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Studies in the Marchantiales (Hepaticae) from southern Africa. 8. The genus *Plagiochasma* (Aytoniaceae: Aytonioideae) and six local taxa

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Keywords: Hepaticae, Marchantiales, *Plagiochasma appendiculatum*, *P. beccarianum*, *P. eximium*, *P. microcephalum* var. *microcephalum*, *P. rupestre* var. *rupestre*, *P. rupestre* var. *volkii*, southern Africa

ABSTRACT

A taxonomic account is given of the genus *Plagiochasma* Lehm. & Lindenb. and its two subgenera, *Micropylum* Bischl. and *Plagiochasma*. The first subgenus is represented in southern Africa by *P. rupestre* var. *rupestre* (J.R. & G. Forst.) Steph. and *P. rupestre* var. *volkii* Bischl.; the second by *P. appendiculatum* Lehm. & Lindenb. (newly recorded for the region), *P. beccarianum* Steph., *P. eximium* (Schiffn.) Steph. and *P. microcephalum* (Steph.) Steph. var. *microcephalum*. Descriptions and illustrations of these taxa together with distribution maps and a key to the subgenera and species are provided.

UITTREKSEL

'n Taksonomiese verslag oor die genus *Plagiochasma* Lehm. & Lindenb. en sy twee subgenusse *Micropylum* Bischl. en *Plagiochasma* word gegee. Eersgenoemde subgenus word in Suider-Afrika deur *P. rupestre* var. *rupestre* (J.R. & G. Forst.) Steph. en *P. rupestre* var. *volkii* Bischl. verteenwoordig en laasgenoemde deur *P. appendiculatum* Lehm. & Lindenb. (nuut vermeld vir die streek), *P. beccarianum* Steph., *P. eximium* (Schiffn.) Steph. en *P. microcephalum* (Steph.) Steph. var. *microcephalum*. Beskrywings en illustrasies van hierdie taksons sowel as verspreidingskaarte en 'n sleutel tot die subgenusse en spesies word verskaf.

Plagiochasma *Lehm. & Lindenb.* in Lehm., Novarum et minus cognitarum stirpium pugillis quartus: 13 (1832); Nees: 33, 40 (1838); Gottsche et al.: 511 (1846); Steph.: 775 (1898); A. Evans: 262 (1915); Sim: 16 (1926); K. Müll.: 331 (1951–1958); Hässel de Menéndez: 83 (1963); S.W. Arnell: 65 (1963); Bischl.: 71 (1977); R.M. Schust.: 264 (1992). Type species: *P. cordatum* Lehm. & Lindenb.

Aytonia J.R. & G. Forst.: 147 (1776); Lindb.: 291 (1868); Schiffn.: 30 (1893). Type species: *A. rupestris*.

Aitonia J.R. & G. Forst.: 46, 73 (1787), orth. var. [not of Thunb.: 166 (1776)].

Rupinia L. f.: 69 (1781) nom. illegit.

Ruppinia L. f.: 204 (1783) orth. var. Type species: *R. rupestris*.

Antrocephalus Lehm.: 682 (1838). Type species: *A. nepalensis*.

Teldea Mont. ex Webb & Berthel.: 59 (1840) nom. illegit. Type species: *T. elastica*.

Thalloid, smallish to medium-sized to large, flat to slightly concave, not grooved, firm and somewhat leathery, glaucous to purplish and then dull and waxy to velvety, or else bright green to yellowish green, dorsally hardly perceptibly areolate to distinctly so, in crowded, extensive mats, on calcrete soil, or in rocky crevices, on ledges, under overhangs, at foot of large boulders, at seepages or along stream banks. *Branches* lingulate and simple to pseudodichotomously or variously furcate, with lateral or apical innovations from keel, sometimes articulated; thickened over midrib, thinning toward attenuate, narrowly purple, scalloped margins, apically notched, with scale appendages recurved over edge. *Dorsal epidermis* mostly lacking chloroplasts, thick- or thin-walled with trigones, roughened or smooth and with or without waxy, granular deposit externally. *Air pores* simple, sometimes ± stellate, minute and very inconspicuous or larger and slightly raised, encircled by 1 ring or by 2(3) concentric rings of (4)5–8 cells in each, radial walls of cells often forming continuous lines which may be thickened, pores leading below into small, compact, empty air chambers in several irregular layers, bounding walls chlorophyllose, some scattered cells nearly filled with a single oil body, also present in storage tissue, where cells are closely packed; rhizoids ventral, some smooth, others pegged. *Scales* purple-red to violet, in 2 forwardly directed ventral rows, large, extending beyond thallus margins or not, basal portion broadly ovate, apically with 1 or 2(3) appendages, variable in shape, linear-lanceolate or ovate to orbicular, sometimes constricted or folded at base, containing a few scattered oil cells; scale margin entire or toothed and with papillae in subgenus *Plagiochasma*, but without in subgenus *Micropylum*.

Monoicous, autoicous or paroicous. *Androecia* with antheridia sunken in tumid, sessile, crescentic to broadly U- or V-shaped dorsal cushions, base encircled by short paleae. *Archegoniophores* dorsal, single to several acropetally arranged along length of leading branch, usually with tuft of slender paleae around base and eventually mostly at apex of very short to long unfurrowed stalk, bearing carpocephalum with (1–)2–4(–5) capsules, each on a short seta, capsule wall unistratose, cells lacking thickening bands, dehiscing by an irregularly decaying lid and

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covered by ± spherical, bilabiate involucre with vertically slightly overlapping, somewhat swollen lips, top of carpocephalum slightly raised to nearly flat or somewhat depressed, 3- or 4-sided, with compound air pores. *Spores* 70–105 µm, yellow to brown, triangular-globular, winged, both faces coarsely reticulate, proximal face with distinct triradiate mark. *Elaters* 175–300 µm long, 7.5–20.0 µm wide in middle and tapering to ends, bi- or tri-spiral.

The genus *Plagiochasma* is classified in the family Aytoniaceae Cavers, and in the subfamily Aytonioideae, whereas the other four genera of the family, namely *Asterella*, *Cryptomitrium*, *Mannia* and *Reboulia* are placed in subfamily Reboulioideae Grolle (Grolle 1972). *Plagiochasma* was previously said to include ± 34 species worldwide (Evans 1915), but the number of taxa has been considerably reduced by Bischler (1977, 1978, 1979). Most are confined to the rather warmer, dry regions of the world, although *P. rupestre* var. *rupestre* is nearly cosmopolitan. The other taxa that also occur in southern Africa, are more narrowly restricted in their distribution. Two subgenera, namely *Micropylum* and *Plagiochasma* have been instituted by Bischler (1977), based mainly on the compactness and colour of the thalli, the structure of the dorsal air pores and on the shape, size and margins of the scale appendages.

Key to subgenera and species of *Plagiochasma*

1a Thallus glaucous to greyish green, dull and velvety, dorsally granular, with numerous air pores, tiny and obscure, bounded by a single ring of 4–6 cells but never by an inner hyaline ring of collapsed cells; ventral scales with 1–2(3) narrow appendages, hardly or not constricted at base, with margins not differentiated and lacking teeth and/or papillae (subgenus *Micropylum* Bischl.):

2a Ventral scales reddish pink to purple, rarely more than 2000 µm long, including pink, purple or hyaline appendage(s) (1 or 2), narrowly to broadly triangular, up to 900 µm long, apically shortly pointed, with 1 or 2 (rarely 3) cells in series, thin-walled and quadrate or rectangular; spores up to 92.5 µm in diameter . . . . . 1a. *P. rupestre* var. *rupestre*

2b Ventral scales dark red or purple, large, up to 3000 µm long, including hyaline appendage(s) (1–3), narrowly triangular, up to 1500 µm long, apically with a long point, with 3–5 elongated cells in series, thick-walled; spores more than 92.5 µm in diameter . . . . . 1b. *P. rupestre* var. *volkii*

1b Thallus green to yellow-green, shiny and dorsally smooth with fewer air pores, large and quite conspicuous, raised and bounded by an inner hyaline ring of collapsed cells and then by 2 or 3 concentric rings of 5–8 cells in each; ventral scales with 1–3 appendages, wide or narrow, often constricted or folded at base with margins differentiated into smaller cells, teeth and/or papillae (subgenus *Plagiochasma*):

3a Scales mostly with a single appendage, sometimes with two, round or oval or broadly triangular, widest across middle, constricted or folded at base; along margins 1 or 2 rows of regular, smaller cells or alternating with them cells of usual size, lacking teeth; elaters with evenly thickened spirals:

4a Thallus robust; carpocephalum on short, thick stalk; scale appendage single, rarely double, rounded, large, hyaline above, red or pink below, markedly constricted at base; margins smooth, with small cells here and there alternating with somewhat larger ones . . . . . 2. *P. appendiculatum*

4b Thallus medium-sized; small carpocephalum on thin, short or long stalk; scale appendage single or double, oval or broadly triangular, pink or violet, slightly constricted or folded or horizontally pleated at base; margins with 1 or 2 rows of smaller, regular cells, occasionally with papillae . . . . . 3. *P. microcephalum* var. *microcephalum*

3b Scales with 1, 2 (or 3) appendages, narrowly triangular, slightly constricted to folded at base or evenly tapered; sometimes toothed along margins; elaters with spirals interrupted or evenly thickened:

5a Thalli robust but carpocephala relatively small; dorsal air pores of thalli surrounded by hyaline ring and 3 concentric rings of cells; scale appendages red, not acuminate, slightly constricted or folded at base; elaters with spirals often interrupted . . . . . 4. *P. eximium*

5b Thalli less robust and carpocephala of usual size; air pores surrounded by hyaline ring and 2 concentric rings of cells; scale appendages purple, acuminate, lanceolate, not constricted at base; elaters with spirals evenly thickened . . . . . 5. *P. beccarianum*

Subgenus *Micropylum* Bischl.

Micropylum is characterized by very compact, velvety thalli, the dorsal surface covered with a water-repellent, granular deposit and the numerous air pores tiny and inconspicuous; the ventral scales have acuminate appendages with undifferentiated margins, lacking teeth and papillae. *Plagiochasma rupestre* var. *rupestre* and *P. rupestre* var. *volkii* are placed here.

1. **Plagiochasma rupestre** *(J.R. & G. Forst.) Steph.* in Bulletin de l'Herbier Boissier, Sér. 1, Vol. 6.10: 783 (1898); K. Müll.: 332 (1952); A. Evans: 277 (1915); Sim: 18 (1926); Hässel de Menéndez: 84 (1963); S.W. Arnell: 67 (1963); Bischl.: 64 (1978); Volk: 237 (1979); Bischl. & Sérgio: 173 (1984); R.M. Schust.: 292 (1992). Type: Madeira, Funchal, Quinta do Bom Sucesso, *Sérgio & Nóbrega 3873* [LISU, neo.! selected by Bischl. & Sérgio (1984)]; PC, BM, G, MADJ, iso.).

P. abyssinicum Gola: 62 (1914). Type: Ethiopia, Erythraea, in regione Hamasen prope Asmara n. 132, 24. IV. 1909, leg. *Chiovenda*.

P. algericum Steph.: 780 (1898). Type: Algeria, leg. *Trabut*.

P. capense Sim: 17 (1926). Type: S Africa, Herschel, Cape Province, 5000 ft, leg. *Hepburn*.

P. dschallanum Steph.: 778 (1898). Type: Tanzania, Kilimandscharo, ad lacum Dschalla, leg. *Holst*.

P. muricatum Steph.: 310 (1901a). nom. illegit.

P. tenue Steph.: 779 (1898). Types: S Africa, Transvaal, leg. *MacLea, Wilms*; Tanzania, Usambara, leg. *Holst*; Angola, leg. *Welwitsch*.

The above list of synonyms includes only African plants and was taken from Bischler (1978). Schuster (1992) gives an extensive list of ± all synonyms established largely on the basis of detailed studies by Evans (1915) and Bischler (1978).

Thallus medium-sized to quite large, nearly flat to somewhat concave with the sides slightly raised, oblong to lingulate (Figure 1A), compact, glaucous to greyish green, dull, surface ± water-repellent, narrow purple edge along margins, pores very inconspicuous, almost imperceptible as minute dots, subdorsal air chamber walls hardly visible, when wet; thallus margins incurved or clasped together, exposing deep purple to dull black, transversely striate underside of wings, toward apex sometimes covered with a dull bloom and medianly always by scales, when dry; in crowded, gregarious patches, simple or once, rarely twice furcate or with apical or latero-ventral innovations and then articulated or jointed. *Branches* 8–25 × (3–)4–6 mm, 375–650 µm thick over midrib, laterally thinning out into attenuate wings (Figure 1F); apex notched, with appendages of 8–10 deep pinkish purple or purple, sometimes partly decolorate scales recurved over edge; margins acute, thin, scalloped and undulate; flanks sloping obliquely, purple; ventral face medianly keeled, green, with row of purple-red or purple scales on either side (Figure 1E).

