

STUDIES ON THE EXOSTOME OF BRACHYTHECIACEAE (MUSCI)

ИЗУЧЕНИЕ ЭКЗОСТОМА BRACHYTHECIACEAE (MUSCI)

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Abstract

The exostome structure of Brachytheciaceae was studied with the scanning electron microscope. 63 species of 17 genera were involved: *Brachythecium* (21 species), *Bryoandersonia* (1), *Camptothecium* (2), *Cirriphyllum* (1), *Eurhynchiella* (1), *Eurhynchium* (9), *Homalotheciella* (1), *Homalothecium* (5), *Myuroclada* (1), *Palamocladium* (2), *Platyhypnidium* (4), *Rhynchostegiella* (6), *Rhynchostegium* (5), *Scleropodium* (2), *Scorpiurium* (1), *Steelecleus* (1). *Rhynchostegiella*, *Homalothecium* and *Homalotheciella* have many advanced characters, mostly clearly adaptive to xeric environments. Exostome patterns provide evidences for the segregation of *Camptothecium* from *Homalothecium*, *Platyhypnidium* from both *Rhynchostegium* and *Eurhynchium*, *Steelecleus* from *Rhynchostegium*, *Eurhynchiella* from *Rhynchostegiella*.

Резюме

С помощью сканирующего электронного микроскопа изучено строение экзостомы семейства Brachytheciaceae. Были исследованы 63 вида из 17 родов: *Brachythecium* (21 species), *Bryoandersonia* (1), *Camptothecium* (2), *Cirriphyllum* (1), *Eurhynchiella* (1), *Eurhynchium* (9), *Homalotheciella* (1), *Homalothecium* (5), *Myuroclada* (1), *Palamocladium* (2), *Platyhypnidium* (4), *Rhynchostegiella* (6), *Rhynchostegium* (5), *Scleropodium* (2), *Scorpiurium* (1), *Steelecleus* (1). *Rhynchostegiella*, *Homalothecium* и *Homalotheciella* имеют много подвинутых признаков, в большинстве своем адаптивных к ксерофитным условиям обитания. Особенности строения экзостомы свидетельствуют в пользу выделения *Camptothecium* из *Homalothecium*, *Platyhypnidium* из *Rhynchostegium* или *Eurhynchium*, *Eurhynchiella* из *Rhynchostegiella*.

INTRODUCTION

Brachytheciaceae is a family which is well-delimited from most of other pleurocarpous mosses. At the same time, limits between genera within Brachytheciaceae are not all as distinct. The problems of placement of some species exist for the generic pairs of *Brachythecium*—*Eurhynchium*, *Rhynchostegium*—*Eurhynchium*, *Platyhypnidium*—*Rhynchostegium*, *Cirriphyllum*—*Eurhynchium*, *Homalothecium*—*Brachythecium*, etc. This is because the diagnostic characters of the genera are confusingly combined in some species. Obviously, for the better circumscription of the genera we need new characters. For this reason we have studied the exostomes of some species of Brachytheciaceae with the scanning electron microscope (SEM).

SEM studies of peristomes of pleurocarpous mosses were applied successfully for finding a correct familial placement for many genera (Buck, 1980), for delimiting Entodontaceae and Hylocomiaceae from Hypnaceae (Buck, 1980; Rohrer, 1985a,b), for demonstrating that there is no close relationship between *Pylaisiella* and *Platygyrium* (Ignatov & al., 1996), for an improved classification of Hookeriaceae (Tan & Robinson, 1990), etc. However, Brachytheciaceae were never explored extensively by this method.

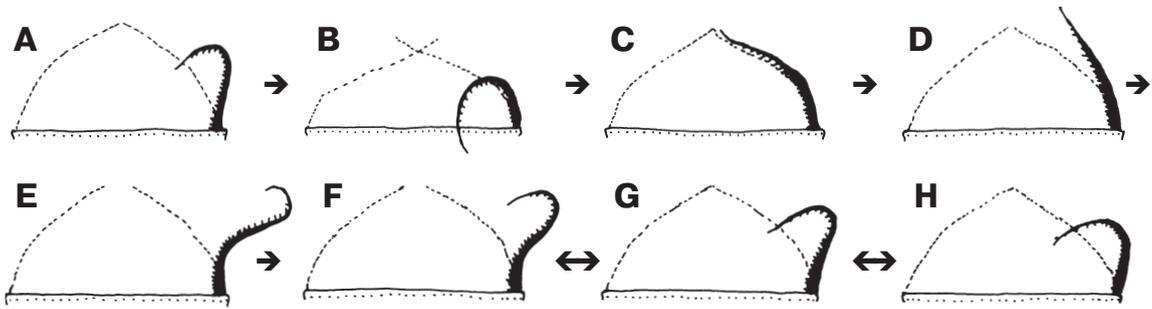
MATERIAL AND METHOD

For the SEM observations capsules from herbarium collections were used (a list of specimens is given in appendix). We studied 84 specimens of 63 species of the following genera: *Brachythecium* (21 species), *Bryoandersonia* (1),

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Scheme 1. Hygroscopic movements of exostome tooth in Brachytheciaceae (based on observation in *Brachythecium oedipodium* (Mitt.) Jaeg. A – open dry capsule; B – immediately after wetting; C – after complete wetting; D – beginning of reflexing movement during drying; E – maximal reflexing during drying; F – median stage of inflexing after stage E; G – return to the starting position. F, G and H show the range of reflexing during changing of air moisture.

*Camptothecium* (2), *Cirriphyllum* (1), *Eurhynchiella* (1), *Eurhynchium* (9), *Homalotheciella* (1), *Homalothecium* (5), *Myuroclada* (1), *Palamocladium* (2), *Platyhypnidium* (4), *Rhynchostegiella* (6), *Rhynchostegium* (5), *Scleropodium* (2), *Scorpiurium* (1), *Stereocleus* (1). A list of specimens is given in the appendix. Peristomes were studied either from deoperculate capsules or from mature capsules after careful operculum removal. Capsules were glued on the stub, covered by gold or platinum and studied at 10 kv with Hitachi S-420 in Museum of Natural History of Smithsonian Institution or at 15 kv with Hitachi S-405 in Moscow State University. In most cases capsules were oriented to make visible the outer surface of exostome and also the inner surface of distal parts of 2-3 teeth. In several species with strongly curved teeth we removed some teeth and glued them separately.

For several species 2-3 specimens were studied, showing that the main pattern of exostome ornamentation is relatively stable within a species. Thus, for most species we studied only one capsule.

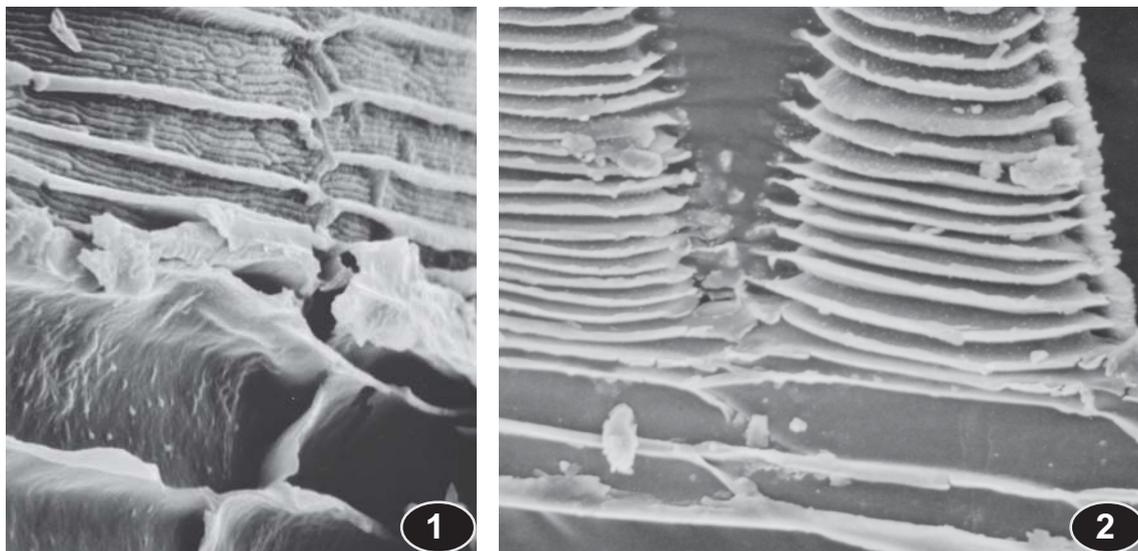
Most species were studied also for the hygroscopic movements of the peristome. For this purpose we mostly used herbarium specimens. A comparisons with the movement of newly opened capsules of living mosses were made for a few species and confirm the principal identity of the movement pattern, though fresh material displays longer “pulsing” movements after the peristome drying. All observations on peristome movement were made under ordinary laboratory condition.

#### GENERAL COMMENTS ON STRUCTURE OF PERISTOME AND TERMINOLOGY

In Brachytheciaceae there are 16 exostome teeth joined with each other in the 2-5 lowermost plates. In species with large teeth (*Eurhynchium angustirete*, *Homalothecium philippeanum*, etc.) they are joined in more plates, in *Palamocladium euchloron* up to 13 plates. The color below is light to dark-brown, sometimes reddish (in wet condition the color becomes paler). In the upper part the teeth are paler to whitish.

The exostomes of most species of Brachytheciaceae are xerocastique (involute when wet, straight or straight-curving when dry), but in *Homalotheciella*, some species of *Homalothecium* s. l., and *Rhynchostegiella* s. l. they are hygrocastique (involute when dry, straight when wet). Hygrocastique behavior of exostome depends, as far as we can see, on the heavier cell material deposition on the outer than on the inner surface of teeth. In *Homalotheciella* and some *Homalothecium* species the dorsal trabeculae<sup>1</sup> are especially high, and they are probably responsible for the outward curving of the teeth after wetting (simulating ventral trabeculae in xerocastique peristomes of most Brachytheciaceae). However, some hygrocastique species (*Rhynchostegiella tenella*, *Homalothecium aeneum*) have quite low dorsal trabeculae, and their curved to straight position after wetting is a result of other features of the outer ornamentation (which is probably thicker than the inner one).

<sup>1</sup> – The terms lamella and trabecula were both applied to the projecting transversal walls on either surface of the exostome tooth. We will name them *dorsal and ventral trabeculae*, because the term “lamella” is sometimes used for the anticlinal cell wall (Mueller & Neumann, 1988), which we here call “plate”.



Figs. 1-2. 1. *Brachythecium reflexum* (Starke) B. S. G. (Russia, Altai, Ignatov 0/442): base of tooth from outside, 1750x; 2. *B. populeum* (Hedw.) B. S. G.. (Russia, Altai, Ignatov 1/16): base of teeth from inside, 635x.

Xerocastique teeth have hygroscopic movements generally similar to those in many other pleurocarps (Hypnaceae, Amblystegiaceae, Thuidiaceae, *Homalia*, etc.). This main pattern was nicely described by Steinbrinck (1897). Teeth in open capsules, as well as separated teeth, are arch-shaped to question-mark-shaped in side view. After wetting they firstly curve strongly near their bases. Then, after a short time teeth straighten and are only a little curved near their bases (so that the complete peristome forms a cone at this stage), and remain in this position until drying. After drying the teeth rather suddenly widely reflex, and then slowly come to the starting position (Scheme 1).

The mechanism of spore dissemination by the movements described above is probably as follows. (A) In dry condition the endostome segments form a more or less complete cone with rather narrow spaces between the teeth, providing little opportunity for spores to escape. The upper parts of the teeth are usually inserted between the endostome segments and force the ciliae move to a more inclined orientation than the segments (sometimes to horizontal), so an additional net is formed against spore release. (B) After wetting the teeth first move fastly well inside the urn. (C) Then after a relatively long time of wetting, straighten and rest upon the cone formed by segments as long as the capsule remains wet; this stage provides virtually no

way for spore release. (D-E) After drying the teeth fastly reflex and then slowly inflex (F) and finally reach the starting position (G). Typically the reflexing movement starts from the bases of the teeth or otherwise from the transition zone (so the upper tooth suddenly raise upward from the segments without jerking of the latter). After reflexing, the inner surface of the exostome bears some spores between the ventral trabeculae (cf. Fig. 57) and other spores loosely stick to papillose surfaces of the teeth. Most of these spores are carried away before the teeth return into the urn next time. Thus, during these movements, the exostome works as an excavator, the scoop being series of ventral trabeculae.

However, this "excavator-mechanism" is probably not the most important and most effective. Its limited role can be assumed already from the fact that only a few spores are released during each drying-wetting cycle. At the same time, the exostome teeth have at least one other type of movement. It can be observed without putting a drop of water on the capsule, but by raising the air humidity (by bringing to tooth a needle with a drop of water into close proximity, or by putting the capsule in dry place in Petri dish with water). Under such condition, teeth from capsules even from old herbarium specimens usually exhibit some movements. After the raising of humidity, the upper parts of the teeth penetrate into the urn somewhat more than in the "starting posi-

tion" (Scheme 1, H). A weak wind (blowings) on the teeth under such a conditions results in a reflexing movement of the teeth (to position F on Scheme 1). During these reflexing movements, teeth pull and jerk the endostome structures (both membrane, segments, and ciliae). The rigid and springy endostome suddenly release tension, resulting in a flight of group of spores from the urn. The peristome movements with the same amplitude (F–G–H) were observed in fresh capsules, soon after their dehiscence, when they release spores especially actively. In this period, the teeth are more flexible and have a "pulsing" movements which continue at least several hours. Slight wind reflexes teeth (to position H), but in a few seconds they inflex again (to position F or G), probably receiving moisture from the spore mass and other structures of a newly opened capsule. Each reflexing cycle results in jerking of endostome and the releasing of spores. Similar "pulsing" movements are known in many mosses with "perfect" double peristome.

There are several structures on the teeth which help in the jerking: (1) ventral trabeculae; (2) a serrate margin (projecting upper angles of dorsal plates); (3) relatively large papillae on the incrassate margin<sup>1</sup> of the upper teeth; (4) a special double teeth on the plate joints in several species (Fig. 101).

The hygroscopic movements of the peristome described above suggest that the following zones are the functionally most important for xerocastic peristome:

(1) *Basal zone*. The dorsal trabeculae are higher and the plates wider than above, and smooth (Figs. 1, 117). The ventral plates are much wider (Fig. 2). These smooth plates are partly below the attachment of peristome to the capsule wall, but in any case they must be considered as still a part of peristome because they work as a single hygroscopic system. This basal zone is obviously responsible for the movements of the basal teeth (at the level of the annulus). However, it can rarely be observed in entire capsules prepared for SEM but usually only after their destruction when the exostome has been detached from both urn and endostome. For this reason, we examined only a few basal zones.

(2) *Transition zone*. This is the second place

where the teeth are bend during their hygroscopic movements. In this zone the teeth (1) become thinner, often abruptly; (2) the ornamentation of the outer plates changes from transversal to longitudinal (in many species several plates of the transition zone are densely covered by large round papillae; (3) the ventral trabeculae become more distantly arranged; (4) the "border" becomes wider and more apparent – it is easily seen under the light microscope as a narrow transparent zone along the margin of the teeth in the upper part. SEM demonstrates that it is composed mainly by OPL cell remains (cf. Figs. 41, 48, 80). The changes in the transition zone are obviously very important for the patterns of hygroscopic movement of the various species. Namely, teeth with more gradual changes of ornamentation and with big round papillae upon the cristae (almost masking the cristae) in the transition zone are less flexible than teeth with more abrupt changes of ornamentation. However, it is important to note that gradual/abrupt transitions in ornamentation do not always correspond with gradual/abrupt taperings of teeth outlines.

(3) *Dorsal plates in lower part of tooth*. These were found to be rather variable in the Brachytheciaceae. The plates usually are covered by transversely oriented cristae, 5–13 per plate in lower part of tooth. The cristae are smooth or, more often, papillose. Papillae on cristae can have different shapes and sizes: (1) "bead-like" papillae (Figs. 26, 93, 118) are round, with diameter less than the width of cristae; (2) "wavy-papillose" we call cristae when their surface is not flat but wavy, and waves are of the same width as the cristae; in high-wavy patterns it is easy to delimit papillae from intra-papillose parts of the cristae (Fig. 54), but in low-wavy cristae the papillae show very gradual transition to intra-papillose parts of the cristae (Figs. 24); (3) conic papillae (Figs. 131); (4) round papillae (Figs. 25). In *Rhynchostegiella*, *Homalothecium* and *Homalotheciella* branched papillae also occur (Figs. 159, 169) and "snowman-like" papillae, the latter are composed of 2–3 more or less globose subunits, with the smaller standing upon larger ones (Figs. 144–145). The pattern of papillosity of the cristae seems to correlate to a cer-

<sup>1</sup> – The margin of the exostome tooth in its distal part is often differentiated, being thicker with sparser but larger papillae. We call this margin incrassate (Figs. 14–17). Rarely the margin is not incrassate (Figs. 179).

tain extent with the environmental preferences of individual species (and also corresponds somewhat to their generic position). For example, branched papillae are known mainly in species growing in xeric areas; bead-like papillae on lower dorsal plates are found also in species with temperate to subtropical distribution, etc.

(4) *Ventral trabeculae in the upper part of tooth.* These are important structures for releasing of spores. They are especially diverse in shape and ornamentation, and some of their characters are more or less correlated with the systematic position of the taxa. Ventral trabeculae typically end at 4-7 plates below teeth apices. However, in some *Rhynchostegium* and *Eurhynchium* species, and more rare in *Brachythecium* ones, the exostome teeth lack ventral trabeculae on 10-15 distal plates. In the lower part of teeth, ventral trabeculae are usually smooth (among xerocastique peristomes exceptions found in *Brachythecium rivulare* and *Eurhynchium asperisetum*). In the transition zone some papillae appear on the trabeculae and somewhat above the transition zone the papillae are densest and highest. The description of the ventral trabeculae in the upper teeth *always refers* to this area of strongest papilosity (usually at about  $3/4$ – $4/5$  of the tooth length). Above this, the ventral trabeculae become lower and usually less papillose (an exception is found in some *Rhynchostegium* species, where the uppermost low trabeculae are more highly papillose than those below).

The three latter characters (2-4) were a main focus of our SEM studies.

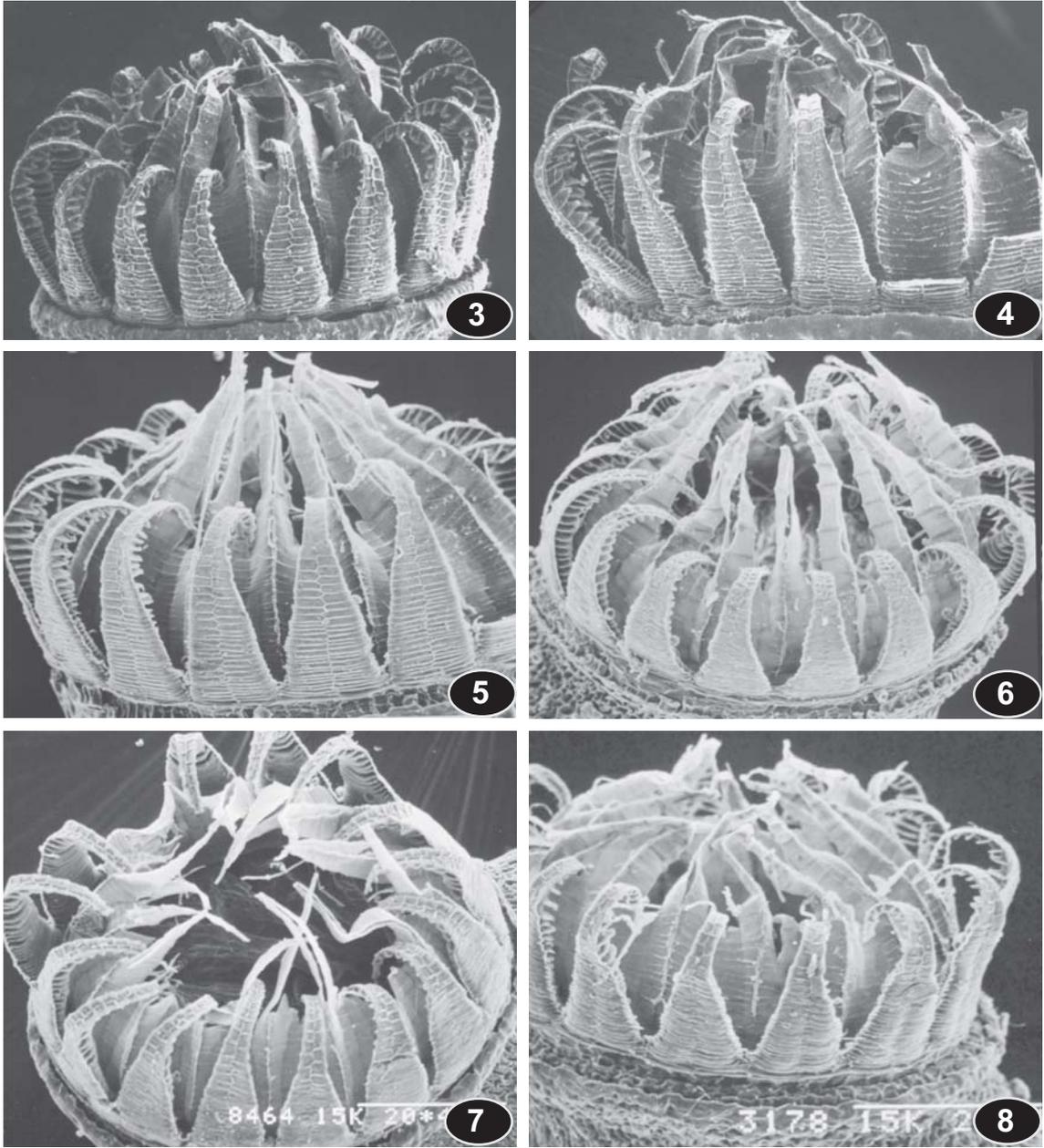
#### **Brachythecium** (Figs. 3-48 & 70, 72, 74)

Species studied: *B. acuminatum* (Hedw.) Aust., *B. albicans* (Hedw.) B. S. G., *B. auriculatum* Jaeg., *B. cirrosum* (Schwaegr.) Schimp., *B. complanatum* Broth., *B. erythrorrhizon* B. S. G., *B. falcatulum* (Broth.) Par., *B. lamprocarpum* (C. Muell.) Jaeg., *B. mildeanum* (Schimp.) Schimp. ex Milde, *B. oedipodium* (Brid.) Mitt., *B. laetum* (Brid.) B. S. G., *B. plumosum* (Hedw.) B. S. G., *B. populeum* (Hedw.) B. S. G., *B. reflexum* (Starke) B. S. G., *B. rivulare* B. S. G., *B. roteanum* De Not., *B. rutabulum* (Hedw.) B. S. G., *B. salebrosum* (Web. et Mohr) B. S. G., *B. starkei* (Brid.) B. S. G., *B. trachypodium* (Brid.) B. S. G., *B. velutinum* (Hedw.) B. S. G.

Twenty-one species (i. e. 20-25% of those in genus) were studied. The main structures of peristome are rather uniform.

