REVISION OF THE NEW SOUTH WALES DEVONIAN BRACHIOPOD "SPIRIFER" YASSENSIS

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(PLATES VII-IX)

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Synopsis

De Koninck (1876) described Spirifer yassensis from the Lower Devonian of the Taemas—Cavan area on the Murrumbidgee River, and the species has been mentioned often since then; however, a systematic revision has never been published. In the present study, the species is redescribed and assigned to the genus Spinella Talent, 1956. The original locality information was imprecise, and the material was destroyed in 1882; therefore a new type locality is selected near the base of the Taemas Formation, and a neotype is chosen. The species is compared morphologically and statistically with the type species Spinella buchanensis; a new subspecies, Spinella yassensis ravinia, is erected by Flood for specimens from the Lick Hole Limestone at Ravine, near Kiandra, New South Wales. Silicified specimens from a horizon near Warroo Creek about 300 metres above that of the type locality of S. yassensis s.s. may prove to be subspecifically distinct, while the subspecific position of material from the Cavan Formation is uncertain.

INTRODUCTION

Historical discussion

From material submitted to him by the Rev. W. B. Clarke, de Koninck (1876, translated 1898) identified five species of spiriferoid brachiopods from the Devonian strata southwest of Yass, New South Wales. The first, *Spirifer multiplicatus*, was erected on one poor specimen from "a grey, very compact limestone in the Yass District" (1898, p. 82). Specimens found "in a black limestone from the Yass District" (1898, p. 83) were attributed to *Spirifer cabedanus* de Verneuil; they were described but not figured. *Spirifer yassensis* was based on specimens "collected by [Clarke] in a compact blackish limestone from the Yass District; also at Duntroon, in a yellow-brown argillaceous limestone, softer than the first, in which it is more common" (1898, p. 84). *Spirifer latisinuatus* was "found on the banks of the Murrumbidgee, in the Yass District, in a blackish, very compact limestone" (1898, p. 84). The last species, attributed to *Spirifer nudus* Sowerby, was based on a single specimen from "a black limestone containing *Atrypa plicatella*... in the Yass District" (1898, p. 85; not figured).

This material, which was subsequently purchased by the Government of New South Wales, was destroyed in the Garden Palace fire of September 22nd, 1882. Since then, all the species have been quoted in faunal lists (Harper, 1909; Benson, 1922), but only "Spirifer" yassensis has been referred to in papers of a systematic nature (e.g. Allan, 1947; Talent, 1956). The only locality mentioned in any of these later works (Talent, 1956; Browne, 1959) is "Shearsby's Wallpaper"—portion 65, parish of Taemas (locality 'CC/109 in Text-fig. 1)—which is in the "Spirifer yassensis Limestone" of Browne (1959), at the base of the Taemas Formation.

Present status of species

Both "Spirifer" multiplicatus and "Spirifer" cabedanus were described as having plicate fold and sulcus; they therefore are unrelated to "Spirifer"

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yassensis and "Spirifer" latisinuatus, which have a simple fold and sulcus. The small specimen referred to "Spirifer" nudus possessed a "very pronounced triangular" ventral interarea with the delthyrium "partly closed by a pseudodeltidium"; this could have been a Cyrtina, but certainly is distinct from "S." yassensis and "S." latisinuatus. Since these last appear to be members of a group of closely related eastern Australian forms, we considered it desirable that their identities be established. An analysis of a collection from near the "Wallpaper" revealed that both forms fell within the total range of variation at this locality. The two forms are therefore probably synonymous. Both because "S." yassensis was the first described of the two, and in the interests of stability in both systematic and stratigraphic nomenclature, we have made "S." latisinuatus the junior synonym.

Selection of a type locality

De Koninck's locality information is vague, as can be seen from the quotations given above. Of the localities quoted for the two forms, the most accurate is Duntroon; however, the outcrops in this suburb of Canberra are of sheared olive calcareous mudstones of the Riverside Formation (Silurian). Not only do the lithologies not match, but also the Duntroon outcrops have failed to yield spiriferoids at all comparable with "S." yassensis. Indeed the lithological description given by de Koninck could well be applied to weathered outcrops of the "Spirifer yassensis Limestone", such as may be seen at "Shearsby's Wallpaper". Blackish compact limestones are known at most levels of the Taemas-Cavan sequence. The locality description for "S." latisinuatus is slightly more specific than that for "S." yassensis. There are, however, several places where such blackish compact limestones rise steeply from the sandy river banks, which since Burrinjuck Dam was completed in 1927 are generally exposed only at periods of low water level. The information is therefore not good enough for us to identify Clarke's locality, and so we have chosen a new type locality for "S." yassensis at which the species is common, and which is not only in accord with the descriptions given by de Koninck for both of his species, but also with later references (Talent, 1956: Browne, 1959).

The new type locality is on the west bank of the Murrumbidgee River below "Shearsby's Wallpaper", which is on an old road between "Mountain Creek" and "Taemas" properties, in portion 65, parish of Taemas, county Cowley (Bur. Miner. Resour. locality CC/109; Canberra 1: 250,000 Sheet, $148^{\circ}49'23'' E$, $35^{\circ}2'19'' S$). The approximate position is shown in Text-fig. 1. The stratigraphic position of this locality is about the middle of the "Spirifer yassensis Limestone".

Stratigraphic distribution and age

In the Taemas-Cavan succession, the species is known from the Cavan Formation through to the "Receptaculites Limestone". Silicified specimens were obtained by Chatterton from several localities at the base of the "Receptaculites Limestone" (especially locality A on Text-fig. 1); these may represent a new subspecies. Specimeus collected from a locality in Spring Creek 1.6 km. (1 mile) above its junction with Mountain Creek (see map in Browne, 1959), in the lower half of the Cavan Formation, belong to Spinella yassensis (ANU 21566-21573). Those features that can be measured (shell width, width of fold, and number of plications) suggest a somewhat closer relationship to S. yassensis ravinia n. subsp. than to S. yassensis yassensis; only single valves were found, but these suggest that the shells are rather thick with a prominent fold, as in the latter subspecies. The understanding of the precise relationship of this form must await discovery



Text-fig. 1. Maps showing positions of localities referred to in the text.

of a locality at which the shells permit the measurement of all relevant features. Flood collected a number of free calcareous shells, here described by him as a new subspecies, from the Lick Hole Limestone at Ravine near Kiandra, New South Wales. The successions are shown in Text-fig. 2.



