

OPHIOGLOSSACEAE : AN EXOMORPHOLOGICAL APPROACH WITH EMPHASIS IN SOUTH AMERICAN SPECIES

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ABSTRACT

An update about exomorphology of Ophioglossaceae family, with special reference to South American species is provided. The morphological characters that have been described in the literature by classical authors are discussed from the perspective of new observations, and its main morphological features are given. In this contribution it recognizes in South American the following genera: *Botrychium* Sw., *Botrypus* Micx., *Sceptridium* Lyon. *Ophioderma* Nakai (included *Cheiroglossa* C. Presl.), and *Ophioglossum* L. It proposed the term "angiostroma" to describe fertile portion of sporophore.

Key Words : Angiostroma, *Botrychium*, *Botrypus*, *Ophioglossum*, *Sceptridium*

INTRODUCTION

Ophioglossaceae, commonly called the adder's tongue ferns, is a putatively ancient lineage of ferns (Bower 1926, Campbell 1905, Clausen 1938, Eames 1936, Gifford & Foster 1989, Kato 1987, Prantl 1884, Presl 1845, Tryon & Tryon 1982, Wagner 1990) with an evolutionary history that is largely enigmatic because of family fossils date only from the earliest Tertiary for *Botrychium wightonii* Rothwell & Stockey [(aff. *B. virginianum* (L.) Sw.] species known for Canada (Rothwell & Stockey 1989) and *B. aff. underwoodianum* Maxon from the Oligocene/Miocene that document the earliest fossil of a *Botrychium* in Bulgaria (Bozukov *et al.* 2010).

The principal attribute distinguishing Ophioglossaceae from other ferns is the division of the frond into a separate sterile (trophophore) and a fertile (sporophore) segments (Figs. 1, 2) (Hauk *et al.* 2003 and authors cited by them). This architecture of the phylomes is a synapomorphy for this group (Ophioglossaceae, or Ophioglossales *sensu* Pichi Sermolli, 1977), moreover all current morphological and molecular data support the monophyly of this family (Hauk *et al.* 2003).

Many species of Ophioglossaceae have a shoot with a simple architecture and frequently with small and inconspicuous leaves, contrasting strongly with the conspicuous and highly complex development of fronds in many other ferns. Morphological simplicity was a feature highlighted repeatedly by botanists who wrote about this family (e.g. Bower 1923, Eames 1936, Clausen 1938). This simplicity in the sporophyte has given much conjecture, although the family has a limited fossil record and its age is uncertain, some botanists have postulated the hypothesis that Ophioglossales would constitute a primitive lineage, and would be a blind lineage of Primofilices from the Carboniferous, and would represent a modernized relic of Paleozoic flora (Smith 1955). These interpretations were

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always open to controversy, as Bateman *et al.* (1998), based on cladistic studies, considered that the extreme simplification would be a derived condition.

In this contribution the main author recognizes these genera for the South American species: *Botrychium* Sw., *Botrypus* Micx., *Sceptridium* Lyon (*Botrychium s.l.*) *Ophioderma* Nakai (included *Cheiroglossa* C. Presl.), and *Ophioglossum* L. (*Ophioglossum s.l.*).

The aim of this paper is to describe collectively the exomorphology of Ophioglossaceae family, with special reference to South American species. The morphological characters have been described in the literature by several authors, but here will be discussed from the perspective of new observations.

A BRIEF REVIEW OF EXOMORPHOLOGICAL FEATURES

Habit :

The family includes terrestrial or epiphytic herbaceous plants (Clausen 1938), some species exhibit an ecological specialization, and some grow in sandy grounds, or exhibit an epiphytic habit as species of *Ophioderma* (Blume) Endl. (Tryon & Tryon 1982).

Root :

The Ophioglossaceous root is described as an unusual organ among vascular plants, since this organ in the Ophioglossaceae lacks absorbent root hairs (Ogura 1972, Smith *et al.* 2008). Within the group of *Ophioglossum s.l.* species, two types of roots are described in the literature. The roots of subgenus *Euophioglossum* (Prantl) R. T. Clausen are described as fleshy and unbranched (Clausen 1938, Mickel & Smith 2004). This root type is present too in the genus *Mankyua* B. Y. Sun, M. H. Kim & C. H. Kim (Sun *et al.* 2001), while the genus *Ophioderma* (sub *Ophioglossum palmatum* L.) shows fleshy and branched dichotomously roots (Mickel & Smith 2004) the gemmiferous character is always attributed to these roots. The latter authors described *Botrychium s.l.* species, also with fleshy roots, a recurring character in the monotypic genus *Helminthostachys* Kaulf. (Clausen 1938), although the gemmiferous character is not mentioned for roots of these two genera.

Rhizome :

Farmer & Freeman (1899) described the rhizome of *Helminthostachys* with dorsiventral symmetry, and the fronds arranged in two lines. These characters are shared with the genus *Mankyua* (Sun *et al.* 2001), and *Ophioderma* (Smith 1955). In all other genera, the radial symmetry character of the rhizomes is shared (Smith 1955). A particular case of radial rhizome is shown in *O. crotalophoroides s.l.*, which is described by Clausen (1938, 1948) and by Mickel & Smith (2004) as globose-bulbous, whereas in many other species of this genus a cylindrical rhizome is present.

Petry (1915) analyzed the ramifications of rhizomes in this family, and attributed a type of dichotomous branching to *Ophioglossum vulgatum* L., because the vascular tissue of rhizome is divided in two equal parts. This author considers that the ramifications in the rhizome of *Helminthostachys* are result of vestigial buds. Axillary buds also would be present in the genera *Botrychium*, *Botrypus*, and *Sceptridium*.

