Taiwania 66(2): 141–159, **2021**
DOI: 10.6165/tai.2021.66.141

Embryology and systematic position of *Corokia* A. Cunn. (Argophyllaceae, Asterales)

Ashok K. BHATNAGAR, Arun K. PANDEY*

Department of Botany, University of Delhi, Delhi-110007, India.
**Corresponding author's Phone No.: +91-9717745993; E-mail: arunpandey79@gmail.com*

(Manuscript received 11 January 2021; Accepted 27 March 2021; Online published 9 April 2021)

ABSTRACT: Embryology of *Corokia* has been studied in order to utilize the data for taxonomic considerations. Anther wall consists of epidermis, endothecium, middle layer and tapetum. The ontogeny conforms to Dicotyledonous type. Pollen grains are spheroidal and three-zonocolporate. The ovules are anatropous, unitegmic, and tenuinucellate with a distinct endothelium. Embryo sac development is of Polygonum type. Development of the endosperm is of Cellular type. Both chalazal and micropylar endosperm haustoria are present. The embryogeny conforms to the Chenopodiad type. At the mature embryo sac stage, the integument consists of 10–12 layers of cells. In the mature seed only the outer epidermis of the integument persists. The ripe fruit is drupaceous with stony endocarp. Based on embryological characters, considered together with relevant information on morphology, anatomy, cytology and chemotaxonomy of groups regarded related in the past, *Corokia* deserves to be elevated to the rank of a family, Corokiaceae. The Corokiaceae can be appropriately placed, along with Stylidiaceae, in the order Asterales.

KEY WORDS: *Corokia*, Gametogenesis, Embryo, Endosperm, Fruit, Seed, Sporogenesis, Taxonomic Relationships.

INTRODUCTION

A genus of seven species and native to New Zealand, Australia and Rapa Iti (French Polynesia), *Corokia* A. Cunn. (family Argophyllaceae) has evoked an unending interest among systematists because of its puzzling affinities. Following Raoul (1846) and Wangerin (1910), Hutchinson (1959), Huber (1963) and Melchior (1964) included *Corokia* in the Cornaceae. However, Engler (1930) assigned *Corokia* to the subfamily Escallonioideae of the Saxifragaceae. After a systematic anatomical study of the flower and fruit, Eyde (1966, 1988) supported closer relationship of *Corokia* with the Escallonioideae-Saxifragaceae rather than with the Cornaceae. Willis (1973) and Thorne (1973) too have favoured this viewpoint. Cronquist (1968, 1988) emphasized Eyde's conclusions but relegated *Corokia*, along with the rest of the escallonioids, to the Grossulariaceae. He pointed out that the characters of *Corokia* overlapped with both the Cornaceae and the Grossulariaceae, and suggested that the status of the genus as a "possible non-missing link" merits consideration. Dahlgren (1980, 1983) has treated *Corokia* as an independent family Corokiaceae within the Cornales (in Corniflorae), which includes the Cornaceae and the Escalloniaceae. Takhtajan (1987) has separated *Corokia* and *Argophyllum* in the Argophyllaceae and placed them next to the Escalloniaceae in his Hydrangeales within the Cornanae.

Because of the divergent opinions expressed regarding the systematic position of *Corokia*, several workers have carried out investigations on this and the related taxa during the last few decades. However, these contributions are based on new comparative data from wood anatomy (Patel, 1973b, stomata (Kapil and Bhatnagar, 1974), cytology (Raven, 1975), palynology (Hideux and Ferguson, 1976), chemotaxonomy and serology (Gibbs, 1974; Fairbrothers *et al.*, 1975; Fairbrothers, 1983). Based on morphological and molecular data, more recently, the genus *Corokia* has been placed in the Asterales along with *Argophyllum* in the family Argophyllaceae (see Lundberg and Bremer, 2003).

Comparative embryological data offer reliable criteria for evaluating the taxonomic relationships, for assessing pre-existing schemes of classification and interpretation of phylogeny at various levels of hierarchy (Kapil and Bhatnagar, 1991). Seeing the importance of embryological data in systematics, Kapil and Bhatnagar (1992) made a pilot study on the embryology of *Corokia* and presented the paper in the symposium held at St. Petersburg, Leningrad in 1990. Nevertheless, detailed embryological data incorporating more species of *Corokia* was never published. Hence, the objectives of the present communication were: (1) to make a comprehensive study of the ontogenetic details of the embryological features in the genus *Corokia* and (2) to assess the systematic position of *Corokia* based on embryological characters.

MATERIALS AND METHODS

Fixed material of buds, flowers and fruits of *Corokia cotoneaster* Raoul was obtained from Woodland Forest Station, University of Auckland and Christchurch Botanic Gardens, New Zealand, *C. buddleioides* A. Cunn.

Table 1. Collection data.

Species	Locality	Collector	Period of Collection
Corokia cotoneaster	Woodland Forest Station, New Zealand	Dr. L. C. Armiger	June 1963
	Auckland University Grounds, New Zealand	Miss Toni Kitchen	September-November 1967
	Auckland University Grounds, New Zealand	Dr. L. C. Armiger	March-October 1973
	Christ Church Botanic Garden, New Zealand	Professor B. A. Fineran	September-November 1973, 1974, December 1975
Corokia buddleioides	Auckland University grounds, New Zealand	Miss Toni Kitchen	September-November 1968
	Auckland University Grounds, New Zealand	Miss E. M. Dickson	September 1973
	Christ Church Botanic Garden, New Zealand	Professor B. A. Fineran	October 1974
Corokia macrocarpa	Golden Gate Park, San Fransisco, U.S.A.	Dr. Elizabeth Mclintock	April 1965
	Christ Church Botanic Garden, New Zealand	Professor B. A. Fineran	October –December 1974
Corokia cheesemanii	Auckland University Grounds, New Zealand	Miss Toni Kitchen	September-November 1968
	University of California, Los Angeles, U. S. A.	Dr. D. S. Varity	September 1974, 1975

from University of Auckland and Christchurch Botanic Garden; *C. macrocarpa* Kirk from Golden Gate park, San Francisco, U.S.A. and from Christchurch Botanic gardens, and *C. cheesemanii* H. Carse (= *C.* x *virgata* Turril) from University of Auckland and Botanical Garden-Herbarium, University of California, Los Angeles, U.S.A. The collection data are given in Table 1.

The material, fixed in FAA, was transferred to 70% ethanol after it was received from foreign collectors. Conventional dehydration and paraffin embedding methods were employed. The material was sectioned at 6-12µm, and stained with safranin-astra blue combination (Feder and O'Brien, 1968).

RESULTS

Flowers are pedicellate, bracteate, actinomorphic, hermaphrodite, epigynous and pentamerous (Fig. 1A), sometimes hexamerous (Fig. 1B, C) or tetramerous (Fig. 1D). Stamens are five, alternipetalous, and anthers are basifixed, dithecous, and introrse dehiscing by longitudinal slits. The number of locules in the ovary is one in *C. macrocarpa*, one or two in *C. cotoneaster* and *C. cheesemanii*, and two-four in *C. buddleioides*. Style has variable length and the number of stigmatic lobes corresponds to the locules (Fig. 1A, E, F). In *C. cotoneaster* a flower with a small vestigial additional style was also seen (Fig. 1G).

Microsporangium

Some hypodermal cells differentiate as archesporial initials at each of the four corners of the anther primordium (Figs. 2A, F). They divide periclinally and form outer primary parietal cells and inner primary sporogenous cells (Fig. 2B, G). The primary parietal cell divide (Fig. 2 H-L) to generate an endothecium, single middle layer and tapetum. The ontogeny conforms to the Dicotyledonous type (cf., Davis, 1966). The endothecial cells elongate tangentially and develop fibrous cellulosic thickenings on their radial walls before dehiscence. A layer of fibrous cells is differentiated toward the connective also (Fig. 2E, O). The middle layer cells stretch considerably as the anther lobe enlarges and at the microspore tetrad stage it becomes virtually compressed (Fig. 2D, N).

While the primary parietal cells are in the division process, the subarchesporial cells divide periclinally, enlarge (Fig. 2G, J) and constitute the tapetum toward the connective. Soon the inner secondary parietal layer is also differentiated similarly so that the tapetum is organized all around the anther locule (Fig. 2K). The tapetum is glandular or secretory type and its cells often become binucleate (Fig. 2M).

Microsporogenesis and Male Gametophyte

Primary sporogenous cells undergo repeated divisions and form a large number of microspore mother cells. A thick layer of callose is deposited around these cells (Fig. 2P). At meiosis I nine pairs of chromosomes are observed (Fig. 2Q). Cytokinesis is of Simultaneous type (Fig. 2R–V), and the tetrads are tetrahedral (Fig. 2N). Pollen is three-celled when shed.

Ovule

Placentation varies according to the number of carpels and locules in the ovary. In unilocular ovaries of *C. macrocarpa*, *C. cotoneaster* and *C. cheesmanii* the ovular primordium is initiated from the carpellary wall (3A). In plurilocular ovaries of *C. buddleioides*, *C. cotoneaster* and *C. cheesmanii* the ovules appear suspended from the central axis which incompletely partitions the ovary (Fig. 3B). There is a single, pendulous ovule in each locule. However, in some abnormal ovaries of *C. buddleioides* a sterile ovule was observed from the upper part of the placental axis.

Integument

The ovular primordium (Fig. 3A) undergoes a curvature due to unilateral divisions and cell enlargement on the dorsal side. The nucellus is soon delimited as a small protuberance of epidermal cells covering a large archesporial cell (Fig. 3B) and a few subdermal cells.