Text-fig. 2. Devonian stratigraphic sequences in the Ravine and Taemas areas, showing approximate correlations suggested by Flood.

The Taemas-Cavan sequence has been described in detail by Browne (1959), and that at Ravine by Adamson (1957) and Flood (1969). Pedder (1968, p. 143) and Philip and Pedder (1968, p. 1032) have discussed the age of the Taemas-Cavan sequence, revising Hill's (1940) late Coblenzian to Couvinian age to one of Siegenian-Emsian. Chatterton is preparing papers on the brachiopod and trilobite faunas of a part of the succession, in which he will be discussing the age in detail. His present view is that the "Spirifer yassensis Limestone" is middle or late Emsian in age, and the "Receptaculites Limestone" is probably late Emsian, but could be early Eifelian. Flood considers the Lick Hole Limestone to be early Emsian.

The "Wallpaper" and Ravine localities yielded enough well preserved specimens for statistical analysis (undertaken by Strusz). The far smaller number of suitable shells from the "*Receptaculites* Limestone" locality was also analyzed, although it was realized that the confidence levels would be much lower. Computation was done in the CSIRO Division of Computing Research, Canberra, on a CDC 3600 computer, using the formulae of Imbrie (1956). Text-fig. 3 shows the features measured, the manner in which the shells were oriented, and the symbols used.



Text-fig. 3. Idealized views of *Spinella yassensis*, showing orientation and symbols used for measurement. Abbreviations: Ws, width of shell; Wh, width of hinge line; Wf, width of fold at commissure; Ls, length of shell; Lp and Lb, lengths of pedicle and brachial valves; Tp and Tb, thicknesses of pedicle and brachial valves; Ts, thickness of shell; Hf, height of fold at commissure; P, number of plications on one dorso-lateral flank.

Terminology

In the descriptions that follow, the terminology for dental supporting structures does not conform precisely to that in the Treatise on Invertebrate Paleontology, part H (Moore, 1965). The terms for which we have restricted the meanings are here defined (see Fig. 4):

Dental plates.—"Variably disposed plates of secondary shell underlying hinge teeth and extending to floor of pedicle valve" (Williams and Rowell, p. H143, in Moore, 1965).

Ventral adminiculum (Brown, 1953).—The ventral portion of the dental plate in some spiriferoids. It is usually at an angle to the dental lamella (see below); it is sometimes differentiated from the dental lamella by a ridge or furrow; and its anterior margin is usually concave. This is regarded by us as a useful term because in many spiriferoid brachiopods the dental plate clearly consists of two distinct parts.

Dental lamella.—The postero-dorsal portion of the dental plate in spiriferoids. It incorporates the dental trace (that part of the shell that functioned as the tooth in earlier growth stages). It consists of the dental trace and a blade of varying length in cross-section, which is produced by deposition of secondary shell tissue along the anterior and antero-ventral margins of the dental trace. It is usually at an angle to the ventral adminiculum, and is present even when the latter is absent (e.g., in Quadrithyrina Havlíček). Its anterior margin is frequently convex.

Repositories

The repositories for the material used in this study are indicated by the following symbols:

AM: Australian Museum, Sydney.

ANU: Department of Geology, School of General Studies, Australian National University, Canberra.

CPC: Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology and Geophysics, Canberra.

GS NSW: Geological Survey of New South Wales, Sydney.

UNE: Department of Geology, University of New England, Armidale.

SYSTEMATICS

Superfamily Spiriferacea King, 1846 Family Delthyribidae Waagen, 1883 Subfamily Acrospiriferinae Termier and Termier, 1949 Genus Spinella Talent, 1956

Type species.—Spinella buchanensis Talent, 1956, by original designation. Taravale Formation, Murrindal, Victoria.

Diagnosis.—Shell subequally biconvex, with rounded to slightly mucronate cardinal extremities, and strong fold and sulcus extending from the beaks; plications rounded and simple; weak median furrow may occur in fold. Oval to elongate-oval spine bases may be arranged quincuncially or sub-radially. Pedicle interarea large, usually incurved, with open delthyrium. Dental plates long, comprising large ventral adminicula and low dental lamellae; delthyrial plate absent, umbonal and delthyrial chambers may be thickened. Short laminar crural bases apically fused to valve floor alongside small cardinal process; surface of cardinal process with more or less distinct median groove separating two sets of sublongitudinal lamellae. Low median ridge often present in brachial valve.

Remarks.—Several features, including the microsculpture, suggest some affinity with the Spinocyrtiidae, despite the absence of a delthyrial plate in *Spinella*. Pitrat's classification (in Moore, 1965) requires some revision, but that is not attempted, as it is beyond the scope of this paper.

Species assigned

Spinella buchanensis Talent, 1956; Proc. R. Soc. Vict., 68: 22-27, Pl. 1, figs. 1-5, Pl. 11, figs. 4-10.

Spinella maga Talent, 1956; Proc. R. Soc. Vict., 68: 28–29, Pl. 1, fig. 8. Spirifer yassensis de Koninck, 1876; Mém. Soc. r. Sci. Liège, ser. 2, t. 2: 104–105, Pl. 111, figs. 6–6b.

Species tentatively assigned

Spirifer incertus Fuchs in Spriestersbach and Fuchs, 1909; Abh. preuss. geol. Landesanst., 58: 63, Pl. x, figs. 1–2. Vandercammen, 1963, pp. 63–68, Pl. vi, figs. 1–12, referred the species to Spinella.

Spirifer subspeciesa Verneuil, 1850; Bull. Soc. geol. France, 2 (7): 179, Pl. 1x, figs. 5a-c. See also Comte, 1938, p. 66, Pl. vi, figs. 9–11a. In Vandercammen and Krans, 1964, pp. 6–12, figs. 3–4, and Krans, 1965, pp. 105. 136–139, Pl. x, fig. 3, Pl. xv, fig. 5, this species was referred to Spinella.

