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# New light on the enigmatic *Xenoturbella* (phylum uncertain): ontogeny and phylogeny

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*Xenoturbella* is an enigmatic animal that is merely a ciliated bag with epithelial epidermis and gastro-dermis, a subepidermal nerve plexus and a ventral mouth, but without an anus or any distinct organs. It is marine, free living, and up to 4 cm long. Its simplicity in organization has led to diverse inter-pretations during the last 50 years: as an acoelomorph flatworm, a paedomorphic holothurian or enteropneust, or a unique representative of a plesiomorphic phylum. I report here the previously unknown embryology of *Xenoturbella* that unequivocally corroborates a bivalve relationship and thus once and for all dismisses the potential new phylum. The simplicity of the adult *Xenoturbella* is due to neither plesiomorphy nor paedomorphy. It is caused by metamorphosis from a trochophore larva of molluscan type with a defined organ system, including a concentrated nervous system with ganglia, to an adult without any defined organs.

**Keywords:** embryology of *Xenoturbella*; ontogeny of *Xenoturbella*; pericalymma larva; protobranch bivalves; trochophore larva; *Xenoturbella*

## 1. INTRODUCTION

*Xenoturbella bocki* Westblad, 1949 is a strange animal with an epithelial epidermis and gastrodermis, a subepidermal nerve plexus and a ventral mouth, but without an anus, concentrated nervous system, or any other distinct organs except for a 'statocyst' containing flagellated statoconia (Ehlers 1991). It has only been found off the Swedish west coast, in the Oslo Fjord, in the North Sea (Westblad 1949, 1952), and in the Adriatic Sea (Riedl 1956), and it is neither parasitic nor microscopic. Despite its peculiarities and possible relevance to the early phases of metazoan evolution, *Xenoturbella* has been neglected by most text-books. Since its discovery, it has been the subject of most diverse interpretations: as one of the most primitive metazoans due to its simplicity in organization (Ehlers & Sopott-Ehlers 1997; Jägersten 1959) (a unique representa-tive of a plesiomorphic phylum); as a primitive relative of acoelomorph flatworms (Franzén & Afzelius 1987; Lundin 1998; Westblad 1949) due to similarities in the locomotory cilia (Franzén & Afzelius 1987); or as a paedomorphic larvae of a holothurian, an enteropneust or an extinct animal (Reisinger 1960), due to superficial similarities in the epithelium (Pedersen & Pedersen 1986; Pardos 1988). Recent studies of oogenesis (Israelsson 1997) and 18S rRNA and cytochrome oxidase I nucleo-tide sequences (Norén & Jondelius (1997), although no sequences have yet been submitted to GenBank) indicate a possible relationship of *Xenoturbella* with protobranch bivalves within the Mollusca.

## 2. A NEW SPECIES OF *XENOTURBELLA*

The material in the Swedish Museum of Natural History (SMNH) collected by Sixten Bock in 1915 and described later by Westblad consists of two species, the larger *Xenoturbella bocki* and a smaller undescribed species. Most of the specimens (including those originally described) belong to *X. bocki*.

### (a) **X. bocki *Westblad, 1949***

(i) *Type material*

All serially sectioned. Lectotype here designated to be SMNH 4987, collected off Skår, Gullmarsfjorden, Bohuslän, Sweden, from soft mud at 70–80 m. Paralecto-types, 20 specimens: SMNH 4988–5000, from type locality; SMNH 5001–5007, Flatholmsrännan, Gullmars-fjorden from mud at 70–80 m depths. All specimens were collected and sectioned by Bock and Westblad.

(ii) *Diagnosis*

An animal moving slowly, up to 4 cm long, with an irregular and flattened shape, yellow–white, darkly pigmented by small spots (each formed by numerous pigment granules just below the body surface) in the epidermis. The body is fully and homogeneously ciliated, anteriorly with a lateral sensory furrow on each side; the midpoint of the body is transversed by a sunken circum-feral 'girdle'. The mouth is ventral and central; no anus is present. There are no distinct organs except for an anterior sense organ containing motile, flagellated cells. Body layers comprise an epidermis with supporting cells (containing supporting filaments) and subepidermal nerve net, thick basal lamina, circular and longitudinal muscular layers, parenchyma, gastrodermis (basally with gonadial tissue), and stomach cavity. Gametes develop in
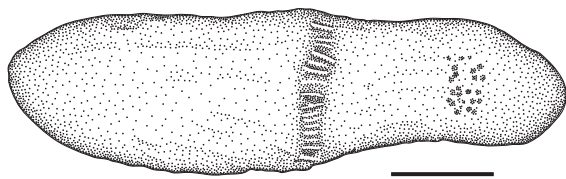
Figure 1. *Xenoturbella westbladi*, new species. Live specimen collected in April 1998, off Sydhällsö Island, Koster area. Anterior end to the right. The dots at the anterior are pigmented dots and not eyes. Scale bar, 2 mm.

the parenchyma or basally in the gastrodermis; eggs are large (up to 140 µm long), with numerous micronucleoli, covered by thick (approximately 12 µm) envelope; the spermatozoa are of a primitive type and free from each other; embryology is unknown, probably extramaternal development.

