Systematics of *Cheilolejeunea* (Spruce) Schiffn. (Lejeuneaceae) in Continental Africa and its Ecological Significance in Conservation of Kakamega and Budongo Rainforests

Dissertation

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Contents

LIST OF TABLES	. IV
LIST OF FIGURES	V
SUMMARY	. Vl
CHAPTER 1. GENERAL INTRODUCTION	1
1.1 Specific Objectives	4
CHAPTER 2. HISTORICAL TAXONOMIC SURVEY	5
2.1. THE GENERAL DEVELOPMENT OF <i>CHEILOLEJEUNEA</i> TAXONOMY	
CHAPTER 3. METHODOLOGY	21
3.1. MORPHOLOGY	21 24 26
RAINFORESTS	
3.2.1. Introduction	
3.2.2. Kakamega Forest	
3.2.3. Budongo Forest	
3.2.4. Sampling techniques	32
CHAPTER 4. RESULTS	35
4.1. MORPHOLOGY AND ANATOMY	35
4.1.1. Sporelings	35
4.1.2. Merophytes	
4.1.3. Stem anatomy	
4.1.4. Branching	
4.1.5. Leaves	
4.1.6. Lobules	
4.1.7. Underleaves and Rhizoids	
4.1.8. Vegetative reproduction	
4.1.9. Sex distribution	
4.1.11. Gynoecia	
4.1.12. Sporophyte	
4.1.12. Sporophyte	
4.2. PHENETIC ANALYSIS	
4.3. PHYLOGENETIC ANALYSIS	
4.4. BRYOGEOGRAPHY AND ALTITUDINAL DISTRIBUTION	
4.4. BRYOGEOGRAPHY AND ALTITUDINAL DISTRIBUTION	45
4.5. THE ECOLOGY AND CONSERVATION OF CHEILOLEJEUNEA IN KAKAMEGA AND BUDONGO RAINFORESTS	5 0
4.5.1. Diversity of corticolous bryophytes	
4.5.2. Bryophyte cover	
4.5.3. Correlation between phorophyte and bryophyte diversity	
4.5.4. Cheilolejeunea diversity in response to forest disturbance	
CHAPTER 5 DISCUSSION AND CONCLUSIONS	65

5.1. GENERIC RELATIONSHIPS	65
5.2. Phenetic Observations	68
5.3. PHYLOGENETIC RELATIONSHIPS	71
5.3.1. Conspectus of the genus Cheilolejeunea	
5.4. BRYOGEOGRAPHY AND ALTITUDINAL DISTRIBUTION OF AFRICAN CHEILO	OLEJEUNEA 75
5.5. THE IMPLICATION OF THE ECOLOGY OF CHEILOLEJEUNEA IN CONSERVATI	ON OF KAKAMEGA
AND BUDONGO FORESTS	76
5.6. CONCLUSIONS AND RECOMMENDATIONS	
5.7. SYSTEMATIC TREATMENT OF AFRICAN CHEILOLEJEUNEA	79
5.7.1 Doubtful and excluded species	141
6. REFERENCES	146
APPENDICES	156
ACKNOWLEDGEMENT	177

List of Tables

Table 1: Generic delimitations of <i>Cheilolejeunea</i> and <i>Euosmolejeunea</i>	7
Table 2: Distinction between Cheilolejeunea and Pycnolejeunea	8
Table 3: Character and character states coded for phenetic analysis	3
Table 4: Character and character states used in phylogenetic analysis2	5
Table 5: Vegetation succession status in Kakamega Forest	1
Table 6. Data matrix of species and character states used for phylogenetic analysis4	6
Table 7. Tropical African <i>Cheilolejeunea</i> species: Distribution range (by endemism /bryodiversity centre), altitude, main habitat, forest condition and substrate5	3
Table 8: List of <i>Cheilolejeunea</i> species recorded in Kakamega and Budongo forests6	3
Table 9. Taxonomic placement of the genus <i>Cheilolejeunea</i> by different authors6	7

List of Figures

Figure 1. Sporelings, branching, leaves, underleaves, oil bodies and capsule	37
Figure 2. Phenogram of the genus <i>Cheilolejeunea</i> using UPGMA	
Figure 3. The Most Parsimonious tree, with number of characters/states supporting each of	
Figure 4. Bootstrap/ Jacknife analysis of the generated tree.	47
Figure 5. Distribution of Cheilolejeunea species within bryological centres of endemism in	n
Africa (see Appendix III for individual species distribution maps)	
Figure 6. Altitudinal abundance of <i>Cheilolejeunea</i> species	
Figure 8. Families of epiphytic bryophytes	58
Figure 9. Generic diversity of epiphytic bryophytes	60
Figure 10. Diversity and cover of bryophytes in the study area	60
Figure 11. Species diversity and cover as influenced by abiotic factors along disturbance	61
Figure 12. Correlation of phorophyte and bryophyte diversity	
Figure 13. Frequency of <i>Cheilolejeunea</i> species in various tree substrates	
Figure 14. Cheilolejeunea krakakammae (Lindenb.) R.M.Schust. (
Figure 15. Cheilolejeunea ngongensis Malombe & Pócs sp. nov	
Figure 16. Cheilolejeunea fischeri Malombe & Pócs sp. nov	
Figure 17. Cheilolejeunea pluriplicata (Pearson) R.M.Schust	
Figure 18. Cheilolejeunea camerunensis S.W.Arnell.	
Figure 19. Cheilolejeunea pocsii E.W. Jones	101
Figure 20. Cheilolejeunea usambarana (Steph.) Grolle	
Figure 21. Cheilolejeunea convexa (S.W.Arnell) S.W.Arnell	
Figure 22. Cheilolejeunea cordistipula (Steph.) Grolle ex E.W.Jones	
Figure 23. Cheilolejeunea ruwenzorensis (Steph.) R.M.Schust	
Figure 24. Cheilolejeunea omphalogastria Pócs	
Figure 25. Cheilolejeunea decursiva (Sande Lac.) R.M.Schust	
Figure 26. Cheilolejeunea serpentina (Mitt.) Mizut	
Figure 27. Cheilolejeunea diversifolia Augier	
Figure 28. Cheilolejeunea intertexta (Lindenb.) Steph	
Figure 29. Cheilolejeunea exinnovata E.W.Jones	
Figure 30. Cheilolejeunea trifaria (Reinw. et al.) Mizut	
Figure 31. Cheilolejeunea montagnei (Gottsche) R.M.Schust	
Figure 32. Cheilolejeunea ulugurica Malombe, Pócs, Eb. Fisch. & Masinde sp. nov	
Figure 33. Cheilolejeunea trapezia (Nees) Kachroo & R.M. Schust	
Figure 34. Cheilolejeunea rotundistipula (Lehm.) Malombe, comb. nov	
Figure 35. Cheilolejeunea unciloba (Lindenb.) Malombe comb. nov	
Figure 36. Cheilolejeunea xanthocarpa (Lehm. et Lindenb.) Malombe comb. nov	
Figure 37.Cheilolejeunea latiflora Steph.	
Figure 38. Cheilolejeunea laurentii Steph	
Figure 39. Cheilolejeunea sp. (Strepsilejeunea vatovae Gerola)	

Summary

The genus Cheilolejeunea (Spruce) Schiffn. (Lejeuneaceae, Jungermanniopsida) is represented by 23 species in continental tropical Africa. The morphological characters such as features of the stem, leaf, lobule and perianth traditionally used to separate the taxa at both species and generic level have been found to be unstable. The species are variably ranked in several subgenera including Cheilolejeunea (Spruce) Schiffn., Euosmolejeunea Schiffn., Strepsilejeunea (Spruce) Schiffn. and Xenolejeunea Kachroo & Schust. Although the genus has never been monographed, there are a few regional taxonomic accounts for America, Australia and China. A comprehensive revision of *Cheilolejeunea* species is lacking in Africa where the existing studies are based on single subgenus and sub-regional flora or checklist compilations, which are sometimes without identification keys. This study revises the taxonomy of Cheilolejeunea and the closely allied genus Leucolejeunea A. Evans, in continental Africa based on morphological data analysed using phenetic and phylogenetic methods. At the subgeneric level, different species of *Cheilolejeunea* are known to be limited by altitudinal changes. A bryogeographical survey of the species including an altitudinal gradient analysis in Africa was therefore undertaken. In addition, investigations were carried out along disturbance gradient to establish the ecological importance of the species as indicators of biodiversity change following fragmentation in Kakamega (Kenya) and Budongo (Uganda) tropical rainforests. A total of 276 phytosociological relevés (25 x 25 cm) were established in nine study sites and the presence or absence of *Cheilolejeunea* species noted.

The phylogenetic analysis supported by phenetic observations resulted in two major clades, a monophyletic subg. *Strepsilejeunea* and paraphyletic subg. *Cheilolejeunea*, based on leaf morphological characters. The species belonging to subg. *Strepsilejeunea* are characterised by strongly convex and falcate lobes, which are usually ovate with the apex strongly decurved. Those affiliated to subg. *Cheilolejeunea* exhibit flat, ovoid to orbicular lobes with broadly rounded apices, which are plane and rarely deflexed. The genus *Leucolejeunea* and subgenera *Euosmolejeunea* and *Xenolejeunea* Kachroo & Schust., were combined into subg. *Cheilolejeunea*. Characters used to separate the genus *Leucolejeunea* from *Cheilolejeunea* such as the width of ventral merophyte, type of subgynoecial innovations and the position of hyaline papilla are variable. At subgeneric level, features of lobule including the apical tooth

cells and the width of underleaves used to delineate species among the subgenera (*Cheilolejeunea*, *Xenolejeunea* and *Euosmolejeunea*) were also unstable.

The analysis was supported by bryogeographical observations. The majority of the *Cheilolejeunea* species allied to subg. *Cheilolejeunea* are of Afro-Asian distribution. They are common in lowland forests and rarely occur in montane vegetation. Except *Cheilolejeunea krakakammae* (Lindenb.) R.M.Schust. and *Ch. pluriplicata* (Pearson) R.M.Schust, which have disjunct populations in Asia, most of the species in subg. *Strepsilejeunea* are endemic to Africa. They are usually distributed in the afromontane vegetation, sometimes spreading to the subalpine zone. They are occasionally corticolous or ramicolous and hardly epiphyllous. This suggests that the subg. *Cheilolejeunea* is more derived as most of its species inhabit living leaves.

Six species of *Cheilolejeunea* (*Ch. krakakammae*, *Ch. intertexta*, *Ch. trifaria*, *Ch. trapezia*, *Ch. decursiva* and *Ch. fischeri*) were recorded in Kakamega and Budongo Forests. Kakamega Forest was dominated by *Ch. krakakammae* and Budongo forest characterised by *Ch. intertexta*. Most of the *Cheilolejeunea* records were associated with forest pioneer species such as *Harungana madagascariensis* and *Polyscias fulva*, which occupy young and open secondary forests.

This study combines the genus *Leucolejeunea* into *Cheilolejeunea* and proposes two subgenera; *Cheilolejeunea* and *Strepsilejeunea*. Twenty three species were recognised namely *Ch. camerunensis*, *Ch. convexa*, *Ch. cordistipula*, *Ch. decursiva*, *Ch. diversifolia*, *Ch. exinnovata*, *Ch. fischeri*, *Ch. intertexta*, *Ch. krakakammae*, *Ch. montagnei*, *Ch. ngongenis*, *Ch. omphalogastria*, *Ch. pluriplicata*, *Ch. pocsii*, *Ch. rotundistipula*, *Ch. ruwenzorensis*, *Ch. serpentina*, *Ch. trapezia*, *Ch. trifaria*, *Ch. ulugurica*, *Ch. unciloba*, *Ch. usambarana* and *Ch. xanthocarpa*. These include three species, *Ch. fischeri*, *Ch. ngongensis* and *Ch. ulugurica*, which are new to science. Two species, *Ch. newtonii* and *Ch. surrepens* were reduced to synonyms. The species of *Cheilolejeunea* are common in disturbed tropical rainforests. They are therefore valuable indicators of forest quality and can be used in rapid assessments for biodiversity conservation.

CHAPTER 1. GENERAL INTRODUCTION

The family Lejeuneaceae is characterised by lack of ventral branching, incubous bifid leaves with water sac known as 'lobule' and bundles of rhizoids. It is usually represented by many epiphyllous species, which is typical of a highly advanced clade of Porellales (Gradstein et al., 2001; Wilson et al., 2007a). Represented by approximately 90 genera consisting of 1000-1500 described species Lejeuneaceae is the largest family of liverworts (Schuster, 1963; He, 1996a; Gradstein et al., 2003). It also contributes more than three-quarters of the hepatic bryoflora of the tropical lowland rainforests (Gradstein, 1995). Due to these high extant species diversity, Lejeuneaceae has been used as the first example of land plants to infer the cradle of plant biodiversity in relation to the long-term effects of global climate change for terrestrial biomes (Wilson et al., 2007b). The gametophytic characters of the underleaves were traditionally used to classify Lejeuneaceae into two artificial groups, the 'Holostipae' and the "Schizostipae," based on whether they are unlobed or lobed, respectively (Schuster, 1963). Mizutani (1961) used constant characters of sporophyte to recognise the two groups and renamed them accordingly as Ptycanthoideae (most members with undivided leaves) and Lejeuneoideae (most members with divided leaves). These subfamilies have been widely accepted and has been the basis of studying the generic phylogenetic relationships within the family as found in Schuster (1980a), Gradstein et al., (2003), Ahonen (2005) and Wilson et al., (2007a). The genus Cheilolejeunea (Spruce) Schiffn. has been placed in the subfamily Lejeuneoideae (Schuster, 1963, 1980a) within the Lejeuneeae clade (Gradstein et al., 2003).

Cheilolejeunea consisting of 70 to 80 species widely distributed in subtropical and tropical regions is the third largest genus of the family Lejeuneaceae. Most of the species are ephemerals usually inhabiting tree trunks (corticolous), tree branches (ramicolous) and living leaves (epiphyllous) in lowland rainforests (Jones, 1983; Pócs, 1985, 1994; Gradstein *et al.*, 2001; Zhu & So, 2001). All these microhabitats can be temporarily dry and hot. They exist in open environments from sea level to the afroalpine belt dominated by elfin heath vegetation. Furthermore, most bryophytes in the lowland rainforests are regulated by conditions of light, temperature and humidity. The sun loving species which are 'usually in threadlike forms' like the Lejeuneaceae and other xerophytic species of the canopy of primary forest will live in the same conditions as those in open secondary forests or gaps created by any disturbance

(Richards, 1984; Gradstein, 1995; Frahm, 2003). Other microhabitat variables, which influence the distribution of the bryophytes, include forest age, size and age of gaps (Eldridge *et al.*, 2003). The morphological features of the species may also influence its adaptation to the various habitats. The epiphyllous species for example exhibit strongly flattened perianth on the dorsal view as an adaptation for retaining moisture (Zhu & So, 2001). Such species communities are very sensitive to external impacts like forest fragmentation (Pócs, 1996).

Taxonomic reviews of *Cheilolejeunea* are limited and like other genera with extreme variability of morphological characters such as Lejeunea Lib. in Lejeuneaceae, bryologists have been reluctant to study them. Schuster (1980b) cautioned the use of dry herbarium specimens and preferred living collections with oil bodies, which is an excellent character for delimiting the group. Earlier, Schuster (1955, 1963) and Kachroo and Schuster (1961) had attempted to revise the genus in relationship to the affiliated genera using features of stem, leaves, perianth and position of hyaline papilla of the lobule. They reduced several genera such as Euosmolejeunea, Strepsilejeunea and Anomalolejeunea (Spruce) R.M. Schust. to subgeneric level and created subgenus *Xenolejeunea* to accommodate several species initially placed in *Pycnolejeunea* (Spruce) Schiffn. and characterised by distal hyaline papilla. Subsequent treatments have however experienced difficulties in the placement of Cheilolejeunea species at the subgeneric level owing to increased variation of the distinguishing characters (Theirs, 1985, 1992; Zhu et al., 2002; Gradstein, 2003; Zhu & Grolle, 2004). When revising the *Cheilolejeunea* in China, Zhu et al., (2002) found most of the morphological characters such as the stem anatomy, leaves, oil bodies, lobule morphology and perianth shape quite variable. They combined species formerly in subg. Strepsilejeunea to subg. Euosmolejeunea and reduced subg. Anomalolejeunea to a synonym. On the treatment of Cheilolejeunea in West Africa, Wigginton (2004a) observed the substantial overlap of characters distinguishing the subgeneric ranks and was unable to place Cheilolejeunea cordistipula (Steph.) Grolle ex E.W. Jones in any of these subgenera.

At the generic level, *Cheilolejeunea* has been viewed as a "clandestine complex" comprising of *Cheilolejeunea-Leucolejeunea-Omphalanthus* Lindenb. as well as *Evansiolejeunea* Vanden Berghen and *Aureolejeunea* R.M. Schust. (Schuster, 1980a; Gradstein *et al.*, 2003). This complex is characterised by distal hyaline papilla, large oil bodies and spores with more than

10 rosettes (Gradstein et al., 2003). The characters used to separate Leucolejeunea from Cheilolejeunea such as ventral merophytes, lobule structures and underleaves have been found to be variable. Cheilolejeunea revoluta (Herzog) Gradst. & Grolle (Gradstein et al., 1993) and Ch. trapezia (Nees) Kachroo & R.M. Schust. (Zhu et al., 2002) sometimes have 4 or more ventral merophytes while Ch. montagnei (Schuster, 1980a) has undivided underleaves. Recent molecular studies in preparation of Lejeuneaceae phylogeny by Wilson et al., (2007a) resolved a polyphyletic *Cheilolejeunea* clade. They proposed adoption of a broader concept of Cheilolejeunea to include all the five related genera; Cheilolejeunea, Leucolejeunea, Evansiolejeunea, Omphalanthus and Aureolejeunea. Only two genera of the Cheilolejeunea complex namely Cheilolejeunea and Leucolejeunea are widely distributed in tropical Africa. The genus *Omphalanthus* is of American distribution (Schuster, 1980a), while *Aureolejeunea* and Evansiolejeunea have narrow distribution in Africa. The former is found in St. Helena and Uganda while the latter is localised in Rwanda and DR Congo (Wigginton, 2004b). Furthermore, Schuster (1963, 1980a) found the two genera more affiliated to *Omphalanthus* clade than to Leucolejeunea or Cheilolejeunea. He also noted that Evansiolejeunea lacks subgynoecial innovations and Aureolejeunea has retained cell wall pigmentation, a common plesiomorphic character in the subfamily Ptycanthoideae.

The genus *Cheilolejeunea* has never been monographed on a worldwide basis but some regional or floral treatments are available. They include 12 species in Japan (Mizutani, 1982), 13 species in western Melanesia (Grolle & Piipo, 1984), 21 species in Borneo (Menzel, 1988), nine species in India (Asthana *et al.*, 1995), 17 species in Australia (Thiers, 1997) and 20 species in China (Zhu *et al.*, 2002). Twenty three to twenty eight species have been recorded in Africa including the eastern islands (Grolle, 1995; Wigginton & Grolle, 1996; Wigginton, 2004b). The African species numbers are bound to change with critical revision, but currently the continent remains a major centre of evolutionary diversification of the genus. New taxa, combinations and extension of distribution range of the *Cheilolejeunea* species continue to be described as shown in Thiers (1992b), Gradstein *et al.*, (1993), Pócs (1994), Grolle *et al.*, (2001), Zhu *et al.*, (2002), Dauphin and Gradstein (2003), Renner and Glenny (2003), Bastos and Gradstein (2006), Reiner-Drehwald (2006) and Zhu (2006). This may imply a gap of taxonomic knowledge or general neglect of the group.

There are several taxonomic notes and species descriptions on *Cheilolejeunea* in Africa; Augier (1972), Arnell (1953, 1958, 1963), Jones (1954a, 1954b, 1976, 1985, 1988), Jones & Harrington (1983), Tixier (1995), Vanden Berghen (1951d, 1953d, 1960b, 1965) and Wigginton (2004a). Except for scattered taxonomic evaluation by Jones between 1950 and 1980s, the majority of descriptions of *Cheilolejeunea* on the continent have been opportunistic. They are mainly based on descriptions of individual species, checklists, single subgeneric accounts or regional flora compilations sometimes lacking identification keys (see Jones, 1988 and Wigginton, 2004a). A complete revision of the genus in Africa is lacking. Infrageneric delimitations or specific names are unclear and species placement often erroneous. In addition, some of the species may be relegated to synonymy because they are represented by single collections and there is limited information about them. A comprehensive taxonomic revision of the genus *Cheilolejeunea* in Africa has therefore been long overdue.

This study attempts to establish a taxonomic revision of the genus *Cheilolejeunea* in continental Africa, putting into considerations the infrageneric status and comprehensive species delineations. The phylogenetic relationship of the genus as well as their ecological significance in fragmented lowland rainforests of Kakamega (Kenya) and Budongo (Uganda) has also been assessed.

1.1 Specific Objectives

- 1. To investigate the phylogenetic relationships of *Cheilolejeunea* species in continental tropical Africa and determine their relationships with closely affiliated genera.
- 2. To revise the taxonomy of *Cheilolejeunea* on continental Africa based on morphological data.
- 3. To investigate the ecological significance of *Cheilolejeunea* species following anthropogenic disturbance and fragmentation of tropical rainforests in Kakamega (Kenya) and Budongo (Uganda).

CHAPTER 2. HISTORICAL TAXONOMIC SURVEY

2.1. The General Development of *Cheilolejeunea* Taxonomy

The prefix "cheilo" is derived from Greek word meaning lip probably referring to the nature of the lobule apex shape. Lobules of the leaves in *Cheilolejeunea* are unique in that they are usually inflated up to the widened apex, leaving an open end or the 'mouth' and the sac formed is frequented by tiny insects such as Bdelloid rotifers, perhaps the *Habrotrocha sp.* group. "*Lejeunea*" on the other hand refers to the ability of the apical cells to develop into a single archegonium. Consequently, *Cheilolejeunea* may be referred to *Lejeunea* species with open mouthed and inflated leaf lobules. However, Evans (1906) and Schuster (1980a, page 858) think that the name "*Cheilolejeunea*" is derived from features of the perianth, which dehisces along the lateral faces becoming two lipped upon emergence of mature capsule. It is noted in Stearn (2004) that '*Ch*' translates to '*K*' in Latin and, for the first time, *Cheilolejeunea* species are abbreviated as "*Ch.*" and not '*C.*".

The name "Cheilo-Lejeunea" was introduced by Spruce (1884) for one of the subgenera of the diverse tropical genus Lejeunea. The genus Lejeunea like Cheilolejeunea belongs to the artificial group of "schizostipae", recognized by their bifid underleaves as opposed to the "holostipae" that are characterized by undivided or weakly emarginate underleaves of the leafy hepatics in the family Lejeuneaceae. Schiffner (1893) raised the subg. Cheilolejeunea Spruce to generic rank. His work was supported by Evans (1906) when he revised the hepatics of Puerto Rico focusing on Cheilolejeunea, Rectolejeunea A. Evans, Cystolejeunea A. Evans and Pycnolejeunea (Spruce) Schiffn. However, Evans noted the great variability of characters used to describe Cheilolejeunea especially the lobule type and perianth. He suggested that species of *Cheilolejeunea* should have a strongly inflated lobule with more or less abrupt contraction on outer part, giving way to a circular opening of the water-sac, as seen in the type Cheilolejeunea aneogyna (Spruce) A. Evans. In addition, the hyaline papillae are placed in a small depression at the distal base of the lobule's apical tooth. According to Evans, the species with proximal hyaline papillae should be placed to either *Rectolejeunea* or *Cystolejeunea*. Although he gave a comprehensive description of *Cheilolejeunea*, he cautioned that some of the species could still be classified into Euosmolejeunea (Spruce) Schiffn. or Pycnolejeunea.

Franz Stephani (1842-1927), a renowned German hepaticologist undertook a substantial contribution to the taxonomy of *Cheilolejeunea*. He received several large collection consignments including those of African liverworts between 1886 and 1924 and described over 31 taxa. Most of these were new to science, either belonging to this genus or affiliated taxa, a few of which have been reduced to synonyms. Eighteen species were published in the Species Hepaticarum in 1913 and 1914. Jones (1954a, 1954b) made remarkable progress in the taxonomy of *Cheilolejeunea* when he revised the genus in relationship to closely affiliated genera like Euosmolejeunea and Strepsilejeunea in Africa (Table 1). He reviewed most of the species described by Stephani and confirmed only four in Euosmolejeunea (Euosmolejeunea montagnei (G.) Schust., E. robillardii Steph., E. grandistipula Steph. and E. brachytoma Gottsche) and five in Cheilolejeunea (Ch. tisserantii, Ch. principensis Steph., Ch. inflata Steph., Ch. newtonii Steph. ex Schiffn. and Ch. africana Steph.). According to Jones (1954a), Euosmolejeunea was separated from other genera by having large underleaves, which are deeply cordate at base, areolation and form of lobule with its distal papilla and short apical tooth. It differs from Cheilolejeunea by the perianth, which is less compressed, and large underleaves.

Cheilolejeunea was delimited based on rounded leaves, an inflated lobule with long spiniform apical tooth and distal hyaline papilla. Other important characters were the underleaves which are 3 (2-4) times the stem width, bilobed to a third or a half their length with narrow sinus and cuneate at the base, and obovate subcomppressed perianth. Jones (1954a) however cautioned on existence of wide variations of most morphological characters within a single collection. He reiterated the most reliable features to be the shape of the lobe and lobules. According to him, Ch. latiflora Steph. is closely allied if not identical to Ch. newtonii or Ch. inflata while Ch. laurentii Steph. does not comply with the genus description (Jones, 1954b). Considering the lobule shape, he noticed that Ch. tisserantii by Jovet-Ast and Vanden Berghen (1951) is uniquely inflated beneath but flattened and bent upwards in its distal part elevating the lobes, and that the apical tooth is spiniform as compared to short single celled blunt apical tooth of the other species.

Table 1: Generic delimitations of Cheilolejeunea and Euosmolejeunea

Character/	Cheilolejeunea	Euosmolejeunea
Character state		
Trigones	small	Large
Underleaves	Small, shortly incised at base, orbicular or long than width, 2- 3(4)x wider than stem width	Large, cordate-based, usually wider than long and 4x wider than stem width
Perianth	Sub-compressed	Less compressed

Like in Evans (1906), Jones (1954b) doubted the majority of species described by F. Stephani in the genus *Pycnolejeunea*. He recommended transfer of the species to *Cheilolejeunea* after confirmation be carried out using more fertile materials and exact position of hyaline papilla. Particularly, he noted that *Pycnolejeunea involuta* Steph. collected from Usambaras resembles *Ch. africana* in relation to the lobule apex. Two collections (Mauritius; *Voltzkow, 1904*, and Madagascar; Betsileo, *Villaume, 286*) in Geneva herbarium assigned to *Pycnolejeunea silvestris* had distal hyaline papilla, hence similar to *Cheilolejeunea*. He maintained *Pycnolejeunea decurrens* Steph. (Cameroon, *Dusén* 803) probably because he could not observe the position of the hyaline papilla (Jones, 1954b).

It is however, the work of Schuster (1955, 1980a) and Kachroo and Schuster (1961) which became a major turning point for the taxonomy of *Cheilolejeunea*. Importantly, most of their comparisons for the genus were made on global perspective. Perhaps guided by recommendations by Evans (1906) and Jones (1954a), Schuster (1955) reduced the genus *Euosmolejeunea* to subgeneric level under *Cheilolejeunea* during the revision of the neotropical Lejeuneaceae. He observed that characters initially separating the two genera like perianth and underleaves were variable. Species limited to *Cheilolejeunea* were known to have apical tooth of lobule with 1-spiniform cell, somewhat compressed perianth with vestigial or lacking keels and small remote underleaves averaging up to twice the width of the stem (see Evans, 1906 and Jones, 1954a & b). Although the perianth of *Euosmolejeunea* has sharp keels, sometimes it exhibits obsolete dorsal keels. In addition, some of the species are characterised by smaller underleaves (2-5 times the width of stem) which may be slightly remote to imbricate (Schuster, 1955).

Kachroo and Schuster (1961) reviewed the genus *Pycnolejeunea* and discussed in details the characters separating the species from Cheilolejeunea. The most reliable characters included the position of the hyaline papillae and presence or absence of ocelli (Table 2). Like in Euosmolejeunea, they noted the variability of distinguishing features such as shape of apical tooth, leaf-lobule, leaves and underleaves, stem anatomy, oil bodies and perianth. They suggested that they could only be applicable at infraspecific levels. They proposed subg. Xenolejeunea to include 15 species, especially those with several cells in the apical tooth and distal hyaline papilla, hitherto placed in Pycnolejeunea (Kachroo & Schuster, 1961; Thiers, 1992a). They proposed the subgenus to be subdivided into five sections based on number of cells of the lobule apical tooth and the stem anatomy. However, they were quick to note some existing similarities between subg. Xenolejeunea and other subgenera in Cheilolejeunea especially Euosmolejeunea. They even thought the infrageneric division comprising of Cheilolejeunea-Euosmolejeunea-Strepsilejeunea-Xenolejeunea complex might be after all artificial and could just be retained for convenience. Despite the broad lobules, some species in subg. Xenolejeunea had 1, rarely 2, cell of the apical tooth typical of subg. Euosmolejeunea. Equally variable are characters of the perianth and stem anatomy usually eclipsing the known features in other subgenera such as dostriventral compression and 7 cortical cells, respectively. In particular, they tentatively hinted that it might be difficult to separate subgenera Cheilolejeunea, Euosmolejeunea and Xenolejeunea.

Table 2: Distinction between Cheilolejeunea and Pycnolejeunea

Character Genus	Cheilolejeunea	Pycnolejeunea
Hyaline papillae	Distal to lobule apical tooth	Proximal to lobule apical tooth
Ocelli	absent	present

Schuster (1963) undertook an outlined review of the genera and subgenera of Lejeuneaceae. He established the key to distinguish the newly established subgenera (*Cheilolejeunea*, *Euosmolejeunea*, *Xenolejeunea* and *Strepsilejeunea*) in *Cheilolejeunea* complex. He also doubted the recognition of *Ch. montagnei* as *Cheilolejeunea* or even its suitability to subg. *Euosmolejeunea*. He introduced subg. *Renilejeunea* to accommodate this "holostipous" species characterised by winged lobule of female bracts, orbicular-reniform and entire

underleaves. Although Kachroo and Schuster (1961) proposed subg. *Strepsilejeunea*, it is Schuster (1963) who provided valid taxonomic description. He described the subg. *Strepsilejeunea* as typically having falcate lobes with apices deflexed, bluntly to acutely pointed and female bracts with reduced lobules. The three major subgenera (*Cheilolejeunea*, *Euosmolejeunea* and *Xenolejeunea*) have orbicular to ovate lobes with rounded apex, which are flat and never or distinctly deflexed. Their female bracts have well developed bracts. In addition, he noted for the first time that *Cyrtolejeunea* A. Evans was indeed close to *Cheilolejeunea* complex. It has characteristic 7 cortical cells only differing from *Cheilolejeunea* by being small with aspects of the genus *Microlejeunea*.

Schuster (1980a) attempted the most modern re-evaluation of *Cheilolejeunea* at generic and subgeneric level. His broad discussions on the genus in relevance to the revision of the North American bryoflora shed more light on the clear delimitation of *Cheilolejeunea* and allied genera. Such genera included Euosmolejeunea, Strepsilejeunea, Anomalolejeunea (Spruce ex Pears.) Schiffn and Pycnolejeunea, most of which were earlier sank into Cheilolejeunea at subgeneric level (Schuster, 1955; Kachroo & Schuster, 1961; Schuster, 1963). On Euosmolejeunea, which is characterised by large and orbicular cordate underleaves, and a less compressed perianth (Schiffner, 1893; Evans, 1903; Jones, 1954a), Schuster (1980a) noted persistent intermediate species characters thus confirming his earlier observations and those of other hepaticologists (e.g. Evans, 1918; Jones, 1954a; Mizutani, 1961; Schuster, 1963). He noted Euosmolejeunea parvula Evans, which is common in tropical North America, has much smaller underleaves with cuneate bases and low postical and nearly obsolete dorsal perianth keels just as in Cheilolejeunea. The perianth of Cheilolejeunea polyantha Evans has vestigial keels and a pair of low postical keels as well as moderately large underleaves and 1 to 2 subgynoecial innovations typical of Euosmolejeunea (Schuster, 1980a). Jones (1954) also noted usual occurrence of 1 to 2 subgynoecial innovations in *Cheilolejeunea* as opposed to the absence of innovations as indicated by Schiffner (1893).

Characters distinguishing genus *Strepsilejeunea* such as deflexed, blunt to pointed leaf lobes and reduced lobules of female bracts were also found unreliable. Schuster (1980a) noted the lobules of *Cheilolejeunea camerunensis* S.W.Arnell well developed. Likewise, *Anomalolejeunea* was sunk in *Cheilolejeunea* at subgeneric level for the first time. Except the

perianth having 6-10 plicates, the monotypic genus represented by *A. pluriplicata* resembles the latter in all the other characters (Schuster, 1980a). In addition, Schuster (1980a) established subg. *Tegulilejeunea* Schust. to accommodate species close to subg. *Renilejeunea* but differentiated by short notched apices of the underleaves and bracteoles of androecia spread along the whole axis as well as unwinged keels of the female bracts.

Schuster (1980a) was non-committal in identifying actual differences between *Cheilolejeunea* and its closest African relative the genus *Leucolejeunea* Evans. He noted that subg. *Renilejeunea* (i.e. *Cheilolejeunea montagnei*) and species of *Leucolejeunea* could be shuffled either way. *Leucolejeunea* as argued by Schuster (1980a), Zhu and So (2001), and Grolle and Piipo (1990) has not been sharply differentiated from *Cheilolejeunea* and some intermediate features as well as species have been noted. The two genera resemble each other in texture, colour, ventral merophytes, oil bodies, lobule form, distal hyaline papilla and the nature of perianth. Some perceived differences have been cited as the positioning of hyaline papilla at least four cells below the base of apical tooth (Jones, 1973; Wigginton, 2004a). However, as shown in Schuster (1980a), *Leucolejeunea unciloba* and *L. clypeata* has the same position of hyaline papillae about 2 to 3 cells difference similar with *Cheilolejeunea cordistipula*. Schuster (1980a) finds the difference between the two genera as only gynoecial innovation patterns. While the *Leucolejeunea* is usually presented by pycnolejeuneoid innovations, *Cheilolejeunea* have a combination of lejeuneoid and pycnolejeuneoid and that of usual occurrence of free innovations.

Jones (1985) adopted infrageneric divisions recommended by Schuster (1980a) and described *Cheilolejeunea* (subg. *Strepsilejeunea*) *cordistipula* (Steph.) Grolle ex E.W. Jones comb. nov. He distinguished the species from related members by the usually flattened lobule free margin, which is visible *in situ*. He attempted a more diverse account of subg. *Strepsilejeunea* three years later and described five species in Africa. These were *Cheilolejeunea krakakammae*, *Ch. pluriplicata* (Pears.) R.M.Schust., *Ch. usambarana* (Steph.) Grolle, *Ch. pocsii* E.W.Jones, *Ch. convexa* S.Arnell and *Ch. camerunensis*. One of these species (*Ch. pocsii*) was named in honour of the best collector of Tanzanian hepaticological flora, Dr Tamás Pócs (Jones, 1988). Jones did not attempt construction of identification keys for the subgenus, reckoning that most of the infraspecific characters were variable. He however noted the type of subgynoecial

innovation as a good character especially when used in combination with others such as the underleaves, lobules and perianth. He maintained that the members of the subgenus are usually afromontane, and usually corticolous with few shoots, mixed with other species and hardly as pure stands. They are characterised by strongly convex, ovate to acuminate and deflexed lobes with subacute or acute lobe apices and the much reduced lobules of the female bracts. Importantly, he noted that some phenotypes of *Strepsilejeunea* usually have short and broadly rounded leaf apices thus confirming its closeness to *Cheilolejeunea* as argued by Schuster (1980a). Interestingly, Jones (1988) did not discuss his taxonomic view of the genus *Anomalolejeunea* but seems to have combined it with subg. *Strepsilejeunea*.

In the study of the Australian *Cheilolejeunea*, with focus to subg. *Xenolejeunea* revision, Thiers (1992a) recognised five subgenera of the genus Cheilolejeunea; Strepsilejeunea, Euosmolejeunea, Cheilolejeunea and Xenolejeunea. He however observed that several of the subgeneric taxa may be synonymous and reluctantly established a taxonomic key for their identification. As in Schuster (1980a) and Jones (1988), he recognised subg. Strepsilejeunea species having convex leaves with blunt to sharp apices while subg. Euosmolejeunea and subg. Cheilolejeunea have flattened leaves with rounded apices. The latter two are further differentiated by apical tooth of lobule, which is longer, and spiniform in Cheilolejeunea. He revised all the 15 species listed in subg. Xenolejeunea as established by Kachroo and Schuster (1961). He identified important characters as those of stem anatomy, underleaf and the shape of the lobule apex. He retained only 10 species distributed in Australasia, Oceania and tropical Asia, and formalised three sections; Gigantae, Meyeniane and Xenolejeunea. In addition, he reduced subg. Tegulilejeunea to a synonym of subg. Xenolejeunea citing incorrect observation by Schuster (1980a) that the type species Cheilolejeunea excisula (Steph.) Mizut., had bracteoles spread on the entire axis of the androecium. Related plants usually produce strongly inflated lobules on the spicate vegetative branches, which resemble androecia but will only have bracteoles at the base.

Schuster (1992) described cytological characters including cell shape, size, walls, lamellae and intermediate thickenings in 23 species of *Cheilolejeunea* in five subgenera (*Cheilolejeunea*, *Strepsilejeunea*, *Euosmolejeunea*, *Xenolejeunea* and *Anomalolejeunea*). He proposed *Saccophoropsis* and *Pseudopycnolejeunea* as probable new subdivisions. As in his earlier

recommendations (Schuster, 1980a) he reiterated that features of the oil bodies and cell wall, i.e. types of trigones and presence or absence of lenticular or boss-like thickenings of cell wall to be important in delimiting species. Other important characters include the stem anatomy, sexuality innovation and merophyte sequencing. He observed that the cell trigones of subg. *Cheilolejeunea* have a characteristic tendency to be triradiate as well as clear intermediate thickenings. In subg. *Euosmolejeunea* intermediate thickenings are lacking. The latter observation however contradicts his observation of the same (Schuster, 1980a), citing *Cheilolejeunea adnata* (Kunze) Grolle. Schuster (1992) further reiterated on the poor taxonomic understanding of the genus *Cheilolejeunea* terming it as quite 'impenetrable' and contains 'tenuous' boundaries where a species is placed in either of the subgenera.

He (1995) transferred *Pycnolejeunea* species *P. decurrens* Steph. and *P. fitzgeraldii* Steph. to *Cheilolejeunea*. He based his decision on the recommendations by Jones (1973) that *P. decurrens* resembles *P. involuta* and *P. africana*, which have already been sank in *Cheilolejeunea*. Furthermore, Kachroo and Schuster (1961) had reduced *Pycnolejeunea* species with distal hyaline papilla to *Cheilolejeunea* subg. *Xenolejeunea*. *Pycnolejeunea decurrens* is known from a single collection (*Dusén* 803) in Cameroon while *Ch. fitzgeraldii* is distributed in Asia and Oceania including New Guinea and Mauritius. He further noted that *Ch. decurrens* (Steph.) X.-L. He shared features with *Ch. surrepens* and recommended further scrutiny as more material becomes available. He (1996a) also transferred the South American species *Pycnolejeunea decurviloba* Steph. and *P. valenciae* Gott. ex Steph. to *Cheilolejeunea* after he found the original description indicating that they had distal hyaline papillae and lacking ocelli. He found the number of ventral merophytes for the two species to be variable (i.e. 3-8).

He (1996b) reviewed the importance of lobule characters in the family Lejeuneaceae. He supported the observation by Jones (1984) that the number of cells along the free margin of lobule is variable in the genera having distal hyaline papillae including *Cheilolejeunea*. He noted the variation of the character at intraspecific levels and concluded that it has no significant taxonomic value.

A morphotaxonomic treatment showing the phenotypic variations as well as reproductive

structures of the Indian *Cheilolejeunea* was published by Asthana *et al.*, (1995). They recognized nine species and described two new species (*Cheilolejeunea ghatensis* and *Ch. udarii*) in four subgenera; *Cheilolejeunea* (*Ch. intertexta*, *Ch. serpentina*, *Ch. ghatensis*), *Euosmolejeunea* (*Ch. giraldiana* (C.Massal.) Mizut., *Ch. udarii*, *Ch. laeviuscula* (Mitt.) Steph.), *Strepsilejeunea* (*Ch. birmensis* (Steph.) Mizut., *Ch. subopaca* (Mitt.) Mizut.) and *Xenolejeunea* (*Ch. imbricata*). Their subgeneric divisions clearly support Thiers (1992) who combined subg. *Tegulijeunea* with subg. *Xenolejeunea*.

Zhu & So (1999) reviewed phytogeographic data of a well-known afromontane species *Cheilolejeunea pluriplicata* and newly collected in China and Nepal giving detailed description and illustrations. They predicted that the species might have migrated to Laurasia by drifting on the Indian plate northwards during the Tertiary period. Importantly, they noted that when sterile the species is not easily distinguished from the Indian species *Ch. khasiana* (Mitt.) N. Kitag. and postulated that it may occur on that subcontinent. Jones (1988) too observed the difficulties of differentiating *Ch. pluriplicata* from *Ch. krakakammae* when relying on sterile collections. Besides, Zhu & So (1999) maintained the monotypic subg. *Anomalolejeunea* accommodating *Ch. pluriplicata* as proposed by Schuster (1980a). They suggested that it is closely affiliated to subg. *Euosmolejeunea*, differing only by having 6 to 10 keels of the perianth. Jones (1988) included *Ch. pluriplicata* in the subg. *Strepsilejeunea* and, as mentioned above, equated it with *Ch. krakakammae* differing only by bearing the characteristic 8 to 10 keels of the perianth.

Grolle *et al.*, (2001), reduced the neotropical holostipous genus *Cyrtolejeunea*, found in Brazil and Bolivia, to a synonym of *Cheilolejeunea*. As observed by Schuster (1963), they argued that the only difference between the two genera was the sub erect leaves and miniature size of *Cyrtolejeunea*. Their enthusiasm to review the genus was justified by the discovery of two intermediate species, *Cheilolejeunea chenii* R.L. Zhu & M.L. So and *Ch. insecta* Grad. & Grolle, from China and Brazil, and Bolivia in 1999, respectively. Although these two new species had short bifid underleaves, those of *Cyrtolejeunea holostipa* (Spruce) Grolle & R.-L. Zhu also tend to behave the same or are emarginate especially on the female bracts. Furthermore holostipous species such as *Ch. montagnei* and *Ch. mariana* (Gottsche) B. Thiers & Gradst. are found in Africa and Asia respectively. Schuster (1992) had separated *Ch.*

holostipa with small and finely segmented (Jungermannia-type) oil bodies from Cheilolejeunea with large botryoidal Leucolejeunea-Calypogeia type. However, the new species, Ch. insecta, had Jungermannia type of oil bodies as also recorded in Ch. obtusifolia (Steph.) S.Hatt. in eastern Asia.

Studies of Cheilolejeunea in China were recorded by Piipo (1990), So & Zhu (1996), Zhu & So (1996, 1999 & 2001), Zhu et al., (2000) and Zhu et al., (2002). It is however Zhu et al., (2002) who carried out a comprehensive study of all the species existing in the country. They listed 20 species including the description of two new ones. They observed variation of the stem anatomy (e.g. Ch. ryukyuensis Mizut., has 7-20 cortical cells), oil bodies, presence of ocelli (e.g. Ch. insignis Ast & Tixier and Ch. falsinervis (Sande Lac.) Kachroo & R.M. Schust.) as well as perianth characters. Following the observed variation of perianth keels, such as strongly compressed dorsiventral keels in *Ch. obcordata* Herzog (subg. Euosmolejeunea), they suggested that Cheilolejeunea subg. Anomalolejeunea is a synonym of subg. Euosmolejeunea. They reduced subg. Strepsilejeunea to a synonym in subg. Euosmolejeunea citing weak subgeneric characters. Three subgenera including subg. Xenolejeunea were therefore retained in the genus Cheilolejeunea. They delimited the subgenera by features of the lobule type and size, apices of the underleaves (i.e. bifid or entire), subgynoecial innovations and number of keels of the perianth. Species retained in subg. Cheilolejeunea were autoicous, miniature and leaf lobules rectangular or oblong with elongated and spiniform apical tooth. Evidently, therefore, Zhu et al., (2002) seems to have dropped the basic features defining Cheilolejeunea s. str. including stem anatomy and underleaves. Inevitably, some well known species belonging to subg. Cheilolejeunea in Africa such as Ch. intertexta and Ch. serpentina were included in subg. Euosmolejeunea. The species Ch. pluriplicata was found to be strictly corticolous while Ch. intertexta and Ch. trifaria occur in various strata mainly corticolous or epiphyllous (Zhu et al., 2002).

Zhu and So (2001) gave a detailed account of the epiphyllous liverworts of China giving brief descriptions of species taxonomy and ecology. They recorded ten species of *Cheilolejeunea* in this substratum. Some of these included *Ch. trifaria* and *Ch. trapezia* (=*Ch. imbricata*), which are also spread in Africa. The former is usually corticolous but 'occasionally' epiphyllous while the latter is 'typical' epipyllous on trees, shrubs and fern leaves.

While revising *Cheilolejeunea* for Brazil, Gradstein (2003) recognised three subgenera; *Cheilolejeunea*, *Euosmolejeunea* and *Strepsilejeunea*. He distinguished the subg. *Strepsilejeunea* from the rest by the characteristic acute to bluntly pointed and usually recurved lobes. Like Schuster (1963, 1980a), he noted the other two subgenera (*Cheilolejeunea* and *Euosmolejeunea*) had broadly rounded leaf apices. He however failed to indicate the distinguishing characters between them.

A worldwide study of the taxonomy and distribution of *Cheilolejeunea krakakammae* has recently been undertaken by Zhu (2006). According to him, the species is variable in several features such as leaves, lobules, angular tooth, underleaves and perianth keels. After detailed studies of equally variable species *Ch. khasiana* (Mitt.) N. Kitag. found in Asia and *Ch. comitans* (Hook.f. & Taylor) R.M. Schust., known from Australia and New Zealand he concluded they are conspecific with *Ch. krakakammae*. *Cheilolejeunea khasiana* was earlier observed to exhibit perianth, which is mostly ecarinate, but sometimes has 3 to 4 keels (Zhu *et al.*, 2002). He observes that *Ch. krakakammae* is separated from the close allies such as *Ch. laevicalyx* (J.B.Jack & Steph.) Grolle, *Ch. mimosa* (Hook.f. & Taylor) R.M.Schust., *Ch. osumiensis* (S.Hatt.), *Ch. pluriplicata* (Pearson) R.M.Schust. and *Ch. ecarinata* Vanden Berghen by having small shoots which are autoicous. Other peculiar features include the lejeuneoid leaf sequence of gynoecial innovations, perianth that are eplicate with distinct beak, acute to obtuse apices of leaves, usually approximate underleaves and mostly unicellular second tooth of the leaf lobule.

There are *ca*. 80 species of *Cheilolejeunea*, which are widely distributed in subtropical and tropical regions (Thiers, 1997; Zhu & So, 2001; Zhu *et al.*, 2002; Gradstein, 2003; Zhu & Grolle, 2004). Although a global monograph is lacking for the genus, some detailed taxonomic reviews have been undertaken at generic and subgeneric levels especially in North America (Schuster, 1980a), Australia (Thiers, 1997) and Asia (Zhu *et al.*, 2002).

2.2. Status of Cheilolejeunea Taxonomy in Africa

Several collectors such as E. Vanden Berghen, E.W. Jones, F. Stephani, J. Augier, M.J. Wigginton, P. Tixier, S. Arnell, S. Jovet-Ast and T. Pócs have made descriptions of the species in the genus *Cheilolejeunea* in Africa. Except the revisions done by Jones (1954, 1973) on *Cheilolejeunea* in comparison with affiliated genera like *Euosmolejeunea* and *Pycnolejeunea*, most of the descriptions were based on single species observations or general floral checklists of hepatics.

Perhaps the first record of *Cheilolejeunea* on the African continent was made in 1844 by Lindenberg who described *Lejeunea krakakammae* from the Cape Province in Uitenhage, Krakakamma, of South Africa (Gottsche *et al.*, 1845). Several other species, which later proved to be related were described and published at the same time. Since the election of the genus by Schiffner (1983), the majority of the African species have been described by F. Stephani, 18 of which were published in the *Species Hepaticarum* in 1913 and 1914.

Major hepaticological collection missions were made in Africa early 20th century, such as explorations in the 1940s by E.W. Jones. However, publications on *Cheilolejeunea* resumed nearly 25 years after the Stephani publications (1886-1923). For example, Vanden Berghen in association with Jovet-Ast (1951) described a new species *Cheilolejeunea tisserantii* Vanden Berghen et Jovet-Ast (=*Ch. decursiva* (Sande Lac.) R.M.Schust.) from Central African Republic. Arnell (1953) described three new species from South Africa; *Strepsilejeunea georgensis*, *S. knysnana* (which he later transferred to *S. krakakammae*) and *Lejeunea convexa*. He later transferred *L. convexa* to *Cheilolejeunea* (Arnell, 1955).

As mentioned elsewhere, Jones (1954 a & b) reviewed the genus *Cheilolejeunea* in relationship to other close genera. In particular, he supported observations by Evans (1906) that the genus *Euosmolejeunea* was very closely related to *Cheilolejeunea* and difficult to separate them. He also proposed the transfer of some species in *Pycnolejeunea* to *Cheilolejeunea* based on the position of hyaline papilla in lobules.

Arnell (1958) described three new species of hepaticae from Mount Cameroon, one of them as

Cheilolejeunea camerunensis. According to him, Ch. camerunensis differed from other known species in the genus by its triplicate perianth. Five years later, he published his book on the Hepaticae of South Africa (Arnell, 1963) describing Anomalolejeunea pluriplicata Pears., Strepsilejeunea krakakammae (Linden.) Steph., and S. brevifisa (G.) Steph, which where later transferred to genus Cheilolejeunea (Schuster, 1980a; Jones, 1988). He noted that A. pluriplicata was not significantly different from S. krakakammae especially when sterile. He recommended the size and shape of basal cells of the lobes and oil bodies as the distinguishing characters of the species. Nevertheless, as Jones (1988) observed the basal cells are short or rounded in both species and that oil bodies were never seen.

Augier (1972) described *Cheilolejeunea diversifolia* as a new species from Mount Cameroon. According to him, the species is distinct from other taxa by having 4 to 5, or often less, medullary cells of stem and seemingly less compressed perianth. Jones (1976) reduced *Cheilolejeunea silvestris* E.W. Jones to a synonym of *Cheilolejeunea surrepens* (Mitt.) E.W. Jones. However, he did not indicate whether *Ch. silvestris* var. *involuta* should be referred to as *Ch. surrepens* var. *involuta*. Jones (1982) described yet another new epiphyllous species, *Cheilolejeunea exinnovata*, among other African Lejeuneaceae taxa mainly *Lejeunea* species from unexploited primary lowland rainforest in Sierra Leone. The new species also occurs in Ghana, Zimbabwe and Brazil. He noted the distinguishing characters of the *Ch. exinnovata* as the invariable absence of subgynoecial innovation, frequent occurrence of a step between the ventral margin of leaf and keel of lobule. It resembles *Ch. decursiva* in having a spiniform apical tooth of the lobule. He however opined that the Williams collection (no 19RSES) of *Ch. exinnovata* from Zimbabwe might form extreme phenotype or even a different species. The collection is of larger sizes including longer tooth of lobule.