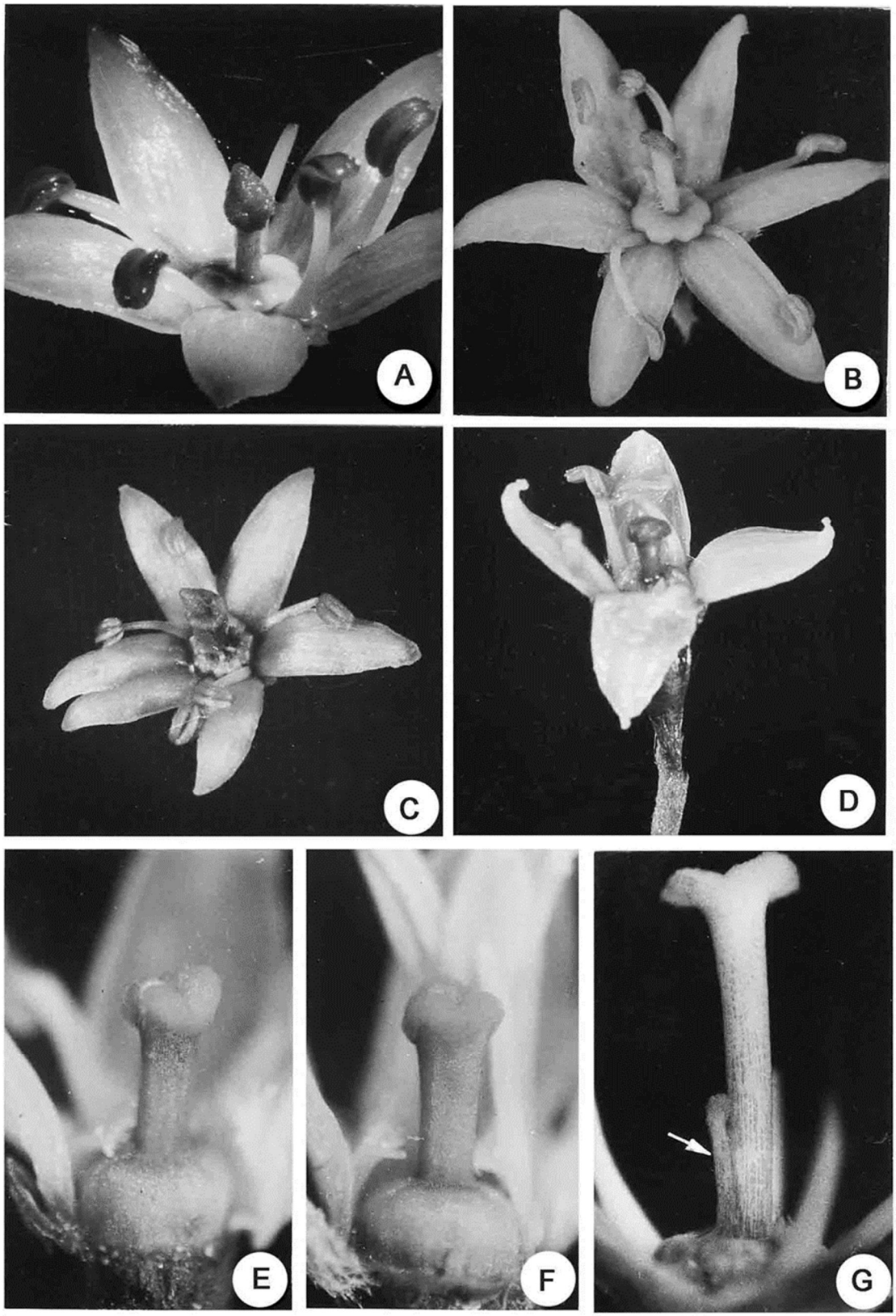

Fig. 1. ***Corokia*** spp., Flower **A.** ***C. cotoneaster***, pentamerous flower with alternipetalous stamens, clavate stigma and nectariferous disc (x8). **B**. ***C. cheesmanii***, a flower with six petals (x 6). **C.** ***C. cheesmanii***, a flower with one cleaved petal (x 6). **D.** ***C. buddleioides***, tetramerous flower (x 6). **E**–**F.** ***C. buddleioides***, magnified veins of the stylar portion showing two- and three- lobed stigmas, respectively (x16). **G.** ***C. cotoneaster*** part of the flower with an extra style (arrow) arising independently from the disc (x 26).

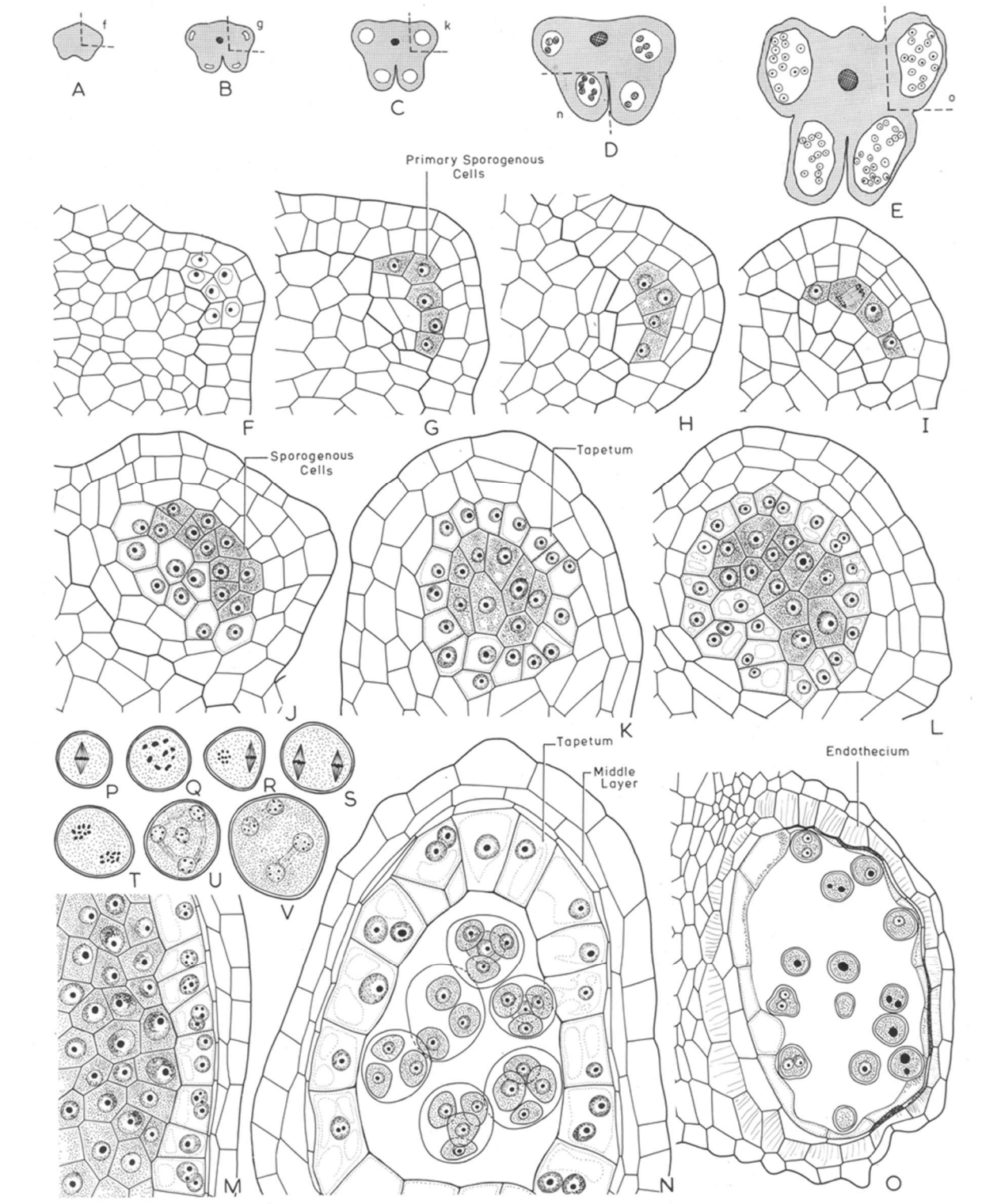

Fig. 2. ***Corokia cotoneaster***, Microsporagium and microsporogenesis. **A–E.** Transection of anthers at various stages of development (diagrammatic) (x65). **F.** Portion f of marked in A enlarged to show periclinal divisions in hypodermal cells (x635). **G.** Differentiation of primary sporogenous and primary parietal cells as seen in portion g enlarged from B (x635). **H–I.** Periclinal divisions in primary parietal cells (x635). **J.** Formation of secondary parietal layers and sporogenous cells; note differentiation of tapetum towards connective (x635). **K.** Sector k marked in C enlarged to show inner secondary parietal layer differentiating as tapetum (x635). **L.** Anther lobe in cross section showing four layered wall; tapetal cells have become bilayered towards connective (x635). **M.** Portion of anther wall with some binucleate tapetal cells (x635). **N.** Portion n marked in D enlarged to show four wall layers enclosing microspore tetrads (x635). **O.** Mature anther lobe having endothecium, degenerating middle layers and tapetum (x270). **P–V.** Some stages of microsporogenesis (x 1,000).

Meanwhile, three or four cells of the dermal layer around the nucellar protuberance undergo periclinal (Fig. 3B) or somewhat oblique divisions, marking the initiation of the integument. The subjacent cells do not participate in the development of integument.

As a result of vigorous periclinal (sometimes anticlinal or oblique) divisions the integument grows to the nucellus level (Fig. 3C–E). Simultaneously, more intense division activity and cell enlargement on the dorsal side of the funiculus and chalaza result in a gradual curvature that eventually causes the anatropy of the ovules (Fig. 3F–I). The cells of the subdermal layer adjoining the archesporial cell, however, do not divide.

Continued divisions in the dermal initials result in a massive integument covering nucellus (Fig. 4A) and then continues growth upwards so as to form a long micropylar canal (Fig. 4B). The protoderm lining the micropylar canal elongate radially or divide anticlinally so that the micropylar canal becomes very narrow (Fig. 4C). The form and structure of the ovule are similar in *C. cotoneaster* and *C. macrocarpa*. As compared to these, in *C. buddleioides* (Fig. 4D) and *C. cheesmanii* the ovular growth is much more rapid and the micropylar canal is longer.

In *C. cotoneaster*, *C. buddleioides,* and *C. cheesmanii* the integumentary cells surrounding the nucellus, with four-nucleate embryo sac, elongate radially (Fig. 4C) and divide anticlinally. At the organized embryo sac stage, they differentiate as endothelium which surrounds most of the embryo sac except the micropylar and chalazal poles.

Nucellus

The nucellar layer extends by anticlinal divisions. In one ovule of *C. cotoneaster* the subdermal cells formed an irregular layer between the nucellar epidermis and megasporocyte. During megagametogenesis the nucellus degenerates, but a collar of cells surrounding the chalazal part of the embryo sac persists (Fig. 4C). At organized embryo sac stage, the nucellus degenerates completely and the embryo sac is surrounded by cells of integumentary tapetum.

Megasporogenesis and Female Gametophyte

The hypodermal archesporial cell differentiates directly from the megaspore mother cell. Meiosis I in the megasporocyte is followed by forming a transverse wall resulting in two superposed dyad cells. In *C. cotoneaster* and *C. macrocarpa* linear tetrads of megaspores are produced (Fig. 5A, B). T- (Fig. 5C) or inverted T-shaped (Fig. 5D) disposition of megaspores is also encountered in *C. buddleioides* and *C. cotoneaster*, respectively. In *C. cotoneaster* triads with functional chalazal megaspore and persistent healthy micropylar dyad cell were observed (Fig. 5E). Mostly the chalazal megaspore develops into an embryo sac (Fig. 5F, I) and the other three degenerate. Less often the chalazal megaspore is first to degenerate (Fig. 5G, H).

Three meiotic divisions in the functional megaspore successively result in the formation of two- (Fig. 6A), four- (Fig. 6B) and eight-nucleate embryo sac conforming to the Polygonum type.

The gametophyte of *C. cotoneaster* appears narrow, spindle-like (Fig. 6C, D) or broad with rounded edges (Fig. 6E) according to the plane of sectioning of the ovule. Cells of the egg apparatus form a triangular configuration. The egg nucleus is placed close to the broad tip surrounded by several vacuoles. The newly formed synergids are densely cytoplasmic but subsequently large vacuoles appear in the apical part of each displacing the nucleus to the middle portion. The synergids possess a prominent filiform apparatus. Antipodal cells may form a T-shaped arrangement (Fig. 6D) or, equally often, two of them occupy the chalazal concavity of the embryo sac and the third is laterally placed (Fig. 6E). The central cell has several large vacuoles separated by strands of cytoplasm. These strands join near the cell center where the polar nuclei meet and fuse before fertilization.

Some variations were noted in the organization of the embryo sac in *C. cotoneaster*. For example, in one of the 12 mature embryo sacs examined, the antipodal cells show an arrangement similar to that of the egg apparatus (Fig. 6F). Another contained four synergids and two eggs at the micropylar pole, seven antipodal cells at the chalazal pole and two nuclei in the central cell (Fig. 6G), the upper larger presumably formed by the fusion of two micropylar nuclei.

In *C. macrocarpa* the antipodal cells are arranged in a trihedral manner and polar nuclei fuse close to the egg. An embryo sac with one of the synergids divided by transverse wall was also observed (Fig. 6H). In *C. cheesmanii* the embryo sac is relatively more elongated and the antipodals are arranged in an inverted T-shaped manner (Fig. 6I). The embryo sac in *C. buddleioides* has broader ends and the wall is considerably thickened at the micropylar pole (Fig. 6J). In this species the antipodal cells also are arranged tetrahedrally, but the egg does not protrude much beyond the synergids.

Fertilization

The pollen tube enters the embryo sac through the filiform apparatus (Fig. 7A). At this stage both the synergids are healthy, but they degenerate soon after fertilization.

