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ALLENIELLA AEGAEA BLOCKEEL & HUGONNOT (NECKERACEAE), A NEW MOSS SPECIES FROM THE AEGEAN ISLANDS OF GREECE

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Abstract: A new moss species, *Alleniella aegaea* (Neckeraceae) is described and illustrated from the Greek islands of Crete, Samos and Evvia based on morphological and molecular evidence. According to phylogenetic analysis of nuclear ITS and plastid *trnS-F* sequences it is sister to *A. complanata*, which it also morphologically resembles, but it differs from that species e.g. in its distinctly flattened habit, lack of caducous branchlets, more rounded leaf apices, and shorter median laminal cells. *Alleniella aegaea* is dioicous and the sporophytes remain unknown.

Keywords: *Alleniella aegaea*, mosses, Neckeraceae, new species, phylogeny, taxonomy

INTRODUCTION

Traditionally the pleurocarpous moss genus *Neckera* Hedw. s.l. (Neckeraceae) comprised dozens of species sharing some distinctive characters, such as being relatively large plants with glossy, often transversely undulate and asymmetric leaves with the costa short or even absent. The distribution of the broadly defined genus covered all continents except Antarctica. In the 21st century however *Neckera* s.l. has been shown to be paraphyletic and its species have been transferred into several newly described genera and certain existing genera, especially *Forsstroemia* Lindb., which has 19 species (Olsson *et al.* 2011; Enroth *et al.* 2019, 2022; Fedosov and Ignatov 2019). In its current circumscription *Neckera* s.str. contains c. 10

species (Enroth *et al.* 2022). The main segregates are *Alleniella* S. Olsson, Enroth & D. Quandt with 15 species, *Exsertotheca* S. Olsson, Enroth & D. Quandt with 3 species, and the resurrected unispecific *Metaneckera* Steere (Olsson *et al.* 2011; Draper *et al.* 2011; Enroth *et al.* 2022). The morphological differences between *Neckera* s.str., *Alleniella*, *Exsertotheca* and *Forsstroemia* are not clear-cut but there are some. Species of *Forsstroemia* have a distinct single costa, while those in the other three genera lack a costa or have a very short one, sometimes bifurcate. Twelve out of the 15 species of *Alleniella* have paraphyllia, which are absent or rare in the other three genera. *Metaneckera menziesii* (Drumm.) Steere is distinct in the combination of a single costa reaching to mid-leaf, strongly incrassate and porose laminal cell walls, and abundant paraphyllia.

The geographic distributions of the five genera mentioned above are partly different. *Forsstroemia* has a wide distribution, but the species are heavily concentrated in Asia, mainly in the non-tropical zone. *Exsertotheca* is predominantly a Western Palaearctic genus, distributed from Macaronesia and North Africa through most of Europe to Turkey and the Caucasus region. *Neckera* is distributed in the temperate Northern Hemisphere, while species of *Alleniella* occur mainly in the tropics (but not in tropical Asia) and the Southern Hemisphere; only the first-diverging lineages *A. complanata* (Hedw.) S. Olsson, Enroth & D. Quandt and *A. besseri* (Lobarz.) S. Olsson, Enroth & D. Quandt are from the temperate Northern Hemisphere (Enroth *et al.* 2022). *Metaneckera menziesii* has a strongly disjunct distribution of a Mediterranean character. It is known from north-western and western North America and southern and Central Europe, reaching Turkey and the Caucasus region to the east.

In this paper we describe a third species of *Alleniella* in the temperate Northern Hemisphere. Material of the new species has been known for 50 years in the Aegean region of Greece, but with a confused history. It was first collected by the late Prof. Ruprecht Düll on 22 March 1972 near Aghios Ioannis / Nea Roumata in western Crete (Düll and Düll-Hermanns 1973). Prof. Düll identified his collection as *Neckera besseri* (Lobarz.) Trevis. (*Alleniella besseri*). The original packet in his herbarium indicates that the locality was 3 km below Ag. Ioannis, but it remains unclear which Ag. Ioannis is meant. In a later paper, Düll treated *Neckera besseri* as a synonym of *Homalia webbiana* (Mont.) Mitt. (*Pseudomalia webbiana* (Mont.)

Enroth), and listed the record from Crete under the name *Neckera webbiana* (Mont.) Düll (Düll 1979). In his more recent publication (Düll 2014), he reverted to the treatment of *Neckera besseri* and *Homalia webbiana* as separate species, but transferred the Cretan record to *H. webbiana*. In the same publication he also referred several collections from the Aegean island of Samos to *H. webbiana*. The earliest of these was by H. van Melick, and according to a specimen in Düll's herbarium it was collected during a field trip with Prof. Düll in the 'Valley of Nightingale' north of Manolates on 5 June 2006.

During a visit to Samos in 2012, TLB had independently collected specimens of a distinctive species of Neckeraceae which he could not identify with confidence. Though similar to *Alleniella complanata*, it differed in having lingulate leaves with a very broad, often shortly apiculate apex. Düll's (2014) publication prompted TLB to compare his specimens with Macaronesian material of *Homalia webbiana*, and he was also able to examine two of the original specimens cited by Düll from Crete and Samos. It was clear that TLB's material was identical to the specimens from Düll's herbarium, but that they differed significantly from *H. webbiana*, which is distinct in its leaves being strongly narrowed towards the base. He sent some of the material from Samos to JE, but in the absence of molecular data it was uncertain whether these plants belonged to an extreme form of *A. complanata* or to a separate species. In 2017 TLB found morphologically similar plants in the Dimosari gorge in the southern part of the island of Evvia. They appeared distinct from a population of *A. complanata* found growing in a different part of the same gorge.

In April 2022, VH visited Crete and found abundant material of the unusual '*Neckera*' in the Boriano Gorge. He forwarded material to JE and MSI, and contacted TLB about the previous records. MSI and OIK were able to obtain nuclear and plastid sequences using VH's material from Crete and TLB's earlier specimens from Samos and Evvia. On the basis of both morphological and molecular data, we were able to confirm that the Aegean plants represented a distinct species sister to *Alleniella complanata*. A search of the bryological literature for Europe, Macaronesia and the wider Mediterranean region did not reveal any existing taxa which matched the Aegean plant in having smooth, lingulate leaves with a broad apex, often bearing a small apiculus (*Figure 3c*). In their treatise on the bryophytes of South-west Asia, Kürschner and Frey

(2020) cite the non-European *Homalia woronowii* Thér. as occurring in Turkey. We have seen type material of this species, and morphologically it matches *Pseudomalia webbiana*, as previously indicated by He (1997). In North Africa, Ros *et al.* (1999) do not cite any names or synonyms within *Neckera* s.l. and *Homalia* Brid. other than those known from Europe.

