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Ponder, Winston F., & Clark, G.A., 1990. A radiation of hydrobiid Snails in threatened artesian springs in western Queensland. *Records of the Australian Museum* 42(3): 301–363. [16 November 1990].

doi:10.3853/j.0067-1975.42.1990.119

ISSN 0067-1975

Published by the Australian Museum, Sydney

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A Radiation of Hydrobiid Snails in Threatened Artesian Springs in Western Queensland

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ABSTRACT. A radiation of hydrobiid snails exhibiting diverse morphology is described from western Queensland. All but one of the species live in springs west of the Great Dividing Range, most of them derived from water emanating from the Great Artesian Basin. Twelve species contained in the genus *Jardinella* are described from eight springs or small spring groups, spread over an area of about 260,850 km². Most of the species are found in springs that are highly vulnerable to damage and are thus under threat of extinction. Only one species is located in a protected area. The 12 species, all of them new, are discriminated primarily using shell and anatomical characters. A cladistic analysis is used to indicate the probable evolution of the group which is shown to be a monophyletic radiation separated from related genera on opercular and genital morphology. Discriminate analysis shows that the species can be distinguished on shell characters alone. Seven allopatric species are found in separate springs or small groups of springs, the remaining five (and a sixth undescribed species) live in Edgbaston Springs, all six species living sympatrically in at least one of these springs. The genus *Jardinella* is thought to consist of the relictual endpoints of a radiation that commenced in the (mid?)Tertiary. The type species is found in coastal streams and rivers in north Queensland and represents a rather derived member of the group. All but one of the spring-associated species is considered to be endangered because the springs in which they are found have no conservation status and are threatened by pastoral activities and drawdown caused by artesian bores.

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Permanent arid-zone springs are known to be sites of some spectacular radiations of aquatic animals, examples being the pup fishes of western North America (Deacon & Minckley, 1974) and hydrobiid snails in the Cuatro Ciénegas Basin, Coahuila, Mexico (Hershler, 1985). Recently Ponder *et al.* (1989) demonstrated a significant radiation of hydrobiids from springs near the south-western side of Lake Eyre South in South Australia.

While the fishes of artesian springs associated with the Great Artesian Basin (GAB) have been rather well studied (see Glover, 1982 and 1989 for references) the invertebrate fauna is only belatedly gaining some attention (Ponder, 1985, 1986; Mitchell, 1985). An account of the natural history of Dalhousie Springs in the far north of South Australia has been recently published with information on the aquatic fishes, crustaceans and molluscs (Zeidler & Ponder, 1989) but there is only one brief report on the endemic invertebrates in artesian springs in Queensland (Ponder, 1986).

The conservation importance of the artesian springs associated with the Great Artesian Basin has recently been discussed by Harris (1981), Ponder (1985, 1986, in press) and Zeidler & Ponder (1989). Work on their faunas is hampered by their inaccessibility and public awareness is slight, partly because of their remoteness and partly because most of the endemic fauna has a small body size and much of it remains undescribed. The fragility of these environments is not reflected by their conservation status. Only one group of South Australian artesian springs is located in a National Park and, similarly, of the Queensland springs that contain endemic fauna dealt with in this report, only one group is located within a National Park. All of the remaining artesian springs associated with the Great Artesian Basin are located on pastoral land and are thus potentially threatened by pastoral activities.

There is little published information on the geology and hydrology of Queensland artesian springs but Habermehl (1982) and Ponder (1986) review the literature. Habermehl (1982) recognises six spring-groups in Queensland which he names, and this classification is followed by Ponder (1986) who refers to the spring-groups as spring supergroups (see also Figure 1).

The present study is based on material collected during a survey of Queensland artesian springs in 1984 with some additional material collected in 1988. There remain many springs that are yet to be visited and it is very likely that additional species will eventually be found.

Materials and Methods

Material for this paper results from two collections, one in September to October 1984 by W.F. Ponder and P.H. Colman (with M.A. Habermehl) and the other in May 1988 by W. and L. Zeidler. A list of stations is given in Appendix 1. The station numbers cited are those assigned in the field. The hydrological data for the 1984 stations will be published separately by M.A. Habermehl. Some of the sites containing hydrobiids are illustrated in Figures 2 and 3. All tables referred to throughout the text are listed in Appendix 2.

Collections were made by hand using a small sieve (approximately 1 mm mesh) and by washing substratum (rocks, wood, vegetation etc.) into a plastic bowl. The untreated residue was left to stand over night in water taken from the collection site with a few menthol crystals added to narcotise the snails. The sample was then fixed in 10% neutral formalin and the residue later sorted in the laboratory. In localities where more than one species was present numbers of each species were recorded and percentage frequencies calculated.

A subsample of adult shells (i.e. at terminal growth) was chosen from each sample randomly (see Table 3 for number measured from each sample). They were measured using a digitising pad linked to a microcomputer, a program automatically converting the input to millimetres. These data were utilised in constructing the descriptions and subjected to discriminate analysis.

The shell parameters measured were shell length, shell width, length of body whorl, length of aperture, width of aperture, width of umbilicus, and protoconch diameter. In addition the spire angle was calculated by the

computer from points entered along the spire, and the slope of the outer lip was determined in a similar manner. The whorl convexity was determined at the junction of the last whorl with the penultimate whorl and was estimated by the calculation of a convexity ratio. Three points were entered via the digitising pad, one at the middle of the whorl outline and one at each of the sutures above and below this point. The length of a line (a) from the middle of the outer edge of the whorl vertical to a line (b) drawn between the two sutures at the junction of the penultimate and body whorls was calculated by the computer and the ratio a/b (the convexity ratio) then determined. The number of protoconch and teleoconch whorls were counted.

The shells of the measured individuals were then

gently cracked and the animals sexed after being removed from their shells. The operculum of each individual was removed from the foot, and the length, the distance of the nucleus from the edge opposite the end of the last whorl (i.e. at half the last whorl) and the length of the white smear (if one was present) were measured using the digitising pad.

Some shells (including juveniles for protoconch details) were mounted for scanning electron microscope (SEM) examination after cleaning with a mild solution of bleach and using an ultrasonic cleaner.

Heads (including penes in the case of males) and female genitalia were prepared for SEM examination using critical point drying. The shell was dissolved in dilute HCl

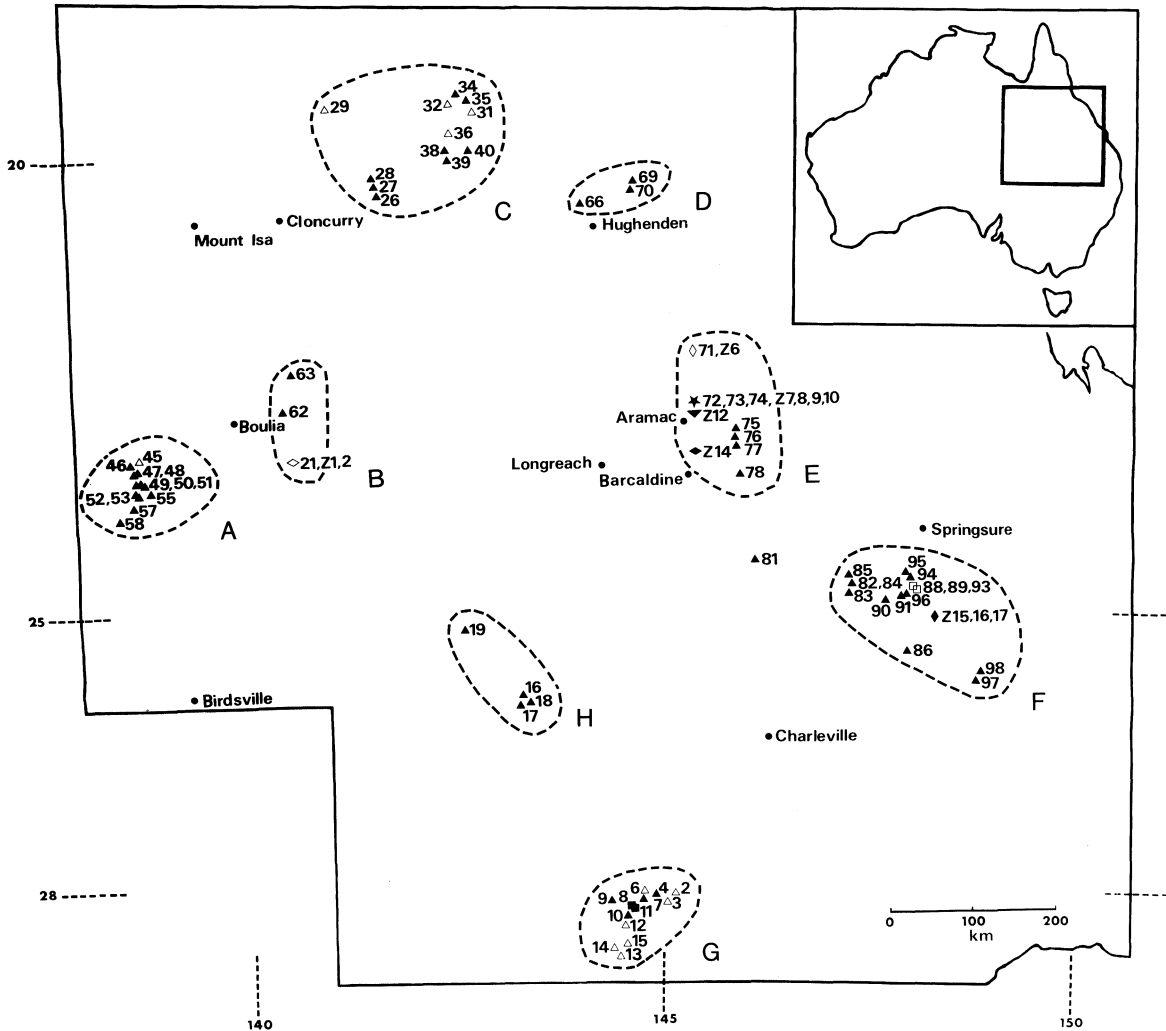


Fig.1. A map showing the locations of the springs sampled in Queensland and their hydrobiid fauna. The numbers are the field station numbers and correspond to those used in the text and in the Appendices. The dotted lines outline the main spring supergroups:- A, Mulligan River Supergroup; B, Springvale Supergroup; C, Flinders River Supergroup; D, Hughenden Supergroup; E, Barcaldine Supergroup; F, Springsure Supergroup; G, Eulo Supergroup; H, a group of non-artesian springs associated with Tertiary sediments and basalts. open triangle - extinct spring(s); closed triangle - active springs lacking hydrobiids; closed square - *J. eulo*; open horizontal diamond - *J. isolata*; open vertical diamond - *J. colmani*; closed vertical diamond - *J. carnarvonensis*; open square - *J. exigua*; closed inverted triangle - *J. zeidlerorum*; closed horizontal diamond - *J. coreena*; closed star - Edgbaston species (*J. edgbastonensis*, *J. corrugata*, *J. acuminata*, *J. pallida*, *J. jesswisae* and *J. sp.*)

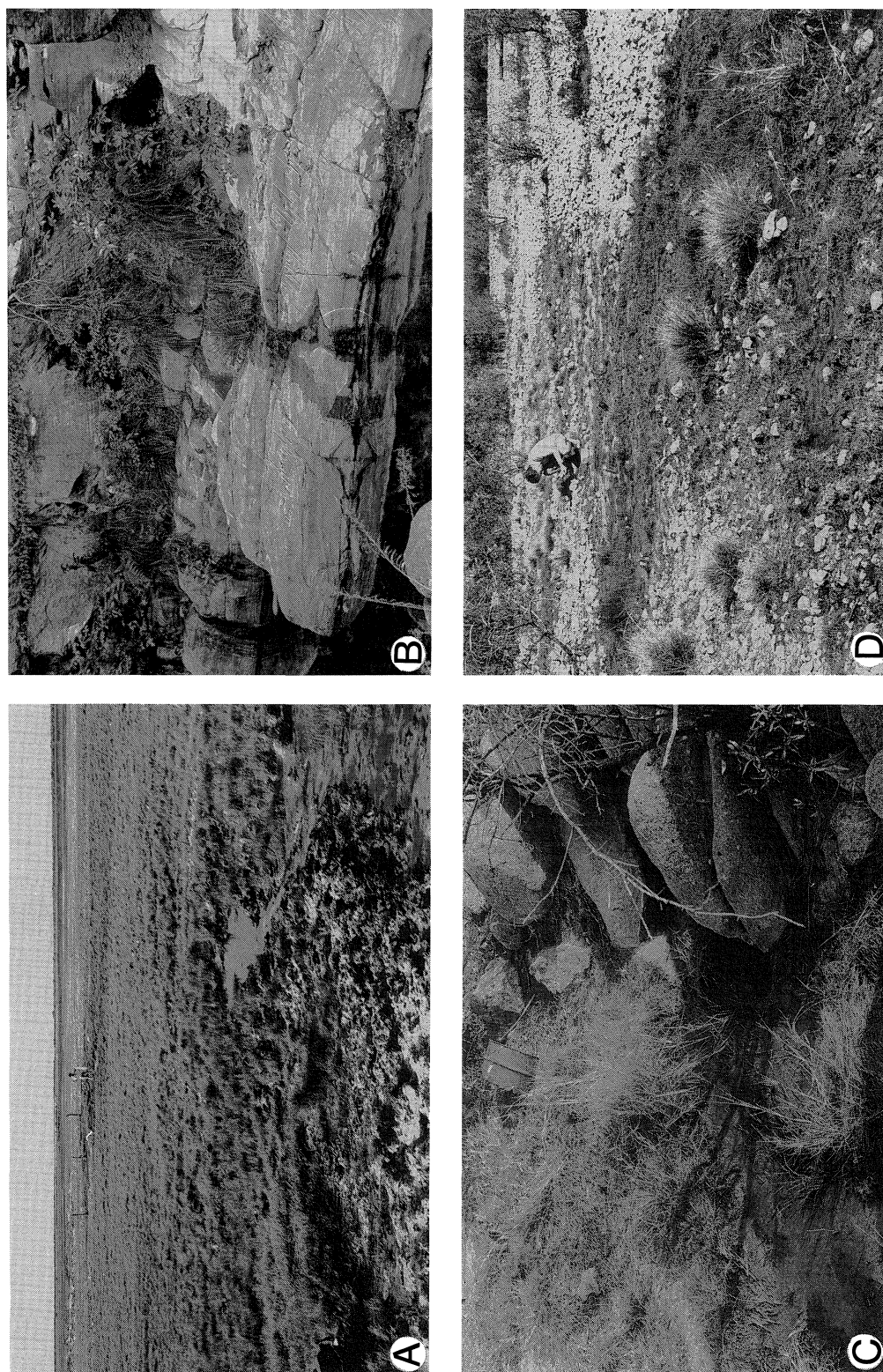


Fig.2. Some of the springs containing hydrobiids. A, Elizabeth Springs, near Springvale (Stn 21), photo W.F. Ponder (locality for *J. isolata*); B, Carnarvon Gorge National Park, springs at the beginning of Kooraminya Gorge (Stn Z16), photo W. Zeidler (locality for *J. carnarvonensis*); C, "Rocky Springs", near Eulo (Stn 11), photo W.F. Ponder (locality for *J. eulo*); D, spring at Tunga Bore, near Eulo (Stn 8), photo W.F. Ponder (locality for *J. eulo*).

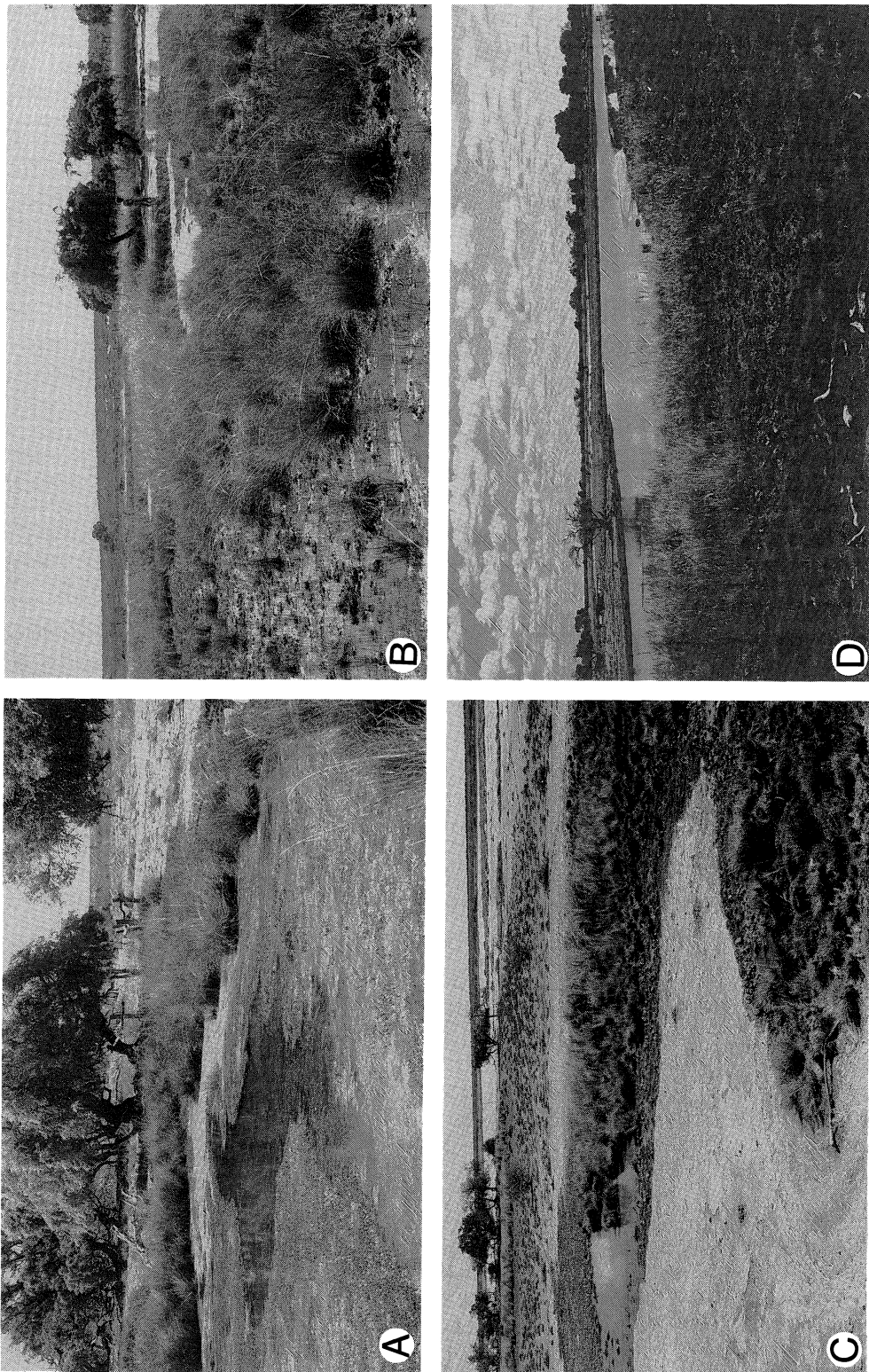


Fig.3. Some of the Edgbaston springs containing hydrobiids. A, the upper part of the outflow of “Big Spring” (Stn 73), photo W.F. Ponder; B, lower outflow of “Big Spring” (Stn 73), photo W.F. Ponder; C, small spring in Edgbaston group (Stn Z10), photo W. Zeidler; D, spring near Edgbaston group (Stn Z12), photo W. Zeidler (locality for *J. zeidlerorum*).

and the animal transferred to 70% ethanol. The structure required for examination was then carefully removed under a stereoscopic dissecting microscope. The specimens were then dehydrated through a series of acetone baths of increasing concentration (70%-100%) with 20 minutes in each bath and 20 seconds of ultrasound in an attempt to remove mucus residues. Critical point drying was done in an Emscope CPD750 at the School of Biological Sciences, Macquarie University. The dried specimens were mounted on aluminium stubs using electroconductive glue for SEM scanning. Most female genitalia were not used further because of lack of success in getting good results.

Because species could be readily discriminated using shell characters, anatomical investigation of each species was limited to a minimum of two individuals of each sex of each species. If differences were found between the first two individuals additional specimens were examined. A preliminary examination revealed several easily scored characters that assisted in discriminating the species (see Table 1). Dissections were carried out in a mixture of Bouin's fluid and water on a black wax background. Three to four specimens of each sex of eight species were serially sectioned and stained with Mallory's triple stain. These sections were used to confirm some of the observations made using gross dissection.

The radulae of a few individuals of each species were removed using KOH, washed with distilled water and mounted for photographing with a scanning electron microscope (SEM). The radular characters listed in Table 1 were scored from examination of the SEM photos.

All characters (see Table 1 for a full list) were entered into a computer file for use with the taxonomy package DELTA (Dallwitz & Paine, 1986). The output was used as the basis for the descriptions used in this paper. It also generated the initial data file used in the phylogenetic analyses. This was refined to produce the list of characters in Table 2 which were used in the final analysis.

The full range of measurements of several characters are given in the description of the shells and opercula, as well as the means for males (M) and females (F) for those characters. Means are also given in Table 3, in addition to standard deviations.

Phenetic analysis. Quantifiable evidence of differences in shell characters between the initially defined taxa were obtained by the use of multivariate statistics [discriminate analysis, using the statistical package BIOSTAT (Pimentel & Smith, 1986)]. The characters shell length, shell width, aperture length, body whorl length, convexity, width of umbilicus, protoconch diameter, and number of teleoconch whorls were used in this analysis. Those taxa that were not well discriminated were identified and statistical comparisons (t-test) between similar species pairs were carried out, using shell and opercular measurements (pooled sexes), with the statistical package SYSTAT (Wilkinson, 1987). Sexual dimorphism in shell size was also tested for using t-tests on shell length and width.

Phylogenetic analysis. The phylogenetic package PAUP (Swofford, 1985) was used to construct

phylogenetic trees using the genus *Tatea* as an outgroup to root the trees and including the genera *Fluvidona* and *Fonscochlea* (with its subgenus *Wolfgangia*). *Fluvidona* is a freshwater genus widespread in south-eastern Australia and shares many characters with *Jardinella*. *Fonscochlea* is also morphologically similar to *Jardinella* and is found in artesian springs in South Australia (Ponder *et al.*, 1989). The options MULPARS and SWAP=GLOBAL were used. Shell characters and other characters judged to show considerable homoplasy were excluded from the analysis.

Not all of the characters used in generating the descriptions were appropriate for use in phylogenetic analysis. They must have at least two states, each state should exist in at least two taxa and should be, as far as can be determined, homologous. Homology is difficult to identify with certainty because of homoplasy and no guarantee can be given for any character state. After analysis convergences can be identified, but a meaningful result is always dependent on the relative proportion of correctly identified homologous apomorphies.

Characters were chosen for use in this analysis from the characters used in the descriptions (indicated by an asterisk in Table 1; listed in more detail in Table 2). Characters were excluded that were considered to exhibit a high level of homoplasy or which could not be readily assigned to discrete character states. No shell characters are used, with the exception of the number of protoconch whorls, and this was included because of the choice of outgroup. *Tatea* T. Woods, 1879 was chosen as the outgroup because this estuarine genus appears to be one of the most plesiomorphic of the group of genera to which *Jardinella* belongs. It is similar anatomically, including the reproductive systems, to species of *Hydrobia*, another estuarine group that is considered to be primitive within the family (Ponder, 1988, and unpublished observations). The characters listed for *Tatea* are based on dissections and SEM investigations of species of *Tatea* from Tasmania and New South Wales, including topotypes of the type species.

Museum abbreviations used are: AMS – Australian Museum Sydney; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide.

Results

Systematics

Hydrobiidae

Jardinella Iredale & Whitley

Jardinella Iredale & Whitley, 1938: 67.

Type species. *Petterdiana thaanumi* Pilsbry, 1900 (by original designation).

Diagnosis. Shell variable in shape (depressed

trochoid to elongate conic), with evenly convex whorls, umbilicate to nonumbilicate, usually lacking true sculpture but rarely (in one species) with axial growth lines thickened as riblets. Growth lines and outer lip of aperture prosocline; periphery of body whorl evenly convex. Protoconch of 1.2-1.5 whorls, sculptured with minute pits.

Operculum yellow to reddish brown, with eccentric nucleus, inner surface with or without white smear, sometimes with small horny lump on inner surface near nucleus, lacking pegs.

Radula taenioglossan, each central tooth typically with 2 pairs of basal processes, innermost larger; sometimes with 1

or 3 pairs. Cutting edge formula (2-5):1:(2-5). Each lateral tooth with narrow, straight, short to long outer flange (ratio of cutting edge to length of flange 1.3-2.6); cutting edge formula (2-4):1:(3-5). Marginal teeth with numerous, small, sharp cusps, those on inner marginal teeth larger.

Head-foot pigmented with grey to varying extent, usually with a dark grey patch behind eyes. Cephalic tentacles usually bear 1-3 longitudinal tracts of cilia ventrally, some species with 1 tract dorsally, only on right side in some. No pallial tentacle(s).

Pallial cavity (Figs 4A,B, 5D-F): ctenidium (c) well developed, with broadly triangular filaments, osphradium

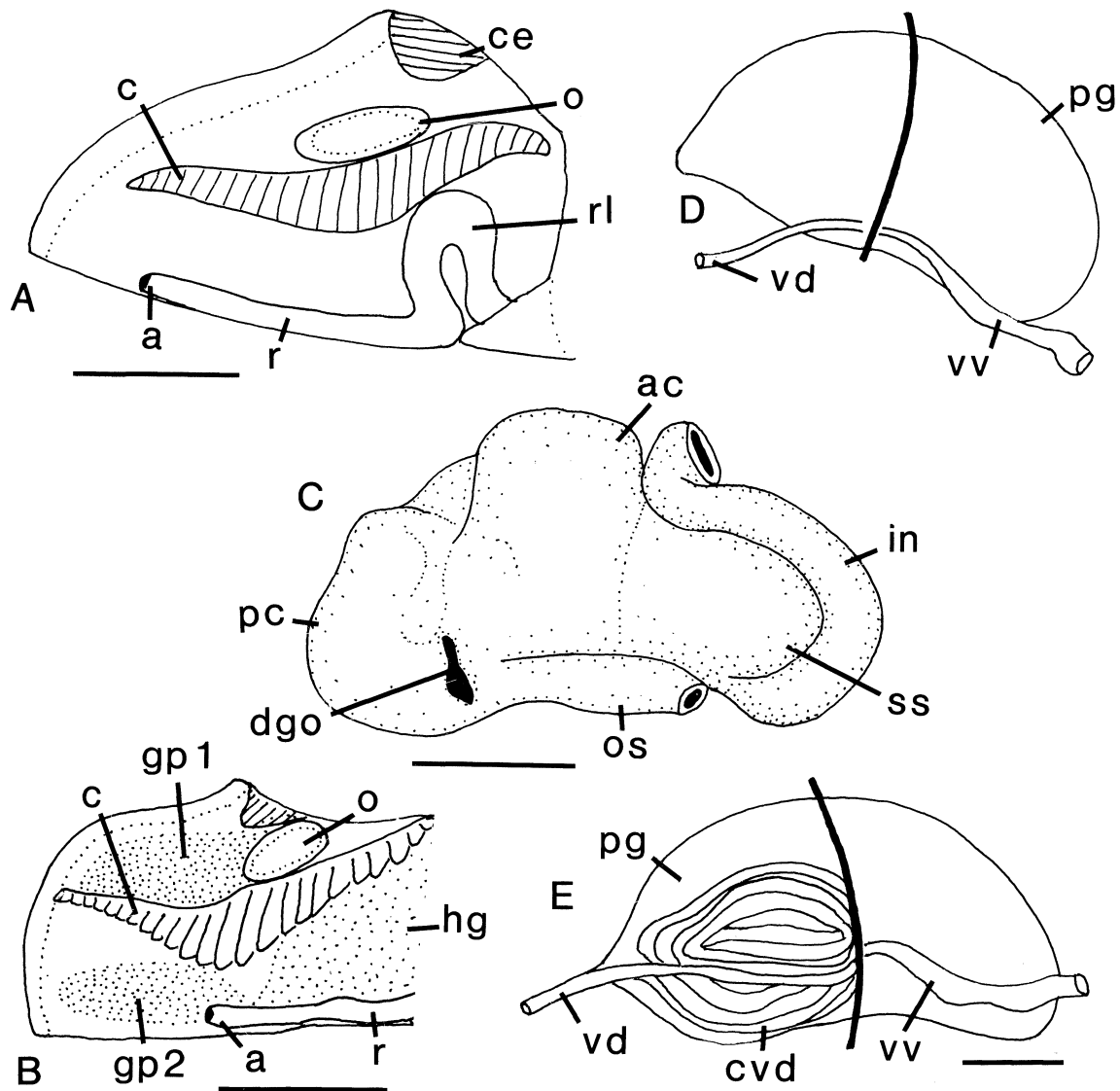


Fig.4. A,B, the inside of the pallial roof of *Jardinella carnarvonensis* (A) and *J. acuminata* (B) showing the main pallial structures. C, stomach of *J. edgbastonensis*. D,E, prostate glands of *Jardinella* sp. (D) (generalised and shows the prostate form for the majority of species) and *J. exigua* (E). The heavy black line represents the posterior wall of the pallial cavity. a – anus; ac – anterior chamber; c – ctenidium; ce – cut area; cvd – coiled pallial vas deferens; dgo – digestive gland opening; gp1 – glandular pad to left of ctenidium; gp2 – glandular pad near anus; hg – hypobranchial gland; in – intestine; o – osphradium; os – oesophagus; pc – posterior chamber; pg – prostate gland; r – rectum; rl – rectal loop; ss – style sac; vd – pallial vas deferens; vv – visceral vas deferens. Scales:- A,B,C – 0.5 mm, E – 0.1 mm.

(o) elongately oval, situated alongside posterior half of ctenidium, not extending to posteriormost part of ctenidium. Hypobranchial gland (hg) very well developed to absent, restricted to posterior part of pallial cavity when present. Glandular pads near anus (gp2) and left of ctenidium (gp1) present in 2 species. Renal organ abuts against posterior end of pallial cavity and, in some species, extends dorsally a little into pallial roof. Stomach (Fig. 4C) short, stomach/style sac ratio 0.9-1.9, with well-developed posterior (pc) and anterior (ac) chambers, the anterior chamber larger. Digestive gland opening (dgo) a simple slit above the oesophageal opening.

Male with penis situated on right side of neck and curled back into pallial cavity when at rest. Penis with broad basal portion, with surface concentrically folded when at rest, and smooth, often cuticularised, distal portion which, in some species, forms papilla. Simple, flattened, non-glandular, often pigmented lobe(s) present on distal part of penis in some species. Penial duct undulating in basal part of penis, more or less straight in distal part. Pallial vas deferens narrow, simple tube lying just below pallial floor, typically with multiple loops in section anterior to prostate, sometimes coiled over pallial part of prostate (Fig. 4E, cvd). Prostate gland (Fig. 4D,E, pg) about half to one third in pallial roof, with visceral vas deferens entering gland just behind posterior pallial wall and pallial vas deferens emerging from gland just in front of posterior pallial wall. Seminal vesicle long and coiled, anteriorly on stomach and posteriorly lying beneath about first half whorl of testis.

Female with large yolky eggs. Pallial oviduct mainly large capsule gland, posterior albumen gland usually immediately behind posterior pallial wall. Ventral channel simple (Fig. 5F, vc) and with anterior pallial opening in few species but typically with large, muscular vestibule at least partly separated from capsule gland (Fig. 5D,E, v), some species with pallial opening set off on short papilla. Type species with pallial opening about one third length of capsule gland posterior to anterior end of capsule gland. Vestibule, when present, often with deeply folded walls internally (Fig. 5E) and used for (short term?) sperm storage. Coiled oviduct non-pigmented, thinly muscular, basically U-shaped, lying on inner (left) side of albumen gland, with additional folds in some species. Bursa copulatrix posterior to albumen gland, ovate, with duct emerging from anterior face and joining oviduct at variable points from just in front of seminal receptacle duct to posterior wall of pallial cavity. Bursa copulatrix missing in one species. Seminal receptacle small, thin walled, usually on anterior edge of bursa copulatrix, rarely more posteriorly located.

Remarks. The original introduction of this genus name barely meets the requirements of the code [*Jardinella* (type *Petterdiana thaanumi* Pilsbry), a small globose freshwater rissoid, of unknown relationship"]. The genus is based on a species found in rivers and streams in the vicinity of Cairns, north-east Queensland. The type species shows the essential features exhibited by the species in the Queensland spring radiation described

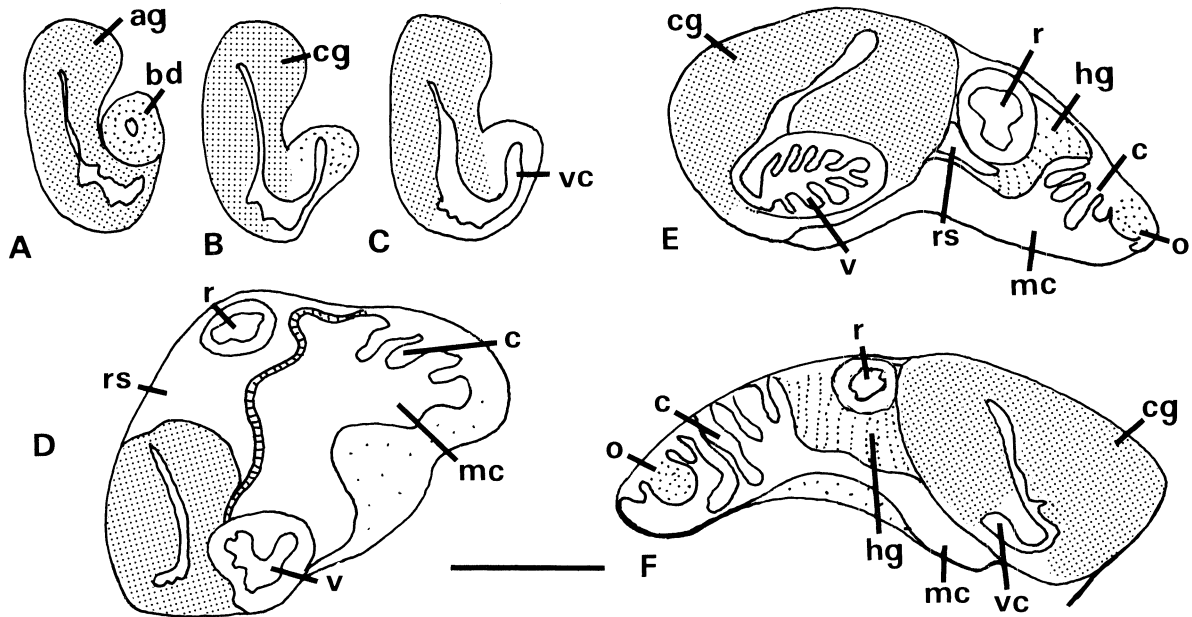


Fig.5. Sections of female pallial genital ducts and pallial cavities of species of *Jardinella*. A-D, *J. colmani*, Stn 71, A-C, sections through the anterior albumen gland (A) and posterior part of the capsule gland (B,C); D, section through the pallial cavity and the anterior part of the capsule gland; E, *J. jesswiseae*, Stn 73(A), section through the pallial cavity and capsule gland showing the vestibule; F, *J. acuminata*, section through the pallial cavity and middle part of the capsule gland. ag - albumen gland; bd - bursal duct; c - ctenidium; cg - capsule gland; hg - hypobranchial gland; mc - pallial cavity; o - osphradium; r - rectum; rs - rectal sinus; v - vestibule; vc - ventral channel. Scale:- 0.2 mm.

below, including a coiled pallial vas deferens, a smooth distal penis (lacking lobes), a white smear on the operculum and two pairs of basal cusps on the central teeth of the radula. Females lack a swollen anterior vestibule but the ventral channel is wide and internally thickened. This species is not dealt with in this paper but is treated in detail elsewhere (Ponder, in press).

