

Pecluma, a New Tropical American Fern Genus

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The species of *Pecluma* were submerged in *Polypodium* until modern taxonomists separated Grammitids from Polypods. Then, Copeland (1956) included some members of *Pecluma* in a generic treatment of the Grammitid *Ctenopteris*. That provided the impetus for three papers which supplied evidence that *Pecluma* species indeed belonged with *Polypodium* (Stokey, 1959; Wilson, 1959; Sota, 1963). A later revision of the individual species by Evans (1969) has facilitated a new examination of the relationships of the group, and I have come to the conclusion that those authors who reaffirmed an alliance with *Polypodium* are correct, but that Copeland's error may be partly excused on the grounds that *Pecluma* also has many features reflecting a shared ancestry with *Ctenopteris*, features that mark it as abundantly distinct from *Polypodium*. The most conspicuous of these differences from *Polypodium* are: rhizomes short and non-branching, paleae basally attached, axes terete, and fronds pectinate. From *Ctenopteris*, diagnostic differences are: spores neither trilete nor green, hairs never acicular from a broad base and not dark maroon, and stipes articulate. These and other characters are detailed below.

Pecluma Price, gen. nov.

Polypodium subg. *Pectinatum* Lellinger, Amer. Fern J. 71:93. 1981.

"*Polypodium pectinatum-plumula* complex" Evans, Ann. Missouri Bot. Gard. 55:193-293. 1969.

Rhizoma breve, non ramificans nec glaucescens, radices saepe prolificas procreans. Paleae basifixae, non clathratae, nec in lamina conspersae, cellulis ad margines non valde differentiatis. Stipites articulatae, rachidesque teretes, in vivis siccisve non sulcatae, atrantes. Segmenta laminae conferta, numerosa, longa angustaque, plerumque sursumdecurrentia, marginibus non cartilagineis pilis ascendentibus multiseptatis dispositis, infra pagina pilis multiseptatis glandulosis appressis praedita. Venae liberae vel fortuito anastomosantes. Stomata polocytica atque anomocytica vel copolocytica. Sori orbiculati paraphyses trichoideas continentes. Sporae monolaetae, non chlorophyllosae.

✓TYPE: *Polypodium pectinatum* L.

ETYMOLOGY: *Pecluma* is a compound of the epithets *pectinatum* and *plumula* which have been used to exemplify the group.

DISTRIBUTION: Tropics and subtropics of the New World, from Bermuda, Florida, and northern Mexico to southern Brazil and northern Argentina (Evans, 1969). Species about 28, generally epiphytic or epipetric.

The only previous author to accord formal taxonomic rank to *Pecluma* was Lellinger (1981), who noted that it was "sharply distinct" from the rest of *Polypodium*. As a genus, *Pecluma* is immediately recognizable and clearly defined and circumscribed. Separation from *Polypodium* (sensu stricto or lato) is important for the portrayal of the evolutionary lines involved, since *Pecluma* appears to have preserved characters that are possibly primitively simple among Polypods. Some of these character elements, especially of rhizomes, paleae, and axes, are fundamentally different from the usual condition in not only the genus *Polypodium* but also

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the entire subfamily Polypodioideae (the Polypods). The removal of *Pecluma* thus leaves *Polypodium* far more uniform, definable, recognizable, and phylogenetically meaningful. However, *Pecluma* does agree with *Polypodium* in a number of crucial features that require microscopy for detection (characters of the spores, sporangial stalks, and gametophytes), as well as the articulate stipes, which taken together are my basis for maintaining it in the Polypodioideae. In the other direction, *Pecluma* agrees with many members of subfamily Grammitidoideae in various characters by which it differs from the other genera of subfamily Polypodioideae, again characters of rhizomes, paleae, and axes, and also of frond-form and venation.