The teeth taper gradually in the transition zone and form a wide arch (Figs. 3-6) or rarer taper rather abruptly, without an obvious arch (Figs. 10-12). In the upper part teeth are serrulate (rarely subentire). The median zig-zag line in the lower half of teeth is not immersed. The dorsal trabeculae in the proximal part of teeth are smooth, somewhat exerted above the cristae level, rarely moderately exerted (*B. oedipodium*), or partly sinking among cristae (*B. plumosum*, *B. populeum*, *B. rivulare*). The cristae are dense and straight to slightly flexuose, smooth to relatively lowly wavy-papillose (typical variant is illustrated in Fig. 24; exceptions are seen in *B. complanatum*, with loose and strongly flexuose cristae; in *B. falcatulum*, with small rare "bead-like" papillae on the few lowermost plates, though most of the lower cristae are smooth; in *B. rivulare*, with cristae papillose almost to the base). Towards the transition zone the papillae are always become more prominent. The papilosity patterns are gradually changing from low-wavy papillose below to high-wavy papillose and then, in most of species dense round papillae totally mask the cristae on 1-2 plates in the transition zone (cf. Figs. 18, 19, 21), rarely dense papillae cover more plates below the transition zone (in *B. falcatulum*, *B. salebrosum*, *B. laetum*, *B. rivulare*, *B. mildeanum* – cf. Figs. 22, 25). In some species the plates with transversal cristae having high-wavy papillae are immediately changing to plates with longitudinal cristae, which are typical for the upper part (cf. Figs. 20). In the upper part the dorsal trabeculae are low and lowly papillose. The incrassate margins of teeth are usually well defined and less densely papillose than the plates, but often its papillae are larger, especially on the lateral surface. On the plates in upper teeth papillae are rare and arranged in longitudinal rows, or more rarely papillae are denser, masking the longitudinal rows. The ventral trabeculae are lowly semiorbicular, triangular to high-ligulate, relatively thin to incrassate, with a smooth to rugose surface, and densely to sparsely papillose, or smooth. The papillae are typically restricted to several ventral trabeculae, and are rarely found below the transition zone (*B. rivulare*).

The ventral trabeculae are densely and evenly high-papillose in *B. velutinum* and in the related *B. falcatulum* (Figs. 34-35, 37); *B. rivulare* (Fig.



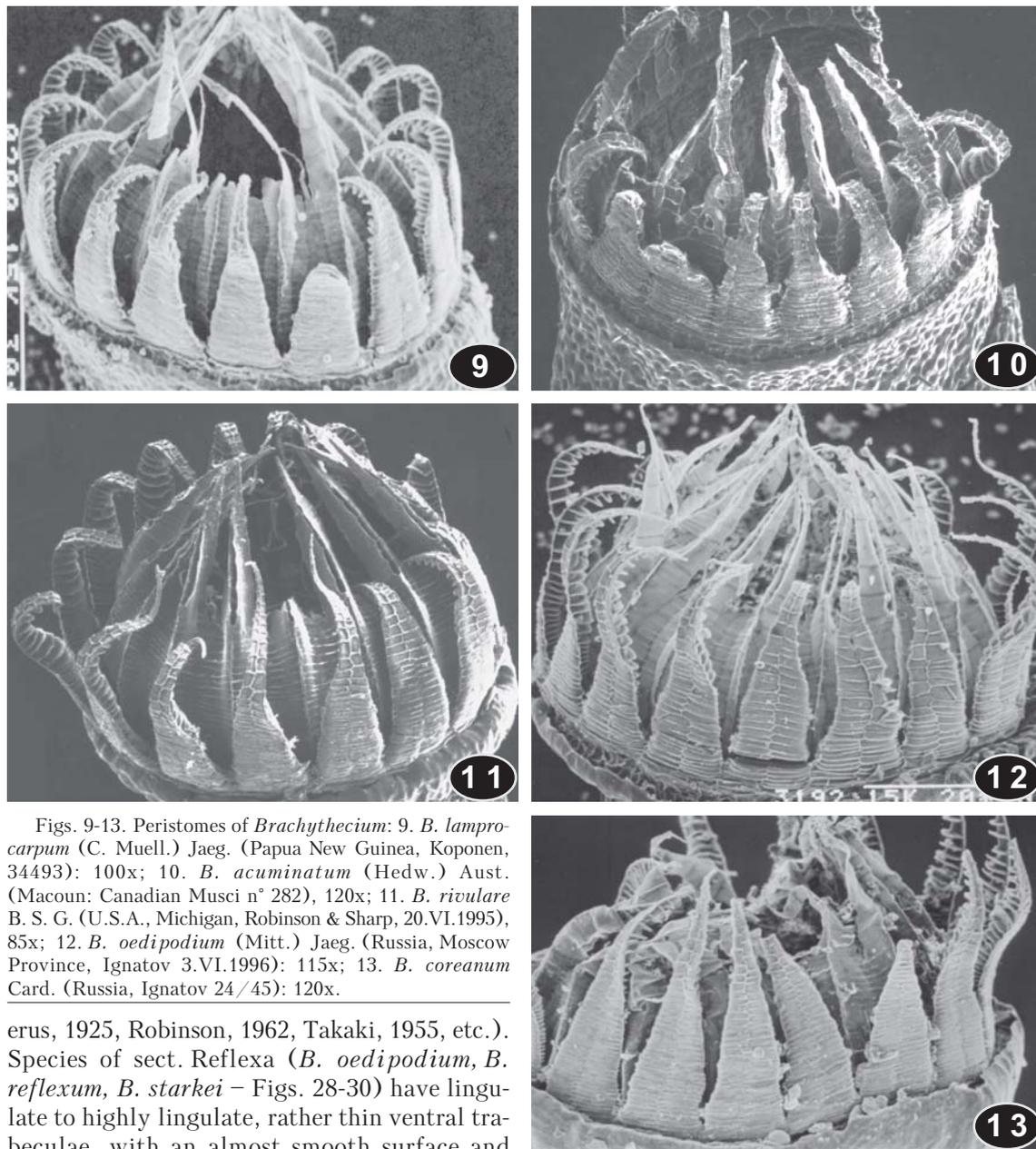
Figs. 3-8. Peristomes of *Brachythecium*: 3. *B. populeum* (Hedw.) B. S. G. (Russia, Altai, Ignatov 1/16): 130x; 4. *B. salebrosum* (Web. et Mohr) B. S. G. (Sweden, Lule Lappmark, Hj. Moller): 120x; 5. *B. rutabulum* (Hedw.) B. S. G. (Russia, Moscow, Ignatov 27.VI.1994): 150x; 6. *B. mildeanum* (Schimp.) Schimp. ex Milde (Russia, Moscow Province, Ignatov 16.V.1986): 120x; 7. *B. velutinum* (Hedw.) B. S. G. (Russia, Moscow Province, Ignatov 20.VII.1988): 115x; 8. *B. plumosum* (Hedw.) B. S. G. (Russia, Altai, Ignatov 16/29): 150.

36); *B. acuminatum*. In these species the papillae are high, cylindric, about  $1.5 \times 0.3 \mu\text{m}$ , very similar to papillae commonly occurring in many *Eurhynchium*-species (cf. Figs. 57, 59, 60, 62 etc.).

However, 16 of 21 species studied have only low papillae on the ventral surface, or otherwise have rows of high papillae only along the mar-

gin of the ventral plates and trabeculae (Figs. 29, 45, 48).

Species without dense papillae on the ventral trabeculae can be classified into several groups, which more or less correspond to the sections of the genus that are accepted in most of treatments of *Brachythecium* (cf. Broth-

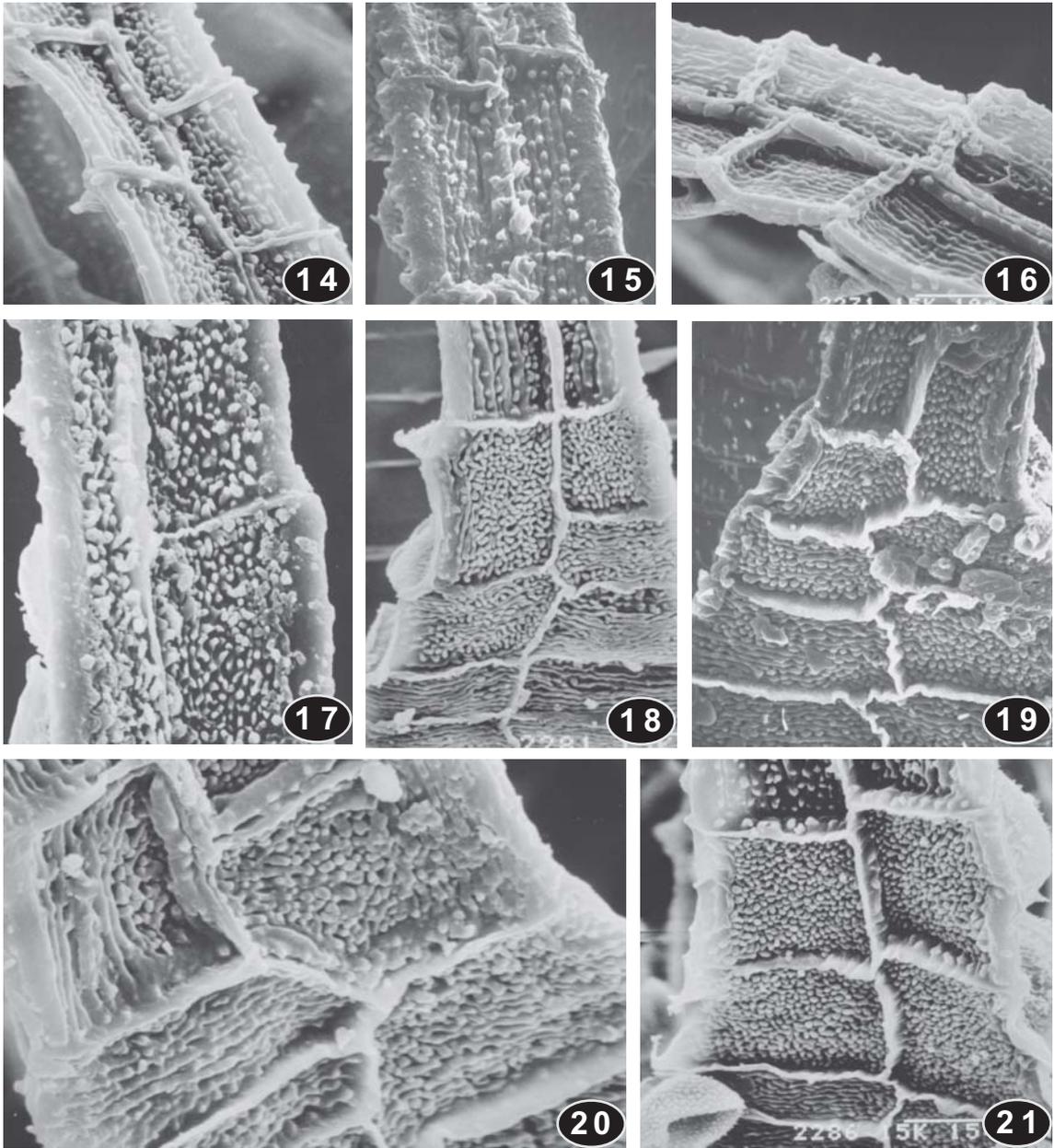


Figs. 9-13. Peristomes of *Brachythecium*: 9. *B. lamprocarpum* (C. Muell.) Jaeg. (Papua New Guinea, Koponen, 34493): 100x; 10. *B. acuminatum* (Hedw.) Aust. (Macoun: Canadian Musci n° 282), 120x; 11. *B. rivulare* B. S. G. (U.S.A., Michigan, Robinson & Sharp, 20.VI.1995), 85x; 12. *B. oedipodium* (Mitt.) Jaeg. (Russia, Moscow Province, Ignatov 3.VI.1996): 115x; 13. *B. coreanum* Card. (Russia, Ignatov 24/45): 120x.

erus, 1925, Robinson, 1962, Takaki, 1955, etc.). Species of sect. *Reflexa* (*B. oedipodium*, *B. reflexum*, *B. starkei* – Figs. 28-30) have linguulate to highly linguulate, rather thin ventral trabeculae, with an almost smooth surface and sparse, small, low papillae, and sometimes with higher thin papillae concentrated along the margin of the inner plates and ventral trabeculae. Species of sect. *Salebrosa* (*B. salebrosum*, *B. laetum*, *B. albicans*, *B. rotaeianum*, *B. erythrorrhizon*) have low and semiorbicular relatively incrassate ventral trabeculae, with  $\pm$ rugulose surfaces, which are moderately to sparsely lowly papillose with papillae that are often uneven in shape (Figs 39-42, 44, 47). The group of species around *B. rutabulum* (*B. rutabulum*, *B.*

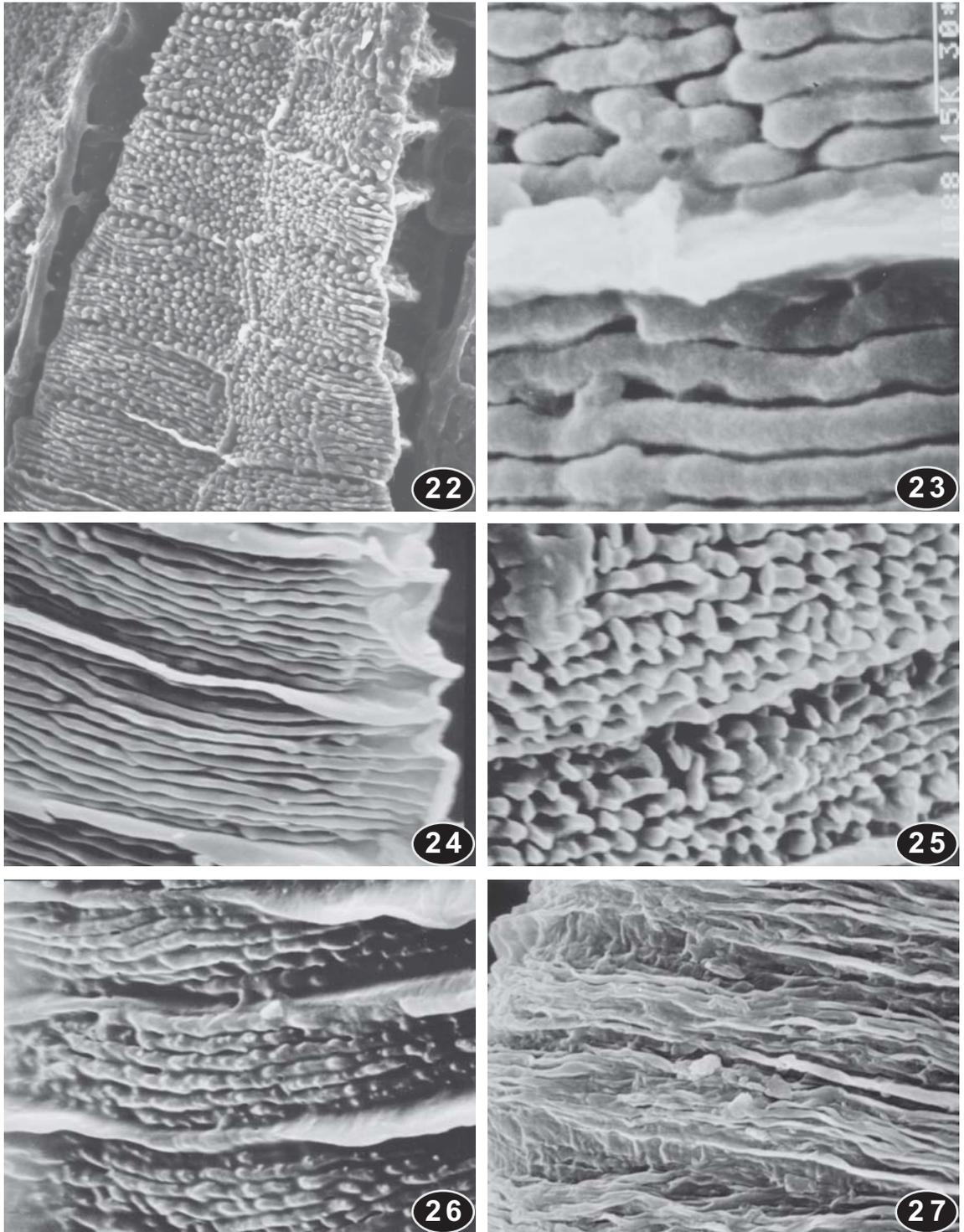
*complanatum*, *B. mildeanum* – Figs. 31-33) have intermediately incrassate ventral trabeculae and sparse low papillae (more resembling those in sect. *Reflexa*). The species of sect. *Cirriphylloidsis* (*B. populeum*, *B. plumosum*) have incrassate semiorbicular ventral trabeculae, which sometimes bear higher papillae, especially near the margin (Figs. 45-46, 48).

Especially deviating exostomes in *Brachythecium* were found in *B. complanatum* and *B. rivulare*. In *B. complanatum* the teeth are espe-

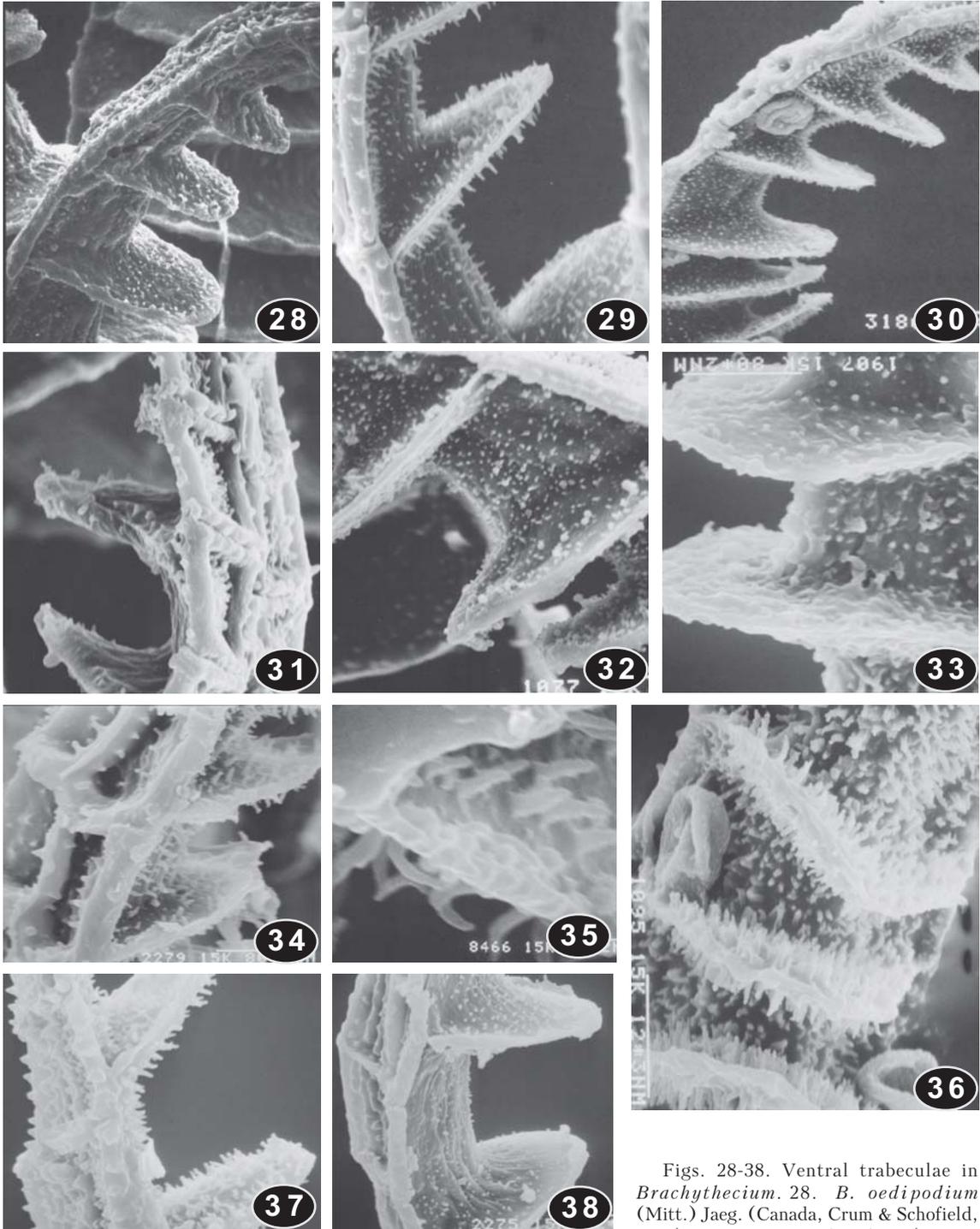


Figs. 14-21. Upper (14-17) and middle (18-21) parts of teeth from outside. 14. *B. rutabulum* (Hedw.) B. S. G. (Russia, Moscow, Ignatov 27.VI.1994): 1400x; 15. *B. populeum* (Hedw.) B. S. G. (Russia, Altai, Ignatov 1/16): 2000x; 16. *B. erythrorrhizon* B. S. G. (Russia, Ignatov & Bezgodov, 133): 1850x. 17. *B. rivulare* B. S. G. (Russia, Moscow Province, Ignatov, 4.5.1985): 2100x; 18. *B. trachypodium* (Brid.) B. S. G. (Russia, Ignatov 31/227): 1220x. 19. *B. populeum* (l. c.): 1350x; 20. *B. erythrorrhizon* B. S. G. (Russia, Ignatov & Bezgodov, 133): 2300x. 21. *B. falcatulum* (Broth.) Par. (Russia, Altai, Ignatov 0/1680): 1400x.

