

***Alexgeorgea*, a Bizarre New Genus of Restionaceae from Western Australia**

Sherwin Carlquist

Claremont Graduate School and Rancho Santa Ana Botanic Garden,
Claremont, Calif. 91711, United States.

Abstract

The genus *Alexgeorgea* is described as new to science. Two species were discovered during field work in 1974: *A. subterranea*, from the Jurien Bay-Badgingarra sandplain, W.A., and *A. arenicola*, from sand areas short distances north and east of Perth. *Alexgeorgea* is highly distinctive in bearing single-flowered female inflorescences on sessile horizontal rhizomes c. 10-15 cm below the sand surface. In flower, only the tips of the bracts and the three ephemeral styles appear above the ground, so that female flowers are invisible most of the year and inconspicuous even at anthesis. Fruits are exceptionally large for Restionaceae, indehiscent, one-seeded and borne sessile on underground rhizomes. Difficulty in dispersal of these fruits would explain the existence of presumptive all-female colonies of *A. arenicola* which may have originated from single-fruit introductions to sites at the periphery of the range of that species. Increase in the size of colonies is mostly vegetative, by branching of the elongate subterranean rhizomes. It is suggested that the underground flowering and fruiting habit is related to fire resistance. *Alexgeorgea* appears most closely related to Western Australian species of *Restio* on account of striking vegetative similarities. The two species of *Alexgeorgea* are illustrated by habit photographs and macrophotographs of living plants taken during the field work.

Introduction

During field work in Western Australia, from 8 July to 21 October 1974, I paid particular attention to the Restionaceae. Interest in this family was developed as a result of field work in Cape Province, South Africa, in 1973 with Miss Elsie Esterhuysen, a well-known South African botanist and student of restiads. She showed me the essential features of this family and the necessity for collecting male plants in flower, female plants in flower and fruit, and underground portions. On 2 September 1974, I discovered a population of the plant named *Alexgeorgea subterranea* along the Cockleshell Gully road north from Jurien Bay, W.A. This was recognized as restionaceous from its male inflorescences, but no female flowers and fruits could at first be located. Then I noticed purple thread-like structures emerging from the sand in this population and realized that female flowers were, in fact, borne underground, with only styles emergent above the soil surface. Had I not seen female flowers at anthesis I would never have discovered them, for the emergent styles are inconspicuous and wilt soon after anthesis. Only the uppermost purplish tips of inflorescence bracts of the female inflorescences emerge from the sand surface; presumably these bracts form a sheath through which the long styles can emerge without the abrasion they would otherwise suffer. *Alexgeorgea subterranea* was abundant in certain sand areas near Jurien Bay, and in several locations I dug up

alti, basi squamis hyalinis 4–45 mm longis. Ramuli crassi, applanati, flexuosi vel recti, circa 2 mm lati. Folia caulium erectiorum acuta, circa 5–7 mm longa, distincte mucronata, mucrone 2–4 mm longa. Inflorescentia masculina capituliformis, bractee capitulorum 5–6 mm longae (setae inclusae), deltoideae; seta circa 3 mm longa, minute scabra. Perianthium circa 2 mm longum; filamenta circa 3 mm longa. Bractee inflorescentiarum foeminearum 2–80 mm longae, apicibus bractearum longissiorum purpureis. Styli circa 60 mm longi, 30 mm supra terrae protrudentes. Tepala deltoidei-lanceolata, acuta, in fructibus 12–15 mm longa. Fructus circa 15 mm longi, 6 mm lati.

All the characters as included in the generic description. Rhizomatous stems creeping below ground, covered with hyaline scales about 8 mm long. Erect stems borne singly at intervals along the underground rhizome, 7–25 cm tall, underground scales at bases of erect shoots hyaline, 4–45 mm long. Leaves of the erect branches all distinctly mucronate, 5–7 mm long (not including mucro), mucro 2–4 mm long. Male inflorescence a head about 10 mm long. Bracts of male heads 5–6 mm long, including setae, deltoid, seta about 3 mm long, minutely scabrous. Perianth of male flowers about 2 mm long, filaments about 3 mm long. Bracts of female inflorescences 2–80 mm long, the tips of the longer (inner) bracts purple where they emerge above the sand surface. Styles about 60 mm long, of which the above ground portions are about 30 mm long. Perianth segments of female flowers deltoid-lanceolate, acute, 12–15 mm long in fruit. Fruits about 15 mm long, 6 mm in diameter at widest point.

Type. Along road to Mt. Lesueur, about 10 km west of junction with Eneabba-Gingin road, 3.x.1974, *Carlquist* 5925 (holotype: RSA; isotypes: PERTH, K, NSW, US).

