American Journal of Botany

Some Morphological Features for Generic Characterization Among the Casuarinaceae
Author(s): John G. Torrey and R. Howard Berg
Source: *American Journal of Botany*, Vol. 75, No. 6 (Jun., 1988), pp. 864-874
Published by: Botanical Society of America
Stable URL: http://www.jstor.org/stable/2444006
Accessed: 23/08/2011 15:52

Amer. J. Bot. 75(6): 864–874. 1988.

SOME MORPHOLOGICAL FEATURES FOR GENERIC CHARACTERIZATION AMONG THE CASUARINACEAE[1]

JOHN G. TORREY AND R. HOWARD BERG

Harvard Forest, Petersham, Massachusetts 01366; and Biology Department,
Memphis State University, Memphis, Tennessee 38152

ABSTRACT

The family Casuarinaceae has been divided recently into four genera on the basis of differences in chromosome numbers, morphological characters including stem morphology, structures of the male and female flowers and fruits, their modern biogeography, and fossil record. All members of the family are characterized by highly reduced leaves, photosynthetic deciduous branchlets, and adaptations to xeric or hot humid environments. The genus *Gymnostoma* is characterized by multiple rows of naked stomata along the central vertical faces of the stem internodes. *Casuarina* and *Allocasuarina* develop vertically aligned rows of stomata in deep furrows that alternate with stem ridges. Epidermal hairs, formed within the furrows, occur in different species in conformity with other xeric characters. The characters described in this paper conform to the view that the morphological structures represent reduction and specialization rather than primitiveness.

THE FAMILY Casuarinaceae is comprised of four genera: *Allocasuarina* L. Johnson, *Casuarina* Adans., *Gymnostoma* L. Johnson and a fourth genus, *Ceuthostoma,* still to be described (Johnson and Wilson, 1981; Johnson, 1982, in press). The family is a large group native to Australia, Malaysia and Polynesia. Members of the genus *Casuarina* sensu stricto have been disseminated by man to most parts of the tropical and subtropical world where they serve as important sources of fuel wood (National Academy of Sciences, 1980), and multi-use trees for windbreaks, dune stabilization and for soil improvement by virtue of their symbiotic association with the root-nodulating nitrogen-fixing actinomycete *Frankia* (Midgley, Turnbull, and Johnston, 1983; National Academy of Sciences, 1984).

Taken as a whole, the family probably includes some 90 species distributed among the four genera in the following ratio: *Allocasuarina* 54 spp., *Casuarina* 16 spp., *Gymnostoma* 18 spp. and *Ceuthostoma,* 2 species (Johnson, 1982, and personal communication). Separation of the four genera is based on a series of characters including chromosome numbers, morphology of the vegetative shoot, including the distribution of stomata on the branches, structures of the male and female inflorescences and fruits together with their biogeography and fossil record (Johnson and Wilson, 1981). All members of the family show highly reduced vegetative morphology with reduced scale-like leaves and needle-like branchlets that serve as photosynthetic organs. The reduction or simplification of the vegetative axis characterizes the xeromorphy of the shoot in this family whose growth habits range from low-growing woody shrubs a meter or so in height (e.g., *Allocasuarina nana*), to tall trees in excess of 35 meters in height as in *Casuarina cunninghamiana* or *C. grandis* (Doran and Hall, 1981). According to Moseley (1948), members of the Casuarinaceae were derived in brackish areas, sand dunes or dry, marginal, low-nutrient sites that were either physiologically or climatically arid environments. After study of structures within the family, Moseley concluded that their morphological characteristics represent reduction rather than primitiveness.

Of special interest in the group is the development of cuticular modifications accompanying their xeromorphic characters, the variation in distribution of stomata on the branchlets and reduced scale leaves, and the occurrence and distribution of epidermal hairs (Withers, 1978). Five species among three of the four genera in the Casuarinaceae have been selected as representative of the morphological characteristics among the major groups. Some of their distinctive features based on scanning electron microscopy (SEM) are presented here.

MATERIALS AND METHODS—For the most part, material for SEM was taken from living plants started from seed and grown in the greenhouse at the Harvard Forest in Petersham, Massachusetts.

---

[1] Received for publication 16 February 1987; revision accepted 26 August 1987.

This research was supported in part by the Maria Moors Cabot Foundation for Botanical Research of Harvard University and by USDA Grant 83-CRCR-1-1315 to RHB.

Sources of seed were as follows:

Casuarina cunninghamiana Miq. From collection by Division of Forest Research, CSIRO, Canberra, Australia.

Casuarina equisetifolia Forst. & Forst. Collected from coastal sand dunes at Indialantic, Florida. Figures 3–6 were photographs of shoots from tissue cultures derived from axenically-grown seedlings.

Allocasuarina lehmanniana (Miq.). L. Johnson. Seeds made available from collections of the King's Park Botanical Garden, Perth, Western Australia.

Allocasuarina decaisneana (F. Muell.) L. Johnson. Collected from trees near Alice Springs, Northern Territory, Australia.

Gymnostoma papuanum (S. Moore) L. Johnson. Collected from trees at The Waiakea Arboretum, U.S. Forest Service, Institute of Pacific Islands Forestry, near Hilo, Hawaii.

For scanning electron microscopy shoots were fixed in 2.5% redistilled glutaraldehyde in 0.1 M Na cacodylate buffer at pH 7.2. After primary fixation for 1.5–2.5 hr, the tissue was rinsed 30 min in 3 changes of buffer and postfixed in several changes of buffered 2% osmium tetroxide at 25 C for 48 hr. Specimens were critical-point dried after dehydration to 100% ethanol. After being coated with gold, samples were examined in a Hitachi S-450 SEM, using an accelerating voltage of 20 kv.

OBSERVATIONS—In Table 1 are summarized the major features of these five species brought together from available sources and from the SEM observations made during this study. The chromosome numbers of the genera are listed according to Barlow (1983) and reflect the distinctness of the three different genera. According to Barlow, *Gymnostoma* may be the least specialized with *Allocasuarina* the most specialized. The geographical occurrence of these species and the climatic conditions are taken from Doran and Hall (1981) and from Johnson (1982). The sites and climates epitomize the differences in the distributions of these genera and further emphasize the distinctions among the genera.

