

Upper Devonian microvertebrates from the Canning Basin, Western Australia

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ABSTRACT:

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A diverse microvertebrate fauna is described from the Virgin Hills and Napier formations, Bugle Gap Limestone Canning Basin, Western Australia. Measured sections at Horse Spring and Casey Falls (Virgin Hills Formation) and South Oscar Range (Napier Formation) comprise proximal to distal slope carbonates ranging in age from the Late Devonian Frasnian to middle Famennian. A total of 18 chondrichthyan taxa are identified based on teeth, including the first record of *Thrinacodus tranquillus*, *Cladoides wildungensis*, *Protacrodus serra* and *Lissodus lusavorichi* from the Canning Basin. A new species, *Diademodus dominicus* sp. nov. is also described and provides the first record of this genus outside of Laurussia. In addition, the upper range of *Australolepis seddoni* has been extended to Late Devonian conodont Zone 11, making it the youngest known occurrence for this species. The Virgin Hills and Napier formations microvertebrate faunas show close affinities to faunas recovered from other areas of Gondwana, including eastern Australia, Iran, Morocco and South China, which is consistent with known conodont and trilobite faunas of the same age.

Key words: Vertebrate palaeontology; Chondrichthyes; Thelodonti; Frasnian; Famennian; Lennard Shelf; Gondwana.

INTRODUCTION

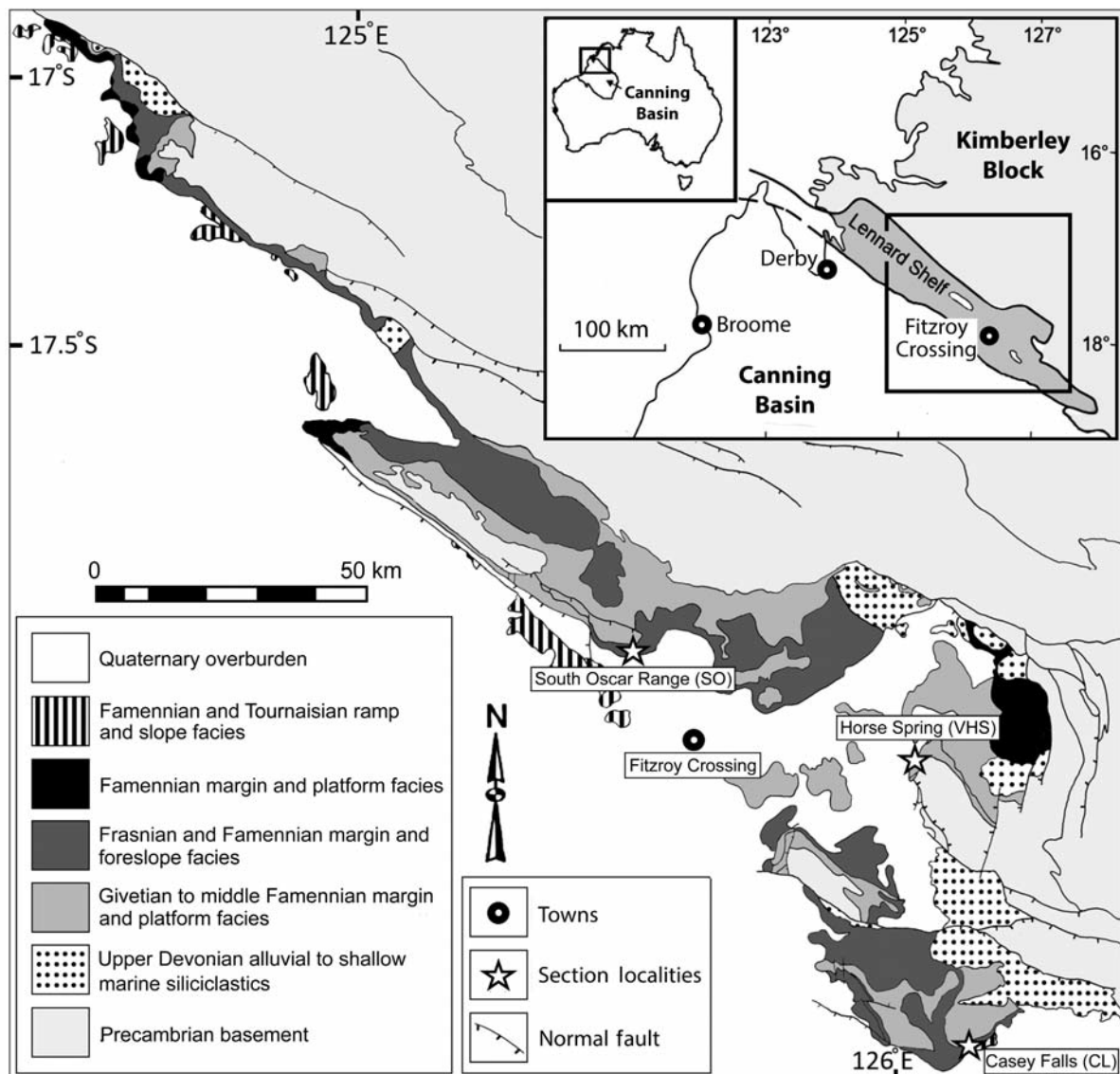
The Canning Basin, Western Australia (Text-fig. 1) is well known for the preservation of Devonian reef complexes as well as both invertebrate and vertebrate fossils (Playford *et al.* 2009; Klapper 2007; Becker *et al.* 1993), many of which have proved important in studies of biostratigraphy and correlation. Conodont and ammonoid faunas have both been extensively used in biostratigraphy over the past century with conodont

zonations established for the Frasnian (Glenister and Klapper 1966; Klapper 2007; Nicoll and Playford 1993; Metzger 1994) as well as ammonoid zonations for the Frasnian and Famennian (Peterson 1975; Becker *et al.* 1993; Becker 2000) recognised in the Canning Basin. These fossils have proven useful in determining ages of slope and basin strata enabling successful correlation across physically disconnected localities (Glenister and Klapper 1966; Becker *et al.* 1993; Becker 2000). However, correlation between slope and platform facies

within the Canning Basin remains problematic as many conodont and ammonoid faunas are absent or undiagnostic in shallow water environments. In contrast, microvertebrates have proven useful in correlating such environments (Turner 1997; Hairapetian *et al.* 2000; Trinajstic and George 2009). To date, globally correlative microvertebrate zonation schemes are best resolved for the Silurian and early to middle Devonian (Turner 1993; Young 1995; Burrow and Simpson 1995; Valiukevicius 1995; Burrow 1996, 1997; Turner 1997; Burrow and Turner 1998, 2000; Basden *et al.* 2000; Valiukevicius and Kruczek 2000). Furthermore, a Late Devonian zonation scheme based on phoebodont sharks has been established from the Frasnian to the end Famennian (Ginter and Ivanov 1995a; Ginter 2000; Jones and

Turner 2000; Young and Turner 2000). Where known, the Devonian shark fauna of Western Australia (Trinajstic and George 2009; Trinajstic *et al.* 2014) has been correlated to the Frasnian phoebodont zonation of Ginter and Ivanov (1995a). However, to date little work has been published on Famennian shark taxa from Western Australia. Thelodont zonation has also recently been extended into the Famennian (Hairapetian *et al.*, in press), although the known taxa are currently restricted to Iran and north-western Australia because other thelodonts appear to have become extinct at the end of the Givetian in other areas of the world (Turner 1997; Trinajstic 2001; Märss *et al.* 2007).

Detailed taxonomic studies on vertebrate faunas of Frasnian-age strata have been undertaken in the



Text-fig. 1. Simplified geological map of the Devonian Reef complexes of the Lennard Shelf, northern Canning Basin, showing the South Oscar Range, Horse Spring and Casey Falls measured sections and main facies types (modified after Playford *et al.* 2009)

Carnarvon (Turner and Dring 1981; Long 1991; Trinajstic and George 2009) and Canning basins of Western Australia (Long and Trinajstic 2000; Trinajstic and George 2009; Long and Trinajstic 2010) with greatest number of studies in Western Australia done on the Frasnian macrovertebrate faunas of the Gogo Formation (see Trinajstic *et al.* 2014 for a review). Biostratigraphic studies into vertebrate faunas, from both the Canning and Carnarvon basins however, are less common.

The utility of Western Australian microvertebrates to date strata has been, in part, due to the ability to identify isolated scales through comparison with the exceptionally preserved fauna from the Frasnian Gogo Formation. This has been most successful with placoderms (Trinajstic 1999a), acanthodians (Burrow *et al.* 2010) and palaeoniscoids (Trinajstic 1999b). However, a single articulated shark (Long and Trinajstic 2010), which is not comparable with any of the isolated teeth recovered so far, has been reported from the Gogo Formation. A second, incomplete specimen comprising meckels cartilage, a shoulder girdle and associated teeth has highlighted the high degree of heterodonty present in Frasnian sharks and the recognition of this variation is important when diagnosing species

from isolated teeth. Previous microvertebrate studies in the Canning and Carnarvon basins have revealed the presence of the youngest-recorded thelodont scales, first in early Frasnian strata of the Carnarvon Basin (Turner and Dring 1981) and later, younger scales in the middle Frasnian (Trinajstic and George 2009) and middle Famennian of the Canning Basin (Hairapetian *et al.*, in press).

In contrast to Frasnian vertebrate faunas, Famennian macrovertebrates from Western Australia are rare (Trinajstic *et al.* 2014), with bothriolepid and phyllolepid placoderms reported from the Willaraddie Sandstone in the Carnarvon Basin (Long and Trinajstic 2000) and coccosteid and dinichthyid placoderms described from the Napier and Virgin Hills formations in the Canning Basin (Long 1987; Trinajstic *et al.* 2014). Microvertebrate taxa from the Famennian in Canning Basin are even more understudied than those of the Frasnian with only a few reports of dipnoan, acanthodian and chondrichthyan remains from the Gumhole Formation and lower parts of the Yellow Drum Formation (Young 1987; Turner 1993; Edwards 1997; Burrow *et al.* 2010; Trinajstic *et al.* 2014). Although rare, thelodont scales as well as the teeth of *Stethacanthus cf. thomasi* and *Thrinacodus ferox*

Taxa	Localities		Casey Falls (CL)						South Oscar (SO)	Horse Spring (VHS)				
	CL-9	CL127.5	CL-471	1984-94	1984-96	1984-97	1984-98	SO-200	VHS-308	VHS-310	VHS-311	VHS-312	VHS-315	
<i>Australolepis seddoni</i>													1	
<i>Phoebodus bifurcatus</i>									2	1		1	2	
<i>Phoebodus fastigatus</i>										1	4	8	1	
<i>Phoebodus cf. fastigatus</i>											1	2		
<i>Phoebodus latus</i>										4	3	1		
<i>Phoebodus</i> sp. 1												1		
<i>Diademodus dominicus</i> sp. nov.										2				
<i>Thrinacodus tranquillus</i>		1	3			7	2							
<i>Stethacanthus</i> sp. 1			1				1							
<i>Cladoides cf. wildungensis</i>	1												1	
Ctenacanthiform gen. et sp. indet 1								1						
Ctenacanthiform gen. et sp. indet 2						1		1						
<i>Protacrodus serra</i>				1		1								
<i>Deihim mansureae</i>			1		1	2	4							
<i>Deihim cf. mansureae</i>							2							
<i>Deihim</i> sp. 1			1											
Protacrodontidae gen. et sp. indet. 1				1										
?Protacrodontidae fam. gen. sp. indet.							1							
<i>Lissodus lusavorichi</i>							2							
Total	1	1	6	2	1	11	12	2	2	8	8	13	5	

Table 1. Distribution and abundances of microvertebrate remains from sections measured at Horse Spring, South Oscar and Casey Falls, Canning Basin, Western Australia

Turner, 1982, and a possible Late Famennian otolith have been reported from the Middle to Late Famennian in the Napier Formation (Turner 1993; Trinajstić *et al.* 2014; Hairapetian *et al.*, in press). Even with a small number of Famennian microvertebrate fossils, the presence of *Thrinacodus ferox* and Famennian thelodonts, indicates a faunal connection with other areas in north Gondwana.

This work readdresses a previous lack of study through the description of a microvertebrate fauna recovered from measured sections (Text-fig. 2; Table 1) that encompass distal slope to platform top facies and crop out along the Lennard Shelf in the Canning Basin of Western Australia. The discontinuous nature of the reef complexes has meant the use of microvertebrates adds a significant control to how the Lennard Shelf carbonate system is correlated and reconstructed. Microvertebrates recovered from sampled strata are compared with the known age ranges reported from other sites globally as well as those species previously described from north-western Australia. In addition to providing the first comprehensive study into Late Famennian chondrichthyans within the Canning Basin, this work also determines faunal links between the Canning Basin and other areas along the margins of northern Gondwana and southern Laurussia.

