

Studies in the Marchantiales (Hepaticae) from southern Africa. 5. The genus *Exormotheca*, *E. pustulosa* and *E. holstii*

S.M. PEROLD *

Keywords: Exormothecaceae, *Exormotheca holstii*, *E. megastomata*, *E. pustulosa*, *E. youngii*, Hepaticae, Marchantiales, southern Africa

ABSTRACT

A taxonomic account of the genus, *Exormotheca*, and its local representatives, *E. pustulosa* and *E. holstii*, together with their distribution in southern Africa as currently known, is given. *Exormotheca megastomata* is here treated as a synonym of *E. holstii* since no distinct morphological differences could be found between them.

UITTREKSEL

'n Taksonomiese verslag oor die genus *Exormotheca* en die plaaslike verteenwoordigers, *E. pustulosa* en *E. holstii*, saam met hul verspreiding in Suider-Afrika, soos tans bekend, word gegee. *Exormotheca megastomata* word hier as a sinoniem van *E. holstii* beskou, aangesien geen duidelike verskille tussen hulle gevind kon word nie.

Exormotheca (Godm.) Mitten in Natural history of the Azores or Western Islands: 325 (1870); Schiffn.: 29 (1893–1895); Solms: 2 (1897); Steph.: 218 (1899); K. Müll.: 292 (1905–1916); Schiffn.: 40 (1942); K. Müll.: 398 (1951–1958); Hässel de Menéndez: 193 (1962) Type species: *E. pustulosa*.

Myrriorhynchus Lindb. & H.W. Arnell: 8 (1884). Type species: *M. fimbriatus*.

Corbierella Douin & Trab.: 321 (1919). Type species: *C. algeriensis*.

Thalloid, small to medium-sized to quite large, silvery glaucous green, dorsally with numerous conical evaginations of the epidermis; in crowded patches, in damp to rather dry, exposed areas on gravelly or sandy soil or on soil overlying rocky outcrops, xerophytic. *Branches* simple, or once, sometimes twice pseudo-dichotomously furcate, apex entire to shallowly notched, dorsally not grooved, slightly concave. *Dorsal epidermis* raised as pustular or conical evaginations over low or tall air chambers, opening above via simple air pores, encircled by thin-walled cells and basally occupied by chlorophyllose, sometimes branched, cell filaments, the lateral walls vertical, hyaline; storage tissue $\frac{2}{3}$ or $\pm \frac{1}{2}$ the thickness of thallus, a rather loose mesh of open, round spaces or so-called 'Schleimzellen' surrounded by smaller angular cells, single oil bodies in scattered upper and lower cells; ventrally keeled to rounded, green to purple, flanks sloping obliquely upward and outward; rhizoids some smooth, others tuberculate. *Scales* smallish to medium-sized, purple, oblong or rounded, occasionally with 1 or 2 appendages, otherwise large, hyaline with purple base, obliquely triangular, with long, filiform appendages from apex.

Monoicous or dioicous. *Antheridia* in rows along middle of thallus, in shallow groove where development of

air chambers temporarily suppressed, sunken, necks protruding conspicuously. *Gynoecea* raised on stalk with single rhizoidal furrow, receptacle erect or horizontal, when hammer-like, the parenchymatous centre covered by air chambers that open via simple pores, above or laterally, with 1 or 2 capsules, each supported by a seta, exerted from bilabiate involucre and dehiscing by 4 or 5 valves after shedding operculum; otherwise subsessile, lacking stalk, central dome with air chambers above, epidermis extended laterally and turning purple, forming involucre that cover capsules on either side; capsule wall with cells containing semi-annular thickenings. *Spores* 70–75 μm or almost twice as large, $\pm 140 \mu\text{m}$, triangular-globular, distal face with large hollow, conical papillae or convoluted areas covered with granules, proximal face without triradiate mark, heavily encrusted with granules; elaters tapering, up to 150 μm long and trispiral or blunt at one end, much shorter and unispiral or ringed.

Two genera are classified in the family Exormothecaceae K. Müll. ex Grolle (1983): *Exormotheca* Mitten and the Indian *Stephensoniella* Kashyap. Three subgenera are recognized in the genus *Exormotheca*: *Exormotheca* (for *E. pustulosa* and *E. tuberifera*), *Corbierella* (Douin & Trab.) Schiffn. (for *E. welwitschii*, *E. algeriensis* and *E. holstii*) and *Myrriorhynchus* Lindb. & H.W. Arnell (for *E. fimbriata*) (Schiffner 1942).

Exormotheca pustulosa Mitten in Natural history of the Azores or Western Islands: 326 (1870); Solms: 2 (1897); Steph.: 218 (1899); K.I. Goebel: 244 (1905); K. Müll.: 292 (1906–1912); Schiffn.: 46 (1942); K. Müll.: 399 (1951–1958); S.W. Arnell: 74 (1963); O.H. Volk: 232 (1979). Type: Madeira, Pico de Barcellos, leg. Johnson (NY, holo.).

E. africana Steph.: 18 (1917). Type: Transvaal, in Waterfall gorge near Belfast, leg. Pole Evans (G).

* National Botanical Institute, Private Bag X101, Pretoria 0001.
MS. received: 1993-03-26.

