

A new species of the family Thyasiridae (Mollusca: Bivalvia) from the oxygen minimum zone of the Pakistan margin

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A new species of Thyasiridae, *Leptaxinus' indusarium* sp. nov. is described from the Indus margin, off Pakistan. The generic affinity is tentative and possible alternatives are discussed. It occurs between 800 m and 1000 m water depth in a low oxygen environment, where it is relatively abundant. The ecological setting is described and data suggest that this species is not chemosymbiotic.

INTRODUCTION

A large study of effects of the oxygen minimum zone on organic matter cycling was conducted on the Indus margin (off Pakistan) by British, Dutch and American investigators during 2003 (Cowie, 2004a,b, 2005). Systematic sampling of the margin between 140 and 1850 m by trawl and core revealed strong effects of the oxygen minimum zone ($<0.5 \text{ ml l}^{-1}$; located between 100 and 1200 m), with many species exhibiting narrow depth distributions, presumably influenced by availability of oxygen. At depths of around 900 m a bivalve tentatively identified as a thyasirid was found to be relatively abundant and was illustrated in Cowie, 2004a,b.

Thyasirid bivalves are unusual in that some are chemosymbiotic and some are not (Dufour, 2005), and that they inhabit a wide range of environments from extreme chemosynthetic communities such as hydrothermal vents to intertidal mudflats. With the exception of the genus *Conchocele*, they are not common, as compared to the Vesicomidae and Bathymodiolinae, in chemosynthetic communities (Oliver & Sellanes, 2005). Oxygen minimum zones are characterized by having high levels of nutrients and reducing conditions, apparently ideal for chemosymbiotic organisms, yet molluscs are generally rare (Levin, 2003). On the Oman margin thyasirids were present but at depths beyond 1000 m where the oxygen concentrations were above 0.25 ml l^{-1} (Levin et al., 2000). The taxa found included small species assigned to the genus *Mendicula* (Levin et al., 2000) as well as larger, carinate-shelled species such as *Thyasira' investigatoris* (Smith, 1895) (P.G. Oliver, personal observation). The Pakistan margin thyasirid was found at lower oxygen concentrations and in greater abundance than any of those from the Oman margin. Thyasirids have not been reported from other oxygen minimum zone sites outside the Arabian Sea such as those off Peru, West Africa or in the Santa Barbara Basin.

The species under study here is therefore unusual within the Thyasiridae as well as being one of the

few bivalve species that can tolerate such low oxygen conditions.

SYSTEMATICS

Order VENEROIDA H.&A. Adams, 1856

Family THYASIRIDAE Dall, 1901

Genus *Leptaxinus* Verrill & Bush, 1898

Leptaxinus' indusarium sp. nov.

Figures 1–3

Material examined

All material was collected during the RRS 'Darwin' cruise, on the Indus margin of Pakistan, Station 55912#1 by trawl from $22^{\circ}54.10'N$ $66^{\circ}38.88'E$ to $22^{\circ}54.62'N$ $66^{\circ}37.81'E$, 879 m, 13 May 2003.

Holotype: a complete shell, NMW.Z.2005.34.1; length 3.7 mm; height 3.5 mm; tumidity 2.2 mm.

Paratypes: 1 shell and 1 valve on scanning electron microscopy stubs, NMW.Z.2005.34.2; 5 specimens in alcohol, GENBANK reference material, Natural History Museum, London.

Diagnosis

Thyasirid with ctenidium of a single demibranch, multi-lobed lateral pouches and foot with a heel. Shell with only weak posterior truncation, posterior slope not sulcate, outline subovate with posterior margin more broadly rounded than anterior. Lunule large, asymmetric. Escutcheon cleft. Hinge with small median tubercle.

Description

The shell (Figures 1A–C & 2A–I)

Shell small, to 5 mm in length, fragile. Subequilateral, beaks at or just behind the midline. Beaks prosogyre. Equivalve, becoming inflated in some (length to tumidity ratio 1.5:1 to 1.75:1). Outline subovate, broad posteriorly, more narrowed anteriorly, length slightly greater than height; posterior dorsal slope steep and gently curved; posterior truncate, slightly indented; ventral and anterior

