= Aiphanes =

Aiphanes is a genus of spiny palms which is native to tropical regions of South and Central America and the Caribbean . There are about 26 species in the genus (see below) , ranging in size from understorey shrubs with subterranean stems to subcanopy trees as tall as 20 metres (66 ft) . Most have pinnately compound leaves (leaves which are divided into leaflets arranged feather @-@ like , in pairs along a central axis) ; one species has entire leaves . Stems , leaves and sometimes even the fruit are covered with spines . Plants flower repeatedly over the course of their lifespan and have separate male and female flowers , although these are borne together on the same inflorescence . Although records of pollinators are limited , most species appear to be pollinated by insects . The fruit are eaten by several birds and mammals , including at least two species of amazon parrots .

Carl Ludwig Willdenow coined the name Aiphanes in 1801 . Before that , species belonging to the genus had been placed in Bactris or Caryota . The name Martinezia had also been applied to the genus , and between 1847 and 1932 it was generally used in place of Aiphanes . Max Burret resurrected the name Aiphanes in 1932 , and laid the basis for the modern concept of the genus . Aiphanes is most closely related to several other genera of spiny palms ? Acrocomia , Astrocaryum , Bactris and Desmoncus . Two species are widely planted as ornamentals and the fruit , seeds or palm heart of several species have been eaten by indigenous peoples of the Americas for millennia .

= = Description = =

Aiphanes is a genus of spiny palms ranging from 20 @-@ metre (66 ft) tall subcanopy trees to small shrubs with subterranean stems growing in the forest understorey . Its name combines the Ancient Greek ai , meaning " always " , with phaneros , meaning " evident " , " visible " or " conspicuous " . In their 1996 monograph on the genus , botanists Finn Borchsenius and Rodrigo Bernal pointed out that " ironically , species of Aiphanes are generally very hard to spot and find in dense vegetation and , accordingly , are among the most poorly collected neotropical palms " .

= = = Stems = = =

While some species are single @-@ stemmed , others form multi @-@ stemmed (caespitose) clumps . Coupled with variation in stem size , this produces a diversity of growth forms in the genus ? solitary (single @-@ stemmed) palms that grow into the subcanopy of the forest , solitary or caespitose palms that grow in the forest understorey and acaulescent palms which lack an aboveground stem .

Two species are characterised by an acaulescent growth habit ? A. acaulis and A. spicata . Two other species ? A. ulei and A. weberbaueri ? occur in both acaulescent populations and those which produce above @-@ ground stems . Several species are single @-@ stemmed understorey palms , an unusual growth form . Aiphanes grandis and A. minima are single @-@ stemmed palms which grow to be more than 10 metres (33 ft) tall , while the remainder are multi @-@ stemmed understorey species . Multi @-@ stemmed palms range from plants with a single main stem and a few basal suckers to caespitose clumps of 20 densely packed stems . A variety of growth forms can exist within a single species and this appears to be influenced by habitat and environmental conditions .

= = = Leaves = = =

The leaves of Aiphanes species are usually pinnately divided ? rows of leaflets emerge on either side of the axis of the leaf in a feather @-@ like or fern @-@ like pattern . The sole exception to this is A. macroloba which has entire leaves . They are usually spirally arranged , but some species have a distichous leaf arrangement , a condition that is normal in palm seedlings but uncommon among adults . Old leaf bases detach cleanly from the stem , except in A. hirsuta subsp. fosteriorum

, which often has old leaf bases attached to the newer portions of the stem .
Leaves are spiny but the degree varies both within and among species . Leaf sheaths are always densely spiny but the spines usually become smaller and sparser towards the ends of the leaves .

= = = Spines = = =

Spines are characteristic of Aiphanes and other members of the subtribe Bactridinae . They are found almost everywhere on the plants and are especially well @-@ developed on the stem , leaf bases , and the peduncle . In Aiphanes , the spines are formed from the outer tissues of the plant and are not derived through the modification of other plant organs . They range from less than 1 millimetre (0 @.@ 04 in) to more than 25 centimetres (9 @.@ 8 in) long .

