Epiphytic and Lithophytic Fern and Lycophyte Genera of BELIZE

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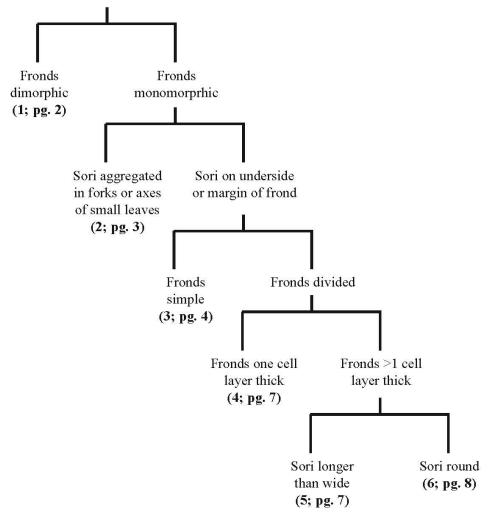
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Of the 79 fern and lycophyte genera known from Belize, 34 grow exclusively, or in part as *epiphytes* on trees and shrubs, as *lithophytes* on rocks, or as *hemiepiphytes* living in the canopy but maintain connection to the forest floor. These genera are distinguished based on **frond shape, sori, growth habit,** and **rhizome** characteristics. Definitions of these features, and the different characteristics they exhibit may be found at the end of this guide. Ferns and lycophytes (*Phlegmariurus* is the only known epiphytic lycophyte genus in Belize) can be distinguished by the presence of small leaves (microphylls) in lycophytes, the location in which the sori are produced (between stem and microphyll axes in lycophytes, on the underside, forks, or tips of fronds and microphylls in ferns) and differences in anatomical development.

This guide provides brief descriptions for each genus, along with photographs displaying key characters for identification. The number of species for each genus found within Belize is provided in parentheses following the genus name. Species names are denoted in each figure caption by the first letter of the focal genus and the specific epithet.



To the left is a small key to the morphological groups recognized in this guide. Numbers in parentheses indicate the group number based on morphology, followed by the page on which genera with those characteristics can be found.

District Abbreviations: Belize (B), Cayo (Ca), Corozal (Co), Orange Walk (OW), Stann Creek (SC), Toledo (T). Elevations are for Belize only.

Photos by RM and MS are not from Belize. Other photos not taken of Belize plants are identified in the text.

Identification Guide to the Epiphytic and Lithophytic Fern Genera of Belize

Anemia (1 sp.)

- Found in Ca, SC, T; 210-720 m elev.
- Terrestrial; rhizomes short, creeping and hairy; hemidimorphic, with lower pinnae fertile.
- Not likely to be confused with other taxa in Belize.



Hemidimorphic frond, fertile pinnae at base (all A. speciosa; E,



Sori on fertile frond, lacking indusia (EB)



Compact growth habit; note the Compact rhizome with reddish, slightly iridescent frond (EB)



brown hairs (EB)

Blechnum (2 spp.)

- Found in Ca, SC, T; 900-1130 m elev.
- Terrestrial to hemiepiphytic; rhizomes creeping and scaly, may be arborescent; fronds reddish when young, dimorphic in some species; sori paired, linear, straddling the costae.
- Resembles Polypodium, but has linear sori with indusia.



rarely simple (B. sp.; EB)



Fronds pinnatisect to 1-pinnate, Sori paired, linear, with indusium Terrestrial, rarely hemiepiphytic (B. ensiforme; BH) open toward costae (B. sp.; EB)





Rhizomes scaly, creeping or erect (B. sp.; EB)

Bolbitis (2 spp.)

- Found in Ca, SC, T; 60-580 m elev.
- Terrestrial, lithophytic or hemiepiphytic; rhizomes creeping; fronds dimorphic; buds may be produced at tips of sterile fronds.
- The buds, anastomosing veins, and acrostichoid sori distinguish Bolbitis from other fern genera in Belize.



natifid (all B. portoricensis; BH)



Fronds simple to 1-pinnate-pin- Acrostichoid sori on fertile frond Example of terrestrial habit (BH) Rhizomes scaly creeping (MS) (EB)



Elaphoglossum

(13 spp.)

