

Pseudoparaphyllia in the European and Macaronesian species of *Neckera* Hedw. (Neckeraceae, Musci)

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Abstract – Pseudoparaphyllia in the European and Macaronesian species of *Neckera*: *N. crispera*, *N. complanata*, *N. pumila*, *N. pennata*, *N. besseri*, *N. cephalonica* and *N. intermedia* are studied with SEM to assess their variability and taxonomic significance. Univariate ANOVA showed that the specific differences in the mean number of pseudoparaphyllia around branch-buds and in the size of pseudoparaphyllia are statistically significant. This result evidences the utility of these structures as determinative and taxonomic characters.

Biometrics / *Neckera* / pseudoparaphyllia / taxonomy

Resumen – Han sido estudiados los pseudoparáfilos en las especies europeas y macaronésicas del género *Neckera*: *N. crispera*, *N. complanata*, *N. pumila*, *N. pennata*, *N. besseri*, *N. cephalonica* y *N. intermedia* con microscopio electrónico de barrido (SEM) para determinar su variabilidad y su significación taxonómica. El análisis univariante ANOVA muestra diferencias significativas entre las especies en la media de pseudoparáfilos por yema y en el tamaño de los pseudoparáfilos. Esto demuestra la utilidad de estas estructuras como carácter determinativo y taxonómico.

Biometría / *Neckera* / pseudoparáfilos / taxonomía

INTRODUCTION

Pseudoparaphyllia of pleurocarpous mosses have been shown to be of considerable, although somewhat taxon-dependent, taxonomic significance (Iwatsuki, 1963; Ireland, 1971; Newton & De Luna, 1999; Hedenäs, 2001). Iwatsuki (1963) defined the pseudoparaphyllia as “small paraphyllum-like appendages surrounding the branch primordium, which also remain at the base of mature branches”. He distinguished two main types: foliose pseudoparaphyllia, which

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resemble tiny leaves, and filamentous pseudoparaphyllia, which are usually narrow, fragile structures consisting of a single row of narrow cells, and frequently having a long apical cell. Akiyama & Nishimura (1993a, 1993b) discovered that the term pseudoparaphyllum was in fact used for two types of structures that sometimes looked very similar but had different origins, *i.e.*, the structures were not homologous. Branch primordia are closely protected by what those authors termed “scaly leaves”, referring to small, leaf-like structures originating from the edges of branch buds; Enroth (1994a) called these structures embryonic leaves and emphasized that they have a clear, consistent phyllotaxy, implying that they are modified leaves. According to Akiyama & Nishimura (1993a, 1993b) pseudoparaphyllia *sensu stricto* are homologous with trichomes. Newton & De Luna (1999) proposed to interpret pseudoparaphyllia as structures that originate on the dark, thick-walled cells of the epidermis, and “scaly leaves” as structures that originate on the pale, thin-walled cells surrounding the branch primordium. This is a clear-cut separation, since it establishes the distinction between modified leaves and pseudoparaphyllia, and it is the one followed in this paper.

Characters of pseudoparaphyllia have been used successfully at the generic and specific levels in the families: Hypnaceae (Hedenäs, 1992): *Calliergonella* and *Breidleria*, Brachytheciaceae (Ignatov, 1999): *Brachythecium*, *Rhynchostegiella* and *Brachytheciella*, Meteoriaceae (Ignatov, 1999): *Meteoriella*, Sematophyllaceae (Seki, 1968): *Neacroporium* (Iwatsuki & Noguchi, 1971), *Acanthocladium* (Schofield, 1966), Neckeraceae: *Curviciadium* (Enroth, 1993a), *Homaliodendron* (Ninh, 1984), *Neckeropsis* (Enroth, 1993b), *Porotrichum* (Schofield & Thompson, 1966), *Pinnatella* (Enroth, 1994a), *Homalia* (He, 1997) and Plagiotheciaceae: *Plagiothecium* (Ireland, 1969), *Taxiphyllum* (Iwatsuki, 1963) among others (Nishimura & Matsui, 1990). Most of these studies treated mainly non-European taxa. This is probably due to the fact that the European moss flora is comparatively well known and thus in somewhat less need of thorough revisions than floras from other, especially tropical, areas. Thus, small structures such as pseudoparaphyllia, have been largely neglected and considered unimportant by researchers on European taxa (Hedenäs, 1989), although they are useful characters for taxonomic and phylogenetic analyses.

