A Comparative Study of the Australian Fossil Shark Egg-Case *Palaeoxyris duni,* with Comments on Affinities and Structure

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The enigmatic fossil noted by Dun in 1913 as *Spirangium* and named by Crookall in 1930 as *Palaeoxyris duni* is described in detail in the light of the discovery of other *Palaeoxyris* specimens, which are now accepted by most workers to be shark egg-cases. *Palaeoxyris duni* is the only Australian shark egg-case yet described and is one of the largest *Palaeoxyris* species so far discovered. Comparison of the macro morphology of *P. duni* with other described *Palaeoxyris* specimens confirms that it is a separate form species. The palaeoenvironment in which *P. duni* was deposited was a Triassic low lying fluvial and lacustrine coastal floodplain. One of the Triassic species of hybodontid sharks was the possible egg producer as these fishes have been shown to penetrate freshwater environments. The process of egg production in the nidamental gland of modern sharks is applied to conjecture about the egg-case structure of ancient sharks. The egg-cases of *Heterodontus* have a helical structure broadly similar to that of *Palaeoxyris* except that *Palaeoxyris* have four or six bands in their construction compared to two for the modern *Heterodontus*. Evidence of shark nurseries, clustered egg-cases and tendril attachment of *Palaeoxyris* egg-cases indicates ancient shark breeding behaviour was similar to that of modern oviparous sharks.

INTRODUCTION

Palaeoxyris was an enigmatic fossil when first described by Brongniart (1828) as a rhombic patterned capsule with tapered ends. Plant and animal affinities were subsequently suggested for these fossils, but mounting evidence of their shark egg-case origin has finally been accepted by most workers (Fischer and Kogan 2008).

Dun (1913) briefly described four imperfect specimens found at the Beacon Hill Quarry in Brookvale, NSW, Australia, classifying them as *Spirangium* and alluding to the possibility that they could be either fructifications of plants or the egg-cases of primitive selachians. Since then, work has been carried out by Crookall (1928, 1930, 1932), Brown (1950), Zidek (1976), Böttcher (2010), Fischer et al. (2010, 2011, 2013) and others on specimens found in Britain, Europe, Kyrgizstan and North America and a considerable amount of taxonomic data has been assembled for specimens found in the northern hemisphere. However, apart from the Brookvale specimens mentioned by Dun (1913) there have been no further specimens described in the southern hemisphere and no detailed comparative taxonomic study has been carried out on the Brookvale specimens.

This paper provides a detailed description of the Brookvale specimens and compares them to other specimens described from the northern hemisphere, as well as discussing the palaeoenvironmental implications and the links to extant shark behaviour and egg-case structure.

BRIEF REVIEW OF HISTORICAL RESEARCH

A thorough historical literature review on *Palaeoxyris* has previously been presented by Fischer and Kogan (2008), but a brief summary of that paper and other references will help put this study into context.

In 1828 Brongniart was the first to describe a rhombically patterned enigmatic fossil which he named *Palaeoxyris regularis,* considering it a plant inflorescence. During the 19th century further similar specimens were discovered. Three form genera were erected (*Palaeoxyris, Vetacapsula* and *Fayolia*) and a number of species named. Workers continued to allocate a plant origin to them, until Beer (1856) compared them to a specimen tentatively identified as an egg-case. Schenk (1867) noted their external similarity to egg-cases of extant sharks. The rhombic pattern on specimens was recognised as a taphonomic effect of compressing a body with spirally wound ribs (Quenstedt 1867; Schenk 1867). However, by the end of the 19th century many workers still considered the fossils to be of plant origin.

Moysey (1910) advanced the argument for a shark origin with a detailed morphological description of pedicle, body and beak and the concept that ancient sharks could enter river estuaries to breed. It was at this time that the only Australian specimens of *Palaeoxyris* were found at the Beacon Hill Quarry in Brookvale, a northern suburb of Sydney. These specimens were referred to the genus *Spirangium* in a brief note by Dun (1913). Crookall (1928, 1930, 1932) presented a series of detailed studies of the morphology and affinities of the three form genera, drawing on specimens from the Carboniferous Coal Measures of Britain and Europe, and named many new species, including the Australian specimens which he named *Palaeoxyris duni.* Crookall (1932) rejected a plant origin for these genera and advocated the elasmobranch egg-case hypothesis. After Crookall's thorough analyses, discussion turned to the most likely producer of the eggs. Both xenacanthid and hybodontid sharks were suggested, and palaeoecological studies were carried out to link shark remains with the egg-case sites (Zidek 1976). Additional specimens were described from North America (Brown 1950; Zidek 1976).

By the beginning of the 21st century new evidence pointed to hybodontid sharks being the producers of *Palaeoxyris* and xenacanthids being producers of *Fayolia* (Fischer and Kogan 2008), whereas the producer of *Vetacapsula* has been attributed to the holocephalans (Fischer et al. 2013). Elasmobranch egg-cases were found in Kyrgyzstan (Fischer et al. 2007), Triassic *Palaeoxyris* have been found in North America (Fischer et al. 2010) and Germany (Böttcher 2010), and Triassic juvenile shark teeth microfossils have been discovered in association with *Palaeoxyris* in Kyrgyzstan (Fischer et al. 2011). Fischer et al. (2013) carried out a phylogenetic analysis of the morphology of ancient and modern chondrichthyan egg-cases as a step towards resolving the identity of the egg producers.

GEOLOGY AND PALAEOENVIRONMENT

Palaeoxyris duni was found within a shale lens embedded in the Middle Triassic Hawkesbury Sandstone of the Sydney Basin (Fig. 1a,b). This sandstone was probably deposited on a vast coastal floodplain that lay close to sea level and contained braided rivers, scour channels, sand dunes and lakes (Conaghan 1980). The shale lenses were formed by deposition of finely suspended sediment in low energy basins (Conaghan 1980), which provided ideal anaerobic conditions in which organisms could be preserved and fossilised.

A comparison between the flora of the Late Carboniferous and the Middle Triassic of this area indicated that the climate had returned to cool temperate after the glaciation of the Permian (Retallack 1980), even though by the Middle Triassic the Sydney Basin was within the Antarctic Circle (the poles were ice free during this period) (Fig. 1c).

The shale lens quarried on Beacon Hill was deposited during the Anisian Stage of the Middle Triassic and was composed of fine grey to black laminated mudstone about eight metres thick. It preserved a wide range of Triassic fossils including the bony fishes *Ceratodus, Megapteriscus, Agecephalichthys, Belichthys, Mesembroniscus, Myriolepis*, *Brookvalia, Cleithrolepis, Macroaethes, Leptogenichthys, Geitonichthys, Molybdichthys, Phlyctaenichthys, Schizurichthys, Manlietta, Procheirichthys, Saurichthys, Promecosemina* (Wade 1932, 1933, 1935; Hutchinson 1973,1975), the temnospondyl *Parotosuchus brookvalensis* (Watson 1958; Welles and Cosgriff 1965), insects *Clatrotitan, Choristopanorpa, Austroidelia, Mesacredites, Prohaglia, Fletcheriana, Mesonotoperla, Triassocytinopsis, Beaconella, Triassodoecus* (Tillyard 1925; McKeown 1937; Riek 1950, 1954; Evans 1956, 1963; Béthoux and Ross 2005), crustaceans *Anaspidites, Synaustrus, Palaeolimnadiopsis* and *Estheria* (Chilton 1929; Brooks 1962; Riek 1964, 1968; Webb 1978), the xiphosurian *Austrolimulus fletcheri* (Riek 1955, 1968), the mollusc *Protovirgus brookvalensis (*Hocknull 2000) and plants *Lepidopteris, Dicroidium*, *Cladophlebis, Ginkgoites, Rissikia, Taeniopteris, Xylopteris, Phyllotheca, Marchantites, Rienitsia, Asterotheca, Cylostrobus* (Townrow 1955; Retallack 1977, 1980, 2002; Holmes 2001). This biota points strongly to a freshwater environment.