Only a few species of *Neckera* s.l. have been described from the Mediterranean region. *Neckera mediterranea* H. Philib. and *N. turgida* Jur. both have a long single costa and undulate leaves and are generally regarded as synonymous with *Metaneckera menziesii. Neckera gennati* Rota has a long single costa and is presumably also a synonym of *M. menziesii. Neckera cephalonica* Jur., described from the Greek island of Kefalonia, differs markedly from the Aegean moss in its undulate leaves with finely acuminate, dentate or ciliate apices.

Within Europe, several names exist that are widely regarded as synonyms of *Alleniella besseri* or *A. complanata*, the two species that most closely resemble the Aegean plant morphologically. *Neckera sendtneriana* Schimp., *N. leiophylla* W. Gümbel and *Homalia pourretiana* Roum. are all described as having rounded ('rotund-obtuse' or 'subrotund-ovate') leaves, and indeed the protologues of *N. sendtneriana* and *N. leiophylla* both refer to material collected by Sendtner at 'Draga d'Orlich' near Tergestum (Trieste). The third author JE has traced and examined nine voucher specimens originally named *N. sendtneriana* in S.O. Lindberg's herbarium in Helsinki (H-SOL), and all of them were annotated as *N. besseri* by S. He in 1989. We have not seen type material of these names but we find no reason to doubt their synonymy with *Alleniella besseri. Neckera rotundifolia* Hartm. (isotype H-SOL 1463009!, examined by JE) from Scandinavia is also described as having rounded, obtuse leaves, and Nyholm (1954–1969) considered it to be a form of *A. besseri* from dry, strongly shaded habitats. *Neckera rabenhorstii* Warnst. from Saxony, according to the protologue, has asymmetric, long ovate, shortly pointed leaves; it is treated as a variety of *N. complanata* by Podpěra (1954). Sotiaux *et al.* (2009) described *Leptodon corsicus* Enroth, Sotiaux, D. Quandt & Vanderpoorten from Corsica and noted its morphological resemblance to *A. besseri.* It is a much smaller plant than *A. aegaea*, with the stem leaves up to only 0.9 mm long and the median laminal cells up to 15 μm long. It was also clearly nested within *Leptodon* in the phylogenetic analysis based on molecular data.

There are rather many infraspecific taxa described in Europe for *Alleniella complanata* and *A. besseri.* Most of them were described from Central and Northern Europe and, according to the protologues of those that we have traced, they each differ in some respect from the Aegean plants. In conclusion, we have not found any taxa described in the literature for Europe and the wider Mediterranean region that match the collections from Crete, Samos and Evvia. In this paper, therefore, we describe the Aegean plant as a new species.

MATERIAL AND METHODS

Morphological characters were observed using stereo and compound light microscopes. Slides were mounted with tap water.

We sequenced two regions: the nuclear internal transcribed spacer region, ITS (including ITS1, gene 5.8S RNA and ITS2), and the plastid region *trn*S–F (the plastid cluster *trn*S–*rps*4–*trn*T*trn*L–*trn*F, in-cluding four tRNAs (*trn*S (partial), *trn*T, *trn*L, *trn*F (partial)), a fast evolving gene (*rps*4), four spacers separating the coding regions, as well as one group I intron). These markers were sequenced for plants of the putative new species, as they have proved to be informative in previous studies of the Neckeraceae (Olsson *et al.* 2009a, b, 2011). The molecular analysis followed the laboratory protocol for DNA extraction, amplification and sequencing described in, e.g., Gardiner *et al.* (2005) for ITS, and Olsson *et al.* (2009a) for *trn*S–F. Preliminary results revealed the close relationship of the putative new species with *Alleniella complanata.* Therefore, datasets were built using sequences most similar to this species in a BLAST search (https://blast.ncbi.nlm.nih.gov/Blast.cgi in November 2022), but excluding accessions identified only to generic level. One additional specimen of *A. complanata* was added subsequently: it was considered of special relevance because it was collected from the same locality as our putative new species on the island of Evvia. Sequences were aligned using MAFFT v. 7.505 (2022/Apr/10) with the E–INS–i alignment strategy with otherwise default options, and afterwards checked for obvious inconsistencies manually. Bayesian analysis was performed separately for the nuclear and plastid *trn*S–F datasets, as the Genbank data only partly belonged to the same species and specimens. The analyses were performed in MrBayes

3.2.6 (Ronquist *et al.* 2012) with the GRT+G model, following the Akaike information criterion by MegaX (Kumar *et al.* 2018), and run with 5,000,000 generations (reaching all PSRF equal to 1.000, and ESS > 1000). Partitioning followed the initially suggested partitions, nruns=4, nchain=6, temp=0.02. Maximum parsimony analyses were performed in Nona (Goloboff 1994) in the Winclada shell (Nixon 1999), with bootstrap calculations for 1000 replications (using the following parameters: N search reps 100, starting trees per rep 100, max trees 100, 'do max').

Vouchers of newly sequenced specimens and GenBank accession numbers of all used sequences are listed in *Table 1*. Full details of the sequenced specimens of *Alleniella aegaea*, identified by voucher number in the Table, are cited in the description of the new species. Details of the newly sequenced specimen of *A. complanata* are: Greece, Evvia, upper part of the Dimosari Gorge, 38°04'34" N, 24°27'55" E, ca 665 m, at the base of an ancient *Platanus* tree, *T.L. Blockeel* 46/121, 26 March 2017 (Priv. Herb. T. Blockeel, MHA, MW).

Table 1. Newly sequenced *Alleniella* specimens and their GenBank accession numbers.