Jardinella is distinguished from all other related genera in usually possessing two pairs of cusps on the central teeth of the radula and in never developing "calcareous" pegs on the operculum, although there is often a white smear. Some specimens of *Fonscochlea*, one of two described genera from South Australian artesian springs (Ponder *et al.*, 1989), resemble *Jardinella* in these characters but species of the former genus develop opercular pegs in most specimens of all but one species and even that species usually has rudimentary pegs. In addition, species of *Fonscochlea* have the osphradium very close to the posterior end of the ctenidium, not positioned in the third quarter (from the anterior end of the ctenidium) of the length as in species of *Jardinella*, and never develop a lobulate penis or coiled pallial vas deferens as is seen in most species of *Jardinella*. However, the major distinguishing autapomorphy of *Fonscochlea* is that females possess two equal-sized sperm sacs which lie alongside the posterior end of the albumen gland. The only other described hydrobiid genus from the South Australian mound springs is *Trochidrobia*. The species in that genus resemble the trochiform species of *Jardinella* in shell characters but differ in lacking a lobulate penis and coiled pallial vas deferens and in possessing only a single sperm sac (bursa copulatrix) in females. In addition, the opercular nucleus is located subcentrally in *Trochidrobia* and there is no trace of white material on the operculum. An undescribed genus, apparently related to *Jardinella*, from Dalhousie springs, South Australia (Ponder, 1989) differs from *Fonscochlea* and *Jardinella* in having only a single sperm sac (the bursa copulatrix). Species in that genus resemble those of *Jardinella* in lacking or having weak opercular pegs (as do a few taxa of *Fonscochlea*).

Another related genus, *Fluvidona* Iredale, 1937, is widespread in south-eastern Australia. It has been known under several names in recent literature including *Pupiphryx* Iredale, 1943 and *Rivisessor* Iredale, 1943 (used by Smith & Kershaw, 1979) and *Hemistomia* (as used by Ponder, 1982). Another synonym is *Angrobia* Iredale, 1943, and *Posticobia* Iredale, 1943 is at best a subgenus. The New Zealand genus *Potamopyrgus* Stimpson, 1865 and the south-western Pacific genus *Fluviopupa* Pilsbry, 1911 are also related. *Fluvidona* differs from *Jardinella* in having three or more pairs of basal cusps and in never developing penial lobes, a coiled pallial vas deferens or a vaginal papilla. In addition, most species of *Fluvidona* have well-developed white pegs on the inner surface of the operculum. Species of *Potamopyrgus* (see Winterbourn, 1970) resemble species of *Fluvidona* in both radular characters and anatomically, but never develop pegs on the operculum, although they often have a white smear. Some species of *Potamopyrgus* brood

embryos in the modified capsule gland. *Fluviopupa* species (see Ponder, 1982) have an accessory lobe on the penis and do not brood but otherwise resemble *Potamopyrgus*.

The genera listed above (with the possible exception of *Trochidrobia*) form a clade within the Hydrobiidae for which the subfamilial name Tateinae Thiele, 1925 is available (see Ponder & Warén (1988) for additional synonyms). No Australasian genera that fall outside this group have white material on the inner surface of the operculum. The origin and relationships of *Jardinella* are further discussed in the phylogenetic section below.

There is a considerable amount of diversity in the shell and anatomical characters in the group of species that we have included in *Jardinella*, although further subdivision may prove to be warranted when additional information, particularly biochemical data, becomes available. The considerable geographic spread of the genus and the divergence in anatomical and shell morphology, are in accord with the idea that it is the remnants of a much larger group of at least mid-Tertiary origin (see Discussion).

The species are described below in the four geographic areas in which they occur (see Fig. 1). These are:-

1. *Barcaldine Supergroup*:— springs on the eastern edge of the Basin north east of Longreach, including Edgbaston Springs.
2. *Springsure Supergroup*:— springs on the eastern side of the Basin west of Rolleston.
3. *Springvale Supergroup*:— springs on the western edge of the Basin south east of Boulia.
4. *Eulo Supergroup*:— springs on the southern side of the Basin west of Eulo.

Species from the Barcaldine Supergroup

Jardinella edgbastonensis n.sp.

Localities. Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaborra 338 486. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 220 m, on open plain. A – general; C – on sheep skull; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 170 m. B – lower part of outflow; C – small seep. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaborra 338 487. WZ, 3 May 1988. No mound but extensive seepage.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 72(A) C.156738 (holotype), C.156739 (250 paratypes), Stn 72(C) C.156744 (11 paratypes), Stn 72(E) C.156741 (160 paratypes), Stn 72(F) C.156740 (460 paratypes), Stn 73(B) C.156742 (15 paratypes), Stn 73(C)

C.156743 (120 paratypes), SAM Stn Z7 D.18524 (4 paratypes), Stn 72(F) D.18525 (20 paratypes), QM Stn 72(F), MO.20075 (5 paratypes).

Diagnosis. Shell trochiform, of medium size (up to 3.2 mm), smooth or with weak, rounded axial ribs, umbilicate. Penis with long, tapering distal portion, pigmented distally. Pallial oviduct with wide vestibule and ventral opening anterior to capsule gland.

Description. *Shell* (Figs 6A, 7): trochiform, of medium

size, 2.47-3.22 mm in length [mean 2.80 (M), 2.98 (F)]; 2.36-2.86 mm in width [mean 2.43 (M), 2.58 (F)]; sexually dimorphic in size (P less than 0.05); of medium thickness, translucent white, with indistinct, transparent periostracum. Spire angle $75.49-92.92^\circ$ [mean 83.17 (M), 84.47 (F)]. Protoconch (Fig. 7A,B) of 1.2-1.4 whorls [mean 1.31 (M), 1.35 (F)]. Teleoconch of 2.75-3.2 convex whorls [mean 2.99 (M), 3.03 (F)]. Convexity ratio 0.19-0.31 [mean 0.26 (M&F)]. Teleoconch sculpture of faint, prosocline growth lines sometimes strengthened to form rounded riblets (Fig. 7D). Aperture length/shell length ratio 0.51-0.6 [mean 0.57 (M), 0.56 (F)]. Inner lip of medium thickness, of medium width.

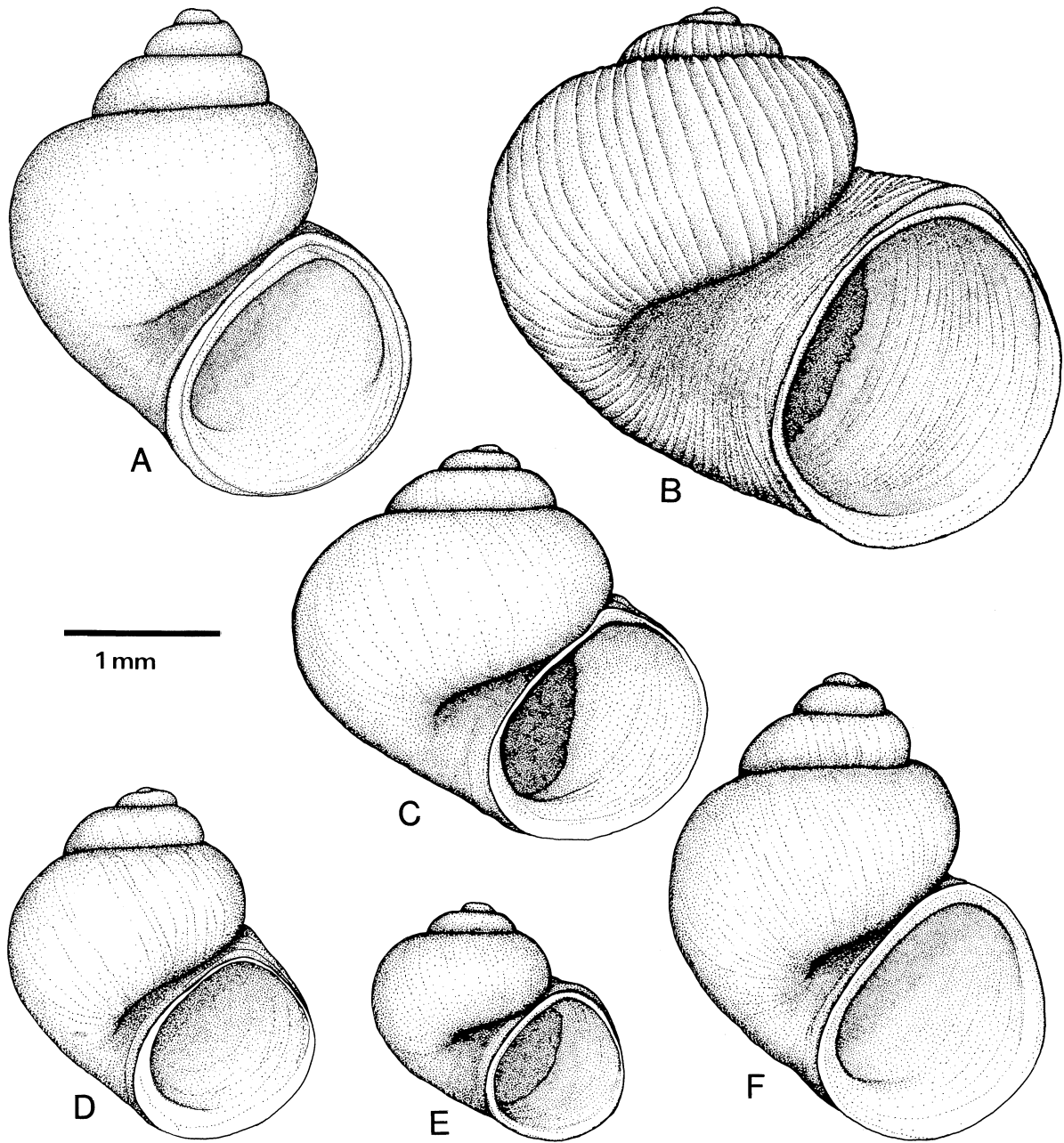


Fig.6. Shells of holotypes of species of *Jardinella*. A – *J. edgbastonensis*; B – *J. corrugata*; C – *J. eulo*; D – *J. carnarvonensis*; E – *J. exigua*; F – *J. coreena*.

Outer lip prosocline, angle $14.31-26.27^\circ$ [mean 20.33 (M), 22.18 (F)]. Umbilicus of medium width [$0.27-0.43$ mm; mean 0.33 (M), 0.35 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 3.08 mm, width 2.54 mm, length of aperture 1.68 mm, number of teleoconch whorls 3.10 .

Operculum (Fig. 8A): thin, pale yellow, $1.21-1.61$ mm in length [mean 1.36 (M), 1.45 (F)]. With or without white smear up to 0.93 mm in length [mean 0.15 (M), 0.24 (F)]. Ratio of opercular length to position of nucleus $2.94-3.55$ [mean 3.24 (M), 3.30 (F)].

Dimensions: see Table 3.

Radula (Fig. 8B,C): each central tooth with 2-3 lateral cusps; ratio of length of central cusp/length of adjacent

cusp $1.4-1.5$; 2 (rarely 3) pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula (2-3).1.4; ratio of length of primary cusp/length of adjacent outer cusps $1.6-1.8$; with small basal bulge; outer shaft 1.6 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig. 9A) oval in section, with no dorsal ciliated bands present; 2 distinct ciliated bands along most of ventral surface. Snout dark grey to black; anterior end unpigmented; dorsal sides of cephalic tentacles pale to dark grey with unpigmented patch either around eye or anterior to eye; sides of foot and opercular lobe pale to dark grey. Visceral coil pigmentation mostly black or dark grey.

Anatomy. Mantle cavity: ctenidium with 27-31 filaments;

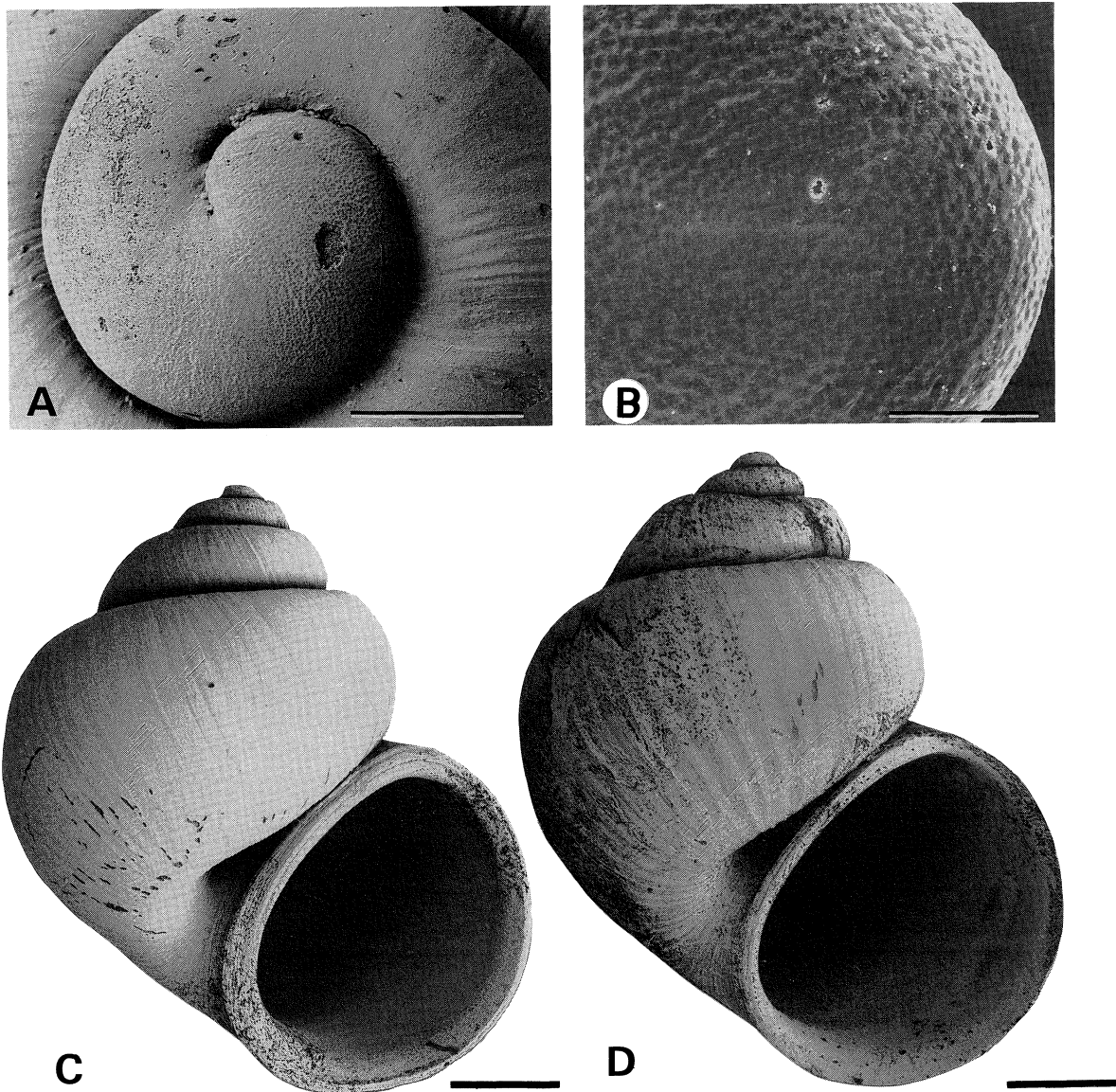


Fig. 7. *Jardinella edgbastonensis* n.sp., Stn 72(F), shell. A, dorsal view of protoconch; B, protoconch microsculpture; C, D, shells showing variation in sculpture. Scales:- A - 0.1 mm, B - 0.02 mm, C,D - 0.5 mm.

apex on right or towards centre. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus with intermediate position relative to mantle edge. Kidney either not extending forward into pallial roof or extends

forward slightly.

Male reproductive system (Figs 10A, 11A,B): penial lobe(s) absent; distal end of penis tapering; with broad grey band at proximal end of terminal portion; remainder unpigmented except for grey basal fold. Vas deferens with several loops/coils anterior to prostate gland

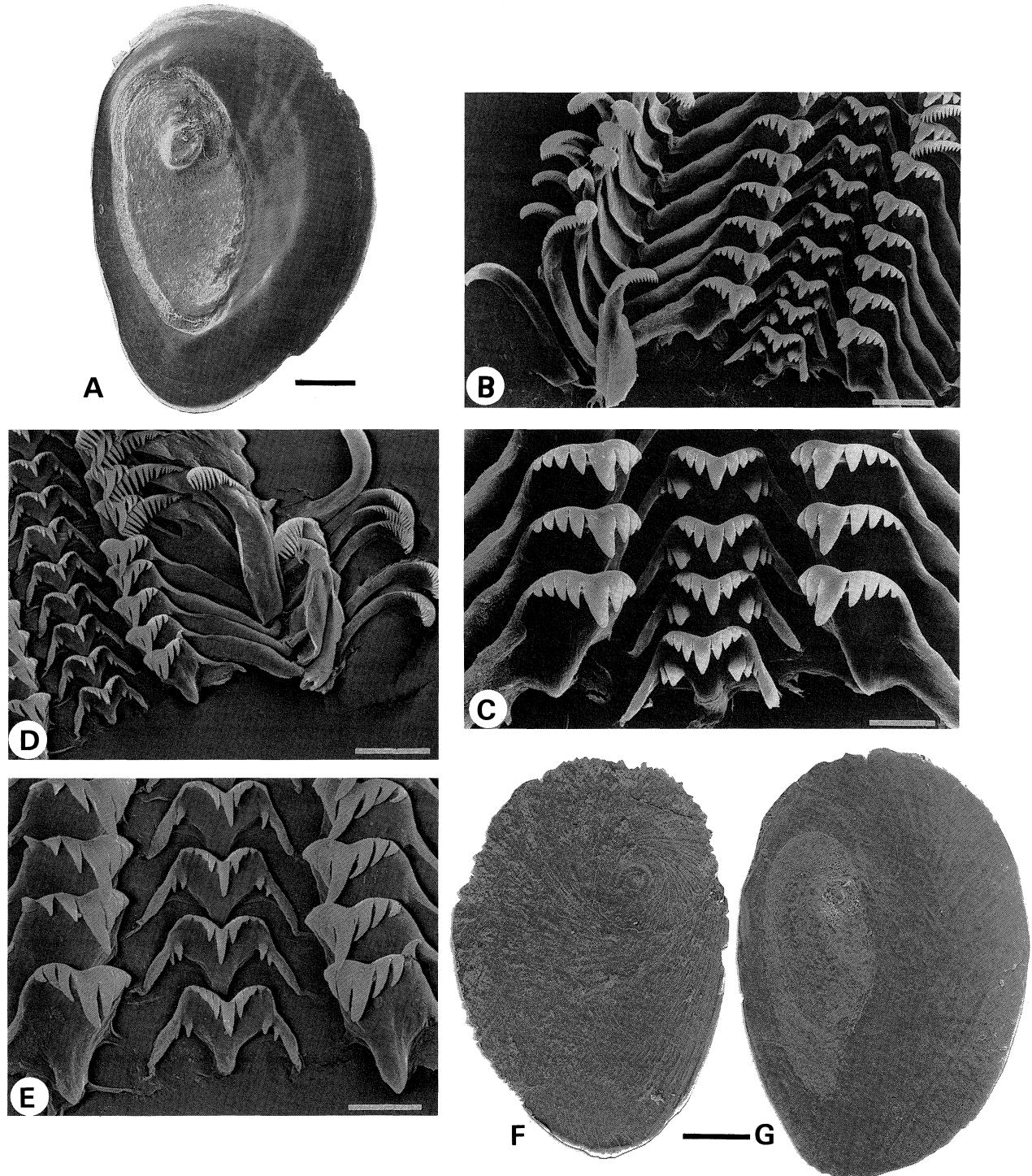


Fig.8. *Jardinella edgbastonensis* n.sp. and *Jardinella corrugata* n.sp., opercula and radulae. A–C, *J. edgbastonensis*, Stn 72(F); A, inner view of operculum; B,C, radula, C showing detail of central and lateral teeth. D–G, *J. corrugata*, Stn 73(C); D, E, radula, E showing detail of central and lateral teeth; F, G, outer (F) and inner (G) sides of operculum. Scales:- A,F,G – 0.250 mm, B,D – 0.02 mm, C,E – 0.01 mm.

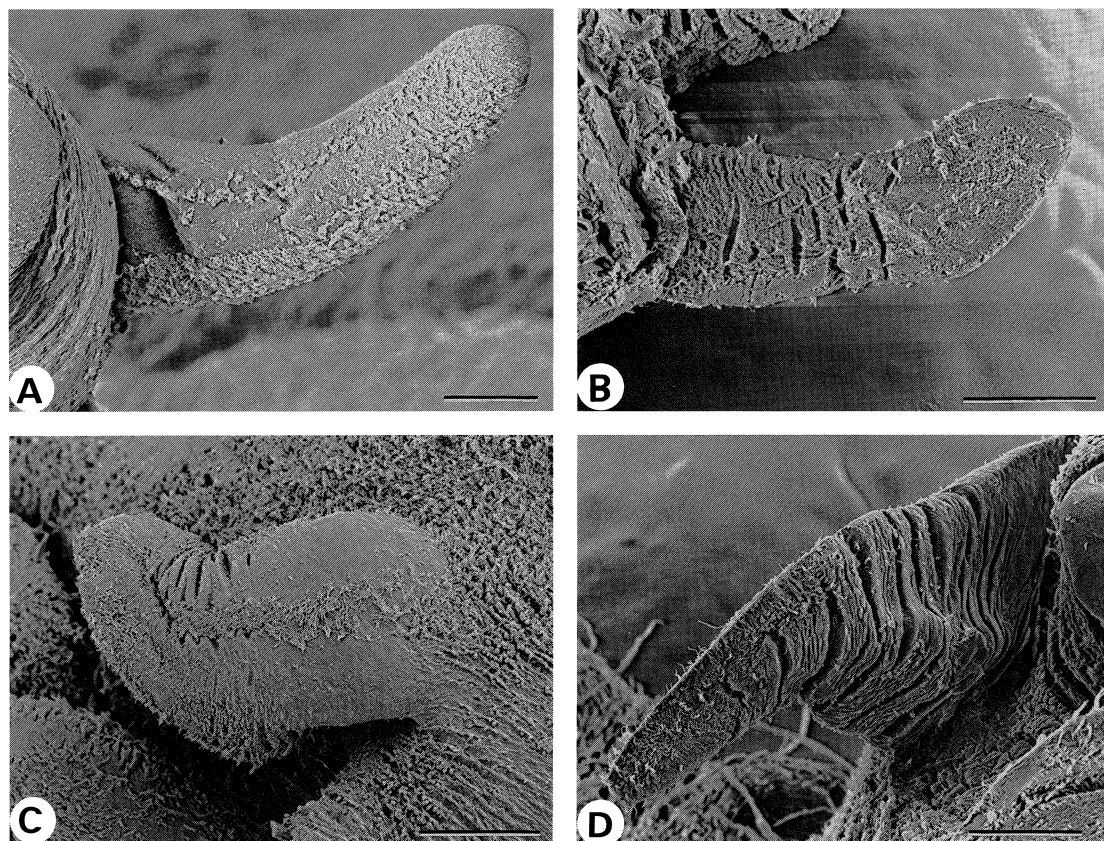


Fig.9. Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A, *J. edgbastonensis*, Stn 72(A), ventral view of left tentacle; B, *J. exigua*, Stn 93, ventral view of left tentacle; C, *J. corrugata*, Stn Z9(A), dorsal view of right tentacle; D, *J. carnarvonensis*, Stn Z15, ventral view of right tentacle. Scales:- A,C – 0.1 mm, B,D – 0.05 mm.

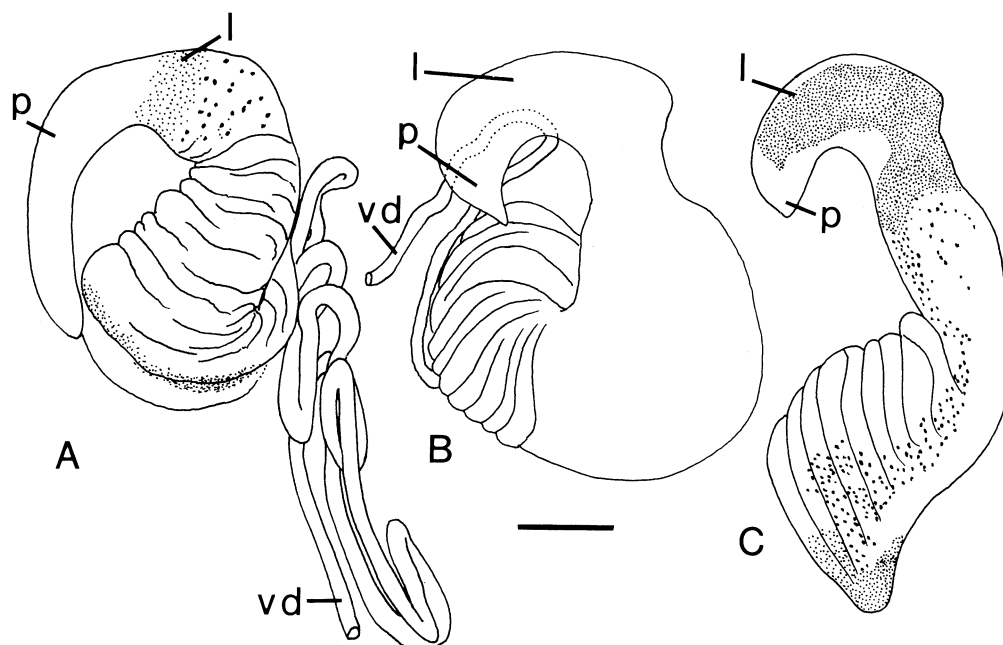


Fig.10. Penes of species of *Jardinella*. A, *J. edgbastonensis*, Stn 72(A); B, *J. coreana*, Stn Z14; C, *J. corrugata*, Stn Z9(A). The stipple indicates pigmentation. l – penial lobe or homologous area; p – penial papilla; vd – pallial vas deferens. Scale:- 0.25 mm.

(Fig. 10A, vd).

Female reproductive system (Fig. 12A,B): pallial oviduct with ventral channel modified as wide, muscular vestibule, duct extended anterior to capsule gland as ventrally located papilla. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix, which lies posterior - posterioventral to, and is smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

Remarks. This species is anatomically and conchologically the most similar of the spring species to the coastal type species of the genus. The rather large (for the genus) trochiform shell somewhat resembles that of two other spring species, *J. corrugata* n.sp. and *J. coreena* n.sp. from which it is distinguished in the following descriptions of these two species. It lives in the Edgbaston Springs along with five other species (Table 4) but appears to prefer the shallow, marshy outflows where it occurs together with *J. corrugata* in Stn 73 (*J. corrugata* was not found in Stn 72).

Etymology. Named for Edgbaston Station, north-east of Aramac.

***Jardinella corrugata* n.sp.**

Localities. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 170 m. A - upper outflow; B - lower part of outflow; C - small seep. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WZ, 4 May 1988. Large spring. A - outflow; B - from flood plain (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaborra 339 483. WZ, 4 May 1988.

Material examined. HOLOTYPE AND PARATYPES - AMS Stn Z9(B) C.156769 (holotype), Stn 73(B) C.156770 (40 paratypes), Stn 73(C) C.156771 (70 paratypes), SAM

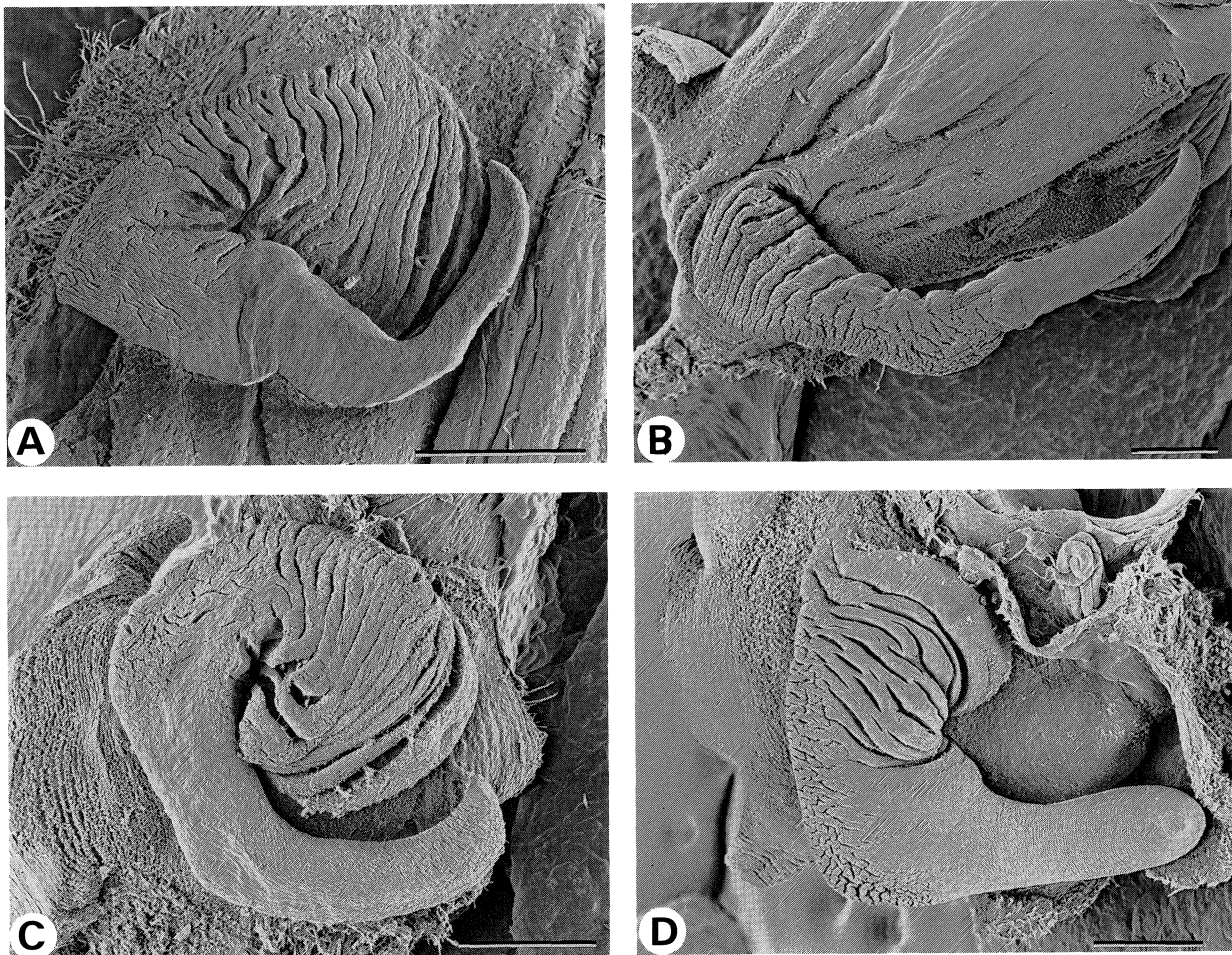


Fig.11. Scanning electron micrographs of critically point dried penes of species of *Jardinella*. A,B, *J. edgbastonensis*, Stn 72(A); C, *J. coreena*, Stn Z14; D, *J. corrugata*, Stn Z9(A). Scales:- 0.2 mm.

Stn Z9(A) D.18526 (60+ paratypes), Stn Z9(B) D.18527 (60+ paratypes), Stn Z10 D.18528 (60+ paratypes), Stn Z10 C.157421 (3 paratypes), QM Stn 73(C) MO.20076 (3 paratypes).

Diagnosis. Shell trochiform, large for genus (up to 4 mm in length), sculptured with weak, sharp riblets, widely umbilicate. Penis pigmented, with flattened distal lobe. Pallial oviduct with very wide, laterally located vestibule and terminal, laterally located opening.

Description. *Shell* (Figs 6B, 13): trochiform, large, 3.46-4.06 mm in length [mean 3.66 (M), 3.73 (F)]; 3.22-3.69 mm in width [mean 3.44 (M), 3.49 (F)]; not sexually dimorphic in size (P greater than 0.5); of medium thickness, translucent white, with indistinct, transparent periostracum. Spire angle 85.96 - 102.39° [mean 91.05 (M), 93.81 (F)]. Protoconch (Fig. 13D,E) of 1.25-1.35 whorls [mean 1.28 (M), 1.26 (F)].

Teleoconch of 2.7-2.9 convex whorls [mean 2.80 (M), 2.79 (F)]. Convexity ratio 0.28-0.38 [mean 0.32 (M), 0.33 (F)]. Teleoconch sculpture of faint to distinct, sharp axial riblets, and prosocline growth lines. Aperture length/shell length ratio 0.52-0.66 [mean 0.63 (M), 0.60 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 19.28 - 31.88° [mean 23.68 (M), 24.72 (F)]. Umbilicus wide [1-1.29 mm in width; mean 1.07 (M), 1.16 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 3.49 mm, width 3.65 mm, length of aperture 2.33 mm, number of teleoconch whorls 2.70.

Operculum (Fig. 8F,G): thin, very pale yellow, 1.77-2.11 mm in length [mean 1.93 (M), 1.97 (F)]. With white smear 0.01-0.71 mm in length [mean 0.33 (M), 0.42 (F)]. Ratio of opercular length to position of nucleus 2.47-3.71 [mean 3.22 (M), 3.32 (F)].

Dimensions: see Table 3.

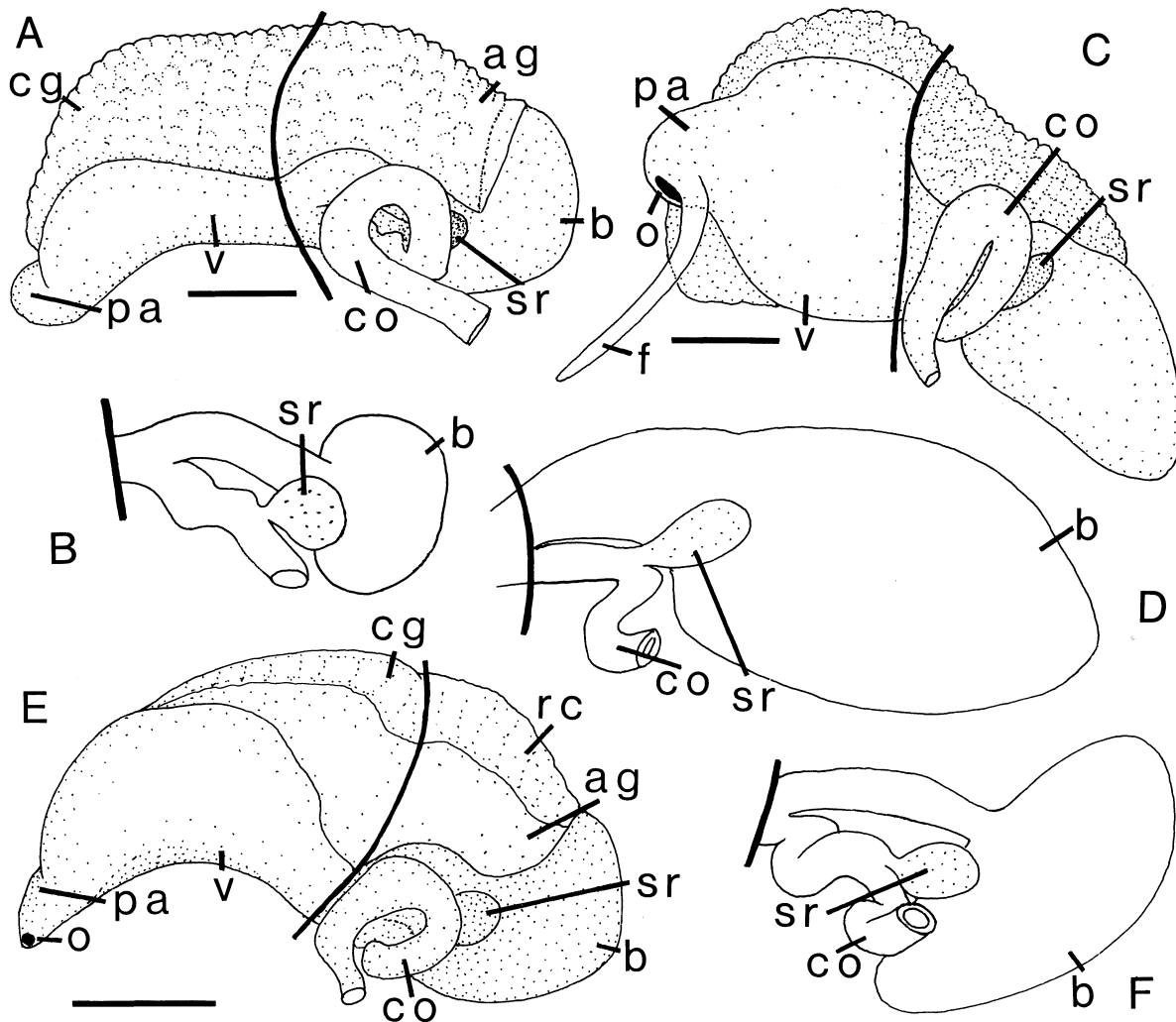


Fig.12. Female genitalia of species of *Jardinella*. A,B, *J. edgbastoniensis*, Stn 72(A); C,D, *J. corrugata*, Stn Z9(A); E,F, *J. coreena*, Stn Z14. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; f – fold; o – oviduct opening; pa – papilla with oviduct opening; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule. Scales:- 0.25 mm.

