LETTER

Reply to Brougham and Brusatte: Overall anatomy confirms posture and flight model offers insight into the evolution of bird flight

Brougham and Brusatte (1) agree with us that *Microraptor* was an arboreal glider but disagree with the posture of our model's hind limbs (1). They offer no suggestion for an alternative, other than the implied parasagittal posture of a typical dromaeosaur, which we showed was aerodynamically and mechanically unlikely (2). They cast doubt on the sprawled (abducted) hind-limb posture of our reconstruction—a key feature—by claiming that dromaeosaurid hips have structures (antitrochanters and supracetabular crests) that prevent abduction and that our specimen was too flattened to see such features. Whereas large dromaeosaurids may possess such structures, apparently, in small ones such as *Microraptor*, these structures are greatly reduced (3). The authors (1) misrepresent the small dromaeosaurid *Hesperonychus* as providing evidence against a sprawling posture, when the original description of *Hesperonychus* specifically mentions the lack of processes on the acetabulum preventing abduction and states that the "acetabulum opens dorsolaterally rather than laterally. . . suggesting the ability to partially abduct the hind limbs. This morphology is of interest in light of proposals that *Microraptor gui* abducted its feathered hind limbs to act as airfoils" (reference 4 in ref. 1). Their crushed flat claim is based on examining an incomplete cast (1). They did not examine the original fossil or its X-rays and X-ray computed tomography scans, and thus made a judgment using incomplete information. This *Microraptor* pelvis has been figured and described (4), and a complete 3D cast of the specimen is also available in our collections for examination. Furthermore, our pelvic morphology was checked against dozens of other specimens (as stated in ref. 2). We stand by our anatomical observations and are currently describing this specimen, along with other material, which will support the accuracy of our interpretation.

Brougham and Brusatte (1) devote a large portion of their letter to defending the dinosaurian origin of birds. We find this somewhat puzzling, because we did not address that issue in our paper. They choose to regard this feathered dromaeosaur as a derived member of the group, although most cladistic analyses show it as basal (5) or even as the primitive sister group of that clade (3). Moreover, much older taxa with large, pennaceous feathers on the lower hind limb (*Pedopenna*, *Anchiornis*) have been discovered from radiometrically dated Jurassic rocks in China (5). *Anchiornis* is cladistically a troodontid, suggesting that four-winged gliding is also primitive for deinonychosaurs. Brougham and Brusatte (1) suggest that *Microraptor* is of no relevance to understanding bird flight, because they doubt that it inherited its mode of gliding from an ancestor that it shared with birds. We think that such a shared ancestry is actually reasonable given the feathered hind limbs of *Anchiornis*, to which other authors have attributed an aerodynamic function (5). We never argued that *Microraptor* must be a direct ancestor of birds to be informative about the origin of avian flight, any more than *Archaeopteryx* must be ancestral to modern birds to be informative about avian origins. We think *Microraptor* displays a four-winged mode of gliding that it inherited from more primitive, arboreal ancestors, and we are confident that our model is anatomically reasonable.

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1. Brougham J, Brusatte SL (2010) Distorted *Microraptor* specimen is not ideal for understanding the origin of avian flight. *Proc Natl Acad Sci USA* 107:E155.
2. Alexander DE, Gong E, Martin LD, Burnham DA, Falk AR (2010) Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proc Natl Acad Sci USA* 107:2972–2976.
3. Hwang SH, Norell MA, Qiang J, Keqin G (2002) New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *Am Mus Novit* 3381:1–44.
4. Burnham DA (2010) *Maniraptoran "Dinosaurs": Paleoenvironment, Paleoecology, and Evolution* (VDM Verlag, Müller, Mauritius), p 128.
5. Hu D, Hou L, Zhang L, Xu X (2009) A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461:640–643.

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