The genus *Phycopeltis* (Trentepohliales, Chlorophyta) from tropical Southeast Asia

by

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Abstract: Twelve species of the aerophytic green alga *Phycopeltis* from epiphyllous biotopes in Peninsular Malaysia, Sumatra and Java are reported. *Phycopeltis theaensis* sp. nov. is described as a new species from leaves of *Thea sinensis* at mountainous tea estates in Peninsular Malaysia. Two of the species found during the investigation (*P. arundinacea P. epiphyton*) seem to have a cosmopolitan distribution in tropical, subtropical and temperate ecosystems. Seven species (*P. amboinensis*, *P. aurea*, *P. irregularis*, *P. pseudotreubii*, *P. treubii*, *P. treubioides*, *P. vaga*) appear to have a pantropic distribution. *Phycopeltis kosteriana*, *P. prostrata* and *P. theaensis* have yet to be reported outside the Indo-Malayan-North Australian phycogeographical region.

Introduction

The genus *Phycopeltis* was established by Millardet (1870) with *P. epiphyton* as the type species. The alga was found on needles and perennial leaves of several plant species in central Europe. However, since that time the infrequent occurrence of *Phycopeltis* has been reported mainly from subaerial biotopes in the tropics and subtropics.

In the original description the genus was characterized as an epiphytic aerophytic alga forming a pseudoparenchymatous discoidal or ramulate thallus with gametangia (Kugelsporangien) developing from vegetative cells. Karsten (1891) ascertained the presence of a second type of reproductive structures – the sporangia (Hakensporangien) on hooked suffultory cells (Kopfzellen) homologous to similar structures in the related genera *Trentepohlia* and *Cephaleuros*.

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Printz (1939) in his preliminary monograph of the Trentepohliaceae reported 12 species within *Phycopeltis*, eight of them with exclusive tropical distribution. The cell dimensions, presence/absence of gametangia (Kugelsporangien) and sporangia (Hakensporangien) and the shape of the thallus were considered the most important characters for delimiting of species.

Unfortunately, the life cycle was not ascertained in most of these early *Phycopeltis* descriptions. However, Trentepohliaceae are known to have a complex life cycle with both sexual and asexual modes of reproduction. Without the knowledge of the life cycle, each type of thallus in the field material was often described as a separate species.

The recent monograph of Thompson & Wujek (1997) is a milestone in *Phycopeltis* taxonomy. The authors have worked out a critical revision of the genus and investigated the life cycle of various *Phycopeltis* species. Homothallic, isogamous and isomorphic alternations of generations in the *Phycopeltis* life cycle were detected. The old descriptions were revised and a number of new species from tropical ecosystems were described. Thompson & Wujek (1997) stressed the importance of several characters for *Phycopeltis* infrageneric taxonomy. The most important characters are the following: the apical/terminal nature of sporangia and gametangia and their position within the thallus, the shape of the thallus, cell dimensions and width:length ratio on both gametophyte and sporophyte, the possibility of asexual duplication of the gametophyte, the presence of sterile hairs or glandular-like cells on the thallus and whether the sporangiophores are produced by apical cell or by successive proliferation of the suffultory cell. In the present study the species concept within the genus *Phycopeltis* and the respective terminology as worked out by Thompson & Wujek (1997) are adopted in substance.

The species of *Phycopeltis* are among the most abundant and distinct representatives of cryptogamic epiphyllous communities in tropical rainforests ecosystems (Kiew 1988). Particularly in mountainous tropical locations the epiphyllous *Phycopeltis* growths are virtually omnipresent with considerable ecological significance for the ecosystem as a whole (Whitten et al. 2000). However, our knowledge of biodiversity, ecology and distribution of individual *Phycopeltis* species is still very scarce. With the exception of the above mentioned monograph of Thompson & Wujek (1997) there are no other modern studies concerning the distribution of *Phycopeltis* species in different biotopes and areas of a single region in the tropics. Recently, Rindi & Guiry (2002) published a study dealing with the distribution and taxonomy of *Phycopeltis* in Ireland. They found only one *Phycopeltis* species (identified as *P. arundinacea*) occurring in Ireland, predominantly in western and southern parts of the island with pronounced oceanic climate.

In the present study, the data on the occurrence and morphology of epiphyllous *Phycopeltis* species from several regions with perhumid climate in Southeast Asia are given. Alongside with the determination and description of the species, attention was paid also to the basic ecological conditions of the investigated regions. The differences in the *Phycopeltis* flora between the particular localities and the ecological preferences of investigated species are discussed.

Material and methods

Collections of epiphyllous algal growths were made in January and February of the years 2000 and 2001 in selected localities of lowland and mountainous tropical rainforests of Peninsular Malaysia and western parts of Indonesia (Fig. 29). All the investigated localities belong to the perhumid, everwet type of climate with annual precipitation exceeding 2500 mm.

The specimens were examined alive in the field as well as in the laboratory using a binocular dissecting microscope and light microscope Carl Zeiss AMPLIVAL and Olympus BX 51. Microphotographs were made using Olympus BX 51 light microscope and Olympus Z 500 microphotograph equipment.

The separation of *Phycopeltis* plants from the substrate, which is crucial for *Phycopeltis* specific determination, was made either manually or using a sonicator bath.