MATERIALS AND METHODS

Carbonate rock samples (~20 kg each) were processed in a 10% buffered acetic acid solution at Macquarie and Curtin universities (following the methodology of Jeppsson *et al.* 1999), with resulting residues further separated by either heavy liquid fractionation (Macquarie University) or sieving (0.125 mm sieve; Curtin University) before being picked under a Nikon stereomicroscope. Both conodont and microvertebrate remains were well preserved with the conodont elements indicating a Conodont Alteration Index (CAI) of 1. For SEM photography, specimens were mounted on adhesive carbon tape fixed to 10 mm diameter aluminium stubs and coated with 5 µm of platinum. Specimens were imaged using a Zeiss Evo 40XVP SEM at the Centre for Materials Research at Curtin University as well as a Hitachi TM-3030 desktop SEM at Applied Geology at Curtin University with accelerating voltages ranging from 5–15 kV and under variable pressure.

The 13-fold Montagne Noire (MN) conodont Zonation (Klapper 1989, 2007) modified by Girard *et al.* (2005) was used to determine the age ranges of the

associated Frasnian microvertebrates recovered in this study, as it provides greater resolution than that of Zeigler and Sandberg (1990). The standard conodont Zonation (Zeigler and Sandberg 1990) is used in the Famennian.

Microvertebrate specimens are housed at the Western Australian Museum (WAM).

GEOLOGICAL SETTING

Throughout the Devonian, the Canning Basin (Text-fig. 1) occupied an equatorial position, approximately 12–14° south of the equator, along the northern margins of Gondwana (Scotese and McKerrow 1990). Development of the basin was initiated during the Ordovician. Following a period of uplift and erosion in the early Devonian, extension during the middle Devonian to early Carboniferous led to rapid subsidence of the NW trending Fitzroy Trough along the northern margin of the Canning Basin (Drummond *et al.* 1991). The margin successions include the late Givetian to late Famennian reef complexes, which are well exposed along the inner Lennard Shelf, and include numerous well-preserved fossilised fringing reefs and atolls (Playford 1980). Difficulty in correlating Frasnian and Famennian sections within the Lennard Shelf is partly due to a complex underlying topography on which the reef was established, as well as depositional heterogeneity (Playford *et al.* 2009). Tectonic activity during the period of reef building (Chow *et al.* 2013) and deformation following post-depositional exhumation have also added to a fragmentary Frasnian and Famennian record across the basin (Playford *et al.* 2009).

Studied sections

Casey Falls

A section was measured at Casey Falls (18°44'0" S, 126°05'8" E; Text-figs 1 and 2) approximately 80 km south east of Fitzroy Crossing (Text-fig. 1). The measured section represents 420 m of toe-of-slope to upper slope carbonate sediments of the Virgin Hills Formation and overlying Bugle Gap Limestone, respectively (Table 2). The lower 100 m of the section mainly comprises resedimented silty skeletal to non-skeletal wackestone/packstones derived from platform, margin and slope environments. The upper 320 m consists mostly of stromatactoid microbial boundstones and microbially stabilised packstones and grainstones (Playton *et al.* 2013). Minor platform derived skeletal-peloidal pack-

stones and grainstones occur in the upper 40 m of the section. The Frasnian strata within the section are limited to the first 2 m of the section and range from Conodont zones (CZ) 13a to 13b, with zone 13c not resolvable. The Frasnian–Famennian boundary is located

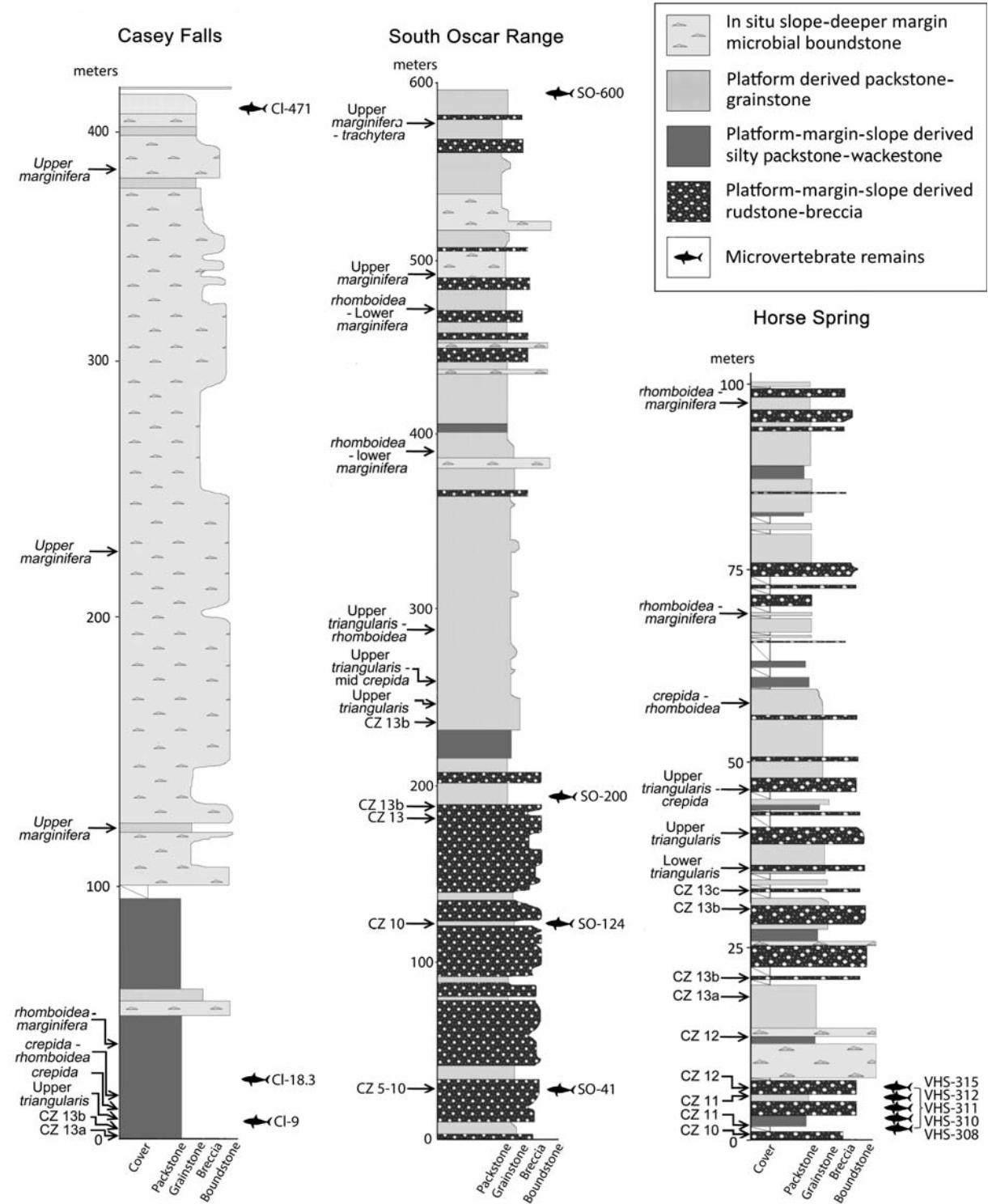
between 2.2 and 7.9 m above the section base, however finer biostratigraphic resolution was impossible at this level due to a paucity of conodonts. Overlying Famennian sediments, from 7.9 m, yield conodont zones from Late *triangularis* to Late *marginifera* CZ. Addi-

CARBONI-FEROUS									FAIRFIELD GROUP		
LOWER		Tournaisian									
DEVONIAN		UPPER		Framennian			zones				
MIDDLE		Givetian	Frasnian		conodont			Reef Complexes			
			Lower	Middle	Upper	Lower	Middle	Upper			
				<i>falsiovalis</i>							
				<i>transistans</i>							
				<i>punctata</i>							
				<i>hassi</i>							
				<i>jamieae</i>							
				<i>rhenana</i>							
				<i>linguiformis</i>							
				<i>triangularis</i>							
				<i>crepida</i>							
				<i>rhomboidea</i>							
				<i>marginifera</i>							
				<i>trachytera</i>							
				<i>postera</i>							
				<i>expansa</i>							
				<i>praesulcata</i>							

Table 2. Correlation table of Upper Devonian and Lower Carboniferous units on the Lennard Shelf (after Playford *et al.* 2009). The discontinuous nature of the reef complexes coupled with the large geographic range of the outcrops resulted in contemporaneous facies receiving different formation names. Dashed lines represent chronostratigraphic boundaries; bold line represents the cessation of reef building in the Canning Basin

tional samples were taken from poorly outcropping beds approximately 580 m north (samples 1984–95 and 1984–96) and 600 m (samples 1984–97 and 1984–98) north-north-east from the top of the measured section at

Casey Falls with conodonts indicating a Late *marginifera* age. These samples represent the shallow water carbonate derived material of the Bugle Gap Limestone.



Text-fig. 2. Simplified stratigraphic columns of the sections at Horse Spring, Casey Falls and South Oscar Range, showing main facies types and locations of recovered microvertebrate remains (modified after Playton *et al.* 2013)

South Oscar Range

The section measured at the southern end of South Oscar Range (17°54'53" S, 125°17'56" E, Text-figs 1 and 2) spans 585 m of the Napier Formation and represents the seaward side of an offshore island and fringing reef complex (Playford *et al.* 2009). The preserved sequence comprises transported slope facies dominated by platform derived packstones and grainstones/rudstones with commonly occurring peloids, coated grains and skeletal fragments. Debris deposits consisting of allochthonous blocks and megabreccias of reefal margin material can occur locally and are concentrated in particular parts of the section, reflecting brittle failure of the early-lithified bound margin. Bioclasts are abundant throughout the entire section and dominated by branching and laminar stromatoporoids (in the Frasnian; George 1999; Stephens and Sumner 2003), crinoids, corals and brachiopods. The Frasnian beds range from MN 6 to 13b CZ and in addition to conodonts, yielded chondrichthyan teeth and scales as well as acanthodian scales. The Frasnian–Famennian boundary was located between 228.7 and 233 m above the section base. The Famennian portion of the section ranges from Upper *triangularis* to *marginifera* CZ with only the uppermost bed containing microvertebrate remains including acanthodian and palaeoniscoid scales as well as the youngest thelodont scales currently known (Hairapetian *et al.*, in press).

Horse Spring

The section measured at Horse Spring (GSWA reference section WCB 364) is located approximately 42 km east of Fitzroy Crossing, at the northern extremity of the Hull and Horse Spring Ranges (18°41'11" S, 126°05'12"; Text-figs 1 and 2). The section represents a lower slope succession dominated by platform derived skeletal to non-skeletal packstones and grainstones, slope derived rudstones, and margin-derived megabreccias. Stromatolitic and stromatactoid boundstones are minor and found in Frasnian beds, representing periods of deep-water in situ encrustation. The section at Horse Spring has been previously dated using conodonts (Klapper 1989; 2007) and goniatites (Becker *et al.* 1993), with the Frasnian–Famennian boundary located between 34.6 and 36.6 m above the section base. A diverse Frasnian microvertebrate fauna has also been recorded by Trinajstić and George (2009) with scales of the thelodont *Australolepis seddoni* Turner and Dring, 1981 recorded as occurring with conodont elements and phoebodont teeth for the first time, thus allowing the age of *A. seddoni* to be constrained to MN 4–10 CZ. The phoebodont teeth were

also correlated to the known phoebodont based zonation of Ginter and Ivanov (1995a).

SYSTEMATIC PALAEONTOLOGY

Class Thelodonti Jaekel, 1911
Order Thelodontiformes Kiaer, 1932
Family Turiniidae Obruchev, 1964
Genus *Australolepis* Turner and Dring, 1981

TYPE SPECIES: *Australolepis seddoni* Turner and Dring, 1981

Australolepis seddoni (Turner and Dring, 1981)
(Text-fig. 3A)

1969. Fish tooth type b; Seddon, p 30, fig. 2a–b.
1981. *Australolepis seddoni* sp. nov.; Turner and Dring, 43, figs 3A–P, 4A–K.
1981. Nikoliviid gen. et sp. indet. Turner and Dring: 46, fig. 6A–C.
1993. *Australolepis seddoni* Turner and Dring, 1981; Turner, p. 183, fig. 8.3.
1997. *Australolepis seddoni* Turner and Dring, 1981; Turner, p. 309, fig. 8.
2000. *Australolepis seddoni* Turner and Dring, 1981; Long and Trinajstić, p. 472, fig. 1.
2000. *Australolepis seddoni* Turner and Dring, 1981; Yazdi and Turner, p. 225, fig. 2.1.
2001. *Australolepis seddoni* Turner and Dring, 1981; Trinajstić, p. 239, fig. 2A–L, fig. 4.
2002. *Australolepis seddoni* Turner and Dring, 1981; Turner *et al.*, p. 151, fig. 8.
2009. *Australolepis seddoni* Turner and Dring, 1981; Trinajstić and George, p. 647–648, pl. 1, figs 1–8.
2013. *Australolepis seddoni* Turner and Dring, 1981; Chow *et al.*, pl. 1C.
2014. *Australolepis seddoni* Turner and Dring, 1981; Hairapetian *et al.*, in press.

