On Myriocoleopsis Schiffn. (Lejeuneaceae)

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Abstract. A new locality of the rare Brazilian liverwort *Myriocoleopsis puiggarii* (Lejeuneaceae) the only species in the genus, was discovered in the river Pardo near Barra do Turvo, Sao Paulo State. Data on stem-anatomy, oil-bodies, sporophyte and ecology are provided here for the first time. The species grows on rocks and trunks of shrubs in or near running water. Sporophytes are developed only in plants growing on emerged substrates. *Myriocoleopsis* seems to be most closely related to *Cololejeunea* subg. *Chlorolejeunea* (type: *C. madothecoides*). The stem in *Myriocoleopsis*, consisting of c. 30 cortical cells surrounding 1 large medullary cell, is more complex than in all species of *Cololejeunea* except *C. madothecoides*. Striking variation in the stem-anatomy of the latter species was observed.

Резюме. На реке Парду близ Барра ду Турву. Штат Сан-Паулу, обнаружено новое местонахождение редкой бразильской печеночницы *Myriocoleopsis puiggarii (Lejeuneaceae)*, единственного вида рода. Тут впервые составлены данные об анатомии стебля, густоте масла. спорофите и экологии. Этот вид растет на камнях и стволах кустарников в воде или близ нее. Спорофиты развиты лишь в растениях, растущих на выступивших субстратах. *Myriocoleopsis*, повидимому, больше всего связана с *Cololejeunea* подр. *Chlorolejeunea* (тип *C. madothecoides*). Стебель *Myriocoleopsis*, состоящий из примерно 30 коровых клеток, окружающих одну большую сердцевинную клетку, более сложный, чем во всех видах *Cololejeunea*, кроме *C. madothecoides*. Обнаружена разительная вариация в анатомии стебля последнего вида.

Introduction

The monotypic genus *Myriocoleopsis* SCHIFFN., including *M. puiggarii* from Brazil, is one of the most remarkable neotropical endemics of the *Lejeuneaceae*. Up to now the species has been known only from type-material, gathered near Iporanga, Sao Paulo State, by PUIGGARI in 1873. Part of this material was studied by GOTTSCHE, who named it *Jungermannia typhacella*, a name which apparently remained unpublished. STEPHANI, apparently mislead by the peculiar habit of the plant, annotated the species in his herbarium as *Clasmatocolea typhacella* (fide GROLLE 1956)!

SCHIFFNER (1944) finally recognized it as a new species (and genus) of *Lejeuneaceae*, comparing it in his original publication with the odd Amazonean endemic *Myriocolea* SPRUCE. The most outstanding characters of *Myriocoleopsis* appeared to be the presence of a prostrate caudex with ascending leafy axes, the inconspicuous lobule which is reduced to a linear fold along the postical margin of the lobe, the absence of underleaves, the 5-keeled, *Lejeunea-type* perianth and the long male spikes. The sporophyte remained unknown.

GROLLE (1956) showed that *Myriocoleopsis* has a pendular leaf-segmentation (*two* underleaves or rhizoid-bundles per leaf-pair) and therefore belongs in the subf.

Cololejeuneoideae HERZ. (*Paradoxae* LACOUT.). *Myriocolea* differs essentially from *Myriocoleopsis* in having the usual helical leaf-segmentation (*one* underleaf per leaf-pair). SCHUSTER (1963) considered *Myriocoleopsis* a "specialised derivative of the *Cololejeunea-Leptocolea* Complex".

In November 1971 the junior author discovered a rich locality of *Myriocoleopsis puiggarii* near Barra do Turvo, Sao Paulo State, at the border of Sao Paulo and Parana. This locality is c. 20 km South-East of the type-locality at Iporanga. Both localities are situated in the Ribeira river basin. The species was found growing in great masses on emerging rocks in the river Pardo, possessing mature gametoecia and young sporophytes. In December 1973 the junior author revisited this locality and made some observations on the ecology of the species. *Myriocoleopsis* was abundantly fruiting at that time and copious material with mature sporophytes could be collected. Most of the material was sent to Dr. INOUE (Tokyo) who will distribute the species in Fasc. VI of his "Bryophyta Selecta Exsiccata".