- Found in Ca, OW, T; 185-1100 m elev.
- Epiphytic; fronds simple or pinnatifid; rhizome long creeping, may have phyllopodia, scales, or hairs.
- Free veins and acrostichoid sori separate Elaphoglossum from other genera in Belize.



Pinnatifid frond with free veins Acrostichoid sori covering entire (all E. peltatum; DA)



underside of fertile frond (WC)



Epiphytic growth habit (DA)



Long creeping rhizome with light brown scales (RM)

Lomariopsis (3 spp.)

- Found in Ca, SC, T; 60-1000 m. elev.
- Hemiepiphytic; rhizome long creeping; fronds dimorphic and 1-pinnate.
- Apical pinnae are similar to adjacent pinnae, which distinguishes the genus from Polybotrya.



costae (L. vestita; RM)



on fertile frond (L. vestita; RM) fronds extended (L. vestita; RM)



Free veins, which may fork near Acrostichoid sori, green spores Hemiepiphytic habit, with fertile Apex of long creeping rhizome



(L. recurvata; MS)

Olfersia (1 sp.)

- Found in Ca, SC, T; 80-920 m elev.
- Terrestrial to low climbing; rhizome compact; fronds dimorphic; sterile pinnae are 1-pinnate, and have a submarginal collecting vein.
- May be confused with Polybotrya, but venation differs in these genera.



1-pinnate sterile frond (all O. cervina; PN)



Fertile fronds are taller than sterile fronds and 2-pinnate (PN)



Predominantly terrestrial (MS) Rhizome compact with clathrate



scales (MS)

Ophioglossum (1 sp.)

- Found in **Ca. T:** 700– 1100 m elev.
- Terrestrial, sometimes epiphytic; roots creeping; sori borne on spike-like structure near base of fronds.
- Not likely to be confused with other genera in Belize.



Fronds are fleshy and lack a costa (all O. palmatum; RM)



Spike-like sori growing off the leaves (RM)



Epiphytic habit (RM)



Creeping roots lacking hairs (MS)

Polybotrya (3 spp.)

- Found in Ca, SC, T; 60-1000 m elev.
- · Hemiepiphytic; rhizome creeping; fronds dimorphic. Morphologically, fertile fronds are reduced versions of sterile fronds.
- Differs from *Lomariop*sis by the pinnatifid frond apex, and from Olfersia by the lack a collecting marginal leaf pinnatifid apex (all P. caudata; vein.



Fronds 1 to 4-pinnate; note the



Fertile fronds lacking indusia (RM)



Hemiepiphytic climbing habit (RM)



Creeping rhizome with scales (RM)

Group 2. Sori aggregated in axils or forks of small leaves

Groups 3–6. Sori located on underside or margins of frond (page 4)

Phlegmariurus (5 spp.)

- Found in **Ca**, **SC**, **T**; 10–1140 m elev.
- Epiphytic; rhizomes short creeping; sori along the main branches in leaf axes.
- Not likely to be confused with other genera in Belize.



Elongated stems with scale-like leaves (*P. linifolius*; EB)



Sori borne is leaf axes next to stem (*P. linifolius*; EB)



Pendent epiphytic habit (*P. di-chotomus*; EB)



Example of short, creeping rhizome (*P. linifolius*; EB)

Psilotum (1 sp.)

- Found in **B**, **Ca**, **Co**, **SC**, **T**: 250–400 m elev.
- Epiphytic or terrestrial; true roots absent; stems photosynthetic, pinnae highly reduced, forked; sori found in the forks of reduced pinnae.
- Not likely to be confused with other genera in Belize.



Photosynthetic stems with reduced pinnae (all *P. nudum*; WC)

Fronds simple, with striking

venation (C. sp.; BH)



Fused sori resembling three spheres (DA)



Pendent, epiphytic habit (BH; photo taken in FL)



Rhizome with rhizoid-like projections present (DA)

Group 3. Fronds simple (see also *Hymenophyllum* in Group 4, *Asplenium* in Group 5, and *Pleopeltis* in Group 6). Groups 4–6. Fronds divided to or near the rachis (page 6)

Ananthacorus (1 spp.)