Dorsal epidermal cells unistratose, hyaline, polygonal, 5–7-sided, 25–47 × 20–37 µm, thin-walled but thickened at corners, in transverse section 25–37 µm thick, externally covered with granules, occasionally containing an oil body, along margins cells rectangular (Figure 1I), ± 27 × 15 µm, air pores numerous, 88–250 µm distant from each other, not raised (Figure 1H), simple, tiny, mostly appearing plugged, but lacking small inner hyaline ring of collapsed cells, surrounded in one series by 3–5 small, bluntly triangular cells (Figure 1G), 10–20 µm long, 17–25 µm across widest part, partly overlying dorsal cells, radial walls often thickened. *Assimilation tissue* 175–220 µm thick, ± ⅓ the thickness of thallus, air chambers empty, in several layers, vertical medianly, sloping obliquely toward the sides, 37–55(–125) µm wide, cells in bounding walls rounded, rather irregular in size, but averaging 25 × 22–25 µm, some with oil bodies, these also present in storage tissue which occupies remaining ⅔ thickness of thallus, cells angular, 25–32 µm wide; rhizoids mostly pegged, 20–30 µm wide, occasionally smooth, 17.5 µm wide. *Scales* reddish pink or purple, occasionally with a faint bloom, appendages and base sometimes hyaline, arranged in 2 forwardly directed ventral rows, one on either side of midrib, rather asymmetric, obtusely triangular with flatly arched base, gradually narrowed above, without constriction into 1 (Figure 1K) or 2(3) (Figure 1J) acuminate to ovate-lanceolate appendages, margins entire, total length (including (600–)900–1450 µm long appendage) 1200–3000 µm, width at base (600–)900–1250 µm, cells in body of scale 4–6-sided, 30–62(–75) × 17–25 µm, becoming smaller toward base and rectangular or not along margin, 30–40 × 20 µm, sometimes bulging outwards, where cells join, at apex ending in 1–4 uniseriate cells, scattered throughout scale several cells that had contained oil bodies, 20–37 × 25 µm.

Monoicous. *Androecia* in sessile cushions, round or crescentic, up to ± 2 × 3 mm, medianly on leading branch or on apical or latero-ventral innovations with immersed antheridia that open above via raised, 37.5 µm high, conical papillae (Figure 1D), at base encircled by tapering, purple paleae (Figure 1N), up to 600 µm long, 180 µm wide at base, cells 4- or 5-sided, ± 50 × 30–37 µm, apical cell ± 32 × 20 µm. *Archegoniophores* in acropetal sequence medianly along main branch, or paired on pseudodichotomously furcate branches, enclosed by tall tuft of tapering, purple-red paleae, up to 1500 µm long, 220 µm wide at base, most of them later carried to tip of stalk (Figure 1M), cells in body of paleae rectangular, 37–53 × 20–25 µm, toward apex elongating and narrowing, up to 62 × 17 µm, 3 or 4 serially arranged. *Carpocephala* 2–3 mm wide, on top initially slightly raised (Figure 1B), later becoming depressed, air pores compound, with 1–3(–5) lobes, involucral lips vertical and swollen, slightly overlapping, each enclosing a single oval capsule, 1500 × 1000 µm, on a short seta and with decaying lid, wall unistratose, cells 25.0–37.5 × 22.5–32.5 µm, polygonal, thin-walled with corners thickened, lacking thickening bands (Figure 1L); stalk at maturity usually remaining very short, only rarely up to 6 mm long, lacking rhizoidal furrow, 640 × 430 µm in transverse section (Figure 1C), cortical cells thicker-walled externally, rounded, 17.5 × 15.0 µm, medullary cells thin-walled, angular, ± 25 µm wide. *Spores* 80–105 µm in diameter, triangular-globular, polar, light brown to yellow brown, translucent, wing up to 12 µm wide, margin undulate, crenulate; ornamentation similar on both faces: distal face (Figure 2A, F) with ± 4 areolae across, ± 20 µm wide, areolar walls wide and studded with granules (Figure 2B, G); proximal face with narrow triradiate mark, clearly elevated and distinct (Figure 2C), each of 3 facets with 6–9 areolae, up to 25 µm wide, walls raised and wide, studded with granules (Figure 2D, H). *Elaters* light brown to yellow brown, 175–235 µm long, 12.5 µm wide in middle, tapering toward ends, ± 5 µm wide, bispiral (Figure 2E, I). *Chromosome number:* n = 9, 18 (Bischler 1978).

Two varieties are recognized: *P. rupestre* var. *rupestre* and *P. rupestre* var. *volkii*. They are distinguished by the longer, acuminate, hyaline appendages of the ventral scales and slightly larger spore dimensions of the latter.

1a. **P. rupestre** var. **rupestre**

Obliquely lunate ventral scales rarely longer than 2000 µm and 1050 µm across base; 1 or 2 narrowly to broadly triangular appendages up to 900 µm long, 1.7–2.7 times longer than wide, and apically acuminate with uniseriate 1 or 2(3) terminal cells, quadrate or rectangular in shape and thin-walled; cells in curved margin of body of scale rectangular, sometimes bulging slightly outward where 2 cells join; male paleae around basal part of androecium 550–580 µm long, 110–180 µm wide at base, tapering to a narrow tip, with 1–3 cells in series, ± 32 × 20 µm (Figure 1N); female paleae 1030–1375 µm long, 150–220 µm wide at base, tapering to a narrow tip, with up to 4 cells in series, 30–40 × 17 µm (Figure 1M); spores 80.0–92.5 µm in diameter (Figure 2A, D).

The typical variety is subcosmopolitan and widely distributed, especially in xerothermic regions. Frey & Kürschner (1988) regard it as a xerothermic Pangaean taxon. In southern Africa it is quite common and frequently collected in rocky crevices, moist ledges, under boulders, or at seepages, on calcareous substrates or on soil overlying cave sandstone or dolomite. It sometimes grows together with *Targionia hypophylla*, *Athalamia*

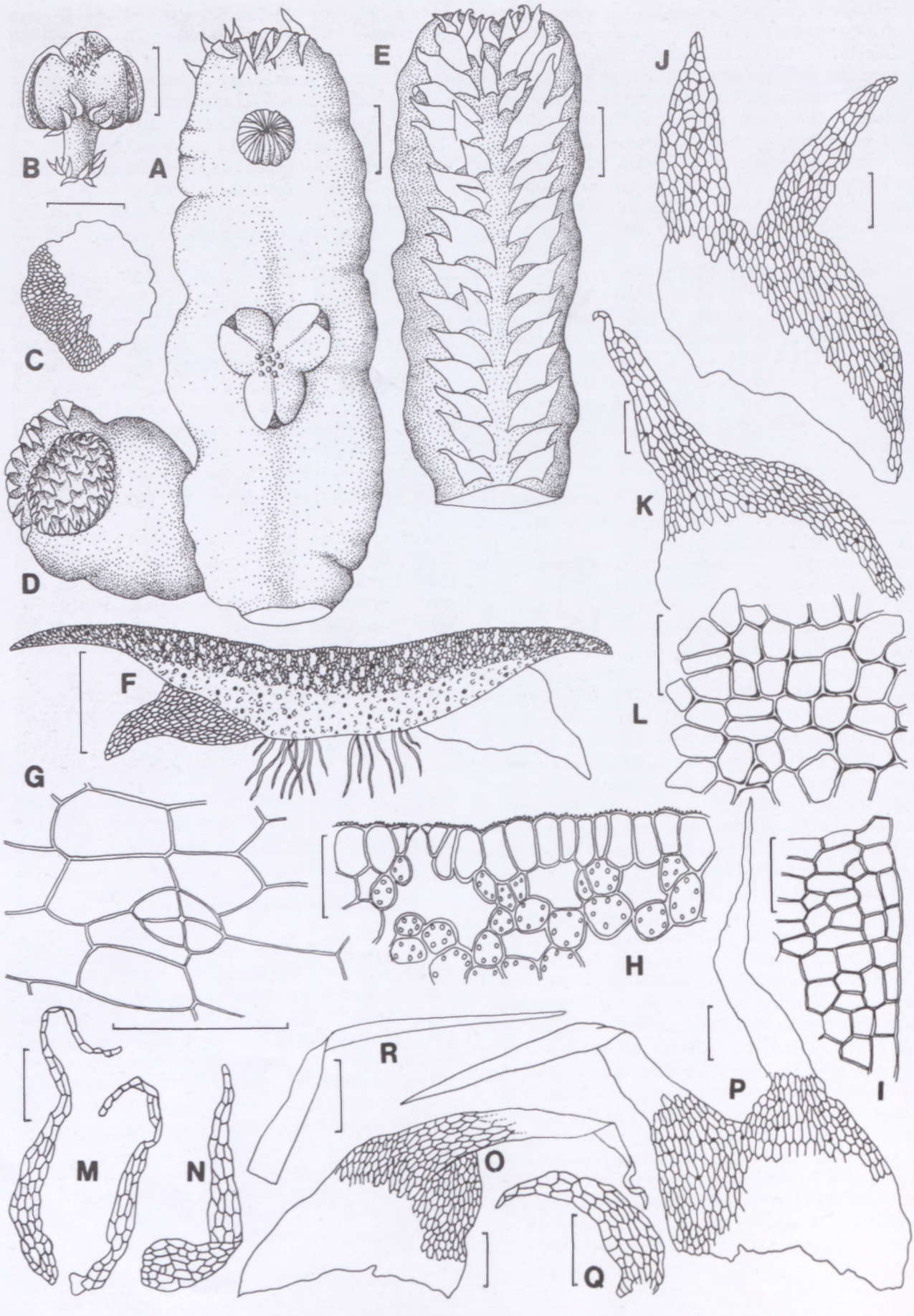

FIGURE 1.—A–N, *Plagiochasma rupestre* var. *rupestre*: A, E, F, I, thallus: A, dorsal face, with archegoniophore and carpocephalum; E, ventral face; F, t.s.; I, margin. B, carpocephalum, side view; C, t.s. of stalk; D, androecium at apex of latero-ventral branch; G, air pore and dorsal cells from above; H, t.s. of air pore, dorsal cells and air chambers. J, K, ventral scale: J, with 2 appendages; K, with 1 appendage. L, cells in capsule wall; M, female paleae; N, male palea. O–R, *Plagiochasma rupestre* var. *volkii*. O, P, ventral scale: O, with 1 appendage; P, with 2 appendages. Q, male palea; R, female palea. A, B, D, E, L, N, *Heilgendorff CH 13611*; C, *Manning CH 13590*; F, H, *Anderson 1230*; G, I–K, M, *S.M. Perold 3058*; O–R, *Mogg 37590*. Scale bars: A, B, D, E, 2 mm; F, 1 mm; C, J, K, M–R, 250 µm; G–I, L, 50 µm.

