

On the homology of the scales in *Gunnera* (Gunneraceae)

LIVIA WANNTORP^{1,*}, HANS-ERIK WANNTORP¹ and ROLF RUTISHAUSER²

¹Department of Botany, University of Stockholm, SE-106 91, Stockholm, Sweden

²Institute of Systematic Botany, University of Zurich, CH-8008, Zurich, Switzerland

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In the genus *Gunnera*, the species of subgenus *Panke* are unique in having large, triangular scales between the leaves on the rhizomes. The morphological significance of these scales has been extensively debated in the past. They have been interpreted as stipules, ligules, or cataphylls, with attempts made to identify homologous structures in representatives of the other subgenera. In the stoloniferous subgenus *Misandra*, the shoot apex is covered by a hood-like structure, usually termed ochrea, generally considered homologous to the scales in *Panke*. Efforts to find similar structures in the remaining subgenera were unsuccessful. Due to the lack of a phylogenetic hypothesis, the homology of the scales has remained unresolved. In this study, the shoot apices of species from all subgenera were examined by light and scanning electron microscopy and the results interpreted in a phylogenetic context. The tip of the stolons in subgenera *Pseudogunnera* and *Milligania* carries two opposite cataphylls at the base of the new shoot. These are homologous to the ochrea in *Misandra* which is in turn homologous to the scales in *Panke*; the latter are thus neither stipules nor ligules but cataphylls. The stems of subgenera *Ostenigunnera* and *Gunnera* have no similar structures. © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, 142, 301–308.

ADDITIONAL KEYWORDS: cataphyll – *Gunnera* – *Milligania* – *Misandra* – ochrea – *Ostenigunnera* – *Panke* – phylogeny – *Pseudogunnera* – stolon.

INTRODUCTION

Panke, the largest subgenus within the genus *Gunnera* L., includes more than 20 species found in South and Central America (and an additional two species endemic to Hawaii). All species, which can often reach impressive dimensions, are characterized by palmately lobed leaves surrounding stout and erect rhizomes. Between the leaf bases, the rhizomes are densely covered by large, triangular, often frilled, scales which cover and protect the rhizome tips (Fig. 1). Hidden under these scales are specialized wart-like organs, often called glands which host colonies of symbiotic cyanobacteria of the genus *Nostoc*.

The nature of the scales in *Gunnera* has attracted the interest of morphologists since the 19th century. The primary issue of those studies concerned the interpretation of the conspicuous scales in *Panke* and the subsequent search for homologous structures in

other subgenera. A comparison between the species of *Panke* and the stoloniferous *G. magellanica* Lam. (subgenus *Misandra*) and *G. monoica* Raoul (subgenus *Milligania*) was therefore sometimes included in the studies. The scales in *Panke* were generally interpreted as stipules (Reinke, 1873; Petersen, 1898) or ligules, depending on the definition of such organs. The major problem was that the homology and evolution of the scales could not be discussed within a phylogenetic context.

In the present study we review the previous interpretations of the scales in *Gunnera* and attempt to interpret the evolution of these structures within a phylogenetic context (Fig. 2).

HISTORICAL REVIEW: PREVIOUS INTERPRETATIONS OF THE SCALES

The first study was made by Reinke (1873), who described the scales of *G. chilensis* Lam. (subgenus *Panke*) as consisting of a central 'ligula', surrounded by two 'stipules'; he also claimed that the ochrea of

*Corresponding author. E-mail: livia.wanntorp@botan.su.se



Figure 1. *Gunnera manicata*. Tip of upright stem. Bunch of bud scales, surrounded by stalked foliage leaves. Maximum diameter of smallest leaf is c. 25 cm.

