Journ. Hattori Bot. Lab. No. 64: 327–334 (June 1988)

HAESSELIA, A NEW GENUS OF CEPHALOZIACEAE (HEPATICAE) FROM MT. RORAIMA, GUYANA[1]

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In early 1985 the junior author joined an international botanical expedition to Guyana organised by the Institute of Systematic Botany, Utrecht. During this expedition the famous flora of the Mt. Roraima (Guayana Highlands), at the western border of Guyana, was explored. Details of the route have been described by Gradstein (1986).

At the northern foot of Mt. Roraima, at an elevation of 550–1550 m, the junior author met with a striking liverwort of *Plagiochila*-like habit but with a hypogonianth, trigonous perianth. Though common in the area and rather handsome, it did not fit any of the known genera. After a joint study by the authors it was concluded that a new genus of the Cephaloziaceae is at hand. We are proposing the name *Haesselia* gen. nov. for this interesting new neotropical endemic, as a tribute of our respect to the excellent contributions to hepaticology by Dr. Gabriela G. Hässel de Menendez (Buenos Aires), who founded high standard hepaticology in Latin America.

Haesselia roraimensis gen. nov. et spec. nov. (Fig. 1–3)

Dioicae, caespitosae, ascendentes, sparsim ramosae ramis semper gyrothecalibus lateralibus, sine stolonibus vel flagellis. Caulis crassus, tenax, dorso limite 2(4) cellulas lato sine insertione foliorum, in sectione transversali e cellulis subaequimagnis, parietibus tenuibus in cortice 1–3-stratosa, valde incrassatis in medulla. Folia succuba, plagiochilacea, convexa (a dorso visa), apice truncato, bidentato, margine dorsali integro, obliquo, substricto, basi breviter angustato, margine ventrali irregulariter (sub)dentato, arcuato, basi valde ampliato et verticaliter ad ventrem patente. Cellulae foliorum leptodermaceae, sine trigonis, maximae, medianae (50)66(83) × 66–100 μm. Cuticula levis. Amphigastria desunt. Gametoecia in surculo primario terminalia. Androecia longissima, bracteis basi dorsali lobulo instructa et bursatim excavata. Antheridia bina, pedicello bicellulariseriato. Gynoecia interdum unilateraliter innovata ramo gyrothecali laterali. Folia subinvolucralia et involucralia libera, valde elongata, profunde 2–4-laciniata, laciniis longe subulatis, attenuatis, perianthio attingentibus. Amphigastria subinvolucrale et involucrale adsunt, foliis suis similia. Perianthia adulta longe exserta, anguste cylindrica, in dimidio superiore trigona (plicis duabus lateralibus et una ventrali), facie dorsali plana, ore truncato, irregulariter setuloso. (Descriptio generico-specifica).

Type: *H. roraimensis* spec. nov.

Type: GUYANA, Upper Mazaruni District, North slope of Mt. Roraima, 700 m, *S. R. Gradstein 5100*, 13 February 1985 (JE holotype; isotypes in ALTA, B, BA, BM, BRG, CINC, COL, F, FLAS, G, H, MEXU, MICH, NICH, NY, PC, PRC, SP, TNS, U, US).

Further specimens: Guyana, Upper Mazaruni District, east bank of river Waruma near Mt. Roraima, 550 m, *S. R. Gradstein 5066* (JE, U); North slope of Mt. Roraima, 1200–1600 m, *S. R. Grad-*