According to Akiyama (1990), the branch buds in the Neckeraceae belong to the *Climacium*-type, which means that they are formed prior to dormancy and protected by “scaly leaves” and small young leaves, subtype **SO**, which means that they have pseudoparaphyllia that show much variety in shape. Enroth (1994b) commented that, in the Neckeraceae, the branch buds are covered by embryonic leaves and are usually but not consistently, accompanied by foliose pseudoparaphyllia.

Our studies on the pseudoparaphyllia of the European species of *Neckera* were carried out to find out whether they can be taxonomically used in this genus and consistently at the specific level and whether the morphological differences are also statistically significant.

MATERIAL AND METHODS

This paper is based on specimens from the bryophyte herbaria MA, H, TFC and from the private herbarium of J. I. Cubero, collected in several countries in Europe (see annex “selected studied specimens”). We studied specimens of the seven

species of *Neckera* from Europe and Macaronesia (Nyholm, 1965; Smith, 1968; Casas, 1991; Dirkse *et al.*, 1993): *Neckera crispa* Hedw., *Neckera pumila* Hedw., *Neckera pennata* Hedw., *Neckera besseri* (Lob.) Jur., *Neckera cephalonica* Jur. & Unger and *Neckera intermedia* Brid. Dry specimens were placed in a few drops of 2% potassium hydroxide solution (KOH) on a microscope slide and later they were washed with 96° ethanol (Koponen, 1967). Of each specimen 30 branch buds of main stem were selected. Of each bud the number of pseudoparaphyllia was counted. The length and the maximum width of each pseudoparaphyllum were also measured.

The taxa were compared with a univariate ANOVA. Tukey HSD-tests were used as post hoc tests. The untransformed data met the assumptions of ANOVA.

In the morphological study, a great number of specimens was used, of which drawings were made and photographs taken. SEM observations were done using the Akiyama & Nishimura (1993b) technique, except that the dehydration in successive acetone dilutions took place at 10%, 20%, 50%, 70% and 100%.

RESULTS

Comparison of taxa

The results of the basic statistical evaluation are summarized in Table 1, and depicted in Figure 1. The ANOVA analysis of length and width was supported only in the foliose pseudoparaphyllia.

Neckera complanata has the highest number of pseudoparaphyllia per branch bud, with a mean value of 5.42 ± 0.19 (mean \pm s.e.). The largest pseudoparaphyllia are present in *Neckera crispa*, with a length of 367.46 ± 12.59 μm and a width of 57.66 ± 2.36 μm . The lowest number of pseudoparaphyllia per branch bud occurs in *Neckera pumila* (2.04 ± 0.18), in which they are also the shortest (158.73 ± 15.82 μm), although the narrowest are found in *Neckera besseri* (22.22 ± 3.39 μm) (Fig. 4).

Table 1. Basic statistical evaluation of pseudoparaphyllia number branch buds and foliose pseudoparaphyllia in studied specimens.