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SYDNEY BASIN TRIASSIC STRATIGRAPHY			
Ma	**GROUP**	**FORMATION**	**TOPOGRAPHY**
230	WIANAMATTA	Bringelly Shale	streams, lagoons, deltas
		Minchinbury sandstone	shoreline, alluvial
		Ashfield Shale	lagoons, back swamps
240	HAWKESBURY SANDSTONE	*Brookvale (Beacon Hill) shale lens*	braided river systems with still, blind channels
	NARRABEEN	Newport	lagoons, deltas
		Bald Hill Claystone	soils, flood plains
		Bulgo Sandstone	meandering streams
250		claystones / sandstones	flood plains, lakes and streams, alluvial fans

a

b

c

Figure 1 - a. Sydney basin stratigraphic timeline showing the position of the Brookvale (Beacon Hill) shale lens and the topographies during sedimentation. (Data sourced from Packham 1969; Herbert and Helby 1980) b. Location of the Brookvale (Beacon Hill) site (modified after Damiani 1999). c. In the Early Triassic the Sydney Basin entered the Antarctic Circle as Gondwana, containing Australia, drifted south (modified after Hallam 1994).

INSTITUTIONAL ABBREVIATIONS

AM – Australian Museum, Sydney, New South Wales.
BMNH – Natural History Museum, London.
MM – Geological Survey of New South Wales (refers to Mining Museum).

SYSTEMATIC DESCRIPTION

Genus: *Palaeoxyris* Brongniart 1828

Type species: *Palaeoxyris regularis* Brongniart 1928 – Anisian, Middle Triassic. Vosges, France.

Diagnosis: (after Fischer et al. 2011:943) – "Chondrichthyan egg capsule; three-fold division into beak, body, and pedicle; body broadly fusiform, gradually tapering toward each end, composed of three or more parallel helicoidally twisted bands; anterior end gradually tapering into shorter pointed beak; posterior end tapering to long slender pedicle marked by either spiral ribbing or parallel ribs; collarettes accompanying band margins; fine longitudinal striations on bands and collarettes; compressed specimens with transverse rhomboidal pattern".

Palaeoxyris duni Crookall 1930

Synonomy: *Spirangium*: Dun 1913, 205-206 pl.14.
Holotype: MMF 42697a (Figs 2, 3a,b,c, 4a)
Paratype: MMF 42697b (Figs 2, 3d, 4b)
Type Horizon: Hawkesbury Sandstone Formation, Anisian, Middle Triassic (within a shale lens).
Type Locality: Beacon Hill Quarry, Brookvale, New South Wales, Australia.
Etymology: Named after W.S. Dun, the palaeontologist who first presented the specimen to the Royal Society of New South Wales on Dec 12, 1912 (published 1913).
Storage Location: The two specimens are contained on one block which is deposited in the collection of the Geological Survey of New South Wales at Londonderry, New South Wales, Australia.

Description

Palaeoxyris duni is a chondrichthyan egg-case divided into a beak, a body and a pedicle. The beak is greater than 25 mm long and tapers to a point. The body is fusiform and shows a spiral pattern of ribs, and is approximately 90 mm long and 30 mm wide. The two specimens are compressed and exhibit a rhomboidal pattern of ribs and grooves on the body, which is a result of the rear spiral ribs being impressed as grooves on the front spiral pattern of ribs. The pedicle is slightly waisted, tapers, then proceeds as a parallel stem to its end. The pedicle is at least 90 mm long. The body structure consists of four helical bands with a total clockwise twist of 630 degrees from the beak to the pedicle. The bands are an average of 7 mm wide and the twist rate forms seven segments. The ribs formed by the longitudinal suturing of the bands are 2 mm wide. The tapered ends of the bands form tendrils which run parallel to each other to form the beak and pedicle (i.e. there is no twist in the beak or pedicle).

Remarks

Although Dun (1913) stated that he had four

Figure 2. *Palaeoxyris duni* **holotype MMF 42697a (left) and paratype MMF 42697b (right) on a single slab. Scale bar 10 mm.**

imperfect specimens in his possession, only the block figured in Dun (1913) can now be located.

The single block of fine grey shale (MMF 42697) holds two specimens, one almost complete (MMF 42967a) and one with the beak and a section of the body missing (MMF 42697b) (Fig. 2). MMF 42967a appears to have been abraded after discovery and has lost some of its relief. MMF 42967b retains more structural detail. They are compressed specimens.

MMF 42697a has an incomplete beak 25 mm long and a body 90 mm long. At the first impression it has a pedicle 80 mm long. However, microscopic examination of the apparent end of the pedicle shows that the pedicle appears to be broken at this point and bent back at an acute angle. The broken section can be traced back for five mm, but this still may not be the end which could be buried in the substrate. There is a rhomboidal pattern of ribs and grooves on the body of the specimen. The rhomboidal pattern can be interpreted as four bands spiralling clockwise (Fig. 4c). The bands make an angle of 40 degrees with a latitudinal line running through the centre of the body. Each band travels around the body for 630 degrees,

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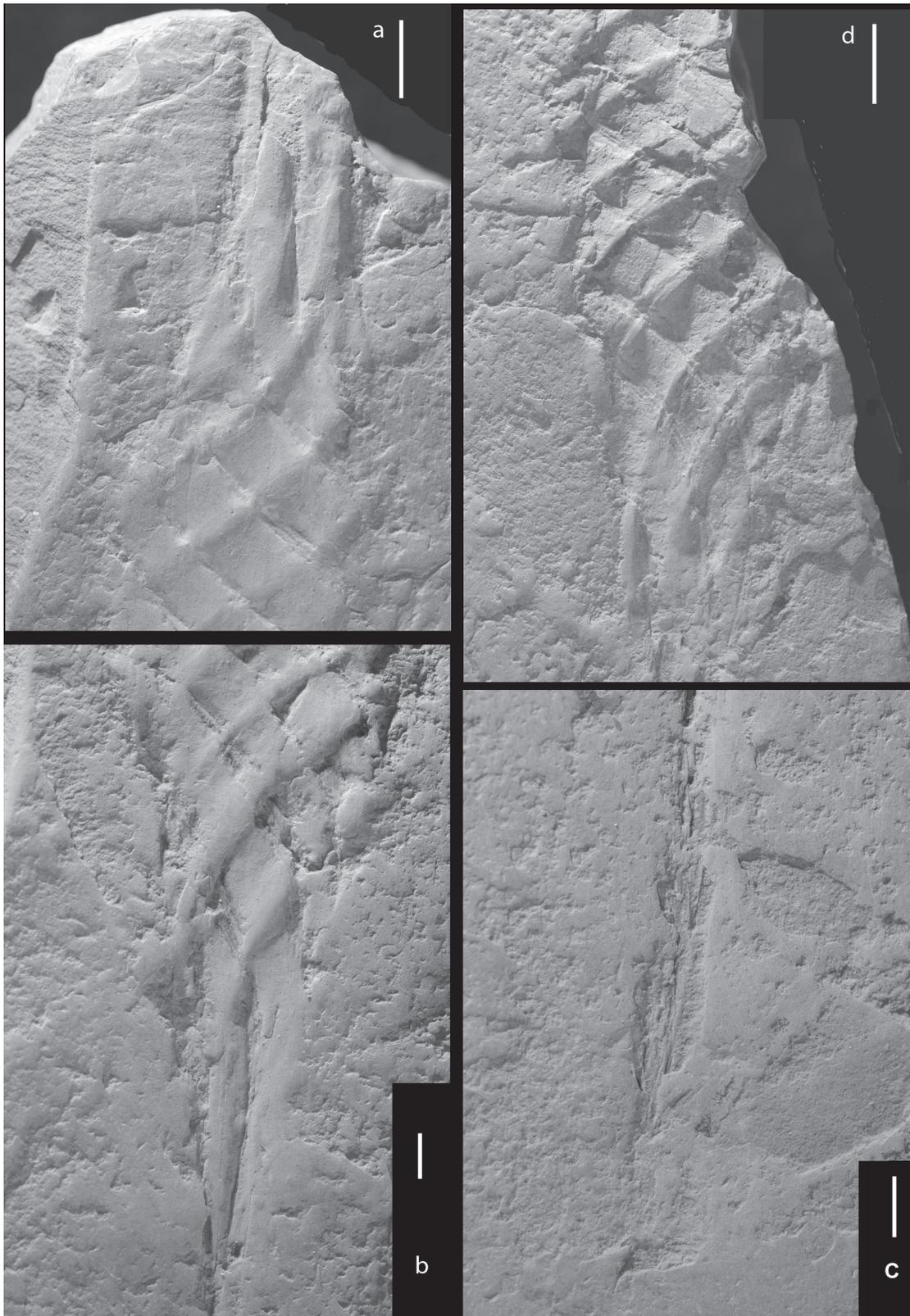
Figure 3 – a. Detail of MMF 42697a beak structure. Scale bar = 7.5 mm.   **b.** Detail of MMF 42697a pedicle structure. Scale bar = 5 mm.   **c.** Detail of MMF 42697a pedicle tip. Scale bar = 5 mm. **d.** Detail of MMF 4267b ribs showing striae. Scale bar = 10 mm.