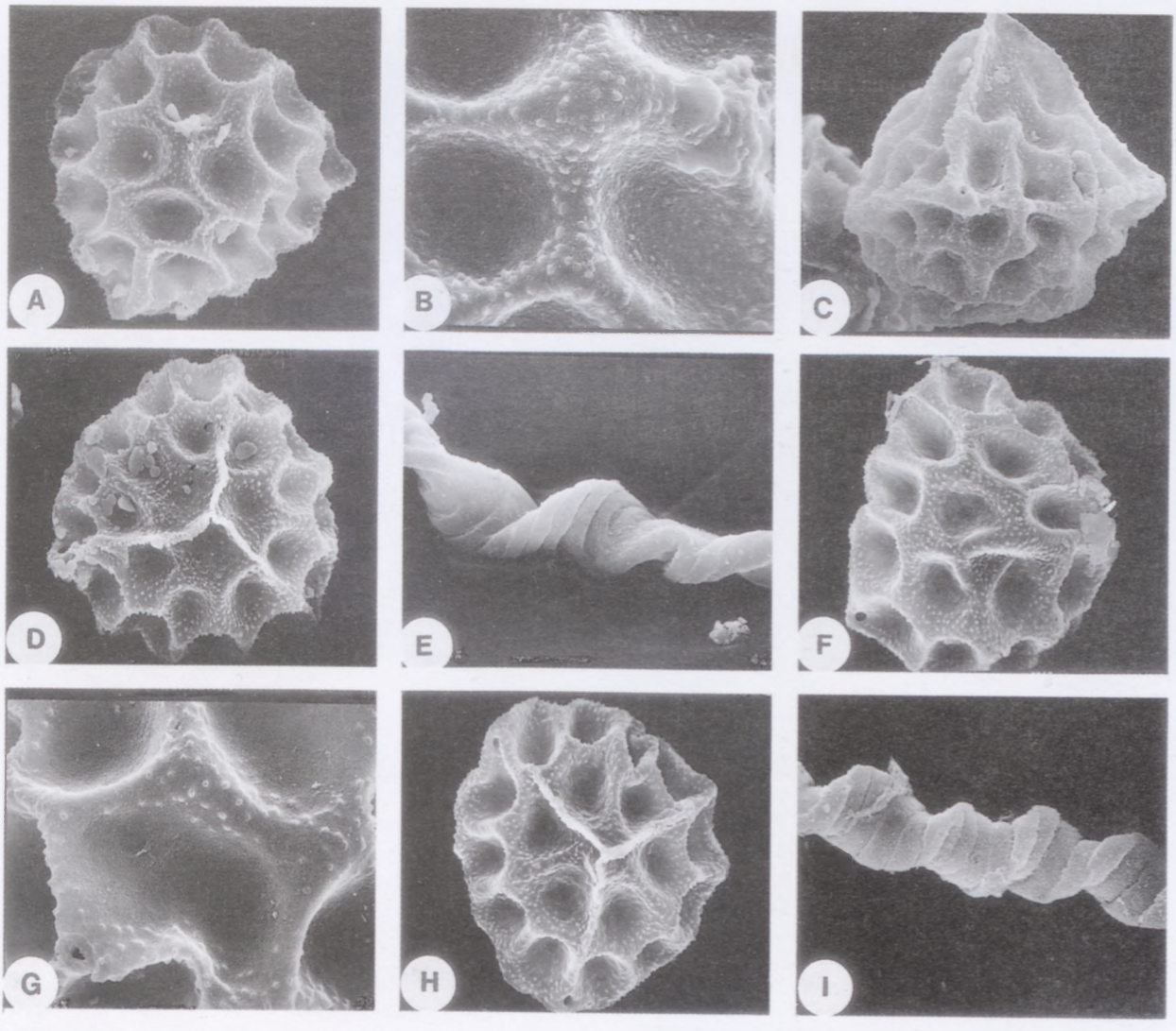

FIGURE 2.—SEM micrographs of spores and elater. A–E, *Plagiochasma rupestre* var. *rupestre*: A, distal face; B, much enlarged view of some areolae and walls on distal face; C, side view; D, proximal face; E, part of elater much enlarged. F–I, *P. rupestre* var. *volkii*: F, distal face; G, much enlarged view of some areolae and walls on distal face; H, proximal face; I, part of elater much enlarged. A, *G.W. Sim CH 1145*; B, neotype, *Sérgio & Nobréga 3873*; C, *Volk 00639*; D, *Pole Evans 458*; E, *Cooper 962*; F–I, *Mogg 37590*. A, × 452; B, G, × 1150; C, × 464; D, × 440; E, I, × 936; F, H, × 402.

spathysii and *Riccia* spp. It is known from Namibia, the Northwest, Northern and Eastern Transvaal, Gauteng (PWV), Orange Free State, Lesotho, KwaZulu-Natal, as well as from Northern, Western and Eastern Cape (Figure 3). Its range in Africa extends northward into Zimbabwe from where it was also reported by Best (1990) and by Bischler (1978), who reported it from Kenya, Tanzania, Uganda, Ethiopia, Djibouti, Sudan, Chad, Morocco, Algeria and Angola, as well as from the islands of Madeira, Azores, Ascension, Cape Verde, St Helena and Réunion (Bischler 1990).

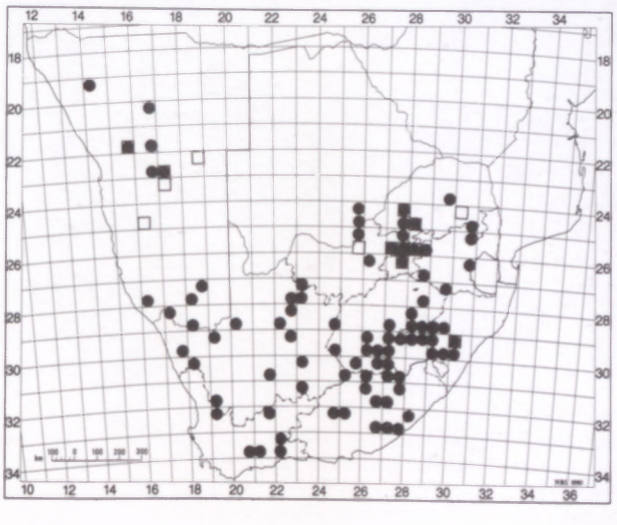

FIGURE 3.—Distribution of *Plagiochasma rupestre* var. *rupestre*, ●; and *P. rupestre* var. *volkii*, ❑, in southern Africa.

Plagiochasma rupestre var. *rupestre* is easily identified by its dull, velvety and glaucous thalli with simple, very inconspicuous pores and by its reddish pink or purple scales, with ovate-lanceolate or acuminate appendages, the margins of which are entire.

1b. **P. rupestre** var. **volkii** *Bischl.* Type: Namibia, Neudamm bei Windhoek, *Volk 948* (JE).

Purple ventral scales larger (up to 3000 × 1350 µm) and more conspicuous than those of typical variety, especially 2 or 3 hyaline appendages, which are narrowly triangular, 1370–1450 µm long and 4 or 5 times longer than

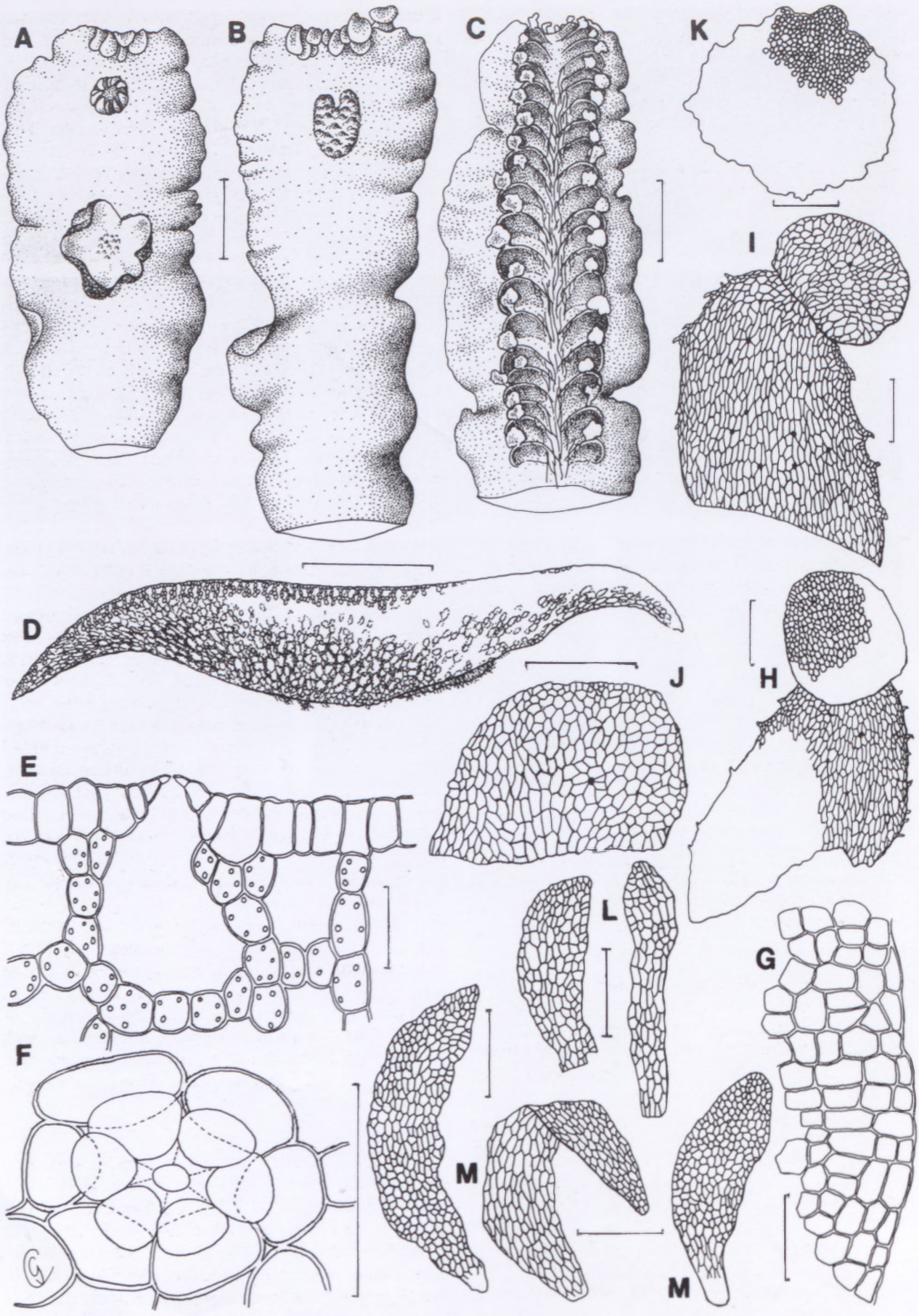

FIGURE 4.—*Plagiochasma appendiculatum*. A–D, thallus: A, dorsal face with archegoniophore and carpocephalum; B, dorsal face with androecium; C, ventral face; D, transverse section. E, transverse section of air pore, dorsal cells and air chambers; F, air pore and surrounding cells from above; G, margin of thallus; H, I, scales; J, scale appendage; K, transverse section of stalk; L, male paleae; M, female paleae. A, C, F, G, K, M, *Bottomley CH 268*; B, D, E, H–J, L, *S.M. Perold 854*. Scale bars: A–C, 2 mm; D, 1 mm; E, F, G, 50 µm; H–M, 250 µm.

wide (Figure 1O, P). Apex rather fragile, 3–5 elongated cells in series, walls thickened; cells at rounded margin of body of scale irregular in shape and size, cross walls often oblique; male paleae ± 600 µm long, 150 µm wide at base, tapering to a narrow tip where up to 4 cells, 50 × 15 µm, are in series (Figure 1Q); female paleae up to 1500 µm long, 100–150 µm wide at base, tapering to a narrow tip with 3 or 4 cells, 37.5–42.5 × 12.5–17.5 µm, in series (Figure 1R); spores (Figure 2F–H) 92.5–105.0 µm in diameter, slightly larger but very similar in appearance to those of typical variety.

This variety is quite rarely collected in southern Africa, but fairly frequently both varieties grow together. In the present investigation specimens of *P. rupestre* var. *volkii* from Namibia, the Northwest, Gauteng (PWV), Northern Transvaal, as well as KwaZulu-Natal have been examined (Figure 3). Bischler (1978) had also studied plants from the Western Cape, Orange Free State, Lesotho and Zimbabwe, so that it occurs throughout most of southern Africa. Schuster (1992) states that *P. rupestre* var. *volkii* also occurs in Peru and Argentina and it is thus not endemic to southern Africa.

In *P. rupestre* var. *volkii* the thallus is generally somewhat narrower than in the typical variety, but otherwise it is very similar in colour, appearance and composition. The very long, decolorate scale appendages are conspicuous, however, and make it easily separable.

Subgenus *Plagiochasma*

Most species are assigned to subgenus *Plagiochasma*, which is characterized by less compact green or yellow-green thalli, dorsally with quite large, raised air pores, surrounded by a hyaline ring and 2 or 3 concentric rings of (5)6–8 cells in each, radial walls generally forming continuous radiating lines that can be somewhat thickened; air chamber walls faintly visible from above and scale and appendage margins differentiated with smaller cells, teeth or papillae.

2. **Plagiochasma appendiculatum** *Lehm. & Lindenb.* in Lehmann, Novarum et minus cognitarum stirpium pugillus quartus: 14 (1832); Gottsche et al.: 517 (1844–1847); Steph.: 782 (1898); Kashyap: 318 (1914); Bischl.: 228 (1978). Type: Nepal, Punjab, Dehra Doon, *Wallich*.

P. appendiculatum Lehm. & Lindenb. var. *erythraeum* Gola: 62 (1914). Type: Ethiopia, Eritrea, Hamasen, sul Monte Bizen nella valle Nabaret a Mai Electi, *Ragazzi 253*.

P. fischerianum (Steph.) Steph.: 786 (1898) (*P. fischeri*). Type: Kenya, Ligaijo, *Fischer 692* [as *Aitonia fischeriana* Steph.: 301 (1895)].

For a complete synonymy see Bischler (1978).

