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Kurt Ockelmann's unpublished studies on the Thyasiridae (Mollusca: Bivalvia) of the North Atlantic, held in the Natural History Museum of Denmark

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Abstract. The archive of illustrations and graphics relating to the research of Kurt Ockelmann (1924–2021) on the bivalve family Thyasiridae is reviewed. Although he published only one short paper on the family, the archive reveals that he undertook a substantial series of studies and shows his continuing influence on the taxonomy and life history of this family in the North Atlantic. Ockelmann was the first to recognise amphi-Atlantic species, their life habits and larval biology. He mapped the distribution of 19 species, drew their prodissoconchs and made superb drawings of the adult shell and their hinges. He made accurate anatomical diagrams of representative species of the genera. Given the excellence of illustrations many are reproduced here, as they are among the best available and a valuable resource when identifying species.

Keywords. Ockelmann, history, Thyasiridae, retrospective, archive.

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Introduction

Kurt Wolfgang Ockelmann (1924–2021) was one of Denmark's most respected and well-loved marine biologists of the twentieth century. The photograph in Fig. 1 was taken at the celebration conference in Helsingør in 2014 to mark his 90th birthday. Ockelmann's early life from German soldier to Danish marine biologist is told in Kristiansen (2021) and a full retrospective of his scientific life will be found in Jensen & Dinesen (in prep). His interests strayed across a wide range of taxa and found him following whatever took his curiosity throughout his forty years at the Marine Biological Laboratory, Helsingør. His primary interest was in the Mollusca, probably sparked by his mentor, the great Danish biologist, Gunnar Thorson (1906–1971) (Ankel 1972). Through Thorson, Ockelmann became familiar with the collections in the Zoological Museum, Copenhagen (now incorporated into the Natural History Museum of Denmark) and in particular the large collections from Greenland made by Thorson during

the Godthab expeditions of the early 1930s (Higgins 2010). Ockelmann began work on the bivalves of Greenland publishing an account on the genus *Yoldia* Møller, 1842 in 1954 (Ockelmann 1954) and a large monograph on all the bivalves in 1958 (Ockelmann 1958). It was in this latter study that he encountered the Thyasiridae Dall, 1900 (1895) and the taxonomic difficulties posed by these, rather nondescript, small white bivalves. Following up on this study, in 1959, he spent time in the United States National Museum studying the type material in the J.G. Jeffreys and A.E. Verrill & K.J. Bush collections where he recognised type material and, in some instances, selected lectotypes and neotypes. From this study, he wrote a short paper on the status of three species of *Thyasira* Lamarck, 1818 described by Verrill & Bush (1898) (Ockelmann 1961). Despite his long interest in the Thyasiridae, this was the last and only paper he published on them.

However, Ockelmann became known as the expert on Atlantic Thyasiridae, probably through his generosity and willingness to help anyone who came to him for advice, a trait I personally benefitted from in my study on the Thyasiridae of the UK North Sea oilfields (Oliver & Killeen 2002). In 1961, McIntyre acknowledged Ockelmann's help in identifying *Thyasira equalis* (Verrill & Bush, 1898) from the North Sea and many such acknowledgments can be found, e.g., in Bowden & Heppell (1968), Lande (1975), Lubinsky (1976), Southward (1986), Dando & Southward (1986) and Payne & Allen (1991). A reference in Bowden & Heppell (1968: 263) is especially informative: “The arrangement of British Thyasiridae given here will be modified considerably by Ockelmann, 1968 (*Ophelia*, in press)”, as it suggests a paper had been completed and submitted, but as we know, it was never published. The following acknowledgement is typical: “Thanks are also due to Dr. K. Ockelmann at Helsingør for the many ideas and the help he gave in identification during a short stay with him” (Blacknell 1973). C.M. Payne told me, when working on the deep-sea thyasirids (Payne & Allen 1991), she visited Ockelmann and recalled seeing some of the contents of his study. It is these papers that were archived by the Natural History Museum of Denmark (NHMD), under Archive number T 926 and which form the core of this paper.



Fig. 1. Portrait of Kurt Ockelmann at the conference to celebrate his 90th birthday at Helsingør Marine Biological Laboratory, 2014.

The hope was that I would be able to publish some, if not all, of Ockelmann's monograph in one or more taxonomic papers, but this will not be possible simply due to the advances made in techniques and papers published over the intervening years. Rather, this will be a commentary on Ockelmann's work, but also an opportunity to publish many of the fine graphics and illustrations that he had prepared. We may not know why this monograph was not published, but from the note in Bowden & Heppell (1968) and annotations on the illustrations, it appears that it was Ockelmann's intention to publish in the journal "*Ophelia*", which was merged into "*Marine Biology Research*" in 2005.

The Thyasiridae Dall, 1900 (1895)

Students of the thyasirids are, and have always been, few. From a conchological focus, most are non-descript, small, white bivalves with a preference for the colder and deeper parts of the oceans. In historical literature, they appear mainly in expedition reports under descriptions of new species; typical of these are the works by Jeffreys (1876, 1881) and Verrill & Bush (1898) or as faunistic works from northern latitudes, such as Sars (1878). Ockelmann's attention to this family was drawn by the very large numbers he encountered in East Greenland (Ockelmann 1958). Ockelmann remained the only serious student until the material collected from the deep Atlantic, by American and French cruises, was studied by John Allen and Cathy Payne (Payne & Allen 1991). Allen (2008) listed 27 named species and 52 unnamed thyasirid species from the deep Atlantic (500 to 5000 m), an indication of their diversity and importance in deep-sea benthic communities. Despite detailed anatomical observations made by Ockelmann and Payne & Allen, they did not recognise that many thyasirids are chemosymbiotic. This observation was first made by Eve Southward (1986), and kindled a new interest in thyasirids, with the work of Dufour (2005) seminal here. While most chemosymbiotic bivalve families are strictly so, Dufour (2005) showed that there is a range of dependency on chemosymbiosis in the thyasirids, and this is reflected in their gill anatomy. In the last decades, most publications were taxonomic, with only a single paper attempting to look at phylogeny through DNA sequencing (Taylor *et al.* 2007). This study revealed that the current generic systematics is probably inadequate, a view supported by Huber (2015). Further research is hampered by the difficulty in acquiring suitably preserved material for DNA extraction, especially of the smaller taxa from deep water. An intriguing observation among the smaller taxa are the large geographic and bathymetric ranges cited. Some are considered cosmopolitan, others pan-Atlantic with ranges from shelf to abyssal depths. It was these that Ockelmann studied most, and along with Payne & Allen, being responsible for confirming their distributions. However, the benthic fauna of the continental margins is strongly zoned (Carney 2005) and in the North Atlantic, it is unusual to find the same species inhabiting the shelf on both American and European margins. A detailed study using DNA sequencing is needed to resolve the bathymetric and geographic ranges exhibited by the Thyasiridae. A final conundrum thrown up by thyasirids is the relationship between arctic and boreal populations of species such as *T. gouldii* (Philippi, 1845a) and *T. dunbari* Lubinsky, 1976. Much of the accepted position on North Atlantic thyasirids came from Ockelmann's unpublished monograph via personal communications, and this paper is an opportunity to examine his work in detail.

After some nomenclatural explanations and a description of the contents of NHMD archive number T926, the results are presented in five sections. The first provides details on four unpublished species that Ockelmann had identified, followed by a section on four Amphi-Atlantic thyasirids studied by him in detail. A section on larval shells is followed by an account of his studies on living thyasirids, in particular their anatomy, life habits and the ciliary currents they produce. Finally, a number of miscellaneous shell drawings are presented.

Material and methods

Reference will be made throughout this paper to manuscript species names applied by Ockelmann, but which were never published. There is no intention here of introducing these names into nomenclature and their inclusion here should not be interpreted as a nomenclatural act.

Ockelmann's use of generic names, as seen in the archive, was rather inconsistent and he sometimes referred all species to "*Thyasira sensu lato*" while also using other genera such as *Mendicula* Iredale, 1924, *Axinulus* Verrill & Bush, 1898 and *Leptaxinus* Verrill & Bush, 1898 as genera or subgenera. When referring to Ockelmann's annotations, I have not altered them to the current accepted nomenclature in MolluscaBase (2025) or added generic names to his labels.

The archive consists of graphic material only; there are no texts, but most of the illustrations carry pencil identifications of species but are not allocated to a particular genus. Frequently, the pencil notations are very faint, so for the purposes of publication these have been enhanced to make them legible. Many of the items are on card, attached to larger pieces of card, such that on copying there is often a shaded border. Also, the colour of the card is no longer pure white, and some discolouration has taken place; in such instances, no attempt has been made to retouch the scans so some shadows and shading may be present. The archive is listed in the Natural History Museum of Denmark under accession T 926. An overview of the contents of this archive is provided here and presented in detail in the Results section.

Pen and ink diagrams of anatomy

Seven species were illustrated, labelled as: *croulinensis*, *dunbari*, *gouldi*, *minutus*, *orbiculata*, "*perplexa*", *pygmaea*.

Stipple illustrations of the shells, including those by K. Olsen and P. Winther

Some of the shell illustrations can be directly linked to specimens in the collection and these are annotated with "Tegnet [= drawn by] K. Olsen" or "Tegnet P. Winther" and dated 1971 by Ockelmann. Those done by P. Winther must have been executed earlier as he died in 1966. The following species are represented as the entire shell and/or their hinges. The majority of these illustrations are probably by Ockelmann himself as he was known to be a good scientific illustrator (Jensen & Dinesen in prep.). Stipple drawings of twenty-two species labelled as follows are present: *brevis*, *croulinensis*, *dunbari* = "*frigida*", *equalis*, *eumyaria*, *ferruginea*, *flexuosa*, *gouldi*, *grandis*, *granulosa*, *incrassata*, "*ingolfi*", *obsoleta*, *orbiculata*, "*perplexa*", *perplicatus*, *pygmaea*, *sarsi*, "*scandica*", *subovata*, *succisa*, *tortuosa*.

Distribution maps

The distribution maps are all based on a map of the Atlantic Ocean or restricted to the North Atlantic and Arctic Oceans from 40° to 85° N. Occurrences relate to data associated with collections and are represented by single symbols. Open and closed symbols are present but not explained; I assume that the open symbols represent dead collected shells or literature records. Some maps pertain to a single species whereas others combine data for up to three species.

The following species have distribution maps but only those in bold font are reproduced here: *brevis*, *croulinensis*, *dunbari* = "*frigida*", *equalis*, *eumyaria*, ***ferruginea***, *flexuosa*, ***gouldi***, ***incrassata***, "*ingolfi*", ***obsoleta***, *orbiculata*, ***pygmaea***, ***sarsi***, "*scandica*", *subovata*, *succisa*, ***tortuosa***. Some maps include more than one species and in some cases, these have been simplified by me.

Line drawings of the prodissoconchs

Two plates of line drawings illustrate the larval shells (prodissoconchs) of the following species and labelled by Ockelmann as: Plate 1: *Axinopsida orbiculata*, *T. gouldi*, *flexuosa*, *sarsi*, *croulinensis*, *succisa*,

granulosa, “*frigida*” = *dunbari*, *equalis*, *subovata*; Plate 2: *tortuosa*, “*scandica*”, *minutis*, *incrassata*, “*ingolfi*”, *pygmaea*, *ferruginea*, ?*eumyaria*, *brevis*.

Data presented in graphical form

Bar-charts indicating the bathymetric ranges of 10 species, *gouldi*, *obsoleta*, *sarsi*, “*frigida*”, *flexuosa*, *orbiculata*, *equalis*, *eumyaria*, *pygmaea*, *ferruginea*.

Line charts of the relation between height and length of the prodissoconch of 18 species not annotated.

Scatter diagram of the shell length against depth of 18 species.

Life observations

Pen and ink drawing of *T. flexuosa* (Montagu, 1803) in life position.

Diagram of the ciliary currents of the mantle.

Diagrammatic transverse section showing mantle currents.

Methods

The supplementary illustrations of photographed shells and scanning electron micrographs (SEMs) were made by the author. The photographs were made using a Leica Z6 macroscope producing digital images enhanced by Helicon Focus stacking software. The SEMs were made on a Jeol JCM-7000 Benchtop in the National Museum of Wales. Specimens from the Ockelmann collection of his unpublished species were not gold coated and were viewed at the low vacuum setting.

Institutional acronyms

MCZ = Museum of Comparative Zoology, Harvard
NHMD = Natural History Museum, Denmark, Copenhagen
NHMUK = Natural History Museum, London
USNM = United States National Museum, Washington, USA

Results

Unpublished manuscript names by Ockelmann

Among the archive and in his collection are four undescribed species annotated with the following manuscript names: *T. “frigida”*; *T. “perplexa”*; *T. (Leptaxinus) “scandica”*; *T. (Mendicula) “ingolfi”*.

Thyasira “frigida” Ockelmann MS Figs 2–4

In Ockelmann's monograph (1958) on the bivalves of East Greenland, he illustrated a shell from Jan Mayen as *Thyasira equalis* (Verrill & Bush, 1898) (Ockelmann 1958: fig. 7). He noted that this species was widely distributed in East Greenland and was in general a little larger than *T. equalis* from NE America. In McIntyre (1961), it became evident that Ockelmann changed his mind and that the *T. equalis* illustrated by him was probably undescribed. In his collections, Ockelmann labelled this form as “*Thyasira “frigida”* n. sp.” and selected a prospective holotype (NHMD-1175760) from “Ingolf” stn 126; 67°19' N, 15°52' W, at a depth of 535 m, N of Iceland. The Danish Ingolf Expedition of 1895/96 was reviewed by Wolff (2008). Ockelmann's map of distribution for *T. “frigida”* gives a widespread range across the cold regions of the North Atlantic into the Arctic Ocean at 80° N. Then, around 1975/76 he corresponded with Irene Lubinsky who subsequently described *T. dunbari* Lubinsky, 1976 from Arctic

Canada. Ockelmann was gifted a specimen of *T. dunbari* (NHMD-1175909) and from then on dropped his name *T. “frigida”* in favour of *T. dunbari*.

I find this surprising as the shapes of the shell are quite different, *T. “frigida”* being polygonal rather than the pyriform shell of *T. dunbari*. Furthermore, the prodissoconch sizes, which Ockelmann gave emphasis to throughout his studies, are quite different with a mean of 165 μm in *T. “frigida”*, but 193 μm in *T. dunbari*. Perhaps he considered *T. dunbari* to represent a larger, gerontic form of his *T. “frigida”*, but there are no shells resembling *T. dunbari* in any of the collections in the Natural History Museum of Denmark from East Greenland, northern Norway or Svalbard. Here, I present his illustrations (Fig. 2) and map (Fig. 4) from the archive along with photographs of the type specimen of *T. “frigida”* from Ockelmann’s collection (Fig. 3B) and a paratype of *T. dunbari* (Fig. 3A). From this simple comparison, I would not consider *T. dunbari* and *T. “frigida”* to be conspecific. However, samples of *T. “frigida”* do vary and are close to *T. rotunda* (Jeffreys, 1881), a taxon not considered by Ockelmann in his monograph. A full consideration of *T. dunbari*, *T. “frigida”* and *T. rotunda* will be presented in a forthcoming paper on the Thyasiridae of the UK Atlantic margin (Oliver in prep).

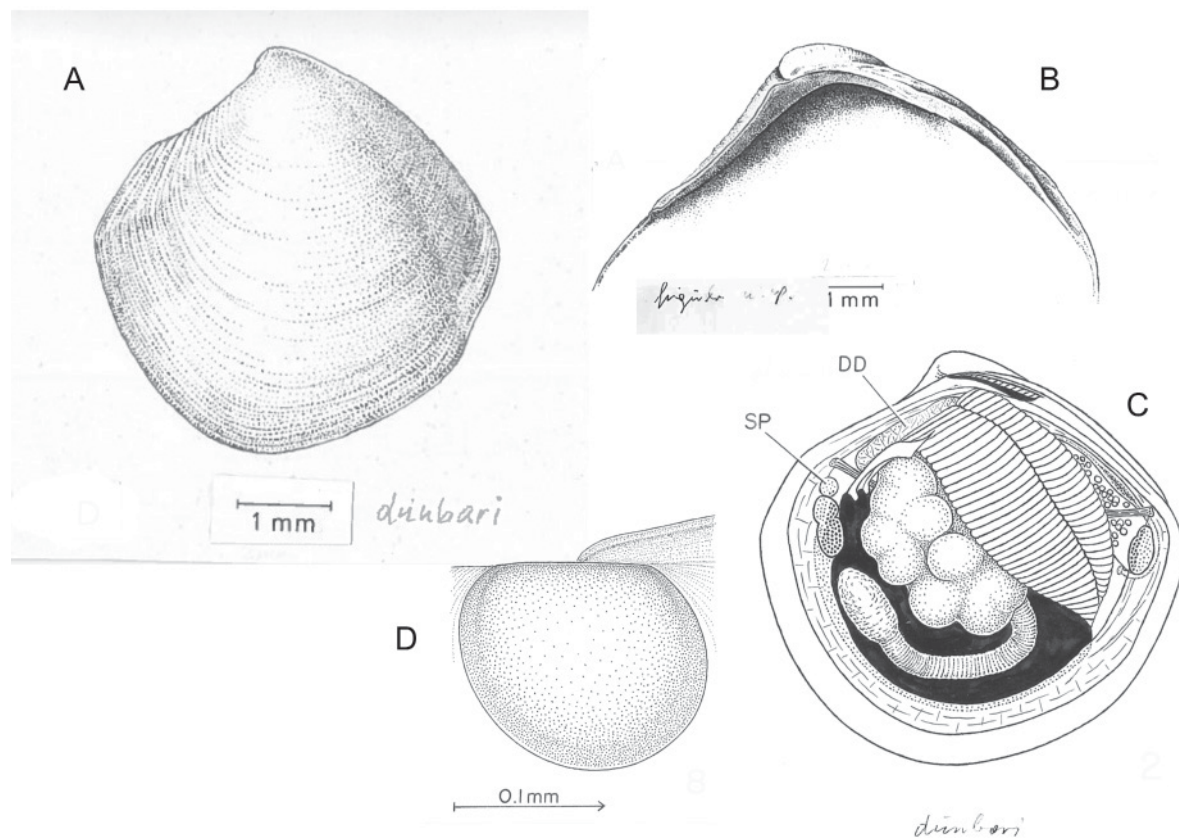


Fig. 2. Stipple drawings from the Ockelmann archive of *Thyasira “frigida”* Ockelmann MS/*dunbari* Lubinsky, 1976. **A.** Exterior of shell. **B.** Hinge of right valve. **C.** Diagram of the anatomy. **D.** Prodissoconch. Abbreviations: DD=digestive diverticula; SP=separate portion of anterior adductor.

