

Investigations on the genus *Phycopeltis* (Trentepohliaceae, Chlorophyta) from South-East Asia, including the description of two new species

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Abstract – In the course of an investigation of the genus *Phycopeltis* from South-East Asia, two new species, *P. javanica* and *P. juarensis*, were discovered; *P. arundinacea* and *P. dorsopapillosa* were also recorded. *P. javanica* is characterised by obligate alternation of generations, intercalary gametangia and zoosporangia, absence of a sporangiophore and presence of dorsal papillae. *P. juarensis* is characterised by obligate alternation of generations, intercalary gametangia, terminal zoosporangia and presence of a sporangiophore up to five cells long. For *P. dorsopapillosa* the present record is the first for South-East Asia, suggesting the possible pantropical distribution of the species.

Phycopeltis / Southeast Asia / aerophytic algae / Chlorophyta / Trentepohliales

Résumé – Etudes sur le genre *Phycopeltis* (Trentepohliaceae, Chlorophyta) en Asie du Sud-Est, description de deux nouvelles espèces. Lors de l'étude du genre *Phycopeltis* en Asie du Sud-Est tropicale, deux nouvelles espèces (*P. javanica* et *P. juarensis*) ont été découvertes. *P. javanica* se caractérise par l'alternance obligée de générations, de gamétanges et zoosporanges en position intercalaire, par l'absence de sporangiophore et la présence de papilles dorsales. *P. juarensis* se caractérise par l'alternance obligée de générations, gamétanges en position intercalaire, zoosporanges en position terminale et la présence d'une sporangiophore de cinq cellules au maximum. L'auteur présente aussi les résultats des observations de *P. arundinacea* et *P. dorsopapillosa*, nouvellement récoltés dans la région. Pour *P. dorsopapillosa*, il s'agit d'une première récolte dans le Sud-Est de l'Asie tropicale; cette espèce pourrait avoir une distribution pantropicale.

Phycopeltis / Asie Sud-Est / algues aérophytiques / Chlorophyta / Trentepohliales

INTRODUCTION

Species of the genus *Phycopeltis* are often an important part of cryptogamic epiphyllous growths in tropical ecosystems (Lücking, 2001). *Phycopeltis* is one of the five genera currently included in the green algal order Trentepohliales, which has been recently shown to belong to the ulvophycean lineage (López-

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Bautista *et al.*, 2002; López-Bautista & Chapman, 2003). Molecular phylogenetic studies at the inter-generic level have shown the monophyly of the Trentepohliales (López-Bautista *et al.*, 2002; López-Bautista *et al.*, 2003), a conclusion that is in agreement with the unique, exclusively terrestrial ecology of the order.

The members of the genus *Phycopeltis* occur in subaerial conditions, growing mainly on perennial leaves of vascular plants. Descriptions of individual species date back to the 19th century (Millardet, 1870). Printz (1939) included in the genus 12 species, eight of which occurring exclusively in the tropics. However, the current taxonomic circumscription at species level is based primarily on the monograph of Thompson & Wujek (1997). These authors examined a great number of samples, collected mainly in tropical regions of the New World, and stressed the importance of several morphological features for the identification of individual specimens. The most important were the type of life-cycle (possibility of asexual gametophyte reproduction), the position of sporangia and gametangia and their arrangement within the thallus, cell dimensions, width: length ratio of gametophyte and sporophyte cells, presence of glandular outgrowths and sterile hairs, and characteristics of the sporangiophore. Thompson & Wujek (1997) included 18 species in the genus, 15 of which with an exclusive tropical distribution. Neustupa (2003) reported twelve species of *Phycopeltis* in a study dealing with the diversity of the genus in some regions of Southeast Asia. Only three species – *P. arundinacea* (Montagne) De Toni, *P. epiphyton* Millardet and *P. umbrina* (Kützing) Thompson *et* Wujek (for which the inclusion in *Phycopeltis* by Thompson & Wujek (1997) is, however, somewhat problematic) – have been reported as common in temperate regions. In the tropics, species of *Phycopeltis* frequently occur as phycobionts of epiphyllous lichens, forming communities with free-living members of the genus (Lücking, 2001; Grube & Lücking, 2002; Lücking & Grube, 2002). Lichenised specimens of *Phycopeltis* have been reported to differ markedly from free-living forms (Grube & Lücking, 2002; Lücking & Grube, 2002). As these lichenised thalli do not produce reproductive structures, which are essential for species identification, *Phycopeltis* phycobionts remain mostly undetermined (Grube & Lücking, 2002). However, Grube (pers. comm.) noted a high genetic diversity of lichenised *Phycopeltis*, which indicates a considerable and largely unexplored infrageneric diversity of the tropical populations.

On the other hand, Scannell (1978) and Rindi & Guiry (2002) found only one species, *P. arundinacea*, in Ireland. Rindi *et al.* (2003) and Rindi *et al.* (2004) reported two species of the genus from western France and north-western Spain. These marked differences in species number among different climatic zones indicate that constantly humid tropical ecosystems, with their stable environment and multitude of different microhabitats, may be regarded as the centre of biodiversity and evolutionary radiation for *Phycopeltis*.

For such a complex and diverse genus as *Phycopeltis*, it is not surprising that there are some ambiguities in the delimitation of several species (Rindi & Guiry, 2002; Rindi *et al.*, 2003; Rindi *et al.*, 2004; Neustupa, 2003). For example, the principal features of *P. arundinacea* as reported by Rindi & Guiry (2002), Rindi *et al.* (2003) and Rindi *et al.* (2004), differ considerably from those described by Thompson & Wujek (1997) for tropical populations of the species. European populations exhibit generally smaller cells and lower W: L ratio than tropical populations. However, as the European specimens are in agreement with Montagne's (1846) type material, Rindi *et al.* (2003) suggested the possibly different taxonomic nature of Thompson & Wujek's (1997) populations. The availability of molecular data would certainly be very useful for these investigations. However, recent taxonomic criteria allow to distinguish and to identify natural populations, if it is pos-

sible to assess in detail the characteristics of reproductive structures and other important morphological features. In the present study, two well defined populations of *Phycopeltis* from tropical ecosystems of Southeast Asia are described as new species. The paper provides a new contribution to my recent studies on the considerable and still little known biodiversity of tropical aerophytic algae in this region (Neustupa, 2003; Neustupa & Šejnohová, 2003; Neustupa, 2004).

