plan. Here we report the first detailed molecular phylogenetic assessment of *Lynx* relationships. Our data suggest that the Iberian lynx is a distinct species relative to its European and North American counterparts.

The complete mitochondrial control region (D-loop) was sequenced for the Iberian lynx, Eurasian lynx (*Lynx lynx*), Canadian lynx (*Lynx canadensis*), bobcat (*Lynx rufus*) and related felid species (caracal, serval, jaguarundi and ocelot). Phylogenetic analyses of the D-loop performed using both maximum parsimony



Phylogeny derived using a maximum-parsimony analysis (branch and bound option) of aligned sequences. The single most parsimonious tree had a length of 410, a consistency index of 0.670 and a retention index of 0.791. Bootstrap values (1,000 replicates) are shown along branches, with the number of extra tree lengths needed to collapse a node separated by a slash. All specimens are unrelated individuals. The Iberian lynxes are from two different populations in Spain. Specific details of primers and experimental procedures are available from the authors on request.

- Sereno, P. C. & McKenna, M. C. *Nature* **377**, 144–147 (1995).
- Meng, J. & Wyss, A. R. *Nature* **377**, 141–144 (1995).
- Wible, J. R. *J. Vert. Paleont.* **11**, 1–28 (1991).
- Luo, Z. in *In The Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (eds Fraser, N. C. & Sues, H.-D.) 98–128 (Cambridge Univ. Press, New York, 1994).
- Krebs, B. *Berliner geowiss. Abh.* **133**, 1–110 (1991).
- Jenkins, F. A. Jr & Schaff, C. R. *J. Vert. Paleont.* **8**, 1–24 (1988).
- Kielan-Jaworowska, Z. & Gambaryan, P. P. *Fossils Strata* **36**, 1–92 (1994).
- Presley, R. *Nature* **377**, 104–105 (1995).
- Jenkins, F. A. Jr & Parrington, F. R. *Phil. Trans. R. Soc. B* **273**, 387–431 (1976).
- Sun, A. & Li, Y. *Verteb. palasiat.* **23**, 135–153 (1985).
- Cheng, C. J. *Morph.* **97**, 415–471 (1955).
- Miao, D. & Lillegraven, J. A. *Natn. geogr. Res.* **2**, 500–507 (1986).
- Novacek, M. J. *Marim. Rev.* **7**, 131–149 (1977).
- Gates, G. R., Saunders, J. C., Bock, G. R., Aitkin, L. M. & Elliot, M. A. *J. acoust. Soc. Am.* **56**, 152–156 (1974).
- Kielan-Jaworowska, Z. & Qi, T. *Verteb. palasiat.* **28**, 81–94 (1990).
- Sereno, P. C. & McKenna, M. C. *J. Vert. Paleont. Suppl.* **10**, 42A (1990).
- Seeley, H. G. *Phil. Trans. R. Soc. B* **186**, 59–148 (1895).
- Romer, A. S. *Breviora* **407**, 1–26 (1973).
- Zeller, U. in *Mammal Phylogeny Vol. 1* (eds Szalay, F. S., Novacek, M. J. & McKenna, M. C.) 95–107 (Springer, New York, 1993).
- Miao, D.-S. *Univ. Wyoming Cont. Geol. Spec. Pap.* **4** (1988).
- Presley, R. & Steel, F. L. D. *Anat. Embryol.* **154**, 95–110 (1978).
- Zeller, U. *Die Entwicklung und Morphologie des Schädels von Ornithorhynchus Anatinus* (Kramer, Frankfurt, 1989).

and neighbour-joining resulted in identical topologies (see figure).

These results are significant for several reasons. First, the monophyly of the genus *Lynx* is strongly supported, a finding similar to that of Werdelin² but contrasting with some morphological accounts³. Second, relationships among the felid taxa are congruent with previous molecular data⁵. Third, the Iberian lynx is divergent from both the Eurasian lynx and Canadian species, and so can be considered an evolutionary unit (or valid phylogenetic species) in that from both a morphological and a genetic standpoint it is unique. The Iberian lynx revealed a lower level of nucleotide sequence divergence (0.006%) than the bobcat (0.61%) or Eurasian lynx (0.69%). It will be interesting to conduct a detailed study of the remaining isolated populations of Iberian

lynx in an effort to learn more about the overall phylogeographical pattern and levels of genetic variation in this rapidly vanishing species.

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1. Werdelin, L. *Ann. Zool. Fenn.* **18**, 37-71 (1981).
2. Corbet, G. B. & Hill, J. E. *A World List of Mammalian Species* (Br. Mus. Nat. Hist., London, 1986).
3. Rodríguez, A. & Delibes, M. *Biol. Conserv.* **61**, 189-196 (1992).
4. Saites, L. O. *Am. Mus. Novit.* **3047**, 1-67 (1992).
5. Janczewski, D. N., Modi, W. S., Stephens, J. C. & O'Brien, S. J. *Molec. Biol. Evol.* **12**, 690-707 (1995).

Right-pawedness in toads

SIR—Preferential limb use, of which human handedness is the most clear example, is a prominent aspect of brain lateralization and has been reported in both birds and mammals¹. There are reports of significant 'footedness' in avian species that use their feet to manipulate food and objects²; lateralized forelimb usage in large samples of inbred mice³; and in primates, recent

assessments have revealed handedness in several species⁴. Neural lateralization for control of vocalizations has recently been reported in anurans⁵, raising the possibility that preferences in limb use may exist in lower vertebrates, such as amphibians. Here we report the first evidence for behavioural asymmetry in forelimb usage at the population level in two species of

anurans. Our findings suggest that pawedness has a long evolutionary history, dating back at least to early tetrapods.