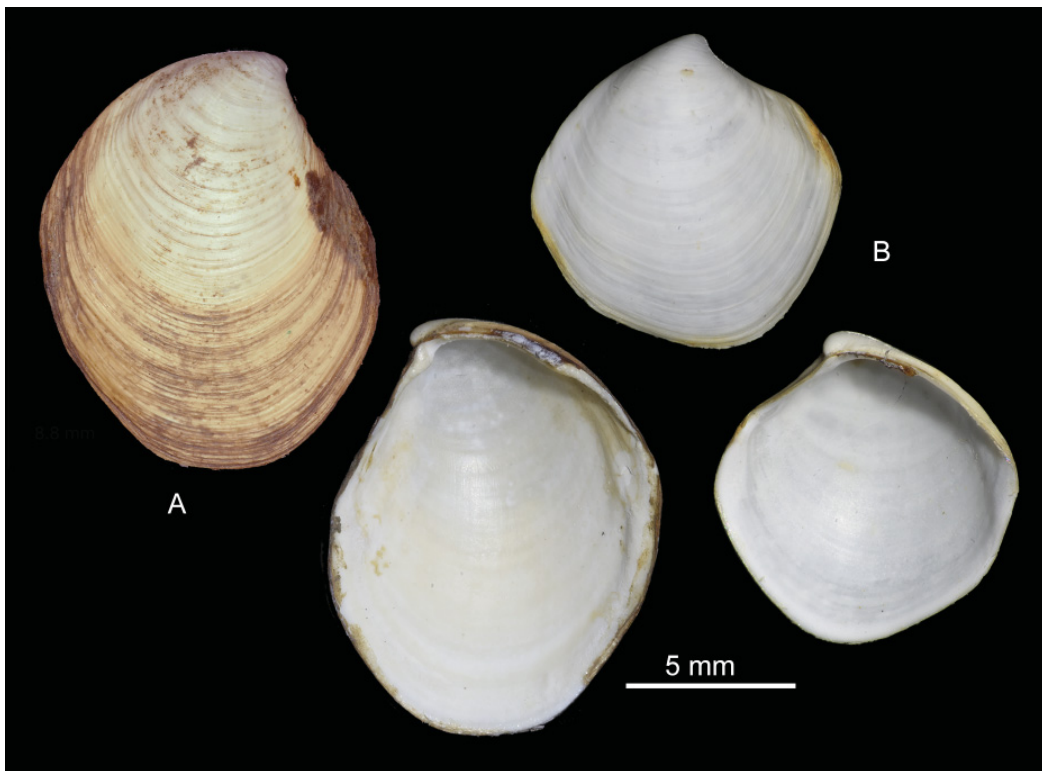


Fig. 3. A. Paratype of *Thyasira dunbari* Lubinsky, 1976 (NHMD-1175909). B. Holotype of *T. "frigida"* Ockelmann MS (NHMD-1175760) selected by Ockelmann. Images by P.G. Oliver.

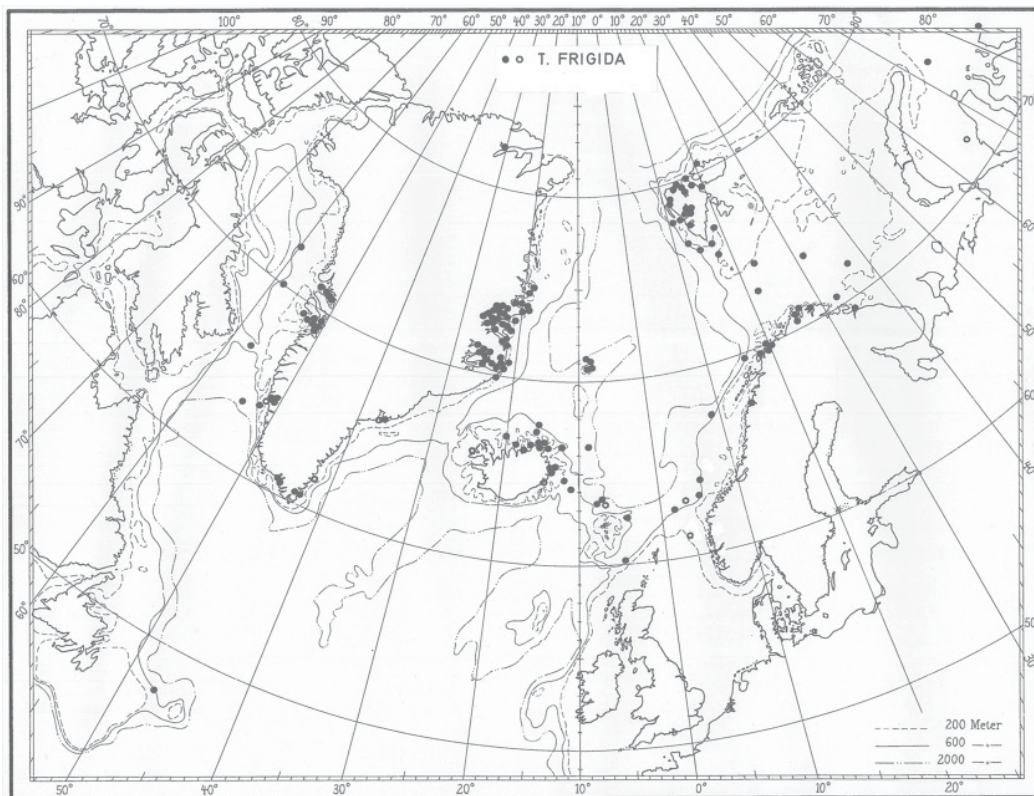


Fig. 4. Ockelmann's map of the distribution of his *T. "frigida"* MS.

Thyasira “*perplexa*” Ockelmann MS
Figs 5–6

In the archive, this species is represented by stipple drawings of two shells, hinge and anatomy (Fig. 5). Drawn shells (2 valves) + 6 valves + 2 shells from Ria de Arosa, N Spain stn 1566 (all NHMD-1175772), are present. There is no correspondence relating to these shells and further information on their provenance could not be found. The Ria de Arosa is situated on the north-west coast of Spain, approximately 40 km N of Vigo. Its deepest point is 60 m and *T. flexuosa* has been recorded from here (Cadee 1968).

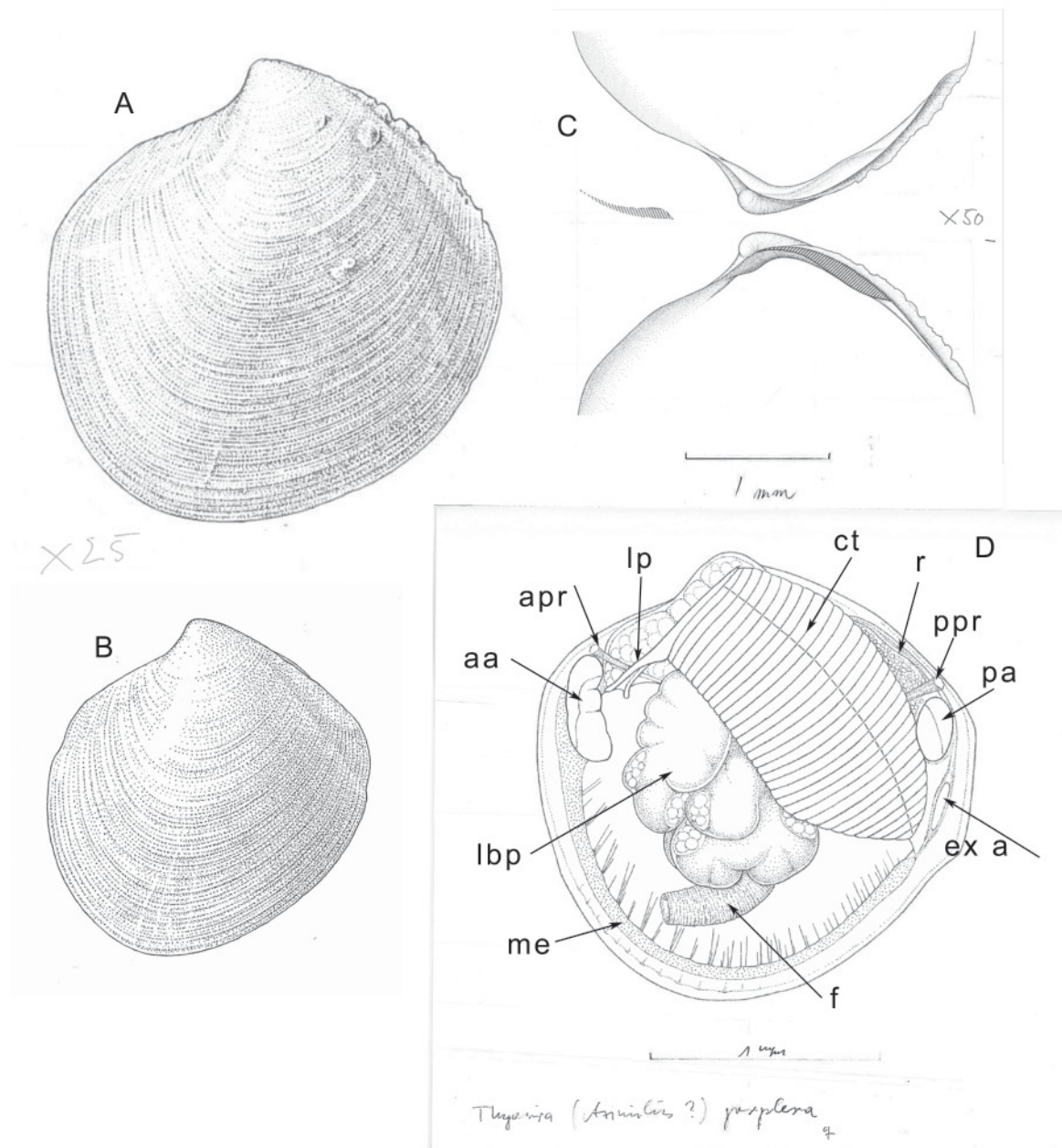


Fig. 5. Stipple drawings from the Ockelmann archive of *Thyasira* “*perplexa*” Ockelmann MS. **A–B.** Exterior of shell. **C.** Hinge of both valves. **D.** Diagram of the anatomy. Abbreviations: aa=anterior adductor muscle; apr=anterior pedal retractor muscle; ct=ctendium; ex a=exhalant aperture; f=foot; lbp=lateral body pouch; lp=labial palp; me=mantle edge; pa=posterior adductor muscle; ppr=posterior pedal retractor muscle; r=rectum.

At first, this did appear to be an undescribed species, but scanning electron microscopy of the prodissoconch revealed two morphologies, one with what I call a “menorah” sculpture of ridges (Fig. 6G) and the other almost smooth (Fig. 6F). The larger shell (Fig. 6A) with the “menorah” prodissoconch sculpture is not too dissimilar from *T. equalis*, but the serrated edge to the submarginal sulcus is unusual and may indicate that a distinct species is present in northern Spain. All the smaller shells, with a smooth prodissoconch, are similar to *Axinulus alleni* (Carrozza, 1981) (Fig. 6D–E) and the anatomy matches

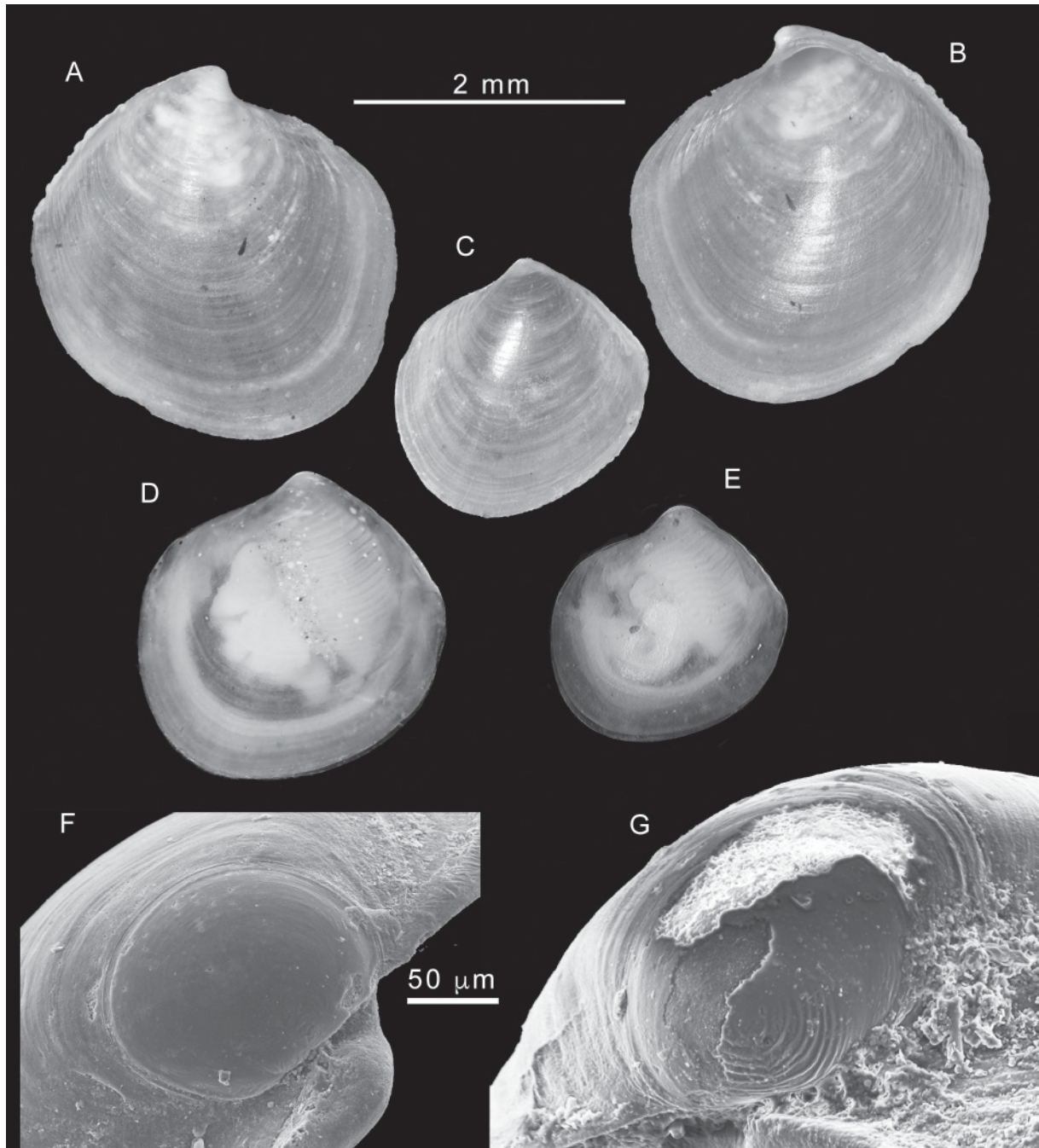


Fig. 6. A–C. Shells drawn by Ockelmann of his *Thyasira* “*perplexa*” MS (NHMD-1175772). D–E. Specimens of *Axinulus alleni* (Carrozza, 1981), Cañón de Motril, Mediterranean Sea off Andalusia Spain, 244–284 m depth, University of Malaga, AN258. F–G. Scanning electron micrographs of the prodissoconchs of shells labelled *T. ‘perplexa’* MS by Ockelmann.

that in Ockelmann’s diagram. The shell outline and anatomy here are, however, quite divergent from that illustrated by Payne & Allen (1991: figs 78–79) but are similar to that illustrated by Carrozza (1981: figs 1–3). The shell illustrated by Payne & Allen (1991) came from the Cape Basin off Angola and is probably a distinct species.

Leptaxinus “*scandica*” Ockelmann MS
Figs 7–9

In the archive, this species is represented by stipple drawings of the shell, hinge and prodissoconch (Fig. 7) and a prospective holotype (NHMD-1175765) is present from Ingolf stn 117, 69°13’ N, 08°03’ W,

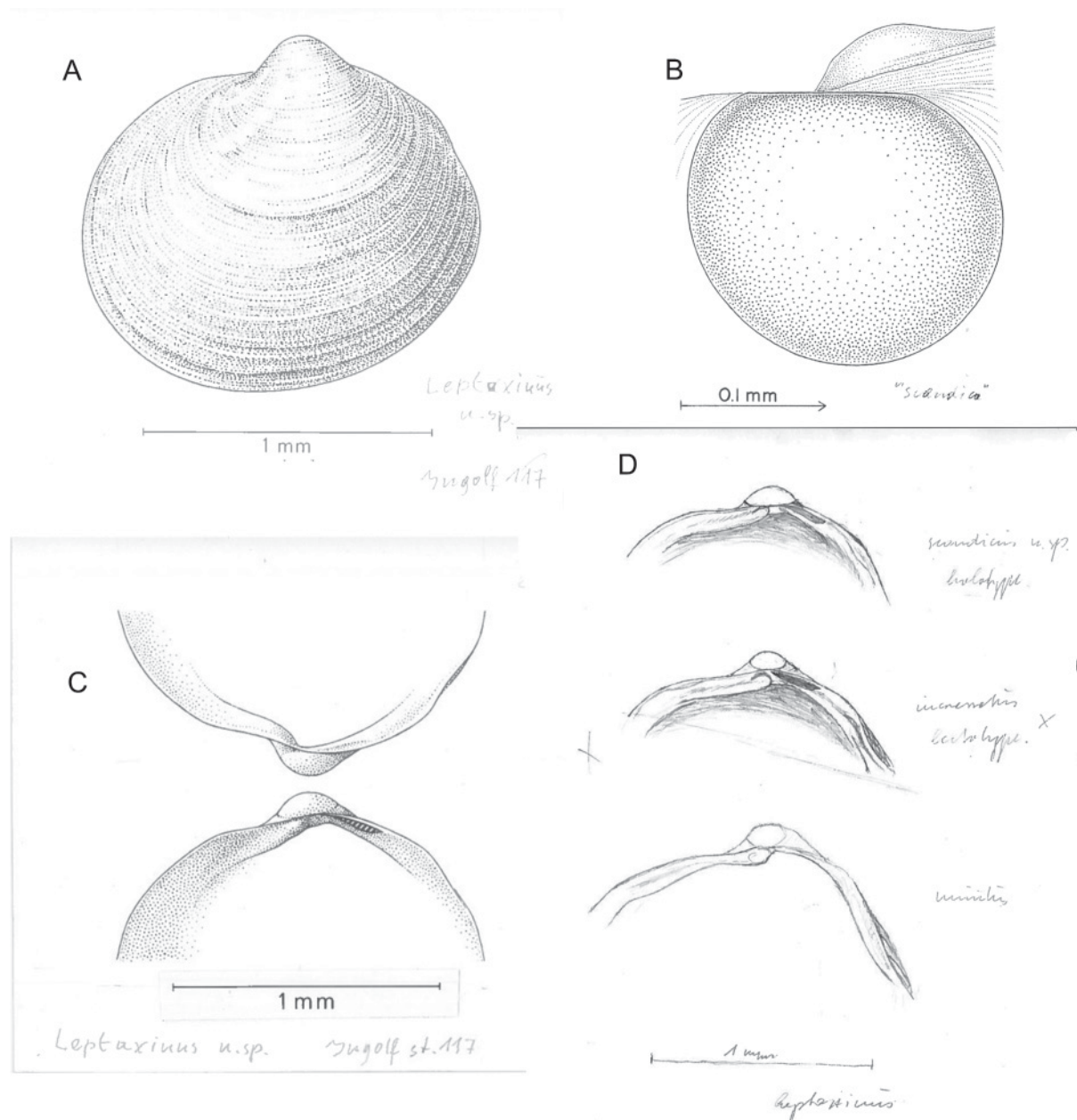


Fig. 7. Drawings from the Ockelmann archive of *Leptaxinus* “*scandica*” Ockelmann MS. **A–C.** Stipple drawings of shell, prodissoconch and hinge. **D.** Pencil sketch of comparisons of *L.* “*scandica*”, *L. incrassatus* (Jeffreys, 1876) and *L. minutus* Verrill & Bush, 1898.

at a depth of 1843 m, S of Jan Mayen in the Norwegian Sea (Fig. 8). Related samples are: 1 dry shell, labelled “*T. (Leptaxinus) incrassatus* (Jeffr.) Ingolf stn 36, Tagnet K. Olsen; 61°50' N, 56°21' W, 2702 m, 1895” (NHMD-1175773); 3 valves+1 broken, labelled “*Leptaxinus* n. sp. *incrassatus* aff. [Ingolf] stn 119” (NHMD-1175749); 12 valves, labelled “*Leptaxinus incrassatus* (Jeffreys) Ingolf stn 18, det. Ockelmann” (NHMD-1175752).

