

CLEVEACEAE-MARCHANTIALES

SAUTERIA NYIKAENSIS, A NEW LIVERWORT SPECIES FROM MALAWI

INTRODUCTION

In the Cleveaceae the dorsal air pores of the thalli are simple and the radial walls of the surrounding cells are often thickened. Three genera have traditionally been grouped together in this family, namely *Athalamia* Falc., *Peltolepis* Lindb. and *Sauteria* Nees. *Peltolepis* and *Sauteria* have not been reported from Africa, but *Athalamia* (formerly *Clevea*) has long been known from

this continent, with two species that occur here, namely *A. spathysii* (Lindenb.) Nees and *A. pulcherrima* (Steph.) Hatt. (Vanden Berghen 1965). A third species, *Clevea* (*Athalamia*) *crassa* Trabut, from the Atlas Mountains (Magreb), is considered to be a *nom. inval.* (Grolle 1976).

Sauteria is a small genus of \pm five (Bischler 1998) or six species (Schuster 1992), although some authorities recognize only three species worldwide (Gradstein *et al.* 2001). The

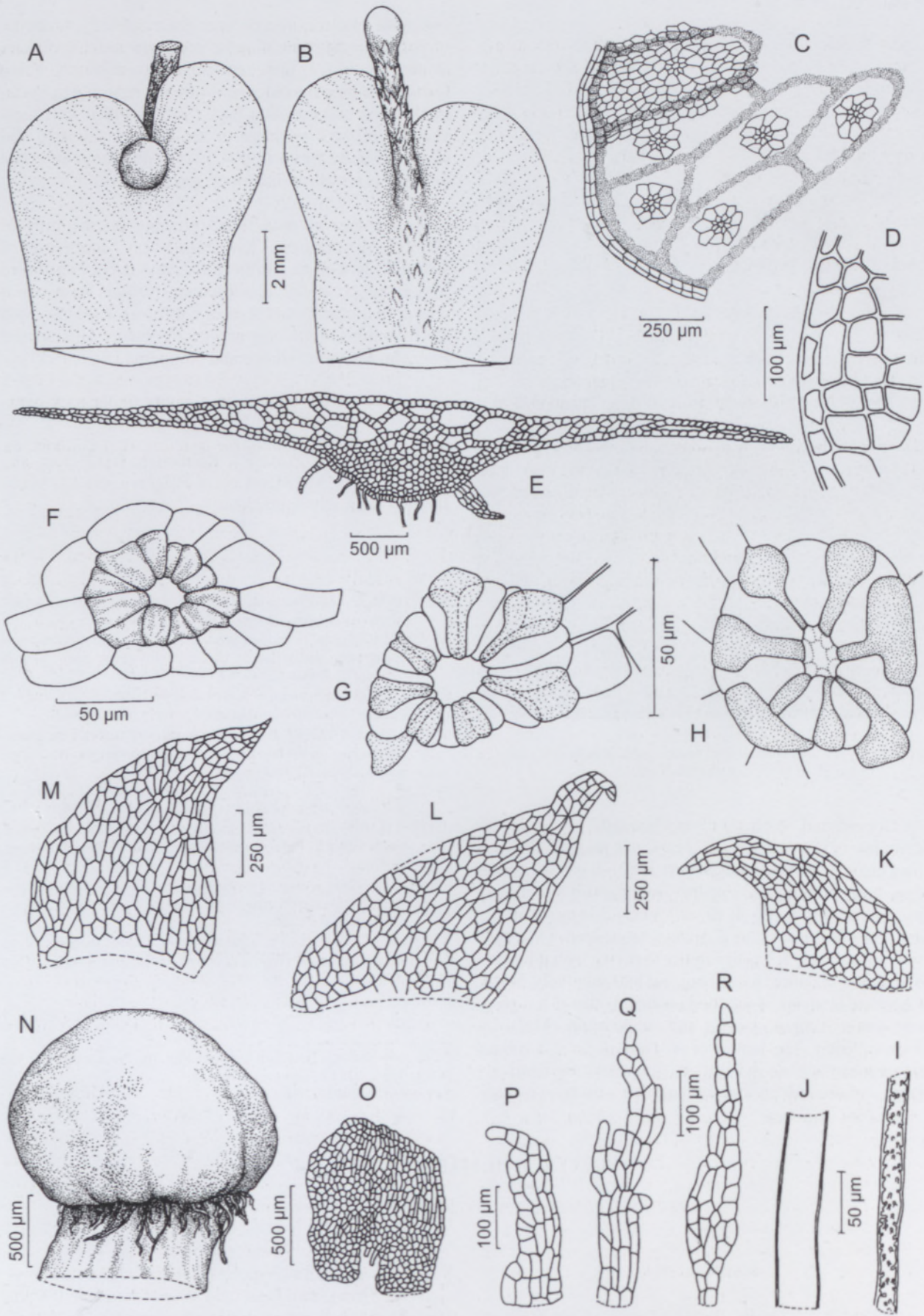


FIGURE 6.—*Sauteria nyikaensis*, Koekemoer 1874. A–E, thallus: A, dorsal face with young female receptacle, stolon cut off apically; B, ventral face with stolon uncut, covered with scales and rhizoids; C, air chambers partly exposed beneath dorsal epidermal cells and air pores surrounded by thickened cells; D, marginal cells and some dorsal epidermal cells; E, c/s. F–H, air pore and surrounding cells from above. I, J, rhizoids: I, tuberculate; J, smooth-walled. K–M, ventral scales; N, young female receptacle from side; O, c/s stalk with single rhizoid furrow; P–R, paleae. Drawings by M. Steyn.

genus is widespread, but is restricted to high mountain environments, often above 3 000 m, although it also occurs at lower elevations on islands (Gradstein *et al.* 2001). In Europe, Russia, Siberia, Tibet, the Himalayas and northern Japan, the distribution of its members is arctic or montane. Its western range includes areas in Iceland, east and west Greenland, as well as east and west Canada (Müller 1951–1958). Hitherto, the only known records in the southern hemisphere are those from the Andes of Peru, northern Argentina and Chile, as well as the Galapagos Islands, where it was found at an altitude of about 1 200 m (Gradstein *et al.* 2001).

