Sinistral nematode population

SIR — Several animal taxa display a consistent left–right asymmetry of the body plan. In nematodes, dextrality predominates¹. However, we have now found a nematode species that has sinistral populations.

In nematodes of the order Rhabditida, the anterior gonadal arm generally lies on the right of the intestine. Together with other asymmetries at the cellular level found in other nematode orders^{1,2}, this defines the overall body handedness. After looking at many wild isolates of free-living soil nematodes, we found one population (strain PS1158) with reversed handedness. We identified it as *Acroboloides bodenheimeri* Steiner, 1936³, Family Cephalobidae, Order Rhabditida. Type specimens for this species and for two independent isolates are also sinistral (see table). Other fixed and cultured isolates, previously identified by morphological criteria as *A. bodenheimeri*⁴, are dextral (for example, strain PS2052). PS2052 crosses with neither PS1158 nor PS2160 (which themselves cross). PS1158/PS2160 and PS2052 thus form two biological species that are mirror images of one another at the cellular level. Because type specimens for *A. bodenheimeri* are sinistral, we conclude that this species name applies to PS1158/PS2160. (We will report elsewhere on the identity of the species represented by PS2052.)

Reverse handedness does not, as in some snails⁵, prevent mating *per se*: mating actually occurred in crosses between PS1158 and PS2052, as revealed by the copulatory plug left by the male over the female's vulva. Also, crosses between sinistral males and rare dextral females from PS1158 yielded progeny, and the converse was also true.

Handedness is apparent from the early cleavages of the nematode embryo, in the

second division of the AB blastomere⁶. The axis of this division can be experimentally inverted in *Caenorhabditis elegans*, causing handedness reversal in the adults⁷. The respective fates of left and right blastomeres are set one cell cycle later by asymmetrical cell interactions⁸. In *Acroboloides* sp. PS2052, as in other dextral nematodes, the left granddaughters of the AB blastomere are positioned anteriorly to their sisters (8/8 embryos). The converse is true in *A. bodenheimeri* PS1158 (8/8) (see figure; in contrast to *C. elegans*, in these species the division of AB is delayed until P1 has divided three times). The asymmetry extends to the next cell cycle in the pattern of contacts to the blastomere MS. This is strikingly similar to the situation in snails, where the cleavage pattern reflects body-plan handedness, and is only rarely reversed^{9,10}.

We believe the present observation to be only the second example of handedness reversal of the whole body plan in an animal phylum. Reversal must be constrained, either because the transition is mechanistically difficult, or because of negative selection on reversed organisms¹¹. Our finding shows that the transition can nevertheless occur and leads to a complete reversal of the population, not only to an equal distribution of handedness.

Developmentally, cleavage handedness could be defined by some chiral cytoskeletal structure^{12–14}. The evolutionary reversal of the cleavage pattern could act at this level, or in the inversion of some component of another embryo axis. We hope that this can be investigated in these

Handedness reversal of the cleavage pattern. Dorsal views of embryos of *Acroboloides* spp. a, PS1158; b, PS2052 at the 9-cell stage. Anterior is to the left of the picture. Cells ABar and ABpr are anterior to their respective sisters ABal and ABpl in PS1158, posterior in PS2052. The other 5 cells at this stage are C, D, P4, MS and E (MS and E are located ventrally). Scale bar, 10 μ m.

closely related nematode species with opposite handedness.

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SINISTRAL AND DEXTRAL NEMATODES

Designation	Status	Origin	Sinistral*	Dextral*
PS1158	In culture	California	186	14
PS2160	In culture	California	198	2
<i>A. bodenheimeri</i>	Type specimens Steiner, 1936	Israel	15	1
<i>A. bodenheimeri</i>	Fixed specimens	Libya	10	0
PS2052	In culture	Senegal	2	198
' <i>A. bodenheimeri</i> '	Fixed specimens	Malawi	0	12

We determined handedness of fixed specimens by the position of the gonad relative to the intestine (these species have a single gonadal arm extending anterior to the vulva). For living populations, handedness was determined on juveniles by the concordance of at least two criteria from ref. 7. Details on the left–right asymmetries at the cellular level and on strain isolations are available on request. Gonad position in the type specimens was not explicitly mentioned by Steiner, but does appear in his original drawings³. Every female of PS1158, irrespective of its phenotype (or of that of the father), produces some dextral progeny, showing that handedness is not imprinted on the embryo by the phenotypic handedness of the mother. The changes in gonad position noted by Lorenzen¹⁵ outside the order Rhabditida could be indicative of changes in handedness of the whole-body plan but may well have evolved independently of handedness.

*Number of animals.

Correction

In the Scientific Correspondence "Turing patterns in fish skin?" by Thomas Höfer and Philip K. Maini (volume 380, page 678), the lettering of two parts of the figure was incorrect: part *b* should have been labelled as part *d*, and part *d* as part *b*. Parts *a* and *c* are labelled correctly.