There exist much discussion and controversy over the appropriate descriptive terminology for the vegetative features of these genera. The following general description of the vegetative body utilizes terms which seem most acceptable based on existing evidence. For extended discussions of the features of the vegetative axis one is referred to the published work of Moseley (1948), Metcalfe and Chalk (1950), Flores (1977, 1978, 1980), Barlow (1983), and Woodall and Geary (1985).

The stem comprises two types of structures: indeterminate persistent branches which undergo secondary thickening and form the permanent aboveground plant body and determinate deciduous branchlets that have radial, jointed stems, possessing green photosynthetic tissues and widely distributed stomata. The deciduous branchlets are the photosynthetic organs of the plant, rather than the scale leaves. They are characterized by ribbed and furrowed longitudinal internodes with nodes defined by whorls of scale leaves. In *Gymnostoma* the stems are always quadrangulate but such 4-sided branchlets occur also in some species of *Allocasuarina.*

Leaves are reduced lateral appendages, white or brown and scale-like. The symmetrical lamina is linear or lanceolate with 1 or 3 veins. The leaves in whorls are fused laterally at their bases, and alternate at successive nodes with those below.

Stomata occur in characteristic fashion in the different genera, typically oriented transversely with respect to the long axis of the internode and either within deep vertical furrows or grooves running longitudinally along the internodes or slightly sunken on the flat face of the branchlet stem surface. Epidermal hairs are typically uniseriate either branched or unbranched, and associated with stomatal distributions in furrows or on leaf adaxial faces or leaf edges. The epidermis of the stem typically shows elaborate, waxy surface incrustations with heavy cuticle and warty surface modifications.

The number of scale leaves per whorl at each node is not a particularly useful taxonomic character within the Casuarinaceae (Doran and Hall, 1981). In *Casuarina* and *Allocasuarina* the number of scale leaves and leaf ridges may range from 4 to about 16; in contrast, in *Gymnostoma* the branchlets are consistently 4-sided, the number of leaves 4 and the stomata are located on the four faces of the branchlets as will be described below. In Table 1 are given the number of scale leaves per leaf whorl found on the specimens described in this study.

Two characters of particular interest in defining these genera, i.e., the occurrence of stomata and epidermal hairs which are described in this paper, are listed in summary form in Table 1 and are illustrated in the SEM's presented in the figures. Emphasis will be placed on stomatal distribution on the stem or branchlet surfaces and on the adaxial surfaces of the leaf scales. The occurrence of epidermal hairs, especially in relation to the stomata, is also