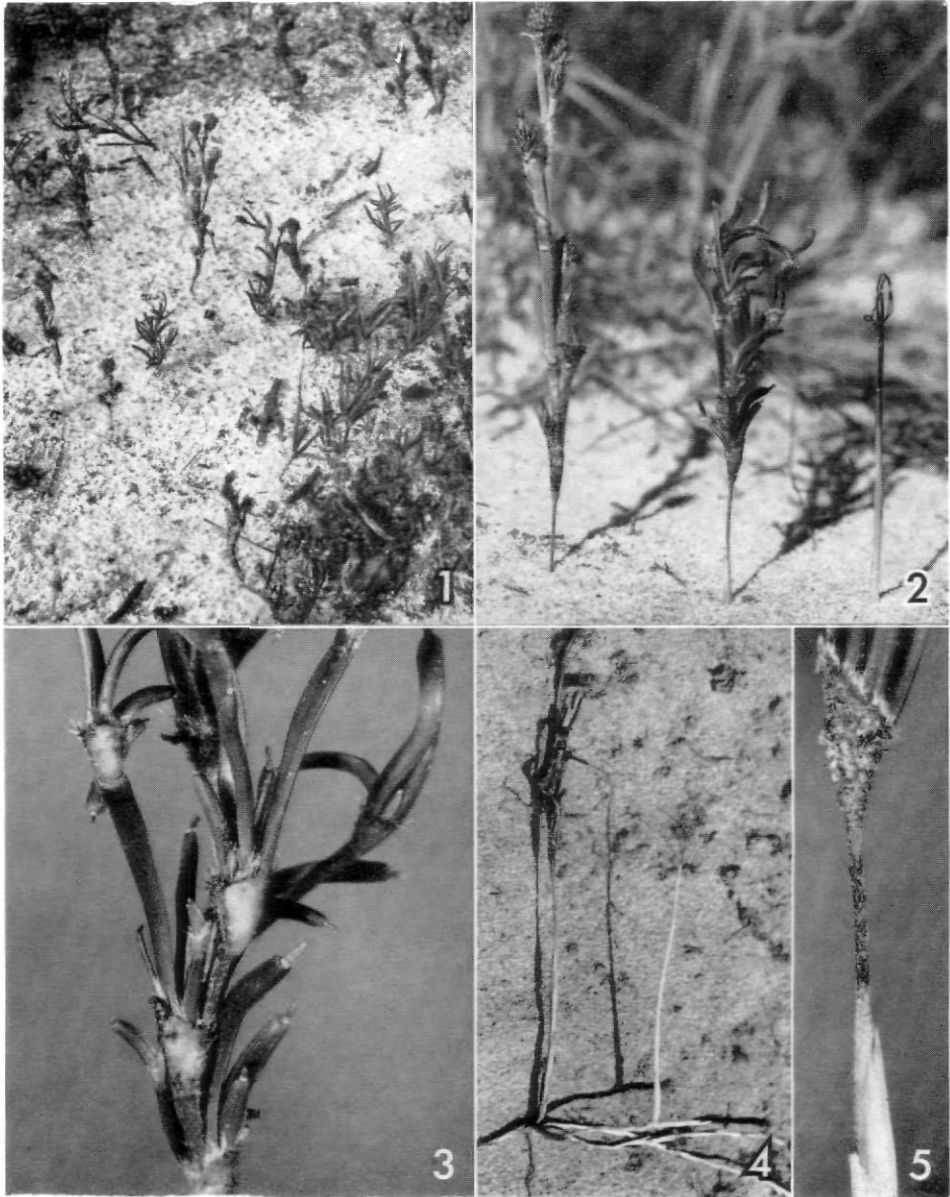
Other collections. Along Cockleshell Gully road about 7 km north of junction with road to Jurien Bay, 29.viii.1974, *Carlquist* 5485 (RSA, PERTH), *De Buhr* 3408 (RSA); same locality, 31.viii.1974, *Carlquist* 5510 (RSA, PERTH, NSW, US, K, CANB, CAS), *De Buhr* 3448 (RSA); along the Coorow to Greenhead road, about 3 km east of junction with Cockleshell Gully road, 4.x.1974, *De Buhr* 3920 (RSA); also at type locality on 3.x.1974, *De Buhr* 3901 (RSA).

Illustrations of this species may be seen in Figs. 1–20.

2. *Alexgeorgea arenicola* sp. nov.

Planta omnibus ut cognita characteribus generis (vide supra) sed flores foeminei et planta juvenilia ignoti. Rhizomata repentes subterranei, squamis nitidis, brunneis, circa 7 mm longis obiectum. Caules erecti fasciculati vel singularis, squamis brunneis, 4–45 mm longis. Ramuli flexuosi vel tortuosi, subtereti vel applanati, circa 1 mm lati, minute mucronati. Folia caulium erectiorum circa 2–6 mm longa, saepe mucronata; mucrone 1–2 mm longa. Capitula masculina circa 6 mm longa; bractee capitulorum circa 3 mm longae (setae inclusae); setae circa 1 mm longae. Perianthium circa 2 mm longum; filamenta 1–2 mm longa. Inflorescentia foeminea ad anthesin ignota. Bractee inflorescentiarum in fructibus 2–80 mm longae. Tepala deltoideo-lanceolata, acuta in fructibus, 15–20 mm longa, brunnescentia. Fructus circa 15 mm longus, 7 mm latus.

All the characters as included in the generic description, but seedling and female flowers not seen. Rhizomatous stems creeping below ground, covered by shiny brown scales about 7 mm long. Erect stems borne singly or in fascicles on the rhizomes.