Localities

- 1. Cameron Highlands, Pahang, Malaysia, slopes of Mt. Jasar, 1400 meters a.s.l., 4°25'15"N and 101°25'30"E, col. 10.2.2001, mountainous rainforest, leaves of an unidentified epiphytic orchid.
- 2. C.H., Pahang, Malaysia, slopes of Mt. Beremban, 1700 meters a.s.l., 4°25′05″N and 101°25′10″E, col. 12.2.2001, mountainous rainforest, leaves of an epiphytic fern.
- 3. C.H., slopes of Mt. Beremban, 1550 meters a.s.l., 4°25′10″N and 101°25′15″E, col. 11.2.2001, mountainous rainforest, leaves of *Calamus* sp. (Arecaceae).
- 4. C.H., slopes of Mt. Beremban, 1550 meters a.s.l., 4°25'10"N and 101°25'15"E, col. 11.2.2001, mountainous rainforest, leaves of *Calamus* sp. (Arecaceae).
- 5. C.H., slopes of Mt. Beremban, 1600 meters a.s.l., 4°25'07"N and 101°25'12"E, col. 11.2.2001, mountainous rainforest, leaves of *Calamus* sp. (Arecaceae).
- 6. C.H., slopes of Mt. Beremban, 1600 meters a.s.l., 4°25'07"N and 101°25'12"E, col. 11.2.2001, mountainous rainforest, leaves of *Calamus* sp. (Arecaceae).
- 7. C.H., slopes of Mt. Jasar, 1450 meters a.s.l., 4°25'17"N and 101°25'34"E col. 10.2.2001, mountainous rainforest, leaves of *Lithocarpus* sp. (Fagaceae).
- 8. C.H., slopes of Mt. Jasar, 1450 meters a.s.l., 4°25'17"N and 101°25'34"E col. 10.2.2001, mountainous rainforest, leaves of *Lithocarpus* sp. (Fagaceae).
- 9. C.H., slopes of Mt. Jasar, 1450 meters a.s.l., 4°25'17"N and 101°25'34"E col. 10.2.2001, mountainous rainforest, leaves of *Lithocarpus* sp. (Fagaceae).
- 10. C.H., slopes of Mt. Jasar, 1520 meters a.s.l., 4°25'25"N and 101°25'45"E col. 10.2.2001, mountainous rainforest, leaves of *Lithocarpus* sp. (Fagaceae).
- 11. C.H., slopes of Mt. Beremban, 1550 meters a.s.l., 4°25'10"N and 101°25'15"E, col. 11.2.2001, mountainous rainforest, leaves of *Litsea* sp. (Lauraceae).
- 12. C.H., slopes of Mt. Beremban, 1550 meters a.s.l., 4°25'10"N and 101°25'15"E, col. 11.2.2001, mountainous rainforest, leaves of *Litsea* sp. (Lauraceae).
- 13. C.H., slopes of Mt. Brinchang, 1900 meters a.s.l., 4°26'15"N and 101°25'05"E, col. 13.2.2001, cloud mountainous rainforest, leaves of unidentified tree.
- 14. C.H., near by Tanah Rata, 1400 meters a.s.l., 4°25'20"N and 101°25'20"E, col. 14.2.2001, mountainous rainforest, leaves of the fern *Drynaria* sp. (Polypodiaceae).
- 15. C.H., Pahang, Malaysia, slopes of Mt. Beremban, 1700 meters a.s.l., 4°25'05"N and 101°25'10"E, col. 12.2.2001, mountainous rainforest, leaves of the fern *Dicranopteris* sp. (Gleicheniaceae).
- 16. C.H., slopes of Mt. Brinchang, 1950 meters a.s.l., 4°26'18"N and 101°25'05"E, col. 13.2.2001, cloud mountainous rainforest, leaves of an unidentified tree.
- 17. C.H., slopes of Mt. Jasar, 1520 meters a.s.l., 4°25'25"N and 101°25'45"E col. 10.2.2001, mountainous rainforest, leaves of an unidentified epiphytic orchid.
- 18. C.H., Sungai Palas Boh Tea Estate, 1700 meters a.s.l., 4°26'55"N and 101°24'40"E, col. 13.2.2001, tea plantation, leaves of *Thea sinensis* (Theaceae).

- 19. C.H., Sungai Palas Boh Tea Estate, 1650 meters a.s.l., 4°26'42"N and 101°24'50"E, col. 13.2.2001, tea plantation, leaves of *Thea sinensis* (Theaceae).
- 20. C.H., Sungai Palas Boh Tea Estate, 1630 meters a.s.l., 4°26'39"N and 101°24'57"E, col. 13.2.2001, tea plantation, leaves of *Thea sinensis* (Theaceae).
- 21. C.H., slopes of Mt. Brinchang, 1900 meters a.s.l., 4°26'15"N and 101°25'05"E, col 13.2.2001, cloud mountainous rainforest, leaves of an unidentified member of *Lauraceae*.
- 22. C.H., Mt. Brinchang, 2000 meters a.s.l., 4°26'18"N and 101°25'05"E, col. 13.2.2001, cloud mountainous rainforest, leaves of an unidentified epiphytic fern.
- 23. C.H., Mt. Brinchang, 2000 meters a.s.l., 4°26'18"N and 101°25'05"E, col. 13.2.2001, cloud mountainous rainforest, leaves of *Nepenthes* sp. (Nepenthaceae).
- 24. Bukit Barisan Mts., Bengkulu, Sumatra, Indonesia, 500 meters a.s.l., 2°25'18"S and 101°30'05"E, col. 21.1.2001, lowland rainforest, leaves of unidentified shrub.
- 25. B.B., Bengkulu, Sumatra, Indonesia, 600 meters a.s.l., 2°24'55"S and 101°30'30"E, col. 18.1.2001, lowland rainforest, leaves of the palm *Iguanura wallichiana* (Arecaceae).
- 26. B.B., 600 meters a.s.l., 2°24'55"S and 101°30'30"E, col. 21.1.2001, lowland rainforest, leaves of unidentified member of Dipterocarpaceae.
- 27. B.B., 900 meters a.s.l., 2°20′50"S and 101°39′30"E, col. 17.1.2001, hill dipterocarp rainforest, leaves of *Shorea* sp. (Dipterocarpaceae).
- 28. B.B., 750 meters a.s.l., 2°22'15"S and 101°34'20"E, col. 18.1.2001, hill dipterocarp rainforest, leaves of the palm *Johannesteijsmannia* sp. (Arecaceae).
- 29. B.B., 550 meters a.s.l., 2°28'25"S and 101°22'18"E, col. 23.1.2001, lowland rainforest, leaves of an unidentified tree.
- 30. B.B., 400 meters a.s.l., 2°28'25"S and 101°22'18"E, col. 23.1.2001, lowland rainforest, leaves of *Calamus* sp.(Arecaceae).
- 31. B.B., 450 meters a.s.l., 2°26'25"S and 101°27'35"E, col. 21.1.2001, lowland rainforest, leaves an unidentified tree.
- 32. B.B., 700 meters a.s.l., 2°23'05"S and 101°34'40"E, col. 18.1.2001, hill dipterocarp rainforest, leaves an unidentified tree.
- 33. B.B., 600 meters a.s.l., 2°24'40"S and 101°30'38"E, col. 18.1.2001, lowland rainforest, leaves of the palm *Eugeissona* sp. (Arecaceae).
- 34. B.B., 600 meters a.s.l., 2°25′50″S and 101°29′10″E, col. 19.1.2001, lowland rainforest, leaves of the palm *Pinanga* sp. (Arecaceae).
- 35. B.B., 1000 meters a.s.l., 2°20'30"S and 101°40'05"E, col. 17.1.2001, hill dipterocarp rainforest, leaves of an unidentified tree.
- 36. Hulu Kelantan, Malaysia, 550 meters a.s.l., 5°15'30"N and 101°50'35"E, col. 31.1.2000, secondary lowland rainforest, leaves of *Bambusa* sp. (Gramineae).
- 37. Hulu Kelantan, Malaysia, 370 meters a.s.l., 5°13'10"N and 101°48'00"E, col. 29.1.2000, secondary lowland rainforest, leaves of an unidentified palm.
- 38. Tioman Island, Pahang, Malaysia, 300 meters a.s.l., 2°50'10"N and 104°13'30"E, col. 6.2.2001, lowland rainforest, leaves of the palm *Eugeissona* sp. (Arecaceae).
- 39. T.I., Pahang, Malaysia, 7 meters a.s.l., 2°50′00″N and 104°12′58″E, col. 4.2.2001, coastal beach vegetation, leaves of *Barringtonia* sp. (Lecythidacae).
- 40. T.I., 300 meters a.s.l., 2°50'10"N and 104°13'30"E, col. 6.2.2001, lowland rainforest, leaves of an unidentified tree.
- 41. T.I., 350 meters a.s.l., 2°50'28"N and 104°13'55"E, col. 6.2.2001, lowland rainforest, leaves of the palm *Calamus* sp. (Arecaceae).
- 42. T.I., 470 meters a.s.l., 2°49'50"N and 104°14'30"E, col. 7.2.2001, lowland rainforest, leaves of *Xanthophyllum* sp. (Polygalaceae).
- 43. Bogor Botanical Garden, West Java, Indonesia, 290 meters a.s.l., 6°55'50"S and 106°50'05"E, col. 20.2.2001, leaves of *Xanthophyllum vitellinum* (Polygalaceae).