Thallus large, robust, flat with sides sometimes curved slightly downwards or upwards, broadly lingulate (Figure 4A, B), bright green, shiny, with narrow purple edge along margins, pores visible, small and slightly raised, when wet; thallus margins incurved or inflexed, exposing shiny, reddish purple to deep purple transversely striate and wrinkled underside of wings, not covered by scales, when dry; in crowded, gregarious patches, simple or once, sometimes twice furcate, rarely jointed with apical or latero-ventral innovations. *Branches* 10–20 × 5–8 mm, 750–925 µm thick over midrib, laterally thinning out into attenuate wings (Figure 4D); apex notched, with large orbicular reddish or partly hyaline scale appendages recurved over edge in 2 layers; margins acute, thin, scalloped and slightly undulate; flanks sloping very obliquely, reddish or purple; ventral face medianly keeled, green, with row of deep red or purple red scales on either side (Figure 4C). *Dorsal epidermal cells* unistratose, hyaline, ± rectangular to polygonal, 22.5–42.5 × 15.0–27.5 µm, walls thin but thickened at corners, in transverse section 30.0–37.5 µm thick, smooth externally, along margins 2 or more rows of cells, rectangular, up to 25 × 12 µm or shorter than broad, ± 15 × 22 µm (Figure 4G); air pores not so numerous, 125–225 µm distant from each other, slightly raised (Figure 4E), simple, 7.5–10.0 µm wide, surrounded by an innermost ring, ± 2.5 µm wide, of tiny collapsed cells and then by 2 (occasionally partly by 3) concentric rings of larger cells, 5 or 6 inner ones transversely oval or round, 10–15 × 15–20 µm (Figure 4F) partly overlying outer row of 5 or 6 bluntly triangular cells, ± 22.5 × 30.0 µm across widest part, radial walls not thickened. *Assimilation tissue* 375–500 µm thick, ± ½ thickness of thallus, air chambers empty, in several layers, upper ones ± 25 µm wide, lower down wider, ± 62.5 µm wide, cells in bounding walls 30–45(–50) × 22–37 µm, some with a brown oil body, 25–30 µm wide; storage tissue occupying ventral ½ of thickness of thallus, cells angular, up to 45 µm wide, with spaces between them, some smaller cells also with oil bodies; rhizoids either smooth, 12.5–25.0 µm wide, or pegged, 12.5 µm wide. *Scales* deep red, appendages mostly decolorate and sometimes base as well, arranged in 2 forwardly directed ventral rows, one on either side of midrib, asymmetric, obtusely triangular with flatly arched base, gradually narrowed above, deeply constricted and folded where joined with large, mostly single, orbicular appendage (Figure 4H, I), the latter up to 750 µm long, 550 µm across widest part in middle, 300–375 µm wide at base, at margin 1 or 2 rows of small rectangular cells 10.0–17.5 × 7.5–12.5 µm, alternating with somewhat larger cells, in centre of appendage toward base, cells large, rectangular, ± 75.0 × 37.5 µm, surrounded by several rows of irregularly shaped cells, variable in size (Figure 4J); body of scale up to 1250 µm long, 1100 µm across base, cells rectangular or 5-sided, ± 70 × 25 µm, 6 or 8 smaller, scattered ones with remains of oil bodies, ± 27.5 × 20.0 µm; at margins cells small, ± 25.0 × 12.5 µm, walls thin, curved, occasionally with long, projecting papillae.

Monoicous, but male and female receptacles often on separate plants. *Androecia* in sessile cushions, oval, horseshoe- or heart-shaped, 1.5–2.5 × 2.0 mm, on leading branch medianly, near apex, proximally partly surrounded by shallow curved groove in thallus, base encircled by blunt, hyaline or partly purple paleae, 550–580 × 130–180 µm (Figure 4L), cells rectangular or 5-sided, ± 57.5 × 20.0 µm, toward apex smaller, quadrate, ± 25 × 25 µm, near to base margins with some projecting papillae, 25.0 × 12.5 µm. *Archegoniophores* single or several in acropetal sequence medianly along main branch, initially enclosed by arching hyaline paleae, ± 850 × 120 µm (Figure 4M), lower cells mostly rectangular, 40–45 × 22 µm, toward apex smaller, ± 20 × 15 µm and at margin 15 ×

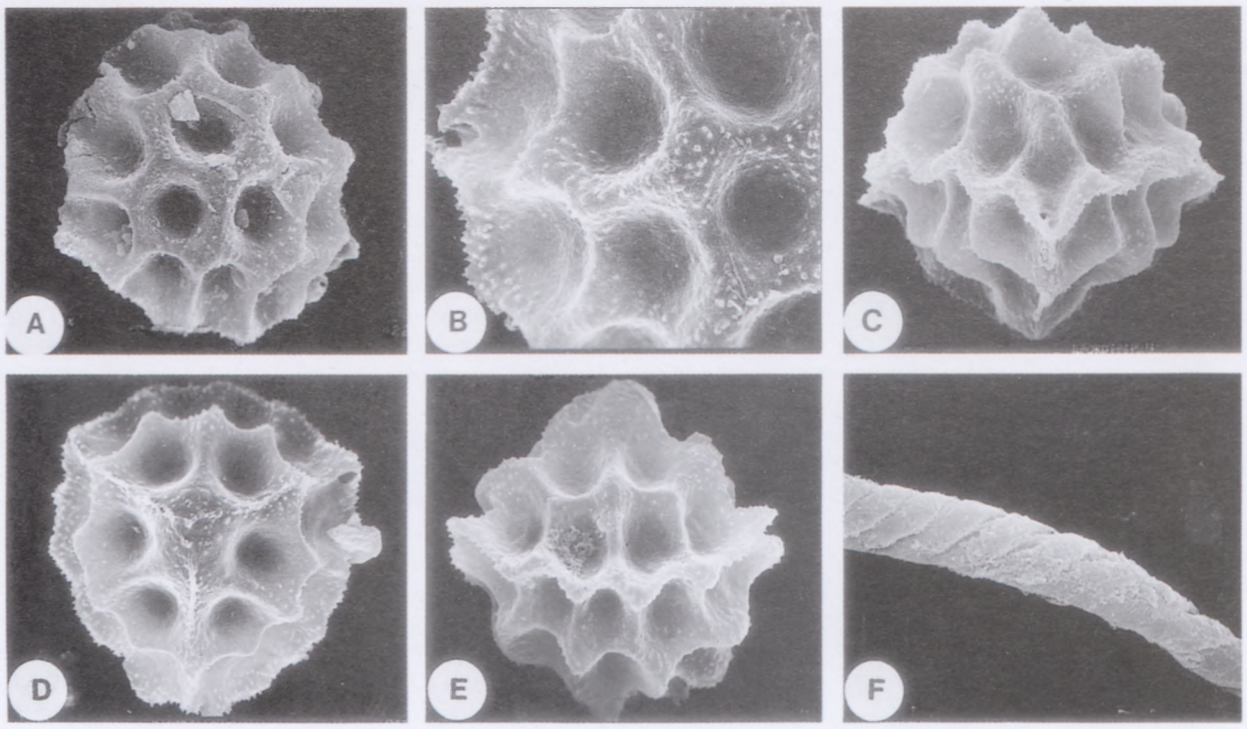

FIGURE 5.—*Plagiochasma appendiculatum*. SEM micrographs of spores and elater, A–F. A, distal face; B, much enlarged view of some areolae, walls, wing and pore on distal face; C, side view, distal face above; D, proximal face; E, side view, proximal face above; F, part of elater much enlarged. A, F, *Hook 8204*; B–E, *S.M. Perold & M. Koekemoer 3135*. A, × 511; B, × 959; C, × 577; D, E, × 534; F, × 940.

25 µm, lacking papillae. *Carpocephala* 2 × 2 mm when 4 lobes present, raised on stalk, 1.25–2.00 mm long, ± 750 µm in diameter (Figure 4K), in transverse section 1 or 2 rows of cortical cells, 17.5–27.5 × 17.5–30 µm, medullary cells angular, up to 37.5 µm wide, thin-walled. *Spores* 75–85 µm in diameter, triangular-globular, polar, light brown, translucent, wing ± 10 µm wide, porate at corners, margin undulate, finely crenulate; ornamentation similar on both faces: distal face (Figure 5A–C) with 5 areolae across, ± 22 µm wide, walls finely granular; proximal face (Figure 5D, E) with very narrow triradiate mark, each of 3 facets with 6 or 7 areolae, walls wide and studded with granules. *Elaters* pale brown, 187–240 µm long, 10 µm wide in middle, tapering toward ends, 5 µm wide, bi- or tri-spiral (Figure 5F). *Chromosome number*: n = 9 (Bischler 1978).

After *P. rupestre*, *P. appendiculatum* was one of the earliest species in the genus to be described. It is generally a large plant and is easily recognized by its mostly single, very rarely double, large, orbicular scale appendages. Bischler (1978) examined a large number of specimens and found quite considerable variation in the size of the thallus and spores as well as in the thickness of the radiating cell walls at the air pores. In the present study only three southern African specimens were available for study; a fourth one is from Zimbabwe and was collected at Essexvale by Borle (also reported by Bischler), but the exact locality could not be traced. Three other specimens seen, were from elsewhere. *Plagiochasma appendiculatum* has not previously been reported from southern Africa, although it had been collected by Bottomley in 1930 at Pelindaba, the specimen being held at PRE. Unfortunately it was misidentified as a species of *Asterella* and was not sent on loan to Bischler, when she was revising the genus. Recently I have collected specimens of it twice (the second time with M. Koekemoer) in Bakker's Pass, east of Thabazimbi in southwestern Northern Transvaal (Figure 6), where it grew between boulders in a shady, damp gulley, together with *Fissidens* sp. and *Philonotis* sp. Arnell (1963) refers to *P. fischeri*, the synonym of *P. appendiculatum*, in his key to the species of *Plagiochasma*, but there is no description or illustration of the species.

Plagiochasma appendiculatum is chiefly an Asiatic species and has been reported from Afghanistan, Burma, Celebes, China, Taiwan [Formosa], India, Kashmir, Nepal, Pakistan, Philippines, Sikkim and Vietnam by Bischler (1978). She has also reported it from Yemen and Socotra as well as from Ethiopia, Kenya and Zimbabwe, where it is rare. Bizot *et al.* (1985) reported it as new from Tanzania and regard it as a palaeotropical species. Frey &

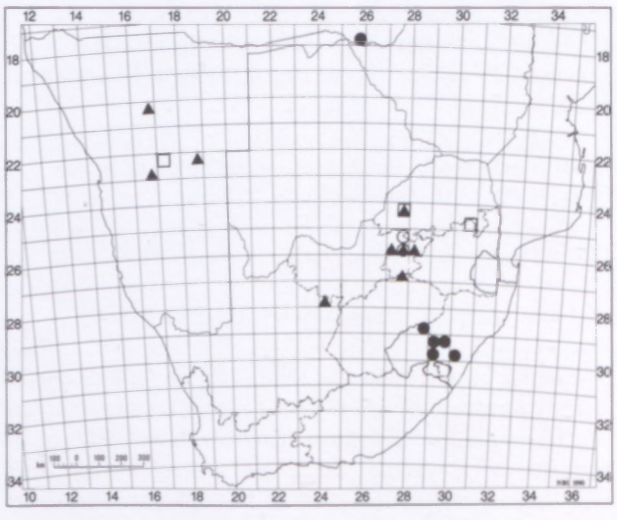

FIGURE 6.—Distribution of *P. appendiculatum*, ○; *P. beccarianum*, □; *P. eximium*, ●; and *P. microcephalum* var. *microcephalum*, ▲, in southern Africa.

Kürschner (1988) also reported it from the Arabian Peninsula and from Socotra; they assume that it is of xerothermic Pangaean origin.

3. **Plagiochasma microcephalum** *(Steph.) Steph.* in Bulletin de l'Herbier Boissier, Sér. 1, Vol. 6.10: 781 (1898); Bischl.: 237 (1978); Volk: 240 (1979).

P. dinteri Steph.: 762 (1901b). Type: Namibia (= Deutsch-Südwest-Afrika). Hereroland: Kransfontein, leg. *Dinter*.

Aitonia microcephala Steph.: 301 (1895). Type: Tanzania, Usambara, leg. *Holst 362* (G, holo.!).

Thallus smallish to medium-sized, flat to slightly concave medianly, with the sides somewhat raised or gently arching downwards, ligulate to oblong (Figure 7A), bright green, along margins red-brown to purple; finely and irregularly areolate, with pores faintly visible, when wet; thallus margins tightly inflexed, exposing shiny, deep purple or dark red transversely striate underside of wings, not covered by scales except partly toward apex, when dry; in crowded, gregarious patches, simple to several times pseudodichotomously furcate, occasionally with apical or latero-ventral innovations. *Branches* 6–12 × 3–4(–6) mm, 450–850 µm thick over midrib, laterally thinning out into attenuate wings (Figure 7E); apex notched with broadly ovate, purple or partly decolorate appendages recurved over edge; margins acute, thin, somewhat transversely pleated or crinkled, scalloped; flanks sloping obliquely, deep purple or dark red, ventral face medianly keeled, green, partly obscured by 2 rows of purple scales, one on either side (Figure 7B).

