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NEW SPECIES OF *STYLIDIUM*, WITH COMMENTS ON
EVOLUTIONARY PATTERNS IN TROPICAL STYLIDIACEAESherwin Carlquist¹

The tropical species of *Stylidium* Sw., which range from southeast Asia to Queensland (Erickson, 1958) are less conspicuous than the species of temperate Australia. The tropical species represent a wide range of adaptations, however. These adaptations seem linked to the summer-wet climate of northern Australia. Most of the tropical species are annuals which flower during the winter months—the least propitious time for pollinators, so that self-pollination is a much more advantageous habit than it would be in southern Australia. The fact that such a high proportion of the tropical species are annuals suggests that there is a selective advantage in the ephemeral habit. There does seem to be a more rapid completion of the life cycle in tropical species as a consequence of greater irregularity of rainfall and lower total rainfall compared to conditions in temperate Australia. My observations during field work in 1977 in tropical Australia suggest that white sand areas or other acidic localities favorable for *Stylidium*s are neither as extensive nor as frequent as are the temperate sand areas which host *Stylidium*s. These factors not only have the effect of favoring smaller plant size, they appear to favor sparser populations. Brief flowering season and sparse population structure are features which, like the winter-flowering habit, tend to favor autogamy.

I have commented earlier (1969) that the flattened and doubly hinged column, seen in *Stylidium repens* R. Br. *diplectroglossum* Erickson & Willis and other southwestern Australian *Stylidium*s, is a self-pollination mechanism. In accordance with the factors cited in the preceding paragraph, this type of column characterizes most species of *Stylidium* in tropical Australia. The variation and evolution patterns of these column mechanisms will be detailed in another paper. Column mechanisms are relevant in a strictly taxonomic context, however. The seemingly lateral column of *S. evolutum* (Fig. 6-8) is not a change in the column, it is a change in size, orientation, and angle of presentation of the corolla parts so that a curious mimicry of floral patterns occurs. *Stylidium reductum* (Fig. 9-12) is an example of diminution in column length and sensitivity. Within the tropical flat-column group of species, it is an equivalent to *S. insensitivum* Carlquist within the southwestern Australian group.

Selfing theoretically has an effect on variation patterns. If selfing predominates, populations will tend to become more uniform. Where even moderate distances separate adjacent populations, differences among the populations may develop and be preserved, owing to a kind of "founder ef-

fect." This appears to have happened in *Stylidium schizanthum* F. Muell. The population of *S. schizanthum* along Nemarluk Drive in Darwin (*Carlquist 15136*) has yellow corollas, all corolla lobes erect and forming a somewhat hooded appearance. The population just south of Berrimah (*Carlquist 15160*) has the larger corolla lobes pointing downward and all lobes light rose in color. The *S. schizanthum* from Hobart Springs (*Carlquist 15180*) has creamy white flowers with the larger corolla lobes pointing downwards; near Koolpinyah (*Carlquist 15205*) the flowers have the same form, but lower lobes are rose, upper lobes green. There were also differences among the populations in leaf form and in corolla markings. Such small differences, or even conspicuous single-character differences among populations, should not be accorded specific status. During my 1977 field work, I found that plants referable to *S. ericksonae* Willis (*Carlquist 15188*, juncture Shoal Bay Road and Stuart Hwy) differed from typical *S. pedunculatum* R. Br. (e.g., *Carlquist 15145*, 40 km S. of Darwin) only by its hairy leaves. Indeed, Erickson (1958) shows this to be the only difference between the two taxa. In addition, *S. ericksonae* occurs only near Darwin (Willis, 1956), so that it is a local variant of *S. pedunculatum*. The treatment most congruent with biological facts and the taxonomy of the Stylidiaceae would be recognition at the varietal level.²

Habit photographs and photomacrophs from the field and field-collected specimens are presented for two of the three new species described and for two of the species compared with the novelties.

Stylidium evolutum Carlquist, spec. nov.