Species	Locality	Voucher number	Isolate	ITS	trnS-F
A. aegaea	Greece, Crete	Hugonnot 22/425	OK3421	OQ275098	OQ275267
A. aegaea	Greece, Evvia	Blockeel 46/065	OK3435	OQ275099	OQ275268
A. aegaea	Greece, Samos	Blockeel 41/108	OK3436	OQ275100	OQ275269
A. aegaea	Greece, Samos	Blockeel 41/218	OK3437	OQ275101	OQ275270
A. complanata	Greece, Evvia	Blockeel 46/121	OK3438	OQ275102	OQ275271

RESULTS

The phylogenetic trees (*Figures 1, 2*), both nuclear and plastid based, were rooted on *Taxiphyllum aomoriense* (Besch.) Z.Iwats., a species found in a clade sister to a large clade with numerous subclades which include species of Neckeraceae (Enroth *et al.* 2019), and also *Pseudomalia webbiana*, a species superficially similar to species of *Alleniella*. The earliest divergent lineages in the ITS tree (*Figure 1*) comprise the genera *Enrothia* Ignatov & Fedosov, *Heterocladiella*

Ignatov & Fedosov, *Indoneckera* Enroth, *Pseudomalia* Enroth and *Thamnobryum* Nieuwl. They are followed by a highly supported clade (PP=1, BS=99), composed mostly of mosses previously classified in the genus *Neckera* s.l. The species of *Neckera* s.str. plus *Metaneckera* form a monophyletic group, constituting one of two subclades of this clade, albeit with low support. The second subclade of the Neckera s.l. clade is rather highly supported (PP=1, BS=99), and comprises a tritomy of an unsupported *Forsstroemia*-clade, a monospecific *Alleniella besseri*-clade (PP=1, BS=96), and a large clade that is also trichotomous: it includes *Cryptoleptodon* Renauld & Cardot, an *Exsertotheca*-clade (PP=1, BS<66) and an unsupported *Alleniella*-clade, which includes all species of this genus except *A. besseri.* The *Alleniella*-clade is subdivided into two subclades, the first composed of exotic *Alleniella* species (from Africa, Australia and New Zealand, South America and Mexico): *A. urnigera* (Müll. Hal.) S. Olsson, Enroth & D. Quandt, *A. hymenodonta* (Müll. Hal.) S. Olsson, Enroth & D. Quandt, *A. submacrocarpa* (Dixon) S. Olsson, Enroth & D. Quandt, *A. chilensis* (Schimp. ex Mont.) S. Olsson, Enroth & D. Quandt, *A. ehrenbergii* (Müll. Hal.) Enroth, *A. remota* (Bruch & Schimp. ex Müll. Hal.) S. Olsson, Enroth & D. Quandt, *A. platyantha* (Müll. Hal.) Enroth, *A. brownii* (Dixon) S. Olsson, Enroth & D. Quandt, and *A. scabridens* (Müll. Hal.) S. Olsson, Enroth & D. Quandt. The second subclade of the *Alleniella*-clade consists of unispecific clades of: (1) seven accessions of *A. complanata* (PP=1, BS=99), and (2) four accessions of the Aegean plants, *A. aegaea* (PP=1, BS=99).

The plastid *trnS-F* phylogenetic tree (*Figure 2*) has divergent lineages rather similar to the ITS tree: the earliest diverging genera are *Pseudomalia*, *Heterocladiella*, *Thamnobryum* and *Enrothia.* As in the ITS tree, they are followed by a highly supported clade of mostly 'former *Neckera*' species, where *Neckera* s.str. is resolved as monophyletic and forms one of two subclades. The second subclade includes (1) the *Forsstroemia*-clade (PP=1, BS=81), (2) the *Exsertotheca*-clade (PP=1, BS=99), and (3) the *Alleniella*-clade (PP=0,97, BS=96). The latter includes a poorly supported clade of four species (*A. besseri, A. ehrenbergii, A. remota, A. platyantha*), and a clade occupied by the *A. complanata*-clade and the clade of the putative new species *A. aegaea*, respectively. The latter has high support (PP=1, BS=97), unlike the *A. complanata* clade, which is unsupported.

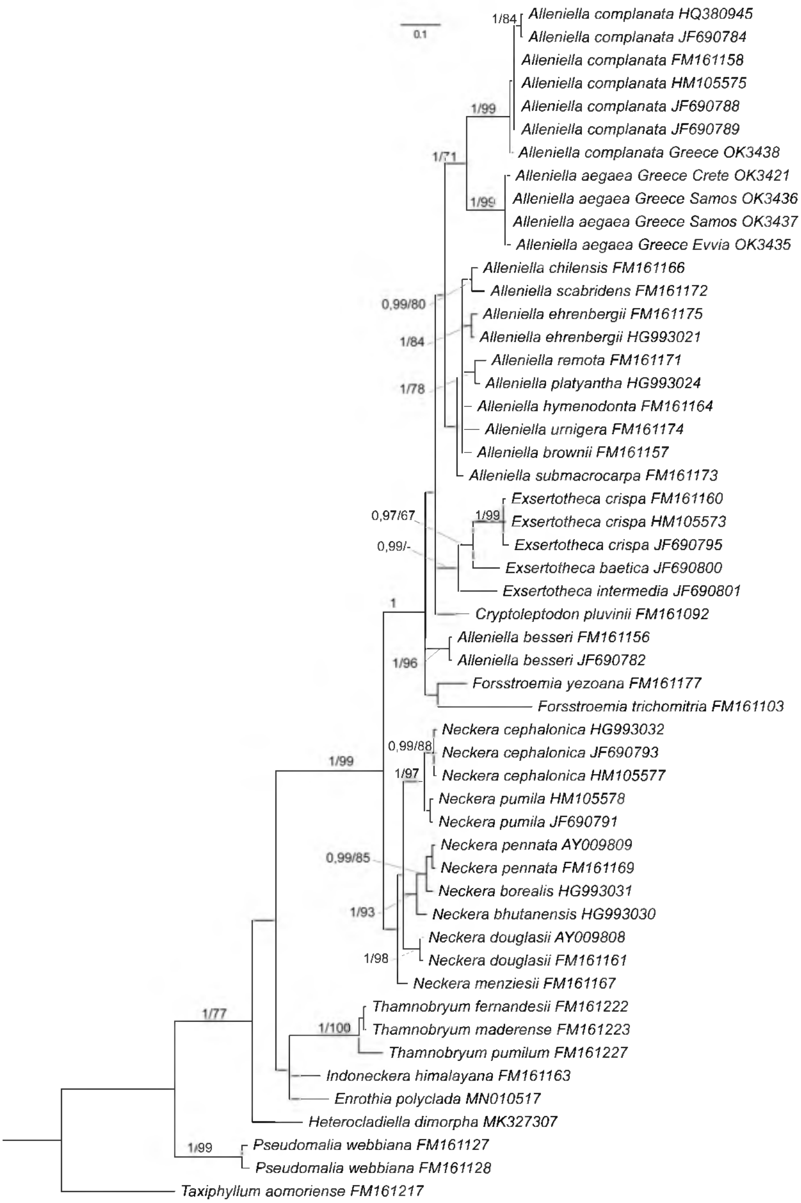

Figure 1. Bayesian phylogenetic tree based on nuclear ITS sequences, supporting the independence of *Alleniella aegaea* as a species, and its sister position to *A. complanata*. The posterior probabilities > 0.95 from Bayesian inference, and the Bootstrap support > 65 from the parsimony analysis are shown on the branches (first and second values respectively).