Results and discussion

In total, 12 *Phycopeltis* species were determined in the course of the investigation. In species that are not included in Thompson & Wujek's monograph the respective synonymous names are given.

Phycopeltis amboinensis (G. Karsten) Printz, Nytt Mag. Naturvidensk. 80: 176 (1939)

The alga consists of open-branched ramuli, mostly produced by a single dichotomizing vegetative filament. The intercalary vegetative cells often produce erect vegetative filaments consisting up to 50 cells. The primary gametangia develop from the apical cells of the ramuli, the secondary gametangia are produced successively centripetally in the vegetative filament within the ramuli. Tertiary gametangia develop on the erect filaments in an intecalary, lateral or terminal position. The sporangia are terminal on sporangiophores of 5-20 cells. Sporangiophores are produced by apical cells. However, the repetitive production of sporangiate-laterals adds to the cellularity of the sporangiophore in older plants. Gametophytes can produce both gametangia and sporangia.

The dimensions of vegetative cells (central part of the ramuli, width of the central area of the cells) are (5.4-)6.2-10.5(-11.0) × (11.5-)12.5-24.0(-26.5) µm. The width: length (W:L) ratio is 1:1.2-2.6. The cells of erect filaments and sporangiophores: (6.0-)7.5-11.5(-13.0) × (11.0-)12.0-23.8(-25.0) µm. The W:L ratio is 1:1.2-2. The dimensions of primary and secondary gametangia are 10.5-21.8 × 18-28 µm. The tertiary gametangia are globular with the dimensions 15.0-19.6 µm. Sporangia: 13.5-16.5 × 22.0-25.5 µm.

The species was found in numerous localities in the tropical regions of America and in some localities in tropical Southeast Asia in the past (Printz 1939; Thompson & Wujek, 1997). In this study it was found in central Sumatra in altitudes 200-800 m a.s.l. and in samples from Tioman Island (altitude 300 m a.s.l.). The Tioman population differs from Sumatran material and the published data in some features. The specimens bear long and branched erect filaments consisting up to 70 cells (width 5-9 µm). The cells of the filaments often produce ramulate tillers which serve as vegetative propagules (Fig. 11). Such a function for erect filaments has never been observed in any *Phycopeltis* species previously. Sporangia were not present in the Tioman population. Whether the peculiarities of this population indicate a different specific nature or whether such features could be found in all populations of *P. amboinensis* throughout the tropics remains to be answered in the course of future research.

The W:L ratio of all investigated populations differs significantly from that assigned by Thompson & Wujek (1997). However, it concurs well with the specimens pictured as *P. amboinensis* in their study.

Localities: 24, 26, 27, 31, 35, 40.

Phycopeltis arundinacea (Montagne) de Toni, Sylloge Algarum I., Sylloge Chlorophycearum omnium hucusque cognitarum, Patavii, 532 pp. (1889) Fig. 2

The populations matching this species as it is perceived by Thompson & Wujek (1997) were found in higher altitudes of the Malay Peninsula in ecosystems of upper mountainous tropical forest characteristic with a continuous high humidity and relatively low temperature (minimum temperature less than 10°C). The organism consists of circular discs up to 5 mm in diameter. The primary gametangia are intercalary within the thallus, the secondary gametangia successively develop from neighbouring vegetative cells, centripetally and centrifugally. The rarely observed sporangiate-laterals are intercalary. Sporangiophores of up to 7 cells develop as a result of successive production of sporangiate-laterals from old suffultory cells.

The dimensions of vegetative cells are (7.5-)8.5-14.3(-16.0) \times (18-)23-35(-43) μ m. The W:L ratio is 1:(2.0-)3.2-4.3(-4.7). The dimensions of gametangia are 11-18 \times 22.5-35.0 μ m. The dimensions of sporangia: 18.8-25.5 \times 22.5-30.0 μ m.

Sometimes, isolated specimens lacking gametangia or sporangia are hardly distinguishable from old plants of P. treubii. This species differs from P. arundinacea by the position of the gametangia and some other features. Regarding the variability and the somewhat uncertain status of broadly defined P. treubii, the complete delimitation of P. arundinacea vis-a-vis this species will be the task of future research. Apart from tropical ecosystems *P. arundinacea* was found also in temperate regions with cold and wet climate without frosts [Ireland (Scannel 1978, Rindi & Guiry 2002)]. However, their observations differ from tropical specimens depicted in Thompson & Wujek (1997) mainly in cell dimensions, W:L ratio of the vegetative cells and structure of the sporangiophore. Rindi & Guiry (2002) found the sporangiatelaterals growing up always directly from vegetative cells. No stalk cells were observed. On the other side, Thompson & Wujek (1997) found sporangiophores up to several cells on their material. Our specimens correspond, rather with Thompson & Wujek's observations. Thus, the splitting of tropical and temperate populations classified recently into *P. arundinacea* in two separate species is possible in the future. However, the close proximity of our populations to *P. treubii* – a species not occurring outside the tropics – should once again be noticed.

Assuming our observations we regard this species as adapted to low temperature but requiring high humidity.

Localities: 13, 16, 25, 29, 30, 31.

Phycopeltis aurea G. Karsten, Ann. Jard. Bot. Buitenzorg 10: 1-66 (1891) Figs 3, 12, 13

The alga consists of a circular or somewhat irregular disc up to 1 mm in diameter. The elongated primary gametangia develop from terminal cells of the filaments within the thallus. The secondary gametangia develop by repeated proliferation of the subtending vegetative cells into the empty primary gametangium. The sporangia are mainly intercalary in origin. The short sporangiophores develop by repeated

proliferation of new sporangiate-laterals from old suffultory cells. The species has the obligatory alternation of generations with gametophytes bearing gametangia only.

The dimensions of the gametophyte vegetative cells are $(1.5\text{-})2.3\text{-}4.7(\text{-}6.0) \times (4.2\text{-})6.0\text{-}8.8(\text{-}11.3) \ \mu\text{m}$. The dimensions of sporophyte vegetative cells: $(2.0\text{-})2.8\text{-}5.8(\text{-}6.0) \times (4.2\text{-})6.0\text{-}9.6(\text{-}11.5) \ \mu\text{m}$. The W:L ratio is 1:(1.2-)1.5-2.2(-2.6). The dimensions of gametangia are 6-12 × 10-18 μ m. The dimensions of sporangia: 11.5-14.0 × 13.0-15.8 μ m.