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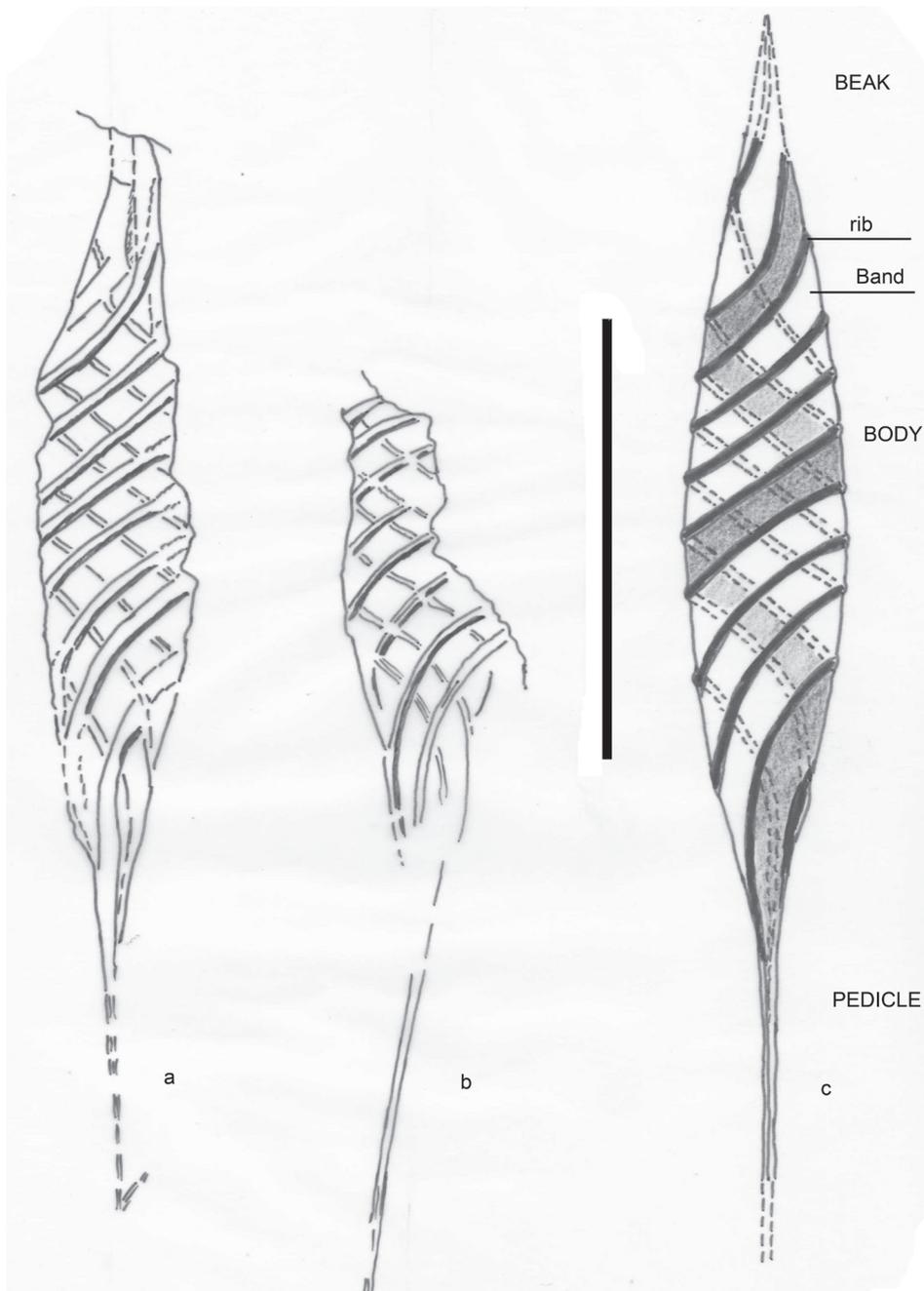
Figure 4 – a. Line tracing of MMF 42697a. b. Line tracing of MMF 42697b. c. Idealised structure of *P. duni* showing the bands wrapping around the body and the band terminations in the beak and pedicle. Scale bar = 100 mm.

then tapers, forming a tendril, and runs parallel with the others longitudinally along the beak and pedicle. The number of segments visible on the body formed by the spiralling bands is seven. Including the ribs, the body is 28 mm wide at the widest point. The ribs have a width of 2 mm. Striae running parallel to the bands are visible on some sections of the grooves. The band margins are defined by ribs, but there are no obvious flanged collarette extensions from the ribs.

MMF 42697b has similar dimensions and a similar rhomboidal pattern of ribs and grooves to MMF 42697a, and is also composed of four bands. Its pedicle is at least 90 mm long. The full length of the pedicle is uncertain as it, too, may have been broken.

However, its total length matches closely the total observable length of the pedicle (including the broken section) of MMF 42697a. The beak and an upper section of the body are missing. Striae are observable in the grooves and there is a faint indication of striae on some sections of the ribs (Fig. 3d).

Comparison with Some Other *Palaeoxyris* Species

From Table 1 it can be seen that *P. duni* has the longest body of any of the Mesozoic taxa and the widest body except for *P. friessi*. Only one species from the Carboniferous has a longer body (*P. bohemica*) and the specimens attributed to this species display a wide range of body sizes which may indicate that more than one species is involved.

The basic structure of all *Palaeoxyris* species is made up of a number of spirally wound bands sutured together longitudinally. Palaeozoic specimens studied early in the 20th century were not analysed for the number of bands. Mesozoic specimens studied later (e.g. Böttcher 2010; Fischer et al. 2010, 2011) were analysed for band number and this analysis showed that all Mesozoic species (with the one exception of one *P. humblei* specimen) were determined to be constructed with four or six bands (Table 1). *P. duni* is one of four Mesozoic taxa to have four bands, whereas another four species have six bands. The total wrap angles of these bands around the body vary from 180 to 630 degrees for those species known. *P. duni* has the highest total band wrap angle of 630 degrees. This high total band wrap angle is a product of a high wrap angle rate and a large body size. Böttcher (2010) observed that all *Palaeoxyris* species have bands that twist in a clockwise direction. Based on the premise that the grooves in the rhombic pattern on the body are the impressed spiral ridges from the unexposed side of the specimen (Böttcher 2010), the bands on *P. duni* twist in a clockwise direction, conforming to this observation.