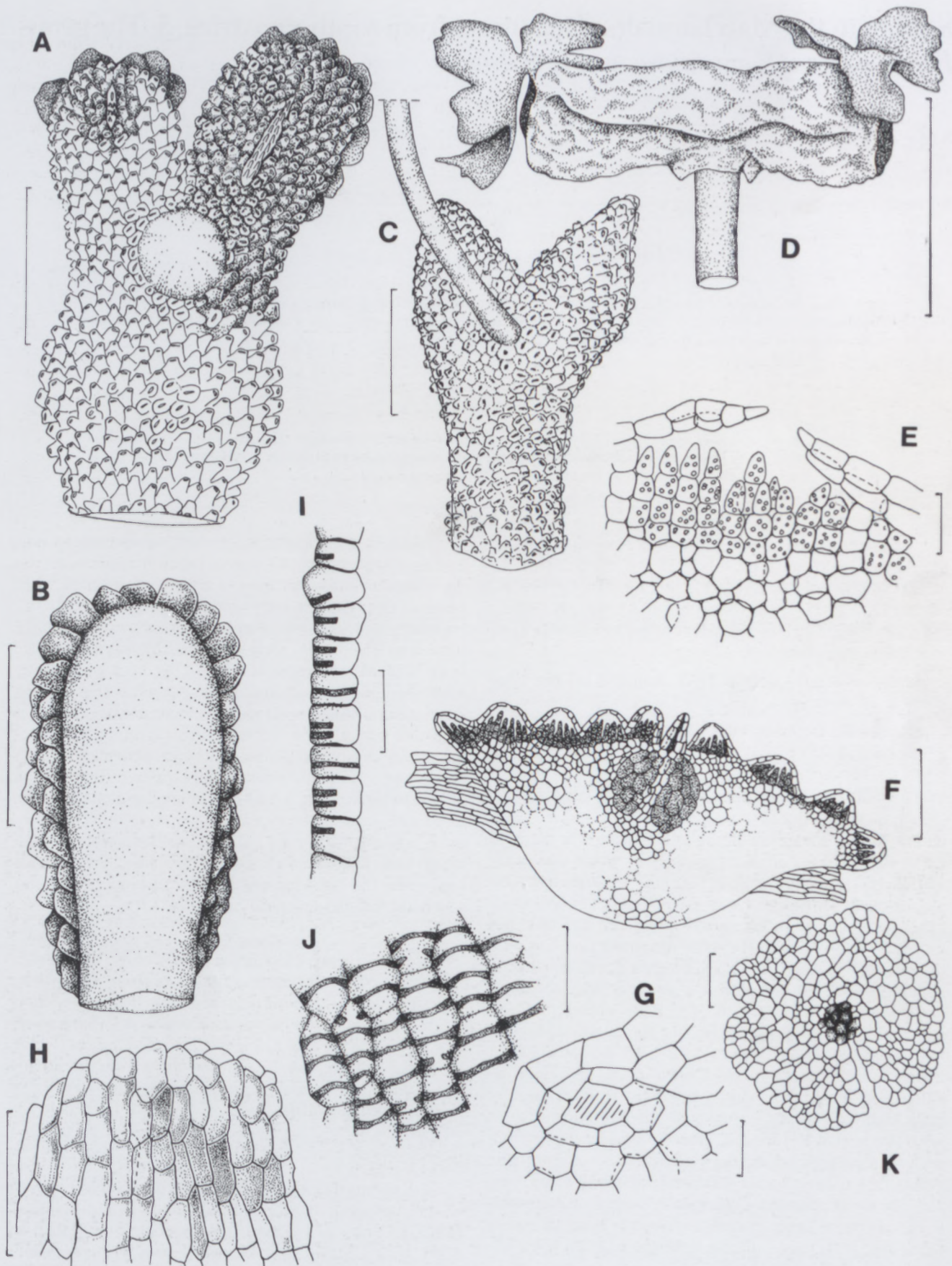


FIGURE 1.—*Exormotheca pustulosa*. Anatomy of thallus. A, dorsal face of monoicous thallus seen from above, with rows of antheridia in grooves toward apices and with young gynoeceium at furcation; B, ventral face of thallus, showing scales; C, stalk (cut off) emerging just proximal to furcation of thallus; D, 'hammer-like' head of carpocephalum with 2 dehiscent capsules; E, air chamber with assimilation tissue filaments and some storage tissue cells; F, transverse section of thallus showing two antheridia; G, air pore and surrounding cells from above; H, scale; I, capsule wall in transverse section; J, capsule wall from above; K, transverse section of stalk with one rhizoidal furrow. A, B, F, H, S.M. Perold 2604; C, D, I–K, S.W. Arnell 791; G, Cl. Reid 1107a. Scale bars: A–D, 1 mm; E, G, I, J, 50 μ m; F, H, 500 μ m; K, 100 μ m. Drawings by A. Pienaar.

Thallus rather small, linear to ligulate, glaucous green, with numerous conspicuous, partly adjoined conical evaginations of the air chambers forming pustules (Figures 1A; 2E), opening above via air pores, dorsally toward apex slightly concave medianly, otherwise flat and not grooved along midline, margins with scales extending above or hardly so, when wet; flanks covered by imbricate, purple or partly hyaline scales, generally tightly incurved over whitish, dorsal face when dry; in crowded patches, simple, or once, occasionally twice (–3 times) symmetrically or asymmetrically pseudo-dichotomously furcate. *Branches* with total length up to 8 or 9 mm, segments 3–5 mm long, variously divergent, 2(–3) mm wide, $\pm 1000 \mu\text{m}$ thick; apex slightly tapering to rather blunt, shallowly notched or entire; margins somewhat obtuse, becoming more acute proximally; ventrally quite strongly keeled, green, flanks sloping obliquely upward and outward, covered by scales (Figure 1B). *Dorsal epidermal cells* unistratose, hyaline, rectangular to 5-sided or polygonal, $30\text{--}75 \times 22\text{--}25 \mu\text{m}$, thin-walled and completely lacking trigones, raised into conical protuberances (Figures 1E; 2F); $\pm 300 \mu\text{m}$ high and $150\text{--}180 \mu\text{m}$ wide, in (8)9–11 irregular rows across width of thallus; air pores (Figure 1G) at or near top of cone, simple, round or oval, up to $62 \mu\text{m}$ wide, bounded by 2 concentric rings of smaller, thin-walled cells, inner cells mostly 8, $\pm 20.0 \times 12.5 \mu\text{m}$, outer cells $\pm 45 \times 25 \mu\text{m}$; assimilation tissue $\pm 200 \mu\text{m}$ thick, occupying lower $\pm 2/3$ of air chambers, and consisting of densely crowded filaments, sometimes branching from close to base, top 3–5 cells free, apical cell conical, $25\text{--}50 \times 15 \mu\text{m}$, those below rectangular, $27\text{--}32 \times 22\text{--}25 \mu\text{m}$, filled with numerous chloroplasts; storage tissue $\pm 700 \mu\text{m}$ thick, loosely composed, with larger empty spaces or so-called 'slime' cells, up to $80 \mu\text{m}$ wide, encircled by smaller cells $\pm 50 \mu\text{m}$ wide, in between a number of cells, also $\pm 50 \mu\text{m}$ wide, each containing a brown, granular oil body, $37.5 \times 30.0 \mu\text{m}$; rhi-

zoids arising from ventral epidermis, some smooth, $12.5\text{--}20.0 \mu\text{m}$ wide, but mostly tuberculate, $\pm 12.5 \mu\text{m}$ wide. *Scales* imbricate, apical ones oblong to rounded (Figure 1H), proximally shorter than wide, $500\text{--}1000 \times 540\text{--}850 \mu\text{m}$, occasionally with 1 or 2 appendages at margin, purple, generally with 1 or 2 cell rows at apex and base hyaline, rarely entirely hyaline, projecting above thallus margins or not, cells in body of scale 5- or 6-sided, up to $137.0 \times 37.5\text{--}42.5 \mu\text{m}$, smaller at margin and often brick-shaped, $17.5 \times 50.0 \mu\text{m}$, lacking oil cells.

Monoicous (or rarely ?dioicous). *Androeceia* in 1–3 rows along middle of thallus, close to female receptacle (distal or proximal to it), antheridia sunken, their necks $\pm 175 \mu\text{m}$ long, protruding above surface between air chambers, which are suppressed here to form a shallow groove (Figure 1A). *Gynoeceia* just proximal to bifurcation of 2 terminal branches, emerging as a central, round green cushion, at maturity raised on a cylindrical stalk (Figure 1C), basally purple-streaked, the remainder yellowish, length variable, up to 10 mm, diameter $350 \mu\text{m}$, with a single rhizoidal furrow, in transverse section (Figure 1K) cortical cells similar to medullary ones, average size $25.0 \times 17.5 \mu\text{m}$, top of stalk loosely sheathed in a short collar-like outgrowth of the head, the latter internally filled with parenchymatous tissue and covered by a row of filament-containing air chambers that open via hardly raised simple air pores, laterally with a capsule exserted from bilabiate involucre on either side, 3 mm across and hammer-like in appearance (Figure 1D), frequently, however, bearing only 1 capsule above, when erect and oblong. *Capsule* sheathed in thin calyptra, \pm spherical, wall brown, unistratose, upper part forming an operculum, cells somewhat smaller, otherwise similar to the rest, $\pm 57.5 \times 25.0 \mu\text{m}$, spindle- or irregularly shaped with semi-annular thickenings (Figure 1J), in transverse section $30 \mu\text{m}$ thick, with 'rods' projecting inwardly (Figure 1I), dehiscing by