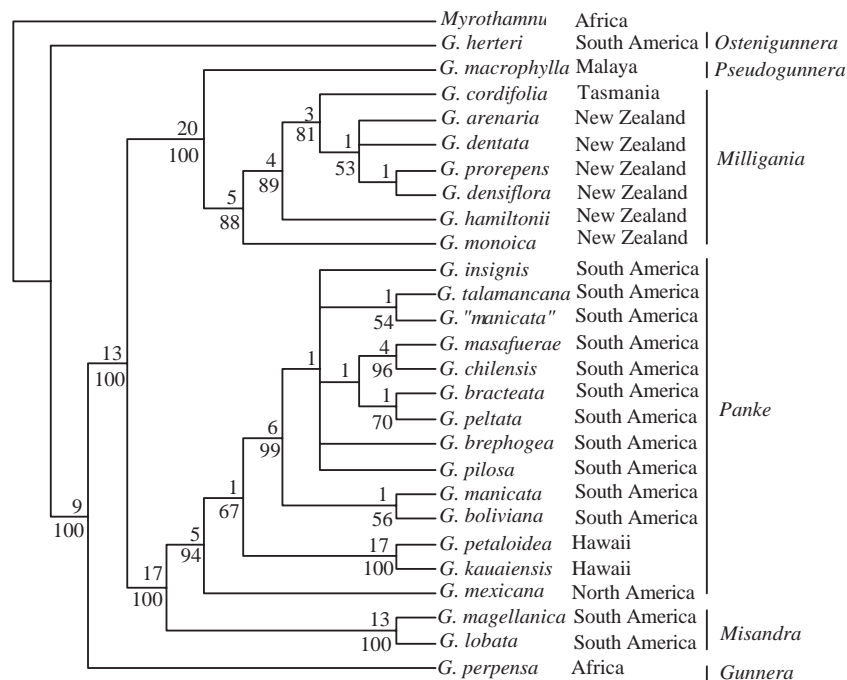


Figure 2. Phylogeny of *Gunnera* based on the *rbcL rps16* intron, the nuclear ribosomal DNA ITS region and on morphology (fig.2 in Wanntorp L. & Wanntorp, H.-E., 2003).

G. magellanica was of stipular origin. In addition, he reported a single unlobed ligula in *G. monoica* (subgenus *Milligania*). The same interpretation of the nature of the scales of *Panke* and of the ochrea of *Misandra* was given by Petersen (1898). In his monograph of the genus, Schindler (1905) treated Reinke's stipular

interpretation caustically, maintaining that these organs were without doubt all 'ligulis'. Schnegg (1902) made a study of some species of *Milligania*. He did not observe any such organs, but described two opposite cataphylls, serving as bud scales at the apex of each stolon.

Table 1. List of species and subgenera examined

Subgenus/species	Material studied
<i>Gunnera</i>	
<i>Gunnera perpensa</i> L.	L. & H.-E. Wanntorp 558 (S); South Africa
<i>Milligania</i>	
<i>Gunnera cordifolia</i> Hooker f.	L. & H.-E. Wanntorp 515 (S); Tasmania
<i>Gunnera monoica</i> Raoul	L. & H.-E. Wanntorp 536 (S); J. Dryden (1989); New Zealand
<i>Misandra</i>	
<i>Gunnera magellanica</i> Lam.	L. & H.-E. Wanntorp 551 (S); Chile cultivated specimen (Zurich); unknown source
<i>Ostenigunnera</i>	
<i>Gunnera herteri</i> Osten	L. & H.-E. Wanntorp 555 (S); Uruguay
<i>Panke</i>	
<i>Gunnera manicata</i>	Linden ex André cultivated specimen (Zurich); unknown source
<i>Pseudogunnera</i>	
<i>Gunnera macrophylla</i> Blume	L. & H.-E. Wanntorp 540 (S); Sumatra