The species was found in samples from Tioman Island in altitudes of 0-300 m a.s.l. Previously it was reported from different tropical regions worldwide (Thompson & Wujek 1997).

Localities: 38-41.

Phycopeltis epiphyton Millardet, Mem. Soc. Sci. Nat. Strasbourg 6: 37-50 (1870) Fig. 14

The alga consists of discoidal thalli up to 1,2 mm in diameter. The primary gametangia are mainly intercalary, in the central part of the disc often somewhat raised over the surface of the thallus. The secondary gametangia are produced successively centrifugally or centripetally to the primary one. The sporangia typically develop from apical vegetative cells and usually terminate the growth of the filament. In some cases sporangiophores in subterminal or occasionally in intercalary position are also present. The suffultory cells often develop directly from vegetative cells within the disc. However, sporangiophores of up to 5 cells may be produced by proliferation of new sporangiate-laterals from previous suffultory cells. The gametophyte can produce both gametangia and sporangia, but sporangial production on gametophytes was only rarely observed.

The dimensions of the gametophyte vegetative cells are $(2.5\text{-})3.2\text{-}5.5(-6.0) \times (5.0\text{-})5.5\text{-}11.2(-14.0)$ µm, W:L ratio is 1:(1.2-)1.4-3.0(-3.2). Sporophyte vegetative cells: $(2.5\text{-})3.2\text{-}6.0(-7.5) \times (4.8\text{-})5.3\text{-}10.5(-12.8)$, W:L ratio is 1:(1.3-)1.5-2.5(-2.8). The dimensions of the gametangia are 4-15 × 11-24 µm. Sporangia: 14.5-17.5 × 16-25 µm.

The species was found in samples from the botanical garden in Bogor, Java and in some samples from Peninsular Malaysia. It was reported from numerous localities in temperate to tropical ecosystems. The identity of populations from different climatic zones should be critically investigated in the future.

Localities: 36, 37, 43.

Phycopeltis irregularis (Schmidle) Wille, Conjugatae und Chlorophyceae. In: Engler, A. & K. Prantl (eds): Die Natürlichen Pflanzenfamilien, Leipzig, Nachträge zum Teil I, Abt. 2: 1-134 (1909)

Figs 15, 27

The alga forms microscopic epiphyllous growths and is composed of widespreading branched prostrate filaments. Pseudoparenchymatic discs or ramuli are never formed

but the filaments can sometimes be congested to an irregular expanse. The vegetative cells are of cylindrical to irregular shape. Gametangia develop in an intercalary position within the thallus. Rarely, the sporangia were observed. They are produced by intercalary vegetative cells.

The dimensions of vegetative cells are $(4.0\text{-})5.2\text{-}9.5(-10.0) \times (10.0\text{-})11.5\text{-}16.5$ (-17.5) µm. The W:L ratio is 1:(1.5-)2.0-3.0(-3.2). The dimensions of gametangia correspond to those of vegetative cells.

This species was found in samples from localities over 500 m a.s.l. in Peninsular Malaysia and Sumatra. This species probably frequently occurs in tropical ecosystems, but it may have been overlooked in the past. It was reported from Samoa and from different localities of tropical America (Schmidle 1897a; Thompson & Wujek 1997).

Localities: 22, 29, 32.

Phycopeltis kosteriana Cribb, Blumea 15: 3 (1967)

Figs 16, 28

The thallus of pale green to yellowish colour consists of an irregular disc composed of loose prostrate branched filaments. The dimensions of the discs are up to 0,3 mm. Unlike in other discoid or ramulate *Phycopeltis* species the vegetative cells within the disc are of irregular elongated shape. Thus, perforations between the cells can often be observed. The gametangia develop intercalary from the vegetative cells within the thallus. The sporangia were not observed.

The dimensions of the vegetative cells are $(1.8\text{-})2.2\text{-}3.8(\text{-}5.2) \times (5.0\text{-})7.0\text{-}12.0$ (-13.5) µm. The W:L ratio is 1:2.3-3.2. The dimensions of gametangia correspond with those of vegetative cells.

This species was described by Cribb (1967) from epiphyllous communities in tropical ecosystems of Northern Australia. It is characterised mainly by inconspicuous pale green discs composed of irregular cells. The species was not encompassed into Thompson & Wujek's (1997) monograph. However, the observed populations fit well into the original description. The organism differs significantly from other *Phycopeltis* species in its cell shape and dimensions. It differs also from the members of the allied genus *Cephaleuros* by its epicuticular way of life, the small dimensions of the vegetative cells and the complete absence of sporangiophores.

The species was found in two Sumatran localities. However, it had been overlooked in some samples and its presence was not revealed until supplementary examinations were made. Thus, we can hypothesize a wider distribution of this inconspicuous organism in the epiphyllous microbiotopes of the region. Investigations of the reproduction and the life cycle of the organism should be undertaken in the future to ascertain its taxonomic status within the genus *Phycopeltis*.

Localities: 32, 34.

Phycopeltis prostrata (De Wildeman) Schmidle emend. Sarma, Nova Hedwigia Beih. 58: 86 (1986) Figs 17-19

- ≡ *Phycopeltis prostrata* Schmidle, Ber. Deutsch. Bot. Ges. 15: 457 (1897).
- = Trentepohlia prostrata De Wildeman, Notarisia 11(2/3): 88 (1896).
- = Hansgirgia polymorpha Schmidle, Hedwigia 36: 277-287 (1897).

The general appearance of this alga ranges from circular or somewhat irregular compact discs up to 1 mm to loose growths of branched prostrate filaments. The occasionally branched erect filaments of up to 10 cells develop intercalary from the prostrate system. The gametangia are lateral or terminal on erect filaments. The sporangiate-laterals are produced either intercalary within the thallus or in some cases in a lateral or terminal position on erect filaments.

The dimensions of vegetative cells are $(3.5\text{-})4.0\text{-}6.5(-7.5) \times (8.0\text{-})10.0\text{-}20.5$ (-22.0) μm . The W:L ratio is 1:(1.8-)2.1-2.8(-3.2). The dimensions of cells of erect filaments: $3.6\text{-}5.5 \times 8.5\text{-}15.0 \ \mu\text{m}$. The W:L ratio is 1:1.8-2.8. The dimensions of gametangia are 8-12 \times 8-14 μm . Sporangia: 9.5-12.5 μm .

The species was originally described from Java by De Wildeman (1896) as *Trentepohlia prostrata*. Later, it was found in Samoa (Schmidle, 1897a) and transferred to the genus *Phycopeltis* (Schmidle 1897b). Sarma (1986) found the species in several localities of New Zealand. He observed the branched pattern of erect filaments and emended the description of the species. Thompson & Wujek (1997) did not include this species in their investigation. However, the observed material fits well into Sarma's description and differs significantly from other *Phycopeltis* species. The species was found in several Sumatran hill rainforest localities in altitudes of about 550-800 m a.s.l. The species seems to be distributed in tropical and subtropical regions of Southeast Asia and Oceania.

