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A rhabdocoel turbellarian (Platyhelminthes, Typhloplanoida) in Baltic amber with a review of fossil and sub-fossil platyhelminths

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Abstract. *Palaeosoma balticus* n. g., n. sp. (Rhabdocoela, Typhloplanoida), the oldest body fossil of a turbellarian and the first representative of the phylum Platyhelminthes found in fossilized resin, is described from Baltic amber 40 million years old. Characters of the fossil turbellarian are epidermal cilia, rhabdoids, a rosulate pharynx, adhesive papillae, and sensory bristles. The body cavity contains developing eggs or capsules. The fossil demonstrates that rhabdocoels had developed a terrestrial habit and were producing subitaneous eggs by the Eocene. A summary of the fossil and sub-fossil records of platyhelminths is presented.

Additional key words: fossil flatworm, microturbellarian

The phylum Platyhelminthes, considered by some as the most primitive of the bilaterally symmetrical animals (Hyman 1951), has an almost non-existent fossil record (Wills 1993). The paucity of platyhelminth fossils has made determining the relationships within the phylum especially difficult and subsequently based solely on morphology and molecular methods (Carranza et al. 1997). The Rhabditiphora is considered to be a monophyletic clade that branched early in the evolution of the protostomates (Carranza et al. 1997). These flatworms are mostly marine and free-living, although a number inhabit freshwater and some have adapted to terrestrial life. They are ovoid to elongate, dorso-ventrally flattened animals, which lack a definitive anus and have a ciliated, cellular or syncytial epidermis.

Amber is known for its ability to preserve soft-bodied inclusions that normally escape other modes of fossilization. Thus, nematodes, rotifers, tardigrades, annelids, and even amebas can be found in an excellent state of preservation in this medium (Poinar 1992). Here, I report that a small, flattened, appendage-less, soft-bodied invertebrate fossil from Baltic amber possesses a ciliated epidermis, rhabdoid tracts, sensory hairs, and a rosulate pharynx and thus appears to be a turbellarian. No other invertebrate is known to have this combination of characters. The fossil resembles extant terrestrial forms in the microturbellarian order Rhabdocoela. I describe this specimen, discuss its significance, and summarize the fossil record of the Platyhelminthes.

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Methods

The piece of light brown amber containing the turbellarian originated from the Kaliningrad region in Russia. The amber was re-cut and polished in order to better view the specimen. Baltic amber has been dated at ~40 million years (Eocene) (for a discussion of the age of these deposits, see Poinar 1992 and Larsson 1978). Observations and photographs were made with a Nikon Optiphot microscope and a Nikon SMZ-10 stereoscopic microscope at magnifications of 400×.

Results

The fossil represents a complete specimen. The presence of a ciliated epidermis, prominent rhabdoid tracts, pharynx rosulatus, ventral mouth, absence of a permanent sheathed proboscis, single gonopore, and terrestrial habits places the fossil in the Typhloplanoida (Hyman 1951; Cannon 1986; Kolasa 2001). Because, on the basis of the available characters, the fossil could not be placed into an existing genus, it is described below in a new genus and species.

Taxonomic account

Order Rhabdocoela Graff 1904
Suborder Typhloplanoida Graff 1908
Palaeosoma n. g.

Diagnosis: Small forms <3 mm long; body shape ovoid, slightly narrower at anterior end; body covered with cilia (best observed along body edges); with prominent rhabdoids and rhabdoid tracts often orientated with long axis parallel to or at oblique angles to