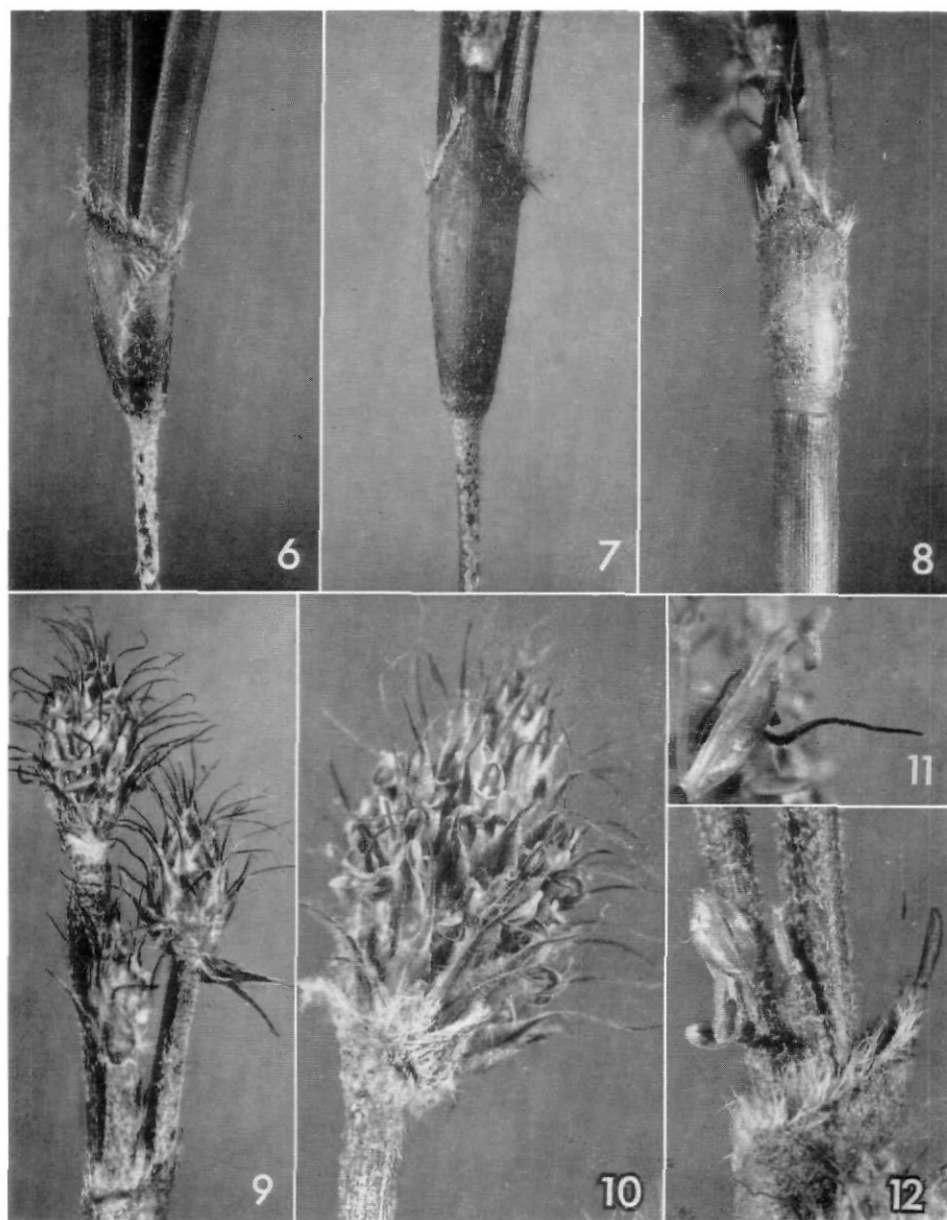
Figs. 1-5. *Alexgeorgia subterranea* (Carlquist 5485).

Fig. 1. View of habit of a colony. $\times 0.1$.

Fig. 2. *Left to right*: male shoot, female vegetative shoot, female flower. In order to photograph the three together the female flower was removed from a plant and inserted into the sand here; under natural conditions the white portions of the bracts would be buried, and only the purplish tips of the uppermost bracts and the three styles would be visible above the sand surface. $\times 0.5$.

