

Development of the Sexual Phase of *Pseudocolysis bradeorum* (Polypodiaceae)

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ABSTRACT.—The development and morphology of the sexual phase of *Pseudocolysis bradeorum* (Polypodiaceae) are described from material collected in Finca La Selva, near Puerto Viejo, Province of Heredia, Costa Rica. Spores were sown in Thompson medium with agar (25 Petri dishes) and germinated after seven days; the germination pattern was *Gleichenia*-type and the prothallial development *Drynaria*-type. Gametangia were typical of homosporous leptosporangiate ferns. Sporophytes appeared after seven months of culture. The sexual phase of this species shares many morphological characteristics with Old and New World species of Polypodiaceae. There is a tendency for vegetative propagation with *Pseudocolysis* gametophytes.

Pseudocolysis bradeorum (Rosenst.) L. D. Gómez (Polypodiaceae) is a rare terrestrial fern growing in tropical rain forest soils rich in organic matter, mainly cellulosic. *Pseudocolysis bradeorum* inhabits *Pinus-Quercus-Liquidambar* forests, and coffee and cacao plantations. It has been reported from Mexico (Veracruz, Chiapas), Belize, Nicaragua, Costa Rica, and Panama. Plants have long-creeping rhizomes and sub-dimorphic to dimorphic leaves. Vegetative leaves are simple-lanceolate whereas fertile leaves vary from simple to deeply pinnatifid with long petioles. Venation is anastomosing with veinlets included within the areoles. Sori are regularly to irregularly linear, oblique and exindusiate; the spores are smooth and oblong. The habit of this plant resembles some *Colysis* spp. [= *Leptochilus*, Flora Malesiana, vol. 3, 1998] and *Pleopeltis* (Evans and Mickel, 1969; Gómez, 1977).

Tryon and Tryon (1982) placed *Pseudocolysis* in the subtribe Polypodieae, but with uncertain relationships. Moran & Riba (1995) suggested a probable hybrid origin because of the highly variable lamina, the variable petiole length, and the occasionally interrupted sori.

Development of the sexual phase of *P. bradeorum* is unknown, although there is information about the morphology of the gametophytes from other genera of Polypodiaceae. For example, Nayar (1962) studied several species of the *Polypodium-Pleopeltis* group [*Arthromeris tenuicaudata* (Hook.) Ching, *A. wallichiana* (Spreng.) Ching, *Campyloneurum angustifolium* (Sw.) Fée, *Colysis elliptica* (Thunb.) Ching, *C. hemionitidea* (Wall.) C. Presl, *C. pedunculata* (Hook. et Grev.) Ching, *Crypsinus griffithianus* (Hook.) Copel., *Crypsinus hastatus* (Thunb.) Copel., *Lemmaphyllum carnosum* (Hook.) C. Presl, *Pleopeltis excavata* (Bory ex Willd.) T. Moore, *Pleopeltis normalis* T. Moore, and *Polypodium amoenum* Wall.].

Prothalli of about 20 genera of Polypodiaceae have been described by several authors (Nayar 1954, 1963a, 1963b, 1964, 1965; Bajpai 1964; Nayar and Chandra 1965; Nayar and Kaur 1969, 1971; Schmelzeisen 1933). Authors reported that, in Polypodiaceae, the development and morphology of the prothalli are perhaps more significant for the understanding of evolutionary processes, in the polypodiaceous ferns than for other fern groups.

Nayar and Raza (1970) studied prothallial development and morphology of three species of Pleopeltidoideae [*Lepisorus loriformis* (Wall.) Ching, *L. thunbergianus* (Kaulf.) Ching and *Weatherbia accedens* (Blume) Copel.], and one species of Polypodioideae (*Polypodium vulgare* L.)]. However, prothallial morphology for most species of Pleopeltidoideae and Polypodioideae is poorly known. Most taxa for which the prothallus has been described belong to subfamilies Microsorioideae, Crypsinioideae, and Platycerioideae.