Dorsal epidermal cells unistratose, hyaline, 5- or 6-sided or polygonal, 22.5–35.0(–40.0) × 17.5–25.0 µm, rarely containing an oil body, walls thin, except at corners, where thickened and rounded with trigones, in transverse section 25.0–32.5(–37.5) µm thick, smooth externally, along margins generally 2 or 3(4) rows of ± quadrate or transversely rectangular cells, 12.5–20.0 × 12.5–25.0 µm (Figure 7H); air pores varying from not so numerous to numerous, distances between them (50–)100–185 µm, slightly raised (Figure 7F), simple, round or oval, 12.5 × 7.5–10.0 µm, surrounded by an innermost ring, ± 2.5 µm wide, of small collapsed cells and then by 2 concentric rings of 5–7(8) cells in each (Figure 7G), inner cells transversely oval, 12.5–17.5 × 15.0–20.0 µm, partly overlying next row of bluntly triangular cells, 12.5–22.5 µm long, 25.0–32.5 µm across widest part, narrowing to base of ± 12.5 µm wide, radial walls sometimes thickened (Figure 7G). *Assimilation tissue* 200–400 µm thick, ± ½ thickness of thallus, air chambers empty, in several layers, upper ones smaller, 30–50 µm wide, lower down up to 85 µm wide, cells in bounding walls 20.0–37.5 × 27.5–35.0 µm, some with a spherical oil body almost filling cell; storage tissue occupying ventral ½ of thickness of thallus, cells angular, closely packed, 35.0–52.5 × 35.0–42.0 µm, a few scattered ones also containing an oil body; rhizoids either smooth, 17.5–25.0 µm wide, or pegged, 12.5–17.5 µm wide. *Scales* and appendages purple or reddish or partly decolorate, arranged in 2 forwardly directed ventral rows, one on either side of midrib, asymmetric, obliquely triangular with base hardly arched, narrowed above into 1 (Figure 7J) or sometimes 2 (Figure 7I) broadly ovate or triangular appendages (Figure 7K, L), equal in size or not, 350–600 µm long, 350–450 µm across middle, constricted or folded or transversely pleated at base where joined to rest of scale, cells toward centre quadrate or rectangular and fairly regular, 25.0–40.0 × 22.5–37.5 µm, apically small and blunt, 10 × 10 µm, 1 or 2 rows along margins ± 17.5 × 20.0 µm, some transversely rectangular, ± 15 × 35 µm, thinner-walled, occasionally with an outwardly projecting papilla; body of scale up to 675 µm long, 800–1500 µm across base, cells 4–6-sided, 37.5–70.0 × 25.0–30.0 µm, ± 10 with remains of oil body, 42.5 × 32.5 µm, cells smaller and thinner-walled toward margins, sometimes curved or bent, a few with projecting papilla.

Monoicous. *Androecia* in small sessile cushions, rounded or V-shaped, ± 1 mm wide, medianly along length of thallus and alternating with archegoniophores, occasionally paired at pseudodichotomy of branches, antheridia opening above via prominent papillae, basally cushions encircled by shallow groove in thallus and surrounded by inconspicuous purple paleae that taper slightly toward apex (Figure 7M), ± 400 × 200 µm, cells 32.5–37.5 × 15.0–20.0 µm, several mucilage papillae projecting along margins and from apex. *Archegoniophores* acropetally arranged along length of thallus and alternating with androecia, enclosed by arching, hyaline or purple paleae, ± 500 × 150 µm, tapering toward apex (Figure 7N), cells rectangular, 35.0–45.0 × 17.5–22.5 µm, sometimes with a few mucilage papillae at margins. *Carpocephala* small, 1.0 × 2.0 mm, when 2 lobes present (Figure 7C), raised on stalk, up to 15 mm long and variously twisted, striate and dark red, ± 310 µm in diameter, in transverse section (Figure 7D) cortical cells in 1 row, thick-walled externally and rounded, 12.5–17.5 × 12.5–15.0 µm, medullary cells thin-walled, angular, 12.5–17.5 µm wide. *Spores* 70–75 µm in diameter, triangular-globular, polar, light brown, translucent, wing ± 10 µm wide, pore at corners occasionally present, margins undulate, finely crenulate, ornamentation similar on both faces: distal face (Figure 8A, B) with 4 areolae across, 15–20 µm wide, walls narrow, only ± 2.5 µm wide, almost smooth to granular; proximal face with distinct triradiate mark, arms thin, 5.0–7.5 µm high, 4 areolae on each of 3 facets, walls almost smooth (Figure 8C–E) to granular. *Elaters* light brown, 212–300 µm long, 7.5 µm wide in middle, tapering toward ends, ± 5.0 µm wide, bi-or trispiral (Figure 8F). *Chromosome number*: n = 9 (Bischler 1978).

Bischler (1978) recognized two varieties of *P. microcephalum*, namely var. *microcephalum* and var. *tunesicum* Bischl. The latter appears to be restricted to Tunisia, whereas she reported the former from the following African countries: Ethiopia, Uganda, Angola, Namibia and South Africa. It is also known from Madagascar, Yemen and southwest India. In the present investigation, a few more specimens from Northern Transvaal, Gauteng (PWV), the Northwest and Northern Cape have been identified (Figure 6). It can be distinguished by the green colour of the fresh thallus and by the generally large, broadly ovate or triangular scale appendages which have one or two rows of smaller cells along the margin. Bischler (1978) reported that plants growing in dry habitats have scales with a single, broadly ovate appendage which is constricted at the base, whereas those from more humid sites usually have one or two triangular

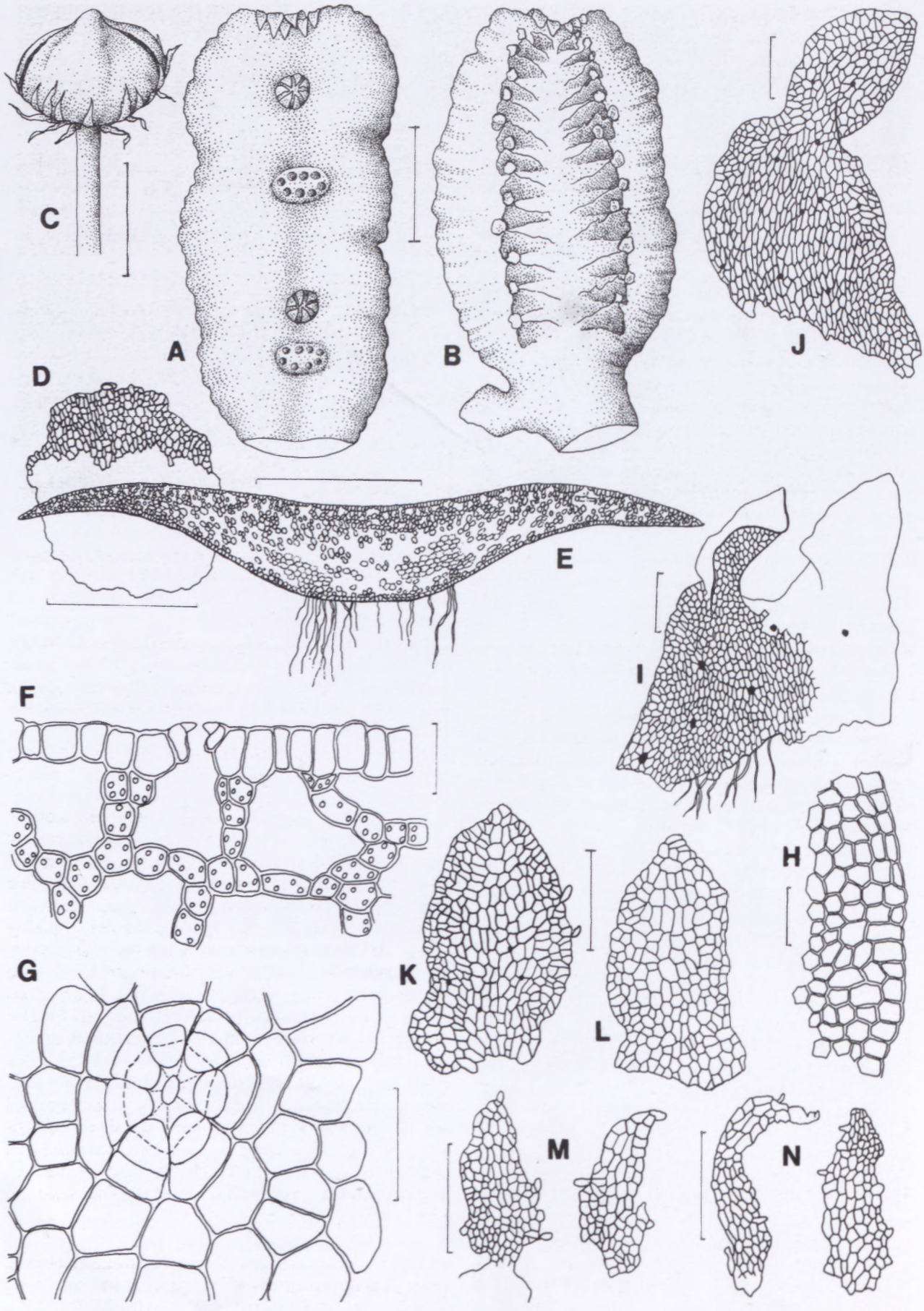

FIGURE 7.—*Plagiochasma microcephalum* var. *microcephalum*. A, dorsal face of thallus with young receptacles; B, ventral face of thallus; C, carpocephalum on stalk; D, transverse section of stalk; E, transverse section of thallus; F, transverse section of air pore, dorsal cells and air chambers; G, air pore and dorsal cells from above; H, margin of thallus; I, scale with 2 appendages; J, scale with single appendage; K, L, scale appendages; M, male paleae; N, female paleae. A, B, F, G, *Condy 47*; C, D, *Holst 362*; E, *S.M. Perold 2976*; H–K, M, N, *Bottomley CH 175*; L, *Burtt Davy 15176*. Scale bars: A–C, E, 1 mm; D, 100 µm; F–H, 50 µm; I–N, 250 µm.

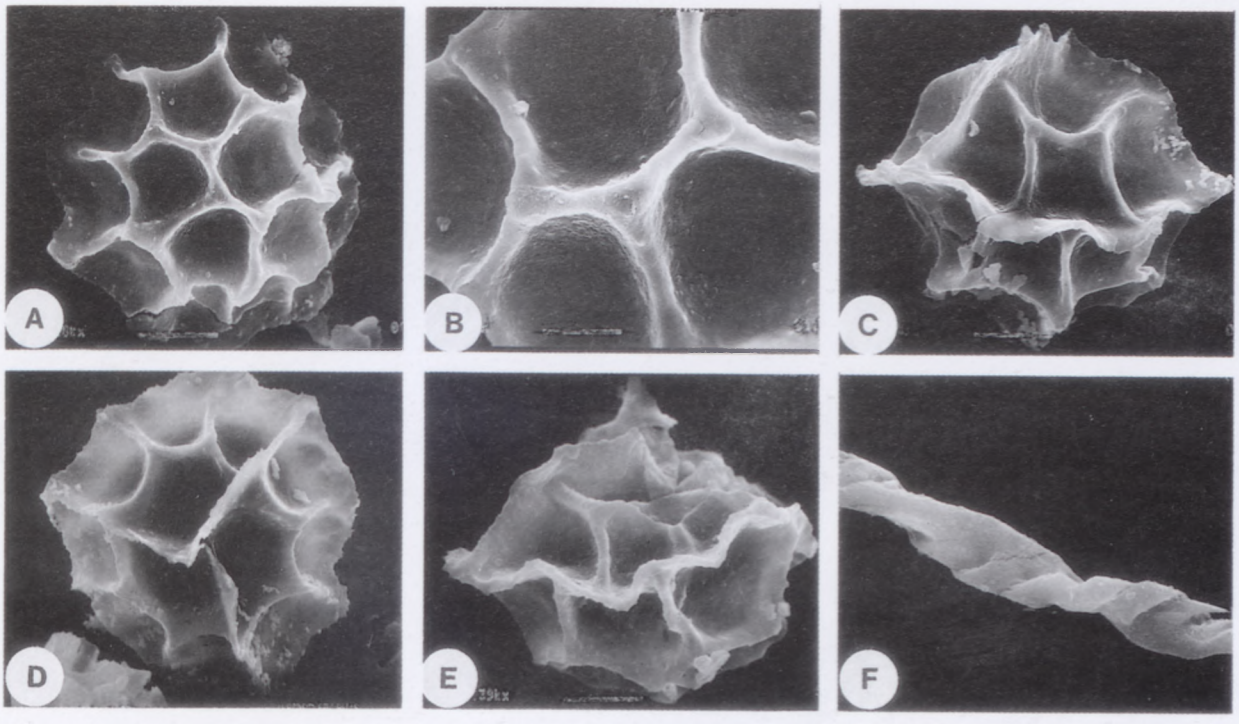

FIGURE 8.—*Plagiochasma microcephalum* var. *microcephalum*. SEM micrographs of spores and elater. A, distal face; B, much enlarged view of some areolae and walls on distal face; C, E, side view; D, proximal face; F, part of elater much enlarged. A–F, *Holst 362*. A, × 600; B, × 1357; C, × 679; D, × 585; E, × 647; F, × 940.

scale appendages horizontally folded at the base and hardly constricted. My observations appear to confirm this.