The vegetation and hepatics of Sierra Leone and Ghana were briefly described by Jones and Harrington (1983). They gave detailed information of seven species of the genus *Cheilolejeunea (Ch. decursiva, Ch. intertexta, Ch. newtonii, Ch. exinnovata, Ch. serpentina, Ch. surrepens* and *Ch. trifaria*) with notes on their ecology and taxonomy. They reluctantly maintained *Ch. intertexta* and *Ch. newtonii* separate, despite an earlier suggestion in Jones (1973) to combine them. They based their decision on observation by Grolle (1979) that *Ch. intertexta* has persistent pycnolejeuneoid subgynoecial innovations. Moreover, they noted that

the two species as well as *Ch. serpentina* and *Ch. surrepens* tend to grow mixed together usually on similar habitats except that *Ch. newtonii* may prefer wetter forests. Ecologically most of the species were found to be desiccation tolerant and rather 'xerophytic' supporting observations by Jones (1954b) and Schuster (1980a). They are also occasionally epipyllous as well as corticolous or ramicolous on farms and open or edges of lowland forests. *Cheilolejeunea surrepens* and *Ch. serpentina* grew near the sea level and seemed to tolerate salty and high humid environments. *Cheilolejeunea trifaria*, however, doubled as semi afromontane species.

Pócs (1985) made a checklist of 94-liverwort species of the Usambara Mountains in Tanzania, which included four species of Cheilolejeunea (Ch. decursiva, Ch. surrepens, Ch. brachytoma and Ch. brevifissa). Jones and Harrington (1983) had found Ch. surrepens to be rare in living leaves but in Tanzania it tends to be more epiphyllous whereas *Ch. decursiva* and *Ch.* brachytoma (=Ch. trifaria) are corticolous (Pócs, 1985). It was however surprising to find epiphyllous Cheilolejeunea brevifissa (=Ch krakakammae), a species with less compressed perianth, which is poorly adapted to such environments as observed by Zhu & So (2001). Following the great bryological expedition to Zaire and Rwanda in the early 1990's, Pócs (1994) recorded three afromontane species all affiliated to the African subg. Strepsilejeunea; Cheilolejeunea krakakammae, Ch. pocsii and a new ramicolous species, Ch. omphalogastria. He noted that, except for the longer and rounded lobes of the underleaves, the new species slightly resembles Strepsilejeunea cordistipula Steph (= Ch. cordistipula). According to him, intermediate characters exhibited by the new species such as the largely cordate underleaves and acute apex of the lobes justified the reduction of Euosmolejeunea and Strepsilejeunea to sub generic status by Schuster (1963; 1980a). The new species Ch. omphalogastria has never been recollected despite several visits to the type locality (E. Fischer, pers.com.).

Tixier (1995) collected *Ch. trapezia* (Nees) Kachroo & R.M. Schust. from Zaire extending the range of the formerly Pacific species. Thiers (1992) had reduced this species to synonymy of a variable and common species in Asian and Oceanic species *Ch. imbricata* (Nees) A. Hatt belonging to *Cheilolejeunea* subg. *Xenolejeunea* Sect. *Xenolejeunea*. Zhu & Grolle (2004) confirmed that the two species are conspecific but *Ch. trapezia* should be given priority according to the ICBN nomenclatural rules.

Cytological studies emphasizing the oil body types and range of sizes in various genera of the African hepaticae were attempted by Kis and Pócs (1997). Observations of 200 specimens investigated over a 12-year period distinguished nine different types of oil bodies (*Diplasiolejeunea, Leptolejeunea, Leucolejeunea, Radula, Riccardia, Massula, Bazzania, Jungermannia* and *Calypogeia*). They recognized greater variation of oil body types, which occur even on individual leaf of a species and coined intermediate oil body types to accommodate such variations. The *Cheilolejeunea* oil bodies were of *Leucolejeunea* type, which are 1-2 (-5) in number, medium to very large, coarsely botryoidal and crescent shaped, as observed by Schuster (1992). They however observed intermediate type, *Calypogeia*, which is usually present and can occur even in an individual leaf mixed with *Leucolejeunea* type.

Chuah-Petiot (2003) listed eight species of *Cheilolejeunea* occurring in Kenya and briefly described four of them giving diagnostic keys and distributions. She mainly used the leaf apex characters but did not state the species affiliation to the various subgenera of *Cheilolejeunea*. A comprehensive taxonomic revision of West African Hepaticae is credited to Wigginton (2004a), who compiled descriptions of 12 species of *Cheilolejeunea* in the *E.W. Jones*' Liverwort and Hornwort Flora of West Africa. The publication was in the honour of E.W. Jones tireless efforts in contribution to the African bryology. Like most of his predecessors, he noted difficulties in the infrageneric descriptions. He tentatively described three subgenera namely Cheilolejeunea (Ch. decursiva, Ch. diversifolia, Ch. exinnovata, Ch. intertexta, Ch. newtonii, Ch. serpentina, Ch. surrepens), Euosmolejeunea(Ch. montagnei, Ch. trifaria) and Strepsilejeunea (Ch. camerunensis, Ch. usambarana). He however left Ch. cordistipula unranked in any of the three subgenera. Like Jones (1988), he associated the species with subg. Strepsilejeunea but noted the species lack brown pigmentation. He also observed that characters of Ch. diversifolia key to either Ch. intertexta or Ch. surrepens. This indicates that Ch. diversifolia could be one of the extreme forms of either of these two species. Further, Wigginton downgraded Ch. decurrens to synonym of Ch. surrepens as suggested by He (1995).

Cheilolejeunea is to date represented by 23 species recorded on the mainland Africa (Grolle, 1995; Wigginton & Grolle, 1996; Wigginton, 2004b). They are listed in Wigginton (2004b) as

follows: Ch. camerunensis, Ch. convexa, Ch. cordistipula, Ch. decursiva, Ch. diversifolia, Ch. exinnovata, Ch. intertexta, Ch. krakakammae, Ch. latiflora, Ch. laurentii, Ch. montagnei, Ch. newtonii, Ch. omphalogastria, Ch. pluriplicata, Ch. pocsii, Ch. rufescens (Lindenb.) Grolle, Ch. ruwenzorensis (S.W. Arnell) R.M. Schust., Ch. serpentina, Ch. surrepens, Ch. trapezia, Ch. trifaria, Ch. usambarana and Ch. sp. (= Strepsilejeunea vatovae Gerola, Cheilolejeunea vatovae). Several of these are of narrow distribution and known from few collections. Other species like Ch. latiflora, Ch. laurentii, Ch. rufescens and Ch. vatovae a little known (Jones, 1954b; Wigginton, 2004b). Despite the recent revision of the genus in other continents, there is no modern and comprehensive taxonomic evaluation in African. As mentioned elsewhere, the species descriptions are opportunistic based on general checklist of hepatics, new species or extension of range. Identification keys as well as subgeneric and generic delimitations in accordance to the taxonomic advancement of the genus in Lejeuneaceae are lacking as attested by Jones (1988). For example, the subg. Xenolejeunea seems to have been ignored in the continent despite species such as *Ch. surrepens* exhibiting clear affiliation (Jones, 1954b; Harrington & Jones 1973). The need of such a revision is also necessitated by the continued discovery of new species in other regions, some related to African taxa.

CHAPTER 3. Methodology

3.1. Morphology

Morphological data was obtained from dry specimens preserved at the East African Herbarium (EA) and others exchanged or sent on loan from the herbaria at Bolus, Cape Town University (BO), Botanical Gardens of Malawi Herbarium (NHBG), British Museum (BM), Brussels (B), Eger (EGR), Geneva (G), Paris (P), Pretoria (PRE) and University of Koblenz-Landau. The observations were augmented with data from fresh specimens collected from Kakamega Forest, Mumoni, Ngong and Cherengani hills in Kenya. Others included Budongo and Mabira Forests in Uganda, Nyungwe Forest in Rwanda, Minlova Inselberg in Yaounde, Cameroon, and Gabon. Specimens were observed by placing the whole collection on the dissecting microscope and the required specimen searched. A drop of distilled water was then applied on the specimen to moisten and avoid breaking of the brittle parts. Observable material of the desired plant part(s) was isolated or sorted out and placed on a glass slide exposing both sidesventral and dorsal. Dissection was carried out to ease observation of medullary cells of the stem, ventral merophytes of the stem, sequence of leaf innovation, apical or free lateral margin of leaf lobule, leaf shape and cells, insertion of leaf lobule and underleaf to stem, and sporophyte. Transverse sections of stem, leaves and perianth were made by hand using a sharp blade. The measurements of the plant parts were made using a graticule inserted in the microscope eyepiece. Illustrations of the species parts were made from images taken using a digital camera and traced on drawing paper. Oil bodies from fresh plant collection were observed under a light microscope at least within a day or before two weeks after collection and photographed without chemical treatment. The data obtained was analysed using both phenetics and phylogenetic methods to establish the species relationships.

3.1.1. Phenetics

The phyletic approach to taxonomic classification was noted to be subjective citing the manner of selecting different characters and character states using the comparisons and consequent ranking of groups formed (Sokal & Sneath, 1963; Sneath & Sokal, 1973). Sokal and Sneath attempted to reduce the subjectivity of the groupings experienced in phyletics by considering assigning equal weight to all the phenological characters of a taxon irrespective of ancestral or evolutionary affiliation. In addition, they emphasized quality and precise

descriptions and measurement as well as standardising the data analytical procedures. They recommended application of authenticated numerical analytical methods. Phenetics, defined by Stuessy (1990) as a classification based on numerous precisely delimited and carefully coded characters and character states of equal weight and their comparison by an explicit method of grouping, was therefore born. Sneath (1976) finds phenetic analysis valuable at all taxonomic ranks. On the hand, Stuessy (1990) and Jessen (2006) recommend more applications of phenetics methods in the delimitation of taxa at species and infraspecific levels. However, Sneath (1976) cautions that phenetic methods are sometimes faced with some difficulties such as determination of homologies, incompleteness of data and shortage of constant characters.

The operation of phenetic classification involves the selection of individuals or taxa 'not necessarily species' of study usually referred to as Operational Taxonomic Units (OTUs). The number of OTUs required to represent a homogeneous cluster is estimated to be at least 10 and preferably 25 or more (Sneath, 1976). When the OTUs are known, characters are then selected and description and/or measurements of the character states are undertaken. The data for the OTUs is coded into a matrix and overall similarity between each individual pair of OTUs is determined through grouping of the units using appropriate taxonomic analytical system with the help of computers. The OTUs are then sorted into clusters according to overall similarity based on Euclidean Distance. The greater the disparity between two OTUs the greater will be their distance and the more likely group of OTUs will be drawn into different ranks in a phenogram or dendrogram.

Twenty-three species of the genus *Cheilolejeunea* and three species in the genus *Leucolejeunea*, occurring in continental Africa were studied in detail. The herbarium studies were supplemented with literature surveys and field observations in tropical forests of Kenya (Kakamega, hills of Ngong, Mumoni, Nuu, Mutha and Cherengani) and Uganda (Budongo and Mabira Forests). Thirty-two taxonomically informative characters including substratum preference and geographical distribution were selected for study as listed in Table 3.

Table 3. Character and character states coded for phenetic analysis

Character	Character	State
number		
1.	Vegetative branches	Mainly <i>Lejeunea</i> type (few <i>Frullania</i> type) (0); mainly or exclusively <i>Frullania</i> type (1); exclusively <i>Lejeunea</i> type (2)
2.	Plant width	$< 1.1 \text{ mm } (0); \ge 1.1 \text{ mm } (1)$
3.	Stem diameter	$\leq 100 \mu \text{m} (0); > 100 \mu \text{m} (1)$
4.	Ventral merophytes	mostly 2-3 (0); 4 or more (1)
5.	Size of epidermal cells	Distinctly larger than medullary cells (0); not (or scarcely) larger than medullary cells (1)
6.	Thickening of epidermal cell walls	Not or scarcely thickened (0); clearly thickened (1)
7.	Lobes	Caudicous (0); semi caudicous (1); not caudicous (2)
8.	Lobes orientation	Flat (0); shallowly to Strongly convex (1)
9.	Lobe shape	Ovate or so (0); ovoid to orbicular or oblong (1)
10.	Lobe apex shape	Acute or subacute (0); broadly rounded or rounded(1)
11.	Lobe apex orientation/ recurved	Plane or rarely shortly recurved (0); strongly recurved (1)
12.	Mean leaf length	$\leq 550 \ \mu m (0); >550 \ \mu m (1)$
13.	Lobe Length/lobe Width ratio	$\leq 1.2 (0); 1.3-1.4 (1); \geq 4 (2)$
14.	Oil body size/number or type	Large, filling the lumen/ \leq 5, Leucolejeunea or rarely Calypogeia type (0); small />5, other types (1)
15.	Ocelli	Absent (0); present (1)
16.	Trigones	Small-medium, without intermediate thickening/ $\leq 6 \mu m$ (0); large/ $\geq 7 \mu m$, without intermediate thickening (1); various size, with intermediate thickening (2); absent (3)
17.	Lobule shape	Cylindrical-triangular (0), rectangular-oblong (1)
18.	Lobule/ lobe length	<0.5 (0), ≥0.5 (1)
19.	Lobule free margin	Recurved / semi-flattened(0); Flattened-visible (1)
20.	Lobule free marginal cells	<7 (0); usually 8-12 (1); usually ≥13 (2)
21.	Hyaline papillae	Distal (0); proximal (1)
22.	Underleaf, width/stem	<4 (0); ≥4 (1)
23.	Underleaf length/width ratio	Longer than wider/> (0); orbicular/wider than longer/ \leq (1)
24.	Underleaf apex type	Entire/retuse (0); bifid (1)
25.	Underleaf, length/sinus	$0(0); 1/10-(1/4)1/3(1); \ge 2/5(2)$
26.	Seta cross section: number of cells	> 20, \ge 2 circles (0); 20 (4 + 16), 2 circles (1); 16 (4 + 12), 2 circles (2)
27.	Lobule width at base/ Lobule width at apex ratio	<0.5 (0); ≥0.5 (1)
28.	Lowland (0-500 m)	No (0); Yes (1)
29.	Submontane (ca.500-1400 m)	No (0); Yes (1)
30.	Lower montane (ca. 1450-2000 m)	No (0); Yes (1)
31.	Upper montane (2050-3000 m)	No (0); Yes (1)
32.	Subalpine (>3000 m)	No (0); Yes (1)

3.1.2. Phylogeny

Phylogeny, commonly referred to as cladistics, is a branching diagram or cladogram that shows the most recent common ancestor shared between a species or group of species (Stuessy, 1990). Like in phenetic classification, phylogenetic analysis seeks to introduce objectivity to the analytical data. The character states used to determine routes of evolutionary change are selected *a priori* in phylogenetic reconstruction as opposed to overall importance of characters in phenetic methods. This approaches however employs the principle of parsimony inference founded by Wagner (1980) and Henning (1966) in which a phylogenetic tree is best regarded if there are less evolutionary changes in a character state (Stace, 1989).

In phylogenetic analysis, characters are analyzed to distinguish between *homologies* i.e. characters shared between two or more species that were present in their common ancestor, from *analogies* i.e. characters shared between two or more species that were not present in their common ancestor. Homologous characters will have in principle the same structure, related to the surrounding parts and well developed in a set of species (Stuessy, 1990). Once then homology is established, the polarity of change in a character state is determined using either fossil evidence or, more practically, out group comparisons (Stace, 1989; Stuessy, 1990; Judd *et al.*, 2002). This involves dividing the characters into *plesiomorphies* i.e. those shared with the common ancestor or primitive one, and *apomorphies* i.e. those which evolved in the common ancestor and not shared with other distant relatives or derived ones.

The fundamentals of parsimony requires establishment of an 'unrooted' and 'rooted' tree. A rooted tree will help to deduce the position of the deepest ancestor of a group of species. An unrooted tree on the other hand is less informative than the rooted tree since it will only show the branching patterns and relationship between the species without indication of most recent common ancestor or time dimension. Whilst a rooted tree can be matched with one unrooted tree, the unrooted tree will lock with a number of possible rooted trees, resulting in only one 'true' tree, depending on the root cause. The method of parsimony inference therefore involves two stages. Firstly, the unrooted tree of a group of species is estimated and secondly the root or ancestor is located. All the possible unrooted trees for a group of species are inferred and then the minimum numbers of evolutionary events are enumerated using most

informative shared character states. It is advisable therefore to isolate the most informative characters from the continuum of characters to arrive at the shortest evolutionary pathway. This introduces *a priori* selection of characters used to determine species relationships and routes of evolutionary change in phylogenetic analysis.

Table 4. Character and character states used in phylogenetic analysis

Character number	Character	State State
1.	Vegetative branches	Mainly <i>Lejeunea</i> type (few <i>Frullania</i> type) (0); mainly or exclusively <i>Frullania</i> type (1); exclusively <i>Lejeunea</i> type (2)
2.	Plant width	$< 1.1 \text{ mm } (0); \ge 1.1 \text{ mm } (1)$
3.	Stem diameter	$\leq 100 \ \mu m (0); > 100 \ \mu m (1)$
4.	Ventral merophytes	2 or 3 (0); 4 or more (1)
5.	Size of epidermal cells	Distinctly larger than medullary cells (0); not (or scarcely) larger than medullary cells (1)
6.	Thickening of epidermal cell walls	Not or scarcely thickened (0); clearly thickened (1)
7.	Lobes	Caudicous (0); semi caudicous (1); not caudicous (2)
8.	Lobes orientation	Flat (0); shallowly to strongly convex (1)
9.	Lobe shape	Ovate or so (0); ovoid to orbicular or oblong (1)
10.	Lobe apex shape	Acute or subacute (0); broadly rounded or rounded(1)
11.	Lobe apex orientation/ recurved	Plane or shortly recurved (0); strongly recurved (1)
12.	Mean leaf length	$\leq 550 \mu \text{m} (0); >550 \mu \text{m} (1)$
13.	Lobe Length/lobe Width ratio	\leq 1.2 (0); 1.3-1.4 (1); \geq 4 (2)
14.	Oil body size/number or	Large, filling the lumen/ ≤5, <i>Leucolejeunea</i> or rarely
	type	Calypogeia type (0); small />5, other types (1)
15.	Ocelli	Absent (0); present (1)
16.	Trigones	Small-medium, without intermediate thickening/ ≤6 μm (0); large/ ≥7 μm, without intermediate thickening (1); various size, with intermediate thickening (2); absent (3)
17.	Lobule shape	Cylindrical-triangular (0), rectangular-oblong (1)
18.	Lobule/ lobe length	<0.5 (0), ≥0.5 (1)
19.	Lobule free margin	Recurved / semi-flattened(0); Flattened-visible (1)
20.	Lobule free marginal cells	$<7 (0)$; up to 12 (1); \ge 13 (2)
21.	Hyaline papillae	Distal (0); proximal (1)
22.	Underleaf, width/stem	<4 (0); ≥4 (1)
23.	Underleaf length/width ratio	Longer than wider/> (0); orbicular/wider than longer/ \leq (1)
24.	Underleaf apex type	Entire/retuse (0); bifid (1)
25.	Underleaf, length/sinus	$0 (0); 1/10-(1/4)1/3 (1); \ge 2/5(2)$
26.	Seta cross section:	$> 20, \ge 2$ circles (0); 20 (4 + 16), 2 circles (1); 16 (4 + 12),
	number of cells	2 circles (2)
27.	Lobule width at base/ Lobule width at apex ratio	<0.5 (0); ≥0.5 (1)

Evolutionary Units (EUs) are the basic units subjected to phylogenetic analysis. A data set for the primitive characters in relationship to the derived character states is obtained to form a matrix. The matrix is then analysed to obtain cladograms based upon the minimal (most parsimonious) way in which the EUs can be connected to account for the data in the matrix. The nodes in a cladogram are considered to represent hypothetical ancestral monophyletic taxonomic units (Stace, 1989).

In this study, 27 character states of morphological and sporophyte data were selected and coded as shown in table 4 above. The resultant matrix was analysed using PAUP4.0b4a for Macintosh (Swofford, 1999).

3.1.3. Bryogeography of Cheilolejeunea in Africa

The establishment of spatial distribution of bryophytes, or simply "bryogeography," is key to bryological studies. This is because floristic analysis, which involves grouping together species with related distribution patterns, can assist to deduce the origin and evolution of a flora (Stace, 1989; Shaw & Goffinet, 2000). Recent studies in bryology based on molecular phylogeny and taxonomy abound, but investigations of phytogeography are minimal (Pócs, 2006).

Conflicting hypothesis have been put forth concerning the factors contributing to wide distributions of majority of bryophytes as given by Zanten & Pócs (1981), Shaw (2001), Shaw & Goffinet (2000), Gradstein & Pócs (1989) and Schofield & Crum (1972). The majority of the bryophyte species have small sized spores (<25 µm). They are also commonly dioicous and several such as *Radula*, frequently produce gemmae and abundant gametophytic materials. The spores of such species are therefore transported easily across landscapes and continents either by air currents as jet stream in upper atmosphere or by insects or birds in case of sticky spores (Schofield & Crum, 1972; Shaw & Goffinet, 2000; Shaw, 2001). Spores of the majority of tropical rainforest hepatics are however intolerant to desiccation, extreme temperatures and high UV radiation. Their dispersal is slow occasioned through forest as well as island or mountain hopping. Other taxa such as the lowland tropical rainforest Lejeuneaceae have large multicecullar spores, 40-60 µm, and are unlikely to be dispersed through air currents in large quantities over long range. They have the advantage of being mostly

autoicous, which increases their chances of successful establishment after the spore translocations (Gradstein & Pócs, 1989).

Bryophytes have well defined patterns of disjunctions especially at infraspecific levels despite the broad geographical distributions. At generic level, they depict the discontinuous distribution of angiosperms, usually induced by ancient vicariance associated with continental movements and global climate change during the tertiary and quaternary periods (Shaw & Goffinet, 2000; Shaw, 2001). Show and Goffinet (2000) categorized tropical Africa into four major bryological patterns namely Arctic-alpine, boreal, north and south temperate and tropical distributions based on worldwide climatic zones. Pócs (1992) further noted a very close association between the Asia-Oceania and African bryoflora especially at the species level.

The bryogeography of the genus *Cheilolejeunea* in Africa was investigated in accordance to the seven-phytochorian range of endemism listed by Shaw and Goffinet (2000). An eighth distribution centre, lowland tropical rainforest, was however introduced. This accommodates species restricted to lowland altitudes with wet and humid climates found in West through central to East Africa (as defined by Bizot & Pócs, 1982). The altitudinal distribution of the *Cheilolejeunea* species was analyzed according to the five-altitudinal belts developed by Frahm and Gradstein (1991). This was also used by Dauphin (2000) with some modifications. Subsequently, the altitudinal zonation of *Cheilolejeunea* species in Africa was coded and applied in the phenetic analysis, Table 3, in order to find out whether their distribution was correlated to adaptations of various climatic regimes.

3.2. Ecology and Conservation Status of *Cheilolejeunea* in Kakamega and Budongo Rainforests

3.2.1. Introduction

Tropical lowland rainforests are complex and characterised by a variety of microhabitats. They harbour a diverse bryophyte flora estimated to be about thirty percent of all bryophytes in the world (Gradstein & Pócs, 1989). Richard (1984), Gradstein (1995) and Frahm (2003) indicate that the distribution of bryophytes in the tropical forests is largely dependant on the

altitude, humidity of the air, the total annual rainfall, and seasonal environmental changes such as droughts and temperature regimes. Further, Pessin (1922) stressed the importance of high humidity and moderate temperature for epiphytic bryophytes to flourish. Unlike in most vascular plants, the gametophytes of bryophytes are poikilohydric and absorb moisture from the environment to equilibrate with the ambient vapour pressure. Frahm (2003) states that although desiccation of species is specific, bryophytes are known to have most turgidity at relative humidity of about 80 and above and many will start to wilt below this mark. In addition, different bryophyte communities in the rainforest are attributed to the forest type, microhabitat, substrate and height of the tree including bark texture (smooth, fissured, flaky, or striped), and some have been found to be host specific (Gradstein, 1992).

The bryoflora in the warm lowland tropical forests is largely dominated by pantropical families like Calymperceae, Hookeriaceae and Lejeuneaceae (Gradstein & Pócs, 1989; Gradstein, 1992). The species are usually transoceanic and few are endemic probably due to younger age and isolation of upland regions. It could also arise from assumed lower speciation rates in these regions. These intercontinental disjunctions arise owing to short range or long-range air dispersal of the spores. Long range species have spores that are drought resistant and can survive freezing up to minus 30°C thus are able to migrate over long distance under heavy rains. They are usually common as pioneer species in secondary forests or habitats, largely autoicous and adapted to the forest crown or forest margins. Majority of the species such as in Lejeuneaceae are characterised by endosporous protonemata. This allows rapid germination soon after the spore is released from the capsule and hence a high proliferation in the rainforests despite frequent alteration of the forest structure (Gradstein, 1992).

Most of the species in the lowland rainforests are epiphytic, inhabiting tree trunks, branches and twigs or leaves. The desiccation-tolerant species characteristically occur in compact tufted or mat forms closely appressed to the substrate and thread-like growing amongst other species. Good examples include members of Lejeuneaceae family, which occupy the twigs and branches of the upper canopy in climax primary forest and occur on the trunks only in disturbed ones. They may also be common in secondary forest on the lower structure of the forest. The sun epiphytes are commonly profuse spore producers and are widely distributed. Shade tolerant species however produce few spores and usually exhibit asexual reproduction

(Richards, 1984).

Bryophytes offer enormous support to the lowland rain forest ecosystem despite their small and inconspicuous sizes. They act as reservoirs of rainwater, which assist in regulation of forest humidity (Pócs, 1980), and are reliable substrates for anchorage of various organisms such as vascular plants, invertebrates and micro organisms. The short life cycle and ability to react rapidly to environmental changes makes them suitable in monitoring pollution levels and indicators of forest quality (Gradstein, 1992 & 1995).

Tropical rainforests have become increasingly fragmented following high deforestation rates especially in the developing countries. Forest destruction is often triggered by increase in human population in search of land for cultivation, food and pasture, among other factors. The forests are sensitive ecosystems. Any environmental changes usually lead to alteration of species composition and may result in decline in biodiversity and even species extinction. Forest remnants are usually in different stages of development and structure. Secondary forests, which arise from disturbance, have tree composition dominated by fast growing species. In case of selective logging, mixed primary forest and weedy secondary vascular species colonize emerging gaps (Gradstein, 1992).

Secondary tropical forest fragments are dominated by several desiccation tolerant species of bryophytes. They also exhibit less diversity of species as compared to the primary forests (Pócs, 1982). In contrast, Fischer (2004) recorded higher diversity of lichens and bryophytes in the secondary remnants as compared to the primary forests in the lowland rainforests of Kakamega in Kenya.

3.2.2. Kakamega Forest

Kakamega forest is known to be the eastern-most relic of the Guineo-Congolean tropical forest basin closely related to most of the tropical forest of western Uganda. Some common peculiar species are *Pouteria altissima* (A.Chev.) Baehni, *Harungana madagascariensis* Poir, *Maesopsis eminii* Engl. and *Englerophytum oblanceolatum* (S. Moore) Pennington (Fischer, 2004). The forest is found about 43 km north of Lake Victoria in the Western Province of Kenya. It lies between latitudes 00°08'30.5" N and 00°22'12.5" and longitudes 34°46'08" E

and 34°57′26.5° E. Most of the forest area lies on flat to undulating terrain with a few steep hills rising abruptly above the general elevation range of 1500 to 1700 m above sea level. It is mainly underlain by acid and basic volcanic lava rocks of the Kavirondo and Nyanzian age. The annual average rainfall is about 1500 to 2300 mm, which is well distributed throughout the year. They emanate from Intertropical Convergence Zone (ITCZ) influenced by the close proximity to Lake Victoria. The rains peak from April to November and a short dry spell is experienced between December and January (KIFCON, 1994). The average monthly temperatures have been recorded to be between 11°C and 29°C. Althof (2005) found the humidity in the forest correlated with the environmental conditions of any of the studied site and that it was inversely correlated with temperatures. The more open an area the less the humidity was found.

The forest is bordered on the eastern side by the Nandi Hills escarpments, which stretch north to south and are capped with indigenous forest patches. It is largely surrounded by densely populated area of intensively cultivated farms with maize, tea and sugarcane. The human activities, pose great pressure to the forest resources constantly extracting timber, fuelwood, fodder and thatch. Major forest disturbances appeared in the 1930's following heavy forest clear-felling or selective logging and plantation establishment using exotic species (Mitchell, 2004).

Illegal forest destruction continued in some areas despite formal timber extraction ban in 1975. To date the forest exists in five main fragments consisting of the Kakamega main forest (8537 ha), Ikuywa (1370 ha), Yala (1199 ha), Kisere (420 ha), Malava (190 ha) and Kaimosi (132 ha) as found by BIOTA (2004). Kokwaro (1988), Tsingalia (1990), KIFCON (1994) and Mutangah (1996) have studied the vegetation and floristic status of the forest. The recent studies by BIOTA (2004) and Althof (2005) established the most comprehensive status especially on the different vegetation associations and floristic composition of the various forest fragments. They divided the forest fragments into five classes based on vegetation succession stage and plant community types as shown in the Table 5.

Table 5. Vegetation succession status in Kakamega Forest

Succession stage	Vegetation type	Sites
Young secondary	Harungana madagascariensis -	Buyangu, Camp forest, Vihiga,
forest	Bridelia micrantha	Isiukhu
Middle aged	Antiaris toxicaria-Funtumia africana /	Salazar, Busambuli, Shiamololi,
secondary forest	Craibia brownii-Croton	Buyangu hill, Colobus,
	megalocarpus-Celtis mildbraedii	Ghostland, Isecheno, Ikuywa
Old secondary	Antiaris toxicaria-Funtumia africana /	Yala, Buyangu hill top
forest	Craibia brownii-Croton	
	megalocarpus-Celtis mildbraedii	
Near primary	Antiaris toxicaria-Funtumia africana	Kisere
forest		
Plantation forest	Planted species e.g. Bischofia	Malava, Kaimosi, Kibiri, Ileho
	javanica, Maesopsis eminii	

3.2.3. Budongo Forest

Budongo Forest Reserve is situated in western Uganda between latitude 1°37' to 2°00' N and longitude 31°22' to 31°6' E along the Albertine Rift, east of the western Rift Valley escarpment and lake Albert within Hoima and Masindi districts. It is found in a gently sloping and well-drained topography with a mean altitude of 1100 m a.s.l. Altogether, it comprises close to 435 km² of continuous forest cover consisting of semi-deciduous species. It is underlain by Precambrian gneiss, schist and granulites rocks and ferrallitic soils (Karani, *et al.*, 1997; Babweteera, 2002; Reynolds, 2005). The rainfall varies between 1340 mm and 2187 mm per annum with a mean of 1600 mm. The rainfall is well distributed over the year with most rain falling in the March-May and September-December period. A short dry spell is experienced between December and February.

Vegetation changes and succession regimes have been discussed by Eggeling (1947), Horward (1991) and Plumptre (1996). Howard (1991) classified the forest into three types thus dominated by *Celtis, Cynometra* and *Khaya* species. Eggeling (1947) had already observed similar associations including swamp-like vegetation along some parts of the Sonso River. He noted that colonizing species such as *Maesopsis eminii* Engl. are later replaced by mixed forest of *Cynometra alexandri* C.H. Wright with *Khaya anthotheca* (Welwitsch) C. DeCandolle as emergent, which finally form climax forest characterised by general paucity of species.

Logging of the valuable timber such as the *K. anthotheca* and *Entandophragma utile* (Dawe & Sprague) in Budongo Forests started around 1910 and intensified with the gazettement of the forest by the British administrators in the early 1930s through cyclical regimes of 40 to 80 years. Largely, regeneration of the forest has been natural after a short stint of enrichment planting was found inferior to the former. In the 1950s and 1960s, arboricides were applied in the forest to suppress the weedy, less valuable species like *C. alexandri* (Reynolds, 2005). Major harvesting of the forest was discontinued in the mid 1970s and 1980s owing to increased political instability and since then exploitation has been selective either legally or illegally.

Sampling was carried out within the area of the field research station in compartments W3/4, W22 and N15. Compartment W22 and N3/4 were harvested at different regimes between 1960 and 1980s. Although the forest regeneration is good, they lack distinct canopy storeys, and sometimes have dense cover of young shrubs and trees in the understorey. Compartment N15 designated as a forest nature reserve since 1930s has never been harvested. It is typical mature rainforest characterised by four distinct canopy storeys. Besides the dominant canopy species as *Cynometra* and mahoganies in the upper canopy, the lowest storey between 10 and 12 m is made of largely *Rinorea beniensis* Engl. Because of the dense canopy strata, the ground is heavily shaded and lacks a shrub layer in many areas (Wagner, 2001). However, fallen trees due to wind throws of the old trees have created some gaps in a few areas.

3.2.4. Sampling techniques

Six study sites namely Colobus, Campsite, Salazar, Kisere, Yala and Isecheno were selected in Kakamega Forest and three (Compartments N3-N4, W22 and N15 within the field station research area as mentioned above) in Budongo Forest, Uganda. In each of these nine sites, transects ranging from 500 m to 1000 m were established along the disturbance gradient to capture different forest types and age structure. Where possible, the transects ran from forest edge, through young secondary forest, characterised by *Harungana madagascariensis* mixed with *Psidium guajava* bushes to more advance secondary vegetation. In Budongo forest, however, transects were laid only in the main advanced forest vegetation because there was

less recent disturbance or edge effect and age structure is over 20 years.

Transects were divided into several points of 10 m interval in young and old secondary or primary forest in each site. Sixteen sampling plots were then selected randomly for each of the succession stage for every study site. This was on the assumption that *Cheilolejeunea* species are distributed in a ratio of 4 to 1 between the young and old secondary or primary forest conditions. Thus, at least 32 sample plots were targeted in each study site. Exceptions included all the three sites in Budongo Forest and Isecheno in Kakamega Forest with more or less uniform age structure and disturbance history. Such sites also experienced minimal edge effect. In this case, only 16 sample plots were established.

In each of the selected sample plots, Point Centred Quadrants' (PCQ) method was used to establish four sub-quadrants. One sub-quadrant was then selected randomly and the nearest tree identified. In every selected tree, one relevé of 25 by 25 cm was established using a well marked and subdivided wire mesh. With a minimum of 16 sample plots studied in each site, a total of 276 relevés were established. The relevés were located at different heights up to 3 m high depending on the location of the chosen microhabitat on the phorophyte tree trunks. In addition, trees fallen owing to natural effects like windy rainfalls or anthropogenic factors including ecological indicator tree species such as *Polyscias fulva* (Hiern) Harms, *Harungana madagascariensis* and *Funtumia africana* (Benth.) Stapf. were examined for the presence of *Cheilolejeunea species*.

The presence or absence of *Cheilolejeunea* species was noted and the data on the general bryophyte flora in each of the 276-substrate relevés were recorded. Other parameters recorded included species density, frequency and cover. The compass direction (e.g. North or South) of the established relevés were also recorded. Relative humidity and temperature were recorded at least for two bright days in different seasons using portable calibrated data loggers (GLM Version 2.3) and hygrometer. The data loggers were calibrated to record both temperatures and humidity data in every minute for a length of one hour taken between 12. 00 and 1 p.m. Frahm (2003) found humidity in such forests to decrease with the rise of the sun experiencing various values over the day, which depends on insulation may be due to forest cover or clouds, and increase again in evening with the fall of temperatures. It usually reaches the peak around

noon. Most of the lowland forests in the examined areas will experience rains usually by 1 p.m. or so and therefore measurement of the abiotic factors between noon and 1 pm was ideal since it avoids low temperatures of the early morning and sudden fall of the same and increase of humidity in the afternoon due to imminent rains. The person recording data was therefore compelled to be at the one end of the transect to start reading the measurements and time for every sample relevé along the transect. Humidity and temperature records were in addition taken from different positions of the transect for the one hour period to avoid skewed data as temperatures may tend to increase as time advances. The readings of the data loggers and generated graphs were downloaded into a laptop computer.

In addition, the tree diameter, height and canopy cover as well as the diversity of vascular plants were also recorded. In the primary forests, presence of *Cheilolejeunea* species was documented through collection of fallen branches or leaves of trees and where possible vertical structure on the fallen mature trees occasioned by wind or storm. General surveys of bryophytes and particularly *Cheilolejeunea* species were also undertaken in other sites of both Kakamega (Buyangu, Busambuli, Isiukhu and Malava) and Budongo (Compartment N2 around the Royal mile and compartment W21) forests.

Sørensein similarity index was calculated between different forests as follows; SI = (2C)* 100/ A+B, Where A= total number of species in site A, B=Total number of species in site B and C= is the common species between the two sites.

CHAPTER 4. RESULTS

4.1. Morphology and Anatomy

4.1.1. Sporelings

Spores in the genera of Lejeuneaceae are shed from the chlorophyllose capsule. After dispersal, the spore elongates and forms three walls at right angle with the long axis containing four cells. A wall is then formed parallel to the long axis in each of the four cells to produce a unistratose thallus of 2x4 cells, with a papillose cell wall from the exospore. An apical cell with two cutting faces develops from one of the cells. The activity of this cell produces a secondary thallus with smooth cell walls, which is first two cells wide, but through irregular, almost periclinal division, becomes four cells broad (Figure 1). After several divisions, the apical cell transforms into an apical cell with three cutting faces, which produces a juvenile leaf shoot (Goebel, 1930).

4.1.2. Merophytes

Merophytes originate from three cutting faces of the apical cell. The two lateral merophytes produce leaves. A ventral merophyte produces underleaves and rhizoids (see underleaves and rhizoids, 4.1.7). The width of ventral merophytes, expressed as the number of epidermal cell rows across the ventral surface of stem between and below the opposite bases of underleaf, is a measure of the robustness of the stem and an important character in taxonomy of Lejeuneaceae (Wigginton, 2004a). The ventral merophytes in *Cheilolejeunea* are basically two but robust species like *Ch. trapezia* and *Ch. cordistipula* may have 3 or 4. It has been used to separate *Cheilolejeunea* from *Leucolejeunea*, known to have 4 or 6 (8) merophytes, until recent studies in Asian species showed some overlap (e.g. Zhu *et al.*, 2002).

4.1.3. Stem anatomy

The anatomy of the stem in subfamily Lejeuneoideae has been studied by Evans (1935), Kachroo & Schuster (1961), Bischler (1964) and Thiers (1992a). The stem of *Cheilolejeunea*, like other lejeuneoids, is composed of seven cortical rows in cross section (2 ventral, 2-3 lateral), and a variable number of (4 i.e. *Ch. diversifolia*) 10-21 smaller medullary cells. The cortical cells are \pm thick-walled and usually constant, but sometimes may increase to eight or

more. Although the stem anatomy has been found stable for the genus (Thiers, 1992a), Zhu *et al.*, (2002) observed variations in several species such as *Ch. imbricata* and *Ch. ryukyuensis* where the medullary cells can be up to 46 in well developed stems. However, as Schuster (1980a) insists that old and mature stems should be used in stem anatomy, the observations by Zhu *et al.*, So (2002) should be taken with some caution. Cross sections of old stem in the slender *Leucolejeunea rotundistipula* consistently showed possession of 7 cortical cells, casting doubt on the actual difference between *Cheilolejeunea* and *Leucolejeunea*. Evans (1935) and Bischler (1966) observed linear reduction pattern of cortical and medullar cells. I observed *Leucolejeunea* pattern of many undifferentiated cells in young shoots of *Cheilolejeunea* that reduced tremendously, with corticular cells forming hyalodermis, at the basal old parts.

4.1.4. Branching

The branching patterns in Lejeuneaceae are described in Mizutani (1970) and Thiers (1985). The detailed branch patterns are ascertained by Crandall-Stotler (1972). The *Cheilolejeunea* species exhibit the *Lejeunea*-type i.e. branches originating from the lateral side of the stem, from behind a leaf (Figure 1). They consist of basiscopic cortical cell, which do not endure periclinal division and is never displaced. The cell finally divides into an ellipsoidal mass of cells, which swell and then split into one dorsal and two ventral lobes as the branch grows.

4.1.5. Leaves

The leaves in *Cheilolejeunea* have the unique kind of insertion found in Lejeuneaceae (Crandall-Stotler, 1972; Wigginton, 2004a). The mature leaf is divided into a dorsal lobe and a ventral lobule (complicate bilobed), being attached to the stem along a J-shaped insertion line. They are usually incubous-complicate i.e. insertion oblique, with the dorsal leaf margin nearer to the shoot apex than the ventral margin (Figure 1). They usually cover the stem dorsally with most species with the lobe base trailing the stem. The leaf lobes can be plane or strongly convex and appressed to the substratum. The shape is variable from ovate to orbicular or ovoid, with the apex rounded or acute ±strongly recurved. The margin is usually entire or slightly crenulate with mammillose cells (e.g. *Ch. diversifolia* or *Ch. usambarana*). The lobes may be caudicous at the lobule apex (e.g. *Ch. serpentina* and *Ch. pocsii*).

The leaf cells in *Cheilolejeunea* are thin to slightly thick-walled, with small to large radiate, triangular or nodulose trigones. The marginal cells are subquadrate, median cells hexagonal or oblong and basal cells similar to median ones or distinctly elongate (Figure 1).

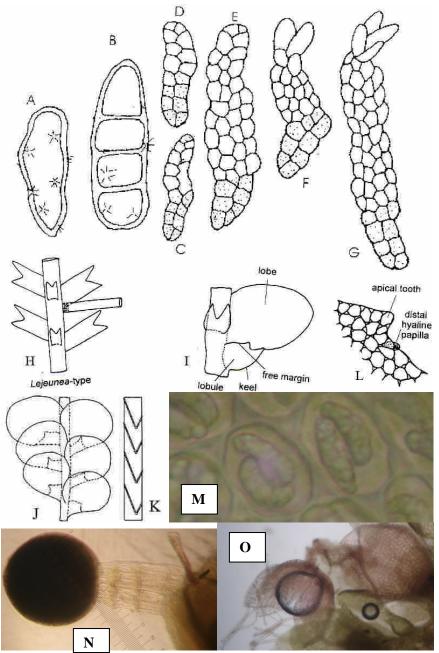


Figure 1. Sporelings, branching, leaves, underleaves, oil bodies and capsule. (A-C) Spores from capsule; (C-D) Eight-celled thallus within the exospore; (E-G) Early development of Sporelings and shoots. (H) Branching-*Lejeunea*-type; (I) Leaf and underleaf; (J,K) Leaf insertion and orientation, incubous-complicate; (L) Lobule apical tooth and distal hyaline papillae. (M) Oil bodies (*Ch. fischeri*); (N) Developing seta (*Ch. intertexta*) and (O) valves with elaters in mature capsule (*Ch. krakakammae*). E-G redrawn from Fulford 1944, H-L from Wigginton, 2004a; M from *Malombe & Chituyi* 5006 Sii 2bs1x, N from *Malombe & Mwale* 6002 N3x6, and O from *Malombe* 5004.A.2

The oil bodies are membrane-bound, terpene-containing organelles suspended in a carbohydrate- or protein-rich matrix found in most cells of the liverworts (Furuki & Higuchi, 1996), originating from cytoplasm and are absent in mosses and hornworts (Schuster, 1966). The function of oil bodies is not yet clear but they are assumed to repel herbivores or offer protection against ultraviolet radiation (Ahonen, 2005). They are useful in taxonomy of Jungermanniales especially at species and generic levels. Gradstein *et al.*, (1977), Schuster (1992) and Kis and Pócs (1997) made the first major strides in revising taxonomy of tropical Lejeuneaceae using oil bodies, which are significant in delimitation of species in *Cheilolejeunea* complex (Schuster, 1966). Species recognised here are provided with *Leucolejeunea*-type, which are (1)-4(-6), very large, coarsely botryoidal or septate oil bodies (Figure 1). Sometimes they may also resemble *Calypogeia*-type as observed by Kis and Pócs (1997). The latter is smaller and seems to lack a discrete external membrane and the independent globules finally disintegrate as observed in some collections of *Ch. krakakammae*.

The oil bodies do not persist in preserved herbarium material and should be examined, preserved in refrigerator at about 6 °C within two weeks of collection (Gradstein *et al.*, 1977). I have however observed some almost complete oil bodies of *Ch. intertexta* preserved for over two years. Pócs (pers. comm.) maintains that the rate of disintegration of the oil bodies depends on the weather conditions at the time the material were collected. They last longer when collected during dry days compared to humid wet conditions. It is however advisable to observe oil bodies immediately or the same day after collection.

Most *Cheilolejeunea* species in tropical Africa lack true ocelli. However, *Ch. falsinervis* (Sande Lac.) Kachroo & R.M.Schust. in Asia has been found to have a linear type of ocelli (Zhu *et al.*, 2002).

4.1.6. Lobules

The lobule is referred to as the ventral lobe of the leaf (He, 1996b). It is normally folded against the dorsal lobe and attached to the stem with a sigmoid long insertion line in Lejeuneaceae. Lobules are widely recognised to have developed as reservoirs of water and

provide suitable environment of symbiotic or mutualism relationship between micro metazoans such as *Rotifers* or other micro organisms and the plants (Ahonen, 2005). Most of the *Cheilolejeunea* collections made in Kakamega harboured lots of Rotifer colonies probably belonging to the *Habrotrocha sp.*, which were active even after two or three weeks of collecting.

Although occasionally variable, several characters such as the shape, free marginal cells, apical tooth and position of hyaline papillae are important in the taxonomy of Lejeuneaceae including *Cheilolejeunea*. The shape of *Cheilolejeunea* lobule is usually ovate to triangular (e.g. Figure 15,16) but also occasionally rectangular to obovate (*Ch. trapezia, Ch. ulugurica*; Figures 32-36) and has been used to separate different subgenera (Zhu *et al.*, 2002).

The ventral free margin is exhibited as the margin of the lobule between the stem and the distal end of the keel, which may also include the apical tooth (He, 1996b). It varies from plane or flattened and visible *in situ* (e.g. *Ch. cordistipula*) to strongly inrolled (e.g. *Ch. krakakammae, Ch. fischeri*) forming an inflated water-sac. It has been used sufficiently by Evans (1906) to segregate *Cheilolejeunea* complex into three genera (*Cheilolejeunea, Rectolejeunea* and *Cystolejeunea*). Jones (1984) found the free margin in *Cheilolejeunea* variable because the length of the lobule teeth and the number of cells in the free margin have considerable intraspecific variation. Species of subgenera; *Cheilolejeunea, Strepsilejeunea* and *Xenolejeunea* s. str. however demonstrate some consistence of the free marginal cell numbers. Most of the species belonging to subg. *Cheilolejeunea* usually have up to 7 cells, while subg. *Strepsilejeunea* exhibit 8-13 cells, or rarely more. Subgenus *Xenolejeunea* can have up to 38 cells.

The apical or second tooth of lobule in *Cheilolejeunea* is usually distinct, being straight or falcate, much reduced or up to 7 or 9 cells. Usually the first tooth is obsolete or in form of blunt projections and rarely the two teeth are present (i.e. *Ch. cordistipula*). This is why the hyaline papilla is seemingly distal. The number of cells and type of teeth is important in the taxonomy of *Cheilolejeunea* as used by Schuster (1980a), Thiers (1990) and Zhu *et al.* (2002). Several species portray single to multicellular blunt cells (e.g. *Ch. krakakammae* and *Ch. intertexta*) while others have spiniform teeth (e.g. *Ch. ulugurica, Ch. pocsii, Ch.*

The seemingly distal position of the hyaline papillae separates the *Cheilolejeunea* complex (*Cheilolejeunea*, *Leucolejeunea*, *Omphalanthus*, *Evansiolejeunea* and *Aureolejeunea*) from other genera in Lejeuneaceae. It is placed near the distal base of apical tooth in most of the *Cheilolejeunea* species and at least 4-6 cells in *Leucolejeunea* (Jones, 1988). A few species of *Cheilolejeunea* (e.g. *Ch. cordistipula*), however have the hyaline papilla placed slightly in more than two cells along the lobule apical sinus away from distal base. Schuster (1980a, pg 854) also believe the position of hyaline papilla does not separate *Leucolejeunea* from *Cheilolejeunea*.

4.1.7. Underleaves and Rhizoids

The shape of the underleaves (Figure 1) in *Cheilolejeunea* vary from ovate, orbicular to obovate or sometimes reniform (e.g. *Ch. montagnei, Ch. omphalogastria* and *Ch. trifaria*). The most important character is the apex, which is occasionally used in taxonomy. Majority are usually of 'schizostipous' type with the apices lobed. Species of subg. *Cheilolejeunea* are known to be deeply lobed up to half while the sinus in subg. *Strepsilejeunea* is shallow (Jones, 1954, 1988). However, *Ch. montagnei* is 'holostipous', which is entire or simply retuse to emarginate, while *Ch. ulugurica* exhibit notched apex. The shape of the sinus also vary greatly. It is usually V-shaped, but occasionally U-shaped (e.g. *Ch. trifaria, Ch. usambarana* and *Ch. convexa*) or rounded (e.g. *Ch. omphalogastria*). The underleaf lobes may be somewhat rounded (e.g. *Ch. convexa* and *Ch. cordistipula*), acute or acuminate. The acute to acuminate lobes end with a one or two-celled acumen. The margin is usually entire but can be rarely coarsely crenulate and wavy when mammillose. The underleaf base could also be cordate or rounded, with deeply arched insertion line (e.g. *Ch. trifaria* and *Ch. omphalogastria*) but is usually of narrow arc in most species.

The rhizoids in *Cheilolejeunea* are basal to the underleaf. Like other genera in Lejeuneaceae, they develop from a disc cell emerging from the basal part of the underleaf (Bischler, 1964). They are normally sparingly developed (Evans, 1906), but in epiphyllous species (e.g. *Ch. trapezia*, *Ch. intertexta*) they become profuse and digitate (Zhu & So, 2001).

4.1.8. Vegetative reproduction

Vegetative reproduction consists of direct regeneration of a plant from the leaf lobe or underleaf cell without protonemal intermediaries. Schuster (1980a) reports frequent vegetative propagation in Latin America especially with caudicous species of subg. *Cheilolejeunea*, while Pócs & Ninh (2005) describes vegetative reproduction by caudicous branches from Asia. These types are unknown for the African *Cheilolejeunea*.

4.1.9. Sex distribution

The majority (70%) of the 23 species of *Cheilolejeunea* treated in the current study are monoicous. Paroicous (26%) and dioicous (30%) species are also wide spread. Some of the commonly paroicous species included *Ch. cordistipula* and *Ch. krakakammae*. The sex type in a few species like *Ch. ulugurica* and *Ch. omphalogastria* is not yet certain as there are few materials known. The sex distribution of some of the species such as *Ch. trapezia* may not be consistent. It is known to be usually dioicous but autoicous populations sometimes occur.

4.1.10. Androecia

The androecia are occasionally subsessile developed on lateral short branches. They can also be terminal or intercalary on long shoots, where by the branch continue to elongate after formation of androecial spike. The hypostatic bracts i.e. overlapping the next younger bract, consists of 1-10, or rarely more. The antheridia are usually in pair or single in the axils of bracts. Bracteoles are smaller than underleaves and resemble in the apex. There are usually 1-2 or 3 bracteoles per spike basally placed, but a rare species *Ch. omphalogastria* from Nyungwe Forest in Rwanda has bracts spread on the entire axis.

4.1.11. Gynoecia

The innovation types in the Lejeuneaceae were first studied by Mizutani (1970). They were revised by Grolle (1980), who recognised 'lejeuneoid' i.e. the leaf appearing before underleaf, and 'pycnolejeuneoid' i.e. the underleaf preceding the leaf. They have been extensively used in the delimitations of species in *Cheilolejeunea* such as in Jones (1954, 1983, 1985, 1988); Schuster (1980a), Zhu *et al.*, (2002) and Wigginton (2004a). I however concur with Jones (1983 and 1988) that it may be difficult to ascertain when one type of innovation is prominent

and that many collections have to be observed. In several species such as *Ch. krakakammae*, described as having majority lejeuneoid innovations, have also persistent pycnolejeuneoid types. The character was found to be variable in *Ch. intertexta* and *Ch. newtonii*. The latter is here reduced to *Ch. intertexta* as earlier opined by Jones (1954a, 1973). Sometimes the underleaf is almost at the same position with leaf making it difficult to determine the innovation type (Jones, 1988). Innovations may also be completely absent (*Ch. exinnovata*) or occasionally lacking (e.g. *Ch. krakakammae* and *Ch. intertexta*).