MATERIAL AND METHODS

Samples were collected in January, August and September 2002 from leaves of *Lithocarpus* sp. and another unidentified tree in the Cibodas Botanical Garden, West Java, Indonesia (6°45'30"S and 107°00'10"E, altitude 1,450 meters above sea level) and from leaves of *Ficus* sp. in a primary lowland rainforest on Tioman Island, Pahang, Peninsular Malaysia (2°50'15"N and 104°13'55"E, altitude 200 meters a.s.l.). The first locality consists of parks and mountain gardens, more than 150 years old, located beside the mountainous tropical rainforest of Gede-Pangrango N.P. The second locality is a typical equatorial primary rainforest with multiple canopy cover resulting in shaded ever-wet conditions in the undergrowth and lower tree level. Both these localities belong to the very humid climate type, with annual precipitation exceeding 2500 mm.

The specimens were examined alive in the field using a PEAK field microscope and in the laboratory as glycerol preparations using an Olympus BX51 light microscope with differential and phase contrast and Olympus C5050 digital micro-photographic equipment. The photographs were processed with Adobe Photoshop 5.0. The separation of plants of *Phycopeltis* from the substratum, crucial for their observation and identification, was made by carefully peeling off the thalli with a blade or by using a sonicator bath.

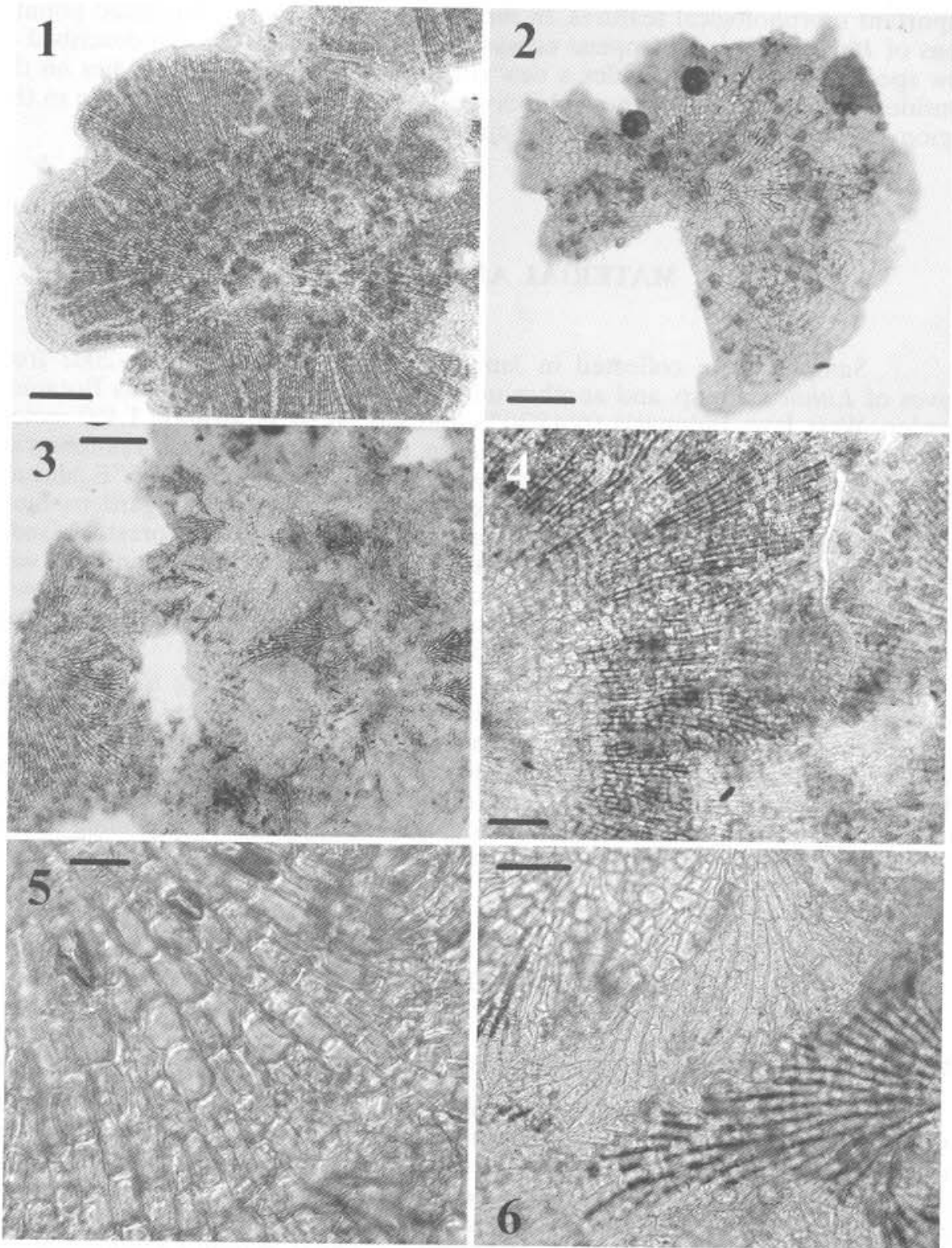
RESULTS AND DISCUSSION

Phycopeltis javanica Neustupa sp. nov.

