DISCUSSION
Pedicularis elephantoides Benth. and P. pyramidata Royle are perennial species of parasitic Scrophulariaceae (like Orobanchaceae). Some genera are annual, with an occasional exception, such as Striga, Rhinanthus, Euphrasia, Melampyrum, and Orobanche. Others are predominantly or entirely perennial (Castilleja and Sophua; Williams, 1960; ) and Lathraea, Boschniakia and Conopholis (Kuijt, 1969). The occurrence of rhizomes is very uncommon in perennial species. Pedicularis canadensis and some others of the same genus reproduce vegetatively by means of rhizomes (Praim, 1891). This seems to be true also of Agalinis linifolia (Pennell, 1928); Bartsia, Tozzia, Lathraea (Hegi, 1907–1931), and possibly Aeginetia (Tiegi, 1952b). Alectra parasitica (Kau, 1961) has greatly swollen and branched squamate rhizomes.

The aerial stem is characterized by slenderness, though some Pedicularis species are somewhat fleshy. The fleshy condition seems to correspond to a more advanced feature associated with total parasitic nature and decrease in chlorophyll content (Kuijt, 1969).
The floral variability of parasitic figworts is difficult to convey (Kuijt, 1969). The flowers are generally bisexual and zygomorphic, although many Pedicularis flowers are almost fantastically twisted out of any symmetry. The calyx is usually greenish with the visual attraction of pollinators falling to the corolla or bracts. The corolla rarely approaches the actinomorphic condition as in Seymeria (Pennell, 1935), and falls short of it even in Gerardia and Harveya (Kuijt, 1969). Euphrasia has zygomorphic flowers and the same situation is more so in Castilleja and related genera—Melampyrum, Pedicularis (present study) and Rhinanthus (Kuijt, 1969).

In both the species of Pedicularis (P. elephantoides and P. pyramidata) the calyx and corolla are 5-lobed and gamopetalous. 4-5 lobed corollas are characteristic of other species of the genus. The corolla in both the species is pink. In P. elephantoides it develops a 2 cm. long beak and corolla tube in P. pyramidata is 10-15 mm long and narrow. Long tubular corollas have developed in some Newzealand Euphrasia (Kuijt, 1969). Chinese
species of *Pedicularis* attain a tube length of 11 cm (Li, 1948, 1949).

Stamens in *P. pyramidata* are attached in the middle part of corolla tube and the upper part of filaments is hairy. In *P. elephantoides* the stamens are attached at the top of corolla tube. The four stamens, in general, are implanted on petals, often very near the latter's base, and are of two different lengths. The anthers are basically two chambered, frequently having trigger-like spurs extending into the floral tube. The spurs must be pushed out of the way by pollinators (Kuijt, 1969) to cover the intruding animal with a shower of pollen. But no such spurs are present in *P. pyramidata* and *P. elephantoides*. The same effect is achieved in other ways in *Harveya* and *Hyobanche* of South Africa (Marloth, 1932).

Stamens are dorsifixed while in majority of the species the stamens are normally basifixed. Even versatile anthers are also known as in *Gerardia lanceolata* (Kuijt, 1969).

In *Pedicularis sudetica* (Schulten, 1975),
the petals are fused in the form of a long tube. The lower portion of the tube is cleft into 3 lobes while the upper portion forms an inflated helmet-like structure bearing anthers and stigma.

The parasitic Scrophulariaceae (fig-worts) are the only group of parasitic angiosperms in which variously divided leaves occur (Kuijt, 1969). The basal leaves of Seymeria, Pedicularis, and Gerardia (Pediculariaceae) are pinnatifid and have a fern-like appearance. Non-parasitic Scrophulariaceae have entire leaves, coarsely dentate, and even scale-like (Kuijt, 1969). The leaves which are part of the floral axis are often different from the lower vegetative ones.

With respect to the morphology of leaves in Scrophulariaceae, two opposite trends exist. The leaves become acropetally simplified towards the inflorescence tip so that most floral bracts are simple and narrowly lanceolate as in P. pyramidata and P. elephantoides. On the other hand, in some cases such as in Melampyrum (Kuijt, 1969) the floral bracts are deeply incised, whereas the basal foliage leaves are nearly entire and
linear in outline.

The complexity of venation is related to the variations in the leaf shape. Leaves of *Pedicularis* have the usual intricate dicotyledonous venation, with small, few celled glands or trichomes. In *P. elephantoides*, *P. pyramidata*, and in other species of the genus conspicuous hydathodes are present in leaf margins. These according to Kuijt, 1969 may bear a relation to the parasitic mode of life of these taxa.

The phyllotaxis in parasitic scrophs is mostly opposite. However, it varies from alternate to whorled condition in *P. elephantoides* and *P. pyramidata*, respectively. The shift from whorled to alternate status of the phyllotaxis is considered to be a feature of more advanced parasites such as *Harveya*, *Hyobanche*, *Alectra* etc. (Kuijt, 1969). But, the present investigation does not support this view because the two parasitic species of *Pedicularis* show both the types of phyllotaxis.
Regarding venation, the most remarkable feature of Pedicularis is the occurrence of hydatodes. Hydatodes and hydatode-like structures are found only in the leaves of desert plants like Anticharis (Varghese, 1966), and those of Euphrasia (Varghese, 1966) growing at high altitudes. The development of such structures seems to be an adaptation to mesic environments. According to Kuijt (1969) the condition may bear a relation to the plant's parasitic mode of life. But the accumulation of tracheids in members of Euphrasias (Varghese, 1966) either at the tip of lobules (Pedicularis) or at marginal serrations (Euphrasia), appears to be a consistent feature of the tribe. Hence it appears to be an important taxonomic criterion. A detailed investigation of this feature in other members of the tribe is necessary to reach a definite conclusion.

The diagnostic character of such features as epidermal and cuticular morphology has been amply demonstrated recently and the utility of such studies in taxonomy of angiosperms has been brought to light in different groups of plants (Stace, 1965; Uphof, 1962; Bhat and Kachroo, 1973).
Iriohomes are perhaps most often enlisted for systematic comparison because of their variety, almost universal presence in angiosperms, ease of preparation and close relation of variation patterns in relation to the taxonomic system (Akhbar and Kachroo, 1981).