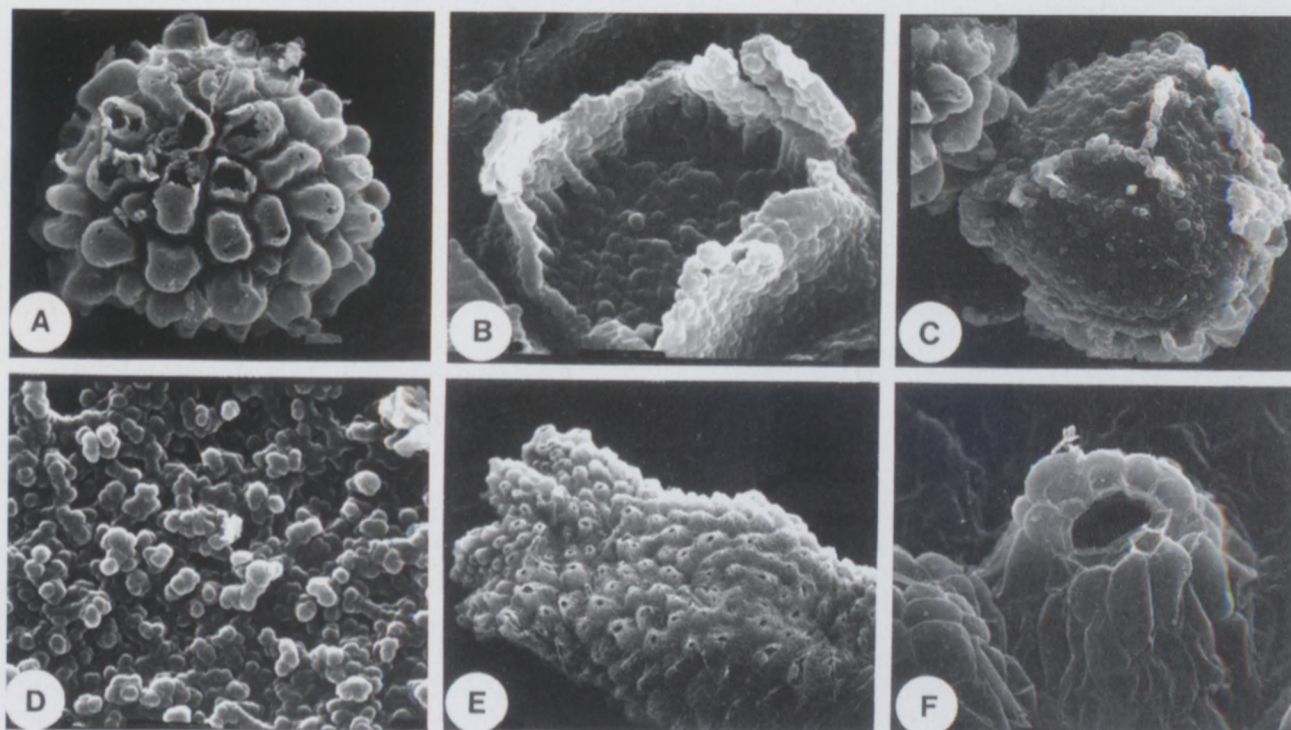


FIGURE 2.—*Exormoetheca pustulosa*. Spores and thallus. A, distal face of spore; B, outer wall of papilla broken down, showing minute internal granular 'pillars'; C, proximal face of spore; D, granules on proximal face; E, thallus; F, conical air chamber opening above via air pore. A–D, S.W. Arnell 791; E, F, S.M. Perold 2604. A, C, $\times 515$; B, D, $\times 3980$; E, $\times 16$; F, $\times 265$.

4 or 5 irregularly shaped valves and folding back, petal-like, seta up to $1625 \times 500 \mu\text{m}$, with ± 30 rows of cortical cells in transverse section, foot rounded. *Spores* 70–75 μm in diameter, polar, triangular-globular, bright honey-brown, distal face (Figure 2A) rounded, with up to ± 50 crowded, hollow, conical papillae, 10 μm high and 10 μm wide, walls of papillae composed of numerous adjoining granules stacked into tiny pillars in some areas and only exposed where wall has broken down (Figure 2B); proximal face with vestigial triradiate mark or part of it occasionally present (Figure 2C), entirely encrusted with fine granules (Figure 2D); wing absent, margin scalloped by protruding papillae on distal face. *Elaters* honey-brown, not tapering toward ends, up to $150 \times 10 \mu\text{m}$, trispiral. *Chromosome number*: $n = 16$ (Bischler 1976).

DISCUSSION

As a member of this rather rare genus *Exormotheca*, *E. pustulosa* is quite widespread, although the single, highly disjunct record from Mexico (Bischler 1976) may be an introduction (Gradstein *et al.* 1983). The latter authors regard it as an Afro-American disjunct with a sub-tropical-Mediterranean range. It is known from the following Mediterranean countries: Portugal, Spain, France (with only one locality (Bischler & Jovet-Ast 1981)) and Italy, as well as from the Atlantic islands: Azores, Madeira, the Canaries, Cape Verde and St Helena; also from two island groups (or islands) in the Indian Ocean: the Comores and Réunion (Bischler 1976). It is further known from Saudi Arabia, United Arab Emirates and Oman (Frey & Kürschner 1988) as well as from the following African countries: Morocco, Chad, Ethiopia, and also from Kenya, Tanzania (Bizot & Pócs 1979), Angola, Zimbabwe and southern Africa. In southern Africa (Figure 3) *E. pustulosa* has been quite rarely collected in Namibia (O.H. Volk pers. comm.), as well as in western, central, southern and eastern Transvaal, Orange Free State, Lesotho and southwestern Cape.

Frey & Kürschner (1988) regard *E. pustulosa* as a xerothermic Pangaean taxon. They define the xerothermic Pangaean element as comprising representatives with a present pattern of distribution corresponding to the Permian-Triassic continental Pangaea region. *Exormotheca pustulosa* grows in association with other liverworts, such as *Riccia* species and *Mannia capensis* on soil around granite or sandstone outcrops, which are generally only temporarily wet. Under rather wetter conditions the ventral scales are less conspicuous and almost entirely hyaline. Vegetative reproduction is by ventral tubers (Knöllchen) which were spherical, scale-clad, 500 μm wide structures in S.W. Arnell 791, one of only three southern African specimens that had mature sporophytes.

Schiffner (1942) had already placed *E. africana* Steph. in synonymy under *E. pustulosa*, when Arnell (1953a) stated that he could not find any real differences between *E. pustulosa* and *E. africana*. The Indian species, *E. tuberifera*, described by Kashyap (1914), seems very closely related to *E. pustulosa* and so does *E. ceylonensis* Meijer (1956). *Exormotheca pustulosa* can be distinguished by its low conical air chambers $\pm \frac{2}{3}$ filled with chlorophyllose cell filaments, by its small size, oblong or rounded purple scales, by its stalked carpocephala, by its spore ornamentation and by its spherical tubers.

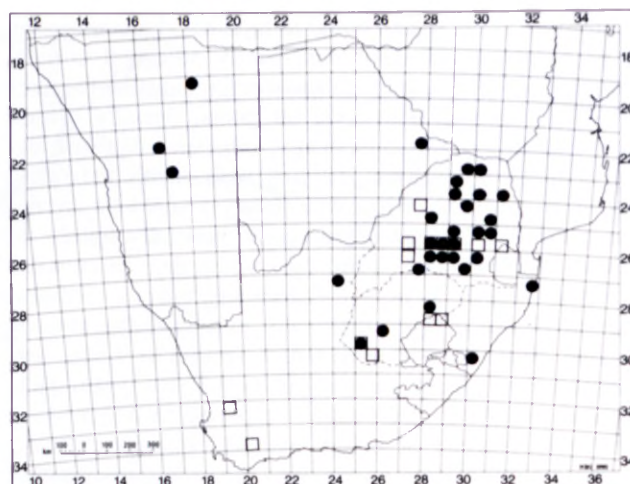


FIGURE 3.—Distribution of *Exormotheca pustulosa*, \square , and *E. holstii*, \bullet , in southern Africa.