- Found in Ca, SC, T; 10–600 m elev.
- Monotypic genus; epiphytic; rhizomes compact; veins anastomosing; sori just inside the margin of the frond; paraphyses abundant.
- Resembles *Radiovit-taria* and *Vittaria*, but has more than one row of areoles between costa and margin.

Campyloneurum (8 spp.)

- Found in **B**, **Ca**, **OW**, **SC**, **T**; 5–750 m elev.
- Epiphytic, rarely terrestrial; rhizomes compact; fronds simple; sori round in 1–4 rows between veins and located at the tip of small veins.
- May be confused with *Niphidium*, but differs based on soral arrangement.



Fronds simple, entire; Sori just inside leaf margin (all *A. angustifolius*; DA)



Sori at tips of small veins (*C. re-pens*; EB)



Clumped, epiphytic habit (DA)



Rhizomes short creeping, with clathrate scales (DA)



Epiphytic habit(C. sp.; BH)



Rhizomes scaly, short to long creeping, may have phyllopodia (*C. costatum*; EB)

Cochlidium (2 spp.)

- Found in B, Ca, SC, T; 30-1140 m elev.
- Epiphytic or terrestrial: rhizome compact; fronds small and simple: sori located at the tip of the frond.
- May be confused with *Lellingeria*, but lacks clathrate rhizome scales.



(C. serrulatum; EB)



Simple fronds, entire or serrate Sori may be linear, shown here, or round (C. linearifolium; MS)



Example of epiphytic habit (C. serrulatum; EK)



Compact rhizome with brown scales (C. serrulatum; BH)

Elaphoglossum

(13 spp.)

- Found in Ca, OW, T; 185-1100 m elev.
- Epiphytic; rhizome long creeping with scales or hairs; fronds simple or pinnatifid, may have phyllopodia.
- Free veins and acrostichoid sori separate *Elaphoglossum* from other genera in Belize.



Simple fronds with free veins (E. sp.; EB)



Acrostichoid sori covering underside of frond (E. rigidum; EB)



Epiphytic habit (E. latum; EK)



Phyllopodia, darkened portion of leaf base remaining after leaf fall (E. sp.; MP)

Enterosora (1 sp.)

- Found in T; 820 m elev.
- Epiphytic, rarely lithophytic; rhizome compact; fronds simple to pinnatifid, thick and fleshy; sori slightly sunken in to frond tissue.
- Not likely to be conconfused with other genera in Belize.



Small ferns with fleshy frond tissue (E. ecostata; RM)



Round to elongate sori slightly sunken in to tissue (E. ecostata; RM)



Epiphytic habit (E. ecostata; RM)



Golden brown rhizome scales (E. trifurcata, species not in Belize, MS)

Microgramma (4 spp.)

- Found in B, Ca, OW, SC, T; 0-1050 m elev.
- Epiphytic, occasionally lithophytic; rhizomes elongate; fronds simple and small; veins anastomosing with areoles. Dimorphic fronds are common.
- May resemble Pleopeltis, but Microgramma lacks clathrate scales.



Small, simple fronds (M. sp.;



Sori round, in a single row (M. reptans; EB)



Epiphytic habit (M. sp.; BH)

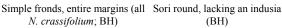


Long creeping rhizome with peltate scales (M. sp.; EB)

Niphidium (1 sp.)

- Found in Ca, SC, T; 0-1000 m elev.
- Terrestrial or epiphytic; rhizome compact; fronds simple with rigid texture, sori arranged in a single row between veins.
- May be confused with Campyloneurum but differs by the number of sori between the veins.







(BH)



Epiphytic growth habit (BH)



Roots pubescent, rhizomes scaly

Oleandra (1 sp.)

- Found in **T**; 760–1050 m elev.
- Epiphytic or terrestrial; rhizomes long creeping, scaly; fronds simple, veins free.
- May be confused with Elaphoglossum or simple Polypodiaceae ferns, but has round sori and free veins.



