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Two new aerophytic species of the genus *Podohedra* DÜRINGER (Chlorophyceae)

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With 37 figures and one table in the text

Abstract: Two new species of the aerial green algal genus *Podohedra* from the tropical epiphytic aerial biotopes are described. Both species were found on trentepohliacean filamentous algae. The infrageneric taxonomy of the genus *Podohedra* based on morphological characters of the vegetative cells is discussed. The characters for discriminating of aerophytic *Podohedra* species are given. The shape comparison of both organisms with similar aerial green algal species Keratococcus bicaudatus is provided by means of outline fitting method based on elliptic Fourier analysis.

Key words: *Podohedra, Keratococcus,* Chlorophyta, aerial algae, tropical rainforest, outline fitting, geometric morphometrics, elliptic Fourier analysis.

Introduction

The genus *Podohedra* was erected by DÜRINGER (1958) to accommodate sessile coccal green algae attached to the substrate with a stalk and reproducing entirely by means of autospores. In its overall appearance the members of the genus resemble *Characium* species, differing in type of asexual reproduction and mostly also in considerably smaller cell dimensions. The cells possess one nucleus and the single parietal chloroplast. The shape of the cells varies from ellipsoidal to beaked-elongate within the genus. Both pyrenoid bearing (*P. longipes*) and pyrenoid-less species (*P. falcata*) were encompassed within *Podohedra* by DÜRINGER (1958) in the original generic concept. The same approach was applied also by GEITLER (1965) in his taxonomic revision of the genus *Podohedra* where two other species (*P. bicaudata* and *P. distincta*) were described.

HINDÁK (1970) investigated the species of the genera *Monoraphidium* and *Keratococcus*. These genera classified traditionally into the subfamily Ankistrodesmoideae of the family Chlorellaceae are differing mainly by the presence or absence of the pyrenoid in *Keratococcus* and *Monoraphidium* respectively. Both genera accommodate species with elongated cells which are not attached to the

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substrate and whose apical cell outgrowths are mostly symmetrical. However, HINDÁK investigated morphology and variability of these organisms and found the much higher shape diversity than in original descriptions. He criticised the GEITLER´s (1965) broad conception of the genus *Podohedra* stating that the species *Podohedra bicaudata* GEITLER is in fact identical with *Keratococcus bicaudatus* (HANSGIRG) BOYE-PETERSEN and *P. distincta* GEITLER with *Monoraphidium rhaphidioides* (HANSGIRG) HINDÁK. Following these findings HINDÁK (1970) synonymised both the above mentioned *Podohedra* species with *K. bicaudatus* and *M. rhaphidioides* respectively. HINDÁK (1970) also mentioned the resemblance of other *Podohedra* species with the genus *Keratococcus*, especially with *Keratococcus bicaudatus*. This species often abounds in subaerial biotopes similar to those from which both the original DÜRINGER´s *Podohedra* species (*P. longipes*, *P. falcata*) were described.

The further taxonomic investigation of the genus *Podohedra* was worked out by HINDÁK (1988). He redefined the generic concept of *Podohedra* so that the genus accommodates only the pyrenoid bearing species *P. longipes*. Consequently, he described the new genus *Podohedriella* HINDÁK for pyrenoidless species previously classified within *Podohedra* and added two new organisms within this genus (*Podohedriella carpatica*, *P. recta*).

Thus, until recently seven species originally classified into genera *Podohedra* and *Podohedriella* and differing in overall cell morphology and dimensions were described (DÜRINGER 1958, GEITLER 1965, HORTOBÁGYI 1969, HINDÁK 1988). Four of them: *Podohedriella falcata* (DÜRINGER) HINDÁK, *Podohedra longipes* DÜRINGER, *Podohedra bicaudata* GEITLER (later synonymized with *Keratococcus bicaudatus*) and *Podohedra distincta* GEITLER (later synonymised with *Monoraphidium rhaphidioides*) occur in mucilaginous aerial algal growths dominated by *Coccomyxa dispar* and *C. confluens* (DÜRINGER 1958, GEITLER 1965, NEUSTUPA et al. 2002). These growths often abound in temperate ecosystems in moist conditions on bare and withered spruce wood. Two *Podohedriella* species – *P. carpatica* HINDÁK and *P. recta* HINDÁK – were described from periphyton and metaphyton of small forest pools from Slovakia (HINDÁK 1988). One species – *P. georgei* HORTOBÁGYI (1969) – was described from tropical freshwater plankton. However, neither the reproduction type, nor the stipitate nature of the cells were presented.

In the course of the investigation of algal flora in aerial epiphytic growths of tropical rainforests in Southeast Asia two populations accordant to *Podohedra* generic description were encountered. In ever-wet aseasonal climatic conditions of tropical rainforest the species-rich aerial algal and cyanobacterial communities are developing. Generally, they are dominated with members of green algal genera *Trentepohlia* and *Phycopeltis* or cyanobacterial genus *Scytonema*. However, the coccal green algae of the morphologically delimited genera *Chlorella*, *Chlorolobion*, *Choricystis*, *Dictyochloropsis* and others account for the most part of the almost unexplored species diversity in these communities (NEUSTUPA 2002).

In this paper the two organisms characterized with stalked asymmetrical elongated cells and single pyrenoid bearing chloroplasts from these localities are presented and their description as new species of the genus *Podohedra* is proposed.

For the morphological comparison of both organisms and similar species *Keratococcus bicaudatus* the outline fitting method based on elliptical Fourier analysis was applied (ROHLF 1990). This approach is based on digitising of the points along the contour of the object. Subsequently, the points are fitted with function of elliptical Fourier analysis and the curves are compared using the coefficients of the function as shape variables. The results can be demonstrated by multivariate analysis (e.g. PCA). The changes in outlines represented by particular principal components can subsequently be reconstructed and visualised (ROHLF 1990, BACHNOU et al. 1999, IWATA & UKAI 2002). The method provides the possibility of complex analysis of shape and its variability within the investigated objects independently of their size and orientation.