MATERIAL: One broken scale from the Virgin Hills Formation, Horse Spring, sample VHS-315.

DESCRIPTION: A damaged scale, less than 1 mm in length, with part of the base and neck not preserved. Unornamented, conically shaped crown possessing six primary ribs radiating from the apex, with the two anterior ribs bifurcating towards the crown base (Text-fig. 3A). The posterior of the scale is complete and preserves a shallow neck separating the crown from the elliptical base that has a well-developed pulp canal surrounded by tubercular swellings.

REMARKS: Scales attributed to *A. seddoni* are found along the northern margins of Gondwana (Yazdi and Turner 2000; Turner *et al.* 2002; Märss *et al.* 2007; Hairapetian *et al.* 2006; Trinajstić and George 2009) and their presence in mainly shallow-water facies indicate that they inhabited a near-shore, marine to marginal marine environment (Burrow 1997; Turner 1999; Märss *et al.* 2007). Within the Canning Basin, the majority of scales (46) have been recovered from the Virgin Hills Formation at Horse Spring (Trinajstić and George 2009; this work). This locality represents a distal slope environment formed in depths in excess of 200 m (Playford *et al.* 2009). This is in contrast to the high numbers (730) recovered from the shallow marine environment of the contemporaneous, Gneudna Formation, Carnarvon Basin, Western Australia (Turner and Dring 1981; Trinajstić 2001) and suggests that the scales were transported downslope, to deeper water prior to fossilization. This transport and likely consequential abrasion might have contributed to the lack of fine ornament, diagnostic for the taxon. However, as the co-occurring phoebodont teeth preserve the delicate lateral carinae and striations on the cusps, this explanation no longer seems likely for all scales. Another possibility for the absence of ornament is intraspecific variation, with both ornamented and non-ornamented scales present in shallow water facies at Hull Range (Chow *et al.* 2013).

DISTRIBUTION AND STRATIGRAPHIC RANGE: Associated conodont elements extend the upper-known age range of *A. seddoni* in the Canning Basin from MN 10 CZ to MN 11 CZ. As the upper age of the Gneudna Formation type section is constrained by the remains of *A. seddoni*, the youngest age for the Gneudna may now be extended to MN 11 CZ. Outside Australia scales of *A. seddoni* have been reported in the Shishtu Formation, Shotori Range, eastern Iran and Chahriseh section, Esfahan, Central Iran from *falsiovalis* to *rhenana* CZ (= MN 1–10 CZ) (Yazdi and Turner 2000; Turner *et al.* 2002; Hairapetian *et al.* 2006).

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Phoebodontiformes Ginter, Hairapetian and Klug, 2002
 Family Phoebodontidae Williams, 1985
 Genus *Phoebodus* St. John and Worthen, 1875

TYPE SPECIES: *Phoebodus sophiae* St. John and Worthen, 1875

Phoebodus bifurcatus Ginter and Ivanov, 1992
 (Text-fig. 3B–E)

1991. *Phoebodus* sp.; Ginter 1991; p. 74, pl. 8, figs 1–2.
 1992. *Phoebodus bifurcatus* sp. nov.; Ginter and Ivanov, p. 65–66, figs 4A–F, 5D–H, 6A.
 1995a. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Ginter and Ivanov, pl. 1, figs 5–6.
 1995. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Ginter, p. 61, fig. 1F–G.
 1995. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Turner and Youngquist, p. 390–391, fig. 1.
 1995. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Wang and Turner, p. 65, pl. 7, fig. 7.
 2009. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Trinajstić and George, p. 648, pl. 1, fig. 9.
 2010. *Phoebodus bifurcatus* Ginter and Ivanov, 1992; Hairapetian and Ginter, p. 360–361, fig. 2B–C.

MATERIAL: Six teeth from the Virgin Hills Formation, Horse Spring, samples VHS-308, VHS-310, VHS-311, VHS-315.

DESCRIPTION: Teeth with three lingually inclined cusps bearing a thin, lateral carinae extending from the bases of the cusps to the apices and lacking a distinct neck between the base and crown (Text-fig. 3B–E). The cusps are generally of nearly equal size however the size of the central cusp is significantly reduced in one specimen (WAM 14.8.2, Text-fig. 3D). The base is characterised by a labially directed semicircular arch which defines the lingual border and varies between specimens from strongly (Text-fig. 3C) to weakly bifurcated (Text-fig. 3E). A distinct button is lacking on most specimens, although a rounded thickening, close to the lingual rim is sometimes present (Text-fig. 3E). A large foramina is located in the centre of the lingual arch and in some specimens there are smaller adjacent canal openings.

REMARKS: The teeth typical of *Phoebodus bifurcatus* Ginter and Ivanov, 1992 are characterised by having five ornamented cusps and a bifurcating base with a distinct button surrounded by foramina (Ginter and Ivanov 1992). However, tricuspid forms, lacking intermediate cusplets, are known from the Confusion Range, Utah, USA and were attributed to juveniles (Turner and Youngquist 1995). Within the Canning Basin only tricuspid forms of *Ph. bifurcatus* have been identified but were previously attributed to juvenile sharks based on deeply bifurcated bases, an indistinct button and lack of ornament on the cusps (Trinajstić and George 2009,

pl. 1, fig. 9). The teeth attributed to juvenile individuals have been found in association with adult forms in the South Urals, Holy Cross Mountains and central Iran (Ginter and Ivanov 1992; Hairapetian and Ginter 2010) whereas in the Confusion Range, Utah, USA and the Canning Basin only juvenile teeth have been reported. Here we question the assignment of these tricuspid teeth to juvenile sharks as the size of some deeply bifurcated, tricuspid teeth (Text-fig. 3C–D, measuring up to 1.2 mm from furthest point on the lingual margin of the base to the labial edge), recovered from Horse Spring, are of comparable or larger size than other teeth attributed to adult forms previously reported (Ginter and Ivanov 1992, fig. 4B–F)). It is also unlikely that these larger teeth are symphyseal due to the asymmetry of the base and crown on one specimen (WAM 14.7.4, Text-fig. 3C). This would leave the possibility that the Canning Basin teeth, and potentially other smaller tricuspid teeth, represent sexual dimorphism (e.g. Peyer 1968; Bass *et al.* 1973; Pfeil 1983; Straube *et al.* 2008), a subspecies of *Ph. bifurcatus*, intraspecific variation or even a separate, closely related species.

DISTRIBUTION AND STRATIGRAPHIC RANGE:

In the Canning Basin, Australia *Ph. bifurcatus* has only been recorded from MN 11 CZ; within the Holy Cross Mountains, Poland, South Urals, Russia, southern China and Utah, USA *Ph. bifurcatus* ranges from MN 11–12 CZ; in Kale Sardar, eastern Iran the range extends from the *rhenana*–lower *linguiformis* Zones (MN 11–13b CZ).

Phoebodus fastigatus Ginter and Ivanov, 1992 (Text-fig. 3D–F)

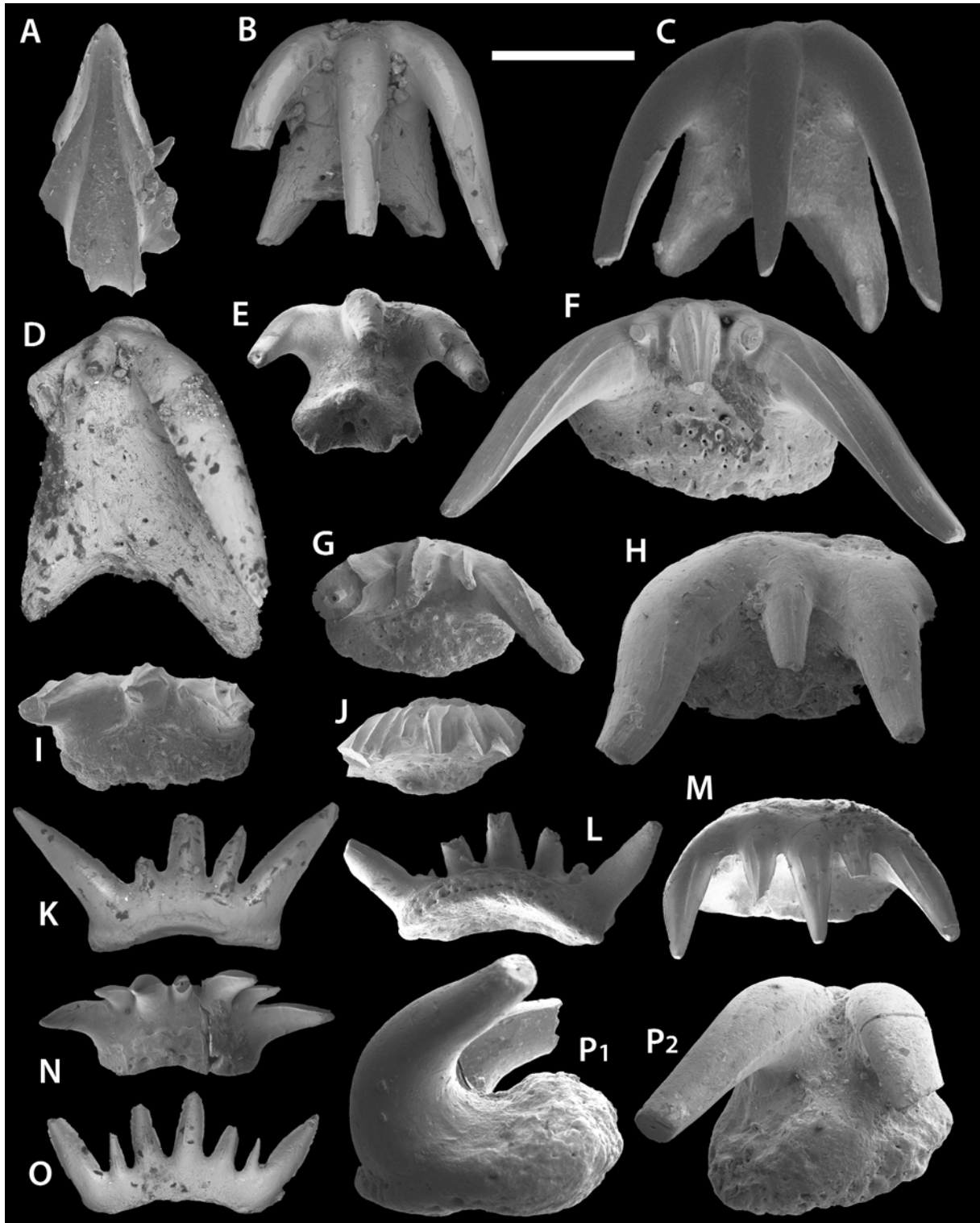
1973. *Phoebodus floweri* Wells, 1944; Gross, p. 131, pl. 35, fig. 7a–b.
 1990. *Phoebodus limpidus* sp. nov.; Ginter, p. 75–76, pl. 4, fig. 6a–b.
 1992. *Phoebodus fastigatus* sp. nov.: Ginter and Ivanov, p. 66–67, fig. 3A–B, G.
 1993. *Phoebodus* sp.: Liszkowski and Racki, fig. 3F, H, K.
 1995. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Ginter, p. 59, fig. 1C–D.
 1995. *Phoebodus* aff. *fastigatus* Ginter and Ivanov, 1992; Wang and Turner, p. 65, pl. 7, fig. 6.
 1997. *Phoebodus* cf. *Ph. fastigatus* Ginter and Ivanov, 1992; Turner, p. 112–113, figs 4, 11, 12.
 1998. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Kaufmann, pl. 13, figs 1–4.
 2000. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Ginter and Ivanov, p. 327, pl. 1, fig. E.

2003. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Abousalam, pl. 27, figs 13–16.
 2004. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Ginter, fig. 2H–J.
 2004. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Hampe *et al.*, p. 494–495, fig. 5.
 2007. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Liao *et al.*, p. 173, fig. 3A–M.
 2008. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Ginter *et al.*, p. 170, text-fig. 2E–H.
 2009. *Phoebodus fastigatus* Ginter and Ivanov, 1992; Trinajstić and George, p. 649–650, fig. pl. 1, figs 11–16.

