

## THE FEMALE GAMETANGIUM OF *TOLYPELLA NIDIFICA* A.BR.: A MISINTERPRETATION

E. X. MAIER

Hugo de Vries-laboratorium, Universiteit van Amsterdam

### SUMMARY

The conclusion of KAUSIK & BHATTACHARYA (1971) that in the genus *Tolypella* there are two stalk cells in the female gametangium and only one such cell in *Chara* and *Nitella* is repudiated. *Tolypella*, *Chara* and *Nitella* have in fact one stalk cell, sometimes two. The "stalk cells" of Kausik and Bhattacharya are usually called sterile oogonium cells. *Chara* has one sterile oogonium cell, *Nitella* three, and *Tolypella* two. This confirms the intermediate position of *Tolypella*. In this connection the systematic position of gyrogonites (fossil remnants of female gametangia), rather generally referred to *Tolypella*, is discussed.

### 1. FEMALE GAMETANGIUM: DEVELOPMENT AND TERMINOLOGY

The development of the female gametangium, also called sporophydium or nucule, of *Chara* and *Nitella* was described in great detail by DE BARY (1871), GOETZ (1899), FRITSCH (1935), and HORN AF RANTZIEN (1956). The development proceeds, briefly, as follows: – The basal node of the male gametangium (globule) forms five peripheral cells, the uppermost of which develops into the sporophydium. The sporophydium initial divides twice to form a row of three cells. The uppermost cell gives rise to the egg cell and the sterile oogonium cell(s); the middle cell forms the five spiral cells, the coronula cells, and the node cell; and the innermost cell forms the pedicel cell(s).

HORN AF RANTZIEN (1956) has given an excellent survey of all the difficulties associated with the terminology of the female gametangium. His summary shows that the terms pedicel cell(s) and sterile oogonium cell(s) are the most appropriate, apart from such terms as "Stielzelle", stalk cell or stalk for pedicel cell, and "Wendungszelle", turning cells for sterile oogonium cells. He clearly pointed out the misleading use of the term stalk cell for sterile oogonium cell. He stated: "as moreover the inadequate expression stalk cell Smith 1938, p. 138 not stalk cells of other authors", is used for the sterile oogonium cell(s). SMITH (1938, 1950) used the term "stalk cell" for both the sterile oogonium cell(s) and the node cell, which view he maintained in his publication of 1955, but now referring to the node cell as "central cell".

KAUSIK & BHATTACHARYA (1971) did not realize which difficulties may arise from the use of the term "stalk cell" for a sterile oogonium cell. They thus came to the conclusion that *Tolypella* has two "stalk cells" and *Chara* and *Nitella* only one. This conclusion must be rejected. By the two "stalk cells" of *Tolypella*

they meant two sterile oogonium cells, but by the "stalk cells" of *Chara* and *Nitella* the pedicel cells. It is evident from their list of references that they must have compared the "stalk cells" of Smith (1955), which are sterile oogonium cells, with those of Fritsch (1935), which are pedicel cells. Their conclusion should have been: *Tolypella* has two sterile oogonium cells ("stalk cells" sensu Smith 1955), *Chara* one (see, e.g., Fritsch 1935), and *Nitella* three (see, e.g., Fritsch 1935). For details see *figs. 1A, B and C*.

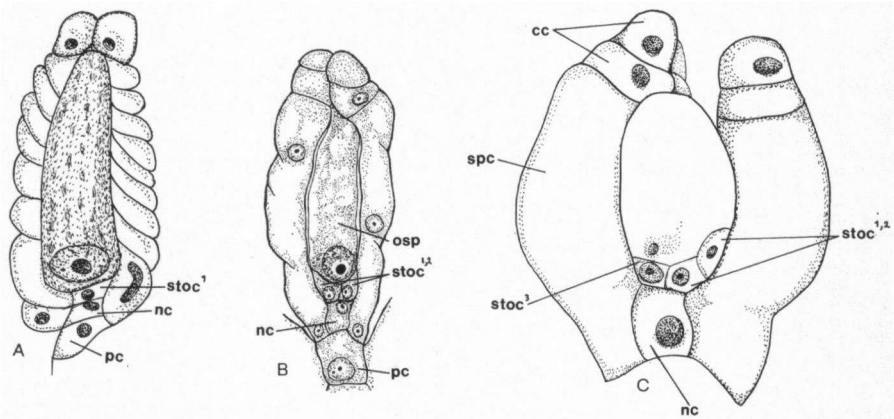


Fig. 1. Vertical sections of female charophyte gametangia. A. *Chara vulgaris* L.; B. *Tolypella nidifica* A. Br.; C. *Nitella flexilis* Ag. cc: coronula cells, nc: node cell, osp: oosphere, pc: pedicel cell, spc: spiral cell, stoc<sup>1,2,3</sup>: sterile oogonium cells. A and C after GOETZ (1899); B after KAUSIK & BHATTACHARYA (1971).

## 2. PHYLOGENETIC IMPLICATIONS

For different reasons the genus *Nitella* is considered to be the most derived within the *Charophyta*, see, e.g., DESIKACHARY & SUNDARALINGAM (1962). One of the arguments is the greater degree of sterilization in the female gametangium of *Nitella*. The genus *Tolypella* is supposed to be intermediate between *Chara* and *Tolypella*. The fact that *Tolypella* has two sterile oogonium cells, *Chara* one, and *Nitella* three, confirms the intermediate position of the genus *Tolypella*. For details see *table 1*.