Several studies are important for our understanding of gametophytes of New World polypods, in particular ones by Stokey (1945, 1954) on *Polypodium pectinatum* L. and *P. plumula* Humb. & Bonpl. ex Willd.; Atkinson & Stokey (1964, 1970) on *Polypodium chnoodes* Spreng.; Reyes and Pérez-García (1994) on *Polypodium lepidotrichum* (Fée) Maxon; Reyes et al. (1996) on *Niphidium crassifolium* (L.) Lellinger; Pérez-García et al. (1998) on three species of *Phlebodium* (R. Brown) J. Smith; and Ramírez and Pérez-García (1998) on *Microgramma nitida* (J. Sm.) A. R. Sm. (see comparative Table 1).

An attempt to classify the various known patterns of spore germination in homosporous ferns was made by Momose (1942), he described three types of spore germination: *centrifugal*, *centripetal*, and *tangential*. Later, Nishida (1965) renamed the *centripetal* and *tangential* types *aspidiod* and *polypodiod*, respectively, and added another which he called the *tripolar* type. Recently, Nayar and Kaur (1968) pointed out that these interpretations of spore germination are incorrect inasmuch as they ignored the polarity of the germinating spore. Nayar and Kaur (1971) gave a detailed account of the patterns of spore germination, classifying them on the basis of the planes of cell division in relation to the polarity of the spore and directions of growth of the primary rhizoid and prothallus. Thus among homosporous ferns there are three distinct categories: *polar*, *equatorial*, and *amorphous*, all differing in the plane and sequence of cell divisions.

The prothallus of the homosporous ferns follows a definite pattern of development leading ultimately to the characteristic adult form. This pattern is constant for each species and commonly to taxa of higher order. In general seven different patterns of prothallial development are recognized among homosporous ferns by Nayar and Kaur (1969): *Adiantum*-type, *Ceratopteris*-type, *Drynaria*-type, *Kaulinia*-type, and *Osmunda*-type. These differ in the sequence of cell divisions, in the stage of development and the region at which a meristem is established, presence or absence of trichomes, and in the final form of the adult thallus.

Thus the type of prothallial development in which an apical cell is established early during the formation of a prothallial plate (*Adiantum*-type) appears to be primitive compared to those in which the establishment of a mer-

TABLE 1. Comparison of the different development stages of the gametophytes of the some genera of the Polypodiaceae family.

Taxa	Type of spore	Types of spore germination	Filamentous phase	Prothallial development
<i>Pseudocolysis bra-deorum</i>	Monolete, yellow, ovate to elliptic	Gleichenia-type	Germinal filaments of 2–3 cells long	Drynaria-type
¹ <i>Arthromeris tenuicauda</i>	Monolete, brown, plano convex or concavo convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate more or less strap-shaped a cordate
¹ <i>Arthromeris wallichiana</i>	Monolete, dark brown, plano convex or concavo convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate more or less strap-shaped a cordate
¹ <i>Campyloneurum angustifolium</i>	Monolete, golden yellow, plano convex or concavo convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate
¹ <i>Colysis elliptica</i>	Monolete, golden yellow, prominently concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate more or less strap-shaped a cordate
¹ <i>Colysis hemionitidea</i>	Monolete, golden yellow prominently concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate more or less strap-shaped a cordate
¹ <i>Colysis pedunculata</i>	Monolete, golden yellow, prominently concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate more or less strap-shaped a cordate
¹ <i>Crypsinus griffithianus</i>	Monolete, pale brown, prominently concavo-convex	No mentioned	Germinal filaments of 8–10 cells long	Young prothalli strap-shaped a cordate
¹ <i>Crypsinus hastatus</i>	Monolete, pale brown, prominently concavo-convex	No mentioned	Germinal filaments of 8–10 cells long	Young prothalli strap-shaped a cordate
¹ <i>Lemmaphyllum carnosum</i>	Monolete, brownish yellow, plano-convex or slightly concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli spatulate
¹ <i>Pleopeltis excavata</i>	Monolete, golden yellow, plano-convex or slightly concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli cordate
¹ <i>Pleopeltis normalis</i>	Monolete, golden yellow, plano-convex or slightly concavo-convex	No mentioned	Germinal filaments of 3–7 cells long	Young prothalli cordate

TABLE 1. Extended.