In a pencil sketch (Fig. 7D), Ockelmann compared *L. “scandica”* with *L. incrassatus* (Jeffreys, 1876) and *L. minutus* Verrill & Bush, 1898, the major difference being the very large size of the prodissoconch of *L. “scandica”* at 207 µm. Ockelmann's map (Fig. 9) indicates he had it from three stations in the deep Norwegian Sea, but I have seen only the one shell designated as the holotype. Comparisons with species illustrated by Payne & Allen (1991) reveal no identical species and the hinge details do not match that of *L. minutus* as illustrated by Verrill & Bush (1898). It is also possible that Ockelmann's N Atlantic “*scandica*” is the same as the more recently described *Mendicula ockelmanni* (Keuning & Schander, 2010), as both come from abyssal depths in the Norwegian Sea. Another similar form is the “*Thyasira* n. sp.” illustrated by Bouchet & Warén (1979) and collected from the deep Norwegian Sea.

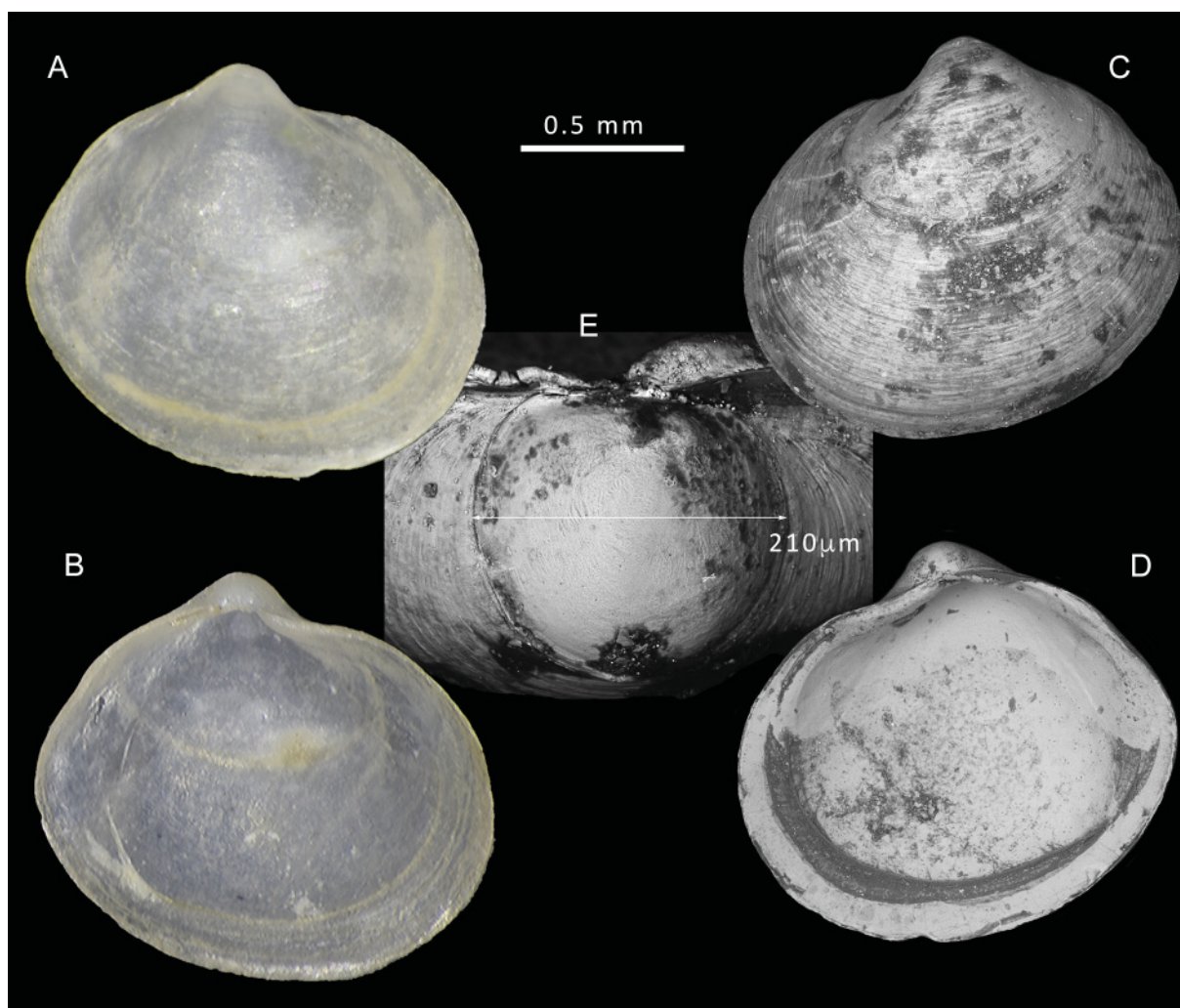


Fig. 8. Holotype of *Thyasira (Leptaxinus) “scandica”* Ockelmann MS (NHMD-1175765). **A–B.** Photographs of external (right valve) and internal (left valve). **C–D.** Scanning electron micrographs (low vacuum, uncoated) of external (left valve) and internal (right valve). **E.** SEM of prodissoconch with a diameter of 210 microns. All images by P.G. Oliver.

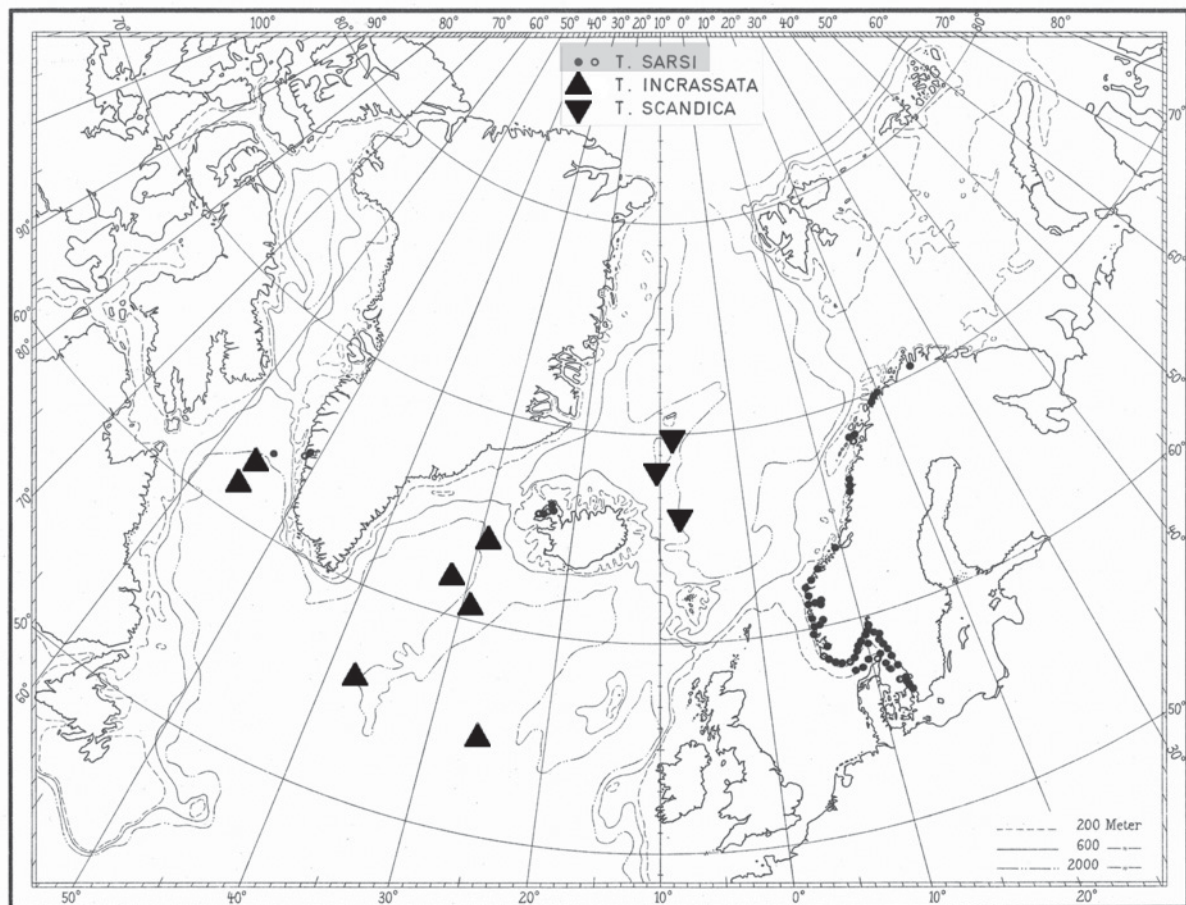


Fig. 9. Ockelmann’s map of the distribution of his *T. (L.) “scandica”* Ockelmann MS and *T. (L.) incrassatus* (Jeffreys, 1876). Relevant symbols enlarged for clarity.

They stated that many specimens were given to Ockelmann, who intended to describe this species but never did, nor are there any notes in the archive. The specimens are in the Ockelmann collection, but my observations suggest it is not the same species as “*scandica*”, due primarily to the size and sculpture of the produssoconch.

Mendicula “ingolfi” Ockelmann MS

Figs 10–12

In the archive, this species is represented by stipple drawings of the shell (Fig. 10A), hinge (Fig. 10B) and produssoconch (Fig. 10C) from Ingolf stn 36; 61°50' N, 56°21' W, at a depth of 2600 m, off SW Greenland in the Labrador Sea. It would appear that Ockelmann was never very sure about this species as the following specimens are present: 1 specimen in spirit from Ingolf stn 36 labelled “Ingolf Stn 36 1435 fathoms [=2624m], type” (NHMD-1175754); 4 specimens in spirit labelled “Ingolf Bundprove [bottom sample] stn 36” (NHMD-1175755) (Fig. 11G); 1 specimen labelled “*Thyasira* n. sp. Ingolf Bundprove stn 25” (NHMD-1175761); 1 dry shell labelled “*T. (Mendicula) ‘ingolfi’* n. sp. L.G.O. stn 49 Tagnet K. Olsen Ockelmann 197” and on reverse “L.G.O. stn 49 1957; 56°43' S, 27°41' W, 1497f [=2737m]” (NHMD-1175747) (Fig. 11A–C); 1 dry shell labelled “*Thyasira subovata* (Jeffreys) L.G.O.

stn 49 Tagnet K. Olsen Ockelmann 1971" and on reverse "L.G.O. stn 49, 1957, 56°43' S, 27°41' W, 1497f [=2737 m]" [this latter appears to be the shell in the drawing by K. Olsen and labelled "*subovata* S. Atlantic" (NHMD-1175764)]; 1 shell + 5 valves dry labelled "*Axinulus* n. sp. (*Th. subovata* aff.) L.G.O. stn 49, 1957, 56°43' S 27°41' W, 1497f [=2737 m]" (NHMD-1175751) (Fig. 11F); 1 dry shell labelled "*Thyasira* (*Mendicula*) '*ingolfi*' n. sp. L.G.O. stn 51, 45°34' S, 06°02' E, (2507f) 4585 m" (NHMD-1175750) (Fig. 11D–E). The distribution of these specimens is shown in Fig. 12.

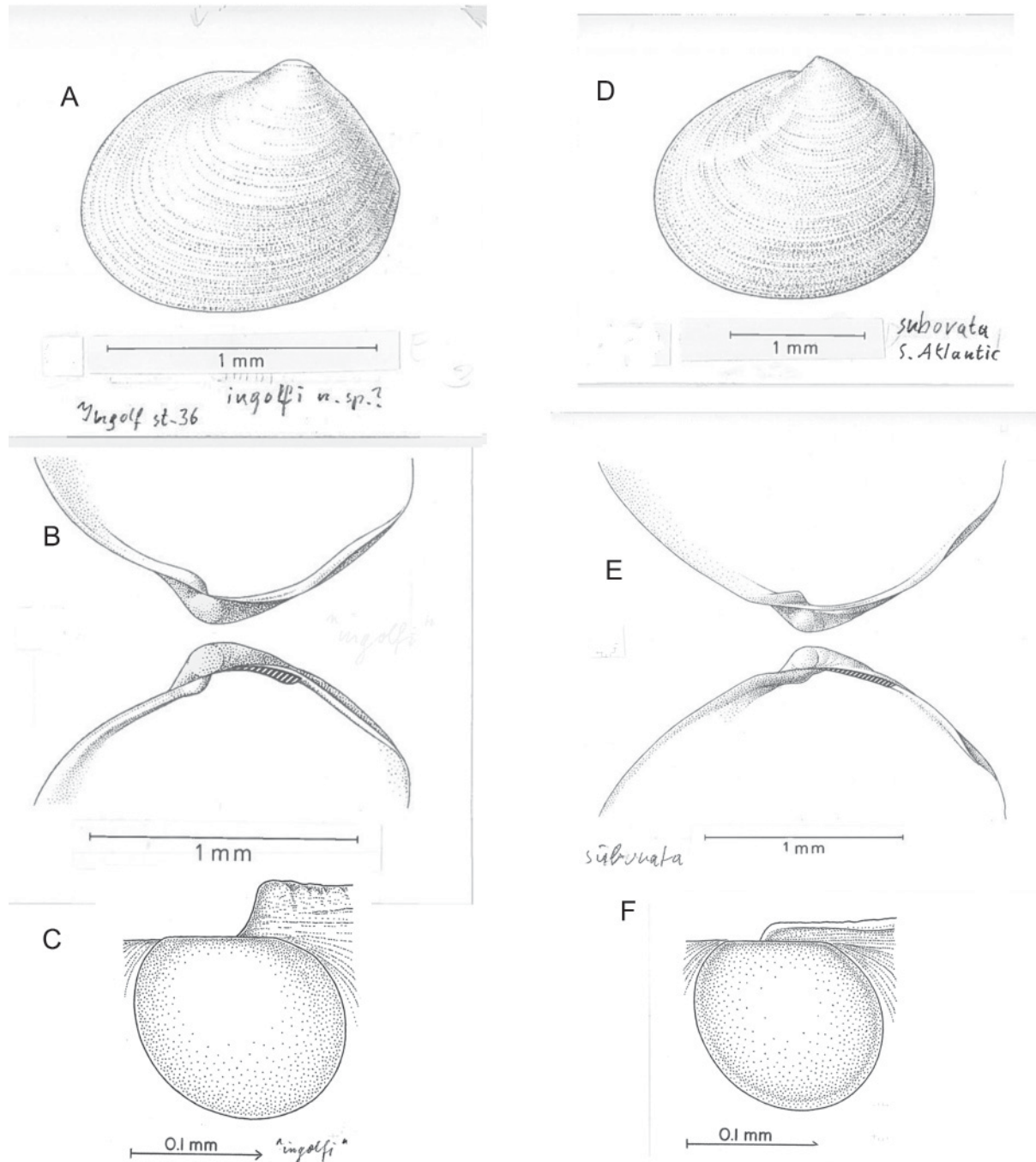


Fig. 10. Stipple drawings from the Ockelmann archive. **A.** Shell of *M. "ingolfi"* from Ingolf stn 36. **B–C.** Hinge and prodissoconch of *M. "ingolfi"*. **D.** Shell of *Thyasira subovata* (Jeffreys, 1881) from the South Atlantic. **E–F.** Hinge and prodissoconch of *T. subovata*.

L.G.O. stations refer to the Vema expedition of 1957 to the South Atlantic (see Clark 1961). Jørgen Knudsen (1970) noted that, while the bulk of the Vema samples were in the Museum of Comparative Zoology in Harvard, some had been transferred to the Zoological Museum in Copenhagen (now incorporated into the Natural History Museum of Denmark) where presumably Ockelmann had access to them. Knudsen also noted that Ockelmann was working on the Ingolf material but had not published on it. It is rather surprising that no Thyasiridae are included in Knudsen's (1970) *Galathea Reports*, although the material in Ockelmann's possession was most definitely abyssal in origin.