The method of outline fitting using Fourier analysis was successfully applied in a wide range of morphometric studies investigating morphology and taxonomy of invertebrates (e.g. BACHNOU et al. 1999, TORT 2003); fish (e.g. LOY et al. 2000, TORRES et al. 2000); human skeletal bones (e.g. SCHMITTBUHL et al. 2001); vascular plant leaves (e.g. JENSEN et al. 2002) or diatoms (PAPPAS et al. 2001). The benefits of outline analysis in comparison with traditional morphometric were illustrated by JENSEN et al. (2002). The demonstration of the potential of outline fitting method to green algal taxonomy and morphology is one of subsequent goals of the presented study.

Material and methods

The investigated algae were isolated from two aerial localities in Peninsular Malaysia. *Podohedra tropica* was isolated from the leaf of an unidentified shrub in secondary lowland rainforest in the of Hulu Kelantan, geographical coordinates 5°13'10"N and 101°48'00"E, altitude 450 m a s.l., collected 27. 1. 2000. *Podohedra saltans* was isolated from the stalk of *Bambusa* sp. growing in The Forest Research Institute Malaysia (FRIM), Selangor, Peninsular Malaysia, geographical coordinates 3°13'20"N and 101°32'30"E, altitude 400 m a s.l., collected 8.2.2000. For the morphological comparison the strain CAUP H 3301 (identical with SAG 202-11) of Keratococcus bicaudatus was used. This strain was isolated by PRINGSHEIM in the year 1955 from a small pool near Kiel, Germany.

For the morphological investigation and comparison the strains were cultivated on both agar-solidified and liquid BBM (BISCHOFF & BOLD 1963) and in biphasic cultures (PRINGSHEIM 1954); in the temperatures 13°C and 25°C; under the illumination of about 2500 lux (light source: Tungsram 36W F33, cool white). The set of standard cytological solutions stains (cotton blue, methylene blue, India ink, nigrosine) were used. The photographs were made on the Olympus BX51 light microscope and Olympus Z300 microphotograph equipment.

The strains are kept in The Collection of Algae of Charles University of Prague, Czech Republic (CAUP) (http://botany.natur.cuni.cz/algo/caup.html).

The outline analysis was conducted using elliptic Fourier analysis (KUHL & GIARDINA 1982). The SHAPE version 1.2. – a software package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors (IWATA & UKAI 2002) – was used for the conducting of the analysis. The contours of the cells were digitised from the photographs using Chain Coder program. In total, 75 randomly chosen objects of three compared populations were analysed. The photographs were taken from 4 weeks old cultures growing in the same standard conditions (agar-solidified BBM, 20°C, 12:12 hours light:dark cycle, 2500 lux – artificial source Tungsram 36W F33, cool white plus the diffuse daylight).

The elliptic Fourier descriptors of the outlines were computed using Chc2Nef program (IWATA & UKAI 2002). The coefficients of first 30 harmonics were computed. The appropriate number of harmonics was empirically tested beforehand for the sufficient description of the outline information. The coefficients were used in subsequent principal component analysis (PCA). The analysis and the scores of particular objects in ordination space of principal components were computed using PrinComp program. The PrinPrint program was used for the visualisation of shape information accounted for by each computed principal component.

Results and discussion

Podohedra saltans **NEUSTUPA sp. nova** Figs 1–10, 19–24

Diagnosis: Cellulae epiphyticae, adultae fusiformes, pedicellatae, apice obtusatae, uninucleates. Dimensiones cellulae (7,2–)9,5–12,5(13,5) x (3,2-)3,7–5,2 μm, pedicellus 1,5–4 μm. Membrana cellulae laevis. Chromatophorus parietalis. Pyrenoide distincto granulis amylaceis induto. Propagatio per 2 autosporas effecta.
Iconotypes: Fig. 19 – 24.

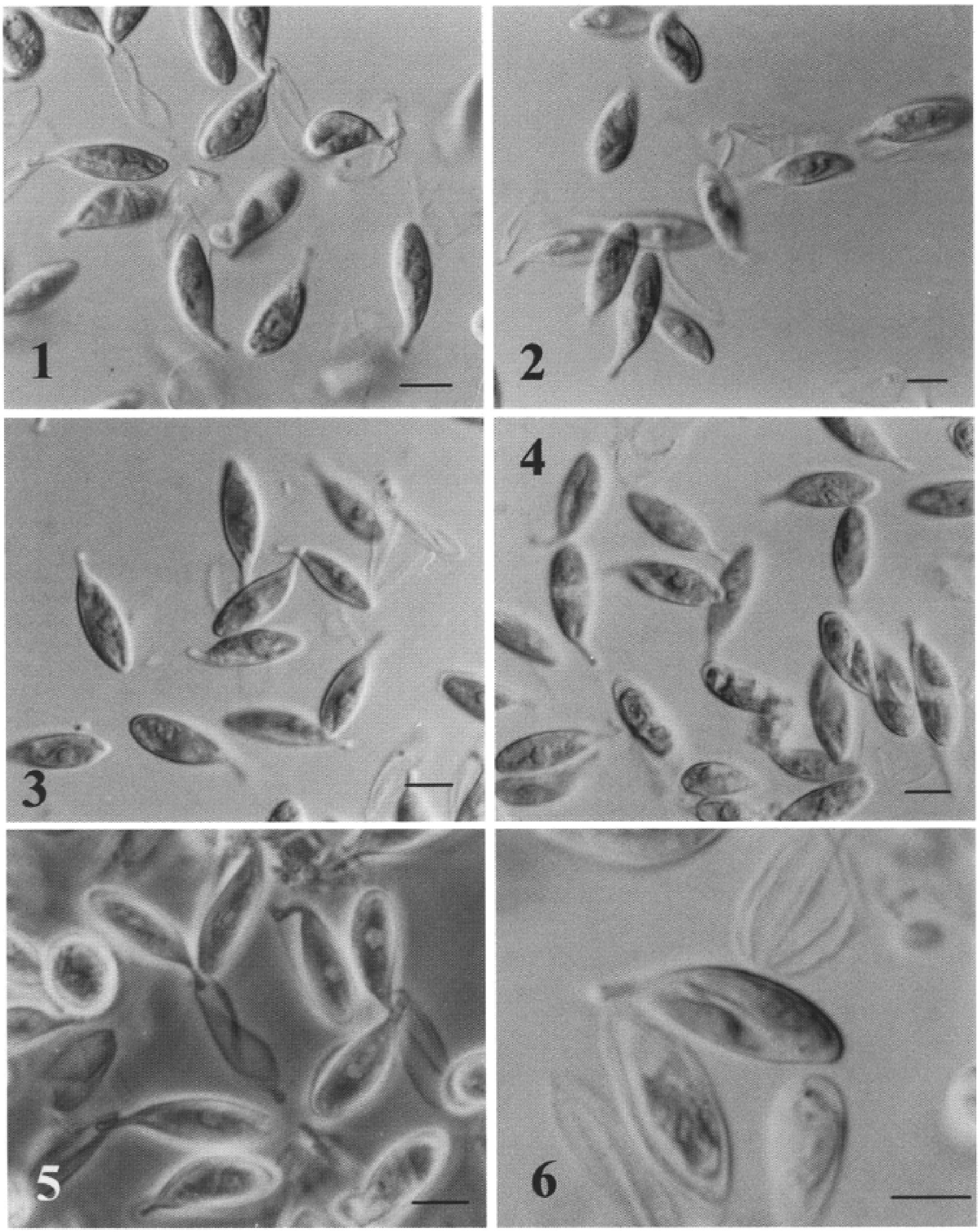
The vegetative cells are stipitate, attached to the substrate, straight to slightly inflexed, ellipsoidal to reverse-egg-shaped. The apical pole of the cells is obtuse-rounded to oval in some cases and without any cell wall thickening. The stalk is slightly widened in its basal part. The cell dimensions without the stalk are (7,2–) 9,5–12,5(–13,5) x (3,2–)3,7–5,7(–6,2) μm. The stalk: 1,5–4 μm. The width : length ratio is 1: 1,8–3. The cells possess the single chloroplast in a lateral position with conspicuous pyrenoid and sometimes with slightly a lobed margin. The envelope of pyrenoid is composed of separated globular to oval starch grains. The reproduction takes place entirely by autosporogenesis. The division plane between two daughter autospores originates in diagonal or more rarely in transverse position within the mother cell. The stalks of daughter cells are fully developed in mature autosporangium. The autospores are released by rupture of the autosporangium cell wall. Neither sexual reproduction nor the production of zoids was observed.