Various types of trichomes occur on different plant organs and their taxonomic significance has been emphasized by several workers especially with respect of Compositae (Carlquist, 1958, 1959; Ramayya, 1963); Icacinaceae (Heintzelman and Howard, 1948); Labiatae (Mathur, 1961); Lentibulariaceae (Farooq and Siddiqui, 1966) and Scrophulariaceae (Kaur, 1968; Kapoor, 1975).

The pattern in which the trichomes are distributed over various parts of the plant and in different kinds of plants, differ widely. The character of this pattern is partly determined by the specific nature of the plant, and partly by the influence of external circumstances (Uphof, 1962).

In Pedicularis elephantoides and P. pyramidalis, two well defined trichome systems, namely, uniseriate multicellular hairs and glandular
hairs with capitate heads are met with. Moreover, the trichomes are full of granular material in early stages but there is a gradual loss of grains as the development reaches its climax. Weiss (1867) pointed to the presence of starch and tannin in the secretory cells in some Scrophs e.g. Antirrhinum and Pentstemon (Uphof, 1962). Moreover, the stigmatic papillae of various Scrophulariaceae show secretory activity (Uphof, 1962).

Allan (1924) conducted experiments to induce hydathode formation in New Zealand Scrophulariaceae (Veronica amplexicaulis) and succeeded in changing the xerophytic habit of this plant. Moreover, he obtained a considerable increase in the number of capitate hairs. The capitate hairs are provided with a two-celled apical part (2 to 4-celled in P. elephantoides and P. pyramidata), and belong to a type that is very common in the Scrophulariaceae.

According to Metcalf and Chalk (1950), the hairs in Scrophulariaceae are often numerous and exhibit a considerable diversity of forms. The non-glandular hairs are mostly uni-cellular or uniseriate.
The simple hairs are calcified in _Euphrasia_, or contain structures resembling cystoliths in species of _Melampyrum_ and _Odontites_. Club-shaped bodies resembling cystoliths also occur in _Craterostigma_. Trichomes and associated cells are silicified in _Melasma hispidum_ Benth. Branched multicellular trichomes have been recorded in _Leucophyllum_, _Paulownia_ and _Verbascum_. Glandular hairs with unicellular or uniseriate stalks of varying length and heads usually composed of 1–4 cells have been reported in genera like _Alonsoa_, _Antirrhinum_, _Bartsia_, _Calceolaria_, _Celsia_, _Chelone_, _Digitalis_, _Erinus_, _Euphrasia_, _Gratiola_, _Limosella_, _Linaria_, _Mazus_, _Melampyrum_, _Mimulus_, _Nemesia_, _Rhinanthus_, _Pedicularis_, _Scoparia_ and others as _Scrophularia_, _Torenia_, _Tozzia_, _Verbascum_ and _Veronica_ (Adamson, 1912). Peltate glands occur in species of the genera like _Bartsia_, _Euphrasia_, _Melampyrum_, _Pedicularis_, _Rhinanthus_ and _Tozzia_ (Solereder, 1908). Peltate glands in _Castilleja_, _Lamourouxia_, _Orthocarpus_, porous glands in _Pedicularis_, and extrafloral nectaries in _Melampyrum_ have been recorded by Federowicz (1915).

However, the developmental and distribu-
tional patterns of various trichome types in various uninvestigated species of *Pedicularis* will provide opportunities for an overall taxonomic revision of this large genus of the family.

Scrophulariaceae is a widely distributed family of herbs including some shrubs and a few trees. *Pedicularis elephantoides* Benth. and *P. pyramidata* Royle are perennial herbs. In both the species, root develops cork. Its formation is rare in the family and was reported in *Sophronanthe* by Holm (1924). Cork is lacking in the stem of *Pedicularis* and it is often absent from herbaceous species. However, it may arise in pericyclic region in *Leucophyllum* (Metcalf and Chalk, 1950) and in sub-epidermal zone in genera like *Veronica* (Gray, 1937). As in other investigated genera like *Melampyrum* and *Rhinanthus* (Metcalf and Chalk, 1950), the cortex of *Pedicularis* contains collenchyma with intercellular spaces. Endodermis, which is conspicuous, is absent in *Pedicularis* (present study). According to Metcalf and Chalk (1950), the presence or absence of endodermis is not reliable as a diagnostic character. Pericycle in *Pedicularis elephantoides* Benth. and *P. pyramidata* Royle
occurs in isolated strands as in other investigated genera like Alonsoa, Antirrhinum, Linaria and Nemesia. It may even be absent from or very rare in Euphrasia, Mimulus, Pedicularis and Rhinanthus; may form a loose or dense ring in species of Celsia, Digitalis and Bartsia; and may occur in bands in species of Chelone and Linaria (Metcalf and Chalk, 1950).

Vessel arrangement in Scrophulariaceae is variable even within the same genus. In Pedicularis they are either solitary and in short radial rows, fairly evenly distributed throughout the wood (P. pyramidata) or numerous and crowded, in radial rows (P. elephantoides). The former condition is also present in genera like Diascia and the latter arrangement is characteristic of such Scrophs as Digitalis purpurea Linn., Gratiola officinalis and Paulownia (Metcalf and Chalk, 1950). On the basis of the nature of xylem, Metcalf and Chalk (1950) classified the investigated species of Scrophulariaceae into 11 categories.

Petiole in Pedicularis is winged with
single median crescent shaped ( _P. pyramidata_ ) and arch shaped ( _P. elephantoides_ ) strand, together with accessory bundles in the wings. The observations conform to the situations occurring in other investigated genera of the family (Metcalf and Chalk, 1950).

Leaf of Scrophulariaceae is very variable ranging from dorsiventral to isobilateral condition. Sometimes it is composed of a homogeneous mass of isodiametric cells. While in _P. pyramidata_ it is dorsiventral, in _P. elephantoides_ it is dorsiventral, but homogeneous at certain places.

Presence of the tetrasporangiate anthers is the characteristic feature of the family Scrophulariaceae. Some members show reduction and sterilization of their sporangia. In _Calceolaria_ (Varghese, 1964) the connective is extended laterally bearing two fertile sporangia and two sterile locules. In _Striga_ (Tiagi, 1956) and _Sopubia_ (Varghese, 1964) anther is bilocular. The anther wall is usually made up of an epidermis, fibrous endothecium, 1/2 middle layers and a glandular tapetum. The study on _Pedicularis elephantoides_ and _P. pyramidata_ has
revealed a single middle layer. *Torenia* and *Lindernia* (Varghese, 1964) possess a few layers of cells in between the epidermis and endothecium. These subepidermal layers in *Lindernia* contain deeply staining granules. A multilayered endothecium has been reported in *Calceolaria* and *Chelone* by Varghese (1964) and Arekal (1963 b), respectively.