MATERIAL: Fourteen teeth from Virgin Hills Formation, Horse Spring, samples VHS-310, VHS-311, VHS-312 and VHS-315.

DESCRIPTION: Teeth with three main cusps. The medial cusp is approximately a third of the length of the lateral cusps and one half to one third the size at the base of the lateral cusps (Text-fig. 3F–H). When present, the accessory cusps are reduced in size, approximately half the size of the central cusp. The lateral cusps are long and slender with some specimens bearing slight torsion (Text-fig. 3F). The central and lateral cusps are all rounded in cross section (Text-fig. 3G), however, the labial faces of the cusps vary between teeth from smooth (Text-fig. 3H) to ornamented with faint to strongly developed striations (Text-fig. 3F). The base is rectangular to trapezoidal in outline, extending further mesio-distally than labio-lingually and bearing a straight to slightly convex thin lingual edge. The lingual face of the base is perforated by numerous small foramina with a round to slightly ovoid centrally located button (Text-fig. 3F).

REMARKS: The teeth are attributed to *Phoebodus fastigatus* Ginter and Ivanov, 1992 based on the thin elongate lingual base with a straight lingual margin and centrally located ovoid button (Ginter and Ivanov 1992). The tooth crowns vary from the diagnostic thin elongate recurved lateral cusps (Text-fig. 3F–G) to shorter more robust cusps with less distal divergence (Text-fig. 3H). A smooth labial cusp face is described as a diagnostic feature of *Ph. fastigatus* (Ginter and Ivanov 1992, 2000) and one of the features distinguishing it from *Ph. bifurcatus*. This feature is not present in all teeth from the Canning Basin with faint to coarse cristae observed here and on teeth previously described by Trinajstić and George (2009, pl. 1, figs 11–16). As there is no correlation between tooth size and the presence of or lack of ornament, these differences are attributed to intraspecific variation rather than ontogeny.



Text-fig. 3. Late Frasnian phoebodonts from the Virgin Hills Formation, Horse Spring, Canning Basin, Western Australia. A – *Australolepis seddoni* scale, WAM 14.7.3, sample VHS-315, in crown view; B–E, *Phoebodus bifurcatus* teeth in occlusal view. B – WAM 14.8.1, sample VHS-315; C – WAM 14.7.4, sample VHS-310; D – WAM 14.8.2, sample VHS-315; E – WAM 14.7.5, sample VHS-310. F–H, *Phoebodus fastigatus* teeth in occlusal view. F – WAM 14.7.9, sample VHS-311; G – WAM 14.7.11, sample VHS-312; H – WAM 14.7.10. I–J, *Phoebodus cf. fastigatus* in occlusal view. I – WAM 14.8.5, sample VHS-311; J – WAM 14.7.12, sample VHS 310. K–O, *Phoebodus latus*. K – WAM 14.8.3, sample VHS-312, in labial view; L – WAM 14.7.7, sample 311, in occlusal view; M – WAM 14.7.8, sample 312, in lingual view; N – WAM 14.9.13, sample VHS-312, in occlusal view; O – WAM 14.8.4, sample 311, in labial view; P – *Phoebodus* sp. 1 WAM 14.7.6, in lateral and occlusal views. Scale bar 0.5 mm

DISTRIBUTION AND STRATIGRAPHIC RANGE:

This species ranges from MN 6–11 CZ in the Canning Basin, Western Australia. Worldwide the range is greater, from the Givetian to Frasnian *rhenana* CZ in the USA, Morocco, Mauritania, Spain, Poland, China, Russia and eastern Australia.

Phoebodus cf. fastigatus (Ginter and Ivanov 1992)
(Text-fig. 3I–J)

MATERIAL: Three teeth from the Virgin Hills Formation, Horse Spring, sample VHS-312.

DESCRIPTION: Three small teeth, measuring less than 0.5 mm mesiodistally across the base, with damage to both the cusps and bases (Text-fig. 3I–J). Crowns with three to five lingually inclined cusps, comprising a main central cusp, two lateral cusps and, when present, smaller intermediate cusplets (Text-fig. 3J). The lateral cusps, when preserved, are slightly larger in size than the medial cusp and in one specimen show torsion towards the apex of one lateral cusp (Text-fig. 3I). When present, the intermediate cusps are small and fused to the base of the mesial margin of the lateral cusps. Prominent striations are present on the labial faces of the cusps, whereas the lingual faces are smooth. The base forms a roughly rectangular to trapezoid outline and is perforated by numerous small foramina. A rounded oval button is often difficult to determine on most specimens, however a faint outline can be seen, positioned centrally on one specimen (Text-fig. 3I).

REMARKS: The teeth described here are too poorly preserved for a definitive diagnosis, however they share similarities to the teeth attributed to the ornamented forms of *Ph. fastigatus* in this work. When preserved, the lingual margin of the base in *Ph. cf. fastigatus* is thin; a diagnostic feature of *Ph. fastigatus* (Ginter and Ivanov 1992), however, the cusps of *Ph. cf. fastigatus* are ornamented with strong striations, ovoid in cross section and lack a distinct rounded button. The bases are not well enough preserved for an outline to be determined. Despite poor preservation, in one specimen the base appears lingually narrow (Text-fig. 3I). The teeth described here are consistently smaller than other teeth attributed to *Ph. fastigatus* and this may be evidence of ontogenetic variation. Furthermore the teeth commonly lack a distinct button, a feature attributed to juvenile forms in both *Phoebodus gothicus* Ginter, 1990 and *Phoebodus bifurcatus* (Ginter and Ivanov 1992). One tooth (WAM 14.7.10, Text-fig. 3G) may represent an intermediate form between teeth desig-

nated *Ph. fastigatus* and the smaller teeth of *Ph. cf. fastigatus* as it possesses an elongate lateral cusp and more prominent ovoid button similar to *Ph. fastigatus*, but exhibits the coarse cristae and smaller size of *Ph. cf. fastigatus*. Therefore an ontogenetic series is supported by the presence of this transitional form.

Phoebodus latus Ginter and Ivanov, 1995a
(Text-fig. 3K–O)

1992. *Phoebodus* sp. A Ginter and Ivanov 1992, p. 70, fig. 7A–1.

1993. *Phoebodus* sp. Liszkowski and Racki, p. fig. 5L–M.
1995a. *Phoebodus latus* sp. nov.; Ginter and Ivanov, p. 355, pl. 1, figs 3, 4.

1995b. *Phoebodus latus* Ginter and Ivanov, 1995b; Ginter and Ivanov, p. 19, fig. 1.

1995. *Phoebodus latus* Ginter and Ivanov, 1995b; Ginter, fig. 1E.

2009. *Phoebodus latus* Ginter and Ivanov, 1995b; Trinajstić and George, pl. 1, figs 18, 19.

2011. *Phoebodus latus* Ginter and Ivanov, 1995b; Ivanov and Lucas, fig. 2A, B.

MATERIAL: Eight teeth from the Virgin Hills Formation, Horse Spring, samples VHS-310 VHS-311 and VHS-312.

DESCRIPTION: The teeth here attributed to *Phoebodus latus* Ginter and Ivanov, 1995a are highly variable with three different morphotypes identified here. The first morphotype (Text-fig. 3K–L) comprises five to seven smooth and almost straight conically shaped cusps with well-developed lateral carinas. The cusps diverge from the centre of the crown, which is defined by a central cusp with a base approximately 25% smaller than the base of the two lateral cusps (Text-fig. 3K–L). A pair of intermediate cusplets, slightly smaller than the medial cusp, are present on all specimens. One specimen (WAM 14.7.7, Text-fig. 3L) exhibits a second pair of small broken cusplets fused at the base of the lateral cusps. The base is roughly trapezoidal in outline, thickened along the lingual edge and slightly arched. A faint outline of an ovoid button is preserved.

A single, well preserved tooth represents the second morphotype (Text-fig. 3M). The crown comprises three main cusps of almost equal size with a pair of intermediate cusplets approximately a third of the length of the lateral cusps. The cusps are ovoid in cross section and all lingually directed, with the medial and lateral cusps extending beyond the lingual margin of the base (Text-fig. 3M). The cusps exhibit a well-defined lateral

carina as well as striations on the labial faces. The lingual faces of the cusps are smooth. The base forms a roughly rectangular outline with the very faint outline of a centrally located ovoid button. Morphotype three (Text-fig. 3N–O) is characterised by three main cusps and two pairs of intermediate cusplets, all of which are smooth with well-developed lateral carinas and a slight lingual inclination. The size of the central cusp ranges from small (Text-fig. 3O), with the basal width approximately half of the size of the first intermediate cusplets, to significantly larger (Text-fig. 3N), almost the same size as the lateral cusps. The second pair are approximately half the size of the intermediate cusplets. The base is arched and slightly bifurcated (Text-fig. 3N) along the lingual rim which is also perforated by a horizontal row of foramina. The mesio–distally elongate button is positioned toward the edge of the lingual rim of the base (Text-fig. 3N).

REMARKS: The crown morphology of *Phoebodus latus* Ginter and Ivanov, 1995a is highly variable with the presence of intermediate cusplets greater than other known species attributed to *Phoebodus* (Ginter 2008). The third morphotype (Text-fig. 3N–O) resembles other *Ph. latus* teeth recovered from the South Urals, Russia and the Holy Cross Mountains, Poland (Ginter and Ivanov 1992, fig. 7A). The tooth also bears strong resemblance to another tooth from Horse Spring, previously described by Trinajstić and George (2009, pl. 1, figs 18, 19). The first and third morphotypes identified here lack the ornament on the labial faces of the cusps (Text-figs 3K, O) seen in other examples of *Ph. latus* (Ginter and Ivanov 1995a). The crown of the second morphotype more closely resembles other teeth from *Ph. latus* (Text-fig. 3M) with the presence of three almost equally sized main cusps ornamented with ridges on the labial faces. However the base does not show the diagnostically distinct ovoid button positioned close to the lingual rim (Text-fig. 3M). There appears to be a great deal of diversity attributed to *Ph. latus* that would suggest a high degree of heterodonty. Until more specimens are found, it is difficult to determine whether the teeth attributed to *Ph. latus* in the Canning Basin are products of heterodonty or if they represent intraspecific variation.

DISTRIBUTION AND STRATIGRAPHIC RANGE: Within the Canning Basin, the range of this species is confined to MN 9–11 CZ. In other regions, the species is longer ranging, from the *falsiovalis* to *linguiformis* conodont Zones (MN 1–13b) in Poland, the Middle and South Urals, and Timan of Russia.

Phoebodus sp. 1
(Text-fig. 3P)

MATERIAL: One tooth from the Virgin Hills Formation, Horse Spring, sample VHS-312.

DESCRIPTION: A robust tooth comprising two lingually inclined, almost equally sized laterally diverging cusps, which are rounded in cross section and bear a single faint lateral carina on the inner face (Text-fig. 3P_{1–2}). There is no evidence of a third cusp forming. The base is asymmetric and perforated by numerous pores concentrated along the basal rim (3P₂). The base is thickest along the lingual rim, forming a rounded bulbous edge. A well-defined circular button is located centrally on the base and reaches almost to the lingual edge. A rounded, striated labiobasal thickening extends from the base (Text-fig. 3P₁).

REMARKS: The thin, smooth cusps, which are rounded in cross section, and the centrally located spherical button are similar to the morphological features that diagnose *Ph. fastigatus* (Ginter and Ivanov 1992, fig. 3A–B). In addition, the tooth shares a similar cusp morphology to teeth from the same horizon, attributed to *Ph. fastigatus* (Text-fig. 3H). However, the bicuspid crown, asymmetric outline of the base and thickened lingual rim makes an accurate diagnosis problematic. It is suggested that these differences are pathological, and that the tooth is most likely from *Ph. fastigatus*. However, as less than 1% of chondrichthyan teeth, both fossil and extant (Becker *et al.* 2000) are known to exhibit pathology the diagnosis of *Ph. fastigatus* cannot be confirmed and until further teeth are recovered this tooth is placed in open nomenclature.

Genus *Thrinacodus* St. John and Worthen, 1875

TYPE SPECIES: *Thrinacodus nanus* St. John and Worthen, 1875

Thrinacodus tranquillus Ginter, 2000
(Text-fig. 4A–C)

2000. *Thrinacodus tranquillus* sp. nov.; Ginter, p. 374–377, figs 2a–c, 3a–f, 4a–c, 5h–k.
2000. *Thrinacodus* cf. *ferox* (Turner); Long and Hairapetian, p. 214–216, fig. 4n.
2002. *Thrinacodus tranquillus* Ginter, 2000; Ginter *et al.*, p. 186–188, text-fig. 9f–h, pl. 2, fig. h, pl. 3, fig. h, pl. 11, figs h–I.