SPECIMENS EXAMINED

TRANSVAAL.—**2427** (Thabazimbi): Kransberg, Farm Geelhoutbos, NE of Thabazimbi, at T-junction of upper 2 kloofs, (–BC), S.M. Perold 2993 (PRE); Waterberg, Welgevonden Estate, drift on Sterkstroom above farmhouse on cliffs, (–BD), Glen 2140, 2145 (PRE). **2527** (Rustenburg): Rustenburg Golf Course, (–CA), Hean CH 3664 (PRE). **2528** (Pretoria): Baviaanspoort, (–CB), Bosman CH 1533 (PRE); 18 km NE of Cullinan, on road to Sybrandskraal, near turnoff to De Tweede-spruit, Konsensusgrotte above Malanspruit, on soil under overhanging rock, (–DA), S.M. Perold 2604 (PRE). **2529** (Witbank): Loskop Dam Nature Reserve, Rhenosterhoek, in gully under vegetation on edge of exposed rock sheet, on loamy soil, small local population with *Riccia natalensis*, (–AD), Cl. Reid 1107(a) (PRE); Krantz, 3 miles N of Middelburg, high above river, on moist soil, (–CD), Van der Merwe CH 229 (PRE). **2627** (Potchefstroom): 6 km N of Carltonville, on the road to Pretoria, at rock outcrop immediately N of Wonderfontein, with *Riccia* spp., (–AD), S.M. Perold 1207 (PRE).

O.F.S.—**2925** (Jagersfontein): Fauresmith, on Reserve koppie, (–CB), Liebenberg CH 3659 (PRE). **3025** (Colesberg): 4 miles south of Trompsburg, at round boulder bases on S aspect of outcrop, (–BB), Schelpe 5284 (BOL).

LESOTHO.—**2828** (Bethlehem): ± 35 km before Oxbow on road from Butha-Buthe, on vertical soilbank of small stream, (–CB/CD), Perold & Koekemoer 2941 (PRE); ± 18 km before Oxbow on road from Butha-Buthe, at seepage area above road, (–DC), Perold & Koekemoer 2952 (PRE).

CAPE.—**3219** (Wuppertal): Olifants River Valley, between Klawer and Citrusdal, on moist soil by wayside, (–AC?), Wilman 664 (BOL, PRE). **3320** (Montagu): Kogmanskloof, (–CC), S.W. Arnell 791, 798 (BOL).

Exormotheca holstii Steph. in Bulletin de l'Herbier Boissier 7: 145 (1899); Schiffn.: 66 (1942); S.W. Arnell: 76 (1963); O.H. Volk: 231 (1979). Type: Deutsch-Ost-Afrika (Tanzania), Muse, plains, in moist sandy spots [regio campestris, in locis arenosis humidis], leg. Holst 3107 (G 024591, holo.).

E. youngii S.W. Arnell: 283 (1953b). Type: Transvaal, Pilgrim's Rest, Hendriksdal, on dry rocky veld, leg. E.M. Young (Duthie 5211) (BOL 54651, holo.).

E. megastomata C. Marquand: 237 (1930). Type: Transvaal, Krantz, 3 miles N of Middelburg, leg. F. Van der Merwe CH 214 (BM, holo.), CH 214 (PRE, iso.); BOL 54643 (Duthie 5042), iso., synon. nov.

Thallus medium-sized to quite large, broadly linear to \pm ovate (Figure 4A), silvery green, with numerous conspicuous, conical evaginations of the air chambers (Figure 5B, C), medianly narrow and somewhat lower, laterally mostly wider and taller, each opening above via an air pore (Figure 5A), dorsally flat to centrally slightly concave or shallowly grooved toward apex, scales at margins, except at apex, mostly hidden when wet; concave to apparently slightly grooved along midline of dorsal face, white, with hyaline, apical and distal scales incurved over margins or erect, when dry; in crowded patches, simple or once, rarely twice or 3 times pseudo-dichotomously furcate, symmetrical or not. *Branches* with total length 8–15(–22) mm, terminal segments generally 4–7(–10) mm long, moderately divergent, (2.5–)3.0–5.0(–7.0) mm wide, 2125–2900 μ m thick; apex slightly tapering, with shallow notch, margins obscured by air chambers; ventrally rounded to flattish, green, or with transverse extensions of purple scale bases or entirely purple, flanks basally tinged with purple, sloping slightly obliquely upward and outward (Figure 4C) covered with large hyaline scales. *Dorsal epidermal cells* unistratose, hyaline, raised into 4–6-sided air chambers, centrally 1000 \times 150 μ m and marginally 1500 \times up to 500 μ m, in 8–12 irregular rows across width of thallus, attached to each other at sides, but narrower apical part free (Figure 4E) for \pm 250 μ m, at margins of thallus at least 500 μ m at top free; cells mostly 5- or 6-sided (Figure 4E) near top of elevated cones 65–75 \times 42–50 μ m, lower down elongated, 125–175(–260) \times 30–50 μ m, thin-walled, air pores at or near tip of cone (Figures 4D; 5D), simple, rounded or elongated, (80–)125–137 \times 50–75(–85) μ m, bounded by smaller cells, 75–112 \times 27–30 μ m, sometimes a single cell, \pm 37 \times 37 μ m, or part of a larger cell jutting into lumen of air pore; assimilation tissue 350–400 μ m thick, occupying basal $\frac{1}{5}$ – $\frac{1}{3}$ of air chambers, and composed of densely crowded filaments (Figure 4F), 7 or 8 cells long, top cell with conical tip, 62.5 \times 17.5 μ m, others 67.5 \times 32.5 μ m, some filaments branching from near base, filled with chloroplasts; storage tissue 1000–1150 μ m thick, cells forming a rather open mesh with 'rounded spaces', 150 \times 100 μ m, surrounded by smaller, mostly angular cells, \pm 62 \times 50 μ m, toward the top and base of storage tissue and quite numerous, cells containing oil bodies, these transversely oval, 67.5 \times 55.5 μ m, yellow, not entirely filling cells; ventral epidermal cells isodiametric or not, giving rise to rhizoids, some smooth, 17.5 μ m wide, others tuberculate, 12.5 μ m wide. *Scales* imbricate (Figure 5E, F), large, 1250–1625 μ m long, 900–1500 μ m wide at base, hyaline but base purple, somewhat obliquely triangular with vertical side \pm entire, facing toward apex of thallus, diagonal side often toothed, cells in body of scale long-hexagonal, 225–250 \times 37–62 μ m, smaller at base, lacking oil bodies, apex mostly with branched or unbranched, filiform appendages up to 5 (Figure 4G), 700–1000 μ m long, cells 150 \times 20 μ m.

Monoicous or dioicous or ?protandrous, rarely producing gametangia of both sexes simultaneously. *Androecia* in 2–4 irregular rows along midline of thallus (Figure 4B), in 1 or 2 successive linear groups, antheridia sunken, necks protruding conspicuously, \pm 1000 μ m, between central air chambers, development of the latter here temporarily suppressed. *Gynoecia* developing near apex of thallus (which continues growth), causing widening and

hollowing of latter, somewhat sunken, sessile, mostly in single groups (Figure 4A) \pm 4 mm wide, occasionally with a second one behind the first, supported on central core of dense parenchymatous tissue, 1500 μ m wide, on either side 1(or 2) slightly obliquely held capsules, 1500 μ m wide, wall with cells containing semi-annular thickenings (Figure 4I, J), on short seta, 500 \times 550 μ m, \pm oval in shape, cortical cells hardly differentiated from medullary ones (Figure 4K), sheathed in thin calyptra, capsules separated by taller central dome, \pm 2250 μ m wide, containing elongated air chambers (Figure 4H), basally with cellular filaments and opening above via simple air pores, surrounded by thin-walled cells, and otherwise covered by larger cells with thicker, purple-stained walls; covering layer of dome forming a groove laterally and continuing on both sides as deeply purple-stained extensions; the involucre, containing numerous cells with oil bodies, partly covering capsules and at scalloped margins with smaller, thinner-walled cells. *Spores* 117.5–142.5 μ m in diameter, polar, triangular-globular, dark red, distal face (Figure 6A) rounded, with 6–8 highly convoluted, raised areas across, 22.5–27.5 μ m wide, bordered by superimposed layers of granules and hollowed in the centre, distinctly or poorly separated by deep furrows (Figure 6B); proximal face with triradiate mark absent (Figure 6D), but with slight flattening of the 3 facets, entirely encrusted with numerous, tiny granules; wing absent (Figure 6C, E), margin scalloped by projecting convoluted areas from distal face. *Elaters* brownish red, tapering slightly at one end, blunt and thicker at the other, 70–90 \times 20 μ m, unispiral or ringed (Figure 6F). *Chromosome number*: $n = 18, 32$ (T. Bornefeld pers. comm. via O.H. Volk).