Comparison of beak and pedicle lengths is not a strong diagnostic tool, as they are often broken, incomplete or missing. However, in general, beak lengths are shorter than pedicle lengths (except for those of *P. friessi,* which are virtually equal*). P. duni* has a longer observable pedicle than all others except *P. friessi*, but its incomplete beak does not allow length comparison.

A number of structural features noted on other *Palaeoxyris* specimens are not observable on *P. duni*. These are flanged collarette extensions reported *on P. alterna* (Fischer et al. 2011), *P. friessi* (Böttcher 2010), *P. humblei* (Fischer et al. 2010) and on a Mazon creek specimen (Brown 1950), and long tendril extensions to the beak reported on *P. alterna* (Fischer et al. 2011).

There are no close matches with specimens listed in Table 1 to the combined parameters of 'body length', 'body width', 'band number' and 'total band wrap angle' for *P. duni*.

AFFINITIES AND STRUCTURE

Over the last 190 years there has been sporadic discussion concerning the origins of *Palaeoxyris*. Initially its cone-like shape with rhombic patterning caused Brongniart (1828) and Schenk (1864) to allocate a plant origin to these specimens. The realisation by Schenk (1867) and Quenstedt (1867) that the rhombic patterning could be produced by compression of a spirally wound object led to the comparison by Renault and Zeiller (1888) to shark egg-cases with spiral collarettes produced by *Heterodontus* sharks. Specimens were tested for plant cell structure but none was found (Crookall 1932). With no evidence of plant structure, opinion swung strongly to the specimens being of shark origin (Moysey 1910; Crookall 1932; Zidek 1976).The palaeoenvironment in which all *Palaeoxyris* species had been found is considered to be one of either deltaic or shallow, freshwater fluvial or lacustrine conditions (Moysey 1910; Crookall 1928; Fischer and Kogan 2008). Ancient sharks are known to have inhabited these environments (Patterson 1967; Rees and Underwood 2008). In at least two instances, in North America and Kyrgyzstan, shark remains have been found closely associated with *Palaeoxyris* specimens (Fischer et al. 2010, 2011). Fischer et al. (2013) carried out a cladistics analysis of ancient and modern chondrichthyan egg-cases based on morphological traits. Their results showed the egg-case *Vetacapsula* (Fig.5b) clustered with the egg-cases of the Chimaeridae (ratfishes), while the egg-cases *Palaeoxyris* and *Fayolia* (Fig.5a) were clustered next to all egg-cases of the neoselachans (modern sharks and rays). Egg-cases of the Heterodontidae were positioned as the basal egg-case type morphology of the neoselachans.

This circumstantial evidence has led to conjecture about the actual egg producer, its breeding behaviour and its egg-case structure.

The Egg Producer

Sharks being cartilaginous do not leave frequent evidence of their existence in the fossil record – teeth, fin spines and scales are the main indicators (Kemp 1982). However, there is enough evidence to plot the time span of the existence of possible egg producer families. Xenacanthids (Fig.5d) appeared in the Carboniferous (Garvey and Turner 2006;

Table 1 – List of the *Palaeoxyris* species described in some taxonomic detail in literature. A small number are yet to be described and these have been omitted. Where there are no data shown, the parameters have not been published. This particularly applies to the Carboniferous species which were described in the early 20th century. The referenced paper(s) are the source of the parameters in Table 1 and are not necessarily the original taxonomic papers. Note the puzzling lack of Permian specimens.

SPECIES	AGE	BODY LENGTH mm	MAX BODY WIDTH mm	NO. OF BANDS	TOTAL WRAP ANGLE degrees	NO. OF SEGMENTS	BEAK LENGTH mm	PEDICLE LENGTH mm	REFERENCES
P. (Spirangium) jugleri	Cretaceous	40 to 50	30 to 40	6			30	80 (incompl)	Crookall 1930, 1932.
?Palaeoxyris sp. (Kansas)	Cretaceous	28	14	3		8 (incompl)	30		Crookall 1930, Brown 1950.
P. muelleri	Rhaetian, Late Triassic	20 to 25	11	4	180	3	17	35	Bottcher 2010.
P. muensteri (quenstedti)	Rhaetian, Late Triassic	30 to 40	23	6		9	25	58	Crookall 1930, Bottcher 2010
P. humblei	Norian, Late Triassic	13	9	3 & 4		6	12.5	(incompl)	Fischer et al. 2010.
P. alterna	Ladinian-Carnian, Mid-Late Triassic	22 to 25	11 to 14	6	540	11	24	55	Fischer et al. 2011.
P. friessi	Ladinian, Middle Triassic	53	39	6	300	6	112	110	Bottcher 2010.
P. becksmanni	Anisian, Middle Triassic	15		4					Bottcher 2010.
P. regularis (Type species)	Anisian, Middle Triassic	35 to 40	13	6		8	55	85	Brongniart 1828, Crookall 1930, Bottcher 2010.
P. duni	Anisian, Middle Triassic	90	28	4	630	7	25	(incompl)85 & 90	This paper.
P. bohemica	Carboniferous	50 to 140	15 to 50	6		11 to 13	20	missing	Crookall 1930.
P. helictoroides	Carboniferous	26 to 60	7 to 30			8 (alternating broad/narrow)	25	20 (incompl)	Crookall 1928.
P. carbonaria	Carboniferous	26 to 32	8 to 12			6 to 8	missing	missing	Crookall 1928.
P. prendeli	Carboniferous	25 to 34	12 to 18			4 to 8	missing	missing	Crookall 1928.
P. trispiralis	Carboniferous	90	30 to 34			3	17	17	Crookall 1928.
P. warei	Carboniferous	18	7			6	6	10 (incompl)	Crookall 1928.
P. pringlei	Carboniferous	22	10			14	20	missing	Crookall 1928.
P. edwardsi	Carboniferous	22	3.5			5			Crookall 1928.
P. lewisi	Carboniferous	42	7.5			10	9	8 (incompl)	Zidek 1976.
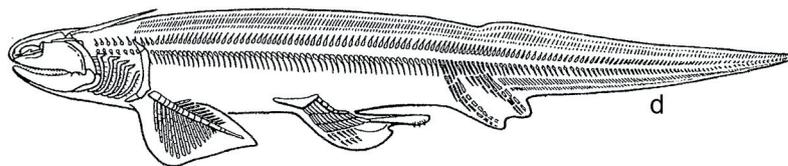
Figure 5 – a. Carboniferous *Fayolia crenulata*, BMNH V12057, part and counterpart, attributed to xenacanthid sharks, showing diagnostic scar-lines parallel to the collarette. b.Carboniferous *Vetacapsula cooperi*, BMNH V12058, tentatively attributed to the Holocephali. (Photos of shark egg-cases by courtesy of the Natural History Museum, London ©) c. Triassic *Xenacanthus* (*Pleuracanthus*) *parvidens*, MMF 13430, from St. Peters Brickpits, Sydney, Australia (photo courtesy of Geological Survey of New South Wales). d. The xenacanthid shark *Xenacanthus sessilis* (after Schaeffer and Williams 1977:297, by permission of the Oxford University Press).