Fig. 1-8

Annua gracilis erecta, 7-30 cm alta, caulis sparse foliatus, rubra. Folia linearis, 2-5 mm long, $\frac{1}{2}$ -1 mm lata, sessilis, apice acuta, bracteiformis. Flores sessiles in paniculam laxam dispositi. Bracteae infra flores binae oppositae lineares, acutae, 2-5 mm longae. Calycis tubus angustus, ca. 1 cm longus, lobi liberi, lineari-lanceolati acuti, sparse glanduloso-pubescentes, aequilongi. Corolla extus glanduligeris. Corolla extus alba; intus alba, laciniae ad basin roseae. Faux aureus. Faus appendices minimae, connatae. Corollae laciniae inaequales, pseudoanteriores 2 minores, connatae; pseudoposteriores 2 majores, ca. 4 mm longae, connatae. Columna lateralibus disposita. Columnae apex acuta. Labellum triangulatum, exappendiculatum. Capsula fusiformis, 1-1.3 cm longa. Placenta filiformis. Semina minuta, 0.3 mm longa, pyriformis.

Annual erect herb 7-30 cm tall, stem sparsely leaved, reddish. Leaves linear, bractlike, 2-5 mm long, $\frac{1}{2}$ -1 mm wide, sessile, tip acute. Flowers sessile in a loose panicle which comprises the plant above the unbranched portion of the stem. Bracts in pairs below the flowers, acute, 2-5 mm long.

Figs. 1-4. *Stylidium evolutum* (Carlquist 15190), S of Darwin.—1. Habit of plant 20 cm tall.—2. Base of plant, showing lack of either branches or a basal rosette. $\times 5$.—3. Portion of inflorescence, showing bracts, nature of capsules. $\times 2.5$.—4. Capsule dissected so as to show placenta, to which some seeds remain attached. $\times 5$.

Ovary slender, ca. 1 cm long, calyx lobes free, linear-lanceolate, acute, sparsely glandular-pubescent, equal and not united. Corolla glandular outside. Corolla white outside; white inside, the corolla lobes marked red near their bases. Throat yellow. Throat appendages very small, connate so as to form a ridge or ring around the throat. Corolla lobes united as an upper pair 2 mm long and a lower pair 4 mm long, with the column apparently lateral, an appearance due to dorsiventral rather than lateral display of the four elongate lobes. Labellum triangular, without appendages. Capsule fusiform, 1–1.3 cm long. Placenta filiform. Seeds minute, about 0.3 mm long, pyriform.

Holotype.—*Carlquist 15190*, scattered individuals in wet muddy pockets of grassland containing *Pandanus* trees and *Melaleuca* shrubs, with such mesophytes as *Byblis liniflora* Salisb. and *Goodenia* sp. Road west from Stuart Hwy opposite juncture with the Shoal Bay Road. June 25, 1977 (Holotype, RSA; Isotype, PERTH).

Additional collection.—*S. Carlquist 15185*, in white sandy depressions with *Eriocaulon* and other ephemerals. Only one individual seen. Along Stuart Hwy 40 km S of Darwin. June 23, 1977. Also seen, but not collected, at Koolpinyah, NE of Darwin, June 27, 1977.

Stylidium evolutum may be closest to *S. fluminense* Erickson & Willis. That species, described in detail by Erickson and Willis (1966), is quite different, however. It grows in riparian sites in sandstone ranges, whereas *S. evolutum* was found in deep, relatively wet sand deposits, not along rivers. *Stylidium fluminense* has several stems from the base, whereas *S. evolutum* can be said to have a single paniculate inflorescence per plant on a single stem not branched below the lowermost flower. In that respect, *S. evolutum* is like *S. fissilobium* F. Muell. Leaves of *S. evolutum* are very narrow and short, and thereby are like those of *S. fissilobium* rather than those of *S. fluminense*.

Calyx lobes, corolla throat appendages, and, in a vague way, corolla color patterns of *S. evolutum* recall those of *S. fluminense*. The color patterns are really unlike those of any other species, however, because they are related to the orientation of the floral parts.

