Atypical Development in Plant and Soil Nematodes

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Abstract: Observations of atypical developmental and anatomical characteristics have been recorded for many taxa of soil nematodes. They include the unusual occurrence of extra feeding structures, aberrant configuration of features of both male and female reproductive systems, and the occurrence of intersexes assumed to be functionally female, functionally male, or non-functional. In many cases, hypotheses have been advanced regarding the genetic or developmental mechanisms and environmental stimuli that control, regulate, or facilitate abnormalities, but many are quite speculative and lack experimental verification. Further, the fitness costs or advantages, and the heritability of aberrant characters are largely unknown, except where they clearly preclude reproduction, either apomictic or amphimictic. Underlying mechanisms and ecological consequences may be difficult to study in organisms that are not readily cultured under axenic or sterile laboratory conditions, however information on developmental processes in *Caenorhabditis elegans* represents an important resource in which to seek homologies.

Key words: developmental abnormalities, extra odontostyle, multivulval condition, intersexes, developmental control, fitness costs, homologies.

Observations of aberrant anatomical and morphological characteristics in plant and soil nematodes trigger questions regarding their fitness costs and the underlying control mechanisms that allow or facilitate them. The occurrence of a "sixth" odontostyle in two females of *Dorylaimoides* sp. was described by Choudhary et al. (2004) as the rarest of rare phenomena. The same phenomenon has been observed in females of *Dorylaimoides* sp. in Japan (Okada, pers. com.). The senior author recently observed an extra odontostyle in a female of *Aporcelaimium* sp. with a fully developed reproductive system (Fig 1. A, B). The extra odontostyle was about 20% longer than the functional odontostyle. The phenomenon has been reported on several occasions in *Xiphinema* and *Longidorus* spp. (Fig. 2A,B; Fig. 3A,B) (Dalmasso, 1967; Loof and Maas, 1972; Zheng et al., 2000; Kumari, pers. com.).

The dorylaimid odontostyle develops and is stored in a cell in the anterior part of the pharynx. The replacement odontostyle in the first juvenile (J1) stage, which will become the odontostyle of the J2 stage, is embedded in the base of the J1 odontophore. In subsequent juvenile stages, the cell in which the odontostyle develops migrates backwards in the pharynx until the final molt occurs, at which time it migrates anteriorly and replaces the shed odontostyle of the previous stage (Coomans and De Coninck, 1963; Grootaert and Coomans, 1980; Carter and Wright, 1984). Because of

their direct damage to plants and their virus-vector attributes, nematodes of the Longidoridae are the most studied of the Dorylaimida. Yeates and Boag (2002) documented growth spurts in Longidoridae based on body volume assessments. Differences in length of attenuated odontostyles in Longidoridae are readily measurable and have been used, in part, to infer development stage. The replacement odontostyle is 14 to 20% longer than the extant odontostyle in all juvenile stages of Longidoridae where measurements are available (Yeates, 1972, 1973; Yeates and van Etteger, 1991; Yeates and Boag, 1992; Yeates et al., 1992; Yeates et al., 1997; Zheng et al., 2000; Ye and Robbins, 2004a, 2004b; Handoo et al., 2005).

