Ann. Bot. Fennici 33: 311–316
Helsinki 13 December 1996
ISSN 0003-3847

On the taxonomic significance of lobule characters in the Lejeuneaceae (Hepaticae)

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Received 18 April 1996, accepted 3 June 1996

The taxonomic importance of some lobule characters in the Lejeuneaceae is reviewed and clarified in this paper: (1) The free margin of lobule is defined as the margin between the stem and the distal end of the keel. The number of the cells along the free margin is variable. This is especially true in the genera with distal hyaline papilla, in which the length of the lobule tooth and the number of the cells in the free margin exhibit considerable intraspecific variation. There is no consistent difference in the number of the cells in the free margin between the genera with a proximal hyaline papilla and those with a distal hyaline papilla. (2) This paper emphasizes the use of "the first tooth", "the second tooth" etc. from distal to proximal for describing lobule teeth, in order to avoid confusion. In the Ptychanthoideae the free margin bears 1–11 distinct lobule teeth, and the number, form and position of the lobule teeth sometimes provide taxonomic criteria in the separation of both genera and species; in the Lejeuneoideae the free margin has no more than two lobule teeth. Often the first tooth or the second tooth is reduced, or sometimes both lobule teeth are obscure. (3) Two positions of the hyaline papilla occur in the Lejeuneaceae: hyaline papilla on the free margin, proximal to the first tooth; or hyaline papilla on the inner side of the lobule, near the proximal base of the first tooth. The species of the Lejeuneaceae in which the hyaline papilla occurs on the inner side of the lobule, usually have more than two lobule teeth; the taxa with 1–2 lobule teeth usually have a marginal hyaline papilla. Therefore, different positions of the hyaline papilla strongly depend on the appearance of the lobule teeth. The position of the hyaline papilla shows less taxonomic importance than the lobule teeth.

Key words: Hepaticae, hyaline papilla, Lejeuneaceae, lobule characters, taxonomy

The Lejeuneaceae is the largest family of the Hepaticae, comprising about 70 genera and 1 500 described species. The great morphological diversity of the family brings not only a large number of species, but also different concepts of taxonomic characters promoted by various authors. In this study the family classification proposed by Gradstein (1994) is used in the following discussions of the lobule characters.

Lobule characters were not described in detail in the Lejeuneaceae until Evans (1902–1912) for the first time made an outstanding study of lobule

structure in his work of "Hepaticae of Puerto Rico". He pointed out that lobule shape, the free margin, the apical tooth and the position of the hyaline papilla of lobule are significant criteria in delimitation of genera in the Lejeuneaceae. Eight new Lejeuneaceae genera were described by him mainly based on lobule features. Since then, lobule features have been recognized as important characters for distinguishing genera and species in the Lejeuneaceae.

The lobule, i.e. the ventral leaf lobe, is normally folded against the dorsal lobe, and attached to the stem with a slightly arched insertion line; the free margin varies from plane to strongly inrolled and forming an inflated water-sac, with 0–11 marginal teeth; the hyaline papilla is usually situated near the lobule apex. In the course of my taxonomic work on the genus *Pycnolejeunea* (Spruce) Schiffn. and with further data gathered from other studies on the Lejeuneaceae, I have found that understanding of the taxonomic importance of the lobule characters still remains somewhat vague. Therefore it is necessary to review and clarify the lobule characters, especially those of the free margin, the lobule teeth and the position of the hyaline papilla .

FREE MARGIN OF LOBULE

The free margin of lobule in the Lejeuneaceae has been explained in various ways. In his descriptions and illustrations, Evans (1902–1912) exhibited the free margin as the margin of the lobule between the stem and the distal end of the keel. This concept is accepted by most hepaticologists (cf. Mizutani 1961, Gradstein 1975, 1994, Schuster 1980, van Slageren 1985, Thiers & Gradstein 1989). On the other hand, Jones (1984) considered the free margin of lobule as the margin between the stem and the apical tooth in his study of some European and African Lejeuneoideae. It seems more comfortable to describe species with the latter concept in the Lejeuneoideae, because the whole margin of lobule is normally involuted throughout a part of its length, tipped by a single cell at the apex, and then continuing as a sinus to the distal end of the keel. It is easily demonstrated that the lobule margin consists of two portions: the free margin (Jones 1984) or free lateral margin (Grolle 1988) and the apical margin, the latter being the margin between the apical tooth and the keel (Mizutani & Piippo 1986, Piippo 1986, Grolle 1988). In the Lejeuneoideae the apical margin with the lobule tooth represents a suite of taxonomically significant characters. However, in the Ptychanthoideae, the lobule margin is usually plane or curved from the base to the lobule apex with several teeth, and shortly continuing into the ventral margin of the leaf lobe. Therefore it appears reasonable to recognize the whole lobule margin as the free margin.