The female bracts are usually bigger than the leaves preceding them, but leaves on robust and sterile shoots may sometime be larger. They are usually obovate and unequally bifid, the lobe broadened and falcate, the lobule linear (especially subg. *Strepsilejeunea* except *Ch. camerunensis*) to lanceolate or obovate and acute, with the keel usually *ca.* 0.5 the lobe length. The bracteoles resemble underleaves, but is larger and shallowly bifid in schizostipous species.

The perianth shape varies from obovate, pyriform, fusiform to longly clavate. The morphology has been used to delineate taxa at generic or lower levels (Evans, 1906; Jones, 1954; Schuster, 1963 and 1980a). Traditionally, the species belonging to *Cheilolejeunea* s. str (Evans, 1906) where believed to be dostriventrally compressed, with the lateral keels being sharp and dorsal ones reduced. However, several species in subg. *Strepsilejeunea* (e.g. *Ch. camerunensis* and *Ch. pocsii*) are also dostriventrally subcompressed, with *ca.* tricarinate perianth. The keels vary from 2-5, but in *Ch. pluriplicata* and possibly *Ch. cordistipula* are usually up to 10 shallow keels. Sometimes the perianth may be terete as found in *Ch. krakakammae*, a character believed to occur in most of the species as the perianth nears maturity. The rostrum can be short but is elongated in *Ch. ngongensis* and *Ch. cordistipula*.

4.1.12. Sporophyte

The spherical capsule splits after maturity from the apex down into 4 non-recurving valves (Figure 1). The hyaline seta is articulate, with 7-10 articulations, 12 outer cells surrounding 4 inner cells in transverse section. The elaters are linear, slightly to strongly sinuately thickened, sometimes with one \pm distinct spiral bands of thickenings. The spores are irregularly oblong in shape, with the surface minutely papillose and usually with several minute rosettes. The

characters of the sporophyte are useful at the higher taxonomic ranks such as family, subfamily and genera (Weis, 1999).

4.1.13. Growth habit

The growth form of *Cheilolejeunea* species is primarily of mat to thread-like form following classification of Richards (1984). They are rarely of hanging type, which seems induced by ramicolous nature where the shoots surpass the substrate width (e.g. *Ch. cordistipula, Ch. trifaria*).

4.2. Phenetic Analysis

This analysis aimed at integrating overall morphological relationships among the *Cheilolejeunea* species in continental Africa. Of the twenty three species initially recorded from the mainland Africa, four species (*Ch. latiflora*, *Ch. laurentii*, *Ch. rufescens* and *Ch. cf. vatovae*) are little known and enough material was not available for the study. *Cheilolejeunea surrepens* and *Ch. newtonii* were recognised as synonyms of *Ch. trapezia* and *Ch. intertexta*, respectively. Meanwhile, three species new to science were described and illustrations provided. These were *Ch. fischeri* Malombe and *Ch. ngongensis* Malombe & Pócs from Kenya and *Ch. ulugurica* Malombe, Eb.Fisch. & Pócs from Uluguru mts in Tanzania. Twenty species of *Cheilolejeunea* and three species belonging to *Leucolejeunea* were therefore included in the phenetic analysis using STATISTICA version 5.1.

Cluster analysis by Unweighted Pair-Group Average (UPGMA) method yielded two major phenons at 4.0 Euclidian distance (Figure 2). The important characters useful in separating the phenons included the underleaf (width size compared to its length or stem diameter and depth of the sinus) and the lobule (shape and length).

Phenon one (1) was composed of three species of the genus *Leucolejeunea* (*L. xanthocarpa*, *L. unciloba* and *L. rotundistipula*) and one species of *Cheilolejeunea*, *Ch. trapezia*. Although the *Leucolejeunea* species are holostipous, their lobule shape and free marginal cells ensemble that of *Ch. trapezia*. Interestingly, *Ch. trapezia* is characterised by single *Leucolejeunea* type of oil body, hardly more, and subgynoecial innovations are usually pycnolejeuneoid,

characters known to be unique in Leucolejeunea.

The second large phenon (2) consisted most of the species of the genus *Cheilolejeunea*. It was further subdivided into two sub-phenons (A and B) at 3.7 Euclidean distances. At a Euclidean distance of 3.3, subphenon 'A' consisted of species belonging to subg. *Cheilolejeunea*. These species are featured by flattened lobes, which are usually rounded at the apex, ovate to triangular lobules, small underleaves with deep sinus and relatively sub-compressed perianth. The apical lobular teeth of the species can be longly spiniform (*Ch. decursiva*, *Ch. exinnovata*), short and blunt (*Ch. intertexta*) or intermediate (*Ch. serpentina*). *Cheilolejeunea trifaria* belonging to subg. *Euosmolejeunea* was also placed at the base of subphenon A at Euclidean distance of 3.4. Except for the large broad underleaves, all the other features resemble those of subg. *Cheilolejeunea*.

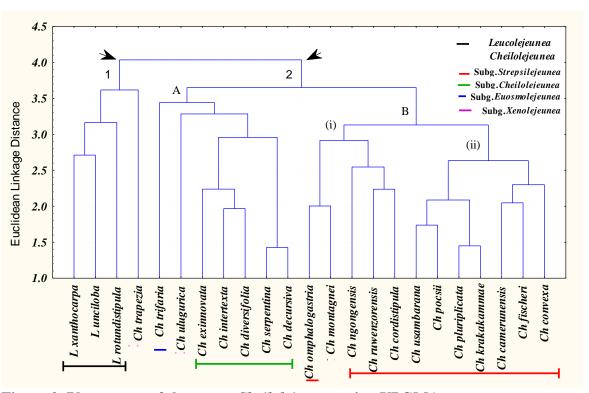


Figure 2. Phenogram of the genus Cheilolejeunea using UPGMA

The sub-phenon 'B' was made up of subg. *Strepsilejeunea* species characterised by strongly convex and recurved lobes usually with acute apices. It was further subdivided at ca. 3.1 Euclidean distance into two clusters. The first cluster 'i' consisted of broadly underleaved species (*Ch. omphalogastria, Ch. ngongensis, Ch. ruwenzorensis* and *Ch. cordistipula*) with

the breadth at least 4, sometimes up to 6, times large than the stem diameter. The robust species of subg. *Euosmolejeunea* (*Ch. montagnei*) was also clustered in this group closely linked to *Ch. omphalogastria*. The former has 'holostipous' underleaves but with strongly convex lobes like most of the species in the subg. *Strepsilejeunea*. The general leave shape is however, oval and apex broadly rounded and shortly recurved, never acute or acuminate. Cluster 'ii' consisted species of subg. *Strepsilejeunea* with sharply acute leaf apices compared to somehow acuminate, sometimes broadly rounded, apices of species in cluster 'i'.

4.3. Phylogenetic Analysis

This analysis aims at providing a hypothesis about the phylogenetic relationships among the *Cheilolejeunea* species in continental tropical Africa. Twenty species of *Cheilolejeunea*, including the three new taxa (*Ch. ulugurica, Ch. fischeri* and *Ch. ngongensis*) were involved. Six outgroup species; *Frullania ericoides* (Nees) Mont., *Archilejeunea abbreviata* (Mitt.) Vanden Berghen, *Odontolejeunea lunulata* (F.Webber) Schiffn., *Drepanolejeunea pocsii* Grolle, *Lejeunea flava* (Sw.) Nees and *L. amaniensis* E.W.Jones were used and three known *Leucolejeunea* species (*L. xanthocarpa, L. unciloba* and *L. rotundistipula*) applied as sister groups. The 29 species were scored for 27 morphological and gametophytic characters and character states as mentioned above (Table 4) resulting to the matrix in Table 6 and Appendix II.

All the characters were treated as unordered. Heuristic searches was done on the matrix using at list 10 replicates of random stepwise taxon addition to find islands of equally most parsimonious trees, holding on tree at each step (Maddison, 1991). This was followed by Tree Bisection Reconnection (TBR) swapping for no more than 100000 trees of score (length) greater than or equal to one saved in each replicate. Clade support was assessed with 1000 bootstrap replicates with simple taxon addition and TBR branch swapping, while permitting only 10 trees per replicate to be held.

Table 6. Data matrix of species and character states used for phylogenetic analysis

Taxon	12345678911111111112222222
	012345678901234567
Chconvexa	200001210010000101000001120
Chcordistipula	211001210011100101120011120
Chdecursiva	2 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 1
Chdiversifolia	2 0 0 0 0 1 2 1 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 2 1
Chexinnovata	20000120110010000010011221
Chfischeri	$2\ 0\ 0\ 0\ 0\ 1\ 2\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 1\ 1\ 2\ 0$
Chintertexta	2 0 0 0 0 1 2 0 1 1 0 0 0 0 0 0 0
Chkrakakammae	2 0 0 0 0 1 2 1 0 0 1 0 0 0 0 0 0 0 0 1 0 0 1 1 1 2 1
Chmontagnei	$2\ 0\ 1\ 0\ 0\ 1\ 2\ 1\ 0\ 1\ 1\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0\ 2\ 0$
Chngongensis	$2 \; 1 \; 0 \; 0 \; 0 \; 1 \; 2 \; 1 \; 0 \; 0 \; 1 \; 1 \; 1 \; 0 \; 0 \; 0 \; 0$
Chomphalogastria	201001210011000100101
Chpluriplicata	$2\ 0\ 0\ 0\ 0\ 1\ 2\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 1\ 1\ 2\ 1$
Chpocsii	$2\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 1\ 1\ 2\ 1$
Chserpentina	2 0 0 0 0 1 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 1
Chtrapezia	$2\; 1\; 1\; 0\; 0\; 1\; 2\; 0\; 1\; 1\; 0\; 1\; 1\; 0\; 0\; 0\; 1\; 1\; 0\; 2\; 0\; 0\; 0\; 1\; 2\; 2\; 1$
Chtrifaria	$2\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 2\ 0$
Chulugurica	20000120110010001111
Chusambarana	$2\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 1\ 1\ 2\ 1$
Lrotundistipula	$2\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 1\ 0\ 2\ 0\ 0\ 1\ 0\ 0\ 2\ 1$
Chcamerunensis	$2\ 0\ 0\ 0\ 0\ 1\ 2\ 1\ 0\ 0\ 1\ 1\ 1\ 0\ 0\ 1\ 0\ 0\ 1\ 0\ 1\ 1\ 1\ 2\ 0$
Chruwenzorensis	$2\ 0\ 1\ 0\ 0\ 1\ 2\ 1\ 0\ 0\ 1\ 1\ 1\ 0\ 0\ 1\ 0\ 1\ 0\ 2\ 0\ 0\ 1\ 1\ 1\ 2\ 0$
Dpocsii	$2\ 0\ 0\ 0\ 0\ 1\ 2\ 0\ 1\ 0\ 0\ 1\ 2\ 1\ 1\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 1\ 1\ 2\ 2\ 1$
Lunciloba	$2\ 1\ 1\ 1\ 1\ 1\ 1\ 0\ 1\ 1\ 0\ 1\ 1\ 0\ 0\ 0\ 1\ 1\ 0\ 2\ 0\ 0\ 1\ 0\ 0\ 2\ 1$
Lxanthocarpa	2 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 1 1 0 2 0 1 1 0 0 2 1
Lamaniensis	$2\ 0\ 1\ 0\ 0\ 0\ 2\ 1\ 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 1\ 2\ 1$
Lflava	$2\ 0\ 0\ 0\ 0\ 0\ 2\ 1\ 0\ 1\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 2\ 0$
Olunulata	$0 \; 1 \; 1 \; 0 \; 0 \; 0 \; 2 \; 1 \; 0 \; 0 \; 0 \; 1 \; 0 \; 1 \; 0 \; 1 \; 0 \; 2 \; 1 \; 0 \; 0 \; 0 \; 1 \; 0 \; 1 \; 0 \; 1 \; 1$
Aabbreviata	$0 \; 1 \; 1 \; 1 \; 1 \; 1 \; 2 \; 1 \; 1 \; 1 \; 0 \; 1 \; 1 \; 1 \; 0 \; 2 \; 0 \; 0 \; 0 \; 0 \; 1 \; 0 \; 1 \; 0 \; 0 \; 1 \; 1$
Fericoides	1 1 1 1 1 1 2 1 1 1 0 1 0 1 0 3 1 1 0 ? ? 0 0 1 1 0 1

Twenty six (96%) of the characters were informative. A total of 2968 most parsimonious trees were recovered and the best tree was obtained at length 101, Consistency Index (CI) 0.347, Homoplasy Index (HI) 0.6535 and Retention Index (RI) 0.641 (Figure 3). The results and phylogeny tree topology was well supported by both Strict Consensus and Majority 50% trees.

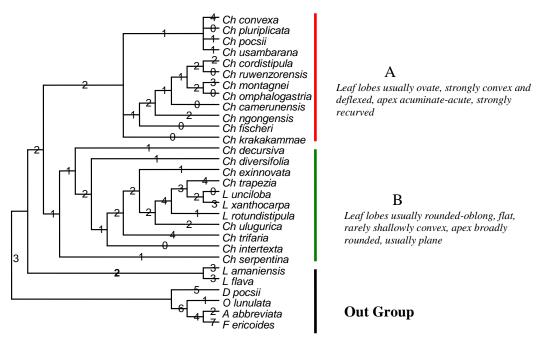


Figure 3. The Most Parsimonious tree, with number of characters/states supporting each clade

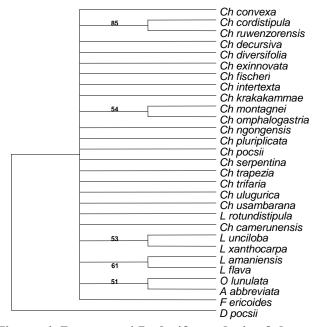


Figure 4. Bootstrap/ Jacknife analysis of the generated tree.

In all cases, the genus *Cheilolejeunea* is presented into two major lineages (A) and (B). Clade 'A' consisted mostly species belonging to subg. *Strepsilejeunea* characterised by usually ovate and strongly convex leaf lobes, which are strongly recurved and with acute apices. In addition, the apex of the underleaves is shallowly bilobed up to 1/3 of its length and majority exhibit

vestigial lobule of the female bracts. The robust species, *Ch. montagnei* belonging to subg. *Euosmolejeunea* is also embedded in this clade closely allied to equally broad underleaved species *Ch. omphalogastria*. Although the species has rounded leaf lobes, they are sometimes shallow to strongly convex and slightly recurved but never with acute apex. Except *Ch. krakakammae* and *Ch. pluriplicata*, which seems to have disjunct populations recently recorded in Australasia, all the species of subg. *Strepsilejeunea* seems to be narrow endemics restricted to afromontane climate with occasional extension to the alpine zones frequented by ericaceous heath. They are occasionally corticolous, hardly epiphyllous, and rarely found below the upper montane altitude zones.

Clade 'B' was a mixture of taxa belonging to three known subgenera; *Cheilolejeunea* (*Ch. serpentina*, *Ch. decursiva*, *Ch. exinnovata*, *Ch. intertexta*, *Ch. ulugurica*, *Ch. diversifolia*), *Xenolejeunea* (*Ch. trapezia*) and *Euosmolejeunea* (*Ch. trifaria*). They are all characterised by rounded to oblong and flat or shallowly convex leaf lobes, which are rounded at the apex and hardly recurved. The three species of the genus *Leucolejeunea* (*L. rotundistipula*, *L. unciloba* and *L. xanthocarpa*) were well embedded within clade 'B' affiliated to species belonging to subg. *Xenolejeunea*. The subgenus is known by ovoid to oblong leaf lobes and rectangular or oblong leaf lobules, which are more than ½ the length of the lobe, with the free ventral margin made up of 13 or more cells. Majority of the species in clade B are usually epiphyllous occurring in lower altitudes, widely distributed in tropical and sometimes neotropical implying that they may be very ancient and highly derived.

The tree collapsed when a bootstrap/ Jacknife analysis was carried out (Figure 4) due to low support of the changes involved. Only a few nodes such as between *Ch. cordistipula* and *Ch. ruwenzorensis* or *L. unciloba* and *L. xanthocarpa*, where recovered.

4.4. Bryogeography and Altitudinal Distribution

The distribution of bryophytes in various ecozones is influenced by day length, humidity, location to the water bodies, altitude and sometimes the soil. These factors vary considerably in different regions of tropical Africa due to a wide variety of landscapes and habitats ranging from deserts to afromontane climate. As such, the bryoflora have an uneven distribution pattern dominated by tropical species, which spill over to temperate, boreal and alpine vegetation types especially on high mountains in central and southern Africa. While, the central African mountains mainly support distinctive alpine paramo vegetation with many endemics, the southern Africa highlands favour the temperate Gondwanic species some with Australasian and Andean relationships (Shaw & Goffinet, 2000).

Whilst the phytogeography of African vascular plant species is described by White (1983) and Clarke (1998), who recognised 20 phytochoria based on species endemism, the bryoflora is at preliminary level. Checklists of bryophytes in Africa are summarised by Grolle (1995) and Wigginton and Grolle (1996) for the sub-Saharan region. They only show the areas of exploration with little reflection of the actual regions of endemism (Shaw & Goffinet, 2000). Endemism of bryophytes in Africa is low with many of species affiliated to Asian-Pacific or Neotropical bryoflora (Gradstein *et al.*, 1984; Pocs, 1992). Shaw and Goffinet (2000) recognise seven-phytochorian range of bryodiversity endemism in Africa. An eighth species distribution, lowland tropical rainforest, can also be recognised to accommodate species restricted to lowland altitudes with wet and humid climates found in West through Central to East Africa usually of tropical rainforests (Bizot & Pócs, 1983). The distribution and diversity of *Cheilolejeunea* in these regions is as described below and shown in Figure 5 (including appendix III for individual species maps) as well as Table 7:

1. Mt. Cameroon (2 spp.). Located in Cameroon in Gulf of Guinea. The forest receives one of the highest amounts of rainfall in the tropics, ranging from 6000 to 9000 mm annually and shares flora with similar habitats of the Atlantic islands of Bioko, Sao Tome and Principe. It contains an endemic species, *Ch. camerunensis*, known only here and in Nigeria. The only other species recorded is *Ch. cordistipula*. It is restricted to afromontane and subalpine

distributions in other parts of Africa.

- 2. Gabon (4 spp.). It has hot and high humid temperatures typical of equatorial climate influenced by off coastal meeting of the cold Benguela Current from the south and the warm Guinea Current from the north. The species recorded in the area includes *Ch. usambarana*, *Ch. intertexta*, *Ch. trapezia* and *Ch. trifaria*. *Cheilolejeunea usambarana* is an afromontane species only known in Africa while the other three are widespread Afro-Asian species dominating the lowland forests. However, *Ch. trifaria* may portray disjunct distribution in Africa usually found in lowlands but sometimes in upper montane elevations.
- 3. East Zairean to Rwandan mts (9 spp.). *Ch. trapezia, Ch. trifaria, Ch. montagnei, Ch. serpentina, Ch. pluriplicata, Ch. krakakammae, Ch. pocsii, Ch. omphalogastria* and *Ch. cordistipula*. *Cheilolejeunea pocsii, Ch. omphalogastria* and *Ch. cordistipula* are African endemics. *Cheilolejeunea omphalogastria* is confined to Nyungwe Forest and has not been recollected in the last 18 years.
- 4. Afromontane (12 spp.). These are the mountains in East Africa such as Ruwenzori, Mts Kenya, Elgon and Kilimanjaro. Also included are the high mist bryophyte refugiums such as volcanic Ngong and Cherengani hills, which occupy typically the lower and upper montane climates. Twelve species, *Ch. montagnei*, *Ch. trifaria*, *Ch. decursiva*, *Ch. intertexta*, *Ch. serpentina*, *Ch. usambarana*, *Ch. pluriplicata*, *Ch. ngongensis*, *Ch. krakakammae*, *Ch. pocsii*, *Ch. ruwenzorensis* and *Ch. cordistipula* were represented here. Four of these species (*Ch. krakakammae*, *Ch. cordistipula*, *Ch. pluriplicata* and *Ch. pocsii*) occur frequently in the subalpine elevations of the high mountains and the rest frequent the lower montane tropical forests. In particular, species of subg. *Cheilolejeunea* represented by *Ch. decursiva*, *Ch. intertexta* and *Ch. serpentina* rarely occur above the lower montane regions. At least five species belonging to subg. *Strepsilejeunea*; *Ch. pocsii*, *Ch. usambarana*, *Ch. ngongenis*, *Ch. cordistipula* and *Ch. ruwenzorensis* are endemic to afromontane forests.
- 5. Eastern Arc mountains in south western Kenya, eastern Tanzania including Malawi (12 spp.). This region is composed of hard quartzite caps overlying metamorphic rocks of the Mozambique Belt system. The climate is influenced by the close proximity to the Indian

Ocean where constant heavy mist-laden clouds maintain the humidity of the area. With 12 species, it was among the richest region with *Cheilolejeunea* species. These included *Ch. trapezia*, *Ch. ulugurica*, *Ch. montagnei*, *Ch. trifaria*, *Ch. intertexta*, *Ch. serpentina*, *Ch. decursiva*, *Ch. usambarana*, *Ch. pluriplicata*, *Ch. krakakammae*, *Ch. pocsii* and *Ch. cordistipula*. Of these, five species are endemic to Africa with newly described species *Ch. ulugurica* endemic to Uluguru mountains.

- 6. Drakensberg in Natal and Lesotho (2 spp.). Cheilolejeunea krakakammae and Ch. pocsii.
- 7. The Cape (3 spp.). These include *Ch. pluriplicata*, *Ch. krakakammae* and *Ch. convexa*. The first two species are Afro-Asian and somehow common in central and eastern Africa. They may however have radiated from this region. *Cheilolejeunea convexa* is however, endemic to the Cape confined in wet rocks as extensive mats.
- 8. Lowland tropical rainforest (9 spp.). They included *Ch. trapezia*, *Ch. decursiva*, *Ch. intertexta*, *Ch. trifaria*, *Ch. diversifolia*, *Ch. exinnovata*, *Ch. serpentina*, *Ch. krakakammae* and *Ch. fischeri*. Except *Ch. krakakammae*, most of the species are lowland specialists common in the high humid tropics, sometimes found near high salty water table (e.g. *Ch. serpentina* and *Ch. trapezia*) and frequently epiphyllous. Several are Afro-Asian, but a few such as *Ch. diversifolia*, *Ch. exinnovata* and *Ch. fischeri* are endemic, only recorded in this region.

The three species in the genus *Leucolejeunea*; *L. xanthocarpa*, *L. unciloba* and *L. rotundistipula*, are restricted to the submontane and lower montane vegetation (Table 7) distributed from South Africa through East Africa to Rwandan forests of Nyungwe and Cyangugu. Although of cosmopolitan distribution, *L. xanthocarpa* has narrow range in Africa, from Ethiopia to South Africa and restrict to Cameroon and Bioko Island in West Africa. It can sometimes exceed the upper montane and reach the subalpine forest regions. However, *L. rotundistipula* is rare and only known from a few localities in South Africa and recently collected in dry lowland mist affected inselberg hilltops with semi evergreen vegetation in SE Kenya.

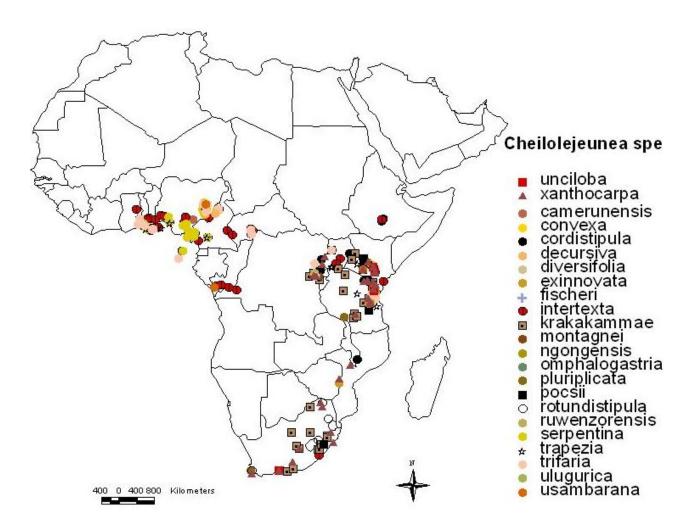


Figure 5. Distribution of *Cheilolejeunea* species within bryological centres of endemism in Africa (see Appendix III for individual species distribution)

Table 7. Tropical African *Cheilolejeunea* species: Distribution range (by endemism/bryodiversity centre), altitude, main habitat, forest condition and substrate

Species	Range	Altitude zones (m)	Main forest habitat	Forest status	substrate
Ch. trapezia	3,5, 8	300-460, 700-1400,	Lowland to lower	Dry mist or wet	Corticolous, ramicolous,
		1600-1880 (2575)	montane, rarely upper	secondary and	epiphyllous, decaying
			montane	primary forests	wood
Ch. ulugurica	5	1650-1880	Lower montane	Primary forest	ramicolous
L. rotundistipula	5,6	757-1400 (2424)	Submontane, rarely	Dry mist primary	Rupicolous, corticolous,
			upper montane	forest	ramicolous, epiphyllous
Ch. montagnei	3,4,5	1600-2000 (2100-	Lower to upper	Moist primary	Rupicolous, corticolous,
		2700)	montane	forest	ramicolous, epiphyllous
Ch. trifaria	2,3,4,5,	450-550, 642-1400,	Lowland to upper	Mist secondary &	Terricolous, rupicolous,
	8	(1500-1950)	montane	primary forests	corticolous, ramicolous
Ch. decursiva	5,8	(90, 1370) 1595-	Lowland to upper	Secondary and	Corticolous, epiphyllous
		2000, 2100-2440	montane	open wet or mist	
				primary	
Ch. diversifolia	8	800	submontane	Open wet primary	rupicolous
Ch. exinnovata	8	1000!	submontane	Primary	Deadwood, epiphyllous
Ch. intertexta	4,5, 8	0-450, 550-1130	Lowland to	Dry or humid open	Terricolous, rupicolous,
		(2600)	submontane, rarely	primary &	corticolous, ramicolous,
			upper montane	secondary forest	epiphyllous, decaying
					tussocks
Ch. serpentina	3,4,5,8	0-515, 650-1080,	Lowland to lower	Dry or humid open	Terricolous, rupicolous,
		1785-1850 (2420)	montane, rarely upper	primary &	corticolous, ramicolous,
			montane	secondary forest	epiphyllous, decaying
					wood
Ch. camerunensis	1	(1000) 1600	(Submontane) to lower	Secondary forest	Corticolous, ramicolous
			montane		
Ch. usambarana	4,5	(460-461, 975-1400)	Rarely lowland or	Mist secondary &	Corticolous, ramicolous,
		1636-1900, 2420	submontane, usually	open primary forest	decaying wood
			lower to upper montane		

Ch. pluriplicata	3,4,5,7	(900-1000) 1650,	Rarely submontane,	Primary wet forest	Corticolous, ramicolous
		2300-3000, (3225)	lower montane to upper		
			montane or subalpine		
Ch. ngongensis	4	2400	Upper montane	Mist secondary or open primary forest	ramicolous
Ch. krakakammae	3,	(150) 1000-1225,	Rarely lowland, mainly	Moist secondary &	Rupicolous, corticolous,
	4,5,6,7,8	1500-2000, 2100-	lower to upper montane	open primary forest	ramicolous, decaying
		3000 (3040-3200)	or subalpine		wood
Ch. pocsii	3,4,5,6	1000-1240, 1700-	mainly lower to upper	Moist secondary &	Rupicolous, corticolous,
		2000, 2100-2250, (3040)	montane or subalpine	open primary forest	ramicolous,
Ch. omphalogastria	3	2000	Lower montane		ramicolous
Ch. fischeri	8	1580-1620	Lower montane	Secondary wet	corticolous
				forest	
Ch. convexa	7	910 (1670)	Submontane to lower montane	Primary forest!	rupicolous
Ch. ruwenzorensis	4	2200	Upper montane wet	Primary moist	corticolous
			forest	forest	
Ch. cordistipula	1,3,4,5	(960-1100) 1650-	submontane, usually	Mist or wet	corticolous, ramicolous,
•		2000, 2100-3000,	lower montane to	secondary &	humus /rupicolous,
		3040-3900	subalpine	primary	
L. unciloba	5,7,8	1235-1410, (1800)	Usually submontane-	Mist dry & wet	Rupicolous, corticolous,
			lower montane	open primary	ramicolous
L. xanthocarpa	3,5,6,7,8	(545), 775-1450,	lowland, usually	Mist or wet	Rupicolous, corticolous,
-		1575-2000, 2100-	submontane-upper	secondary & open	ramicolous
		2900, (3900)	montane or subalpine	primary	

Altitudinal zonations

The distribution patterns of bryophyte species in the different regions of the tropics is influenced by the presence of the different altitudinal belts. These belts have been suggested to be pivotal in species delineations. The African *Cheilolejeunea* species allied to subg. *Strepsilejeunea* were found to be more inclined to the afromontane climates compared to the species of subg. *Cheilolejeunea*, which may dominate the lowland rainforests (Jones, 1988). Five altitudinal belts developed by Frahm and Gradstein (1991), and modified by Dauphin (2000), were adopted to establish *Cheilolejeunea* distribution in Africa. The altitudinal tropical forest zonations were based on the understanding that bryophytes are usually good indicators of climatic change and occur in few species numbers usually with wide geographical distribution. The species are also characteristic constituents of the structure of the tropical rain forests. The distribution of the species in different ecozones is described below and summarised in Table 7 and Figure 6.

(1). The lowland forest; 0-500 m (7 spp.). These forests occur mainly on flat plains and on low undulating terrain occasioned by light intensities at the floor, except in disturbed secondary forests. There is general lack of dense bryophyte mats and most species restricted to the inner upper canopy experiencing higher light intensities. Common corticolous species were *Ch. intertexta*, *Ch. serpentina*, *Ch. trapezia*, *Ch. decursiva* and *Ch. trifaria*. They frequented heavily disturbed open deciduous forests and abandoned farmlands with relatively few bryophytes, sometimes forming pure stands. The species are known to grow mixed together and among the most drought tolerant elements of other schizostipulean Lejeuneaceae. *Cheilolejeunea serpentina* is capable of tolerating salty conditions as it frequently grows near the high water table (*Jones* 1444 c, in Toke, Sierra Leone).

Other species with limited distribution in this zone included the common afromontane and widely distributed species of subg. *Strepsilejeunea*, *Ch. krakakammae*, in lowland Cape. Also some populations of *Ch. usambarana* were recorded in Congo.

2. The submontane forest; ca. 500-1400 m (14 spp.). It occurs on sloping ground usually confined to the lower slopes of the mountains characterised by *ca.* 3% of day light. The lowland species of *Cheilolejeunea* (*Ch. trapezia*, *Ch. trifaria*, *Ch. intertexta*, *Ch.*

serpentina, Ch. decursiva) were the most dominant, either rupicolous, corticolous or ramicolous in cloudy mist inselbergs and mountainous secondary forests, becoming epiphyllous in crown of primary rainforests. The African endemics such as Ch. diversifolia and Ch. exinnovata are confined to this range, occasionally growing in open wet rocks and decaying wood. Species of subg. Strepsilejeunea (Ch. pocsii, Ch. camerunensis, Ch. pluriplicata, Ch. cordistipula and Ch. convexa) begins to emerge in small distributions. Other species included Ch. usambarana and Ch. krakakammae, which were rare confined to mist influenced seemingly afromontane habitats in the Eastern Arc and southern Africa.

- (3) Lower montane forest; ca. 1450-2000 m (15 spp.). Bryophytes in this zone have prominence in the vegetation cover including the soil cover. Species of subg. Strepsilejeunea; Ch. usambarana, Ch. krakakammae, Ch. cordistipula and Ch. pocsii, including continental endemics Ch. camerunensis, Ch. fischeri and Ch. convexa dominate the composition. They are mainly corticolous or ramicolous on disturbed secondary wet or mist rainforests. The few species of subg. Cheilolejeunea (e.g. Ch. decursiva and Ch. serpentina), subg. Euosmolejeunea (Ch. trifaria and Ch. montagnei) and subg. Xenolejeunea (Ch. trapezia and Ch. ulugurica) are usually epiphyllous and ramicolous. They can also occur in gaps of wet primary tropical forests.
- (4) The upper tropical montane forest; 2050-3000m (12 spp.). The species of the subg. *Strepsilejeunea* dominate the forests usually ramicolous on open ericaceous vegetation. Occurrence of species of the other subgenera is rare and only few populations are known. For example, *Ch. intertexta* was collected in Mt. Kenya and *Ch. trifaria* in Eastern DR Congo. This is understandable because Frahm and Gradstein (1991) noted that the lower montane belt might extend to 2400 m in the equatorial mountains.
- (5) The subalpine forest; >3000 m (4 spp.). Only four species of subg. *Strepsilejeunea* were distributed in this belt. However, *Ch. cordistipula* was favoured in such altitude with occasional records where as the rest are seldom collected.

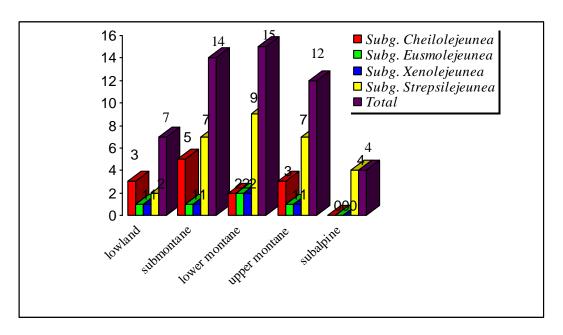


Figure 6. Altitudinal abundance of Cheilolejeunea species

Substrate types

The species of *Cheilolejeunea* occur in six different substrate types as shown in Figure 7. Fifteen species (72%) were collected either on the bark of trees or stems of shrubs and young branches in ericaceous heath or crown of primary forests. About 14% were terricolous, 47% rupicolous, 33.3% epiphyllous and 24% on dead or decaying wood.

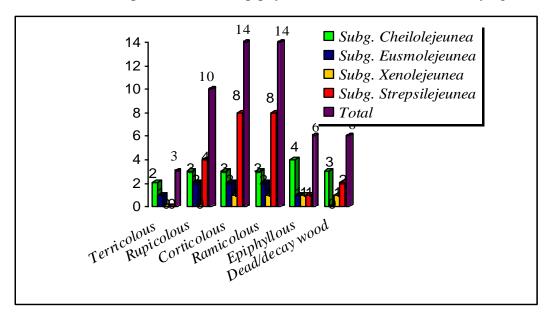


Figure 7. Preference substrate by the *Cheilolejeunea* species

Species of subg. *Cheilolejeunea* were found in all substrates and most of them on living leaves. Other epiphyllous species belong to the subg. *Xenolejeunea* (*Ch. trapezia*) and Subg. *Euosmolejeunea* (*Ch. montagnei*). Species of subg. *Strepsilejeunea* did not occur on

the soil and seldom on living leaves. Pócs (1985) observed epiphyllous collection of *Ch. krakakammae* in the Usambara mountains.

4.5. The Ecology and Conservation of *Cheilolejeunea* in Kakamega and Budongo Rainforests

4.5.1. Diversity of corticolous bryophytes

Ninety-seven species of epiphytic bryophytes (90), lichens (4) and pteridophytes (3), in 32 families and 61 genera, were recorded from the nine study sites involving 276 sample plots and relevés. Seventy-nine (81%) species were recorded in Kakamega forest and only 32 (33%) in Budongo forests. Sørensein similarity index between the two forests was found to be 25.2 showing great dissimilarity of bryophyte species between the two forests.

Lejeuneaceae was the most diverse and consequently the most ecologically significant bryophyte family in terms of species numbers (Figure 8). It represented close to 40% of all the epiphytic species recorded. Other important families included Neckeraceae (5%), Plagiochilaceae (5%), Metzgeriaceae (4%) and Radulaceae (4%).

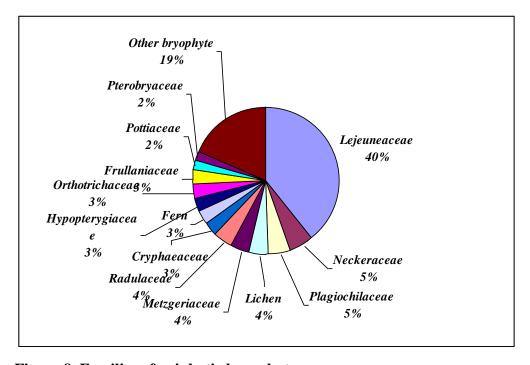


Figure 8. Families of epiphytic bryophytes

Cheilolejeunea and Lejeunea genera were the most diverse and common in the entire study

sites (Figure 9). The species of the two genera were recorded in 45.7% and 47.5% of the total sample area, respectively. However, the frequency of *Lejeunea* (47.5%) taxa was slightly higher than that of *Cheilolejeunea* (45.7%). Further, despite *Frullania* and *Orthostichella* being less diverse, they exhibited high frequency in the lowland tropical rainforests. Other common genera included *Plagiochila*, *Radula* and *Metzgeria* as indicated in Figure 9.

In Kakamega, the highest species diversity of bryophytes was recorded in Salazar (45.4%) and Kisere (44.3%) forest fragments (Figure 10). While Kisere forest is classified as near primary or in climax stage and relatively less disturbed, Salazar and Colobus sites are ranked among the middle-aged secondary forest (Althof, 2005). The young forests of Udo's Campsite and highly disturbed Isecheno area recorded one of the poorest species compositions in the Kakamega Forests. Each of the study sites in Budongo Forest contained less than a quarter of the species diversity. The most diverse was compartment N15 (23.7%) which has never been logged, except recent isolated cases of illegal selection cutting and occasional throw fall of the huge old tree species which has created some forest gaps. It was closely followed by compartments N3 and N4 which are middle aged forest following selective felling of mid the 1970's. The relatively young forest compartment W22 was the least diverse.

Comparisons of the species diversity along the disturbance gradient revealed that the disturbed forest sites exhibit higher species diversity. The much-disturbed forest edge in Kisere forest fragment had the highest diversity of 37.7% followed closely by Salazar with about 32%. Conversely, disturbed forest areas of both Yala and Colobus forests registered slightly lower species diversity than older, intact sites (Figure 11).

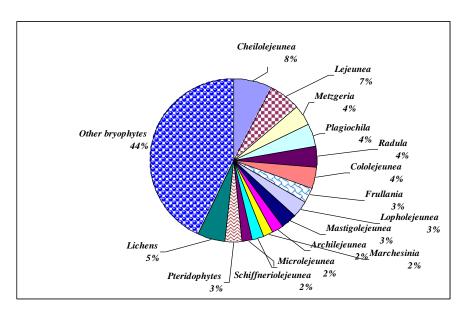


Figure 9. Generic diversity of epiphytic bryophytes

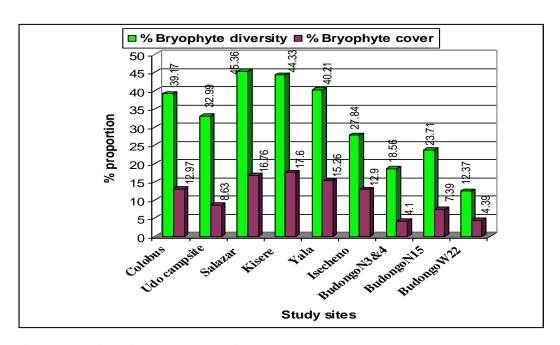


Figure 10. Diversity and cover of bryophytes in the study area

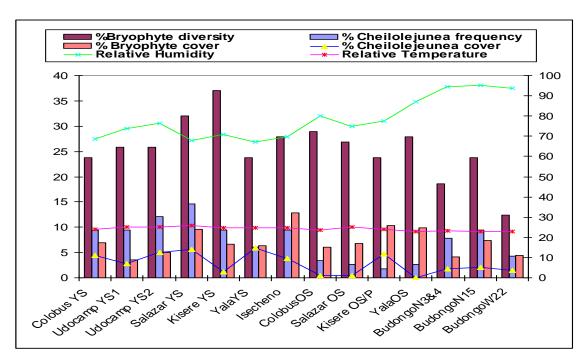


Figure 11. Species diversity and cover as influenced by abiotic factors along disturbance gradient

4.5.2. Bryophyte cover

The estimated bryophyte cover was directly correlated with species diversity in most of the sites studied. In Kakamega forest, the highest cover of about 17% was found in Kisere and Salazar forests. Young forests of Udo's Campsite and Isecheno recorded the lowest bryophyte cover. Primary forests of compartment N15 in Budongo forest of Uganda also recorded highest cover compared to compartment W22 and N3 (Figure 10).

Investigation of bryophyte cover along the disturbance gradient in each of the study sites showed significantly high cover in more disturbed sites and forest edges in majority of the middle-aged forests such as Salazar and Colobus. Conversely, the older or near primary forests such as Kisere and Yala tend to have higher cover in the main undisturbed forest areas. This observation was true for the sites in Budongo forest where compartment N15 recorded the highest cover. The overall bryophyte cover was however highest in the youngest forest site in Isecheno (Figure 11).

4.5.3. Correlation between phorophyte and bryophyte diversity

All the tree substrates in the 276 relevés were identified and frequencies calculated.

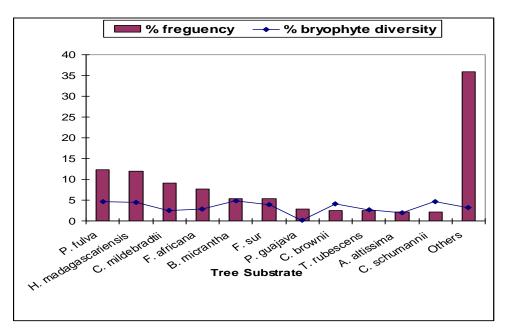


Figure 12. Correlation of phorophyte and bryophyte diversity

Polyscias fulva (Hiern) Harms. and Harungana madagascariensis Lam. ex Poir. constituted 12% each for the 276 sample plots studied (Figure 12). Other important tree phorophytes included Celtis mildbraedii (9.0%), Funtumia africana (Benth.) Stapf. (7.8%), Bridelia micrantha (Hochst) Baill. and Ficus sur with a frequency of 5.4% each. Average bryophyte diversity in each of these tree species however showed that B. micrantha (4.9%) and P. fulva (4.7%) to be the most favourable for bryophyte microhabitats. Other favourite phorophytes with significant bryophyte diversity included Combretum schumannii (4.6%) and H. madagascariensis (4.5%). Most of trees of P. guajava (0.3%) were devoid of any bryophyte species despite their high occurrence (Figure 12).

4.5.4. Cheilolejeunea diversity in response to forest disturbance

The diversity and frequency of the species of the genus *Cheilolejeunea* was recorded alongside the general bryophyte composition as indicated in other subsections in 4.3 above and elaborated in Figure 11. The genus was among the most diverse and frequently encountered in 113 relevés in the study area (Figure 9). It was represented by six species namely *Ch. decursiva*, *Ch. fischeri*, *Ch. intertexta*, *Ch. krakakammae*, *Ch. surrepens* and *Ch. trifaria*. One species, *Ch. fischeri*, was new to science, while *Ch. decursiva* is new to Kenya and *Ch. trifaria* and *Ch. intertexta* were first records for Budongo Forest. A seventh species *Ch. newtonii* was recognised as a synonym of *Ch. intertexta* in this study. Interestingly, except for *Ch. krakakammae*, Kakamega and Budongo forests contain different species of *Cheilolejeunea* (Table 8). Kakamega Forest was dominated by

afromontane species *Ch. krakakammae* and Budongo forest characterised by a lowland and common Afro-Asian species *Ch. intertexta. Cheilolejeunea krakakammae*, which is thriving profusely in Kakamega forest was recorded only once on a decaying branch of *Cordia abyssinica* in Budongo Forest.

Table 8. List of Cheilolejeunea species recorded in Kakamega and Budongo forests

Species	Kakamega	Budongo
Cheilolejeunea Krakakammae (Lindenb.) R.M.Schust.	X	X
Cheilolejeunea intertexta (Lindenb.) Steph		X
Cheilolejeunea decursiva (Sande Lac.) R.M. Schust.	X	
Cheilolejeunea trapezia (Nees) Kachroo & R.M.		X
Schust.		
Cheilolejeunea trifaria (Reinw. et al.) Mizut.		X
Cheilolejeunea fischeri Malombe sp. nov.	X	

Most of the *Cheilolejeunea* records were associated with *H. madagascariensis*, *P. fulva*, *F. africana* and *B. micrantha* tree phorophytes (Figure 13), which were common in disturbed young forests (Figure 11-13). The young and disturbed forest edge of Salazar, which experienced frequent burning, exhibited the highest concentration of *Cheilolejeunea* species mainly *Ch. krakakammae*. Other disturbed sites important for *Cheilolejeunea* proliferation included Udo's campsite and Kisere forest edges in Kakamega, and compartment N15 in Budongo. The two forests in Kakamega are young or influenced by illegal tree cutting and general edge effect (Althof, 2005). Compartment N15 in Budongo forest, on the hand, is a primary forest but with numerous gaps owing to wind throw from mature trees allowing penetration of light to the base. The percentage cover of *Cheilolejeunea* species was directly correlated with forest structure (Figure 11). It increased in young and open forest edges and diminished with increasing forest age. It was however inversely related to the general bryophyte cover especially in closed and older forest sites.

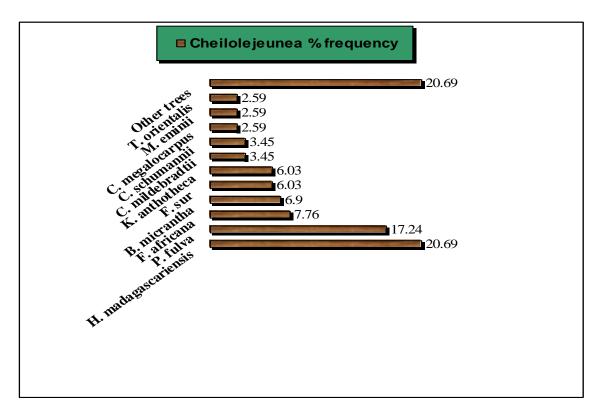


Figure 13. Frequency of *Cheilolejeunea* species in various tree substrates

Records of abiotic factors involving temperature and relative humidity are presented in Figure 11. The variation of average temperature among the different sites and disturbance gradient was minimal. However, a slight change of temperature inversely affected the relative humidity. The relative humidity was always lower in young and open edges of forests compared to the advanced secondary and primary forest sites. The *Cheilolejeunea* species diversity and population concentration were directly influenced by abiotic factors. The higher the temperature and lower the humidity, the more concentration of *Cheilolejeunea* species. Most of the collections of *Cheilolejeunea* made in the least disturbed sites of the forest were largely from crowns of fallen trees as experienced in Compartment N15 in Budongo Forest.

CHAPTER 5. DISCUSSION AND CONCLUSIONS

5.1. Generic Relationships

The genus *Cheilolejeunea* has generally been recognized as a natural entity since its first description by Spruce in 1884 (Evans, 1906; Schuster, 1980a; Zhu *et al.*, 2002). Placed within the monophyletic subfamily Lejeuneoideae and tribe *Lejeuneae* Dumort., it is characterised by the distal position of hyaline papillae in relation to the apical tooth of leaf lobule. The oil bodies are of *Leucolejeunea*-type and rarely *Calypogeia*-type, typically 1-4(-6) per cell, medium to very large, coarsely botryoidal, crescent shaped and nearly filling the lumen (Gradstein *et al.*, 2003; Wigginton, 2004a; Kis & Pócs, 1997). Other important character, according to Schuster (1980a) includes thick-walled or distinctly collenchymatous cells, strongly inflated lobule with apex usually constricted to form small circular opening. It also has firm stems with thick-walled cortical cells. The chronological taxonomic placement of the genus by different authors is shown in Table 9.

Within the tribe Lejeuneeae, Gradstein et al., (2003) recognised putative clade of Cheilolejeunea complex comprising of Aureolejeunea, Evansiolejeunea, Omphalanthus, Leucolejeunea and Cheilolejeunea. The clade was characterised by distal hyaline papillae, very large oil bodies, frequent undivided underleaves and more than 10 rosettes on spore surfaces. It resembled the complexes observed previously such as Cheilolejeunea (Schuster, 1980a, 2001) and Omphalanthus (Gradstein et al., 1981). While studying the molecular phylogeny of Lejeuneaceae, Wilson et al., (2007a) also recovered the Cheilolejeunea clade and noted that it was non-monophyletic. They suggested adoption of a wider concept of the genus Cheilolejeunea to include the other four genera. Aureolejeunea is localised in the Neotropics and in the Atlantic island of St. Helena, Evansiolejeunea restricted to afroalpine regions of Rwanda, Uganda and DR Congo, and Omphalanthus is only found in the Neotropics. Aureolejeunea and Evansiolejeunea are more allied to Omphalanthus than to Leucolejeunea or Cheilolejeunea (Schuster, 1963, 1980a).

Many authors have been unable to draw clear delimitation between *Cheilolejeunea* and *Leucolejeunea* (see Schuster, 1980a; Grolle & Piippo, 1990; Zhu & So, 2001). Schuster (1980a) was even of a general opinion to propose *Leucolejeunea* as a "mere subgenus of *Cheilolejeunea*". Except for the "malleable" gynoecial innovation patterns, which are often

pycnolejeuneoid and rarely with sterile innovations, the genus *Leucolejeunea* according to him resemble *Cheilolejeunea*. The resemblance is portrayed in texture, colour, stem, ventral merophytes, oil bodies, lobule morphology, distal hyaline papillae and perianth type. In the studies of *Cheilolejeunea* in China, Zhu *et al.*, (2002) noted substantial variation of several important diagnostic features used at generic and subgeneric levels. Zhu & So (2001), who listed some intermediaries, had already noted unsuitability of known characters to seperate Asian *Cheilolejeunea* and *Leucolejeunea*.

The *Cheilolejeunea* species are pantropical and common in Africa. Together with *Ceratolejeunea*, *Cyclolejeunea* and *Lepidolejeunea* within Lejeuneoideae, they have species with entire underleaves (Gradstein, 1985). They however differ by the absence of brown cellular pigmentation, horned utriculi and perianth, and except very few Asian *Cheilolejeunea*, they lack ocelli (Dauphin, 2000).