The tapetal cells in the family are uninucleate or sometimes multinucleate (Raju, 1973 a,b) and the nuclei may fuse often. In *Pedicularis elephantoides* and *P. pyramidata* tapetal cells are uninucleate. Moreover, the tapetum becomes bilayered at some places, more so in *Pedicularis pyramidata*. There are reports of occasional periclinal divisions in the tapetal cells which result in its becoming irregularly 2-layered. This is not a consistent feature in any taxon and it appears to be the expression of a latent potentiality to periclinal divisions which is possessed by all parietal cells (Davis, 1966). In *Asclepiadaceae*, a 2-3 layered tapetum occurs in several genera and in *Calotropis* it becomes multilayered. A multilayered tapetum has also been reported in *Anticharis linearis* (Joshi and Varghese, 1963).
The occurrence of a multilayered tapetum has been regarded as an abnormality, having an adverse effect on the development of pollen (Vasil, 1957 a,b; 1962). Steil (1949) reported such a situation in *Lilium longiflorum* and attributed it to some enzymatic disturbances. Presence of the multilayered tapetum may most probably be attributed to the parasitic nature of the *Pedicularis* species.

In both the species of *Pedicularis* under investigation, the size of the tapetal cells is uniform as compared to some other members of the family where the tapetal cells show dimorphism (Vijayaraghavan and Ratnaparkhi, 1973). Apart from Scrophulariaceae to which *Pedicularis* belongs, the families Acanthaceae and Labiatae also contain species with dimorphic tapetal cells (Maheshwari, 1950). Little is known, however, of the manner of development of the two populations of tapetal cells in these plant species (Vijayaraghavan and Ratnaparkhi, 1973).

The anther tapetum of angiosperms is presumed to be the tissue that serves the nutrition of the microsporogenous cells during the development of the latter into the microspores (Periasamy and
Swamy (1960), Ubisch (1927), Johri and Liagi (1952), Johri and Shatnagar (1955) and Maneshwari (1950) have stated that tapetum provides the material for the development of the exine. Evidences are available regarding the nutritional role of the tapetum in pollen formation and have mainly come from histochemical studies. In majority of the plants belonging to Acanthaceae (related to Scrophulariaceae) and other bicarpellatae (Maheshwari, 1950), the tapetal cells on the inner surface elongate radially to a marked extent in comparison to those on the outer surface. In Torenia asiatica (Periasamy and Parameshwaran, 1965), the tapetum on the outer surface consists of a single layer of regularly aligned cells, but on the inner surface it comprises more than one layer of irregularly arranged cells.

The mode of wall formation (cytokinesis) in the microspore tetrads is a very constant feature in angiosperms and is considered to have some taxonomic value (Maheshwari, 1950). The microspore mother cells undergo simultaneous type of cytokinesis and tetrahedral, rarely isobilateral or decussate
tetrads are characteristic of the family Scrophulariaceae. In Pedicularis species (present material), tetrahedral and irregularly iso-bilateral tetrads have been observed. At the time of dehiscence, the adjacent microsporangia coalesce. Generally the dehiscence takes place by means of a longitudinal slit (Kuijt, 1969). But in some members of the family like Seymeria (Pennell, 1925) the dehiscence is poricidal. In Calceolaria (Arekal and Raju, 1971), the microsporangia do not coalesce.

Pollen grains are shed as monads, sometimes in tetrads (Anticharis). They are tricolpate in Torenia, tricolporate in majority of Scrophulariaceae, mono / 2 - syncolpate (oblate to prolate spheroidal) in Pedicularis elephantoides and prolate spheroidal in P. pyramidata.

The megasporangium together with its protective coats, the integuments, is called ovule (Bhojwani and Bhatnagar, 1975). Excluding the Balanophoraceae and Loranthaceae, where ovules as such are not formed, information has been derived from 315 families out of which 266 (i.e. 84%) are
dicotyledonous (Davis, 1966). Ovule morphology is constant in 248 families, of which 204 are characterised by the anatropous form, and among these 84.6% are dicotyledonous. Orthotropous ovules are typical of 20 families, 14 being dicotyledonous, and hemianatropous ovules occur exclusively in 13 families (Davis, 1966).

The ovules in Scrophulariaceae range from anatropous, hemianatropous to campylotropous. In Pedicularis elephantoides and P. pyramidalata each ovule is unitegmic, tenuinucellate and campylotropous born on axile placenta in bicarpellary syncarpous ovary, on short stalks. The inner epidermis of the integument gets modified into a typical endothelium. The same situation has been observed in other species of Pedicularis (Berg, 1954).

In Euphrasia arctica (Arekal, 1963a), a genus related to Pedicularis, however, the ovules are hemi-anatropous with axile placentation at the base of the ovary shifting to parietal position in the upper region. In Orthocarpus luteus (Arekal, 1963a) the ovules are campylotropous and the lower pair is hemianatropous. Nevertheless, in both cases
the ovules are tenuinucellate with massive integument. According to Maheshwari (1950), the unitegmic condition may arise by the elimination of one integument or the fusion of two separate primordia. Reed (1955) writes "there seems to be a correlation between the number of integuments present and the degree of semi-parasitism to root parasitism in the tribes of the Olacaceae". According to Bocquet (1959) Orthotropous and anatropous ovules are the basic types and all others are derived.

The female archesporium in P. elephantoides and P. pyramidalata is multicelled. According to Schnarf (1929) the female archesporium in Scrophulariaceae is one celled indicating thereby that a multicelled condition is an abnormal feature or a variation. Berg (1954) reported a multicelled female archesporium in P. silvatica where the number of archesporial cells varies from ovule to ovule comprising 2 - 3 cells per ovule. Jonsson (1879-80) observed a great number of megaspore mother cells in P. oederi, P. lapponica and P. silvatica supported by Schmid (1906) in P. palustris. Of 3 megaspore mother cells in Euphrasia arctica (Arekal, 1963 a), only a single megaspore mother
cell differentiates. In other related genera such as *Melampyrum lineare* and *Orthocarpus luteus* (Arekal, 1963 a), a single megaspore mother cell differentiates leading to the formation of embryo sac.