Prothallial hairs	Adult prothallus	Sexual expression	Sporophytes
No hairs	Cordiform-spatulate	♂ and ♀, dioic, ♀ type usual, neck 4–6 cells long	7 months
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
No hairs	Perennial, ribbon-shaped branched	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
No hairs	Perennial, ribbon-shaped branched	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
No hairs	Perennial, ribbon-shaped branched	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 5–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 5–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ globular, ♀ type usual, neck 4–6 cells long	No sporophyte
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte
Branched or more complex	Ribbon-shaped	♂ small, ♀ type usual, neck 4–6 cells long	No sporophyte

TABLE 1. Continued.

Taxa	Type of spore	Types of spore germination	Filamentous phase	Prothallial development
¹ <i>Polypodium am-moenum</i>	Monolete, hyaline to yellowish, plano-convex or slightly conca-vo-convex	No mentioned	Germinal filaments of 8–10 cells long	Young prothalli spatulate
² <i>Pseudodrynaria coronans</i>	Monolete hyaline	No mentioned	Germinal filaments of 3–4 cells long	Young prothalli spatulate
³ <i>Lepisorus lorifor-mis</i>	Monolete, yellow-ish oil globules	Vittaria-type	Germinal filaments of 4–5 cells long	Kaulinia-type, young prothalli elongate a rib-bon-like
³ <i>Lepisorus thunber-gianus</i>	Monolete, yellow-ish oil globules	Vittaria-type	Germinal filaments of 4–5 cells long	Drynaria-type, young prothalli elongate a near-ly strap-like
³ <i>Weatherbya acce-dens</i>	Monolete, yellow-ish oil globules	Vittaria-type	Germinal filaments of 6–8 cells long	Drynaria type, young prothalli cordate
³ <i>Polypodium vulga-re</i>	Monolete, yellow-ish oil globules	Vittaria-type	Germinal filaments of 6–8 cells long	Drynaria-type, young prothalli cordate
⁴ <i>Polypodium pectin-atum</i>	Monolete	No mentioned	Germinal filaments of 4–8 cells long	No mentioned
⁴ <i>Polypodium plumu-la</i>	Monolete	No mentioned	Germinal filaments of 4–8 cells long	No mentioned
⁵ <i>Polypodium chnoo-des</i>	Monolete, brown	No mentioned	Germinal filaments of 3–4 cells long more common, 3–6 cells long	No mentioned, spatulate plate
⁶ <i>Polypodium lepidotrichum</i>	Monolete, brown	No mentioned	Germinal filaments of 4–5 cells long	No mentioned, spatulate plate
⁷ <i>Niphidium crassi-folium</i>	Monolete, yellow-green	Vittaria-type	Germinal filaments of 4–7 cells long	Drynaria-type, spatulate plate
⁸ <i>Phlebodium ara-neosum</i>	Monolete, golden	Vittaria-type	Germinal filaments of 2–7 cells long	Drynaria-type, spatulate plate
⁸ <i>Phlebodium decumanum</i>	Monolete, golden	Vittaria-type	Germinal filaments of 2–7 cells long	Drynaria-type, spatulate plate
⁸ <i>Phlebodium pseu-do-aureum</i>	Monolete, golden	Vittaria-type	Germinal filaments of 2–7 cells long	Drynaria-type, spatulate plate
⁹ <i>Microgramma niti-da</i>	Monolete, yellow	Vittaria-type	Germinal filaments of 4–6 cells long	Drynaria-type, spatulate plate

¹ Nayar, 1962; ² Nayar, 1954; ³Nayar & Raza, 1970; ⁴ Stokey, 1959; ⁵ Atkinson & Stokey, 1970; ⁶ Reyes & Pérez-García, 1994; ⁷ Reyes *et al.*, 1996; ⁸ Pérez-García *et al.*, 1998; ⁹ Ramírez & Pérez-García, 1998. ♂ = anteridia, ♀ = archegonia.

TABLE 1. Continued. Extended.