2008. *Thrinacodus tranquillus* Ginter, 2000; Derycke *et al.*, p. 988, text-fig. 4(1–2).
2009. *Thrinacodus tranquillus* Ginter, 2000; Hairapetian and Ginter, p. 191, text-fig 9c–d.
2010. *Thrinacodus tranquillus* Ginter, 2000; Ginter *et al.*, p. 41, fig. 33A.
2010. *Thrinacodus tranquillus* Ginter, 2000; Ginter and Turner, p. 1668, fig. 2C.

MATERIAL: Four teeth from the Virgin Hills Formation, Casey Falls, samples CF-127.5 and CF-471; ten teeth from the Bugle Gap Limestone, Casey Falls, samples 1984-97 and 1984-98.

DESCRIPTION: A total of three morphotypes are attributed to *Thrinacodus tranquillus* in this work. The first morphotype (Text-fig 4A), is the most common and features a symmetrical crown with three sub-equal cusps, often with one dominant lateral cusp. When preserved, the lingually extended base is positioned asymmetrically in relation to the crown. A centrally located canal is present on the occlusal face of the base, which also shows slight torsion towards the distal end.

The second morphotype (?symphyseal teeth *sensu* Ginter 2000; symphyseal tooth Ginter pers comm.), represented by a single tooth (Text-fig. 4B), comprises a symmetrical crown with three thin, straight, equally sized and lingually directed cusps, each with lateral carinae and faint striations on the labial face. The base is thin, extends lingually further than the cusp apices and bears a small nutritive canal approximately half way down the occlusal face of the base. There is no obvious sign of torsion towards the end of the base.

The third morphotype is represented by a single asymmetric tooth (WAM 14.7.29, Text-fig. 4C) that is characterised by a crown consisting of three unequal cusps. The straight, lingually directed central cusp is preserved with lateral carinae and faint striations on the labial face. The thin base extends further lingually than the apex of the central cusp and is curved distally in relation to the crown. The posterior end of the base is contorted toward a vertical orientation with a small nutritive canal located approximately half way down the occlusal face.

REMARKS: These teeth largely conform to the diagnosis of *Thrinacodus tranquillus* Ginter, 2000, and the differences between the tooth forms are attributed to heterodonty. Previous work (Ginter 2000; Ginter *et al.* 2002; Duncan 2003; Ginter and Turner 2010) has suggested the presence of two tooth types; the first with a flattened base positioned asymmetrically in relation to the crown and a smaller almost completely sym-

metrical form (Duncan 2003). The first morphotype (Text-fig 4A) is the most common tooth form attributed to *Th. tranquillus* and has been reported from various locations across northern Gondwana (Ginter and Turner 2010). The second, smaller morphotype (Text-fig. 4B), which has had its assignment to *Th. tranquillus* recently questioned (Ginter and Turner 2010), is less common and with few examples recorded from the Montagne Noire (Ginter 2000). Based on reconstructions of tooth placement within thrinacodont jaws (Turner 1982; Ginter *et al.* 2002; Duncan 2003), the supposed symmetrical symphyseal teeth only comprise a small proportion of teeth thus likely lower yields of these teeth are to be expected.

A third morphotype (Text-fig. 4C) has been attributed to *Th. tranquillus* with similar teeth previously recorded from Montagne Noire and Oum El Jerane and Tizi Nersas, Morocco, conversely these specimens were designated *Thrinacodus cf. ferox* (Ginter 2000, fig. 2; Ginter *et al.* 2002, fig. 9A–E). It was suggested by Ginter *et al.* (2002) that the teeth of *Th. cf. ferox* may represent the lateral most teeth of *Th. tranquillus*, which was supported by the presence of intermediate forms between the typical teeth of *Th. tranquillus* and *Th. cf. ferox*. A similar variety of tooth forms is present in the Canning Basin, however the teeth are recovered from Late *marginifera* CZ dated deposits making their attribution to the *Th. ferox* unlikely as it is regarded as a late Famennian to late Tournaisian species (Ginter and Turner 2010).

DISTRIBUTION AND STRATIGRAPHIC RANGE: In the Canning Basin this species is recorded from the Late *marginifera* CZ. A similar age *rhomboidea* or Late *marginifera* CZ is recorded for Chahriseh, Iran (Long and Hairapetian 2000; Ginter *et al.* 2002; Hairapetian and Ginter 2009) and also a *marginifera* CZ for Hunan, China (Lelièvre and Derycke 1998). In Oum El Jerane and Tizi Nersas, Morocco this species ranges from *rhomboidea* or Late *marginifera* CZ to Middle to Late *expansa* (Ginter *et al.* 2002; Derycke *et al.* 2008). Younger known occurrences have been recorded from the Late *trachytera* CZ, Holy Cross Mountains, Poland, Lower to upper *expansa* CZ, Thuringia, Germany and *expansa* CZ in Montagne Noire. Within the South Urals the range of this species is recorded from the Late *expansa* to Early *praesulcata* CZ (Ivanov 1996).

Genus *Diademodus* Harris, 1951

TYPE SPECIES: *Diademodus hydei* Harris, 1951

Diademodus dominicus sp. nov.
(Text-fig. 4D–E)

ETYMOLOGY: In honour of Mr Dominicus ‘Tim’ Mueller, M.Sc., who guided the careers of many aspiring geoscientists.

HOLOTYPE: Specimen WAM 14.7.1 from the Virgin Hills Formation, Horse Spring, Canning Basin, Western Australia; sample VHS-310; Frasnian, MN 11 CZ; Text-fig. 4D.

MATERIAL: Two teeth from the Virgin Hills Formation, Horse Spring, sample VHS-310.

DIAGNOSIS: Teeth with a multicuspid phoebodont type crown comprising three cusps and three to four pairs of intermediate cusplets (Text-fig. 4D). The cusps are thin and ovoid in cross section, becoming circular towards the cusp apex and bearing prominent lateral carinae. A slight lingual inclination is present on all cusps with the larger lateral cusps recurving occlusally. The base is highly arched, trapezoid in outline and becoming narrower labially (Text-fig. 4E₂). The labial margin is rounded and perforated by a row of foramina. A mesiodistally elongate hump occupies the majority of the basolabial shelf with the labial margin abutting the base of the cusps. There is a slight decrease in height of the shelf towards the lingual margin.

DESCRIPTION: Distinctive teeth with symmetrical crowns that fan out mesiodistally and comprise three main cusps and three to four pairs of lateral cusps (Text-fig. 4D–E). The medial cusps are broken in both specimens, however the bases are approximately half the width of the lateral cusps. A pair of small, first lateral cusplets are independent of the medial cusp but are fused at the base with the second lateral cusplets which are slightly smaller in size than the lateral cusps. In one holotype (WAM 14.7.1, Text-fig. 4E) a small fourth cusplet is present and erupts from the base of the lateral cusp. The preserved cusps appear ovoid in cross section (elongate labio-lingually), at the base and exhibit smooth lingual and labial faces with well-developed lateral carinae. No discernible crown-base interface is present on the labial faces of the teeth. The base is highly arched (Text-fig. 4E₁), approximately twice as long mesiodistally as it is labiolingually (Text-fig. 4E₂). A roughly trapezoid to almost rectangular shape of the base can be determined, with rounded lingual corners. A row of foramina is present running along the lingual rim. An ovoid button is positioned centrally on the base extending between the third lateral cusplets

and gradually dissipates towards the lingual margin of the base. The labial face of the button preserves the openings to a row of canals and terminates abruptly, close to the base of the crown.

REMARKS: The teeth of the type specimen *Diademodus hydei* Harris, 1951 are partially obscured in matrix thus similarities to the genus are based on the visible labial tooth face of *Diademodus hydei* as well as comparison to the other member of this genus, *Diademodus utahensis* Ginter, 2008. The teeth of *Diademodus* all share the typical phoebodont tooth crown but can be differentiated on the number of intermediate cusplets (Ginter 2008). The cusp arrangement and variation in cusplet size present in *D. dominicus* sp. nov. (Text-fig. 4E) is similar to *D. utahensis* (Ginter 2008, fig. 1B) and differs from the original description of *D. hydei* which was figured having two prominent central cusps and intermediate cusplets of almost equal size (Harris 1951, fig. 3b), however, reinterpreted by Ginter (2008) as possessing a single prominent central cusp. The teeth of *D. dominicus* sp. nov. are further distinguished as some cusplets are fused at the base with the adjacent cusp or cusplets, a feature not apparent in *D. hydei* or *D. utahensis*. The lingual face of teeth from *D. dominicus* sp. nov. most closely resemble those of *D. hydei* as these teeth lack both the mesiodistal extension of the base beyond the crown as well as the presence of a basolabial shelf, features both present in *D. utahensis*. The tooth is distinguished from both *D. hydei* and *D. utahensis* by a shorter mesiodistal length of the base which is also significantly arched. The basal outline of *D. dominicus* sp. nov. narrows lingually and is substantially different from that of *D. utahensis* which forms a trapezoid shape becoming wider lingually and slightly compressed centrally on the lingual margin. The orolingual hump of *D. dominicus* sp. nov. is also far more prominent than that of *D. utahensis*. We believe these differences are significant enough for the establishment of the species *Diademodus dominicus* sp. nov.

Despite the low number of teeth recovered from *D. utahensis* and the obscured nature of teeth from *D. hydei*, heterodonty within each species is so far limited to variation in the number of intermediate cusplets, reported in *D. utahensis* (Ginter 2008) and *D. dominicus* sp. nov. Ginter (2008) suggests that anterior teeth of *D. utahensis* may be narrower and speculates they would be similar in form to teeth attributed to *Ph. fastigatus* (in Ginter 2008, fig. 3B). This would appear more likely than the teeth of *D. dominicus* sp. nov. representing anterior *D. utahensis* teeth as the base and cusp morphology is far more similar between *D. utahensis* and the *Ph. fastigatus* tooth examples.

Order Symmoriida Zangerl, 1981
 Family Stethacanthidae Lund, 1974
 Genus *Stethacanthus* Newberry, 1889

TYPE SPECIES: *Physonemus altonensis* St. John and Worthen, 1875.

Stethacanthus sp. 1
 (Text-fig. 4F–G)

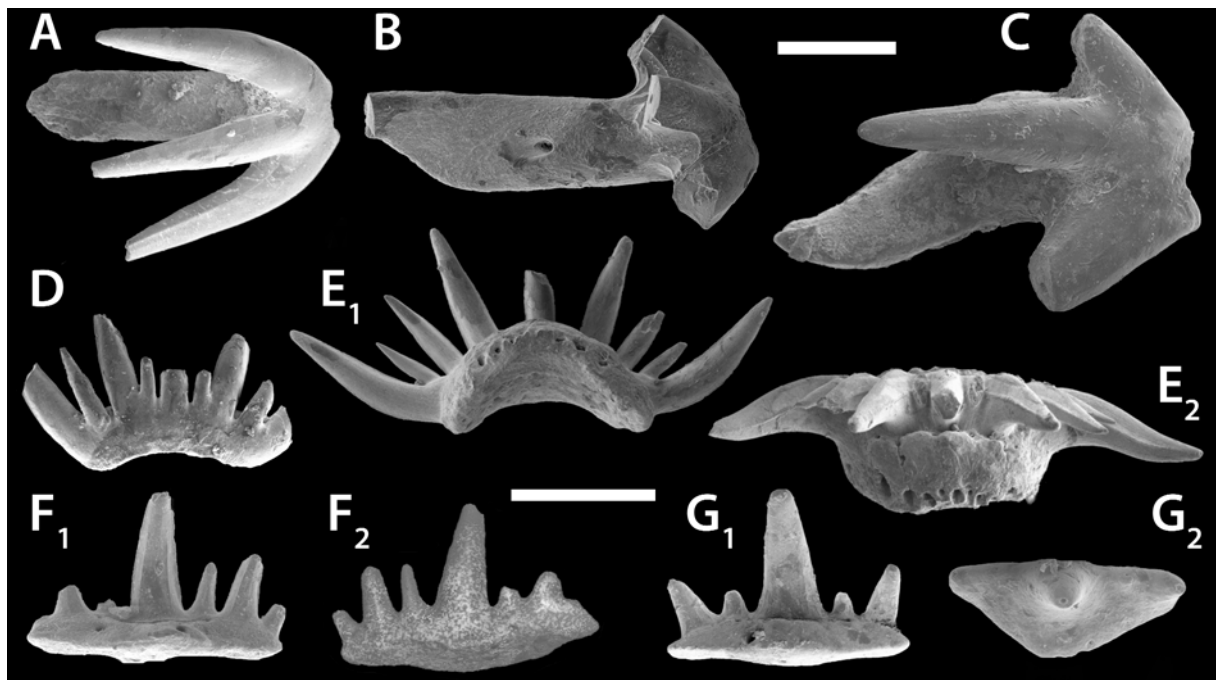
MATERIAL: One tooth from the Virgin Hills Formation, Casey Falls, sample CL-471; one tooth from the Bugle Gap Limestone, Casey Falls, sample 1984-97.

