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## Abstract

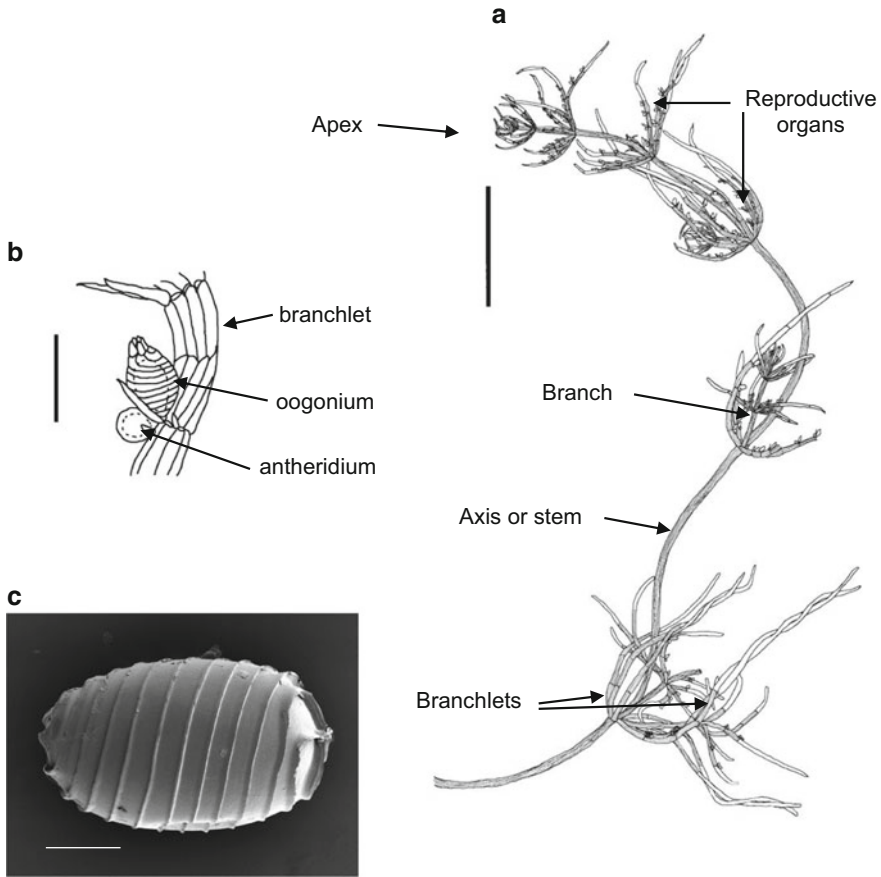
The aim of this chapter is to give physiologists a thorough grounding in the morphology, taxonomy and ecology of the characean plant. The morphology of characean plants is depicted and explained, with specific examples of the morphological characteristics of different species or species groups that are used in physiological studies. The details of characean cellular structure in growing plants and in the reproductive organs are reviewed. The history of taxonomy and nomenclature is outlined, along with the most recent approaches to systematics (and what name to use for characean plants in physiological studies), and finally the patterns of characean plant distribution and requirements for growth in natural situations are explained and related to the culture and growth of characean plants for physiological studies.

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## 1.1 General Morphology

The characean thallus (or plant body) is similar in appearance and size to the plant body of other submerged plants such as *Ceratophyllum* or *Myriophyllum*. Characean plants consist of long photosynthetic stem-like structures (axes) anchored in the soil, with whorls of leaf-like organs (branchlets) along the stem (Fig. 1.1a). Close examination reveals that the structure of characean plants is very different to that of flowering plants. Instead of roots they have colourless rhizoids, instead of leaves they have whorls of branchlets of limited growth, instead of stems they have an axis of giant cells joined end on end and instead of flowers and fruit they have relatively simple reproductive structures (the oogonium and antheridium, Fig. 1.1b) that produce gametes. The product of fertilisation of the gametes is an oospore (Fig. 1.1c) rather than a seed.