Turner and Burrow 2011). Well preserved articulated xenacanthid fossils have been discovered in the Middle Triassic rocks of the Sydney Basin at St Peters Brickpits (Woodward 1908) (Fig.5c), at Picton (an as yet undescribed specimen held in the Australian Museum – AM F 137124) and at Somersby Quarry (two as yet undescribed specimens – AM F 78948,

AM F 78958 and their counterparts) (pers. comm. S. Turner, Queensland Museum). They died out by the Late Triassic (Kemp 1982), whereas the hybodontids (Fig.6e) appeared in the Carboniferous and became extinct by the end of the Cretaceous (Springer and Gold 1989). By matching the span of *Palaeoxyris* ages with the family life spans of sharks, some workers
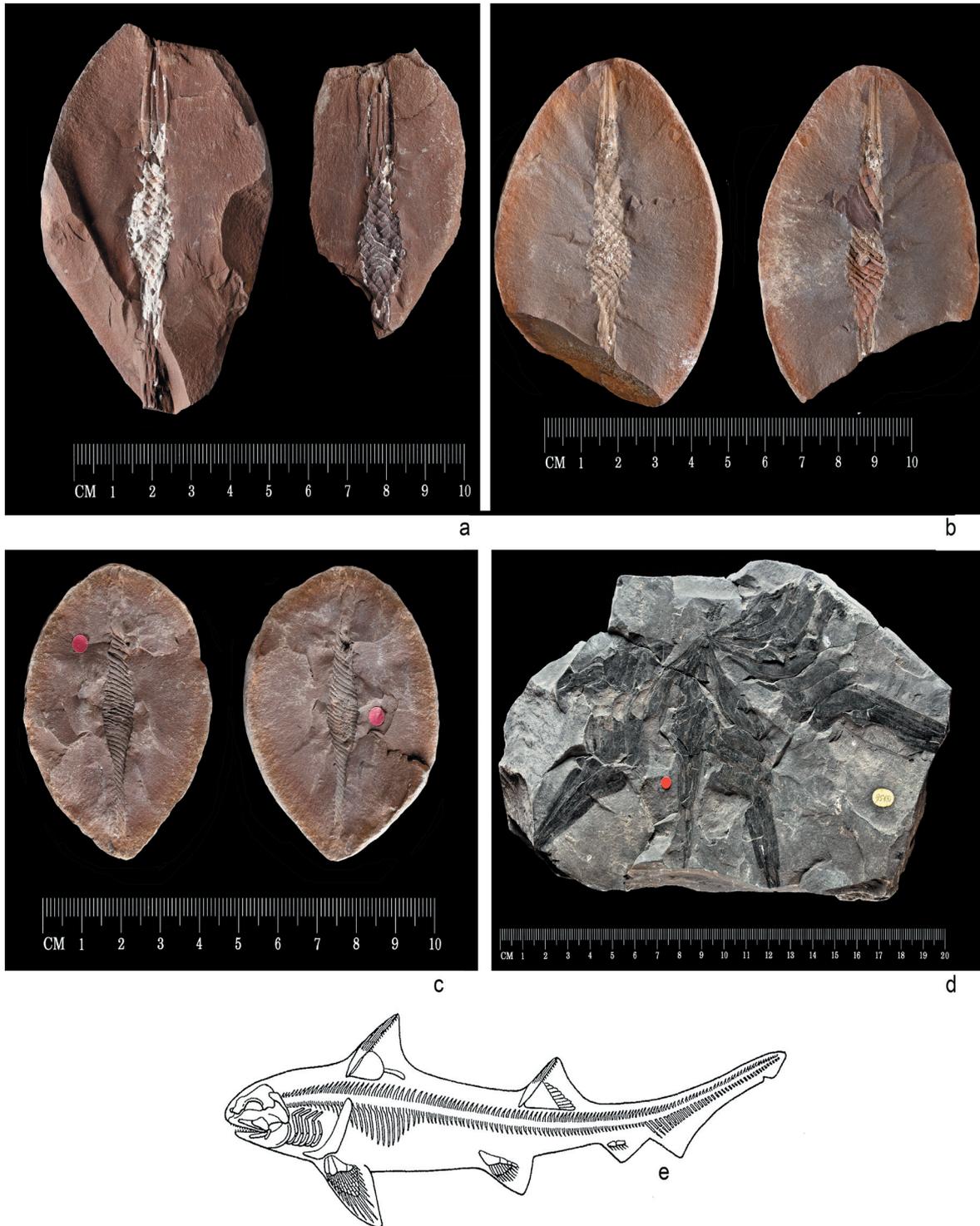
Figure 6 – a. Carboniferous *Palaeoxyris carbonaria*, BMNH V1173, part and counterpart, showing rhombic impressions on body and pedicle. b. Another *Palaeoxyris carbonaria*, also registered as BMNH V1173, part and counterpart, showing partly uncompressed banding on left specimen. c. *Palaeoxyris carbonaria*, BMNH V12928, part and counterpart, showing uncompressed spiral banding. d. Clustered group of Cretaceous *Palaeoxyris* (*Spirangium*) *jugleri*, BMNH 38856, with joined beaks. (Photos of shark egg-cases by courtesy of the Natural History Museum, London ©). e. The hybodontid shark *Hybodus* (after Schaeffer and Williams 1977:300, by permission of the Oxford University Press).

(Crookall 1932; Zidek 1976; Böttcher 2010; Fischer et al. 2010, 2011, 2013) have proposed hybodontid sharks as the producers of *Palaeoxyris*. The earliest *Palaeoxyris* species (e.g. Figs 6a,b,c) were found in the Carboniferous and the latest in the Cretaceous (e.g. Fig.5d), the most recent specimens being discovered in the Wealden Group of the Lower Cretaceous rocks near Hastings, England.

Hybodontids grew to about two metres in length, had an amphistylic jaw and a terminal mouth (Springer and Gold 1989). Their two dorsal fins each contained a spine at the leading edge, and they had heterodont dentition (piercing and crushing) which allowed a range of food options such as fish, crustaceans and molluscs (Springer and Gold 1989). Claspers were present on the male (Springer and Gold 1989) which confirmed they practiced internal fertilisation.

Hybodontid teeth have been found in deposits interpreted as originating in estuarine and river palaeoenvironments (Patterson 1967; Rees and Underwood 2006, 2008) and oxygen and strontium isotopic analyses of juvenile teeth found in lacustrine sediments in Kyrgyzstan have confirmed that the young sharks had developed in fresh water (Fischer et al. 2011). Some hybodontids therefore appear to have inhabited brackish and freshwater environments, at least to breed.

Modern Shark Breeding Behaviour

Many workers have noted similarities between modern Heterodontidae egg-cases and *Palaeoxyris* (Moysey 1910; Brown 1950; Zidek 1976; Böttcher 2010; Fischer et al. 2010). Heterodontidae is a family of extant oviparous sharks that produce egg-cases with helical ribs (in the form of collarettes). Fossil evidence of this family has been found in the early Miocene sediments of Victoria (Kemp 1982; Long and Turner 1984). They have an external spine on the leading edge of each dorsal fin and crushing toothplates suitable for a diet of molluscs. They breed in marine waters (O'Gower 1995).

The egg-case of the Port Jackson Shark, *Heterodontus portusjacksoni*, is constructed of two spiral bands of collagenous material approximately 0.25 mm thick that are overlapped and sutured longitudinally. The overlapping along the sutures forms the collarettes (Figs 7a,b). The egg case is cone shaped with a vent at the larger (anterior) end which opens a few weeks after deposition allowing the circulation of water through the egg during incubation. Finally the young shark escapes fully formed through this vent at the larger end, leaving a durable, empty egg-case.

The egg-case of the Crested Horn Shark, *Heterodontus galeatus*, is similar to *H. portusjacksoni* (Whitley 1940), but has two long tendrils that are extensions of the collarettes. These tendrils are used to anchor the egg-case to algae (Fig. 7c).