Figs. 22-27. Lower parts of teeth from outside. 22. *Brachythecium laetum* (Brid.) B. S. G. (Crum & Anderson, Mosses of North America, n° 871): just below transition zone, 1300x; 23. *B. populeum* (Hedw.) B. S. G. (Russia, Altai, Ignatov 1/16): cristae demonstrating transition from clear striolate to papillose pattern, 10000x; 24. *B. oedipodium* (Mitt.) Jaeg. (Russia, Moscow Province, Ignatov 3.VI.1996): cristae in lower part – pattern typical for many other species, 3800x; 25. *B. rivulare* B. S. G. (Russia, Moscow Province, Ignatov, 4.5.1985): papillose

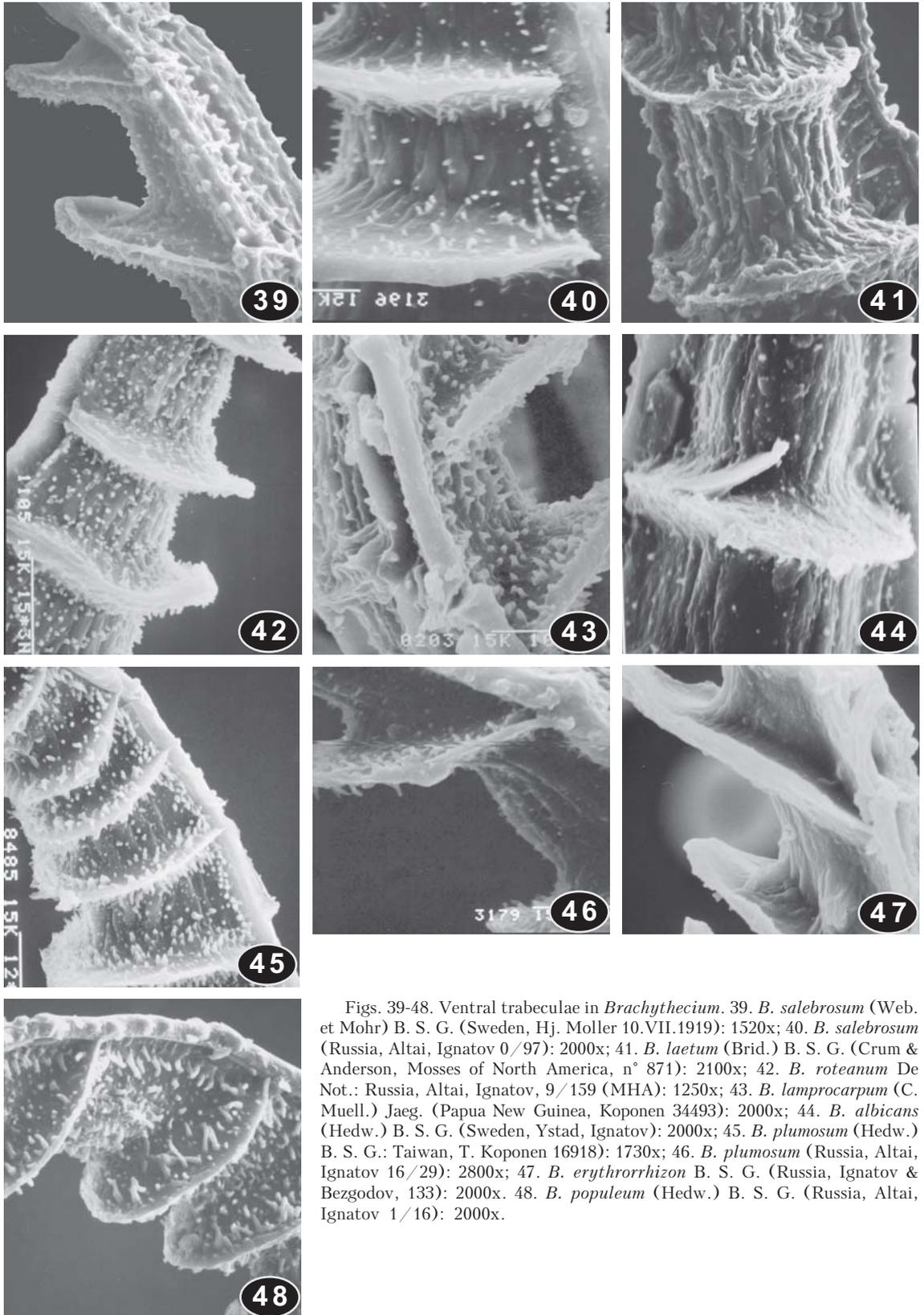


cristae in lower part of tooth, 5400x; 26. *B. falcatulum* (Broth.) Par. (Russia, Altai, Ignatov 0/1680): “bead-like papillae” on lowermost cristae, 3900x; 27. *B. coreanum* Card. (Russia, Altai, Ignatov 24/45): anomalous rare cristae in lower part of tooth, 3000x.

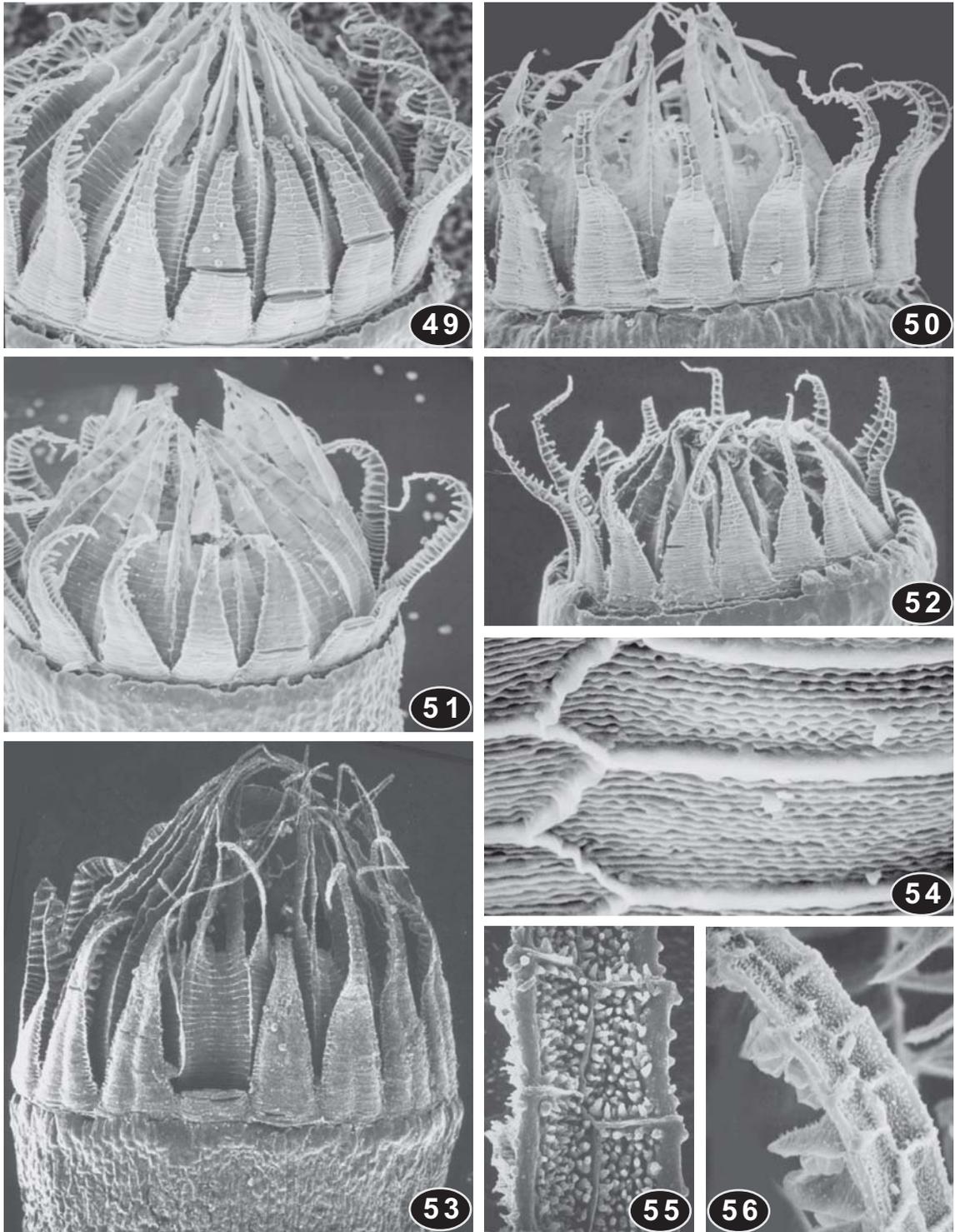


Figs. 28-38. Ventral trabeculae in *Brachythecium*. 28. *B. oedipodium* (Mitt.) Jaeg. (Canada, Crum & Schofield, 4841): 960x; 29. *B. oedipodium* (Russia, Moscow Province, Ignatov 3.VI.1996), 1540x; 30. *B. reflexum* (Starke) B. S. G. (Russia, Altai, Ignatov 0/442): 1350x; 31. *B. mildeanum* (Schimp.) Schimp. ex Milde (Russia, Moscow Province, Ignatov, 16.V.1986): 1750x; 32. *B. rutabulum* (Hedw.) B. S. G. (Russia, Moscow, Ignatov 27.VI.1994): 1380x; 33. *B. coreanum* Card. (Russia, Ignatov 24/45): 2530x; 34. *B. velutinum* (Hedw.) B. S. G. (Russia, Ignatov 13/134): 1950x; 35. *B. velutinum* (Russia, Ignatov 20.VII.1988): 7600x; 36. *B. rivulare* B. S. G. (Russia, Ignatov, 9.IV.1994): 1730x; 37. *B. falcatum* (Broth.) Par. (Russia, Altai, Ignatov 0/1680): 1850x; 38. *B. trachypodium* (Brid.) B. S. G. (Russia, Ignatov 31/227): 1370x.

Moscow Province, Ignatov 3.VI.1996), 1540x; 30. *B. reflexum* (Starke) B. S. G. (Russia, Altai, Ignatov 0/442): 1350x; 31. *B. mildeanum* (Schimp.) Schimp. ex Milde (Russia, Moscow Province, Ignatov, 16.V.1986): 1750x; 32. *B. rutabulum* (Hedw.) B. S. G. (Russia, Moscow, Ignatov 27.VI.1994): 1380x; 33. *B. coreanum* Card. (Russia, Ignatov 24/45): 2530x; 34. *B. velutinum* (Hedw.) B. S. G. (Russia, Ignatov 13/134): 1950x; 35. *B. velutinum* (Russia, Ignatov 20.VII.1988): 7600x; 36. *B. rivulare* B. S. G. (Russia, Ignatov, 9.IV.1994): 1730x; 37. *B. falcatum* (Broth.) Par. (Russia, Altai, Ignatov 0/1680): 1850x; 38. *B. trachypodium* (Brid.) B. S. G. (Russia, Ignatov 31/227): 1370x.



Figs. 39-48. Ventral trabeculae in *Brachythecium*. 39. *B. salebrosum* (Web. et Mohr) B. S. G. (Sweden, Hj. Moller 10.VII.1919): 1520x; 40. *B. salebrosum* (Russia, Altai, Ignatov 0/97): 2000x; 41. *B. laetum* (Brid.) B. S. G. (Crum & Anderson, Mosses of North America, n° 871): 2100x; 42. *B. roteanum* De Not.: Russia, Altai, Ignatov, 9/159 (MHA): 1250x; 43. *B. lamprocarpum* (C. Muell.) Jaeg. (Papua New Guinea, Koponen 34493): 2000x; 44. *B. albicans* (Hedw.) B. S. G. (Sweden, Ystad, Ignatov): 2000x; 45. *B. plumosum* (Hedw.) B. S. G.: Taiwan, T. Koponen 16918): 1730x; 46. *B. plumosum* (Russia, Altai, Ignatov 16/29): 2800x; 47. *B. erythrorrhizon* B. S. G. (Russia, Ignatov & Bezgodov, 133): 2000x. 48. *B. populeum* (Hedw.) B. S. G. (Russia, Altai, Ignatov 1/16): 2000x.



Figs. 49-56. Peristomes (49-53), outer surface of tooth in lower part (54), and outer surface of teeth in upper part (55-56) of *Eurhynchium*. 49. *E. angustirete* (Broth.) Kop. (Russia, Moscow Prov., Ignatov 29.IV.1985): 115x; 50. *E. striatum* (Hedw.) Schimp. (Russia, Krasnodar Territory, L. Vasil'eva, 16.VIII.1935): 115x; 51. *E. pulchellum* (Hedw.) Jenn. (Russia, Altai, Ignatov 0/1226): 115x; 52. *E. hians* (Hedw.) Sande Lac. (Russia, Pskov Province, Ignatov & Zolotov 20.X.1996): 80x; 53. *E. praelongum* (Hedw.) B. S. G. (Aslatia, Schimper): 220x; 54. *E. striatum* (l. c.): 2300x; 55. *E. praelongum* (l. c.): 1500x; 56. *E. angustirete* (l. c.): 650x.

cially massive, slightly curved, with rather stout dorsal trabeculae (Fig. 13), and cristae in lower part flexuose and very loose, exposing a rugose surface (Fig. 27) [similar loose cristae we have otherwise seen among other studied taxa only in *Homalia trichomanoides* (Hedw.) B.S.G.].

In *B. rivulare* the teeth are less hygroscopic and more papillose than in other species of the genus. Round papillae are found on cristae from the transition zone far into the lower part, in one specimen nearly to the base. In the upper part the dorsal plates are densely papillose, totally masking the longitudinal cristae. The ventral trabeculae are densely papillose not only above, but also in the lower part of the teeth (Figs. 17, 25).

It is rather interesting, that the general characters of the exostome remain the same in some tropical species, growing in quite different environment, for example in *B. lamprocarpum* (Figs. 9).

#### **Eurhynchium** (Figs. 49-65)

Species studied: *E. angustirete* (Broth.) Kop., *E. asperisetum* (C. Müll.) Bartr., *E. hians* (Hedw.) Sande Lac., *E. praelongum* (Hedw.) B. S. G., *E. pulchellum* (Hedw.) Jenn., *E. savatieri* Schimp. ex Besch., *E. schleicheri* (Hedw. f.) Jur., *E. striatum* (Spruce) B. S. G., *E. vagans* (Jaeg.) Bartr.

The teeth are abruptly tapered in the transition zone (cf. Figs. 49, 50, 52, 53), more rarely gradually tapered (*E. pulchellum*, Fig. 51). In the lower part the dorsal trabeculae are exerted (Fig. 54), more rarely not exerted above cristae (*E. praelongum*, *E. pulchellum*, *E. savatieri*). The cristae below are smooth or almost so (*E. pulchellum*, *E. savatieri*, *E. schleicheri*, *E. vagans*), wavy-papillose (*E. angustirete*, *E. praelongum*, *E. striatum*), or more or less papillose (in *E. asperisetum*, *E. hians*). In the upper part the plates are papillose, without clear longitudinal rows of papillae (Figs. 54, 55), more rarely with papillae in more or less distinct rows (*E. schleicheri*, *E. vagans*). The margin is incrassate and weakly papillose. The ventral trabeculae are relatively high, lingulate to triangular, rarely lowly semiorbicular (*E. vagans*), relatively thin in most species, more rarely somewhat incrassate and rugulose (*E. schleicheri*). The papillae on the ventral trabeculae show several patterns: (1) papillae moderately dense, high cylindrical, to 2.0 µm high, 0.3 µm in diameter, found in *E. angustirete*, *E. striatum*, *E. praelongum*, *E. pulchellum*, *E. savatieri*; (2) papillae absent or

nearly so, found in *E. hians* and *E. schleicheri*; (3) papillae dense and low, seen in *E. vagans*; (4) upper ventral trabeculae densely unevenly papillose, papillae spinulose to shortly conic, in lower part papillae on ventral trabeculae high-spinulose, found in *E. asperisetum*.

Thus, all the characters of the exostome of *Eurhynchium* are similar to those in *Brachythecium*, but in the former (1) the teeth are more commonly abruptly tapered in the transition zone; (2) the dorsal plates in the upper teeth are more papillose and usually without distinct longitudinal rows; (3) the ventral trabeculae are almost always higher and thinner and often bear dense high cylindrical papillae (rare in *Brachythecium*).

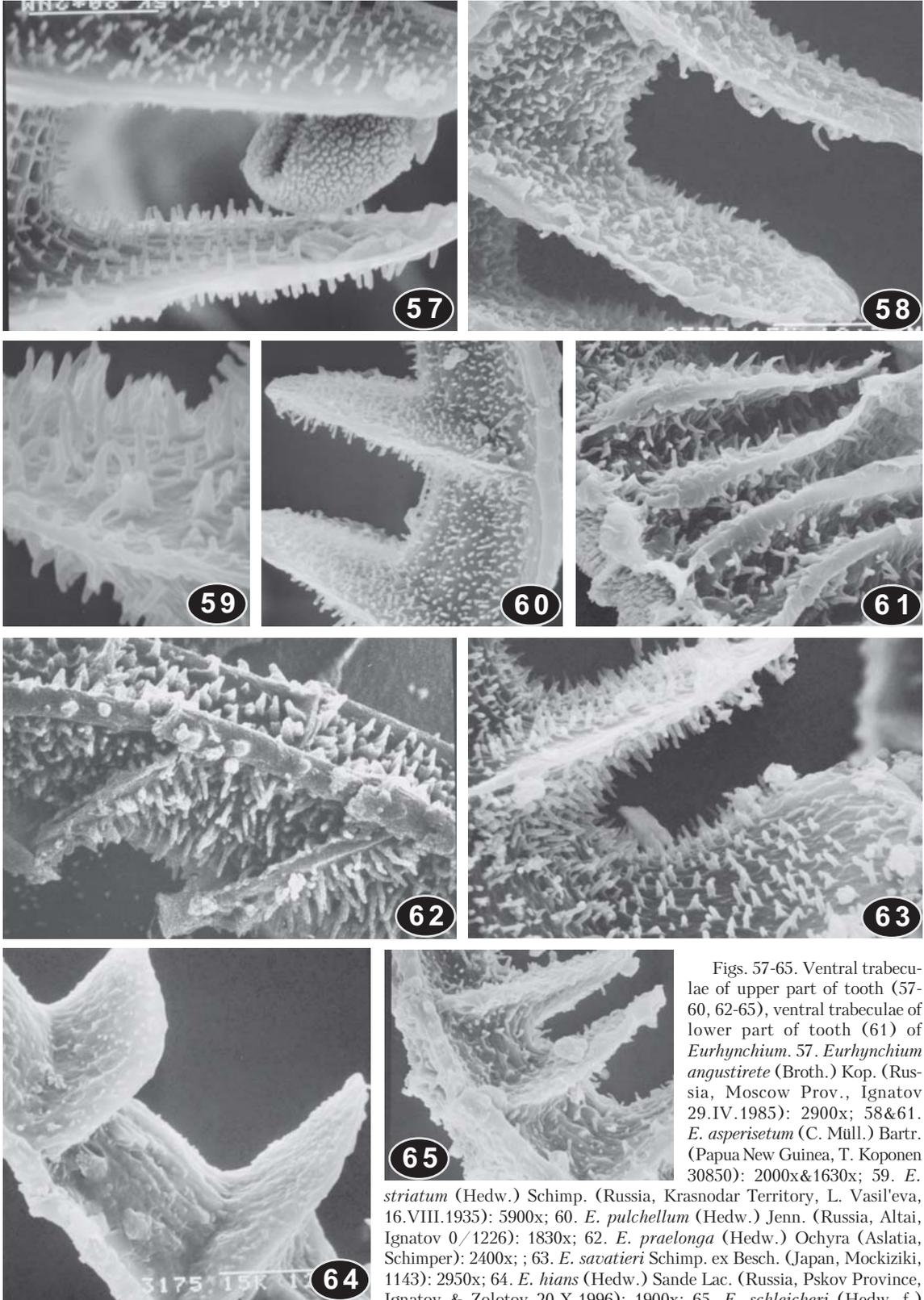
Some infrageneric units are correlated with the papillosity of ventral trabeculae. Species of *Eurhynchium* s. str. (*E. striatum*, *E. angustirete*, *E. pulchellum*, *E. savatieri*) have very dense and high papillae, whereas *E. hians*, classified often in the subgenus or genus *Oxyrrhynchium* (Bruch & al., 1851-55; Warnstorf, 1906; Brotherus, 1925) has smooth ventral trabeculae. However, character state in other species disagrees with the recognition of *Oxyrrhynchium* as a distinct unit: *E. asperisetum* (close to *E. hians*) has papillose ventral trabeculae, whereas *E. schleicheri* (belonging to *Eurhynchium* s. str.) has smooth ones.

*Eurhynchium praelongum* is often segregated in *Kindbergia* by many authors, but Ignatov (1998) failed to delimit it from *Eurhynchium*. The exostome of *E. praelongum* is similar to other species of this genus, especially in their dense high papillae on the ventral trabeculae and in densely papillose dorsal plates in the upper tooth. The only difference from other *Eurhynchium* species includes the rather limited flexibility of the transition zone and the restricted hygroscopic movement (though this might be an artifact, because we studied the peristome of a 150 years old capsule, the only we could obtain for this study). Also, the character of flexibility may be of a limited taxonomic importance (cf. *Brachythecium rivulare*).

#### **Bryhnia** (Figs. 66-68)

Species studied: *B. novae-angliae* (Sull. et Lesq.) Grout.

The teeth are abruptly tapered in the transition zone. In the lower part the stout dorsal trabeculae are somewhat exerted above the cris-



Figs. 57-65. Ventral trabeculae of upper part of tooth (57-60, 62-65), ventral trabeculae of lower part of tooth (61) of *Eurhynchium*. 57. *Eurhynchium angustirete* (Broth.) Kop. (Russia, Moscow Prov., Ignatov 29.IV.1985): 2900x; 58&61. *E. asperisetum* (C. Müll.) Bartr. (Papua New Guinea, T. Koponen 30850): 2000x&1630x; 59. *E. striatum* (Hedw.) Schimp. (Russia, Krasnodar Territory, L. Vasil'eva, 16.VIII.1935): 5900x; 60. *E. pulchellum* (Hedw.) Jenn. (Russia, Altai, Ignatov 0/1226): 1830x; 62. *E. praelonga* (Hedw.) Ochyra (Aslatia, Schimper): 2400x; 63. *E. savatieri* Schimp. ex Besch. (Japan, Mockiziki, 1143): 2950x; 64. *E. hians* (Hedw.) Sande Lac. (Russia, Pskov Province, Ignatov & Zolotov 20.X.1996): 1900x; 65. *E. schleicheri* (Hedw. f.) Jur. (C. Jensen, Musci Danici, 5.11.1899): 1500x.

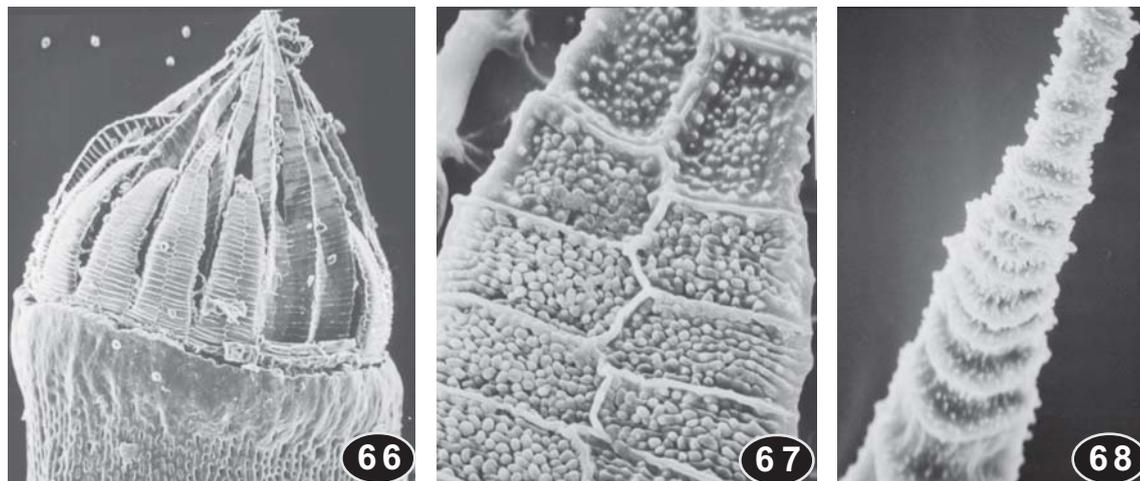


Fig. 66-68. *Bryhnia novae-angliae* (Sull. et Lesq.) Grout (China, T. Koponen). 66. Peristome, 105x; 64. Outer surface of middle part of tooth, 1400x; 65. Inner surface in upper part of tooth, 1000x.

tae, the cristae are straight, smooth to lowly wavy-papillose. In the transition zone a few plates are densely papillose, in the upper part the plates are lowly papillose, with papillae in longitudinal rows. The dorsal trabeculae are exserted, and the margin is incrassate, lowly papillose, but relatively highly papillose in the uppermost non-trabeculate zone. The ventral trabeculae are smooth to sparsely and lowly papillose.