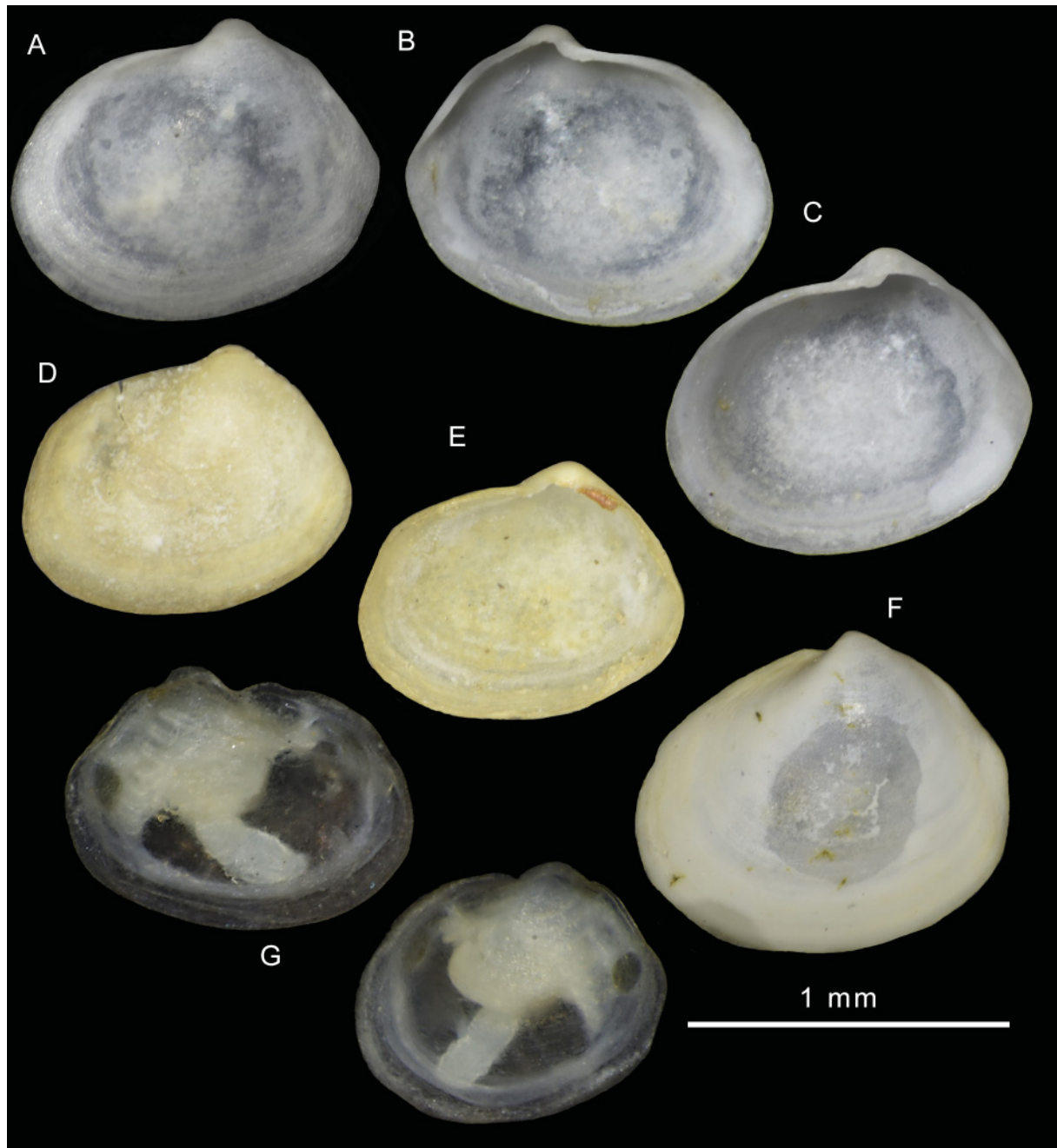


Fig. 11. A–C. *Mendicula* “*ingolfi*” Ockelmann MS Vema Stn 49 (NHMD-1175747). D–E. *Mendicula* “*ingolfi*” Vema stn 51 (NHMD- 1175750). F. *Thyasira subovata* (Jeffreys, 1881) Vema stn 49 (NHMD-1175751). G. Decalcified specimens of *M.* “*ingolfi*” from Ingolf stn 36 (NHMD-1175755). All images by P.G. Oliver.



Fig. 12. Ockelmann's map of the distribution of *Mendicula* "ingolfi" Ockelmann MS. Relevant symbols enlarged for clarity.

Unfortunately, the specimens from Ingolf stn 36 are partially decalcified and I cannot equate them with the stipple drawings labelled "*ingolfi* n. sp." These specimens are very small, around 1 mm in diameter, but they have a single demibranch and could therefore be a *Mendicula* or a *Leptaxinus*. Furthermore, Ockelmann conflated material from Ingolf stn 36 with Vema material from the South Atlantic that he suggested had affinity with *T. subovata* (Jeffreys, 1881). Examination of these shells suggests that South Atlantic shells labelled "*ingolfi* n. sp." are not *T. subovata*. The South Atlantic shells most closely resemble those of the genus *Mendicula* and only SEM examination will tell if they could be a species of *Adontorhina* Berry, 1947. Without the shells from Ingolf stn 36 it is not possible to tell whether they are conspecific with the Vema shells from the South Atlantic, and without a larger number of specimens, including those with soft parts, it is not possible to determine whether it is indeed a new species.

Amphi-Atlantic species

In 1959, as an adjunct to his Greenland monograph (Ockelmann 1958), Ockelmann visited the USNM in Washington to examine the type material in the Jeffreys and Verrill & Bush collections. It must have been a result of this visit that he concluded that some of the American species could also be found in European waters. During this visit, he selected lectotypes and neotypes of a number of species, but he

never formally published these designations. Neither did he ever publish descriptions or illustrations comparing American and European examples.

Comparisons with type material are essential to verify synonymy and identifications of ampho-Atlantic species. Many type selections have been validly made, but some have now crept into the literature following their incorporation through the curation of the collections. Ockelmann selected type material from the Jeffreys collection and some have been validly published by Warén (1980), as follows under their original genus:

- *Clausina croulinensis* Jeffreys, 1847; neotype USNM 62048.
- *Axinus incrassatus* Jeffreys, 1876; lectotype USNM 61969.
- *Axinus planatus* Jeffreys, 1882: not found.
- *Axinus polygona* Jeffreys, 1864; not found.
- *Axinus rotunda* Jeffreys, 1881; not found, subsequently noted in collection under USNM 61942/a but see under *T. granulosa* below.
- *Axinus subovatus* Jeffreys, 1881; syntype USNM 61895, subsequently noted as lectotype under USNM 61895.
- *Axinus succisa* Jeffreys, 1876; lectotype USNM 61973.
- *Axinus tortuosus* Jeffreys, 1881; lectotype USNM 61904 and paralectotype USNM 683898, but see note by Ellen Strong in USNM catalogue on line: EZID: <http://n2t.net/ark:/65665/3ce7ffe52-e280-48e9-a33c-2423b208bff0>.

Although not cited in the USNM on-line catalogue, Ockelmann was responsible for selecting lectotypes from the Verrill & Bush collection, as indicated on annotations in the collection, but unlike Warén, he never published them:

- *Cryptodon obsoletus* Verrill & Bush, 1898; lectotype USNM 159886, but this was never published and should be cited as a figured syntype.
- *Cryptodon (Axinulus) pygmaea* Verrill & Bush, 1898; lectotype USNM 78368, but this was never published and should be cited as a figured syntype.
- *Cryptodon equalis* Verrill & Bush, 1898; holotype USNM 74302, but this was not selected by Verrill & Bush and should be a syntype or figured syntype.

A fourth ampho-Atlantic species to be confirmed by Ockelmann was *Thyasira gouldii*, originally described as *Lucina gouldii* Philippi, 1845 (Philippi 1845a). No type specimens have been isolated and there is no record of them in the MCZ in Harvard (Coan & Kabat 2017). Ockelmann did not visit the MCZ and we assume his concept of this species was based on material in the USNM.

Thyasira equalis (Verrill & Bush, 1898)

Fig. 13

Following his investigations in the USNM, Ockelmann began to apply some of Verrill & Bush's names to European specimens. The first of these was to identify a species from the Fladen Ground in the North Sea as *T. equalis* following communications with Alistair McIntyre (McIntyre 1961). However, *T. equalis* was not included in the British fauna by Tebble (1966) but was listed by Bowden & Heppell (1968). It appears in the Norwegian literature in 1975 (Lande 1975), but the first figures of European specimens were published by Payne & Allen (1991), and illustrations of specimens from the North Sea are in Oliver & Killeen (2002). Comparisons of the shells from NE America, the North Sea and northern Norway show that they share the same characters and in particular the micro-sculpture of the prodissoconch. This has the characteristic "menorah" pattern (Fig. 22A) which Ockelmann did not see. Ockelmann's map (Fig. 13) shows a discontinuous distribution with a western Atlantic range from New England northwards into the Labrador Sea but absent from the entire east of Greenland. In the east, it ranges from the North Sea into the Kattegat and all along the Norwegian coast into the Barents Sea.

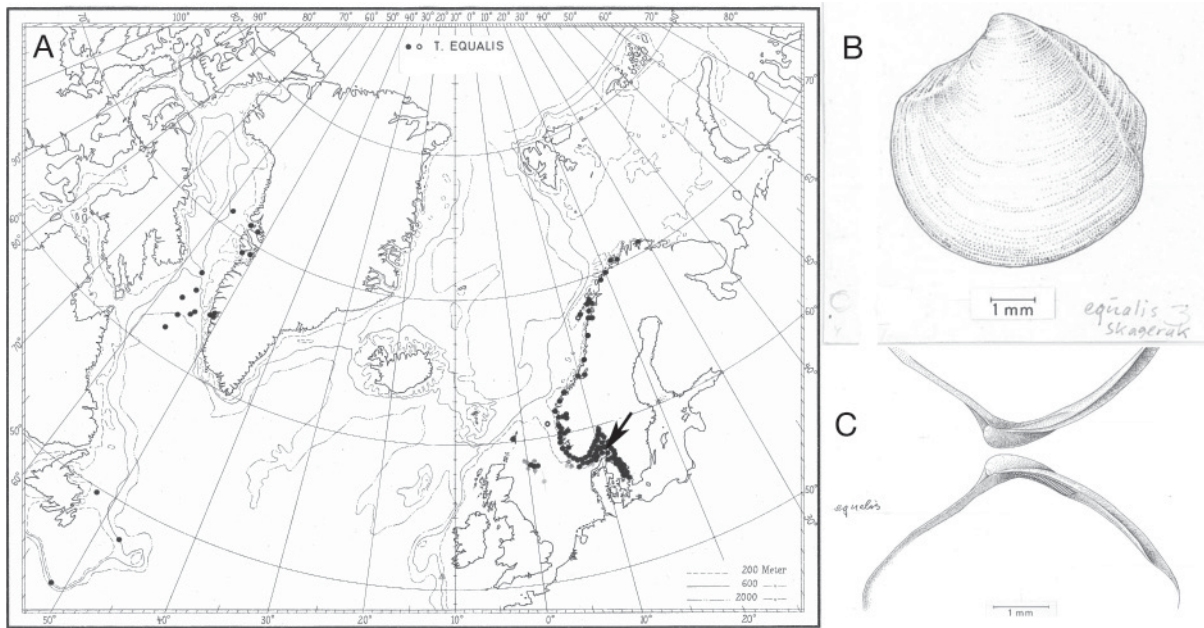


Fig. 13. *Thyasira equalis* (Verrill & Bush, 1898). **A.** Ockelmann's map of the distribution, arrow indicates locality of figured shell, Skagerrak. **B–C.** Stipple drawings of the shell and hinge.

Thyasira obsoleta (Verrill & Bush, 1898)

Fig. 14

For a great many years this species (Fig. 14) was confused with *Axinulus croulinensis* (Jeffreys, 1847) and was widely recorded as such from the eastern Atlantic from the Bay of Biscay to northern Norway (see Payne & Allen 1991 for details). It was not until Ockelmann formally recognised this species in

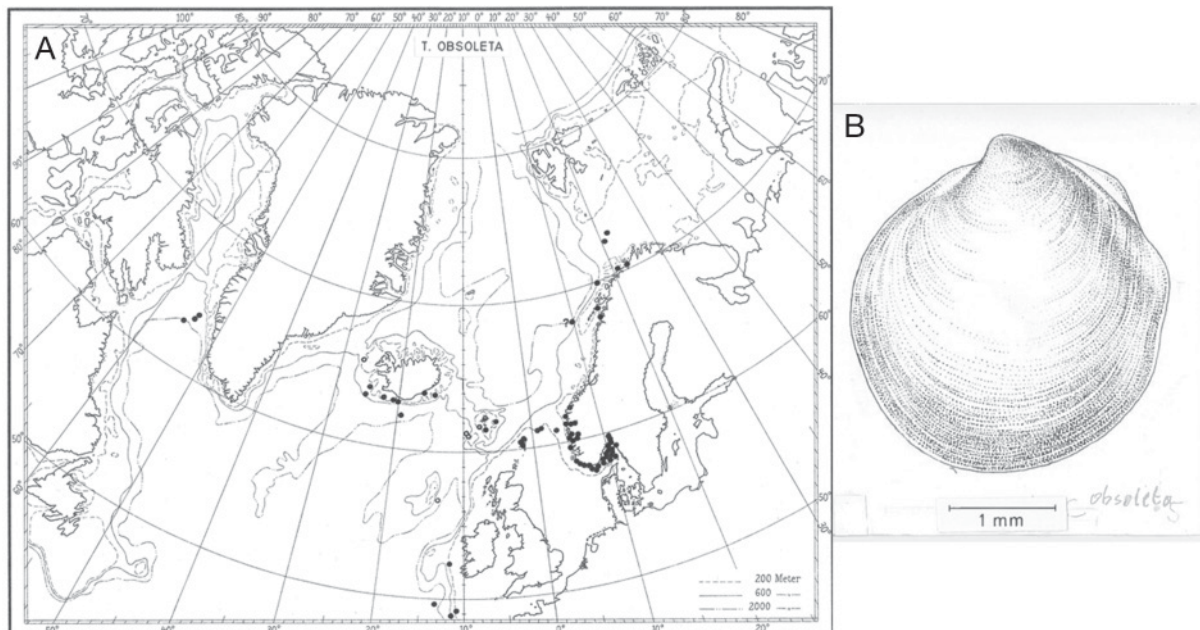


Fig. 14. *Thyasira obsoleta* (Verrill & Bush, 1898). **A.** Ockelmann's map of the distribution. **B.** Stipple drawing of the shell.

the British fauna (Ockelmann pers. comm. in Bowden & Heppell 1968: 263) that the name became established in Europe. Lande (1975) recorded this species from Norway and credits Ockelmann with its identification.

Thyasira gouldii (Philippi, 1845)

Fig. 15

This species was originally described from off north-eastern USA and was known from high latitudes in the eastern Atlantic as early as 1878 (Sars 1878) (Fig. 15). Records from farther south in Norway appear in Lande (1975) and from Scotland (Blacknell 1973), both noting Ockelmann's confirmation of identifications.

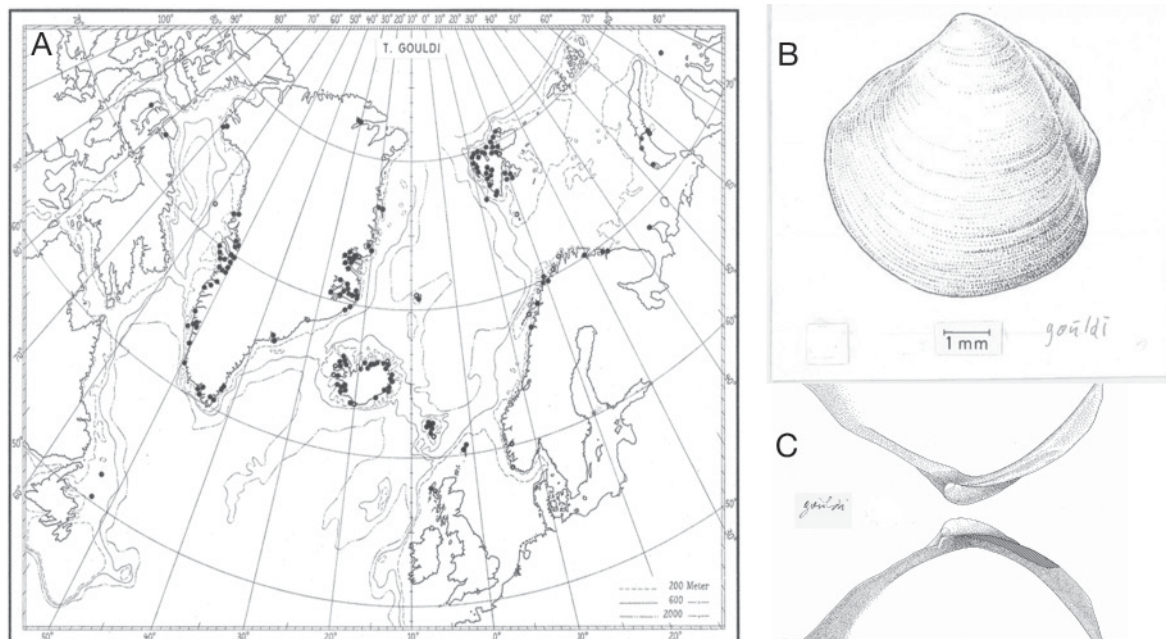


Fig. 15. *Thyasira gouldii* (Philippi, 1845). **A.** Ockelmann's map of the distribution. **B–C.** Stipple drawings of the shell and hinge.

Mendicula pygmaea (Verrill & Bush, 1898)

Fig. 16

Mendicula pygmaea was described from off the coast of New England and appears in the European literature in Lande (1975), and Høisæter (1986) recorded it from the coast of Norway between 60° and 63° N. Ockelmann's unpublished map (Fig. 16) shows a wide range but sparse distribution across the N Atlantic Ocean. It was listed from the Skagerrak by Wikander (1989) and later was cited from the North Sea oilfields by Oliver & Killeen (2002). Unfortunately, both Ockelmann and Oliver & Killeen had overlooked the fact that the material from the North Sea was not *M. pygmaea* but was a neglected species of *Adontorhina* published subsequently by Barry & McCormack (2007) as *A. similis*. It is most unlike Ockelmann to have overlooked *A. similis*, but without recourse to the SEM, he probably could not discern the denticulate dorsal margin typical of *Adontorhina*. Oliver & Killeen (2002) did figure the denticulate margin, but failed to notice the significance taking the *M. pygmaea* identification for granted.