Forms excluded

Spinella sp. Johnson, 1966; J. Paleont., 40: 1048, Pl. cxxix, figs. 12-15.

SPINELLA YASSENSIS (de Koninck, 1876)

Synonymy.—See under subspecies.

Diagnosis.—*Spinella* differing from the type species *S. buchancusis* in smaller size, slightly more elongate shell, somewhat higher fold, relatively more numerous plications at least in large shells, and sparser, more elongate cuneate spine bases.

Original description.—"Coquille subglobuleuse, à peu près aussi large que longue. Valve ventrale régulièrement courbée sur elle-même; deux fois plus profonde que la valve opposée; crochet assez fortement recourbé sur lui-même et pointu; area assez elevée, creusée en gouttière, à extrémités faiblement arrondis; sinus profond, très-large eu égard à la taille de la coquille et anguleux au fond. Valve dorsale munie d'un bourrelet saillant correspondant au sinus de la valve opposée; surface des deux valves ornée de chaque côté de quatorze ou quinze plis rayonnants, dont les derniers sont très-minces et quelquefois très-bien séparés par des sillons de même largeur que les plis adjacents. Sur les bon échantillons on observe quelques stries d'accroissement vers les bords." (De Koninck, 1876, pp. 104–105).

Dimensions of specimen figured by de Kouinck

Ls = 18 mm., Lb = 15 mm., Ws = 21 mm., Wh = 18 mm., Tp = 9 mm., Tb = 7 mm., Ts = 16 mm., Wf = 8 mm., Hf = 3 mm., P = 10.

SPINELLA VASSENSIS VASSENSIS (de Koninck, 1876)

- (Pl. VII, figs. 1–14, Pl. VIII, figs. 1–3, 7, 9–10, Pl. IX, fig. 16; Text-figs. 5.1–5.3, 6–10.)
- 1876 Spirifer yassensis W. B. Clarke, in de Koninck, pp. 104–105, Pl. 111, figs. 6–6b (species attributed to Clarke by de Koninck as a courtesy; nominate subspecies).
- 1876 Spirifer latisinuatus, L. G. de Koninck, pp. 105-106. Pl. 111, figs. 7-7b.
- 1898 Spirifer yassensis, W. B. Clarke, in de Koninck (transl. David et al.), pp. 83-84, Pl. 111, figs. 6-6b.
- 1898 Spirifer latisinuatus, L. G. de Koninck (transl. David et al.), p. 84, Pl. III, figs. 7-7b.
- pars 1905 Spirifer yassensis de Koninck; Chapman, pp. 16-18 (refers to the Taemas occurrence—the nominate subspecies; and describes specimens from Murrindal, figured Pl. v, figs. 2-3, placed in Spinclla buchanensis by Talent, 1956).
 - ? 1909 Spirifera yassensis, De Kon.; Harper, pp. 45. 46 (in faunal lists, from the Cavan Limestone; probably the nominate subspecies).
- pars 1914 Spirifer yassensis de Koninck; Chapman, p. 161, ?fig. 86E (references to occurrences at Taemas—the nominate subspecies and at Buchan—S. buchanensis; no locality is given for the figured specimen).
 - 1914 Spirifer yassensis; Süssmilch, p. 65 (a copy of de Koninck's figures).
 - 1922 Spirifer yassensis; Süssmilch, p. 65 (the same as in 1914).
- pars 1922 Spirifera latisinnata, de Koninck; Benson, p. 182 (only the reference to the original description; the 'Lobb's Hole' specimens are S. yassensis ravinia).
- pars 1922 Spirifera yassensis; Benson. p. 183 (those specimens referred to Cavan and Taemas are probably the nominate subspecies; the Ravine specimens (loc. 33) are S. yassensis ravinia; those from Victoria at least partly belong to S. buchanensis; the specimen tentatively referred to S. yassensis from Capertee remains to be confirmed).
 - 1947 Spirifer yassensis de Koninck: Allan, pp. 446-447 (refers to material from the "Wallpaper").

- pars 1950 "Spirifer" yassensis; David and Browne, non pp. 232, 233
 (Buchan—S. buchanensis, S. maga); non p. 233 (Quedong—not Spinella—and Lobb's Hole—S. yassensis ravinia); p. 234 (Taemas); ?p. 235 (east of Capertee—identity unknown); pars p. 259 (includes all forms).
- non 1953 Acrospirifer yassensis; Fairbridge, p. V/9 (Buchan, quoting an unpublished report by Teichert—S. buchanensis).
 - 1953 "Spirifer" yassensis; Fairbridge, p. V/12 (Taemas).
 - 1954 Spirifer yassensis; Browne, p. 9 (occurrence in the Taemas-Cavan succession; would at least include the nominate subspecies).
 - 1956 "Spirifer" yassensis de Koninck; Talent, pp. 25, 26, 33 (reference to the Taemas form, particularly material from the "Wallpaper", which is the nominate subspecies).
- non 1958 "Acrospirifer yassensis"; Teichert in Teichert and Talent, pp. 11, 14–16, 19 (Buchan and Murrindal—S. buchanensis, S. maga).
 - 1959 Spirifer yassensis de Kon.; Browne, pp. 119, 120 (details of distribution in the Taemas-Cavan succession; at least partly the nominate subspecies).
 - 1968 "Spirifer" yassensis; Pedder, p. 145 (teilzone shown in fig. 2).
 - 1968 "Spirifer" yassensis de Koninck; Philip and Pedder, p. 1032 (mentioned in a discussion of the age of the Taemas-Cavan-Wee Jasper succession; at least partly the nominate subspecies).

Type series and locality.—Neotype (here chosen) CPC 10695 (Pl. 1, figs 1-5); free calcareous shell. Paraneotypes CPC 10650-56 (serial sections), 10657-59, 10660-64 (serially ground), 10665-94, 10696-10706; all calcareous shells, measured for statistical analysis. CPC 10707-37; variously preserved shells and valves. CPC 10738—a bulk collection of less well preserved specimens. All collected from about 2.5 m. of thinly bedded silty calcarenite and marl at locality CC/109 (see discussion above).