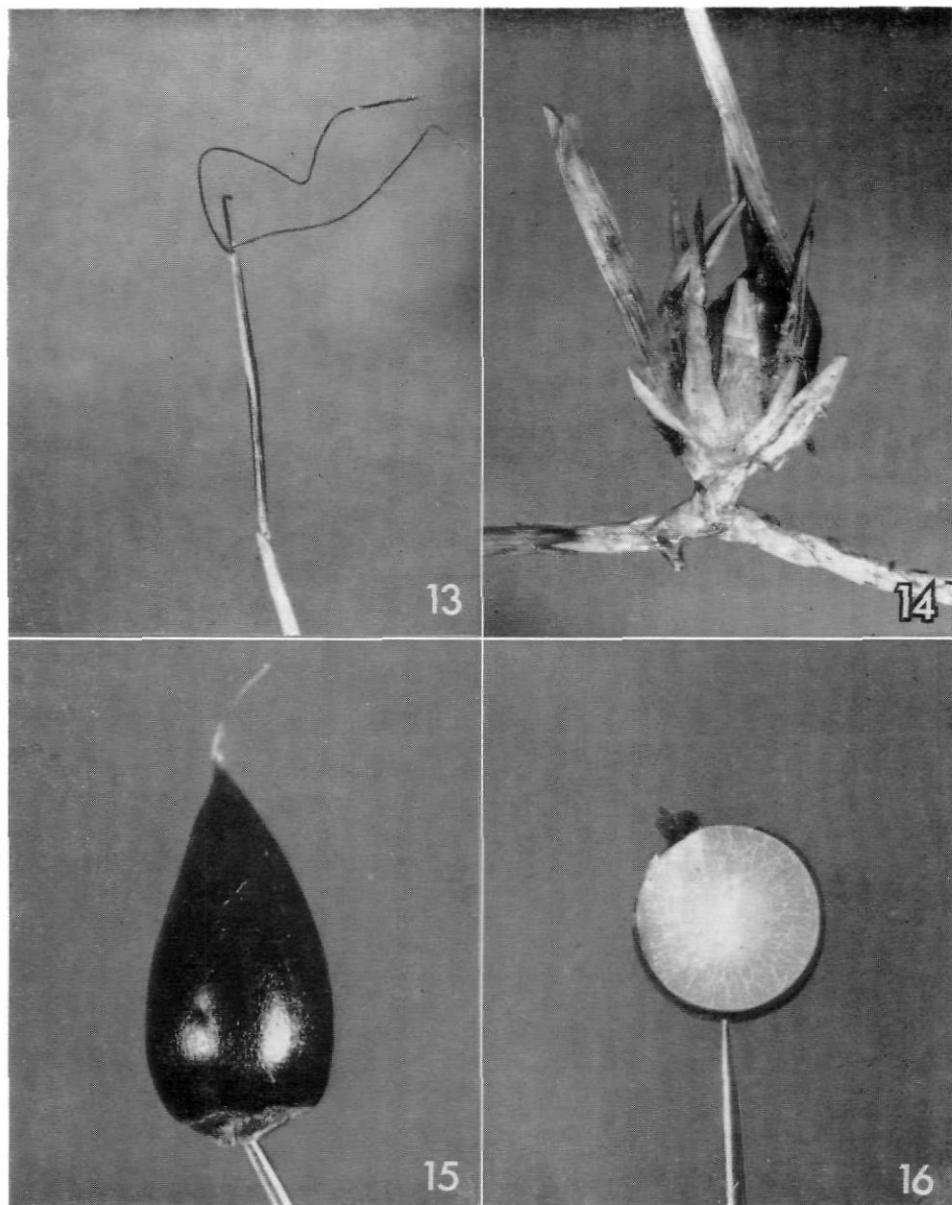
Fig. 3. Enlarged portion of a vegetative shoot from a female plant, showing angular nature of stems, mucronate stem tips, leaf sheaths and branching pattern. $\times 2.0$.

Figs. 4, 5. Unearthed portion of a female plant, showing horizontal stolon bearing a vegetative shoot and a flower respectively. $\times 0.3$.



Figs. 6–12. *Alexgeorgea subterranea* (Carlquist 5485), enlarged portions of a male plant.

- Fig. 6. First above-ground node, showing leaf sheath and sheath margins. $\times 5.5$.
- Fig. 7. First above-ground node, showing back of sheath with mucronate tip. $\times 5.5$.
- Fig. 8. Upper node, showing grooved nature of stem, sheath of leaf with mucronate tip. $\times 5.5$.
- Fig. 9. Fascicle of male inflorescences; note conspicuously setose tips of bracts. $\times 2.8$.
- Fig. 10. Single male inflorescence, with unilocular anthers scattered among the bracts. $\times 5.5$.
- Fig. 11. Male flower dissected from the spike; two anther-bearing filaments, a carinate tepal and the setose tip of the bract associated with the flower are shown. $\times 9.5$
- Fig. 12. Male flower dissected from spike and placed (upper left) on a branchlet node; hairy margins and mucro of the leaf sheath may be seen, as well as the pilose nature of the stems (above). $\times 7.0$.