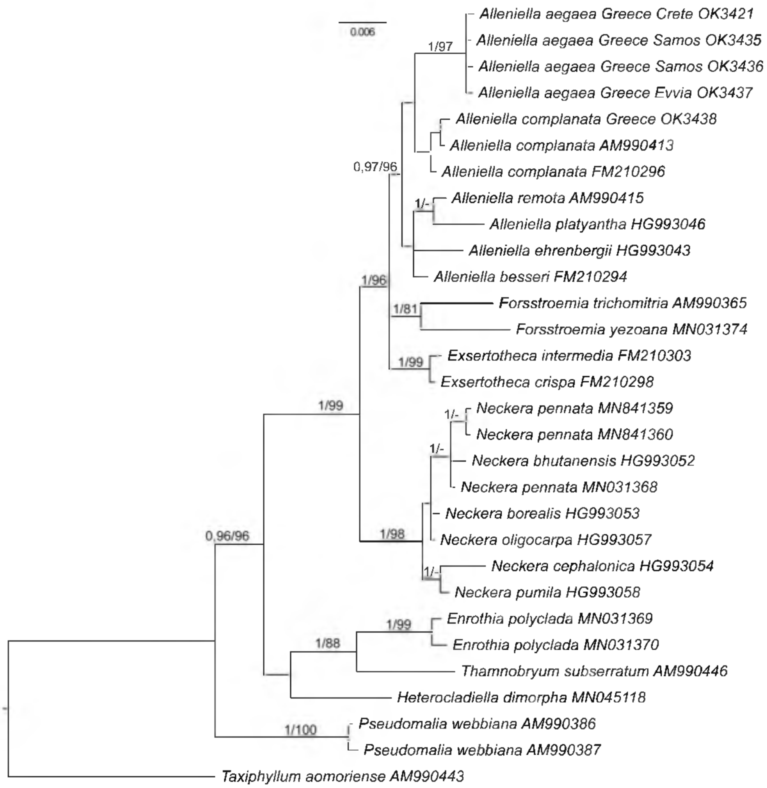

Figure 2. Bayesian phylogenetic tree based on plastid *trn*S-F sequences, supporting the independence of *Alleniella aegaea* as a species, and its sister position to *A. complanata*. The posterior probabilities > 0.95 from Bayesian inference, and the Bootstrap support > 65 from the parsimony analysis are shown on the branches (first and second values respectively).

Taxonomy

Alleniella aegaea Blockeel & Hugonnot, sp. nov. (*Figures 3–5*)
TYPE: GREECE. Crete, Chania region, Mousoures Municipality, Boriano Gorge, ca 290 m, 35°24’24” N, 23°54’42” E, vertical rock face, forming large fans, *V. Hugonnot* 22/425, 26 April 2022 (holotype: PC; isotypes: CLF, H, MHA, MW).

PARATYPES: GREECE. Crete. Chania: Hauptbach der Schlucht 3 km unterhalb Ag. Joannis gen Nea Roumata, ca 390 m, Kalk, *R. Düll*, 22 March 1972 (Priv. Herb. R. Düll); Evvia: lower part of Dimosari Gorge, 38°05’46” N, 24°28’23” E, ca 420 m, on moist shaded rock, *T.L.*

Blockeel 46/065, 24 March 2017 (Priv. Herb. T. Blockeel, Priv. Herb. V. Hugonnot, MHA, MW); Samos: Valley of Nightingale N of Manolates, steep shaded basic wall, *H. van Melick* 211144, 5 June 2006 (Priv. Herb. R. Düll); wooded stream along forest road ca 2 km south of Drakei, approx. 37°44'35" N, 26°36'54" E and 37°44'41" N, 26°37'00" E, ca 500–530 m and 600–625 m, on moist rock faces, *T.L. Blockeel* 41/108 (Priv. Herb. T. Blockeel, Priv. Herb. V. Hugonnot, MHA, MW) & 41/116 (Priv. Herb. T. Blockeel, H), 3 March 2012; stream gully, a little north of Kastania, approx. 37°45'44" N, 26°40'55" E, ca 230 m, on side of massive shaded boulder, *T.L. Blockeel* 41/218, 6 March 2012 (Priv. Herb. T. Blockeel, Priv. Herb. V. Hugonnot).

Vivid green, crisp, moderately shiny, medium-sized plants, fronds to 10 cm long x 3 cm wide, decaying in older parts, leafy stems to 3.8 mm wide, forming extended mats on vertical rock surfaces, and often forming brackets, distal parts of fronds appearing flattened because of the complanate form of both branches and leaves. Primary stems profusely branched, prostrate, stolon-like, bearing several bundles of yellow-brown, smooth rhizoids and minute scale-like leaves, producing secondary stems irregularly (bi)pinnately branched. Apex of shoots not flagelliform; caducous, flagelliform branchlets absent. Stem rigid, with well-developed outer cortex (3–5 strata of yellow stereids), inner parenchymatous firm-walled cells, and no central strand. Pseudoparaphyllia few (rarely found on stem at short distance from branch base or branch primordium) linear to long triangular, pluriseriate at base, to 250 µm long. Axillary hairs few, to 100 x 5 µm, with 2–4 brown, short basal cells, and 1 or 2 hyaline longer apical cells. Stem leaves more or less decurrent, widely diverging from stem (60 to 80 deg.), occasionally very minutely plicate in 1/3 to proximal half, otherwise smooth (or rarely with weak transverse undulations), very slightly falciform toward substrate or not, 1.5–1.9 x 0.53–0.74 mm, narrowly lingulate or lingulate, weakly asymmetric, straight to slightly laterally arched, with one margin largely inflexed to narrowly recurved, sometimes widened in apical part; apex largely rounded, usually distinctly apiculate, occasionally indistinctly so; margin distinctly but finely denticulate in upper 1/3 (to 1/2), with a more or less regular alternance of longer and shorter teeth; teeth made of prominent cells with cell walls antrorsely projecting. Costa very short (to 1/3 leaf length) to absent, or rarely reaching mid-leaf, often double.

Median cells oblong-rhombic, 22–40(–45) x 6–10 µm with thin to moderately thickened walls (0.9–2 µm); upper cells mostly oval to shortly rhombic to nearly isodiametric, 10–21 x 8–10 µm, thin-walled or moderately incrassate; basal cells rectangular, 25–50 x 8–10 µm; cells at leaf insertion porose and often lightly yellow-coloured; alar cells shortly rectangular to quadrate, in small indistinct quadrate group of ca 25 cells or less. Branch leaves less narrowly lingulate, 1.1–1.2 x 0.52–0.6 mm, more acute than stem leaves. Dioicous, male and female individuals observed, but no fertilized female gametangia or sporophytes seen. Perigonial leaves ovate, shortly acuminate. Pre-fertilization perichaetial leaves ovate with long acumen.

