

Review Article

MORPHOLOGY, CYTOLOGY AND CHEMICAL CONSTITUENTS OF SOME *PIPER* SPECIES FROM INDIA

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INTRODUCTION

The genus *Piper*, the largest in the family Piperaceae, consisting of more than 3000 species, occurs throughout the tropical and subtropical regions (Index Kewensis, 1895-1970). The distribution of *Piper* species ranges from sea level to the high ranges of Andes and the sub-Himalayas (Royle, 1839). In India, two independent centres of distribution are recognised viz., (1) Trans-Gangetic region and (2) South Deccan (Hooker, 1886). Several species of *Piper* occur in the forests of Western and Eastern Ghats of South India. The submountainous tracts of Western Ghats are believed to be the centre of origin of black pepper, *P. nigrum* Linn. (Rahiman et al., 1979). Brazil, Central America, Andes Zone, N. W. South America, Malaysia, Mexico, Indian sub-continent, Tropical Australia, East Africa, Malagasy Republic, West Indies, Pampas area and Siam-Burma region are considered to be the centres of world distribution (Datta and Dasgupta, 1977c).

ECONOMIC IMPORTANCE

The genus includes important cultivated species like *P. nigrum* the black pepper and betel vine *P. betle* Linn. The dried fruits, either ground or as a whole and oils and oleoresins extracted from the berries are used throughout the world. It is considered as the world's most important spice and rightly known as the "King of Spices".

Eventhough 108 species of *Piper* have been reported from Indian Sub-continent, besides *P. nigrum*, *P. betle* is the only other species widely cultivated.

Several species of *Piper* are used as important medicinal plants. In modern Indian medicine, black pepper is also used as an aromatic stimulant and antiperiodic in malarial fever.

The use of long pepper (*P. longum* Linn.) in Ayurvedic and Unani systems of medicine goes far back into antiquity (Atal and Ojha, 1965). Based on their experiments on rats, Atal, Zutshi and

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Rao (1981), showed that both long pepper and black pepper are capable of increasing the bio-availability of certain drugs. Fruits and oil extract of tailed pepper (*P. cubeba* Linn.) are used in treatment of asthma, chronic bronchitis, dysentery and catarrh. Roots of Kava pepper (*P. methysticum* Frost.) is used to make a non-alcoholic but narcotic drink *Kava*, a ceremonial drink among the Polynesians since ancient period. The roots of *P. sylvaticum* Roxb. are widely used in indigenous medicines as an effective antidote to snake poison (Banerji and Dhara, 1974). *P. hookeri* Miq. and *P. futokadsura* Seib. were found to possess crotopoxide, an antitumor factor (Kupchan et al., 1968; Singh, 1969; Takahashi, 1969).

Practice of chewing *pan* or betel leaves (along with other ingredients like arecanut and lime) is prevalent from time immemorial among the people from Pakistan in the west to Pacific Islands in the east (Ghani and Sial, 1952).

P. nigrum is a perennial climber cultivated in India, Indonesia, Malaysia and Brazil and to a small extent in Sri Lanka and West Indies (Trimen, 1895; Backer and Brink, 1963; Anonymous, 1969; Howard, 1973). In India, black pepper is grown mainly in Kerala and to a limited extent in other states like Karnataka, Tamil Nadu and Assam.

Betel leaf or *pan* is the leaf of a perennial, dioecious creeper *P. betle*, widely cultivated in India and South-east Asian countries and is probably a native of Malaysia. The cultivated vines are usually the male plants. They are

cultivated in almost all states of India, except in the dry north-west region.

Long pepper is the dried female inflorescence of a slender, aromatic creeper *P. longum*. Long pepper is reported from Central Himalayas, Assam, Khasi Hills, Bengal, Western Ghats and Nicobar Islands. Long pepper, as sold in Indian market, appears to be a product derived from three different species viz., *P. longum*, *P. peepuloides* Roxb. and *P. retrofractum* Vahl. Among these, only the first two are native to India and *P. retrofractum* is from Singapore. Indian long pepper of commerce is mostly collected from the wild plants. These are also reported to be cultivated in Cherrapunji region of Assam, Circar hills of Andhra Pradesh and Anamalai of Tamil Nadu (Royle, 1839; Atal and Ojha, 1965; Anonymous, 1969). The roots and thicker parts of the stem are used in medicine and is known as *Piplamul* (Anonymous, 1969).

Tailed pepper is the fruit (having a long stalk) of *P. cubeba* a liana-like climber. It shows extreme variability in morphological characters and is cultivated mostly in Java and Sumatra. It is also reported to be cultivated in Karnataka region in India (Anonymous, 1969).

TAXONOMIC HISTORY OF INDIAN *PIPER*

The earliest known reference of plants belonging to *Piper* was of Bauhin. His '*Pinax theatri botanici*' published in the year 1563 included *Piper rotundum nigrum* (*P. nigrum*) and *Piper longum orientale* (*P. longum*). In 1678 Rheede Tot published '*Hortus Indicus Malabaricus*' in which five species of *Piper* were