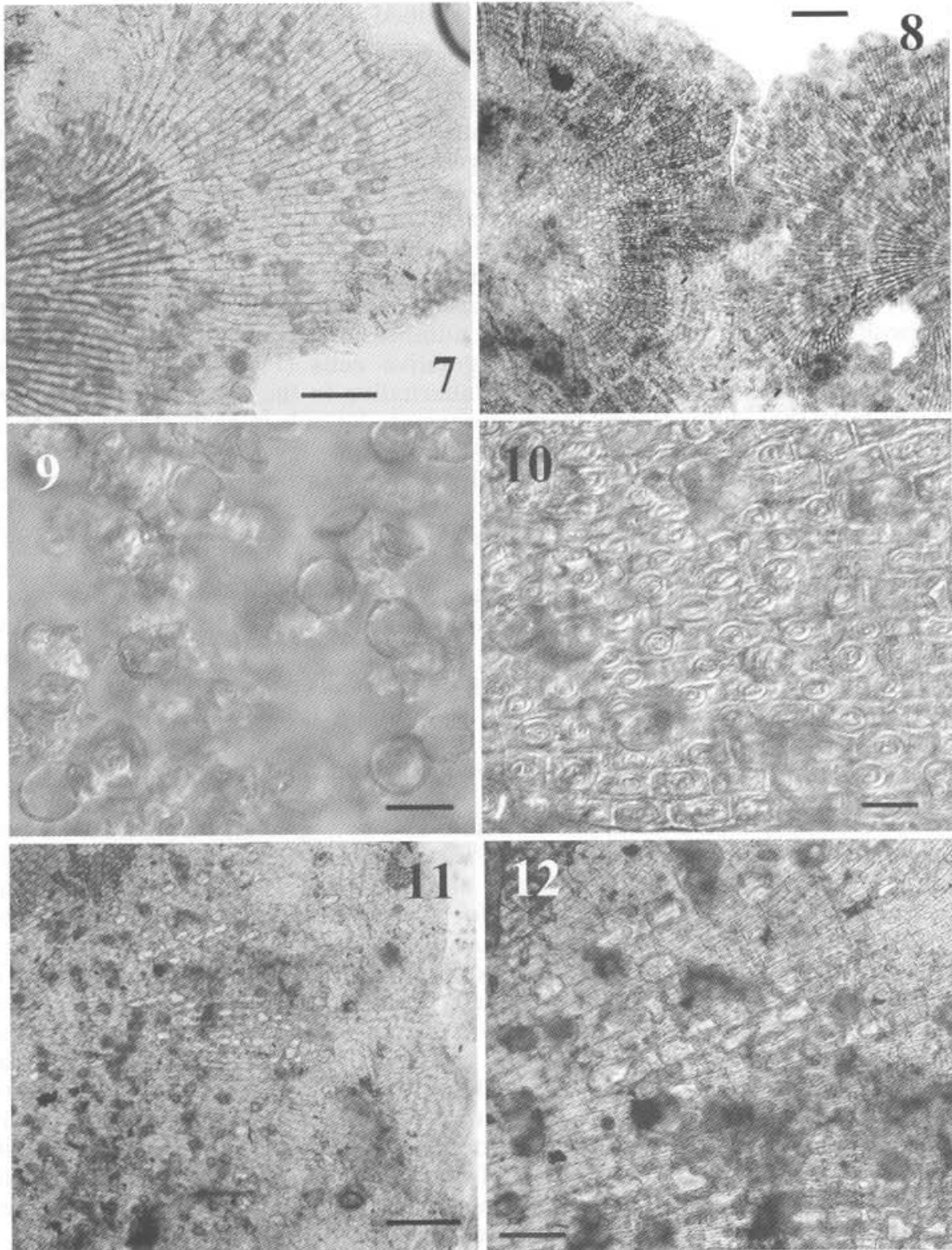
Figs 1-10

Alga discoidalis, crenata in margine vel late et irregulariter ramulata cum angustis vel latis sinubus. Thallus dimensiones tenuis 1.5 mm. Gametangia primaria intercalaria, gametangia secundaria proximaliter ab isdem filamentis centrifuga et centripeta evoluta. Sporangia intercalaria et fortuita ab origine producta. Sporangio-phora non observata. Plurimi thalli sporophytorum unicellulares nucleatas papillas medialiter et dorsaliter producent. Cellulae marginis ramulorum crebro papillae unicellulae producta. Gametangia et sporangia in plantis separatis solis producta.

Gametophytum: cellulae (3.5-)4.7-8.9-(10.2) μm latae et (7-)8.7-17.5-(18.8) μm longae, ratio 1:(1.8-)2-2.9(-3.1), gametangia ovalia, 6.2-14 μm lata et 11.5-25 μm longa. Sporophytum: cellulae (4.6-)7-13.2-(13.8) μm latae et (8-)9.4-25.5-(27) μm longae, ratio 1:(1.5-)1.7-3.1(-3.3), sporangia 12.5-20.8 μm lata et 14-21.5 μm longa.



Figs 1-6. *Phycopeltis javanica*. **1.** A mature sporophyte. **2.** Two adjacent sporophytic and gametophytic plants. **3.** A mixture of sporophytes and gametophytes. **4.** Detail of the marginal part of a gametophyte with abundant gametangial production (and adjacent sporophyte). **5.** Detail of empty gametangia. **Fig. 6.** Marginal part of a gametophyte. Scale bars: 150 μm for Figs 1-3; 50 μm for Fig. 4; 20 μm for Fig. 5; 40 μm for Fig. 6.



Figs 7-12. *Phycopeltis javanica* and *P. arundinacea*. Figs 7-10. *P. javanica*. **7.** A sporophyte with abundant intercalary sporangiate-laterals. **8.** Two adjacent gametophytic and sporophytic plants. **9.** Surface view of zoosporangia. **10.** Surface view of a sporophyte with abundant dorsal papillae. Figs 11,12. *P. arundinacea*. **11.** A gametophyte producing both gametangia and sporangia. **12.** Detail of gametangia. Scale bars: 40 μm for Figs 7, 12; 20 μm for Figs 9, 10; 100 μm for Figs 8, 11.

Holotypus: Indonesia, West Java, Cibodas Botanical Garden. On the leaves of *Lithocarpus* sp. and an unidentified tree, 1450 meters a.s.l., leg. J. Neustupa, 18.1.2002. Holotype is deposited in PRC (n° 2004/09).

The alga consists of discoidal thalli formed by wide ramuli laterally appressed to form a disc with crenate or irregularly lobed, wide-to-narrow sinuses (Figs 1-3). Thalli are up to 1.5 mm in diameter. The primary gametangia develop from intercalary cells, the secondary gametangia develop subsequently, centripetally and centrifugally to the primary ones (Figs 4-6). Usually, the gametangia develop continuously in or around the central area of the thallus. The sporangiate-laterals arise from intercalary cells, irregularly within the thallus (Figs 1, 7-9). Production of a sporangiophore was not observed; the suffultory cells grow directly from vegetative cells of the thallus. In the zoosporangia, the papilla-pore is opposite to the end of attachment. A number of sporophytic thalli bear one-celled dorsal papillae produced by vegetative cells (Fig. 10). Perhaps, these papillae are formed as a developmental alternative to the production of sporangiate-laterals; they differ clearly from sporangiate-laterals in early stages and their possible transformation into sporangiate-laterals was never observed, even when a large number of reproductive sporophytes were inspected. Similar glandular cells may also be formed in the points of contact of different thalli or sinuses. The gametangia and sporangia are never formed on the same plants, indicating obligate alternation of generations (Figs 2-4, 6, 8). In addition, the vegetative cells of the sporophyte have a larger size than the gametophyte cells.