Orientation of the floral parts in *S. evolutum* is unique within the genus *Stylidium*. To explain it, one should say that in most tropical *Stylidium*s, the column works from above downwards. The upper pair of corolla lobes is smaller, the lower pair larger as befits a landing platform (e.g., *S. floodii* F. Muell., Fig. 26, 27). The type of flower seen in such species as *S. fluminense*, *S. multiscapum* Schwarz, etc., on the contrary, features four identical corolla lobes. Therefore an insect approach pathway would lead from the left or from the right rather than from below, as in *S. floodii*. *Stylidium evolutum* represents the *S. multiscapum* or *S. fluminense* type with diminution of the left-hand pair of united corolla lobes, enlargement of the right-

Figs. 5-8. Flowers of *Styloidium evolutum* (Carlquist 15190).—5. Flower with a withered corolla, showing the triangular labellum; unopened bud. $\times 10$.—6. Flower with poised column; the pattern of the red blotch around the throat is the configuration most typical for the species. $\times 7$.—7. Flower with column triggered; red blotch on "upper" portion of corolla, pale rose area below throat on "lower" portion of corolla. Upper portion of corolla somewhat malformed. $\times 10$.—8. Flower with column halfway repoised. Rose markings on upper and, to a lesser extent, on the lower corolla portion. $\times 10$.

hand pair, and reorientation of the flower clockwise 90° so that the large pair is below, the smaller pair is above, and the *S. floodii* pattern is achieved.

The above floral pattern is remarkable in that a mimic of the predominant pattern in the tropical species (*S. floodii*, *S. schizanthum*, *S. fissilobium*, etc.) is achieved by shifting from one form of bilateral symmetry to another. The new pattern is not totally bilaterally symmetrical, because the column is, of course, lateral with the new orientation of the flowers, not vertical as in most tropical Stylidiids. The complete union of the upper pair of lobes and of the lower pair of lobes is attributable to the fact that the column operates laterally. In the *S. floodii*-*S. schizanthum* type, the column operates from above downward, and thus a space at least as wide as the column must occur between the pair of upper corolla lobes. The red markings in *S. evolutum* are large, relatively crude blotches centered on the throat; the markings in *S. fluminense* are small and precise. As figures 6-8 show, there is variation in the way flowers of *S. evolutum* are blotched with red, from little to considerable. This suggests that *S. evolutum* is still in a flexible state with regard to color patterning. This is quite interesting, for although one might hypothesize unstable marking patterns in *Stylidium* flowers as one type evolves into another, the presence of those patterns at any one point in time would be scarce.

The achievement of this mimicry pattern in *S. evolutum* flowers suggests a strong selective advantage for the predominant floral form in the tropical Stylidiids. This uniformity may be related to the fact that in the tropics a diversity of appeals presented to a small number of insects during the brief flowering season of ephemerals would be unsuccessful in pollinator attraction. In southwestern Australia, greater population density and longer flowering season make diversity of appeals to pollinators a viable strategy.

Stylidium reductum Carlquist, spec. nov.

Fig. 9-12

Herba annua semper acaulis. Folia omnia basalia herbacea rosulata, elliptica ovata usque suborbicularia, plus minusque manifeste petiolata. Lamina 2-4 mm longa, 1-3 mm lata, margine albo-hyalina limbata. Petiola 1 mm longa. Scapi 1-4, uniflori, glabri. Pedicelli 2-15 mm longi, unibracteati vel rarius bibracteati. Bractee minutae. Inflorescentia rubra, glabra. Calycis tubus 7-8 mm longus, linearis. Calycis lobi in labia 2 brevius lata indivisa uniti. Corollae laciniae subaequales, integrae vel emarginatae. Faux nuda. Labellum subulato-attenuatum, exappendiculatum. Columna 2-3 mm longa, recurvata, insensitiva. Capsula ignota. Semina ignota.

Minute annual herb, acaulescent. Leaves in a rosette, basal. Leaves green, glabrous, petiolate. Lamina elliptical to orbicular, 2-4 mm long, 1-3 mm wide, with a hyaline margin. Petiole about 1 mm long. Inflorescences one to four always one-flowered. Pedicel 2-15 mm long. Bract at base of pedicel

Figs. 9–12. *Stylidium reductum* (Carlquist 15230), Millstream Falls, Queensland.—9. Habit of two plants in type locality. $\times 2$.—10. Flower, half of corolla removed; column displaced outside of corolla tube because of dissection. $\times 10$.—11, 12. Pairs of plants. Note that column, in permanently poised position, is no longer than the corolla tube and would not be able to dust pollen on an insect visitor even if the column were normally sensitive. $\times 5$. (Compare with Fig. 16).

or at base of ovary, occasionally both. Pedicels, ovaries and calyx lobes reddish brown, glabrous. Ovary at anthesis linear, 7–8 mm long. Calyx united into two identical orbicular lobes $\frac{1}{2}$ –1 mm in diameter. Corolla glabrous, 2–3 mm long, sordid white, throat bare; four corolla lobes equal, upright. Labellum triangular, without appendages. Column 2–3 mm long, recurved, insensitive. Fruit and seeds not available in the material collected.