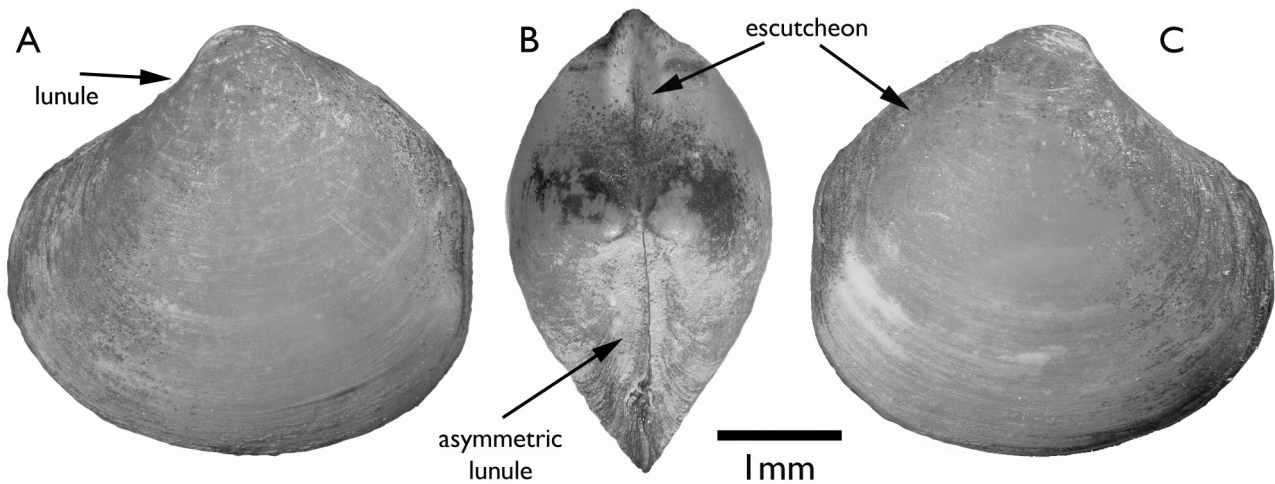


Figure 1. '*Leptaxinus*' *indusarium* sp. nov. Holotype NMW.Z. 2005.34.1. Shell, imaged using AutoMontage™. (A) Left valve; (B) dorsal view; and (C) right valve.

margins forming a smooth broad curve; anterior dorsal margin distinct, long and gently incurved. Lunule distinct (Figures 1B & 2E–F), demarcated by a low ridge, asymmetrical, larger in the right valve and overlapping left valve anteriorly where there is a small twist; microsculpture (Figure 2H–I) of irregular transverse raised ridges in right valve, these absent in left valve. Escutcheon (Figures 1B & 2E) distinct, cleft, running length of posterior dorsal margin. Auricle absent. Posterior slope not sinuate but distinct as flattened area especially towards the truncate margin. Ligament small (Figure 2A & C), about one-fifth the length of escutcheon, deeply sunken and not visible externally. Hinge plate weak with only a single small tubercle in each valve (Figure 2A & C). Sculpture more or less smooth with occasional fine concentric lines; surface with a thin veneer of brown periostracum and ferruginous deposit. Prodissoconch smooth, 191 µm in diameter (Figure 2G).

Anatomy

Mantle thin, mantle edge free except at junction with gill axis, smooth, without any modifications (Figure 3A,B). Exhalant aperture large, between termination of gill axis and posterior adductor muscle (Figure 3A,B).

Adductor muscles unequal, anterior approximately four times longer than posterior, anterior muscle elongate partly divergent from mantle edge (Figure 3A,B).

Foot small (Figure 3E,F), toe elongate with a swollen tip in some, not present in others and probably dependent on preservation. Heel distinct, but small. Retractor muscles weak.

Ctenidium (Figure 3A–D) of inner demibranch only, consisting of about 40 filaments, ascending arms shorter than descending but not greatly so. Gill filaments of Type 2 (Dufour, 2005). Labial palps very small, sorting ridges not observed.

Lateral body pouches (Figure 3C,D) large, multilobed, digestive gland also present as small lobes dorsal to oesophagus (Figure 3E,F). Gut simple (Figure 3E,F), hind gut and mid gut forming a simple S loop, stomach cylindrical with a large opening to lateral body pouch and a smaller

opening to the dorsal digestive gland. Rectum running around posterior adductor, attached to base of pedal retractor so that anus opens close to exhalant aperture.

Kidney large with distinct golden concretions in posterior section (Figure 3E,F).

Etymology

Named after the type locality the Indus margin of Pakistan.

Distribution

Known only from the Indus margin of Pakistan in water depths of 800 m to 1000 m.