The dimensions of the gametophyte vegetative cells are (3.5-)4.7-8.9-(10.2) × (7-)8.7-17.5-(18.8) μm. The W:L ratio is 1:(1.8-)2-2.9(-3.1). The gametangia are oval, 6.2-14 × 11.5-25 μm. Vegetative cells of the sporophyte are (4.6-)7-13.2-(13.8) × (8-)9.4-25.5-(27) μm, with the W:L ratio 1:(1.5-)1.7-3.1(-3.3). Sporangia are 12.5-20.8 × 14-21.5 μm.

The name of the species is derived from the island of origin.

Phycopeltis javanica, described here as a new species, differs from all currently known members of the genus *Phycopeltis*. Thompson & Wujek (1997) reported several species with obligate alternation of generations. *Phycopeltis aurea* G. Karsten differs from our alga for the typically terminal position of the gametangia, the much smaller size of the vegetative cells and the production of sporangiophores formed by 10 or more cells (Thompson & Wujek, 1997; Neustupa, 2003). *Phycopeltis costaricensis* Thompson & Wujek is characterised by the typical subterminal position of both gametangia and sporangia (even if the only picture of this species in Thompson & Wujek (1997) does not show this feature very well). However, *P. costaricensis* has significantly smaller dimensions of vegetative cells and reproductive structures, with cells of the sporophyte scarcely differing in size from those of the gametophyte, which is definitely not the case in *P. javanica*. In addition, the production of dorsal papillae has not been reported in *P. costaricensis*. *Phycopeltis flabellata* Thompson & Wujek differs from our species for its open ramulate habit and for the terminal position of the gametangia.

Several species of *Phycopeltis* with discoidal thallus form a relatively homogeneous group, for which, however, the relationships at species level are uncertain. Since *P. javanica* is morphologically similar to several of these species, a detailed discussion of their differences is necessary.

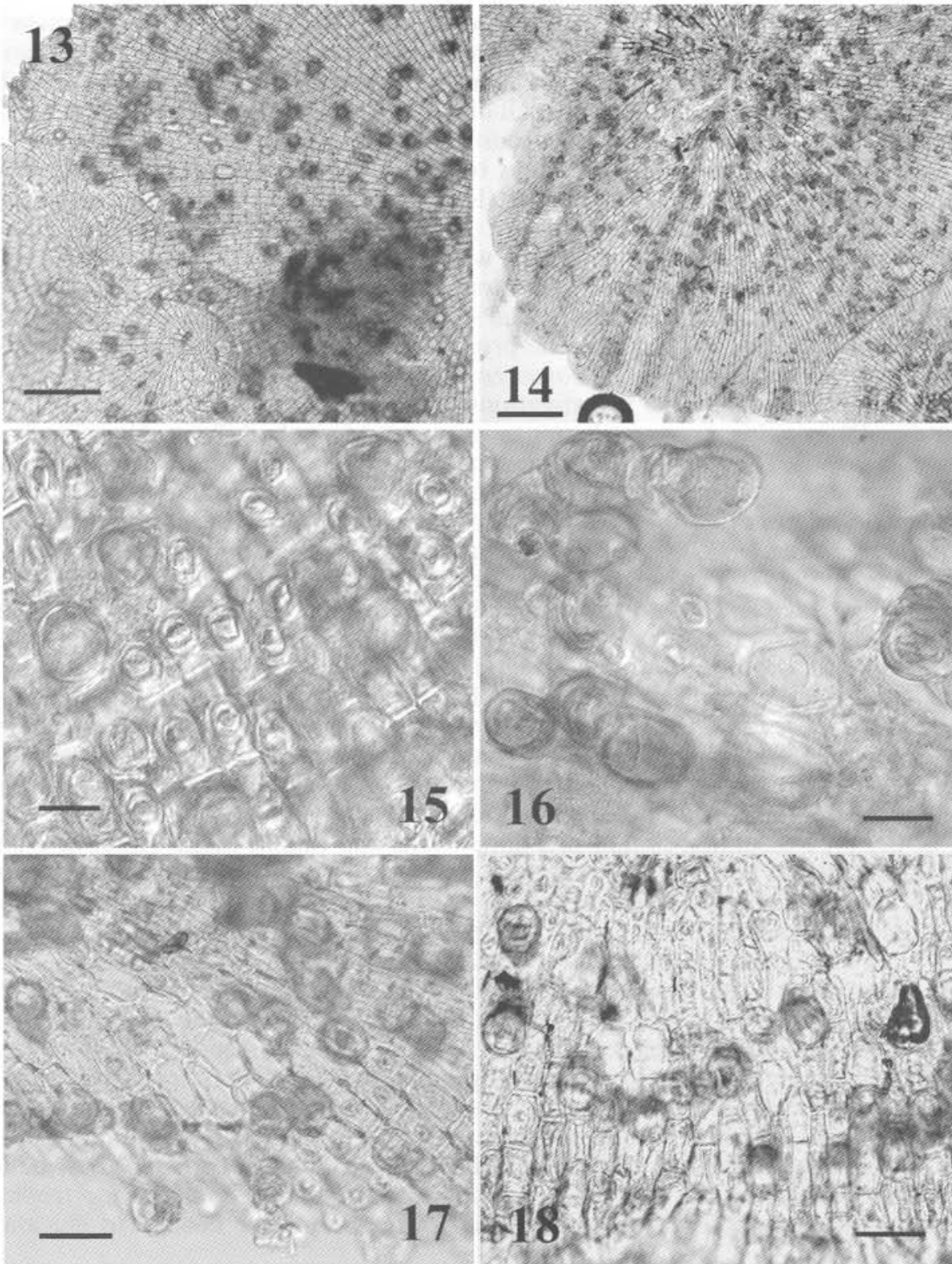
Phycopeltis novae-zealandiae Thompson & Wujek was described from Tokapuna, North Island of New Zealand, and reported also from Hawaii and Costa Rica (Thompson & Wujek, 1997). The species was circumscribed mainly on the basis of the circular arrangement of the gametangia and the obligate alterna-

