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A revised familial classification for certain cirrhitoid genera (Teleostei, Percoidei Cirrhitoidea), with comments on the group's monophyly and taxonomic ranking

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CONTENTS

SYNOPSIS. Previous suprageneric classifications of cirrhitoid fishes were based mainly on superficial characters. Recent anatomical studies show that five morphologically distinct types of urohyal bone occur within the group, and that on this basis certain taxa have been misplaced at both the generic and familial levels. The monophyly of the cirrhitoid fishes, tacitly assumed by previous authors, is reviewed, and an hypothesis of their monophyly erected on the basis of several synapomorphic features. It is also proposed, on the basis of those synapomorphies, that the lineage be given subordinal rank within the Perciformes.

INTRODUCTION

During an investigation into the cranial and branchial muscles associated with feeding in certain cirrhitoid fishes from South African waters, it became apparent that five distinct morphotypes of urohyal occur within the group. Two very distinct types are found in genera currently classified as members of the Cheilodactylidae; of these two forms, one also occurs in genera referred to the family Latridae by Regan. Despite the passage of over 80 years since Regan's (1911) paper was published, it remains the most recent suprageneric classification of these fishes, which he arranged in five families, *viz* Cirrhitidae, Cheilodactylidae, Aplodactylidae, Chironemidae and Latridae, grouping them informally as the 'cirrhitiform percoids'.

Like its predecessor, namely Gill's more detailed paper of 1862, Regan's later analysis was based mainly on external features. Apart from some comments by Regan on cranial features, vertebral numbers and vertebral morphology, neither paper included any other anatomical information on these fishes.

Although Regan (1911) expressed some doubts about the familial status given by him to the five generic assemblages he recognised (suggesting that subfamilial rank could be more appropriate) he did not comment on Gill's (1862) earlier classfication which recognised four subfamilies within a single family, the Cirrhitoidae; indeed, and inexplicably, Regan (*op. cit.*) makes no reference at all to Gill's paper.

Gill's (*op.cit*) four subfamilies correspond, almost entirely, to Regan's families, except that Gill's Latridinae included two genera, *Nemadactylus* Richardson, 1839, and *Cheilodactylus* Lacépéde, 1803, which Regan incorporated in his family Cheilodactylidae; Gill's list of included taxa in his concept of the Latridinae also contained two genera not mentioned by Regan, despite their being recognised at that time and still being recognised today (*viz Latridopsis* Gill, 1862, and *Acantholatris* Gill, 1862).

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† Dr Greenwood died 3 March 1995.

The present contribution, it is hoped, will play some part in rewakening an interest in a phylogenetically based taxonomy of Regan's 'cirrhitiform percoids', and of their interrelationships within, or perhaps outside, the Percoidei. Regan (1911) gave no formal suprafamilial ranking to his 'cirrhitiforms', but in some recent classifications (Nelson, 1994) the group has been raised to a superfamily, the Cirrhitoidea. The use of the terms 'cirrhitoid' and 'cirrhitoids' in this paper is thus to be interpreted as a reference to the superfamily and not to the suborder suggested for these fishes on p. 9.

METHODS AND MATERIALS

Species of the percoid families Serranidae and Centropomidae served as outgroup representatives of basal members of the Percoidei. The condition and composition of the sternohyoideus muscles, and the morphology of the urohyal in these taxa were taken to represent the plesiomorphic percoid conditions.

Wherever possible, dry skeletal preparations and alizarin transparencies were examined, as were radiographs and dissections of preserved specimens.

STUDY MATERIAL. The symbols used in the following list are: D. Sternohyoid muscle dissected and the urohyal removed or examined *in situ*; X. Radiographed; S. Dry skeletal material examined; an asterisk following a binomen indicates that this name appears on the box housing the skeleton, and that its specific identity could not be checked on the basis of the characters preserved.

The familial grouping used in the list is that resulting from the conclusions reached in this paper, and thus differs in some respects from the classifications of Gill (1862) and Regan (1911), and in some cases that of later authors (see p. 5 relating to the species '*bergi*' and '*gayi*' previously placed in the genus *Cheilodactylus* and in the family Cheilodactylidae).

Institutional abbreviations are: BMNH, The Natural History Museum, London; DIFS, The Department of Ichthyology and Fisheries Science, Rhodes University, South Africa; RUSI, J.L.B. Smith Institute of Ichthyology, South Africa; SAM, South African Museum, Cape Town.

STUDY MATERIAL.

(i) Outgroups.

Centropomidae; Glaucosomatidae; Ambassidae: The osteological and other material listed in Greenwood (1976).

Serranidae: as above, together with *Epinephalus alexandrinus* BMNH 1867.2.1: 69–72; (D).

(ii) Cirrhitoid fishes.

Aplodactylidae: *Aplodactylus punctatus* * (type species of the genus): BMNH 1873.4.3: 157 (S).

A. lophodon: BMNH 1914.8.20: 214 (D).

Cheilodactylidae: *Cheilodactylus fasciatus* (type species of the genus): 3 specimens, DIFS unregistered (D).

C. fuscus: 1 specimen, DIFS unregistered (D).

C. pixi: 6 specimens, DIFS unregistered (D).

2 specimens, DIFS unregistered (S).

4 'paperfish' larvae, 44–50 mm standard length, RUSI 19842 (D).

1 'paperfish' larva, 44 mm standard length, RUSI 19842 (S).

C. zonatus: BMNH 1907.12.23: 238 (S).

Chirodactylus brachydactylus: 3 specimens, DIFS unregistered (D).

2 specimens, DIFS unregistered (S).

2 'paperfish' larvae, 33 & 38 mm standard length. RUSI, unregistered (D).

C. grandis: 1 'paperfish' larva, 57 mm standard length. RUSI 18404 (D).

*Dactylophora nigricans**: BMNH 1869.2.24:8 (S).

Chironemidae: *Chironemus marmoratus**: BMNH 1871.3.29: 28 (S).

Chironemus marmoratus: BMNH 1861.11.7: 6 (D).

Cirrhitidae: *Amblycirrhitus pinos:* 2 alizarin preparations *ex* BMNH 1976.7.14: 453–7 (S).

Amblycirrhitus pinos: BMNH 1984.7.16: 96 (D).

*Cirrhitus maculatus**: BMNH unregistered (S).

Cirrhitichthys oxycephalus: RUSI 11658; BMNH 1929.9.20: 8 (D).

Cirrhitichthys oxycephalus: BMNH 1908.3.23: 77–79 (X).

Cyprinocirrhites polyactis: RUSI 12339 (D).

Gymnocirrhites arcatus (type species of the genus):BMNH 1965.12.20: 10 (D).

*Gymnocirrhites arcatus**: BMNH unregistered, collected by Richardson (S).

Gymnocirrhites arcatus: BMNH 1865.3.2: 82–83 (X).

Oxycirrhites typus (type species of the genus): BMNH 1929.6.12: 2 (D).

Paracirrhites forsteri: BMNH 1852.9.13: 119 (S)

Paracirrhites forsteri: BMNH 1969.7.16: 28–32; one specimen(D).

Latridae: *Acantholatris bergi* BMNH 1936.18.26: 439 (D) & (X).

Acantholatris gayi: BMNH 1879.5.14: 278; 1890.2.26: 49 (D) & (X).

Acantholatris monodactylus (type species of the genus): BMNH 1960.1.8: 6–13; one (D), all (X).

Acantholatris monodactylus: BMNH unregistered, *ex* Gough Isl.; 2 specimens,both (S).

Acantholatris monodactylus: RUSI 33484; 33485; 33624 (D).

Latridopsis ciliaris (type species of the genus): BMNH 1872.7.1: 32 (S).

Latridopsis ciliaris: BMNH 1873.12.13: 55 (D) & (X).

Latris lineata: BMNH 1855.9.19: 124 (D).

Latris lineata: SAM 22623 (D).

Mendosoma lineatum (type species of the genus): BMNH 1960.1.8: 14–21; one (D), all (X).

Mendosoma lineatum: RUSI 33613; 33625 (D).

Nemadactylus macropterus: BMNH 1855.9.19: 314 (X).

Nemadactylus macropterus: BMNH 1872.7.1: 21 (D) & (X).

Urohyal morphology and the suprageneric classification of cirrhitoid fishes, particularly the genus *Acantholatris* and species currently referred to the genus *Nemadactylus*

Within the cirrhitoid fishes, five morphologically distinct types of urohyal can be recognised (Figs 1 & 2). Since each

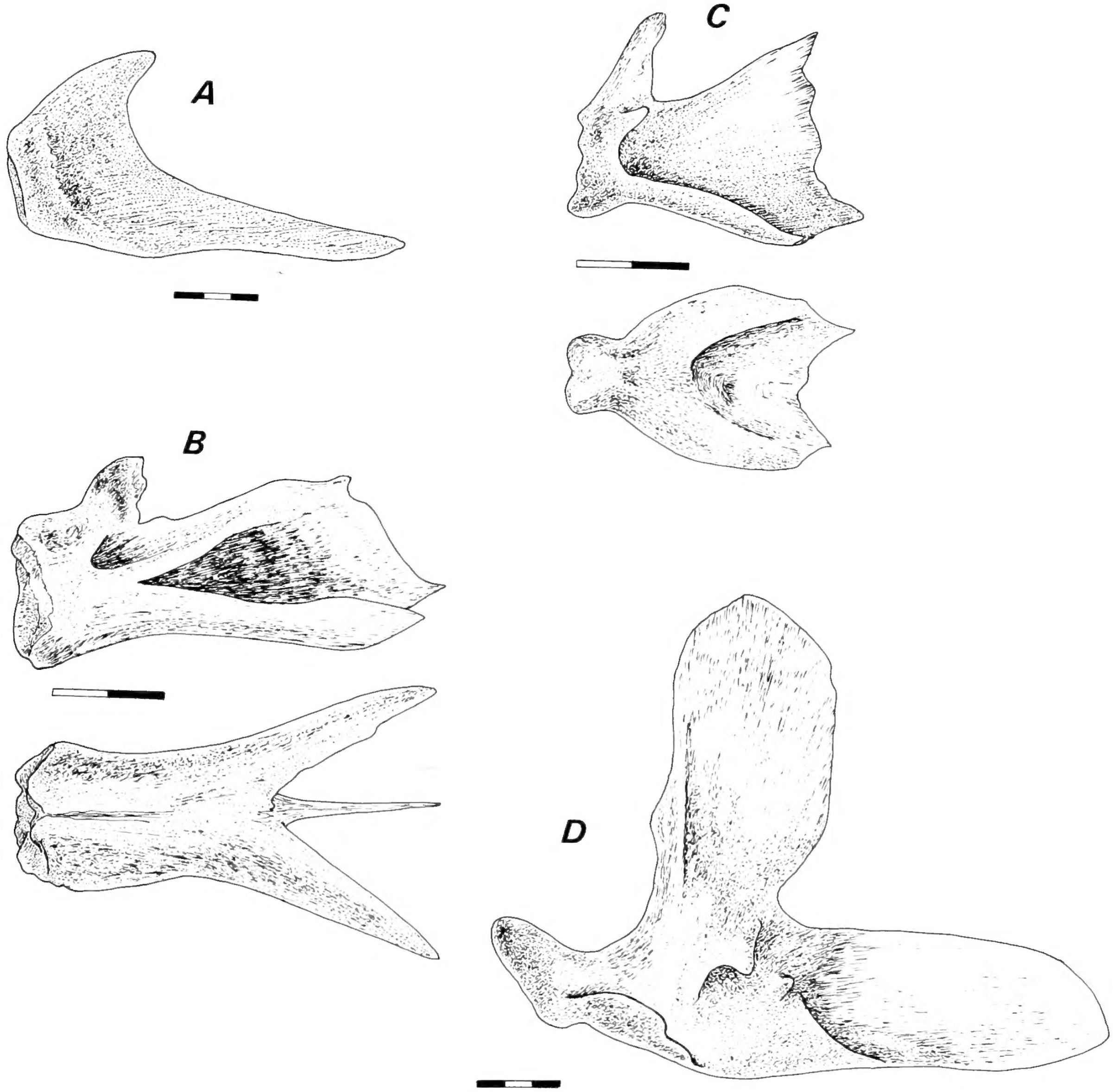

Fig. 1 The urohyal of: A. *Paracirrhites forsteri*; Cirrhitidae; left lateral view (BMNH 1852.9.13: 119). B. *Chironemus marmoratus*; Chironemidae; left lateral and ventral views. (BMNH 1871.3.29:28). C. *Aplodactylus punctatus*; Aplodactylidae; left lateral and ventral views. (BMNH 1873.4.3: 157). D. *Dactylophora nigricans*; Cheilodactylidae; left lateral view. (BMNH 1869.2.24:8). Relative to other figures, this bone has been rotated through 90° to the left; arrow indicates dorsal prominence. Scale in millimetres. Drawn by Gordon Howes.

type can be correlated with one of the five family groups recognised by Regan (1911), these will be referred to as the cirrhitid, latrid, chironemid, aplodactylid and cheilodactylid types respectively.

The cirrhitid type (Fig. 1A) appears to be a plesiomorphic form, one fundamentally similar to that found in several basal percoids (see Kusaka, 1974; also personal observations).

The latrid urohyal (Fig. 2) differs markedly from the cirrhitid type, and also shows slightly more intrafamilial variation, particularly with regard to its posterior margin's degree of indentation, the extent to which the ventral margin is produced bilaterally into a narrow or broader shelf, the extent to which the bone is produced ventrally, and whether the bone's upper margin is sharp or somewhat flattened. Like the cirrhitid type, the latrid urohyal is also of a pleisomorphic form, one occurring in such basal percoids as the Serranidae and Centropomidae (Kusaka, 1974; Greenwood, 1976: 39, fig. 21, and other personal observations).

Departure from the basal percoid form of urohyal is most pronounced in the chironemid, aplodactylid and cheilodactylid types of bone. In chironemids (Fig. 1B) the bone is shallow, the ventral margin greatly flattened and expanded bilaterally to form a broad shelf, while the dorsal margin is also noticeably flattened and bilaterally produced into a shelf, albeit one relatively narrower than that on the ventral aspect of the bone; when compared with the urohyal in cirrhitids,

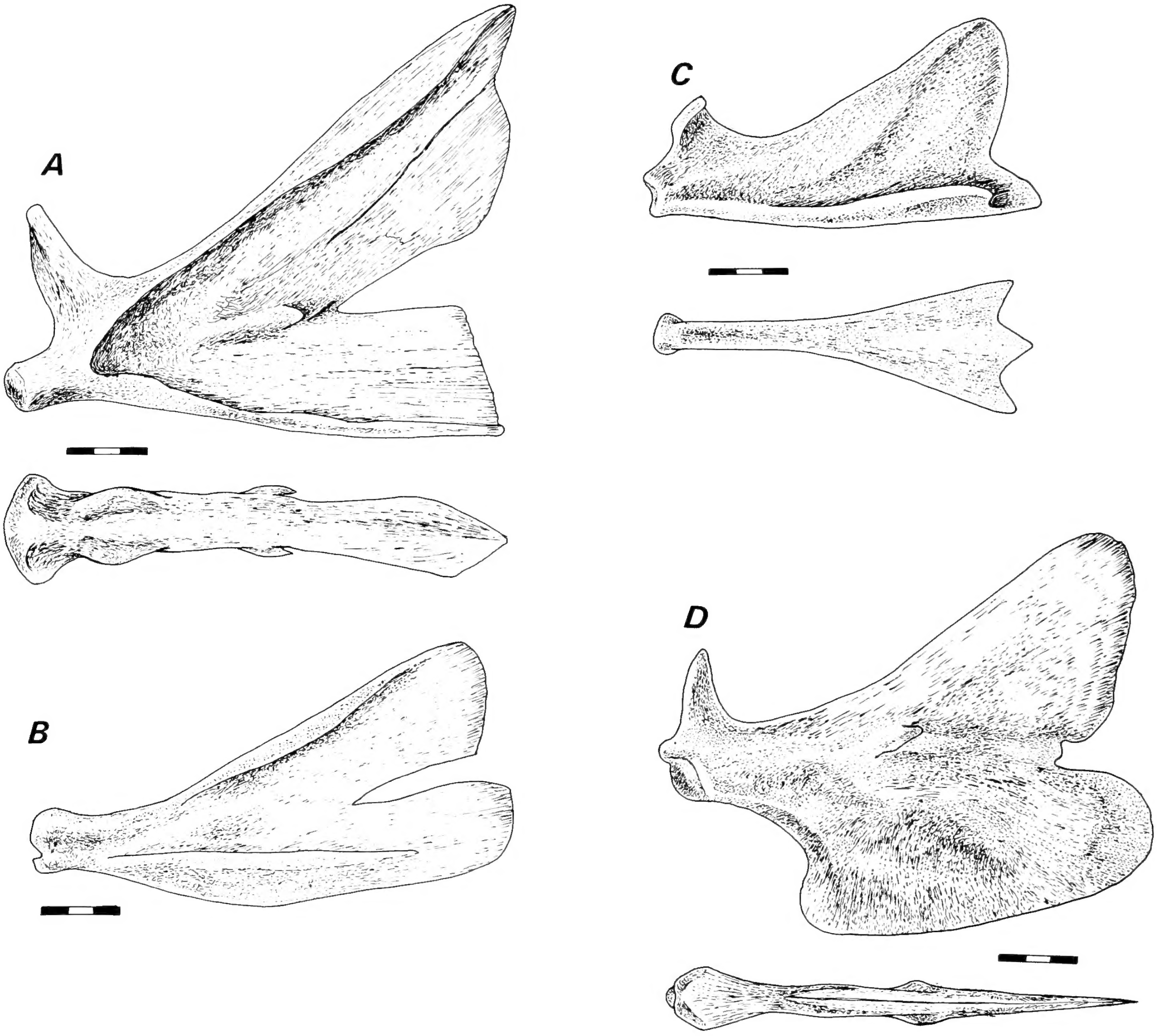

Fig. 2 The urohyal of four latrid species. A. *Acantholatris monodactylus* (BMNH unregistered; *ex* Gough Island); left lateral and ventral views. B. *Latris lineata* (BMNH 1855.9.19:194); left lateral view. C. *Mendosoma lineatum* (BMNH 1960.1.8:14-21); left lateral and ventral views. D. *Latridopsis ciliaris* (BMNH 1872.7.1:31); left lateral and ventral views. Scale in millimetres. Drawn by Gordon Howes.

the chironemid type is relatively foreshortened (cf Figs 1A & 1B).

A pronounced ventral shelf and overall foreshortening of the bone is also characteristic of the aplodactylid urohyal (Fig. 1C), but in this type the bone is relatively deeper than is the chironemid urohyal, and the dorsal surface is produced into only a narrow shelf.

When compared with all other types, the cheilodactylid urohyal (Fig. 1D) is very distinctive. In lateral view it has virtually the shape of an arrow-head with its tip directed anteriorly, and with the two arms meeting at the somewhat thickened apex from which a dorsally directed process arises. The anterior edges of both arms are slightly broadened to form a very narrow bilateral shelf that does not quite extend to the posterior tip of either arm. Although, morphogenetically, the cheilodactylid type of urohyal could be derived from a latrid type by a marked anterior extension and deepening of the latter's posterior indentation, coupled with an increase in the angle subtended by the two arms so formed, the two morphotypes are readily distinguishable. Interestingly, the urohyal in the so-called 'paperfish' juvenile stage (see p. 7) of a 44 mm standard length *Cheilodactylus pixi* Smith, 1980, resembles that of the latrid type more closely than does this bone in larger specimens; nevertheless, the upper and lower arms of the urohyal in the 'paperfish' stage are more widely separated, the division between them extends further anteriorly, and the anterior body of the bone is less compressed and more barrel-like than that in any of the adult latrid urohyals I have examined.

In his monograph on urohyal bones Kusaka (1974) described and illustrates this bone in *Goniistius zonatus* (Cuv., 1839), a taxon now, and previously (Gill, 1862), referred to the family Cheilodactylidae (see Allen & Heemstra, 1976, for comments on the status of this genus; also p. 6 below). Kusaka, however, lists the species under the heading Aplodactylidae. The bone depicted is certainly of the cheilodactylid type and not of the aplodactylid type, and I presume Kusaka's placing the species in the Aplodactylidae is a *lapsus*. This author (*op. cit*:) also figured and described the urohyal from a specimen supposedly of *Cirrhitichthys aureus* Temm. & Schl., 1843 (Cirrhitidae). Unfortunately I have not been able to examine a specimen of this species, but the bone illustrated (and described as 'shaped like a standing rat') is unlike that in any cirrhitoid taxon I have examined, particularly amongst members of the Cirrhitidae and even in a taxon such as *Oxychirrhites typus* Bleeker, 1857, whose elongate and tubular snout is an unusual morphotype within both the Cirrhitidae and the cirrhitoids as a whole. If Kusaka's figure and description are accurate and the specimen was correctly identified, then a sixth and highly distinctive form of urohyal, one far removed from that of other cirrhitids must be recognised, and the higher taxonomic position of its possessor or posessord be reconsidered (assuming, that is, the bone Kusaka examined was not teratological or damaged during preparation).

A typical cheilodactylid urohyal (Fig. 1D) occurs in all members of the family (*sensu* Regan [1911] and subsequent authors) I have examined apart from *Nemadactylus* and members of the genus *Acantholatris*, *viz* the type species *A. monodactylus* (Carmichael, 1818), and the species *A. gayi* (Kner, 1869) and *A. bergi* (Norman, 1937).

Parenthetically it should be noted that *A. gayi* and *A. bergi* were both placed in the genus *Cheilodactylus*, and the family Cheilodactylidae, by Norman (1937). The former species was later transferred by Fowler (1945) to the genus *Acantholatris*, with no explanation given for the change, but was retained in the family Cheilodactylidae. Neither author appears to have been aware, however, that Gill (1862) had included *Acantholatris* in his subfamily Latridinae. Mann (1954: 266) followed Fowler's generic and familial placing of *A. gayi*, and listed the species *bergi* under *Acantholatris* in the index to that publication. The reader is there referred to page 266 of the text. No mention is made of *A. bergi* on that page, but on page 85 (*op. cit.*) *Acantholatris bergi* Norman (the author's name not enclosed in brackets) is listed amongst the 'Invasores del Atlantico'. Mann (*op cit.*) is thus the first author to employ this particular combination of names for the species. As noted earlier (p. 1) Regan did not include *Acantholatris* in any of his cirrhitiform families.

The familial classification of *Acantholatris* Gill, 1982 and *Nemadactylus*

The urohyal in all three *Acantholatris* species examined, and in *Nemadactylus macropterus*, is virtually identical and differs markedly from that in the cheilodactylids, cirrhitids, aplodactylids and chironemids (see pp. 2–5 and *cf* Fig. 1 with Fig. 2A). Instead, it resembles the latrid type, both in detail and in its gross morphology (*cf* Figs. 2A, B and C), especially in its fan-like outline. This marked difference would suggest that the latrid genera (as listed in Regan, 1911), together with *Acantholatris* and *Nemadactylus* shared a recent common ancestry distinct from that of the cheilodactylids. It also suggests that the phyletic relationships of the two groups are obscured by uniting the cheilodactylids with the latrids in a single subfamily, as did Gill (1862).

Thus, in my view, based essentially on their urohyal morphology and not negated by other characters (see, however, the pectoral fin character discussed below), *Acantholatris* and *Nemadactylus* should be included in the family Latridae, currently comprising species of the genera *Latris, Latridopsis* and *Mendosoma*, the latter recently shown to be monotypic by Gon & Heemstra (1987). In addition to the urohyal characters, the genera listed above lack a suborbital shelf, which in cheilodactylids is a prominent feature formed from the posterior upper margin of the lachrymal bone and the entire upper margins of the second and third suborbitals. Also, unlike cheilodactylids, these genera have the basal scaly sheath to the soft dorsal fin somewhat higher and thus more prominent than that at the base of the spinous part of the fin.

As in cheilodactylids, the latrids (here taken to include *Acantholatris* and *Nemadactylus)* have 35 vertebrae (14 abdominal + 21 caudal elements including the urostylar element; data from radiographs and dry skeletons listed on p. 2). To judge from the dry skeletal and dissected material available to me, parapophyses are present on all precaudal centra in both families, and no ribs are sessile.

Possible lineages within the Latridae as now expanded to include the genera *Acantholatris* and *Nemadactylus*

Acantholatris and *Nemadactylus* differ noticeably from *Latris, Latridopsis* and *Mendosoma* in having one of the lower, unbranched pectoral rays (*i.e.* the fifth, sixth or seventh ray from the bottom of the series) greatly elongated, its tip, which extends beyond the fin's margin, reaching to at least the level of the anus and sometimes as far as the midpoint of the anal fin.

There are also differences in the following features:

(i) In scale size, as shown by lateral-line scale counts. In *Latris, Latridopsis* and *Mendosoma* these range from 112 to 120 in the two former taxa, and from 68–78 in *Mendosoma* (data from Last *et. al.*, 1983; Gon & Heemstra, 1987; pers.obs.). In *Nemadactylus macropterus* the count is 59 or 60, and in other species 47–68 (pers obs.; Last *et. al.*, 1983) and in *Acantholatris monodactylus*, *A. bergi* and *A. gayi* the range is from 50–60 (Norman, 1937; pers. obs.).

(ii) Anal fin length. In *Latris*, *Latridopsis* and *Mendosoma*, the number of branched anal rays ranges from 17–35 (the lowest counts occurring in *Mendosoma*, *viz*. 17–21, whereas in *Acantholatris* species and *Nemadactylus macropterus* the range is from 12–15, and other species of the genus, 16–19 (sources as above).

Pending a detailed generic revision of the various taxa involved, especially the several Australian and New Zealand species currently referred to the genus *Nemadactylus* it would be premature to formally recognise the two groups as, for instance, tribes or subfamilies of the Latridae, although phylogenetically some split seems to have occurred within the lineage.

The condition of the pectoral fin in the *Latris-Latridopsis-Mendosoma* group of latrids provides something of a puzzle since these taxa are the only cirrhitiforms not showing any marked elongation of the uppermost unbranched ray in the lower section of the pectoral fin, nor, as in most other cirrhitoids, do any of these rays clearly extend beyond the fin membrane, and none is markedly thickened. In having the lowermost 5–9 rays unbranched, these fishes are, however, typically cirrhitoid. This latter condition can be considered one of the synapomorphies uniting cirrhitoid fishes.

A typically derived pectoral fin configuration occurs in the Cirrhitidae, yet the family would appear to be the least derived of all cirrhitoid taxa (see p. 8). In contrast, except for the condition of the pectoral fin, members of the *Latris-Latridopsis-Mendosoma* assemblage within the Latridae share with *Acantholatris* and *Nemadactylus*, and with the cheilodactylids, aplodactylids and chironemids, the derived condition for all the osteological and myological features discussed on page 5. That being so, it is unlikely that the pectoral fin form in *Latris*, *Latridopsis* and *Mendosoma* can be interpreted as a true retention of the plesiomorph condition. If that was the case, then the derived condition must have evolved more than once within the cirrhitoids. A more parsimonious solution to the problem therefore, would, be to interpret the pectoral fin form in *Latris, Latridopsis* and *Mendosoma* as a secondary reversal to a seemingly more plesiomorphic condition than is found in any other cirrhitiforms, including the family with the greatest number of plesiomorphic features, the Cirrhitidae (see p. 8).

The geographical distribution of the two groups within the Latridae has an interesting pattern. Of the taxa in the long-finned assemblage, *Nemadactylus* (see p. 5) occurs only in Australia, Tasmania and New Zealand, thus overlapping the entire range of *Latridopsis* a member of the short-finned group and one restricted to that region; it overlaps in part (New Zealand and Tasmania) that of the widely distributed *Mendosoma lineatum*, also a member of the short-finned group, and in part, that of *Latris*, another member of the short-finned group (Australia; New Zealand; Gough and Tristan da Cunha islands; Vema Seamount; St Paul and Amsterdam islands). The other long-finned taxon, *Acantholatris*, does not occur in Australasia, but has a wide western distribution, including St Paul, Amsterdam, and Gough Islands, Tristan da Cunha, Vema Seamount Chile, Juan Fernandez and the western coast of South America from Rio de Janeiro southwards. This distribution thus widely overlaps that of the short-finned, monotypic genus *Mendosoma lineatum*, *viz* St Paul, Amsterdam and Gough islands, the coast of Chile and, as noted above, New Zealand and Tasmania (the latter being areas where *Acantholatris* does not occur); data from Norman, 1937; Fowler, 1945; Mann, 1954; Smith 1984; Last *et. al.*, 1983; Gon & Heemstra, 1987; Paulin *et. al.* 1989; Andrew & Hecht, 1992; Andrew, pers.comm., 1993).

TAXONOMIC AND PHYLOGENETIC CONCLUSIONS

Taxonomy

The material studied indicates, on osteological and myological grounds (p. 5), that the species currently named *Nemadactylus macropterus* (the type species of Gill's (1862) genus *Dactylopagrus*; see Wheeler, 1986) should be classified in the Latridae and not the Cheilodactylidae as it is at present.

The genus *Acantholatris* Gill (1862, type species *Chaetodon monodactylus* Carmichael, 1818), was overlooked by Regan (1911) in his synoptic review of cirrhitoid families, but is currently placed in the family Cheilodactylidae (see p. 5). However, on the basis of its urohyal morphology, and its lacking a suborbital shelf (see p. 5) the genus should be classified in the Latridae. Regan (1911) differentiated the Latridae from the Cheilodactylidae on the basis of the latrids having feeble, unbranched pectoral rays that are not produced beyond the fin's margin, and by their lacking a suborbital shelf; in other feaures he noted that the two families are similar. With the inclusion of *Acantholatris* and *Nemadactylus* in the Latridae the nature of the pectoral fin no longer serves as a differentiating feature (see p. 5), the principal diagnostic characters for the family now lying in the form of the urohyal bone, the absence of a suborbital shelf, and in the more prominent arrangement of the basal sheathing scales of the soft dorsal fin (see p. 5).

Gill's (1862) suprageneric classification included *Nemadactylus* as a division – Nematodactyli – of his subfamily Latridinae, in which subfamily but as another division to which he gave the name Latrides he also included *Latris, Latridopsis, Mendosoma, Acantholatris, Chirodactylus, Cheilodactylus* and *Goniistius*. Regan (1911) on the other hand, but without reference to Gill's paper, treated the latter author's four subfamilies as families, and recognised a fifth, the Cheilodactylidae, for two genera, *viz Cheilodactylus* and *Nemadactylus*; no mention is made in Regan's paper of the other taxa in Gill's Latridinae except for *Latris* and *Mendosoma*, which Regan retained in his family Latridae.

The evidence presented here (pp. 2–5), especially that based on urohyal morphology, would support Regan's (1911) classification with regard to the separation of *Cheilodactylus* (and, although not mentioned by Regan, *Chirodactylus* and *Goniistius*) from the other taxa included in Gill's Latridinae, and would support the inclusion of all three taxa in one family, the Cheilodactylidae. The same evidence would also support Gill's inclusion of *Latris, Latridopsis, Acantholatris, Mendosoma* and *Nemadactylus* in a single suprageneric taxon. Since Regan's (1911) familial ranking has been accepted and used since that time, and until contraindicative evidence is available to suggest otherwise, that ranking (i.e. Latridae) is retained.

The anatomical and other features used in this paper (pp. 2–5) would support the recognition of Gill's (1862) and Regan's (1911) other suprageneric lineages, again, for the reasons given above, as families and not subfamilies, *viz*. the Cirrhitidae, Aplodactylidae (Gill's Haplodactylinae) and Chironemidae.

At an intrafamilial taxonomic level, Allen & Heemstra (1976) note that 'The currently accepted classification of the Cheilodactylidae . . . is most unsatisfactory' a sentiment I would not only endorse, but would extend to other cirrhitiform families as well. In part this situation has resulted from the use of mainly superficial characters, with little or no attention paid to anatomical features, especially myological and osteological ones. Thus on those grounds I cannot agree with Allen & Heemstra's (*op.cit.*) treating *Acantholatris* as a subjective synonym of *Cheilodactylus* and its consequent placement in the Cheilodactylidae (see above, p. 5). However, at least on the characters and specimens I have examined, I would endorse their synonymy of Whitley's (1957) genus *Morwong* (type species *Cheilodactylus fuscus* Castelnau, 1879) with *Cheilodactylus*.

The cirrhitoids as a monophyletic lineage

On the basis of several apparently synapomorphic characteristics (see below) the cirrhitoids would seem to be a monophyletic lineage, a conclusion implied by both Gill (1862) and Regan (1911) who described the group as a 'natural' one but gave no reasons for that conclusion. The derived characters on which I would base an hypothesised monophyly of the cirrhitoids are, taken in conjunction, a reduced number (15) of principal caudal fin rays, the unbranched lowermost five to nine rays in the pectoral fin (usually with their tips produced beyond the fin membrane), the lower part of each cleithrum greatly expanded anteroposteriorly and meeting its antimere in a deep, carinate symphysis, an increased number of vertebrae relative to other percoids (26–35, comprising 10–16 abdominal and 15–21 caudal elements), and the presence, ventrally, in subadults of a peculiar, lipoid-filled sac (Fig. 3), free from the overlying hypaxial muscles, and extending from the urohyal, to which it is attached, to the anus, with the lipoidal material apparently contained in hexagonal compartments.

To the best of my knowledge, this lipoid sac has not previously been noted as a feature of subadult cirrhitoid fishes, nor indeed of any other perciforms except the stichaeid *Lumpenus maculatus* (see Falk-Petersen *et al.*, 1984). I first observed it in small specimens (the so-called 'paperfish' stage) of *Cheilodactylus pixi ca* 43 to 44 mm standard length (Fig. 3), where its presence results in the 'pouter-pigeon'-like ventral profile of the paperfish stage in this and other cirrhitoid species (see photographs in Whitley, 1957; Allen & Heemstra, 1976, and Nielsen, 1963). Subsequent dissections revealed a lipoid sac in members of all but two of the cirrhitoid families I have dissected (see p. 2). The exceptions are a chironemid, *Chironemus marmoratus* Günther, 1860 (160 mm standard length) and an aplodactylid, *Aplodactylus lophodon* Günther, 1859 (180 mm S.L.). Since, however, the sac is a juvenile (*i.e.* sub-adult) feature in the other taxa, and the exceptional specimens were, to judge from their gonadial development, young adults, I suspect that it would also be present in smaller specimens of these species. In *Cheilodactylus pixi*, for example, the sac is well-developed in a specimen of 44 mm standard length, but has disappeared in one of 46 mm. Likewise, in *Chirodactylus brachydactylus* (Cuv., 1830), it is present in a fish of 38 mm standard length, but absent in one of 42 mm. The presence of a lipoid sac in specimens from 128 to 243 mm standard length of other species (referred in the current literature to the Latridae and Cheilodactylidae) whose maximum adult lengths are from 50 cm to one metre, suggests that the size at which the lipoid sac disappears is positively correlated with that at which members of a species become adult. This supposition is borne out by the presence of the sac in a juvenile *Chirodactylus grandis* (Günther, 1860) of 57 mm standard length, a species whose adults reach a length of one metre, whereas it has disappeared, at a length of 42 mm, in young *Chirodactylus brachydactylus*, whose adults reach a length of 40 cm. Again, it is present in a specimen of *Acantholatris monodactylus* 243 mm S.L.; adults of this species attain a standard length of at least 65 cm. Thus, the sac's apparent absence in chironemids and aplodactylids could be artefactual, and related to the size-range of the specimens I was able to examine.

It is hoped to carry out a more detailed examination of the lipoid sac when specimens suitably fixed for detailed histo-

Fig. 3 *Chirodactylus pixi*, 49 mm standard length (RUSI 19842) in right lateral view; partially dissected, and with the greater part of the pectoral and the entire pelvic fin removed. The large anterior portion of the lipoid sac (LS) is clearly visible; part of its posterior portion is also visible (x). Throughout its length, the wall of the sac, unlike the muscles above it, is heavily peppered with melanophores.

logical and histochemical study are available.

Intragroup relationships within the cirrhitoids, and the ranking of the group

Within the cirrhitoids, the Cirrhitidae should be ranked as the most plesiomorphic taxon, a view seemingly implicit in Regan's (1911) diagram of relationships. My reasons for giving the family this ranking are based on urohyal form, the low vertebral count (26–28) relative to that in other families, the absence of parapophyses on the first three abdominal vertebrae, sessile ribs associated with these vertebrae, the presence of 3 predorsal bones (2 in the other cirrhitoids radiographed or dissected) and the presence of a suborbital shelf (which, however, is also developed in the Cheilodactylidae [but see below]). Furthermore, the Cirrhitidae are the only cirrhitoids with a basal percoid type of myotome arrangement in the sternohyoideus muscle, a feature not previously noted. That is, one in which the three pairs of hypaxial myomeres forming the sternohyoideus muscle are all arranged in a vertical series, with the first block covering the anterior part of the urohyal (Fig. 4A). Members of all other cirrhitoid families, in contrast, have the first (*i.e.* anterior) hypaxial myotome of each side displaced ventrally so that it now lies medially and horizontally (not, as in cirrhitids, laterally and vertically) to form, with its antimere, a ventral muscle, paired in most species but in some with the left and right parts fused over most of their lengths to form a single median muscle (Fig. 4B). Single or paired, this ventro-medial component of the sternohyoid runs from the urohyal tip to the prominent ventral projection at the symphysis of the left and right cleithra, its origin thus being immediately before that of the anterior infracarinalis muscle insertion.

In both the Cirrhitidae and in the other families, the sternohyoideus myotomes, except the horizontal first myotome in the latter group, are chevron-shaped with the apex directed anteriorly. However, in the latrids, cheilodactylids, chironemids and aplodactylids, the angle between the upper and lower arms of the chevron is more acute, and the lower arm is relatively longer than in cirrhitids.

Judging from the rather scant literature on the sternohyoid muscle in teleosts (see Winterbottom, 1974), and from a personal knowledge of the situation in percoids, the condition of the muscle in the Cirrhitidae should be ranked as plesiomorphic, that in the other cirrhitoid families as derived and possibly a unifying synapomorphy for the Aplodactylidae, Chironemidae, Latridae and Cheilodactylidae within the lineage.

In Regan's (1911) figure of cirrhitoid intrarelationships referred to above, the Cirrhitidae occupy a basal (*i.e.* stem position) and are linked, on the one hand to the Chironemidae and Aplodactylidae, and on the other to the Cheilodactylidae and Latridae (the generic composition of the families being those given by Regan). No reasons were provided by Regan for these supposed relationships, which presumably were based mainly on superficial characters as well as a few anatomical ones. With the anatomical information now available a different scheme of intragroup relationships at the family level can be proposed (see Fig. 5, and Table 1).

In this scheme, apomorphic features (see Table 1) are taken to be: (i) The derived form of urohyal, of which there are three distinct types (see p. 3). (ii) The presence of a

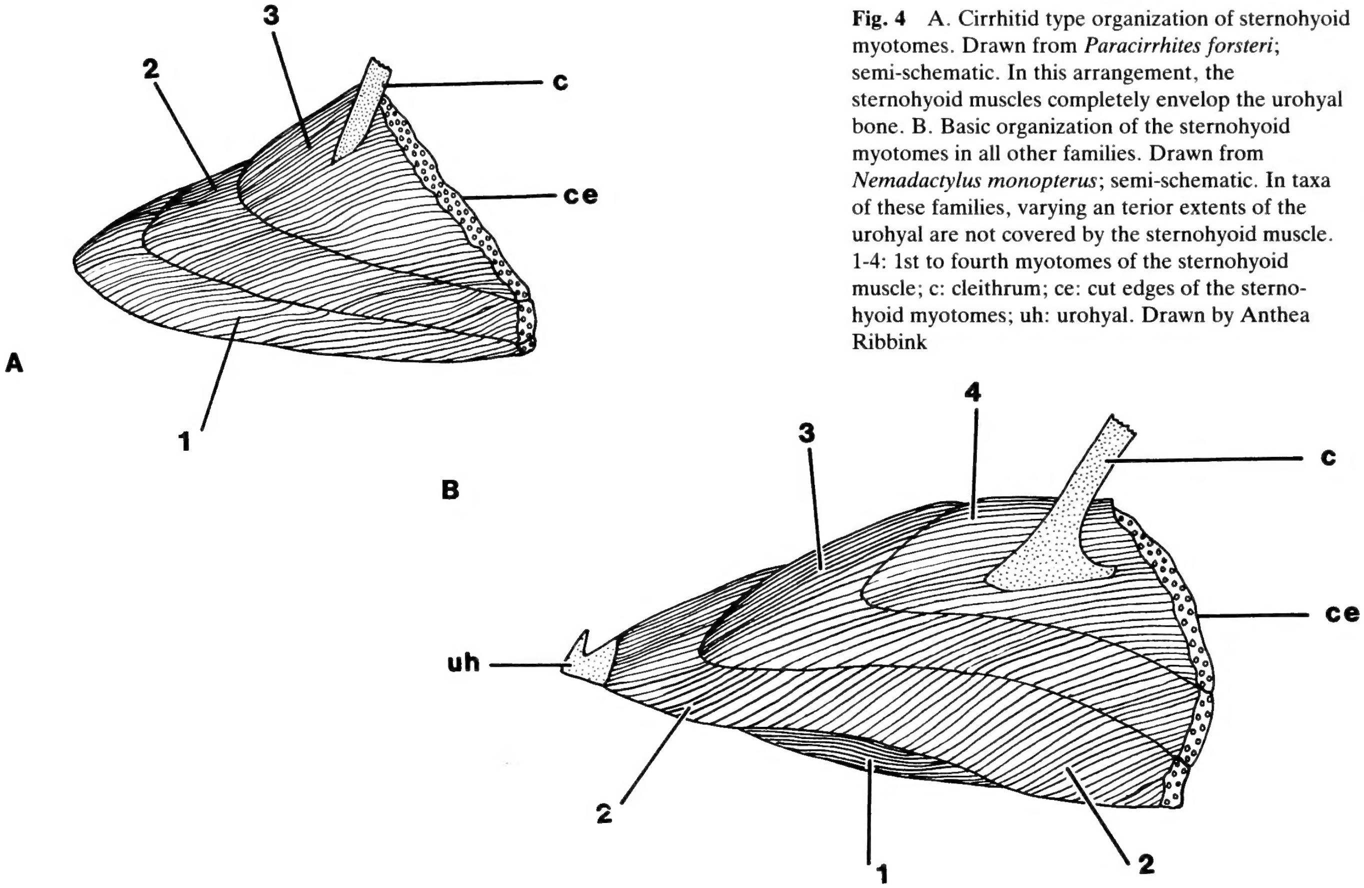

Fig. 4 A. Cirrhitid type organization of sternohyoid myotomes. Drawn from *Paracirrhites forsteri*; semi-schematic. In this arrangement, the sternohyoid muscles completely envelop the urohyal bone. B. Basic organization of the sternohyoid myotomes in all other families. Drawn from *Nemadactylus monopterus*; semi-schematic. In taxa of these families, varying an terior extents of the urohyal are not covered by the sternohyoid muscle. 1-4: 1st to fourth myotomes of the sternohyoid muscle; c: cleithrum; ce: cut edges of the sternohyoid myotomes; uh: urohyal. Drawn by Anthea Ribbink

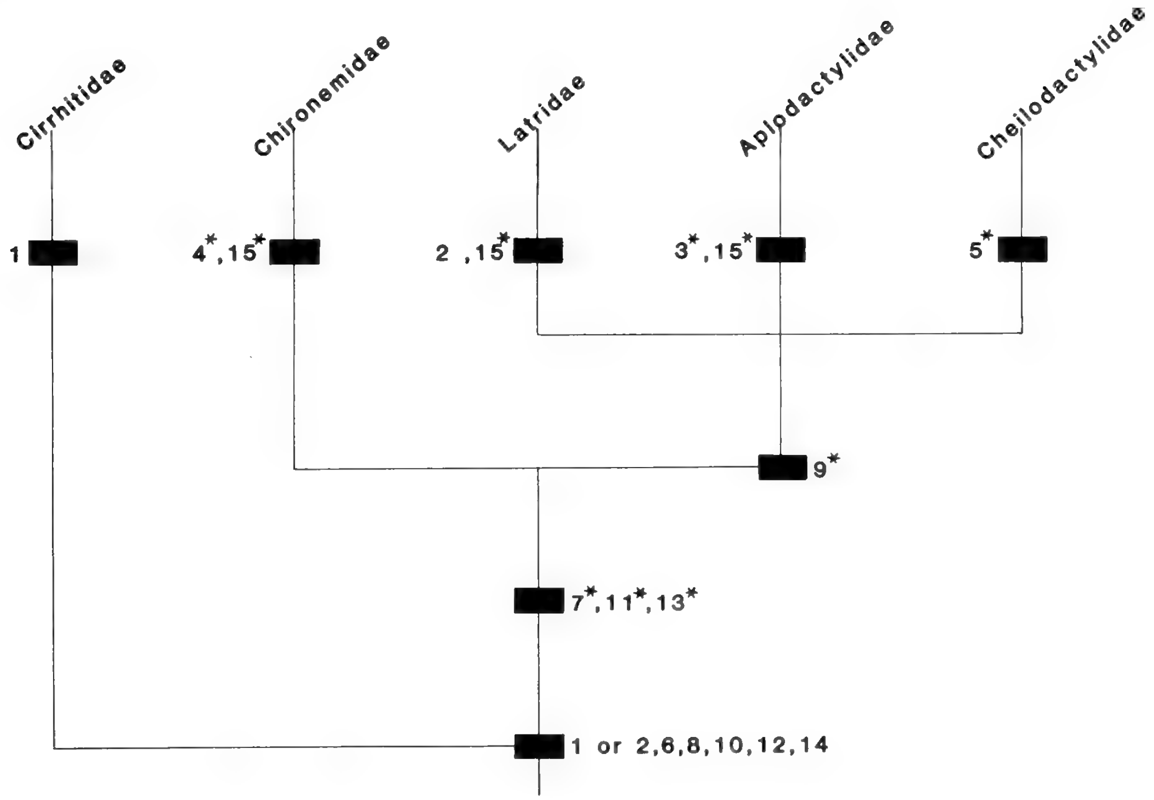

Fig. 5 Tentative scheme of phyletic relationships within the Cirrhitoidei. Asterisks indicate apomorphic characters (see also Table 1). Since both the cirrhilid (1) and latrid (2) condition of the urohyal are rated as pleisomorphic, that bone in the common ancestor of all lineages is taken to be 1 or 2.

derived myotomal arrangement of the sternohyoideus muscles (p. 8). (iii) More than 28 vertebrae. (iv) Parapophyses developed on the first three abdominal vertebrae, with the first pleural rib associated with the second or third vertebrae. (v) Predorsal bones reduced to 2. The three different types of derived urohyal morphology (pp. 2–5) (*ie* in chironemids, aplodactylids and cheilodactylids) are each taken to be independently evolved apomorphies. Relationships (Fig.) suggested by these data are: (i) That the cirrhitids are the plesiomorph sister group to the other four families combined. (ii) The chironemids are the sister taxon of the aplodactylids, latrids and cheilodactylids combined, and that for the moment this assemblage should be treated as an unresolved trichotomy since no two lineages uniquely share a recognisable synapomorphic feature. For example, the urohyal in the latrids is of a basal percoid type, and although that bone in the cheilodactylids and aplodactylids is highly derived, each is unique to the families respectively. The cheilodactylids it will be noted, retain the plesiomorphic suborbital shelf, whereas it is lost in the latrids and aplodactylids (and in the chironemid lineage as well). The value of this feature as an indicator of relationship, however, is problematical because it involves a loss (and not an acquisition) in the lineages concerned. Clearly, a greater number and variety of characters must be sampled and their polarity determined before this hypothesis of cirrhitoid intrarelationships can be improved and the trichotomy resolved.

The same reservation would apply before any sister-group hypothesis can be erected regarding the relationships of the cirrhitoids within the Percomorpha. However, based on the synapomorphic features discussed (above pp. 6–7) it seems reasonable to hypothesize that the five families comprising the lineage, given informal ranking as the 'cirrhitiform percoids' by Regan (1911), and suprafamilial status by recent authors (Nelson, 1994), should be elevated to subordinal status (Cirrhitoidei) within the Perciformes.

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To Dr Phil Heemstra of the J.L.B. Smith Institute goes my gratitude for the many discussions we have had about cirrhitoids, and for his advice on the relevant literature, and to Tony Booth of DIFS my appreciation for his painstaking preparation of several skeletons. Once again it is a great pleasure to thank my old colleague Gordon Howes for his elegant and accurate draftmanship, and also to thank another former colleague, Oliver Crimmen of the Fish Section, The Natural History Museum, London for his untiring help with matters radiographic and bibliographical. Yet again, my special thanks go to Huibre Tomlinson, for her patience and skills in producing the typescripts, and to Robin Stobbs for producing certain of the radiographs, and the photograph, used in this paper.

Table 1 Data matrix and characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Cirrhtidae															
Amblycirrhitus pinos	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Cirrhitus maculatus	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Cirrhitichthys oxycephalus	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Cyprinocirrhites polyactus	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Gymnocirrhites arcatus	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Oxycirrhites typus	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Paracirrhites forsteri	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
Chironemidae															
Chironemus marmoratus	0	0	0	+	0	0	+	+	0	0	+	0	+	0	+
Latridae															
Acantholatris bergi	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
A. gayi	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
A. monodactylus	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
Latridopsis ciliaris	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
Latris lineata	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
Mendosoma lineatum	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
Nemadactylus macropterus	0	+	0	0	0	0	+	0	+	0	+	0	0+		+
Aplodactylidae															
Aplodactylus punctatus	0	0	+	0	0	0	+	0	+	0	+	0	+	0	+
A. lophodon	0	0	+	0	0	0	+	0	+	0	+	0	+	0	+
Cheilodactylidae															
Cheilodactylus fasciatus	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
C. fuscus	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
C. pixi	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
C. zonatus	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
Chirodactylus brachydactylus	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
C. grandis	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
Dactylophora nigricans	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0

Characters: 1. Cirrhitid-type urohyal (*i.e.* of a basal percoid type, but one differing from the latrid condition); 2. Latrid-type urohyal (*i.e.* of basal percoid type; see 1); *3. Aplodactylid-type urohyal; *4. Chironemid-type urohyal; *5. Cheilodactylid-type urohyal; 6. Less than 28 vertebrae; *7. More than 28 vertebrae; 8. Parapophyses not developed on the first three (sometimes 4) abdominal vertebrae, but sessile pleural ribs on one or two of these centra; *9. Parapophyses developed on the first three abdominal vertebrae. No sessile pleural ribs; 1st pleural rib articulating with the parapophyses of the third abdominal vertebrae; 10. Three predorsal bones; *11. Two predorsal bones; 12. Basal percoid-type of sternohyoid muscle; *13. Derived condition of the sternohyoid muscle; 14. Suborbital shelf present; *15. Suborbital shelf absent. Asterisk indicates an apomorphic feature.

REFERENCES

Allen, G.R. & Heemstra, P.C. 1976. *Cheilodactylus rubrolabiatus*, a new species of Morwong (Pisces:Cheilodactylidae) from Western Australia, with a key to the Cheilodactylid fishes of Australia. *Records of the Western Australian Museum*, **4**(4): 311–325.

Andrew, T.G. & Hecht, T. 1992. Feeding biology of *Acantholatris monodactylus* (Pisces:Cheilodactylidae) at Tristan da Cunha and Gough Island, South Atlantic. *South African Journal of Antarctic Research*, **22**: 41–49.

Bloch, M.E. & Schneider, J.G. 1801. *Systema ichthyologia*. 584 p. Berolini.

Falk-Falk-Petersen, S., Falk-Petersen, I-B, & Sargent, J.R. 1986. Structure and function of an unusual lipid storage organ in the arctic fish *Lumpenus maculatus* Fries. *Sarsia*, **71**: 1–6.

Fowler, H.W. 1945. Fishes of Chile. Systematic catalog. *Apartado de la Revista de Historia Natural*, Anos XLV–XLVII: 1–171.

Gill, T.H. 1862. Synopsis of the family of cirrhitoids. *Proceedings of the Academy of Natural Sciences of Philadelphia* **14**: 102–124.

Gon, O. & Heemstra, P.C. 1987. *Mendosoma lineatum* Guichenot 1848, first record in the Atlantic Ocean, with a re-evaluation of the taxonomic status of other species of the genus Mendosoma (Pisces, Latridae). *Cybium* **11** (2): 183–193.

Greenwood, P.H. 1976. A review of the family Centropomidae (Pisces, Perciformes). *Bulletin of the British Museum (Natural History)* Zoology **29**: 1–81.

Kusaka, T. 1974. *The urohyal of fishes*. xiv + 320 p. University of Tokyo Press, Tokyo.

Last, P.R., Scott, E.O.G. & Talbot, F.H. 1983. *Fishes of Tasmania*, viii + 563 p. Tasmanian Fisheries Development Authority, Hobart.

Mann, G. 1954. *Vida de los Peces en aguas Chilenas*. 342 p. Ministero de Agricultura and Universidad de Chile, Santiago.

Nelson, J.S. (1994). *Fishes of the world;* 3nd edition. xvii+600 p. J. Wiley & Sons, New York.

Nielsen, J.G. 1963. On the development of *Cheilodactylus variegatus* Valenciennes, 1833 (Cheilodactylidae) *Copeia* **1963**(3): 528–533.

Norman, J.R. 1937. Coast fishes, part II. The Patagonian Region. *Discovery Reports*. **16**: 1–150.

Paulin, C., Stewart, A., Roberts, C. & McMillan, P. 1989. New Zealand fish, a complete guide. *National Museum of New Zealand, Miscellaneous Series.*, no. 19: xiv + 279.

Regan, C.T. 1911. On the cirrhitiform percoids. *Annals and Magazine of Natural History* (8)**7**: 259–262.

Smith, M.M. 1984. Cheilodactylidae. *In*: Fishcher, W. & Bianchi, G. (eds). *FAO identification sheets for fishery purposes, western Indian Ocean*. F.A.O. Rome.

Wheeler, A.C. 1986. Catalogue of the natural history drawings commissioned by Joseph Banks on the *Endeavour* voyage 1768–1771, held in the British Museum (Natural History). Part 3: Zoology. *Bulletin of the British Museum (Natural History)* Historical Series **13**: 1–172.

Whitley, G.P. (1957). Ichthyological illustrations. Proceedings of the Royal Zoological Society of New South Wales, **1955–56**: 56–71.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia* **125**: 225–317.

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Studies on the deep-sea Protobranchia (Bivalvia); the Subfamily Yoldiellinae

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CONTENTS

Synopsis. Four species of the genus *Portlandia* and twenty-nine species and five subspecies of the genus *Yoldiella* from the deep Atlantic are described – many for the first time. The subfamily Yoldiellinae includes more species than any other higher taxon of deep–sea protobranchs. The differences in morphology are for the most part subtle and there are many closely related species. These close relationships have been analysed, the analysis taking into account shell shape, hinge morphology, musculature and the extent and course taken by the hindgut. Taken together with geographical and depth distribution a pattern of evolution is derived. This supports the view that the derivation of the deep-water species of *Yoldiella* in the Atlantic has been derived mainly via downslope migration and speciation rather than by deep water migration from the Southern Ocean.

INTRODUCTION

This is the eighth paper in a series on the biology and ecology of the deep-sea protobranch bivalves of the Atlantic (Allen & Sanders, 1973, 1982; Allen & Hannah (1989); Rhind & Allen (1992); Sanders & Allen 1975, 1977, 1985. Our interest is widespread and includes, ecology and adaptations to life at great depths, morphology, reproduction, distribution and evolution. Here we turn to the subfamily Yoldiellinae and what has become our major and most difficult task of all our protobranch studies to date. Nowhere have the problems of elucidating evolutionary trends and specific and subspecific divisions within the Protobranchia been so acute as in this large group. Of necessity descriptive and taxonomic studies have played a major role in all our studies. This is because so many species from the deep oceans are new. Now that we have studied more than three quarters of the protobranch material in our collections, it has become obvious that major questions on the evolution of the subclass – particularly those taxa in the deep ocean – remain to be answered. We have described (Sanders & Allen, 1985) intra- and inter-population variations in various species and the difficulties in separating even higher taxa with satisfactory, clear cut, definitions (Allen & Hannah, 1986). These difficulties can be no better illustrated than in our studies on the Yoldiellinae. A considerable effort has been put into the analysis of the most subtle differences in shape and form of the many species of the subfamily. As a consequence we have decided to record our observations in two parts. In the first, here, we describe 36 species in a way that has become standard for this series of papers, describing those population variations that are pertinent to description and taxonomy. In the second, we will report in detail on diversity and the quantitative aspects of the ecology of sibling species which are distributed widely in many Basins of the Atlantic.

Species of the subfamily Yoldiellinae, are among the most common protobranchs of the deep sea and many are recorded in the literature. The difficulties we have experienced in accurately distinguishing the species is not new and confusion is apparent in both past and recent literature and in museum identifications of this group.

Descriptions of genera and higher taxa are based on the recent studies of Shileiko (1985) and Allen & Hannah (1986), but complemented from the results of this study. Holotypes have been lodged in either the Natural History Museum, London, or the Museum National d'histoire Naturelle, Paris. The paratypes, together with the remainder of the specimens collected, for the time being are in the care of JAA, but at the conclusion of the studies will be lodged in appropriate Museums.

Measurements of height, length, width and postumbonal length have been taken and in the case of larger samples ratios have been plotted. For species of which we have few specimens the measurements have been tabulated. While these record the variation in the major axes, they do not measure subtle variation in shell outline and curvature. Much time has been spent on computerized analysis of shell shape and on this work we hope to report later but, to date, this has not improved on visual recognition from comparative accurate drawings. We prefer drawings to photographs for their clarity.

In recognizing subspecies we comply with the ICZN. Subspecies occur at different depth ranges and/or different basins. In a few cases we recognize 'forms', infrasubspecific units which, in compliance with ICZN, cannot clearly be distinguished in their distribution patterns but which may indicate a species in the process of subspeciation.

ABBREVIATIONS TO TEXT FIGURES

AA	anterior adductor muscle
AN	anus
AS	anterior sense organ
BG	'byssal' gland
CG	cerebral ganglion
CS	combined siphon
DD	digestive duct
EG	digestive diverticula
DH	dorsal hood
ES	exhalent siphon
FA	feeding aperture
FM	pedal muscles
FT	foot
GC	gland cells
GD	duct of gland
GI	gill
GS	gastric shield
HG	hind gut
HT	heart
IF	inner muscular fold
IS	inhalent siphon
LI	ligament
ME	mantle edge
MT	major typhlosole
NV	nerve
OE	oesophagus
PA	posterior adductor muscle
PG	pedal ganglion
PL	palp
PM	pallial muscles
PP	palp proboscis
PR	pedal retractor muscle
PSA	posterior sorting area
RM	longitudinal muscle
SC	statocyst
SE	siphonal embayment
SF	sole of foot
SS	style sac
ST	stomach
SY	fold of sensory organ
TE	tentacle
TM	transverse muscle
TS	tooth of gastric shield
VG	visceral ganglion

Family Nuculanidae Adams & Adams 1858

Shell elongate, usually moderately compressed, may be rostrate, shell gape if present, restricted to short posterior margin where siphons protrude, concentric sculpture usually present which may be strongly incised, middle and inner shell layers non-nacrous; teeth chevron-shaped; ligament internal or external with resilium; combined siphons present, usually a simple siphonal tentacle attached to the left or right side of the siphonal embayment.

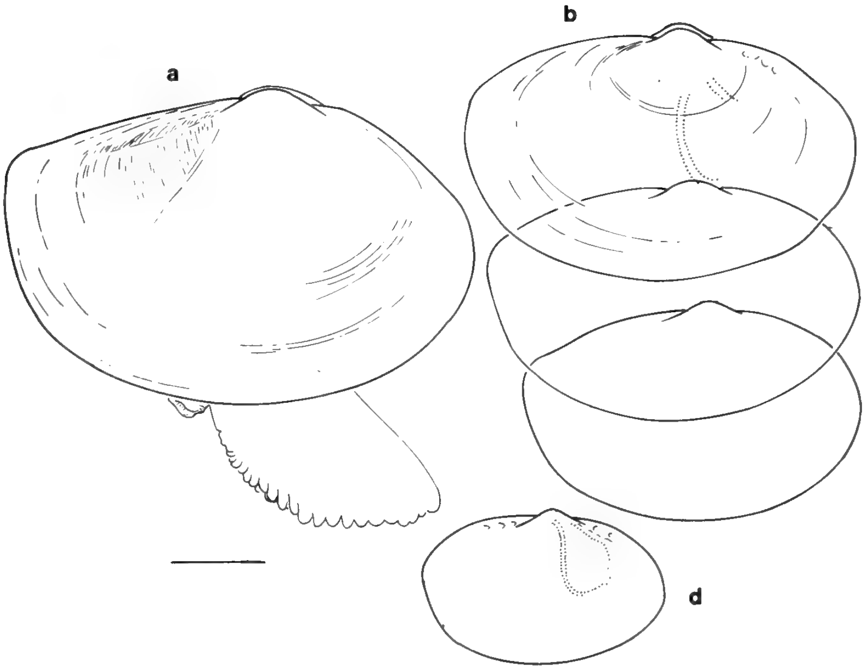

Fig. 1 *Yoldiella lucida*. Lateral views of shells of different size seen from the right side to show variation in shell outline. Collected by R.V. Dana 1922; a & b, 50°20'N 9°00'E, 350 m; c & d, 58°13'N, 9°34'E, 650 m. (Scale = 1.0 mm).

Subfamily Yoldiellinae Allen & Hannah 1986

Shell small, usually compressed, ovate or elongate subovate, occasionally with ill-defined rostrum, not gaping, smooth, or very fine concentric sculpture; ligament amphidetic, largely internal; combined siphons with various degrees of tissue fusion, siphonal embayment small; hind gut with various configurations.

Genus *Yoldiella* Verrill & Bush 1897

TYPE SPECIES. By original designation, *Yoldia lucida* Lovén, 1846.

Shell small, fragile, usually slender, subovate, usually glossy, no escutcheon or lunule, no carina, not gaping, occasionally fine concentric sculpture, postero-ventral margin may be slightly sinuate, postero-dorsal margin usually slightly convex, maybe posteriorly angulate; umbo usually anterior occasionally posterior or central; chevron-shaped hinge teeth may or may not extend beyond the inner limit of adductor muscles; no chondrophore; except for very small external componant, ligament internal and amphidetic, but may extend anteriorly and/or posteriorly to a small degree, hind-gut with various configurations, mostly deep-water species beyond shelf-slope break.

Note. A detailed account of an internal morphology is given under *Y. lata* (p. 34).

Yoldiella lucida (Lovén 1846)

TYPE LOCALITY. Hammerfest, northern Norway (desig. A. Warén, 1989).

TYPE SPECIMEN. Lectotype (desig. A. Warén, 1989), Swedish Museum of Natural History, No. 1533.

Yoldia lucida Lovén 1846, p.34.

Leda lucida Jeffreys 1869, p. 173. pl.100, Fig. 1; Jeffreys 1879, p. 578;Locard 1898, p. 351, 362.

Portlandia lucida Sars G.O. 1878, p.37. pl. 4, Figs. 8a, 8b; Norman 1893, p. 364; Posselt 1898, p. 36; Ockelmann 1958, 122, p. 29.

Yoldiella iris Verrill & Bush 1898, 20, p. 863–864, pl. 80. Fig. 1,2, pl. 82, Fig. 11; Type specimen U.S., Natl. Mus. 159722.

Yoldiella lucida Tebble 1966, p. 29, Fig. 156.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORWEGIAN BASIN							
Thor	273	610					
		350	50	58°20'0N	09°00'0E		
Dana	2896	60		58°13'0N	09°34'0E		
NORTH AMERICAN BASIN							
Chain 58	105	530	124	39°56'6N	71°03'6W	ET	5.5.66
Chain 88	207	805–	264	39°51'3W	70°54'3W	ES	21.2.69
		811	–	39°51'0W	70°56'4W		
WEST EUROPEAN BASIN							
Incal	DS03	609	2	57°57'0N	10°43'0W	CP	16.7.76
	DS04	619	1	57°58'0N	10°43'0W	CP	16.7.76

Museum material examined is listed in the text.

Specimens of *Yoldiella lucida* have most subtle differences in shape that taxed the descriptive powers of our predecessors and as they do ours. Jeffreys (1879) recognized three varieties (*lucida, declivis* and *truncata*) while Locard (1898), accepting the form figured by Sars (1878) as the type, recognized five varieties (*truncata* – the form figured by Jeffreys, *intermedia, minor, depressa,* and *ventricosa*).

Three thousand miles to the west, and in the same year as Locard, Verrill & Bush (1898) described what they thought to be *Y. lucida* from the North West Atlantic and two closely related north-east Atlantic species (*Yoldiella iris* and *Yoldiella inflata*).

We have examined material from the Zoological Museum, Copenhagen, specimens identified by Verrill & Bush, the Jeffreys collections in London and Washington and Scandinavian material from a variety of sources which includes specimens identified by Dr. Kurt Ockelmann in his study of Greenland material. To prevent even more confusion we accept as our baseline that specimens from Eastern Arctic and northern temperate shallow water populations of the east Atlantic adjacent to the type locality and which are described in the earliest accounts, as *Yoldiella lucida* s.s. We have also examined West Atlantic material some of which was misidentified and which we recognize as *Y. lucida* s.s. namely:-

MCZ No. 137266 labelled *Yoldiella inflata,* S. Block Island, 180– 190 m.
MCZ No. 227737 labelled *Yoldiella lucida* V & B, off Bradlees Bank, 120 m.
MCZ No. 159722 (unlabelled).
MCZ No. 202847 (which includes specimens from a number of Stations mixed together).
MCZ No. 78292 labelled Sta. 2697, off Halifax N.S., 377 m.
USNM No. 73172 labelled *Y. lucida*, 200 m.
USNM No. 202847 labelled Gulf of Maine. Mixture from several stations.