Table 9. Taxonomic placement of the genus *Cheilolejeunea* by different authors

Taxon rank	Spruce 1884	Schiffner 1893	Evans 1906; Stephani 1913- 14; Jones 1954	Schuster 1955, 1963; Kachroo & Schuster 1961	Schuster 1980a; Including Jones	Thiers 1992; Asthana <i>et al.</i> 1999
Family	Jungermanniaceae	Jungermanniaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae
Subfamily				Lejeuneoideae	Lejeuneoideae	Lejeuneoideae
Tribe		Jubuloideae- Lejeuneae		Schizostipae		Lejeuneae
Genus	Lejeunea Lib.	Cheilolejeunea (Spruce) Schiffn.	Cheilolejeunea (Spruce) Schiffn.	Cheilolejeunea (Spruce) Schiffn.	Cheilolejeunea (Spruce) Schiffn.	Cheilolejeunea (Spruce) Schiffn.
Subgenus	Cheilo-Lejeunea			Cheilolejeunea Euosmolejeunea Xenolejeunea Strepsilejeunea Renilejeunea	Cheilolejeunea Strepsilejeunea Euosmolejeunea Anomalolejeunea Xenolejeunea Renilejeunea Tegulilejeunea	Cheilolejeunea Strepsilejeunea Euosmolejeunea Xenolejeunea

Taxon rank	Zhu & So 1999	Grolle <i>et al.</i> ,. 2001; Zhu & So 2002	Gradstein et al., 2003 & Wilson et al., 2007a	Wigginton 2004	Malombe 2007a
Family	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae
Subfamily	Lejeuneoideae	Lejeuneoideae	Lejeuneoideae	Lejeuneoideae	Lejeuneoideae
Tribe			Lejeuneeae	Lejeuneae	Lejeuneae
Genus	Cheilolejeunea (Spruce) Schiffn	Cheilolejeunea (Spruce) Schiffn.	Cheilolejeunea (Spruce) Schiffn. (including Leucolejeunea, Omphalanthus, Evansiolejeunea, Aureolejeunea)	Cheilolejeunea (Spruce) Schiffn	Cheilolejeunea (Spruce) Schiffn. (Including Leucolejeunea)
Subgenus	Anomalolejeunea	Cheilolejeunea Euosmolejeunea Xenolejeunea		Cheilolejeunea Euosmolejeunea Strepsilejeunea	Cheilolejeunea Strepsilejeunea

5.2. Phenetic Observations

The phenetic results emphasized the importance of morphological characters in the taxonomic treatment of *Cheilolejeunea* species. The useful characters applied in the separation of the phenons included features of the leaf lobes and lobules (shape and length) and underleaves (width size compared to its length or stem diameter and depth of the sinus). These characters have been used to delineate species of *Cheilolejeunea* at intra and infra-generic levels as demonstrated by Evans (1906), Jones (1954a & b, 1983, 1985, 1988), Schuster (1980a), Thiers (1992), Zhu *et al.*, (2002) and Wigginton (2004a).

The uniqueness of the subg. *Strepsilejeunea* species as observed by Schuster (1963, 1980a) and Jones (1988) has been retained. Zhu et al., (2002) had reduced the subgenus to a synonym of subg. Euosmolejeunea citing lack of reliable characters. The subg. Strepsilejeunea is characterised by broadly ovate, strongly convex and falcate lobes with a recurved acute apex. The apical sinus of the underleaves is shallow, usually up to 1/3 of its length, and except Ch. camerunensis, majority of the species exhibit rudimental lobular bracts of the female inflorencense. The other subgenera in Africa including Cheilolejeunea, Euosmolejeunea and Xenolejeunea are noted to have ovoid to oblong flat or shallow convex leaves, never falcate, with the apex broadly rounded and hardly recurved. Except for the subg. Euosmolejeunea, the underleave sinus is deeply placed up to ½ of its length. They also exhibit large and oblong lobular bracts of the female inflorencense. Further evidence of the identity of subgen. Strepsilejeunea is maintained in attributes of altitudinal distributions. The species are usually of afromontane, several of them appearing in the subalpine-ericaceous or elfin, vegetation and rarely on lower montane distribution. As observed by Jones and Harrington (1983) the majority species of the other three subgenera are lowland generalists with occasional epiphyllous habitation.

The morphological phenetic analysis did not however clearly delineate species belonging to subg. *Cheilolejeunea* and allied subgenera as shown in Subphenon 'A' in Figure 2. Except for large shallowly lobed underleaves and less compressed perianth, *Ch. trifaria* placed within the subg. *Euosmolejeunea* species has characters similar to subg. *Cheilolejeunea*. Several specimens belonging to *Ch. intertexta* in subg. *Cheilolejeunea* have been found to have developed 4-5 keels, with well developed antical ones. The collection by *Pócs T* and *Faden AR* (6601 AD) from Mt Kenya along Kamweti Track and *Assel M* (608) from Central Africa Republic serves as good examples. Zhu *et al.*, (2002)

demonstrated that the perianth shape is not constant and may vary considerably depending on the level of perianth development as also observed by Evans (1906) and Schuster (1980a). The possession of broad reniform underleaves in *Ch. trifaria* seems to be common in other subgenera as found in subg. Strepsilejeunea citing Ch. omphalogastria and Ch. cordistipula. Furthermore, when Zhu et al., (2002) sunk the species of subg. Cheilolejeunea into subg. Euosmolejeunea seems to have disregarded the traditional characters known to separate the subg. Cheilolejeunea, Euosmolejeunea and Xenolejeunea. As shown in Evans (1906), Jones (1954) and Schuster (1961, 1963 and 1980a), species belonging to subg. Cheilolejeunea s. str. will tend to have triangular lobule with spiniform apical tooth. The subg. Euosmolejeunea is characterised by short and broadly rounded lobular apical teeth while subg. Xenolejeunea exhibit rectangular to oblong leave lobules with long multicellular apical teeth. Zhu et al. (2002) retained to subg. Cheilolejeunea only one miniature species Ch. chenii, characterised by oval-rectangular lobule and spiniform apical tooth. The species is allied to the currently described African species Ch. ulugurica, endemic to Uluguru mts in Tanzania, which has intermediate characters between subg. Xenolejeunea and subg. Cheilolejeunea owing to rectangular oblong shape, more than ½ as long as the lobe length. The lobule is however short and the postical free margin has up to 10 cells compared to longer and slender rectangular lobules with up to 22 or more free marginal cells in subg. Xenolejeunea. The African species Ch. decursiva and Ch. exinnovata also with spiniform apical tooth are better suited to subg. Cheilolejeunea as in the original description of the subgenus as used by Wigginton (2004a). As in Zhu et al., (2002), Wigginton (2004a) included Ch. intertexta and Ch. diversifolia, which have reduced lobular apical tooth, and a seemingly suitable subg. Xenolejeunea species Ch. trapezia in subg. Cheilolejeunea. In fact, subg. Xenolejeunea has never been recognised in Africa since its inception by Kachroo and Schuster (1961).

The generic delineation of *Cheilolejeunea* is also unstable. As observed earlier, there seems to be no succinct differences between the genus *Cheilolejeunea* and *Leucolejeunea*. The latter has been separated from the former by having four or more ventral merophytes, almost equal sizes of cortical and medullary cells, hyaline papillae placed 4 or more cells distal to the apical tooth and unlobed underleaves. Schuster (1980a) also observed consistent pycnolejeuneoid innovations, which where hardly sterile in *Leucolejeunea*. The current study has however found species *L. rotundistipula*, which is little known according to Jones (1973), with consistent seven cortical cells, which are larger than medullary cells,

clearly resembling species of *Cheilolejeunea*. A paratype of *L. xanthocarpa* from South Africa (Arnell S 1492) surprisingly had at least seven cortical and few medullary cells. Several species of *Cheilolejeunea* mostly abundant in Asia (*Ch. revoluta, Ch. asperrima* and Ch. trapezia) portrays elastic ventral merophytes, which are usually 3-4 but sometimes up to 8 cells wide (Gradstein et al., 1993; Bastos & Gradstein, 2006). The possession of only pycnolejeuneoid innovations in Leucolejeunea as opposed to having both lejeuneoid and a pycnolejeuneoid subgynoecial innovation in *Cheilolejeunea* as noted by Jones (1973), Schuster (1980a) and Wigginton (2004a) is partially incorrect. The trio probably never observed persistent intermediate characters such as lack of innovations in both cases. Many species of Cheilolejeunea (e.g. Ch. exinnovata and Ch. krakakammae) are characterised by terminal perianth on short shoots a phenomenon frequently observed in L. xanthocarpa. Examples of the latter include materials collected by Pocs T & Lye KA 97132 AX (Uganda), Pocs T & Jones EW 6364/ Jones EW 1641 (Tanzania) and Arnell S 1492 (South Africa). In respect to the position of hyaline papilla, Schuster (1980a) found several Leucolejeunea species with almost basal placement like in Cheilolejeunea. It is also noted that in Ch. cordistipula, as illustrated by Jones (1988), clearly shows the hyaline placed along the sinus at least 2-3 cells ensembling illustrations on L. unciloba by Schuster (1980a). The clustering of *Ch. trapezia* together with the three species of African Leucolejeunea in Phenon one (1) was therefore expected and may confirm the possible overlap between the two genera. Cheilolejeunea trapezia belongs to subg. Xenolejeunea, and just like the species of *Leucolejeunea*, its characterised by broad width of the shoot, prolonged rectangular or oblong leaf lobule with the free postical margin bordered by more than 13, usually up to 22 or more and single oil body is common (Thiers, 1992a; Asthana et al., 1999; Zhu et al., 2002). About three of the species including Ch. trapezia can even grow mixed together in the same colony. Example collections include *Malombe I &* Muasya J 4024 C7 collected in 2005 in Mumoni hills 'inselberg' SE Kenya and Esterhuysen E 25664 from Cape Table Mountains in South Africa. In such circumstances and except for the unlobed underleaves, it becomes difficult to separate L. unciloba from Ch. trapezia as all other characters are similar (Jones, 1973).

At the species level, clustering of several species seem to be somehow incongruent with morphological basis. For example in subphenon B consisting of subg. *Strepsilejeunea* species, the subdivision seems basically on the width ratio between the stem and underleave. Although a significant character as used in Wigginton (2004a), it requires

combination of several other features for successful utilization. Jones (1988) declined to provide identification keys for the subg. *Strepsilejeunea* following unclear morphological delineations. However, at least some allied species are seen to be placed in same cluster as found with *Ch. usambarana* and *Ch. pocsii*. The two species are unique in subg. *Strepsilejeunea* as they posses acute to spiniform tooth and semi caudicous leaves. *Cheilolejeunea decursiva* and *Ch. serpentina* belonging to subg. *Cheilolejeunea* have been currently found related as the latter has extreme cases with short spiniform apical lobular tooth.

5.3. Phylogenetic Relationships

The phylogenetic analysis recovered the *Cheilolejeunea* complex here represented by *Cheilolejeunea* and *Leucolejeunea* as established by Schuster (1980a), Gradstein *et al.*, (1981, 2003) and Wilson *et al.*, (2007a). It was segregated from the seemingly sister genus *Lejeunea* by two plesiomorphic characters thus distal hyaline papilla and *Leucolejeunea* or rarely *Calypogeia* type of oil bodies. *Lejeunea* has proximal hyaline papilla and different type of oil bodies, which are mainly compound and minute, sometimes of *Calypogeia* type. The two genera however belong to the tribe *Lejeuneae* of the most advanced subfamily Lejeuneoideae in Lejeuneaceae characterised by remarkable polymorphism following recent evolutionary explosion alongside the Angiosperm diversification witnessed in the late Cretaceous and Tertiary period (Schuster, 1980a; Wilson et al., 2007a & b). It has reduced morphological structures especially general plant size, its frequently autoecious and corticolous or epiphyllous as pioneer species in adaptation to suit the fast changing environmental conditions (Schuster, 1980a; Gradstein *et al.*, 2003; Ahonen, 2005).

The *Cheilolejeunea* complex was subdivided into two subclades mainly based on leaf characters as proposed by Schuster (1963, 1980a). The seemingly primitive and monophyletic subclade 'A' consisting of all the African species belonging to subg. *Strepsilejeunea* is distinguished by ovate lobes, which are usually falcate and convex with the apex strongly acute and recurved (Figure 3). Although majority of the subg. *Strepsilejeunea* species appear endemic and probably of a recent speciation, the homoplaxious species *Ch. krakakammae* placed at the base of the subclade has been recently proven to be a common Afro-Asian taxa (Zhu, 2006). Equally distributed is *Ch. pluriplicata* found also in Asia (Zhu & So, 1999). Importantly, the species of subg.

Strepsilejeunea are restricted to Afromontane vegetation belts sometimes reaching the subalpine zones (Schuster, 1980a; Jones, 1988; Pócs, 1994). Except again for the *Ch. krakakammae*, they are hardly found in lowland altitudes and on living leaves. They seem to be less desiccation tolerant, adapted to more cold and misty mountain zones and higher altitude hilltops in open vegetation as corticolous or ramicolous.

The more derived and paraphyletic subclade 'B', with *Ch. montagnei* placed within subg. Strepsilejeunea subclade 'A', is characterised by flattened to shallowly convex leaf lobes, which are ovoid to oblong with rounded plane apex, rarely shortly recurved (Figure 3). Thus, they are strongly 'adnate' to the substrate and coupled with flattened perianth and numerous rhizoids are well suited to epiphyllous conditions (Schuster, 1980a; Zhu & So, 2001; Shaw & Renzaglia, 2004). These characters are common with species belonging to the subg. Cheilolejeunea s. str. and partially true for subgenera Euosmolejeunea and Xenolejeunea species (Evans, 1906; Jones, 1954a&b; Schuster 1963). The species were facultative epiphylls in the sense of Pócs (1996) and majority with altitudinal range of the lowland rainforests from sea level to lower montane vegetation characterised by high humidity. Although several species seems dioicous and a few endemic in the region, most of the species in subclade B are wide spread in tropical Africa, Asia and Australia as well as Oceania, and are massively bippinate small branched as attested in *Ch. trapezia* and *Ch.* intertexta (Asthana et al., 1995; Zhu et al., 2002; Wigginton, 2004a). These minute branches may not be microphyllous but they are usually fertile seemingly a derived mechanism of survival in the fragile lowland tropical rainforests (Schuster, 1980a).

The species of subg. *Euosmolejeunea*, (*Ch. trifaria* and *Ch. montagnei*) only differ from subg. *Cheilolejeunea* and some species of subg. *Xenolejeunea* by the large reinform underleaves (Kachroo & Schuster, 1961; Schuster, 1963, 1980a). The reinform or large underleaves character seems of little taxonomic value in *Cheilolejeunea* complex. It is shared with other species in the subg. *Strepsilejeunea* and *Xenolejeunea*. Such members of subg. *Strepsilejeunea* include *Ch. omphalogastria* and *Ch. cordistipula* in Africa, and the recently described species *Ch. rupestris* C. Bastos & Gradst. in Brazil (Bastos & Gradstein, 2006). The Asian *Ch. gigantea* (Steph.) Schust. & Kachroo is a good example of a reinform underleaved species in subg. *Xenolejeunea*. Gradstein *et al.*, (1993) and He (1996) placed the robust South American species *Ch. revoluta*, *Ch. decurviloba* and *Ch. valenciae* characterised by broad ventral merophytes in subg. *Euosmolejeunea* based on

traditional characters like small triangular lobules with short-celled apical tooth. As discussed by Kachroo and Schuster (1961) and Schuster (1963) as well as the placement of Asian *Cheilolejeunea* species by Zhu *et al.*, (2002), such characters have been found unstable. Thus, the three species form a clear intermediary between subg. *Euosmolejeunea*, *Xenolejeunea* and genus *Leucolejeunea*. As noted by Schuster (1955, 1980a) and Gradstein *et al.*, (2003), robust stems with broad ventral merophyte is a plesiomorphic character associated with primitive 'holostipous' Lejeuneaceae subfamily Ptycanthoideae. Some members of subfamily Lejeuneaceae, such as the holostipous genus *Leucolejeunea* and few members of *Cheilolejeunea* (e.g. *Ch. Gigantae* in subg. *Xenolejeunea*) seems to have retained the broad ventral merophyte character. Occasionally, the broad ventral merophytes is associated with more epidermal and medullary stem cells as seen with *Ch. revoluta*, *Ch. decurviloba* and *Ch. rupestris* in southern America. It therefore seems natural for the phylogenetic analysis to have recombined the genus *Leucolejeunea* into a broader *Cheilolejeunea* as recommended by Wilson *et al.*, (2007a).

Supported by at least two synapomorphic characters of underleave sinus length and caudicous lobes, the three African species of the *Leucolejeunea* (*L. rotundistipula*, *L. unciloba* and *L. xanthocarpa*) were embedded within subg. *Cheilolejeunea*, closely allied to members of subg. *Euosmolejeunea* (*Ch. trifaria*) and *Xenolejeunea* (*Ch. trapezia*). A newly described species *Ch. ulugurica* was also closely grouped with this association. Zhu *et al.*, (2002) placed *Ch. chenii* allied to the latter in subg. *Cheilolejeunea*. It seems however an intermediate link between subg. *Cheilolejeunea* and *Xenolejeunea* owing to rectangular oval to oblong lobule with spiniform lobular apical tooth. *Cheilolejeunea decursiva* and *Ch. serpentina* were placed at the base of subclade 'A'. Some phenotypes of the two species exhibit shallow convex leaves portrayed in subg. *Strepsilejeunea*. The high Homoplasy Index and low Consistency Index of the phylogenetic analysis did not however guarantee the tree hypothesis as a basis for an evolutionary classification of the species within the subgenera. They are therefore presented as per the perceived observable morphological characters as seen in the conspectus in 5.3.1 below.

5.3.1. Conspectus of the genus Cheilolejeunea

Subgenus Strepsilejeunea (Spruce) R.M. Schust.

Leaf lobes usually ovate, strongly convex and falcate, apex acute or acuminate, decurved. Underleaves bilobed up to 1/3 of its length. Lobule of \mathcal{P} bracts less developed, usually linear.

- 1. *Ch. krakakammae* (Lindenb.) R.M.Schust.
- **2.** *Ch. ngongenis* Malombe & Pócs sp. nov.
- 3. Ch. fischeri Malombe sp.nov.
- 4. *Ch. pluriplicata* (Pearson) R.M.Schust.
- **5.** *Ch. camerunensis* S.W.Arnell
- 6. Ch. pocsii E.W.Jones
- 7. Ch. usambarana (Steph.) Grolle
- 8. *Ch. convexa* (S.W.Arnell) S.W.Arnell
- **9.** *Ch. cordistipula* (Steph.) Grolle ex E.W.Jones
- **10.** *Ch. ruwenzorensis* (S.W.Arnell) R.M.Schust.
- 11. Ch. omphalogastria Pócs

Subgen. Cheilolejeunea (Spruce) Schiffn.

Leaf lobes usually rounded-oblong, flat, rarely shallowly convex, apex broadly rounded, plane, hardly recurved. Underleaves occasionally entire to very shallowly notched or deeply incised up to 1/5 of its length. Lobule of \mathcal{Q} bracts developed, usually spatulate.

- 12. *Ch. decursiva* (Sande Lac.) R.M.Schust.
- 13. *Ch. serpentina* (Mitt.) Mizut
- **14.** *Ch. diversifolia* Augier
- **15.** *Ch. intertexta* (Lindenb.) Steph.
- **16.** *Ch. exinnovata* E.W.Jones
- 17. *Ch. trifaria* (Reinw. *et al.*) Mizut.
- 18. *Ch. montagnei* (Gottsche) R.M.Schust.
- 19. Ch. ulugurica Malombe, Eb.Fisch., Pócs & Masinde sp. nov.
- 20. Ch. trapezia (Nees) Kachroo et R.M.Schust.
- 21. Ch. rotundistipula (A.Evans) comb. nov.
- **22.** *Ch. unciloba* (A.Evans) comb. nov.
- **23.** *Ch. xanthocarpa* (A.Evans) comb. nov.

5.4. Bryogeography and Altitudinal Distribution of African Cheilolejeunea

The distribution of *Cheilolejeunea* species in tropical Africa conforms to the eight known areas of bryophytic endemism (Shaw & Goffinet 2000; Pócs, pers. comm.). The most diverse regions were the afromontane and equally hilly sites of Eastern Arc Mountains with more than half of the species distributed. Other rich areas included the mountainous region east of DR Congo (Zaire), Rwanda and Burundi (e.g. Biega, Virunga and Nyungwe mts) and the high humid lowland rainforests with at least 45% of the species recorded. Several species endemic to Africa such as Ch. pocsii, Ch. usambarana, Ch. ulugurica and Ch. omphalogastria are restricted to these two regions, some with only one known locality. Surprisingly Ch. krakakammae, which is locally common in these two regions as well as in Drakensberg and Table mts in South Africa, does not cross to West Africa. Phenotypes of the species have recently been confirmed in China and are believed to occur in India. This may partly imply that African mountains are centres of Cheilolejeunea speciation with most of the species spread to Asia. It may be also true that the distribution or dispersal of Cheilolejeunea species is through hopping (i.e. step by step) of spores from suitable habitat to another and not necessary long range dispersal as proposed by Gradstein and Pócs (1989). The high species polymorphism may arise due to vicariance as suitable habitats like mountains are widely separated and the tropical lowland rain forests have been undergoing severe fragmentation.

Species belonging to subg. *Cheilolejeunea* dominated the lowland rainforests while species of subg. *Strepsilejeunea* were afromontane as observed by Jones (1988). The submontane and lower montane altitudinal zones harbour the most concentrations of *Cheilolejeunea* diversity where the subgenera *Cheilolejeunea*, *Xenolejeunea* and *Euosmolejeunea* reach climax. The species of the subg. *Strepsilejeunea* were favoured by the montane vegetation and a few were occasionally distributed in the subalpine belt where they become more robust. It is also noted that species of lower altitude rainforest mountains may resemble those in higher mountain altitude zonation resulting from *massenerhebung* effect (Grubb & Whitmore, 1966). This may explain the occurrence of afromontane species *Ch. krakakammae* in lowland forest belt in the Cape.

Most species of the genus Cheilolejeunea were primarily corticolous or ramicolous on

trees or shrubs in disturbed open secondary or primary tropical forests. They can however be generalists found in most substrates including soil, rock and leaves given favourable environment conditions such as humidity and temperature. According to Pócs (1996), many liverworts may grow in living leaves in very wet conditions of super humid rainforests. Zhu and So (2001) reiterated that many bryophytes are usually "occasional epiphyllous" on leaves, but predominantly on other substrates usually transported by wind or other agents.

The seemingly more desiccation tolerant species of subg. *Cheilolejeunea* (e.g. *Ch. intertexta*, *Ch. serpentina* and *Ch. decursiva*) were found in most of the substrates especially on living leaves. Other epiphyllous species belongs to the subg. *Xenolejeunea* (*Ch. trapezia*) and Subg. *Euosmolejeunea* (*Ch. montagnei*). In Asia, Zhu and So (1999, 2001), also reported occasional occurrence of *Ch. intertexta*, *Ch. trapezia* and *Ch. trifaria* on living leaves. Species belonging to subg. *Strepsilejeunea* hardly occur on the soil or living leaves. This confirms the results of altitudinal belts were the species are almost devoid of lowland high humid tropical rainforests. They dominated the afromontane belts some hopping over to subalpine zones with low sun radiation and heavy cloudy mist conditions specializing in corticolous and ramicolous substrates. Most of the species exhibit inflated perianth, the lobes are strongly convex compared to subcomppressed perianth, and much flattened leaf lobe characteristics of occasional epiphyllous species (Zhu & So, 2001). Previously, Zhu and So (1999) had described *Ch. pluriplicata* as having an epiphloeodic habitat and never occurring on living leaves like the *Ch. intertexta*, *Ch. trifaria* and *Ch. trapezia*.

5.5. The Implication of the Ecology of *Cheilolejeunea* in Conservation of Kakamega and Budongo Forests

The ecological studies of bryophytes in Kakamega and Budongo lowland rainforests showed Lejeuneaceae as the dominant family. As observed by Gradstein (1992) and Gradstein & Pócs (1989), the species of Lejeuneaceae like the other dominant taxa in tropical lowland forests contain few endemics, as they are largely autoicous and characterised by endosporous protonemata. They germinate rapidly and are adapted to the forest crown or secondary forests including the margins. The high record of Lejeuneaceae

diversity on tree trunks in these forests led by *Cheilolejeunea* and *Lejeunea* species therefore indicates that the two forests are still under either severe encroachment or are yet to recover from the past disturbance.

The highest species diversity was recorded in primary or advanced forest fragments such as in Kisere and Salazar (Kakamega), and N15 compartment (Budongo). These high species diversity and cover was however more pronounced in the open disturbed forest edges or large gaps and fallen branches in primary forests. The sites or fragments were never clear felled or selectively logged like most other sites, but they are experiencing anthropogenic and imminent edge effect especially in Kisere near settlement boundaries. Thus, several mother plants remaining atop the forest canopy may have been producing spores, which easily colonize the tree trunks and emerging species on the well-illuminated forest edge including the occasional gaps. This confirms earlier observations by Fischer (2004), who found high diversity of lichens and bryophyte species in the young open secondary rainforest in Kakamega. Acebey et al., (2003) also noted high species diversity of bryophytes in fallows compared to primary forests in Bolivia. The young developing forests or the edge effects lead to convergence of generally diverse species due to striking shifts and specialized growth types to lower heights of trees. Nevertheless, as the forest advances, only specialised shade tolerant species survive. The sun tolerant species either are retained as small fragments utilizing small forest gaps or are relegated to the forest crown with enough sunlight.

The diversity of *Cheilolejeunea* species in Kakamega Forest was different from Budongo forest. Whilst Kakamega Forest was dominated by species belonging to subg. *Strepsilejeunea* (*Ch. krakakammae* and *Ch. fischeri*), Budongo Forest contained largely species of subg. *Cheilolejeunea* (*Ch. intertexta* and *Ch. trapezia*) and subg. *Euosmolejeunea* (*Ch. trifaria*). These different taxa have been found to occupy different altitudinal ecozones, the subg. *Strepsilejeunea* favoured by afromontane related vegetation and the others inclined to lowland tropical vegetation (Schuster, 1980a; Jones, 1988). This could be because Kakamega Forest lie around 1600 m a.s.l., which is well within lower montane zone of tropical vegetation. Budongo Forest rise to an average of 1100 m a.s.l. qualifying to lowermontane vegetation common with species of subg. *Cheilolejeunea*. As most other bryophytes in Africa as noted by Pócs (1992), several species of *Cheilolejeunea* recorded such as *Ch. krakakammae*, *Ch. intertexta*, *Ch. trapezia*, *Ch. decursiva* and *Ch.*

trifaria are of Afro-Asian distribution.

The species of *Cheilolejeunea* showed minimal preference of the tree phorophyte. They usually occupied the most common pioneer tree species such as *P. fulva* and *H. madagascariensis*. The bark texture could however determine their distribution. For example, the smooth trunks of *P. guajava* were devoid of *Cheilolejeunea* species.

The study of *Cheilolejeunea* ecology in tropical lowland forests in Kakamega and Budongo generally underscores the importance of bryophytes as vital components of the ecosystem and applications in rapid environmental evaluation of forest quality. A quick survey of the presence and distribution of *Cheilolejeunea* species can be therefore useful to indicate forest types or ages including the history of anthropogenic disturbance in lowland rainforests. High concentrations of *Cheilolejeunea* populations may indicate highly disturbed young forests or open secondary forests.

5.6. Conclusions and Recommendations

The phenetic analysis of the African Cheilolejeunea morphological data shows only two major phenons separating the species with strongly convex leaf lobes from those with flattened and rounded lobes. Further, it reemphasize that species of Leucolejeunea are related to Cheilolejeunea and, for the first time, affiliated to subg. Xenolejeunea. These results were well supported by phylogenetic analysis, which aligned the three species of Leucolejeunea within subg. Cheilolejeunea. The differences between Cheilolejeunea and Leucolejeunea has been doubted by many hepaticologists including Schuster (1963, 1980a) and Zhu and So (2001). The current study had found Leucolejeunea rotundistipula to have two ventral merophytes with 7-8 cortical cells, which clearly ranks it within the genus Cheilolejeunea. Recent molecular data on the family Lejeuneaceae by Wilson et al., (2007a) found the genus *Cheilolejeunea* paraphyletic having species of *Leucolejeunea* and other related genera placed together. They proposed adoption of a wider genus retaining Cheilolejeunea name in place of the old but less diverse Omphalanthus. This study combines the Leucolejeunea with Cheilolejeunea based on the above observations and recognises 23 species in two subgenera, the monophyletic subg. Strepsilejeunea and a more derived subg. *Cheilolejeunea* (see species list in 5.3.1). The results are well supported by bryogeography of *Cheilolejeunea* in Africa where the species of subg. Strepsilejeunea occur in afromontane and subalpine vegetation and those of subg.

Cheilolejeunea restricted to more humid lowland and submontane vegetation.

The ecological studies of the *Cheilolejeunea* species in tropical rainforests showed that Kakamega forest is dominated by afromontane species *Ch. krakakammae*, while Budongo forest is characterised by common Afro-Asian lowland tropical rainforest species *Ch. intertexta*. Importantly, the species were among the habitat pioneers characteristic of disturbed secondary or open primary forests. They can therefore be useful in rapid evaluation of forest quality and determination of the disturbance level attributed to natural or anthropogenic environmental changes.

This study using the gametophytic characters allows segregation and identification of the species of *Cheilolejeunea*. It did not provide substantial information for a well founded evolutionary classification. Use of broader phenetic and phylogenetic characters such as secondary metabolites and DNA data sequences is therefore recommended. Future studies should take into account the robust species distributed in the Indian Ocean islands such as Madagascar, Mauritius, Comoros and the Mascarenes.

5.7. Systematic Treatment of African Cheilolejeunea

- Cheilolejeunea (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 118, 124.1893. Type [lectotypified by Grolle (1983)]: Cheilolejeunea decidua (Spruce) A. Evans (Lejeunea decidua Spruce).
- Anomalolejeunea (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 118, 127.1893. Type: Anomalolejeunea pluriplicata (Pearson) Schiffn. (Lejeunea pluriplicata Pearson).
- Euosmolejeunea (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 118, 124. 1893. Type [lectotypified by Vanden Berghen (1948)]: Euosmolejeunea trifaria (Reinw. et al.) Schiffn. (Jungermannia trifaria Reinw. et al.).
- Strepsilejeunea (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 119, 127.1893. Type [lectotypified by Grolle (1983)]: Strepsilejeunea inflexa (Hampe ex Lehm.) Steph. (Lejeunea inflexa Hampe ex Lehm.).
- Cyrtolejeunea A. Evans, Bull. Torreya Bot. Club 30: 553, 1903. Type: Cyrtolejeunea holostipa (Spruce) A. Evans (Lejeunea holostipa Spruce).
- Leucolejeunea A. Evans, Torreya, 7: 225-229, 1907, comb. nov. Lejeunea G.L. & N., Syn. Hep. p. 330, 1945. Type: Leucolejeunea clypeata (Schwein.) Evans.

Placolejeunea Herzog, Svensk Bot. Tidskr. 42: 234, 1948. Type: *Placolejeunea subarrhyncha* Herzog.

Plants dull (never glossy), light to deep green, brown green to olive green or glaucous, sometimes yellowish-brown, appressed or ascending, rarely pendent. Shoots 25 mm long, rarely more, 0.4-1.8 mm wide, irregularly branched, branching of the *Lejeunea*-type, sparse to profuse, sometimes ± microphyllous, leaf sequence of vegetative branches lejeuneoid. Stem 58-159 µm in diameter, transverse section of mature or old parts consisting of usually seven or eight, sometimes up to 24 enlarged cortical cells, the cells \pm thick-walled, medullary cells usually smaller, (10)14-21. Ventral merophytes usually of two cells, occasionally wider in Ch. unciloba and Ch. xanthocarpa. Rhizoids numerous, fasciculate, at base of underleaves. Leaves imbricate, rarely approximate, widely spreading from stem, sometimes caudicous. Leaf lobes ovate, obovate, suborbicular, oblong or broadly obovate, ± falcate, flat to shallowly convex or strongly convex, apex rounded to sharply acute, plane or recurved, margins smooth, or sinuately mammillose cells, dorsal margin ± arched. Cell of leaf lobe thin to slightly thick-walled, trigones small to large, radiate, triangular or conspicuously nodulose, sometimes well visible dorsally, marginal cells subquadrate, median cells hexagonal or oblong, basal cells similar to median ones or distinctly elongate. Oil bodies of *Leucolejeunea*-type (rarely *Calypogeia*-type), 1-4(-6) per cell, medium to very large, coarsely granular, botryoidal or crescent shaped and nearly filling the cell lumen. Ocelli or vitta lacking. Leaf lobules 0.15-0.74 the length of the lobe, triangular to ovate, oblong to rectangular, rather strongly inflated, free lateral margin slightly to strongly incurved, sometimes visible in situ (Ch. cordistipula, Ch. rotundistipula, Ch. unciloba, Ch. trapezia and Ch. ulugurica), usually consisting of 4-6 or occasionally up to 13 cells or more (Ch. cordistipula, Ch. trapezia, Ch. unciloba and Ch. xanthocarpa), apex obliquely truncate, attenuate or constricted, apical tooth obtuse or acute, rarely spiniform, 1-6 celled, short or long, sometimes rather reduced, straight or recurved, hyaline papillae distal to the second tooth, usually at the base or sometimes displaced to 2 or 6 cells, keel straight or arched, smooth or mammillose. Underleaves imbricate, sometimes remote, suborbicular or oblong, 1.5-6.2 times as wide as stem, apex bifid (0.08-0.60 underleaf length) or emarginate to entire, sinus wide-U shaped to acute, rarely orbicular, margin entire, the base cuneate, truncate or cordate; insertion line shallowly curved to strongly arched. Dioicous or autoicous, occasionally paroicous. Androecia on very short or long branches, terminal or often intercalary, bracts in 1-11

pairs, rarely more, densely imbricate, obliquely spreading, bracteoles 1-2(3), smaller than underleaves, usually restricted to the base of androecium, hardly up to the apex (*Ch. omphalogastria*). Gynoecia on long or short shoots, with 1-2 lejeuneoid or pycnolejeuneoid innovations, sometimes sterile, bracts leaf-like, usually sharply pointed and larger than normal vegetative leaves, the lobules linear or spatulate, bracteole entire or bifid at apex. Perianth obovate or long clavate with 3-10 smooth keels (occasionally sterrate in *Ch. krakakammae*), beak 10-125(-198 in *Ch. xanthocarpa*) µm long. Capsules spherical, dehiscing from the apex down into four non-recurving valves; seta with 12 outer cells surrounding four inner cells in transverse section.

Distribution. Pantropical, primarily on bark of trees or shrub, including young and small branches. It is also frequently epiphyllous and rupicolous on wet rocks or rarely terricolous on wet soil and decaying logs in lowland to afromontane or sometimes-subalpine tropical forests. Twenty-three species of *Cheilolejeunea*, including three newly described and currently combined three species formerly known to *Leucolejeunea*, belonging to two subgenera are recognised in continental tropical Africa.

Key to subgenera and species of Cheilolejeunea in continental Africa

,	, 1	,	innovations persistently
			6. Ch. pocsii
J			1
3. Autoicous; leaf lob	es rarely caudicous; peri	anth keel 5 cari	nate, usually deeply seated;
underleave sinus	occasionally wide, V-U	shaped; micro	phyllous shoots unknown;
subgynoecial innov	ations most pycnolejeun	eoid, sometimes	lejeuneoid4
			o < 0.5; underleaf lobes
			se, appressed, mixed with
other species			7. Ch. usambarana
4. Perianth oblong;	lobule-leaf length ratio	$0 \ge 0.5$; underl	eaf lobes rounded; plants
rupicolous, forming	g thick mats with ascendi	ng shoots	8. Ch. convexa
5. Underleave width a	at least 4 or more x stem	width; leaf lobe	es length and width ratio at
			6
			and width ratio up to 1.2
			8
			cordate; androecium bracts
	······		
			ded to obcordate, insertion
			7
			in flattened, visible in situ;
		_	-striata, up to 2/3 length of
-			9. Ch. cordistipula
-		-	iform, rectangular, keels 5,
	_		10. Ch. ruwenzorensis
_		•	ranching dichotomous; leaf
			pycnolejeuneoid, a few
			3. Ch. fischeri
		_	nching never dichotomous;
-		-	ty lejeuneoid, sometimes
			9
			terminal on short lateral
huan ah aa			

9. Perianth tricarinate; androecia usually on proximal part of branches
10. Rostrum exerted; perianth keels (6)7-10, inflated, fusiform, widest at the middle
10. Rostrum inserted; perianth with keels 3-4 (5), sometimes terete, pyriform11
11. Perianth inserted, almost covered by bracts; rostrum long, 99-125 µm; shoots 1.2-1.5
mm wide
11. Perianth exserted above bracts; rostrum shorter, 30-94 µm; shoots 0.6-1.2 mm
wide
12. Leaf lobule rectangular or oblong, usually more than ½ as long as the leaf lobe, apical
tooth angular, usually long, ventral free margin cells (10) 15-38 or more; subgynoecial
innovations pycnolejeuneoid only; oil bodies one, rarely more
12. Leaf lobule ovate or triangular, usually up to 2/5, rarely up to ½, as long as leaf lobe;
subgynoecial innovations lejeuneoid or pycnolejeuneoid; oil bodies more than
one
13. Underleaves reniform to orbicular, usually more than 4x larger than the stem width,
completely covering most of the leaf lobules, strongly sinuately inserted on stem,
shortly/shallow bifid or entire at apex; lobule apical tooth usually short
13. Underleaves oblong or suborbicular, usually less than 4x larger than the stem width,
rarely covering the whole length of the leaf lobules, shallowly sinuately inserted on the
stem, most bifid up to half length at apex; lobule apical teeth usually longer,
differentiated
14. Dioicous; leaf lobes 1.1-1.3x as long as wide, often caudicous13. <i>Ch. serpentina</i>
14. Autoicous; leaf lobes 1.2-1.5x as long as wide, never or rarely semi
caudicous
15. Lobule apical tooth long, 20-30 μm long, spiniform; leaf lobes somehow shallowly
convex, apex sometimes deflexed
15. Lobule apical tooth short, 12-20 μm long, blunt; leaf lobes usually flat, apex never
deflexed
$16. \ \ Cortical \ \ cells \ \ 4-5; \ lobule-leaf \ \ lobe \ \ length \ \ ratio \ > 0.5; \ leaves/lobules \ \ conspicuously$
mammillose
16. Cortical cells 7; lobule-leaf lobe length ratio <0.5; leaves/lobules mammillose
inconspicuously
17. Leaves rounded-oval, delicate or semi-caudicous, ca 0.3 mm long; gynoecia with 1-2

- isotypes: JE H1595, S B 30192, W).
- Lejeunea comitans Hook.f. & Taylor in Taylor, London J. Bot. 5: 400. 1846.
 Strepsilejeunea comitans (Hook.f. & Taylor) Steph., Sp. Hepat. 5: 291. 1913.
 Cheilolejeunea comitans (Hook. f. & Taylor) R.M.Schust., J. Hattori Bot. Lab. 26: 245. 1963; syn. nov. Type: New Zealand. 1844, Hooker s.n. (lectotype designated by Grolle (1982): FH; isolectotypes: G 19688, S B47667, S B47666, W).
- Lejeunea khasiana Mitt., J. Proc. Linn. Soc., Bot. 5: 115. 1861. Strepsilejeunea khasiana (Mitt.) Steph., Sp. Hepat. 6: 395. 1923. Cheilolejeunea khasiana (Mitt.) N. Kitag., Hikobia suppl. 1: 68. 1981; syn. nov. Type: India "India Orient". Khasia, region subtrop., 4000 ped., Hooker & Thomson 1516 (holotype: BM).
- Lejeunea brevifissa Gottsche, Abh. Naturwiss. Ver. Bremen 7: 356. 1882. Strepsilejeunea brevifissa (Gottsche) Steph .in Engler, Pflanzenw. Ost.-Afrikas C: 65. 1895. Cheilolejeunea brevifissa (Gottsche) R.M.Schust., Beih. Nova Hedwigia 9: 113. 1963. Type: Madagascar. Rutenberg 1511(holotype: G 17874).
- Euosmolejeunea giraldiana C.Massal., Mem. Accad. Agric. Verona 73: 34. 1897. Strepsilejeunea giraldiana (C.Massal.) Steph., Sp. Hepat. 5: 288. 1913. Cheilolejeunea giraldiana (C.Massal.) Mizut., J.Hattori Bot. Lab. 27: 141. 1964. Type: China .Shanxi [Schen-si]. Mt. Kuantou-san, July 1894, Giraldi s.n. (holotype: VER?; isotype: G 001934).
- Strepsilejeunea inflata Steph., Sp.Hepat. 5: 278. 1913. Type: Madagascar. Betsileo, Herb. Lacouture 140 (holotype: G 17669; isotype: JE).
- Strepsilejeunea ontukensis Steph., Sp.Hepat. 5: 289. 1913. Euosmolejeunea ontukensis (Steph.) S.Hatt., J.Hattori Bot.Lab.5:85.1951. Cheilolejeunea ontukensis (Steph.) S.Hatt., Misc. Bryol. Lichenol. 1: 1. 1957.Type: Japan. Naganoken, Mt. Onktake, Fuurie s.n. (holotype: G 19379).
- Strepsilejeunea gomphocalyx Herzog in Handel-Mazzetti, Symb. Sin. 5: 47. 1930.
 Euosmolejeunea gomphocalyx (Herzog) S.Hatt., Bull. Tokyo Sci. Mus.11: 106.
 1944. Type: China. Hunan "Hunan." "An lebender Rinde von Rhus verniciflua auf dem Yiin-schan bei Wukang," 1200 m, 19 June 1918, Handel-Mametti 12156 (lectotype designated by Zhu et al. (2002): WU; isolectotypes: W, JE).
- Strepsilejeunea tereticalyx Herzog, Trans. Roy. Soc. New Zealand 77:256.1949.

 Cheilolejeunea rereticalyx (Herzog) Hamlin, Rec. Dom. Mus.7: 255. 1972. Type: New Zealand. Nordth Is., Wairoa, Morere Bush, Hodgson 292 (holotype, JE).
- Strepsilejeunea georgensis S.Arnell, Bot. Not.106: 179. 1953. Type: South Africa. Cape

Province, George, Wilderness, 20 Nov. 1951, Arnell 1381 (lectotype designated here: BOL 1109321!; isolectotype: S B476688).

Strepsilejeunea knysnana S.Arnell, Bot. Not.106: 178. 1953. Type: South Africa. Cape Province, Knysna, Gouna Forest, 26 Nov. 1951, Arnell 1741 (holotype: BOL 110932!).

Plants yellowish green, strong shoots 0.6-1.2 mm wide, irregularly branched, stem 65.0-110.9 µm in diameter. Leaves imbricate, diverging from the stem at an angle of ca. 45-60(70)°, weakly interlocking dorsally; the *leaf lobe* ovate, weakly to strongly convex, somewhat falcate, 418.0-621.2(696.0) µm long, apex subacute to sharply acute, usually recurved, lobe median cells 17.1-28.3 µm long and 11.5-19.7 µm wide, trigones small, rarely large, 2.3-8.5 µm long, usually triangular, oil bodies *Leucolejeunea*-type, occasionally with Calypogeia-type, (1-)2-4(-6); leaf lobule ovate, strongly inflated, (125.3)142.7-254.0 (311.0) µm long, 1/5-2/5(-1/2) as long as the lobes, lateral free margin strongly incurved, bordered by (5-)8-11(-12) cells, keel arched, ca. perpendicular at base with stem and postical lobe margin, but occasionally wider than the latter, apex narrow, usually constricted to overlie apical tooth, the apical tooth 1(2-4) celled, sometimes indistinct, 6.5-33 µm long, obtuse to subacute. *Underleaves* remote to approximate, 177-368 µm long, 174-435 µm wide, slightly wider than long, 2.1-4.0(-5.0) times as wide as stem, orbicular to shortly obovate, apex bilobed to 1/5-1/3 of its length, lobes acuminate, apex broadly rounded to subacute, base weakly cordate or \pm cuneate in weaker shoots, insertion mostly arched. Autoicous, occasionally paroicous. Androecia, subsessile, usually axillary or terminal on short lateral branches, bracts in (1-) 2-6(-11) pairs, 177.5-355.0 µm long, bracteole (0)1-2, restricted to the base of androecium. Gynoecia on main stems or on lateral branches, with 1 or 2 innovation(s), occasionally lacking, innovation lobe sequence usually lejeuneoid or pycnolejeuneoid; bracts obovate, narrowly spreading, slightly shorter than perianth, the lobule linear to obovate, up to 0.5 the length of the bract lobe, obovate, apex subacute, keel almost straight; bracteole oblong to suborbicular, 271-477 µm long, the apex lobed, sinus to 0.10-0.13 of the bracteole length, lobe apices rounded, slightly reflexed, margins entire. Perianth usually exserted, obovate (370-)473-864 µm long, (225-)365.4-584.6 µm wide, keels 3(4-5) or occasionally terete (two lateral and wide, and 1-2 ventral), rostrum narrow, 30-94 µm long.

REPRESENTATIVE SPECIMENS EXAMINED. UGANDA. Bunyoro; Budongo

Forest, road from Sonso Camp towards N Reserve, near compartment W22, 1.43685 N 31.3318 E 1100 m, 19 May 2006, *Malombe I & Mwale G* 6002 N3x20 (EA). **KENYA**. West Pokot: Cherengani hills on side of the road from Kitale, 1.15 N 35.27 E, 17 Dec. 2004, Malombe I & Mlangeni E 4029 a (EA); Kaibwibich, 1.12 N 35.17 E 2600 m, 16 Apr. 1975, Friis IB 2730 (EGR). Aberdare National Park, on the Nyandarua Range below the fishing Camp on the Southern part of the Aberdare Plateau in the Magura River Valley, 18 Mar. 2002, Pócs T & Chuah MS 02031 V (EGR, NAI, EA); South of Aberdare hills, along Thika-Kijabe road, 2400 m, 27 Jan. 2003, Pócs T, Chuah-Petiot & Students 03002 N (EA, EGR) & Nyandarua Peak, along Magura River, below Fishing Camp, 3000 m, Pócs T & Chuah MS 02031 V (EA, EGR). Kakamega forest, Buyangu, Colobus forest fragment, along Mukhangu trail, near Mwanzu, 0.2107 N 34.5207 E 1610 m, 12 Sep. 2005, Malombe I & Chituyi BB 5002 Co.2bSx1 (EA, EGR); Kisere forest fragment, northern corridor, near forest edge, 14 Oct. 2005, Malombe I & Soita L 5008 K. (EA); 1aS5Malombe I & Soita L 5008 K.1bS2 (EA); Salazar, along Hiking trail, 13 Sep. 2005, Malombe I & Chituyi BB 5006 Si.1cS3x (EA); along path towards Isiukhu river, 14 Sep. 2005, *Malombe I & Chituyi* BB 5006 Si.2aS4 (EA); along Salazar road near circuit towards Isiukhu river, 13 Sep. 2005, Malombe I & Chituyi BB 5006 Si.1aS1 & 5006 Si.1aS5 (EA) & near Buzambuli A trail, W. Salazar Circuit, 14 Sep. 2005, Malombe I & Chituyi BB 5006 Sii.2bS3 (EA). Kajiado; Ngong Hills, SE slopes, below the aviation satelite station on edge of mist forest, 2420 m, 19 Mar. 2005, *Malombe I Fischer E & Mwachala G* 5009 G (EA) & 1.25 S 36.38 E 2420 m, 10 Mar. 2002, Chuah MS & Pócs T 02025 K (EGR, NAI). Taita Taveta; Vuria Hill, the summit around telecommunication tower, 3.2456 S 38.1763E 2210 m, 1 Apr. 2004, Pócs T, Chuah-Petiot MS & TABC Students 04042 BC (EA, EGR) &. 3.25 S 38.18 E 2200 m, 2 May 1975, Friis IB 2756 (EGR). TANZANIA. Moshi; Umbwe, Mt Kilimanjaro, along Umbwe route, 2450 m, 1 Jul. 1976, Pócs T 6931 J (EGR). Lushoto; W Usambara Mts, Ndamanyiru range on the rocky summit, 13 Feb. 1985, *Pócs T* 8547 AE (EA, EGR); Mazumbai, University Forest Reserve, Sagara ridge, 1800-1900 m, 2 Feb. 1985, *Pócs T* 8531 C (EA, EGR); near "Kambo", 1620 m, 8 Jan. 1971, Pócs T, Tanner & Jones EW 6374 (EGR) & Pócs T & Jones EW 6371 BF (EGR). Morogoro; Bondwa Peak, top of peak near Uluguru Mts, above Morogoro town, 2100 m, 29 Aug. 1970, Pócs T 6233 P (EGR); Mindu Mts, on the NE slope of hill above Kasanga II, SW of Morogoro town, 650 m, 4 Jun. 1988, *Pócs T* 88101 DB (EA, EGR); Nguru Mts, between Chazi and Dikurura valleys, W of Magole, N-NW of Mhonda Mission, 1580 m, 14 Sep. 1988, Pócs T & Minja A 88184 R (EA, EGR). **SOUTH AFRICA.** Natal; Cathkui Peak, 1000 m, Jan. 1918, Sim TR CH

2079 (PRE); Polela, 4000 ft, 1914, *Haygarth WJ* CH 2120 (PRE); Evelyn Valley, Kaffraria, 1902, *Sim TR* CH 2047 (PRE). Cape; Uitenhage, Urwaldung von Krakakamma, Jul. 1832, *Anon.* S.N.(BO).

afromontane (in *Ocotea-Allanblackia stuhlmanii* or *Syzygium and Podocarpus sp.* dominated forest) to subalpine (elfin or *Erica* heath) tropical forest species. Though mainly corticolous or ramicolous in disturbed secondary forest edges of wet, dry misty semi evergreen primary forests or mossy rocky cliffs, it can also be rupicolous, on decaying materials or rarely epiphyllous between 1000-3200 m (recorded at 150 m a.s.l. in the Cape Province, South Africa) usually mixed with *Plagiochilla sp., Lopholejeunea sp., Lejeunea sp., Frullania sp.*, or *Radula sp.* Sometimes it behaves like a pioneer species able to withstand most disturbances, including frequent fires and exposure, but wanes out as forest closes and more species emerge. It is a paleotropical species occurring from Central Africa in DR Congo to South Africa (Congo Brazaville, DR Congo, Burundi, Rwanda, Ethiopia, Uganda, Kenya, Tanzania, Malawi, Zimbabwe and South Africa) including Madagascar, Réunion and Comoros Is. It was recently described in Asia as well as India, Papua New Guinea and Australia.

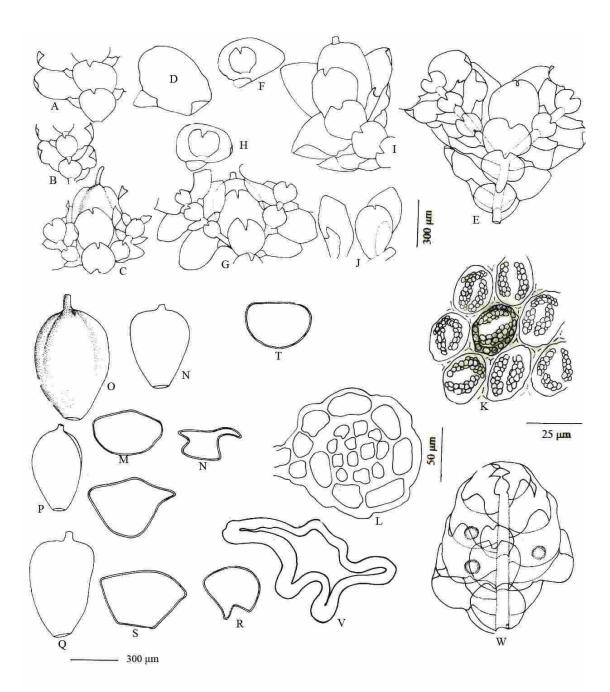


Figure 14. *Cheilolejeunea krakakammae* (Lindenb.) R.M.Schust. (A,B) Part of sterile shoot, ventral view; (C) Gynoecium with bluntly carinate perianth and two lejeuneoid innovations; (D) leave, ventral view; (E) Part of shoot with one gynoecium, ventral view; (F) Leave with adjacent underleaf; (G) gynoecium with perianth; (G) Leave with adjacent underleaf; (I) Gynoecium with terete perianth and without subgynoecial innovations; (J) Female bracts and bracteoles; (K) median cells with oil bodies; (L) Transverse section of stem; (N-Q) Perianth, ventral view; (M, R-V) Transverse section of perianth; (w) Androecia. A-H, M-U drawn from *Ecklon s.n.* (Isotype, *Lejeunea krakakammae* S) and I, J from *E.W. Jones* 665 (from Jones, 1988 and Zhu, 2006); K, L, V and W from *Malombe I & Kilei P* 5008 K 1as5.