= = = Flowers = = =

Aiphanes species are pleonanthic ? they flower repeatedly over the course of their lifespan ? and monoecious , meaning that there are separate male and female flowers , but individuals plants bear both types of flowers . In Aiphanes , male and female flowers are borne together on the same inflorescence . Usually only a single inflorescence is borne at each node , although A. gelatinosa often bears then in groups of three at a single node . The inflorescence usually consists of a main axis consisting of a peduncle and a rachis . The rachis bears rachillae , which are smaller branches which themselves bear the flowers , while the peduncle is the main stalk connecting the rachis with the stem of the plant . In some species there is second @-@ order branching ? the rachillae themselves are branched and the flowers are borne on these branches .
Flowers are usually borne in groups of three ? one female flower together with two male flowers . In some species groups of four flowers (two male and two female) have been reported . At the far end of the inflorescence , away from the axis of the tree , pairs of male flowers replace the triads of male and female flowers . Flower colour is poorly known . It must be recorded from live plants , since preserved flowers lose their colour over time , and records of these species in the wild are incomplete . Male flowers tend to fall into two groups ? those with cream or yellow flowers and those with some amount of purple in the flowers . Female flowers are even less well known than male flowers .
Pollen grains are usually spherical to ellipsoid in shape , sometimes triangular , about 20 to 30 micrometres along their long axis and 20 to 30 µm in diameter . They are typically monosulcate , meridionosulcate or more rarely trichotomosulcate . The sulcus is a furrow which runs along the surface of the pollen grain and is usually the site at which pollination occurs . Monosulcate pollen has a single furrow that runs along the pole of the pollen grain . Meridionosulcate pollen have a furrow that runs along the equator of the pollen grain . Trichotomosulcate pollen , on the other hand , has three furrows . The outer layer of the pollen is covered to a greater or lesser extent with ridges , spines or warts . This " sculpting " tends to be more pronounced in species that are fly @-@ pollinated and less pronounced in those that are pollinated by beetles or bees .

= = = Fruit = = =

The fruit of Aiphanes species is usually a red , spherical , single @-@ seeded drupe . A thin skin (or epicarp) , which can be either smooth or spiny , covers the fleshy mesocarp , which is typically orange and sweet . The mesocarp of A. horrida has one of the highest reported carotene contents of any plant product and is also rich in protein . The endocarp , which encases the seed , is brown or black and very hard at maturity . Seeds are light brown with a thin seed coat (or testa) and white endosperm , which is sweet and tastes somewhat like coconut .

= = = Karyotype = = =

Published chromosome counts exist for two species , Aiphanes minima and A. horrida ; haploid

chromosome counts vary from 15 to 18 . Borchsenius and Bernal report that it is difficult to get accurate chromosome counts in palms and that differences in chromosome counts may reflect these difficulties .

= = Taxonomy = =

Aiphanes is placed in the subfamily Arecoideae , the tribe Cocoseae and the subtribe Bactridinae , together with the genera Desmoncus , Bactris , Acrocomia and Astrocaryum .

In his 1932 revision of the genus , German botanist Max Burret recognised 32 species . Seventeen of these were new species , mostly based on collections made by German botanist Wilhelm Kalbreyer in northern Colombia between 1877 and 1881 . Working with a very narrow species concept , and not being familiar with the variation present in natural populations , Burret placed almost every specimen into a distinct species . The bombing of the Berlin Herbarium during the Second World War destroyed the only known collections for 13 of these 32 species , further complicating the situation .

The International Code of Botanical Nomenclature requires each species to be represented by a type collection . The destruction of Burret 's type collections left many species only known from his original descriptions , which generally lacked illustrations . Other specimens (called neotypes) were designated to replace these , either by Rodrigo Bernal and colleagues in 1989 or by Borchsenius and Bernal in their 1996 monograph of the genus . Bernal and colleagues attempted to retrace Kalbreyer 's travels in northern Colombia and collect specimens from as close as possible to the location of the original collections .