Choudhary et al. (2004) speculated that hormonal changes inactivate the odontostyle forming cell after the J4 stage. In some nematodes with long or heavy odontostyles, including *Longidorus, Xiphinema, Actinolaimus* and *Discolaimus*, a small spear tip or mucro has sometimes been observed in the odontostyle-forming cell in adults, suggesting that cessation of activity in that cell is not absolute (Coomans and De Coninck, 1963; Coomans and van der Heiden, 1971; Loof and Yassin, 1971; Grootaert and Coomans, 1980; Choudhary et al., 2004). Where a complete extra odontostyle has been observed and measured in adult specimens (e.g. Dalmasso, 1967; specimens documented herein), the extra odontostyle is longer than the functional odontostyle, consistent with the observations for juvenile stages. Dalmasso (1967) speculated that the two odontostyle phenomenon in adults might represent either a genetic mutation or a throwback to ancestral dorylaimid forms in which all stages, including adults, had two odontostyles. As an alternative, Loof and Maas (1972) suggested that the time at which the spearforming cell ceases its activity is somewhat variable resulting in adults either without or with a mucro or a complete extra odontostyle.
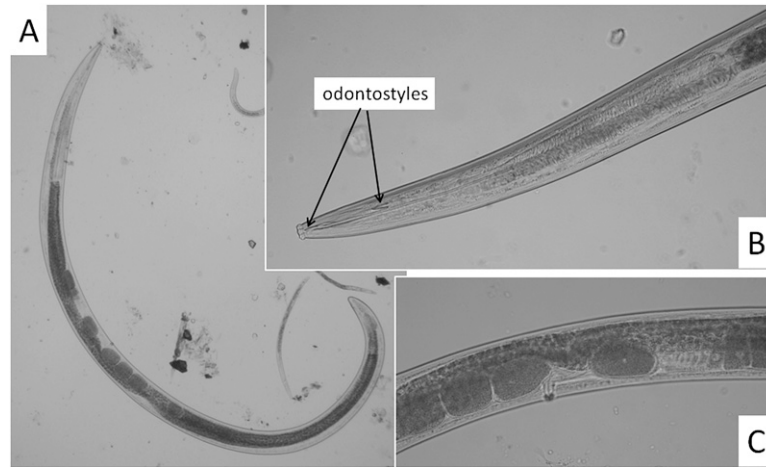
Fɪɢ. 1.   An extra odontostyle in a female of *Aporcelaimium* sp. (A-C). A: Entire nematode; B: Anterior region; C: Vulva region (photographs by H. Ferris).

It is difficult to study life stage events in nematodes of the Dorylaimida since most are not readily cultured in transparent media. When an extra odontostyle has been observed in an adult nematode, the number of developmental stages through which the individual has progressed is generally unknown; also, the number (or variability in number) of developmental stages of the species in which the phenomenon was observed has typically not been documented. From observation, and inferred from body size measurements, some long-idorids pass through only three juvenile stages rather than the four stages documented for Tylenchida and assumed for many other soil nematodes (Yeates and van Etteger, 1991; Halbrendt and Brown, 1992). However, three juvenile stages are reported in several genera of the Plectidae (Holovachov, 2004), and completion of the J1 stage within eggs of some Tylenchida could be construed as a trend towards shortening the life cycle. The loss of a developmental stage has been considered to result from hormonally-mediated heterochrony (Robbins et al., 1995, 1996).

Heterochrony is a change in the timing of developmental events in a species in relation to the ancestral state exhibited by other species. One might hypothesize that an extra odontostyle in an adult nematode is not a developmental abnormality but an indication that there is sufficient heterochronic plasticity in life course events such that, under some circumstances, individuals reach reproductive maturity at the fourth stage and that some developmental processes for the fifth life stage still proceed. Such life course plasticity would allow individuals to achieve reproductive supremacy over competitors. If an extra adult odontostyle results from heritable genetic change due to a mutation, we assume that the trait would be inherited by others and appear frequently within the same population. If it is controlled by ambient conditions, it might also occur commonly among similarly-exposed individuals. However, if the extra odontostyle appeared in response to local resource availability, resource-controlled heterochrony could be postulated and might affect individuals only at the patch level.

Determination of the number of juvenile stages requires careful observation and measurement. Most nematode species have been assumed, rather than observed, to have four juvenile stages. It would be
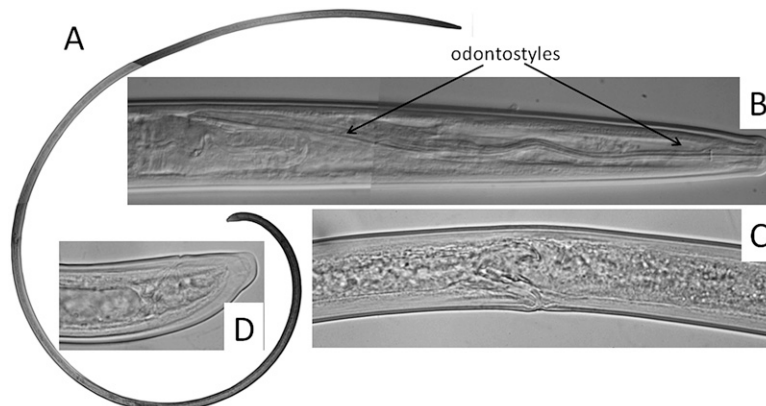