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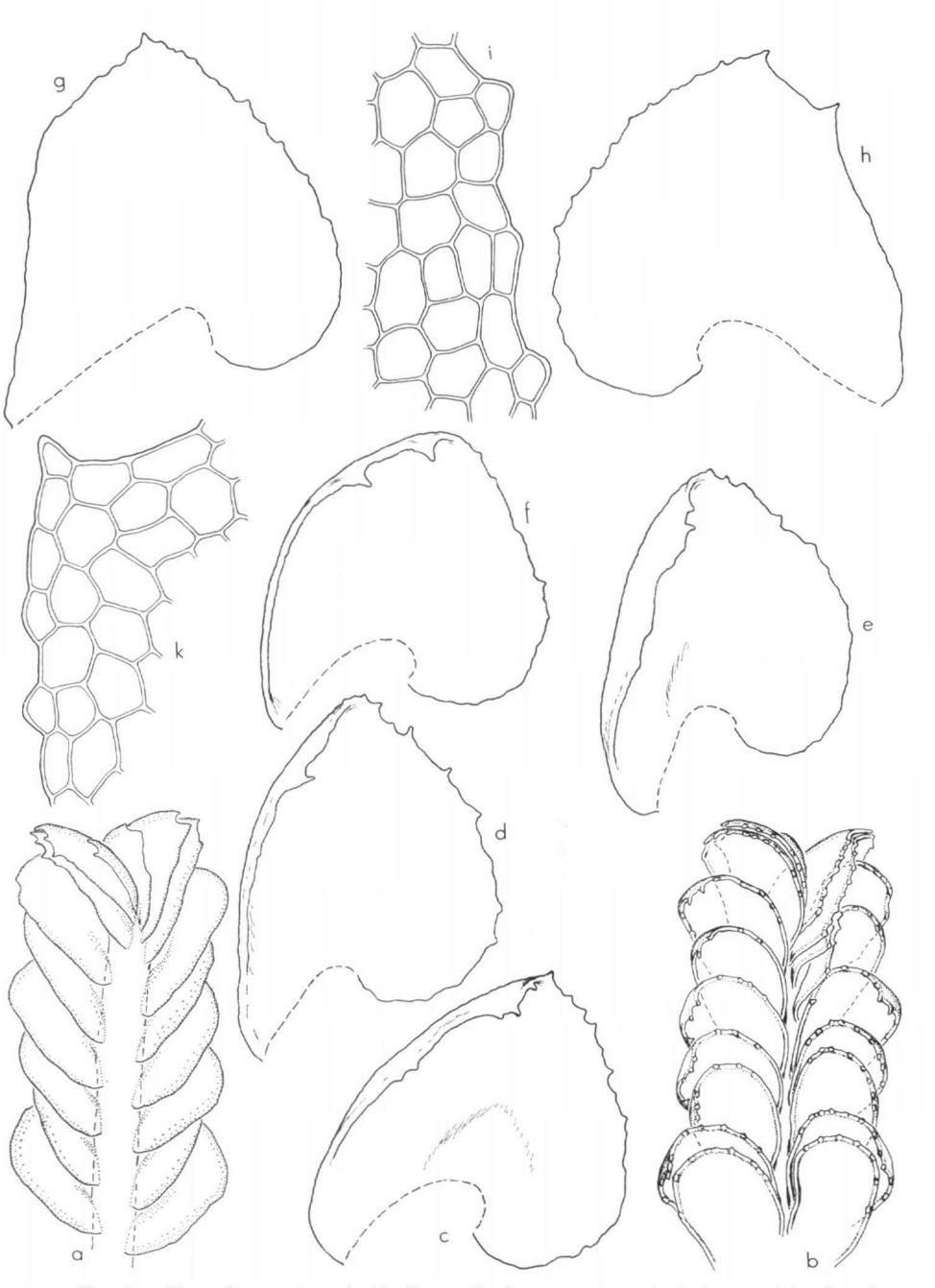

FIG. 1. *Haesselia roraimensis* Grolle et Gradst.: a. shoot (apical sector) in dorsal view, 12×. b. shoot (apical sector) in ventral view, 12×. c–f. leaves, 21×. g–h. leaves, flattened, 21×. i. cell pattern at ventral margin of leaf, 100×. k. cell pattern at apical margin of leaf, 100×. – All from *Gradstein 5100* (Type).

stein 5280, 5296, 5435 (JE, U).

Dioicous, glossy brownish, in the herbarium becoming light-brown, loosely caespitose, *Plagiochila-like*. Shoots 2–3 cm long, 2.5–3.0 cm wide, ascending, apparently with limited growth, often with slightly decurved apex. Branching gyrothecal, sparse and irregular, always lateral, branches soon similar to the primary shoot, athecal branching lacking. Stolons and flagella lacking.

Stems thick, 500–600 μm in diameter, cartilaginously tenaceous, light-brown to slightly reddish light-brown, in vegetative shoot sectors dorsally with a strip of 2(4) cell rows free of leaf insertion. Cortical cells thin-walled, the dorsal cortical cells in optical view ± isodiametric, sometimes transversely elongate, (30)60(90) × (20–30)50(65) μm, the ventral cortical cells rectangular, 40–60 × 85–135 μm. Cross section of stem slightly applanate above, about 12 cells high, hyalodermis weakly marked, dorsally made up of one layer of thin-walled outer cells, ventrally 2–3 layers of thin-walled outer cells, the outer cells surrounding a medulla of hardly smaller but strongly thick-walled cells. Rhizoids in many plants lacking, when present usually sparse, mostly restricted to the lower, ventral part of gyrothecal branches, arising only from the cortex and mainly from the ventral merophytes, colourless, long, about 20 μm thick.

