COI matrix (3,000 replicates with branch swapping, 5 random additions). Thus both data sets analysed independently and in combination support *Xenoturbella bocki* as a member of the Eutrochozoa.

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...and molluscan embryogenesis

Xenoturbella bocki Westblad[1] is a strange animal — a 2-cm-long, slowly moving ciliated bag with no anus and no organs except for a position-sensing statocyst containing flagellated statoconia[2]. Despite the animal's peculiarities, it has been neglected by most textbooks. I now report a study of oogenesis in *X. bocki* which, together with the nucleotide data of Norén and Jondelius[3], contradicts earlier hypotheses as to the phylogeny of the animal and instead suggests a molluscan relationship close to or within the protobranch bivalves.

Because of its simplicity in organization, *X. bocki* has been interpreted as one of the most primitive metazoa[4,5], a neotenous deuterostome[6], or a relation of acoelomorph flatworms[1,7], although the latter two hypotheses have recently been rejected[8,9]. Its proposed position as an early offshoot from the metazoans has brought *X. bocki* into the spotlight, as this might significantly influence our understanding of metazoan radiation and evolution. Norèn and Jondelius's study[3] of 18S ribosomal RNA and cytochrome oxidase I (COI) nucleotide sequences rejects all earlier hypotheses and suggests a molluscan relationship, perhaps a relationship with protobranch bivalves. Morphological data neither support nor reject this hypothesis[1,5,7,9–11].

The oogenesis of *X. bocki* has been described only briefly[1]. The oogonia have nuclei with a peripheral rim of heterochromatin and a single, homogeneous nucleolus. The chromatin becomes dispersed, and a previtellogenous oocyte is formed. Most oocytes continue to grow in the parenchyma, whereas others develop within the gastrodermis close to the parenchyma. The nucleus has amoeboid processes. After a growth period, the nucleus becomes rounded again and vacuoles are formed in the centre of the nucleolus. The nucleoli seem to migrate to the periphery before vitellogenesis.

The oocyte attaches to the gastrodermis, yolk granules begin to accumulate, and the nucleolus becomes homogeneously basophilic and disintegrates into numerous micronucleoli so that the main nucleolus completely disappears. The micronucleoli arrange around the periphery beneath the nuclear envelope opposite to the attachment area of the ovum (Fig. 1a), persisting until the ovum becomes mature. The mature ova, which were not found by Westblad[1], have irregularly rounded nuclei without any remaining nucleoli. There are no nurse or nutritive cells.

The arrangement of nucleolar vacuoles is similar to that of most molluscs and sipunculoids, and micronucleoli are known from different metazoans but not from placozoans, poriferans, cnidarians, or acoelomorph flatworms (refs 12, 13 and references therein; data not shown). However, they are dissolved before the end of vitellogenesis or, if they persist, they remain scattered within the nucleus or along the whole nuclear envelope. In protobranch bivalves on the other hand, in which oogenesis has not yet been described, as well as a main nucleolus, micronucleoli are present and are arranged along one end of the germinal vesicle. They also persist throughout vitellogenesis (Fig. 1b). This character is a synapomorphy that is shared exclusively by *Xenoturbella* and Protobranchia (Fig. 2).

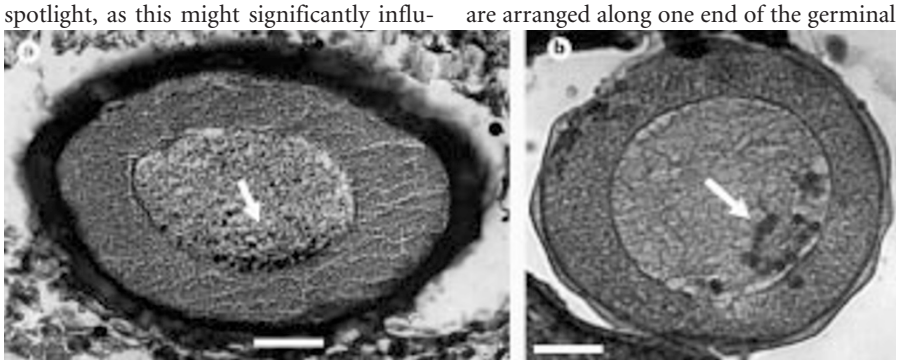

Figure 1 Relationship of *Xenoturbella bocki* to molluscs. Late vitellogenous oocytes of **a,** *Xenoturbella bocki* and **b,** the protobranch mollusc *Nucula nucleus*. Scale bars, 20 μm.

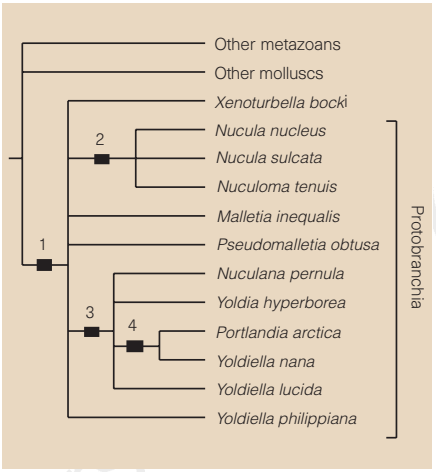

Figure 2 Cladistic analyses of oogenesis indicates that *Xenoturbella bocki* is a sister group or a subgroup of protobranch bivalves. The analysed characters, with their apomorphic states, are: **1,** micronucleoli migrate at one end of the germinal vesicle; **2,** few, large micronucleoli; **3,** chromatin is not scattered but accumulated at the same end as the micronucleoli; and **4,** large, red lipid droplets are present in the ooplasm. The molluscan data include information from refs 12, 13, and references therein, and from observations of 2 caudofoveatans, 3 solenogastres, 2 polyplacophores, 29 gastropods, 3 scaphopods, and 24 bivalves.

The oogenesis and nucleotide data are not fully conclusive by themselves but in combination they provide concordant morphological and molecular data showing that *Xenoturbella bocki* is neither a sister group of Bilateria nor from any other basal metazoan group but is a mollusc related to or within Protobranchia. This conclusion is drawn from apomorphies and not plesiomorphies and autapomorphies as earlier hypotheses. Further investigation, especially of embryology and biology, is needed for a complete understanding of *X. bocki.*

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