The exostome character states are within the variation of *Brachytecium*.

#### **Cirriphyllum** (Figs. 69, 71, 73)

Species studied: *C. piliferum* (Hedw.) Grout

The teeth are abruptly tapered in the transition zone, and serrulate above. In the lower part the dorsal trabeculae are lowly exserted above the cristae. The cristae are dense, smooth to lowly wavy-papillose. In the transition zone 4-5 plates are densely covered by large round papillae, and the dorsal trabeculae here are relatively higher, and somewhat flexuose. In the upper part of teeth the dorsal trabeculae are low, and the papillae are arranged in longitudinal rows. The margin is incrassate and sparsely lowly papillose. The ventral trabeculae are highly ligulate, thin, with sparse and low papillae.

The exostome character states of *Cirriphyllum* are within the variation of *Brachytecium*. However there are a number of differences between *C. piliferum* and *Brachytecium cirrosomum*, a species often treated within *Cirriphyllum*. However according to Robinson (1962) and Ignatov (1998), the latter species should

not be placed in *Cirriphyllum*. The present study adds two more differences between these species. In *B. cirrosomum* the teeth are abruptly tapered in the transition zone, and the ventral trabeculae have relatively high papillae (like in *Eurhynchium spp.*, *Brachytecium velutinum*, etc.). *Cirriphyllum piliferum* has gradually tapered teeth with 4-5 plates covered by round-papillae, and the ventral trabeculae are covered by sparse and low papillae (cf. Figs. 69-74).

#### **Myuroclada** (Figs. 75-78)

Species studied: *M. maximowiczii* (Borszcz.) Steere et Schof.

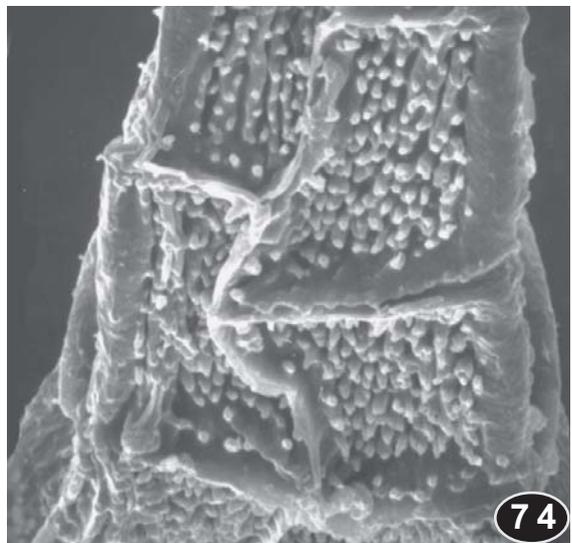
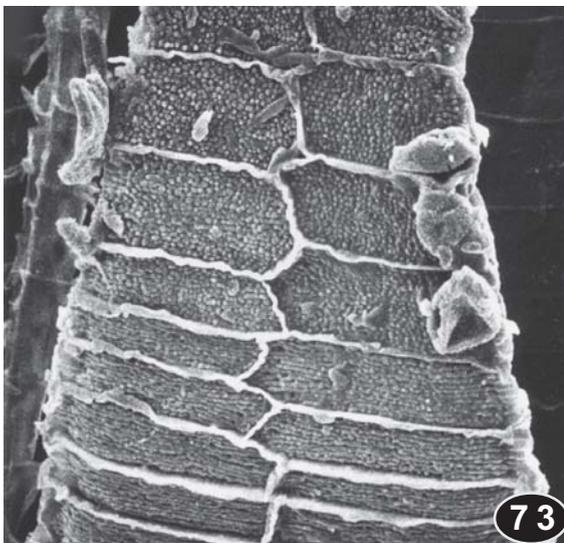
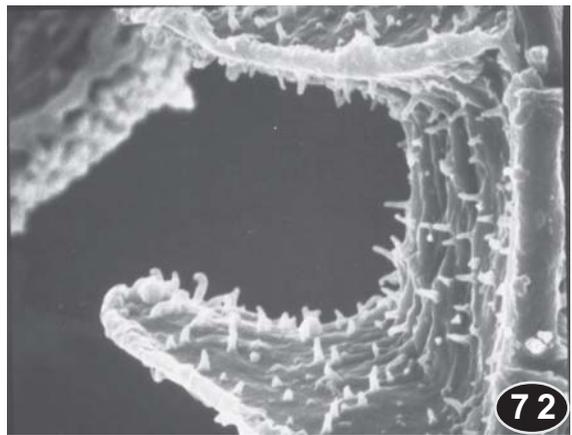
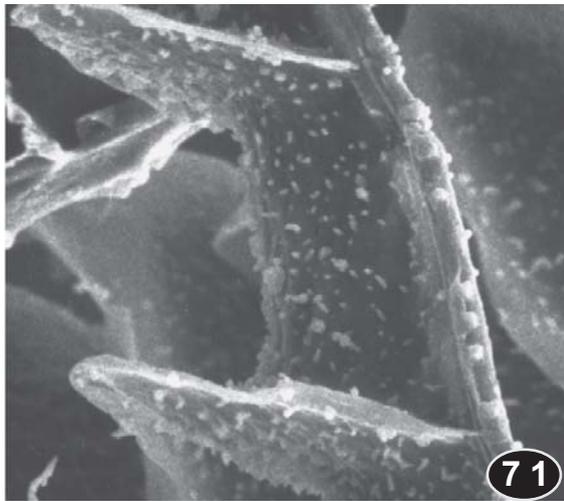
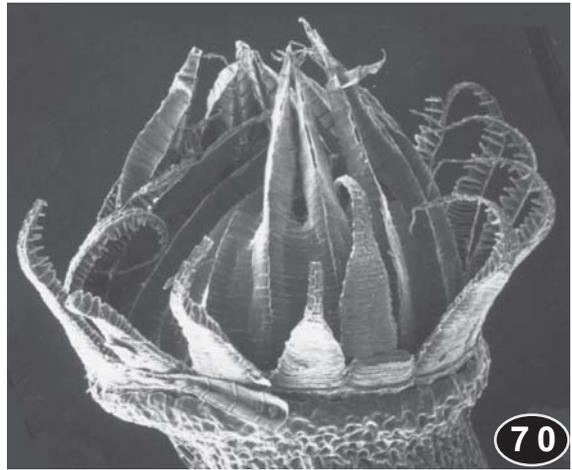
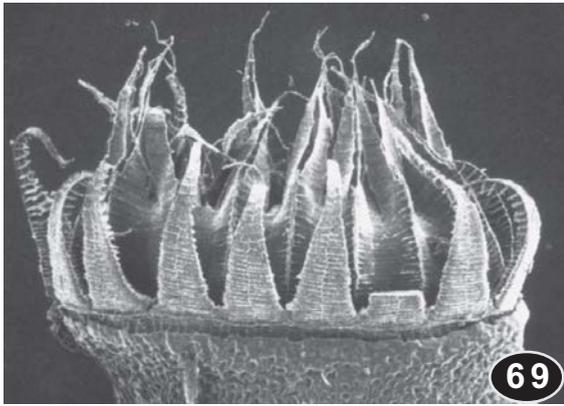
The teeth are abruptly tapered, and are serrulate above. In the lower part the dorsal trabeculae are lowly exserted. In the transition zone 2-4 plates have dense, round papillae, masking the cristae. In the upper part the plates are papillose, without clear longitudinal rows. The dorsal trabeculae are low and lowly papillose, and the margin is moderately incrassate and papillose. The ventral trabeculae are semi-orbicular, incrassate, and densely conic-papillose.

The exostome character states are within the variation of *Brachytecium* and are especially similar to those in some *Eurhynchium* species.

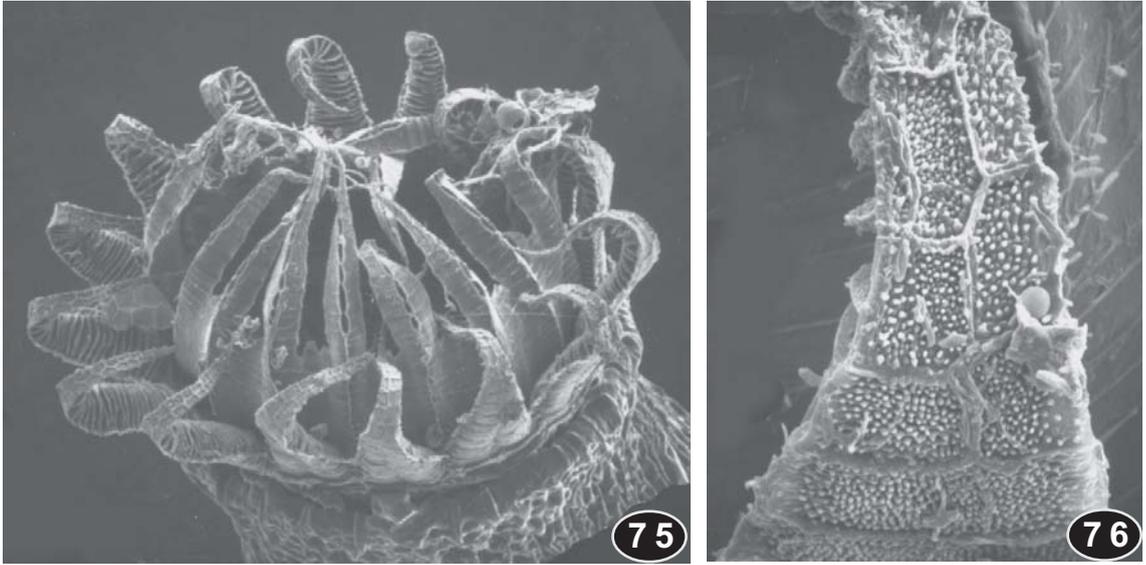
#### **Bryoandersonia** (Figs. 79-81)

Species studied: *B. illecebra* (Hedw.) Robinson.

The teeth are gradually tapered in the transition zone and are serrulate above. In the lower part the dorsal trabeculae are lowly exserted above the cristae. In the transition zone 4-5 plates are densely covered by large round papillae. The dorsal trabeculae in the transition zone are relatively



Figs. 69-74. 69, 71, 73 – *Cirriphyllum piliferum* (Hedw.) Grout (Finland, Roivainen, 13.V.1961) and 70, 72, 74 – *Brachythecium cirrosum* (Schwaegr.) Schimp. (China, Sichuan, Si He, 30410). 69&70 – peristome, 73&74 – outer surface of tooth in middle part, 850x&2700x; 71&72 – side view of upper tooth, showing inner trabeculae, 2950x&2570x.



Figs. 75-78. *Myuroclada maximowiczii* (Borszcz.) Steere et Schof. (Verdoorn, Exs. n° 282): 75. Peristome, 127x; 2. Outer surface of tooth in the middle, 960x; 3 - outer surface of tooth in upper part, 1600x; 4 - side view of tooth, showing inner trabeculae, 1600x.

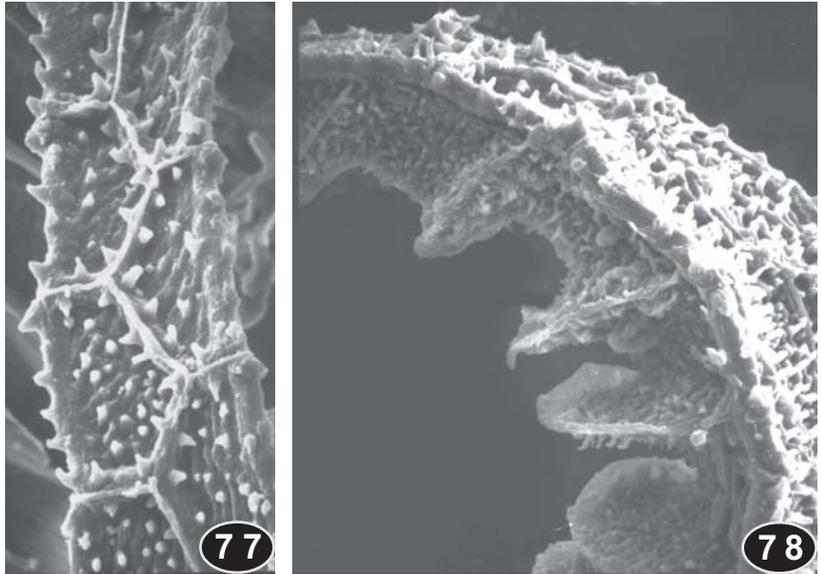
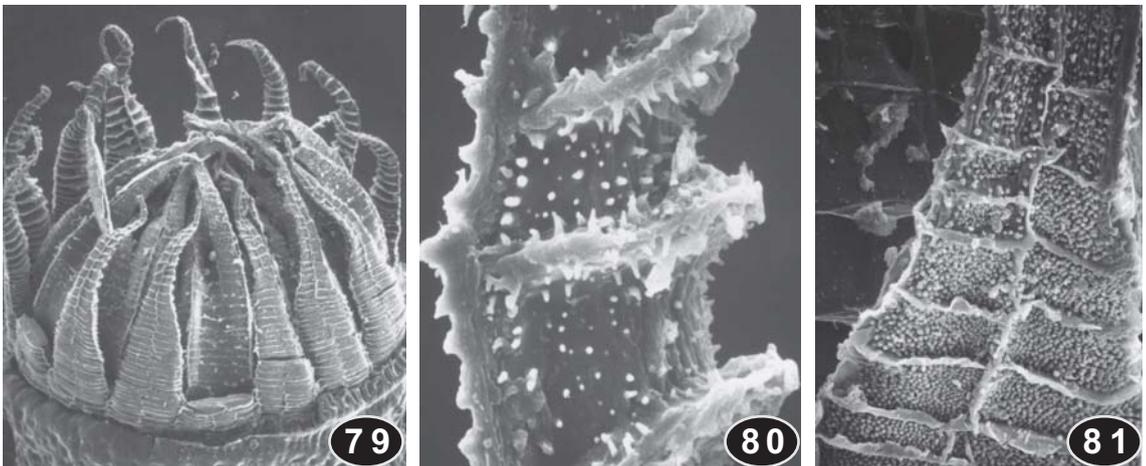


Fig. 79-81. *Bryoandersonia illecebra* (Hedw.) Robinson (USA, Evans, X.1890): 79. Peristome, 85x; 80. Ventral surface and trabeculae, 2050x; 81. Outer surface of tooth in the middle, 640x.



high, in the upper part the dorsal trabeculae are prominent, with round papillae as well as the distinctly incrassate margin. The plates are longitudinally striolate, and the cristae covered by small scattered papillae. The ventral trabeculae are semiorbicular, somewhat incrassate, rugulose, with relatively high papillae near the margin of the inner plates and ventral trabeculae, and with lower papillae in their central (median) part.

The exostome character states are within the variation of *Brachythecium*.

### **Scleropodium** (Figs. 82-87)

Species studied: *S. caespitans* (C. Müll.) L. Koch, *S. tourettii* (Brid.) L. Koch.

In two species studied exostomes were found different in many characters:

|                            | <i>S. caespitans</i>                          | <i>S. tourettii</i>                    |
|----------------------------|---|--|
| teeth shape                | gradually tapered                             | abruptly tapered                       |
| margins above              | entire  | serrulate                              |
| cristae in transition zone | loose with sparse small papillae upon cristae | dense with high-wavy papillose cristae |
| ventral trabeculae         | with sparse very low papillae                 | densely, highly conic-papillose        |

The diversity of exostome character states in *Scleropodium* is within that of *Brachythecium*, but the former is a small genus and such heterogeneity could indicate a polyphyletic origin of species presently included in *Scleropodium*. Further studies are needed to understand if this genus is monophyletic or not.

### **Rhynchostegium** (Figs. 88-99 & 101) and **Steerecleus** (Figs. 100)

Species studied: *R. confertum* (Dicks.) B.S.G., *R. herbaceum* (Mitt.) Jaeg., *R. inclinatum* (Mitt.) Jaeg., *R. javanicum* (Bel.) Besch., *R. murale* (Hedw.) B.S.G., *R. pallidifolium* (Mitt.) Jaeg., *Steerecleus serrulatum* (Hedw.) Robinson.

The teeth in *Rhynchostegium* are abruptly tapered in the transitional zone and are slightly serrulate to subentire above. The lower part is relatively massive, with a somewhat immersed median line. The ventral trabeculae end shortly above the transition zone, so that the uppermost, non-trabeculate part is relatively long (10-15 plates). In the lower part the dorsal trabeculae are shortly exerted above the cristae. The cristae below are dense, straight, wavy-papillose or with bead-like papillae (*R. pallidifolium*, *R. in-*

*clinatum*, *R. herbaceum* – Fig. 93), further above, closer to the transition zone the cristae are papillose. In the upper part the dorsal trabeculae are relatively low and papillose (the uppermost non-trabeculate part is more densely papillose on both surfaces, Fig. 94). The margin is incrassate and papillose, the papillae on the plates are arranged in longitudinal rows, or rarely not in rows. The ventral trabeculae are semiorbicular, slightly incrassate, evenly densely lowly papillose in most species (high-papillose in *R. murale*), but the ventral plates are sometimes more strongly papillose than the trabeculae. The uppermost low trabeculae are often more densely papillose, with high, cylindric papillae.

Two species are peculiar in their exostome characters:

*R. inclinatum*. In the upper part of teeth the outer plate angles bear high papillae, which are paired at the joint of the plates, forming “swallow-tail”-shaped double papillae (Figs. 89, 101). This character is clearly seen under the compound microscope and can be used for the identification of this species.

*R. murale*. The teeth are relatively gradually tapering upward in the transition zone, have an extensive area in the transition zone covered by big round papillae (like in *Brachythecium laetum*, Fig. 22), and the ventral trabeculae in the upper part have relatively dense high papillae (Fig. 99) [though another specimen studied had lower and sparser papillae on the ventral trabeculae, and higher papillae were restricted to the uppermost non-trabeculate part].

As a whole, *Rhynchostegium* resembles *Brachythecium*, but many species are peculiar in their very abruptly tapering teeth, with a relatively incrassate lower part (so median line somewhat immersed), long uppermost non-trabeculate part, and relatively uniform, thin semiorbicular ventral trabeculae with evenly arranged low papillae. *Rhynchostegium* differs from *Platyhypnidium* by teeth that are massive only below and in the long, narrow and delicate upper part.

*Steerecleus serrulatus* was traditionally placed in *Rhynchostegium*, but Robinson (1987) segregated it and some other neotropical species in a new genus *Steerecleus*. The present study supports this idea, since *S. serrulatus* would be anomalous in *Rhynchostegium* with its strongly adaxially papillose teeth, more resembling *Eurhynchium*.