**Figure 3.** *Gunnera manicata* (natural size).

Skottsberg (1928) made a detailed study of living material of three species of *Panke* without identifying any of the patterns previously described by Reinke from *G. chilensis*. Like Schindler, he rejected Reinke's interpretation of a stipular derivation. He identified pairs of scales at the base of each leaf in very young plants, interpreting them as cataphylls ('Niederblätter'), i.e. leaf homologues (Fig. 3). This was primarily based on the observation that the scales can sometimes be leaf-like. Also, the axillary buds (which usually do not develop in *Panke*) carry scales basally, outside the first leaf primordia. Skottsberg also studied the ochrea of *G. magellanica*, comparing it with the scales in *Panke* and arguing for homology between these two structures based on their identical position, between the new leaf and the axillary bud. He inter-

preted the ochrea as a single cataphyll enclosing the shoot apex. Shortly afterwards, he was able to study another stoloniferous species, the Malayan *G. macrophylla* Blume (subgenus *Pseudogunnera*), of which he collected fresh material at the Tjibeurum waterfalls in Java (Skottsberg, 1930). In that species, the axillary buds develop into stolons, just as in *G. magellanica*, while opposite cataphylls surround the stolon apically. Skottsberg interpreted this as support for his theory that the ochrea of *G. magellanica* and the scales of *Panke* also represented cataphylls. He also observed some narrow structures in the leaf axils of *G. macrophylla* which he thought might be reduced scales.

Mattfeld (1933) described the newly discovered *G. herteri* Osten. Looking for scales, he identified 2–5

minute trichomes in the leaf axils. He interpreted these as homologous to the scales in other species of *Gunnera*. Some years later, Troll (1939) rejected these previous hypotheses and instead interpreted the structures as intravaginal scales, completely free from the leaves which enclose them.

MATERIAL AND METHODS

Fresh material of *G. cordifolia* Hooker f., *G. monoica* (both subgenus *Milligania*), *G. magellanica* (subgenus *Misandra*), *G. herteri* (subgenus *Ostenigunnera*), *G. perpensa* L. (subgenus *Gunnera*) and *G. manicata* Linden ex André (subgenus *Panke*) was examined; ethanol-fixed material of *G. macrophylla* (subgenus *Pseudogunnera*) was also studied (see list in Table 1).

The specimens were critical-point dried and gold sputter coated. Micrographs of the apical tips of young stolons of *G. magellanica*, *G. cordifolia* and *G. monoica*, as well as of stems of *G. herteri* and *G. perpensa* were taken with a Cambridge S4 scanning electron microscope at the University of Zurich. The phylogeny used in the present paper is based on Wanntorp, Wanntorp & Källersjö (2002) and in Wanntorp & Wanntorp (2003).

RESULTS

SUBGENUS *PSEUDOGUNNERA* – *GUNNERA* *MACROPHYLLA*

Gunnera macrophylla (Fig. 4A) grows on wet, more or less perpendicular slopes in the Malayan rainforest. It is about 50 cm tall, with reniform leaves on long stalks from a somewhat thickened rhizome. Axillary buds grow into stolons produced by the elongation of the first internode, up to 50 cm or more in length. Apically, the stolons carry a single pair (not two pairs as described by Skottsberg, 1930) of opposite scale-like cataphylls. These serve as bud scales to the thickened upright, leafy part of the shoot. Figure 4A shows a relatively young stolon, surrounded by two opposite cataphylls (c). At the base of the cataphylls are two glands (only one visible in figure) (g). Below these, primordia of adventitious roots are present, some of which develop into roots (not visible in figure). In older stolons, the two cataphylls persist at the base of the upright part. Between the cataphylls and opposite to each other are the primordia of the first two foliage leaves (l) (mistakenly described as cataphylls by Skottsberg).

SUBGENUS *MILLIGANIA*

Axillary buds of the upright shoots grow into stolons by the elongation of the first internode, usually about

5–10 cm. Apically, these stolons carry two opposite cataphylls enclosing the upright, brachyblastic portion of the shoot. This in turn will form new stolons from the axils of its leaves, leading to the mat-forming habit of these species. The morphology described in *G. cordifolia* and *G. monoica* (see below) was also found in *G. prorepens* Hooker f., *G. hamiltonii* Kirk, *G. dentata* Kirk and *G. arenaria* Cheesem. of subgenus *Milligania*.