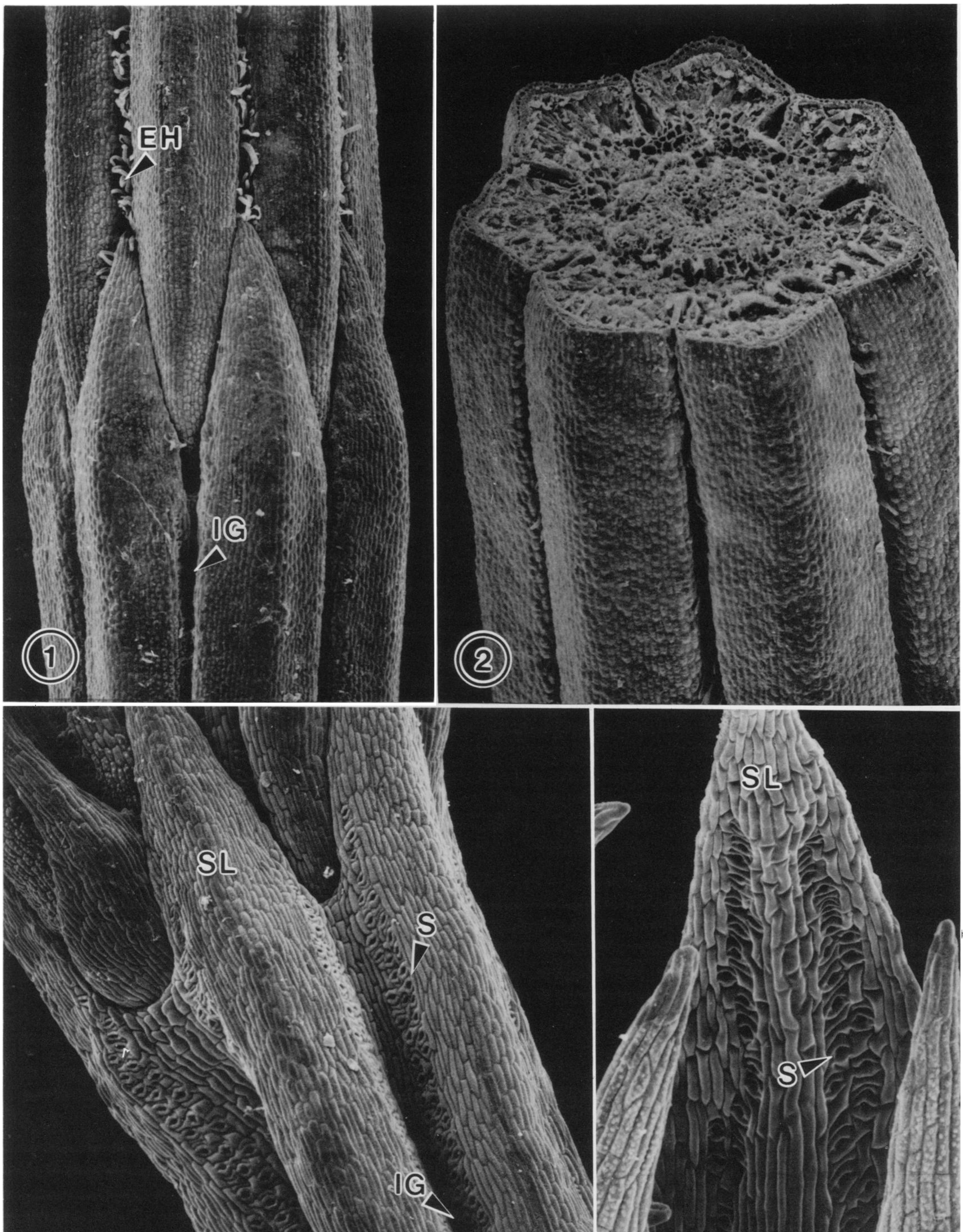


Fig. 1–4. *Casuarina equisetifolia* stem and leaves of deciduous branchlet. **1.** Nodal region of stem showing alternation of leaves in successive nodes. Epidermal hairs (EH) erupt from internodal grooves (IG). ×70. **2.** Transverse face of stem showing 7 ribs and furrows with stomata lining grooves. ×100. **3.** Rows of stomata (S) in grooves (IG) extending to scale leaf (SL) bases. Note lack of epidermal hairs. ×80. **4.** Adaxial surface of scale leaf (SL) showing 2 double rows of stomata (S) along either side of midrib. ×250.

TABLE 1. *Summary of several characters used in the separation of genera in the Casuarinaceae*

Genus and species	Chromosome no. of genus (Barlow, 1983)	Geographical occurrence and climate	Number of scale leaves (in sample)	Stomatal distribution		Epidermal hairs		
				On stem surface (abaxial)	On leaf scale (adaxial)	On stem surface (abaxial)	On leaf scale (adaxial)	Surface appearance of stem
Casuarina equisetifolia	$N = 9$	Australia: coastal areas of Queensland, New South Wales, warm to hot subhumid	7	In deep grooves on two facing sides with 2–3 vertical rows, exposed near node	Two vertical rows each with staggered double rows; frequent	In grooves toward base of internodes, lacking at upper end of grooves	Absent	Smooth and rounded with no "midrib"
C. cunninghamiana	$N = 9$	Australia: Queensland, Northern Terr., New South Wales Freshwater sites, warm to hot, subhumid to humid	10	In grooves, totally hidden	Two vertical rows; infrequent and scattered vertically	Short epidermal hairs in grooves along full length of internode	Frequent on edges of leaf scales. None on adaxial surface	Smooth but angular with beaded papillae
Allocasuarina lehmanniana	$N = 10$–14 or polyploid	Australia: western Australia	7	In grooves, hidden. Double rows on inner face of grooves	Two vertical rows each with 1–2 rows; sparse	No hairs on abaxial surface or grooves	Frequent on edges of scale leaves and on adaxial surface among stomata	Evident "midrib" with prominent rounded papillae
A. decaisneana	$N = 10$–14 or polyploid	Central Australia: Northern Terr., and W. Australia, hot, dry	4	In grooves, near edges. 2–3 vertical rows on each interface of groove	Two vertical rows each with two rows of stomata; frequent	In grooves all along internode. Elongate and arched over grooves	Along edges of lower portion of leaf scales and on adaxial face over stomata	Smooth rounded surface. No evident "midrib"
Gymnostoma papuanum	$N = 8$	Papua New Guinea, hot, humid	4	Naked central vertical rows from 2–5 stomata wide	Two rows of stomata each with two rows wide; scattered	No hairs on abaxial surface. No grooves	Short epidermal hairs on scale leaf edges None on adaxial surface	Prominent "midrib" but rounded and smooth

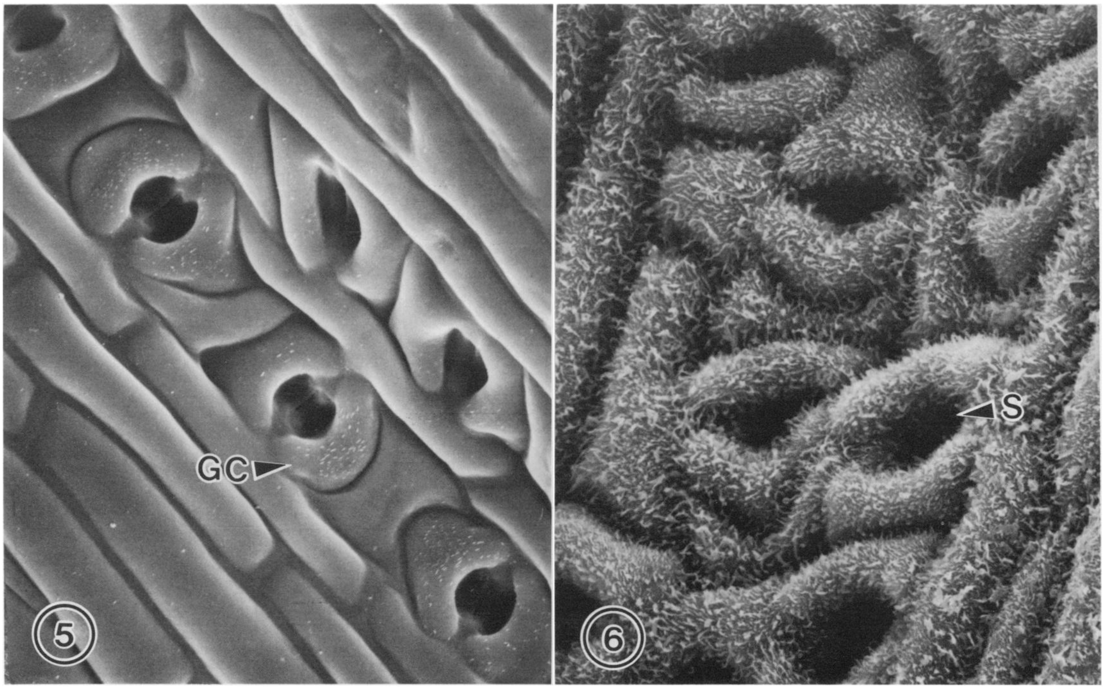


Fig. 5, 6. *Casuarina equisetifolia* leaf epidermis showing stomata. **5.** Epidermal cells, including guard cells (GC) lacking waxy deposits. ×1,200. **6.** Epidermal cells surrounding stomata (S) encrusted with waxy deposit. ×1,350.

described for each species. Finally, comments are made on the nature of epidermal modifications and appearance of the abaxial surfaces of scale leaves and branchlet stems.