During April 2000, an unusual thallose liverwort was collected on the Nyika Plateau at an altitude of 2 343 m, on soil, in a cavity under a rock overhang. Unfortunately, neither of the two female receptacles present is mature, and antheridia are absent. Nevertheless, in order to draw attention to this plant, it is described here and has been referred to the genus *Sauteria* for the following reasons: 1, the thalli are light green and fragile, the assimilation tissue is spongy and there is no trace of pigmentation; 2, the cells surrounding the simple air pores are strongly thickened; 3, the air chambers are empty, lacking both filaments and papillae, medianly in 2 or 3 layers and, visible beneath the epidermal cells in the wings, are the parallel outlines of what appears to be a single layer, obliquely orientated toward the thallus margins; 4, the ventral scales do not extend to the thallus margins; they are hyaline, with a single, tapering appendage, and are arranged in ill-defined rows, mostly confined to the prominent midrib; oil bodies are very rare and apical slime papillae are absent; 5, the female receptacle originates from a deep notch at the apex of the thallus; 6, in cross section the stalk of the receptacle has a single rhizoid furrow, whereas *Athalamia* species have none and *Peltolepis* species have two.

According to Schuster (1992), '*Sauteria* is separated from the other two genera of the Cleveaceae by one absolute feature (solitary rhizoid furrow of carpocephalum stalk)'. He also mentions 'distinct, scattered oil cells' in the ventral scales, in some (but not all) cases, adding that isolated ventral scales in Greenland *Sauteria alpina* often lack oil cells. Shimizu & Hattori (1954) describe the oil cells in *S. alpina* as 'scattered in the ventral scales and the dorsal epidermis of thallus, rare'. In their description of *S. alpina* var. *japonica* (later elevated to *S. yatsuensis*), they note that, 'oil-cells scattered in ventral tissue of thallus and bractlets of female receptacle (and also in ventral scales of thallus?), very rare', their question mark clearly indicating uncertainty. In a later description of *S. alpina*, Hattori & Shimizu (1955) remark that 'oil-cells rare, scattered in ventral tissue, ventral scales and bractlets'. They do not, however, illustrate oil cells in their 'Text-fig. XXI', although figs F–H of the ventral scales show groups of 5–7 cells surrounding a much smaller central cell, which does not contain an oil body. This is also seen in Figure 6K–M of the Nyika plant. Oil bodies in *Sauteria* have been observed to be long-persisting; those in the scales of *S. alpina*, leg. S.O.Lindberg & E.Rettig (held at PRE), are still present 120 years after collection.