	Pseudoparaphyllia by brunch bud					Length of foliose pseudoparaphyllia (μm)					Maximum width of foliose pseudoparaphyllia (μm)				
	Media	Stnd. Error	Min.	Max.	N	Media	Stnd. Error	Min.	Max.	N	Media	Stnd. Error	Min.	Max.	N
<i>N. besseri</i>	2.04	0.2	1.64	2.45	44	187.98	18.12	150	225.89	57	22.22	3.39	15.12	29.32	57
<i>N. cephalonica</i>	4.23	0.18	3.86	4.61	51	469.76	20.18	427.55	511.96	46	45.75	3.78	37.84	53.66	46
<i>N. complanata</i>	5.42	0.19	5.02	5.82	45	180.47	11.73	155.9	205	136	31.94	2.16	27.34	36.54	136
<i>N. crispa</i>	3.63	0.18	3.24	4.01	49	367.46	12.59	341.11	393.81	118	57.66	2.36	52.73	62.6	118
<i>N. intermedia</i>	3.36	0.21	2.91	3.81	36	312.99	14.19	283.31	342.67	93	60.39	2.65	54.83	65.95	93
<i>N. pennata</i>	3.76	0.2	3.35	4.18	42	242.89	11.96	217.88	267.9	131	51.54	2.24	46.85	56.22	131
<i>N. pumila</i>	2.04	0.18	1.66	2.41	51	137.4	21.12	93.24	181.57	42	42.95	3.96	34.68	51.23	42
					318					623					623

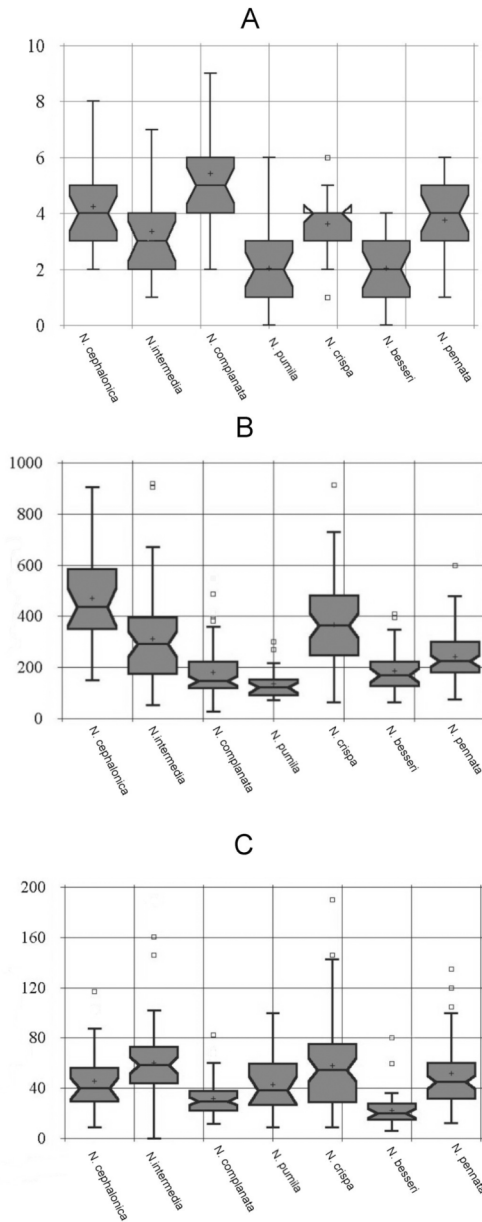


Fig. 1. **A:** Box plot of number of pseudoparaphyllia by branch bud. **B:** Box plot of foliose pseudoparaphyllia length (μm). **C:** Box plot of foliose pseudoparaphyllia maximum width (μm).

- ⌈ Range between maximum and minimum (mean values per specimens)
- Outlier symbol
- ⌋ Interquartile range, median
- + Mean

According to the results of the three ANOVA tests (length: $F = 48.35$, $P < 0.0005$; width: $F = 25.05$, $P < 0.0005$; number per branch bud: $F = 40.73$, $P < 0.0005$), there are significant differences among the taxa in the three studied variables. Statistical tests (Tukey HSD) on pairs of taxa revealed that:

1. The number of pseudoparaphyllia per branch bud separates three groups with significant differences among them (at the 5% level). *Neckera pumila* (2.04 ± 0.18) and *Neckera besseri* (2.04 ± 0.2) form a distinct group, as do also *Neckera intermedia* (3.36 ± 0.21), *Neckera crispa* (3.63 ± 0.18), *Neckera cephalonica* (3.76 ± 0.2) and *Neckera pennata* (4.23 ± 0.18). Within the latter group, *Neckera cephalonica* and *Neckera intermedia* have significant differences between them but not from the rest. Finally, *Neckera complanata* (5.42 ± 0.19) differs from all other studied taxa. (Fig. 1A)