described and four species were illustrated. Later in 1796 Casparus published his 'Flora Malabarica sive Horti Malarici Catalogue' wherein five *Piper* species were included. Linnaeus (1753) established the genus *Piper*. He described 17 species and assigned five of them to Indian peninsula. Roxburgh (1832) described 18 species of which seven were from Indian peninsula. Miquel (1843-1859) described more than 600 species of which only eight were from India. Wight (1853) illustrated 16 species from Indian Peninsula under six different generic names. Of the 640 species described by de Candolle (1866-1923), 52 were from Indian peninsula. Hooker (1886) described 45 species of which 29 were assigned to the peninsula. Brandis (1906) described eight species. Apart from these, several Indian Taxonomists treated *Piper* in their Regional Floras. There are 108 species so far recorded from Indian subcontinent. They are: *P. accrescens* Heurck & Muell., *P. anisotis* Hook. f., *P. arborescens* Miq., *P. arborigandens* C.DC., *P. argyrophyllum* Miq., *P. attenuatum* Ham., *P. aurantiacum* Wall., *P. aurorubrum* C.DC., *P. barberi* Gamble., *P. bengalens* C.DC., *P. betle* Linn., *P. betleoides* C.DC., *P. boehmeriaefolium* Wall., *P. brachystachyum* Wall., *P. calvilimum* C.DC., *P. caninum* Blume., *P. carnistigma* C.DC., *P. caudilimum* C.DC., *P. chaba* Hunter, *P. clarkei* C.DC., *P. clypeatum* Wall., *P. cornilimum* C.DC., *P. crassistipes* C.DC., *P. crenulibracteum* C.DC., *P. cubeba* Linn., *P. curtistipes* C.DC., *P. dekkooanum* C.DC., *P. diffusum* Blume, *P. exasperatum* Vahl, *P. falconeri* C.DC., *P. filipedunculum* C.DC., *P. galeatum* C.DC., *P. gallatlyi* C.DC., *P. Gamblii* C.DC., *P. gammiei*

C.DC., *P. gibsoni* C.DC., *P. glabramentum* C.DC., *P. glabrirhache* C.DC., *P. grandipedunculum* C.DC., *P. griffithii* C.DC., *P. guigual* Ham. ex Don., *P. hamiltonii* C.DC., *P. hapnium* Miq., *P. hookeri* Miq., *P. hymenophyllum* Miq., *P. isopleurum* C.DC., *P. japvonum* C.DC., *P. jenkinsii* C.DC., *P. kapruanum* C.DC., *P. khasianum* C.DC., *P. laeve* Vahl, *P. lainatakanum* C.DC., *P. lanatum* Miq., *P. laxivenum* C.DC., *P. lesteri* C.DC., *P. longum* Linn., *P. maingayi* Hook f., *P. makruense* C.DC., *P. malamaris* Linn., *P. mannii* C.DC., *P. meeboldii* C.DC., *P. mullesua* Ham., *P. muneporensis* C.DC., *P. mungpooanum* C.DC., *P. nagaense* C.DC., *P. nepalense* Miq., *P. nigramentum* C.DC., *P. nigrum* Linn., *P. obtusistigma* C.DC., *P. oldhamii* C.DC., *P. ootacamundense* C.DC., *P. opacilimum* C.DC., *P. ovatistigma* C.DC., *P. ovatoacuminatum* C.DC., *P. ovatostamon* C.DC., *P. pallidum* Heurck & Muell., *P. parvilimum* C.DC., *P. podicellatum* C.DC., *P. peepuloides* Roxb., *P. petiolatum* C.DC., *P. phalangense* C.DC., *P. puberulipes* C.DC., *P. pykarahenes* C.DC., *P. retrofractum* Vahl, *P. ribesioides* Wall., *P. rhytidocarpum* Hook. f., *P. sarmentosum* Roxb., *P. schmidtii* Hook. f., *P. saxatile* Wall., *P. sikkimense* C.DC., *P. siriboa* Linn., *P. spnadense* C.DC., *P. subpedicellatum* Willd., *P. suipigua* Ham., *P. subrigidilimum* C.DC., *P. sylvaticum* Roxb., *P. sylvestre* Lamk., *P. syringaefolium* Vahl., *P. talbotti* C.DC., *P. tenuibracteum* C.DC., *P. thermale* Vahl., *P. thomsoni* Hook. f., *P. trichostachyon* C.DC., *P. trioecum* Roxb., *P. tristachyon* C.DC., *P. voigtii* C.DC., *P. wightii* Miq., *P. zuccarinii* C.DC.

Very little attempt has been made so far to collect and conserve the wild relatives of black pepper, long pepper and betel in any pepper growing

countries. Recently (1973-'78) a survey for the wild relatives of black pepper from the forests of the Western Ghats in South India was organised by the Central Plantation Crops Research Institute. Based on a detailed study of the herbarium specimens collected, in comparison with the *Piper* specimens preserved in various Indian herbaria, Rahiman et al., (1979) recorded the following eight species from the Western Ghat regions of Karnataka: *P. argyrophyllum* Miq., *P. attenuatum* Buch-Ham., *P. galeatum* C.DC., *P. hookeri* Miq. (*P. hymenophyllum* Miq.), *P. mullesua* D. Don (*P. brachystachyum* Wall. ex Hook.), *P. nigrum* Linn. and *P. trichostachyon* C.DC.

Piper species, in Karnataka are found to occur in evergreen and semi-evergreen forests and also in certain pockets in moist deciduous forests. *P. nigrum* is found from sea level to a height of 1450 m. *P. attenuatum* is confined to lower elevation. *P. mullesua* occurs only at higher altitudes such as Kemmanagundi (1320 m), Agumbe (800 m) and Mercara (1200 m) (Karnataka State). All species mostly occur in the middle elevation forests, though *P. trichostachyon* occurs at higher elevation also. *P. nigrum* is the most widely distributed species. In distribution, *P. nigrum* is followed by *P. trichostachyon*, *P. hookeri*, *P. attenuatum*, *P. argyrophyllum*, *P. longum*, *P. mullesua* and *P. galeatum* in decreasing order (Rahiman, et al., 1979, Rahiman, 1981a).