Burret divided Aiphanes into two subgenera , Brachyanthera and Macroanthera . Eleven species were placed in Macroanthera , while the remainder were placed in Brachyanthera . In their 1996 monograph , Borchsenius and Bernal questioned the applicability of these subgenera . They recognised that if Macroanthera was reduced to three species (A. horrida , A. eggersii and A. minima) it could form a viable grouping , but that this would leave Brachyanthera overly heterogeneous . Consequently , they abandoned Burret 's use of subgenera .

In the three decades following Burret 's delimitation of the genus a further 15 species were described , bringing the total species count to 47 . Borchsenius and Bernal determined that many of these names were synonyms , although American botanist George Proctor disagreed with their decision to lump A. acanthophylla into A. minima . Borchsenius and Bernal also described one new species , Aiphanes spicata , bringing the total number of accepted species to 22 . In two cases the destruction of the only known collections made it impossible to be absolutely certain that a name was a synonym . The current World Checklist of Selected Plant Families , maintained by Rafaël Govaerts at the Royal Botanic Gardens , Kew , recognises 26 species , including four species described since the publication of Borchsenius and Bernal 's monograph .

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= = = History = = =

The earliest botanical description of a species in the genus was made by French botanist Charles Plumier , who described two species based on his visits to the West Indies between 1689 and 1695 . Both of Plumier 's species are now considered to be Aiphanes minima . The same species was described by Dutch botanist Nikolaus Joseph von Jacquin in 1763 . Spanish botanist José Celestino Mutis produced a detailed description of A. lindeniana and illustrations of that species and what is thought to be A. horrida in 1779 .

In 1791 Joseph Gaertner included a species of Aiphanes in his De Fructibus et Seminibus

Plantarum , calling it Bactris minima . This is the oldest validly published name for any member of the genus . The name Aiphanes was coined by German botanist Carl Ludwig Willdenow in 1801 . He described a single species , A. aculeata , in 1806 .

Jacquin had used the name Caryota horrida to describe a plant that belonged to the same species (and may have been the same individual) described by Willdenow . Borchsenius and Bernal cite an 1809 publication date for Jacquin 's description , which gave precedence to Willdenow 's name . However , the more recent World Checklist (2006) gives an 1801 publication date for Jacquin 's description , making A. horrida the correct name for the species .

In 1816 Alexander von Humboldt , Aimé Bonpland and Carl Sigismund Kunth described Martinezia caryotifolia , adding another name to the list of synonyms for A. horrida . Since the original diagnostic characters of Martinezia did not fit any existent species , it was redefined by Kunth to fit M. caryotifolia . Consequently , Martinezia came to replace Aiphanes and the latter name was rarely used between 1847 and 1932 . In 1857 Hermann Karsten created a new genus , Marara , to accommodate two Colombian species , M. bicuspidata (later shown to be a synonym for A. horrida) and M. erinacea (now A. erinacea) . Hermann Wendland attempted to resurrect Aiphanes in 1878 , merging Martinezia and Marara into it , but his proposal was ignored . In 1901 Orator F. Cook created two new genera ? Curima , into which he put A. minima , and Tilmia , which housed A. horrida . In 1932 , after publishing a species in Martinezia , Burret changed his mind about the genus and synonymised it with Aiphanes . This led to the current delimitation of the genus .

= = = Species = = =

Species accepted by the World Checklist of Selected Plant Families :

= = Distribution and status = =

The genus Aiphanes ranges from the Dominican Republic and Panama in the north , to Trinidad and Tobago in the east , across Colombia and down along the Andes to Bolivia . In Brazil it only occurs along the border with Peru . Aiphanes is primarily South American ? one species (A. hirsuta) is present in Panama and two others (A. horrida and A. minima) are found in the Caribbean . Aiphanes minima , which is endemic to the insular Caribbean , is the only species absent from the South American mainland . Although A. horrida has been reported from Guyana and southern Venezuela these reports have not been verified with herbarium vouchers .