Tagged *Heterodontus portusjacksoni* has been tracked from Cape Naturaliste, north-east Tasmania (latitude 41°S) to Sydney (latitude 38°S), a distance of 850 km, during an annual migration cycle to lay eggs in specific sites, thus exhibiting breeding fidelity as well as spatial memory of long migration routes (O'Gower 1995). Females have been observed carrying an egg-case in their mouth and egg-cases have been found pushed into crevices so that the collarettes hold the egg-case firmly in place (Springer and Gold 1989; O'Gower 1995) (Fig. 7d).

The pattern of modern shark breeding behaviour, particularly that of the oviparous sharks such as the *Heterodontus*, leads to speculation about similar ancient shark behaviour, particularly relating to migration, breeding fidelity and the finding of ancient shark egg-cases in consistently similar fluvial and lacustrine environments around the world.

Modern Shark Egg-Case Structure

Knight et al. (1996) described in detail the macrostructure, biochemistry and microstructure of selachian egg-case formation in the nidamental (or shell) gland of oviparous sharks. Briefly, they explained that the nidamental gland lies in line with the oviduct (Fig.8a). The anterior end of the gland faces the ostium, which is the source of the fertilised ovum. The gland in recent species is composed of two similar halves surrounding a lumen. Each half works in parallel to extrude a complex collagenous lamellated sheet along its internal surface from the anterior zone (Fig 8b). The extruding sheets are fed by material secreted by tubules through a row of spinnerets, and a jelly is secreted between the sheets to divide and "inflate" the egg-case within the lumen. As the two parallel sheets progress down the gland the fertilised ovum enters the anterior end of the gland and is held between the forming sheets. The sheets continue forming around and past the ovum and finally join together to provide full encapsulation. During the extrusion of the sheets that form the two enclosing walls of the egg-case, special rib material is also secreted to "glue" the lateral edges of the laminar sheets together to form lateral ribs. In egg-cases that develop horns or tendrils (which are extensions of the lateral ribs), the posterior horns or tendrils form initially and the anterior ones form as the very end of the process. The final result for almost all recent

a

b

c

d
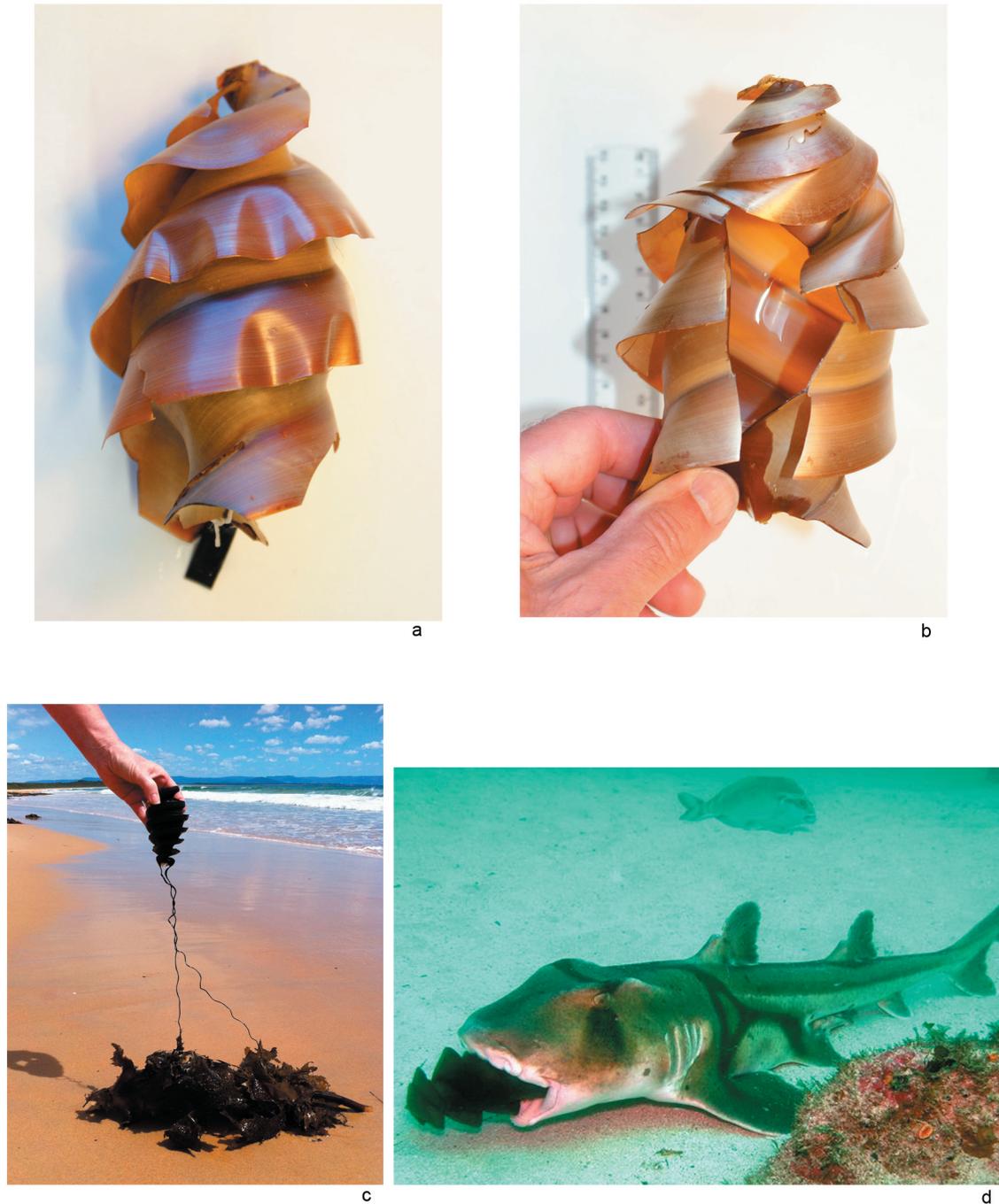
Figure 7 – a. Egg-case of *Heterodontus portusjacksoni* specimen AMS IB.673. Note the striae on the collarettes and bands. b. Sectioned egg-case of *Heterodontus portusjacksoni* specimen AMS I.30753-002. c. Egg-case of the Crested Horn Shark *Heterodontus galeatus* showing its long tendrils attached to marine algae. d. An *Heterodontus portusjacksoni* carries an egg for safe placement in a crevice. (Photos a,b courtesy of the Australian Museum, Sydney. Photo c courtesy of Mark McGrouther at the Australian Museum, Sydney. Photo d courtesy of Jayne Jenkins).
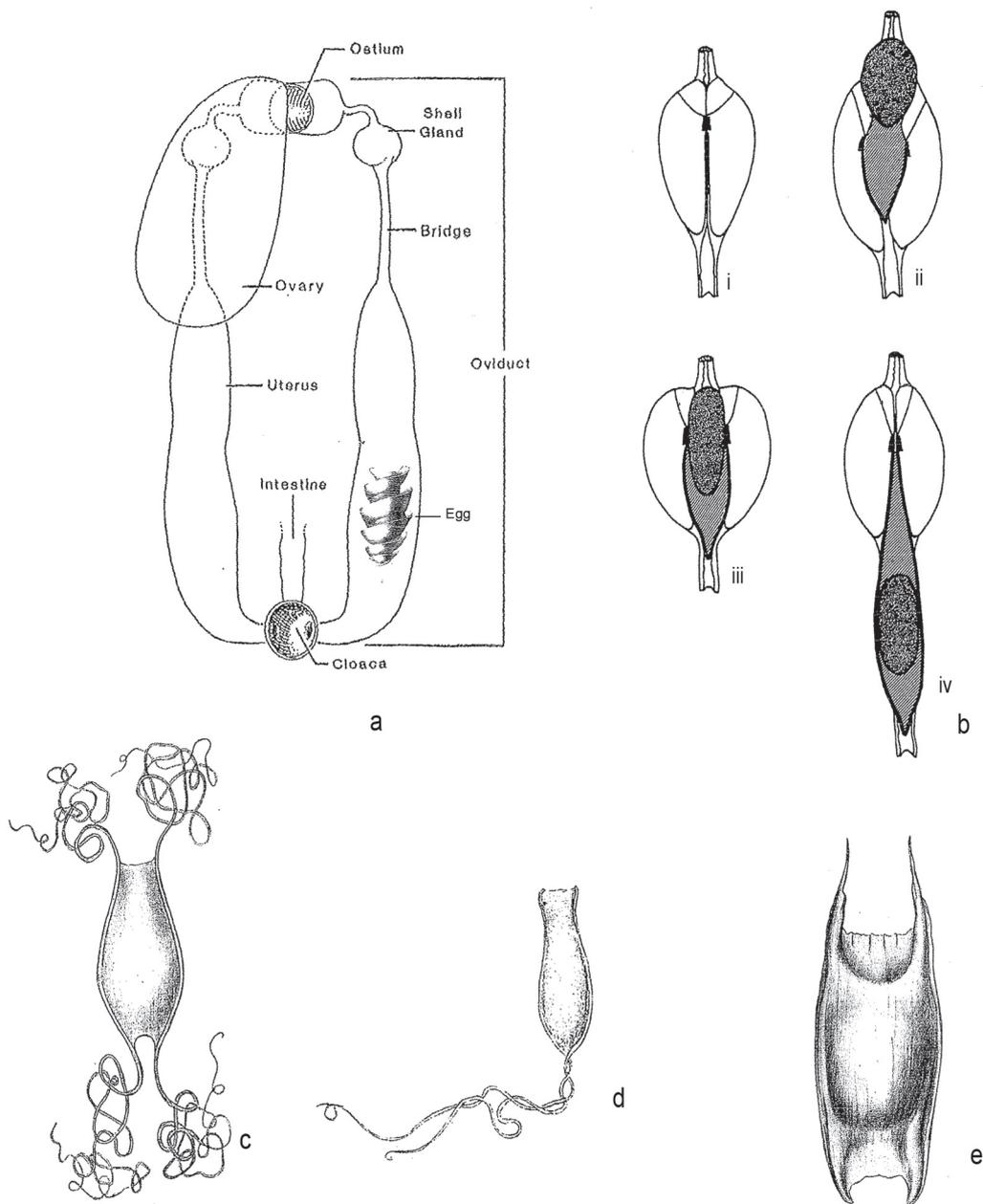
Figure 8 – Modern sharks and egg-cases. a. Simplified diagram of a modern shark reproductive system (modified after Springer and Gold 1989:68). b. Simplified diagram of a section through an active nidamental gland of a modern shark – i. resting gland. ii. formation of the posterior section of the egg case wall with fertilised ovum ready to enter the lumen. iii. the fertilised ovum enters the lumen. iv. production of the walls of the egg case continues around and behind the ovum forming the anterior end of the egg-case and sealing it. (modified after Knight et al. 1996:98). c. Egg-case of an *Atelomycterus* (a catshark) from the China Sea. d. Egg-case of an unknown species of catshark from the Timor Sea. e. Egg-case of *Zearaja nasuta* (a skate) from New Zealand. (Egg-case drawings after Whitley 1940:42,44).