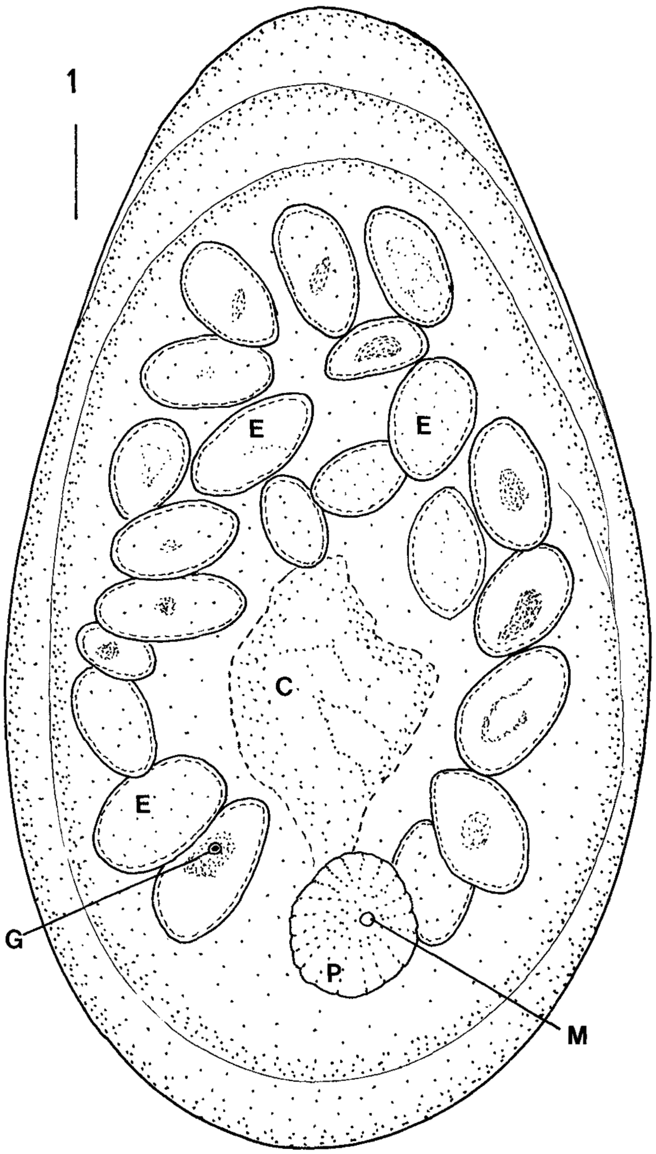


Fig. 1. *Palaeosoma balticus* n. g., n. sp. Ventral view showing mouth (M), pharynx (P) (dorsal to mouth), gonopore (G), collapsed gut (C), and subitaneous eggs (E). Presumed anterior end at top. Scale bar, 134 μm.

body surface; adhesive papillae and sensory hairs present; eggs in mesenchyme; mouth ventral, rosulate pharynx dorsal to mouth; pharynx, gut, and gonopore in posterior portion of body.

Etymology: "Palaeo" is Greek for old or ancient and refers to the fossilized condition of the specimen.

Palaeosoma balticus n. sp. (Figs. 1–7)

Body color tan; L = 1.54 mm; greatest width = 0.85 mm; body flat, widest in center; with numerous rhabdoids and rhabdoid tracks; cilia at body edges 5–9 μm long, cilia tracks present in amber adjacent to body; rosulate pharynx roughly spherical in shape, with greatest diameter = 189 μm; gut collapsed, pharynx dorsal to mouth; mouth posterior, located above pharynx on ventral surface of body, 315 μm from posterior end, leading dorsally into pharyngeal cavity; posteriorly located gonopore positioned on right side of body, opening on ventral surface of body ~220 μm from mouth; sensory hairs and adhesive papillae present; shape of rhabdions variable, many curved, 3–5 μm long; reproductive and excretory organs not discernable; body filled with eggs of various sizes and shapes, ranging 126–202 μm long (mean = 173 μm, n=10) and 75–140 μm wide (mean = 110 μm, n=10); eyes not detected.

Type locality: Baltic amber from Kaliningrad dated at ~40 million years (Eocene).