Radula (Fig. 8D,E): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.3-1.6; 2 pairs of basal denticles; dorsal edge concave to dorsal edge inverted U-shaped; basal process long, tongue shaped; does not protrude beyond basal margin. Each lateral tooth with cusp formula (3-4).1.(3-4); ratio of length of primary cusp/length of adjacent outer cusps 1.6-1.9; with well-developed basal bulge; outer shaft 1.7-2 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig. 9C) triangular in section, with dorsal ciliated band present on right tentacle only; 3 ciliated bands along most of ventral surface. Head and foot black to dark grey, sometimes with thin, mid-dorsal unpigmented line on cephalic tentacles. Visceral coil pigmentation mostly black or dark grey.

Anatomy. Mantle cavity: ctenidium with 26-28 filaments; apex on right, or towards centre. Osphradium near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus near mantle edge. Kidney not extending forward into pallial roof.

Male reproductive system (Figs 10C, 11D): penial lobe distal; distal end of penis blunt; penis with black zone at proximal end of terminal portion; small black spots proximal to this; proximal part of base partially black. Vas deferens with few loops/coils anterior to prostate gland.

Female reproductive system (Fig. 12C,D): pallial oviduct with ventral channel modified as wide, laterally located, muscular vestibule, duct extended as laterally placed papilla protruding beyond blunt anterior edge of capsule gland. Thin fold of tissue runs from oviduct opening anteriorly. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate to subtriangular bursa copulatrix which is about equal in size to albumen gland and posterior to it. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

Remarks. This species is generally similar to *J. edgbastonensis* n.sp. in size and shape but is distinguished from it by the tendency of the last whorl of the shell to become separated from the parietal wall in adults,

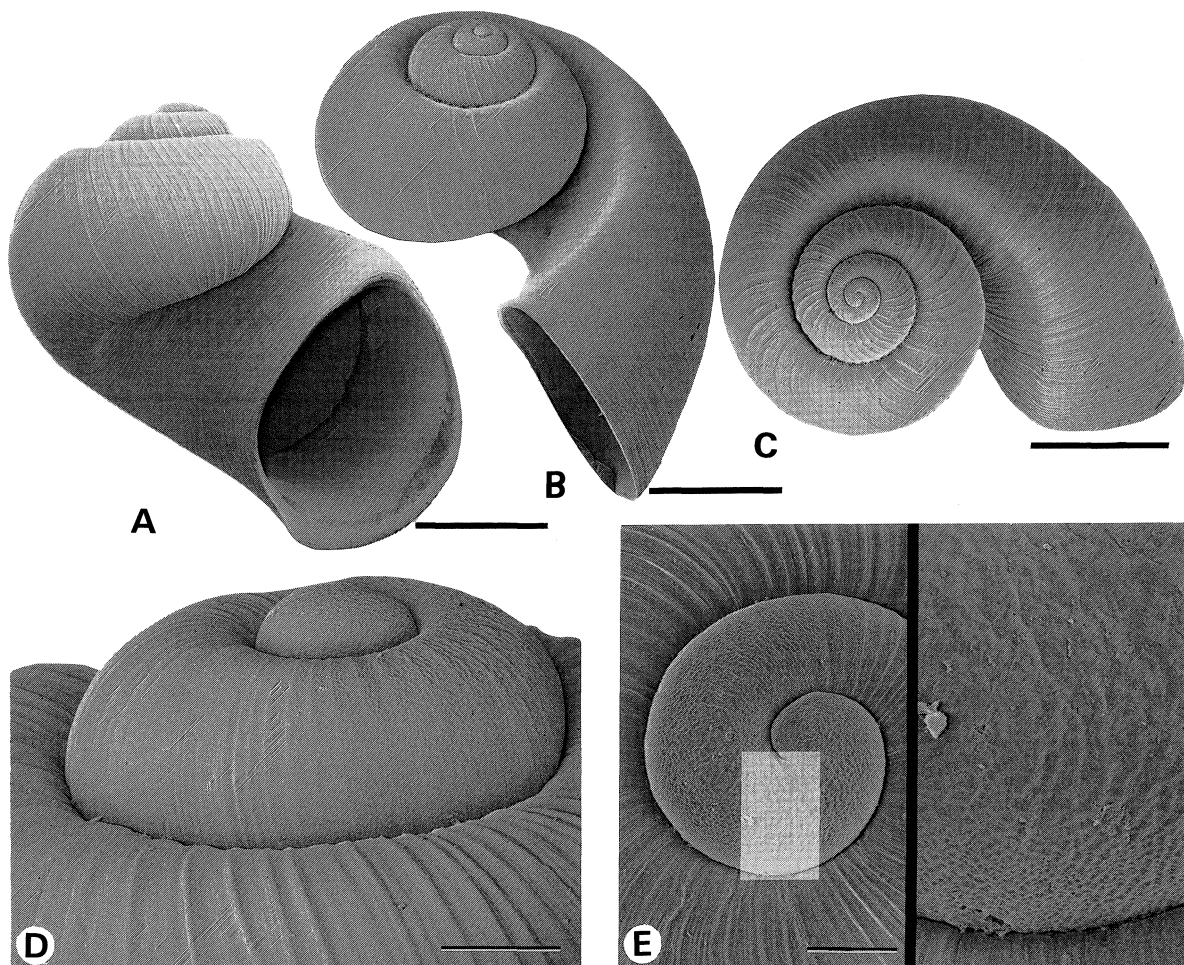


Fig. 13. *Jardinella corrugata* n.sp., shell. A-C, shell, Stn 73(C); D-E, protoconch, Stn 73(C), D, side view; E, dorsal view and microsculpture. The highlighted area shows the area magnified in the adjacent frame a further 4X. Scales:- A,B,C - 1.0 mm, D,E - 0.1 mm.

by the presence of sharp axial riblets, and a wider umbilicus [mean width relative to shell width 0.2 (males) and 0.3 (females) compared with 1.5 (males) and 1.1 (females) in *J. edgbastonensis*]. Of the shell and opercular characters measured, shell length and width, number of teleoconch whorls, aperture length and width, body whorl length, convexity, spire angle, umbilical width, opercular length, and the length of the white smear on the operculum are all significantly different (P equal to or less than 0.001), as are protoconch diameter and number of protoconch whorls (P equal to or less than 0.005). The two species also separate very well in the discriminant analysis (Figs 35-37), and *J. corrugata* also discriminates markedly from all other taxa.

Several anatomical characters separate *J. edgbastonensis* and *J. corrugata*, particularly genital differences. The pigmented penis is expanded and flattened (lobed) distally whereas that of *J. edgbastonensis* is unpigmented and narrow distally (compare Figs 10C and A, and 11D and A,B). The female genitalia differ mainly in the relative proportions of the oviduct glands and the development of the vestibule, the glandular oviduct being relatively short and broad compared with that of *J. edgbastonensis* (compare Figs 12C and A). The vestibule is much more massive in *J. corrugata*, with the oviducal opening placed higher and the bursa copulatrix is relatively larger and longer. In addition the oviduct anterior to the opening of the seminal receptacle is straight in *J. corrugata* but has a fold in *J. edgbastonensis* (compare Fig. 12D and B).

Although this species has only been collected from two springs at Edgbaston Springs, it may possibly occur in some of the other springs in the Edgbaston Group.

Etymology. From the Latin word *corrugo*, meaning to wrinkle up.

Jardinella coreena n.sp.

Type locality. Z14, large unnamed spring just south of "Coreena" homestead, about 32 km north-east of Barcardine, 23°17'S 144°24'E. Longreach 337 425. WZ, 5 May 1988.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn Z14 C.156792 (holotype), C.156793 (12 paratypes), SAM D.18529 (100+ paratypes), QM MO.20077 (2 paratypes).

Diagnosis. Shell trochiform, of medium size (up to 3.1 mm in length), smooth, umbilicate. Penis with distal lobe, unpigmented. Pallial oviduct with wide vestibule, pallial opening ventral and anterior to capsule gland.

Description. *Shell* (Figs 6F, 14E,F): trochiform, of medium size, 2.61-3.09 mm in length [mean 2.72 (M), 2.84 (F)]; 2.17-2.55 mm in width [mean 2.27 (M), 2.36 (F)]; not

sexually dimorphic in size (P greater than 0.2); of medium thickness, translucent to opaque white, with indistinct, transparent periostracum. Spire angle 76.58-89.9° [mean 79.07 (M), 80.86 (F)]. Protoconch (Fig. 14F) of 1.25-1.3 whorls [mean 1.25 (M), 1.26 (F)]. Teleoconch of 2.55-3.1 convex whorls [mean 2.85 (M), 2.93 (F)]. Convexity ratio 0.24-0.31 [mean 0.28 (M), 0.27 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.52-0.56 [mean 0.55 (M), 0.54 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle 15.97-28.84° [mean 23.93 (M), 21.12 (F)]. Umbilicus of medium width [0.22-0.4 mm in width; mean 0.27 (M), 0.34 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 2.97 mm, width 2.47 mm, length of aperture 1.59 mm, number of teleoconch whorls 2.80.

Operculum (Fig. 15A): thin, yellow, 1.22-1.4 mm in length [mean 1.26 (M), 1.31 (F)]. Without white smear. Ratio of opercular length to position of nucleus 3-3.58 [mean 3.41 (M), 3.19 (F)].

Dimensions: see Table 3.

Radula (Fig. 15B,C): each central tooth with 3-4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6-1.7; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 2.1.(3-4); ratio of length of primary cusp/length of adjacent outer cusps 1.5-1.7; with well-developed basal bulge; outer shaft 1.8-1.9 times longer than cutting edge.

Head-foot: cephalic tentacles triangular in section; lacking obvious dorsal and ventral ciliated tracts. Head and foot grey to dark grey; distal end of cephalic tentacles sometimes unpigmented. Visceral coil pigmentation mostly black or dark grey.

Anatomy. *Mantle cavity:* ctenidium with 25-28 filaments; apex on right. Osphradium between posterior end and middle of ctenidium to near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum without arch, position of anus varies from near mantle edge to intermediate position. Kidney either behind, or extends forward slightly into, pallial roof.

Male reproductive system (Figs 10B, 11C): penial lobe in medial part of distal part of penis; distal end of penis tapering; penis unpigmented. Vas deferens with one loop/coil anterior to prostate gland.

Female reproductive system (Fig. 12E,F): pallial oviduct with ventral channel modified as wide, muscular vestibule, duct extended anterior to capsule gland as ventrally located papilla. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix, which lies posteroventral to, and smaller to subequal in size to, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct basically U-shaped but with extra bend distally. Rudimentary penis absent in females.

Remarks. This species is isolated from the others in the

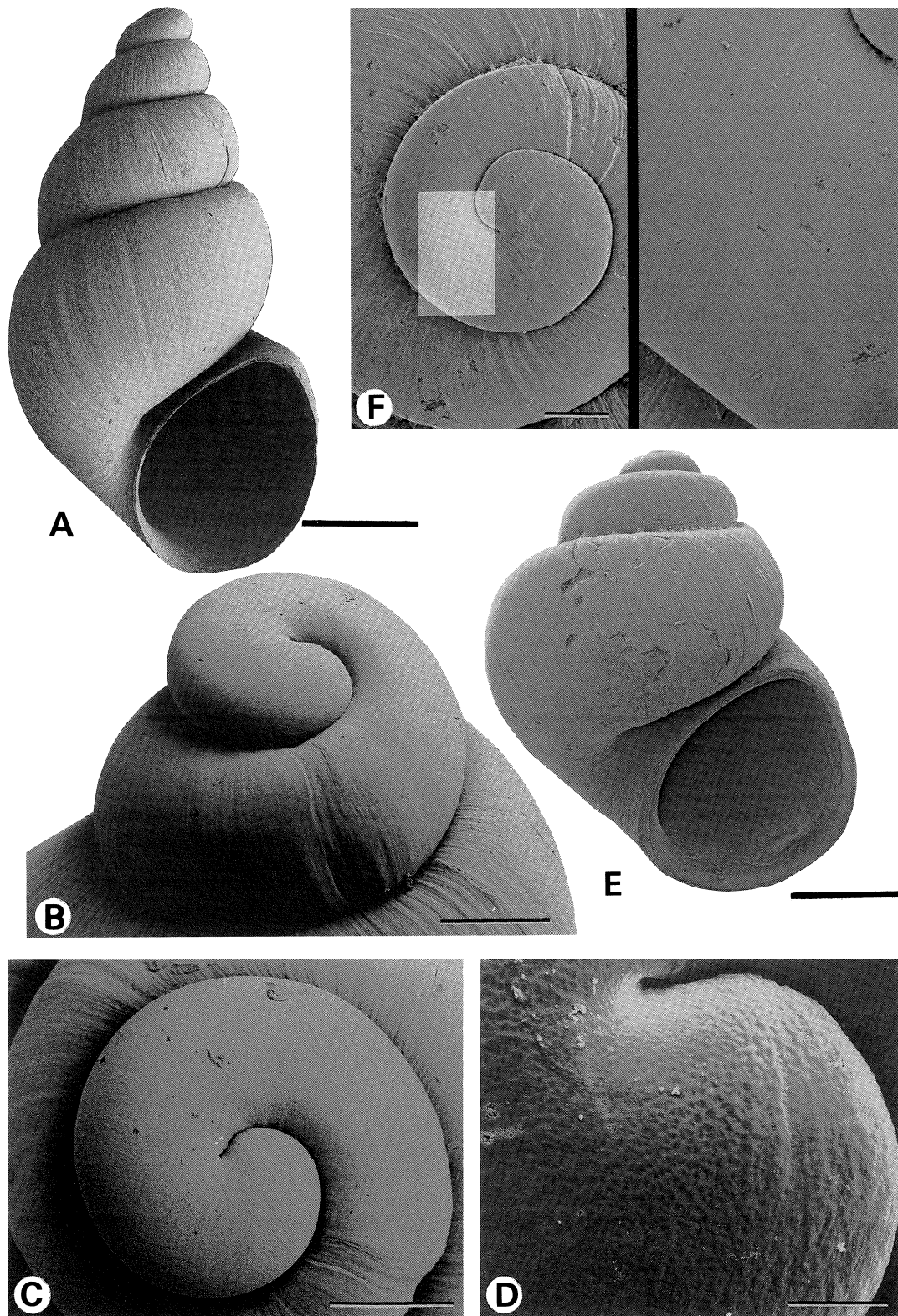


Fig.14. Shells of *Jardinella jesswiseae* n.sp. and *J. coreena* n.sp. A–D, *J. jesswiseae*, Stn 73(A); A, shell; B–D, protoconch, D showing microsculpture. E, F, *J. coreena*, Stn Z14; E, shell; F, protoconch, dorsal view and microsculpture. The highlighted area shows the area magnified in the adjacent frame a further 4X. Scales:– A,E – 0.5 mm, B,C,F – 0.1 mm, D – 0.02 mm.

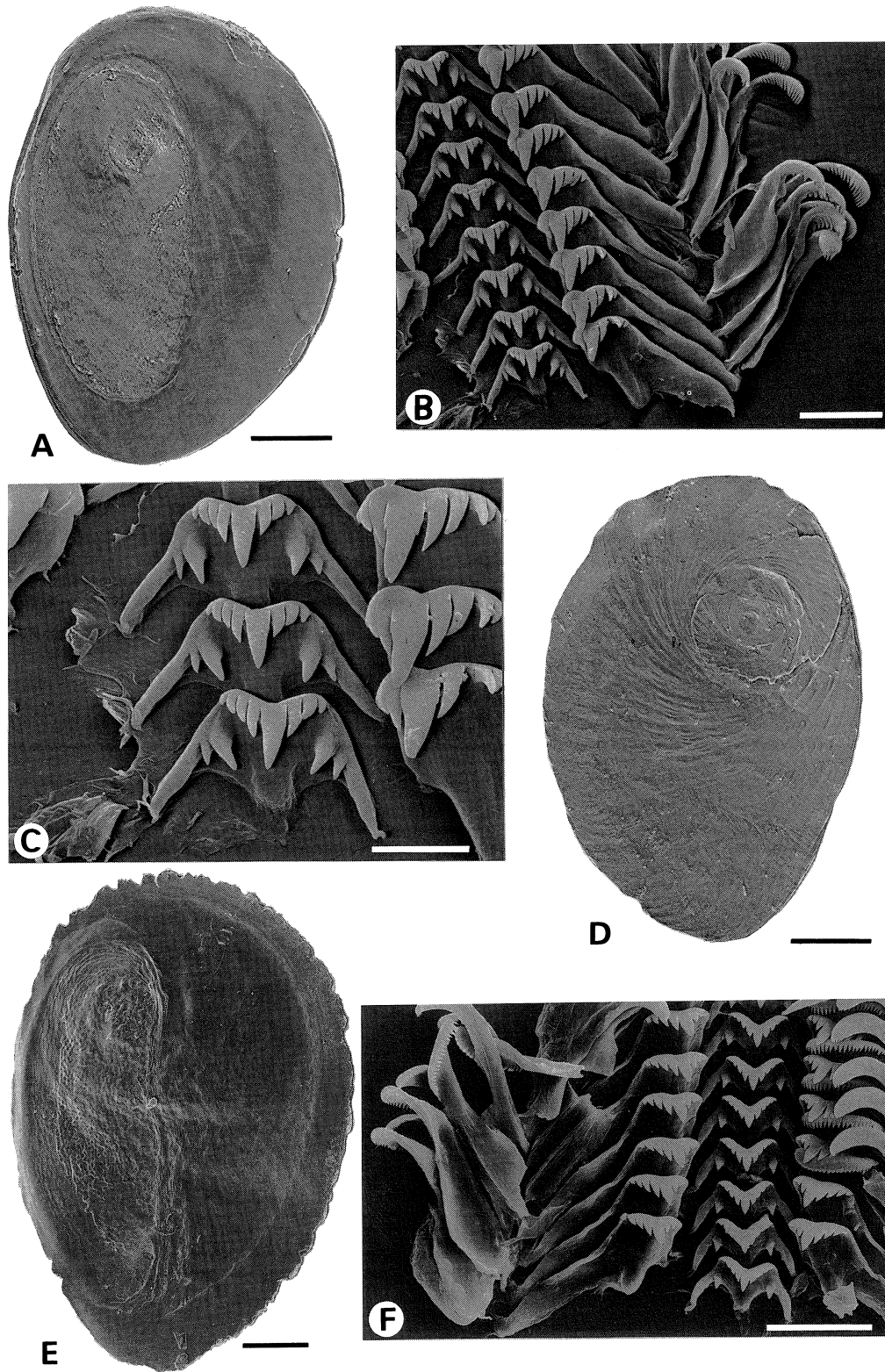


Fig.15. *Jardinella coreena* n.sp. and *Jardinella jesswiseae* n.sp., opercula and radulae. A–C, *J. coreena*, Stn Z14; A, inner view of operculum; B,C, radula, C showing detail of central and lateral teeth. D–F, *J. jesswiseae*, Stn 73(A); D,E, outer (D) and inner (E) sides of operculum; F, radula. Scales:- A,D,E – 0.1 mm, B,F – 0.02 mm, C – 0.01 mm.

area, being found 61 km south of the main Edgbaston Spring Group. It most closely resembles *J. edgbastonensis* n.sp. in shell characters but has a slightly smaller shell (P less than 0.3 for shell length and P less than 0.003 for shell width). Other shell characters that differ (P less than 0.006) include the number of protoconch whorls and the protoconch diameter (*J. edgbastonensis* is larger). Another similar species, *J. carnarvonensis* n.sp., is contrasted below. In the discriminant analysis the "trochiform" species do not separate well (with the exception of *J. corrugata* n.sp.). Comparisons of their generalised distances (Table 5) shows that *J. coreena* and *J. edgbastonensis* are the two most similar species, *J. carnarvonensis* the next most similar. The Euclidean distance comparisons (Table 6) show that *J. edgbastonensis* is the most similar but the next most similar species are *J. eulo* n.sp. and *J. isolata* n.sp., both these species being contrasted below.

Anatomically *J. coreena* also resembles *J. edgbastonensis*, having somewhat similar female genital characters, although differing in detail, notably in a more expanded vestibule and in having a small fold in the oviduct on both sides of the duct of the seminal receptacle. The penis has an expanded distal end (i.e. is lobed) and, apart from being unpigmented, is more similar to that of *J. corrugata*, not *J. edgbastonensis*. It would, however, be possible to derive the penis of *J. edgbastonensis* from that of *J. coreena* (or *J. corrugata*) by reduction of the folds. It also shares a general resemblance in shell characters to the two species described from the second group of springs (*J. carnarvonensis* and *J. exigua* n.sp.) but differs from them in its larger size and in genital characters.

Etymology. The species is named after the Coreena Homestead.

Jardinella pallida n.sp.

Localities. Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaborra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring, in *Phragmites*; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep. Stn 74, unnamed spring about 3.6 km south-east of "Edgbaston" homestead, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaborra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km east of Aramac, 22°42'45"S 145°25'25"E. Muttaborra 338 487. WZ, 3 May 1988. No mound but extensive seepage. Stn Z8, unnamed spring about 2.3 km north-east of "Edgbaston" homestead, about 33 km north-

east of Aramac, 22°43'S 145°25'30"E. Muttaborra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WZ, 4 May 1988. Large spring. A – outflow (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km east of Aramac, 22°45'30"S 145°25'40"E. Muttaborra 339 483. WZ, 4 May 1988.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 73(A) C.156759 (holotype), C.156760 (270 paratypes), Stn 73(B) C.156762 (10 paratypes), Stn 73(C) C.156761 (5 paratypes), Stn 72(A) C.156763 (80 paratypes), Stn 72(B) C.156767 (10 paratypes), Stn 72(D) C.156764 (90 paratypes), Stn 72(E) C.156766 (45 paratypes), Stn 72(F) C.156765 (340 paratypes), Stn 74 C.156768 (100+ paratypes), Stn Z7 C.157425 (1 paratype), Stn Z8 C.157426 (2 paratypes), Stn Z10 C.157423 (2 paratypes), SAM Stn Z7 D.18530 (30+ paratypes), Stn Z8 D.18531 (15 paratypes), Stn Z9(A) D.18532 (6 paratypes), Stn Z10 D.18533 (20+ paratypes), QM Stn 73(A) MO.20078 (5 paratypes).

Diagnosis. Shell conical, small (up to 1.8 mm in length), smooth, narrowly umbilicate. Penis lacking distinct lobe(s) but with median, pigmented part of distal portion swollen and with long, narrow papilla. Pallial oviduct with narrow vestibule, pallial opening subterminal and subventral.

Description. *Shell* (Figs 16B, 17C,D,G,H): conic, small, 1.34-1.82 mm in length [mean 1.41 (M), 1.62 (F)]; 0.82-1.03 mm in width [mean 0.86 (M), 0.94 (F)]; sexually dimorphic in size (P less than 0.001); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 58.97-77.4° [mean 73.52 (M), 68.88 (F)]. Protoconch (Fig. 17C,G,H) of 1.2-1.3 whorls [mean 1.24 (M), 1.24 (F)]. Teleoconch of 2.15-2.6 convex whorls [mean 2.25 (M), 2.45 (F)]. Convexity ratio 0.12-0.29 [mean 0.19 (M), 0.22 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.39-0.47 [mean 0.43 (M), 0.42 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 11.32-27.96° [mean 21.06 (M), 16.71 (F)]. Umbilicus small [0-0.12 mm in width; mean 0.06 (M), 0.05 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 1.77 mm, width 0.96 mm, length of aperture 0.67, number of teleoconch whorls 2.50.

Operculum (Fig. 18C): thin, very pale yellow, 0.59-0.77 mm in length [mean 0.63 (M), 0.70 (F)]. With or without white smear up to 0.3 mm in length [mean 0.13 (M), 0.15 (F)]. Ratio of opercular length to position of nucleus 2.68-4.28 [mean 3.36 (M), 3.30 (F)].

Dimensions: see Table 3.

Radula (Fig. 18D): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.4-1.6; 2 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula (3-4).1.5; ratio of length of primary cusp/length of adjacent outer cusps 1.5-1.6; with well-developed basal bulge; outer shaft 1.9 times longer than cutting edge.

Head-foot: cephalic tentacles triangular in section, with dorsal ciliated band present on both tentacles; 3 ciliated bands along most of ventral surface. Unpigmented except for smudge of grey behind eyes and proximal sides of snout. Visceral coil essentially unpigmented.

Anatomy. *Mantle cavity*: ctenidium with 20-22 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus near mantle edge. Kidney extending well forward into pallial roof.

Male reproductive system (Figs 20H, 21A): distinct

penial lobe(s) absent but these represented by swollen median part of distal portion of penis; distal end of penis with long papilla; penis unpigmented except pale grey distal end (excluding papilla). Vas deferens with about 2 loops/coils anterior to prostate gland.

Female reproductive system (Fig. 20F,G): pallial oviduct with ventral channel modified as narrow, muscular vestibule located subventrally, opening subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall

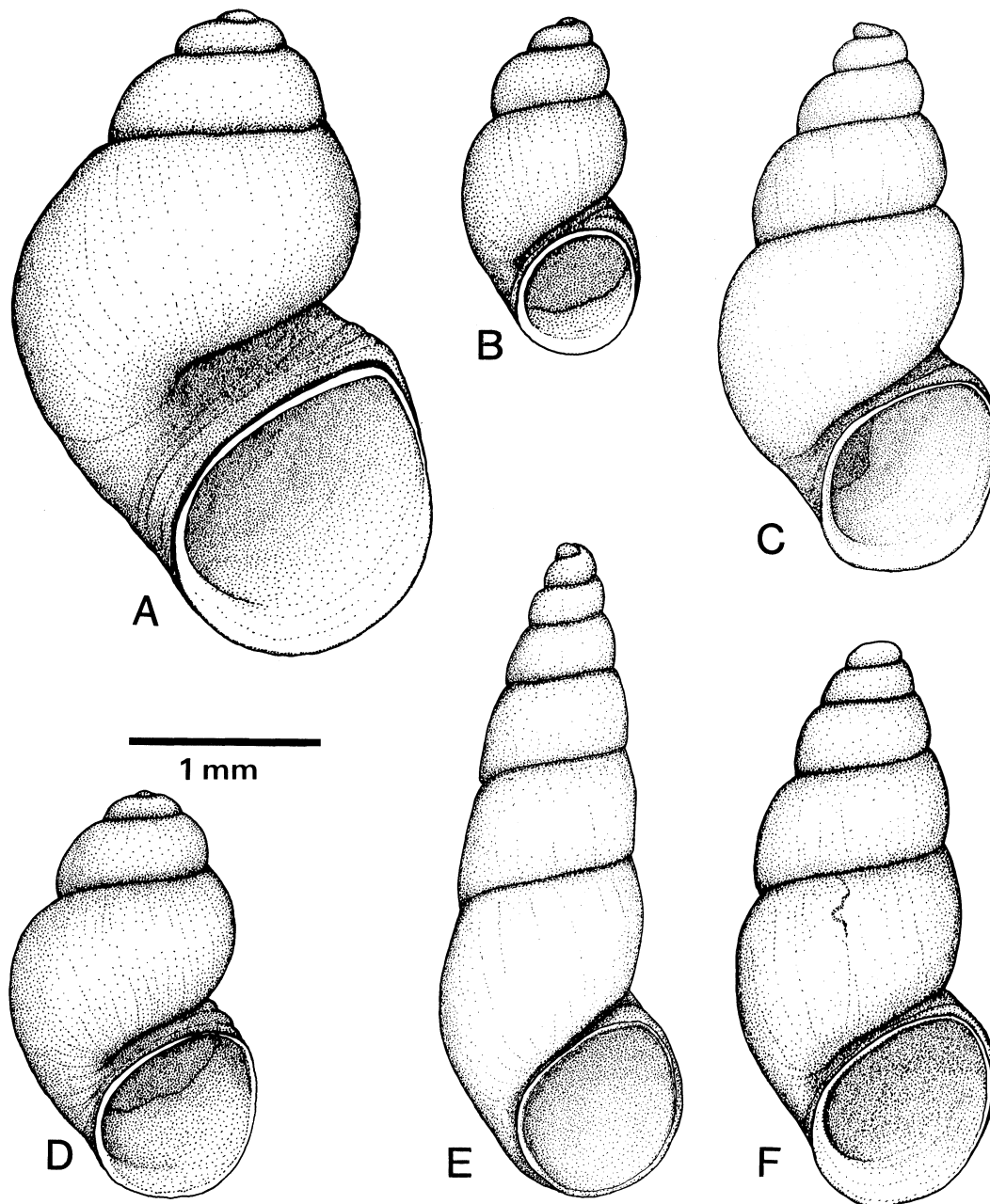


Fig.16. Shells of holotypes of species of *Jardinella*. A, *J. isolata*; B, *J. pallida*; C, *J. jesswiseae*; D, *J. colmani*; E, *J. acuminata*; F, *J. zeidlerorum*.

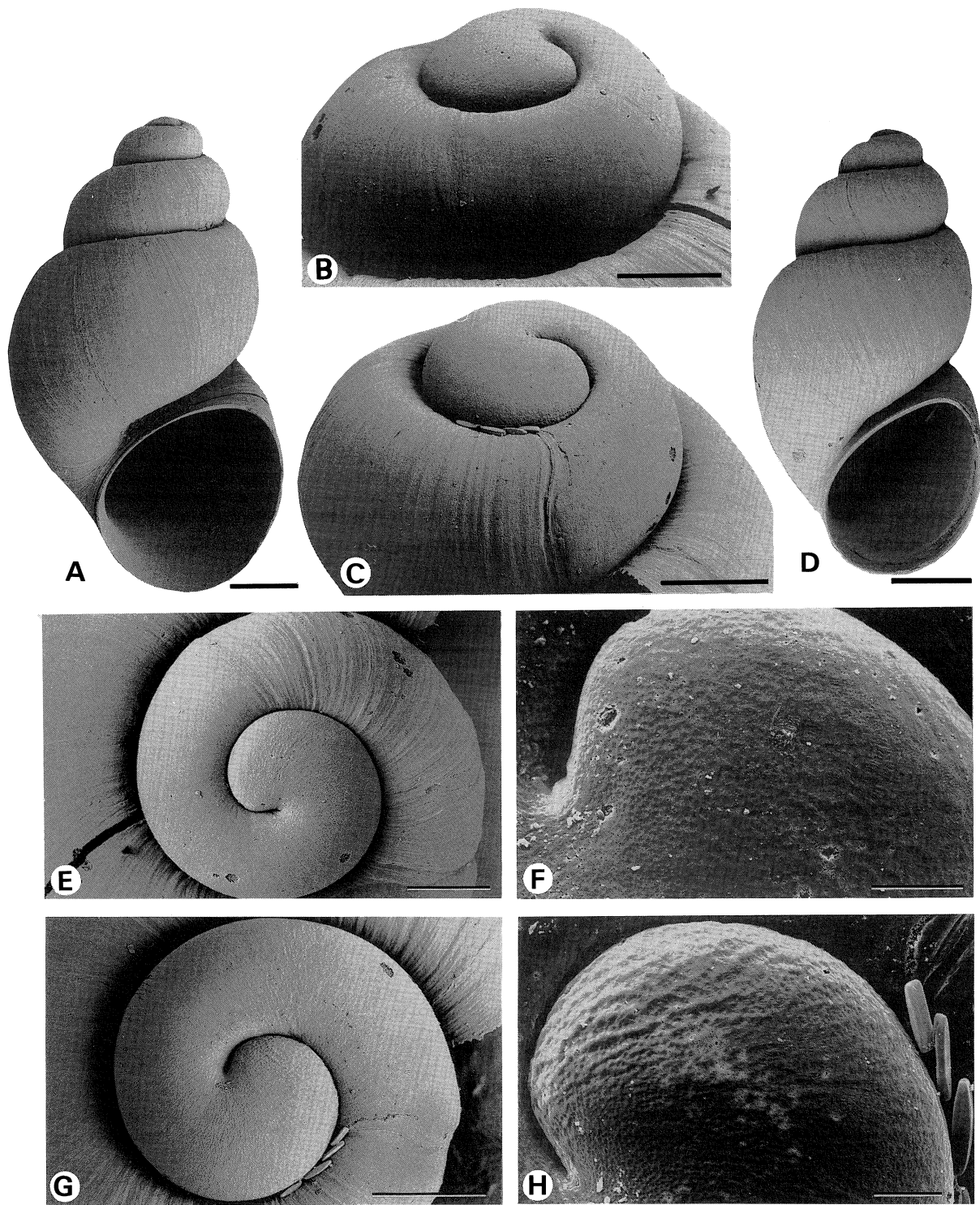


Fig.17. Shells of *Jardinella colmani* n.sp. and *J. pallida* n.sp. A,B,E,F, *J. colmani*, Stn 71; A, shell; B, E,F, lateral (B) and dorsal (E,F) views of protoconch, F showing microsculpture. C,D,G,H, *Jardinella pallida*, Stn 73(A); C, lateral view of protoconch, D, shell, G, H, dorsal view of protoconch and microsculpture (H). Scales:- A,D – 0.3 mm, B,C,E,G – 0.1 mm, F,H – 0.02 mm.

from seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend distally. Rudimentary penis absent in females.

Remarks. This species and the next appear to be closely related and are contrasted below. This species is the smallest in the Edgbaston Springs, being readily distinguished from all of the other species by its small size, pale body colour and medium-conical spire shape. It lives in the outflows of the springs in sympatry with all of the other species (see Table 4), being most abundant in Stn 72 in the lower outflow and in the upper outflow of Stn 73, but occurring throughout both springs.

Etymology. From the Latin word *pallidus* (a) meaning pale.

***Jardinella colmani* n.sp.**

Localities. Stn 71, unnamed spring near Smokey Creek about 8 km east-north-east of "The Springs" homestead, about 83 km north-north-east of Aramac, 22°12'20"S 145°22'30"E. Muttaborra 332 544. WFP and PHC, 25 Sept. 1984. Stn Z6, unnamed spring about "11 km north-east of "The Springs" homestead, about 83 km north of Aramac", 22°12'20"S 145°22'30"E. Muttaborra 332 544. WZ, 2 May 1988. Low mound (fenced) with ill-defined source and small outflow (almost certainly the same spring as Stn 71).

Material examined. HOLOTYPE AND PARATYPES – (all Stn 71) AMS C.156776 (holotype), C.156777 (500+ paratypes), SAM Stn Z6 D.18534 (2 paratypes), D.18535 (20 paratypes), QM MO.20079 (5 paratypes).

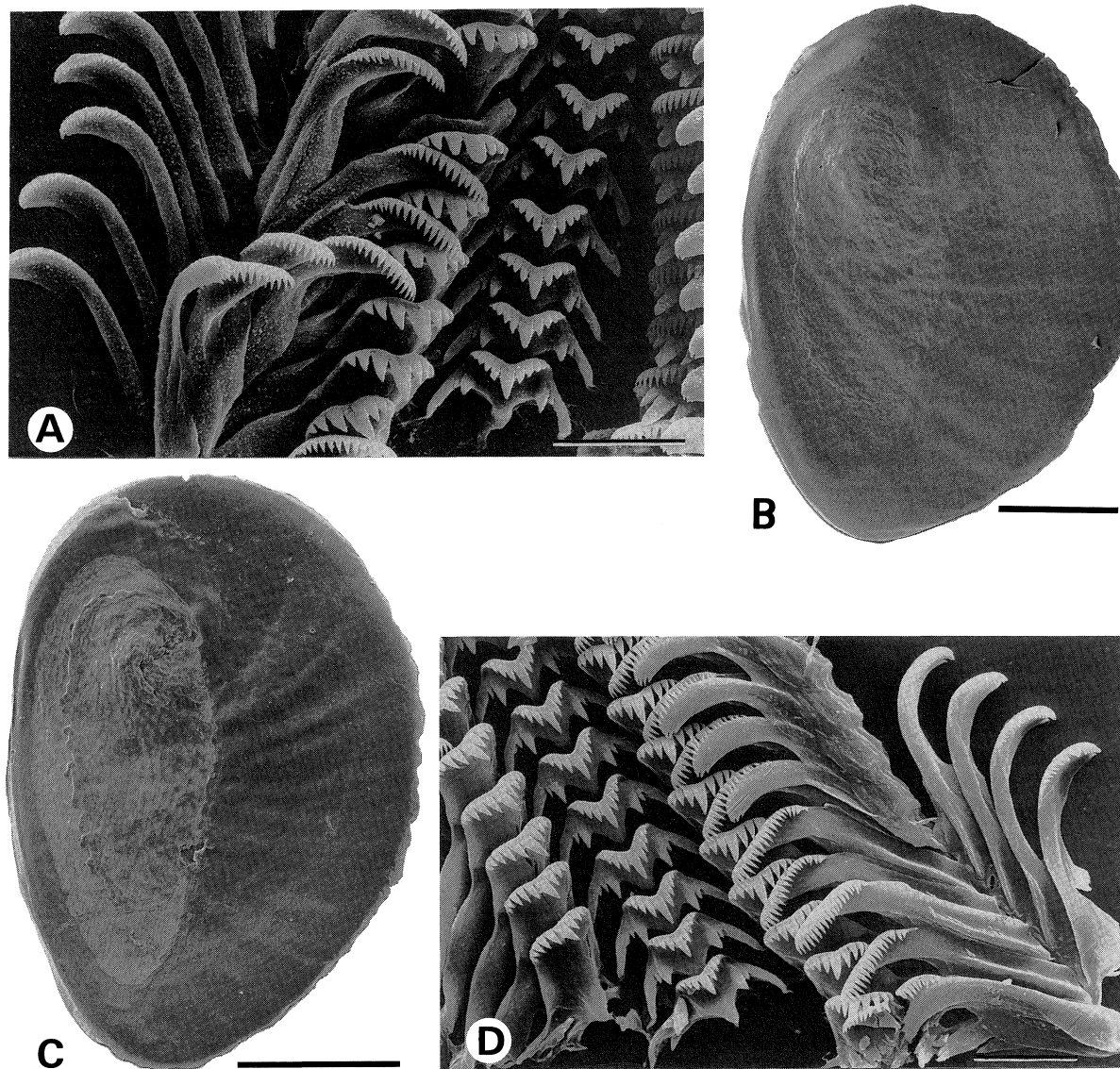


Fig.18. *Jardinella colmani* n.sp. and *Jardinella pallida* n.sp., opercula and radulae. A,B, *J. colmani*, Stn 71; A, radula; B, inner side of operculum. C,D, *J. pallida*, Stn 73(A); C, inner side of operculum; D, radula. Scales:- A,D – 0.01 mm, B,C – 0.2 mm.