Aiphanes horrida is the most widely distributed species . It ranges from Trinidad to Bolivia but is absent from Ecuador and northern Peru . Other species have narrower ranges with one centre of diversity in western Colombia and Ecuador and another minor one in northeastern Peru . The 2006 IUCN Red List includes three species which are endangered by habitat destruction ? A. grandis , A. leiostachys and A verrucosa ? and three others considered vulnerable to the same threat ? A. chiribogensis , A. duquei and A. lindeniana . Rodrigo Bernal and Gloria Galeano expanded this list in a 2005 review of the status of Colombian palms . They listed two species as critically endangered ? A. graminifolia , a species that was first described in 2002 , and A. leiostachys (which was classified as endangered in the IUCN Red List) . They classified two species as endangered ? A. acaulis and A. parvifolia ? and two species as vulnerable ? A. gelatinosa and A. pilaris . They also classified six species as near threatened ? A. erinacea , A. hirsuta , A. lindeniana (vulnerable according to the IUCN Red List) , A. linearis , A. macroloba and A. simplex . The threats to these species were not listed , but Jens @-@ Christian Svenning reported that A. erinacea was threatened by logging given its limited distribution and poor ability to regenerate in disturbed forests . In addition to these , A. deltoidea , which is widely distributed across the western Amazon Rainforest , is present at such low densities that it was classified as a rare species by Francis Kahn and Farana Moussa in 1994 .

= = Habitat and ecology = =

Aiphanes species are palms of the forest understorey and subcanopy . The most widely distributed species , A. horrida , occurs both in tropical dry forest and in more humid forest types , but there is a gap in its distribution which coincides with the wettest forests of the upper Amazon Basin . Two other species , A. minima and A. eggersii , are also found in drier environments ; A. eggersii is found in areas receiving as little as 500 mm (20 in) of precipitation annually . The remaining species are found in montane forests at high elevations or in wet ? often very wet ? lowland forests , including areas receiving as much as 9 @,@ 000 mm (350 in) of annual precipitation .

Records of visits by pollinators exist for only a few species , but most of these suggest that the species are pollinated by insects . Flowers of A. chiribogensis produce small quantities of nectar , but lack a scent . Fruit flies (Drosophilidae) , fungus gnats (Mycetophilidae , Sciaridae) , midges (Cecidomyiidae , Ceratopogonidae) and micromoths (Lepidoptera) were recorded visiting these flowers , but bees and hover flies were not . Aiphanes eggersii was thought to be pollinated by bees and possibly by wind . Fruit flies (Drosophilidae) , hover flies (Syrphidae) , biting midges (Ceratopogonidae) and leaf beetles (Chrysomelidae) were recorded visiting the flowers of A. erinacea , but bees were not . Aiphanes horrida was reportly pollinated by wind , bees (Meliponidae) , weevils (Curculionidae) and bugs (Hemiptera) . Flies and weevils were observed on the flowers of A. simplex .

The fruit of A. horrida is rich in vitamins and energy and likely to be eaten by many animals . Oilbirds are reported to eat its fruit and disperse its seeds . Squirrels are also reported to consume the fruit , despite the spiny nature of the tree . The fruit , flowers and seeds of A. minima are consumed by the vulnerable Saint Vincent amazon (Amazona guildingii) and is also considered a potentially important food species for the critically endangered Puerto Rican amazon (Amazona vittata) .

Several species show clumped distributions . Dispersal limitation has been invoked to explain the clumped distribution of adults and limited recruitment of seedlings in both A. erinacea in Ecuador and A. minima in Puerto Rico . Similarly , the rarity of A. lindeniana and A. simplex in Colombian forests may be linked to limited seed production and the limited effectiveness of seed dispersal by avian and mammalian frugivores .

= = Uses = =

Aiphanes species have a long history of human use . The remains of carbonised seeds thought to belong to A. horrida have been found in archaeological sites in Colombia dating back to about 2800 BP ; seeds of this species are still consumed and are traded in local markets . Aiphanes horrida is also widely planted as an ornamental , as is A. minima . The fruit or seeds of A. deltoidea , A. eggersii , A. linearis and A. minima are all consumed locally . The palm heart of A. macroloba is consumed by the Coaiquer people of northwestern South America . Aiphanol , a compound isolated from A. horrida , has shown significant inhibitory activity against cyclooxygenases ; inhibition of these enzymes can provide relief from the symptoms of inflammation and pain .