Specimens misidentified as *Y. iris* in the U.S. National Museum, but which are clearly *Y. lucida* s.s. :-

USNM No. 74517 labelled Gulf of Maine, 172 m.
USNM No. 159717 labelled Gulf of Maine, 40m.
USNM No. 159718 labelled Gulf of Maine, 134 m.

Samples of *Y. lucida* from the Skaggerak, loaned by the University Museum, Copenhagen, agree well with the figure of Sars (1878) and which Locard (1898) considered as the type (Fig. 1). These are also very similar to the shallow water, North American specimens referred to as *Y. lucida* and *Y. iris* by Verrill & Bush (1898). These latter specimens are very slightly more inflated but otherwise identical to the specimens taken from North American Basin Stations 105 and 207 (Figs. 4 & 7).

Thus, *Y. lucida* s.s. is found in Arctic and North Atlantic waters at shelf and upper slope depths, including the northern part of North America Basin, off Nova Scotia, Norwegian Sea, Greenland, Iceland, Skagerak and West European Basin. Depth range: 38–811 metres.

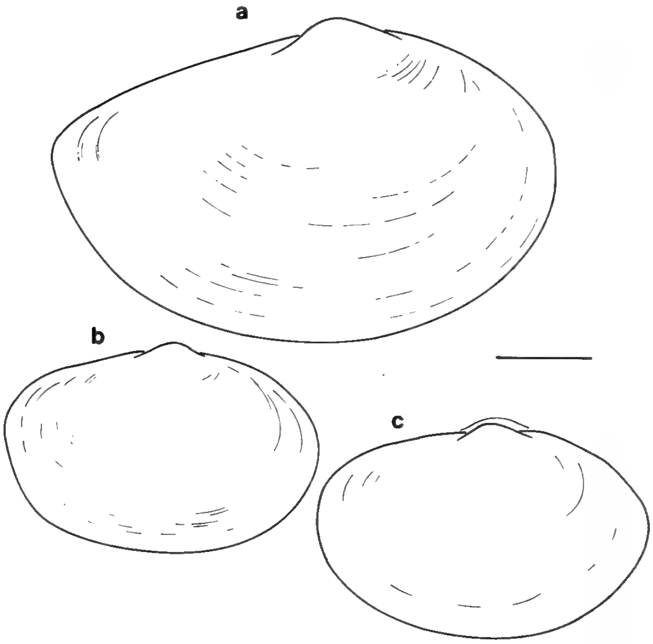

Fig. 2 *Yoldiella lucida*. Lateral views of shells from off the northeast coast of America; a, USNM No. 73172, 200 m; b, USNM No. 74517 labelled *Yoldiella iris*, Gulf of Maine, 172 m; c, USNM No. 159717 labelled *Yoldiella iris*, 40 m. (Scale = 1.0 mm).

SHELL DESCRIPTION (Figs. 1–4 & 15, Table 1). Shell elongate, ovate, moderately inflated, inequilateral, irregular concentric ridges, partially opaque, umbos moderately large, inwardly directed, proximal dorsal margin close to umbos depressed in many but not all specimens, antero-dorsal and postero-dorsal margins raised to form sharp, low, keel on either side of umbo, distally antero-dorsal margin extends in almost straight line to point opposite anterior limit of hinge plate then curves to the anterior margin, ventral margin long, even curve, distal postero-dorsal margin slopes in almost straight line, close to dorsal limit of posterior margin maybe slightly upturned, limit of posterior margin supramedial, slightly truncate, postero-ventral margin not sinuous, but may be slightly flattened; hinge plate moderately broad, except where narrow below umbo, anterior plate elongate extends opposite anterior margin of adductor muscle, posterior plate relatively short, does not reach posterior margin of posterior adductor muscle, hinge teeth chevron-shaped, moderately stout, maximum of 14 recorded in each series, occasionally anterior series has one more tooth than posterior; ligament amphidetic, moderately elongate, anterior and posterior lobes extend ventral to hinge plate.

The above description is of a fully grown animal. In smaller

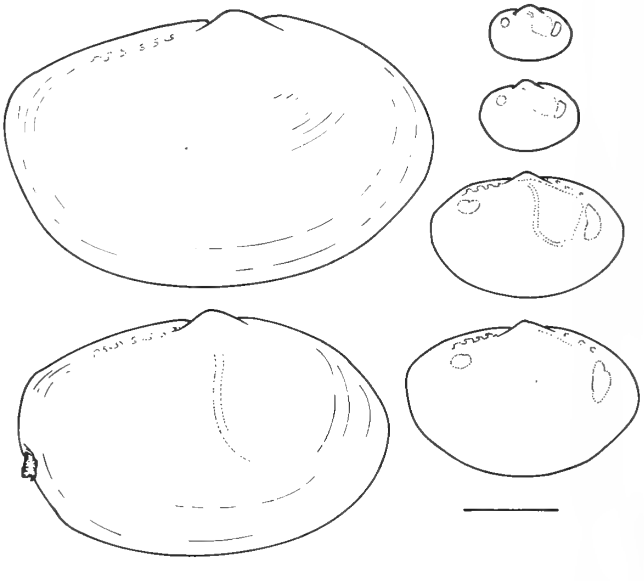

Fig. 3 *Yoldiella lucida*. Outline drawings of shells from the right side from Sta. 105 to show change in shape with increase in size. (Scale = 1.0 mm).

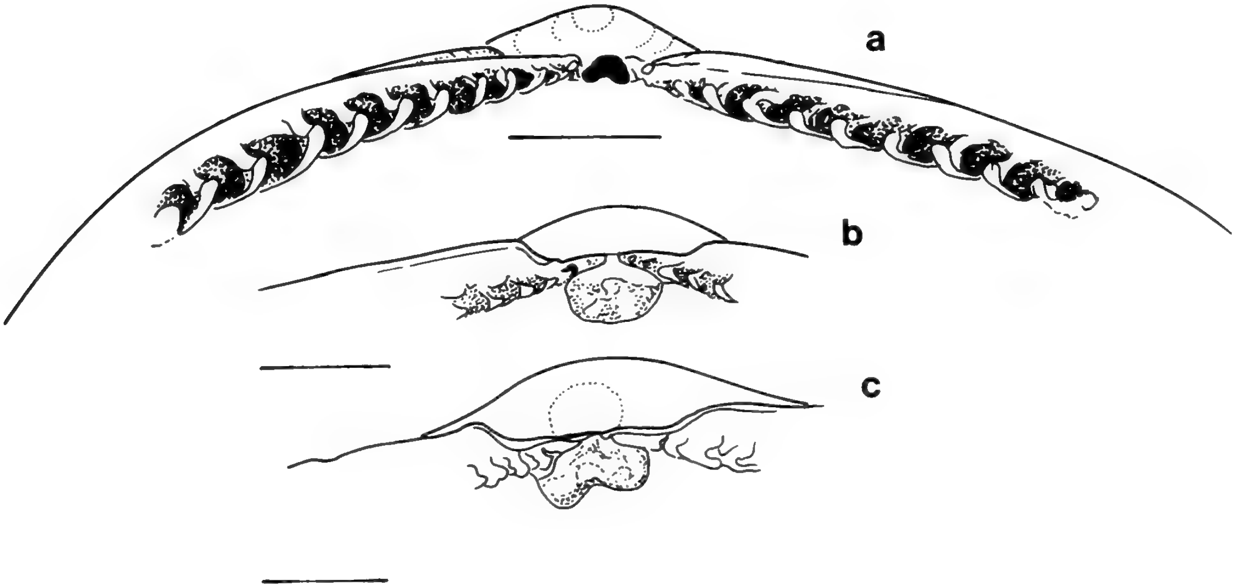

Fig. 4 *Yoldiella lucida*. Hinge plates of a, right valve of a specimen from Sta. 105 (North America Basin); b & c, right and left valve of specimens from 'Thor' Sta. 28 to show variation in the shape of the ligament. (Scales = 0.5 mm).

specimens the antero-dorsal margin is more convex, the postero-dorsal margin is normally angulate and the posterior margin more rounded (Fig. 4). As in many species of *Yoldiella* older specimens tend to become subrostrate.

Prodissoconch length: 198 μm. Maximum recorded shell length: 6.9 mm.

INTERNAL MORPHOLOGY. (Figs. 5 & 6) The mantle margin has a well-developed anterior sense organ. Posteriorly the siphons are combined, the inhalent siphon being open ventrally. A well-developed feeding aperture lies immediately ventral to the siphons with numerous gland cells present in what is a broadened region of the inner muscular lobe. A long siphonal tentacle originates usually on the left side of the siphonal embayment near the base of the siphon. The adductor muscles are large and unequal in size. The posterior muscle is oval in cross-section and between 1/2 and 1/3 the size of the anterior which is more circular in section.

The visceral and cerebral ganglia are relatively large, club-shaped, with an exceptionally thick connecting commissure. The pedal ganglia are also large but more round in outline, and each with a large statocyst dorsal to it. The foot is anteriorly directed with well-developed pedal retractor muscles. The byssal gland is moderate in size. The gills are well-developed with between 16–23 gill filaments, the number depending on the size of the individual. Posteriorly the gill axes attach to the junction between the two siphons. The labial palps are moderately large extending approximately a third across the body with between 13–23 palp ridges on the inner face. The palp proboscides are well-developed and are long and muscular. A wide ciliated oesophagus opens into a large stomach, the dorsal hood of which lies close to the dorsal margin of the body. There is a large style sac which penetrates the lower posterior half of the foot. The hind gut forms a single loop on the right side of the body. It has a typhlosole along its entire length. There are two digestive diverticula to the left and one on the right of the stomach. Material similar to that present in the stomach was observed in the left hand digestive diverticulum. The kidney is relatively small in comparison with *Yoldiella* species from deeper waters. The sexes are separate, and the gonads overlie the viscera dorsally and laterally. 203 ova were present in a specimen of 3.4 mm total length.

Yoldiella obesa obesa (Stimpson 1851)

TYPE LOCALITY. Original not known; Type locality here designated, St. Georges Bank, U.S. Fish Comm. Sta. 2072, 2.10.1883, 43°53′N, 65°35′W, Beam Trawl, 858 fms.

TYPE SPECIMEN. Holotype believed lost in Chicago fire. Neotype here selected, USNM No. 38419.

Leda obesa Stimpson 1851, p. 113; Stimpson 1851, p. 10, pt. II, Fig. 1; Tryon 1873, p. 184, pl. 38, Figs. 500, 501.

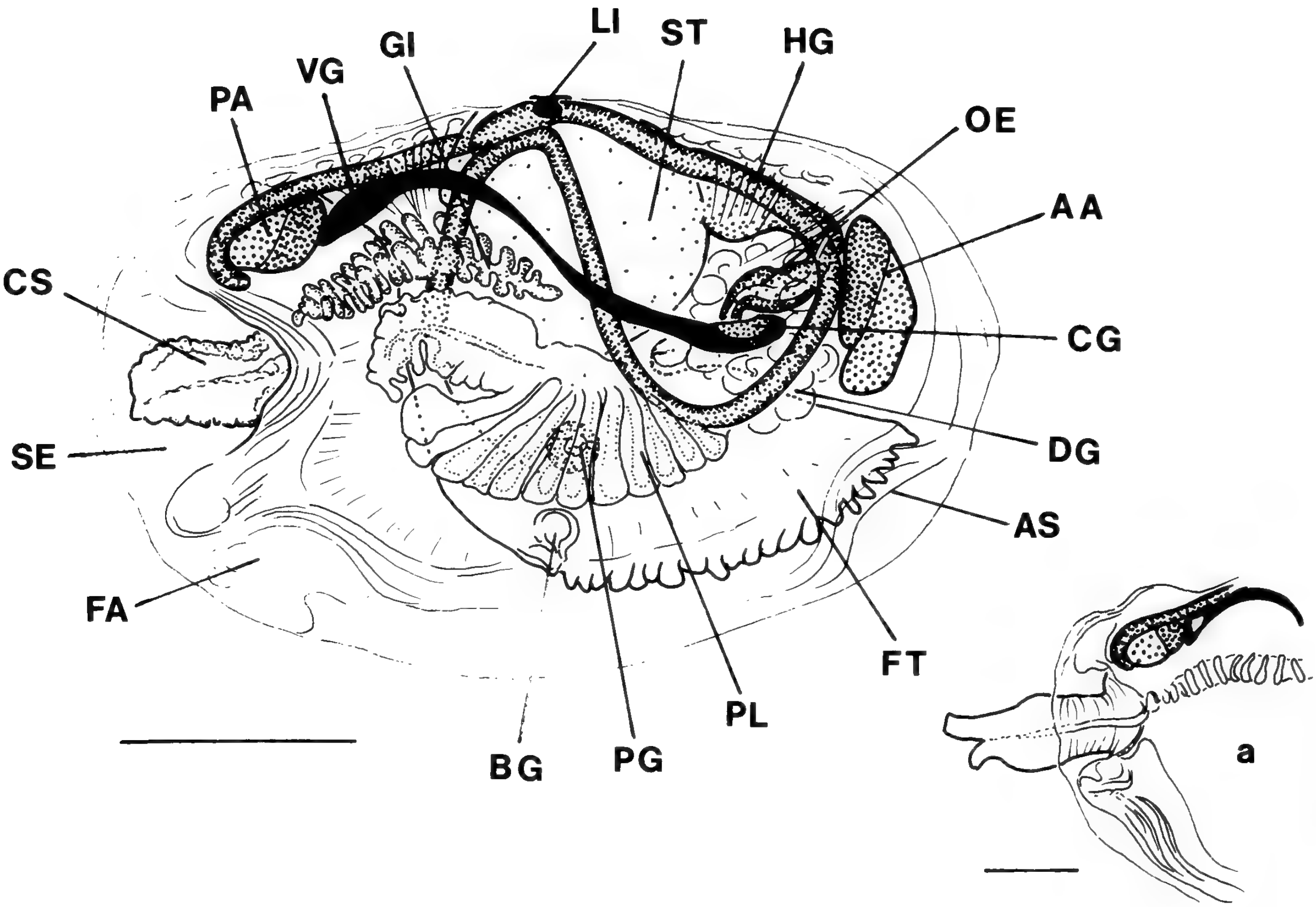

Fig. 5 *Yoldiella lucida*. Lateral view of the internal morphology from the right side with detail of the posterior part of the mantle cavity and the partially expanded siphon. (Scales = 0.5 mm).

Yoldia obesa Gould 1870, p. 155, Fig. 463; Verrill 1874, p. 46, p. 412, p.503; Smith & Harger 1874, p. 18, p. 23; Verrill 1874, p. 352, p. 368; Verrill 1874, p. 396.

Yoldia lucida Verrill 1881, pl. XLIV, Fig. 1; Verrill 1884, p. 279 (in part); Verrill 1885, p. 576 (in part); Bush 1893, p. 233.

Yoldiella lucida Verrill & Bush 1897, p. 55. Fig. 14; Verrill & Bush 1898, p. 861, 862, 863, pl. 77, Fig. 2, pl. 80, Fig. 3.

Yoldiella inflata Verrill & Bush 1897. p. 56. Figs. 3, 4. 11; Verrill & Bush 1898, p. 864, 865, pl. 80, Fig. 8, pl. 82, Fig. 5, 6.

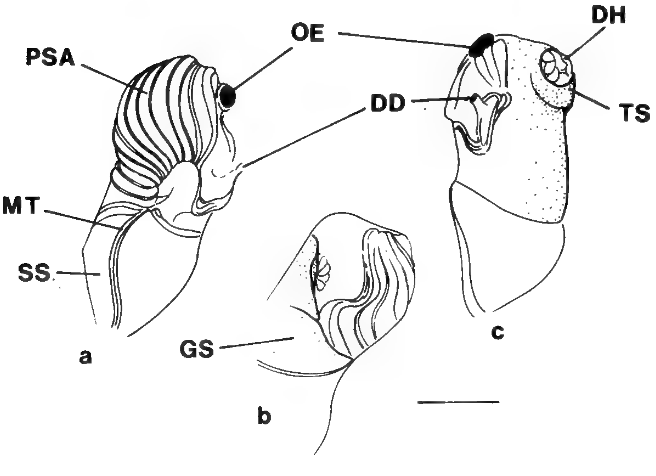

Fig. 6 *Yoldiella lucida*. External view of the stomach as seen from a, antero-frontal; b, right lateral; c, left lateral aspects. (Scale = 0.5 mm).

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICAN BASIN							
Atlantis II 12	62	2496	6	36°26.0′N	70°33.0′W	ET	21. 8.64
	64	2886	8	38°46.0′N	70°06.0′W	ES	21. 8.64
	72	2864	11	38°16.0′N	71°47.0′W	ES	24. 8.64
Chain 58	103	2033	28	39°43.6′N	70°37.4′W	ET	4. 5.66
Atlantis II 30	128	1254	11	39°46.5′N	70°45.2′W	ES	16.12.66
	131	2178	51	39°38.5′N – 39°39.0′N	70°36.5′W 70°37.0′W	ES	18.12.66
Chain88	210	2024– 2064	11	39°43.0′N – 39°43.2′N	70°46.0′W 70°49.5′W	ES	22/ 23. 2.69

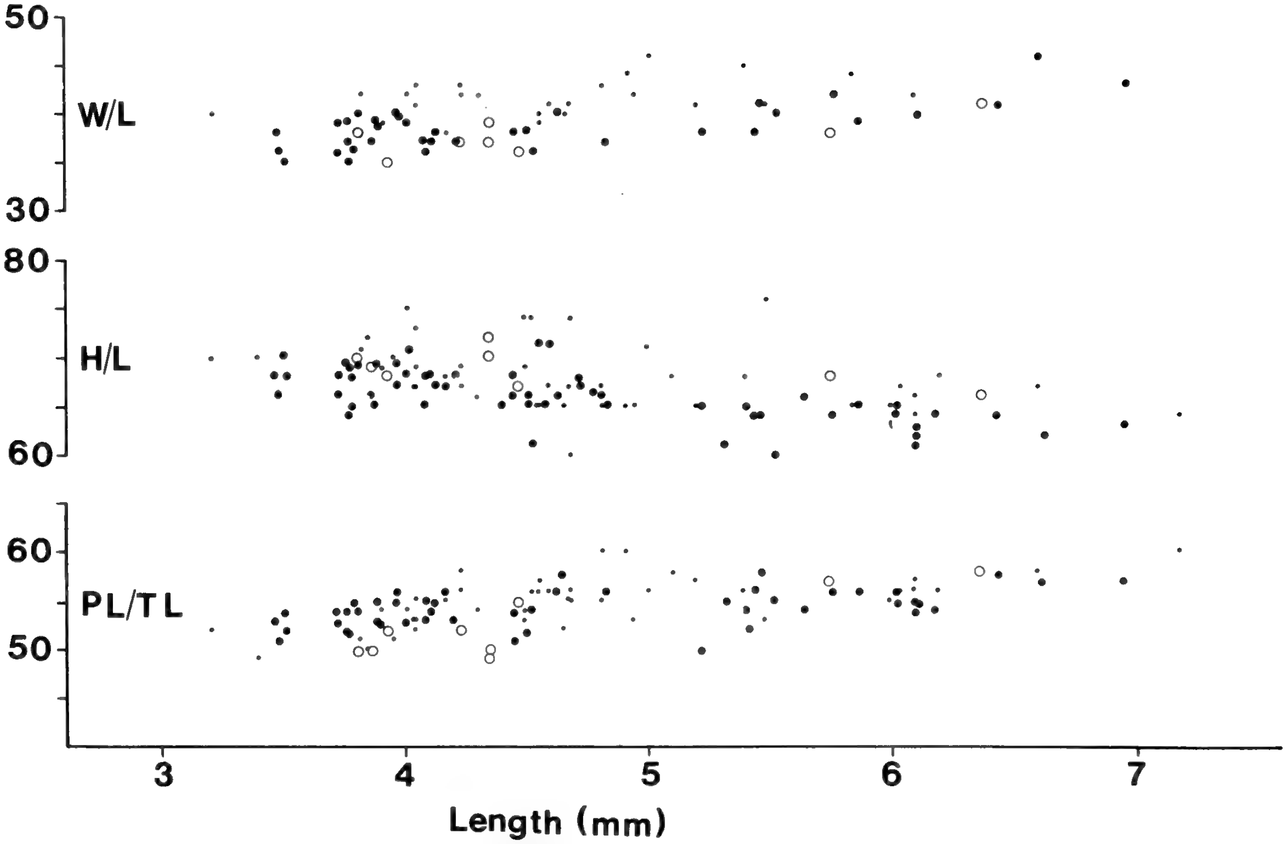

Fig. 7 *Yoldiella lucida*. Comparison of the shell proportions of three populations; small closed circles, Gulf of Maine USNM 202847; large closed circles, a subsample from 'Thor' Sta. 28; open circles, a subsample from Sta. 105. H/L height/length, PL/TL postero-umbonal length/total length, W/L width/length – all against length.

Also examined:

U.S. Fish Comm. USNM 73163 labelled *Y. lucida* (Lovén), Cisco Bay 1873 m; Station 2072 USNM 38419 labelled *Yoldiella inflata* (young), off Georges Bank 1569 m; USNM 35189 labelled *Yoldiella inflata* off Georges Bank 2360 m.

Restricted to the North American Basin at lower slope depths. Depth range 1254–2886 metres.

SHELL DESCRIPTION (Figs. 8–9 & 15). Shell moderately fragile, elongate, ovate, with fine concentric ridges, inequilateral; umbo moderately inflated, anterior, inwardly directed; dorsal margin in the region of the umbos in all but a few specimens, slightly concave, dorsal margins form sharp raised edge, antero-dorsal margin smooth curve joining anterior margin with no angulation, ventral margin smooth, relatively deep curve, postero-dorsal margin in large specimens almost straight, subangulate with posterior margin, extreme posterior limit of shell dorsal to horizontal midline; hinge plate moderately strong, parallel to margin, chevron-shaped teeth fairly stout, anterior and posterior hinge plates with same number of teeth, occasionally with one additional tooth on posterior plate; ligament amphidetic, circular in lateral view, extends ventral to hinge plate but without chondrophore, short anterior and posterior secondary external periostracal extensions.

Prodissoconch length: 215 μm. Maximum recorded shell length: 4.45 mm.

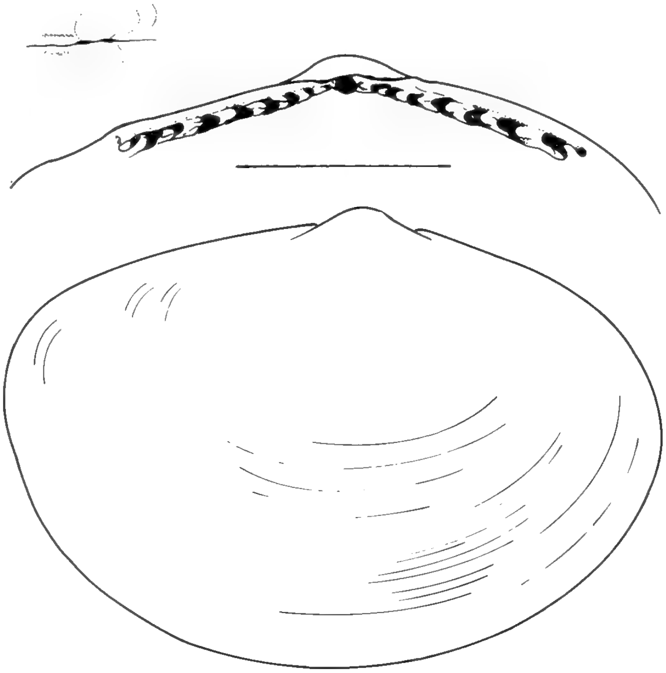

Fig. 8 *Yoldiella obesa obesa*. Neotype: USNM No. 38419. Lateral view of a right valve and a hinge plate of left valve, also a dorsal view of the umbos showing the outline of the prodissoconch. (Scale = 1.0 mm).

Table 1 *Yoldiella lucida*; numbers of anterior and posterior hinge teeth in specimens from different localities.

	Biscay			North Atlantic				'Thor' N. European		
	Length (mm)	Teeth Ant.	No. Post.	USNM. No.	Length (mm)	Teeth Ant.	No. Post	Length (mm)	Teeth Ant.	No. Post.
INCAL DS 02	2.28	6	6	738419	3.07	8	8	2.50	8	7
INCAL DS 01	2.42	7	7	159718	3.22	10	10	2.77	8	9
INCAL DS 01	2.75	7	7	74517	3.35	11	10	2.91	9	9
INCAL DS 01	2.95	8	8	202847	3.84	11	11	3.44	9	9
INCAL CP 01	3.24	9	9	202847	3.94	11	11	3.49	9	10
INCAL DS 01	3.28	8	8	202847	4.03	11	10	4.31	11	11
INCAL CP 01	3.49	8	8	202847	4.51	12	12	4.39	12	12
INCAL DS 02	3.57	9	9	202847	4.67	11	11	4.67	11	11
POLYGAS DS 26	3.61	11	11	73172	4.93	12	12	5.02	11	12
INCAL DS 01	3.77	10	10	202847	5.98	12	14	5.02	14	14
INCAL DS 01	4.31	10	10	202847	6.02	15	14	5.10	13	14
								5.10	11	12
								5.10	11	12
								5.10	13	13
								5.19	12	11
								5.61	13	13

Very similar to *Y. lucida* (for points of difference see p. 19), past records e.g. (Verrill & Bush, 1898; Warén, 1989) testify to this.

INTERNAL MORPHOLOGY (Fig. 10). The internal morphology is similar to that of *Y. lucida*. There is a well-developed ciliated anterior mantle sense organ. The inhalent and exhalent siphons are combined for most of their length, and the inhalent siphon is not fused along its ventral margin. The siphonal tentacle is well-developed and usually attached to the left of the base of the siphons. The feeding aperture is also well-developed and provided with numerous gland cells. The broad and, in preserved specimens, convoluted part of the inner muscular lobe which forms the feeding aperture, extends anteriorly beyond the limit of the aperture and is

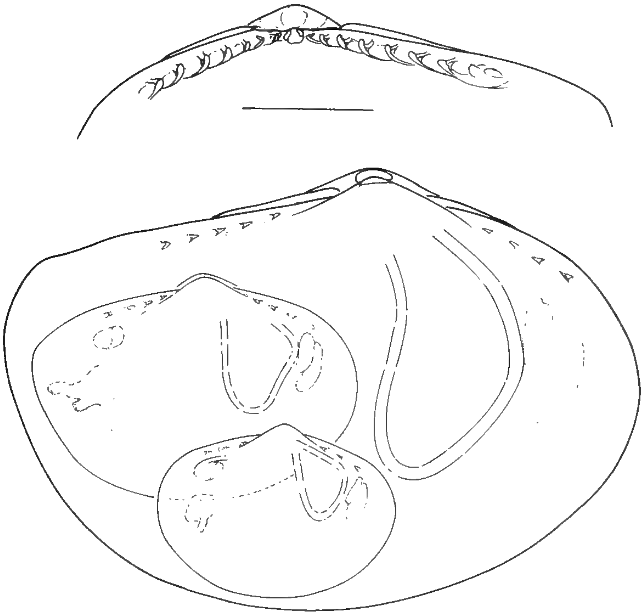

Fig. 9 *Yoldiella obesa obesa*. Lateral views of shells from the right side to show change in shape with increasing size and detail of hinge plate. Specimens from Sta. 62 North America Basin. Note adductor muscles and hind gut loop seen through the transparent shell. (Scale = 1.0 mm).

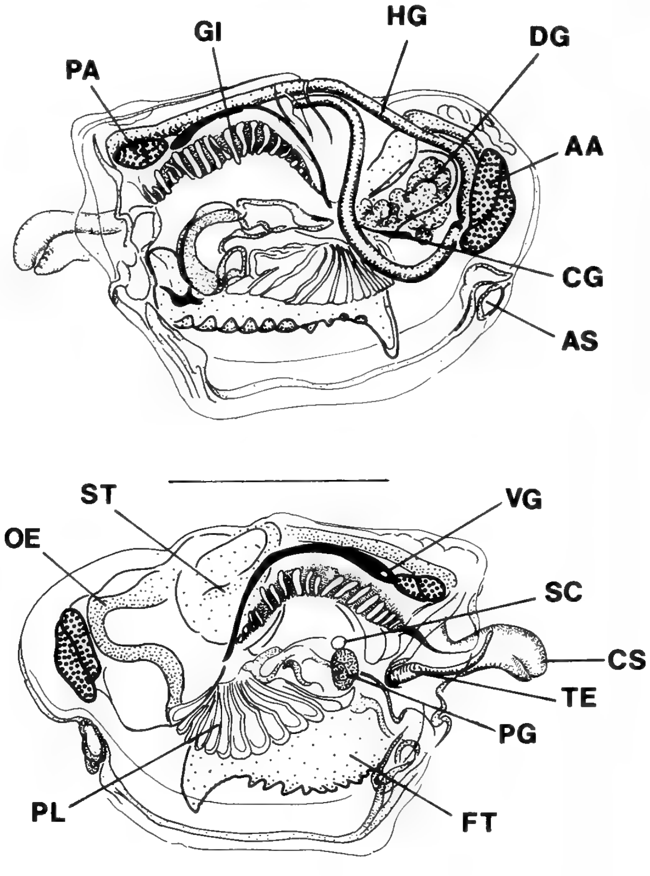

Fig. 10 *Yoldiella obesa obesa*. Lateral views of the internal morphology from right and left side. (Scale = 1.0 mm).

heavily ciliated throughout. The adductor muscles are relatively large and unequal in size. The posterior muscle is oval in outline and is approximately 1/2 to 1/3 the size of the anterior muscle.

The gills are well-developed with up to 16 gill filaments depending on the size of the individual. The number of ridges on the inner surface of the labial palp varies between 12–17. The palps extend over approximately half the body width and have long, moderately thick palp proboscides. The visceral and cerebral ganglia are elongate and each large pedal ganglia has a large statocyst dorsal to it. The foot is large and directed anteriorly, with well-developed retractor muscles. There is a moderately large byssal gland in the heel. The oesphagus is wide and opens into a voluminous stomach. The style sac penetrates into the lower portion of the foot. The hind gut forms a single loop on the right side of the body and has a typhlosole along its entire length. The digestive diverticula, as in other species, are situated one to the right and two to the left of the stomach. The ducts to the left hand diverticula enter the stomach close together, ventral to the gastric shield one posterior to the other. The kidney is small. Gonads overlie the lateral and dorsal sides of the viscera and the sexes are separate.

Y. obesa s.s. and *Y. lucida* differ as follows:- (1) The ventral margin of *Y. obesa* is slightly deeper and more rounded. (2) The anterior adductor of *Y. obesa* is relatively smaller when compared with a specimen of *Y. lucida* the same size. (3) The internal ligament of *Y. obesa* is smaller, shorter and more rounded. (4) The umbo is more anterior in *Y. obesa* and slightly larger and more prominent. (5) The posterior margin is more rostrate and tapered in *Y. obesa* and less truncate. (6) The posterior section of the loop of the hind gut is less curved and almost vertical in *Y. obesa*.

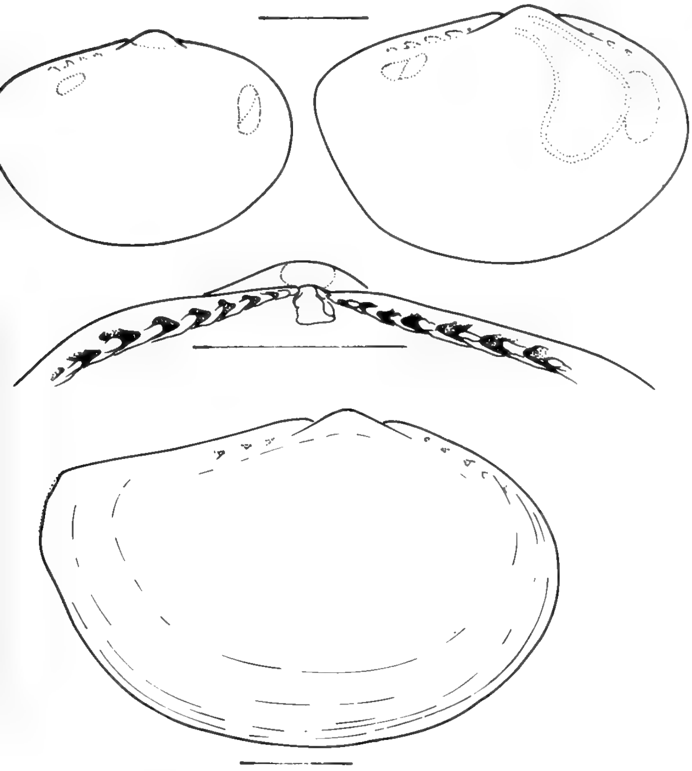

Fig. 11 *Yoldiella obesa incala*. Lateral view of shells from the right side to show change in shape with increasing size, and detail of the hinge plate of a right valve. Specimens from Incal Sta. DS02. (Scales = 1.0 mm).

Yoldiella obesa incala (new subspecies)

TYPE LOCALITY. R.V. Jean Charcot, Cruise INCAL, Sta. DS01, East of Rockall Island, 15.7.1976, 57°59′N, 10°40′W, Epibenthic Trawl, 2091 m.

TYPE SPECIMEN. Holotype: Museum National d'Histoire Naturelle, Paris, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Jean Charcot	DS25	2096	3	44°08.2′N	4°15.7′W	DS	1.11.71
(Polygas)	DS26	2076	3	44°08.2′N	4°15.0′W	DS	1.11.71
Jean Charcot (Biogas IV)	DS51	2430	1	44°11.3′N	4°15.4′W	DS	12. 2.74
(Biogas V)	CP07	2170	4	44°09.8′N	4°16.4′W	CP	21. 6.74
(Biogas VI)	DS80	4120	2	46°29.5′N	10°29.5′W	DS	27.10.74
	DS86	1950	7	44°04.8′N	4°18.7′W	DS	31.10.74
	DS87	1913	5	44°05.2′N	4°19.4′W	DS	1.11.74
(Incal)	DS01	2091	518	57°59.0′N	10°40.0′W	DS	15. 7.76
	DS02	2081	452	57°58.0′N	10°49.0′W	DS	16. 7.76
	CP01	2068–2040	35	57°57.0′N	10°43.0′W	CP	16. 7.76
	CP02	2091	3	57°58.0′N	10°43.0′W	CP	16. 7.76

Restricted to the West European Basin at lower slope depths. Depth range: 1913–2170 mm.

SHELL DESCRIPTION (Figs. 11 & 12). *Y. obesa incala* is similar to *Y. obesa* s.s. and requires little description other than to identify points of differences with the North American subspecies.

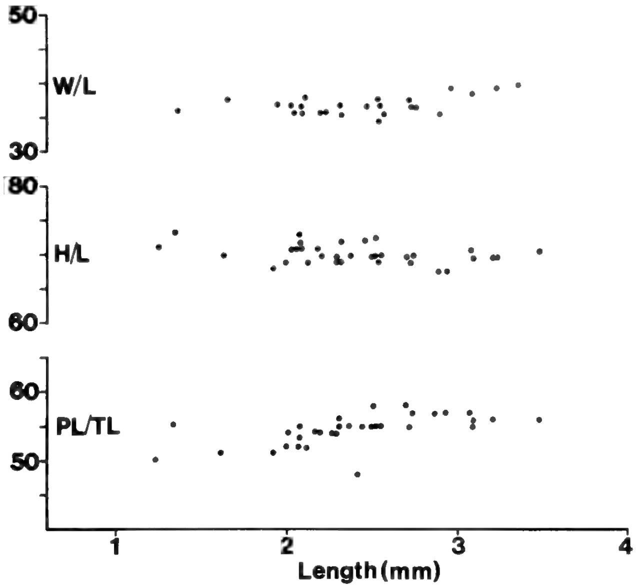

Fig. 12 *Yoldiella obesa incala*. Variation in the ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of a sample from Incal Sta. CP01 from the Bay of Biscay.

The subspecies has been long confused with *Y. lucida* s.s. (Warén, 1989) and there is little doubt that records of the latter species from deeper than 1000 m are of *Y. obesa incala*. In large specimens in particular, elongation and narrowing of the posterior margin together with a slightly upturned distal end of the postero-dorsal margin, resembles *Y. lucida*. A population from Rockall although similar in outline is relatively smaller and less inflated than the Biscay populations.

Prodissoconch length: 187–208 μm. Maximum recorded shell length: 4.8 mm.

INTERNAL MORPHOLOGY. Mantle structures are similar to those in *Y. obesa* s.s., for example the ventral margin of the inhalent siphon is open ventrally, however the feeding aperture is not particularly well-developed. The posterior adductor muscle is oval in shape and half the size of the crescent-shaped anterior muscle. There is a large stomach and style sac, and a single loop of the hind gut on the right side of the body. The byssus gland is moderately small. The palp proboscides are long and palp ridges number up to 21. The gills are well-developed with up to 17 plates present.

Points of distinction are as follows:- (1) The umbo in *Y. obesa incala* is slightly more medial than in *Y. obesa* s.s. (2) The posterior dorsal section of the hind gut loop takes a slightly more anterior course than in *Y. obesa* s.s. (3) The anterior adductor is relatively more ventral in position than in *Y. obesa* s.s. (4) Although the ligament is relatively short and, in many specimens rounded as it is in the North American subspecies, in some specimens the anterior and posterior ends are slightly swollen giving a 'dumb bell' appearance.

In a specimen 3.03 mm length, 281 ova were counted, with a maximum diameter 119 μm. In two specimens less mature, 240 and 387 ova were present in animals measuring 3.06 mm and 4.23 mm respectively.

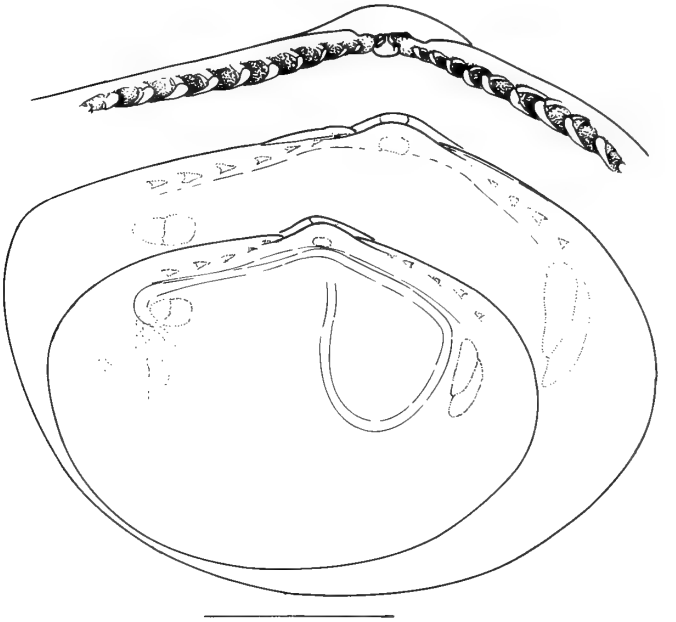

Fig. 13 *Yoldiella similirus*. Lateral views of shells from the right side and a hinge plate of a left valve. Specimens from Sta. 236 Argentine Basin. (Scale = 1.0 mm).

Yoldiella similiris (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 60. Sta. 236, Argentine Basin, 11.3.1971, 36°27.0'S, 53°31.0'W–36°28.1'S, 53°32.3'W, Epibenthic Trawl, 409–518 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992028. Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II 60	236	409–518	86	36°27.0'S – 36°28.1'S	53°31.0'W 53°32.3'W	ES	11.3.71
	237	993–1011	5	36°32.6'S	53°23.0'W	ES	11.3.71

Restricted to shallow slope depths in the Argentine Basin. Depth range: 497–1011 metres.

SHELL DESCRIPTION (Figs. 13, 15–17). Shell small, subovate, moderately inflated, smooth, fine irregular concentric lines, inequilateral; umbos small, anterior of midline, inwardly directed; antero-dorsal margin convex, curves evenly to anterior margin, ventral margin convexity increases slightly posteriorly, posterior margin obliquely subtruncate, postero-dorsal margin approximately straight, gently sloping, posteriorly forming a blunt angle, dorsal margins on either side of umbo form an acute edge; hinge plate well-developed, anterior slightly arched, posterior almost straight, 11 anterior and 12 posterior strong angular teeth in individual 3.75 mm long; ligament amphidetic, small secondary external periostracal extensions on either side of umbo, internal primary ligament moderately large, extends below hinge line.

Prodissoconch length: 198 μm. Maximum recorded shell length: 3.75 mm.

The shell and internal morphology of *Y. similiris* is very similar to that of *Y. lucida* s.s. The following differences are noted:- The umbo of *Y. similiris* is slightly more anterior, this

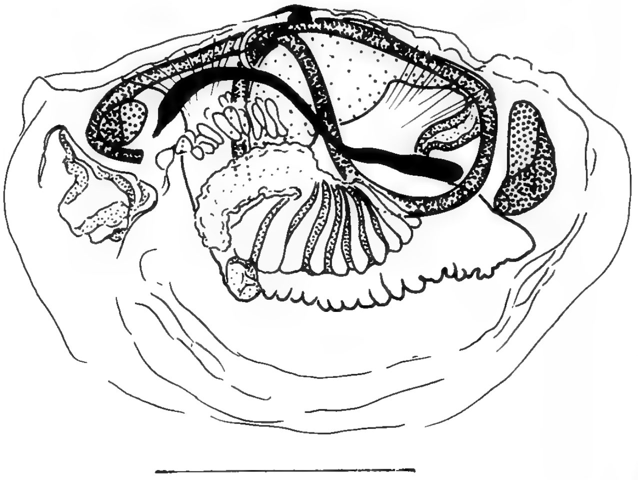

Fig. 14 *Yoldiella similiris*. Lateral view of internal morphology from the right side. (Scale = 1.0 mm). For identification of parts see Fig. 5.

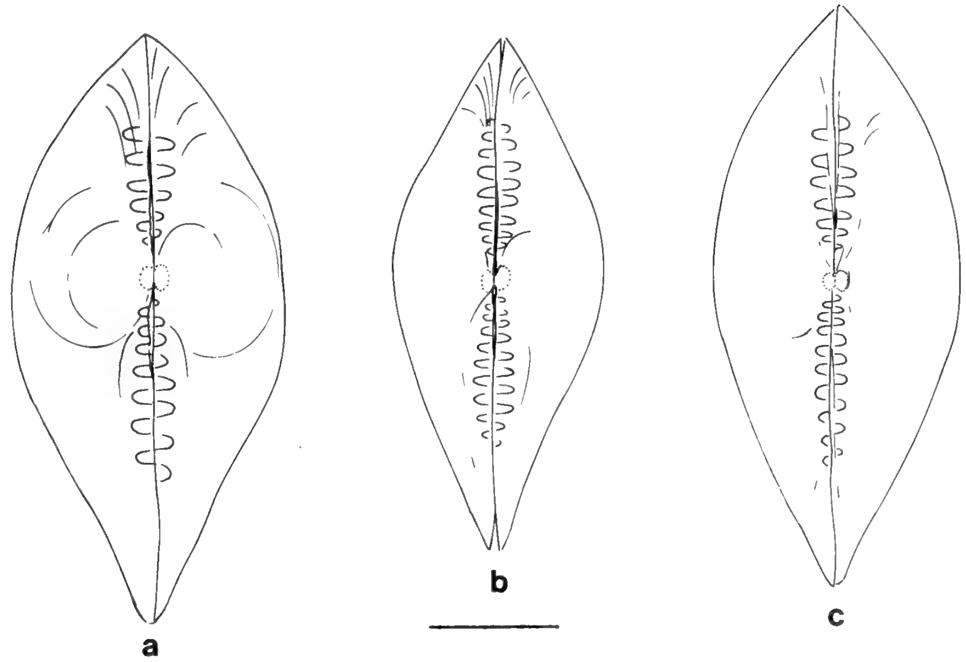

Fig. 15 *Yoldiella* spp. Dorsal views of shells of a, *Y. obesa obesa*; b, *Y. similiris* and c, *Y. lucida*. (Scale = 1.0 mm).

is particularly noticeable in the larger specimens. The height to length ratio is greater in *Y. similiris*.

INTERNAL MORPHOLOGY (Fig. 14). The internal morphology is very similar to that of *Y. lucida*. The adductor muscles are unequal in size, the posterior muscle is oval and approximately 1/3 the size of the anterior. There are a smaller number of gill filaments (maximum of 11 observed) and the labial palp ridges vary between 11–13. The stomach and style sac appear relatively smaller than those in *Y. lucida* and the hind gut, while making a single loop on the right side of the body, is not as deep as it is in the latter species. A maturing female (3.4 mm total length) had 203 ova with a maximum

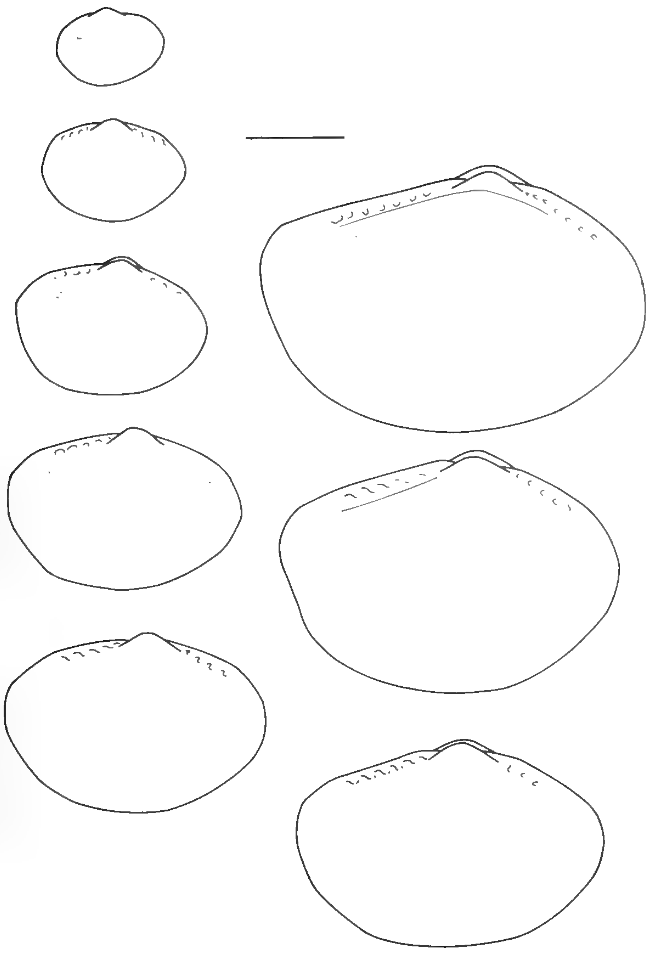

Fig. 16 *Yoldiella similiris*. Lateral views of a series of shells to show changes in shape with growth. Specimens from Sta. 236 Argentine Basin. (Scale = 1.0 mm).

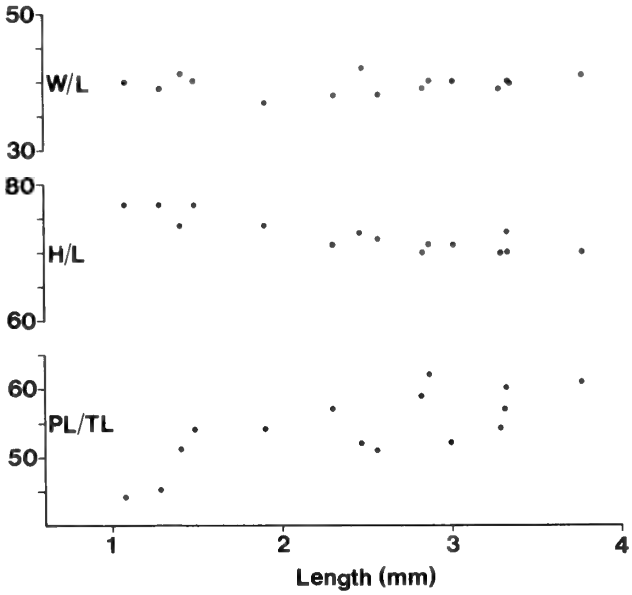

Fig. 17 *Yoldiella similiris*. Variation in the ratios of height H/L, width W/L and postero-umbonal length to length against length of a subsample from Sta. 236. Argentine Basin.

diameter of 83 μm (probably less than half their eventual maximum size).

Yoldiella hanna (new species)

TYPE LOCALITY. R.V. Atlantis II Cruise 42, Sta. 186, Cape Basin, 15.5.1968, 22°57′S, 13°05′E, Epibenthic Trawl, 439–481 m.

TYPE SPECIMEN. Holotype BM(NH) 1992022, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CAPE BASIN							
Atlantis II 42	186	439–481	21	22°57.0′S	13°05.0′E	ES	16.5.68
	188	619–622	7	23°00.0′S	12°58.0′E	ES	16.5.68

The species is restricted to the upper slope in the Cape Basin. Depth range: 439–622 metres.

SHELL DESCRIPTION (Fig. 18). Shell small, ovate, relatively inflated, inequilateral (posterior umbonal length 52–57% of the total length), sculpture, fine concentric lines at ventral margin, pale straw-coloured periostracum; umbos slightly raised, inwardly directed; dorsal margin slightly convex, antero-dorsal margin slopes gradually and smoothly to anterior margin, dorsal part of which more convex, ventral margin long, smooth, curve, postero-dorsal margin almost straight maybe slightly concave, slopes gently to blunt-angled supramedial posterior margin; hinge plate very strong, wide, except centrally under umbo; 10 strong chevron-shaped teeth on each side of ligament in largest specimen; ligament amphidetic, goblet-shaped, extends below margin of hinge plate.

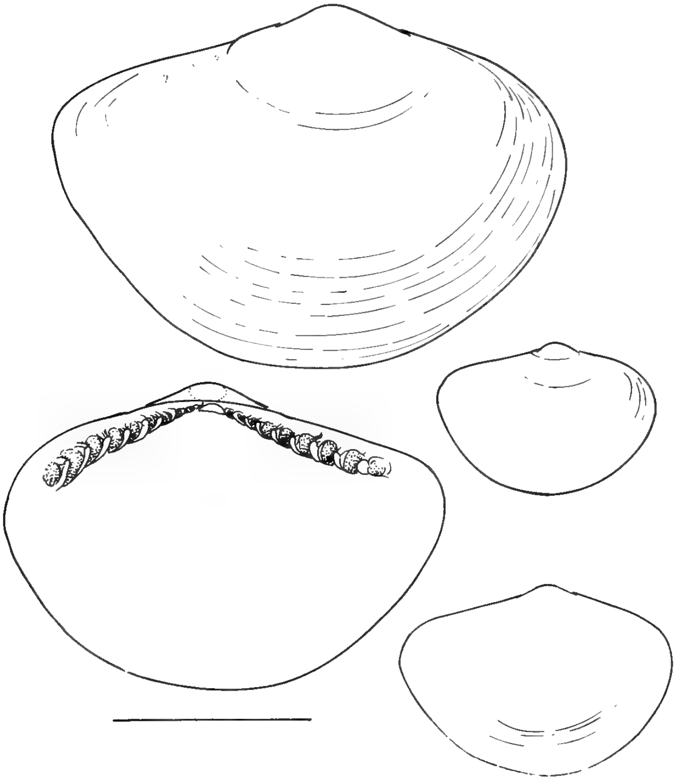

Fig. 18 *Yoldiella hanna*. Lateral views from the right side of three shells and an internal view of a right valve to show detail of the hinge plate. Specimens from Sta. 186 Cape Basin. (Scale = 1.0 mm).

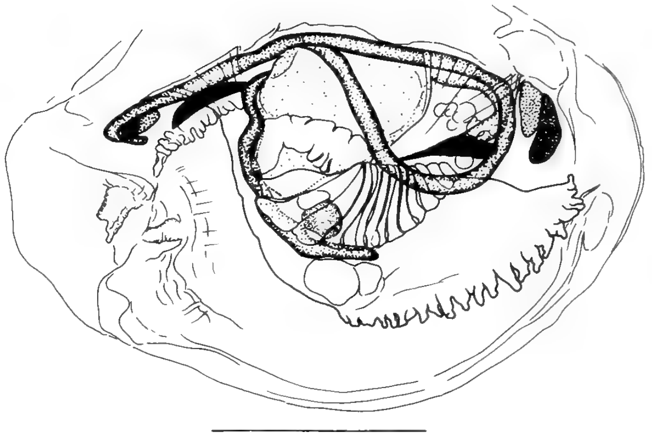

Fig. 19 *Yoldiella hanna*. Lateral view from right side of the internal morphology. Specimen from Sta. 186 Cape Basin. (Scale = 1.0 mm). For identification of parts see Fig. 5.

Prodissoconch length: 200 μm. Maximum recorded shell length: 3.2 mm.

INTERNAL MORPHOLOGY (Fig. 19). Well-developed combined siphons are present with a well-developed feeding aperture ventral to them. The siphonal tentacle lies to the left. The posterior adductor muscle is very small and elongate oval in cross-section. The anterior adductor muscle is crescent-shaped

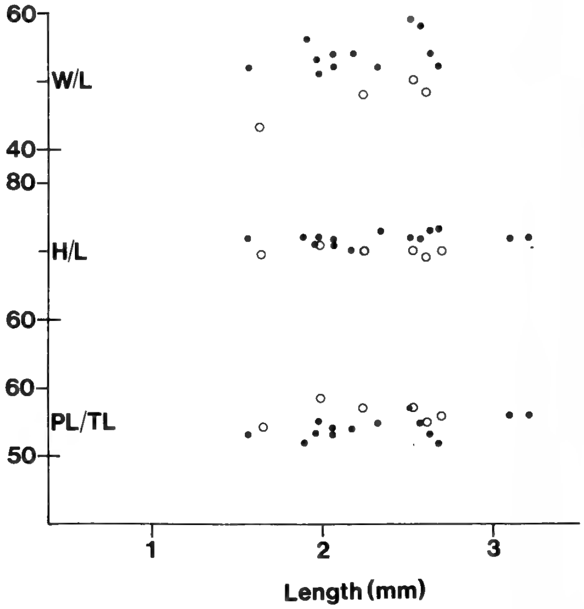

Fig. 20 *Yoldiella* spp. Comparison of the shell proportions of *Y. hanna* (closed circles) and *Y. artipica* (open circles). Height H/L, width W/L and postero-umbonal length PL/TL to length against length.

and at least three times as large as the posterior. The foot is large, anteriorly directed and with a large byssal gland. The cerebral and visceral ganglia are relatively large, club-shaped with a stout commissure. The pedal ganglia are also large but more rounded. The labial palps are well-developed and extend across approximately half of the body and have up to 14 broad internal ridges present on their inner face. The palp proboscides are moderately long. The gills are small with up to 18 alternating filaments.

The stomach is large and laterally distended. The proximal part of the hind gut penetrates deep into the foot, ventral to the pedal ganglia. It forms a single loop on the right side of the body.

In external appearance the shells of the species can be easily confused with *Yoldiella artipica* (p. 25) although *Y. hanna* is slightly more inflated and the height/length ratio is slightly greater (Fig. 20). Nevertheless, hinge and teeth differ markedly, as does the hind gut configuration.

Yoldiella capensis (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 42, Sta. 189, Cape Basin, 15.5.1968, 23°00′S, 12°45′E, Epibenthic Trawl, 1007–1014 m.

TYPE SPECIMEN. Holotype BM(NH) 1992026, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CAPE BASIN							
Atlantis II 42	188	619–622	70	23°00.0′S	12°58.0′E	ES	16.5.68
	189	1007–1014	918	23°00.0′S	12°45.0′E	ES	15.5.68
	190	974–979	15	23°05.0′S	12°45.0′E	AD	17.5.68

Only found at slope depths of the Cape Basin. Depth range: 619–1014 m.

SHELL DESCRIPTION (Figs. 21 & 22). Shell, subovate, moderately inflated, inequilateral, posteriorly somewhat wedge-shaped, smooth with a few fine concentric lines, periostracum pale straw-coloured; umbos slightly raised, inwardly directed; antero-dorsal margin convex, slopes steeply from umbo to anterior margin, dorsally posterior margin produced into rounded point, postero-dorsal margin long, varying from slightly convex in smaller specimens (usually) to slightly concave, slopes gradually to posterior margin, hinge plate strong, relatively long, plates approach shell margin below umbo, anterior plate arched with up to 9 erect chevron teeth, posterior plate extends to anterior margin of adductor, straighter than anterior, with up to 11 teeth and does not extend beyond posterior margin of adductor; ligament amphidetic, bilobed in lateral view, extends below hinge line.

Prodissoconch length: 170 μm. Maximum recorded shell length: 8.0 mm.

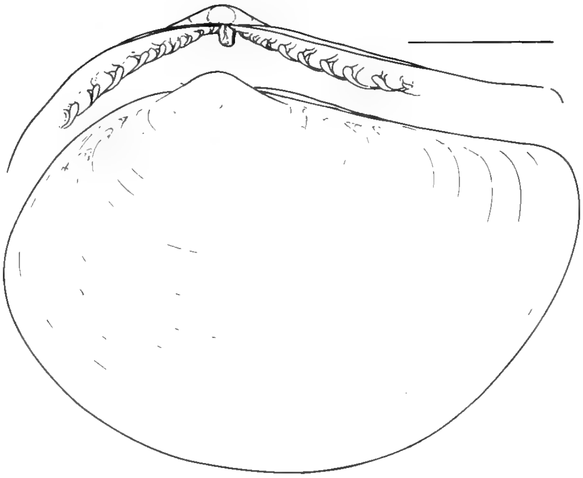

Fig. 21 *Yoldiella capensis*. Lateral view from the left side of the largest shell taken from Sta. 189 Cape Basin and hinge detail of right valve of the same specimen. (Scale = 1.0 mm).

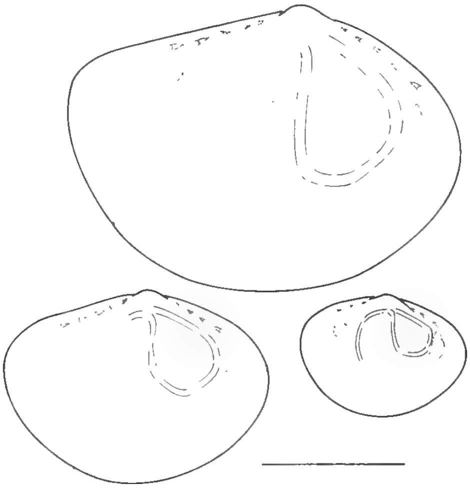

Fig. 22 *Yoldiella capensis*. Lateral views of shells from the right side to show change in shape with growth. Specimens from Sta. 188 Cape Basin. (Scale = 1.0 mm).

With increasing size this species becomes more posteriorly elongate and the distal posterior dorsal limit more pointed (Figs. 21 & 22). Furthermore the posterior dorsal margin becomes less curved with increasing size, so much so that without a size series it would be difficult to equate small specimens with large. Other shell ratios (H/L and W/L) remain more or less constant as length increases (Fig. 23).

INTERNAL MORPHOLOGY (Fig. 24). Specialization of the mantle includes a well-developed anterior sense organ and combined exhalent and inhalent siphons. The latter are well-developed with thick muscular walls. A siphonal tentacle lies to the left of the siphons. There is a feeding aperture ventral to the siphons which is much folded in the contracted state. The adductor muscles are relatively small. The posterior muscle is narrow and elongate, while the anterior is 2 to 3 times larger and crescent-shaped.

The gills are well-developed with up to 20 plates. The labial palps are moderate in size. They extend between 1/4 – 1/3 distance across the body and have long and slender palp proboscides. The nervous system is well developed with large club-shaped visceral and cerebral ganglia and massive commissures which link them. Large, round, pedal ganglia each have a large statocyst full of refractile granules dorsal to

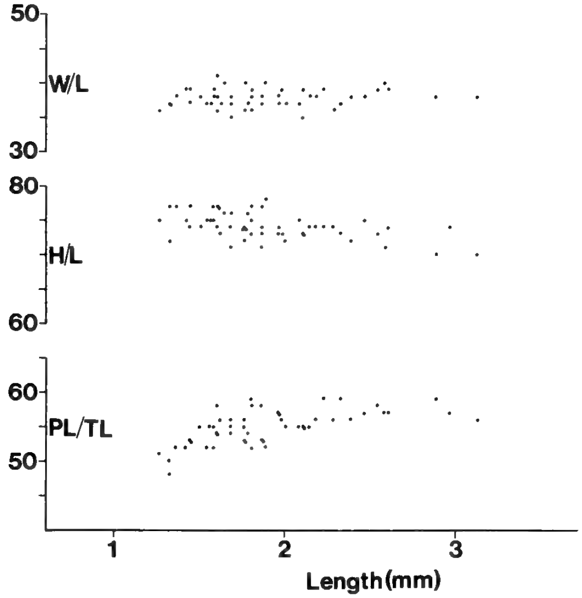

Fig. 23 *Yoldiella capensis*. Variation in the ratios of height H/L, widthW/L, and postero-umbonal length PL/TL to length against length of a subsample of specimens from Sta. 188 Cape Basin.

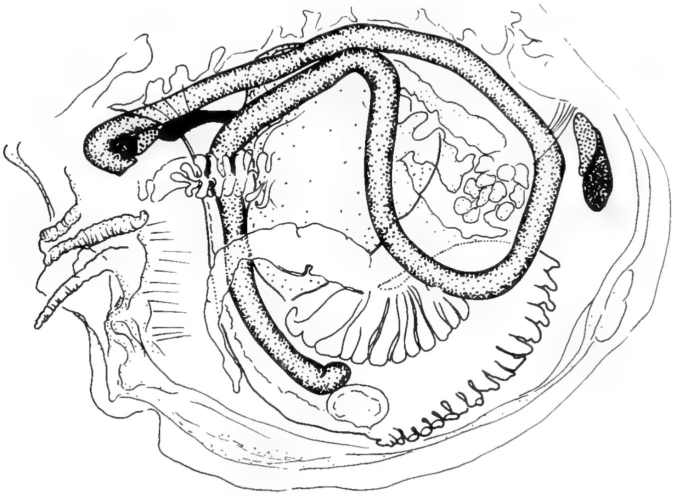

Fig. 24 *Yoldiella capensis*. Lateral view from the right side of the internal morphology. Specimen from Sta. 188, Cape Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 5.

them. The foot is large, well-developed with an anteriorly directed attitude. The stomach and style sac are also large. The hind gut forms a single loop on the right side of the body. This species bears some resemblance to *Yoldiella lucida* and to *Y. bilanta* (Fig. 137).

Yoldiella bilanta (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 42, Sta. 192, Cape Basin, 17.5.1968, 23°05.0′S, 12°31.5′E, Epibenthic Trawl, 2117–2154 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992027, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CAPE VERDE BASIN							
Atlantis II 31	138	1944–1976	1	10°36.0′N	17°52.0′W	ES	4.2.67
	141	2131	2	10°30.0′N	17°51.5′W	ES	5.2.67
	142	1624–1796	1	10°32.0′N	17°51.5′W	ES	5.2.67
	144	2051–2357	22	10°36.0′N	17°49.0′W	ES	5.2.67
CAPE BASIN							
Atlantis II 42	191	1546–1559	1025	23°05.3′S	12°31.5′E	ES	17.5.68
	192	2117–2154	1697	23°02.0′S	12°19.0′E	ES	17.5.68

Found in the Cape Verde and Cape Basins at lower slope depths. Depth range: 1446–2357 metres.

SHELL DESCRIPTION (Fig. 25). Shell slender, elongate ovate, inequilateral, smooth with few fine concentric lines, periostracum pale straw-coloured; umbos anterior to midline, slightly inflated, orthogyrate; antero-dorsal margin moderatley convex, curves evenly to anterior margin, ventral margin long, smooth curve, anterior curvature slightly more convex than posterior, posterior margin narrow, slightly produced with supramedial rounded angle, postero-dorsal margin slopes gradually more or less straight or slightly concave from umbo to posterior limit of hinge plate, then more acutely to posterior margin; hinge plate, strong, long, relatively narrow and straight with 9 anterior and 10 posterior teeth in largest specimen; anterior and posterior plates approach margin below umbo; ligament amphidetic, bilobed goblet-shaped, extends below hinge line, short anterior and posterior external extensions of fused periostracum.

Prodissoconch length c 190 μm: Maximum recorded shell length: 8.0 mm.

The morphology of the shell is similar to that of *Yoldiella capensis* (Fig. 21). With increasing size the shell becomes more posteriorly elongate and the postero-dorsal margin becomes more straight so that the slight angulation at the level of the limit of the posterior hinge margin becomes much less obvious (Figs. 25 & 26). There is little change with growth in the height and length and width to length ratios. The hinge plate is more narrow and teeth less robust than in *Y. capensis* and the lateral 'dumb bell' outline of the ligament is very different from the more rectangular and deeper ligament of the latter species.

