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Developmental biology

Variable cell number in nematodes

Studies of the nematode worm *Caenorhabditis elegans* have led to the widely held belief that individuals of a given nematode species are characterized by a property known as eutely, in which all individuals have the same total number of cells¹. This property, which is peculiar to nematodes and a few other phyla, has raised the question of whether the developmental mechanisms of nematodes differ from those of larger metazoans. Here we show that many, perhaps most, nematode species are not eutelic in at least one organ, the epidermis, and that in this respect they resemble other model organisms such as fruitflies and mice.

Although most *C. elegans* cell lineages are invariant, a few are not (such as intestinal lineages)^{2–4}. Limited cell-lineage variation has also been found in other species of nematode^{5–8}: for example, in *Pelodera strongyloides*, the ventral epidermal cells P3.p and P9.p divide in about half the females⁷. To test whether a variable cell number is more widespread than such isolated cases suggest, we determined the among-individual variance (V_i) of epidermal nuclear number in adults of 13 species of free-living nematode from three families (Cephalobidae, Panagrolaimidae and Rhabditidae), which between them span the range in adult body size and adult epidermal cell number typical of free-living terrestrial nematodes (Fig. 1a). All these species have epidermal syncytia containing nuclei produced by a series of lateral seam cells that stop proliferating before adulthood.

V_i for epidermal nuclear number in *C. elegans* is not significant (likelihood ratio test, $P > 0.05$). This is to be expected, as there are no reports of variation in lateral-seam-cell lineages². Four other species (*Caenorhabditis* sp. PS1010, *Oscheius myriophila*, *Panagrolaimus rigidus* and *Rhabditella octopleura*) do not deviate significantly from eutely. The remaining eight species show significant V_i for nuclear number, with *Panagrellus redivivus*, *Pellioditis* sp. EM434 and *Rhabditoides regina* having $V_i > 100$ (Fig. 1b).

Among species, V_i increases with the number of epidermal nuclei, N (Spearman's rank correlation, $\rho = 0.84$, $P < 0.001$; Fig. 1b). This relationship has evolved many times (regression through the origin of phylogenetically independent contrasts, assuming that branch lengths are equal⁹,

$\log V_i = 3.38 \log N$; $P = 0.006$). Body length (L) also increases with the number of nuclei ($\rho = 0.73$, $P = 0.004$; Fig. 1c), and this relationship has also evolved repeatedly ($\log L = 0.514 \log N$; $P = 0.003$). However, the relationship between V_i and body length is only weakly positive ($\rho = 0.59$, $P = 0.03$) and disappears after correcting for phylogeny ($\log V_i = 3.27 \log L$; $P > 0.1$). Reproductive mode (parthenogenetic, hermaphroditic and gonochoristic) does not have a significant effect on any of the traits studied ($P > 0.1$).

The evolution of V_i must be caused by changes in lateral-seam-cell lineages. We have modelled the V-cell lineages of *C. elegans*, *P. redivivus*, *R. octopleura* and *O. myriophila*^{2,5,10} as discrete-time multitype branching processes and determined the

resulting distribution of epidermal nuclear counts by simulation¹⁰.

The simulations suggest two reasons why species with many nuclei may be more variable than those with fewer¹⁰. First, V_i increases with the probability of deviating from the species' canonical lineage. Second, for a given probability of lineage variation, more complex lineages yield a higher V_i than simpler lineages. We conclude that the high observed value of V_i for *P. redivivus* results not only from the complexity of its lineage, but also from a greater propensity to deviate from the canonical lineage compared with the other species¹⁰. This is consistent with observations of variability in the V-cell lineages of *P. redivivus*⁵ and *R. regina*, which have high V_i values. Loss of hypodermal eutely also occurs in several species of primitive marine nematode that have a cellular, rather than syncytial, hypodermis¹¹.

Given that the terrestrial free-living nematodes studied here are smaller and have fewer epidermal nuclei than most marine and animal parasitic nematodes, it is likely that most nematode species are not eutelic and so resemble other metazoans.

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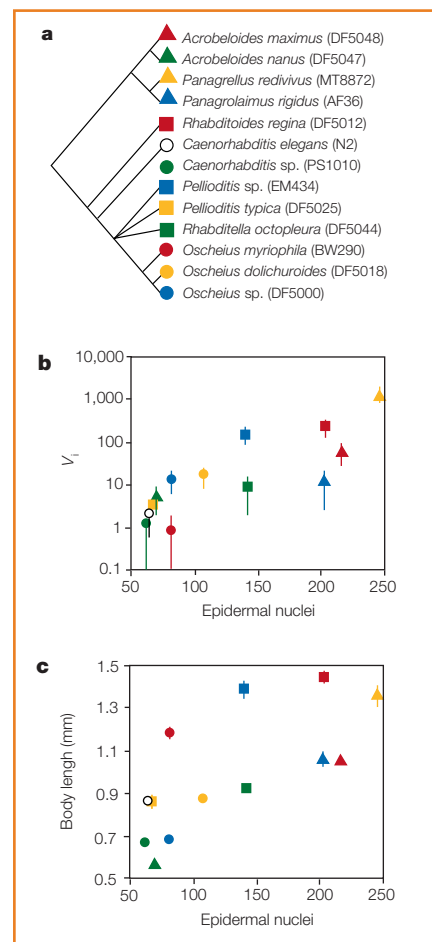


Figure 1 Relationship between body length, the number of epidermal nuclei and the among-individual variance in 13 nematode species. Lateral epidermal nuclei were independently counted 2–3 times (to account for measurement error) on one side of 10–14 early adult females or hermaphrodites from each species. For each species, among-individual variance (V_i) was estimated by maximum likelihood using a random effects one-way linear model. **a**, Phylogeny of the species studied (strain names in parentheses)^{12,13}. *Acroboloides* species are parthenogenetic; the rest are gonochoristic, except *C. elegans*, *O. myriophila* and *Oscheius* sp. DF5000, which are hermaphroditic. **b**, Plot of V_i (log scale) against number of epidermal nuclei, N . **c**, Plot of body length against N . Error bars show standard errors.

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Nanoelectronics

Growing Y-junction carbon nanotubes

The synthesis of connections between two or more different carbon nanotubes is an important step in the development of carbon nanotube-based electronic devices and circuits^{1–4}. But this is difficult to achieve using conventional methods to grow carbon nanotubes⁵ because the straight tube structure cannot be controllably altered along its length. Various ideas for post-growth modifications have been suggested⁶,