BIOLOGY OF THE GENUS

Plants belonging to the genus *Piper*, as occurring in India, are usually shrubs, rarely herbs, erect or scandent, often

glandular and aromatic. Branches are with swollen nodes. Leaves are alternate, entire, often unequal sided and range from very thin and membranous to thick and coriaceous, leaf surface varies from smooth to rugose, some are entirely glabrous and other pubescent. Majority of the species have small but conspicuous glandular dots, frequently on leaves but some times on other tender and fleshy parts as well, petiole varies in length among different species and often within the same species; leaves are rarely sessile. Leaves of majority of the species have 5-9 principal nerves which are multiple-, palmately-, or rarely pinnately-nerved. Stipules none to two, connate or adnate to the petiole (Hooker, 1886; Hains 1924; Gamble, 1925; Saldanha and Nicolson, 1976).

Spikes are always opposite to the leaves, predominantly filiform, sometimes cylindrical and rarely subglobose or globose; peduncle may be glabrous, hirtellous or puberulous. The flowers are many, sessile, naked and compactly arranged on the inflorescence axis. Each flower is subtended by a bract. In some species the bracts are peltate with a small stalk, in others they are adnate and decurrent and in the remaining ones, they are transformed into a fleshy cup like structure. In some species stamens are two in number, occupying either side of the ovary, in others, three, of which the third is posterior, rarely more than three, filaments short, anther lobes two, rarely one, each lobe with two pollen sacs, which after dehiscence, become united due to confluence. Ovary is single, sessile, subglobose or flask shaped, one-ovuled, stigma is usually

sessile, orthotropous. Fruit is a small one-seeded drupe; seed small, testa thin, cartilaginous, albumen floury, embryo antitropous, occupies a cavity in the albumen at the top of the fruit. Cotyledons minute or absolent, radicle superior (Le Mount and Decaisne, 1876; Hooker, 1886; Gamble, 1925; Lawrence, 1951; Murthy, 1959 b).

In cultivated varieties of black pepper, variations ranging from complete hermaphrodite to entirely male or female flowers are found. In commercial cultivation a high ratio of hermaphrodite flowers are essential for good yield (Blacklock, 1954). In the cultivars of black pepper, within 15 days of soaking rain the vines resume flushing. From the tip of the flowering branches, a minute, elastic, brownish, sickle-shaped growth starts. This cap-like structure is pushed aloft by the growing sheath underneath. The sheath falls off within ten to twelve days of its appearance, exposing a very minute spike with tiny young leaf subtending it. The flowers are protogynous, the stigma being exerted several days before anther dehiscence. The development of two stamens in flower is not simultaneous, one may come out 2-3 days in advance of the other. Anthesis proceeds from base to tip of the spike, taking about a week for all flowers to open (Anandan, 1924; Semple, 1974). Barber (1956) and Anandan (1924) attributed pollination to the splashing of rain and the latter ruled out the role of insects in pollination. According to Anandan (1924) heavily falling rain drops scatter the pollen grains in different directions. The rain drops either wash down the pollen to the lower spikes (self pollina-

tion) or carry them from vine to vine (cross pollination). However, Semple (1974) observed that insects visit the flowers and are probably involved in pollination. Martin and Gregory (1962) presumed that the pendent spike is practically assured of self-pollination from the anthers of upper flowers. Excellent fruit set on some spikes during the dry months made them to suggest that self-pollination is the rule in cultivated plants and rain is neither the sole nor a necessary agent in pollination. Because of the globular nature of the pollen, they presumed that wind and rain are not significant pollination agents. De Waard and Zeven (1969) suggested five types of possible pollinations viz., insect pollination, wind pollination, geitanogamy, autogamy and pollination between neighbouring spikes. Gentry (1955) reported apomixis in a female clone of black pepper but Martin and Gregory (1962) failed to observe any such development in cultivar *Uthirankotta* which is an entirely female clone.

ANATOMY

The genus *Piper* has attracted much attention because of the anomalous vascular structures. The distinguishing feature of the genus is the distribution of vascular bundles in the axis which are often scattered and widely spaced resembling that of monocotyledons. It is noteworthy, however, that unlike the monocotyledons, the stem of *Piper* grows in thickness through the cambial activity (Metcalf and Chalk, 1950). Another interesting feature is the presence of an endodermis in the stems of many species.

Chibber (1913) and Datta and Dasgupta (1977 a, b, c) studied the anatomy of *P. betle*. The upper epidermis of the leaf is many layered. Hypodermis is 1-2 layered and lower epidermis single layered. Stomata are confined to lower epidermis and are scattered and irregularly oriented. Occasionally the stomata may be contiguous or in groups, (Datta and Dasgupta, 1977 a). A circle of four subsidiary cells are generally seen, sometimes an additional outer circle is also observed. Stomata show diversity in different varieties; most of them are tetracytic, some are anisocytic, anomocytic and cyclocytic (Mohandas and Shah, 1980). Pant and Banerji (1965) described in detail the development of stomata. Hairs are restricted to the veins, they are unicellular in some varieties and multicellular in others. Hairs have a sunken stalk cell and a curved apical cell having a tapering apex and a rounded base and are frequently found on both sides of the leaves and these are regarded as hydathodes (Chibber, 1913, Pant and Banerji, 1965). Mesophyll is bifacial type. Pallisade tissue is irregularly stratified. Spongy tissue is made up of irregular rounded cells. Secretory cells are present in upper and lower hypodermis, mesophylls and spongy tissues. The entire assimilatory tissue is characterised by the presence of large amount of calcium oxalate in the form of crystal or fine sands.