Localities: 29, 33, 34.

Phycopeltis pseudotreubii R.H. Thompson & Wujek, Trentepohliales: *Cephaleuros, Phycopeltis* and *Stomatochroon*. Morphology, taxonomy and ecology. Sci. Publ., Enfield, 86 (1997)

The alga consists of a broadly ramulate thallus appressed into a disc up to 1,5 mm in diameter. The gametangia develop from terminal or intercalary cells within the thallus. The terminal cells develop into the primary gametangia only in the position at the margin of lateral mutually folded ramuli. The intercalary primary gametangia are often somewhat raised over the surface of the thallus. The secondary gametangia develop successively centrifugally and centripetally to the primary one. The sporangia develop on intercalary sporangiophores of 4 to more cells. The first 4-5 cells of the sporangiophores are produced by the apical cell before the first sporangiate-lateral is formed. The proliferation of new sporangiate-laterals from old suffultory cells adds to the cellularity of the sporangiophore. The length of the primary sporangiophore cells exceeds their width. In contrast, the secondary sporangiophore cells are distinctly about twice as wide as long. The gametophyte bears both gametangia and sporangia, which are often found at once on the same plant.

The dimensions of the vegetative cells are $(4.0\text{-})4.2\text{-}7.7(\text{-}9.0) \times (8.5\text{-})10.5\text{-}17.0$ (-18.8). The W:L ratio is 1:(1.5-)1.7-2.8(-3.3). The dimensions of the gametangia: $9\text{-}12 \times 10.5\text{-}23.0 \,\mu\text{m}$. The dimensions of primary sporangiophores cells: $(8.0\text{-})8.7\text{-}11.8(\text{-}12.2) \times (10.0\text{-})11.0\text{-}20.5(\text{-}23.0) \,\mu\text{m}$. The W:L ratio is 1:1.2-2.4. The dimensions of sporangia are $10.5\text{-}12.0 \times 12.5\text{-}15.2 \,\mu\text{m}$.

The species was found in one locality of lowland tropical rainforest in Sumatra (altitude 450 m a.s.l.). Thompson & Wujek (1997) reported the species from tropical South and Middle Americas. The species is reported for the first time from Southeast Asia.

Localities: 31.

Phycopeltis theaensis Neustupa sp. nov.

Figs 5-7, 20-22

Descriptio:

Alga discoidalis integrimargine. Thallus dimensiones tenus 1 mm. Gametangia primaria intercalaria, interdum in fascia producta. Gametangia secondaria ex cellulis successivis centripetis et centrifugis primariis producta. Sporangia intercalaria et fortuita ab origine producta. Sporangiophorum per proliferationem successivam ex cellulis suffultis provectionibus producta.

Thalli pleni non nullae unicellulares nucleatas papillas medialiter, dorsaliter producta.

Gametophytum et gametangia et sporangia producit. Sporophytum solus sporangia producit.

Gametophytum: cellulae (3.8-)4.6-8.7(-9.9) μ m latae et (7.0-)7.5-17.5(-20.4) μ m longae, ratio 1: (1.3-)1.5-2.8(-3.3), gametangium ovales, 8.3-16.4 μ m latae et 13.7-25.0 μ m longae, sporangium 10-17 μ m latae et 14.0-18.8 μ m longae.

Sporophytum: cellulae (5.0-)6.2-11.5(-12.7) μm latae et (9.0-)10.0-23.6(-25.0) μm longae, ratio 1:(1.3-)1.5-2.4(-2.8), sporangium 15.0-18.3 μm latae et 16.2-22.7 μm longae.

Holotypus: Malaysia, Pahang, Cameron Highlands, On leaves of *Thea sinensis*, Sungai Palas Boh Teh Estate, 1630 meters a.s.l., leg. J. Neustupa, 13.2.2001 (holotype deposited at PRC).

The alga consists of discoidal thalli up to 1 mm in diameter. The primary gametangia develop mainly from intercalary vegetative cells. The secondary gametangia develop successively centripetally and centrifugally to the primary one. Usually, the gametangia develop continuously in or around the central area of the disc. In some cases the gametangia form a single, irregular broad band around the disc. The sporangiate-laterals are produced irregularly, entirely by intercalary vegetative cells. The short sporangiophores up to 5 cells develop entirely by secondary proliferation of new sporangiate-laterals from old suffultory cells. The gametophyte is capable of producing both gametangia and sporangia, even if more often only the gametangia are produced. The putative sporophyte plants, with slightly larger vegetative cells and sporangia, produce sporangiate-laterals only.

In old mature thalli of both gametophytes and sporophytes one-celled median dorsal papillae are formed. These are most often found on thalli with intensive sporangial production.

The dimensions of the gametophyte vegetative cells are $(3.8\text{-})4.6\text{-}8.7(\text{-}9.9) \times (7.0\text{-})7.5\text{-}17.5(\text{-}20.4)$ µm. The W:L ratio is 1:(1.3-)1.5-2.8(-3.3). The dimensions of the sporophyte vegetative cells: $(5.0\text{-})6.2\text{-}11.5(\text{-}12.7) \times (9.0\text{-})10.0\text{-}23.6(\text{-}25.0)$ µm. The W:L ratio is 1:(1.3-)1.5-2.4(-2.8). The dimensions of gametangia: 8.3-16.4 × 13.7-25.0 µm. The dimensions of sporangia produced by gametophytes: 10-17 × 14.0-18.8 µm. The dimensions of sporangia are 15.0-18.3 × 16.2-22.7 µm.

The name of the species is derived from the host plant at the type locality.

The species differs from all the other described members of the genus *Phycopeltis* in having a unique combination of attributes. However, it is somewhat similar to some known species. *Phycopeltis novae-zealandiae* Thompson & Wujek is characterised by concentric rings of intercalary gametangia. This species shares with *P. theaensis* also the pattern of sporangiate-laterals occurrence and the vegetative cells dimensions. However, it differs from *P. theaensis* in following attributes. The alternation of generations is obligatory according to Thompson & Wujek (1997) in *P. novae-zealandiae*, whereas in *P. theaensis* gametophytes are capable of producing sporangia too. The gametangial rings were never observed in a concentric pattern in *P. theaensis* where the irregular bands of gametangia are usually concentrated in the central part of the disc with or without the inclusion of the thallus centre. The dorsal papillae were never observed in *P. novae-zealandiae* (Thompson & Wujek 1997).