GUNNERA CORDIFOLIA

Gunnera cordifolia (Figs 4B, C, 5) is low, densely mat-forming, and grows in boggy areas in the uplands of Tasmania. Young stolons carry two cataphylls apically, which like bud-scales protect the primordium of the erect part of the shoot (Fig. 4B). On each side, between the bases of the cataphylls, is a gland just breaking through the epidermis of the shoot. Below each gland is a primordium of an adventitious root (r) (Fig. 4C). In somewhat older plants, the two cataphylls have opened and the tip of the shoot has emerged between them, carrying two young opposite leaves (Figs 4C, 5). Dark colonies of cyanobacteria have by this stage invaded the glands. The shoot will soon become erect and carry many leaves, although no more cataphylls will develop.

GUNNERA MONOICA

Gunnera monoica (Figs 4D–F, 8) is low, loosely mat-forming, and grows on disturbed ground in New Zealand. The growth pattern is identical to that of *G. cordifolia*. Two opposite cataphylls enclose the tip of young stolons (Figs 4D, 8). Below each cataphyll is one gland, and below this a primordium of an adventitious root (Fig. 4F). The leaves of the upright part begin to develop early, before the final elongation of the stolon (Fig. 4E). The foliage leaves soon develop between the two cataphylls and buds of new stolons (s) emerge (Figs 4E, F, 8).

SUBGENUS *MISANDRA* – *GUNNERA MAGELLANICA*

Gunnera magellanica (Figs 4G, 6, 7) is low, mat-forming, and grows in wet ground from the shores of Patagonia to the high Andes in Colombia. From the leaf axils develop stolons, normally 5–10 cm long. The stolons in *Misandra* are formed by two successive internodes. Apically, the stolons turn into upright brachyblastic leafy shoots. The first node of the stolon does not show a foliage leaf but is surrounded by a cap-like ochrea (o). The tip of the stolon penetrates the tip of this structure, which remains as a collar surrounding the base of the second internode of the stolon