Fɪɢ. 2.   An extra odontostyle in a female of *Longidorus paravineacola* (A-D). A: Entire nematode; B: Anterior region; C: Vulva region; D: Tail (photographs by R.T. Robbins).
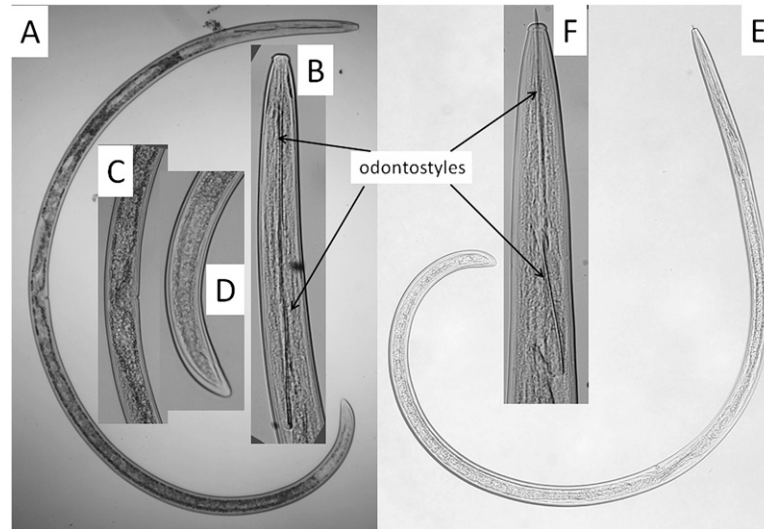
Fɪɢ. 3.   Extra odontostyles in two females of *Xiphinema brevicollum* (A-F). A, E: Entire nematode; B, F: Anterior region; C: Vulva region; D: Tail (slide: S. Kumari; photographs by R.T. Robbins).

interesting to know if the extra odontostyle in long-idorids only occurs in those species known to have three juvenile stages or if the phenomenon occurs independently of the number of juvenile stages. Certainly, the observations that the extra odontostyle is longer than the extant odontostyle allows the alternative explanation that it is not the odontostyle cell that has continued activity but that sexual maturity is achieved at an earlier life stage in some individuals. Also of interest in the developmental ecology of these taxa would be to determine whether a shortened life cycle is obligate for all individuals of the species or facultative depending on resource availability or some other factor. Development of methods for culture and study of the biology of these organisms would greatly facilitate such observations.

These are not the only areas in which developmental control of nematodes is poorly known. Features are sometimes observed in nematodes that appear to be developmental abnormalities rather than indicators of plasticity or mutation and the occurrence of an additional odontostyle might fall into that category. For example, the occasional occurrence of two or more vulvas in longidorids (Fig. 4) (Robbins, 1986; Robbins and Rubtsova 1996; Rubtsova et al., 1999; Kumari and Decraemer, 2006), the observation of specimens with two and three vulvas in *Mesodorylaimus bastiani* (Valocká and Sabová, 1980), differences in number of supplements in males of some *Plectus* species (Holovachov, 2004), and other examples in mononchids and tylenchids as reviewed by Kumari and Decraemer (2006). Abnormalities in development of the vulva are well understood in hermaphrodites of *Caenorhabditis elegans*. The vulva is initiated when the *lin-3*/EGF (epidermal growth factor) gene of the anchor cell produces signals which induce development of vulva precursor cells in the epidermis. Disruption of those signals, or interference with their pathways, results in vulva abnormalities. In wild-type *C. elegans*, there are six cells capable of responding to the initiation signals, however only three develop into the vulva. When the signal is weak, or the pathway is compromised, hermaphrodites may develop without vulvas. When *lin-3*/EGF is over-expressed, or there is a failure of control of the signalling molecules so that they are not received by the appropriate cells, more than three or even all six vulva precursor cells respond to the signals and a multivulval condition results (Sternberg and Horvitz, 1986; Hill and Sternberg, 1992; Sternberg 2005; Saffer et al., 2011). Are there similar transcriptional accidents or mutations that result in multivulval conditions of Dorylaimida? When there are two or more vulvas present, are all connected to the uterus(i) and functional?
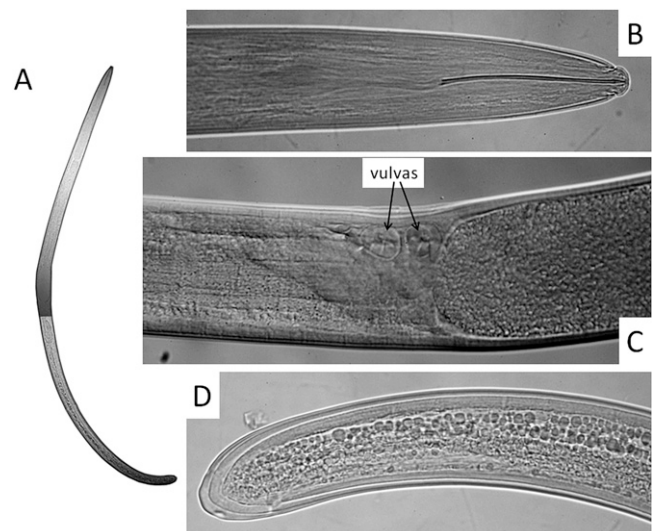