Prothallial hairs	Adult prothallus	Sexual expression	Sporophytes
Unicellular papillate with a extracellular cap-like secretion	Cordate with midrib 4–8 cells thick	♂ cap cell large, basal cell columnar, barrel-shaped, rather than saucer or funnel-shaped	No sporophyte
Unicellular papillate	Cordate	♂ globose and sessile, 2 months ♀ type usual, neck 4–5 cells long, 3–4 month	No sporophyte
Unicellular papillate secretory	Elongate, ribbon-like	Type usual in Polypodiaceae, neck short 3–4 cells	No sporophyte
Unicellular papillate secretory	Elongate cordate	Type usual in Polypodiaceae, neck short 3–4 cells	No sporophyte
Unicellular papillate secretory	Cordate	Type usual in Polypodiaceae, neck short 3–4 cells	No sporophyte
Unicellular papillate secretory	Cordate	Type usual in Polypodiaceae, neck short 3–4 cells	No sporophyte
Unicellular	Cordate	♂ and ♀ type usual, 2–4 months	Sexual
No hairs, only hairs acicular in gametophytes apogamic	Cordate	♂ and ♀ 4 months, type usual	embryo apogamous 3 months
Unicellular papillate in margin, hairs branched in surface	Cordate	♂ globose and elongated, ♀ neck 3–4 cells long	Sexual
Unicellular simple	Cordiform and reniform	♂ globose 3 cells and ♀ usual, dioic	Sexual, 3–4 months
Unicellular papillate	Cordiform with wide wings	♂ globose, ♀ necks 4 cells long	Sexual, 3 months
Unicellular capitate	Cordate-spatulate to cordate-reniform	♂ small, spherical or subglobose, ♀ necks 5–7 cells long	Sexual
Unicellular capitate	Cordate-spatulate to cordate-reniform	♂ small, spherical or subglobose, ♀ necks 5–7 cells long	Sexual
Unicellular capitate	Cordate-spatulate to cordate-reniform	♂ small, spherical or subglobose, ♀ necks 5–7 cells long	Sexual
No hairs	Cordiform-alargate	Monoic, ♂ small barrel-shape, ♀ necks 5 cells long	Sexual

istematic cell is delayed (*Drynaria*-type). Usually accompanying this delayed establishment of the meristematic cell there is also a distinct reduction in its activity. Thus in prothalli having an *Adiantum*-type of development, growth and expansion of the young prothallus is mainly by the activity of the meristematic cell. In those having a *Drynaria*-type of development, the meristematic cell does not play a very active part in the growth and expansion of the young prothallus, as is the case in the majority of the Polypodiaceae (Nayar, 1962, 1963a, 1965).

The elimination of the meristematic cell altogether and the establishment of a pluricellular meristem directly from some of the marginal cells of a broad, non-meristic prothallial plate, has been recorded in several cases among the more advanced groups of homosporous ferns. The elimination of meristic cells and the presence of a pluricellular meristem as found in the *Kaulinia*-type of development appears to represent the most advanced condition.

In this paper, we describe the morphology and development of the sexual phase of *Pseudocolysis bradeorum*.

MATERIALS AND METHODS

Spores of *P. bradeorum* were obtained from fertile specimens of plants (Gómez 26045, USJ) growing in Finca La Selva, near Puerto Viejo, province of Heredia, Costa Rica, at an elevation of 50 m. Fertile leaves were sealed in paper envelopes and allowed to dry under natural conditions to favor the release of spores from the sporangia. After several days, the contents of the envelopes were sifted to eliminate sporangial fragments and other debris (Pérez-García *et al.*, 1998).

Spores were sown in 20 Petri dishes (two replicates) on 10% agar supplemented with Thompson medium (Klekowski, 1969; Pérez-García, 1989); one of which was kept in darkness to test for photoblastism. Petri dishes were kept in transparent, sealed plastic bags to avoid dessication and contamination, given a light regime of 12 h light/12 h darkness, with daylight Solar lamps (75w/t 38/A1-D) placed 35 cm above the cultures, and maintained at temperature 25–28°C. Cultures were examined periodically (except the Petri dish maintained in darkness) until germination was detected on the seventh day. After that, dishes were checked every 15 days to record data on the development of the prothallia. Cultures were moistened with sterilized water to prevent desiccation and, in the last stages, to favor the antheridia opening and movement of antherozoids. The culture maintained in darkness was opened 100 days after sowing. Spores were also sown in previously sterilized, natural organic soil.

Photomicrographs were taken from living material with an AO microscope and Tmax B/W film. Pictures of spores were taken with a Zeiss SEM DSM 94DA.