Diagnosis.—As for species.

Description (type series): exterior.—The shell is transversely elliptical, with a hinge line which is generally a little less than the greatest width (see Tables 1 and 2 for this and other size relationships). The cardinal angles may be as low as 90° , when the hinge line equals the greatest width, but more often they are somewhat obtuse $(95^{\circ} \text{ to } 105^{\circ})$, the extremities being angular to rounded. The profile is slightly ventri-biconvex; maximum curvature of both valves is in the umbonal region. A prominent fold and sulcus extend from the beaks; the sulcus is simple, but there may be a faint median furrow on the fold. The fold is wider than high, and rather more than a quarter of the shell width at the commissure. The brachial flanks usually bear eight to eleven rounded plications, separated by narrower grooves; the plications are strong near the fold, but towards the cardinal extremities become narrow and faint. The pedicle beak is sharp, the umbo moderately to strongly incurved over a strongly longitudinally curved apsacline interarea with an apical angle of about 90°. The delthyrium is open, clearly bounded by tooth ridges; measured along the interarea surface it is nearly twice as long as wide. A pair of narrow grooves separates the tooth ridges from the longitudinally and transversely striated surface of the interarea (see Pl. VII, fig. 4). The low brachial umbo is slightly incurved, and surmounts a short curved anacline to slightly apsacline interarea (apical angle 75° to 78°). The postero-ventral surface of the cardinal process protrudes into the apex of the wide notothyrium.

Shell microsculpture comprises fine growth lines and small spines (Pl. VIII, figs. 9, 10, Pl. IX, fig. 16). The short spines are about 0.1 mm. in diameter, and rise obliquely from the shell surface. Their bases are elongate cuneiform, with expanded anterior "heads" about 0.2 mm. long, and slender "tails". The latter originate within the primary shell layer, gradually emerging forward onto the shell surface, so that up to half their anterior length (as much as 0.6 mm. in the sulcus) is visible as a fine ridge. With shallow weathering the "tail" becomes much longer, but once the weathering has removed the primary layer the spine bases are no longer visible.

The spine bases do not normally occur in radial lines, but are oriented approximately radially, tending to slant gradually up the sides of the plications, towards their crests, where they are radial. Near the anterior margin in adult shells the spine bases become more crowded and arranged along prominent growth lines, giving rise to a subdued fimbriate structure.

Pedicle interior (Text-figs. 4, 5).—The teeth are triangular in section, rounded distally, with distinct crural fossettes grooving their inner sides. Their traces are expanded ventrally to form narrow dental lamellae, which meet the tops of the ventral adminicula at a slight angle. The adminicula diverge antero-ventrally, have concave forward edges, and extend forward along the valve floor generally for about half (occasionally as much as two thirds) its length. The umbonal chambers, and to a lesser extent the lower walls of the delthyrial chamber, are slightly to moderately thickened by secondary deposits in adults, so that the portion of the delthyrial chamber which constitutes the posterior part of the muscle field becomes noticeably depressed. The crest of the inner surface of the sulcus is flattened to form a long narrow adductor muscle scar within the diductor scar.



Text-fig. 4. Internal structure of brachial valve, *Spinella yassensis*; reconstruction based on silicified specimens of *S. yassensis*, n. subsp?, and on cleaned specimens and serial sections of *S. yassensis yassensis*. Cardinalia and spiralia in solid black.

Brachial interior (Pl. VIII, fig. 7; Text-figs. 4, 5).—The narrow dental sockets are widely divergent. The inner socket ridges, which articulate with the crural fossettes, merge dorsally with the laminar crural bases, which meet the valve floor only alongside the cardinal process. Forward of this, the steadily widening inner surfaces of the crural bases face ventro-medially. The long tapering crura maintain this inclination as they curve gently forward to become parallel a little behind the hook-like jugal processes, whose points are directed ventrally and slightly medially. The primary lamellae of the spiralium are attached to the jugal processes near their bases. The spiralium, of some ten to twelve turns, is elliptical in cross-section, with a somewhat asymmetric oval profile, and is directed slightly ventral of laterally, towards the widest part of the shell. The cardinal process, a pad of secondary tissue uniting the proximal ends of the crural bases, is more or less distinctly bilobed. Each lobe bears about four or five parallel low ridges, the two sets diverging forward at a small angle. In most shells there is a slender median ridge on the floor of the valve, starting a little forward of the beak and extending to about the mid-length.

Variability.—The measured features of the shell show the amount of variability common to most articulate brachiopods (see Table 1), and their relationships during growth are mostly well correlated (see Table 2, and Text-figs. 6–10). The most notable exception to the latter is the correlation between number of plications and the various shell dimensions. The correlation coefficients are relatively low, ranging between r = 0.436 (P:Tb) and r = 0.567 (P:Lb) for N = 49.

Remarks.—The description and illustrations of "Spirifer" latisinuatus suggest that it only differs from S. yassensis in having a relatively smaller number of plications—the most variable feature measured in the neotype series. The form falls in the upper part of the size range for S. yassensis yassensis.

SPINELLA YASSENSIS RAVINIA Flood, n. subsp.

(Pl. IX, figs. 1-14, 17; Text-figs. 5.4, 5.5, 6-10)

- 1901 Spirifera yassensis de Koninck; Dun in Andrews, p. 16 (listed only).
- 1902 Spirifera yassensis de Kon.; Dun, p. 175 (listed only).
- 1913 Spirifer yassensis; Harper, p. 179 (listed only).
- pars 1922 Spirifera latisinuata, de Koninck; Benson, p. 182 (only the specimens from "Lobb's Hole" (= Ravine), which are presumably S. yassensis ravinia).
- pars 1922 Spirifera yassensis; Benson, p. 183 (only the specimens from Ravine, loc. 33).
- pars 1950 "Spirifer" yassensis; David and Brown, p. 233 (only from Lobb's Hole), pars p. 259 (includes all described Australian forms).
 - 1957 Spirifer yassensis de Koninck; Fletcher in Adamson, p. 15.