Endosperm

In *C. cotoneaster* the primary endosperm nucleus divides near the resting zygote resulting in a small micropylar and a large chalazal chamber (Fig. 7B). The micropylar cell then divides by a vertical wall, whereas the chalazal divides transversely (Fig. 7C). Subsequent divisions are more rapid in the micropylar cells. They

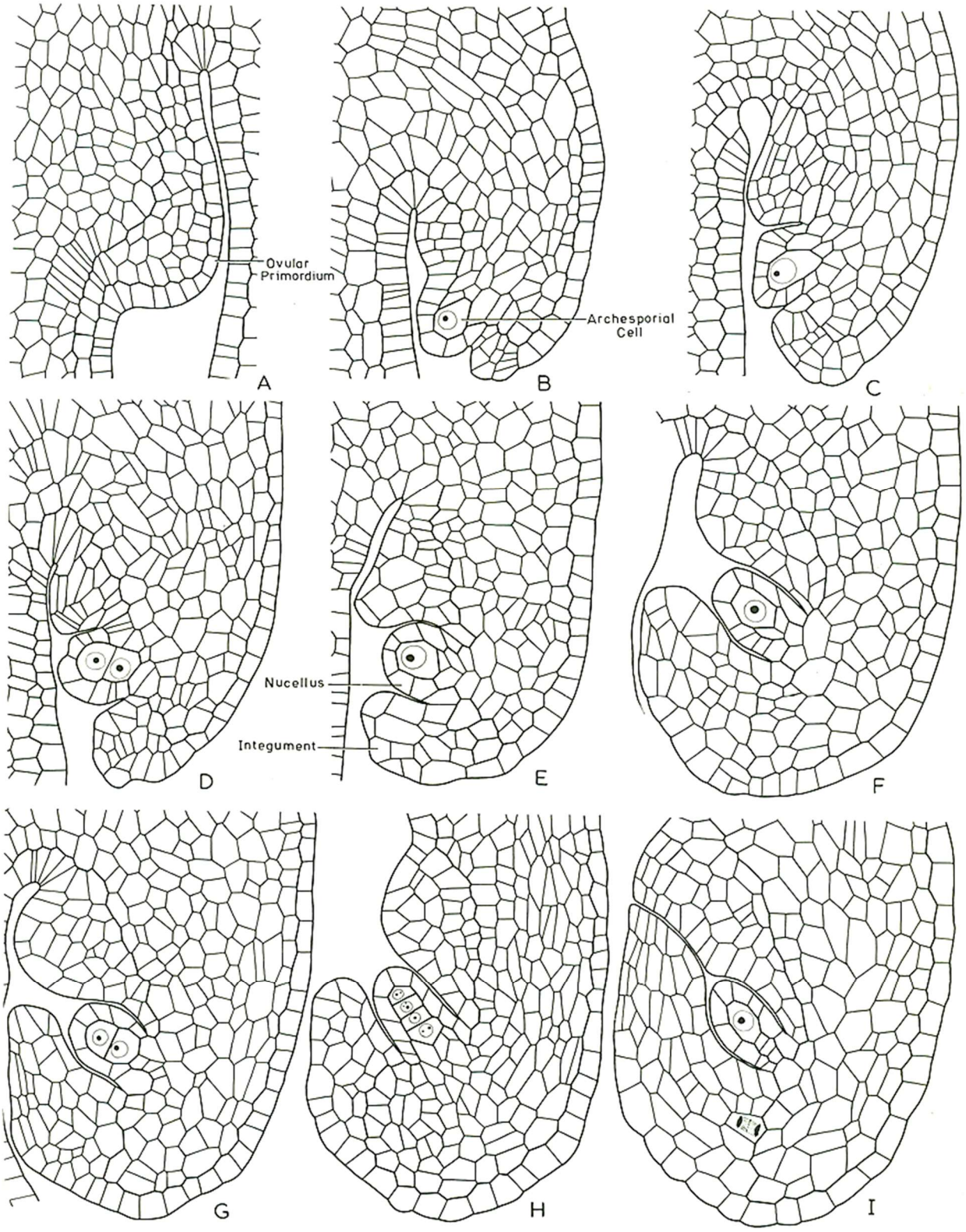

Fig. 3. ***Corokia cotoneaster***, Megasporangium. **A.** Longisection through ovular primordium; growth has occurred chiefly in the subdermatogen (separated by thick lines) (x400). **B.** Longisection of young ovule; hypodermal archesporial cells have differentiated and adjoining epidermal cells have divided periclinally to form integumentary initials (x400). **C**–**L.** Further growth of integuments and gradual curvature of ovule; mark the precise correlation between stage of megasporogenesis and extent of integument development (x400).

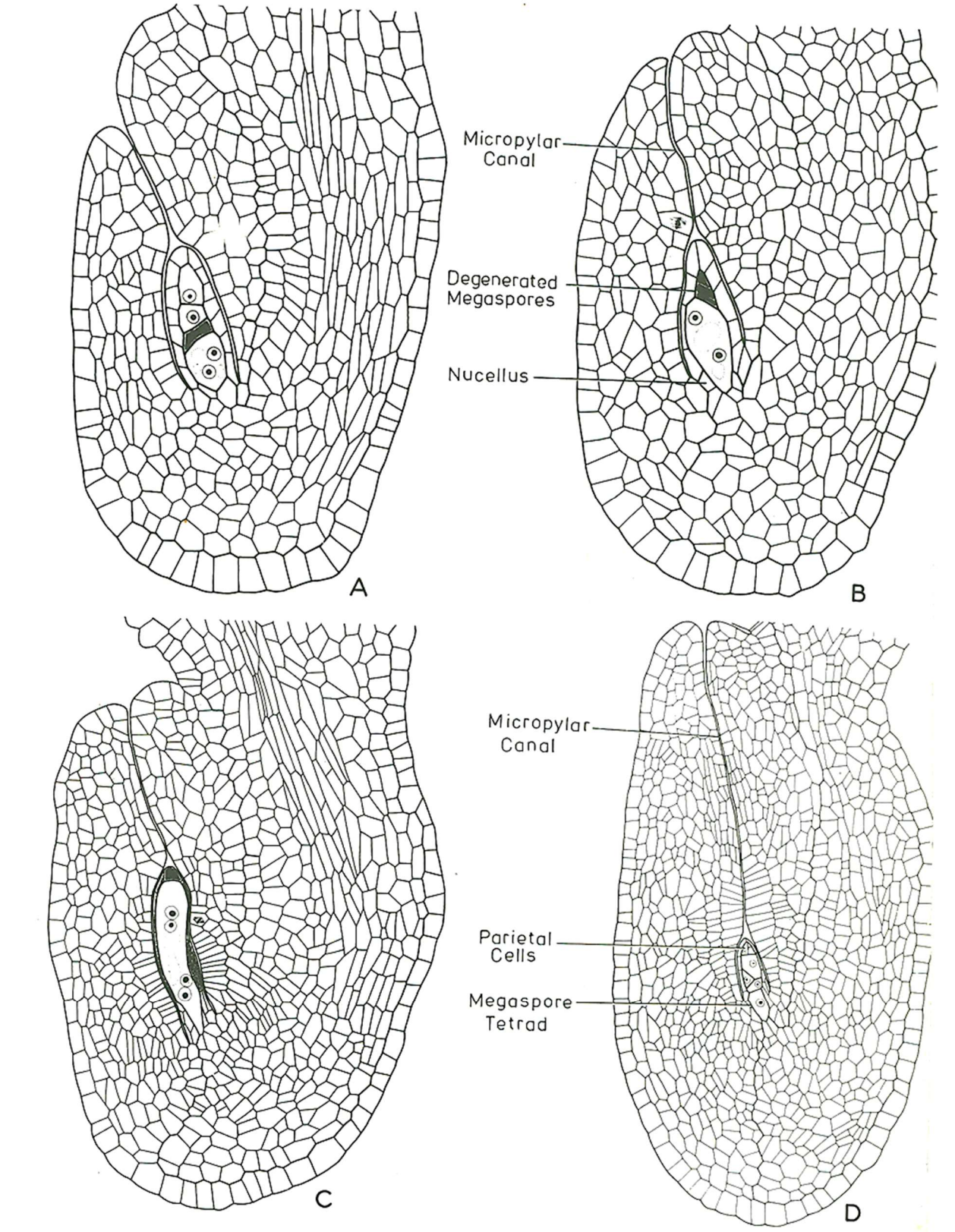

Fig. 4. ***Corokia*** spp., Megasporangium. **A**–**C.** ***C. cotoneaster***, longisections of ovule showing tetrad with binucleate chalazal cell, and two– and four–nucleate embryo sacs, respectively; note differentiation of integumentary tapetum in C. (A, B x425; C x300). **D.** ***C. buddleioides***, ovule at megaspore tetrad stage with the long micropylar canal (x265).

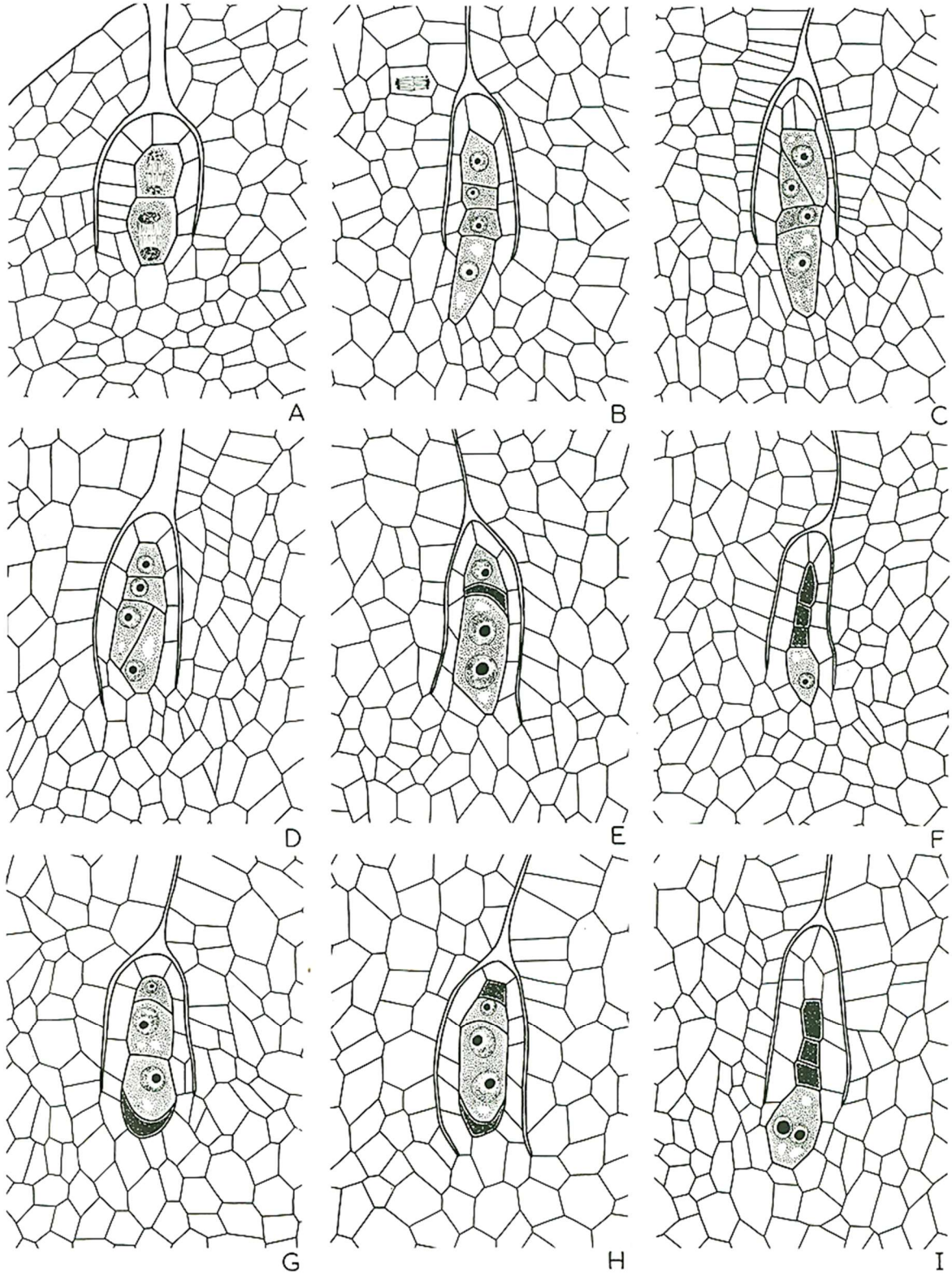

Fig. 5. ***Corokia*** spp., Megasporogenesis. **A**–**B.** ***C. cotoneaster***, young nucelli showing dyad cells in the synchronous division, and linear, megaspore tetrad, respectively (x735). **C.** ***C. buddleioides,*** tetrad with an oblique wall separating micropylar megaspores, the primary parietal cell has divided anticlinally (x735). **D.** ***C. cotoneaster***, inverted T-shaped tetrad (x735). **E.** ***C. cotoneaster,*** triad with two-nucleate chalazal cells (x 735). **F.** ***C. cotoneaster***, tetrad with chalazal functional megaspore (x735). **G**–**H.** ***C. cotoneaster***, chalazal megaspore has degenerated in G, and subchalazal megaspore has formed two-nucleate embryo sac in H (x735). **I.** ***C. buddleioides***, tetrad with chalazal functional megaspore; the primary parietal cell is persistent (x735).