This species is equally well adapted to dry or to damp habitats. It grows in dry river beds between limestone boulders or on granite hills or on damp stream banks, but has not been frequently collected. Plants with mature female receptacles are rare. The carpocephala are small (hence the specific epithet) and are raised on a slender, short or long, dark red stalk.

Frey & Kürschner (1988) regard it as a palaeotropical taxon with a tropical African distribution. Sim (1926) stated that *P. dinteri* [placed in synonymy under *P. microcephalum* by Bischler (1978)] was not known to him and he quoted a few particulars from Stephani (1901b). Arnell's (1963) description of *P. dinteri* contains several inexactitudes as already observed by Bischler (1978): thallus dimensions '15 cm long and 16 mm wide; peduncle apical, spores 40–50 µm in diameter, without a wing or with a rudimentary one, occasionally with a wing up to 4 µm wide; surface irregularly areolate'. One of the specimens seen by him [Essendale (sic)] is the Borle collection from Essexdale and belongs to *P. appendiculatum*. The collection from Hennops River, of which he illustrates the spores, has not been traced. The Holst specimen (the type of *P. microcephalum*) was seen by Arnell and under *P. tenue* he states that it belongs to another species, which is certainly correct, since *P. tenue* is a synonym of *P. rupestre*, but he failed to notice the similarity between *P. microcephalum* and *P. dinteri*.

4. **Plagiochasma eximium** *(Schiffn.) Steph.* in Bulletin de l'Herbier Boissier, Sér. 1, Vol. 6.10: 781 (1898); Bischl.: 248 (1978).

P. schimperi Steph.: 788 (1898). Type: Ethiopia (Abyssinia). In monte Semen, leg. *Schimper*.

Aitonia eximia Schiffn. in Steph.: 300 (1895). Type: Kamerun, Buea, an den Höhlen eine Stunde östlich von Manus-Quelle, 2 500 m, 4-II-1891, leg. *Preuss 731* (FI, lecto.!).

Grimaldia abyssinica Gola: 63 (1914). Type: Abyssinia, leg. *Chiovenda 2993* (FI).

Thallus large, robust, ± flat to sometimes medianly concave with sides raised or slightly incurved, broadly ovate (Figure 9B) to lingulate (Figure 9C), yellow green, along margins narrowly to widely dark red; finely and irregularly areolate with pores slightly raised, when wet; thallus margins tightly inflexed or incurved, exposing shiny, dark red, somewhat wrinkled and transversely striate underside of wings, ventrally covered in wine red or deep pink scales, when dry; in crowded, gregarious patches, simple or once pseudodichotomously furcate (Figure 9A), sometimes with one or more apical innovations and articulated (Figure 9B). *Branches* 16.5–22.0 × 5.0–8.5 mm, ± 750 µm thick over midrib, laterally thinning out into attenuate wings (Figure 9E); apex notched with lanceolate, reddish pink or dark red scale appendages recurved over edge; margins acute, thin, scalloped and undulate; flanks sloping obliquely, dark red, ventral face medianly keeled, green, with a row of deep red scales on either side (Figure 9C).

Dorsal epidermal cells unistratose, hyaline, oblong, ovate or polygonal, walls with trigones at corners, 25–40 × 20–35 µm, in transverse section 30.0–37.5 µm thick, smooth externally, along margins 2(3) rows of cells (Figure 9H), rectangular, 25–35 × 10–20 µm, or shorter than broad, ± 17.5 × 35.0 µm; air pores not numerous, distances between them variable, 230–440 µm, slightly raised (Figure 9F), simple, round or oval, 12.5–27.5 × 15.0–27.5 µm, surrounded by an innermost ring, ± 7.5 µm wide, of

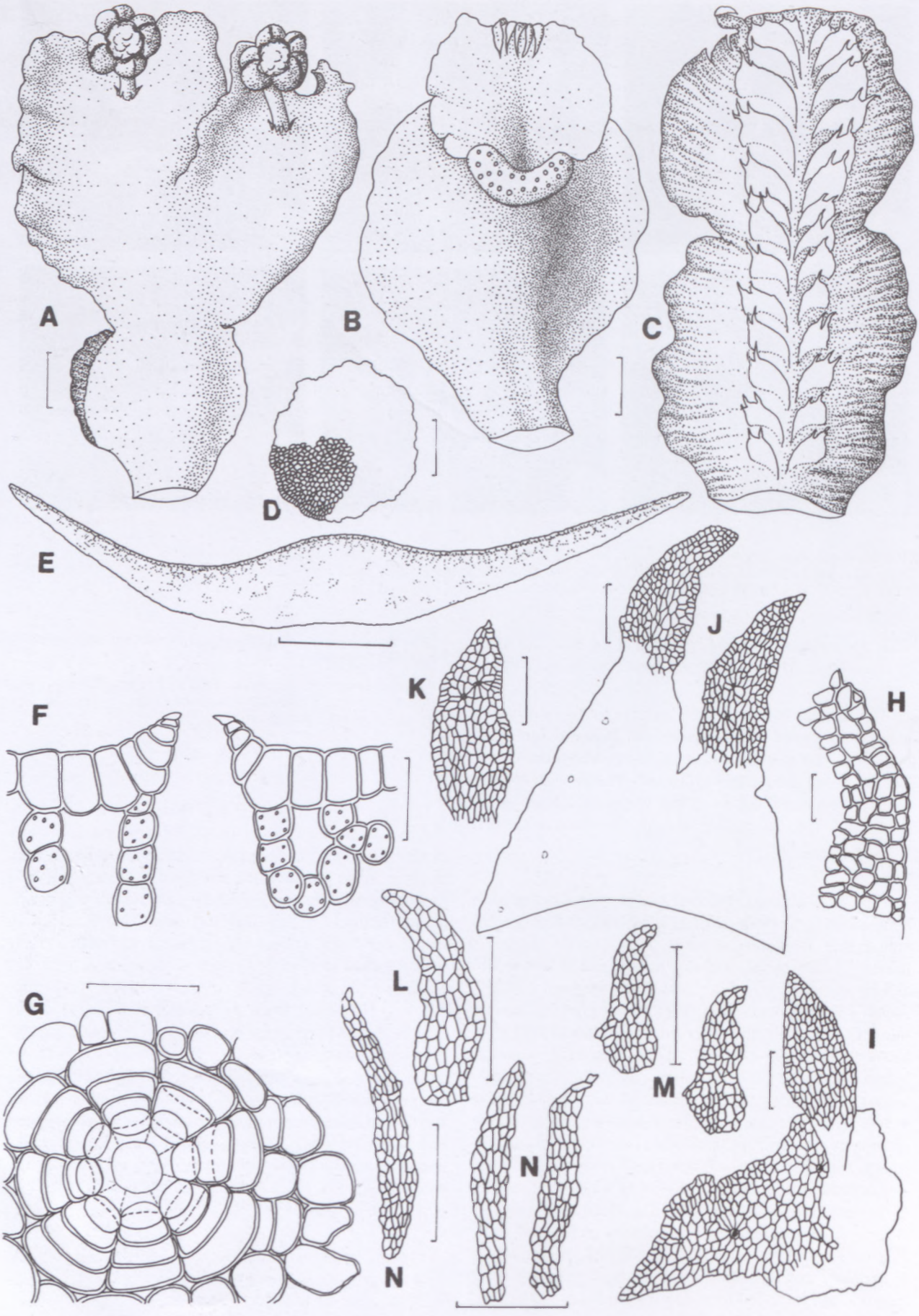

FIGURE 9.—*Plagiochasma eximium*. A, thallus with 2 carpocephala; B, thallus with androecium; C, ventral face of thallus; D, transverse section of stalk; E, transverse section of thallus; F, transverse section of air pore, dorsal cells and air chambers; G, air pore and dorsal cells from above; H, margin of thallus; I, scale with single appendage; J, scale with 2 appendages; K, scale appendage; L, M, male paleae; N, female paleae. A–C, L, *S.M. Perold 2498*; D–I, N, *Sim CH 1163*; J, K, *H. Anderson CH 4498*; M, *Sim CH 1200*. Scale bars: A–C, 2 mm; D, 100 µm; E, 1 mm; F–H, 50 µm; I–N, 250 µm.

small collapsed cells and then by 3 concentric rings of 7 or 8 larger cells in each (Figure 9G), inner cells transversely oval, ± 12.5 × 17.5 µm, partly overlying next row of transversely oblong cells, ± 12.5–15.0 × 25.0–32.5 µm, outermost ring of cells ± 17.5 × 40.0–45.0 µm, radial walls sometimes thickened. *Assimilation tissue* 375–475 µm thick, ± ½ or more than ½ thickness of thallus, air chambers empty, in several layers, upper ones ± 35 µm wide, lower down ± 110 µm wide, cells in bounding walls 22.5–27.5 × 25.0–27.5 µm, gradually enlarging to 42.5 × 32.5 µm, some with spherical dark brown oil body, ± 32.5 µm in diameter, almost filling cell, these also present in storage tissue, which occupies ventral part of thallus, cells angular, up to 37.5 µm wide; rhizoids some smooth, 12.5–17.5 µm wide, others pegged, 10.0–17.5 µm wide. *Scales* and appendages deep pink to wine red, arranged in 2 forwardly directed ventral rows, one on either side of midrib, asymmetric, obtusely triangular with arched base and narrowed above into 1 (Figure 9I) or 2 (Figure 9J) and sometimes 3 tapering appendages, 650–900 µm long, slightly constricted or pleated at base (Figure 9K), 250–350(–400) µm wide, cells long-rectangular or hexagonal, 37.5–55.0 × 20.0–25.0 µm, apex not acuminate but often unicellular, 20.0–30.0 × 20.0–27.5 µm; body of scale ± 950 µm long, 1650 µm across base, cells 4–6-sided, 37.5–62.5 × 27.5–35.0 µm, ± 14 with remains of oil body, scattered and smaller, 25.0 × 22.5 µm, at margins cells narrowly rectangular, ± 22.5 × 10.0 µm, occasionally with a projecting papilla, 15 × 15 µm.

Monoicous, but male and female receptacles sometimes on separate plants. *Androecia* in sessile cushions, kidney- or sausage-shaped, 1 mm wide, medianly at base of smaller articulated, apical innovation (Figure 9B) of leading branch, proximally partly surrounded by shallow curved groove in thallus, encircled by apically tapered, dark red paleae, 250–500 × (90–)100–120 µm, cells rectangular, 40–55 × 17–20 µm, smaller toward apex, 32.5 × 15.0 µm, and along upper part of margin 25.0–37.5 × 12.5–15.0 µm, sometimes with a projecting papilla supported on a narrow base and also above at apex. *Archegoniophores* single or occasionally paired when branches bifurcate (Figure 9A), medianly near apex of branch, enclosed by arching, hyaline paleae, ± 550 × 80 µm, tapering toward apex with single cell, ± 22.5 × 12.5 µm, lower down cells larger, rectangular, up to 42.5 × 15.0 µm, margins sometimes with a papilla. *Carpocephala* 3.25 × 3.25 mm, when 4 lobes present, raised on stalk, 3–6(–9) mm long, striate and dark red, in transverse section (Figure 9D) ± 850 × 750 µm, cortical cells in 1 row, ± 20.0 × 17.5 µm, thick-walled externally, medullary cells thin-walled, angular, up to 37.5 × 30.0 µm. *Spores* 82.5–90.0 µm in diameter, triangular-globular, polar, golden brown, translucent, wing up to 12.5 µm wide, porate at corners, margins undulate, finely crenulate; ornamentation similar on both faces: distal face (Figure 10A–C) with 4 or 5 areolae across, 22.5–32.5 µm wide, walls wide and finely granular; proximal face (Figure 10D, E) with distinct triradiate mark, arms ± 5 µm high, mostly 4 shallow areolae on each of 3 facets, walls sparingly sprinkled with granules. *Elaters* light brown, 175–225 µm long, 15–20 µm wide in middle, tapering toward ends, 5.0–7.5 µm wide, laxly bispiral or spirals interrupted (Figure 10F). *Chromosome number*: n = 9 (Bischler 1978).