Casuarina species—In Fig. 1–6 are shown distinctive features of the stem and scale leaves of *C. equisetifolia.* Seven scale leaves arise from the stem forming seven ridges, visible in cross-section of the stem (Fig. 2), with deep grooves between the ridges, each groove arranged with two double or triple vertical rows of stomata facing inward along the grooves (Fig. 3). Epidermal hairs which are absent on the scale leaves (Fig. 4) occur along the lower third of the grooves between internodes (Fig. 1) but are lacking along the upper portions of the grooves. The adaxial face of each scale leaf shows two parallel rows of stomata arranged typically in two rows each of alternating stomata (Fig. 4). Thus along much of the length of the green photosynthetic stem, the stomata face into a partially enclosed groove, allowing for gas exchange but probably reducing moisture loss. The adaxial surfaces (Fig. 5) show less epicuticular wax deposition than abaxial surfaces around stomata (Fig. 6).

In *C. cunninghamiana* vertical grooves between stem ribs are less evident (Fig. 9, 10) than in *C. equisetifolia.* Stomata occur in vertical rows within these grooves almost totally hidden by epidermal hairs (Fig. 8, 9). Scale leaves typically exhibit epidermal hairs along the distal edges of the leaves (Fig. 7) continuing up from the stem grooves. The adaxial face of the scale leaves shows two parallel uniseriate rows of stomata unadorned by hairs (Fig. 7). Beading of the stem epidermal cells and the midrib cells is usual. These two *Casuarina* species have in common, therefore, the distribution of stomata in deep grooves in the stem surface and limited occurrence of epidermal hairs in relation to the groove.

Allocasuarina species—Both *A. lehmanniana,* which occurs in western Australia, and *A. decaisneana* in central Australia show morphological characters presumed to be adaptations to the hot, seasonally dry sites in which they may be found. Both show elongate epidermal hairs clustered around and along deep grooves in which stomata occur. In *A. lehmanniana* the vertical grooves of the stem are lined with stomata in scattered vertical rows (Fig. 12) and are partially covered by branched epidermal hairs (Fig. 12). Elongate epidermal hairs edge the scale leaves and the adaxial surfaces of the scale leaves over and around the two rows of stomata (Fig. 13). The stem ridge midribs are prominent and the surfaces beaded (Fig. 11, 14).

Allocasuarina decaisneana, which grows in

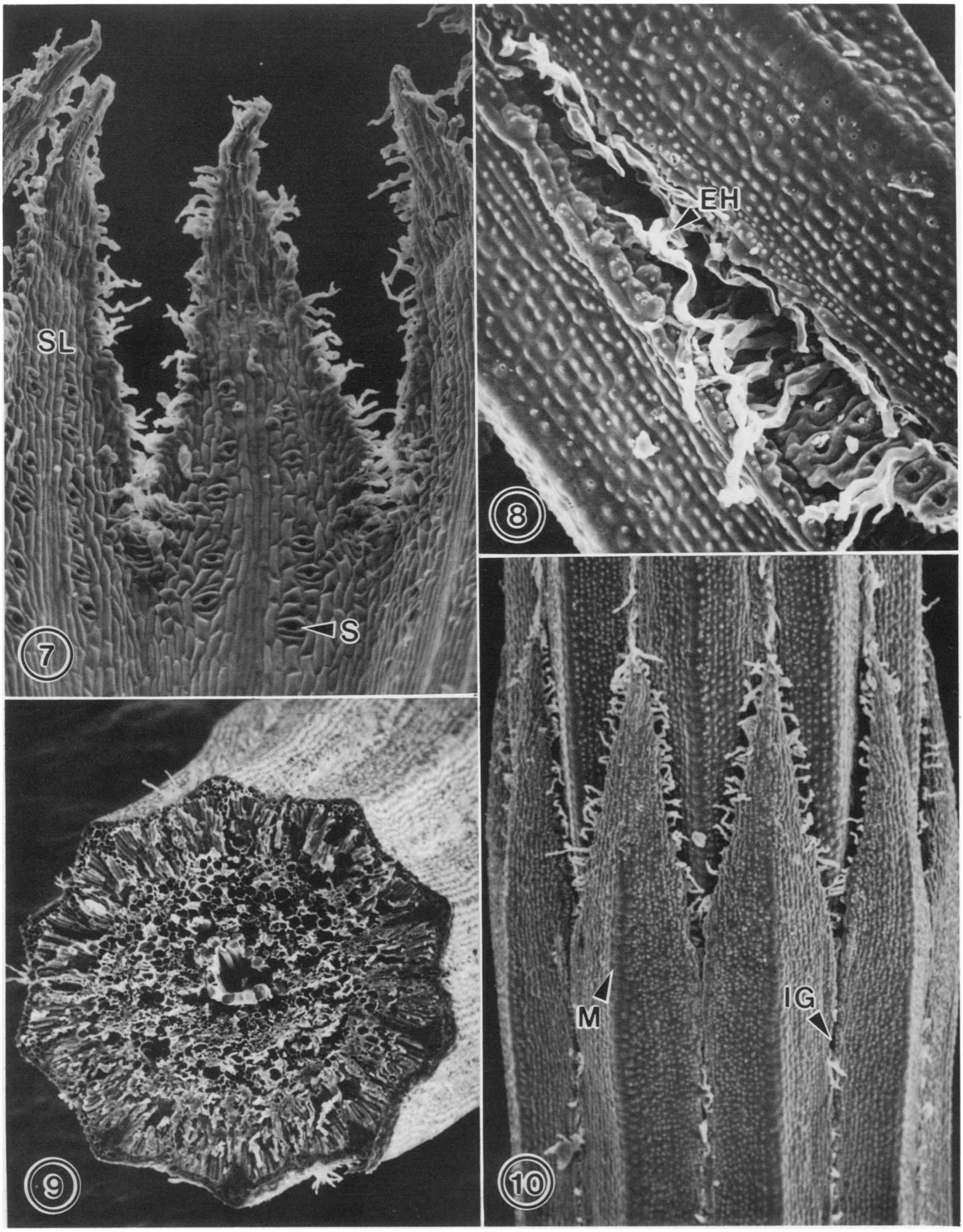


Fig. 7–10. *Casuarina cunninghamiana* stem and leaves of deciduous branchlet. **7.** Adaxial surface of scale leaves (SL), showing 2 single rows of stomata (S) paralleling midrib and numerous epidermal hairs along leaf edge. ×160. **8.** Enlarged view of internodal groove showing stomatal rows within groove and emerging epidermal hairs (EH). ×250. **9.** Transverse view of stem showing 10 shallow grooves alternating with stem ribs. Note epidermal hairs emerging from grooves. ×90. **10.** Scale leaves with epidermal hairs merge into the internodal ribs separated by grooves (IG). Grooves show emergent epidermal hairs. Scale leaves and internodal ribs have a midrib (M). ×90.