Out of the multicelled female archesporium, ultimately only one cell takes the lead; the rest degenerate and get resorbed. In exceptional cases (Berg, 1954), two archesporial cells may develop in the same ovule. In *Pedicularis silvatica* (Berg, 1954), two archesporial cells were observed to form two linear tetrads in a row in a single instance in an abnormal ovule.

In *Pedicularis* species (present study), it is the chalazal megaspore of the linear tetrad which is functional. According to Berg (1954), the three other megaspores do not degenerate simultaneously. The symptoms are first noticeable in the spore which is originally the smallest, then in the second smallest and finally in the second largest. The factors responsible for this selective degeneration are explained by Berg (1954) who says: "It has been assumed that such selectivity may be due to the position of the megaspore in relation to the flow of nutritive materials. Nutrient supply is
scanty and goes mostly through the chalaza. The spores nearest to chalaza, thus, has an easy access to the nutrition supply and, therefore, grows ahead of the others." However, in *Pedicularis silvatica* (Berg, 1954) the chalazal megaspore sometimes degenerates while another develops. Berg attributes it to an extra amount of nutrition available from sterile archesporial cells. This view was initially put forth by Palm (1915). Another factor which Berg adds is the initial size of the megaspores. The megaspore with the greatest surface area absorbs nutrition more easily and is, therefore, successful. This explanation appears to be the decisive factor in selective germination of the functional megaspore in *Pedicularis* species with multicelled archesporium.

The embryo sac is monosporic, 8-nucleate (*Polygonum* type; Maheshwari, 1950). At four nucleate stage, the embryo sac of *Pedicularis* species under investigation breaks the nucellar epidermis and protrudes to become extramicropylar. This holds true of other species of *Pedicularis* (Berg, 1954). In the family Scrophulariaceae, there are many instances
where such a situation occurs. In *Pentaphragma horsfieldii* (Kapil and Vijayaraghavan, 1962) and *Torenia violacea* (Yamazaki, 1954 a), the tip of the embryo sac protrudes beyond the micropyle even at the four nucleate stage. In *Torenia*, the upper part comes to lie beside the funiculus (Yamazaki, 1954 a) at maturity.

In *Acanthaceae* (related to *Scrophulariaceae*) a schizogenous cavity develops in the funicular region of the ovule of *Justicia simplex* (Mohan Ram and Sengal, 1956) and the tip of the 4-nucleate embryo sac extends into this cavity. The caecum later functions as micropylar haustorium. In *Dipteracanthus patulus* (Maheshwari and Negi, 1955) and *Elytraria acaulis* (Johri and Singh, 1959) the tip of the embryo sac extends reaching upto the ovular hypodermis especially in *Elytraria*. The situation obtained in the present investigation is in conformity with observations on *Euphrasia* and *Orthocarpus* (Schmid, 1906; Wurdinger, 1910 and Arekal, 1963 a); as also on *Pedicularis* (Berg, 1954; Iyengar, 1942 c; Schmid, 1906) and *Lathraea* (Glisic, 1932). The situation is also characteristic of *Alectrolophus* and *Tozzia* (Schmid, 1906). In *Melampyrum lineare*
(Arekal, 1963a), however, the female gametophyte extends towards the chalaza, destroying the cells in that region. Schmid (1906), had also noted this feature earlier in *Melampyrum silvaticum* and *M. pratense*, attributing it to the behaviour of an ingrowth of the micropylar tissue plug. The tubular extensions of the embryo sac near micropylar region is not seen in *P. elephantoides*. However, these exist in *P. pyramidata* and have been reported also in *Melampyrum* by Arekal (1963a).

The mature embryo sac is long and narrow. It is expanded near micropylar end with a few protuberances in *Pedicularis pyramidata*. The chalazal end in both the investigated species is tapering. Similar condition has been reported by Schmid (1906) and Berg (1954) in other species of *Pedicularis*. According to Hofmeister (1858a) the cell walls in the egg apparatus contain cellulose.

The antipodal cells are short living and degenerate soon after their formation. Balicka-Iwanowska (1899) says that the antipodal cells of *Pedicularis palustris* are: "tres pronounces et persistent jusque a la formation complete due haustorin..."
chalazien". However, this does not appear to be true in Pedicularis species. According to Schmid (1906), "... Sind aber nur von kurzer existent und gehen bald nach der Betruchlung zu Grunde..."

Ontogenetic variability of the embryo sac development in the same species is rather rare (Ratnaparkhi, 1973). But the co-existence of Polygonum (Monosporic) and Allium (bisporic) type of embryo sac developments has been reported in Tridax trilobeta of Compositae (Hjelmqvist, 1951), Ehertia laevis of Boraginaceae (Johri and Vasil, 1956) and in Tillinia grandiflora of Saxifragaceae (Ratnaparkhi, 1973). In Scrophulariaceae to which Pedicularis belongs, such a situation has been reported in Alectra thomsonii (Ratnaparkhi, 1973) and Scrophularia himalensis (Natesh and Bhandari, 1975). The mode of female gametophyte development in Calceolaria mexicana (Calceolariaceae) is of Polygonum type (Arekal and Raju, 1971) as in Pedicularis.

Pedicularis elephantoides and P. pyramidata possess a typical endothelium. It is formed from the inner epidermis of the integument. The cells are
larger in size, with denser consistency and contain large size nuclei. As the development proceeds, the endothelium becomes restricted to only chalazal region of the embryo sac. Endothelium is a characteristic feature in as many as 57 families (Davis, 1966). In certain families e.g. Acanthaceae (closely related to Scrophulariaceae) it is formed only in certain members. Characteristic feature of only tenuinecellate ovules (as in the present material), the endothelium is used as a taxonomic character at family level in 54 families (Davis, 1966).