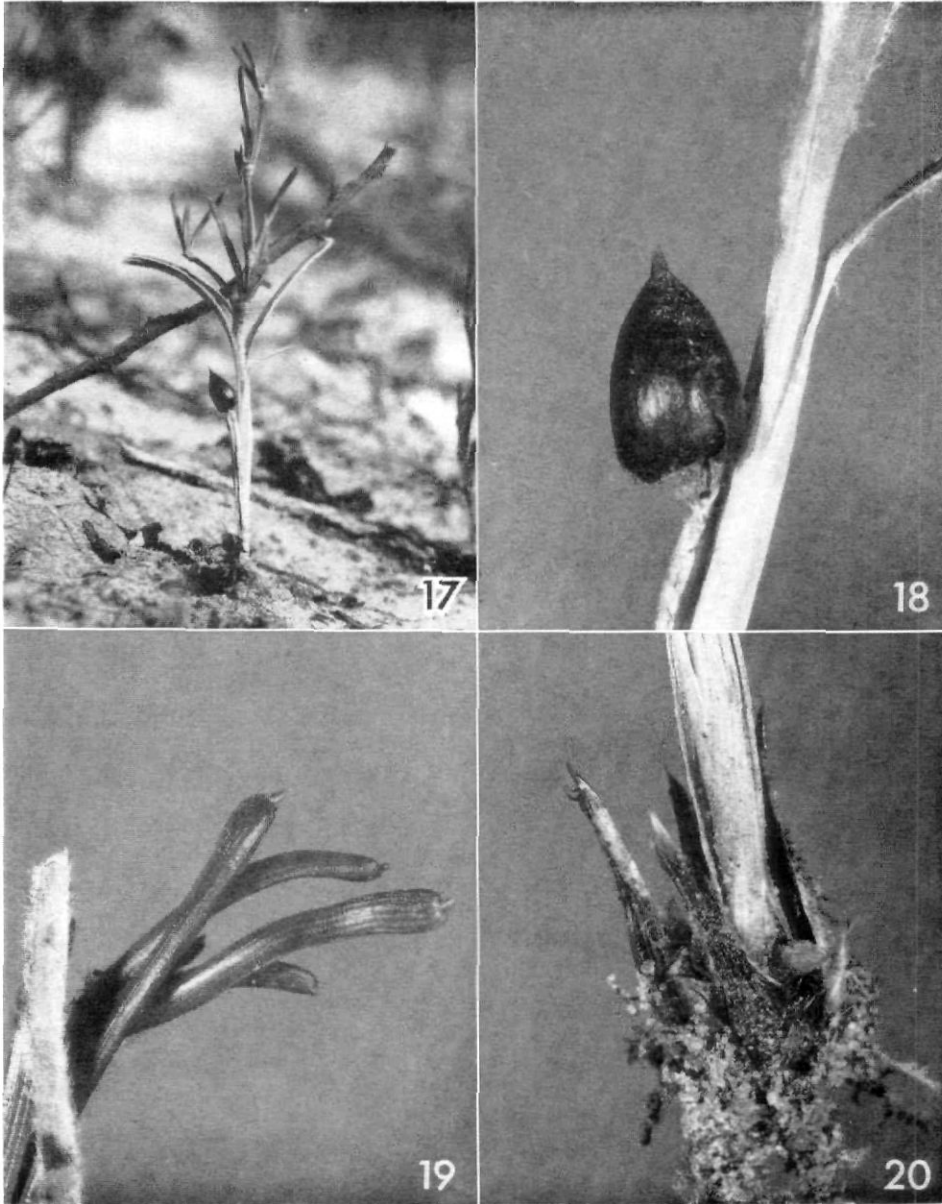
Figs. 13–16. *Alexgeorgea subterranea* (Carlquist 5485). Enlarged portions of female flower and fruits.

Fig. 13. Tip of female flower showing the three styles (two at left broken) emerging from the tubule formed by the inner bracts. $\times 1.5$.

Fig. 14. Fruit, surrounded by perianth segments and bracts, in its natural sessile position on the horizontal stolon. $\times 1.8$.

Fig. 15. Fruit, dissected from bracts and tepals, mounted on a needle. $\times 3.0$.

Fig. 16. Fruit transection mounted on a needle; thin nature of fruit wall is apparent; the endosperm of the single seed fills the fruit. $\times 3.0$.



Figs. 17–20. *Alexgeorgea subterranea* (Carlquist 5925), seedling and enlarged portions of seedling.

Fig. 17. Unearthed seedling propped against a twig for photograph; when growing naturally the lower half of this plant (to the point where leaves bend outward) would be underground. Note cotyledon tipped by fruit at left; four juvenile leaves are present. $\times 0.4$.

Fig. 18. Portion of seedling enlarged, showing fruit remaining on tip of cotyledon. Portions of juvenile leaves and their sheaths can be seen. $\times 1.8$.

Fig. 19. Lamina (tip rounded) of hairy juvenile leaf (*left*) and mucronate tips of adult branches. $\times 1.8$.

Fig. 20. Base of seedling with persistent perianth parts and sheaths of juvenile leaf bases. A rhizome is beginning to grow out from the base of the seedling. $\times 1.8$.

Branchlets flexuous or twisted, subterete or with two margins, about 1 mm in diameter, minutely mucronate. Leaves of the erect stems 2–6 mm long (the longer leaves at lower nodes), some (the lower ones) mucronate; mucro 1–2 mm long. Male inflorescence a fusiform head about 6 mm long. Bracts of the male inflorescence about 3 mm long, seta included; seta about 1 mm long. Perianth of male flower about 2 mm long; filaments 1–2 mm long. Female inflorescence at anthesis not seen. Bracts of the female inflorescence 2–80 mm long in fruit. Perianth segments of the female flower deltoid-lanceolate, acute, 15–20 mm long in fruit, brownish. Fruits about 15 mm long, 7 mm wide at widest point.