Phycopeltis epiphyton in the concept used by Thompson & Wujek (1997) shares the general cell dimensions and central position of gametangia with P. theaensis. On the other hand, P. epiphyton never produces dorsal papillae and is characterised by the terminal or subterminal position of sporangiate-laterals. Phycopeltis dorsopapillosa Thompson & Wujek is the only other *Phycopeltis* species with production of median dorsal papillae by vegetative cells. However, in P. theaensis the vegetative cells are considerably smaller than in P. dorsopapillosa and there is a different pattern of gametangial production within the thallus. Moreover, the pattern of papillae production is different. In P. dorsopapillosa the papillae are found on most thalli with the exception of heavily reproducing ones. On the contrary, the dorsal papillae in P. theaensis are mostly found on a few intensively reproducing old mature plants. The temperate populations of *P. arundinacea* described by Rindi & Guiry (2002) differ from P. theaensis in the absence of sporangiophores, higher W:L ratio and the absence of dorsal glandular papillae. Phycopeltis expansa Jennings, an uncertain species not included in Thompson & Wujek's monograph, differs from P. thaeansis in structure of sporangiophore, which is always single-celled in the former species.

Phycopeltis theaensis was found to be a dominant species of epiphyllous growths on the tea leaves at the Sungai Palas Boh plantation. The plantation is surrounded by natural mountainous rainforest vegetation, which, however, hosts a quite different Phycopeltis flora with P. treubii and P. treubioides. In view of the considerably different microclimatic conditions of a tea plantation and a primary rainforest, we can hypothesize that P. theaensis is adapted to direct light exposure and significant circadian changes of air humidity.

Localities: 18-20.

Phycopeltis treubii G. Karsten, Ann. Jard. Bot. Buitenzorg 10: 1-66 (1891) Figs 8, 23, 24

The alga consists of a broadly ramulate thallus appressed to form an irregular disc or open-branched thallus. The dimensions of the thallus are up to 3-6 mm. The terminal cells at the margins of mutually folded adult ramuli often produce dorsally "glandular" papillae (Fig. 23). The primary gametangia develop terminally along the margins of the ramuli. The secondary gametangia are intercalary centripetal to the primary one. In young thalli, primary gametangia in an intercalary position were also sporadically observed. The sporangiate-laterals develop in an intercalary, often subterminal position. The sporangiophores of up to 7 cells always develop by secondary proliferation of new sporangiate-laterals from old suffultory cells. The gametophyte bears both gametangia and sporangia. The sporophyte plants were not observed.

The dimensions of the vegetative cells: $(6.0\text{-})7.2\text{-}14.0(\text{-}16.5) \times (10.0\text{-})13.0\text{-}30.5$ (-37.0) μ m. The W:L ratio is 1:(2.0-)2.3-3.3(-3.6). The dimensions of the gametangia are 7.0-19.5 \times 15-28 μ m. Sporangia: 12.5-15.0 \times 16.2-20.5 μ m.

Phycopeltis treubii is one of the most frequently reported tropical epiphyllous species in the literature (Printz 1939; Thompson & Wujek 1997). In this study the species was found in a number of samples as a dominant part of epiphyllous synusiae in altitudes over 400 meters a.s.l. However, considerable variability was revealed in the specimens investigated. In contrast to Malaysian samples, the populations found in the Barisan Range of Sumatra comprised the considerable proportion of plants with more open-branched ramuli. On the other hand, Sumatran specimens mostly lacked glandular papillae. The dimensions of the plants differed between Malaysian and Sumatran populations. The old individuals from Sumatra ranged up to 6 mm whereas the Malaysian populations were only up to 3 mm in diameter. Occasionally, primary intercalary gametangia, which were not reported by Thompson & Wujek (1997), were encountered both in Malaysian and Sumatran populations. Given the current state of the knowledge in *Phycopeltis* taxonomy all the investigated specimens were determined as a broadly defined P. treubii. However, the future description of several similar species recently encompassed within *P. treubii* should not be entirely surprising.

Localities: 1, 3-12, 14, 17, 21-34, 36, 42.

Phycopeltis treubioides R.H. Thompson & Wujek, Trentepohliales: *Cephaleuros*, *Phycopeltis* and *Stomatochroon*. Morphology, taxonomy and ecology. Sci. Publ., Enfield, 88 (1997)

Figs 9, 25, 26

The thallus is composed of an irregular disc or broad mutually folded ramuli. The dimensions of the thalli are up to 1,5 mm. The primary gametangia are produced along the margins of the ramuli in a terminal position. The secondary gametangia develop successively centripetal to the primary one. Sporangiophores of up to 5 cells, produced by an apical cell, develop from intercalary, often subterminal cells within the thallus. The proliferation of the new sporangiate-laterals from old suffultory cells adds to the cellularity of the sporangiophore. The gametophytes bear gametangia

only. The sporangiate-laterals are produced on separate plants considered to be sporophytes. This suggests the obligate alternation of generations in the life cycle of this species.

The dimensions of the gametophyte vegetative cells are $(4.8\text{-})6.2\text{-}10.0(\text{-}11.5) \times (12.0\text{-})13.8\text{-}19.0(\text{-}23.8) \ \mu\text{m}$. The W:L ratio is 1:(1.5-)1.8-2.8(-3.5). The dimensions of sporophyte vegetative cells: $(7.5\text{-})8.7\text{-}11.2(\text{-}11.6) \times (12.0\text{-})14.0\text{-}21.0(\text{-}25.0) \ \mu\text{m}$. The W:L ratio is 1:(1.7-)2.0-3.0(-3.5). The dimensions of primary sporangiophores cells are $(7.8\text{-})8.0\text{-}14.0(\text{-}17.0) \times (9.0\text{-})10.5\text{-}17.5(\text{-}18.5) \ \mu\text{m}$. The W:L ratio is 1: (1.0-)1.1-1.8(-2.3). The dimensions of gametangia: $10.0\text{-}17.5 \times 15.5\text{-}25.0 \ \mu\text{m}$. The dimensions of sporangia: $17.5\text{-}29.0 \times 16.2\text{-}21.5 \ \mu\text{m}$.

The delimitation of this species is based mainly on the presence of primary sporangiophores produced by an apical cell and the obligate alternation of generation within its life cycle. Otherwise, *P. treubioides* shares many characters typical for *P. treubii*. Thompson & Wujek (1997) reported the species from epiphyllous growths in Costa Rica. In the present study *P. treubioides* was found in several samples from mountainous rainforest in Malay Peninsula (altitude 1500-1800 m a.s.l.). In most other samples from this area *P. treubii* was a dominant *Phycopeltis* species. This is the first report of *P. treubioides* from Southeast Asia.

Localities: 2, 15, 17.

Phycopeltis vaga R.H. Thompson & Wujek, Trentepohliales: *Cephaleuros*, *Phycopeltis* and *Stomatochroon*. Morphology, taxonomy and ecology. Sci. Publ., Enfield, 89 (1997)

This species is characterised by a narrow open-branched ramulate thallus. In some cases, ramuli appressed to form a perforate irregular disc could be observed. The prominent primary gametangia develop from apical cells of the thallus filament and terminate their growth. The secondary gametangia develop by proliferation of the subtending cells into the empty cell wall of the primary one. The sporangiate-laterals develop from intercalary, often subterminal cells. Sporangiophores are produced entirely by secondary proliferation of new sporangiate-laterals from old suffultory cells. The gametophyte bears both gametangia and sporangia. The sporophyte was not observed.