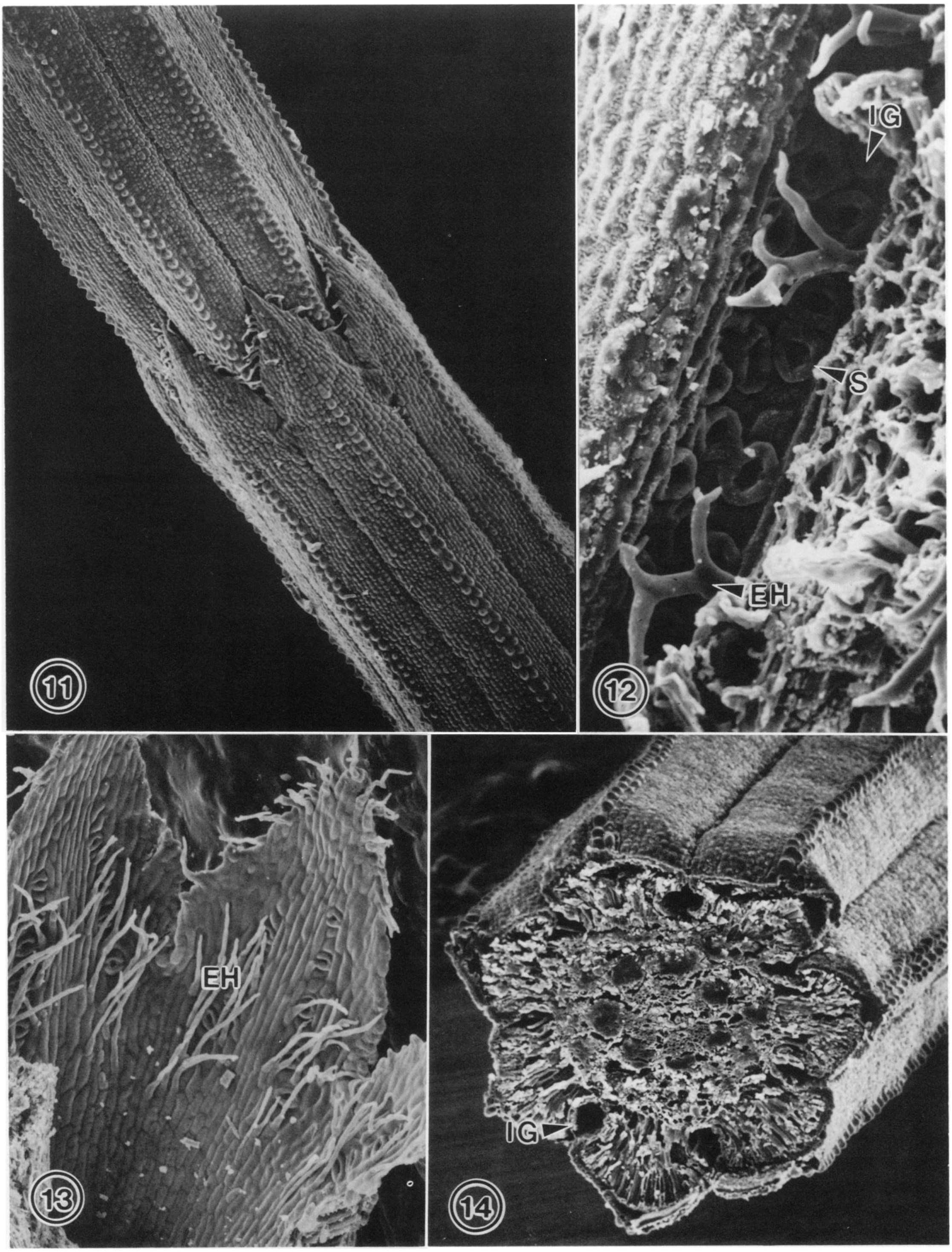


Fig. 11–14. *Allocasuarina lehmanniana* stem and leaves of deciduous branchlet. **11.** Node and portions of two internodes of branchlet showing prominent ribbing and deep grooves. Leaves and ribs alternate at each node. Epidermal hairs emerge from the scale leaves. ×70. **12.** Enlarged view looking into internodal groove (IG) showing multiple rows of stomata (S) with branched epidermal hairs (EH) overarching. ×340. **13.** Adaxial surface of scale leaves showing 2 rows of spaced single stomata hidden by epidermal hairs (EH). Small epidermal hairs are at edges of leaves. ×140. **14.** Transverse view of stem showing deep grooves (IG) alternating with prominently ribbed internodal surfaces of stem. ×90.