Sauteria nyikaensis Perold, sp. nov.

Thalli magnitudine media vel sat magna, apice semel dichotome ramificantes, interdum irregulariter; laete

virides, sine pigmento, fragiles spongiosique. Cavernulae aerae, circumscriptione clare visibile, in medio thalli parallele, apicem versus dispositae, sed marginem thalli versus oblique dispositae. Pori dorsales non elevati, simplices, ab 1 vel 2 annulis concentricis cellularum circumscripti, pro parte vel pro parte maxima incrassationibus conspicuis tecti. Squamae ventrales hyalinae appendiculo acuminato non semper manifesto, in seriebus incertis supra costam dispositae. Costa saepe producta stolonem magnum geotropicum formans. Antheridia non visa. Receptaculum gynoeceale immaturum, in incisura apicali setae brevi tereti, sulco uno rhizoidali insidens. Guttae olei omnino absentes, semel tantum in squama ventrali visae.

TYPE.—Malawi, 1033: Nyika National Park, Jalawe viewpoint, (–BD), on soil, in a cavity under rock overhang, at altitude 2 343 m, 3 April 2000, *Koekemoer 1874* (PRE, holo.) with *Lunularia cruciata* (L.) Dumort. ex Lindb. and *Plagiochasma eximium* (Schiffn.) Steph.

Thalli prostrate, in crowded patches, obovate, apically notched or incised, on either side with rounded lobes (Figure 6A, B), continuing sometimes as smaller lobes along slightly decurved (Figure 7A) attenuate margins; medium-sized to fairly large, up to 12 mm long and 5–9 mm wide distally, narrowing gradually or abruptly up to ± 4 mm wide proximally, branching dichotomously once, but in young plants often irregularly or rather diffusely; light green, without any pigmentation, margins colourless; fragile and spongy, with clearly visible outlines of elongated, empty air chambers medianly running parallel toward apex, but soon becoming obliquely orientated toward thallus margins (Figure 6C), each one apparently opening by a simple air pore; along dorsal midline, slightly concave and not grooved, laterally margins acute, flanks sloping obliquely, ventral face medianly keeled with a prominent midrib, rounded distally but flattening proximally, covered with rhizoids and ill-defined rows of hyaline scales; midrib rarely branched at its apex, ensuing laminae irregularly shaped, most commonly continuing growth distally and occasionally proximally as well, forming very large tuberosus, geotropic stolons (Figures 6AB; 7D), up to 850 μm diam., filled with starch grains. Dried plants with flanks sometimes flat, incurved or ascending.

Dorsal epidermal cells rarely chlorophyllose, unistratose, thin-walled, without trigones, 4- to 6-sided, shorter than wide, generally $30\text{--}45 \times 60.0\text{--}72.5 \mu\text{m}$, in cross section $32.5\text{--}40.0 \mu\text{m}$ thick; margins unistratose, with 2 juxtaposed cell rows (Figure 6D), mostly rectangular, others 5-sided, outermost cells $22.5\text{--}50.0 \times 15.0\text{--}32.5 \mu\text{m}$, some with thickened walls between adjoining cells; second row of cells 4- or 5-sided, $22.5\text{--}45.0 \times 27.5\text{--}45.0 \mu\text{m}$, walls not thickened; air pores (Figures 6F–H; 7B; 8A) one per air chamber, not raised, simple, oval or rounded, $10\text{--}15 \times 10\text{--}20 \mu\text{m}$, with or without faint inner ring of small cells and then bounded by 1, occasionally 2 concentric rings of cells, variable in number, and covered partly to sometimes almost entirely by conspicuous thickenings, $15\text{--}25 \times 12.5\text{--}20.0 \mu\text{m}$, also obscuring several of the radial cell walls, width of air pore together with surrounding cells $62.5\text{--}100.0 \mu\text{m}$; row of dorsal epidermal cells adjoining thickened cells often