Type series and locality.—Holotype CPC 10771, paratypes CPC 10739 (serial sections), 10740–70, 10772–89, and UNE F10026–28. Collected from approximately 305 m. (1,000 feet) above the base of the Lick Hole Limestone near Ravine (Bur. Miner. Resour. locality WAG/1; Flood, 1969, Text-fig. 1, grid reference 2948.1756; approximate location shown on Text-fig. 1). Free calcareous shells.

Other material.—AM F43427-32, collected by Andrews, 1901. GS NSW F14703-07, mentioned in Adamson, 1957. UNE F9958-10025, 10029-83. collected by Flood in 1967 from between 73 m. (240 feet) and 366 m. (1.200 feet) above the base of the Lick Hole Limestone near Ravine (see measured section in Flood, 1969).

Derivation of name.—From Ravine post office plus latin suffix "-ia". pertaining to.



2.—S. yassensis yassensis, paraneotype CPC 10656, \times 2. 3.—Idem., brachial valve at cardinal process, \times 10. 4.—S. yassensis ravinia, paratype CPC 10739; brackial valve at cardinal process, \times 10.

5.—8. yassensis ravinia, paratype UNE F10027, \times 2; drawn from photographs mound surfaces original destroyed by grinding

Diagnosis.—Small *Spinclla*, differing from *S. yassensis yassensis* in having a significantly shallower shell with a relatively narrower and flatter fold, and a slightly larger number of plications.

Description.—This subspecies is known only from calcareous specimens. It differs from Spinella yassensis yassensis in the following ways (see also Tables 1 and 2, and Text-figs. 5–10). The shells tend not to attain as large a size as has been observed in the nominate subspecies, and are also rather flatter, with a relatively flatter and slightly narrower fold. The observed maximum number of plications is fourteen in both subspecies, but the mean value in S. yassensis ravinia (11.2). is significantly larger than that for S. yassensis (9.8).

Internally, the cardinal process tends to have a few more lamellae, there is a larger divergence between the adminicula and dental lamellae, and the lateral extent of the dental sockets is greater (see Text-fig. 5.5g).

Variability.—This would appear to be about the same as for S. yassensis s.s. As the scattergrams and statistics show (see below), the degree of overlap in the ranges of variation for the two forms is too great to permit specific distinction.

SPINELLA YASSENSIS, n. subsp?

(Pl. VIII, figs. 4-6, 8; Text-figs. 6-10)

Material, locality.—ANU 18966a-e, g, and i-k. Collected by Chatterton from the base of the "*Receptaculites* Limestone" near his Locality A (Chatterton, 1969, unpublished), about 3 km. (2 miles) south of "Hume Park", near the eastern bank of the Murrumbidgee River, west of the mouth of Warroo Creek (Goulburn 1: 250,000 Sheet, grid reference 182.682; see Text-fig. 1). Silicified shells and valves.

Description.—In general structure, these specimens agree with the description given for *S. yassensis s.s.* However, they tend to reach a slightly larger size, and show greater variability in shape—the cardinal angles may be strongly asymmetrical, and as sharp as 60° . The curvature of the ventral interarea is less pronounced.

Internally also, the structures do not differ significantly, allowing for the different preservation. The umbonal and delthyrial chambers are more strongly secondarily thickened in adult shells, and the muscle fields in both valves rather more strongly impressed. The ventral muscle field is broadly fusiform to sub-pyriform, and impressed more strongly between the ventral adminicula than further forward. The field bears a series of shallow near-longitudinal furrows which medially define a long narrow adductor scar. In large valves, superimposed on these is a series of pinnately radiating furrows confined to the diductor scar (see Pl. VIII, figs. 5, 6). Behind the muscle field, particularly in large valves, the delthyrial chamber may be strongly thickened. The layers were deposited more rapidly at the base of the ventral adminicula than on the valve floor, and so met along a distinct medial furrow. Shallow pits in this secondary tissue may have been sites of attachment for the pedicle adjustor muscles. The dorsal muscle field is generally indistinct. The spiralia in large shells have 12–18 turns.

Remarks.—Since only a few shells could be measured, statistical comparison with the type series of *S. yassensis*, suggesting significant differences (see Table 4), must be considered inconclusive. However, more abundant material may show that the differences in size, proportion, and the degree of secondary thickening within the umbones, are sufficiently consistent for subspecific differentiation. The same pattern of variability as occurs in the type series of *S. yassensis yassensis* can be discerned in the seven silicified shells measured.