Endothelium is absent around chalazal haustorium in Chaenorrhinum minus (Arekal, 1963b). Cook (1924) mistook the endothelium of Linaria vulgaris for a persistent layer of nucellar cells around the endosperm. Bachmann (1882) studied the course of endothelial cells and thickenings of their walls in some species of Linaria (Scrophulariaceae). In Celsia coromandeliana (Kapoor and Vijayaraghavan, 1975-76), the integumentary cells bring about the rumination of endosperm by undergoing irregular ingrowth. In Mimulus trigrinus and Torenia fournieri (Guilford and Fisk, 1952) a chalazal hypostase
is present. Such a structure has been reported also for other members of the family (Balicka-Iwanowska, 1899; Sevenssen, 1928; and Iyengar, 1940a-c, 1941).

Iyengar (1941) observed that in some members of the Scrophulariaceae the endothelium is a repository of food material during pre-fertilization stages. Its subsequent behaviour varies, however, in many plants (Kapil and Vasil, 1963). Its cells either lose contents or enlarge and show denser cytoplasmic contents associated with larger nuclei as in Celsia, Vandellia, Verbasum and Torenia. This holds true for the Pedicularis species also. In Centranthera hispida (Iyengar, 1942c), these cells in the chalazal region enlarge and seem to be haustorial in function.

The epidermal origin of the integumentary tapetum noted in Pedicularis pyramidata and P. elephantoides corresponds to Euphrasia arctica, Orthocarpus luteus and nearly all the investigated species of the tribe (Arekal, 1963a). In Melampyrum lineare (Arekal, 1963a) it is
hypodermal while in *Melampyrum nemerosum* and other species (Balicka-Iwanowska, 1899) it was assumed to have arisen from the conversion of the inner epidermis of the integument. Schmid (1906), however, did observe and illustrated a tapetum such as found in *Melampyrum lineare*. He maintained that it belonged to the inner epidermis of the integument. Moreover, in *Pedicularis* a tissue plug develops from the micropylar summit of the integument and grows down the micropylar canal, finally surrounding the nucellus in the young ovule. There is no formation of a special tissue plug at any stage in *M. silvaticum* and *M. pratense* (Schmid, 1906).

The endothelium in *Pedicularis palustris* (Steffen - 1956) is 32-ploid by endomitosis. Such a condition is reminiscent of polyploidy in anther tapetum (Witkus, 1945).

Endosperm has been reasonably recognised as an important nutritive tissue for the differentiation and development of the embryo (White, 1950). Recent researches have shown that endosperm plays a significant role in the growth and differentiation of the embryo. Attention is being paid to a study of its physiology and cytology. The culture of
endosperm on artificial media, isolation of endosperm nuclei for culturing other plant organs, and chemical analyses of the endosperm are some of the promising lines of approach for the elucidation of endosperm physiology. Of importance also are cytogenetical investigations concerned with the causes of hybrid seed collapse (Chopra and Sachar, 1963).

The study of the development of endosperm in the family Scrophulariaceae dates from the year 1849 when Tulasne made his classical observations. Since then a large number of works (Hofmeister, 1859; Balicka-Iwanowska, 1899; Schmid, 1906; Glisic, 1932; Srinath, 1934, 1940; Iyengar, 1937, 1939 a-c, 1940 a-c, 1941, 1942 a-c; Raghavan and his co-workers, 1941 a, b; Grete, 1948, 1949, 1950 a-c, 1952-54 a-b, 1958 and Yamazaki, 1953 a, 1954 a-b, 1957 a) have also contributed to our knowledge of the endosperm in Scrophulariaceae. Samuelsson's work in 1913 followed by those of Schnarf (1929, 1931), Glisic (1932, 1933, 1937), Iyengar (1947) and Grete (1951, 1955 a) have thrown light on the nature of the endosperm and its haustorial processes. They have also indicated
phylogenetic relationships between the different genera of Scrophulariaceae. Yamazaki (1953a, b, 1954a-b, 1957a-b) worked extensively on several genera of Scrophulariaceae and established phylogenetic relationships and affinities in the different genera on the basis of morphological and embryological characters.

The formation of a cellular type of endosperm is characteristic of the family Scrophulariaceae (Banerji, 1961). The first division of the endosperm in all the plants so far investigated is transverse leading to the formation of a micropylar and a chalazal chamber. In Pedicularis elephantoides and P. pyramidalata also the first division is transverse. Next division is vertical in the upper cell followed by a transverse one in both. In this way two longitudinal tiers of 2 cells each are formed. Out of these, the lower 2 cells act as main endosperm initials while the upper two act as micropylar haustorial initials.

The micropylar initials give rise to a four nucleate micropylar haustorium while the main
endosperm initials form the storage endosperm.

In Scrophulariaceae, the second division in the endosperm is vertical with the exceptions of some related genera like Melampyrum, Euphrasia and Tozzia (Hofmeister, 1859; Schacht, 1863; Schmid, 1906; Lundqvist, 1915; Iyengar, 1942c). Similar sequential division is reported in other members of the family such as Alonsoa, Sopubia, Vandellia, Bonnava and Illysanthes (Iyengar, 1937, 1940a-c).

In Angelonia (Srinivasan, 1940) and Nemesia (Crete, 1950a,b). However, the sequence is altogether different. In the former, all the early divisions are said to be transverse, and in the latter, the microphylar chamber precociously differentiates into a uninucleate haustorium instead of undergoing any further divisions. In Pedicularis elephantoides and P. pyramidata, there were seen some instances where all the early divisions in the endosperm were transverse. Schmid (1906), however, recorded the occurrence of the free nuclear endosperm in a single instance in Pedicularis foliosa.
The chalazal haustorium in *Pedicularis elephantoides* and *P. pyramidata* is 2-nucleate. The structure of this haustorium is very variable in different species of the family ranging from a single uni-nucleate, or binucleate or tetra-nucleate cell to two or four uninucleate juxtaposed cells (Banerji, 1961). In *Gratiola* (Glisic, 1933; Yamazaki, 1953b), these cells, however, are superposed. The haustorium is also not equally aggressive in different members of the family (Banerji, 1961). In *Lindenbergia indica* (Pal, 1956) the haustorium is composed of a uninucleate cell while in *Mazus japonicus* (Pal, 1958) there are two such cells which are later converted into a two-nucleate cell by the dissolution of the common vertical wall between them.