In my opinion, taking the whole margin of the lobule as the free margin is appropriate in the Lejeuneaceae, because the tipped lobule tooth is attached to the apical portion of the lobule, and derived from the lobule margin. If the term "apical margin" is considered necessary, it can be taken as a part of the free margin.

Taxonomic importance of the free margin in the Lejeuneaceae remains insufficiently known. Evans (1906) segregated *Cheilolejeunea* into three genera based on the lobule features, and these three genera *Cheilolejeunea*, *Rectolejeunea* Evans and *Cystolejeunea* Evans are distinct from each other in characters of the lobule free margin. Jones (1984) studied the number of cells in the free margin of some European and African Lejeuneoideae, and concluded that the somewhat constant number of cells in the free margin afforded a useful taxonomic character. He mentioned that the number of cells in the free margin is variable in many species, but generally the species with a proximal hyaline papilla have constantly 4 cells in the free margin, while the species with a distal hyaline papilla usually have at least 5 cells. Furthermore, Jones noted that the lobule provided less taxonomically useful features in the genera with a distal hyaline papilla, because in these genera the length of the lobule tooth and the number of cells in the free margin of the lobule both bear considerable intraspecific variation. According to my observations of the species of *Pycnolejeunea* and *Cheilolejeunea,* I agree with Jones that the number of the cells of the free margin is variable, and I have also observed that in some species the lobule tooth of the genus *Cheilolejeunea* is variable. However, I cannot see significant and constant difference in the number of cells in the free margin between the genera with proximal and distal hyaline papilla. I assume that this one missing cell in the free margin in the genera with a proximal hyaline papilla results from reduction of the second lobule tooth.

The free margin of lobule is certainly a good character for generic delimitation in the Lejeu-

neaceae. It is also useful for distinguishing species within a genus; for example, the apices of the free margin are considerably different between *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. and *A. securifolia* (Nees) Watts (Gradstein 1975). I believe that better understanding of the taxonomic value of the free margin of lobule will be achieved after more detailed taxonomic and monograpic work of the Lejeuneaceae is done.

TEETH OF LOBULE

Lobule tooth has been accepted as a significant character in the taxonomy of the Lejeuneaceae. Characters of generic importance can be derived from the number of teeth on the free margin. In the Ptychanthoideae the free margin bears 1–11 distinct marginal teeth (Fig. 1a). The first tooth or the apical tooth is situated near the apex of lobule, with a greater distance from the neighbouring tooth; several other teeth are usually regularly spatiated, as in *Acrolejeunea fertilis* (Reinw. *et al*.) Schiffn. (Gradstein 1975), and *Frullanoides corticalis* (Lehm. & Lindenb.) van Slageren (Slageren 1985). For the Ptychanthoideae the number, length, width, form and position of the lobule teeth provide significant criteria in the separation of both genera and species. Gradstein (1994) segregated the tribe Brachiolejeuneae from the Ptychanthoideae and placed it in the Lejeuneoideae based on the sporophytic features, but in all genera of Brachiolejeuneae except *Neurolejeunea* (Spruce) Schiffn., the character of lobule teeth is shared with the Ptychanthoideae.

In the remaining Lejeuneoideae the apex of the free margin has two lobule teeth, which are situated within a certain distance or rarely side by side. In some taxa one of the lobule teeth is usually reduced. Mizutani (1961) discussed the lobule teeth and first proposed to use "the first tooth", "the second tooth" and so on from distal to proximal to avoid confusing the individual teeth (see also Gradstein 1975). He demonstrated that in *Cheilolejeunea* and *Leucolejeunea* Evans the first tooth is reduced, the remaining tipped lobule tooth being the second tooth. I favour Mizutani's proposal, and suggest to avoid the terms "apical tooth" (Jones 1954, 1979, Kachroo & Schuster 1961, Pócs 1975, Tixier 1979, Mizutani 1980, 1981, 1982, Schuster 1980, 1992, Gradstein *et al*. 1989, He 1995), "true apical tooth" (Schuster 1980), "preapical tooth" (Tixier 1979, Schuster 1980), "proximal tooth" (Pócs 1975, 1980, Thiers & Gradstein 1989, Thiers 1992) and "distal tooth" (Thiers 1992), because the apical tooth can mean either the first tooth or the second tooth. As I understand it, the true apical tooth and the distal tooth are the same as the first tooth, while the preapical tooth and the proximal tooth mean the second tooth.