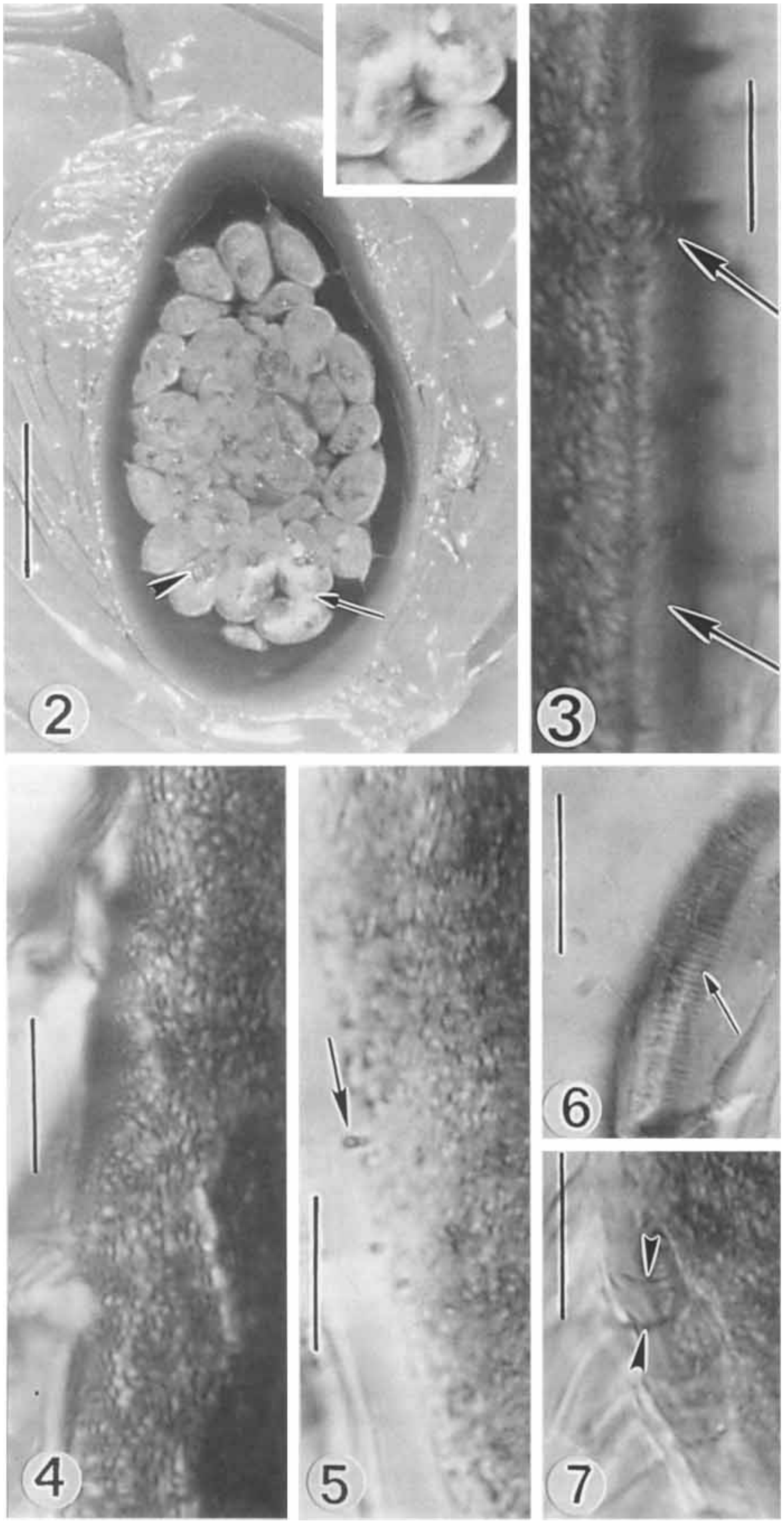
Holotype: Accession number PT-3-1, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, USA.

Etymology: "Balticus" refers to the region of origin of the fossil.