INTERNAL MORPHOLOGY (Fig. 27). The most conspicuous difference from *Y. capensis* is the size and shape of the adductor muscles which are larger and more rounded in *Yoldiella bilanta* The labial palps are relatively small and extend approximately 1/3 distance across body. They bear up to 16 palp ridges. The gill plates are relatively narrow and number up to 18. The single loop of the hind gut has a greater diameter but is not as ventrally deep as that in *Yoldiella capensis*. Similar features to *Yoldiella capensis* include well-developed combined siphons, nervous system, and a large,

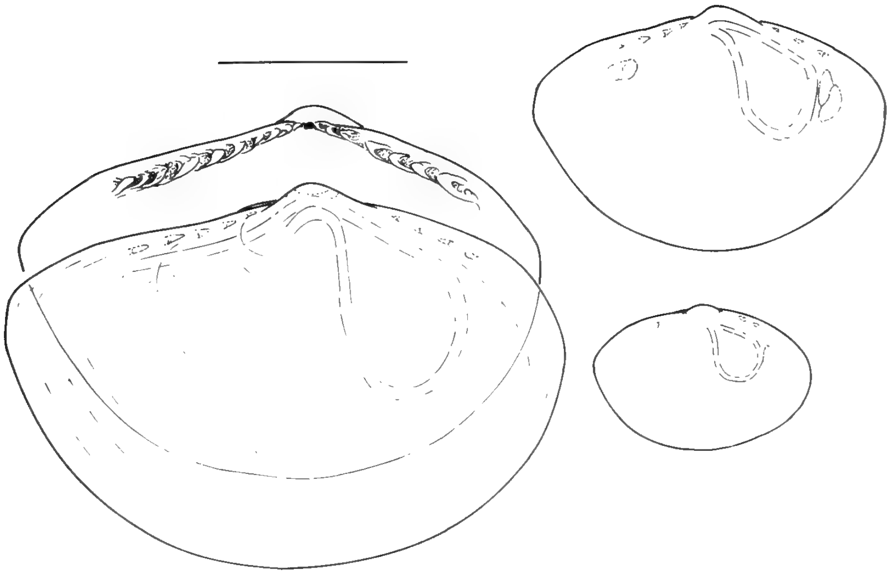

Fig. 25 *Yoldiella bilanta*. Lateral views of three shells from the right side and internal view of a left valve to show the hinge-plate. Specimens from Sta. 192 Cape Basin. (Scale = 1.0 mm).

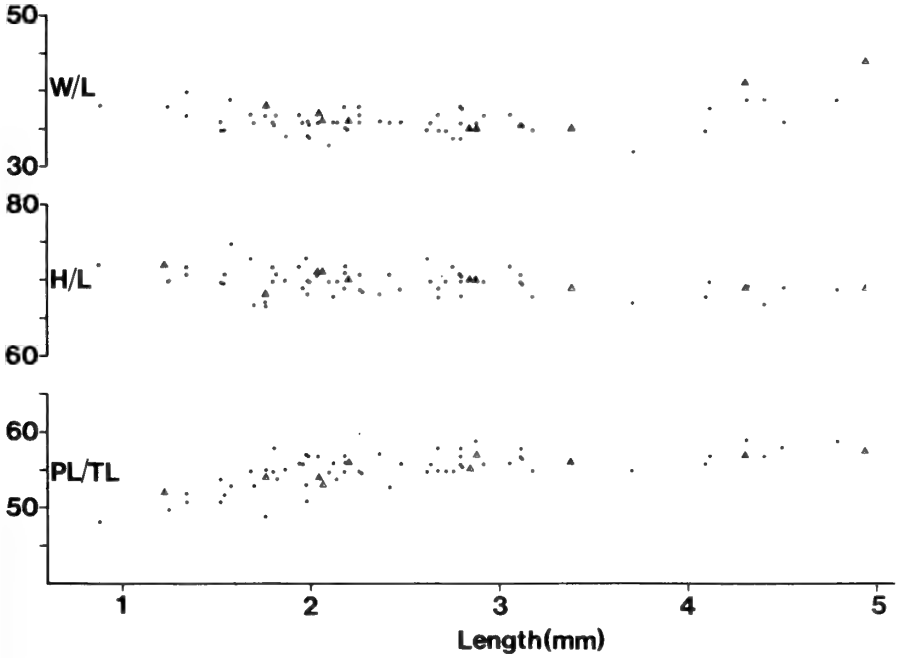

Fig. 26 *Yoldiella bilanta*. Variation in the ratios of height H/L, width W/L, and postero-umbonal length PL/TL to length against length of samples from Sta. 191 (open triangles) and Sta. 192 (closed circles) Cape Basin.

anteriorly directed foot. The lateral papillae of the foot are not so well-developed as those in *Y. capensis*.

The specimens from the Cape Verde Basin are somewhat smaller and have a slightly deeper shell than those from the Cape Basin. There appear also slight differences in the size of the posterior adductor muscle and the gills, but these may be a result of distortion following preservation. Such small differences are within the normal variation of yoldiellid species and at most represent a population difference.

Yoldiella artipica (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 42, Sta. 200, Angola Basin, 22.5.1968, 9°43.5′S, 10°57′0E – 9°41.0′S – 10°55.0′E, Epibenthic Dredge, 2644–2754 m.

TYPE SPECIMEN. : Holotype: BM(NH) 1992021, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ANGOLA BASIN							
Atlantis II 42	200	2644–2754	25	9°43.5′S – 9°41.0′S	10°57.0′E 10°55.0′E	ES	22.5.68
Walda	DS20	2514	2	2°32.0′S	8°18.1′E	ES	–.–.71

Restricted to the abyssal rise of the south east Atlantic. Depth range: 2514–2754 m.

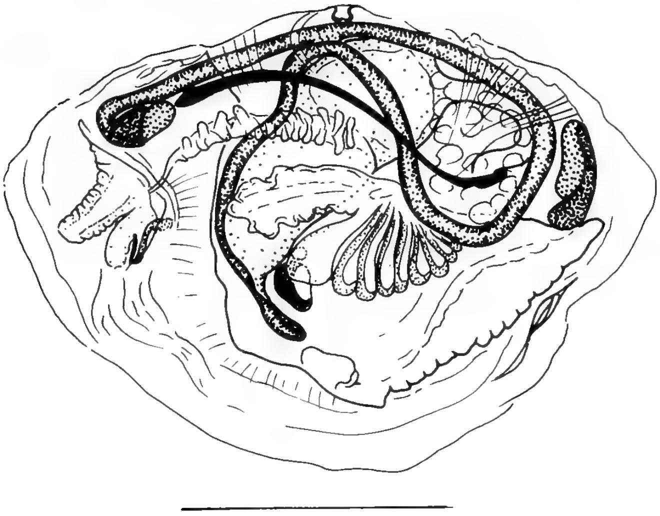

Fig. 27 *Yoldiella bilanta*. Lateral view of the internal morphology from the right side of a specimen from Sta. 192 Cape Basin. (Scale 1.0 mm). For identification of parts see Fig. 5.

SHELL DESCRIPTION (Fig. 28). Shell small, ovate, not inflated, inequilateral (posterior umbonal length 54–58% of total length), in larger specimens antero-ventrally, very fine concentric lines form broadly spaced ridges, periostracum pale yellow, umbo slightly raised, inwardly directed; dorsal margin slightly convex, antero-dorsal margin curves moderately steeply and evenly with anterior margin, ventral margin smooth curve, postero-dorsal margin slopes gently from umbo to extended posterior margin; ligament amphidetic, small, rounded, not extending below hinge plate, with small secondary anterior and posterior external extensions of fused periostracum ; hinge plate moderately long, relatively narrow, small chevron-shaped teeth, 7 anterior and 8 posterior.

Prodissoconch length: 200 μm. Maximum recorded shell length: 2.78 mm.

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
2.00	1.46	–	0.73	–	0.54
2.69	1.89	–	0.70	–	0.56
2.78	1.98	–	0.71	–	0.58
1.64	1.13	0.53	0.69	0.33	0.54
2.23	1.55	0.84	0.70	0.38	0.57
2.60	1.80	1.01	0.69	0.38	0.55
2.52	1.76	1.01	0.70	0.40	0.57

PL = postumbonal length

INTERNAL MORPHOLOGY (Fig. 29). The combined exhalent and inhalent siphons are large. The inhalent is somewhat shorter than the exhalent and open ventrally. A large siphonal tentacle originates on the left side of the siphonal embayment close to the base of the siphon. The feeding aperture is not particularly well-developed. There is a large anterior sense organ. The posterior adductor muscle is long and narrow, and only half the size of the bean-shaped anterior muscle. The gills are well-developed with up to 20 gill plates. The labial palps are relatively small with up to 12 internal palp ridges with long, thin palp proboscides. The foot is extremely long and slender with an extended sole fringed with deep papillae. There is a large byssal gland in the heel with large pedal ganglia dorsal to it. The visceral and cerebral ganglia are of moderate size and club-shaped. The hind gut is similar to that in *Yoldiella lata* (p. 32) with one complete turn of a double loop to the right side. That in *Y. artipica* entends further posteriorly than that in *Y. lata*. As in many yoldiellid species the body wall enclosing the hind gut loops overhangs the palps on the right side (Fig. 29).

Yoldiella similis (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 42, Sta. 197, Angola Basin, 21.5.1968, 10°24′S, 9°09′E – 10°29′S, 9°04′E, Epibenthic Trawl, 4559–4566 m.

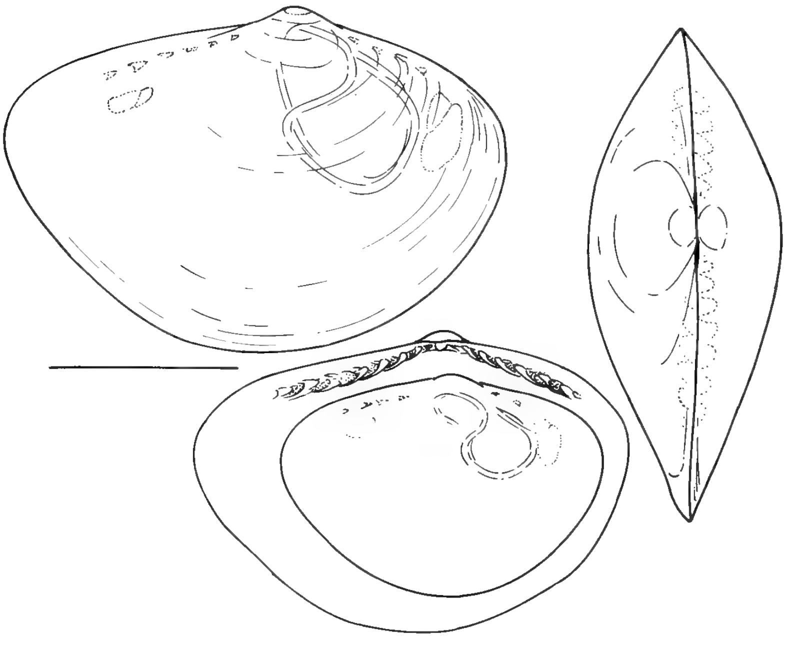

Fig. 28 *Yoldiella artipica*. A dorsal and two right lateral views of shells, and one lateral view of a left valve to show detail of hinge-plate. Specimens from Sta. 200 Angola Basin. (Scale = 1.0 mm).

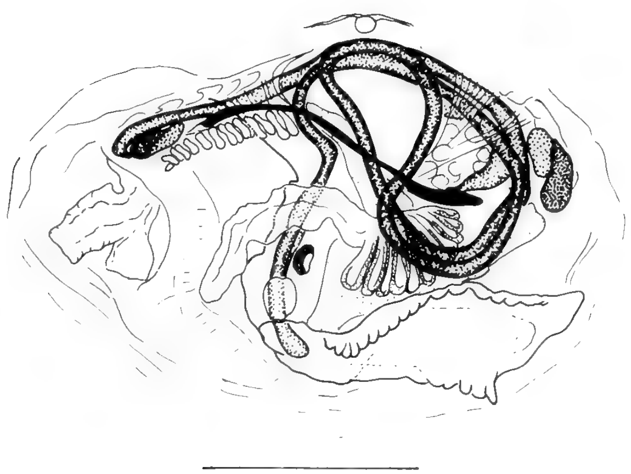

Fig. 29 *Yoldiella artipica*. Lateral view from the right side of the interal morphology of a specimen from Sta. 200 Angola Basin. (Scale = 1.0 mm). For identification of parts see Fig. 5.

TYPE SPECIMEN. Holotype: BM(NH) 1992023, Paratypes: in collection held by J.A. Allen.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ANGOLA BASIN							
Atlantis II 42	196	4612–4630	1	10°19.0'S	9°04.0'E	ES	21.5.68
	197	4596	35	10°29.0'S	9°04.0'E	ES	21.5.68
	198	4559–4566	12	10°24.0'S – 10°29.0'S	9°09.0'E 9°04.0'E	ES	21.5.68

Found at abyssal depths in the Angola Basin. Depth range: 4559–4630 m.

SHELL DESCRIPTION (Fig. 30). Shell small, ovate, very slightly inflated, inequilateral with posterior margin supramedially subrostrate, shell with very fine concentric lines, forming ridging on ventral half of shell; periostracum pale yellow; umbos slightly raised, internally directed; dorsal margin slightly convex, antero-dorsal margin slopes from umbo to form even curve with anterior margin, ventral margin smoothly curved, posterior margin sharply curved where it meets postero-dorsal margin; hinge strong, moderately broad, extends to anterior and posterior limits of the anterior and posterior adductors respectively; hinge teeth well-developed, equal numbers (maximum 9) on anterior and posterior hinge plates, ligament amphidetic, moderately large, goblet-shaped with very small external extensions.

Prodissoconch length: 173 μm. Maximum recorded shell length: 2.92 mm.

The shell outline of this species is similar to that of specimens of *Y. jeffreysi* from the Cape Verde Basin. The two species can be distinguished by the larger ligament, broader hinge and more rostrate posterior margin of *Y. similis*.

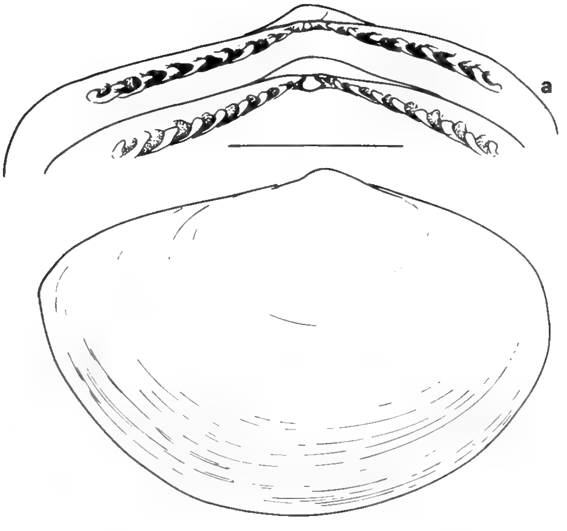

Fig. 30 *Yoldiella similis*. Lateral view of a shell from right side and a hinge-plate of a left valve compared with the hinge-plate of a specimen of *Y. jeffreysi* (a) Specimens from Sta. 197, Angola Basin and Sta. 316, West European Basin, respectively. (Scale = 1.0 mm).

Shell measurements (mm) and ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
1.0	0.71	0.78	0.71	0.38	0.42
1.93	1.39	0.80	0.72	0.41	0.50
1.72	1.43	0.80	0.83	0.46	0.54
2.90	2.06	1.39	0.71	0.48	0.55

PL = postumbonal length

INTERNAL MORPHOLOGY (Fig. 31). The internal morphology of *Y. similis* is very similar to that of *Y. jeffreysi*. The exhalent siphon is combined with the less well-developed inhalent siphon. The adductor muscles are unequal in size, the anterior being approximately three times larger than the posterior. In lateral view the posterior adductor muscle is oval in outline while the anterior is 'bean-shaped'. The foot has a long, extended, narrow sole with a large byssal gland in the heel. The nervous system is extremely well-developed with large visceral and cerebral ganglia with short stout commissures joining them. Gills appear to have relatively few plates (up to 10) and the number of palp ridges is also few (up to 12) but the latter are relatively broad. This species has a large stomach and the hind gut makes one complete double coil to the right side of the body.

Yoldiella sinuosa (new species)

TYPE LOCALITY. R.V. Knorr, Cruise 25, Sta. 299, Surinam Basin, 29.2.1972, 7°55.1'N, 55°42.0'W, Epibenthic Trawl, 1942–2076 m.

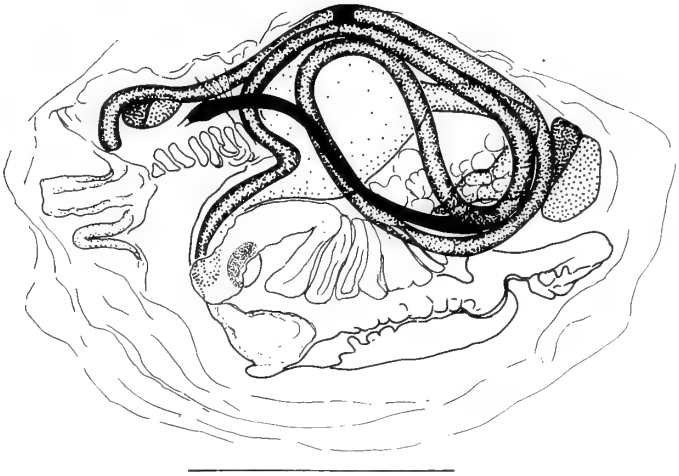

Fig. 31 *Yoldiella similis*. Lateral view from the right side of the internal morphology of a specimen from Sta. 197. Angola Basin. (Scale = 1.0 mm). For identification of parts see Fig. 5.

TYPE SPECIMEN. Holotype: BM(NH) 1992025, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SURINAM BASIN							
Knorr 25	299	1942–2076	54	7°55.1′N	55°42.0′W	ES	29.2.72

Restricted to one Station on the lower slope of the Surinam Basin. Depth range: 1942–2076 m.

SHELL DESCRIPTION (Figs. 32 & 33). Shell small, ovate, moderately inflated, slightly inequilateral, surface smooth in small individuals, ridges on ventral half of shell of larger specimens, periostracum pale yellow; umbo small, slightly raised, internally directed; no lunule or escutcheon; dorsal margin convex, anterior and posterior margins slope at similar angle from umbo, anterior margin smooth curve, posterior margin slight extended and slightly subrostrate, postero-dorsal margin slightly angled at posterior limit of hinge plate, postero-ventral margin sinuous, ventral margin slightly more convex posteriorly; hinge plate strong, relatively long, with up to 9 anterior and 10 posterior chevron-shaped teeth, hinge plate narrow below umbo; ligament amphidetic, internal, 'goblet-shaped'.

With increasing shell length, there is little change in the height to length ratio but there is a slight increase in the width to length ratio. There is also gradual post-umbonal extension with the sinuous nature of the postero-ventral margin becoming more conspicuous (Fig. 35).

Prodissoconch length: 179 μm. Maximum recorded shell length: 3.69 mm.

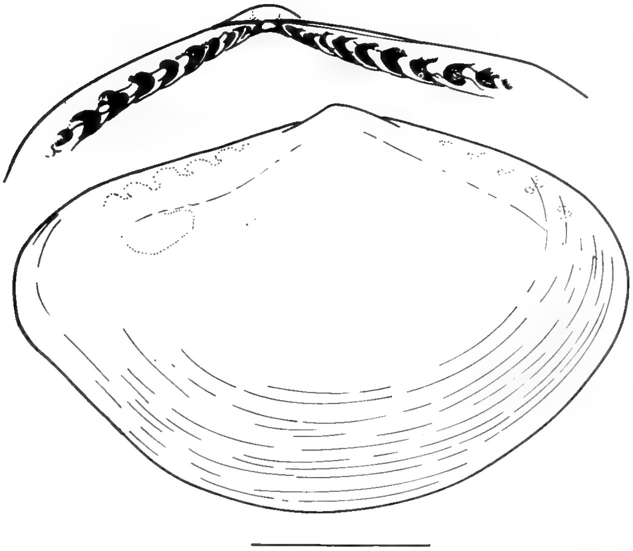

Fig. 32 *Yoldiella sinuosa*. Lateral view of a shell from the right side and detail of the hinge-plate of a right valve. Specimens from Sta. 299 Guyana Basin. (Scale = 1.0 mm).

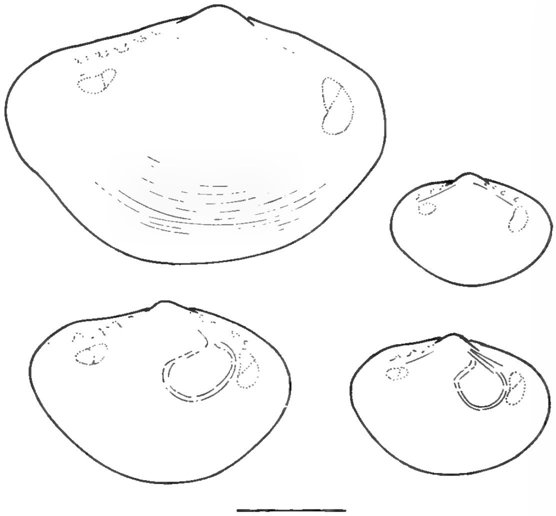

Fig. 33 *Yoldiella sinuosa*. Outline drawings of shells of different sizes from the right side to show change in shape with growth. Specimens from Sta. 299 Guyana Basin. (Scale = 1.0 mm).

INTERNAL MORPHOLOGY (Fig. 34). The combined siphons, the siphonal tentacle (usually on the left side), and the anterior sense organ are as in *Y. similis*. The adductor muscles are approximately oval, the anterior muscle being the larger and being almost twice the size of the posterior. The gills have up to 17 plates. The labial palps are moderate in size and extend 1/3 way across the body. They have up to 15 moderately broad ridges and each bears a long palp proboscis. The pedal ganglia are large, round, with large statocysts dorsal to them. The cerebral ganglia are slightly larger than the visceral, both are club-shaped and well-developed. The foot is large with a large byssal gland. The stomach is large with a small, narrow style sac. The hind gut takes an 'S-shape' course to the right side of the body before returning to the mid dorsal margin and thence to the anus. There is a fine typhlosole present along the length of the hind gut. Ingested material was seen in part of the left digestive diverticulum. The kidney is well-developed, extending anteri-

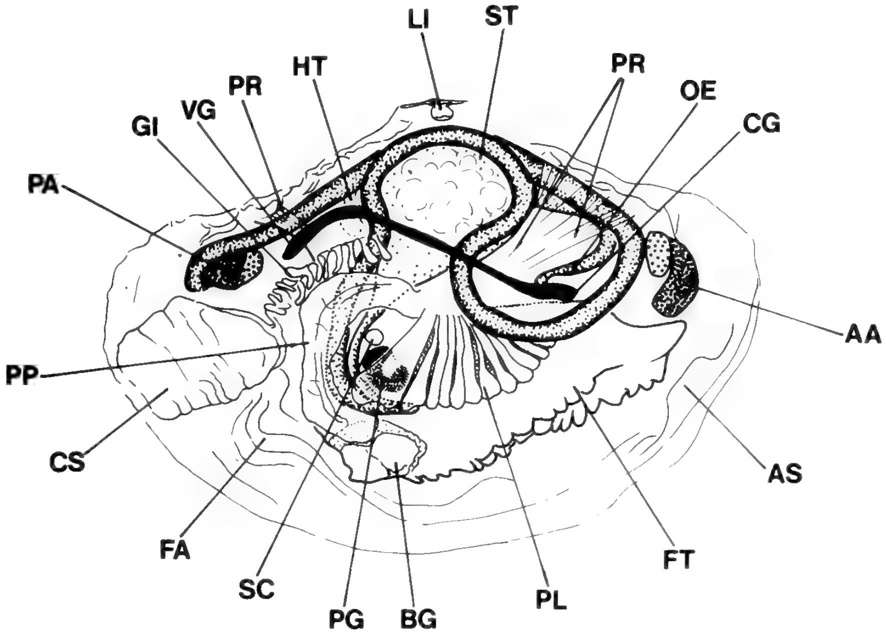

Fig. 34 *Yoldiella sinuosa*. Lateral view from the right side of the internal morphology of a specimen from Sta. 299 Guyana Basin. (Scale = 1.0 mm).

orly on either side of the stomach, anterior to the lateral pedal retractor muscles. It also pentrates the foot posterior to the stomach.

Only male specimens were observed in which the testes were restricted to the anterior dorsal and ventral limits of the viscera.

Yoldiella sinuosa is characterized by its slightly sinuous postero-ventral shell margin and the s-shaped course of the hind gut (see p.).

Yoldiella blanda (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 60, Sta. 247, Argentine Basin, 17.3.1971, 43°32.0'S, 48°58.1'W, Epibenthic Trawl, 5208–5223 m.

TYPE SPECIMEN. Holotype: BM(HM) 1992020, Paratypes: in a collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	119	38°16.9'S	51°56.1'E	ES	13.3.71
	245	2707	1	36°55.7'S	53°01.1'E	ES	14.3.71
	247	5208–5523	106	43°33.0'S	48°58.1'E	ES	17.3.71
	252	4435	42	38°29.8'S	52°09.1'E	ES	22.3.71
	256	3906–3117	63	52°19.3'S	52°19.3'E	ES	24.3.71
	259	3305–3317	20	37°13.3'S	52°45.0'E	ES	26.3.71

This species is restricted to abyssal depths in Argentine Basin. Depth range: 2707–5223 m.

SHELL DESCRIPTION (Figs. 36 & 37). Shell ovate, laterally

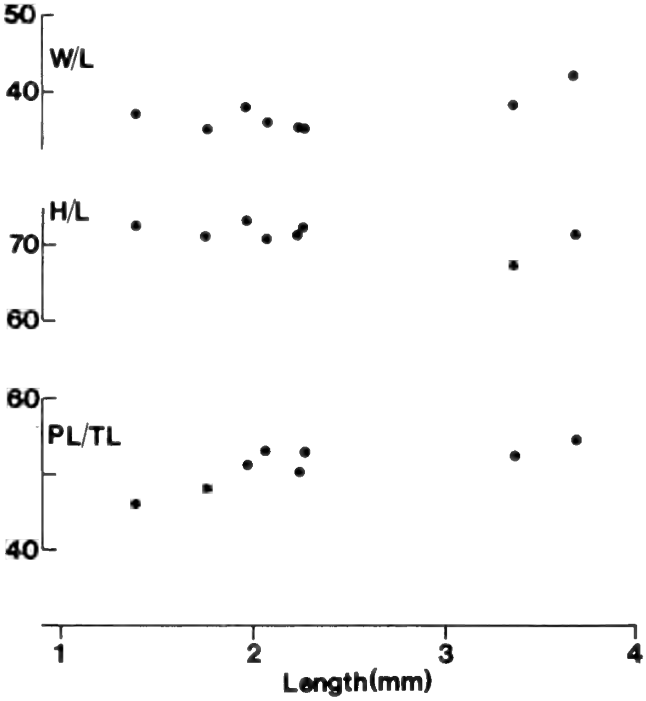

Fig. 35 *Yoldiella sinuosa*. Variation in the ratios of height H/L, width W/L, and post-umbonal length PL/TL to length against length of a subsample from Sta. 299 Guyana Basin.

compressed, fragile, slightly inequilateral; umbos small, not markedly raised or inflated, slightly anterior to the mid line; antero-dorsal, anterior and ventral margins, evenly curved, postero-dorsal margin slopes in almost straight line from umbo, anterior and posterior limits dorsal to mid horizontal line; hinge plate moderately strong, parallel to dorsal margin, anterior and posterior series of teeth equal in number; ligament amphidetic and extends slightly below hinge plate with very small anterior and posterior marginal extensions of fused periostracum.

INTERNAL MORPHOLOGY (Fig. 38). Exhalent and inhalent siphons combined, the inhalent siphon is shorter than the exhalent and open at the ventral margin. There is a siphonal tentacle to the left side. The posterior adductor muscle is oval and approximately half the size of the crescent-shaped anterior muscle. The gills are moderately well-developed and the plates number up to 16. The labial palp ridges number between 14–18 depending on size of individual. The foot is large with a conspicuous byssal gland. There is a single hind gut loop to the right of the body which has a characteristic course that approaches an 'S' in shape.

Prodissoconch length: 198 μm. Maximum recorded shell length: 5.61 mm.

Most closely resembles *Y. sinuosa* but without the postero-ventral sinuosity (Fig. 139).

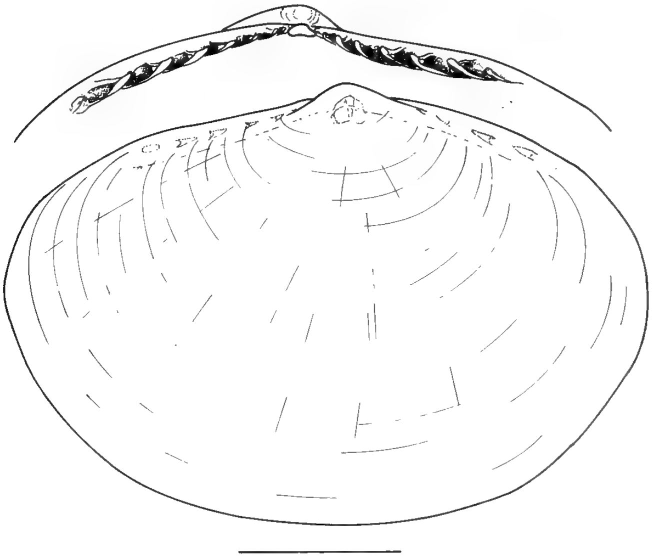

Fig. 36 *Yoldiella blanda*. Lateral view of a shell from the right side and detail of the hinge-plate of a right valve. Specimens from Sta. 242 Argentine Basin. (Scale = 1.0 mm).

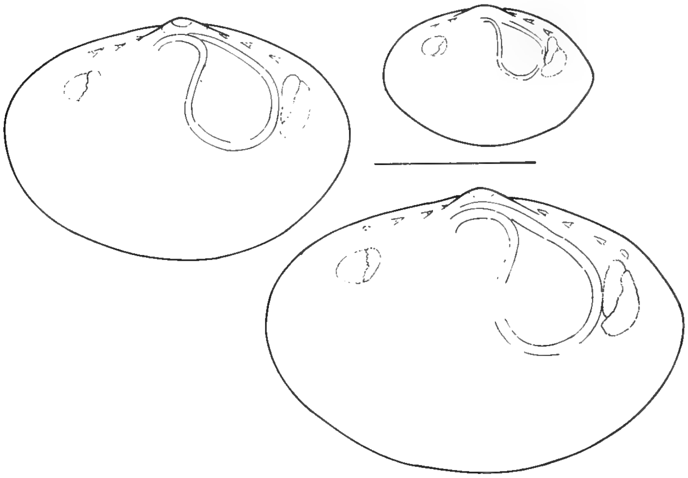

Fig. 37 *Yoldiella blanda*. Outline drawings of shells of differing sizes from the right side to show change in shape with growth. Specimens from Sta. 242 Argentine Basin. (Scale = 1.0 mm).

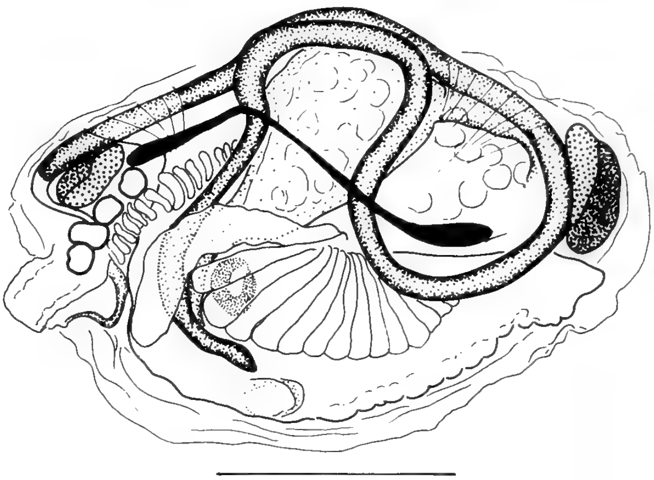

Fig. 38 *Yoldiella blanda*. Lateral view from the right side of the internal morphology of a specimen from Sta. 242 Argentine Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

Yoldiella biscayensis (new species)

TYPE LOCALITY. R.V. Chain, Cruise 106, Sta. 326, Bay of Biscay, 22.8.1972, 50°04.9′N, 14°23.8′W, Epibenthic Trawl, 3859 m.

TYPE SPECIMEN. Holotype BM(NH) 1992024, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Jean Charcot							
(Polygas)	DS20	4226	10	47°33.0′N	9°36.7′W	DS	24.10.72
	DS21	4190	6	47°31.5′N	9°40.7′W	DS	24.10.72
	DS22	4144	21	47°34.1′N	9°38.4′W	DS	25.10.72
	DS23	4734	17	46°32.8′N	10°21.0′W	DS	26.10.72
(Biogas II)	DS31	2813	11	47°32.5′N	9°04.2′W	DS	19. 4.73
(Biogas III)	DS44	3992	4	47°33.2′N	9°42.0′W	DS	27. 8.73
	DS41	3548	20	47°28.3′N	9°07.2′W	DS	26. 8.73
	DS45	4260	6	47°33.9′N	9°38.4′W	DS	27. 8.73
	DS48	4203	2v	44°29.0′N	4°54.0′W	DS	31. 8.73
(Biogas IV)	DS53	4425	11	44°30.4′N	4°56.3′W	DS	19. 2.74
	DS54	4659	20	46°31.1′N	10°29.2′W	DS	21. 2.74
	DS55	4125	76	47°34.9′N	9°40.9′W	DS	22. 2.74
	DS56	4050	1	47°32.7′N	9°28.2′W	DS	23. 2.74
	DS59	2790	3	47°31.7′N	9°06.2′W	DS	24. 2.74
	DS60	3742	24	47°26.8′N	9°07.2′W	DS	24. 2.74
	KR35	4140	1	47°26.0′N	9°08.7′W	KR	25. 2.74
(Biogas V)	DS66	3480	31	47°28.2′N	9°00.0′W	DS	16. 6.74
	DS67	4150	4	47°31.0′N	9°35.0′W	DS	17. 6.74
	DS68	4550	2+2v	46°26.7′N	10°23.9′W	DS	19. 6.74
	DS69	4510	1	44°21.9′N	4°52.4′W	DS	20. 6.74
	DS70	2150	1	44°08.8′N	4°17.4′W	DS	21. 6.74
(Biogas VI)	DS74	2777	7	47°33.0′N	9°07.8′W	DS	22.10.74
	DS75	3250	9	47°28.1′N	9°07.8′W	DS	22.10.74
	DS76	4228	101	47°34.8′N	9°33.3′W	DS	23.10.74
	DS77	4240	11	47°31.8′N	9°34.6′W	DS	24.10.74
	DS78	4706	47	46°31.2′N	10°23.8′W	DS	25.10.74
	DS79	4715	106	46°30.4′N	10°27.1′W	DS	26.10.74
	DS80	4720	19	46°29.5′N	10°29.5′W	DS	27.10.74
	DS81	4715	9	46°28.3′N	10°24.6′W	DS	27.10.74
	DS82	4462	27	44°25.4′N	4°52.8′W	DS	29.10.74

	DS85	4462	2	44°23.2'N	4°50.8'W	DS	30.10.74
	CP13	3134	2	47°34.4'N	9°38.0'W	CP	23.10.74
	CP16	4825	1	46°27.3'N	10°25.0'W	CP	26.10.74
	CP17	4706	2	46°30.8'N	10°19.5'W	CP	26.10.74
	CP19	4434	1	44°24.9'N	4°51.3'W	CP	28.10.74
	CP22	4475	2	44°22.9'N	4°54.8'W	CP	30.10.74
Jean Charcot	CP11	4823	1	48°20.4'N	15°14.6'W	CP	1. 8.76
(Incal)	OS02	4829	2	48°19.2'N	15°15.7'W	OS	2. 8.76
	WS03	4829	3	48°19.2'N	15°23.3'W	WS	1. 8.76
					– 15°22.5'W		
	DS14	4254– 4348	7	47°32.8'N	9°35.4'W	DS	7. 8.76
	DS15	4211	6	47°33.6'N	9°39.1'W	DS	8. 8.76
					– 9°38.5'W		
	DS16	4268	13	47°29.8'N	9°33.4'W	DS	9. 8.76
				– 47°30.3'N			
	OS05	4296– 4248	4	47°31.3'N	9°34.6'W	DS	7. 8.76
				– 47°32.2'N	9°34.7'W		
	OS06	4316	5+1v	47°27.3'N	9°36.2'W	OS	9. 7.76
int9.347°27.9'N					9°36.0'W		
int3.9OS07		4249	12	47°31.8'N	9°34.3'W	OS	10.8.76
				– 47°31.3'N			
	OS08	4327	13	47°29.8'N	9°32.9'W	OS	11. 8.76
				– 47°29.5'N	9°38.8'W		
	WS07	4281	9	47°30.6'N	9°37.1'W	WS	7. 8.76
				– 47°31.2'N	9°35.7'W		
	WS08	4287– 4301	13	47°30.5'N	9°33.7'W	WS	9. 8.76
				– 47°29.3'N	9°34.1'W		
	WS09	4277	8	47°28.8'N	9°34.0'W	WS	10. 8.76
				– 47°27.9'N			
	WS10	4354	18	47°27.3'N	9°39.9'W	WS	11. 8.76
				– 47°28.2'N	12°43.9'W		
	KR07	2891	8	55°02.9'N	12°43.9'W	KR	20. 7.76
Chain 106	321	2890– 1868	2	50°12.3'N	13°35.8'W	ES	20. 8.76
	323	3356– 3338	39	50°08.3'N	13°53.7'W	ES	21. 8.76
					– 13°50.9'W		
	326	3859	29	50°04.9'N	14°23.8'W	ES	22. 8.76
	328	4426– 4435	13	50°04.7'N	15°44.8'W	ES	23. 8.76
	330	4632	29	50°43.5'N	17°51.7'W	ES	23. 8.76
				– 50°43.3'N	17°52.9'W		

Restricted to abyssal depths in West European Basin, the majority of specimens were taken from depths greater than 3500 mm. Depth range: 2150–4829 m.

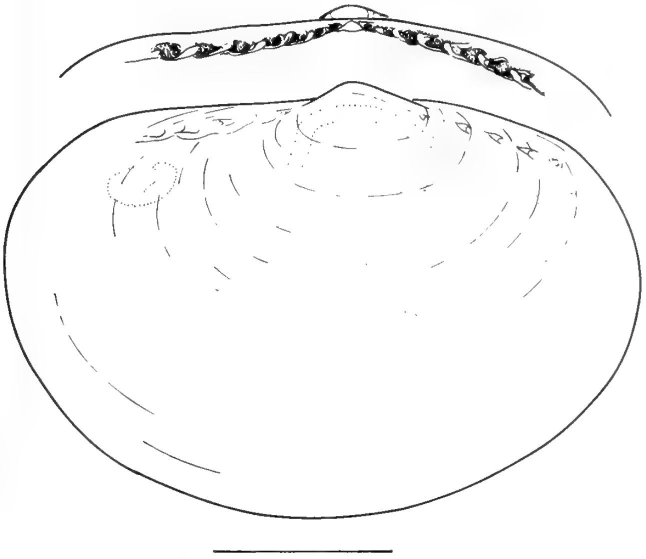

Fig. 39 *Yoldiella biscayensis*. Lateral view of a shell from the right side and detail of the hinge-plate of a left valve. Specimens from Sta. 326 West European Basin. (Scale = 1.0 mm).

SHELL DESCRIPTION (Figs. 39–42). The form of the shell varies somewhat from locality to locality.

Form A: The following description is based on specimens found in Bay of Biscay at 4000 m and below.

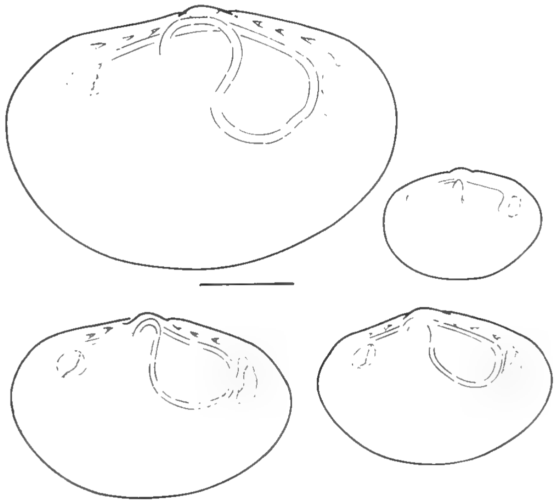

Fig. 40 *Yoldiella biscayensis*. Outline drawings of shells of different sizes from the right side to show change in shape with growth. Specimens from Sta. 326 West European Basin. (Scale = 1.0 mm).

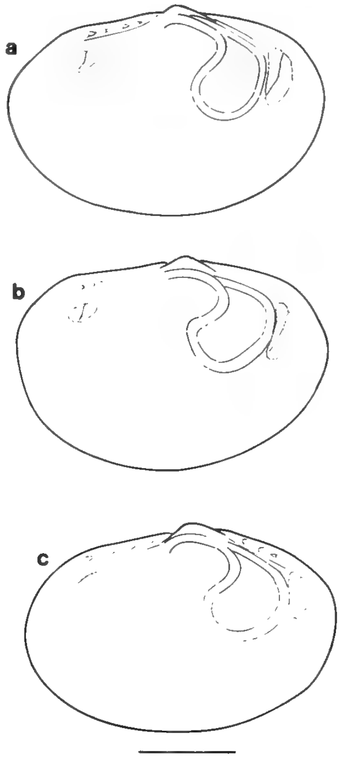

Fig. 41 *Yoldiella biscayensis*. Outline drawings of three shells of similar size from the right side to show differences in shape. Specimens a & b from Sta. BGVI DS 76 (4228 m); specimen c from Sta. BG II DS 31 (2813 m). (Scale = 1.0 mm).

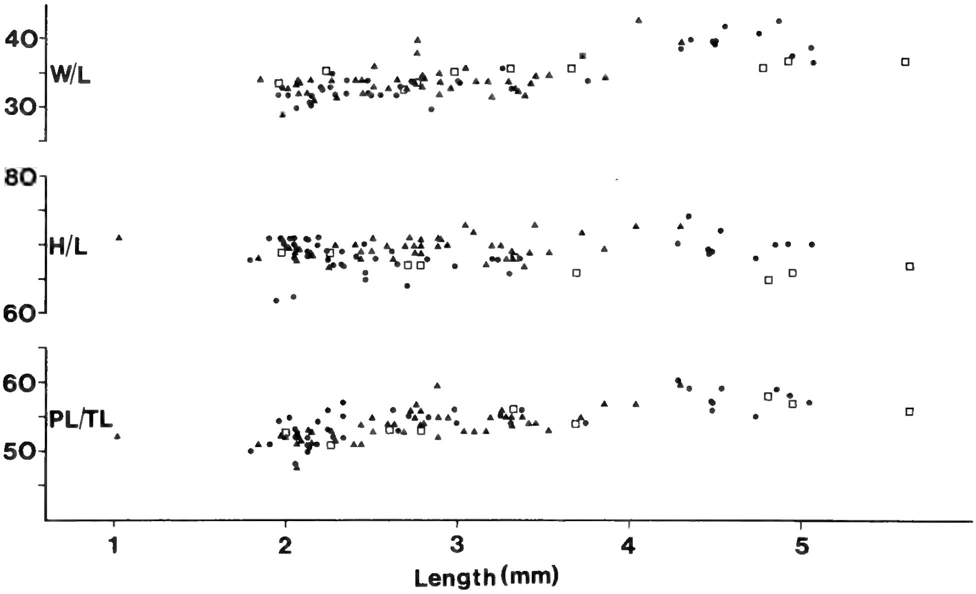

Fig. 42 *Yoldiella biscayenesis*. Variation in the ratios of height H/L, width W/L, and postero-umbonal length PL/TLL to length against length of the three shape forms illustrated in Fig. 41. Solid circles, angulate specimens from Sta. BG VI DS76; solid triangles, rounded specimens from Sta. BG VI DS76; open squares, specimens from Sta. BG II DS31; West European Basin.

Shell compressed, ovate, fragile, inequilateral, post-umbonal length 48–62% of total length, sculpture of fine irregular concentric lines, pale yellow periostracum; umbo slightly raised, posteriorly directed; antero-dorsal margin convex curving gradually to broadly rounded anterior margin, ventral margin evenly curved, postero-dorsal margin very slightly sinuous, slopes gradually to distal limit of hinge plate, then more sharply inclined to posterior margin; hinge plate moderately long, moderately well-developed with up to 10 well developed teeth on each side of ligament, occasionally one additional tooth in posterior series; ligament amphidetic, large, internal, goblet-shaped, extends ventral to and somewhat posterior to proximal limit of posterior hinge plate.

Prodissoconch length: 187–198 μm. Maximum recorded shell length: 5.82 mm.

Form B: This was taken between approximately 3000–4100 metres and at about 4000 m may be mixed with Form A. The shell is distinguished from Form A by a more marked concavity in the proximal part of the postero-dorsal margin and by a more rounded posterior margin. Internally the hinge and ligament are similar. Form B on average is somewhat smaller than Form A.

Maximum recorded shell length: 4.19 mm.

Form C: Recorded at 2076 and 1891 metre depths. This form is intermediate between Forms A and B. It has an almost straight postero-dorsal margin.

Maximum recorded shell length: 7.39 mm.

INTERNAL MORPHOLOGY (Fig. 43). The three forms are anatomically indestinguishable from each other. Exhalent and inhalent siphons are combined. There is a siphonal tentacle that lies either to the left or the right of the siphons. A feeding aperture is present ventral to the siphon embayment and there is a well-developed anterior marginal sense organ.

The adductor muscles have conspicuous 'quick' and 'catch' parts. The posterior muscle is approximately half the size of the anterior and oval in outline. The anterior muscle is crescent-shaped. The gills are well-developed with a relatively large number (up to 28) of gill plates alternating on either side of the gill axis. The labial palps are relatively large and, depending on the size of the animal, have up to 25 internal ridges. The palp proboscides are long and thin. The foot is large with a large byssal gland. There is a small single papilla posterior to the aperture of the gland and the posterior surface of the foot is well-supplied with secretory cells. As in other species, there is histological evidence of a secretion being released along the whole length of the sole of the foot. Large, round, pedal ganglia are situated dorsal to the byssal gland. The visceral ganglia are 'club'-shaped and relatively slender, the cerebral ganglia are slightly more inflated. The oesophagus, stomach and style sac are similar to those described for other *Yoldiella* species, the hind gut is relatively broad and forms a single loop on the right side of the body. The posterior section of the loop describes a conspicuous and characteristic 'S'-shaped course. There is a typhlosole along the length of the hind gut. The digestive diverticula are similar to those of other species of *Yoldiella*. The sexes are separate. All individuals more than 3.0 mm in length show some gonadial development. A specimen 4.9 mm in length contained 190 ova (maximum diam. 150 μm).

Most closely resembles *Y. sinuosa* and *Y. blanda* and distinguished by more angulate postero-dorsal margin and lack of postero-ventral sinuosity.

Yoldiella lata (Jeffreys 1876)

TYPE LOCALITY. Valorous Sta. 9, Davis Strait, 14.8.1875, 59°10′N, 50°25′W, dredge, 1750 fms.

TYPE SPECIES. Lectotype: U.S. Natl. Mus., No. 199695 as here designated.

Specimens from Biogas Sta. DS87 are housed in the Museum National d'Histoire Naturelle, Paris.

Leda lata Jeffreys 1876, p. 431 (in part).

As is pointed out under *Y. jeffreysi* (p. 63) when the 'Valorous' material was examined, it was found that two species had been grouped together under the name *Leda lata*. Furthermore, the original description is such that it is not

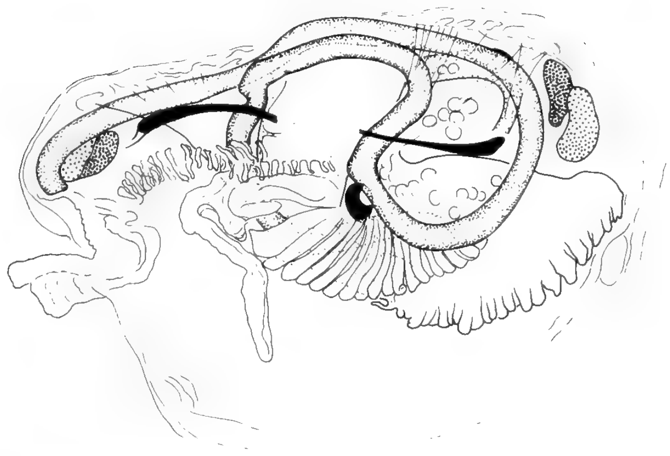

Fig. 43 *Yoldiella biscayensis*. Lateral view from the right side of the internal morphology of a specimen from Sta. BG VI DS76 West European Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

possible to identify which of the two is *L. lata*. We have separated the two species and chosen lectotypes from the 'Valorous' material.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Sarsia	44	1739	18	43°40.8′N	3°35.2′W	ED	16. 7.67
	65	1922	25	46°15.0′N	4°50.0′W	ED	25. 7.67
La Perle							
(Biogas I)	DS06		3				
	DS07		2				
	DS11	2205	8	47°35.5′Ne	8°33.7′	WDS	8. 8.72
	DS12	2180	2	47°28.5′N	8°35.5′W	DS	9. 8.72
	DS13	2165	5+1v	47°33.7′N	8°39.9′W	DS	9. 8.72
	OS01		2v			OS	
Chain 106	313	1491–1500	457	51°32.2′N	12°35.9′W	ES	17. 8.72
	316	2173–2209	1653	50°58.7′N	13°01.6′W	ES	18. 8.72
Jean Charcot							
(Polygas)	DS15	2246	8	47°35.2′N	8°40.1′W	DS	21.10.72
	DS16	2325	1	47°36.1′N	8°40.5′W	DS	21.10.72
	DS18	2138	10	47°32.2′N	8°44.9′W	DS	22.10.72
	DS25	2096	255	44°08.2′N	4°15.7′W	DS	1.11.72
	DS26	2076	1095 +17v	44°08.2′N	4°15.0′W	DS	1.11.72
	CV10	2108	2	47°30.7′N	8°40.6′W	CV	22.20.72
Jean Charcot							
(Biogas II)	DS32	2138	26	47°32.2′N	8°05.3′W	DS	19. 4.73
(Biogas III)	DS35	2226	9	47°34.4′N	8°40.7′W	DS	24. 8.73
	DS36	2147	7+2v	47°32.7′N	8°36.5′W	DS	24. 8.73
	DS37	2110	12+2v	47°31.8′N	8°34.6′W	DS	24. 8.73
	DS38	2138	13	47°31.5′N	8°35.8′W	DS	25. 8.73
	DS49	1845	177+ 25v	44°05.0′N	4°15.6′W	DS	1. 9.73
	DS50	2124	153+ 61v	44°09.9′N	4°15.9′W	DS	1. 9.73
(Biogas IV)	DS51	2430	421+ 101v	44°11.3′N	4°15.4′W	DS	18. 2.74
	DS52	2006	183+ 190v	44°06.3′N	4°22.4′W	DS	18. 2.74
	DS61	2250	3	47°34.7′N	8°38.8′W	DS	25. 2.74
	DS62	2175	48+1v	47°32.8′N	8°40.0′W	DS	26. 2.74
Jean Charcot	DS64	2156	12+ 14v	47°29.2′N	8°30.7′W	DS	26. 2.74
	CV33	1913	1	44°04.6′N	4°18.1′W	CV	18. 2.74
	CP01	2245	19+4v	47°34.6′N	8°38.8′W	CP	25. 2.74
(Biogas V)	DS70	2150	6	44°08.8′N	4°17.4′W	DS	21. 6.74
	CP07	2170	136+ 4v	44°09.8′N	4°16.4′W	CP	21. 6.74
(Biogas VI)	DS71	2194	19	47°34.4′N	8°33.8′W	DS	20.10.74
	DS86	1950	325+ 13v	44°04.8′N	4°13.7′W	DS	31.10.74
	DS87	1913	550+ 4v	44°05.2′N	4°19.4′W	DS	1.11.74
	DS88	1894	40+2v	44°05.2′N	4°15.7′W	DS	1.11.74
	CP08	2177	12+1v	44°33.2′N	8°38.5′W	CP	20.10.74
	CP09	2171	34	47°33.0′N	8°44.1′W	CP	20.10.74
	CP24	1995	23	44°08.1′N	4°16.2′W	CP	31.10.74
Jean Charcot	CP01	2068–2040	29	55°57.0′N	10°55.0′W	CP	16. 7.76
(Incal)	CP02	2091	4	57°58.4′N – 57°57.7′N	10°42.8′W 10°44.6′W	CP	16. 7.76
	CP08	2644 –	1	50°14.7′N 50°15.2′N	13°13.5′W 13°14.8′W	CP	27. 7.76
	QS01	2634	2	50°14.4′N – 50°15.2′N	13°10.9′W 13°11.0′W	OS	30. 7.76
	DS01	2091	234	57°59.7′N – 57°59.2′N	10°39.8′W 10°41.3′W	DS	15. 7.76
	DS02	2081	262	57°58.8′N – 57°58.5′N	10°48.5′W 10°49.2′W	DS	16. 7.76
	DS05	2053	7	56°28.1′N – 56°17.6′N	11°11.7′W 11°12.0′W	DS	18. 7.76
	DS06	2494	86	56°26.6′N – 56°15.9′N	11°10.5′W 11°10.7′W	DS	18. 7.76
	WS01	2550–2539	6	50°19.4′N – 50°19.3′N	13°08.0′W 13°06.9′W	WS	30. 7.76
	WS02	2498–2505	4	50°19.3′N – 50°20.0′N	12°55.8′W 12°56.0′W	WS	30. 7.76
CANARIES BASIN							
Discovery	6701	1934	9	27°45.2′N	14°13.0′W	ED	16. 3.68
SIERRA LEONE BASIN							
Atlantis II 31	139	2099–2187	1	10°33.0′N	17°53.0′W	ES	4. 2.67

Largely restricted to lower slope and abyssal rise depths in the northeastern Atlantic, but predominantly in the West European Basin with a few specimens taken in the Canaries and Sierra Leone Basins. Depth range: 1491–3220 m.

SHELL DESCRIPTION (Figs. 44 & 45). Shell transversely ovate, fragile, inequilateral, postumbonal length 53–65% of total length, moderately inflated, very fine concentric lines forming ridges ventrally, more conspicuous in larger specimens, irridescent, pale yellow/brown periostracum, light and dark banding patterns; umbo moderately inflated, inwardly directed; dorsal margin raised, anterior and posterior margins smoothly curved with anterior margin more convex than posterior, antero-dorsal margin short, joins anterior margin in smooth curve, postero-dorsal margin approximately straight, gradually inclining distally to posterior limit of hinge plate, then curves sharply to posterior margin, posterior margin more convex dorsally, ventral margin smoothly curved; hinge plate narrow, anterior and posterior hinge plates merge with margin below umbo, teeth small, chevron-shaped, number on each plate depending on size (up to 9/10), usually with one or two less on anterior hinge plate; ligament amphidetic, small, internal rectangular in cross-section.

Prodissoconch length: 198 μm (average) range 190–220 μm. Maximum recorded shell length: 4.43 mm.

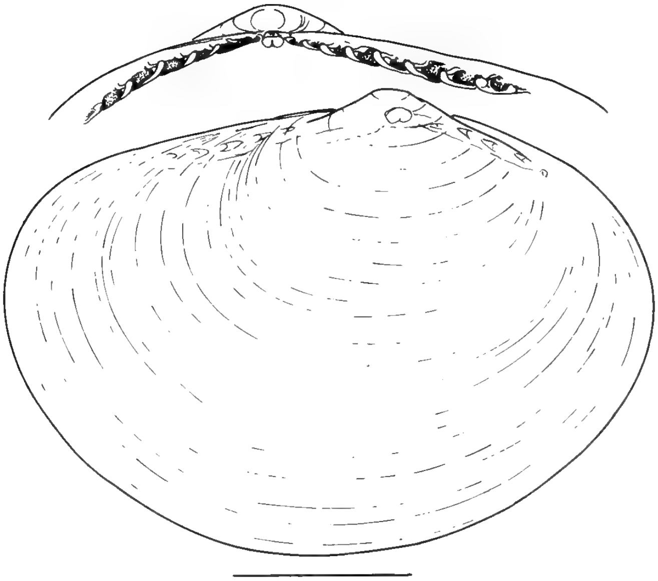

Fig. 44 *Yoldiella lata*. Lateral view of a shell from the right side and detail of the hinge-plate of a right valve. Specimens from Sta. 316 West European Basin. (Scale = 1.0 mm).

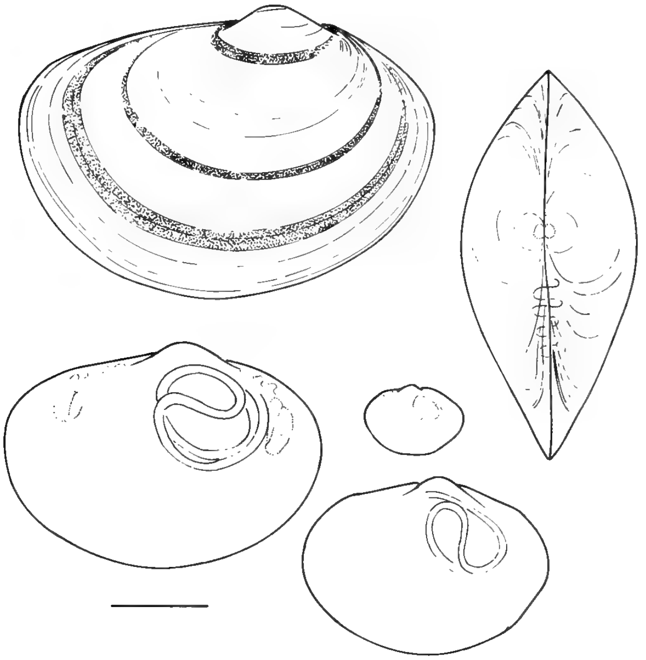

Fig. 45 *Yoldiella lata*. Right lateral and dorsal views of shells to show changes in shape with growth. Specimens from Sta. INCAL/DS 06 West European Basin. (Scale = 1.0 mm).

The shell is similar in shape to *Yoldiella jeffreysi* but more fragile, more compressed, and has fewer hinge teeth on a narrower hinge plate. With increasing length there is a gradual increase in the posterior umbonal length/total length ratio. There is little change in the height/length or width/length ratios (Fig. 46). Hydroids are present on several specimens at the antero-ventral shell margin.

INTERNAL MORPHOLOGY (Fig. 47). With the exception of the

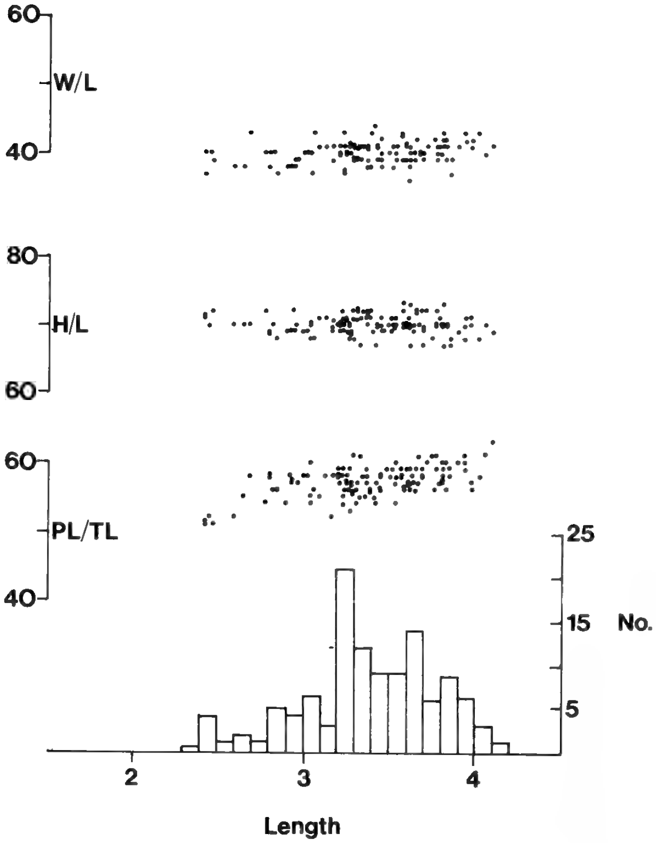

Fig. 46 *Yoldiella lata*. Variation in the ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of a sample from Sta. BG V CP 07 from the West European Basin.

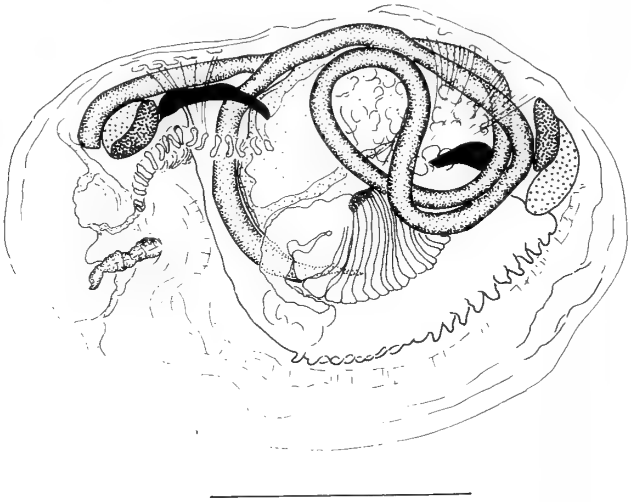

Fig. 47 *Yoldiella lata*. Lateral view from the right side of the internal morphology of a specimen from Sta. BG III DS 50 West European Basin (Scale = 1.0 mm). For identification of parts see Fig. 34.

posterior margin, the mantle edge is little modified and comprises three marginal lobes. The middle sensory lobe forms a frill while the inner muscular fold is thickened, being approximately twice the thickness of the general mantle epithelium and is relatively broad. Posteriorly combined exhalent and inhalent siphons are formed by fusion of the opposing inner muscular lobes. The inhalent siphon is shorter than the exhalent siphon and remains open ventrally. The siphonal wall is relatively thin. A narrow band of longitudinal muscles lies immediately internal to the basal membrane of the outer and inner epithelia. Internal to the longitudinal fibres are circular and transverse muscle fibres with sub-epithelial gland cells scattered throughout the layer. Between the exhalent and inhalent siphons, there is a pair of haemocoelic channels within the muscle layer (Fig. 48a). The proximal end of the gill axes join laterally at the junction between the siphons. The gill axes probably act as a channel to guide faecal rods into the lumen of the exhalent siphon. The anus lies immediately dorsal to the inner margins of the siphon.

The siphonal tentacle, is developed from the middle sensory lobe of the mantle and originates from a pocket in the siphonal embayment at the base of the siphon, usually on the left side. It consists of an elongate finely-tapering cone which in transverse section comprises a large central nerve surrounded by several muscle fibres (Fig. 48b). These in turn are surrounded by a layer of connective tissue with gland cells interspersed throughout and a layer of epithelial cells with fine granular contents.

Ventral to the siphon is a broad, deep, specialized area of the mantle – the feeding aperture. Ventral to the inhalent aperture there is an inner secondary muscular fold. Peripheral to this the inner muscular layer is enlarged both in thickness and width. In preserved specimens this area is highly convoluted. In life the muscular and sensory layers are probably extended beyond the shell margin as a flap on each side. The epithelial cells in this region are densely ciliated (Fig. 48a).

The adductor muscles are unequal in size with the 'quick' and 'catch' parts obvious. The posterior adductor is round in outline. The anterior is approximately twice the size of the posterior and crescent-shaped. At the mantle margin ventral to the anterior adductor muscle there is a well-developed anterior sense organ. This is derived from the middle sensory fold which is greatly extended to form two flaps. The epithelial cells of the outer flap are ciliated. Internal to this the epithelium is glandular (Fig. 48c). Underlying this epithelium is a thick layer of connective tissue containing the pallial nerve.

The gills lie parallel to the postero-dorsal shell margin. They are well-developed with up to 22 alternating gill plates (the number relates to the size of the individual).

The labial palps are moderately large and, also depending on the size of the animal, have up to 24 ridges on their inner face. The palp proboscides are relatively slender. The palps are wedge-shaped and extend 1/4–1/2 way across the body. The mouth is set posterior to the anterior adductor muscle.

The foot is well-developed, and of typical nuculanid form. The divided sole is elongate with papillate edges. At the tips of the papillae, lying between muscle fibres are glandular cells with ducts to the surface of the foot. Secretions from these may be used to lubricate the movement of the foot through the sediment. A large well-developed byssal gland is present in the heel of the foot (Fig. 49a). The byssal gland is spherical, composed of large, hyaline cells, surrounded by muscle fibres. It opens medially at the posterior limit of the divided sole and several glandular epithelial cells surround the opening. A very small medial papilla lies posterior to the opening at the heel of the foot. Histochemical tests have been carried out to identify type secretion from the gland. Tests did not confirm any protein component but this could have been masked by other muco-substances. The main component at the centre of the byssal gland appears to be a keratin-sulphate (PAS-ve with no glycol groups, and carboxyl groups). It has the character of cartilage. (Secretions from the gland cells in the foot do, however, possess carboyxyl groups).