Leaves alternate, succubously inserted, the insertion line about half as long as leaf width, in the dorsal half straight and almost parallel to the stem axis, in the ventral half almost semicircularly curved; leaves neither on dorsal nor on ventral side decurrent, always densely imbricate, laterally spreading at an angle of 45°, the lamina in the dorsal half almost horizontal and slightly, evenly convex (in dorsal view), in the ventral half much more strongly convex, strongly ventrad, reaching far below stem, in the median basal third sheathing; leaf outline in situ rounded broadly triangular (about as long as wide), the dorsal margin and dorsal half of the leaf apex broadly ± decurved, the ventral margin and ventral half of the apex almost flat, when flattened (flattening often impossible without tearing) leaf outline rounded trapezioid, the apex obliquely truncate-retuse, bidentate, the two teeth 1–3 cells long and at their base 1–3 cells wide, sometimes the dorsal tooth ± obsolete, the dorsal margin almost straight, entire, rounded-angustate at base, the ventral margin in the upper 2/3 slightly curved, irregularly and short dentate, the teeth unicellular and mostly ± rounded broadly triangular, in the lowermost third vertical, very strongly ampliate, entire, the opposite ventral leaf bases approaching but not touching each other, forming a comb with a narrow longitudinal slit along the ventral side of the shoot. Leaf cells almost empty, penta- or hexagonal, in the upper middle of leaf (50)66(83) × 66–100 μm, near the base up to 150 μm long, with thin to slightly thickened walls (in the latter case the median wall sector thinner), trigones lacking. Cuticle smooth. Oil bodies not investigated.

Underleaves lacking, near shoot apex replaced by a single, pyriform, soon decaying slime papilla.

Androecia almost always terminal on leading shoots, only occasionally on a longer gyrothecal branch, sometimes becoming intercalary, the transition from vegetative shoot to androecium very gradual, firstly the leaf insertion extending to the middle line, then a lobule of variable shape developing, transition zone (antheridia not yet developed) ten or more leaf cycles long. Antheridial bracts in 4–12 pairs, almost transversely inserted, a little smaller and more densely crowded than vegetative leaves, strongly saccate with pouched dorsal base and a large lobule fused along its whole length with the slightly reduced free leaf lamina, the saccate bract bases imbricate, not leaving a dorsal strip free of leaf insertion. Antheridia restricted to the dorsal half of bracts, usually paired, without admixed paraphyses, stalk strong, straight,