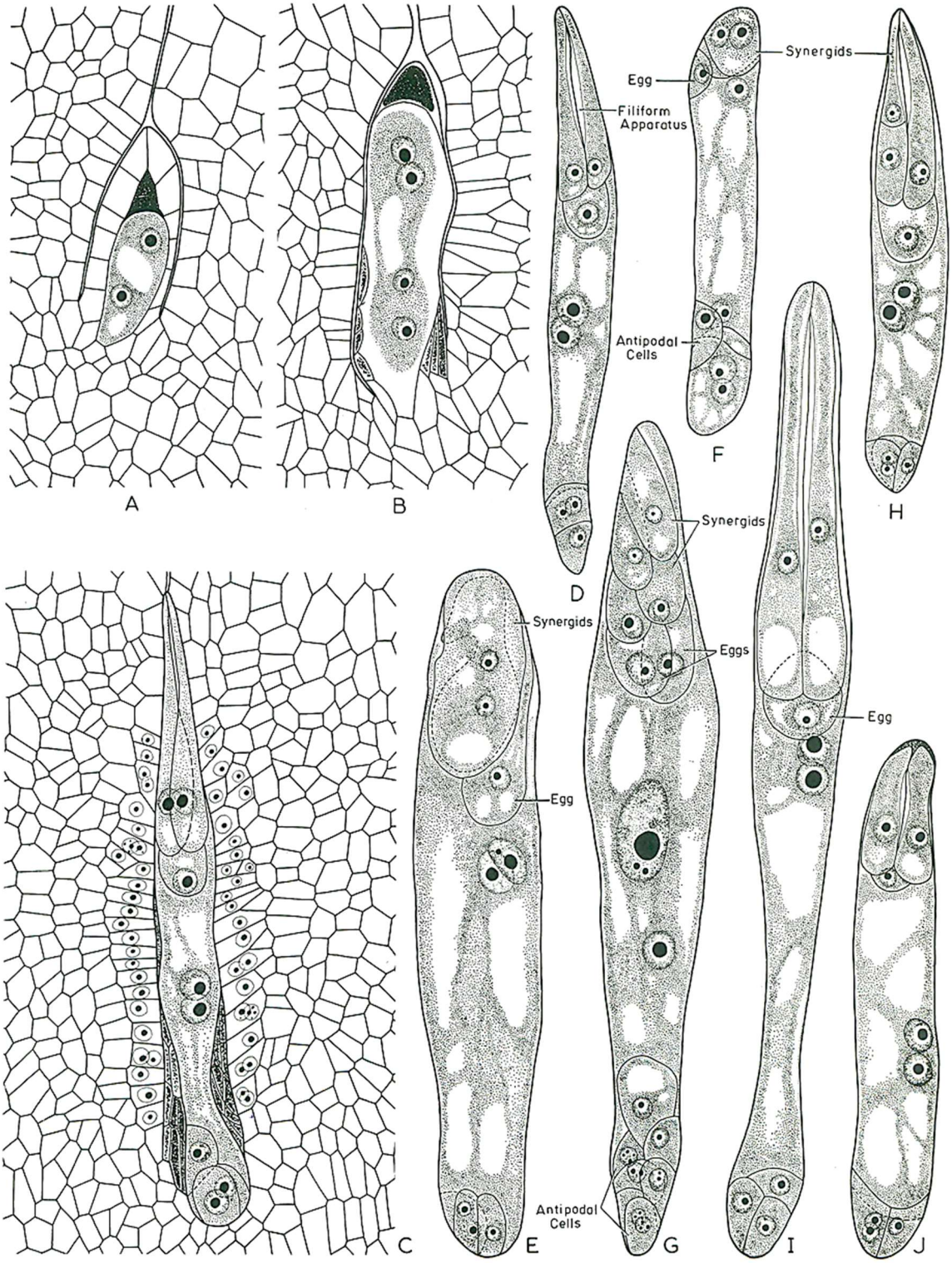

Fig. 6. ***Corokia*** spp., Megagametogenesis and female gametophyte. **A**–**B.** ***C. cotoneaster***, parts of longisectioned ovules with two- and four-nucleate embryo sacs respectively; remnants of non-functional megaspores and degenerated nucellar cells are seen in B (x 625). **C.** ***C. cotoneaster***, organised embryo sac; some endothelium cells are binucleate (x625). **D.** ***C. cotoneaster***, embryo sac with T- shaped arrangement of antipodal cells (x625). **E.** ***C. cotoneaster***, embryo sac in an ovule cut cross the raphe plane; one antipodal cell is laterally placed (x625). **F.** ***C. cotoneaster,*** embryo sac with antipodals stimulating egg apparatus (x625). **G.** ***C. cotoneaster***, abnormal embryo sac with double egg apparatus, two central cell nuclei and seven antipodal cells (x625). **H.** ***C. macrocarpa***, embryo sac with one synergid segmented transversely (x625). **I.** ***C. cheesmanii***, embryo sac with polars fusing below egg apparatus; antipodals are arranged in an inverted T- shaped manner (x625). **J.** ***C. buddleioides***, embryo sac with trihedrally arranged antipodal cells (x 625).

divide transversely, and their micropylar derivatives become multinucleate (Fig. 7D), whereas chalazal divide in various planes and constitute a part of the storage endosperm. The cells derived from the chalazal chamber divide in various planes. Together with the adjacent micropylar cells they form the bulk of the endosperm. One or two cells adjoining the persistent antipodal cells, however, become multinucleate (Fig. 7E). The micropylar and chalazal endosperm haustorial cells become richly cytoplasmic, multinucleate and possess prominent thickenings on that portion of the wall that is not covered by endothelium (Fig. 7F, G). The integumentary cells surrounding the micropylar haustorium degenerate and break down showing its aggressive nature. The basal ends of the zygote and proembryo are entirely surrounded by the haustorial endosperm cells. The endosperm haustoria remain active until the torpedo-shaped stage of the embryo.

There is some variation in the pattern of early endosperm development in other species of *Corokia*. In *C. buddleioides* the first division is transverse but the second is vertical in both the cells (Fig. 7H). The micropylar tier divides transversely (Fig. 7I) and, as in *C. cotoneaster*, the endosperm cells surrounding the basal part of the suspensor constitute a haustorium. On the other hand, in *C. cheesmanii* the first transverse division is followed by another transverse wall in the micropylar and a vertical wall in the chalazal chamber (Fig. 7J). In *C. macrocarpa* four-celled linear endosperm is formed (Fig. 7K). Its micropylar and chalazal cells give rise to haustoria (Fig. 7K) and the two central cells divide into various planes to form the bulk of endosperm.

Embryogeny

In *C. cotoneaster* the zygote elongates considerably and divides transversely (Fig. 8A) forming a small apical cell and a large, vacuolate basal cell (Fig. 8B). Both the derivatives divide transversely again forming a linear, four-celled proembryo (Fig. 8C). Further divisions in the apical cell derivatives of the apical cell are not as rapid as in those of the basal cell. Cells *m* and *ci* undergo transverse divisions and form two to six cells each (Fig. 8D, E). At the eight- to ten-celled filamentous proembryo stage, the cell *cc* divides by a longitudinal wall, whereas *cd* divides transversely forming two superposed daughter cells (Fig. 8F, G). Next longitudinal division may precede in either derivative of the *cd*. Meanwhile, both the cells in *cc* are segmented by a vertical wall, perpendicular to the previously formed wall (Fig. 8H), resulting in a quadrant of four circumaxial cells.

The derivatives of *ci* and *m* continue to divide transversely and a uniseriate suspensor of ten or more cells (Fig. 8I, K) is produced. Occasionally some cells may divide by a longitudinal (Fig. 8L) or oblique (Fig. 8J) wall. The cells derived from *m*, adjacent to *cd*, however, regularly divide by vertical walls. Derivatives of *cd* also undergo vertical or oblique divisions (Fig. 8I). Transverse or oblique divisions in *cc* result in an octant of two tiers of four cells (Fig. 8J), divided further by periclinal walls initiating the dermatogen (Fig. 8K). The dermatogen undergoes anticlinal divisions, but occasionally periclinal divisions also occur. Periblem initially divides anticlinally. Later divisions are periclinal and more profuse below the apical part (Fig. 8M, N). Cells of plerome divide in various planes.

Finally, the derivatives of *cc* constitute the initials of the cotyledons and stem apex. The tiers derived from *cd* divide periclinally and form concentric rows (Fig. 8L), forerunners of the hypocotyl. The embryogeny, thus, conforms to the Chenopodiad type (cf., Johansen, 1950).

The pattern of divisions and destiny of proembryonal cells are more or less similar in the other species. In *C. buddleioides* the first two cell divisions result in a linear four-celled proembryo (Fig. 9A, B). However, in contrast to *C. cotoneaster*, vertical walls are laid down in *cc* and *cd* when the proembryo is six- or seven-celled (Fig. 9C, D). The cell *cc* forms a quadrant and an octant (Fig. 9E), but transverse divisions in the *cd* are delayed until several vertical divisions have occurred in this cell and periclinal walls have already begun forming in *cc* (Fig. 9F). The destinies of various cells are the same as in *C. cotoneaster*, but the suspensor is barely three or four cells long. In *C. cheesmanii* the first two cell divisions also lead to a filamentous four-celled proembryo (Fig. 9G, H). Vertical divisions in *cc* and *cd* take place when the proembryo is six-celled (Fig. 9I). As in *C. buddleioides* the transverse division in tier *cd* is delayed. The quadrants are formed (Fig. 9J) as in other species, but octants are not regularly produced. The occurrence of oblique divisions in the cells of the quadrant is common (Fig. 9K). The suspensor is five (Fig. 9L) to eight cells long.

After the globular stage of proembryo (Fig. 9M), the hypocotyl elongates rapidly. The heart-shaped stage is missed altogether, and when the cotyledons are initiated the embryo is torpedo-shaped (Fig. 9N). The mature embryo is cylindrical with well-developed root cap and hypocotyledonary axis but the cotyledons are minute (Fig. 9O).

Seed Coat and Pericarp

At the mature embryo sac stage the integument consists of 10-12 layers of cells (Fig. 10A). In the mature seed only the outer epidermis of the integument persists (Fig. 10B). At the archesporial cell stage, the ovary wall in *C. cotoneaster* consists of about 25 layers of cells and is distinguishable into two zones: (i) an outer comprising nine or 10 layers of large, vacuolated cells; (ii) an inner of 15 to 18 layers of small, relatively more densely staining cells. The hypodermal layer of the ovary wall is tanniniferous. Before fertilization the inner zone becomes 27- to 30- cell-thick (Fig. 10 C).