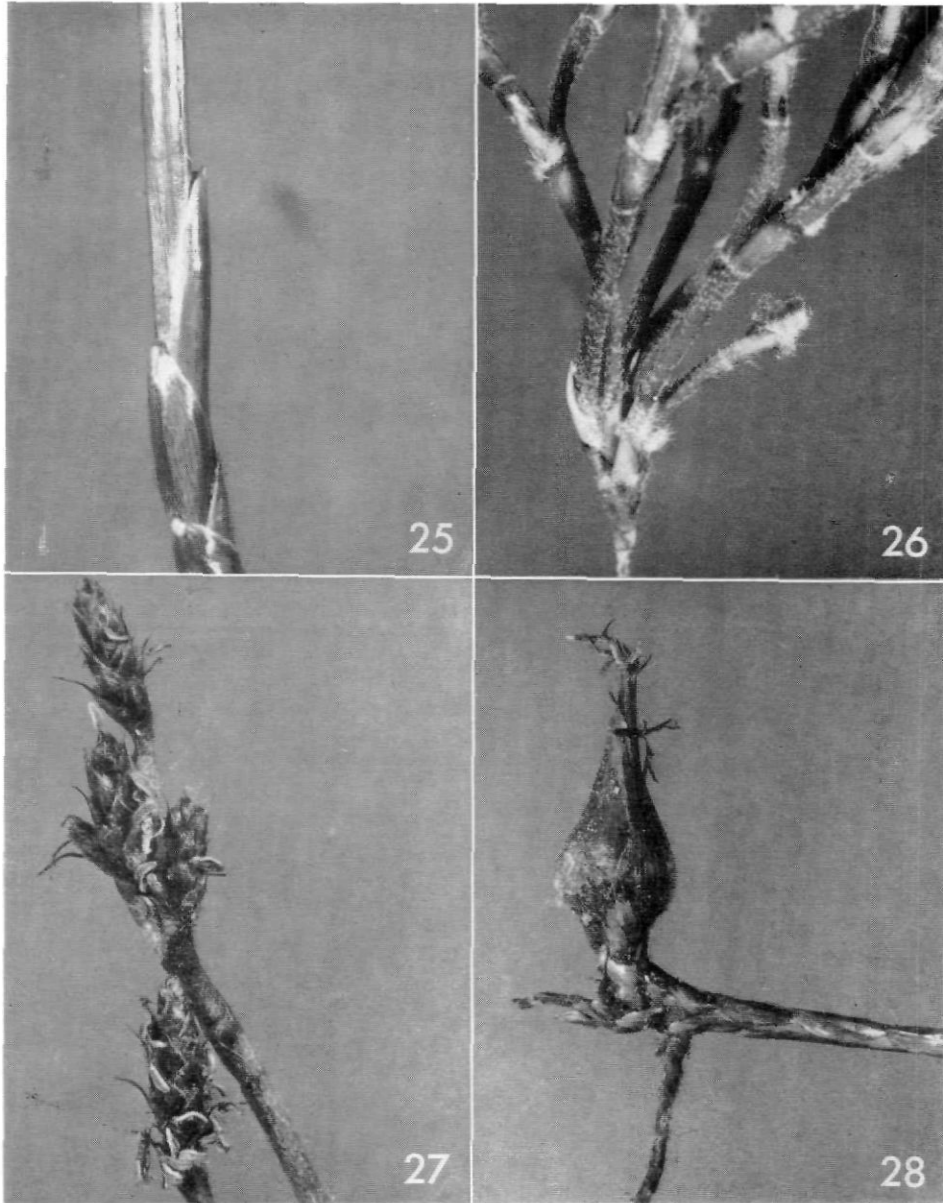
Type Swampy area about 7 km north of Bullsbrook, on sandy rises within the swamp with *Banksia grandis*, *Hibbertia*, *Patersonia* and *Xanthorrhoea*, 16.ix.1974, *Carlquist* 5643 (holotype: RSA; isotypes: PERTH, NSW, US, K, CANB, CAS, UC, GH).

Other collections. On sandy rises with *Anigozanthos manglesii*, *Lyginia barbata* and *Restio leptocarpoides* in the Helena Vale swamp, near junction of Maida Vale Road, 15.ix.1974, *Carlquist* 5641 (RSA); in *Banksia grandis* woodland on upslope from swampy areas at the 37-mile peg on the Great Northern Highway, colony all female, 15.ix.1974, *Carlquist* 5653a (RSA).

Critical features of this species are shown in Figs. 21–32.