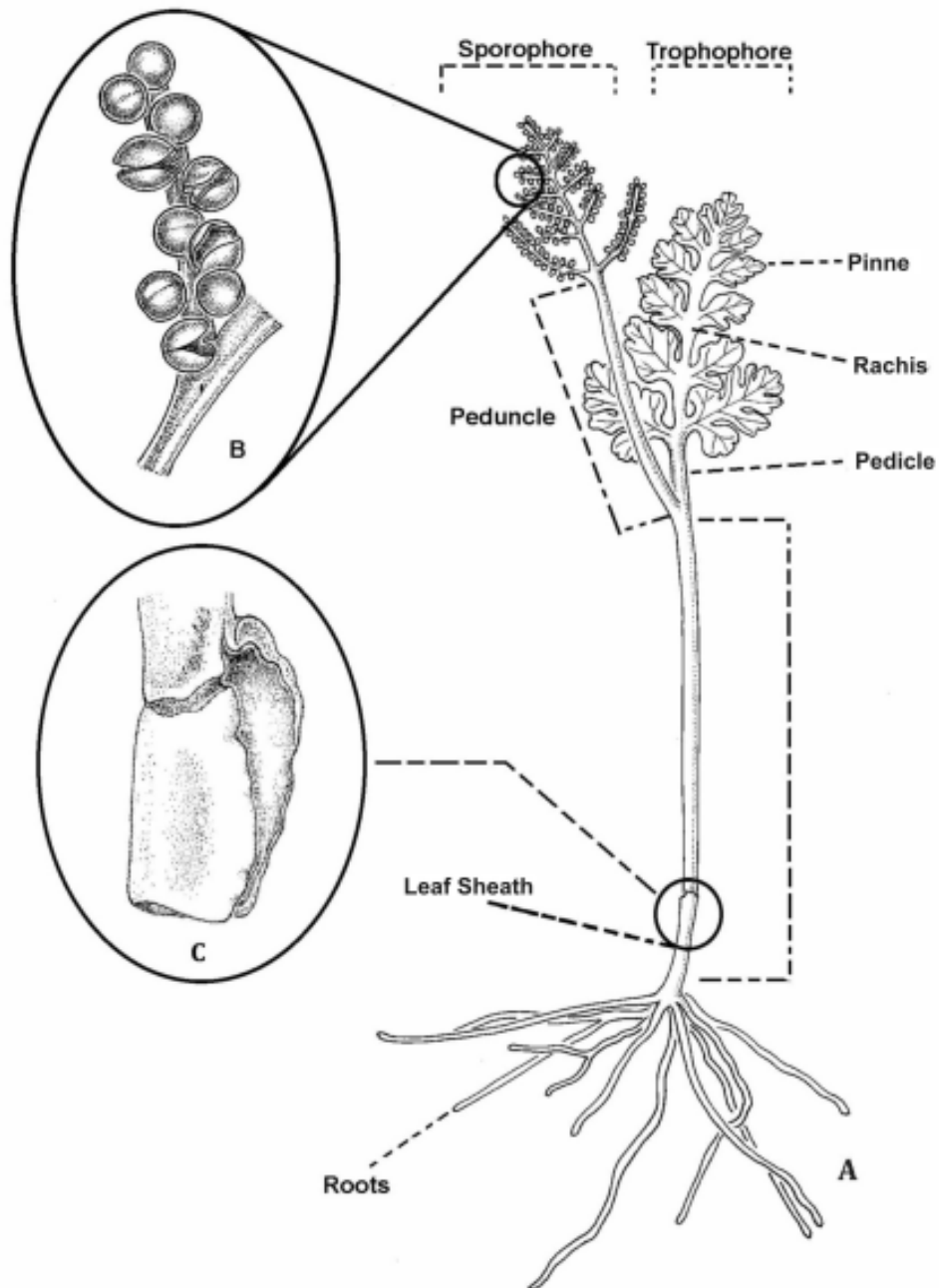


Figure 1. Basic model architecture of the sporophyte of Botrychioid species. **A.** General view of plant indicating the trophophore and sporophore. **B.** Details of the disposition of sporangia. **C.** Detail of the distal portion of the sheath [C, from specimen of *Sceptridium schaffneri*, Meza Torres et al. 807)]. A : Drawing modified of Chanda Skelton, published by Farrar, 2006.

