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BIOMÔR 3

The Thyasiridae (Mollusca: Bivalvia) of the British Continental Shelf and North Sea Oilfields

An Identification Manual

Thyasira sarsi

P. Graham Oliver & Ian J. Killeen
with contributions from
Kurt W. Ockelmann

With the Author's Compliments.

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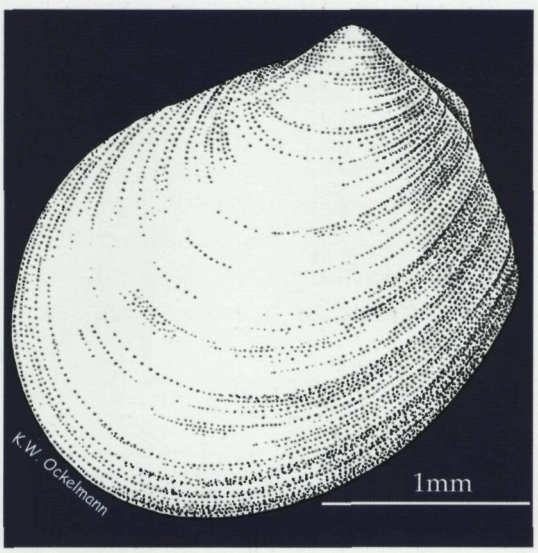

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Foreword

Over the last decade usage of the term biodiversity has exploded, triggered in part by the Convention on Biological Diversity and Edward O. Wilson's book "The Diversity of Life" both of 1992. Today, the word biodiversity is incorporated into the titles of all manner of local, national and international ecological studies and conservation initiatives. It is included in departmental names and is being embraced by the oil and other industries.

Fundamental to understanding biodiversity is the ability to distinguish different species. What we need is a Genetic Identification of Molluscs Probe – but until it is developed, we will continue to rely on keys, handbooks and papers to allow the identification of species.

There is a widely held perspective that European marine species are well known – and a European Register of Marine Species (www.erms.soton.biol.ac.uk) reassuringly lists everything down to species. However, probing a little deeper, the uncertainties and the lack of adequate identification tools are all too evident.

The International Council for the Exploration of the Sea 1980's synoptic survey of North Sea benthos found that one third of the most abundant 30 animals had identification problems associated with them, necessitating analyses based on multispecies taxa. Some of these difficulties have been resolved, generally through the efforts of individual systematists rather than any strategic biodiversity programme, but many remain – including the bivalve family Thyasiridae.

The Thyasiridae are speciose and ecologically important in both undisturbed and polluted systems. Many *Thyasira* species have symbioses with chemosynthetic bacteria and of particular applied interest is their role in promoting the recovery of organically enriched sediments through sulphide mining bioturbation. Enrichment of sediments may be natural e.g. through seaweed accumulation or seepage of methane, or caused by human activities such as the discharge of oily drilling wastes. Piles of oily drill cuttings exist beneath many oil production platforms in the central and northern North Sea and their long term fate and effects have recently been the subject of a £6million series of studies.

Unpublished results of a 1999 survey of the NW Hutton field cuttings pile provide an indication of the potential role of *Thyasira* species in the recovery of these polluted areas. In depth sectioned cores, *Thyasira sarsi* was present at densities of 1000-3000/m^2 and down to 5 to 6cm in cuttings material containing up to nearly 2% by weight oil. This scale of bioturbation must significantly influence the ability of oxygenated, sulphate rich seawater to penetrate into the cuttings and hence promote microbial degradation of hydrocarbons.

This identification manual represents a major advance. I hope it will serve as a stimulus and a catalyst to the production of similar works which will help to fill the yawning gap between a societal desire to document and protect biodiversity, and the availability of the tools needed for an assessment of the biodiversity status of an area.

But the ability to correctly identify *Thyasira* and related species is only the first step – it will then allow appropriate targeting of conservation efforts (for example, does *Thyasira gouldi* still require a UK Biodiversity Action Plan?). And there are many ecological questions outstanding, such as do small *Thyasira* species also contain chemosynthetic bacteria and if so, how do they compete for the sulphide resource with larger, deeper burrowing congeners - do they partition the resource by occupying the burrow walls of large organisms like *Nephrops* and *Calocaris*? Do the genetics of the species support the present systematic hierarchy and views on biogeographic distributions?

I strongly support the conclusion of the US National Research Council workshop report "Understanding Marine Biodiversity" (1995) which called for a "partnership between ecology and taxonomy, with a major focus on reinvigorating the field of marine taxonomy and systematics". This is manual is an example of such a partnership and is a pointer to the future.

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Abstract

Benthic biodiversity studies have become a frequent element of the environmental monitoring programmes related to the exploration for and extraction of oil and gas in the seas around the British Isles. This intense interest has highlighted some serious taxonomic deficiencies within the literature covering the bivalve family Thyasiridae. This study attempts to resolve this deficiency for those taxa living on the continental shelf and shelf margins of the North Sea.

Collections from 41 oil/gas fields were examined along with collections from museums and private individuals. From these collections twelve species were recognised: *Thyasira (Thyasira) flexuosa, T. (T.) polygona, T. (T.) gouldi, T. (T.) sarsi, T. (Parathyasira) equalis, T. (P.) granulosa, T. obsoleta, T. succisa, Axinulus croulinensis, Axinulus (Genaxinus) eumyarius, Mendicula ferruginosa, M. pygmaea.* A dichotomous key and tabular key are presented. All species are illustrated at all stages of growth. In addition, putative or doubtful taxa associated with the region are reviewed: *T. dunbari, T. subovata, Axinopsida orbiculata* and *Leptaxinus minutus.* The species and generic nomenclature is reviewed and the subgenus *Genaxinus* is introduced into the British nomenclature for the first time.

Crynodeb

Mae astudiaethau o fioamrywiaeth dyfnforol yn ymddangos yn aml bellach fel elfen o raglenni monitro amgylcheddol mewn perthynas â gweithgareddau archwilio ac alldynnu olew a nwy yn y moroedd o gwmpas Ynysoedd Prydain. Mae'r sylw manwl yma wedi amlygu gwendidau tacsonomig difrifol yn y llenyddiaeth sy'n ymdrin â'r teulu *Thyasiridae* o ddwygragenogion. Mae'r llyfr hwn yn ymdrechu i unioni hyn ar gyfer y tacsonau sy'n byw ar y silff gyfandirol ac ar ymylon silff Môr y Gogledd.

Archwiliwyd casgliadau o 41 maes olew/nwy, ynghyd â chasgliadau amgueddfeydd ac unigolion preifat. O'r casgliadau hyn, llwyddwyd adnabod 12 rhywogaeth :*Thyasira flexuosa, T.polygona, T.gouldi, T.sarsi, T. (Parathyasira)equalis, T. (P.) granulosa, T.obsoleta, T.succisa, Axinulus croulinensis, Genaxinus eumyarius, Mendicula ferruginosa, M.pygmaea.* Cyflwynir allwedd ddwyrannol ac allwedd dablaidd yma. Darlunir y rhywogaethau i gyd ar bob cam o'u tyfiant. Yn ychwanegol at hyn, adolygir tacsonau tybiedig neu amheus â gysylltir â'r rhanbarth: *T.dunbari, T.subovata, Axinopsida orbiculata.* Adolygir y gyfundrefn enwau generig a'r un ar gyfer y rhywogaethau a chaiff yr is-genws *Genaxinus* ei adnabod am y tro cyntaf o blith ffawna Prydain.

Contents

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Special thanks are due to Kurt Ockelmann not only for reviewing the manuscript but making much data and his illustrations available to this project. Kurt Ockelmann has been studying Thyasiridae since the late 1950's and has amassed much information not only on the taxonomy but on life histories and habits.

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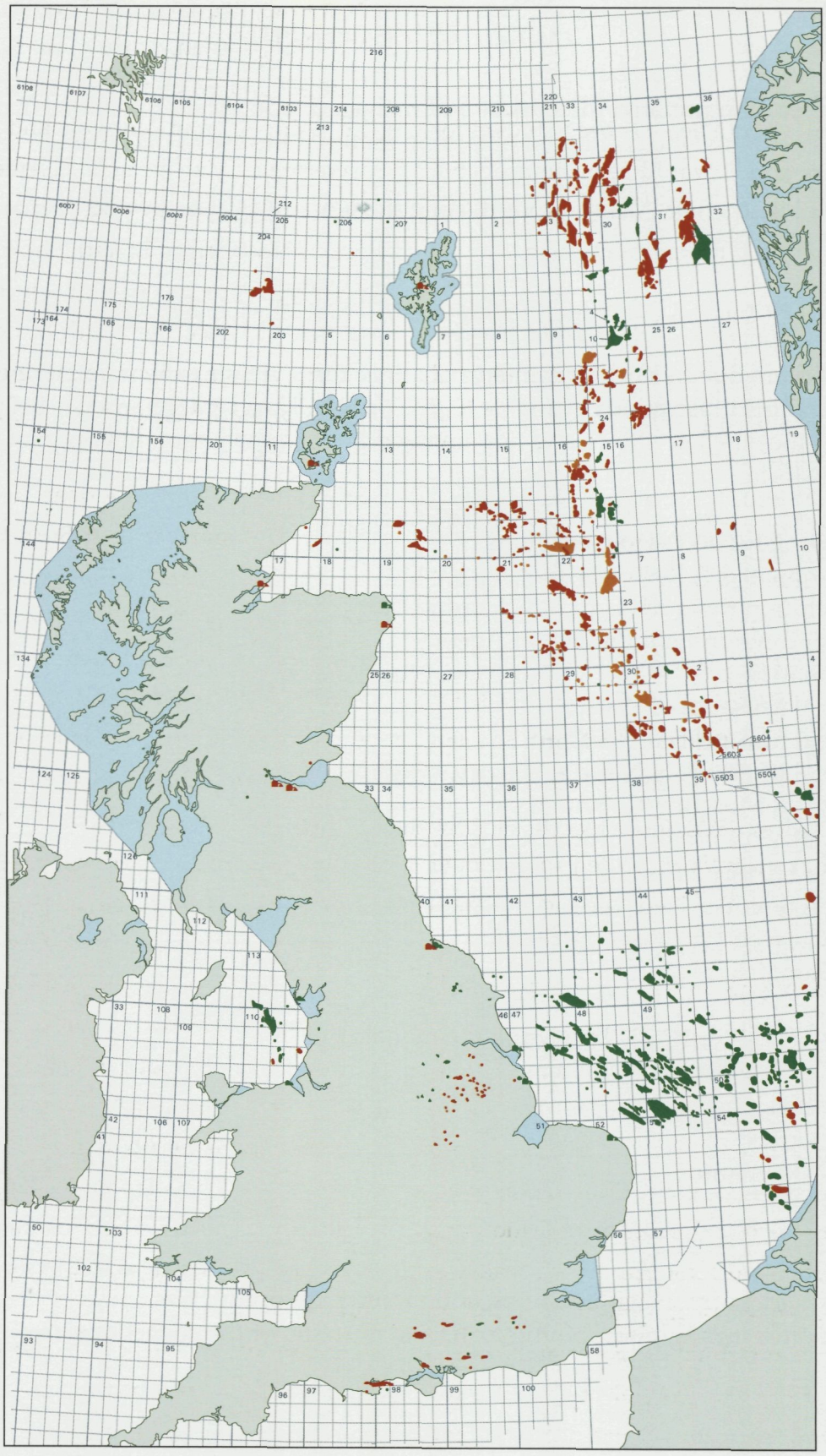


Figure 1. Distribution of oil (red), gas (green) and gas condensate (orange) fields in the North Sea and adjacent areas.

1. Introduction

Background

The fauna of the North Sea has been studied for over 200 years and it would seem improbable that taxonomic sufficiency had not yet been reached in, at least, the more studied groups such as the Mollusca. Yet in 1989 Eleftheriou & Basford were moved to report that for the Thyasiridae "even with the above type material specific identification proved impossible". Oil production platforms began to be installed in the North Sea in the mid 1970's, and a variety of benthic baseline and monitoring surveys were undertaken. Since then, benthic contaminant and ecological monitoring effort has been substantial with over 500 surveys conducted around UK oil and gas fields (UKOOA 1999). The current distribution of oil and gas fields in the North Sea and adjacent areas is shown in Figure 1. Seabed sampling for habitat assessment and environmental monitoring has recently extended into deeper waters to the west of Scotland. Benthic ecological (e.g. Künitzer et al. 1992) and environmental impact studies require extensive taxonomic support and it is evident that the available identification guides were insufficient when applied to the central and northern North Sea. The Thyasiridae are of particular interest because several species have chemosynthetic associations with sulphide oxidising bacteria (Southward 1986; Dando and Southward 1986) and some species are found in high numbers in areas of natural or pollution linked organic enrichment *e.g.* methane seeps (Dando et al. 1991 and 1994), oil spills (Kingston et al. 1995) and oily drill cuttings (Olsgard and Gray 1995).

The Thyasiridae is not an obscure family and has been recorded extensively over the years. During the latter half of the nineteenth century interest in the northern waters of the British Isles was high as evidenced in the "dredgings" of Jeffreys, Marshall, Jordan, Forbes and Norman. At this time M. and G. O. Sars described and reported Thyasiridae from Norway, and Verrill & Bush were similarly active in N. E. America. The twentieth century saw a waning of interest and taxonomy also declined, with the result that this northern fauna has never been comprehensively reviewed. When the North Sea oil explorations began, identifications of marine bivalves were based primarily on Tebble (1966), but only a few identifiers had access to the nineteenth century Scandinavian and American literature such as Sars (1878) and Verrill & Bush (1898). With the advent of the deep sea sampling programmes it was realised that many elements of the shallow boreal fauna underwent equatorial submergence and could be found as part of the shelf edge or upper slope faunas further south. Ockelmann, working on the fauna of Greenland (1958), brought both the pan-Atlantic nature of the boreal fauna and the consequent need to consider the work of Americans such as Gould and Verrill & Bush in the identification of British material, into recognition. Species originally described from America or the high latitudes started to appear in more recent Scandinavian literature e.g. Høisaeter (1986), but these new records were not accompanied by illustrations. Consequently, checklists such as Smith & Heppell (1991) gave ten *Thyasira* species from British shelf waters but there was no single source of illustrations or key to these.

Our understanding of the northern North Sea fauna needs to take account of :

- recognition of incompleteness of the British biodiversity inventory
- submergence of shallow water Scandinavian

	Field	Depth (m)	Co-ordinates	Sediment	Source/Code	Museum Accession No
1	Magnus	180-196	61°37'N, 01 o18'E		BP survey	NMWZ.1988.114
1	Magnus	180-196	61o37'N, 01 °18'E		OPRU 1979	NMWZ.1996.080
2	Block 211/12a (well)	186	61°36.47'N, 01 °15.71'E	Sand	ERT 96/062/1	NMWZ.2001.113
3	Thistle	165	61°21'N, 01 °35'E		OPRU 1988	NMWZ.1996.110
4	Murchison	150	61°23.77'N, 01 °44.43'E	Fine to medium sand	ERT 87/631	NMWZ.2001.092
4	Murchison	156	61°23.77'N, 01 °44.43'E	Gravelly sand	ERT 90/1057/2	NMWZ.2001.093
4	Murchison	150	61°23.77'N, 01 ° 4.43'E	Fine to medium sand	ERT 93/047/1	NMWZ.2001.101
5	Statfjord	145	61°12'N, 01 °48'E	Fine to medium sand	OPRU 1992	
6	Statfjord North		61°32'N, 01 °54'E		Aquanal	
7	Gullfaks	205-220	61°13'N, 02 °17'E	Medium sand	OPRU 1992	NMWZ.1996.065
8	North Cormorant	161	61°14.43'N, 01 °08.07'E	Sand	ERT 94/050/1	
9	Cormorant	150	61°10'N, 01 °06'E		ERT 91/125	NMWZ.2001.094
10	NW Hutton	145	61°06'N, 01 °19'E		Unicomarine 1999	
11	Brent South	140	61°04'N, 01 °43'E		ERT 94/050/3	NMWZ.2001.107
12	Strathspey	136-150	60°57'N, 01 °43'E	Fine to medium sand	ERT 91/190	NMWZ.2001.096
12	Strathspey	136-150	60°57'N, 01 °43'E	Fine to medium sand	ERT 94/032	NMWZ.2001.104
13	Lyell	150	60°55'N, 01 °14'E	Very fine sand	ERT 91/150/3	NMWZ.2001.095
14	Veslefrikk	180	60°47'N, 02 °53'E	Sand	ERT VFR50	NMWZ.2001.118
15	Alwyn	125	60°47'N, 01 °44'E	Fine sand	ERT 92/082A	NMWZ.2001.098
16	Troll	170	60°37"N, 03°50"E	Clay	Aquanal	
17	Dunbar	130-145	60°36'N, 01 °39'E	Very fine sand	ERT 92/082	NMWZ.2001.097
18	Beryl	120	59°34'N, 01 °32'E		OPRU1991	NMWZ.1996.028
19	Crawford		59°07.34'N, 01 °29.29'E	Very fine sand	OPRU 1991	
20	Block 16/3 (Braemar)	124–127	58°58'56"N, 01°28;57"E	Mud/Fine sand/Silt	(ex P Garwood)	
21	Brae	112	58°45'N, 01 °18'E		ERT MB1	NMWZ.2001.116
21	Brae	112	58°45'N, 01 °18'E		ERT MB59A	NMWZ.1997.055
21	Brae	112	58°45'N, 01 °18'E		ERT MB59C	NMWZ.2001.117
22	Miller		58°42'N, 01 °26'E		(ex P Garwood)	
23	Sleipner Vest	110	58°27'N, 01 °42'E	Very fine sand	OPRU	NMWZ.2001.047
24	Thelma	130	58°23'N, 01 °18'E		ERT 94/062	NMWZ.2001.110
25	Donan	140	58°22.48'N, 00 °50.43'E	Sandy mud	ERT BD6	NMWZ.2001.115
26	Beatrice	30-60	58°08'N, 03 °03'W		OPRU1982	NMWZ.1996.024
27	Cromarty	30-60	57°41'N, 04 °01'W		OPRU 1982	NMWZ.1996.040
28	SE of Ross (pock marks)	129	58°00.74'N, 00 °12.40'W		Ex Hartley	NMWZ.2001.046
29	S of Alba (pock marks)	140	57°59'N, 01 °09'E		Ex Hartley	NMWZ.2001.046

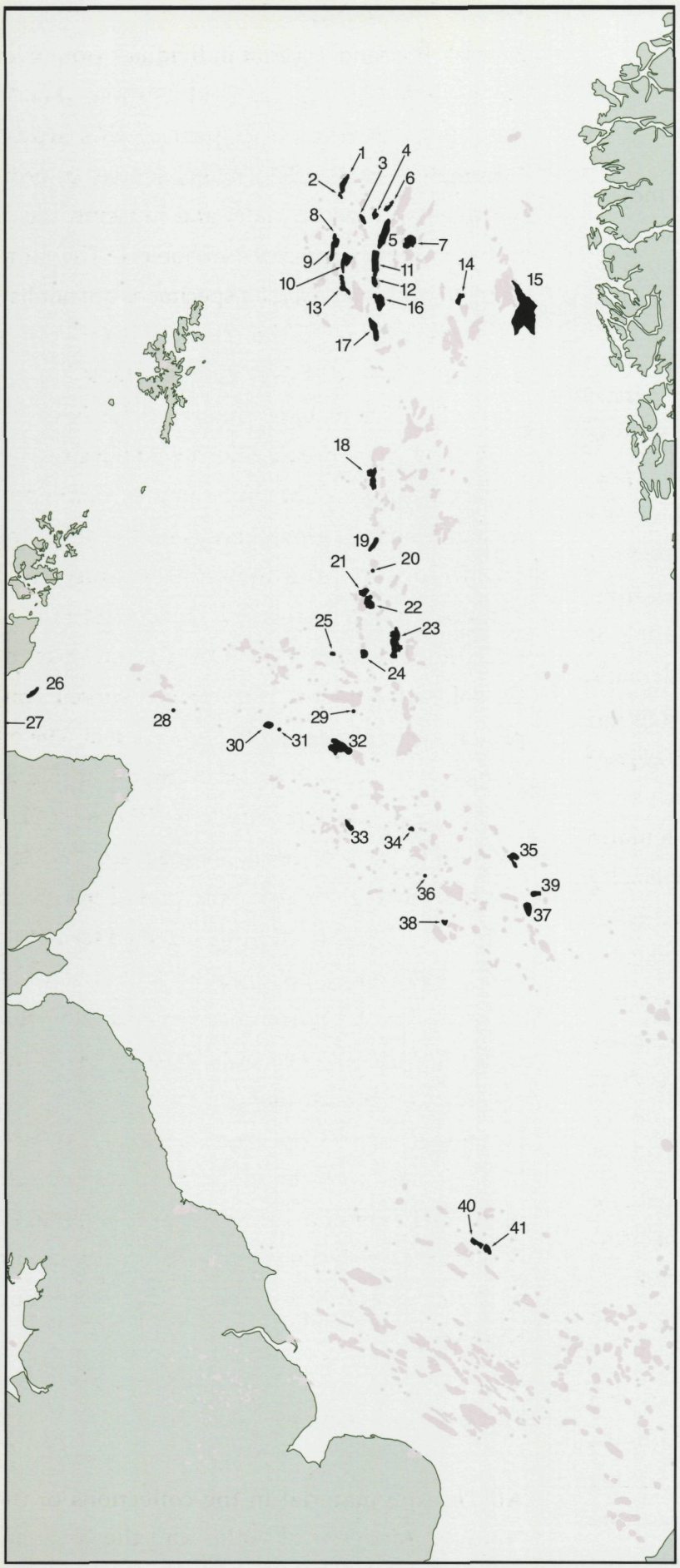
	Field	Depth (m)	Co-ordinates	Sediment	Source/Code	Museum Accession No
30	Buchan	129	57°54'N, 00 °02'E		OPRU 1988	NMWZ.1996.036
31	Block 21/1b (Single well)	115	57°51.85'N, 00 °07.56'E	Muddy sand	ERT 94/050/4	NMWZ.2001.048
32	Forties	90-100	57°43'N, 01 °02'E		OPRU 1982/84	NMWZ.1996.096
33	Gannet	95	57°12'N, 01 °00'E		ERT 94/050/2	NMWZ.2001.106
34	Heron	92	57°08.94'N, 01 °47.06'E	Muddy sand	ERT 94/050/5	NMWZ.2001.109
35	Gyda		56°53'N, 03 °05'E		OPRU 1992	NMWZ.1996.072
36	Single well Block 29/10	75	56°48.53'N, 01 °57.09'E	Muddy sand	ERT 96/213	NMWZ.2001.114
37	Ekofisk	65-70	56°32'N, 03 °16'E		OPRU	NMWZ.1996.052
38	Fulmar	85	56°29'N, 02 °01'E	Fine sand	ERT 92/151	NMWZ.2001.100
39	Magne	70	56°37'N, 03°28'E	Fine sand	ERT 92/126	NMWZ.2001.099
40	Murdoch	32	54°15'N, 02 °18'E	Fine to medium sand	ERT 93/047/3	NMWZ.2001.102
41	Caister	42	54°12'N, 02 °26'E		ERT 93/048	NMWZ.2001.103

Table 1. Oil and gas fields from which Thyasiridae material was obtained along with its location, depth, sediment type. Original source and museum numbers are also presented.

	Field	flexuosa	polygona	sarsi	equalis	granulosa	obsoleta	succisa	croulinensis	eumyarius	ferruginosa	pygmaea
1	Magnus						x	x	x		x	
1	Magnus						x	x	x			
2	Block 211/12a (Single well)			x	x		x	x	x			
3	Thistle			x			x	x	x		x	
4	Murchison								x		x	x
4	Murchison			x					x			x
4	Murchison	x		x			x	x	x		x	x
5	Statfjord	x		x			x	x	x			
6	Statfjord North	x					x	x	x			x
7	Gullfaks			x			x	x	x			
8	North Cormorant	x			x		x	x	x		x	x
9	Cormorant	x		x			x	x	x		x	x
10	NW Hutton			x			x		x		x	x
11	Brent South			x			x		x		x	x
12	Strathspey			x			x	x	x		x	x
12	Strathspey	x		x			x	x			x	x
13	Lyell			x			x	x	x			
14	Veslefrikk							x				
15	Troll					x				x	x	
16	Alwyn			x			x		x			x
17	Dunbar	x		x	x		x		x		x	x
18	Beryl	x		x	x		x		x		x	x
19	Crawford			x			x		x		x	
20	N of Brae (pock marks)				x		x					
21	Brae										x	x
21	Brae			x	x							
21	Brae			x	x		x		x		x	x
22	Miller			x	x		x		x		x	x
23	Sleipner Vest	x	x	x	x				x		x	
24	Thelma				x				x		x	x
25	Donan	x		x	x				x		x	
26	Beatrice	x										
27	Cromarty	x										
28	SE of Ross (pock marks)		x		x							
29	S of Alba (pock marks)				x							
30	Buchan				x						x	x

	Field	flexuosa	polygona	sarsi	equalis	granulosa	obsoleta	succisa	croulinensis	eumyarius	ferruginosa	pygmaea
31	Block 21/1b (Single well)	x	x		x				x		x	x
32	Forties	x	x	x	x				x		x	x
33	Gannet	x							x			x
34	Heron				x				x		x	x
35	Gyda	x										
36	Single well Block 29/10											x
37	Ekofisk	x										
38	Fulmar	x		x	x				x		x	x
39	Magne	x										
40	Murdoch	x										
41	Caister	x										

Table 2. Presence/ absence table for eleven species of Thyasiridae in North Sea oil and gas fields.



1 – Magnus
2 – Block 211/12a, well
3 – Thistle
4 – Murchison
5 – Statfjord
6 – Statfjord North
7 – Gullfaks
8 – North Cormorant
9 – Cormorant
10 – NW Hutton
11 – Brent South
12 – Strathspey
13 – Lyell
14 – Veslefrikk
15 – Troll
16 – Alwyn
17 – Dunbar
18 – Beryl
19 – Crawford
20 – pockmarks N of Brae
21 – Brae
22 – Miller
23 – Sleipner Vest
24 – Thelma
25 – Donan
26 – Beatrice
27 – Cromarty
28 – pockmarks SE of Ross
29 – pockmarks S of Alba
30 – Buchan
31 – Block 21/1b, well
32 – Forties
33 – Gannet
34 – Heron
35 – Gyda
36 – Block 29/10, well
37 – Ekofisk
38 – Fulmar
39 – Magne
40 – Murdoch
41 – Caister

Figure 2. Distribution map of the fields and well sites from which thyasirid samples were examined.

species with decreasing latitude

- pan-Atlantic north boreal species
- south-ranging circum-arctic species

Taking into account the above gives an indication of the total fauna likely to be encountered, but the Thyasiridae has issues that further complicated their taxonomy and led to the current state of confusion.

Original descriptions and illustrations are generally poor and have rarely been revised. Such is the case for the type of the genus *Thyasira*, *T. flexuosa* (Montagu, 1803) and as a consequence one can observe the ubiquitous use of this name for a wide variety of Recent and Cenozoic taxa from many parts of the world. Our understanding of those taxa described by Jeffreys is problematic because of confusion created by Jeffreys himself and the many years before modern type designations were published (Warén, 1980). Even so, a number of Jeffreys' taxa remain problematic because of the lack of type material especially relating to the varieties which were erected without full descriptions. Type material of species described by Philippi is apparently lost and neotypes have never been designated. Most recently the work of Payne & Allen (1991) has described the Atlantic deep sea thyasirid fauna, but in doing so has left many of the species which extend into the outer shelf and upper bathyal zones unresolved. The thyasirid shell has few discrete characters and these are often subtle in expression rendering identification difficult to the inexperienced eye.

The primary aim of this study is to produce a practical identification guide but in doing so much ground work had to be laid. The resulting discussions on nomenclature and taxonomy are placed in the appendices.

Material Examined

Several thousand *Thyasira* individuals from over 40 North Sea oil and gas field locations (Fig. 2) have been examined as part of this study. Information on the field name, source, co-ordinates, environmental data, and museum accession numbers is presented in Table 1. The numbers of individual *Thyasira* specimens are not listed, but the species composition on a presence/absence basis is shown in Table 2.

The bulk of the material from oil fields has been provided by two organisations who have carried out the analyses of benthic samples from environmental monitoring surveys on behalf of the oil producers: Environmental Resource and Technology Ltd, Edinburgh (ERT), and the Oil Pollution Research Unit (OPRU), now part of Cordah Ltd. We have also received survey samples from Unicomarine Ltd and Aquanal. The oil fields are generally sampled along linear or cruciform transects usually up to a distance of 5km away from the well head. Samples are collected using a Van Veen or Day grab, passed over a 0.5 or 1mm sieve and fixed in 4% buffered formaldehyde, followed by preservation in 70% alcohol. The samples of *Thyasira* made available for this study had either been bulked to represent all *Thyasira* from a particular survey, or bulked as all individuals of each species from a survey. Only in a few cases were the specimens supplied from individual sampling stations. All of this material is now in the collections at the National Museum of Wales (NMW) (See Table 1 for Accession Numbers).

We have also examined the following:

All *Thyasira* material in the collections of the National Museum of Wales and the National Museums of Scotland (NMS). The latter collection includes the material from the following:

research cruises of *RRS Challenger*, in deep waters to abyssal depths, between 1973 and 1991 under the direction of Dunstaffnage Marine Laboratory; cruises west of Shetland between 1996 and 2000 under the direction of the Atlantic Frontier Environmental Network (AFEN); sampling from the environmental impact assessment following the *Braer* oil spill off SE Shetland in 1995.

Samples of *T. gouldi* and *T. equalis* were obtained from the Zoological Museum, University of Copenhagen (ZMC).

Type material of *T. equalis, T. succisa, T. obsoleta, T. croulinensis* and *T. pygmaea* were borrowed from the National Museum of Natural History (USNM). Type material of *T. dunbari* was borrowed from the National Museum of Natural Sciences, Canada.

All thyasirid material from the private collection of Dr Shelagh Smith, Carlisle (SMSC) was examined.

All material of *T. flexuosa, T. polygona* and *T. gouldi* studied by Killeen & Oliver (2002a, b) has also been included in this study. Only localities are given but all material is available through the National Museum of Wales, National Museums of Scotland and the private collection of Dr. Shelagh Smith:

West Scotland: Firth of Clyde, Loch Fyne, Loch Sween & Loch na Cille, Firth of Lorn & Loch Spelve, Loch Etive, Loch Eil, Loch Creran, Loch Ailort, Loch Torridon, Loch Laxford, Loch Eriboll, Jura, ***Northern & Western Isles***: Isle of Lewis; Orkney, Water Sound; Shetland, Sullom Voe. ***East Scotland***: Cromarty Firth, Firth of Forth. ***North Sea***: from Magnus oil field (61°35'N to Caister gas field (54°12'N). ***Irish Sea and South West England***: Weymouth, Salcombe Falmouth, Milford Haven, St. Georges Channel, Cardigan Bay, Morecambe Bay.

In addition to the above material the contributions from Kurt Ockelmann are based on his examination of over 40,000 specimens representing 40 species

Abbreviations used in text

Institutional abbreviations: NMS, National Museums of Scotland; NMW, National Museum of Wales (pre-1970); NMW.Z National Museum of Wales (post-1970). RSMNH, Royal Museum of Scotland = National Museums of Scotland. SMSC, private collection of Dr. Shelagh M. Smith. ZMC, Zoological Museum, Copenhagen. USNM, United States National Museum.

Shell characters:

ar, anterior ridge; **as**, anterior slope; **au**, auricle; **lm**, lunule margin; **l**, lunule; **lig**, ligament; **pa**, posterior area; **pr**, posterior ridge; **ps**, posterior sulcus; **sn^1**, umbo-auricle marginal sinus; **sn^2**, marginal sinus; **sn^3**, posterior sinus; **sms**, submarginal sulcus; **LV**, left valve; **RV**, right valve.