The posterior pedal retractor muscles comprise a thick, wide, strap that inserts on the shell on either side of the hind gut anterior to the posterior adductor muscle. A small postero-lateral pedal retractor muscle is present on either side of the stomach. Three major pairs of anterior pedal retractor muscles pass from the neck of the foot anteriorly to insert posterior to the anterior adductor muscle on either side

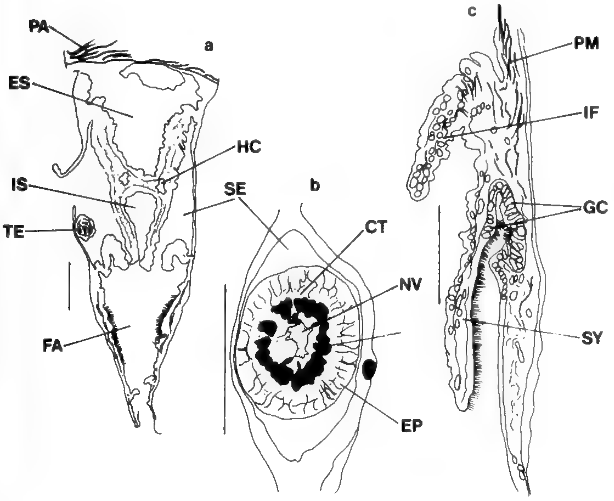

Fig. 48 *Yoldiella lata*. Transverse sections through a, the inhalent, exhalent and feeding apertures; b, the base of the siphonal tentacle; c, the anterior sense organ of a specimen from Sta. BG III DS 49 West European Basin. (Scales = 0.1 mm).

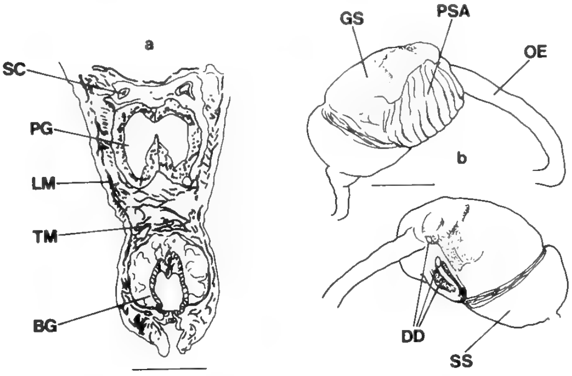

Fig. 49 *Yoldiella lata*. a, transverse section through the heel and 'byssal' gland of the foot and b, right and left lateral external views of the stomach and style sac of specimens from Sta. Polygas DS 26 West European Basin. (Scales = 0.1 mm).

of the oesophagus and lateral to the hind gut loop.

The cerebral ganglia are relatively small and oval while the visceral ganglia are elongate and relatively thickened. The pedal ganglia are large and elongate/oval, conjoined, and each has a large dorsal statocyst associated with it and which contains numerous small refractile crystals.

The mouth is displaced posteriorly to a small extent. It opens into a relatively long, ciliated oesophagus which curves first anteriorly to the posterior face of the anterior adductor before passing posteriorly to the stomach. The oesphagus is positioned almost centrally rather than dorsally within the body. The longitudinal axis of the stomach and style sac lies diagonally within the body, the style sac penetrating into the upper half of the foot. The stomach and style sac are large, taking up much of the central body space. Externally the stomach is brown in colour. A large gastric shield covers part of the dorsal wall and extends laterally, mainly to the left side. To the right of it are approximately nine sorting ridges. The organization of the stomach appears similar to that described for *Ledella* (Allen & Hannah, 1989). The stomach is cradled by the pedal retractor muscles. The digestive diverticla are in three parts which for the most part lie anterior to the stomach but also to the right and left of the body. A duct from the right diverticulum joins the stomach on the right anterior face just ventral to the oesophageal opening. Immediately posterior to this, a duct from one of the two left diverticula enters the stomach on the lower left side (Fig. 49b). The third diverticulum opens into the stomach immediately below the tooth of the gastric shield. The epithelial cells which line these ducts contain highly refractile golden granules. In the case of the third diverticulum the duct is reduced to a small collar of cells around the aperture. Material was present in the lumen of this diverticulum but not in the other two diverticula.

From the style sac, the hind gut passes posteriorly into the foot, as far as the pedal ganglia. It then passes anterior for a short distance between ganglia and byssal gland and then takes a dorsal course parallel to the posterior margin of the foot to a point immediately ventral to the ligament. It then forms a loop on the right side of the body which skirts the posterior face of the anterior adductor and then passes dorsally and posteriorly parallel to shell margin to the anus. A deep typhlosole is present along the entire length of the hind gut. Slight variations in the arrangement of the loop of the hind gut are seen in this species. Material in the gut consists of fine clay particles and skeletal fragments of various kinds.

The sexes are separate. The gonads overlie the lateral and dorsal sides of the viscera of the body. Gonads are present in all specimens over 2 mm in length. Numbers of ova are relatively high and vary with the size of the animal. A maximum of c.730 ova were counted in a specimen 3.54 mm in length. The maximum observed diameter of the ova range from 126–190 μm. There is some indication of an annual reproductive cycle. Ova of maximum size were present in October and February. April and June samples show little ovarian development, but increasing maturity was observed in July and August. The gonadial apertures open into the supra-mantle cavity, close to those of the kidney, anterior to the posterior pedal retractor muscle.

The kidney is well-developed. It lies anterior to the posterior pedal retractor muscle and extends on either side of the stomach, tapering to its anterior limit close to the lateral pedal retractor mucles. The kidney epithelium is a single layer of cuboid cells. The heart, through which the hind gut passes is well-developed in this species with numerous muscle fibres in a relatively thick-walled ventricle.

Distinctive features include the hind gut on the right hand side of body forming an extended single loop which turns back on itself; the light and dark banding pattern of shell, and the more rounded posterior adductor muscle. The hind gut, although similar, is simpler in form than that in *Yoldiella jeffreysi*.

Yoldiella frigida Torrell 1859

TYPE LOCALITY. Spitzbergen, Ice Sound 55 m.

TYPE SPECIMEN. Holotype not known; lectotype (desig. A. Warén, 1989) Swedish Museum of Natural History No. 1986.

Yoldia frigida Torrell 1859, p.148, pl. 1, Fig. 3; Friele 1878, p. 222; Leche 1878, pl. 1, Fig. 6 a–d; Sars G.O. 1878, pl. 4, Fig. 11a–b; Friele 1879, p. 266.

Leda frigida Jeffreys 1870, p. 440; Jeffreys 1879, p. 570.

Portlandia frigida Norman 1893, p. 344, p. 364; Posselt 1898, p. 34–35; Friele & Grieg 1901, p. 15; Hogg 1905, p. 112; Jensen 1905, p. 320; Grieg 1909, p. 534; Ohdner 1915, pl. 1, Figs. 30–32;

Portlandia frigida Grieg 1916, p. 8; Ockelmann 1958, pl. 1. Fig. 14.

Portlandia (Yoldiella) frigida Soot–Ryen 1939, p. 9; Clarke 1963, p. 100, pl. 2, Figs. 6–8.

Yoldiella frigida Soot-Ryen 1958, p. 10; Warén, 1989; Figs. 7E & F & 10 G & H.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICAN BASIN							
Atlantis	4	400	304	39°56.6′N	70°39.9′W	AD	30. 8.62
Chain 58	105	530	121	39°56.6′N	71°03.6′W	ET	5. 5.66
Chain 88	207	805– 811	153	39°51.3′N – 39°51.0′N	70°54.3′W 70°56.4′W	ES	21. 2.69
WEST EUROPEAN BASIN							
Thalassa	2425	700	1	48°28.9′N	09°44.0′W	PBS	25.10.73
Jean Charcot	DS04	619	1	57°23.0′N	11°07.0′W	DS	17. 6.76
Incal	DS03	609	16	57°25.1′N	11°03.7′W	DS	17. 6.76

In addition to the above, material from Ingolf Sta. 115 (det Ockelmann), Spitzbergen, Franz Joseph Fjord, East Greenland (USNM No. 219726 det. Odhner) and off Martha's Vineyard Sta. 934 (USNM No. 193343 det. Verrill & Bush) has been examined.

Predominantly a North Atlantic high arctic species from shelf seas and upper slope depths (Warén (1989). Clarke (1963) reports it as being present at abyssal rise depths but there must be some doubt about this. There is some indication that in north temperate seas at the southern extremity of its range the population is found deeper at the shelf slope break, thus suggesting a relationship with temperature. Greenland, Jan Mayen, Spitzbergen, Novaya Zemlya, Kera Sea, West Siberia, Iceland, North American and West European Basins (see Ockelmann (1958) for other more doubtful records). Depth range: 5–811 m.

SHELL DESCRIPTION (Fig. 50 & 51). Shell subelliptical,

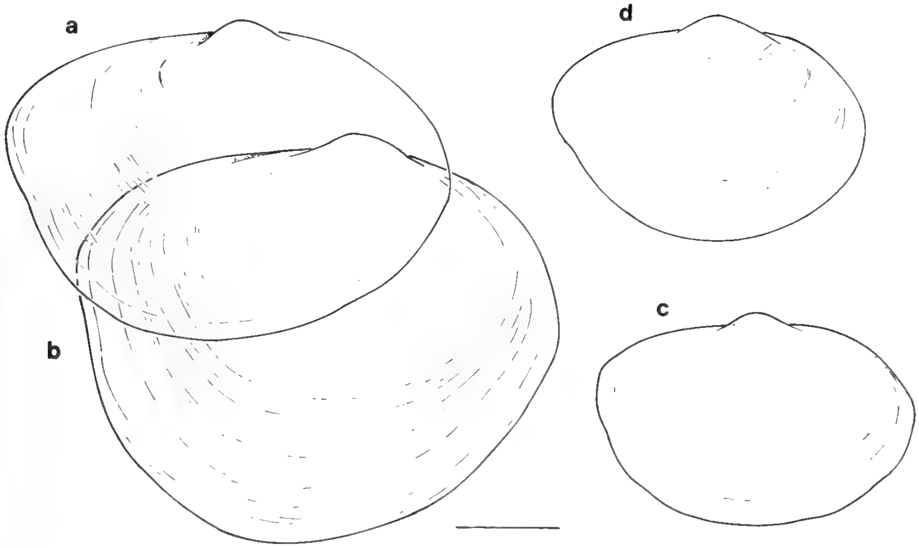

Fig. 50 *Yoldiella frigida*. Lateral views of shells from the right side. Specimens a & b from Franz Joseph Fjord, E. Greenland; c, from Sta. INCAL DS 04 Bay of Biscay; d, from off Martha's Vineyard (USNM No. 193343). (Scale = 1.0 mm).

approximately equilateral (postumbonal length 45–50% of total length), smooth, moderately thin, pale yellow irridescent periostracum, with banding patterns, narrow dark bands and broader light bands between; umbo slightly raised directed somewhat posteriorly; dorsal margins proximally straight, distally curving to anterior and posterior margins, posterior and anterior dorsal margins very slightly angulate at limit of hinge plate, limit of anterior margin submedial, limit of posterior margin supramedial, postero-ventral margin relatively flattened, very slightly sinuous particularly in larger specimens; hinge plate relatively short, not extending beyond inner margin of adductor muscles, 5 anterior teeth and 6 posterior teeth in specimen 2.5 mm, ventral part of chevron reduced; ligament amphidetic, large elongate internal part, with small external extensions either side of umbo; adductor muscle scars distinct, particularly anterior, line of attachment of pallial sinus also visible. Hydroids may be present, dorsally, close to umbo and on the posterior and postero-ventral margins.

Prodissoconch length: 166–208 μm. Maximum recorded shell length: 3.98 mm, (Sta. 207), however, specimens from Greenland donated by Ockelmann measure 6.1 mm.

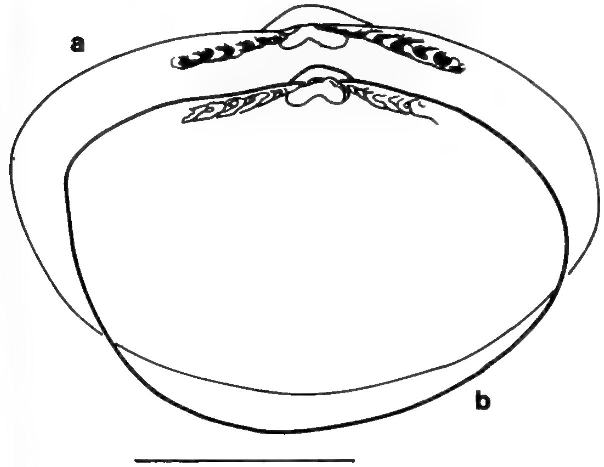

Fig. 51 *Yoldiella frigida*. Lateral views of left valves showing detail of the ligament and the hinge-plates; a, a specimen from Stor Fjord Spitzbergen (USNM No. 219726); b, a specimen from Sta. 105 North America Basin. (Scale = 1.0 mm).

Comparing height/length, width/length and post-umbonal length/total length ratios of specimens from the North American Basin (Sta. 105 & 207) and West European Basin (Incal DS03), it was found that in the latter case the average for each of the three parameters is slightly less than those from the two North American Stations and whose ranges for the most part overlap (Figs. 52 & 53). Specimens from Sta. 105 appear to be somewhat wider than specimens from Sta. 207.

It is highly likely that many records of *Y. frigida* from the North Atlantic relate to other species. This is a view also expressed by Warén (1989). For example, *Y. frigida* (USNM No. 193343) figured by Verrill & Bush (1898) and here (Fig. 50), closely resembles *Yoldiella nana* again confirming the observations of Warén (1989). (*Y. nana* has a straighter dorsal margin, a slightly more inflated umbo and fewer hinge teeth). Further comparing USNM No. 193343 with high arctic specimens of *Y. frigida* the former has a larger umbo, and thicker hinge. In addition, we believe that many shallow water specimens of *Yoldiella inconspicua* from the North American Basin have been misidentified as *Y. frigida*. Subtle differences seen here, as in many other deep-sea protobranch bivalves, are particularly difficult to disentangle (Fig. 53) and in the case of *Yoldiella* this particularly applies to species found at shallower slope depths.

INTERNAL MORPHOLOGY (Fig. 54). Mantle structures include a well-developed anterior sense organ and long slender combined siphons with a single lumen. A siphonal tentacle is present originating, but not without exception, on the left side of the inner limit of the siphon embayment. The adductor muscles are unequal in size the anterior being the somewhat larger and oval in outline whereas the posterior muscle is more circular in outline. The gill axes attach ventrally to the siphon and with the exception of the ventral margin, the latter must be assumed to be largely exhalent in origin. There is a well-developed feeding aperture ventral to the siphon. The gills are well-developed, the number of filaments range from 12–22 according to the size of the specimen. The palps are large and extend over approximately half the length of the body. There are between 11 and 20 relatively broad palp ridges and the palp proboscides are also well-developed. The

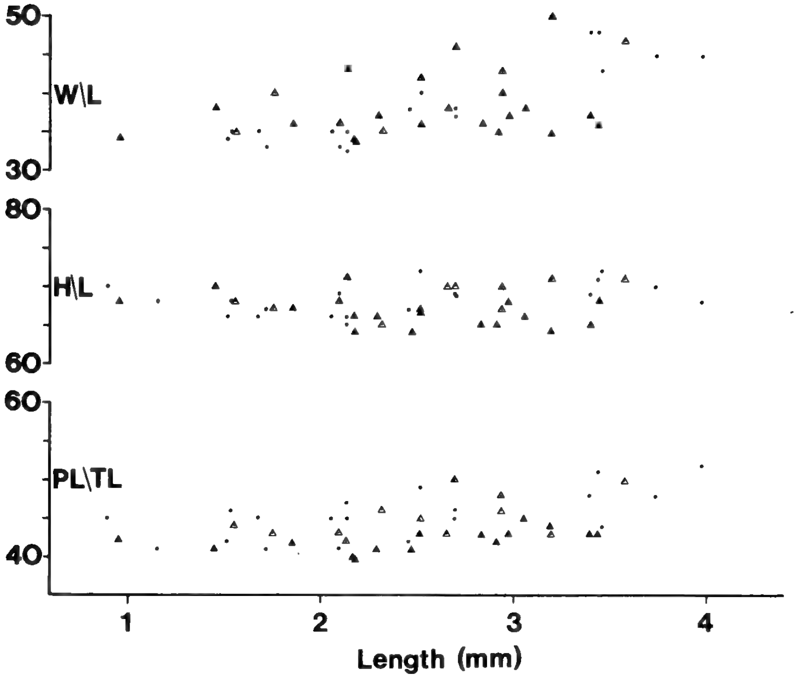

Fig. 52 *Yoldiella frigida*. Variation in ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of samples from; open triangles, Sta. 105 North America Basin; closed triangles, Sta. INCAL DS 03 Bay of Biscay; closed circles Sta. 207 North America Basin.

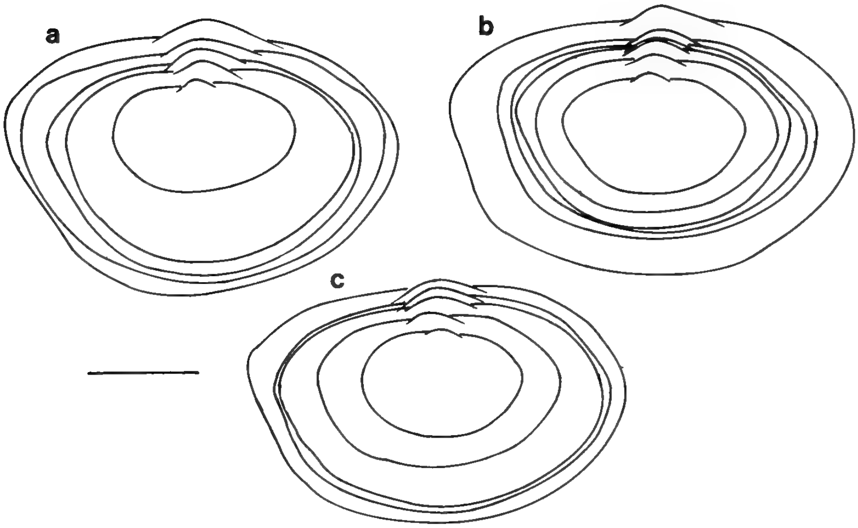

Fig. 53 *Yoldiella frigida*. Outlines of shells from the right side from three Stations to show variation in shape within and between populations and with increasing size. Specimens from a, Sta. Ingolf 115 (det Ockelmann); b, Sta. 105 North America Basin; c, Sta. INCAL DS 03 Bay of Biscay. (Scale = 1.0 mm).

foot which tends to be largely hidden by palps is also relatively large with well-developed retractor muscles. This is particularly true of the anterior series. There is a moderate-sized byssal gland. The pedal ganglia are elongate each with a large statocyst dorsal to it. The visceral ganglia lie relatively ventral in position, distant from the posterior section of the hind gut. The visceral and the cerebral ganglia are not particularly large.

The gut describes a single loop on the right side of the body. The size of the hind gut and the path it describes on the right side of the body is highly characteristic of a species even in those with a single loop and is particularly useful in distinguishing, for instance, *Y. frigida* from *Y. inconspicua* (Figs. 53 & 63). The oesophagus is particularly wide in cross-section, the stomach is large with two sorting areas clearly visible to the right side of the gastric tooth. The more ventral of the two, which has not been observed in other species, is broad and close to the aperture of the right digestive duct. Ingested material was seen in the dorsal part of the left digestive diverticulum. The duct to the right digestive diverticulum overlies the dorsal section of the hind gut. The kidney is well-developed and the pericardial cavity is large.

The sexes are separate. The developing gonads surround the hindgut loop in the usual manner. In one sectioned specimen (2.3 mm total length) 59 ova were present with a maximum diameter of 120 μm. The ova were present ventral and internal to the digestive diverticula, with fewer numbers overlying the viscera dorsally.

Yoldiella robusta (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 60, Sta. 280, Argentine Basin, 29.3.1971, 36°18.0′S, 53°23.9′W, Epibenthic Trawl, 256–293 m.

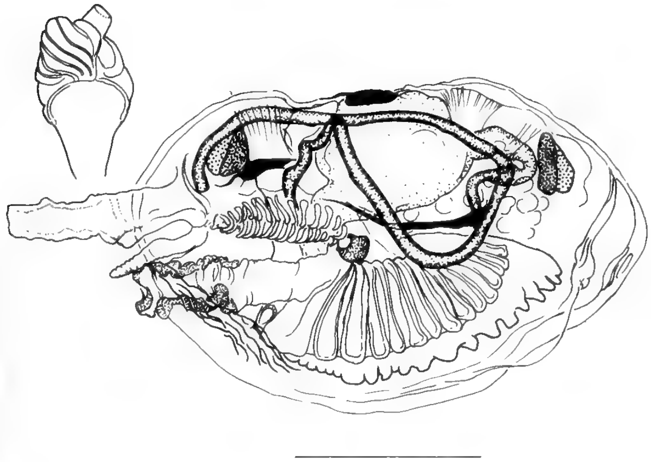

Fig. 54 *Yoldiella frigida*. Lateral view from the right side of the internal morphology of a specimen from Sta. 105 North America Basin. Inset is a right-frontal external view of the stomach. (Scale = 1.0 mm). For identification of parts see Figs. 34 & 49.

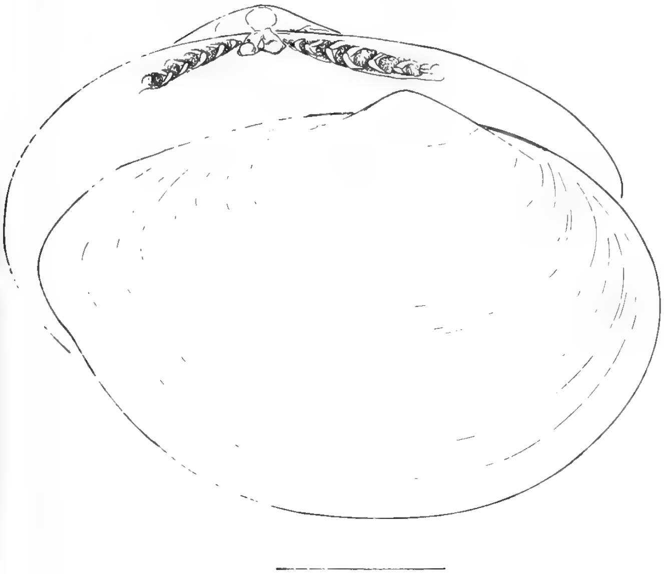

Fig. 55 *Yoldiella robusta*. Lateral view of a shell from the right side and detail of hinge-plate of a left valve. Specimens from Sta. 280 Argentine Basin. (Scale = 1.0 mm).

TYPE SPECIMEN. Holotype : BM(NH) 1992030, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II	280	256–293	3495	36°18.0′S	53°23.9′W	ES	29.3.71

Restricted to one Station at the shelf/slope break of the Argentine Basin. Depth range: 256–293 m.

SHELL DESCRIPTION (Figs. 55 & 56). Shell subovate, moderately inflated, irregular concentric growth lines and small ridges best developed posteriorly, periostracum pale yellow; umbos anterior to mid line, slightly raised and inwardly

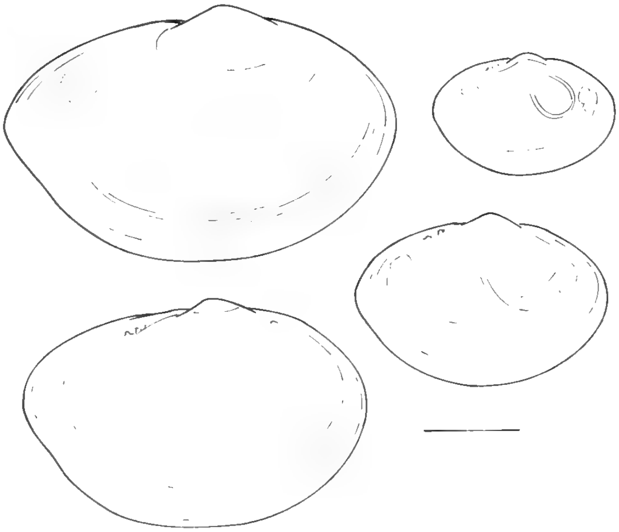

Fig. 56 *Yoldiella robusta*. Outlines of shells from the right side to show change in shape with growth. Specimens from Sta. 280 Argentine Basin. (Scale = 1.0 mm).

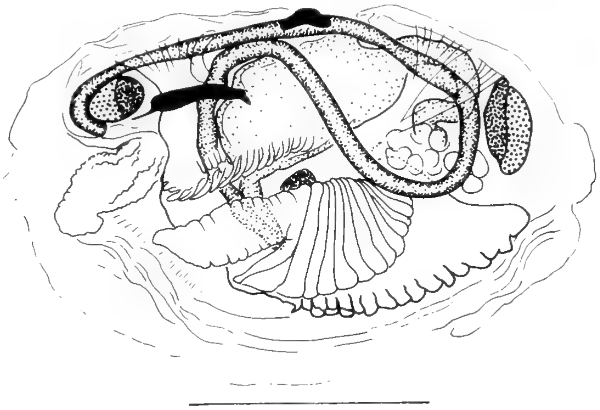

Fig. 57 *Yoldiella robusta*. Lateral view from the right side of the internal morphology of a specimen from Sta. 280 Argentine Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

directed; proximal antero-dorsal margin horizontal for very short distance before curving steeply to anterior margin, proximal postero-dorsal margin horizontal or slightly convex, distally slightly angled opposite posterior limit of hinge, postero-ventral margin slightly sinous giving a relatively narrow rounded medial tip to posterior margin, ventral margin smooth convex curve. Hinge plate short, moderately narrow with up to 9 small chevron-shaped teeth on each series, one additional tooth on posterior plate. Ligament large, amphidetic, bilobed in lateral view, with short, narrow, secondary external extensions anterior and posterior to umbo.

Prodissoconch length: c. 200 μm. Maximum recorded shell length: 4.0 mm.

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL	Teeth(A/P)
1.89	1.31	0.70	0.70	0.37	0.51	–
2.58	1.76	0.98	0.68	0.38	0.53	–
2.62	1.80	0.94	0.69	0.36	0.56	–
2.81	1.89	1.09	0.67	0.39	0.55	–
3.05	2.05	1.23	0.67	0.40	0.54	
3.44	2.21	0.64	–	–	0.57	8/9
3.55	2.38	1.44	0.67	0.40	0.55	–
3.61	2.46	0.68	–	–	0.53	7/8
3.81	2.67	1.52	0.70	0.40	0.56	–
3.98	2.62	1.58	0.66	0.40	0.59	–

INTERNAL MORPHOLOGY (Fig. 57). The internal morphology is very similar to that described for *Y. frigida*. The siphons are combined and there is a siphonal tentacle to the left. The anterior sense organ is well-developed. The adductor muscles are relatively large, the posterior being more round and slightly smaller than the anterior muscle. The foot is also large with a moderately-sized byssal gland. The gills are well developed and suspended more ventral within the mantle cavity than other species. There are approximately 15 alternating gill filaments. The labial palps extend across about half the body and have 12–16 internal ridges and well-developed palp proboscides. The visceral and cerebral ganglia are relatively large. The viscera are also more ventral in position than in most other *Yoldiella* species. The pedal ganglia are large and elongate. The hind gut forms a single loop on the right side of the body.

***Yoldiella extensa* (new species)**

TYPE LOCALITY. R.V. Atlantis II, Cruise 60, Sta. 245, Argentine Basin, 14.3.1971, 36o55.7′S, 53o01.4′W, Epibenthic Trawl, 2707 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992036, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II 60	245	2707	26	36°55.7′S	53°01.4′W	ES	14.3.71

Only found at the one Station at abyssal depth in Argentine Basin. Depth range: 2707 m.

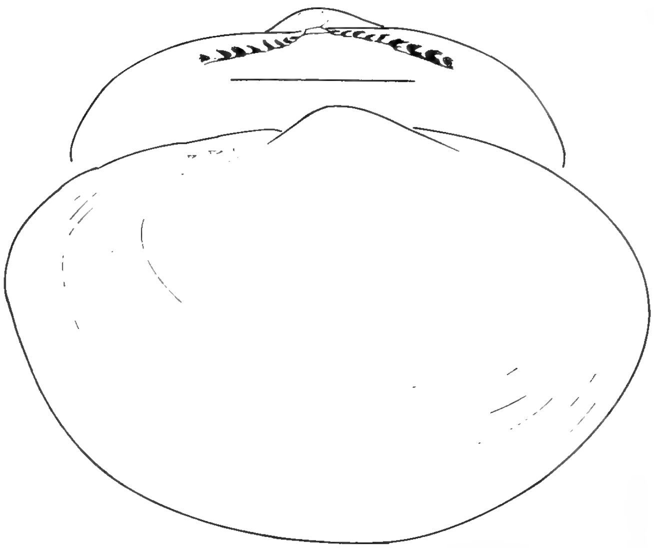

Fig. 58 *Yoldiella extensa*. Lateral view of a shell from the right side and detail of the hinge-plate of a right valve. Specimens from Sta. 245 Argentine Basin. (Scale = 1.0 mm).

SHELL DESCRIPTION (Figs. 58 & 59). Shell oblong-ovate, moderately robust, moderately inflated, nearly equilateral, very fine concentric lines, periostracum pale yellow; umbo inflated, raised slightly, directed posteriorly; dorsal margin slightly convex, antero-dorsal margin gradually slopes to broad rounded anterior margin, ventral margin long, curvature similar to that of dorsal margin, posterior margin slightly extended with faint suggestion of postero-ventral sinus; ligament amphidetic, moderate size, elongate, but slightly asymmetric in lateral view with posterior part slightly longer and wider than anterior, slight external extension on either side of umbo; hinge plate narrow, relatively short, with small eden-

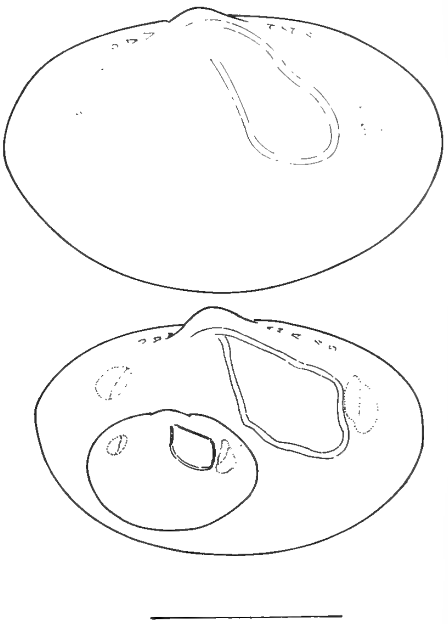

Fig. 59 *Yoldiella extensa*. Outlines of shells from the right side to show change in shape with growth (see also Fig. 58). Specimens from Sta. 245 Argentine Basin. (Scale = 1.0 mm).

tulous space below umbo, anterior plate follows curvature of antero-dorsal margin, posterior plate with slight convex arch, equal number of teeth on each plate, teeth with prominent dorsal arm and reduced ventral arm.

Prodissoconch length: c 170 μm. Maximum recorded shell length: 4.62 mm.

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
2.56	1.81	1.26	0.70	0.49	0.51
2.60	1.76	1.22	0.68	0.47	0.53

INTERNAL MORPHOLOGY (Fig. 60). The siphons are combined, with a single lumen present. A siphonal tentacle occurs on the right side of the siphonal embayment. The adductor muscles are unequal in size the anterior being one and a half to two times larger in cross-section than the posterior. Both are more or less oval in shape. The gills are well-developed with 13–16 plates. The labial palps are small in the contracted state, extending about 1/4 distance across body, and have 8–10 moderately narrow palp ridges. In contrast the palp proboscides are well-developed. The pedal ganglia are large and elongate, similarly the visceral and cerebral ganglia are also well-developed. They are club-shaped with the cerebral ganglia being slightly larger than the visceral. The foot is long and narrow, with a large byssal gland in the heel. The stomach is large and there is a single hind gut loop on the right side of the body.

Yoldiella inconspicua inconspicua **Verrill & Bush 1898**

TYPE LOCALITY. Off Martha's Vineyard, 318 fm. Original specimens were taken from North American Basin between Lat. 42°33′N, Long. 69°58.5′W and Lat. 35°12.10′N and 74°57.15′W by the U.S. Fish Commission Steamers Fish Hawk and Albatross.

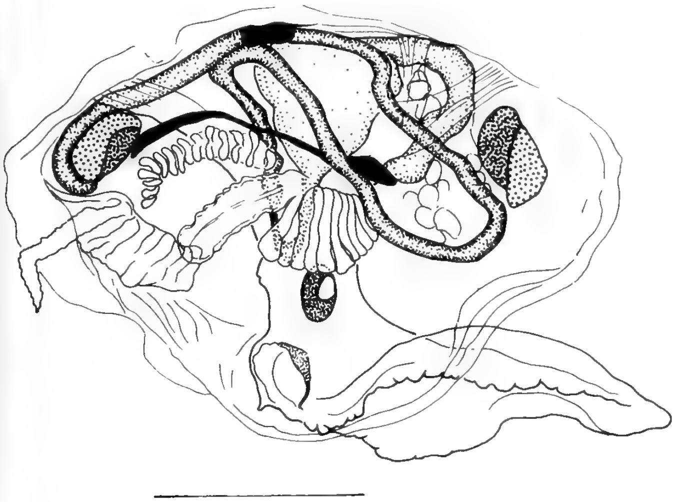

Fig. 60 *Yoldiella extensa*. Lateral view from the right side of the internal morphology of a specimen from Sta. 245 Argentine Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

TYPE SPECIMEN. Holotype: U.S. Natl. Mus. No. 48867.

Yoldiella inconspicua Verrill & Bush 1898, p. 869, pl. 79, Figs. 5–3.
Yoldiella nana Warén 1989 (in part), p. 227.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Sarsia	S44	1739	11	43°40.8′N	3°35.2′W	ED	16. 7.67
	S50	2379	343	43°46.7′N	3°38.0′W	ED	18. 7.67
Jean Charcot	DS20	4226	2	47°33.0′N	9°36.7′W	DS	24.10.72
(Polygas)	DS21	4190	3	47°31.5′N	9°40.7′W	DS	24.10.72
	DS22	4144	3	47°34.1′N	9°38.4′W	DS	25.10.72
	DS28	4413	2	44°23.8′N	4°47.5′W	DS	2.11.72
Chain 106	316	2173– 2209	20	50°58.7′N	13°01.6′W	ES	18. 8.72
	318	2868– 2890	72	50°04.9′N – 50°05.3′N	14°23.8′W 14°24.8′W	ES	20. 8.72
	323	3338– 3356	16	50°08.3′N – 50°08.3′N	13°53.7′W 13°50.9′W	ES	21. 8.72
	326	3859	3	50°04.9′N – 50°05.3′N	14°23.8′W 14°24.8′W	ES	22. 8.72
	330	4632	30	50°43.5′N – 50°43.4′N	17°51.7′W 17°52.9′W	ES	24. 8.72
Challenger	10	2540	1	56°36.0′N	11°04.0′W	ES	4. 7.73
Jean Charcot (Biogas III)	DS41	3548	5	47°28.3′N	9°07.2′W	DS	26. 8.73
(Biogas IV)	DS55	4125	58	47°34.9′N	9°40.9′W	DS	22. 2.74
(Biogas V)	DS66	3480	3	47°28.2′N	9°00.0′W	DS	16. 6.74
	DS67	4150	1	47°31.0′N	9°35.0′W	DS	17. 6.74
(Biogas VI)	DS71	2194	1	47°34.3′N	8°33.8′W	DS	20.10.74
	DS75	3250	1	47°28.1′N	9°07.9′W	DS	22.10.74
	DS76	4228	26	47°34.8′N	9°33.3′W	DS	23.10.74
	CP13	4134	4	47°34.4′N	9°38.0′W	CP	23.10.74
	DS77	4240	1	47°31.8′N	9°34.6′W	DS	24.10.74
	DS82	4462	1	44°25.4′N	4°52.8′W	DS	29.10.74
(Incal)	DS01	2091	2	57°39.8′N – 57°59.2′N	10°39.8′W 10°41.3′W	DS	15. 7.76
	DS02	2081	4	57°58.8′N – 57°58.5′N	10°48.5′W 10°49.2′W	DS	16. 7.76
	C003	2466	12	56°38.0′N – 56°37.3′N	11°64.0′W 11°07.8′W	CP	17. 7.76
	C004	2483– 1513	9	56°33.2′N – 56°32.5′N	11°11.3′W 11°12.4′W	CP	17. 7.76
	DS05	2503	270	56°28.1′N – 56°27.6′N	11°11.7′W 11°02.0′W	DS	18. 7.76
	DS06	2494	277	56°26.6′N – 56°25.9′N	11°10.5′W 11°10.7′W	DS	18. 7.76
	DS07	2884	280	55°00.7′N – 55°01.0′N	12°31.0′W 12°21.0′W	DS	19. 7.76
	DS08	2891	58	55°02.0′N – 52°01.9′N	12°34.6′W 12°33.4′W	DS	19. 7.76
	CP05	2884	149	55°00.4′N – 55°00.9′N	12°29.4′W 12°31.1′W	CP	19. 7.76
	CP06	2888– 2893	218	55°02.3′N – 55°02.6′N	12°40.3′W 12°41.7′W	CP	19. 7.76
	KR06	2891	1	55°02.9′N – 55°02.2′N	12°43.7′W 12°39.0′W	KR	20. 7.76
	KR07	2891	1	55°02.9′N – 55°02.2′N	12°43.9′W 12°39.0′W	KR	20. 7.76
	CP07	2895	488	55°03.4′N – 55°04.4′N	12°46.2′W 12°46.7′W	CP	20. 7.76
	DS09	2897	867	55°07.7′N – 55°08.1′N	12°52.6′W 12°53.2′W	DS	20. 7.76
	CP08	2644	135	50°14.7′N – 50°15.2′N	13°13.5′W 13°14.8′W	CP	27. 7.76
	DS10	1719	21	50°12.7′N – 50°13.2′N	13°16.6′W 13°16.4′W	DS	27. 7.76

QS01	2634	322	50°14.4′N – 50°15.2′N	13°10.9′W 13°11.0′W	OS	30. 7.76
WS01	2550	221	50°19.4′N – 50°19.3′N	13°08.1′W 13°06.9′W	WS	30. 7.76
WS02	2498	287	50°19.3′N – 50°20.0′N	12°55.8′W 12°56.0′W	WS	30. 7.76
CP10	4823	2	48°25.5′N – 48°26.3′N	15°10.7′W 15°09.8′W	CP	31. 7.76
WS03 (broken valve)	4829	1	48°19.2′N – 48°19.1′N	15°23.3′W 15°22.5′W	WS	1. 8.76
WS07	4281	5	47°30.6′N – 47°31.2′N	9°37.1′W 9°35.7′W	WS	7. 8.76
DS14	4254–4307	1	47°32.6′N – 47°32.9′N	9°35.7′W 9°35.1′W	DS	7. 8.76
OS06	4316–4307	2	46°27.3′N – 47°27.9′N	9°36.2′W 9°36.0′W	OS	9. 8.76
DS16	4268	7	47°29.8′N – 47°30.3′N	9°33.4′W	DS	9. 8.76
QS07	4249	2	47°36.8′N – 47°31.3′N	9°34.3′W 9°34.3′W	OS	10. 8.76
QS08	4327	1	47°29.8′N – 47°29.5′N	9°39.2′W 9°38.8′W	QS	11. 8.76

NORTH AMERICA BASIN

Atlantis II 12	62	2496	25	39°26.0′N	70°33.0′W	ET	21. 8.64
	64	2886	80	38°46.0′N	70°06.0′W	ET	21. 8.64
	72	2864	120	38°16.0′N	71°47.0′W	ET	24. 8.64
	73	1330-1470	1	39°46.5′N	70°43.3′W	ET	25. 8.64
Chain 50	76	2862	53	39°38.3′N	67°57.8′W	ET	29. 6.65
	78	3828	3	38°00.8′N	69°18.7′W	ET	30. 6.65
	85	3834	32	37°59.2′N	69°26.2′W	ET	5. 7.65
	87	1102	17	39°48.7′N	70°40.8′W	ET	6. 7.65
Atlantis II 24	126	3806	14	39°37.0′N – 39°37.5′N	66°47.0′W 66°44.0′W	ET	24. 8.66
Chain 106	334	4400	5	40°42.6′N – 40°44.0′N	46°13.8′W 46°14.6′W	ES	30. 8.72
	335	3882–3919	12	40°25.3′N	46°30.0′W	ES	31. 8.72
Knorr 35	340	3264–3356	95	38°14.4′N – 38°17.6′N	70°20.3′W 70°22.8′W	ES	24.22.73

We have examined the Verrill & Bush material housed in the U.S. National Museum. With the exception of specimen No. 49390, which is more inflated and slightly more inequilateral than is typical of specimens of *Y. inconspicua* and which is probably *Y. frigida,* the Verrill & Bush collection is correctly described.

Warén (1989) synonymizes *Y. inconspicua* with *Y. nana*. We disagree with this view. *Y. nana* is essentially a high latitude species from the shelf and upper slope while *Y. inconspicua s.s.* is restricted to temperate latitudes at lower slope to abyssal depths in the North American and West European Basins.

Depth range: 1102–4829 m, but most common between 2400–3000 m.

SHELL DESCRIPTION (Fig. 61). The shell is very well described by Verrill & Bush (1898). We would add that although the shell is small, compressed and an ovate wedge-shape, the width, height and thickness of shell for any given length is variable (Fig. 62). Some specimens have a slightly sinuous postero-ventral margin. In many specimens the gut and internal organs are visible through a transparent shell, in others light and dark banding patterns are present on thicker shells. Hydroids may be present over most of the shell margin. The large elongate, slightly 'saddle-shaped', internal ligament is characteristic. The hinge teeth are small, the total number ranges from 6 in an individual 2.42 mm in length to 13 in an individual of 3.44 mm in length. There is normally an additional tooth in the anterior series (3/3–7/6). Although the shape varies between individuals there is an overall trend of a slight increase in posterior umbonal length and in width with increasing shell length. The height ratio remains more or less constant (Fig. 62). Analysis of shell length of two samples from the east and west Atlantic showed marked size differences (Fig. 64) probably indicative of the differences in time of successful settlements. Individual peaks in the sample from the Bay of Biscay perhaps might indicate an annual breeding event and a lifespan of 5 or 6 years.

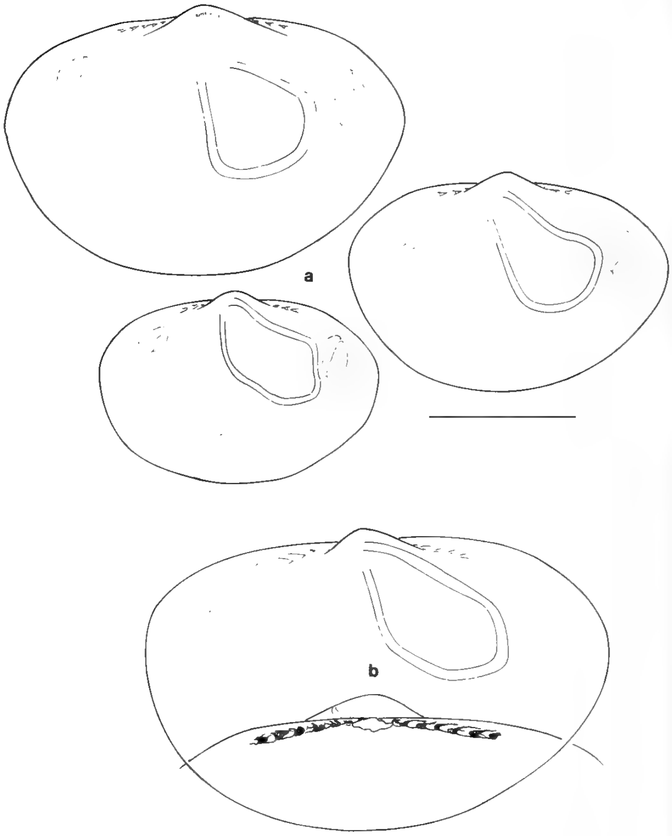

Fig. 61 *Yoldiella inconspicua inconspicua*. Lateral views of shells from the right side and detail of hinge from a right valve; a, variation in shape of three specimens from Sta. 76 North America Basin with b, a specimen from Sta. INCAL CP 06 West European Basin. (Scale = 1.0 mm).

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
4.20	2.87	1.66	0.68	0.39	0.53
4.03	2.78	1.54	0.69	0.38	0.51
3.79	2.71	1.53	0.71	0.40	0.50
3.66	2.45	1.43	0.66	0.39	0.53
3.58	2.50	1.38	0.70	0.38	0.50
3.41	2.75	–	0.72		0.53
1.49	1.02	0.54	0.69	0.36	0.48
0.99	0.76	–	0.77	–	0.48
0.93	0.62	–	0.67	–	0.50

INTERNAL MORPHOLOGY (Fig. 63). The morphology of the mantle is essentially the same as in other nuculanoid species. There are typically three mantle lobes. Specialization of the mantle margin includes an anterior sense organ, in position

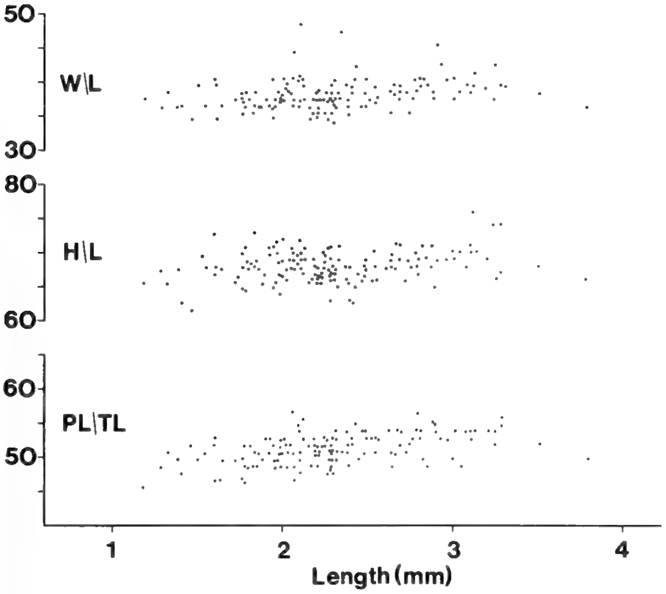

Fig. 62 *Yoldiella inconspicua inconspicua.* Variation in the ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of a sample from Sta. INCAL CP 08 West European Basin.

vertically below the anterior adductor muscle. A large siphonal tentacle is usually attached on the right side of the innermost wall of the siphonal embayment, but was recorded on the left in a few specimens. Siphons are combined and form a wide tube with a single lumen. The feeding aperture is not particularly well-developed, being represented in *Y. inconspicua* by two small flaps ventral to the combined siphon. The inner muscular layer is not expanded anterior to these, as it is in some other *Yoldiella* species. The adductor muscles are large and approximately equal in size. The posterior muscle is circular and the anterior more 'crescent-shaped'.

The gills are well-developed and filaments number from 12–23, the latter in a large individual 3.55 mm in length. The distal gill filaments lie close to the siphon and the gill axis attaches to the siphon ventro-laterally. The labial palps are moderately large with between 12–22 ridges on the internal face. The palp proboscides are long and thin. The cerebral ganglia are large, the visceral ganglia are moderate in size and the pedal ganglia are large and elongate oval in shape. They lie more dorsal in position in the foot than in most other *Yoldiella* species. The foot is divided and fringed with papillae and has a large byssal gland in the heel.

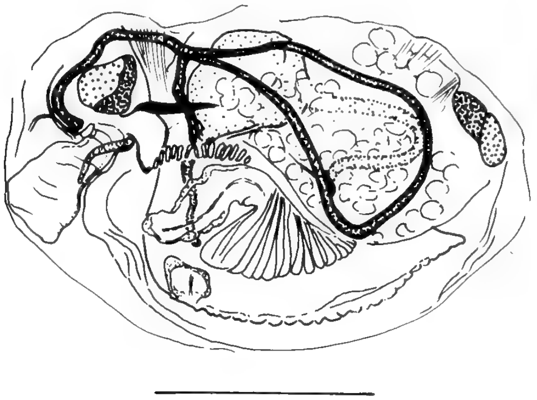

Fig. 63 *Yoldiella inconspicua inconspicua.* Lateral view from the right side of the internal morphology of a specimen from Sta. 72, North Atlantic Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

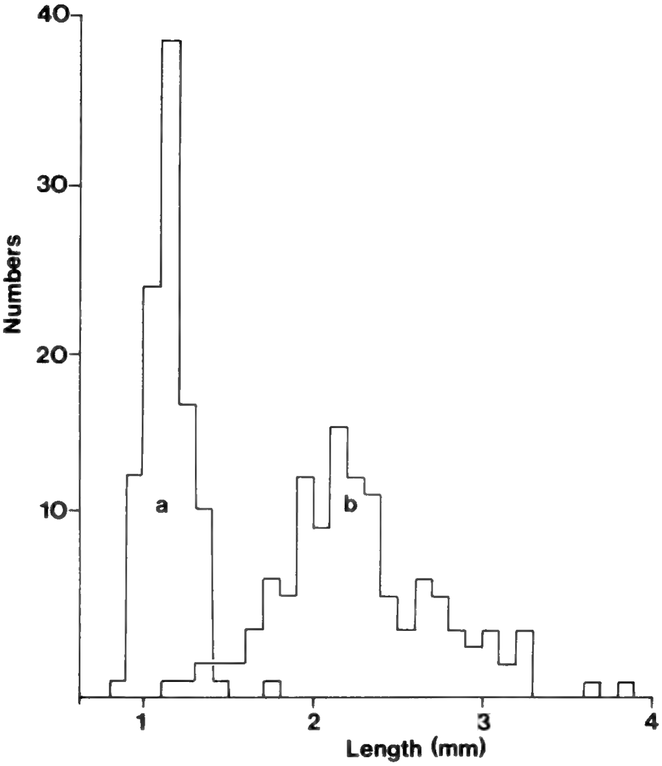

Fig. 64 *Yoldiella inconspicua inconspicua.* Length frequency histograms of two samples from a, Sta. 72 North America Basin and b, Sta. INCAL CP 08 West European Basin.

The oesophagus is distended and wide in diameter. The longitudinal plane of the stomach lies at an angle to the vertical sagittal plane, and anteriorly is displaced to the right while posteriorly it lies to the left. The stomach is large but somewhat laterally flattened. The style sac is small. The first section of the hind gut which lies within the foot is wide in section from thence it curves dorsally parallel to the posterior margin of the foot. At its dorsal limit of its course there are two small kinks to the left of the body (possibly a result of contraction in preserved specimens) before it crosses to the right side to form a single anterior loop the outline of which is characteristic of the species. The diameter of the gut appears to vary somewhat between populations, western Atlantic specimens appear to have a more slender hindgut although the dimensions fall within the overall range of eastern Atlantic specimens. A typhlosole is present along the whole length of the gut. A considerable amount of food material is frequently present in the left hand digestive diverticulum. The digestive diverticula extend well posterior within the

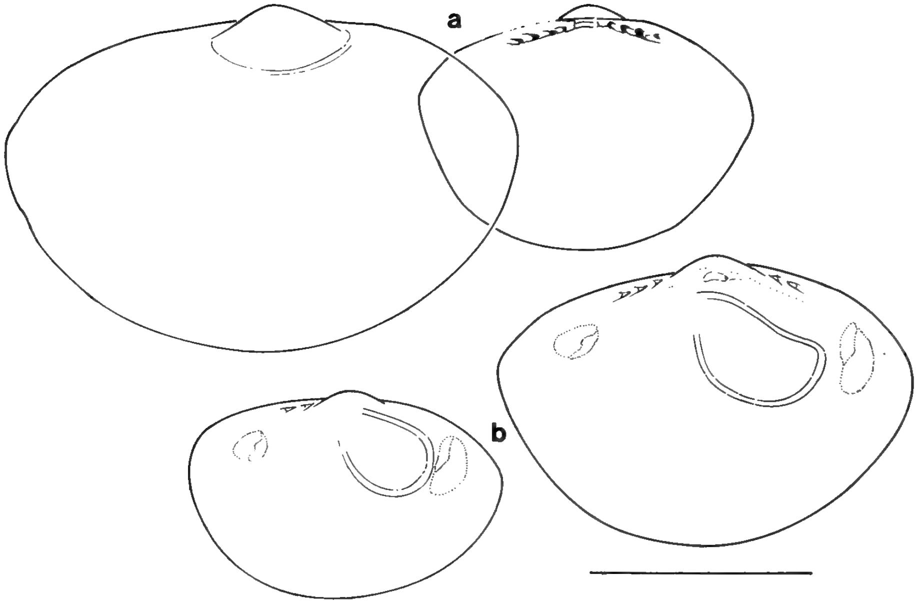

Fig. 65 *Yoldiella inconspicua africana*. Outlines a, of a shell from the right side and a left valve to show detail of the hinge-plate from Sta. 8532^{6} Cape Verde Basin and b, two shells from the right side from Sta. 201 Angola Basin. (Scale = 1.0 mm).

body. A large well-developed kidney extends anteriorly close to the posterior limit of the diverticula.

The sexes are separate. The gonads lie dorsal and ventral to the viscera and anteriorly they occur internal to the digestive diverticula. A female 2.8 mm in length collected in July (Incal CP 07) contained 255 closely packed ova with a maximum diameter of 132 μm.

Yoldiella inconspicua africana (new subspecies)

TYPE LOCALITY. R.V. Atlantis II, Cruise 42, Sta. 201, Angola Basin, 23.5.1968, 9°25′S, 11°35′E to 9°29′S, 11°34′E, Epibenthic Trawl, 1964 m.

TYPE SPECIMEN. Holotype BM(NH) 1992039, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SIERRA LEONE BASIN							
Atlantis II	145	2185	29	10°36.0′N	17°49.0′W	ES	6.2.67
31	147	3984	5	10°38.0′N	17°52.0′W	ES	6.2.67
CAPE BASIN							
Atlantis II	192	2117–	55	23°02.5′S	12°19.0′E	ET	17.5.68
42		2154					
	194	2864	28	22°54.0′S	11°55.0′E	ET	17.5.68
ANGOLA BASIN							
	201	1964	109	9°25.0′S	11°35.0′E	ET	23.5.68
				– 9°29.0′S	11°34.0′E		
CAPE VERDE BASIN							
Discovery	8521^{1}	3058–	2	20°46.9′N	18°53.4′W	WS	25.6.74
		3053		– 20°47.6′N	18°53.5′W		
	8521^{6}	3070–	1	20°47.9′N	18°53.4′W	WS	26.6.74
		3964		– 20°48.6′N	18°53.4′W		
	8521^{1}	3113–	34	13°47.8′N	18°14.0′W	WS	4.7.74
		3119		– 13°48.0′N	18°14.8′W		
	8532^{6}	2958–	12	13°48.2′N	18°08.0′W	WS	5.7.74
		2952		– 13°47.6′N	18°07.5′W		
Walda	DS20	2514	5	2°32.0′S	8°18.1′W	DS	

Y. inconspicua africana is found off the West coast of Africa in the Sierra Leone, Cape Verde, Angola and Cape Basins at lower slope to abyssal depths. Depth range: 1964–3119 m.

SHELL DESCRIPTION (Fig. 65). Shell very small, short, relatively compressed, ovate wedge-shape, very slightly inequilateral, except for some very fine lines shell surface smooth, periostracum pale yellow, iridescent; umbos just anterior to midline, slightly raised; antero-dorsal margin slightly convex, nearly horizontal close to umbos, then curving to slightly pointed anterior margin, ventral margin broadly rounded, often slightly swollen posteriorly, ascending steeply to posterior supramedial angle, postero-dorsal margin nearly horizontal close to umbo, then slightly convex, sloping gradually to posterior margin; posterior hinge plate narrow; teeth small, oblique v-shape, 4–5 on each hinge plate; ligament short, amphidetic, relatively wide, yoke-shaped, slight external extension on either side of umbo.

Prodissoconch length: 166 μm. Maximum recorded shell length 2.56 mm (Discovery Sta. 8521^{b}).

INTERNAL MORPHOLOGY (Fig. 66). The siphons are combined but with a single lumen. The combined siphon is large and long, with relatively thin muscular walls. The single tentacle is large, attached to the right or the left at the base of the siphonal embayment. The feeding aperture is moderately well-developed with a small internal secondary fold. The mantle epithelial in the area of the feeding aperture and anterior to it is well supplied with gland cells, similar to those present in *Yoldiella curta* (p. 47). The anterior sense organ lies far anterior and is covered dorsally by an extended and particularly well-developed hood derived from the middle sensory lobe. The adductor muscles are slightly unequal in size; the larger anterior muscle is bean-shaped and the posterior is round in outline. The gills are well-developed with up to 12 filaments. The labial palps are relatively large with up to 15 broad ridges on the inner face. The palps extend across approximately one third of the body. The palp proboscides are long and relatively slender. The foot is well-developed with a deeply divided sole. The byssal gland is moderately small. The ganglia are large. Both cerebral and

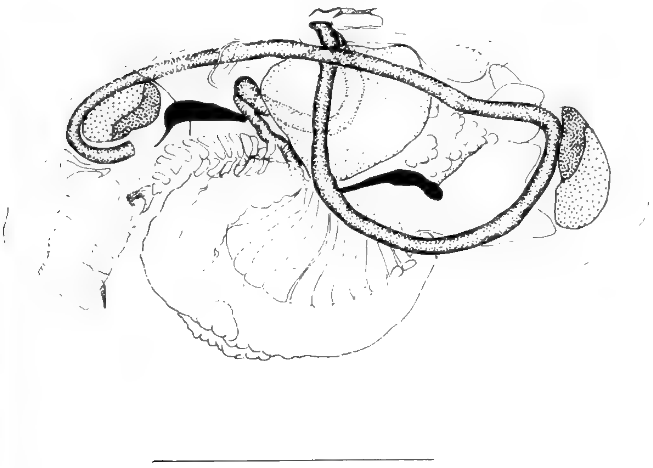

Fig. 66 *Yoldiella inconspicua africana*. Lateral view from the right side of the internal morphology of a specimen from Sta. 8532^6 Cape Verde Basin. (Scale = 1.0 mm). For identification of parts see Fig. 12.

visceral ganglia are 'club'-shaped, the visceral being the larger. The ovoid pedal ganglia lie central in the foot, just dorsal and anterior to the byssal gland. A large statocyst lies dorsal to each pedal ganglion.

The mouth is set posterior to the anterior adductor muscle. The oesophagus is relatively narrow while the stomach is large with a small style sac which does not penetrate the foot. The duct of the right digestive diverticulum passes dorsally around the hind gut to join the stomach close to the oesophageal aperture. One of the two left diverticula opens ventral to the gastric tooth while the second opens adjacent to that from the right. No ingested material was observed in the diverticula. From the style sac, the hind gut passes between the pedal ganglia and the byssal gland before turning dorsally. It makes a very small flexure on the left side immediately before crossing to the right side at the dorsal limit of the body posterior to the ligament. On the right side of the body the hind gut makes a broad sweeping loop as far as the posterior face of the anterior adductor before passing dorsally and posteriorly to the anus.

The gonads overlie the posterior, dorsal and dorso-lateral sides of the viscera and extend antero-dorsally with part lying centrally between the digestive diverticula. The kidney is small in comparison to the other species of *Yoldiella* described here, extending no further than the posterior edge of stomach. The heart is relatively large.

This subspecies differs from *Y. inconspicua s.s.* in having a more elongate outline and a more pointed posterior shell margin. The dorsal margin is slightly more convex, the height/length ratio is slightly greater. The hind gut differs slightly in the course taken to the right of the body (Figs. 60 & 66).

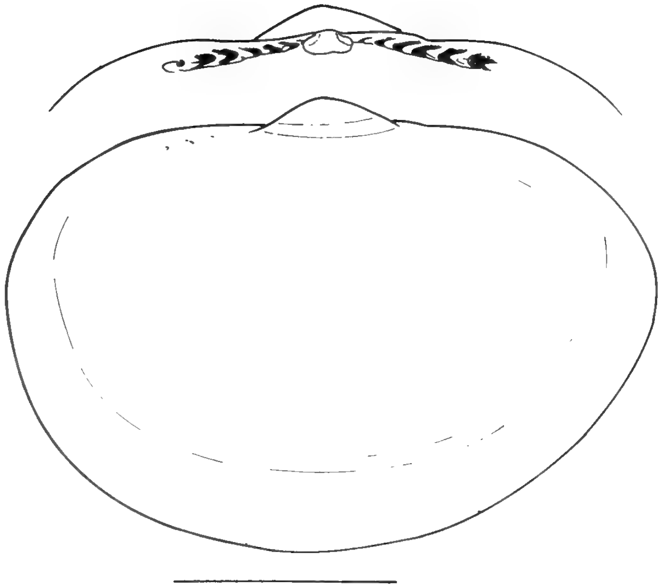

Fig. 67 *Yoldiella inconspicua profundorum*. Lateral view of shell from the right side and detail of the hinge-plate of a left valve. Specimens from Sta. 242 Argentine Basin. (Scale = 1.0 mm).

Yoldiella inconspicua profundorum (new subspecies)

TYPE LOCALITY. R.V. Atlantis II, Cruise 60, Sta. 256, Argentine Basin, 24.3.1971, 37°40.9′S, 51°19.3′W, Epibenthic Trawl, 3906–3917 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992038, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	50	38°16.9′S	51°56.1′W	ES	13.3.71
	243	3815–3822	1	37°36.8′S	52°23.6′W	ES	14.3.71
	245	2707	2	36°55.7′S	53°01.4′W	ES	14.3.71
	247	5208–5223	1	43°33.0′S	48°58.1′W	ES	17.3.71
	252	4435	23	38°29.8′S	52°09.1′W	ES	22.3.71
	256	3906–3917	19	37°40.9′S	51°19.3′W	ES	24.3.71
	259	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
	264	2041–2048	6	36°12.7′S	52°42.7′W	ES	28.3.71

Restricted to the Argentine Basin at lower slope and abyssal depths. Depth range: 2041–5223 m.

SHELL DESCRIPTION (Fig. 67). Shell small, equilateral, moderately inflated, subovate, fine concentric lines; umbos slightly raised, inwardly directed; shell outline somewhat variable, anterior and posterior dorsal margins straight proximal to umbo, curve distally to broadly rounded anterior and slightly pointed posterior margins, ventral margin smooth curve; anterior and posterior hinge plates relatively narrow

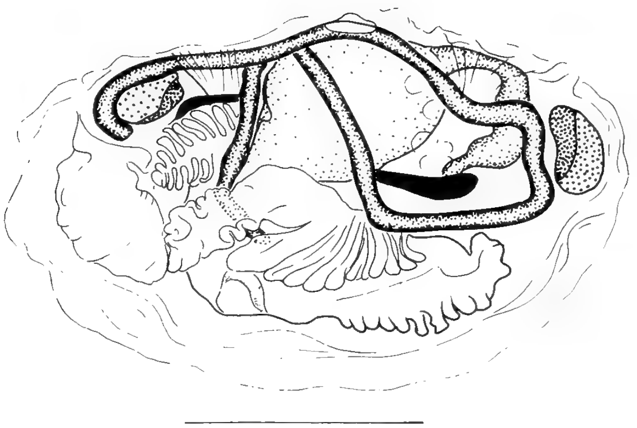

Fig. 68 *Yoldiella inconspicua profundorum*. Lateral view from the right side of the internal morphology of a specimen from Sta. 242 Argentine Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

(but broader than in *Y. inconspicuous s.s.*) short, with up to 7 teeth on each side; ligament amphidetic, large, slightly elongate, short external secondary extensions of fused periostracum on either side of umbo.

The shell shape of this subspecies while similar to that of *Y. inconspicua s.s.* is slightly more rounded, in particular the posterior limit of the shell margin is medial instead of supramedial. The hinge plate is broader and the teeth stronger in *Y. i. profundorum*.

Maximum recorded shell length: 3.31 mm.

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
2.90	2.09	1.25	0.72	0.43	0.52
3.31	2.25	1.47	0.68	0.44	0.52

INTERNAL MORPHOLOGY (Fig. 68). Very similar to that of *Y. inconspicua s.s.* and *Y. argentinea*. In *Y. i. profundorum*, size for size, the posterior adductor muscle is more elongate than in *Y. inconspicua s.s.*, the palps are slightly smaller and the ridges are broader but not as long and slightly fewer in number (12–14 internal ridges).

Yoldiella argentinensis (new species)

TYPE LOCALITY. R.V. Atlantis II, Cruise 60, Sta. 237, Argentine Basin, 11.3.1971, 36°32.6′S, 53°23.0′W, Epibenthic Trawl, 993–1011 m.

TYPE SPECIMEN. presently housed in the Sanders collection, Woods Hole Oceanographic Institution, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
ARGENTINE BASIN							
Atlantis II	236	497–518	3	36°27.0′S	53°31.6′W	ES	11.3.71
60	237	993–1011	26	36°32.6′S	53°23.0′W	ES	11.3.71
	239	1661–1679	26	36°49.0′S	53°15.4′W	ES	11.3.71

Y. argentinensis has only been recorded from Argentine

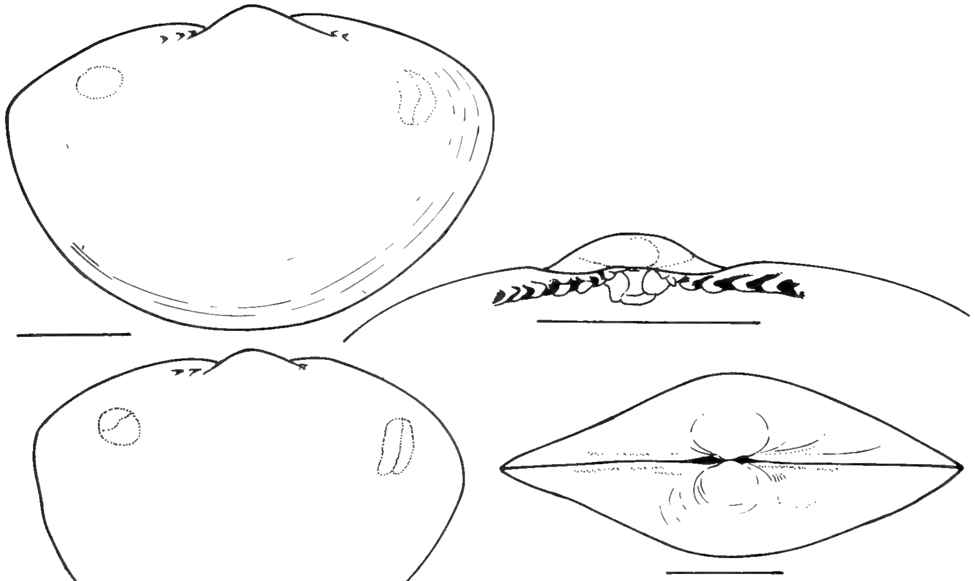

Fig. 69 *Yoldiella argentinensis*. Lateral view of the shells from the right side to show variation in shape; detail of the hinge-plate of a left valve; dorsal view of a shell. Specimens from Sta. 237 Argentine Basin. (Scales = 1.0 mm).