Holotype.—*S. Carlquist* 15230 (In RSA). In gray depressions, with small *Melaleuca* trees, and plants of other ephemerals such as *Drosera indica* L. and *Stylidium uliginosum* Sw. Millstream Falls Park, along the Ravenshoe—Mt. Garnet Road, N. Queensland. July 5, 1977.

The floral morphology of *S. reductum* marks it as clearly related to *S. rotundifolium* R. Br. (Fig. 13–17). I was able to study material of both species in the field in Queensland during July, 1977. *Stylidium rotundifolium* showed larger corolla lobes, calyx lobes, and columns than did *S. reductum*. The stouter columns in *S. reductum* are related to their apparent lack of sensitivity. The column is recurved at all times (Fig. 10–12), which seems a correlate of obligate self-pollination. The way in which flattened columns, so abundantly represented in tropical *Stylidiums*, are adapted for autogamy has been described earlier (Carlquist, 1969).

The inflorescence of *S. rotundifolium* may have fewer flowers than those of other species of *Stylidium*, but they are quite long. As with many other tropical species, inflorescences have a pair of bracts at the base of each pedicel. Inflorescences of *S. reductum* are single-flowered, even in the most vigorous individuals. There is no vestige of paired bracts in *S. reductum*—usually a single bract is present, either at the base or the top of the pedicel, rarely both. More vigorous plants of *S. reductum* do have more numerous inflorescences, even though the inflorescences are one-flowered.

At best the most vigorous plants of *S. reductum* are quite small compared to those of *S. rotundifolium*: the leaves of *S. rotundifolium* (Fig. 15) are about ten times the length and width of those of *S. reductum*. Leaves of *S. rotundifolium* have a prominent red callous margin. This margin is white and much finer in leaves of *S. reductum*.

The diminutive size of plants of *S. reductum* is more than a mere ecotypic variant of *S. rotundifolium*. It is an adaptation, together with the obligate selfing mechanism, for life in the small pans of gray (probably basaltic) soil which probably are wet for a brief season. Plants of *Drosera indica* and of *Stylidium uliginosum* on these pans are a little smaller than is typical for those species, but they are within the normal range of size variation, whereas *S. reductum* does not fall within the range of *S. rotundifolium*.

When plants come into flower for such a brief time in a habitat with such a short growing season, autogamy is obviously a character favored by selection, for reasons detailed in the opening paragraphs of this paper. The tendency toward obligate autogamy in *S. reductum* appears fairly recent,

Figs. 13-17. *Stylidium rotundifolium* (Carlquist 15250), Bamaga, Queensland.—13. Habit of plant, $\times 0.8$.—14. Portion of inflorescence, showing one capsule dehiscent, one still closed. $\times 3$.—15. Leaf, showing red callous margin. $\times 5$.—16, 17. Flower portions. $\times 10$.—16. Column poised.—17. Same flower, column sprung.

for the space through which the column would spring if it retained sensitivity is almost wide enough to permit movement of the column. Corollas and calyces are slightly shorter in *S. reductum* than in *S. rotundifolium*. The plant size and adaptation to autogamy of *S. reductum* is reminiscent of the similar adaptation by *Levenhookia* R. Br. is the case of *L. dubia* Sond.

Stylidium desertorum Carlquist, spec. nov.

Fig. 18–20, 23

Annua robusta, caudice caespitoso vel breviter ramoso. Folia omnia radicalia, dense rosulata, linearia, filiformia, apice acuta setaceo-mucronata, 3.5–4.5 cm longa. Scapi fere semper complures, glanduloso-pubescentes plerumque rubrescentes, 8–16 cm alti. Scapi dichotomo-ramosi, cymosi, ramosi elongati, pluriflores. Pedicelli ca. 4 mm longi, glanduloso-pubescentes. Calycis tubus obovato-turbinatus, glanduloso-pubescentis. Calycis lobi liberi, ovati, acuti. Corolla rosea. Corollae tubus brevism laciniae dentae-oblongae. Laciniae extus glanduloso-pubescentes. Faux minute denticulata. Columna filiformia. Labellum minutum, exappendiculatum. Capsula obovoidea, reticulate-venosa, 4 mm longa. Calycis lobi 2 mm longi. Semina numerosa.