Diagnosis. Shell conical, small to medium (up to 2.3 mm in length), smooth, narrowly umbilicate. Penis with slightly swollen area medially behind tapering distal end; swollen part (medial) pigmented. Pallial oviduct with narrow vestibule, pallial opening located on prominent

lateral, subterminal papilla.

Description. *Shell* (Figs 16D, 17A,B,E,F): conic, small to medium size, 1.6-2.31 mm in length [mean 1.66 (M), 1.96 (F)]; 1.02-1.48 mm in width [mean 1.11 (M), 1.26 (F)]; sexually

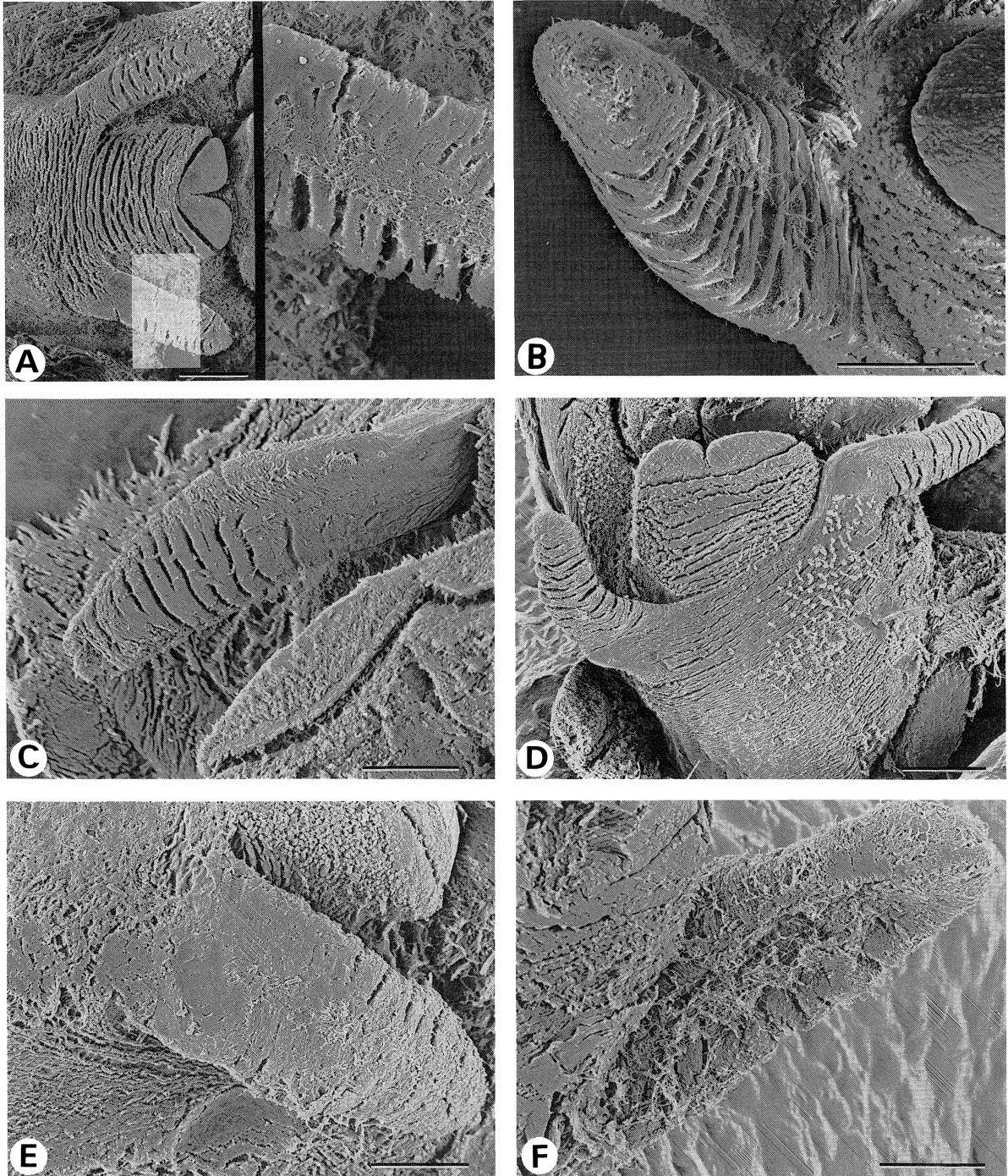


Fig.19. Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A,B, *J. colmani*, Stn 71; A, dorsal view of head, the highlighted area showing detail of cilia on right tentacle at 4X additional magnification; B, ventral view of left tentacle with part of the snout also showing. C,D, *J. zeidlerorum*, Stn Z12; C, ventral view of left tentacle with part of anterior edge of foot also showing; D, dorsal view of head showing ciliary tract at base of right tentacle. E,F, *J. jesswiseae*, Stn 73(A); E, dorsal view of right tentacle; F, ventral view of left tentacle. Scales:- A,D – 0.1 mm, B,C,E,F – 0.05 mm.

dimorphic in size (P less than 0.002); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle $70.95\text{--}86.79^\circ$ [mean 82.83 (M), 77.19 (F)]. Protoconch (Fig. 17B,E,F) of 1.2–1.35 whorls [mean 1.26 (M), 1.27 (F)]. Teleoconch of 2–2.65 convex whorls [mean 2.20 (M), 2.45 (F)]. Convexity ratio 0.16–0.28 [mean 0.22 (M), 0.21 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.42–0.51 [mean 0.47 (M), 0.44 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle $5.39\text{--}28.31^\circ$ [mean 12.57 (M), 15.74 (F)]. Umbilicus small [0.05–0.13 mm in width; mean 0.09 (M), 0.09 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 2.11 mm, width 1.30 mm, length of aperture 0.88, number of teleoconch whorls 2.50.

Operculum (Fig. 18B): thin, very pale yellow, 0.69–0.95 mm in length [mean 0.75 (M), 0.85 (F)]. With or without white smear up to 0.37 mm in length [mean 0.00 (M), 0.04 (F)], without pegs (note: of a sample of 21 only females had any sort of white smear). Ratio of opercular length to position of nucleus 2.63–3.52 [mean 3.05 (M), 3.04 (F)].

Dimensions: see Table 3.

Radula (Fig. 18A): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6–1.7; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp

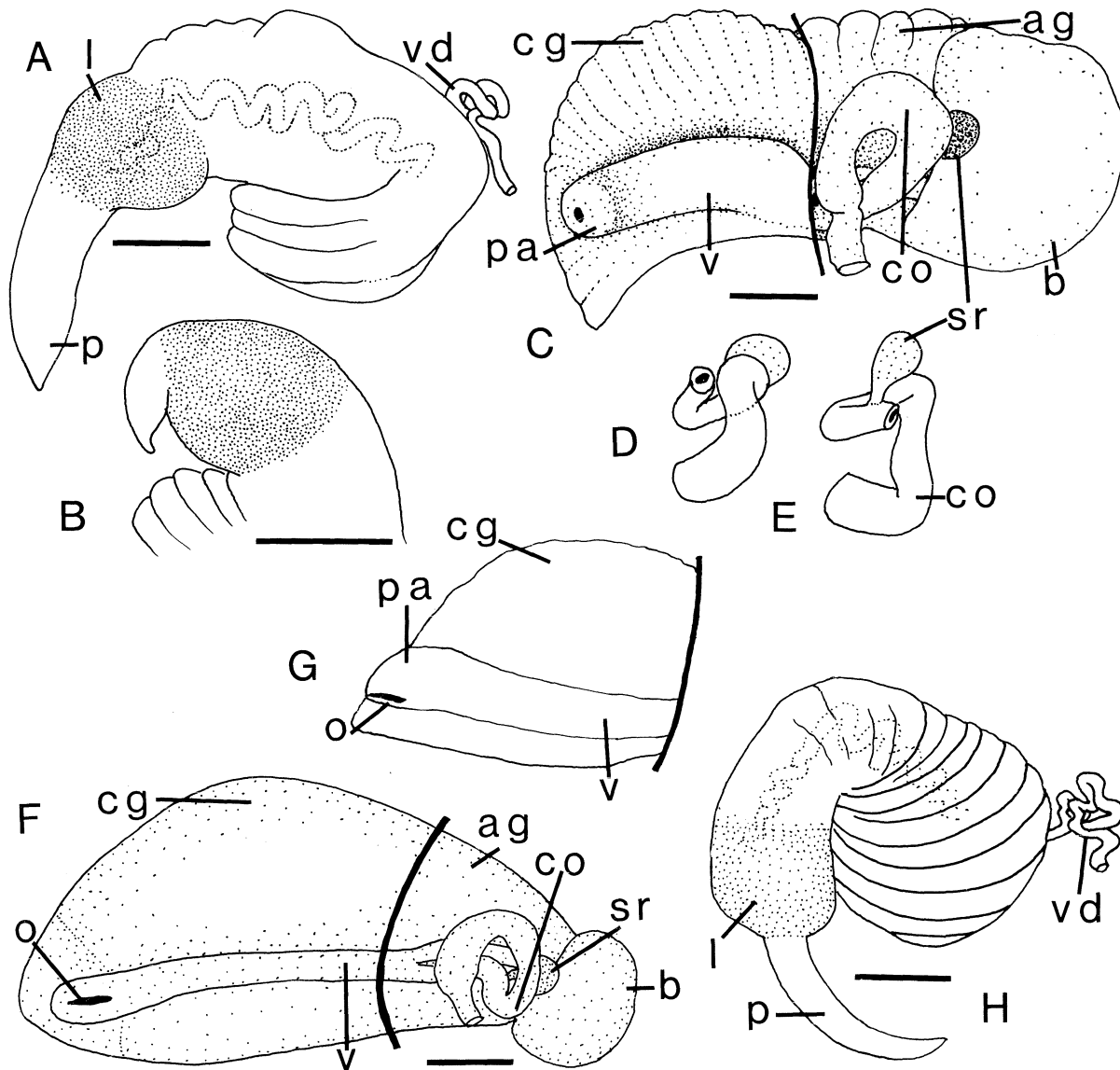


Fig. 20. Genitalia of species of *Jardinella*. A–E, *J. colmani*, Stn 71, A,B, penis, showing the range of variation in the length of the penial papilla; C–E, oviduct; F–H, *J. pallida*, Stn 73(A), F,G, oviduct, H, penis. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; pa – papilla with oviduct opening; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:– A,C,F,H – 0.1 mm, B – 0.2 mm.

formula 3.1.3-4; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.6; with well-developed basal bulge; outer shaft 1.3-1.4 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig.19A,B) triangular in section, with 1 mid-dorsal ciliated band on right tentacle only and 3 ventral bands on both tentacles. Proximal sides of snout and bases of cephalic tentacles black or

grey, pigment extending along sides of neck. Cephalic tentacles with mid-dorsal streak in proximal half in some specimens; sides of foot and opercular lobe pale grey.

Anatomy. Mantle cavity: ctenidium with 17-23 filaments; apex on right. Osphradium between posterior end and

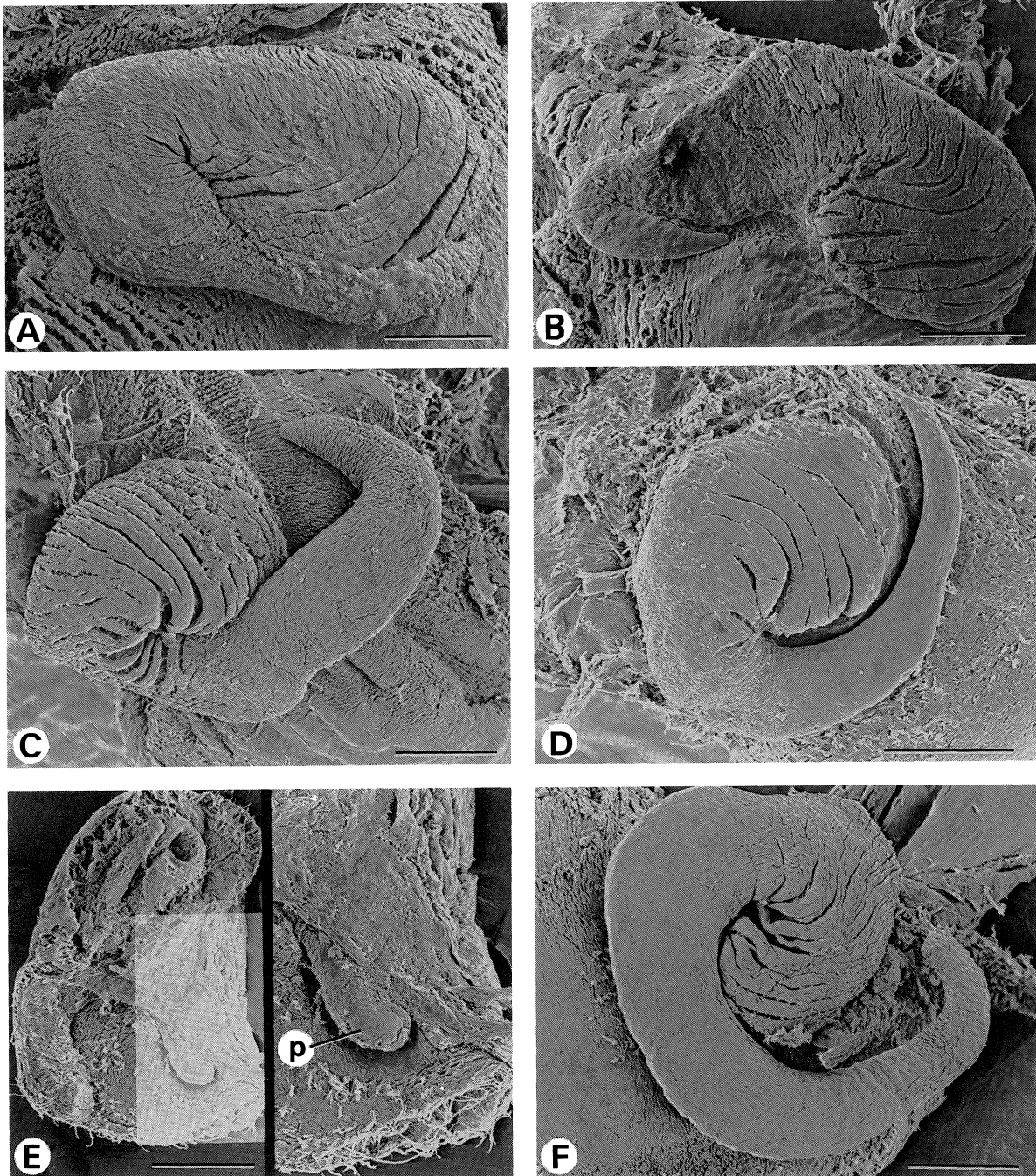


Fig.21. Scanning electron micrographs of critical point dried genitalia of species of *Jardinella*. A, *J. pallida*, Stn 73(A), penis; B, E, *J. colmani*, Stn 71, B, penis; E, glandular oviduct, the highlighted area is magnified 2X in the adjacent figure and shows the papilla-like structure with the pallial opening at its anterior end; C, *J. jesswiseae*, Stn 73(A), penis; D, *J. acuminata*, Stn 73(B), penis; F, *J. zeidlerorum*, Stn Z12, penis. p – papilla. Scales:- A – 0.05 mm, B,C,D,F – 0.1 mm, E – 0.2 mm.

middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus with intermediate position relative to mantle edge. Kidney extending well forward into pallial roof.

Male reproductive system (Figs 20A,B, 21B): penial lobe not obvious, appears to be developed as medial (pigmented) swollen area; distal portion tapering, distal extremity with very short papilla in some specimens; swollen medial area grey, rest unpigmented. Vas deferens with few loops/coils anterior to prostate gland.

Female reproductive system (Figs 20C–E, 21E): pallial oviduct with ventral channel modified as narrow, lateroventrally placed muscular vestibule, duct extended as prominent lateral papilla opening laterally and subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from anterodorsal side of ovate bursa copulatrix which lies posterior to, and is slightly larger than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall from seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend in middle part. Rudimentary penis absent in females.

Remarks. This species is most similar to *J. pallida* n.sp. and the two taxa are located about 58 km apart. *Jardinella colmani* differs from *J. pallida* in its larger size darker body pigmentation and more developed vestibule, the opening of which is located on a distinct papilla midlaterally on the anterior part of the capsule gland. The penis is similar in both species but the long, distal filament is narrower, relative to the rest of the penis, in *J. pallida* than in *J. colmani*.

Discriminate analysis shows *J. colmani* to be most similar to *J. pallida* and both species are more similar to one another than to any other species. Comparisons of the measurement data showed that all shell and opercular characters, except convexity, the number of teleoconch and protoconch whorls and aperture angle, differ significantly (P less than 0.001) from those of *J. pallida*. The only other somewhat similar species is *J. jesswiseae* n.sp. which is more darkly pigmented, has a taller shell with more whorls and a deviated protoconch, as well as several anatomical differences.

A visit to what is almost certainly the same spring in 1987 by W. Zeidler failed to locate living material of *J. colmani* (2 empty shells were found) so the population may have considerably declined in numbers or even be extinct.

Etymology. The species is named after Phillip Colman of the Australian Museum.

Jardinella jesswiseae n.sp.

Localities. Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaborra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring,

in *Phragmites*; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep; D – head of spring. Stn 74, unnamed spring about 3.6 km south-east of "Edgbaston" homestead, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaborra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaborra 338 487. WZ, 3 May 1988. No mound but extensive seepage. Z8, unnamed spring about 2.3 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°43'S 145°25'30"E. Muttaborra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaborra 339 483. WZ, 4 May 1988.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 73(B) C.156748 (holotype), C.156749 (330 paratypes), Stn 73(C) C.156750 (45 paratypes), Stn 73(A) C.156751 (1620 paratypes), Stn 73(D) C.156752 (165 paratypes), Stn 72(A) C.156753 (300+ paratypes), Stn 72(B) C.156757 (9 paratypes), Stn 72(D) C.156754 (460 paratypes), Stn 72(E) C.156756 (20 paratypes), Stn 72(F) C.156755 (40 paratypes), Stn 74 C.156758 (500+ paratypes), Stn Z10 C.157422 (4 paratypes), Stn Z7 C.157424 (2 paratypes), Stn Z8 C.157427 (2 paratypes), SAM Stn Z7 D.18536 (50+ paratypes), Stn Z8 D.18537 (500+ paratypes), Stn Z9(A) D.18538 (500+ paratypes), Stn Z9(B) D.18539 (1 paratype), Stn Z10 D.18540 (30+ paratypes), QM Stn 73(B) MO.20080 (5 paratypes).

Diagnosis. Shell conical, small to medium in size (up to 2.8 mm in length), smooth, umbilicate. Penis with expanded, pigmented distal half, lacking distinct lobe(s), with small terminal papilla. Pallial oviduct with wide vestibule, pallial opening ventral and subterminal.

Description. *Shell* (Figs 14A–D, 16C): conical, small to medium size, 1.87–2.84 mm in length [mean 2.08 (M), 2.43 (F)]; 1.09–1.4 mm in width [mean 1.18 (M), 1.29 (F)]; sexually dimorphic in size (P less than 0.003); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 46.83–63.09° [mean 57.06 (M), 55.35 (F)]. Protoconch (Fig. 14B–D) deviated; of 1.2–1.4 whorls [mean 1.26 (M), 1.25 (F)]; minutely pitted. Teleoconch of 2.9–3.85 convex whorls [mean 3.20 (M), 3.55 (F)]. Convexity ratio 0.13–0.24 [mean 0.20 (M), 0.20 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.33–0.45 [mean 0.40 (M), 0.37 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 10.25–28.15° [mean 19.73 (M), 20.16 (F)]. Umbilicus minute to

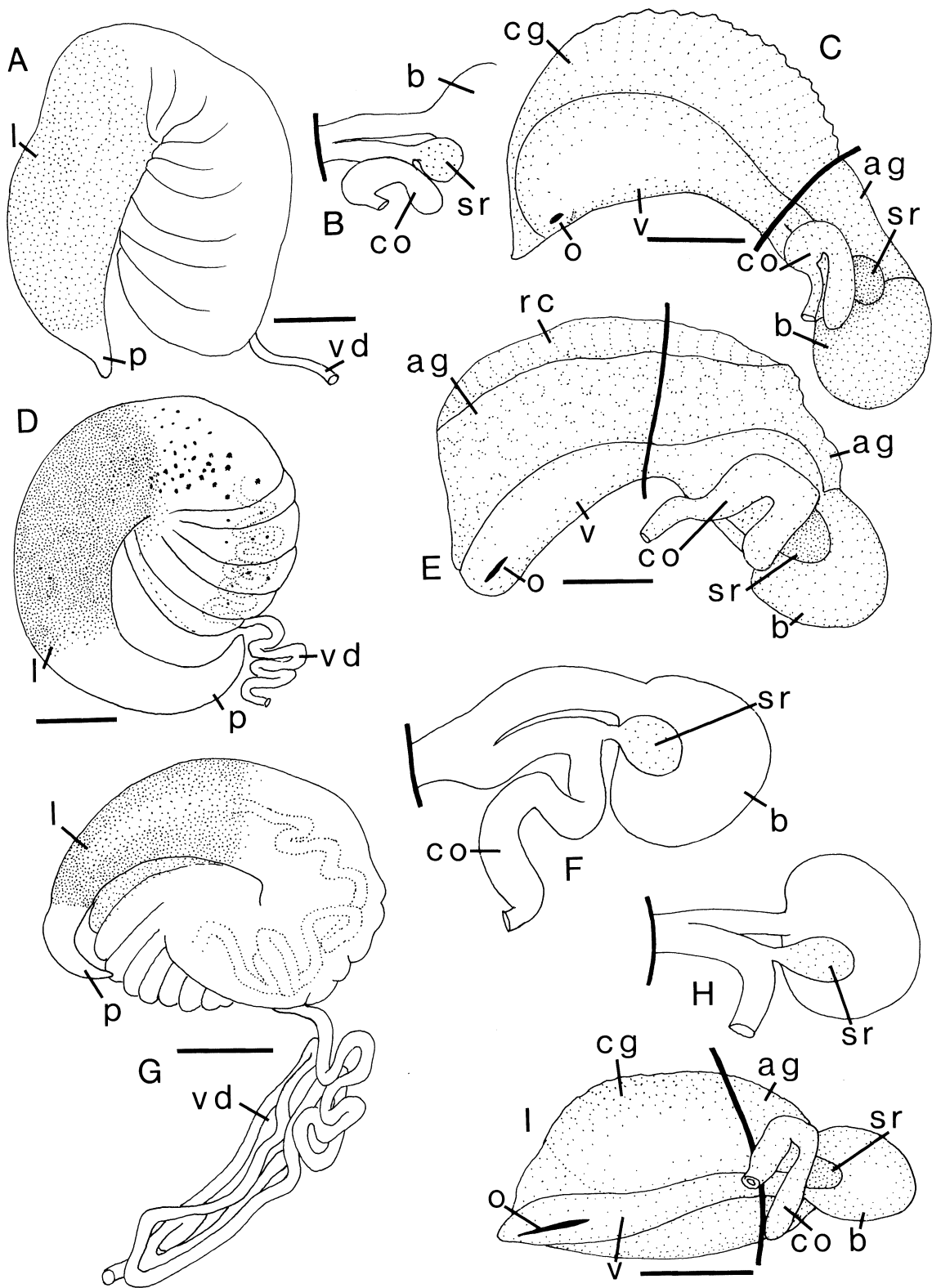


Fig.22. Genitalia of species of *Jardinella*. A–C, *J. jesswiseae*, Stn 73(A), A, penis, B,C, oviduct; D–F, *J. zeidlerorum*, Stn Z12, D, penis, E,F, oviduct; G–I, *J. acuminata*, Stn 73(B), G, penis, H,I, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- A,D,G – 0.1 mm, C,E,I – 0.2 mm.

closed [0-0.07 mm in width; mean 0.03 (M), 0.04 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 2.86 mm, width 1.42 mm, length of aperture 0.98 mm, number of teleoconch whorls 3.75.

Operculum (Fig. 15D,E): thin, very pale yellow, 0.71-0.95 mm in length [mean 0.80 (M), 0.88 (F)]. Without white smear. Ratio of opercular length to position of nucleus 3.21-4.25 [mean 3.80 (M), 3.70 (F)].

Dimensions: see Table 3.

Radula (Fig. 15F): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.7-1.9; 1 pair of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 3.1.4; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.5; with well-developed basal bulge; outer shaft 2-2.1 times longer than cutting edge. Inner and outer marginal teeth with cusps about equal in size.

Head-foot: cephalic tentacles (Fig. 19E,F) triangular in section, with dorsal ciliated band present on right tentacle only; distinct ciliated band along most of ventral surface. Head and foot black with black cephalic tentacles except for narrow unpigmented mid-dorsal line. Visceral coil pigmentation mostly black or dark grey.

Anatomy. *Mantle cavity*: ctenidium with 24-32 filaments; apex on right, or towards centre. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus distant from mantle edge. Kidney extends forward slightly into pallial roof.

Male reproductive system (Figs 21C, 22A): distinct penial lobe(s) absent but distal, pigmented part of penis swollen; distal extremity of penis with short papilla; distal half of penis (except papilla) grey, distal part of base grey or unpigmented, rest of base unpigmented. Vas deferens with few loops/coils next to anterior extremity of prostate gland.

Female reproductive system (Fig. 22B,C): pallial oviduct with ventral channel modified as wide muscular vestibule, opening subterminal and ventral and thickened to form very short papilla-like structure. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is slightly smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis present in some females.

Remarks. *Jardinella jesswiseae* is the most abundant of the Edgbaston snails in the middle part of the outflows (Table 4). In shell characters it is most similar to *J. zeidlerorum* n.sp., as also shown by discriminant analysis (Tables 5,6; Figs 35-37). It is distinguished from that species by its smaller size, uniformly black body (visible through the shell), rather tall spire, more convex whorls and deviated protoconch. The genitalia are similar except that the vestibule is more expanded in *J. jesswiseae*.

The two following species are similar to *J. jesswiseae* but have even more elongate shells.

Etymology. The species is named for Mrs Jess Wise, a long serving volunteer in the malacology section of the Australian Museum.

Jardinella zeidlerorum n.sp.

Locality. Stn Z12, unnamed spring about 11 km south-south-east of "Edgbaston" homestead, about 0.8 km south of main road, about 28 km north-east of Aramac, 22°47'20"S 145°25'40"E. Muttaborra 339 479. WZ, 4 May 1988. Mud mound supporting large natural pool.

Material examined. HOLOTYPE AND PARATYPES – (all Stn Z12) AMS C.156790 (holotype), C.156791 (18 paratypes), SAM D.18541 (200+ paratypes), QM MO.20081 (2 paratypes).

Diagnosis. Shell elongate conic, of medium size (up to 2.9 mm in length), smooth, non-umbilicate. Penis lacking lobe(s), pigmented medially, distal end tapering. Pallial oviduct with unmodified ventral channel, pallial opening terminal and ventral.

Description. *Shell* (Figs 16F, 23D-F): elongate conic, of medium size, 2.41-2.93 mm in length [mean 2.57 (M), 2.62 (F)]; 1.16-1.46 mm in width [mean 1.19 (M), 1.25 (F)]; not sexually dimorphic in size (P greater than 0.1); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 42.72-47.65° [mean 44.39 (M), 45.28 (F)]. Protoconch (Fig. 23E,F) strongly deviated; of 1.25-1.3 whorls [mean 1.25 (M), 1.26 (F)]. Teleoconch of 3.75-4.4 convex whorls [mean 4.15 (M), 4.05 (F)]. Convexity ratio 0.1-0.17 [mean 0.12 (M), 0.14 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.35-0.4 [mean 0.36 (M), 0.38 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 1.05-7.67° [mean 4.18 (M), 3.95 (F)]. Umbilicus closed.

Dimensions: see Table 3.

Dimensions of holotype: length 2.92 mm, width 1.30 mm, length of aperture 0.96 mm, number of teleoconch whorls 4.25.

Operculum (Fig. 24B): thin, very pale yellow, 0.71-0.9 mm in length [mean 0.76 (M), 0.79 (F)]. With white smear 0.22-0.43 mm in length [mean 0.26 (M), 0.30 (F)]. Ratio of opercular length to position of nucleus 3.46-4.61 [mean 4.13 (M), 4.04 (F)].

Dimensions: see Table 3.

Radula (Fig. 24D,E): each central tooth with 4-5 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.2-1.4; 2 pairs of basal denticles; dorsal edge inverted U-shaped; basal process long, tongue shaped. Each lateral tooth with cusp formula (3-4).1.5; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.4; with well-developed basal bulge; outer shaft 1.7-1.9 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig. 19C,D) triangular in section, with dorsal ciliated band present on right tentacle only; scattered ventral cilia only (this latter observation not entirely certain as the preparations are not very good). Head and foot black, distal end of tentacles unpigmented but with black pigment dorsally in proximal part and narrow stripe in distal part; eye

surrounded by heavy narrow unpigmented ring. Visceral coil pigmentation mostly black or dark grey.

Anatomy. *Mantle cavity*: ctenidium with 24-27 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. Thinly developed

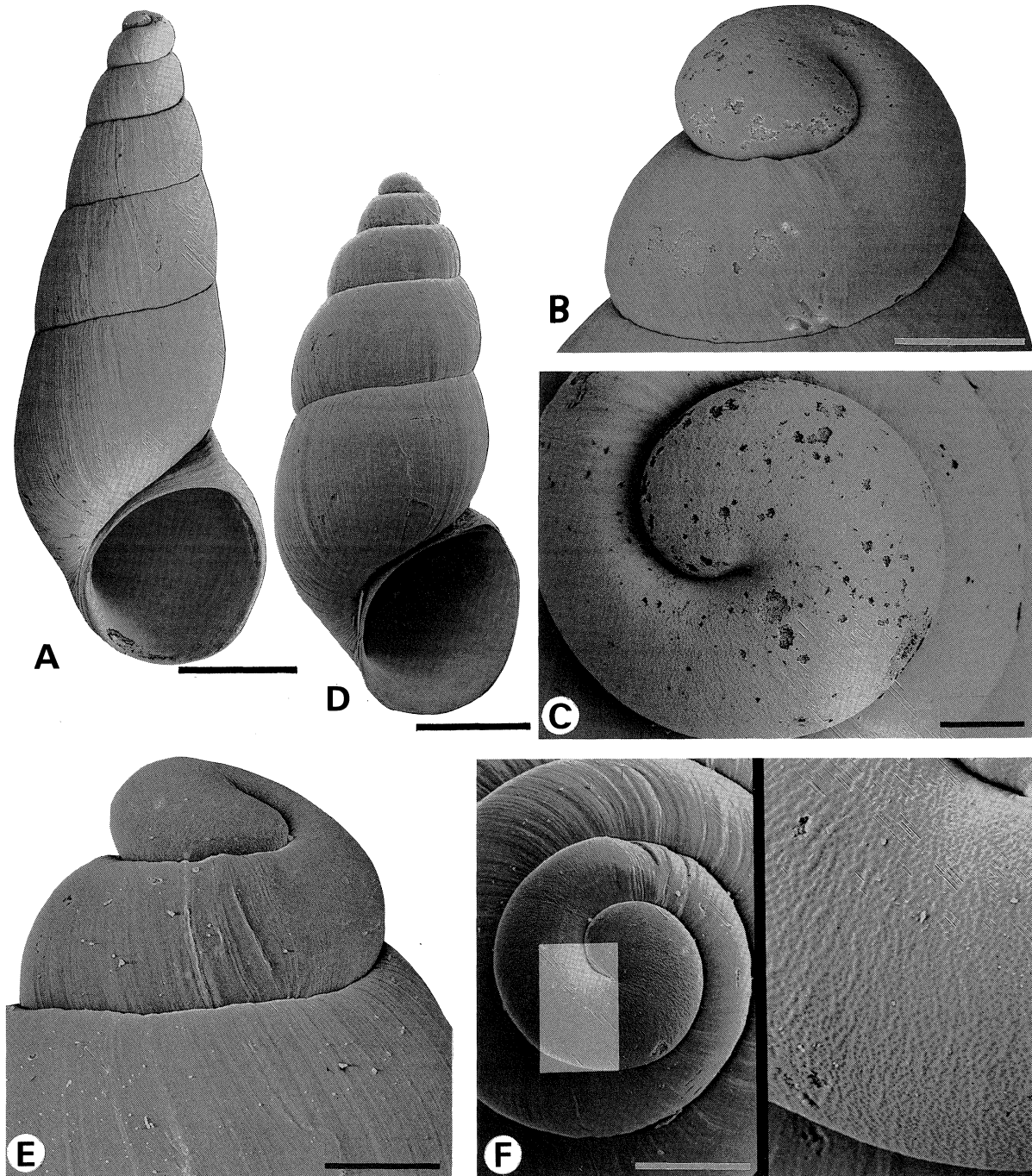


Fig.23. Shells of *Jardinella acuminata* n.sp. and *J. zeidlerorum* n.sp. A–C, *J. acuminata*, Stn 73(A); A, shell; B,C, lateral (B) and dorsal (C) views of protoconch; D–F, *J. zeidlerorum*, Stn Z12; D, shell; E,F, lateral (E) and dorsal (F) views of protoconch. The highlighted area in F is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,D – 0.5 mm, B,E,F – 0.1 mm, C – 0.05 mm.

glandular layer to left of ctenidium and near anus. Rectum without arch, anus distant from mantle edge. Kidney not extending forward into pallial roof.

Male reproductive system (Figs 21F, 22D): penial lobe(s) absent, distal portion tapering; middle section of penis and most of distal section dark grey to black; base with scattered black spots and grey proximal basal fold; distal end unpigmented. Vas deferens straight or undulating with one to few loops/coils anterior to prostate gland.

Female reproductive system (Fig. 22E,F): pallial oviduct with unmodified, rather wide ventral channel, with pallial opening ventroterminal. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall from seminal receptacle duct. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

Remarks. This species is similar to the last but has about

an extra half whorl (about 4 compared with about 3.5), less convex whorls and a relatively narrower spire (length/width ratio about 1.8 compared with about 2.1). Shell length, aperture length, body whorl length, number of teleoconch whorls, convexity, spire angle, aperture angle, protoconch diameter, and the position of the opercular nucleus all differ significantly (P equal to or less than 0.001).

The female genital system differs from that of *J. jesswiseae* n.sp. in having a thin-walled, unmodified ventral channel and the albumen gland is relatively larger, being only slightly shorter than the capsule gland (less than half the length of the capsule gland in *J. jesswiseae*). The uniformly tapering distal end of the penis differs from that of *J. jesswiseae* which has a short papilla, and the pigmented part of the penis is located much nearer to the distal end in *J. jesswiseae* than in *J. zeidlerorum*.

This species lives in a spring separated from the perimeter of the main Edgbaston group by about 3.5 km.