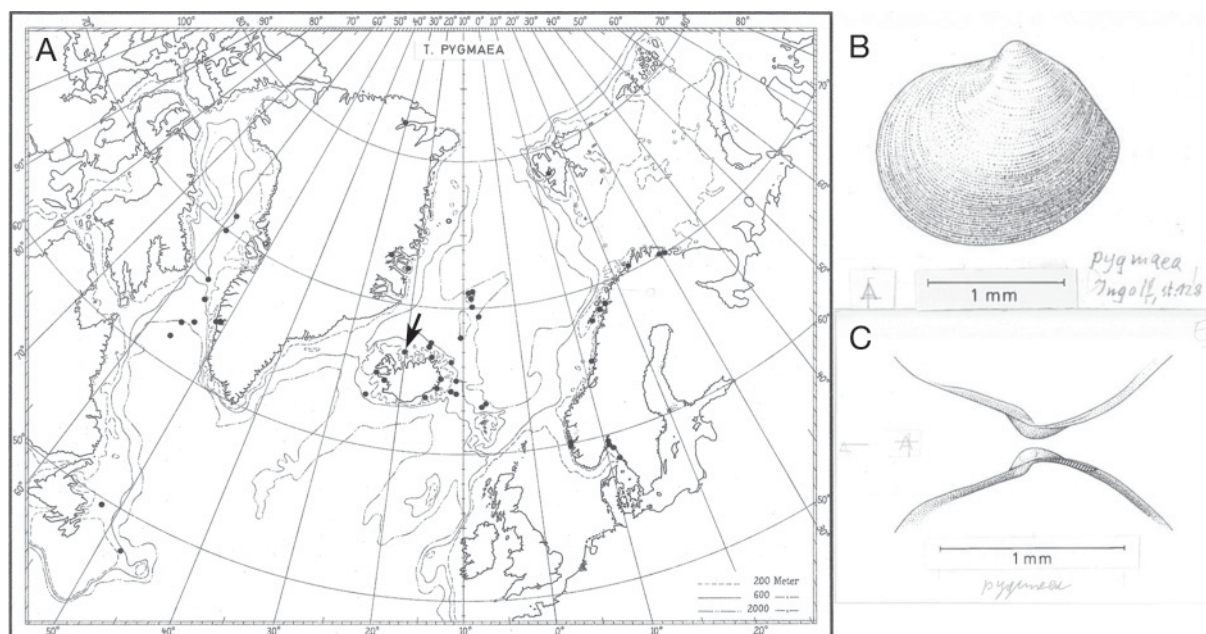
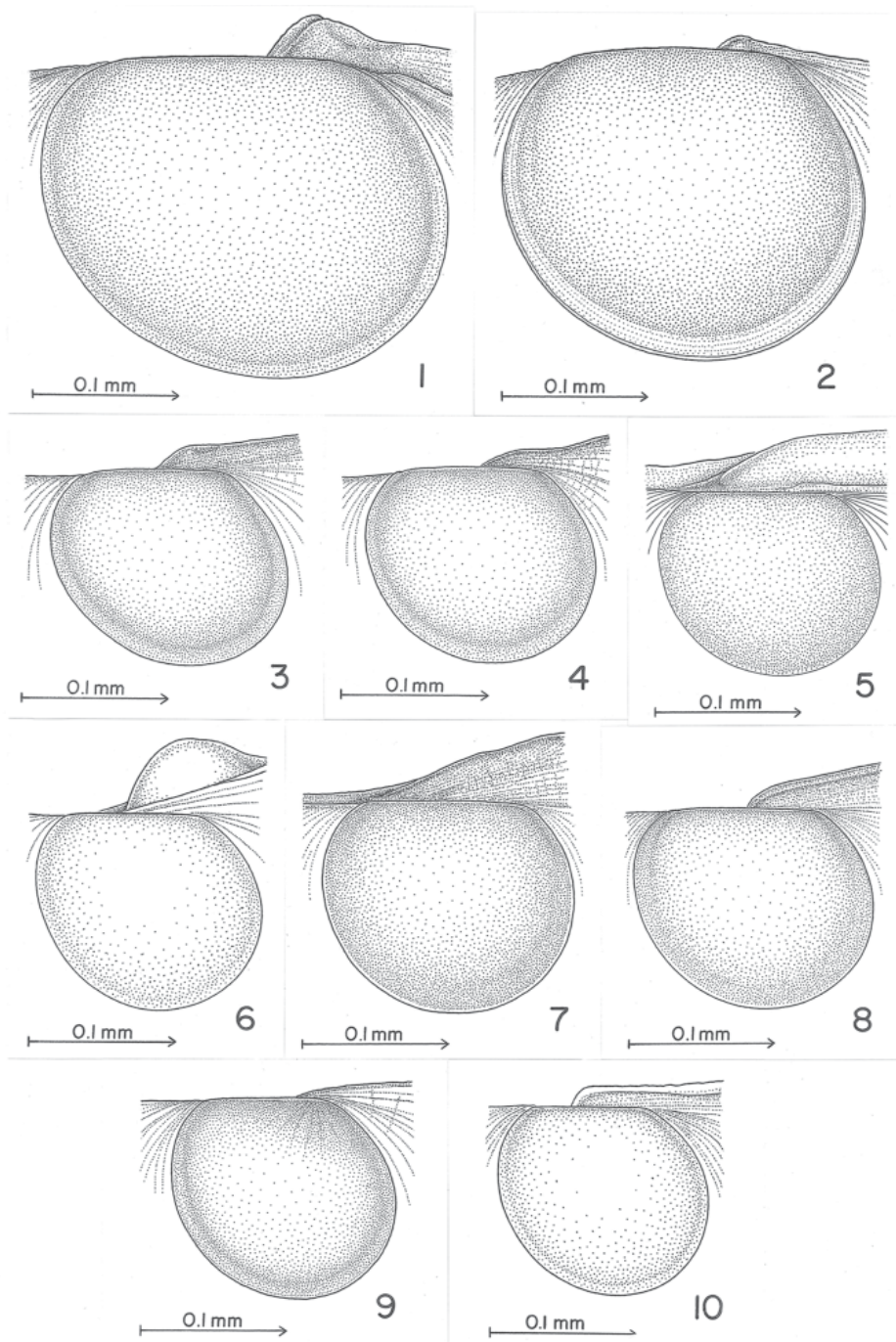


Fig. 16. *Mendicula pygmaea* (Verrill & Bush, 1898). **A.** Ockelmann's map of the distribution, arrow indicates locality of figured shell, Ingolf stn 218. **B–C.** Stipple drawings of the shell and hinge.

Larval shells (prodissoconchs)

Ockelmann was mentored by Gunnar Thorson who postulated Thorson's rule concerning the relationship of egg size and larval development to latitude. Egg size and larval development can be inferred in bivalves from their prodissoconch size and this was an area of interest for Ockelmann throughout his research. In his thyasirid archive, we find two very detailed plates of the drawings and sizes of prodissoconchs of 20 species of Thyasiridae (Figs 17–18). In addition, there are scatter-charts of the length to height ratios of prodissoconchs (Fig. 19), shell size plotted against depth (Fig. 20) and bar charts of bathymetric ranges (Fig. 21). All of these can be related to prodissoconch size and ultimately to Thorson's rule. Ockelmann would also have been familiar with Rass's rule which relates to the variation in larval development within a species affected by latitude or temperature (Laptikhovsky 2006). Unfortunately, we only have the drawings and charts in the archive without any written commentary, so we cannot discern how Ockelmann was going to interpret his results.

The effort he made in compiling this data was impressive for the charts in Fig. 21 were compiled from 21 252 individual observations on 10 species. This data was probably compiled before 1976, as it includes *T. "frigida"* rather than *T. dunbari*. By contrast, the legend on his prodissoconch plate cites "*T. "frigida"* n. sp. = *T. dunbari*" so at least the legend was added after 1976. A selection of these images was sent to the author and published in Oliver & Killeen (2002). At the time we (Oliver & Killeen) were puzzled by the faint radial lines indicated on Ockelmann's drawing of the prodissoconch of *T. equalis* (Fig. 17: no. 9) for we were unable to see any. In a forthcoming paper on NE Atlantic thyasirids, using scanning electron microscopy, I compare the prodissoconchs of a number of species and will demonstrate that *T. equalis* has a very distinct arrangement of raised ridges on the apex of the larval shell that I will describe as the "menorah" pattern, as they resemble to arms on the Jewish candlestick of that name. Furthermore, far from the smooth appearance inferred by Ockelmann's drawings, the prodissoconch displays a variety of distinctive microsculptures that can be used to differentiate species (Fig. 22). While Ockelmann's drawings adequately indicate the sizes of the prodissoconchs, the details are missing, and this would have made it difficult to publish after the establishment of scanning electron microscopy.



1. *Axinopsida orbiculata*. - 2. *Thyasira gouldi*. - 3. *Thyasira flexuosa*. -
 4. *Thyasira sarsi*. - 5. *T. croulinensis?* - 6. *T. succisa*. 7. *T. granulosa*.
 8. *T. frigida* n. sp. = *T. dunbari*. 9. *T. equalis*. 10. *T. subovata* (Jeffr.).

Fig. 17. Fig. 17. Stipple drawings of 10 species of Thyasiridae from the Ockelmann archive, numbering is original and identifications as per annotations. 1. *Axinopsida orbiculata* (G.O. Sars, 1878). 2. *Thyasira gouldi* (Philippi, 1845). 3. *T. flexuosa* (Montagu, 1803). 4. *T. sarsi* (Philippi, 1845). 5. *Axinulus croulinensis?* (Jeffreys, 1847). 6. *T. succisa* (Jeffreys, 1876). 7. *Parathyasira granulosa* (Monterosato, 1874). 8. *T. "frigida* n. sp." = *T. dunbari* Lubinsky, 1976. 9. *T. equalis* (Verrill & Bush, 1898). 10. *T. subovata* (Jeffreys, 1881).

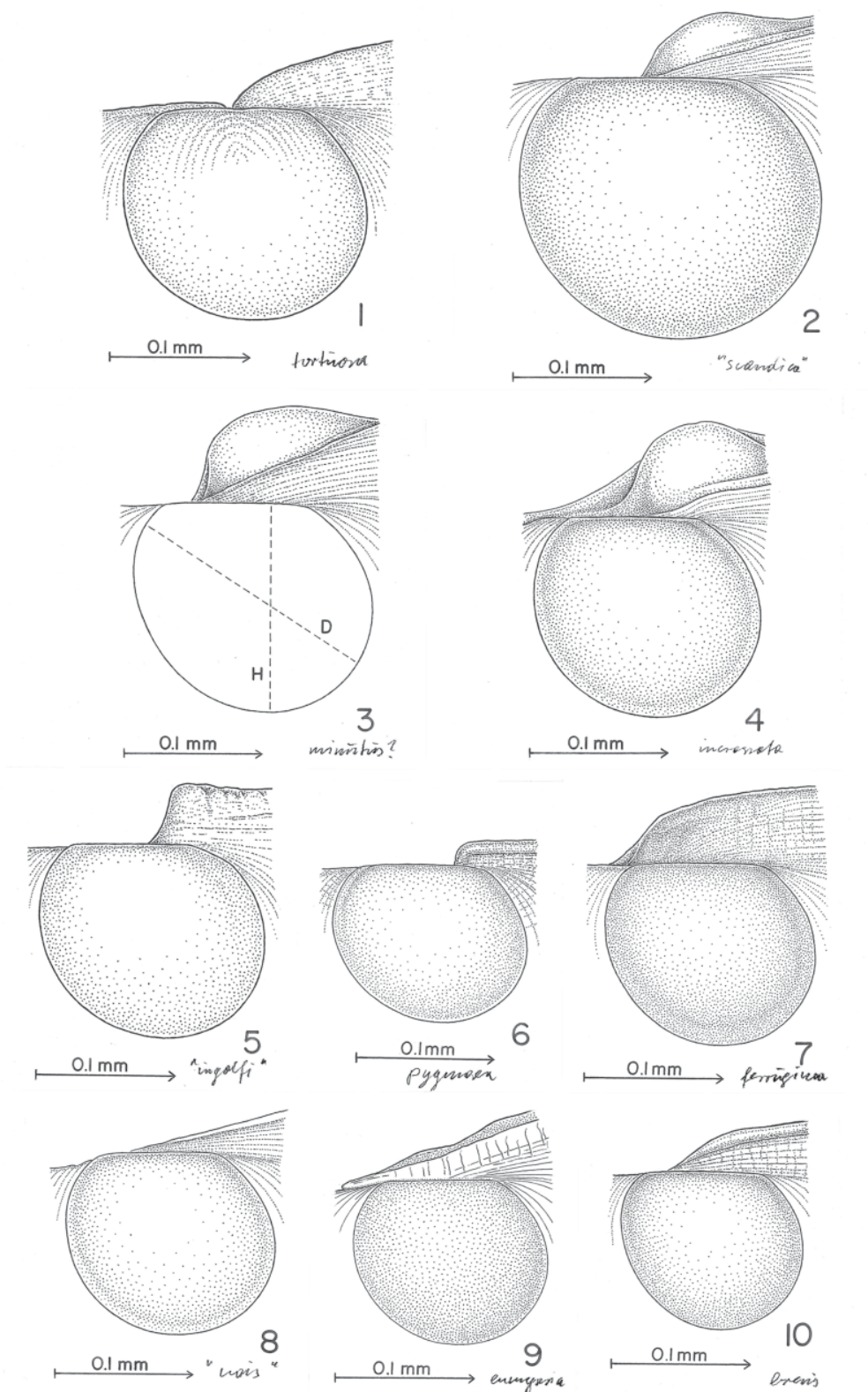


Fig. 18. Stipple drawings of 10 species of Thyasiridae from the Ockelmann archive, numbering is original and identifications as per annotations. **1.** *Thyasira tortuosa* (Jeffreys, 1881). **2.** *T. "scandica"* Ockelmann MS. **3.** *Leptaxinus. minutus* Verrill & Bush, 1898. **4.** *Leptaxinus. incrassatus* (Jeffreys, 1876). **5.** *T. "ingolfi"* Ockelmann MS. **6.** *Mendicula pygmaea* (Verrill & Bush, 1898). **7.** *Mendicula ferruginosa* (Forbes, 1844). **8.** ? **9.** *Genaxinus eumyrius* (M. Sars, 1870). **10.** *Axinulus brevis* (Verrill & Bush, 1898).

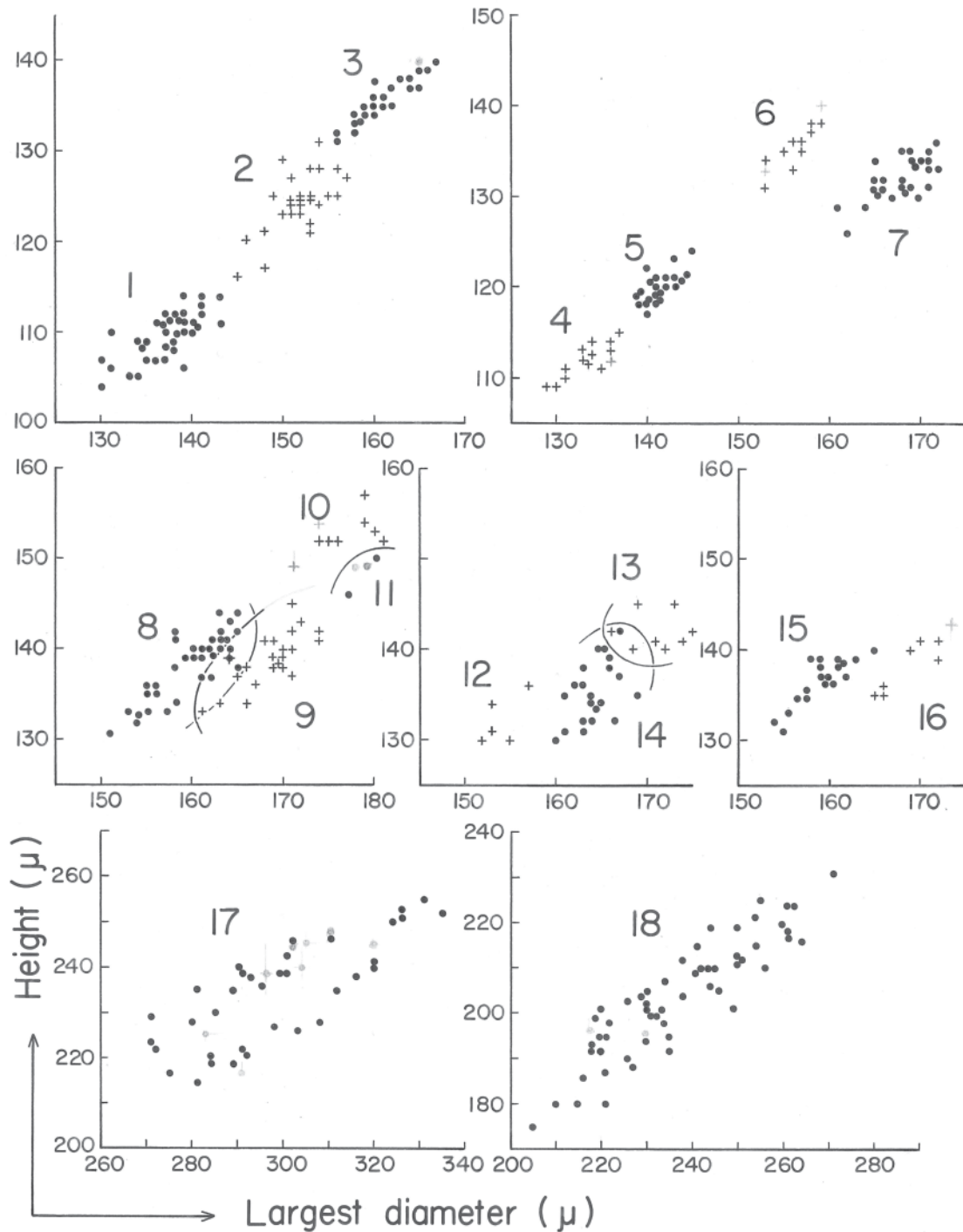


Fig. 19. Scatter diagrams from the Ockelmann archive of the height and largest diameters of the prodossoconchs of eighteen species of Thyasiridae. The identities of the species are not given.