Fɪɢ. 4.   Two vulvas in a female of *Californidorus cralleyi* (A-D). A: Entire nematode; B: Anterior region; C: Vulva region; D: Tail (slide: USDA collection; photographs by R.T. Robbins).

Other examples of aberrant development include the rare occurrence of male nematodes of various nominal species or their occurrence in only some populations as observed in *Xiphinema insigne* (Robbins et al., 2000). Similarly, the apparent occurrence of males at times of population stress is a phenomenon that may reflect genetic, heterochronic or environmentally-mediated mechanisms. Also, polyploidy is well known in several nematode genera, including *Ditylenchus* and *Meloidogyne*, with consequences to development and morphology (Triantaphyllou, 1991; Subbotin et al., 2005). For example, tetraploid females of *Synonchium pacificum* (Chromadorida) were regarded by Yeates (1967) as having non-functional ovaries. The underlying molecular and chromosomal mechanisms of these varied features contribute to genome plasticity, genetic variation and adaptive responses (Castagnone-Sereno, 2006). They may also underlie accidents and variability in genome transcription.

In his interesting paper on the frequent occurrence of intersexes in mermithid nematodes, Steiner (1923) summarized several reports dating from the late 19th and early 20th centuries of intersexes in both soil and marine nematodes. Recent observations on intersexes include the occurrence of female nematodes with male features such as ventromedian supplements in a population of *Longidorus biformis* (Ye and Robbins, 2004a) and of a vulva, supplements and rudimentary spicules in intersexes of *L. elongatus* (Fig. 5; Robbins, 1986), *Leptonchus obtusus* (Goseco and Ferris, 1973) and *Enchodelus veletensis* (Pedram et al., 2009). Interestingly, at least in the *L. obtusus* example, the intersexes with male features occurred in a species where males were otherwise unknown. Among the Secernentea (or Chromadorea *sensu* De Ley and Blaxter, 2004), intersex males of *Meloidogyne javanica* with vulvas have been reported (Chitwood, 1949; Triantaphyllou, 1960;

Davide and Triantaphyllou, 1968; Eisenback et al., 1981) and the occurrence of intersexes is documented for *Ditylenchus triformis* (Hirschmann and Sasser, 1955) and *Tylenchorhynchus capitatus* (Wouts, 1966). Zhou et al. (2009) listed intersexes of 30 species of plant nematodes representing nine genera and seven families.