Single celled uninucleate chalazal haustorium has also been reported in *Torenia* (Balicek - Iwanowska, 1899; Iyengar, 1941; Guilford and Fisk, 1952); *Limosella* (Samuelsson, 1913; Schnarf, 1925; Sevenssen, 1928); *Lathraea* (Glisic, 1932); *Limnophila* (Iyengar, 1939b); *Moniera* and *Bacapa* (Safeeulla and Govindu, 1949,
The chalazal haustorium consisting of two uni-nucleate cells, later becoming bi-nucleate, occur in *Mazus japonicus*, *Alonsoa*, *Sopubia*, *Bonnaya* and *Vandellia* (Iyengar, 1937, 1940a-c; Srinivasan, 1940).

The micropylar haustorium of *Pedicularis elephantoides* and *P. pyramidata* is 4 nucleate. It is formed from the micropylar haustorial initials which get differentiated after the second division in the micropylar chamber. This is quite contrary to Schmid's (1906) finding, where it has been reported to get differentiated precociously as in *Nemesia* and *Ellisiopyllum* (Schmid, 1906; Iyengar, 1942c; Crete, 1950a-b; Yamazaki, 1957a).

The micropylar haustorium, like the chalazal one, differs widely in its structure as well as in the degree of aggressiveness in different species of the family. In *Pedicularis*
species (present study) the same shows variations in shape and degree of ramification, particularly in Pedicularis elephantoides.

The occurrence of lateral tubular extensions from the micropylar haustorium in Pedicularis also holds true for other investigated genera of the tribe Rhamnaceae like Euphrasia (Schmid, 1906; Arekal, 1963 a; Wurdinger, 1910) and Tozzia (Schmid, 1906). Although the haustorium is 4 nucleate usually, in Euphrasia arctica (Arekal, 1963 a) a 2-nucleate condition occurs sometimes.

By way of contrast, in Orthocarpus luteus (Arekal, 1963 a) and in Alectrolophus (Schmid, 1906) no lateral extensions occur. Moreover, the haustorium remains two-nucleate unlike Pedicularis (Iyengar, 1942 c; Schmid, 1906; Steffen, 1956). In species of Pedicularis under present investigation, one of the lateral extensions enlarges and enters into the funicular tissue as in Melampyrum lineare (Arekal, 1963 a), M. nemerosum (Balicka-Iwanowska, 1893), M. silvaticum, M. pratense (Schmid, 1906) and Striga (Tiagi, 1956).

However, only two tubes were observed in the last two species.
The presence of a uni-nucleate and unicellular (chalazal or micropylar) haustorium is regarded as a highly advanced feature (Arekal, 1963a). Transitional species connect them to so-called primitive multicellular haustorium observed in *Verbascum* (Håkansson, 1926; Soueges, 1935; Iyengar, 1942a) and *Chelone* (Arekal, 1962). The micropylar and chalazal haustoria are four-celled, uni-nucleate, unbranched and least aggressive in *Celsia coromandeliana* (Kapoor and Vijayaraghavan, 1976). But, the absence of chalazal haustorium in *Nemesia* (Crete, 1950a-b), and, again the absence of micropylar haustorium in *Linaria genistaefolia* (Perisidsky, 1934) and *Chaenorrhinum minus* (Arekal, 1963c) present some difficulties (Arekal, 1963a).

In 32 families of dicotyledons, both micropylar and chalazal haustoria are present. Included in these are *Acanthaceae* and *Epacridaceae* in which certain members possess only a micropylar haustorium, and *Bignoniaceae* where presence of a chalazal haustorium is the usual condition (Davis, 1966).
Scrophulariaceae is the most variable family: although terminal haustoria (chalazal and micropylar) are usually formed, yet it is the chalazal one only which is present in Chaenorhinum minus and Linaria genistaefolia. Haustorial development is absent in some genera of the family (Davis, 1966).

In Pedicularis elephantoides and P. pyramidata the endosperm on micropylar and chalazal ends cuts off a densely staining group of small cells. These may be regarded as 'secondary micropylar' and 'secondary chalazal' haustoria. Srinivasan (1946) also considered this group of cells to be a secondary haustorium at the chalazal end in Striga. Tiagi (1956) regards this tissue to be conductive in function. The formation of a group of small cells, rich in cytoplasm, by endosperm tissue at one or both ends (i.e. chalazal and micropylar) just below the haustoria has been recorded in many members of the family (Mitchell, 1915; Glisic, 1933; Souejes, 1935; Iyengar, 1937, 1939 a-b, 1940 a-c, 1941, 1942 a-c; Srinath, 1940; Guilford and Fisk, 1952; Crete, 1953; Yamazaki, 1953 b, 1954 b.
'Secondary haustorium' in *Linaria cymbalaria* (Balicza-Iwanowska, 1899) and 'cutis forming cells' in *Pedicularis silvatica* (Berg, 1954) are also possibly identical in nature (Banerji, 1961). In *Lindenbergia indica* (Pal, 1958), however, these cells are absent at the chalazal end. At the micropylar end of the endosperm of *L. indica* and *Mazus japonicus* (Banerji, 1961), these endosperm cells become further specialized. Banerji (1961) has presented a comprehensive account on the evolutionary tendencies in the development of endosperm haustoria in Scrophulariaceae on the basis of: a. sequence of early divisions in endosperm; b. occurrence and behaviour of the partition walls (if any) in the haustoria; c. number of cell or cells and/or nuclei in the haustoria, and d. plane of wall formation (if multicellular), in the haustoria.

Observations of Berg (1954) on *Pedicularis silvatica* seem to invalidate the conception of 'Pedicularis type' (as proposed by Glisic)
of endosperm formation. He clearly demonstrated the formation of a vertical wall in the micropylar chamber and suggested that interpretations were possibly erroneous due to several reasons as has already been admitted by Schmid,(1906). The present observations support this view.

The presence of endosperm haustoria, as such, is probably an expression of convergent evolution and, consequently, has little or no taxonomic significance. On the other hand, details of the origin and formation of haustoria are probably consistent within taxa.

Out of the two investigated species, Pedicularis pyramidata alone has shown the development of suspensor haustorium. According to Maheshwari(1950) the suspensor cells show an increase in size or give rise to prominent haustorial structures which penetrate between the cells of the endosperm and encroach upon the surrounding tissues of the ovule.

