

Die evolusie van gametangiofore in Suider-Afrikaanse Marchantiales (Hepaticae): 'n hipotese

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UITTREKSEL

Die tallusagtige lewermos-orde, Marchantiales, toon sowel 'n groot diversiteit in die gametangiosore (gespesialiseerde gametangiumdraende vertakkings) as in die sporofiete (gewoonlik bestaande uit 'n voet, seta en spoorbevattende kapsel). 'n Poging word aangewend om die filogenie of afstammingsgeskiedenis van die Suider-Afrikaanse lede van die orde na te spoor deur die vermelde strukture by 'n paar sleutelvoorbeweide soos die genusse *Oxymitra*, *Exormotheca*, *Targionia*, *Riccia*, *Lunularia*, *Asterella*, *Cryptomitrium* en *Marchantia* te ondersoek en met mekaar te vergelyk. Daar is tot die gevolgtrekking gekom dat daar 'n mosaïk van voorvaderlike en gevorderde kenmerke in die gametangiosore van die aangehaalde voorbeeld is, ook dat 'n afstammingssmodel, waar die stadiums lineêr gerangskik word, onaanvaarbaar is, en dat 'n vertakte tipe konfigurasie¹⁰ meer waarskynlik is.

ABSTRACT

The evolution of gametangiophores in Southern African Marchantiales (Hepaticae) : a hypothesis

Members of the thallose liverwort order, Marchantiales, display great diversity in their gametangiophores (specialized gametangium-bearing branches), as well as in their sporophytes (typically consisting of a foot, seta and spore-containing capsule). An attempt is made to trace the phylogeny or evolutionary history of Southern African members of the order by examining and comparing the aforementioned structures in a few key examples such as the genera *Oxymitra*, *Exormotheca*, *Targionia*, *Riccia*, *Lunularia*, *Asterella*, *Cryptomitrium* and *Marchantia*. It is concluded that there is a mosaic of primitive and advanced characters in the gametangiophores of the examples cited and that a linear mode of descent is not acceptable, but that a branched type of configuration¹⁰ is more probable.

INLEIDING

Die kenmerke van sowel die gametangiosore (geslagseldraende strukture met gespesialiseerde vertakkings) as die sporofiete wat later vorm en gewoonlik uit 'n voet, seta en kapsel bestaan, is belangrike maatstawwe by die klassifisering en filogenie van lede van die orde Marchantiales, die mees gevorderde tallusagtige lewermosse. Daarenteen word die hoogte en kompleksiteit van die gametofiet (d.i. die tallus) deur die akwatiese bevrugtingsmilieu (waarin die spermselle na die eiersel swem) beperk en dié toon gevolglik groter eenvormigheid.

By verteenwoordigers van die genus *Marchantia* (fig. 1A) word die mees komplekse gametangiosore, wat hier by altwee geslagte op stèle gedra word, aangetref. Daarenteen het *Riccia*-spesies (fig. 1H) die eenvoudigste gametangiosore en word die spoordraende kapsel inwendig gehou en deur tallusweefsel omsluit. Voorheen is die familie Ricciaceae as die primitiefste beskou, omdat hulle eenvoudigheid met primitiwiteit verwarr is en daar beweer is dat die geslagseldraende strukture toenemend steeds komplekser geword het. Die voorstanders van die reduksieteorie beweer egter dat daar 'n geleidelike verlies van die stèle en ook van die gametofietweefsel rondom die kapsels plaasgevind het. Uiteindelik het die sporofiet, soos by *Riccia*, slegs uit 'n spoordraende kapsel bestaan, en dit word tans as die