egg-cases is a subrectangular structure containing the ovum and comprising two curved sheets sealed at the two lateral margins by ribs and sealed at the posterior and anterior ends, with tendrils or horns protruding from the four corners (Figs 8c,d,e). After many months (in the case of the genus *Heterodontus* between 9 to 12 months (Springer and Gold 1989)) the hatching fish finally escapes through the anterior

end of the egg-case after the anterior seal has opened into a slit.

However, the egg-cases of the genus H*eterodontus* have a strikingly different shape – that of a helix. At first sight it appears very different to that of all other recent oviparous sharks. Knight et al. (1996) point out that if the ribs are flattened and the egg-case is twisted during formation, the above process will produce the egg-case of the *Heterodontus* complete with collarettes which are the flattened ribs. Thus a bifurcated nidamental gland can produce a spiral egg-case with two parallel bands. Striae are observable on *H. portusjacksoni* egg-case collarettes, possibly due to the extrusion process during formation (Figs 7a,b). Understanding the process of formation of the modern egg-case with two bands has implications for the study of fossil helical egg-cases with four or six bands.

DISCUSSION

Morphology

The macromorphology of MMF 42697a and MMF 42697b conforms to the diagnosis of *Palaeoxyris* thus confirming Crookall's decision. As the pedicle is not twisted this confirms previous observations by Fischer and Kogan (2008) and Böttcher (2010) that all Mesozoic *Palaeoxyris* have pedicles constructed with tendrils laid parallel longitudinally, whereas Carboniferous species have twisted pedicles which, when compressed, exhibit rhomboidal patterning (Figs 6a,b,c).

Comparison with other *Palaeoxyris* species (e.g. Table 1) indicates that the body length of *P. duni* is only matched or exceeded by one specimen of *P. bohemica* and *P. trispirilis* which are both Late Carboniferous in age. Although some extant sharks such as the catshark *Scyliorhinus canicula* produce an intra-species range of egg-case sizes which is determined by the size of the female and its habitat (Springer and Gold 1989), the range is still limited and it is therefore reasonable to conjecture that the size of the egg-case of *P. duni* indicates that the egg producer was one of the comparatively larger Triassic hybodontids.

The combination of the *P. duni* macro morphology parameters of 'body length', 'body width', 'band number' and 'total band wrap angle' is unique and therefore justifies its classification as a definite form species.

A particular feature of the modern *Heterodontus* egg-case is the wide flanged collarette (Figs 7a,b). Flanged collarettes have been detected on Palaeozoic

and Mesozoic *Palaeoxyris* specimens (Brown 1950; Böttcher 2010; Fischer et al. 2010, 2011), although they are not seen on *P. duni*. The Carboniferous *P. helictoroides* exhibits a wide/narrow pattern of segments. The narrow segments could possibly be a collarette impression. The *Heterodontus* collarette is thin (0.25 mm) and friable when dry. It is possible that many more ancient egg-cases might have had flanged collarettes but that these were destroyed during the taphonomic process.

Striae running longitudinally parallel span the bands and collarettes of *Heterodontus* egg-cases (Figs 7a,b). It is likely that these are produced by the extrusion process within the nidamental gland by the array of spinnerets that form the bands. Striae are observable in many *Palaeoxyris* specimens (Crookall 1932; Fischer et al. 2010) including *P. duni*, particularly in the sheltered regions like the grooves. Striae are thus strong circumstantial evidence that *Palaeoxyris* had a similar egg-case formation process to that of the modern shark genus *Heterodontus*.

Palaeoenvironment

The interpreted palaeoenvironment in which *P. duni* was produced bears a close resemblance to that described for many other northern hemisphere species. The eggs were laid in a still, shallow, freshwater lacustrine or lagoonal environment, most likely accessible from the sea. Fossils recovered from the fine grained shale lens in which *P. duni* was found (Dun 1913) are a close match to those found with other Triassic *Palaeoxyris* specimens, for example the plants *Taeniopteris*, *Cladophlebis* and horsetails, and invertebrates such as conchostrachans and brackish water bivalves (Böttcher 2010). A similar environment was described for *P. alterna* (Fischer et al. 2011), *P. friessi* (Böttcher 2010) and *P. humblei* (Fischer et al. 2010). Carboniferous species described by Crookall (1928, 1930, 1932) were found in the British Coal Measures that formed in freshwater swamps. Fischer et al. (2011) postulated that the producers of *P. alterna* might have lived as adults in an enclosed freshwater lake. Patterson (1967) and Rees and Underwood (2008) conjectured that hybodonts, already capable of travelling up rivers and lakes to breed, might have radiated and diversified within wholly freshwater environments under pressure of the developing marine neoselachians in the early Jurassic and Cretaceous.