A section of the midrib at the basal portion shows three large and a variable number of smaller vascular bundles, all arranged in a crescent. There is a large mucilage canal in the centre. The midrib shows only a single

bundle at the apical region i.e., after the midrib has given of all the secondary ribs. Vascular bundles are open, collateral, number of tracheary elements in transverse section are about 20-40 in different varieties. Proportion of phloem to xylem is almost equal, cambium layer vary in number (Chibber, 1913; Datta and Dasgupta, 1977 a).

A young stem near the apical region reveals a central mucilage canal surrounded by varying number of smaller canals. Vascular strands are arranged in two rings, the inner one lies within the circle of mucilage-canals in the medulla. It consists of 6-12 bundles. They may or may not occur in regular circles. The peripheral ring consists of 5-6 large bundles and 12-24 or more smaller bundles. Outside this ring there is a narrow pericycle of about five cells thickness. It is bounded by an endodermis. The cortex, contains isolated arcs of collenchyma. The parenchyma is only two or three cells deep. The epidermal cells are unequal sized, the hairs are sparsely distributed and are unicellular or multicellular. The cortex is characterized by abundant secretory cells (Chibber, 1913; Datta and Dasgupta, 1977 b).

A mature stem shows one, or rarely two central mucilage canals and about 12 peripheral ones. There are two types of vascular bundles viz., medullary bundles and peripheral bundles. The medullary bundles are about 20 in number and are arranged in one or two sinuous rings. Peripheral ring may have as many as 50 bundles. This ring is surrounded by an outer sheath of sclerenchyma. Endodermis occurs as a

continuous ring. In the cortex the parenchyma layer is rather thin. It is succeeded by groups of collenchyma, which appear in the form of detached arcs. The cork layer consists of radially compressed cells. This layer is traversed by lenticels. The cortex contains secretory cells. Starch may be seen at certain times of the year in almost every cell of the stele and cortex. Pith contains calcium oxalate crystals, stone cells and secretory cells (Chibber, 1913; Datta and Dasgupta, 1977 b).

Hoffstadt (1916) studied the histology of *P. methysticum* and *P. umbellatum*. Both the species show almost identical structure. The stem contains at maturity three rings of bundles, one peripheral and two medullary. Sometimes an irregular half-ring may be seen along the latter. The peripheral bundles are of two sizes, the large (primary) and the small (secondary), latter are the branches of the former and lie between the primary bundles. The pericycle consists of only a few cells outside the bundle. There is no differentiation of endodermis. Secondary growth takes place by cambial activity and the division is restricted to the inner side only. Interfascicular cambium appears late and cuts off segments on inside only. There is no growth ring. Garner and Beakbane (1968) studied the anatomy of the stem of *P. nigrum* (clone *Kutching* of Sarawak and cultivar *Uthirankotta* of India). According to them when the secondary thickening is initiated the cambial sheath becomes continuous by the formation of inter-fascicular cambium across the medullary rays. Later fiber groups are formed over the rays. Sclerification proceeds until these fibres become

continuous with those capping the phloem. Eventually they penetrate deeply between the vascular strands so that once again cambial sheath is broken at various regions. Endodermis is observed over medullary rays and outer vascular strands in the form of a continuous strand.

In addition to different varieties of *P. betle*, Datta and Dasgupta (1977a,b,c) studied the anatomy of *P. brachystachyum* Wall., *P. cubeba* Linn., *P. longum* Linn., *P. magnificum* Hort. ex Gentil, *P. pedicellosum* Wall., *P. nepalense* Miq., *P. nigrescence* C.DC. and *P. nigrum* Linn. According to them the leaf epidermis is single layered, glabrous or hairy. Leaves are hypostomatic, stomata are always surrounded by a rosette of cells which differ from the remaining cells. The hypodermis in different species may vary from 1-3 layers, in some it may be even absent. Mesophyll is 1-2 layered. In some species the spongy parenchyma and mesophyll cells are distinguishable and in others not.

Murthy (1959a) studied the vegetative anatomy of *P. betle*, *P. longum* and *P. subrubrispicum*. According to him, adult internodes of all the three species studied, agree in general and especially in the arrangement and structure of the vascular bundles. There is a very conspicuous mucilage canal in the centre of the internode of *P. betle* and *P. subrubrispicum* but not in *P. longum*. The numerous vascular bundles are arranged in two or three concentric rings. The bundles of the outermost ring are always greater in number than those of the inner. Murthy

(1959b) also studied the floral morphology and anatomy of 10 species, viz., *P. betle*, *P. gaudichaudianum*, *P. longum*, *P. nigrum*, *P. nigrescens*, *P. obtusilimum*, *P. schmidtii*, *P. subrubripicum*, *P. tucumanum* and *P. unguiculatum*. Floral vasculature in these species are essentially similar. The inflorescence axis consists of two rings of bundles, an outer 10 or more and an inner of about five. The vasculature of the flowers in all these species is essentially similar. A flower is always supplied by a single branch of vasculature that first gives out a trace to the subtending bract. The remaining vascular supply gives out traces to the stamens and then to the ovary. The ovary supply splits up at its base into three peripheral and one central strand. The central strand furnishes a ovular trace. The three peripheral bundles may or may not branch and supply the ovary wall.