In this paper we present a description of the genus *Myriocoleopsis* which is more complete than the description given by SCHIFFNER. Data on stem-anatomy, oil-bodies, sporophyte structure and ecology are new. On the basis of the new data available we will shortly review the systematic position of the genus.

Description

Myriocoleopsis puiggarii SCHIFFN., Hedwigia 81: 235, figs. 1–9 (1944); VAN DEN BERGHEN, Lejeunia 6: 53 (1948); GROLLE (1956): 301; BISCHLER (1961): 235; SCHUSTER (1963): 185.
Jungermannia typhacella GOTT. *ex* SCHIFFN. Hedwigia 81: 234 (1944); *nom. nud.*
Clasmatocolea typhacella STEPH. ex GROLLE, Revue Bryol. & Lichénol. 25: 301 (1956); *nom. nud.*
Typus: Brazil, Sao Paulo State, Iporanga, Estate of J. A. DE SILVA, on rocks in a stream (?), leg. PUIGGARI, VII. 1873 (not seen).

Plants autoicous, growing in dense, pale-greenish mats with short, creeping, stoloniform primary stems and ascending to erect secondary stems up to 3 cm long, which arise in bundles from the creeping primary stems; secondary stems in the lower half stoloniform with reduced leaves, irregularly branched with numerous *Lejeunea*-type branches (arising ventro-laterally with a conspicuous 3-lobed collar) and with *Radula*-type innovations; primary and secondary stems rigid, 150–170 μm in diam., with thick-walled, quadrate to rectangular cortical cells, 30–80 μm long, their lumina filled with numerous small, papillose oil-bodies; stem in transverse section with a cortex of c. 30 cells, arranged in (1–)2(–3) layers and surrounding one large, hyaline medullary cell without chlorophyll; cortex about as wide as the medulla, 40–45 μm; medullary cells in longitudinal section 250–400 μm long, 4–8 × the length of the cortical cells; rhizoids virtually absent, when present arising in dense bundles from a multicellular rhizoid-pad on the ventral side of the stem near the base of each leaf. Leaves laxly inserted, not imbricated, widely spreading, c. 1 mm long, obovate with a widely rounded apex and a very short and almost transverse line of insertion; lobule reduced to an obscure, flat or slightly upcurved fold along the postical margin of the lobe, reaching up to ⅔ the length of the lobe, at apex crowned with an erect hyaline papilla; leaf areolation homogeneous, the cells subisodiametric-hexagonal, 15–20 × 18–24 μm, the lumina filled with chlorophyll-bodies, the walls thin or slightly thickened with small trigones; oil-bodies (2–)3–6(–8) per cell, becoming more numerous in the slightly elongated basal leaf-cells, papillose-granulose, sphaerical to ellipsoid, 3–5 × 3–8 (–12) μm; underleaves absent.

Androecia in long spikes terminating a short leafy branch; male bracts in (6–)10–20 series, densely imbricated, unequally bilobed, much smaller than the leaves and strongly saccate, each bract with 2(–3) globose antheridia; male bracteoles absent.