Etymology

The epithet *aegaea* refers to the Aegean Sea. All of the known localities of the new species are located on Aegean Islands.

DISCUSSION

Molecular analysis

The molecular phylogenetic trees (*Figures 1, 2*) are congruent with previous results (Enroth *et al.* 2019, 2022; Fedosov and Ignatov 2019; Ignatov *et al.* 2019; Olsson, 2009a, b, 2011) in the general tree topology (where the earlier divergent lineages include *Thamnobrum*, *Enrothia*, and *Pseudomalia*), and also in the separate position of *Alleniella* and *Exsertotheca* from *Neckera* s.str.

The monophyly of the genus *Alleniella* is not always apparent. The ITS analysis (*Figure 1*) resolves it in three subclades within the terminal clade that also includes *Exsertotheca*, *Forsstroemia* and *Cryptoleptodon*. *Alleniella complanata* and *A. aegaea* are well separated from a clade of *Alleniella* species from South America, Africa and Australasia.

The molecular distinction of *Alleniella aegaea* from *A. complanata* is very strong in the nuclear analysis. Statistical support for the separate status of *A. aegaea* in the plastid tree is also very high, while the lower support for *A. complanata* is partly explained by the less complete sequence data for this species in GenBank.

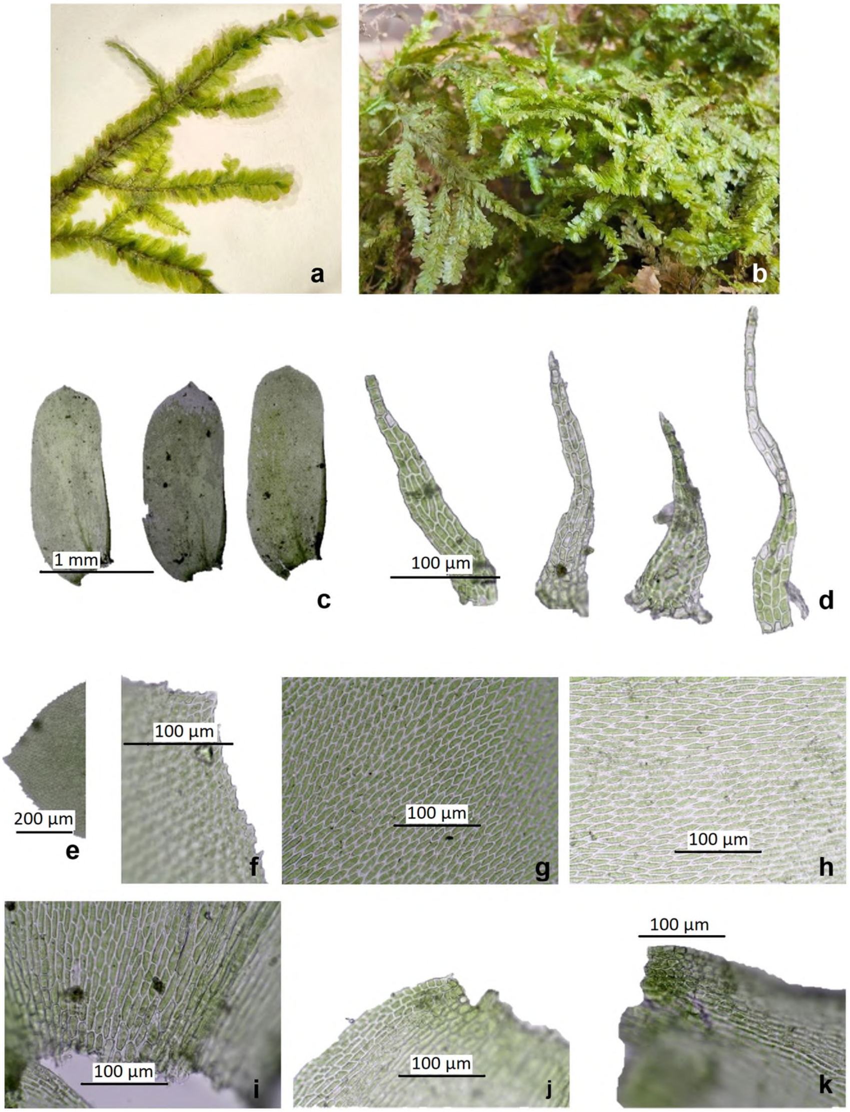

Figure 3. *Alleniella aegaea* Blockeel & Hugonnot: **a**: habit; **b**: colony; **c**: branch leaves; **d**: pseudoparaphyllia; **e**, **f**: leaf apex; **g**, **h**: mid-leaf areolation; **i**: leaf base; **j**, **k**: alar cells (from Crete, Greece, *Hugonnot* 22/425).

Morphology

Morphologically, *Alleniella aegaea* is an almost unmistakable species which is readily distinguished by its general appearance in the field and a set of gametophytic characters. It forms large colonies, mostly on rocks, of flattened shoots that tend to be arranged horizontally above one another, like many other Neckeraceae. The flat appearance of the leaves and branches, the widely spreading and contiguous leaves, and the absence of caducous branchlets give the plant a much more regular outline than in the well-known *A. complanata*, which is sister to *A. aegaea* (*Figures 1, 2*).

On casual examination *Alleniella aegaea* could nevertheless be confused with species of *Homalia* or *Pseudomalia webbiana.* This is partly because the margins of the shoots, consisting of juxtaposed, very broad leaf apices, appear regular in these taxa. Indistinct plications are sometimes visible on the leaf bases of *A. aegaea* (when dry), as in *Homalia* spp. and *P. webbiana*, and the apical parts of the leaves tend to be broad.

However, the two European species of *Homalia*, *H. trichomanoides* (Hedw.) Brid. and *H. lusitanica* Schimp. have a long costa which is constantly absent in *A. aegaea.* In addition, *H. trichomanoides* lacks pseudoparaphyllia which are few but present in *A. aegaea*, as shown in *Figure 4.* We use the term ‘pseudoparaphyllia’ here in its traditional sense, but the homology and terminology of foliose structures around branch primordia admit different interpretations, since such pseudoparaphyllia may have a more or less apparent phyllotaxis (Ignatov *et al.* 2021; Spirina *et al.* 2020). The subject requires further study.