Bond (1931) studied the stem endodermis in eight species viz., *P. angustifolium* Ruiz and Pav., *P. celtidifolium*, *P. chaba* Hunter, *P. decurrens* C. DC., *P. excelsum* Frost., *P. nigrum*, Linn., *P. porphyrophyllum* N. E. Br. and *P. tilioefolium* Schlecht. According to Bond (1931) endodermis develops to varying degrees in different species. In some, it forms a continuous cylinder around the bundles and in some other species it is absent, being replaced by a layer of relatively large cells without casparian thickenings. In a third group it is present but inconsistently distributed. The casparian strips are of exceptionally large size in all the species. Pits are present in the radial and tangential walls. Secretory cells are present in the endodermal layer. Endodermis was not

detected in the leaf. Bond tentatively concluded that in the genus *Piper*, and possibly in the shoots of all Phanerogams, the endodermis is a vestigial structure of no primary importance.

POLLEN MORPHOLOGY

Anandan (1924) described pollen grains of black pepper as small, hyaline in appearance, round and smooth in outline and about 8.0–8.8 μ in diameter. Erdtman (1951) described pollen morphology of *P. aduncum* Linn., *P. majusculum* Blume and *P. subscrabrum*. In *P. aduncum* grains were monosulcate, 6.5 \times 10.5 \times 8.0 μ in size, sulcus membrane granulate. In *P. majusculum*, they are 7.0 \times 13.0 \times 11.0 μ monosulcate but occasionally trichomosulcate and in *P. subscrabrum*, 7.0 \times 12.0 \times 9.5 μ in size. Mitroiu (1970) gave a generalized description of pollen grains of *P. berlandieri* C. DC., *P. siriboa* Heyne, *P. cubeba* Linn. and a detailed account of *P. nigrum* Linn. and *P. aduncum* Linn. According to him, pollen grains of *P. nigrum* are small, subprolate to prolate monosulcate, polar axis 8.4–9.6 μ in diameter, equatorial axis 9.6–18.8 \times 7.2–9.6 μ , sporoderm 0.7 μ in thickness, exine warty. Agababian (1969) gave simple diagram of pollen grains of *P. argyrophyllum*, *P. brachystachyum* and *P. nigrum*. Smith (1975) furnished scanning electron microscope photograph of the pollen grains of *P. insectifugum*. Rahiman (1981b) studied pollen morphology of eight species of *Piper*. According to him pollen grains of all the eight species are characterised by a uniform morphology though they vary in their size. Grains were small, spheroid to suboblate, monosulcate, exine reticulate,

the brochi being large and irregular on the distal polar surface and small and uniform in the rest of the surface.

STRUCTURE AND DEVELOPMENT OF OVARY

Joshi (1944) studied the structure and development of ovule and embryo-sac in *P. longum*. He observed special cells secreting volatile oil scattered throughout the wall of the ovary. The ovary contains a single basal orthotropous ovule with two integuments of which the inner forms the micropyle. He also described in detail the structure of the embryo-sac in *P. longum*.

Johnson (1902) studied development and structure of ovary in *P. medium* and *P. aduncum*. Development of ovary was found to be quite alike in both the species. In these species also, the wall of the ovary has numerous oil-secreting cells scattered.

In *P. medium*, the ovule which is terminal on the axis of the carpel, arises just as the carpel lobes are closing in above. The primary archesporial cell divides to form a tapetal cell which divides further to form 4 or 5 layers of cells, above the embryo-sac and the definitive archesporial cell below, which will become a megaspore directly, without further division. Later the megaspore divides and redivides to form a group of eight cells and form the embryo-sac. The ripe embryo sac has a large egg, two smaller synergids, a large endosperm nucleus and distinct antipodals which become sunken in the very bottom of the embryo sac (Johnson, 1902).

Development of embryo-sac in *P. aduncum* is similar to that of *P. medium* (Johnson, 1902). Johnson (1910) also studied the structure and development of the ovary of *P. betle* var *monoicum* and according to him the female gametophyte develops according to 'Adoxa type' of embryo-sac development. Maheswari (1937) drew attention to the figures and text of Johnson's papers on *P. betle*, rearranged the figures and interpreted them as depicting some characteristic phases of 'Fritillaria type' of embryo-sac development. Swamy (1944) reinvestigated the embryo-sac of *P. betle* and showed that the development is 'Fritillaria type' rather than 'Adoxa' type. Murthy (1959b) studied the embryo-sac development of *P. gaudichaudianum* and concluded that this species also belongs to 'Fritillaria type'.

MICROSPOROGENESIS

Mathew (1958) observed that in *P. nigrum* microsporogenesis takes place when the spike is about 3 - 5 cm long and almost all the stages of division are observed in anthers of a single spike. During meiosis, the bivalents condensed appreciably and are distributed on the periphery of the nucleus. Some bivalents are held together by only one chiasma. Sharma and Bhattacharyya (1959) reported meiotic abnormalities like laggards, early and late separation of chromosomes and secondary associations between the bivalents. According to Martin and Gregory (1962) pairing is normal among the bivalents except for the occurrence of occasional quadrivalents. The development of the microsporangium has been studied in *P. schmidtii*, *P. gaudichaudianum*, *P. longum*

and *P. unguiculatum*. The anther has four microsporangia and a wall consisting of four layers. The innermost layer, tepetum, remains uninucleate. At maturity endothecium becomes fibrous and the middle layer is completely crushed (Murthy, 1959b).