2. The pseudoparaphyllium length also separates three groups with significant differences among them (at the 5% level). The first group is formed by *Neckera cephalonica* ($469.76 \pm 20.18 \mu\text{m}$) with the longest pseudoparaphyllia. The second one, with intermediate pseudoparaphyllium length, consists of *Neckera crispa* ($367.46 \pm 12.59 \mu\text{m}$) and *Neckera intermedia* ($312.99 \pm 14.19 \mu\text{m}$). Finally the third group comprises *Neckera pennata* ($242.89 \pm 11.96 \mu\text{m}$), *Neckera besseri* ($187.98 \pm 18.12 \mu\text{m}$), *Neckera complanata* ($180.47 \pm 11.73 \mu\text{m}$) and *Neckera pumila* ($137.4 \pm 21.12 \mu\text{m}$). In this group, *Neckera pennata* differs significantly from *Neckera complanata* and *Neckera pumila*, but not from *Neckera besseri* (Fig. 1B).

3. The pseudoparaphyllium width does not separate groups with significant differences among them (at the 5% level) although these exist between individual species. *Neckera besseri* ($22.22 \pm 3.34 \mu\text{m}$) differs significantly from all other species except *Neckera complanata* ($31.94 \pm 2.16 \mu\text{m}$). *Neckera intermedia* ($60.39 \pm 2.65 \mu\text{m}$) has non-significant differences only with *Neckera crispa* ($57.66 \pm 2.32 \mu\text{m}$) and *Neckera pennata* ($51.54 \pm 2.24 \mu\text{m}$) (Fig. 1C).

DESCRIPTIONS

In these descriptions we include the mean value, absolute minimum and absolute maximum of the studied parameters in pseudoparaphyllia.

***Neckera besseri*:** Pseudoparaphyllia linear (almost filamentous) to linear-lanceolate, margin entire to slightly denticulate, cells rectangular. 0-(2)-4 pseudoparaphyllia by branch bud, 6-(22)-59 \times 65-(187)-348 μm (Figs 2 A, B and 3 A).

***Neckera cephalonica*:** Pseudoparaphyllia linear-lanceolate and acuminate or filamentous. 2-(5)-10 pseudoparaphyllia by branch bud. Filamentous with 1-2 rows of polygonal basal cells that remain in an only rectangular row above 6-(12)-51 \times 45 -(227)- 672 μm . Foliose with basal cells quadrate, cells above rectangular to linear-rectangular, margin denticulate, sometimes with 1 or 2 marginal teeth 9-(45)-117 \times 151-(469)-905 μm . (Figs 2 C and 3 B).

***Neckera complanata*:** Lanceolate, linear-lanceolate to linear, acuminate, margin entire to denticulate, basal cells rectangular, linear-rectangular to linear above, 2-(5)-9 pseudoparaphyllia by branch bud, 6-(32)-82 \times 27-(180)-547 μm (Figs 2 D and 3 C).

***Neckera crispa*:** Ovate-lanceolate to lanceolate or filamentous, 1-(4)-6 by branch bud, foliose with a long acumen, margin denticulate, basal cells rectangular, linear above, 10-(57)-190 \times 68-(367)-915 μm . Filamentous pseudoparaphyllia almost equal to *Neckera cephalonica*, 9-(15)-30 \times 64-(196)-394 μm . (Figs 2 E and 3 D).