After fertilization there is a multiplication of the cells

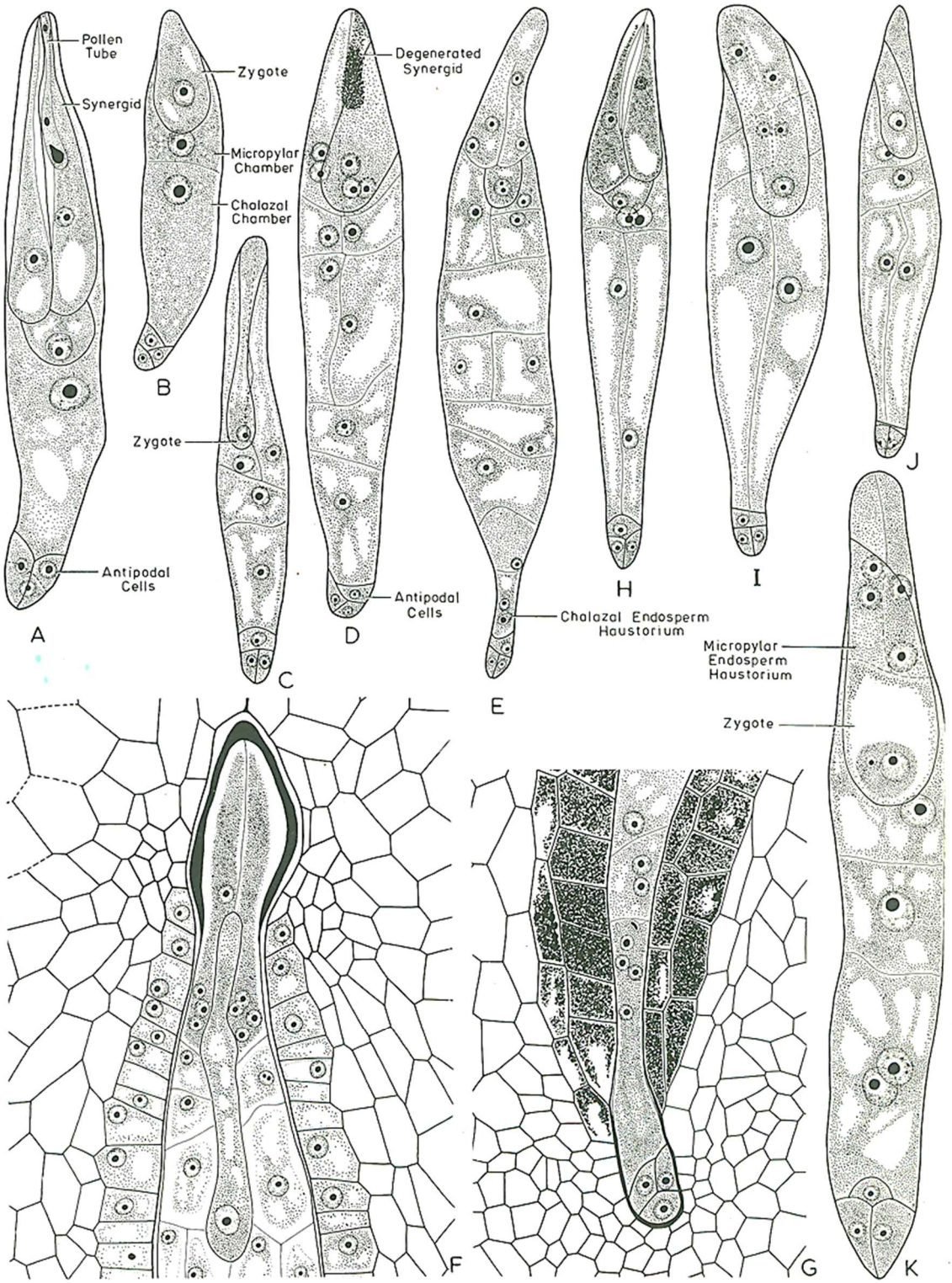

Fig. 7. ***Corokia*** spp., Fertilization and endosperm. **A.** ***C. cotoneaster***, embryo sac showing pollen tube in a synergid (x665). **B**–**C.** ***C. cotoneaster***, two- and four- celled endosperm, respectively; the micropylar chamber is smaller in B (x 235). **D**–**E.** ***C. cotoneaster***, differentiation of micropylar and chalazal haustoria (x285). **F.** ***C. cheesmanii***, densely cytoplasmic, multinucleated cells of micropylar haustorium surrounding basal part of the zygote (x665). **G.** ***C. cotoneaster***, multinucleate chalazal haustorium; persistent antipodals and tannin-filled cells of the endothelium are also seen (x485). **H**–**I.** ***C. buddleioides***, four- and six-celled endosperm, respectively, synergids are persisting in H (x285). **J.** ***C. cheesmanii***, four-celled endosperm (x285). **K.** ***C. cheesmanii***, five-celled endosperm with binucleate micropylar and chalazal cells (x665).

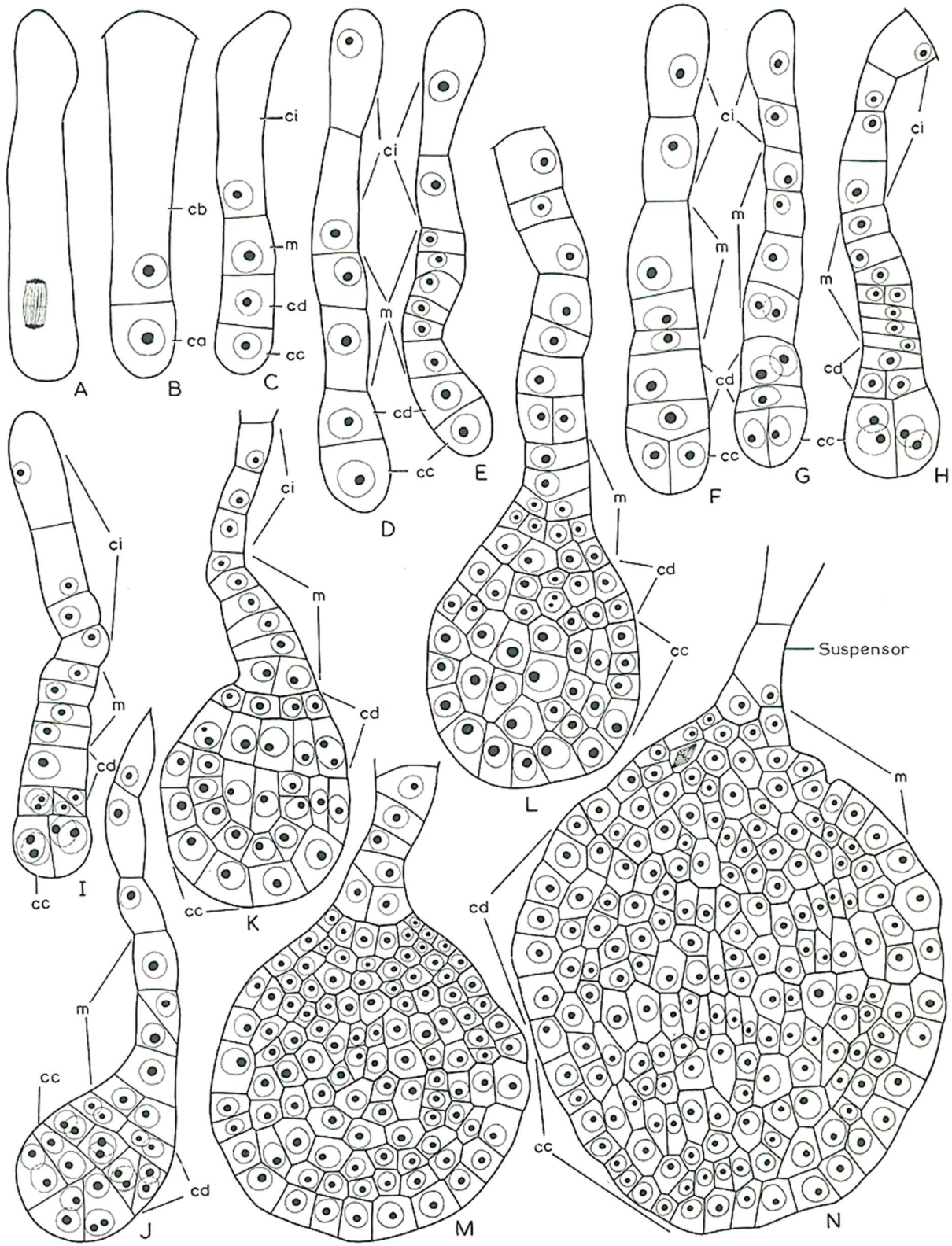

Fig. 8. ***Corokia cotoneaster***, Embryogeny. **A.** zygote in division (x615). **B**–**E.** Young linear proembryos (x615). **F**–**G.** Filamentous proembryos with longitudinally divided terminal cell (x615). **H**–**I.** Quadrant stages (x 615). **J.** Octant stage (x615). **K**–**N.** Developmental stages leading to the formation of the globular proembryo (x 615).