Anatomical characters:

aa, anterior adductor muscle; **agt**, anterior glandular tissue; **agr**, anterior glandular ridge; **ct**, ctenidium; **dg**, digestive gland; **dt**, digestive tubules; **f**, foot; **id**, inner demibranch of ctenidium; **lp**, labial palps; **od**, outer demibranch of ctenidium; **pa**, posterior adductor muscle; **pgr**, posterior glandular ridge; **ppr**, posterior pedal retractor muscle; **r**, rectum

Morphology & Terminology

The shell (Plate 1)

The shells of the Thyasiridae are all rather similar in that they lack strong sculptural detail, are approximately ovate in outline and have poorly developed hinge structures. Consequently, iden-

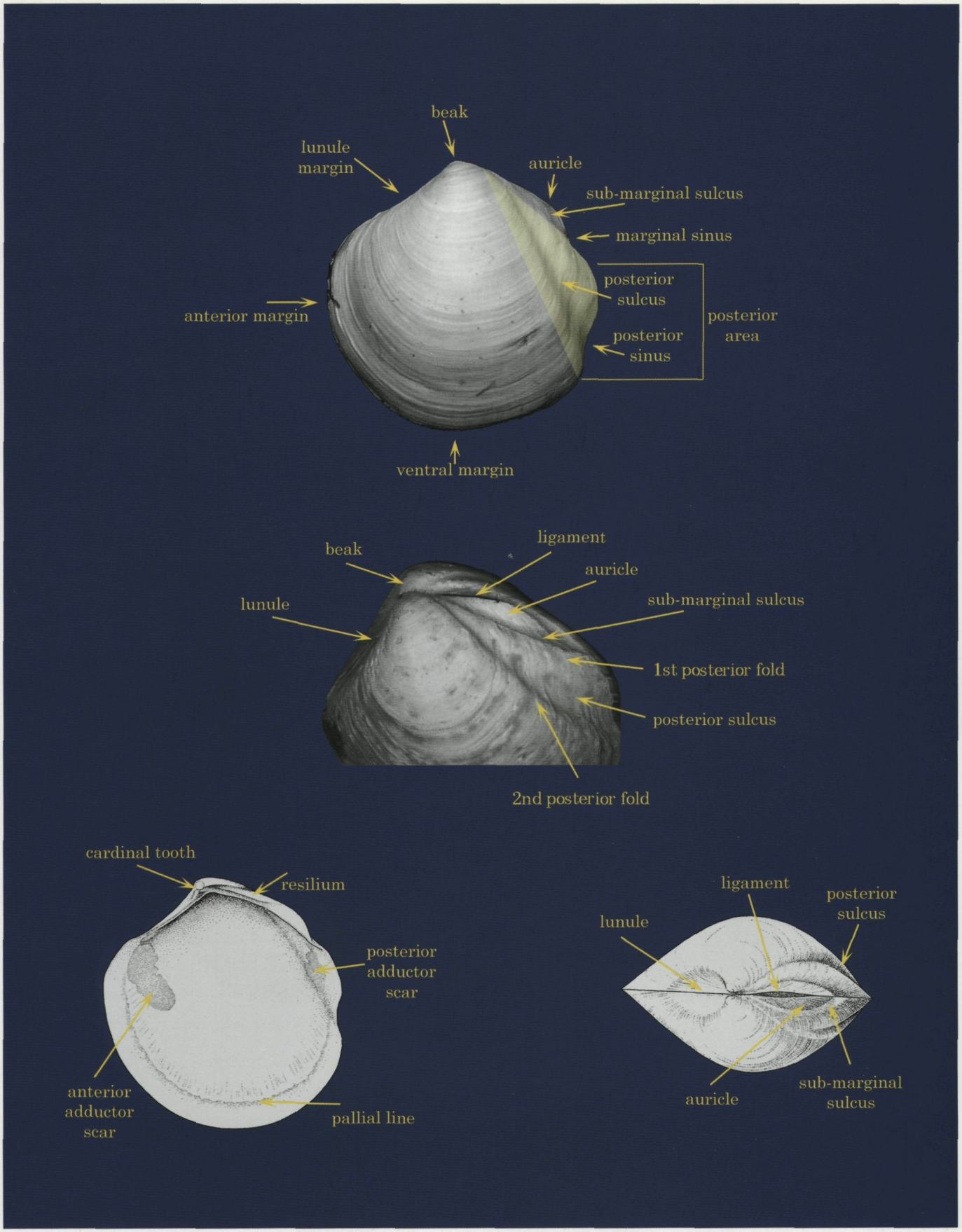


Plate 1. Structures of the thyasirid shell and the terminology used in the text.

tification relies on difference in shell outline and the form of the posterior and anterior areas. It is therefore important to understand the terminology used in defining these characters. We have compared Payne & Allen (1991) and Kauffman (1969) and mostly follow these. Where our terms differ we indicate those changes which have been made to simplify their understanding.

Outline in the Thyasiridae considered herein can be classified as follows (Fig. 3).

Equilateral – ovate: Beaks in the midline, height a little greater than length, lunule margin sloping, anterior rounded, ventral rounded, posterior curved but variously sinuate.

Equilateral – ovate-polygonal: Beaks in the midline, height a little greater than length; junctions of all margins well defined and posterior deeply sinuate.

Equilateral – subcircular: Beaks in the midline, height a little greater than or equal to length; posterior weakly sinuate.

Subequilateral – rhomboidal: Beaks a little to the anterior, height a little greater than or equal to length; anterior, ventral and posterior margins subacute

Equilateral – oval: Beaks in the midline, height a little greater than length; lunule margin and posterior dorsal margins short and not sloping, giving a more regular ellipse.

Inequilateral obliquely-ovate: Beaks behind the

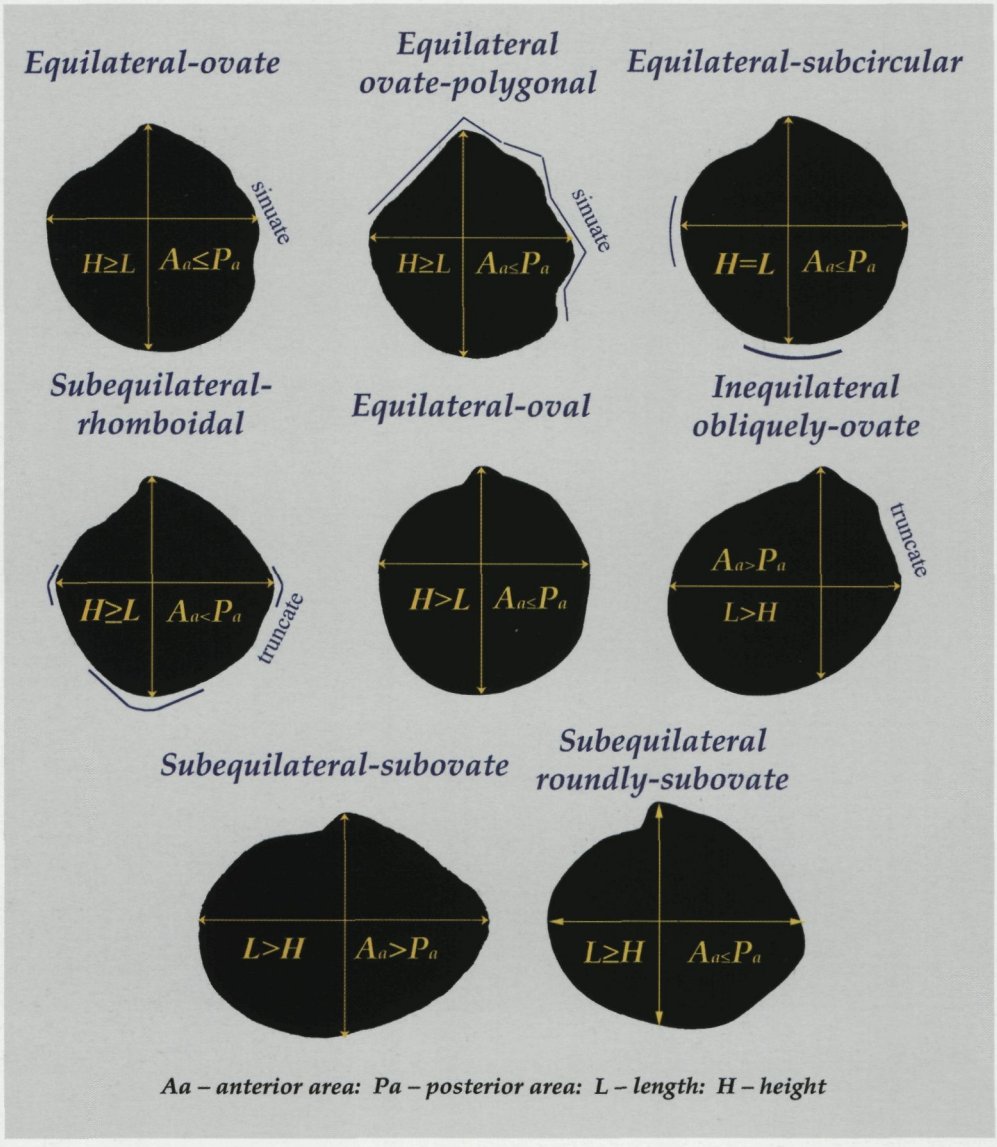


Figure 3. Lateral outlines of thyasirid shells, relative proportions and terminology as used in the text.

midline, anterior and ventrally expanded.

Subequilateral – subovate: Beaks behind the midline, anterior expanded laterally, posterior margin narrower than anterior margin.

Subequilateral – roundly subovate: Beaks just behind the midline, anterior expanded laterally, posterior margin narrower than anterior margin.

The posterior of the shell can variously express a complex of folds that can be defined as follows.

The **auricle** (posterior auricle of Payne & Allen, 1991) is a raised acute ridge formed from the posterior dorsal margins and encloses the **ligament**. It can vary in length and height. In highly umbonate shells there may be a shallow marginal sinus formed by the umbo and the auricle.

Bordering the auricle (if present), or ligament, there may be an incised line that can be developed further into a **submarginal sulcus** (referred to as SMS). This sulcus can extend down the posterior margin and borders the posterior area. The junction between the submarginal sulcus and the posterior area may form a sharp angled fold (**1st posterior fold**) or may be indistinct. The posterior area may be undefined, flat or sulcate, the latter termed the **posterior sulcus** (primary sulcus of Payne & Allen, 1991 & Kauffman, 1969). The junction between the posterior area and median area may be obscure or marked by a fold or ridge (**2nd posterior fold**), especially in those species with a prominent posterior sulcus.

The submarginal sulcus may cause an indentation in the marginal outline, the **marginal sinus** and similarly the posterior sulcus may cause a second indentation, the **posterior sinus**. In species with strong marginal and posterior sinuses the posterior outline may be termed **bisinuate** but when the marginal indentations are absent the posterior outline may be entire or more often **biangulate**. If there is a depression between the umbo and the auricle then the posterior outline in bisinuate shells will become **trisinuate**.

The lunule is, in most cases, poorly expressed but can be flat, medially elevated or depressed. The boundaries of the lunule are usually not defined except in one species where weak ridges are developed. The lunule margin as seen in lateral view may be sloped, quite steeply in most cases, but may be almost horizontal.

The hinge is poorly developed with a single cardinal tooth present in some species. The cardinal tooth is poorly formed and expressed as a rounded protuberance, a projecting flange or small peg. Its presence often is not consistent within some species and it may be eroded in aged specimens. Lateral teeth are absent, although lateral thickenings have been recorded from species not included herein.

The ligament is set in a sunken resilifer lying along the dorsal margin. It may easily be visible or if deeply sunken may be almost invisible from the external view.

The larval or embryonic shell, the prodissoconch, can be a useful character but is impractical to use for routine identificatipn where many specimens are present, and where the umbos are eroded. Prodissoconch size is a valuable character in separating *T. flexuosa* from *T. gouldi*.

Internal muscle scars are generally very obscure and offer no discrimination, with the exception of *A. eumyarius* where the adductor scars are thickened and raised.

Most species have some ferruginous deposit on the outer surface of the shell. It is concentrated around the anterior and posterior apertures. In one species the coating develops from an early stage and quickly envelops the entire shell. Only in *M. ferruginosa,* where the coating is consistently present, is this character valuable. *M. pygmaea, A. croulinensis, T. succisa* and *T. obsoleta* are frequently coated to some degree.

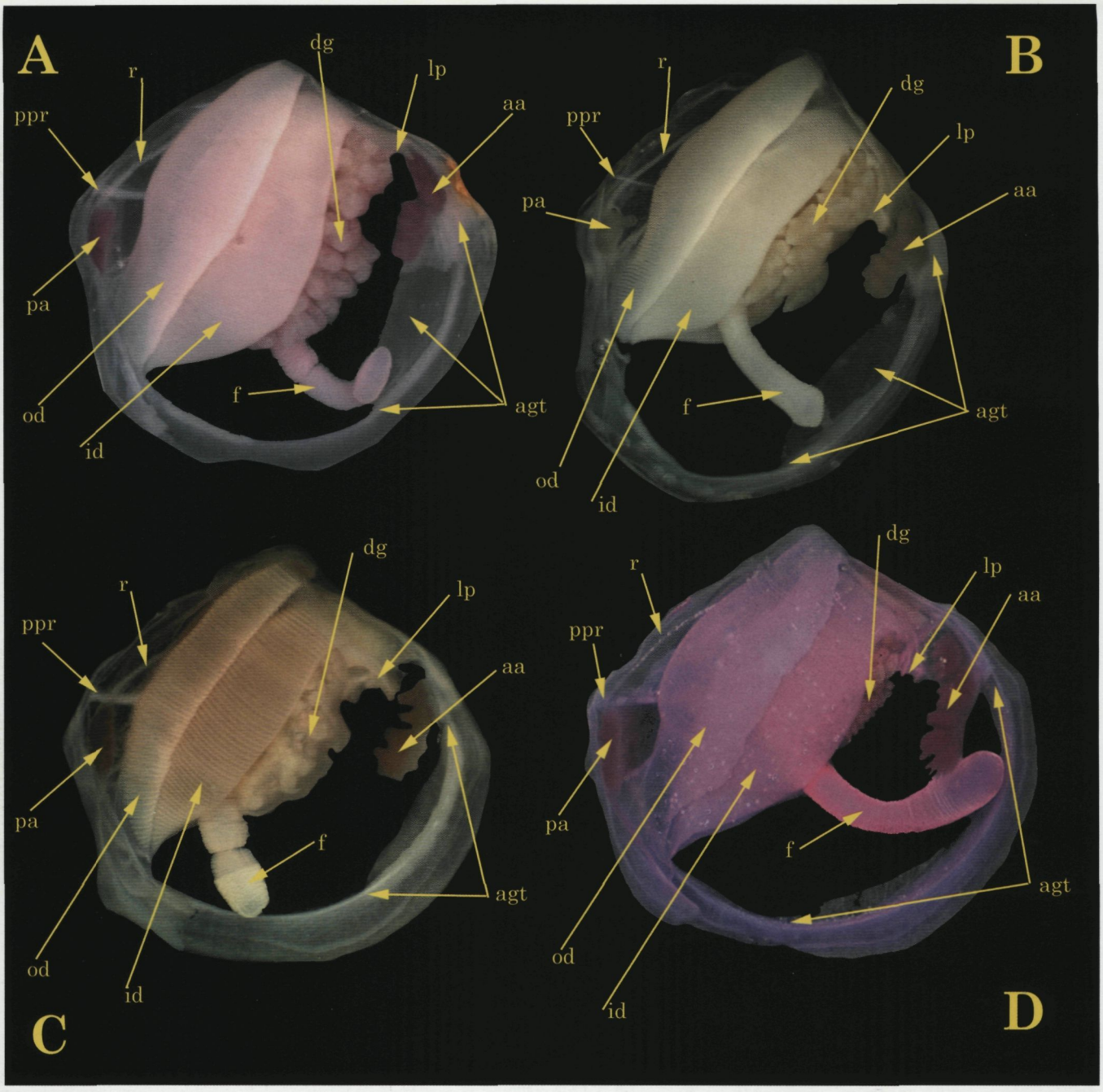


Plate 2. Gross anatomy of four species of Thyasiridae. **A**, *Thyasira flexuosa*. **B**, *T. polygona* **C**, *T. gouldi*. **D**, *T. sarsi*.
Abbreviations: aa, anterior adductor muscle; agt, anterior glandular tissue; dg, digestive gland tubules; f, foot; lp, labial palps; id, inner demibranch of ctenidium; od, outer demibranch; pa, posterior adductor; ppr, posterior pedal retractor; r, rectum.

Anatomy (Plates 2–3)

The Thyasiridae together with the majority of the Lucinoidea have a modified anatomy (Allen, 1958), related to nutritional dependence of many species on chemosymbiosis with sulphide oxidising bacteria located in the gills (Southward, 1986).

In the Thyasiridae the adductor scars are unequal in size with the anterior adductor larger and elongate rather than oval. The exception is *Mendicula*, where the adductor scars are more equal in size. The pedal retractor muscles are small and attached to the shell immediately dorsal of the adductors.

The foot is vermiform with a bulbous tip and is capable of considerable extension. The bluntly pointed tip is often demarcated by a ridge and there is rarely a developed heel.

The mantle is fused posteriorly to form an exhalant aperture beneath the posterior adductor. The

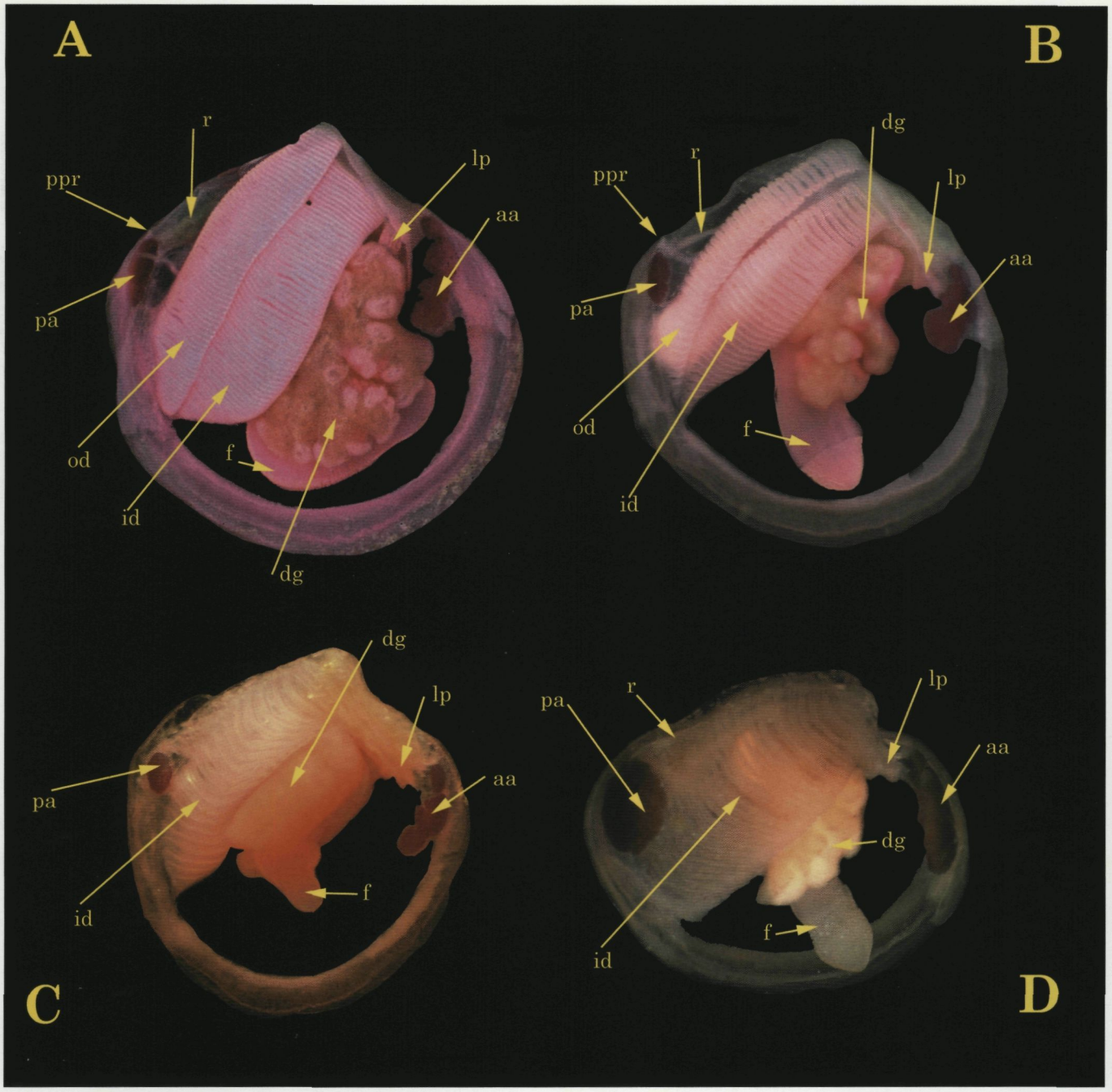


Plate 3. Gross anatomy of four species of Thyasiridae. **A**, *T. equalis*. **B**, *T. obsoleta*. **C**, *Axinulus croulinensis*. **D**, *Mendicula ferruginosa*.

Abbreviations: aa, anterior adductor muscle; agt, anterior glandular tissue; dg, digestive gland tubules; f, foot; lp, labial palps; id, inner demibranch of ctenidium; od, outer demibranch; pa, posterior adductor; ppr, posterior pedal tetractor; r, rectum.

ventral and anterior margins are not fused but can be adhered by ciliary junctions. The foot creates an inhalant aperture immediately below the anterior adductor and can also create feeding burrows at points along the ventral margin. The mantle adjacent to the anterior adductor is frequently modified by glandular tissue that can form a distinct ridge inside the anterior-ventral margin.

As many species are heavily reliant on chemosymbiotic nutrition the normal feeding and digestive structures are modified. The ctenidia (gills) can consist of both inner and outer demibranchs or the inner only. In those with both demibranchs the outer has much shorter filaments. The growth of the outer demibranch varies between species and this is important to taxonomy because it can give rise to confusion between small species which never develop the outer demibranch and juveniles of large species

Species	Outer demibranchs appear at shell length (mm)	Sexual maturity is reached at shell length (mm)
Thyasira flexuosa	0.9 – 1.0	3.5 – 4.0
Thyasira gouldi	1.3 – 1.5	3.0 – 3.5
Thyasira sarsi	0.9 – 1.0	4.0 – 5.0
Thyasira equalis	1.1 – 1.2	2.5 – 3.0 (Denmark)
		2.0 – 2.5 (W. Greenland)
Thyasira dunbari	1.6 – 1.7	2.5 – 3.0
Thyasira granulosa	1.7 – 2.0	–

Table 3. Sizes at which the outer demibranchs appear, and sizes at which sexual maturity is first reached, for six species of *Thyasira*.

which develop both demibranchs. Table 3 gives the sizes of shell at which the outer demibranch appears in six of the larger species of *Thyasira*.

The labial palps are poorly developed and sorting ridges are indistinct in most species. The digestive gland is usually contained in digestive diverticula within the body cavity but in the Thyasiridae there are pouched extensions either side of the foot. These pouches may be simple or greatly divided. The gut is simplified and a rectum, normally easily visible due to faecal pellets, is mostly seen as a pale thin apparently empty tube.

Anatomical features are a useful adjunct to species identification and those that are easily visible without dissection are the number of demibranchs, form of the foot, extent and development of anterior mantle glandular ridges and development of sorting ridges on the labial palps.

Ecology

All the species considered here live buried in mud or muddy sand in which they make three-dimensional burrow systems (Dando & Southward, 1986). Size for size they burrow deeply with the foot capable of extending up to 14 times the diameter of the shell (Kurt Ockelmann pers. comm.). The shell when fully buried is oriented with the beaks uppermost. The foot constructs an inhalant tube used to bring oxygenated water from the surface to the gills. This tube may be rather amorphous or take the form of a lined tube. There is no exhalant siphon and often no exhalant tube, the exhalant currents usually following the path of the burrow, as in *Mendicula pygmaea* (Fig. 4). In *T.*

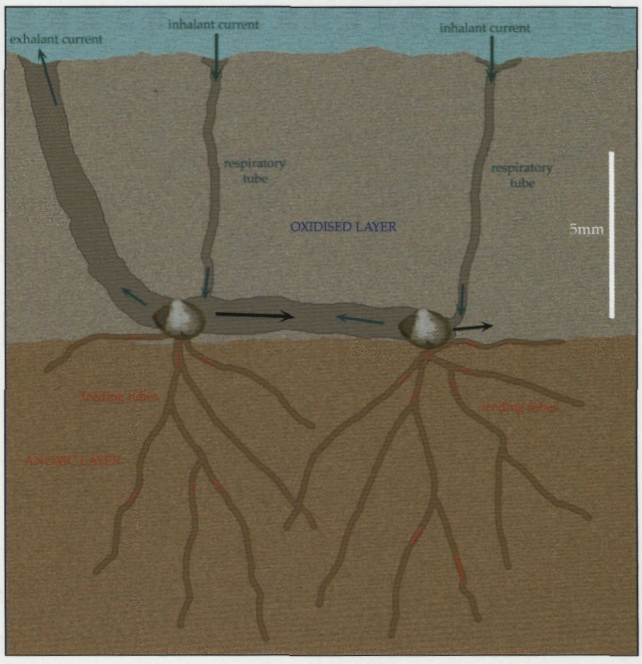


Figure 4. Mode of life of *Mendicula pygmaea*, redrawn from Ockelmann, pers obs.

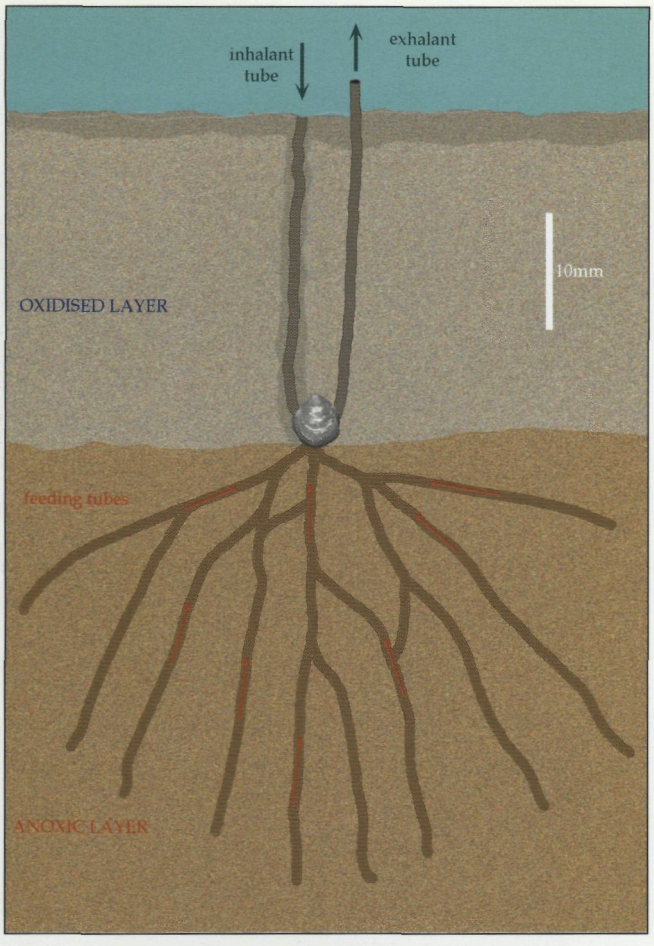


Figure 5. Mode of life of *Thyasira (Parathyasira) equalis,* redrawn from Ockelmann pers. obs.

(Parathyasira) equalis (Fig. 5) the foot also builds an exhalant tube and this frequently ends in a small chimney projecting above the sediment surface. It was originally believed that particulate food items were drawn in through the inhalant tube. A number of species are now known to be chemosymbiotic and with the use of micro-aquaria the ventral feeding tubes have been observed. The foot forms tubes in a radiating pattern into the sulphide or methane rich sediments. Water flowing into the mantle cavity brings the necessary nutrients to the bacteria held within the gills.

This mode of life explains the distribution of Thyasiridae and the occurrence of many in highly enriched sediments with an anoxic layer as well as in discrete habitats such as cold methane seeps and artificial sources of sulphide such as hydrocarbons originating from the offshore drilling operations.

Contents of the manual

Smith & Heppell (1991) list 19 species of Thyasiridae from British waters but this list includes species from slope and abyssal depths. In this study we recognise ten species from waters of the British contintal shelf and shelf edge, and include two more, *Axinulus eumyarius* and *Thyasira granulosa*, because they occur in the Norwegian sector of the North Sea and at upper slope depths on the British continental margin.
The taxa under detailed consideration are as follows:

Thyasira (Thyasira) flexuosa (Montagu, 1803)
Thyasira (Thyasira) polygona (Jeffreys, 1864)
Thyasira (Thyasira) gouldi (Philippi, 1845)
Thyasira (Thyasira) sarsi (Philippi, 1845)
Thyasira obsoleta (Verrill & Bush, 1898)
Thyasira succisa (Jeffreys, 1876)
Axinulus (Axinulus) croulinensis (Jeffreys, 1847)
Axinulus (Genaxinus) eumyarius (M. Sars, 1870)
Mendicula ferruginosa (Forbes, 1844)
Mendicula pygmaea (Verrill & Bush, 1898)

The nomenclature used here is slighlty modified from that of Smith & Heppell (1991) and is discussed in the "Nomenclature and Taxonomic History" section of this paper.

Some other species have previously been listed from shelf waters in the eastern Atlantic but are unconfirmed in the area of this study. We have illustrated two high latitude species *Thyasira dunbari* and *Axinopsida orbiculata* to avoid further confusion and because they may yet be encountered in British shelf or continental margin zones. *Leptaxinus minutus*, a species described from the western Atlantic, has been found in Norwegian fjords but has not yet been found in British waters although it yet may do so. *Thyasira subovata*, a deep water species, is also illustrated as it has been incorrectly identified from shelf waters off Iceland.
"Thyasira" subtrigona is not included because it is not a thyasirid but a *Kellia*. Records of this species from the North Sea are referable to *Mendicula pygmaea*.

The guide presents a tabular key and a dichotomous key supported by detailed descriptions and illustrations that include growth series.
In most species, shell morphology is variable and discrete characters are few. Identification is consequently difficult and constructing traditional keys using couplets is not entirely satisfactory. The dichotomous key must be used with reference to the illustrations with care taken when examining small species and juveniles of larger species.
The tabular key gives a visual comparison of typical examples of each species together with a set of distinguishing characters. Again, care must be taken when juveniles are present in the samples.
Given the range of variation and changes in shape with growth, the keys cannot be constructed to cover all variations. It is therefore necessary to refer to the plates of individual species and there can be no denying that the task of identification becomes less problematic with experience.