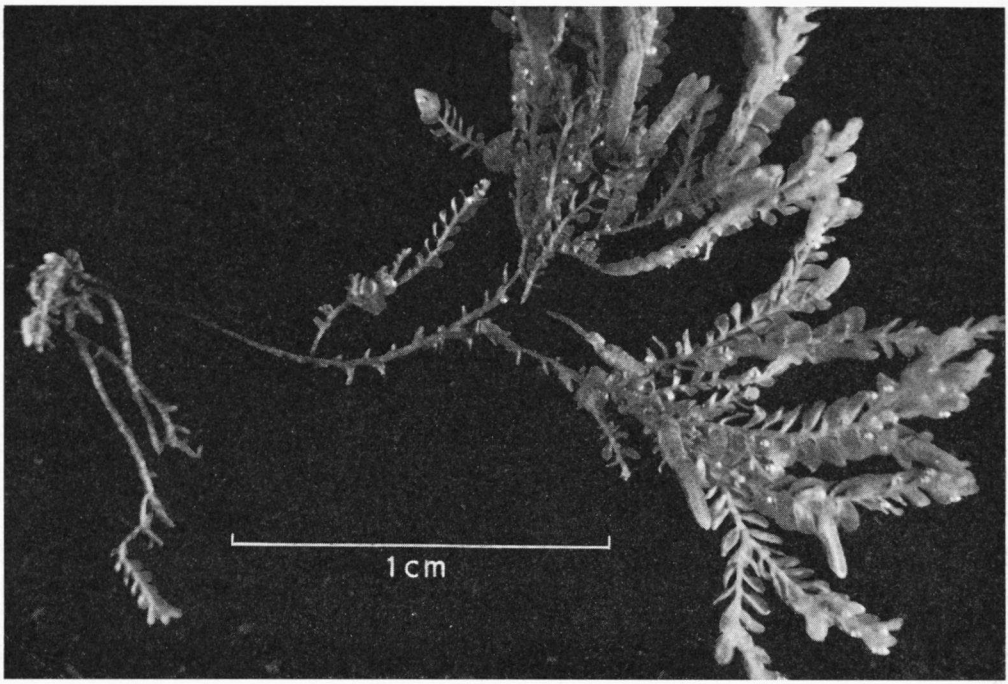
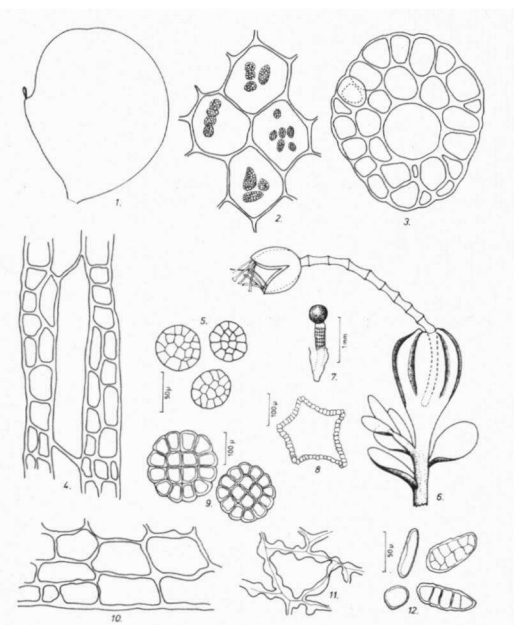


Photo 1: habitus of *Myriocoleopsis puiggarii* SCHIFFN.



Gynoecia arranged in cymose clusters of up to 10 perianths (the innovations becoming "floriferous" again), the lower gynoecia in dichasia (2 innovations), the upper ones in monochasia (1 innovation) or dichasia; female bracts similar to leaves; female bracteole absent; perianth at ma-

Figs 1–12: *Myriocoleopsis puiggarii* SCHIFFN. 1: leaf (60×); 2: leaf-cells with oil-bodies (ca. 750×); 3: stem in transverse section (360×); 4: stem in longitudinal section (225×); 5: gemmae; 6: gynoecium with sporophyte after dehiscence (35×); 7: calyptra and mature sporophyte just before dehiscence; 8: perianth in transverse section; 9: seta in transverse section; 10: cells of the outer layer of the capsule wall (500×); 11: cell of the inner layer of the capsule wall (500×); 12: spores, showing precocious germination. All figs drawn from VITAL 2779.

turity obpyriform, 1 mm long, inflated, with a short beak and 5 isomorphic and smooth keels; the base of the perianth often stalk-like elongated up to 250 μm long; calyptra of thinwalled, quadrate cells, 1–stratose, becoming slightly thicker towards base. Sporophyte pale, at maturity elevated on a very thin seta up to 2 mm above the perianth, the seta 2–3 mm long, 200 μm in diam., articulate, in transverse section with 16 cells of equal size: 12 outer cells and 4 inner cells; foot of the sporophyte composed of large and bulging thick-walled cells in 3 layers: one basal cell, four intermediate cells and ten to twelve upper cells (the 4th layer of sixteen cells is the basal segment of the seta!); capsule globose, splitting over ¾ of its length into four valves, the valves pale, hardly spreading, at apex with few elaters sticking out (only the elaters attached to the marginal cells of the valves stick out, the others remain appressed to the inner side of the valves); capsule wall 2-stratose, the inner layer of large, thick-walled cells with nodulose-sinuose wall-thickenings, the outer layer with small quadrate cells in the basal half and large cells above, the cells of the outer layer slightly sinuately thickened only; each capsule producing c. 150 green spores of irregular shape, 40–70(–100) × 21–25 μm, their surface finely papillose and with a few rosettes of larger, sharp papillae arranged in a circle; elaters pale, long and narrow, c. 300 × 12–15 μm, with one rudimentary spiral.