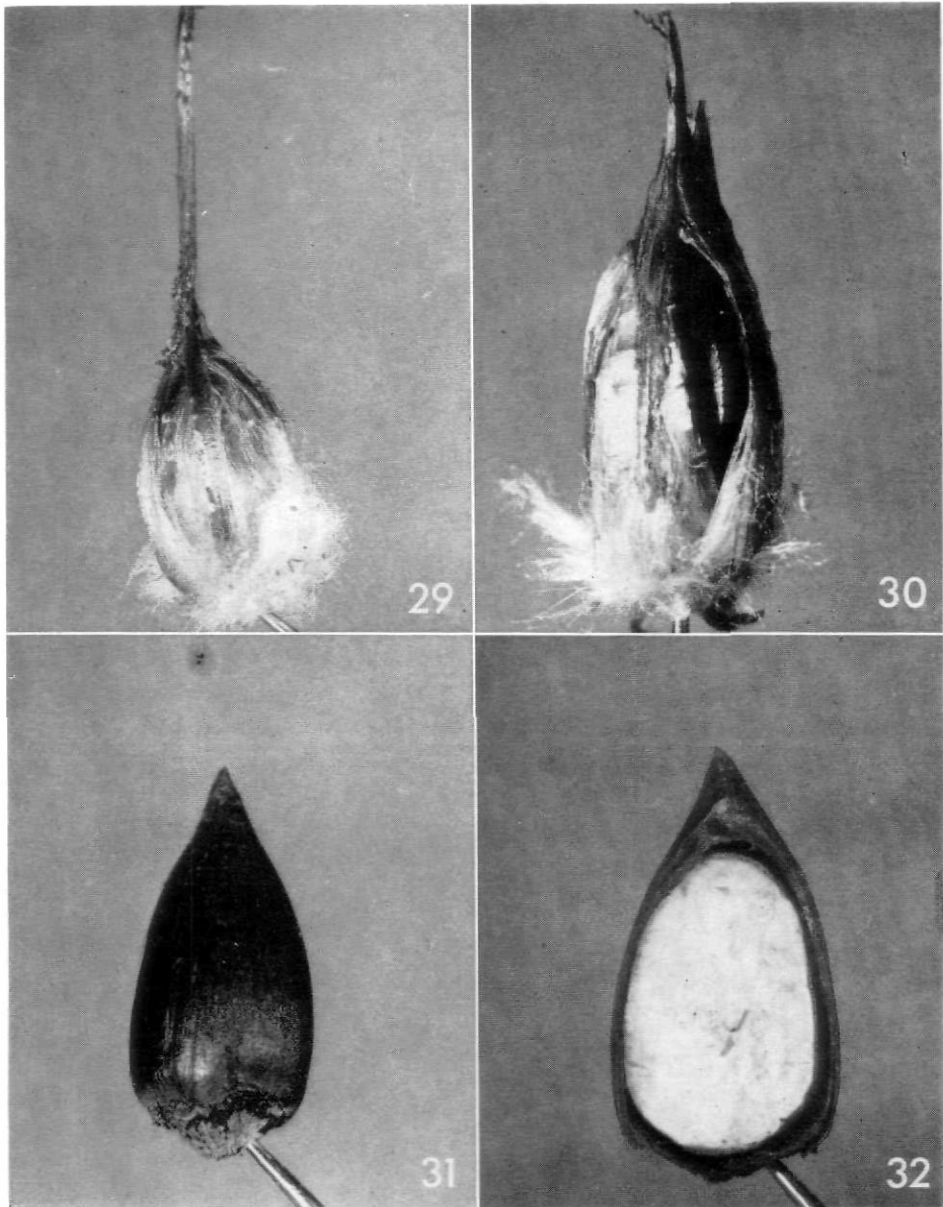
Distribution and Ecology

In addition to the localities cited as collections, other sand areas in the vicinity of Jurien Bay support colonies of *Alexgeorgea subterranea*. It is a common plant characteristic of deep white sand where *Banksia prionotes* and *B. hookeriana* grow, as well as many other characteristic sand-heath genera and species. *A. subterranea* tends to occur in open areas among the scattered shrubs. In fact, road cuts have encouraged expansion of colonies: the underground rhizomes invade newly denuded or deposited sand areas. Plants of *A. subterranea* were mostly collected in such areas because rhizomes, bearing fruits from the preceding year, were easily unearthed. The species seems in no danger of extinction in view of its abundance and pioneering qualities. In the Mt. Lesueur locality (*Carlquist* 5925), an area of sand which had drifted as a result of road-cutting operations bore a number of seedlings (Figs. 17–20). These seedlings were mixed among adult plants, and their positions suggested that seeds had germinated *in situ*, with little or no dispersal. During germination, growth of the long (but achlorophyllous) cotyledon does force the fruit closer to the soil surface, but it still remains underground. The first-formed stem is at first very short and bears the strap-shaped juvenile leaves, which are achlorophyllous in their below-ground portions; the above-ground portions are green and tend to lie on the soil surface. The seedling stem directly initiates an erect shoot (Fig. 17) and, soon after, the first rhizomatous stem (Fig. 20). Rhizomatous stems of adult plants branch occasionally, especially at points from which erect shoots arise. Most reproduction or expansion of a plant could be said to be vegetative multiplication by means of the growth of these rhizomes. At all localities where *A. subterranea* was observed, both male and female plants were present. Thus, occasional seedlings probably do occur within populations, in contrast to some populations of *A. arenicola* mentioned below. The very ephemeral nature of the female flowers and their extreme inconspicuousness undoubtedly explain why both species of *Alexgeorgea* remained undiscovered for so long.



Figs. 25-28. *Alexgeorgea arenicola* (Carlquist 5643), enlarged portions of plants.

- Fig. 25.** Bract leaves of an erect vegetative shoot, a short distance above departure from the horizontal rhizome. $\times 5.5$.
- Fig. 26.** Portion of a vegetative shoot of a female plant, showing pilose nature of stems, hirsute nature of leaf sheath margins and mucronate nature of leaf. $\times 5.5$.
- Fig. 27.** Four male inflorescences on shoot formed preceding year. $\times 3.7$.
- Fig. 28.** Abortive fruit, sessile on a horizontal rhizome; bract leaves covering the rhizome and a single root are present. $\times 3.7$.