Dichotomous Key

see also Tabular Key, Pls 4–5

1 Shell outline inequilateral-subovate, longer than high. **2**

Shell outline ovate, oval or pyriform, height equal to or greater than length. **3**

2 Posterior outline rounded, entirely coated with a granular ferruginous deposit from early in growth. ***Mendicula ferruginosa***

Posterior outline pointed, never entirely coated ***Mendicula pygmaea***

3 Adductor scars elevated, visible through shell ***A. (Genaxinus) eumyarius***

Adductor scars not elevated **4**

4 Posterior bisinuate, posterior sulcus present **5**

Posterior truncate or angulate, posterior area not sulcate **8**

5 Outline subcircular, posterior sulcus and SMS very weak, ligament exposed with length more than 50% of shell length ***T. (Thyasira) sarsi***

Outline ovate, ovate pyriform or polygonal, posterior sulcus distinct, ligament more concealed with length less than 45% of shell length **6**

6 Outline polygonal and posterior trisinuate, posterior sulcus and SMS excavated with acute folds, auricle short and elevated. ***T. (Thyasira) polygona***

Outline ovate to ovate pyriform and posterior bisinuate, sulci distinct but folds rounded, auricle medium to long but not greatly elevated. **7**

Dichotomous Key

7 Outline variable from roundly ovate to ovate pyriform, SMS weak, auricle long, periostracum silky, prodissoconch < 200μm. *T. (Thyasira) gouldi*

Outline ovate, SMS distinct, auricle short, periostracum obscure, prodissoconch > 180μm *T. (Thyasira) flexuosa*

8 SMS long with acute margins, auricle absent **9**

SMS absent or if present then auricle also present **10**

9 Shell surface smooth. *T. (Parathyasira) equalis*

Shell surface granular *T. (Parathyasira) granulosa*

10 No auricle, no SMS, outline oval, dorsal margins almost horizontal *Axinulus croulinensis*

Auricle present, outline expanded anteriorly. **11**

11 Outline obliquely pyriform, auricle very short, SMS well developed, lunule depressed and bordered by low ridges, cardinal protuberance large. *T. succisa*

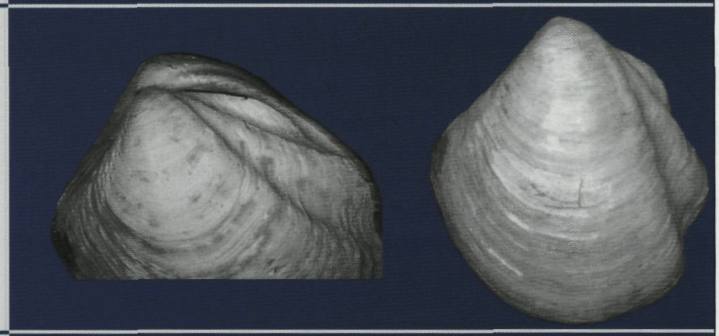
Outline obliquely ovate to pyriform, auricle indistinct but over 50% of indistinct SMS, lunule not depressed and lacking bordering ridges, hinge without teeth. *T. obsoleta*

Thyasira (Thyasira) flexuosa

Outline equilateral-ovate, posterior bisinuate.
SMS and posterior sinus distinct,
edges prominent. Lunule margin depressed.
Auricle weak to distinct, 1/2 length of SMS.
Ligament deeply sunken, half length of auricle.
Larval shell 162-177mm.

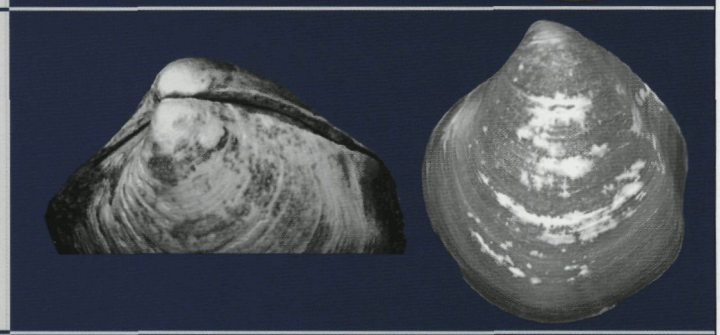
Thyasira (Thyasira) polygona

Outline ovate-polygonal, posterior
distinctly trisinuate.
SMS and posterior sinus strong,
edges acute. Lunule margin long.
Auricle high, 1/2 length of SMS.
Ligament deeply sunken, half length of auricle



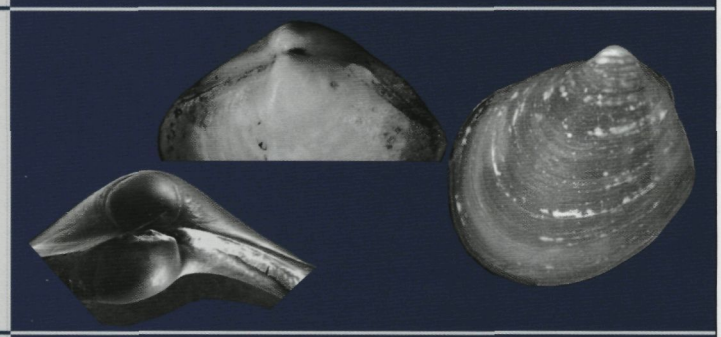
Thyasira (Parathyasira) equalis

Outline ovate-rhomboidal, subequilateral,
posterior weakly sinuate to truncate.
SMS strong, edge acute, posterior
flattened not sulcate.
Auricle absent. Sculpture smooth.
Paired demibranchs



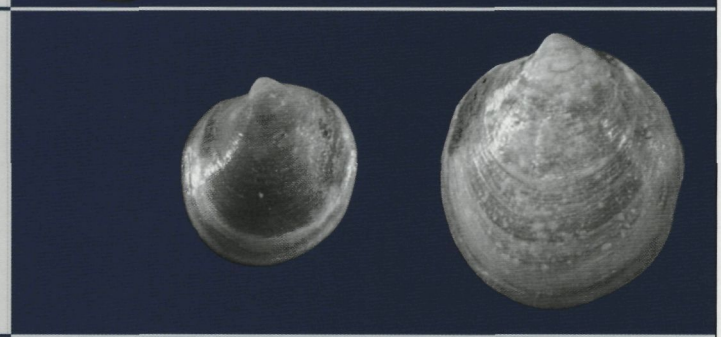
Thyasira succisa

Outline obliquely ovate, inequilateral,
anterior expanded, posterior truncate
SMS long, boundaries angled, posterior area
flattened.
Auricle prominent about 1/4 length of SMS.
Lunule depressedwith marginal ridges.
Hinge with single tooth and opposing socket.
Paired demibranchs.



Axinulus (Axinulus) croulinensis

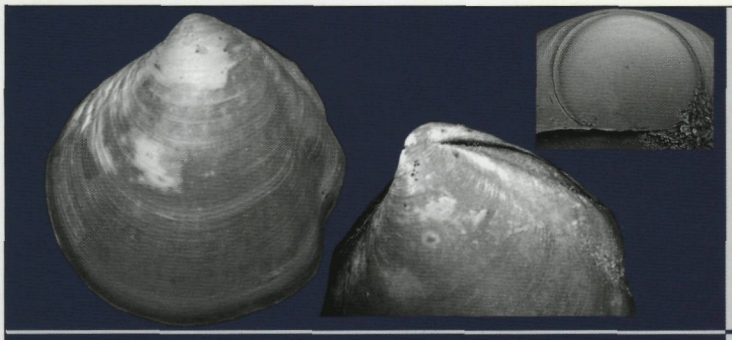
Outline oval, dorsal margins almost horizontal,
equilateral, posterior weakly angled to rounded.
SMS obscure to absent, posterior area poorly defined.
Auricle present as a weak crest.
Single demibranch.



Mendicula ferruginosa

Outline subequilateral roundly subovate, anterior
expanded, posterior rounded.
Lunule excavated with anterior umbonal notch.
Heavily coated with a ferruginous deposit
from early stages.
Single demibranch.

Plates 4–5. Tabular key to twelve species of Thyasiridae.



Thyasira (Thyasira) gouldi

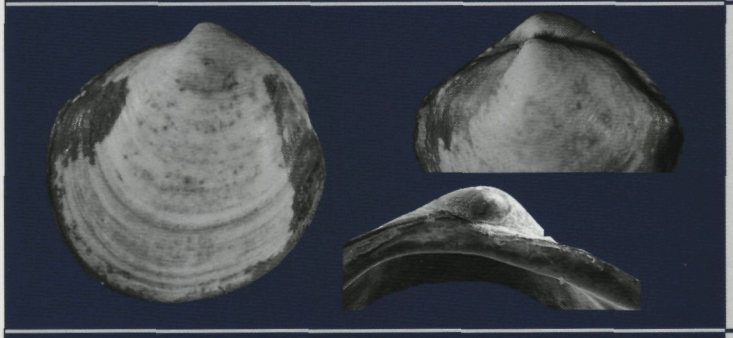
Outline equilateral-ovate, posterior bisinuate. SMS and posterior sulcus distinct, 1st and 2nd posterior folds rounded. Auricle prominent, over 1/2 of SMS. Ligment exposed. Larval shell 205 - 270mm.

Thyasira (Thyasira) sarsi

Outline equilateral-subcircular, posterior weakly bisinuate.
SMS and posterior sinus weak, edges obscure.
Auricle prominent, over 1/2 length of SMS.
Ligament exposed, visible along length of auricle.

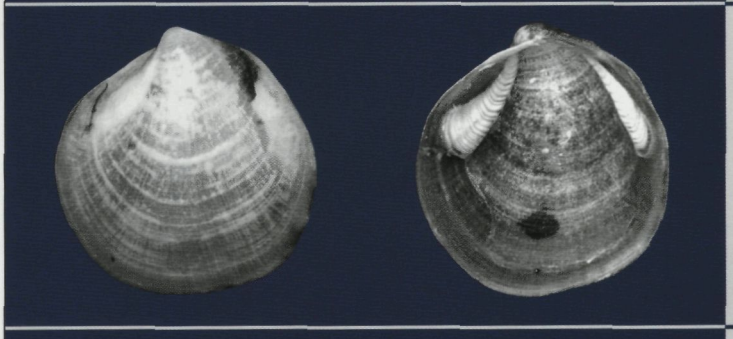
Thyasira (Parathyasira) granulosa

Outline ovate-rhomboidal shaped, posterior weakly sinuate to truncate.
SMS strong, edge acute, posterior flattened not sulcate. Lunule concave.
Auricle absent. Sculpture granulose.
Paired demibranchs



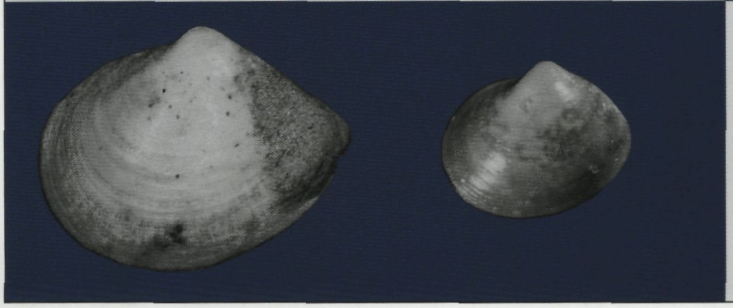
Thyasira obsoleta

Outline obliquely ovate, inequilateral, anterior expanded, posterior truncate
SMS weak, posterior area flattened.
Auricle about 1/2 length of SMS.
Lunule as a weak crest but some flattened, lacking boundary ridges.
Hinge without teeth.
Paired demibranchs.



Axinulus (Genaxinus) eumyarius

Outline equilateral-oval, posterior weakly angled.
SMS obscure to absent, posterior area slightly flattened.
Auricle present as a weak crest.
Adductor scars prominently raised and visible through shell.
Single demibranch.



Mendicula pygmaea

Outline subequilateral-subovate, anterior expanded, posterior pointed.
SMS and auricle not defined.
Single demibranch.

Plate 5.

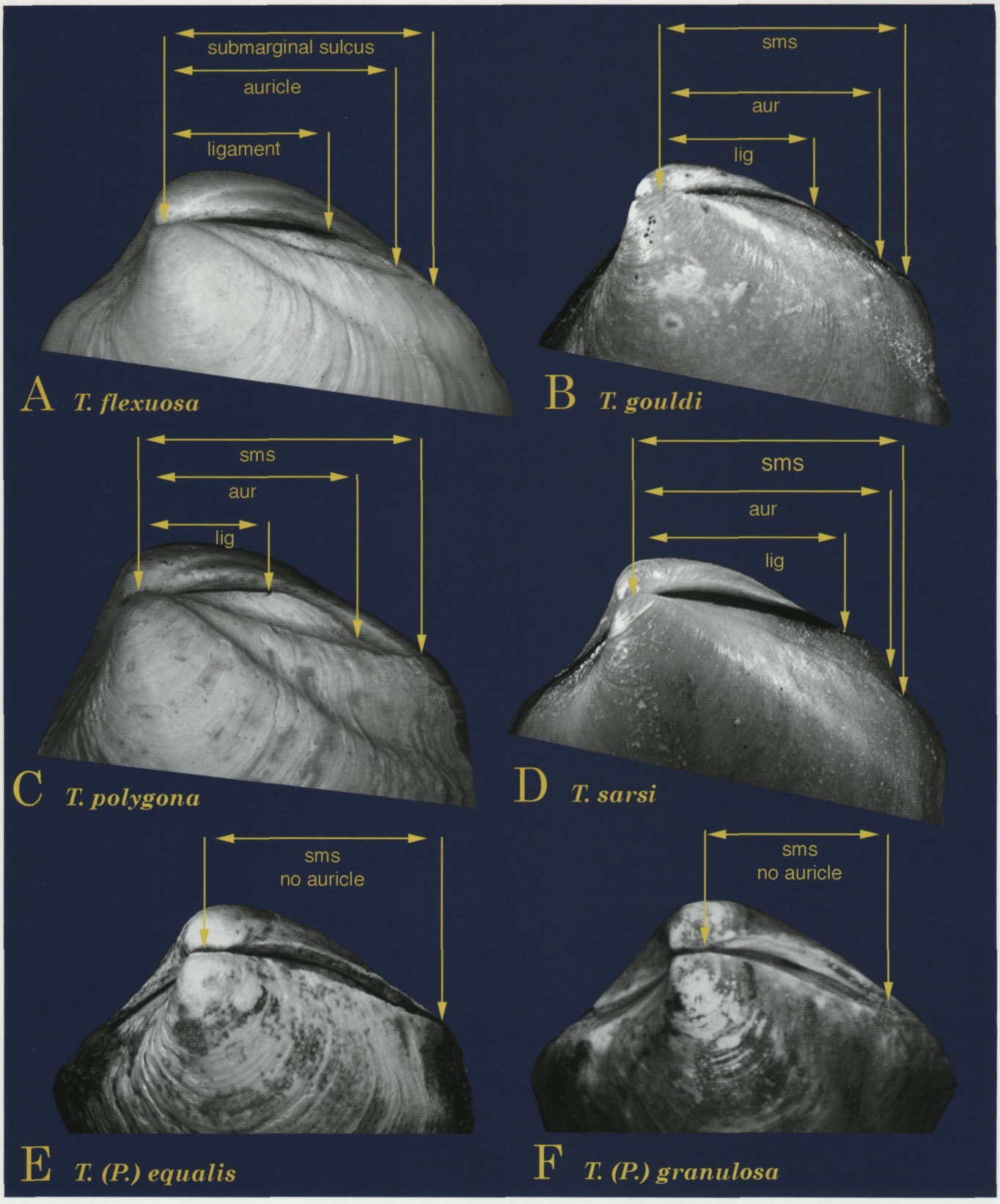


Plate 6. Oblique dorsal views of the shell of six species of *Thyasira* showing the comparative expression of the auricle, ligament and submarginal sulcus.

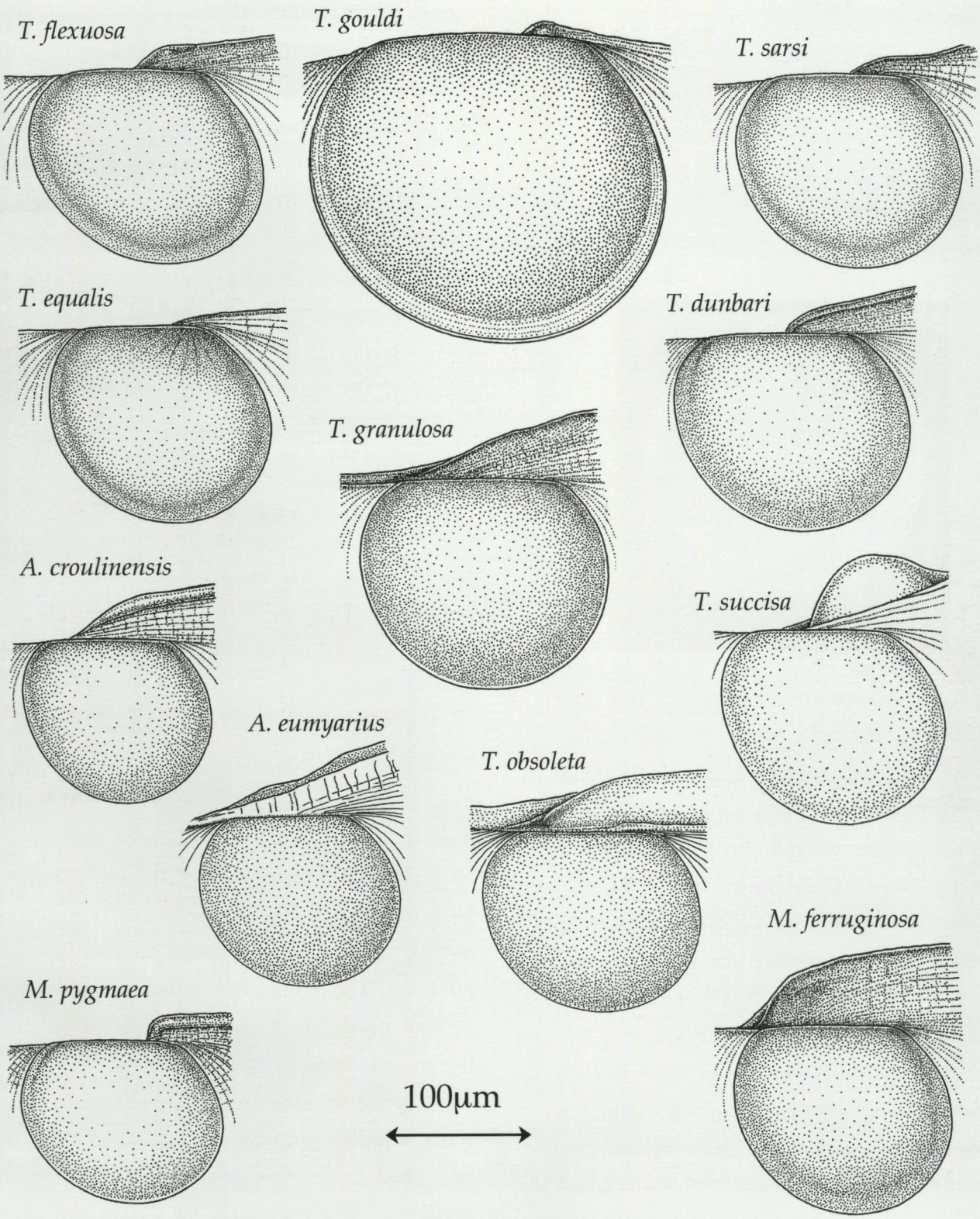


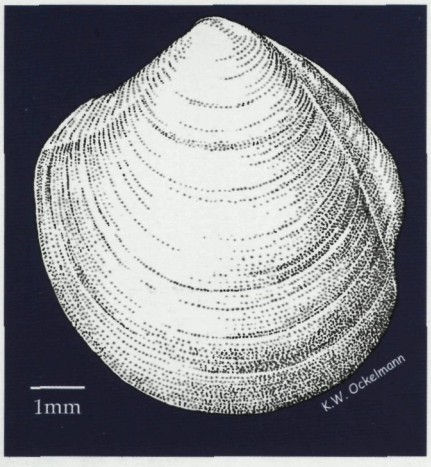
Figure 6. Prodissoconchs of twelve species of Thyasiridae. *All illustrations by K. W. Ockelmann.*

Species Accounts

Thyasira (Thyasira) flexuosa
(Montagu, 1803)

Plates 2A, 6A, 7 & 8, 9C–D, 10B

Tellina flexuosa Montagu, 1803: 72–73



Description: Maximum size, 12mm. Equivalve. Equilateral. Moderately tumid. Outline equilateral-ovate, umbos projecting, higher than long with prominent posterior folds and bisinuate posterior outline. Auricle projecting, poorly to distinctly demarcated, about 2/3 the length of the submarginal sulcus which itself is deeply excavated, ligament sunken about 1/2 the length of the auricle. The submarginal sulcus frequently forms a marginal sinus but always to a lesser extent than the posterior sinus. First posterior fold acute. Posterior sulcus well developed giving rise to a strong posterior sinus. Second posterior fold also prominent and subacute. Ventral margin rounded to narrowly rounded verging on being angulate. Anterior roundly angulate at junction with lunule. Lunule margin long, slightly concave. Lunule broad, weakly excavated. Umbo narrow, projecting.

Hinge weak with a single small cardinal tooth, in the form of flattened peg, in the RV. LV with a corresponding small depression below the beak. Sculpture of weak concentric lines and growth stops and frequently with irregular dents, weak ridges and other damage marks. Lunule rather smooth. Periostracum thin, often worn away, transparent over white, chalky shell.

Larval shell (Fig. 6.1) ranging in length from 162 – 177µm (measured shells from Norway & Denmark, N = 73).

Ctenidium with two demibranchs. Inside the anterior mantle margin there is a distinct thickened glandular ridge that runs to a point not quite at the middle of the ventral margin. Interior to this ridge the mantle is opaque but not thickened.

Growth changes: Juvenile shells up to 2mm in length are slightly inequilateral and expanded anteriorly. They exhibit strong posterior folds and can therefore be separated from similarly sized *T. obsoleta*.

Variations: The outline can vary from ovate to almost diamond-shaped, the latter almost as seen in *T. equalis*. This is primarily the result of variations in the curvature of the ventral margin from rounded to roundly angulate. The auricle is usually well developed but in some it is weakly elevated. These variations have no geographic pattern and can be found within samples.

Given Ockelmann's (1958) assertion that *T. flexuosa* is primarily Lusitanian/Boreal in distribution those samples from the very north of the North Sea, and close to the shelf edge (Stafjord, Sleipner, Cormorant, N. Cormorant and Murchison fields), were carefully examined. The prodissoconch size and form agree with *T. flexuosa* from further south.

Type locality: Falmouth Harbour, Cornwall.

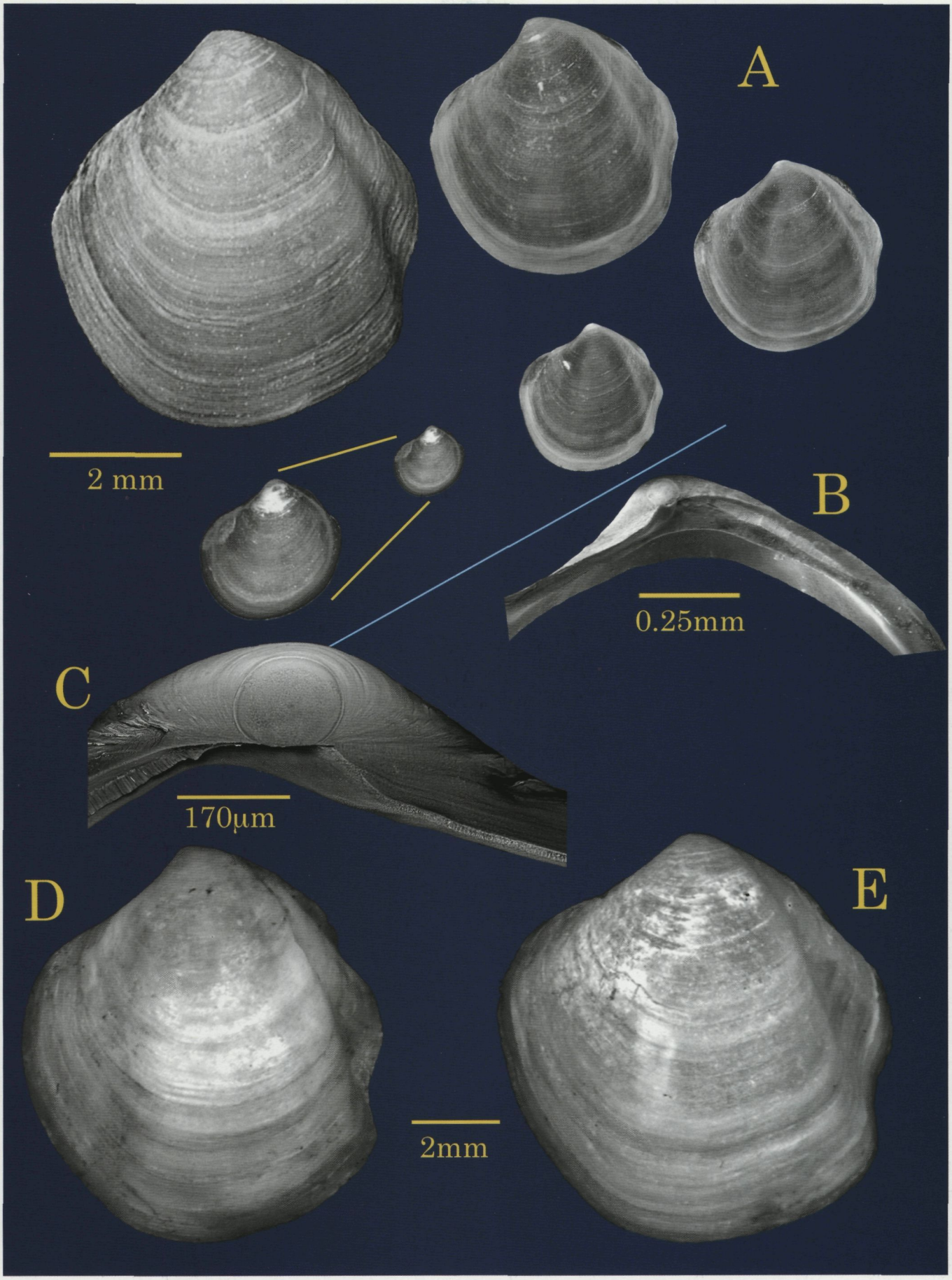


Plate 7. *Thyasira (Thyasira) flexuosa*. **A–C**, Irish Sea. **A**, growth series. **B**, hinge of RV. **C**, scanning electron micrograph of prodissoconch. **D**, Firth of Clyde. **E**, Falmouth, type locality.

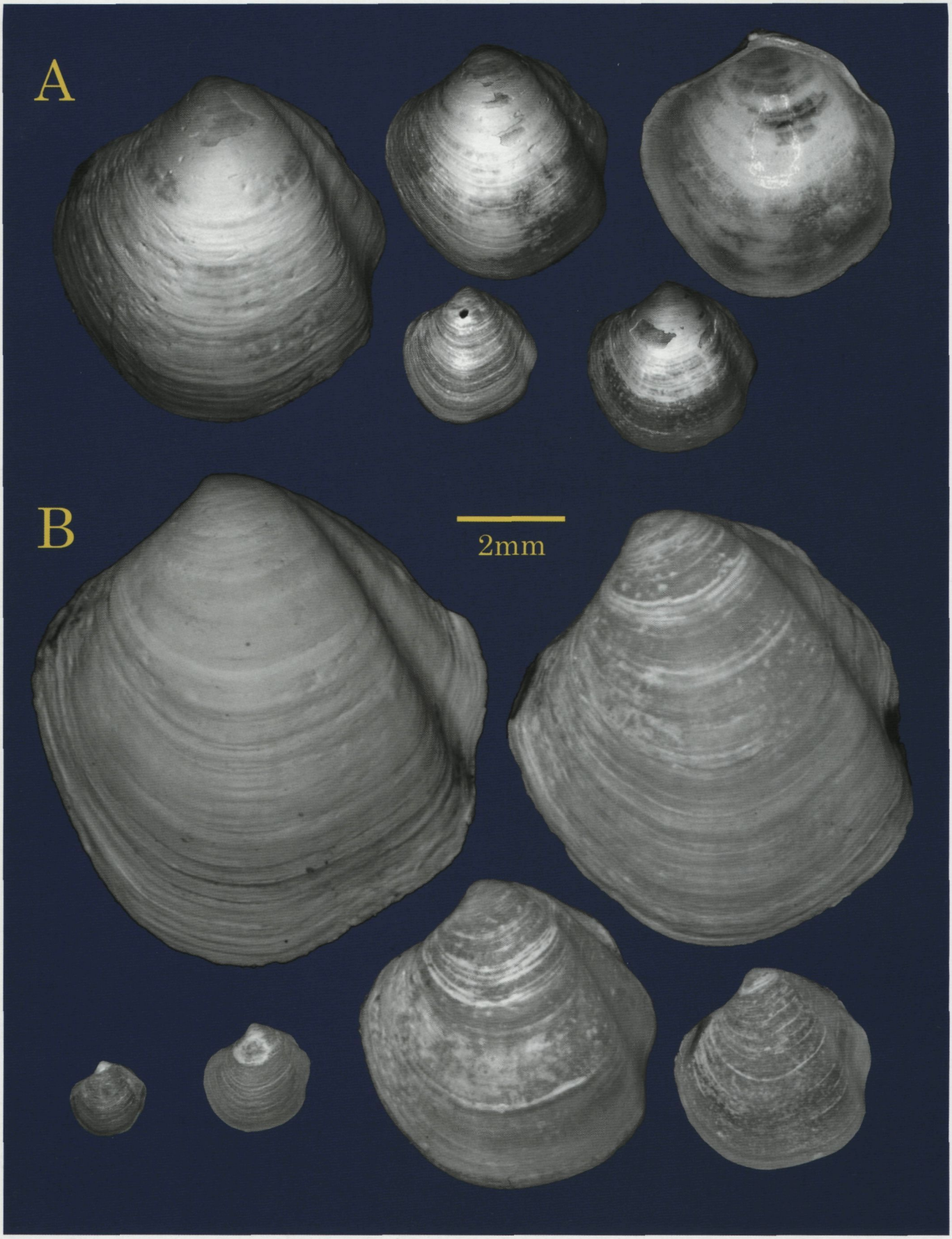


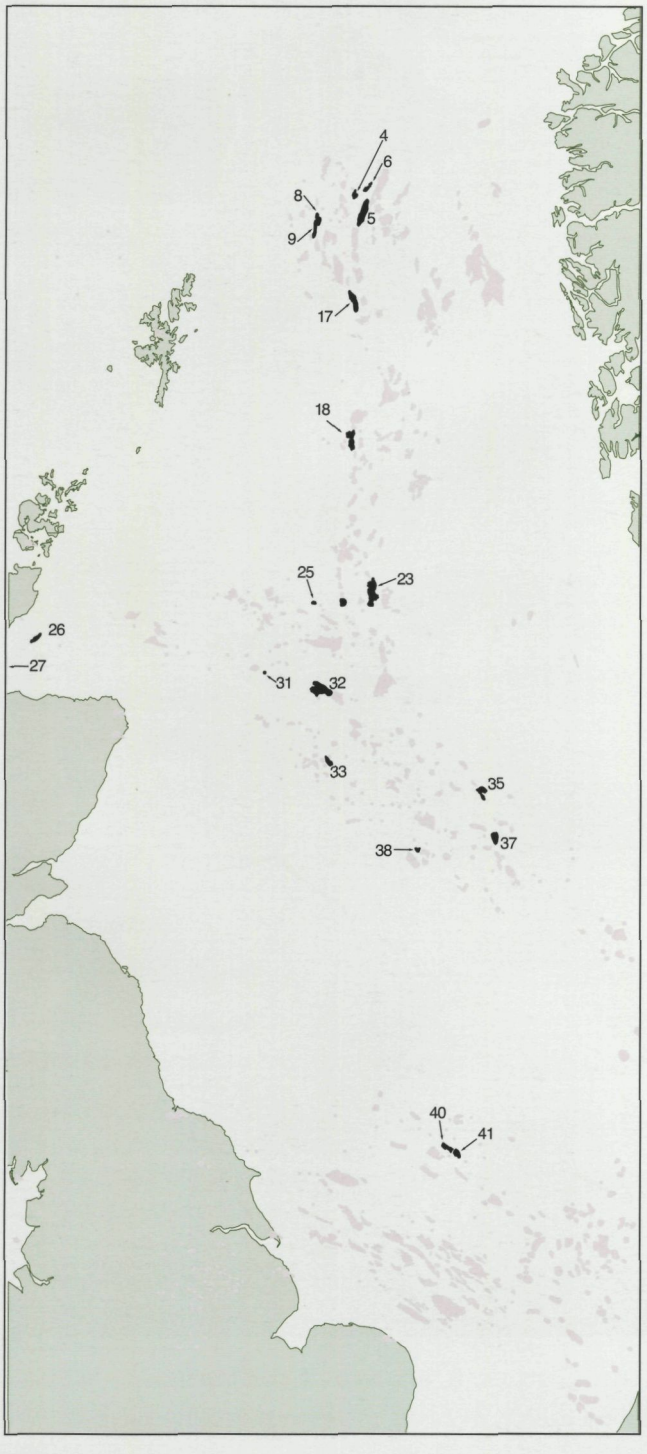
Plate 8. *Thyasira (Thyasira) flexuosa*. **A**, size series from Statfjord. **B**, size series from Murdoch.