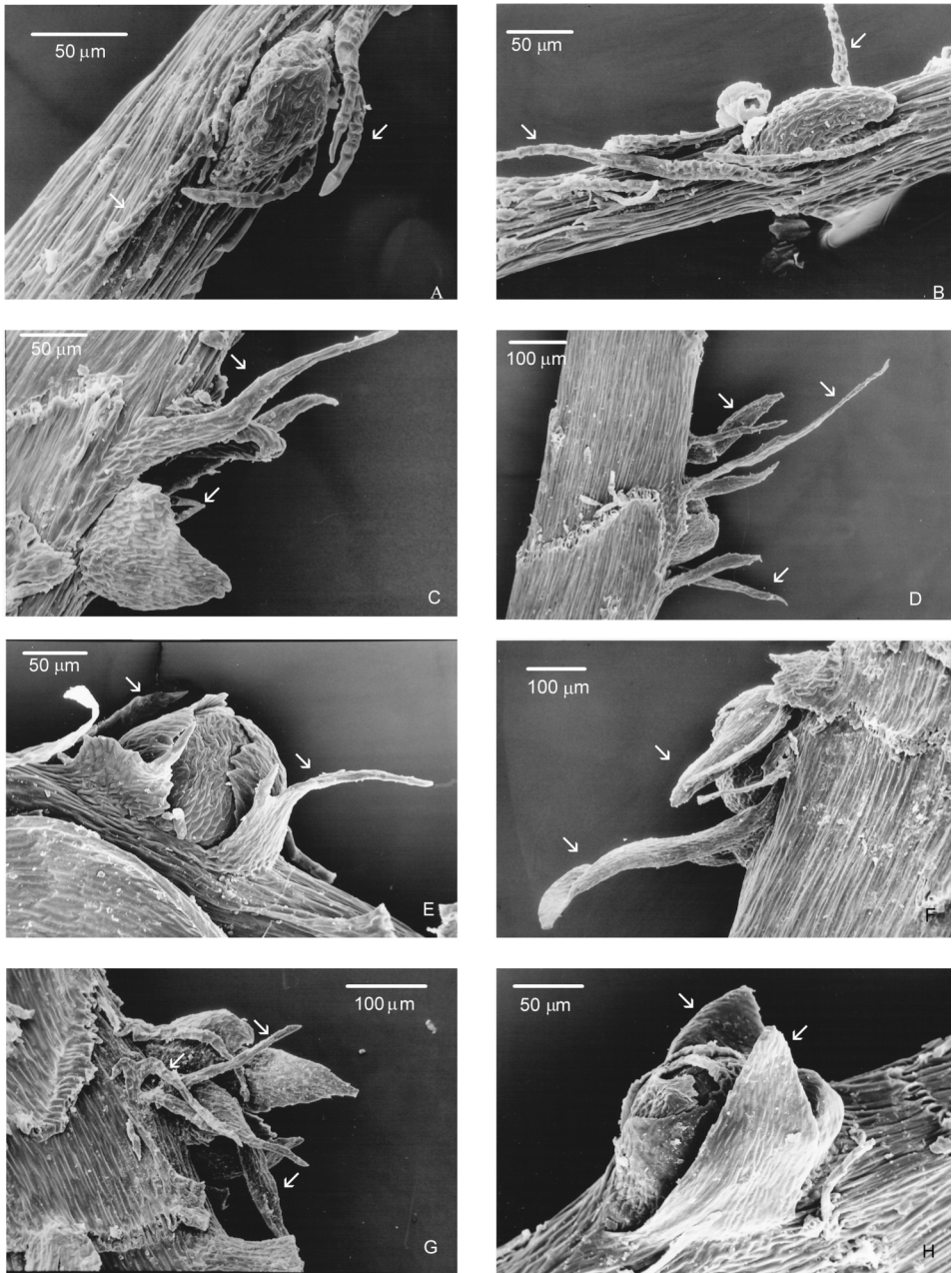


Fig. 2. SE-micrographs of brunnal-buds of European and Macaronesian species of *Neckera*. Arrows indicate pseudoparaphyllia. **A, B:** *Neckera besseri* (Lob.) Jur. **C:** *Neckera cephalonica* Jur. & Unger. **D:** *Neckera complanata* (Hedw.) Hüb. **E:** *Neckera crispa* Hedw. **F:** *Neckera intermedia* Brid. **G:** *Neckera pennata* Hedw. **H:** *Neckera pumila* Hedw.