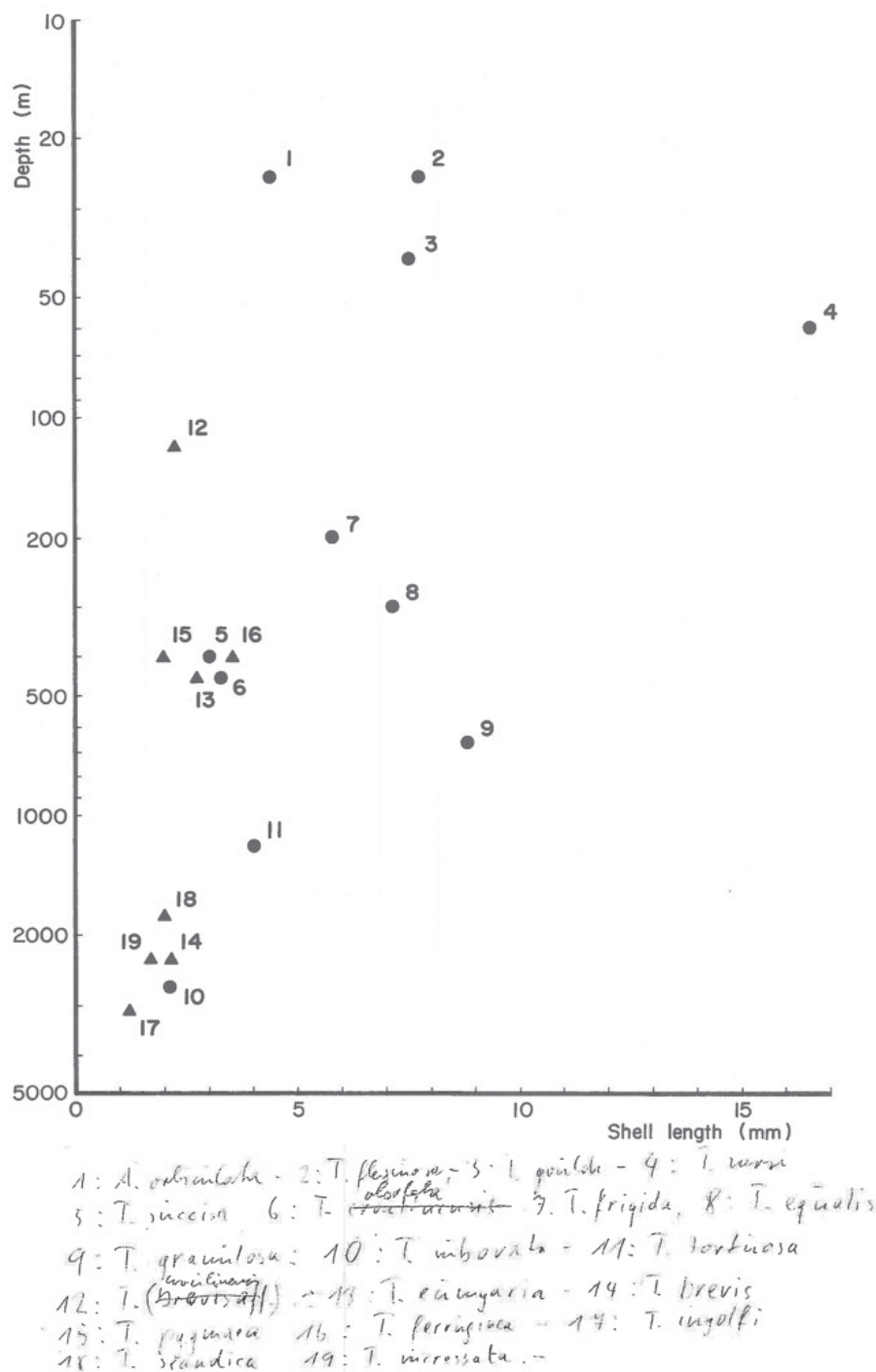


Fig. 20. Chart from the Ockelmann archive of the sizes of species, as shell length plotted against bathymetric distribution of nineteen species of Thyasiridae. Numbering is original and identifications as per annotations. 1. *Axonopsida orbiculata* (G.O. Sars, 1878). 2. *Thyasira flexuosa* (Montagu, 1803). 3. *T. gouldi* (Philippi, 1845). 4. *T. sarsi* (Philippi, 1845). 5. *T. succisa* (Jeffreys, 1876). 6. *T. obsolata* (Verrill & Bush, 1898). 7. *T. "frigida"* Ockelmann MS. 8. *T. equalis* (Verrill & Bush, 1898). 9. *T. granulosa* (Monterosato, 1874). 10. *T. subovata* (Jeffreys, 1881). 11. *T. tortuosa* (Jeffreys, 1881). 12. *T. croulinensis* (Jeffreys, 1847). 13. *T. eumyaria* (M. Sars, 1870). 14. *T. brevis* (Verrill & Bush, 1898). 15. *T. pygmaea* (Verrill & Bush, 1898). 16. *T. ferruginea*. 17. *T. "ingolfi"* Ockelmann MS. 18. *T. "scandica"* Ockelmann MS. 19. *T. incressata* (Jeffreys, 1876).

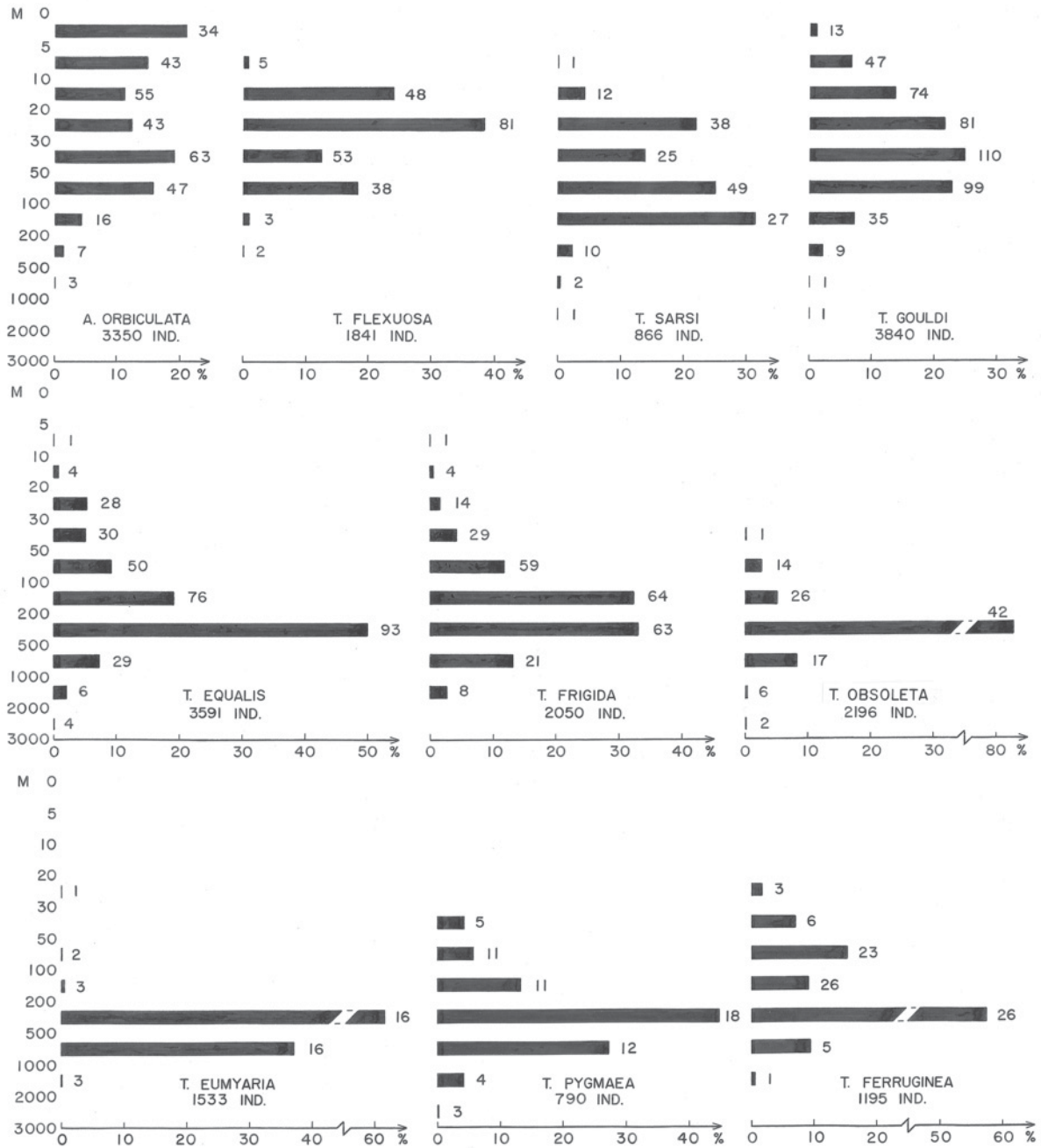


Fig. 21. Bar charts from the Ockelmann archive of the bathymetric distribution of 10 species of Thyasiridae. The depth is given on the x-axis and the percentage of individual recorded on the y-axis. The number on the bars are the actual numbers used.

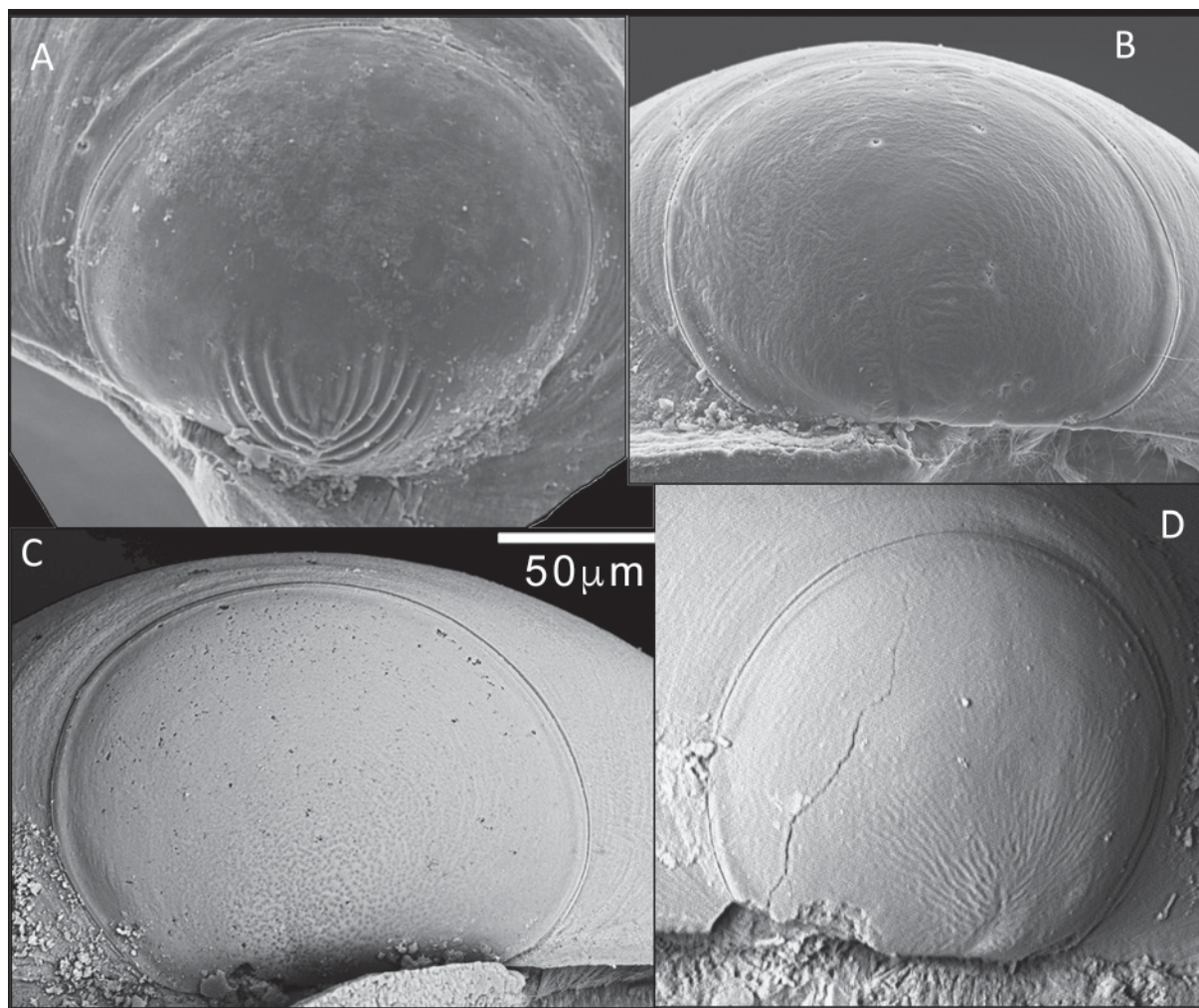


Fig. 22. Scanning electron micrographs of four species of Thyasiridae. **A.** *Thyasira equalis* (Verrill & Bush, 1898) showing “menorah” pattern. **B.** *T. obsoleta* (Verrill & Bush, 1898). **C.** *T. “frigida”* Ockelmann MS. **D.** *Mendicula ferruginea* (Forbes, 1844). All by P.G. Oliver.

The living animal

Ockelmann was what one terms as a “whole animal zoologist” and making observations on living animals in the laboratory was, I believe, a passion of his and is evidenced in other papers of his (e.g., Ockelmann 1964a, 1965; Ockelmann & Muus 1978). He made observations on the burrowing behaviour of at least 3 species of Thyasiridae, *T. flexuosa*, *T. equalis* and what he called *M. pygmaea*. The latter two were modified from rough sketches and reproduced in Oliver & Killeen (2002). The fully worked up reconstruction for *T. flexuosa* is reproduced below (Fig. 23) but not in its original size that was portrait A3. This diagram shows the bivalve living at depth in the sediment with an anterior inhalant tube and the exhalant flow posteriorly into the surrounding sediment. Once buried in this position, the foot probes further into the sediment and makes a network of such tubes (Dando & Southward 1986). I do not know if Ockelmann had an explanation for such behaviour, but he probably thought that pedal feeding was involved where particles of detrital food were brought into the mantle by the foot. It was not until Southward (1986) and Dando & Southward (1986) discovered that the foot was probing into the anoxic zone to supply its commensal chemoautotrophic bacteria with sulphides that the behaviour

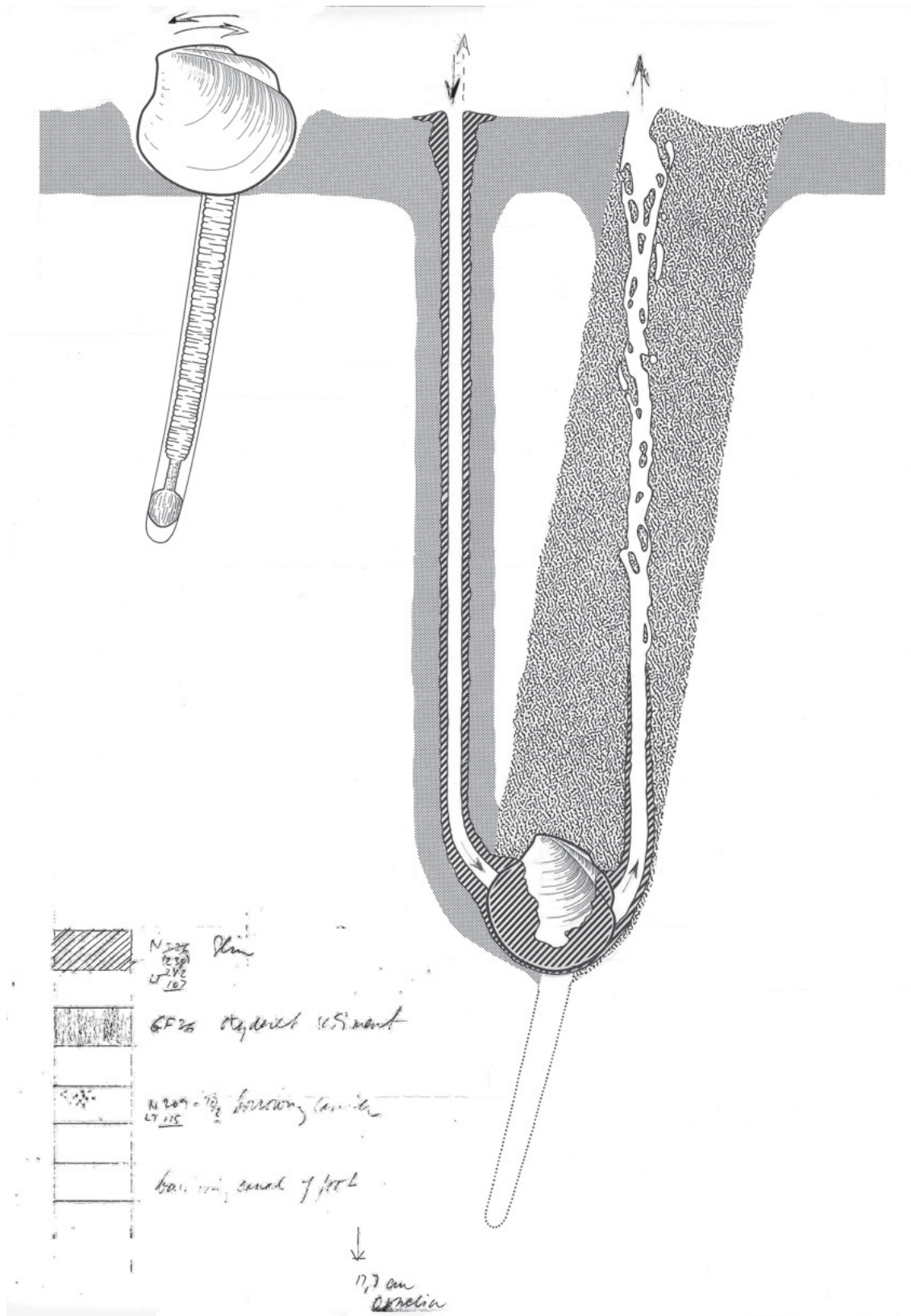


Fig. 23. Drawing by Kurt Ockelmann of *Thyasira flexuosa* (Montagu, 1803) in life position. The annotation “17.7 cm *Ophelia*” at the base suggests the eventual reproduction size of the diagram for the journal “*Ophelia*”.

was truly recognised. This symbiosis of *T. flexuosa* with chemoautotrophic bacteria was discussed with Ockelmann by Paul Dando (pers. comm.) who recounts here: “Kurt described using India ink particles to study the flow of water through the pathways and noted that the inhalant tube flow was sometimes reversed, as noted by the dotted arrow line in Fig. 23. He also noted that the bivalve did not pump water from above and from below at the same time. This then made sense, since it avoided chemical oxidation of sulphide by oxygen before either reached the gills. The figure also shows that Ockelmann appreciated the oxidation of the sediment by water drawn down through the inhalant tube.” Eve Southward (1930–2023) (Dando *et al.* 2024), on 10 June 1986, wrote to Ockelmann asking for his comments on her interpretation of the burrowing behaviour, and urging him to publish his observations and to join a European consortium to apply for funds to further their research. There is no reply in Eve Southward's correspondence file, but Ockelmann did not publish his observations or join a research consortium.