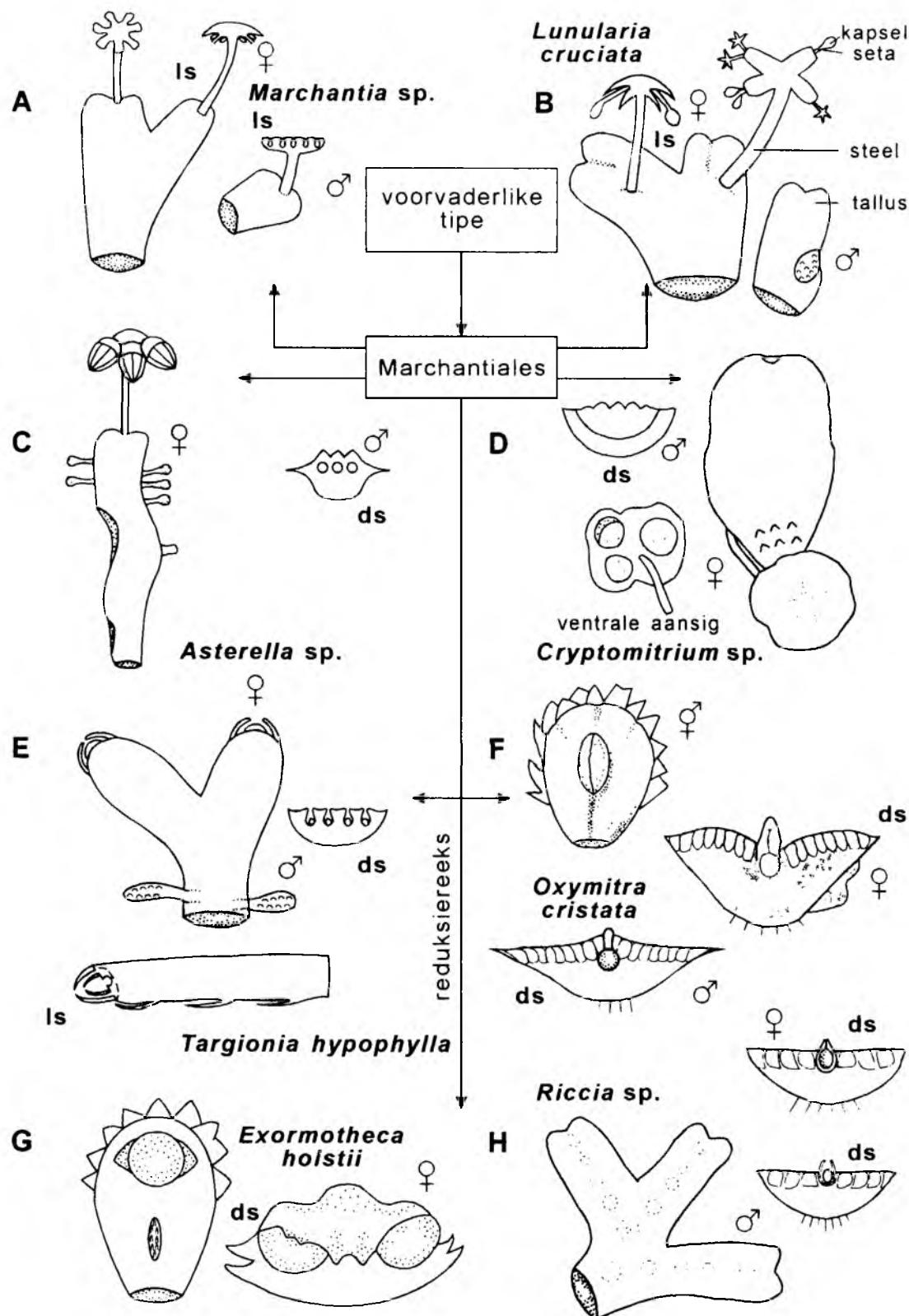
gevorderdste genus beskou.² Dit is duidelik dat hierdie twee klassifikasiestelsels mekaar reëlgreg weerspreek.

RESULTATE EN BESPREKING

Vermoedelik het evolusie by die Marchantiales vanuit 'n voorvaderlike prototipe, waar die gametangiums (argegoniums met eierselle; anteridiums met spermselle) in eenvoudige akropetale volgorde (d.i. progressief jongerwordend in die rigting van die voorste punt) in 'n ry bo-kant die middelrif van 'n gevleuelde tallus gerangskik was, geskied. Die kapsel is deur 'n kort seta en voet ondersteun, die wand het langs vier lengtesplete oopgegaan, en elaters (bi- of trispirale stafies) wat kronkelbewegings uitvoer, is met die spore gemeng. Die gametangiums het geleidelik in diskrete dorsale groepe vergader en die gametangiosore en uiteindelike kapsels met spore, was sit-tend op die tallus.

Die stelsel wat tans die meeste aanhang by kenners geniet, sal vervolgens met behulp van 'n paar sleutelvoorbeweide bespreek word.

Die ligging van die gametangiums by *Oxymitra cristata*³ (fig. 1F) stem waarskynlik die naaste ooreen met dié van die voorvaderlike tipe. Die argegoniums (en latere sporofiete) is net effens in flesvormige holtes ingesink en bo-oor met 'n onreëlmataige, vlesige, kamvormige rif



FIGUUR 1: Hipotetiese evolusie van die gametangiofore van 'n paar sleutelvoorbeelde by die Marchantiales (gedeeltelik volgens Schuster 1992).