NOTES. *Cheilolejeunea krakakammae* exhibits substantial variations in several features. For example, the leaf lobes are usually acute or obtuse at apex, sometimes rounded especially near shoot bases, while the lobes are usually strongly convex and apex recurved, occasionally shallow and weakly recurved in some populations. Majority of leaf lobules

are less than half the leaf lobe length but a few are longer (e.g. *Malombe I & Chituyi* BB 5002 Co2aSx1, *Malombe I & Soita L* 5007 Ya.1bS2, *Pócs T* 6931 J and *Pócs T & Chuah MS* 02031 V). The cells of the lateral lobule free margin vary from 8-10, but some indicated up to 11 or 12, and one collection had 5 cells. Underleaves are usually up to 4 times as wide as stem while some extremes are up to 5 times. Perianth usually has 3-4 keels but terete or five carinate are common even on the same branch. Jones (1988) observed an almost all lejeuneoid subgynoecial innovations in *Ch. krakakammae* and recommended the character as useful in the species delimitation (Wigginton, 2004a), sediments shared by Zhu (2006) in the description of the species in Asia. However, the current study noted many collections of *Ch. krakakammae* with either lejeuneoid or pycnolejeuneoid subgynoecial innovation(s) as well as frequent sterile perianth, which are placed at terminal of the fertile branch. It is difficult to decide the most common type of innovation.

Some collections from Kakamega forests exhibited extreme length of 2.6 cm and wider shoots (e.g. *Malombe & Chituyi* 5006 Si 2aS4). Most of these were within old forest gaps in advanced secondary forest and probably never dried completely during dry conditions and continued to grow in favarouble weather. Most of the collections by *Pócs T* (e.g. 7145, 6512, 6021 and 8167) from Rwanda were mistakenly identified as *Ch. krakakammae*. I find these specimens a replica of *Ch. cordistipula* (and currently determined so) owing to large lobule lobe length ratio, majority with conspicuously flattened postical margin of lobule and large trigones. Also the perianths are elliptic with acute apex and 5-6 carinate which extend halfway the length.

2. Cheilolejeunea ngongensis Malombe & Pócs sp. nov.

Diagnosis: *Differt ab* Cheilolejeunea krakakammae (Lindenb.) R.M. Schust., Beih. Nova Hedwigia 9: 112, 1963. *perianthiis brevioribus immersis cum rostris elongatis*.

Plants green to light green, strong shoots 1.15-1.48 mm wide, stem 88.7-105.0 μm in diameter. *Leaves* distant to loosely imbricate, the lobes ovate to orbicular, very narrowly convex, 506.0-693.0 μm long, 396.7-525.0 μm wide, apex subacute to broadly rounded, a few lobes shortly recurved, margin smooth, base rounded, shortly crossing the stem; lobe median cells 23.13-26.88 μm long and 15.0-18.5 μm wide, trigones small, 2.1-3.3 μm long, usually triangular, oil bodies 2-3. *Leaf lobule* triangular, 135.7-232.5 μm, 1/3 as long

as the lobes, distal free margin 8-12(14) celled, keel straight to weakly curved at an angle of 40°-60°, occasionally at 90° especially at the basal lobes, forming wide angle with postical lobe margin, apical tooth 1 celled, ca. 14.75 μm long. *Underleaves* distant to approximate, 3.8 times wider than the stem width, 306-327 μm long, 355-381 μm wide, slightly wider than length, orbicular, lobed 0.2-0.4 of their length, lobes ovate, apex broadly rounded to subacute, subcordate. *Gametagia* autoicous. *Androecia* bracts in 2-4 pairs, imbricate and saccate, male bracteole 1. *Gynoecia* innovations 1-2, innovation lobe sequence usually lejeuneoid, rarely pycnolejeuneoid; bracts usually erect, slightly longer than perianth, 574.2-635.9 μm long, the lobule up to 0.6 the length of the bract, narrowly linear, apex acute; bracteole obovate, apex sinus 0.13-0.17 of the bracteole length, lobe apices rounded, margins entire. *Perianth* appressed, pyriform, dorsiventrally subcomppressed, 440-679 μm long by 295-470 μm wide, covered by the bracts except the emerging rostrum, keels 4, lateral ones longer; rostrum 99-125 μm long. Rhizoids several, spreading to radiant, 224 μm.

SPECIMENS EXAMINED. KENYA. Kajiado District; Ngong Hills, SW of Nairobi city, near the top ridge, 2400 m, 25 Feb. 2004, *Pócs T*. with EA staff 04011 AN (EGR, holotype) and 19 Mar. 2005, *Malombe et al.*, 5009 Lb2 (EA, EGR).

ECOLOGY AND DISTRIBUTION. Only known from the type locality *ca.* 2400 m a.s.l in Ngong hills, a cloudy and mist afromontane open forest of volcanic type usually affected by the easterly winds. Ramicolous.

NOTES. *Cheilolejeunea ngongensis* is described under the subg. *Strepsilejeunea* usually characterized by species with strongly, sometimes shallow, convex lobes with broadly acute apices and usually linear lobule of female bracts (Jones, 1988; Schuster, 1980a). The number of cells on the leaf lobule margin are 8-12, which is characteristic of this subgenus. It is however differentiated from the closest relative *Ch. krakakammae* by the wider shoots and short perianth usually covered by the female bracts with exceptionally elongated and protruding rostrum. Although Jones (1988) reports long rostrum in *Ch. krakakammae*, all the observed specimens were relatively shorter.

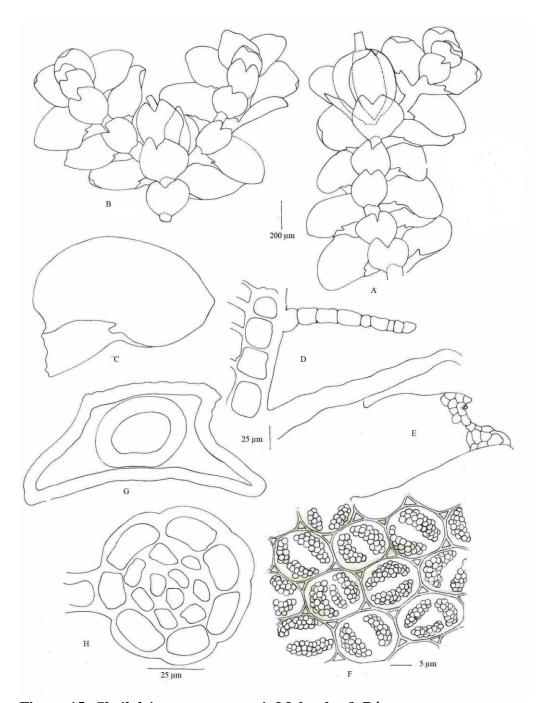


Figure 15. *Cheilolejeunea ngongensis* **Malombe & Pócs sp. nov.** (A, B) Fertile shoots with lejeuneoid gynoecial innovations, ventral view; (C) Leave, ventral view; (D) Free margin cells of lobule; (E) Lobule with apical tooth and papilla; (F) Median cells of lobe with oil bodies; (G) Transverse section of perianth with capsule; (H) Transverse section of stem. B-H drawn from *Malombe et al.*, 5009 Lb2 and A from *Pócs T* 04011 AN (holotype). By author and N. Maundu

3. Cheilolejeunea fischeri Malombe sp. nov.

Diagnosis: Differt a Cheilolejeunea krakakammae (Lindenb.) R.M. Schust., Beih. Nova Hedwigia 9: 112, 1963 colore olivaceo, lobis apice acutis incurvatis, oleocorporibus fere permanenter duabus et surculis dichotomis.

Plants olive green, strong shoots up to 2.5 cm long, 0.7-0.9 mm wide, seldom branching, dichotomously branched, stem 81.4-95.3 µm in diameter. Leaves strongly imbricate, shortly appressed near the base, the lobes ovate, falcate, strongly convex above and raised from the stem, 404.0-561.0 µm long, 342.4-467.2 µm wide, apex subacute to sharply acute, strongly recurved, the tips somehow inrolled, base rounded, widely crossing the stem; lobe median cells 15.8-23.1 µm long and 12.5-17.5 µm wide, trigones medium sized, 4.8-7.5 µm long, usually triangular, occasionally nodulose, oil bodies 2, rarely 3. Leaf lobule triangular to ovate, entirely inflated, 120.9-215.0 µm long and 90.0-135.7 µm wide at base, 1/3 to 2/5 as long as the lobes, distal free margin strongly incurved, 8-12(14) celled, keel strongly arched ca. perpendicular at base with stem and postical lobe margin, apex narrow, incurved and constricted to overly apical tooth, the apical tooth 1-2 (4) celled, 12.5-24.4 (39) µm long, broadly rounded, rarely subacute, straight but occasionally elongated and recurved towards the keel. *Underleaves* distant to approximate, 217-325 µm long, 271-471 µm wide, slightly longer than wide, 3.2 x wider than the stem width, orbicular to shortly obovate, apex bilobed to 1/5-1/4 of their length, sinus V shaped, lobes acuminate, apex broadly rounded to subacute, margin raised making the underleaves look bowel like, subcordate. Autoicous. Androecia subsessile, axillary or terminal on short branches, bracts in 2-6 (10) pairs, 198-219 µm long, bracteole 1-2, restricted at the base. Subgynoecia innovations 1 or 2 (and shortly fertile), sometimes lacking, innovation lobe sequence usually lejeuneoid, rarely pycnolejeuneoid, female bracts slightly shorter than perianth, lobule up to 0.5 the length of the bract, linear-shortly obovate, apex subacute; bracteole elliptic to narrowly obovate, 271-477 µm long, the apex lobed, sinus to 0.10-0.13 of the bracteole length, lobe apices rounded, slightly reflexed, margins entire. Perianth pyriform or obovate, dorsiventrally slightly compressed, exserted by 1/3 to completely exposed probably by maturity, keels four (3-5 or terete), lateral ones wider, rostrum 41.8-55.7 µm long, 5 celled.

SPECIMENS EXAMINED. KENYA. Kakamega forest, Buyangu, along Arboretum drive at Birds' Observatory site, 1610 m, 11 Sept. 2005 *Malombe I & Chituyi BB* 5002 Co 1bS1; Salazar II fragment, along the path towards Buzambuli A, W. Salazar Circuit, 14 Sept. 2005 *Malombe I & Chituyi BB* 5006 SII 2bS1x (EA holotype, EGR isotype); Salazar forest fragment, along Hiking Trail off the path to Isiukhu River, 13 Sept. 2005 *Malombe I & Chituyi BB* 5006 SI 1cS5; Udo Campsite, ca. 1 km from Udo's camp, along Hiking Trail, 29 Jun. 2005, *Malombe I & Kilei P* 5009 Ca 3.6 & 1aS8B.

ECOLOGY AND DISTRIBUTION. It inhabits the bark of pioneer forest trees such as *Polyscias fulva* or rarely *Harungana madagascariensis* and *Combretum schumannii* usually in more shaded and advanced secondary forest edges than its closest relative, *Ch. krakakammae*. It is usually isolated and rarely mixed with few other bryophytes. Endemic to Kakamega lowland rainforest at about 1620 m a.s.l.

NOTES. Cheilolejeunea fischeri is distinguished from related species especially *Ch. krakakammae* by its olive green coloration, which is clearly observed in fresh collections. The occurrence of olive colour in *Cheilolejeunea* is rare and has only been reported in Latin America for *Cheilolejeunea evansii* (M.S. Tayl.) Schust. (Schuster, 1980a) and China for *Cheilolejeunea ceylanica* (Zhu & So, 2001). Other distinguishing characters include strongly convex lobes with apices usually sharply acute and somewhat inrolled, large oil bodies, persistently two (rarely three) per cell, and long shoots, which are somewhat dichotomously branched. The lobule apical tooth is occasionally elongated and recurved inwards.

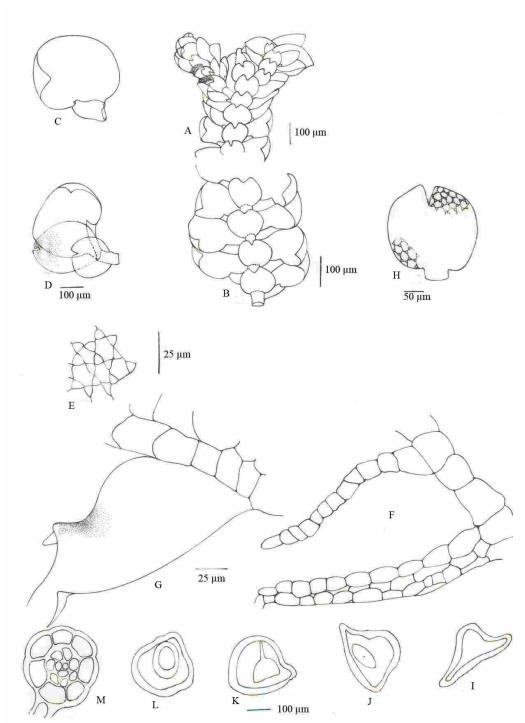


Figure 16. *Cheilolejeunea fischeri* **Malombe & Pócs sp. nov.** (A) Habit, dorsal view; (B) Portion of shoot with 1-2 pycnolejeuneoid gynoecial innovations, ventral view; (C) Middle portion of shoot; (D) leave, ventral view; (E) Female bract and bracteole, ventral view; (F-H) Median lobe cells and oil bodies; (I) Cells of lobule free margin with apical tooth; (J) lobule with apical tooth; (K) underleave; (L-O) Transverse section of perianth, some with capsule; (P) Transverse section of stem. All drawn from *Malombe I & Chituyi BB* 5006 SII 2bS1x (Holotype). By author and N. Maundu

4. Cheilolejeunea pluriplicata (Pearson) R.M.Schust., Phytologia 45: 430. 1980. Lejeunea (Anomalo-Lejeunea) pluriplicata Pears., Christiana Vidensk. –Selsk. Forhandl. nr 1: 5 (1887). Anomalolejeunea pluriplicata Schiffn., Engler & Prantl. Nat. Pflanzenfam. I (3), 127 (1893). Anomalolejeunea decemplicata Steph. Spec. Hep. 5: 298 (1913).

Plants up to 2.0 cm long, strong shoots 0.8-0.9 mm wide, stems 78.3-96.6 µm in diameter. Leaves imbricate, diverging from the stem at an angle of ca. 45-60(70)°, the lobes ovate, rarely ovoid, strongly convex, 400.2-522.0 µm long, 409.8-430.8 µm wide, apex broadly rounded- sharply acute, usually strongly recurved, trigones medium to large, 5.0-7.8 µm long, nodulose; oil bodies 2-3(-5) per cell; leaf *lobule* small, triangular-ovate, inflated, 150.3-175.4 µm long and 92.7-104.4 µm wide at base, 1/4-2/5 as long as the lobes, lateral free margin usually slightly incurved to the base, bordered by 8-11, keel straight to slightly arched, the apical tooth 1(2) celled, 10-13 µm long, obtuse. Underleaves remote to approximate, wider than long, 265.2-317.0 µm long, 288.1-393.0 µm wide, 3-4 times as wide as stem, orbicular to cuneate, apex bilobed to 1/4-1/3 of its length, sinus V shaped, base cuneate, insertion mostly arched. Autoicous, occasionally paroicous. Androecia usually axillary or terminal on short lateral branches, sometimes intercalary (Perold SA 71b, South Africa), the bracts in 2-9 pairs, 237.5-284.5 µm long, bracteole 1-2, restricted to the base of androecium. Gynoecia usually on main long stems, with 1 or 2 innovation(s), innovation lobe sequence usually lejeuneoid; bracts obovate to ovate, 652.5-678.6 µm long, the lobule lingulate-oblong, up to 0.5 the length of the bract lobe, apex subacute, truncate, margin entire, keel almost straight, slightly winged, 3/4-4/5 length of bract lobule; bracteole oblong, 476.8-703.0 µm long, the apex lobed, the sinus to 0.04-0.07 of the bracteole length, lobe apices rounded, slightly reflexed, margins entire. Perianth usually exserted, fusiform, 835.2-924 µm long, 448.9-471.9 µm wide, keels (6)7-10, inflated, widest at the middle; rostrum 55.3-67.9 µm long, base exserted.

SPECIMENS EXAMINED. DR CONGO. Biega, Kivu, Kahuzi-Biega National Park, 2.22047 S 28.4101 E 2600 m, 28 Aug. 1991, *Pócs T* 7138 (EA, EGR). **TANZANIA.** Moshi; Mt. Kilimanjaro, Umbwe, near the first Bivouac. 3.135 S 37.175 E 2850 m, 1 Jul. 1976, *Pócs T* 6962 NB (EGR). Southern highlands, Mt Rungwe 2300 m, 17 Dec. 1970, *Pócs T* 6328 A /*J.W. Jones* 1947 (EA, EGR). **SOUTH AFRICA**. Cape Province, Kynsna, upper part of River Gouma, 500-1000 m, 26 Nov. 1951, Arnell S 1683 (PRE).

ECOLOGY AND DISTRIBUTION. *Cheilolejeunea pluriplicata* is corticolous or ramicolous usually in afromontane-subalpine habitats dominated by *Erica* species. It is often mixed with other species of *Cheilolejeunea* or different genera like *Lejeunea* and *Drepanolejeunea*. It is distributed from Central to Southern Africa (DR Congo, Ethiopia, Uganda, Kenya, Tanzania, Malawi, Mozambique, Angola and South Africa) and Madagascar between elevations of 800 and 3225 m. Elsewhere it is reported in China (south of Yunnan), India and Nepal.

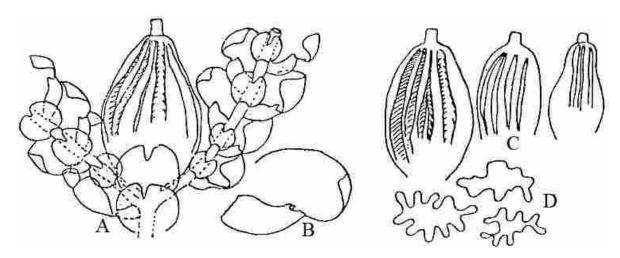


Figure 17. *Cheilolejeunea pluriplicata* (**Pearson**) **R.M.Schust.** (A) Portion of shoot with 1-2 lejeuneoid gynoecial innovations, ventral view; (B) Leave, ventral view; (C) Perianth; (D) Perianth transverse section. Drawn from Arnell, 1963.

NOTES. Description of *Cheilolejeunea pluriplicata* has been revisited by Vanden Berghen (1951), Arnell (1953, 1963), Jones (1988) and Zhu & So (1999). As Jones (1988), Zhu *et al.*, (2002) and Wigginton (2004a) and observed, the species clearly resembles *Ch. krakakammae* and *Ch. usambarana* by characters of the leaf lobule, apical tooth and cells on the free margin of the lobule, which is 'usually slightly inrolled and hardly distinguishable in sterile conditions'. The leaf lobule length is less than half the length of leaf lobes i.e. 1/4-1/3, observations confirmed by Zhu and So (1999).

Cheilolejeunea pluriplicata however has fusiform perianth with (6)7-10 carinae, a character it compares well with *Ch. cordistipula*. This is observed for the first time in the current study and attested in collections by *Pócs T* 02030 AE and 90022 T. *Cheilolejeunea cordistipula* has the leaf lobule length being more than half the length of lobe and the free margin composed of 13-22 rectangular cells, flatted as if to be in contact with the lobe and visible *in situ*. Many authors too had confusion on the diagnosis of the species. As Schuster

(1980b) notes, illustration given by Arnell (1963) are different from the lobule drawings given by Vanden Berghen in 1951. Vanden Berghen had already doubted the true representation of his drawings. Based on these observations, majority of the collections hitherto identified as Ch. pluriplicata (including Pócs T & Chuah MS (+others) 9215 AB 12 Jan. 1992, Pócs T 02030 AE 17 March 2002, Pócs T 9237 N 3 Feb. 1992, Pócs T 7138 B2 28 Aug. 1991, Pócs T, Frater T., & Kosa G. 87173 G, Miehe G & S 1942 C, Pócs T & *Orban S* 89176 S, *Lewinsky J.* 28 Dec. 1875 and *Pócs T & Lye K.A.* 97142 BH 21 Sep. 1997) are transferred to Ch. cordistipula. All these except Pócs T 6328 A, a paratype as used by Jones (1988) to describe the African Ch. pluriplicata from East Africa, ensemble Ch. cordistipula. Jones (1985) also assigned all the collections from Bale Mts above Rira village, in Ethiopia to Ch. cordistipula. Furthermore, when describing the Chinese Cheilolejeunea, Zhu et al. (2002) indicated that Ch. pluriplicata is mostly a Southern African species in the continent. It is therefore possible that *Ch. pluriplicata*, although once thought wide spread in East and Southern Africa, is rather rare and usually confused with Ch. cordistipula as they can grow mixed together. There are few materials suited to Ch. pluriplicata s. str. and the provided distribution is in doubt.

5. Cheilolejeunea camerunensis S.W.Arnell. Svensk Bot. Tidskr. 52: 63. 1958.

Plants up to 2.0 cm length, weakly appressed, strong shoots 0.8-1.0 mm wide, branches of young shoots accumulate towards apex, ascending, stem 90-100 μm wide. *Leaves* strongly imbricate, the lobes ovate, asymmetrical, weakly to strongly convex, 550-800 μm long, 420-560 μm wide, apex conspicuously narrow, strongly acute and recurved, antical margin strongly arched, the postical one nearly straight, making a sinus of *ca.* 90-120° with keel, lobe of median cells (10-)15-20(-24) μm long, (18-)20-30 μm wide, trigones small or absent, (5-)6-9 μm long, nodulose, oil bodies 1-3(-4), 10.3-14.0 μm long; *Leaf lobule* small, ovate, proximally strongly inflated, distally contracted to a narrow curved narrow neck, 150-200 μm long, ¼-2/5 as long as the lobes, lateral free margin strongly incurved, bordered by (6-)8 cells, keel strongly arched, the apical tooth straight, 12-17 μm long, subacute or rounded; *Underleaves* distant or approximate, 240-270 μm long, 300-400 μm wide, largely broader than long (1.5), 2.5-4.0 times as wide as stem, bilobed to 1/6-1/4 of its length, sinus V shaped, lobes acuminate, apex broadly rounded to subacute. *Autoicous*. *Androecia* sessile, usually on short lateral branches, mostly on proximal part of the main axis, bracts in 1-4 pairs. *Gynoecia* either on short lateral branches from the distal part of

the main axis or terminal on branching main axis (each of which is quickly fertile forming a dischasial cyme), with 1 or 2 innovation(s), innovation lobe sequence usually lejeuneoid or pycnolejeuneoid; the bracts as long as leave, falcate-ovate, acute or obtuse, strongly recurved, the lobule narrowly oblong, up to 0.5 the length of the bract lobe, the apex shortly free, one keel more or less winged and another connate with the bracteole; bracteole obovate, the apex shortly lobed. *Perianth* longly exserted, obovate, 800-1000 μ m long, 400-600 μ m wide, tricarinate, plane dorsally and with long, deep, ventral keel; rostrum short.

SPECIMENS EXAMINED. NIGERIA. Ogoja, Obudu Cattle Ranch, *McFarlane I* 384 b (BM). **CAMEROON.** Mt Cameroon, Buea, near the Forest Department, *Bystrom K* 10 c. (UPPS, lectotype, isotype in Herb. E.W. Jones); *Bystrom K* 24 & Mimbia, *Jones EW* 313 D.

ECOLOGY AND DISTRIBUTION. Epiphytic on trees and shrubs, 1000-1600 m a.s.l. Known only from W Africa, with a few collections from Mt. Cameroon and one from Eastern Nigeria.

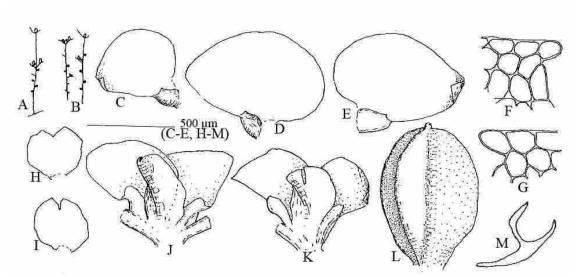


Figure 18. *Cheilolejeunea camerunensis* **S.W.Arnell.** (A,B) Cladograms; solid symbols, androecia, hollow symbols, gynoecial; (C,D,E) Leaves; (F,G) Apical teeth of lobules; (H,I) Underleaves; (J,K) Female bracts; (L) Perianth; (M) Transverse section of perianth. (B, F,G) *E.W. Jones* 313D and (A,D,I,JL,M) *I. McFarlane* 384b after Jones (1988).

6. Cheilolejeunea pocsii E.W.Jones, J. Bryol. 15: 149-160. 1988.

Plants yellowish green, strong shoots 0.7-1.0 mm wide, but robust with, sometimes, *microphyllous branches*, stem 88.7-103.5 µm in diameter. *Leaves* usually caudicous,

weakly interlocking dorsally, the lobes ovate to oval on weaker shoots, weakly to strongly convex, (318.4)413.4-637.0 µm long, apex obtuse, subacute, broadly rounded on week branches, ± strongly recurved, ventral margin somewhat arched or nearly straight, making a sinus of ca. 90° with keel, lobe of median cells 20.0-24.6 µm long, 14.4-17.5 µm wide, trigones usually large, (5-)6-9 µm long, nodulose; *leaf lobule* ovate, proximally inflated, distally contracted to a narrow curved neck, 167.5-300.2 µm long, (1/3)2/5-1/2 as long as the lobes, lateral free margin strongly, bordered by 7-8 cells, keel strongly arched extending about a third the distance to apex of lobe, the apical tooth usually 1-celled, rarely more, 18-27 µm long, almost parallel to the lobule apex, spiniform. *Underleaves* remote to approximate, 174.9-347.0 µm long, 177.5-394.0µm wide, usually broader than long, 1.8-4.0 times as wide as stem, bilobed to 1/5-1/4 of its length, sinus V shaped. Dioicous or autoicous. Androecia, usually axillary or terminal on short lateral branches, 428-720 µm long, 438-616 µm wide; bracts in 2-5 pairs. Gynoecia innovation lobe sequence usually lejeuneoid, rarely pycnolejeuneoid. *Perianth* exerted for about half its length, pyriform, 739-859 µm long, 450.7-497.6 µm wide, tricarinate, emanating from plane dorsal and bicarinate ventral, the keels close to each other dorsally, but merge into the broadly inflated median region on proximal side; rostrum long, 42.8-58.2 μm.

REPRESENTATIVE SPECIMENS EXAMINED. KENYA. Aberdare National Park on the Nyandarua Range, below the fishing Camp on the south part of the Aberdare Plateau in the Magura River valley, 3040 m, 18 Mar. 2002, *Pócs T 02031 O* (EGR, EA, NAI) & above Chania Falls 17 Mar. 2002, *Pócs T* 02030 AQ (EGR, NAI). TANZANIA. Morogoro; Lukwangule Plateau, S Uluguru Mts, Chenzema escarpment on top of the granitic rock, 10 Jun. 1988, *Pócs T, Ochyra R & Bednarek-Ochyra H* 88114 S (EA, EGR); Mindu, W Morogoro, 1100 m, 12 Apr. 1972, *Pócs T* 6152 AQ (EGR, EA, isotype); Uluguru Mts, NE ridge, 1750 m, *Pócs T* 6578 (BO). SOUTH AFRICA. Natal, Onrust, Nelsrust, 2000 m, Dec. 1916, *Sim TR* CH 2053 (PRE, syntype).

ECOLOGY AND DISTRIBUTION. Usually a corticolous or ramicolous, rarely rupicolous, afromontane or subalpine species common in East Africa especially in Uluguru Mts. Found mixed with other species like *Odontolejeunea* and *Frullania sp.* between 1000 and 3040 m a.s.l. in *Allanblackia-Podocarpus* or *Rapanea* and *Erica-Hagenia* vegetation. Elsewhere, it is recorded in Rwanda (Nyungwe Mts.), Malawi, South Africa and Madagascar.

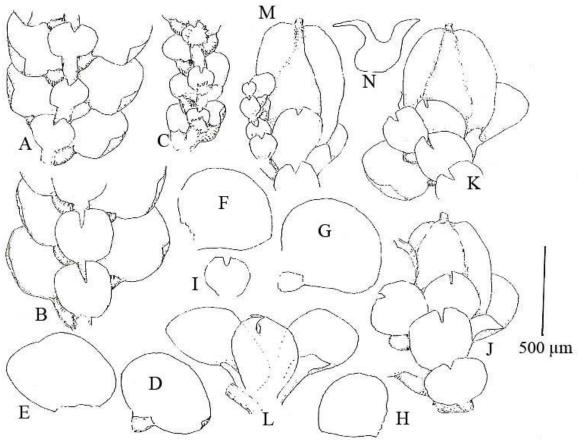


Figure 19. *Cheilolejeunea pocsii* **E.W. Jones.** (A,B) part of shoot, ventral view; (C) Microphyllous stolon; (D,G) Leaves, ventral view; (E,F,H) Caducous lobes; (I) Underleave; (J,K,M) Gynoecia with perianth; (L) Female bracts; (N) Transverse section of perianth. After Jones (1988), where (F,G,I) are drawn from *Pócs* 6708/P; (M) *Pócs* 6991/J and others from *Pócs* 6253/AP (type).

NOTES. *Cheilolejeunea pocsii* is distinguished from *Ch. usambarana*, *Ch. convexa* and *Ch. krakakammae* by usually caudicous nature of leaves and the frequently microphyllous shoots. The dioicous character of the species is however doubtful as Jones (1988) observed. Three collections (*Pócs T* 02031 O, *Pócs T* 02030 AQ, *Pocs T* & *Ochyra R* & *Bednarek-Ochyra* 88114 S) were found to be autoicous with subgynoecial innovations sometimes pycnolejeuneoid. *Cheilolejeunea pocsii* has been described as common with lejeuneoid type of subgynoecial innovations.

7. *Cheilolejeunea usambarana* (**Steph.**) **Grolle**. J. Hattori Bot. Lab. 46: 344. 1979; *Strepsilejeunea usambarana* Steph., Sp. Hepat. 5: 277. 1913. *Strepsilejeunea brevifissa, sensu* Vanden Berghen 1960, *p.p.*, [non (Gottsche) Steph.]. Plants yellowish green turning pale brown on drying, strong shoots 0.6-0.9 mm wide, stem 74.1-104.4 µm in diameter. *Leaves* imbricate, sometimes semi-caudicous, the lobes asymmetrically ovate, almost semi-circular, weakly to strongly convex, 350-549 µm long, 302-436 μ m wide, apex obtuse to sharply acute, \pm strongly recurved, the dorsal base arching across the stem; lobe median cells 20.0-25.4 µm long and 12.0-23.3 µm wide, trigones medium to large, (4-)5-11.3 µm long, nodulose, rarely triangular, oil bodies 1-3(-4). Leaf lobule ovate, strongly inflated, 122.7-225.5 µm long, 1/3-2/5 as long as the lobes, lateral free margin strongly incurved, bordered by (5-7) 8 subquadrate to rectangular marginal cells, keel strongly arched, forming a sharp sinus or ca. straight with postical lobe margin, usually constricted to overly apical tooth, the apical tooth 1-2(-3) celled, 10-17 (28-51) µm long, usually parallel to the lobule apex, acute-spiniform. *Underleaves* remote to approximate, 170-268(-495) µm long, 157-257(-551) µm wide, usually longer than wide, 1.5-2.6(-6.0) times as wide as stem, bilobed to 1/5-2/5 of its length, sinus V-U shaped, lobes apex broadly rounded to subacute. Autoicous, sometimes paroicous. Androecia on short lateral branches or intercalary on long shoots, bracts in 2-5 pairs. Gynoecia on main stems or on lateral branches, with 1 or 2 innovation(s), innovations lejeuneoid or pycnolejeuneoid. Perianth slightly exserted, suborbicular-subcompressed or pyriform, obovate, 557-793 µm long, 365-561 µm wide, 4-5-carinate, keels equal but usually the dorsal surface plane with a weak keel; rostrum 23.5-52.2 µm long.

REPRESENTATIVE SPECIMENS EXAMINED. CONGO, Brazaville. Montota Foret, Sur tronc pourri, 28 Apr. 1966, *Assel M* 894 (EGR, EA). GABON. ? Apr. 2007 *Fischer E* s.n. (EA, Koblenz). KENYA. Kajiado; Ngong Hills, SW of Nairobi town, E slope of the summit ridge, 1.2385 S 36.383 E, 2420 m, Mar. 2004, *Pócs T; S* 04011 BH & *Pócs T & S* 04011 AH (EGR, EA, NAI) & 19 Mar. 2005, *Malombe I Fischer E & Mwachala G* 5009 E2 (EA). TANZANIA. Lushoto; W Usambara Mts, University Forest Reserve near Mazumbai, 1800 m, 7 Jan. 1971, *Pócs T & Jones EW* 6373 P (EGR, EA); Kambo, 1850 m, 8 Jan. 1971, *Jones EW* 1710 (EGR, EA); SSW of Balangai village, on steep rock summit, 27 2 1984, Pócs *T 8412 C* (EGR, EA); above Kambi Falls, 30 Jan. 1985, *Pócs T 8528 P* (EGR, EA) & *Pócs T 8528 Q* (EGR, EA). Morogoro; Uluguru Mts. SW of Kinole village, in the Tegetero Mission garden, 980 m, 15 Apr. 1971, *Pócs T* 6424 N (EA, EGR).

ECOLOGY AND DISTRIBUTION. Epiphytic (ramicolous and corticolous) on trees and shrubs in shade or sunny ericaceous heath between 1640 and 2420 m a.s.l., rarely below, sometimes mixed with other Lejeuneaceae species like *Drepanolejeunea ternatensis* (Gott.) Schiffn. and *Taxilejeunea conformis*. It is found in Kenya, Tanzania, Malawi, Congo, and is rare in W Africa (Gabon, Sierra Leone i.e. Loma Mts, Guinea and Cameroon). Also known from Reunion and is new to Madgascar.

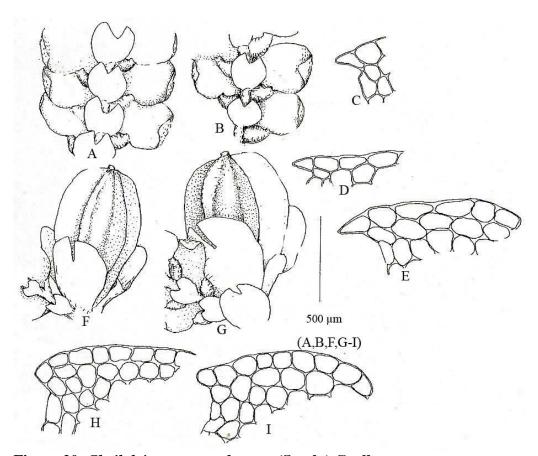


Figure 20. *Cheilolejeunea usambarana* (Steph.) Grolle. (A,B) part of shoot, ventral view; (C-E) Lobule apical tooth; (F,G) Gynoecia with mature perianth and pycnolejeuneoid innovations. (A,B,G) Tanzania, Jones 1710; (C, F) Sierra Leone, *Jones* 1512; (D) Tanzania, *Brunnthaler* G19693 (type) and (E) Tanzania, *Jones* 1702. *Cheilolejeunea krakakammae*. (H, I) Apical tooth and free margin of lobules. (H) South Africa, *Ecklon* 1832; (I) Tanzania, *Jones* 2014 (After Jones 1988).

8. *Cheilolejeunea convexa* (**S.W.Arnell**) **S.W.Arnell**, Bot. Notiser 108, 310 (1955); *Lejeunea convexa* S.W.Arnell, Bot. Notiser 106, 272 (1953)

Plants shoots up to 1.2 cm long, making extensive and thick pure cushions on wet rocks, 0.5-0.7 mm wide, usually semi-erect, somewhat dichotomous branching, few branches, stem 75.7-95.3 µm in diameter. *Leaves* weakly interlocking dorsally, the lobes ovate,

almost semi-circular, usually strongly convex, 355.0-426.3 µm long, apex broadly rounded to rarely subacute, strongly recurved, lobe median cells 22.8 µm long and 13.6 µm wide, trigones usually large, rarely medium, (5.3)7.5-8.0 µm long, nodulose, rarely triangular. Leaf lobule strongly inflated, 187.9-203.6 µm long, (2/5) 1/2 as long as the lobes, lateral free margin strongly incurved, bordered by 7-8(10) cells, keel strongly arched, the apical tooth 1 celled, 16-20 µm long, almost straight, forward or parallel to the lobule apex, spiniform. *Underleaves* usually ascending, distant to approximate, 193.2-233.0 µm long, 183.5-220.0 µm wide, usually longer than wide, 2.0-2.6 times as wide as stem, orbicular to shortly obovate, bilobed to 1/3 of its length, sinus V-U shaped, lobes obtuse without any clear apical cell, apex clearly rounded, never acute. Autoicous. Androecia usually axillary or intercalary on short lateral branches, bracts in 2-5(7) pairs, 209-261 µm long. Gynoecia on main stems or on lateral branches, with (1)2 innovation(s), innovation lobe sequence usually pycnolejeuneoid, few lejeuneoid; bracts 465-663 µm long, the lobule up to 0.5 the length of the bract lobe; bracteole sinus 0.13-0.18 of its length. *Perianth* slightly exerted to over 1/3 emerging, 765.6-1162.3 µm long, 452.4-626.4 µm wide, 5(6)-carinate, keels sharp, sub-equal; rostrum short, up to 29.6 µm long.

SPECIMENS EXAMINED. SOUTH AFRICA. Cape Province; Table Mts, Platteklip Ravine, Jan. 1919, *Sim TR* 2401 (PRE); on Hills N of Woodhead Reservoir, at base of cliff facing south, Jan. 1919, *Pillans NS* 3333 (BO, Syntype)& 23 Sep. 1951, *Arnell S* 968 (BO) & Pearl, Wemmershocks Tafelberg, 27 Apr. 1952, *Esterhuysen E* 20083 (BO).

ECOLOGY AND DISTRIBUTION. Rupicolous on shaded and damp or wet vertical rocks forming dense mats. Rare and only known from the Table Mts in Cape, South Africa, bewteen 910-1670 m a.s.l., mixed with *Jamesoniella colorata* or *Plagiochilla wilmsiana*.

NOTES. The sterile specimen collection by *Esterhuysen E* 20083 has small trigones and the lobule lobe length ratio slightly smaller than well established specimens of *Ch. convexa*. It has less convex lobes which resemble that of *Ch. pocsii*.

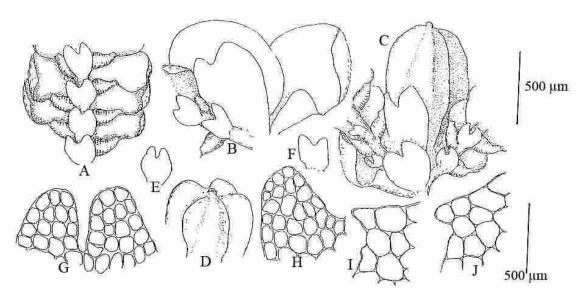


Figure 21. *Cheilolejeunea convexa* **(S.W.Arnell) S.W.Arnell.** (A) Part of shoot, ventral view; (B,C) Gynoecia showing pycnolejeuneoid innovations, C with perianth; (D) apex of perianth; (E,F) underleaves; (G,H) underleave lobes; (I,J) Apical teeth of lobule. (A-C,I) from *Arnell* 964, (d) *Wilms* 2544, (E,F,J) *Arnell* 955. Extracted from Jones, 1988.

9. Cheilolejeunea cordistipula (Steph.) Grolle ex E.W.Jones. J. Bryol. 13: 395, 1985;
Strepsilejeunea cordistipula Steph., Sp. Hepat. 5: 276, 1913.
Pycnolejeunea angustiflora Steph., Sp. Hepat. 5: 601, 1914

Plants weak or strongly appressed to slightly pendent, shoots 0.8-1.5 mm wide, irregularly branched, stems 80-130 µm in diameter, composed of 7(8) cortical cells and about 14 (16) smaller isodiametric medullary cells; ventral merophytes of the stem 2, rarely 3 cells. Leaves imbricate, the lobes ovate, strongly convex, 573.0-871.0 μm long, 750.0-405.0 μm wide, apex narrow, rounded to acute, strongly recurved, median cells isodiametric, 18.2-30.0 μm long, 13.8-23.8 μm wide, trigones very large, (5.7-6.7) 7.0-11.5 μm long, nodulose, oil bodies 2-3(-8) per cell, Leucolejeunea-Calypogeia type. Leaf lobule large, triangular-ovate, inflated proximally and along the slightly arched keel, 288.2-468.0 µm long, 0.5-0.6 as long as the lobes, the distal free margin flattened, lying against the lobe, and visible in situ, bordered by 13-22 cells, the apical tooth 1-2(3) celled, sometimes oblique, 11-20(31) µm long, obtuse. *Underleaves* remote to imbricate, usually wider than long, 205-480 µm long, 223-619 µm wide, (2.4) 3.0-5.0 times as wide as stem, rounded to obcordata, apex bilobed to 1/10-1/4 (1/3) of its length. Autoicous, occasionally paroicous. Androecia usually axillary or terminal on short lateral branches, sometimes very long, up to 1320 µm long, bracts in 2-7(10) pairs. Gynoecia usually on main long stems, with 1 or 2 innovation(s), occasionally lacking, innovation lobe sequence usually lejeuneoid,

occasionally pycnolejeuneoid; bracts obovate to ovate, nearly convolute around the perianth; bracteole oblong-oval, 449-867 μ m long, the apex retuse to slightly lobed, the sinus 0.003-0.18 (ca. 0.03) of the bracteole length. *Perianth* longly emergent up to 1/2, narrowly obovate or fusiform, 818-1330 μ m long, 305-795 μ m wide, keels 5-10, inflated, widest at the middle; rostrum (22-31) 41-90 (100-105) μ m long.

REPRESENTATIVE SPECIMENS EXAMINED. DR CONGO. Kivu, Kahuzi, Biega National Park, Mt. Biega, 2.22047 S 28.4101 E 2600 m, 28 Aug. 1991, *Pócs T* 7145 (EGR) & Pócs T 7138 (EGR). **RWANDA**. Cyangugu, Nyungwe Forest along highway from Butare to Cyangugu, 2.2925 S 29.1052 E 2330 m, 15 Aug. 1991, *Pócs T* 6512 (EGR) & Fram JP 6128; 31 Mar. 2005, Fischer E 2-65, E 4-67, Fischer E 4.2; Rwasenoko, 2500 m, *Pócs T* 6074 (EGR) & Sikongoro 2.3134 S 29.2121 E, 11 Aug. 1991, *Pócs T* 6021 (EGR). Ruhengeri, in the saddle between Mt. Visoke and Mt. Karisimbi, 1.3028 S 29.265 E 3000 m, 13 Sep. 1991, *Pócs T* 8167 (EGR). **ETHIOPIA**. Bale Mts, above Goba, E to SSE facing slopes of valley, 2 Mar. 1990, Miehe G & S 3063 (EA, EGR); above Rira, W Aduka Range, 30 degrees SE facing rocky slope, 3400 m, 12 Feb. 1990, Miehe G & S 2510 a (EGR); on 5 degrees SSE facing slope, 3590 m, 5 Feb. 1990, *Miehe G & S* 1942 C (EGR) & North facing upper slope 5-8m high, 3370 m, 8 Feb. 1990, *Miehe G & S* 2050 (EA, EGR). UGANDA. Mbale; Mt Elgon, W approach of Mountain along Sasa trail, around and above Sasa River Camp, 1.103 N 34.2627E 2700-2900 m, 21 Sep. 1997, Pócs T & Lye KA 97142 BH (EGR) & Pócs T & Lye KA 97142 BD (EGR); Ruwenzori, 0.1952 N 29.552 E 2700 m, Stuhlmann G 922. KENYA. Trans-Nzoia; S slope of Chemwote, Mt Elgon National Park, 12 Jan. 1991, *Pócs T & Chuah* 9215 AB (EGR, EA) & 3900 m 15 Jan. 1992, Pócs T & Szabo A 9218 FC (EA, EGR). Aberdare National Park, on the Nyandarua range around and above Chania Falls on the E slopes, 3040 m, 17 Mar. 2002, Pócs T 02030 AF (EGR, EA) & 2980 m18 Mar. 2002. Pócs T 02031 U (EGR, NAI). Nyeri; Naro Moru, Mt Kenya National Park, 3040 m 2 Feb. 1992, Pócs T 9237 N (EA, EGR) & Pócs T 9237 C (EA, EGR). **TANZANIA.** Moshi; Mt Kilimanjaro, Nkweseko,1 Jan. 1971, *Pócs T* 6358 E (EA, EGR) & Pócs T& Jones EW 6359 AF (EGR, EA); Machame Hut, below the hut, 22 Jun. 1987, Pócs T, Fráter E & Kósa G 87173 G (EA, EGR); trail from Mweka to Kibo Peak, 28 Jul. 1968, Sharp AJ, Gilbert V.C., Vesey-Fitzgerald D.E.F. & Bigger M 7425 D (EGR); Mawenzi, NE, W-SW of Tarakea, N of Nesikiria River, 1 Feb. 1990, Pócs T, Mjatta SHK & Linden J 90022 T (EA, EGR). Arusha; Mt Meru, W slope, N branch of Engare Narok valley, on the W slope, 3200 m,16 Jun. 1989, *Pócs T* 89186 AS (EA, EGR).

Lushoto; Shume-Magamba Forest on the summit, 17 Mar. 1984, *Pócs T* 8448 BO (EA, EGR) & W Usambara Mts, Mtumbi Forest Reserve, 10 Feb. 1985, *Borhidi A* 8542 AL (EA, EGR). Morogoro; Bondwa, Uluguru Mts, NW slope of Bondwa, 1650 m, *Pócs T* 6006 E (EA EGR); Nguru ya Ndege, NNW of Morogoro town below the summit, going down in the valley, 6 Jun. 1989, *Pócs T & Orbán S* 89176 S (EA, EGR). **MALAWI**. Mulanje Mt., Path to S of Minunu Hut, 15.55031 S 35.38052 E 1980 m, 20 Jun. 1991, *Wigginton M.J.* 1275 b (NHBG).

ECOLOGY AND DISTRIBUTION. It is widespread in Africa (Uganda, Kenya, Tanzania, Ethiopia, Malawi, Rwanda, DR Congo, Cameroon, Bioko (Fernando Po) including Madagascar and Réunion on bark or twigs of shrubs and trees usually forming loose mats. It has a wide range of habitats from the dry evergreen afromontane vegetation and usually upper montane to subalpine concentrations composed of mainly *Erica* species, but also Bamboo (*Arudinaria alpina*) and *Philippia-Hagenia* associations, some of which are disturbed by frequent fires. Sometimes mixed with other species of Lejeuneaceae such as *Lejeunea flava* (Swartz)Nees.

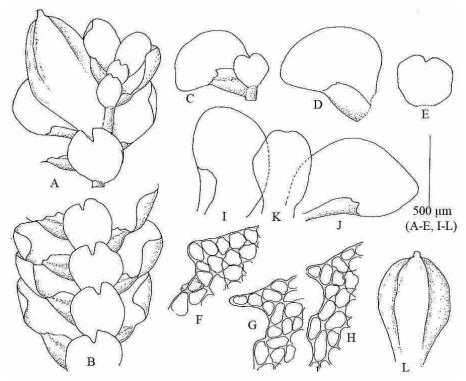


Figure 22. *Cheilolejeunea cordistipula* (Steph.) Grolle ex E.W.Jones. (A) Apex of shoot with perianth, showing pycnolejeuneoid innovation, ventral view; (B) Part of shoot, ventral view; (C) Leaf and underleave; (D) Leaf; (E) Underleave; (F-H) Apical part of lobule, "F" with hyaline papillae; (I,J) Female bracts; (K) Bracteole; (L) Perianth. (A,C,G,H) Tanzania, *Jones* 1642; (B) Bioko, *Newton* 1894 (Type of *Pycnolejeunea angustiflora*) and (D, E, I-L) Cameroon, *Jones* 431 from Jones (1985).

NOTES. Most of the specimens were initially assigned to *Ch. pluriplicata* as explained above. It has been found for the first time that the perianth of *Ch. cordistipula*, like *Ch. pluriplicata*, sometimes exhibit up to 10 keels. This might have led to misidentification of the collections. However, the leaf lobule ventral free margin is flattened and visible *ex situ*, while in *Ch. pluriplicata* is inrolled resembling those of *Ch. krakakammae*.

10. *Cheilolejeunea ruwenzorensis* (**Steph.**) **R.M.Schust**. Hepaticae collected by O. Hedberg *et al.*, Arkiv for Botanik. Bd 3 nr 16.

Plants up to 3 cm length, shoots 0.8-1.0 mm wide, irregularly branched, stem ca. 120 μm in diameter. *Leaves* imbricate, strongly convex, 573.0-871.0 μm long, 750.0-405.0 μm wide, apex narrow, subacute, strongly recurved, median cells 20-22 μm long, trigones large, (5.7-6.7) 7.0-11.5 μm long, nodulose; *leaf lobule* medium, triangular-ovate, convex, inflated proximally, keel arched, 288.2-468.0 μm long, 0.5-0.6 as long as the lobes, bordered by more than 10 cells, the apical tooth 1-3 celled, 11-20(31) μm long, subacute. *Underleaves* approximate, 205-480 μm long, 223-619 μm wide, usually wider than long, 3.0-5.0 times as wide as stem, orbicular, apex shortly bilobed up to 1/10-1/4 (1/3) of its length, sinus V shaped, lobes acuminate, apex broadly rounded to subacute, margin entire, base usually cordate, insertion mostly arched. *Dioicous. Androecia* on short lateral branches, bracts in 4-8 pairs, bracteole restricted to the base of androecium. *Gynoecia* usually on main long stems, with 2 innovation(s), innovation lobe sequence pycnolejeuneoid; bracts apex subacute; bracteole oblong-oval, 449-867 μm long, the apex shortly incised, the sinus shallow. *Perianth* pyriform to oblong, 818-1330 μm long, 305-795 μm wide, keels 5, inflated, keels on dorsal side confluent; rostrum 40 μm long.

SPECIMEN EXAMINED. **DR CONGO**. Mukaba, Kahuzi-Biega National Park, 30km W of Bukavu, 20 Aug. 1991, *Pócs T* 6574(EGR).

ECOLOGY AND DISTRIBUTION. Only known from Uganda and DR Congo, usually corticolous on liana in montane tropical forests dominated by *Dombeya goetzenii*, *Zanthoxylum gillettii*, *Hagenia abyssinica* and *Alangium chinense*, mixed with *Taxilejeunea conformis* (Mont.) Steph.

NOTES. Cheilolejeunea ruwenzorensis is transferred to subg. Strepsilejeunea based on the

strongly convex lobes with acute and recurved apices.

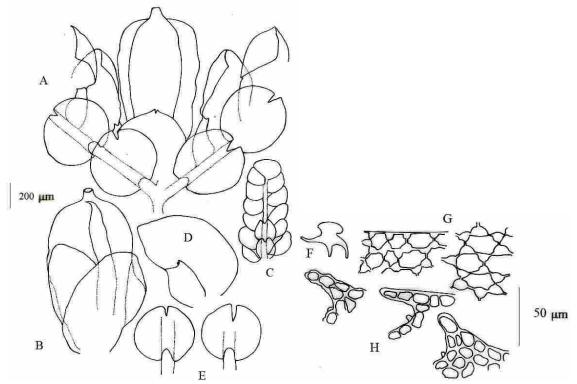


Figure 23. Cheilolejeunea ruwenzorensis (Steph.) R.M.Schust. (A) Perianth, ventral view showing pycnolejeuneoid innovations; (B) Perianth and bracts, dorsal view; (C) Androecium; (D) Leave, ventral view; (E) Underleaves; (F) Perianth transverse section; (G) Leaf cells; (H) Apex of the lobule. All by S. Arnell (1958)

11. Ch. omphalogastria Pócs. Tropical Bryology 9: 131-136, 1994.

Plants appressed or somewhat pendent on twigs, shoots 0.9 mm wide, branches few, perpendicular, stem 100-113.3 μm in diameter. *Leaves* approximate, the lobes ovate, rarely ovoid, strongly convex, 603 (650) μm long, 400-500 (590) μm wide, apex subacute to mucronate, strongly recurved, postical margin strongly arched making a wide sinus with keel; median cells 8-26 μm long, 8-19 μm wide, trigones very large, up to 12 μm long, triangular, occasionally nodulose; *leaf lobule* small, triangular, inflated entirely, 175-200 μm long, ca. 0.3 as long as the lobes, the apical tooth 1-3 celled, forward facing, up to 24 μm long, obtuse. *Underleaves* appressed, imbricate, large, 480-535 μm long, 470-600 μm wide, largely wider than long, 5-6 times as wide as stem, ca. orbicular, apex bilobed to 1/5-1/4 of its length, sinus V-U shaped, lobes acute, apex acuminate, margin weakly sinuate, base cordate, insertion of deep-navel like sinus, overlapping auricles. *Dioicous!*. *Androecia* usually axillary on short lateral branches, 793 μm long, 522 μm wide; bracts in 3(4) pairs, 230-418 μm long; bracteole spread on the entire androecium. *Gynoecia* unknown.