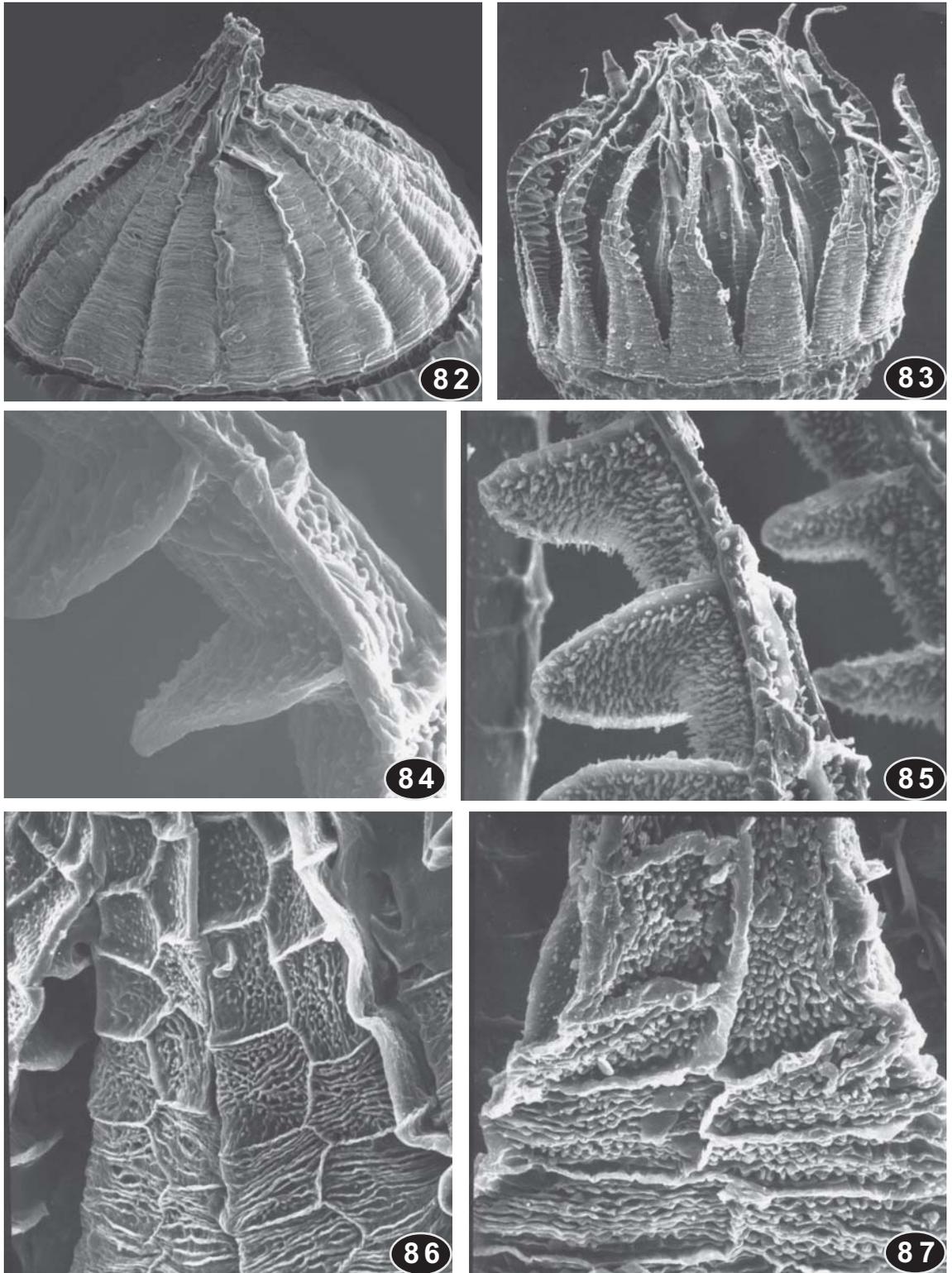
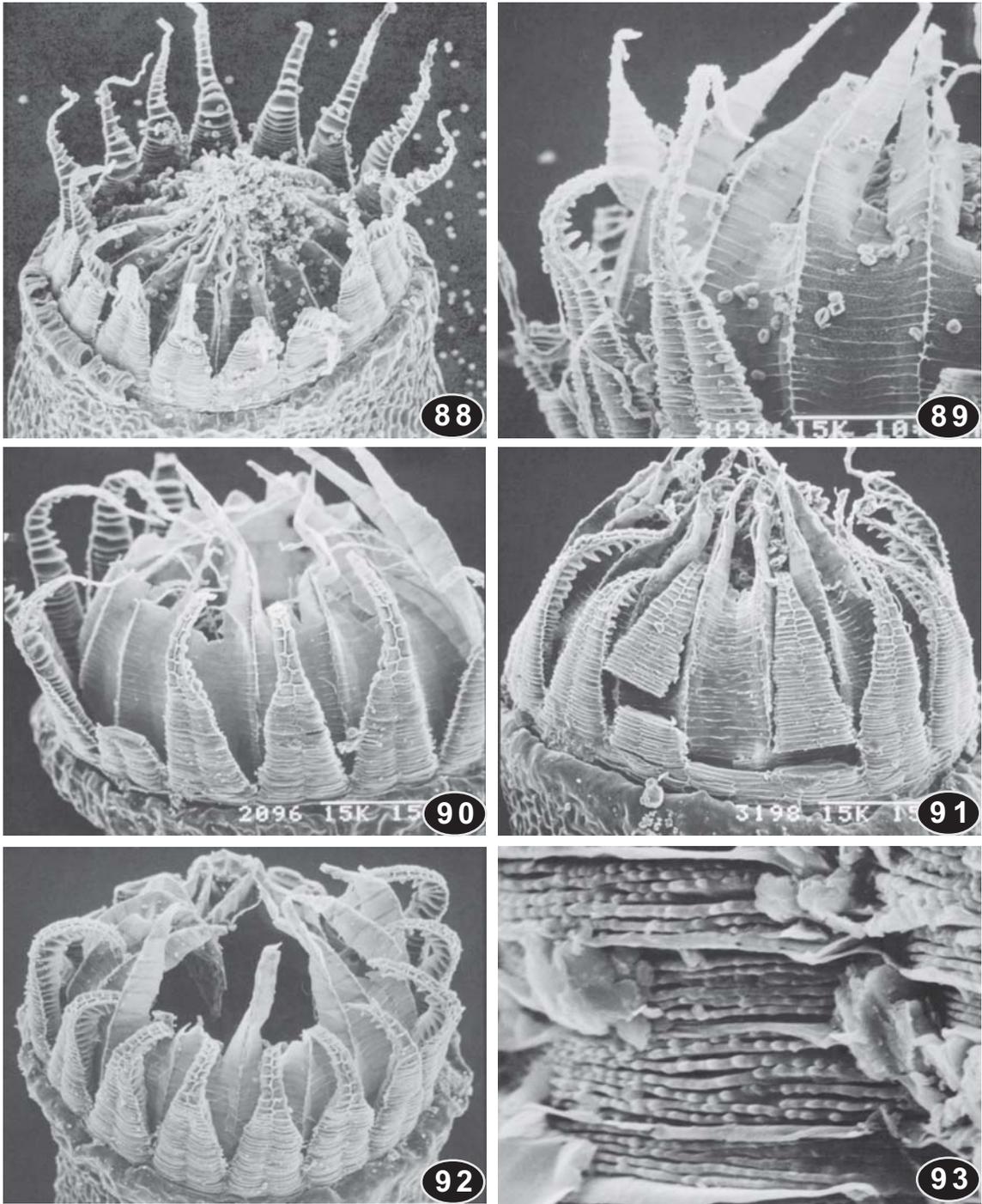
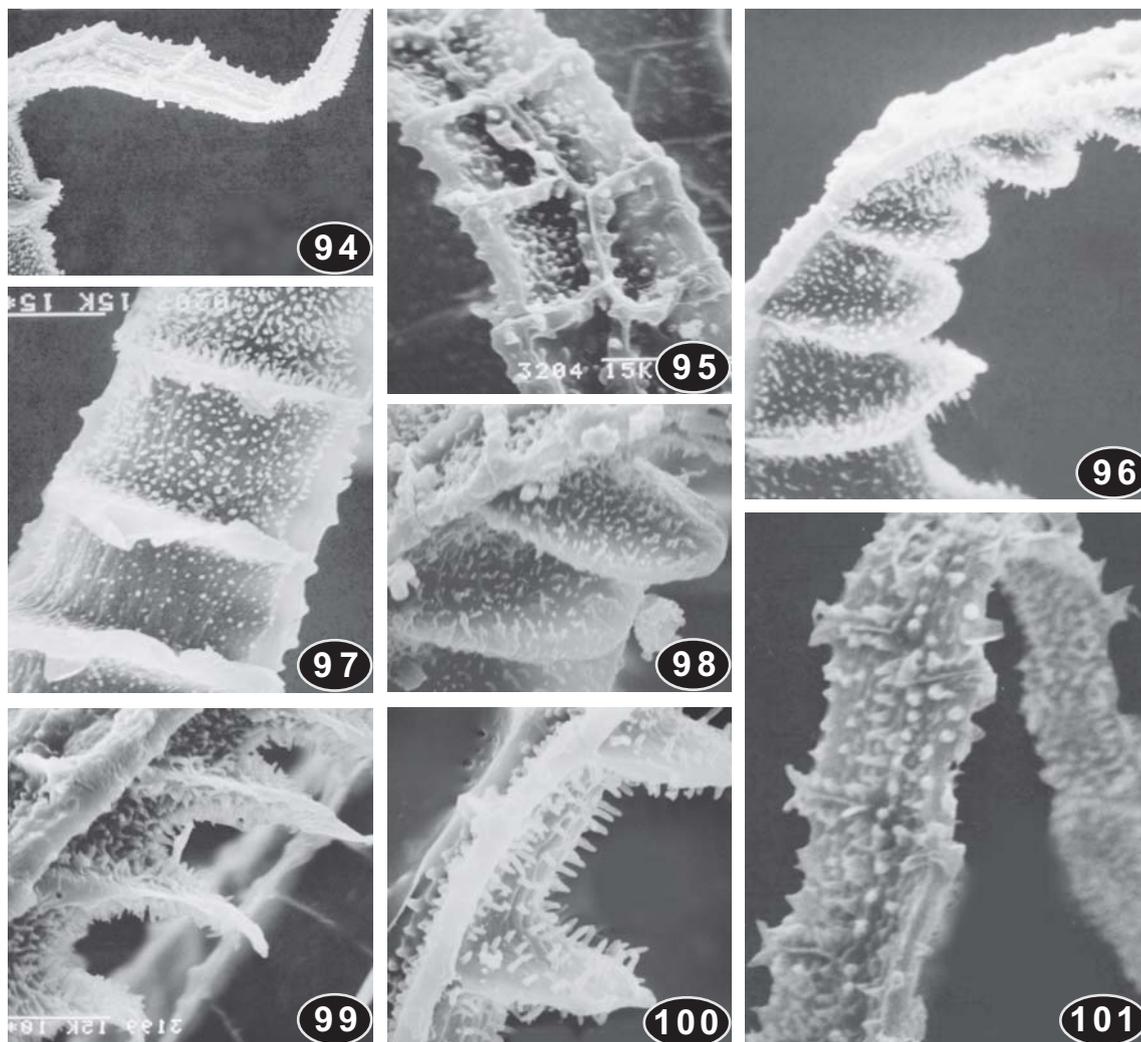


Fig. 82-87. *Scleropodium*. 82, 84, 86 – *S. caespitans* (C. Muell.) L. Koch (Canada, Schofield 20410); 83, 85, 87 – *S. tourettii* (Brid.) L. Koch (USA, California). 82&83. Peristomes, 176x&108x; 84&85. Side view of teeth, showing inner trabeculae, 2400x&1600x; 86&87. Outer surface of teeth in transition zone, 1040x&1600x.



Figs. 88-93. Peristomes (88-92) and outer surface of tooth in lower part (93) of *Rhynchoszegium*. 88. *R. javanicum* (Bél.) Besch. (Papua New Guinea, Koponen, 34252): 95x; 89. *R. inclinatum* (Mitt.) Jaeg. (Taiwan, J. Suzuki 1.I.1927): 260x; 90. *R. pallidifolium* (Mitt.) Jaeg. (Japan, Uematsu, 425): 150x; 91. *R. murale* (Hedw.) B.S.G. (Russia, Moscow Province, Ignatov, 6.VII.1988): 150x; 92. *R. confertum* (Dicks.) B.S.G. (USSR, Abkhazia, Ignatov, 27.VII.1987): 160x; 93. *R. inclinatum* (l. c.): 3130x.



Figs. 94-101. Upper parts of teeth of *Rhynchostegium* and *Steerecleus* (94 – uppermost non-trabeculate part; 95, 101 – outer surface; 96-100 – side views showing ventral trabeculae). 94. *R. javanicum* (Bél.) Besch. (Papua New Guinea, Koponen, 34252): 865x; 95. *R. confertum* (Dicks.) B.S.G. (USSR, Abkhazia, Ignatov, 27.VII.1987): 1650x; 96. *R. pallidifolium* (Mitt.) Jaeg. (Japan, Uematsu, 425): 1350x; 97. *R. javanicum* (l. c.): 1450x; 98. *R. confertum* (l. c.): 1650x; 99. *R. murale* (l. c.): 1700x; 100. *Steerecleus serrulatum* (Hedw.) Robinson (U.S.A., Norris 11456): 2180x; 101. *R. inclinatum* (Mitt.) Jaeg. (Taiwan, J. Suzuki 1.I.1927): 1900x.

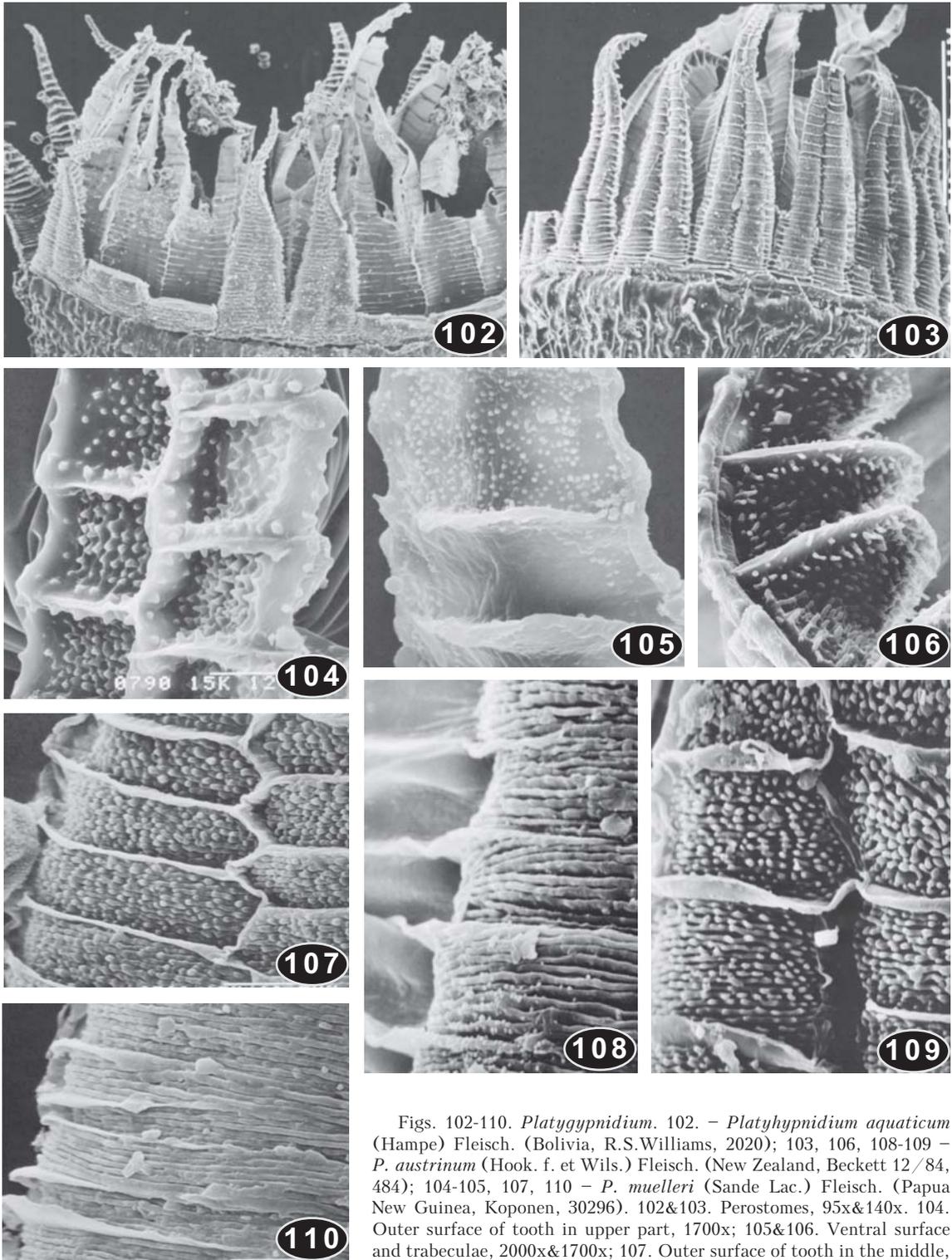
### **Platyhypnidium** (Figs. 102-113)

Species studied: *P. aquaticum* (Hampe) Fleisch., *P. austrinum* (Hook. f. et Wils.) Fleisch., *P. muelleri* (Sande Lac.) Fleisch., *P. riparioides* (Hedw.) Dix.

The important character state of all of species studied is the strongly incrassate teeth, due to additional deposits of cell-wall material of both OPL and PPL. Most material is deposited on the central part of the OPL cell wall, so the columns of the OPL' cell remains appear somewhat convex whereas the median line appears somewhat immersed. In the lower tooth the latter is slightly zig-zag-shaped, or in *P.*

*austrinum* straight. Hygroscopic movements in *Platyhypnidium* are more limited and unusually slow comparatively with *Rhynchostegium* or *Eurhynchium*. In addition, the following are characteristic for all species of *Platyhypnidium*. In the lower teeth the cristae are smooth. In the transition zone, several plates have dense large papillae. In the upper tooth, longitudinal rows of papillae on the outer plates are indistinct to lacking. Finally, the ventral trabeculae are relatively densely and lowly papillose.

*Platyhypnidium austrinum* is the most pe-



Figs. 102-110. *Platygygnidium*. 102. – *Platygygnididium aquaticum* (Hampe) Fleisch. (Bolivia, R.S.Williams, 2020); 103, 106, 108-109 – *P. austrinum* (Hook. f. et Wils.) Fleisch. (New Zealand, Beckett 12/84, 484); 104-105, 107, 110 – *P. muelleri* (Sande Lac.) Fleisch. (Papua New Guinea, Koponen, 30296). 102&103. Peristomes, 95x&140x. 104. Outer surface of tooth in upper part, 1700x; 105&106. Ventral surface and trabeculae, 2000x&1700x; 107. Outer surface of tooth in the middle, 1500x; 108. Side view of tooth in lower part, showing small papillae on cristae, 2450x; 109. Outer surface of tooth in lower part showing immersed median line, 1750x; 110. Outer surface of tooth in lower part, 1700x.

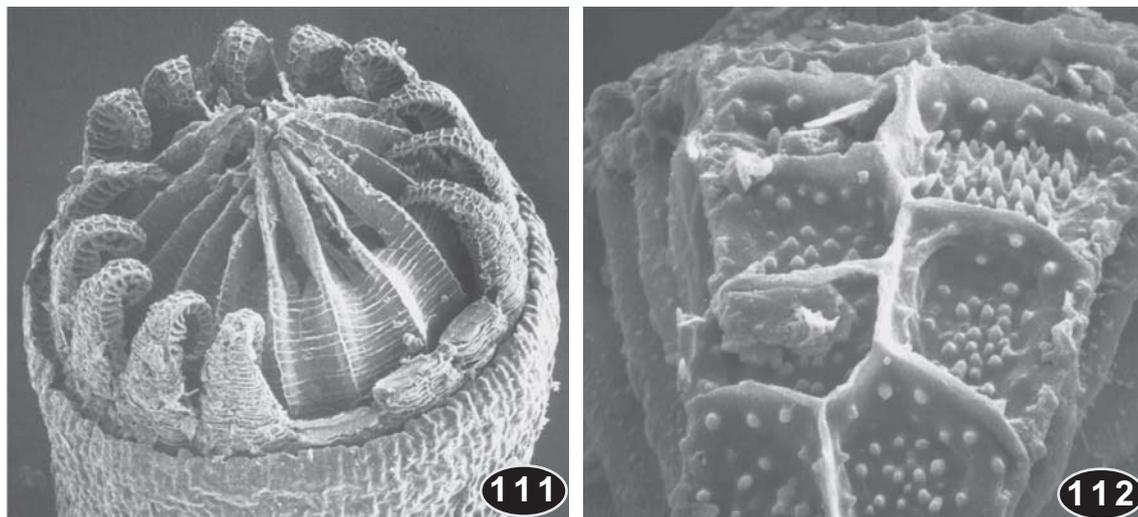


Fig. 111-113. *Platyhypnidium riparioides* (Hedw.) Dix. (USA, Reed, 64277). 111 – peristome, 130x; 112 – outer surface of tooth in upper part, 2000x; 113 – side view of tooth, showing ventral trabeculae, 1650x.

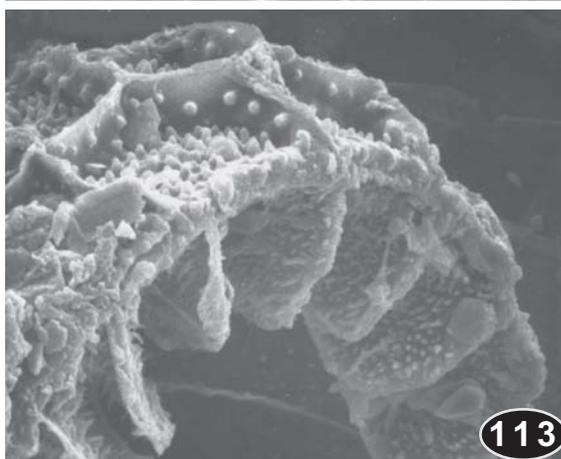
cular species in its clearly straight median line and relatively slightly curved teeth (Figs. 103, 109), and in its more strongly papillose ventral trabeculae (Fig. 106). This species has also the most special gametophytic characters in the genus.

Differences between the species include characters of the dorsal trabeculae in the lower part of the teeth (exserted above cristae in *P. riparioides* and *P. aquaticum*, not-exserted in *P. austrinum* and *P. muelleri*) and the dorsal upper trabeculae (much higher in *P. riparioides* than in the other species).

#### **Palamocladium** (Figs. 114-123)

Species studied: *P. euchloron* (C. Muell.) Wijk et Marg., *P. leskeoides* (Hook.) Britt.

Both species studied have unique character states not observed in the other *Brachytheciaceae*. Relatively high and solid longitudinal cristae on the outer surface of the upper tooth (more similar to the cristae of the lower teeth, than to the longitudinal ridges of the upper teeth of *Brachythecium*). Both species have also relatively massive teeth that gradually taper in the transition zone and are joined by 5-13 basal plates. The dorsal trabeculae in the lower teeth are high, reaching upwards above the middle. In the lower part the cristae have small bead-like papillae, in the upper part the longitudinal cristae are distinct and high, smooth or covered by sparse, small papillae. In the uppermost, non-trabeculate part of



the teeth the papillae are denser. The dorsal trabeculae are low, with relatively high conic papillae, and the margin is moderately incrassate and highly conic papillose. The ventral trabeculae are triangular, incrassate, unevenly papillose, with spinulose to short-conic papillae.

In *P. leskeoides* the marginal zone of teeth in the lower and middle parts is exceptionally thin and wide, forming “wings”. This feature was not observed in *P. euchloron* and was not reported for *P. leskeoides* by Hofmann (1997), who illustrated American specimen of this species.

The exostomes of *Palamocladium euchloron* and *P. leskeoides* differ in the extensive transition zone of the former, with many plates having high and dense papillae that mask the cristae, whereas in *P. leskeoides* the transition from transversal to longitudinal cristae is very abrupt (Figs. 118, 122).