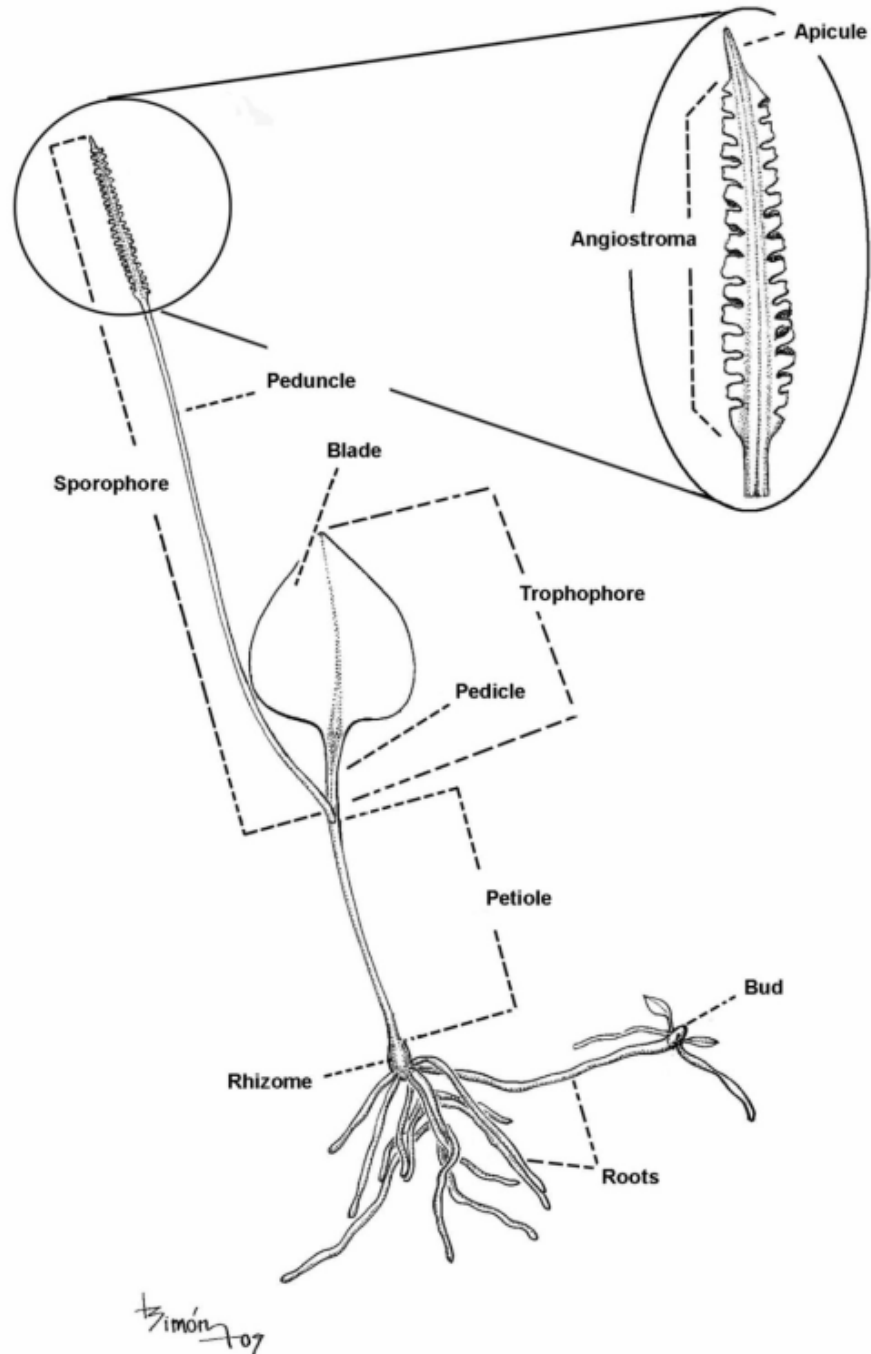


Figure 2. Basic model architecture of the sporophyte of Ophioglossoid species. General view of plant, indicating the trophophore and sporophore.

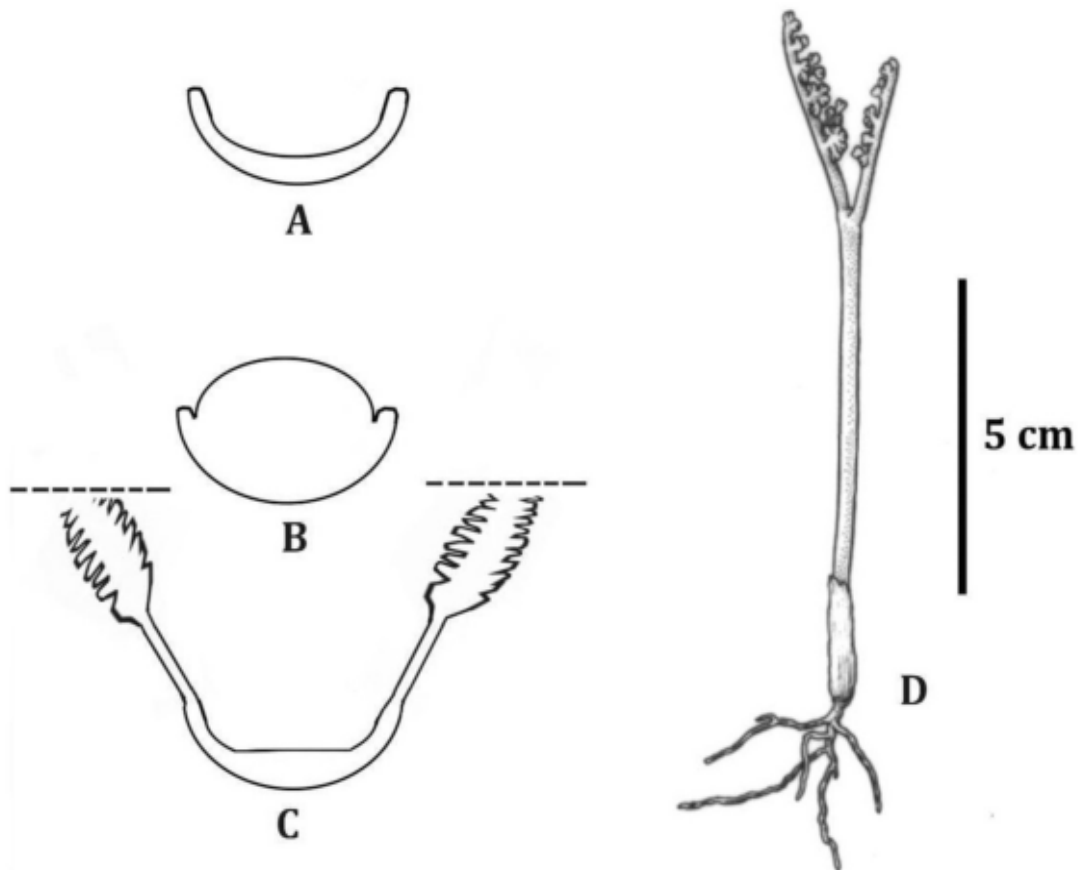


Figure 3. Structural variation of petioles associated with sporophores in Ophioglossaceae. **A-C** : Cross sections diagrams of *Ophioglossum* (A, B), and *Ophioderma* (C) petioles. **A** : Petiole without sporophores. **B** : Petiole with sporophores. **C** : Cross section of petiole at level insertion of sporophores. **D** : General view of *Botrychium paradoxum* W. H. Wagner, showing sporangia along the entire frond. (D, available in www.eFloras.org).