Loxogramme exhibits a mosaic of characters otherwise associated with either the Polypodioideae or the Grammitidoideae, and therefore is living evidence that those two are linked evolutionarily. A subfamily Loxogrammoideae may therefore be appropriate. I believe that *Pecluma* must be retained in subfamily Polypodioideae, rather than be placed in a subfamily of its own, but I am convinced that its numerous character states so similar to those widespread in the Grammitidoideae cannot be attributed to evolutionary convergence or reversal, but rather indicate shared ancestry. *Pecluma*, then, provides further evidence of the affinity between the Polypod and the Grammitid ferns and strengthens the case for ranking them as subfamilies of a greater Polypodiaceae, as apparently first done by Wagner (1961).

In the following discussion of the characteristics of *Pecluma*, I will not attempt to repeat the morphological observations made in the excellent paper of Evans (1969), except to place emphasis on certain character states. A summary of major characters compared with *Polypodium* and *Ctenopteris*,¹ both confused with *Pecluma* in the past, is presented in Table 1.

In *Polypodium*, the rhizome is wide-creeping, even rampant, regularly branching or producing short, dormant side branches, and is often glaucous beneath the paleae. *Pecluma* differs strongly in all these features, with the rhizome invariably short, whether ascending or creeping, and even when creeping having phyllopodia close together (exceptionally to 1 cm apart), and never regularly branching. The absence of rhizome branches is sometimes compensated for by the production of proliferations from the roots, already confirmed for seven species by Evans (1969, pp. 195, 196, and 203), and one more first noted here, *P. funicula*. The rhizome surface is never glaucous. All these rhizome characters, as they contrast with *Polypodium*, are the general condition of Grammitid ferns, which usually have short, non-branching, non-glaucous rhizomes, although the Malesian *Ctenopteris taxodioides* and the American *C. moniliformis*, for example, have slender, long-creeping rhizomes. Root proliferations are known among Polypods only in the highly-specialized *Platyserium*, where they should not be construed as evidence of affinity to *Pecluma*. Among Grammitids, root prolifery has only been confirmed for *Adenophorus* subg. *Oligadenus* (Bishop, 1974), perhaps first shown in the careful illustration of *A. pinnatifidus* Gaud. by Brackenridge (1855, pl. 2, fig. 3.). In the Poly-

¹The name *Ctenopteris* is used here for expedience to refer to miscellaneous pinnate or subpinnate species of Grammitids, although its Malesian type is very closely related to the type of the earlier described genus *Prosaptia*.

TABLE 1. COMPARISON OF MAJOR CHARACTERS OF *Pecluma* WITH *Polypodium* SENSU STRICTO AND THE PINNATE OR SUBPINNATE GRAMMITIDS ("Ctenopteris").

Structure	<i>Polypodium</i>	<i>Pecluma</i>	<i>Ctenopteris</i>
Rhizome	long-creeping freely branching often glaucescent	short unbranched not glaucous	usually short unbranched not glaucous
Roots	not proliferous	often proliferous	sometimes proliferous
Paleae	peltately attached often clathrate sometimes with rhizoids often marginate	basally attached not clathrate sometimes with rhizoids margin not differentiated	basally attached usually not clathrate sometimes with rhizoids margin usually not differentiated
	often scattered on lamina	only along axes or absent from lamina	not on lamina
Stipes	articulate	articulate	usually not articulate
Axes	variously channeled usually not dark	perfectly terete dark	usually terete often dark
Lamina segments	usually relatively few often lanceolate occasionally sursumcurrent	numerous linear usually sursumcurrent	usually numerous usually linear occasionally sursumcurrent
Hairs	various or glabrescent	multiseptate, dense on rachis above, appressed on lamina below and glandular	various, often acicular, broad-based, dark maroon
Venation	free to regularly anastomosing	free or casually anastomosing	free or casually anastomosing
Stomates	usually polocytic + copolocytic and/or anomocytic	polocytic + anomocytic or copolocytic	usually polocytic + anomocytic
Paraphyses	scales, hairs, or apparently none	hair-like	hair-like or apparently none
Sporangial stalks	2 or 3 cells thick throughout	2 or 3 cells thick throughout	uniseriate at base
Spores	monolete not green	monolete not green	trilete chlorophyllose
Chromosome numbers	$x = 37$	$x = 37$	$x = 37$

podaceae as here circumscribed, root prolifery is also exhibited by *Anarthropteris*, a close ally of *Loxogramme*.