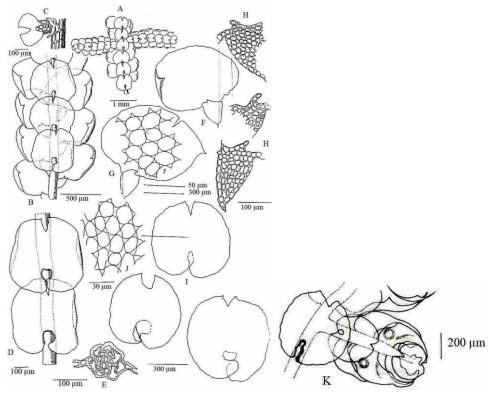


Figure 24. *Cheilolejeunea omphalogastria* **Pócs.** (A,B) Part of plant, ventral view; (C) Thecal, *Lejeunea* type of branching; (D) Incubous underleaves, on stem; (E) Transverse section of stem; (F) Leaf attached to stem, ventral view; (G) Leaf with median cells; (H) Apical teeth of lobule; (I,J) Underleaves; (K) Androecium. (A-J) from type by Pócs (1994) and (K) by author and N. Maundu.

SPECIMEN EXAMINED. RWANDA. Pref. Cyangugu, W edge of Nyungwe Forest near Gisakura, (Loc. 155), 10 Sep. 1991, *Pócs T.* 8044b (EGR, isotype)

ECOLOGY AND DISTRIBUTION. A ramicolous pendent species usually on upper canopy of trees. It can however be found on fallen twigs of shrubs and rotting materials. Only known from the type locality, Nyungwe montane rainforest in Rwanda, and has never been recollected.

NOTE. Cheilolejeunea omphalogastria may resemble the American species Cheilolejeunea decurviloba (Steph.) X.-L. He. The latter is however distinguished by the rounded leaf apices, lobule with decurved free margin line and underleaves with shallow insertion (He, 1996; Bastos & Gradstein, 2006). Bastos and Gradstein (2006) claimed that the Bolivian Cheilolejeunea asperrima (Steph.) Grolle and Ch. omphalogastria are related and the two species may be conspecific. It seems they had not seen the type or the protoloque of Ch. omphalogastria because the two species differ considerably. Comparison of the basionym illustrations of Taxilejeunea asperrima Steph. (Stephani,

1985; microfile 009996) shows the *Ch. asperrima* lacks the mucronate lobe apices and auriculate underleaves, features common with *Ch. omphalogastria*. *Cheilolejeunea asperrima* is further differentiated by presence of tipped large pappilae in all cells (Stephani, 1923). In addition, *Ch. omphalogastria* has only two ventral merophytes of the stem and is characterised by bracteoles spread on the entire androecium. On the contrary, *Ch. asperrima* has four or more ventral merophytes and bracteoles are restricted to the base of androecia. Except a few species such as the south American *Ch. revoluta* (Herz.) Gradst. & Grolle (Gradstein *et al.*, 1993), there are no other species of *Cheilolejeunea* known to exhibit androecia bracteoles spread on the entire length in Africa. *Cheilolejeunea revoluta* differs from *Ch. omphalogastria* by lack of auriculate underleaves and mucronate strongly decurved lobe apices.

Subgenus Cheilolejeunea

- **12.** Cheilolejeunea decursiva (Sande Lac.) R.M.Schust. Beih. Nova Hedwigia 9: 112. 1963;
- Lejeunea decursiva Sande Lac., Nederl. Kruidk. Arch. 3: 522. 1855; Strepsilejeunea decursiva (Sande Lac.) Herzog, Feddes Repert. 54: 252. 1951.
- Cheilolejeunea tisserantii Vanden Berghen et Jovet-Ast, Rev. Bryol. Lichénol. 20: 105. 1951.

Plant shoots 0.55-1.0 mm wide, irregularly branched, delicate, stems 50-96 (105) μm in diameter. *Leaves* imbricate, the *leaf lobe* broadly rounded, moderately convex, 309.7-492.7(530) μm long, 220.0-455.2 μm wide, the apex broadly rounded, rarely acuminate, plane or involute, lobe median cells 15-23 μm long and 12.0-18.5 μm wide, trigones small-medium, 3.5-5.5μm long, triangular, oil bodies *Leucolejeunea*-type, 2-3 per cell, ca. 15 μm long and 5 μm wide; *leaf lobule* large, largely ovate, strongly inflated, narrowed to the mouth and with carved apex, 123.0-187.9 μm long, ¼-1/3 or ca. ½, as long as the lobes, lateral free margin bordered by 7-8(-9) cells, keel strongly arched, ca. 90° with postical lobe margin forming a deep sinus, the apical tooth 1celled, (11-12)25-30 μm long, spiniform, slightly recurved, abutting into a group of swollen cells on the inner face of the lobe at the base of the lobule apex; hyaline papilla large. *Underleaves* remote to approximate, 135-300 μm long, 128.8-275.0 (315) μm wide, about as long as wide, or slightly longer than wide, 1.7-3.0 times as wide as stem, orbicular or obovate, apex bilobed

to ½-2/5 of its length. *Autoicous*, sometimes paroicous. *Androecia* terminal or axillary on short or long branches, bracts in 3-7 pairs. *Gynoecia* on long shoots or on short lateral branches, with usually 1-2 innovation(s), innovation lobe sequence usually lejeuneoid, rarely pycnolejeuneoid. *Perianth* scarcely compressed, fusiform-claviform, 300-600 (1096) μm long, 480-522 μm wide, keels ca. equally 5-carinatey; rostrum up to 60 μm long.

REPRESENTATIVE SPECIMENS EXAMINED. KENYA (First record for Kenya). Kakamega, Malava Forest fragment, forest edge, 1640 m, Jun. 2005, *Malombe I & Soita* L 5010 Ma x2; Kajiado; Ngong Hills, SW of Nairobi town, East slope of the summit ridge, 1.2385 S 36.383 E 2040 m, 25 Feb. 2004, *Pócs T. & S & EA Staff* 04011 AW (EA, EGR). TANZANIA. Lushoto; Mazumbai, Usambara Rain Forest Research Project to the W of Mazumbai village, E slope of Kwagoroto above Kambi, 1750-1900 m, 23 Feb. 1982, *Pócs T* 6955 U (EGR). Morogoro; Bondwa Peak, near Uluguru mts, top of peak above Morogoro, 2100 m, 29 Aug. 1970, *Pócs T* 6233 J (EGR); Lupanga Track, South end of Ridge above Mbere, 15 Nov.1970, *Pócs T & Nchimbi KBG* 6287 AW (EGR) & Kanga Mts, Southern slopes of the main top by the water falls, 1370 m, 27 Nov. 1970, *Pócs T*

with other small species of subfamily Lejeuneoideae such as *Lejeunea caespitosa*, *L. eckloniana*, *Microlejeunea africana* Steph., and *Drepanolejeunea cuetrella* (Mitt.) Steph on the bark or epiphyllous, usually between 1590 and 2450 m, sometimes in lower altitudes up to 90 m a.s.l. Recorded in Tanzania, Kenya (first record), Malawi, Congo-Brazzaville, Central African Republic, Cameroon, Sierra Leone and Guinea, including Madagascar, Comoro and Réunion isl in Africa. It is also reported in Hawaii, Sri Lanka and N. Borneo (Pócs, per. com.).

6140 AP (EGR).

NOTES. Collections from Tanzania (*Pócs T* 6955 U & 6233 J) form extreme phenotypes of *Ch. decursiva*. The leaf lobes are relatively ovate and apex round to narrowly acute. Although the lobes are never decurved, they resemble basal forms in the subg. *Strepsilejeunea* especially *Ch. usambarana* owing to the spiniform lobular apical tooth. The apical tooth is however longer and straight.

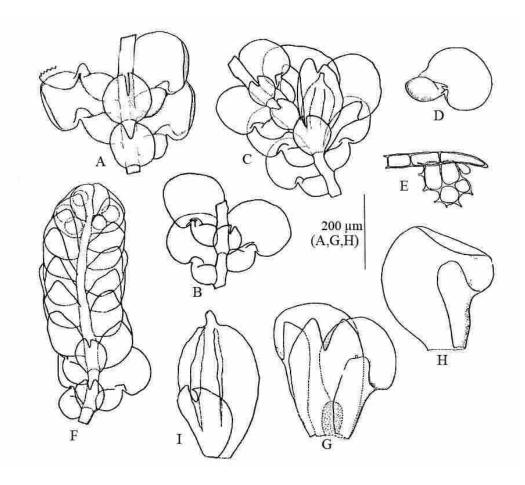


Figure 25. *Cheilolejeunea decursiva* (Sande Lac.) R.M.Schust. (A,B) Part of shoot, ventral view; (C) Part of shoot, with gynoecium; (D) Leaf; (E) Apical tooth of lobule; (F) Terminal androecium; (G) Bracts and bracteole; (H) Female bract; (I) Perianth and bracteole. (A,E,G,H) D.R Congo, *Symoens* 5326 from Vanden Berghen, 1972, and (B-D, F,I) Central Africa Republic, *Tisserant* 11090 p.p. after Jovet-Ast & Vanden Berghen, 1951, as *Ch. tisserantii*.

13. Cheilolejeunea serpentina (Mitt.) Mizut., J. Hattori Bot. Lab. 26: 171. 1963; Lejeunea serpentina Mitt., J. Proc. Linn. Soc., Bot. 5: 112. 1861; Euosmolejeunea serpentina (Mitt.) Steph., Sp. Hepat. 5: 590. 1914.

Cheilolejeunea principensis Steph. ex Paris, Rev. Bryol. 33: 38. 1906, Steph., Sp. Hepat. 5: 649. 1914; Euosmolejeunea principensis (Steph. ex Paris) R.M. Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968.

Cheilolejeunea crenulata Steph. ex Paris, Rev. Bryol. 29: 82. 1902, nom. inval. Cheilolejeunea madagassa Steph. Sp. Hepat. 5: 648. 1914.

Plants yellowish green, shoots robust, 0.6-0.8 (-1.0) mm wide, occasionally slender in weak shoots, pinnately branched, stems 60-90 (100) µm in diameter. *Leaves* remote or approximate or imbricate, flat or moderately convex, the lobes often caudicous, shortly

oval, 343.2-472.0(500) μm long, 292.3-417.6 μm wide, typically 1.1-1.3 x as long as wide, the apex broadly rounded, the ventral margin arched to form a clear sinus of 90-130° with arched keel, the base rounded and scarcely cross the stem, lobe of median cell trigones small, 3.0-5.4µm long, triangular, oil bodies 2-3 per cell, ca. 15 µm long and 5 µm wide; leaf lobule inflated proximally and narrowed to the mouth, rarely with carved apex, (99)-127.9-170.4 µm long, 1/3-2/5 as long as the lobes, lateral free margin bordered by 4-6 cells, the apical tooth 1(2) celled, 15-21 µm long, obtuse but occasionally spiniform and recurved. Underleaves remote to approximate, 120-249 µm long, 172-159 µm wide, about as long as wide, or slightly longer than wide, 2-3 times as wide as stem, orbicular or obovate, apex bilobed to $(\frac{1}{4})1/3(\frac{2}{5})$ of its length. *Dioicous*, male plants occasionally slender than female ones. Androecia usually intercalary, rarely axillary on short lateral branches, bracts in 3-6 pairs. Gynoecia on long shoots or on short lateral branches, with usually 1, sometimes 2 innovation(s), innovation lobe sequence usually lejeuneoid, pycnolejeuneoid very rare; bracts oval, 365-522 µm long, the lobule narrow, up to ½-4/5 the length of the bract lobe, obovate, keel almost straight, slightly winged, ¾-4/5 length of bract lobule; bracteole obovate, 370-640 µm long, apex sinus to 0.10-0.33 of the bracteole length. Perianth usually exerted over 0.5 their length, compressed, pyriform, 700-800 µm long, 500-563 µm wide, keels 4-plicate with 2 lateral and 2 ventral sharp plicate, plane dorsally, inflated ventrally; rostrum up to 63 µm long.

REPRESENTATIVE SPECIMENS EXAMINED. SIERRA LEONE. Oriel Mts., 13.1403 W, 23 Dec. 1951, *Arnell S* 1387 (BO). COTE DIVORE. Tabou, Troya, route de tabou, foret entre troya et le fl., Cavally, 27 Nov. 1975, *Assi AL* 12772 A (EA, EGR). GHANA. Aiyinasi Station, 15 Feb. 1971, *Jones EW* 1383 (EGR). DR CONGO. Kivu; Irangi Forest Station, 110 km W of Bukavu, 2.3003 S 28.51039 E, 22 Aug. 1991, *Pócs T* 6610 (EGR). CAMEROON. Yaounde, Eloumdeu, 6 km au SW de Yaounde, Sommet de cult Eloumdeu. Foret primaire, 6 Dec. 1986, ? B 3059(EGR) & Minlova inselberg, near the summit, 800 m, 28 Feb. 2007, *Malombe, I* 7001 C1 (EA). KENYA. Mwingi, Mumoni hills, 0.3119 S 38.002 E 1745 m, 10 May 2005, *Malombe I, Mwachala G & Kirika P* 4026 L15B(EA). Kajiado; Ngong Hills, SE slopes, below the aviation satellite station, 1.25 S 36.38 E 2420 m, 19 Mar. 2005, *Malombe I Fischer E & Mwachala G* 5009 J2 (EA). TANZANIA. Lushoto; Amani, E Usambara Mts, on the ridge above Sigi Valley, 950 m, 20 Feb. 1987, *Pócs T* 87040 D (EA, EGR); Amani Forest Reserve, 1800 m, 27 Dec. 1969, *Pócs T & S* 6100 B (EGR); Baga Forest Reserve, W Usambara Mts. 2 Mar. 1984, *Pócs T*

8419 BU (EA, EGR); Mazumbai, W Usambara Mts, on the isolated peak between Kwagoroto summit and Mazumbai village, 1850 m, 23 Feb. 1984, *Pócs* 8404 U (EA, EGR). Morogoro; Mindu, Uluguru Mts, NE slope, Hill above Kasanga II, W-SW of Morogoro town, 650 m, 4 Jun. 1988, *Pócs T* 88101 DA (EA, EGR); Nguru ya Ndege, NNW of Morogoro town, 6 Jun. 1989, *Pócs T & Orban S* 89175 S (EA, EGR).

ECOLOGY AND DISTRIBUTION. Epiphytic on shrubs and trees on rather dry open places dominated by *Euphorbia sp.*, sometimes on rocks and rarely terricolous forming pure or mixed patches of thin sheets. A paleotropical species common in lowland rainforests, sometimes at high water mark near the sea, and rarely upland dry moist (submontane) forest. It is known from Sierra Leone, Guinea, Ghana, São Tomé, Rio Muni, Annobón, Bioko, Principe, Nigeria, Cameroon, Congo-Brazaville, DR Congo, Tanzania and Kenya as well as Mauritius, Comoros, Seychelles, Madagascar and Réunion Is. and Mascarenes. Others include Japan, Korea, China, India, Nepal, Sri Lanka, Singapore, Java, Philippines, Caroline Is. and Sumatra. Also recorded in Cuba and Brazil.

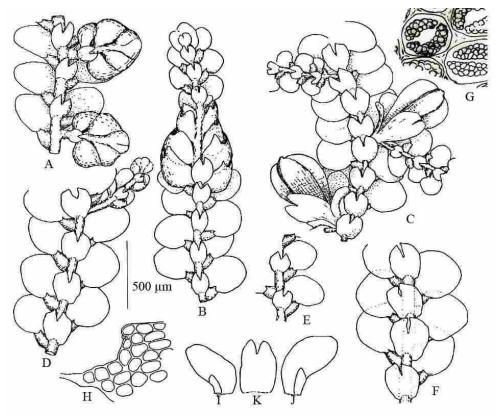


Figure 26. *Cheilolejeunea serpentina* (**Mitt.**) **Mizut.** (A) Part of male plant with androecia on lateral branches, ventral view; (B) Male plant with intercalary androecium; (C) Female plant with gynoecia, showing lejeuneoid and pycnolejeuneoid innovations; (D-F) Part of sterile shoots, ventral view; (G) Leaf median cells with Leucolejeunea type of oil bodies; (H) Distal part of lobule; (I,J) Female bracts and (K) Bracteole. (A,I,K) Cameroon, *Jungner* 201; (B, D-F) Cameroon, *Linnell* 12; (C) Nigeria, *Jones* 195 and (H) Sierra Leone and *Arnell* 2507 after Jones (1954b). (G) Kenya, *Malombe, et al.*, 5009 J2 by Author and N. Maundu.

NOTES. The Kenyan collections from Ngong hills (*Malombe I Fischer E & Mwachala G* 5009 J2) and Mumoni hills (*Malombe I, Mwachala G & Kirika P* 4026 L15B) are large form of *Ch. serpentina*. Unlike several collections of the species, the lobular apical tooth is relatively acute to spiniform, a character only known for *Ch. decursiva* and *Ch. exinnovata*. *Cheilolejeunea serpentina* is however distinguished by the frequently caudicous leaf lobes. These collections may form a subspecies or an intermediary between the two species. They are currently placed under *Ch. serpentina* until fertile materials are obtained.

14. Cheilolejeunea diversifolia Augier, Ann. Fac. Sci. Cameroun 11: 65. 1972.

Plants small, shoots up to 0.4 cm long, 0.25-0.6 mm wide, irregularly branched, some branches microphyllous, stems 40-70 μm in diameter, medullary cells (3-)4(-5). *Leaves* and lobules conspicuously mammillose, the *leaf lobe* loosely imbricate, sometimes remote, oval, flat to moderately convex, 250-350 μm long, 170-250 μm wide, the apex rounded, trigones small to *ca.* absent, 1.3-2.5 μm long; *leaf lobule* strongly inflated, with marked depression near apex, the apex raised and postical lobe margin deflexed, gently narrowed to the mouth and slightly carved, 110-150 μm long, *ca.* ½ as long as the lobes, free margin bordered by 5-6(-7) cells, keel strongly arched, forming a wide sinus with postical postical lobe margin, apical tooth 1 celled, 13-16 μm long, blunt. *Underleaves* remote, rarely imbricate, 90-145 μm long, 90-130 μm wide, 2 x as wide as stem, apex bilobed to 1/3-1/5 of its length. *Autoicous. Androecia* usually in 2 pairs of bracts. *Gynoecia* on short lateral branches, with 1(-2) innovation(s), innovation lobe sequence pycnolejeuneoid; bracts lobule broad, up to 3/4 the length of the bract lobe, largely lingulate-obovate; bracteole 450 μm long, the apex sinus to 0.2 of the bracteole length. *Perianth* subcomppressed, pyriformoblong, 400-450 μm long, ca. 330 μm wide, keels 5-carinate; rostrum up to 30 μm long.

SPECIMEN EXAMINED. CAMEROON. Yaounde, sur rochers granitiques exposes, 1972, *Augier J* (EGR, holotype).

ECOLOGY AND DISTRIBUTION. Rupicolous on wet granitic rocks. Only known from Cameroon.

NOTES. I find *Ch. diversifolia* unique based on small size, with usually (3)4 medullary cells and lobule keel strongly arched on strong branches. It is characterized by big lobule-lobe length ratio (*ca.* 0.5), large mammillae glands and lacks the bippinate branching common with *Ch. intertexta*.

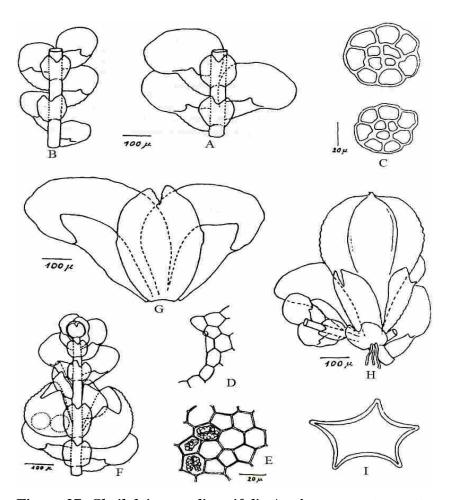


Figure 27. *Cheilolejeunea diversifolia* **Augier.** (A,B) Diverse forms of shoot, ventral view; (C) Transverse section of stem; (D) Lobule apical tooth, with rounded hyaline papillae; (E) Middle leaf cells, with oil bodies; (F) Androecia; (G) Female bracts and bracteole; (H) Perianth showing pycnolejeuneoid innovations; (I) Transverse section of perianth. Drawn from Augier, 1972.

- **15.** *Cheilolejeunea intertexta* (**Lindenb.**) **Steph.**, Bull. Herb. Boiss. 5: 79. 1897; *Lejeunea intertexta* Lindenb. in Gottsche *et al.*, Syn. Hep. 379. 1845. Type: Karolinen. Martens s.n. [lectotype designated by (Grolle 1979): W!, S, isotype].
- Cheilolejeunea newtonii Steph. ex Schiffn., in Engler & Prantl., Naturl. Pflanzenfam. 1(3): 124. 1893; Cheilo-Lejeunea newtonii Steph., Hedwigia 27: 109. 1888, nom. inval. syn. nov.

Cheilolejeunea kurzii Steph., Bot. Gazette 15: 284. Nov 1890 "Cheilo-Lejeunea"; Lejeunea

kurzii (Steph.) Steph., Bot. Gazette 15: 349. Dec 1890.

Cheilolejeunea inflata Steph., Sp. Hepat. 5: 645. 1914; Euosmolejeunea inflata (Steph.) R.M.Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968.

Rectolejeunea santae-mariae Steph., Sp. Hepat. 5: 680. 1914, probably synonymous.

Cheilolejeunea subrotunda Herzog & Noguchi, J. Hattori Bot. Lab. 14: 48. 1955. Type:China. Taiwan. Botel Tobago. Baumwurzel in schattigem Bachbett, 2 June 1947,G.H. Schwabe 72 p.p. (JE, holotype)

Plants green to yellowish, strong shoots 0.68-1.1(-1.3) mm wide, irregularly pinnately branched, stems 60 to 120 µm diameter. Leaves remote to weakly imbricate, usually diverging from the stem perpendicularly; the *lobes* asymmetrically oblong-oval, nearly flat, 337-750 µm long, (266-290)307-620 µm wide, the apex broadly rounded, the ventral margin nearly weakly arched, forming a very wide angle with the keel, or almost in line with it, the base weakly arched, not crossing the stem; the trigones usually small, 1-5 µm long, sometimes bigger, oil bodies 1-2(-3) per cell, up to 25 µm long and 10 µm wide; leaf lobule small, ovate-conical, inflated proximally, narrowed towards the neck, 62-200 µm long, 1/5-2/5, or less (0.15), as long as the lobes, lateral free margin bordered by 4-6 cells, keel straight or slightly arched, usually diverging from the stem at a wider angle of 80-90°, sometimes at a narrower angle of up to 45°, apical tooth short, 1celled, ca. 20 µm long, blunt. Underleaves remote to imbricate, 156-379 µm long, 153-363 µm wide, 2-3.5 (4) x as wide as stem, apex bilobed 1/3-1/2 of its length, sinus V, rarely U shaped. Autoicous, sometimes paroicous. Androecia on short lateral branches, sometimes intercalary or terminal on long branches, 365-756 µm long, 364-485 µm wide, bracts in 1-5(-7) pairs. Gynoecia on short lateral branches or on long shoots, usually with 1(-2), occasionally lacking, lejeuneoid or pycnolejeuneoid innovations. Perianth compressed, oblongpyriform, 0.41-1.04 mm long, 0.33-56 mm wide, exserted to about 0.5 their length, plane and ecarinate dorsally, bicarinate ventrally, the apex truncate-slightly cordate; rostrum 17-40 (60) μm long.

REPRESENTATIVE SPECIMENS EXAMINED. SIERRA LEONE. Leicester Peak, Freetown Peninsula, about 20 m below the summit of the hill, 2 Mar.1971, *Jones EW* 1430 (EGR, EA, BO). **COTE D'IVOIRE**. Sakre, Cavally, 15 Aug. 1975, *Assi LA* 12980 D (EGR); Ono, 27 Aug. 1975, *Assi LA* 13025 B (EGR). **GHANA.** Volta, Amedzofe just below the summit of the hill, 31 Jan. 1971, *Jones EW & Hall JB* 1255 (BO). Bunso, near

the Tafo road, 6 Feb. 1971, Jones EW & Dall JB 1317 a part (EA, EGR). BENIN. Lama Forest, 4 Apr. 1998, Dilg C 6.12 (EA, EGR); 3 Apr. 1998, Dilg C 5.5 (EGR); Dilg C 7.5 (EGR); Dilg C 4.16 (EA, EGR) & Dilg C (EGR, EA). CENTRAL AFRICA REPUBLIC. Damara, Bangui, Route de Damara, Surtroucd'arbre. 8 Jan. 1961, Assel M 58/134 (EGR, EA); 3 Mar. 1962, Assel E 351 (EGR); Pócs T 68 (EGR) & 3 Mar. 1962, Pócs T 354 C (EGR); Galerie Forest, Ligala, 25 Oct. 1962, Assel M 608/134 (EGR, EA); Bozo on sur ecorces, 9 Dec. 1961, Assel M 338 B (EA, EGR). DR CONGO. Saturne, Envitons de l'anneau de Saturne on Broussailles, 29 Dec. 1964, Pócs T (EGR). CONGO- Brazzaville. Chute, Fulakau, R.C Chute dela fulakari, sur arbustes. 14 Apr. 1965, Assel E 257 (EGR). Mbete, River Mbete, 17 Jan. 1966, *Pócs T* 436 (EA, EGR). M'bote, 17 Jan. 1966, *Pócs T* 450 (EGR). Ngamissaku, Ruisseau, 22 Apr. 1966. Pócs T 864 (EGR). ETHIOPIA. Bale, Harenna escarpment, 24 Dec. 1989, *Miehe G & S* 157 (EGR). **UGANDA**. Bunyoro; Budongo rainforest, transect B, 1100 m, Malombe I & Mwale G 6004 N15bS5 (EA); Malombe I 6002 N3x15 (EA); Malombe I & Mwale G 6005 W22S2x (EA); Mwale G 6007 N2x5 (EA) & Malombe I & Mwale G 6007 N2x7 (EA). Mengo; Jungo Forest near Mweno village in the SE part of Bugala Island, 0.262 S 32.164 E 1100m, 7 Sep. 1997, Pócs T, Lye KA & Samuela A 97107 E (EGR, EA, MAK, N) & Mabira Forest along the main track from the Ecotourism site, 0.23886 N 33.01202 E, 22 May 2006, *Malombe I* 6008 F (EA). **KENYA**. Kirinyaga; Kamweti Track along the track, 2600 m, 29 Nov. 1971, *Pócs T*, Faden RB & Faden A 6601 D (EA). Gede, Arabukosokoke forest, ca. 1 km off Malindi Mombasa highway, along the track opposite Mida Gate, 3.19358 S 39.5688 E 10 m, 10 Nov. 2006, Malombe I, Mugambi, GK & Miyawa D 6011 A (EA). TANZANIA. Lushoto, Amani, Forest House, 7 Aug. 1974, Baagøe J & Vollesen K 303 a (EGR). **SOUTH AFRICA**. Port St. John, Cape. 31.36021 S 29.31011 E 370 m, Wager D 3705 (PRE).

ECOLOGY AND DISTRIBUTION. Usually epiphylic on shrub and tree trunks, branches and twigs, but occasionally epiphyllous and sometimes on rocks and decaying wood. It is one of the common species in secondary tropical humid lowland rainforests forming pure mats or mixed with other common species such as the equally variable *Ch. serpentina* and *Ch. trapezia*. Occurs from sea level up to 1130 m, and it is rarely recorded in the upper montane forests. Its widespread in Africa (Ivory Coast, Sierra Leone, Guinea, Ghana, Benin, Nigeria, Cameroon, Central African Republic, Congo-Brazaville, Gabon, São Tomé, Príncipe, Ethiopia, Uganda, Kenya, Tanzania, South Africa, Réunion, Madagascar and Mascerenes) as well as Asia (Thailand, India, China, Sumatra, Samoa,

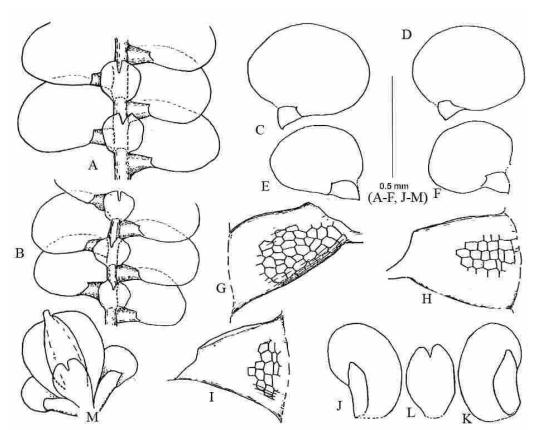


Figure 28. *Cheilolejeunea intertexta* (Lindenb.) Steph. (A,B) Part of shoot, ventral view; (C-F) Leaves; (G-I) Lobules; (I,K) Female bracts; (L) Bracteole; (M) Perianth with bracts and bracteoles. (A,B,I,M) Nigeria, *Jones*; (C,D) Nigeria, *Berrie*; (E) Nigeria, *Jones* 226; (I-L) Nigeria, *Jones* 11. *Cheilolejeunea serpentina*. (F) Príncipe, *Newton* 1 (Type, *Ch.. principensis*). All from Jones (1954b).

NOTES. Jones (1954) was first to doubt the difference between *Ch. intertexta* (*Ch. inflata*) and *Ch. newtonii* and about two decades later he concluded the two species were conspecific (Jones, 1973). He noted that several leaf lobes of the *Ch. intertexta* formed narrow angle with stem and slightly marked sinus with ventral leaf margin. Grolle (1979) however maintained that the subgynoecial innovation is pycnolejeuneoid in *Ch. intertexta* while in *Ch. newtonii* is lejeuneoid. As Jones (1983) still doubts, these two features are malleable and common in both species. They are definitely therefore bad characters to separate the two species. As shown in the illustrations by Asthana *et al.* (1995), the keel of leaf lobe lobule can also form narrow sinus with stem and with a marked one with ventral margin. I observed several collections in Africa with related characters even on the same shoot and the subgynoecial innovations frequently being either lejeuneoid or pycnolejeuneoid in both species. Wigginton (2004a) also found difficulties in use of innovation characters especially with species exhibiting both lejeuneoid and

pycnolejeuneoid form and recommends the use of several materials to ascertain the more frequent type of innovation. The size of shoot width was also used to differentiate the two species, with *Ch. newtonii* thought to have larger width. Collections characteristic of *Ch. newtonii* by *Assel M* 608/134, 450 and 338 B from Congo Brazaville has the width of shoots less than 900 µm clearly enclipsing the size of *Ch. intertexta*. *Cheilolejeunea newtonii* is therefore reduced to a synonym of *Ch. intertexta*.

16. Cheilolejeunea exinnovata E.W.Jones, J. Bryol. 12: 37. 1982.

Plants 0.55-1.1 mm wide, irregularly pinnately branched, stems up to 80 μm in diameter. *Leaves* asymmetrically oval or ovate, flat, 448-750 μm long, 359-550 μm wide, the apex broadly rounded, the ventral margin nearly straight but with more or less sharp angle just distal to the lobule and disoriented with the keel; *leaf lobule* small, ovate-conical, inflated proximally, narrowed to a small mouthed neck, which sometimes is curved forward, *ca*. 140 μm long, ¼-(1/3) as long as the lobes, lateral free margin sometimes visible at extreme apex, bordered by 4-5(9-11) cells, keel slightly arched, the apical tooth spiniform, 20-30 (37 Zimbabwe) μm long. *Underleaves* 145-250 μm long, ca. 154 μm wide, ca. 2 times as wide as stem, apex bilobed 1/3-1/2 of its length. *Autoicous. Androecia* on short lateral branches and intercalary on long branches, rarely terminal. *Gynoecia* on very short lateral branches, innovations absent. *Perianth* compressed, oblong to pyriform, 500-840 μm long, 360-600 μm wide, exserted to about 0.5 their length, plane and ecarinate dorsally, bicarinate ventrally, the apex truncate- slightly cordate; rostrum 15-20 μm long.

SPECIMENS EXAMINED. ZIMBABWE. Melsetter, Makuripini Forest, about 3 ft from ground, 14 Jan. 1969 *Williams O.J.* 19RSES (MISS, EGR). **SIERRA LEONE.** Kenema District; Gola North Forest Reserve, *Jones* EW 1568 (BM, holotype). **GHANA.** Western Region, Ankasa River Forest Reserve, *Jones EW* 1375.

ECOLOGY AND DISTRIBUTION. Epiphyllous and rare in primary lowland rainforests in Sierra Leone and Ghana. Also recorded in Zimbabwe (on deadwood) and Brazil.

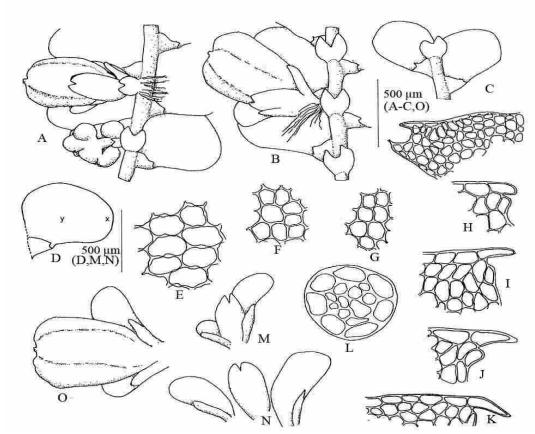


Figure 29. *Cheilolejeunea exinnovata* **E.W.Jones.** (A) Part of shoot with gynoecium and androecium, in ventral view; (B) Part of shoot with gynoecium; (C) Leaf and underleaves; (D) Leaf, ventral view; (E-G) Cells, 'E' and 'F' from D's x and y respectively, 'G' from different leaf; (H) Distal part of lobule; (I-K) Apical tooth of lobule; (L) Transverse section of stem; (M,N) Female bracts and bracteoles; (O) Perianth with bracts. (A-G, I, L-O) Sierra Leone, *Jones* 1568 (type); (H) Ghana, *Jones* 1375 and (J,K) Zimbabwe, *Williams* 19RSES from Jones, 1982.

- 17. Cheilolejeunea trifaria (Reinw. et al.) Mizut., J. Hattori Bot. Lab. 27: 132. 1964; Jungermannia trifaria Reinw. et al., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 226. 1824; Lejeunea trifaria (Reinw. et al.) Nees, Syn. Hepat.: 361. 1845. Euosmolejeunea trifaria (Reinw. et al.) Steph., Hedwigia 27: 292. 1888. Type: Indonesia. Java. Specific locality unknown, Blume s.n. & s.d. (L, holotype; STR, isotype).
- Lejeunea brachytoma Gottsche, Abh. Naturwiss. Ver. Bremen 7: 355. 1882; Euosmolejeunea brachytoma (Gottsche) Steph., Sp. Hepat. 5: 577. 1914; Cheilolejeunea brachytoma (Gottsche) R.M.Schust., Phytologia 45: 431. 1980.
- Lejeunea grandistipula Steph., Bot. Jahrb. Syst. 8: 89. 1886 "1887"; Euosmolejeunea grandistipula (Steph.) Steph., Sp. Hepat. 5: 578. 1914.
- Euosmolejeunea robillardii Steph., Sp. Hepat. 5: 578. 1914; Cheilolejeunea robillardii (Steph.) R.M.Schust., Phytologia 45: 431. 1980.

Euosmolejeunea latifolia Horik., J. Sci. Hiroshima Uni., Ser. B, Div. 2, Bot. 2: 269. 1934. Type: China. Taiwan "Formosa". Taichu, Zitsugetsutan, on the barks of tree, 14 Aug. 1932, Y. Horikawa 8880 (HIRO, holotype).

Plants green, up to 3 cm long, strong shoots 0.7-1.0 mm wide, irregularly branched, stems 89.5-114.8 µm in diameter. *Leaves* strongly imbricate, semi caudicous, the lobes broadly rounded, varying from flat to moderately convex, 450-700µm long, 404-550 µm wide, the apex rounded, semicircular, the base broadly rounded, often crossing the stem, lobe median cells 20-30 µm long and 15-22 µm wide, trigones large, 8.5-10.9 µm long, usually nodulose, the cells prominent dorsally, oil bodies 2-3 per cell, ca. 17.5 µm long and 8.3 µm wide; leaf lobule small, inflated, narrowed to the mouth and with shortly carved apex, 118-174 μm long, 1/5-1/4, rarely 1/3, as long as the lobes, lateral free margin strongly incurved, bordered by 4-6(-7) cells, keel strongly arched, ca. 90° with postical lobe margin; the apical tooth 1 celled, 14-20(27) µm long, blunt-subacute, straight, rarely slightly recurved. Underleaves strongly imbricate, 317-491 µm long, 406-547 µm wide, wider than long, nearly as large as the lobes, 3.8-5.0 times as wide as stem, apex bilobed to ca. 1/5-2/5 of its length, sinus usually V, sometimes U or semicircular shaped, base cordate, insertion strongly arched. Autoicous. *Androecia* forming short lateral branches, sometimes intercalary or terminal on long branches, bracts in 2-6 pairs, 285-380 µm long, often distant from female branches. Gynoecia either on short lateral branches or terminal on long shoots, usually with 1 lejeuneoid innovation (occasionally with none, very rarely with 2), the innovation either short and sterile, or short and quickly fertile; bracts broadly rounded, 438-576 µm long; bracteole obovate, up to 582 µm long, apex sinus 0.23-0.32 of the bracteole length. Perianth oblong or narrowly pyriform, 715-1008 µm long, 465-626 µm wide, keels long and almost equal, 5(-6) carinate; rostrum up to 70 μm long.

REPRESENTATIVE SPECIMENS EXAMINED. CENTRAL AFRICAN

REPUBLIC. Boali, Chute de la Boali, 450 m, 28 Dec. 1960, *M. Assel* 44 (EA, EGR); Bozo, 29 Dec. 1961, *Assel E* 338 A (EGR). Bangui, Kassai, 1 May 1961, *Assel E* 217 (EGR). **UGANDA**. Bunyoro; Budongo Forest near Sonso River, along track B, Nature reserve in Compartment N15, 1.43587 N 31.31672 E 1100 m, 17 May 2006, *Malombe I & Mwale G* 6004 N15aS1x5 (EA) & *Malombe I & Mwale G* 6007 N2x4b (EA). **KENYA** (new record for Kenya). Kitui; Mutha hill at the summit, S facing side, 1400 m, 8 Oct. 2004, *Malombe I & Muasya J* 4022 E1 (EA). **TANZANIA.** Lushoto, E Usambara Mts,

Amani Forest Reserve behind the Forest Houses, 960 m, 19 Feb. 1982, *Pócs T* 6946 A (EA, EGR); Amani Government Rest House, 10 Jan. 1971, *Pócs T, & Jones EW* 6381 B(EGR); Kwamkoro, near sawmill, 960 m, 11 Feb. 1987, *Pócs T, Hamilton A & Mwasha I* 87032 BH (EGR). Morogoro; Mindu Mts, W Morogoro town, 1150 m, 12 Apr. 1970, *Pócs T* 6152 AB (EA); WSW of Morogoro town, on the S end of the main ridge, 12 Dec. 1972, *Pócs T & Crosby M & C* 6843 Z (EGR, EA); Nguru ya Ndege, Hill NNW of Morogoro town, on the North ridge, 900-1080 m, 6 Jun. 1989, *Pócs T & Orban S* 89175 Q (EA, EGR) & 22 Oct. 1988, *Pócs T & Knox E* 88250 M (EA, EGR).

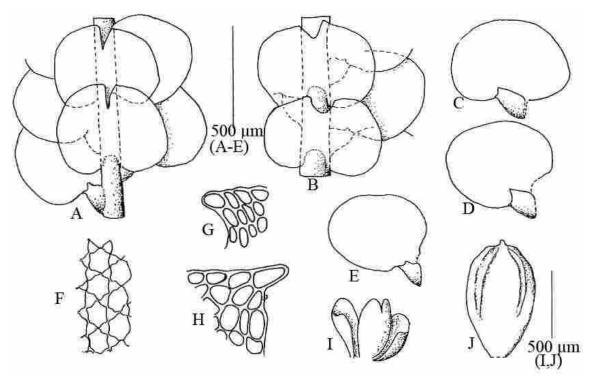


Figure 30. *Cheilolejeunea trifaria* (**Reinw. et al.**) **Mizut.** (A,B) Part of shoot, ventral view; (C-E) Leaves, ventral view; (F) Cells, mid-lobe; (G,H) Apex of lobule, 'H' showing position of hyaline papilla; (I) Female bracts and bracteole; (J) Perianth. (A, C-F, H-J) Sierra Leone, *Jones* 476; (B) Mauritius, *Robillard* s.n. (type of *Euosmolejeunea robillardii*); (C,D,G) Tanzania, *Fischer* 30. All from Jones (1954a).

ECOLOGY AND DISTRIBUTION. A pantropical species with a wide but disjunct distribution in tropical Africa, occurring largely on tropical lowland rainforests but sometimes in afromontane dry mist primary forests, from 450 up to 1950 m a.s.l. It is common on tree trunks, but also on the tree crown, soil and steep rocks. In Africa, *Ch. trifaria* is known from Togo, Sierra Leone, Ghana, Bioko, Sáo Tomé, Central African Republic, DR Congo, Cameroon, Gabon, Rwanda, Uganda, Kenya (first record), Tanzania and Zimbambe, and is common in East African islands and Asia.

18. Cheilolejeunea montagnei (Gottsche) R.M.Schust., Beih. Nova Hedwigia 9: 112, 1963; Lejeunea montagnei Gottsche, Ann. Sci. Nat., Bot. Sér. 2, 19: 261. 1843; Euosmolejeunea montagnei (Gottsche) Steph., Bot. Jahrb. Syst. 20: 318. 1895; Leptocolea montagnei (Gottsche) Steph., Sp. Hepat. 5: 845. 1916.

Euosmolejeunea thomeensis Steph., Sp. Hepat. 5: 580. 1914.

Plants pale green, strong shoots 2-3 (-7) cm length, 0.7-1.2 mm wide, irregularly branched, stems 113-142 µm in diameter, cortical cells seven and medullary cells 12-16. Leaves strongly imbricate, lobes broadly ovate, sub symmetrical, strongly convex, 577-760 µm long, 440-600 µm wide, the apex rounded, recurved, the base broadly rounded, often crossing the stem, lobe median cells 20-26 µm long and 16-22 µm wide, trigones large, ca. 10.4 µm long, often irregularly nodulose; *leaf lobule* relatively small, triangular, strongly inflated, narrowed to the mouth and with shortly carved apex, 180-340 µm long, 1/3-2/5, rarely ca. 1/2, as long as the lobes, lateral free margin strongly incurved, keel arched, forming an angle with postical lobe margin; the apical tooth 1-4 celled, 13-16 µm long, blunt-subacute, straight or recurved. *Underleaves* distant to approximate, 386-600 µm long, 440-712 µm wide, 3.4-5.4 times as wide as stem, reniform, apex entire, rounded to very shallowly retuse, base broadly cuneate, truncate or somewhat cordate, insertion strongly arched. *Dioicous. Androecia* forming short lateral branches, up to 2 mm long by 0.7 mm µm wide, bracts in 3-8 pairs, 323-506 µm long, bracteole 1-3, restricted to the base of androecium, antheridia 2 per bract. Gynoecia usually with 2 lejeuneoid innovations; bracts broadly rounded-obovate, ca. 800 µm long, the lobule oblong-lanceolate, up to 1/3 the length of the bract lobe, acute, apex rounded, margin entire, keel straight; bracteole obovate, up to 550 µm long, the apex entire. *Perianth* rare, oblong, 4-5 keels; rostrum large.

REPRESENTATIVE SPECIMENS EXAMINED. DR CONGO. Biega Mts, Kahuzi, Biega National Park, 2700 m, 28 Aug. 1991, *Pócs T* 7180 (EA, EGR). RWANDA. Cyangugu, Nyungwe Forest, Kamitanzovu swamp forest, 2000 m, 13 Aug. 1991, *Pócs T* 6355 (EGR); Nyungwe Forest, 31 Mar. 2005 *Fischer E* s.n. KENYA. Taita Taveta; Kasigau on lower slopes of the peak in mist forest, 1400-1600 m, 6 Feb. 1971, *Faden RB*, *Evans A, Kariuki & Smeenk C* s.n. (EGR). TANZANIA. Lushoto; W Usambara Mts, Balangai, Kilimandege, 20 Jan. 1985, *Pócs T* 8508 L (EA, EGR) & Mazumbai, University

Forest Reserve, on the ridge, 1800-1880 m, Jan. 1971, *Pócs T & Jones EW* 6373 C (EA, EGR).

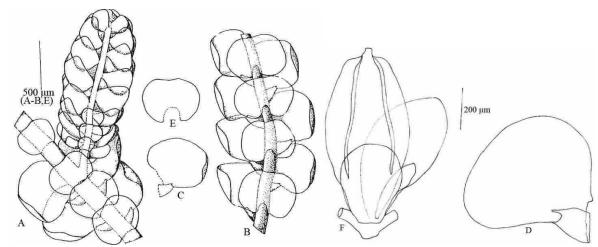


Figure 31. *Cheilolejeunea montagnei* (**Gottsche**) **R.M.Schust.** (A,B) Part of shoot, 'A' with androecium, in ventral view; (C,D) Leaves, ventral view; (E) Underleaf; (F) Perianth. (A) Rwanda, *Marlier-Spirlet s.n.* and (B,C,E) Rwanda, *Symoens* 5381 from Vanden Berghen, 1965, as *Euosmolejeunea montagnei*, and (D,F) Mauritius?, redrawn from Stephani Icones, Microfiche 002761 (Stephani, 1985).

ECOLOGY AND DISTRIBUTION. It is an African species known from São Tomé, DR Congo, Rwanda, Ethiopia, Uganda (Ruwenzori mts), Kenya (Taita hills) and Tanzania. Also collected in Madagascar, Mauritius, Comoro Is. and Réunion. Usually afromontane species on bark or branches especially of *Erica sp.*, among other species. Also sometimes on rocks or epiphyllous between 1400 and 2000, rarely up to 2700, m a.s.l.

NOTES. Cheilolejeunea montagnei is easily differentiated from other species in Cheilolejeunea by the large entire or notched underleaves. It forms a strong link between subg. Cheilolejeunea and Strepsilejeunea due to strongly convex lobes, which may be sometimes recurved. The lobe apex is however broadly rounded ant acute as the latter. As observed by Wigginton (2004a), it differs from Evansiolejeunea roccatii, which may grow in the same environment by having small lobules and presence of 2 innovations. E. roccattii lacks innovations and lobules are large. The collection by Fischer E s.n. 2005 from Nyungwe Forest is 7 cm, a record length in Cheilolejeunea. I also noted specimens (Fischer E s.n. 2007) with wide ventral merophytes (up to 8), large lobules with near flattened ventral free margin and sometimes with at least one subgynoecial innovation. These collections do not guilify to be Ch. montagnei neither true E. roccatii. It calls for urgent evaluation of the genus Evasiolejeunea.

19. Cheilolejeunea ulugurica Malombe, Pócs, Eb. Fisch. & Masinde sp. nov.

Diagnosis: Cheilolejeunea chenii R.L. Zhu & M.L.So, Taxon 48: 663, 1999 similis sed differt foliis sigmoideis lobulis longioris (longitudine 2/3 lobi aequantia), margine libera lobuli 10 cellulae longi et margine distali solum 2-3 cellulae lati.

Plants green, shoots up to 12 mm long, 560-776 μm wide, with few seldom branches, stem 64-84 μm in diameter. *Leaves* usually imbricate, spreading from the stem at an angle of 80-130°, the lobes obovate, 378-488 μm long, 340-392 μm wide, apex broadly rounded, plane, bend towards the antical stem base, base flat, the lobe cells slightly thickened, mid cells hexagonal, 32-64 μm long and 22.4-27.2 μm wide, marginal cells rectangular, 20.0-26.0 μm long and 16-32 μm wide, trigones very small, up to 2.6 μm in length. *Leaf lobule* ovoid to oblong, usually over 2/3 as long as the lobes, lateral free margin usually flattened starting from the base of the lobule, forming a strongly conspicuous fold which run diagonally to nearly the entire length as to join the much incurved keel apex, *ca.* 10 cells, the keel forming a narrow sinus (<45°) with postical lobe margin, apical tooth moderately long, usually incurved to form a club-like appendage with the incurved keel side, rarely straight, 64-105 μm, spiniform, the distal hyaline papillae obovate, large. *Underleaves* distant, appressed, 304-488 μm long, 336-484 μm wide, transversely inserted, orbicular, base subcordate, sinus very shallow or notched, *ca.* 0.08 times the length of the underleaves. Gametagia and asexual reproduction organs unknown.

SPECIMEN EXAMINED. TANZANIA. Uluguru Mts, N side of Bondwa peak, 26 Dec. 1985, *Pócs, B. & T.* 8565 S, (EGR, holotype).

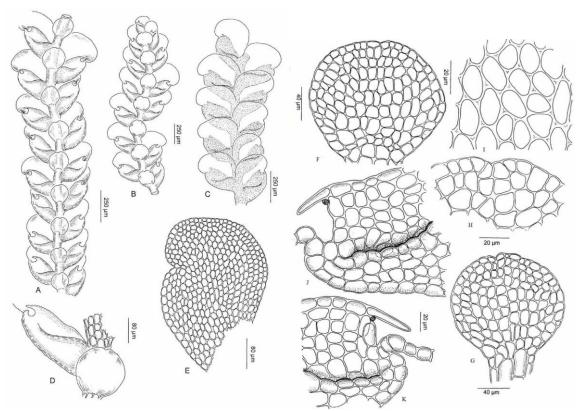


Figure 32. *Cheilolejeunea ulugurica* **Malombe, Pócs, Eb. Fisch. & Masinde sp. nov.** (A-C) Part of shoot, 'B' terminal, 'C' dorsal view; (D) Lobule; (E) Leaf; (F,G) Underleaves; (H) Apical part of underleaf showing shallow sinus; (I) Median cells of lobe; (J,K) Apical part of lobule, showing apical teeth and hyaline papillae. All from the type by E. Fischer and I. Malombe.

ECOLOGY AND DISTRIBUTION. Ramicolous on ericaceous stems always mixed with other species at the edge of montane forest. Endemic to Uluguru Mts between 1650 and 1800 m a.s.l.