The discovery of suspensor haustoria dates back to the year 1658 when Hofmeister showed their occurrence in some members of the family
Eubiaceae. Further details of these haustoria have been given by Lloyd (1902) and Soueges (1925). According to Lloyd, "the function of the suspensor in these forms is, therefore, not only to bring the embryo into a favourable position with relation to food supply in a mechanical sense, but to act as a temporary embryonic root". However, Fagerlind (1937) states that the suspensor cells soon lose their connection with the main body of the haustorium and occur merely as islands within the endosperm. Moreover, according to him they degenerate sometimes even before the connection is lost.

The occurrence of a suspensor haustorium in P. pyramidata is the first record of this kind in the genus in particular and in the family Scrophulariaceae in general. The structure has been recorded in a variety of angiospermic families since its discovery in Rubiaceae by Hofmeister (1858 b). More information is now available about their occurrence in many angiospermic families like Halorrhagidaceae (Stolt, 1926; Soueges, 1940), in Fumariaceae (Soueges, 1943 a, b; 1946 a-b), Crassulaceae (Mauritzon, 1933), Tropaeolaceae (Walker, 1947) and Orchidaceae (Swamy, 1949).
Fruits of scrophulariaceae are capsules, opening in various ways (Weberbauer, 1901). Sutures may develop at the locules or at the septa of the fruit, and reach down to varying extent (Kuijt, 1969). In Pedicularis species, at the time of dehiscence, sutures develop at the septa and reach far below the middle of the capsule. In Rhinanthus (Kuijt, 1969) only the apex opens; so the large seeds stay in the capsule for a long time. The capsule opens up on wetting in Striga; it is pushed by growing seeds in Melampyrum silvaticum (Kuijt, 1969). In Lathraea the seeds are violently expelled (Becxv. Mannagetta, 1930).

The average seed size varies up to 4 mm in Pedicularis pyramidata and P. elephantoides. Seeds are ovate - acute at both ends. In general the seed size in Rhinanthae ranges from about 0.3 mm (Striga, Orobanche) to 5 mm (Rhinanthus, and Melampyrum arvense; Kuijt, 1969). On average basis, the investigated species of Pedicularis produce about 15 seeds per capsule. There is a tremendous variation in the number
of seeds produced per capsule in Rhinantheae.
Some New Zealand species of *Euphrasia* have no
more than two seeds per flower (Du Rietz, 1931).
In *Melampyrum*, *Pedicularis* and *Rhinanthus* the
number is only slightly larger (Tiaigi, 1966).
Beyond this point there appears a relation
between the number and size of seeds per flower,
and the degree of dependence on the host (Kuijt, 1969).
At any rate, *Striga*, one of the most advanced
'fig worts', produces minute seeds in great
numbers (Kuijt, 1969). The seeds of all the
members of Rhinantheae have endosperm, enclosing
a small embryo.

The seeds of *Pedicularis* contain a
characteristic elaiosome which acts as seed
disjuncteur. Some authors consider it synonymous
with caruncle or strophiole (Netolitzky, 1926).
Elaiosomes have been described for other investigated
species of *Pedicularis* (Berg, 1954). This peculiar
structure has also been described in a number of
plants belonging to families Amaryllidaceae,
Aristolochiaceae, Juncaceae, Papaveraceae,
Resedaceae and Violaceae (Sernander, 1906).
In *Pedicularis* species under report, the seed functions as a dispersal unit. This holds true in other investigated species of the genus (Berg, 1954). The elaiosome of *Pedicularis* is formed from an endosperm haustorium while the other elaiosomes are formed from the seed coat, the raphe, the funicle or parts of the placenta (Berg, 1954). Phylogenetically, this organ primarily performed a haustorial function, the elaiosome function was taken up secondarily (Berg, 1954). According to him "the elaiosome of *Pedicularis silvatica* might be regarded as an 'intelligent' exploitation of a potentiality. It is a new example of an organ which consequently fulfils two quite different functions".

Plants dispersed by ants have a small and reduced number of seeds in each capsule (Sernander, 1906). The capsule of *P. elephantoides* and *P. pyramidalis* contains an average of 15 seeds per capsule as compared to the capsule of *P. silvatica* with an average of 8 seeds in each locule.
Lange, 1870 - 71). It is a high figure compared to the related myrmecochorous Melampyrum and Veronica species. The former have only 1 - 2 seeds in each locule (Nordhagen, 1940), the latter 1 - 6 (Sernander, 1906). The 32 species of Pedicularis examined by Lange (1870 - 71), contained from 6 to 20 seeds while P. palustris, has an average of 10 - 12 per capsule locule. The reduction in seed number is often accompanied by an increase in the size of the remaining seeds. The ant dispersed plants often have larger seeds than their non-myrmecochorous relatives (Sernander, 1906). The seeds of Pedicularis silvatica (Berg, 1954), however, are among the smallest in the whole genus. According to Groenlund (1870-71), the seeds get detached before the opening of the capsule due to the formation of abscission layer in the funicle. The elaiosome also helps as a lever (Berg, 1954). Myrmecochorous diaspores are particularly well equipped with seed disjunctors (Sernander, 1927), and the mature seeds are set free very quickly. The seeds very rarely remain
Capsules of myrmecochores usually are marked by signs of degeneration and alteration. The amount of mechanical tissue in the wall is often small and reduced, the opening mechanism is lost, and the capsules open because of the pressure caused by the large sized seeds e.g. *Melampyrum silvaticum* L. (Weberbauer, 1901) and *Veronica* species (Sernander, 1906). Capsule may remain intact and retain green colour until after the maturity of the seeds. However, the capsule of *Pedicularis* species under investigation did not show any signs of degeneration. Berg (1954) observed few signs of degeneration in the capsules of *Pedicularis silvatica*. The opening device of capsules in non-myrmecochorous and myrmecochorous species of Scrophulariaceae, according to Weberbauer (1901), is similar.

Several myrmecochorous plants have capsules that turn downwards when mature. They open at the apex, and as a result, the seeds drop down to the
ground where the ants can easily seize them. (Sernander, 1906). The capsules of Pedicularis silvatica (Berg, 1954) and those of P. elephantoides and P. pyramidata, however, remain erect and ascending.

The Scrophulariaceae includes a wide variety of seed types. From their study much relevant taxonomic and phylogenetic information can be obtained (Thieret, 1955). On the basis of a study on Veronica and allied genera, Thieret (1955) and Yamazaki (1957 a-b) noted certain evolutionary tendencies in seed morphology, such as: (Primitive condition stated first) seeds reticulate to loss of reticulation; seeds ellipsoidal to seeds flattened, to seeds cochlidiospermous; seeds relatively numerous and small to seeds relatively few and large.