RESULTS

The spores of *P. bradeorum* are monolete, bilateral, yellow, and ovate to elliptic in polar view. They are 56 (54) 53 m long $\times$ 34 (33) 32 m broad [$n =$

50]. The spores are chlorophyllous but also contain yellow oily globules. The thin granulate perine (Figs. 1, 2) is psilate, smooth to verrucate, or variously ornamented. The laesurae are short.

Germination was of the *Gleichenia*-type and commenced seven days after sowing. The first division produced a wall parallel to the polar axis of the spore, cutting off a lateral initial rhizoid cell (Figs. 3, 4). This simple equatorial form is found in many members of the Polypodiaceae.

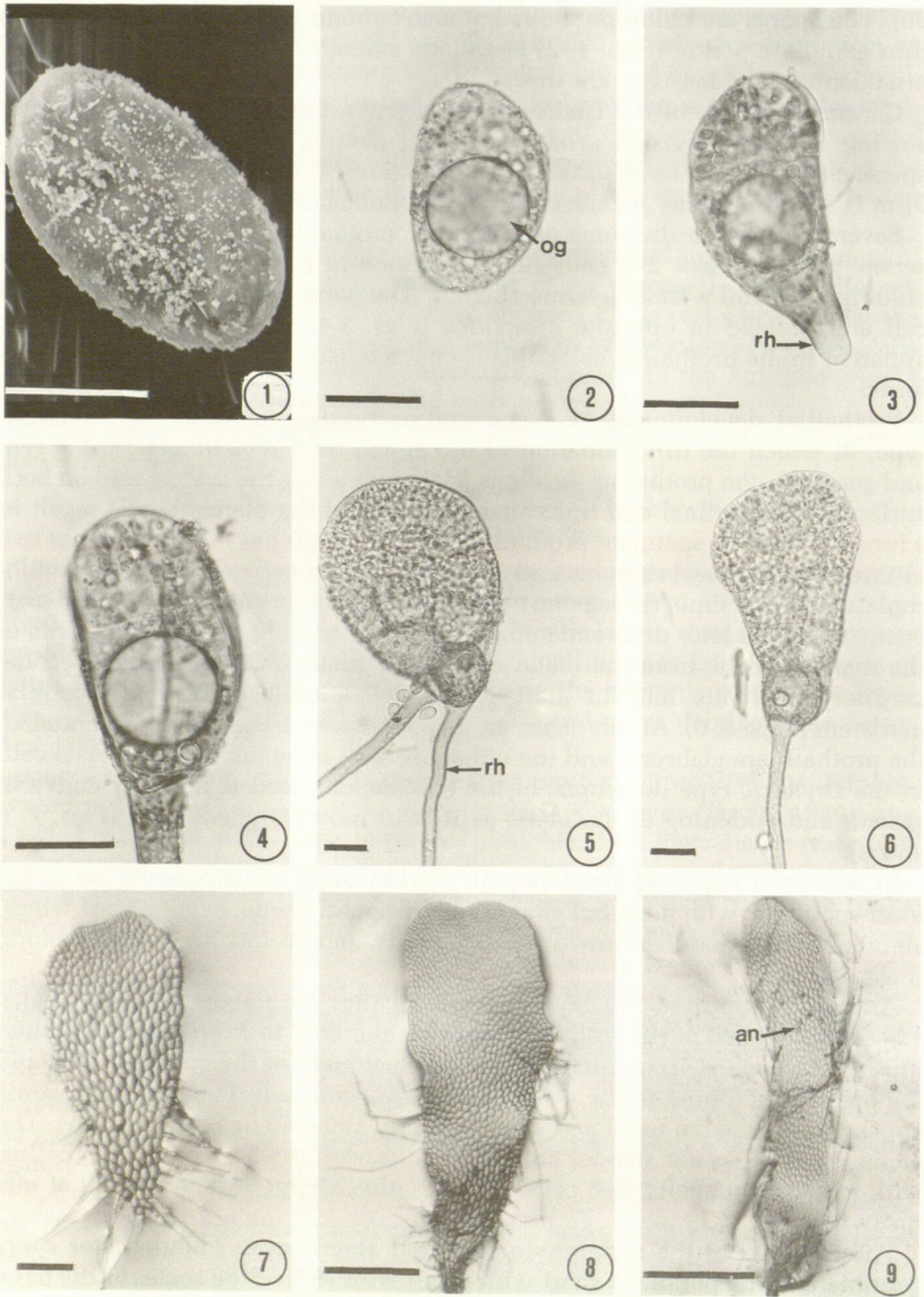
Several transverse divisions of the initial prothallial cell resulted in a uniseriate germ filament 2–3 cells long (each one of these cells with abundant chloroplasts) and a short hyaline rhizoid. The germ filament and the rhizoid cell are oriented in opposite directions (Figs. 3, 4). A large oil globule was apparent in the prothallial cells; this is characteristic in many polypodiaceous ferns.