Simple, entire frond (all O. artic- Randomly scattered round sori ulata; EK)



(EK)



Epiphytic growth habit (EK)



Rhizomes long, covered in dense scales (EK)

Polytaenium (3 spp.)

- Found in Ca, SC, T; 10-750 m elev.
- Epiphytic; rhizome, may be long creeping, scales clathrate; fronds simple, veins anastomosing, sori following these veins or scattered.
- May be confused with Scoliosorus, but sori lack paraphyses or *Elaphoglossum* but has clathrate scales.



Simple fronds with obvious venation on underside of frond (P. citrifolium; EB)



nation (P. feei; RM)



Sori arrangement following ve- Epiphytic growth habit (P. feei;



Rhizome covered in clathrate scales (P. feei; BH)

Radiovittaria (1 spp.)

- Found in Ca, SC, T; 250-750 m elev.
- Epiphytic; rhizomes compact, scales clathrate; fronds simple, entire, arranged in a row petioles dark. Paraphyses abundant with funnel shaped apical cell.
- Differs from Vittaria, by frond arrangement, petiole color, and pical cell on paraphyses.



Fronds simple, entire; young fronds redish (all R. stipitata; MS)



Sori linear, just inside frond margin (RM)



Pendent, epiphytic habit (RM)

Scoliosorus (1 sp.)

- Found in **T**; 700–750 m elev.
- Epiphytic; rhizome scales clathrate; fronds simple, with anastomosing veins, sori following these veins.
- May be confused with Polytaenium, but paraphyses with a spherical apical cell are present among sporangia.



Simple, fleshy fronds (all S. ensi-formis; MS)



Sori at angle to costae, following veins (MS)



Clumped, epiphytic growth habit. Rhizomes covered in clathrate scales, not shown here. (RM).

Vittaria (2 spp.)

- Found in Ca, SC, T; 0-1100 m elev.
- Epiphytic; rhizomes compact with clathrate scales; fronds thin, long; sori sunken in grooves just inside the margin of the frond.
- Vittaria distinguished from Radiovittaria or Ananthacorus by thin fronds and paraphyses



Thin long fronds that resemble a grass (V. sp.; BH)



Sori arranged in sunken linear grooves (V. sp.; EB)



Pendent, epiphytic habit (V. sp.; BH)



Rhizomes compact, with clathrate scales (V. lineata; EB)

Group 4. Frond tissue extremely thin and delicate, one cell layer thick Groups 5–6. Fronds multiple cell layers thick, as in most fern species (page 7)

Hymenophyllum (7 spp.)

- Found in Ca, T; 30– 1140 m elev.
- Epiphytic or lithophytic; rhizome long creeping; fronds thin and delicate, sori in clam-shaped indusium.
- May be confused with Trichomanes, but has a bivalve indusium housing the sori.





Sori inside a clamshell-shaped structure (EB)



Epiphytic habit (EB)



Rhizomes long creeping and pubescent (EB)

Trichomanes (20 spp.)

- Found in Ca, SC, T; 10-1140 m elev.
- Epiphytic or terrestrial; rhizome long creeping; fronds highly variable, tissue thin, sori in tube shaped indusium; one species in Belize is dimorphic.
- May be confused with Hymenophyllum, but has a tubular indusium and a black receptacle.



Fronds 1 to 4-pinnate (all T. sp.; Sori located inside a tubular in-



dusium (EB)



Epiphytic habit (EB)



Rhizomes long creeping and pubescent (EB)

Group 5. Sori longer than wide (linear or oblong, to broadly elliptic; see also Pleopeltis in group 6) Group 6. Sori round (page 8)

Asplenium (17 spp.)

- Found in Ca, Ow, SC, T; 20–1100 m elev.
- Epiphytic or terrestrial; rhizome scales clathrate; frond variable, sori linear or elliptical with flap-like indusium.
- Look for clathrate rhizome scales, and linear sori, to distinguish this genus from others in Belize.

Hecistopteris (1 sp.)