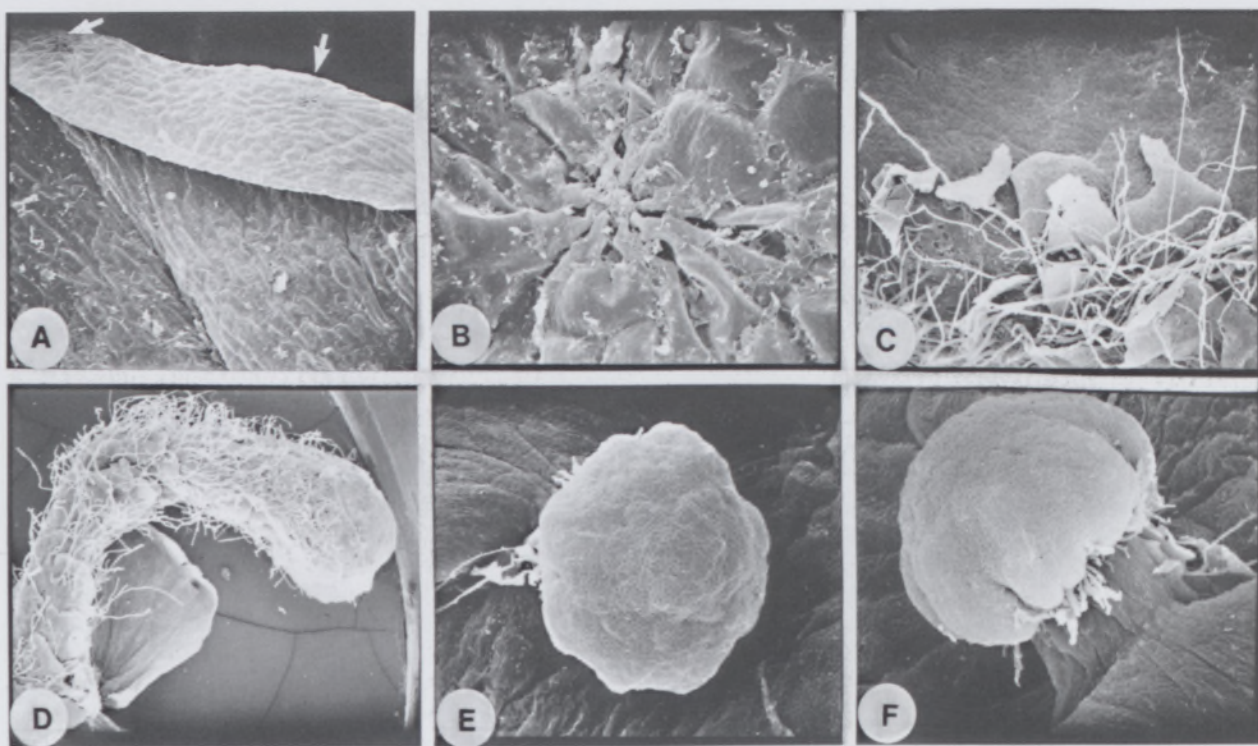


FIGURE 7.—*Sauteria nyikaensis*, Koekemoer 1874. SEM micrographs. A, margin of dorsal face of thallus decurved over lateral part of ventral face, arrows indicating positions of some dorsal air pores with thickenings; B, thickened cells around contracted air pore in concentric rings, partly shown; C, irregular rows of ventral scales mostly over midrib, between rhizoids; D, massive ventral stolon with scales and rhizoids, partly overlying apical part of ventral face of thallus; E, young female receptacle from above; F, young female receptacle from side. A, $\times 58$; B, $\times 430$; C, $\times 18.5$; D, $\times 8.5$; E, $\times 18$; F, $\times 21$.

somewhat smaller than average, partly arranged in a concentric ring, occasionally the thickenings extending slightly onto a few of them as well.

Assimilation tissue, as seen below and through dorsal epidermis, with parallel outlines of empty air chambers 200–350 μm apart, running obliquely across wings to margins of thallus, partitioned in wings by slanting, unistratose cross walls at intervals of up to 600 μm between them, at thallus margins air chambers somewhat smaller; in cross section (Figure 6E), thallus over midrib 700–1150 μm thick, \pm upper half with polyhedral air chambers in 2 or 3 layers, 65–175 \times 150–220 μm , with lower ones smaller, unistratose walls consisting of chlorophyllose cells, spherical or ovoid, 37.5–50.0 \times 25.0–42.5 μm ; storage tissue occupying $\pm 1/6$ of width of thallus medianly and ± 12 rows of cells in lower half of thickness of thallus, decreasing laterally, soon disappearing and flanks bounded beneath by ventral epidermis only, cells crowded together, angular, 27.5–40.0 \times 50–65 μm , no sclerotic cells, oil bodies or mucilage cavities present; rhizoids densely covering midrib, fewer beneath wings, some smooth (Figure 6J), 27.0–47.5 wide, others pegged (Figure 6I), 15–25 μm wide. **Ventral scales** (Figure 6K–M), hyaline, in 2–4 poorly defined rows over midrib and extending onto adjacent ventral face of thallus (Figure 7C), also on continuation(s) of midrib as geotropic stolon(s) (Figures 6B; 7D); inconspicuous, asymmetrically triangular, one side obliquely rounded, margins entire, tapering gradually and not constricted where joined with acuminate, apically pointed and not sharply differentiated appendage, 725–1025 μm long (including appendage), width across base 375–725 μm , cells 4–6-sided, 45–75 \times 30–45 μm , in each scale 1–3 groups of cells surrounding 1 much smaller, central cell, not containing an oil body; oil bodies very rare