Type material: None.

Remarks: The three species, *T. flexuosa*, *T. polygona* and *T. gouldi* have been confused in the past and continue to require careful examination because of the variability shown in outline and expression of the auricle.

Compared to *T. flexuosa*, *T. polygona* is trisinuate rather than bisinuate, has a longer and less concave lunule margin, an auricle which is always strongly elevated and sharper posterior folds.

The bisinuate form is characteristic of both *T. flexuosa* and *T. gouldi* but most *T. gouldi* shells have a longer auricle, rounded posterior folds, and weak submarginal and posterior sulci. However, some shells are more sinuous and reference to the larval shell is the most diagnostic character. In T. *gouldi* it is not only much larger (over 200μm) but is raised and easily visible at low magnifications. Anatomical and sperm structure data confirm the separate specific status of *T. flexuosa* and *T. gouldi* (Blacknell, 1973)



Map 1. Distribution of *Thyasira flexuosa* in North Sea oil fields.

Distribution: This species occurs sporadically throughout the North Sea oil fields, and is the only *Thyasira* recorded in the oil and gas fields to the south of Fulmar (56°30'N). Depth range, 32m (Murdoch) to 161m (North Cormorant). Elsewhere, *T. flexuosa* is recorded from almost all British and Irish-based Sea Areas (Seaward 1990).

Thyasira (Thyasira) polygona
(Jeffreys, 1864)

Plates 2B, 6C, 9A–B, E–H

Axinus flexuosus var. *polygona* Jeffreys 1864: 248

Thyasira polygona (Jeffreys) – Killeen & Oliver, 2002a: 383-389

Description: Shells to 9mm in height. Outline polygonal, umbos narrow, pointed. Posterior margin strongly trisinuate, first sinus (sn^1) formed by slope of umbo and auricle, second (sn^2) by the auricle and submarginal fold and third (sn^3) by the posterior sulcus. Anterior angulate, lunule margin straight, very long, reaching almost to the mid point and sloping steeply, anterior ventral margin curved, some slightly angulate at ventral extremity. Auricle prominent, raised posteriorly. Submarginal sulcus and poste-

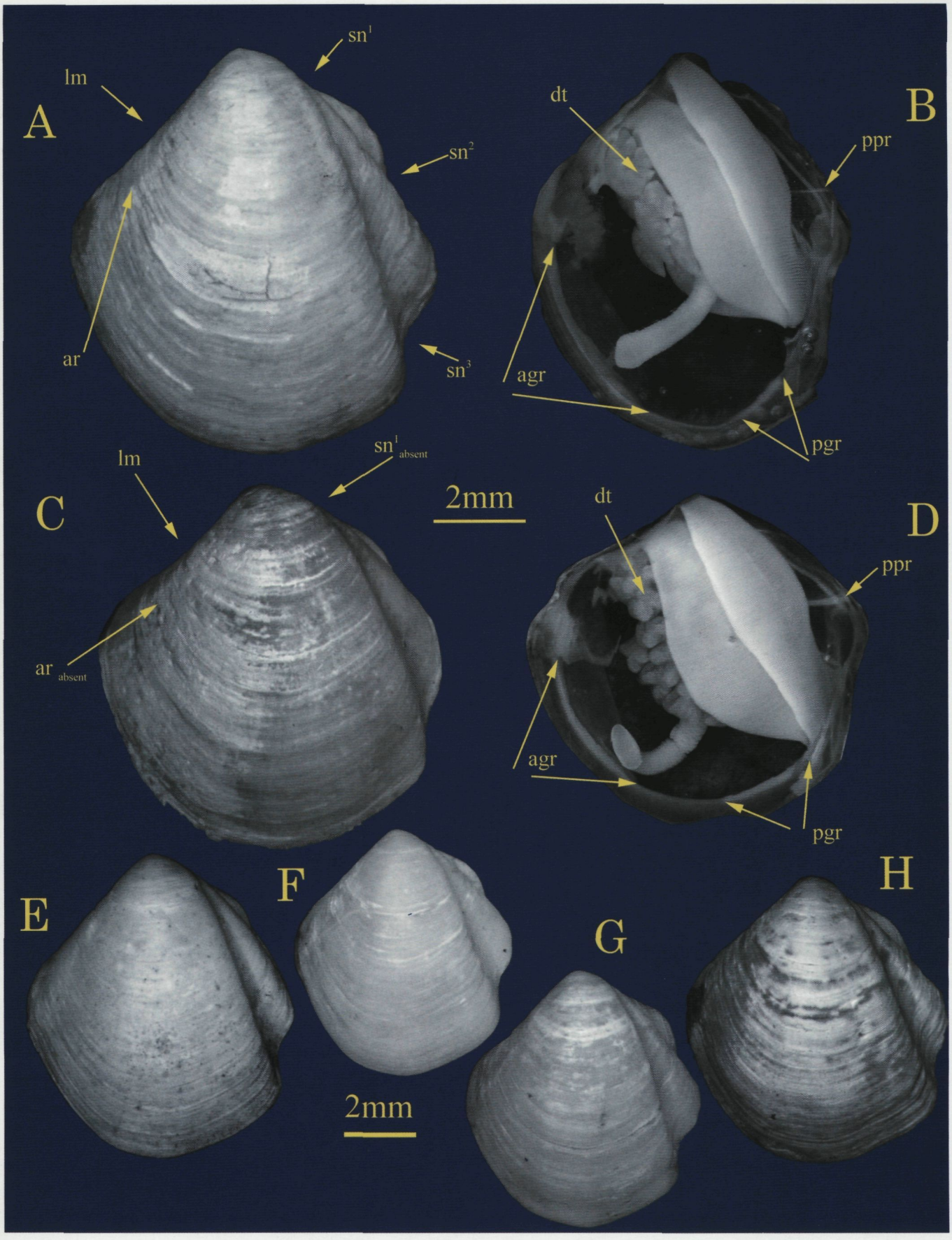


Plate 9. **A–B, E–H,** *Thyasira (Thyasira) polygona*; **A,** LV from Forties. **B,** anatomy from Forties. **E,** Gairloch. **F,** Sound of Jura. **G,** Firth of Lorn. **H,** North Sea, Block 21/1b.
C–D, *T. (T.) flexuosa*, LV and anatomy from Murdoch.
Abbreviations: agr, anterior glandular ridge; ar, anterior ridge; dt, digestive tubules; lm, lunule margin; pgr, posterior glandular ridge; ppr, posterior pedal retractor; sn^1, first posterior sinus; sn^2, marginal sinus; sn^3, posterior sinus.

rior sulcus very strong and demarcated by sharply angled folds, narrow anterior slope flattened, demarcated by a faint ridge (ar).
Hinge weak with a small or obsolete cardinal tooth. Muscle scars indistinct.

Larval shell size unknown, no specimens with uneroded beaks were available for this study.

Adductor muscles strongly different in size, anterior elongate, posterior small and rounded. Pedal retractor muscles very weak, the posterior almost thread-like and attached well above the adductor. Anterior inner mantle edge with a narrow thickened glandular ridge extending to a point in line with the beak; inside a weakly opaque area is present; a small but less developed posterior glandular ridge is present. The gills are composed of both inner and outer demibranchs neither especially thick and with the filaments clearly visible. The digestive tubules are deeply divided and terminate in pointed finger like tips.

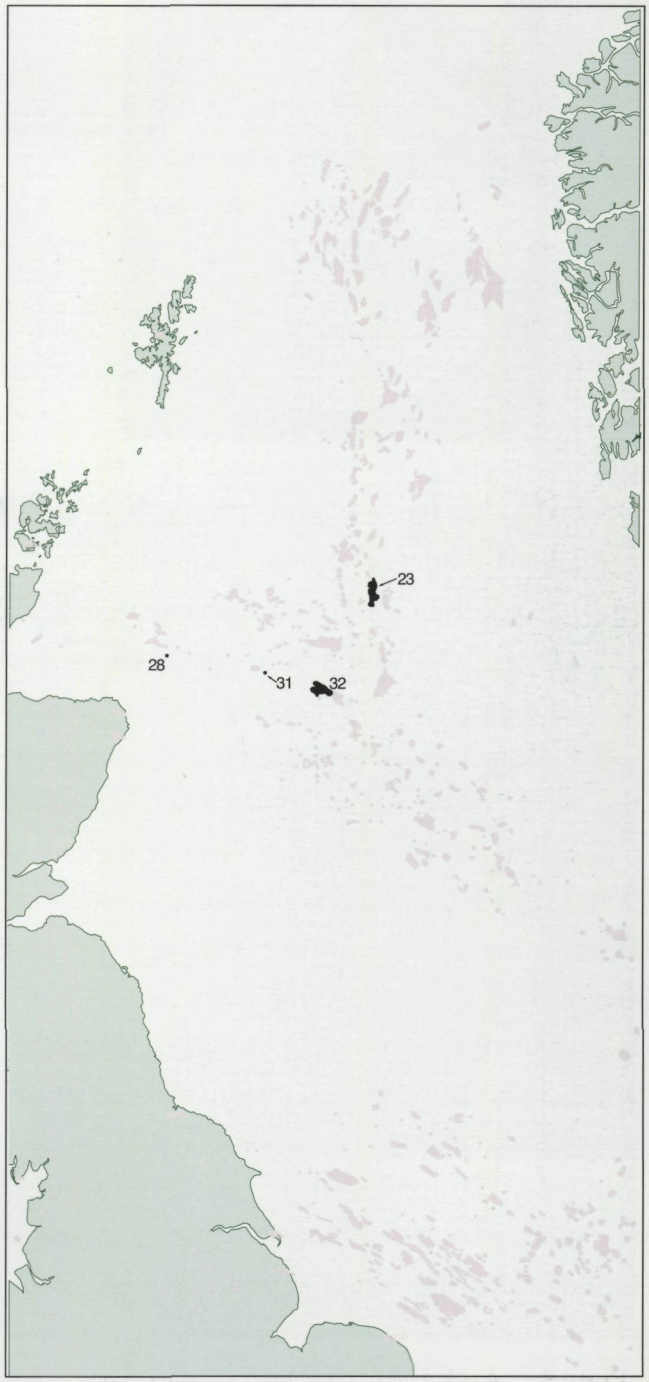
Variations: The form of this species is relatively constant.

Type locality: East of Shetland

Type material: Warén (1980) reports that no type material could be found in the Jeffreys collection in the Smithsonian Institute.

Remarks: For discrimination from *T. flexuosa* see under *T. flexuosa* and in Killeen & Oliver (2002b).

Distribution: Recorded in samples from three North Sea oil fields: Forties, Sleipner and a well in Block 21/1b, plus an additional site in the Fladen Ground. Elsewhere, shells have been recorded from sites on the west coast of Scotland: Gairloch c. 57°43'N 05°44'W, Leg. Marshall, NMW 1953.183, the Firth of Lorn, 56°28'N 05°36'W, 61m, Leg. S. M. Smith private collection and the Sound of Jura, c. 56°N 05°45'W, NMS.1977.105.337. Full details of the material examined are given in Killeen & Oliver (2002b).



Map 2. Distribution of *Thyasira polygona* in North Sea oil fields.

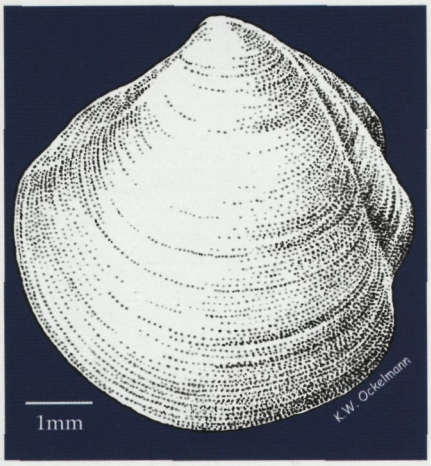
Thyasira (Thyasira) gouldi
(Philippi, 1845)

Plates 2C, 6B, 10A, 11–13

Lucina flexuosa Mont. – Gould, 1841: 72

Axinus gouldii, Philippi, 1845: 74–75

Thyasira gouldi (Philippi) – Killeen & Oliver, 2002b: 391-402



Description: Maximum size, 10mm. Equivalve. Equilateral. Moderately tumid. Outline equilateral-ovate, umbos projecting, higher than long with posterior folds and bisinuate posterior outline. Auricle weakly projecting, weakly demarcated, almost extending the total the length of the submarginal sulcus which itself is weakly defined, ligament sunken about half the length of the auricle. The submarginal sulcus frequently forms a marginal sinus but always to a lesser extent than the posterior sinus. First posterior fold weak. Posterior sulcus well developed giving rise to a strong posterior sinus. Second posterior fold prominent but rounded. Ventral margin narrowly rounded verging on being weakly angulate in some specimens. Anterior narrowly rounded to subtruncate at junction with lunule often with associated anterior flattened area. Lunule margin moderately long, sloping moderately. Lunule broad, not sunken.

Hinge weak with a single small cardinal tooth, in the form of a flattened peg, in the RV. LV with a corresponding small depression below the beak. Sculpture of weak concentric lines and growth stops and frequently with irregular dents, weak ridges and other damage marks. Lunule with compressed lines. Periostracum often persistent, silky and translucent over white shell.

Embryonic shell (Fig. 6.2) large, 205 – 270μm in length (measured shells from Norway, Faroes, New England and Greenland, N = 55). There is a latitudinal trend where the embryonic shell increases in size from south to north (Ockelmann pers comm).

Ctenidium with two demibranchs. Inside the anterior mantle margin there is a distinct thickened glandular ridge that runs to a point not quite at the middle of the ventral margin. Interior to this ridge the mantle is not opaque and not differentiated from the remainder.

Growth changes: Shells up to 2mm in length are more circular in outline and slightly inequilateral with the anterior somewhat expanded. The posterior folds are developed from early on but the margin is biangulate rather than bisinuate.

Variations: There is considerable variation in the outline of the shell in that while most specimens are roundly ovate with a short lunule margin, others have a longer sloping lunule margin giving a more attenuated appearance to the umbonal area. All varieties examined possessed the large embryonic shell and shells of each type could be found within samples, confirming that the observed variations are intra-specific.

Type locality: Off Massachusetts, U.S.A.

Type material: (not examined) MCZ State Coll., No 196, Soc. Cab,. No. 2413

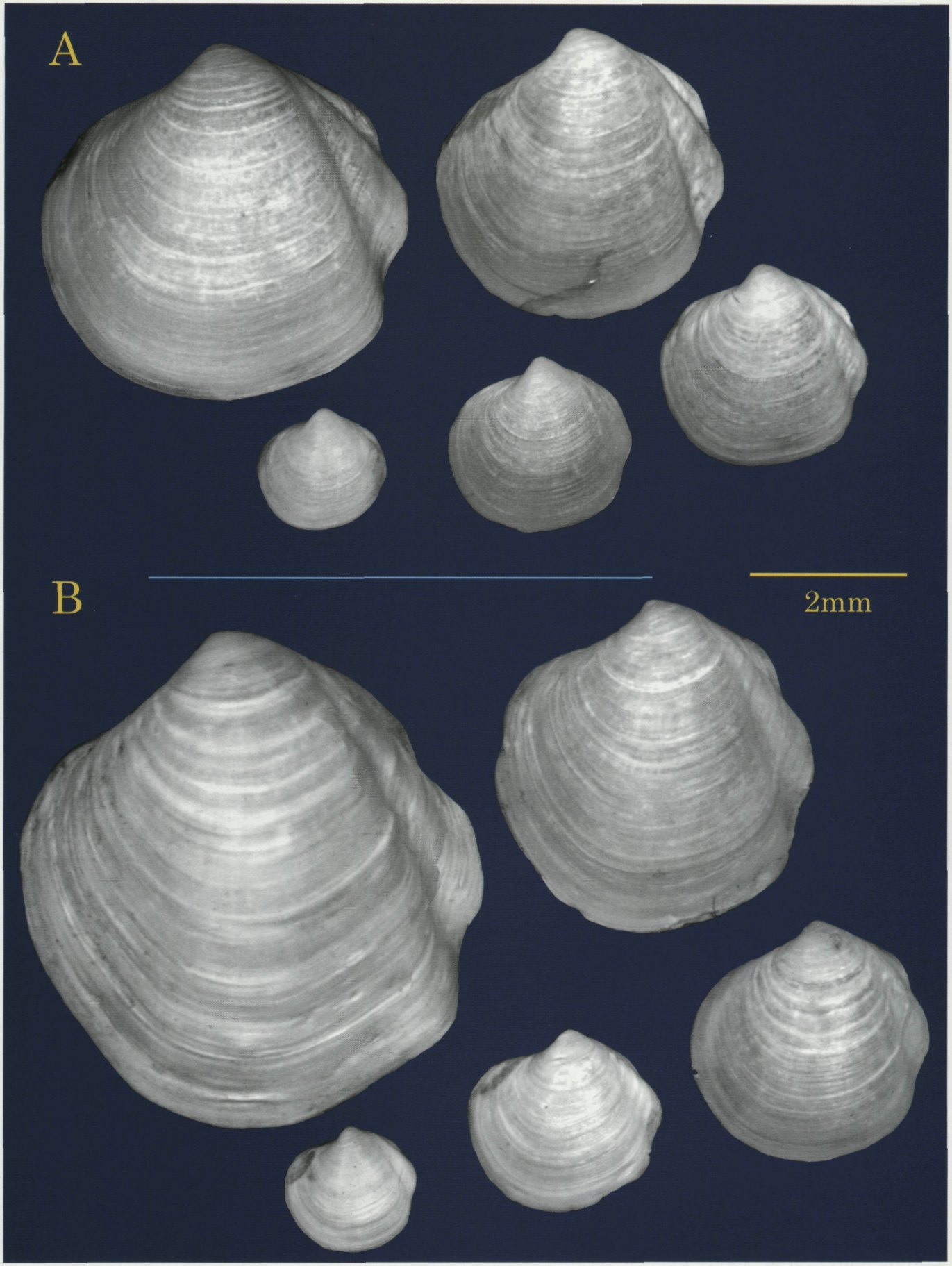


Plate 10. **A**, *Thyasira (Thyasira) gouldi* size series from Sullom Voe, Shetland.
B, *Thyasira (Thyasira) flexuosa*, size series from Sullom Voe, Shetland.

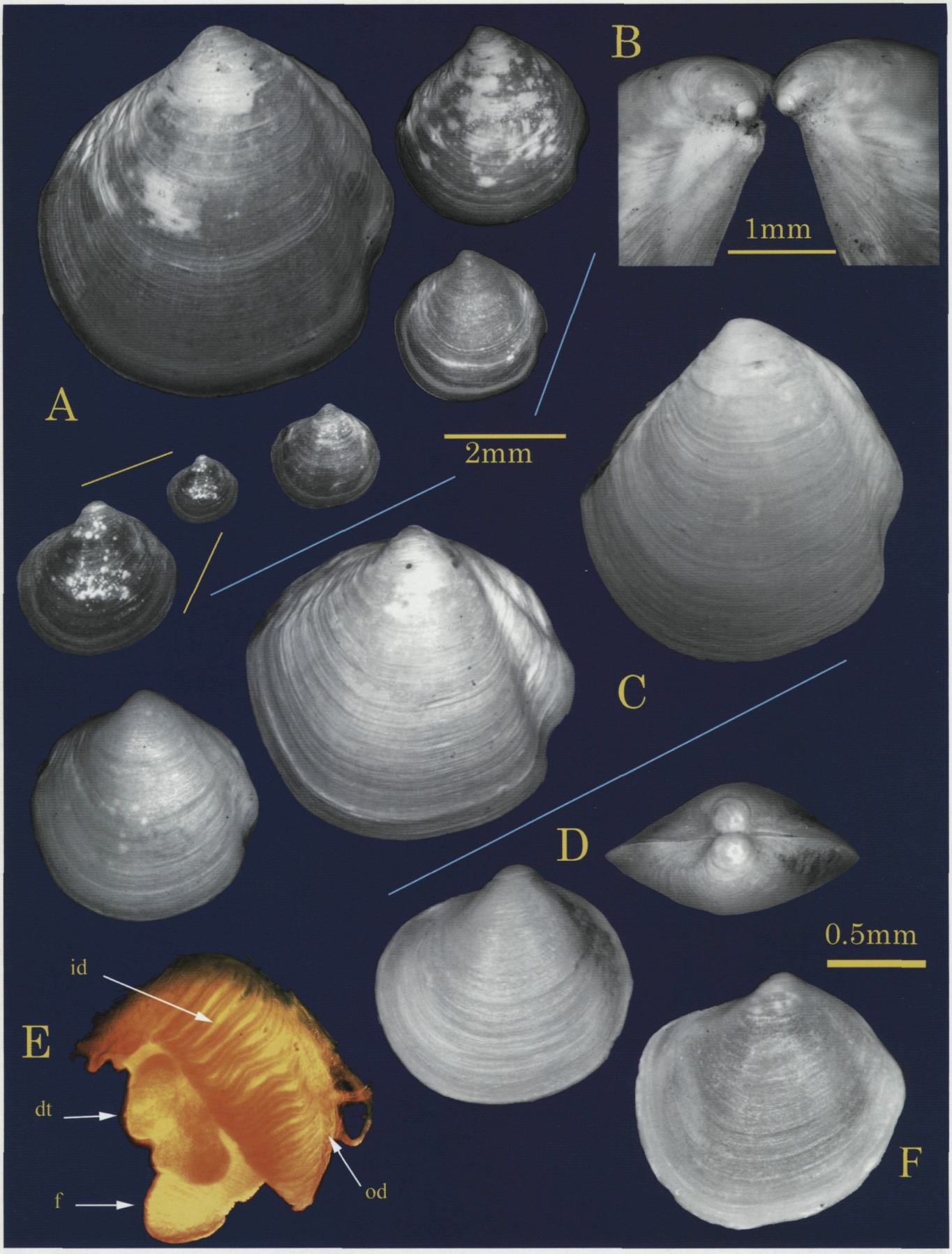


Plate 11. **A–E**, *Thyasira (T.) gouldi*. **A**, Size series, Loch Etive. **B**, Embryonic shell under low magnification, Loch Etive. **C**, Variations, Loch Eil. **D**, dorsal and lateral views of newly settled specimen, Cape Wrath. **E**, soft parts of newly settled specimen, Cape Wrath.**F**, *T. (T.) flexuosa* newly settled specimen, Cape Wrath.
Abbreviations: dt, digestive tubules; f, foot; id, inner demibranch; od, outer demibranch.

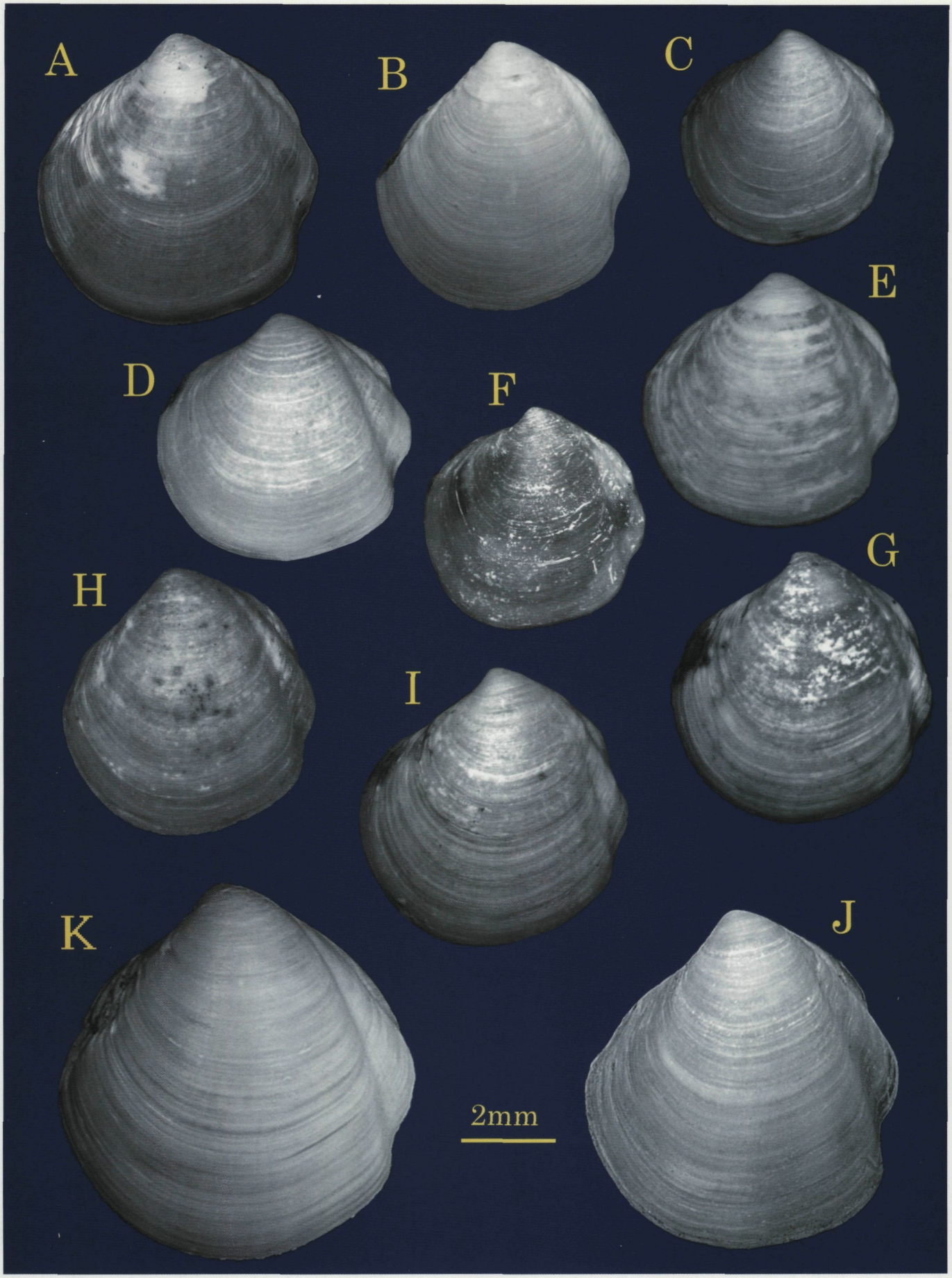


Plate 12. *Thyasira (Thyasira) gouldi*. **A**, Loch Etive. **B**, Loch Eil. **C**, Jura. **D**, Sullom Voe **E**, Loch Sween. **F**, Firth of Forth. **G**, Norway. **H**, Maine. **I**, Spitzbergen. **J**, Faroes. **K**, Greenland.

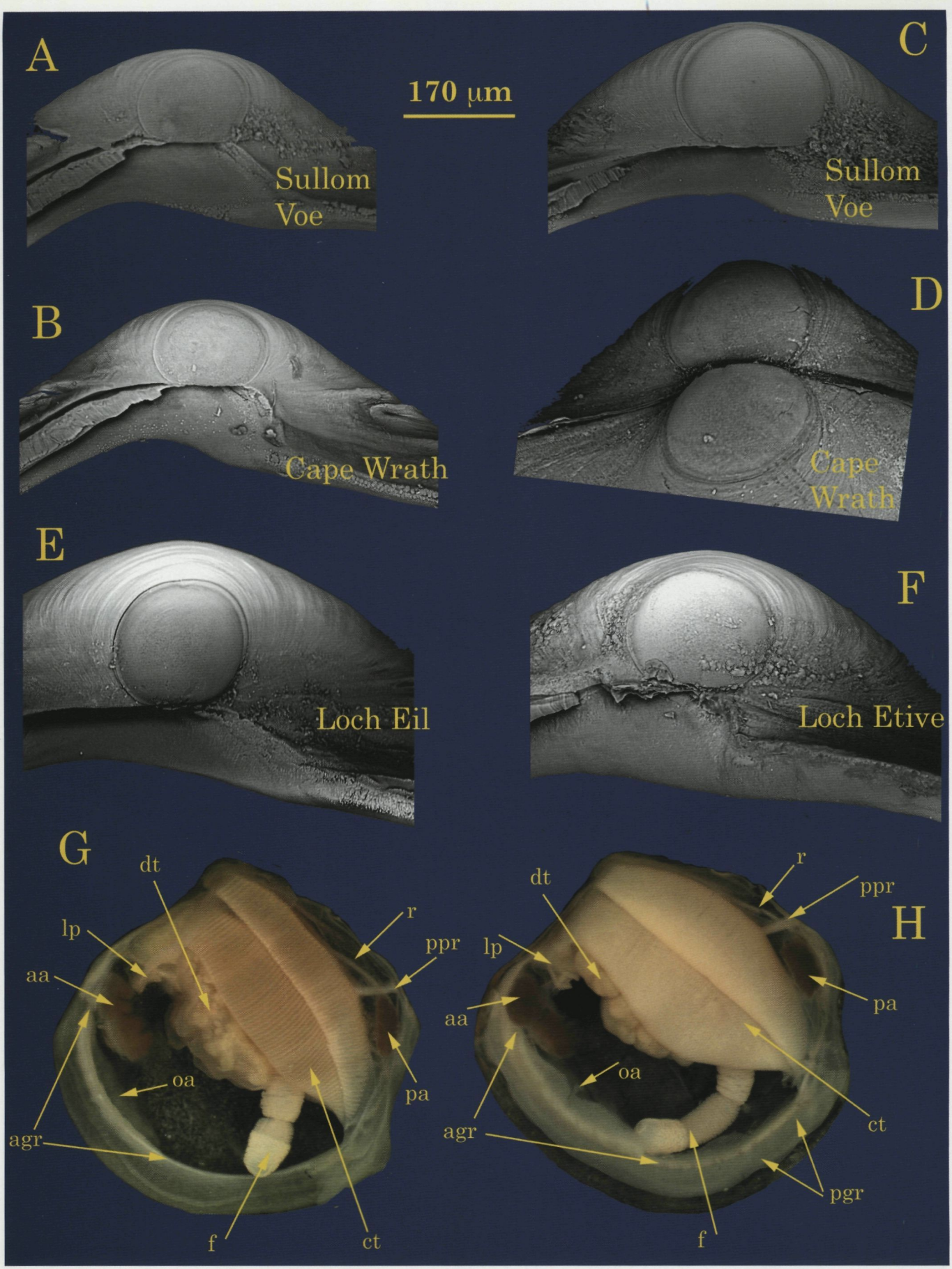


Plate 13. **A–F**, scanning electron micrographs of prodissoconchs. **A–B**, *Thyasira (T.) flexuosa*. **C–F**, *T. (T.) gouldi*. **G**, *T. (T.) gouldi*, Anatomy, Sullom Voe. **H**, *T. (T.) flexuosa*, Anatomy, Sullom Voe.
Abbreviations: aa, anterior adductor muscle; agr, anterior glandular ridge; dg, digestive gland tubules; f, foot; lp, labial palps; id, inner demibranch of ctenidium; od, outer demibranch; pa, posterior adductor; pgr, posterior glandular ridge; ppr, posterior pedal retractor; r, rectum.