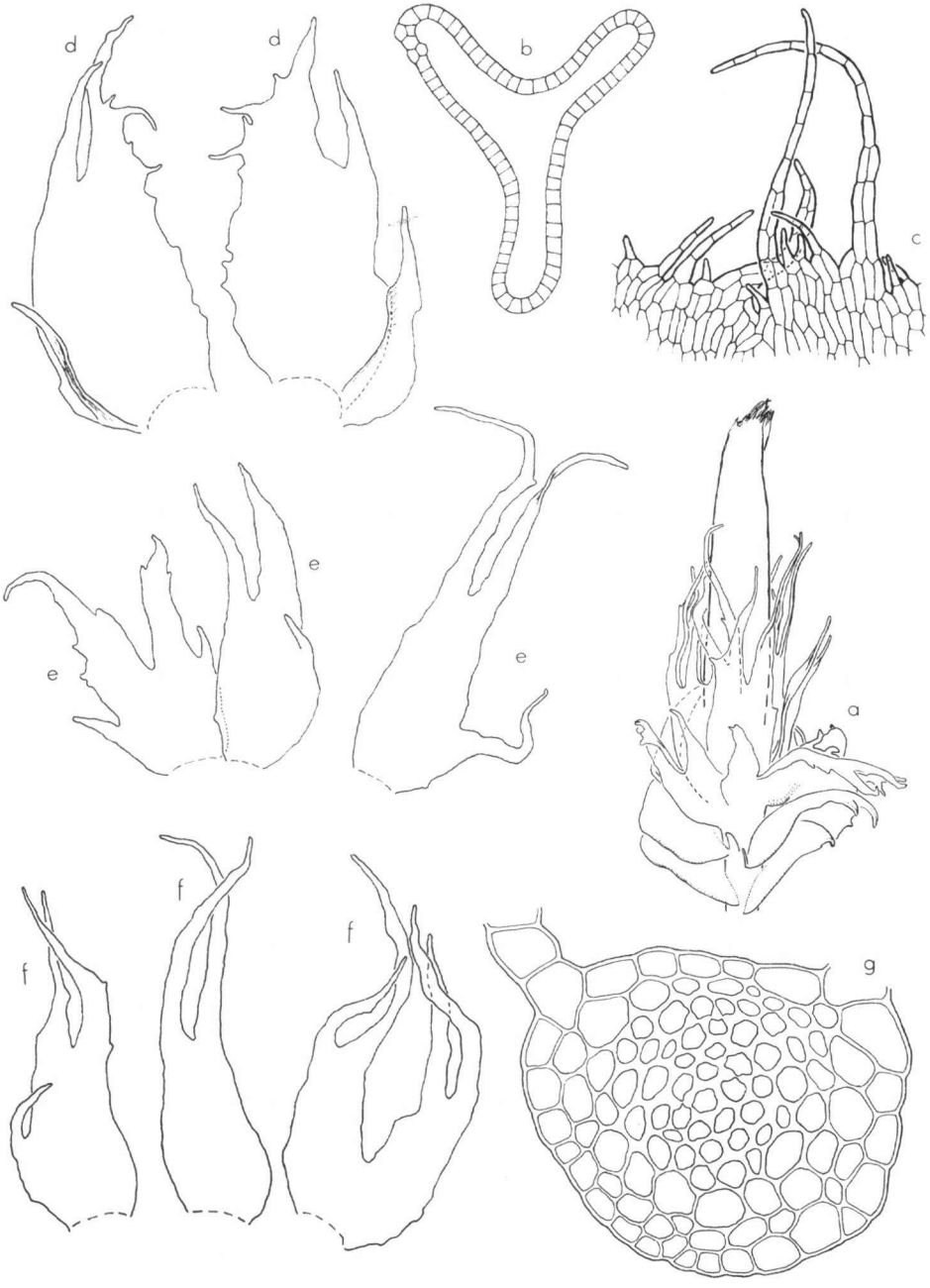

FIG. 2. *Haesselia roraimensis* Grolle et Gradst.: a. gynoecium with perianth, 12×. b. cross section of perianth in upper half, 42×. c. sector of perianth mouth, 52×. d. leaf pair below subinvolucre, 16×. e. subinvolucre, 16×. f. involucre, 16×. g. cross section of stem, 104×. – a from *Gradstein 5100*, b–g from *Gradstein 5280*.

a little shorter than the body, biseriate, each row made up of about twelve narrow disciform cells, body obovate, median part of the body wall distinctly tiered by three tiers of elongate cells. Male bracteoles lacking.

Gynoecia mostly at the tip of leading shoots, sometimes terminating ±long branches, usually without innovation, occasionally innovated on one side by a gyrothecal branch. Leaves increasing in size at least 3–4 leaf cycles below the perianth, becoming more transversely inserted, in the dorsal half more convex, in the median base more sheathing, the margins stronger dentate to thorny, the apex unequally bilobed up to 1/3 of leaf length, the dorsal base provided with a rather large lobule, underleaves (still) lacking. Subinvolucral and involucral bracts free, not fused, strongly different from ordinary leaves, strongly elongate, up to 1/2–3/4 of length divided into 2–4 unequal segments, the segments subulate, long attenuate, often ±twisted, almost entire. Underleaves present in the subinvolucral and involucral leaf cycles, free, often asymmetrically divided up to 1/2 of length into two segments, otherwise resembling bracts. Subinvolucre and involucre brush-like compressed in absence of fertilization, after formation of the perianth closely adhering to the latter. Perianth before fertilization a primordium surrounding the archegonia, after fertilization becoming very long cylindrical, long exserted from the involucre, the lower half with a two- to pluri-layered wall, tubular, the upper half with a single-layered wall, deeply trigonous, two folds lateral, one fold ventral, the dorsal face ±flat, the mouth truncate, densely and irregularly setulose, the setae formed by rather elongate cells, 1–12 cells long, at base 1–3 cells wide. Archegonia about eight.

Mature sporophyte unknown. Special organs of vegetative reproduction lacking.