Vegetative propagation (rare) by means of multicellular disciform gemmae arising from leaf-surfaces.

Specimens seen: Brazil, Sao Paulo State, Municipio de Barra do Turvo, Fazenda Sanharao, Rio Pardo, on rocks and trunks of shrubs in the river, D. M. VITAL 1856, 12.IX.1971 (ABSH, NICH, SP, U, private coll. FULFORD, GROLLE, SCHUSTER); ibid., D. M. VITAL 2779, 5.XII.1973 (SP, U; to be distributed in Fasc. VI of "Bryophyta Selecta Exsiccata", ed. Dr. H. INOUE)

Ecology

Myriocoleopsis puiggarii grows mainly on bare rocks and small rocky cliffs in the middle and along the edges of the river Pardo.

Sometimes it also occurs in small patches on the base of low shrubs with thick and rigid stems growing among large rocks and in rocky crevices. The species is always found in exposed places in or near running water. In the area where *Myriocoleopsis* occurs the river Pardo becomes moderately sloped over a distance of c. 2½ km, running swiftly over a rocky bed with small waterfalls, numerous emerging rocks and even some small rocky islets.

The species seems to thrive on emergent substrates and only there it become fertile. When submerged for a period of 5–15 days, the leafy shoots die and only the stoloniform stems survive. At almost every small rocky cliff the following phases of development could be observed: 1) submerged plants consisting of few stoloniform stems only; 2) plants growing at water-level or slightly above the water having well-developed leafy shoots with young perianths; 3) plants growing on the upper part of the emerging cliff being profusely branched and bearing sporophytes. The patches on the trunks of shrubs are also well-developed, bearing sporophytes in great quantity. An exception to this was observed in slightly submerged plants which grow on top of rocks, over which water runs very swiftly. These plants, being more directly exposed to sunlight than plants growing on the sides of rocks, grow quite well and even bear some young perianths.

SCHIFFNER (1944) suggested that *Myriocoleopsis* was an aquatic species because he found some diatoms inside tufts of the liverwort. In our recent collections of the species there are indeed many diatoms, e. g. *Melosira* (in great number), *Gomphonema, Synedra, Cymbella* and some *Naviculaceae.* However, the occurrence of diatoms in tufts of bryophytes does not necessarily im-

ply that the bryophytes came from an aquatic environment. It is well known that diatoms occur in many different habitats, such as humid banks, cliffs, soil, tree-trunks and also in water accumulated in the imbricated leaves of *Bromeliaceae* (LYRA 1971). From the foregoing we must conclude that *Myriocoleopsis puiggarii* SCHIFFN. is not a truly aquatic liverwort but a rheophytic species.

Taxonomic relationship

Within the subf. *Cololejeuneoideae, Myriocoleopsis* has tentatively been placed near *Aphanotropis* (tribe *Diplasiae*) by HERZOG (in GROLLE 1956) and near *Cololejeunea* (tribe *Aphyllae*) by SCHUSTER (1963).

Aphanotropis HERZ. is a rare monotypic genus from Borneo, including *A. saxicola* HERZ. which is only known from one little stem-fragment. The genus agrees with *Myriocoleopsis* in several striking respects: 1) the presence of a creeping caudex and erect axes, 2) the reduced fold-like leaf-lobule, 3) the cymose arrangement of the gynoecia, and 4) the occurrence on boulders in running water. However, *Aphanotropis* has underleaves and therefore belongs in the tribe *Diplasiae* of the *Cololejeuneoideae,* where it is placed close to *Diplasiolejeunea* (HERZOG 1952). *Myriocoleopsis* lacks underleaves and therefore should be put in the tribe *Aphyllae.*

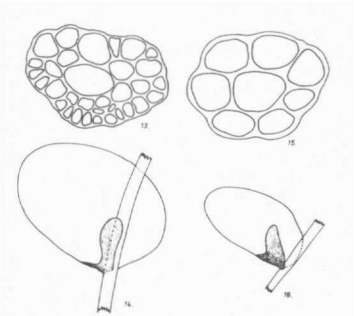
Because of the ecological similarity of *Aphanotropis* and *Myriocoleopsis* it is likely that the morphological congruence of the two genera illustrates analogy – a very common phenomenon in *Lejeuneaceae* – rather than close phylogenetic relationship.