DISCUSSION

Exormotheca holstii and *E. pustulosa* are the only two species belonging to this rather rare genus, that also occur in southern Africa. *Exormotheca holstii* has been reported in southern Africa (Figure 3) from Namibia [several collections recorded by Volk (1979)]. Botswana, northern, central, eastern and southern Transvaal, Natal, Orange Free State and northern Cape Province. Most gatherings are from the Transvaal, as in recent times it has become a more thoroughly collected area, as far as bryophytes are concerned. *Exormotheca holstii* has also been found elsewhere in Africa, namely Tanzania (*locus classicus*) and Zimbabwe (Best 1990). It appears to prefer quite dry, somewhat sandy or gravelly soil, sometimes between grass or in exposed areas that are only occasionally wet and that overlie sandstone or quartzitic or granitic rock. It sometimes grows in association with *Riccia* species, such as *R. volkii*, *R. rosea* and *R. albovestita*.

Marquand (1930) described a new species of *Exormotheca*, *E. megastomata*, based on a sterile specimen from Middelburg, Transvaal. This plant and its scales are somewhat larger than in *E. holstii* Steph., but the ratio of the surface area of an apical scale to that of a section of the thallus, works out to the same for both; no other significant differences between *E. megastomata* and *E. holstii* could be found after careful study of the type specimens of both species. I, accordingly, regard them as conspecific and place *E. megastomata* in synonymy under *E. holstii*. Marquand stated that *E. megastomata* 'is distinct from all previously described species of that genus in the very tall

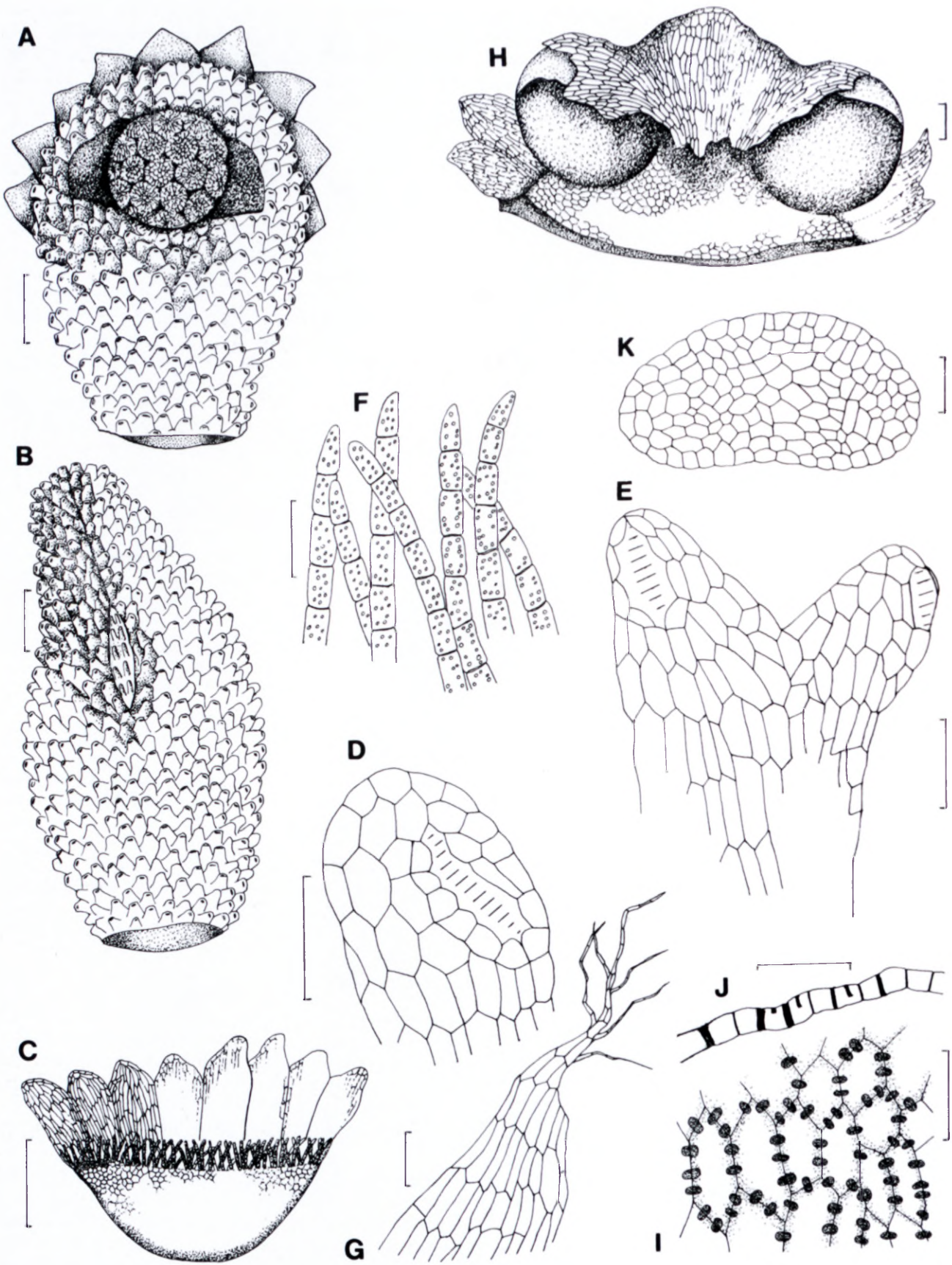


FIGURE 4.—*Exormotheca holstii*. Anatomy of thallus. A, thallus with sessile carpocephalum from above; B, thallus with antheridial necks emerging between air chambers in midline; C, transverse section of thallus showing tall air chambers, chlorophyllose cell filaments and storage tissue; D, air pore and surrounding cells from above; E, top part of two partly adjoining air chambers; F, assimilation tissue with cell filaments; G, scale with branched filiform appendages; H, carpocephalum, upper half three dimensional, lower half in transverse section; I, capsule wall from above; J, capsule wall in transverse section; K, transverse section of seta. A, H, K, *Germishuizen* 2839; C, *Perold & Koekemoer* 2872; D, *S.M. Perold* 2702; E, F, *Glen* 2190; G, I, J, *Holst* 3107. Scale bars: A–C, H, 1 mm; D–F, I–K, 100 μ m; G, 500 μ m. Drawings by A. Pienaar.