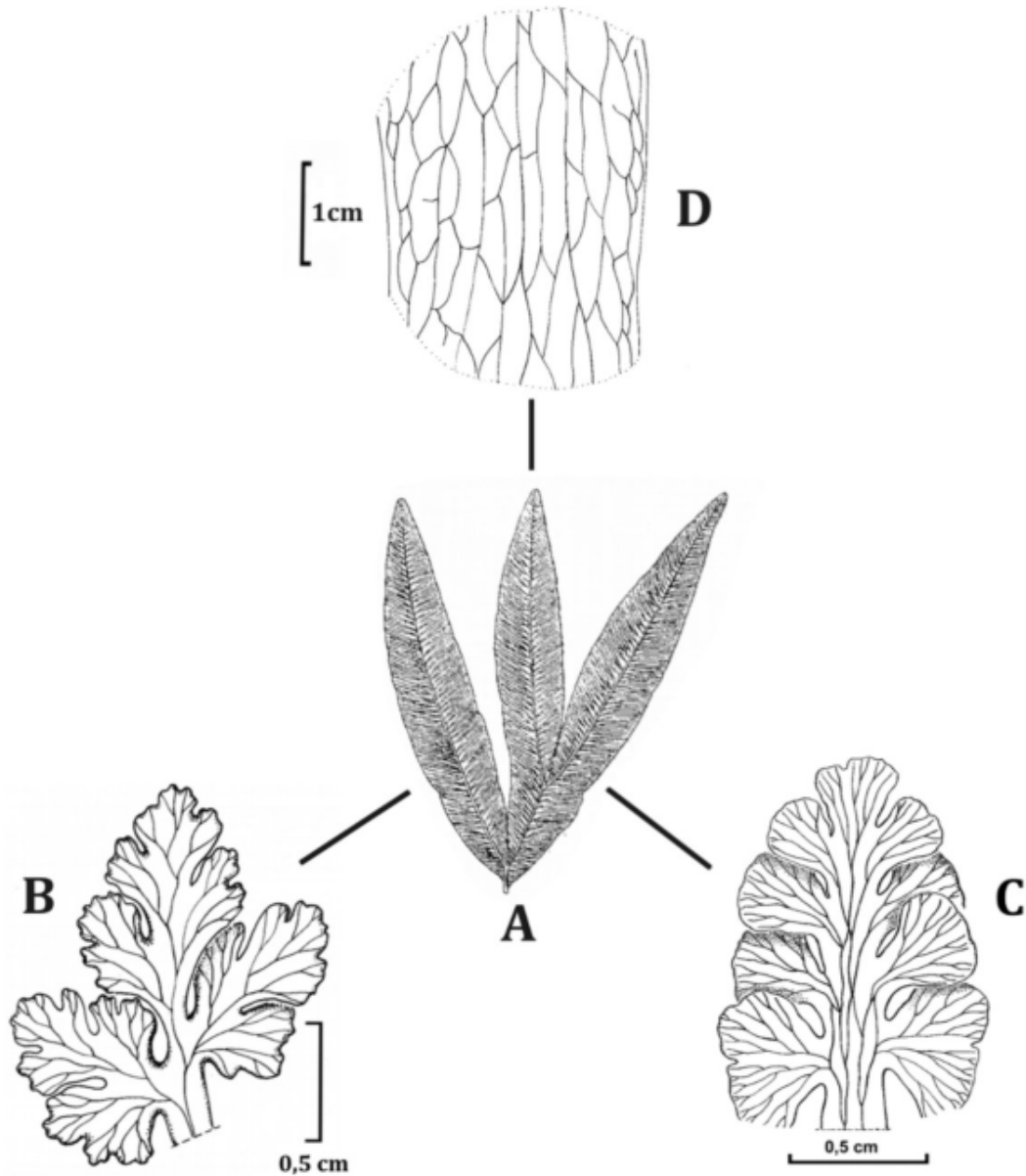


Figure 4. Hypothesized diagram of evolutionary trends in the venation pattern in Ophioglossaceae. **A** : *Helminthostachys zeylanica*, pinnate and furcate venation; with bifurcate and parallel veinlets. **B** : *Sceptridium schaffneri*, furcate venation, with veinlets laxly arranged. **C** : *Botrychium dusenii*, furcate venation, with veinlets laxly arranged, anastomosing and forming elongated areoles in areas close to the rachis. **D** : *Ophioderma palmata*, reticulate venation, also seen in *Ophioglossum*. (A : extracted from Bower, 1926).

Sporophore :

The sporophore (sub “sporophyll”, in Kato 1987) usually consists of an axis, lacking blade, and having eusporangiate sporangia (Fig. 5). This structure is seemingly inserted in the distal and adaxial region of the petiole, but in an organographic point of view, the sporophore emerge of the lateral flanks (Clausen 1938, Ogura 1972).

The sporophore may be pinnate and its segmentation similar to its homologous sterile (Kato 1987). The sporangia are grouped into clusters that were classified by Clausen (1938) as “spike” (Fig. 5C & E), when the sporophore is simple, unbranched and the sporangia are included in the tissue, or racemes or panicles (Fig. 5A, B & D), when clusters are compound. The sporangia are described as bivalvate, and produce spores in mass (Bower 1926, Clausen 1938, Kato 1987).

Indumentum :

The epidermal surface is described as glabrous in *Botrychium s.s.*, *Ophioderma*, and *Ophioglossum s.s.* or pubescent with uniseriate hairs in the genera *Botrypus*, *Japanobotrychium*, and *Sceptridium* (Fig. 6E) (Wagner 1990, Mickel & Smith 2004).

DISCUSSION AND CONCLUSIONS

All Ophioglossaceae species are herbaceous; the majority is terrestrial and vegetates in grasslands, having also species that inhabit the undergrowth (e.g. *Botrypus* Michx.). The genus *Ophioderma* (Blume) Endl. differs by having an epiphytic habit.

The roots have a morphology that could be used as a diagnostic character to the genera or to species group's level. Thus, the species of the *Ophioglossum* have fleshy, gemmiferous, and unbranched roots, with the exception of *Ophioglossum crotalophoroides* Walter. The genus *Ophioderma* has fleshy roots too, but branch dichotomously. In the genera *Botrypus* [*B. virginianus* (L.) Michx.] and *Sceptridium* the roots are axonomorphous. These roots have lateral branchings, which seem to follow a monopodial pattern. The genus *Botrychium* [e.g. *B. dusenii* (H. Crist) Alston] presents branching in its roots with the particularity that the lateral axis tends to be arranged in a horizontal plane, while a principal root grows vertically, in *B. dusenii* lateral roots are gemmiferous .

Cases of branching of rhizomes are reported for all genera, but this condition seems to be more an unusual character than a consistent one. Petry (1915) mentioned in his work that only five specimens showed ramifications from 300 specimens analyzed of *O. vulgatum*, while in *Ophioderma palmata* (L.) Nakai were found two specimens with branched rhizomes in a sample of 100 individuals. For the other genera of *Botrychium s.l.* group, Petry (1915) also concluded that the branching could be product to lesions during development. In the review of specimens from southern South America were no found cases of branching in studied genera. The species of *O. crotalophoroides s.l.* represent a particular case of rhizomes, since these exhibit spherical rhizomes with an inner cavity, which gives a similar morphology to that of a “vessel”. The apical meristem is located in the base inside the vessel. This structure could be interpreted as a specialization of the rhizome.