Hybodontid Sharks in Eastern Australia

There is scant evidence for the presence of hybodontids along the coast of eastern Australia in the Triassic and Jurassic. Woodward (1890) described a selachian with two dorsal fins complete with spines

found in the Narrabeen Group of the freshwater Triassic sediments of Gosford, NSW. (Unfortunately, that specimen has not been traced (pers. comm. Susan Turner 2012)). Another eastern Australian Triassic hybodontid is in the process of being described (pers. comm. Susan Turner 2012). There is also a Jurassic specimen from the freshwater deposits of Talbragar, NSW yet to be described (Turner et al. 2009).

Shark Behaviour

Heterodontus portusjacksoni has been shown to migrate long distances to feeding sites, and to return regularly to known, shallow water marine breeding sites (O'Gower 1995). The palaeogeographic position of the Sydney Basin in the Triassic was within the Antarctic Circle (Hallam 1994), meaning that during winter there was probably a long, unbroken period of darkness. During this darkness it was likely that food sources for the hybodontids would either migrate north or seasonally reduce in numbers (as do modern krill). This would force hybodontids to migrate north in winter. It is therefore likely that hybodontids in these latitudes followed an annual migration pattern of northern migration in winter, then a return to known breeding sites in the rivers and lakes of the Sydney Basin in summer.

Modern oviparous sharks, such as *Heterodontus*, have been observed to gather at common shark nurseries to lay their eggs (O'Gower 1995). It is an advantage to a marine species that produces only a few eggs to secure them in a safe place and protect them from predation, random current transport and storms. *H. portusjacksoni* does this by pushing them into rocky crevices (Springer and Gold 1989; O'Gower 1995) (Fig.7d), *H. galeatus* anchors its eggs to marine algae using long, flexible tendrils (Fig. 7c). A flexible tendril has been discovered protruding from beak of one *Palaeoxyris alterna* specimen (Fischer et al. 2011). Fischer et al. (2010) noted the finding of a *Palaeoxyris* specimen from Mazon Creek, attached to wood fragments by beak tendrils. Crookall (1932) described and figured five *P. jugleri* jointly attached by their beaks (Fig. 6d). MMF 42697 shows the beaks of the two *P. duni* oriented in the same direction, which indicates they may have been joined or jointly anchored by their beaks. Fischer et al. (2011) describe the finding of 31 specimens of *P. alterna* (some fragmentary) in association with juvenile shark teeth. This circumstantial evidence links ancient shark breeding behaviour to modern shark nursery breeding habits.

Egg-Case Formation

Fischer et al. (2013) identified nine ancient and modern morphotypes of chondrichthyan egg-cases,

seven of which appeared in the fossil record. They carried out a cladistics analysis of 11 taxa, based on 15 morphological characters, which clustered *Palaeoxyris* and *Fayolia* and grouped this cluster next to neoselachan egg-cases.

Considering the process by which the nidamental gland produces a shark egg-case leads to some valuable insights into the morphology of ancient shark egg-cases. Although the shapes of extant shark, ray and skate egg-cases (except for the genus *Heterodontus*) at first sight appear quite different from the helically twisted *Palaeoxyris* (Figs 8c,d,e), they are in fact all variations on a fundamental structure. This structure comprises extruded posterior tendrils, enclosing sheets (or bands), the longitudinal suturing of these bands together, the sealing of the ends and the final production of anterior tendrils. The egg-case of each species varies in the size, the number or absence of pairs of tendrils, the shape of the end seals and the size and shape of the longitudinal sutures. In the case of the genus *Heterodontus* the complete structure is twisted into a helix. All extant sharks, rays and skates produce egg-cases with two enclosing sheets (or bands). The morphology of *Palaeoxyris* reveals all the same elements of the fundamental structure – sheets (or bands) longitudinally sutured forming ribs, twisted into a helix, and a beak and pedicle formed by the joining of tendrils which each originate at the end of a rib. *Palaeoxyris* species, however, have four or six bands. This leads to the conjecture that ancient nidamental glands were divided into four or six parallel sections, which each extruded a separate band. This in turn leads to the conclusion that the combination of egg-case body size (within a tolerance), the number of bands and the helical twist rate would identify separate egg producer species, as each egg producer species would have a common nidamental gland structure.

Diagnostic Parameters

Based on the premise that each egg producing species would have a common nidamental gland structure, for the reasons set out above, the number of bands and the helical twist rate for each egg-case form species would be diagnostic, coupled with body size. Böttcher (2010) commented that all Mesozoic *Palaeoxyris* specimens so far described had even numbers of bands (either four or six or even greater). Recent egg laying sharks and rays all have two bands, thus supporting the concept that the fossil egg-cases were produced by a different clade, such as the hybodonts.

However, there is one recent paper that tests this concept. Fischer et al. (2010) reported the finding of three specimens of *P. humblei*, two with four

bands and one with three bands. Due to taphonomic distortion it is often difficult to determine the exact number of bands (Böttcher 2010), particularly if the specimens are compressed and the edges of the body are not well defined or are buried in the substrate. If further evidence of variation of band number within form species is found, doubt may be thrown on band number as a significant diagnostic parameter.

CONCLUSIONS

The basic morphology of *Palaeoxyris duni* shows a strong relationship to northern hemisphere Mesozoic *Palaeoxyris* species, but the essential diagnostic indicators of 'body size', 'band number' and 'total wrap angle' in combination do not match other specimens, confirming that *P. duni* is a separate form species.

The existence of common structures, such as helical bands, collarettes, tendrils and striae in *Palaeoxyris* form species and modern oviparous shark egg-cases is convincing evidence that ancient sharks produced *Palaeoxyris*. Geographic, temporal and environmental constraints lead to the initial consideration that either xenacanthid or hybodontid sharks produced *Palaeoxyris* species. Currently the weight of circumstantial evidence favours the family Hybodontidae. If hybodontid species were the egg-case producers, specimen MMF 42697 is further evidence of their presence on the eastern coast of Australia during the mid-Triassic along with the specimens known from the Sydney Basin.

It is probable that the nidamental glands of hybodont shark species produced egg cases in a similar manner to modern oviparous sharks, except that the glands were divided into more than two parallel sections. Thus the diagnostic features that define a *Palaeoxyris* form species by association define a shark species.

The palaeoenvironment in which *P. duni* was deposited matches that described for most, if not all, other *Palaeoxyris* species. This is essentially a deltaic or shallow, freshwater, fluvial, lacustrine or lagoonal coastal environment accessible from the sea. A significant body of evidence for hybodontid movement into freshwater systems, particularly the finding of fossil teeth and fin spines, shows that these sharks were capable of making the transition from marine to freshwater, if only to breed. There are indications that breeding habits such as the formation of shark nurseries and egg-case attachment were practiced by ancient sharks in a similar manner to those of modern sharks.

As the Sydney Basin where the *P. duni* specimens were found was within the Antarctic Circle during the Middle Triassic Period, it is likely that hybodontids followed an annual migration pattern of northward winter movement and a return to regular favoured breeding areas to the south during summer for breeding purposes.

Most workers accept the hypothesis that *Palaeoxyris* are shark egg-cases. There are still some questions to be answered. The search is on for any fossil egg-cases, including *Palaeoxyris,* containing embryonic shark remains.

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