Figs. 29–32. *Alexgeorgea arenicola* (Carlquist 5643), views of fruit.

- Fig. 29.** Fruit enclosed by bracts which are markedly woolly at base; above, bracts persist around the withered style. $\times 1.8$.
- Fig. 30.** Ridge of fruit visible through portions of persistent bracts and tepals. $\times 3.0$.
- Fig. 31.** Fruit dissected from bracts and tepals; one of the three ridges is at left. $\times 3.0$.
- Fig. 32.** Longitudinal section of fruit showing endosperm of the single seed. Fruit wall is thicker than the seed coat. $\times 3.3$.

precise relationships of *Alexgeorgea*. The shift from 'typical' restiad inflorescences as in *Restio* with small, short-styled dehiscent three-seeded fruits to the indehiscent single-seeded fruits of *Alexgeorgea* would seem a remarkable divergence. However, no one would expect preservations of species or genera representing a complete series between the two, because the adaptive modes of each are clear, whereas the intermediate types might be assumed to be less adaptive.

Single-seeded indehiscent fruits occur within the Restionaceae in the genera *Cannamois*, *Chaetanthus*, *Hypodiscus*, *Mastersiella*, *Onychosepalum*, *Staberoha* and *Thamnochortus*—genera representing both South Africa and Australia (Bentham and Hooker 1883). The occurrence of indehiscent fruits in *Alexgeorgea* does not necessarily imply relationship to any of the genera named. The fact that fruits in *A. arenicola* are angled (Figs. 30, 31) might suggest retention of a vestige of the three-valved fruits characteristic of genera with dehiscent fruits. Indehiscent fruits have quite likely originated on more than one occasion in restiads.

Although the deeply buried fruits of *Alexgeorgea* are unique in the Restionaceae, flowering at ground level is a phenomenon of many groups of Australian angiosperms. Such inflorescences have evolved in the genera *Dryandra*, *Banksia*, *Grevillea* and *Isopogon* among Australian Proteaceae, and this habit has developed in a series of South African species of *Protea* and *Leucopogon*. Interestingly, the conifer *Actinostrobus acuminatus* (Cupressaceae), endemic to the Jurien Bay–Badgingarra sandplain where *Alexgeorgea* occurs, bears its cones at ground level, a habit unique among conifers. Many more examples—especially from Western Australia—of angiosperms that flower at ground level could be cited.

The selective advantage of underground flowering and fruiting, as well as ground level flowering in the examples named and others, seems primarily related to fire. The pervasive influence of fire in the evolution of the plants of Western Australia has been discussed elsewhere (Carlquist 1974). Diels (1906) stressed adaptations to summer heat and drought in Western Australia, but seemed to neglect fire as a factor. To be sure, both factors might educe similar morphological adaptations in some cases, such as woolliness. However, one would expect adaptations to summer heat to be represented in leaves (e.g. microphyllly) and those portions of the plant near a soil surface likely to absorb considerable heat (e.g. wiry or woolly stems), whereas the portions of the plant well above or below the soil surface would be expected to reflect adaptations to fire. For example, the large corky fruits of *Hakea* and the massive fruits of other genera in the Proteaceae or in *Eucalyptus* seem to represent primarily adaptations to fire. The exceptionally high degree of adaptation to fire by the flora of Mediterranean type climatic zones of Australia is without parallel except for the flora of Cape Province, South Africa. In *Alexgeorgea*, the deeply buried nature of horizontal rhizomes and fruits (c. 10–15 cm below the surface) offers maximal protection from fire. The hairy nature of inflorescence bracts (Figs. 29, 30) may provide insulation from summer heat as well as from fire. The effects of extreme heat from fires are less at ground level compared with above-ground levels, and are least of all below ground.

A shift to new pollination mechanisms may occur concomitantly with development of the ground-flowering habit, but is a secondary phenomenon attendant on the primary selective force of resistance of fruits and renewal buds to fire. The fact that an anemophilous plant such as *Alexgeorgea* possesses remarkable mechanisms for achieving pollination despite the position of the flowers demonstrates that the shift to new

pollination mechanisms (anemophily is presumed to occur in all Restionaceae) is not a primary factor in development of the ground-flowering habit in Western Australia. The example of ground-flowering Proteas in South Africa is relevant. Shrubby *Protea* species are ornithophilous. A few of the ground-flowering species may be (e.g. *P. acaulos*, a species with colourful bracts in which I have observed claw scars of birds in the coriaceous leaves above flowering heads), although other acaulescent *Protea* species may rely on other pollinators, such as beetles. However, fire resistance, not a shift to a new pollination scheme, is obviously the prime selective factor.

The example of Australian and South African Proteaceae is germane in discriminating between fire resistance and resistance to the heat of summer. If resistance to summer heat were the prime factor, flowering and fruiting at ground level would be disadvantageous, since heat absorption at the soil surface would expose fruits to much higher temperatures than they would experience if borne aerially.

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