### (iii) *Distribution and habitat*

Gullmarsfjorden, west coast of Sweden. Lives in soft and very soft mud rich in organic material at 60–120 m depths.

### (iv) *Remarks*

The external ciliation was illustrated by Franzén & Afzelius (1987), and the mature oocytes were illustrated by Westblad (1949) and Israelsson (1997). The lateral sensory furrow has been described as a separate furrow at each side (Ehlers & Sopott-Ehlers 1997; Westblad 1949) but, at least in *X. westbladi*, there is a single continuous furrow. The anterior connection runs just below the tip of the anterior end and can be visualized by vital staining in a dilute solution of neutral red in seawater for 15 min (the furrow remains unstained).

### (b) **X. westbladi *sp. nov.***

(i) *Type material*

Holotype: SMNH 5008 was serially sectioned, collected south of Sydhällsö Island, Koster area, Bohuslän, Sweden at 60–70 m depths in soft mud. Paratypes: 12 serially sectioned specimens, SMNH 5009–5020, and 22 whole specimens, SMNH 5021–5022, from type locality; 15 serially sectioned specimens, SMNH 5023–5037, between Blåbergsholmen and Lysekil, Gullmarsfjorden, Bohuslän, Sweden, at 40–50 m; one serially sectioned specimen, SMNH 5038, off Skipella, Dröbak, Oslo Fjord, Norway, at 50–100 m. The material from Sydhällsö Island is newly collected, the other is material from Bock and Westblad.

### (ii) *Diagnosis*

As for *X. bocki* except for the following: an animal (figure 1) quickly gliding on surfaces (even in air), slender, small (up to 12 mm long), pink, with only a few dark pigment spots (primarily in the anterior part of body); circumferal girdle is raised, but in large specimens is occasionally sunken. A consecutive hermaphrodite; the spermatozoa are attached to each other (probably forming spermatozeugmata); eggs are small (about 55 µm long), with a thin envelope (figure 3a); there are ciliated canals through the gastrodermis in females during the mating season (figure 2a), separate from each other after
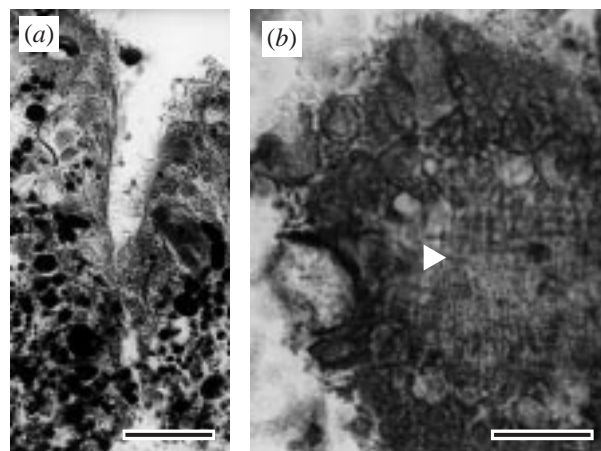
Figure 2. *Xenoturbella westbladi*, new species. (a) Ciliated canal through the gastrodermis of a female during the mating season. Scale bar, 50 µm. (b) Epithelium of late trochophore. Note the striated pattern (arrowhead) that is probably formed by the supporting filaments of epithelial cells. Scale bar, 20 µm.

copulation; spermatozoa are transferred from males to females and fertilization is internal; brooding takes place in the parenchyma; larval development occurs via spiral cleavage, stereoblastulae and trochophore as described below.

### (iii) *Etymology*

Named after Einar Westblad who found the first specimens.

### (iv) *Distribution and habitat*

Gullmarsfjorden and Koster Area, west coast of Sweden; Oslo Fjord, Norway. Soft mud rich in organic material and some silt at a depth of 40–70 m. It seems that *X. westbladi* prefers slightly coarser and shallower habitats than *X. bocki*.

### (v) *Remarks*

I have examined about 300 specimens collected at different months during the year. None of them exceeded one-third of the length of *X. bocki*, therefore it is improbable that *X. westbladi* only represents immature specimens. They are also sexually mature.