Etymology. The species is named for Wolfgang

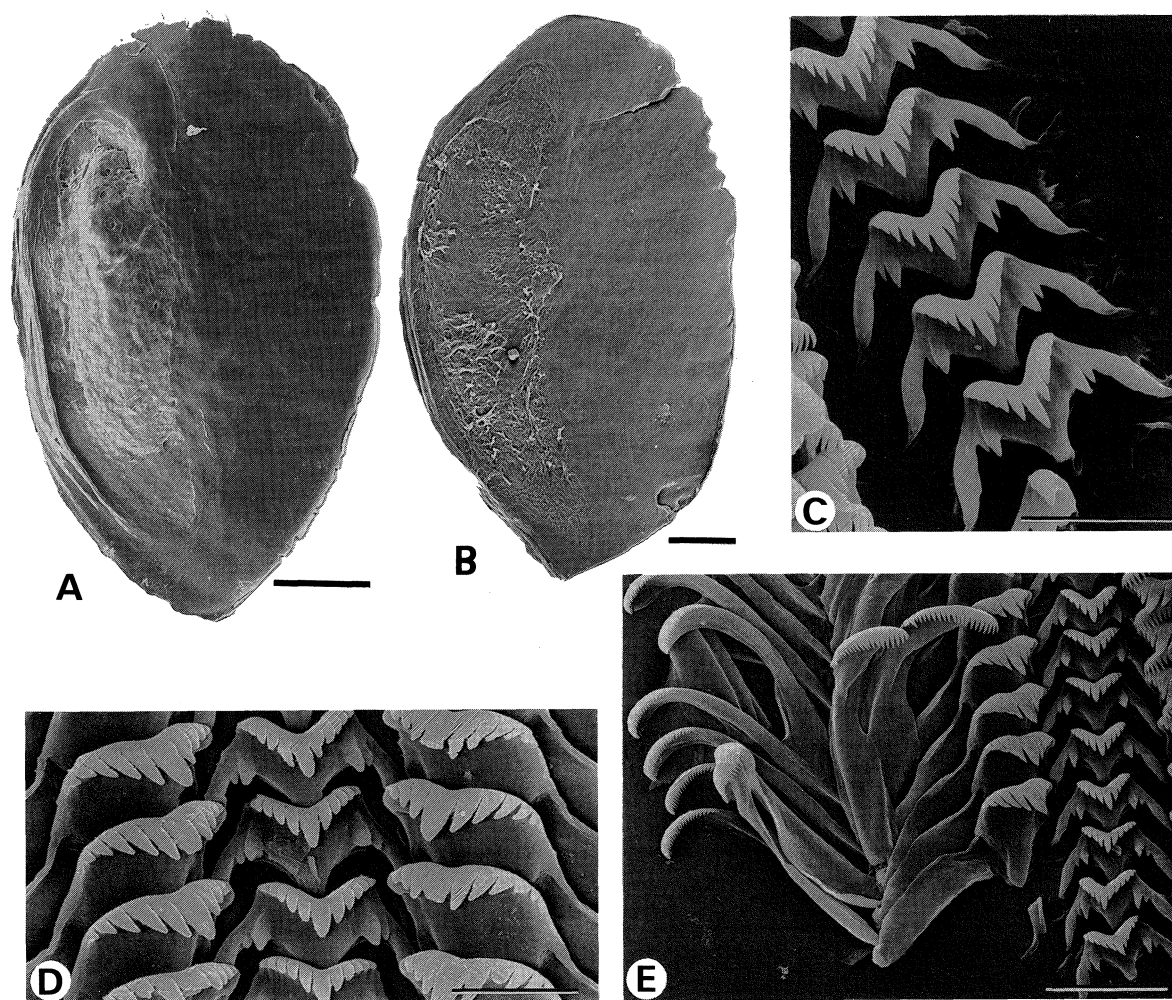


Fig. 24. *Jardinella acuminata* n.sp. and *Jardinella zeidlerorum* n.sp., opercula and radulae. A,C, *J. acuminata*, Stn 73(A), A, inner side of operculum; C, central teeth of radula; B,D,E, *J. zeidlerorum*, Stn Z12; B, inner side of operculum; D,E, radula, D, detail of central and lateral teeth. Scales:- A,B - 0.2 mm, C,D - 0.01 mm, E - 0.02 mm.

and Lyn Zeidler.

Jardinella acuminata n.sp.

Localities. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 433. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 73(B) C.156745 (holotype), C.156746 (100 paratypes), Stn 73(A) C.156747 (310 paratypes), SAM Stn Z9(A) D.18542 (4 paratypes), Stn Z9(B) D.18543 (100+ paratypes), QM Stn 73(A) MO.20082 (5 paratypes).

Diagnosis. Shell elongate conic, of medium size (up to

3.6 mm in length), smooth, non-umbilicate. Penis without lobe(s), distal part pigmented and tapering, terminal part unpigmented. Pallial oviduct with unmodified ventral channel, opening subterminal and ventral.

Description. *Shell* (Figs 16E, 23A–C): very elongate conic, of medium size, 2.29–3.58 mm in length [mean 2.91 (M), 3.00 (F)]; 0.96–1.29 mm in width [mean 1.12 (M), 1.15 (F)]; not sexually dimorphic in size (P greater than 0.4); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 31.51–43.38° [mean 36.75 (M), 36.40 (F)]. Protoconch (Fig. 23B,C), strongly deviated; of 1.3–1.5 whorls [mean 1.39 (M), 1.40 (F)]. Teleoconch of 4.25–5.75 convex whorls [mean 5.00 (M), 4.92 (F)]. Convexity ratio 0.06–0.14 [mean 0.09 (M), 0.09 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.26–0.32 [mean 0.29 (M), 0.28 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 2.47–9.84° [mean 6.31 (M), 5.16 (F)]. Umbilicus closed.

Dimensions: see Table 3.

Dimensions of holotype: length 3.36 mm, width 1.21 mm, length of aperture 0.89 mm, number of teleoconch whorls 5.50.

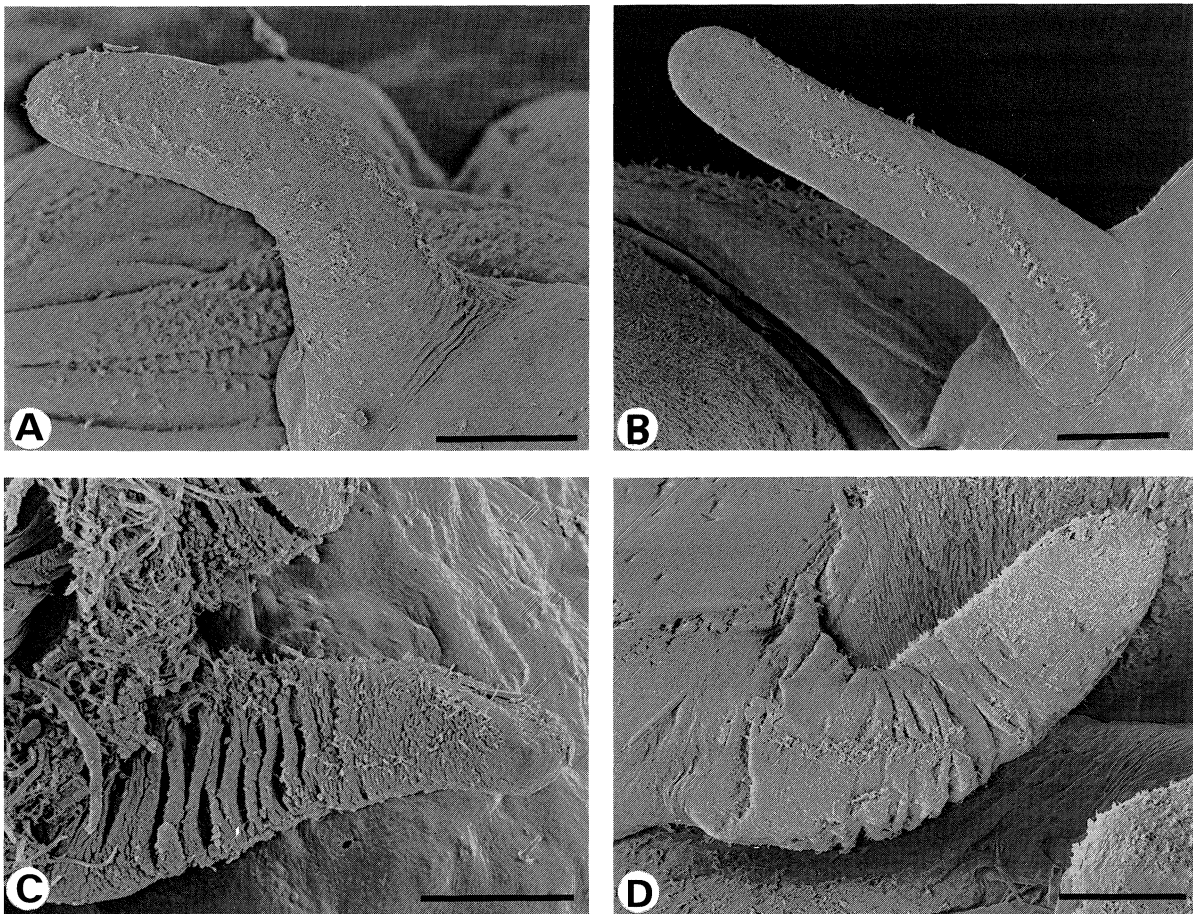


Fig.25. Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A,B, *J. eulo*, Stn 11; A, dorsal view of right tentacle; B, ventral view of right tentacle; C, *J. acuminata*, Stn 73(B); ventral view of left tentacle; D, *J. isolata*, Stn 21(C); ventral view of left tentacle. Scales:- A,B,D – 0.1 mm, C – 0.05 mm.

Operculum (Fig. 24A): thin, very pale yellow, 0.58-0.81 mm in length [mean 0.69 (M), 0.73 (F)]. With white smear 0.15-0.41 mm in length [mean 0.33 (M), 0.34 (F)]. Ratio of opercular length to position of nucleus 3.52-5.82 [mean 4.46 (M), 4.35 (F)].

Dimensions: see Table 3.

Radula (Fig. 24C): each central tooth with 5 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.4-1.5; 2 pairs of basal denticles; dorsal edge inverted U-shaped; basal process long, tongue shaped. Each lateral tooth with cusp formula 3-4.1.3-4; ratio of length of primary cusp/length of adjacent outer cusps 1.8-2; with small basal bulge; outer shaft 1.3-1.7 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig. 25C) triangular in section, with no dorsal ciliated band on left tentacle, 1 on right; 2 ventral longitudinal ciliated bands on right tentacle, 1 band medial, 1 (weak) posterior. Head mostly black, pigment extending to, and covering eyes; cephalic tentacles with median black stripe developed to greater or lesser extent. Visceral coil pigmentation mostly black or dark grey.

Anatomy. Mantle cavity: ctenidium with 26-27 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. Well-developed glandular pad to left of ctenidium, and near anus. Rectum without arch, anus distant from mantle edge. Kidney extends forward slightly into pallial roof.

Male reproductive system (Fig. 21D, 22G): penial lobe(s) absent, distal portion tapering; penis with grey area proximal to base of terminal part. Vas deferens with 1 to several loops/coils anterior to prostate gland.

Female reproductive system (Fig. 22H, I): pallial oviduct with unmodified ventral channel with ventral, slit-like pallial opening located subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is subequal in size to, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

Remarks. This species lives in the outflow of Big Spring (Stn 73) (see Table 4), one of the Edgbaston springs, and is distinguished from all others in the genus by its large, elongate shell and straight-sided spire. The only other species with similar shell features (confirmed by discriminate analysis) is *J. zeidlerorum* n.sp., the shell of which differs in its slightly convex spire outline and more convex whorls. Statistical comparison of the measurement data for these two species showed that they differ (P equal to or less than 0.001) in shell length and width, aperture length, convexity, spire angle, number of protoconch and teleoconch whorls, opercular length and position of the opercular nucleus.

A thick glandular pad to the left of the ctenidium (Fig. 4B, gp1) and another in front of the anus (Fig. 4B, gp2) are autapomorphies of *J. acuminata*. Homologous, but thinly developed, pads of epithelial glands are apparent in the

same areas in *J. zeidlerorum* and are have been scored as the same character in the phylogenetic analysis. None of the other species show any special development of epithelial glands in these areas.

The genital systems of *J. acuminata* and *J. zeidlerorum* are similar, the male genitalia differing in pigmentation details and in the vas deferens being more looped in *J. acuminata*.

Etymology. The specific name is based on the Latin word *acumen* meaning sharp point.

Jardinella sp.

Locality. 73(D), "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Head of large spring with outflow about 170 m.

Material examined. AMS Stn 73(D) C.157167.

Remarks. A single empty shell (Fig. 26) was found and is not named although it almost certainly represents an additional species. It probably lives in a specialised microhabitat in the head of the spring.

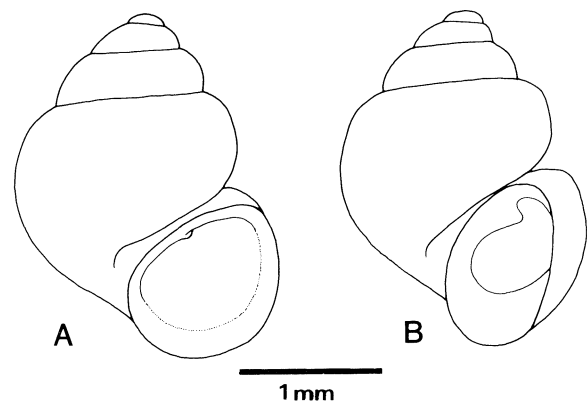


Fig.26. A,B, shell of *Jardinella* sp., Stn 73(D), B, rotated slightly to show the columellar fold.

This specimen (length 2.44 mm, width 1.86 mm, length of aperture 1.08 mm, number of teleoconch whorls 3.25) differs from all of the other species in the genus in possessing a prominent columellar fold (Fig. 26B).

Species from the Springsure Supergroup

Jardinella carnarvonensis n.sp.

Localities. Stn Z15, unnamed spring about 5 km north-west of Rangers HQ, just north of 13th river crossing, Carnarvon Gorge National Park, 25°02'30"S 148°11'20"E. Eddystone 619 229. WZ, 8 May 1988. Stn Z16, small seep from rock face east side of Kooramina

Creek, about 200 m up gorge, about 7.3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°02'20"S 148°11'E. Eddystone 619 229. WZ, 8 May

1988. Stn Z17, unnamed side spring, about 300 m up Hellhole Gorge (Koolaro Creek), about 3 km west of Rangers HQ, Carnarvon Gorge National Park,

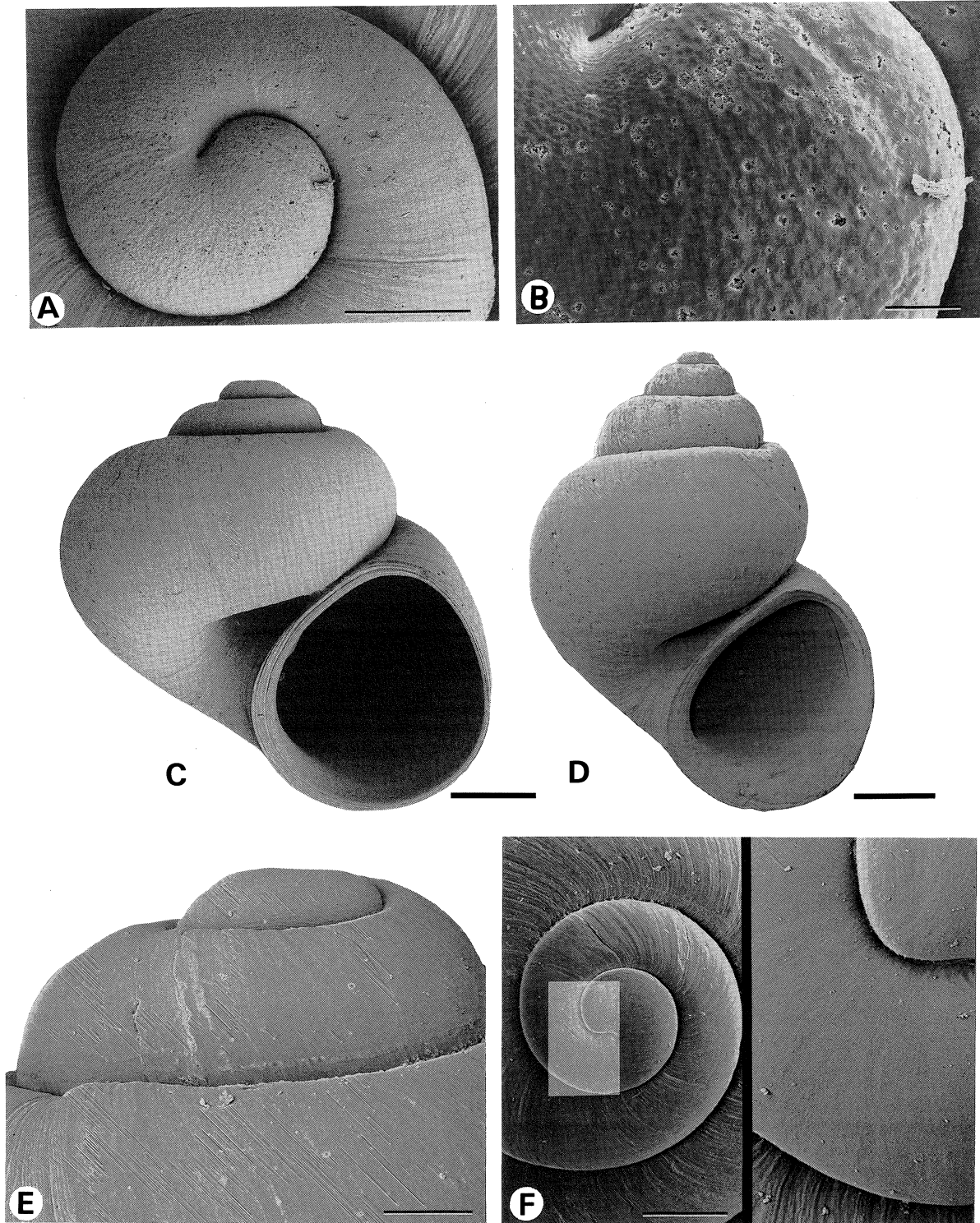


Fig.27. Shells of *Jardinella exigua* n.sp. and *J. carnarvonensis* n.sp. A–C, *J. exigua*, Stn 89; A,B, dorsal view of protoconch (A) and detail of microsculpture (B); C, shell; D–F, *J. carnarvonensis*, Stn Z15; D, shell; E,F, lateral (E) and dorsal (F) views of protoconch. The highlighted area in F is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,E – 0.1 mm, B – 0.02 mm, C – 0.3 mm, D – 0.5 mm, F – 0.2 mm.

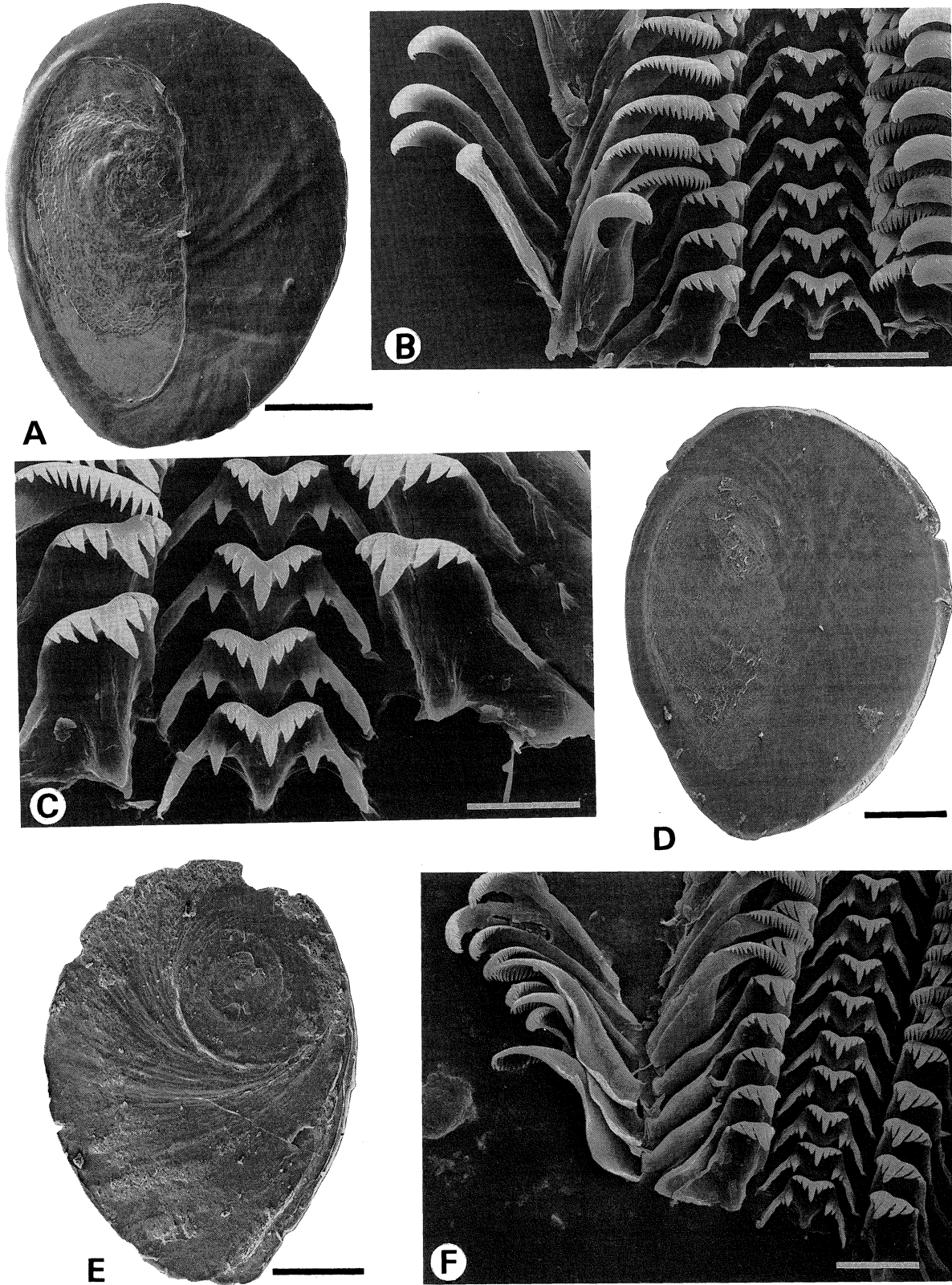


Fig.28. *Jardinella exigua* n.sp. and *J. carnarvonensis* n.sp., opercula and radulae. A-C, *J. exigua*, Stn 89, A, inner side of operculum; B,C, radula, C, detail of central and lateral teeth of radula; D-F, *J. carnarvonensis*, Stn Z15; D,E, inner (D) and outer (E) sides of operculum; F, radula. Scales:- A,D,E - 0.2 mm, B - 0.01 mm, C,F - 0.02 mm.

25°03'30"S 148°12'30"E. Eddystone 622 228. WZ, 8 May 1988.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn Z15 C.156786 (holotype), Stn Z15 C.156787 (14 paratypes), Stn Z16 C.156788 (5 paratypes), Stn Z17 C.156789 (5 paratypes), SAM Stn Z15 D.18544 (80+ paratypes), Stn Z16 D.18545 (50+ paratypes), Stn Z17 D.18546 (50+ paratypes), QM Stn Z15 MO.20083 (2 paratypes).

Diagnosis. Shell trochiform, small (up to 2.5 mm in length), smooth, umbilicate. Penis with expanded, pigmented distal end and small, terminal papilla. Pallial oviduct with wide vestibule, pallial opening terminal and ventral.

Description. *Shell* (Figs 6D, 27D–F): trochiform, small to medium size, 1.8–2.53 mm in length [mean 2.06 (M), 2.14 (F)]; 1.57–2.13 mm in width [mean 1.81 (M), 1.90 (F)]; not

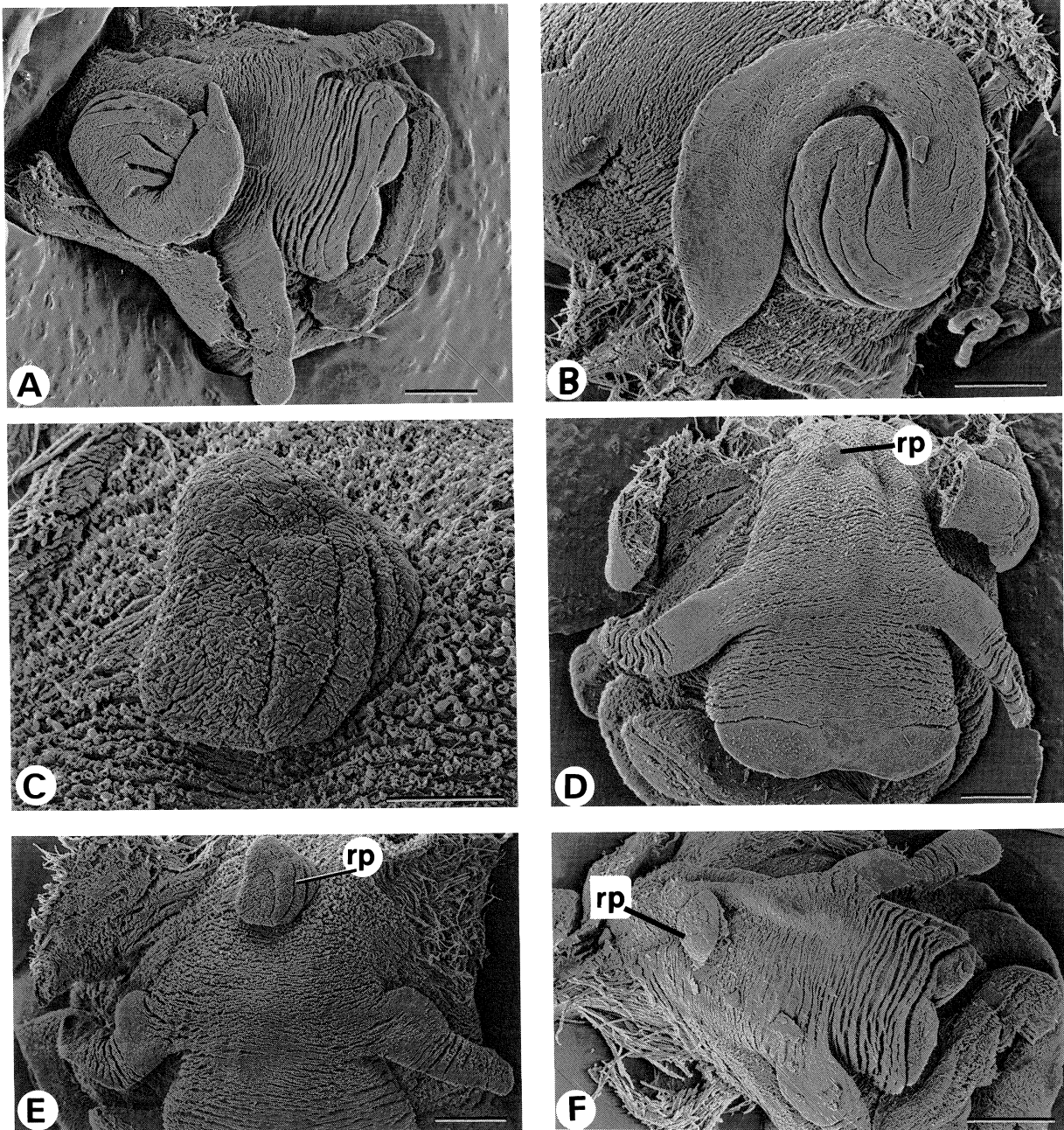


Fig.29. Scanning electron micrographs of critically point dried penes and rudimentary penes of species of *Jardinella*. A,F, *J. exigua*, Stn 93(A); A, penis; F, head of female with rudimentary penis; B–E, *J. carnarvonensis*, Stn Z15; B, penis; C–E, rudimentary penis in females; D,E, dorsal view of head and neck with rudimentary penis (rp) on neck, C, detail of the rudimentary penis of the specimen shown in E. rp – rudimentary penis. Scales:- A,B,D-F – 0.1 mm, C – 0.05 mm.

sexually dimorphic in size (P greater than 0.05); of medium thickness, translucent to opaque white, with indistinct, pale yellowish brown periostracum. Spire angle $80.62\text{--}112.68^\circ$ [mean 95.31 (M), 93.87 (F)]. Protoconch (Fig. 27E,F) of 1.2–1.3 whorls [mean 1.24 (M), 1.25 (F)]. Teleoconch of 2.3–2.9 convex whorls [mean 2.51 (M), 2.57 (F)]. Convexity ratio 0.16–0.33 [mean 0.25 (M), 0.25 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.49–0.61 [mean 0.55 (M), 0.54 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle $22.82\text{--}40.19^\circ$ [mean 30.52 (M), 31.43 (F)]. Umbilicus of medium width [0.13–0.36 mm in width; mean 0.25 (M), 0.25 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 2.25 mm, width 1.94 mm, length of aperture 1.25, number of teleoconch whorls 2.50.

Operculum (Fig. 28D,E): thin, yellow, 0.81–1.19 mm in length [mean 0.97 (M), 1.01 (F)]. Without white smear. Ratio of opercular length to position of nucleus 2.6–3.66 [mean 3.04 (M), 3.12 (F)].

Dimensions: see Table 3.

Radula (Fig. 28F): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6–1.8; 2–3 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula 3.1.3; ratio of length of primary cusp/length of adjacent outer cusps 1.4–1.5; basal bulge absent; outer shaft 1.8–2.1 times longer than cutting edge.

Head-foot: cephalic tentacles (Figs 9D, 29D,E) triangular in section, with no dorsal ciliated bands present; scattered ventral cilia only. Degree of pigmentation variable, snout with grey to black sides, mid-dorsal stripe and distal end

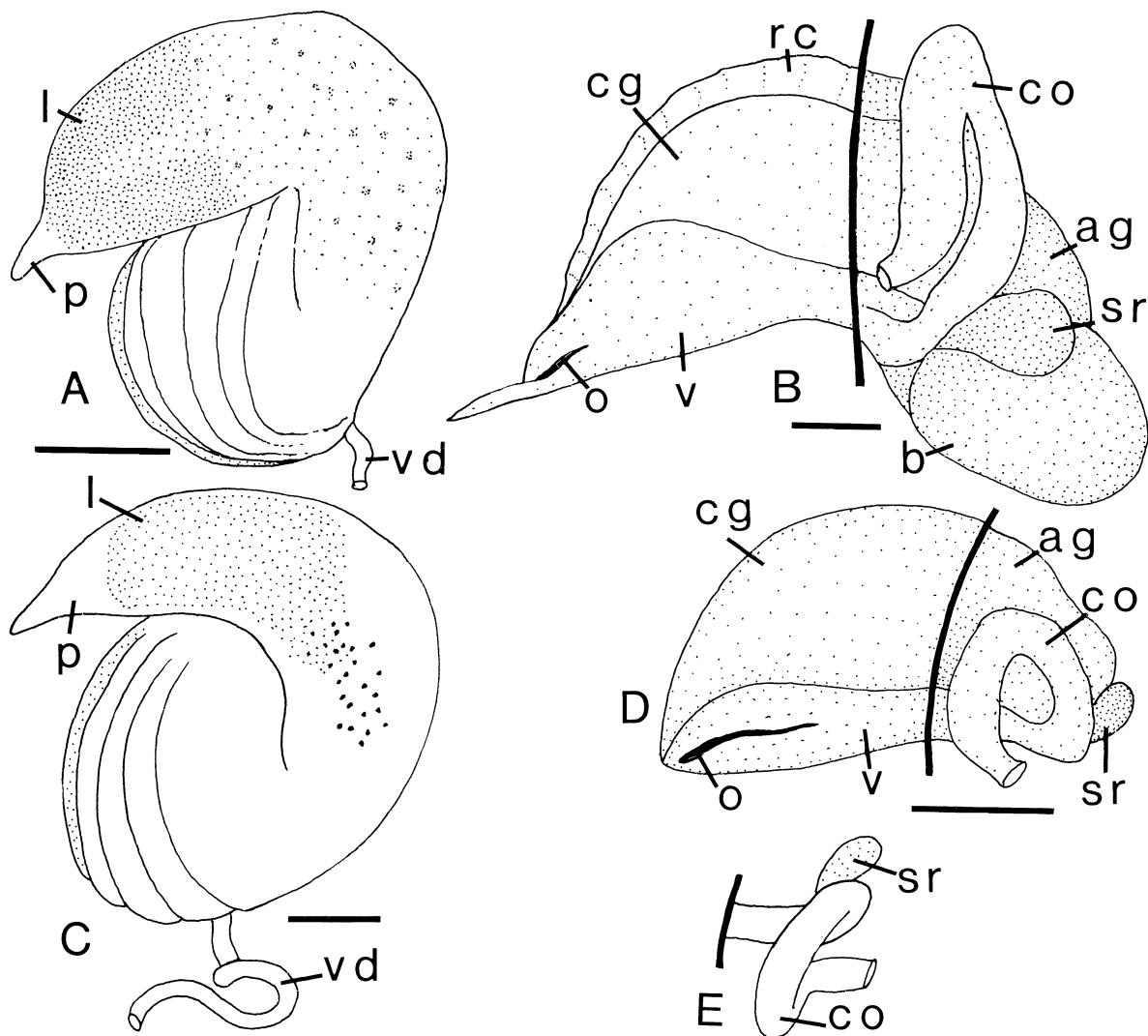


Fig. 30. Genitalia of species of *Jardinella*. A,B, *J. exigua*, Stn 89, A, penis, B, oviduct; C–E, *J. carnarvonensis*, Stn Z15, C, penis, D,E, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:– A,D – 0.2 mm, B,C – 0.1 mm.

unpigmented; black patch behind each eye; cephalic tentacles grey to black dorsally; foot pale to dark grey. Visceral coil pigmentation mostly black or dark grey.

Anatomy: *Mantle cavity:* ctenidium with 15-19 filaments; apex on right, or towards centre. Osphradium near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with prominent arch, anus near mantle edge. Kidney not extending forward into pallial roof.

Male reproductive system (Figs 29B, 30C): penial lobe(s) absent but smooth distal part expanded (swollen); distal end of penis with very short papilla; distally penis (except for papilla) black or grey, with few grey spots in middle section and grey proximal basal lobe, rest unpigmented. Vas deferens with few loops/coils on anterior end of prostate gland and additional loops/coils anterior to prostate gland.

Female reproductive system (Fig. 30D,E): pallial oviduct with ventral channel modified as wide, muscular vestibule, ventral pallial opening short slit located terminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is slightly smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis present in most or all females (Fig. 29C-E).

Remarks. This species is similar in shell shape to *J. coreena* n.sp. but is smaller in size [all teleoconch characters, including shell length and width (but excluding convexity) are significantly different (P less than 0.001)]. Comparing the generalised distances between the species generated by discriminate analysis on shell characters this species is most similar to *J. coreena*, and also similar to *J. exigua* n.sp. (Table 5). The Euclidean distances, show this species having most similarity with *J. colmani* n.sp. (Table 6).

The springs in Carnarvon Gorge flow from sandstones that are part of the same series making up the aquifer of the Great Artesian Basin. The water flowing from them, however, is not derived from the Great Artesian Basin (M.A. Habermehl, personal communication). They flow into Carnarvon Creek, a tributary of the Brown River, a tributary of the Fitzroy River. This river has an eastern drainage, unlike all of the other drainages with which the springs are associated which are west of the Great Divide.

Etymology. The species is named for Carnarvon Gorge.

Jardinella exigua n.sp.

Localities. Stn 88, small unnamed spring on hillside about 2.5 km north-west of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Stn 89, small unnamed spring on hillside about 100

m south-east of Stn 88, about 2.5 km north-west of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Head of spring fenced off and a small pipe leading from it. Stn 93, small seep about 1.2 km north-east of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°48'E. Springsure 581 249. WFP and PHC, 1 Oct. 1984. With small pipe leading from it. A - head of spring; B - outflow.

Material examined. HOLOTYPE AND PARATYPES - AMS Stn 93(B) C.156781 (holotype), C.156782 (200+ paratypes), Stn 93(A) C.156785 (100+ paratypes), Stn 88 C.156783 (500+ paratypes), Stn 89 C.156784 (500+ paratypes), SAM Stn 88 D.18547 (20 paratypes), QM Stn 88 MO.20084 (5 paratypes).

Diagnosis. Shell trochiform, small (up to 1.7 mm in length), smooth, umbilicate. Penis with slightly tapering distal end and short, terminal papilla; middle part of distal half pigmented. Pallial oviduct with unmodified ventral channel, ventral pallial opening slit-like and subterminal.