The seeds of the investigated species of Pedicularis contain a reticulate seed coat, which consists of the remnants of the integumentary tapetum in addition to the outer most wall of the integument. A seed coat of similar
nature has been reported for other investigated members of the tribe (Arekal, 1963a) and other species of the genus. In most of the Pedicularis species, it is the very thick walls in the epidermis which protect the seed (Lange, 1870-71; Groenlund, 1870-71; Bachmann, 1862). In Pedicularis silvatica (Berg, 1954), the epidermis, only to a limited extent, gives such protection. The seed coat is made up of the remains of the integumentary tapetum and outermost layers of the thick-walled cells in Euphrasia arctica (Arekal, 1963a). In Orthocarpus luteus (Arekal, 1963a), the seed coat consists of persistent, heavily thickened inner tangential walls of endothelial cells together with the outer epidermis of the integumentary tapetum. In the latter the radial and outer tangential walls are thick. In Melampyrum lineare (Arekal, 1963a), however, the seed coat is a smooth delicate membrane consisting of 1-3 layers of degenerated thin-walled integumentary cells.

The pollination mechanism has been
briefly described by Weed (1884), who suggested nectar foraging bumble bees as the most effective pollinators. Meehan (1873) and Weed (1884) recorded bumble bees securing nectar by corolla perforation without pollinating the flower.

Taxonomic summaries of the genus *Pedicularis* in Asia by Prain (1891); Pennell (1925) and Li (1946, 1949) have indicated a great degree of variation in the floral forms among numerous species. Recent studies of pollination dynamics of the genus *Pedicularis* by Sprague (1962a, b), Macior (1966a–b, 1969–1970, 1973, 1974, 1975 and 1977), MacInnes (1972), and Faegri and van der Pijl (1971) indicate that floral diversity in *Pedicularis* is closely related to the form and behaviour of pollinating insects foraging for nectar and/or pollen. The divergence in sympatric species of *Pedicularis* is almost surely due to a high degree of specificity of visiting insects (Li, 1951).

Wind pollination does not seem to occur. Insects play, by far, the most important role in pollination. Many genera, such as *Rhinanthus*, *Pedicularis* and *Melampyrum* have typical bee—or bumble bee
flowers, complete with landing platform, copious nectar and bright colours. The usual two lipped condition of these flowers, with anthers and papillar, bilobed stigma associated with the upper lip; the frequent honey guides (Euphrasia; Gerardia, Pennell, 1935) and contrasting colours arround the floral entry in Melampyrum, some Rhinanthus and Orobanche (Kuijt, 1969), and Pedicularis are all aspects of the same mechanism. It is an interesting fact that Pedicularis and Bombus are co-existing geographically (Sprague, 1962a-b).

The extent of involvement of Lepidoptera in pollination is unknown, but it is likely to be considerable in the long tubed Pedicularis (Pennell, 1948) and perhaps in similar Euphrasia in New Zealand (Kuijt, 1969). Orobanche lutea and O. purpurea, not withstanding their bright colours, are said to lack nectar (Hegi, 1907-1931).

Birds only exceptionally function as pollinators (Kuijt, 1969). The humming bird, pollination of a single species of Pedicularis (P. densiflorus), has been well documented (Sprague, 1962b), although even here bumble-bee...
are active. Bird pollination has been also reported in South African Harvey (Marloth, 1932) and Castilleja (Grant and Grant, 1966).

It has been found that the location of a plant has a remarkable influence upon the dispersal mechanisms of that particular plant (Sernander, 1906). For the present investigation, the material of Pedicularis pyramidata was collected from Snopian and Ahrabal where it grows in mesic environment, in rice fields and along the lower region of Ahrabal Forest (2260 m). The material of Pedicularis elephantoides was collected at a very high altitude (2900 - 3400 m) above sea level, falling in block F, compartment 5 of Dudhanga forest constituting a part of Yus forests in Kashmir Himalayas. The area of collection is a triangular compartment occupying the southern slope of the Kali-ali Keri overlooking Dregtolan Maidan. The species grows there in clayey loam underlying rocks. The area gets maximum annual rain fall and is dominated by a pure fir (Abies pindrow) forest, mostly middle aged and slightly mixed with young Pinus walchiana and broad leaved species.
confined to Nala. The density of the area varies from 0.4 to 0.6 having scanty regeneration and with sparse undergrowth consisting of Guchh and Sambucus.

Both the species of Pedicularis mentioned above are myrmecocochores. According to Sernander (1906), the myrmecochory is developed only in mesic - xeric conditions. Pedicularis pyramidata, no doubt is mesic but Pedicularis elephantoides is a nyctrophyte. This species adds one more to the recorded number of myrmecocochores found on damp places. P. elephantoides also grows on damp places where maximum moisture is available. Berg (1954) for the first time reported a myrmecochorous Pedicularis species (P. silvatica) from a similar habitat.

Sernander (1906) pointed out that myrmecocochores usually were tachysporous, i.e. a relative short time elapses between flowering and seed dispersal. Hence the dispersal units are already developed when the activity of ants (about mid summer) reveals its height. It has been confirmed by Berg (1954). The present investigatio...
also substantiates the fact.

Berg (1954) conducted experiments on the dispersal mechanisms in Pedicularis (P. silvatica) and proved that it is strongly myrmecochorous. The appendage of the seed according to him serves as an elaiosome. Ants were found to be the chief dispersing agents. Regarding the other dispersal possibilities Berg writes,

"Although the myrmecochory of Pedicularis silvatica is proved, the plant may be adapted to other agencies of seed dissemination as well, i.e., the species may be polychorous. P. silvatica has, however, neither autochorous nor anemochorous dispersal devices. It shows no structures, either, that could cause an epizoic or endozoic scattering of its seeds. The stem and the capsule stalk are too weak for the plant to be a ballista. Accordingly, the only possibility, apart from dispersal by ants is dispersal by water .... Although Pedicularis silvatica shows no concrete dispersal adaptation apart from that for ants, it is quite probable that haphazard dispersal occurs in various ways. The plant wilts early, and those seeds left in the capsules, fall to the ground. They may be then easily transported away by water ...."