

Placozoa

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Placozoa is a phylum of multicellular animals that are only a few mm in diameter and are continuously changing shape by forming folds at the dorsal surface. Its natural habitat is seawater.

Basic Design

The phylum Placozoa was established in 1971 comprising only two genera and species: *Trichoplax adherens* and *Treptoplax reptans*. Morphologically, its main feature is dorsoventrality. The animal is described as a plate measuring 2–3 mm in diameter, lacking polarity, defined organs or bilateral symmetry, and continuously changing shape by forming folds at the dorsal surface. As the name ‘adherens’ indicates, it attaches to the surface of the vessel in which it is contained (Figure 1).

Histologically primitive compared with other metazoa (multicellular animals), *T. adherens* has no defined nervous or muscular system. It is composed of three layers of cells: two epithelia (dorsal and ventral) and a central region

(interspace) of fluid and ‘star-shaped’ cells termed the mesenchyme.

The dorsal epithelium is seen as a monolayer of flattened, flagellated cells. Their nucleus is localized in sac-like inward protrusions. Proximal to the cell surface several vesicles are observed, and ‘shiny spheres’ comprised of lipid are found regularly dispersed in deep inclusions of the dorsal epithelium.

The ventral epithelium, thought to be responsible for nutrition, is composed of cylindrical cells – flagellated and nonflagellated (gland cells). The higher density of flagella on this epithelium is the result of the tight packing of the cylindrical cells. As in the dorsal epithelium, the nuclei of cells constituting the ventral epithelium are located away

Introductory article

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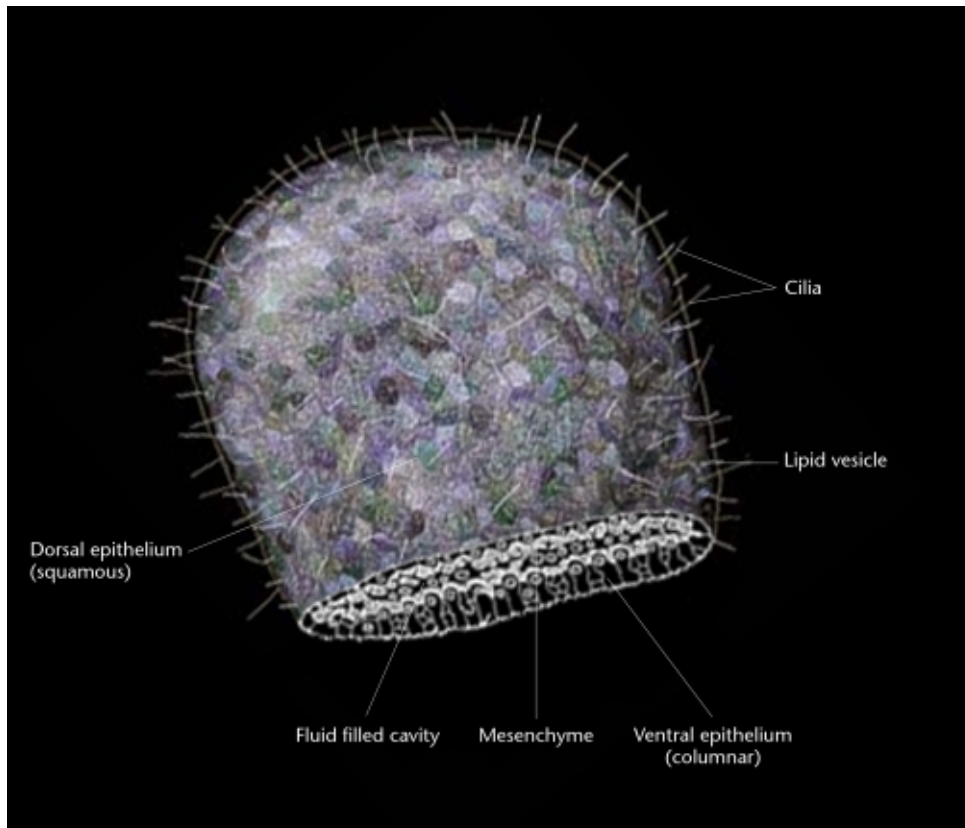


Figure 1 Drawing of *T. adherens* (adapted from Wim van Egmond).

from the outer cellular membrane. The gland cells are filled with secretory vesicles that presumably produce and export enzymes for the extrasomatic digestion of food organisms.

The interspace between the dorsal and ventral surfaces is filled with fluid and fibre (star-shaped) cells. The fibre cells are connected with cells on each epithelium and to one another. The fibre cells composing this primitive mesenchyme form a syncytium in which zones of cytoplasm are separated from one another by osmophilic discs and the plasma membranes are continuous. It has been proposed that these disc-like structures connecting each fibre cell may represent primitive synapses (prosynapses). Another peculiar feature of the fibre cells is their contractile capacity, which, if acting in coordination, may be responsible for the changes in shape of the organism and folding of the dorsal epithelium. These observations suggest that fibre cells are primitive motor nerve cells.