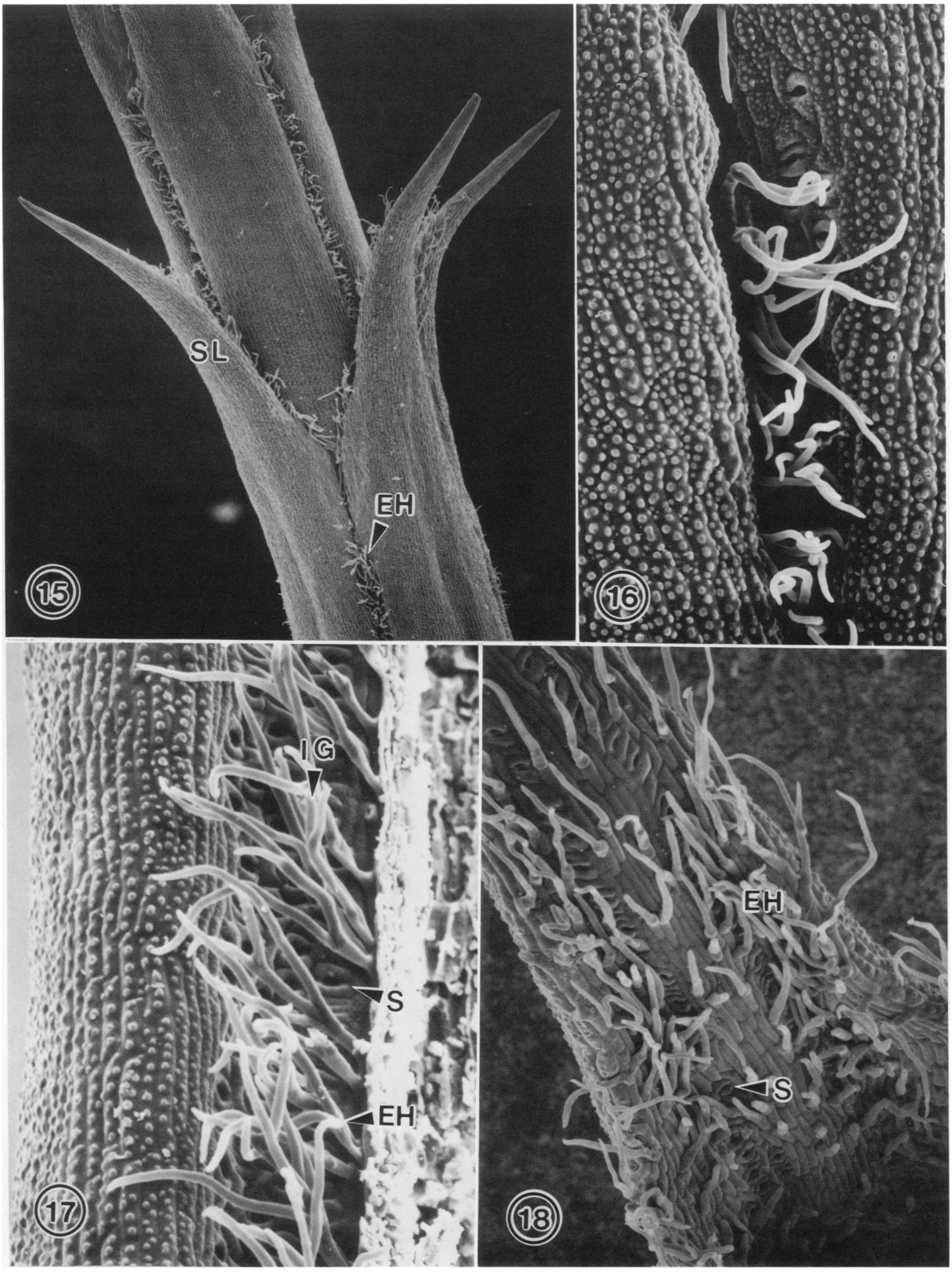
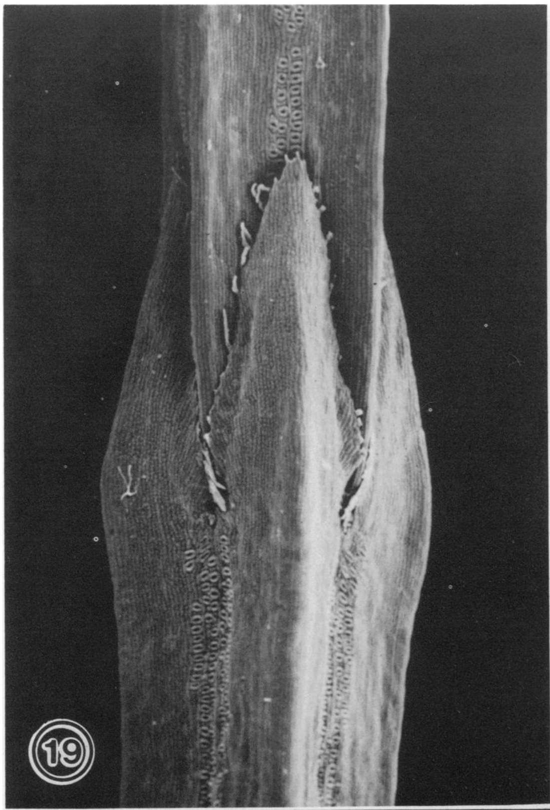
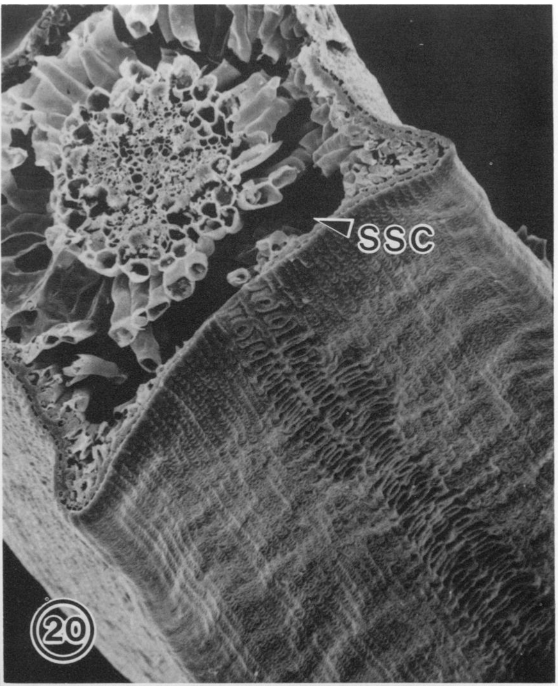
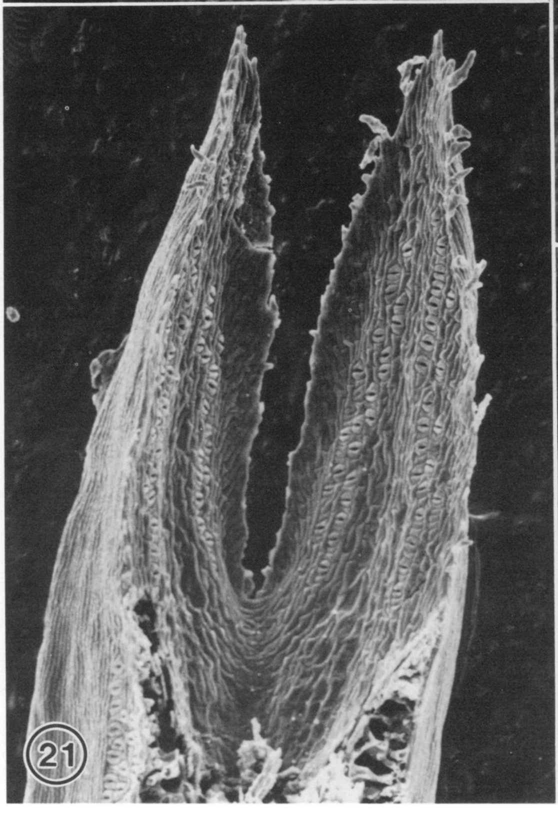
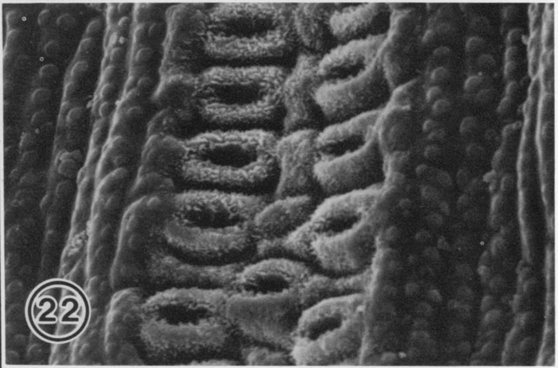