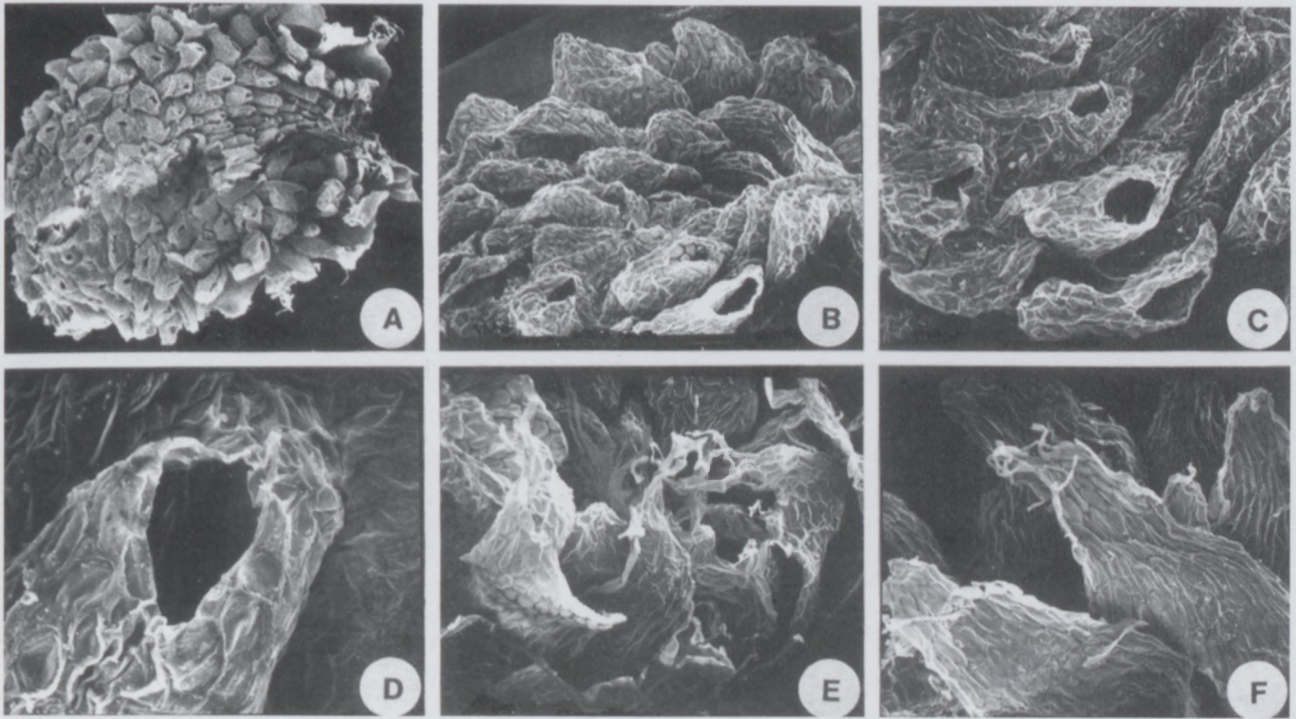


FIGURE 5.—*Exormothecha holstii*. Thallus, A, thallus from above, with conical air chambers; B, air chambers seen from side; C, air pores seen from above; D, air pore at apex of cone; E, scales inflexed over apex of thallus; F, scales seen from side. A–F, R. Smit s.n. A, $\times 8$; B, $\times 26$; C, E $\times 34$; D, $\times 150$; F, $\times 35$.

stomata', for which he named it, and so he made the same error as Stephani (1899) in referring to an entire air chamber as a stoma—Schiffner (1942) had already drawn attention to this. In his protologue, Marquand compared only *E. africana* Steph. (a synonym of *E. pustulosa*) to his new species, which is a much larger plant and differs in several other aspects as well, such as the tall air chambers and the conspicuous, triangular, mostly hyaline scales

with filiform apical appendages. Curiously, Marquand reported the marginal scales of *E. megastomata* as 'minute' and was followed in this by Arnell (1963), who also referred here, but not elsewhere, to the air chambers as stomata. In his description of a new species, *Exormothecha youngii*, Arnell (1953b) reported that it differed from *E. megastomata* by the large marginal scales and by the free air chambers ('free from one another down to the base').

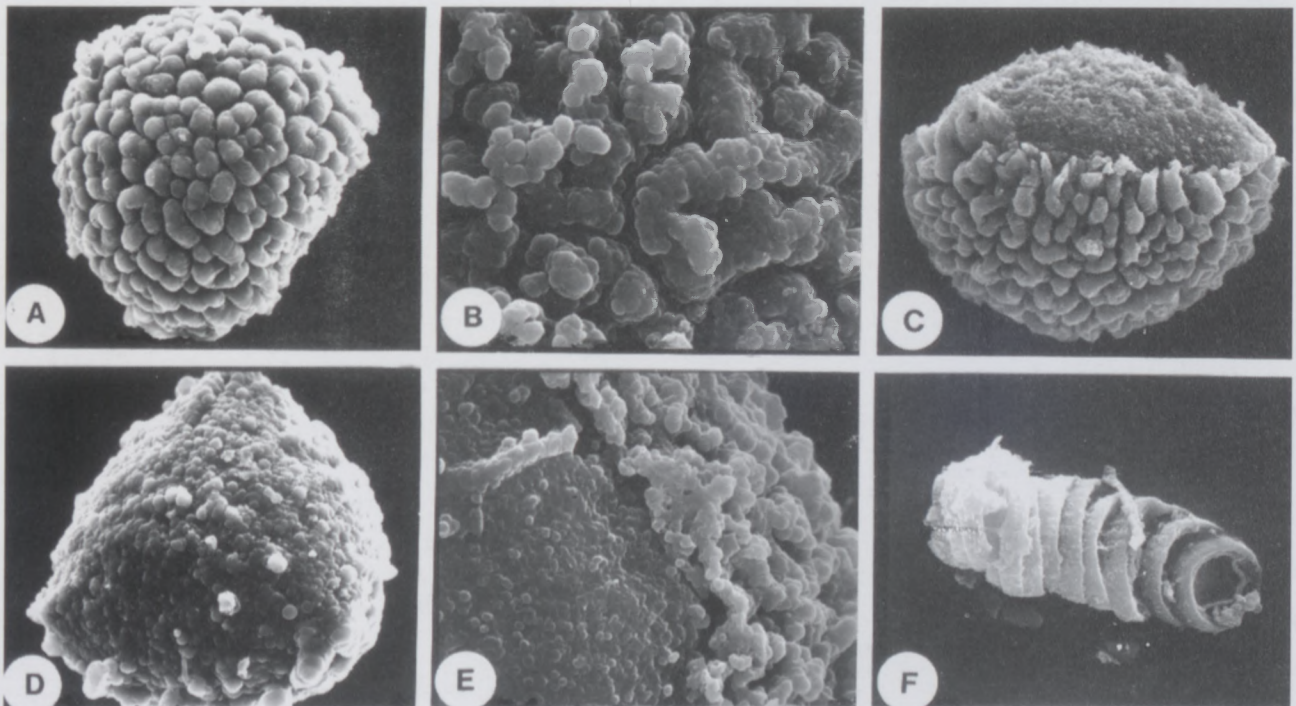


FIGURE 6.—*Exormothecha holstii*. Spores. A, distal face; B, granules on distal face much enlarged; C, side view; D, proximal face; E, boundary between proximal and distal face; F, elater. A, D, Volk 011670; C, Volk 85-766; B, E, F, Holst 3107. A, $\times 293$; B, E, $\times 794$; C, $\times 324$; D, $\times 300$; F, $\times 700$.

Arnell (1963) later placed *E. youngii* in synonymy under *E. holstii*. In his key to three species of *Exormotheca*, Arnell (1963) also referred to the air chambers in *E. holstii* as being free almost to the base. This is contrary to my findings (see above). Stephani (1899) also described the stomata (sic) of *E. holstii* as 'densissima altissima, ad $\frac{2}{3}$ coalita, tertio supero libera', and Schiffner (1942) referred to the air chambers as 'seitlich bis drei Viertel verwachsen'. Arnell's observations must, therefore, have been based on an error. In Schiffner's (1942) monographic study of the genus *Exormotheca*, he makes no reference to *E. megastomata*. In this work he refers to the controversy between himself and Müller (1940, 1941) concerning the application of the epithet, *E. bullosa*, which he suggested 'als Art einzuziehen ... ist'. I discussed this in greater detail in Perold (1991), urging a return to its earlier epithet, *E. welwitschii*, and furnishing reasons for it.