DESCRIPTION: Small teeth, less than 1 mm mesiodistally and consisting of a slender prominent central cusp and two smaller, slightly diverging lateral cusps approximately one third of the size of the medial cusp (Text-fig. F–G₁). A pair of small intermediate cusplets is present with one specimen possessing a second pair of cusplets on the distal side of the lateral cusps (Text-fig. 4F_{1–2}). Thin vertical striations extend from the base to tip on the lateral and intermediate cusps on the well preserved cusps. The base forms a distinct triangular outline (Text-fig. G₂), extending beyond the crown mesio-distally with rounded edges and a low profile. The apex of the lingual projection on the base is slightly

thickened and possesses multiple foramina along the lingual rim.

REMARKS: The teeth described here possess characters found in other stethacanthid tooth types including upright, unconnected cusps ornamented in sub-parallel cristae and a base lacking a labial depression. The triangular shaped lingual extension of the base (Text-fig. 4G₂) is a common feature of Moroccan stethacanthid teeth (Ginter *et al.* 2002, pl. 10C) and also seen in other Famennian teeth from the Montagne Noire (Ginter 2000, fig 7C) and Dalmeh, Iran (Long and Hairapetian 2000, fig 4I). The teeth from the Canning Basin also appear to exhibit a thickening around the lingual apex of the base, which is similar to a tooth from Dalmeh, Iran (Long and Hairapetian 2000, fig. 4e) but lack a well-formed labial boss. One tooth variant (WAM 14.7.26, Text-fig. 4F) exhibits a sixth cusp, a feature not usually found in Famennian stethacanthid teeth from Morocco and Iran (Ginter *et al.* 2002). Further specimens are required to determine if this tooth represents a non-typical variant of *Stethacanthus* sp. 1 or if there is a degree of heterodonty within this species.

Order Ctenacanthiformes Glikman, 1964
 Family Ctenacanthidae Dean, 1909
 Genus *Cladoides* Maisey, 2001



Text-fig. 4. Shark teeth from the middle Famennian at Casey Falls (A–C, F–G) and Upper Frasnian at Horse Spring (D–E). A–C, *Thrinacodus tranquilus* in occlusal view. A – WAM 14.7.15, sample 1984-97; B – WAM 14.7.16, sample 1984-97; C – WAM 14.7.29, sample 1984-98. D–E, *Diademodus dominicus* sp. nov. teeth, sample VHS-310. D – WAM 14.7.2, in lingual view; E – WAM 14.7.1, holotype, in lingual and occlusal views; F–G – *Stethacanthus* sp. 1. F – WAM 14.7.26, sample CL-471, in lingual and labial views; G – WAM 14.7.27, sample 1984-98 in lingual and occlusal views. A–E, scale bar = 0.5 mm; F–G, scale bar = 0.5 mm

Cladodoides wildungensis Jaekel, 1921
(Text-fig. 5A)

1921. *Cladodoides wildungensis* sp. nov.: Jaekel, 1921.
1991. *Stethacanthus* sp.; Ginter, p. 75, pl. 8: 4, pl. 9: 2, 3.
1992. *Cladodus* cf. *C. thomasi* Turner; Ivanov *et al.*, p. 89, pl. 36: 3, 4.
1992. *Stethacanthus thomasi* Turner [sic]; Derycke, p. 39–40, fig. 14, pl. 2: 10, 11.
1995b. *Stethacanthus* cf. *thomasi* Turner; Ginter, fig. 2A.
1996. “symmoriid with button partially divided”; Ginter and Ivanov, fig. 4C.
1996. “stethacanthid?”; Ginter and Ivanov, fig. 5C, D.
2000. *Stethacanthus* cf. *thomasi* (Turner); Ginter and Ivanov, pl. 1: J.
2002. *Stethacanthus resistens* sp. nov.; Ginter *et al.*, figs 2, 3, 4C–I, 5C.
2010. *Cladodoides wildungensis* Jaekel; Ginter *et al.*, fig. 66A–J.

MATERIAL: Two teeth from the Virgin Hills Formation, Horse Spring, sample VHS-310; Casey Falls, sample CI-9.

DESCRIPTION: Symmetrical teeth with five lingually inclined and strongly diverging cusps. The central cusp is large, almost twice the width at the base of the lateral cusps (Text-fig. 5A₁). The intermediate cusps are significantly smaller, approximately half the height of the lateral cusps. Both the lingual and labial faces of the cusps are ornamented with sub parallel ridges. The base is ovoid in outline, slightly arched and elongated mesiodistally, extending beyond the crown. A small basiolabial projection is preserved on one tooth (Text-fig. 5A₂₋₃), between the distal edges of the medial cusp. Due to abrasion, only the remnants of a mesiodistally elongate button are preserved on both teeth. One tooth (Text-fig. 5A₁) preserves an outline of a button, extending the distance between the two intermediate cusps, as well as a series of grooves, presumably once pore canals running labiolingually.

REMARKS: Ginter *et al.* (2010) recognises two morphotypes of *Cladodoides wildungensis* Jaekel (1921). The first morphotype, characterised by its larger size and long, slender medial cusp; and the second smaller morphotype, to which the Canning Basin teeth are here assigned, that are less than two mm across the length of the base with diverging cusps ornamented in coarse sub-parallel cristae. The teeth described here are markedly similar to the holotype of *C. wildungensis* (figured in Ginter *et al.* 2010, fig. 66I) as well as resembling teeth from Poland (Ginter *et al.* 2002, fig. 2C–

F) designated *Stethacanthus resistens*. Ginter *et al.* (2010) suggests that it is possible that some, if not all teeth previously attributed to *Stethacanthus resistens* belong to the *C. wildungensis*. If so, it appears *C. wildungensis* is considerably cosmopolitan in nature.

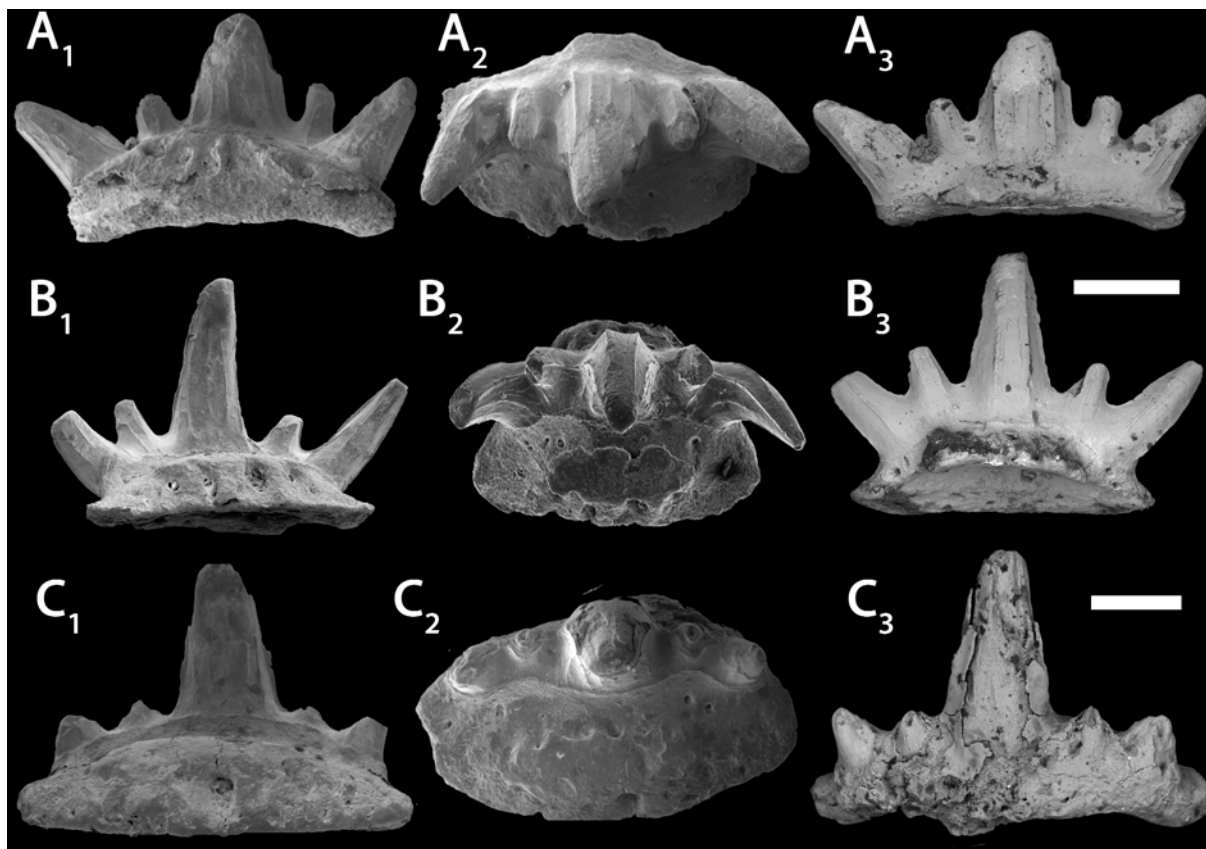
DISTRIBUTION AND STRATIGRAPHIC RANGE: This species ranges from MN 11 CZ– lower *crepida* in the Canning Basin, Western Australia. Due to a degree of synonymy with *S. cf. thomasi* a definitive range is difficult to ascertain, however a range from the Upper Frasnian – middle Famennian is likely in Poland, Moravia, Germany, Morocco and Russia.

Ctenacanthiform gen. et sp. indet 1
(Text-fig. 5B)

MATERIAL: One tooth from the Napier Formation, South Oscar Range, sample SO-200.

DESCRIPTION: This highly symmetrical tooth is well preserved, by comparison to other teeth in the sample, and possesses five slender, lingually inclined cusps that fan out mesio distally (Text-fig. 5B₁₋₂). A large prominent central cusp is flanked by two smaller intermediate cusps. The lateral cusps are approximately two thirds the length of the medial cusp and diverge at approximately 45 degrees to the medial cusp. In labial view, the cusps appear more triangular and connected at the bases (Text-fig. 5B₃). All cusps are ovoid in cross section and ornamented on both the lingual and labial faces with strong vertical striations. The base is trapezoid in shape extending further lingually than labially and broadest along the lingual margin (Text-fig. 5B₂). The base is thickest in a trapezoid area between the labial edge of the lingual button and lateral cusps. A thin baso-labial projection is present with a row of foramina. A well developed, ovoid shaped button is positioned close to the lingual border and perforated by a row of four large foramina (Text-fig. 5B₁).

REMARKS: The tooth shares commonalities between many cladodont-like teeth outlined by Duffin and Ginter (2006). The connection of the tooth cusps by an enameloid or orthodentine layer (Text-fig. 5B₃) excludes this tooth from belonging to the symmoriids and stethacanthids. The tooth lacks a basiolabial depression as seen in *Cladodus* and *Ctenacanthus* and is thereby more similar to *Cladoides* which may also lack this feature. The baso-labial shelf is straight which is characteristic of *Cladoides* but is far more developed in Ctenacanthiforme gen. et sp. indet 1 and this pro-



Text-fig. 5. Ctenacanthiform teeth from the Famennian at Casey Falls (A) and South Oscar Range (B-C). A – *Cladoides wildungensis*, WAM 14.7.14, sample CL-9, in lingual, occlusal and labial views. B – Ctenacanthiform gen. et. sp. indet 1, WAM 14.7.19, sample SO-200, in lingual, occlusal and labial views; C – Ctenacanthiform gen. et. sp. indet 2, WAM 14.7.20, sample SO-200, lingual, occlusal and labial views. A–B, scale bar = 0.5 mm; C, scale bar 1 mm

jection may obscure the presence of any basolabial depression. The tooth is differentiated from other Ctenacanthiformes based on the strongly rounded or bi-convex central cusp and lateral cusps, which are almost two thirds the size of the central cusps. The tooth is referred to the Ctenacanthiformes, perhaps temporally, based on the orthodontine or enameloid connective tissue present between the cusps and similarities with the genus *Cladoides*.

Ctenacanthiform gen. et sp. indet 2
(Text-fig. 5C)

MATERIAL: One tooth from the Virgin Hills Formation, Casey Falls, sample 1984-97; one tooth from the Napier Formation, South Oscar Range, sample SO-200.