Robust annual, caespitose but tending to be branched, branches with cass stems up to 5 cm long, 5 mm in diameter (mostly shorter and slenderer). Leaves in a dense rosette, green, fleshy, linear, filiform, 3.5–4.5 cm long, leaf tips setose, mucronate, the mucro composed of fibroid epidermal cells. Inflorescences usually several per rosette or rosette branch, reddish, glandular-pubescent, crass (about 3 mm in diameter at base). Inflorescences dichotomously branched, cymose in structure with the two branches elongate and bearing many flowers. Pedicels about 4 mm long, glandular-pubescent. Bracts borne in pairs at bases of pedicels, acute, 1–3 mm long, glandular-pubescent. Ovary obovate-turbinate, glandular-pubescent. Calyx lobes free, ovate, acute. Corolla rose. Corolla tube short. Corolla lobes ovate-oblong, corolla lobes glandular-pubescent. Throat minutely denticulate. Labellum small, without appendages. Capsule obovoid, with a prominently reticulate-veined surface, 4 mm long. Longitudinally oriented veins on capsule surface numerous. Calyx lobes in fruit 2 mm long. Seeds numerous, less than 1 mm long.

Holotype.—D. K. Latz 4085 (Holotype, AD; Isotypes, BRI, CANB, DNA, NSW, NT, PERTH). Salt Beef Lake, Tanami, N. T. 20°53'S., 130°25'E. Common in whitish sand, *Plectrachne* sp.-dominate depression area above salt lake. Erect herb with bright pink flowers and fleshy terete leaves. July 22, 1973.

Additional collections.—G. Chippendale 3813 (AD, NT). 9.6 mi. W of Georgina Downs H.S., N. T. Oct. 1, 1957. P. K. Latz 4422 (AD, CANB,

Figs. 18–23. *Stylidium desertorum* and *S. floodii*, portions from dried specimens.—18, 19. *S. desertorum* specimens (magnification scale to right of Fig. 19).—18. Branched plant, P. K. Latz 4422 (AD).—19. Unbranched plant, G. Chippendale 3813 (AD).—20. *S. floodii* (Carlquist 15178), leaf tip. $\times 10$.—21. *S. desertorum*, type, leaf tip. $\times 10$.—22. *S. floodii* (Carlquist 15178). Immature capsule. $\times 7$.—23. *S. desertorum*, type, capsule. $\times 7$.

DNA, NSW). Rare in sandy soil, large "swamp-like" depression on *Triodia basedowii* sandplain. NW Simpson Desert, 23°33'S., 136°16'E., N.T. Nov. 2, 1973.

Stylidium desertorum is perhaps most closely related to *S. floodii* (Fig. 20, 22, 24–27), although equally to some other tropical species, such as *S. inequipetalum* Black. The paired bracts at the bases of pedicels could be used as a character to delimit the species to which *S. desertorum* is related. In inflorescences of *Stylidium*, dichasial structure would be accompanied by pairs of bracts at each branching. Alteration of the structure to an unequal cyme rather than a dichotomous cyme, as in the abovementioned species, would tend to result in pairs of bracts, rather than single bracts, beneath each pedicel in a racemose, or elongate, inflorescence branch phylogenetically derived from dichasial branchings.