The species was found growing epiphytic on the filaments of *Trentepohlia bossei* on the stalk of *Bambusa* sp. in The Forest Research Institute Malaysia (FRIM), Selangor, Peninsular Malaysia.

Podohedra tropica **NEUSTUPA sp. nova** Figs 11–18, 25–30

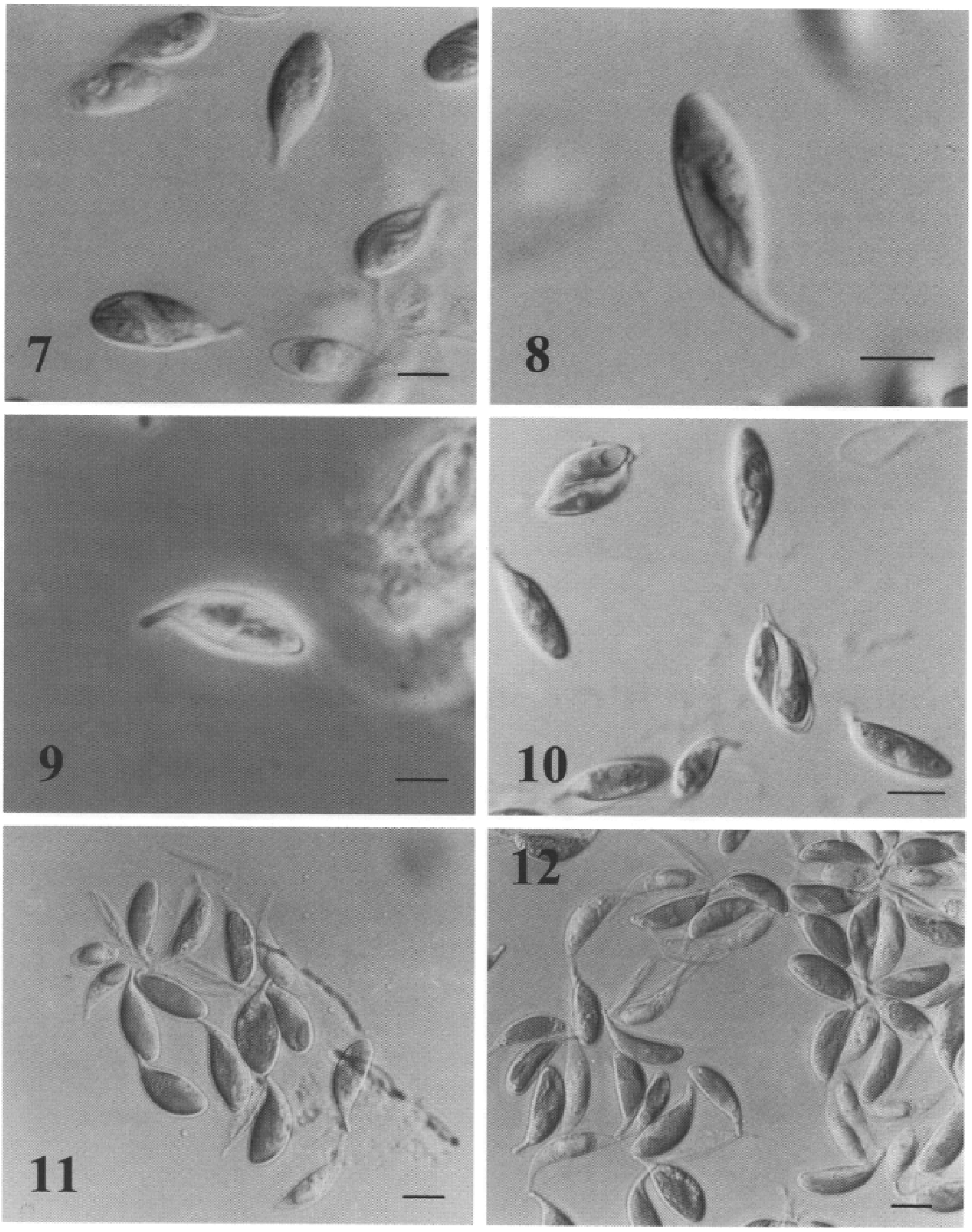
Diagnosis: Cellulae epiphyticae, adultae fusiformes, curvatae, pedicellatae, apice obtusatae et rostratae, uninucleates. Dimensiones cellulae (9–)10–13,2(–14,7) x (2,4–)3–5,5(–6,8) μm, pedicellus 2,5–5(–8) μm. Membrana cellulae laevis. Chromatophorus parietalis, cum pyrenoide inconspicuo. Propagatio per 2 autosporas effecta.
Iconotypes: Fig. 25 – 30.

