

## Predominant occurrence of apical cell divisions in *Oedogonium pakistanense* and its phylogenetic significance

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A rare terrestrial species, *Oedogonium pakistanense*, was first recorded from Hubei Province, south-central China. Morphological characters, including the predominant occurrence of apical cell division and unique lateral apical caps, are described. The growth of the filaments in *O. pakistanense* from China is usually the result of the repeated divisions of the apical cells and intercalary divisions are rare. It is suggested that this species may represent an evolutionary transition between *Oedogonium* and *Oedocladium*, the latter being a terrestrial genus with branched filaments and cell division more often terminal than intercalary.

### INTRODUCTION

Up to now, more than 500 species have been described in the genus *Oedogonium* Link (Mrozińska 1985). Most are aquatic and usually found in small water bodies such as pools and ponds. Nine species are known to be terrestrial; all of them are recorded from South Asia (Randhawa 1939; Venkataraman 1958; Islam & Sarma 1963; Chacko 1970; Srivastava & Srivastava 1987; Panikkar & Ampili 1990; Mahato 1999). Of these, seven species are monoecious and two dioecious. The terrestrial life-form is thus rare in *Oedogonium* and some evolutionary significance has been attributed to it (Jao 1979).

We collected an *Oedogonium* specimen from sandy soil in a village of Xiantao County, Hubei Province, China, in 1992. It was the dominant species in this habitat and grew together with some other filamentous soil algae such as *Rhizoclonium hieroglyphicum* Kützing, *Lyngbya* C. Agardh sp. and *Oedocladium prescottii* Islam. But we could not identify it because its filaments were all vegetative. It was the first discovery of a terrestrial *Oedogonium* species from China. Six years later, we found the alga again at the same locality. At this time, we cultured the filaments successfully in the laboratory. Unlike what happens in most species of *Oedogonium* (Fritsch 1948; Smith 1950; Jao 1979), the cell division of this species was often more apical than intercalary; hence, developing apical caps were found laterally attached to septa in growing filaments. We confirmed the alga was *O. pakistanense* Islam & Sarma.

### MATERIAL AND METHODS

Field material of *O. pakistanense* was collected from sandy soil from Hengdi village in Xiantao County (113°30'N, 30°50'E), Hubei Province, China. The samples were fixed in 4% formaldehyde solution. We also cultured it in liquid soil

extract medium (10 ml soil extract added to 90 ml H<sub>2</sub>O containing 0.09 mM MgSO<sub>4</sub>, 0.13 mM K<sub>2</sub>HPO<sub>4</sub>, 2.2 mM KNO<sub>3</sub>) and on 1% agar plates for studying the life cycle and relative position of the apical caps on the filaments. Cultures were grown in this medium at 25 ± 1°C with 50 μmol photons m<sup>-2</sup> s<sup>-1</sup> 14:10 h light–dark photoperiod. The culture strain investigated was LW-052, collected on 2 August 1998 by one of us (G.L.) and kept in the freshwater algae herbarium of the Institute of Hydrobiology, Chinese Academy of Sciences. Observations were made with a Vanox (Olympus, Tokyo, Japan) light microscope and an Amray-1830 (Amray, Bedford, MA, USA) scanning electron microscope.