*Xenoturbella* has also been found in the Firth of Clyde, Scotland (Westblad 1949), off Bergen, Norway (Westblad 1952), and off Valdibora, Rovinj, Croatia, Adriatic Sea (Riedl 1956). Riedl (1956) stated that Adriatic material might belong to another group of *Xenoturbella* (other than *X. bocki*). Unfortunately, there is no remaining material.

## 3. ONTOGENY OF *XENOTURBELLA*

The ontogeny has been suggested as instrumental for understanding the phylogeny of *Xenoturbella* (Westblad 1949; Israelsson 1997). There are several serially sectioned specimens of both species at the SMNH (collected in 1915–1955) that have been available all this time. One specimen (collected in April 1944) contains numerous fertilized eggs and blastulae, another (September 1955) with a larva. I recently (April 1998) collected specimens
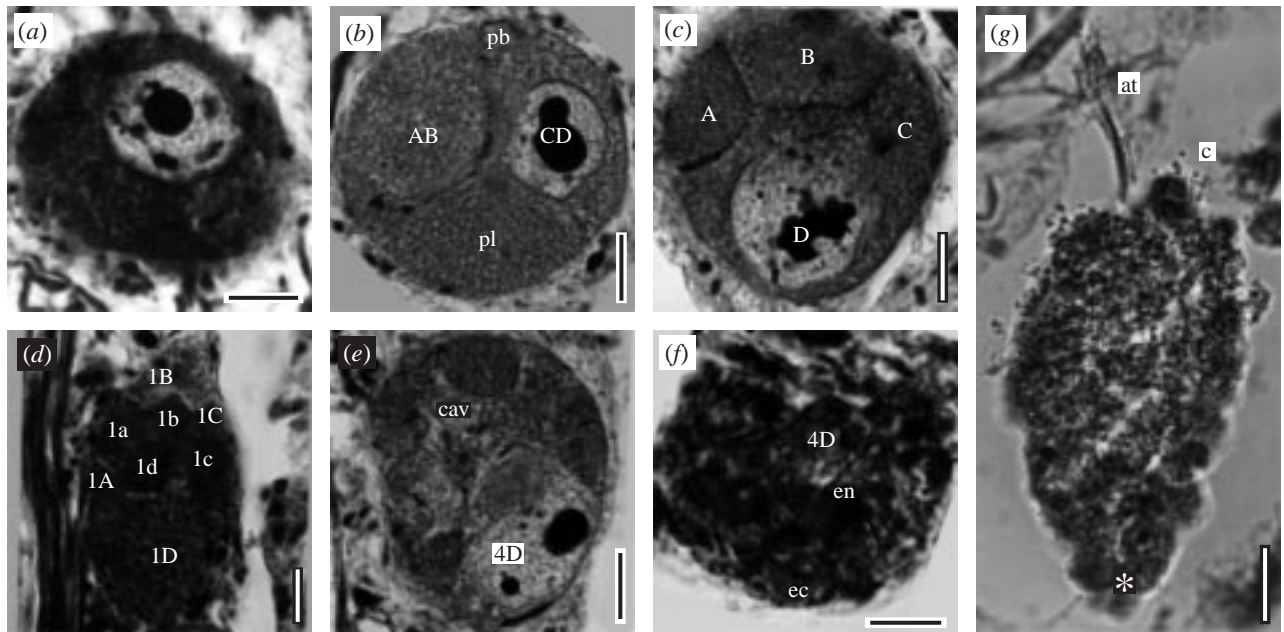
Figure 3. *X. westbladi*, new species. Early embryological stages. (*a*) Mature egg (section through the nucleus, actual length 55 μm). (*b*) Two-cell stage with two small polar bodies (pb) and a large polar lobe (pl). (*c*) Four-cell stage. (*d*) Eight-cell stage. (*e*) Stereoblastula with a large 4D surrounded by a cap of smaller cells; there is only a thin cavity (cav) within the blastula. (*f*) Gastrula. (*g*) Early trochophore larva with an apical tuft (at), a blastopore (not visible but its position indicated by an asterix); at least some of the cells bear cilia (c). ec, ectoderm; en, endoderm. Blastomeres CD, D, 1D, 2D, 3D, and 4D, respectively, are always larger than the other cells at each stage. (*a–e*) Collected in April 1943 between Blåbergsholmen and Lysekil, Gullmarsfjorden; (*f–h*) collected in April 1998 off Sydhällsö Island, Koster area. Scale bar, 10 μm.

off Sydhällsö Island with blastulae, gastrulae, and early larvae. Furthermore, I have been able to get *Xenoturbella* to mate spontaneously in a partly closed jar (they escape otherwise) without water circulation or any sediment (October l998). All specimens belong to *X. westbladi*.

