Observations on the glands of the male reproductive system in dorylaims and its phylogenetic importance

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SUMMARY

A description is given of the ejaculatory and rectal glands and their outlets in dorylaims and mononchs. The outlets of the rectal glands describe a peculiar loop caudally or dorsocaudally of the spicules, which is considered a synapomorphy that, together with the position of the outlets of the pharyngeal glands, proves the monophyly of this group. The authors, therefore, stress that mononchs should not be dissociated from dorylaims to form a separate order.

Resumé

Observations sur les glandes du système reproducteur mâle des Dorylaimides et sur leur importance phylogénétique

Les auteurs donnent une description des glandes éjaculatoires et rectales, ainsi que de leurs conduits, observés chez les Dorylaimides et les Mononchides. Les conduits des glandes rectales forment une boucle typique située dans la queue ou plus dorsalement par rapport aux spicules; cette structure considérée comme synapomorphe, de même que la position des conduits des glandes pharyngiennes, prouve la monophylie de ce groupe. Les auteurs estiment en conséquence que les Mononchides ne doivent pas être séparés des Dorylaimides pour former un ordre particulier.

While preparing the redescription of Actinca (Parastomachoglossa) costata (Coomans & Loof, 1986) and two species of Laimydorus (Loof & Coomans, 1985), the authors were struck by the exceptionally well developed male genital gland system. Although basically the same in the two genera the glands were especially prominent in the Actinca species. The description of the gland system given below is based primarily upon that genus, but has been checked in other dorylaim genera so that apart from quantitative details it can be considered as valid for the whole group of dorylaims. It has further been compared with the male genital system of mononchs and its phylogenetic implications are discussed.

The ejaculatory gland system

There are usually eight unicellular ejaculatory glands, the cell bodies of which lie either at both sides of the intestine (4 + 4) or partly at one lateral side of the intestine and ventrally from it so that all of them can be observed from one side (Fig. 1 C). Sometimes there are less than eight glands (down to five observed). Depending on the length of the prerectum the cells may be partly anterior to the intestine-prerectum junction (Fig. 1 C). The cell bodies lead to long ducts situated at both sides of the prerectum and/or vas deferens (Figs 1 C-E & 2 A-C). The ducts merge with the ventral wall of the vas deferens (Fig. 2 D-G) and then open into the lumen of the vas deferens.

The rectal gland system

The rectal glands consist of three pairs of cells located dorsolaterally or laterally from the prerectum (Fig. 1 C, E). Their ducts first parallel the prerectum (Figs 1 C & 2 A-C, G), then run dorsolaterally above and along the spicules (Fig. 2 J-L), curve inwards opposite or just behind the cloacal opening, run anteriorly between the spicules into the dorsal wall of the cloaca and open into the cloaca just behind the junction between rectum and vas deferens (Figs 1 C, F & 2 J-M). The gland cells produce refractive granules that may fill up the ducts (cf. Fig. 1 F) even to such an extent that the granulation obscures the spicules as in Laimydorus tenuistriatus (noted expressly by Schneider, 1935).
Fig. 1. *Actinca (P.) costata*: Male. A: Cross section just in front of the intestine-prerectum junction, comparable to level 1 in Fig. C; B: C.S. through an ejaculatory gland cell at a level comparable to level 2 in Fig. C; C: Posterior body region of male showing seven ejaculatory glands, three rectal glands and their ducts. Figures 1-18 indicate levels of cross sections as illustrated in A, B, D and in Fig. 2; D: C.S. at level 3 in C; E: C.S. at level 4 in C (the ventral chord contains cells of the supplements of the posterior fascicle); F: Cloacal region showing junction of *vas deferens* and rectum and terminal part of the rectal gland ducts (spicules omitted except for distal part); G: Cloacal, spicular and caudal muscles.

an. d. = anal dilator; cl. m. = cloacal muscles; c.c.m. = caudal copulatory muscle; c.m. = copulatory muscle; ej.gl.c. = ejaculatory gland cell; ej.gl.d. = ejaculatory gland duct; int. = intestine; prer. = prerectum; r.gl. = rectal gland; r.gl.c. = rectal gland cell; r.gl.d. = rectal gland duct; sp.pr. = spicule protractor; sp.r. = spicule retractor; sv.p. = subventral papilla; v.ch. = ventral chord; v.d. = *vas deferens*; v.d.r.j. = junction between *vas deferens* and rectum. Arrow in C indicates intestine-prerectum junction.
Fig. 2. *Actinca (P.) costata*: Male. Cross sections through the posterior body region, comparable to levels 5-18 in Fig. 1 C, with A = level 1 to N = level 18.