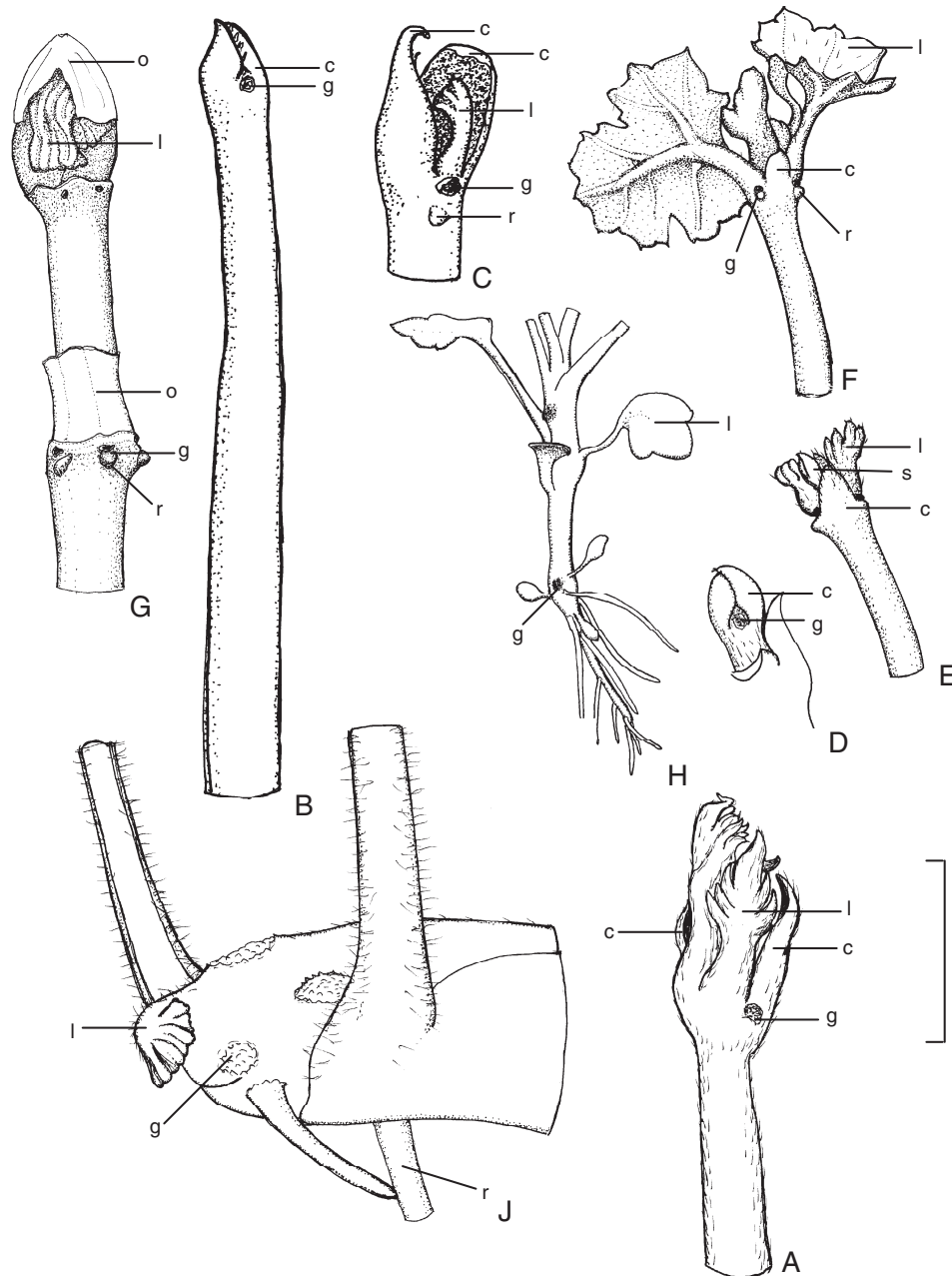


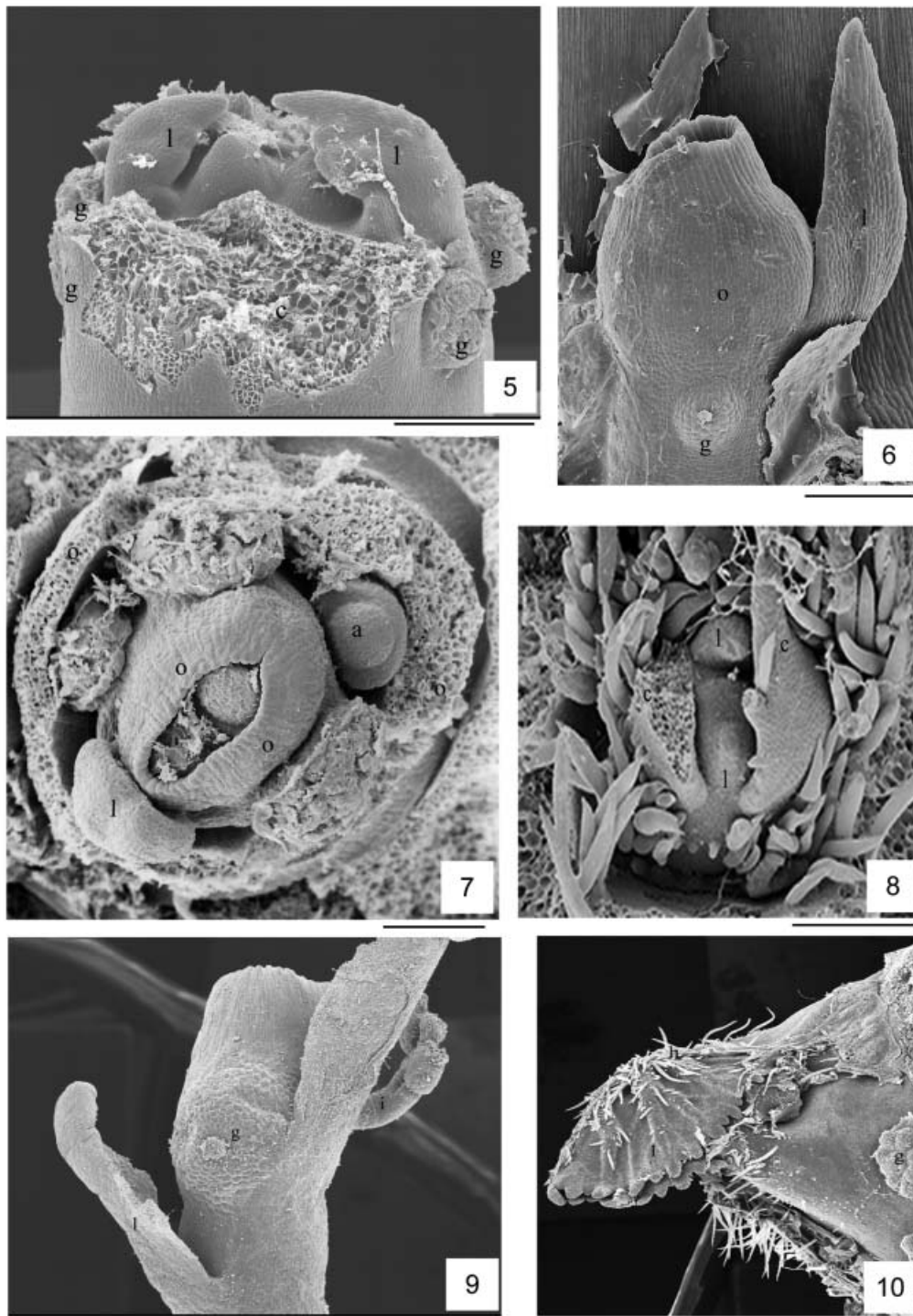
Figure 4. Scales in *Gunnera*. A, *G. macrophylla*. Relatively young stolon. B & C, *G. cordifolia*. B, young stolon. C, slightly older stolon. D–F, *G. monoica*. D, young stolon. E & F, older stolons. G, *G. magellanica*. Young stolon. H, *G. herteri*. Habit. J, *G. perpensa*. Section of rhizome. Abbreviations: (c) cataphylls, (g) glands, (r), roots, (l) leaves, (o) ochrea and (s) young stolon. Scale bars: A, B, E–J = 10 mm; C, D = 5 mm.