CYTOGENETICS

Cytological investigations in the genus *Piper* has been confined to determination of the chromosome number of different species. The diploid chromosome numbers reported so far for different species of *Piper* are given in Table I. Reports on chromosome morphology in the genus have been limited so far (Mathew, 1958, 1973; Sharma and Bhattacharyya 1959; Dasgupta and Datta, 1976; Jose 1981), probably because of the large number and small size of chromosomes.

P. nigrum: Mathew (1958, 1973) studied 11 cultivated and six wild types of *P. nigrum*. In all the cultivated and four wild types, he reported a somatic chromosome number of $2n=52$ and in two wild types the number was $2n=104$ each. Chromosomes were very small and ranged in length between 1.0 and 3.0 μ . According to Sharma and Bhattacharyya (1959), diploid number in *P. nigrum* was $2n=48$ and the chromosomes varied in length from 0.7 to 3.4 μ . Four pairs of chromosomes possessed secondary constrictions. According to Dasgupta and Datta (1976) diploid numbers of North Indian species were $2n=36$ and the South Indian species, $2n=60$. In the former, the chromosome length ranged between 0.77 and 1.9 μ and in the latter between

0.77 and 2.3 μ . North Indian group possessed four pairs of chromosomes with secondary constrictions and the South Indian group, two pairs.

P. longum: Mathew (1958, 1973) observed 52 chromosomes in the somatic cells and the chromosome size varied from 1.3 to 3.0 μ . Sharma and Bhattacharyya (1959) reported $2n=48$, and 96 and $n=24$ for three types studied by them. Dasgupta and Datta (1976) observed chromosome length ranging from 0.77 to 1.5 μ in a *P. longum* type with $2n=48$ and a pair of secondary constriction.

P. betle: According to Mathew (1958) diploid number in *P. betle* was $2n=78$. Chromosomes were short, thick and small and ranged from 1.0 to 2.0 μ . Sharma and Bhattacharyya (1959) noted 64 chromosomes in the somatic cells and the size ranged between 0.7 and 2.5 μ . Six pairs of chromosomes were found to possess secondary constrictions. Dasgupta and Datta (1976) reported chromosome number for two cultivars of *P. betle* and both had diploid number, $2n=64$. In both cultivars, chromosome length ranged from 0.77 to 1.2 μ , but in the former, two pairs of chromosomes possessed secondary constrictions and in the latter 3 pairs had secondary constrictions.

P. attenuatum: Karyomorphology of this species was attempted only recently by Jose (1981). According to him the diploid chromosome number was $2n=52$. Chromosomes ranged from 0.7 to 1.9 μ in length. Two pairs of chromosomes showed secondary constriction and one pair, a satellite.

Table I. Chromosome number in Piper species

Species	Diploid number (2 n)	Author/s and year
<i>P. argyrophyllum</i> , Miq.	26,39	Samuel and Bavappa (1981)
<i>P. attenuatum</i> , Ham.	26,39	-do-
-do-	52	Jose (1981)
<i>P. betle</i> , Linn.	32	Johnson (1910)
-do-	32	Janaki Ammal (1945)
-do-	78	Mathew (1958)
-do-	64	Sharma and Bhattacharyya (1959)
-do-	64	Dasgupta and Datta (1976)
-do-	26,52	Samuel and Bavappa (1981)
<i>P. chaba</i> , Hunt.	24	Janaki Ammal (1945)
<i>P. chuvya</i> , Roxb.	52	Samuel and Bavappa (1981)
<i>P. cubeba</i> , Linn.	24	Janaki Ammal (1945)
-do-	24	Dasgupta and Datta (1976)
<i>P. futokadzura</i> , Sub. and Zuce.	24	Yoshida (1960)
<i>P. geniculatum</i> , Sw.	28	Maugini (1951)
<i>P. grissico-argenta</i> , Yunck.	22	Smith (1966)
<i>P. longum</i> , Linn.	24	Tjio (1966)
-do-	52	Mathew (1958)
-do-	48,96	Sharma and Bhattacharyya (1959)
-do-	48	Dasgupta and Datta (1976)
-do-	26	Samuel and Bavappa (1981)
<i>P. magnificum</i> , Trel.	26	Smith (1966)
-do-	24	Dasgupta and Datta (1976)
<i>P. medium</i> , Jacq.	28	Maugini (1951)
<i>P. ornatum</i> , N. E. Br.	80	Sharma and Bhattacharyya (1959)
<i>P. nigrum</i> , Linn.	c. 128	Janaki Ammal (1945)
-do-	48	Sharma and Bhattacharyya (1959)
-do-	36,60	Dasgupta and Datta (1976)
-do- (cultivated)	52	Mathew (1958, 1973)
-do- -do-	52	Martin and Gregory (1962)
-do- -do-	52	Samuel and Bavappa (1981)
-do- (wild)	52,104	Mathew (1958; 1973)
-do- -do-	52,65	Samuel and Bavappa (1981)
<i>P. sylvestre</i> , Lamk.	26,39	-do-
<i>P. thwaitseii</i> , C. DC.	39,65	-do-
<i>P. trineuron</i> , Miq.	26	-do-
<i>P. unguiculatum</i> , Ruiz and Pav.	28	Maugini (1951)
<i>P. zeylanicum</i> , Miq.	39	Samuel and Bavappa (1981)
<i>Piper</i> sp. undetermined	104	Mathew (1958)

P. ornatum: The only report on this species was that of Sharma and Bhattacharyya (1959). The diploid number for this species was $2n=80$. Chromosome length ranged from 0.7 to 1.9 μ . Four pairs were found to possess secondary constrictions.