DESCRIPTION: Heavily abraded teeth with a large medial cusp flanked by four smaller triangular shaped cusps consisting of a pair of small lateral cusps and a

pair of intermediate cusplets approximately half the size of the lateral cusps (Text-fig. 5C₁₋₂). The medial cusp is inclined slightly and convex along the lingual edge in cross section. Where the outer enameloid is preserved on the central cusp, faint vertical striations can be observed. The intermediate and lateral cusps do not show any ornamentation with the lateral cusps diverging at a 45 degree angle. A distinct rim is preserved on the labial face of the teeth and marks the crown base interface (Text-fig. 5C₁₋₂). The base extends lingually almost three times the width of the crown and forms a large dome shape that extends beyond the crown mesiodistally (Text-fig. 5A₂). A very faint ovoid button, approximately twice as long as it is wide, is preserved on one specimen and positioned closer to the lingual margin than the crown (Text-fig. 5A₂). A series of foramina perforate the lingual face of the base with a single large nutritive canal positioned centrally along the lingual margin. The labial face of the base in both specimens is highly abraded (Text-fig. 5A₃), however remnants of a thickened baso-labial shelf and slight depression are present.

REMARKS: These teeth have been attributed to the Ctenacanthiformes based on features shared with other members of this group. The prominent central cusp and diminished lateral and intermediate cusps are similar to *Cladodus conicus* Agassiz, 1843 although the base on the tooth from the Canning Basin specimens is much thicker and the striations preserved on the cusps are coarser. The central cusp is flattened along the labial face and exhibits a convex lingual face, and in this respect closely resembles *Cladodus*. The significant abrasion to the labial faces of the teeth does not allow further taxonomic refinement. The teeth do feature a unique rim running across the crown base interface that is not typically seen in other cladodont type teeth.

DISTRIBUTION AND STRATIGRAPHIC RANGE: Frasnian conodont Zone 13b to Late *marginifera* conodont Zone in the Canning Basin, Western Australia.

Cohort Euselachii Hay, 1902
Order indet.
Family *Protacrontidae* Zangerl, 1981
Genus *Protacrodus* Jaekel, 1925

TYPE SPECIES: *Protacrodus vetustus* Jaekel, 1925

Protacrodus serra Ginter, Hairapetian and Klug, 2002
(Text-fig. 6A–B)

1990. “*Cladodus*” sp.; Ginter, p. 77, pl. 4, fig. 9.
2000. *Protacrodus* cf. *vetustus* Jaekel; Ginter, p. 378–379, fig. 8.
2002. *Protacrodus serra*, sp. nov.; Ginter, Hairapetian and Klug, p. 195, text-fig. 11; pl. 2, figs L–N; pl. 11, figs. A–C.
2007. *Protacrodus serra* Ginter, Hairapetian and Klug, 2002; Gillis and Donoghue, p. 40, fig. d–e.
2007. *Protacrodus* cf. *serra* Ginter, Hairapetian and Klug, 2002; Ginter and Sun, p. 711, 4C.
2010. *Protacrodus serra* Ginter, Hairapetian and Klug, 2002; Ginter *et al.*, p. 87, fig. 80A–C.
2011. *Protacrodus serra* Ginter, Hairapetian and Klug, 2002; Ginter *et al.*, p. 168, fig. 10I–J.

MATERIAL: Two teeth from the Bugle Gap Limestone, Casey Falls, samples 1983–94; 1984–97.

DESCRIPTION: The teeth described here can be assigned to morphotype one of *Protacrodus serra* (Ginter *et al.* 2002, text-fig. 11 C–E) and comprise asymmetrical crowns with three cusps directed distally to one

side (Text-fig. 6A). The medial cusp is large, over twice the size of the lateral cusps with a narrow labiolingual profile. Both the lingual and labial faces of the cusps are ornamented in strong cristae. In one specimen (WAM 14.7.23, Text-fig. 6B), a row of small pointed cusplets is present along the crown base interface on the labial face. The base is narrow lingually, with a slightly extended and straight lingual rim (Text-fig. 6B) that is perforated by a large canal located centrally. The labial face of the base does not protrude and is perforated by a row of small foramina (Text-fig. 6A₂).

REMARKS: Evaluating variation present in the teeth of different shark taxa is difficult as odontological studies remain incomplete (Straube *et al.* 2008). The presence of labial cusplets (Text-fig. 6B) on *P. serra* may be evidence of intraspecific variation or the presence of sexually based heterodonty which is seen in the dentition of some fossil (Parmley and Cicimurri 2003) and extant shark species (Raschi *et al.* 1982). The same labial cusplets are apparent in other teeth attributed to *P. serra* from Iran (Ginter *et al.* 2002, pl. 2L–M; Ginter *et al.* 2011, text-fig 10I–J), which rules out regional influences for variation. Cusplets also appear on teeth independent of size (Text-fig. 6A–B) and morphotype (Ginter *et al.* 2002, pl. 2L–M) which makes ontogenetic variation unlikely.

DISTRIBUTION AND STRATIGRAPHIC RANGE: This species has an older occurrence in the Canning Basin, Western Australia (Lower *crepida* to Upper *marginifera* Zone) as compared to other areas of the world where it occurs in the Early *expansa* Zone in Dalmeh, Iran, Late *expansa* Zone, Tizi and Oum El Jerane, Morocco and probable *expansa* Zone Khor Virap, Armenia. In China this species has been recorded from the middle Tournaisian. Another protacrodont species, *D. masureae* (Burrow *et al.* 2010) is known to range from the Late Devonian into the Carboniferous.

Genus *Deihim* Ginter, Hairapetian and Klug, 2002

TYPE SPECIES: *Deihim masureae* Ginter, Hairapetian and Klug, 2002

Deihim masureae Ginter, Hairapetian and Klug,
2002
(Text-fig. 6C–D)

2000. ?*Protacrodus* sp. Long and Hairapetian, p. 217–218, fig. 40.

2000. *Protacroodus* sp. cf. "*P. aequalis*" sensu Ginter and Turner; Yazdi and Turner, p. 226, figs 3.4–7, 4.4.
2002. *Deihim mansureae* gen. et sp. nov.; Ginter, Hairapetian and Klug, p. 191–193, text-fig. 10; pl. 1, fig. r; pl. 2, fig. k; pl. 4, figs F–G, J–M; pl. 5, figs A–M.
2005. Polycrodontidae *insertae sedis* Derycke-Khatir, p. 76, pl. VII, figs 7–10.
2005. *Bobbodus* sp. Derycke-Khatir, p. 95–96, pl. XII, figs 1–2.
2009. *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; Hairapetian and Ginter, p. 176, 179, fig. 2D, 4H.
2010. *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; Hairapetian and Ginter, p. 362, fig. 3A.
2010. *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; Ginter *et al.*, p. 88, fig. 81A–J.
2011. *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; Ginter *et al.*, p. 166, 169, 8A–E, 11C.
2011. *Deihim mansureae* Ginter, Hairapetian and Klug; Ivanov and Lucas, p. 60, fig. 8.
2013. *Deihim mansureae* Ginter, Hairapetian and Klug; Habibi *et al.*, p. 30, fig. 4.

MATERIAL: One tooth from the Virgin Hills Formation, Casey Falls, sample CL-471 and seven teeth from the Bugle Gap Limestone, samples 1984-96, 1984-97, 1984-98.

DESCRIPTION: Four morphotypes were originally assigned to the species *Deihim mansureae* Ginter *et al.* 2002, of which, two are represented here (Text-fig. C–D). A single tooth attributed to morphotype one (Text-fig. D_{1–2}) appears to possess a significantly worn central and lateral cusps with only the base of the crown preserved. The base of a large main central cusp can be distinguished, flanked by two smaller highly fused lateral cusps. Cristae is present on the base of the lateral cusps on the lingual face. The labial face of the crown possesses three large, robust cusplets (Text-fig. 6D₂), immediately above the base. The crown-base interface on the lingual face is highly arched and defined by a shallow groove. The base is narrower, mesiodistally, than the crown and extends lingually with a series of deep canals.

Two teeth (Text-fig. 6C_{1–2}), assigned to morphotype four were recovered and are characterised by an elongate central cusp and two well-spaced diverging lateral cusps approximately a third of the size of the medial cusp. Sub-parallel cristae are present on both the labial and lingual faces of each cusp. Four cusplets are present above the crown-base interface on the labial face. The base is roughly ovoid in outline (Text-fig. 6C₂) and does not extend beyond the crown mesiodistally. The lingual face of the base forms an arch, protruding lingually and is perforated by a few foramina.

REMARKS: The teeth described here conform to the diagnosis of *D. mansureae* with the presence of a prominent central cusp and lateral cusps that bear strong cristae, on a convex crown-base interface. A row of labial cusplets present above the crown base interface is also characteristic of this species. The teeth assigned to morphotype four resemble those of Ginter *et al.* (2010, pl. 5 D–F) with the presence of a slender central cusp with two lateral cusps, approximately half the size of the central cusp and diverging at 45 degree angles. These teeth also appear less perforated by foramina on the lingual face of the base and lack the fusing of the central and lateral cusps that is seen in the other morphotypes of this species.

DISTRIBUTION AND STRATIGRAPHIC RANGE: *D. mansureae* ranges from the Late *marginifera* CZ to possibly the Tournaisian in the Canning Basin. An older occurrence of this species is known from the *rhenana* (MN 11 CZ) in Kale Sardar area of Iran (Hairapetian and Ginter 2010). In the Famennian of Iran and Armenia *D. mansureae* ranges into the Upper *crepida* conodont Zone. Teeth attributed to this species have also been found in the Sly Gap Formation, New Mexico, USA (Ivanov and Lucas 2011), however no concise age range beyond the Late Devonian and Early Carboniferous can be ascertained.

Deihim cf. mansureae Ginter, Hairapetian and Klug, 2002 (Text-fig. 6E)

MATERIAL: Two teeth from the Bugle Gap Limestone, Casey Falls, sample 1984-98.

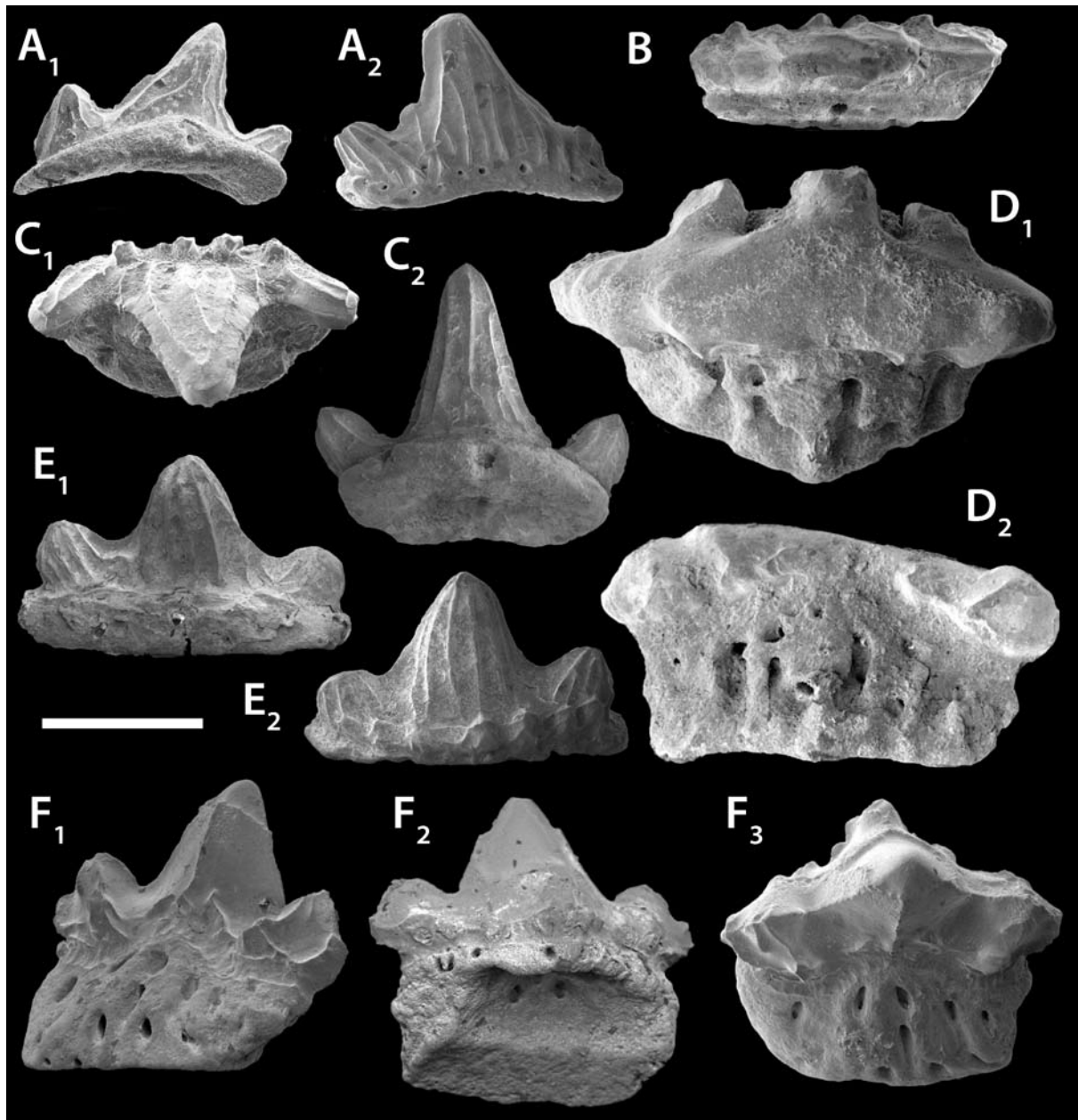
DESCRIPTION: Teeth with prominent central cusps and two smaller lateral cusps approximately one third the size of the medial cusp, diverging at approximate 45 degree angles (Text-fig. 6E₁). Each cusp is rounded with sub parallel striations on both the labial and lingual faces. A row of seven rounded cusplets, ornamented in strong cristae are present on the base of the crown along the labial face (Text-fig. 6E₂). The base is ovoid in outline, extending lingually and possessing a single small pore located centrally on the lingual rim. On the labial face the base is thin and forms an undulated contact with the crown.