(Figs 4G, 7). At the base of the ochrea several glands penetrate the epidermis, each followed by successive root primordia (Fig. 4G). An ochrea also subtends the base of the upright part of the shoot. In Figure 4G, the upper part of this ochrea has been severed basally, and is carried like a cap, covering the shoot apex. Inside this, the first leaf of the upright stem can be seen. In

G. magellanica, each successive leaf of the upright part is surrounded by an ochrea (Fig. 7).

SUBGENUS *PANKE*

The morphology of this subgenus has been thoroughly studied (Reinke, 1873; Petersen, 1898; Skottsberg,



Figures 5–10. Scales in *Gunnera*. SEMs. Fig. 5. *G. cordifolia*, lateral view of tip of young stolon. Scale bar = 400 μm . Figs 6, 7. *G. magellanica*, lateral and top views, respectively, of young stolons. Scale bars: Fig. 6 = 300 μm .; Fig. 7 = 170 μm . Fig. 8. *G. monoica*, top view of apex of stolon. Scale bar = 257 μm . Fig. 9. *G. herteri*, lateral view of basal part of stem. Fig. 10. *G. perpensa*, lateral view of shoot tip. Scale bars, both figs. = 1000 μm . Abbreviations: (a) axillary bud, (c) cataphylls, (g) glands, (h) hairs, (i) inflorescence, (l) foliage leaves, (o) ochrea. (Figs 7–9 reproduced with permission from Reiner, 1991).

1928; Rutishauser, 1989; Reiner, 1991) and is therefore not described in detail here. It is characterized by stout, more or less erect, rarely branching rhizomes. The plants usually stand in individual clumps but sometimes form extensive stands by seed propagation. The rhizomes carry large to very large, usually palmate, leaves. Between these are large, often brightly coloured, reddish scales, usually much more numerous than the leaves. The scales may have smooth edges, but are mostly frilled and may have a green, more or less leaf-like lamina (Fig. 3).