A, *Marchantia* sp.; B, *Lunularia cruciata*; C, *Asterella* sp.; D, *Cryptomitrium* sp.; E, *Targionia hypophylla*; F, *Oxymitra cristata*; G, *Exormotheca holstii*; H, *Riccia* sp.
ds = dwarsnitt; *Is* = lengtesnit

bedek. Die spore word vrygestel deur die disintegrasie van die omringende weefsel. Elaters het verlore gegaan, 'n toestand wat as gevorderd beskou word. Die anteridiums is in die tallus ingesink en is lineêr in akropetale volgorde gerangskik, net proksimaal tot die argegoniums - 'n voorvaderlike kenmerk.

Exormotheca holstii het sittende sporofiete⁴ (fig. 1G). Hier ondersteun 'n sentrale kern van parenchiematische weefsel 'n effens skuins georiënteerde kapsel aan albei kante. Beringde of enkelspiraal elaters is teenwoordig - 'n voorvaderlike kenmerk. Die anteridiums wat ingesink en akropetaal langs die sentrale groef van die tallus gerangskik is, is ook voorvaderlik. Net die lang nekke van die anteridiums steek uit; dit is 'n gevorderde kenmerk.

By *Targionia hypophylla*⁵ (fig. 1E) het sekondêre welwing van die weefsel aan die bopunt van die tallus, boordie aanvanklik dorsaal geleë argegoniums, waarskynlik plaasgevind. Die sporofiet is toe na benede die bopunt van die tallus, ventraal verplaas. Elaters is hier aanwesig, weereens 'n voorvaderlike kenmerk. Die anteridiums word opaansienlik gereduseerde ventrale sytakke gevorm en is nie akropetaal gerangskik nie, 'n gevorderde kenmerk.

By die familie Ricciaceae (fig. 1H) het reduksie van die sporofiete, waar 'n voet en seta ontbreek, tesame met uitbouing van die gametofietweefsel rondom die gametangiums, waarskynlik plaasgevind, totdat hulle in die tallus versink het. Die spore is groot, plus-minus 100 µm in deursnee, en word deur disintegrasie van die tallus vrygestel. Verspreiding van die spore word deur spoelende reënwater of deur klewing aan die pote van voëls en ander diere bewerkstellig. Hulle is waarskynlik te groot vir verspreiding deur die wind. Elaters is afwesig, 'n gevorderde kenmerk. Die anteridiums (sowel as die argegoniums) is in akropetale volgorde in 'n ry langs die sentrale dorsale groef van die tallus versink, 'n voorvaderlike kenmerk.⁶

Die voorbeeld in die voorafgaande verteenwoordig 'n reduksiereeks, maar dit is moontlik dat 'n tweede, teenoor gestelde evolusionêre rigting ook kon bestaan het. Dit word dan veronderstel dat die gametofietiese strukture wat die gametangiums steun, geleidelik meer kompleks geword het, soos by *Marchantia*-spesies en by *Lunularia cruciata*, asook by die meeste verteenwoordigers van die *Marchiales*.

In die opsoring van die hipotetiese ontstaan en ontwikkeling van hierdie strukture, word weereens by die eenvoudige akropetale rangskikking van die gametangiums op die boonste oppervlak van die tallus, begin. Dit word opgevolg deur die samevoeging van die gametangiums in diskrete groepe. Die fertiele sone is toe waarskynlik tot die eindpunte van die tallussegment aan die basis benede die fertiele sone, en deur reduksie en invouing van die vleuels van die tallus, is 'n steel gevorm waarop die sporofiet gedra word. Verheffing van die sporofiete op 'n steel het moontlik geskied in reaksie op seleksie vir verspreiding van die heelwat kleiner spore deur die wind, wat waarskynlik meer effektiief as reënwater of diere is wat groter spore versprei.