tion of gametophyte and sporophyte generations. However, both Rindi & Guiry (2002) and Rindi *et al.* (2003) expressed some doubts about the distinctiveness of *P. novae-zealandiae*. They noticed the resemblance of the European populations of *P. arundinacea* to *P. novae-zealandiae* in the arrangement of the gametangia, the general habit of the thallus and the cell dimensions. However, differently from the obligate alternation of generations occurring in *P. novae-zealandiae* (Thompson & Wujek, 1997), the European specimens of *P. arundinacea* produce both gametangia and sporangia on the same plants (Rindi *et al.*, 2004). This life-cycle pattern seems also to be common to all tropical populations of *P. arundinacea* that I have so far investigated. Therefore, I agree with Rindi *et al.* (2004) that the possible conspecificity of *P. novae-zealandiae* and *P. arundinacea* remains a subject for future studies. Unfortunately, Thompson's type material of *P. novae-zealandiae* has been lost (Rindi & Guiry, 2002). The problem could be elucidated by future findings of typical populations of *P. novae-zealandiae* – possibly from the type locality – and detailed comparative investigations of these species.

Phycopeltis expansa Jennings was also described from New Zealand (Jennings, 1895). The species was characterised mainly by its unique pattern of sporangial production, where the suffultory cell is borne on a sporangiophore formed by a single cell. In other features, the species was reported to be similar to *P. arundinacea* by Printz (1939). *P. expansa* was regarded as a synonym of *P. arundinacea* by Scannell (1978), who did not attribute any taxonomic value to the presence/absence and type of sporangiophores. Sarma (1986) recorded this species again from several localities in New Zealand, but several of his specimens apparently did not produce the single-celled sporangiophores. Thompson & Wujek (1997) did not mention this species, but Rindi & Guiry (2002), investigating Irish populations of *P. arundinacea*, remarked that their populations were characterised by the complete absence of sporangiophores. Consequently, they concluded that *P. expansa*, with the single-celled sporangiophore described by Jennings (1895), could nevertheless represent an independent taxonomic entity. Given the proximity of the type localities, similar cell dimensions and thallus habit, Rindi & Guiry (2002) and Rindi *et al.* (2004) suggested the possible conspecificity of *P. expansa* and *P. novae-zealandiae*. However, until further investigations of populations of *Phycopeltis* from New Zealand are carried out, this issue remains unresolved.

For *P. arundinacea*, Rindi *et al.* (2003) noticed the difference between the type material and the European population of *P. arundinacea* on one hand, and Thompson & Wujek's (1997) tropical reports of this species on the other. The main differences included greater cell dimensions, the presence of sporangiophores and the extremely high W:L ratio in tropical populations. However, as for the original collections of *P. novae-zealandiae*, the specimens of *P. arundinacea* investigated by Thompson & Wujek (1997) have been lost. After a detailed examination of European specimens of *P. arundinacea*, Rindi *et al.* (2004) expressed their belief that there is no need at present to reject records of *P. arundinacea* for tropical regions. Still, they pointed out that further observations are needed to elucidate this problem.

In the course of my *Phycopeltis* investigation in Southeast Asia, I have encountered several times populations fitting well into the delimitation of *P. arundinacea*. In the course of this study, specimens referable to this species were collected on leaves of *Garcinia* sp. in the Bogor Botanical Garden (altitude approximately 200 meters a.s.l.) and in the area of the Cibodas Botanical Garden (Figs 11-13). The plants had discoidal thalli, with vegetative cells $6.6-12 \times 13-25 \mu\text{m}$ and W:L ratio 1: 1.8-3.3. They bore intercalary sporangia and gametangia, which regularly occurred on the same plants. No production of dorsal papillae or



Figs 13-18. *Phycopeltis arundinacea* and *P. dorsopapillosa*. **13.** *P. arundinacea*. A gametophyte with both gametangia and sporangia. **Figs. 14-18.** *P. dorsopapillosa*. **14.** A gametophyte plant with intercalary gametangia and sporangia. **15.** Detail of dorsal papillae and zoosporangia. **16.** Detail of some sporangiate-laterals and an empty gametangium. **17, 18.** Marginal parts of gametophytic thalli showing production of sporangiate-laterals, gametangia and dorsal papillae. Scale bars: 75 μm for Figs 13, 14; 10 μm for Figs 15-17; 20 μm for Fig. 18.

secondary sporangiophores was observed. Except for the size of the cells, these populations concur well with the specimens presented by Rindi *et al.* (2004) and they can therefore be conspecific with European *P. arundinacea*. In agreement with Rindi & Guiry (2002), I conclude that the differences in size and W:L ratio between European and tropical specimens could be due to environmental conditions favouring a more vigorous growth in the tropics.

In any case, *Phycopeltis javanica* differs from both the original descriptions of *P. expansa* (Jennings, 1985) and *P. novae-zealandiae* (Thompson & Wujek, 1997) and from European and tropical populations of *P. arundinacea*. *P. javanica* typically develops dorsal papillae on vegetative cells – a prominent feature never observed in any of the aforementioned species. My observations indicate that the dorsal papillae are a stable morphological feature and occur consistently throughout the populations examined; they should therefore be considered a useful taxonomic character for identification at species level. For the complete absence of sporangiophores *P. javanica* differs from *P. expansa*, whose specific delimitation relies exclusively on this feature. In contrast to *P. novae-zealandiae*, our species never produces circular gametangial bands and the gametangia are typically produced in the central area of the thallus. In addition, the secondary sporangiophores, which have been reported for *P. novae-zealandiae*, were never observed during my examination of *P. javanica*. Similarly to *P. arundinacea*, the absence of secondary sporangiophores (causing the suffultory cells to arise directly from the vegetative cells of the disc) seems to be a stable feature of *P. javanica*. Although the taxonomic relevance of this feature was neglected by Thompson & Wujek (1997), on the basis of my observations I can only support the statement of Rindi *et al.* (2003) and Rindi *et al.* (2004) advocating its taxonomic value. However, *P. javanica* produces dorsal papillae on vegetative cells and it has obligate alternation of generations, which clearly separates this species from *P. arundinacea*.

Another species with both intercalary sporangia and gametangia, *Phycopeltis theaensis* Neustupa, was described from mountainous regions of Peninsular Malaysia (Neustupa, 2003). This species, resembling *P. novae-zealandiae* in the circular arrangement of gametangia and the regularly discoidal shape of the thallus, produces dorsal papillae in sporophyte plants. However, differently from *P. javanica*, *P. theaensis* is capable of joint gametangial and sporangial production on gametophytes, is characterised by a smaller thallus and smaller vegetative cells, and produces sporangiophores.