Description. *Shell* (Figs 6E, 27A-C): trochiform, small, 1.21-1.68 mm in length [mean 1.45 (M), 1.38 (F)]; 1.29-1.67 mm in width [mean 1.52 (M), 1.46 (F)]; not sexually dimorphic in size (P greater than 0.08); thin, fragile, translucent white, with indistinct, very pale orange brown to colourless periostracum. Spire angle 82.96-118.28° [mean 103.68 (M), 105.04 (F)]. Protoconch (Fig. 27A,B) of 1.2-1.4 whorls [mean 1.26 (M), 1.27 (F)]. Teleoconch of 1.6-2.2 convex whorls [mean 1.87 (M), 1.93 (F)]. Convexity ratio 0.18-0.37 [mean 0.26 (M), 0.26 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.53-0.69 [mean 0.62 (M), 0.61 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 21.35-36.35° [mean 27.47 (M), 29.58 (F)]. Umbilicus of medium width [0.16-0.31 mm in width; mean 0.27 (M), 0.25 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 1.52 mm, width 1.65 mm, length of aperture 0.98 mm, number of teleoconch whorls 2.00.

Operculum (Fig. 28A): thin, very pale yellow, 0.7-0.92 mm in length [mean 0.83 (M), 0.80 (F)]. Without white smear. Ratio of opercular length to position of nucleus 2.26-3.52 [mean 2.97 (M), 2.85 (F)].

Dimensions: see Table 3.

Radula (Fig. 28B,C): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.5-1.7; 2 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula 3.1.3; ratio of length of primary cusp/length of adjacent outer cusps 1.7-2; with small basal bulge; outer shaft 1.7-1.8 times longer than cutting edge.

Head-foot: cephalic tentacles (Figs 9B, 29A,F) triangular in section, with no dorsal ciliated bands present; distinct ciliated band along most of ventral surface. Unpigmented except for variable sized dark grey to black patch behind eyes continuous with small patches on sides of snout; sides of foot and opercular lobes sometimes grey. Visceral coil

pigmentation variable, mostly with black or dark grey dorsally.

Anatomy. *Mantle cavity:* ctenidium with 11-17 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with prominent arch, anus near mantle edge. Kidney extending well forward into pallial roof.

Male reproductive system (Figs 29A, 30A): penial lobe(s) absent; distal end of penis with short papilla; distal third of penis pale grey, last basal fold pale grey, rest unpigmented. Pallial vas deferens with many loops/coils which lie over anterior end of prostate gland.

Female reproductive system (Fig. 30B): pallial oviduct with unmodified ventral channel; opening slit-like, commences subterminally and extends to a little over half length of pallial ventral channel. Seminal receptacle lies at posterior edge of albumen gland. Bursa copulatrix and its duct absent. Coiled oviduct simple U-shape. Rudimentary penis present in almost all females (Fig. 29F).

Remarks. The long, slit-like oviducal opening and absence of a bursa copulatrix are important characters which separate this species from the last, with which it is generally most similar. These characters could be considered to be of generic significance except that this species probably shares a common ancestor with *J. carnarvonensis* n.sp., that species having most characters in common, including a slit-like (but shorter) oviducal opening. Both species also have a rudimentary penis in females (Fig. 29C–F).

These two species can be distinguished using shell characters by the larger size of *J. carnarvonensis*, shell length and shell width both being significantly different (P less than 0.001), as are aperture length and width, length of body whorl, spire angle, protoconch diameter, teleoconch whorls, opercular length and the position of the opercular nucleus. Generalised distances between the species generated by discriminate analysis show this species to be most similar to *J. carnarvonensis* (Table 5), but the Euclidean distances between the groups show, as with *J. carnarvonensis*, that *J. colmani* n.sp. is the most similar species (Table 6).

The shell of this species is somewhat similar to that of species of *Trochidrobia* but they lack a seminal receptacle, have a simple penis, a more subcentral opercular nucleus, a radula with more numerous cusps on the central and lateral teeth and 1-2 basal denticles on the central teeth.

The small springs in which this species lives flow from Tertiary basalts and are thus not derived from the Great Artesian Basin.

Etymology. The specific name is from the Latin word *exiguus(a)* meaning small.

Species from the Springvale Supergroup

Jardinella isolata n.sp.

Localities. Stn 21, Elizabeth Springs about 26 km north-north-west of Springvale, 23°20'30"S 140°34'40"E. Springvale 457 418. WFP and PHC, 10 Sept. 1984. A – top of spring; B – outflow; C – large seep; D – small seeping pool on side of creek. Stn Z1, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Low mound nearest creek. Stn Z2, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Mound adjacent to spring with old fence about 300 m north of Stn Z1.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 21(C) C.156772 (holotype), C.156773 (500+ paratypes), Stn 21(A) C.156775 (7 paratypes), Stn 21(B) C.156774 (70 paratypes), SAM Stn Z1 D.18548 (50+ paratypes), Stn Z2 D.18549 (50+ paratypes), QM Stn 21(C) MO.20085 (5 paratypes).

Diagnosis. Shell conical, medium to large (up to 3.9 mm in length), smooth, umbilicate, last part of body whorl sometimes detached from parietal wall. Penis with pigmented distal lobes and small, terminal papilla. Pallial oviduct with unmodified ventral channel and ventral, terminal pallial opening.

Description. *Shell* (Figs 16A, 31C–F): conical, medium to large, 2.67–3.88 mm in length [mean 3.05 (M), 3.23 (F)]; 1.86–2.45 mm in width [mean 2.05 (M), 2.17 (F)]; not sexually dimorphic in size (P greater than 0.1); of medium thickness, translucent white to yellowish white, with indistinct, transparent periostracum. Spire angle 63.01–79.32° [mean 71.11 (M), 70.01 (F)]. Protoconch (Fig. 31D,E) of 1.25–1.35 whorls [mean 1.27 (M), 1.28 (F)]. Teleoconch of 2.5–3.3 convex whorls [mean 2.91 (M), 2.81 (F)]. Convexity ratio 0.15–0.24 [mean 0.19 (M), 0.19 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.43–0.54 [mean 0.49 (M), 0.47 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 4.34–20.86° [mean 11.13 (M), 13.36 (F)]. Umbilicus medium [0.32–0.71 mm in width; mean 0.41 (M), 0.46 (F)].

Dimensions: see Table 3.

Dimensions of holotype: length 3.29 mm, width 2.20 mm, length of aperture 1.63 mm, number of teleoconch whorls 2.70.

Operculum (Fig. 32D): thin, very pale yellow, 1.28–1.64 mm in length [mean 1.41 (M), 1.46 (F)]. With white smear 0.34–0.74 mm in length [mean 0.52 (M), 0.53 (F)]. Ratio of opercular length to position of nucleus 2.96–3.68 [mean 3.27 (M), 3.26 (F)].

Dimensions: see Table 3.

Radula (Fig. 32C): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.8–2; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 2.1.4; ratio of length of primary cusp/length of

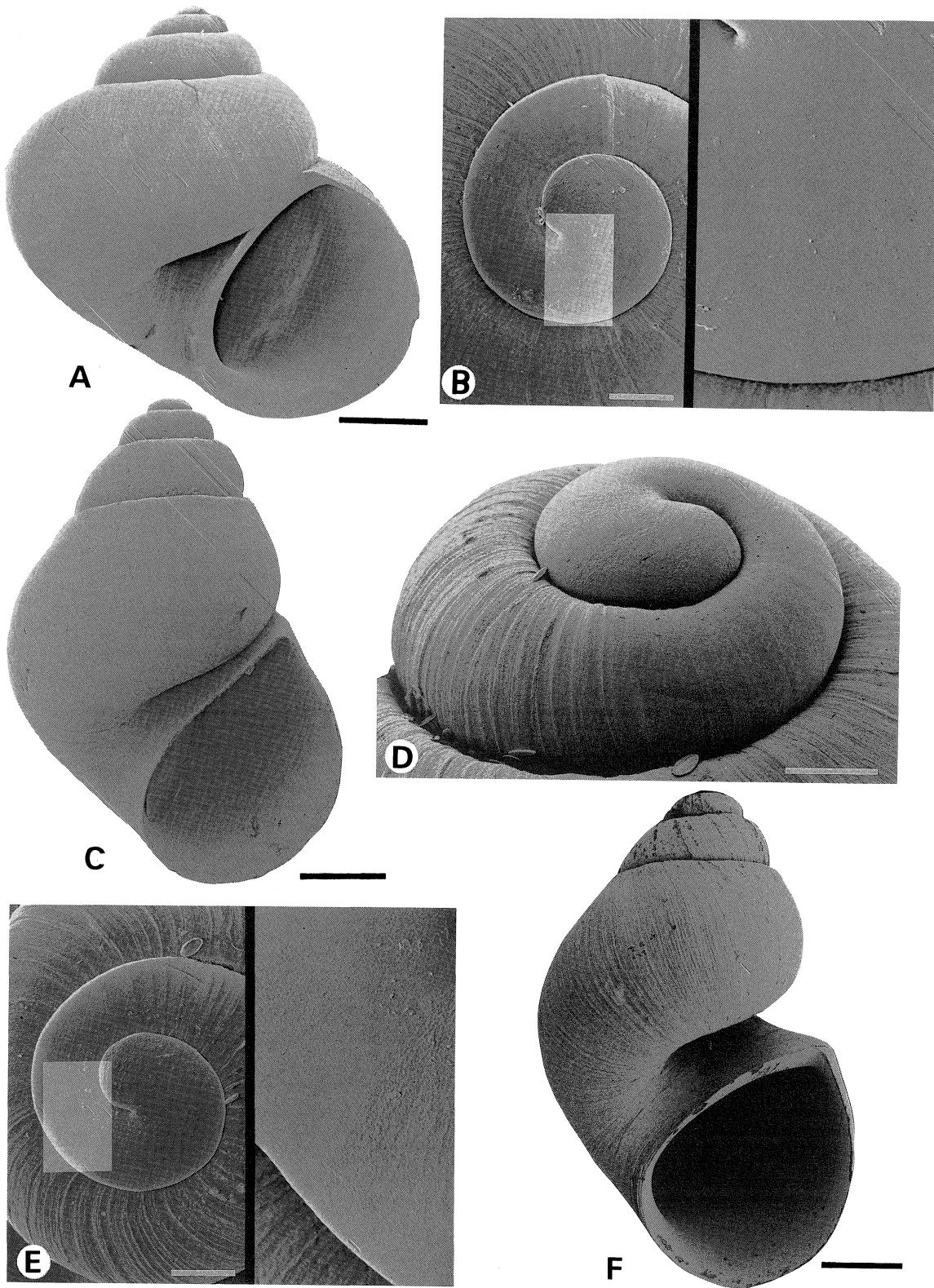


Fig.31. Shells of *Jardinella eulo* n.sp. and *J. isolata* n.sp. A,B, *J. eulo*, Stn 11; A, shell; B, dorsal view of protoconch; the highlighted area is magnified a further 4X in the adjacent figure to show the microsculpture. C–F, *J. isolata*, Stn 21(C); C,F, shell; D,E, lateral (D) and dorsal (E) views of protoconch. The highlighted area in E is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,C,F – 0.5 mm, B,D,E – 0.1 mm.

adjacent outer cusps 1.4-1.5; with small basal bulge; outer shaft 1.6-1.8 times longer than cutting edge.

Head-foot: cephalic tentacles (Fig. 25D) oval to circular in section, or triangular in section, with dorsal ciliated band present on both tentacles; 2 distinct ciliated bands along most of ventral surface. Head and dorsal snout grey to black; if grey has black patch at base of tentacles behind eyes; unpigmented patch in front of eyes; rest of dorsal surface of cephalic tentacles grey except unpigmented distal end; foot grey to unpigmented. Visceral coil pigmentation mostly black or dark grey.

Anatomy. Mantle cavity: ctenidium with 24-26 filaments; apex on right. Osphradium between posterior end and

middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus with intermediate position relative to mantle edge. Kidney not extending forward into pallial roof.

Male reproductive system (Figs 33A,B, 34A): penial lobes represented by flattened, expanded portion distally; short papilla terminally; distal half of penis grey, expanded distal area dark grey. Pallial vas deferens straight or undulating.

Female reproductive system (Fig. 34B,C): pallial oviduct with unmodified ventral channel. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from anteroventral side of elongately-ovate

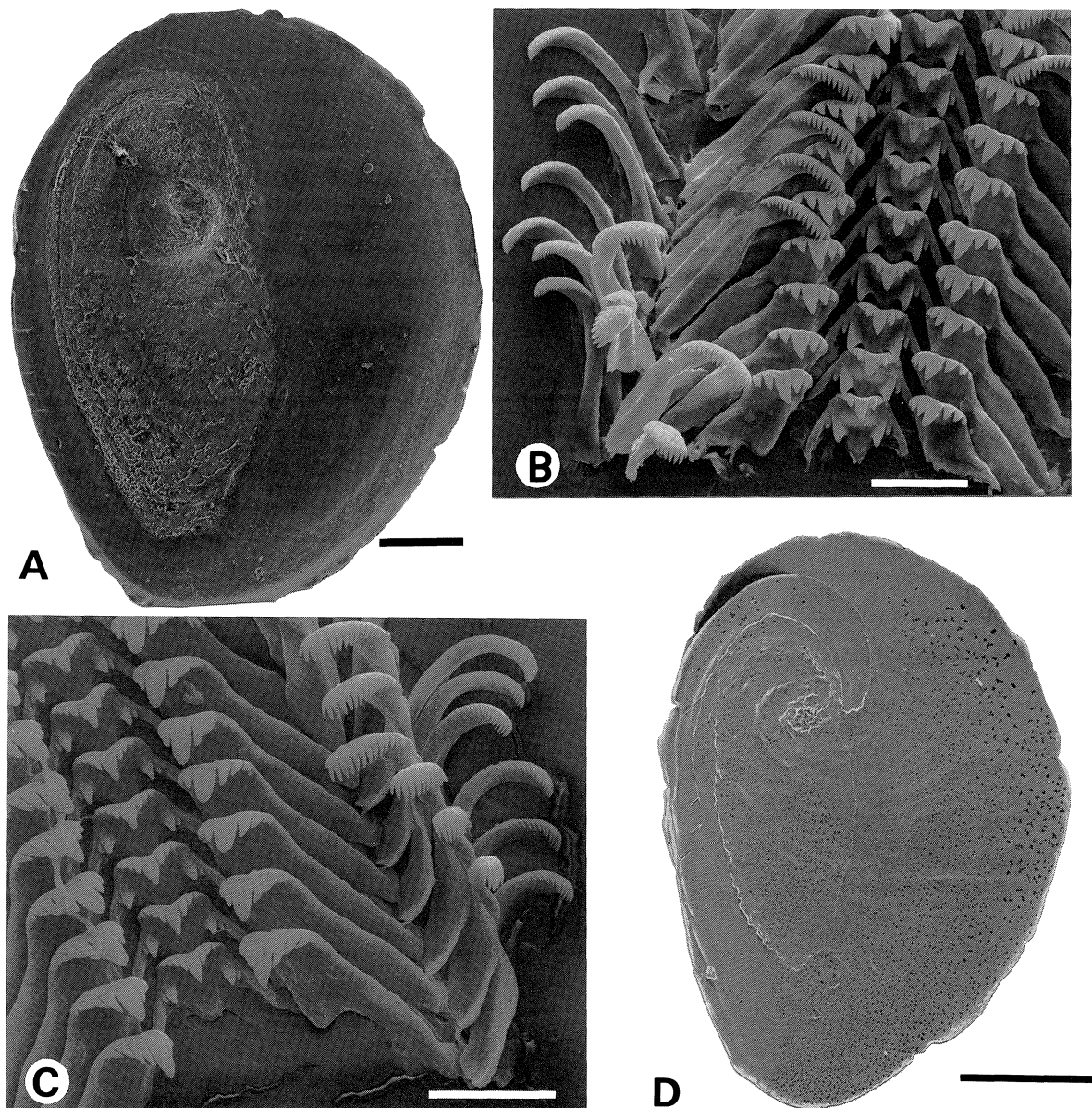


Fig.32. *Jardinella eulo* n.sp. and *J. isolata* n.sp., opercula and radulae. A, B, *J. eulo*, Stn 11, A, inner side of operculum; B, radula. C,D, *J. isolata*, Stn 21(C); C, radula; D, inner side of operculum. Scales:- A,D - 0.2 mm, B,C - 0.025 mm.

bursa copulatrix which lies posteroventral to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct just in front of seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend proximally. Rudimentary penis absent in females.

Remarks. This species, like *J. corrugata* n.sp., has a tendency for the aperture to become detached from the parietal wall. It is readily distinguished from all other species of *Jardinella* by its rather large, smooth, broadly conical shell. Discriminate analysis shows that this species is closest to *J. coreena* n.sp. in shell characters but it differs from that species in the more elongate shell and particularly in both male and female genital characters.

The female genital system is similar to that of several other species of *Jardinella* and has a simple ventral channel. The male reproductive system differs in detail in having a simple pallial vas deferens and the penis differs from all other species in detail in having a broad, flattened distal end with a very short papilla.

This species lives in the very isolated Elizabeth Springs in far western Queensland, south-east of Boulia and is the

only species living in this area.

Etymology. The specific name is taken from the New Latin word *isolatus* meaning detached, separated, based on *solus* (Latin) meaning alone.

Species from the Eulo Supergroup

Jardinella eulo n.sp.

Localities. Stn 8, unnamed spring at Tunga Bore near Mount Tunga, about 43 km west-south-west of Eulo, 28°13'S 144°38'E. Eulo 252 498. WFP and PHC, 6 Sept. 1984. Stn 11, "Rocky Springs" near Mount Francis about 52 km south-west of Eulo, 28°18'S 144°32'E. Eulo 244 489. WFP and PHC, 7 Sept. 1984.

Material examined. HOLOTYPE AND PARATYPES – AMS Stn 11 C.156778 (holotype), C.156779 (500+ paratypes), Stn 8 C.156780 (500+ paratypes), SAM Stn 11 D.18550 (20 paratypes), QM Stn 11 MO.20086 (5 paratypes).

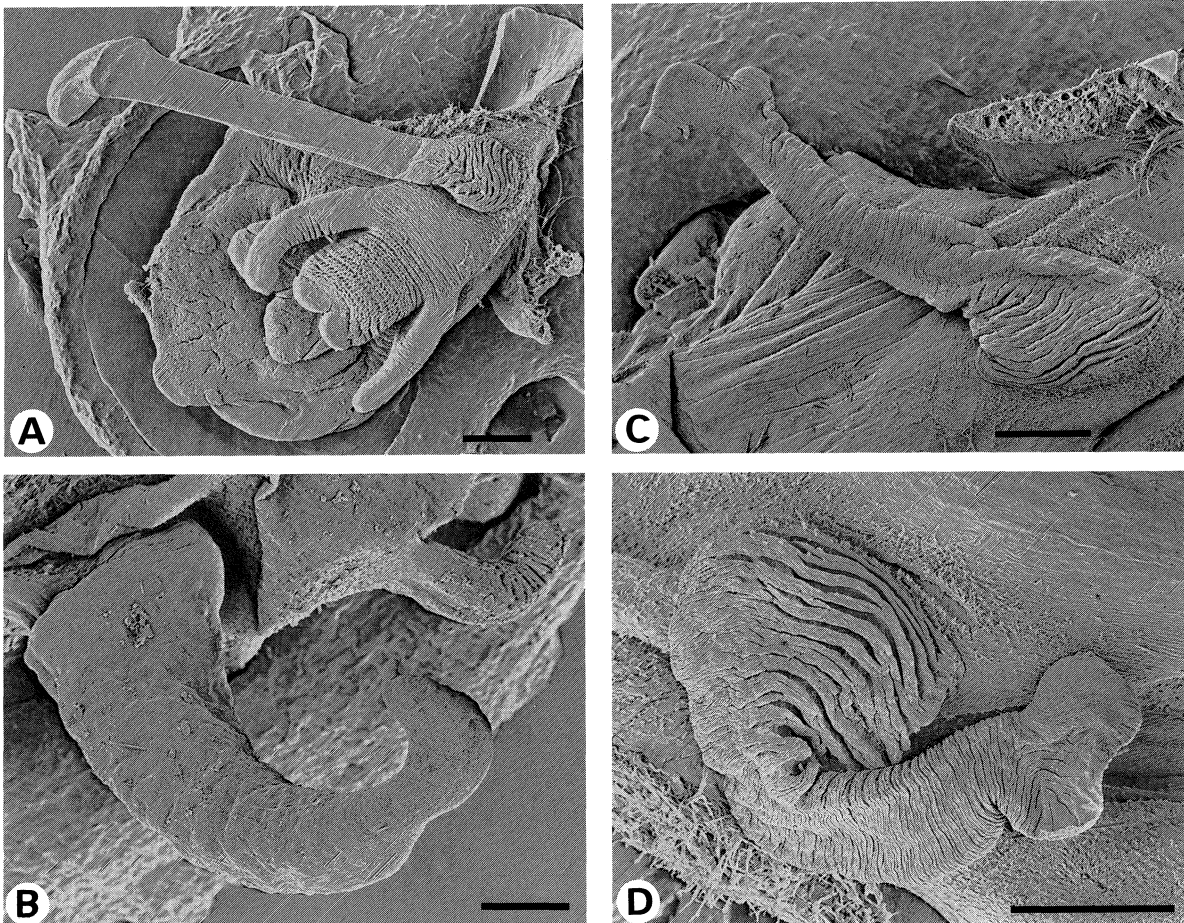


Fig.33. Scanning electron micrographs of critically point dried penes of species of *Jardinella*. A,B, *J. isolata*, Stn 21(C), A, penis extended, also showing dorsal view of head-foot; B, penis contracted; C, D, *J. eulo*, Stn 11; C, penis partially extended; D, penis contracted. Scales:- 0.2 mm.

Diagnosis. Shell trochiform, of medium size (up to 2.8 mm in length), smooth, umbilicate. Penis with terminal lobes and short, reflected papilla. Pallial oviduct with unmodified ventral channel, pallial opening terminal and ventral. Coiled oviduct extends nearly to posterior end of bursa copulatrix (unlike all other species).

Description. *Shell* (Figs 6C, 31A,B): trochiform, of medium size, 2.03-2.84 mm in length [mean 2.36 (M), 2.58 (F)]; 2.19-2.91 mm in width [mean 2.46 (M), 2.75 (F)]; sexually dimorphic in size (P less than 0.03); of medium thickness,

translucent orange brown, with indistinct, transparent periostracum. Spire angle $92.01-108.07^\circ$ [mean 100.29 (M), 99.79 (F)]. Protoconch (Fig. 31B) of 1.25-1.4 whorls [mean 1.29 (M), 1.28 (F)]. Teleoconch of 2.5-3 convex whorls [mean 2.64 (M), 2.73 (F)]. Convexity ratio 0.17-0.24 [mean 0.22 (M), 0.20 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.56-0.67 [mean 0.60 (M), 0.63 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle $19.57-32.1^\circ$ [mean 27.94 (M), 24.15 (F)]. Umbilicus medium [0.2-0.53 mm in width; mean 0.34 (M), 0.40 (F)].

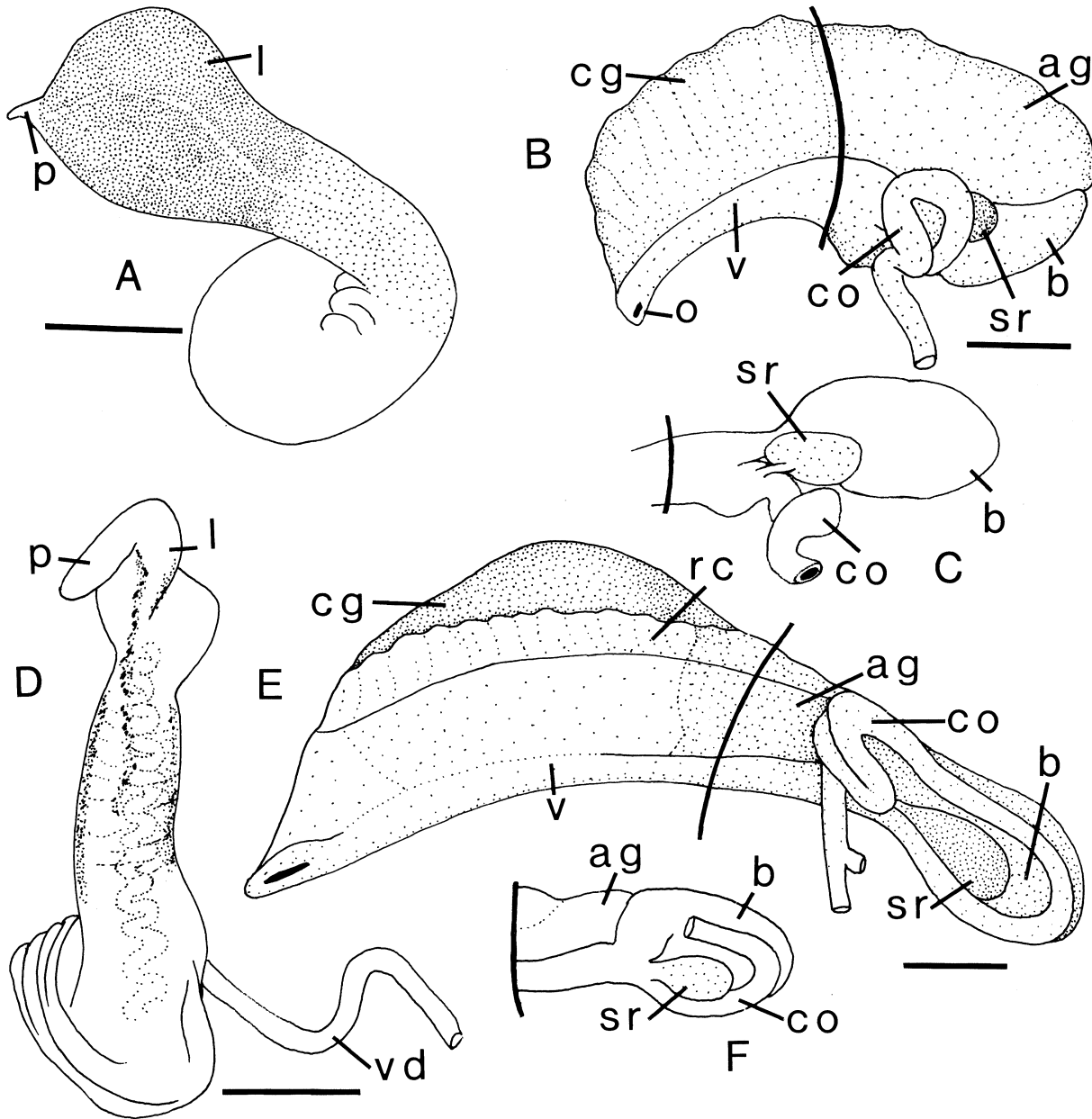


Fig.34. Genitalia of species of *Jardinella*. A-C, *J. isolata*, Stn 21(C), A, penis, B,C, oviduct; D-F, *J. eulo*, Stn 11, D, penis, E,F, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- 0.25 mm.

Dimensions: see Table 3.

Dimensions of holotype: length 2.55 mm, width 2.64 mm, length of aperture 1.55 mm, number of teleoconch whorls 2.75.

Operculum (Fig. 32A): thin, light brown, 1.13–1.61 mm in length [mean 1.29 (M), 1.46 (F)]. With or without white smear up to 0.45 mm in length [mean 0.27 (M), 0.26 (F)]. Ratio of opercular length to position of nucleus 2.73–3.26 [mean 3.02 (M), 3.11 (F)].

Dimensions: see Table 3.

Radula (Fig. 32B): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.7–1.9; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped, or basal process long, tongue shaped. Each lateral tooth with cusp formula (2-3).1.(2-3); ratio of length of primary cusp/length of adjacent outer cusps 1.7–1.8; with small basal bulge; outer shaft 2.4–2.6 times longer than cutting edge.

Head-foot: cephalic tentacles oval to circular in section, with no dorsal ciliated bands present; 2 distinct ciliated bands along most of ventral surface. Snout black on tops of concentric ridges, unpigmented between these ridges; distal end of snout unpigmented; dorsal sides of cephalic tentacles grey with unpigmented patch anterior to eyes; head and neck dark grey to black; sides of foot and opercular lobes pale grey. Visceral coil pigmentation mostly black or dark grey.

Anatomy. *Mantle cavity*: ctenidium with 24–25 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus with intermediate position relative to mantle edge. Kidney extends forward slightly into pallial roof.

Male reproductive system (Figs 33C,D, 34D): penial lobes distal; distal portion wrinkled, with short papilla at tip; middle part of penis with about 3 pale grey longitudinal stripes or unpigmented. Vas deferens straight or undulating.

Female reproductive system (Fig. 34E,F): pallial oviduct with unmodified ventral channel. Seminal receptacle lies opposite middle of bursa. Bursal duct arises from anterodorsal side of elongate bursa copulatrix which lies posterior to, and is larger than, albumen gland. Coiled oviduct and bursal duct fused to form common duct just in front of seminal receptacle duct. Coiled oviduct with proximal U-shaped loop and long posterior loop reaching almost to posterior edge of bursa copulatrix. Rudimentary penis absent in females.

Remarks. This species resembles *J. exigua* n.sp. in shape but is much larger and, unlike that species, possesses a bursa copulatrix. It differs from all other species of *Jardinella* in genital characters, having a penis bearing a club-shaped head and, like only *J. isolata* n.sp., has a non-coiled pallial vas deferens. The female system differs from all other species in the genus in having the coiled oviduct extending posteriorly almost to the posterior

end of the bursa copulatrix after making a large loop in its proximal part.

Discriminate analysis shows that this species is most similar to *J. coreena* n.sp. and *J. edgbastonensis* n.sp. (Tables 5,6, Figs 35–37) in shell characters. It does, however, have a relatively broader spire than both of these species.

This species is known to live in two small springs near Eulo in southern Queensland. One potentially suitable habitat (Stn 10) close to Stn 11 had been dug out to form a large pond and no snails were present.

Etymology. The species is named for the town of Eulo in south-western Queensland.

Phenetic Analysis

The discriminate analysis clearly indicates that all species are well distinguished on shell characters. Only two discriminate at less than 100% (18% of *J. edgbastonensis* are classified as *J. coreena* and 5% of *J. eulo* are classified as *J. carnarvonensis*). The generalised distances (given in Table 5) are discriminate space distances among centroids expressed in standard deviation units, the larger the number, the greater the difference between the groups. The Euclidean (or taxonomic) (see Table 6) distances assess the between centroid differences in reference to original variable coordinate axes. Plots of each population on the first three coordinates are given in Figs 35–37. Table 7 gives the percentage of the variance of each variable in each canonical variate to indicate the relative participation of each variable in each axis.

Phylogenetic Analysis

A phylogenetic analysis was carried out to attempt to ascertain whether *Jardinella* was a monophyletic group and to try to obtain a picture of the evolution of the species within the genus. The data used in the phylogenetic analysis is given in Table 8. With one exception, all shell characters were omitted from the analysis as were all but two radular characters. Most shell and radular characters were omitted because they are mostly continuous (rather than discrete) and subject to homoplasy. Anatomical characters listed in Table 1 and not used in the phylogenetic analysis (i.e. not listed in Table 2) were either more-or-less uniform throughout all the taxa in the analysis, continuous (rather than discrete) characters, or considered to be of low value in determining relationships because of their plasticity and/or considerable homoplasy.

All of the taxa included in the analysis are part of what appears to be a monophyletic Australasian group of hydrobiids that share several characters. These include a non-glandular penis, non-pigmented coiled oviduct, a white layer on the inner side of the operculum

and two or more pairs of basal cusps on each central tooth of the radula. The subfamily name Tateinae is available for this group, but because higher category relationships in the hydrobiids are in need of major revision, we refer to this group as the *Tatea* group for the purposes of this paper.

We included *Jardinella thaanumi*, the type species of *Jardinella*, in the analysis although it falls well outside the spring radiation.

The outgroup chosen for this analysis is the estuarine genus *Tatea* which is judged to be the most plesiomorphic of all the Australian *Tatea* group. It has a protoconch of about two whorls with a distinctly separated protoconch 1 and protoconch 2. This latter character is assumed to be plesiomorphic and suggests a planktotrophic larval stage. It is the only genus in the *Tatea* group (including non Australian genera) to have this character. The remainder of the taxa in the analysis

are assumed to be direct developers with a simple protoconch of about one and a half-whorls. Species of *Tatea*, *Fluvidona* and *Fonscochlea* typically have an operculum bearing pegs on its inner side, a character that is judged to be plesiomorphic for Australian Tateinae. A white smear, such as that seen in species of *Potamopyrgus* and *Fluviopupa*, may be more primitive but, in the case of these genera could equally well be secondarily reduced from an originally pegged condition.

The radula of species of *Tatea* and *Fluvidona* has three or more pairs of basal cusps on each central tooth, a character state plesiomorphic for the *Tatea* group. The outer shaft of each lateral tooth is more than 1.5 times as long as the length of the cutting edge in *Tatea* and most other genera of hydrobiids and this is taken to be the plesiomorphic state.

The pallial cavity is rather uniform throughout the

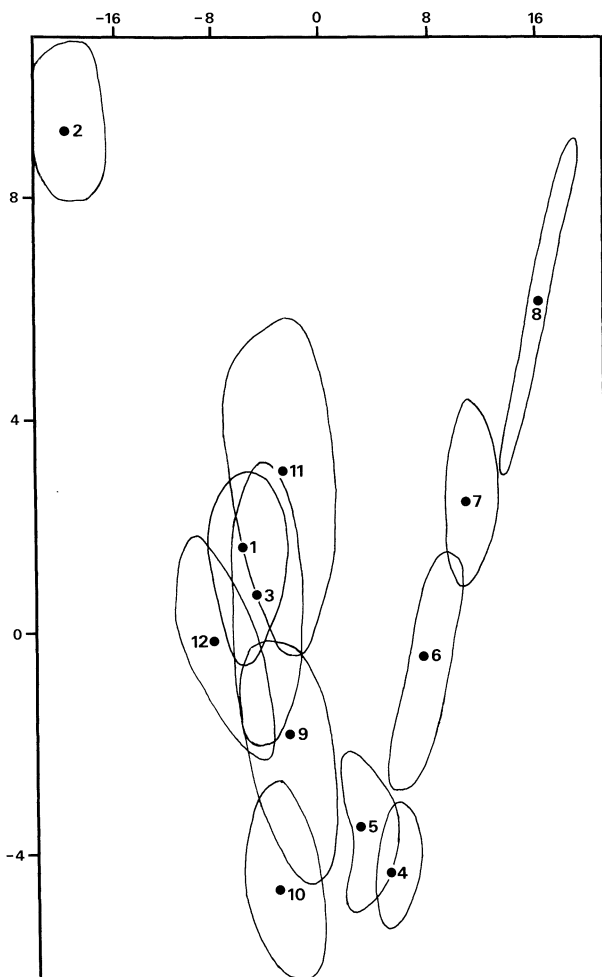


Fig.35. Plot of the results of the discriminate analysis using the first (vertical) and second coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 - *J. edgbastonensis*; 2 - *J. corrugata*; 3 - *J. coreena*; 4 - *J. pallida*; 5 - *J. colmani*; 6 - *J. jesswiseae*; 7 - *J. zeidlerorum*; 8 - *J. acuminata*; 9 - *J. carnarvonensis*; 10 - *J. exigua*; 11 - *J. isolata*; 12 - *J. eulo*.

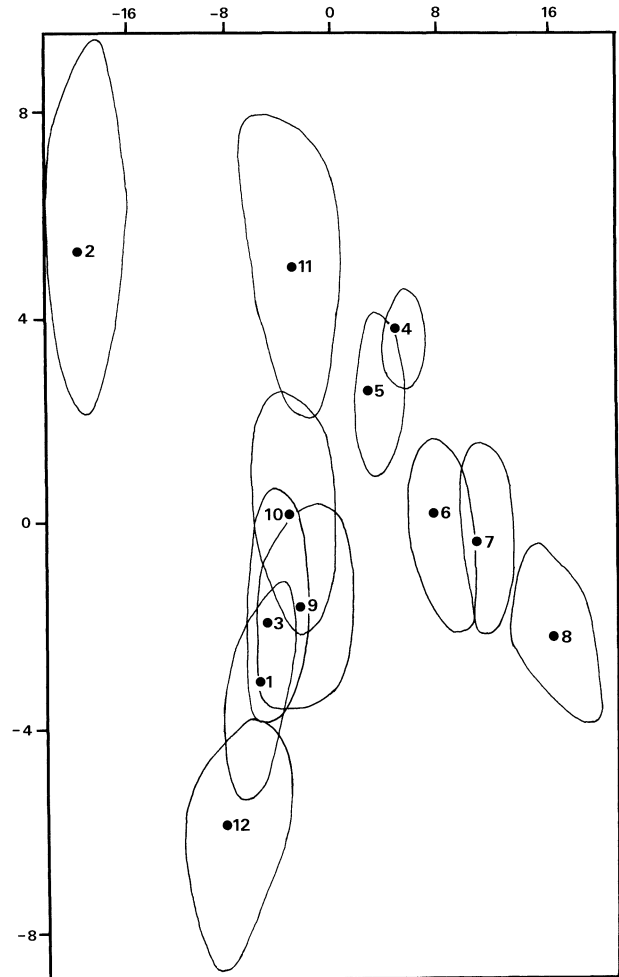


Fig.36. Plot of the results of the discriminate analysis using the first (vertical) and third coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 - *J. edgbastonensis*; 2 - *J. corrugata*; 3 - *J. coreena*; 4 - *J. pallida*; 5 - *J. colmani*; 6 - *J. jesswiseae*; 7 - *J. zeidlerorum*; 8 - *J. acuminata*; 9 - *J. carnarvonensis*; 10 - *J. exigua*; 11 - *J. isolata*; 12 - *J. eulo*.

group although the position of the osphradium relative to the posterior end of the gill varies from group to group. In *Tatea* and in *Hydrobia* it is located near the middle of the ctenidium and, consequently, this position is considered to be the plesiomorphic one. The presence of a hypobranchial gland is considered to be plesiomorphic as this structure is found in most neotaenioglossans. There is no glandular pad to the left of the ctenidium in species of *Tatea* or any other genus that we have examined, other than in two species of *Jardinella*.