Die kruisvormige rangskikking van die sporofiet by *Lunularia cruciata* (fig. 1B) met min lugkamerweefsel

(gereduseer en daarom 'n gevorderde kenmerk) tussen die vier omwindsels, het waarskynlik ontstaan uit twee pare digotome vertakkings van die vroulike struktuur. Dit is opgevolg deur verdere kondensering en verkorting. Die sporofiet, waarvan daar twee of selfs drie per omwindsel kan ontwikkel, het 'n groot, bolvormige voet, die seta is lank en die kapsel splits langs vier kleppe, almal voorvaderlike kenmerke. Die steel toon verlies van 'n risoïedkanaal, 'n gevorderde kenmerk. Klein, groen, dunwandige spore word gevorm en elaters is teenwoordig. Die anteridiums is in 'n sittende skyf op die manlike tallus versink en is nie akropetaal gerangskik nie, 'n gevorderde kenmerk.

By *Asterella*-spesies (fig. 1C) is die vrughofie ook gekondenseer en elke lob is 'n gereduseerde fertiele tak van 'n digotome vertakking. Heelwat lugkamerweefsel en porieë het hier behoue gebly, 'n voorvaderlike kenmerk. Vanaf die basis van die argegonium ontwikkel daar 'n kenmerkende skede, die pseudoperiant, 'n gevorderde kenmerk, wat in 'n aantal smal lengtesplete verdeel waardeur die spore en elaters sif. Die steel bevat 'n enkele risoïedkanaal. Die anteridiums is in sittende skywe, digby die bopunt van die hooftak van die tallus, of op baie gereduseerde sytakke, versink.

In 'n nuwe spesie wat voorlopig na die genus *Cryptomitrium* (fig. 1D) verwys is, maar nog nie deur my beskryf is nie, was daar waarskynlik nog verdere verkorting van die segmente van die digotome vertakkings, en het dit 'n meer kompakte sisteem tot gevolg gehad. Elaters is aanwesig. Die steel bevat 'n enkele risoïedkanaal. Die anteridiums is ingesink en bymekaar op die tallus in ongedefinieerde andresiums gegroepeer, 'n gevorderde kenmerk.

Marchantia-spesies (fig. 1A) het die hoogtepunt van die ingewikkeldheid bereik en hier word die hofies van beide geslagte op stele wat twee risoïedkanale bevat, gedra. Die argegoniofore het vier tot elf arms, as gevolg van herhaalde digotome vertakkings. Die argegoniums word ventraal op die argegoniofore in akropetale volgorde verplaas, 'n voorvaderlike kenmerk. Die kapsel word ondersteun deur 'n gereduseerde seta en 'n smal voet, wat albei gevorderde kenmerke is. Die anteridiofore is sambreelagtig as gevolg van kondensering en vereenvoudiging van die oorspronklike digotome vertakkings.⁹

GEVOLGTREKKING

Uit bogenoemde voorbeeld is dit duidelik dat daar by elke groep sowel 'n mosaïk van gevorderde as voorvaderlike kenmerke aanwesig is. 'n Afstammingsmodel waar die stadiums lineêr gerangskik is, het dus in onguns verval. In die plek daarvan stel Schuster¹⁰ 'n tipe konfigurasie met veelvoudige vertakkings as 'n meer aanneemlike model voor. Uit eie ondervinding blyk dit dat Schuster wel op die regte spoor is, maar die fossielerekord van lewermosse is ongelukkig baie skraal,¹¹ sodat daar geen bewyse vir bogenoemde spekulasie is nie.

Pogings word tans aangewend om verwantskappe tussen groepe deur chemiese analises, ribosomale RNA-volgordes en kladistiese metodes te bepaal, en hopelik sal dit ook lig op die filogenie kan werp.

SUMMARY

Characteristics of the gametangiophores (specialized branches bearing gametangia, i.e. archegonia with egg cells and antheridia with sperm cells), as well as the sporophytes (typically consisting of a foot, seta and spore-containing capsule), are important criteria in the classification and phylogeny of members of the order Marchantiales, which are the most complex thallose liverworts. Great diversity is displayed by these structures and an effort is made to trace the phylogeny of Southern African members of the order by comparing these structures in a few key examples.

Members of the genus *Marchantia* (Fig. 1A) have the most elaborate gametangiophores, which are borne on stalks in both sexes, whereas the *Riccia* species (Fig. 1H) have the simplest, which are enclosed by thallus tissue. Previously the Ricciaceae were regarded as the most primitive because of their simplicity, and it was thought that the gametangiophores became progressively more elaborate.⁸ However, advocates of the theory of reduction hold that there had been a gradual loss of the stalks and also of the gametophytic tissues surrounding the capsule. Finally, the sporophyte consisted solely of a capsule containing spores as in *Riccia*, and this is now regarded as the most advanced genus.⁹ It is clear that these two classification systems are contradictory.