We have examined the forepaw use by European toads (*Bufo bufo*) of natural populations during attempts to remove either a plastic balloon wrapped around the head (expt 1) or a strip of paper stuck onto the mouth/nose region (expt 2). In both experiments, toads showed a bias for right forepaw use at the population level (see table).

It is often assumed that laterality of limb use evolved only in those species that use their limbs for manipulative activities⁶. Domestic chickens (*Gallus gallus*), however, do not use their feet to pick up or manipulate objects, but they use their right foot preferentially during ground scratching⁷. Thus, it has been suggested that it is not manipulative ability alone which confers a population bias of footedness in avian species, but rather active use of the feet for feeding or searching for food^{1,2}. *B. bufo* makes some use of the feet in feeding and also commonly wipes its head using one of its forepaws⁷. Active use of the forelimbs associated with feeding or grooming behaviour could thus produce asymmetrical forepaw usage in this species.

The South American cane toad (*Bufo marinus*) does not show asymmetry in the paper-strip test (see table; expt 3), but does have asymmetry in another behavioural test. We measured to which side *B. marinus* turned when positioned underwater, with the ventral surface of the toad uppermost (expt 4). From videotapes we determined that the toads pivoted preferentially to their left side. During the pivot, the left forepaw was released, and the right forepaw controlled rolling to the upright position.

Pawedness and motor asymmetries found in natural populations of toads could represent a precursor of handedness in higher vertebrates and thus contribute to our understanding of the evolution of brain lateralization.

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EXPERIMENTS TO ASSESS PAWEDNESS							
	Per cent 'right-pawed'	Student's t-test (two-tailed)	Probability	No. of animals showing preference 'Right pawed' 'Left-pawed'		χ^2 test	Probability
<i>Bufo bufo</i>							
Expt 1 (n = 24)	59.2 ± 3.9	2.325	<0.05	14	4	5.55	<0.02
Expt 2 (n = 46)	55.2 ± 2.5	2.039	<0.05	26	10	7.11	<0.01
<i>Bufo marinus</i>							
Expt 3 (n = 18)	48.2 ± 5.5	-0.330	>0.1				
Expt 4 (n = 18)	66.4 ± 2.8	5.795	<0.001	15	2	9.940	0.002

Mature *B. bufo* were collected from natural populations (Valsanzibio, Colli Euganei, north Italy; expt 1: spring 1994; expt 2: spring 1995) and kept individually for at least 3 days before testing. Toads were placed in the middle of a circular tank (60 cm diameter) with a small plastic balloon wrapped around their head (expt 1), or a small wet piece of paper stuck on their mouth and nose (expt 2). They were given 10 successive trials; in each trial the first forepaw used in attempts to remove the annoyance was recorded. In expt 1 the animals were manipulated in turn by two experimenters (one right-handed and one left-handed); this produced no significant effect ($\chi^2(1) = 2.28$). In expt 2 the animals were manipulated in turn by two right-handed experimenters, different from those of expt 1 and unaware of its results. In both experiments experimenters were alternated, one placing the annoyance and the other keeping and placing the toad in the arena. Mean percentages of right forepaw use (with s.e.m.) and number of animals showing predominant right or left forepaw use are shown. *B. marinus* were collected from north Queensland (expts 3 and 4; autumn 1995) and group-housed for at least 1 week before testing. Paper-strip tests (expt 3), followed by submersion-inversion tests (expt 4), were performed on each toad for 6 successive days. Expt 3: toads were placed in a circular tank, with a small strip of wet paper placed across their mouth and nose equidistant from the midline. One trial per day was performed for each toad, the first paw used in attempts to remove the strip being recorded. Expt 4: each toad was turned upside down and, still clasping the experimenter's fingers, immersed in a small tank of water. The side to which the toads turned when righting was recorded. Three trials per toad per day were performed. Every effort was made to randomize the direction of rotation of the toad when inverting and the orientation of the toad with respect to the experimenter. On day 1, nine toads were tested with the left hand and the remaining with the right hand for each trial. On day 2, they were tested alternately with left or right hand (random sequence of toads). From day 3 onwards each toad was tested (in random order) with R, L, R or L, R, L hands, for each of 3 trials. Results show mean % of right forepaw use and left side turning (with s.e.m.), and number of animals showing prevalent left or right turning over the 6 days.

1. Bradshaw, J. L. & Rogers, L. J. *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect* (Academic, San Diego, 1993).
2. Rogers, L. J. & Workman, L. *Anim. Behav.* **45**, 409-411 (1993).
3. Waters, N. S. & Denenberg, V. H. *Behav. Brain Res.* **63**, 195-204 (1994).
4. Ward, J. P. & Hopkins, W. D. (eds) *Primate Laterality: Current Behavioural Evidence of Primate Asymmetries* (Springer, New York, 1993).
5. Bauer, R. H. *Psychobiology* **21**, 243-248 (1993).
6. Walker, S. F. *Br. J. Psychol.* **71**, 329-367 (1980).
7. Ewert, J.-P. *Neuro-Ethology* (Springer, Berlin, 1980).

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