In *X. westbladi*, all stages of the gametogenesis as well as the embryogenesis take place basally in the gastrodermis, or in the parenchyma enclosed inside the basal lamina of the gastrodermis. Even those that seem to be freely floating in the parenchyma are enclosed by the basal lamina. The oocytes (figure 3*a*) undergo vitellogenesis during summer–winter and mature into slightly telolecithal eggs in spring–summer. The spermatozoa are arranged in large bundles with their tails directed inwards and possibly forming spermatozeugmata. The sperm masses are transferred from the male to the intestinal cavity of females, where they probably enter into the parenchyma via ciliated openings through the gastrodermis were the fertilization may occur; these ciliated ducts are only present in females during the mating season. The spermatozoa inside the females are separate from each other. The fertilized egg changes shape from elongated to spherical and undergoes meiosis with the formation of two polar bodies, and a stereoblastula is formed through unequally holoblastically spiral cleavage with the presence of a polar lobe (figure 3*b–e*); there seems to be no molluscan cross. The blastula gastrulates (figure 3*f*) and develops further into an elongated cell mass with an apical tuft and a blastopore (figure 3*g*; larvae maximum 55 μm long). The cell mass grows and differentiates into a spherical, ciliated larva (figures 4*a*, 5 and 6; 180 μm in diameter) surrounded by a ciliated test

with an apical tuft, a hemicircumferal prototroch, and a ciliated lateral band on each side of the apical tuft; all trochs consist of two rows of ciliated cells. I have not found any telotrochs. The epithelial area behind the apical tuft consists of supporting cells (figure 2*b*) with intracellular supporting fibres surrounded by mucus glands, both structures being similar to those found in the epithelium of adults (Pedersen & Pedersen l988). The mouth is equatorial, the anus ventral. The pallial cavity is well-developed and the mantle skirt is thickened at its margin. There is a structure of unknown function (figure 5*b*, u) with ciliated cells and gland cells that might be a residual shell gland. The alimentary tract consists of a mouth, buccal cavity lined by the buccal musculature, foregut, midgut with the openings of the tubules of the digestive glands that occupy a large portion of the larva, hindgut partly lined by cuboidal epithelium, and anus. The respiratory, circulatory and reno-genital systems consist of: a single (right) ctenidium with six small gill filaments, of which the posterior ones are more developed than the others; a kidney surrounded by a thick layer of extracellular matrix; a pericardium (not shown in the figures) with a duct that opens into the kidney or externally close to it; and an epithelium of undifferentiated cells that may be the primordial gonad. The cerebral ganglion is connected to the pedal and pleural ganglion. The pedal area is formed by the pedal muscle, the pedal ganglia, and a statocyst without statoliths. There is a second structure that is histologically similar to the statocyst but opens through a duct, the opening of which is surrounded by single gland cells; it may the pedal (byssal) gland. Around the mouth there are large cells
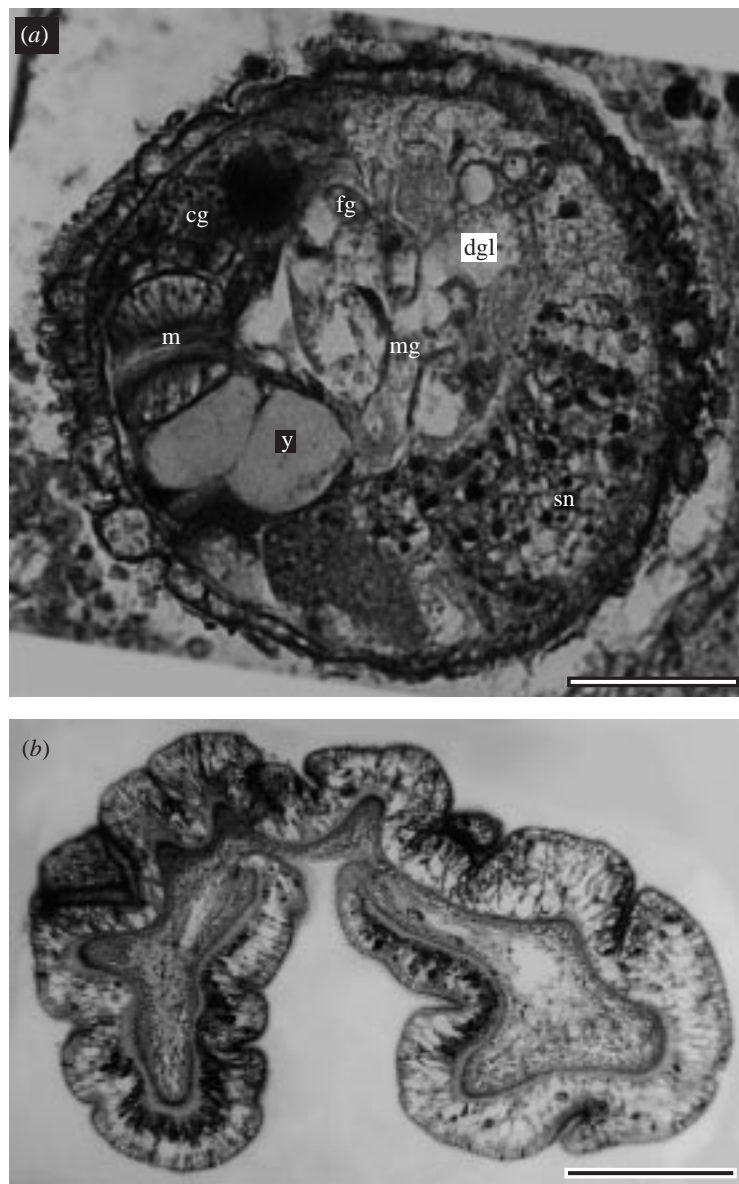
Figure 4. *X. westbladi*, new species. (*a*) Late trochophore larva, collected in September 1955, off Dröbak, Oslo Fjord. cg, cerebral ganglion; dgl, tubule of digestive gland; fg, foregut; m, mouth; mg, midgut; sn, stored nutrients; y, yolk. Scale bar, 50 μm. (*b*) Juvenile, collected in April 1943, between Blåbergsholmen and Lysekil, Gullmarsfjorden. Scale bar, 500 μm.