Remarks: See under *T. flexuosa* and Killeen & Oliver (2001a)

Distribution: *T. gouldi* has not been found in any samples from the North Sea oil fields (Killeen & Oliver 2002a). Following an examination of *Thyasira flexuosa/gouldi* from around the British Isles, *T. gouldi* has been identified from the following Scottish and North Sea sites in depths generally less than 25m.

Loch Etive: 56°32.5'N 05°03.5'W (NMWZ). Loch Etive: Sailean Ruadh 56°27.3'N 05°16.3'W. (Killeen, Light & Smith private collections). Loch Eil: no precise data (SMSC). Loch na Cille (outer Loch Sween) 55°57.4'N 05°42.0'W (SMS). Shetland: around Calback Ness, Sullom Voe, 60°29.6'N 01°17'W, NMS1977.100.337, and NMWZ1997.092. 'Cape Wrath': This sample was part of a sea loch survey which included Lochs Laxford, Inchard and Eriboll but only carries the "Cape Wrath" survey title (NMW). Jura/Islay, RSMNH 1983009.337.03. Firth of Forth: 56.04050°N 03.26967°W (NMS).

Both *T. flexuosa* and *T. gouldi* can occur in the same sample, notably in Sullom Voe, Shetland and also in the Faeroes (Ockelmann pers comm).

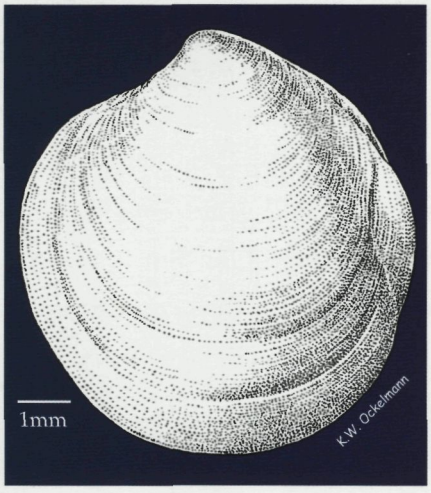
The occurrences of *T. gouldi* in Scottish sea lochs and southerly Norwegian fjords are considered to be glacial relicts but those in the Shetland voes and the Firth of Forth are more difficult to explain in this way

Map 3. Distribution of *Thyasira gouldi* in British waters, Faroes and southern Norway

Thyasira (Thyasira) sarsi
(Philippi, 1845)

Plates 2D, 6D, 14

Axinus sarsii, Philippi, 1845: 94



Description: Maximum size, 25mm. Equivalve. Not inflated. Outline equilateral-subcircular, just higher than long with weak posterior folds, posterior outline weakly bisinuate. Auricle projecting, weakly demarcated, almost extending the total length of the submarginal sulcus which itself is weakly defined, ligament exposed about three quarters the length of the auricle. The submarginal sulcus forms a slight marginal sinus but always to a lesser extent than the posterior sinus. First posterior fold, low and rounded. Posterior sulcus weakly developed giving rise to a slight posterior sinus. Second posterior fold weak and rounded. Ventral margin broadly rounded. Anterior rounded or becoming slightly truncated at junction with lunule margin. Lunule margin short, weakly depressed. Umbo narrow, projecting.

Hinge weak, cardinal tooth rudimentary or lacking, in the RV. LV with indistinct corresponding small depression below the beak.

Sculpture of weak concentric lines and growth stops and frequently with irregular dents, weak ridges and other damage marks. Lunule often with transverse crimping. Periostracum mostly persistent, translucent and giving a silky appearance over the white shell.

Larval shell (Fig. 6.3) 160-170µm in length (measured shells from W. Norway & Denmark, N = 32).

Ctenidium with two demibranchs. Inside the anterior mantle margin there is a narrow thickened glandular ridge that runs to a point beyond the middle of the ventral margin.

Growth changes: Shells up to 2 mm in length are slightly expanded anteriorly but the overall appearance changes little with growth.

Variations: The North Sea shells are very consistent and display no notable variation.

Type locality: "Norwegian Seas".

Type material: Unknown.

Remarks: Of the four bisinuate species *T. sarsi* should be the least confusing owing to its rounded outline and weak sulci. Its form is uniform in the North Sea but Sars (1878) recognised a large variety as 'monstr *oblonga*' and Ockelmann (1961) states "However, *T. sarsi* varies rather much in shape...." suggesting that elsewhere in its range it is more variable. However if there is variation in shell form as suggested by Ockelmann (1961) then the disposition of the glandular ridge is useful for separating *T. sarsi* from both *T. flexuosa* and *T. gouldi*.

Distribution: *T. sarsi* is present in most of the oil fields as far south as Fulmar (56°30'N), in depths ranging from 85m (Fulmar) to 220m (Gullfaks). It is absent in oil and gas fields further south or in

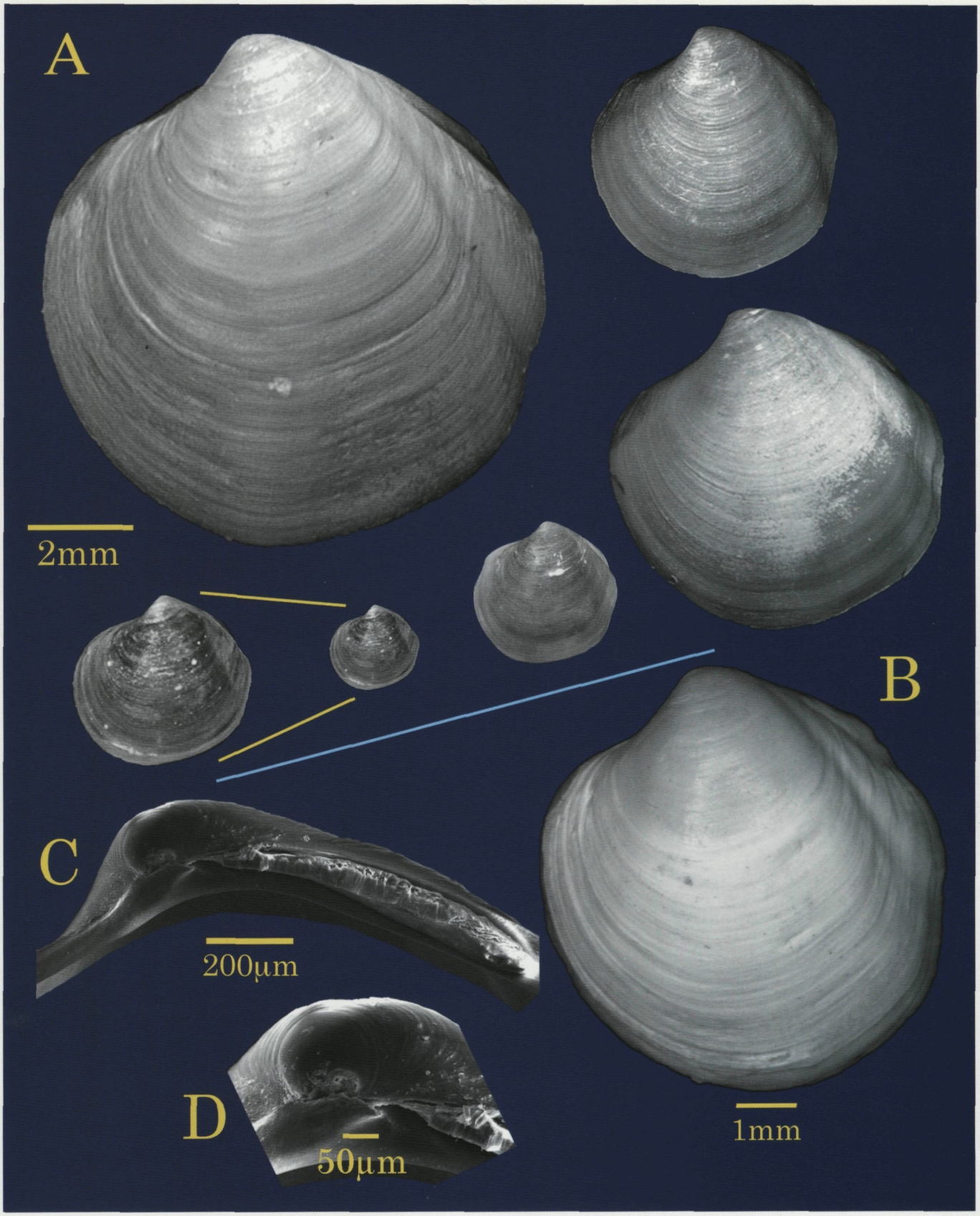
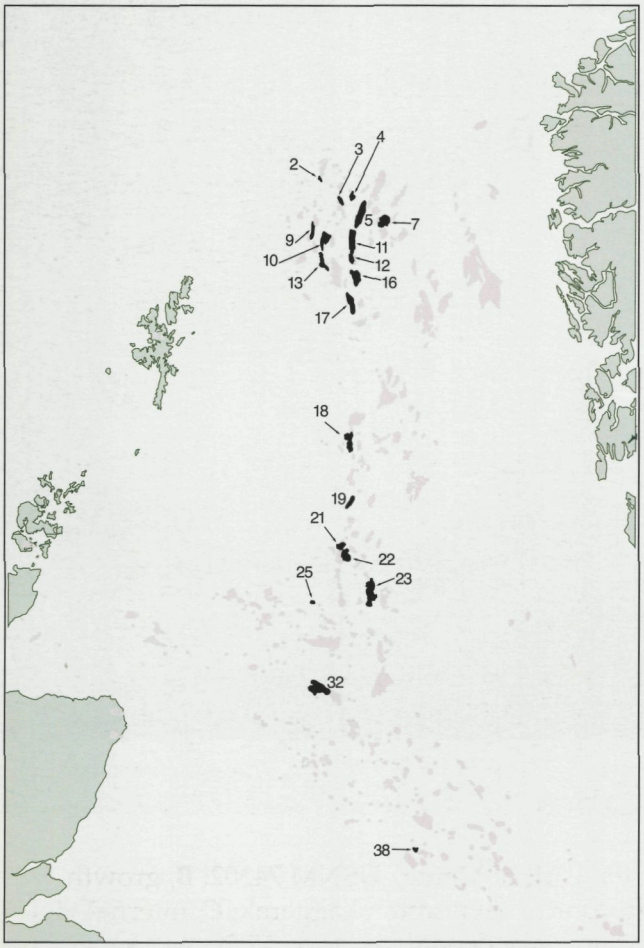


Plate 14. *Thyasira (Thyasira) sarsi*. **A**, growth series from Alwyn. **B**, large shell from Norway. **C–D**, scanning electron micrographs of shell from Alwyn; **C**, hinge of right valve. **D**, prodissoconch.

shallower water. Although we have material from individual sampling stations only from a limited number of fields, there is evidence that *T. sarsi* occurs in highest densities around the well heads, where it is often the dominant, or only, *Thyasira* species. The species then decreases in abundance away from the drilling centre. In Scandinavia this species is associated with high concentrations of organic detritus in water depths of 50–150m. High H_2S concentrations appear to be favoured and in this there is similarity between the fjordic conditions and the hydrocarbon concentrations around drilling centres.

There are no records of *T. sarsi* in British waters prior to the onset of drilling activities. It was present in samples from the Forties field collected in 1982 but was not distinguished from *T. flexuosa*. The species may well have been present around oil and gas seeps, but the paucity of benthic surveys in the northern North Sea may have meant that *T. sarsi* was not collected. However, we cannot overlook the possibility that the species has also spread and increased rapidly as a result of drilling activities. We have not seen any specimens of *T. sarsi* in any sample stations from the AFEN or *Challenger* cruises.



Map 4. Distribution of *Thyasira (Thyasira) sarsi* in North Sea oil fields.

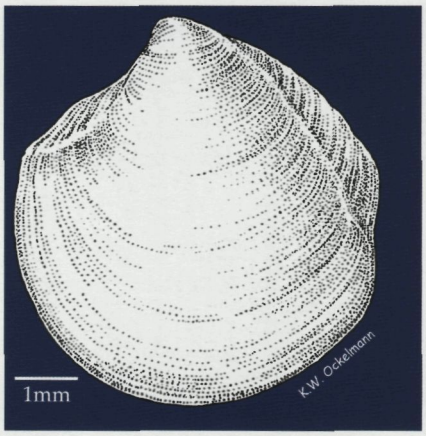
Thyasira (Parathyasira) equalis
(Verrill & Bush, 1898)

Plates 3A, 6E, 15

Cryptodon equalis Verrill & Bush, 1898: 788, fig. 5-6

Thyasira spec. a Ockelmann, 1958: 197

not *Thyasira equalis* in Ockelmann, 1958: 104–110, fig. 7



Description: Maximum size, 8mm. Equivalve. Equilateral. Moderately tumid. Outline ovate to diamond shaped, higher than long and lacking prominent posterior folds. Auricle absent. Submarginal sulcus long, deeply incised with almost vertical margins. Ligament deeply sunken, extent not visible on surface. The submarginal sulcus not forming a marginal sinus. First posterior fold absent. Posterior area flat or weakly sulcate , posterior margin weakly indented or truncated. Second posterior fold weak and rounded. Ventral margin narrowly rounded often angulate. Anterior roundly angulate to obliquely truncate at junction with lunule. Lunule margin short, sloping steeply. Lunule

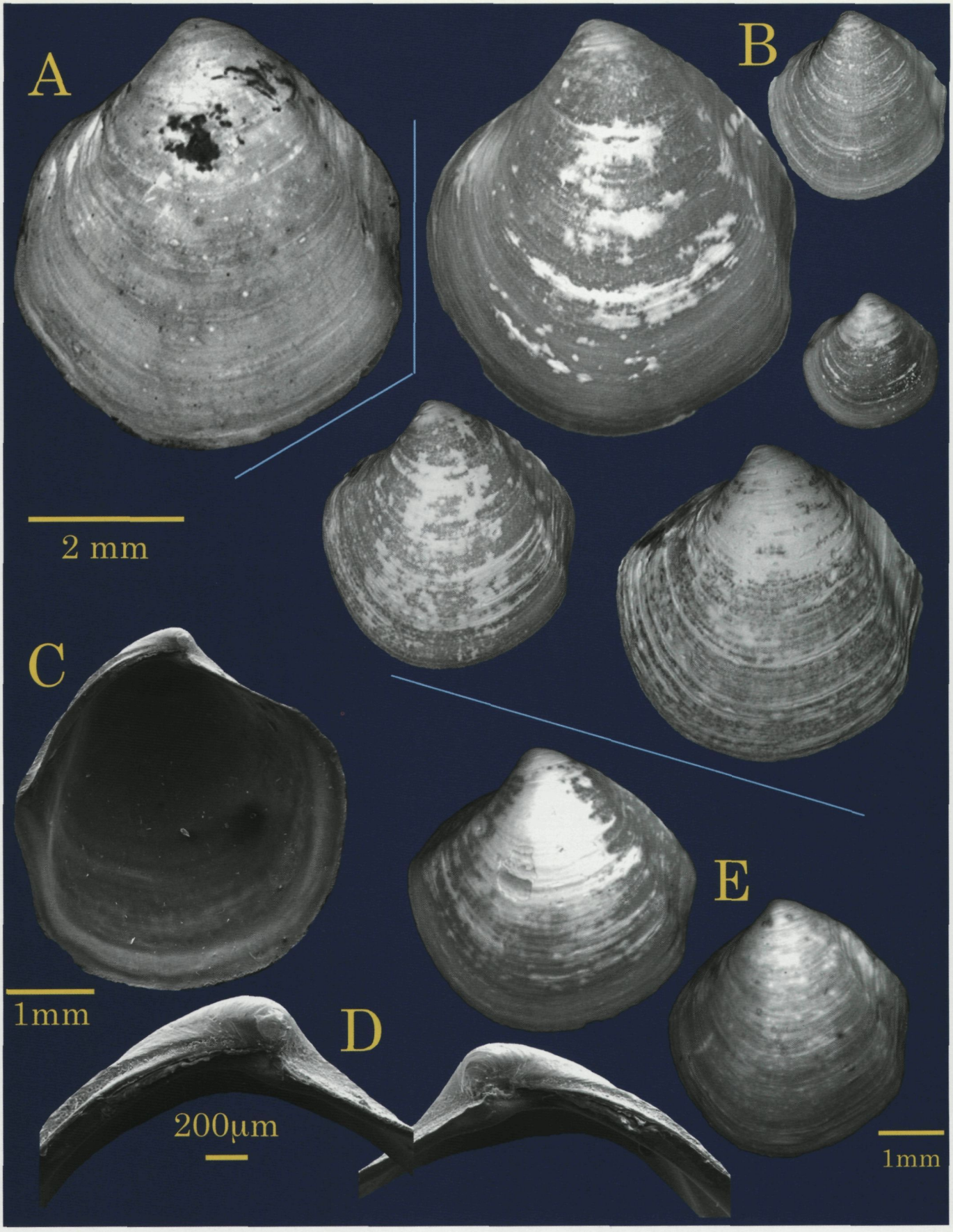


Plate15. *Thyasira (Parathyasira) equalis*. **A**, Type specimen, Gulf of Maine, USNM 74302. **B**, growth series from Block 21/1b. **C–D**, scanning electron micrographs of shell from Skaggerak; **C**, internal view of left valve. **D**, hinge of left and right valve. **E**, 2 shells from west Greenland, top - 57°N, bottom - 65°N

small, weakly excavated. Umbo narrow, projecting.

Hinge weak with a single, almost rudimentary, cardinal tooth, in the form of a flattened peg, in the RV. LV with a corresponding small depression below the beak.

Sculpture of weak concentric lines and growth stops and frequently with irregular dents, weak ridges and other damage marks. Lunule rather smooth. Periostracum thin, often worn away, transparent over white shell.

Larval shell (Fig. 6.4) 155–167μm in length (measured shells from Norway & Denmark, N = 81). There is a series of folds or wrinkles radiating from the anterior end of the apex.

Ctenidium with two demibranchs. Inside the anterior mantle margin there is a narrow thickened glandular ridge that runs to a point not quite at the middle of the ventral margin. The labial palps have prominent sorting ridges and the rectum is wide.

Growth changes: At sizes below 2mm the outline is subcircular rather than ovate and the posterior area is scarcely demarcated. Above 2mm growth related changes are insignificant.

Variations: This species is relatively constant in outline except that some show a greater angulation of the ventral margin than others which leads to the diamond shaped outline. The posterior margin is mostly truncate but can also be very slightly sinuous.

Type locality: Gulf of Maine

Type material: 1 shell, USNM 74302.

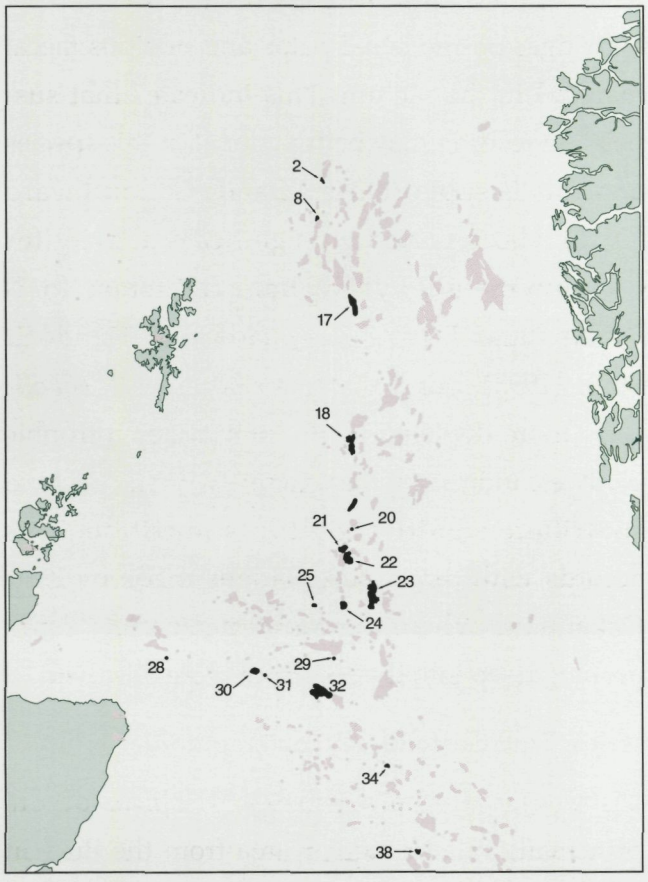
Remarks: The incised submarginal sulcus, lack of auricle and flattened rather than sulcate posterior are distinctive of this species and it should not be confused with others in the shelf waters of the North Sea. *Thyasira granulosa*, from more northerly, deep waters, also lacks the auricle but the granulose micro-sculpture of that species is distinctive. The similarities between the American type specimen of *T. equalis* and the eastern Atlantic material are strong, as are those with material that we have examined from West Greenland. McIntyre (1961) quotes Kurt Ockelmann in stating that "it (McIntyre's material) is identical with his '*Thyasira* spec. a' (Ockelmann, 1958: p.100), while his '*Thyasira equalis*' (op. cit.: p.104) is probably a previously undescribed species. This statement is repeated by Bowden & Heppell (1968) and by Payne & Allen (1991). This statement can now be clarified; the *T. equalis* of Ockelmann, 1958 is *T. dunbari* Lubinsky and the *Thyasira* "spec. a" is *T. (P.) equalis*.

The anatomy of *T. equalis* differs from the other larger species with the presence of distinct sorting ridges on the labial palps and obvious faecal material in the rectum. This indicates that suspension feeding may be functional in this species and this is supported by Dando & Southward (1986) who reported no significant activity for the enzyme adenylsulphate reductase in *T. equalis* (and *T. ferruginea*). However, Dando & Spiro (1993) found that the tissues of *T. equalis* were more depleted in ^{13}C than in heterotrophic bivalves, indicating that chemosynthetic bacteria contribute significantly to its nutrition. This accords with direct observations made by Kurt Ockelmann where the radiating feeding tubes probing deep into the sediment were observed.

Distribution: In the North Sea, *T. equalis* occurs principally in a triangular area from the Buchan field in the west, to Fulmar in the south, and around Brae in the north. Generally the species is

uncommon in oil field samples. However, it is often very common, sometimes dominant, in the pockmarks and Fladen Ground samples. We also have records of occasional specimens from more northerly fields (North Cormorant, Dunbar, Strathspey). *T. equalis* had been previously recorded from the Fladen Ground (McIntyre 1961), and from the Forties field by Hartley (1984), who recorded it in densities as high as $72m^{-2}$. Voucher material from these two studies is in the collections at NMS and NMW respectively.

Specimens of a taxon with a shell morphology similar to *T. equalis* are present in samples from the AFEN cruises at depths of 600-1100m, and in the *Challenger* material below 400m. However, we believe that further research is necessary to establish whether these are the same as the species referred to as *T. equalis* in the North Sea.



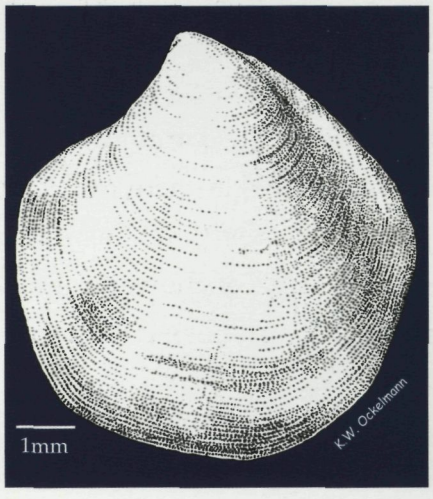
Map 5. Distribution of *Thyasira equalis* in North Sea oil fields.

In Scandinavian waters *T. equalis* is most often found between 100–300m while off New England it is generally deeper. A total depth range of 10–2700m is suggested by Kurt Ockelmann.

Thyasira (Parathyasira) granulosa
(Monterosato, 1874)

Plate 6F, 16

Axinus granulosus Monterosato 1874: 251



Description: Maximum size, 10mm. Equivalve. Equilateral. Moderately tumid. Outline ovate to diamond shaped, higher than long and lacking prominent posterior folds. Auricle absent. Submarginal sulcus long, deeply incised with almost vertical margins. Ligament visible, about half length of SMS. The submarginal sulcus not forming a marginal sinus. First posterior fold absent. Posterior area flat or weakly sulcate , posterior margin weakly indented or truncated. Second posterior fold weak and rounded. Ventral margin narrowly rounded often angulate. Anterior roundly angulate to obliquely truncate at junction with lunule. Lunule margin short, distinctly concave. Lunule excavated. Umbo narrow, distinctly projecting.

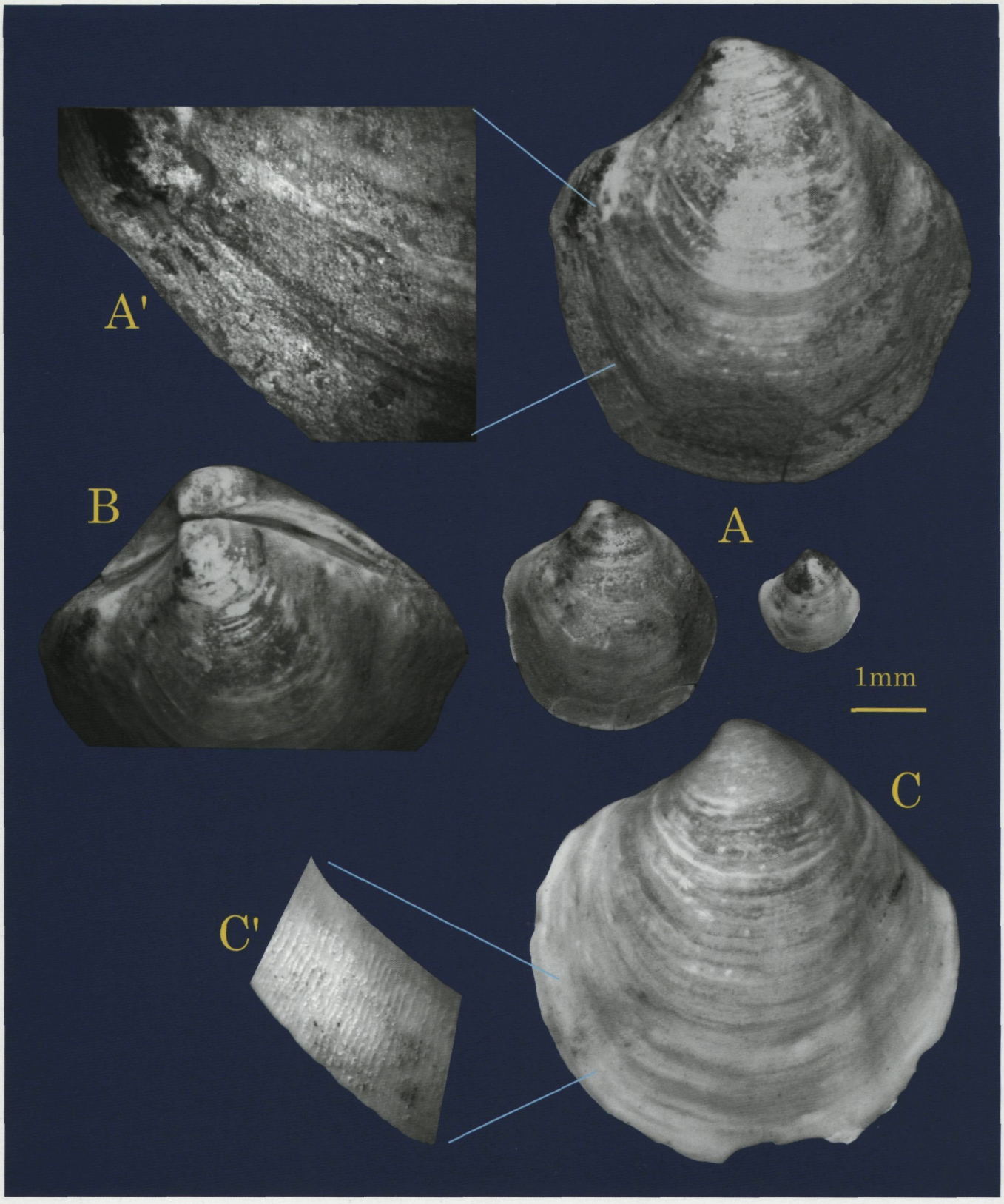


Plate 16. *Thyasira (Parathyasira) granulosa*. **A**, growth series, Troll Gasfield. **A'**, coated granular sculpture. **B**, oblique dorsal view, Troll Gasfield.
C, *Thyasira (P.) cf. subcircularis*, Challenger st. ES 255. **C'**, radial arrangement of granules.

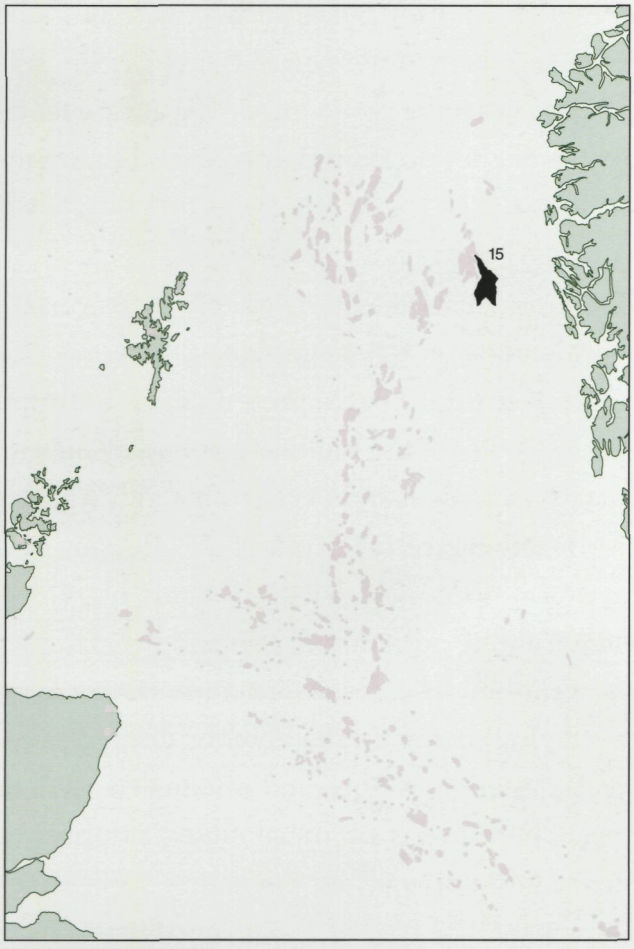
Hinge weak with a single, almost rudimentary, cardinal tooth, in the form of a flattened peg, in the RV. LV with a corresponding small depression below the beak.

Shell fragile with sculpture of weak concentric lines, growth stops and irregular dents overlaid by a granular micro-sculpture which is arranged radially. The granular micro-sculpture best seen at margins where it is often exaggerated by a thin ferruginous coating.

Larval shell (Fig.6.5) 76–182μm in length, (measured shells from Norway, N = 20)

Ctenidium with both demibranchs and gross morphology similar to that of *T. equalis*. The bulbous tip of the foot is very large.

Growth changes: The umbonate appearance, overall outline and micro-sculpture are present in individuals down to 1mm in size.



Map 6. Distribution of *Thyasira (Parathyasira) granulosa* in North Sea oil fields

Variations: The outline is a little variable in that some are more rounded and some diamond shaped. The 2nd posterior fold can be very weak and consequently the posterior area can be indistinct.

Type locality: Probably Cape Santo Vito, Sicily.

Type material: 1 syntype Natural History Museum, London. BM(NH).1885.11.5.933

Remarks: The granular micro-sculpture is unique among the thyasirids under consideration here and in outline the only similarity is with *T. (P.) equalis*. Payne & Allen (1991) describe a granulose species, *T. (Parathyasira) subcircularis* (pl. 16, fig C) from the western European basin in depths as shallow as 800m. This species has the granules arranged radially and care should be taken when identifying granulose species from bathyal depths, especially as *T. granulosa* has been recorded from 1800m off the west of Shetland (pers. obs).