The dimensions of the central area of vegetative cells are $(3.5-)4.2-8.5(-10.0) \times (10.5-)13.5-22.0(-25.0)$ µm. The W:L ratio is 1:(1.2-)1.4-2.7(-3.0). The dimensions of gametangia: $15.0-20.5 \times 19-26$ µm. Sporangia: $10.0-14.5 \times 13.0-15.5$ µm.

The species was found in several samples from different regions in altitudes up to 600 meters a.s.l. This is the first report of *P. vaga* from Southeast Asia.

Localities: 29, 33, 34, 40, 42.

Out of the 12 species found during the investigation, two (*P. arundinacea*, *P. epiphyton*) seem to have a cosmopolitan distribution in tropical, subtropical and temperate ecosystems. Seven species (*P. amboinensis*, *P. aurea*, *P. irregularis*, *P. pseudotreubii*, *P. treubii*, *P. treubioides*, *P. vaga*) appear to have a presumably pantropic

distribution. *Phycopeltis kosteriana*, *P. prostrata* and *P. theaensis* nov sp. have not yet been reported outside the Indo-Malayan-North Australian phycogeographical region.

The species composition of epiphyllous *Phycopeltis* growths from a single investigated area appears to be very similar, regardless of the host plant. Rather, the *Phycopeltis* growths typical for a given area develop on every suitable plant surface - perennial leaves but also the fruits, stems or twigs. Instead, the distribution of particular species seems to be determined by climatic factors (temperature, rainfall) and reflects the specific microclimatic condition of a single locality (e.g. tea plantation with extreme circadian humidity changes and direct sun exposure vs. undergrowth of the rainforest with relatively stable humidity and low illumination). In equatorial climates of the investigated region the distribution of certain *Phycopeltis* species in forest ecosystems appears to be primarily well determined by altitude, which generally reflects changes both in temperature and relative humidity.

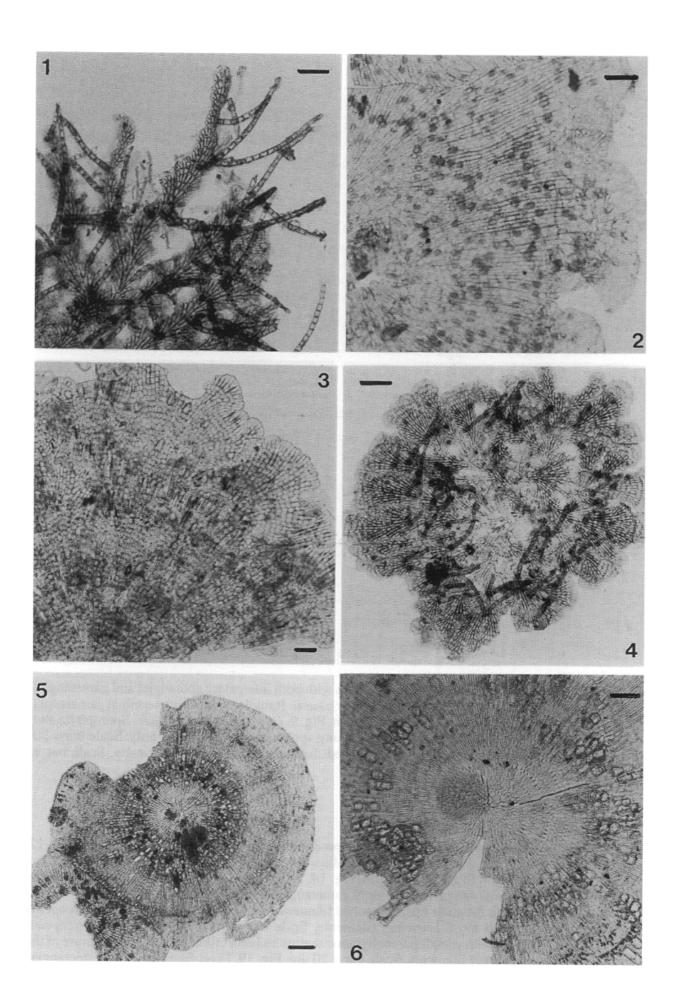
However, as has been discussed above, the uncertain species concept in some taxa (e.g. *P. epiphyton*, *P. treubii*) hinders in some respect the definition of their biogeographical distribution areas. Taxonomic studies focused on these broadly defined species could generate a valuable knowledge for their taxonomic delimitation in the future. The algae of the family Trentepohliaceae exhibit both sexual and asexual modes of reproduction in their life cycle. Thus, hybridisation as well as polyploidisation should be taken into account as possible speciation mechanisms within this algal group (López-Bautista et al. 1998).

Regarding the fact that some species are clearly associated with specific ecological conditions, we should also look at the possibility of phenotypic changes of some species growing in different environments. Molecular approaches might be helpful for investigating of species boundaries within the genus. In addition to this, floristically and ecologically oriented studies (especially in tropical ecosystems) should reveal the ecological preferences and distributional patterns of particular *Phycopeltis* species in the future.

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Fig. 1. Phycopeltis amboinensis. Open-branched ramuli with elevated filaments. Scale bar = $50 \, \mu m$. Fig. 2. Phycopeltis arundinacea. Thallus with intercalary sporangiate-laterals. Scale bar = $40 \, \mu m$. Fig. 3. Phycopeltis aurea. Gametophyte plant with terminal gametangia. Scale bar = $20 \, \mu m$. Fig. 4. Phycopeltis pseudotreubii. Plant with extensive intercalary sporangial production. Scale bar = $60 \, \mu m$. Figs 5-6. Phycopeltis theaensis. Fig. 5. Gametophyte plant with intercalary gametangia forming circular ring and the part of the sporophyte plant with intercalary sporangia in the lower left part of the picture. Scale bar = $50 \, \mu m$. Fig. 6. Gametophyte plant with intercalary gametangia forming a circular ring. Scale bar = $30 \, \mu m$.