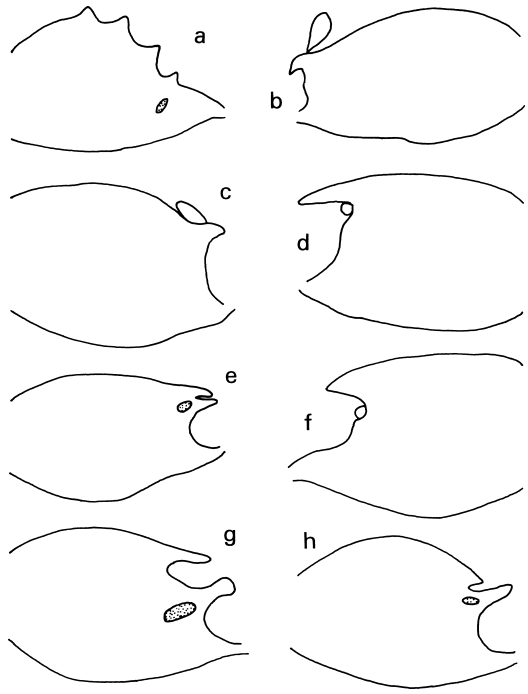

Fig. 1a–h. A schematic illustration of typical lobule teeth and the positions of the hyaline papilla in the Lejeuneaceae. — a: Ptychanthoideae. — b, c: Lejeuneoideae. — d, e: *Cheilolejeunea*. — f: *Leucolejeunea*. — g: *Tuyamaella*. — h: *Cololejeunea*.

In many genera of the Lejeuneoideae, such as *Ceratolejeunea* (Spruce) Schiffn., *Lejeunea* Libert, *Pycnolejeunea, Lepidolejeunea* Schuster, *Rectolejeunea, Drepanolejeunea* (Spruce) Schiffn., etc., the inflated, well-developed lobule usually bears a single 1-celled lobule tooth, which is the first tooth (Fig. 1b and c). The reduced second tooth is usually invisible. This appearance of the lobule tooth is constant among these genera. However, in *Cheilolejeunea* and *Leucolejeunea*, the second tooth is usually distinct, being straight or falcate, varying from 0 to 7 cells in length, and the first tooth is usually

obsolete or presents as a blunt projection; sometimes both teeth are seen in certain species (Fig. 1d–f), such as one species of *Cheilolejeunea* (He, in prep.), and *Leucolejeunea unciloba* (Lindenb.) Evans (Schuster 1980). The variation of the lobule tooth has been used in delimitation of the subgenera of *Cheilolejeunea* (see Schuster 1980, Thiers 1992). The tendency for reduction of the first lobule tooth can also be found in the genera *Omphalanthus* Lindenb., *Neurolejeunea* and *Blepharolejeunea* S. Arnell (Gradstein 1994).

In the genera *Cololejeunea* (Spruce) Schiffn., *Tuyamaella* Hattori and *Nipponolejeunea* Hattori, the lobule also has paired lobule teeth (Fig. 1g and h), but the distribution and form of the teeth along the lobule margin are remarkably different from the other genera of Lejeuneoideae. Normally both the first and the second tooth are distinct, with some distance from each other. The first tooth is prominent, acuminate or subulate, sometimes broadened at the base and T-shaped; the second tooth is less prominent, different in shape, occasionally obscure or involute.

Lobule teeth show great morphological diversity in the Lejeuneaceae. Even though lobules are liable to be reduced in response to environmental conditions, the available monographic work of the family shows that well-developed lobules provide taxonomically important features. According to my view, the free margin with several lobule teeth is a primitive character, while the free margin with 1–2 lobule teeth is an advanced character. This opinion turns out contrary to the concept proposed by the previous authors (Mizutani 1961, Schuster 1963). A phylogenetic analysis is, however, necessary to establish the correct polarization.