Species comparisons

Most descriptions of thyasirid species are based on shells only. Consequently, the hinge, dorsal margin structures and general outline are important. '*Leptaxinus*' *indusarium* is unusual in that the posterior area is more broadly rounded than the anterior with its deeply indented lunule margin. It also has distinctive lunule and escutcheon characters. Considering the fauna of the Arabian Sea and wider Indian Ocean then this species may have been encountered by the exploration cruises of the 'Investigator' (Smith, 1894, 1895, 1906), 'Valdivia' (Thiele & Jaeckel, 1931), and the 'John Murray' (Knudsen, 1967). The species encountered were *Cryptodon investigatoris* Smith, 1894, *C. acuticarinata* Smith, 1895, *C. omanensis* Smith, 1906, *Thyasira aequitoralis* Thiele & Jaeckel, 1931 and *T. valdiviae* Thiele & Jaeckel, 1931. All of these species are bicarinate and none of these warrants further comparison.

The wider Indo-Pacific fauna is poorly known except for Japan (Matsukuma, 2000) and the north-eastern Pacific (Coan et al., 2000) but although there are superficially similar taxa none have the same combination of characters. Perhaps the most studied thyasirid fauna is that of the Atlantic Ocean (Payne & Allen, 1991; Oliver & Killeen, 2002) and there is similarity to *Thyasira succisa* (Jeffreys, 1876) in the lunule and escutcheon but not in outline or gill type.