Phycopeltis dorsopapillosa Thompson & Wujek, described from Costa Rica and Salvador, is another species for which production of dorsal papillae has been reported. There is some ambiguity in the original description of this species by Thompson & Wujek (1997). These authors reported the simultaneous occurrence of gametangia and sporangia on the gametophytes, whereas sporophytes were absent from the populations investigated. However, the corresponding illustrations depict plants exhibiting rich sporangial production and designated as sporangial plants. Furthermore, there are no illustrations of plants producing both gametangia and sporangia.

In the present study, populations corresponding to Thompson & Wujek's (1997) description of *P. dorsopapillosa* were recorded (Figs 14-18). These occurred on leaves of several plants in the secondary vegetation covering the slopes of Mt. Galunggung in the province of West Java, Indonesia, at an altitude of approximately 800 meters a.s.l. The diameter of the discoidal plants was up to 2 mm; the vegetative cells were 6.8-13.5 × 18-28 μm and the W:L ratio was 1: 1.8-3.6. Sporangia and gametangia were intercalary and were borne on the same plants; the plants frequently produced dorsal papillae (Fig. 15). These specimens

are in good agreement with the original description of *P. dorsopapillosa* and I assume that this should be regarded as the first record of *P. dorsopapillosa* from Southeast Asia, indicating the possible pantropical distribution of the species.

Apart from the smaller cell dimensions, *P. javanica* differs from this species mainly in its obligate alternation of generations and by a somewhat different thallus morphology, which is regularly discoidal in *P. dorsopapillosa*, but widely ramulate in *P. javanica*. This combination of characteristics makes these organisms readily distinguishable on careful investigation.

***Phycopeltis juarensis* Neustupa sp. nov.**

Figs 19-26

Alga discoidalis integrimargine. Thallus dimensiones tenuis 0.4 mm. Gametangia primaria intercalaria, gametangia secundaria proximaliter ab isdem filamentis centrifuga et centripeta evoluta. Sporangia terminalia, sporangiophora, fortasse ab cellulis per proliferationem successivam novorum sporangiophorum lateraliorum, latiora quam longiora producta. Gametangia et sporangia in plantis separatis solis producta.

Gametophytum: cellulae (2.5-)3.7-7.6-(8.6) μm latae et (7.5-)8-12.5-(13.5) μm longae, ratio 1:(1.3-)1.5-2.7(-3), gametangia ovalia, 4.8-13 μm lata et 8.5-25.5 μm longa. Sporophytum: cellulae (2.5-)3.5-8-(8.8) μm latae et (7.5-)9-22.5-(25) μm longae, ratio 1:(1.8-)2-4.4(-4.7), sporangia 10-17.5 μm lata et 10.5-18.8 μm longa.

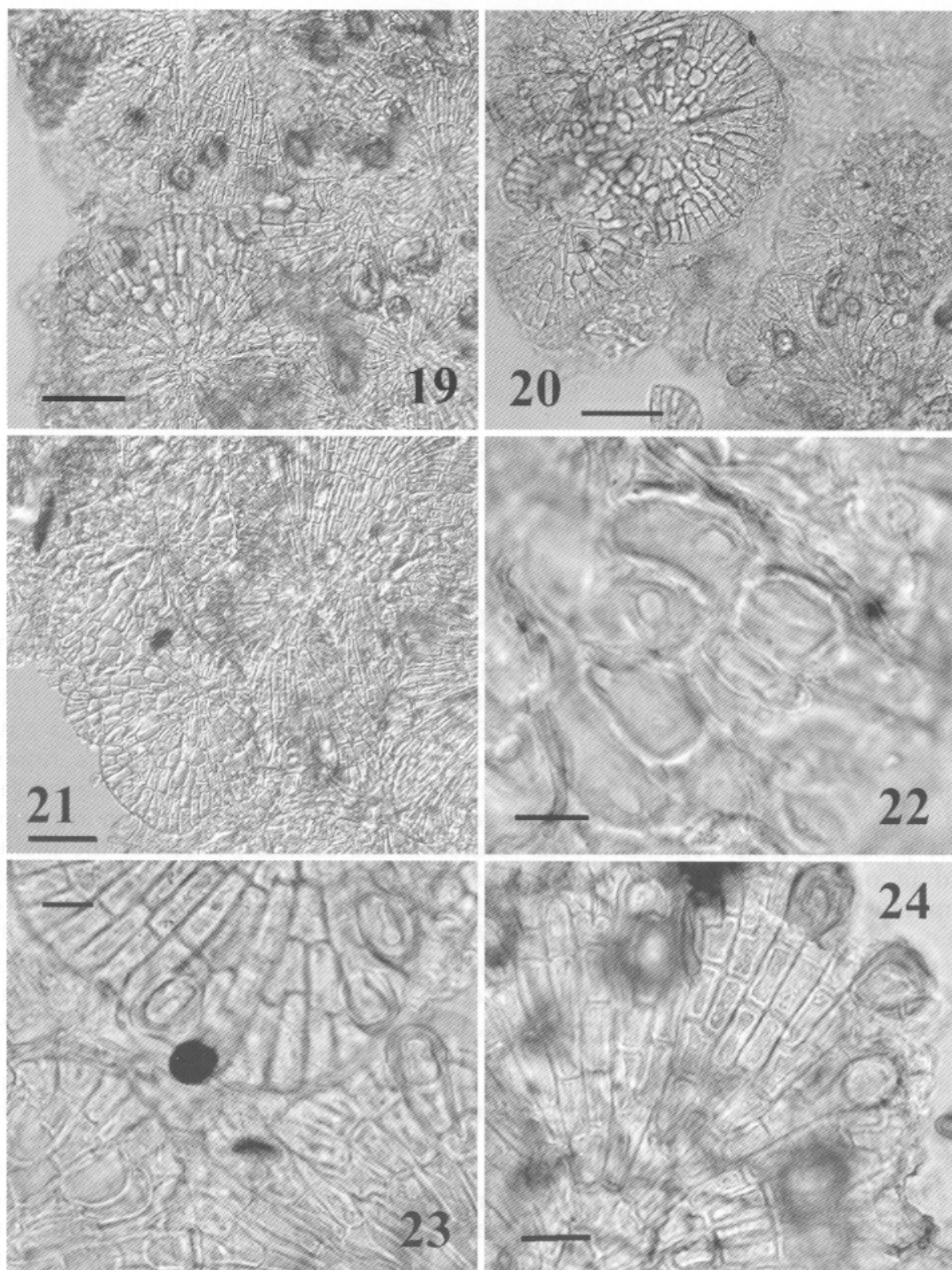
Holotypus: Malaysia, Pahang, Pulau Tioman. On leaves of *Ficus* sp. in a primary lowland rainforest, 300 meters a.s.l., leg. J. Neustupa, 28.8.2002. Holotype is deposited in PRC (no. 2004/10).