The male genital system in species of *Tatea*, and in most other members of the *Tatea* group, is characterised by a simple, tapering penis, the distal end of which is wrinkled (in preserved material), a prostate gland that lies about half in and half behind the pallial roof and a more or less straight pallial vas deferens. The female system has a nonpigmented, U-shaped coiled oviduct with the small, ovoid seminal receptacle opening to it.

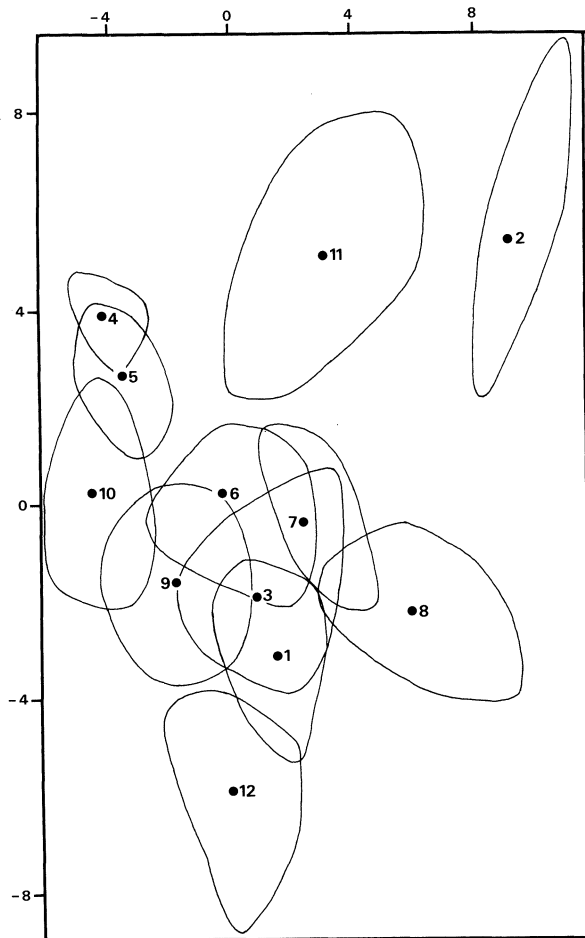


Fig.37. Plot of the results of the discriminant analysis using the second (vertical) and third coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 - *J. edgbastonensis*; 2 - *J. corrugata*; 3 - *J. coreena*; 4 - *J. pallida*; 5 - *J. colmani*; 6 - *J. jesswiseae*; 7 - *J. zeidlerorum*; 8 - *J. acuminata*; 9 - *J. carnarvonensis*; 10 - *J. exigua*; 11 - *J. isolata*; 12 - *J. eulo*.

The large bursa copulatrix lies behind the albumen gland, its duct running anteriorly from the anteroventral side of the bursa to join with the oviduct at the posterior wall of the pallial cavity. The oviduct opens to the ventral channel of the capsule gland which opens anteriorly by a simple, small opening. There is no rudimentary penis developed. All of these characters are taken to be plesiomorphic for the *Tatea* group for the purposes of this analysis.

Characters based on the patterns of ciliation of the cephalic tentacles are included in the analysis but we make no *a priori* assumptions about their polarity because of insufficient data about many of the other genera. The cephalic tentacles are oval in section in the majority of genera and this state is considered to be the plesiomorphous one.

The data was run (using PAUP) and 39 equally parsimonious trees (length = 55, consistency index = 0.60) were produced (Fig.38). *Tatea* was used as the outgroup to produce the consensus tree illustrated but using *Tatea* + *Fluvidona* or *Tatea* + *Fluvidona* + *Fonscochlea* as outgroups produced trees that were identical for the *Jardinella* clade and of the same length.

The ingroup is separated from the outgroup (*Tatea*) by two apomorphies, a reduced number of protoconch whorls, and the osphradium moving slightly posteriorly. *Fluvidona* is distinguished, in this analysis, by only one apomorphy — three ventral bands of cilia on the cephalic tentacles.

The clade formed by *Fonscochlea* and *Jardinella* is supported by three apomorphies, the only significant one being a reduction in the pairs of basal cusps on each central tooth of the radula to two (character 3B). The other two characters (dorsal ciliation of the cephalic tentacles and hypobranchial gland) are subject to reversals in the rest of the tree. The *Jardinella* clade is supported by three apomorphies:— the loss of opercular pegs and two related penial characters (the development of penial lobes and a smooth distal end).

Although this cladogram supports the monophyly of *Jardinella*, it also demonstrates the distinctiveness of *J. isolata* and *J. eulo*. This latter group is characterised by a unique apomorphy, an extra bend proximal to the U-shaped coiled oviduct (character 17C). It is also plesiomorphic in having the cephalic tentacles rounded in section (character 5A, of questionable value) and an uncoiled pallial vas deferens (character 13A). The branch leading to the remainder of the species of *Jardinella* is distinguished by the cephalic tentacles changing from oval to triangular in section (character 5B) and the acquisition of a coiled pallial vas deferens (character 13B).

The main cluster of species is not well resolved in the consensus tree and the following brief discussion outlines the main patterns observed. The characters given as distinguishing clades are the character state changes which occur at the stem of those groups. Several of these are, of course, subject to other state changes or reversals within the groups. Within this cluster *J. thaanumi* and *J. jesswiseae* form a polycotomy with the roots of three monophyletic groups which are present in all of

the trees. *Jardinella edgbastonensis*, *J. corrugata*, *J. coreena* and *J. pallida* + *J. colmani* form the largest of these monophyletic groups, which is distinguished by the pallial oviduct developing a papilla (character 20B). Within this clade, *J. pallida* and *J. colmani*, which are similar in shell characters, are defined in all trees as a monophyletic group in which the penis has reduced lobes and a long papilla (character 11D), the oviduct opening moves a little posteriorly (character 20C), and the oviduct and bursal duct join behind the posterior pallial wall (character 16B). This latter character is developed as an apomorphy of another pair of species having similar shell characters, *J. zeidlerorum* and *J. acuminata*, which are also characterised by anterior glandular pads in the pallial cavity (character 10B). The remaining pair of species, *J. carnarvonensis* and *J. exigua*, are distinguished by females having a rudimentary penis (character 21B) and a slit-like genital opening (character 19B).

Examination of the individual trees shows that the species in the eastern spring radiation (plus *J. thaanumi*) fall into three groups. In one group (16 trees) two clades are formed - one with *J. jesswiseae*, *J. carnarvonensis* and *J. exigua* separated by two ventral bands of cilia on the tentacles (character 7B) and, in about half of these trees, a modified ventral channel (character 14B). The remainder of the species fall into the other group, which is distinguished by only one apomorphy, a long penial papilla (character 11D). This latter character change was the only one separating a group consisting of *J. thaanumi*, *J. zeidlerorum* and *J. acuminata* in ten trees, although in three additional trees this same group was distinguished by an additional character, a reversal of the development of the hypobranchial gland. In these 13 trees the remainder of the species are distinguished by two characters in eight trees, modification of the ventral channel and two ventral ciliary tracts of the tentacles,

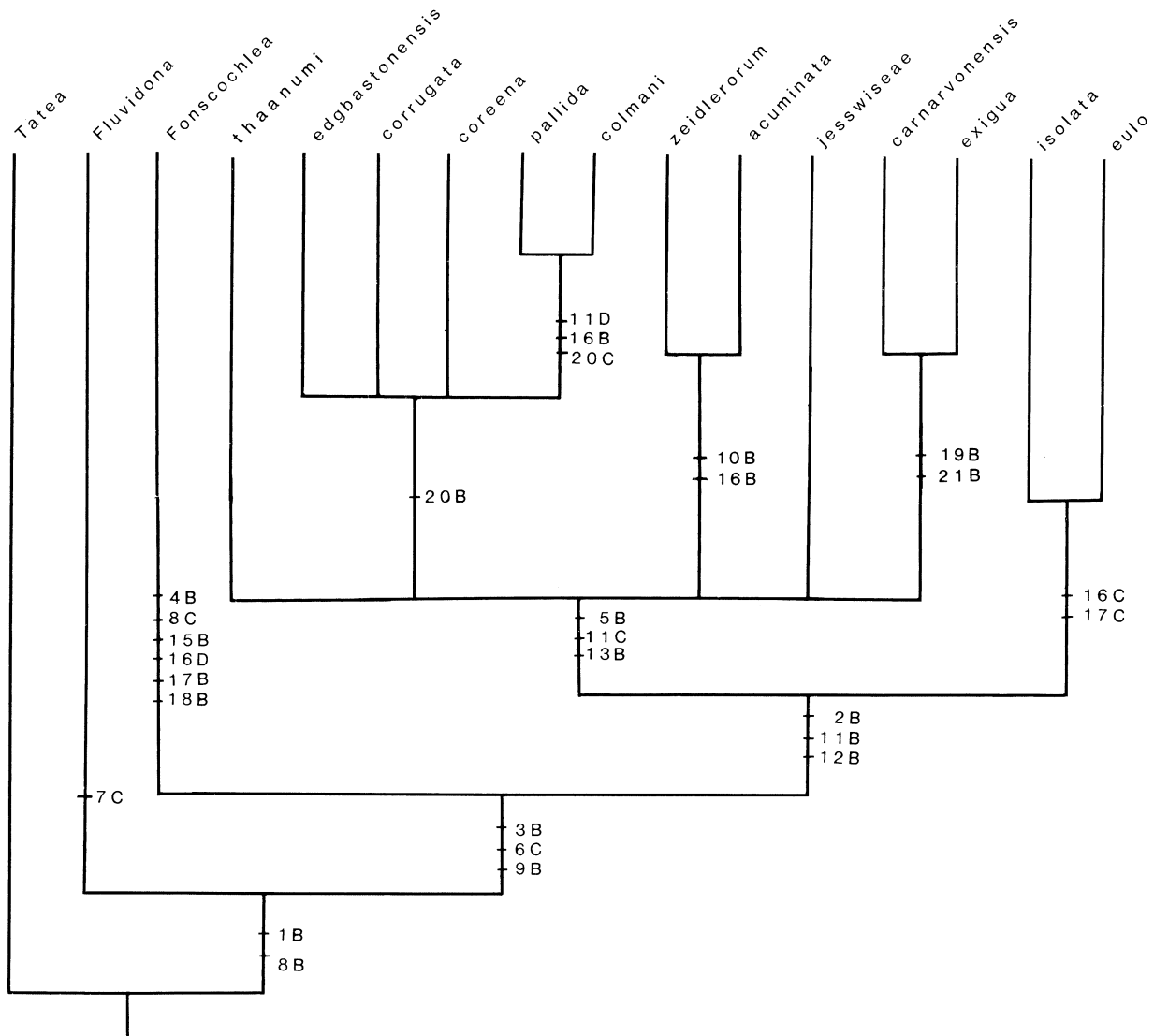


Fig.38. Strict consensus tree produced from 39 trees generated from the data given in Table 8. The numbers and letters along branches forming clades supported in all trees indicate character state changes. The branch lengths in no way reflect relative phylogenetic distance.

whereas in the other five trees either one of these two characters is utilised. The third pattern, seen in the remaining ten trees, *J. zeidlerorum* and *J. acuminata* separate as a separate group in the initial split which is distinguished by the characters given above (glandular pad + posterior joining of the oviduct and bursal duct). The stem giving rise to the remaining species shows no character changes.

Further resolution of species-level relationships probably requires utilising additional characters, or character weighting, the latter not having been attempted with this data set. The analysis does, however, support the monophyly of *Jardinella*, its relationship to *Fonscochlea* and the basic division of the genus into western and eastern groups of species.

Discussion

Relationships with other genera. *Jardinella* belongs to a group of mainly Australasian genera including *Tatea*, *Potamopyrgus* and *Fluvidona* which are similar anatomically and several of them possess the unusual feature (in the Hydrobiidae) of white material on the inner side of the operculum forming a smear or raised into one or more pegs. In mainland Australia, *Fluvidona* (*sensu lato*) is the only significant representative of this group of genera in freshwater and species referable to this genus extend around the coastal areas and along the Great Dividing Range from southern Queensland southwards to western South Australia and north into the Flinders Ranges as well as in south Western Australia (Ponder, unpublished). The only related genera, apart from the estuarine genus *Tatea*, are those found in Artesian springs associated with the Great Artesian Basin in South Australia [*Fonscochlea* (Ponder *et al.*, 1989) and a new genus from Dalhousie Springs (Ponder, 1989)] and Queensland (*Jardinella*). Although there is as yet insufficient data to demonstrate the detailed evolutionary relationships of these groups, we suggest that the cladogram shown in Fig. 38 indicates that the inland species evolved from a *Fluvidona*-like ancestor and that the artesian springs fauna may share a common ancestry.

The Queensland radiation (of *Jardinella*) is so diverse in shell and anatomical characters that this fauna must have been in existence for a considerable period of time. The Pleistocene radiation at Dalhousie Springs, while showing some divergence in shell shape and size and some physiological divergence (Ponder, 1989) has hardly differentiated anatomically (Ponder, unpublished observations). The radiation of *Fonscochlea* in the Lake Eyre Supergroup is diverse in shell characters but anatomically much more conservative (Ponder *et al.*, 1989) than seen in the *Jardinella* radiation. The sympatric *Trochidrobia* are, however, anatomically differentiated (Ponder *et al.*, 1989) but the relationships of this genus remain obscure. The Lake Eyre Supergroup hydrobiid fauna is presumably older than that at Dalhousie Springs as it was already well differentiated in the Pleistocene (from observations on fossils in Pleistocene mounds; Ponder,

unpublished) and Miocene fossils from the general vicinity are similar to some *Fonscochlea* species (Ponder *et al.*, 1989). A mid-Tertiary origin of the Queensland artesian spring hydrobiid fauna is supported by the existence of Miocene limestones containing hydrobiids south-east of Springvale Homestead, north west of the Diamantina River in western Queensland (McMichael, 1968), about 46 km south-east of Elizabeth Springs where *J. isolata* is found living today. Thus both the Lake Eyre Supergroup hydrobiids and *Jardinella* may have had a common ancestor in the Miocene or even earlier.

The existence of two species (*J. exigua* and *J. carnarvonensis*) in springs not emanating from the Great Artesian Basin, but closely associated with the recharge areas on the eastern edge of the Basin (Springsure Supergroup), suggests that more similar species may be found in the extensive hinterland along the Great Dividing Range in this section of Queensland. The cladistic analysis clearly shows that these species are derived from the artesian spring radiation. Similarly *J. thaanumi*, the type species of *Jardinella*, lives in coastal streams and rivers in north Queensland (Ponder, in press B) and is clearly part of the same radiation.

The genus occurs in only four of the six supergroups of artesian springs recognised in Queensland (Habermehl, 1982; Ponder, 1986; see also Fig. 1) and currently there is no evidence to suggest that they once occurred in the other groups. It is, however, possible that further work may reveal living or extinct populations in those areas. The springs emanating from Tertiary basalts in the middle of the Great Artesian Basin and on the north eastern edge near Hughenden (Habermehl, 1982; see also Fig. 1D,H) lack hydrobiids of any sort. The only hydrobiid found in the other springs sampled was *Fluvidona* (*Posticobia*) cf. *brazieri* (Smith, 1882) from Stn 82 in a non-artesian spring in the Great Dividing Range west of Bundaberg. *Fluvidona* (*Posticobia*) *brazieri* is widely distributed in coastal rivers in northern New South Wales and southern Queensland.

The radiation. The species included in *Jardinella* consist of two main groups - the south-western group and the eastern group which probably diverged very early in the history of the genus. The south-western group (*J. eulo* and *J. isolata*) uniquely (within the genus) share some characters, some plesiomorphic (no coils in pallial vas deferens) and some derived (distal penial lobes) but also differ markedly from one another in other features (e.g. shell shape, posterior female genital characters) suggesting a long separation. These two species may be the surviving end points of what may have been a much larger radiation in this area. The eastern group of species is located in the Barcardine and Springsure Supergroups on the eastern side of the Great Artesian Basin and, because more species still exist, it is possible to speculate on the evolution of this group.

The most derived members of this group may be the two species *J. acuminata* and *J. zeidlerorum*. These species possess a thick hypobranchial gland and autapomorphic glandular pads near the anus and on the left side of the ctenidium. The most similar species in shell characters,

J. jesswiseae, has the ventral channel modified as a vestibule, a character that is regarded as an autapomorphy of the eastern species of the genus (the exceptions are interpreted as reversals). Females of *J. jesswiseae* occasionally have a rudimentary penis and this feature is characteristic of the two species found in non-artesian springs (*J. carnarvonensis* and *J. exigua*). These latter two species have short-spined shells, a character shared with several species living in the artesian springs. *Jardinella coreena* and *J. corrugata* appear to be related, sharing rather similar reproductive characters, especially the penial lobes. *Jardinella edgbastonensis* also has a similar shell, but a different penis, although it would be possible to

derive the penis of that species from one like that in *J. coreena* and *J. corrugata* by reduction of the penial folds. Presumably *J. thaanumi* was derived from a species somewhat similar to *J. edgbastonensis* that evolved on the western side of the Great Dividing Range rather than the artesian spring radiation being derived from the east because the more primitive members of the *Jardinella* clade are present in western-most Queensland.

Two allopatric species sharing similar shells and genital characters are *J. colmani* and *J. pallida* which are intermediate in shell shape between species such as *J. jesswiseae* and *J. edgbastonensis*.

All of the springs containing hydrobiids have a single

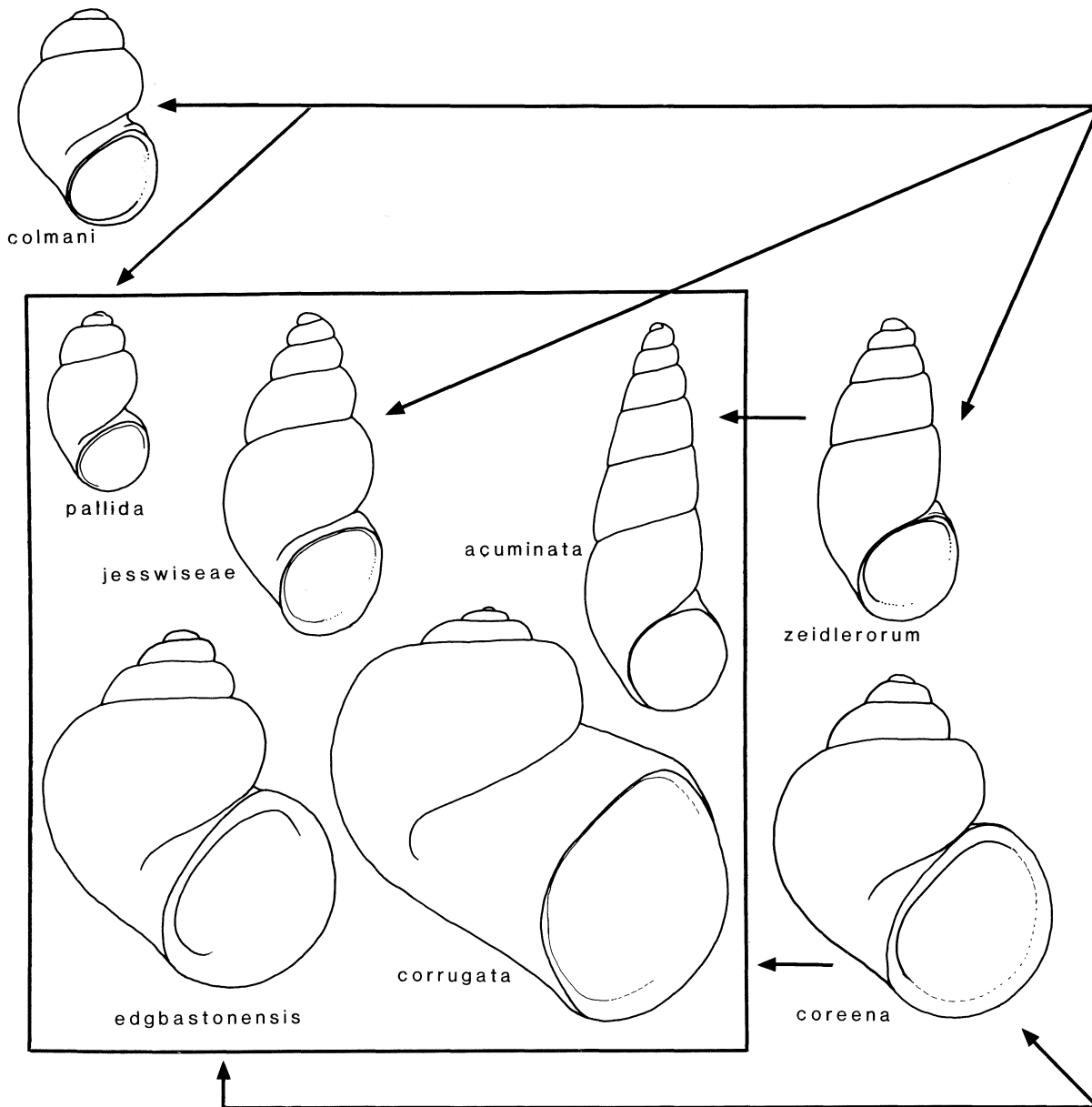


Fig.39. A diagrammatic representation of the possible origin of the hydrobiid fauna of Edgbaston springs. The species enclosed in the square are those living sympatrically at Edgbaston Springs, those outside the square live in the general vicinity. The lines represent probable relationships, the arrows the possible migration of an ancestral taxon in relation to Edgbaston Springs.

species except Edgbaston Springs. Of the five described species living in Edgbaston Springs (the sixth undescribed species cannot be included in this discussion because only the shell characters are known) there is some evidence to suggest that three of these evolved allopatrically and subsequently differentiated after dispersal events carried them to Edgbaston Springs (Fig. 39). *Jardinella pallida* is rather similar to *J. colmani* which occurs in springs about 58 km to the north. There are a number of springs in this area, some of which are recently extinct or heavily degraded and some of which have not been investigated. It is quite possible that *J. colmani* was (or is) more widespread or that other similar species are living in the general area. *Jardinella acuminata* is clearly closely allied to *J. zeidlerorum* which lives in a spring only about 11 km from Edgbaston Springs. These two species are not clearly related to any others. The Edgbaston species *J. corrugata* is similar, as noted above, to *J. coreena*, which lives 61 km to the south, and they may have shared a common ancestry but, again, there is no clear relationship with other species except perhaps *J. edgbastonensis*.

In these three cases allopatric evolution followed by dispersal to Edgbaston Springs appears to have occurred because it can be shown that existing species outside Edgbaston Springs are morphologically similar. The idea that these species have migrated to Edgbaston Springs (and not vice versa) is supported by most Edgbaston derivatives being more apomorphic.

The relationships of *J. jesswiseae* are more obscure. It may be an offshoot from the common ancestor to *J. colmani* + *J. pallida* and *J. acuminata* + *J. zeidlerorum*. Certainly the possession of a deviated protoconch allies it to the latter two species (this character was not included in the cladistic analysis).

Other species of molluscs at Edgbaston Springs included *Gabbia* sp. (Bithyniidae), a species somewhat similar in size and shape to *J. corrugata* and *J. edgbastonensis*. The families Ancyliidae and Planorbidae represented by one (*Ferrissia* sp.) and two (*Gyrulus* sp. and *Isidorella* sp.) species respectively.

Evolution of major characters. *Shell.* The acceptance of the remarkable diversity of shell form as part of a single radiation is perhaps made more acceptable because there is a gradation between all of the shell types. The uniformity of the group is also supported by the identical microsculpture of the protoconch in all species.

Operculum. The operculum differs from most related genera in lacking pegs on the inner surface (although sometimes there is a low horny swelling) but usually has a white smear. This latter character strongly suggests that the pegs were present in an ancestral form but have subsequently been lost. Likewise the white smear is lacking in some individuals of most species and in all individuals of some species.

Radula. The radular characters are similar to those of *Fonscochlea* in typically having only two pairs of basal cusps on the central teeth but those of *Jardinella* are

more plesiomorphic because they have longer shafts on the lateral teeth in almost all species. Occasional specimens of *Jardinella* are found with a third pair of cusps (usually only on one side of the tooth) supporting the idea that the two-cusp condition is derived from a multi-cuspid state.

Male genitalia. A distinctive character of several of the species of *Jardinella* is the development of flattened, pigmented, non-glandular lobes on the penis. The ancestral condition of this state appears to have been the development of this structure in the medial part of the penis, with a smooth (i.e. essentially non-contractile), portion distal to it that tapers to a point where the penial duct opens. The relative development of the lobes and the length of the distal portion relative to the rest of the penis appear to explain the majority of variation in penial morphology in the group. Those species appearing to have a simple penis, resembling that of species of *Fluvidona*, differ from species in that group in having the distal part of the penis non-contractile (i.e. smooth when fixed in the resting position), not contractile (i.e. wrinkled when fixed in the resting position). For this reason it is assumed that these species have lost the lobes/swellings and resemble the simple, tapering penis of species of *Fluvidona* only superficially.

Another apomorphy of most species of the genus is the coiled pallial vas deferens, a character seen in all species except *J. isolata* and *J. eulo*. *Fonscochlea* species have a plesiomorphic penial morphology and pallial vas deferens resembling those of *Fluvidona*.

Female genitalia. In its plesiomorphic state the ventral channel is open to the capsule gland along its entire length. The most unusual feature of the pallial oviduct in some species of *Jardinella* is the formation of a muscular vestibule characterised by being partially separated from the capsule gland and with folded internal walls. This feature, however, is absent in both the western species and in three of the eastern species. The sperm channel is separated by a flap of ciliated tissue (the lateral fold) in the plesiomorphic state, this becoming separated as a wide duct lying on the inner (left) side of the capsule gland when defined as a vestibule. There may have been reversals to a plesiomorphic-like state in *J. acuminata*, *J. zeidlerorum* and *J. exigua*. Some evidence for a reversal in the latter species is that it appears to have been derived from an ancestor similar to *J. carnarvonensis* with a vestibule but has reverted to a state resembling the ancestral one, apart from sharing the long pallial opening.

A rudimentary penis is found consistently in females of *J. exigua* and *J. carnarvonensis* and in a few females of *J. jesswiseae*. The latter was scored as state A in the cladistic analysis because, given the small number of individuals examined for most species, occasional rudimentary penes could have been missed in other species. We have no explanation as to why rudimentary penes should occur. Certainly there is no evidence of protandry.

Conservation considerations. Of the species described in this paper, all but one is endangered. While

J. carnarvonensis is contained in a National Park, the habitat of none of the others is protected in any way, all being on pastoral land. Several species are in small springs that are easily damaged — for example *J. eulo* is known from only two springs, but a dam had been dug out of a third one (Stn 10) which was located close to one of the springs containing snails (Stn 11) and no snails were present. All species are found only in single springs or in small, tightly grouped springs.

There are several ways the habitats could be degraded causing the extinction of the molluscs and other aquatic fauna. These include:-

1. Direct damage by pastoralists — e.g. damming, digging out, placing a well on or near the spring, overstocking.

2. Indirect damage — general drawdown from artesian wells leading to reduced flow (with consequent reduction of habitat) and eventual cessation of flow.

Feral and pastoral stock damage caused by overstocking and inadequate control of feral animals (e.g. horses, camels, donkeys) is a problem but generally the springs should recover unless the damage is extreme.

Direct damage from pastoralists can be prevented by education or specifically protecting the spring areas. The problem of drawdown caused by the over-exploitation of artesian water is a far reaching one that needs to be addressed on an interstate level [see Habermehl (1980) for a general overview]. Many Queensland, and virtually all New South Wales artesian springs have become extinct since the 1880's (Habermehl, 1980, 1982; Ponder, 1986; see also Fig. 1). If the removal of artesian water is not adequately controlled the extinction of most of the remaining Queensland artesian springs is assured. Many of the springs recorded by Habermehl (1980) proved to be extinct when visited on the 1984 survey (Fig.1).

ACKNOWLEDGMENTS. We thank Wolfgang and Lyn Zeidler for making available material that they collected and Dr M.A. Habermehl and Mr P.H. Colman for their companionship and support in the field with W.F.P. Mr G. Avern mounted all of the material for SEM examination and took the photographs. Mrs Jess Wise sorted many of the samples used in this and other studies. Histological work was done by Ms K. Jackes of the School of Zoology, University of Sydney and critical point drying was done using the facilities of the School of Biological Sciences, Macquarie University. A free copy (and free advice) of DELTA was kindly provided by Dr M. Dallwitz. This work has been supported in large part by ARC and ARGS grants (No. A18831777).

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Accepted 8 August 1989

APPENDIX 1

List of Stations

In the list of stations given below, the original field numbers are given. Distances from major locations (e.g. towns) are straight line distances taken from the map. Minor distances are generally distances by road measured with a vehicle speedometer. Map sheet names are the Queensland 1:250,000 series.

SPRINGS CONTAINING HYDROBIIDS

- 8, unnamed spring at Tunga Bore near Mount Tunga about 43 km west-south-west of Eulo, 28°13'S 144°38'E. Eulo 252 498. WFP and PHC, 6 Sept. 1984.
- 11, "Rocky Springs" near Mount Francis about 52 km south-west of Eulo, 28°18'S 144°32'E. Eulo 244 489. WFP and PHC, 7 Sept. 1984.
- 21, Elizabeth Springs about 26 km north-north-west of Springvale, 23°20'30"S 140°34'40"E. Springvale 457 418. WFP and PHC, 10 Sept. 1984. A – top of spring; B – outflow; C – large seep; D – small seeping pool on side of creek.
- Z1, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Low mound nearest creek.
- Z2, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Mound adjacent to spring with old fence about 300 m north of Stn Z1.
- 71, unnamed spring near Smokey Creek about 8 km east-north-east of "The Springs" HS, about 83 km north-north-east of Aramac, 22°12'20"S 145°22'30"E. Muttaborra 332 544. WFP and PHC, 25 Sept. 1984.
- 72, unnamed spring 2.3 km north-east of "Edgbaston" HS, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaborra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring, in *Phragmites*; C – on sheep's skull; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow.
- 73, "Big Spring" about 3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep; D – head of spring.
- 74, unnamed spring about 3.6 km south-east of "Edgbaston" HS, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaborra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan.
- Z6, unnamed spring about 11 km north-east of "The Springs" HS, about 83 km north of Aramac, 22°12'20"S 145°22'30"E. Muttaborra 332 544. WZ, 2 May 1988. Low mound (fenced) with ill-defined source and small outflow.
- Z7, unnamed spring about 2.4 km north-east of "Edgbaston" HS, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaborra 338 487. WZ, 3 May 1988. No mound but extensive seepage.
- Z8, unnamed spring about 2.3 km north-east of "Edgbaston" HS, about 33 km north-east of Aramac, 22°43'S 145°25'30"E. Muttaborra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m.
- Z9, "Big Spring" about 3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaborra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain.
- Z10, unnamed spring about 3.3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaborra 339 483. WZ, 4 May 1988.
- Z12, unnamed spring about 11 km south-south-east of "Edgbaston" HS, about 0.8 km south of main road, about 28 km north-east of Aramac, 22°47'20"S 145°25'40"E. Muttaborra 339 479. WZ, 4 May 1988. Mud mound supporting large natural pool.
- Z14, large unnamed spring just south of "Coreena" HS, about 32 km north-east of Barcaldine, 23°17'S 145°24'E. Longreach 337 425. WZ, 5 May 1988.
- 82, Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°50'S 147°11'45"E. Springsure 519 254. WFP and PHC, 29 Sept. 1984. Large spring with outflow about 120 m.
- 88, small unnamed spring on hillside about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984.
- 89, small unnamed spring on hillside about 100 m south-east of Stn 88, about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Head of spring fenced off and a small pipe leading from it.
- 93, Small seep about 1.2 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°48'E. Springsure 581 249. WFP and PHC, 1 Oct. 1984. With small pipe leading from it. A – head of spring; B – outflow.
- Z15, unnamed spring about 5 km north-west of Rangers HQ, just north of 13th river crossing, Carnarvon Gorge National Park, 25°02'30"S 148°11'20"E. Eddystone 619 229. WZ, 8 May 1988.
- Z16, small seep from rock face east side of Kooraminya

Creek, about 200 m up gorge, about 7.3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°02'20"S 148°11'E. Eddystone 619 229. WZ, 8 May 1988.

Z17, unnamed side spring, about 300 m up Hellhole Gorge (Koolaro Creek), about 3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°03'30"S 148°12'30"E. Eddystone 622 228. WZ, 8 May 1988.

SPRINGS NOT CONTAINING HYDROBIIDS

2, unnamed springs about 10 km east-north-east of Eulo, on tributary of Gumble Creek, 28°07'S 145°09'E. Eulo 307 513. WFP and PHC, 5 Sept. 1984. 15-20 small springs extinct to nearly extinct (damp mud).

3, unnamed springs about 2 km south-west of Eulo, 28°10'30"S 145°01'E. Eulo 294 506. WFP and PHC, 5 Sept. 1984. A few low extinct mounds.

4, unnamed springs about 10 km west of Eulo, on side of road, 28°08'45"S 144°57'E. Eulo 288 508. WFP and PHC, 5 Sept. 1984. Three large mounds all slightly damp.

5, mud spring about 20 km west of Eulo, Yowah Creek, on side of road, 28°07'30"S 144°51'30"E. Eulo 277 510. WFP and PHC, 5 Sept. 1984.

6, Dewalla "Spring" near bore about 34 km west of Eulo on Dewalla Creek, 28°07'50"S 144°43'30"E. Eulo 263 511. WFP and PHC, 5 Sept. 1984. One old low mound.

7, unnamed spring at "Bingara" HS about 38 km west of Eulo, 28°09'30"S 144°43'30"E. Eulo 263 507. WFP and PHC, 5 Sept. 1984.

9, Wombula Springs near Tunga Bore about 73 km west-south-west of Eulo, 28°16'20"S 144°19'20"E. Eulo 220 492. WFP and PHC, 6 Sept. 1984. About 10 mud mounds and several seepages.

10, Granite Springs near Mount Francis about 53 km south-west of Eulo, 28°19'S 144°32'E. Eulo 243 487. WFP and PHC, 6 Sept 1984. Large spring bulldozed to make deep pool for water supply.

12, unnamed springs 7 km south of "Granite Springs" HS, about 60 km south-west of Eulo, 28°23'45"S 144°30'30"E. Eulo 240 476. WFP and PHC, 7 Sept. 1984. Several extinct mound springs.

13, unnamed springs about 7.5 km north-west of "Currawinya" HS, about 90 km south-south-west of Eulo, 28°47'S 144°28'30"E. Eulo 231 431. WFP and PHC, 7 Sept. 1984. Large group of extinct mounds with a few damp ones on the eastern edge of group.

14, unnamed spring north of Fish Spring Bore about 89 km south-south-west of Eulo, 28°44'30"S 144°25'E. Eulo 231 435. WFP and PHC, 7 Sept. 1984. Two extinct mounds.

15, unnamed springs near Shire Council Tank about 85 km south-west of Eulo, 28°40'30"S 144°24'45"E. Eulo 231 441. WFP and PHC, 7 Sept. 1984. A few extinct mound

springs.

16, unnamed spring (not artesian) in Touro Creek about 88 km south-east of Windorah, 25°57'30"S 143°17'30"E. Windorah 652 771. WFP and PHC, 8 Sept. 1984. Large pool and small runoff from a smaller pool, both with stagnant, oily water.