This part of his studies included collecting and observing the larvae, their settlement and early life history. Paul Dando also recalls discussing such matters, including Ockelmann's observations that the larvae of *T. flexuosa* and *T. sarsii* (Philippi, 1845) (Philippi 1845b) were benthopelagic and that on settlement, the larvae chose organic-rich areas such as sunken mats of *Zostera* leaves. Ockelmann observed that, in his laboratory tanks, the young bivalves lived at the surface of the sediment for about a year before burrowing and taking up the life position seen in the above diagram. Paul Dando also recalls Kurt explaining to him how he studied the ciliary currents entering and exiting the mantle cavity by jamming open the valves so that he could see inside. Kathe Jensen (pers. comm.) also recalls Kurt's enthusiasm for these observations in 1972. This study was aided by Ockelmann's invention of a detritus sledge for collecting meiobenthos and newly settled larvae (Ockelmann 1964b).

Ciliary currents

A routine part of the description of the function of a bivalve is to record the ciliary currents on the mantle and gill as pioneered by Ridewood (1903) and later by Atkins (e.g., 1937). Two diagrams (Fig. 24A–B) illustrate ciliary currents in the mantle of what appears to be *Thyasira flexuosa*. The mantle ciliary currents are shown in great detail and would have taken very careful observation to record. This diagram is instructive as it indicates mantle apertures both fixed by tissue fusion and by ciliary junctions. The presence of two posterior apertures has been noted in some species by Payne & Allen (1991) and Zelaya (2009); the former suggested the second (ex a2 here) was a second inhalant aperture while the latter only recorded their presence. Ockelmann's diagram clearly shows a small current exiting at ex a2 and I suggest this is expelling pseudofaeces. It also shows that only the upper exhalant aperture is created by mantle fusion (solid black line) while the other apertures are created by weaker ciliary junctions that most frequently are not preserved in preserved specimens.

Figure 24C shows glandular areas on the mantle in four species and that their extent is different in the four illustrated. The extent of the glandular areas has been shown to be a useful taxonomic character and was cited by Oliver & Killeen (2002).

Gross anatomy

One assumes that in preparation of the monograph that as each shell was illustrated, so too was the gross anatomy, but only six anatomical diagrams are present in the archive. These are a mixture of stipple drawing and ink, are morphologically exact but stylised interpretations that reflect Ockelmann's knowledge of the anatomy and mastery of the pen (Fig. 25).

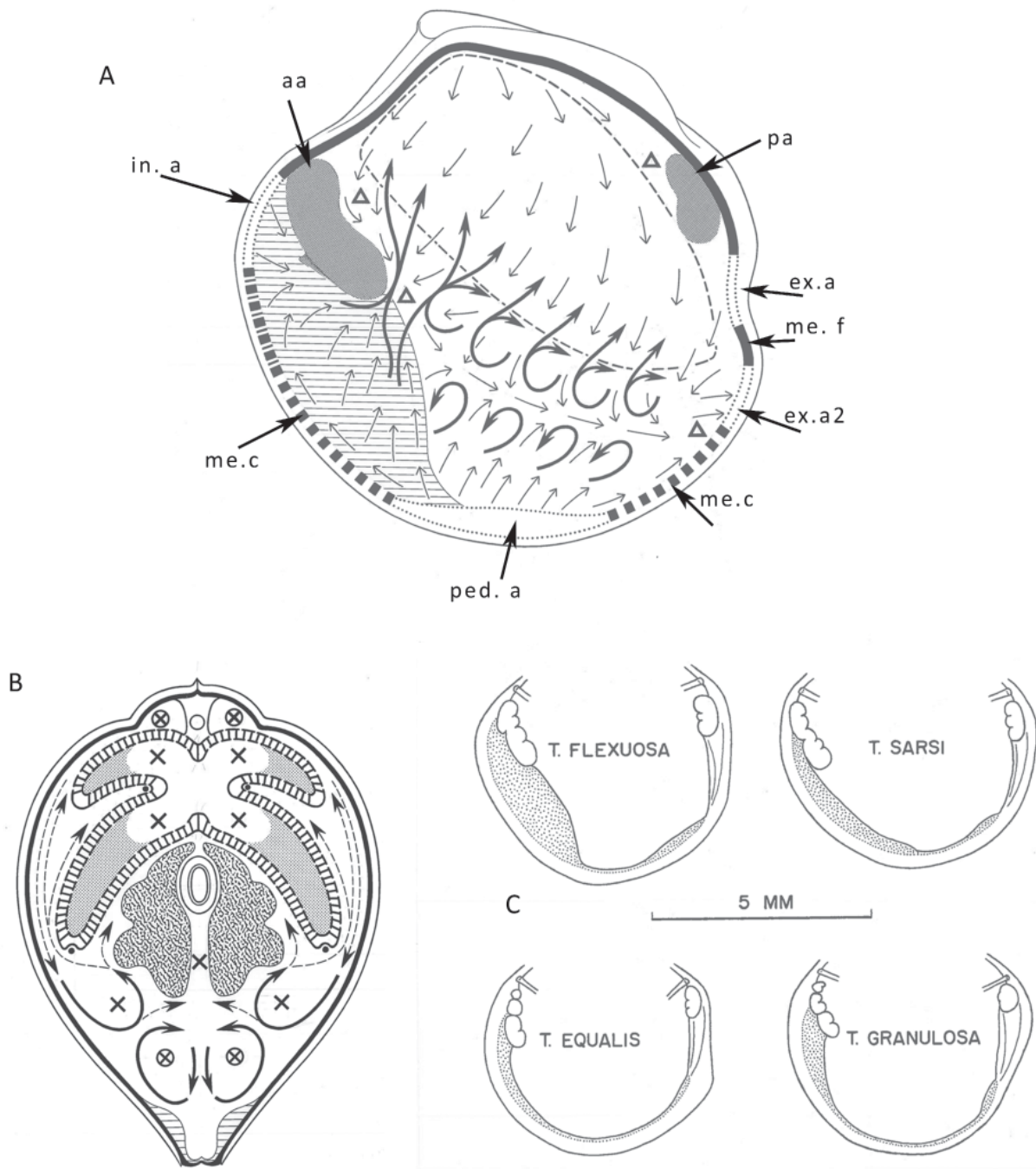


Fig. 24. **A.** Drawing by Kurt Ockelmann of the ciliary currents of the mantle of *Thyasira flexuosa* (Montagu, 1803) (my identification). Abbreviations added by me: aa=anterior adductor muscle; ex. a=exhalant aperture; ex. a2=second exhalant aperture; in. a=inhaling aperture; me. c=mantle edge with ciliary junctions; me. f=mantle edge fused; pa=posterior adductor muscle; ped. a=pedal aperture. The significance of the open triangles on the original is unclear. **B.** Diagrammatic transverse section of a thyasirid showing ciliary currents. The x indicates direction of current towards the anterior. **C.** Sketches of four species of thyasirid indicating the extent of glandular tissues (stippled areas) on the mantle.

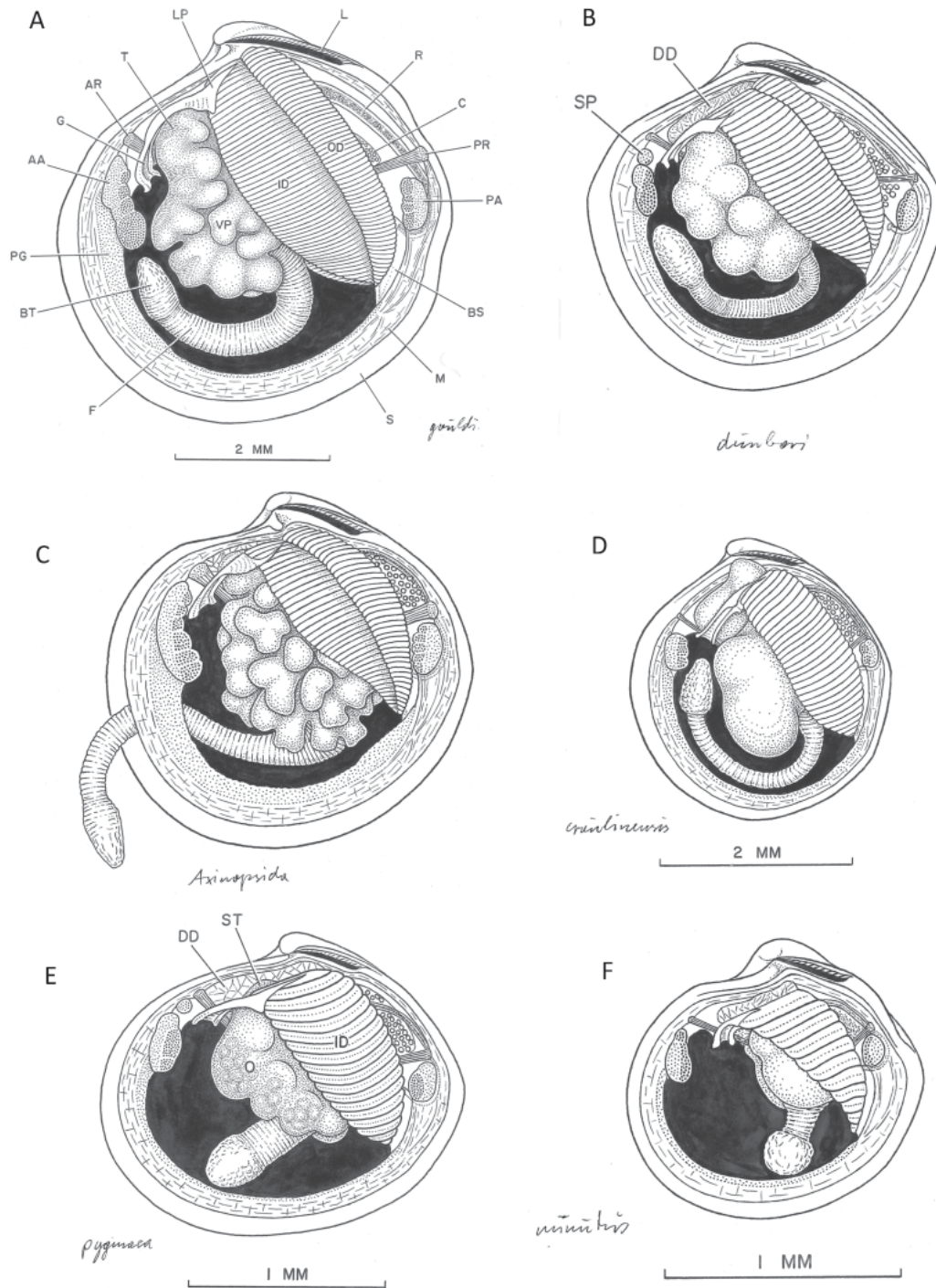


Fig. 25. Six anatomical diagrams drawn by Kurt Ockelmann. **A.** “gouldi” is *Thyasira gouldii* (Philippi, 1845). **B.** “dunbari” is *Thyasira dunbari* Lubinsky, 1976. **C.** “Axinopsida” is *Axinopsida orbiculate* (G.O. Sars, 1878). **D.** “croulinensis” is *Axinulus croulinensis* (Jeffreys, 1847). **E.** “pygmaea” is *Mendicula pygmaea* (Verrill & Bush, 1898). **F.** “minutis” is *Leptaxinus minutus* Verrill & Bush, 1898. Original annotations: AA=anterior adductor; AR=anterior retractor; BS=branchial septum; BT=bulbous toe; C=gonad; DD=digestive diverticula; F=foot; G=food groove; ID=inner demibranch; L=ligament; LP=labial palp; M=mantle; O=ova; OD=outer demibranch; PA=posterior adductor; PG=pedal gland; PR=posterior retractor; R=rectum; S=shell; SP=separate part of adductor; ST=stomach; T=testis; VP=visceral pouch.

Other shell drawings

- *Thyasira tortuosa* (Jeffreys, 1881)

Within the archive, besides the typical stipple drawings, is a rough sketch (Fig. 26C) of the anatomy of *T. tortuosa* made from a dried specimen from the French *Travailleur* expedition of 1880, dredge 10. It might be assumed that Ockelmann was sent this material, for there is no evidence that he visited the Paris museum where the bulk of this collection is kept. However, there are 2 lots in the Smithsonian, USNM 61983/61984, which are ex *Travailleur* in Jeffreys collection and it is likely it was one of these that he drew during his visit in 1959. Lot number USNM 61984 is listed as a lectotype, selected by Ockelmann, in the Smithsonian catalogue, but this was never formally published. By chance, one of these (USNM 61983) was illustrated by Payne & Allen (1991: fig. 45). Ockelmann indicates that the prodissoconch is sculptured and indeed it has a “menorah” pattern (Fig. 26E) as seen in *T. equalis* (Fig. 22A); this was not mentioned by Payne & Allen (1995). Also not mentioned by Payne & Allen (1995) and not commented upon by myself is Ockelmann’s observation that the uppermost part of the anterior adductor is separate from the remainder. It is indicated here as a “separate portion of ant add” and he also indicated in his anatomical diagram of *T. dunbari* (Fig. 25B), where it is annotated as “SP”.

- *Thyasira (Parathyasira) granulosa* (Monterosato, 1874) (Fig. 27A–C)

Here, Ockelmann illustrated the typical radially arranged microspicules on the shell surface (Fig. 27B). These spicules can be seen on the supposed lectotype and paralectotype of *Thyasira flexuosa* var. *rotunda* in the Smithsonian, USNM 61942 and 61942a. This selection was never formally published and is now superceded by the presence of type material from the type locality in the NHMUK.

- *Thyasira succisa* (Jeffreys, 1876) (Fig. 27D–E)
- *Axinopsida orbiculata* (G.O. Sars, 1878) (Fig. 27F–G)
- *Thyasira (Axinulus) brevis* (Verrill & Bush, 1898) (Fig. 28A–B)
- *Thyasira (Axinulus) croulinensis* (Jeffreys, 1847) (Fig. 28C–D)
- *Thyasira (Genaxinus) eumyaria* (M. Sars, 1870) (Fig. 28E)
- *Mendicula ferruginosa* (Forbes, 1844) (Fig. 28F)
- *Thyasira flexuosa* (Montagu, 1803) (Fig. 29A–C)
- *Thyasira sarsii* (Philippi, 1845b) (Fig. 29D–E)
- *Channelaxinus perplicatus* (Salas, 1996)

The illustrated shell (Fig. 30A) is not identified, but is a typical example of what was known as *Thyasira plicata* (Verrill, 1885) but is now *Channelaxinus perplicatus*.

- *Axinus grandis* (Verrill & Smith, 1885)

The stipple drawing of the hinge of *A. grandis* is labelled “holotype” and is probably one of the shells in the Smithsonian under USNM 44824. There is a little variance in the literature, as Payne & Allen (1991) cite the holotype as being in the MCZ Harvard, the station data is the same for both USNM and MCZ shells.

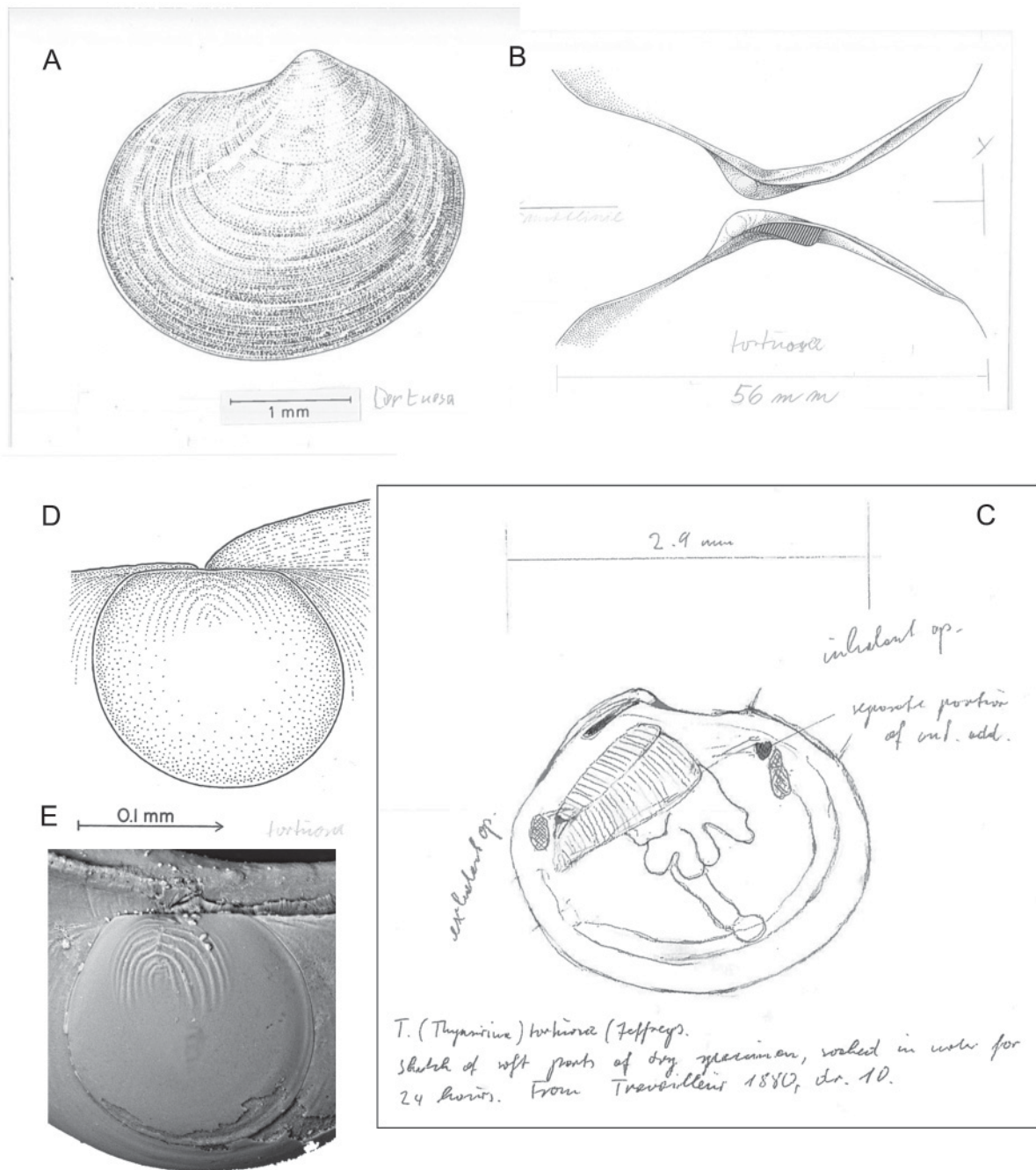


Fig. 26. *Thyasira tortuosa* (Jeffreys, 1881). **A.** Stipple drawing of shell. **B.** Stipple drawing of hinge. **C.** Pencil sketch of the anatomy. **D.** Stipple drawing of the prodissoconch. **E.** Scanning electron micrograph of the prodissoconch, specimen from off New England (USNM 1495804), by P.G. Oliver.