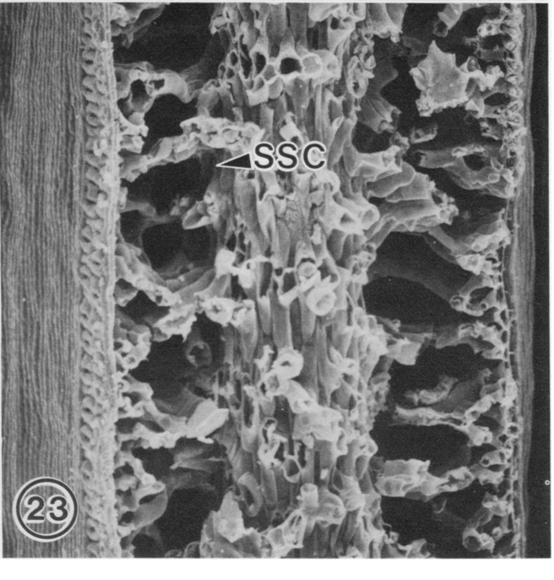
Fig. 15–18. *Allocasuarina decaisneana* stem and leaves of deciduous branchlets. **15.** Node of stem with prominent scale leaves (SL) and alternating internodal tissues above. Note abundant epidermal hairs (EH) exerted from internodal grooves and on adaxial face of scale leaves. ×50. **16.** Enlarged view of internodal groove showing epidermal hairs and rows of stomata within groove. ×460. **17.** View into internodal groove (IG) showing multiple vertical rows of stomata (S) and overarching epidermal hairs (EH). ×260. **18.** Adaxial view of scale leaf covered with epidermal hairs (EH) arising from cells around vertically oriented rows of stomata (S). ×190.


19


SSC
20


21


22


SSC
23

one of the driest habitats in central Australia, shows elaborated epidermal hairs along the stem grooves (Fig. 15–17) surrounding and overarching the stomatal rows that run longitudinally in the sunken grooves of the stem. Epidermal hairs cover the lower half of the adaxial face of the scale leaves (Fig. 15), nearly obscuring the two rows of stomata (Fig. 17, 18). The paired stomatal rows extend nearly to the tip of the scale leaves where epidermal hairs are lacking (Fig. 15, 18). Scale leaves are rounded abaxially showing no midrib but epidermal cells are covered with beaded cuticular incrustation.

Gymnostoma species—Although less familiar because, unlike *Casuarina* spp., *Gymnostoma* has not been distributed worldwide by man, it is a large genus comprised of about eighteen species (Barlow, 1983). *Gymnostoma* is restricted to the hot, humid tropics on the islands of the South Pacific and Malaysia. The genus, as the name given by Johnson (1980) adapted from a term used by Poisson (1871) indicates, is distinctive in having naked stomata located in vertical rows along each face of the quadrangular stem. Each row consists of two to five axial series of stomata (Fig. 19, 20, 22). In *Gymnostoma papuanum* sections of the stem (Fig. 20, 23) show that the stomata open internally into large intercellular chambers that facilitate gas exchanges between the atmosphere and the green photosynthetic tissues of the stem, an adaptation lacking in the more xeromorphic genera of the family. Stomata also occur almost at random in vertical arrays on the adaxial surfaces of the scale leaves (Fig. 21). Epidermal hairs are reduced and restricted to the distal edges of the scale leaves (Fig. 19, 21). The prominent "midrib" is rounded, smooth and shows little epidermal cuticular development. The morphology reflects adaptations to a moist environment.

DISCUSSION—Genera of the Casuarinaceae pose intriguing problems for the morphologist, systematist, physiologist and biologist interested in biogeography and evolution. Due to the presence of numerous deciduous, needle-like branchlets with highly reduced leaves, members of this family have a deceptively conifer-like habit. This impression is augmented by the occurrence of cone-like infructescences. On careful examination one observes its basic angiospermous traits. The simplified and reduced male and female flowers are unisexual, borne on plants that are monoecious or dioecious. These plants are adapted to wind pollination. The family has been considered primitive within angiosperms or in more recent years as moderately specialized and reduced. (For the review of these arguments, consult the papers by Moseley, 1948; Flores, 1977, 1978, 1980; Flores and Moseley, 1982; and Barlow, 1983.)