The vegetative cells are stipitate, attached to the substrate. The cells are of inflexed fusiform elongated shape. The apical pole is usually obtuse to sharply



Figs 1–6
1–4 – *Podohedra saltans*, vegetative cells. **5** – *P. saltans*, vegetative cells in phase contrast showing separated starch grains of the pyrenoid. **6** – *P. saltans*, maturing autosporangium. [Bar = 5 μm]

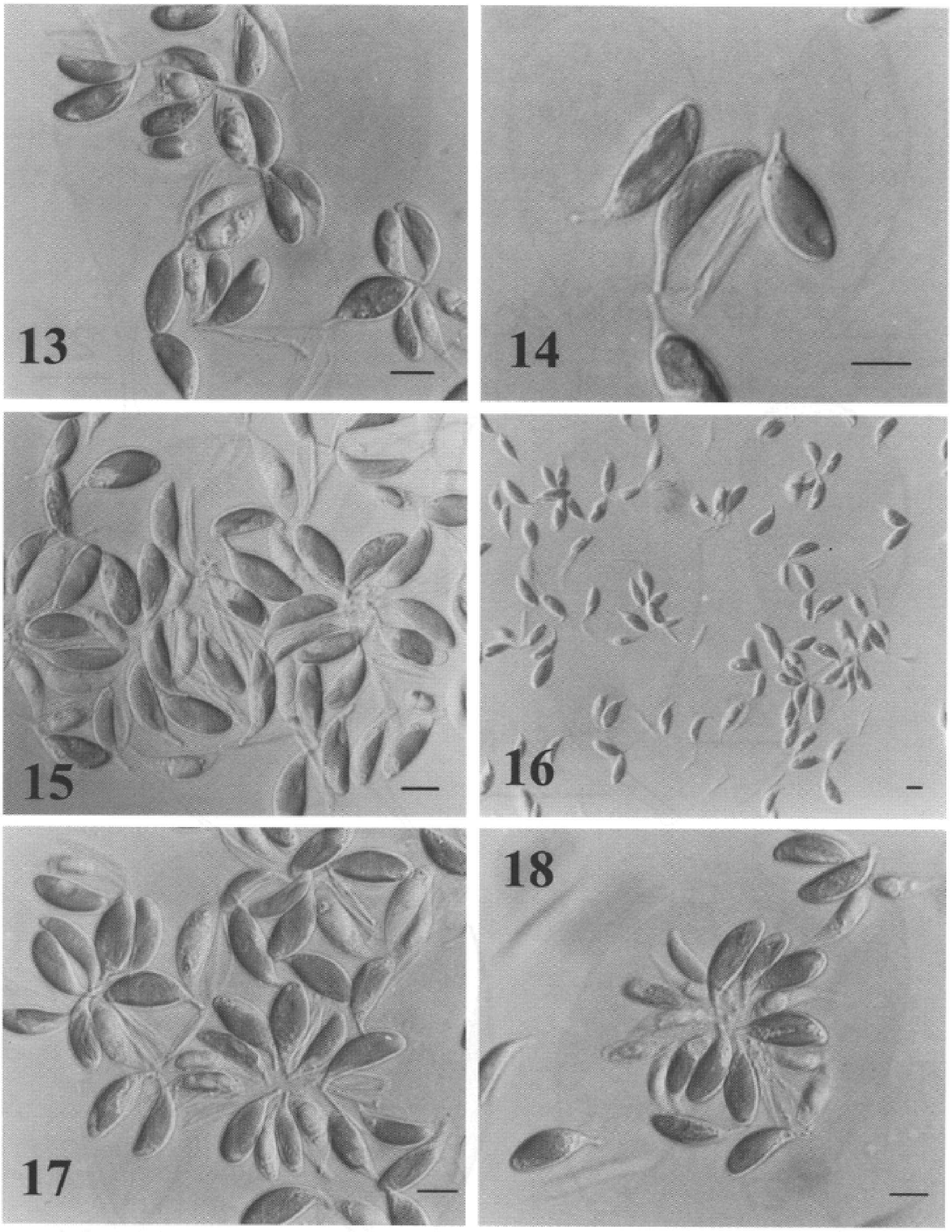
pointed; in older cells sometimes more rounded. The stalk is slightly widened in its basal part. The cell dimensions without the stalk are (9–)10–13,2(–14,7) x (2,4–)3–5,5(–6,8) μm. The stalk: 2,5–5(–8) μm. The width : length ratio is 1: 2 – 4,5. The cells possess the single chloroplast in lateral position with inconspicuous and sometimes hardly distinguishable pyrenoid. The reproduction takes place



Figs 7–12
7, 9, 10 – *Podohedra saltans*, vegetative cells and autosporangia in different stages of maturity, 9 – phase contrast. **8** – *P. saltans*, vegetative cell with typical lateral chloroplast. **11, 12** – *Podohedra tropica*, vegetative cells. [Bar = 5 μm]

entirely by autosporogenesis. The division plane between two daughter autospores originates in diagonal position within the mother cell. The autospores are released by rupture of the autosporangium cell wall. Neither sexual reproduction nor the production of zoids was observed.