The stem leaves of *Pseudomalia webbiana* are widely obovate, less than 1.4 mm long, and very finely denticulate, whereas the stem leaves of *A. aegaea* are more or less narrowly lingulate, more than 1.5 mm long and more strongly denticulate. The median laminal cells of *P. webbiana* are to 20 µm long and quite thick-walled, whereas in *A. aegaea* they reach 40(–45) µm long and have thinner walls.

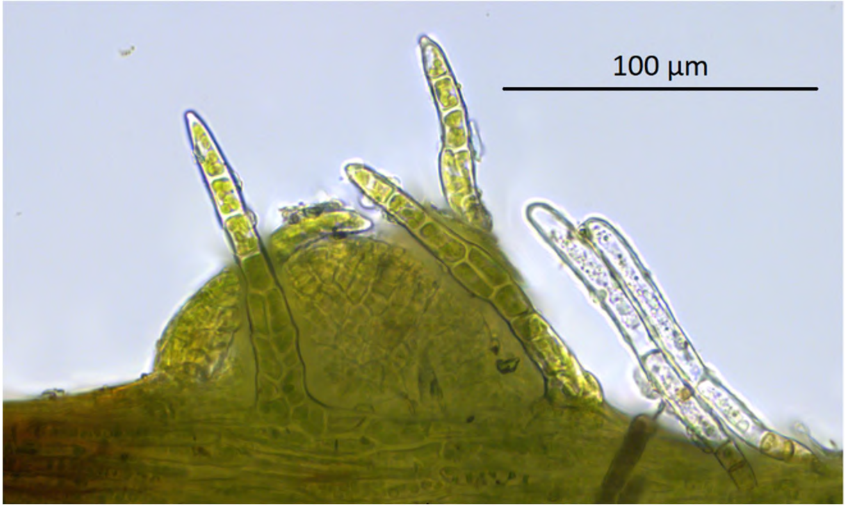

Figure 4. Pseudoparaphyllia of *Alleniella aegaea* Blockeel & Hugonnot (from Crete, Greece, *Hugonnot* 22/425).

Alleniella complanata bears some resemblance to *A. aegaea*, but there are many differences. The shoots of *A. complanata* have a rather different appearance from those of *A. aegaea*; they are glossy and pale green in colour; the leaves are oriented mostly at an angle of 40–60° from the axis, and are rather widely spaced along the branches (with gaps between them often visible); the apices are markedly decurved. The shoots of *A. aegaea* are less glossy, and pure green or slightly blue-green; the leaves on average spread more widely from the axis, typically at an angle of 60–80°, and are more closely spaced, with few gaps visible; the apices are plane or only weakly decurved. Overall the shoots of *A. aegaea* appear a little more robust, partly because of the flattened nature of the branches and the broader leaf apices. Delicate plicae can sometimes be observed in the lower part of the leaf in *A. aegaea* but we have not seen anything comparable in *A. complanata*. The length of the mid-leaf cells offers another important diagnostic character between the two species. In *A. complanata* they are mostly in the range 50–70 µm long, while in *A. aegaea* they are much shorter, 22–40(–45) µm long (*Figure 5*). This difference in cell length explains the differences in glossiness observed in the two species. Long cells give a glossier appearance than short cells, perhaps because there are fewer transverse cell walls that interfere with light reflection.

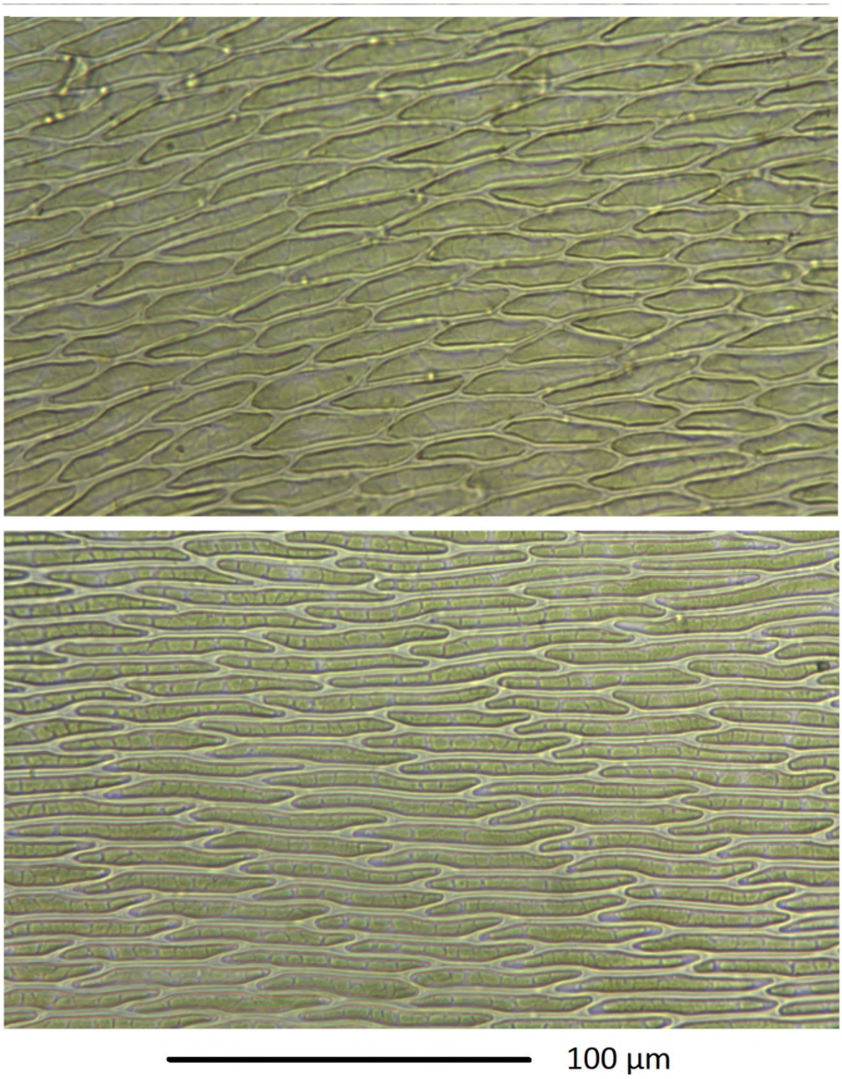

Figure 5. Mid-leaf cells of *Alleniella* species. Upper image: *A. aegaea* Blockeel & Hugonnot (from Samos, Greece, *Blockeel 41/218*); lower image: *A. complanata* (Hedw.) S. Olsson, Enroth & D. Quandt (from Derbyshire, England, *Blockeel* 51/315).