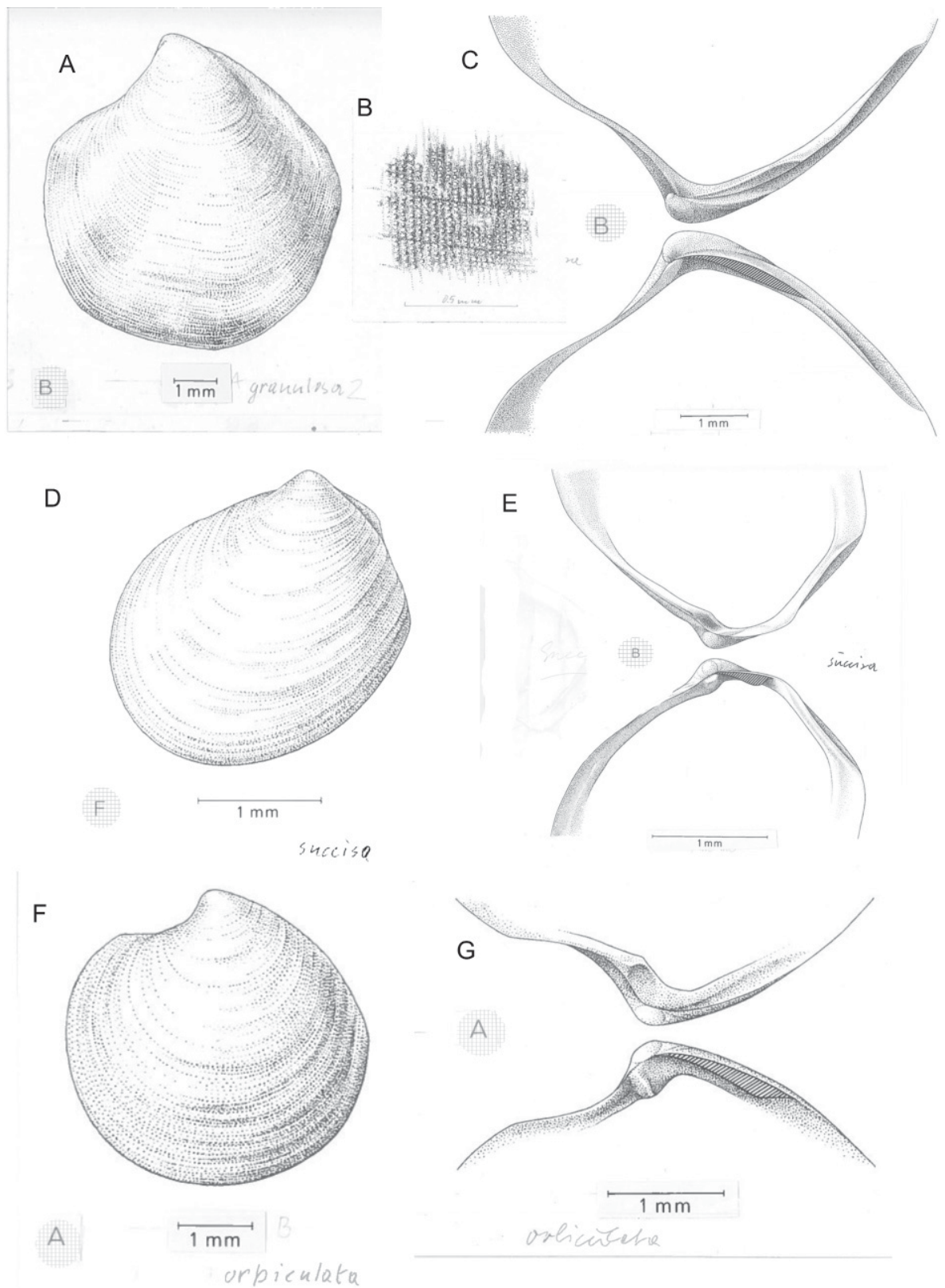


Fig. 27. Stipple drawings by Kurt Ockelmann of three species of Thyasiridae. **A.** Shell labelled “granulosa” is *Parathyasira granulosa* (Monterosato, 1874). **B.** Detail of the microsculpture. **C.** Hinge of *P. granulosa*. **D–E.** Shell and hinge of “succisa” is *Thyasira succisa* (Jeffreys, 1876). **F–G.** Shell and hinge of “orbiculata” is *Axinopsida orbiculata* (G.O. Sars, 1878).

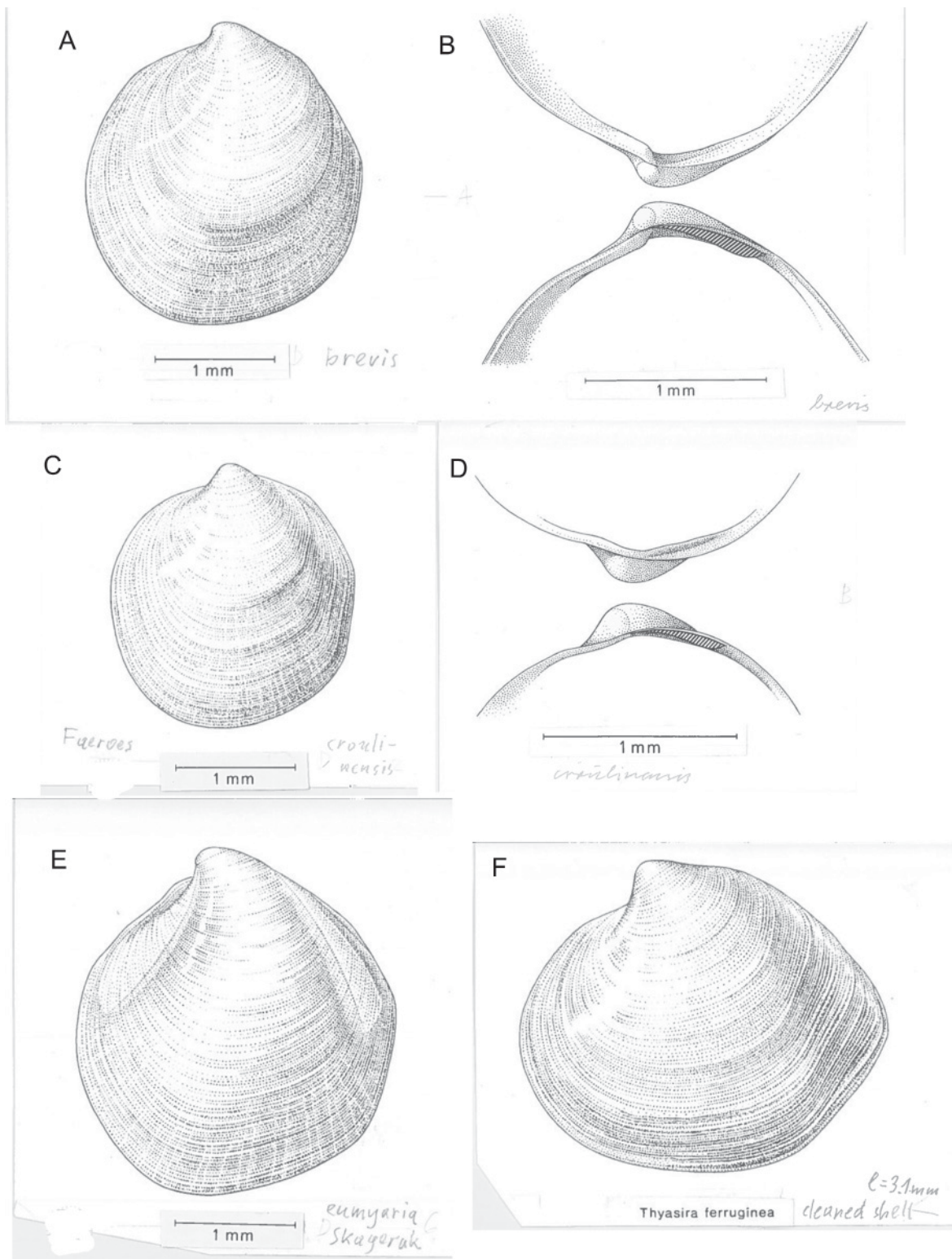


Fig. 28. Stipple drawings by Kurt Ockelmann of four species of Thyasiridae. **A–B.** Shell and hinge of “brevis” is *Axinulus brevis* (Verrill & Bush, 1898). **C–D.** Shell and hinge of “croulinensis, Faeroes” is *Axinulus croulinensis* (Jeffreys, 1847). **E.** Shell of “eumyaria Skagerrak” is *Genaxinus eumyarius* (M. Sars, 1870). **F.** “Cleaned shell of *Thyasira ferruginea*” is *Mendicula ferruginea* (Forbes, 1844).

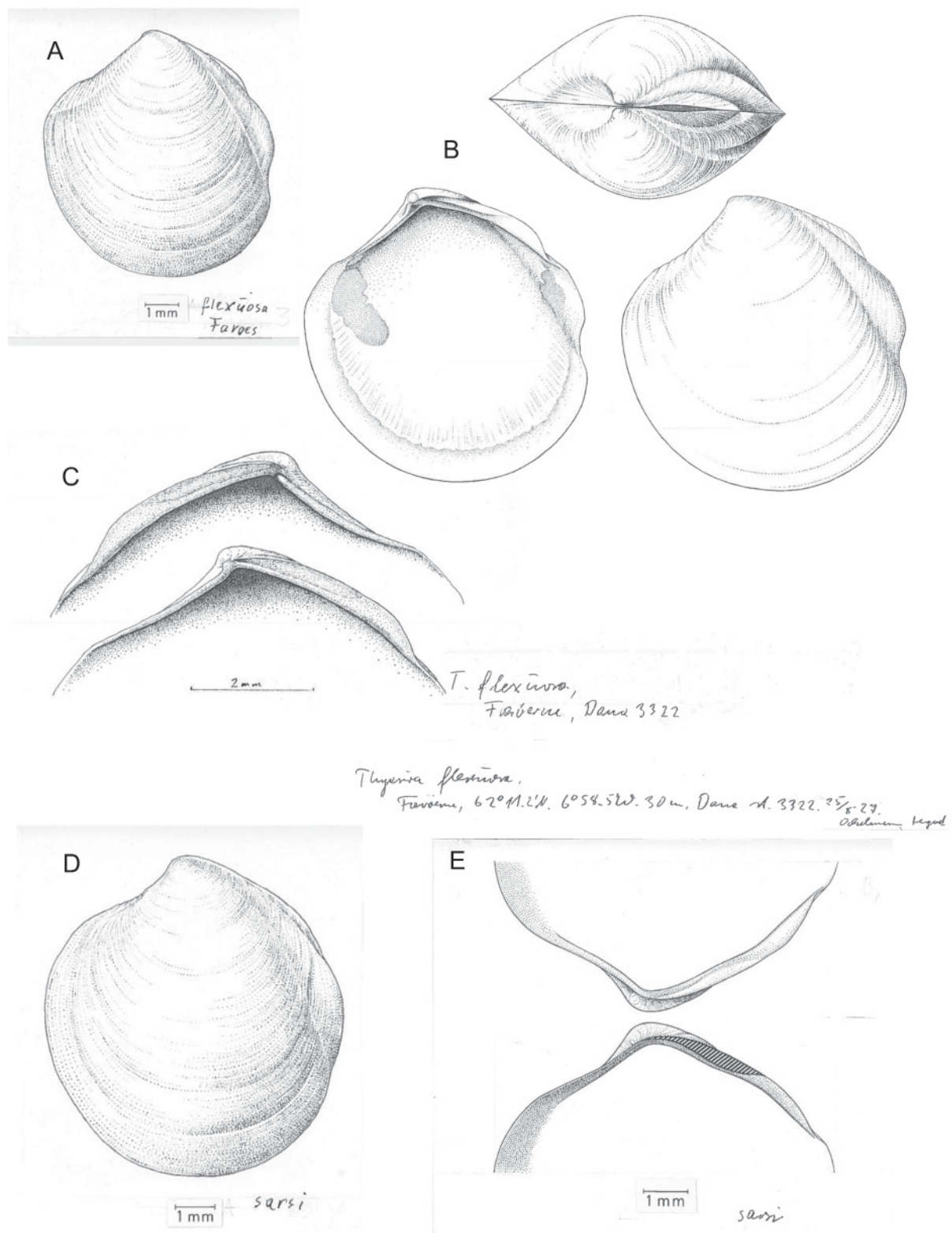


Fig. 29. Stipple drawings by Kurt Ockelmann of two species of Thyasiridae. **A.** Shell labelled “*flexuosa* Faroes” is *Thyasira flexuosa* (Montagu, 1803). **B.** Internal, external and dorsal views of the shell of *T. flexuosa*. **C.** Stipple drawing of the left and right hinges of *T. flexuosa*, the annotation indicates that the shell was from the Faroes at 62°11.2' N, 6°58.5' W and was from “*Dana*” stn 3322. **D-E.** *T. sarsi* (Philippi, 1845) shell and hinge, no locality indicated.

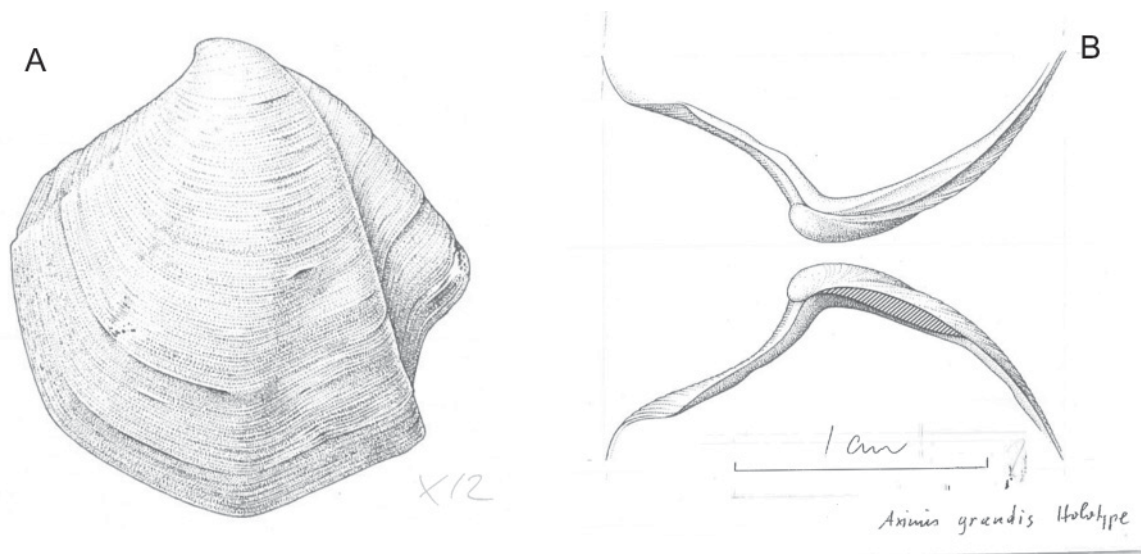


Fig. 30. **A.** *Chanellaxinus perplicata* (Salas, 1996), stipple drawing by Kurt Ockelmann lacking any legend. **B.** Stipple drawing by Kurt Ockelmann of the hinge of *Axinus grandis* (Verrill & Smith, 1885), labelled holotype.

Discussion

It is undoubtedly true that Ockelmann made many new observations on the Thyasiridae based on many detailed observations on both living and preserved specimens. It is also true that he had a great influence on others interested in the Thyasiridae. But what of his legacy and what can we derive from his surviving monograph? I fear that, by not publishing or actively collaborating, his research will be overlooked.

Of the undescribed species, three, *T. "perplexa"*, *T. "scandica"* and *T. "ingolfi"*, are represented by too few specimens to sustain description today. The fourth, his *T. "frigida"*, should have been published as he had considerably more material than Lubinsky (1976) and from a far greater geographical and bathymetric range.

He was the first to recognise amphi-Atlantic species inhabiting the continental margins of both north-east American and European waters but without published papers, he has no visible credit for this. With DNA sequencing, it will be possible to investigate the phylogenetic relationships of these amphi-Atlantic populations and test the validity of their distributions.

He was among the first to observe the unusual burrowing behaviour of thyasirids and if he had collaborated with Southward and Dando, he would have been at the forefront of the investigations into the ecology of chemosymbiotic species. If he had continued his observations on the settling of thyasirid larvae he may have helped to discover when, and from where, they acquired their symbiotic bacteria.

He was the first to document the larval shells, prodissoconchs, of all known N Atlantic species but his work has become largely irrelevant through the advent of scanning electron microscopy. I am sure he could have had access to scanning electron microscopy but he did not use it, rather choosing to stay with familiar techniques.

He was meticulous as evidenced in the thousands of shells he processed to compile bathymetric ranges for N Atlantic species and map their distribution.

Yet, he published but one short paper specifically on thyasirids after his major work on the bivalves of East Greenland and because of this, his name does not feature as much as it should in the literature on the thyasirids. Despite this, he had a wide and lasting influence through his generosity of sharing his knowledge with others and being satisfied with mentions in acknowledgments of many papers. His beautiful stipple illustrations are far superior to any others published and his anatomical diagrams are striking for their clarity.

Unfortunately, time passes, and new techniques and thinking have made it impossible to go back and publish his work as prepared by him. Others have now published on many aspects of his study and in some instances, new techniques have revised his work radically. In this retrospective, I hope by reproducing many of Ockelmann's drawings, one can see the excellence of his work and powers of observation.

I cannot explain why Ockelmann never published his monograph or any part of it. I did not know him well enough to know if it was down to a streak of perfectionism or perhaps the making of observations was enough for him and the laborious process of preparing papers was just too much. Tom Schiøtte recalls: "I believe this is what Jørgen Knudsen, Godtfred Høpner Petersen and others who asked Kurt about it were convinced was the reason. He said something like "These things lie very well in my drawers". I once asked him if he wouldn't like to be remembered for having solved the riddle of *Thyasira*, and he actually scolded me for thinking that such concerns should be on the mind of a true scientist".

Perhaps Kurt would not approve of publishing this retrospective, but I hope that it will be cited and give due acknowledgement to his enormous contributions to the study of these small, non-descript, but fascinating bivalves.

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