Vari- able	Mean	Standard Error	Standard Deviation	Observed Range	N	Taxon	Locality
	$15 \cdot 0$	0.49	$3 \cdot 556$	$8 \cdot 7 - 24 \cdot 1$	52	yassensis s.s.	CC/109
\mathbf{Ls}	$17 \cdot 1$	0.96	$2 \cdot 538$	$13 \cdot 3 - 21 \cdot 4$	7	yassensis, n.subsp. ?	" A "
(mm.)	13.9	0.29	2.071	$9 \cdot 3 - 17 \cdot 3$	50	yassensis ravinia	WAG/1
	19.6	1.86	5.885	11.0-26.0	10	buchanensis	Murrindal
	12.7	0.38	$2 \cdot 721$	$7 \cdot 7 - 19 \cdot 9$	52	yassensis s.s.	CC/109
$\mathbf{L}\mathbf{b}$	14.5	0.70	$1 \cdot 852$	$11 \cdot 4 - 17 \cdot 3$	7	yassensis, n.subsp. ?	" A "
(mm.)	$11 \cdot 5$	$0 \cdot 22$	1.559	$8 \cdot 0 - 14 \cdot 5$	50	yassensis ravinia	WAG/I
			Not measur	ea		oucnanensis	Murrindal
	$19 \cdot 4$	0.56	$4 \cdot 024$	$12 \cdot 0 - 30 \cdot 1$	51	yassensis s.s.	CC/109
Ws	$23 \cdot 6$	0.79	$2 \cdot 100$	$20 \cdot 1 - 26 \cdot 0$	7	yassensis, n.subsp. ?	" Á "
(mm.)	$17 \cdot 7$	0.41	$2 \cdot 870$	$11 \cdot 0 - 25 \cdot 6$	50	yassensis ravinia	WAG/1
	$27 \cdot 9$	1.92	6.638	16.0-37.0	12	buchanensis	Murrindal
	18.0	0.71	$4 \cdot 366$	$10 \cdot 4 - 28 \cdot 4$	38	yassensis s.s.	CC/109
$\mathbf{W}\mathbf{h}$	$21 \cdot 7$	0.80	$2 \cdot 109$	$17 \cdot 8 - 24 \cdot 3$	7	yassensis, n.subsp. ?	" À "
(mm.)	$15 \cdot 8^*$	0.41	$2 \cdot 890$	$10 \cdot 0 - 25 \cdot 6$	50 - 50	yassensis ravinia	WAG/1
	$24 \cdot 9$	2.96	7.834	$14 \cdot 0 - 35 \cdot 0$	7	buchanensis	Murrindal
	$7 \cdot 4$	0.23	1.693	4-1-11.0	52	yassensis s.s.	CC/109
Tp	$8 \cdot 4$	0.50	$1 \cdot 331$	$6 \cdot 4 - 10 \cdot 1$	7	yassensis, n.subsp. ?	" Á "
(mm.)	$6 \cdot 5$	0.15	$1 \cdot 091$	$3 \cdot 6 - 8 \cdot 7$	50	yassensis ravinia	WAG/1
		-	Not measure	ed		buchanensis	Murrindal
	$5 \cdot 6$	0.19	1.386	3.0- 9.9	52	yassensis s.s.	CC/109
$^{\mathrm{Tb}}$	$5 \cdot 7$	0.38	0.996	$4 \cdot 3 - 6 \cdot 9$	7	yassensis, n.subsp. ?	" A "
(mm.)	$3 \cdot 8$	0.12	0.877	$2 \cdot 3 - 6 \cdot 1$	50	yassensis ravinia	WAG/1
			Not measure	əd		buchanensis	Murrindal
	$12 \cdot 9$	0.41	$2 \cdot 978$	$7 \cdot 3 - 20 \cdot 9$	52	yassensis s.s.	CC/109
\mathbf{Ts}	$14 \cdot 2$	0.79	$2 \cdot 077$	$11 \cdot 7 - 17 \cdot 0$	7	yassensis, n.subsp. ?	" A "
(mm.)	$10 \cdot 2$	0.24	$1 \cdot 695$	$6 \cdot 2 - 13 \cdot 5$	50	yassensis ravinia	WAG/1
	17.5	$1 \cdot 42$	4.936	$11 \cdot 0 - 23 \cdot 0$	12	buchanensis	Murrindal
	$6 \cdot 5$	0.31	$1 \cdot 838$	$3 \cdot 1 - 10 \cdot 0$	36	yassensis s.s.	CC/109
Wf	$8 \cdot 2$	$0 \cdot 23$	0.618	$7 \cdot 6 - 9 \cdot 0$	7	yassensis, n.subsp. ?	" A "
(mm.)	$5 \cdot 2$	0.14	0.993	$2 \cdot 6 - 7 \cdot 2$	50	yassensis ravinia	WAG/1
	$9 \cdot 2$	0.74	$2 \cdot 563$	$5 \cdot 5 - 13 \cdot 5$	12	buchanensis	Murrindal
	$4 \cdot 2$	0.27	$1 \cdot 521$	$1 \cdot 6 - 7 \cdot 0$	32	yassensis s.s.	CC/109
Hf	$4 \cdot 6$	0.51	$1 \cdot 341$	$2 \cdot 7 - 5 \cdot 2$	7	yassensis, n.subsp. ?	" A "
(mm.)	$2 \cdot 6^{+}$	0.12	0.875	$1 \cdot 0 - 5 \cdot 1$	50	yassensis ravinia	WAG/1
	$5 \cdot 1$	0.52	1.793	$2 \cdot 2 - 8 \cdot 0$	12	buchanensis	Murrindal
	9.8	0.25	1.748	7 -14	49	yassensis s.s.	CC/109
P	$10 \cdot 6$	0.30	0.787	10 -12	7	yassensis, n.subsp. ?	" Å "
	$11 \cdot 2$	0.17	$1 \cdot 229$	8 -14	50	yassensis ravinia	WAG/1
	$12 \cdot 1$	0.61	$2 \cdot 109$	9 - 15	12	buchanensis	Murrindal

		TABLE 1				
Mean	Values	and	Ranges	of	Measured	Features

* Skewness $(1 \cdot 009)$ and kurtosis $(2 \cdot 552)$ both significant at the 95% level.

[†] Skewness (0.708) but not kurtosis significant at the 95% level. N=number of observations; other abbreviations as in Text-fig. 3. Locality details in text—Murrindal is the type locality of *S. buchanensis*.

Equation	σa	r	Ν	Taxon	Locality
$L_{s} = 0.87W_{s} - 1.7$	0.059	0.874	51	vassensis s.s.	CC/109
$1 \cdot 21 W_8 - 11 \cdot 4$	0.284	0.783	7	vassensis, n.subsp. ?	·· A
0.72Ws + 1.1	0.066	0.764	50	yassensis ravinia	WAG/1
0.83Ws - 3.0	0.079	0.954	10	buchanensis	Murrindal
Ts = 0.72Ws - 1.0	0.027	0.852	51	yassensis s.s.	CC/109
0.99 Ws - 9.1	0.311	0.556	7	yassensis, n.subsp. ?	" Á "
0.59 Ws - 0.3	0.047	0.827	50	yassensis ravinia	WAG/1
0.74Ws - 3.2	0.069	0.947	12	buchanensis	Murrindal
Wf = 0.49Ws - 2.4	0.040	0.876	36	yassensis s.s.	CC/109
$0\cdot 29\mathrm{Ws}+1\cdot 3$	0.081	0.686	7	yassensis, n.subsp. ?	·· A ''
0.34Ws - 0.9	0.035	0.681	50	yassensis ravinia	WAG/1
0.39Ws - 1.6	0.033	0.960	11	buchanensis	Murrindal
P = 0.44 Ws + 1.3	0.017	0.508	48	yassensis s.s.	CC/109 ·
$0\cdot 37\mathrm{Ws}+\ 1\cdot 9$	$0 \cdot 110$	0.617	7	yassensis, n.subsp. ?	" А "
0.45Ws + 3.3	0.062	0.250	50	yassensis ravinia	WAG/1
0.32Ws + 3.1	0.071	0.689	11	buchanensis	Murrindal
Lb = 0.77Lp + 1.2	0.023	0.977	52	yassensis s.s.	CC/109
0.73 Lp + 2.1	0.052	0.982	7	<i>yassensis</i> , n.subsp. ?	"А"
0.75Lp + 1.0	0.012	0.902	50	yassensis ravinia	WAG/1
Tb = 0.82Tp - 0.5	0.020	0.825	52	yassensis s.s.	CC/109
0.75 Tp - 0.6	0.088	0.951	7	yassensis, n.subsp. ?	" A "
0.80 Tp - 1.4	0.101	0.450	50	yassensis ravinia	WAG/1
Hf = 0.85Wf - 1.3	0.072	0.879	32	yassensis s.s.	CC/109
$2 \cdot 17 \text{Wf} - 13 \cdot 2$	0.586	0.700	7	yassensis, n.subsp. ?	" A "
0.88Wf - 1.9	0.080	0.770	50	yassensis ravinia	WAG/1
$0 \cdot 70 \mathrm{Wf} = 1 \cdot 3^{\circ}$	$0 \cdot 123$	0-793	12	buchan ensis	Murrindal