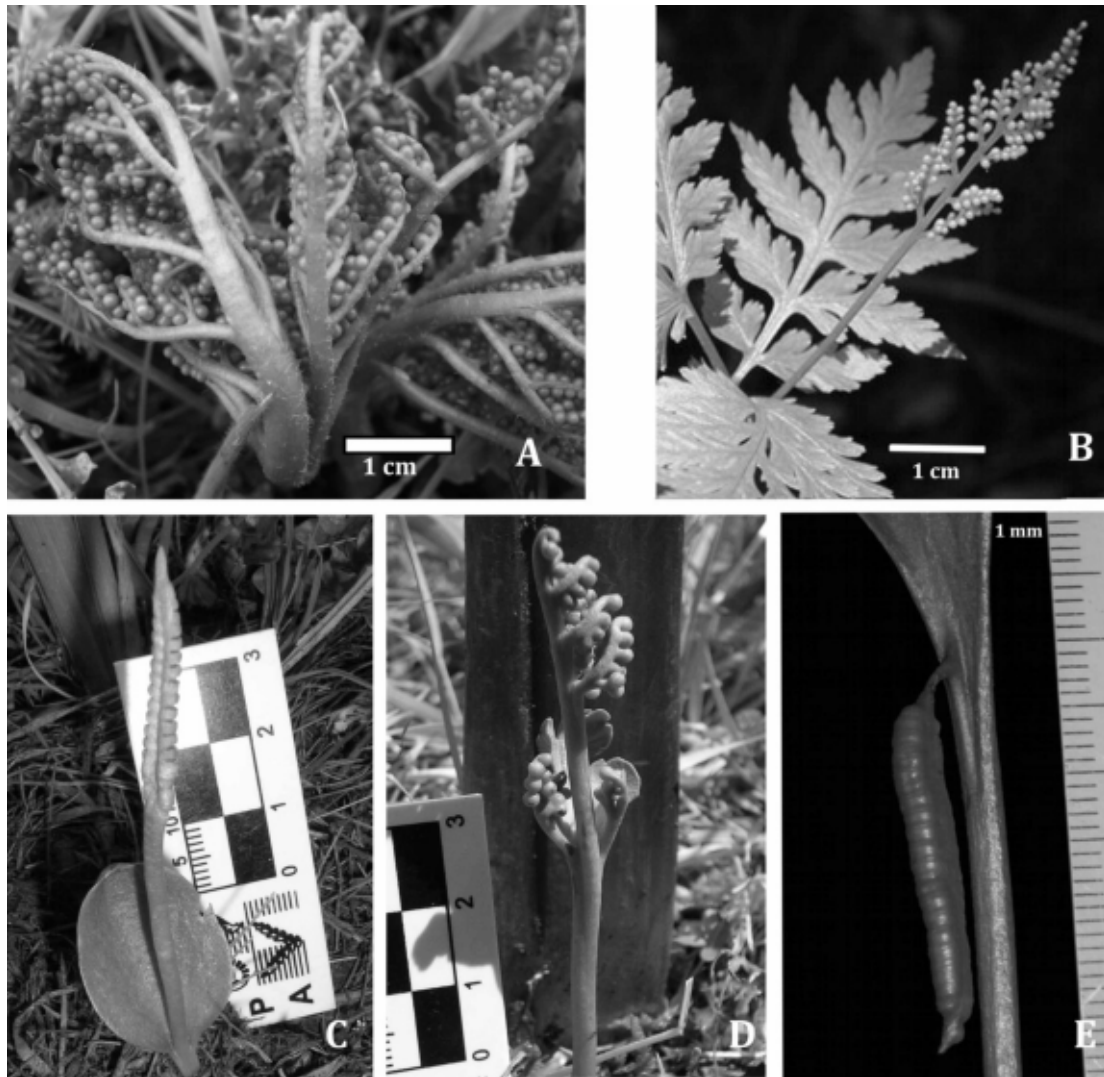


Figure 5. Sporophore morphology in five genera of Ophioglossaceae. **A-B** : Pinnate sporophore (**A**) *Sceptridium negeri* (**B**) *Botrypus virginianum*, and (**D**) *Botrychium dusenii* [Meza Torres et al. 1058 (CTES)]. Sporophore, where it can be differentiated peduncle, angiostroma, and apicule in (**C**) *Ophioglossum vulgatum* [Meza Torres et al. 699 (CTES)] y (**E**) *Ophioderma palmata*. [Meza Torres & Andrade Kersten 1410 (CTES)] (A, courtesy of Carla Jara. B, courtesy of Carlos Brussa).