Kurt Ockelmann has examined much of the material from 19th century reports and notes that in part the material described by Jeffreys (1881, p. 702) as *Axinus flexuosus* var *rotunda* includes small examples of *T. granulosa*. He also notes that in Sars (1878), figures 4a-b on plate 19 represent *T. granulosa* and not *Axinus flexuosus* as labelled.

Distribution: *T. granulosa* was recorded in samples from the Troll field at depths of 170m. This species was not found in any of the oil fields in the North Sea Basin and there are no other records for the British shelf elsewhere. In the AFEN (west of Shetland) cruise material, a few individuals were recorded from stations at depths of 900-1800m. Depth ranges in Norwegian waters are 100–1300m.

Thyasira obsoleta

(Verrill & Bush, 1898)

Plates 3B, 17 & 18

not *Clausina croulinensis* Jeffreys, 1847:19

Clausina croulinensis Jeffreys:- Jeffreys, 1864: 250, 1869: pl. 33, fig. 2

Axinus pusillus M. Sars, 1868: 257 nomen nudum

Axinus croulinensis Jeffr:- Sars, 1878: 62, pl. 19, fig8

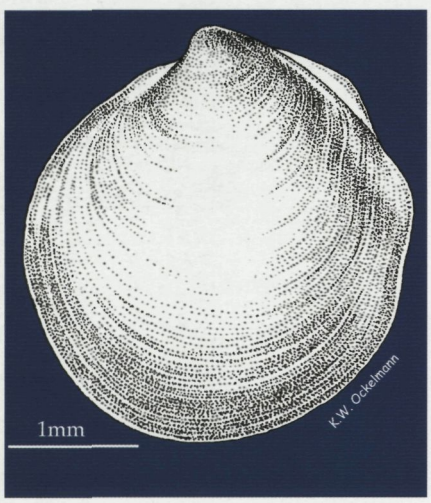
Cryptodon obsoletus Verrill & Bush, 1898: 789–790, pl. LXXXIX, figs 1, 2.

Axinus croulinensis var. *truncatus* Marshall, 1914: 186-187

Axinulus subovatus Jeffreys:- Madsen, 1949: 53, Fig. 6

Axinulus pygmaeus Verrill & Bush:- Madsen, 1949, in part, Fig. 7c

Thyasira (Thyasira) obsoleta (Verrill & Bush, 1898):- Payne & Allen, 1991: 493–496



Description: Maximum size, 4mm. Equivalve. Inequilateral, beaks slightly to the posterior. Moderately tumid. Outline obliquely-ovate to pyriform (tear-drop shaped) and extended anteriorly, slightly higher than long. Umbo narrow, projecting. Posterior margin biangulate, anterior broadly rounded. Posterior folds weak, submarginal sulcus shallow. Auricle present, confluent with most of SMS but projection variable. Ligament not visible on surface. Posterior sulcus as a flattened area, sulcus margin straight, not indented. Ventral and anterior margins forming a broad curve into the lunule area. Lunule weakly defined, lacking boundary ridges, valve margin junction typically raised.

Hinge weak, cardinal tooth mostly absent. Ligament mostly internal on a sunken resilifer and half the length of the auricle

Sculpture of weak concentric lines and growth stops and frequently with irregular dents. Ferruginous deposits confined mostly to anterior dorsal and posterior areas.

Larval shell (Fig. 6.9) 148–157μm in length (measured shells from Norway & Denmark, N = 44). Ctenidium with two demibranchs.

Growth changes: Shells around 1mm in length are obliquely rounded with poorly developed posterior features. With growth the posterior features strengthen and the posterior area becomes flattened and the fold defining the submarginal sulcus becomes more pronounced. The auricle tends to be more developed in larger shells but is subject to variation.

Variations: This is the most variable species under consideration with three recognisable forms. The 'typical' form is that represented by the type specimen where the outline is obliquely subcircular, the lunule margin is curved and the posterior features are moderately developed. The 'pyriform' form has a sloping lunule margin, a more truncate posterior margin and projects anterior ventrally. The 'expanded' form differs from the 'typical' in the greater anterior development, weak posterior features and a flattened median area. These forms occur as mixed samples in most cases although the 'expanded' form is not as frequent. The type of *T. croulinensis* var *truncatus* Marshall, 1914 is a large shell of *T. obsoleta* with the 'typical' form. However, in most of the

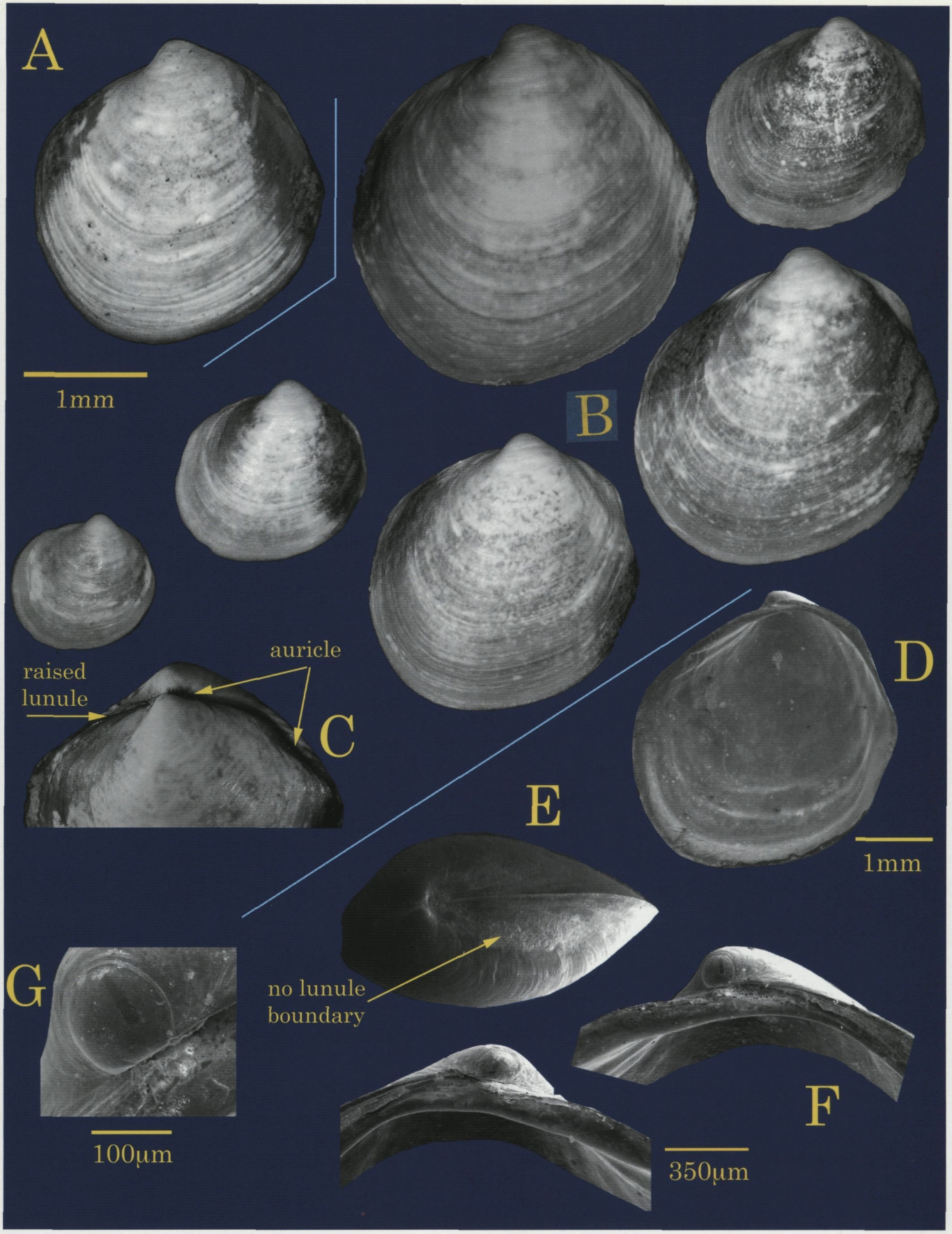


Plate 17. *Thyasira obsoleta*. **A**, Lectotype, Off Martha's Vineyard, USNM 159886. **B**, Size series from Cormorant and Lyell. **C**, oblique view of dorsal area. **D–G**, scanning electron micrographs of shells from Cormorant: **D**, internal view of right valve. **E**, lunule area. **F**, hinge of right and left valve. **G**, prodissoconch.

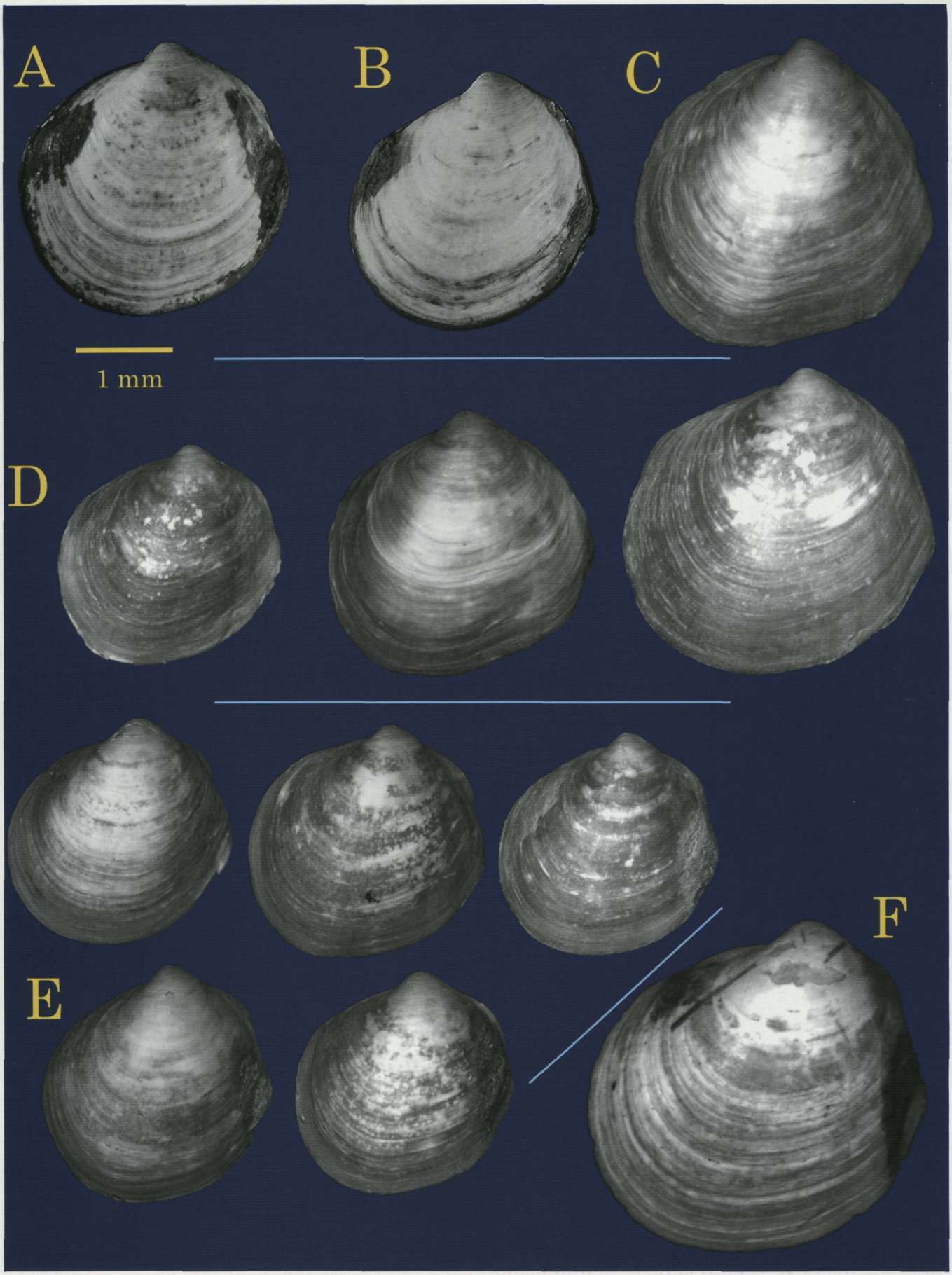


Plate 18. *Thyasira obsoleta*, variations in external form. **A–C**, Three recognisable morphs; **A**, typical (Cormorant), **B**, "tear-drop " (Cormorant), **C**, "expanded" (Thistle). **D**, variations from Thistle. **E**, variations from Lyell. **F**, lectotype of *Axinus croulinensis* var. *truncata* Marshall, NMW 1953.183.

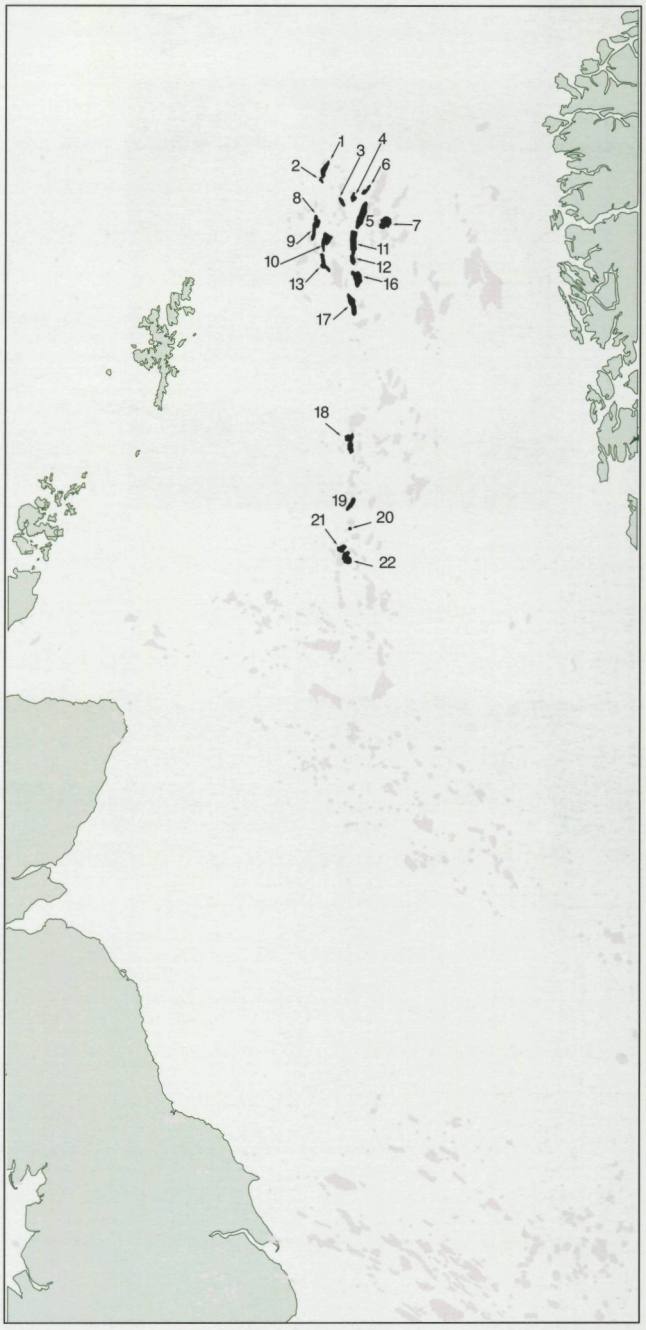
material at hand the hinge lacks any obvious development of the cardinal, but in Marshall's shells there is a depression in front of the beak in the left valve and a corresponding plate-like extension of the hinge in the right valve.

Type locality: Off Martha's Vineyard

Type material: 1 shell, USNM 159886.

Remarks: Our examination of the large number of samples and the large number of specimens available revealed no pattern in the occurrence of the different forms. They are found mixed in any one sample and the forms show morphological convergence. Our conclusion on the current evidence is that *T. obsoleta* is a variable species.
Madsen (1949) illustrates a shell as *Axinulus subovatus* Jeffreys from 326-216m off Iceland that we interpret as the 'pyriform' form of *T. obsoleta.* We consider *T. subovata* to be a truly deep water species and disagree with Payne & Allen's (1991) inclusion of Madsen's material in *T. subovata.* Madsen (op. cit. p.54, fig. 7c) also illustrates a small typical *T. obsoleta* under *Axinulus pygmaeus.* For comparative remarks with *T. succisa* see p. 48.

Distribution: This species was present in virtually every oil field north of 60°N. Further south, it was present (in large numbers) in the Beryl field (59°33'N), and occasionally in Block 16/3 (58°58'N) and the Miller oil field (58°42'N). Depth range 125m (Alwyn) to 220m (Gullfaks). Specimens were present in the *Braer* samples S of Shetland in 128m depth. We have not seen material of *T. obsoleta* from any other location on the continental shelf in the British sea area and literature records have been regarded as unreliable (see *T. croulinensis*). *T. obsoleta* is present in samples from the AFEN and *Challenger* cruises in depths from 500-1300m. The depth distribution of material from Norway and the Faroes is 43–1159m.



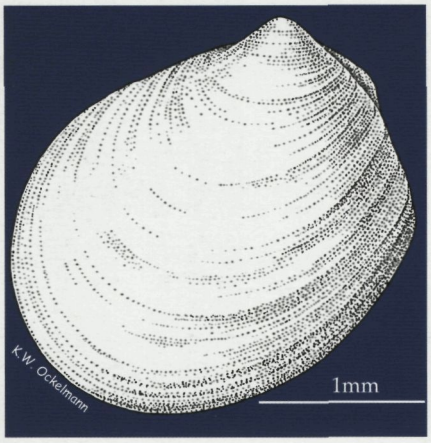
Map 7. Distribution of *Thyasira obsoleta* in North Sea oil fields

Thyasira succisa

(Jeffreys, 1876)

Plate 19

Axinus incrassatus var *succisa* Jeffreys, 1876: 492–493.



Description: Maximum size, 3.5mm. Slightly inequivalve with LV a little larger, this is most noticeable on the lunule and between the beaks. Inequilateral, beaks slightly to the posterior. Not inflated. Outline obliquely pyriform (tear-drop shaped), extended anteriorly, slightly higher than long. Umbo narrow, projecting. Submarginal sulcus narrow but distinct. First posterior fold distinct. Auricle prominent but short. Ligament deeply sunken, extent not visible on surface. Second posterior fold rudimentary but posterior area rather flattened and posterior margin distinctly biangulate. Ventral and anterior margins forming a broad curve into the lunule area. Lunule well defined, slightly sunken and bordered by slightly raised ridges.

Hinge with a prominent cardinal boss in LV and a corresponding socket in RV. Ligament mostly internal on a sunken resilifer and half the length of the auricle.

Surface rather smooth and a little glossy, sculpture of faint concentric lines and growth stops. The relatively thick shell remains less blemished than *T. obsoleta*. Ferruginous deposits confined to anterior dorsal and posterior areas.

Larval shell (Fig. 6.10) 154–165µm in length (measured shells from NE. Atlantic and Mediterranean, N = 21).

Ctenidium with two demibranchs.

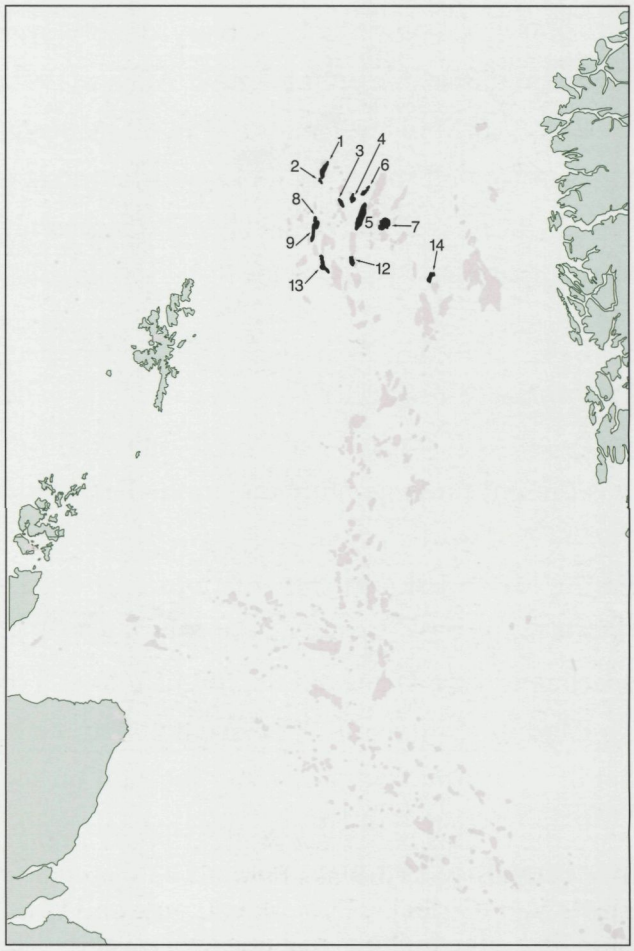
Growth changes: Changes are not marked and the distinct posterior angulation and oblique form are present in shells under 1mm in length.

Variations: The outline of the shell is rather uniform but the expression of the lunule ridges can vary a little.

Type locality: Adventure Bank, Mediterranean

Type material: Lectotype, 1 shell, USNM 61973

Remarks: The pyriform variety of *T. obsoleta* is easily confused with *T. succisa* primarily because



Map 8. Distribution of *Thyasira succisa* in North Sea oil fields.

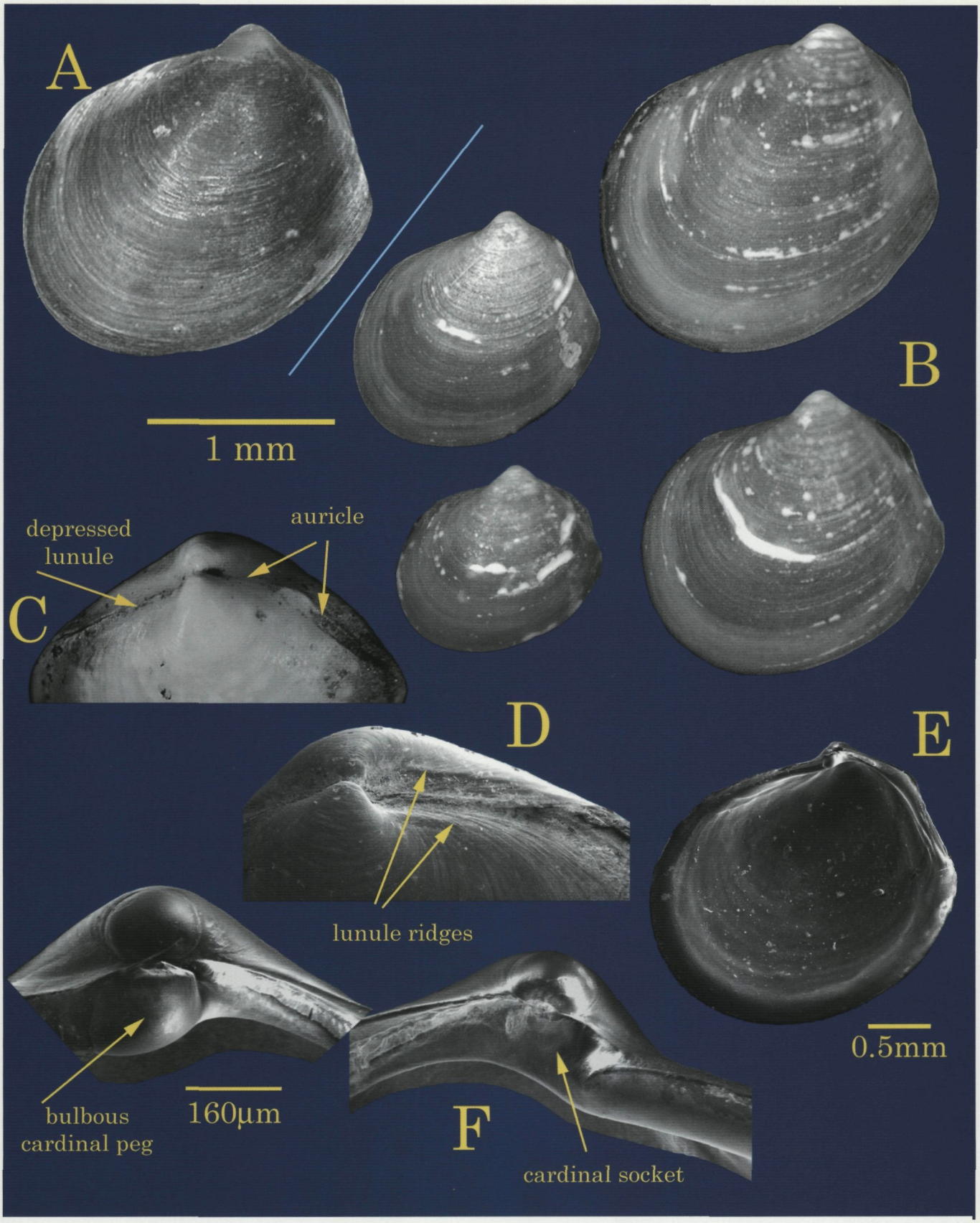


Plate 19. *Thyasira succisa*. **A**, lectotype, Adventure Bank, Mediterranean, USNM 61973. **B**, growth series, Gullfaks field. **C**, oblique view of dorsal area. **D–F**, scanning electron micrographs of shells from Gullfaks; **D**, sunken lunule and boundary ridges. **E**, internal view of right valve. **F**, hinge showing large bulbous peg and socket.

the outlines are similar, and also because in the pyriform *T. obsoleta*, the lunule is flat and the valve margins not raised. It should be noted that in none of the varieties of *T. obsoleta* are there boundary ridges to the lunule and this feature is found only in *T. succisa*.

Distribution: This is a northern species in the North Sea occurring in most of the oil fields north of 60°55'N, but not further south. Depth range 145m (Statfjord) to 220m (Gullfaks). There are no other records of *T. succisa* from the continental shelf in the British sea area (Seaward 1990). However, in the AFEN material this species is a common component of the upper slope, west of Shetland, in a depth range of 200 to c. 600m. *T. succisa* was also present in the *Challenger* material from upper slope stations on the Wyville Thomson Ridge and Hebrides Terrace.

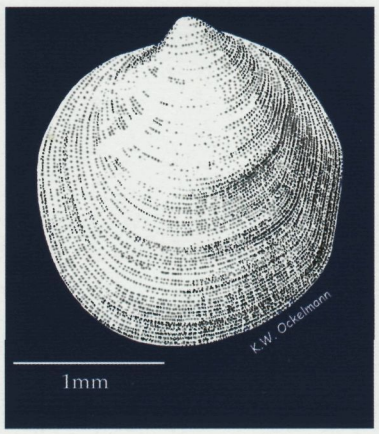
Axinulus croulinensis

(Jeffreys, 1847)

Plates 3C, 20

Clausina croulinensis Jeffreys, 1847: 19.

Thyasira ferruginea Winckworth:- Tebble, 1966, Fig. 35a only.



Description: Maximum size, 2.5mm. Fragile. Equivalve. Equilateral. Distinctly tumid. Outline oval, conspicuously higher than long. Posterior folds obsolete but posterior area a little flattened and posterior margin weakly biangulate. Auricle indistinct but post dorsal margin initially straight before merging into posterior curve. Ventral margin more narrowly curved than anterior margin. Lunule absent, anterior dorsal margin horizontal, valve edges raised "pinched". Umbo small, projecting with distinct anterior notch to lunule margin.

Hinge weak, cardinal tooth absent but hinge plate slightly swollen below beak. Ligament mostly internal on a sunken resilifer and one third the length of the dorsal margin.

Sculpture of weak concentric lines and growth stops, mostly glossy with a radial texture under transmitted light. Ferruginous deposits confined to anterior dorsal and posterior areas.

Larval shell (Fig. 6.7) 131–141μm in length (measured material from Norway and the Faroes, N = 52).

Ctenidium with one demibranch.

Growth changes: The initial outline is roundly quadrate with the posterior dorsal margin relatively long with the junction to the posterior margin distinctly angled. With growth the shell becomes more oval and the angles at the junctions of the margins diminish..

Variations: The neotype is not typical of the majority of the material collected from the northern North Sea in that it is more circular in outline. Remains of the ctenidium dried onto the inner surface of the type reveal the single demibranch structure indicative of this species. Similar shells have been examined from Gairloch (north of the Crowlins) at a depth of 60m [ex Preston coll, NMW.1955.158]. In the North Sea

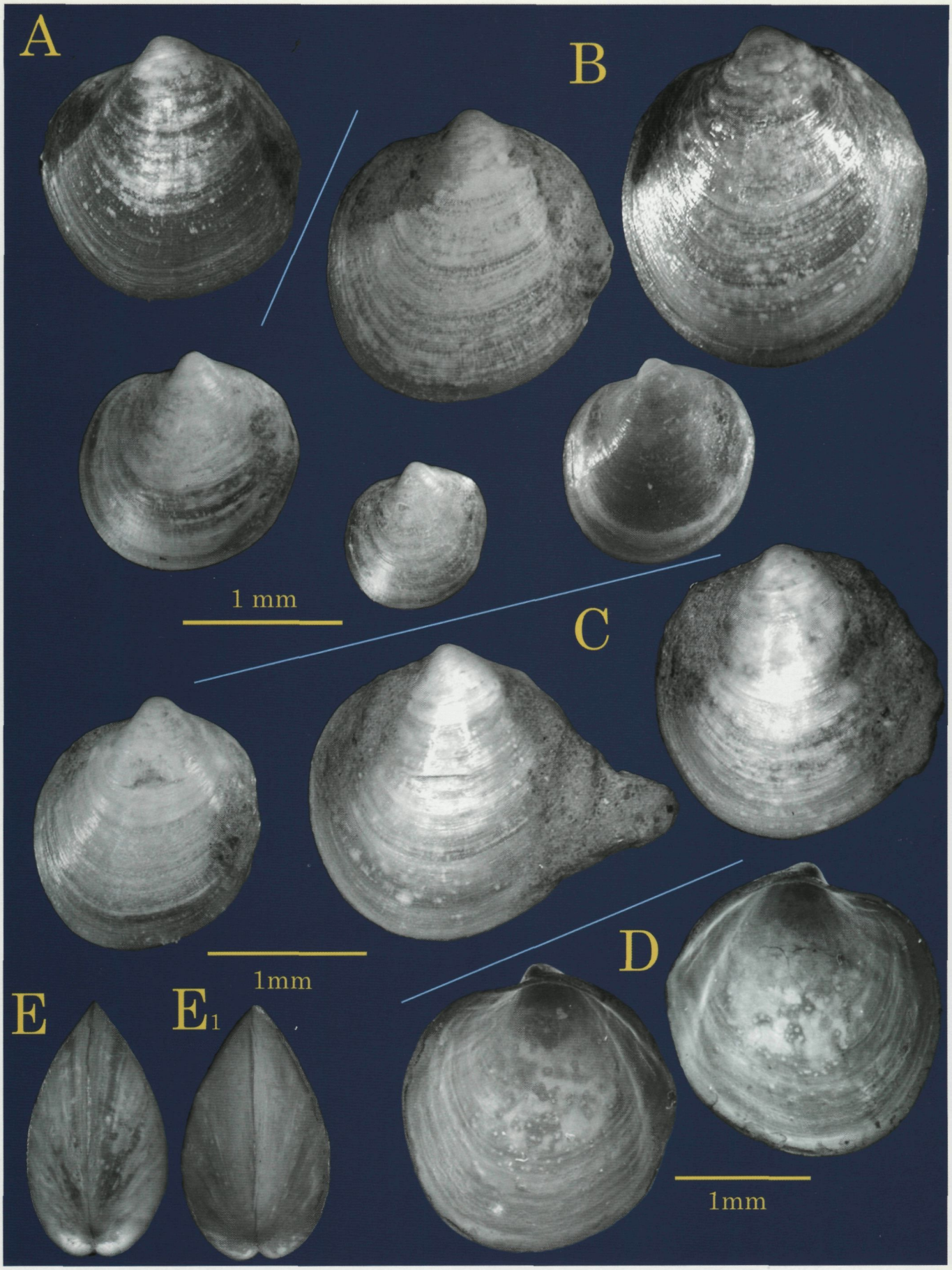
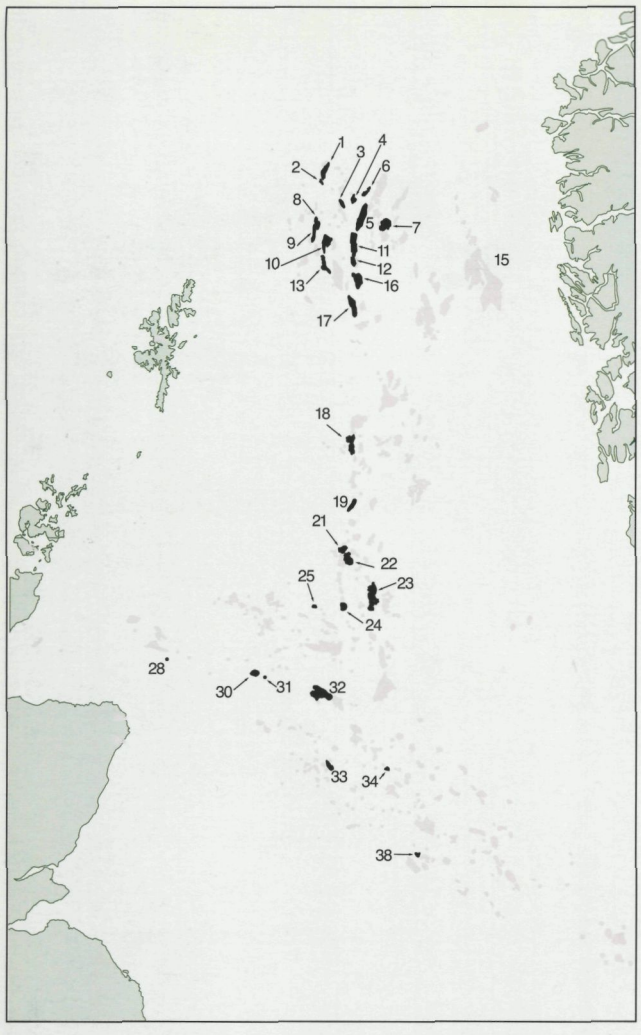


Plate 20. **A–E**, *Axinulus(Axinulus) croulinensis*. **A**, neotype, USNM 62048, Loch Fyne, Scotland. **B**, growth series from Gullfaks/Magnus. **C**, variations in encrustation from Gullfaks. **D**, scanning electron micrographs of internal views from Gullfaks. **E**, lateral view from Gullfaks. **E_1**, *Thyasira obsoleta*.