Plagiochasma eximium has previously been reported from southern Africa by Bischler (1978), who had examined a specimen, *Sim CH 1163*, from Mont-aux-Sources which had earlier been identified as *P. rupestre*. Two other specimens, *Sim CH 1200* (Pietermaritzburg) and *Sim CH 1186* (Victoria Falls), have now been identified as *P. eximium*, as well as some later collections from the

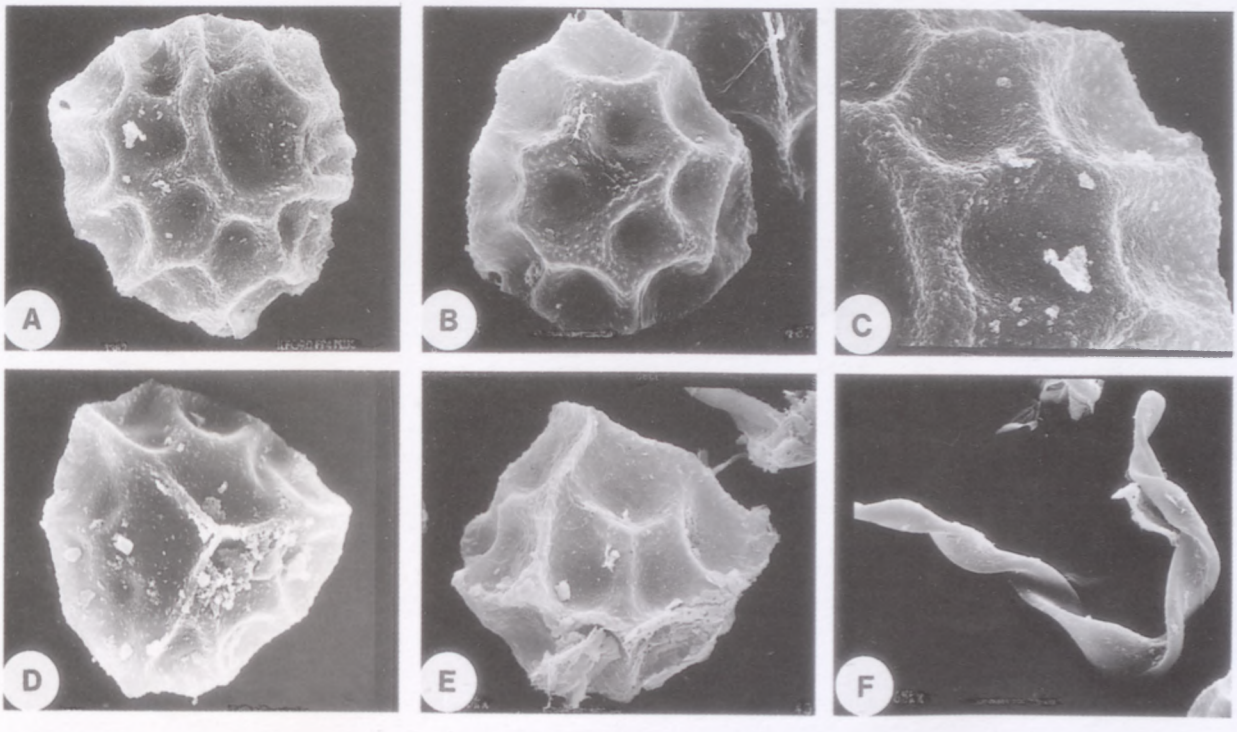

FIGURE 10.—*Plagiochasma eximium*. SEM micrographs of spores and elater. A, B, distal face; C, much enlarged view of margin, some areolae and walls on distal face; D, proximal face; E, side view of proximal face; F, elater. A, C, D, *T.R. Sim CH 1163*; B, E, F, *T.R. Sim CH 1186*. A, × 470; B, × 482; C, × 925; D, × 459; E, × 501; F, × 308.

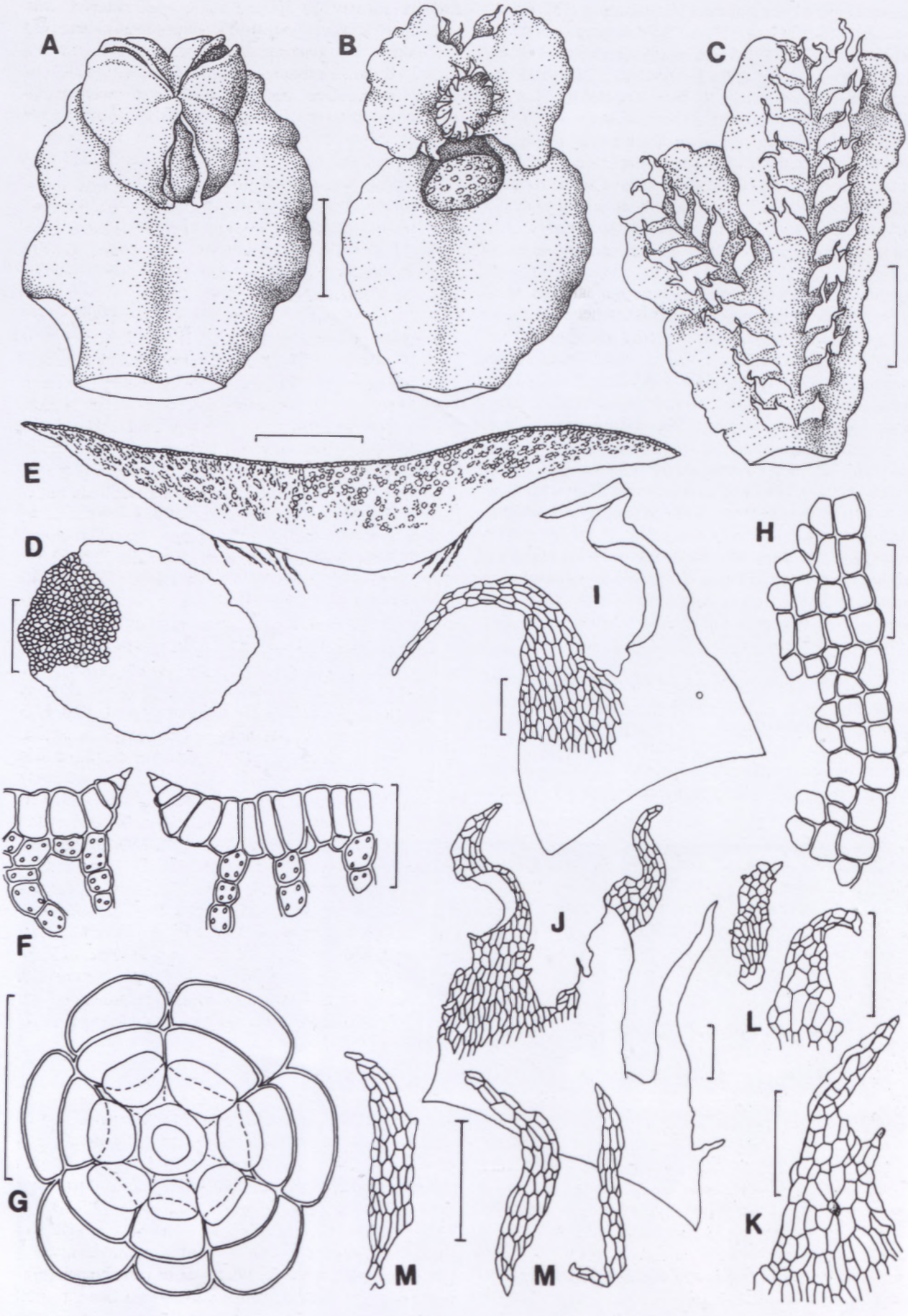

FIGURE 11.—*Plagiochasma beccarianum*. A, thallus with mature carpocephalum; B, thallus with archegoniophore and androecium; C, ventral face of thallus; D, transverse section of stalk; E, transverse section of thallus; F, transverse section of air pore, dorsal cells and air chambers; G, air pore and surrounding cells from above; H, margin of thallus; I, scale with 2 appendages; J, scale with 3 appendages; K, scale appendage; L, male paleae; M, female paleae. A, B, D–K, M, *Volk 00950*; C, *S.M. Perold 2992*; L, *S.M. Perold 2995*. Scale bars: A–C, 2 mm; D, 100 µm; E, 1 mm; F–H, 50 µm; I–M, 250 µm.

Drakensberg by H. Anderson, E. Esterhuysen, S.M. Perold and O.H. Volk (Figure 6). Arnell (1963) gave no description or illustration of *P. eximium*, merely listing it in his key to the species of *Plagiochasma*. This species is widespread in Africa and has been reported by Bischler (1978) from Sierra Leone, Guinea, Cameroons, Zaïre, Djibouti, Ethiopia, Uganda, Kenya, Tanzania, Malawi and the following islands: Cape Verde, Réunion and Madagascar (Bischler 1990). Its distribution extends to the Arabian Peninsula: Saudi Arabia, Yemen, Oman and to Socotra. Frey & Kürschner (1988) consider *P. eximium* to be a palaeotropical taxon with tropical African distribution.

Many of the collections are from high altitudes, such as the Drakensberg in southern Africa, where the plants grow in shady kloofs on muddy rock faces or on soil covering rocks or under boulders. As far as could be ascertained, the specimen, *Sim CH 1186*, from Victoria Falls seems to be the first record of this species from Zimbabwe.

Plagiochasma eximium can be distinguished by its robust, yellow-green thalli with large, deep pink to wine-red ventral scales narrowed above into (1)2 or 3 tapering appendages which are only a little constricted or pleated at the base. Ventrally the flanks are wrinkled and deep red, not dark purple. Elaters from the few spore-bearing plants studied are bispiral, but Bischler (1978) also found them to be 3- or 4-spiral and generally distinct along only a small part of their length.

Bischler (1978) states that herbarium specimens of *P. eximium* can look quite different from each other. Those from damp, shady places (e.g. a cave) have thin, olive-green thalli and decolorate margins, large epidermal cells with thin walls, and smaller, pale scales. Others have thicker, yellowish green thalli with pigmented margins, slightly smaller epidermal cells with well-developed trigones and large, dark red scales. Bischler (1978) considers them to be ecological variants of the same species. Other characters that are quite variable are the width of the thalli, the thickness of the radial walls at the air pores, the presence or absence of teeth at the base of the scale appendages, the spore ornamentation and the presence or absence of spiral thickenings in the elaters.

5. **Plagiochasma beccarianum** *Steph.* in Bulletin de l'Herbier Boissier, Sér. 1, Vol. 6.10: 781 (1898); Bischl.: 257 (1978); Volk: 240 (1979). Type: Abyssinia (Bogos), Keren, in Monte Deban, inter 4500′ & 5500′, 1870, *Beccari* (FI, holo.; 009583G, iso.!).

Thallus medium-sized to rather large, flat to very slightly concave medianly and gently arching downward toward margins, ligulate to lingulate or broadly ovate (Figure 11A, B), bright green, shiny, along narrow edge of margins purple; finely and irregularly areolate, pores distinctly visible, raised, when wet; thallus margins frequently tightly inflexed or sometimes incurved, exposing shiny, ink-black or very dark purple, transversely striate underside of wings, partly covered by purple scales, when dry; in crowded, gregarious patches, once or twice pseudodichotomously furcate, sometimes with apical innovations and then articulated. *Branches* 8.0–20.0 × 3.5–5.0(–6.0) mm, 600–850 µm thick over midrib, laterally thinning out into attenuate wings (Figure 11E); apex notched, with several purple ovate-lanceolate scale appendages recurved over edge; margins acute, thin, sparingly scalloped and slightly undulate; flanks sloping obliquely, black or purple, ventral face medianly keeled and green, partly obscured by 2 rows of purple scales, one on either side (Figure 11C).

Dorsal epidermal cells unistratose, hyaline, rectangular to polygonal, 25.0–37.5 × 20.0–27.5 µm, walls thin, except at corners where thickened and rounded with trigones, in transverse section 30–35 µm thick, smooth externally, along margins (Figure 11H) 2 or 3 rows of short rectangular cells, ± 25.0 × 22.5 µm; air pores not so numerous, distances between them quite variable, 137–287 µm, slightly raised (Figure 11F), simple, round or oval, 15.0–30.0 × 17.5–25.0 µm, surrounded by an innermost hyaline ring, 5 µm wide, of collapsed cells, and then by 2 (or partly by 3) concentric rings of 6–8 cells in each, inner cells ± rounded or transversely oval, 10.0–15.0 × 15.0–27.5 µm, partly overlying next row of bluntly triangular cells, 12.5–17.5 × 25.0–35.0 µm, outermost row of cells (if present), 20–25 × 35 µm, radial walls not thickened (Figure 11G). *Assimilation tissue* 300–400 µm thick, ± ½ thickness of thallus, air chambers in several layers, 30.0–57.5 µm wide, cells in bounding walls 22.5–32.5 × 22.5–27.5 µm, occasionally with dark brown oil body almost filling cell, 37.5 × 35.0 µm; storage tissue occupying ventral part of thallus, cells transversely oval to rounded or angular, 30.0–37.5 µm wide, walls mostly faintly reddish and thickened at corners, intercellular spaces here and there, some cells containing an oil body; rhizoids either smooth, 12.5–25.0 µm wide, or pegged, 10.0–12.5 µm wide. *Scales* and appendages deep purple to violet, in 2 forwardly directed ventral rows, one on either side of midrib, ± asymmetric, with flatly arched base, gradually tapered above into 2 (Figure 11I) or 3 (Figure 11J) lanceolate appendages up to 1000 µm long, not constricted at base (Figure 11K), ± 400 µm wide, cells mostly rectangular to 6-sided, 62.5–100.0 × 27.5 –30.0 µm, at apex often a single conical cell, 22.5 × 20.0 µm, at margins lower down a few prominent teeth, ± 50 × 20 µm, sometimes basally supported on 1 or 2(3) cells in series; body of scale ± 850 µm long, 1750 µm across base, cells 4- or 6-sided, 50–75 × 25–30 µm, at margin narrower, ± 17.5 µm wide and thinner-walled, also present a few (± 10) scattered smaller cells, which had contained an oil body.