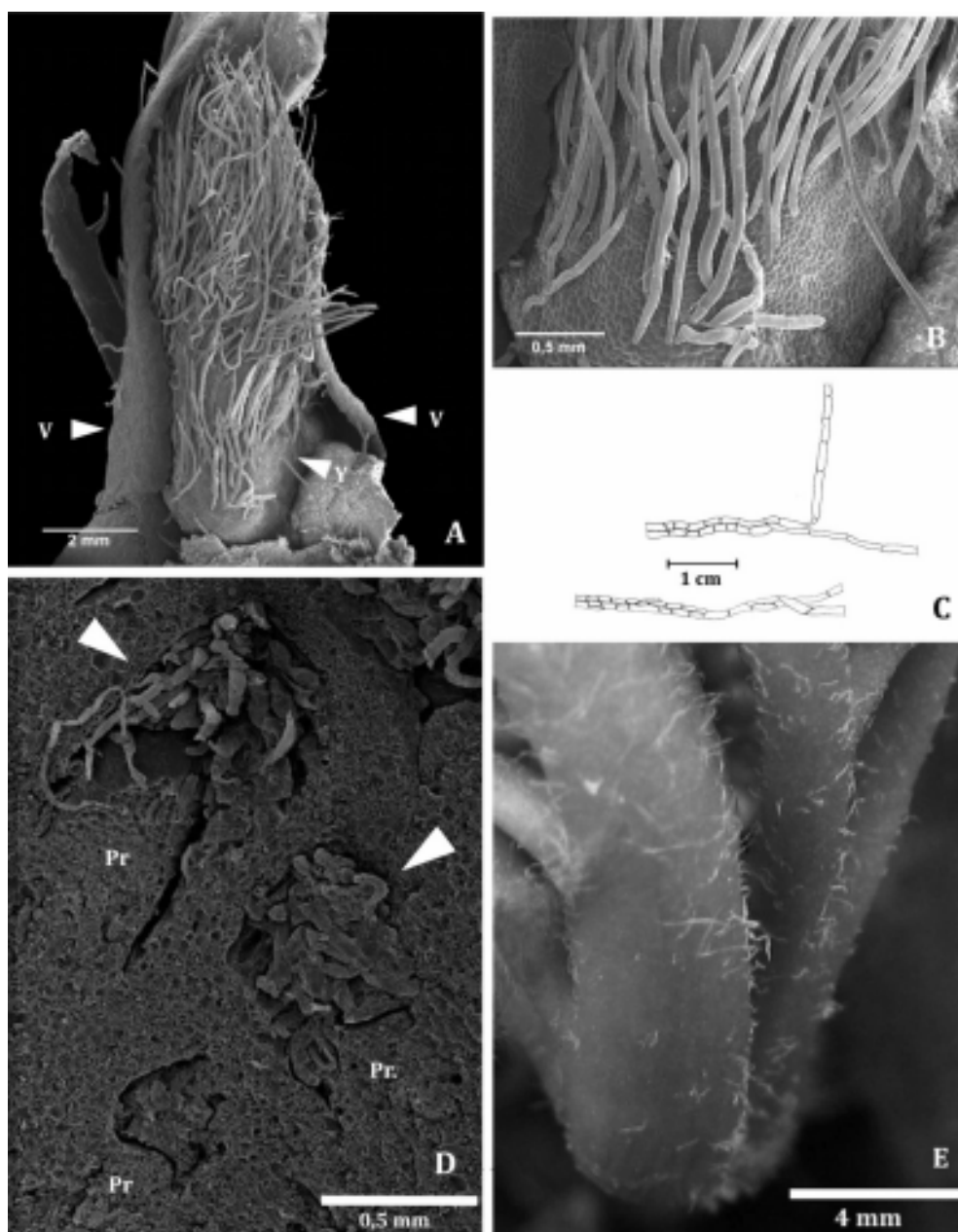


Figure 6. Indument present in the family Ophioglossaceae. **A.** Filiform hairs present in the leaf primordia of *Botrypus virginianus*; v : sheath, and: apical bud. **B.** Filiform hairs, detail. **C.** Septate hairs of the rhizomes of *Ophioderma palmata*. **D.** Filiform hairs inside rhizome of *Ophioglossum crotalophoroides*. Arrows indicate the hairs; Pr: leaf primordia. **E.** Developing trophophore with hyaline filiform hairs in *Sceptridium negeri*. (**A, B** : Meza Torres et al. 1283 (CTES); **C** : Sousa, J. P. 836 (ESA); **D** : Meza Torres 504 (CTES); **E** : courtesy of Carla Jara).

Fronds :

The megaphyllous development in Ophioglossaceae is usually described as conduplicate, not circinate (Wagner 1990). The phyllom in this family possesses a particular organization, considering the segments producing spores, which are separated from the photosynthetic portion of the blades, for this reason, this type of fronds are known as hemidimorphic fronds (Lellinger 2002). Bower (1926) and Clausen (1938) divided the blade in two parts, the laminate photosynthesizing portion is called “sterile leaf-like segment”, and the portion with sporangia is described simply as fertile segment. Wagner (1990) assigned the terms trophophore and sporophore (Figs. 1 and 2) to designate sterile and fertile segments respectively.

Leaf sheaths :

A special feature of this family is that the apical meristem and leaf primordia are enclosed by the enlarged base of the fronds, forming a sheath that protects the meristem and leaf primordia (Fig. 1.C) (Bower 1923, 1926; Clausen, 1938; Eames, 1936; Gifford and Foster, 1989; Imaichi, 1989; McAlpin, 1971; Wagner, 1990)., and other authors cited), but *Botrypus* presents incomplete development of this sheath (Imaichi 1989).

Petiole :

The special configuration of the fronds in Ophioglossaceae had led to different interpretations. Thus, the portion of fronds below sporophore insertion, and that inserted the phyllom with the caulinar axis is referred as “common stalk” (Fig. 1 & 2) (Bower 1926, and Clausen 1938). Nozu (1950) called “phyllomophore” to this appendicular portion, which is considered a special organ with intermediate characters between stem and leaf. The section of this appendicular organ is described as circular (Ogura 1972).

Trophophore :

The trophophore is described as deltoid to oblong in Botrychioid species, with blades pinnate, palmate or decompound, and entire, spatulate to linear in Ophioglossoid species (Clausen 1938, Wagner 1990). The blade of the trophophore can be immediately connected to the sporophore, or connected by an appendicular portion, sometimes cuneiform, called trophophore stalk (Fig. 1 & 2) by Clausen (1938), Wagner (1990), and Farrar (2006).

Venation :

The veins are free in *Botrychium*, *Botrypus* and *Helminthostachys* (Fig. 4A-C) and anastomosed in *Ophioglossum* (Kato 1987). The venation of *Helminthostachys* is described by Clausen (1938) as pinnate, parallel, usually 1-forked (Fig. 4A), similar pattern is found in *Mankyua* (Sun *et al.* 2001). Kato (1987) considered that the reticulated venation of *Ophioglossum* (Fig. 4D) would be a specialized state, whereas the open venation of the other three genera would be a primitive state. Within open venation genera, Kato (1987) proposed that *Botrychium* s.s. and *Helminthostachys*, for showing veins anastomosed would be more specialized than *Sceptridium* and *Botrypus*.