SUBGENUS *OSTENIGUNNERA* – *GUNNERA HERTERI*

Gunnera herteri (Figs 4H, 9) is a tiny annual, forming dense mats on seepage ground between the coastal dunes of Uruguay and southern Brazil. It has thin upright branching stems with long internodes. Both ordinary branches and inflorescences are ‘extra-axillary’, i.e. they are united to the main axis for some distance above the axil and thus seem to emerge directly from the stem, seemingly without subtending leaf. At the base of each leaf is a gland. There are no stolons and no cataphyll-like leaves at all.

SUBGENUS *GUNNERA* – *GUNNERA PERPENZA*

Gunnera perpensa (Figs 4J, 10) is about 50 cm high with reniform leaves on slender stalks. It forms dense stands by means of stout, creeping, somewhat flattened rhizomes which branch intermittently. The leaf bases are decurrent on the rhizome to form elongate somewhat cushion-like structures, demarcated by sharp edges. At the base of the leaves, numerous glands are visible as well as adventitious roots departing from the rhizomes (Fig. 4J). No stolons and no cataphylls or other scale-like structures are present.

DISCUSSION

The scales in *Panke* have been the subject of detailed morphological attention over the years (studies by, *inter alia*, Reinke, 1873; Schnegg, 1902; Skottsberg, 1928, 1930). However, mainly due to typological thinking and the lack of a phylogenetic framework, these studies did not succeed in resolving the scales’ homology. The approach they used was to try to apply the same interpretation to both the scales in *Panke* and the ochrea in *Misandra* (considered a homologous structure by all authors). Almost none included representatives of *Milligania*. According to the phylogeny presented in Figure 2, subgenera *Ostenigunnera* and *Gunnera*, represented by *G. herteri* and *G. perpensa*, respectively, are sister groups to the other four subgenera. On the stems of these two species, however, there are no traces of any scales or cataphylls

(Figs 4H–J, 9, 10). Following the successive branchings of the cladogram, it is obvious that the interpretation of the scales in *Panke* should be addressed by departing from the structures of the stoloniferous subgenera, *Milligania*, *Pseudogunnera* and *Misandra* (Fig. 11).

Skottsberg (1930) identified opposite cataphylls on the stolons of *G. macrophylla*. According to our results, the conditions in subgenus *Milligania* and in *G. macrophylla* (subgenus *Pseudogunnera*) are identical. In all these species there are two cataphylls protecting the apex of the stolon. These cataphylls are not only found at the same position, but are also morphologically very similar (Fig. 4A–F). The most parsimonious interpretation from the phylogeny is thus that the presence of stolons with opposite cataphylls represents an apomorphy at this level. A less parsimonious hypothesis is that stolons with apical cataphylls may have been ancestral in the genus *Gunnera* and subsequently been lost in subgenera *Ostenigunnera* and *Gunnera*. This hypothesis has the advantage of not requiring a *de novo* appearance of opposite cataphylls within the genus.

The sister group of *Pseudogunnera*/*Milligania* is *Misandra*/*Panke* (Fig. 2). In this group, the conditions in subgenus *Misandra* are very similar to those described. While the stolon is formed by two internodes instead of one, the apex is surrounded by a cap-like structure, the ochrea, in exactly the same position as the cataphylls of *Milligania* and *Pseudogunnera*. From the morphological similarity and the identical position on the stolon, our interpretation is that the ochrea is indeed homologous to a cataphyll. A novel trait in *Misandra*, however, is the existence of an ochrea below every foliage leaf, protecting the shoot

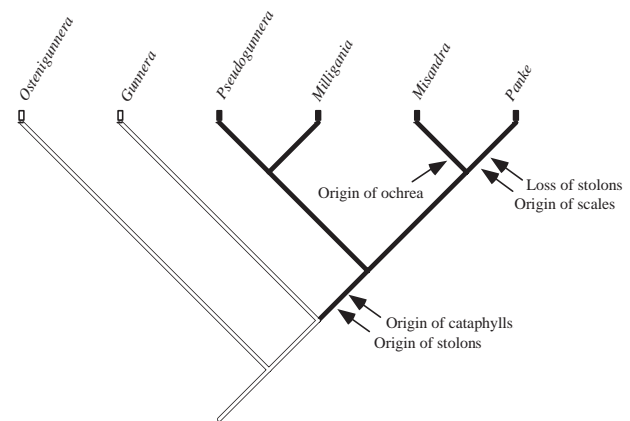


Figure 11. Evolution of scales in *Gunnera*. Black indicates presence of cataphylls or cataphyll derivatives (ochrea, scales).