Monoicous, but receptacles often on separate plants. *Androecia* in single sessile cushions, kidney-shaped or rounded, up to 2 mm wide, medianly and generally just proximal to apical innovation (Figure 11B), basally surrounded by purple paleae, 300–400 × 160–200 µm, apically pointed or blunt (Figure 11L), cells 32.5–37.5 × 15.0–20.0 µm, occasionally containing an oil body and some marginal ones with a papilla. *Archegoniophores* generally single, medianly near apex of main branch (Figure 11A) or on apical innovation, sometimes 2 in acropetal sequence, basally surrounded by dark paleae with pointed apex (Figure 11M), up to 500 × 80 µm, cells rectangular, ± 45.0 × 22.5 µm, sometimes a few papillae at marginal cells. *Carpocephala* up to 3.5 × 3.5 mm, when 4 lobes present (Figure 11A), raised on stalk, 1.2–3.5 mm long, in transverse section (Figure 11D), 825 × 675 µm, cortical

cells in 1 row, thick-walled externally, 15–20 × 15–20 µm; medullary cells thin-walled, rounded or polygonal and then angled, up to 37.5 × 25.0 µm. *Spores* 80–90 µm in diameter, triangular-globular, polar, light brown, translucent, wing 10 µm wide, porate at corners, margin finely crenulate; ornamentation similar on both faces: distal face (Figure 12A–C) with 3 or 4 areolae across, 20–25 µm wide, walls ± 7.5 µm wide and finely granular; proximal face (Figure 12D, E) with distinct triradiate mark, ridge ± 7.5 µm high, each of 3 facets with 4 areolae, walls wide and sprinkled with granules. *Elaters* (Figure 12F) light brown, 195–258 µm long, 12.5 µm wide in middle, tapering toward ends, 7.5 µm wide, occasionally branched, bispiral except at tips. *Chromosome number*: n = 9 (Bischler 1978).

Plagiochasma beccarianum is regarded as quite a heterogeneous species, but so closely resembling *P. eximium* that the two species are often difficult to distinguish when sterile (Bischler 1978). In the few southern African specimens of *P. beccarianum* available for study, it appears that the fresh thalli are a clear green dorsally, not yellow-green, and the underside of the wings as well as the scales are deep purple and not dark red as in *P. eximium*. The two or three scale appendages of *P. beccarianum* are ± acuminate or narrowly triangular and not constricted at the base; their margins are irregularly toothed.

This species is rare and has been reported from relatively few places in Africa; except for Namibia (*Volk 00950*), it is mostly found along the eastern part of the continent, namely Ethiopia, Tanzania and Zambia (Bischler 1978). It has also been reported from the Arabian Peninsula (Frey & Kürschner 1988) and from Socotra (Bischler 1978; Frey & Kürschner 1988). Some specimens from the Northern and Eastern Transvaal have recently been collected (Figure 6), where they grew in a shady kloof under boulders or in a rocky crevice in Blyde River Canyon respectively. Frey & Kürschner (1988) regard it as a palaeotropical taxon with a tropical African distribution.

Bischler (1978) states that *P. beccarianum* belongs to a complex represented by several species in Asia and America. She thinks that this group probably diversified more rapidly on these two continents than in Africa and that the heterogeneity of *P. beccarianum* could be due to a slower African evolution of the complex which has not as yet achieved the separation of distinct taxonomic units.

SPECIMENS EXAMINED

(held at PRE, unless otherwise indicated)

H. Anderson 1230, 1245, 1254 (1a); *CH 13477, CH 13512* (1b); *CH 13588* (1a); *CH 4498–CH 4500* (4). *T. Anderson 13* (1a).

Badenhorst CH 4360 (1a). *Bean & Oliver 2354* (1a). *Bester 15* (1a). *Bews CH 1132, CH 1152, CH 1232* (1a). *Borle CH 1340* (2). *Botha 136=145, CH 1170, CH 13240* (1a). *Bottomley CH 155, CH 160, CH 173* (1b); *CH 175* (3); CH 198 (1a); *CH 268* (2); *CH 269* pp. (1b); *CH 269, CH 3661* (1a). *Brueckner 225* (3) BOL. *Brusse 4123, 4124, 4126–4130, 4261* (1a). *Burrows 2363, 2520* (1a). *Burtt Davy 15176* (3).

Condy 45 (1a); *47* (3); *82, 83* (1b); *84* (3); *CH 13629, CH 13631* (1a). *Cooper 962* (1a).

Dieterlen 793C (1a). *Doidge CH 169, CH 3601* (1a). *Du Preez 2107, 2108* (1a).

Edwards CH 1153 (1a). *Esterhuysen 26166A* (1a); *26166* (4) BOL. *Eyles 937, 1181* (1a).

Germishuizen 5393, 5385 (1a). *Giess, Volk & Bleissner 6768* (1a, 1b, 3). *Giffen 2 (CH 1228)* (1a). *Glen 1250* (5); *1644* (1b); *1722, 2241, 2846, 3171* (1a). *Götze 16* (1a). *Graham CH 1174* (1a).

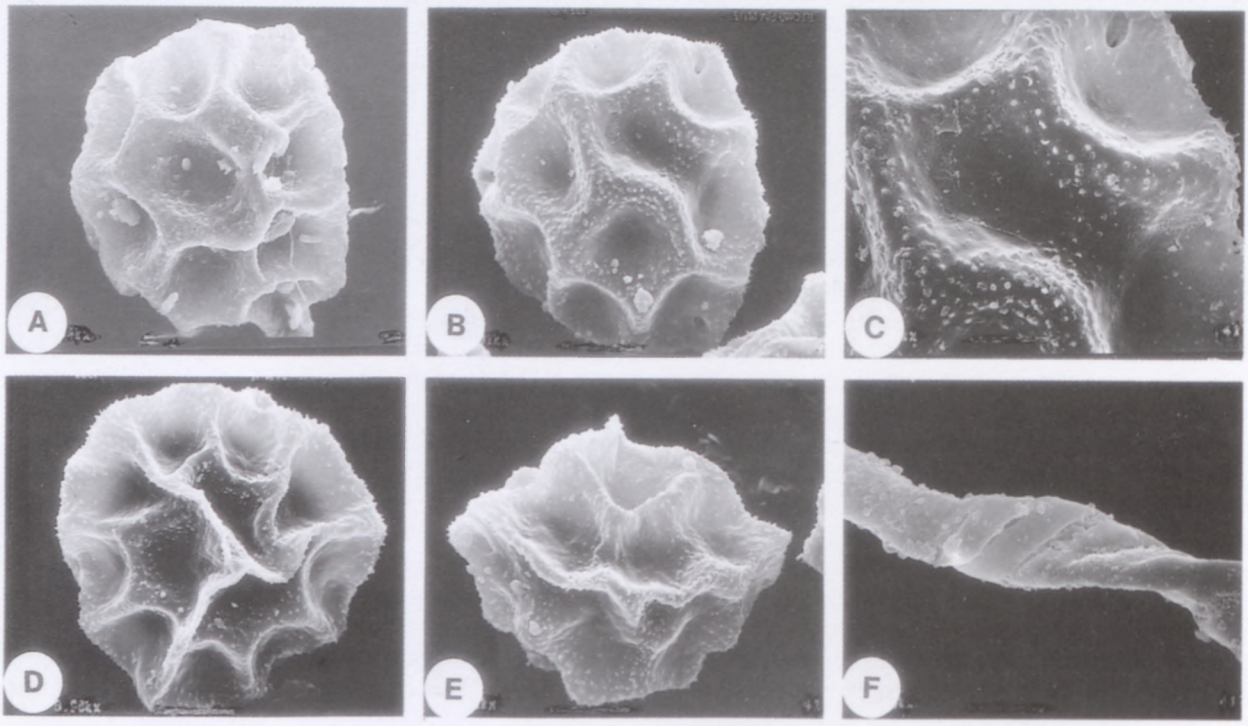

FIGURE 12.—*Plagiochasma beccarianum*. SEM micrographs of spores and elater. A, B, distal face; C, much enlarged view of margin, pore, some areolae and walls; D, proximal face; E, side view; F, part of elater much enlarged. A, *Glen 1250*; B–F, *Volk 00950*. A, × 437; B, E, × 472; C, × 936; D, × 460; F, × 1014.

Hansen 3241 (1a). *Hedberg 2150* BOL (4). *Heilgendorff CH 13611* (1a). *Hepburn 3 (= CH 1155)* (1a). *Herman 338* (1a). *Heymann, Cloete & Burgoyne 67* (1b); *68* (3). *Hilton 54706* (1a) BOL.

Jacot Guillarmod CH 3675, CH 3791, CH 4187 (1a). *Jacot Guillarmod, Getliffe & Mzamane 114, 287* (1a). *Jensen 442* (1a).

Koekemoer 104, 296 (1a); *637* (1b); *842, 912, 1024a* (1a). *Kreiner (= Volk 89-31)* (1b).

Leighton 3284 (1a) BOL. *Liebenberg 7593* (1a). *Lyle 7085* (1a).

Magill 6372, 6398, 6413, 6418, 6431, 6480 (1a). *Manning CH 13590* (1a). *Mogg 144* (1a); *CH 3720, 37590* (1b). *Moore CH 55* (1a). *Morley 358* (1a). *Moss CH 1256* (1a). *Mott 860* (1a).

Oliver 1449 BOL, *1464, 10133* (1a). *Örtendahl 696A* (1a).

Pearson 9849 (1a). *S.M. Perold 55* (1a); *176–178* (1b); *224* (3); *225* (1b, 3); *229* (3); *260, 301, 852* (1a); *854* (2); *947, 948, 1292, 1297, 1477, 1504, 1514, 1876, 2167, 2168* (1a); *2498* (4); *2508* (1a); *2586* (1b); *2799, 2803* (1a); *2974* (1b); *2976* (3); *2984* (1a); *2985* (1b); *2992, 2995* (5); *2997, 2998* (1b); *3002, 3058, 3062* (1a). *Perold & Koekemoer 2944, 2949, 2950, 2972* (1a); *3135* (2). *Perold, Koekemoer & Smook 3020* (1a). *Pieterse 100* (1a). *Playford CH 1264* (1a). *Pole Evans CH 11, CH 14* (1b); *CH 457, CH 1154* (1a). *Potts CH 1168, CH 1173, CH 1230, CH 1258* (1a).

Retief 1543, 1675a (1a). *Retief & Germishuizen 170, 408* (1a). *Retief & Shearing 1228* (1a).

Saaiman 309 (1a). *Schelpe s.n. (BOL 54717), 2019* (1a); *4781* (1b); *4782, 4852* BOL, *5283, 5290* BOL (1a); *5587 BOL* (1b); *5823, 5834, 6360* (1a). *Scott 21* (1a). *G.W. Sim 8109* (1a). *T.R. Sim CH 1157* (1a); *CH 1163* (4); *CH 1166, CH 1180–CH 1185* (1a); *CH 1186* (4); *CH 1189, CH 1199* (1a); *CH 1200* (4); *CH 1201, CH 1209, CH 1225* (1a). *Smook 4425, 4486, 5176a, 7929, 7952, 8240a, 8639, 8745* (1a).

Tidmarsh CH 3175 (1a, 1b).

University of Durban-Westville 2152 (1a).

Vahrmeijer CH 13145 (1a). *Van der Bijl 498* (1a). *Van der Westhuizen & Deetlefs 1* (1a) BOL. *Van Rooy 690, 734, 779, 791, 1166, 1347, 1467, 2025, 2366, 2379, 2408, 2423, 2525, 2595, 2621, 2657, 2679, 2726, 2771, 2777, 2782, 3160, 3197, 3212, 3293, 3542* (1a). *C.M. Van Wyk 2679, 3190* (1a). *Venter 8612* (1a). *Viljoen CH 4524* (1a). *Vlok 2662* (1a). *Volk 212, 00482, 00554, 00639, 00684, 00909* (1a); *00948* (1b); *00950* BOL (5); *01000, 01348* (1a); *5020, 6105, 6657, 6854* (1b); *6900, 11361, 11363, 11406, 12728, 81/063, 81/093* (1a); *81/183* (3); *81/194, 81/274, 81/287* (1a); *84/630, 84/650* (1a, 4); *84/724* (1a). *Vorster 655* (1a).

V. Wager 100 (1a). *Welman CH 1141* (1a).

Young CH 1164 (1a).

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