Alleniella besseri and *A. complanata* frequently produce caducous, flagelliform branchlets with reduced leaves. Such branchlets are unknown for *A. aegaea*. Additionally, the shoot apices of *A. besseri* and *A. complanata* tend to be flagelliform, a feature not so apparent in *A. aegaea.* In *A. complanata* the leaves of flagelliform branchlets are triangular-acuminate, whereas in (rare) sub-flagelliform branchlets of *A. aegaea* they are broadly pointed.

Alleniella besseri is a much smaller plant than *A. aegaea*, with leaves less than 0.6 mm long (always more than 1 mm long in *A. aegaea*), and not or indistinctly apiculate (distinctly apiculate in *A. aegaea*), and with shorter median laminal cells (less than 30 μm long vs. to 40(–45) μm in *A. aegaea*). The prominent leaf apex denticulation of *A. aegaea* differs clearly from the entire or very finely denticulate leaf apices of *A. besseri.*

Habitat

Alleniella aegaea is characteristic of deep gorges and stream gullies in a Mediterranean environment. Shelter is provided by the topography but also by tree cover. The presence of seasonal or semi-permanent streams helps to maintain relatively high humidity. All of the known collections are from mildly to markedly base-rich rock faces, often vertical or steeply inclined, on limestone and schist (*Figure 6*). The rocks are typically moist but not wet, and may become dry in the summer season. On Samos, relatively high humidity at one site was indicated by an abundance of *Lejeunea cavifolia* (Ehrh.) Lindb. on the rock faces; *Plasteurhynchium meridionale* (Schimp.) M. Fleisch., *Porella platyphylla* (L.) Pfeiff. and *Thamnobryum alopecurum* (Hedw.) Gangulee were present on the same rocks. *Lejeunea cavifolia* was also an associate at the locality on Evvia, and *Cirriphyllum crassinervium* (Taylor ex Wilson) Loeske & M. Fleisch. *and Homalia lusitanica* were also present, though not in close contact with *A. aegaea.* In the Boriano gorge in Crete accompanying species were *Plasteurhynchium meridionale, Homalothecium sericeum* (Hedw.) Schimp. (very scarce), *Radula complanata* (L.) Dumort. and a great abundance of *Lejeunea cavifolia.* The latter species has been observed growing epiphytically on populations of *A. aegaea* on all of the islands from which it is recorded.

Figure 6. Habitat of *Alleniella aegaea* Blockeel & Hugonnot on Samos, Greece, March 2012, with bracket-like shoots visible in the lower centre of the image.

Reproduction

We did not observe sporophytes in any of the four known localities. The dioicy in the description is inferred from our observations of unisexual stems and colonies. In Boriano gorge (Crete), only male individuals were recorded whereas in Samos and Evvia only female individuals were seen. Reproduction may be limited in this species since it apparently does not produce specialized vegetative branchlets or propagula. We assume that sporophytes are produced somewhere in the species' area, but that they must be rare. It is possible that the species reproduced sexually in earlier times, especially if it was more common then, but has now lost the ability as a result of a more restricted and scattered distribution. Clearly this issue deserves to be studied further.

Distribution

In addition to the specimens cited above, the following published reports by Düll (2014) under the name *Homalia webbiana* are thought to represent *Alleniella aegaea.* We have not seen the corresponding specimens.

Greece. Samos. Potami, 40 m, *R. Düll*, no date; in a gorge below Platanos, above Idrousa, 250 m, *R. Düll*, no date; west of Manolates, in direction Stavrinides , ca. 350-360 m, under an exceeding [sic] limestone rock, *B. Duell-Wunder*, 2011.

Thus, all of the known localities for *A. aegaea* are in the Aegean islands of Greece. It is known from two localities in western Crete, and five localities on the eastern Aegean island of Samos. In addition there is one known population in the southern part of the island of Evvia in the western Aegean. Such a restricted distribution would be unusual among bryophytes but, in view of its occurrence on Samos, *A. aegaea* is very likely to occur in Turkey, and perhaps elsewhere in the eastern Mediterranean region. This pattern of distribution can be compared with that of *Bryoerythrophyllum duellii* Blockeel, currently known only from Crete, Ikaria and Cyprus (Blockeel *et al.* 2017), and *Oncophorus dendrophilus* Hedd. & Blockeel, known only from Crete, Cyprus and north-western Turkey (Hedderson and Blockeel 2006; Yayintas 2013). Indeed, the Aegean region is known for a number of other rare and/or disjunct bryophytes, for example *Asterella africana* (Mont.) Underw. ex A. Evans, *Campylostelium strictum* Solms, *Campylopus brevipilus* Bruch & Schimp., *Timmiella flexiseta* (Bruch) Limpr., *Rhamphidium purpuratum* Mitt. and *Solenostoma handelii* (Schiffn.) Müll. Frib. (Düll 1966; Gradstein 1970; Blockeel 2011, 2016, 2017; Blockeel and Nieuwkoop 2016).

In view of the identification of collections from Crete and Samos as *Homalia webbiana* (*Pseudomalia webbiana*) by Düll (2014), we considered the possibility that other reports of *H. webbiana* in eastern Europe and the eastern Mediterranean might belong to *Alleniella aegaea.* Hodgetts and Lockhart (2020) include doubtful reports of *Pseudomalia webbiana* in Montenegro, Romania and Ukraine, while Düll (1985) and Çetin (1988) list this species for Turkey. However, many reports of *H. webbiana* in the bryological literature in the 1980s and 1990s were based on the synonymisation of *H. webbiana* with *Alleniella* (*Neckera*) *besseri* by Düll (1979). This synonymisation was accepted in the European checklist of Corley *et* *al.* (1981) and thereby gained wide acceptance. It acquired further visibility in Düll's Distribution Catalogue of European and Macaronesian mosses (Düll 1985). Although Düll subsequently retracted the synonymisation (Düll 1992), the synonym remained widespread in the literature for many years. This is certainly (or very probably) the reason for the reports of *H. webbiana* from the territories of Montenegro, Romania and Ukraine.

Romania. *Homalia webbiana* was included in the Romanian checklist of Ştefănuţ and Goia (2012). Sorin Ştefănuţ (pers. comm.) has confirmed that this was based on the presumed synonymy with *Neckera besseri*.

Montenegro. *Homalia webbiana* was recorded from Montenegro by Grgić (1989) in the Tara River Canyon. In a later paper Dragićević *et al.* (2003) indicated that they had not re-found it during their own study of the Canyon. According to Snežana Dragićević (pers. comm.), *H. webbiana* should be excluded from the flora of Montenegro. It is likely that the report by Grgić was based on *Neckera besseri*.

Ukraine. A number of publications on the bryoflora of Ukraine accept the synonymy of *H. webbiana* and *N. besseri* (e.g. Danylkiv *et al.* 2002; Bachurina and Melnichuk 2003; Partyka 2005). We have not traced any reports of *H. webbiana* in Ukraine as a species distinct from *N. besseri*.