 TABLE 2
 Selected Growth Equations and Bivariate Correlations

Abbreviations and locality symbols as for Table 1; $\sigma_a = \text{standard error of } a$ in the growth formula "y = ax + b".



Text-fig. 6. Scattergram of shell length Ls against shell width Ws for the forms described, with S. buchanensis s.s. for comparison. Data envelopes and calculated growth lines shown for S. yassensis yassensis and S. yassensis ravinia.



Text-fig. 7. Scattergram of shell thickness Ts against shell width Ws, as in Text-fig. 6.



Text-fig. 8. Scattergram of number of plications P against shell width Ws, as in Text-fig. 6.



Text-fig. 9. Scattergram of fold width Wf against shell width Ws, as in Text-fig. 6.



Text-fig. 10. Scattergrams of (left) fold height Hf against fold width Wf, and (right) thickness of brachial valve Tb against thickness of pedicle valve Tp, as in Text-fig. 6; no data for Tb, Tp, for S. buchanensis.

Discussion

Intraspecific Discrimination

The differences between the two named subspecies of Spinella yassensis have been described above. The tests for statistical discrimination suggested by Imbrie (1956) have also been applied, and indeed helped in making subsequent qualitative distinctions. The results are shown in Table 3. At the 95% probability level, there is a significant difference in slope for Ts: Ws, and for the relative width of the fold. In S. yassensis ravinia the rate of increase in shell thickness is less than in S. yassensis yassensis. The fold, in juveniles lower in S. yassensis ravinia than in S. yassensis s.s., becomes less different with increasing size. Most growth lines are significantly different in position, although only marginally so for relative fold width (the range of values in "z" is for the limits of overlap in observed values for the two subspecies). The shell in S. yassensis ravinia is thinner, with a slightly narrower fold, more plications, and a relatively thinner brachial valve; the two forms cannot be distinguished for Ls : Ws.

The difference in thickness/width ratio at least seems to be both statistically significant, and usable even with small collections of shells.

Variables	Test	Values of	" z "
Compared	for	$(1 \cdot 96)$	$(2 \cdot 58)$
Ls : Ws	slope	1.54	
	position	$1 \cdot 63 - 1 \cdot 74$	
Ts : Ws	slope	$2 \cdot 40$)
	position		$2 \cdot 58 - 7 \cdot 07$
P : Ws	slope	0.19	
	position		$5 \cdot 19 - 5 \cdot 3$
Wf:Ws	slope		2.77
	position	0.93-2.22	
Hf:Wf	slope	0.93	
	position	1.41	-2.58
Tb:Tp	slope	1.94	
F	position	2.17	3:08

TABLE	z 3
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Despite the small number of whole shells obtained from the base of the "Receptaculites Limestone" at Locality A, discrimination tests were also applied between S. yassensis yassensis and S. yassensis, n. subsp?, to determine whether there were any differences sufficiently large to be usable. These tests are summarized in Table 4.

Variables	Test	Values of "z"
Compared	for	$(1 \cdot 96)$ $(2 \cdot 58)$
Ls : Ws	slope	1.17
	position	$1 \cdot 102 \cdot 84$
Ts : Ws	slope	0.87
	position	$1 \cdot 41 - 2 \cdot 42$
P : Ws	slope	0.63
	position	1.16
Wf:Ws	slope	2.21
	position	0.932.22
Hf : Wf	slope	$2 \cdot 24$
	position	0.04 - 2.46
Th : Tn	slone	0.78

TADLE 4

Except for the shape and relative width of the fold, the calculated growth lines for the two collections are statistically indistinguishable in slope at the 95% probability level. All are distinguishable in position— P: Ws only in large shells. These figures have suggested to us the possibility of differentiation at the subspecific level, but this would have to be confirmed by a study of a larger collection from the basal "Receptaculites Limestone".

Interspecific Discrimination

The two named subspecies of *Spinella yassensis* were also statistically compared with the type series of *Spinella buchanensis*, using measurements made by Chatterton in 1968. The results are shown in Tables 5 and 6.