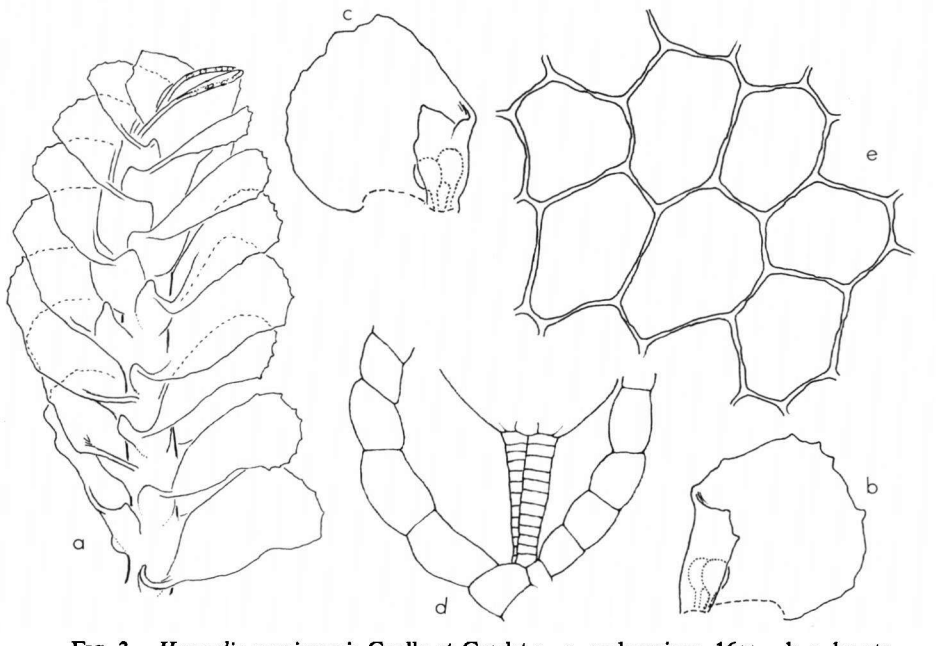

FIG. 3. *Haesselia roraimensis* Grolle et Gradst.: a. androecium, 16×. b–c. bracts, each with two antheridia, 21×. d. antheridial stalk with surroundings, 100×. e. cell pattern in upper middle of leaf, 200×. – a–d from *Gradstein 5066*, e from *Gradstein 5100*.

ECOLOGY: in periodically flooded, riverine forest and in dense, submontane "mossy" forest at the very humid, hilly foot of Mt. Roraima at the northern, Guyana-side of the mountain. Growing on rotten logs and dead wood, often in extensive mats, together with *Anomoclada mucosa*, *Leucobryum crispum*, various Hookeriaceae and Sematophyllaceae spp., *Micropterygium trachyphyllum* and *Riccardia* spp. Occasionally also on trunk bases and roots. Altitudinal range 550–1550 m, optimum between 700 and 1400 m.

DISCUSSION

The succubous leaf insertion, the very large, almost empty, thin-walled cells without trigones, the lack of underleaves on vegetative shoot sectors, the diffusely scattered rhizoids along the row of ventral merophyte, the free subinvolucral and involucral leaves deeply divided into 2–4 long, subulate laciniae, the presence of free subinvolucral and involucral underleaves similar to the associated leaves, the long cylindrical perianth with hypogonianth trigonous upper half, and the androecia with pouched bracts and with antheridial walls formed by distinctly tiered, elongate cells, justify placement of *Haesselia* in the Cephaloziaceae.

At present 14–15 genera are recognised in this family, which is subdivided into six subfamilies (Schuster 1979). Among the genera of Cephaloziaceae, *Fuscocephaloziopsis* Fulf. (Fulford 1968, Plates 93–94) and *Trabacellula* Fulf. (Fulford 1968, Plate 92; Schuster 1984, Fig. 67) show closest affinities to *Haesselia*. All three are dioicous, neotropical plants with ± brownish pigmentation, convex leaves, large almost empty thin-walled leaf cells without trigones, ampliate ventral leaf bases, a strip free of leaf insertion on the dorsal side of the stem of vegetative shoots, androecia predominantly on leading shoots, no underleaves, no athecal branching and no stolons. However, both *Fuscocephaloziopsis* (=*Cephalozia* subg. *Macrocephalozia* Schust., see Schuster 1974: 697–699) and *Trabacellula* differ considerably from *Haesselia*. The differences are listed in Table 1.

Within the Cephaloziaceae, both *Haesselia* and *Trabacellula* have several specialized features such as the ascending growth, the ventrad plagiochiloid leaf orientation, the dentate ventral leaf margin, the strongly ampliate, vertical ventral leaf bases associated with comb formation along the ventral side of the shoot and the ±multilayered lower portion of the perianth in *Haesselia*, and the numerous thickening bands on the cell surface, the undivided leaf apex, the semicircular appendage at the ventral leaf base and the female involucre, which is loosely patent in the absence of fertilization in *Trabacellula*. *Fuscocephaloziopsis* is much less specialized, yet approaches *Haesselia* and *Trabacellula* in the slightly convex leaves, the shallow leaf sinus, the somewhat ampliate ventral leaf base, etc.