17, about 4-5 small non-artesian seeps and small pool in Touro Creek about 89 km south-east of Windorah, 25°58'30"S 143°17'30"E. Windorah 651 768. WFP and PHC, 8 Sept. 1984.

18, two pools (not artesian) in Touro Creek about 91 km south-east of Windorah, 25°57'30"S 143°19'30"E. Windorah 655 770. WFP and PHC, 8 Sept. 1984. One large and one small pool, the small probably spring fed.

19, unnamed spring (not artesian) about 23 km north-north-west of Windorah, 25°14'S 142°34'30"E. Windorah 575 863. WFP and PHC, 9 Sept. 1984. The spring has been dug out to form a well about a metre deep.

26, mud pan about 25 km north-north-west of Julia Creek, 20°26'S 141°40'E. Julia Creek 569 739. WFP and PHC, 13 Sept. 1984. Pan about 100 m wide with a few small mud "bubbles" just damp, no standing water.

27, spring remains about 2 km north-north-west of "Alva Downs" HS, about 28 km north-north-west of Julia Creek, 20°24'S 141°38'30"E. Julia Creek 567 744. WFP and PHC, 13 Sept. 1984. A few low sand and clay mounds along spring bank.

28, unnamed spring about 6 km north of "Alva Downs" HS, about 35 km north-north-west of Julia Creek, 20°21'S 141°38'E. Julia Creek 567 744. WFP and PHC, 13 Sept. 1984.

29, unnamed spring on Spring Creek a tributary of Flinders River about 37 km north-west of "Numil" HS, 19°33'S 141°06'E. Millungera 412 551. WFP and PHC, 14 Sept. 1984. The spring has been made into a well, there are several other extinct springs in the area.

30, bore on Boorabin Creek about 0.5 km downstream from Malpas Bore, about 10 km east of "Malpas" HS, 19°35'S 142°19'20"E. Millungera 553 544. WFP and PHC, 15 Sept. 1984.

31, "Plain Spring" on tributary of Currajong Creek, about 6.5 km north-east of Stn 30, about 15 km east of "Malpas" HS, 19°33'30"S 142°21'30"E. Millungera 557 549. WFP and PHC, 15 Sept. 1984. A large low mound, spring extinct.

32, unnamed spring about 12 km north-north-east of "Malpas" HS, 19°30'30"S 142°17'30"E. Millungera 550 555. WFP and PHC, 15 Sept. 1984. Extinct spring.

33, pool just north of Stn 32, about 12.3 km north-north-east of "Malpas" HS, 19°30'30"S 142°18'E. Millungera 551 555. WFP and PHC, 15 Sept. 1984. Circular depression scrapped out and full of water.

34, large shallow muddy pool about 1.8 km north of Stn 32,

on east side of road, about 13.8 km north-north-east of "Malpas" HS, 19°30'S 142°17'45"E. Millungera 552 556. WFP and PHC, 15 Sept. 1984. Probably a spring.

35, "Black Spring" about 25 km north-east of "Malpas" HS, 19°29'S 142°25'E. Millungera 565 558. WFP and PHC, 15 Sept. 1984. Large mound spring.

36, unnamed spring about 20 km south-east of "Malpas" HS, 19°46'S 142°20'E. Millungera 554 525. WFP and PHC, 16 Sept. 1984. Extinct spring.

38, unnamed spring at "Saxby Downs" HS, 20°02'S 142°29'E. Julia Creek 655 784. WFP and PHC, 16 Sept. 1984. Spring with deposits of sulphur and iron, with no signs of life present in the spring.

39, Waddy Springs about 1.5 km south-east of "Saxby Downs" HS, 20°03'S 142°29'E. Julia Creek 657 783. WFP and PHC, 16 Sept. 1984. Small muddy pools with algae, badly polluted and damaged by cattle.

40, unnamed spring about 6 km east-south-east of "Saxby Downs" HS, 20°03'S 142°32'E. Richmond 661 783. WFP and PHC, 16 Sept. 1984. Small muddy spring in hollow, heavily polluted.

45, Peelunga Spring about 9.5 km north-west of Mount Whelan, 23°24'30"S 138°48'45"E. Mount Whelan 276 411. WFP and PHC, 18 Sept. 1984. An extinct travertine spring.

46, Peanunga Spring about 8.5 km west of Mount Whelan, 23°26'S 138°48'30"E. Mount Whelan 275 407. WFP and PHC, 18 Sept. 1984. A large low seeping mound spring.

47, New Carlo Spring about 6.5 km west of Mount Whelan, 23°26'30"S 138°49'30"E. Mount Whelan 277 406. WFP and PHC, 18 Sept. 1984. A mound of carbonate with large hole in one side containing water, and a pool with mud spring feeding it about 60 m away, heavily polluted by cattle.

48, Kendalls Spring about 8.5 km west-south-west of Mount Whelan, 23°28'S 138°49'E. Mount Whelan 276 403. WFP and PHC, 18 Sept. 1984. Small mud spring with shallow muddy pool.

49, unnamed springs about 12.5 km south-south-west of Mount Whelan, 23°30'30"S 138°47'30"E. Mount Whelan 274 398. WFP and PHC, 19 Sept. 1984. Several damp sand mounds on a large flood plain.

50, unnamed spring about 14 km south-south-west of Mount Whelan, 23°31'S 138°47'E. Mount Whelan 273 398. WFP and PHC, 19 Sept. 1984. A low, flowing spring on a large flood plain.

51, unnamed spring about 0.5 km east of Stn 49, about 13 km south-south-west of Mount Whelan, 23°31'S 138°48'E. Mount Whelan 274 399. WFP and PHC, 19 Sept. 1984. Cattle trampled spring.

52, Allawonga Springs about 27 km south-west of Mount Whelan, 23°33'30"S 138°40'E. Mount Whelan 262 392. WFP and PHC, 19 Sept. 1984. A low mound spring, with

some cattle damage.

53, Allawonga Springs about 27 km south-west of Mount Whelan, 23°33'30"S 138°40'30"E. Mount Whelan 263 392. WFP and PHC, 19 Sept. 1984. Two small springs about 6 m apart.

54, Mulligan River, about 29 km south-south-west of Mount Whelan, 23°40'S 138°45'E. Mount Whelan 272 381. WFP and PHC, 19 Sept. 1984. Several still, clear connected pools.

55, unnamed springs on north-west side of Mulligan River about 1 km south-west of Stn 54, about 30 km south-south-west of Mount Whelan, 23°40'30"S 138°45'E. Mount Whelan 271 381. Several small low oozing mud springs. WFP and PHC, 19 Sept. 1984.

56, Wongitta Waterhole about 44 km south-west of Mount Whelan, 23°45'S 138°38'30"E. Mount Whelan 259 371. WFP and PHC, 19 Sept. 1984. Long, shallow pool.

57, Pitchamurra Spring about 46.5 km south-south-west of Mount Whelan, 23°47'S 138°39'30"E. Mount Whelan 261 367. WFP and PHC, 20 Sept. 1984. Very polluted spring, cattle trodden.

58, Mirrica Springs about 61.5 km south-west of Mount Whelan, 23°51'30"S 138°30'E. Mount Whelan 246 369. WFP and PHC, 20 Sept. 1984. Tiny pools of water in creek.

62, unnamed springs near Datson Bore, about 54 km east of Boulia, 22°51'S 140°24'30"E. Boulia 336 151. WFP and PHC, 21 Sept. 1984. Line of small springs and seeps along a creek bed.

63, Pathungra Spring about 5 km south-west of "Pathungra" HS, about 83 km north-east of Boulia, 22°24'30"S 139°35'E. Boulia 352 205. WFP and PHC, 21 Sept. 1984. Old bore on what was a spring.

66, Soda Gorge Spring about 27.5 km north-west of Hughenden, 20°37'S 144°05'30"E. Hughenden 197 717. WFP and PHC, 23 Sept. 1984.

69, Mickey Spring on tributary of Flinders River, about 67 km north-east of Hughenden, 20°23'S 144°37'30"E. Hughenden 252 743. WFP and PHC, 24 Sept. 1984.

70, downstream of Mickey Spring, about 65 km north-east of Hughenden, 20°24'30"S 144°37'E. Hughenden 251 742. WFP and PHC, 24 Sept. 1984. Small seeping spring.

75, unnamed spring at "Texas" HS, about 64 km north-west of Jericho, 23°05'S 145°50'30"E. Jericho 382 447. WFP and PHC, 26 Sept. 1984. Large spring with calcrete rock in abundance but dug out and covered at head.

76, Four Mile Spring about 59 km north-west of Jericho, 23°08'S 145°50'E. Jericho 381 441. WFP and PHC, 26 Sept. 1984. Spring with a pumping mill associated with it.

77, small unnamed spring about 200 m south of Ten Mile Spring, about 51 km north-west of Jericho, 23°12'30"S 145°51'E. Jericho 382 433. WFP and PHC, 26 Sept. 1984.

- 78, small unnamed seepage/spring about 1 km north of "Igtham" HS, about 21 km west of Jericho, 23°34'S 145°54'30"E. Jericho 389 394. WFP and PHC, 27 Sept. 1984. Small flow, with heavy cattle pressure.
- 81, small unnamed spring about 51 km north-west of Tambo, 24°27'45"S 146°03'30"E. Tambo 403 294. WFP and PHC, 28 Sept. 1984. Two small springs one with piping feeding from it, with cattle degradation extensive for both springs.
- 83, Major Mitchell Springs, Salvator Rosa Section, Carnarvon Gorge National Park, 24°51'40"S 147°11'E. Springsure 519 251. WFP and PHC, 29 Sept. 1984. Large valley with swampy springs on floor.
- 84, peat bogs about 2.5 km north of Major Mitchell Springs and about 1.5 km south of Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°50'30"S 147°11'30"E. Springsure 519 252. WFP and PHC, 29 Sept. 1984. Large swampy gullies with swift narrow channels and numerous seeps.
- 85, small unnamed bog/spring on side of track on tributary of Nogoia River, about 5.2 km north along track from Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°48'30"S 147°11'E. Springsure 518 256. WFP and PHC, 29 Sept. 1984.
- 86, large unnamed spring, in Reedy Creek at "Crystalbrook" HS, south of Carnarvon Gorge National Park, 25°30'30"S 147°58'30"E. Eddystone 598 179. WFP and PHC, 30 Sept. 1984. Cattle damage throughout spring but not very bad.
- 90, small seep/spring in narrow gully, about 1 km north of Stn 88, about 3.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°51'S 147°47'E. Springsure 579 250. WFP and PHC, 1 Oct. 1984.
- 91, small seep/spring in narrow gully, about 1 km south-west of Stn 88, about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°46'E. Springsure 578 248. WFP and PHC, 1 Oct. 1984.
- 92, small seep, in large creek gully, about 1.5 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°51'30"S 147°48'20"E. Springsure 582 248. WFP and PHC, 1 Oct. 1984.
- 94, "Black Bull Spring" about 11 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°47'S 147°51'E. Springsure 587 258. WFP and PHC, 1 Oct. 1984. Large spring.
- 95, unnamed spring about 13 km north of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°46'S 147°49'E. Springsure 583 259. WFP and PHC, 1 Oct. 1984. Similar to last spring but smaller.
- 96, Paddys Spring about 8 km south-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°56'S 147°50'45"E. Springsure 585 242. WFP and PHC, 1 Oct. 1984. Large waterhole in narrow sandstone gully/gorge.
- 97, unnamed spring about 1.5 km north of "Mount Hutton" HS, about 21.5 km east of Injune, 25°49'50"S 148°46'40"E. Taroom 678 143. WFP and PHC, 2 Oct. 1984. Large swampy spring in depression near Injune Creek.
- 98, unnamed springs about 1.5 km north of Stn 97, about 21 km east of Injune, 25°48'S 148°46'E. Taroom 678 146. WFP and PHC, 2 Oct. 1984.

APPENDIX 2

Table 1. List of characters and character states used in compiling the descriptions. Those also used in the phylogenetic analysis are indicated by an asterisk (*).

SHELL	Ratio of length of primary cusp/length of adjacent outer cusp
Shell shape	Basal bulge
1. trochiform (length/width ratio 0.50-1.30)	* Outer shaft - number of times longer than cutting edge
2. conical (length/width ratio 1.30-2.01)	<i>Marginal teeth</i>
3. elongate conic (length/width ratio 2.01-2.30)	Cusps
4. very elongate conic (length/width ratio 2.30-2.80)	1. inner marginal teeth with larger cusps than outer marginal teeth
Shell size	2. inner and outer marginal teeth with cusps about equal in strength
1. small (length 1.0-2.0 mm)	
2. of medium size (length 2.0-3.6 mm)	
3. large (length greater than 3.6 mm)	
Shell length and width	
Shell thickness (not quantified)	EXTERNAL FEATURES – HEAD-FOOT
Shell colour (observed dry)	* Cephalic tentacles – cross sectional shape
Periostracum - including colour	* Dorsal ciliation of cephalic tentacles
Spire angle	* Ventral ciliation of cephalic tentacles
* Number of protoconch whorls	Pigmentation of head foot
Protoconch microsculpture	Pigmentation of visceral coil
Number of teleoconch whorls	
Convexity ratio	PALLIAL CAVITY
Teleoconch sculpture	Number of ctenidial filaments
Slope of growth lines on teleoconch	Position of ctenidial apex
Shape of periphery of body whorl	* Position of osphradium relative to posterior end of ctenidium
Aperture length/shell length ratio	* Hypobranchial gland
Thickening of inner lip	* Presence or absence of glandular pad to left of ctenidium
Width of inner lip	Presence or absence of glandular pad near anus
Columellar swelling present or absent	Rectal arch present or absent
Slope and angle of outer lip	Position of anus relative to mantle edge [near mantle edge, well back (i.e. about one third of length of pallial cavity from mantle edge), or intermediate between these two positions]
Umbilicus	Renal organ (kidney) – extent of protrusion into mantle roof
1. closed	
2. minute (width of body whorl/width of umbilicus greater than 26)	MALE REPRODUCTIVE SYSTEM
3. small (width of body whorl/width of umbilicus 10-26)	* Presence or absence of penial lobes
4. medium (width of body whorl/width of umbilicus 4-10)	* Distal portion of penis wrinkled or smooth
5. wide (width of body whorl/width of umbilicus 1-4)	Shape of distal end of penis
Umbilicus diameter	Pigmentation of penis
	* Pallial vas deferens coiled or straight; location of coils, if present.
OPERCULUM	FEMALE REPRODUCTIVE SYSTEM
Opercular thickness	* Ventral channel of pallial oviduct simple or modified as vestibule
Opercular colour	Position of seminal receptacle relative to bursa copulatrix
Opercular length	Point of origin of bursal duct from bursa copulatrix
* Presence or absence of white smear on inner surface of operculum	Shape and size (relative to albumen gland) of bursa copulatrix
Length of white smear	* Fusion of oviduct and bursal duct
Ratio of opercular length/distance of nucleus from edge of last whorl at half whorl point	* Loops of coiled oviduct
	* Shape of oviduct opening
RADULA	* Presence or absence, and position, of papilla with pallial opening
<i>Central teeth</i>	* Rudimentary penis present or absent in females
Number of lateral cusps	
Ratio of length of central cusp/length of adjacent cusp	
* Number of pairs of basal denticles	
Shape of dorsal edge	
Shape of basal process	
Thickness of lateral edge	
Extension of lateral edges ventrally	
<i>Lateral teeth</i>	
Cusp formula	

Table 2. Characters used in the phylogenetic analysis. The data used in the analysis is given in Table 8 and the character numbers given here correspond to the character numbers given in that table. Characters are ordered unless otherwise noted. An asterisk (*) indicates those character states considered to be plesiomorphic.

SHELL

1. Number of protoconch whorls
 - * A. with more than 1.6 whorls
 - B. with less than 1.6 whorls.

OPERCULUM

2. Presence or absence of pegs
 - * A. with pegs
 - B. without pegs (white smear present or absent)

RADULA

3. Number of pairs of basal denticles
 - * A. more than two
 - B. two or less
4. Outer shaft – number of times longer than cutting edge
 - * A. more than 1.5 times as long
 - B. less than 1.5 times as long

HEAD-FOOT

5. Cephalic tentacles
 - * A. oval to circular in section
 - B. triangular in section
6. Dorsal ciliation of cephalic tentacles (unordered)
 - A. with dorsal ciliated band present on both tentacles
 - B. with dorsal ciliated band present on right tentacle only
 - C. with no dorsal ciliated bands present
7. Ventral ciliation of cephalic tentacles (unordered)
 - A. distinct ciliated band along most of ventral surface
 - B. two distinct ciliated bands along most of ventral surface
 - C. three ciliated bands along most of ventral surface
 - D. cilia not arranged in bands on ventral surface
8. Osphradium
 - * A. near middle of ctenidium
 - B. between posterior end and middle of ctenidium
 - C. near posterior end of ctenidium
9. Hypobranchial gland
 - * A. moderately to well developed
 - B. very reduced or absent
10. Glandular pad to left of ctenidium
 - * A. no glandular pad to left of ctenidium
 - B. well-developed glandular pad to left of ctenidium

GENITALIA:MALE

11. Penial lobes
 - * A. absent, simple tapering penis
 - B. papilla short, distinct lobes present or distinctly swollen area

C. papilla short, folds or swelling slightly to moderately developed

D. papilla long, folds or swelling slightly to moderately developed

E. long folds to distal end of penis

12. Distal end of penis

* A. simple, tapering, wrinkled when at rest

B. modified as papilla and/or lobes, not conspicuously wrinkled when at rest

13. Pallial vas deferens

* A. straight or undulating

B. with loops/coils

GENITALIA:FEMALE

14. Ventral channel

* A. unmodified

B. modified as muscular vestibule

15. Orientation of bursal duct

* A. runs anteriorly

B. runs vertically (ventral to bursa) or posteriorly

16. Coiled oviduct and bursal duct (unordered)

* A. separate to posterior mantle wall

B. fused to form common duct about halfway to mantle wall from seminal receptacle duct

C. fused to form common duct just in front of seminal receptacle duct, bursal duct sloped anteriorly

D. fused to form common duct, bursal duct vertical to sloped posteriorly

17. Coiled oviduct (unordered)

* A. simple U-shape

B. basically U-shaped but with extra bend distally

C. basically U-shaped but with extra bend proximally

D. basically U-shaped but with extra bend in middle part

18. Relative size of bursa copulatrix

* A. bursa copulatrix much larger in size than thin-walled seminal receptacle

B. bursa copulatrix about equal in size to thick-walled seminal receptacle

19. Opening of oviduct

* A. short (small)

B. long, slit-like

20. Papilla bearing oviduct opening (unordered)

* A. not developed

B. anterior to capsule gland

C. behind anterior end of capsule gland

21. Rudimentary penis

* A. absent in females or present in a few females

B. present in most or all females

Table 3. Shell and opercular measurements of species of *Jardinella*. AA - angle of outer lip of aperture; AL - aperture length; AW - aperture width; BW - body whorl length; CS - length of white smear; CV - convexity ratio; f - females; OL - opercular length; ON - distance of opercular nucleus from opercular edge; m - males; PD - protoconch diameter; PW - number of protoconch whorls; SA - spire angle; SD - standard deviation; SL - shell length; SW - shell width; TW - number of teleoconch whorls; UW - umbilical width; X - mean.

		<i>J. edgbastonensis</i>	<i>J. corrugata</i>	<i>J. coreena</i>	<i>J. pallida</i>	<i>J. colmani</i>	<i>J. jesswiseae</i>	<i>J. zeidlerorum</i>	<i>J. acuminata</i>	<i>J. carnarvonensis</i>	<i>J. exigua</i>	<i>J. isolata</i>	<i>J. eulo</i>
stn. No.		72(A)	Z9(A)	Z14	73(A)	71	73(A)	Z12	73	Z15	93(B)	21(C)	11
number		22	12	12	22	21	22	15	22	39	33	21	22
SL (m)	X	2.80	3.66	2.72	1.41	1.66	2.08	2.57	2.91	2.06	1.45	3.05	2.36
	SD	0.21	0.27	0.17	0.05	0.04	0.21	0.09	0.29	0.12	0.12	0.13	0.22
	(f) X	2.98	3.73	2.84	1.62	1.96	2.43	2.62	3.00	2.14	1.38	3.23	2.58
	SD	0.17	0.21	0.16	0.11	0.18	0.17	0.14	0.37	0.18	0.10	0.31	0.17
SW (m)	X	2.43	3.44	2.27	0.86	1.11	1.18	1.19	1.12	1.81	1.52	2.05	2.46
	SD	0.17	0.11	0.11	0.03	0.06	0.08	0.03	0.07	0.15	0.10	0.14	0.19
	(f) X	2.58	3.49	2.36	0.94	1.26	1.29	1.25	1.15	1.90	1.46	2.17	2.75
	SD	0.14	0.18	0.11	0.04	0.10	0.06	0.08	0.11	0.13	0.09	0.16	0.13
AL (m)	X	1.58	2.29	1.48	0.60	0.77	0.84	0.92	0.84	1.13	0.89	1.49	1.42
	SD	0.12	0.25	0.10	0.02	0.03	0.08	0.01	0.07	0.11	0.07	0.08	0.13
	(f) X	1.65	2.22	1.54	0.68	0.87	0.89	0.98	0.85	1.15	0.83	1.51	1.62
	SD	0.10	0.12	0.10	0.03	0.07	0.05	0.06	0.07	0.12	0.08	0.12	0.09
AW (m)	X	1.42	1.73	1.37	0.60	0.74	0.75	0.79	0.78	1.07	0.84	1.30	1.30
	SD	0.11	0.12	0.07	0.03	0.04	0.06	0.03	0.05	0.09	0.06	0.05	0.10
	(f) X	1.50	1.75	1.38	0.66	0.82	0.82	0.83	0.79	1.11	0.81	1.34	1.47
	SD	0.09	0.08	0.06	0.02	0.06	0.06	0.07	0.07	0.08	0.05	0.10	0.09
BW (m)	X	2.15	3.31	2.22	1.12	1.35	1.46	1.56	1.61	1.74	1.28	2.49	2.02
	SD	0.38	0.25	0.12	0.03	0.02	0.14	0.05	0.12	0.11	0.10	0.09	0.19
	(f) X	2.31	3.39	2.31	1.27	1.58	1.67	1.66	1.64	1.81	1.21	2.62	2.19
	SD	0.32	0.19	0.13	0.06	0.14	0.08	0.08	0.15	0.15	0.09	0.21	0.12
UW (m)	X	0.33	1.07	0.27	0.06	0.09	0.03	0.00	0.00	0.25	0.27	0.41	0.34
	SD	0.05	0.03	0.06	0.03	0.03	0.01	0.00	0.00	0.07	0.03	0.09	0.07
	(f) X	0.35	1.16	0.34	0.05	0.09	0.04	0.00	0.00	0.25	0.25	0.46	0.40
	SD	0.04	0.10	0.04	0.02	0.02	0.02	0.00	0.00	0.05	0.04	0.10	0.06
CV (m)	X	0.26	0.32	0.28	0.19	0.22	0.20	0.12	0.09	0.25	0.26	0.19	0.22
	SD	0.03	0.02	0.02	0.04	0.04	0.03	0.02	0.03	0.03	0.05	0.03	0.02
	(f) X	0.26	0.33	0.27	0.22	0.21	0.20	0.14	0.09	0.25	0.26	0.19	0.20
	SD	0.03	0.04	0.03	0.04	0.03	0.02	0.02	0.02	0.04	0.05	0.02	0.02

Table 3 (cont'd).

		<i>J. edgbastonensis J. corrugata J. coreena J. pallida J. colmani J. jesswiseae J. zeidlerorum J. acuminata J. carnarvonensis J. exigua J. isolata J. eulo</i>												
stn. No.		72(A)	Z9(A)	Z14	73(A)	71	73(A)	Z12	73	Z15	93(B)	21(C)	11	
number		22	12	12	22	21	22	15	22	39	33	21	22	
SA	(m)	X	83.17	91.05	79.07	73.52	82.83	57.06	44.39	36.75	95.31	103.68	71.11	100.29
		SD	3.47	2.52	2.86	2.92	3.02	3.05	2.09	3.57	7.23	7.97	3.64	4.42
	(f)	X	84.47	93.81	80.86	68.88	77.19	55.35	45.28	36.40	93.87	105.04	70.01	99.79
		SD	4.25	6.79	3.95	4.34	2.89	4.16	1.75	3.26	5.96	8.42	5.03	4.25
AA	(m)	X	20.33	23.68	23.93	21.06	12.57	19.73	4.18	6.31	30.52	27.47	11.13	27.94
		SD	4.12	0.91	2.70	4.54	4.35	5.74	3.86	2.32	3.67	4.46	3.76	3.52
	(f)	X	22.18	24.72	21.12	16.71	15.74	20.16	3.95	5.16	31.43	29.58	13.36	24.15
		SD	2.41	3.64	4.09	3.37	4.95	4.06	2.00	2.12	4.97	4.00	4.80	3.50
PD	(m)	X	0.41	0.37	0.44	0.30	0.39	0.34	0.33	0.30	0.42	0.39	0.43	0.43
		SD	0.03	0.01	0.02	0.03	0.02	0.03	0.01	0.02	0.03	0.04	0.03	0.03
	(f)	X	0.42	0.38	0.45	0.32	0.40	0.34	0.31	0.31	0.43	0.40	0.45	0.43
		SD	0.03	0.04	0.03	0.03	0.04	0.02	0.02	0.02	0.03	0.03	0.06	0.03
PW	(m)	X	1.31	1.28	1.25	1.24	1.26	1.26	1.25	1.39	1.24	1.26	1.27	1.29
		SD	0.10	0.03	0.00	0.02	0.04	0.05	0.00	0.07	0.02	0.04	0.02	0.02
	(f)	X	1.35	1.26	1.26	1.24	1.27	1.25	1.26	1.40	1.25	1.27	1.28	1.28
		SD	0.06	0.04	0.02	0.03	0.03	0.05	0.02	0.08	0.01	0.05	0.04	0.05
TW	(m)	X	2.99	2.80	2.85	2.25	2.20	3.20	4.15	5.00	2.51	1.87	2.91	2.64
		SD	0.15	0.07	0.27	0.06	0.15	0.17	0.14	0.38	0.12	0.16	0.22	0.15
	(f)	X	3.03	2.79	2.93	2.45	2.45	3.55	4.05	4.92	2.57	1.93	2.81	2.73
		SD	0.14	0.06	0.13	0.09	0.08	0.22	0.20	0.34	0.16	0.15	0.21	0.14
OL	(m)	X	1.36	1.93	1.26	0.63	0.75	0.80	0.76	0.69	0.97	0.83	1.41	1.29
		SD	0.08	0.14	0.03	0.03	0.03	0.06	0.01	0.06	0.07	0.06	0.07	0.10
	(f)	X	1.45	1.97	1.31	0.70	0.85	0.88	0.79	0.73	1.01	0.80	1.46	1.46
		SD	0.09	0.09	0.06	0.04	0.07	0.04	0.05	0.06	0.08	0.05	0.09	0.08
ON	(m)	X	0.42	0.61	0.37	0.19	0.25	0.21	0.19	0.16	0.32	0.28	0.43	0.43
		SD	0.03	0.13	0.01	0.02	0.01	0.02	0.02	0.03	0.03	0.03	0.04	0.03
	(f)	X	0.44	0.60	0.41	0.22	0.28	0.24	0.20	0.17	0.33	0.28	0.45	0.47
		SD	0.03	0.08	0.03	0.02	0.04	0.03	0.02	0.02	0.04	0.03	0.04	0.04
CS	(m)	X	0.15	0.33	0.00	0.13	0.00	0.00	0.26	0.33	0.00	0.00	0.52	0.27
		SD	0.10	0.17	0.00	0.06	0.00	0.00	0.04	0.06	0.00	0.00	0.08	0.10
	(f)	X	0.24	0.42	0.00	0.15	0.04	0.00	0.30	0.34	0.00	0.00	0.53	0.26
		SD	0.25	0.24	0.00	0.11	0.11	0.00	0.07	0.08	0.00	0.00	0.13	0.10

Table 4. The distribution of hydrobiids and *Gabbia* sp. in the Edgbaston Springs. Percentage frequencies are given except for the undescribed hydrobiid species (which is known from only one shell) and *Gabbia*.

	<i>edgbastonensis</i>	<i>acuminata</i>	<i>jesswiseae</i>	<i>pallida</i>	<i>corrugata</i>	n.sp.	<i>Gabbia</i>
Station 73							
Head of spring	—	—	100.0	—	—	—	—
Upper outflow	—	11.3	76.0	12.7	—	*	*
Lower outflow	2.1	21.2	67.5	2.1	7.0	—	*
Small seep	51.2	—	18.9	1.4	28.6	—	—
Station 72							
Head of spring	—	—	47.4	52.6	—	—	—
Middle of middle outflow	—	—	84.2	15.8	—	—	—
Edge of middle outflow	71.4	—	9.4	19.2	—	—	*
Lower outflow	54.4	—	4.8	40.8	—	—	*

Table 5. Comparisons of generalised distances between groups (species) generated by discriminate analysis.

	<i>J. edgbastonensis</i>	<i>J. acuminata</i>	<i>J. colmani</i>	<i>J. eulo</i>	<i>J. corrugata</i>	<i>J. pallida</i>	<i>J. exigua</i>	<i>J. carnarvonensis</i>	<i>J. coreena</i>	<i>J. jesswiseae</i>	<i>J. zeidlerorum</i>	<i>J. isolata</i>
<i>J. edgbastonensis</i>	0.000	21.649	11.417	5.188	17.817	13.911	8.523	5.722	3.226	13.249	16.159	9.422
<i>J. acuminata</i>	21.649	0.000	16.959	24.326	34.478	16.394	21.457	19.804	21.111	11.293	7.431	20.498
<i>J. colmani</i>	11.417	16.959	0.000	14.004	24.936	3.543	7.168	7.111	9.788	6.148	10.405	9.363
<i>J. eulo</i>	5.188	24.326	14.004	0.000	18.419	16.443	9.468	7.252	6.405	16.096	19.091	12.766
<i>J. corrugata</i>	17.817	34.378	24.936	18.419	0.000	26.555	21.211	20.631	18.282	27.468	29.875	17.580
<i>J. pallida</i>	13.911	16.394	3.543	16.443	26.555	0.000	8.912	9.758	12.589	6.228	10.101	11.547
<i>J. exigua</i>	8.523	21.457	7.168	9.468	21.211	8.912	0.000	4.448	7.740	11.359	15.488	10.643
<i>J. carnarvonensis</i>	5.722	19.804	7.111	7.252	20.631	9.758	4.448	0.000	4.118	9.937	13.745	8.892
<i>J. coreena</i>	3.226	21.111	9.788	6.405	18.282	12.589	7.740	4.118	0.000	11.978	15.162	7.797
<i>J. jesswiseae</i>	13.249	11.293	6.148	16.096	27.468	6.228	11.359	9.937	11.978	0.000	4.711	12.029
<i>J. zeidlerorum</i>	16.159	7.431	10.405	19.091	29.875	10.101	15.488	13.745	15.162	4.711	0.000	14.667
<i>J. isolata</i>	9.422	20.498	9.363	12.766	17.580	11.547	10.643	8.892	7.797	12.029	14.667	0.000

Table 6. Euclidean (=Taxonomic) distances between groups (species) generated by discriminate analysis.

	<i>J. edgbastonensis</i>	<i>J. acuminata</i>	<i>J. colmani</i>	<i>J. eulo</i>	<i>J. corrugata</i>	<i>J. pallida</i>	<i>J. exigua</i>	<i>J. carnarvonensis</i>	<i>J. coreena</i>	<i>J. jesswiseae</i>	<i>J. zeidlerorum</i>	<i>J. isolata</i>
<i>J. edgbastonensis</i>	0.000	2.622	2.099	0.567	1.979	2.638	2.469	1.289	0.258	1.798	1.925	0.641
<i>J. acuminata</i>	2.622	0.000	2.832	2.921	4.137	3.011	3.486	2.705	2.607	1.708	0.989	2.699
<i>J. colmani</i>	2.099	2.832	0.000	1.844	3.905	0.574	0.771	0.865	1.903	1.133	1.875	2.165
<i>J. eulo</i>	0.567	2.921	1.844	0.000	2.214	2.376	2.070	0.985	0.526	1.813	2.121	0.998
<i>J. corrugata</i>	1.979	4.137	3.905	2.214	0.000	4.456	4.153	3.098	2.106	3.691	3.693	1.901
<i>J. pallida</i>	2.638	3.011	0.574	2.376	4.456	0.000	0.814	1.398	2.451	1.399	2.115	2.720
<i>J. exigua</i>	2.469	3.486	0.771	2.070	4.153	0.814	0.000	1.212	2.295	1.808	2.541	2.618
<i>J. carnarvonensis</i>	1.289	2.705	0.865	0.985	3.098	1.398	1.212	0.000	1.105	1.154	1.753	1.468
<i>J. coreena</i>	0.258	2.607	1.903	0.526	2.106	2.451	2.295	1.105	0.000	1.657	1.851	0.553
<i>J. jesswiseae</i>	1.798	1.708	1.133	1.813	3.691	1.399	1.808	1.154	1.657	0.000	0.749	1.899
<i>J. zeidlerorum</i>	1.925	0.989	1.875	2.121	3.693	2.115	2.541	1.753	1.851	0.749	0.000	2.020
<i>J. isolata</i>	0.641	2.699	2.165	0.998	1.901	2.720	2.618	1.468	0.553	1.899	2.020	0.000

Table 7. Percentage of the variance of each variable in each canonical variate from a canonical analysis of discriminance. AL – aperture length; BW – body whorl length; CV – convexity ratio; PD – protoconch diameter; PW – number of protoconch whorls; SL – shell length; SW – shell width; TW – number of teleconch whorls; UW – umbilical width.

	1	2	3	4	5	6	7	8	9
SL	60.330	0.327	31.706	6.094	0.620	0.637	0.058	0.006	0.221
SW	83.066	4.058	12.716	0.070	0.000	0.006	0.039	0.037	0.008
AL	45.156	47.269	4.643	1.057	0.378	0.007	0.230	1.094	0.166
BW	1.873	1.386	55.416	13.632	9.686	6.441	4.915	4.725	1.928
UW	54.776	32.822	7.675	4.561	0.115	0.005	0.028	0.020	0.000
CV	91.832	4.999	0.467	0.307	0.762	0.773	0.781	0.078	0.000
PD	12.934	3.341	62.198	9.527	7.064	1.409	3.010	0.492	0.025
PW	38.222	26.624	5.324	19.408	0.114	8.406	1.093	0.537	0.271
TW	73.437	18.382	6.873	1.062	0.064	0.164	0.007	0.003	0.008

Table 8. Data used in the phylogenetic analysis. The characters (1–21) and character states (A–E) are listed in Table 2 (Note:– *J. thaanumi* was omitted from the primary analysis).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Unordered char.(*)			*	*												*	*			*	
<i>Tatea</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
<i>Fluvidona</i>	B	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	?	A	A	A	A
<i>Fonscochlea</i>	B	A	B	B	A	C	A	C	B	A	A	A	A	A	B	D	B	B	A	A	A
<i>J. thaanumi</i>	B	B	B	A	?	C	A	B	A	A	D	B	B	A	A	A	A	A	A	A	A
<i>J. edgbastonensis</i>	B	B	B	A	A	C	A	B	B	A	D	B	B	B	A	A	A	A	A	B	A
<i>J. corrugata</i>	B	B	B	A	B	B	C	A	B	A	E	B	B	B	A	A	A	A	A	B	A
<i>J. coreena</i>	B	B	B	A	B	C	D	B	B	A	E	B	B	B	A	A	B	A	A	B	A
<i>J. pallida</i>	B	B	B	A	B	A	C	B	A	A	D	B	B	B	A	B	B	A	A	C	A
<i>J. colmani</i>	B	B	B	B	B	B	C	B	B	A	D	B	B	B	A	B	D	A	A	C	A
<i>J. jesswiseae</i>	B	B	B	A	B	B	B	B	A	A	C	B	B	B	A	A	A	A	A	A	A
<i>J. zeidlerorum</i>	B	B	B	A	B	B	D	B	A	B	D	B	B	A	A	B	A	A	A	A	A
<i>J. acuminata</i>	B	B	B	?	B	C	A	B	A	B	D	B	B	A	A	B	A	A	B	A	A
<i>J. carnarvonensis</i>	B	B	B	A	B	C	D	A	B	A	C	B	B	B	A	A	A	A	B	A	B
<i>J. exigua</i>	B	B	B	A	B	C	B	B	B	A	C	B	B	A	?	?	A	A	B	A	B
<i>J. isolata</i>	B	B	B	A	A	A	A	B	A	A	B	B	A	A	A	C	C	A	A	A	A
<i>J. eulo</i>	B	B	B	A	A	C	A	B	B	A	B	B	A	A	A	C	C	A	A	A	A