The alga consists of discoidal thalli with dimensions up to 0.4 mm (Figs 19, 20). The primary gametangia develop randomly from intercalary cells, the secondary gametangia develop centripetally and centrifugally to the primary ones (Figs 19-22). Along the margins of adjacent thalli gametangia can also develop from terminal cells. The sporangiate-laterals develop on terminal vegetative cells (Figs 23, 24). They are formed either along the margins of the thallus or within the disc (in the second case, they terminate the growth of the vegetative filament on which they are produced, which is then overgrown in length by the adjacent filaments). The secondary sporangiophores, up to 5 cells long, are formed by the proliferation of new sporangiate-laterals from previous suffultory cells (Figs 25, 26). The cells of the sporangiophores are typically wider than long. The papilla-pore is in terminal position on the zoosporangia. The organism has obligatory alternation of sporophyte and gametophyte generations. Thus, the gametangia and the sporangiate-laterals are always found on separate plants.

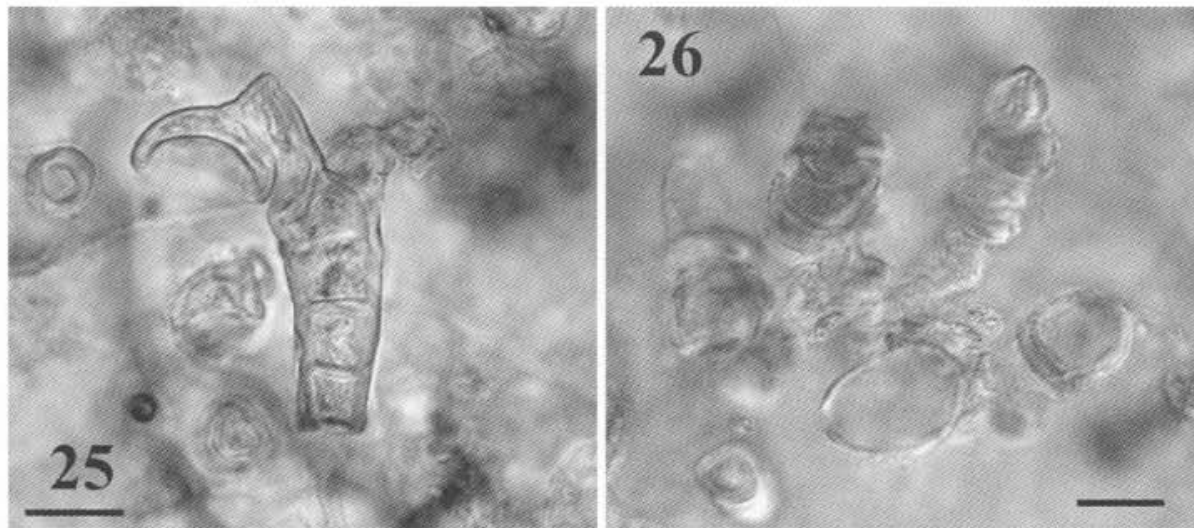
The dimensions of the gametophyte vegetative cells are (2.5-)3.7-7.6-(8.6) \times (7.5-)8-12.5-(13.5) μm . The W:L ratio is 1:(1.3-)1.5-2.7(-3). The gametangia are oval, 4.8-13 \times 8.5-25.5 μm . Vegetative cells of the sporophyte are (2.5-)3.5-8-(8.8) \times (7.5-)9-22.5-(25) μm , with W:L ratio 1:(1.8-)2-4.4(-4.7). Sporangia are 10-17.5 \times 10.5-18.8 μm .

The name of the species is derived from the name of a village near the type locality.

From the morphological point of view, *P. juarensis* is one of the very small discoidal species of *Phycopeltis*. In this group, *P. aurea* differs from *P. juarensis* for the terminal position of the gametangia and the characteristically low W:L ratio of the vegetative cells (Thompson & Wujek, 1997; Neustupa, 2003). Another species with terminal gametangia – *P. terminopapillosa* Thompson & Wujek – is characterised by the abundant presence of glandular cells along the margins of the thalli.



Figs 19-24. *Phycopeltis juarensis*. **19-21**. Mixture of sporophytes and gametophytes. **22**. Detail of empty gametangia. **23**. Detail of two sporophytes with terminal sporangiate-laterals and a gametophyte with gametangia. **24**. Detail of a sporophyte with terminal sporangiate-laterals. Scale bars: 40 μm for Figs 19-21; 10 μm for Figs 22-24.



Figs 25-26. *Phycopeltis juarensis*. **25.** Detail of a sporangiophore. **26.** Surface view of sporangia. Scale bars: 10 μm .

Finally, the type species of the genus – *Phycopeltis epiphyton* Millardet – has intercalary gametangia developing mostly in the central part of the disc and sporangiate-laterals developing in terminal position. This species has also been reported from subtropical and temperate regions (Millardet, 1870; Printz, 1939; Thompson & Wujek, 1997). Recently, European specimens of this species have been examined by Rindi *et al.* (2004). The European plants exhibit minute dimensions, obligate alternation of generations and production of sporangiate-laterals without a sporangiophore on terminal vegetative cells. The gametangia are regularly produced from vegetative cells located in the central portion of the thallus and in older plants the central parts are often formed by clusters of empty gametangia. Rindi *et al.* (2004) discussed the probable ambiguity in the interpretation of tropical findings of *P. epiphyton* (e.g. Thompson & Wujek, 1997; Krishnamurthy, 2000 (without an illustration); Neustupa, 2003). In these studies, the sporangia and gametangia are reported to occur frequently on the same plants (e.g., Fig. 3.30. in Thompson & Wujek, 1997). In addition, Rindi *et al.* (2004) reported absence of sporangiophores in European populations and differences in cell size. I agree with these authors that the tropical reports of *P. epiphyton* may possibly represent populations of different specific nature and that they should be evaluated critically in the future.