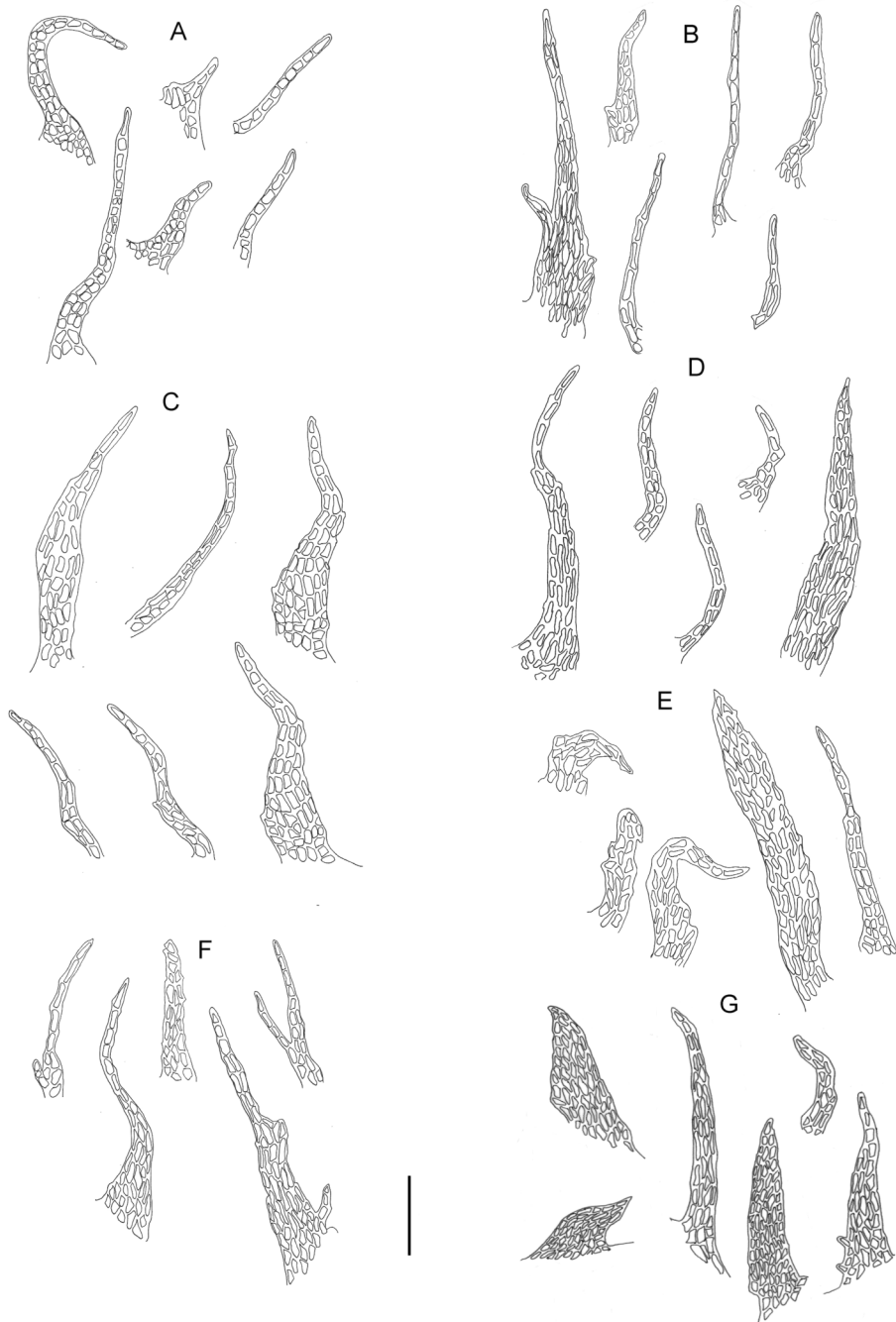


Fig. 3. Pseudoparaphyllia of European and Macaronesian species of *Neckera*. **A:** *Neckera besseri* (Lob.) Jur. **B:** *Neckera cephalonica* Jur. & Unger. **C:** *Neckera complanata* (Hedw.) Hüb. **D:** *Neckera crispa* Hedw. **E:** *Neckera intermedia* Brid. **F:** *Neckera pennata* Hedw. **G:** *Neckera pumila* Hedw. Line indicates 100 μ m.