NOTES. Cheilolejeunea ulugurica is currenly ranked in the subg. Cheilolejeunea subclade. It partly resembles species initially placed in the subg. Xenolejeunea based on the large lobules, > than ½ the leaf lobe length. It also partly resembles species of subg. Cheilolejeunea s. str. owing to small sizes, long spiniform lobular apical tooth and flattened lobes. A related species in China, Ch. chenii was placed in the latter (Zhu et al., 2002). The two species are so close to each other such that even the measurements of shoot width, leaf lobes and underleaves almost overlap (see Zhu et al., 1999). However, Ch. ulugurica is characterized by a sharp, ca. notch, angle between leaf lobule keel and ventral lobe margin. The leaf lobule ventral free margin consists of up to 10 cells. Cheilolejeunea chenii has a wider and clear angle between leaf lobular keel and ventral lobe margin. The free margin of lobule consists of 7-8 subquadrate cells.

- 20. Cheilolejeunea trapezia (Nees) Kachroo & R.M. Schust. J. Linn. Soc. London, Bot. 56: 509. 1961 (Feb.); Jungermannia trapezia Nees, Enum. Pl. Crypt. Jav.: 41. 1830. Lejeunea trapezia (Nees) Gottsche et al., Syn. Hepat.; 357. 1845. Pycnolejeunea trapezia (Nees) Steph., Hedwigia 29: 76. 1890, nom. inval. (Art. 43.1). Pycnolejeunea trapezia (Nees) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1(3): 124. 1893. Cheilolejeunea trapezia (Nees) Mizut., J. Hattori Bot. Lab. 24: 282. 1961 (Oct.). Type: Indonesia. Java, "in Collemate bullata," Blume & Reinwardt s.n. (holotype STR; isotypes FH fide Thiers 1992, W Lindenb. Hep. 6401).
- Lejeunea trapezia (Nees) Gottsche et al., var. minor Gottsche et al., Syn. Hepat.: 358. 1845. Pycnolejeunea trapezia (Nees) Schiffn. var. minor (Gottsche et al.) Schiffn., Consp. Hepat. Arch. Ind: 261. 1898. Type: Indonesia. Java, "ad pedem Merapi montis inter Muscos arboreos legit Junghuhn (Herb. Nees)" (isotype G 16573).
- Jungermannia thymifolia var. imbricata Nees, Enum. Pl. Crypt. Jav.: 42. 1830. Lejeunea imbricata (Nees) Gottsche et al., syn. Hepat.: 359. 1845. Pycnolejeunea imbricata (Nees) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1(3): 124. 1893.
 Cheilolejeunea imbricata (Nees) S. Hatt., Misc. Bryol. Lichenol. 1(14): 1. 1957.
 Type: Indonesia. Java, without specific locality, collector or date, Herb. Nees, Herb. Lindenberg 6406 (holotype STR; isotype G 16567, G 16568).
- Lejeunea surrepens Mitt., Phil. Trans. Roy. Soc. London 168: 399. 1879. Cheilolejeunea surrepens (Mitt.) E.W.Jones, J. Bryol. 9: 49. 1976. syn. nov.
- Lejeunea silvestris Gottsche, Abh. Naturwiss. Ver. Bremen 7: 354. 1882; Cheilolejeunea silvestris (Gottsche) E.W. Jones, J. Bryol. 7: 548. 1974 "1973".
- Pycnolejeunea tosana Steph., Bull. Herb. Boissier 5: 94. 1897. Cheilolejeunea tosana (Steph.) Kachroo & R.M.Schust., J. Linn. Soc., Bot. 56: 509. 1961. Type: Japan. Kochi Pref. (Prov. Tosa). Sakawa-machi, April 1896, T. Inoue 63 (holotype: G-20604; isotype: TNS).
- Pycnolejeunea decurrens Steph., Sp. Hepat. 5: 600. 1914; Cheilolejeunea decurrens (Steph.) X.-L.He, Ann. Bot. Fennici 32: 251. 1995. Cheilolejeunea decurrens (Steph.) X.-L. He, (comb. nov.) Ann. Bot. Fennici 32: 251-258. 1995.
- Pycnolejeunea involuta Steph., Sp. Hepat. 5: 601. 1914; Cheilolejeunea silvestris var. involuta (Steph.) E.W.Jones, J. Bryol. 7: 548. 1974 "1973".
- Pycnolejeunea africana Steph., Sp. Hepat. 6: 412. 1923; Cheilolejeunea africana (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 388. 1954; Euosmolejeunea africana

(Steph.) R.M.Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968. *Pycnolejeunea longiloba* Steph. ex G.Hoffm., Ann. Bryol. 8: 114. 1935. *Cheilolejeunea longiloba* (Steph. ex G.Hoffm.) J.J.Engel & B.C.Tan, J. Hatori Bot. Lab. 60:294. 1986; syn. nov. Type: Philippines. Polillo I., Oct.-Nov. 1909, R.C. McGregor s.n. (holotype: FH; isotype; NY).

Placolejeunea subarrhyncha Herzog, Svensk. Bot. Tidskr. 42: 234. 1948. Type: Indonesia. West Borneo, Bukit Bajah, 1240 m, *winkler 3360 p.p.* (holotype JE).

Plants up to 3 cm length, or more, strongly appressed to form thin mats, yellowish green, strong shoots 1.0-1.7 mm wide, but frequently with smaller younger branches, pinnately or dendroid irregularly branched; the stems 73-122(130-158) µm in diameter, ventral merophytes usually 2(-4) cells wide. *Leaves* strongly imbricate, diverging from the stem at an angle of ca. 75-90°, the lobes obliquely oval, varying from moderately convex to nearly flat, 473-968 µm long, 344-694 µm wide, the apex broadly rounded, ± slightly incurved, the base broadly rounded, often crossing the stem, lobe median cells 15-28 µm long and 14-24 µm wide, trigones usually oblique, small-medium sized, 1-5 µm long, sometimes large, oil bodies 1(2-3) per cell, up to 22.5 µm long and 10 µm wide; leaf *lobule* large, cylindrical (occasionally tapering at both ends), oblong to rectangular, 260-491 µm long, ½-2/3 as long as the lobes, usually slightly inflated, lateral free margin slightly incurved, bordered by (13-15)16-22 cells, keel straight, apical teeth vary from almost obsolete to 4 (-5) cells, 20 µm long and 1-3 cells wide at base, straight forward pointing, sometimes ascending or incurved towards leaf apex, blunt-subacute. Underleaves distant or approximate, 195-438 µm long, 181-408 µm wide, usually a little longer than wide, 1.9-3.6 times as wide as stem, orbicular or oval, apex bilobed to ca. 1/4-1/2 of its length, sinus variable, usually V, but also U or orbicular in cases of apex joining, base obtuse, insertion strongly arched. Autoicous or dioicous. Androecia forming short lateral branches, terminal on long shoots or often intercalary, bracts in 2-8 (-10) pairs, bracteole 1-2, restricted at base. Gynoecia on short or long branches, with 1(-2) pycnolejeuneoid innovations; bracts longly oblong, 400-710 µm long, usually obtuse-rounded at apex, the lobule linear to narrowly oblong, ca. ½ the length of the bract lobe, acute to truncate at apex; bracteole oblong, the apex lobed, the sinus to 0.25-0.50 of the bracteole length. *Perianth* pyriform, subcomppressed, 438-1010 µm long, 187-580 µm wide, keels long and almost equal, 4 carinate (2 ventral and 2 lateral); rostrum 10-28 µm long.

REPRESENTATIVE SPECIMENS EXAMINED. COTED'VOIRE. Banco, 450 m31 May 1976, Assi LA 13399 D (EGR). CAMEROON. Yaounde, SW, Minlova hillinselberg, near the summit, 800 m, 28 Feb. 2007, Malombe I 7001 C2 (EA). DR CONGO. Bukavu, Irangi Forest Station, 110 km W Bukavu, 2.3003 S 28.51039 E 850 m, 22 Aug. 1991, Fischer E 8500 64b (EA, EGR). UGANDA. Bunyoro; Budongo Forest near Sonso river, along track B, Nature reserve in Compartment N15, 1100 m, 17 May 2006, Malombe I & Mwale G 6004 N15aS1x1 (EA). Masaka; Katera 1 km ENE of Katera village, 1140 m, 9 Sep. 1997, Pócs T, Lye KA & Samuela A 97113 Q (EGR) & 3km ENE of Katera village, 0.54 S 31.397 E, 9 Sep. 1997, Pócs T, Lye KA & Samuela A 97114 O (EA, EGR). Mengo; Mukono, Sezibwa Falls, 4 km S Namataba village, 10 Sep. 1997, Pócs T & Lye KA 97115 N (EGR). **KENYA**. Mwingi; Mumoni hill on top of the highest ridge, 0.31 S 38.1 E, 1740 m, 8 May 2005, Malombe I, Mwachala G & Kirika P 5026 L1a (EA); & Malombe I, Mwachala G & Kirika P 4026 L2 (EA); Nuu hill, along foot path, SE near summit of ridge overlooking Nuu market, 1.0222 S 38.19218 E, 1380 m, 21 Oct. 2004, Malombe I & Muasya J 4024 C7 (EA). Taita Taveta; Taita hills, Kasigau on S slope above Bungule, 31 Dec. 1970, Faden RB, Faden A & Msafiri F s.n. (EA) & 16 Feb. 1971, Faden RB, Evans A, Kariuki & Smeenk C s.n. (EGR); Mbololo Forest, 1700-1800 m, 31 Dec. 1971, Faden RB, Faden AJ & Smeenk C 71 1020 AB (EGR). TANZANIA. Lushoto; E Usambara Mts, near Amani Forest House, 920 m, 10 Jan. 1971, Pócs T & Jones EW 6376 A(EGR); in valley of the Hunga stream, 9 Jan. 1971, Pócs T & Jones EW 6378 (EA, EGR); Amani Botanical Garden and experimental forest, 20 Feb. 1987, Pócs T 87040 C (EGR, BP). W Usambara Mts, Baga Forest Reserve, 1800 m, 2 Mar. 1984, Pócs T 8419 BS (EA, EGR); Mazumbai, University Forest Reserve, 7 Jan. 1971, Pócs T & Jones E.W. 6371 BA; Pócs T & Jones E.W. 6372 DM & 8 Jan. 1971, Pócs T, Jones E.W. & Tanner 6374 A. Morogoro, Nguru ya Ndege, NW Morogoro town, on the ridge, 1200-1350 m, 22 Oct. 1988, Pócs T & Knox E 88251 L (EA, EGR); Dindili Forest Reserve, 30km E-NE of Morogoro on the E slope and on the summit, 9 Jun. 1989, *Pócs T* 89182 CA (EA, EGR, SUA, EGR); Mtai Forest Reserve, on the main ridge and summit of Mountain, 850-1050 m, 14 Nov. 1986, Borhidi A, Iversen S, Steiner M & Temu RPC 86248 B (EA, EGR); Hululu Falls, Mgeta river, Guru/Uluguru mts, 27 Mar. 1973, Pócs T 6912 AB (EA, EGR); Kimboza Forest Reserve, E foothills, near Matombo, 6 Sep. 1970, Pócs T & S 6236 H (EGR); N Kinole sawmill, 4 Feb. 1973, Pócs T, & Lungwecha M 6874 AF (EGR) & Pócs T & Harris B.J. 6172 B; Kitulanghalo Forest Reserve, 35 km E-NE of Morogoro town, on the top of ridge, 700 m, 7 Jun. 1989, *Pócs T* 89181 H (EA, EGR); Mindu, SW Morogoro town, main ridge,

12 Dec. 1972, *Pócs T & Crosby M & C* 6843 Q; W-SW of Morogoro town, on the summit, 1200-1250 m, 15 Apr. 1987, *Pócs T & Pócs A* 87057 F (EA, EGR), *Pócs T* 88102 BB (EA, EGR) & *Pócs T, Crosby M & Crosby C* 6842 B (EGR); Nguru ya Ndege, Hill N-NW of Morogoro town, on the summit, 1250 m, 22 Oct. 1988, *Pócs T & Knox E* 88252 T (EA, EGR).

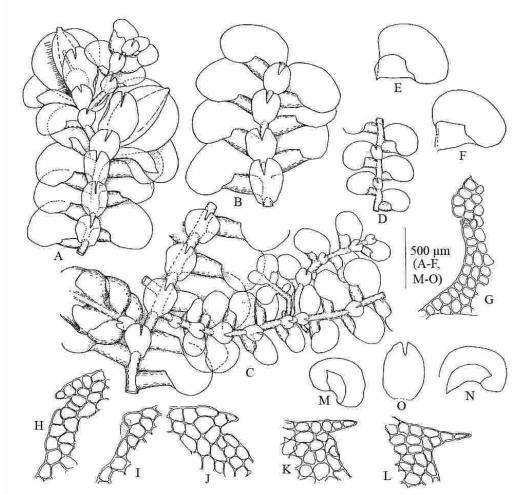


Figure 33. *Cheilolejeunea trapezia* (Nees) Kachroo & R.M. Schust. (A-C) Part of shoot, 'A' with perianth and 'C' with androecium, in ventral view; (D) Slender shoot; (E, F) leaves; (G-L) Apices of lobule; (M,N) Female bracts and (O) Bracteole. (A-G, M-O) Nigeria, *Jones* 192; (H,I) Ghana, *Jones* 1237a; (J) Uganda, *Jones* 66; (K) Tanzania, *Jones* 1825; (L) Mauritius, *Le Pouce*. (A-G, M-O) from Jones 1954b, as *Ch. africana*, (H-L) from Jones 1974a, as *Ch. silvestris*.

ECOLOGY AND DISTRIBUTION. Usually corticolous, ramicolous or epiphyllous on smaller branches and twigs in the crowns of forest trees, and sometimes on decaying wood, either in secondary (including abandoned farmlands) and primary montane rainforests or in lowland dry rocky, cloudy and mist semi-evergreen hilltops/ inselbergs dominated by Newtonia buchannii, Ricinodendron heudelotii, Croton sp., Nuxia congesta, Bombax rhodognaphalan, Euphorbia candelabrum, E. nyikae and Sterculia africana. It's usually a lowland species but spreads up to afromontane climate with altitude ranging from 300 to

1875 m, rarely up to 2575 m, where it's occasionally mixed with other species of Lejeuneaceae or Jubulaceae families.

Cheilolejeunea trapezia is Paleotropical common in Africa from W Africa through E Africa to Malawi. Also found in Madagascar and the Mascarenes. In Asia, it's distributed in China, Taiwan, Hong Kong and Oceania, extending northwards to Japan and Korea.

NOTES. The variable African species *Cheilolejeunea surrepens* is reduced to synonym as the width of the shoot once thought distinct is variable and overlapping with *Ch. imbricata*. The latter was combined with *Ch. trapezia* by Thiers (1992) and epithet name *Ch. trapezia* adopted according to ICBN priority (Zhu & Grolle, 2004). Sample collections from African material include those by *Pócs T*, *Crosby MR* & *CA* 6843 Q, *Pócs T* 88102 BB and *Pócs T* 6912 AB. Several African collections are seemingly dioicous since perianth is rare. A dioicous phenotype *Ch. decurrens* (Steph.) X.-L. He (=*Pycnolejeunea decurrens* Steph.) was sunk in *Ch. surrepens* (He, 1995) indicating some forms of the latter may exhibit dioicous nature. Asthana *et al.*, (1995) described *Ch. imbricata* as being both dioicous and autoicous in India. Except on the basis of altidunal distribution, Tixier (1995) could not distinguish the two African species *Ch. surrepens* and *Ch. trapezia*. He recommended the eastern African lowland phenotypes to be transferred to *Ch. trapezia*.

I have not seen the type of *Ch. parvidens* B. Thiers, but the description of the Australian species fits well into *Ch. trapezia* (Thiers, 1997), which may later proof to be a synonym. It was separated from *Ch. imbricata* (= *Ch. trapezia*) on the basis of narrow ventral merophytes and less cortical cells, characters which have been found variable (see Zhu *et al.*, 2002).

21. Cheilolejeunea rotundistipula (Lehm.) Malombe, comb. nov.

Jungermannia rotundistipula Lindenb. ex Lehm. Linnaea 4: 360. 1829. Lejeunea
rotundistipula (Lindenb. ex Lehm.) Mont. in Sagra: Hist. Phys. Cuba 9: 484. 1842.
Lejeunea rotundistipula Lindenb. in Gottsche, Lindenb. & Nees: Syn. Hep. 331.
1845. Lejeunea (Archilejeunea) rotundistipula Steph. Hedwigia 29: 21. 1890.
Leucolejeunea rotundistipula (Lindenb. ex Lehm.) Evans 1907. Torreya 7: 229

Plants up to 3 cm length, loosely appressed, glaucous yellowish green; strong shoots 0.8-1.1 mm wide, short pinnate, irregularly branched form thin mats on substrate, sometimes microphyllous; stems 81-90(118) µm in diameter, cortical cells 7, medullary cells 10, smaller, ventral merophytes 2 cells wide. Leaves distant to loosely imbricate, diverging from the stem at an angle of ca. 45-60°, weakly interlocking dorsally, the lobes obliquely oval, ovate, moderately convex, 459-563 µm long, 360-445 µm wide, rotundate, the apex broadly rounded, ± slightly incurved, the base broadly rounded, often crossing the stem, trigones small-medium sized, 1-5 µm long, visible from dorsal end, oil bodies 1 per cell, 12-22 µm long and 5-12 µm wide; *leaf lobule* large, oblong to rectangular or ovate, 261-372 μm long, ½-2/3, as long as the lobes, or more, dorsally slightly inflated, lateral free margin flattened almost to base, bordered by 18-19 subquadrate to rectangular marginal cells, keel gently arched; second teeth 1-4(-5) cells, 17-30 µm long and 1-3(4) cells wide at base, straight, blunt-spiniform; hyaline papillae 2-4 cells distal to apical tooth. *Underleaves* usually distant, 188-274 µm long, 230-296 µm wide, 2.5-3.3 times as wide as stem, orbicular or oval, apex entire, base obtuse, insertion arched. Dioicous. Androecia forming short lateral branches; bracts up to 5 pairs. Gynoecia on short branches, usually with 1 pycnolejeuneoid innovations, sometimes lacking; bracts longly oblong, shorter than perianth, apex rounded, the lobule 3/4 the length of the bract lobe; bracteole obovate, up to 624 µm long, the apex rounded-truncate. *Perianth* pyriform, subcomppressed, emerging from bracts by more than 2/3, keels 5 carinate, the 2 ventral ones sharp; rostrum 49 µm long.

REPRESENTATIVE SPECIMENS EXAMINED. KENYA (first records). Kitui; Mutha hill summit, 1.46432 S 38.34461 E, 1400 m, 8 Oct. 2004, *Malombe I & Muasya J* 4022 C4c (EA). Mwingi, Nuu hill along foot path SE near summit of ridge overlooking Nuu market, 1.0222 S 38.19218 E 1380 m, 21 Oct. 2004, *Malombe I & Muasya J* 4024 C8c (EA); Meru, Chogoria Track, E slope of Mt Kenya, SW of Meru town, 0.1211 S 37.2951 E 2460 m, 22 Feb. 2004, *Pócs T & S & Chuah P* 04009 A (EA, NAI, EGR). MALAWI. Mulanje, Chisongoli forest along path, 16.01026 S 35.43026 E, 17 Jun. 1991, *Magombo Z* 4067 a. SOUTH AFRICA. Natal, Drakensberg, Pearl, Bains Kloof, Cliffs, W slopes, 7 Apr. 1956, *Esterhuysen E* 25587 (BO) & Bergville, Cathkin area on the summit of Turret Peak, 29.06 S 29.24 E, Jun. 1956, *Esterhuysen E* 26147(BO). Cape, Table Mts., Platteklips, 25 Oct. 1953, *Esterhuysen E* 22177 (BO).

ECOLOGY AND DISTRIBUTION. Usually corticolous or ramicolous, but sometimes rupicolous on wet rocks or epiphyllous in submontane dry forests or rarely upper montane moist primary forest between 760 and 2420 m a.s.l. Commonly mixed with *L. xanthocarpa* and *L. unciloba*. It was initially thought to be endemic to the Drakensberg and Cape Province mts in South Africa, but was recently collected in Malawi and Kenya. Elsewhere, it is known from Lesotho, Mauritius and Réunion. Manyanga & Perold (2004) also reported possible occurrence of *Ch. rotundistipula* in Zimbabwe.

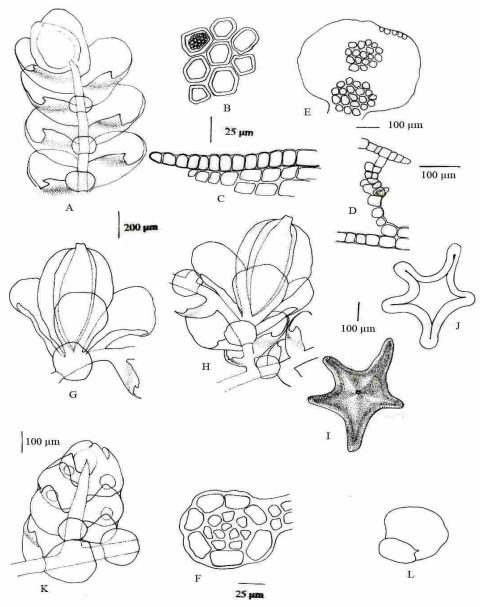


Figure 34. *Cheilolejeunea rotundistipula* (Lehm.) Malombe, comb. nov. (A) Apical shoot, ventral view; (B) Median leaf cells; (C) Free marginal cells of lobule; (D) Apical lobule showing hyaline papilla; (E) Underleaf; (F) Transverse section of stem; (G,H) Perianths; (I,J) Transverse section of perianth, 'I' showing apex rostrum; (K) Androecium, and (L) Leaf. (A-E, G-J) South Africa, *EA Schelpe* 5993; (F) South Africa, *E. Esterhuysen* 26147 (K) Kenya *Malombe & Muasya* 4024 C8 and (L) South Africa by Arnell, 1963. Others by author and N. Muema.

NOTES. Evans (1907) and Jones (1973) failed to describe *L. rotundistipula* and never provided illustrations. Jones (1973) did not study the specimens and accepted decision by Evans to retain the species in *Leucolejeunea*. Except the unlobed underleaves, most of the other characters are ensemble of *Cheilolejeunea* including the 2 ventral merophytes. Following recent collections in Kenya and small shoot size, the species may be wide spread especially in Eastern and Southern Africa but usually overlooked because it frequently grows mixed with *Ch. unciloba*, *Ch. xanthocarpa* and *Ch. trapezia*. It closely resemble *Ch. trapezia* and *Ch. unciloba* but the small sizes with rotundate leaf lobes are unique to the species.

- 22. Cheilolejeunea unciloba (Lindenb.) Malombe comb. nov.; Lejeunea unciloba Lindenb., in G. L. & N., Syn. Hep.: 331. 1845; Lejeunea (Archilejeunea) unciloba Spr., Trans. Proc. Bot. Soc. Edinburgh 15: 91, 1884. Archilejeunea unciloba Schiffn., Steph., in Engler & Prantl, Nat. Pflanzenfam. 1(3): 130, 1893. Stephani, Hedwigia 34: 62, 1895 (exclusive of A. florentissima Spr.). Leucolejeunea unciloba (Lindenb.) A.Evans, Torreya 7: 228. 1907. comb. nov.
- Lejeunea (Archilejeunea) florentissima Spr., Trans. Proc. Bot. Soc. Edinburgh 15: 91, 1884.
- Archilejeunea sellowiana Steph., Hedwigia 34: 62, 1895; Evans, Mem. Torrey Bot. Club 8: 125, 1902, pl. 16: 12-20. Leucolejeunea sellowiana Steph., Spec. Hep. 4: 737, 1912.

Leucolejeunea knysnana S.W.Arnell, Bot. Notiser 106: 286. 1953.

Plants pale glaucous to light green; strong shoots 1.3-1.8 mm wide, irregularly branched; stems (88) 112-139 μm in diameter, cortical 12-14, medullary cells many, slightly smaller than corticular; ventral merophytes 4-6 cells wide. *Leaves* imbricate, the lobes oblong to ovate, often slightly falcate, flat or nearly so, 622-1023 μm long, 586-814 μm wide, the apex rounded; cells distinctly convex to produce a slightly crenulate leaf margin, median cells 18-24 μm, trigones medium, oil bodies 1 per cell, rarely with second smaller one, 20 x 10 μm; *leaf lobule* rectangular, 331-584 μm long, 2/5-1/2 as long as the lobes, sometimes more, inflated, the lateral free margin slightly involute basally, distally plane, visible, bordered by 20-35 cells, keel form obtuse arch, postical margin never involute, apical tooth long, 1-7(9) x 2-4 celled, spiniform; hyaline papillae 2-4 cells distal to apical tooth.

Underleaves usually remote, rarely imbricate, orbicular or slightly reniform, slightly wider than long, 341-466 μm long, 3 times as wide as stem, apex entire or retuse, base rounded to subcordate. *Autoicous*. *Androecia* sterile lateral on short lateral branches or intercalary or terminal on long branches; bracts 2-6 (12) pairs. *Gynoecia* terminal on main axis or on short branches with 1 pycnolejeuneoid innovation; bracts oblong-obovate; bracteole broadly obovate. *Perianth* obovate, emergent to *ca*. 0.5, with 5 keels; rostrum slender, 80-125 μm long.

REPRESENTATIVE SPECIMENS EXAMINED. KENYA. Kitui, Mutha hill at the summit, S facing side, uphill route from Mutha market, 1.46432 S 38.34461 E 1410 m, 8 Oct. 2004, *Malombe I & Muasya J* 4022 A1 (EA); Mwingi, Nuu hill along foot path SE Nuu market, top of the centre ridge, 1.0219 S 38.1903 E 1380 m, 3 May 2005, *Malombe I, Mwachala G & Kirika P* 4024 N5B (EA); 19 Oct. 2004, *Malombe I & Muasya J* 4024 B4 (EA); & 1.0222 S 38.19218 E 1235.m, 21 Oct. 2004, *Malombe I & Muasya J* 4024 C8c (EA). TANZANIA. Lushoto, Mazumbai, West of Mazumbai village, East slope of Kwagoroto above Kambi, 1800 m, 23 Feb. 1982, *Pócs T* 6955 Z(EGR,VB). SOUTH AFRICA. Cape, Knysna, Gouna Forest, 26 Nov. 1951, *Arnell S* 1741(BO, holotype).

ECOLOGY AND DISTRIBUTION. Paleotropical and neotropical, corticolous or ramicolous. Found in eastern (Uganda, Kenya, Tanzania) and South Africa as well as Reunion and Mascarenes.

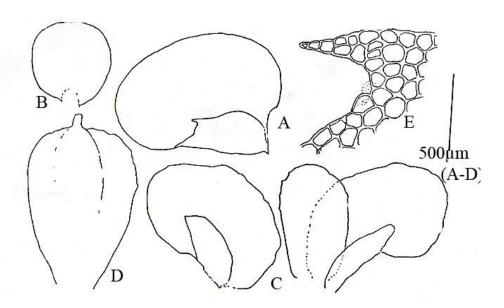


Figure 35. *Cheilolejeunea unciloba* (Lindenb.) Malombe comb. nov. (A) Leaf; (B) Underleaf; (C) Female bracts and bracteole; (D) Perianth. From Jones, 1973.

- 23. Cheilolejeunea xanthocarpa (Lehm. et Lindenb.) Malombe comb. nov. Jungermannia xanthocarpa Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 5: 8. 1833; Lejeunea xanthocarpa (Lehm. et Lindenb.) Gottsche et al., Syn. Hep.: 370. 1845; Archilejeunea xanthocarpa (Lehm. et Lindenb.) Steph., in Engler, Pflanzenw. Ost-Afrikas C: 65. 1895. Leucolejeunea xanthocarpa (Lehm. et Lindenb.) A.Evans, Torreya 7: 225. 1907. Type: Brazil, locality unknown. Beyrich s.n. & s.d. [lectotype designated by Grolle & Piipo (1990): S; isolectotypes: NY, STR, W].
- Jungermannia microscypha Hook.f. et Taylor, London J. Bot. 4: 90. 1845; Phragmicoma microscypha (Hook.f. et Taylor) Mitt., in Melliss, St. Helena: 371. 1875;Mastigolejeunea microscypha (Hook.f. et Taylor) Steph., Sp. Hepat. 4: 762. 1912.
- Acrolejeunea fuscescens Gola, Annali di Botanica, Roma 6: 275. 1907; Ptychocoleus fuscescens (Gola) Step., Sp. Hepat. 5: 32. 1912, hom. illeg. [non (Hampe ex Lehm.) Trevis. 1877].

Leucolejeunea capensis S.W.Arnell, Bot. Notiser 106: 286. 1953.

Plants pale glaucous to, or light to light, green; strong shoots 0.9-1.8 mm wide, irregularly scarcely pinnately branched; stems (88) 108-152 µm in diameter, cortical (7-8) 10-24, medullary cells many, slightly smaller than corticular; ventral merophytes 4-6 cells wide. *Leaves* imbricate, spreading widely, the lobes oval, convex, (522-627) 705-1068 µm long, 465-855 µm wide, the apex rounded, together with ventral margin strongly and conspicuously involute; cells distinctly convex to produce a slightly crenulate leaf margin, median cells 18-24 µm, trigones usually small, oil bodies 1 per cell, rarely with second smaller one; *leaf lobule* oblong to rectangular or ovoid, 302-501 µm long, 2/5-1/2 as long as the lobes, sometimes more, inflated, the lateral free margin strongly involute, bordered by 25-38 cells, keel straight to slightly arched, continuous with the involute distal margin of the lobe, apical tooth variable, usually 1 celled or much reduced, blunt; hyaline papillae 3-4 cells distal to apical tooth. *Underleaves* imbricate, reniform, wider than long, 4-6 times as wide as stem, rarely 3, apex entire, base cordate. *Autoicous*, occasionally paroicous. *Androecia* forming on short lateral branches; bracts 2-6 (10) pairs. *Gynoecia* terminal on

main axis or on short branches with 1-2 pycnolejeuneoid innovations; bracts oblongobovate; bracteole broadly obovate. *Perianth* obovate, emergent, with 5 keels; rostrum prominent, 104-198 μm long.

REPRESENTATIVE SPECIMENS EXAMINED. DR CONGO. Mukaba, Kahuzi-Biega National Park, Mt. Biega, 2.22047 S 28.4101 E 2650 m, 28 Aug. 1991, Pócs T 7184 (EGR). **RWANDA**. Cyangugu, W end of Nyungwe forest near Gisakura, 2.2729 S 29.0505 E 2000 m, 10 Sep. 1990, *Pócs T* 8044 L (EGR); Nyungwe, Rwasenoko, on the drier slopes of valley, 2500 m, 11 Aug. 1991, Fischer E 6101(EGR). UGANDA. Toro, Kibale Forest, North-most part of reserve along Mpanga River, 13km E from Fort Portal, 0.38 N 30.236 E 1450-1460 m, 15 Sep. 1997, Pócs T & Lye KA 97132 AX (EGR). **KENYA**. Mwingi, Mumoni hills at highest peak, 0.3119 S 38.002 E 1745 m, 10 May 2005, Malombe I, Mwachala G & Kirika P 4026 L14A(EA) & Malombe I, Mwachala G & Kirika P 4026 L17(EA); Nuu hill along foot path SE near summit of ridge overlooking Nuu market, 1.0222 S 38.19218 E 1235 m, 21 Oct. 2004, Malombe I & Muasya J 4024 C8a (EA); Kitui, Mutha hill at the summit, South facing side, uphill route from Mutha market, 1.46432 S 38.34461 E 1340 m, 8 Oct. 2004, Malombe I & Muasya J 4022 B1 (EA); Kajiado, Ngong Hills, SW of Nairobi town 1.2385 S 36.383 E 2420-2440 m, 25 Feb. 2004, Pócs T, Pócs S & EA Staff 04011 Y (EA, EGR); Taita Taveta, Kasigau hill, 1250-1400 m, 6 Feb. 1971, Faden RB, Evans A, Kariuki & Smeenk C 112(EGR) & Vuria Hill on the NE ridge of hilltop along Land rover track leading to the summit in plantation forest, 3.2425 S 38.18 E, 2900-1980 m, 31 Mar. 2004, Pócs T, Pócs S, Chuah-Petiot MS & TABC Students 04041 J (EA, EGR). TANZANIA. Arusha, Kitoto, Arusha NP, E slope of Mt. Meru, 2450-2650 m, 25 Dec. 1970, Jones EW & Pócs T 6340 E(EGR); Moshi, Marangu, Mt Kilimanjaro, 1900-2200 m, 2 Jan. 1971, *Pócs T & Jones EW* 6364 B (EA, EGR) & Umbwe, S slopes of Kibo, 3.135 S 37.175 E 1800 m, 30 Dec. 1970, Pócs T 6351 (EA, EGR). Morogoro, Uluguru Mts, top of Bondwa Peak above Morogoro, 2100 m, 29 Aug. 1970, *Pócs T* 6233 T (EGR); Kinole, Midhani, NE of village, 880 m, 8 Feb. 1973, *Pócs T* & Lungwecha M 6881 AJ (EA, EGR); Iringa, Mufindi Escarpment near the Fishing Camp, 1730 m, 16 Dec. 1970, *Pócs T & Jones EW* 6322 A (EGR). **ZIMBABWE**. Umtali, Vumba mts, Cloudland, 5200 ft, 25 Jun. 1955, Schelpe EA 5771 (BO). MOZAMBIQUE. Manica & Sofala, Yonangora mts near Yagago peak, 16.52013 S 34.33019 E 1760 m, 6 Jul. 1955, Schelpe EA 5575 (BO). SOUTH AFRICA. Natal, Eshowe, Dhlinza Forest, 28.8883 S 31.4483 E 550 m, 27 Jan. 1955, Schelpe EA 5171 (BO); Transvaal, Pietersbury,

Woodbush, E 1700 m, 10 Jul. 1956, *Schelpe EA* 6076 (BO) & Zoutpansberg, Shafeera Estates, 1210 m, 7 Jul. 1956, *Schelpe EA* 5994 (BO). Cape, Caledon, Rivierzanderand Mts, Kloof near Zanderand, 11 Feb. 1956, *Esterhuysen E* 25346 (BO) & Knysna, Sourflats Forest, Aug. 1952, *Taylor C* 491 A (BO); Table mts, Cape province, W side, Rock face, S side, 780 m, 15 Apr. 1956, *Esterhuysen E* 25664 (BO); Knysna, Weepwall Forest Reserve, 23 Nov. 1951, Arnell S 1616 (BO, syntype-lectotype by Zhu 2003) & 23 Nov. 1951, *Arnell S* 1492(BO, syntype).

ECOLOGY AND DISTRIBUTION. Common on small branches and twigs of tree and shrubs in open and well-illuminated windy areas where it may form almost pure mats. It is also occasionally corticolous or rarely rupicolous in open scrub and ericaceous woodland. It grows on the branches of closed forest trees where it can sometimes be epiphyllous mixed with other species of Lejeuneaceae. Unlike most of the other species in subg. *Cheilolejeunea*, it seems to be more robust in altitudinal adaptations. Athough common in lowlands, it is also freguent in afromontane and rarely in subalpine vegetation ranging from (540) 770 to 2900 (3900) m a.s.l.

A pantropical species common in eastern (Ethiopia, Uganda, Kenya and Tanzania) and Southern (Malawi, South Africa, St. Helena) Africa including the eastern islands (Mauritius, Madagascar, Reunion). Sparse localities are known from Rwanda, Burundi, DR Congo, Cameroon, Bioko and Cape Verde Is.

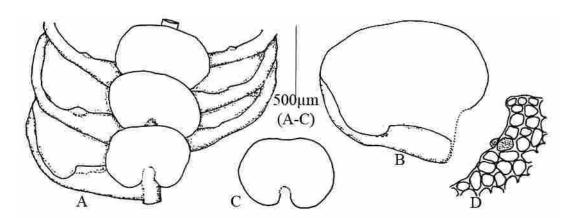


Figure 36. *Cheilolejeunea xanthocarpa* (Lehm. et Lindenb.) Malombe comb. nov. (A) Part of shoot, ventral view; (B) Leaf, ventral view; (C) Underleaf; (D) Lobule apex with hyaline papilla. Modified from Jones, 1973.

NOTES. Cheilolejeunea xanthocarpa, Ch. unciloba, Ch. trapezia and Ch. rotundistipula

may frequently grow mixed together. *Cheilolejeunea xanthocarpa* is however readily recognized even in the field by the closely imbricate suborbicular convex leaves with longly involute apical and ventral margin, the large entire underleaves and strongly involute leaf lobule with short blunt apical tooth. *Cheilolejeunea unciloba* has flattish leaf lobes, which lack the involute postical margin. The leaf lobule free margin is distally flattened with the longly spiniform apical tooth visible and the underleaves are smaller usually suborbicular. It can further be separated from *Ch. trapezia*, which also grows together, by the much arched lobule keels, entire orbicular underleaves and short rostrum. *Cheilolejeunea rotundistipula* can easily be confused with young branches of *Ch. xanthocarpa* owing to the involute postical leaf margin. However, it is recognised by the small size, 2 ventral merophytes, moderately convex leaf lobes which are rotundate and the involute margin hardly reaching the lobe apex, and lobule free margin less involute with distal margin visible and long spiniform apical tooth.

5.7.1 Doubtful and excluded species

1. Cheilolejeunea latiflora Steph., Spec. Hepat. 5, 646. 1914.

Monoicous, olivaceous or yellowish green, tiny, flaccid, grows together with mosses. *Stem* up to 2 cm long, irregularly branching. Stems *leaves* continuous, straight patent, little concave, when flattened, almost round (1 mm long, 0.83 mm wide), symmetric, at base short inserted, dorsal base rounded truncate. Upper cells 18x18 μm, basal ones 18-27 μm, almost no trigones, walls thin. *Lobule* small, 1/6 leaf length, conical ovate, keel obliquely ascendant, almost straight,..., flattened triangular ovate, apex 3 times narrower than the base, rectangularly truncate....*Underleaves* slightly larger, ovato-elliptic, more than three times wider than the stem, transversally inserted, halfway incised with straight sinus and straight, obtuse, lanceolate lobules. *Perianths* with one sided innovation, almost round with narrowing base, rounded apex, small beak, narrow, long decurrent ventral folds and almost obsolete dorsal fold. *Bracts* slightly shorter than the *perianth*, oblong-ovate, obtuse, with half-long, obtuse, linear lobule. *Bracteole* small, obovate, at apex shortly incised with equally long, round lobules. *Male branch* sessile with 3 pairs of bracts.

DISTRIBUTION. Central Africa Republic (Ubangi)

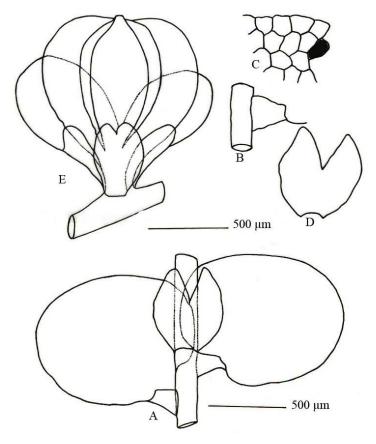


Figure 37. *Cheilolejeunea latiflora* **Steph.** (A) Part of shoot. (B) Lobule. (C) Lobule apex-showing tooth and hyaline papilla. (D) Underleave. (E) Perianth with bracts and bracteole. Redrawn from Stephani 1985, Icones no. 1739.

NOTES. As quoted in Wigginton and Grolle (1996), Jones (1954b) remarks that this taxon 'sounds from the description to be closely allied to, if not identical with, *Ch. newtonii* or *Ch. inflata*'. In addition, the type of trigones 'ca. lacking' as well as confirmed by the original illustrations provided by Stephani (1985, Microfiche 1739) confirm that *Ch. latiflora* is conspecific with *Ch. intertexta*. However, the material was not available for study.

2. Cheilolejeunea laurentii Steph., Spec. Hep. 5: 647. 1914.

Dioicous, small, reddish-yellow, growing together with other liverworts. Stem up to 12 mm long, irregularly many branched. Stem leaves slightly imbricate, straight spreading, slightly concave, when flattened, broad ovate (0.75 mm long, 0.67 mm wide), subsymmetric, with rounded apex,, dorsal base rounded truncate. Upper cells 18x18 μm, basal 18x38 μm, with moderately large trigones. Lobules moderately large, 4x shorter than leaves, subrectangular, slightly longer than wide with straight keel,...., with a narrow, long decurrent fold from the apex to the base......Bracts as long as the perianth, obconic-

obovate with broadly rounded apex. Their lobule shorter than half-length, linear...with rounded apex. *Bracteoles* longer than the *perianth*, oblong-elliptic (0.83 mm long, at middle 0.4 mm wide), at apex to 1/5 length incised, sinus almost straight, lobules triangular acute to apiculate. *Androecia* not seen.

DISTRIBUTION. DR Congo-Zaire, Congo ?Brazaville, Cameroon, Guinea and Principe Island. Nevertheless, Wigginton (2004b) indicates Zaire as the only distribution of the species.

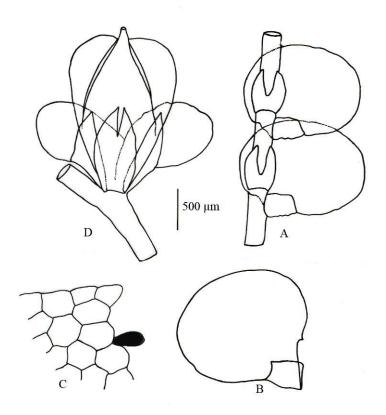


Figure 38. *Cheilolejeunea laurentii* **Steph.** (A) Part of shoot. (B) Lobule. (C) Lobule apex-showing tooth and hyaline papilla. (D) Perianth with bracts and bracteole. Redrawn from Stephani 1985, Icones no. 1741.

NOTES. Jones (1954b) remarks that 'neither the colour..nor the underleaves.. nor the female bracts agree with the genus *Cheilolejeunea*'. Red colour has not been recorded in any other *Cheilolejeunea* species while the underleaves resembles those of *Lejuenea*. I have also not seen such sharp and deep keels at the rare of perianth in *Cheilolejeunea*.

3. Cheilolejeunea rufescens (Lindenb.) Grolle. Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität 31: 212. 1982. Lejeunea rufescens Lindenb. Syn.

NOTES. Grolle (1982) listed *Ch. rufescens* under doubtififul species and suggested it may be endemic to tropical southern America. He stated that "the NY-Isotype makes it obvious that neither the identification by Mitten 1859 p. 235 with *Ch. mimosa* (Hook. f. & Tayl.) Schust., *Ch. implexicaulis* (Hook. F. & Tayl.) Schust. and *Ch. albovirens* (Hook. F. & Tayl.) Hodgs. nor the identification by Stephani 1890, p. 80 with *Ch. trifaria* is true. It is more probable that *Ch. rufescens* is an endemic of the patagonic South America". Wigginton (2004b) recomments for a re-evaluation of specimens from South Africa by Mitten.

4. Cheilolejeunea sp. (=Strepsilejeunea vatovae Gerola). Lavori di Botanica. Istituto Botanico Dell'Universitá di Padova: volume pubblicato in occasione del 70° genetliaco del Prof. G. Gola. Pp 471-487. 1947. Type! Torrente Hallo, pr. Uondo, 22/11/1937 (TO?).

Stem up to 1 cm long, simple or sparsely branched. Leaves inserted to middle, apex obtuse, decurved upper cells 18 μm, with thickened walls, basal cells slightly smaller. Lobules much smaller than lobes, oblong, inflated, shortly ascended, twice as long than large, keel smoothly arcuate, excurrent with wide angle in leaf, apex obliquely truncate, acute or apiculate. Underleaves large, 4 times larger than stem, contiguous, transversely inserted, up to ¼ bifid, with acute sinus and obtuse lobes. Autoicous. Androecia in terminal branches, longly spicate, with 5 bracts. Gynoecium with 2 dichotomous innovations. Perianth small, pyriform, slightly plicate, keels minutely crenulate, the rest smooth, rostrum small; bracts as large as the stem leaves or slightly larger, rotundate, lobule 2x shorter than in stem leaves, subquadrangular, acute; bracteoles similar to those of stem leaves, slightly larger.

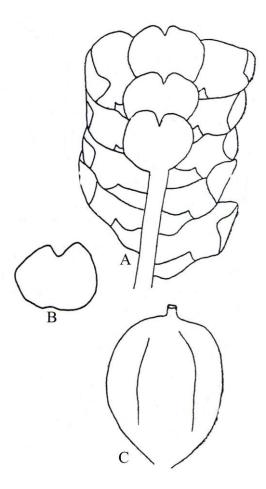


Figure 39. *Cheilolejeunea sp.* (*Strepsilejeunea vatovae* Gerola). (A) Part of shoot, ventral view. (B) Underleaf. (C) Perianth. From Gerola 1947.

NOTES. Described by Gerola (1947) among the hepatics collected by Torrente Hallo from Ethiopia in 1937 near Uondo *ca*. 2500 m a.s.l. The illustration he provided (Gerola, 1947; pg 484, 14a-c) clearly show the species belongs to *Cheilolejeunea* subg. *Strespilejeunea* owing to strongly convex and recurved leaf lobes. Given the original description especially mode of the leaf apex recurving, type of lobules and pyriform perianth, the species may be a form of the robust *Ch. krakakammae*. However, the collections were not available for a detailed species diagnosis.

6. References

- Acebey, A., Gradstein, S.R. & Krömer, T., (2003). Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18 Cambridge University Press.
- Ahonen, I., (2005). Evolutionary relationships of liverworts with a special focus on the order Porellales and the family Lejeuneaceae. Academic dissertation, Department of Biological and Environmental Sciences, University of Helsinki, Finland.
- Althof, A.J., (2005). Human impact of flora and vegetation of Kakamega forest, Kenya: structure, distribution and disturbance of plant communities in an East African rainforest. PhD dissertation, Universität Koblenz-Landau.
- Arnell, S., (1953). Hepaticae collected in South Africa 1951. New and little known species. II. *Bot. Not.* **108**: 309-313.
- Arnell, S., (1955). Notes on South African Hepatics II. Bot. Not. 106: 163-186.
- Arnell, S., (1958). New Hepaticae from Cameroon Mountain. *Svensk Bot. Tidskr.* **52**: 63-67.
- Arnell, S., (1963). Hepaticae of South Africa. Swedish Natural Science Research Council. Stockholm. 411 pp.
- Asthana, G., Srivastava, S.C. & Asthana, A.K., (1995). The genus *Cheilolejeunea* in India. *Lindbergia* **20**: 125-143.
- Augier, J., (1972). Cheilolejeunea diversifolia sp. Nov. Annals de la Faculté des Scinces du Cameroun 11: 65-70.
- Babweteera, F., (2002). Forest canopy closure: implication for seedlings growth and species composition. MSc. Thesis, University of Oxford. UK.
- Bastos, C.J.P. & Gradstein, S.R., (2006). Two new species of *Cheilolejeunea* (Spruce) Schiffn. (Lejeuneaceae) from Brazil: *C. lacerata* sp. nov. and *C. rupestris* sp. nov. *J. Bryol.* **28**: 133-138.
- Bischler, H. (1964). Recherches sur l'anatomie de la tige chez les Lejeuneaceae. III. Les sous-families Lejeuneoideae, tribus Lejeuneeae, et Tuyamaelloideae. *Rév. Bryol. et Lichén.* **30**: 601-675.
- BIOTA, East Africa (2004). Biodiversity in conversion: the influence of fragmentation and disturbance on the biodiversity of East African highland rainforests. *Final Report Phase I, 2001-2004*: 1-16. < http://biota-africa.de/Library/papers_east/final_report.pdf>
- Bizot, M. & Pócs, T. (1983). East African Bryophytes, V. Acta Bot. Acad. Sci. Hung. 28:

15-64.

- Clarke, G.P., (1998). A new regional centre of endemism in Africa. In: C.R. Huxley, J.M. Lock and D.F. Cutler (eds.). Chorology, Taxonomy and ecology of the floras of Africa and Madagascar. Pp. 53-65. Royal Botanic Gardens, Kew.
- Chuah-Petiot, M.S., (2003). Mosses, liverworts & hornworts of Kenya: an illustrated guide with descriptions and figures of over 300 species and keys for identification. Min S. Chuah-Petiot. 1. publ. Nairobi. 273 pp.
- Crandall-Stotler, B., (1972). Morphogenetic patterns of branch formation in the leafy Hepaticae –a résumé. *Bryologist* **75**: 381-403.
- Dauphin, G.L., (2000). The genus *Ceratolejeunea* Jack & Steph. (Hepaticae: Lejeuneaceae) in Tropical America. Dissertation zur Erlangung des Doktorgrades, der Georg-August Universität zu Göttingen.
- Dauphin, G.L. & Gradstein, S.R., (2003). A new species of *Cheilolejeunea* (Spruce) Schiffn. from Panama. *J. Bryol.* **25**: 259-261.
- Eggeling, W., (1947). Observations on the ecology of Budongo rainforest, Uganda. *J. Ecol.* **34**: 20-87.
- Eldridge, D, Skinner, S. & Entwisle, T.J., (2003). NSW biodiversity report: Survey guidelines for non-vascular plants. Botanic Gardens Trust. Sydney.
- Evans, A.W., (1903). Hepaticae of Puerto Rico. 3. *Harpalejeunea, Cyrtolejeunea, Euosmolejeunea* and *Trachylejeunea*. In: R.M., Schuster, 1980a. The Hepaticae and Anthocerotae of North America, Vol. IV. Columbia University Press, New York. 1334 pp.
- Evans, A.W., (1906). Hepaticae of Puerto Rico. VI. *Cheilolejeunea*, *Rectolejeunea* and *Pycnolejeunea*. In: X-L., He, 1996. On the taxonomic significance of lobule characters in the Lejeuneaceae (Hepaticae). *Ann. Bot. Fenn.* **33**: 311-316.
- Evans, A.W., (1908). Hepaticae of Puerto Rico. IX *Brachiolejeunea*, *Ptychocoleus*, *Archilejeunea*, *Leucolejeunea* and *Anoplolejeunea*. *Bull. Torrey Bot. Club*, **35**: 155-179
- Evans, A.W., (1918). -.In: R.M., Schuster, The Hepaticae and Anthocerotae of North America. Vol. IV. Columbia University Press, New York. 1334 pp. 1980a.
- Evans, A.W., (1935). The anatomy of the stem in the Lejeuneaceae. *Bull. Torrey Bot. Club*, **62**: 187-214; 259-280.
- Fischer, E., (2004). Influence of anthropogenic and natural fragmentation on diversity of flora and vegetation in montane rainforests in East Africa. *BIOTA East Africa*,

- *Final Report Phase I*, 2001-2004: 61-72. < http://biota-africa.de/Library/papers_east/final_report.pdf>
- Frahm, J-P., (2003). Climatic habitat differences of epiphytic lichens and bryophytes. *Cryptogamie*, *Bryologie*, **24**(1): 3-14.
- Frahm, J-P. & Gradstein, S.R., (1991). An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeography*, **18**: 669-678.
- Furuki, T & Higuchi, M., (1996). Studies of oil bodies and oil droplets of some Hepatics (Jungermanniales) from New Caledonia. *Bull. Nat. Sci. Mus., Tokyo, Ser. B*, **22**(2): 59-75.
- Gerola, F.M., (1947). Epatiche deli'Abissinia meridionale. Lavori di Botanica. Istituto Botanico Dell'Universitá di Padova: volume pubblicato in occasione del 70° genetliaco del Prof. G. Gola. Pp 471-487.
- Goebel, K., (1930). Organographie die Pflanzen, zweiter Teil. In: G. Dauphin & S.R. Gradstein. A new species of *Cheilolejeunea* (Spruce) Schiffn. from Panama. *J. Bryol.* **25**: 259-261. 2003.
- Gotsche, C.M., Lindenberg, J.B.G. & Nees, C.G., (1945). *Syn. Hepat.* pp 834, p 353. Hamburg.
- Gradstein, S.R., (1985). A guide to the holostipous Lejeuneaceae. *Beih. Nova Hedwigia* **80**: 13-29.
- Gradstein, S.R., (1992). The vanishing Tropical Rain Forest as an environment for bryophytes and lichens. In: J.W. Bates and A.R. Farmer (eds), Bryophytes and lichens in a Changing Environment, p. 232-256. Oxford University Press.
- Gradstein, S.R., (1995). Bryophyte diversity of the tropical rainforests. *Archs Sci. Genéva*. **48**(1): 91-96.
- Gradstein, S. R. & Costa, D.P., (2003). The Liverworts and Hornworts of Brazil. *Memoirs New York Bot. Garden* 87: 1-317.
- Gradstein, S.R. & Pócs, T., (1989). Bryophytes. *Tropical Rain Forest Ecosystems*. H. Lieth and M.J.A Werger (eds). Elsevier Science Publishers B. V., Amsterdam.
- Gradstein, S.R., Matsuda, R. & Asakawa, Y., (1981). Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. *J. Hattori Bot. Lab.* **50**: 231-248.
- Gradstein, S.R., Pócs, T. & Vána, J. (1984). Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Acad. Sci. Hung.* **29**: 127-171.
- Gradstein, S.R., Churchill, S.P. & Salazar Allen, N., (2001). Guide to the bryophytes of tropical America. *Memoirs New York Bot. Garden* **86**: 1-577.