- Found in SC; ca. 50 m
- Epiphytic or lithophytic; fronds 4 cm or smaller, lacking a petiole. Rhizome long creeping, capable of producing buds.
- Not likely to be confused with other genera in Belize.



Fronds range from simple to 3-pinnate (A. cristatum; EB)



Elongate sori, with flap-like indusium (A. serratum; EB)



Epiphytic habit, often clumped appearance (A. formosum; EB)



Rhizome with clathrate scales (A. formosum; DA)



Small divided, fronds lacking a petiole (all H. pumila; RM)



Sori linear, borne toward the leaf apex, lacking an indusium (RM)



Growth habit of this small, creeping fern (RM)

Group 6. Sori round (this is the largest group in terms of species numbers, with a great diversity of frond shape)

Alansmia (1 sp.)

- Found in **T**; 700–750 m
- Epiphytic genus that is pinnatiscect to 1-pinnate. Fronds, sori, and rhizomes covered in hair or hair-like scales.
- May be confused with Pecluma, but the fronds pinnae are more pubescent in Alansmia.



species not in Belize; MS)



Indeterminate growth leafs cro- Sori round, lacking an indusium, zier at frond tip (all A. sensilis, note the hair-like trichomes (MS)



Pendent epiphytic habit (MS)

Lellingeria (1 sp.)

- Found in **Ca**, **T**; 400– 880 m elev.
- Epiphyte or hemiepiphyte with clathrate scales on the rhizomes. Fronds are pinnatifid to 1-pinnate-pinnatifid.
- Small ferns that may be confused with Cochlidium, but Lellingeria has clathrate scales.



Fronds with forked, pale, trichomes (L. humilis, species not in Belize; MS)



Sori round to slightly elongate (L. suspensa, species not in Belize; RM)

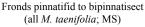


Epiphytic habit, may also be lithophytic (L. suspensa, species not in Belize; RM)

Moranopteris (1 sp.)

- Found in **Ca. T:** 920-1135 m elev.
- Epiphytic and small. Fronds nearly lacking a petiole, with 20-80 paired pinnae.
- Single sorus per pinna, reddish hair-like trichomes, and clathrate rhizome scales distinguish this genus from others in Belize.







(RM)



Fronds pinnatifid to bipinnatisect Sori one per lamina segment Compact epiphytic habit. Rhizomes with golden, orange, yellow or brownish scales, not shown here (RM)

Nephrolepis (7 spp.)

- Found in B. Ca. SC. T: 5-1050 m elev.
- Terrestrial or epiphytic; fronds 1-pinnate, apex indeterminate.
- May be confused with Pecluma and Polypodium, but sori have indusia.



minate apex (N. sp.; EB)



Frond 1-pinnate with an indeter- Sori round, covered by indusia (N. sp.; EB)



Rachis persistent after pinnae have fallen (N. sp.; BH)



Rhizomes compact, stolons present (N. brownii; RM)

Pecluma (6 spp.)

- Found in B, Ca, Co, **OW.** T: 10–1000 m elev.
- Epiphytic; rhizomes short creeping and scaly, phyllopodia present; fronds pinnatisect to pinnatifid with thirty or more pinnae, reducing in size at base of frond.
- The tops of the rachises
 Fronds resemble a hair comb (P. Sori round, exindusiate, with paare pubescent, distinguishing this genus from Polypodium.

Phlebodium (1 sp.)

- Found in Ca, Co; 5-610 m elev.
- Epiphytic or terrestrial genus with creeping rhizome. Rachis and costae lacking hair on upper surface.
- May be confused with Pecluma, Polypodium, Serpocaulon but has clathrate scales on the rhizome.



camptophyllaria, not found in Belize; RM)



raphyses (P. plumula; BH). Photo taken at Everglades National Park.



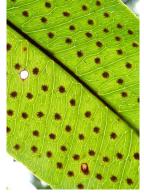
Epiphytic habit (P. plumula; BH). Photo taken at Everglades National Park.