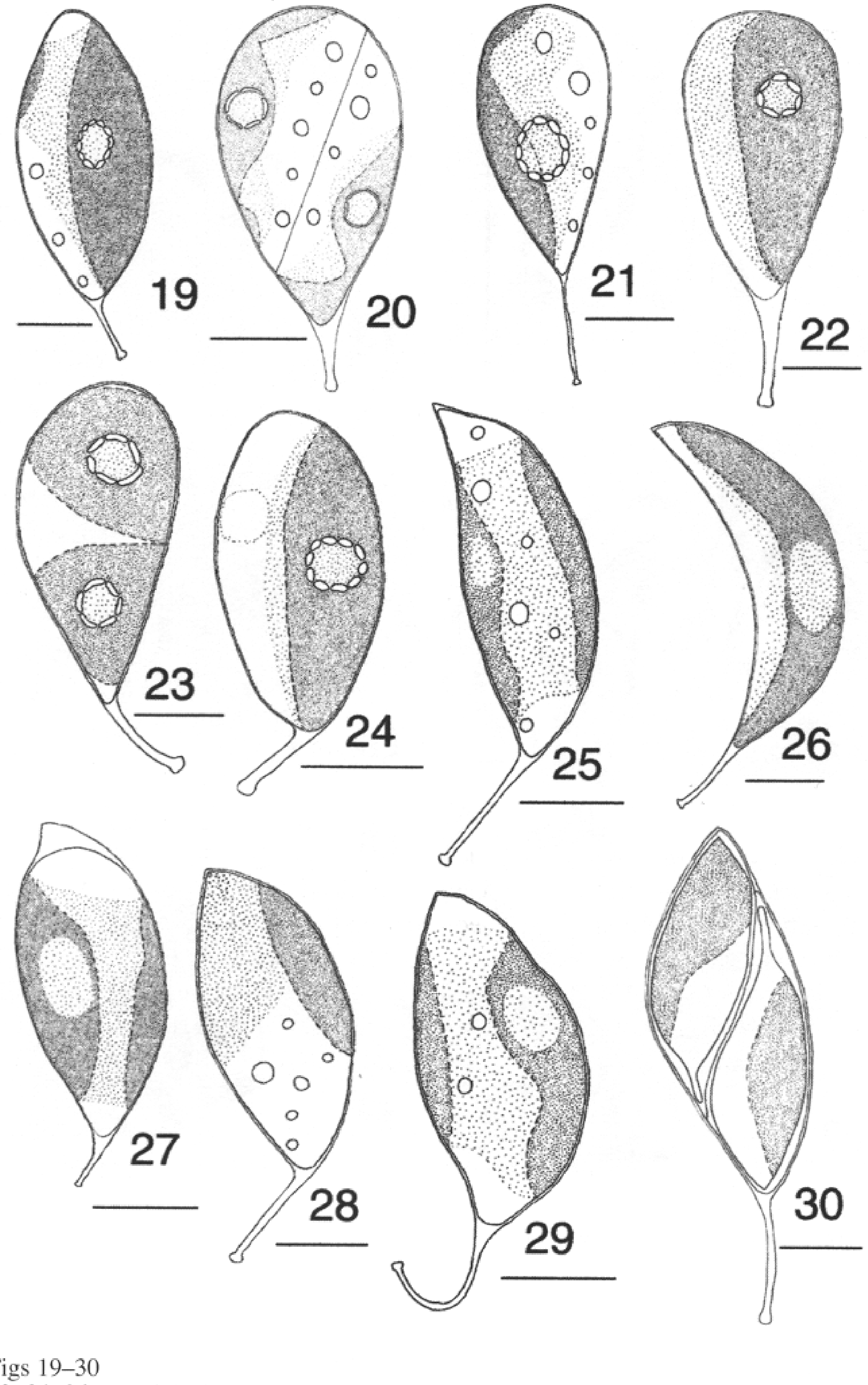
The species was found growing epiphytically on the filaments of *Trentepohlia*



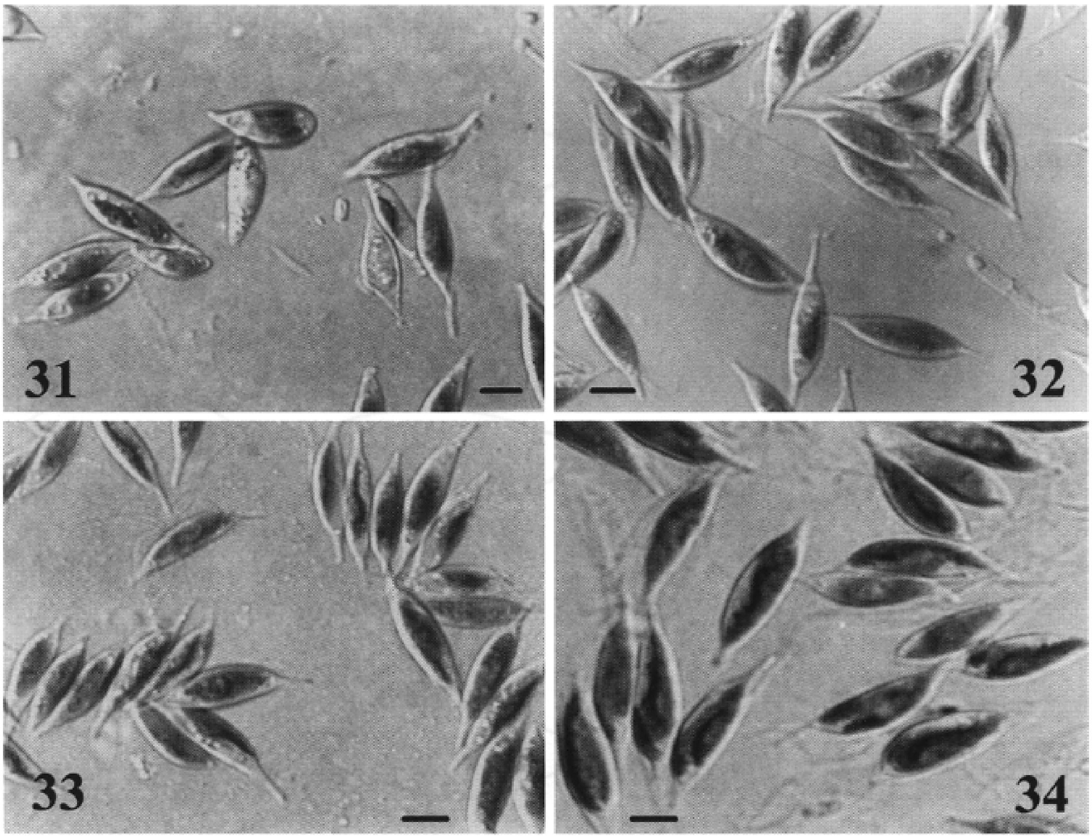
Figs 13–18
13–18 – *Podohedra tropica*, vegetative cells. [Bar = 5 μm]

aurea growing on the leaf of an unidentified shrub in secondary lowland rainforest in the area of Hulu Kelantan, Peninsular Malaysia.