that are filled with condensed yolk. There is no post-anal organ; see Zardus & Pardus (1998) for a description of this organ. The digestive glands are surrounded by masses of different stored nutrients. All organs seem to be unpaired with a possible exception of the digestive glands. The (free-living) juveniles (2–3 mm long; figure 4*b*) do not differ morphologically from the adults except for some allometries such as that their mouth region is proportionally larger. Intermediates between the late larva and the free juvenile have not been observed.

## 4. DISCUSSION

Do the described larvae represent the embryology of *Xenoturbella* or are they larvae of another animal? I think that it is improbable that the described larvae do not belong to *Xenoturbella* since: (i) brooding is present—the larva develops inside the female within the membranes of the 'gonad' and separated from the exterior, therefore making an external contamination improbable; (ii) mating and early cleavage of the egg have been observed in living specimens and thus provide direct evidences of a link between the adult *Xenoturbella* and the early larva; (iii) different embryological stages are linked to each other with a simultaneous presence in the same individual (egg to blastula; blastula to gastrula; gastrula to early trochophore); (iv) the late larva is partly covered by an epithelium that is similar to that of adult *Xenoturbella* and that has not been described from any other animal (including the protobranch bivalve *Nucula sulcata*; O. Israelsson, personal observation), thus providing a morphological link between the late larva and the adult *Xenoturbella*; and (v) the juveniles do only possess allometric differences from the adults. Important data, such as on the transition of the early trochophore into the late larva, and the late larva into the juvenile, are
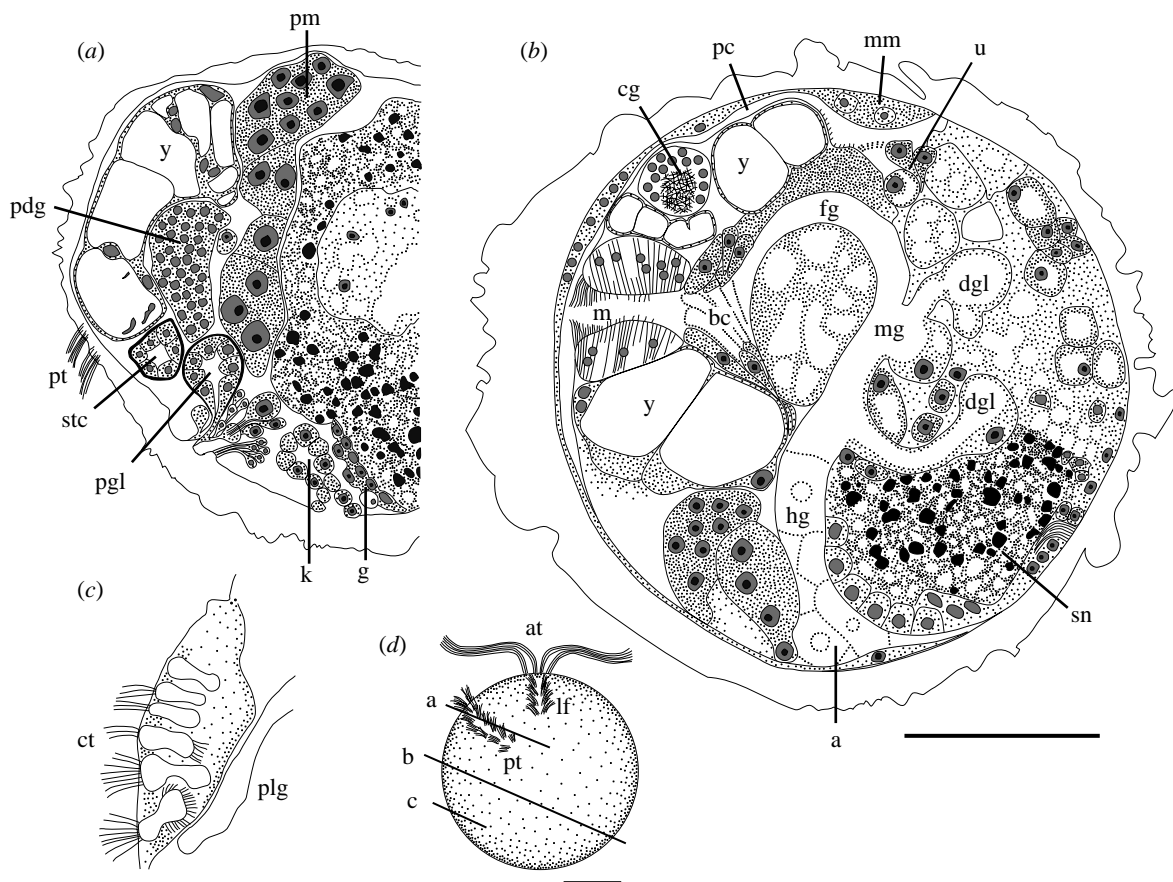
Figure 5. *X. westbladi*, new species. Reconstruction of the late trochophore larva. The sections are seen from below and their position shown in (*d*). Section (*b*) corresponds partly to figure 3*a*. a, anus; at, apical tuft; bc, buccal cavity; cg, cerebral ganglion; ct, ctenidium (gill); dgl, tubule of digestive gland; fg, foregut; g, gonad; hg, hindgut; k, kidney; lf, lateral ciliated field; m, mouth; mg, midgut; mm, mantle margin; pc, pallial cavity; pdg, pedal ganglion; pgl, possible pedal (byssal) gland; plg, pleural ganglion; pm, pedal muscle; pt, prototroch; sn, stored nutrients; stc, statocyst; u, structure of unknown function, might be a residual shell gland; y, yolk. Scale bar, 50 $\rmu m$.