POSITION OF HYALINE PAPILLA

The hyaline papilla occurring on the leaf-lobule has been recognized taxonomically valuable since Evans' early studies. Evans separated the genus *Rectolejeunea* from *Cheilolejeunea* (1906), and *Aphanolejeunea* from *Cololejeunea* (1911) partly based on the different position of the hyaline papilla. Ever since the trend in taxonomic work on the Lejeuneaceae has been to emphasize the position of the hyaline papilla as being either proximal or distal to the apical tooth, or borne on the inner side of the lobule. In 1961 Mizutani pointed out that in all species of the Lejeuneaceae, the hyaline papilla is situated at the proximal base of the first tooth, or on the inner surface of lobule at or near the first tooth. Therefore describing hyaline papilla as proximal or distal depends only on the different lobule tooth, and there is no great taxonomic difference in distal and proximal positions. As was discussed above, hyaline papilla with a distal position merely means that the first tooth is reduced, and the tipped lobule tooth is replaced by the second one. I have found Mizutani's studies to be valuable. Basically two types of hyaline papilla positions in the Lejeuneaceae can be recognized.

Hyaline papilla on the free margin, proximal to the first tooth

In many genera of the Lejeuneoideae, the hyaline papilla is situated on the free margin at the proximal base of the first tooth, for example in *Ceratolejeunea*, *Cystolejeunea*, *Prionolejeunea* (Spruce) Schiffn., *Cyclolejeunea* Evans, *Trachylejeunea* (Spruce) Schiffn., *Pycnolejeunea, Lepidolejeunea, Echinocolea* Schuster, *Lejeunea, Rectolejeunea, Macrolejeunea* (Spruce) Schiffn., *Harpalejeunea* (Spruce) Schiffn., *Drepanolejeunea, Leptolejeunea* (Spruce) Schiffn., *Rhaphidolejeunea* Herzog etc. In this case, the first tooth and the hyaline papilla are usually distinct and constant; only when the lobule is reduced or vestigial, for example, in some species of *Lejeunea*, the hyaline papilla is positioned on a single projecting cell of the lobule apex. In the genus *Cololejeunea*, however, the lobule tooth shows great variation, e. g. when the first tooth is distinct but the second one is obsolete, with the hyaline papilla usually positioned on the free margin, proximal to the first tooth, as in *Cololejeunea siamensis* (Steph.) Bened. (Mizutani 1965) and *C. floccosa* (Lehm. & Lindenb.) Schiffn. (Mizutani 1984, Thiers 1988); or when both lobule teeth are distinct, with hyaline papilla proximal to the first tooth, as in *Cololejeunea mamillata* (Ångstr.) Hodgs. and *C. falcata* Bened. Some other variations of the lobule teeth in *Cololejeunea* are explained in the latter part of the paper.

A monograph on the large genus *Cheilolejeunea* remains lacking. A broad ventral merophyte (4 or more cells wide), which is one of the diagnostic features in the Ptychanthoideae, has been demonstrated in some species of the genus (Kachroo & Schuster 1961, Mizutani 1980, 1982, Thiers 1992, Gradstein *et al.* 1993, He 1995, 1996). Moreover, also the lobule characters exhibit a link between the subfamilies

Lejeuneoideae and Ptychanthoideae. In many species of *Cheilolejeunea*, the hyaline papilla occurs on the free margin; however, it also exists on the inner side of the lobule. This occurrence is typical in the Ptychanthoideae. The genus *Cheilolejeunea* has close relationships with *Leucolejeunea*; both genera have species with entire underleaves, broad ventral merophytes and reduced first tooth.

Hyaline papilla on the inner side of the lobule, near the proximal base of the first tooth

In the Ptychanthoideae, all genera have hyaline papillae on the inner side of the lobule near the proximal base of the first tooth. This type of position of the hyaline papilla is also present in the Brachiolejeuneae (except *Neurolejeunea*; Gradstein 1994), in *Pictolejeunea* Grolle (Grolle 1977) and in most species of *Cololejeunea* in the Lejeuneoideae. Those species of the Lejeuneaceae in which the hyaline papillae occur on the inner side of the lobule mostly have more than two lobule teeth; the taxa with 1–2 lobule teeth usually have marginal hyaline papillae. In my opinion, the different position of the hyaline papilla strongly depends on the different appearance of the lobule teeth, and thus the position of the hyaline papilla shows less taxonomic importance than the lobule teeth.

Acknowledgements. Thanks are due to Dr. Sinikka Piippo for the valuable discussions and corrections on the manuscript; to Dr. Barbara Thiers and an anonymous referee for the helpful comments; to Prof. Dr. Rob Gradstein and Prof. Tamás Pócs for the important advice and references; and to the curatorial staff of B, BM, FH, G, JE, L, NY, P, S, and U for specimens sent on loan for my studies.

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