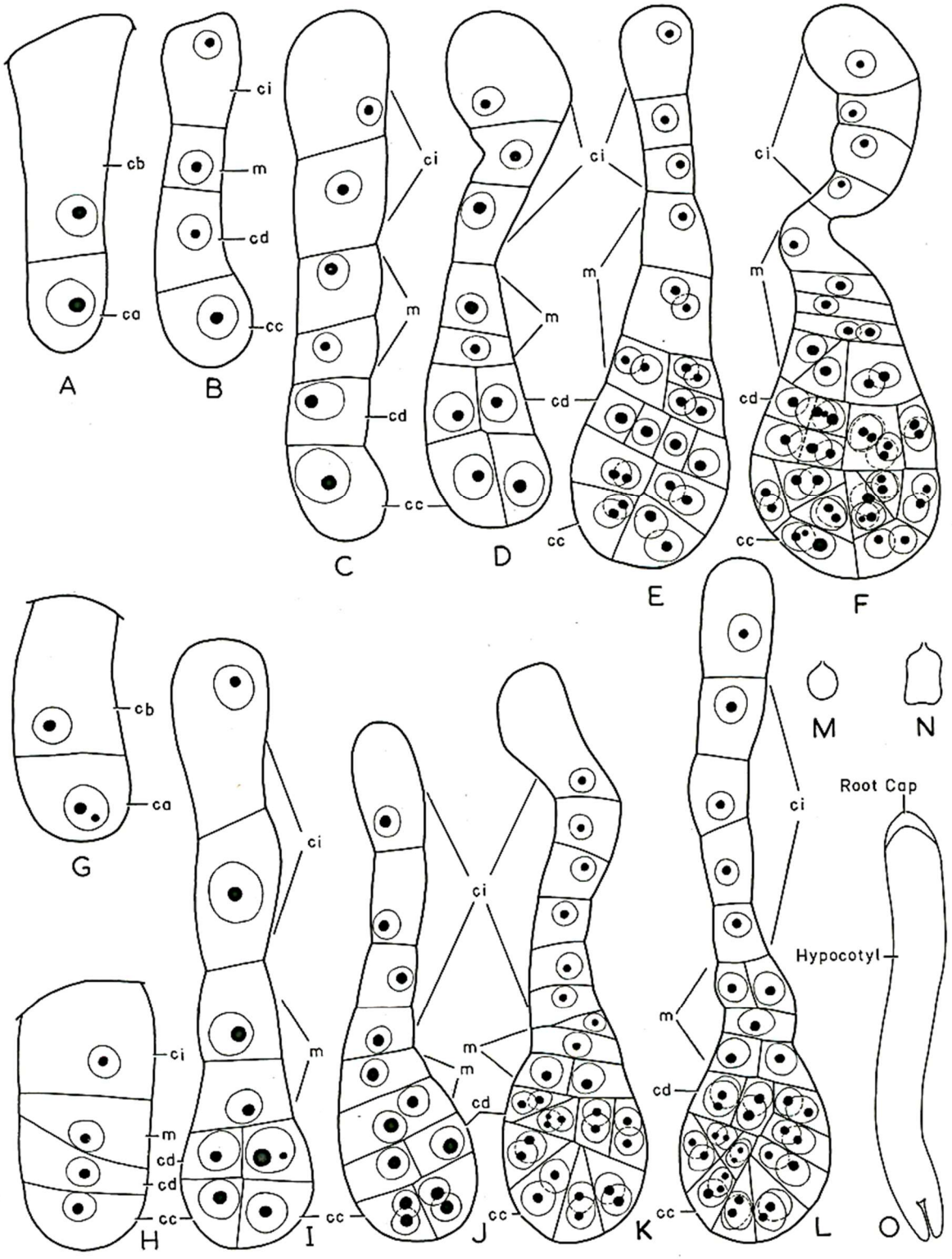

Fig. 9. ***Corokia*** spp., Embryogeny. **A.** ***C. buddleioides***, two-celled proembryo (x 800). **B**– **C.** ***C. buddleioides***, four-celled and filamentous proembryos (x800). **D.** ***C. buddleioides***, proembryo will longitudinally divided terminal and subterminal cells (x800). **E.** ***C. buddleioides***, proembryo at octant stage (x800). **F.** ***C. buddleioides***, proembryo showing delimitation of dermatogen (x800). **G**–**H.** ***C. cheesmanii***, two- and four-celled proembryos, respectively (x800). **I.** ***C. cheesmanii***, proembryo with logitudinally divided terminal cells (x800). **J.** ***C. cheesmanii***, quadrant stage (x 800). **K**–**L.** ***C. cheesmanii***, proembryos showing oblique walls and irregular divisions in quadrant cells; cells of tier *cd* divide in a variable manner (x800). **M**–**O.** ***C. cheesmanii***, globular, torpedo-shaped and mature dicot embryos, respectively (x28).

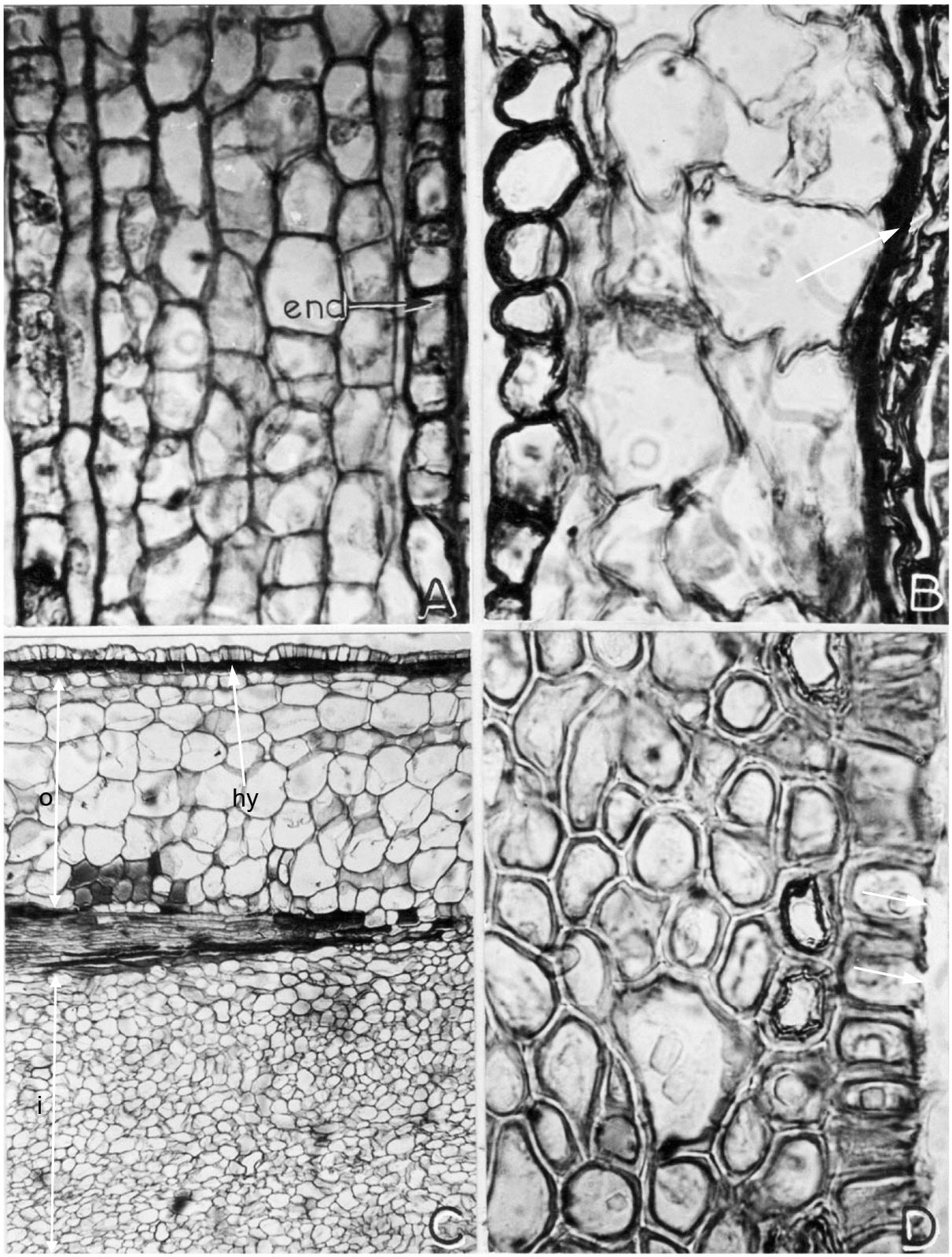

Fig. 10. ***Corokia cotoneaster***. Seed coat and pericarp. **A.** Part of longisection of integument at organized embryo sac stage; endothelial cells (end) are thick–walled (x680). **B.** Endothelium and adjoining integumentary layers have become obliterated (arrow) at torpedo stage of embryogeny (x1300). **C.** Part of ovary wall before fertilization showing demarcation of the outer (o) zone of large and inner (i) of small cells; hypodermis (hy) is filled with tannin (x275). **D.** Endocarp at the heart-shaped stage of the embryo; cells are sclerosed and contain prismatic crystals. Walls facing fruit cavity are interrupted (arrows) (x690).

of the ovary wall cells, resulting in more than 50 cell layers at the globular stage of the proembryo. The inner epidermal cells of the pericarp become sclerosed. The inner zone cells are gradually transformed into thick-walled sclereids with simple pits (Fig. 10D). At the mature fruit stage these cells disorganize and form large cavities. The fleshy exocarp is produced by the outer zone of the ovary wall.

DISCUSSION

The genus *Corokia* has been considered to be related to the Cornaceae or the Escalloniaceae, Grossulariaceae since it shares several morphological as well as anatomical characters with these families (see Eyde, 1966; Philipson, 1967). Nevertheless, the precise relationships have been rather difficult to establish partly because these taxa are not properly defined. Harms (1898) included 15 genera in the Cornaceae: *Alangium*, *Aucuba*, *Camptotheca*, *Cornus*, *Corokia*, *Curtisia*, *Davidia*, *Garrya*, *Griselinia*, *Helwingia*, *Kaliphora*, *Mastixia*, *Melanophylla*, *Nyssa and Torricellia.* In his monograph, Wangerin (1910) retained 10 of these in the Cornaceae and assigned *Nyssa*, *Camptotheca* and *Davidia* to Nyssaceae, *Alangium* to Alangiaceae and *Garrya* to Garryaceae. It seems that some of the genera are erroneously placed even in Wangerin's smaller Cornaceae. Subsequent investigators, therefore, found it desirable to reassess their systematic position. For example, at one time or the other *Toricellia* was removed to Toricelliaceae (Takhtajan, 1969) or Toricelliales (Takhtajan, 1987); *Helwingia* to Araliaceae (Hutchinson, 1959) or a separate family Helwingiaceae within Apiales (Takhtajan, 1987). *Curtisia*, *Kaliphora* and *Melanophylla* were believed to have no affinities with the Cornaceae (see Hegnauer, 1965); and *Aucuba* and *Griselinia* were raised to the rank of an independent family, Aucubaceae (Philipson, 1967; Thorne, 1973). *Mastixia* was likewise placed in an independent family, Mastixiaceae by several authors including Takhtajan (1969, 1987) or was considered to have aralian affinities (Philipson, 1967; Rodriguez, 1971). Takhtajan (1987) has retained only three genera in the Cornaceae. Thorne (1983) is of the opinion that the Cornaceae should be restricted to *Mastixia*, *Curtisia*, *Afrocrania* and *Cornus*. However, Goldberg (1986) has conceived his Cornaceae rather broadly to include 12 genera, separating out only *Davidia*, *Nyssa* and *Garrya* into independent families within the Cornales.

The Escalloniaceae, Grossulariaceae too constitute a constellation of diverse, relict genera that have been insufficiently studied. Engler (1930) has conceived of the escallonioids as constituting a subfamily Escallonioideae of the Saxifragaceae. Hutchinson (1959) and Takhtajan (1969, 1987) elevated them to the rank of a family, the Escalloniaceae. Cronquist (1968) included these plants in his Grossulariaceae along with some other members such as *Brexia*, *Itea*, *Montinea*, *Phyllonoma*, *Pterostemon* and *Tetracarpa*. In several respects the Grossulariaceae of Cronquist are similar to Takhtajan's (1969) Grossulariaceae, several of these genera are placed in small families, e.g., *Brexia* in Brexiaceae, *Ribes* in Ribesaceae and *Itea* in Iteaceae. Based on seed anatomy, Krach (1976) placed Escalloniaceae and Hydrangeaceae in Grossulariales. However, Takhtajan (1987) has included Grossulariaceae in his Saxifragales in Rosidae and placed Escalloniaceae and Hydrangeaceae in Hydrangeales within his Cornanae.

A comparison of *Corokia* with the Cornaceae and the Escalloniaceae, Grossulariaceae shows resemblance in many embryological features such as axile placentation, anatropous, unitegmic ovule, single-celled archesporium, differentiation of endothelium, Polygonum type of embryo sac, albuminous seed and drupaceous fruit with hard endocarp. Certain anatomical features too overlap among these taxa. For example, the stomata are mostly perigenous and anomocytic, the ovary wall is rich in druses and nodes are trilacunar in *Corokia* as in most of the investigated taxa of the Cornaceae and Escalloniaceae, Grossulariaceae. Several wood characteristics are also common (Patel, 1973 a, b; Meylan and Butterfield, 1975). To cite a few, the vessels are solitary, angular with exclusively scalariform perforation plates, and rays are heterogeneous. Chemical features such as the distribution of iridoid glucosides and phenolics prove inconclusive and permit alliance of *Corokia* with either Cornaceae or the rosalean taxa such as Saxifragaceae s.l. (Hegnauer, 1969). Aucubin-type glycoside, cornin is present in *Cornus* and *Corokia* but not in the Escalloniaceae-Saxifragaceae. Based on such chemical evidence Gibbs (1974) supports retention of *Corokia* in Cornaceae.

Between the Cornaceae and the Escalloniaceae, resemblance of *Corokia* is decidedly greater with the latter taxon. The geographic distribution of the Escalloniaceae in southern hemisphere, with three genera within New Zealand, offers greater chances of relationship than the Cornaceae which are chiefly distributed in north temperate region and central and south America. *Greselinia*, the only genus with suspected cornaceous alliance in New Zealand, seems to be doubtfully placed in Cornaceae and as argued by Philipson (1967) it is anatomically quite distinct from *Corokia*. According to Eyde (1966) the ligule, a tongue-shaped outgrowth arising from the adaxial base of petals in *Corokia* spp., is also present in *Argophyllum*. This, in his opinion, is a strong reason for the placement of *Corokia* in Escalloniaceae, next to *Argophyllum*. A four-layered anther wall noticed in *Corokia*, is not present in either the Cornaceae or Escalloniaceae. In the former the wall is five-layered (Kaur, 1970) and in the latter either three- (*Ribes*, Popova, 1965) or five-layered (*Grossularia*, Berezenko and Liferova, 1970). However, the

multinucleate, secretory tapetal cells are encountered in both the taxa. In particular, the abnormal growth of tapetal cells and degeneration of anther locules observed in *Corokia cotoneaster* (present work) is also seen in *Ribes*. Pollen morphology and the three-celled condition of the pollen in *Corokia* also indicate greater affinity to the Escalloniaceae rather than the Cornaceae.