Prothallial development of *Pseudocolysis bradeorum* is of the *Drynaria*-type, in which the differentiation of the apical meristematic cell is delayed, and generally the prothallus develops trichomes along the margin and on both surfaces. Longitudinal and transverse divisions of the filament cells result in a broadly ovate to spatulate prothallial plate at 20–30 days. The plate has two or three hyaline basal rhizoids and 36–50 prothallial cells with abundant chloroplasts. At this time, there is no evident meristematic zone. An obconic meristematic cell is later differentiated as a result of an oblique division of one of the marginal cells from the distal end of the plate. Young prothalli become cordiform-spatulate, and the meristematic cell is replaced by a pluricellular meristem (Figs. 5, 6). At this stage, an inconspicuous cushion is differentiated, the prothalli are glabrous, and the old spore wall is retained on the basal cell. In the *Drynaria*-type development the meristematic cell is not very active in growth and widening of the plate, as it is in most Polypodiaceae (Figs. 7, 8 and 9).

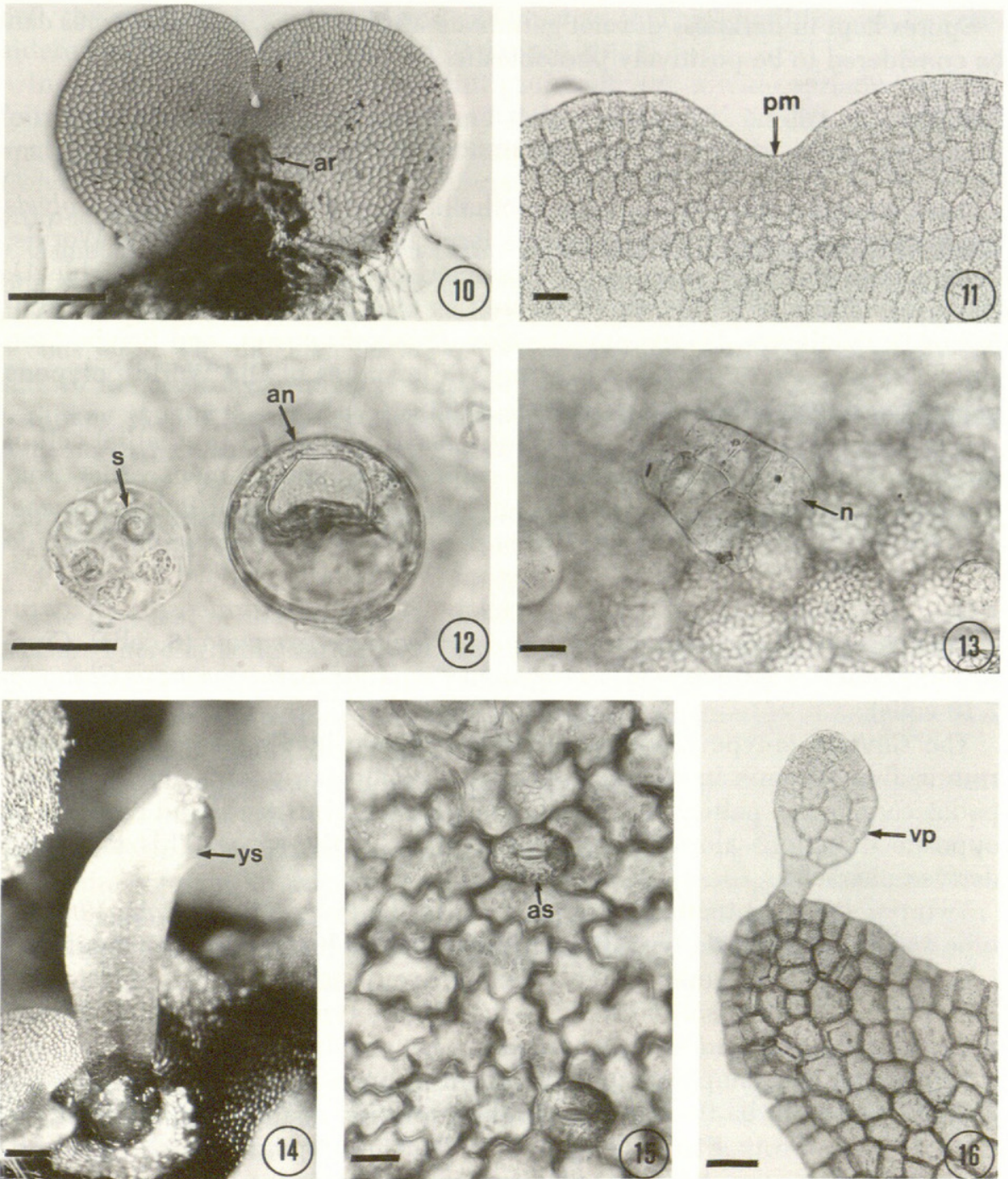
In advanced stages of development, 70–105 days, gametophytes are cordiform-spatulate, with a central shallow meristematic zone, symmetrical wings, abundant short, reddish brown basal rhizoids, and an inconspicuous cushion (Figs. 10, 11).