Basally attached paleae characterize the Grammitids. In *Polypodium*, the ubiquitous condition is peltate attachment; even among the entire Polypodioideae, basally attached paleae occur only in a few highly specialized cases unrelated to *Pecluma*, i.e., *Platyserium*, a few large *Pyrrosia* species, and some drynarioid ferns. *Pecluma* has paleae basally attached both on the rhizomes and the fronds, and if borne on the frond they are situated only along axes, never scattered on the laminar surface, not clathrate in whole or in part, and not strongly differentiated at the margins. Some species of *Pecluma* as well as *Polypodium* and *Ctenopteris* have rhizoids on the surfaces of the rhizome scales which appear to be homologous with root hairs, and so presumably function for absorption. Marginal hairs on the paleae, when they occur in any of these three, are morphologically quite different. Surficial hairs on

the paleae are also found in *Tricholepidium* (Ching, 1978) of Pleopeltid affinity, where they resemble the slender, maroon setae of the Grammitids, in *Leucostegia* of the Davalliaceae, in *Pleurosoriopsis*, where they seem to be rhizoidal, and in the Thelypteridaceae (Holttum, 1971), where they are related to the hairs on the fronds.

Pecluma agrees with the Polypodioideae rather than the Grammitidoideae in the important character of stipes articulate to the phyllopodia, but this is not an exclusive feature, as *Ctenopteris celebica*, for example, has articulate stipes. The stipe and rachis of *Pecluma* are dark and virtually perfectly terete; they do not shrink during drying to become grooved, channeled, or differentially dimensional. No *Polypodium* has this character, although it is widespread in the Grammitidoideae, and occurs in some species of *Pleopeltis* of the Polypodioideae. In checking for this character, one must be wary of several deceptive conditions. If immature, still-developing fronds are dried before the deposition and hardening of the sclerenchymatous sheath responsible for the character, the axes will shrink along certain lines and appear to be channeled, or if unusually heavy or unequal mechanical pressure is used in drying, portions of the axes may appear slightly compressed. Laminar tissue is long-decurrent down the stipe, forming a very narrow strip on each side, but the actual shaft of the stipe is invariably terete.

Laminar segments (pinnae) are very numerous (over 40) and long and narrow, the ratio of length to breadth ranging from 6:1 to 14:1, giving the fronds a marked pectinate appearance, and although nearly the same character state occurs in a few species of *Polypodium*, the situation is far more frequent in *Ctenopteris*. In most species, some or all of the segments are sursumcurrent, the bases extending upwards along the rachis more markedly than downwards. This character is more common in *Polypodium* than in *Ctenopteris*, but occurs in both. The margins are never cartilaginously reinforced as in many Polypods.

Fronds are always hairy with multiseptate hairs, copious on the rachis adaxially, less so abaxially, and at intervals along the margins (except in *Pecluma curvans* and *P. pectinatiformis*); the lamina beneath almost always has appressed, pale, multiseptate hairs with glandular terminal cells (except *P. hygrometrica*, which has erect, non-glandular hairs). The morphology and distribution of these hairs are most similar to those of some species of *Polypodium*, and although a few *Ctenopteris* have hairs of similar appearance and distribution, the widespread condition in the Grammitidoideae of dark maroon, broad-based, slender, acicular hairs is never found in *Pecluma*.

The combinations of stomatal types are similar to those widespread among the Grammitids (van Cotthem, 1970) and Polypods (Sen & Hennipman, 1981). *Pecluma plumula* has a combination of polocytic and copolocytic stomates, whereas the other species I have examined (*P. pectinata*, *P. hygrometrica*, *P. ptilodon*, and *P. pectinatiformis*) combine polocytic with anomocytic stomates.