The reported occurrence of *H. webbiana* in Turkey by Düll (1985) and Çetin (1988) has a different origin. These reports were unlocalised and were based on the synonymisation of *Homalia woronowii* with *H. webbiana* by He (1997). The type locality of *H. woronowii* was thought to be in Georgia (Ignatov *et al.* 2006). In a later paper Düll (1992) caused some confusion by listing *H. woronowii* for both Turkey and Russia, citing Abramova and Abramov (1979) as the source of the Turkish record. However, Abramova & Abramov did not indicate any new localities for *H. woronowii*, but drew attention to the paper by Thériot (1918), in which *H. woronowii* is described. The type locality of *H. woronowii* is stated on the label of the holotype to be 'Lazistania Rossica – Fauces fl. Behlevan cac. reg. sylv. infer'. We interpret the Latin 'fauces fl. Behlevan' to indicate the gorge of the River Behlevan, but we have been unable to trace the name Behlevan. Evidence of its location is provided by the label on a specimen of *Primula megaseifolia* Boiss. et Bal. ex Boiss. in LE, cited by Kovtonyuk (2013): 'Prov. Batum, ad traject. Satibe inter p. Behlevan et Makret, in fagetis, 3300′, 2–

15.06.1902, leg. Alexeenko et Woronow'. Thus Behlevan is close to Makret, now Kale in the District of Borçka in modern Turkey, c. 15 km SSE of the border with Georgia at Sarpi. There is very limited land above 1,000 m near Makret (Kale) in the direction of Georgia, all within Turkey. Thus, we conclude that the type locality of *H. woronowii* is in modern Turkey. The type specimen (MNHN-PC-PC0694189) has been re-examined and found to belong to *Homalia webbiana*, confirming the synonymisation of *H. woronowii* with this species by He (1997).

KEY TO EUROPEAN SPECIES OF *NECKERA* s.l. AND *HOMALIA*

(Neckera s.l. includes the genera *Alleniella*, *Exsertotheca*, *Metaneckera*, *Neckera* s.str. and *Pseudomalia*)

1 Leaves distinctly transversely undulate at least above mid-leaf……**2**
– Leaves not transversely undulate……**9**
2 Costa distinct, reaching above mid-leaf……***Metaneckera menziesii*** (Drumm.) Steere
– Costa absent or indistinct (sometimes double), ending much below mid-leaf……**3**
3 Leaf apex round or obtuse, not or hardly apiculate……**4**
– Leaf apex acute or acuminate or, if obtuse, distinctly apiculate……**5**
4 Branch tips in upper parts of stems curved and turgid; leaves oblong or broadly lingulate, not distinctly widened below mid-leaf; walls of laminal cells incrassate, porose; paraphyllia absent or infrequent……***Exsertotheca intermedia*** (Brid.) S. Olsson, Enroth & D. Quandt
– Branch tips in upper parts of stems not curved or turgid; leaves ovate, distinctly widened below mid-leaf; walls of laminal cells hardly incrassate, eporose; paraphyllia frequent……***Exsertotheca baetica*** (J. Guerra, J.F. Jiménez & J.A. Jiménez) Draper, Gonz.-Mancebo, O. Werner, J. Patiño & Ros
5 Apices of (especially) branch leaves and upper stem leaves often long-acuminate, strongly spinosely denticulate to dentate or ciliate……***Neckera cephalonica*** Jur. & Unger
– Apices of leaves obtuse to acute (rarely acuminate), variously denticulate but not spinosely dentate or ciliate……**6**

6 Plants autoicous, sporophytes common; leaves gradually tapering to apex; capsules immersed or emergent **7**

– Plants dioicous, sporophytes uncommon; leaf apices mostly obtuse and apiculate; capsules exserted **8**

7 Mostly growing on trunks of deciduous trees, rarely on rock; leaves c. 2–3 mm long; seta c. 0.5 mm long, capsules immersed .... ***Neckera pennata*** Hedw.

– Growing on rock; leaves less than 2 mm long; seta c. 1 mm long, capsules emergent .... ***Neckera oligocarpa*** Bruch

8 Leaves less than 2 mm long; both leaf margins narrowly recurved at least below mid-leaf; seta 2–5 mm long .... ***Neckera pumila*** Hedw.

– Leaves 2–4 mm long; leaf margins not recurved; seta c. 5–10 mm long .... ***Exsertotheca crispa*** (Hedw.) S. Olsson, Enroth & D. Quandt

9 Costa distinct, reaching at least to mid-leaf **10**

– Costa absent or short, ending much below mid-leaf **11**

10 Costa reaching 3/4 or 4/5 of leaf length; leaf apices coarsely dentate, teeth often multicellular .... ***Homalia lusitanica*** Schimp.

– Costa reaching to mid-leaf or 3/4 of leaf length at most; leaf apices serrulate to serrate .... ***Homalia trichomanoides*** (Hedw.) Brid.

11 Plants small, fronds mostly less than 5 cm long, in depressed mats; leaves obovate, distinctly narrowed towards base .... ***Pseudomalia webbiana*** (Mont.) Enroth

– Plants of variable size, usually in lax patches or forming hanging brackets; leaves not obovate nor strongly narrowed towards base **12**

12 Plants medium-sized to large, fronds mostly 10–15 cm long, turgid; walls of laminal cells incrassate, strongly porose .... ***Exsertotheca intermedia*** (Brid.) S. Olsson, Enroth & D. Quandt

– Plants small to medium-sized, fronds mostly less than 5 cm long, not turgid; walls of laminal cells not particularly incrassate, eporose or with few pores **13**

13 Branch leaf apices mostly acute to acuminate; flagelliform branchlets common; mid-leaf cells mostly 50–70 µm long .... ***Alleniella complanata*** (Hedw.) S. Olsson, Enroth & D. Quandt

– Branch leaf apices rounded or obtuse, sometimes apiculate, rarely broadly acute; flagelliform branchlets sometimes present; mid-leaf cells ≤ 45 µm long...**14**

14 Leaves to c. 0.6 mm long; leaf apices not or very indistinctly apiculate; flagelliform branchlets often present; mid-leaf cells ≤ 30 µm long...
...........***Alleniella besseri*** (Lobarz.) S. Olsson, Enroth & D. Quandt

– Leaves more than 1 mm long; leaf apices mostly distinctly apiculate; (sub)flagelliform branchlets absent or rare; mid-leaf cells up to 40(–45) µm long...
....***Alleniella aegaea*** Blockeel & Hugonnot

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