Table of Z for S. yassensis yassensis, S. buchanensis							
Variables	Test	V	alues of "z"				
Compared	for	$(1 \cdot)$	$(2 \cdot 58)$				
Ls : Ws	slope	0.41					
	position		$2 \cdot 14 - 3 \cdot 77$				
Ts : Ws	slope	0.27					
	position		$2 \cdot 28 - 4 \cdot 99$				
P : Ws	slope	$1 \cdot 64$					
	position	$0 \cdot 15$	$2 \cdot 28$				
Wf:Ws	slope	$1 \cdot 93$					
	position		$2 \cdot 04$				
Hf:Wf	slope	$1 \cdot 05$					
	position		$2 \cdot 27 7 \cdot 12$				

TABLE 5Table of Z for S. yassensis yassensis, S. buchanensis

 TABLE 6

 Table of Z for S vassensis ravinia, S, buchanensis

Variables Compared	Test for	Values of "z" $(1 \cdot 96)$ $(2 \cdot 58)$			
Ls : Ws	slope position	1.07	2.64-3.00		
Ts_:Ws	slope	$1 \cdot 80 \\ 0 \cdot 81 2 \cdot 14$			
P : Ws	slope	1.38	$4 \cdot 71 - 12 \cdot 26$		
$\mathbf{W}\mathbf{f}:\mathbf{W}\mathbf{s}$	slope	$1 \cdot 04 \\ 0 \cdot 26 2 \cdot 05$			
Hf:Wf	slope position	1.23	3.39- 3.88		

In all cases, the growth lines for S. yassensis s.s. and S. buchanensis show no significant difference in slope at the 95% probability level, but all show significant differences in position (that for P: Ws being marginally so). Analysing the differences, we find that S. yassensis s.s. is relatively longer and thicker than S. buchanensis; in larger shells the former tends to have relatively more plications, and a wider and relatively higher fold.

All of the growth lines for S. yassensis ravinia and S. buchanensis are indistinguishable in slope at the 95% probability level. In position, the lines for Ts: Ws and Wf: Ws are marginally distinguishable, the remainder quite distinct. In other words, the shells of S. yassensis ravinia differ from those of S. buchanensis in being longer, with more plications and a higher fold; they are also distinguishable by the differing relationship between thickness and width during growth.

Taken alone, the differences shown in Tables 3, 5 and 6 are to us sufficient only for subspecific differentiation. However there is a consistent

difference in the pattern of spine bases between S. buchanensis on the one hand and S. yassensis s.l. on the other. In the former, the spine bases are teardrop- to diamond-shaped, crowded, and show a strong tendency to form a quincunx array (particularly near the margins in mature shells), as shown in Pl. IX, fig. 15. In all known subspecies of S. yassensis the spine bases are elongate cuneate, relatively sparse, and rather irregularly spaced along arched growth lines—see Pl. VIII, figs. 9-10, Pl. IX, figs. 16-17; only in large shells is there even a hint of quincuncial arrangement anteriorly.

Topotypic specimens of Spinella buchanensis collected by G. H. Packham of the University of Sydney have revealed a further distinction not readily apparent from Talent's original collections. In our calculations the mean size values are fairly close, but the new material is consistently much larger than the mean values for S. yassensis.

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EXPLANATION OF PLATE VII

Spinella yassensis yassensis. All specimens were whitened with ammonium chloride. All \times 2.

Neotype CPC 10695; dorsal, lateral, ventral, posterior and anterior views. Figs 1-5. Figs 6-8. Paraneotype CPC 10682; dorsal, lateral and posterior views.

Figs 9-11. Paraneotype CPC 10706; dorsal, lateral and posterior views of a pauciplicate individual with its greatest width at the hinge line.

Figs 12-14. Paraneotype CPC 10677; posterior, dorsal and ventral views of a large individual.

EXPLANATION OF PLATE VIII

All specimens were whitened with ammonium chloride.

Figs 1-3. Spinella yassensis yassensis. Paraneotype CPC 10673; dorsal, lateral and posterior views of a small individual, \times 2.

- Fig. 4. Spinella yassensis, n. subsp? Silicified specimen showing cardinalia, and distinction between ventral adminiculum and dental lamella (compare Text-fig. 4); ANU 18966g, × 3.
- Fig. 5. Spinella yassensis, n. subsp? Slightly oblique dorsal view of pedicle valve, to show musculature and secondary thickening in the umbonal cavity: ANU 18966e, \times 2.
- Fig. 6. Spinella yassensis, n. subsp? Dorsal view of pedicle valve, showing musculature; ANU 18966i, × 2.
- Fig. 7. Spinella yassensis yassensis. Calcareous specimen cleaned with an airbrasive unit to show the spiralium (compare Text-fig. 4); paraneotype CPC 10737, \times 2.

Fig. 8. Spinella yassensis, n. subsp? Antero-ventral view of cardinalia (spiralium broken off); ANU 18966b, \times 3.

Figs 9-10. Spinella yassensis yassensis. Paraneotypes CPC 10721, 10719, showing microsculpture; the former is a slightly weathered shell, the latter has been cleaned; ca \times 7.5.

EXPLANATION OF PLATE IX

All specimens whitened with ammonium chloride, except fig. 14.

- Figs 1-5. Spinella yassensis ravinia, n. subsp. Dorsal, lateral, ventral, posterior, and anterior views of holotype CPC 10771, \times 2.
- Figs 6, 7. Spinella yassensis ravinia, n. subsp. Lateral and dorsal views of a small shell, paratype CPC 10769, \times 2.
- Figs 8, 9. Spinella yassensis ravinia, n. subsp. Dorsal and lateral views of a pauciplicate shell, paratype CPC 10739 (plaster cast, original partly destroyed by serial sectioning), $\times 2$.
- Figs 10, 11. Spinella yassensis ravinia, n. subsp. Lateral and dorsal views, paratype UNE F10027, \times 2.
- Figs 12, 13. Spinella yassensis ravinia n. subsp. Dorsal and anterior views of a relatively long shell, paratype UNE F10026, \times 2.
- Fig. 14. Spinella yassensis ravinia n. subsp. Transverse thin section through the cardinal process, 2.7 mm. from the posterior of the shell (compare Text-fig. 5.4); paratype CPC 10739, \times 12.
- Fig. 15. Spinella buchanensis. Microsculpture on un-numbered topotype, ANU collections, $ca \times 7.5$.
- Fig. 16. Spinella yassensis yassensis. Latex impression of an external mould of a specimen from the "Spirifer yassensis Limestone" at Good Hope, west of Yass, showing slender spines: un-numbered specimen. ANU collections. ca × 7.5.
- showing slender spines; un-numbered specimen, ANU collections, ca × 7.5. Fig. 17. Spinella yassensis ravinia n. subsp. Microsculpture on a lightly weathered shell, paratype CPC 10770, ca × 7.5.