Diversity and Lifestyle

The phylum Placozoa has not been carefully studied in its natural habitat, seawater. Little is known about *T. reptans*, whose existence has been put in doubt since it was observed only once in seawater off the Gulf of Naples. *T. adherens* is found in seawater of tropical and subtropical regions, and was first discovered in a seawater aquarium. Although nothing is known about its biology in the natural habitat, *T. adherens* can be cultivated in the laboratory. This has enabled its biological and histological features to be studied in great detail.

T. adherens is a free-living animal, probably a scavenger. In laboratory conditions it feeds on protozoans such as *Cryptomonas*. In its natural habitat it may live on more varied organisms. It has been observed that protozoans in contact with the dorsal epithelium remain intact, while protozoan cells on the ventral side appear as dissolved remnants of the original organism. The absorption of predigested nutrients seems to be effected by pinocytosis through coated vesicles of the ventral cells. Interestingly, the organism has been observed contracting its ventral surface, elevating from the surface, and forming a ventral 'digestive bag' where extrasomatic digestion may occur more effectively. The formation of this digestive bag has been proposed as a model for a primitive form of archenteron.

The most common mode of reproduction is by asexual binary fission, somewhat resembling that of *Amoeba*; the two daughter organisms remain attached to each other for a long time. Agglomerations of organisms have been observed as 'swarmers', formed by the budding of daughter organisms. The mechanism of bud formation is not known and may result from the artificial conditions present in laboratory cultures.

Under specific conditions, related mostly to population density, oocytes may develop in *T. adherens*. In nature this may be a consequence of several factors such as the seasonal changes in salinity, light, temperature and availability of nutrients. Some evidence has accumulated indicating that the oocyte is derived from the ventral epithelium. There is usually only one oocyte per animal, it may reach a diameter of about 120 µm. It is formed from different types of yolk granules and a nucleus containing a large and occasionally vacuolated nucleolus. Reaching the final stage of development, the oocyte migrates to the periphery, with a simultaneous contraction of the ooplasm and the formation of a 'fertilization membrane'. The oocyte is released when the animal degenerates. Oogenesis can be stimulated only during the degenerative phase of the animal. In this condition, a large number of nonflagellated cells of approximately 3–4 µm in diameter are observed in the mesenchyme and are postulated as being the sperm cells. It has not been possible to determine from which somatic cell they derive; however, fibre cells appear to be involved in their differentiation.

Fossil Record and Phylogeny

The origin and evolution of metazoa has been debated with considerable intensity over the years. It is generally accepted that metazoa were derived from Protozoa about 700–1000 million years ago. However, lower metazoan phyla have insufficient morphological homology, the palaeontological record is scant, and there are few indications of the transition from Protozoa to metazoa. Several authors have concluded that the metazoa form a monophyletic taxon with two diverging branches: the diploblasts, which evolved during the Vendian radiation soon after the multicellular animals derived from Protozoa, and the triploblasts, which appeared later during the Cambrian explosion.

Placozoa have the most rudimentary histological organization of all metazoa, and a simpler somatic structure than the majority of Porifera, Ctenophora and Cnidaria larval stage. Only four types of somatic cell are present, comprising the dorsal, ventral and mesenchyme-like interspace. Muscle or nervous systems are lacking, although these functions may be simultaneously satisfied by the interspace syncytium. Whether the primitive aspect of *T. adherens* is an original or derived character remains under debate. The first assumption gains support based on the free-living lifestyle, as a parasitic stage leading to secondary simplification is absent. There is a possibility that *T. adherens* is derived from a spongiaria larval stage, although this seems unlikely.

Recently, a study of 18S ribosomal ribonucleic acid (rRNA) sequences strongly suggested that Placozoa, Bilateria and Cnidaria form a clade, excluding Ctenophora

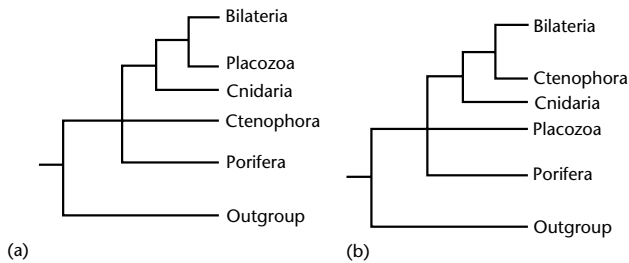


Figure 2 Alternative trees for the evolution of metazoa. (a) Tree supported by parsimony and minimum evolution of 18S ribosomal ribonucleic acid (rRNA). Modified from Collins (1998). (b) Competing phylogeny based on morphological characters and simplicity arguments. Modified from Grell and Ruthmann (1991).

and Porifera (**Figure 2a**). Analysis supported by parsimony and minimum evolution indicates Placozoa as a sister group to Bilateria, and maximum likelihood analysis supports a cnidarian–bilaterian relation to the exclusion of Placozoa. Earlier studies suggested Ctenophora to be a sister group to Bilateria. The simplicity of the Placozoa has also argued to the positioning of this phylum as basal to Cnidaria, Ctenophora and Bilateria (**Figure 2b**). The 18S rRNA data contradict these hypotheses and suggest that the derived features shared by Ctenophora–Bilateria either arose independently or were lost in the Cnidaria–Placozoa. Moreover, the simplicity of Placozoa is suggested as a secondary character.

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