apex above. This observation is in direct contrast with earlier interpretations, in which the position of the ochrea was seen as inside the leaf, and thus interpretable as a structural modification of the leaf base (Skottsberg, 1928). There is thus a strong case for the interpretation of the ochrea of *Misandra* as a cataphyll.

Skottsberg (1928) argued for homology between the scales of *Panke* and the ochrea of *Misandra*. However, the scales are not very similar either to the cataphylls in *Milligania* and *Pseudogunnera* or to the ochrea of *Misandra*. In *Panke*, the vegetative axillary buds are normally suppressed and stolons never develop. These buds, however, also carry scales below the leaf primordia (Skottsberg, 1928). The scales in *Panke* develop between each successive leaf, as does the ochrea in *Misandra*. Since the ochrea in *Misandra* is believed to be a cataphyll, and since it is also homologous to the scales in *Panke*, the most parsimonious interpretation is that the latter are in fact cataphylls as well. We thus agree with Skottsberg (1928). According to our interpretation, cataphylls in *Gunnera* are a synapomorphy for the clade consisting of the subgenera *Milligania*, *Pseudogunnera*, *Misandra* and *Panke* (Fig. 11). The inconspicuous structures observed by Skottsberg (1930) in the leaf axils of *G. macrophylla* and by Mattfeld (1933) in *G. herteri*, are unrelated.

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REFERENCES

- Mattfeld J. 1933.** Weiteres zur Kenntnis der *Gunnera herteri* Osten. *Ostenia* 102–118.
- Petersen OG. 1898.** Halorrhagidaceae. In: Engler A, ed. *Die Natürlichen Pflanzenfamilien*, 7, 8. Leipzig: Wilhelm Engelmann, 226–237.
- Reiner G. 1991.** Morphologie, Anatomie und Biologie dreier *Gunnera*-Arten: *G. manicata*, *G. magellanica*, *G. monoica*. Unpublished PhD, University of Zurich.
- Reinke J. 1873.** *Morphologische Abhandlungen. II. Untersuchung über die Morphologie der Vegetationsorgane von Gunnera*. Leipzig: Wilhelm Engelmann.
- Rutishauser R. 1989.** Exception to acropetal leaf initiation in vegetation shoots of angiosperms. *American Journal of Botany* 75 (6/2): 44–45.
- Schindler AK. 1905.** Halorrhagaceae. In: Engler A, ed. *Das Pflanzenreich*, 4. Leipzig: Wilhelm Engelmann, 1–133.
- Schnegg H. 1902.** Beiträge zur Kenntnis der Gattung *Gunnera*. *Flora* 90: 161–208.
- Skottsberg C. 1928.** Zur Organographie von *Gunnera*. *Svensk Botanisk Tidskrift* 22 (1–2): 392–415.
- Skottsberg C. 1930.** Bemerkungen über die Morphologie von *Gunnera macrophylla* Bl. *Meddelanden från Göteborgs Botaniska Trädgård*. 5: 115–126.
- Troll W. 1939.** *Vergleichende Morphologie der Höheren Pflanzen*, 1(2). Berlin: Borntraeger.
- Wanntorp L, Wanntorp H-E. 2003.** The biogeography of *Gunnera* (L.): vicariance and dispersal. *Journal of Biogeography* 30: 1–9, in press.
- Wanntorp L, Wanntorp H-E, Källersjö M. 2002.** Phylogenetic relationships of *Gunnera* based on nuclear ribosomal DNA ITS region, *rbcL* and *rps16* intron sequences. *Systematic Botany* 27 (3): 512–521.