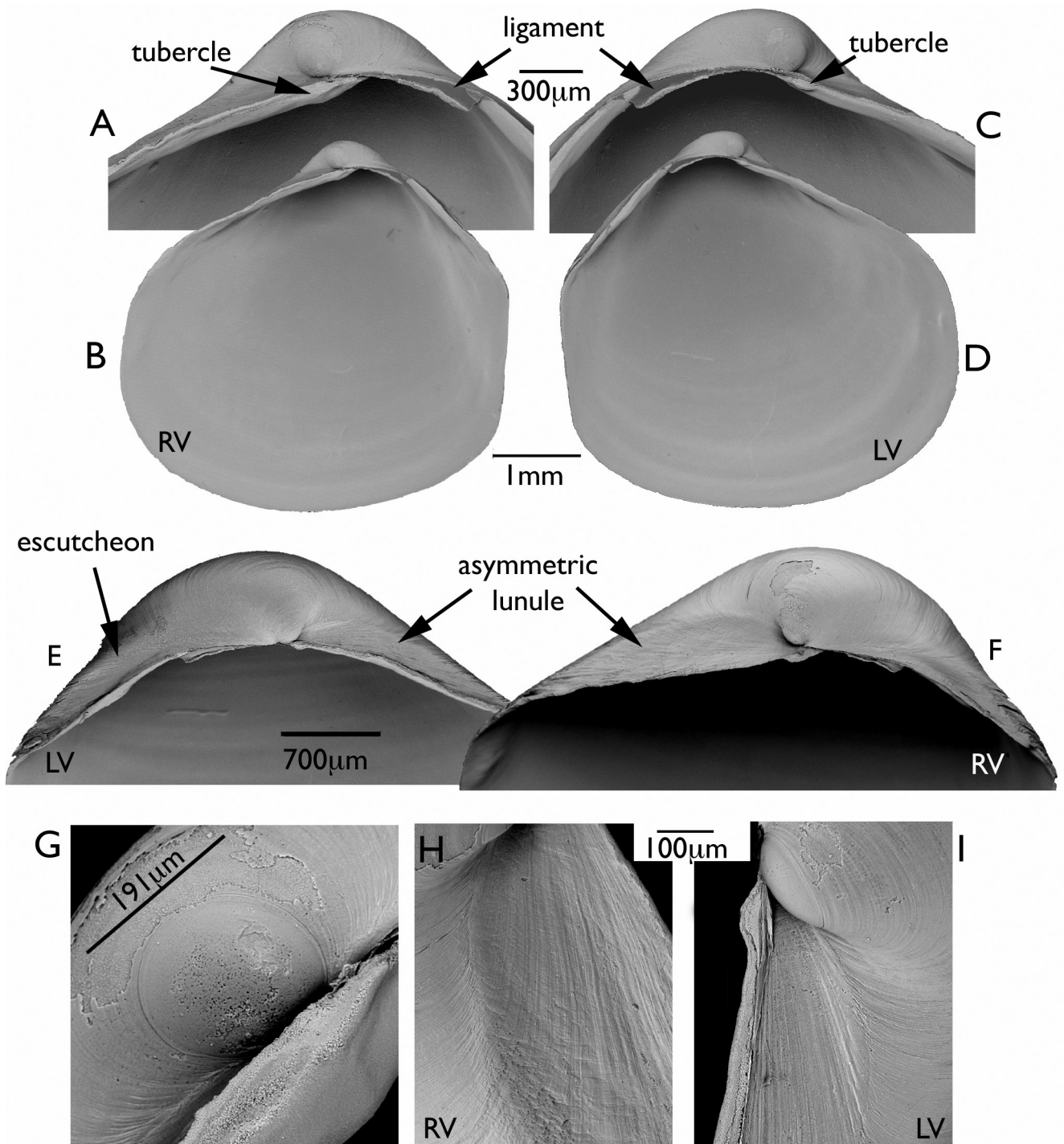


Figure 2. *Leptaxinus* *indusarium* sp. nov. Paratype NMW.Z. 2005.34.2. Scanning electron micrographs of shell. (A, B) Right valve; (C, D) left valve; (E, F) escutcheon and lunule in left valve and right valve respectively; (G) prodissoconch; and (H, I) lunule.

Symbionts (this section by Suzanne Dufour)

Four specimens of *L. indusarium* were immersed in 3% glutaraldehyde in a 0.1 M sodium phosphate buffer (pH 7.3) with 0.35 M sucrose, after the shells had been cracked to allow better infiltration of the fixative. After a minimum of 24 h, the specimens were rinsed in the sodium phosphate buffer, and the gills were dissected and post-fixed for 1 h in 1% osmium tetroxide in the same buffer. The gills were then dehydrated in an ascending ethanol gradient, and embedded in Spurr resin. Semi-thin (1–2 μm) sections were made, and stained with toluidine blue.

The gill filaments, as seen on semi-thin sections, have a simple, homorhabdic filibranch design, and correspond to the Type 2 gill morphotype described for some thyasirids (Dufour, 2005). On all specimens examined, the gill epithelial cells were in poor state: there was much desquamation, with, in many cases, only the structural collagen rods remaining. The gills of two specimens were further processed for transmission electron microscopy, but with unsatisfactory results. The observations did not allow us to determine whether there are bacterial symbionts in *L. indusarium* gills. The simple gill structure does not rule out the possibility