Antheridia appeared 180 days after sowing; they are globose with three cells, a basal funnel cell, a ring cell, and an opercular cell. In *P. bradeorum*, antheridial dehiscence is accomplished by the detachment of the opercular cell and the opening of a pore in the wall of the androgenic cell (Fig. 12). Archegonia appear on the medial basal part of the cushion 130–140 days after sowing. The archegonial necks are slender and oriented toward the base of the prothallus, with four rows of cells, 5–6 cells per row, plus a binucleate neck cell at maturity (Fig. 13).

The first leaf of the sporophyte appeared about seven months after spore germination; the petiole is short with small whitish hyaline scales at the base, the lamina is simple and entire, with smooth margins (Fig 14). The venation is open dichotomous. Anomocytic stomata were observed on the abaxial surface (Figs. 15). Sporophytes only developed on the natural organic soil cultures.



FIGS. 1-9. Germination and prothallial development of *Pseudocolysis bradeorum* (Rosenst.) L. D. Gómez. 1. SEM of spore. 2. Spore with yellow oil globule. 3-4. Germination initiation. 5-6. Young prothallial plate. 7-8. Spatulate gametophytes. 9. Spatulate gametophyte with antheridia. Scale bars in figs. 1-6 = 15 μ m, in figs. 7-9 = 400 μ m.



FIGS. 10–16. Morphology of adult prothallus and sex organs of *Pseudocolysis bradeorum* (Rosenst.) L. D. Gómez. 10. Cordate gametophyte with archegonium. 11. Pluricellular meristem. 12. Antheridia. 13. Neck of archegonium. 14. Sporophyte. 15. Anomocytic stomata. 16. Gametophyte showing vegetative propagation. Scale bars in figs. 10, 14 = 400 μm , in figs. 11, 12, 13, 15 and 16 = 15 μm .

After 71 days, we observed the formation of gemmae on the margins of young gametophytes (Fig. 16). When detached, these small gemmae maintained the capacity to grow and developed into adult gametophytes of typical structure and sexuality. The development followed the same pattern observed in agar, except that adult gametophytes were cordate.

Spores kept in darkness did not germinate after 10 days, so this species can be considered to be positively photoblastic.

DISCUSSION

Analysis and comparison of the prothallial development of *Pseudocolysis bradeorum* with other polypodiaceous ferns from the Old and New Worlds, demonstrate that they share many characteristics (see comparative Table 1). However, spores of *P. bradeorum* as well as the spores of *Niphidium crassifolium* (L.) Lellinger, *Microgramma nitida*, *Phlebodium* spp., and *Polypodium* spp., germinate 7–10 days after sowing, while spores of Old World polypods usually germinate after 30 days (Nayar, 1962).