Basin at shelf slope break and upper slope depths. Depth range: 497–1679 m.

SHELL DESCRIPTION (Fig. 69). Shell small, subovate, approximately equilateral, relatively compressed, 'boat-shaped' in outline except for fine concentric lines, smooth, iridescent; umbos inflated, inwardly directed; anterior and posterior dorsal margins concave proximal to umbo, distal to umbo slightly convex, slope gradually to anterior and posterior margins, anterior margin slightly produced, ventral margin broadly curved, more convex posteriorly to slightly produced, posterior margin; horizontal axis supramedial; hinge plate short, teeth small, 'V'-shaped, proximal teeth very small, difficult to discern, 6 anterior and 6 posterior in individual 3.66 mm long; ligament amphidetic, large with long, narrow, secondary external anterior and posterior extensions.

Prodissoconch length: 150 µm. Maximum recorded shell length: 4.03 mm.

The shape of the shell is similar to that of *Yoldiella inconspicua* s.s. The main differences include the marked proximal concavities of the dorsal margin, the more inflated umbos and detail of the hinge.

INTERNAL MORPHOLOGY (Fig. 70). There is a wide combined siphon with a single lumen. The siphonal tentactle lies to the left side of the siphonal embayment. A feeding aperture is present ventral to the combined siphon. The adductor muscles are slightly unequal in size, in cross-section the posterior is broadly oval in outline while the larger anterior muscle is 'bean'-shaped.

The foot is well-developed and there is a large byssal gland in the heel. The gills are well-developed with between 10–17 alternating filaments (the number varying with the size of the individual). The labial palps are of moderate size, extending approximately one third across the body with between 10–18 internal ridges. The hind gut forms a single loop on the right side of the body (Fig. 70).

Yoldiella curta Verrill & Bush 1898

TYPE LOCALITY. North America Basin, 40°16.5'N, 67°05.3'W. 1290 fm. Original specimens were taken from the North America Basin between 41°11.5'N, 66°12.3'W and 39°38'N – 70°22'W by U.S. Fish Commission Steamer Albatross, 5.10.1883, Beam Trawl.

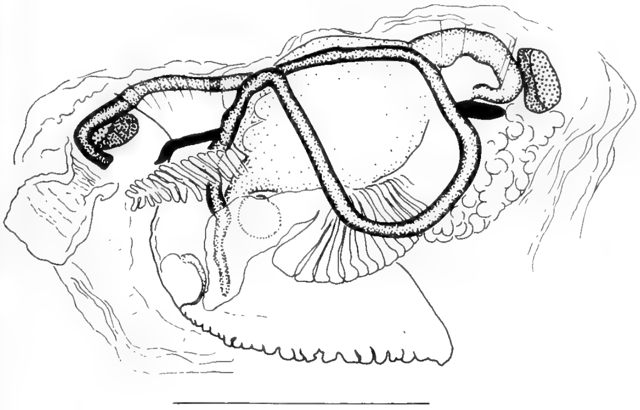

Fig. 70 *Yoldiella argentinensis*. Lateral view from the right side of the internal morphology of a specimen from Sta. 237 Argentine Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

TYPE SPECIMEN. Holotype U.S. Natl. Mus. No. 38457.

Phaseolus ovatus Verrill 1884, p.230.
Yoldia jeffreysi Verrill 1884, p.229; Verrill 1885, p. 576.
Yoldia curta Verrill & Bush 1898, p. 868, pl. 97, Fig. 8; Warén 1989, p. 244.
Yoldiella miniscula Verrill & Bush 1898, p. 870, pl. 79, Figs. 2, 7; Warén 1989, p. 244, Figs. 14 A & B.

Although a very well–defined species in that it is the only known *Yoldiella* with the hind gut configuration described below (p. 51), in its shell shape it is very similar to a number of other species. We believe that *Y. miniscula* Verrill & Bush is synonymous with it, indeed Verrill & Bush (1898) state this latter very minute species may, with a larger series, prove to be the young of one of the preceding species they describe. These latter include *Y. inconspicua, Y. pachia, Y. lucida, Y. iris, Y. inflata, Y. subangulata, Y. lenticula* and *Y. curta*. Verrill & Bush (1898) were correct in their supposition and here we illustrate specimens of *Y. miniscula* to show their similarity (Fig. 71).

Note. The holotype specimen of *Y. miniscula* (U.S. Natl. Mus. No. 38415) is from the same Station as the holotype of *Y. curta*.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
La Perle	DS06		1				
(Biogas I)	DS07		4				
	DS12	2180	1	47°28.5'N	8°35.5'W	DS	9. 8.72
	DS13	2165	15	47°33.7'N	8°39.9'W	DS	9. 8.72
Jean Charcot							
(Polygas)	DS25	2096	16+6v	44°08.2'N	4°15.7'W	DS	1.11.72
	DS26	2076	2	44°08.2'N	4°15.0'W	DS	1.11.72
	CV10	2108	2v	47°30.7'N	8°40.6'W	CV	22.10.72
(Biogas II)	DS32	2138	4	47°32.2'N	8°05.3'W	DS	19.4.73
(BiogasIII)	DS36	2147	5	47°32.7'N	8°36.5'W	DS	24. 8.73
			(1 empty 4 dried)				
	DS38	2138	7+2v	47°32.5'N	8°35.8'W	DS	25. 8.73
	DS49	1845	4+4v	44°05.9'N	4°25.6'W	DS	1. 9.73
(Biogas IV)	DS52	2006	2+4v	44°06.3'N	4°22.4'W	DS	18. 2.74
	DS61	2250	1	47°34.7'N	8°38.8'W	DS	25. 2.74
	DS62	2175	10	47°32.8'N	8°40.0'W	DS	26. 2.74
	DS63	2126	19+2v	47°32.8'N	8°35.0'W	DS	26. 2.74
	DS64	2156	7+4v	47°29.2'N	8°30.7'W	DS	26. 2.74
(Biogas V)	CP07	2170	3	44°09.8'N	4°16.4'W	CP	21. 6.74
(Biogas VI)	DS71	2194	7	47°34.3'N	8°33.8'W	DS	20.10.74
	DS86	1950	28	44°04.8'N	4°18.7'W	DS	31.10.74
	DS87	1913	7	44°05.2'N	4°19.4'W	DS	1.11.74
			(13+8v)				
	DS88	1894	5	44°05.2'N	4°15.4'W	DS	1.11.74
Jean Charcot	CP08	2177	3	44°33.2'N	8°38.5'W	CP	20.10.74
(Biogas VI)	CP09	2171	1	47°33.0'N	8°44.1'W	CP	20.10.74
Jean Charcot	CP01	2068–	38	57°57.7'N	10°55.0'W	CP	16. 7.76
(Incal)		2040		– 57°56.0'N	10°55.0'W		
	CP02	2091	4	57°58.4'N	10°42.8'W	CP	16. 7.76
				– 57°57.7'N	10°44.6'W		
	DS01	2091	468	57°59.7'N	10°39.8'W	DS	15. 7.76
				– 57°59.2'N	10°41.3'W		
	DS02	2081	544	57°58.5'N	10°48.5'W	DS	16. 7.76
				– 57°58.5'N	10°49.2'W		
	DS05	2503	2	56°28.1'N	11°11.7'W	DS	18. 7.76
				– 56°27.6'N	11°12.0'W		
	DS06	2494	6	56°26.6'N	11°10.5'W	DS	18. 7.76
				– 56°25.9'N	11°10.7'W		

	OS01	2634	5	50°14.4′N – 50°15.2′N	13°10.9′W 13°11.0′W	OS	30. 7.76
Sarsia	S–65	1922	19	46°15.0′N	4°50.0′W	ED	25. 7.67
	33/2	1537–1830	8	43°41.0′N	3°36.0′W	AD	13. 7.67
	S–44	1739	68	43°40′8′N	3°35′2′W	ED	16. 7.67
Chain 106	313	1500–1491	106	51°32.2′N	12°35.9′W	ES	17. 8.72
	316	2173–2209	91	50°58.7′N – 50°57.7′N	13°01.6′W 13°01.3′W	ES	18. 8.72
NORTH AMERICA BASIN							
Atlantis II 12	73	1470–1330	699	39°46.5′N	70°43.3′W	ET	25. 8.64
Chain 50	87	1102	354	39°48.7′N	70°40.8′W	ET	6. 7.65
Chain 58	103	2202	303	39°43.6′N	70°37.4′W	ET	4. 5.66
Atlantis II 24	115	2031–2051	249	39°39.2′N	70°24.5′W	ET	16. 8.66
Atlantis II	128	1254	8	39°46.5′N	70°45.2′W	ES	15.12.66
30	131	2178	53	39°38.5′N – 39°39.0′N	70°36.5′W 70°37.1′W	ES	18.12.66
Chain 88	207	805–811	239	39°51.3′N – 39°51.0′N	70°54.3′W 70°56.4′W	ES	21. 2.69
	210	2024–1064	4	39°43.0′N – 39°43.2′N	70°46.0′W 70°49.5′W	ES	22/23.2.69
ARGENTINE BASIN							
Atlantis II 60	239	1661–1679	36	36°49.0′S	53°15.4′W	ES	11. 3.71
	240	2195–2323	1	36°43.4′S	53°10.2′W	ES	23. 3.71
	264	2041–2048	4	36°12.7′S	52°42.7′W	ES	28. 3.71
GUYANA BASIN							
Knorr 25	293	2456–1518	49	8°58.0′N	54°04.3′W	ES	27. 2.72
	295	1000–1022	25	8°04.2′N	54°21.3′W	ES	28. 2.72
SIERRA LEONE BASIN							
Atlantis II 31	142	1124–1796	45	10°30.0′N	17°51.5′W	ES	5. 2.67
	145	2185	1	10°36.0′N	17°49.0′W	ES	6. 2.67
BRAZIL BASIN							
	159	834–939	1	7°58.0′S	34°22.0′W	ES	18. 2.67
	167	943–1007	4	7°58.0′S – 7°50.0′S	34°17.0′W	ES	20. 2.67
	169	587	6	8°03.0′S – 8°02.0′S	34°23.0′W 34°25.0′W	ES	21. 2.67
CAPE BASIN							
Atlantis II 42	189	11007–1014	196	23°00.0′S	12°45.0′E	ES	16. 5.68
	190	974–979	7	23°05.0′S	12°45.0′E	AD	17. 5.68
	191	1546–1559	2	23°05.0′S	12°31.5′E	ES	17. 5.68
Walda	DS10	1432	1	18°40.0′S	10°56.3′E	DS	

Y. curta is probably the most widely distributed species of *Yoldiella*. It occurs throughout the Atlantic at slope and abyssal rise depths. Depth ranges:

Brazil Basin	587–1007 m
Cape Basin	974–1559 m
Guyana Basin	1000–1518 m
Argentine Basin	1661–2048 m
Sierra Leone Basin	1624–2185 m
North American Basin	805–2178 m
West European Basin	1537–2634 m

SHELL DESCRIPTION (Figs. 71 & 72). Verrill & Bush (1898) give a full and accurate description of this species. *Y. curta* has a small, smooth, ovate, semi-transparent shell through which the characteristic, indeed unique, course of the hind gut is usually visible. The latter is usually seen as a double strand on the right side of the body with a single loop on the left extending out from the posterior margin of the anterior adductor. The hinge is short with a large internal ligament. The outline of the shell is variable both within (Fig. 73) and between populations. There is no lunule or escutcheon. The hinge plate is very short and slender and does not reach to the level of the inner margin of the adductor muscles. The number of teeth on each hinge plate varies with size up to a maximum of 7. There is usually one more tooth on the posterior hinge plate. The shell may be confused with other species e.g. *Y. inconspicua*, *Y. lucida* and *Y. frigida*, even though the hinge and the hind gut configuration are characteristic.

In general, with increasing length, the height/length ratio increases thus producing a more rounded outline (Figs. 74 & 75). The outlines of the anterior and posterior margins are variable. The anterior margin may be smoothly rounded or slightly angular, while the posterior margin is slightly extended with the degree of curvature and the position of the posterior limit in relation to the mid horizontal shell axis somewhat variable. With increasing size shells become more inequilateral with the posterior end slightly elongate. There is also a gradual increase in the width to length ratio.

Prodissoconch length: 170 μm. Maximum recorded shell length: 4.77 mm.

INTERNAL MORPHOLOGY (Figs. 76 a & b). As in other *Yoldiella* species the mantle is little modified and for the most part unfused. The inner muscular lobe is relatively broad and somewhat folded in preserved specimens. Posteriorly the inner muscular layer fuses to form a relatively wide, thin-walled combined siphon with a single lumen. In one whole mount several faecal pellets lying one on top of the other were seen within the siphon and in one series of sections two faecal pellets one in the dorsal half and one in the ventral half of the siphonal lumen were seen. The gill axes attach laterally close to the ventral margin of the siphon, thus any inhalent componant is probably restricted to the ventral margin. A large siphonal tentacle originates from a pocket in the siphonal embayment at the base of the siphon, usually on the left side. A small secondary muscular mantle fold marks the inner limit of the feeding aperture which in life must extend beyond the shell margin as a pair of flaps. Here the inner mantle lobe is increased in thickness and width and in the preserved contracted state is much folded. The epithelium on the ventral side of the secondary muscular fold, on the dorsal side of the muscular fold, as well as the epithelium between the two, is well supplied with acidophilic gland cells. The gland cells within the epithelium between the folds extend anteriorly beyond the limit of the feeding aperture for a short distance. The anterior sense organ is well-developed. Over it the middle sensory lobe forms a long thin flap which is well-supplied with glandular epithelial cells. The adductor muscles are large, approximately equal in size with the 'quick' and 'catch' parts clearly visible. The anterior adductor if anything is slightly the larger, it is 'crescent'-shaped in cross section while the posterior muscle is approximately circular.

The gills lie comparatively ventral in position within the

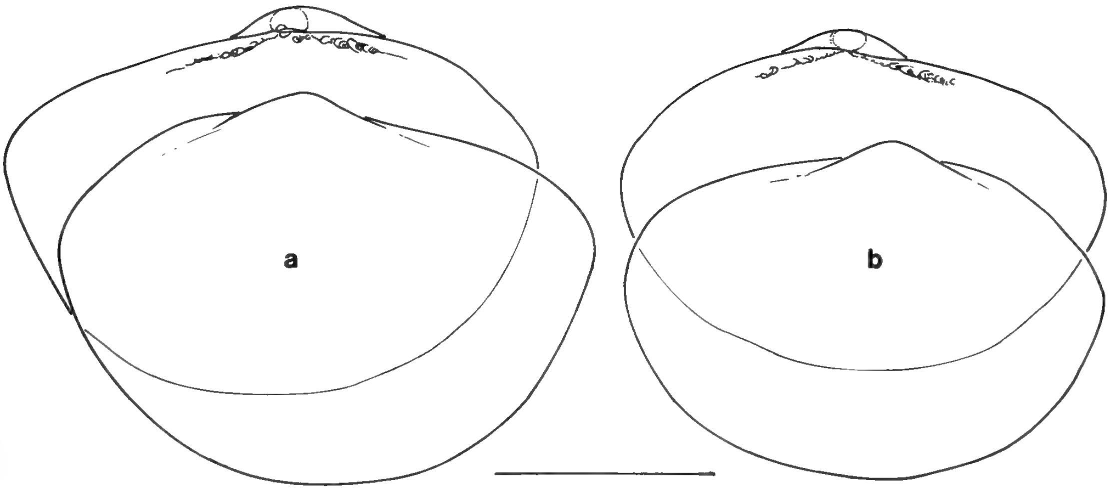

Fig. 71 *Yoldiella curta*. a, lateral external and internal view of left valve of the type specimen of *Y. curta* (USNM No.38457) and b, the lateral external and internal view of the right valve of the type specimen of *Y. miniscula* (USNM No. 38415). Specimens from the U.S. Fish Commission Sta. 2084 North America Basin. (Scale = 1.0 mm).

mantle cavity. The outer and inner demibranchs are attached to the mantle and body respectively by tissue junctions. Depending on the size of the individual there are 11–16 alternating gill plates. The labial palps are moderately large, extending approximately 1/3 across the body and have between 13–19 wide ridges on their inner faces.

The foot is large and well-developed. A large byssal gland is present, with little obvious internal structure as seen in whole mounts. At the point where the gland opens to the exterior the surrounding tissue contains acidophilic gland and basiphilic cells. As in other species of *Yoldiella* there is a broad band of posterior retractor muscles. The latero-posterior retractor muscle is inserted ventrally on lateral body wall. There are three major pairs of anterior pedal retractor muscles which, from the neck of the foot, pass to either side of the oesophagus and insert on the shell posterior to the anterior adductor muscle. Another smaller pair of anterior retractor muscles insert immediately posterior to the anterior adductor and pass within the ventral visceral margin at epithelia to the region of the mouth (Fig. 76b). Posterior to these a second pair of muscles pass vertically from the dorsal shell margin to the labial palps.

The cerebral ganglia are relatively large, as are the elongate-oval pedal ganglia. The visceral ganglia are smaller, cylindrical and lie close to the antero-ventral margin of the posterior adductor muscle.

The mouth is a short distance posterior to the anterior adductor muscle. The oesophagus curves dorsally and anteriorly before turning posteriorly to enter the stomach approximately midway on the left side of the anterior face. No sorting ridges are visible externally on the right side of the stomach. There is a prominent gastric tooth at the left antero-dorsal edge of the gastric shield. The latter extends posteriorly over the left, the dorsal and part of the right wall. The style sac is small, narrow and penetrates the foot to level of pedal ganglia. The digestive diverticula are extensive occurring on the right and left sides of the body and anterior to the stomch. Fine material was observed in the lumen of the left digestive diverticulum. A duct from the left side opens into the stomach below the gastric tooth. The course of the two other ducts are less clear, but from the evidence of other species they probably open into the stomach anteriorly close to the oesophagus. The hind gut sweeps across the ventral right side of the viscera to the anterior adductor muscle, where it crosses to the left side of the body to form a single loop before returning to the right alongside the outward

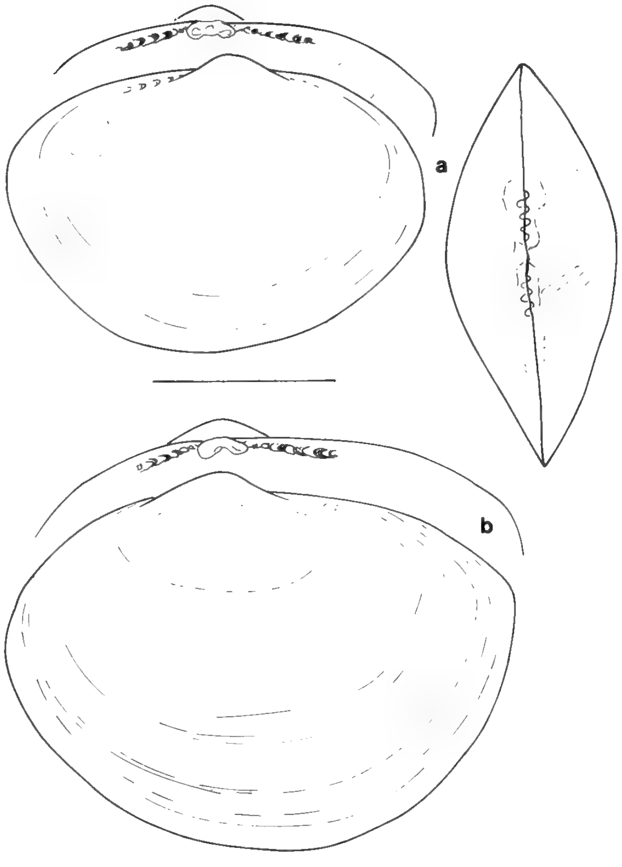

Fig. 72 *Yoldiella curta*. a, lateral view from right side of shell, detail of the hinge-plate of a right valve and dorsal view of a shell from U.S. Fish Commission Sta. 2073 North America Basin, compared with b, a lateral view of a shell from the left side and detail of the hinge-plate of a right valve from Sta. Polygas DS 25 West European Basin. (Scale = 1.0 mm).

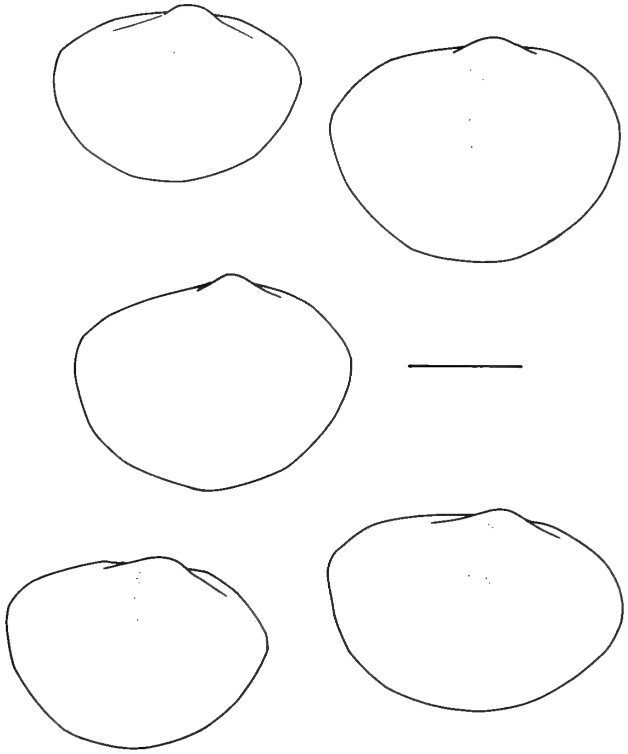

Fig. 73 *Yoldiella curta*. Outlines of shells of a similar size to show intrapopulation differences in shape. Specimens from Sta. BG IV DS 86 West European Bain. (Scale = 1.0 mm).

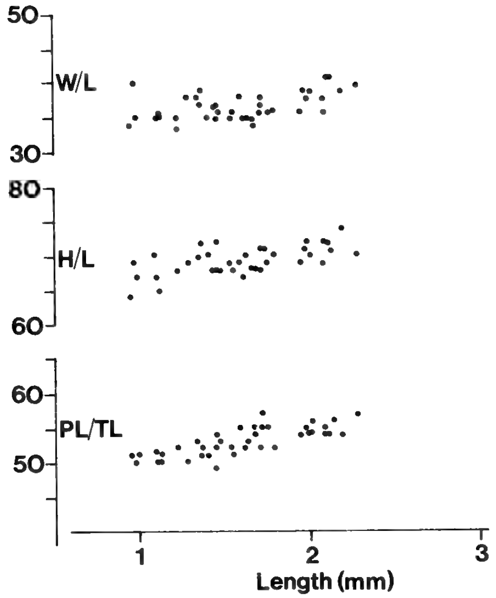

Fig. 74 *Yoldiella curta*. Variation in the ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of a sample from Sta. INCAL CP 01 West European Basin.

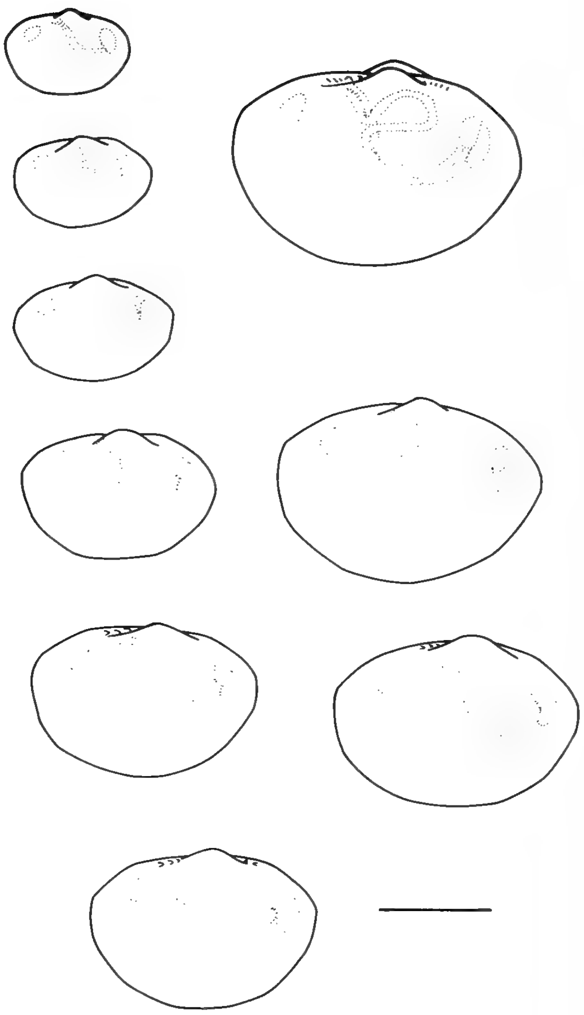

Fig. 75 *Yoldiella curta*. Outlines of shells from the right side to show change in shape with growth. Specimens from Sta. BG I DS 13 West European Basin. (Scale = 1.0 mm).

section of the mid dorsal margin of the body and from there to the anus. A shallow typhlosole is present along the length of the hind gut. Occasional aberrent specimens were recorded with an extra length of gut being accommodated within the general pattern (see Fig. 75).

The kidney is well-developed. There is a large pericardial cavity but the heart is relatively small with few muscle fibres in the wall of the ventricle. Gonads occur dorsally from the anterior adductor muscle to just posterior to the stomach and in the anterior part of the body internal to the digestive diverticula and hind gut. The sexes are separate. In one sectioned female (2.3 mm) 27 ova were counted and in other specimens (1.8 and 2.1 mm) 69 and 70 ova were recorded respectively. The maximum dimension was 108 μm.

This is one of a few deep-water specimens which were brought to the surface alive and from which it was posible to make some observations on the ciliary currents of the mantle and the contained organs. The ciliary sorting mechanisms of the gills, palps, mantle and body were found to be similar to those described by Stasek (1965) for *Yoldia ensifera*.

The ciliation on the frontal surface of the gill plates is axially directed, there those on the posterior 2/3rds of the axis move anteriorly and those on the anterior 1/3rd move posteriorly. Particles thus accumulate at a point which is close to where the palp proboscides join the dorsal palp surface and they are accepted onto the palp. The palp ridges sort in the manner described by Stasek (1965). Rejected particles arrive at the posterior-ventral margin of the palp. A main rejection tract at the mantle edge to the inside of the muscular fold carries these particles to a point of collection at the ventral edge of the feeding aperture. Particles on the body eventually pass to the dorsal margin of the palps and join with those from the gills.

Hydroids were present on the shell margins of a number of specimens.

Yoldiella perplexa (new species)

TYPE LOCALITY. R.V. Knorr Sta. 299, Guyana Basin, 29.2.1972, 7°55.1′N, 54°42.0′W, Epibenthic Trawl, 1912–2076 m.

TYPE SPECIMEN. Holotype BM(NH) 1992031, Paratypes: in collection held by J.A. Allen.

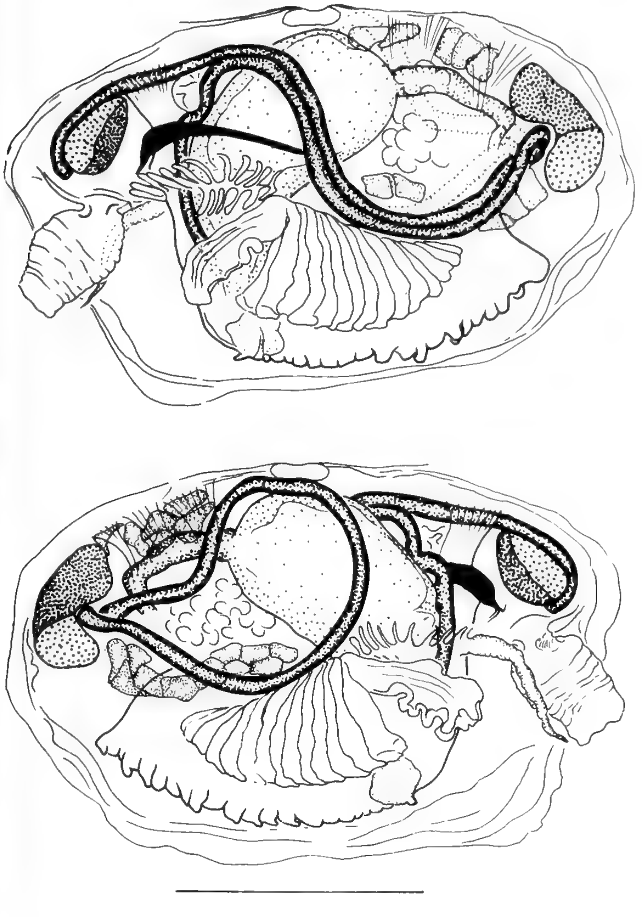

Fig. 76 *Yoldiella curta*. Lateral views from the right and left sides of the internal morphology of a specimen from Sta. BG VI DS 71 West European Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

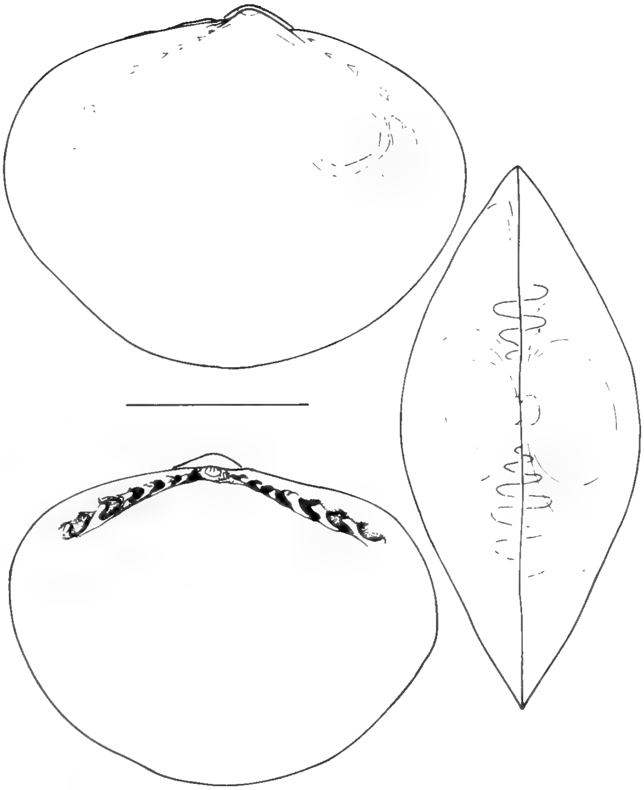

Fig. 77 *Yoldiella perplexa*. Lateral view of shell from the right side, lateral internal view of a right valve to show detail of hinge-plate and a dorsal view of a shell. Specimens from Sta. 299 Guyana Basin. (Scale = 1.0 mm).

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUYANA BASIN							
Knorr 25	293	2456–1518	22	8°58.0′N	54°04.3′W	ES	27.2.72
	299	1942–2076	82	7°55.1′N	54°42.0′W	ES	29.2.72

Recorded from the lower slope of the Guyana Basin. Depth range: 1456–2076 m.

SHELL DESCRIPTION (Fig. 77). Shell small, ovate, moderately inflated, inequilateral, smooth with some fine irregularly spaced concentric lines at ventral margin, periostracum pale yellow; umbos moderately developed, slightly raised, inwardly directed anterior to midline; proximal dorsal margin straight in small specimens, slightly convex in larger, antero-dorsal margin curves gradually to wide anterior margin, dorsal part slightly more convex than ventral, ventral margin deeply convex, postero-dorsal margin slopes gradually to steeply rounded posterior margin, postero-ventral margin relatively straight and in some specimens very slightly sinous; hinge plate moderately broad, not narrow below umbo, hinge teeth strong, few in number, 6 anterior and 6 posterior in individual 2.6 mm; ligament amphidetic, moderate in size, not extending to ventral edge of hinge plate, round in lateral

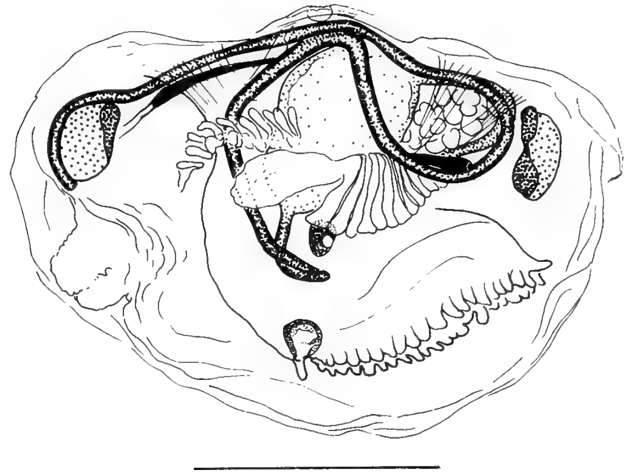

Fig. 78 *Yoldiella perplexa*. Lateral view from the right side of the internal morphology of a specimen from Sta. 299 Guyana Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

view with little external periostracal extension anterior and posterior to the umbo.

Prodissoconch length: 177 μm. Maximum recorded shell length: 3.11 mm.

INTERNAL MORPHOLOGY (Fig. 78). The combined siphons are well-developed. There is a long thin siphonal tentacle attached to the left ventral side of a moderately deep siphonal embayment. The anterior sense organ is well-developed. The adductor muscles are relatively large; the anterior is bean-shaped and slightly larger than the posterior and which is more round.

The gills bear up to 16 alternating plates which are distant from the internal limit of the siphons and to which they are joined by long extended axes. The labial palps are relatively small and extend approximately 1/4 distance across body. There are up to 13 palp ridges on the inner face. The palp proboscides are moderately well-developed.

The foot is also well-developed and anterior in position in preserved specimens. There is a small byssal gland and the pedal ganglia dorsal to the gland are also small. The visceral ganglia are slender and elongate while the cerebral ganglia are slightly larger and more 'club'-shaped. The stomach and style sac are large. The hind gut describes a shallow single loop to the right side of the body. No gonads were seen in the whole mounts.

Y. perplexa is characterized by a rounded high shell which has a slightly sinuous postero-ventral shell margin. Unlike other high rounded species such a *Y. americana* and *Y. subcircularis* it has a simple and not particularly extensive hind gut loop to the right and thus has characters intermediate between *Y. lucida* or *Y. obesa* and species such as *Y. subcircularis*.

Yoldiella americana (new species)

TYPE LOCALITY. R.V. Chain Sta. 84, North America Basin, 4.7.1965, 36°24.4′N, 67°56.0′W, Epibenthic Trawl, 4749 m.

TYPE SPECIMEN. Holotype BM(NH) 1992032, Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II 12	70	4680	190	36°23.0′N	67°58.0′W	ET	23. 8.64
Chain 50	77	3806	1	38°00.7′N	69°16.0′W	ET	30. 6.65
	80	4970	75	34°49.8′N	66°34.0′W	ET	2. 7.65
	81	5042	9	34°41.0′N	66°28.0′W	ET	2. 7.65
	83	5000	4	34°46.5′N	66°30.0′W	ET	3. 7.65
	84	4749	235	36°24.4′N	67°56.0′W	ET	4. 7.65
	85	3834	4	37°59.2′N	69°26.2′W	ET	5. 7.65
	86	3843	268	37°59.0′N	69°18.5′W	ET	5. 7.65
Atlantis II 17	92	4694	3	36°20.0′N	67°56.0′W	ET	13.12.65
	93	5003	6	34°39.0′N	66°26.0′W	ET	14.12.65
Atlantis II 24	121	4800	66	35°50.0′N	65°11.0′W	ET	21. 8.66
	122	4833	25	34°50.0′N – 35°52.0′N	64°57.5′W 64°58.0′W	ET	21. 8.66
	123	4853	94	37°29.0′N	64°14.0′W	ET	22. 9.66
	124	4862	76	37°26.0′N – 37°25.0′N	63°59.5′W 63°58.0′W	ET	22. 8.66
	125	4825	37	37°24.0′N – 37°26.0′N	65°54.0′W 65°50.0′W	ET	23. 8.66
Atlantis II 40	175	4667–4693	145	36°36.0′N – 36°36.0′N	68°29.0′W 68°31.0′W	ES	29.11.67
Chain 106	330	4632	243	50°43.5′N – 50°43.4′N	17°51.7′W 17°52.9′W	ES	24. 8.72
	331	4793	10	41°13.0′N – 41°13.2′N	41°36.7′W 41°38.7′W	ES	29. 8.72
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	8	38°16.9′S	51°56.1′W	ES	13. 3.71
	247	5208–5223	293	43°33.0′S	48°58.1′W	ES	17. 3.71
	252	4435	1	38°29.8′S	52°09.1′W	ES	22. 3.71
GUYANA BASIN							
Knorr 25	287	4980–4034	12	13°16.0′N – 13°15.8′N	54°52.2′W 54°53.1′W	ES	24. 2.72
	288	4417–4429	45	11°02.2′N – 11°03.8′N	55°05.5′W 55°04.8′W	ES	25. 2.72
Biovema	DS03	5150	3	10°47.1′N – 10°47.1′N	42°40.7′W 42°40.3′W	DS	16.11.77
	DS05	5100	28	10°45.9′N – 10°46.8′N	42°40.2′W 42°39.8′W	DS	18.11.77
	CO04	5100	1	10°45.9′N – 10°45.9′N	42°40.2′W 42°39.3′W	CP	18.11.77
	DS09	5875	1	11°36.5′N – 11°37.1′N	32°51.8′W 32°51.3′W	DS	25.11.77
	DS11	5867	2	11°37.5′N – 11°37.6′N	32°43.8′W 32°52.8′W	DS	26.11.77
SIERRA LEONE BASIN							
Atlantis II 31	139	2099–2187	1	10°33.0′N	17°53.0′W	ES	4. 2.62

Y. americana is found mainly in the deep western Atlantic with a few records to east of the Atlantic Ridge at the western edge of the Sierra Leone Basin. Otherwise the species is recorded from the North America, Guyana and Argentine Basins. Depth range: 2099–5867 m.

SHELL DESCRIPTION (Fig. 79). Shell small, ovate, moderately inflated, approximately equilateral; umbos moderately raised, inwardly directed; dorsal margin slightly convex, antero-dorsal margin slopes evenly to join broad curve of anterior margin, ventral margin more convex posteriorly,

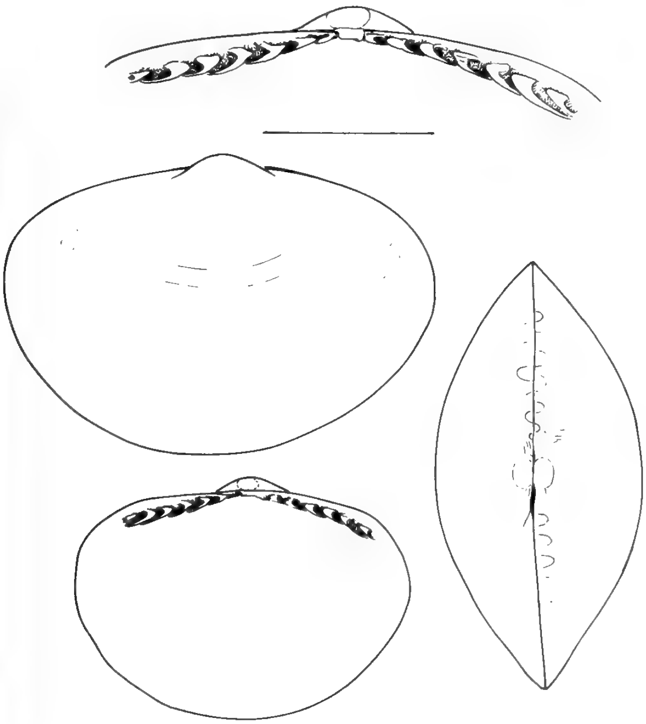

Fig. 79 *Yoldiella americana*. Lateral view of shell from the right side, lateral internal view of a left valve, enlarged view of a hinge-plate of a left valve and a dorsal view of the shells. Specimens from Sta. 80, North America Basin. (Scale = 1.0 mm).

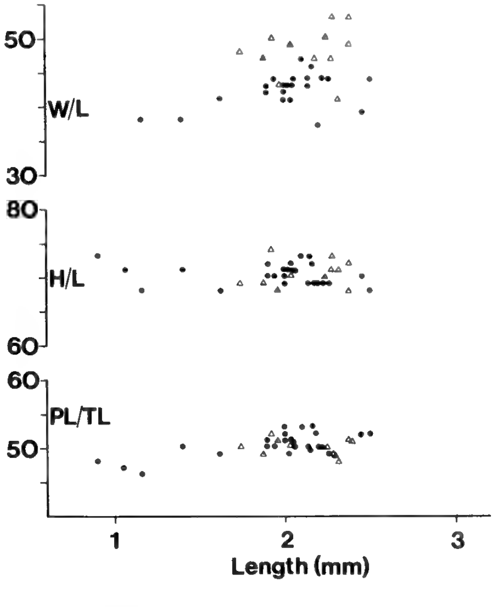

Fig. 80 *Yoldiella americana*. Variation in ratio of height H/L, width W/L and postero-umbonal length PL/TL to length against length of subsamples from Sta. Biovema DS 05, Cape Verde Basin (closed circles) and from Sta. 247 Argentine Basin (open triangles).

posterior margin rounded or with slight angulation forming slight subrostrum; hinge plate moderately strong, long strong chevron-shaped teeth, equal numbers on anterior and posterior plates, 14/14 in a specimen 2.44 mm total length; ligament amphidetic, small, rectangular in shape, small posterior external extension of fused periostracum.

Prodissoconch length: 187 μm. Maximum recorded shell length: 2.5 mm.

There is little change in the posterior umbonal length/total length ratio or the height/length ratio with increasing size, however, individuals tend to become more tumid with increasing length. The width/length ratio is the most variable feature when comparing populations from different areas (Fig. 80). Thus, specimens from the west Atlantic are relatively wider than those from the the east Atlantic although in lateral view (Fig. 81) and in internal anatomy they differ little. Populations are remarkably different in their size range. This is probably indicative of single massive successful spatfalls at different times (Fig. 82).

INTERNAL MORPHOLOGY (Fig. 83). The anterior sense organ is moderately well-developed. The siphons are combined, with the inhalent siphon open at the ventral edge. A siphonal tentacle originates from the base of the siphonal embayment, either on the right or the left side. There is a feeding aperture ventral to the siphons. Anterior to this the inner muscular lobe is enlarged convoluted and heavily ciliated. The adduc-

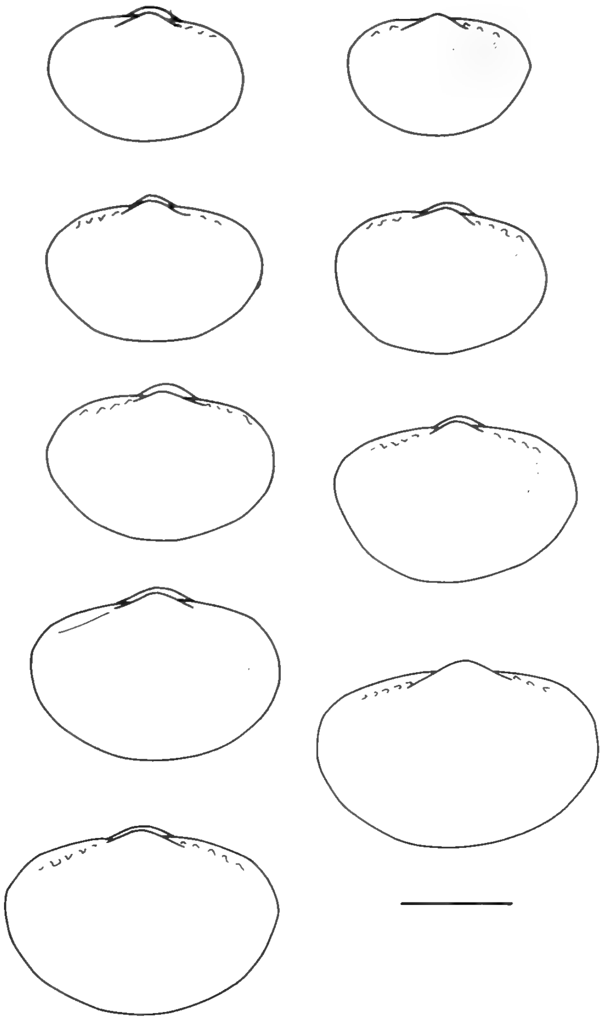

Fig. 81 *Yoldiella americana*. Outlines of shells from the right side to show change in shape with growth of specimens from Sta. Biovema DS 05 Cape Verde Basin (left) compared with specimens from Sta. 247 Argentine Basin. (Scale = 1.0 mm).

tor muscles are relatively small and elongate and approximately equal in size. The gills are well-developed. The exact number of gill plates is difficult to determine but at least 16 are present in the largest specimen. The labial palps are relatively large with up to 17 ridges on the inner face and with long palp proboscides. The foot is elongate with a relatively narrow neck. Many subepithelial gland cells open on to the sole of the foot. There is a relatively large byssal gland in the heel. A small papilla is present immediately posterior to the aperture of the byssal gland. The cerebral and visceral ganglia are 'club'-shaped and of moderate size. The pedal ganglia, in the neck of the foot, are large and elongate.

The hind gut passes from the style sac to the *left* side of the body and forms a loop then crosses to the right side where it forms a similar loop before passing postero-dorsally to the anus. The point of crossover from left to right is ventral to the ligament or slightly posterior to it. A small typhlosole is present along the length of the gut.

The sexes are separate. From whole mounts, it appears that the ovaries contain relatively few large ova. The testes occupy a large part of the anterior half of the body with the digestive diverticula dorsal to them.

Y. americana has a similar rounded shape to *Y. perplexa* although without the slight sinuous postero-ventral margin of the latter species. *Y. americana* is the only species taken with a single hind gut loop to the right *and* left of the body.

Yoldiella subcircularis (Odhner 1960)

Portlandia (Yoldiella) subcircularis Odhner 1960, p. 369, pl. 1, Fig. 1.

TYPE LOCALITY. Swedish Deep-Sea Expedition, Sta. 373, North America Basin, collected by R.V. Albatross, 24.8.1948, 28°25′N, 61°05′W – 28°05′N, 60°49′W, 5,500–5,987 m.

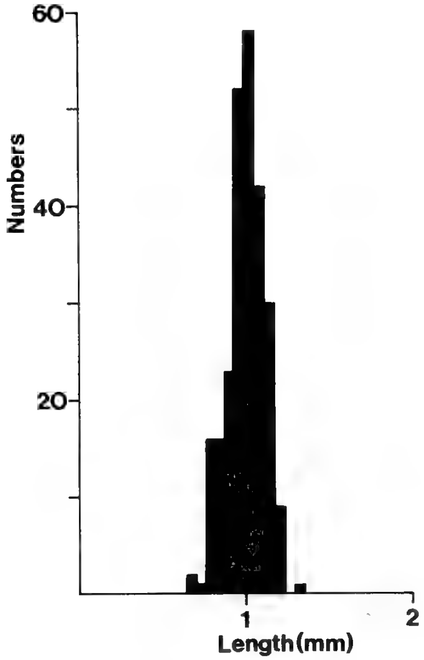

Fig. 82 *Yoldiella americana*. Length frequency histogram of a sample from Sta. 84, North America Basin.

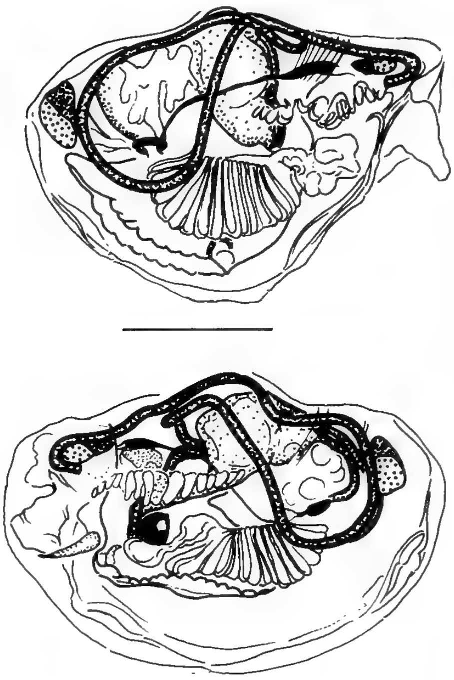

Fig. 83 *Yoldiella americana*. Lateral views from right and left sides of the internal morphology of a specimen from Sta. 84, North America Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

TYPE SPECIMEN. Holotype: Swedish Museum of Natural History, Stockholm.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Jean Charcot	DS20	4226	7	47°33.0′N	9°36.7′W	DS	24.10.72
(Polygas)	DS21	4190	1	47°31.5′N	9°40′7′W	DS	24.10.72
	DS22	4144	4	47°34.1′N	9°38.4′W	DS	25.10.72
(Biogas IV)	DS54	4659	2	46°31.1′N	10°29.2′W	DS	21. 2.74
	DS55	4125	7	47°34.9′N	9°40.9′W	DS	22. 2.74
(Biogas V)	S68	4550	1	46°26.7′N	10°23.9′W	DS	19. 6.74
(Biogas VI)	DS75	3250	1	47°28.1′N	9°07.8′W	DS	22.10.74
	DS76	4228	29+1v	47°34.8′N	9°33.3′W	DS	23.10.74
	DS77	4240	13+2v	47°31.8′N	9°34.6′W	DS	24.10.74
	DS78	4706	4	46°31.2′N	10°23.8′W	DS	25.10.74
	DS79	4715	13	46°30.4′N	10°27.1′W	DS	26.10.74
	DS80	4720	4	46°29.5′N	10°29.5′W	DS	27.10.74
	DS81	4715	1	46°28.3′N	10°24.6′W	DS	27.10.74
Jean Charcot	QS02	4829	2	48°19.2′N	15°15.7′W	OS	2. 8.76
(Incal)	QS05	4296–	1	47°31.3′N	9°34.6′W	OS	7. 8.76
		4248		– 47°32.2′N	9°34.7′W		
	QS06	4316	6	46°27.3′N	9°36.2′W	OS	9. 8.76
				– 47°27.9′N	9°36.0′W		
	QS07	4249	15	47°31.8′N	9°34.3′W	OS	10.8.76
				– 47°31.3′N	9°34.3′W		
	QS08	4327	5	47°29.8′N	9°39.2′W	OS	11. 8.76
				– 47°29.5′N	9°38.8′W		
	WS03	4829	10	48°19.2′N	15°23.3′W	WS	1. 8.76
				– 48°19.1′N	15°22.5′W		
	WS07	4281	4	47°30.6′N	9°37.1′W	WS	7. 8.76
				– 47°31.2′N	9°35.7′W		
	WS08	4287	11	47°30.5′N	9°33.7′W	WS	9. 8.76
	WS09	4277	3	47°28.8′N	9°34.0′W	WS	10. 8.76
				– 47°27.9′N			

	WS10	4354	10	47°27.3′N – 47°18.2′N	9°39.9′W	WS	11. 8.76
Jean Charcot (Incal)	DS11	4823	1	48°18.8′N – 48°18.6′N	15°11.5′W 15°12.0′W	DS	1. 8.76
	DS14	4254– 4248	3	47°32.6′N – 47°32.6′N	9°35.7′W 9°35.1′W	DS	7. 8.76
	DS15	4268	12+2v	47°29.8′N – 47°30.3′N	9°33.4′W 9°33.4′W	DS	9. 8.76
	CP11	4823	1	48°20.4′N – 48°21.2′N	15°14.6′W 15°13.7′W	CP	1. 8.76
Chain 106	330	4632	8	50°43.5′N – 50°43.4′N	51°07.0′W 51°09.0′W	ES	29. 8.72
CANARIES BASIN							
Discovery	6714	3301	3	27°13.0′N	15°41.0′W	ES	20. 3.68
GUYANA BASIN							
Knorr 25	287	4980– 4934	5	13°16.0′N	54°52.2′W	ES	24. 2.72
	288	4417– 4429	64	11°02.2′N	55°05.5′W	ES	25. 2.72
Jean Charcot (Biovema)	DS03	5150	1	10°47.1′N – 10°47.1′N	42°40.7′W 42°40.3′W	DS	16.11.77
	DS05	5100	6	10°45.9′N – 10°46.0′N	42°40.2′W 42°39.8′W	DS	18.11.77
	CP04	5100	1	10°45.9′N – 10°45.9′N	42°40.2′W 42°39.3′W	CP	18.11.77
CAPE BASIN							
Jean Charcot	DS05	4560	3	33°20.5′S	2°34.0′E	DS	30.12.78
(Walvis)	DS06	4585	7	33°24.5′S	2°32.0′W	DS	31.12.78
	DS07	5100	20	26°59.7′S	1°07.1′E	DS	1. 1.79
	DS08	5225	3	26°59.6′S	1°07.3′E	DS	5. 1.79
	DS09	5220	15	26°59.9′S	1°06.7′E	DS	6. 1.79
NORTH AMERICA BASIN							
Atlantis II 12	70	4680	1	36°23.0′N	67°58.9′W	ET	23. 8.64
Chain 50	78	3828	2	38°00.0′N	69°18.7′W	ET	30. 6.65
	80	4970	45	34°49.8′N	66°34.0′W	ET	2. 7.65
	81	5042	14	34°41.0′N	66°28.0′W	ET	2. 7.65
	83	5000	2	34°46.5′N	66°30.0′W	ET	3. 7.65
	85	3834	8	37°59.2′N	69°26.2′W	ET	5. 7.65
Atlantis II 17	92	4694	3	36°20.0′N	67°56.0′W	ET	13.12.65
Atlantis II	93	5007	23	34°39.0′N	66°26.0′W	ET	14.12.65
24	121	4800	2	35°50.0′N	65°11.0′W	ET	21. 8.66
Atlantis II 40	175	4667– 4693	2	36°36.0′N	68°29.0′W	ES	29.11.67

This is a true abyssal species found only in the deepest part of the Basins and, except for the Argentine & Norwegian Basins is widely distributed throughout the Atlantic. Depth range: 3250–5225 m.

SHELL DESCRIPTION (Figs. 84 & 85). Shell small, moderately thick, oval, inflated, inequilateral, posterior margin slightly produced; surface with very fine irregular concentric lines, fine radial striae present in some specimens, dorsal area between umbo and posterior margin furrowed; umbos raised slightly, orthogyrate; dorsal margin proximally straight on either side of umbo, distally antero-dorsal margin joins rounded anterior margin in broad curve which continues to ventral margin, more convex posteriorly, distal postero-dorsal margin curves more gradually to produce slightly drawn out posterior margin, limit of posterior margin supra-medial; hinge plate moderately broad, long, slightly curved, up to 10 small 'V'-shaped, chevron teeth on each side of ligament; ligament amphidetic, small, 'goblet'-shaped, small external extension of fused periostracum on either side of umbo, small chondrophore present.

Prodissoconch length: 146–187 μm. Maximum recorded shell length 4.4 mm.

The description of *Portlandia (Y) subcircularis* (Odhner, 1960) agrees well with that presented above.

With increasing length, the posterior part of the shell becomes slightly more extended and at the same time the postero-dorsal margin becomes more smoothly curved (Figs. 85 & 86). The width to length ratio also increases with increasing size, but little proportionate change occurs in the height to length ratio although this varies in individuals between 0.72 and 0.84. The height/length ratios are the highest recorded for any species of *Yoldiella*. In some larger specimens the dorsal margin immediately anterior and posterior to the umbos may become slightly concave and as a result a small, shallow lunule and escutcheon may be formed. Comparison of specimens from the different Basins show that northerly (W. European) and southerly (Angola) populations in the eastern Atlantic are similar in form as too are the North

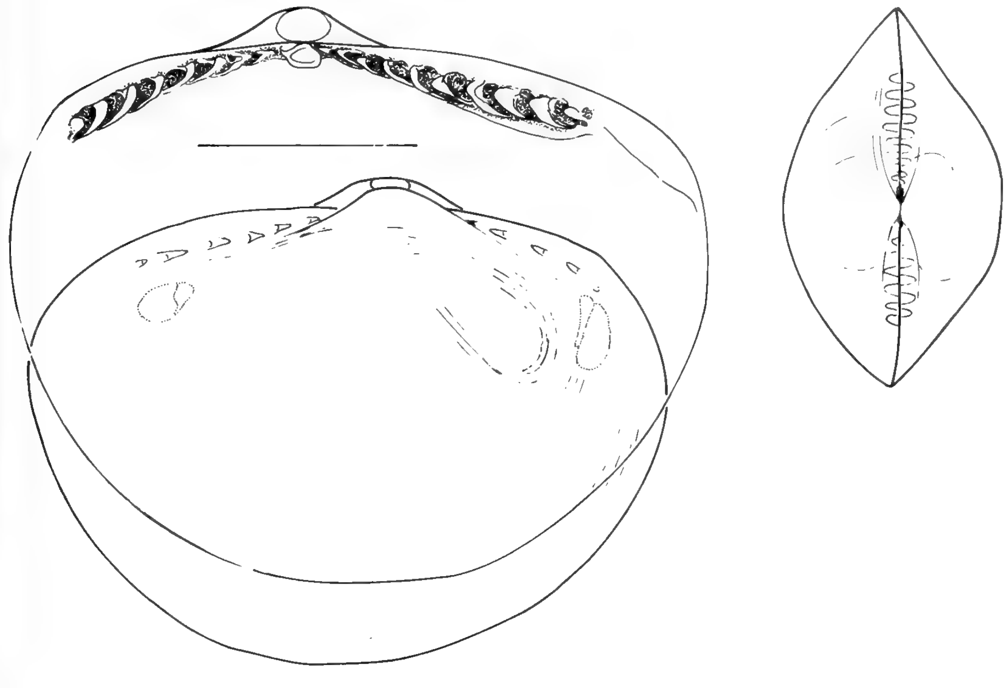

Fig. 84 *Yoldiella subcircularis*. Lateral view of a shell from the right side and a right valve to show the detail of the hinge-plate. Specimens from Sta. 285 Guyana Basin and Sta. 93 North Atlantic Basin respectively. (Scale = 1.0 mm).

America specimens. In contrast the small number of specimens from the Guyana Basin differ slightly in having a lower height/length ratio (significant at the 0.1 level).

INTERNAL MORPHOLOGY (Figs. 87 & 88). In *Y. subcircularis* the volume of the mantle cavity is large compared with that of the body. A well-developed sense organ lies at the far anterior margin. The siphons are combined and the inhalent siphon is shorter than the exhalent and is open ventrally. Both siphons are thin-walled and a pair of lateral haemocoeles are present in the junction between them. There is a moderately large siphonal tentacle, most frequently found on the left side. The feeding aperture is well-developed with areas of glandular mantle epithelium on each side which are probably extended in life as paired, broad flaps. For some distance anterior to these, the inner muscular lobe is particularly well-ciliated and it may be that the feeding area either is separated from the pedal gape by a ciliary junction or it is the region where pseudofaeces are formed. The adductor muscles are small, approximately equal in size, oblong in shape and lie close to the dorsal and anterior and posterior mantle margins respectively.

The gill plates are relatively few in number (18 in a specimen 3.0 mm). Tissue junctions join the demibranchs to the mantle dorsally. The gill plates are particularly muscular

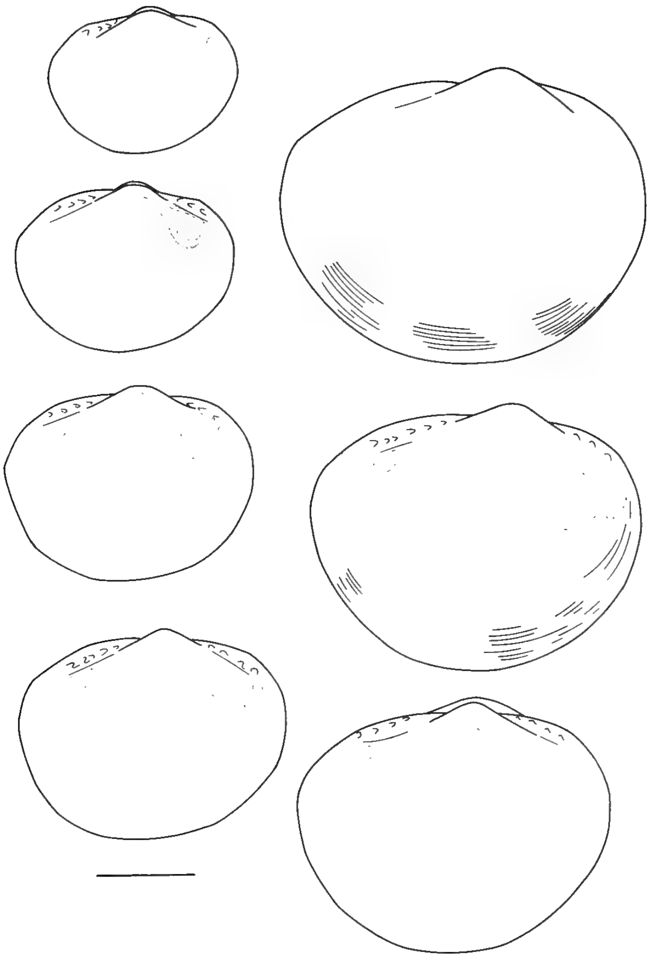

Fig. 85 *Yoldiella subcircularis*. Outlines of shells from the right side to show variation in shape. Specimens taken from Sta. BG VI DS 76, West European Basin. (Scale = 1.0 mm).

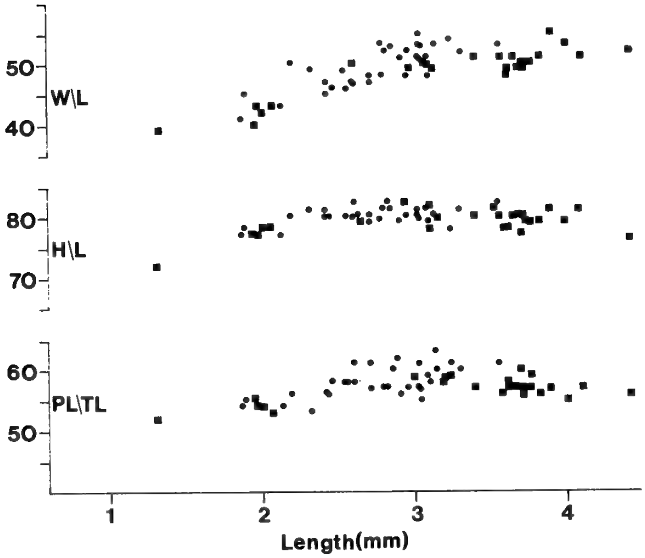

Fig. 86 *Yoldiella subcircularis*. Variation in ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of subsamples from Sta. BG DS 76, West European Basin (closed circles) and Sta. Walvis QS 07, Cape Basin (closed squares).

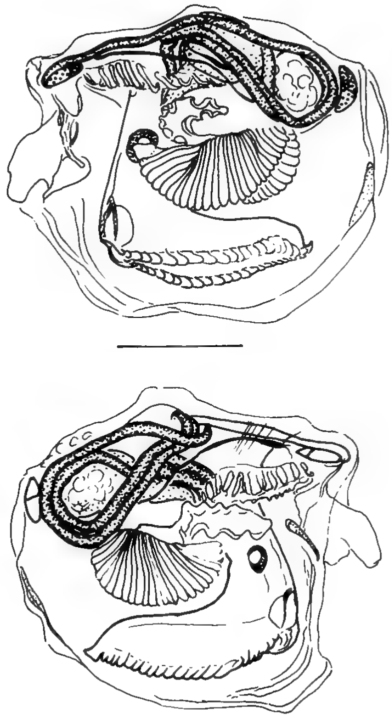

Fig. 87 *Yoldiella subcircularis*. Lateral views from right and left sides of the internal morphology of a specimen from Sta. 80 North America Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

and well-developed. The labial palps are large, with up to 32 closely spaced ridges on each inner face. In some of the largest specimens (> 3.3 mm) the anterior part of the palps are frequently folded in on themselves. The palp proboscides are relatively small and slender. The foot is conspicuous, being long and thin, with a much extended narrow neck and a long divided papillate sole. Gland cells are present along the ventral part of the sole and surrounding the aperture of a large byssal gland. Pedal retractor muscles are less conspicuous in this species than in others described here. The central haemocoele of the foot is extensive. The cerebral and visceral ganglia are relatively small, circular in transverse vertical cross-section. The visceral ganglia are some distance anterior to the posterior adductor muscle. The pedal ganglia lie at the dorsal limit of the extended neck of the foot close to its junction with the body, they are large and elongate with large associated statocysts dorsal to them.