Fruiting collections of those *Exormotheca* species that are characterized by sessile carpocephala, are extremely rare and have only been illustrated once before by Douin & Trabut (1919). They described *Corbierella algeriensis*, a synonym of *E. algeriensis*, as dioicous. Of the specimens studied in the present work, *Giess 15383* is definitely monoicous; of the remaining 53 specimens, only the type specimen of *E. holstii*, *Holst 3107*, *Volk 01160* and *Germishuizen 2839* have mature sporangia and are dioicous or possibly protandrous.

Volk (in litt.) identified his collection *Volk 81/015*, from Middelburg (the type locality of *E. megastomata*), as *E. megastomata*; Bornfeld (in litt.) found its chromosome number to be $n = 18$, whereas specimens from Namibia have $n = 32$ chromosomes. Bornfeld and Volk are of the opinion that the material from Middelburg and from Namibia represents two different species. However, two different chromosome numbers manifested here are not reflected in morphological differences. The same phenomenon was observed in some *Riccia* species, e.g. *R. argenteolimbata* (Volk et al. 1988), where as many as five chromosome numbers were found in the same species.

Exormotheca holstii can be distinguished from other species in the genus by its large size, by its tall air chambers, basal $\frac{1}{5}$ – $\frac{1}{3}$ occupied by chlorophyllose filaments, and laterally adjoined except for the apical 250 μm toward the centre of the thallus and marginally for the apical $\pm 500 \mu\text{m}$; by the large, hyaline, triangularly shaped scales with long filiform appendages and by its subsessile gynoecia. Tubers were not found.

SPECIMENS EXAMINED

NAMIBIA.—1918 (Grootfontein): Gaikos, on quartzite sand, (–AD), *Volk 81/124* (M, PRE). 2116 (Okahandja): Erichsfelde, (–DA), *Volk 11925* (M, PRE); Fort Garden Park, Okahandja, (–DD), *Giess 15383* (PRE). 2217 (Windhoek): WIN 85, Farm Rietfontein, Granitzersatz, flach, durch Sickerwasser zeitweise feucht bis nass, (–CA), *Volk 01160* (BOL, PRE).

BOTSWANA.—2127 (Francistown): Shashe Dam, 30 km S of Francistown, damp soil in sandy wash, (–DA), *Cl. Reid & Barker 14* (PRE).

TRANSVAAL.—2229 (Waterpoort): Farm Driehoek, on top of sandstone koppie, on sandy soil, (–DC), *Fourie 31* (PRE); Lokovhela 793 Farm, campsite near Zwarthoek boundary, near edge of abandoned *Eucalyptus* plantation, on well-drained sand/gravel overlying Waterberg sandstone, (–DD), *Glen 2650* (PRE). 2230 (Messina): Maname, on soil, (–CD), *A.E. van Wyk 5424* (PRE). 2329 (Pietersburg): Soutpansberg, Koedoesvlei 47 Farm, Lejuma, foot of krantzies, stony soil overlying Waterberg quartzite, (–AB), *Glen 2190* (PRE); Pietersburg, Farm Bloedrivier, 6961 R, on ground

in open patches, (–CD), *F. Venter 12229* (PRE). 2330 (Tzaneen): Mountain Home Farm, Woodbush, in exposed positions on southern slopes, (–CC), *Mogg CH 3172* (PRE). 2331 (Phalaborwa): Silonque, in large colonies, in open areas on loamy soil, weakly drained, (–CC), *I.M. Retief 246* (PRE). 2428 (Nylstroom): Loubad, on road between Nylstroom and Alma, near bridge over Sand River, on soil between flat rock outcrops above river, (–CA), *S.M. Perold 820* (PRE). 2429 (Zebediela): Chumiespoort, (–BC), *F. van der Merwe CH 3666* (PRE). 2430 (Pilgrim's Rest): Bourke's Luck Potholes, 27 km N of Graskop on R532 road, (–DB), *S.M. Perold 412* (PRE); on R532 road to Bourke's Luck Potholes, ± 1 km before coming to SADF Dog Training Centre, on dry sandy slope above stream, between grass, (–DB), *S.M. Perold 2702* (PRE). 2528 (Pretoria): Soutpan road, on sandy soil between grass, (–CA), *Odendaal CH 12611* (PRE); Pretoria, (–CA), *Wager CH 3819* (PRE); Zwavelpoort, near Willows road, (–CA), *Watson PRE 56943*; Magaliesberg, summit Boekenhoutsloof, sandy flats, (–CB), *Mogg CH 853* (PRE); Pienaarspoort, (–CB), *Wager CH 852* (PRE); Donkerpoort, (–CD), *Bottomley CH 3566* (PRE), *Bottomley & Doidge CH 3590* (PRE); Donkerhoek, 22.5 km E of Pretoria, along Pretoria-Witbank Freeway, just beyond road cutting, seepage area, (–CD), *M. Crosby 464* (PRE), *Germishuizen 5624* (PRE), *S.M. Perold 330, 2015, 2795, 2796, 2884* (PRE); open veld east of Premier Mine, (–DA), *Pole Evans s.n.* (TR. Sim Herb. 1826) (PRE); Bronkhorstspuit Dist., 19 km N of town on Groblersdank road, at left hand side of road on soil overlying base of granite, (–DC), *S.M. Perold 144* (PRE); 33 km E of Pretoria, on R515 road to Cullinan/Bapsfontein, rock outcrop next to road, at small streamlet on damp soil beneath grass, (–DC), *S.M. Perold 1371* (PRE); between Cullinan and Bapsfontein on R515 road, just after T-junction from Rhenosterfontein, rock outcrop next to road, (–DC), *S.M. Perold 2010* (PRE); near Bronkhorstspuit, (–DC), leg. not known, *CH 3566a* (PRE). 2529 (Witbank): Triegaardts Poort, (–CA), *Verdoorn CH 3759* (PRE); Middelburg, along extension of Noordkant Street, W of town, on hill next to road, (–CB), *Van Rooy & Perold 644, 645* (PRE); on road from Middelburg to township, sandstone, on slope opposite Olifants River, (–CB), *Volk 81/015* (BOL, M, PRE); Witbank, on soil, (–CD), *Reinet Smit s.n.* (PRE); Middelburg, Gravel Krantz, (–CD), *Van der Merwe CH 214* (type of *E. megastomata*), *CH 3657, CH 3665* (PRE). 2530 (Lydenburg): halfway between Dullstroom and Lydenburg, Farm Klipsteen, seepage area, on gravel overlying quartzite, near path, (–AB), *H. Anderson 1244* (PRE); 29 km from Dullstroom on road R540 from Lydenburg, at dirt road turnoff to Boschhoek, near Marmerkop Station, on soil on hillside, (–AB), *S.M. Perold 422* (PRE); south of Lydenburg, Spitskop, on Coromandel Farm (opposite side to homesteads), on soil on ledge above waterfall, (–AB), *Perold & Koekemoer 2872* (PRE); Hendriksdal, on dry rocky veld, (–BB), *Young* (type of *E. youngii*). 2628 (Johannesburg): Benoni, Farrarmere, on soil at rocky outcrop near Homestead Lake, (–AB), *S.M. Perold 461* (PRE); 5 km NE of Kriel on road to Vanwyksdrift, beyond old bridge, coarse rock outcrop, (–BB), *S.M. Perold 2477* (PRE). 2629 (Bethal): 5 km W of Kriel on road to Vandyksdrift, on left side of road, on soil in depression at flat rocks, (–AB), *S.M. Perold 348* (PRE). 2630 (Carolina): Carolina, (–AA), *Van der Merwe CH 3583* (PRE); Knock Dhu Farm, 13 km SE of Lake Chrissie on Lothair road, common on rich black loamy soil, in grassland, (–AD), *Germishuizen 2839, 2887* (PRE).