Notes: The specimen is in good condition. Folds along the contour of the body and impressions of cilia in the resin adjacent to the body suggest that it had contracted upon contacting the resin. Thus, when alive, its length may have been slightly greater.

Because no sexual or excretory organs are discernable (these and other characters appear to be obscured by the eggs), the family status cannot be determined and placement in the Typhloplanoida is based on the discernable morphological characters and terrestrial habit. The size and shape of the body, posteriorly located pharynx, location of mouth and gonopore, presence of sensory hairs, and curved rhabdoids mostly orientated with their long axis parallel to or at oblique angles to the body surface are characters which, taken together, are not characteristic of other genera of Typhloplanoida (Graff 1908; Reisinger 1924; Hyman 1951; Cannon 1986; Kolasa 2001). The absence of eyes makes determination of body orientation of the fossil difficult. The anterior end was determined by the presence of sensory hairs (Fig. 7), structures that supposedly occur only on the head end of the animal (Hyman 1951). It is not uncommon to have the pharynx and mouth in the posterior portion of the body in typhloplanoids (Cannon 1986).

A posteriorly located, off-center gonopore also occurs in members of the genera *Tensopharynx* EHLERS and *Acrumena* KARLING (Cannon 1986). The fossil appears most similar to *Olisthanellinella rotundula* REISINGER (1924), a terrestrial species with the pharynx also located in the posterior third of the body; however, this species is much smaller than the fossil, with



Figs. 2–7. *Palaeosoma balticus* n. g., n. sp. in Baltic amber. **Fig. 2.** Ventral surface showing subitaneous eggs, gonopore (arrowhead) and area of pharynx (arrow). Scale bar, 330 μm. Insert shows higher magnification of pharynx. **Fig. 3.** Edge of body showing cilia (arrows). Scale bar, 20 μm. **Fig. 4.** Edge of body showing rhabdoid tracts. Scale bar, 20 μm. **Fig. 5.** Adhesive papilla (arrow). Scale bar, 20 μm. **Fig. 6.** Cilia tracks (arrow) in amber adjacent to fossil. Scale bar, 20 μm. **Fig. 7.** Sensory hairs (arrowheads) along anterior edge of body. Scale bar, 20 μm.

Table 1. Fossil and sub-fossil* records of Platyhelminthes (in increasing age).

Fossil	Age	Substrate	Location	Reference
Bothriocephelus, eggs	1500 yrs	Bog cadaver	Germany	Szidat 1944
Dicrocoelium, eggs	~2,000 yrs	Roman remains	England	Taylor 1955
Diphyllobothrium, eggs	~4,000 yrs	Indian coprolite	Peru	Callen & Cameron 1960
Turbellarian eggs	Holocene-Pleistocene	Lakes	USA	Frey 1964
Turbellarian eggs	Holocene-Pleistocene	Lakes	England	Harmsworth 1968
Schistosoma, eggs	5,000 yrs	Mummies	Egypt	Ruffer 1910
Schistosoma, DNA	5,000 yrs	Mummies	Egypt	Deelder et al. 1990
Dicrocoelid eggs	5,500 yrs	Bear coprolites	France	Jouy-Avantin et al. 1999
Metacercarial pits	Eocene-Holocene	Bivalves	World-wide	Ruiz & Lindberg 1989
Turbellarians	Miocene	Calcareous nodules	California, USA	Pierce 1960
Palaeosoma balticus	Eocene	Amber	Northern Europe	present study
Terricolichnus permicus	Permian	Locomotion trail	Italy	Alessandrello et al. 1998
Cestode eggs?	Pennsylvanian	Shark	USA	Zangerl & Case 1976
Platyhelminth?	Devonian	Hooks in fishes	Latvia	Upeniece 2001

* Subfossil refers to specimens <10,000 years old.

a body length of only 0.5 mm and the pharynx diameter 46–50 μm.