The mouth is displaced a short distance posteriorly from the anterior adductor muscle. The stomach and style sac are moderately large. Two broad sorting ridges can be seen on the right anterior wall of the stomach. A prominent gastric tooth is present on the left dorsal wall and posterior to it the gastric shield extends over the left and most of the right walls of the stomach. The major typhlosole extends along the right side of the stomach. The digestive diverticula lie either side and anterior to the stomach. The duct of the right digestive diverticulum curves dorsally over the hind gut and enters the stomach on the right anterior dorsal wall. A duct from one left diverticulum enters the stomach far anterior on the left dorsal side, and immediately posterior to it, a short duct from a second left diverticulum enters the stomach, ventral to the gastric tooth. Material similar to that in the stomach was present in the lumen of the latter diverticulum, but this could possibly have resulted from tissue contraction following fixation. The style sac is relatively large and extends into the dorsal part of the foot. The hind gut has a shallow typhlosole along its entire length, the impression of which can be seen on extruded faecal pellets. The hind gut is arranged in two loops on each side of the body. These are usually visible through the shell antero-dorsally. There is also a double vertical extension of the hind gut deep into the foot. Thus, design advantage is taken of the exceptional length of the neck of the foot to accommodate a significant part of the greatly extended hind gut.

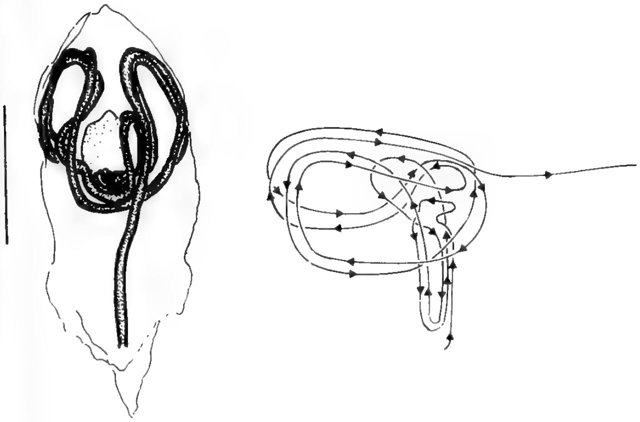

Fig. 88 *Yoldiella subcircularis*. Dorsal view of the hind gut of a specimen from Sta. 80 North America Basin and a diagrammatic view of the course of the hind gut as seen from the left side. (Scale = 1.0 mm).

The sexes are separate. Sectioned specimens larger than 2.8 mm had maturing gonads. The number of ova ranged from 37 (2.80 mm) to approximately 140 (2.91 mm) with a maximum ovum diameter of 132 μm and 156 um respectively. The gonads overlie the lateral and dorsal sides of the viscera. Mature females were present in February, June, August and October samples from the West European Basin. In two specimens from (Sta. DS76, Sta. DS79 respectively both 2.91 mm total length), eggs were partially shed into the mantle cavity and had a maximum dimension of 156 μm. Nevertheless, there is no evidence to show that eggs are retained and incubated within the mantle cavity.

Although the kidney is relatively small, it extends forward on either side of the stomach for a short distance.

Yoldiella biguttata (new species)

TYPE LOCALITY. R.V. Knorr Cruise 25, Sta. 299,Guyana Basin, 29.2.1972, 7°55.1′N, 55°42.0′W, Epibenthic Trawl, 1942–2076 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992029. Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
BRAZIL BASIN							
Atlantis II 31	167	943–1007	5	7°58.0′S – 7°50.0′S	34°17.0′W 34°17.0′W	ES	20.2.67
ARGENTINE BASIN							
Atlantis II 60	245	2707	2	36°55.7′S	53°01.4′W	ES	14.3.71
GUYANA BASIN							
Knorr 25	293	1456–1518	13	8°58.0′N	54°04.3′W	ES	27.2.72
	295	1000–1022	2	8°04.2′N	54°21.3′W	ES	28.2.72
	299	1942–2076	74	7°55.1′N	55°42.0′W	ES	29.2.72
	301	2487–2500	44	8°12.4′N	55°50.2′W	ES	29.2.72
	303	2849–1853	4	8°28.8′N	56°04.5′W	ES	1. 3.72

Y. biguttata is distributed off the coast of eastern South America at mid slope to abyssal depths in the Argentine, Brazil and Guyana Basins. Depth range: 943–2853 m.

SHELL DESCRIPTION (Fig. 89). Shell small, inflated, equilateral, fine concentric striae; umbos posterior to midline, slightly raised, moderately large, inwardly directed; dorsal margin raised, sharp-edged, particularly so anterior to umbo, dorsal margin close to umbo straight, proximal antero-dorsal margin curves to broadly rounded anterior margin, the limit of which is slightly ventral to the midline, ventral margin shallow curve, in some specimens almost straight centrally, postero-ventral margin sinuous giving a characteristic oblique

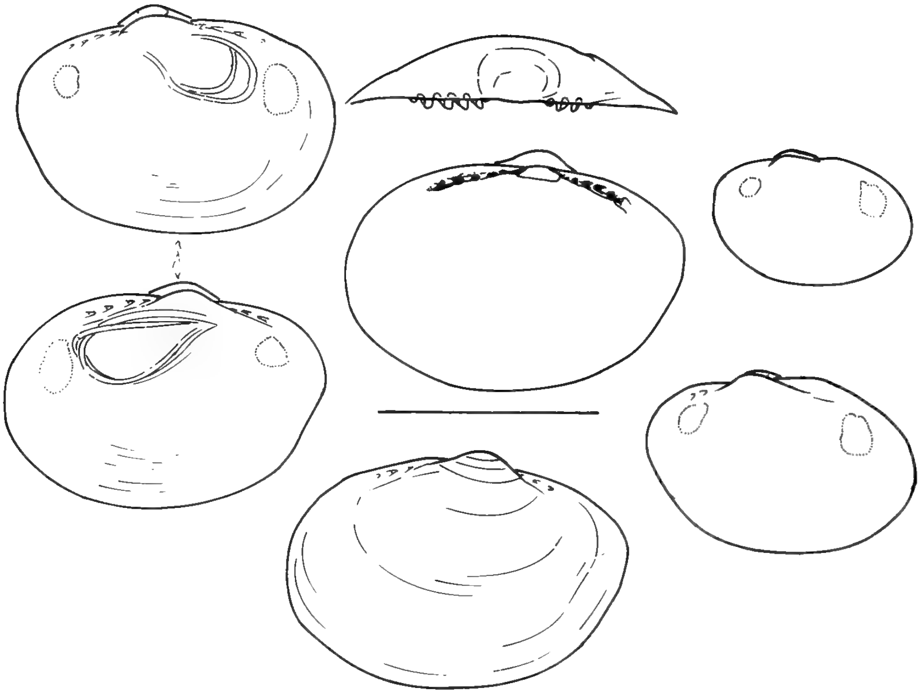

Fig. 89 *Yoldiella biguttata.* Lateral views of shells from the right and left sides and a right valve in inner lateral and dorsal view to show variation in shape and hinge-plate details. Specimens from Sta. 301 and Sta. 299, Guyana Basin. (Scale = 1.0 mm).

configuration to shell in lateral view; hinge plate moderately shallow, short, reaching no further than inner limit of adductor muscles, teeth few, anterior and posterior series either equal or with one additional tooth in anterior series (5/6 in largest specimen); ligament amphidetic, very large in relation to size of shell.

Shell measurements (mm) & ratios are as follows:-

Length	Height	Width	H/L	W/L	PL/TL
1.64	1.24	0.89	0.75	0.54	0.39
1.62	1.12	0.72	0.69	0.44	0.45
1.50	1.07	0.68	0.72	0.45	0.46
1.50	1.08	0.73	0.72	0.49	0.39
1.37	1.02	0.70	0.74	0.51	0.47
1.19	0.81	0.48	0.68	0.40	0.39
0.87	0.62	0.33	0.71	0.38	0.40

Prodissoconch length: 198 μm. Maximum recorded shell length: 1.64 mm.

INTERNAL MORPHOLOGY (Fig. 90). The combined siphon is thin-walled and with a single lumen. In that the gill axis joins the ventral edge of the siphon the inhalent component can be assumed to be largely absent. The siphon is not open ventrally. A single fine, elongate mantle tentacle originates on the left ventral inner limit of the moderately deep siphonal embayment. An area of secretory cells is present at the base of the siphon. Ventral to the siphon is a well-developed feeding aperture. The posterior adductor muscle is round in cross-section while the anterior is slightly larger and 'crescent'-shaped. The visceral and cerebral ganglia are well-developed and joined by a stout commissure. The cerebral ganglia are slightly the larger. The gills have a relatively small number of plates (maximum number recorded 9) most of which are carried posterior to the foot. Labial palp ridges number 14–18, depending on the size of the specimen, and are moderately large. The palp proboscides are also moderately large. The foot papillae contain considerable numbers

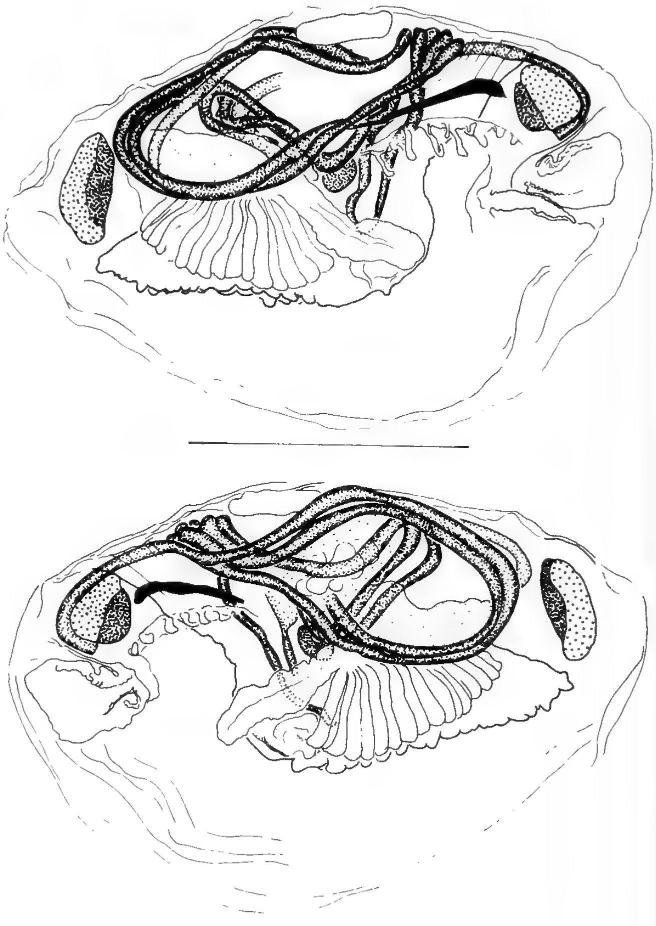

Fig. 90 *Yoldiella biguttata.* Lateral views from the right and left sides of the internal morphology of a specimen from Sta. 299, Guyana Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

of secretory cells. There is a relatively large single posterior papilla immeditely posterior to the aperture of the byssal gland at the heel of the foot. The gland is large and is surrounded by secretory cells. The hind gut is complex with twinned loops on each side of the body, with two recurved sections immediately anterior to the stomach. The main lateral loops of the hind gut cross from one side of the body to the other dorsally and immediately posterior to the resilium. All the specimens examined had well-developed gonads which makes it difficult to determine the exact course of the gut, but from sections we are confident that it has a similar design to that described for *Yoldiella subcircularis*. One sectioned female (1.63 mm total length) from Sta. 299 has 18 large ova present (maximum observed dimension 114 μm).

Despite the similarity of the internal morphology to that of *Yoldiella subcircularis* the shapes of the shell, hinge and ligament are totally different in the two species (p. 55). As we point out elsewhere the various types of hind gut morphology do not necessarily correlate to a particular characteristic suite of shell characters. All that can be said with certainty is that the hindgut of *Yoldiella biguttata* has configuration so far found only in the Yoldiellidae and only in species from the abyss and abyssal rise.

Yoldiella ovata (new species)

TYPE LOCALITY. R.V. Knorr Cruise 25, Sta.300, Guyana Basin, 29.2.1972, 8°14.2′N, 55°53.5′W, Anchor Dredge, 2524–2542 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992035. Paratypes: in collection held by J.A. Allen.

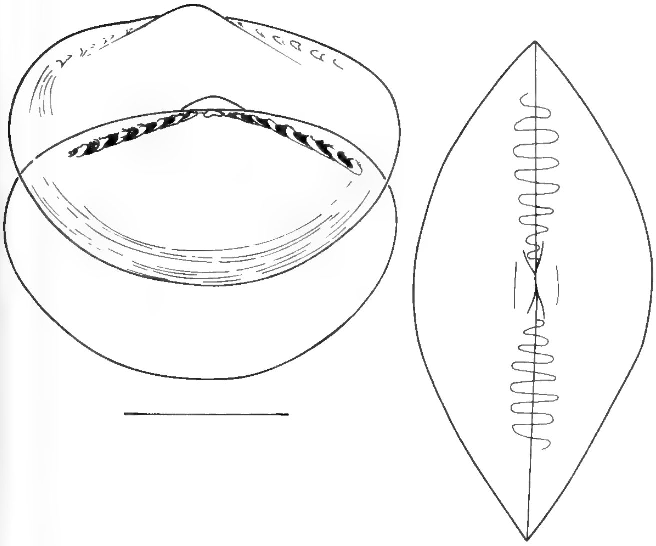

Fig. 91 *Yoldiella ovata*. Lateral views of a shell from the left side and dorsally and an inner view of a left valve to show detail of the hinge-plate. Specimens taken from Sta. 300, Guyana Basin. (Scale = 1.0 mm).

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUYANA BASIN							
Knorr 25	300	2524–2542	208	8°14.2′N	55°53.5′W	AD	29.2.72
	301	2487–2500	324	8°12.4′N	55°50.2′W	ES	29.2.72
	303	2842–2853	13	8°28.8′N	56°04.5′W	ES	1 .3.72

Restricted to the abyssal rise of the Guyana Basin. Depth range: 2487–2853 m.

SHELL DESCRIPTION (Figs. 91 & 92). Shell small, ovate, moderately inflated, inequilateral, transparent, dorsolaterally smooth, ventrally, with very fine concentric lines forming ridges; umbos slightly anterior of midline, moderately inflated, orthogyrate; dorsal margin slightly convex, antero-dorsal and postero-dorsal margins with similar curva-

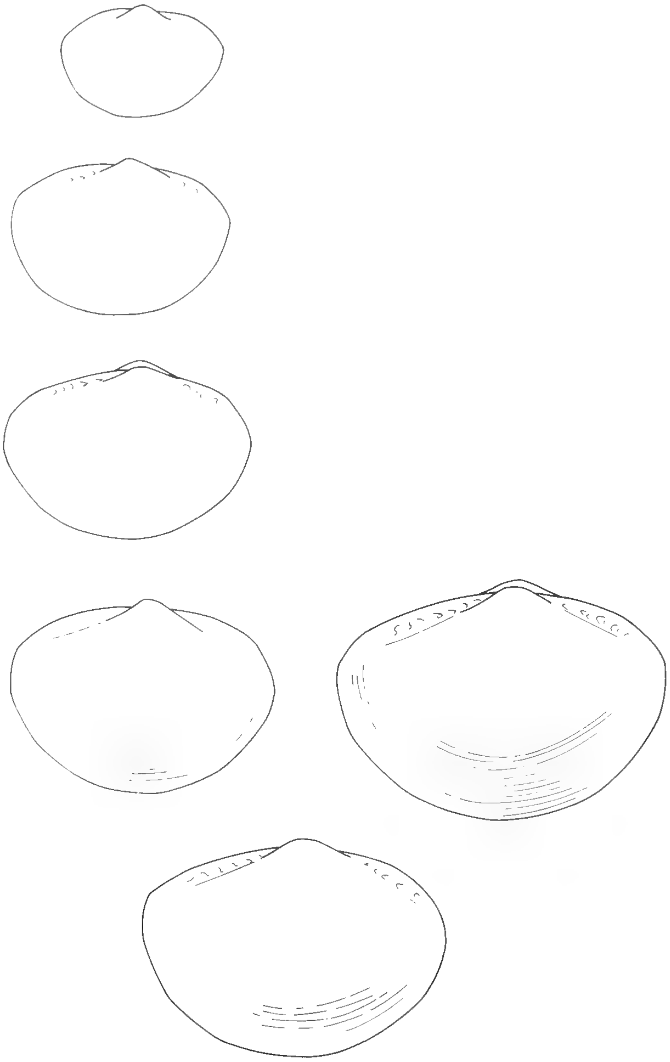

Fig. 92 *Yoldiella ovata*. Outlines of shells from the right side to show change in shape with growth of specimens from Sta. 300, Guyana Basin. (Scale = 1.0 mm).

ture, ventral margin smoothly curved, posterior margin somewhat more convex than anterior and very slightly extended, anterior and posterior margins broad, rounded; hinge plate elongate, moderately wide except below umbo where narrow, moderately strong, acute taxodont teeth, 7 in anterior and 8 in posterior series in specimen 2.3 mm; ligament internal, amphidetic, slightly elongate, barely extends below hinge plate.

Prodissoconch length: 172 μm. Maximum recorded shell length: 2.9 mm.

INTERNAL MORPHOLOGY (Fig. 94). The inhalent and exhalent siphons are combined, the inhalent is open along its ventral margin. The siphonal tentacle is either to the right or left. There is a feeding aperture and anterior to it a heavily ciliated region of the inner mantle fold. There is a well-developed anterior sense organ. The posterior adductor muscle is small and oval, the anterior adductor, also oval, is approximately twice the size of the posterior. The labial palps are moderately large with up to 19 palp ridges and each has a long thin palp proboscis. The gill which is small, dorsal in position in preserved specimens, has up to 14 plates. The visceral and cerebral ganglia are typically 'club'-shaped, the visceral being the smaller. The pedal ganglia are moderately large, elongate and situated high in the foot. The foot is long and thin with deep papillae fringing the sole. A large byssus gland is present in the heel.

The stomach and style sac are small and the latter does not penetrate far into the foot. The hind gut forms double loops to the left and right of the body, recurring anterior to the stomach, thus taking a similar course to *Yoldiella subcircularis* and *Yoldiella biguttata*. A considerable amount of fine material was present in the digestive diverticula of the left side. The kidneys although moderately well-developed do not penetrate anteriorly into the visceral mass to any great extent. The sexes are separate. One sectioned female (2.7 mm) contained approximately 50 ova with a maximum diameter of 80 μm.

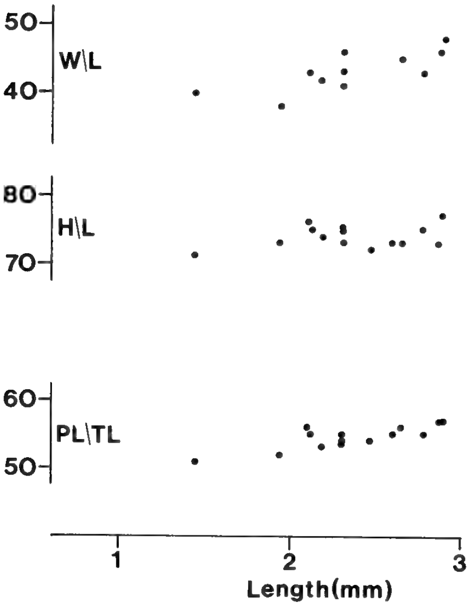

Fig. 93 *Yoldiella ovata.* Variation in the ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of subsample from Sta. 300, Guyana Basin.

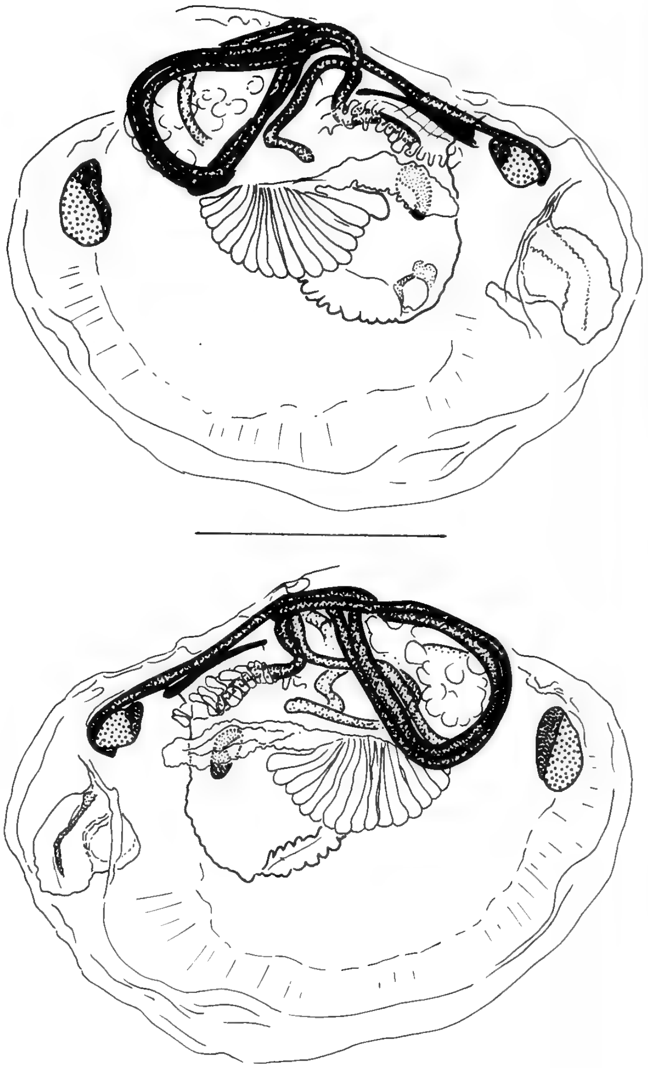

Fig. 94 *Yoldiella ovata.* Lateral views from the right and left side of the internal morphology of a specimen from Sta. 300, Guyana Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

With increasing length, the height/length, width/length and particularly the posterior umbonal length/total length ratios gradually increase (Fig. 93).

Yoldiella ovata is closely related to *Y. biguttata*, but can be distinguished by its more ovate outline and not being flattened at the postero-ventral shell margin.

Yoldiella insculpta (Jeffreys 1879)

TYPE LOCALITY. West of Ireland, H.M.S. Porcupine, 1869, Sta. 16, 54°19′N, 11°50′W, 816 fms.

TYPE SPECIMEN. Holotype: not designated. Lectotype: (here designated) BM(NH) 85.11.5.459.

Leda insculpta Jeffreys 1879, p. 580, pl. 46, Fig. 5; Dautzenberg 1889, p. 80; Dautzenberg & Fischer 1897, p. 204; Locard 1898, p. 355.

We have examined the material designated as syntypes by Warén (1980) and housed in the collections of the U.S. National Museum and the Natural History Museum, London.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
La Perle	DS11	2205	9+2v	47°35.5'N	8°33.7'W	DS	8. 8.72
(Biogas I)	DS13	2165	23+6v	47°33.7'N	8°39.9'W	DS	10. 8.72
Jean Charcot	DS15	2246	5	47°35.2'N	8°40.1'W	DS	21.10.72
(Polygas)	DS16	2325	1	47°36.1'N	8°40.5'W	DS	21.10.72
	DS18	2138	4	47°31.2'N	8°44.9'W	DS	22.10.72
(BiogasII)	DS31	2183	4	47°32.5'N	9°04.2'W	DS	19. 4.73
	DS32	2138	14	47°32.2'N	8°05.3'W	DS	19. 4.73
(BiogasIII)	DS35	2226	18+8v	47°34.4'N	8°40.7'W	DS	24. 8.73
	DS36	2147	5	47°32.7'N	8°35.6'W	DS	24. 8.73
	DS37	2110	12+ 54v	47°31.8'N	8°34.6'W	DS	24. 8.73
	DS38	2138	2	47°32.5'N	8°35.8'W	DS	25. 8.73
(Biogas IV)	DS61	2250	10+2v	47°34.7'N	8°38.8'W	DS	25. 2.74
	DS62	2175	63	47°32.8'N	8°40.0'W	DS	26. 2.74
	DS63	2126	23+ 10v	47°32.8'N	8°35.0'W	DS	26. 2.74
	DS64	2156	18+ 12v	47°29.2'N	8°30.7'W	DS	26. 2.74
	CP01	2245	8+4v	47°34.6'N	8°38.8'W	CP	25. 2.74
(Biogas V)	DS65	2360	1	47°36.1'N	8°40.5'W	DS	15. 6.74
	DS71	2194	6+2v	47°34.3'N	8°33.8'W	DS	20.10.74
	DS87	1913	1	44°05.2'N	4°19.4'W	DS	1.11.74
	CP08	2177	11+2	44°33.2'N	8°38.5'W	CP	20.10.74
	CP09	2171	24+4v	47°33.0'N	8°44.0'W	CP	20.10.74
Sarsia	65	1922	42	46°15.0'N	4°50.0'W	ED	25.7.67
CANARIES BASIN							
Discovery	6701	1934	1	27°45.2'N	14°13.0'W	ED	16. 3.68
	6704	2129	1	27°44.9'N	14°25.0'W	ED	17. 3.68
	6710	2670	2	27°23.6'N	15°39.6'W	ED	19. 3.68
	6714	3301	2	27°13.0'N	15°41.0'W	ED	20. 3.68

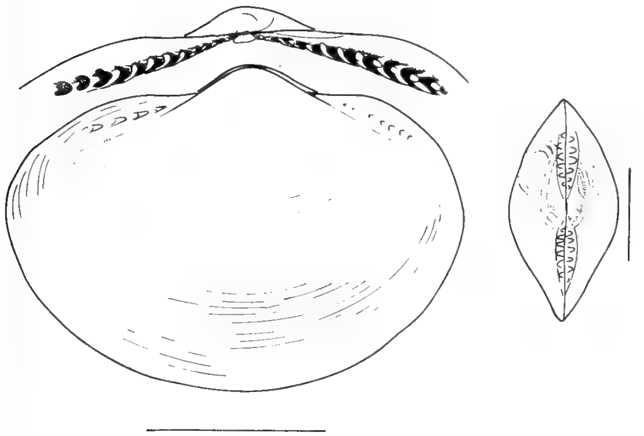

Fig. 95 *Yoldiella insculpta*. Dorsal and lateral view of shell from the right side and a lateral view of the hinge-plate of a left valve. Specimens from Sta. BG IV DS 62, West European Basin. (Scales = 1.0 mm).

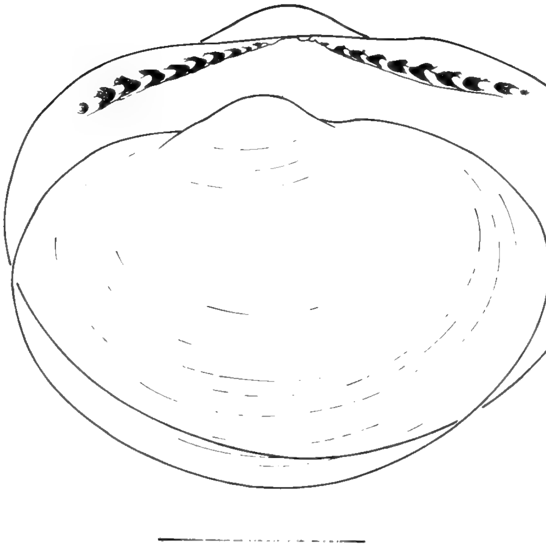

Fig. 96 *Yoldiella insculpta*. Lateral view of shell from the left side and an inner view of right valve. Specimens from Sta. 16 and Sta. 17 Porcupine Expedition, W. of Portugal. (USNM No. 199773). (Scale = 1.0 mm).

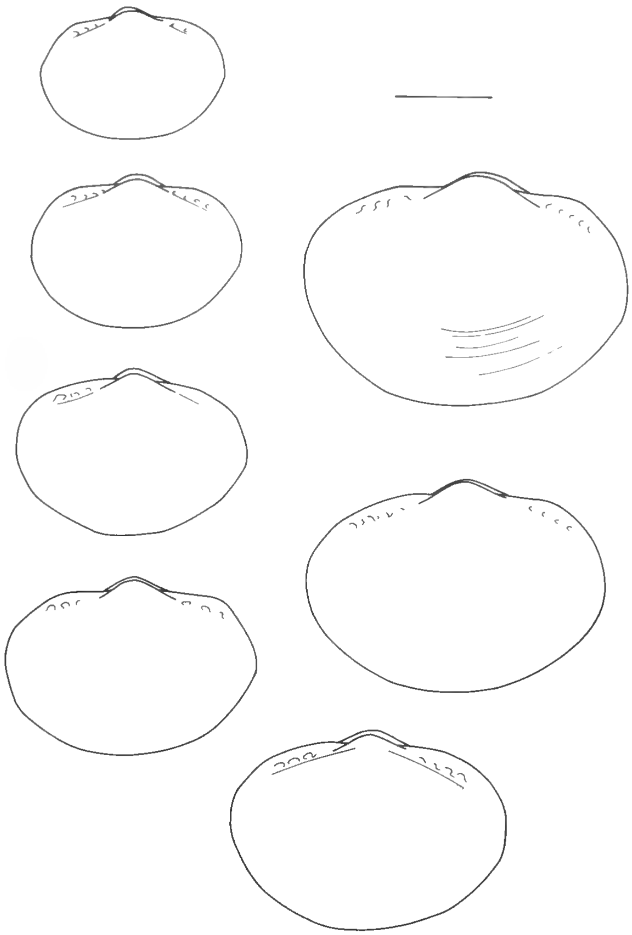

Fig. 97 *Yoldiella insculpta*. Outlines of shells from the right side to show variation in shape. Specimens from Sta. BG DS 63, West European Basin. (Scale = 1.0 mm).

Distributed in the north eastern Atlantic, Bay of Biscay, off northwest Africa and the Azores at abyssal rise depths. Depth range: 1354–3301 m.

Shell description (Figs. 95–98). Shell ovate, moderately inflated, smooth with very fine concentric lines near ventral margin forming slight ridges in larger specimens, occasionally a few faint radial lines are present in larger specimens; periostracum pale straw-coloured, slightly iridescent; umbos very slightly anterior of midline, moderately inflated; proximal dorsal margin straight or slightly concave on either side of umbo, antero-dorsal and anterior margin merge in an even curve in most specimens, distally postero-dorsal margin slopes down to posterior margin; posterior margin with slight angulation, posterior limit of anterior and posterior margins dorsal to horizontal mid-plane, ventral margin a smooth curve; hinge plate relatively narrow, barely extending to outer margins of adductor muscles, anterior hinge line relatively straight, distally slopes away from dorsal shell margin, chevron-shaped teeth small, posterior hinge line slightly curved anteriorly, with same number of teeth in each series (8/8 in a specimen 2.2 mm and 12/12 in a specimen 3.5 mm); ligament amphidetic, small, rounded, extends below hinge plate.

Prodissoconch length: c. 190 μm. Maximum recorded shell length: 3.65 mm.

There is a slight increase in the post-umbonal length as length increases, otherwise the ratios of height/length and width/length remain constant.

Internal morphology (Fig. 99). The mantle edge is well-developed, particularly the inner muscular fold which at its dorsal edge, contains secretory cells beneath the main rejection tract. Postero-ventral to the siphons, both the middle and inner folds are increased in size, convoluted and heavily ciliated and form a feeding aperture. Exhalent and inhalent siphons are combined, the latter being open ventrally. A pair of lateral haemocoelic canals are present the junction between the siphons. The siphonal tentacle is large and found equally to either the right or left side of the siphonal embayment. There is a well-developed anterior sense organ. Adductor muscles are slightly unequal in size, the anterior being the larger.

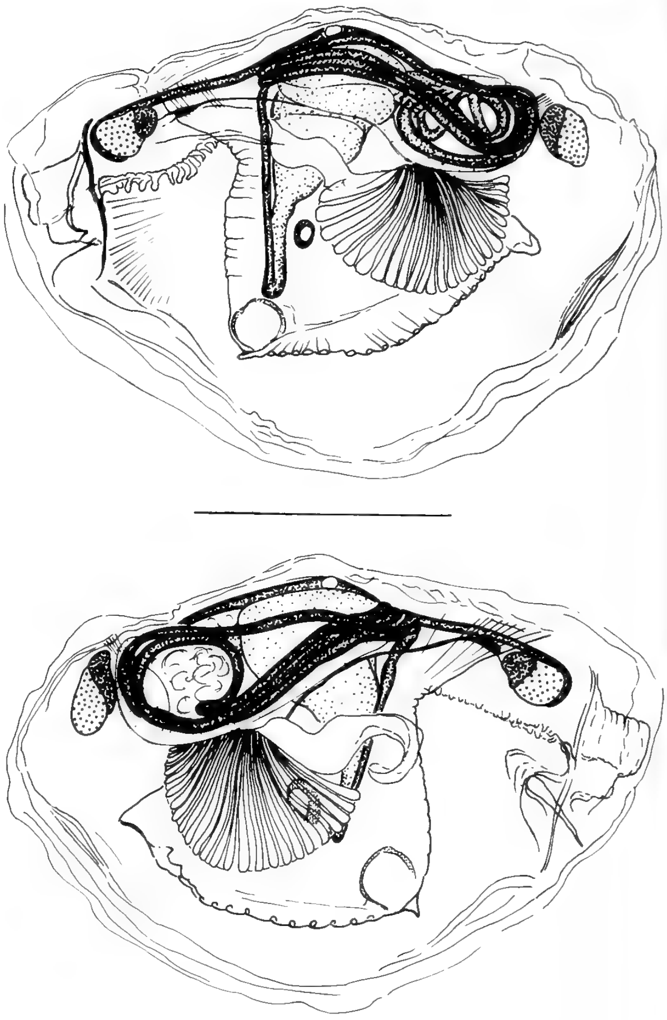

Fig. 99 *Yoldiella insculpta*. Lateral views from the right and left sides of the internal morphology of a specimen from Sta. S 65, West European Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

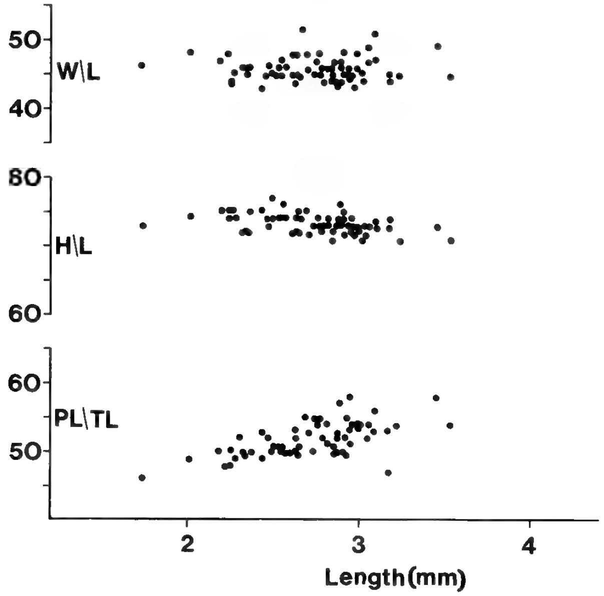

Fig. 98 *Yoldiella insculpta*. Variation in the ratios of height H/L, width W/L and postero-umbonal length PT/TL to length against length of a sample from Sta. BG IV DS 62, West European Basin.

Gill plates are relatively small and difficult to count in preserved specimens (maximum recorded c. 18–20). The labial palps are well-developed with approximately up to 26 closely spaced ridges on each inner face. The palps extend between 1/3–1/2 across the body and each bears a long thin palp proboscis. The mouth is positioned a short distance posterior to the anterior adductor muscle. The foot is relatively large with a broad sole with a small papilla at the posterior limit. There is a large byssal gland in the heel (Fig. 100). The arrangement of pedal retractor muscles is similar to that of other species of *Yoldiella*. The cerebral ganglia are relatively large, the visceral ganglia are small and elongate. The pedal ganglia lie ventral to the style sac in the proximal part of the foot and are moderately large. The stomach is displaced slightly to the right of the body and is of moderate size with a large style sac. The hind gut configuration is unique. There are three loops to the right of the body and two loops to the left of the body with a further double loop passing to the left of the stomach into the foot anterior to the stomach. The loops do vary slightly in their extent and curvature. This is similar to the condition in *Y. subcircularis, Y. biguttata* and *Y. ovata* but with an additional loop on the right. The hind gut has a typhlosole along its entire length. Fine material similar to that present in the stomach was seen in the digestive diverticula of a number of specimens. The kidney is well-developed. Sexes are separate.

The maximum diameter of the ovum as observed in sections of females from samples taken in February and August was similar (130 μm). There seems to be a wide variation in the numbers of ova present. A female collected in August (2.74 mm) had 255 ova while another collected in February (3.09 mm) had only 65 ova. Maturing gonads were recorded for all months sampled.

Yoldiella jeffreysi **(Hidalgo 1877)**

TYPE LOCALITY. H.M.S. Valorous Sta. 16, Iceland Basin, west of Rockall Plateau, south Maury Channel, 55°10′N, 25°58′W, 23.8.1875, Dredge, 1785 fm.

TYPE SPECIMEN. Holotype: not designated; Lectotype: U.S. Natl. Mus., No. 199696 as here designated.

Leda lata Jeffreys 1876, 1876. p. 431 (in part).
Leda jeffreysi Hidalgo 1877, p. 396; Jeffreys 1879, p. 579, pl. 46, Fig. 2; Dall 1881, p. 124; Smith 1885, p. 234; Dautzenberg 1889, p. 75; Dautzenberg & Fischer 1897, p.204; Locard 1898, p. 353.
Portlandia jeffreysi Posselt 1898, p.36.
Yoldiella jeffreysi Verrill & Bush 1898, p. 866, pl. 81, Fig. 5, pl. 83, Fig. 3.

A holotype of *Y. jeffreysi* was never designated but the following USNM specimens were identified as syntypes by Warén (1980):-

No. 1999695, Valorous Sta. 9; No. 199694, and No. 199696, Valorous Sta. 16; No. 199700, Porcupine Sta. 20; No. 199701, Porcupine Sta. 16 & 17; No. 199698 Porcupine Sta. 30.

and in the BM(NH):–

No. 77.11.18.25, Valorous Stas. 9, 12, 13, 16; No. 85.11.5.592–593,Porcupine Sta. 31; No. 85.11.5 366–367, Porcupine Sta. 16; No. 85.11.5. 591, Porcupine Sta. 9.

Jeffreys original specimens were taken from the North Atlantic (Valorous Stations 9, 12, 13 & 16 and from which he described his species *Leda lata* (Jeffreys, 1896). Unfortunately the material from these four 'Valorous' Stations, which we have examined, contains two species of *Yoldiella* which are, superficially, similar in form (p.). Furthermore the 1876 description is so general that there is nothing to indicate which of the two species Jeffreys chose when he described *Leda lata*. Thus, we here accept *Leda jeffreysi* Hidalgo (1877) as the first unequivocal specific designation and which Jeffreys (1879) himself accepted two years later.

We have also examined specimens referred to as *Yoldiella jeffreysi* by Verrill & Bush (1898) (USNM, No. 4888) and these clearly differ from *Y. jeffreysi s.s.* in being stouter, with a more inflated umbo, a broader hinge plate, with teeth of different form and fewer in number.

Y. jeffreysi is a very widespread species. It occurs from the base of the continental slope to the deepest abyssal depth. In our samples it occurs in the Argentine, Guyana, North America, West European, Canary, Cape Verde & Angola Basins. It has also been recorded from the Gulf of Mexico (2416–2868 m) and from off West Greenland (3200 m) and in the Mediterranean off Palermo.

Depth range: 2040–4862 m. The depth distribution is similar throughout the Atlantic.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II	64	2886	7	38°46.0′N	70°06.0′W	ET	21. 8.64
12	72	2864	6	38°16.0′N	71°47.0′W	ET	24. 8.64
Chain 50	76	2862	32	39°38.3′N	67°57.8′W	ET	29. 6.65
	77	3806	109	38°00.7′N	69°16.0′W	ET	30. 6.65
	78	3828	57	38°00.8′N	69°18.7′W	ET	30. 6.65
	84	4749	16	36°24.4′N	67°56.0′W	ET	4. 7.65
	85	3834	413	37°59.2′N	69°26.2′W	ET	5. 7.65
Atlantis II	123	4853	4	37°29.0′N	64°14.0′W	ET	22. 8.66
24	124	4862	1	37°26.0′N – 37°25.0′N	59°59.5′W 63°58.0′W	ET	22. 8.66
	126	3806	138	39°37.0′N – 39°37.5′N	66°47.0′W 66°44.0′W	ET	24. 8.66
Atlantis II 40	175	4667–4693	53	36°36.0′N	68°29.0′W – 68°31.0′W	ES	29.11.67
Chain 106	330	4632	155	50°43.5′N – 50°43.3′N	17°51.7′W 17°52.9′W	ES	24. 8.72
	334	4400	49	40°42.6′N – 40°44.0′N	46°13.8′W 46°14.6′W	ES	30. 8.72
	335	3882–3919	28	40°25.3′N	46°30.0′W	ES	31. 8.72
Knorr 35	340	32164–	13	38°14.4′N	70°20.3′W	ES	24.11.73

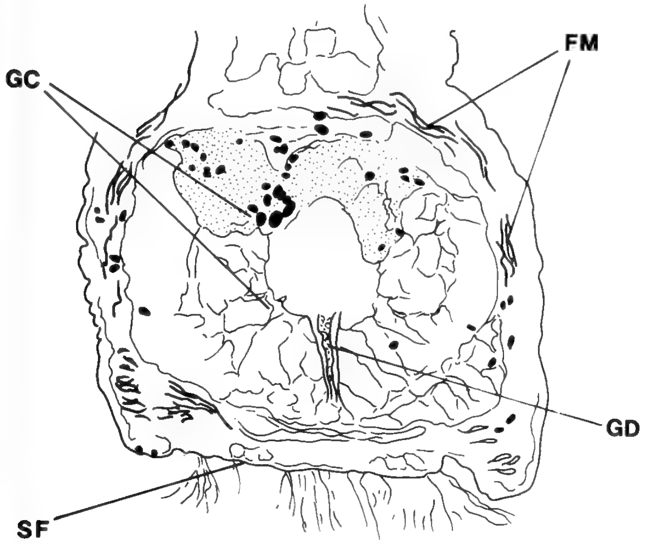

Fig. 100 *Yoldiella insculpta*. Transverse section through the 'byssal' gland. (Scale = 0.1 mm). Abbreviations see p. 12.

		3356		– 38°17.6′N	70°22.8′W		
GUYANA BASIN							
Knorr 25	287	4980– 4934	5	13°16.0′N – 13°15.8′N	54°52.2′W 54°53.1′W	ES	24. 2.72
	288	4417– 4429	31	11°02.2′N – 11°03.8′N	55°05.5′W 55°04.8′W	ES	25. 2.72
	291	3859– 3868	155	10°06.1′N – 10°06.6′N	55°14.0′W 55°15.4′W	ES	26. 2.72
	306	3392– 3429	38	9°31.1′N	56°20.6′W	ES	2. 3.72
	307	3862– 3835	30	12°34.4′N – 12°40.8′N	58°59.3′W 59°09.2′W	ES	3. 3.72
ARGENTINE BASIN							
Atlantis II 60	259	3305– 3317	30	37°13.3′S	52°45.0′W	ES	26. 3.71
WEST EUROPEAN BASIN							
Chain 106	316	2173– 2209	85	50°58.7′N – 50°57.7′N	13°01.6′W 13°01.3′W	ES	18. 8.72
	318	2506	106	50°27.3′N – 50°26.8′N	13°20.9′W 13°19.9′W	ES	19. 8.72
	321	2290– 2968	94	50°12.3′N	13°35.8′W	ES	20. 8.72
	323	3356– 3338	6	50°08.3′N	13°53.7′W – 13°50.9′W	ES	21. 8.72
Jean Charcot	DS23	4734	1	46°32.8′N	10°21.0′W	DS	26.10.72
(Polygas)	DS25	2096	2v	44°08.2′N	4°15.7′W	DS	1.11.72
(Biogas II)	DS31	2813	11	47°32.5′N	9°04.2′W	DS	19. 4.73
(BiogasIII)	DS37	2110	1	47°31.8′N	8°34.6′W	DS	24. 8.73
	DS71	3546	4	47°28.3′N	9°07.2′W	DS	28. 8.73
(Biogas IV)	DS51	2430	27	44°11.3′N	4°15.4′W	DS	18. 2.74
	DS52	2006	1	44°06.3′N	4°22.4′W	DS	18. 2.74
	DS53	4425	1	44°30.4′N	4°56.3′W	DS	19. 1.74
	DS54	4659	1	46°31.3′N	10°29.1′W	DS	21. 2.74
	DS58	2775	10	47°34.1′N	9°08.2′W	DS	23. 2.74
	DS62	2175	1	47°32.8′N	8°40.0′W	DS	26. 2.74
	DS63	2126	1	47°32.8′N	8°35.0′W	DS	26. 2.74
	DS64	2156	2	47°29.2′N	8°30.7′W	DS	26. 2.74
	CV38	2695	2	47°30.9′N	8°59.5′W	CV	24. 2.74
(Biogas V)	DS68	4550	1	46°26.7′N	10°23.9′W	DS	19. 6.74
(Biogas VI)	DS71	2194	2	47°34.4′N	8°33.8′W	DS	20.10.74
	DS74	2777	2+2v	47°33.0′N	9°07.8′W	DS	21.10.74
	DS78	4706	1	46°31.1′N	10°23.8′W	DS	25.10.74
	DS79	4715	2	46°30.4′N	10°27.1′W	DS	26.10.74
	CP10	2878	1	47°29.6′N	9°04.5′W	CP	21.10.74
(Incal)	DS01	2091	73	57°59.7′N – 57°59.2′N	10°39.8′W 10°41.3′W	DS	15. 7.76
	DS02	2081	67	57°58.8′N – 57°58.5′N	10°48.5′W 10°49.2′W	DS	16. 7.76
	CP01	2068– 2040	10	57°57.7′N – 57°56.4′N	10°55.0′W	CP	16.7.76
	CP02	2091	2	57°58.4′N – 57°57.7′N	10°42.8′W 10°44.6′W	CP	16. 7.76
	CP03	2466	4	56°33.2′N – 56°32.5′N	11°11.3′W 11°12.4′W	CP	17. 7.76
	CP04	2483– 2513	2	56°33.2′N – 56°31.5′N	11°11.3′W 11°12.4′W	CP	17. 7.76
	DS05	2503	123	56°28.1′N – 56°27.6′N	11°11.7′W 11°12.0′W	DS	18. 7.76
	DS06	1494	243	56°26.6′N – 56°25.9′N	11°10.5′W 11°10.7′W	DS	18. 7.76
	DS07	2884	267	55°00.7′N – 55°01.0′N	12°31.0′W 12°32.0′W	DS	19. 7.76
	DS08	2891	32	55°02.0′N – 55°01.9′N	12°34.6′W 12°33.4′W	DS	19. 7.76
	CP05	2884	58	55°00.4′N – 55°00.9′N	12°29.4′W 12°31.1′W	CP	19. 7.76
	CP06	2888– 2893	39	55°02.3′N – 55°02.6′N	12°40.3′W 12°41.7′W	CP	19. 7.76
	CP07	2896	17	55°03.4′N – 55°04.4′N	12°46.4′W	CP	20. 7.76
	DS09	2897	274	55°07.7′N – 55°08.1′N	12°52.6′W 12°53.2′W	DS	20. 7.76
	CP08	2644	49	50°14.7′N – 50°15.2′N	13°13.5′W 13°14.8′W	CP	27. 7.76
	DS10	2719	48	50°12.7′N – 50°13.2′N	13°16.6′W 13°16.4′W	DS	27. 7.76
	OS01	2634	794+ 52v	50°14.4′N – 50°15.2′N	13°10.9′W 13°11.0′W	OS	30. 7.76
	WS01	2550– 2539	39+2v	50°19.4′N – 50°19.3′N	13°08.1′W 13°06.0′W	WS	30. 7.76
	WS02	2498– 2505	416	50°19.3′N – 50°20.0′N	12°55.8′W 12°56.0′W	WS	30. 7.76
	CP10	4823	1	48°25.5′N – 48°26.3′N	15°10.7′W 15°09.8′W	CP	31. 7.76
	DS11	4823	1	48°18.8′N – 48°13.6′N	15°11.5′W 15°12.0′W	DS	1. 8.76
	WS03	4829	5+1v	48°19.2′N	15°23.3′W	WS	1. 8.76
	CP11	4823	2	48°20.4′N – 48°21.1′W	15°14.6′W 15°13.7′W	CP	1. 8.76
	OS02	4829	4	48°19.2′N	15°15.7′W	OS	2. 8.76
	DS14	4254– 4248	1	47°32.8′N	9°35.4′W	DS	7. 8.76
	DS16	4268	1	47°29.8′N – 47°30.3′N	9°33.4′W 9°33.4′W	DS	9. 8.76
CANARY BASIN							
Discovery	6704	2129	17	27°44.9′N	14°25.0′W	ED	17. 3.68
CAPE VERDE BASIN							
Discovery	8521	3053– 3058	90	20°46.9′N – 20°47.6′N	18°43.4′W 18°53.5′W	WS	25. 6.74
	8521	3064– 307	52	20°47.9′N – 20°48.6′N	18°53.4′W 18°53.4′W	WS	26. 6.74
	8532	3112– 3119	36	13°47.8′N – 13°48.0′N	18°14.0′W 18°14.8′W	WS	5. 7.74
	8532	2952– 2958	20	13°48.2′N – 13°47.6′N	18°08.0′W 18°07.5′W	WS	5. 7.74
ANGOLA BASIN							
Atlantis II 42	197	4592– 4597	35	10°29.0′S	9°04.6′E	ES	21. 5.68
CAPE BASIN							
Jean Charcot (Walvis)	DS06	4585	1	33°34.5′N	2°32.9′E	DS	31.12.78

SHELL DESCRIPTION (Figs. 101–103). Shell ovate, somewhat inflated, inequilateral, fragile, frequently with broad, opaque, concentric banding which is variable in form; umbo inflated, anterior in position, orientated medially; dorsal shell margins slope gently from umbo, antero-dorsal, anterior and antero-ventral margins form a smooth curve, anterior limit of which lies dorsal to the mid horizontal line, ventral margin smoothly curved, with posterior limit of shell also dorsal to mid horizontal line, postero-dorsal margin slightly convex, slope increases moderately sharply at posterior limit of hinge plate to join posterior margin to form slight subrostration; hinge plate, stout, with relatively large chevron-shaped teeth, posterior series with one or two more teeth than anterior series (maximum 10 in posterior series), teeth extend as far as the anterior and posterior margins of anterior and posterior adductor muscles respectively, hinge plate lies close to shell margin below umbo; ligament moderately sized, amphidetic, 'saddle'-shaped in lateral view, extends below hinge plate.

Prodissoconch length: 187–198 μm. Maximum recorded shell length: 3.7 mm.

The species has a high degree of variation in shape and within a population may range from the form described above (the most common) to a more quadrangular outline in which the deepest part of the ventral margin instead of being approximately central is posterior to vertical line through the beaks (Fig. 104). Such specimens may be more inflated.

Table 2 *Yoldiella jeffreysi*; ratios of Posterior Length (PL), Height (H), Width (W), to Total Length (TL) and other parameters.

Basin	Max.recorded length (mm)	PL/TL (mean)	H/TL (mean)	W/TL (mean)	ProdissoconchN length (μm)
W. European Incal DS07	3.70	48/60 (54)	69/75 (72)	33/53 (45)	187–198 (54)
Canary Sta. 6704	3.49	52/58 (56)	68/75 (70)	32/48 (41)	185–198 (17)
Cape Verde 8521^{6}	2.84	51/56 (54)	70/76 (72)	38/46 (42)	190–200 (52)
N. America Sta. 126	2.54	47/55 (51)	69/77 (73)	35/52 (40)	182–189 (38)
Guyana Sta. 291	2.96	48/58 (54)	69/76 (73)	34/43 (40)	200–210 (35)
Argentine Sta. 259	2.95	44/60 (53)	69/75 (72)	36/49 (41)	182 (25)

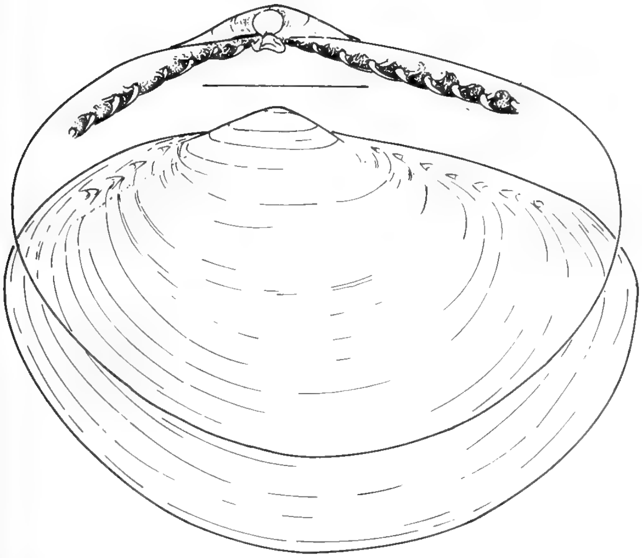

Fig. 101 *Yoldiella jeffreysi*. Lateral view of a shell from the left side and an inner view of a right valve to show detail of the hinge-plate. Specimens from Sta. 316, West European Basin. (Scale = 1.0 mm).

The populations in different basins also differ somewhat in overall shape (Fig. 105). In the Atlantic, more southerly populations are somewhat less inflated and large specimens have an extended posterior margin and thus a more inequilateral shape. Overall, populations in the western Atlantic have a similar shape to the majority of specimens from the northern part of the West European Basin and they are inflated to a similar degree. The more southern populations are more extended posteriorly. Specimens from the Argentine Basin are slightly more inflated but less so than those from the northern West European Basin.

It is a general feature of all populations that the width/length and post-umbonal length/total length increase with increasing length. In contrast, there is little change in the height/length ratio (Fig. 105).

The inter- and intra- variability in the shape of populations of deep sea protobranchs has been noted in many taxa and most recently for the family Malletiidae (Sanders & Allen 1985). Yoldiellid species are no exception and *Y. jeffreysi* is an extreme example (see Table 2). So much so that we have made a particular study of this species and we propose to present our results in more detail in a following publication.

The most closely related (but distinct) species to *Y. jeffreysi* is *Yoldiella lata*. Jeffreys (1876) failed to distinguish between the two species in his samples from depths where their distributions overlap (*Y. lata* is confined to slope depths (see p. 32). In general *Y. jeffreysi* is more inflated than *Y. lata*, has more hinge teeth and the posterior adductor muscle (usually visible through the shell in live specimens) is smaller and more elongate.

INTERNAL MORPHOLOGY (Fig. 106–107). The exhalent and inhalent siphons are combined the latter being open ventrally (Fig. 106). There is a moderately well-developed feeding aperture immediately ventral to the inhalent siphon. A large siphonal tentacle, more frequently on the left side originates close to the base of the siphon. Antero-ventrally there is a well-developed mantle sense organ. The adductor muscles are unequal in size. The anterior is between two and three times larger than the posterior. The posterior is oval in shape while anterior is 'bean'-shaped; the 'quick' and 'catch' parts are clearly distinct.

The gills are relatively well-developed with 12–19 alternating gill plates, the number depending on the size of the animal. The most posterior plate lies close to the junction between the inhalent and exhalent siphons and to which the gill axes join. The labial palps are relatively small with long and slender palp proboscides. In their contracted state they extend across one quarter to one third of the body. The palps have been 11–14 palp ridges, again the number depending on the size of the animal. The foot is large and in some specimens it is preserved in a very long, anteriorly extended fashion. It has a deep papillate sole. A large byssal gland is present and in many specimens in the region of its aperture at the posterior margin of the foot there is a considerable amount of mucous material present.

The species has a very large stomach, the dorsal wall of which lies close to the hinge plate, the stomach lies off centre slightly to the left. A large style sac penetrates deep into the foot. The gastric shield extends close to the opening of the oesophagus, the latter slightly to the right on the antero-dorsal wall. Right and left digestive diverticula are anterior within the body and material similar to that found in the stomach was observed in sections of both right and left diverticula. The hind gut forms a clockwise loop to the right

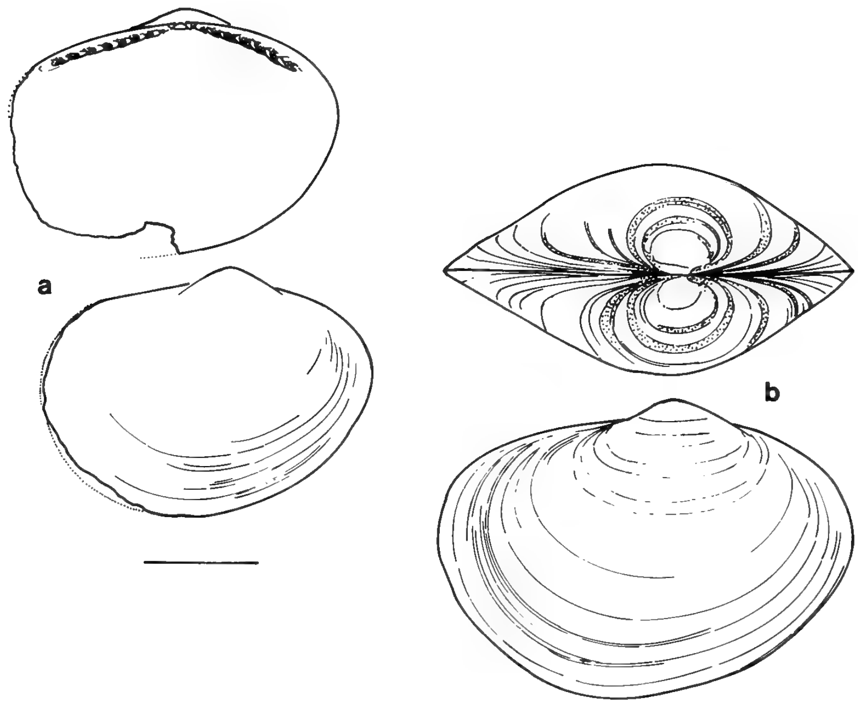

Fig. 102 *Yoldiella jeffreysi*. a, lateral view of a right and left valve of a specimen from the Jeffreys collection labelled *Leda lata* (USNM No. 199695, Valorous Expedition, Sta. 9). b, a dorsal and lateral view from the right side of a specimen from Sta. INCAL DS 06, West European Basin. (Scale = 1.0 mm).

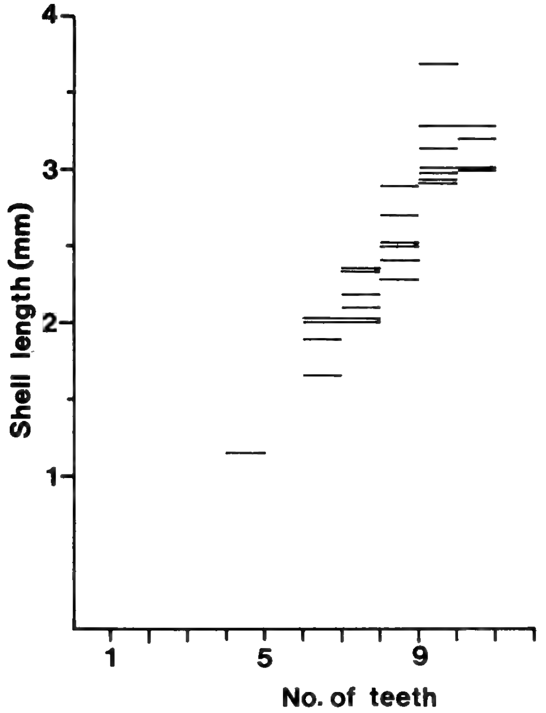

Fig. 103 *Yoldiella jeffreysi*. The relationship of the number of hinge-teeth to shell length of a subsample from Sta. 316, West European Basin. The left and right limits of each bar indicate the number of anterior and posterior hinge-teeth respectively.

anterior of the body, thereafter describing an 'S'-shaped bend before continuing as an anticlockwise loop which partially overlies the first. Thereafter it runs parallel to and immediately below the dorsal margin to the anus (see Fig. 107). A typhlosole is present along its entire length. The configuration of the hind gut on the right side of the body, despite being somewhat variable is characteristic of this species (Fig. 108). It can be very simply visualized as a doubled length of rope making one and a half turns (Fig. 107). In this species, more than any other we have examined, there is a considerable variation in the course of the hind gut which can easily be resolved by reference to the rope analogy (Fig. 107). It would appear that this manner of accommodation of a long hind gut is particularly susceptible to distortion during development, possibly because of displacement due to the large size of the stomach and the anterior arrangement of the digestive diverticula or possibly because the loop tends to impede its own development in this particular configuration (Fig. 105).

The nervous system is well-developed with moderately large 'club'-shaped cerebral ganglia, slightly smaller elongate visceral ganglia and large, oval, pedal ganglia. Dorsal to the latter are large, round, statocysts, filled with refractile granules. The visceral ganglia lie some distance anterior to the posterior adductor.

The populations from the different basins have similar internal morphologies.

Sexes are separate and the gonads overlie other internal organs. Gonad development was followed in two Incal samples (DS07, DS09; West European) and one Discovery sample (8521 No. 1, Cape Verde). In West European specimens the number of ova ranged from 160 (108 um maximum diameter) in a female 2.1 mm long to 350 (144 μm max. diameter) in a female 3.1 mm long. The females from the Cape Verde Basin (2.2, 2.5 & 2.7 mm total length) contained fewer eggs 41–103 but these had a slightly larger size range 130–156 μm.

In July/August samples, maturing gonads had become

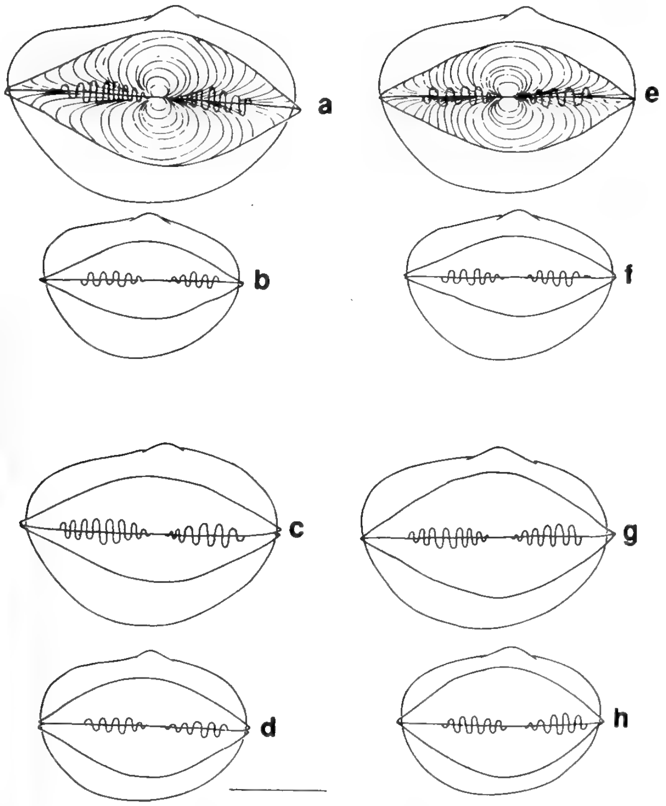

Fig. 104 *Yoldiella jeffreysi*. A comparison of selected specimens from a number of deep-sea Basins showing the range in shell shape. The shell outlines of each specimen are drawn in dorsal and right lateral view. a & b, Sta. 197, Angola Basin; c, Sta. 288, Guyana Basin; d, Sta. 334, North America Basin; e & f, Sta. 259, Argentine Basin; g, Sta. 316, West European Basin; h, Sta. 85, North America Basin. (Scale = 1.0 mm).

obvious (Fig. 109) and by October the gonads had largely filled the body.

