A systematic problem of inter- and intra-generic variation in nephromixia of Terebellidae

Ralph I. SMITH

Department of integrative Biology
University of California
Berkeley, California, 94720, U.S.A.

ABSTRACT

The nephromixial systems of *Pista fimbriata* Moore, 1923 (a typical *Pista*) and of two aberrant "*Pista*", *P. elongata* Moore, 1909 and *P. pacifica* Berkeley & Berkeley, 1942, are described. The latter two species do not belong in *Pista*, but no described genus can accomodate them. If they are congeneric, the differences between their reproductive nephromixia exceed any intra-generic variation previously reported in the nephromixial system of any terebellid genus. Some taxonomic and phylogenetic implications are discussed.

RÉSUMÉ

Un problème systématique de variabilité inter- et intra-générique dans la néphromixie des Terebellidae

Les systèmes néphromixiaux de *Pista fimbriata* Moore, 1923 (une *Pista* typique) et de deux "*Pista*" aberrantes, *P. elongata* Moore, 1909 et *P. pacifica* Berkeley & Berkeley, 1942, sont décrits. Les deux dernières espèces n'appartiennent pas au genre *Pista*, ni à aucun autre genre connu. Si elles sont congénériques, les différences entre leurs nephromixies reproductrices surpassent toutes les variations intragénériques décrites parmi les genres de térébellides. Quelques implications taxonomiques et phylogénétiques sont discutées.

Nephromixia (GOODRICH, 1895, 1945; SMITH, 1988) are complex segmental organs serving excretory and reproductive fonctions. Their morphology show great inter-generic variations in the Terebellidae (MEYER, 1887; HESSLE, 1917; SMITH, 1989), but intra-generic variation in these organs has not previously been described. The study reported herein is the subject of a longer and fully-illustrated paper in the Journal of Morphology (SMITH, 1992). Most of the illustrations used in the oral presentation at this Conference will be found in that paper and so will not be reproduced here. Reprints will be furnished to Conference participants upon requests.

Two Californian species, *Pista elongata* Moore, 1909 and *P. pacifica* Berkeley & Berkeley, 1942, have been found to differ markedly in nephromixia and other respects from typical *Pista*, type *P. cristata* (O.F. Müller,1776). *Pista fimbriata* Moore, 1923 are described and illustrated, and it is confirmed that typical *Pista* (insofar as has

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Typical *Pista* is characterized by two, often unequal, pairs of dendritic branchiae, prominent lateral lappets, and especially by distinctive crested, long-handled, avicular, anterior uncini. In the present study the nephromixia of been reported) has one pair of anterior, pre-septal, non-reproductive, "excretory" nephromixia (ENMX) opening by obscure "renal" apertures on segment III. Post-septally occur two pairs of reproductive nephromixia (RNMX) that open on genital papillae located dorsally, just posterior to the notopodia of segments VI and VII. These RNMX are not united by lateral common ducts (Figs 1B, E). The tubes of *Pista* are usually reported as thick-walled and muddy, without apertural ornamentation.