More plausible seems to be a close phylogenetic relationship between *Myriocoleopsis* and *Cololejeunea* (SPRUCE) SCHIFFN. According to SCHUSTER (1963), these two genera differ mainly in the presence of dimorphic stems in *Myriocoleopsis.* In view of the fact that no data on stem-anatomy, oil-bodies and sporophyte of *Myriocoleopsis* were available, it becomes necessary to review the affinities between the two genera. The oil-bodies and the sporophyte of *Cololejeunea* and *Myriocoleopsis* seem to be basically similar, although it should be noted that in *Myriocoleopsis* the elongated seta becomes up to 3 mm long, whereas in *Cololejeunea* the seta rarely exceeds 1 mm in length. Of interest might be the fact that in *Myriocoleopsis* only few elaters protrude from the apex of the valves of the capsule after dehiscence, e. g. only those elaters which are attached to the marginal cells of the valves. The other elaters remain appressed to the innerside of the valves. We do not know whether this character has any taxonomical significance.

The stem in *Myriocoleopsis,* which consists of c. 30 small, greenish cortical cells surrounding one large central medullary cell, is definitely more complex than is usual in the subf. *Cololejeuneoideae.* According to BISCHLER (1961), who made a thorough survey of the stem-anatomy in this subfamily, in the tribe *Aphyllae* the stem in transverse section usually consists of 1–2 medullary cells and 5–7 cortical cells.

In the tribe *Diplasiae* there are usually 3 medullary cells and 7–8 cortical cells. The only notable exception is *Cololejeunea madothecoides* (STEPH.) BENEDIX from Malesia which, according to BISCHLER, has a stem of 2–5 medullary cells and 11–12 cortical cells. When looking at BISCHLER's fig. 22 of the stem of *C. madothecoides* we even count 16 cortical cells arranged in 1–2 layers and only 1(–2?) large central medullary cells. For comparison's sake, we made stem sections of two different collections of *C. madothecoides* from the HAUSSKNECHT Herbarium (Jena). In a collection from Merapoh, Malaya (CHIN 1527; det. GROLLE) we found relatively rigid stems, which consist of one large medullary cell surrounded by c. 35 cortical cells in 1–3 layers (fig. 13)! The only difference with the stem of *Myriocoleopsis* appears to be the presence of a difference in size between dorsal and ventral cortical cells.

Another collection of the species, from Dana, Sumatra, (RUTTNER s.n., type of *He-*



Figs 13–16: *Cololejeunea madothecoides* (STEPH.) BENEDIX *sensu lato*. 13, 15: stem in transverse section (360×); 14, 16: leaf (35×). Figs 13–14 from plants growing on boulders in a stream (CHIN 1527); figs 15–16 from plants growing on leaves of a tree (WINKLER 3329).

milejeunea ruttneri SCHIFFN.; rev. BENEDIX) had also fairly rigid stems but due to the small amount of material no sections could be made. Both collections came from boulders in rivers, just like *Myriocoleopsis*. According to BENEDIX (1953), *C. madothecoides* also grows on bark of trees and even on leaves. We made stem-sections in a collection, gathered from leaves of trees near Serawei, Borneo (WINKLER 3329; det. BENEDIX) and were amazed to find a thin stem of the usual *Cololejeunea*-type with only 5–7 cortical cells (fig. 15). This material also differed from the two other collections of *C. madothecoides* studied in that the leaves are much narrower and not arching beyond the stem (figs. 14,16), and it therefore seems possible that two different, although closely related, taxa are at hand. This deserves further study. For the time being it should be concluded that within *Cololejeunea madothecoides sensu lato* a striking variation in stem-anatomy occurs, with the number of cortical cells varying from 5–7 (coll. from leaves) to 12–16 (fide BISCHLER 1961) to 35 (coll. from rocks in streams). The stem-anatomy of *Myriocoleopsis* clearly falls within this range of variation and cannot serve to distinguish between *Myriocoleopsis* and *Cololejeunea*.