lacking, and these would be very interesting to study. Unfortunately such a study requires a large number of specimens, since only about 10% of the collected specimens are fertilized females (during the mating season), and the females must be dissected and therefore killed (neither the sex nor the presence of larvae can be observed from the exterior). Although *Xenoturbella* is not rare, it is not common enough for collection of any large amounts. I have examined about 300 specimens of *X. westbladi*, i.e. about three times the number of *Xenoturbella* (both species) collected during 1915–1996. Nevertheless, I regard the present data as sufficient for concluding that the larvae actually are the larvae of *Xenoturbella*.

The late larva lacks metamerism and a hydropore, and has a large vertical muscle mass to the right of the alimentary tract (=foot), a gill composed of parallel filaments, a surrounding skin fold (=mantle skirt), and a sac-shaped nephridium (not protonephridium). These features, together with the organization of the nervous system, indicate a body plane that is different from that of trochophores of annelids (figure 6*c*), echiurids and sipunculids, the tornaria larva of enteropneusts (figure 6*d*), and the different types of flatworm larvae (Bresslau 1909; Harrison 1991, and references therein). It is most unlikely

that this type of larva could be present in a basal offshoot of the Metazoa. Instead, the late larva has numerous features that are characteristic of the trochophore (or pericalymma) larva of protobranch bivalves (figure 6*b*; Drew 1899, 1901; Gustafson & Lutz 1992; Gustafson & Reid 1986; Zardus & Morse 1998), such as the ciliation and general organization, and the presence and organization of mantle