The genus *Helminthostachys* is the probably intermediate taxon between the species of *Ophioglossum s.l.* and *Botrychium s.l.* (Hauk *et al.* 2003). *Helminthostachys* could also be the most primitive taxon of the family. Thereby, it can be hypothesized that the primitive condition for symmetry is dorsiventral rhizomes, present in *Helminthostachys*. The derived state of the rhizomes would be the radial symmetry and cylindrical form, present in *Botrychium*, *Botrypus*, *Ophioglossum*, and *Sceptridium*. Within the group *Ophioglossum s.l.*, hypothetically arise two new lineages, an evolutionary line would be represented in *Ophioderma*, which acquired secondarily dorsiventral symmetry as a result of its adaptation to epiphytic habit. The other line of specialization would be present in *O. crotalophoroides s.l.*, these taxa preserve the radial symmetry, but taking on a spherical morphology with a central cavity. The acquisition of the spherical shape with a central cavity of the rhizome, with the meristem located inside, it probably would be a strategy to protect the meristem.

Ophioglossaceae has been described with not circinate vernation, however in greenhouse-grown specimens of *Sceptridium schaffneri* cultivated by the first author was observed that the sporophores present a curvature toward the adaxial side in developing fronds. Although is not clearly a circinate vernation, as in other ferns, one might infer that development of frond of *Botrychium s.l.* species are rudimentary circinate.

The presence of leaf sheaths in Ophioglossaceae is more conspicuous in genera considered primitive as *Botrychium*, *Botrypus*, and *Sceptridium* (Imaichi 1989). In living specimens was observed that the sheaths of *Ophioglossum* (e.g. *O. nudicaule* L. f.) are membranous and are surrounding the apical bud. During the development of the primordium, the sheath will be broken by the developing blade. In the genus *Ophioglossum* the petioles and sheaths are marcescent, this is notorious in species like *O. nudicaule* and *O. melipillense* J. Remy. No data is available about the sheath in *Ophioderma*. Based on observations in *Ophioderma palmata*, we can infer that probably the sheaths are early caducous or absent. In *O. crotalophoroides* the sheaths also are absent, although in longitudinal section of the rhizome, into the central cavity there are remnants of petioles, these are not enlarged like sheaths. Therefore, the sheaths reduction or loss in these species appears to be a derived character.

For the portion of the frond that was called “common stalk” (Bower 1926, Clausen 1938), or “phyllomophore” (Nozu 1950), in this treatment will be adopted the expression petiole, consistent with the criterion of Ogura (1972) (Figs. 1, 2). The petiole is delimited for its insertion into the rhizome and the insertion of sporophore in the distal portion. The petioles are described as terete (Ogura 1972), but based on FAA preserved specimens, was noted that in the genus *Ophioglossum* petioles of fronds without sporophores are adaxially furrowed or in a “U” expanded. The subsequent frond develops a fertile portion, and the petiole in fertile frond turns terete and marginate (Fig. 3A, B).

The leaves in southern South America species are simply pinnate to 4 pinnate in

Botrychium s.l. (Fig. 1). In the genus *Ophioglossum* the contour of leaf is ovate-lanceolate to chordate. The genus *Ophioderma* presents pendulous fronds, which are narrow-lanceolate in juvenile fronds to palmatisect in adult fronds. The base of the blade in species of *Ophioglossum* and *Ophioderma* are usually connected to the insertion of sporophore by an appendicular portion, called by Bower (1926) and Clausen (1938) as “trophophore stalk”, but here is called pedicle (Figs. 1, 2). In species as *Ophioglossum reticulatum* L. and *Ophioderma palmata* can be cuneiform. In other species as *O. nudicaule* and *O. melipillense* the pedicle may be absent.

In the species of *Sceptridium* and *Botrypus*, the venation patterns are open and furcate without anastomoses. In *Botrychium s.s.* (e.g. *B. dusenii*), the venation presents a degree of anastomosis in the veins near the rachis. Furthermore, all species of *Ophioglossum* have anastomose-reticulated venation, also exist species with veinlets foundling, such as in *Ophioderma palmata*. According with Kato (1987), the reticulated pattern is undoubtedly the most specialized state of this character. However, in *Botrychium s.l.* and *Helminthostachys* species, there are two evolutionary lines, the most primitive venation pattern is present in *Helminthostachys* and *Mankyua*, with a pinnate pattern, forked, with parallel very close veins. From this pattern derived two evolutionary lines of forked and free venation, but with a looser venation. One of these trends was observed in *Botrychium dusenii*, with anastomoses of the central veins, near to the rachis forming elongated areoles. The other trend was found in *Sceptridium* and *Botrypus*, both genera present a forked venation, without apparent anastomoses (Fig. 4).

The appendix sterile portion that connects the sporophore to the petiole is called peduncle (Figs. 1, 2), usually this is cylindrical. Its length may be short as in *Ophioderma* or can exceed the length of trophophore as in *Sceptridium*. In the genera *Ophioglossum s.s.* and *Ophioderma*, the sporangia are arranged in a simple structure and embedded in a connective tissue of the sporangiophore (Fig. 5 C, E). This structure has been called “spike”. Here we propose the term “angiostroma” (gr. $\kappa\upsilon\beta\omicron\nu$, beaker + $\sigma\tau\epsilon\rho\beta\epsilon\delta\omicron\nu$, bed) (Fig. 1) to denominate the fertile region where are inserted the sporangia in the genera *Ophioglossum s.s.* and *Ophioderma*, but, by extension the term could also apply to the genera *Helminthostachys* and *Mankyua*. The angiostroma is also an appendicular structure, consisting of two rows of opposite or subopposite, sessile sporangia, embedded in a connective portion. The terminal portion of sporophore has a sterile and deltoid appendage, the apicule (Fig. 2). The species of *Botrychium s.l.* shows spherical sporangia, arranged pinnately on the sporophore axis, with a degree of division similar to the sterile blade (Fig. 5A, B, D).

Regarding to an organographic standpoint, the nature of the sporophore seems to originate from a basal pair of pinnae that would modify to form these axes. This opinion was given by Bower (1926) and Clausen (1938) and is supported by the example of Kato (1987). In *Botrychium paradoxum* W. H. Wagner (Fig. 3.D) the two axes are each modified

into a sporophore, whereas the blades are reduced. Thus, the Ophioglossaceae would present a homology with the genus *Anemia*.

In petioles in *Ophioglossum* species, sterile fronds are surcate, and the fertile fronds are (sub) terete and marginate. These disparities between petioles carrier sporophores and petioles sterile, gives the possibility of thinking that the origin of the fertile axes in *Ophioglossum* would correspond to a recaulescence case. This would mean that the sporophores could be a frond entirely different to the trophophore, and the fertile axis intimately concrescent with the sterile frond was to be dragged on the petiole for to be developed on its adaxial side. This interpretation would be one of the classical postures (de la Sota 1977).