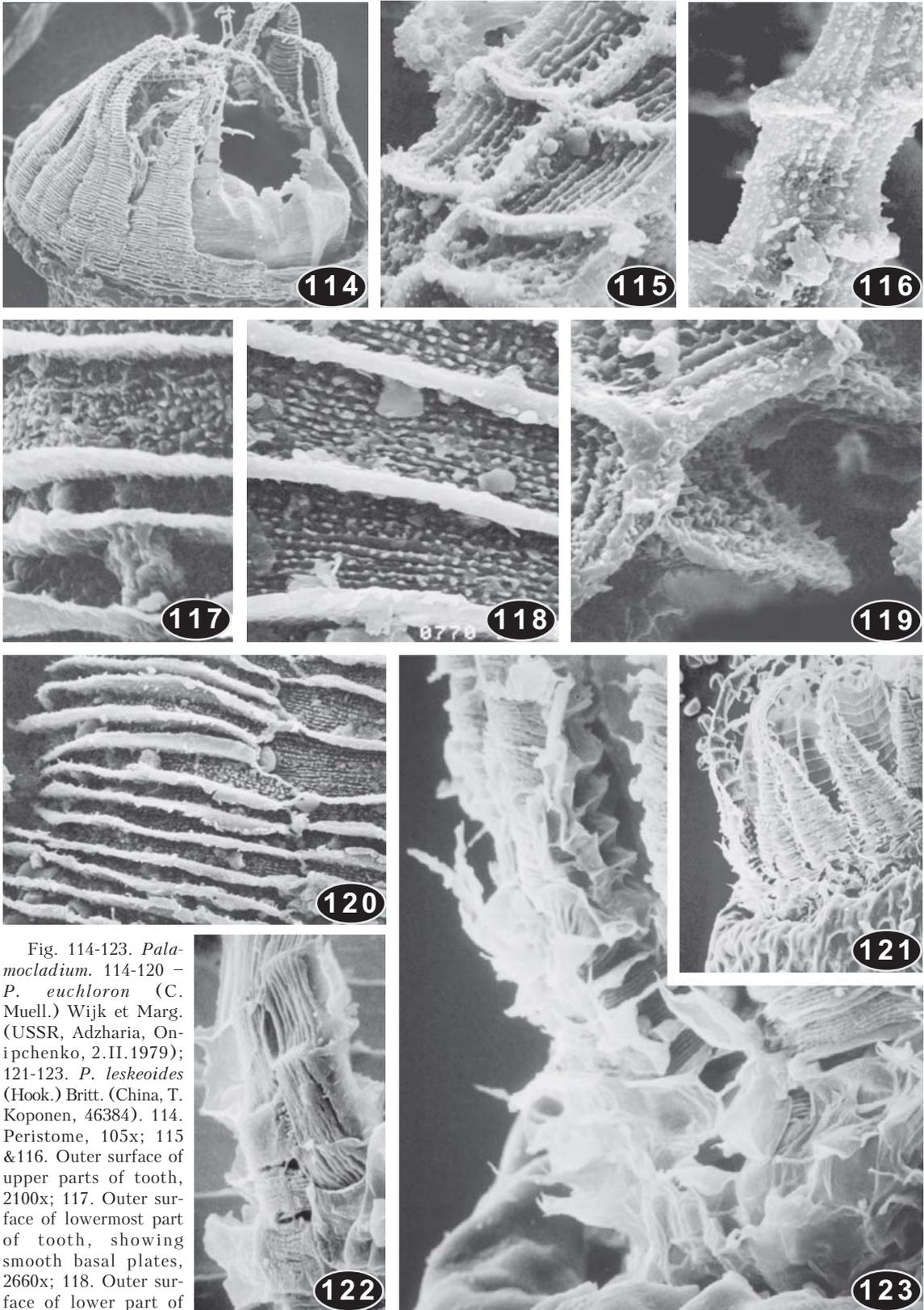
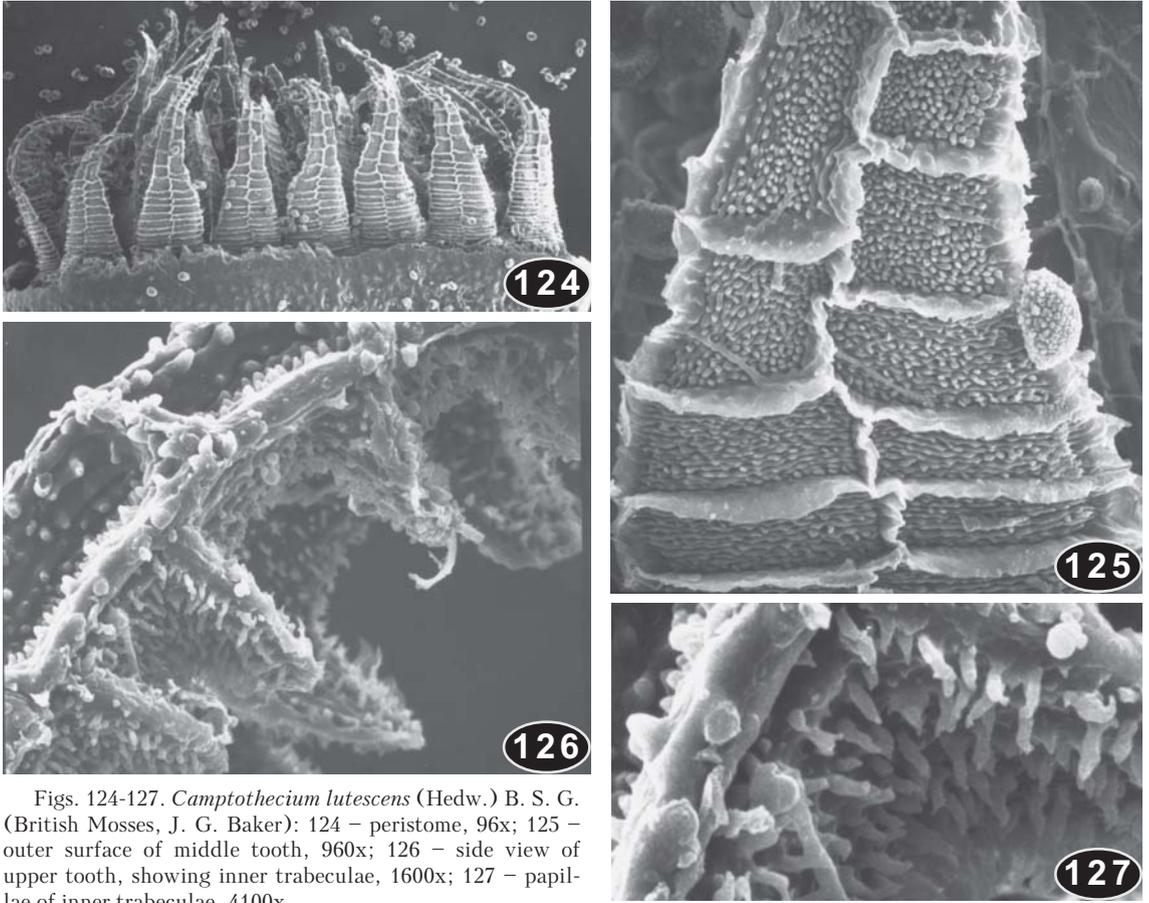


Fig. 114-123. *Palaeocladium*. 114-120 – *P. euchloron* (C. Muell.) Wijk et Marg. (USSR, Adzharia, Onipchenko, 2.II.1979); 121-123. *P. leskeoides* (Hook.) Britt. (China, T. Koponen, 46384). 114. Peristome, 105x; 115 & 116. Outer surface of upper parts of tooth, 2100x; 117. Outer surface of lowermost part of tooth, showing smooth basal plates, 2660x; 118. Outer surface of lower part of

tooth, 2660x; 119. Side view of ventral trabecula, 3370x; 120. Outer surface of lower part of tooth, 980x; 121. Peristome, 210x; 122. Outer surface of tooth in upper part, 1330x; 123. Basal parts of teeth, showing wing-like thin edges of teeth, 1140x.



Figs. 124-127. *Camptothecium lutescens* (Hedw.) B. S. G. (British Mosses, J. G. Baker): 124 – peristome, 96x; 125 – outer surface of middle tooth, 960x; 126 – side view of upper tooth, showing inner trabeculae, 1600x; 127 – papillae of inner trabeculae, 4100x.

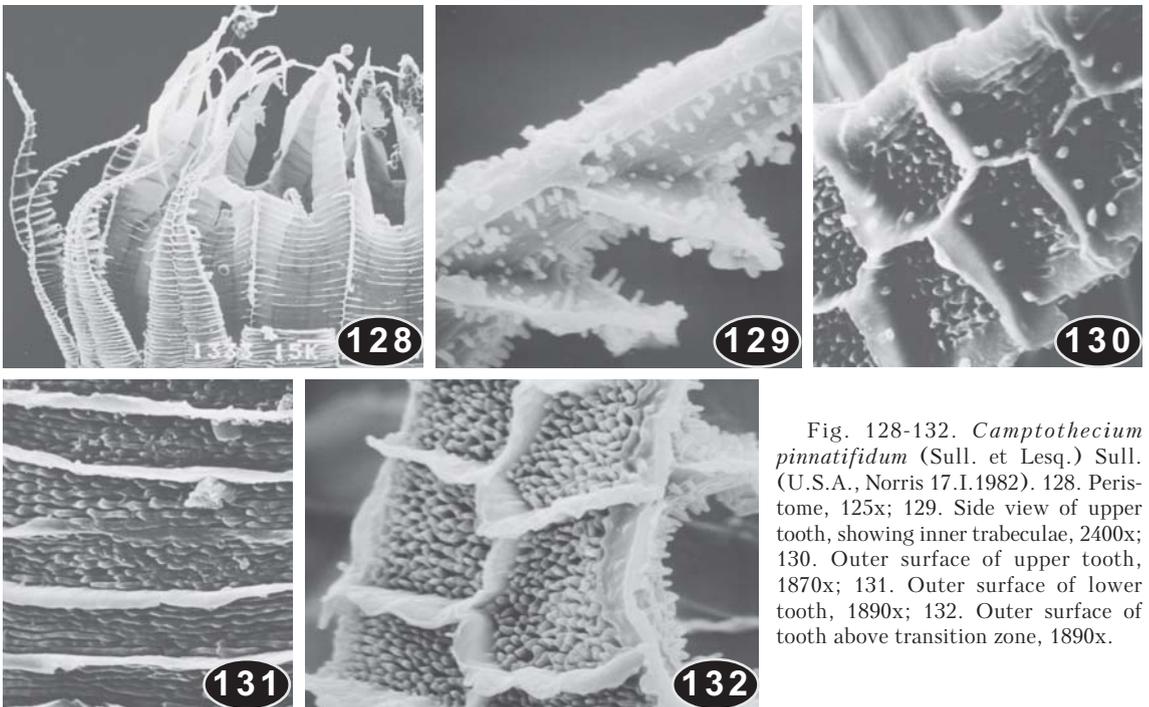


Fig. 128-132. *Camptothecium pinnatifidum* (Sull. et Lesq.) Sull. (U.S.A., Norris 17.I.1982). 128. Peristome, 125x; 129. Side view of upper tooth, showing inner trabeculae, 2400x; 130. Outer surface of upper tooth, 1870x; 131. Outer surface of lower tooth, 1890x; 132. Outer surface of tooth above transition zone, 1890x.

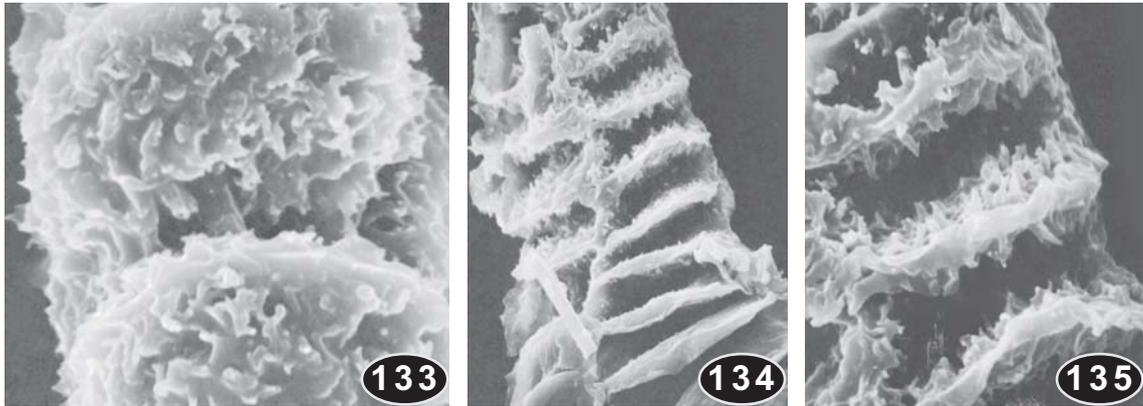


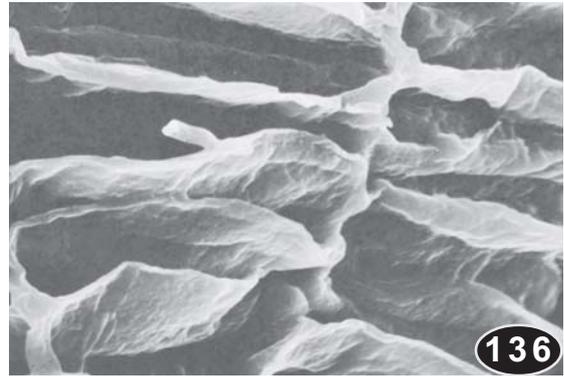
Fig. 133-136. *Homalothecium laevisetum* (Hedw.) B. S. G. (Japan, H. Mayr, 3). 133. Ventral surface and trabeculae, 3110x; 134. Outer surface of tooth in transition zone, 1260x; 135. Outer surface of tooth above transition zone, 3150x; 136. Outer surface of lower tooth, 2300x.

#### **Homalothecium and Camptothecium** (Figs. 124-155)

Species studied: *Camptothecium lutescens* (Hedw.) B. S. G., *C. pinnatifidum* (Sull. et Lesq.) Sull., *Homalothecium aeneum* (Mitt.) Lawt., *H. laevisetum* Sande Lac., *H. nuttallii* (Wils.) Jaeg., *H. philippeanum* (Spruce) B. S. G., *H. sericeum* (Hedw.) B. S. G.

We studied five species of *Homalothecium* s. str. and to of *Camptothecium* (all sometimes considered within *Homalothecium* s. lat.). Peristomes were found to differ considerably between and within this genera. *Homalothecium sericeum*, *H. philippeanum*, *H. laevisetum*, *H. nuttallii*, *H. aeneum* have hygrocastique peristomes (with teeth straight when wet), whereas *Camptothecium lutescens* (*Homalothecium lutescens*) and *C. pinnatifidum* (*H. pinnatifidum*) have xerocastique peristomes (teeth covering the urn when wet). The two latter species are similar to each another in their curved capsules, well-developed endostome and many structural characters of the exostome: (1) in the lower part the dorsal trabeculae are moderately high, thin, smooth; (2) in the lower part the cristae are dense and wavy; (3) in the transition zone the plates are densely papillose, with large round papillae; (4) in the upper part the papillae are arranged in longitudinal rows; (5) the incrassate margin is differentiated; (6) the ventral trabeculae are semiorbicular-triangular, moderately incrassate, and have high cylindrical papillae (Figs. 124-132).

Contrary to this, the five other studied species of *Homalothecium* have straight capsules,



strongly reduces endostomes, and the states of the exostome characters mentioned above are nearly totally different. However these 5 species themselves exhibit strong diversity, which can be understood as a series of reductions as follows:

I. *Homalothecium laevisetum* (Figs. 133-136) has the most derived exostome with: (1) very high and stout dorsal trabeculae, up to 2/3 of teeth length or more; (2) smooth lower dorsal plates and trabeculae, becoming papillose only above the transition zone; (3) high and branched papillae in upper tooth, not arranged in longitudinal rows; (4) low-semiorbicular, much incrassate, rugose and densely papillose ventral trabeculae, with irregular-shaped large papillae.

II. *Homalothecium philippeanum* (Figs. 137-141) has also high dorsal trabeculae, but the plates in the lower teeth are distinctly striolate with cristae covered by small bead-like papillae. In the upper part the papillae are arranged in longitudinal rows.

III. *Homalothecium sericeum* (Figs. 142-146) is similar to two above species in its high dorsal trabeculae in most parts of the tooth, but differs

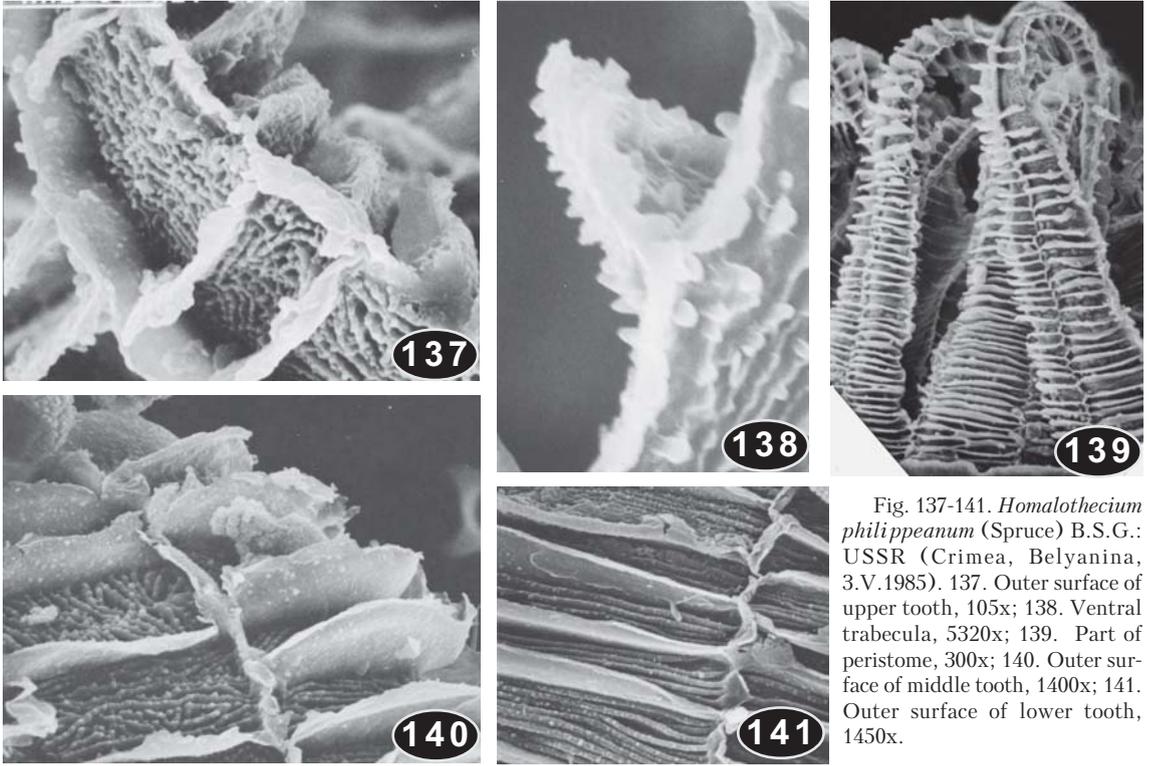


Fig. 137-141. *Homalothecium philippeanum* (Spruce) B.S.G.: USSR (Crimea, Belyanina, 3.V.1985). 137. Outer surface of upper tooth, 105x; 138. Ventral trabecula, 5320x; 139. Part of peristome, 300x; 140. Outer surface of middle tooth, 1400x; 141. Outer surface of lower tooth, 1450x.

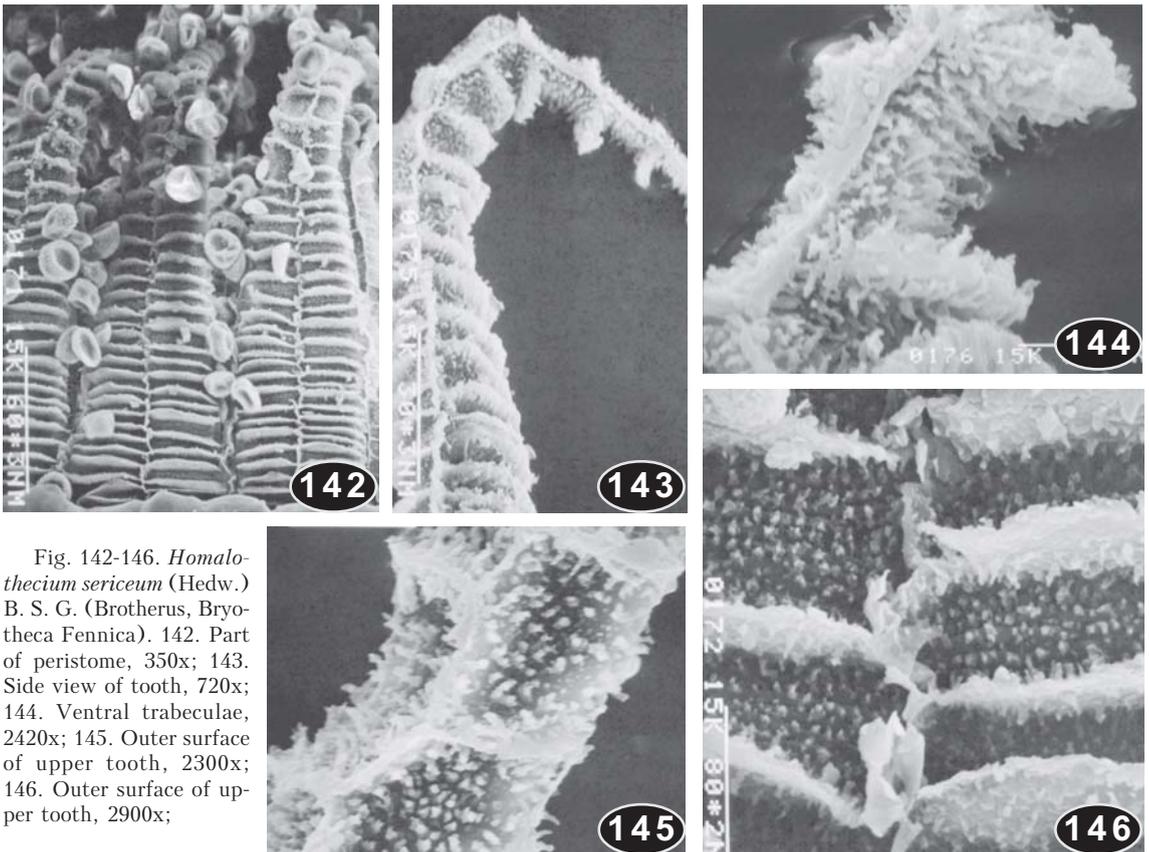


Fig. 142-146. *Homalothecium sericeum* (Hedw.) B. S. G. (Brotherus, Bryotheca Fennica). 142. Part of peristome, 350x; 143. Side view of tooth, 720x; 144. Ventral trabeculae, 2420x; 145. Outer surface of upper tooth, 2300x; 146. Outer surface of upper tooth, 2900x;

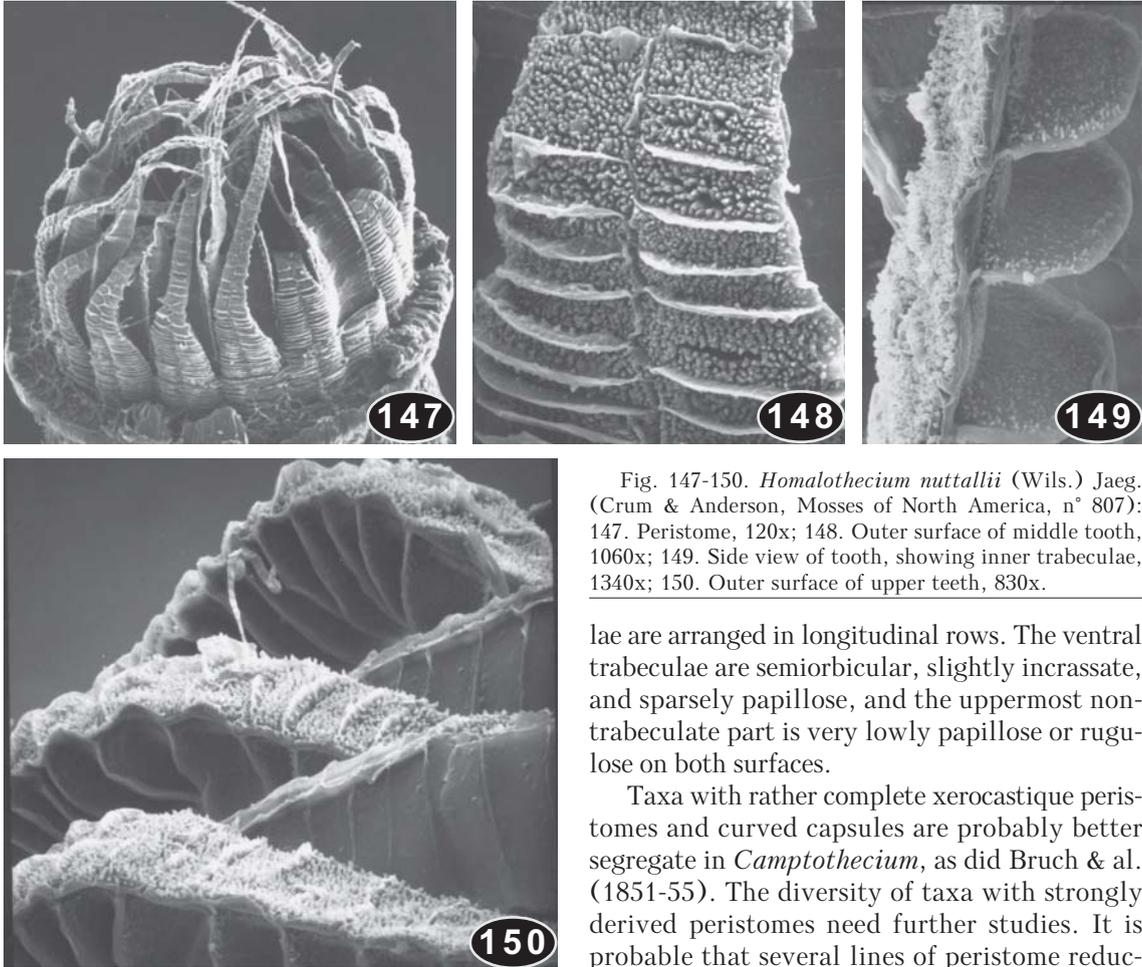


Fig. 147-150. *Homalothecium nuttallii* (Wils.) Jaeg. (Crum & Anderson, Mosses of North America, n° 807): 147. Peristome, 120x; 148. Outer surface of middle tooth, 1060x; 149. Side view of tooth, showing inner trabeculae, 1340x; 150. Outer surface of upper teeth, 830x.

lae are arranged in longitudinal rows. The ventral trabeculae are semiorbicular, slightly incrassate, and sparsely papillose, and the uppermost non-trabeculate part is very lowly papillose or rugulose on both surfaces.