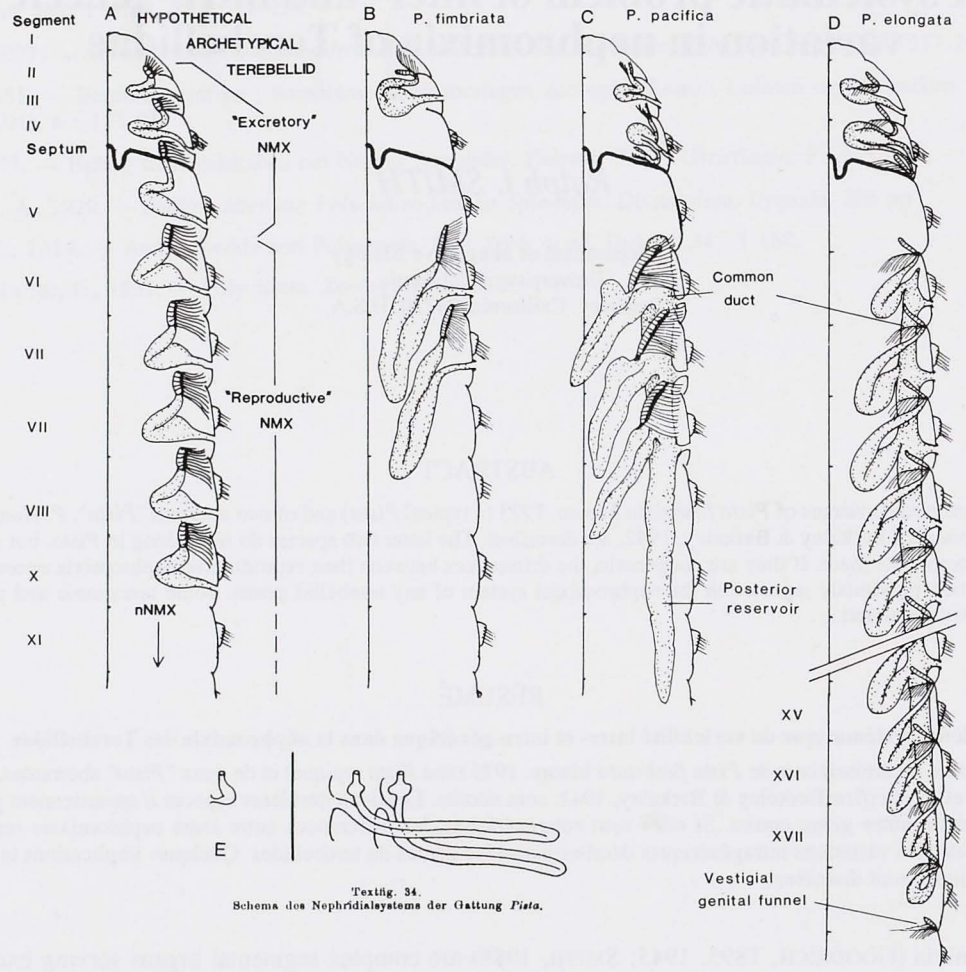

FIG. 1. — A-D, "Procrustacean Bed" representation of nephromixial systems of an hypothetical archetypical terebellid and of *Pista fimbriata* Moore, *P. pacifica* Berkeley & Berkeley, and *P. elongata* Moore. The nephromixia are fitted into a common bed for comparison. E, HESSLE's schema of the nephromixial system of *Pista*.

In contrast, *Pista pacifica* is easily recognized in its habitat in muddy sand flats by its long, chitinous, sandy, vertical tube with a distinctive fringed hood at the surface aperture and a button-like plaque with a cross-shaped slit at its lower end. *Pista pacifica* has lappets and its anterior uncini are long-handled, but are stout and crochet-like, unlike those of typical *Pista*. It differs most markedly from typical *Pista* in its nephromixia (Fig. 1C). There are two pairs of ENMX but three pairs of ciliated renal funnels. The first pair of funnels supply a pair of ENMX opening by papillae at the tops of the second lappets (segment III). The second and third pair of funnels supply the second ENMX, which open by papillae on the third lappets (segment IV). Post-septally, are three pairs of large

and complex RNMX, those on each side united by a lateral common duct with posterior extension, and discharging by obscure genital papillae on segments VI, VII and VIII.

Pista elongata occupies rock crevices and pholad bore-holes. Its tough, membranous, sand-encrusted tube opens within a bilobed reticulated hood. It is pointed out that the morphology of such tubes is often as specifically distinct as other morphological characteristics, as much as is a gastropod shell, and should be included in specific descriptions. *P. elongata* has long-handled anterior crochet-like uncini indistinguishable from those of *P. pacifica*. Likewise, it has been the same arrangement of ENMX, three pairs of ciliated funels supplying two pairs of ENMX opening on lappets of segments III and IV. But it differs from *P. pacifica* in having 9-11 pairs of relatively simple RNMX united on each side by a common duct (Fig. 1D). The number of RNMX exceeds the number of genital papillae, and small, vestigial, genital funnels may occur posterior to the common ducts. This suggests that the posterior extensions of the common ducts seen in *P. pacifica*, as well as in certain other species, may have resulted from the losse of the more posterior RNMX in evolution.

HESSLE (1917) has shown that nephromiwia of terebellid polychaetes exhibit great inter-generic variation, but he suggested little or no intra-generic variation. The differences between *P. pacifica* and *P. elongata* on the one hand and typical *Pista* on the other in respect to anterior uncini, tube morphology, and in ENMX and RNMX are sufficient to justify removal of the two former species from *Pista* but, on present information, no described genus can accomodate them. Further, the differences in RNMX between these species is a great as might characterize separate genera, although on the bases of branchiae, lappets, tubes, anterior uncini, and ENMX they appear congeneric. The differences in RNMX represent a degree of intra-generic variation not previously reported in the Terebellidae. Possibly the patterns of ENMX here demonstrated are only the extremes of intra-generic variation, in which intermediate patterns may have been lost or not yet discovered. Might sub-generic status be justified? Paradoxically, an "intermediate" condition of the RNMX is shown by *Lanice conchilega*, which has four pairs of RNMX joined by common ducts, but in this species the anterior uncini are of an entirely different avicular form, and the ENMX differ as well (MEYER, 1887). Nephromixial patterns seem to have evolved quite independently of the form of the uncini, and the similarity between the latter might represent convergent adaptations to life in comparable tubes.

The information implicit in the diverse patterns of nephromixial morphology in terebellid polychaetes may be useful in phylogenetic studies, and should be included whenever possible in specific descriptions within the Terebellidae.

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