5. T. V. Santulli, *Hosp. Pract.* **9**, 129 (1974); B. Barlow, T. V. Santulli, W. C. Heird, J. Pitt, W. A. Blanc, J. N. Schullinger, *J. Pediatr. Surg.* **9**, 587 (1974).
6. J. J. Bullen, H. J. Rogers, L. Leigh, *Br. Med. J.* **1**, 69 (1972).
7. B. Reiter, J. H. Brock, E. D. Steel, *Immunology* **28**, 83 (1975).
8. D. Burman, in *Iron in Biochemistry and Medicine*, A. Jacobs and M. Worwood, Eds. (Academic Press, New York, 1974), p. 544.
9. M. L. Groves, in *Milk Proteins II: Chemical and Molecular Biology*, H. A. McKenzie, Ed. (Academic Press, New York, 1971), p. 367.
10. D. A. Lipschitz, J. D. Cook, C. A. Finch, *N. Engl. J. Med.* **290**, 1213 (1974).

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Woodruffia metabolica: Exception to the Rule of Desmodexy Questioned

Golder (*1*) has concluded that *Woodruffia metabolica* is an exception to the rule of desmodexy. In this comment I show that Golder's conclusion (*1*) is predicated on the identity of nonhomologous structures. I emend the rule of desmodexy and several contingent definitions of cell structures in order that nonhomologs cannot be used to test the consistency of this rule. Furthermore, I show that *W. metabolica* does not except the emended rule of desmodexy.

Chatton and Lwoff (*2*) proposed the rule of desmodexy as "*Quelle que soit la course de la cinétie, le cinétodesme est á la droite des blepharoplastes*," that is, on the ciliate's right of the blepharoplasts or kinetosomes. The definition of kinety as a file or row of kinetosomes is generally accepted (*3, 4*). However, several definitions of a *cinétodesme* or kinetodesma exist. Chatton and Lwoff (*2*) defined a kinetodesma, which is composed of *fibres cinétodesmales*, as "*un fil ou une bandelette . . . qui unit les cinétosomes entre eux.*" Nonhomologous ultrastructures are identified by this light-microscopic definition (*1, 3, 5*). Sleigh (*5*) and Pitelka (*3*) recognized two categories of nonhomologous kinetodesmal structures: (i) classic kinetodesmal systems of holotrichous ciliates, in which Chatton and Lwoff originally observed *fibres cinétodesmales*, and (ii) Km fibers of heterotrichs. The Lkm fiber of *W. metabolica* (*1*) establishes a third category. The preceding structural categories satisfy Chatton and Lwoff's definition of a kinetodesma and thus may be used to test their rule of desmodexy. To avoid this confusion, Grain (*4*) emended the definition of the components of kinetodesma thus: "*la fibre cinétodesmale est une fibre à structure periodique, qui prend naissance à l'extérieur du cinétosome, vers sa base, du côté antéro-latéral droit, au niveau des triplets 5, 6, 7, 8 et qui se coude pour devenir parallèle à la surface cellulaire en se maintenant dans l'ectoplasme.*" But, kinetodesmal fibers not in the anterior right portion of a kinetosome [such as *Dileptus* proboscis kineties (*6*) and *Chilodochona* circumoral kineties (*7*)] do not qualify as such, although they satisfy the other qualifications of the definition. Furthermore, this definition, because of its spatial criterion (the right anterolateral side), makes the rule of desmodexy tautologous. To avoid these problems, the definition is emended as: The kinetodesmal fiber is a periodically striated fiber which arises near the base of the kinetosome, exterior to any or all of kinetosomal triplets 5, 6, 7, and 8, and extends toward or parallel to the cell surface. The triplets are numbered by convention (*8*). As Chatton and Lwoff (*9*) originally described kinetodesmal fibers in apostomatous ciliates, it seems reasonable to restrict this term to these structures or their homologs. Ultrastructural research on apostomes (*10*) has revealed that their kinetodesmal fibers are identified as such by the emended definition. These "classic" kinetodesmal fibers have been observed in many holotrichs (*3, 4*) and one heterotrich (*11*).

The rule of desmodexy emphasizes the constant relationship of kinetosomes and kinetodesmal fibers within somatic or nonoral kineties. As emended, the rule of desmodexy states that kinetodesma (an assemblage of overlapping kinetodesmal fibers) or nonoverlapping kinetodesmal fibers are to the right of the kinetosomes of a somatic kinety. In order to disprove the rule, nonhomologous structures may not be used; only kinetodesma or kinetodesmal fibers oriented other than to the right of a kinety or its kinetosomes will suffice. Neither the Km fiber of heterotrichs nor the Lkm fiber of *W. metabolica* may be used to except the rule.