- Gradstein, S.R., Cleef, A.M. & Fulford, M.H., (1977). Studies on Colombian cryptogams

 Hepaticae oil body structure and ecological distribution of selected species of

 tropical Andean Jungermanniales. Reprinted from *Proceedings of the Koninklijke*Nederlandse Akademie van Wetenschappen, Amsterdam, series C, **80** (5).
- Gradstein, S.R., Grolle, R. & Schäfer-Verwimp, A., (1993). Two interesting species of Lejeuneaceae from Brazil. *J. Hattori Bot. Lab.* **74**: 59-70.
- Gradstein, S.R., Reiner-Drehwald, M.E. & Schneider, H., (2003). A phylogenetic analysis of the genera of Lejeuneaceae (Hepaticae). *Bot. J. Linnean. Soc.* **143**: 391-410.
- Grolle, R., (1979). Miscellanea Hepatocologica, 191-200. J. Hattori Bot. Lab. 46: 337-355.
- Grolle, R., (1980). Uber Harpalejeunea in Australasien. J. Hattori Bot. Lab. 47: 237-244.
- Grolle, R., (1982). Übersicht der Lejeuneaceae in Tasmanien. Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität. 31: 207--227.
- Grolle, R., (1988). Verzeichnis der Lebermoose von Ascension Island nebst Beschreibung von *Cheilolejeunea ascensionis* (Hook. f. et Tayl.) Grolle, comb. nov. *Haussknechtia* 4: 43--49.
- Grolle, R., (1995). The Hepaticae and Anthocerotae of the East African islands. An annotated catalogue. *Bryophyt. Biblioth.* **48**: 1-178.
- Grolle, R. & Piipo, S., (1984). Annotated catalogue of Western Melanesian bryophytes. I. *Acta Bot. Fenn.* **125**: 1-86.
- Grolle, R., Zhu, R.-L. & Gradstein, S. R., (2002 "2001"). On *Cyrtolejeunea* A. Evans (Lejeuneaceae, Hepaticae). *Taxon* **50**: 1067-1074.
- Grubb, P.J. & Whitmore, T., (1966). A comparison of montane and lowland rainforest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *J. Ecol.* **54**: 303-333.
- He, X.-L., (1995). Type studies on *Pycnolejeunea* (Lejeuneaceae, Hepaticae), I. *Ann. Bot. Fenn.* **32**: 251-258.
- He, X-L., (1996a). Type studies on *Pycnolejeunea* (Lejeuneaceae, Hepaticae), II. *Ann. Bot. Fenn.* **33**: 51-58.
- He, X-L., (1996b). On the taxonomic significance of lobule characters in the Lejeuneaceae (Hepaticae). *Ann. Bot. Fenn.* **33**: 311-316.
- Henning, W., (1966). *Phylogenetic Systematics*. Translated by D.D. Davies and R. Zangerl. Univ. Illinois Press, Urbana.
- Howard, P.C., (1991). Nature conservation in Uganda's Tropical Forest reserves. IUCN, Gland Switzerland.

- Jessen, R.J., (2006). Commentary: reply to Henderson on delimiting species for taxonomic analysis. *Syst. Bot.* 31(2) 432-435.
- Jones, E.W., (1954a). African hepatics VI. The genus *Euosmolejeunea*. *Trans. British Bot. Soc.* **2**: 375-379.
- Jones, E.W., (1954b). African hepatics VII. The genus *Cheilolejeunea*. *Trans. British Bot. Soc.* **2**: 380-395.
- Jones, E.W., (1973 "1974"). African Hepatics XXIV. Lejeuneaceae: some new or little-known species and extensions of range. *J. Bryol.* **7**: 545-561.
- Jones, E.W., (1976). African Hepatics XXIX. Some new or little-known species and extensions of range. *J. Bryol.* **9**: 43-54.
- Jones, E.W., (1979). African hepatics XXXI. Rare or little known Lejeuneaceae and extensions of range. *J. Bryol.* **10**: 387-400.
- Jones E.W., (1982). African Hepatics XXXIII. Some new Lejeuneaceae. *J. Bryol.* **12**: 37-48.
- Jones, E.W., (1984). Notes on the lobule in the Lejeuneoideae. *Cryptog.*, *Bryol. Lichénol.* 5, 1-2: 159-171.
- Jones E.W., (1985). African Hepatics XXXIV. Little-known or new Lejeuneaceae. *J. Bryol.* **13**: 385-398.
- Jones, E.W., (1988). African Hepatics XXXVIII. *Cheilolejeunea* subgenus *Strepsilejeunea* (Spruce) Schust. with special reference to East Africa. *J. Bryol.* **15**: 149-160.
- Jones, E.W. & Harrington, A.J., (1983). The hepatics of Sierra Leone and Ghana. *Bot. Bull. Br. Nat. Hist.* 11(3): 215-289.
- Jovet-Ast, S. & Vanden Berghen, C., (1951). *Cheilolejeunea tisserantii* sp. nov. V.B. et J.-A. *Rev. Bryol. Lichen.* **22**, 105-107.
- Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. & Donoghue, M.J., (2002). Plant systematics, a phylogenetic approach (2nd edition). Sinauer associates, Inc. Massachusetts, USA.
- Kachroo, P. & Schuster, R.M., (1961). The genus *Pycnolejeunea* and its affinities to *Cheilolejeunea*, *Euosmolejeunea*, *Nipponolejeunea*, *Tuyamaella*, *Siphonolejeunea* and *Strepsilejeunea*. *Bot. J. Linnean Soc.* **56**: 475-511.
- Karani, P.K, Kiwanuka, L.S. & Sizomu-Kagolo, M.E., (1997). Forest management for Budongo Forest Reserve July 1997 to June 2007. Forest Department, Kampala, Uganda.
- KIFCON, (1994). Kakamega Forest- the official guide. Kenya Indigenous Forest

- Conservation programme, Nairobi, Kenya.
- Kis, G. & Pócs, T., (1997). Oil body studies on African Hepaticae. *J. Hattori Bot. Lab.* No. **81**: 175-242.
- Kokwaro, J.O., (1988). Conservation status of the Kakamega Forest in Kenya: The easternmost relic of the equatorial rainforests of Africa. *Monographs in Syst. Bot.*, *Missouri Bot. Garden*, **25**: 471-489.
- Maddison, D.R., (1991). The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* **40**, 315-328.
- Manyanga, P & Perold S.M., (2004). A checklist of Zimbabwean bryophytes. South African Botanical Diversity Network Report No. 21.
- Menzel, M., (1988). Annotated catalogue of the Hepaticae and Anthocerotae of Borneo. *J. Hattori Bot. Lab.* **65**: 145-206.
- Mitchell, N., (2004). The exploitation and disturbance history of Kakamega forest, Western Kenya. BIOTA East Report No 1. Bielefelder Ökologische Beiträge, Band 20, Bleher, B. & Dalitz, H. (eds.).
- Mizutani, M., (1961). A revision of Japanese Lejeuneaceae. *J. Hattori Bot. Lab.* **24**: 115-302.
- Mizutani, M., (1970). Branching types of Lejeuneaceae. *Miscellanea bryological et lichenological* **5**:81-90.
- Mizutani, M., (1982). Notes on the Lejeuneaceae. 6. Japanese species of the genus *Cheilolejeunea*. *J. Hattori Bot. Lab.* **51**: 151-173.
- Mutangah, J.G., (1996). An investigation of vegetation status and process in relation to human disturbance in Kakamega forest, western Kenya. Ph.D. thesis, University of Wales, Aberystwyth, Great Britain.
- Pessin, L.J., (1922). Epiphyllous plants and certain regions in Jamaica. In: S.O. Olarinmoye (1975). Ecological studies on epiphyllous liverworts in western Nigeria: I notes in distribution. Tome 41. Fasc. 1.
- Piipo, S., (1990). Annotated catalogue of Chinese Hepaticae and Anthocerotae. *J. Hattori Bot. Lab.* **68**: 1-192.
- Pócs, T., (1980). The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Acad. Sci. Hung.* **26:** 143-167.
- Pócs, T., (1985). East African bryophytes, VII: the hepaticae of the Usambara Rain Forest Project Expedition. *Acta Bot. Hung.* **31**(1-4): 113-133.

- Pócs, T., (1992). Correlations between the tropical African and Asia bryoflora. II. *Bryobrothera*, **1**: 35-47.
- Pócs, T., (1994). Taxonomic results of the BRYOTROP Expedition to Zaire and Rwanda 28. Lejeuneaceae, a ramicolous collection. *Trop. Bryol.* **9**: 131-136.
- Pócs. T., (1996). Epiphyllous liverwort diversity at worldwide level and its threat and conservation. *Anales Inst. Biol. Uni. Nac.* Autón, México, *Ser. Bot.* **67**: 109-127.
- Pócs, T., (1999). New records and additions of the Hepatic flora of Uganda 2. *Trop. Bryol.* **17**: 23-33.
- Pócs, T., (2006). Bryophyte colonization and speciation on Oceanic islands, an overview. *Lindbergia*, **31**: 54-62.
- Pócs, T. & Tran Ninh (2005). Contribution to the bryoflora of Vietnam, VI. On the liverwort flora of Vu Quang Nature Reserve. *Acta Bot. Hung.* **47** (1-2): 151-171.
- Plumptre, A.J., (1996). Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest. Ecol. Man.* **89**:101-113.
- Reiner-Drehwald, M.E., (2006). The studies on Neotropical Lejeuneaceae (Jungermanniopsida). *Cheilolejeunea* and *Lepidolejeunea*. *Nova Hedwigia*, **83** (3-4): 473-482.
- Renner, M.A.M. & Glenny, D., (2003). A new *Cheilolejeunea* (Marchantiopsida: Lejeuneaceae) from montane forests in New Zealand. *J. Bryol.* **25**: 169-174.
- Reynolds, V., (2005). The Chimpanzees of the Budongo forest: ecology, behaviour and conservation. Oxford University Press. 297 pp.
- Richards, P.W., (1984). The ecology of tropical forest bryophytes. In: New Manual of Bryology (R.M. Schuster, ed.), **2**: 1233-1270.
- Schiffner, V., (1893). The oil bodies of the Hepaticae. II. Lejeuneaceae. In A. Engler & K. *Prantl, Nat. Pflanzenfam.* **1** (3): 118, 124.
- Schiffner, V., (1893). Jungermanniaceae Akroginae. In: Engler A. & K. Prantl (eds.), Die *Naturlichen Pflanzenfamilien* **1** (3): 124.
- Schofield, W.B. & Crum, H.A., (1972). Disjunctions in bryophytes. *Ann. Missouri Bot. Garden*, **59**, 174-202.
- Schuster, R.M., (1955). North American Lejeuneaceae, I. Introduction: Keys to Subfamilies and Genera. *J. Elisha Mitschell Scientific Society*. **71**: 106-126.
- Schuster, R.M., (1963). An annotated synopsis of the genera and subgenera of Lejeuneaceae. *Beih. Nova Hedwigia* **9**: 1-203.
- Schuster, R.M., (1966). The Hepaticae and Anthocerotae of North America. Vol. 1. XVII.

- Columbia University Press, New York. 802 pp.
- Schuster, R.M., (1980a). The Hepaticae and Anthocerotae of North America. Vol. IV. Columbia University Press, New York. 1334 pp.
- Schuster, R.M., (1980b). New combinations and taxa of Hepaticae, I. *Phytologia* **45**: 415-437.
- Schuster, R.M., (1992). The oil-bodies of the Hepaticae. II. Lejeuneaceae (part 2). *J. Hattori Bot. Lab.* **72**: 163-359.
- Schuster, R.M., (2001). Studies on Lejeuneaceae, IV. On the circumscription and subdivision of the subfamily Lejeuneoideae. *J. Hattori Bot. Lab.* **91**: 137-172.
- Shaw, A.J., (2001). Biogeographic patterns and cryptic speciation in bryophytes. *J. Biogeography*, **28**: 253-261.
- Shaw, A.J. & Goffinet, B., (2000). Bryophyte biology. Cambridge University Press. Pp 476.
- Shaw, J. & Renzaglia, K., (2004). Phylogeny and diversification of bryophytes. *Am. J. Botany*, **91** (10) 1557-1581.

 http://www.amjbot.org/cgi/content/abstract/91/10/1557
- Sneath, P.H.A., (1976). Phenetic taxonomy at the species level and above. *Taxon* **25**:437-450.
- Sneath, P.H.A. & Sokal, R.R., (1973). Principles of numerical taxonomy. W.H. Freeman. San Francisco.?? Pp.
- So, M.L. & Zhu, R.-L., (1996). Two newly recorded species of the genus *Cheilolejeunea* (Lejeuneaceae, Hepaticae) in Hong Kong and China. *Bot. Bull. Acad. Sin.*, **37**: 275-280.
- Sokal, R.R. & Sneath, P.H.A., (1963). Principles of numerical taxonomy. W.H. Freeman. San Francisco. ?? pp.
- Spruce, R., (1884-85). Hepaticae amazonicae et andinae. *Trans. Proc. Soc. Bot.* Edinburgh. **15**. I-IX, 1-588.
- Stace, C., (1989). Plant taxonomy and biosystematics. Cambridge University Press. 264 pp.
- Stearn, W.T., (2004!). Botanical Latin Illustrated, 4th ed. Timber Press, 560 pp.
- Stephani, F., (1912-1914). Species Hepaticarum. V. Genéva & Bale. 1044 pp.
- Stephani, F., (1923). Species Hepaticarum. VI. Inst. Bot. Univ. Genéva, 763 pp.
- Stephani, F., (1985). Icones Hepaticarum, Microfiches. Leiden: International Documentation Company.

- Stuessy, T.F., (1990). Plant taxonomy: the systematic evaluation of comparative data. New York: Columbia University Press.
- Swofford, D.L., (1999). PAUP: Phylogenetic Analysis Using Parsimony, version 4. 0b4a. Computer Program distributed by Illinois Natural History Survey, Champaign, Illinois.
- Thiers, B. M., (1985). Branching in Lejeuneaceae, III. Nova Hedwigia Beih. 80: 31-61.
- Thiers, B.M., (1992a). A re-evaluation of *Cheilolejeunea* subgenus *Xenolejeunea*. *Trop. Bryol.* **5**: 10-21.
- Thiers, B.M., (1992b). New species of *Cheilolejeunea* and *Otolejeunea* (Hepaticae; Lejeuneaceae) from Australia. *Brittonia*, 44(2): 160-165.
- Thiers, B.M., (1997). *Cheilolejeunea* in Australia: Description of new taxa and Key. J. *Hattori Bot. Lab.* **82**: 321-382
- Tixier, P., (1995). Résultats taxonomiques de l'éxpédition BRYOTROP au Zaire et Rwanda. 30. Bryophytes epiphylls (récoltes de E. Fischer). *Trop. Bryol.* **11**: 11-76.
- Tsingalia, M.H., (1990). Habitat disturbance, severity and patterns of abundance in Kakamega Forest, Western Kenya. *Afr. J. Ecol.*, **28**: 213-226.
- Vanden Berghen, C., (1951d). Note sur quelques hépatiques récoltées par R.E. et T. Fries en 1922 au Mt. Kenya. *Svensk. Bot. Tidskr.* **45**: 362-367.
- Vanden Berghen, C., (1953d). Quelques hépatiques récoltées par O. Hedberg sur les montagnes de l'Afrique orintale. *Svensk. Bot. Tidskr.* **47**: 263-293.
- Vanden Berghen, C., (1960b). Hépatiques récoltées par le Dr J.J. Symoens dans la Région Péritanganyikaise. *Bull. Soc. Belg.* **92**: 111-138.
- Vanden Berghen, C., (1965). Hépatiques récoltées par le Dr J.J. Symoens dans la Région Péritanganyikaise. *Bull. Soc. Belg.* **92**: 111-138.
- Wagner, W.H., (1980). Origin and philosophy of the groundplan-divergence method of cladistics. *Syst. Bot.*, **5**: 173-193.
- Wagner, T., (2001). Seasonal changes in the canopy arthropod fauna in Rinorea beniensis in Budongo Forest, Uganda. *Pl. Ecol.* **153**: 169-178.
- Weis, G., (1999). Neue Untersuchungen zur Sporophytenmorphologie bei Lejeuneaceae und Jubulaceae (Hepaticae). *Syst. Georg. Pl.* **68**: 137-146.
- White, F., (1983). The vegetation of Africa: a descriptive memoir to accompany the UNESCO/ AETFAT/UNSO Vegetation map of Africa. Natural Resource Research 20. UNESCO, Paris.
- Wigginton, E.W., (ed.) (2004a) E.W. Jones's Liverwort and Hornwort Flora of West

- Africa. Scripta Botanica Belgica, 30: i-vii, 1-443.
- Wigginton, M.J., (2004b). Checklists and distribution of liverworts and hornworts of subsaharan Africa, including the East African Islands. Tropical Bryology Research reports no. 5 http://www.tropicalbryologyresearchreports.co.uk.
- Wigginton, M.J. & Grolle, R., (1996). Catalogue of the Hepaticae and Anthocerotae of Sub-Saharan Africa. *Bryophytorum Bibliotheca*, Band **50**. 267 pp.
- Wilson, R., Gradstein, S.R., Schneider, H & Heinrichs, J., (2007a). Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): Evidence for four main lineages. Mol. Phylogenet. Evol. 43: 270-282.
- Wilson, R., Heinrichs, J., Hentschel, J., Gradstein, S.R., Schneider, H., (2007b). Steady diversification of derived liverworts under tertiary climatic fluctuations. *Biol. Lett.* **3**: 566-569. http://www.journals.royalsoc.ac.uk.
- Zanten, B.O. & Pócs, T., (1981). Distribution and dispersal of bryophytes. In Schultze-Motel, W. (ed.): *Advances in Bryology* 1. J.Cramer, Vaduz, 479-562.
- Zhu, R.-L., (2006). Taxonomy and distribution of *Cheilolejeunea krakakammae* (Lejeuneaceae, Jungermanniopsida, Marchantiophyta), with a description and illustrations of *Cheilolejeunea laevicalyx* from Bolivia, Colombia and Ecuador. *Nova Hedwigia* 83(1-2): 187-198.
- Zhu, R.-L. & Grolle, R., (2004). Nomenclatural notes on *Cheilolejeunea inaequitexta* and *C. trapezia* (Lejeuneaceae, Hepaticae). *Ann. Bot. Fenn.* **41**: 445-447.
- Zhu, R.-L. & So, M. L., (1996). Mosses and Liverworts of Hong Kong. 2. Heavenly People Depot. Hong Kong.
- Zhu, R.-L. & So, M. L. (1999). Taxonomic notes and phytogeography of *Cheilolejeunea* pluriplicata (Hepaticae, Lejeuneaceae). *Bryologist*, 102 (1): 45-49.
- Zhu, R.-L. & So, M. L., (2001). Epiphyllous liverworts of China. –*Beih. Nova Hedwigia* **121**: 1-418.
- Zhu, R.-L., So, M. L. & Grolle, R., (2000). *Cheilolejeunea gaoi* (Hepaticae, Lejeuneaceae), a new species from China. *Bryologist* **103**: 499-502.
- Zhu, R.-L., So, M. L. & Wang, Y.-F., (2002). The genus *Cheilolejeunea* (Hepaticae, Lejeuneaceae) in China. *Nova Hedwigia* **75**: 387-408.

Appendices

Appendix I. Data matrix used in phenetic analysis Characters/ states

	Characters/ states																															
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3
species	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Ch. convexa	2	0	0	0	0	1	2	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1_	2	0	0	1	1	0	0
Ch. cordistipula	2	1	1	0	0	1	2	1	0	0	1	1	1	0	0	1	0	1	1	2	0	0	1	1	1	2	0	0	1	1	1	1
Ch. decursiva	2	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1	1	1	1	0
Ch. diversifolia	2	0	0	0	0	1	2	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	2	1	0	1	0	0	0
Ch. exinnovata	2	0	0	0	0	1	2	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	2	2	1	0	1	0	0	0
Ch. fischeri	2	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	1	0	0
Ch. intertexta	2	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	0	1	0
Ch. krakakammae	2	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	2	1	1	1	1	1	1
Ch. montagnei	2	0	1	0	0	1	2	1	0	1	1	1	0	0	0	1	0	0	0	1	0	1	1	0	0	2	0	0	0	1	1	0
Ch. ngongensis	2	1	0	0	0	1	2	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	2	1	0	0	0	1	0
Ch.																																
omphalogastria	2	0	1	0	0	1	2	1	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	0
Ch. pluriplicata	2	0	0	0	0	1	2	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1_	1	1_	2	1	0	1	1	1	1
Ch. pocsii	2	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	2	1	0	1	1	1	1
Ch. serpentina	2	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1	1	1	1	1	0
Ch. trapezia	2	1	1	0	0	1	2	0	1	1	0	1	1	0	0	0	1	1	0	2	0	0	0	1	2	2	1	1	1	1	1	0
Ch. trifaria	2	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	1	1	1	0	0
Ch. ulugurica	2	0	0	0	0	1	2	0	1	1	0	0	1	0	0	0	1	1	1	1	0	0	1	1	1	2	0	0	0	1	0	0
Ch. usambarana	2	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	2	1	1	1	1	1	0
Ch. rotundistipula	2	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	1	0	2	0	0	1	0	0	2	1	0	1	0	1	0
Ch. camerunensis	2	0	0	0	0	1	2	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	1	1	1	2	0	0	1	1	0	0
Ch. ruwenzorensis	2	0	1	0	0	1	2	1	0	0	1	1	1	0	0	1	0	1	0	2	0	0	1	1	1	2	0	0	0	0	1	0
L. unciloba	2	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	2	0	0	1	0	0	2	1	0	1	1	0	0
L. xanthocarpa	2	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	2	0	1	1	0	0	2	1	1	1	1	1	1

Appendix II. Detailed procedure and results of phylogenetic analysis

```
P A U P *
Version 4.0b4a for Macintosh
Tuesday, July 25, 2000 12:23 pm
```

This copy registered to: Eric Knox
Rutgers University
(serial number = B413749)

This is a beta-test version. It will expire on 15 Jan 2001. Please report any crashes, apparent calculation errors, or other anomalous results. There are no restrictions on publication of results obtained with this version, but you should check the WWW site frequently for bug announcements and/or updated versions. See the README file on the distribution media for details.

Processing of file "cheilolejeunea4.paup" begins...

Warning: File does not begin with '#NEXUS'.

Data matrix has 29 taxa, 27 characters Valid character-state symbols: 0123456789 Missing data identified by '?' Gaps identified by '-'

Processing of file "cheilolejeunea4.paup" completed.

Processing of file "cheilolejeunea4.paup" begins...

Warning: File does not begin with '#NEXUS'.

Data matrix has 29 taxa, 27 characters Valid character-state symbols: 0123456789 Missing data identified by '?' Gaps identified by '-'

Processing of file "cheilolejeunea4.paup" completed.

Input data matrix:

Taxon/Node	111111111122222222 123456789012345678901234567
Chconv	200001210010000101000001120
Chcord	211001210011100101120011120
Chdecu	200001110100000000000001121
Chdive	200001211100000001000001221
Chexin	200001201100100000010011221
Chfisc	200001210010000000010011120
Chinte	2000012011000000000000001221
Chkrak	200001210010000000010011121
Chmont	201001210111000100010110020
Chngon	210001210011100000010011121
Chomph	201001210011000100010111120
Chplur	200001210010000100010011121
Chpocs	200001010010000100010011121
Chserp	200001010100000000000011121
Chtrap	211001201101100011020001221

```
200001101100000100000111120
Chtrif
           200001201100100011110011120
Chulua
           200001110010000100010011121
Chusam
           200001111100100011020010021
Chrotu
           200001210011100100010011120
Chcame
           201001210011100101020011120
Chruwe
           200001201001211010001011221
Dpocsi
           211111101101100011020010021
Luncil
            2111111111111100011020110021
Lxanth
Lamani
            201000210010110000001111121
Lflava
            200000210100110000001001120
Olunul
           011000210001010210001010011
Aabbre
           011111211101110200001010011
           1111112111010103110??001101
Ferico
Outgroup status changed:
   4 taxa transferred to outgroup
   Total number of taxa now in outgroup = 4
   Number of ingroup taxa = 25
Heuristic search settings:
   Optimality criterion = maximum parsimony
      Character-status summary:
        Of 27 total characters:
          All characters are of type 'unord'
          All characters have equal weight
          1 character is parsimony-uninformative
         Number of parsimony-informative characters = 26
      Gaps are treated as "missing"
   Starting tree(s) obtained via stepwise addition
   Addition sequence: random
      Number of replicates = 10
      Starting seed = 1118356021
   Number of trees held at each step during stepwise addition = 1
   Branch-swapping algorithm: tree-bisection-reconnection (TBR)
   Steepest descent option not in effect
   No more than 100000 trees of score (length) greater than or equal to 1
will be saved in
     each replicate
   Initial 'MaxTrees' setting = 100 (will be auto-increased by 100)
   Branches collapsed (creating polytomies) if maximum branch length is
zero
   'MulTrees' option in effect
   Topological constraints not enforced
   Trees are unrooted
Heuristic search completed
   Total number of rearrangements tried = 68160211
   Score of best tree(s) found = 101
   Number of trees retained = 2968
   Time used = 00:07:53.5
Tree-island profile:
```

Island	Size	First tree	Last tree	Score	First replicate	Times hit
1 2	2968 170	1 -	2968 -	101 102	1 2	9

Lengths and fit measures of trees in memory: Character-status summary:

```
Of 27 total characters:

All characters are of type 'unord'
All characters have equal weight

1 character is parsimony-uninformative
Number of parsimony-informative characters = 26
Gaps are treated as "missing"

Sum of min. possible lengths = 35
Sum of max. possible lengths = 219

Tree # 1
Length 101
CI 0.347
RI 0.641
```

Tree lengths constant over trees for all characters.

Tree description:

```
Unrooted tree(s) rooted using outgroup method
Optimality criterion = maximum parsimony
Character-status summary:
    Of 27 total characters:
    All characters are of type 'unord'
    All characters have equal weight
    1 character is parsimony-uninformative
    Number of parsimony-informative characters = 26
Gaps are treated as "missing"
Character-state optimization: Accelerated transformation (ACCTRAN)
```

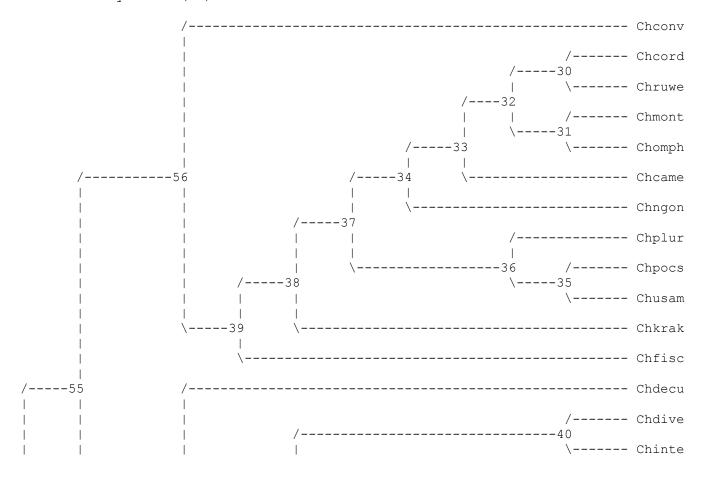
Tree number 1 (rooted using user-specified outgroup)

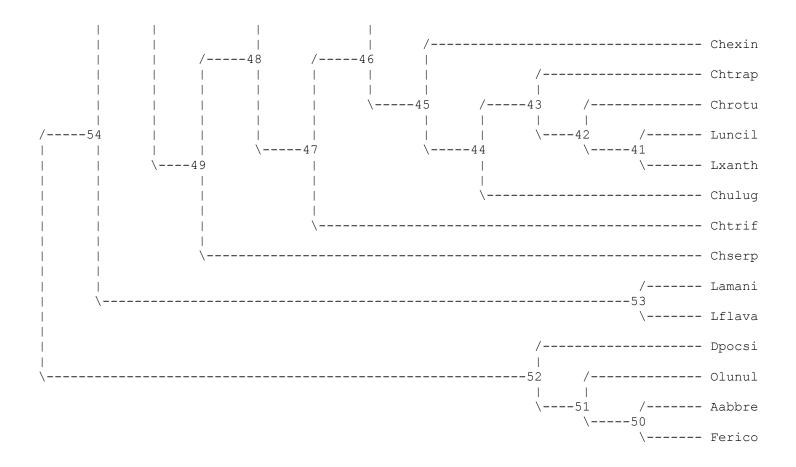
Reconstructed states for internal nodes:

Taxon/Node	111111111122222222 123456789012345678901234567
30	201001210011100101020011120
31	201001210011000100010111120
32	201001210011100100010011120
33	200001210011100100010011120
34	200001210011100100010011121
35	200001010010000100010011121
36	200001210010000100010011121
37	200001210010000100010011121
38	200001210010000000010011121
39	200001210010000000010011120
40	2000012011000000000000001221
41	211111111101100011020010021
42	211001111101100011020010021
43	211001201101100011020011221
44	200001201100100011010011221
45	200001201100100000010011221
46	200001201100000000000011221
47	200001101100000000000011121
48	200001110100000000000011121
49	200001010100000000000011121
50	011111211101010210001010011
51	011001210001010210001010011
52	200001210001010010001011021
53	200000210000110000001011121

54	200001210000010000001011121
55	200001210000000000000011121
56	200001210010000000000011120

Tree length = 101 Consistency index (CI) = 0.3465 Homoplasy index (HI) = 0.6535 CI excluding uninformative characters = 0.3400 HI excluding uninformative characters = 0.6600 Retention index (RI) = 0.6413 Rescaled consistency index (RC) = 0.2222





Apomorphy lists:

Branch	Character	Steps	CI	Change
node_52 <-> node_54	12 17 25	1 1 1	0.250 0.333 0.286	1 <=> 0 1 <=> 0 0 <-> 1
node_54> node_55	14 21	1	1.000	1 ==> 0 1 ==> 0
node_55> node_56	11 27	1 1	0.333	0 ==> 1 1> 0
node_56> Chconv	16 18 23	1 1 1	0.500 0.200 0.167	0 ==> 1 0 ==> 1 1 ==> 0
node_56> node_39 node 39> node 38	20 27	1 1	0.500 0.167	0 ==> 1 0> 1
node_38> node_37	16	1	0.500	0> 1
node_37> node_34	12	1	0.250	0 ==> 1
	13	1	0.333	0 ==> 1
node 34> node 33	27	1	0.167	1 ==> 0
node 33> node 32	3	1	0.200	0 ==> 1
node 32> node 30	18	1	0.200	0 ==> 1
110de_32				
	20	1	0.500	1 ==> 2
node_30> Chcord	2	1	0.200	0 ==> 1
	19	1	0.500	0 ==> 1
node_32> node_31	13	1	0.333	1 ==> 0
	22	1	0.250	0 ==> 1
<pre>node_31> Chmont</pre>	10	1	0.250	0 ==> 1
_	24	1	0.250	1 ==> 0
	25	1	0.286	1 ==> 0
node 34> Chngon	2	1	0.200	0 ==> 1
noue_or / omigen	16	1	0.500	1> 0
nodo 36> nodo 35	7	1	0.333	2> 0
node_36> node_35		1		0> 1
node_35> Chusam	7		0.333	
node_55> node_49	7	1	0.333	2> 0
	10	1	0.250	0 ==> 1
node_49> node_48	7	1	0.333	0> 1
node_48> Chdecu	23	1	0.167	1 ==> 0
node_48> node_47	8	1	0.200	1 ==> 0
	9	1	0.333	0 ==> 1
node_47> node_46	7	1	0.333	1> 2
	25	1	0.286	1 ==> 2
node 46> node 40	23	1	0.167	1 ==> 0
node 40> Chdive	8	1	0.200	0 ==> 1
node_40 > charve	18	1	0.200	0 ==> 1
nodo 16 > nodo 15				0 ==> 1
node_46> node_45	13	1	0.333	
	20	1	0.500	
node_45> node_44	17	1	0.333	
	18	1	0.200	0 ==> 1
node_44> node_43	2	1	0.200	0> 1
	3	1	0.200	0> 1
	12	1	0.250	0> 1
	20	1	0.500	1 ==> 2
node 43> Chtrap	23	1	0.167	1 ==> 0
node 43> node 42	7	1	0.333	2 ==> 1
1000_12	8	1		0> 1
		1		1 ==> 0
	24		0.250	
	25	1	0.286	2 ==> 0
node_42> Chrotu	2	1	0.200	1> 0
	3	1	0.200	1> 0

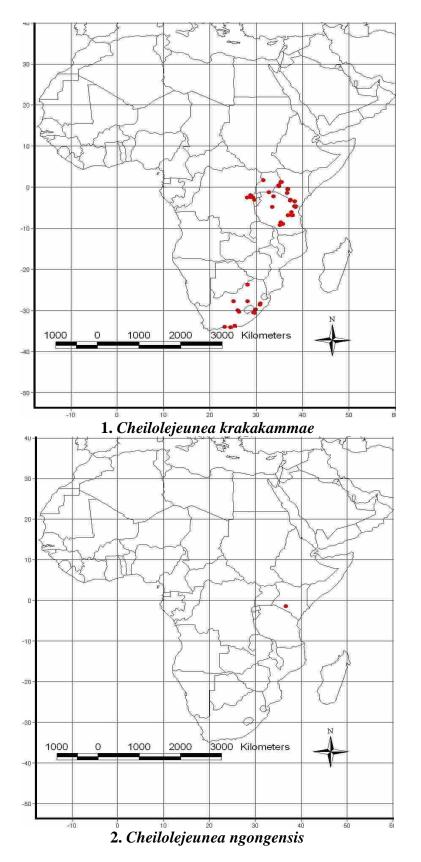
	12	1	0.250	1> 0
node 42> node 41	4	1	0.500	0 ==> 1
	5	1	0.500	0 ==> 1
node 41> Luncil	8	1	0.200	1> 0
node 41> Lxanth	11	1	0.333	0 ==> 1
_	22	1	0.250	0 ==> 1
node_44> Chulug	19	1	0.500	0 ==> 1
	25	1	0.286	2 ==> 1
	27	1	0.167	1 ==> 0
node_47> Chtrif	16	1	0.500	0 ==> 1
	22	1	0.250	0 ==> 1
1 54 > 1 50	27	1	0.167	1 ==> 0
node_54> node_53	6	1	0.500	1 ==> 0
node 53> Lamani	13 3	1 1	0.333	0 ==> 1 0 ==> 1
node_55> Lamani	11	1	0.333	0 ==> 1
	22	1	0.250	0 ==> 1
node 53> Lflava	10	1	0.250	0 ==> 1
nede_ee / EFFava	23	1	0.167	1 ==> 0
	27	1	0.167	1 ==> 0
node 52> Dpocsi	8	1	0.200	1 ==> 0
	9	1	0.333	0> 1
	13	1	0.333	0 ==> 2
	15	1	1.000	0 ==> 1
	25	1	0.286	0> 2
node_52> node_51	1	1	1.000	2 ==> 0
	2	1	0.200	0 ==> 1
	3	1	0.200	0 ==> 1
	16	1	0.500	0 ==> 2
	24	1	0.250	1> 0
nodo E1 > Olympi	26 6	1 1	1.000	2 ==> 1 1 ==> 0
node_51> Olunul node 51> node 50	4	1	0.500	1 ==> 0 0 ==> 1
110de_31> 110de_30	5	1	0.500	0 ==> 1
	9	1	0.333	0> 1
	10	1	0.250	0 ==> 1
node 50> Aabbre	13	1	0.333	0 ==> 1
_	17	1	0.333	1 ==> 0
node 50> Ferico	1	1	1.000	0 ==> 1
_	16	1	0.500	2 ==> 3
	18	1	0.200	0 ==> 1
	23	1	0.167	1 ==> 0
	24	1	0.250	0> 1
	25	1	0.286	0> 1
	26	1	1.000	1 ==> 0

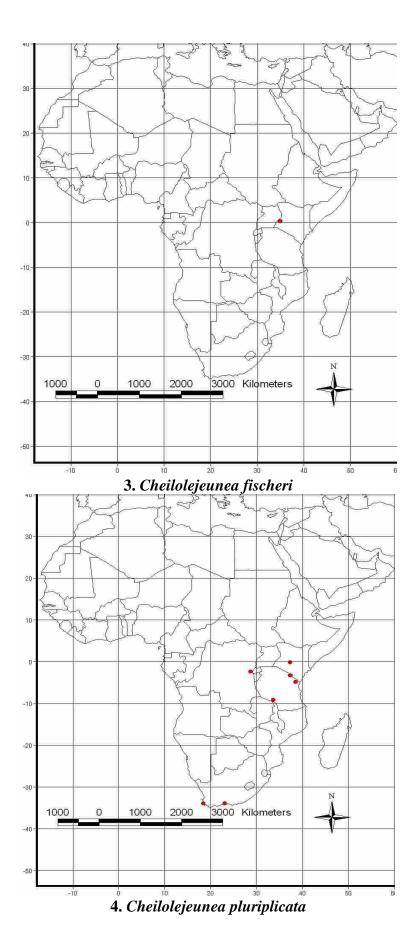
Character diagnostics:

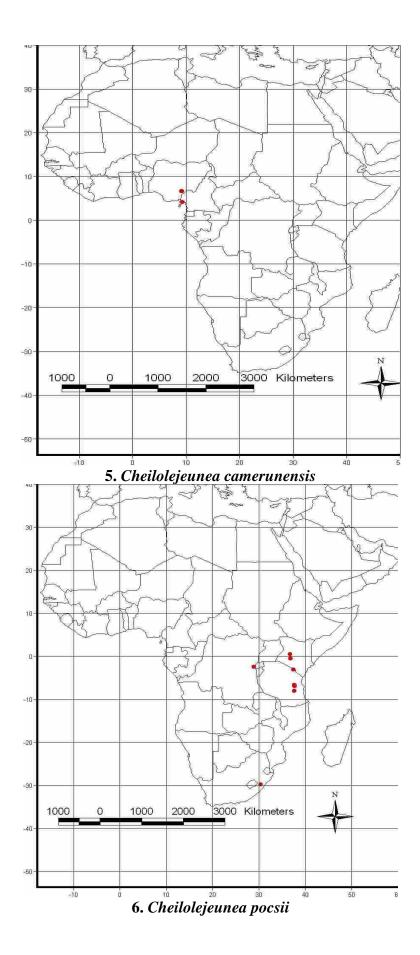
Character	Range	Min steps	Tree steps	Max steps	CI	RI	RC	HI	G- fit
1	2	2	2	3	1.000	1.000	1.000	0.000	1.000
2	1	1	5	8	0.200	0.429	0.086	0.800	0.429
3	1	1	5	11	0.200	0.600	0.120	0.800	0.429
4	1	1	2	4	0.500	0.667	0.333	0.500	0.750
5	1	1	2	4	0.500	0.667	0.333	0.500	0.750
6	1	1	2	3	0.500	0.500	0.250	0.500	0.750
7	2	2	6	8	0.333	0.333	0.111	0.667	0.429
8	1	1	5	7	0.200	0.333	0.067	0.800	0.429
9	1	1	3	12	0.333	0.818	0.273	0.667	0.600
10	1	1	4	14	0.250	0.769	0.192	0.750	0.500

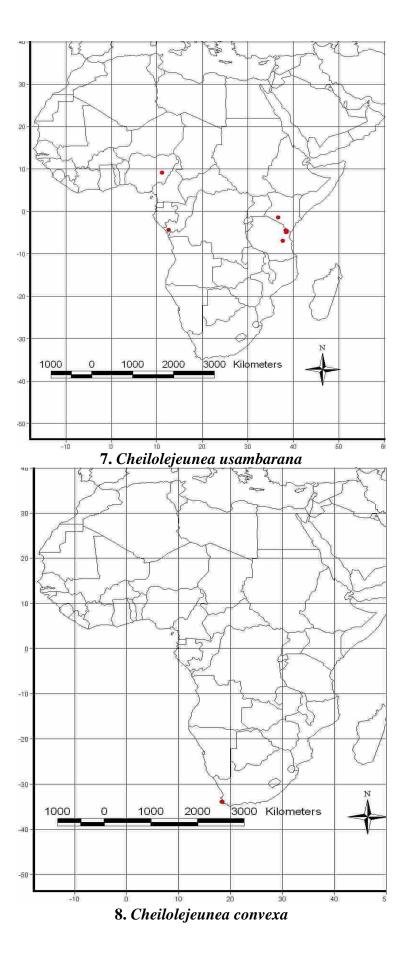
11	1	1	3	14	0.333	0.846	0.282	0.667	0.600
12	1	1	4	13	0.250	0.750	0.188	0.750	0.500
13	2	2	6	14	0.333	0.667	0.222	0.667	0.429
14	1	1	1	6	1.000	1.000	1.000	0.000	1.000
15	1	1	1	1	1.000	0/0	0/0	0.000	1.000
16	3	3	6	13	0.500	0.700	0.350	0.500	0.500
17	1	1	3	8	0.333	0.714	0.238	0.667	0.600
18	1	1	5	10	0.200	0.556	0.111	0.800	0.429
19	1	1	2	2	0.500	0.000	0.000	0.500	0.750
20	2	2	4	17	0.500	0.867	0.433	0.500	0.600
21	1	1	1	5	1.000	1.000	1.000	0.000	1.000
22	1	1	4	5	0.250	0.250	0.062	0.750	0.500
23	1	1	6	7	0.167	0.167	0.028	0.833	0.375
24	1	1	4	6	0.250	0.400	0.100	0.750	0.500
25	2	2	7	11	0.286	0.444	0.127	0.714	0.375
26	2	2	2	3	1.000	1.000	1.000	0.000	1.000
27	1	1	6	10	0.167	0.444	0.074	0.833	0.375

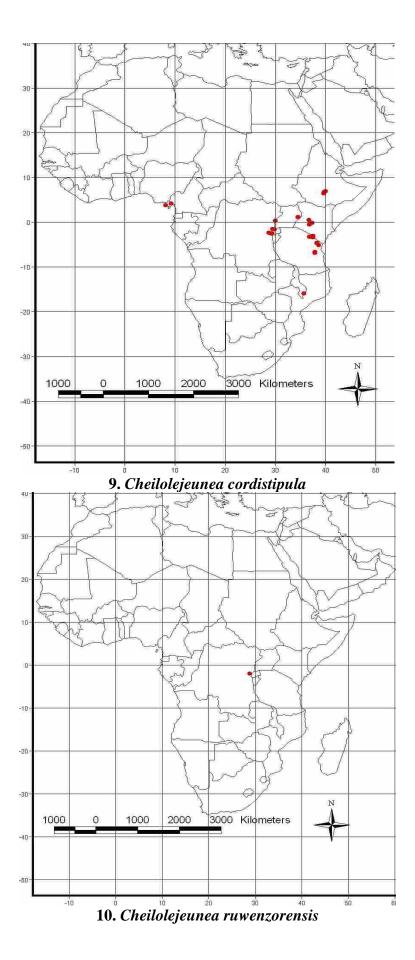
Appendix III. Distribution maps of *Cheilolejeunea* species in continental Africa

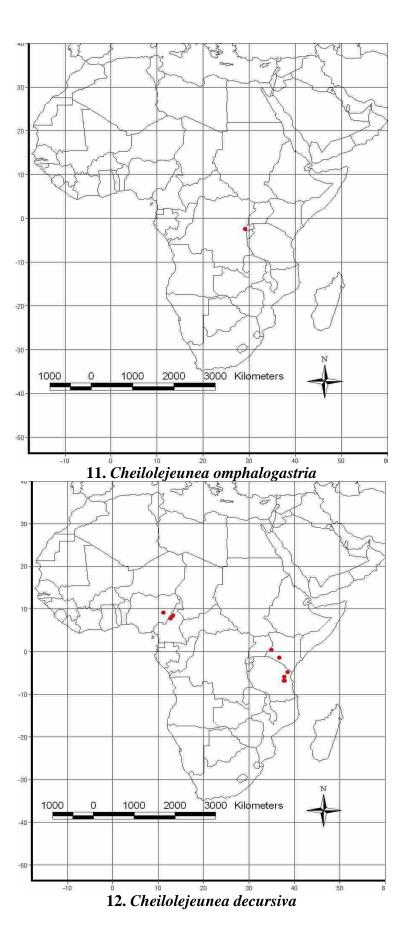


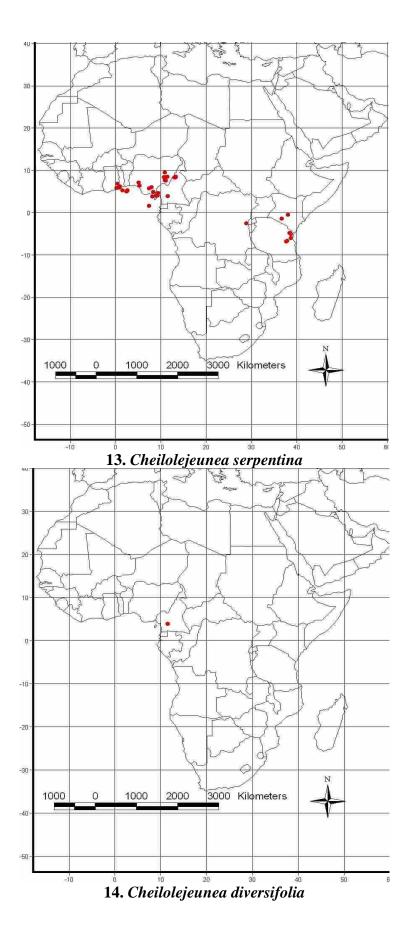


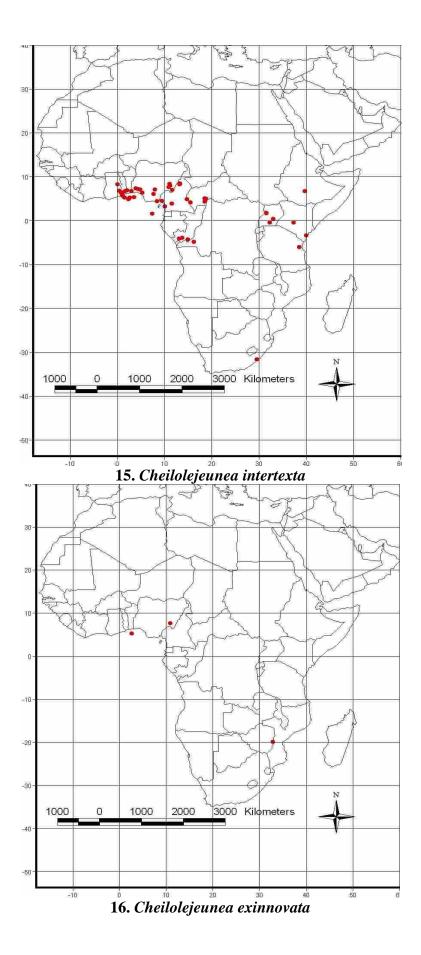


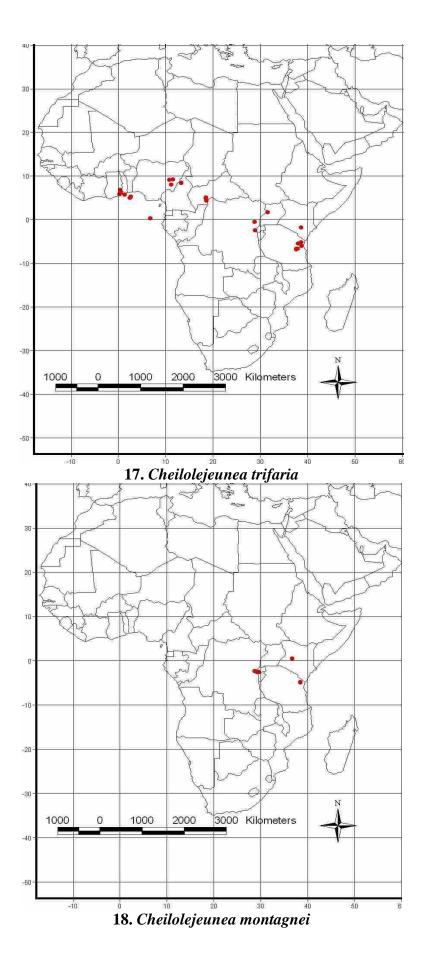


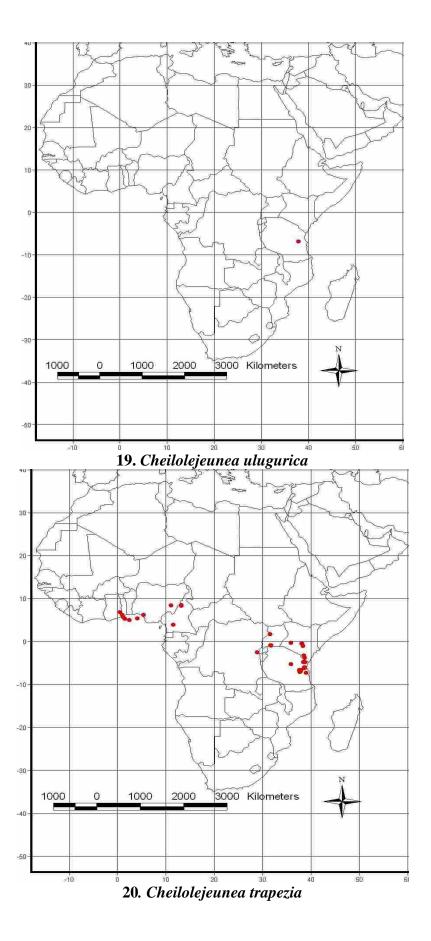


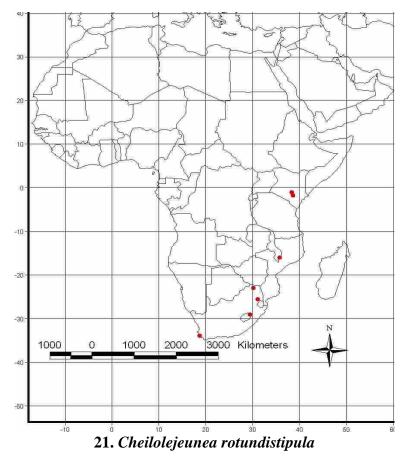


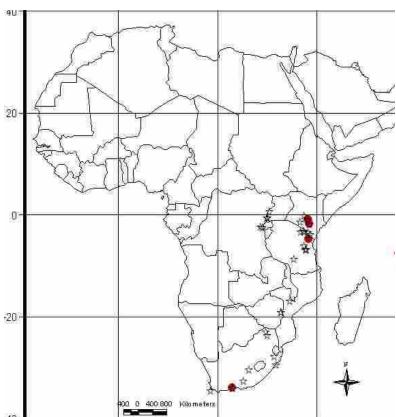












22. Cheilolejeunea unciloba (star) and Ch. xanthocarpa (•-red)

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