



FIG. 2 Phylogeny, total sperm length and length of sperm entering the egg for 12 species of *Drosophila*. The phylogeny was reconstructed and total sperm length determined as described in ref. 8. Length of sperm entering the egg was either estimated or measured directly as in Fig. 1. In the six species for which complete tracing and measurement were not done, determination of whether nearly all (++) or only part (+) of the sperm enters the egg was based on visual observation of sperm in eggs and the position of the sperm tail relative to the egg micropyle. Solid branches indicate that entire sperm enters the egg; hollow branches indicate that only a fraction of sperm enters the egg.

provisioning function of their sperm when anisogamy ratios are large³, the ancestral character state for *Drosophila*.

Although our findings indicate that selection to provision offspring has not significantly contributed to sperm length evolution in *Drosophila*, they demonstrate a previously unrecognized diversity and complexity of sperm–egg interactions. An unappreciated degree of coordinated evolution between sperm and egg has occurred in *Drosophila*. Further studies

are needed to determine whether similar variation in sperm utilization occurs in other animal groups.

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Multituberculate phylogeny

STR — In the recent reports of fossils of multituberculate mammals^{1,2}—pectoral girdle and ear ossicles, respectively—only a few selected characters and taxa are considered: 10 characters and 3 taxa in the report by Sereno and McKenna¹ (the remaining 12 characters are autapomorphies) and 16 characters and 4 taxa in that by Meng and Wyss². Basing phylogenetic hypotheses on a single complex of characters is sometimes necessary because of the fragmentary material available. However, the newly described material should be included in the more general framework of postcranial and cranial or basicranial comparisons (for example, refs 3, 4). We believe that additional taxa and character information are critical for the interpretations presented.

In their analysis, Sereno and McKenna¹ do not integrate the postcranial remains of the dryolestid *Henkelotherium*⁵ and the triconodont *Gobiconodon*⁶. They ally these taxa with multituberculates and therians, but give no rationale for the alliance. In fact, both taxa^{5,6} and other multituberculates (see, for example, refs 7, 8) show a higher degree of humeral torsion than do

therians and the multituberculate cf. *Bulganbaatar*¹. This conflicts with Sereno and McKenna's proposal of a single origin of parasagittal gait in multituberculates and therians. They also restore the scapulo-coracoid of Early Jurassic *Morganucodon* without trace of a supraspinous fossa, yet this portion of the bone is not preserved⁹. Moreover, Tritylodontidae, an outgroup to *Morganucodon*^{3,4}, has a supraspinous fossa in the anterodorsal border of the scapula¹⁰, the same position at which the supraspinous muscle appears embryonically¹¹.

Meng and Wyss² offer four characters of the ear ossicles allying multituberculates with monotremes, but three of them are problematic. First, an incus articulating dorsally with the malleus, as occurs in monotremes, is yet to be documented in multituberculates. The only associated malleus and incus of a multituberculate (*Lambdopsalis*) are not dorsoventrally articulated¹². Second, a horizontal position of the ectotympanic is shared by monotremes and the multituberculate *Lambdopsalis*, but is also probably primitive for placentals¹³. Accepting a horizontal ectotympanic for multituberculates and

using the taxa in Meng and Wyss's tree, this character should diagnose Mammalia and not a Multituberculata–Monotremata clade. Nevertheless, indirect evidence suggests that a horizontal ectotympanic is not repeated in multituberculates other than *Lambdopsalis* and some Cretaceous taeniolabidoids with inflated vestibuli. The orientation of the oval window roughly parallels the ectotympanic in living mammals³ and thus predicts the horizontal ectotympanic of *Lambdopsalis*. Given this correspondence, an oblique ectotympanic is interpreted for most multituberculates, including paulchoffatiids and ptilodontoids³. Third, the 'contact' between the ectotympanic and 'pterygoid' purported for *Lambdopsalis* is between two broken pieces, one from the ectotympanic, the other from the pterygoid. Moreover, in the platypus, the 'pterygoid' does not contact the ectotympanic, which is supported only by connective tissue¹⁴. Consequently, the character becomes equivocal, even accepting the tree topology proposed by Meng and Wyss². In addition, the free monotreme 'pterygoid' is a neomorph under any recent phylogenetic scheme; therefore, its homology with the multituberculate pterygoid is suspect.

The exercise of building a matrix with data combined from both reports yields one phylogenetic tree with the same topology as that presented by Sereno and McKenna¹, which is three steps shorter than the tree reported by Meng and Wyss². The anatomical information provided is welcome; however, evaluation of the competing phylogenetic hypotheses of multituberculate relationships must await the inclusion of additional taxa and characters.

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SERENO AND MCKENNA REPLY — Presley⁸ and Rougier *et al.* have commented on our recent description of a complete multituberculate shoulder girdle and our cladistic analysis which links multituberculates and therians on the basis of six synapomorphies in the shoulder region¹. As evidence against the therian-like structure and function of the multituberculate pectoral girdle and forelimb, they cite the greater degree of torsion in the shaft of the humerus of another multituberculate (*Lambdopsalis*¹⁵). Marked humeral torsion and fossorial habits, however, are clearly correlated among mammals (for example, moles among living therians). Increased humeral torsion in this avowed fossorial multituberculate from the