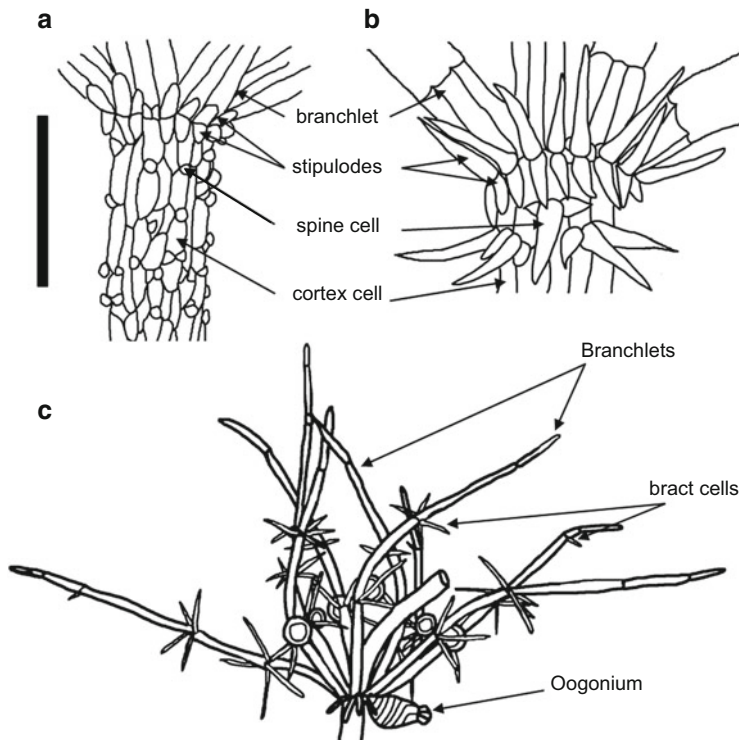
The thallus of characean plants is essentially filamentous. The axes (stems) are made up of long, multinucleate, single cells interrupted by multicellular nodes (Fig. 1.2). There is no development of tissues such as parenchyma, although the axial nodes approach such an arrangement (Sect. 4.3). Several organs of limited



**Fig. 1.1** Thallus of a characean plant (*Chara* sp. r862). (a) Stem showing whorls of branchlets, scale bar = 10 mm. (b) Reproductive organs, scale bar = 1 mm. (c) Scanning electron micrograph of an oospore of *Chara* sp. (r862), scale bar = 200  $\mu$ m

growth (branchlets, stipulodes and cortical filaments) arise in whorls at the nodes (Fig. 1.2). Branchlets are the “leaf-like” organs that occur in spreading whorls, and below these there are often whorls of smaller cells called stipulodes. In many species of *Chara*, the stipulodes occur in two whorls, the upper whorl pointing upwards and the lower whorl pointing downwards (Fig. 1.2a, b). In the genera *Lamprothamnium* and *Tolypella*, and some species of *Chara*, the axial node can also be the site of gametangial development (Fig. 1.2c).

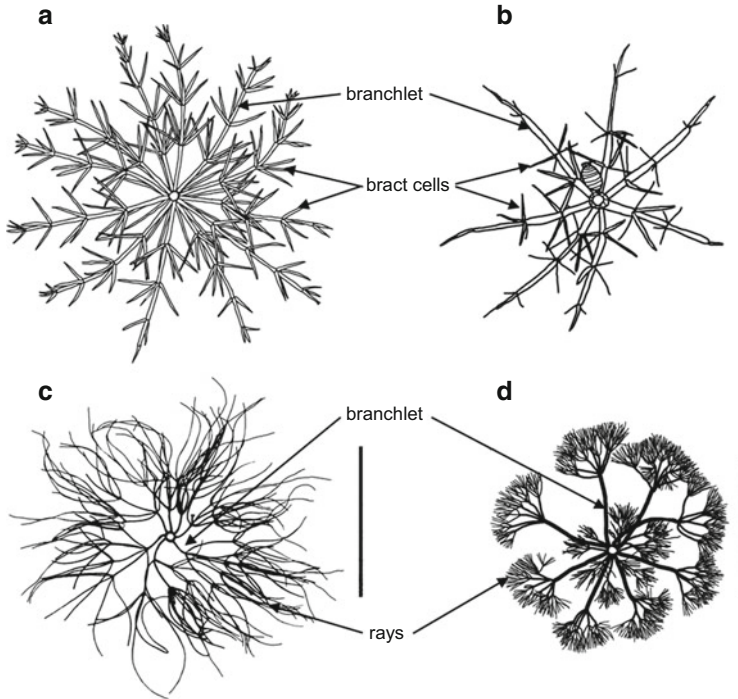
Branchlet arrangement (Fig. 1.3) and morphology (Fig. 1.4) varies among the genera but is characterised by elongate multinucleate cells interrupted by multicellular branchlet nodes. Other cellular structures can be produced at the branchlet nodes, namely bract cells (Figs. 1.3a, b, and 1.4a, b), secondary and tertiary (*et seq.*) branchlet segments or rays (Figs. 1.3c, d, and 1.4c, d), cortical filaments (Fig. 1.4a) and gametangial initials (Fig. 1.4). Some species of *Chara* have elongate bract cells