HINDÁK (1988) stated the similarity of aerial *Podohedra* species with *Keratococcus bicaudatus*. Therefore, the strain CAUP H 3301 of *Keratococcus bicaudatus* was chosen for the morphological comparison (Figs 31–34). The cells



Figs 19–30
19, 21–24 – *Podohedra saltans*, vegetative cells with conspicuous pyrenoid. **20** – *P. saltans*, maturing autosporangium with diagonal division plane. **25–29** – *Podohedra tropica*, vegetative cells. **30** – *P. tropica*, autosporangium with 2 autospores in diagonal position. [Bar = 4 μm]



Figs 31–34
31–34 – *Keratococcus bicaudatus,* strain CAUP H 3301, vegetative cells. [Bar = 5 μm]

of *K. bicaudatus* were found to be widely fusiform, with both apical poles usually obtuse to sharply pointed. As already ascertained by HINDÁK (1970), in some cells one of the cellular poles can become rounded so that the cells are more or less asymmetric. Consequently, these particular cells can be hardly distinguishable from members of the genus *Podohedra*. The cells have a single parietal chloroplast with the pyrenoid. The reproduction takes place by means of two autospores. The dimensions of the cells are (11–)18,5–26,5(–30) x (2–)2,5–7,5(–9) μm.

The results of the outline analysis showed the shape variability of the investigated cultures. The first principal component (PC-1) of PCA encompassed 54,7 % of the total shape variability. This component relates to changes from isopolar fusiform cells with both apical poles obtuse pointed (the objects with positive scores on the component) to markedly heteropolar and assymetric cells with stalk on the proximal apical pole and rounded distal pole (the objects with negative scores) (Fig. 35). The first principal component bears also the most considerable information for the morphological delimiting of the investigating cultures (Figs 36, 37). The cells of *Podohedra tropica* mostly correspond with shapes bearing negative values on PC-1. *Podohedra saltans* is typical with intermediate cells and *Keratococcus bicaudatus* mostly with cells sharing the features typical for the objects with positive scores on PC-1.

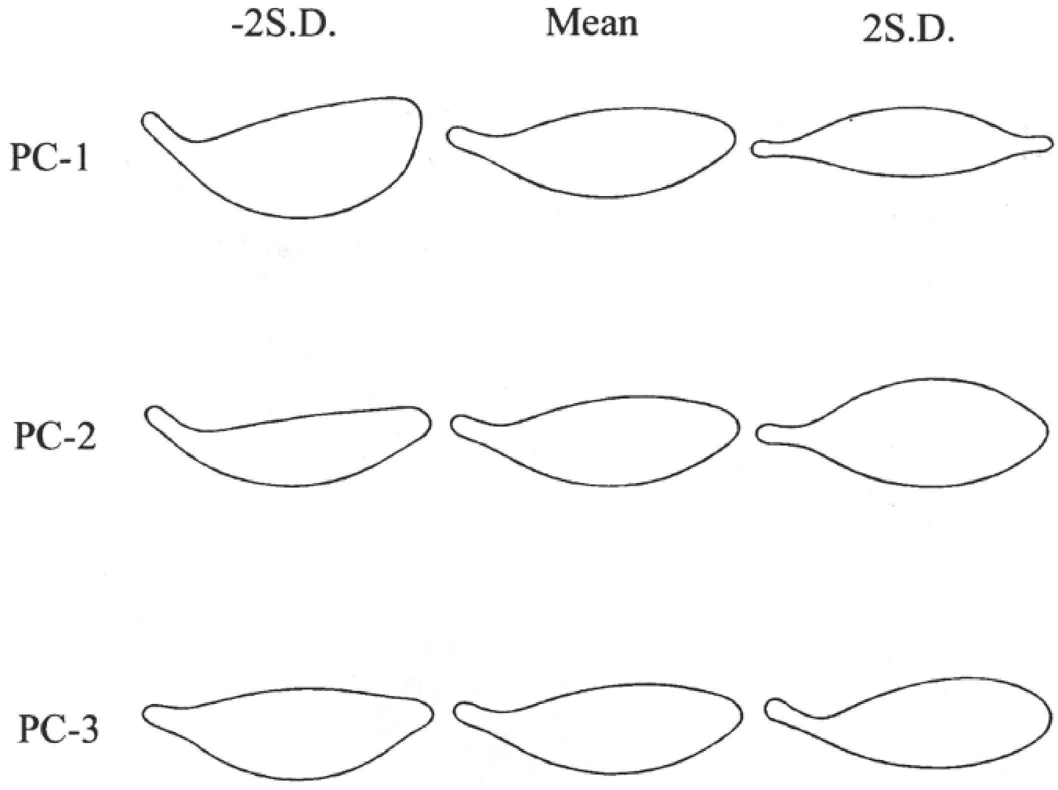


Fig. 35
The changes of cell outlines reconstructed from the elliptic Fourier analysis and encompassed by the principal components 1–3 in PCA. The shapes typical for objects with negative scores on particular principal components are shown in the left part of the figure; the mean shape in central position and the shapes typical for objects with positive scores in the right part.

The second principal component (PC-2) encompassed 27,3 % of the total analysed variability. The component relates to the changes from the fusiform cells with inflexed stalk to the cells with straight stalk and pronounced convex rounded outlines (Fig. 35). However, PC-2 does not distinguish clearly between the cells originating from three investigated cultures (Fig. 36). The third principal component (PC-3) encompassed 7,4 % of the total variability providing good applicable information for the distinguishing of the cultures. The cells with pointed apical pole has negative scores on this component and the cells with obtuse rounded apical pole share the positive scores (Fig. 37). PC-3 distinguishes the cells of *Podohedra saltans* with higher scores indicating the typical more rounded shape of its apical poles (Fig. 35). The cells of *Keratococcus bicaudatus* and *Podohedra tropica* have mostly the negative values of the PC-3 scores with their cells usually typical by obtuse to sharply pointed apical poles.