ads. = adanal supplements; an.d. = anal diator; cl.gl. = cloacal gland; cl.m. = cloacal muscle; c.c.m. = caudal copulatory muscle; c.m. = copulatory muscle; ej.gld. = ejaculatory gland duct; l.b.p. = lateral body pore; l.g.p. = lateral guiding piece; prer. = prerectum; r.gld. = rectal gland duct; r.sph. = rectal sphincter; s. = supplement; sp. = spicule; sp.pr. = spicule protractor; sp.r. = spicule retractor; sv.p. = subventral papilla; v.d. = vas deferens.
The cloaca1 glands

The caudal area contains many cell bodies, partly belonging to the different muscles present in this region as well as to the walls of the cloaca and the caudal nervous system. In lateral view and unstained specimens it is impossible to distinguish between these different types. In cross section, however, two of these cells can be separated from the other on the basis of their position and granular appearance; they seem to be connected with the lateral walls of the cloaca and, because of their appearance are considered to be glandular. Pending more information we call them cloaca1 glands (Fig. 2 L).

Discussion

Few and incomplete reports on ejaculatory glands in dorylaims exist (e.g. Chitwood & Chitwood, 1950), hence this is the first account that not only reports upon the number and position of the gland cells and their ducts but also on the outlets.

Although parts of the rectal glands can be found in some published drawings, the actual position of gland bodies, ducts and outlets has never been reported. Apart from differences in length of ducts, hence gradual differences, the arrangement completely matches that found in mononchs as described by Coomans and Lima (1965) for Anatonchus and since then seen in many species of mononchs by the present authors (Fig. 3).

The situation outlined above was found in the following families and genera:

MONONCHINA

Anatonchus, Iononchus, Mononchus, Mylonchulus, Miconchus and Prionchulus.

DORYLAIMINA

Dorylaimidae sensu lato : Dorylaimus, Idiodorylaimus, Calodorylaimus, Laimydorus, Labronema, Mesodorylaimus and Prodorylaimus.

Fig. 3. Anatonchus : Male. A : A. tridentatus, Ejaculatory glands; B : A. amicius, Rectal glands; C : A. amicius, Rectal glands.
Glands of male reproductive system in dorylaims

Actinolaimidae: *Actinolaimus, Actinca.*
Aporcelaimidae: *Aporcelaimellus, Aporcelaimus.*
Belondiridae sensu lato: *Lindseyus, Axonchium nairi.*
Axonchium heynsi is somewhat aberrant, the rectal glands being located in the tail.

In *Longidorus macrosoma* Aboul-Eid (1969) illustrated a similar loop, but more dorsal than caudal from the spicules. We found this same condition in *L. vineacola, L. caespiticola* and *Xiphinema diversicaudatum*; also in *Nygolaimus aquaticus* and in the belondirid genus *Oxydirus.*

Probably owing to their small size the Leptonchidae sensu lato did not show the glands and outlets distinctly; nor did (poorly preserved) males of *Bathyodontus.*

The male genital system of *Triplonchida* Cobb, 1920 (syn. *Diphtherophorina* Coomans & Loof, 1970) is very aberrant due to the presence of a spicular pouch. Ejaculatory and rectal glands appear to be lacking, which stresses that this group does not belong to Dorylaimida (cf. Siddiqi, 1983).

The very peculiar position of the rectal glands and especially the loops formed by the ducts caudally or dorsocaudally of the spicules, clearly constitute a synapomorphy. Together with the position of the pharyngeal glands and their outlets this synapomorphy proves the monophyly of the group. Hence we still consider mononchs, bathyodonts and dorylaims as three groups belonging to a single higher taxon in which mononchs on the one hand and bathyodonts-dorylaims on the other hand are sister groups (cf. also Coomans & Van der Heiden, 1978). This taxon could be either the order Dorylaimida or the subclass Dorylaimia. The choice can only be made with reference to the overall classification of the Nematoda, but we prefer the lower level to reduce or avoid taxonomic inflation.

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REFERENCES