Many isolated rhabdoids occur in the amber adjacent to the specimen. These presumably were discharged from the worm when it made contact with the resin, because turbellarians, when placed in harmful solutions, lose their rhabdoids (Hyman 1951). The presence of epidermal cilia is supported by fine ciliary tracks present in the amber adjacent to the specimen (Fig. 6). When first contact was made with the resin, the specimen appears to have contracted, which would be a natural reaction of any soft-bodied invertebrate to an irritating environment. The cilia made fine impressions in the amber as they were drawn across the resin when the body contracted.

Discussion

The specimen described is the oldest body fossil of a turbellarian and the first representative of the phylum Platyhelminthes found in fossilized resin. The body measurements of the fossil fall within the known size range of living typhloplanoids, which range from less than a millimeter to several millimeters long (Reisinger 1924; Hyman 1951; Cannon 1986).

Members of the Typhloplanoida, which include most of the terrestrial rhabdocoels, produce 2 types of eggs (or capsules)—thin-shelled (subitaneous) and/or thick shelled (dormant) (Fiore & Ioale 1973). Based on the variability in size and shape of the eggs (or capsules) and in part on their relatively thin shells, the eggs in the fossil are considered to represent subitaneous eggs. Eggs of this type, which are self-fertilized and carried in the uteri or mesenchyme, develop directly into young worms that leave by rupturing the parent's body. Subitaneous eggs appear to be an adaptation for rapid multiplication during favorable climatic conditions. The fossil specimen may not have attained full sexual maturity since subitaneous eggs can be produced before the animal has reached this state (Hyman 1951).

Palaeosoma balticus n. g., n. sp. probably lived under logs or leaves in the amber forest and came out at night to feed. Nematodes are a favorite food item for small typhloplanoids (Sayre & Powers 1966), and free-living nematodes have been reported from Baltic amber (Poinar 1992). Most extant terrestrial turbellarians are limited to tropical or subtropical habitats with high humidity because they are unable to mature sexually under cool or cold conditions (Hyman 1951). Such conditions prevailed in the Baltic amber forest when the resin was forming some 40 million years ago (Eocene) and the climate in northern Europe was subtropical (Larsson 1978; Prothero 1994).

The fossil demonstrates not only that typhloplanoid microturbellarians had developed a terrestrial habit some 40 million years ago but that ovoviviparous development of subitaneous eggs had been established by that time and may have been the dominant method of reproduction, especially if dormant eggs evolved as a result of climatic cooling that followed during the Oligocene (Prothero 1994).

Review of fossils of Platyhelminthes

Although platyhelminth remains are rare, 2 categories have been reported, trace and body fossils (Table 1). Trace fossils include metacercarial pits in bivalve shells (Ruiz & Lindberg 1989), locomotion trails in sandstone (Alessandrello et al. 1988), and schistosome antigen in mummies (Deelder et al. 1990). Body fossils are represented by eggs (and/or cocoons) in archaeological sites (Taylor 1955), coprolites (Jouy-Avantin et al. 1999), mummies (Ruffer 1910), and lakes (Frey 1964; Harmsworth 1968), as well as in marine vertebrates (Zangerl & Case 1976; Upeniece 2001). Remains of post-embryonic forms include, aside from the present report, representatives of the Planariidae and Rhynchodemidae in calcareous nodules (Pierce 1960). The 2 reports concerning fossil cestodes need further study—namely the egg-like objects found in a Paleozoic shark (Zangerl & Case 1976) and circles of hooks found associated with Upper Devonian fishes (Upeniece 2001). In reviewing the former record, Boucot (1990) included a statement that the urea-rich environment of a dead shark would probably autolyse such eggs and considered the report as fairly speculative. It is still unclear whether the hooks in the Devonian fishes belong to a platyhelminth or to an acanthocephalan.

In summary, the fossil record of turbellarians is indeed quite sparse, being limited to some subfossil egg cases, 1 trace fossil, and 2 representatives in calcareous nodules. The present specimen in Baltic amber is the oldest, most complete, and best-preserved fossil representative of the Platyhelminthes.

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