P. cubeba: Dasgupta and Datta (1976) reported diploid number as $2n=24$ for this species. Chromosome length ranged from 0.77 μ to 2.5 μ . Three pairs were found to possess secondary constrictions.

P. magnificum: Dasgupta and Datta (1976) observed 24 chromosomes in somatic cells. Chromosome length ranged from 1.2 μ to 3.7 μ . Three pairs possessed secondary constrictions.

In addition to the above, chromosome numbers of 13 other species viz., *P. argyrophyllum* Miq., *P. chaba* Hunt., *P. chuyva* Roxb., *P. futokadzura* Sub. & Zuce., *P. geniculatum* Sw., *P. grissico-argenta*, *P. magnificum* Hortex Gentil., *P. medium* Jacq., *P. sylvestre* Lam., *P. thwaitseii* C. DC., *P. trineuron* Miq., *P. unguiculatum* Ruiz and Pav. and *P. zeylanicum* Miq., have been recorded. (Table I). In the genus *Piper* so far chromosome numbers of $2n=22, 24, 26, 28, 32, 36, 39, 48, 52, 60, 64, 65, 78, 80, 96, 104$ and c. 128 have been reported.

From the literature it is noticed that though the chromosome numbers do not follow a clear polyploid series, mostly multiples of 12 have been reported from North India and multiples of 13, from South India and Sri Lanka.

The strict arithmetic progression of chromosome numbers in some species and the presence of different chromosome numbers in other species indicated the significance of polyploidy in the evolution of different species of *Piper* (Mathew, 1958; Sharma and Bhattacharyya, 1959; Samuel and Bavappa, 1981).

A comparative study of several complements of chromosomes from both male and female plants of *P. longum* showed a pair of heteromorphic chromosomes. The consistent occurrence of this pair in all the somatic complements of the male plants examined, strongly suggested the presence of sex chromosome in this species (Mathew, 1958). According to him the male had XY type of sex chromosomes and the female, XX, the Y being longer than X.

CHEMICAL CONSTITUENTS

A number of species were investigated by various authors for the chemical contents. Some of the species investigated and the chemical constituents obtained are:

P. betle: Oil extract is found to contain phenols and terpene like compounds (Ghani and Sial, 1952), eugenol, cadinene, eugenol methyl ether, estragol, chavicol and caryophyllene. Leaves are found to contain enzyme diastase and catalase and vitamin A and C (Anonymous, 1969).

P. longum: Leaves subjected to chromatography over silica gel using soxhlet and petroleum ether gave

hentriacontane, hentriacontane-16-one, triacontanol and β -sitosterol (Manavalan and Singh, 1979). Triacontane, 22-23-dihydrostigmasterol, an uncharacterized steroid and two alkaloids, piperine and piperidine amide of 3, 4, 5-trimethoxycinnamic acid are reported by Atal and Banga (1962, 1963). Fruits have shown the presence of piplasterol, piperine and piplartine and a crystalline compound sesamine (Atal and Ojah, 1965; Atal, Girotra and Dhar, 1966). *P. longum* oil contains *n*-hexadecane, *n*-heptadecane, *n*-octadecane, *n*-nonadecane, *n*-eicosane, *n*-heneicosane, *a*-thujene, terpinolene, zingiberene, *p*-cymene, *p*-methoxy acetophenone, dihydrocarveol, phenethyl alcohol and two monocyclic sesquiterpenes. *Piplamul*, the dried roots and thicker parts of the stem, contain piperine, piplartine, triacontane, dihydrostigmasterol etc. New alkaloids like piperlongumine and piperlonguminine have also been isolated (Anonymous, 1969).

P. nigrum: Black pepper owes its characteristic pungency and aroma to its oleoresin content. The alkaloid piperine is considered to be the major constituent responsible for biting taste. Piperine is absent in leaves and stems. α -pinene, β -pinene, *dl*-limonene, 1- α -phellandrene, caryophyllene, dihydrocarveol, epoxydihydrocaryophyllene, piperonal, cryptone, phenylacetic acid, piperidine, citronellol are also observed in some samples of black pepper. Chavicine and pipertine are also reported in small amounts (Anonymous 1969). Two phenolic amides viz. *N*-*trans*-feruloyl tyranine and *N*-5-(4-hydroxyphenyl)-2E, 4E-pentadienoyl

piperidine (Nobuji, Inatani and Fuwa 1980) and four isobutyl amides viz., *N*-isobutyl-13-(3, 4-methylenedioxyphenyl)-2E, 4E, 12E-tridecatrienamide (Guineensin); *N*-isobutyl-2E, 4E 8Z-eicosatrienamide; *N*-isobutyl-2E, 4E-octadecadienamide and *N*-isobutyl-2E, 4E-decadienamide (pellitorine) are recently reported (Nobuji and Inatani, 1981). Three amides viz., (E, E)-*N*-(2-methylpropyl)-2, 4-decadienamide; (E, E, E)-13-(1, 3-benzodioxol-5-yl)-*N*-(2-methylpropyl)-2, 4, 12, tridecatrienamide and (E, E, E)-11-(1, 3-benzodioxol-5-yl)-*N*-(2-methylpropyl)-2, 4, 10-undecatrienamide (Su Helen and Horvat, 1981).