(Figure 8A, B), 22.5–25.0 \times 20.0–27.5 μm , light brown and finely granular.

Monoicous? Antheridia unknown. **Gynoeceal receptacle** terminal, raised on short stalk, (Figures 6N; 7E, F) at crotch of apical incision up to 2.5 mm long, separating 2 thallus lobes, immature, rounded above, ± 1675 μm wide, with 8 lobes below, air pores not seen, but may develop later, as air chambers visible in cross section of receptacle, a single archegonium also seen; stalk terete, with one rhizoid furrow (Figure 6O), 625 μm long at this stage of development, 875 μm wide, without assimilatory strip, naked below, but with paleae at apex; paleae elongated and narrow (Figures 6P–R; 9B) 375–800 \times 75–120 μm , inner cells 25–40 \times 12.5–25.0 μm , with 1 to 3 papillae apically and sometimes 1 at margin, thicker-walled at tip. **Chromosome number** for the genus *Sauteria*: $n = 36$ (Müller 1951–1958; Hattori & Shimizu 1955, count by Dr S. Tatuno for *Sauchia japonica*, later transferred to *Sauteria yatsuensis*; Bischler 1998). The Nyika material was no longer living when examined, and a chromosome count could not be done.

DISCUSSION

In the absence of antheridia, the single archegonium seen in the above specimen, would not have been fertilized. The development of antheridia may have been delayed for some reason, or else they had already disappeared. Bischler (1998) states that in families of the Marchantiales with archegoniophores other than the Marchantiaceae, the stalk elongates after fertilization. In the Nyika plant, however, the stalk is still very short, almost sessile, and fertilization had not taken place.

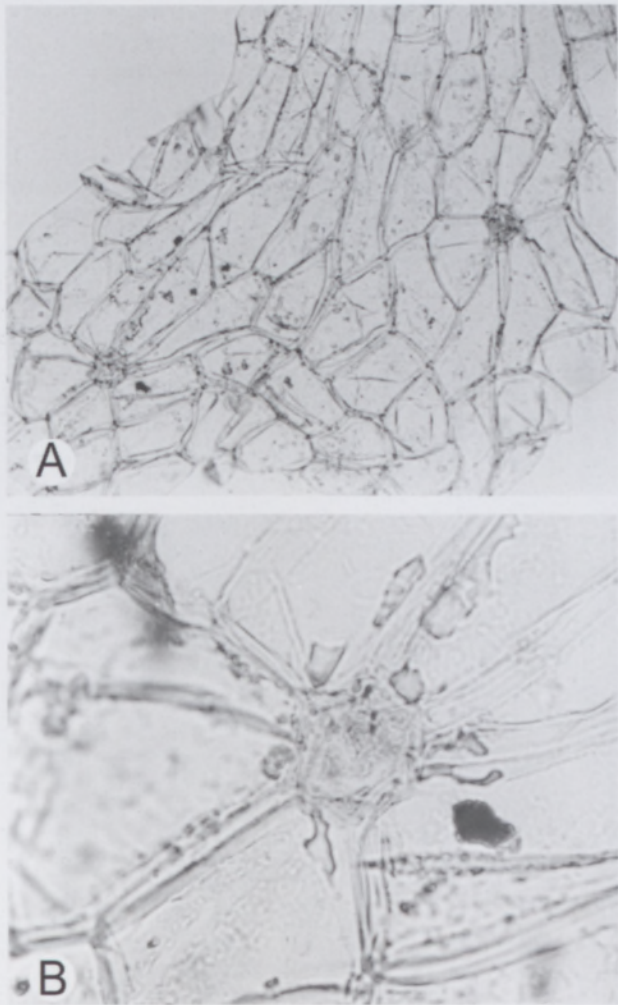


FIGURE 8.—*Sauteria nyikaensis*, Koekemoer 1874. LM micrographs. A, part of ventral scale with 2 oil bodies; B, much enlarged micrograph of one of the oil bodies. A, $\times 198$; B, $\times 790$.