If one arbitrarily selects *S. floodii* for comparison, one finds that *S. desertorum* occurs in localities more toward the center of Australia than does *S. floodii*, according to the data on the latter given by Mildbraed (1908) and Erickson (1958). The rosette of *S. desertorum* is larger than that of *S. floodii*, as are the leaves, stems, and main roots of *S. desertorum*. For example, the branches are short or up to 4 cm long in the specimens of *S. desertorum* examined, with stems 2–4 mm thick—much thicker than stems of *S. floodii* (about 1 mm in diameter). Leaves of *S. floodii* are about 2 cm long and have blunt tips (Fig. 20) not differentiated from the remainder of the leaf. In *S. desertorum*, leaves are nearly all at least 3 cm long (Fig. 18, 19), dry a dark green color (related to the thin-walled nature of leaf cells) and have a mucronate tip. This mucro (Fig. 21) is composed of elongate or fiberlike cells, like those described for leaf epidermis of various *Stylidium* species by Mildbraed (1908). Capsules are about 4 mm long, with calyx lobes 2 mm long in *S. desertorum* (Fig. 23). In *S. floodii*, capsules are about 3 mm long with lobes about 1 mm long (Fig. 22). The inflorescence axes of *S. desertorum* are considerably stouter than those of *S. floodii*. One might think of *S. desertorum*, aside from leaf tips, as a crasser version of *S. floodii*. However, that tendency is quite reversed in any case by pedicel length: the pedicels of *S. floodii* are markedly longer (about 7 mm) than those of *S. desertorum* (about 4 mm).

Because I studied only dried material of *S. desertorum*, the precise shape of corolla lobes and throat appendages could not be determined. As noted in conjunction with *S. pseudohirsutum* Mildbraed (Carlquist, 1969), attempts to discern shapes of corolla lobes from dried materials of *Stylidium* may produce erroneous results. There appear to be minor differences in flowers between *S. floodii* and *S. desertorum*.

In addition to leaf tips, capsules provide another qualitative difference between the two species. Capsules of *S. desertorum* have numerous prominent veins on the outside surface. Although the photograph herewith only

Figs. 24–27. *Stylidium floodii* (Carlquist 15178), S of Darwin.—24. Habit of plant. $\times 1$.—25. View of flower showing calyx, labellum. $\times 7$.—26, 27. Face views of flowers, showing details of corolla-lobe margins, teeth around throat, and column morphology. $\times 7$.

partially suggests it (Fig. 23), a reticulate pattern forming interconnections between the numerous longitudinally oriented veins may be seen. Capsules of *S. floodii* (Fig. 22) bear fewer, less conspicuous veins, and no reticulate pattern is present.

The three specimens of *S. desertorum* cited are from quite different sites, but they are all from areas well to the interior, in contrast to *S. floodii* localities. The three collections also show, despite the distance between the populations, uniformity in all characters, reinforcing the distinctness of *S. desertorum*—much like the distinctness of *S. arenicola* Carlquist from *S. humphreysii* Carlquist (Carlquist, 1969). Specimens of *S. floodii* (all AD specimens seen, as well as my own collections) also show no appreciable variation among themselves.

The description of *S. floodii* by Mildbraed (1908) expands upon Mueller's description. Mildbraed is basically accurate (type concept verified by study of the Schomburgk specimen loaned to me by AD). The parenthetical exceptions given for *S. floodii* by Mildbraed may possibly refer to inclusion of a specimen of *S. desertorum* among the assemblage of *S. floodii* specimens. *Stylidium desertorum* came to light among the collection of Stylidiaceae sent me by the State Herbarium, Adelaide, for identification.

The addition of three species, together with the subtraction of *S. ericksonae*, now brings the number of species in the genus *Stylidium* to 146 (for basis of estimate, see Carlquist, 1976). To that number species may be added or subtracted depending on taxonomic concepts, rediscovery of some questionable species, or discovery of as yet undescribed species. Quite conceivably distinctive new species remain to be uncovered. The reason for suggesting this is the relatively great number of species known from a single collection or from a very restricted area (e.g., *S. xanthopis* Erickson & Willis), or both. Maps showing narrow endemism are given by Erickson (1958).

There may be sterility barriers within some species of Stylidiaceae. The *S. graminifolium* Sw. complex has morphological discontinuities suggestive of such a phenomenon. Some workers are tempted, whenever sterility barriers subdividing a morphological species are discovered, to designate new species. In *Stylidium*, sterility barriers appear to parallel morphological disjunctions very closely. Natural hybrids are extremely rare (Carlquist, 1969). If sterility barriers do occur within some "good species" of *Stylidium*, taxonomists will be faced with very difficult choices.

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Footnotes

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² *Stylidium pedunculatum* R. Br. var. *ericksonae* (J. H. Willis) S. Carlquist, comb. nov. (Basionym: *Stylidium ericksonae* J. H. Willis, Victorian Naturalist 73:43, 1956).