Sori are orbicular, never elongate as in some *Polypodium* and *Ctenopteris*, surficial (slightly impressed in *P. sursumcurrens*), and always contain hair-like paraphyses. Setose sporangia are common in *Pecluma* and *Ctenopteris*, but are rare in *Polypodium*. Wilson (1959) pointed out that although no fundamental differences exist between the sporangial capsules of Polypods and Grammitids, *P. pectinata* and

P. plumula both agree with the Polypodioideae in having two rows of cells at the base of the sporangial stalk (vs. a single row at the base in the Grammitidoideae). Spores are normally monolete and fabiform (globose in *P. dispersa*), finely tuberculate, and achlorophyllous. Spore characters are probably most consistently useful for distinguishing between subfamilies Polypodioideae and Grammitidoideae, as exceptions are very rare, and in only one case is a Grammitid known to have monolete spores (F. S. Wagner, in prep.).

Gametophyte characters agree best with *Polypodium* as to early appearance of the first rhizoid, short duration of the filamentous stage, form of the mature thallus, and distribution and types of hairs (Stokey, 1959), although gametophytes of the apogamous *Pecluma dispersa* agree with the Grammitidoideae in several characters (Evans 1969, p. 207).

Most similar to *Pecluma* is the group of species² around *Polypodium hartwegianum* Hook., as pointed out by Evans (1969, p. 217) and Smith (1981, p. 187), but all these species have the usual differences in rhizomes, paleae, and axes. The Old World *Thylacopteris*, a segregate of *Polypodium*, is similarly pectinate, but has a very slender, long-creeping, branched rhizome, peltate paleae, grooved axes, and glabrescent laminae.

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ENUMERATION OF SPECIES

***Pecluma absidata* (Evans) Price, comb. nov.**

Polypodium absidatum Evans, Ann. Missouri Bot. Gard. 55:238, f. 20. 1969.

***Pecluma alfredii* (Rosenst.) Price, comb. nov.**

Polypodium alfredii Rosenst. Fedde Repert. 22:15. 1925.

***Pecluma atra* (Evans) Price, comb. nov.**

Polypodium atrum Evans, Ann. Missouri Bot. Gard. 55:237, f. 18. 1969.

***Pecluma bermudiana* (Evans) Price, comb. nov.**

Polypodium bermudianum Evans, Ann. Missouri Bot. Gard. 55:228, f. 17. 1969.

***Pecluma boliviana* (Rosenst.) Price, comb. nov.**

Polypodium bolivianum Rosenst. Fedde Repert. 5:236. 1908.

***Pecluma camptophyllaria* (Fée) Price, comb. nov.**

Polypodium camptophyllum Fée, Huit. Mém. 86. 1857.

***Pecluma chiapensis* (Evans & Smith in Smith) Price, comb. nov.**

Polypodium chiapense Evans & Smith in Smith, Amer. Fern J. 70:23, f. 16–17. 1980.

***Pecluma choquetangensis* (Rosenst.) Price, comb. nov.**

Polypodium choquetangense Rosenst. Meded. Rijks Herb. 19:18. 1913.

***Pecluma consimilis* (Mett.) Price, comb. nov.**

Polypodium consimile Mett. Ann. Sci. Nat. (Paris) V, 2:253. 1864.

²These species have often been included in *Polypodium* subg. *Goniophlebium*, but the name *Goniophlebium* when used as a subdivision of *Polypodium* is typified by an Old World species whose relationship with American species remains to be clarified.