The presence of a multilocular ovary, often with free styles and many ovules in each ovarian locule in Escalloniaceae/Grossulariaceae is in sharp contrast to the condition in *Corokia* where the carpellary locules may be reduced to one, and each locule contains only one ovule. However, a tendency toward reduction in the number of carpellary locules and the number of ovules per locule is seen within Grossulariaceae (e.g., *Ixerba* has two ovules in each of its five locules). The presence of more than one ovule in a locule is rarely encountered in *Corokia* (Eyde, 1966) and the occurrence of an occasional second style in flowers of *C. cotoneaster* (present work) certainly points to the possibility of its derivation from such an ancestor. Pluricellular, T-shaped trichomes, axial ventrals in flower, a prominent vascular supply to the disc, tenuinucellate ovule, and presence of hypostase, are some features of *Corokia* which characterize the Escalloniaceae, Grossulariaceae as well. Wood anatomy does not help much decide the issue since most of the characters overlap (Patel, 1973a, b). Lack of axial parenchyma as reported in *Corokia* finds a parallel in *Ribes* (Spongberg, 1972), but the occurrence of septate fibres and presence of fewer bars (15-25) in the vessel perforation plate are in contrast to the Escalloniaceae, and in this respect *Corokia* has greater resemblance with the Cornaceae.

There also exist a large number of characters in which *Corokia* is different from the Cornaceae as well as the Escalloniaceae. The phyllotaxis in *Corokia* is alternate as compared to opposite in Cornaceae and spiral in Escalloniaceae. The distribution of stomata on all floral parts, especially on the inner ovary wall, is not observed in any family member (Kapil and Bhatnagar, 1974). Raven (1975), who investigated the cytology of several cornaceous and saxifragaceous plants, stated that the basic chromosome number, n=9, in *Corokia* spp. has no parallel in the Cornaceae or Escalloniaceae.

The question of whether *Corokia* has closer relatives elsewhere in the Cornales or the Saxifragales also needs to be examined. Embryologically, the Nyssaceae (Tandon and Herr Jr, 1971; Rao, 1972) stand apart from *Corokia* by their six-layered anther wall, two-nucleate pollen, ventral raphe, absence of endothelium and hypostase, ephemeral antipodal cells, multiplicative integument, divisions of epidermal cells of the nucellar apex, Nuclear endosperm, absence of endosperm haustoria and lignification of outer epidermal cells of the ovule during seed formation. Pollen in Nyssaceae (Sohma, 1963) is tricolporate (*Nyssa javanica*) or tricolporoidate (*Davidia involucrata*), but isopolar pollen with perforated exine noticed in *Nyssa* is different from *Corokia*. The basic chromosome number, x=11 (Raven, 1975), substantiates evidence from other sources to show a lack of affinity with *Corokia*. Likewise, the Garryaceae (Kapil and Rao, 1966) are quite distinct with their catkin-like inflorescences, tetramerous flowers, five-layered anther wall, crassinucellar ovules, absence of endothelium, polyantipody, Nuclear endosperm, suspensor polyembryony, and spathulate embryo with large cotyledons. Unicellular trichomes, paracytic stomata (Paliwal and Kakkar, 1970) and the basic chromosome number, x=11 (Raven, 1975) in *Garrya* also show a lack of any affinities of *Corokia* with the Garryaceae.

The genus *Mastixia* with five-layered anther wall, cavities in the anther connective (Bhatnagar and Rawat-Bisht, 2008), crassinucellate ovules, stylar canal with stigmatoid cells, and unicellular T-shaped trichomes (unpublished observations in *M. arborea*), bears greater resemblance with the Cornaceae than with *Corokia*. *Helwingia*, which is variably placed in the Cornaceae (Melchior, 1964; Thorne, 1973), Araliaceae (Hutchinson, 1959), or is treated as an independent family Helwingiaceae (Takhtajan, 1969), has some resemblance with *Corokia* in the structure of ovule and in the presence of an endothelium, but its separate perianth and carpellary bundles (Horne, 1914), unilacunar node and ephemeral antipodal cells (Sato, 1976) are distinct features. Thus, on embryological grounds, *Corokia* does not seem to bear a close relationship with any member of the Cornaceae *s.l.* This is supported by anatomical data provided by Eyde (1966) and cytological evidence presented by Raven (1975). Fairbrothers *et al.* (1976) and Fairbrothers (1983) have also stated that the qualitative and quantitative immunochemical techniques indicate very little serological correspondence of *Corokia* with any tested taxa belonging to the Cornales.

The question of whether *Corokia* could be related to other woody segregates of the Saxifragaceae has not been seriously discussed, chiefly because these plants are generally opposite leaved. Al-Shammary and Gornall (1994) have pointed out that the pluricellular T-shaped trichomes with slits at the junction of the stalk and the T-piece which characterize *Corokia* and *Argophyllum* are also observed in *Deinanthe* of the Hydrangeoideae. In their opinion it is possible that *Corokia* and *Argophyllum* may have a hydrangeoid rather than escallonioid affinity. Members of Hydrangeaceae have tetra- or pentamerous flowers; three-colporoidate, subprolate pollen (in *Philadelphus*); inferior two- to five-locular ovary; anatropous, unitegmic, tenuinucellate ovules borne on two-five axile placentae; cellular endosperm, with micropylar haustorium in *Philadelphus*; and loculicidal or poricidal capsules (Davis, 1966; Spongberg, 1972). However, the presence of numerous stamens (sometimes 20 or more), large number of ovules in each carpel, confinement of endothelium to the lower half of embryo

sac, absence of hypostase, protrusion of embryo sac beyond the micropyle in *Philadelphus*, and multinucleate and haustorial antipodals have no parallel in *Corokia*. Some anatomical features such as ring- or semiring porous wood with small vessels, epidermal cells often containing tannin, raphide sacs containing mucilage common in most tissues and foliar stomata of paracytic or anisocytic type are also not encountered in *Corokia* and thus rule out any affiliations of this genus with the opposite-leaved, woody Saxifragaceae. Terminal endosperm haustoria is not reported in the Saxifragaceae or any of its segregates (see Johri *et al.,* 1992).

Dahlgren (1975) presented classification system of angiosperms based on exomorphology, anatomy, embryology and even chemical characters. His Cornanae included, besides the Cornales, the Ericales, Sarraceniales and Eucommiales. The herbaceous Sarraceniales (with numerous stamens and carpels and several ovules per locule) and the dioecious Eucommiales can be ruled out at first look as repositories *Corokia*. Ericales share several characters with *Corokia*, especially those of the vessels (Meylan & Butterfield, 1975). Ovule (Pyykkö, 1968), embryo (Palser, 1975; Yamazaki, 1975) (Terechin, 1962) and endosperm haustoria. However, the diagnostic characters of Ericales (Palser, 1975; Yamazaki, 1975) such as anthers dehiscing by terminal pores, pollen in permanent tetrads, two-celled pollen, absence of fibrous endothelium, numerous ovules in each carpel locule, female gametophyte with an enlarged micropylar end, antipodals surviving till fertilization, endosperm having a linear arrangement of first four-cells, and loculicidal capsule are not encountered in *Corokia*. The basic chromosome numbers in Ericales (x=8,10 or 12; Raven, 1975) also negate any phyletic relationship with *Corokia*.

Within Dahlegren's Cornales are placed 12 other families (and a few doubtful ones) besides a broadly conceived Cornaceae. Between the Escalloniaceae and Hydrangeaceae are placed two families- Columelliaceae and Stylidiaceae (including *Donatia*). The Australasian family Stylidiaceae (especially its segregate Donatiaceae) bears remarkable similarity with *Corokia* in its embryology. These plants are alternate leaved, much-branched herbs or shrubs distributed in Australia. Flowers are terminal, solitary or in peduncles, and bracteate. There are three to seven sepals, five to ten petals (free in *Donatia*), and two or three stamens inserted on the disc and generally fused with the style to form a column (free from the style in *Donatia*). The ligule of *Corokia* looks remarkably similar to the paracorolla of *Stylidium adnatum* (see Goldberg, 1986, in fig. 161e). The gynoecium in Stylidiaceae is bicarpellary, bilocular with a tendency toward unilocular condition (Subramanyam, 1951). Even in the bilocular ovary the septation is incomplete so that the locule is continuous in the upper region. As in *Corokia*, some lobed structures hang downward from the base of the style and surround the free part of the placenta. Several ovules arise from the placenta. This is in marked contrast to *Corokia* in which only one ovule is borne in each locule. However, in *Corokia* rarely two ovules are present in a locule, and sterile ovules have been observed to arise from the free part of the placenta, thus showing the possibility that the uniovulate condition could have arisen from multiovulate as in Stylidiaceae. The Styliadaceae have Dicotyledonous type of anther wall formation with glandular type tapetum (*Leyenhookia dubia*, Subramanyam, 1950) and the pollen is three-celled when shed (Gardner, 1975). The ovule is anatropous (or hemianatropous toward lower region), unitegmic and tenuinucellate. The single-celled archesporium is hypodermal. Linear or T-shaped tetrads are produced of which the chalazal megaspore forms a Polygonum type of embryo sac. The outer epidermis of ovule is replete with tannin in *Forstera* and *Donatia* (Philipson and Philipson, 1973), endothelium is differentiated, and a glandular, nutritive tissue or hypostase is reported below the antipodal end of embryo sac in *Stylidium squamellosum* (Burns, 1900). The embryo sac tapers at both ends. Synergids are elongated and have prominent filiform apparatus. Antipodal cells are persistent. The lower end of embryo sac forms a process that penetrates the chalazal end of the seed. The endosperm development is remarkably similar–the micropylar and chalazal tiers of cells develop into haustoria, whereas intervening cells form the endosperm tissue (Scutellaria type). The haustoria remain active until the late stage of embryo development. Although the pattern of early divisions in the endosperm varies in different species, the ontogeny and mature endosperm are similar in structure and behavior. An aggressive micropylar and relatively passive chalazal haustoria develop in all these species. The seeds are albuminous.

The seed coat development is identical to *Corokia*-all the integumentary cells except those of the epidermis are consumed during seed development (Corner, 1976). The inner layers of the pericarp become sclerosed and form a hard endocarp as in *Corokia*. In *Forstera* the capsule dehisces apically.

The pollen of *Donatia novae-zelandiae* is three- or four colporate, spheroidal (23 µm) and psilotegillate (Erdtman, 1952) and, thus, bears close resemblance with the pollen of *Corokia cotoneaster*. The subdermal tanniniferous layer in leaves and floral parts, so characteristic of *Corokia* (Eyde, 1966), is also encountered in *Stylidium graminifolium* (Subramanyam, 1951). Cytologically the Stylidiaceae are not well worked out. *Stylidium adnatum* has the somatic chromosome number 2n=36 (Sugiura, 1936), which also agrees with the basic number, x=9, found in *Corokia*.

Thus, *Corokia* has far more resemblance with the Stylidiaceae than with the Cornaceae or Escalloniaceae/ Grossulariaceae. The differences with Stylidiaceae are mostly concerning the number of stamens, carpels and

ovules. Some characters form a part of reproductive adaptation and are considered less important systematically.