NATAL.—2732 (Ubombo): Zululand, Muzi swamp near Phelandaba Cash Store, south of foot-and-mouth barrier, sedge meadow, in bare patches overlain by coarse sand, (–BA), *Cl. Reid 1024* (PRE). 3030 (Port Shepstone): Lynton Farm, N of east end of Oribi Gorge, overlooking Umzimkulu River, ± 2 km W of 'Rock of Gibraltar', on stony soil overlying Natal Mountain sandstone, (–CB), *Glen 2243* (PRE).

O.F.S.—2627 (Potchefstroom): Sasolburg, on soil, (–DD), *Kroon s.n.* (PRE). 2828 (Bethlehem): 14 km E of Paul Roux on road to Bethlehem, at flat weathered sandstone rocks, on soil, (–AC), *S.M. Perold 1349* (PRE). 2925 (Jagersfontein): Fauresmith, Pasture Research Station, (–CB), *Henrici CH 11226* (PRE). 2926 (Bloemfontein): grassveld in University grounds, Bloemfontein, (–AA), *Van Zinderen Bakker 7494* (BOL).

CAPE.—2724 (Taung): Farm Zoetvlei, ± 50 km W of Vryburg and 6 km from turnoff on road to Louwna, 50 m W of pan, on higher ground, with *Riccia volkii*, (–AA), *M. Crosby 1115* (PRE); Vryburg, Heuningvlei Salt Pan, west of town, in shallow damp hollow, occasional, (–AA), *Oliver 1446* (BOL). (A Wager bequest, *PRE CH 3839*, is said to be from Stellenbosch, but this is surely a mistaken locality, as *Exormotheca holstii* has not otherwise been recorded in the southwestern Cape).

ACKNOWLEDGEMENTS

I wish to thank Professors S. Jovet-Ast and T. Pócs for refereeing this article and for their helpful suggestions; also Prof. Dr O.H. Volk, Würzburg, for the loan of his specimens and for fruitful discussions and Dr T. Bornfeld

for chromosome counts. The curators of BOL, G and NY are thanked for the loan of type specimens. My thanks also to my colleagues at NBI for collecting specimens, to the artist, Ms A. Pienaar, the typist, Mrs J. Mulvenna and the photographer, Mrs A. Romanowski, for their valued contributions.

REFERENCES

- ARNELL, S.W. 1953a. Notes on South African Hepaticae. *Revue Bryologique et Lichénologique* XXII, fasc. 1–2.
- ARNELL, S.W. 1953b. A new South African species of *Exormotheca*. *Transactions of the British Bryological Society* 2: 283, 284.
- ARNELL, S.W. 1963. *Hepaticae of South Africa*. Swedish Natural Science Council, Stockholm.
- BEST, E.B. 1990. Bryophyta of Zimbabwe—an annotated checklist. *Kirkia* 13: 293–318.
- BISCHLER, H. 1976. *Exormotheca pustulosa* Mitten. *Revue Bryologique et Lichénologique* 42: 769–783.
- BISCHLER, H. & JOVET-AST, S. 1981. The biological significance of morphological characters in Marchantiales (Hepaticae). *The Bryologist* 84: 208–215.
- BIZOT, M. & PÓCS, T. 1979. East African Bryophytes III. *Acta Botanica Academiae Scientiarum Hungaricae* 25: 223–261.
- DOUIN, C. & TRABUT, L. 1919. Deux Hépatiques peu connues. *Revue générale de Botanique* 31: 321–328.
- FREY, W. & KÜRSCHNER, H. 1988. Bryophytes of the Arabian Peninsula and Socotra. *Nova Hedwigia* 46: 37–120.
- GOEBEL, K.I. 1905. Zur Kenntnis der Verbreitung und der Lebensweise der Marchantiaceen-Gattung *Exormotheca*. *Flora* 95: 244–250.
- GRADSTEIN, S.R., PÓCS, T. & VÁNA, J. 1983. Disjunct hepaticae in tropical America and Africa. *Acta Botanica Hungarica* 29: 127–171.
- GROLLE, R. 1983. Nomina generica Hepaticarum, references, types and synonymies. *Acta Botanica Fennica* 121: 1–62.
- HÄSSEL DE MENÉNDEZ, G.G. 1962. Estudio de las Anthocerotales y Marchantiales de la Argentina. *Opera Lilloana* 7: 1–297.
- KASHYAP, S.R. 1914. Morphological and biological notes on new and little-known West Himalayan liverworts. II. *New Phytologist* 13: 308–323.
- LINDBERG, S.O. & ARNELL, H.W. 1884. *Sandea* et *Myriorrhynchus*, nova hepaticarum genera. *Acta Soc. pro fauna et flora Fennica* 2, 5: 1–9.
- MARQUAND, C.V.B. 1930. XXVI. A new species of *Exormotheca* from South Africa. *Kew Bulletin* 1930: 237–239.
- MEIJER, W. 1956. A new species of *Exormotheca* from Ceylon. *Journal of the Hattori Botanical Laboratory* 16: 72–74.
- MITTEN, W. 1870. Hepaticae. In F.C. Godman, *Natural history of the Azores or Western Islands*: 316–328. Van Voorst, London.
- MÜLLER, K. 1906–1912. Die Lebermoose. *Dr L. Rabenhorst's Kryptogamen-Flora* 6: 1–870.
- MÜLLER, K. 1940. Exormothecaceae. Die Lebermoose Europas. *Dr L. Rabenhorst's Kryptogamen-Flora* 6: 275–280.
- MÜLLER, K. 1941. Beiträge zur Systematik der Lebermoose II. *Hedwigia* 80: 90–118.
- MÜLLER, K. 1951–1958. Die Lebermoose Europas. *Dr L. Rabenhorst's Kryptogamen-Flora* 6: 417–471.
- PEROLD, S.M. 1991. Studies in the genus *Riccia* (Marchantiales) from southern Africa. 23. *R. bullosa*: typification and a full description. *Bothalia* 21: 129–135.
- SCHIFFNER, V.F. 1893–1895. Hepaticae. *Die Natürlichen Pflanzenfamilien* 1: 3–141.
- SCHIFFNER, V.F. 1942. Monographie der Gattung *Exormotheca*. *Hedwigia* 81: 40–74.
- SOLMS-LAUBACH, H. 1897. Über *Exormotheca* Mitten, eine wenig bekannte Marchantiaceengattung. *Botanische Zeitung* 55: 1–16.
- STEPHANI, F. 1899. Species hepaticarum. *Bulletin de l'Herbier Boissier* 7: 198–225.
- STEPHANI, F. 1917. Species hepaticarum. *Bulletin de l'Herbier Boissier* 6: 18.
- VOLK, O.H. 1979. Beiträge zur Kenntnis der Lebermoose (Marchantiales) aus Südwestafrika (Namibia). 1. *Mitteilungen der Botanischen Staatssammlung, München* 15: 223–242.
- VOLK, O.H., PEROLD, S.M. & BORNEFELD, T. 1988. Studies in the genus *Riccia* (Marchantiales) from southern Africa. 10. Two new white-scaled species of the group 'Squamatae': *R. argenteolimbata* and *R. albornata*. *Bothalia* 18: 155–163.