DISCUSSION

It is presumed that evolution in the Marchantiales was from an ancestral type in which the gametangia developed above the costal region of a winged thallus in simple acropetal sequence (i.e. becoming progressively younger toward the apex). In the capsule elaters (bispiral or trispiral rods) were mixed with the spores. The system that is currently in vogue will be discussed with the aid of a few key examples.

The position of the gametangia in *Oxymitra cristata*⁴ (Fig. 1F) probably corresponds most closely to the ancestral position. The sporophytes are only slightly sunken into flask-shaped cavities and are enclosed above by an irregular, crest-like, fleshy ridge. Elaters have been lost, a derived character. The antheridia are linearly arranged in acropetal sequence, a primitive character.

Exormotheca holstii has sessile sporophytes⁶ (Fig. 1G). Ringed or unispiral elaters are present, a relatively primitive character. Also primitive are the antheridia, which are sunken and acropetally arranged along the central groove of the thallus. Only their long necks protrude, which is a derived character.

In *Targionia hypophylla*⁵ (Fig. 1H) secondary overarching of the tissues of the thallus apex over the initially dorsally located archegonia may have taken place. The sporophyte is then ventrally displaced below the apex. Elaters are present, again a primitive character. The antheridia are formed on greatly reduced ventral branches and are not acropetally arranged, a derived character.

In the family Ricciaceae (Fig. 1H) reduction of the sporophytes, which lack a foot and seta, together with elaboration of the gametophytic tissue around the gametangia until they became sunken into the thallus, probably took place. Elaters are absent, a derived character. The antheridia (as well as the archegonia) are sunken

in a row along the dorsal groove of the thallus, in acropetal sequence, a primitive character.²

The examples in the foregoing represent a reduction series, but it is possible that a second, fundamentally opposed, evolutionary pathway may also have existed. Here it is supposed that the gametophytic structures that support the gametangia became progressively more complex, as in *Marchantia* species and in *Lunularia cruciata*, as well as in most of the representatives of the *Marchantiales*.

In tracing the hypothetical origin and development of these structures we commence again with the simple acropetal arrangement of the gametangia above the thallus surface. This is followed by their aggregation into sessile groups. The fertile zone may have become restricted to the thallus apices. The thallus segment at the base below the fertile zone then became narrow and constricted, followed by the wings of the thallus becoming reduced and incurved, thus forming the stalk on which the sporophyte is borne.

The cruciate arrangement of the sporophyte in *Lunularia cruciata* (Fig. 1B) with vestigial air chambers (a derived character) between the four involucres may have resulted from two pairs of dichotomies of the female receptacle. The sporophyte has a large, bulbous foot, the seta is long and the capsule splits into four valves, all primitive characters. Elaters are present. The antheridia are sunken into a sessile disc on the male thallus and are not acropetally arranged,³ a derived character.

In *Asterella* species (Fig. 1C) the female receptacle is also condensed and each lobe is a reduced fertile branch of a dichotomy. Quite a number of air chambers and pores have been retained, both primitive characters. The antheridia are sunken into sessile discs at the apex of the main branch or on greatly reduced lateral branches and are not acropetally arranged, a derived character.⁷

In a new species that has been provisionally referred to the genus *Cryptomitrium* (Fig. 1D), but that has not yet been described by me, there has probably been greater foreshortening of the segments of the dichotomies and this has resulted in a more compact system. Elaters are present. The antheridia are sunken and are grouped together on the thallus in undefined androecia, a derived character.

Marchantia species (Fig. 1A) have attained a summit of complexity and the receptacles of both sexes are raised on stalks. The archegoniophore has four to eleven arms, resulting from repeated dichotomies. The archegonia become ventrally displaced on the archegoniophores in acropetal sequence, a primitive character. The capsule is supported on a shortened seta and small foot, both derived characters. The antheridiophores are umbrella-like by condensation and simplification of the initially dichotomously branching system.¹⁰

CONCLUSION

From the above examples it will be clear that in every group there is a mosaic of derived and primitive characters. A linear model of descent is thus unacceptable and

in its place Schuster¹¹ suggests a type of configuration with numerous branches as a more likely model. From personal experience it would appear that Schuster is on the right track, but the fossil record of liverworts is unfortunately so meagre¹ that there is no way of proving the above speculations.

Nowadays efforts are being made to determine relationships between the groups by chemical analysis, by ribosomal RNA sequences and by cladistic methods, and it is hoped that these will also shed some light on the phylogeny.

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