The rhizomatic indumentum of *Ophioderma* consists in articulate, branched, and brown hairs (Fig. 6.C). This indumentum is present in *Ophioderma palmata* (L.) Nakai and *O. pendulum* (L.) C. Presl, and this character can be used for defining this genus. *Ophioglossum* s.s. has no indumentum on the surface of its organs, but *O. crotalophoroides* shows filiform hairs inside the rhizome, apparently coated the leaf primordia (Fig. 6.D).

Another case of trichomes presence is observed in *Botrypus virginianus*, where they are abundant in leaf primordia (Fig. 6. A, B), but is caducous since the density of indumentum in adult frond is reduced, and *Sceptridium* species (Fig. 6.E) also show a similar indumentum, since both genera have hyaline to brown hairs. The similarities of these two genera in the indument, radical branching pattern, degree of division of the blade and venation pattern could be interpreted as two closely allied genera or could constitute a single genus, near *Botrychium* s.s. although with more primitive characteristics.

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REFERENCES

- BATEMAN R, CRANE P R, DIMICHELE W A, KENRICK P R, ROWE N P, SPECK T, STEIN W E 1998 Early Evolution of Land Plants: Phylogeny, Physiology, and Ecology of the Primary Terrestrial Radiation *Annu Rev Ecol Evol Syst* **29** : 263-292
- BOWER F O 1923 *The Ferns* (Filicales) Vol I, Cambridge University Press Cambridge
- BOWER F O 1926 *The ferns* (Filicales) Vol II, Cambridge University Press Cambridge
- BOZUKOV V, TSENOV B, VATSEV M 2010 A first find of *Botrychium* (Ophioglossaceae) in Bulgarian Palaeomacrolflora *C R Acad Bulg Sci* **63(6)** : 889-892
- CAMPBELL D H 1905 *The Structure and Development of Mosses and Ferns* (Archegoniatae) The MacMillan Company, New York
- CLAUSEN R T 1938 A monograph of the *Ophioglossaceae* *Mem Torrey Bot Club* **19(2)** : 1-177

- CLAUSEN R T 1948 The *Ophioglossum* of the Falkland Islands and relationships and distribution of *Ophioglossum crotalophoroides* *Amer Fern J* **38** : 176-186
- DE LA SOTA ER 1977 Pteridophyta In : “*Flora de Jujuy*”, Ed A Cabrera *Colecc Ci Inst Nac Tecnol Agropecu* **13** : 1-275
- EAMES A J 1936 *Morphology of Vascular Plants* McGraw-Hill, New York and London
- FARMER J B & FREEMAN W G 1899 On the structure and affinities of *Helminthostachys zeylanica* *An Bot* **13** : 422-445
- FARRAR D R 2006 Systematics of Moonworts *Botrychium* Subgenus *Botrychium* www.public.iastate.edu/~herbarium/botrychium/Moonwort-Systematics-June-06.pdf Iowa State University
- GIFFORD E M & FOSTER A S 1989 *Morphology and Evolution of Vascular Plants* W H Freeman, New York
- HAUK W D, PARKS C R & CHASE M W 2003 Phylogenetic studies of Ophioglossaceae : evidence from *rbcL* and *trnL-F* plastid DNA sequences and morphology *Mol Phylogenet Evol* **28** : 131-151
- IMAICHI R 1989 Early Leaf Development and Leaf Sheath Formation of *Botrychium strictum* and *B virginianum* (Ophioglossaceae) *Ann Bot* **63**(2) : 249-256
- KATO M 1987 A phylogenetic classification of Ophioglossaceae *Gard Bull* (Singapore) **40** : 1-14.
- LELLINGER D B 2002 A Modern Multilingual Glossary for Taxonomic Pteridology *Pteridologia* **3** : 263 pp
- McALPIN BW 1971 *Ophioglossum* leaf sheaths : development and morphological nature *Bull Torrey Bot Club* **98** : 194-199.
- MICKEL J T & SMITH A R 2004 The Pteridophytes of Mexico *Mem N Y Bot Gard* **88** : 1-1055
- NOZU I 1950 On the so-called petiole of *Botrychium* *Bot Mag Tokyo* **63** : 4-11
- OGURA Y 1972 *Comparative anatomy of vegetative organs of the pteridophytes* Gebruder Borntraeger, Berlin
- PETRY L C 1915 Branching in the Ophioglossaceae *Bot Gaz* **59**(5) : 345-365
- PICHI SERMOLLI REG 1977 *Tentamen Pteridophytarum genera. Webbia* **31**(2) : 313-512
- PRANTL K 1884 Beiträge zur Systematik der Ophioglosseen *Jb Bot Gart Berlin* **3** : 297-350
- PRESL K B 1845 Ophioglossaceae In : *Supplementum Tentaminis Pteridographiae Abh Böhm Ges Wiss* **4** : 301-320
- ROTHWELL G W, STOCKEY R A 1989 Fossil Ophioglossales in the Paleocene of western North America *Am J Bot* **76** : 637-644
- SMITH A R, PRYER K M, SCHUETTPELZ E, KORALL P, SCHNEIDER H & WOLF P G 2008 Fern classification pp 417-467 In “*Biology and Evolution of Ferns and Lycophytes*” Eds T Ranker & C H Haufler, Cambridge University Press
- SMITH G M 1955 *Cryptogamic Botany II, Bryophytes and Pteridophytes*. McGraw-Hill New York VIII + 399 pp
- SUN B Y, KIM M H, KIM C H & PARK C -W 2001 *Mankyua* (Ophioglossaceae): a new fern Genus from Cheju Island, Korea *Taxon* **50**(4) : 1019-1024
- TRYON R M & TRYON A F 1982 *Ferns and Allied Plants; With Special Reference to Tropical America* Springer-Verlag, New York
- WAGNER W H 1990 Ophioglossaceae In *The Families and Genera of Vascular Plants Vol I : Pteridophytes and Gymnosperms* Eds. K U Kramer & P S Green, Springer-Verlag, New York pp 193-197