**Fig. 1.2** Characean axial nodes. Scale bar = 1 mm. (a) *Chara* sp. (r822) node with two rows of stipulodes, short cortical cells and small spine cells. (b) *Chara canescens* (r020) node with longer stipulodes and spines cells. (c) *Lamprothamnium* sp. (r870) with no cortication, oogonium and stipulodes below the base of the whorl, and spreading bract cells at the branchlet nodes

in whorls (verticillate) at the branchlet nodes, as well as at the apices of the branchlets (Fig. 1.3a). Other species produce unilateral bract cells (Fig. 1.4a). *Lamprothamnium* exhibits the same overall branchlet morphology as *Chara*, but the bract cells are generally inserted at angles of 45–90° to the branchlet, forming a “cage-like” structure around the nodal complexes (Figs. 1.3b and 1.4b). *Nitella* species have branchlets that are divided or forked (furcate) into separate rays or segments (Fig. 1.4c), which can be very evenly arranged (Fig. 1.3d) or irregular (Fig. 1.3c). Some species of *Nitella* can produce more than one whorl of branchlets at the nodal complexes, a condition referred to as “heteroclemous” (Fig. 1.3d). *Tolypella* branchlets are different from those in other genera, usually with a central pluricellular ray, secondary rays and clusters of gametangia (Fig. 1.4d).

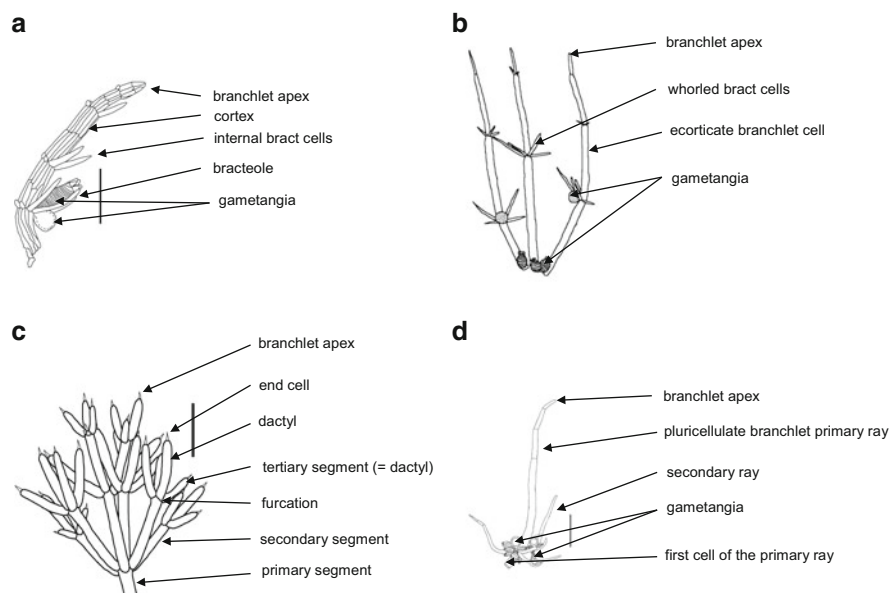
The gametangial initial cell produces the gametangia (oogonia and/or antheridia), bracteoles and sometimes a bractlet (Fig. 1.5). Oogonia have a striped appearance with a small but distinctive crown of cells (coronula) at their apex. Oogonia vary in colour from green to bright orange, and in older parts of the thallus the fertilised oospore within the oogonium becomes darker as it matures. The antheridia can also be green, but are often orange to red in colour, and in dioecious