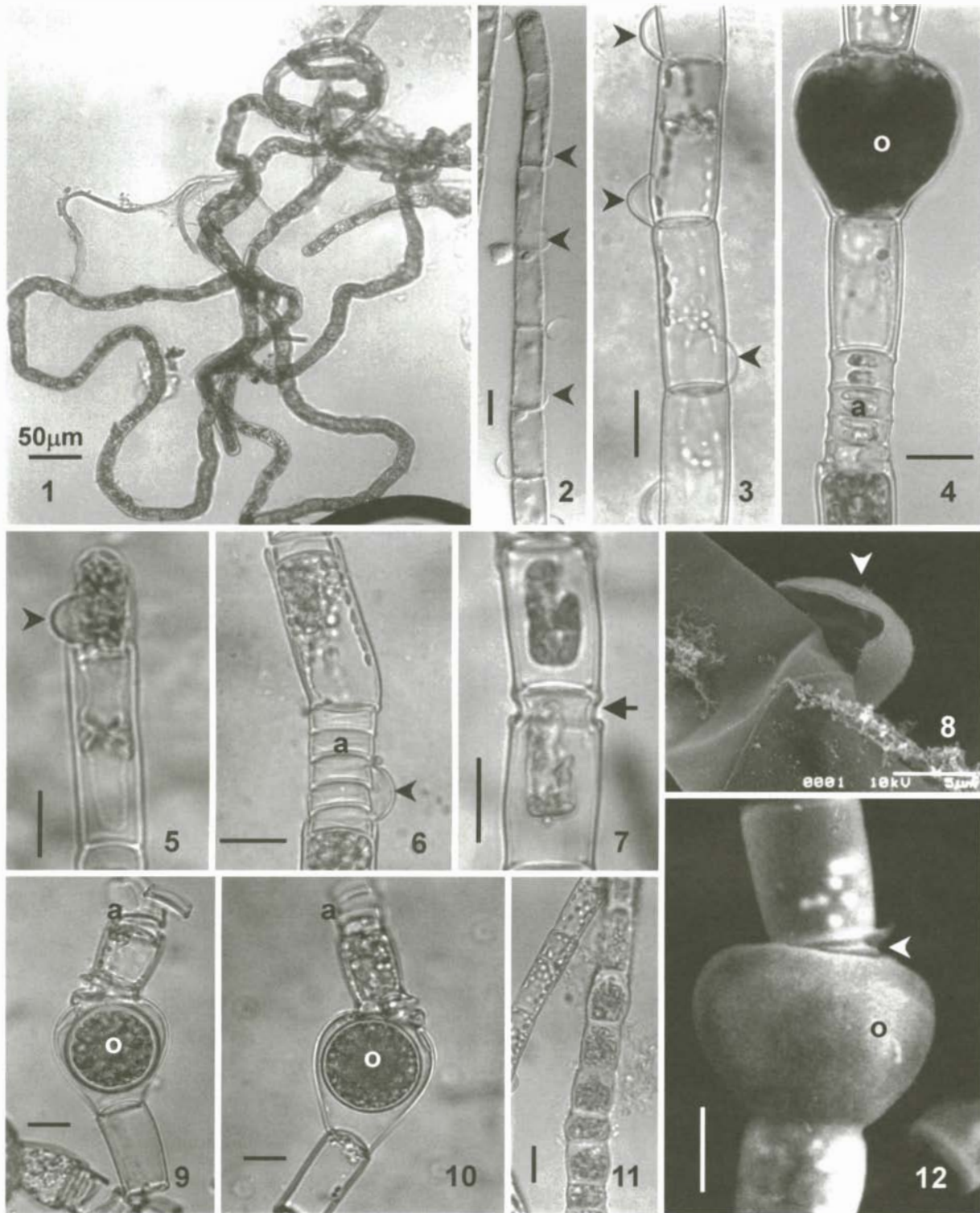
### RESULTS

#### *Oedogonium pakistanense* Islam & Sarma (1963, pp. 75–76, figs 11–16)

*Oedogonium pakistanense* is terrestrial but it also grows well and faster in liquid medium. The filaments are slightly curved in the field (Fig. 1) but straight in culture (Figs 2–4). Vegetative cells are subcylindrical to cylindrical, 9–15 μm in diameter, 28–32 μm long; apical cells are obtuse. On the agar plates, we observed series of apical caps attaching to septa in filaments (Figs 2, 3, 5), suggesting that the growth of filaments is usually the result of repeated divisions of the terminal cell (Figs 2, 5); intercalary divisions do exist but are rare (Fig. 7). The caps are conoid with an obtuse top, 10–12 μm wide and 4–6 μm high (Figs 3, 5, 8). It seems that the lateral apical caps contact the filaments loosely and that, consequently, they tend to drop off after some time. Therefore, the caps are more frequently found in material growing on agar medium than in liquid medium. Occasionally, apical caps can even be found on lateral antheridia (Fig. 6).