Map 9. Distribution of *Axinulus croulinensis* in North Sea oil fields

material the outline itself is not very variable but can be obscured by the ferruginous deposit that can accumulate and mask the true shape.

Type locality: Off the Crowlin Islands, between Skye and Scottish mainland, Inner Hebrides.

Type material: 1 shell, Neotype, USNM 62048, Loch Fyne, Scotland

Distribution: A widespread and common species in the North Sea oil fields extending from the northern shelf edge (Magnus) south to Fulmar (56°30'N). Depth range in oil fields 85m (Fulmar) to 220m (Gullfaks). *A. croulinensis* is recorded at several locations on the shelf around western Scotland (Seaward 1990, Smith & Nunn in press), where it lives in depths as shallow as 20m (e.g. Firth of Lorn, Killeen pers. obs). Many records of *A. croulinensis*, which are not supported by specimens, have been treated as unreliable by Seaward (1990) and Payne & Allen (1991) owing to confusion between this species and *T. obsoleta*. We have also recorded this species from a few localities on the upper slope west of Shetland (AFEN) where it appears to be uncommon.

Axinulus (Genaxinus) eumyarius

(M. Sars, 1870)

Plate 21

Axinus eumyarius M. Sars, 1870: 87–89; pl.12, figs 7–10

Thyasira (Axinulus) eumyaria (M. Sars, 1870): Payne & Allen, 1991: 529–531

Description: Maximum size, 2.5mm. Fragile. Equivalve. Equilateral. Outline oval, higher than long. Posterior folds obsolete but posterior area a little flattened and posterior margin weakly biangulate. Auricle indistinct, post dorsal margin sloping and merging into posterior curve. Ventral and anterior margins broadly rounded. Anterior dorsal margin sloping steeply into prominent forward-facing beaks. Umbo prominent, projecting. Adductor muscle scars raised, and extending into umbonal cavity, usually visible as opaque rays from the outside.

Hinge weak, cardinal tooth absent. Ligament mostly internal on a sunken resilifer and one quarter the length of the dorsal margin.

Sculpture of weak concentric lines and growth stops, with prominent radiating white stripes corresponding to adductor scars. Shell surface slightly glossy. Ferruginous deposits confined to anterior dorsal and posterior areas.

Larval shell (Fig. 6.8) 138–147μm in length (measured material from Norway and Denmark, N = 54)

Ctenidium with one demibranch.

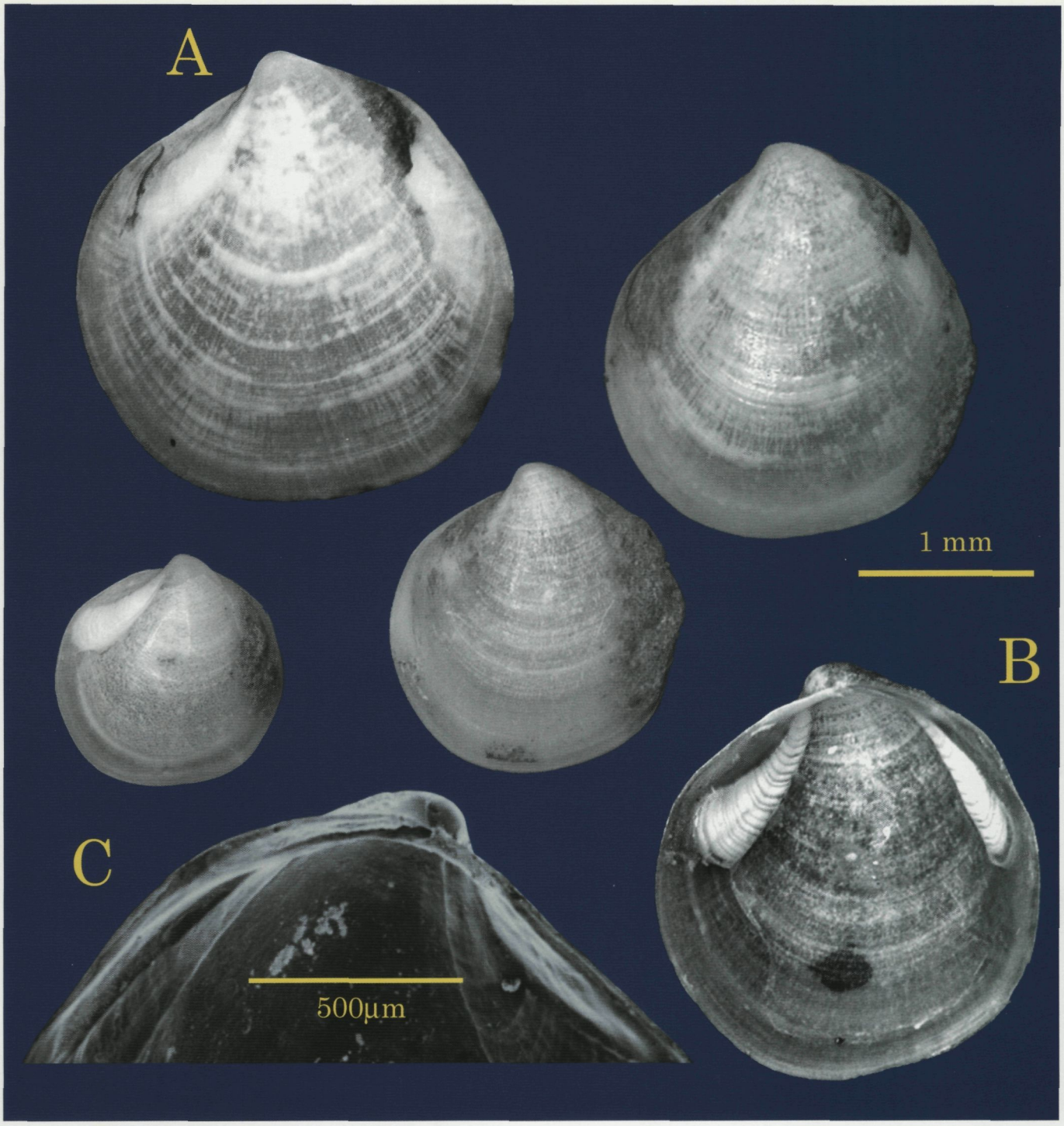


Plate 21. *Axinulus (Genaxinus) eumyarius*. **A–C**, Shells from *Challenger* st. SBC 238. **A**, growth series. **B**, internal view of right valve. **C**, scanning electron micrograph of internal of dorsal area.

Growth changes: In shells under 1mm the outline is rounded with low umbos and the lunule margin not sloping steeply. With growth the slope of the lunule margin increases and the beaks become more prominent giving a more ovate outline.

Variations: No significant variations have been observed.

Type locality: Vallo-Dyb (Cristianafjord, Norway), Lofoten, Hardangerfjord.

Type material: Possibly in the Zoological Museum, Oslo.

Distribution: *Axinulus eumyarius* was not recorded from any of the oil fields on the North Sea continental shelf and there are no other records

for the British shelf elsewhere. It was present in samples from the Troll field at depths of 170m. It is a rather uncommon species in the AFEN (west of Shetland) cruise material, occurring at stations between 900 and 1100m depth. *A. eumyarius* is present in several of the *Challenger* stations at a similar depth. In Norway and other N. Atlantic localities Kurt Ockelmann has noted this species from a depth range of 50–1350m.

Map 10. Distribution of *Axinulus (Genaxinus) eumyarius* in North Sea oil fields.

Mendicula ferruginosa

(Forbes, 1844)

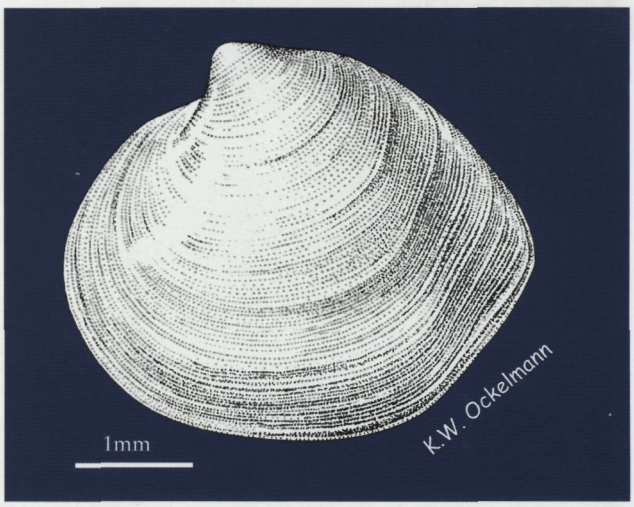
Plates 3D, 22

Kellia ferruginosa Forbes, 1844: 192

Lucina ferruginea/ferruginosa Forbes, 1851: 216,217,235.

Axinus ferrugineus Locard, 1886: 256

Thyasira (Mendicula) ferruginea (Locard, 1886):- Payne & Allen, 1991: 534–539



Description: Maximum size, 4.5mm. Fragile. Equivalve. Inequilateral. Outline subovate to subcircular, slightly longer than high. Adults with a complete coating of ferruginous deposit generally obscuring details of shell form. Posterior folds obsolete. Posterior dorsal margin long and sloping to meet ventral margin at a narrow but rounded angle. Ventral and anterior margins form a broadly rounded curve dipping into sunken anterior dorsal margin. Lunule small, excavated but visible mostly from internal view or in decorticated shells. Umbo prominent, projecting anteriorly.

Hinge weak, cardinal tubercle in LV, RV with marginal flange below beak. Ligament mostly internal on a sunken resilifer and one half the length of the dorsal margin.

Sculpture of weak concentric lines and growth stops obscured by continuous ferruginous deposit in all but the very juvenile stages.

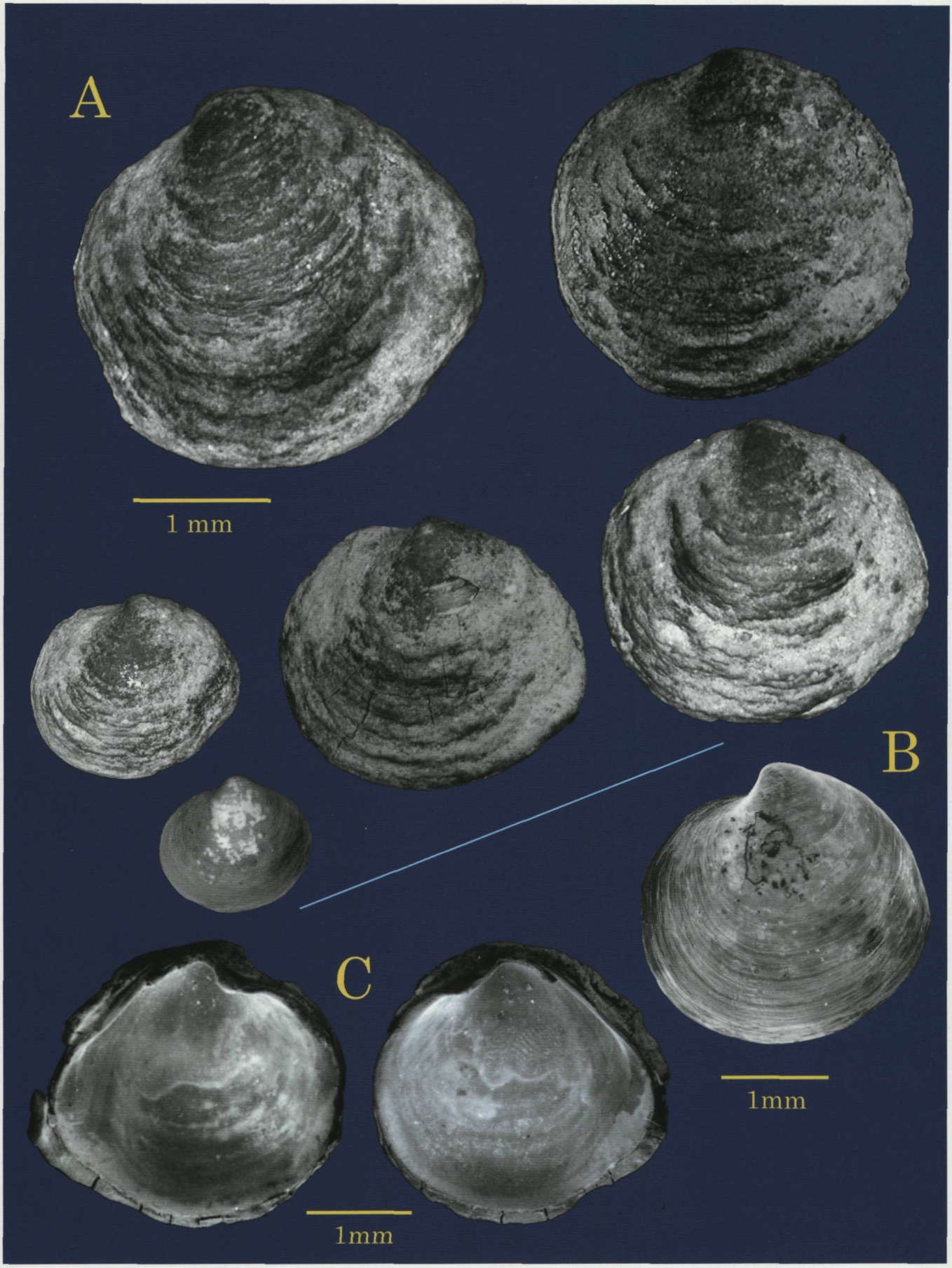


Plate 22. *Mendicula ferruginosa.* **A**, growth series from Murchison. **B**, scanning electron micrograph of left valve with deposit removed from Murchison. **C**, scanning electron micrographs of internal views of left and right valves from Cormorant.

Larval shell (Fig. 6.12) 159–171μm in length (measured material from W. Norway and Skagerak, N = 100+).
Ctenidium with one demibranch.

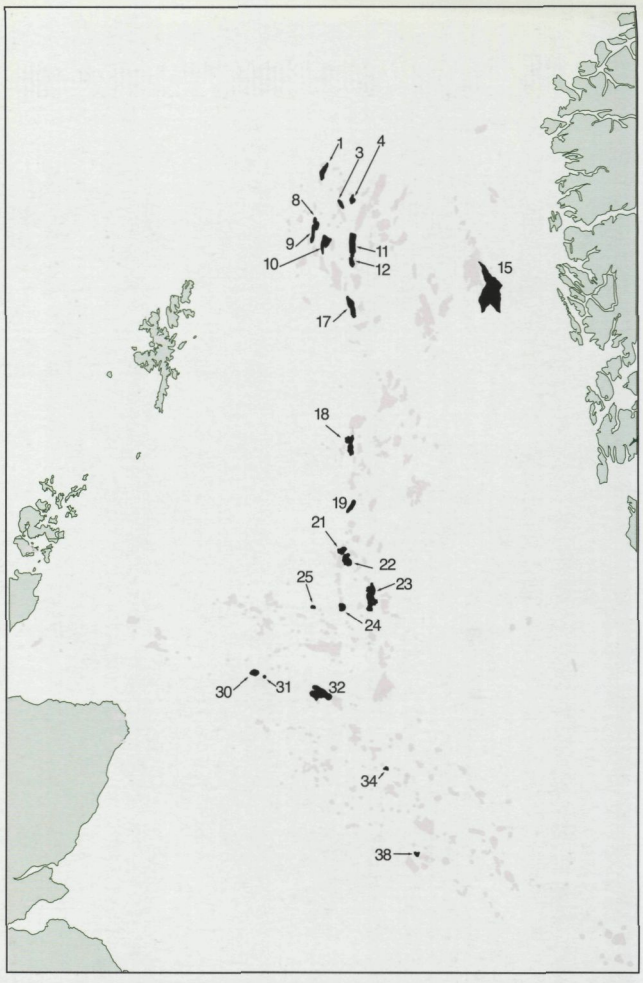
Growth changes: Juvenile shells under 1mm in length are weakly encrusted, but the outline is clearly visible. They are sub-elliptical with the posterior only slightly narrower than the anterior. They become subcircular with age and develop the distinct sunken lunule margin and subacute posterior. However, after 1mm in length they rapidly become heavily encrusted and the outline is obscured.

Variations: Owing to the rapid encrustation of the shell outline variations are not observed. Generally the subcircular outline is retained but the encrustation obscures the sunken lunule margin and subacute posterior.

Type locality: Off Crete, Mediterranean

Type material: not in National Museums of Scotland, probably lost.

Distribution: This is a widespread species in the North Sea oil fields occurring from the northern shelf edge (Magnus), south to Fulmar in depths from 85 to 185m. Specimens were also present in the Troll field at a depth of 170m. However, in the majority of samples, *M. ferruginosa* occurred only as a few individuals. There are numerous records from east and west Scotland in depths as shallow as 30m (McKay & Smith 1979, Smith & Nunn in press). The species is present in material from the AFEN (west of Shetland) and *Challenger* cruises at depths from 200-1850m. In the N. Atlantic it has a recorded depth range of 30–2740m and may have a cosmopolitan distribution.



Map 11. Distribution of *Mendicula ferruginosa* in North Sea oil fields.

Mendicula pygmaea
(Verrill & Bush, 1898)

Plate 23

Cryptodon (Axinulus) pygmaeus Verrill & Bush, 1898: 792–793, pl. 86, figs 3–4

Thyasira (Mendicula) pygmaea (Verrill & Bush, 1898):- Payne & Allen, 1991: 540–541

Description: Maximum size, 2mm. Fragile. Equivalve. Inequilateral, beaks just behind the midline. Outline subovate, slightly longer than high. Submarginal groove weak, posterior folds obsolete, posterior area a little flattened not sulcate. Posterior dorsal margin long and sloping to meet ventral margin at a narrow angle, posterior outline subacute. Anterior ventral and anterior margins form a broadly rounded curve, anterior

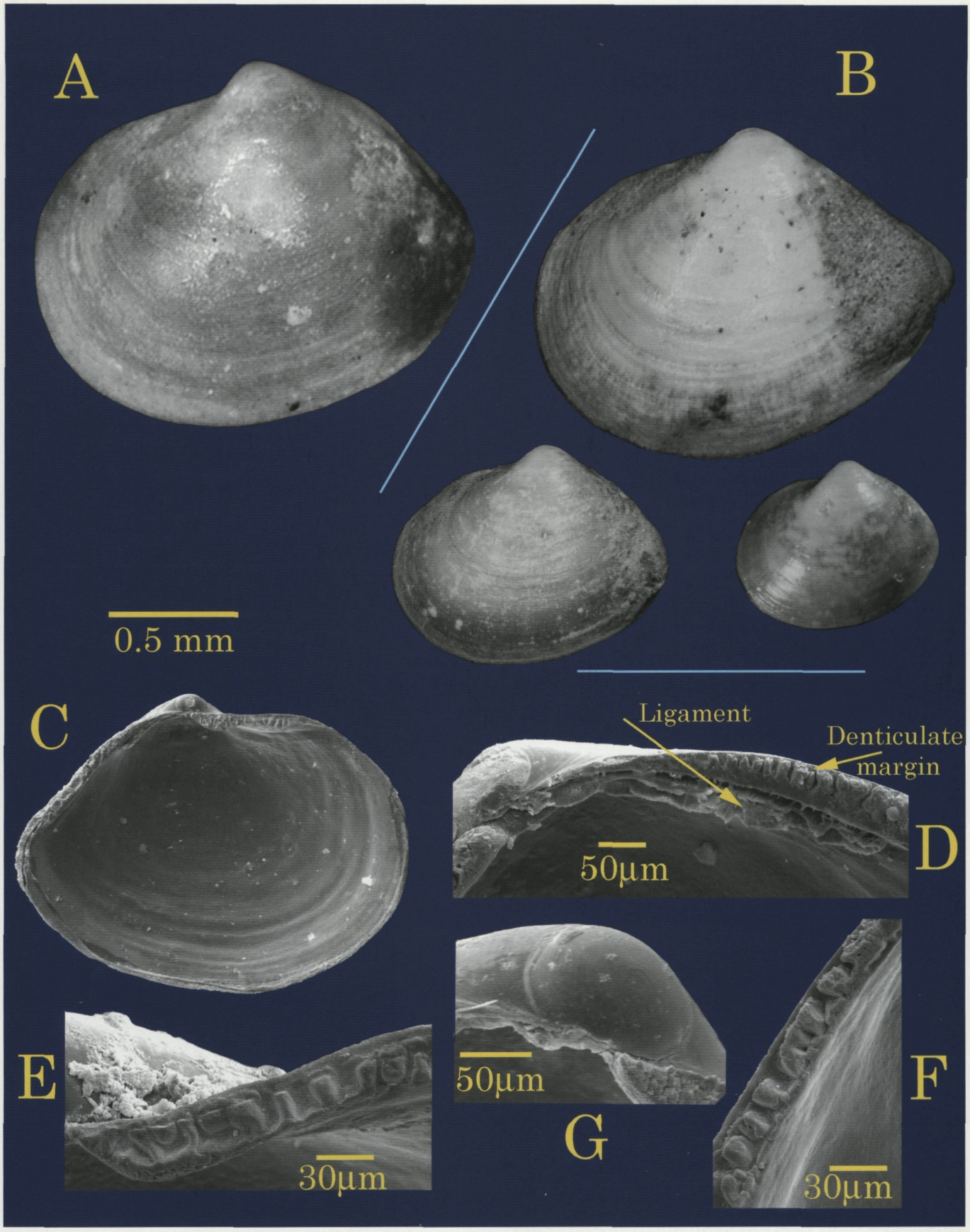


Plate 23. *Mendicula pygmaea*. **A**, Lectotype, Nova Scotia, USNM 78368. **B**, growth series, Murchison. **C–G**, scanning electron micrographs of shell from Murchison; **C**, internal of left valve. **D**, posterior hinge and ligament of right valve. **E**, anterior dorsal denticulate margin. **F**, posterior dorsal denticulate margin. **G**, prodissoconch.

dorsal margin straight not sunken. Umbo prominent, projecting anteriorly.

Hinge with a small cardinal protuberance in the right valve and a corresponding depression in the left valve. Ligament mostly internal on a sunken resilifer and one half the length of the dorsal margin. Anterior and posterior dorsal margins minutely denticulate.

Surface slightly glossy, sculpture of weak concentric lines and growth stops. Ferruginous deposit over posterior area and to a lesser extent on anterior dorsal area.

Larval shell (Fig. 6.11) 132–141μm in length (measured material from Iceland and W. Norway, N = 40).

Ctenidium with one demibranch.

Growth changes: Growth changes are not marked and only the posterior outline changes from narrowly rounded to subacute.

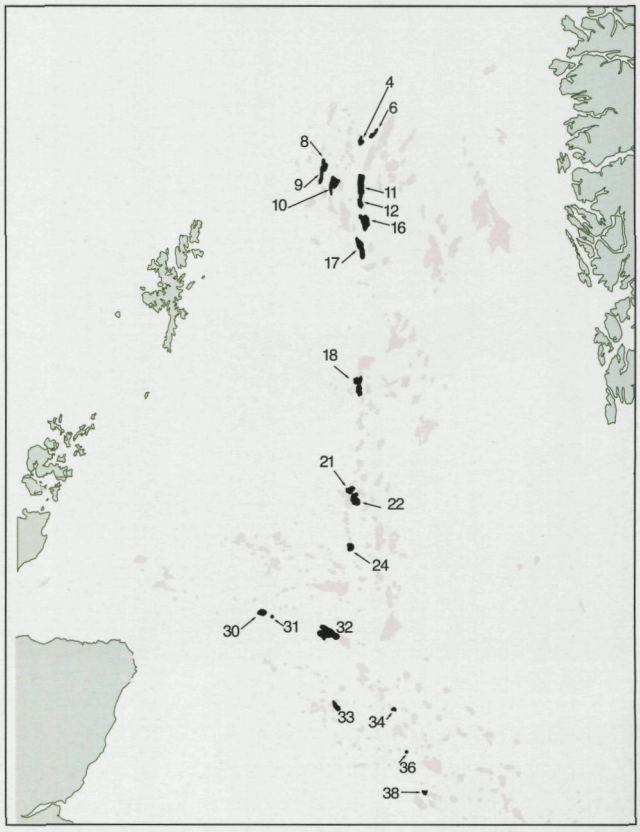
Variations: None of note

Type locality: Off Nova Scotia

Type material: 1 shell, Lectotype, USNM 78368

Remarks: The denticulate dorsal margins have not been previously reported and as the type is a long dried complete shell we could not ascertain whether this character is present. An examination of fresh material from the north west Atlantic would be of interest.

Distribution: This species has been found, often abundantly, in samples from many of the oil fields as far south as Fulmar in depths ranging from 85 to 161m. It is apparently absent from the fields in deeper water towards the shelf edge. On the west coast of Scotland, *T. pygmaea* has been recorded from Raasay Channel (Killeen pers. obs.) and in the Firth of Lorn where it is locally common in muddy gravel at depths of 20-100m (Smith & Nunn in press). We have not recorded this species in samples from the AFEN or *Challenger* cruises. Kurt Ockelmann has recorded material from a total depth range of 30 to more than 2000m. It is apparently common in the high arctic regions but a change in outline and maximum size from north to south suggest a geographical cline or a complex of closely related species. Examination of voucher material from the Forties field collected in 1978 confirms that the records of *T. subtrigona* in Hartley (1984) are actually *M. pygmaea*. Similarly, we suspect that *T. subtrigona* recorded within the *Thyasira* 'complex' by Eleftheriou & Basford (1989) were also *M. pygmaea*. It should be noted that *T. subtrigona*, originally *Poromya subtrigona* is not a thyasirid. It belongs to the Galeommatoidea and is related to *Kellia cycladia* S. V. Wood, 1851 (Ockelmann pers. obs.)



Map 12. Distribution of *Mendicula pygmaea* in North Sea oil fields.

Species not recorded from North Sea oilfields but known from adjacent regions.

Thyasira (Parathyasira) dunbari
Lubinsky, 1976

Plate 24A–E

Thyasira dunbari Lubinsky, 1976: 1667-1670

Thyasira equalis :- Ockelmann, 1958:-104–110, fig. 7, not *Cryptodon equalis* V&B, 1898

Remarks: This is a high arctic species described from the Canadian-Greenlandic region and is widely distributed in the arctic waters of East Greenland (Ockelmann, 1958). It is cold stenothermal and exhibits temperature submergence by appearing at great depth just NE of the Faroes. It has been listed in an environmental impact report from Norway and from the BIOFAR (Faeroes) programme (Stokland, 1992) but we have been unable to confirm the identity. Our understanding of this species is based on examination of type material from the National Museum of Canada (NMC 75803–75804)

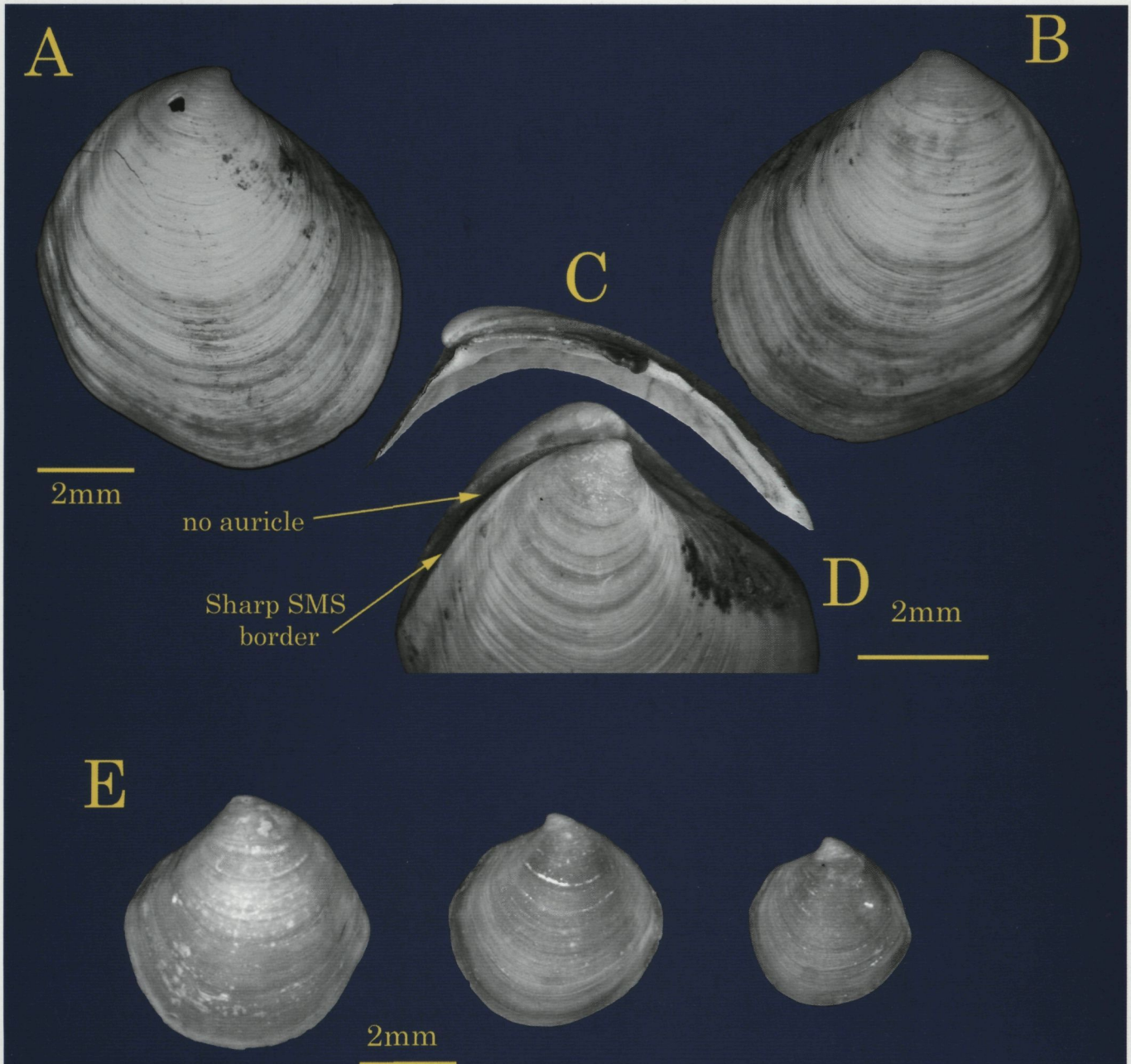


Plate 24. **A–D**, *Thyasira (Parathyasira) dunbari*, Paratypes, Arctic Canada, NMC 75804. **A**, right valve. **B**, left valve. **C**, hinge of right valve. **D**, oblique apical view. **E**, size series from Jan Mayen.