Taxa with rather complete xerocastique peristomes and curved capsules are probably better segregate in *Camptothecium*, as did Bruch & al. (1851-55). The diversity of taxa with strongly derived peristomes need further studies. It is probable that several lines of peristome reductions will be found, so that the genus may need further splitting into smaller and more homogeneous entities.

#### **Homalotheciella** (Figs. 156-159)

Species studied: *H. subcapillata* (Hedw.) Broth.

Exostome ornamentation of *H. subcapillata* is rather similar to that of *Homalothecium sericeum*. Both have very gradually tapered teeth, the dorsal trabeculae are highly exserted in at least 2/3 of the tooth length. The cristae and trabeculae are densely covered by branched papillae, in the upper part also densely papillose with branched papillae that are not arranged in longitudinal rows. The margin is not incrassate and the ventral trabeculae are lowly semiorbicular, incrassate, and papillose. Differences between *Homalotheciella* and *Homalothecium sericeum* include more dense papillae on outer plates in the former, making cristae hardly discernible,

in having densely papillose dorsal trabeculae. It is similar to *H. philippeanum* in having cristae on plates below, but differs in having high and branched papillae – they are high and branched (bead-like in *H. philippeanum*).

IV. *Homalothecium nuttallii* (Figs. 147-150) has high dorsal trabeculae only in the lower part of tooth. The dorsal plates are densely papillose with high papillae below (very rarely branched). The upper part of the tooth has inconspicuous dorsal trabeculae not exserted above dense papillae, and the ventral trabeculae are semiorbicular above, relatively thin, and have small low papillae.

V. *Homalothecium aeneum* (Figs. 151-155) has very low dorsal trabeculae (not exserted above the cristae or papillae level) in all parts of the tooth. The cristae are straight below, not very dense, slightly flexuose, and wavy to nearly smooth. In the upper part of the tooth low papil-

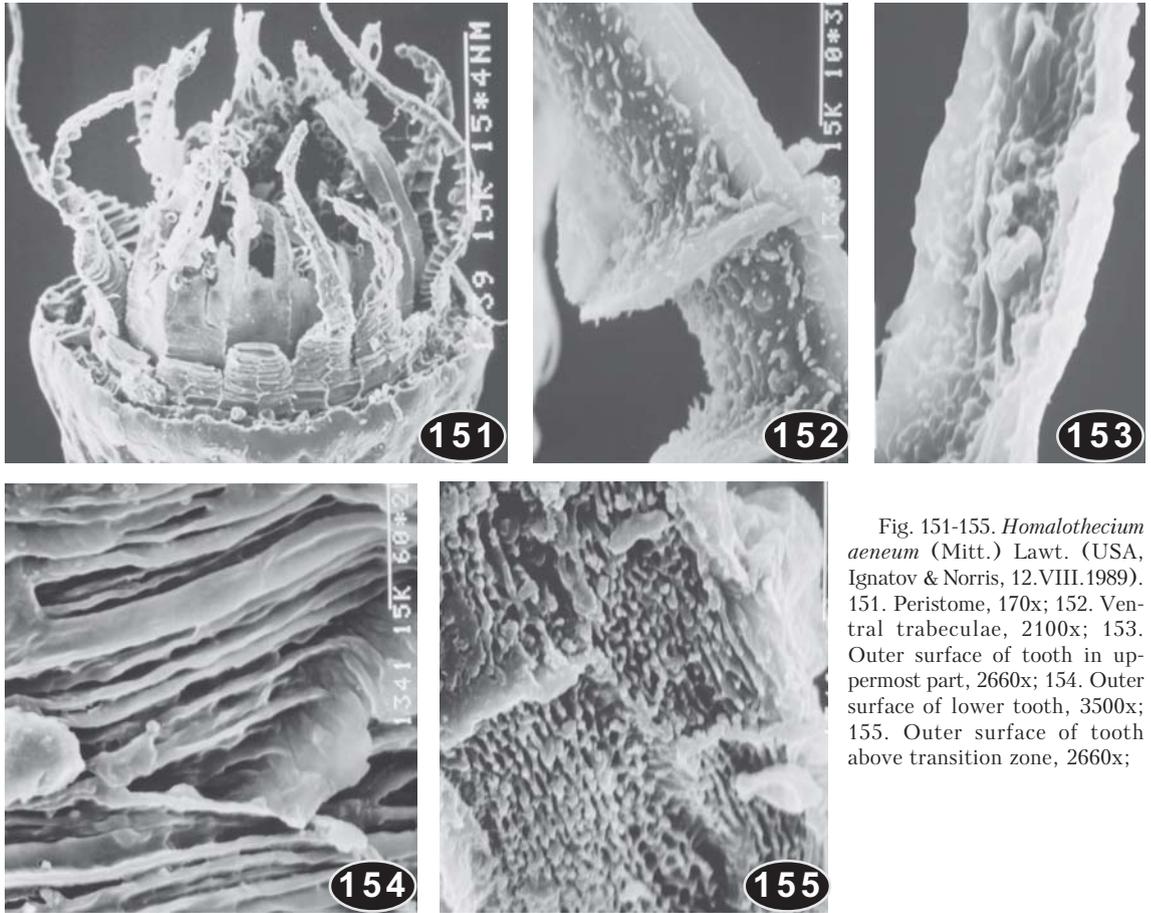
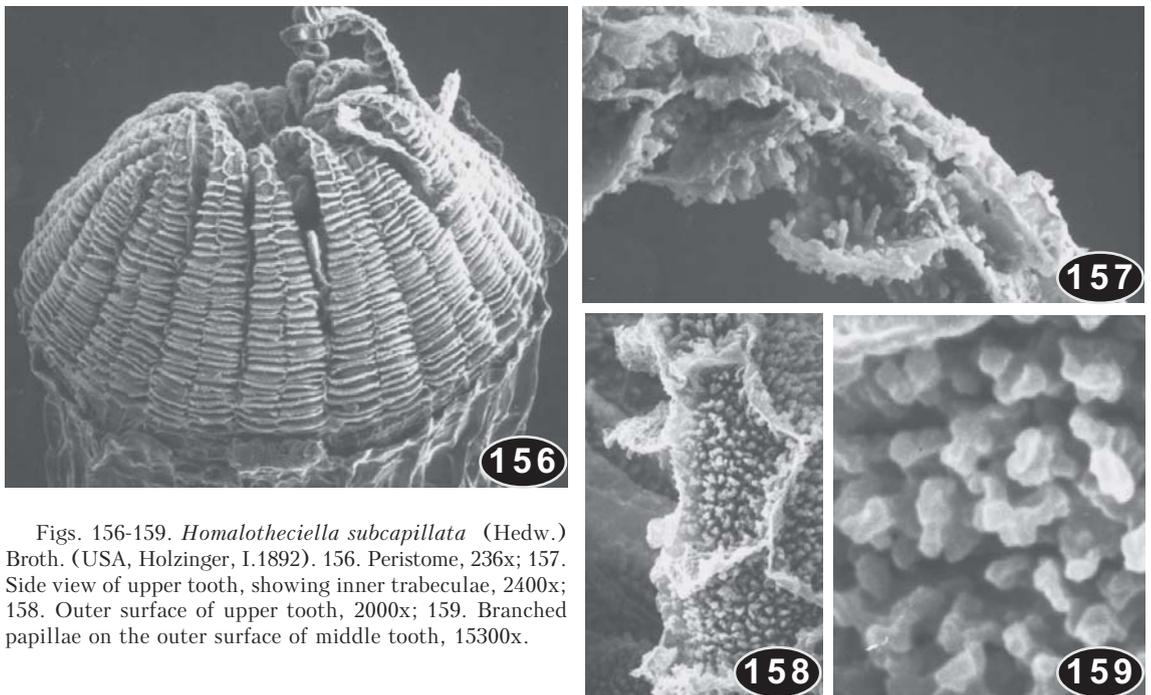


Fig. 151-155. *Homalothecium aeneum* (Mitt.) Lawt. (USA, Ignatov & Norris, 12.VIII.1989). 151. Peristome, 170x; 152. Ventral trabeculae, 2100x; 153. Outer surface of tooth in uppermost part, 2660x; 154. Outer surface of lower tooth, 3500x; 155. Outer surface of tooth above transition zone, 2660x;



Figs. 156-159. *Homalotheciella subcapillata* (Hedw.) Broth. (USA, Holzinger, I.1892). 156. Peristome, 236x; 157. Side view of upper tooth, showing inner trabeculae, 2400x; 158. Outer surface of upper tooth, 2000x; 159. Branched papillae on the outer surface of middle tooth, 15300x.

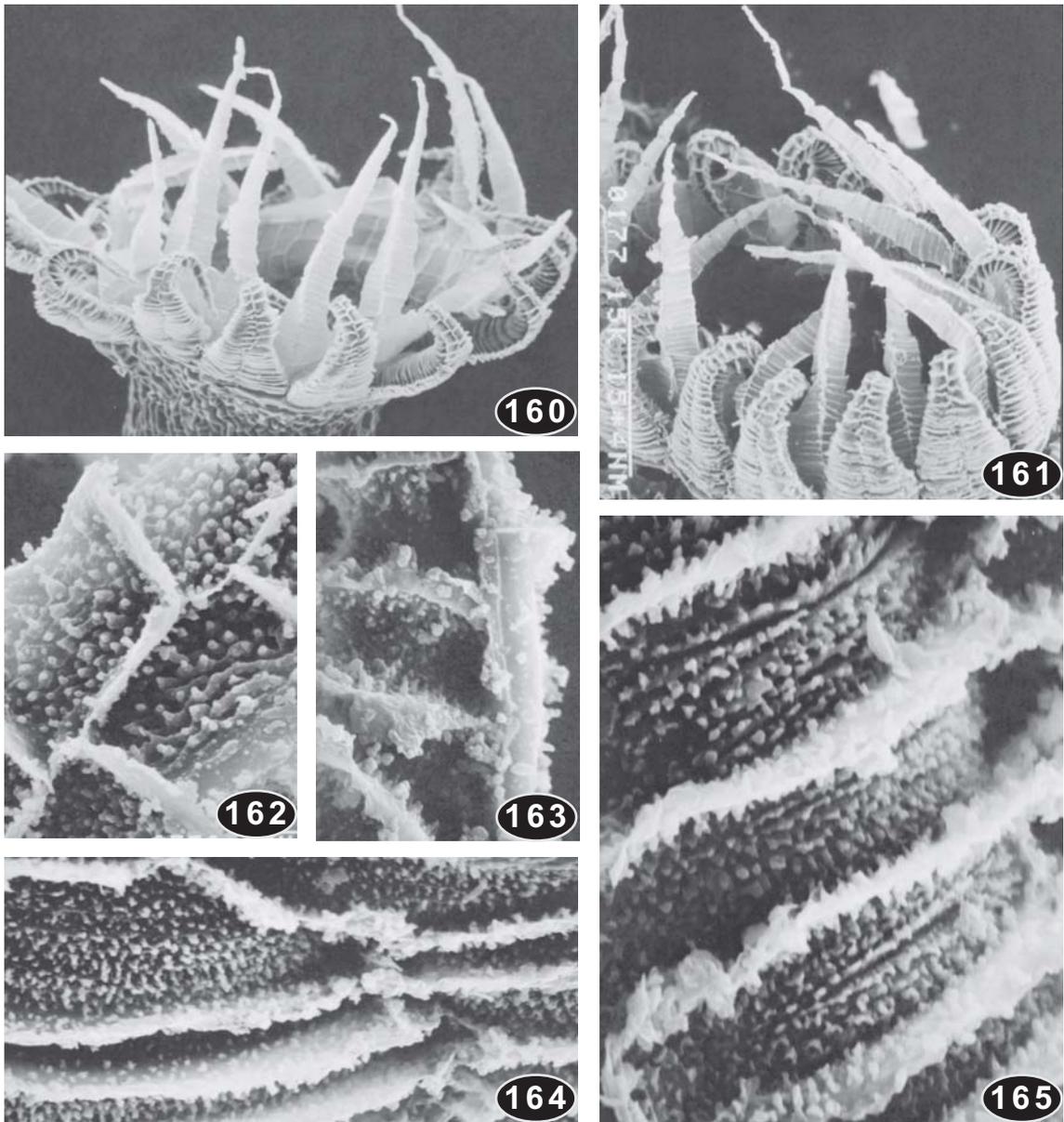


Fig. 160-165. 160, 162-164 – *Rhynchoستيgiella brachypodia* Fleisch. (Papua New Guinea, Norris, 61083); 161, 165 – *R. papuensis* Bartr. (Nederlands Nieuw-Guinea, van Zanten, 571). 160 & 161. Peristomes, 165x for both; 162. Outer surface of upper tooth, 2800x; 163 – side view of upper tooth, showing inner trabeculae, 2870x; 164 & 165 – outer surface of lower tooth, 3220x & 4630x.

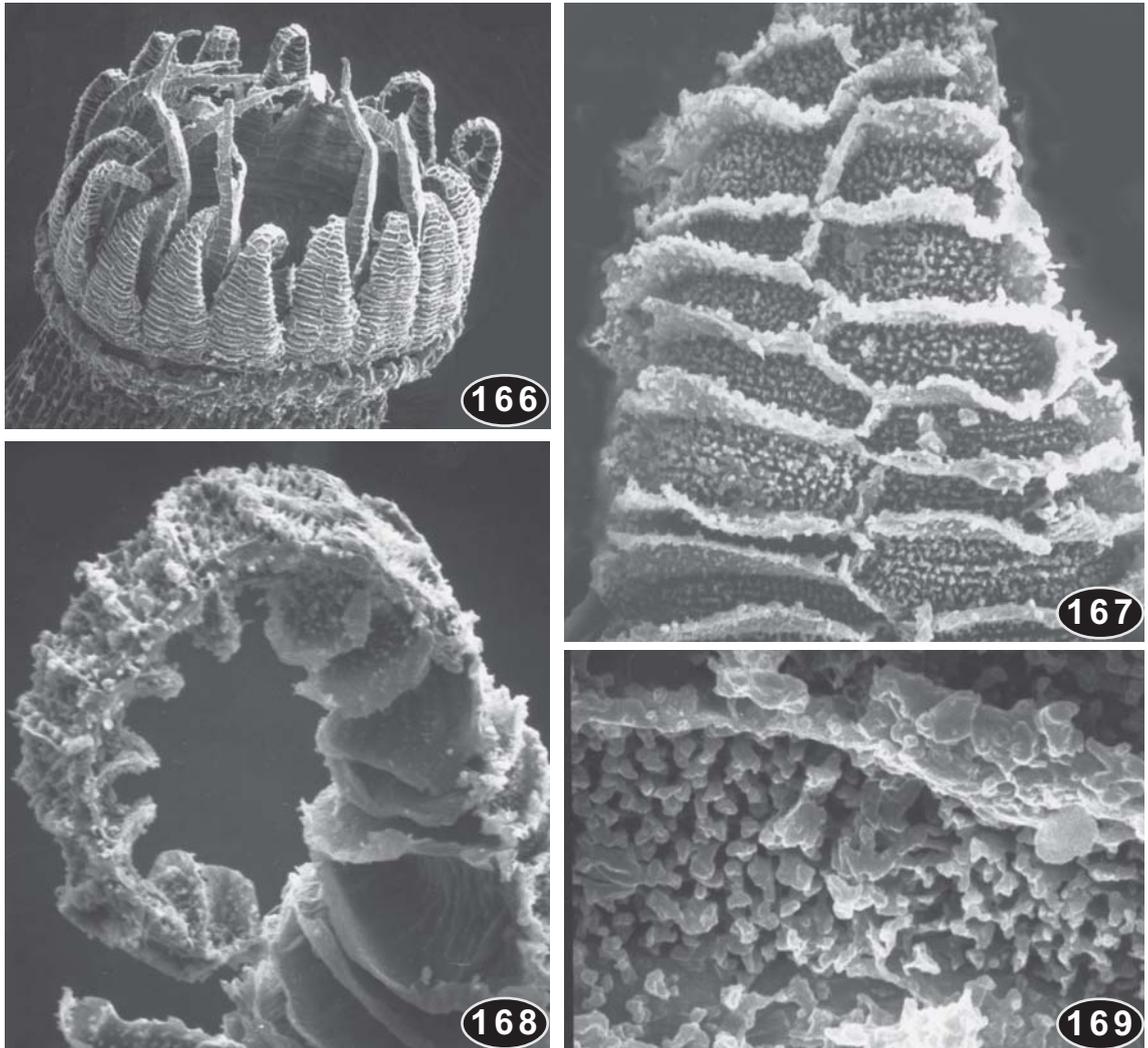
and also less papillose ventral trabeculae. By the presence of branched papillae *Homalotheciella* is also resembling some tropical and subtropical *Rhynchoستيgiella* species (*R. brachypodia*, *R. papuensis*, *R. leptoneura*).

***Rhynchoستيgiella* and *Eurhynchiella*** (Figs. 160-190)

Species studied: *Eurhynchiella zeycheri* (C. Muell.) Fleisch., *Rhynchoستيgiella brachypodia*

Fleisch., *R. leptoneura* Card., *R. menadensis* (Lac.) Bartr., *R. papuensis* Bartr., *R. teesdalei* (B. S. G.) Limpr., *R. tenella* (Dicks.) Limpr. [and *Scorpiurium cucullatum* (Mitt.) Hedenäs (= *E. cucullatum* (Mitt.) Steere et G.A.M.Scott)].

These species is worth discussing together for the following reason. Fleischer (1923) outlined the strong heterogeneity of *Rhynchoستيgiella* and suggested the segregate *Eurhynchiella*



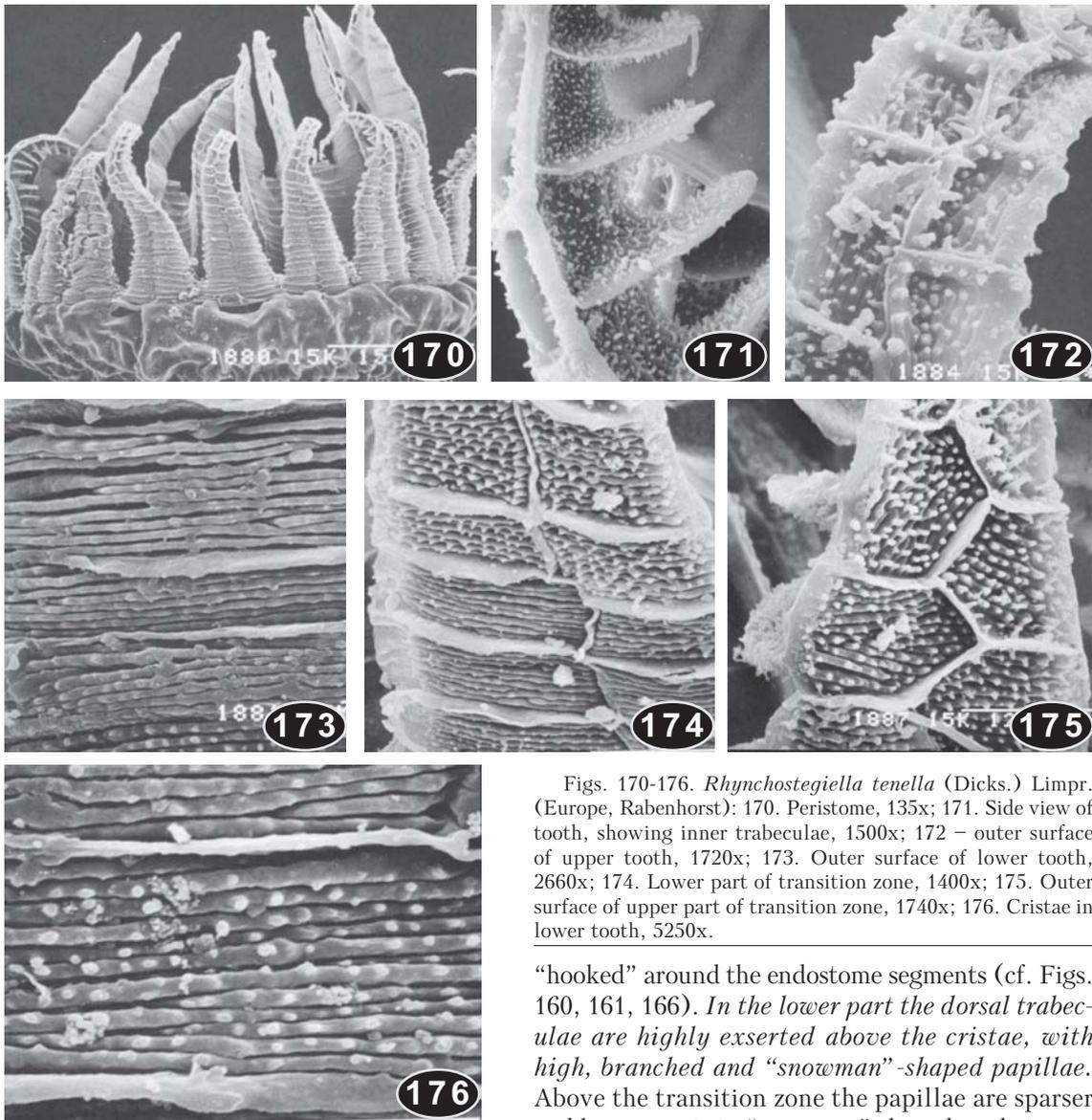
Figs. 166-169. *Rhynchostegiella leptoneura* Card. (China, Yunnan, Magill & al., 7830). 166. Peristome, 120x; 167. Outer surface of middle tooth, 1450x; 168. Side view of upper tooth, 1200x; 169. Ornamentation of outer surface of middle tooth, 5600x.

la for small rather rigid plants, with short thick-walled laminal cells, and a costa ending in a spine (retaining in *Rhynchostegiella* plants of more delicate stature, with long, thin-walled laminal cells, and a costa that does not end in a spine). According to this concept, *Rhynchostegiella papuensis* and *Scorpiurium* (*Eurhynchiium*) *cucullatum* should be placed in *Eurhynchiella*. But if so, the diversity of peristomes within *Eurhynchiella* will be enormously great. Moreover, the advanced characters in *Eurhynchiella zeycheri*, the type of the genus (Ignatov & al., 1998), are quite different from the advanced characters in *R. papuensis*. Obviously, at least these two taxa represent two different lines of evolu-

tion and their correct generic classification need further studies.

Species of this group represent a series of peristome reduction, in some respects similar to those in *Homalothecium*. The peristomes are hygrocastic and xerocastic, some species have dense branched papillae on dorsal plates and trabeculae in lower tooth, other ones have bead-like or nearly smooth cristae.