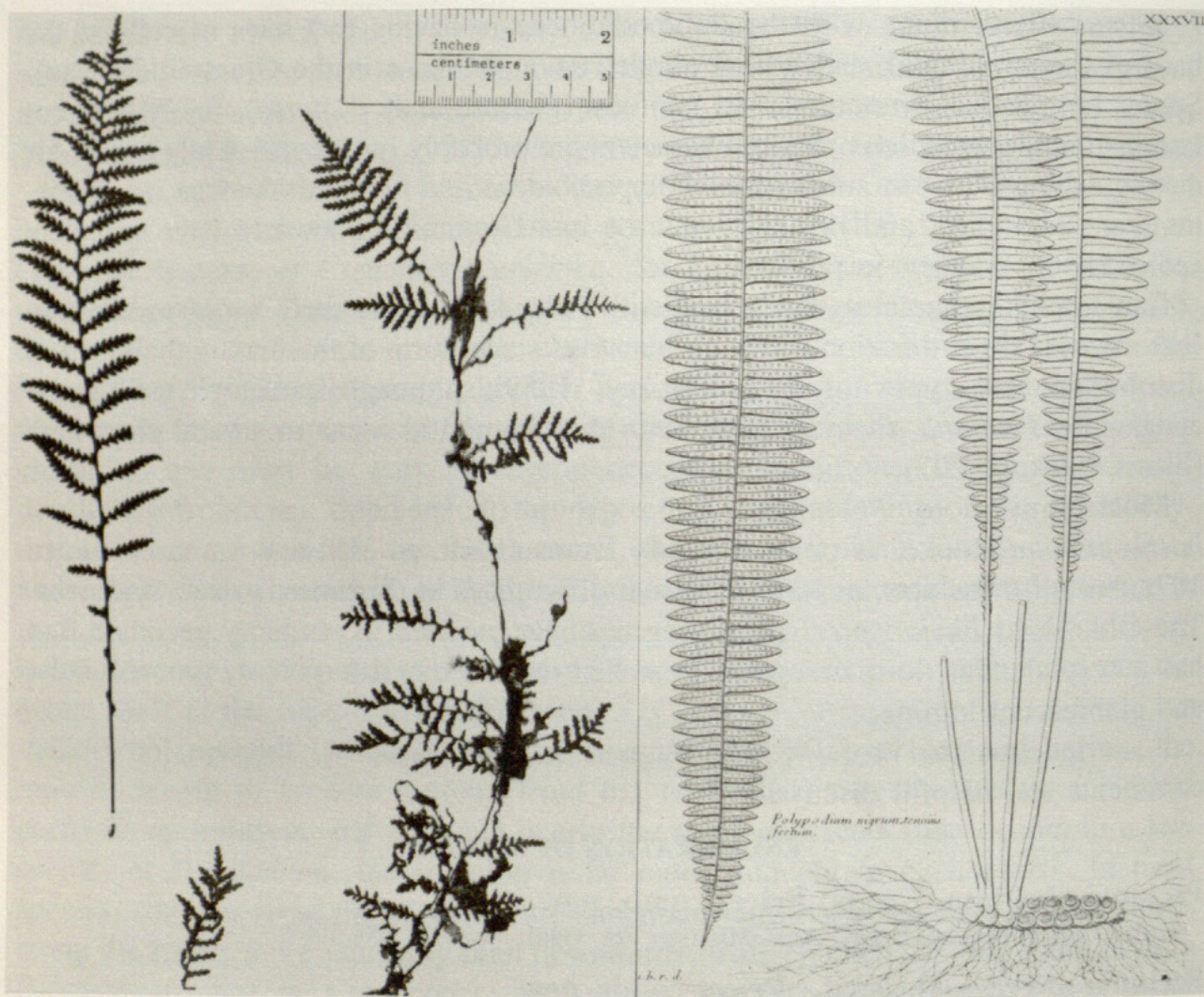


FIG. 1. *Pecluma funicula* showing a fertile frond (left) and an elongate root with a series of plantlets produced by prolifery (Oriente, Cuba, "creeping on trees," von Eggers 5104, MICH).

FIG. 2. Plate 37 of Plumier's "Description des Plantes de l'Amerique."

***Pecluma cupreolepis* (Evans) Price, comb. nov.**

Polypodium cupreolepis Evans, Ann. Missouri Bot. Gard. 55:224, f. 17. 1969.

This species was reduced to *P. alfredii* by Stolze (1981, p. 395).

***Pecluma curvans* (Mett.) Price, comb. nov.**

Polypodium curvans Mett. Ann. Sci. Nat. (Paris) V, 2:253. 1864.