skirt, pallial cavity, stomach with tubular digestive glands, ctenidium, pericardium, nervous system, and pedal musculature with adjacent statocyst. However, it differs from protobranch bivalves by having only an unpaired ctenidium, ctenidial filaments that develops from posterior to anterior, nephridium, statocyst, and cerebral, pedal and pleural ganglia, and presumably lack of shell gland. The cleavage is unequal, involves formation of polar lobes, and does not result in a (distinct) molluscan cross. This pattern is typical for bivalves except for *Solemya* (Gustafson & Lutz 1992; Gustafson & Reid 1986; Verdonk & Van der Biggelaar 1983). The larva is covered by a test and does not possess a velum as do the veliger larvae of gastropods and bivalves. Furthermore, it lacks radula as in bivalves, in contrary to all non-bivalve molluscs. The larval morphology, as well as the early cleavage pattern, blastulation, gastrulation and early larva, clearly indicates that *Xenoturbella* is not only a
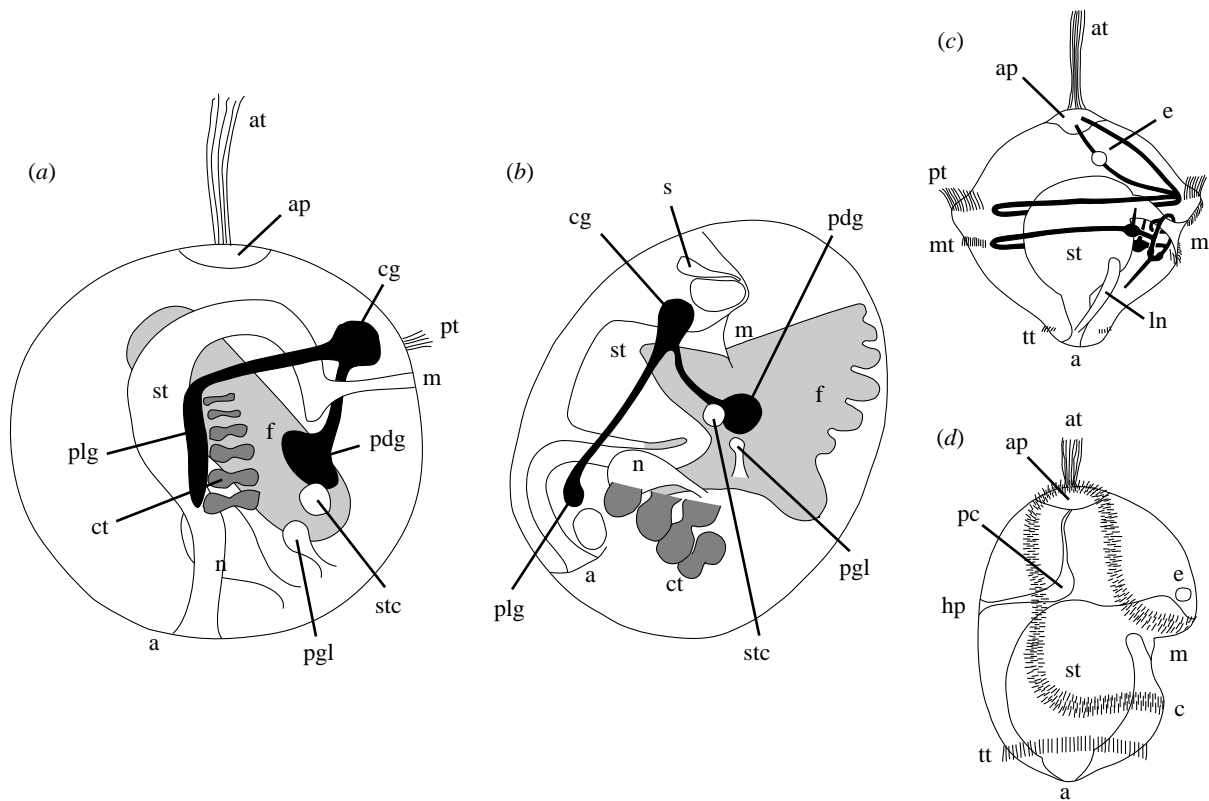
Figure 6. Larval types. (*a*) Late trochophore larva of *X. westbladi*. (*b*) Embryo of the protobranch *N. delphinodonta* (after Drew 1901). (*c*) Trochophore larva of a general annelid (after Dawydoff 1928, and Lacalli 1984). (*d*) Tornaria larva of a general enteropneust (after Stiasny 1914). a, anus; ap, apical plate or apical thickening; at, apical tuft; c, ciliated band; cg, cerebral ganglion; ct, ctenidium; e, eye; f, foot; hp, hydropore; ln, larval nephridium; m, mouth; mt, metatroch; n, nephridium; pc, protocoel; pdg, pedal ganglion; pgl, pedal gland; plg, pleural ganglion; pt, prototroch; s, Stempell's organ; st, stomach; stc, statocyst; tt, telotroch.
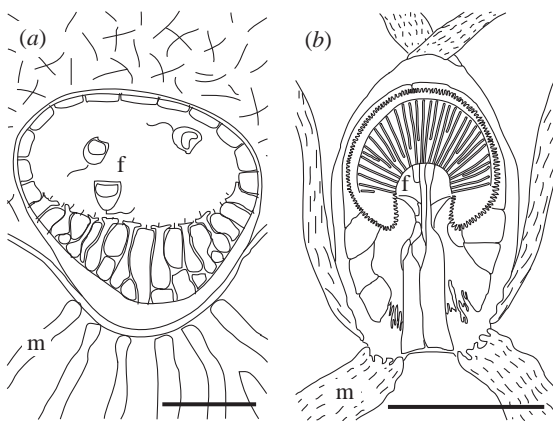