Yoldiella enata (new species)

TYPE LOCALITY. R.V. Knorr, Sta. 301, Guyana Basin, 29.1.1972, 8°12.4′N, 55°50.2′W, Epibenthic Dredge, 2487–2500 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992033. Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUYANA BASIN							
Knorr 25	301	2487–2500	175	8°12.4′N	55°50.2′W	ES	29. 1.72
	303	2842–2853	23	8°28.8′N	56°04.5′W	ES	1. 3.72
NORTH AMERICA BASIN							
Atlantis II	118	1135–1153	20	32°99.4′N – 32°19.0′N	64°34.9′W 64°34.8′W	ES	18. 8.66

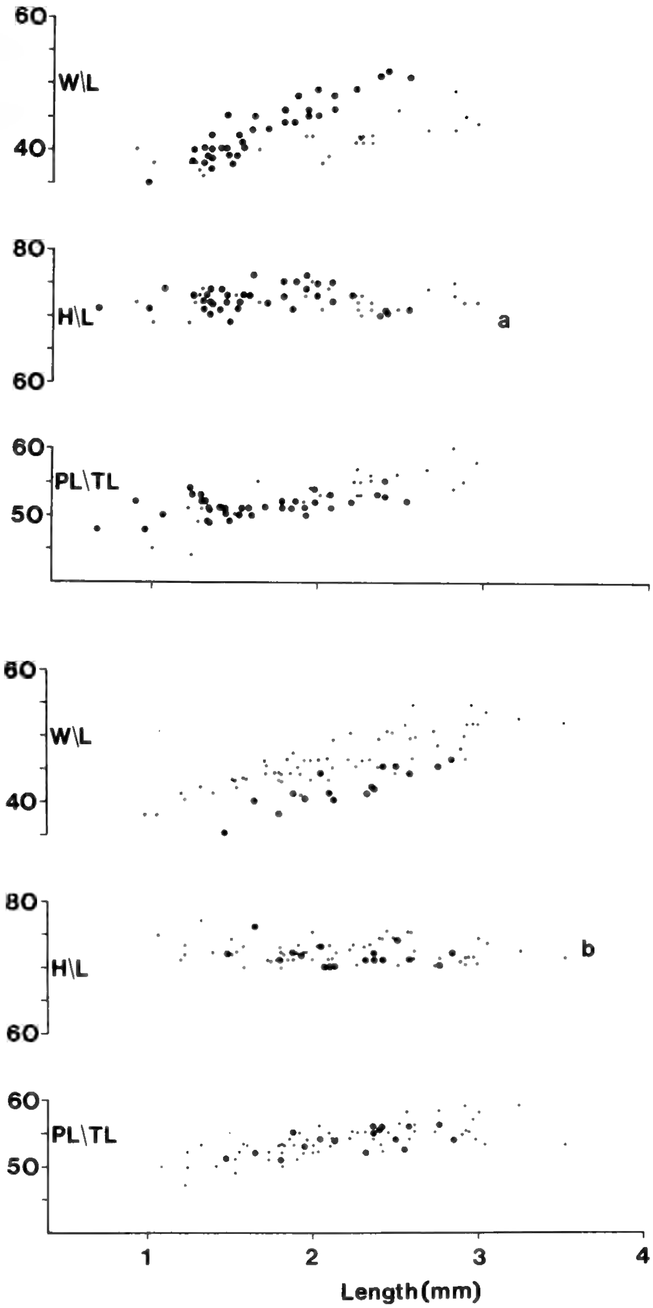

Fig. 105 *Yoldiella jeffreysi*. Variation in ratios of height H/L, width W/L and postero-umbonal length PL/TL to length against length of a, samples from Sta. 126, North America Basin (large closed circles) and Sta. 259, Argentine Basin (points); and of b, samples from Sta. INCAL DS 07, West European Basin (points) and Sta. 6704, Canary Basin (large closed circles).

Several specimens of this species are included in a mixture of species contained with U.S. Natl. Mus. No. 108197, labelled *Yoldiella pygmaea* Munst. None of these correspond to *Leda*

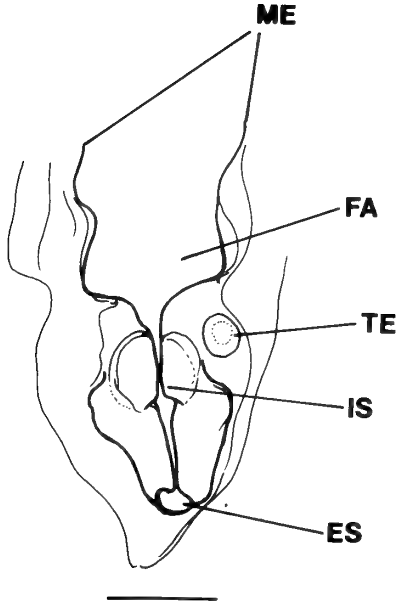

Fig. 106 *Yoldiella jeffreysi.* Siphons as seen from the ventral side of a preserved specimen form Sta. 85, North America Basin. (Scale = 0.1 mm).

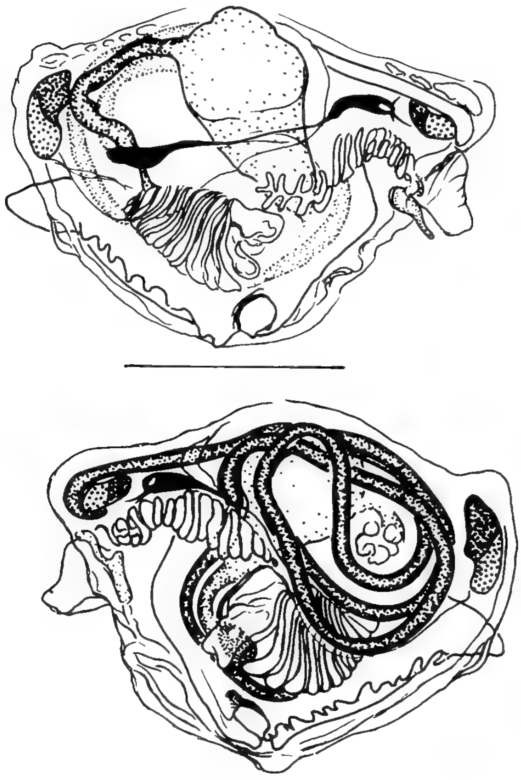

Fig. 107 *Yoldiella jeffreysi.* Lateral views from the right and left sides of the internal morphology of a specimen from Sta. 85, North America Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

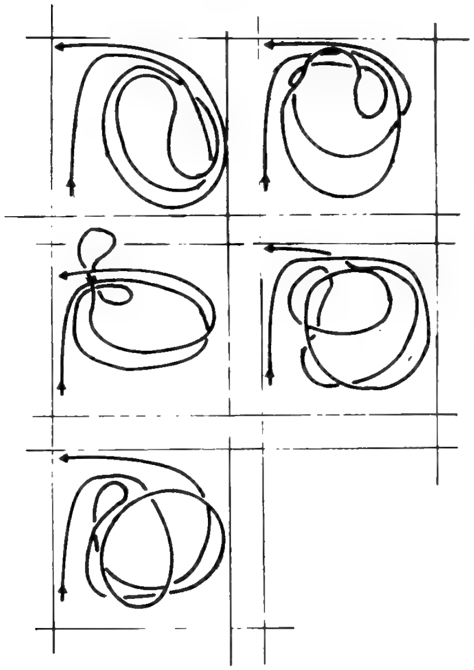

Fig. 108 *Yoldiella jeffreysi.* Diagrammatic views of the course of the hind gut as seen from the right side to show variations in the configuration.

pygmaea Munst. as exemplified by U.S. Natl. Mus. No. 197285.

Distributed in the western Atlantic from southern limit of the North America Basin to Guyana, from mid to lower slope depths. Depth range: 1135–2853 m.

SHELL DESCRIPTION (Figs. 110 & 111). Shell ovate, not particularly inflated, moderately elongate, slightly inequilateral, faint concentric striae particularly close to ventral margin; umbo moderately large; postero-dorsal and antero-dorsal margins slightly convex and slope gently from umbo, anterior margin rounded, anterior limit dorsal to mid horizontal plane, dorsal and ventral margins without angulation, antero-ventral margin smooth curve, postero-ventral margin very slightly sinuous posterior margin not angulated, broadly blunt, posterior limit in mid horizontal plane; hinge moderately broad distally, narrows centrally, chevron-shaped teeth robust, close set with ventral arm twice length of dorsal, anterior and posterior plates with up to 7 teeth; ligament amphidetic, moderately large, extends ventral to hinge plate.

Prodissoconch length: – 287 μm. Maximum recorded shell length: 3.65 mm.

This species is similar to *Yoldiella ella*, however it is less round in outline, shallower dorso-ventrally and less inflated. The ligament is also similar to that of *Y. ella* as is the hinge plate, however, the latter in *Y. ella* is more broad and bears one or two more teeth than that in *Yoldiella enata*.

INTERNAL MORPHOLOGY (Fig. 112). This is similar to that of *Yoldiella ella* so much so that it is extremely difficult to distinguish between the two species. Such distinction as there is is a matter of slight difference in proportion. Thus, the anterior adductor muscle is slightly larger, the diameter of the hind gut is slight less and the exhalent siphon is somewhat larger than in *Y. ella*. Sections of the tightly coiled hindgut

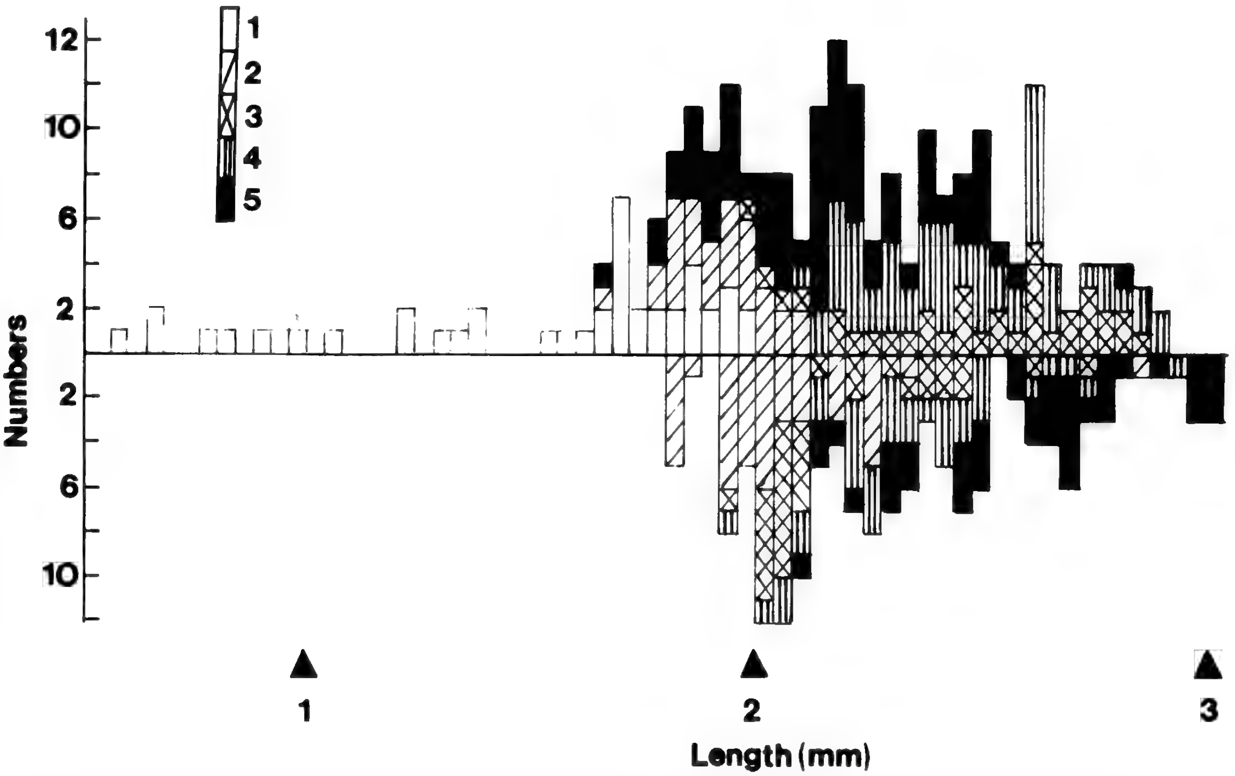

Fig. 109 *Yoldiella jeffreysi*. Length frequency histogram superimposed by a gonadial index. 1, immature, no gonadial development seen in the intact specimen; 2, first sign of gonadial development at ventral edge of visceral mass; 3, gonad surrounds the periphery of the visceral mass; 4, gonad covers half the visceral mass; 5, visceral mass wholly covered by gonad. Top, females; bottom, males.

Fig. 110 *Yoldiella enata*. Lateral view of a shell from the right side and detail of the hinge-plate of a left valve. Specimen from Sta. 301, Guyana Basin. (Scale = 1.0 mm).

show the same number of coils. In a specimen 3.1 mm the palps, which are moderately small, have 14 internal ridges. The palp proboscides are large and broad. The kidney is large and extends anteriorly lateral to the stomach. The largest specimens are mature and in the case of one sectioned specimen a few eggs were present in the mantle cavity. This is not taken as evidence of brooding.

It is clear that *Yoldiella enata* and *Yoldiella ella* are very closely related, however, we have no difficulty in distinguising them from their shell features. It should also be noted that the depth distribution of the two species is very different, *Yoldiella enata* is found on the lower slope while *Yoldiella ella* is truly abyssal.

Yoldiella ella (new species)

TYPE LOCALITY. R.V. Chain Sta. 334, North America Basin, 30.9.1972, 40°42.6'N, 46°13.8'W – 40°44.0'N, 46°14.6'W, Epibenthic Trawl, 4400 m.

TYPE SPECIMEN. Holotype: BM(NH) 1992034. Paratypes in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II 12	72	2864	1	38°16.0'N	71°47.0'W	ET	24. 8.64
Chain 50	76	2862	1	39°38.3'N	67°57.8'W	ET	29. 6.65
	78	3828	5	38°08.0'N	69°18.7'W	ET	30. 6.65
	85	3834	11	37°59.2'N	69°26.2'W	ET	5. 7.65
Atlantis II 24	126	3806	4	39°37.0'N – 39°37.5'N	66°47.0'W 66°44.0'W	ET	24. 8.66
Chain 106	334	4400	44	40°42.6'N – 40°44.0'N	46°13.8'W 46°14.6'W	ES	30. 8.72

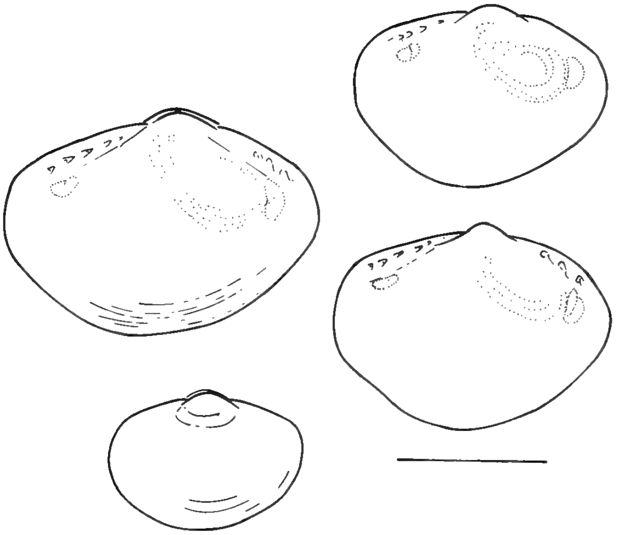

Fig. 111 *Yoldiella enata*. Outlines of shells from the right side to show variation in shape with growth of specimens from Sta. 301, Guyana Basin. (Scale = 1.0 mm).

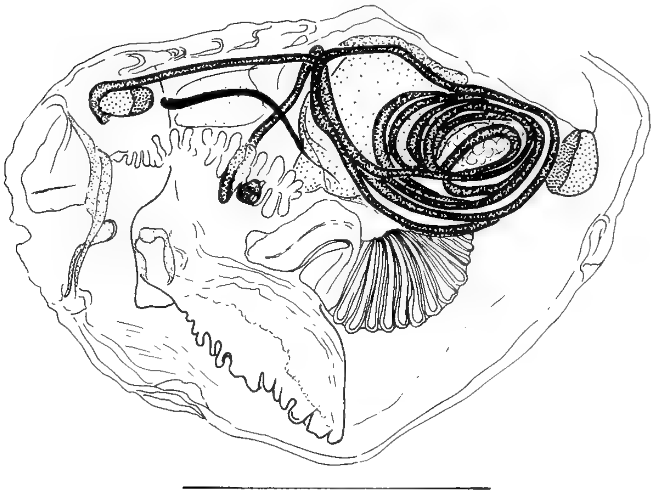

Fig. 112 *Yoldiella enata*. Lateral view from the right side of the internal morphology of a specimen from Sta. 301, Guyana Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

	335	3882–3919	26	40°25.3′N	46°30.0′W	ES	31. 8.72
Knorr 35	340	3264–3356	16	38°14.4′N – 38°17.6′N	70°20.3′W 70°22.8′W	ES	24.11.73
SIERRA LEONE BASIN							
Atlantis II 31	148	3814–3818	1	10°37.0′N	18°14.0′W	ES	7. 2.67
	149	3861	25	10°30.0′N	18°18.0′W	ES	7. 2.67
	155	3730–3783	7	00°03.0′S	27°48.0′W	ES	13. 2.67
	156	3459	4	00°46.0′S – 00°46.5′S	29°28.0′W 29°24.0′W	ES	14. 2.67
ANGOLA BASIN							
Atlantis II 42	197	3865–4595	2	10°29.0′S	9°04.0′E	ES	21. 5.68
	198	4559–4566	4	10°24.0′S	9°09.0′E	ES	21. 5.68
	199	3764–3779	2	9°47.0′S – 9°49.0′S	10°29.0′E 10°33.0′E	ES	22. 5.68
WEST EUROPEAN BASIN							
Chain 106	323	3356–3338	9	50°08.0′N	13°53.7′W – 13°50.9′W	ES	21. 8.72
	326	3859	12	50°04.9′N – 50°05.3′N	14°23.8′W 14°24.8′W	ES	22. 8.72
	328	4426–4435	9	50°04.7′N	15°44.8′W	ES	23. 8.72
	330	4632	137	50°43.5′N – c50°43.4′N	17°51.7′W 17°52.9′W	ES	24. 8.72
Jean Charcot (Polygas)	DS20	4226	25	47°33.0′N	9°36.7′W	DS	24.10.72
	DS21	4190	8	47°31.5′N	9°40.7′W	DS	24.10.72
	DS22	4144	14	47°34.1′N	9°38.4′W	DS	25.10.72
	DS23	4734	2	46°32.8′N	10°21.0′W	DS	26.10.72
(Biogas III)	DS41	3548	1	47°28.3′N	9°07.2′W	DS	26. 8.73
	DS42	4104	1	47°32.1′N	9°35.6′W	DS	27. 8.73
(Biogas IV)	DS55	4125	80	47°34.9′N	9°40.9′W	DS	22. 2.74
	DS56	4050	3	47°32.7′N	9°28.2′W	DS	23. 2.74
	DS60	3742	6	47°26.8′N	9°07.2′W	DS	24. 2.74
Cyros (Biogas V)	DS66	3480	21	47°28.2′N	9°00.0′W	DS	16. 6.74
	DS67	4150	4	47°31.0′N	9°35.0′W	DS	17. 6.74
	DS68	4550	3	46°26.7′N	10°23.9′W	DS	19. 6.74
Jean Charcot (Biogas VI)	DS75	3150	4	47°28.1′N	9°07.8′W	DS	22.10.74
	DS76	4228	243	47°34.8′N	9°33.3′W	DS	23.10.74
	DS77	4240	55	47°31.8′N	9°34.6′W	DS	24.10.74
	DS78	4706	3	46°31.2′N	10°23.8′W	DS	25.10.74
	DS79	4715	9	46°30.4′N	10°27.1′W	DS	26.10.74
	DS80	4720	3	46°29.5′N	10°29.5′W	DS	27.10.74
	CP13	4134	2	47°34.4′N	9°38.0′W	DS	23.10.74
Jean Charcot (Incal)	0S02	4829	8	48°19.2′N	15°15.7′W	OS	2. 8.76
	0S05	4248–4296	9	47°31.3′N – 47°32.2′N	9°34.6′W 9°34.7′W	OS	7. 8.76
	0S66	4316–4307	43	46°27.3′N – 47°27.9′W	9°36.2′W 9°36.0′W	OS	9. 8.76
	0S07	4249	63	47°31.8′N	9°34.3′W	OS	10. 8.76
	0S08	4327	42	47°29.8′N – 47°29.5′N	9°39.2′W 9°38.8′W	OS	11. 8.76
	WS03	4829	7+2v	48°19.2′N – 48°19.1′N	15°23.3′W 15°22.5′W	WS	1. 8.76
	WS07	4281–4274	30	47°30.6′N – 47°31.2′N	9°37.1′W 9°35.7′W	WS	7. 8.76
	WS08	4287–4301	36	47°30.5′N – 47°29.3′N	9°33.7′W 9°34.1′W	WS	9. 8.76
	WS09	4277	11	47°28.8′N – 47°27.9′N	9°34.0′W	WS	10. 8.76
	WS10	4354	37	47°27.3′N – 47°28.3′N	9°39.9′W	WS	14. 8.76
	DS11	4823	3	48°19.2′N	15°23.3′W – 15°22.5′W	DS	1. 8.76
	DS14	4248–4254	20	47°32.6′N – 47°32.9′N	9°35.7′N 9°35.1′W	DS	7. 8.76
	DS15	4211	3	47°33.6′N	9°39.1′W – 9°38.5′W	DS	8. 8.76
	DS16	4268	57	47°29.8′N – 47°20.2′N	9°33.4′W	DS	9. 8.76
	CP11	4823	1	48°20.4′N – 48°21.1′N	15°14.6′W 15°13.7′W	CP	1. 8.76

Widely distributed throughout much of the Atlantic in North America, West European, Sierra Leone and Angola Basins at abyssal depths. With only two exceptions, all records are greater than 3200 m. Depth range: 2862–4829 m.

SHELL DESCRIPTION (Figs. 113–116). Shell ovate, moderately inflated, inequilateral, shell with very fine concentric lines, ventral lines usually more conspicuous, few fine radial lines from umbo to ventral edge, periostracum light straw colour; umbo large, rounded, orthogyrate, anterior to midline, great-

Fig. 113 *Yoldiella ella.* Lateral view of a shell from the right side and a left valve to show detail of the hinge-plate. Specimens from Sta. INCAL OS 06. (Scale = 1.0 mm).

est shell height posterior to umbo; dorsal margin slightly convex, antero-dorsal anterior and ventral margins in a smooth continuous curve, postero-ventral margin rounded posteriorly, posterior margin in small specimens may have very slight, blunt, angulation, posterior limit slightly dorsal to horizontal midline, postero-dorsal margin curves gently from umbo to distal edge to hinge plate then slopes more acutely to posterior margin; hinge plate, long, characteristically angular below umbo, moderately broad proximally, narrow ventral to umbo, anterior and posterior ventral margins of hinge plate more or less straight, teeth strong, well-developed, equal number in anterior and posterior plates, up to 9 in specimen 4.2 mm, ligament amphidetic, moderate in size, rectangular or slightly 'goblet'-shaped, short, wide, posterior external extension and long slender anterior external extension of fused periostracum.

Prodissoconch length: 166 μm. Maximum recorded shell length: 4.2 mm.

There is little change in the width/length or height/length ratios with increasing size, however, posterior umbonal length increases slightly and the posterior margin becomes more smoothly curved.

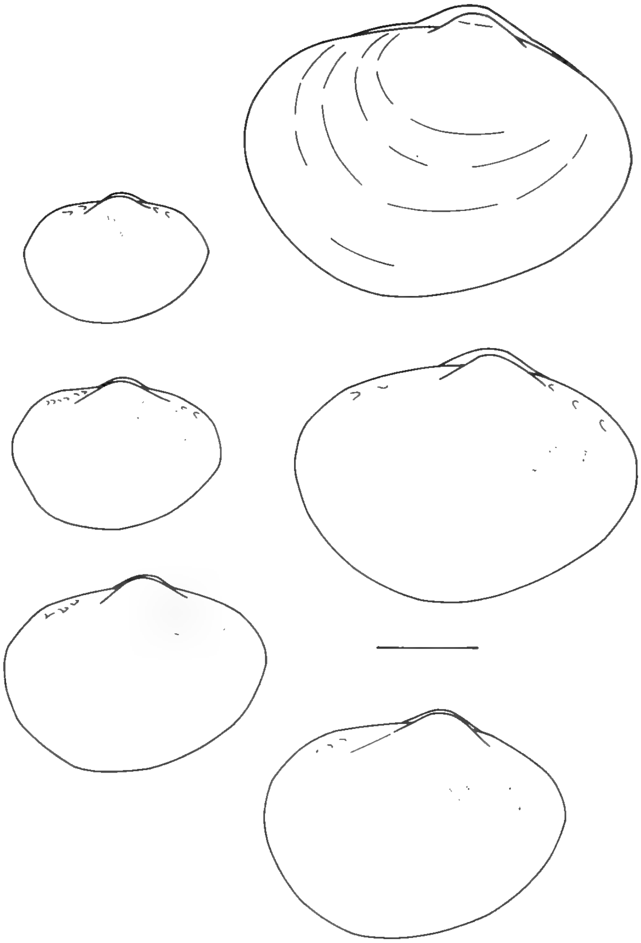

Fig. 114 *Yoldiella ella.* Outlines of shells from the right side to show variation in shape with growth of specimens from Sta. BG VI DS 76, West European Basin. (Scale = 1.0 mm).

INTERNAL MORPHOLOGY (Fig. 117). The anterior sense organ is well-developed. Posterior mantle fusion is minimal, limited to a fine bridge of tissue between the opposing inner mantle lobes forming a short exhalent siphon. The gill axis is attached laterally on either side of the bridge tissue. Ventral to it the inhalent siphon is reduced to a pair of unfused thickened pads of tissue. The feeding aperture is poorly developed with a few gland cells present. Immediately anterior to the feeding aperture, the inner mantle fold is enlarged slightly and more obviously ciliated and may possibly indicate a temporary point of adhesion in the living specimen. The siphonal tentacle is usually to the left ventral side of the shallow mantle embayment. The adductor muscles are relatively small, approximately equal in size and more or less oval in shape. There are up to 16 gill plates and the gills are attached far posterior on the body wall. The gill axis is well-supplied with muscle fibres. The labial palps, like the gills, are relatively small with up to 14 ridges on their inner faces with the result that in preserved specimens, there is a marked separation of gill and palp which is unlikely to be true in life. The palp proboscides are relatively long and broad. The foot is of moderate size with a relatively wide neck and an elongate, deeply divided sole. There is a large byssal gland in the heel with a concentration of cilia around its opening. The heel has a terminal papilla. The cerebral and visceral ganglia are relatively small and 'club'-shaped in lateral view. The pedal ganglia is larger and slightly elongate.

The oesophagus has a wide opening into a large stomach. The combined style sac and mid gut extend into the dorsal half of the foot. The digestive duct from the right diverticulum skirts dorsal to the hind gut loops to open into the anterior wall of the stomach. On the left and close to the oesophageal aperture is a relatively wide digestive duct from

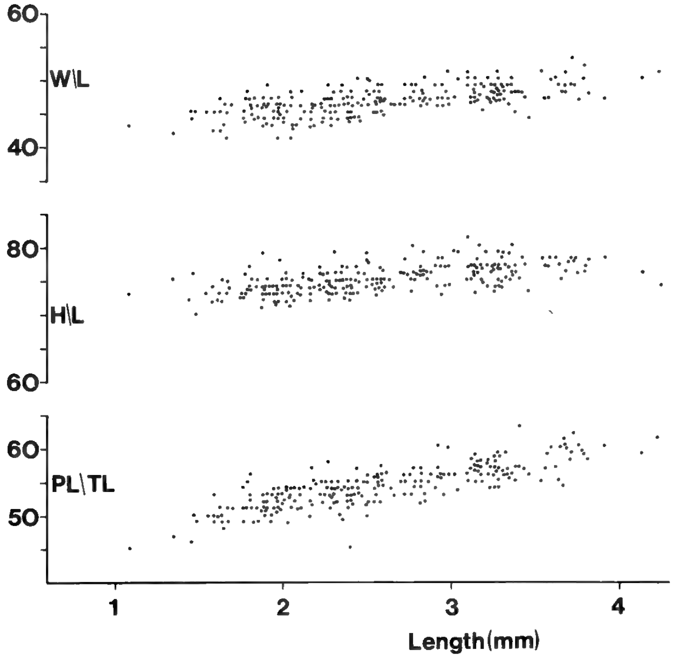

Fig. 115 *Yoldiella ella*. Variation in ratios of height H/L. width W/L and postero-umbonal length PL/TL to length against length of a sample from Sta. BG VI DS 76, West European Basin.

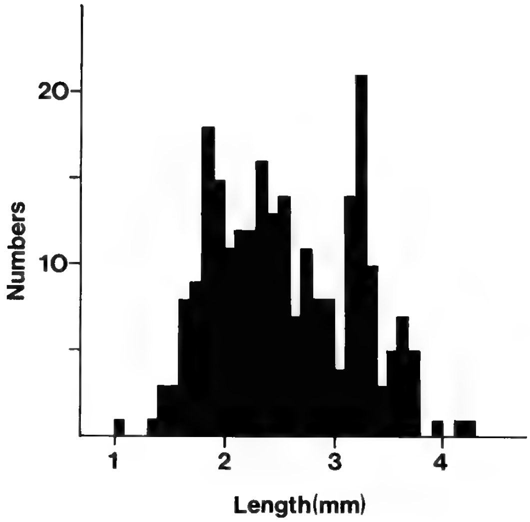

Fig. 116 *Yoldiella ella*. Length frequency histogram of a sample from Sta. BG VI DS 76, West European Basin.

the left anterior diverticulum. This latter opens mid-laterally into the stomach. A second duct from the posterior digestive diverticulum of the left side opens into the left wall of the stomach below the gastric tooth. The course of the hind gut is first anterior and then antero-ventral to the pedal ganglia before turning back on itself to pass dorsally posterior to the stomach. Thereafter it forms a series of complicated coils to the right side of the body the design of which can be derived from a doubled strand coiled clockwise as seen from the right side (Fig. 117). The hind gut then passes to the mid postero-dorsal margin and thence dorsal to the posterior adductor muscle to the anus. There is a relatively shallow typhlosole along the length of the hind gut. Faecal rods were seen cradled by the gill axes between anus and the siphon.

The kidney and heart are well-developed. The sexes are separate. Animals smaller than 2.15 mm total length were all immature with no obvious gonad present. The number of ova varies from 16 in an individual 2.57 mm (maximum diameter of ova 87 mm) to 90 in an individual 3.2 mm long (maximum diameter of ova 132 μm). In samples collected in February, June, August and September in specimens of 2.15 mm and above, all have maturing ova.

Y. ella has all the characteristics of a shallow burrowing or semi-submerged species i.e. a rounded, broad form, with short siphons in a shallow siphonal embayment. Many specimens bear hydroids attached to antero-ventral and ventral margins.

Two intact specimens of a species of *Yoldiella* in which the external shell features appear to be close to *Y. ella* (or possibly *Y. enata*) were taken at Sta. 199 from the Angola Basin at a depth of 3771 metres (Fig. 118). We have hesitated to examine the internal anatomy of these. Unfortunately because of the opaqueness of the shell all that can be seen of the hind gut is part of one or possibly two coils to the right of the body, close to the anterior adductor. These specimens could either prove to be a new species or showing variation of shell form.

Yoldiella fabula (new species)

TYPE LOCALITY. R.V. Chain Cruise 50, Sta, 85, North America Basin, 5.7.1965, 37°59.2′N, 69°26.2′W, Epibenthic Trawl, 3834 m.

TYPE SPECIMEN. Holotype: BM (NH) 1992037. Paratypes: in collection held by J.A. Allen.

Leda sericea Jeffreys 1879, p. 579 (in part). Two specimens were found in the Jeffreys collection (U.S. Natl. Mus. No. 199590 (Fig. 119a) and No. 199589 (Fig. 119b)). Although these are labelled *L. sericea* and must have been so identified by Jeffreys they clearly differ from that species. A specimen stored with and labelled *Yoldiella expansa* (U.S. Natl. Mus. No. 697343 (Fig. 119c)) is also this species. All these specimens were collected off West Ireland in 2500–2670 metres.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II 12	62	2496	4	39°26.0′N	70°33.0′W	ET	21. 8.64
	64	2886	1	38°46.0′N	70°06.0′W	ET	21. 8.64
	70	4680	1	36°23.0′N	67°58.0′W	ET	23. 8.64
	72	2864	2	38°16.0′N	71°47.0′W	ET	24. 8.64
Chain 50	77	3806	1	38°07.0′N	69°16.0′W	ET	30. 6.65
	78	3828	6	38°08.0′N	69°18.7′W	ET	30. 6.65
	84	4749	4	36°24.0′N	67°56.0′W	ET	4. 7.65
	85	3834	c13	37°59.2′N	69°26.2′W	ET	5. 7.65
Atlantis II 17	92	4694	1	36°59.2′N	69°26.2′W	ET	5. 7.65

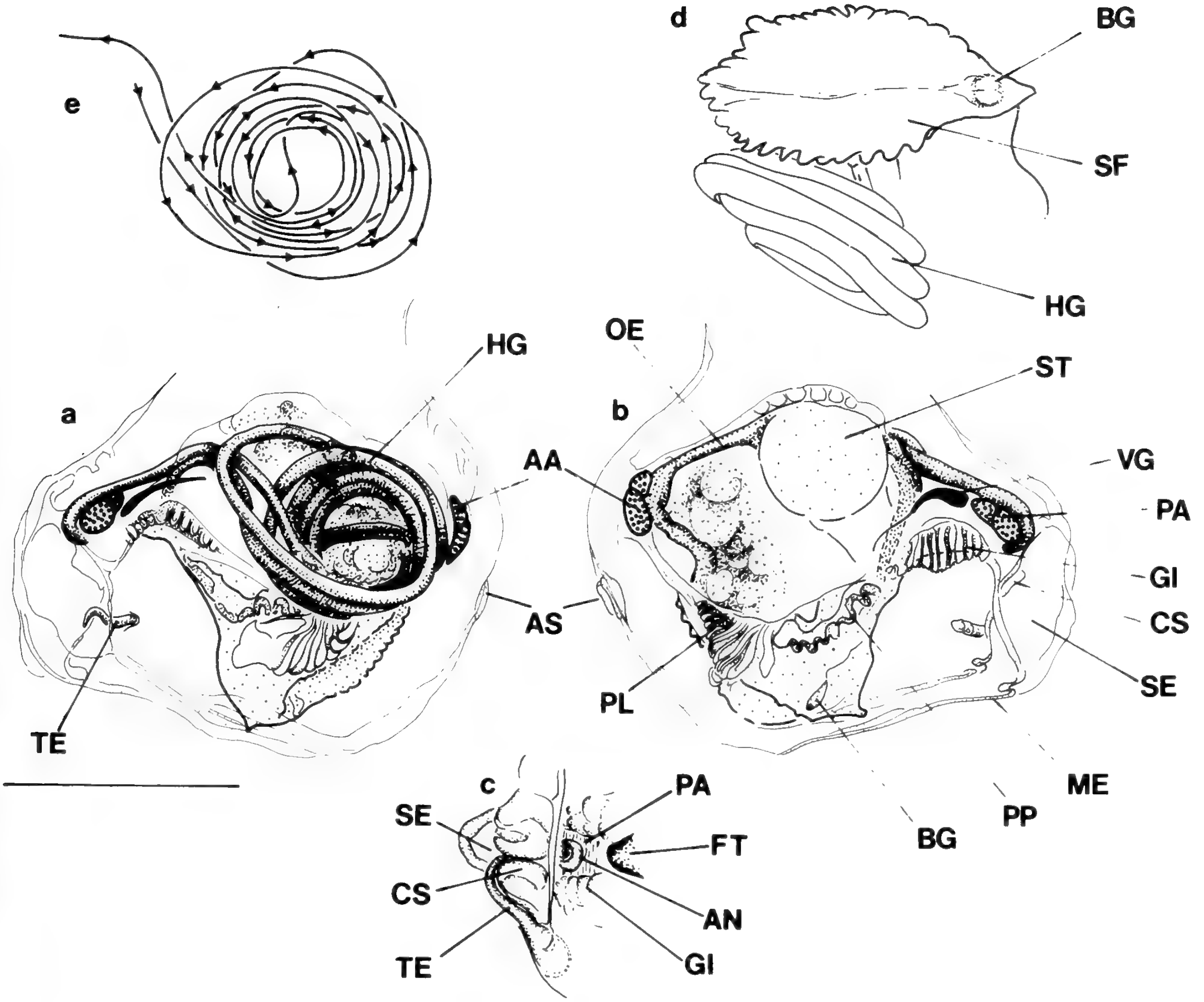

Fig. 117 *Yoldiella ella*. Details of the internal morphology. a & b, whole mounts from the right and left sides respectively; c, ventral view of contracted siphon; d, ventral view of the sole of the foot and hindgut; e, course of the hindgut as seen from the right side. (Scales = 1.0 mm).

Atlantis II	125	4825	1	37°24.0′N	65°54.0′W	ET	23. 8.66
24				– 37°16.0′N	65°50.0′W		
Knorr 35	340	3264–	1	38°14.4′N	70°20.3′W	ES	24.11.73
		3356		– 38°17.6′N	70°22.8′W		

ARGENTINE BASIN

Atlantis II	242	4382–	8	38°16.9′S	51°56.1′W	ES	13. 3.71
60		4402					
	243	3815–	10	37°36.9′S	52°23.6′W	ES	14. 3.71
		3822					
	247	5208–	16	43°33.0′S	48°58.1′W	ES	17. 3.71
		5223					
	256	3906–	3	37°40.9′S	52°10.3′W	ES	24. 3.71
		3917					

WEST EUROPEAN BASIN

Chain106	323	33536–	2	50°08.0′N	13°53.7′W	ES	21. 8.72
		3338		– 50°08.3′N	13°50.9′W		
	330	4632	1	50°43.5′N	17°51.7′W	ES	24. 8.72
				– 50°43.4′N	17°52.9′W		
Jean Charcot	DS21	4190	1	47°31.5′N	9°40.7′W	DS	24.10.72
(Polygas)	DS23	4734	2	46°32.8′N	10°21.0′W	DS	26.10.72
	DS28	4413	1	44°23.8′N	4°47.5′W	DS	2.11.72
	CV13	4252	1	47°31.8′N	9°34.2′W	CV	25.10.72
	DS30	4160	1	47°38.3′N	9°33.9′W	DS	18. 4.73
(Biogas II)							
(Biogas III)	DS41	3548	1	47°18.3′N	9°07.2′W	DS	26. 8.73
	DS50	2124	1	44°08.9′N	4°15.9′W	DS	1. 9.73
(Biogas IV)	DS55	4125	3	47°34.9′N	9°40.9′W	DS	22. 2.74
	DS56	4050	1	47°32.7′N	9°28.2′W	DS	23. 2.74
	DS57	2906	2	47°31.7′N	9°06.2′W	DS	24. 2.74
(Biogas V)	DS66	3480	1	47°28.2′N	9°	DS	16. 6.74
	DS67	4150	2v	47°32.0′N	9°35.0′W	DS	17. 6.74
(Biogas VI)	DS76	4228	1	47°34.8′N	9°33.3′W	DS	23.10.74
	DS84	4466	1	44°25.4′N	4°52.8′W	DS	29.10.74
(Incal)	WS07	4281	1	47°30.6′N	9°37.1′W	WS	7. 8.76
				– 37°31.2′N	9°35.7′W		
	WS08	4287	2	47°30.5′N	9°33.7′W	WS	9. 8.76
				– 47°29.3′N	9°34.1′W		
	QS06	4316	2	46°27.3′N	9°36.2′W	OS	9. 8.76
				– 47°27.9′N	9°36.0′W		
	QS07	4249	2	47°31.3′N	9°34.3′W	OS	19. 8.76
				– 47°31.3′N	9°34.3′W		

	DS05	2503	1	56°28.1'N – 56°27.6'N	11°11.7'W 11°12.0'W	DS	18. 7.76
	DS09	2897	7	55°07.0'N – 55°08.1'N	12°52.6'W 12°53.2'W	DS	20. 7.76
	DS14	4254– 4548	1	47°32.6'N – 47°32.9'N	9°35.7'W 9°35.5'W	DS	8. 8.76
	DS16	4268	2	47°29.8'N – 47°30.3'N	9°33.4'W 9°33.4'W	DS	9. 8.76
GUINEA BASIN							
	DS20	2514	2	2°32.0'S	8°18.1'W	DS	
SIERRA LEONE BASIN							
Atlantis II 31	149	3861	1	10°30.0'N	18°18.0'W	ES	7. 2.67
ANGOLA BASIN							
Atlantis II 42	195	3707	7	14°49.0'N – 14°40.0'N	9°56.0'W 9°54.0'W	ES	19. 5.68
	196	4612– 4630	2	10°29.0'N – 10°29.5'W	9°03.0'W 9°04.0'W	ES	21. 5.68
	197	3865– 4595	5	10°29.0'N – 10°29.0'N	9°04.0'W 9°04.0'N	ES	21. 5.68
	198	4559– 4566	10	10°24.0'N – 9°47.0'N	9°09.0'W 10°29.0'W	ES	21. 5.68
	199	3764– 3779	2	9°49.0'N – 9°41.0'N	10°33.0'W 10°55.0'W	ES	22. 5.68
GUYANA BASIN							
Knorr 25	291	3859– 3868	1	10°06.1'N	55°14.0'W	ES	26. 2.72
	303	2842– 2853	2	8°28.8'N	56°04.0'W	ES	1. 3.72

Y. fabula is wide-spread at abyssal depths throughout the Atlantic in small but persistent numbers in most of the Atlantic Basins. Low population density and low sampling density probably explains the lack of records in the Guyana & Canaries Basins. Depth range: 2503–5223 m.

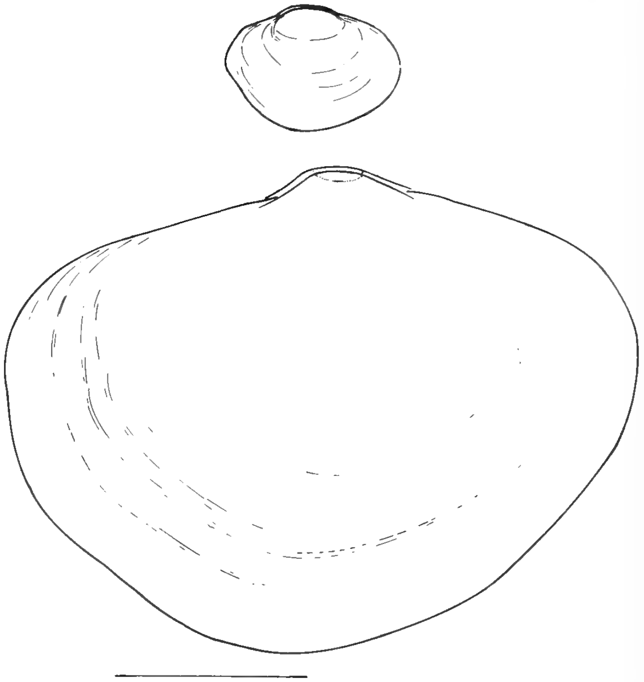

Fig. 118 *Yoldiella sp.* Lateral views of two shells taken from Sta. 119, Angola Basin. (Scale = 1.0 mm).

SHELL DESCRIPTION (Figs. 119–121). Shell small, moderately swollen, 'bean'-shaped, inequilateral, post umbonal length 40–46% of total length, sculpture regular with conspicuous ridges, periostracum straw coloured, often discoloured and brown at valve margins; umbo relatively large, posterior in position and inflated, directed posteriorly; proximal dorsal margins slightly convex either side of umbo, proximally evenly curved to rounded anterior and posterior margins, ventral margin long, smooth curve; hinge plate moderately

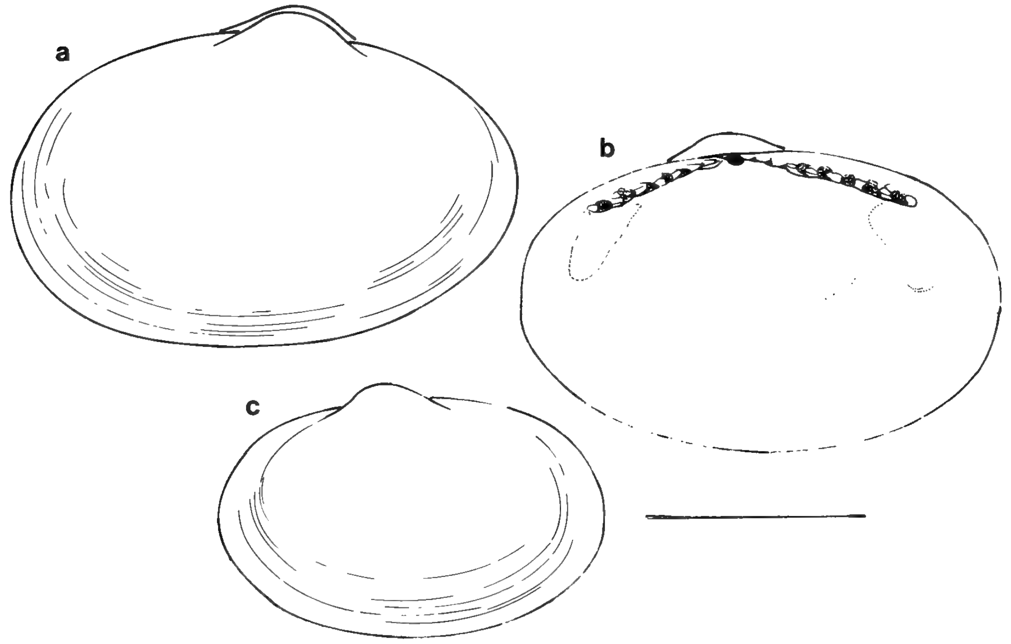

Fig. 119 *Yoldiella fabula.* Lateral views of two shells from the right and left sides respectively and a left valve to show details of the hinge-plate. a, Jeffreys collection USNM No. 199590 labelled *Leda sericea* Jeffr. St. 21, 1476 fm. N.W. Ireland, Porc. Ex. 1870; b, USNM No. 199589 labelled *Leda sericea* Jeff. St. 19a, 1366 fm, W. of Ireland, Porc. Ex. 1869; c, USNM No. 697343 labelled *Yoldiella expansa* Jeffreys 49°37'N, 13°34'W. S.W. of Ireland. (Scale = 1.0 mm).

strong, extends almost to outer limit of both adductor muscles, anterior hinge plate with 1–2 more teeth than posterior, total number of teeth up to 17 depending on size, distal teeth small and difficult to identify; ligament internal, slightly opisthodetic, 'goblet'-shaped with posterior extension ventral to hinge plate.

Prodissoconch length: 229 μm. Maximum recorded shell length: 3.1 mm.

The shell outline in this species is somewhat variable (Figs. 120 & 121). It is the only yoldiellid species indeed species in our collections, with this highly characteristic 'bean'-shape. For a time we misidentified *Yoldiella fabula* as *Y. dissimilis* Verrill & Bush 1898. On closer examination we note that *Y. dissimilis* unlike *Y. fabula* is nearly equilateral, that the anterior hinge is oblique that the number of hinge teeth is greater and that an oblong prominent tooth-like process at the proximal end of the posterior hinge series is not present. *Y. fabula*, as all other yoldiellids, has only very small external anterior and posterior componants visible which are derived from secondary fused periostracum.

The range in length of the specimens in the collection varies from 1.72 mm to 3.08 mm. The following are the overall proportions:- H/L ratio 0.63–0.72; W/L ratio 0.41–0.50; and PL/TL ratio 0.40–0.46. Although these ratios vary the overall range is related to growth and to some variation in the populations.

INTERNAL MORPHOLOGY (Figs. 122 & 123). Ventral to the anterior adductor muscle the middle lobe of the mantle is modified to form a well-developed anterior sense organ. The combined siphon has a single lumen which is open ventrally. The gill axes join laterally indicating an inhalent as well as an exhalent component. A small, single, tentacle is present close to the postero-ventral margin of siphonal embayment. Numerous groups of glandular epithelial mantle cells are found peripheral to the inner siphonal aperture and the feeding aperture and anterior to the latter.The adductor muscles are large and approximately equal in size. The posterior adductor is oval in cross section while the anterior is 'crescent'-shaped with 'catch' and 'quick' portions clearly marked.

The gills are parallel to the dorsal posterior shell margin with up to 17 well-developed plates. The distal gill filaments lie close to the siphon. Moderately large labial palps extend approximately halfway across the body and have up to 20 ridges on their inner surface. The foot is well-developed with a narrow neck and a deeply divided sole. At the heel there is a conspicuous median papilla directly posterior to the opening of the byssal gland. The byssal gland is well-developed. The pedal musculature is similar to *Y. lata*. Both cerebral and visceral ganglia are cylindrical and moderately well-developed with a stout connecting commissure. The pedal ganglia are circular and not particularly large.

The oesophagus, stomach, and style sac are basically similar to those of *Y. lata*. A long duct from the right digestive diverticula passes dorsally over the hind gut to enter the stomach close to the oesophageal aperture. The duct from one left diverticulum opens slightly more posteriorly on left ventral wall, while the duct from the second left diverticulum opens ventral to the gastric tooth on the left side. The hind gut has a typhlosole and forms a single loop to the right side of the body.

Initially the gonads develop ventral to the digestive diverticula and the hind gut loop, but gradually they spread posteriorly and dorsally to the stomach. A female 2.5 mm long, from a July sample had approximately 74 large ova (maximum diameter 180 μm) while a second female of similar size (2.3 mm) had 62 ova (maximum diameter 160 μm). The gonadial aperture is close to that of the kidney, and anterior to the posterior pedal retractor muscle. The large kidney extends from the postero-dorsal margin to the foot and anteriorly over the viscera to a point just anterior to the lateral pedal retractor muscle. A large pericardial cavity is present.

Yoldiella veletta (new species)

TYPE LOCALITY. R.V. Jean Charcot, Biogas VI, Sta. DS87, Bay of Biscay, 31.10.1974, 44°05.2'N, 4°15.7'W, Epibenthic Trawl, 1913 m.

TYPE SPECIMEN. Holotype: Museum National d'Histoire Naturelle, Paris.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CANARIES BASIN							
Discovery	6701	1934	1	27°45.2'N	14°13.0'W	ES	16. 3.68
CAPE VERDE BASIN							
	145	2185	1	10°36.0'N	17°49.0'W	ES	6. 2.67
WEST EUROPEAN BASIN							
Jean Charcot Biogas VI	DS87	1913	1	44°05.2'N	4°15.7'W	ES	31.10.74

Distributed on the lower slope in the eastern Atlantic from the Bay of Biscay to the Cape Verde Islands. Depth range: 1913–2105 m.

SHELL DESCRIPTION (Fig. 124). Shell moderately swollen,

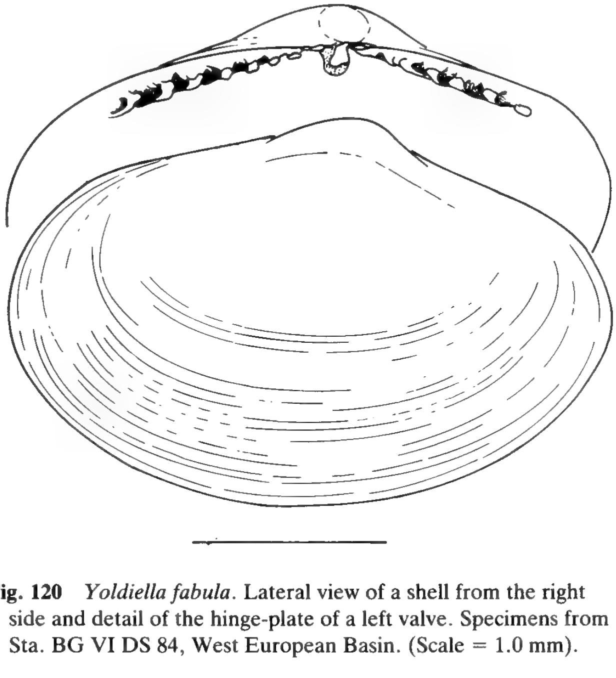

Fig. 120 *Yoldiella fabula*. Lateral view of a shell from the right side and detail of the hinge-plate of a left valve. Specimens from Sta. BG VI DS 84, West European Basin. (Scale = 1.0 mm).

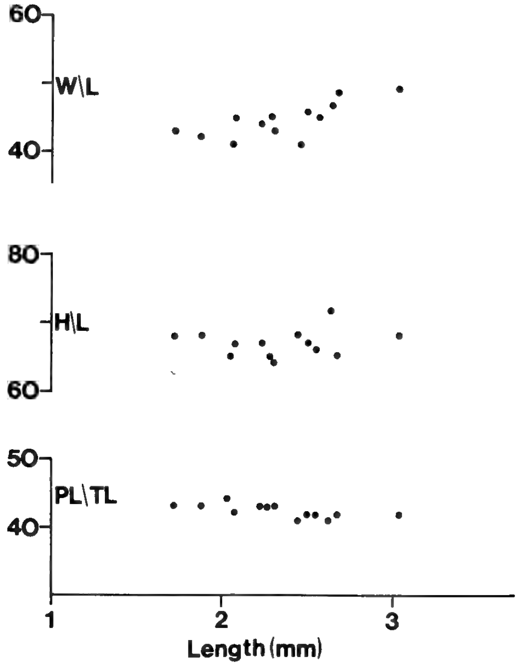

Fig. 121 *Yoldiella fabula*. Variation in ratios of height H/L. width W/L and postero-umbonal length PL/TL to length against length of specimens taken by the Biogas Expeditions as listed in the table of material.

ovate, inequilateral, sculpture, fine concentric lines and growth rings, no lunule, no escutcheon; umbo large, posterior to midline, directed to posterior; antero-dorsal margin merges with anterior margin in smooth curve, limit of anterior margin close to midline, ventral margin long, shallow curve, limit of posterior margin ventral to midline, proximal postero-dorsal margin slopes more steeply than antero-dorsal margin and results in narrowing of post umbonal shell in lateral view; hinge plate moderately strong, except ventral to umbo where it is very narrow, hinge teeth strong, somewhat elongate, 1 or 2 more teeth in anterior series; ligament amphidetic, largely ventral to hinge margin; no chondrophore.

Prodissoconch length: 165 μm. Maximum recorded shell length: 4.56 mm.

INTERNAL MORPHOLOGY (Fig. 125). The combined siphon has a single lumen which is open ventrally, as in *Y. fabula*. The siphonal embayment is deep, a fine tentacle is present on the right side. The adductor muscles are particularly large but approximately equal in size, the anterior being fractionally the larger. The anterior sense organ is not particularly well-developed. The gill is elongate and attenuated with up to 27 plates. The palps are large each with up to 13 internal ridges. The foot is also large and with papillate margins anteriorly directed. The stomach is moderately large and the hind gut forms a single loop to the right side of the body. The hind gut has a wide diameter and a single typhlosole is present along its entire length.

This species has clear affinities with species of *Portlandia*. Nevertheless, it is a fragile shell without any trace of lunule or escutcheon. On the basis of only three specimens, the shell morphology seems most similar to *Y. fabula*.

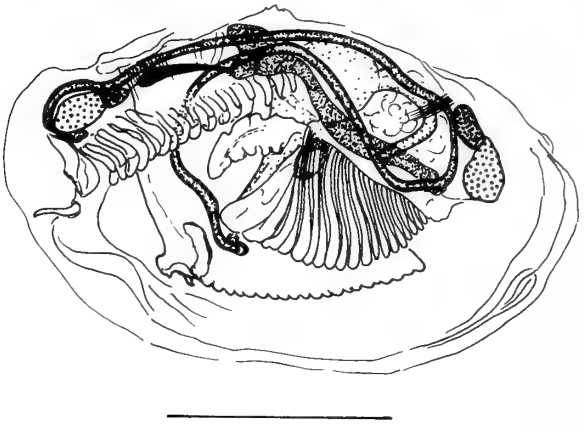

Fig. 122 *Yoldiella fabula*. Lateral view from the right side of the internal morphology of a specimen from Sta. 85, North America Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

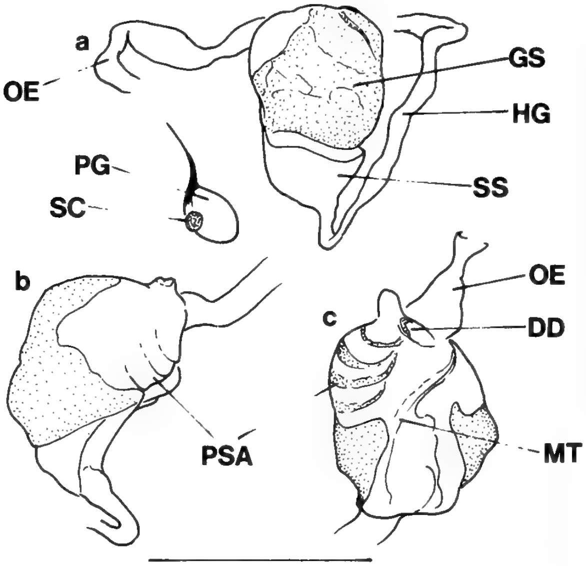

Fig. 123 *Yoldiella fabula*. External views of intact stomach an style sac in a, left; b, right and c, antero-frontal views. Dissected from a specimen from Sta. 85, North America Basin. (Scale = 1.0 mm).

Genus *Portlandia* Mörch 1857

TYPE. By selection (Soot-Ryen, 1984: Opinion 769 ICZN) *Nucula artica* J.E. Grey, 1824.

Shell moderately small, slightly inflated, moderately fragile, oblong, posteriorly angular, more or less truncate, subrostrate, not gaping, escutcheon present, usually defined by weak or occasionally moderate carina, lunule may be present; usually glossy, smooth, postero-ventral margin may be sinuous, proximal postero-dorsal margin almost straight or slightly concave; umbo prominent, anterior, chondrophore variously developed; ligament amphidetic, largely internal with small part external, hind gut single loop to right of body.

Portlandia lenticula (Möller 1842)

TYPE LOCALITY. Greenland.

TYPE SPECIMEN. Lectotype BM(NH) 1843.7.3.31, right-hand

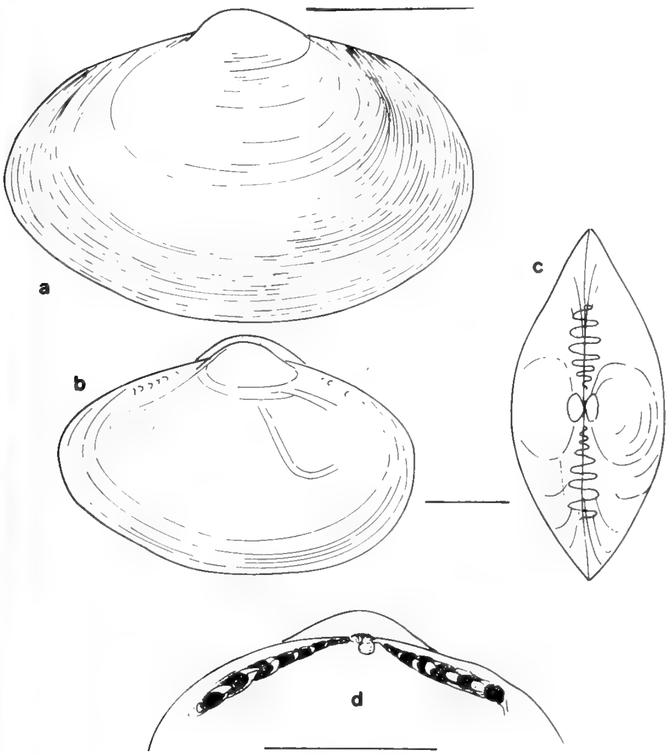

Fig. 124 *Yoldiella veletta*. Lateral views of two shells from the right side, detail of the hinge-plate of a right valve and a dorsal view of a shell. Specimens form a, Sta. 145, Cape Verde Basin; b & c, Sta. BG VI DS 87, West European Basin; d, Sta. 6701, Canaries Basin. (Scales = 1.0 mm).

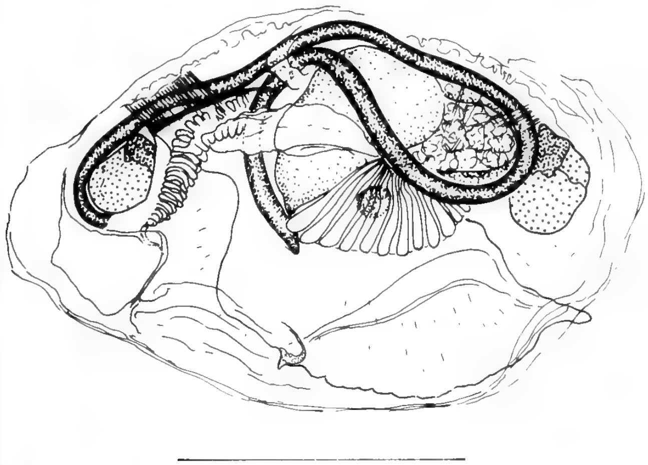

Fig. 125 *Yoldiella veletta*. Lateral view from the right side of the internal morphology of a specimen from Sta. 145, Cape Verde Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

specimen of 5 mounted specimens; Paralectotypes BM(NH) 1843.7.3.27–30 4 mounted specimens.

Nucula lenticula Möller 1842, 17.
Portlandia lenticula Sars 1878, 39, tab. 4, Fig. 10a,b; Thiele 1928, 617; Ockelmann 1958, Fig. 13, pl. 1, Fig. 12.
Yoldia (Yoldiella) lenticula Richards 1962, pl. 1, Figs, 23, 24.

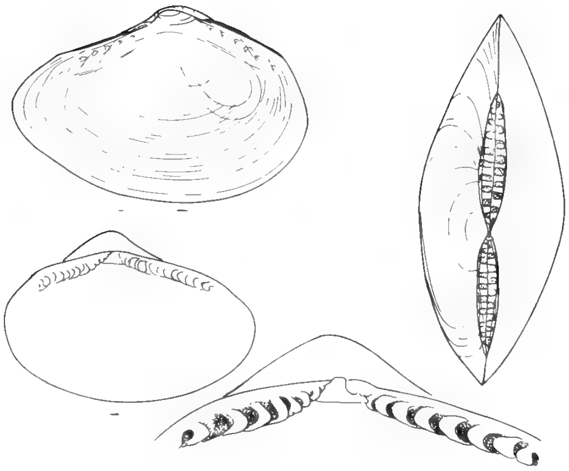

Fig. 126 *Portlandia lenticula*. Lateral view of a shell from the right side from Sta. S44, West European Basin. An interval view of a right valve with an enlarged detail of the hinge-plate and a dorsal view of a shell. Specimens from North East Atlantic (det. K. Ockelmann). (Scales = 1.0 mm).

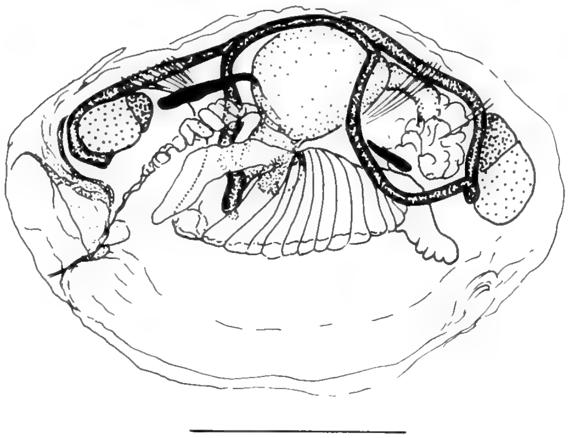

Fig. 127 *Portlandia lenticula*. Lateral view from the right side of the internal morphology of a specimen from Sta. S44, West European Basin. (Scale = 1.0 mm) for identification of the parts see Fig. 34.

Yoldiella lenticula Dautzenberg & Fischer, 1912, 406; Scarlato 1981, 209. Fig. 113.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Sarsia	44	1739	4	43°40.8′N	3°35.2′W	ED	16. 7.67
Thalassa	2438	1400	3	48°33.7′N	10°15.0′W	PBS	26.10.73

Jean Charcot (Biogas III)	DS37	2110	1	47°31.8′N	8°34.6′W	DS	24. 8.73
(Biogas IV)	CP01	2245	2	47°34.6′N	8°38.8′W	CP	25. 2.74
CANARY BASIN							
Discovery	6704	2129	1	27°44.9′N	14°25.0′W	ED	17.3.68

This is predominantly a northern Atlantic species occurring mostly from 10–200 metres (Ockelmann, 1958). Nevertheless, there are sufficient past records to confirm the present identifications that at its southern limits it is present at lower slope depths. Perhaps indicative of a temperature/depth relationship.

SHELL DESCRIPTION (Fig. 126). Shell moderately stout, ovate, slightly inequilateral, fine concentric lines, with elongate lunule and escutcheon, shell very wide dorsally and medially (such that when it rests on a valve the dorsal part is centred so that both umbos are characteristically visible in the lateral view); umbo very large, raised, internally directed, orthogyrate, immediately anterior to midline; antero-dorsal margin joins anterior and antero-ventral margins in a smooth curve, postero-dorsal margin also joins posterior and postero-ventral margin in smooth curve but is more attenuate than anterior margin; hinge plate moderately stout, not quite reaching level with the outer margins of adductor muscles, hinge plate narrows almost to margin below umbo, anterior and posterior hinge teeth equal in number or with one additional on the posterior plate; ligament amphidetic large, globular, extending far ventral to the hinge plate, slight secondary anterior and posterior external extension of fused periostracum. (See Ockelmann 1958, for typical shell dimensions).

INTERNAL MORPHOLOGY (Fig. 127). The combined siphons are short within a relatively shallow siphonal embayment. There is a slender sensory tentacle on the right side. The anterior sense organ and the feeding aperture are not particularly well-developed. The adductor muscles are very large, more or less oval in shape the anterior being the larger in size. The gills are slender with approximately 13 plates in a small specimen 14 mm in length. The palps are large with 13 ridges. The foot is small and in the one whole mount contracted to the level of the ventral edge of the palps. There is a small byssal gland. The stomach is large and the hind gut stout, the latter describes a single loop on the right side of the body.

Portlandia fora **(new species)**

TYPE LOCALITY. R.V. Sarsia, Sta. 56, Bay of Biscay, 19.7.1967, 43°43.0′N, 3°47.8′W, Epibenthic Trawl, 641 m.

TYPE SPECIMEN. Holotype: BM (NH) 1992041. Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPEAN BASIN							
Sarsia	56	641	15	43°43.0′N	3°47.8′W	ED	19.7.67

Only taken from the Bay of Biscay at one Station on the upper slope. Depth 641 m.