Because of the delicate structure of the thalli, the plants are thought to be drought intolerant and to perennate during the dry season by means of the tuberous geotropic stolons.

At the site in northern Malawi (Figure 10), where the plant was collected near the Jalawi View Point, it grew on calcareous soil containing slivers of mica, in a small, cave-like cavity at the base of a large rock. Not much direct sunlight could have reached it there, but species of *Sauteria*, except for *S. chilensis*, lack secondary pigmentation even when growing in open, strongly illuminated sites (Schuster 1992). Shimizu & Hattori (1954) do not regard the presence of thickened radial walls around the dorsal air pores as being of generic value, since they had observed pores with both thickened and thin radial walls on the same plant. All the air pores in the Nyika specimen had thickenings, not just on the radial walls but partly or entirely covering the cells surrounding them, somewhat like those in *Athalamia pulcherrima*, as illustrated by Vanden Berghen (1965). When stained with periodic acid-Schiff's (PAS) reaction (Jensen 1962), the thickenings became intensely pink, much more so than the rest of the tissues.

Bischler (1998) states that the genera *Athalamia*, *Sauteria* and *Peltolepis* are traditionally grouped in the

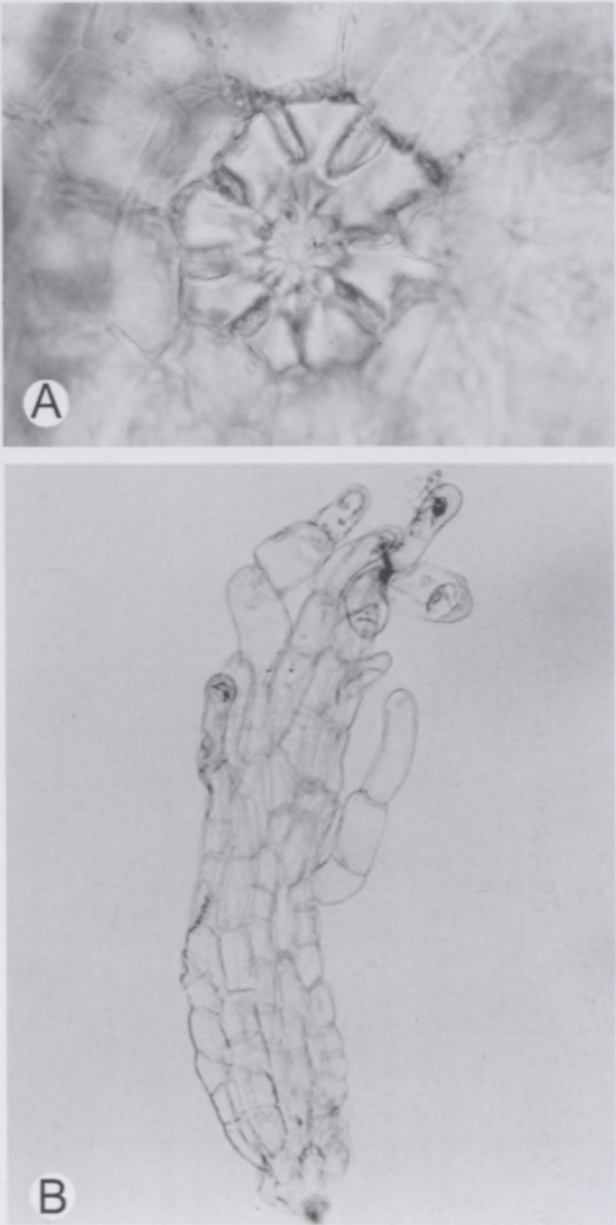


FIGURE 9.—*Sauteria nyikaensis*, Koekemoer 1874. LM micrographs. A, dorsal air pore with thickenings on surrounding cells; B, palea. A, $\times 500$; B, $\times 100$.

same family, the Cleveaceae, but adds that, 'other characters argue against such a classification'. She does not elaborate further.