According to BISCHLER (l.c.), the greatest variation in stem-anatomy within *Cololejeunea* is present in the "*Leptocolea* Complex" which includes *C. madothecoides*, and *C. lanciloba* and its allies (Subg. *Chlorolejeunea* BENEDIX *emend.* SCHUSTER 1963). Several of the species in this group may grow in aquatic habitats, e. g. *C. lanciloba* and *C. raduliloba* from S.E. Asia (MIZUTANI 1962, p. 240–252). They all share with *Myriocoleopsis* the smooth, thin-walled, greenish leaf-cells and the often reduced lobule (resulting from the humid habitat!) which is crowned with a hyaline papilla on its apex. A close phylogenetic relationship between *Myriocoleopsis* and *Cololejeunea* subg. *Chlorolejeunea*, as suggested by SCHUSTER (1963), seems likely to exist. The difference between both taxa may be summarized as follows:

Myriocoleopsis	*Cololejeunea* subg. *Chlorolejeunea* (Typus: *C. madothecoides*)
dimorphic stems (creeping caudex and erect axes)	all stems creeping
stem without dorsi-ventral differentiation	stem with dorsal cortical cells larger than ventral cortical cells
androecia in long spikes of (6–)10–20 pairs of bracts	androecia in short spikes of 3–8(–10) pairs of bracts
gynoecia arranged in compound cymes: dichasial below, monochasial above (with 2 or 1 innovations)	gynoecia simple or arranged in monochasia (1 innovation only)
perianth inflated, with 5 keels (*Physocolea*-type!)	perianth more or less flattened, with 4(–5) keels (*Leptocolea*-type!)

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Postscript

After our manuscript was sent to the editors, an interesting paper on *Cololejeunea* subg. *Chlorolejeunea* was published by SCHUSTER & INOUE (1974). It now appears that epiphyllous plants with thin stems assigned to *Cololejeunea madothecoides* (Pl. II: 15–16 of this paper) most probably belong to *C. raduliloba* STEPH. SCHUSTER & INOUE describe *Cololejeunea (Chlorolejeunea) mizutanii* sp. nov. from Japan, which is very similar to hydrophytic *C. madothecoides* from Indo-Malesia reported in our paper. *C. mizutanii* is said to have a cortex of one layer of cells (22–26), and a medulla of several layers of cells (12–18) including one large cell (SCHUSTER & INOUE l.c., Fig. 1:8). From what we have seen in *Myriocoleopsis* and *C. madothecoides* we would suggest that the stem cells in *C. mizutanii* are all cortical-derived except for the large central cell, which should represent the single medullary cell characteristic for the subfamily *Cololejeuneoideae*.

Literature

BENEDIX, E. H. 1953. Indomalayische Cololejeuneen. – Feddes Repert. Beih. 134, 88 p., 31 Pls.

BISCHLER, H. 1961. Recherche sur l'anatomie de la tige chez les *Lejeuneaceae Paradoxae*. – Rev. Bryol. Lichénol. 30: 232–252, 2 Pls.

GROLLE, R. 1956. Revision der *Clasmatocolea*-Arten. – Rev. Bryol. Lichénol. 25: 288–303, 3 Pls.

HERZOG, TH. 1952. *Aphanotropis* HERZ., eine neue Gattung der *Lejeuneaceae* aus Borneo. – Trans. Brit. Bryol. Soc. 2: 62–65, 2 figs.

LYRA, L. T. 1971. Algumas diatomáceas encontradas em bromeliaceas, Brasil. – Mems. Inst. Oswaldo Cruz, Rio de Janeiro, 69: 129–139, 2 Pls.

MIZUTANI, M. 1962. A revision of Japanese *Lejeuneaceae*. – J. Hattori Bot. Lab. 24: 115–302, Figs. 1–39, maps 1–5.

SCHIFFNER, V. 1944. *Myriocoleopsis*, eine neue Gattung der *Jubuleae*. – Hedwigia 81: 234–237, Figs. 1–9.

SCHUSTER, R. M. 1963. An annotated synopsis of the genera and subgenera of *Lejeuneaceae*. I. Introduction; annotated keys to subfamilies and genera. – Nova Hedwigia Beih. 9: 1–203.

SCHUSTER, R. M. & H. INOUE 1974. – Bull. Nat. Sci. Mus. 17: 233–238.