SHELL DESCRIPTION (Fig. 128). Shell relatively stout,

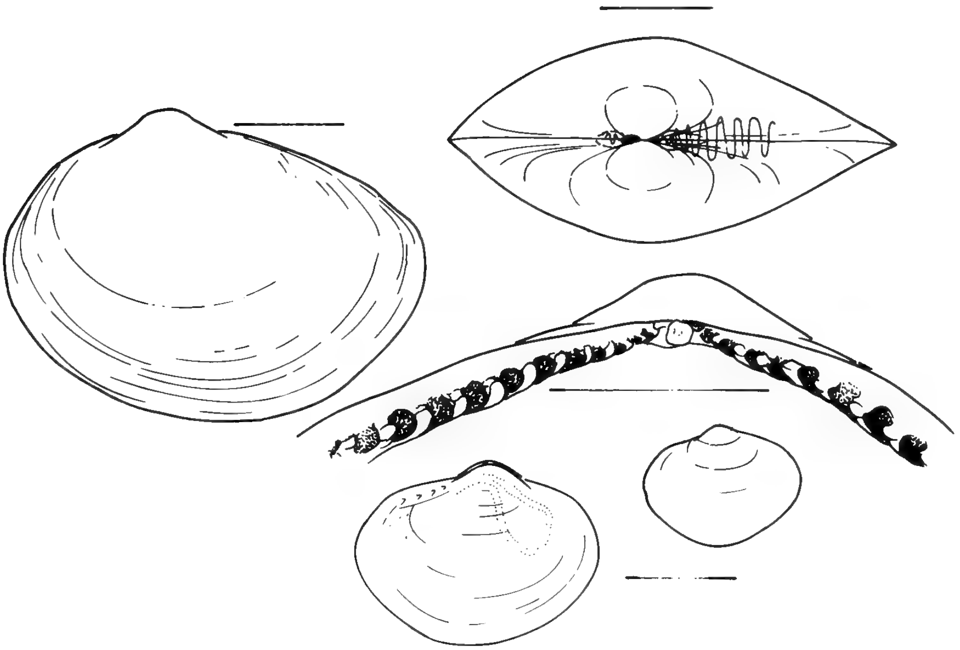

Fig. 128 *Portlandia fora.* Lateral view of a shell from the left side and a dorsal view of the same shell, detail of the hinge-plate of a left valve and lateral views of two small specimens to show variation in shape with growth. Specimens from Sta. S 56, West European Basin. (Scales = 1.0 mm).

inflated, ovate, inequilateral; umbos inflated, orthogyrate, anterior to midline; proximal dorsal margin slightly convex, antero-dorsal margin convex, slightly angulate at limit of hinge plate, then relatively straight section to dorsal limit of anterior margin, antero-ventral margin and ventral margin smoothly curved, posterior margin drawn out into broad rounded medial tip, postero-dorsal margin slightly convex sloping gradually towards tip, slight dip in outline at limit of hinge plate, posterior margin slightly rostrate; no marked rostral ridge but a small lunule and escutcheon present close to umbos; hinge plate moderately broad, long strong teeth, 12 in posterior and 10 in anterior series in largest individual, ligament internal, amphidetic, moderately large, 'goblet'-shaped, short anterior and posterior external extensions of fused periostracal.

Maximum observed shell length: 3.86 mm.

INTERNAL MORPHOLOGY (Fig. 129). Well-developed combined inhalent and exhalent siphons are present, the inhalent siphon is somewhat the shorter than exhalent. The siphonal tentacle is usually on the left side. The anterior sense organ is well-developed. The adductor muscles are relatively small. The anterior adductor is 'cresent'-shaped and approximately twice the size of the oval posterior adductor.

The gills have up to 14 alternating filaments. The labial palps are small, extending over approximately 1/4 distance of body and have up to 9 inner palp ridges. The palp proboscides are long and thin. The visceral ganglia are relatively slender, the cerebral ganglia are larger and more oval in shape and the pedal ganglia are large and round. The foot is moderate in size with a large byssal gland. There is a relatively large stomach with the style sac ventral and slightly posterior to it. The hind gut penetrates deep into the foot ventral and anterior to the pedal ganglia before turning dorsally to umbonal region where it passes to the right side of the body and forms a single loop. The hind gut has a typhlosole along its length.

This species is similar in shell shape and internal morphology to *Portlandia minuta* but differs from the latter in that *P. fora* has a less angulate shell margin, slightly larger internal ligament, a more obvious external ligament, is less inflated and has a greater number of hinge teeth, the hinge plate is narrower, and the post-umbonal length shorter. Anatomically there are relatively few differences, the gill plates and palp ridges are marginally fewer in specimens of a similar size.

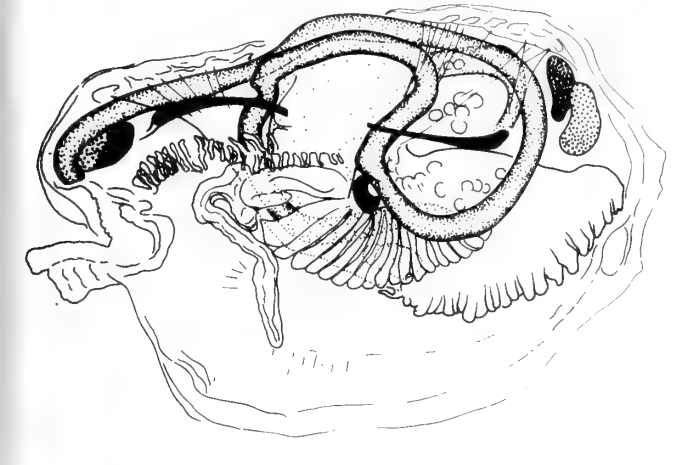

Fig. 129 *Portlandia fora*. Lateral view from the right side of the internal morphology of a specimen from Sta. S 56, West European Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

Portlandia minuta (new species)

TYPE LOCATION. R.V. Atlantis, II Cruise 42, Sta. 203, Angola Basin, 23.5.1968, 8°48′S, 12°52′E, Epibenthic Trawl, 527–542 m.

TYPE SPECIMEN. Holotype BM (NH) 1992040. Paratypes: in collection held by J.A. Allen.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CAPE BASIN							
Atlantis II	188	619–622	33	23°00.0′S	12°58.0′E	ES	16.5.68
ANGOLA BASIN							
Atlantis 42	203	527–542	1352	8°48.0′S	12°52.0′E	ES	23.5.68

Occurs off S.W. Africa at upper slope depths in Angola & Cape Basins. Depth range: 527–622 m.

SHELL DESCRIPTION (Figs. 130 & 131). Shell small, inflated, subovate, posteriorly narrow, robust, fine but somewhat irregular concentric lines; slightly iridescent, pale yellow periostracum; umbos inflated, anterior to midline, internally directed; lunule and escutcheon barely visible; slightly rostrate, slight indication of rostral ridge in some specimens; antero-dorsal margin convex, slopes rapidly and evenly to anterior margin, postero-dorsal margin slightly convex, slopes gradually to posterior margin, slight angle at limit of posterior hinge plate, ventral margin smoothly curved, centrally deep, posterior margin drawn out but moderately rounded, in mid horizontal plane; hinge plate strong, fairly narrow on either side of ligament, broadens out distally, distal teeth prominent, 3–4 small proximal teeth, in total 9 in anterior series and 11 in posterior series of largest specimen; ligament amphidetic, rectangular in shape, small external secondary extensions of fused periostracum on either side of umbo.

Prodissoconch length: 166 μm. Maximum recorded shell length: 2.28 mm.

INTERNAL MORPHOLOGY (Fig. 132). There is a combined siphon with a single lumen, thus there is no separation between inhalent and exhalent lumena, however, the gill axes join mid-laterally. Gland cells are present at the junction of axis and siphon. There is a well-developed elongate anterior sense organ. The adductor muscles are unequal in size. The smaller posterior muscle is oval in shape, the anterior is almost twice the size and 'cresent'-shaped. The gills are well-developed with up to 14 relatively large plates, the most posterior of the inner plates are clearly interlocked even in the preserved specimens. The labial palps are relatively small with up to 8 palp ridges, the most posterior of these being much broader than the rest.

The foot is large but the pedal musculature is not as well-developed as in some *Yoldiella* species. There is a large

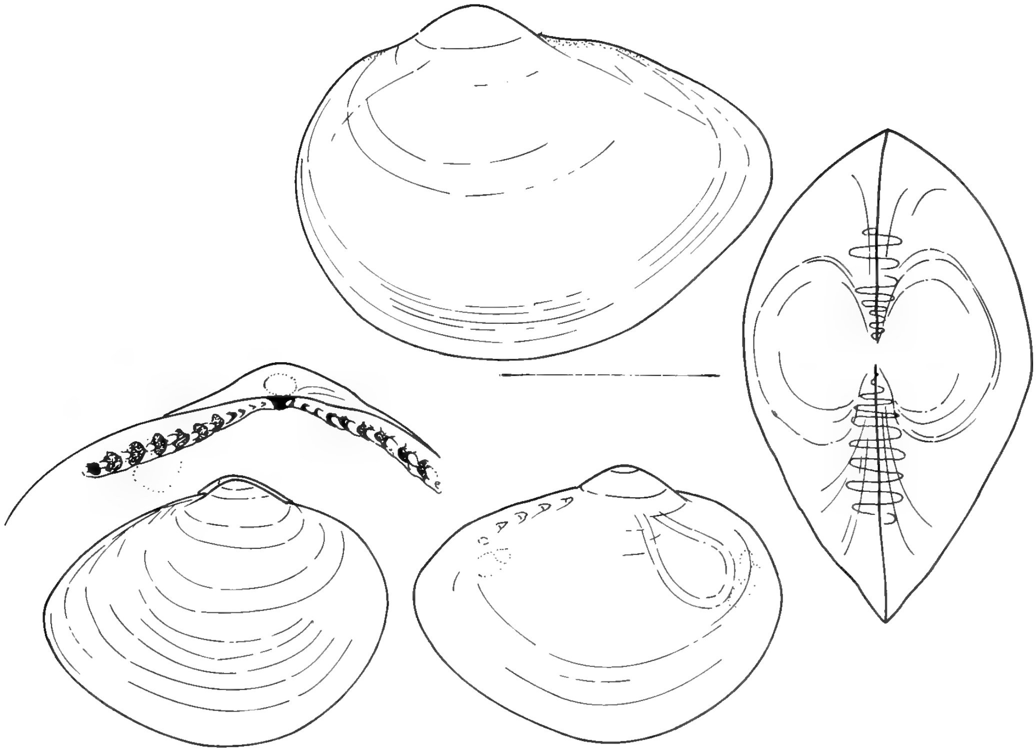

Fig. 130 *Portlandia minuta*. Lateral views of shells from the left and right sides, detail of the hinge-plate of a left valve and the dorsal view of a shell. Specimens from Sta. 203, Cape Basin. (Scale = 1.0 mm).

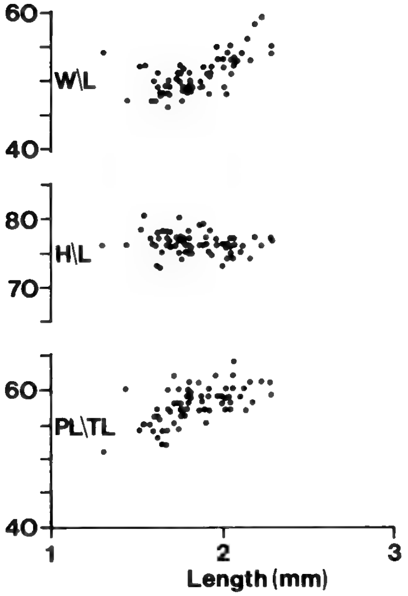

Fig. 131 *Portlandia fora*. Variation in ratios of height H/L, width W/L and postero-umbonal length PT/TL to length against length of a subsample taken from Sta. 203, Cape Basin.

byssal gland in the heel with a relatively large blood space surrounding it. The nervous system is well-developed with large 'club'-shaped visceral and cerebral ganglia and large, round, pedal ganglia with associated large statocysts dorsal to them. The stomach and style sac are large. From the style sac the hind gut penetrates the foot for a short distance before turning dorsally to parallel the posterior edge of the body. Thereafter it makes a single loop to the right side of the body. A small amount of food material was observed in parts of the left digestive diverticulum. The kidneys are small. Gonads are present in specimens larger than 1.6 mm. The testes occur dorsally, ventrally and internally to the digestive diverticula with posterior dorsal and lateral extensions.

In the course of growth, the valves become more inflated and more rostrate but there is little change in the height/ length or posterior umbonal length/ total length ratios (Fig. 131). Hydroids were present on one individual and these covered the dorsal and posterior shell margins.

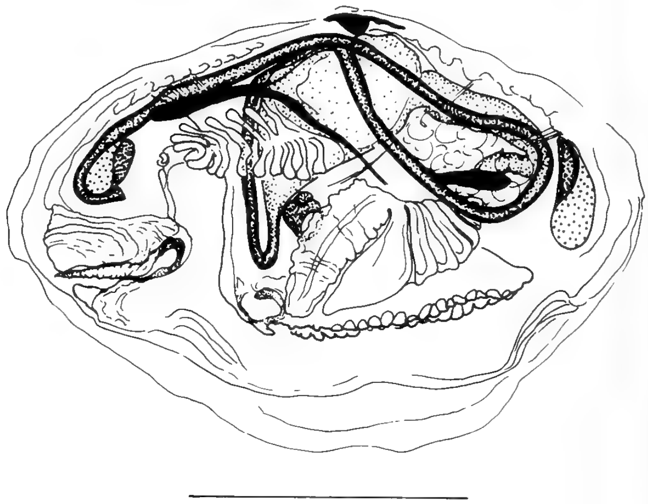

Fig. 132 *Portlandia fora*. Lateral view from the right side of the internal morphology of a specimen from Sta. 203, Cape Basin. (Scale = 1.0 mm). For identification of parts see Fig. 34.

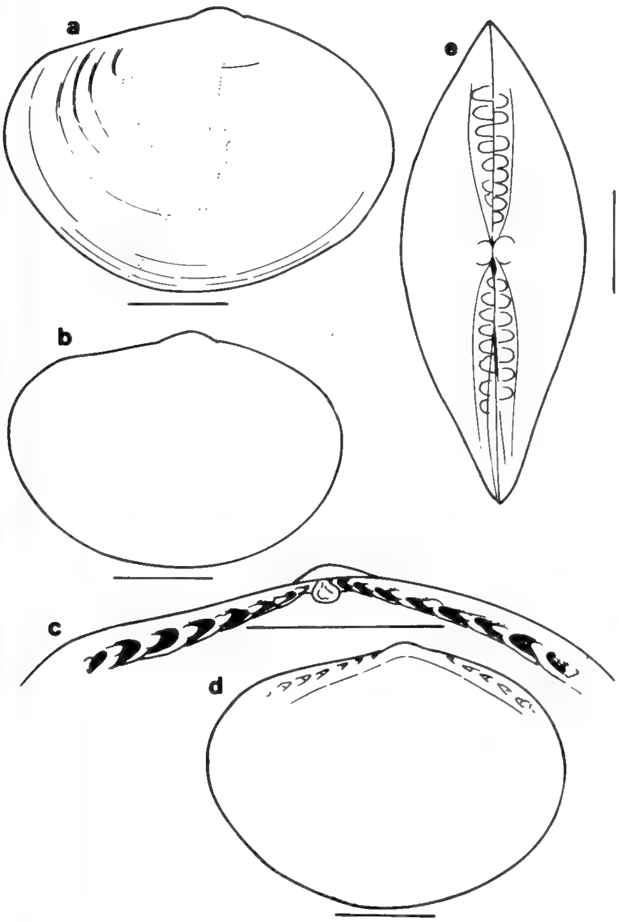

Fig. 133 *Portlandia abyssorum*. Lateral views of three shells from the right side to show variation in shape. Dorsal view of a shell and detail of the hinge-plate of a left valve. Specimens taken from a, Sta. 24, Galathea Expedition, Sierra Leone Basin (Type specimen); b, c & d, Sta. 8528¹, Cape Verde Basin; e, Sta. 8521⁶, Cape Verde Basin. (Scales = 1.0 mm).

Portlandia abyssorum (Knudsen 1970)

TYPE LOCALITY. R.V. Galathea, Sta. 24, E., Atlantic off W. Africa, 1950, 3°54′N, 8°22′W, Trawl, 3196 m.

TYPE SPECIMEN. Holotype: Zoological Museum, University of Copenhagen.

Yoldiella abyssorum Knudsen 1970, 47, Fig. 29, pl. 1, Fig. 17.

MATERIAL.

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
CAPE VERDE BASIN							
Discovery	8521⁶	3070– 3064	6+2v	20°47.9′N	18°53.4′W	WS	26. 6.74
	8528¹	3155– 3150	72+2v	17°38.7′N – 17°38.3′N	18°35.8′W 18°34.9′W	WS	2. 7.74
Atlantis II 31	148	31114– 3828	1	10°37.0′N	18°14.0′W	ES	7. 2.67
	149	3861	3	10°30.0′N	18°18.0′W	ES	7. 2.67
ANGOLA BASIN							
Atlantis II	195	3797	45	14°40.0′S	9°54.0′E	ES	19. 5.68
42	196	4612– 4630	1	10°29.0′S – 10°29.0′S	9°54.0′E 9°04.0′E	ES	21. 5.68
CAPE BASIN							
Jean Charcot	DS05	4560	1	33°20.5′S	2°34.9′E	DS	30.12.78
(Walvis)	CP13	3550	1	32°18.1′S	13°15.9′E	CP	12. 1.79

Occurs at abyssal depths off the west coast of Africa, Cape Verde, Angola & Cape Basins. Depth range: 3064–4630 mm.

SHELL DESCRIPTION (Figs. 133 & 134). An accurate description is given by Knudsen (1970). Populations of this species vary somewhat in the shape of the shell outline from that of the type specimen to specimens with a more straight or slightly concave postero-dorsal margin and a more convex postero-ventral margin with intermediates between these two extremes.

INTERNAL MORPHOLOGY (Fig. 135). In contrast to the description of Knudsen (1970) there is an inhalent as well as an exhalent siphon. The short ventral inhalent siphon is not particularly obvious being much shorter than the exhalent, however, sections show a twin siphon, the inhalent being open ventrally. A siphonal tentacle originates on the left of the siphon and there is a fairly well-developed feeding aperture below. The adductor muscles are large, the anterior being approximately twice the size of the posterior. The gills are well-developed with up to 24 gill filaments. The labial palps are large with a large number of internal ridges (up to 30), the number depending on the size of the individual. The foot is large and extends anterior and ventral to the anterior adductor muscle. It also has a large byssal gland. The cerebral and visceral ganglia are elongate with a moderately thick commissure. The pedal ganglia are large, elongate with large associated statocyts. The hind gut forms a single loop on the right side of the body and has a typhlosole along its length.

Prodissoconch length: 187–198 μm. Maximum recorded shell length: 4.76 mm.

This species at first sight might be confused with *Yoldiella biscayensis*, however there are a number of differences. These include: – the presence of a lunule and escutcheon; the umbo is raised only slightly above the dorsal margin; the posterior and postero-dorsal margin is faintly rostrate; the prodissoconch is much narrower and is shorter in length; the palps have many more ridges.

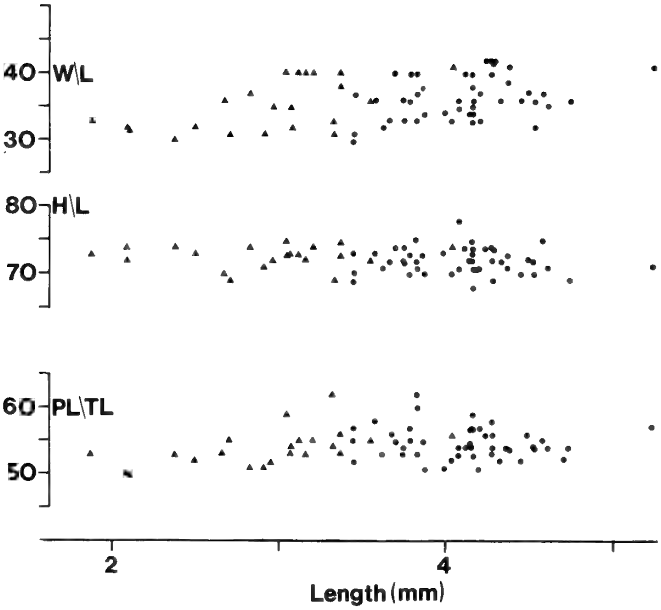

Fig. 134 *Portlandia abyssorum*. Variation in ratios of height H/L width W/L and postero-umbonal length PL/TL to length against length of specimens from Sta. 195, Angola Basin (closed triangles) and Sta. 8528^1, Cape Verde Basin (closed circles).

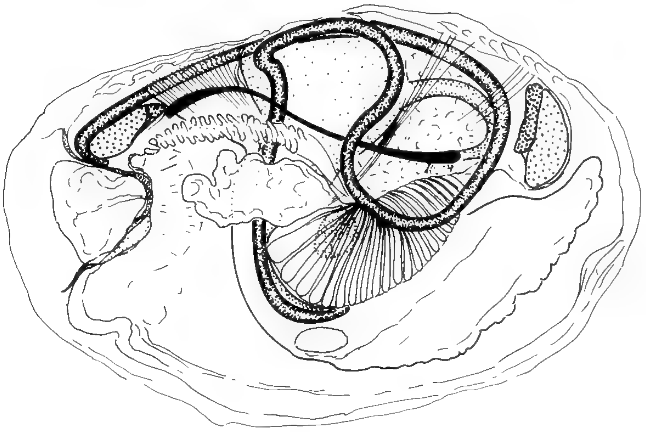

Fig. 135 *Portlandia abyssorum*. Lateral view from the right side of the internal morphology of a specimen from Sta. 8528^1, Cape Verde Basin. (Scale = 1.0 mm). For identification of the parts see Fig. 34.

DISCUSSION

Of all the protobranch bivalves of the Atlantic, the yoldiellids are by far the most difficult nuculanid subgroup in which to discern evolutionary pathways. Despite the large number of species we believe that these are closely related within a subfamily. With possibly one exception, of 28 species of *Yolidella* described here, there is a fine gradation in morphological features that both combines them within a single genus and distinguishes them as a separate group. It must be emphasized that as in all deep-sea protobranch species, the shell proportion changes with increasing size. In general the post-umbonal length increases at a rate greater than the other dimensions. In some cases this also applies to the height of the shell. As a result the small shells of a species may be mistaken as being of a different species. This also creates difficulties in making comparisons between species.

To the experienced eye, species and subspecies can be separated and defined. Of particular diagnostic importance is the form and course taken by the hind gut. Although there may be some variation within a species, the course and diameter of the gut alone is usually diagnostic. Nevertheless, it is often difficult to define and only becomes clear after close comparison of a range of species. We can distinguish eight broad configurations of the hindgut of which the simplest, a single loop to the right of the viscera occurs in 17 of 32 species and subspecies of *Yoldiella* (Table 3) (Allen, 1992). The most complex configuration occurs in only one species (see below).

The species of *Portlandia* form a compact group in which the shells are relatively robust, elongate, with the posterior margin approximately central to the horizontal midline. The hind gut has a single loop to the right and has a large diameter. The adductor muscles are large and oval and more or less equal in size. The hinge plates are long and stout, continuous with the amphidetic internal ligament. The lunule and escutcheon are usually well-defined. Three of the four species are from upper to mid-slope depths and one *P. abyssorum*, is from abyssal depths. The latter, apart from having larger palps, smaller adductor muscles and more dorsal anterior and posterior limits to the shell outline than the other species described, its morphology is basically the same.

One rare species of *Yoldiella, Y. veletta*, has many of the characteristics of *Portlandia* described above. However, it is a fragile shell without lunule or escutcheon. Furthermore, the hinge plates form in a narrow bridge below the umbo with the amphidetic ligament ventral to it. With only three specimens at hand we defer categorical judgement, but hypothesize that the primitive form of *Yoldiella* must have had similar characteristics.

On the premise that the simplest form of hind gut is likely to reflect the primitive condition we derive an evolutionary pattern that originates in species with this character but among others, for it is unwise to base evolutionary conclusions on one character alone. In passing, it should be said that it is a sad fact that for many malacologists, it is the shells rather than the viscera that are all-important.

It seems reasonable to assume that deep-water species in the Atlantic originated either from shallow water, possibly tethyan and arctic seas, or by migration at depth from the Southern Ocean. For reasons that we will describe elsewhere (Allen and Sanders in m/s), we think it unlikely that the major colonization of the deep Atlantic was from high southern latitudes. Yet there are only a limited number of yoldiellids present in shelf sediments, but all of these species have a relatively short hindgut with a simple single loop to the right side of the viscera. This character is also found in other shallow-water nuculanids and in shallow-water neilonellids and tindariids, however, species of *Yoldiella* differ from these latter three groups in not having heavy, concentrically ornamented shells. When concentric ornamentation is present in a yoldiellid it is always of a fine, delicate nature, and more often than not confined to the periphery of the shell.

We identify two species from shallow water in the North and West Atlantic, *Y. frigida* and *Y. robusta* that have characters which we believe a 'stem' group *might* possess. These include, in addition to the single hind gut loop, a symmetrical ovate shell outine, relatively short fragile separate hinge plates and a moderately large central amphidetic ligament (Fig. 148). In addition, they have large siphons with combined lumena which are ventrally unfused, moderately large, oval, subequal, adductor muscles, a few large fringing papillae to the foot, a relatively elongate gill with a moderate number of plates and broad palp ridges which are relatively few in number.

From this basic form, we derive a number of evolutionary pathways. The most simple derivation appears to be that shells become somewhat higher in proportion to length and the antero-dorsal and postero-dorsal margins become more horizontal such that the anterior and posterior limits of the shell are dorsal to the horizontal midline (Figs. 136–147). (For details of the comparative overlay technique, see Fig. 136). In other respects, a characters are similar to those given above. These latter species include *Y. inconspicua*, *Y. extensa* and *Y. argentinensis*, again from the North and West Atlantic but further downslope than *Y. frigida* and *Y. robusta*. In addition, *Y. curta*, a common and widespread species from the base of the continental slope would also appear to belong here, however, unlike the species mentioned so far, the hindgut of *Y. curta* passes anterior to the mouth to form a single loop on the left side of the body. This disposition of the hind gut is a simple derivation from the primitive condition and can be explained simply in terms of elongation and accommodation of the hindgut. In all other respects *Y. curta* is similar to the species of the *Y. frigida* group.

In juxtaposition to this possible stem group is a group of species centred upon *Y. lucida* (shelf/upper slope), *Y. obesa* (mid/lower slope) and *Y. similiris* (upper/mid slope). Although having similar ovate shape to *Y. frigida* and *Y. robusta*, these species have much longer but still separated hinge plates, smaller adductor muscles of which the posterior is significantly smaller than the elongate anterior muscle. The hind gut loops are somewhat longer and more broadly looped and the lumena have a wider diameter. Most other characters are in common with the 'stem group'. These include an internal amphedetic ligament ventral to the hinge plate which is somewhat smaller than that of the stem group, a relatively elongate gill, small palps with broad ridges which are few in number and papillae of the foot which are relatively large. The differences between *Y. lucida*, *Y. obesa* and *Y. similiris* and the species of the 'stem group' relate to the strength of the hinge plate. As the length and robustness of the hinge increases there is less requirement for large adductors and a large ligament to ensure the integrity of the two valves. In addition, as the maximum depth limit of the species increases, the hind gut tends to enlarge either in length or diameter or both.

As in the case of the 'stem group', we believe evolution from the '*lucida*' group also involves an increase in the height of the shell and the antero- and postero-dorsal shell margins becoming more horizontal such that the posterior limit of the shell margin becomes characteristically sharply rounded. The posterior adductor muscle is reduced in size, the hind gut penetrates deep into the foot and the palps are small with very few ridges. The siphonal lumena are separate. Species with these characterstics include *Y. bilanta*, *Y. hanna* and *Y. capensis*, all of which are restricted to slope depths.

Y. artipica is intermediate in its characters to the two above groups, however the hind gut is more sinuous in its course to the right. This represents the initial stage in a trend that leads to the coiling of the hind gut on the right side of the body. Note the *Y. artipica* has a deeper distribution than those species described above and is found on the abyssal rise. Similarly, *Y. sinuosa*, *Y. blanda* and *Y. biscayensis* which have similar characteristics to the '*bilanta*' group, all have sinuous hind guts. There are other internal differences shown by these three species. Thus, while the adductor muscles are dissimilar in size, the posterior muscle is not greatly reduced in size, the palp ridges, although wide, are more numerous and thus the palp is large and the siphon is particularly large with combined lumena. As in the case of *Y. artipica* these are species from the abyssal rise.

The logical sequence to the trend is seen in *Y. lata* in which the hind gut has a larger diameter, has lengthened such that the 'reverse-S' course has progressed to a double-loop. Also to be noted are that the adductors are moderately large and are equal in size, and the hinge plates, although elongate, are narrow and much less robust. Similarly the gill is relatively small and the palp has numerous narrow ridges.

As a continuation of this trend, a specialized group of species comprising *Y. ella*, *Y. enata* and *Y. jeffreysi* is arrived at. A sequence of events can be envisaged. Starting from the condition in *Y. lucida* the hind gut lengthens, remains to the right of the body and becomes increasingly coiled. (Up to four times). The shell becomes characteristically rounded, high with large umbos. The hinge plates become very strong and the ligament small and rounded. The adductor muscles are small, and may be subequal in size. The generating outline curve of the shell is rotated somewhat to the right so that the umbo is distinctly anterior and the maximum ventral limit is posterior to the vertical midline. We can envisage a sequence of increasing hind gut complexity from *Y. lucida* through *Y. blanda*, *Y. lata*, *Y. jeffreysi* to *Y. enata*, however, we have some reservations as to whether *Y. ella* is the terminal species of this line. While *Y. ella* has the most coiled hind gut of all the yoldiellids in our collections, the more evenly rounded shape, the extremely small subequal adductor muscles and the massive hinge plates might indicate a separate derivation or at least a marked terminal divergence in the series. These species have a depth distribution from the abyssal rise to the greatest abyssal depth. There is little doubt in our opinion that the differences in morphology exhibited in both the latter group are related to the requirements of life at abyssal depths.

We also derive an even more complex but distinct group comprising *Y. americana*, *Y. subcircularis*, *Y. biguttata* and *Y. ovata* from the *Y. lucida* stock. These four species also have characteristically rounded, high shells which have large umbos. The evolutionary sequence probably included an intermediate stage with a form similar to that of *Y. perplexa* in which shell characters are similar but in which there is a relatively short single hind gut loop to the right, robust subequal adductor muscles, small palps and gills, large pedal papillae and long hinge plates. *Y. americana* differs relatively little from this, except that the hind gut is considerably lengthened and which takes a course to the left and right of the stomach and the palp is a deep semicircular shape with a large number of ridges (see p. 54). A similar morphology to that of *Y. americana* is found in *Y. subcircularis* except that the hindgut loops are doubled on either side of the body. Similarly, *Y. biguttata* and *Y. ovata* also have two hind gut loops to the right and the left and in *Y. insculpta*, the hind gut

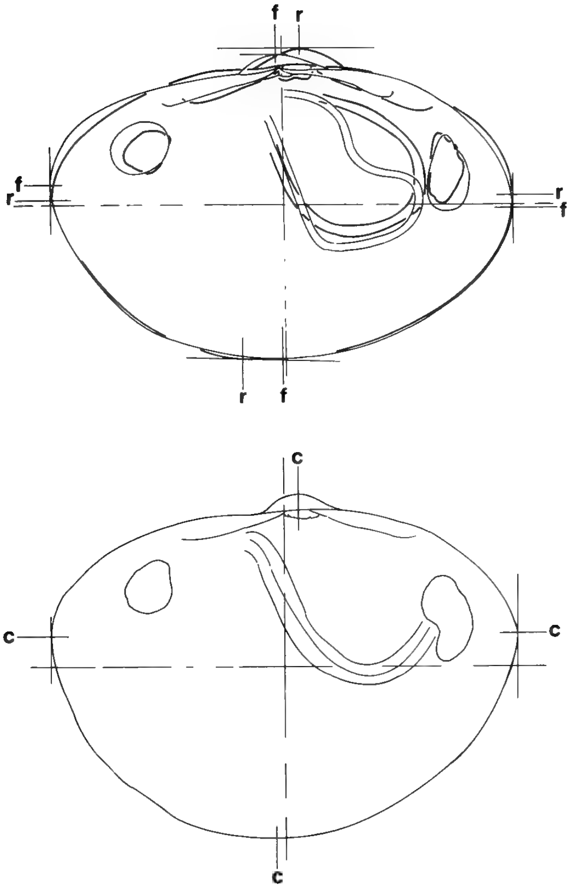

Fig. 136 *Yoldiella frigida* (f), *Y. robusta* (r), & (separately) *Y. curta*(c).

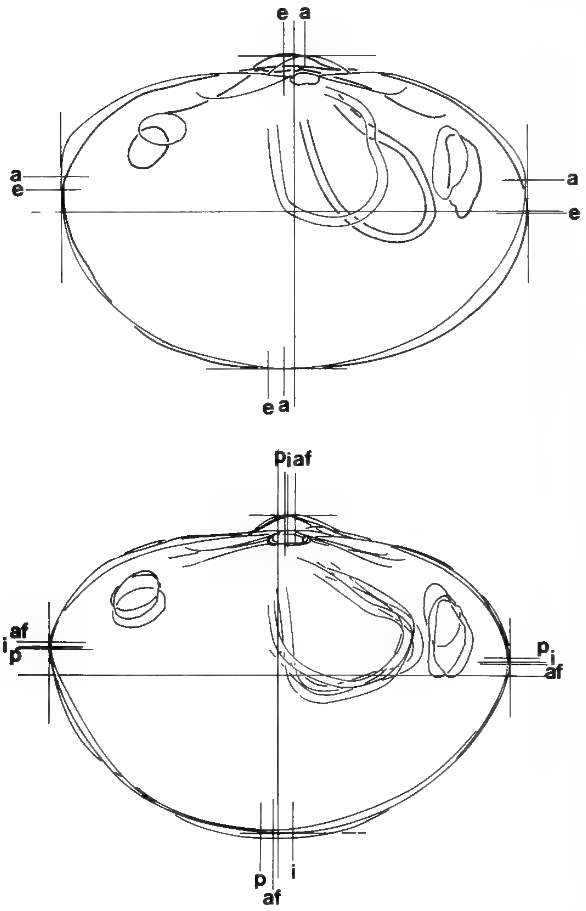

Fig. 137 *Yoldiella argentinensis* (a), *Y. extensa* (e) & (separately) *Yoldiella inconspicua inconspicua* (i), *Y. i. profundorum* (p) & *Y. i. africana* (a).

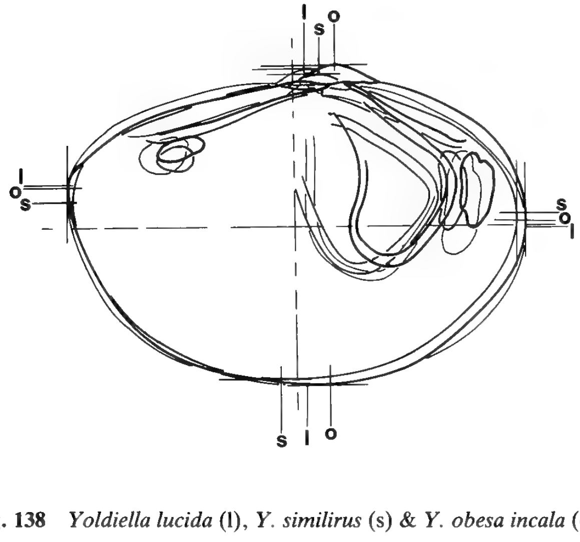

Fig. 138 *Yoldiella lucida* (l), *Y. similirus* (s) & *Y. obesa incala* (o).

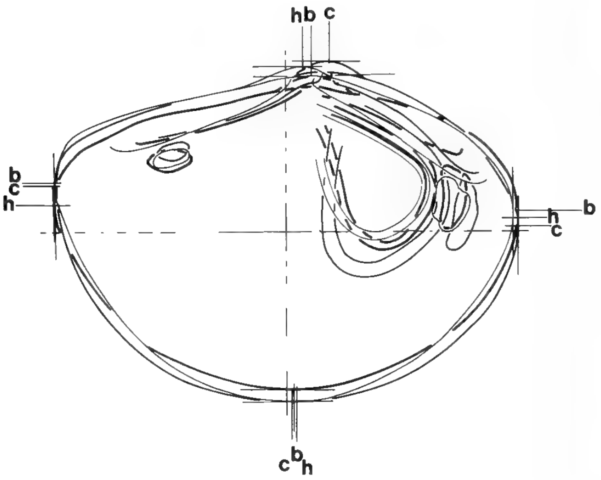

Fig. 139 *Yoldiella bilanta* (b), *Y. hanna* (h) & *Y. capensis* (c).

Figs 136–147 Outline comparisons of species by overlay technique. Each outline is centred with reference to the junction of the centre of the mid-length axis with the centre of the mid-height axis. Outlines are drawn to a similar length. Each shell outline comprises the margin in right lateral view, hindgut loop and anterior and posterior adductor muscles. Anterior, posterior ventral and dorsal limits are indicated parallel to the relevant shell axis as too is the apex of the umbo. Each limit is identified by the first letters of the species name. The figures are in the order of the discussion on the evolution of form. (See text pp. 82–86).

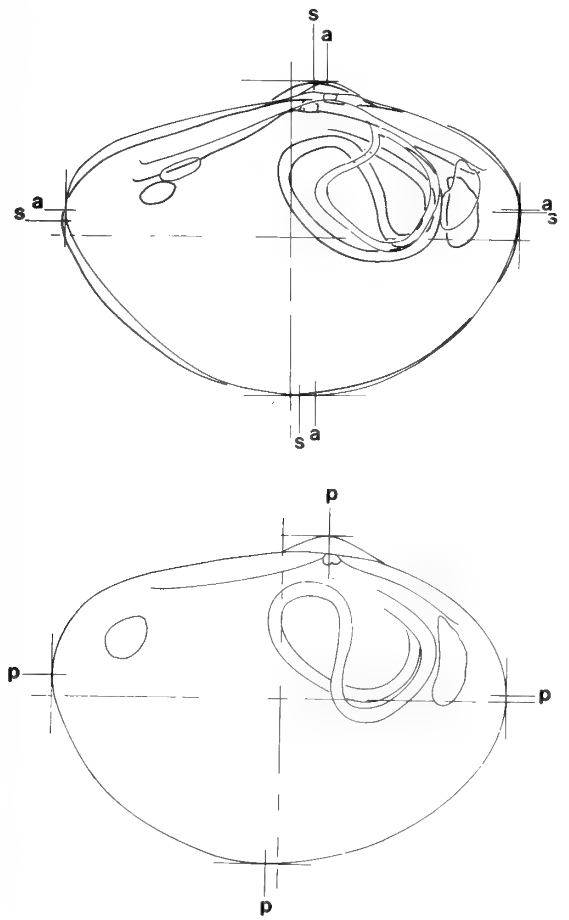

Fig. 140 *Yoldiella artipica* (a), *Y. similis* (s) & (separately) *Y. lata*(p).

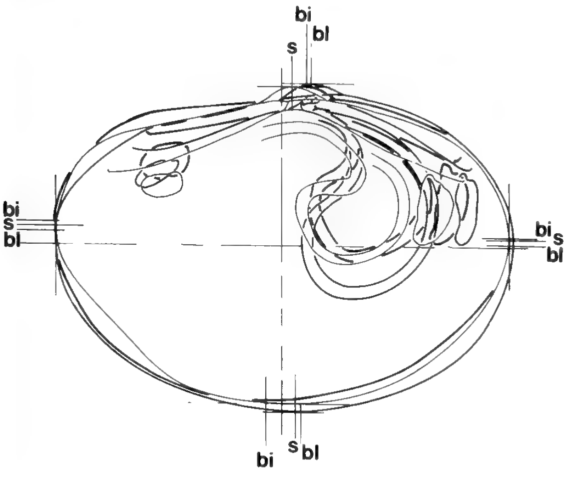

Fig. 141 *Yoldiella sinuosa* (s), *Y. blanda* (bl) & *Y. biscayensis* (bi).

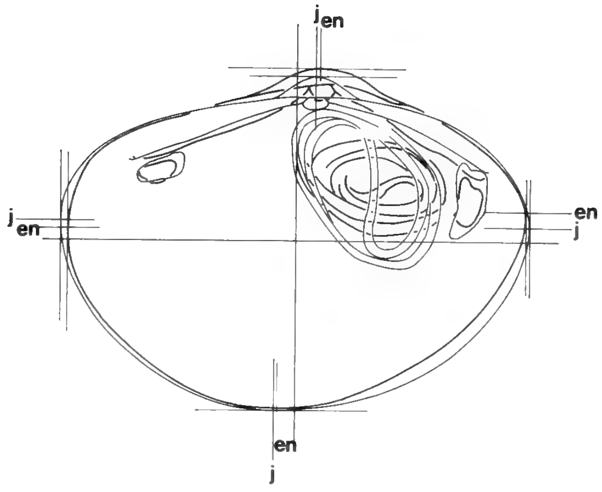

Fig. 142 *Yoldiella jeffreysi* (j) & *Y. enata* (en).

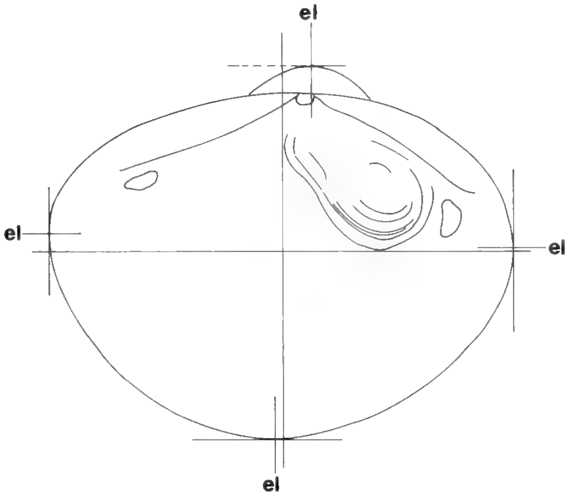

Fig. 143 *Yoldiella ella* (el).

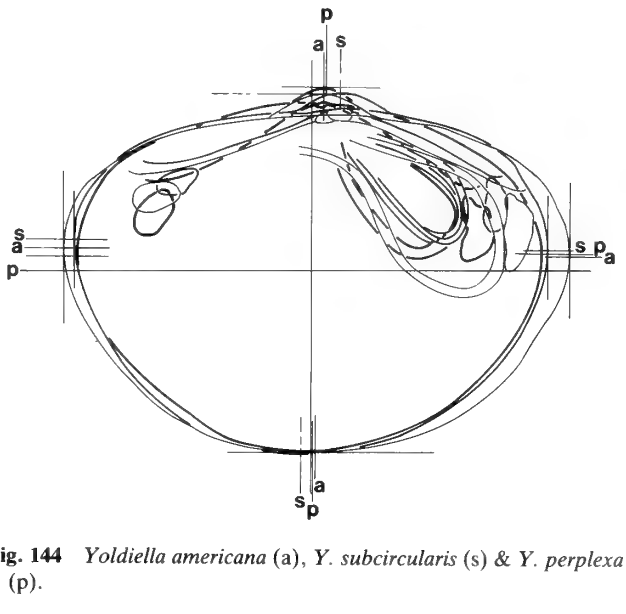

Fig. 144 *Yoldiella americana* (a), *Y. subcircularis* (s) & *Y. perplexa* (p).

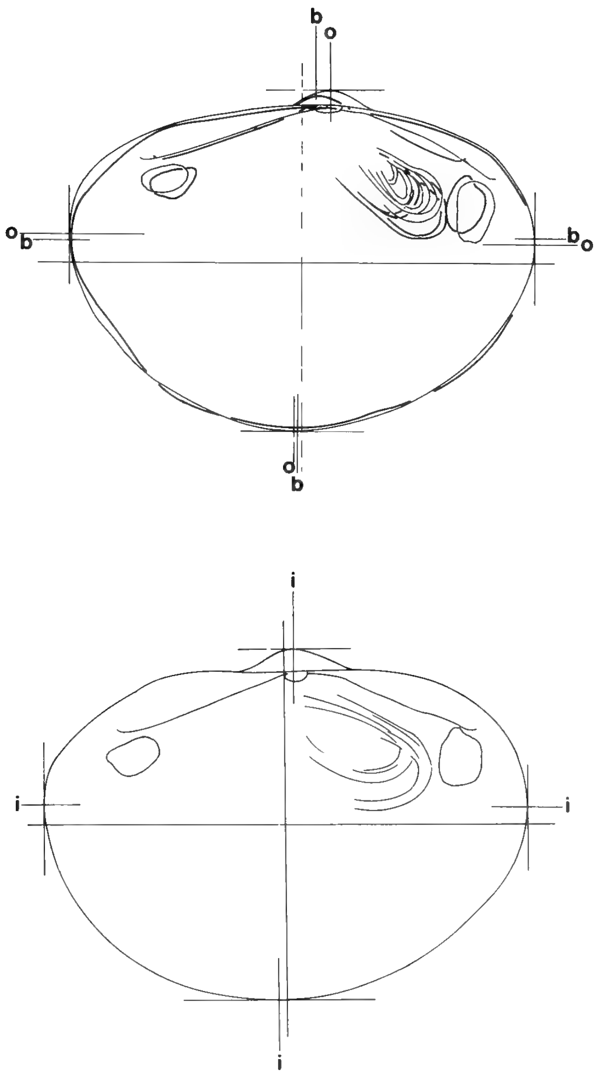

Fig. 145 *Yoldiella ovata* (o), *Y. biguttata* (b) & (separately) *Y. insculpta* (i).

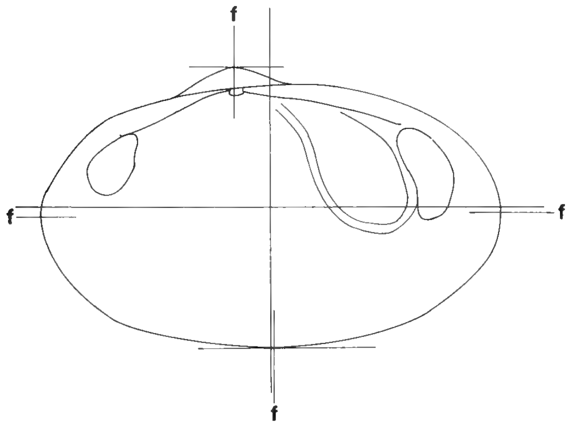

Fig. 146 *Yoldiella fabula* (f).

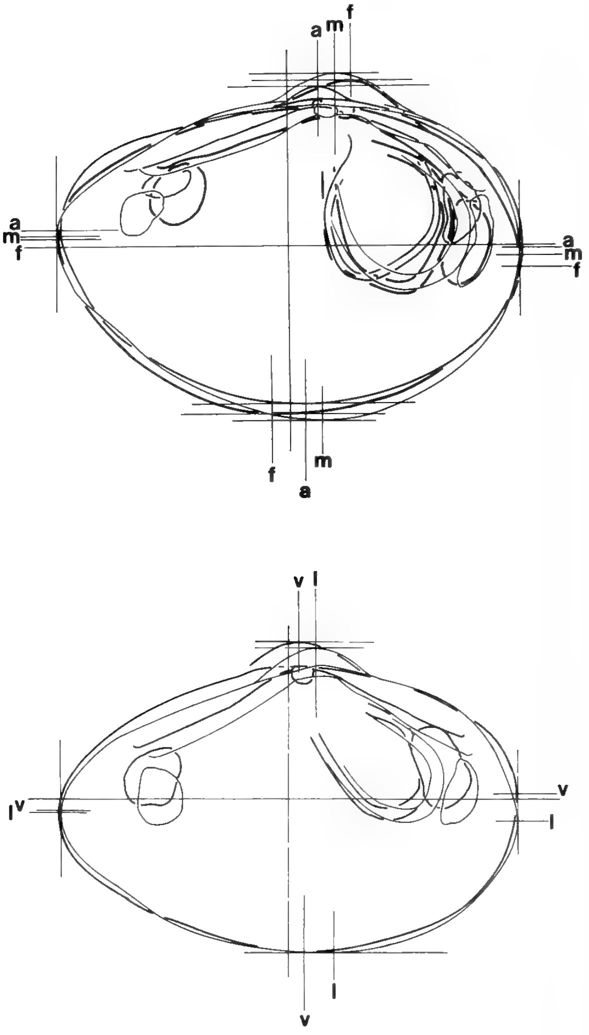

Fig. 147 *Portlandia abyssorum* (a), *P. minuta* (m), *P. fora* (f), (separately) *Yoldiella velleta* (v) & *Portlandia lenticula* (l).

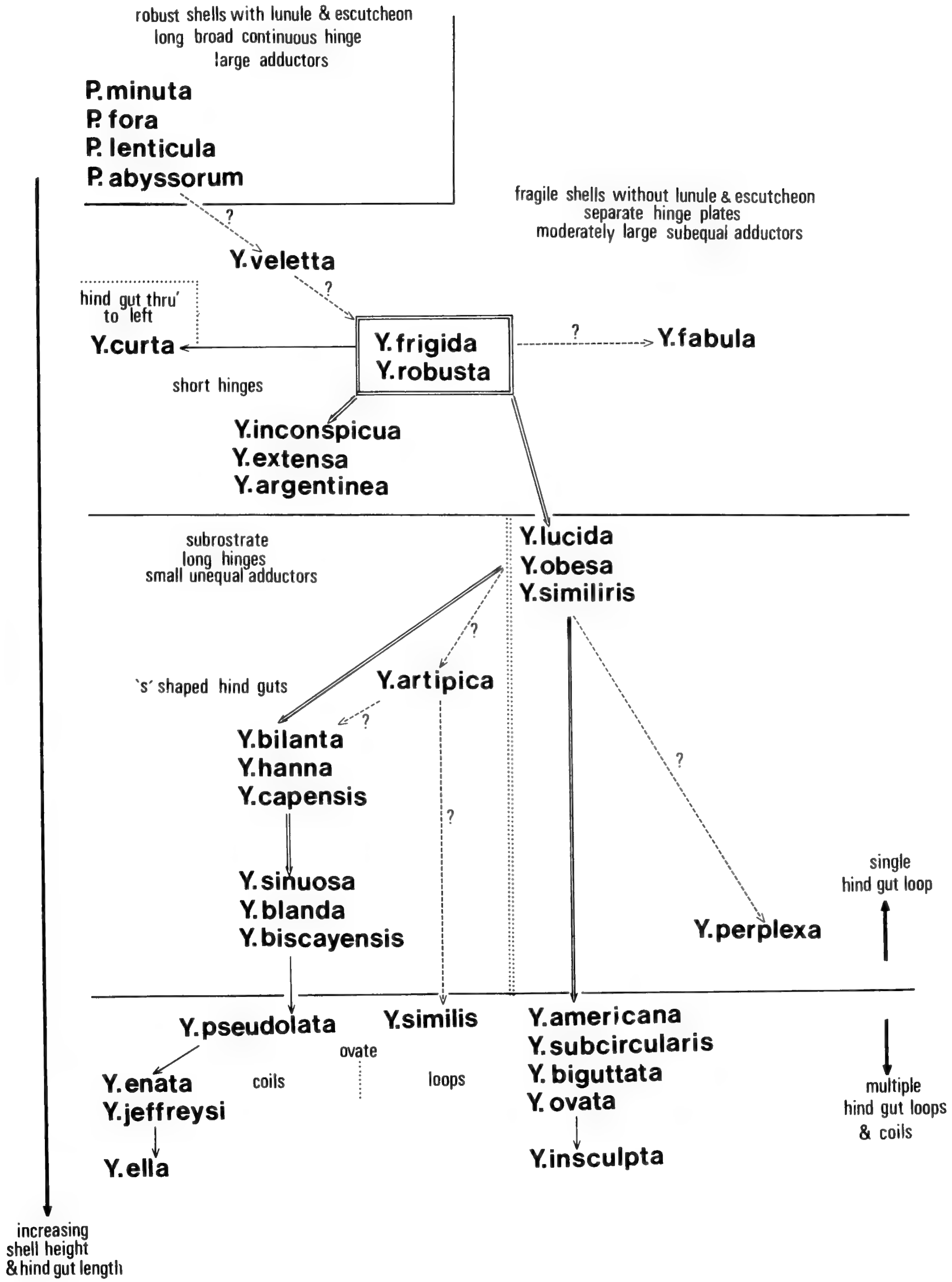

Fig. 148 Diagram to show resemblances in shell form of the deep-sea species of the genus *Yoldiella* found in the Atlantic, arranged in increasing length and complexity of the hindgut and each group of species arranged in increasing depth sequence.

Table 3 An analysis of morphological characters of species of *Yoldiella* arranged according to depth.

		Hindgut configuration								Hinge		Ligament		Adductors					Palps												
	Depth m.	1 loop to R	½ coil to R	1 coil to R	2 coils to R	2+ coils to R	1 loop L & R	2 loops L & R	2+ loops L & R	Short	Long	Short	Long	Small posterior	Medium posterior	Large posterior	Subequal	Heteromyarian	Large	Small	Ar	Br	Gy	NA	WE	Cn	SL	Gn	An	Cp	No
Portlandia minuta	527–622	+									+	+			+			+		+				+					+	+	
P. fora	641	+									+	+				+	+			+					+						
P. lenticula	508–1739	+								+		+				+	+		+						+	+					
P. abyssorum	3064–4630	+									+	+		+				+	+								+		+	+	
Yoldiella frigida	5–811	+								+			+			+	+		+					+	+						+
Y. lucida	38–811	+									+	+		+				+		+				+	+						+
Y. robusta	256–293	+								+			+			+	+		+		+										
Y. hanna	439–622	+									+	+		+				+		+										+	
Y. similiris	497–1011	+									+	+		+				+	+		+										
Y. argentinensis	497–1679	+								+		+			+			+	+		+										
Y. curta	587–2634*	+~								+			+			+		+	+		+	+	+	+	+		+			+	
Y. capensis	614–1014	+									+	+		+				+		+										+	
Y. biguttata	943–2853*							+		+			+	+				+	+		+	+	+								
Y. i. inconspicua	1102–4829*	+								+			+		+		+		+					+	+						
Y. enata	1135–2853*					+					+	+		+			+		+				+	+							
Y. o. obesa	1254–2886*	+									+	+		+				+		+				+							
Y. insculpta	1354–3301*								+		+	+			+		+		+						+	+					
Y. jeffreysi	1426–4802*				+						+	+				+	+		+							+	+				
Y. veletta	1440–2245	+									+	+		+				+		+	+										
Y. perplexa	1456–2076	+									+	+		+				+		+	+		+	+	+	+	+		+	+	
Y. lata	1491–2644*			+						+		+			+			+		+					+	+	+				
Y. bilanta	1546–2358	+									+	+		+				+		+		+					+			+	
Y. o. incala	1913–2170	+									+	+		+				+		+					+						
Y. sinuosa	1924–2076		+								+	+		+				+		+			+								
Y. i. africana	1964–3119*	+								+			+		+			+	+								+	+	+	+	
Y. i. profundorum	2041–5223*	+								+			+		+			+		+	+										
Y. biscayensis	2150–4820*		+								+	+			+			+	+						+						
Y. ovata	2487–2853*							+			+	+		+				+		+			+								
Y. fabula	2503–5223*	+									+	+				+		+	+		+		+	+	+	+	+	+	+		
Y. artipica	2514–2754*			+							+	+		+				+		+								+	+		
Y. extensa	2709*	+								+			+		+			+		+	+										
Y. blanda	2707–5223*		+								+	+		+				+	+		+										
Y. ella	2862–4829*					+					+	+		+			+			+		+		+	+		+		+		
Y. subcircularis	3250–5987*						+				+	+		+			+		+				+	+	+	+				+	
Y. americana	3806–5867*						+				+	+			+		+		+		+		+		+		+				
Y. similis	4559–4630*			+							+	+		+				+		+									+		

Abbreviations of the listed abyssal basins of the Atlantic are:- Ar, Argentine; Br, Brazil; Gy, Guyana; NA, North America; WE, West European; Ca, Canary; SL, Sierra Leone; Ga, Guinea; An, Angola; Ca, Cape; No, Norwegian.

* Species distributed to below 2500 m.

~ Single hindgut loop extending to the left side of body.

is further extended to three loops to the right and two to the left with one loop on each side short and anterior to the stomach. The latter is a configuration unique among protobranchs. In these relatively large rounded species the ligament tends to be relatively large and the hinge plates robust and elongate. Most of these species extend from the abyssal rise across the abyssal plain.

Comparison of this latter group with *Y. similis* is of interest. While *Y. similis* species has a double hind gut loop its anatomy is similar to *Y. artipica*. In particular it has small palps with a few broad ridges.

One species of *Yoldiella* remains to be mentioned. *Yoldiella fabula* differs markedly in its shell characters from all other species of *Yoldiella* (and *Portlandia*) yet in its internal morphology it is close to the basic stem group of the genus. Thus, while it is elongate with the umbo set far posterior to the mid-vertical line, it has relatively short separate hinge plates with a small amphidetic ligament. Very large subequal adductors are present and the hind gut is a simple, single loop to the right. Although its shell outline is unique, these characters fit best with the yoldiellids and we are presently persuaded to keep it within this subfamily.

In the foregoing discussion, stress has been placed on changes in the shape of the shell and the disposition of the gut. It is clear that for the most part species that occur at great depths have longer guts than those in shallow water and that this increased length has been accommodated within a small body space. This in turn relates to the digestive requirement to deal with sparse complex organics in deep-sea sediments. Indeed, in general the body space of deep-sea bivalves as a percentage of shell volume is significantly smaller than that of shallow-water congeners. Similarly, in regard to shell shape, species in shallower depths appear to be of an elongate-ovate shape, whereas those from the deep have higher shells which are either more rounded or have the greatest length measurement dorsal to the mid-horizontal plane. This we believe is related to the softness of the abyssal sediments and the ease of movement within them.

There are other evolutionary trends that may or may not be depth related. For instance, the size of the adductors clearly relates inversely to the strength and length of the hinge plates and the size of the ligament. In contrast, the size of the palps appears to increase with increasing depth range, while gills tend to reduce in size. We believe this is for a different reason from that of the change in shape of gut and shell, and relates in part to a difference of energy demand at high pressures and in part to the lack of importance of the protobranch gill in the feeding process. Because of this latter there is a reduction in the size of the gill, however, the loss in ciliated tissue is compensated by an increase in palp area which is required in order to maintain ciliary flow within the mantle cavity. At the same time it provides ciliary activity where is is most needed in the processing of fine abyssal sediments.

As might be expected the siphons also show modifications. Reduction in the gill area results in lower inhalent siphonal flow rates. In contrast, larger palp surfaces result in higher inflow via the feeding aperture. The processing of large quantities of fine sediment must produce increased numbers of faecal pellets. The predicted result from these changes is realized in the increased importance and size of the feeding aperture, the reduction and in some cases elimination of the inhalent siphon or the loss of division between exhalent and inhalent siphonal lumena such that the combined siphon is largely used for the passage of faecal material to the outside.

Finally, we speculate that not only that the small size of the body in comparison with the shell volume in the deep-water species is related to reduced food resources (as in reduced numbers of ova) but it is also related to the reduction of overall metabolic energy requirements at high pressures.

Like all protobranchs, the yoldiellids have large eggs and larval development is almost certainly short-lasting, nonfeeding and takes place close to the sea floor. Although there are subtle basinal differences in shell form, some of which may be sufficiently distinct to establish subspecies (e.g. *Y. obesa* and *Y. inconspicua*) there is little doubt that either widespread gene flow occurs and/or that genetic change is slow. Clearly, the yoldiellid form is one that is extremely successful. The subfamily contains by far the most species of all the protobranch families and subfamilies.

Much of the scientific discussion on the distribution of the Yoldiellinae will be incorporated into a following and final round-up paper on the diversity and zoogeography of the deep-sea protobranchs of the Atlantic. Nevertheless, because it is such a large group, the distribution of the 29 species of the genus *Yoldiella* described here reflect many of the general features of protobranch distribution. Thus, of the 29 species only a limited number can be regarded as being widespread (Table 3). Only six species are present in five or more of the Atlantic abyssal basins and of these, five are abyssal and one is lower slope/abyssal rise in its depth distribution. There are 16 endemic species, of these five species and one subspecies are restricted to the Argentine Basin. A further four endemic species are found in the Cape or Angola Basins. Thus, it is clear that most endemic species are in the South Atlantic. Furthermore, the South Atlantic has been much less sampled than the North and one would suspect that more rare endemic species will be reported in the future. This is clearly of considerable importance in speculations on the origin of the protobranch fauna of the Atlantic. Although endemic species are not restricted to upper slope depths, most of the species at upper slope depths are endemic and those few that are not, are restricted to the North European and North American Basins. Thus, in general, the deeper the species occurs, the more widespread is likely to be its distribution. This may simply reflect the fact that the abyssal plains contain enormous areas of sediment of similar characteristics and that distribution simply reflects the commonality of the environment.

REFERENCES

Allen, J.A. 1992. The evolution of the hindgut of the deep-sea protobranch bivalves. *American Malacological Bulletin*, **9:** 187–191.

Allen, J.A. & Hannah, F.J. 1986. A reclassification of the Recent genera of the sublass Protobranchia (Mollusca: Bivalvia). *Journal of Conchology*, **32**: 225–249.

Allen, J.A. & Hannah F.J. 1989. Studies on the deep-sea Protobranchia. The subfamily Ledellinae (Nuculanidae). *Bulletin of the British Museum (Natural History), Zoology*, **55:** 123–171.

Allen, J.A. & Sanders, H.L. 1973. Studies on the deep-sea Protobranchia, the families Siliculidae and Lametilidae. *Bulletin of the Museum of Comparative Zoology Harvard*, **145:** 263–310.

Allen, J.A. & Sanders, H.L. 1982. H.L. Studies on the deep-sea Protobranchia. The subfamily Spinulinae (family Nuculanidae). *Bulletin of the Museum of Comparative Zoology Harvard*, **150:** 1–30.

Allen, J.A. & Sanders, H.L. The zoogeography and diversity of the deep-sea protobranch bivalves of the Atlantic (in m.s).

Clarke, A.H. Jr. 1963. Arctic archibenthal and abyssal mollusks. Two mollusks dredged from drifting ice station Charlie (Alpha 2). *Bulletin, National Museum of Canada,* **185:** 90–109.

Jeffreys, J.G. 1876. Preliminary reports of the biological results of a cruise in H.M.S. 'Valorous' to Davis Straits in 1875. *Proceedings of the Royal Society of London,* **25:** 177–237.

Jeffreys, J.G. 1879. On the Mollusca procured during the 'Lightening' and 'Porcupine' Expeditions 1868–1870. Part II. *Proceedings of the Zoological Society of London, 1879:* 553–558.

Knudsen, J. 1970. The symstematics and biology of the abyssal and hadal Bivalvia. *Galathea Reports,* **11:** 241.

Locard, A. 1898. Mollusques Testaces. *Expeditions Scientifiques du Travailleur et du Talisman,* **2:** 1–515.

Ockelmann, K.W. 1955. The Zoology of East Greenland. Marine Lamellibranchiata. *Meddelelser om Grφnland,* **122:** 1–258.

Odhner, N.H. 1960. Mollusca. *Reports of the Swedish Deep-Sea Expedition 2, Zoology,* **(22):** 367–400.

Rhind, P.M. & Allen, J.A. 1992 Studies on the deep-sea Protobranchia (Bivalvia): the family Nuculidae. *Bulletin of the British Museum (Natural History)*, Zoology, **58:** 61–93.

Sars, G.O. 1878. *Bidrag til kundskaben om Norges artiske Fauna 1, Mollusca regionis articae Norvegiae.* 466 p. Christiana.

Sanders, H.L. & Allen, J.A. 1973. Studies on the deep-sea Protobranchia (Bivalvia): Prologue and the Pristglomidae. *Bulletin of the Museum of Comparative Zoology Harvard,* **145:** 237–261.

Sanders, H.L. & Allen, J.A. 1977. Studies on the deep-sea Protobranchia (Bivalvia): the family Tindariidae and the genus *Pseudotindaria. Bulletin of the Museum of Comparative Zoology Harvard,* **148:** 23–59.

Sanders, H.L. & Allen, J.A. 1985. Studies on the deep-sea Protobranchia (Bivalvia): the family Malletiidae. *Bulletin of the British Museum (Natural History), Zoology,* **49:** 195–238.

Shileiko, A.A. 1985. [The genus *Yoldiella* auct. as a combined group (Bivalvia, Protobranchia)]. *Transactions, P.P. Shirshov Institute of Oceanology,* **120:** 165–175.

Stasek, C.R. 1965. Feeding and particle-sorting in *Yoldia ensifera* (Bivalvia: Protobranchia), with notes on other nuculanids. *Malacologia,* **2:** 349–366.

Verril, A.E. & Bush, K.J. 1898. Revision of the deep-water Mollusca of the Atlantic coast of North America with descriptions of new genera and species. Part 1. Bivalvia. *Proceedings of the U.S. National Museum,* **20:** 775–901.

Warén, A. 1978. The taxonomy of some North Atlantic species referred to *Ledella* and *Yoldiella* (Bivalvia). *Sarsia,* **63:** 213–219.

Warén, A. 1980. Marine Mollusca described by John Gwyn Jeffreys, with the location of type material. *Conchological Society of Great Britain and Ireland Special Publication No. 1:* 1–60.

Warén, A. 1989. Taxonomic comments on some protobranch bivalves from the northeastern Atlantic. *Sarsia*: 223–259.

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