P. attenuatum: Column chromatographic study of the petroleum ether extract of the roots over neutral alumina furnished four amides viz., *N*-isobutyl-deca-*trans*-2-*trans*-4-dienamide; piperine, piperlonguminine and guineensine, an amide bearing striking similarity with sylvatine in physical and special properties (Dasgupta and Ray, 1979). Earlier Desai et al. (1975) isolated crotepoxide from this species.

P. sylvaticum: Banerji and co-workers have isolated sylvatin, 4', 7'-dimethoxy-5-hydroxy flavone (Banerji and Ghosh, 1973); aurantiamide acetate; sesamin (Banerji and Dhara, 1974; Banerji et al., 1979); piperine and piperlongumine (Banerji and Dhara, 1974); *N*-isobutyl-deca-*trans*-2-*trans*-4-dienamide; pipatine; 5-hydroxy-3', 4', 7'-trimethoxy flavone and 5-hydroxy-7-methoxy flavone (Banerji and Das, 1977a) and (+)-diaeudesmin (Banerji and Das, 1977a).

P. aurantiacum: Vanillic acid and *dl-N*-benzoylphenylalanine (Banerji et al., 1979), friedelin, *epi*-friedelinol, β -sitosterol, aurantiamide and aurantiamide acetate (Banerji and Das, 1975) and an aliphatic alcohol, (C₃₄H₇₀O₂) was also isolated (Banerji and Das, 1977b).

P. officinarum: Gupta, Atal and Gaiind (1972) isolated methyl piperate from the fruits. Gupta, Dhar and Atal (1976) reported *N*-isobutyl-trideca-13-(3, 4, methylenedioxyphenyl)-2, 4, 12-trienamide.

P. hookeri: Sitosterol was isolated by Desai et al. (1975) and a cyclohexane diepoxide (crotepoxide-I) by Singh (1969).

P. tuberculatum: Piplartine-dimer A, a dimer of pyridone alkaloid piplartine was isolated from the root bark.

P. hispidum Var. *obliquum*: contains 2', 3'-dihydroxy-4', 6'-dimethoxy- and 2'-hydroxy-3', 4', 6'-trimethoxy-chalcones; 6-hydroxy-5, 7-dimethoxy-, 8-hydroxy-5, 7-dimethoxy- and 5, 7, 8-trimethoxy-flavones; and 4-(5'-*n*-hexadecenyl)-phenol.

P. trichostachyon: Vig and Mahajan (1972) isolated *N*-pyrrolidinyloleic-*trans-2-trans-4*-dienamide. Singh, Dhar and Atal (1969) isolated an alkaloid, trichostachine.

P. brachystachyum: Caryophellene epoxide was isolated from the oil by Thappa et al. (1970).

P. peepuloides: An alkaloid, peepuloidin was isolated from this species by Atal, Moza and Pelter (1968) and *N*-isobutyl deca-*trans-2-trans-4* dienamide by Dhar and Atal (1967).

EVOLUTIONARY SIGNIFICANCE

The genus *Piper* shows extreme reduction in floral characters. Flower is achlamydous, ovary 1-celled and 1-ovuled, stigma sessile and ovule orthotropous. Saururaceae and Chloranthaceae also show such reduced reproductive structure. Engler and Diels (1889), Rendle (1925) and Hutchinson (1926) considered these three as distinct families. Bentham and Hooker (1880) clubbed Piperaceae and Saururaceae into a single family and considered Chloranthaceae as a separate family. Rousseau (1927) suggested amalgamation of these three families into a single family.

Piperaceae includes three genera viz., *Piper* Linn., *Peperomia* Ruiz. and Pav. and *Lepianthus* Raf. (= *Heckeria* Kun. = *Pothomorphe* Miq.). Separation of *Peperomia* into a separate family has been suggested by some taxonomists (Datta and Dasgupta, 1977a). The orthotropy and basilar position of the ovule in Piperaceae show its close affinity to Urticaceae, Loranthaceae, Polygoniaceae and even monocotyledonous family Araceae (Rendle, 1925). But in certain anatomical characters, it is related to Ranunculaceae (Datta and Dasgupta, 1977a). Rendle (1925) considered *Piper* as one of the most primitive dicot. Hallier (1912), Bessey (1915) and Hutchinson (1926) considered the family as an independent and terminal off-shoot

of direct Renalian ancestry (Lawrence, 1951). Metcalfe and Chalk (1950) considered wood of *Piper* and *Peperomia* more specialized than *Chloranthus*. On the contrary, Rousseau (1927) assumed that the genus *Piper* is the basic group from which *Chloranthus* is derived by minor modification and *Peperomia* by major modification indicating that *Chloranthus* is more specialised. Cytological and anatomical evidences indicate that *Peperomia* is more primitive than *Piper* (Datta and

Dasgupta, 1977a, b, c; Dasgupta and Datta, 1976). Among the five species studied by Datta and Dasgupta (1977c) the evolutionary advancement is considered to be in sequence of *P. magnificum*, *P. cubeba*, *P. longum*, *P. nigrum* and *P. betle*. Murthy (1956a, 1959b) and Datta and Dasgupta (1971, a, b, c,) favoured establishment of a separate family Peperomiaceae based on the evidences from comparative morphology, anatomy, embryology and vascular pattern.

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