Sauteria nyikaensis is separated from the other species in the genus by collectively considering the following characters listed in Table 1.

The genus *Sauteria* was first described by Nees (1838) and named for the Austrian physician, Anton E. Sauter, 1800–1881, who also collected and studied liverworts.

If more material of *Sauteria nyikaensis* with ripe sporophytes is collected, the above description will, undoubtedly, have to be emended.

ACKNOWLEDGEMENTS

I wish to sincerely thank the curator of PRE, Dr M. Koekemoer, for collecting this specimen while on a South-

TABLE 1.—Comparison of some characters of *Sauteria alpina*, *S. chilensis*, *S. nyikaensis* and *S. yatsuensis*

| | <i>S. alpina</i> (Schuster 1992) | <i>S. chilensis</i> (Hassel de Menéndez 1963) | <i>S. nyikaensis</i> (Perold 2003) | <i>S. yatsuensis</i> (Hattori & Shimizu 1955) |
|-------------------------|--|--|--|---|
| Distribution | Central and northern Europe, Yugoslavia, Siberia, Norway, Sweden, Finland, Iceland, Greenland, Alaska, British Columbia, Alberta | Andes of Peru, northern Argentina and Chile; Galapagos Islands | Nyika Nat. Park, Malawi | Mt Rishiri, Rishiri Island, Hokkaido, northern Japan |
| Thallus | | | | |
| colour | light green, margins decolorate | dark green, margins & ventral face purple | light green, no pigmentation | pale to light or dull green |
| size | 8–17 × 3–5 mm | 6–12 × 1.5–2.5 mm | up to 12 × 5–9 mm distally | 10–15 × (3–)5–7 mm |
| branching | simple or 1–2 × dichotomous | 3–4 × dichotomous | dichotomous or irregular | sparsely dichotomous |
| segments | lingulate | branches with apical innovations | rounded lobes | |
| apex | deeply emarginate | furrowed | notched or incised | |
| texture | fleshy, ± soft | | fragile, spongy | 'not so firm' |
| margins | thin, translucent, ascending | purple | colourless, 2 juxtaposed cells unistratose, attenuate | |
| dorsal epidermis | strongly areolate | cells with chloroplasts | unistratose, cells thin-walled | |
| pores | ± elevated, bounded by 5–7 cells, radial walls thickened | not raised, bounded by 5 or 6 cells, radial walls thickened | not raised, bounded by up to 12 or 13 cells, mostly covered by thickenings | radial walls of cells not so thickened, often thin and indistinct |
| air chambers | inflated, polyhedral, (2)3(4) layers | 1(2) layer(s), narrow-rectangular | polyhedral, 2 or 3 layers | polygonal |
| Ventral scales | not projecting at thallus margins | extending to thallus margins | over midrib and occasionally on adjacent ventral face | hardly reaching thallus margins |
| rows | irregular, 3–6 | in 2 irregular rows | 2–4 poorly defined rows | in 3–5(6) irregular rows |
| colour | hyaline | reddish black or decolorate | hyaline | colourless |
| shape | asymmetrically ovate-lanceolate | base triangular | asymmetrically triangular | ovate or lanceolate |
| appendage | acuminate to longly acute | ciliate, basally constricted or not | acuminate, not sharply differentiated | narrowed to 1-celled apex |
| marginal slime papillae | present, clavate | ephemeral | absent | usually present |
| oil bodies | scattered in scale body | in 1 or 2 isolated cells | very rare | rare |
| Geotropic stolons | not mentioned | not mentioned | present, prominent | not mentioned |
| Androecia | ill-defined group behind female stalk | behind female receptacle | not seen | just below female receptacle or on different branch |
| Gynoeceia | from deep apical notch | at apical bifurcation | from deep apical notch | disc non-convex, lacking pores |
| stalk | colourless, up to 15 mm long | yellow-green, 2–8 mm long | immature, only 625 µm long | |
| palcae | none at base, few at apex | | narrow and elongated, at apex | |

Note: there is little information about *S. spongiosa* Kashyap (1929) from middle and main Himalayas, Kashmir, or about *S. inflata* Gao *et al.* (1981) from Tibet.



FIGURE 10.—Locality of *Sauteria nyikaensis* in Malawi.

ern African Botanical Diversity Network (SABONET) Expedition to the region; also Dr David Long for advice. The referees, the artist, Ms M. Steyn, and the typist, Ms D.

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