Interestingly, the relation of papillosity-pattern to xero-/hygrocastic movements is almost opposite to that in the *Homalothecium-Campthecium* group. Species with especially strongly papillose cristae and dorsal trabeculae exhibit xerocastic movements, whereas hygrocastic



Figs. 170-176. *Rhynchoستيella tenella* (Dicks.) Limpr. (Europe, Rabenhorst): 170. Peristome, 135x; 171. Side view of tooth, showing inner trabeculae, 1500x; 172 – outer surface of upper tooth, 1720x; 173. Outer surface of lower tooth, 2660x; 174. Lower part of transition zone, 1400x; 175. Outer surface of upper part of transition zone, 1740x; 176. Cristae in lower tooth, 5250x.

movement is observed only in one species, *Rhynchoستيella tenella*, which has a relatively “hypnoid” peristome. In its peristome structure the latter species is closest to *R. teesdalei*, which has a xerocastique peristome. Certainly the structural basis for movements of peristomes need much more studies.

The exostome structure of the species can be classified in four types as follows:

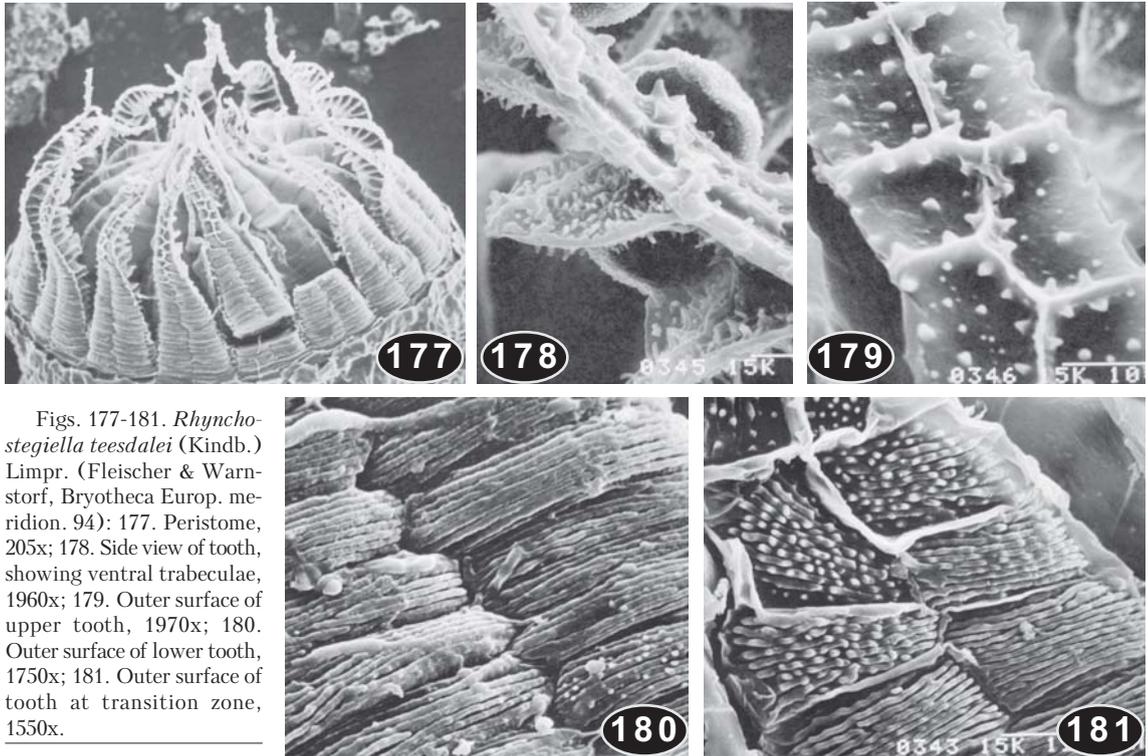
1. *Rhynchoستيella brachypodia*, *R. leptoneura*, *R. papuensis* (Figs. 160-169)

The teeth are abruptly tapered in the transition zone and serrulate above. In the dry condition they are somewhat twisted and

“hooked” around the endostome segments (cf. Figs. 160, 161, 166). In the lower part the dorsal trabeculae are highly exerted above the cristae, with high, branched and “snowman”-shaped papillae. Above the transition zone the papillae are sparser and lower, conic to “snowman”-shaped, and at some places longitudinal or vermicular cristae are seen. In the upper part the dorsal trabeculae are low and papillose. The margin is incrassate (*R. papuensis*) or not incrassate (*R. brachypodia*, *R. leptoneura*). The ventral trabeculae are lowly semiorbicular, moderately to strongly incrassate, and are densely to moderately densely, highly papillose.

2. *Rhynchoستيella tenella* (Figs. 170-176) and *R. teesdalei* (Figs. 177-181)

The teeth are ±abruptly narrowed in the transition zone and serrulate above. The median line is zig-zag-shaped below, somewhat immersed. In the lower part the dorsal trabeculae are lowly exerted above the cristae level (*R. tenella*) or not exerted



Figs. 177-181. *Rhynchoستيgiella teesdalei* (Kindb.) Limpr. (Fleischer & Warnstorf, Bryotheca Europ. meridion. 94): 177. Peristome, 205x; 178. Side view of tooth, showing ventral trabeculae, 1960x; 179. Outer surface of upper tooth, 1970x; 180. Outer surface of lower tooth, 1750x; 181. Outer surface of tooth at transition zone, 1550x.

(*R. teesdalei*). The cristae have scattered small, bead-like papillae near the base, further up slightly wavy to nearly smooth and towards the transition zone with large conic-wavy papillae on the cristae. The cristae are oblique in 1-2 plates in the transition zone. In the upper part the plates are lowly papillose with the papillae arranged in indistinct rows, or in the uppermost, non-trabeculate part with sparse papillae on the smooth surfaces. The dorsal cristae are low and lowly papillose in upper part. The margin is moderately incrassate. The ventral trabeculae are high, ligulate-triangular, incrassate, and densely (*R. tenella*) or moderately densely (*R. teesdalei*) covered by irregular papillae (thinly spinulose, conic, rarely branched).

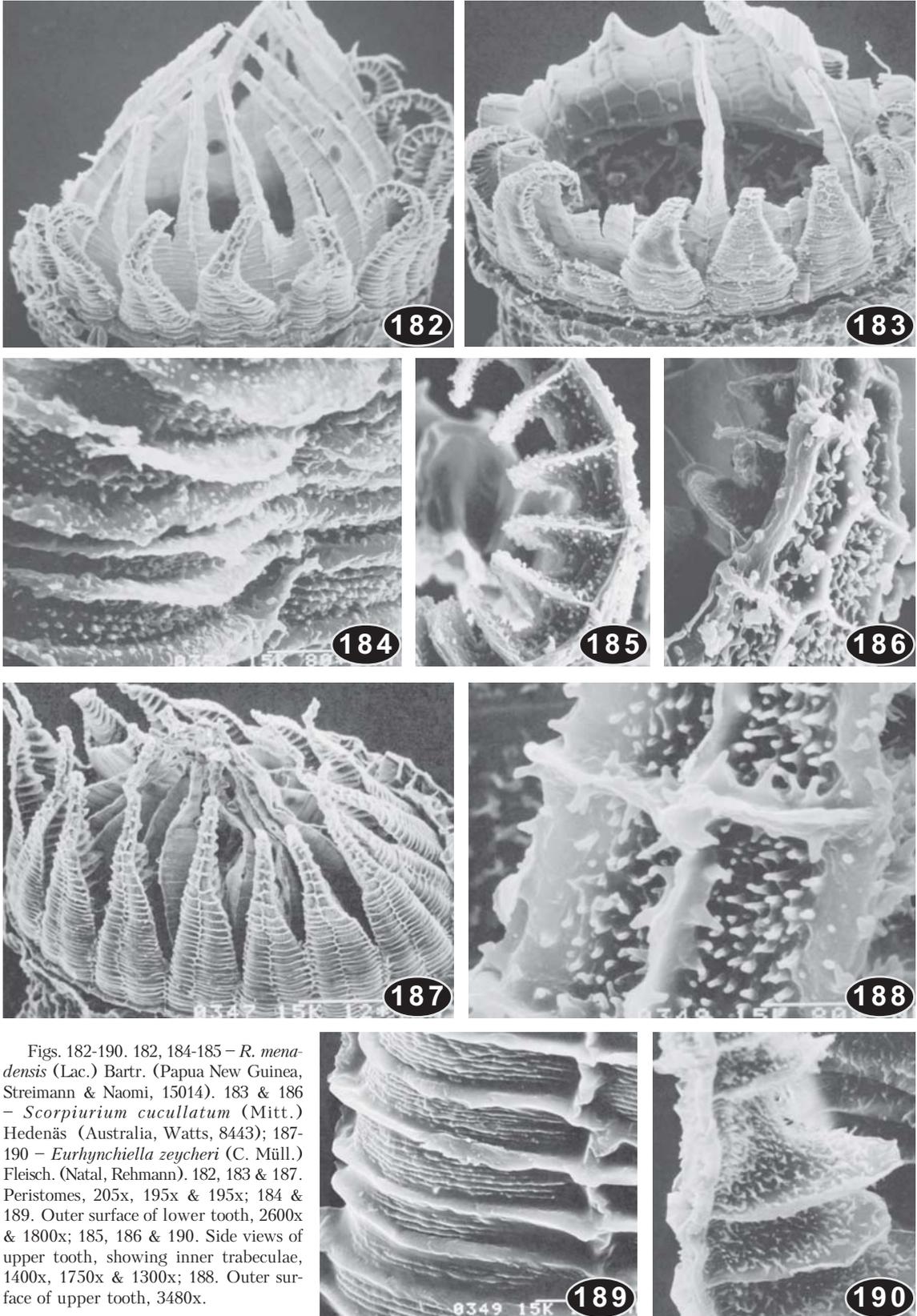
3. *Rhynchoستيgiella menadensis*, *Scorpiurium cucullatum* (Figs. 182-186)

The teeth are abruptly tapered in the transition zone and serrulate above. In the dry condition they are slightly to moderately twisted and form a "hooks" around the endostome segments. In the lower part the dorsal trabeculae are exerted above the cristae and low-papillose (*R. menadensis*), or not exerted (*S. cucullatum*). The cristae are straight and covered with small papillae. In the

upper part the dorsal trabeculae are low and papillose, and the plates have low papillae, that are arranged in indistinct longitudinal rows. The margin is incrassate and lowly-papillose (in *R. menadensis* the papillae near the joints of plates are higher and sometimes form "double"-teeth). The ventral trabeculae are semiorbicular and moderately to strongly incrassate, rarely lowly papillose.

4. *Eurhynchiella zeycheri* (Figs. 187-190)

The teeth are massive, slightly curved when dry, abruptly tapered in transition zone and serrulate above. In the lower part the teeth are incrassate, with a somewhat immersed median line that is zig-zag-shaped to almost straight. In the lower part the dorsal trabeculae are stout, exerted above the cristae and distinctly projecting from the sides of the teeth. The cristae are very dense, straight, and smooth to slightly wavy. In the transition zone the cristae are densely papillose. In the upper part the dorsal trabeculae are exerted, with high-conic papillae. The plates have high papillae arranged in indistinct longitudinal rows. The margin is distinctly incrassate, with relatively sparse high papillae (papillae near the joint of plates higher and sometimes forming "double-tooth"). The



Figs. 182-190. 182, 184-185 - *R. menadensis* (Lac.) Bartr. (Papua New Guinea, Streimann & Naomi, 15014). 183 & 186 - *Scorpiurium cucullatum* (Mitt.) Hedenäs (Australia, Watts, 8443); 187-190 - *Eurhynchiella zeycheri* (C. Müll.) Fleisch. (Natal, Rehmann). 182, 183 & 187. Peristomes, 205x, 195x & 195x; 184 & 189. Outer surface of lower tooth, 2600x & 1800x; 185, 186 & 190. Side views of upper tooth, showing inner trabeculae, 1400x, 1750x & 1300x; 188. Outer surface of upper tooth, 3480x.

ventral trabeculae are semiorbiculate and densely covered by thin papillae.

The great diversity of exostome structure found in the few species studied of *Rhynchostegiella* s. l. do not allow us to draw conclusions other than that this genus is very heterogeneous and needs more studies.

#### CONCLUSIONS

1. Most genera of the Brachytheciaceae have a relatively uniform structure of their exostomes, hardly exceeding the variability found within *Brachythecium*: (*Bryoandersonia*, *Bryhnia*, *Camptothecium*, *Cirriphyllum*, *Eurhynchium*, *Kindbergia*, *Myuroclada*, *Pseudocirriphyllum*, *Rhynchostegium*, *Scleropodium*). At the same time there are some relatively stable minor characters states (especially in the structure of the ventral trabeculae in the upper part of teeth), which are more or less stable within some small natural groups of large genera (e. g. in sections of *Brachythecium* ).

2. The exostomes are especially advanced and heterogeneous in *Homalothecium* and *Rhynchostegiella*. Even after the segregation of *Camptothecium* as a genus with the peristome almost of the *Brachythecium*-type, *Homalothecium* represents several contrasting pattern. *Rhynchostegiella* also exhibits several distinct types of exos-

tomes. The systematics of these genera should not be based on the gametophytic characters only. A description of the peristomes simply as "reduced" often include clearly different lines of evolution.

3. *Scleropodium caespitans* and *S. tourettii* show many differences in their exostome structures and may not belong to one genus.

4. *Platyhypnidium* species have several features which provide additional evidence for its segregation from both *Rhynchostegium* and *Eurhynchium*.

5. Xero/hygrocastique movements of the exostome are not clearly correlated with the patterns of ornamentation. The more or less "hypnoid" peristome of *Rhynchostegiella tenella* is hygrocastique, whereas the much "reduced" exostomes with branched papillae (e. g. in *R. brachypodia* and *R. papuensis*) are xerocastique.

#### ACKNOWLEDGMENTS

We are grateful for the curator of H for the permission of use some collection for SEM studies and to Lars Hedenäs for critical reading and suggestions on the manuscript. The study of Ignatov has been supported by a Smithsonian Institution Short-Term Visitor appointment and the study of Ignatov and Ignatova by the Russian Foundation of Scientific Researches, 96-04-48033.

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- B. albicans* (Hedw.) B. S. G.: U.S.A., Idaho, Hermann 20226 (US).
- B. auriculatum* Jaeg.: China, Sichuan, Tan 95-100 (MHA ex FH).
- B. complanatum* Broth.: Russia, Altai, Ignatov 24/45 (MHA).
- B. erythrorrhizon* B. S. G.: Russia, Ural, Reserve "Basegi", Ignatov & Bezgodov, 133 (MW ex MHA).
- B. falciculatum* (Broth.) Par.: Russia, Altai, Ignatov 0/1680 (MHA).
- B. laetum* (Brid.) B. S. G.: Crum & Anderson, Mosses of North America, n° 871: U.S.A., Tennessee, Schofield 10548 (US).
- B. lamprocarpum* (C. Muell.) Jaeg.: Papua New Guinea, 2070-2200 m, Koponen 34493 (MHA ex H).
- B. mildeanum* (Schimp.) Schimp. ex Milde: Moscow Province, Belye Kolodezi, 16.V.1986 (MHA).
- B. oedipodium* (Mitt.) Jaeg.: Canada, British Columbia, Crum & Schofield, 4841 (US); Russia, Moscow Province, Ignatov 3.VI.1996 (MHA).
- B. plumosum* (Hedw.) B. S. G.: Russia, Altai, Ignatov 16/29 (MHA); Ural, Reserve "Basegi", Ignatov & Bezgodov, 171 (MW ex MHA).
- B. plumosum* (Hedw.) B. S. G. ("B. oedistegium-phenotype"): Taiwan, T. Koponen 16918 (MHA ex H).
- B. populeum* (Hedw.) B. S. G.: Russia, Altai, Ignatov 1/16 (MHA); same 0/45 (MHA).
- B. reflexum* (Starke) B. S. G.: Russia, Altai, Ignatov 0/442 (MHA); same 0/1637 (MHA); Russia, Ural, Reserve "Basegi", Ignatov & Bezgodov, 644 (MW ex MHA).
- B. rivulare* B. S. G.: U.S.A., Michigan, Robinson & Sharp, 20.VI.1995 (US); Russia, Moscow, Ignatov, 9.IV.1984 (MHA); Moscow Province, Ignatov, 4.5.1985 (MHA).
- B. roteanum* De Not.: Russia, Altai, Ignatov, 9/159 (MHA).
- B. rutabulum* (Hedw.) B. S. G.: Russia, Altai, Ignatov 0/1672 (MHA); Russia, Moscow, Ignatov 27.VI.1994 (MHA).
- B. salebrosum* (Web. et Mohr) B. S. G.: Sweden, Lule Lappmark, Hj. Moller 10.VII.1919 (US ex UPS); Russia, Altai, Ignatov 0/97 (MHA).
- B. starkei* (Brid.) B. S. G.: Russia, Altai, Ignatov 0/1675 (MHA).
- B. trachypodium* (Brid.) B. S. G.: Russia, Altai, Ignatov 31/227 (MHA).
- B. velutinum* (Hedw.) B. S. G.: Russia, Altai, Ignatov 13/134 (MHA); Russia, Moscow Province, Ignatov 20.VII.1988 (MHA).
- Bryhnia novae-angliae* (Sull. et Lesq.) Grout: U.S.A., New York, Howe, 1867 (US ex NY); China, Jilin, T. Koponen 37290 (H).
- Bryoandersonia illecebra* (Hedw.) Robinson: U.S.A., Orange (CI), Evans, X.1890 (US).
- Camptothecium lutescens* (Hedw.) B. S. G.: British Mosses, J. G. Baker (US).
- C. pinnatifidum* (Sull. et Lesq.) Sull.: U.S.A., California, Norris 17.I.1982 (MHA ex HSU).
- Cirriphyllum cirrosium* (Schwaegr.) Grout: China, Sichuan, Si He, 30410 (MO).
- C. piliferum* (Hedw.) Grout: Finland, Roivainen, 13.V.1961 (US).
- Eurhynchiella zeycheri* (C. Muell.) Fleisch. (sub *Rhynchostegium austro-strigosum* C. Müll.): Natal, Rehmann (H-BR).
- Eurhynchium angustirete* (Broth.) Kop.: Russia, Moscow Prov., Bogoslovskaya, 28.VI.1961 (MW); Russia, Moscow Prov., Lytkino, 29.IV. 1985 Ignatov (MHA).
- E. asperisetum* (C. Muell.) Bartr.: Papua New Guinea, T. Koponen 30850 (MHA ex H).
- E. hians* (Hedw.) Sande Lac. (from Russia, Pskov Province, Ignatov & Zolotov 20.X.1996 (MHA); Russia, Altai, Ignatov, 35/56 (MHA).
- E. praelongum* (Hedw.) B. S. G.: [Germany], Aslatia, Schimper (US).
- E. pulchellum* (Hedw.) Jenn.: Russia, Moscow Province, Ignatov 29.IV.1985 (MHA); Russia, Altai, Ignatov 0/648 (MHA); same, 0/1226 (MHA).
- E. savatieri* Schimp. ex Besch.: Japan, Mockiziki, 1143 (H, Rel. Broth. 5649).
- E. schleicheri* (Hedw. f.) Jur.: C. Jensen, Musci Danici, Sjaelland, 5.11.1899 (H).
- E. striatum*: Russia, Krasnodar Territory, Kavkazsky Reserve, L. Vasil'eva, 16.VIII.1935 (MW).
- E. vagans* (Jaeg.) Bartr.: Papua New Guinea, Koponen 33209 (MHA ex H).
- Homalotheciella subcapillata* (Hedw.) Broth.: U.S.A., D.C., Holzinger, I.1892 (US).
- Homalothecium aeneum* (Mitt.) Lawt.: USA, California, 1400 m, Ignatov & Norris, 12.VIII.1989 (MHA)
- H. laevisetum* Sande Lac.: Japan Centr., 3000-5000', 20-25.X.1890, H. Mayr, 3 (H-BR).
- H. nuttallii* (Wils.) Jaeg.: Crum & Anderson, Mosses of North America, n° 807: U.S.A., California, Schofield 11164 (US).
- H. philippeanum* (Spruce) B. S. G.: USSR [Ukraine], Crimea, Belyanina, 3.V.1985 (MHA).
- H. sericeum* (Hedw.) B. S. G.: Suecia, Stockholm, [?] 5.VI.1918 (H); Brotherus, Bryotheca Fennica: Nylandia, Lojo, 11.X.1909, Buch (MW).
- Myuroclada maximowiczii* (Borszcz.) Steere et Schof.: Russia, Primorkiy Territory, L. Vasil'eva, 8.V.1946 (MW); Verdoorn, Exs. n° 282 (1939): Russia, Primorkiy Territory, Lazarenko, X.1934 (US).
- Palamocladium euchloron* (C. Muell.) Wijk et Marg.: USSR, [Georgia], Adzharia, Onipchenko, 2.II.1979 (MHA).
- P. leskeoides* (Hook.) Britt. (sub *P. nilgheriense* (Mont.) C. Muell.): China, Sichuan, T. Koponen, 46384 (MHA ex H).
- Platyhypnidium aquaticum* (Hampe) Fleisch.: Bolivia, 2400, R.S.Williams, 2020 (H-BR ex NY).
- P. austrinum* (Hook. f. et Wils.) Fleisch.: New Zealand, Beckett 12/84, 484 (H).
- P. muelleri* (Sande Lac.) Fleisch.: Papua New Guinea, Koponen, 30296 (MHA ex H).
- P. riparioides* (Hedw.) Dix.: U.S.A., Maryland, Reed, 64277 (US).
- Rhynchostegiella brachypodia* Fleisch.: Papua New Guinea, Norris, 61083 (MHA ex H).
- R. leptoneura* Card.: China, Yunnan, Magill & al., 7830 (MO).
- R. menadensis* (Lac.) Bartr.: Papua New Guinea, Streimann & Naomi, 15014 (MHA ex H).
- R. papuensis* Bartr.: Nederlands Nieuw-Guinea, van Zanten, 571 (US ex Leiden).
- R. teesdalei* (Kindb.) Limpr.: Fleischer & Warnstorf, Bryotheca Europ. meridion. 94: Corsica (H).
- R. tenella* (Dicks.) Limpr.: Europe, Rabenhorst [unclear handwriting], (MW).
- R. confertum* (Dicks.) B.S.G.: USSR [Georgia], Abkhazia, Ignatov, 27.VII.1987 (MHA).
- R. inclinatum* (Mitt.) Jaeg.: Taiwan, J. Suzuki 1.I.1927 (H-BR).
- R. javanicum* (Bel.) Besch.: Papua New Guinea, Koponen, 34252 (MHA ex H).
- R. murale* (Hedw.) B.S.G.: Russia, Moscow Province, Grigorichikovo, Ignatov, 6.VII.1988 (MHA); Russia, Lipetzki Province, Samsel, 8.IX.1962, n 61, (MW).
- R. pallidifolium* (Mitt.) Jaeg.: Japan, Sendai, Uematsu, 425 (H-BR).
- Scleropodium caespitans* (C. Muell.) L. Koch: Canada, British Columbia, Schofield 20410 (US).
- S. touretii* (Brid.) L. Koch: U.S.A., California, Santa Clara Co., Schofield & Thomas 11200 (US).
- Scorpiurium cucullatum* (Mitt.) Hedenäs: (type of *Rhynchostegium subconvolutifolium* Broth. et Watts, Australia, Watts, 8443 (H-BR).
- Steeerleus serrulatum* (Hedw.) Robinson: U.S.A., Alabama, Norris 11456 (MHA ex HSU).