***Neckera intermedia*:** Lanceolate to oblong-lanceolate, sometimes acuminate, margin denticulate, cells rectangular, sometimes linear in the intermediate zone, 1-(3)-7 pseudoparaphyllia per branch bud, 9-(60)-190 × 45-(313)-919 µm (Figs 2 F and 3 E).

***Neckera pennata*:** Ovate-lanceolate to lanceolate, margin entire to slightly denticulate sometimes with 1 or 2 marginal teeth, basal cells rectangular; rectangular, linear-rectangular to linear above, 1-(4)-6 pseudoparaphyllia per branch bud. 8-(51)-135 × 72-(243)-600 µm (Figs 2 G and 3 F).

***Neckera pumila*:** Very variable, triangular, lanceolate, acuminate-lanceolate to filamentous, 0-(1)-3 pseudoparaphyllia per branch bud, foliose with margin dentate to denticulate, basal cells quadrangle, linear-rectangular above, 9-(43)-120 × 71-(188)-400 µm, filamentous pseudoparaphyllia 6-(17)-32 × 42-(154)-420 µm (Figs 2 H and 3 G).

DISCUSSION

Ireland (1971) reported pseudoparaphyllia of three species and one variety in *Neckera*: *N. complanata*, *N. douglasii*, *N. pennata* and *N. pennata* var. *tenera*. He included an illustration of a branch bud of *Neckera complanata* with six linear-lanceolate pseudoparaphyllia with an entire margin and rectangular cells. In the rest of the taxa, Ireland observed similar characters. Our observations agree with Ireland's and the similarity between *Neckera complanata* and *Neckera pennata* pseudoparaphyllia is clear although they are not identical.

The SEM study by Nishimura & Matsui (1990) on isobryalean pseudoparaphyllia includes photos and descriptions of *Neckera yezoana*. In their description some elements that we regard as typical of *Neckera* (foliose, lanceolate, acumen, margin serrulate, and a number close to three) were included. In published works on other genera of the Neckeraceae these show generally foliose pseudoparaphyllia, mostly lanceolate to triangular in shape and low in number (*Homaliodendron*, Ninh, 1984; *Handeliobryum*, Ochyra, 1986; *Pinnatella*, Enroth, 1994a, *Neckeropsis*, Enroth, 1993b). Except *Porotrichum* (Schofield & Thompson, 1966) and *Homalia* (He, 1997) that present appreciable differences and *Curviacledium*, *Touwia* and *Pendulothecium* (Enroth, 1994b) that lack pseudoparaphyllia, the remaining genera have pseudoparaphyllia similar to those of *Neckera*.

As Enroth (1994a) and He (1997) have shown for *Pinnatella* and *Homalia*, respectively, there are at least in these genera interspecific differences in the size, shape and number of pseudoparaphyllia. More comprehensive studies on the morphology and biometry of these structures in the Neckeraceae are necessary to clarify the possible taxonomic differences and significance as we hope to have here demonstrated for the European species of *Neckera*.

Selected Studied specimens

Neckera besseri: **SPAIN**. Teruel. Cantavieja. Sierra Palomita. On *Buxus sempervirens* and sandstone. With *Neckera complanata*. 1480m. 24.IV.1999. Cubero J.I. & Marcos N. (herb. Cubero 127). **POLAND**. Wielun, Upland. Cracow, Sikornik Hill. On shady calcareous rocks in deciduous forest. 290m. 1.X.1978. Ochyra R. (H 3096531). **RUSSIA**. Caucasus, Teberda. 10.VIII.1955. Abramov M. S. (H 3096534).