In total we can see that the outline analysis revealed the distinct shape differences between the investigated cultures implicating their different specific nature. On the other side, the occasional occurrence of cells with shape typical for other analysed species in cultures indicates the relationship of the investigated organ-

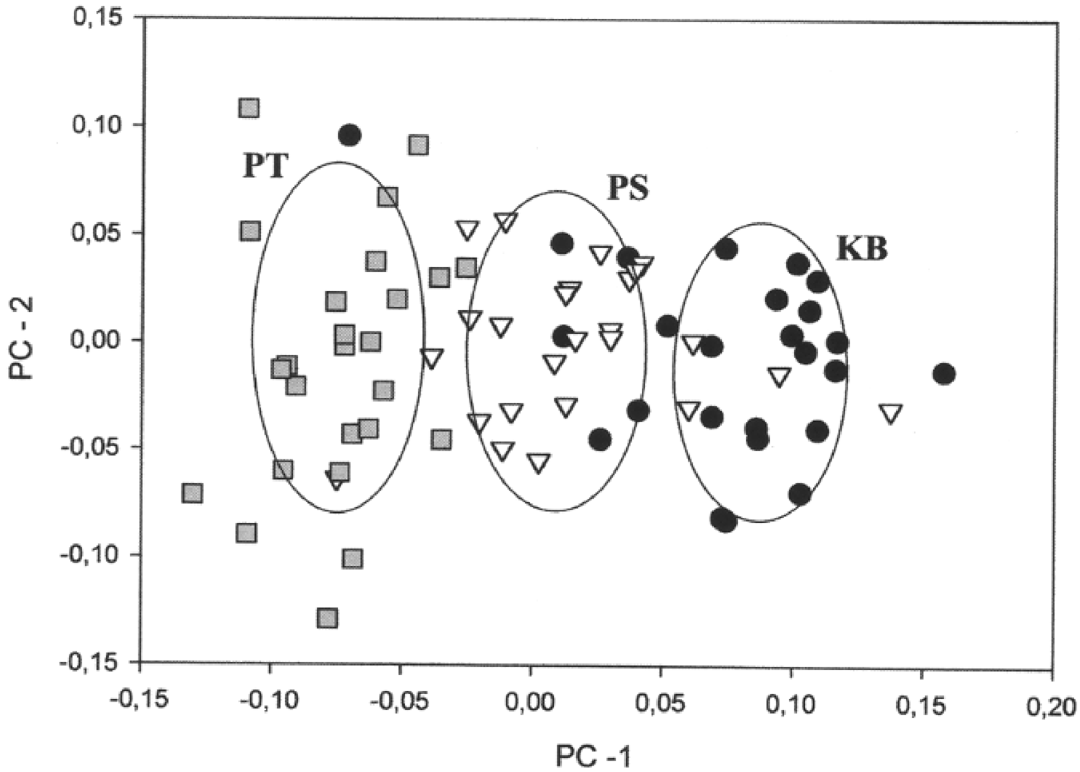


Fig. 36
36 – PCA diagram showing the objects in the ordination space of first and second principal components. The centre areas of occurrence encircling 60 % objects for particular investigated are shown. Symbol "▨" represents *Podohedra tropica*, symbol "∇" *Podohedra saltans* and symbol "O" *Keratococcus bicaudatus*.

isms. Consequently, the need of populational approach for the correct identification of *Keratococcus* and *Podohedra* species is obvious.

The tropical *Podohedra* species described in this paper differ distinctly from their relatives in temperate ecosystems. The discrete morphological characters for the differentiation of the aerial *Podohedra* species described so far, the species which were originally classified in *Podohedra* but later transferred to relative genera and *Keratococcus bicaudatus* are summarised in Table 1. The main characters suitable for species identification in these organisms are the cell and stalk dimension, the overall shape of cell outline (heteropolarity of cells, rounded or pointed apical pole – see the outline analysis), the presence or absence of pyrenoid and the structure of its starch envelope. *Podohedra georgei*, which was described from freshwater plankton differs considerably from aerial species in its overall cell morphology. Moreover, it has been observed only in free living unattached stage (HORTOBÁGYI 1969). Therefore, its position within the genus *Podohedra* remains questionable and should be possibly revised in the future.

The aerial cryptogamic communities in tropical rainforests are globally one of the less known species-rich algal microbiotopes. In floristic study carried out in 17 microlocalities in Peninsular Malaysia, 51 species of microscopic algae and

Table 1. The comparison of morphological characters and ecology of *Keratococcus bicaudatus* and aerial species originally described within the genus *Podohedra*.

Species	The cell dimensions [μm]	The stalk dimensions [μm]	The W : L ratio	The overall cell shape	The shape of the apical pole	Pyrenoid	Starch envelope of the pyrenoid	The number of autospores	Occurrence	References
Keratococcus bicaudatus (HANSGIRG) BOYE-PETERSEN; investigated strain: CAUP H 3301	(11–)18,5–26,5(–30) x (2–)2,5–7,5(–9)	3–5	1 : 2,5–8	fusiform to widely fusiform	pointed to obtuse pointed	yes; in old cells indistinct	separate grains	2 (–4)	species frequently occurs in soil and humid subaerial biotopes	e.g. HINDÁK (1970), KOMÁREK & FOTT (1983), ETTL & GÄRTNER (1995)
Keratococcus bicaudatus (HANSGIRG) BOYE-PETERSEN; material originally described as *Podohedra bicaudata* by GEITLER (1965)	16–23 x 4–6	3–7,5	1 : 3–4	broad fusiform to oval	short, pointed	yes; distinct	several distinct grains	not known	mucilaginous *Coccomyxa* growths on bare spruce wood, Austria	DÜRINGER (1958) (as *Podohedra* sp.), GEITLER (1965), HINDÁK (1970)
Monoraphidium rhaphidioides (HANSGIRG) HINDÁK; material originally described as *Podohedra distincta* by GEITLER (1965)	50–75 x 5–6,5	10–40	1 : 8–12	inflexed, narrow fusiform	elongated, distinctly pointed	yes; distinct	several densely aggregated distinct grains	not known	mucilaginous *Coccomyxa* growths between and on mosses on bare spruce wood, Austria	GEITLER (1965), HINDÁK (1970)
Podohedra longipes DÜRINGER	30–50 x 3–8	10–20	1 : 6–10	somewhat inflexed, fusiform to cask-like	short, obtuse pointed	yes; distinct	a lot of very small widely dispersed grains	(2–) 4	mucilaginous *Coccomyxa* growths on bare spruce wood, Austria, Czech Republic	DÜRINGER (1958), GEITLER (1965), NEUSTUPA et al. (2002)
Podohedra saltans NEUSTUPA	(7,2–)9,5–12,5(–13,5) x (3,2–)3,7–5,2	1,5–4	1 : 1,8–3	straight to slightly inflexed, ellipsoidal to reverse-egg-shaped	obtuse rounded to oval	yes; distinct	several distinct grains	2	on filamentous trentepohliacean algae on the stalk of *Bambusa sp.*, Malaysia	this paper

Table 1 (continued). The comparison of morphological characters and ecology of *Keratococcus bicaudatus* and aerial species originally described within the genus *Podohedra*.