It is interesting to note that oil globules occur in the first prothallial cell of the germ filament, and the number of cells of the germ filament varies from 2–10. A short filament has been found in several species of Polypodiaceae, e.g., *Polypodium chnoodes* Spr. [*Polypodium dissimile*], *Microgramma nitida* (J. Smith) A.R. Sm. (6 cells), *Polypodium lepidotrichum* (Fée) Maxon (4–5 cells), *Niphidium crassifolium* (3–7 cells), *Phlebodium araneosum*, *P. pseudoaureum*, and *P. decumanum* (4–7 cells), *Pleopeltis excavata* (6 cells), *Crypsinus* (9 cells), *Arthromeris* (6–7 cells) and *Pseudodrynaria coronans* Ching (3, 7, 10 cells).

The *Gleichenia*-type germination pattern shown by *Pseudocolysis bradeorum* is also common in advanced groups of homosporic ferns, such as Polypodiaceae. In this pattern, the germ filament and primary rhizoid elongate in opposite directions along the equatorial plane of the spore. This may be a derived character.

Two types of germination patterns occur in the Polypodiaceae, the *Vittaria*-type and the *Gleichenia*-type. Basal groups such as Platycerioideae exhibit the *Gleichenia*-type, and comparatively derived groups as the Crypsinoideae, Drynarioideae, and Microsorioideae have the *Vittaria*-type. In this regard, the germination type of *Pseudocolysis bradeorum* is “primitive”.

In general, the temporary or permanent suppression of organized apical growth appears to be the key note in the evolution of the prothalli of homosporous ferns. Prothallial development is *Drynaria*-type, in which differentiation of the meristematic cell is delayed longer than in the *Adiantum*-type. In Polypodiaceae, prothallial development in basal genera of the Microsorioideae (Nayar, 1962; 1963a and 1963b) and Platycerioideae (Nayar and Chandra, 1965) is closer to the *Adiantum*-type, while in the more derived groups as the Drynarioideae (Nayar, 1965) and Crypsinoideae (Nayar, 1962), the development is *Drynaria*-type, with delay of the formation of the meristematic cell. In comparatively more advanced genera such as *Kaulinia* (Nayar, 1963a), *Colysis* and *Paraleptochilus* (Nayar, 1963b), and *Colysis* (Nayar, 1962) the *Kaulinia*-type prevails.

Some Polypodiaceae (Microsorioideae and Pleopeltoideae) have a prothallial development of the *Kaulinia*-type, with no differentiation of a meristematic

cell, the prothalli is prolonged and ribbon-shaped. This condition can be considered as an advanced condition (Atkinson, 1973).

In regards to the shape of the adult gametophytes, a wide variation can be found, long-cordate in *Niphidium* and *Polypodium* spp., cordate to reniform, spatulate and long-lived in *Polypodium* spp. and *Crypsinus*, strap-shaped in *Colysis* and *Pleopeltis*. In *Pseudocolysis* the prothallia are cordate-spatulate to strap-shaped.

Gametangia are of the common type for homosporous leptosporangiate ferns. Shape and structure of the gametangia agree with the description of those organs given by Davie (1951), Hartman (1931), and Nayar (1962) for some polypodiaceous ferns. This is characteristic of polypodiaceous ferns and previously described in classical papers by Schlumberger (1911) and Hartman (1931).

Stokey (1959) mentioned the presence of unicellular papillate trichomes with an extracellular cap-like excretion, on margins and both surfaces of the prothalli. This is a common condition found in many polypodiaceous ferns (*Campyloneurum*, *Microgramma*, *Niphidium*, *Phlebodium*, *Pleopeltis*, and *Polypodium*). However, the gametophytes of *Pseudocolysis* are glabrous, a condition which, according to Nayar (1962), is advanced.

The first leaf of the sporophyte appeared seven months after spore germination. There is wide variation reported in the age of sporophyte differentiation. Species of *Niphidium* and *Polypodium* appeared after three months, while in *Phlebodium* spp., time until sporophyte production is between five months and 2.5 years (Pérez-García *et al.*, 1998).

Vegetative propagation may allow gametophytes to survive extreme environmental conditions and to propagate vegetatively thus permitting survival of the species in more extreme ecological niches.

Results obtained in this study, in regard to development and characteristics of the gametophytes and comparison with data from New and Old World genera of polypodiaceous ferns, confirm that *Pseudocolysis bradeorum* is closely related to some genera of Polypodiaceae.

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