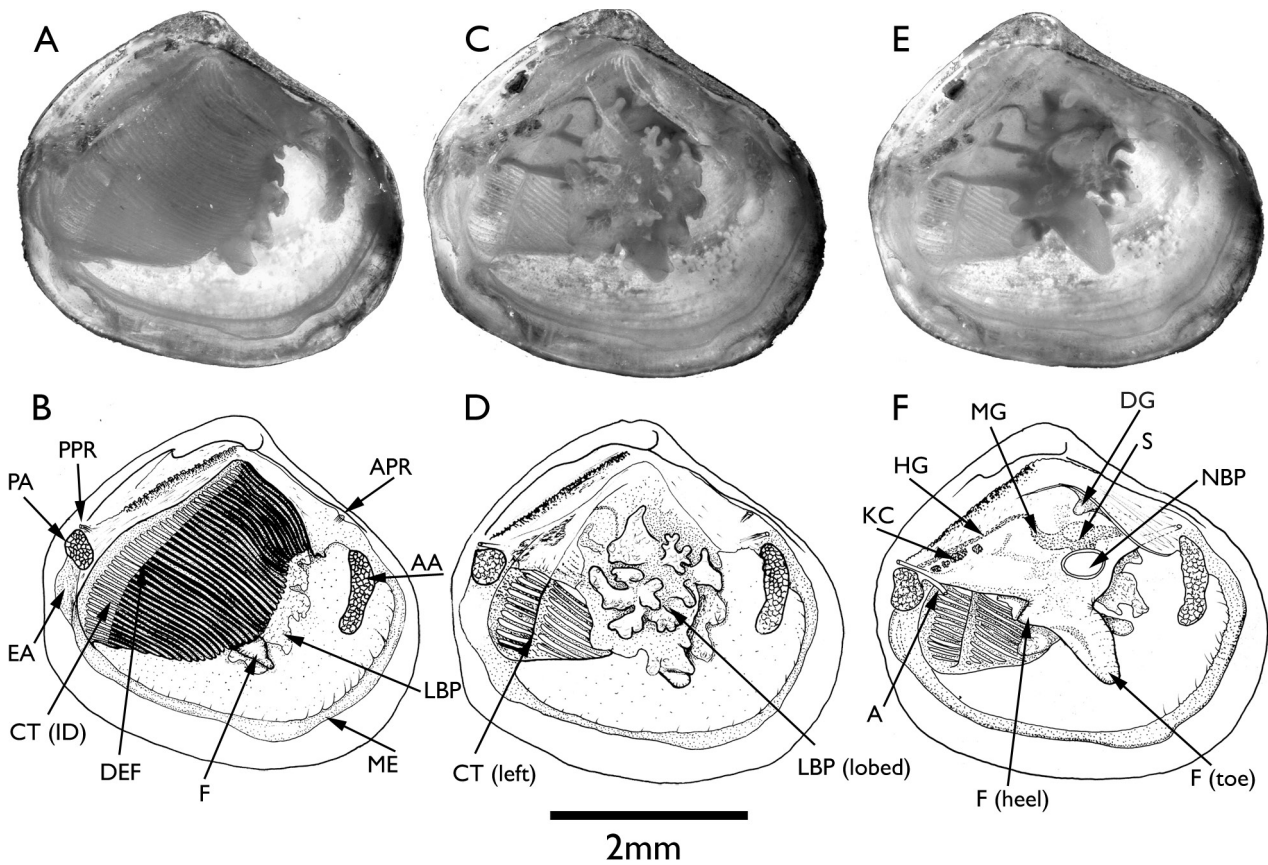


Figure 3. *Leptaxinus indusarium* sp. nov. anatomy, imaged using AutoMontage™ software and line drawings. (A, B) View after removal of right mantle; AA, anterior adductor; APR, anterior pedal retractor; CT(ID), ctenidia (inner demibranch); DEF, dorsal ends of filaments; EA, exhalant aperture; F, foot; LBP, lateral body pouches; ME, mantle edge; PA, posterior adductor; PPR, posterior pedal retractor; (C, D) view after removal of ctenidium; CT, ctenidia; LBP, lateral body pouches; (E, F) view after removal of body pouch; A, anus; DG, digestive gland; F, foot; HG, hind gut; KC, kidney concretions; MG, mid gut; NBP, neck of body pouch; S, stomach.

Table 1. Character matrix for *Leptaxinus indusarium* and the five described genera sharing the Type 2 filament and single demibranch characters; *Axinulus*; *Leptaxinus*; *Mendicula*; *Genaxinus*; *Adontorhina*. Characters shared with '*L.*' *indusarium* are in bold type.

	<i>Axinulus</i>	<i>Leptaxinus</i>	<i>Mendicula</i>	<i>Genaxinus</i>	<i>Adontorhina</i>	<i>Indusarium</i>
Type species	<i>A. brevis</i> V&B, 1898	<i>L. minutus</i> V&B, 1898	<i>M. induta</i> (Hedley, 1907)	<i>G. albigena</i> (Hedley, 1907)	<i>A. cyclia</i> Berry, 1947	
Source	Payne & Allen, 1991	Payne & Allen, 1991	Payne & Allen, 1991 (on <i>M. ferruginosa</i>)	Payne & Allen, 1991 (on <i>G. eumyrius</i>)	Scott, 1986	
Outline	Oval (H>L)	sub-ovate (L>H)	round-ovate (H≥L)	Oval (H>L)	Round (H=L)	sub-ovate (L>H)
Anterior vs posterior curvature	=curvature	Posterior more pointed	Posterior more pointed	=curvature	Posterior more pointed	Anterior more pointed
Escutcheon margin	simple	cleft	simple	simple	simple	cleft
Lunule margin	rounded	rounded	rounded	rounded	rounded	sunken
Adductor scars	normal	normal	normal	raised	normal	normal
Cardinal tubercle	absent	present	present	absent	absent	present
Lateral teeth	absent	present	absent	absent	as denticles	absent
Lateral body pouches	simple	simple	slightly lobed	simple	arborescent	multilobed
Foot with heel	no	yes	yes	no	?no	yes

H, height; L, length.

that symbionts are present, as the thyasirid *Axinulus croulinensis*, having a Type 2 gill with only one demibranch, was shown to have symbionts (Dufour, 2005). However, if '*L. indusarium*' does have symbionts, they cannot be abundant given the limited gill epithelial space available for bacterial colonization; as a result, the nutritional benefit that would be provided by those symbionts would be relatively small.