Differently from *P. epiphyton*, in *P. juarensis* the gametangia do not develop from the central cells of the gametangial plants; they are produced irregularly from intercalary vegetative cells and even in old gametangial plants the central parts of the thallus consist mostly of living vegetative cells. Additionally, there is a prominent production of sporangiophores in *P. juarensis* (in mature sporangial plants almost all the sporangiate-laterals develop into sporangiophores). Frequently, the sporangiate-laterals of *P. juarensis* occur within the thallus and they superficially appear as intercalary. However, with careful observation it is possible to notice that every sporangiate-lateral terminates the growth of its vegetative filament, which eventually becomes overgrown from adjacent filaments.

Another distinctive character of this species is the unusually large W:L ratio of the sporophyte vegetative cells. In contrast to other small species of

Phycopeltis, where the W:L ratio does not exceed 1:3, the sporophyte plants of *P. juarensis* usually have cells with W:L equal to 1:4.5.

The diversity of *Phycopeltis* in the tropics is probably immense. To date, the infrageneric taxonomy of *Phycopeltis* is still entirely based on morphological characters. It can be expected that major modifications in the arrangement at species level will be determined by the use of different approaches, especially molecular. However, in the current state of our knowledge of *Phycopeltis*, individual morphospecies can be circumscribed by careful examination of stable structural and ontogenetic features, enabling identification of natural populations and enumeration of their diversity. In this respect, I agree with Thompson & Wujek (1997) in their assertion of the importance of the life-cycle characteristics (alternation of generations), the position of both sporangiate-laterals and gametangia and the presence/absence of several other structures, e.g. dorsal papillae or sterile filaments, as the most useful attributes for delimitation of morphological species. In my opinion, the presence/absence of sporangiophores and the pattern of gametangial formation are also stable and taxonomically useful features.

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REFERENCES

- GRUBE M. & LÜCKING R., 2002 — Fine structure of foliicolous lichens and their lichenicolous fungi studied by epifluorescence. *Symbiosis* 32: 229-246.
- JENNINGS A.V., 1895 — On two new species of *Phycopeltis* from New Zealand. *Proceedings of the Royal Irish Academy* 3: 753-766.
- KRISHNAMURTHY V., 2000 — *Algae of India and neighbouring countries. I. Chlorophycota*. Enfield, New Hampshire, Science Publishers, 210 p.
- LÓPEZ-BAUTISTA J.M., WATERS D.A. & CHAPMAN R.L., 2002 — The Trentepohliales revisited. *Constancea* 83: http://ucjeps.berkeley.edu/constancea/83/lopez_etal/trentepohliales.html
- LÓPEZ-BAUTISTA J.M. & CHAPMAN R.L., 2003 — Phylogenetic affinities of the Trentepohliales inferred from small-subunit rDNA. *International Journal of Systematic and Evolutionary Microbiology* 53: 2099-2106.
- LÓPEZ-BAUTISTA J.M., RINDI F., GUIRY F., BROADY P., BROOKS F. & CHAPMAN R.L., 2003 — Evolutionary relationships in the family Trentepohliaceae. *Journal of Phycology* 39 (Suppl.): 37.
- LÜCKING R., 2001 — Lichens on leaves in tropical rainforests: life in a permanently ephemeral environment. In: Gottsberger G. & Liede S. (eds), *Life forms and dynamics in tropical forests*. Stuttgart, J. Cramer Verl., pp. 41-78.
- LÜCKING R. & GRUBE M., 2002 — Facultative parasitism and reproductive strategies in *Chroodiscus* (Ascomycota, Ostropales). *Stapfia* 80: 267-292.
- MILLARDET A., 1870 — De la germination des zygospores des genres *Closterium* et *Staurastrum* et sur un genre nouveau d'algues chlorospores. *Mémoires de la Société de Sciences Naturelles de Strasbourg* 6: 37-50.
- MONTAGNE C., 1846 — Phyceae. In: Durieu de Maisonneuve M.C. (ed.), *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842*. Sciences physiques. Botanique. Cryptogamie. Paris, Imprimerie Nationale, pp. 1-197.
- NEUSTUPA J., 2003 — The genus *Phycopeltis* (Trentepohliales, Chlorophyta) from tropical Southeast Asia. *Nova Hedwigia* 76: 487-505.

- NEUSTUPA J., 2004 — Two new aerophytic species of the genus *Podohedra* Düringer (Chlorophyceae). *Archiv für Hydrobiologie* 152, Supplement *Algological Studies* 112: 1-16.
- NEUSTUPA J. & ŠEJNOHOVÁ L., 2003 — *Marvania aerophytica* sp. nov. — a new aerial tropical green alga. *Biologia* 58: 503-507.
- PRINTZ H., 1939 — Vorarbeiten zu einer Monographie der Trentepohliaceen. *Nytt. Magasin for Naturvidenskapene* 80: 137-210.
- RINDI F. & GUIRY M.D., 2002 — The genus *Phycopeltis* (Trentepohliaceae, Chlorophyta) in Ireland: a taxonomic and distributional reassessment. *Phycologia* 41: 421-431.
- RINDI F., GUIRY M.D., CRITCHLEY A.T. & ARGALL E., 2003 — The distribution of some species of *Trentepohliaceae* (Trentepohliales, Chlorophyta) in France. *Cryptogamie, Algologie* 24: 133-144.
- RINDI F., MENÉNDEZ J.L., GUIRY M.D. & RICO J.M., 2004 — The taxonomy and distribution of *Phycopeltis* (Trentepohliaceae, Chlorophyta) in Europe. *Cryptogamie, Algologie* 25: 3-17.
- SARMA P., 1986 — The freshwater Chaetophorales of New Zealand. *Beihefte zur Nova Hedwigia* 58: 1-169.
- SCANNELL M.J.P., 1978 — *Phycopeltis arundinacea* Mont. in Europe. *Revue Algologique* 13: 41-42.
- THOMPSON R.H. & WUJEK D.H., 1997 — *Trentepohliales: Cephaluros, Phycopeltis and Stomatochroon. Morphology, taxonomy and ecology*. Enfield, New Hampshire, Science Publishers, 149 p.