The above interpretation of relationships leads to assigning *Fuscocephaloziopsis* as an unspecialized member to the subfamily Trabacelluloideae (Fulf.) Schust. of Cephaloziaceae, together with the more derived *Haesselia* and *Trabacellula*. The joining of *Fuscocephaloziopsis* and *Trabacellula* in a separate family Trabacellulaceae by Fulford (1968) is apparently based on a similar view. On the other hand, we recognize the existence of a close relationship between *Fuscocephaloziopsis* and *Cephalozia*

TABLE I. A comparison of *Fuscocephaloziopsis*, *Trabacellula* and *Haesselia* (Cephaloziaceae subfam. Trabacelluloideae).

	Fuscocephaloziopsis	*Trabacellula*	*Haesselia*
Plants	creeping, 1.0–1.5 mm wide	creeping, 0.8–1.0 mm wide	ascending, 2.5–3.0 mm wide
Branching	ventral-intercalary	ventral-intercalary	lateral-intercalary
Stems	fragile, ca. 0.25 mm wide, hyaloderm distinct, 1-layered	fragile, ca. 0.20 mm wide, hyaloderm distinct, 1-layered	rigid, 0.5–0.6 mm wide, hyaloderm indistinct, 1–3-layered
Leaves	widely spreading (60–80°) surface± horizontal, insertion sublongitudinal, margins entire or crenulate, dorsal base±decurrent, ventral bases weakly ampliate, widely separated	widely spreading (80°), surface±horizontal, insterion sublongitu-dinal, margins entire, dorsal base not decurrent ventral bases ampliate-auriculate, widely sparated	obliquely spreading (45°), surface ventrad, plagiochiloid, insertion oblique, curved, dorsal margin entire, ventral margin dentate, dorsal base not decurrent ventral bases strongly ampliate, contiguous, forming a high comb
Leaf cells	without thickening bands	with transverse thickening bands	without thickening bands
Underleaves	lacking	lacking, near shoot apex replaced by 2 slime papillae	lacking, near shoot apex replaced by 1 slime papilla
Ventral merophyte	2 cortex cells wide	2–3 cortex cells wide	1 cortex cell wide (wider in areas with rhizoid formation)
Gynoecium	on short ventral branches, involucre "brush-like" in absence of fertilization, perianth 1–2-layered below	on short ventral branches, involucre loosely patent in absence of fertilization, perianth 1–2-layered below	on main stem or on long lateral branches, involucre "brush-like" in absence of fertilization, perianth 2–plurilayered below

(Dum.) Dum., noted earlier by Schuster (1974) who treated *Fuscocephaloziopsis* as a mere subgenus of the latter (as *Cephalozia* subg. *Macrocephalozia* Schust.). Indeed, this close relationship precludes the separation of the two taxa at family rank, as advocated by Fulford. The convex leaves of *Fuscocephaloziopsis*, however, are alien in *Cephalozia* as well as in all other genera of Cephalozioideae listed in Schuster (1979).

Haesselia may be added to the list of ca. 40 genera of Jungermanniales endemic to tropical America (Schuster 1984). Three of them are endemic to the Guayana Highlands: *Odontoseries* Fulf. (Lepidoziaceae), *Trabacellula* and *Haesselia*. Each of these three genera has been collected only in the eastern portion of the Highlands, on the tepuis surrounding the Gran Sabana, which seems to be the area where the most significant endemic taxa of the Guayana bryoflora occur (Robinson 1986). Whether *Haesselia* and the other endemic bryophytes of the eastern tepuis are indeed restricted to this area remains open to question, as the Guayana bryoflora is still very poorly collected. Most of the endemics are known from one or two localities only and have usually been gathered by non-specialists. Further bryological exploration of the Guayana Highlands is needed and may throw more light on the actual distribution of the

bryophytes of this phytogeographically interesting area.

SUMMARY: *Haesselia roraimensis* gen. et spec. nov. (Cephaloziaceae) from the foot of Mt. Roraima (Guyana) is described and figured. The new genus has been assigned to the subfamily Trabacelluloideae together with *Fuscocephaloziopsis* Fulf. and *Trabacellula* Fulf., two other neotropical genera of Cephaloziaceae with convex leaves.

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