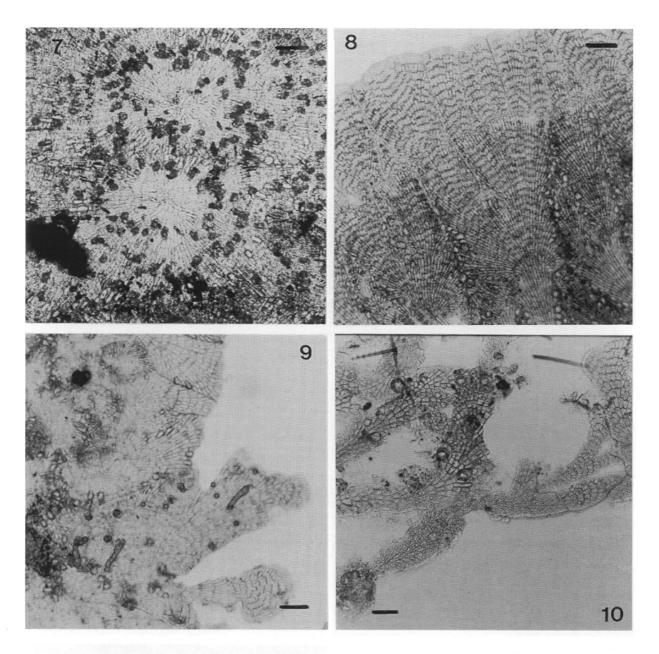
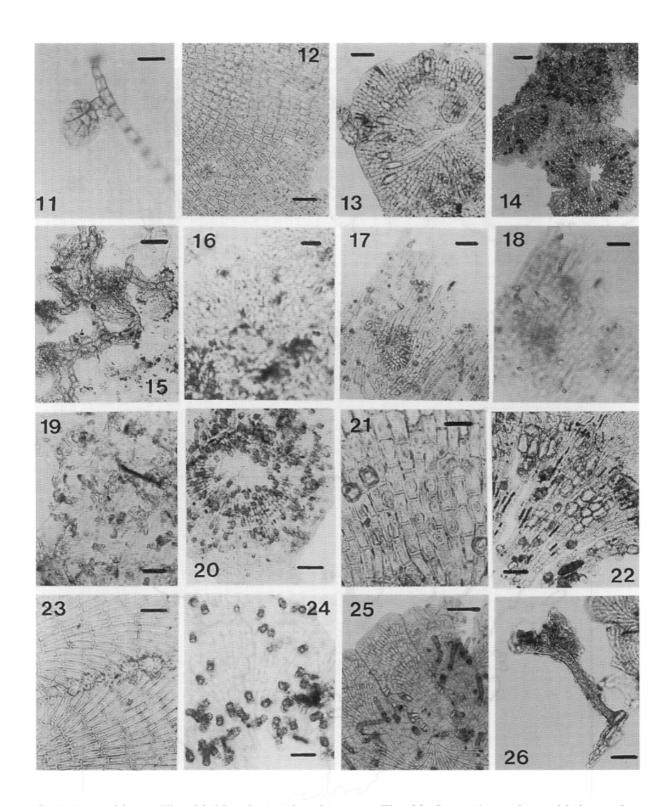


Fig. 7. Phycopeltis theaensis. Gametophyte plants with both intercalary sporangial and gametangial production. Scale bar = $40 \,\mu m$. Fig. 8. Phycopeltis treubii. Ramulate plant with terminal gametangia along the margins of the ramuli. Scale bar = $50 \,\mu m$. Fig. 9. Phycopeltis treubioides. Sporophyte and gametophyte plants growing together and producing sporangia or gametangia only. Scale bar = $50 \,\mu m$. Fig. 10. Phycopeltis vaga. An open-branched thallus with terminal gametangia. Scale bar = $30 \,\mu m$.

Fig. 11. *Phycopeltis amboinensis*. Erect filament producing new ramulus. Scale bar = 25 μ m. Figs 12, 13. *Phycopeltis aurea*. Fig. 12. The vegetative thallus. Scale bar = 10 μ m. Fig. 13. Gametophyte plant with terminal gametangia. Scale bar = 15 μ m. Fig. 14. *Phycopeltis epiphyton*. Plant with intercalary gametangia (the dark cells are gas-filled empty gametangia). Scale bar = 20 μ m. Fig. 15. *Phycopeltis irregularis*. Thallus with irregular open-branched filaments. Scale bar = 25 μ m. Fig. 16. *Phycopeltis kosteriana*. Thallus with loose branched filaments. Scale bar = 10 μ m. Figs 17-19. *Phycopeltis prostrata*. Fig. 17. Plant with pseudoparenchymatic thallus and erect filaments. Fig. 18. Picture of the same plant focused on erect filaments. Scale bar = 20 μ m. Fig. 19. Erect filaments with gametangia.



Scale bar = 20 μ m. Figs 20-22. *Phycopeltis theaensis*. Fig. 20. Sporophyte plant with intercalary sporangia. Scale bar = 40 μ m. Fig. 21. Dorsal papillae on vegetative cells in sporangia producing thallus. Scale bar = 20 μ m. Fig. 22. Intercalary gametangia and sporangia on gametangial plant. Scale bar = 30 μ m. Figs 23, 24. *Phycopeltis treubii*. Fig. 23. Papillae along the margins of the ramuli. Scale bar = 20 μ m. Figs 24. Intercalary sporangiate-laterals in sporangia producing thallus. Scale bar = 20 μ m. Figs 25, 26. *Phycopeltis treubioides*. Fig. 25. Sporophyte and gametophyte plants growing together and producing intercalary sporangiophores or terminal gametangia only. Scale bar = 50 μ m. Fig. 26. Sporangiophore with about 10 cells produced by an apical cell and old suffultory cells which add secondarily to the cellularity of the sporangiophore. Scale bar = 30 μ m.

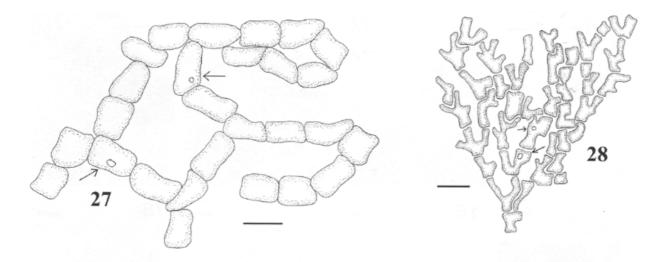


Fig. 27. *Phycopeltis irregularis*. Thallus with irregular open-branched filaments and intercalary gametangia (see arrows). Scale bar = $10 \mu m$. Fig. 28. *Phycopeltis kosteriana*. Thallus with loose branched filaments, irregularly shaped cells and intercalary gametangia (see arrows). Scale bar = $5 \mu m$.

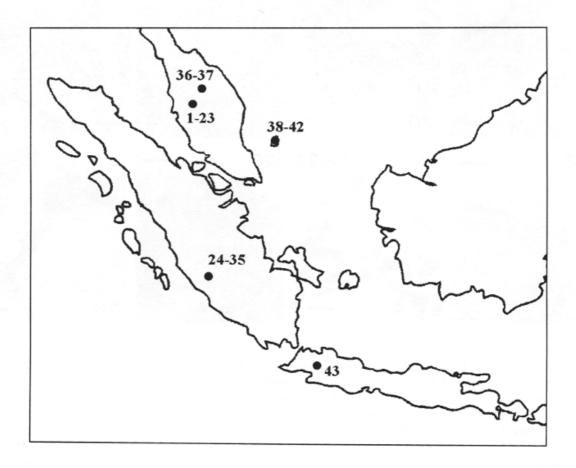


Fig. 29. Map of part of Southeast Asia showing the location of sampling sites.

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