The colpodid *Colpoda cucullus*, which apparently lacks a kinetodesmal fiber (*12*) and possesses an Lkm fiber homolog, is cited as a possible exception to the rule (*1*). A kinetodesmal fiber is observed in *C. maupasi*, a congener of *C. cucullus* (Fig. 1A), when fixation procedures different from those of Didier and Chessa (*12*) are used. *Woodruffia metabolica* is considered to be a colpodid (*13*). As kinetosomes and their fibrillar associates are very similar in taxonomically related forms (*3, 4, 14*), one would expect to find a kinetodesmal fiber

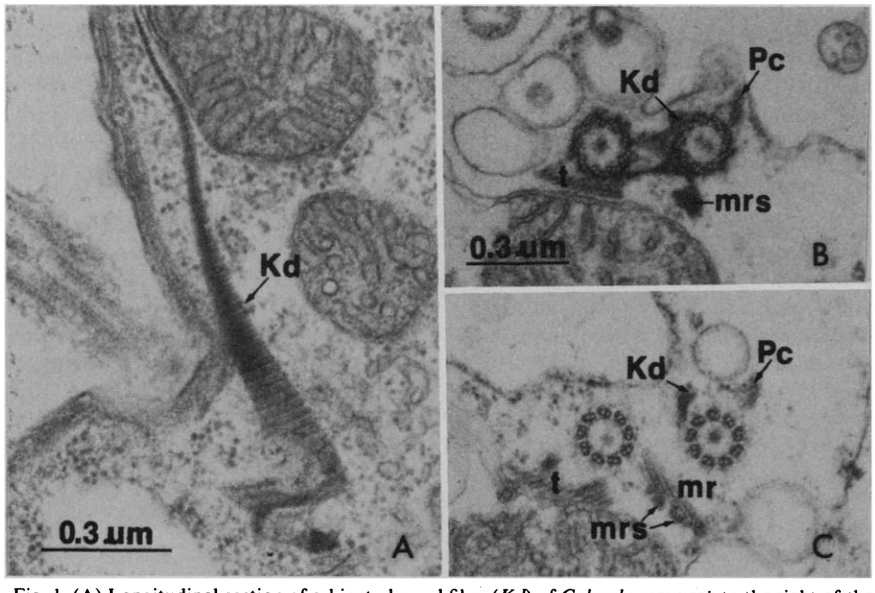

Fig. 1. (A) Longitudinal section of a kinetodesmal fiber (*Kd*) of *Colpoda maupasi*, to the right of the posterior kinetosome of a somatic pair. Specimens were fixed in glutaraldehyde in phosphate buffer and postfixed with osmium tetroxide (× 57,000). (B) Proximal transection of a kinetosome pair of *Woodruffia metabolica*, illustrating the origin of the kinetodesmal fiber homolog (*Kd*) near triplets 5, 6, and 7, the postciliary ribbon (*Pc*) at triplet 9, the transverse ribbon (*t*), and the microtubular ribbon support (*mrs*) (× 45,000). (C) Distal transection of kinetosome pair of *W. metabolica*, illustrating the separation of the kinetodesmal fiber homolog (*Kd*) from the kinetosome, the postciliary ribbon (*Pc*), the transverse ribbon (*t*), and the microtubular ribbon (*mr*) and its support (*mrs*) (× 45,000).

in *Woodruffia*. In this organism, a dense fiber arises near triplets 5, 6, and 7 [Fig. 1B; see also figure 2, A and B, in (*1*)]. It separates from the kinetosome [Fig. 1C; see also figure 2, B to D, in (*1*)] and extends toward the cell surface [note the dense fiber, which extends from mid-kinetosome level toward *Pc*, just to the right of the posterior kinetosome in figure 1C of (*1*)]. This fiber would completely satisfy the definition of a kinetodesmal fiber if it were periodically striated. Its periodicity might be revealed by different fixation procedures. It is considered at least a kinetodesmal fiber homolog, if not a kinetodesmal fiber sensu stricto, which is to the right of the kinetosomes of a somatic kinety. Thus, *W. metabolica* is not an exception to the rule of desmodexy.