## 3. PALAEOBOTANIC IMPLICATIONS

An important diagnostic characteristic of fossil *Charophyta* is the so-called basal plug, a small calcified disc in the lower part of the gyrogonite (= the fossil remnant of the female gametangium). According to GRAMBAST (1956) and MASLOV (1963) the plug represents the sterile oogonium cells. *Nitella*, which has three sterile oogonium cells, might be expected to form, if becoming fossilized, a basal plug consisting of three parts. However, *Nitella* is not certainly

Table 1. Comparison of some diagnostic features of the genera *Chara*, *Tolypella* and *Nitella*.

	<i>Chara</i>	<i>Tolypella</i>	<i>Nitella</i>
number of coronula cells	5	10	10
cortication	+	—	—
calcified oosporangia	+	+ <sup>1</sup>	—
branching	monopodial	monopodial	sympodial
number of sterile oogonium cells	1	2	3

<sup>1</sup> Texturally different from *Chara*.

known as a fossil owing to the fact that no lime-shells are produced. Nevertheless Grambast found gyrogonites with tripartite basal plugs whose three parts easily become detached from one another. He referred this type of gyrogonite to *Tolypella* starting from the assumption that this genus, like the genus *Nitella*, has three sterile oogonium cells (GRAMBAST 1956, 1962). *Tolypella* has only two sterile oogonium cells, however. We must, accordingly, conclude that either such gyrogonites do not represent remains of representatives of the genus *Tolypella*, or that they nevertheless belong to this genus because the third part of the plug was formed by a different calcified cell (e.g., a node cell) or because certain extinct species of *Tolypella* possessed three sterile oogonium cells. As far as we know now, *Tolypella* possesses only two sterile oogonium cells, so that the erstwhile occurrence of species of *Tolypella* with three sterile oogonium cells is not at all probable.

It is noteworthy in this connection that a number of workers such as HORN AF RANTZIEN (1959) and PECK & EYER (1963) doubt whether sterile oogonium cells can calcify at all, since they lie within the innermost two oosporangial membranes. According to MIGULA (1897) and WALTHER (1929) the sterile oogonium cells are even resorbed by the oosphere to disappear completely. The node cell, on the other hand, is supposed to be able to become calcified because it belongs to the outer two oosporangial layers. Later Horn af Rantzien revised his opinion, however, see HORN AF RANTZIEN & GRAMBAST (1962), but without giving arguments for his change of mind.

It will be quite obvious from the above-mentioned diversity of opinion that it is by no means clear whether the basal plug is a derivative of sterile oogonium cells. It follows that the classification of gyrogonites in the genus *Tolypella* on the ground of the tripartite basal disc is highly suspect.

#### ACKNOWLEDGEMENTS

The author thanks Prof. dr. A. D. J. Meeuse for his critical advice and the help with the translation into English, and H. I. Koerts Meijer for making the drawings.

## REFERENCES

- BARY, A. DE (1871): Über den Befruchtungsvorgang bei den Charen. *Monatsber. Kön. Akad. Wiss. Berlin*: 227–239.
- DESIKACHARY, T. V. & V. S. SUNDARALINGAM (1962): Affinities and inter-relationships of the Characeae. *Phycologia* 2: 9–16.
- FRITSCH, F. E. (1935): *The structure and reproduction of the algae*. 1. Cambridge.
- GOETZ, G. (1899): *Über die Entwicklung der Eiknospe bei den Characeen*. Thesis. Freiburg.
- GRAMBAST, L. (1956): La plaque basale des characées. *C. R. Acad. Sc. Paris* 242: 2585–2587.
- (1962): Classification de l'embranchement des charophytes. *Natur. Monspel. sér. Bot.* 14: 63–86.
- HORN AF RANTZIEN, H. (1956): Morphological terminology relating to female charophyte gametangia and fructifications. *Bot. Not.* 190: 212–259.
- (1959): Recent charophyte fructifications and their relations to fossil charophyte gyrogonites. *Arkiv. Bot. ser. 2*, 4: 165–332.
- & L. GRAMBAST (1962): Some questions concerning recent and fossil charophyte morphology and nomenclature. *Stockholm Contrib. Geol.* 3: 135–144.
- KAUSIK, S. B. & S. S. BHATTACHARYA (1971): Structure and development of the sex organs in *Tolypella nidifica* (O. Müll.) A. Br. (Characeae). *Bot. J. Linn. Soc.* 64: 97–104.
- MASLOV, V. P. (1963): The discovery of the calcareous crown and the apical structure of the fruit-bearing organs of fossil charophytes. *Dokl. Akad. Nauk S.S.S.R.* 149: 954–956 (Russian). English transl. 1965, 152 (1–6): 206–208.
- MIGULA, W. (1897): Die Characeen. In L. RABENHORST *Kryptogamenflora* Bd. 5. Leipzig.
- PECK, R. E. & J. A. EYER (1963): Pennsylvanian, Permian and Triassic Charophyta of North America. *J. Pal.* 37: 835–844.
- SMITH, G. M. (1938): *Cryptogamic botany* 1. 1st ed., New York.
- (1950): *Freshwater algae of the United States of America*. 2nd ed., New York.
- (1955): *Cryptogamic botany* 1. 2nd ed., New York.
- WALTHER, E. (1929): Entwicklungsgeschichtliche und zytologische Untersuchungen an einigen Nitellen. *Arch. Julius Klaus-Stiftung Vererb. Forsch.* 4: 23–121 (not seen).