In his revised classification Dahlegren (1983) has included Cornaceae, Escalloniaceae and Stylidiaceae (incl. *Donatia*), along with some other families, in the Cornales within the Corniflorae. *Corokia* has also been treated as an independent family Corokiaceae in the Cornales. The position of *Corokia* as a monogeneric family in the neighborhood of Stylidiaceae (including *Donatia*) seems eminently justifiable on embryological grounds. Since, based on the present level of knowledge, the embryological resemblance is far greater with *Donatia* than with *Argophyllum*. Takhtajan's (1987) inclusion of *Corokia* and *Argophyllum* in a separate family Argophyllaceae in Hydrangeales appears less convincing.

In a more recent analysis of Rolf Dahlegren's (1980) classification, Gertrud Dahlegren (1989) has subdivided the earlier super order Cornanae into two superorders, Cornanae *sensu stricto* and Ericanae. The position of Corokiaceae among these superorders is not indicated. However, the Stylidiales are placed in Ericanae. Since this new classification emphasizes the presence or absence of Cellular endosperm with terminal haustoria as one of the major characters for subdivision, the proper place for the Corokiaceae would be under the Ericanae. The Ericanae are characterized by the production of iridoid (Jensen, 1975). Considering that *Corokia* resembles the Stylidiaceae significantly in embryological, cytological and chemical features, the appropriate place for Corokiaceae would be in the order Stylidiales, along with the Stylidiaceae rather than in the Cornales along with the Cornaceae and Escalloniaceae.

ACKNOWLEDGMENTS

We thank Dr L.C. Armiger, Prof. B. A. Fineran, Miss Toni Kitchen, Dr Elizabeth Mclintock and Dr D.S. Varity who sent us materials from buds to seeds fixed in FAA over many years to complete all embryological stages.

LITERATURE CITED

Al-Shammary, K. and R. Gornall 1994. Trichome anatomy of the Saxifragaceae *s.l.* from the southern hemisphere. Bot. J. Linn. Soc. **114(2)**: 99–131.

Berezenko, N. and V. Liferova 1970. Some observations of embryology of *Grossularia reclinata* Mill. Ukr. Bot. J. **27**: 318–324.

Bhatnagar, A.K. and R. Rawat-Bisht 2008. Air cavities in anther connective of *Mastixia arborea* (Cornaceae). Phytomorphology 58: 81–83.

Burns, G.P. 1900**.** Beitrage zur kenntnis der Stylidiaceen. Flora **87**: 313–354.

Corner, E.J.H. 1976. The Seeds of Dicotyledons. Vols. I & II. Cambridge, U.K.

Cronquist, A. 1968. The evolution and classification of flowering plants. London, U.K.

Cronquist, A. 1988. The evolution and classification of flowering plants. The New York Botanical Garden. New York, USA.

Dahlgren, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. **128**: 119 – 147.

Dahlgren, R. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. **80(2)**: 91–124.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nord. J. Bot. **3(1)**: 119–149.

Dahlgren, G. 1989. The last Dahlgrenogram. System of classification of dicotyledons. In: Davis & Hedge Festchrift: 249–260.

Davis, G.L. 1966. Systematic embryology of the angiosperms. John Wiley, New York

Engler, A. 1930. Saxifragaceae. In: Engler, A., Prantl, K., (eds.) Not. Pflanzenfam. 2. Aufl., 74–226.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms. Waltham Mass and Stockholm.

Eyde, R.H. 1966. Systematic anatomy of the flower and fruit of *Corokia*. Am. J. Bot. **53(8)**: 833–847.

Eyde, R.H. 1988. Comprehending Cornus: Puzzles and progress in the systematics of the dogwoods. Bot. Rev. **54(3)**: 233–351.

Fairbrothers, D., T. Mabry, R. Scogin and B. Turner 1975. The bases of angiosperm phylogeny: chemotaxonomy. Ann. Missouri Bot. Gard. **62(3):** 765–800.

Fairbrothers, D.E. 1983. Evidence from nucleic acid and protein chemistry, in particular serology, in angiosperm classification. Nord. J. Bot. **3(1)**: 35–41.

Feder, N. and T.P. O'Brien 1968. Plant Microtechnique: some principles and new methods. Am. J. Bot. **55(1)**: 123–142.

Gardner, R. 1975. A survey of the distribution of binucleate and trinucleate pollen in the New Zealand flora. N. Z. J. Bot. **13(3)**: 361–366.

Gibbs, R.D. 1974. Chemotaxonomy of Flowering Plants: Four Volumes. McGill-Queen's Press-MQUP.

Goldberg, A. 1986. Classification, evolution, and phylogeny of the families of Dicotyledons Smithsonian contributions to botany. Smithsonian Institution Press, Washington, DC.

Harms, H. 1898. Cornaceae. In: Engler A, Prantl K, (eds.), Naturlichen Pflanzenfamilien. III, 8: 250–270.

Hegnauer, R. 1965. Chemismus and systematische Stellung der Cornaceae. Beitrage zur Biochemie and Physiologie von Naurstoffen. Jena, Germany.

Hegnauer, R. 1969. Chemical evidence for the classification of some plant taxa. In: Harborne, JB, Swain T, eds. Perspectives I Phytochemistry. London, U. K. 121–138.

Hideux, M.J. and I.K. Ferguson. 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae *sensu lato*. In: Ferguson, I.K., Miller, J. (eds.), The Evolutionary Significance of the Exine. New York, U.S.A. 327–377.

Horne, A.S. 1914. VIII. A Contribution to the Study of the Evolution of the Flower, with special reference to the Hamamelidaceae, Caprifoliaceae, and Cornaceae. Trans. Linn. Soc. Lond: Botany **8(7)**: 239–309.

Huber, H. 1963. Verwandtschaftsverhältnisse der Rosifloren. Mitt. Bot. St Samml. Munch. **5**: 1–48.

Hutchinson, J. 1959. The families of flowering plants. Vol. I., 2nd Edition. Oxford, U.K.

Jensen, S.R. 1975. Iridoid compounds, their occurrence and systematic importance in the angiosperms. Bot. Not. **128**:148–180.

Johri, B.M., K.B. Ambegaokar and P.S. Srivastava 1992. Comparative Embryology of Angiosperms. Springer, Berlin, 862–898.

Kapil, R.N. and A.K. Bhatnagar 1974. Stomata on leaves and floral parts of *Corokia*. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie. **94**: 257–266.

Kapil, R.N. and A.K. Bhatnagar 1991. Embryological evidence in angiosperm classification and phylogeny. Bot. Jahrb. Syst. **113**: 309–338.

Kapil, R.N. and A.K. Bhatnagar 1992. Embryology and systematic position of *Corokia* Cunn.. In: Proceedings XI International Symposium on Embryology and seed reproduction (Abstract). Leningrad. 1990. St. Petersburg: Nauka.

Kapil, R.N. and P.M. Rao 1966. Studies of Garryaceae. 2. Embryology and systematic position of *Garrya* Douglas ex Lindley. Phytomorphology **16**: 564–578.

Kaur, H. 1970. Cornaceae. In: Proc. Symp. On *Comparative Embryology of Angiosperms*. Indian Nat. Sci. Acad. Bull. No. 41. New Delhi, India. 230–232.

Krach, J. 1976. Seed anatomy of the Rosiflora. I. The seeds of the Saxifragaceae [Taxonomy]. *Bot.* Jahrb. Syst. **97**:1–60.

Lundberg, J. and K. Bremer 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Int. J. Plant Sci. **164 (4):** 553–578.

Melchior, H. 1964. A. Engler's Syllabus der Pflanzenfamilien 12. Angiospermen **2**: 666 Berlin, Germany.

Meylan, B. and B. Butterfield 1975. Occurrence of simple, multiple, and combination perforation plates in the vessels of New Zealand woods. N. Z. J. Bot. **13(1)**: 1–18.

Paliwal, G. and L. Kakkar 1970. Leaf anatomy of some *Garrya* species. Bot. J. Linn. Soc. **63(1)**: 81–90.

Palser, B.F. 1975. The bases of angiosperm phylogeny: embryology. Ann. Missouri Bot. Gard. **62(3)**: 621–646.

Patel, R.N. 1973a. Wood Anatomy of the Dicotyledons Indigenous to New Zealand: 1. Cornaceae. N. Z. J. Bot. **11(1)**: 3–22.

Patel, R.N. 1973b. Wood anatomy of the dicotyledons indigenous to New Zealand: 2. Escalloniaceae. N. Z. J. Bot. **11(3)**: 421–434.

Philipson, W.R. and M.N. Philipson 1973. A comparison of the embryology of *Forstera* L. and *Donatia* JR & G. Forst. N. Z. J. Bot. **11(3)**: 449–460.

Philipson, W.R. 1967. *Griselinia* Forst. fil. - anomaly or link. N. Z. J. Bot. **5(1)**: 134–165.

Popova, A.E. 1965. Formation and development of generative organs of the black current (*Ribes nigrum* L.). Ukr. Bot. J. **22**: 83–89.

Pyykkö, M. 1968. Embryological and anatomical studies on Finnish species of the Pyrolaceae. Ann. Bot. Fenn. **5**: 153–165.

Rao, P.R.M. 1972. Embryology of *Nyssa sylvatica*, and systematic consideration of the family Nyssaceae. Phytomorphology **22**: 8–21.

Raoul, E. 1846. Choix de plantes de la Nouvelle-Zélande. Fortin. Masson et Cie, Paris.

Raven, P. H. 1975. The bases of angiosperm phylogeny: cytology. Ann. Missouri Bot. Gard. **62(3)**: 724–764.

Rodriguez, R. 1971. The relationships of the Umbellales. In: Heywood, V. H. (ed.). The Biology and Chemistry of the Umbelliferae: 63–91. London, U.K.

Sato, Y. 1976. Embryological studies of some cornaceous plants. Science Reports of the Research Institutes, Tohoku University Ser. IV (Biol.) **37**: 117–130.

Sohma, K. 1963. Pollen morphology of the Nyssaceae, II. Nyssa and Davidia. Science Reports of the Research Institutes, Tohoku University Ser. IV (Biol.) **33**: 527–532.

Spongberg, S.A. 1972. The genera of Saxifragaceae in the southeastern United States. J. Arnold Arbor. **53**: 409–498.

Subramanyam, K. 1950. An embryological study of *Levenhookia dubia* Sond in Lehm. Proc. Nat. Inst. Sci., India B: 245–253.

Subramanyam, K. 1951. A morphological study of *Stylidium graminifolium*. Lloydia **14**: 65–81.

Sugiura, T. 1936. A list of chromosome numbers in angiospermous plants. II. Proc. Imperial Acad. **12(5)**: 144–146.

Takhtajan, A. 1969. Die Evolution der Angiospermen. Gustav. Fischer Verlag, Jena, Germany.

Takhtajan, A. 1987. Systems Magnoliophytorum. Academia Scientiarum URSS, Leningrad.

Tandon, S.R. and J.M. Herr, Jr. 1971. Embryological features of taxonomic significance in the genus *Nyssa*. Can. J. Bot. **49(4)**: 505–514.

Terechin, E.S. 1962. O rasvitie sarodsej u nekotorych Pyroleae Monotropoideae. Botanical Zh., Kyyiv **47**: 1811–1816.

Thorne, R. 1973. Inclusion of the Apiaceae (Umbelliferae) in the Araliaceae. Edinberg Royal Botanical Garden Notes. **32**: 161–165.

Thorne, R.F. 1983. Proposed new realignments in the angiosperms. Nord. J. Bot. **3(1)**: 85–117.

Wangerin, W. 1910. Cornaceae. In: Engler, A. (ed.). Das Pflanzenreich. Heft 41 (IV. 224), Leipzig. 1–110.

Willis, J.C. 1973. A dictionary of the flowering plants and ferns. Ed. 8, Cambridge, U. K.

Yamazaki, T. 1975. Floral anatomy and embryology of *Tripetaleia paniculata* and *T. bracteata* (Ericaceae). Bot. Mag. **88(4)**: 267–279, Tokyo.