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References and Notes

1. T. K. Golder, *Science* **185**, 57 (1974).
2. E. Chatton and A. Lwoff, *C. R. Seances Soc. Biol. Fil.* **118**, 1068 (1935).
3. D. R. Pitelka, in *Research in Protozoology*, T. T. Chen, Ed. (Pergamon, New York, 1969), vol. 3, pp. 280–388.
4. J. Grain, *Ann. Biol. Anim. Biochim. Biophys.* **8**, 54 (1969).
5. M. Sleigh, *J. Protozool.* **13** (Suppl.), 29 (1966).
6. J. N. Dumont, *ibid.* **8**, 392 (1961); J. Grain and K. Golinska, *Protistologica* **5**, 269 (1969).
7. J. Grain and A. Batisse, *J. Protozool.* **21**, 95 (1974).
8. P. de Puytorac, *ibid.* **17**, 358 (1970).
9. E. Chatton and A. Lwoff, *Arch. Zool. Exp. Gen.* **77**, 1 (1935).
10. P. C. Bradbury and D. R. Pitelka, *J. Microsc.* **4**, 805 (1965).
11. P. de Puytorac and J. Grain, *Protistologica* **4**, 121 (1968).
12. P. Didier and M. G. Chessa, *ibid.* **6**, 301 (1970).
13. J. O. Corliss, *The Ciliated Protozoa: Characterization, Classification, and Guide to the Literature* (Pergamon, New York, 1961), p. 310.
14. P. Didier, *Ann. Stn. Biol. Besse-en-Chandesse* **5**, 1 (1970).
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Lynn has pointed out a very important fact, that older concepts based on light microscopic observations need to be reexamined and often redefined when enough electron microscopic data have accumulated.

Chatton and Lwoff (*1*) coined the term kinetodesma when they first observed these structures in apostome ciliates. Subsequently, they observed dextrally oriented fibers accompanying kineties in a wide range of ciliates (*2*), including heterotrichs. All of these fibers were considered kinetodesma by Chatton and Lwoff when they coined the term desmodexy to describe the typical right-handedness of the fiber attachments. They were unaware, however, that they were looking at nonhomologous structures in some of the species observed. Although some of the fibers they were looking at were the striated type now referred to as kinetodesma, the fibers they saw in heterotrichs must have been Km fibers because these are the only heterotrich fibers large enough to be seen with the light microscope. At any rate, both fibers satisfy the rule of desmodexy, as originally proposed.

Grain (*3*) suggested that the use of the term kinetodesmal fiber be restricted to the right anterior striated fiber. Grain also discussed the rule of desmodexy and implied that it only applied to the striated fiber. While there were those who were in agreement with this idea, others were not. In fact, Pitelka (*4*) pointed out that both kinetodesma and Km fibers satisfy the rule.

Lynn now suggests that the rule be officially changed so that it pertains only to kinetodesma. He further states that *Woodruffia metabolica* has a kinetodesmal fiber on the right-hand side of the kinetosomes and therefore does not violate the rule of desmodexy. I have seen periodic striations of approximately 33 nm in the fiber which Lynn describes as kinetodesmal, and I agree that it is a kinetodesmal fiber. However, the fact remains that in *W. metabolica* the major cortical fiber, microscopically visible, accompanies kineties on their left and is in violation of the Chatton-Lwoff definition of desmodexy. It must be remembered that Chatton and Lwoff were looking at both kinetodesma and Km fibers when they proposed desmodexy. Since the rule, as originally proposed, encompassed both of these nonhomologous structures, the left-handed Km stands as an exception to the rule. Had Chatton and Lwoff observed silver-stained preparations of *W. metabolica*, they would have noticed this sinistral fiber and, I'm sure, considered it as an exception to their own generalization.

Whether the fiber observed in *W. metabolica* stands as an exception to the rule of desmodexy thus boils down to how the rule is defined. If defined as Chatton and Lwoff defined it, *W. metabolica* is an exception. According to the changed versions suggested by Grain and Lynn, it is not. Although any of these definitions might be acceptable, there are some reasons for leaving it as Chatton and Lwoff proposed it. Why restrict the rule to one of the two structures when it is applicable to both? The rule, as originally proposed, is a good one because in the vast majority of ciliates which have microscopically visible fibers accompanying their kineties, whether Km or kinetodesma, dextral orientation is evident. Why is it so rare to find elaborate structural differentiation on the kinety's left? The "right-handedness" of ciliates is, as Chatton and Lwoff suspected, a general feature, and dextral orientation is the "rule." It is even more intriguing that this dextral orientation is present in nonhomologous structures.

Whether Lynn's restricted definition of desmodexy or the original interpretation I favor gains widespread acceptance must remain to be seen. At any rate, it is pleasing to see a rekindling of interest in this little-studied area.

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References and Notes

1. E. Chatton and A. Lwoff, *Arch. Zool. Exp. Gen.* **77**, 1 (1935).
2. ———, *C. R. Seances Soc. Biol. Fil.* **118**, 1068 (1935).
3. J. Grain, *Ann. Biol. Anim. Biochim. Biophys.* **8**, 54 (1969).
4. D. R. Pitelka, in *Research in Protozoology* (Pergamon, New York, 1969), vol. 3, p. 280.
5. I thank D. R. Pitelka, L. E. Rosenberg, S. L. Wolfe, and H. Wessenberg for their contributions and opinions regarding this reply.

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