Thalli of *O. pakistanense* are monoecious. After two weeks on agar, the filaments become yellow and form oogonia, which are pyriform and solitary (Figs 4, 9, 10, 12). The open-

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**Figs 1–12.** *Oedogonium pakistanense*, light microscopy (except Figs 8, 12, scanning electron microscopy). o, oogonium; a, antheridium. Scale bars = 5 µm (Fig. 8), 10 µm (Figs 2–7, 9–12) or 50 µm (Fig. 1).

**Fig. 1.** Curved unbranched fresh filaments from nature.

**Figs 2–12.** Different stages from cultures on agar.

**Figs 2–3.** Lateral apical caps (arrowheads) in a row along filament.

**Fig. 4.** Pyriform oogonium and four antheridia with two sperms in each.

**Fig. 5.** Apical cap (arrowhead) pushed to the side of an apical cell.

**Fig. 6.** Five antheridia in a row with a lateral apical cap (arrowhead).

**Fig. 7.** Intercalary division (arrow).

**Fig. 8.** Lateral apical cap (arrowhead) on the filament.

**Figs 9–10.** Globose oospore in a pyriform operculate oogonium.

**Fig. 11.** Filament with serial akinetes; on the left is a 'normal' filament.

**Fig. 12.** Pyriform oogonium with an operculum (arrowhead).

ing of the oogonium is a complete split or a circumscissis (Figs 10, 12). The oospore is globose with a smooth wall; mature oospores do not fill the oogonium completely and are orange-yellow in colour. Antheridia are usually subepigynous, but in rare cases, the antheridia of *O. pakistanense* from China can be subhypogynous (Fig. 4). They are organized with two to eight in a row including two sperms in each antheridium; the sperms are formed by a horizontal division (Fig. 4). Oogonia are 31 µm in diameter and 34–40 µm long; oospores are 25–30 µm in diameter; antheridia are 12–13 µm in diameter and 4–5 µm long.

Zoospores and subsequent germinating stages with distinct basal cells are well known in *Oedogonium*, but they are not found in our material, either field-collected or cultured. Some vegetative cells arose during a period of unfavourable growth conditions that were filled with oil droplets and starch and had a slightly thickened wall (Fig. 11; akinetes?).

## DISCUSSION

Before this report, terrestrial *Oedogonium* was known only from South Asia, for example India and Bangladesh. This is the first report of terrestrial *Oedogonium* from the subtropics, far from South Asia. In fact, the temperature of Xiantao County is often high, over 40°C in summer, so we can only collect this species in summer.

Chinese material of *O. pakistanense* differs from that collected from India by its smaller size in every aspect (Islam & Sarma 1963). The oogonia are always pyriform and the oospores are regularly globose and incompletely fill the oogonia. The remarkable character of the Chinese material is the predominant occurrence of apical cell division, which was not described by Islam & Sarma (1963).

It is a characteristic of *Oedogonium* that the upper end of an intercalary cell may bear a stack of overlapping caps (rings), the number of rings borne by each cell revealing the number of cell divisions it has undergone (Fritsch 1948). Free caps (cap turned to one side and able to drop off after some time) are only formed as a result of the division of terminal cells in another oedogonialean genus *Oedocladium* Stahl or the division of unicells developed from zoospores in *Bulbochaete* C. Agardh (Fritsch 1948; Jao 1979). In our *Oedogonium*, the free caps formed are very similar to those in *Oedocladium*; this is the first *Oedogonium* species we have observed with apical division dominant.

The pattern of cell division is an important criterion for discussion of the phylogenetic relationships between the genera *Bulbochaete*, *Oedocladium* and *Oedogonium*. In many species of *Bulbochaete*, cell division is usually restricted to the basal cell. However, *B. nigerica* Gauthier-Lièrve exhibits

mostly intercalary division, and this is interpreted as a primitive feature and is typical of *Oedogonium*. Therefore Jao (1979) suggested that *Bulbochaete* might be derived from *Oedogonium*. *Oedogonium pakistanense* has unbranched filaments, so it clearly belongs to *Oedogonium*, but the growth of its filaments is usually apical, a character more typical of *Oedocladium*. Therefore, it seems that this terrestrial species represents an evolutionary transition between *Oedogonium* and *Oedocladium*.

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