Rhizome with prominent phyllopodia (P. divaricata; RM)



(all P. decumanum; EB)



Fronds pinnatisect or 1-pinnate Sori round, lacking indusia found in vein areoles (BH)



Epiphytic habit (BH)



Rhizome covered in copious orange scales (EB)

Pleopeltis (4 spp.)

- Found in Ca, SC, T: 20-1000 m elev.
- Epiphytic or lithophytic; fronds simple to 1-pin-nate, scaly, veins anastomosing.
- May be confused with members of the genus Polypodium, which lack prominent scales on the fronds.



- Found in Ca, Co, SC, T; 0-1010 m elev.
- Epiphytic, lithophytic, rarely terrestrial; rhizomes creeping; fronds pinnatisect, rarely 1pinnate, lacking hairs or scales, veins free.
- May be confused with Pecluma but has fewer pinnae, Serpocaulon but has free veins, or Pleopeltis, but lacks scales on fronds.

Serpocaulon (4 spp.)

- Found in Ca, SC, T: 80-1100 m elev.
- Epiphytic; rhizomes creeping, scales clathrate; fronds pinnatifid to pinnate, rarely simple, petioles grooved, phyllopodia present.
- May be confused with Polypodium, but has clathrate rhizome scales, or Pleopeltis, but lacks scales on fronds.

Terpsichore (3 spp.)

- Found in **T**; 580–1100 m elev.
- Epiphytic; rhizomes compact and scaly; fronds pinnatisect to 1pinnate covered in dense scales with long petioles, sori round.
- May be confused with Alansima, but has long petioles, or Pecluma, which lacks hair-like scales on the petioles and laminae.



Clathrate, circular scales on fronds (P. polypodioides; EB)



trolepis; EB)



oides; BH)



scales (P. astrolepis; MP)



Tops of petioles grooved (P. lindenianum; EB)



a single row between costa and margin. (P. plesiosorum; RM)



Sori round, exindusiate, forming Epiphytic habit (P. plesiosorum;



Rhizomes creeping, scales nonclathrate (P. plesiosorum; MS)



Pinnate frond (S. triseriale; RM)



Anastomosing veins with free veinlet, which is where sori develop (S. triseriale; EB)



Epiphytic habit with arching fronds. (S. dissimile; RM)



Peltate scales with clathrate center (S. triseriale; EB)



Petioles long, covered in hairlike scales (all T. asplenifolia; MS)



Round sori with hair-like scales (MS)

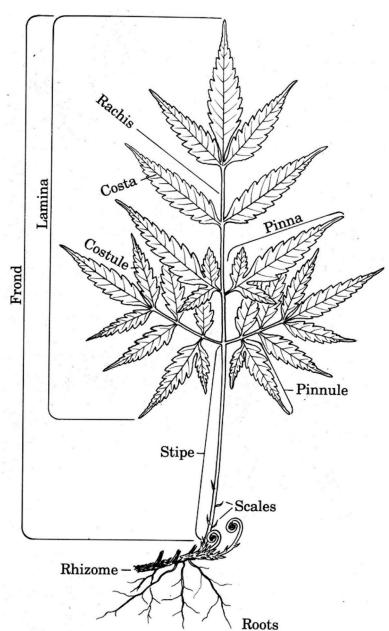


Pendent, epiphytic habit (JM)



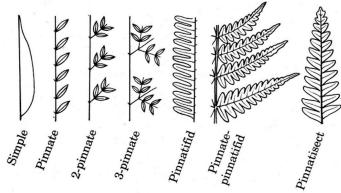
Orange to brown hair-like scales on rhizome (MS)

Morphological Trait Descriptions



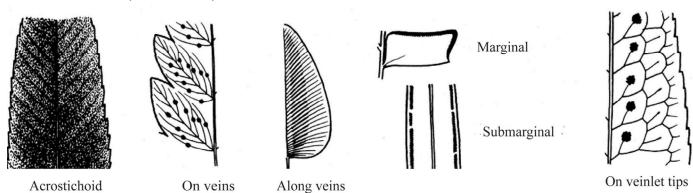
A fern **frond** consists of a stem (*stipe / rachis*) and photosynthetic tissue (*lamina*). Young fronds that are just unfurling have a circular shape at the tip, referred to as a *fiddlehead* or *crozier*. In some species the lamina tissue is divided in to *pinnae*, which are then subdived in to *pinnules* in some species. On pinnae, the central vein is referred to as the *costa*, while this central vein is called the *costule* on further divided pinnules.