Species	The cell dimensions [μm]	The stalk dimensions [μm]	The W : L ratio	The overall cell shape	The shape of the apical pole	Pyrenoid	Starch envelope of the pyrenoid	The number of autospores	Occurrence	References
Podohedra tropica NEUSTUPA	(9–)10–13,2 (–14,7) x (2,4–) 3–5,5(–6,8)	2,5–5(–8)	1 : 2–4,5	inflexed fusiform	short, obtuse to sharp pointed	yes; indistinct	without distinct starch envelope	2	on filamentous trentepohliacean algae on the leaf of an unidentified shrub, Malaysia	this paper
Podohedriella falcata (DÜRINGER) HINDÁK; originally described as *Podohedra falcata* by DÜRINGER (1958)	(20–)30–68 x 1,5–5	2,5–15	1 : 12–20	narrow fusiform	short, obtuse pointed	no	–	2 (–4)	mucilaginous *Coccomyxa* growths between and on mosses on bare spruce wood, Austria	DÜRINGER (1958), GEITLER (1965), HINDÁK (1988)

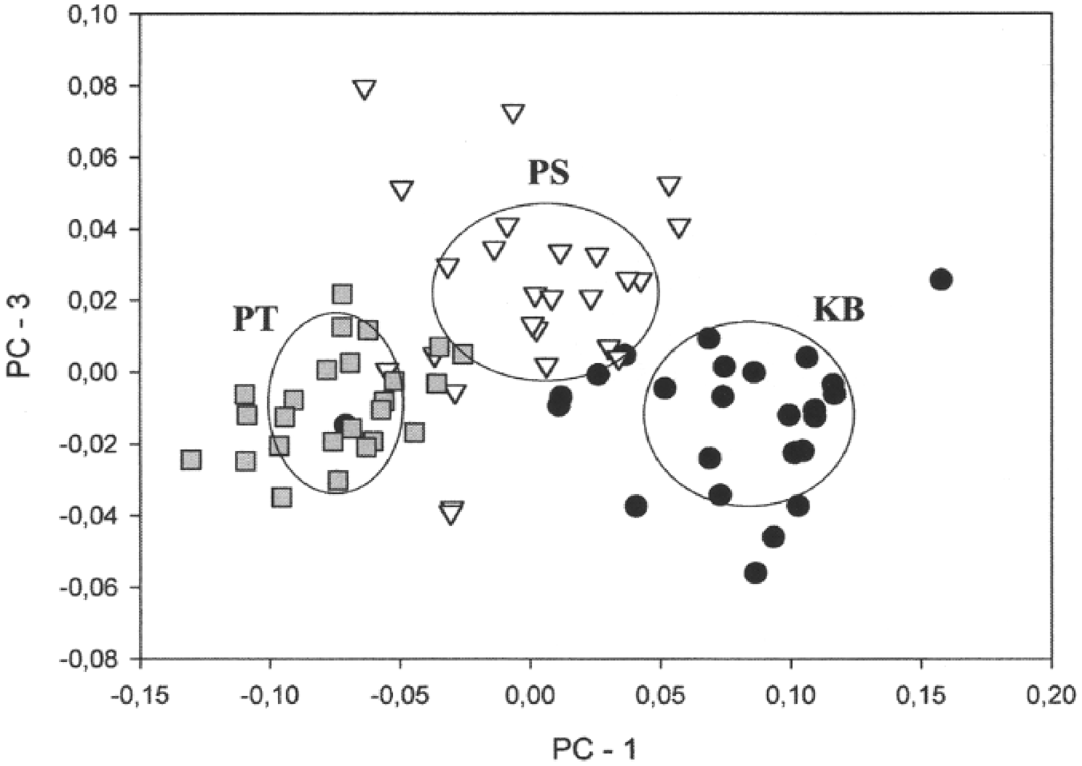


Fig. 37
37 – PCA diagram showing the objects in the ordination space of first and third principal components. The centre areas of occurrence encircling 60 % objects for particular investigated are shown. Symbol "▩" represents *Podohedra tropica*, symbol "∇" *Podohedra saltans* and symbol "O" *Keratococcus bicaudatus*.

cyanophytes were encountered. About 41 % of them have been considered as hardly identifiable or probably undescribed species (NEUSTUPA 2002). Regarding the abundance of different suitable microbiotopes and complexity of tropical rainforest ecosystem, we can assume that there is probably a "hidden continent" of microalgal diversity awaiting future scientific concern in the tropics. Consequently, the discovery of further *Podohedra*-type species would not be entirely surprising.

As well, we can assume the higher diversity of *Podohedra* species in temperate *Coccomyxa* dominated mucilaginous growths. NEUSTUPA et al. (2002) reported the occurrence of two unidentifiable morphotypes distinctly differing from described species in material from Šumava Mts. in Czech Republic. However, the reproduction and variability could not be ascertained in these populations. Therefore, these morphotypes remain undescribed till now.

The generic concept of *Podohedra* is based on cell morphology and the reproduction type. The infrageneric taxonomy relies mainly on morphological differences in shape of the vegetative cells and the cell dimensions (Tab. 1). The analyses of shape can provide valuable information for the taxonomy of these organisms. We assume that the outline fitting analysis will become one of the standard tools for the investigation of morphology and phenotypic plasticity of coccal green algae in the near future. Together with JENSEN et al. (2002) and ADAMS et al. (2003) we believe that geometric morphometrics provides new ground for the fundamental progress in morphology of living organisms in the 21st century.

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