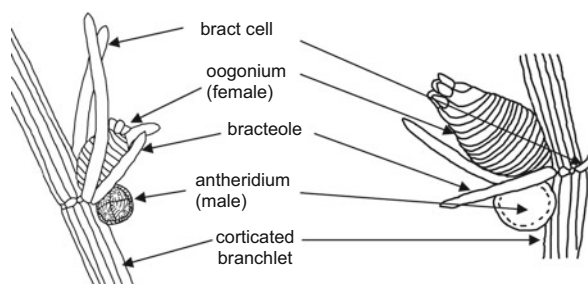
**Fig. 1.3** Whorls of characean branchlets viewed in cross section, with the branchlets spread around the sectioned node. (a) *Chara gymnophytis* whorl with 12 branchlets in a whorl, 12 stipulodes at the base of the whorl, long bract cells at each branchlet node and branchlets terminated by a group of bract cells. (b) *Lamprothamnium* sp. aff. *macropogon* with seven branchlets in a whorl, no apparent stipulodes, long bract cells at the branchlet nodes and an oogonium at the base of the whorl. (c) *Nitella* sp. with seven branchlets in a whorl, the branchlets divided into 3–5 secondary rays and 3–5 tertiary rays. (d) *Nitella hyalina* with two whorls of branchlets at the node (a longer, primary whorl of eight branchlets, and a smaller, inner, secondary whorl of seven branchlets), with the branchlets divided into 3–6 secondary rays, 3–5 tertiary rays and 3–4 quaternary rays, scale bars = 5 mm

species can be so large (approaching 1 mm in diameter) as to be mistaken for “berries” on the branchlets. The gametangia (oogonia and antheridia collectively) are often surrounded by bracteoles (that arise from the base of the gametangia) and bract cells (that arise from the branchlet node). These can be longer (Fig. 1.5a) or shorter than the oogonium (Fig. 1.5b). A bractlet can occur at the base of the oogonium in female dioecious plants instead of an antheridium.

The distinctive characteristic of the characean thallus is that all of the parts consist (with the exception of the gametangia and nodes) of single cells or uniseriate filaments of cells. A notable characteristic of some characean species is the development of a coating of calcium carbonate, “marl” or “lime”, when growing in hard-water lakes or streams. In general, species of *Lamprothamnium*, *Tolypella*, a few species of *Nitella* and corticated species of *Chara* can develop a calcareous layer on the thallus and/or a calcified coating on the oospore (called a lime-shell or gyrogonite). However, the species that do so are not used generally in



**Fig. 1.4** Branchlet morphology in the different genera of characean plants. (a) *Chara*, (b) *Lamprothamnium*, (c) *Nitella* and (d) *Tolypella*



**Fig. 1.5** Branchlet nodes and gametangia of *Chara* spp. In *Chara*, the oogonium (female) is above the antheridium, and bract cells, bracteoles and cortical filaments arise from the nodal complex

physiological studies. Calcium carbonate can be precipitated in bands on the axes and branchlets of many species as a consequence of their photosynthesis and metabolism, but this is generally distinct from the thick encrustation that occurs in calcareous habitats (see Sect. 2.4).

The growing thallus of characean plants varies in complexity and size depending on the species. Most of the species of *Chara* that occur in the Northern Hemisphere (Krause 1997; Han and Li 1994; Scribailo and Alix 2010) have internodes covered by a cortex of smaller, linearly aligned cells (Fig. 1.2a, b). This layer of cortical cells can prevent physical access to the largest cells, and for this reason corticated

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