DISCUSSION

Generic placement

The generic definitions within the Thyasiridae have been recognized to be problematic (Payne & Allen, 1991; Oliver & Killeen, 2002; Oliver & Sellanes, 2005). This situation is reflected here and the adoption of *Leptaxinus* is tentative and requires discussion. Recent research on gill structure (Dufour, 2005) indicates that the present species has affinity with those taxa that also have Type 2 filament form, a single demibranch and lack symbionts; namely *Axinulus* Verrill & Bush, 1898, *Mendicula* Iredale, 1924 and *Adontorhina* Berry, 1947. From Payne & Allen (1991), one would also include the genera *Leptaxinus* Verrill & Bush, 1898 and *Genaxinus* Iredale, 1930s. Although Dufour (2005) indicates a double demibranch condition for *Genaxinus*, the species cited by her do not have the shell characters of the type species, and in our opinion are doubtfully placed. Although Coan et al. (2000) use the generic taxon *Axinodon* Verrill & Bush, 1898 within the Thyasiridae it was, based on the type species, transferred to the Leptonacea (now Montacutidae) by Warén (1980). *Axinodon* is therefore not considered further. Molecular data (J.D. Taylor, personal communication) also supports the separation of these small species from *Thyasira sensu lato*. *Thyasira s.l.* includes most of the strongly carinate-shelled species and this shell character alone precludes assigning the Pakistan margin species to the genus *Thyasira*.

Table 1 compares the characters of those genera with Type 2 gills (based on type species) with the present species and shows that there is no precise affinity with any of the described genera.

Of the described genera, more characters are shared with *Leptaxinus* than with any other genus but the markedly different outline and presence of lateral teeth in *Leptaxinus* appear to be significant.

The character set for *Mendicula* used here is restricted to those of the type species *M. induta* (Hedley, 1907) and its identical sister species *M. ferruginosa* (Forbes, 1844). These species have almost round shells and weakly demarcated lunule and escutcheon. Many other taxa that do not share these characters have been assigned to *Mendicula* and we agree with Payne & Allen (1991) that this genus needs revision. The Pakistan species is therefore only tentatively assigned to *Leptaxinus*, and consequently, a revised generic definition is not given here.

Functional morphology and ecology

The anatomy of '*L. indusarium*' is in plan identical to many of the species described by Payne & Allen (1991). There are no anatomical features suggesting any morphological adaptation to the oxygen minimum zone.

'*Leptaxinus*' *indusarium* was present within a narrow zone on the Pakistan margin. Type specimens were obtained

from a bottom trawl that was sampled at 879 m. In addition to the thyasirid, this trawl contained large numbers of edwardsiid anemones, amphinomid, polynoid, ampharctid and sabellid polychaetes, and a pectinid bivalve.

In quantitative sediment samples taken pre-monsoon during May 2003 by multicorer at roughly 50 m intervals between 700 and 1100 m, specimens were found only at 800 m (531 ind/m²) and 940 m (415 ind/m² in preserved samples and 690 ind/m² in live-sorted samples). Post-monsoon, in October 2003, specimens were found at 940 m (276 ind/m² in preserved samples and 621 ind/m² in live-sorted samples) and 1000 m (69 ind/m² in preserved samples). All of the specimens collected in vertically sectioned cores were found in the uppermost 1 cm pre-monsoon, but about a third of the specimens were found in 1–5 cm fractions post-monsoon, suggesting they had moved deeper into the sediment. The diet of this species is uncertain. Natural abundance isotope signatures (δ13C = -18.4‰ δ15N = 14.1‰) suggest that these animals are not relying heavily on symbionts, and that they are utilizing recycled organic matter originating in the photic zone. However, shipboard exposure to ¹³C-labelled diatoms (Clare Woulds, personal communication) in cores from 940 m yielded minimal uptake by '*Leptaxinus*' (relative to other species present), indicating that they are unlikely to rely heavily on phytodetritus.

Environmental setting

This species occurs firmly within the oxygen minimum zone, with bottom water oxygen concentrations at 800–1000 m between 0.1 and 0.2 ml l⁻¹. Temperature is ~9–9.5°C and salinity is 35.4. Sediments in the upper centimetre where this species lives (940 m) have high water content (68–74%), high organic carbon content (3.4%) and carbon/nitrogen ratios between 9 and 10 (G. Cowie, personal communication).

The narrow depth-distribution of this species suggests that it is adapted to specific features of the environment present between 875 and 1000 m. We hypothesize that there is a fine balance between high food availability (within much of the oxygen minimum zone) and sufficient oxygen to allow the bivalve to utilize this food (found only deeper than 850 m). Competition with other taxa (i.e. an amphinomid polychaete that is extremely abundant at 800 and 850 m) may also influence the distribution of '*L. indusarium*'.

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