Developmental sex reversal from female to male under adverse environmental conditions is well documented in *Meloidogyne* (Triantaphyllou, 1973; Papadopoulou and Triantaphyllou, 1982) and *Globodera* (Trudgill, 1967) and may result in diorchic males as both arms of the original female genital primordia develop. In contrast, Roy and Gupta (1975) speculated that intersexes might result as intermediate stages in sex reversal from males to females. The protandrous hermaphrodites of *C. elegans* indicate flexibility of function in the gonad and its progenitors, as does the development under heat shock and other stressors of functional males in that species (Sulston and Horvitz, 1977; L'Hernault, 1997; Anderson et al., 2010). Hermaphrodites (XX chromosome complement) of a temperature-sensitive mutant of *C. elegans* produced abundant oocytes at 16°C but few at 25°C. Males (XO) produced a normal quantity of sperm at 16°C but developed as intersexes at 25°C, which had characteristics intermediate between males and hermaphrodites and which produce no sperm and few oocytes (Nelson et al., 1978). Intersexes are also determined by the ratio of sex chromosomes to autosomes in polyploid individuals (Madl and Herman, 1979). Interestingly, sexual differentiation in *C. elegans*, and presumably in other nematodes, is not restricted to the reproductive system; most tissues and organs differ between the sexes in anatomy or physiology, with sexual specialization occurring in 40% of male and 30% of hermaphrodite cells. The sexual differentiation of somatic cells is regulated by a global sex determination
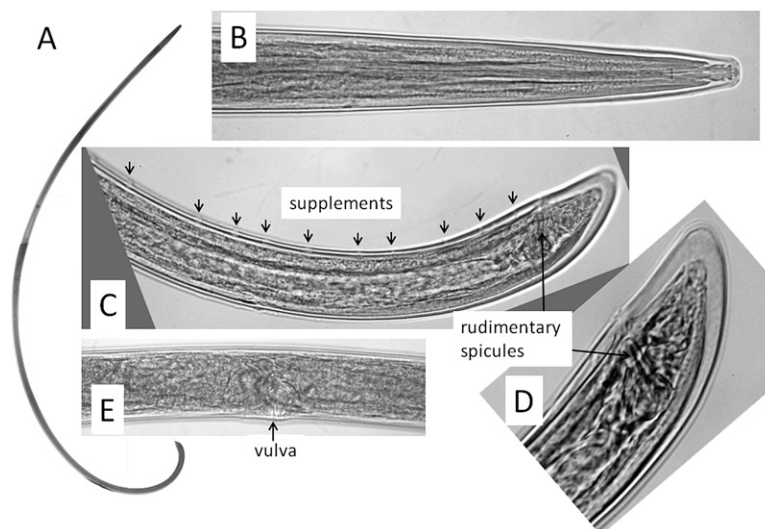

FIG. 5.   An intersex of *Longidorus elongatus* (A-D). A: Entire nematode; B: Anterior region; C,D: Posterior region with male features; E: Vulva region (slide: H. Jensen, USDA collection; photographs by R.T. Robbins).

pathway. Regulated by the number of X chromosomes, a series of inhibitory interactions establishes the activity level of a terminal regulator gene (*tra-1,* transformer 1), which switches differentiation of somatic cells to either male or hermaphrodite configurations (Hodgkin and Brenner, 1977; Sulston and Horvitz, 1977; Hodgkin, 1987; Hunter and Wood, 1990; Zarkower, 2006).

In nematodes, as in the crustacean *Gammarus duebeni,* the occurrence of intersexuality was considered a fitness cost of the flexibility of environmentally influenced sex determination (Dunn et al., 1993). Similar reasoning might be applied to the consequences of developmental plasticity. Does intersexuality impose a fitness cost in nematodes? Are intersex individuals that are functional females less fecund? Are intersexes that are functionally male less competitive for females or produce fewer sperm? Anderson and Kimpinski (1977) observed that cells in the germinal zone of the gonad of an intersex of *Aphelenchoides composticola* did not mature and that, with one exception, mature oocytes had not been reported in intersexes of that genus. Further answers to questions of fitness in a range of nematode taxa will require experimental determination.

The developmental and anatomical aberrations outlined above may result from several quite different mechanisms: 1. Failure to terminate juvenile developmental processes in the adult stage (extra odontostyle); 2. Gender interchangeability perhaps resulting from environmentally-induced stress (intersexes); and, 3. Anatomical aberrations possibly resulting from accidents in transcription of the genetic code or mutations which may or may not be mechanistically limiting to reproduction and therefore may or may not be maintained in the genome through either apomixis or amphimixis. In most cases the abnormalities have been reported for female nematodes, probably because the abundance of females is proportionally much greater than that of males in most soil nematode species. In addition to the important use of valuable molecular tools, as exemplified by the understanding of developmental regulation in *C. elegans*, there remains great value in critical observation of nematode morphology, anatomy and life history as a basis for understanding their biology and roles in ecological processes.

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