Figure 7. Sense organs. (*a*) 'Statocyst' of *X. bocki* (partly after Ehlers 1991). (*b*) Stempell's organ of *N. nucleus* (after Haszprunar 1985). f, flagellated cells; m, muscle fibres. Scale bar, 20 μm.

mollusc but also a protobranch bivalve that is more closely related to nuculanids and nuculids than to sole-myids. Similarities between *Xenoturbella* and molluscs have been discussed by earlier authors (Westblad 1949; Franzén 1956; Pedersen & Pedersen 1988) but the comparisons have never been carried to any actual conclusions.

Westblad (1949) described free oocytes in the intestinal cavity. These oocytes (O. Israelsson, personal observa-tion) are not mature and are probably accidentally released due to decomposition of gastrodermis that has

surrounded the oocytes. The eggs are about 15 times smaller in volume in the brooding *X. westbladi* than in the probably externally developing *X. bocki*. The late larvae of *X. westbladi* are much larger (approximately 35 times in volume) than the eggs; i.e. a much greater larval growth than reported from other protobranchs (Gustafson & Reid 1986). These proportions indicate a transfer of nutrients from the mother to the larva; there is material in the foregut that might represent this transfer. A poorly developed prototroch is shared with the brooding or directly developing *Solemya* (Gustafson & Lutz 1992; Gustafson & Reid 1986) and *N. delphinodonta* (Drew 1901) but not with other protobranchs (Drew 1899; Zardus & Morse 1998); it might be an adaptation to brooding. However, both *N. delphinodonta* and *Solemya* lack an apical tuft, a feature that is present in *Xenoturbella* and the plank-tonic developing protobranchs. The ctenidial filaments seem to develop from the posterior one anteriorly in contrast to *Nucula* were the inner filaments are first formed (Drew 1901). The possible lack of shell gland is unique among gastropods and bivalves; even the shell-less nudibranchs have larvae with shells. The late trochophore larva, described in this paper, is probably close to its metamorphosis into an adult; it has characters that develop late during the ontogeny of protobranchs (Drew 1901), such as the large pallial cavity, the ctenidium, and the well-developed connectives between the ganglia. However, the pedal musculature is less developed than in equally developed protobranchs. The trochophore larva must undergo a remarkably drastic metamorphosis from

its complex organization into an adult without the concentrated nervous system, renal organs, and all other defined organs. This is especially remarkable since *Xenoturbella* is neither a parasite nor microscopic, and probably not short-lived. The presence, in the larva, of epithelial cells similar to those in adults indicates that at least a part of the larval tissue will be included in the adult, i.e. that the adult is not formed fully *de novo* from undifferentiated stem cells. Nevertheless, there is a possible source of such cells. Organs that usually are paired in molluscs are unpaired in the larvae of *Xenoturbella*, and the cells that should have developed into the lacking half may remain undifferentiated until the time of metamorphosis. The lateral ciliated fields possibly form the lateral sense furrows.

The single 'statocyst' in the adult *Xenoturbella* is curious in that it does not contain ordinary statoconia or a statolith. Instead, it contains flagellated cells (figure 7*a*) that have been interpreted as symbiotic flagellates (Ehlers 1991). The organ is situated in the anterior end of the animal and is partly embedded in the subepidermal muscular layer (Westblad 1949). It does not resemble statocysts of molluscs since it is unpaired, its sensory epithelium is unequally thick and histologically different from that of molluscan statocysts, and its lumen contains flagellated cells that move randomly (and do not seem to be affected by gravity). Therefore, I find it more likely that this organ is homologous to the Stempell's organ in the Nuculidae (figure 7*b*), an unpaired mechanoreceptor situated dorsally to the anterior adductor muscle and which probably detects muscular tensions (Haszprunar 1985). Despite their obvious differences, they have features in common: flagellated cells, muscular connections, and asymmetry in the epithelial thickness.

Solving the systematic position of *Xenoturbella* does not make it less puzzling. Why would an animal that is neither parasitic nor microscopic nor short-lived lose all its organs and change its concentrated nervous system with ganglia to a loose network of neurons, especially when its larva has all the features the adult lacks? There is not known a single case in the free-living Mollusca (or any other protosome phylum) in which the nervous system dedifferentiates to a basiepidermal nerve plexus.

Note added in proof. Specimens of *X. bocki* were collected in December 1998 but they did not produce any larvae.

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