Fern taxa are often described based on the number of times the lamina tissue is divided, and these divisions are further characterized by the depth, and number of times, in which the frond is divided. Complete divi-sion is referred to as *pinnate* and incomplete division is referred to as *pinnatifid or pinnatisect*. Fronds may also lack any division, and are thus referred to as *simple*. (e.g., *Elaphoglossum*, *Vittaria*).

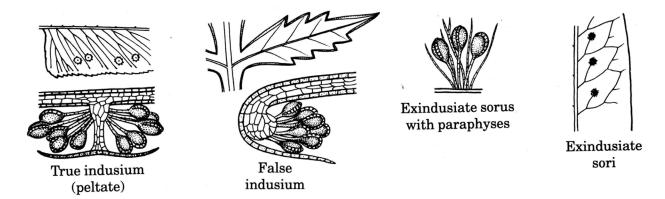


Venation throughout the frond is an additional char-acteristic for defining genera, with some taxa having parallel (free), dividing (forked or dichotomous), or netted (anastomosing) venation. Small veins may also be present (veinlets) in some taxa, and others may have a marginal

Sori are generally located on the underside of fern fronds, however some taxa have dimorphic fronds where sori are borne on differently-shaped, independent pinnae or separate fronds entirely. When sori are located on the underside of fronds, they can form arrangements that appear round, elongate, or cover the entire bottom surface of the frond (*acrostichoid*).



Additionally, sori may be protected by a thin piece of tissue known as an *indusium*. This indusium can appear as a round (*peltate*) or kidney-shaped (*reniform*) umbrella, a bivalve (e.g., *Hymenophyllum*), tube-shaped (e.g., *Trichomanes*), or elongated. Many taxa also have what is known as a *false indusium*, where the indusium is formed from folded leaf tissue along the margin of the frond. Finally, some sori lack an indusium (*exindusiate*) and may contain small hair-like structures (*paraphyses*) mixed in with the sporangia.



The **growth habit** of most fern genera described here are primarily *epiphytic*, however many taxa are also *lithophytic*, and thus may also be found growing on boulders and in crevices of rock outcroppings.

Rhizomes are often characterized by their growth habit (e.g., long creeping) and the presence, colors, and size of *scales* and *trichomes*. Scales that exhibit a mosaic of cells in a lattice-like arrangement, such as in a stained-glass window, are termed *clathrate*. Rhizomes may also have elevated projections, known as *phyllopodia*, which are prominent leaf scars that remain after the fronds have become detached (see *Elaphoglossum*). They may also be intermixed with modified stems that grow underground, termed *stolons* (see *Nephrolepis*). In other genera, rhizomes may converge and become elevated, resembling a small tree trunk, referred to as *arborescent* (see

Notes on nomenclature and hybridization

Some of the nomenclature used here may have changed based on recent efforts to understand fern relationships. The development of rapid and affordable genomic sequencing technology has resulted in the reclassification of genera and species previously based solely on morphological characteristics. For instance, *Polytaenium* and *Scoliosorus* were once lumped together under the genus *Antrophyum*, and the genus *Polytaenium* now includes the *genus Anetium*. Additionally, *Phlegmariurus* was once lumped under the genus *Huperzia*. While this change reflected in this guide, some other nomenclature edits such as these have not been reflected. Of particular note are the species in the Hymenophyllaceae, a family which contains a little less than 30 species in Belize. This family, represented in this guide by two genera (*Hymenophyllum* and *Trichomanes*) has been divided in to nine genera in recent treatments. Additionally, ferns are known to readily hybridize, resulting in intricate species complexes. New hybrids are frequently being discovered and species relationships are still being investigated, though relatively little is known about how ferns hybridize in Belize.

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