Of special interest have been the morphological and physiological adaptations to a great range of soils and climates. One can name species within the family, many of them endemics, adapted to every one of the fifteen described ecosystems on continental Australia (Specht, Roe, and Boughton, 1974) and still others on the South Pacific islands and in Malaysia. In part because of their capacity to form dinitrogen-fixing root nodules in response to infection by the soil actinomycete, *Frankia* (Torrey, 1982), these plants survive in a wide range of nutrient-poor soils.

Particularly striking are the morphological characters involving presumed adaptations to xeric or moist environments. Justification for the generic segregation on morphological and other grounds is summarized by Barlow (1983) and much further detailed information promises to be forthcoming from the studies of L. A. S. Johnson and his associates. The remarkable reduction of the leaf and the question of interpreting the internodal tissue as axial or as related to leaf bases early led to coining the term "phyllichnium" (Loew, 1865) to designate the single leaf base-like components of internodes. More recently, references to the photosynthetic branchlets as "cladodes" have been criticized (Rao, 1972; Flores, 1977) and discarded by them. Arguments over terminology in this group reflect the uniqueness of

---

←

Fig. 19–23. *Gymnostoma papuanum* stem and leaves of deciduous branchlet. **19.** Node of stem showing scale leaves alternating with midribs of adjacent internode. Multiple rows of stomata are distributed along the slightly depressed stem surfaces between prominent ridges of the quadrangulate stem. ×70. **20.** Transverse section of 4-sided stem showing rows of naked stomata on the stem surface and elaborate substomatal cavities (SSC) within the stem. ×170. **21.** Adaxial surfaces of scale leaves show multirowed stomata distributed parallel to midrib region. Short epidermal hairs occur at the leaf edges. ×140. **22.** Waxy deposits on epidermal surfaces of naked stomata on stem. ×600. **23.** Longitudinal section of portion of stem internode showing the substomatal cavities (SSC) beneath stomatal rows. ×140.

the morphologies involved. Descriptive terms used here appear to be the simplest that are useful and accepted by modern students of the family.

Stomatal occurrence, distribution and associated epidermal modifications, such as epidermal hair formation which are emphasized in this SEM study, all suggest adaptation either to xeric or to humid environments and offer one more set of characters which, together with other criteria, present additional bases for Johnson's (1982) generic separations and conform to the view that these structures represent reduction and specialization rather than primitiveness.

LITERATURE CITED

Barlow, B. A. 1983. Casuarinas—a taxonomic and biogeographic review. *In* S. J. Midgley, J. W. Turnbull, and R. D. Johnston [eds.], Casuarina ecology, management and utilization, 10–18. CSIRO, Melbourne, Australia.

Doran, J. C., and N. Hall. 1981. Notes on fifteen Australian *Casuarina* species. Forest Research, CSIRO, Canberra, Australia.

Flores, E. M. 1977. Developmental studies in *Casuarina* (Casuarinaceae). III. The anatomy of the mature branchlet. Rev. Biol. Trop. 25: 65–87.

———. 1978. The shoot apex of *Casuarina* (Casuarinaceae). Rev. Biol. Trop. 26: 247–260.

———. 1980. Shoot vascular system and phyllotaxis of *Casuarina* (Casuarinaceae). Amer. J. Bot. 67: 131–140.

———, and M. F. Moseley, Jr. 1982. The anatomy of the pistillate inflorescence and flower of *Casuarina verticillata* Lamarck (Casuarinaceae). Amer. J. Bot. 69: 1673–1684.

Johnson, L. A. S. 1980. Notes on Casuarinaceae. Telopea 2: 83–84.

———. 1982. Notes on Casuarinaceae II. J. Adelaide Bot. Gard. 6: 73–87.

———. In press. Notes on Casuarinaceae III. The genus *Ceuthostoma.* Telopea.

———, and K. L. Wilson. 1981. Casuarinaceae, then and now. XIII Int. Bot. Congr. Abstr. 278.

Loew, E. 1865. (cited by Flores, 1978) De casuarinearum caulis foliique evolution et structure. Dissertatio inauguralis botanica. Berolini.

Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Oxford University Press, Oxford.

Midgley, S. J., J. W. Turnbull, and R. D. Johnston [eds.]. 1983. Casuarina ecology, management and utilization. CSIRO, Melbourne, Australia.

Moseley, M. F., Jr. 1948. Comparative anatomy and phylogeny of the Casuarinaceae. Bot. Gaz. 110: 231–280.

National Academy of Sciences. 1980. Firewood crops. National Academy Press, Washington, DC.

———. 1984. Casuarinas: nitrogen-fixing trees for adverse sites. National Academy Press, Washington, DC.

Poisson, I. 1871. (cited by Flores, 1977) Récherches sur les *Casuarina* et en particulier sur ceux de la Nouvelle Calédonie. Nouv. Arch. Mus. Hist. Nat. Paris. Ser. I 10: 59.

Rao, A. N. 1972. Anatomical studies on succulent cladodes in *C. equisetifolia* L. Proc. Indian Acad. Sci. LXXVI Sec. 86: 262–270.

Specht, R. L., E. M. Roe, and V. H. Boughton [eds.]. 1974. Conservation of major plant communities in Australia and Papua New Guinea. Austral. J. Bot. Suppl. Ser. 7. CSIRO, Melbourne, Australia.

Torrey, J. G. 1982. Casuarina: actinorhizal dinitrogen-fixing tree of the tropics. *In* P. H. Graham and S. C. Harris [eds.], Biological nitrogen fixation technology for tropical agriculture, 427–439. CIAT, Cali, Colombia.

Withers, J. R. 1978. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. III. Comparative water relations of the major tree species. Austral. J. Bot. 26: 819–835.

Woodall, S. L., and T. F. Geary. 1985. Identity of Florida casuarinas. USDA Forest Service SE Forest Exp. Sta. Res. Note SE-332: 1–10.