- Neckera cephalonica*: **SPAIN**. Tenerife. Los Silos. On *Erica arborea*. 2.VII.1985. Losada A. (TFC Bry 1479). **PORTUGAL**. Madeira. Caramujo- Ribeiro do Inferno (origin). 1100-1200m. 30.VI.1952. Persson H. (H 3097627).
- Neckera complanata*: **SPAIN**. Navarra. Orbaiceta. On calcareous rock inside the *Fagus sylvatica* forest. 800m. 8.VIII.1998. Cubero J.I. (Herb. Cubero 28). **BOSNIA-HERZEGOVINA**. Montes Vranica. Ad corticem trunci in fageto fertili (cum *Mercurialis perenni* et *Salvia glutinosa*) in valle torrentis Borovnica. 1080m. 6.IX.1979. Rusinska A. (H 3096850). **BELGIUM**. Aux confins de Houyet, ruisseau de Vesli (confluent de l'Iwene). Sur rocher (grés calcaire) sous bois. 7.V.1978. De Sloover J.L. (H 3096771). **GREAT BRITAIN**. Wales. Duhonw, near Builth, Breconshire vicecounty 42. On shaded cliff, bank of river. 25.IV.1966. Harrison S.G. (H 3096786).
- Neckera crispa*: **SPAIN**. Huesca. Bielsa. Valle de La Pineta. On calcareous rock. 1250m. 25.VII.1998. Cubero J.I. (Herb. Cubero 13). **RUMANIA**. Comm. Darmanesti. In rupibus. 1600m. 14.IX.1970. Barabas V. & Mihai Gh. (H 3097090). **SLOVAQUIA**. Slovaocia Ctr. Horné Diery mts. Malá Fatra, Loc. Sub monte Rozsutec. 800m. 30.V.1982. Váňa J. (H 3097083). **GERMANY**. Baviera. Oberbayern: Kreis Bad Tölz, Steinbachtal at Bichl (Waldvorlpen). On calcareous rock faces. 750m. 18.VIII.1967. Koponen T. (H 3097146).
- Neckera intermedia*: **SPAIN**. Tenerife. Los Silos. Monte de Aguas y Pasos. Talud húmedo y umbrío. 27.IV.1987. Losada A. (TFC Bry 4976). **PORTUGAL**. Madeira. Caramujo-Ribeiro do Inferno (origin). 1100-1200m. 30.VI.1952. Persson H. (H 3097235).
- Neckera pumila*: **SPAIN**. Málaga. Ronda. Sierra de las Nieves. Pinsapar. On *Abies pinsapo*. 1440m. 21.X.1998. Cubero J.I. & Marcos N. (Herb. Cubero 103). **PORTUGAL**. Biera Litoral. Mata de Margaraca. On *Castanea sativa* and *Quercus robur*. 7.V.1999. Cubero J.I. & Marcos N. (Herb. Cubero 135).
- Neckera pennata*: **STONIA**. Viljandi district. SW of Viljandi, Heimtali. SW slope of the valley of the river Raudna, round an old manor (now a restaurant), very rich grass-herb forest of *Ulmus*, *Acer*, *Tilia*, *Quercus*, *Betula*, *Populus*, *Corylus* and some *Picea*, on trunks of hardwood trees. 26.VIII.1989. Kytövuori I. (H 3097386). **POLAND**. N.E., Plaska, Starozyn, Foret Puszcza Augustowska. Epiphyte sur le tronc de *Quercus robur* dans la forêt mixte. 30.X.1958. Lisowski S. (H 3097416). **SWEDEN**. Jämtlandnd, Untersakers socken Valberget, Waldregion, an den schattigen seiten herabgestürzter Blöcke. 18.VII.1912. Arnell H.W. & Jansen C. (MA- musci 4686)

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