***Pecluma dispersa* (Evans) Price, comb. nov.**

Polypodium dispersum Evans, Amer. Fern J. 58:173, pl. 27. 1968.

***Pecluma eurybasis* (C. Chr.) Price, comb. nov.**

Polypodium eurybasis C. Chr. Svensk. Vet. Akad. Handl. III, 16:71, t. 16, f. 12-13, 1937.

***Pecluma ferruginea* (Mart. & Gal.) Price, comb. nov.**

Polypodium ferrugineum Mart. & Gal. Mém. Acad. Bruxelles 15:36, t. 6, f. 2. 1842.

***Pecluma filicula* (Kaulf.) Price, comb. nov.**

Polypodium filiculum Kaulf. Enum. Fil. 275. 1824, as "filicula."

***Pecluma funicula* (Fée) Price, comb. nov.**

Polypodium funiculum Fée, Gen. Fil. 241. 1852; Six. Mém. 12, t. 8, f. 2. 1854.

Ctenopteris funicula (Fée) J. Smith, Hist. Fil. 185. 1875.

This Cuban species, overlooked by Evans (1969), is one of two members of the genus *Pecluma* with deeply pinnatifid segments, the other being *P. choquetangensis*, known from only Bolivia. *Pecluma funicula* differs conspicuously by the rachis \pm straight (not sinuous) and the pinnae and lobes only slightly ascending (vs. ascending at c. 45°). But the most interesting character of *P. funicula* is the rampant root system (see Fig. 1), freely proliferating and imitating rope-like, long-creeping rhizomes. Fée described these roots as rhizomes, and illustrated an elongate, intertwined clump of roots and fronds.

***Pecluma hygrometrica* (Splitg.) Price, comb. nov.**

Polypodium hygrometricum Splitg. Tijdschr. Nat. Gesch. 7:409. 1840.

***Pecluma paradiseae* (Langsd. & Fisch.) Price, comb. nov.**

Polypodium paradiseae Langsd. & Fisch. Icon. Fil. 11, t. 11. 1810.

***Pecluma pectinatiformis* (Lindm.) Price, comb. nov.**

Polypodium pectinatiforme Lindm. Hedwigia 43:309. 1904.

***Pecluma pectinata* (L.) Price, comb. nov.**

Polypodium pectinatum L. Sp. Pl. 1085. 1753.

This species provides the type of the genus. Its lectotype, chosen by Evans (1969, p. 246), is plate 37 of Plumier's (1693) "Description des Plantes de l'Amerique" (Fig. 2).

***Pecluma plumula* (Humb. & Bonpl. ex Willd.) Price, comb. nov.**

Polypodium plumula Humb. & Bonpl. ex Willd. Sp. Pl. ed. 4, 5:178. 1810.

***Pecluma ptilodon* (Kunze) Price, comb. nov.**

Polypodium ptilodon Kunze, Linnaea 9:42. 1834.

Evans (1969) divided this species into four varieties, two of which are tetraploids. If the two tetraploids are united into a distinct entity, as they were by Löve & Löve (1977), the earliest name for it is *Polypodium robustum* Fée.

***Pecluma recurvata* (Kaulf.) Price, comb. nov.**

Polypodium recurvatum Kaulf. Enum. Fil. 106. 1824.

***Pecluma sicca* (Lindm.) Price, comb. nov.**

Polypodium siccum Lindm. Ark. Bot. 1:234, t. 11, f. 4. 1903.

***Pecluma singeri* (de la Sota) Price, comb. nov.**

Polypodium singeri de la Sota, Opera Lilloana 5:181. 1960.

***Pecluma sursumcurrens* (Copel.) Price, comb. nov.**

Polypodium sursumcurrens Copel. Univ. Calif. Publ. Bot. 19:291, t. 42. 1941.

***Pecluma truncorum* (Lindm.) Price, comb. nov.**

Polypodium truncorum Lindm. Hedwigia 43:309. 1904.

***Pecluma venturii* (de la Sota) Price, comb. nov.**

Polypodium venturii de la Sota, Opera Lilloana 5:186, f. 31. 1960.

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