The type material represents very large shells (7mm in height), which are distinctly pyriform in outline. The posterior area is similar to that of *T. equalis* in that there is a well defined submarginal sulcus without an auricle and the posterior area is flattened, not sulcate. However in the more typical state it is very similar to *T. equalis* in that it is not greatly expanded antero-ventrally. It differs in that the posterior area is poorly defined and the posterior margin is not truncated but is narrowly rounded The larval shell (Fig. 6.6) is slightly larger and lacks the radial folds. The anatomy is also similar to that of *T. equalis* (Ockelmann pers. obs).

Thyasira subovata

Jeffreys, 1881

Plate 25A–B

Axinus subovatus Jeffreys, 1881: 704, pl. 61, fig. 8.

Remarks: This species was recorded by Madsen (1949) from Iceland in depths around 200m. This record was accepted by Payne & Allen (1991) but we believe it to be erroneous and to represent *T. obsoleta*. We believe that *T. subovata* is restricted to bathyal depths and is a common element of the slope fauna surrounding the Rockall Trough. Specimens from this region collected by the *RRS Challenger* are illustrated.

Leptaxinus minutus

Verrill & Bush, 1898

Plate 25C–D

Leptaxinus minutus Verrill & Bush, 1898: 797, pl. 89, figs 3–5.

This species has been found at shelf depths around Bergen, Norway and a single animal has been found from Iceland (Ockelmann, pers. obs). It is possible that this species may occur in the northern North Sea.

It is a small species around 2mm in diameter, rather inflated, ovate in outline with beaks a little behind the mid-line and height a little less than the length. There is small auricle and the rather straight dorso-posterior margin is sulcate and bounded by a distinct ridge on either side. There is no posterior sulcus or flattening of the posterior area. The hinge is strong with, in the RV, a large projecting cardinal, a long lateral groove along the straight dorso-posterior margin and a short lateral groove on the antero-dorsal margin. In the LV there is a cardinal socket but no obvious lateral teeth, the margins of the shell fitting into the corresponding grooves of the RV.

Axinopsida orbiculata

G. O. Sars, 1878

Plate 25E–H

Axinopsida orbiculata Sars, 1878: 63-64, pl. 19, fig. 11

Remarks: This is a common arctic and subarctic species which does not range into the northern North Sea area.

It reaches 8mm in diameter, is circular in outline with a distinct lunule and lacks any posterior folds or sulci. There is a distinct cardinal tooth in the right valve and a corresponding socket in the left valve. The periostracum is persistent and yellowish in colour. The development is direct and the embryonic shell is very large, around 300μm in length.

The ctenidium consists of both demibranchs.

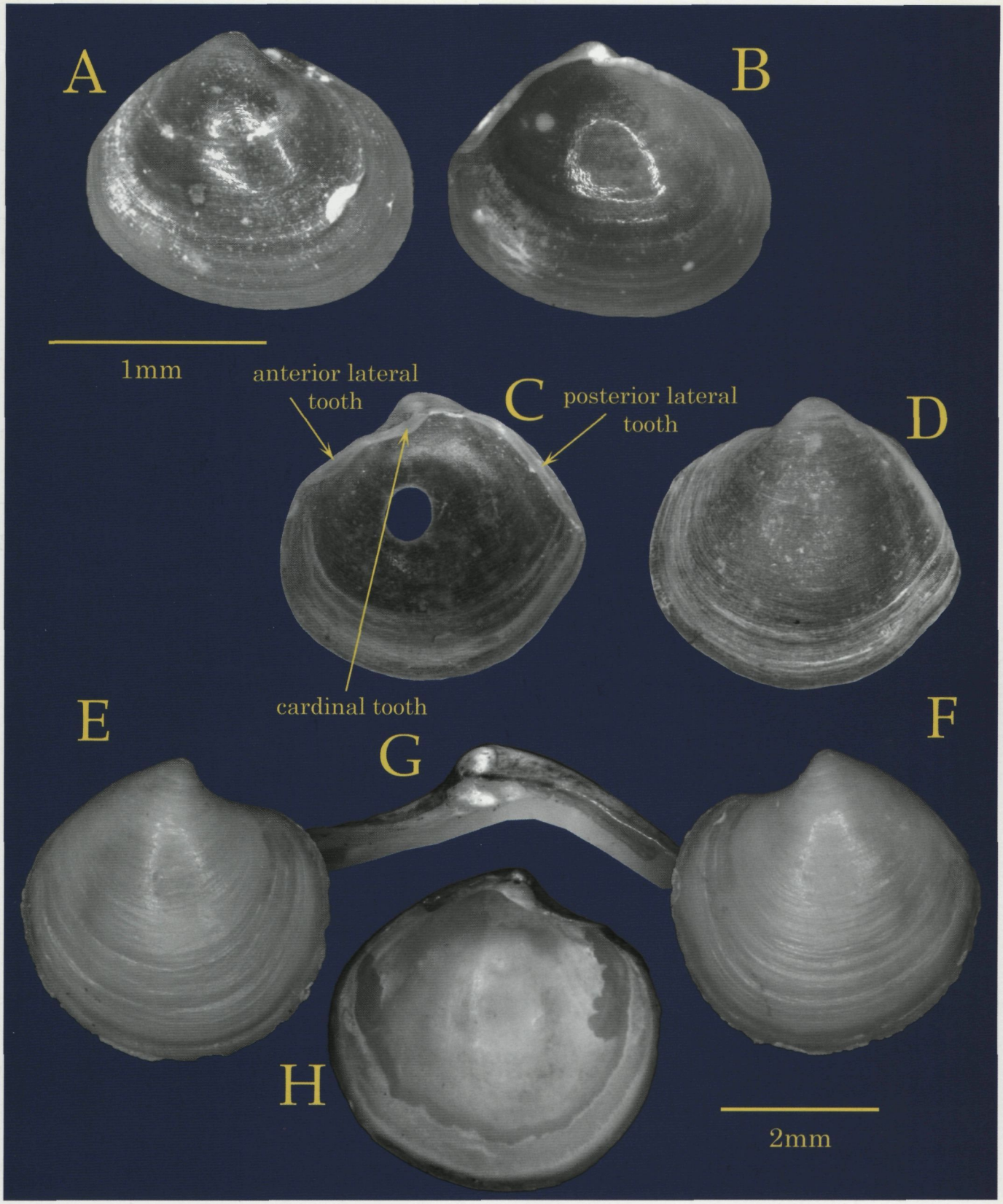


Plate 25. **A–B**, *Thyasira subovata*, Rockall, ES137. **C–D**, *Leptaxinus minutus*, off Bergen. **E–H**, *Axinopsida orbiculata*. Spitzbergen, NMW. 1955.158. **E**, right valve. **F** ,left valve. **G**, hinge of right valve. **H**, internal of left valve.

Nomenclature and Taxonomic History

Notes on the genera and subgenera

Payne & Allen (1991) give the most recent indication on the use of the available generic and subgeneric names and this is the same as adopted by Smith & Heppell (1991). It is, however, often difficult to follow the rationale behind the allocation of the species to the subgenera.

Considering only those species included here, there is more variation within *Thyasira* s.s. than there is between *Thyasira* and *Parathyasira*. In terms of outline and hinge structures *T. succisa* is as distinct from *T. flexuosa* as is *T. equalis*. Payne & Allen (1991) do not introduce any new generic taxa and as they state under *Parathyasira* and *Mendicula*, there are species that doubtfully fit into these subgenera. The consequence is that their usage of subgenera becomes loose, e.g. they include one species in *Parathyasira* that has a single demibranch, yet use this character as indicative of *Axinulus* and *Mendicula*. As a result of adopting only those subgenera already defined for the many forms in their review, it is now not easy to give tight generic and subgeneric definitions. We do however, sympathise with their reluctance to modify further the generic systematics based only on their material. It is sufficient to say that the generic systematics still needs revision. We cannot review the generic systematics of the Thyasiridae as a whole, and cannot comment on the rather radical classification proposed by Bernard (1983) and adopted by Coan *et al.* (2000), where the family is divided into the Thyasirinae and Axinopsidinae, with the latter including *Axinulus* and *Mendicula*.

Alternatively, we consider the generic placements of the species under consideration, and give some definition to these.

Genus *Thyasira* Leach in Lamarck, 1818

Type species *Tellina flexuosa* Montagu, 1803

In the context of this work those species that possess both pairs of demibranchs are included in the genus *Thyasira*. We recognise that the single demibranch condition is probably neotenous and therefore probably polyphyletic but at this time we cannot link the neotenous taxa to their paired demibranch ancestors.

The shells are small to minute, ovate to obliquely ovate in outline with a sulcate or truncated posterior area and usually sinuate posterior margin. The hinge is weak with or without a single cardinal tubercle or flange.

There are other generic taxa that contain species with paired demibranchs but none are considered to have representatives in the shelf waters of the NE Atlantic.

Conchocele Gabb, 1866 (pl.26A) shells are usually large, obliquely ovate in outline with the beaks well in front of the midline, and possess an acutely angled second posterior fold. The gills are large and fleshy (Nakazima, 1958). This genus is widely recognised from many parts of the world and includes the species *C. excavata* that is, in our view, erroneously placed in *Thyasira* by Payne & Allen (1991).

Prothyasira (pl.26C) was erected by Iredale (1930) for species with a bisulcate form but where the second posterior fold is very strong and thus resembles *Conchocele*. Anatomical data may clarify the proximity of *Prothyasira* to *Thyasira* and *Conchocele*.

Axinus Sowerby, 1821 have quadrate shells and the mantle bears modified extensions.

S.g. *Thyasira* s.s.

Type species *Tellina flexuosa* Montagu, 1803

Shells are typically between 5–15mm, bisulcate with both a submarginal and posterior sulcus resulting in a bisinuate posterior margin. They are approximately

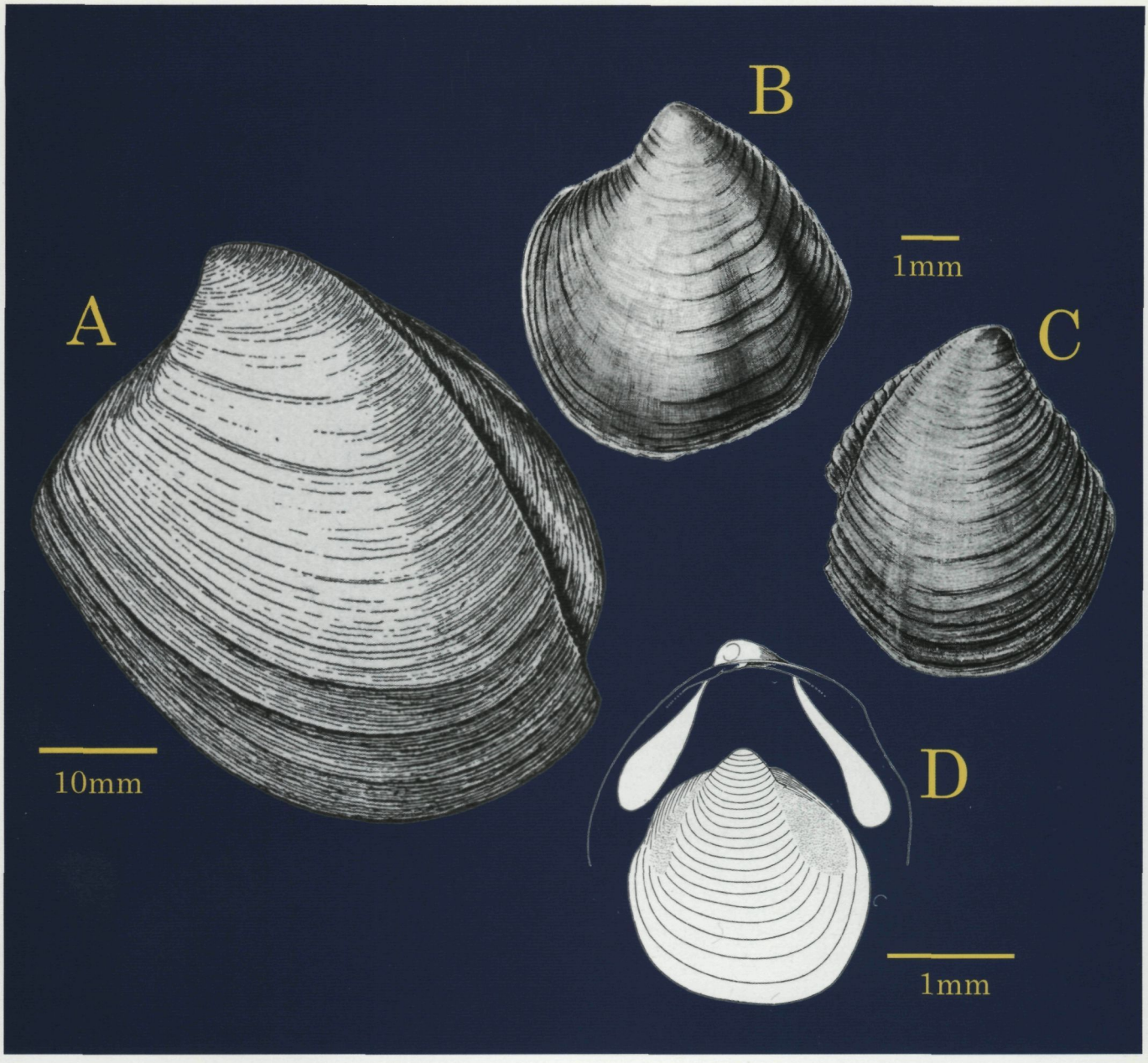


Plate 26. **A**, *Conchocele bisecta*, type of genus, after Dall, 1901. **B**, *Parathyasira resupina*, type of genus, after Iredale, 1930. **C**, *Prothyasira peroniana*, type of genus, after Iredale 1930. **D**, *Genaxinus albigena*, type of genus, after Hedley, 1907.

equilateral, ovate to subcircular in outline with prominent beaks. The hinge is weak with a small laminar cardinal flange and corresponding depression.

The ctenidium is large, of two demibranchs with numerous tightly spaced filaments. The palps are mostly smooth with few sorting ridges.

They are predominantly upper to middle shelf in distribution and their range is worldwide.

Under this definition, *T. flexuosa, T. polygona, T. gouldi* and *T. sarsi* can be included with a high degree of certainty. However, the obliquely pyriform, non-sulcate shells of *T. obsoleta* and *T. succisa* cannot be included within this definition. Furthermore, the strong hinge of *T. succisa* is a quite distinctive character seen only to a similar degree in *Leptaxinus* Verrill & Bush. The ctenidium of *T. succisa* has both demibranchs but that of *Leptaxinus* only one.

In this work we assign *T. obsoleta* and *T. succisa* to *Thyasira sensu lato*.

S.g. *Parathyasira* Iredale, 1930

Type species *Parathyasira resupina* Iredale, 1930

Shells are typically flattened posteriorly with only a submarginal sulcus surrounding the ligament. The posterior margin is angled and truncated but not sinuate. They are approximately equilateral, ovate to ovate-rhomboidal in outline with prominent beaks. The hinge is weak, some with a small laminar cardinal flange and corresponding depression.

Anatomical details of the type species are unknown but if they are similar to those of *T. equalis, T. granulosa and T. dunbari* then: the ctenidium has both demibranchs, the labial palps are very small but with a few distinct sorting ridges. A marked difference between the gills of these *Parathyasira* species and those of *Thyasira sensu stricto* is their much weaker development of abfrontal tissue on the gill filaments. These differences are not great and because of this we retain *Parathyasira* as a subgenus of *Thyasira*.

The introduction of this Australian subgenus in a European context first appears in Høisaeter (1986) following personal communication with K. Ockelmann (Høisaeter, pers. comm.) and then in Payne & Allen (1991). Payne & Allen (1991) note the similarity between *T. resupina* (pl. 26B) *and T. granulosa* in both outline and faint radial striations. The 'granular surface' character is considered here to carry little weight at the subgeneric level and more weight is given to the general form an anatomical characters. Consequently smooth (*T. equalis* forms) and granular (*T. granulosa* forms) species are considered congeneric.

Genus *Axinulus* Verrill & Bush, 1898

S.g. *Axinulus*

Type species *Axinulus brevis* Verrill & Bush, 1898

Shells are posteriorly sloping or a little flattened with a weak submarginal groove defining a low auricle. The posterior margin is weakly biangulate to curved. They are approximately equilateral, oval in outline with prominent beaks. The hinge is weak without cardinal extensions. The ctenidium has only a single demibranch with few, well spaced filaments. The palps are mostly smooth with few sorting ridges. The lateral pouches are large and simple.

The inclusion of *A. croulinensis* is not contentious but that of *A. eumyarius* needs discussion. The buttressed adductor scars of *A. eumyarius* are also found in *G. albigena* Hedley, 1907 which is the type species of *Genaxinus* Iredale, 1930 (pl. 26D). The question is whether the adductor scar character is sufficient to give subgeneric status to those species. As with the other Australian taxa there is no supporting anatomical data. We adopt Genaxinus because it defines a well recognised group of species.

S. g. *Genaxinus* Iredale, 1930

Type species *Thyasira albigena* Hedley, 1907

As *Axinulus* but adductor scars raised, opaque.

To include *A. eumyarius* and *A. albigena*.

Genus *Mendicula*

Type species *Lucina induta* Hedley, 1907

Shells are posteriorly sloping or a little flattened with a weak submarginal groove defining a low auricle. The posterior margin is narrowed the anterior broadly rounded. They are inequilateral with beaks to the posterior, in outline longer than high, subcircular to subovate with low beaks. The hinge has a cardinal flange or tubercle. They are variously encrusted with a ferruginous deposit. The ctenidium has only a single demibranch with few, well spaced filaments. The palps are mostly smooth with few sorting ridges. The foot is vermiform but with a small heel. The lateral pouches are large and occasionally divided.

Hedley (1907) describes the complete ferruginous deposit on the shell and his species is very similar to *M. ferruginosa*. The inclusion of *M. pygmaea*, as Payne & Allen (1991) state for many of their species, is speculative. The grouping of these taxa depends on the subovate outline and single demibranch characters alone. We appear to be the first to note the denticulate margins in *M. pygmaea* and this character may be shared by the many other similar species of *Mendicula*. It is, however, not shared by *M. ferruginosa*.

Notes on the species

Thyasira (Thyasira) flexuosa

Originally described by Montagu from the south coast of England, this species has subsequently been recorded from localities across the northern hemisphere: Japan (Dunker 1882), Pacific coasts of the USA and Canada (Coan *et al.* 2000), Atlantic coasts of USA (Abbott 1974) and Europe, and the Mediterranean (Sabelli *et al* 1992). The validity of this range is questionable and recent Japanese literature excludes it (Higo *et al*, 1999). Pacific American records are also doubtful with Coan *et al.* (2000) retaining synonymy with *T. gouldi*. Payne & Allen (1991), however, restate the Pacific occurrence. Ockelmann (1958) suspected that *T. flexuosa* has a boreal/lusitanian range and excluded it from the circum-subarctic and arctic provinces. He now believes that it is restricted to the NE Atlantic and Mediterranean. This serves to illustrate the uncertainty of the literature data on identification and range of this and other *Thyasira* species. Confirmation of the true range and status of the many forms confused with *T. flexuosa* must follow a cosmopolitan revision based on actual material not on literature records and is beyond the scope of this work. The validity of the taxon in Europe is not in question as the type locality is known (Falmouth *fide* Montagu, 1803) and only *T. flexuosa* has ever been recorded from the inshore waters of the south of England. The type description is clear but the figure cited by Montagu in Donovan (1802, II: pl. 42, fig. 2 as *Venus sinuosa* Pennant) shows a distorted shell with a dent in the ventral margin. Jeffreys (1864) states that this is a shell of *Thracia distorta*.

Thyasira (Thyasira) polygona

This species was recently reviewed by Killeen & Oliver (2002a) and recognised as a species distinct from *T. flexuosa*. It was first described by Jeffreys in 1864 but had been abandoned and not recognised by subsequent British malacologists. It was however regarded (Dall, 1901) as a synonym of the eastern Atlantic species *T. obesa* (Verrill, 1872) and the Caribbean species *T. trisinuata* (d'Orbigny, 1853). A similar form exists in the Mediterranean under *T. plicata* (Philippi, 1836) and the relationships of all of these taxa remains to be resolved.

Thyasira (Thyasira) gouldi

This species was first recognised as distinct from *T. flexuosa* by Philippi (1845) in a paper that reviewed the first edition of "Invertebrates of Massachusetts" by A. A. Gould (1841). Gould initially stated that his shells were indistinguishable from the European examples of *T. flexuosa* and it is unclear whether Philippi based his decision to erect a new species on Gould's description alone or whether he also saw shells collected by Gould. Gould, in a later edition (Gould & Binney, 1870) acknowledged the new species and it became an accepted part of the western Atlantic fauna.

The first records outside American waters were by Ockelmann (1958) who recorded it from Greenland, Faeroes and Northern Norway. The first British reference is in Seaward (1990) which

refers to Ockelmann (pers. comm.) who noted material from Shetland in the USNM.

In the early 1970's a large population was discovered in Loch Etive on the west coast of Scotland and was subsequently published upon (Blacknell, 1973; Blacknell & Ansell 1974, 1975). The identity of this population was confirmed by K. Ockelmann (pers. comm. in Blacknell, 1973). Blacknell & Ansell (1974) refer to a paper in press drawing attention to *T. gouldi* as a species new to the British fauna but this seems never to have appeared. Consequently the Loch Etive shells had not been illustrated outside of Blacknell's thesis (Blacknell, 1973) and neither had his differential diagnoses from *T. flexuosa* been widely available. Examination of a large quantity of material from around Scotland led Killeen & Oliver (2001a) to revise the status of *T. gouldi* in British waters. Not only did they confirm the presence of this species in Shetland but also recorded it from a range of localities on the western coast of Scotland and from the Firth of Forth in the east.

Thyasira (Thyasira) sarsi

This species was described by Philippi (1845) in a short paper on the genus *Axinus*. The description is in Latin, is short and is accompanied by a simple reference to the origin "Norwegian Seas". There is no indication of the source of the material or to type material. One may assume that the shells were sent to Philippi by M. Sars as in 1864 M. Sars published a detailed description of the anatomy of *T. sarsi* (M. Sars, 1864). It was illustrated by G. O. Sars (1878) and is known from many localities along the entire Norwegian coast (Høisaeter, 1986, Brattegard & Holthe, 1997).

It is cited in Seaward (1990) but this refers to the material examined by Southward (1986) and Dando & Southward (1986) collected from Bergen. It was subsequently added to the British list by Smith & Heppell (1991) and Dando *et al.* (1991), but its detailed occurrences are contained within the 'grey literature' on impact surveys from the North Sea oil fields.

In the North Sea *T. sarsi* is highly concentrated around the well heads and drilling platforms. In the Norwegian fjords it is widely distributed and together with *T. flexuosa* increases in numbers when there is organic enrichment. We cannot explain why in the North Sea *T. sarsi* responds positively to hydrocarbon enrichment, but *T. flexuosa* does not. This has led us to examine Norwegian shells more closely and some small differences are apparent, notably the greater expression of the first posterior fold, the shorter auricle and shorter ligament. Overall the Norwegian shells resemble large more rounded *flexuosa,* and we can understand why *T. sarsi, T. flexuosa* and *T. gouldi* have so often been confused.

Thyasira (Parathyasira) equalis

This species was first described from waters off New England (Verrill & Bush, 1898) and then recorded from SW Greenland Norway by Ockelmann as *Thyasira* spec. a (1958). In British waters it was discovered by McIntyre (1961) from the Fladen Ground and identified by Kurt Ockelmann. It is considered not to be a genuine arctic species but extends northward following influxes of warm Atlantic water (KWO). The record of Soot-Ryen (1966) from 1100m off Nova Scotia is doubtful. Miloslavskaja (1970) reports it widely from the arctic and subarctic regions but these may be predominantly misidentifications of *T. dunbari.*

Thyasira (Parathyasira) granulosa

The early nomenclature of this species is complex and has resulted in a variety of dates of

publication and confusion as to the choice of Jeffreys and Monterosato as authors. Concerning the latter there is no publication by Jeffreys in which he describes this species and in his papers and those of Monterosato, all references are to an unpublished manuscript name. The first appearance of the name is in Monterosato (1872) but this consists simply of "*Axinus granulosus*, Jeffr. MS. Palermo!"with no description and should be considered a *nomen nudum*. Monterosato (1874) refers to the Jeffreys manuscript name but accompanies it with a brief description that includes reference to the sculpture. This citation is sufficient to distinguish the taxon and can be regarded as a valid introduction of the name that takes Monterosato as the author. Jeffreys (1881) refers to *T. granulosa* under *Axinus orbiculatus* Seguenza which can be regarded, doubtfully, as a synonym (Lamy, 1920). This paper contains the first illustration of *T. granulosa*, which is re-used by Nordsieck (1969) and Parenzan (1974). These show a strongly biangulate shell which is not represented in material used in this paper. The only recent illustration is in Ardovini & Cossignani (1999), erroneously labelled *T. flexuosa*, and this Mediterranean specimen also lacks strong angles.

Thyasira granulosa has also been recorded from the Gulf of Mexico and West Indies (Dall, 1901) but not from the temperate and boreal waters of the north-west Atlantic. Payne & Allen (1991) recorded no specimens from any of their deep water Atlantic material. The overall geographic range (Mediterranean, Caribbean, north-east Atlantic) and bathymetric range (100 – 1800m) are considerable. There is some cause for enquiry here, and the possibility of more than one granulose taxon being present should not be excluded.

Thyasira obsoleta

Although described by Verrill and Bush (1898) from American waters it was known in Europe much earlier but never recognised through the confusion with *A. croulinensis*. It was not until 1964 that the name *T. obsoleta* became part of the European fauna and arose from research carried out by Kurt Ockelmann. This work was not published as such and is referred to as "personal communication" in Bowden & Heppell (1968).

As noted under *A. croulinensis*, Jeffreys (1864) description and figure is of *T. obsoleta*. Subsequently, other authors followed this and used *A. croulinenis* when recording *T. obsoleta*. The figure of *T. croulinensis* in Sars (1878) is clearly that of *T. obsoleta*. Sars (1878) notes a synonym as *Axinus pusillus* M. Sars and this can be traced back to M. Sars (1870) who cites M. Sars (1868 p. 257). This name is preoccupied by *Axinus pucillus* [*sic*] Brown, 1841 (Sherborn, 1922) and is noted as a *nomen nudum* by Nordsieck (1969).

A number of varietal names of other species can be linked to *T. obsoleta*. *Axinus flexuosus* var *rotunda* Jeffreys, 1881, *Axinus croulinenis* var. *transversa* Locard, 1898, and *Axinus croulinensis* var *truncatus*, Marshall, 1914 are all cited as such by Payne and Allen, 1991. *Axinus flexuosus* var *rotundata* Jeffreys in Locard, 1898 is a mis-spelling for *rotunda*. No figures of these varieties were published and no type material is available for var. *rotunda* of Jeffreys (Warén, 1980). The type of var. *truncatus* is extant [NMW. 1953.183] and is a large *obsoleta* from the Shetland Isles.

Thyasira succisa

Described originally by Jeffreys (1876) as a variety of *Leptaxinus incrassatus*, he recorded it from a number of localities in the north-east Atlantic and Mediterranean ranging from outer shelf to bathyal depths. Dall (1901) was the first to give specific rank and placed *T. succisa* in the sub-

genus *Axinulus*. The ctenidium consists of two demibranchs and therefore generic placement in *Axinulus* or *Leptaxinus* is not appropriate.

Smith & Heppell (1991) include it in their checklist but as a deep water species only and its recognition from the northern North Sea oil fields is very recent and appears in 'grey literature' only.

Thyasira (Leptaxinus) incrassatus is a bathyal to abyssal species and not included here. Although similar in outline it has a thickened hinge plate and strong submarginal folds.

Axinulus (Axinulus) croulinensis

This species was first described by Jeffreys in 1847 from shells collected off the Crowlin Islands, off Skye, west coast of Scotland. Since then it has been the subject of confusion primarily with *T. obsoleta* that resulted from the description and illustration given by Jeffreys in his "British Conchology" (1864). This later description identifies an angular form clearly that of *T. obsoleta* and is most likely the basis for most subsequent identifications by other authors. The extensive citation list given by Payne & Allen (1991) shows how few were accompanied by illustrations thus rendering clarification impossible without reference to the original specimens.

A neotype was selected by K. W. Ockelmann and subsequently published by Warén (1980). The selected shell was originally identified as *T. flexuosa* and came from Loch Fyne

Axinulus (Genaxinus) eumyarius

This species was first described by M. Sars (1870) from Norwegian waters and was soon found by Jeffreys (1876, 1881) in the dredgings of the *Valorous*, *Lightning* and *Porcupine* expeditions. It has been reported widely from the North Atlantic (Payne & Allen, 1991).

Mendicula ferruginosa

This distinctive species has been frequently recorded since its discovery in the Mediterranean by Forbes (1844).

It does however have a confused nomenclature which was recently clarified by Coan et. al, 2000.

To summarise:

It was noted by Winckworth that in Sherborn there were two entries for *Kellia ferruginosa* one authored by Forbes, 1844 and another by Morris, 1843. From this it was concluded that Forbes' *Kellia ferruginosa* was preoccupied and Winckworth introduced the replacement name *Thyasira ferruginea* Winckworth, 1932. This is the name used in Tebble, 1966. Bowden & Heppell (1968) then noted that the name *ferruginea* had previously been used by Locard (1886) and concluded that the correct name was *Thyasira ferruginea* Locard, 1886. Recent Scandinavian checklists assign the author and date to Forbes 1851 and this refers to the occurrence of both *ferruginea* and *ferruginosa* spellings in tables included in that paper.

However on closer examination of Morris, 1843 it was found that he did not erect a new species called *Kellia ferruginosa* he placed the *Mya ferruginosa* of Montagu, 1808 in the genus *Kellia*. Consequently Forbes' *Kellia ferruginosa* is not preoccupied and no replacement was ever necessary.

Mendicula pygmaea

This species was described from the NW Atlantic by Verrill & Bush (1898) and was first noted in European waters from Iceland (Madsen 1949). More recently it was recorded from Norway (Høisaeter 1986), the Skagerrak (Wikander 1989) and in British waters it was first noted from the northern sectors of the North Sea (Seaward 1990).

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