REMARKS: These teeth are similar to the morphotype 1 of *Deihim mansureae* as they comprise a crown with a large central cusp with two strongly diverging lateral cusps, all ornamented in a strong cristae as well

as a row of lingual cusplets along the labial face of the tooth. The cusplets present on the teeth described here are unusual but bear a strong resemblance to the cusplets on a tooth from *D. mansureae* in central Iran (Hairapetian and Ginter 2009, figs 5H₂₋₃). Despite the similarities with *D. mansureae*, the tooth lacks both the arched lingual groove associated with the crown base interface as well as the series of deep pore canals on the lingual face diagnostic of this species (Ginter *et al.* 2002). These features are also lacking on a tooth

attributed to *Protacrodus* cf. *vetustus* from the Montagne Noire (Ginter 2000, fig. 8C). The Montagne Noire tooth shares the similar sub-parallel cristae to the teeth from the Canning Basin, however it lacks labial cusplets.

Deihim sp. 1
(Text-fig. 6F)



Text-fig. 6. Protacrodont teeth from Casey Falls. A-B – *Protacrodus serra*. A – WAM 14.7.21, sample 1984-97, in lingual and labial views; B – WAM 14.7.23, sample CL-471, in occlusal view; C-D – *Deihim mansureae*. C – WAM 14.7.25, sample 1984-98, in lingual and occlusal views; D – WAM 14.7.28, sample 1984-97, in lingual and occlusal views; E, *Deihim* cf. *mansureae*, WAM 14.7.24, sample 1984-98, in lingual and labial views; F, *Deihim* sp. 1, WAM 14.7.17, sample CL-471, in lingual, baso-labial and occlusal views. Scale bar 0.5 mm

MATERIAL: One tooth from Bugle Gap Limestone, Casey Falls, sample CL-471.

DESCRIPTION: A well preserved, almost symmetrical tooth with a prominent central cusp and two pairs of highly fused lateral cusplets (Text-fig. 6F₁). Cusps are ornamented on the lingual face in strong cristae along the base of the cusps with a single ridge running up the centre of the central cusp. A crown-base interface is prominent, marked by a groove on both the lingual and labial faces of the tooth (Text-fig. 6F₁). A triangular labial peg is positioned at the base of the central cusp with accompanying smaller projections on either side (Text-fig. 6F₂₋₃). The base is approximately the same height as the central cusp with a straight lingual edge and rounded distal margins. A series of foramina are present on the lingual face of the base in almost two rows, one slightly below the crown base interface and another close to the lingual rim (Text-fig. 6F₁). A large articulation socket is present on the basolabial face of the base (Text-fig. 6F₂).

REMARKS: The tooth described here comprises a large central cusp with diverging cusps ornamented in strong cristae which are diagnostic of the genus *Deihim* (Ginter *et al.* 2002). Further similarities include the presence of a crown base interface separating a lingually extended base perforated by a series of canals. Despite the similarities, *Deihim* sp. 1 comprises a central cusp which is more prominent than that found on morphotype 1 of *D. mansureae* and it also lacks the characteristic labial cusplets. Instead the tooth from the Canning Basin bears small tubercle-like projections above the crown base interface on the extended labial face of the crown. The general morphology of *Deihim* sp. 1 also bears a slight resemblance to *Protacrodus orientalis* Li, 1988 with the high central cusp, fused laterals and a labial projection of the central cusp (Li 1988, pl. 1, fig. 2), however the size difference in the cusps excludes this tooth from *P. orientalis* (Ginter *et al.* 2002). There is also a very strong resemblance to another tooth attributed to *P. orientalis* from the Menggongao Formation, South China (Lelièvre and Derycke 1998, fig. 7B) which is narrower mesiodistally with the same cusp morphology and deep base. Recently, the inclusion of *P. orientalis* as a species of *Protacrodus* has been questioned (Ginter *et al.* 2010). It is possible that *P. orientalis* belongs to the genus *Deihim* and the tooth from the Canning Basin represents a less abraded form of this species.

Protacrodontidae gen. sp. indet. 1
(Text-fig. 7A)

MATERIAL: One tooth from the Bugle Gap Limestone, Casey Falls, sample 1984–94.

DESCRIPTION: Highly elongate and slightly arched tooth comprising a prominent pyramidal central cusp accompanied by four to five fused lateral cusps approximately a quarter of the size of the central cusp (Text-fig. 7A₁). Both the labial and lingual faces of the cusps are ornamented in coarse wavy cristae directed towards the cusp apices. Approximately 80% of the lingual face of the base is broken, however the preserved section is the same height as the lateral cusps and extends both lingually and further mesiodistally than the crown on one side (Text-fig. 7A₂). A small number of foramina are present on the lingual face of the base. The labial margin of the base is thin and perforated by small foramina and lacks a distinct crown base interface (Text-fig. 7A₂).

REMARKS: The tooth is placed under Protacrodontidae based on the coarse cristae and lack of articulation devices also found in other Devonian Protacrodonts as well as its occurrence within the middle Devonian. The tooth is also similar to a partial tooth of a ?Protacrodontid (Ginter and Sun 2007, fig. 4E) from Muhua, southern China in that it shares the highly elongate shape, with extensively fused lateral cusps flanking a prominent central cusp and a well-developed cristae. However, the tooth described here lacks the festoon-like sculpture on the lower aspect of the crown present on the Chinese tooth (Ginter and Sun 2007).

?Protacrodontidae fam. gen. sp. indet.
(Text-fig. 7B)

MATERIAL: One tooth from the Bugle Gap Limestone, Casey Falls, sample CL-471.

DESCRIPTION: A mesio-distally elongate tooth with a crown consisting of highly fused cusps that are almost indistinguishable. Strong cristae are present on the labial and lingual faces as well as the occlusal surface (Text-fig. 7B₁₋₃). The labial face of the crown is higher and slopes lingually. The distal margins of the crown taper inward to the crown-base interface, whereas the labial and lingual faces are almost straight. The base is roughly rectangular in outline with a slightly thickened, protruding lingual margin. A row of pore canals are present along the lingual face of the base (Text-fig. 7B₂), where as possible remnants of canals are present on the labial face (Text-fig. 7B₃).

REMARKS: Teeth with coarse cristae, a reduced base lacking both a lingual extension and articulation devices are common among Devonian protacrodonts. The crown of the tooth described here, retains more highly fused cusps than other protacrodont teeth and in this respect it more closely resembles an orodont. The reduced base and lack of distinct margin between the crown and base along the labial margin appear similar to the lingual face of the teeth attributed to *P. serra* and *Protacrodus aequalis* Ivanov 1996. The samples taken above the section measured at Casey Falls are dominated by protacrodontid-type teeth (*Protacrodus serra*, *Deihim mansureae*, *D. cf. mansureae*, *Deihim* sp. 1, Protacrodontidae gen. et sp. indet.; Table 1), which could suggest it belongs to the family Protacrodontidae and is highly modified, possibly representing a lateral crushing tooth.

Order Hybodontiformes Cappetta,
Duffin and Zidek, 1993

Superfamily Hybodontoidea Owen, 1846
Family Lonchidiidae Herman, 1977
Genus *Lissodus* Brough, 1935

TYPE SPECIES: *Hybodus africanus* Bloom, 1909.

Lissodus lusavorichi Ginter,
Hairapetian and Grigoryan, 2011
(Text-fig. 7C)

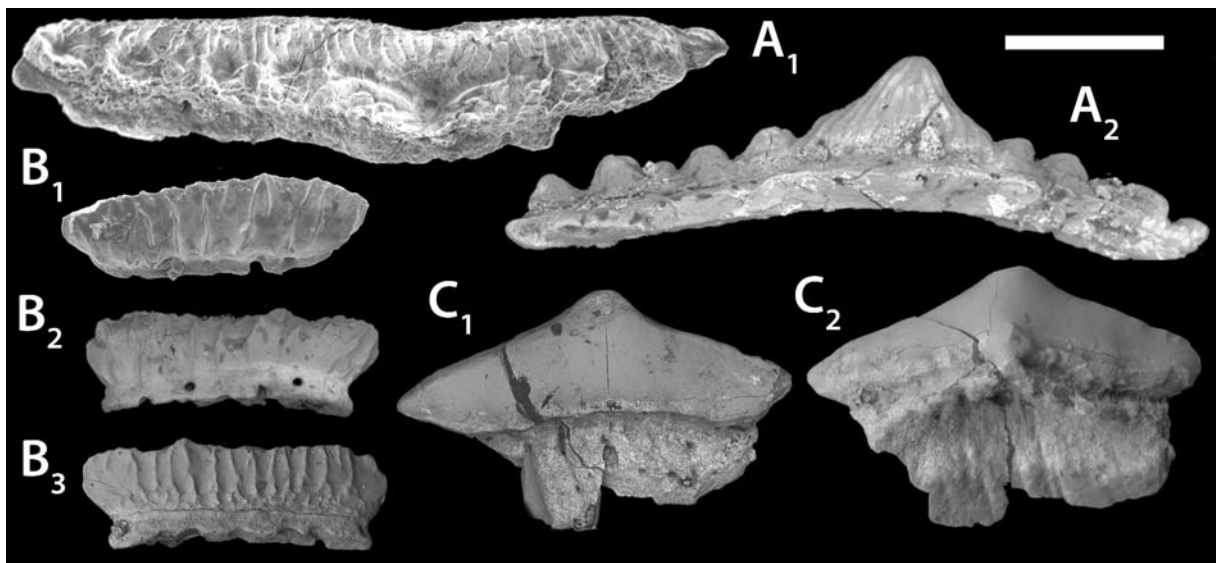
2011. *Lissodus lusavorichi* sp. nov. Ginter, Hairapetian and Grigoryan, p. 160, fig. 10E–F.

MATERIAL: Two teeth from the Virgin Hills Formation, Casey Falls, sample 1983-94.

DESCRIPTION: The tooth crown is broadly triangular with a well-developed occlusal crest (Text-fig. 7C₁). The crown extends laterally beyond the base terminating in triangular shoulders. The crown base interface is slightly arched on the lingual face and prominent on the labial face (Text-fig. 7C₂). A well-developed labial peg is present and accompanied by small cusplets or tubercle like projections. The base is typically euselachian, projecting lingually with a rounded margin. A series of deep, elongated canals perforate the lingual face of the base (Text-fig. 7C₁).

REMARKS: The teeth from Casey Falls are attributed to *Lissodus lusavorichi* Ginter *et al.* 2011, as they possess the same smooth broad triangular crown, well developed occlusal crest and horizontal longitudinal crown shoulders as well as the tubercles associated with the labial peg. The presence of this species represents the oldest record of the family Lonchidiidae in the Canning Basin.

DISTRIBUTION AND STRATIGRAPHIC RANGE: The species has been previously described from the *expansa* zone in Dalmeš, Iran and probable *expansa* zone, Khor Virap Armenia. Its presence in the Upper *marginifera* conodont Zone in the Canning Basin, refines the lower age range of this species.



Text-fig. 7. Shark teeth from the Casey Falls. A – Protacrodontidae gen. et sp. indet 1, WAM 14.7.22, sample 1984-94, in occlusal and labial views; B – ?Protacrodontidae gen. et sp. indet WAM 14.7.31, 1984-98, in occlusal, lingual and labial views; C – *Lissodus lusavorichi*, WAM 14.7.30, sample 1984-98, in labial and lingual views. Scale bar 0.5 mm

DISCUSSION

Biostratigraphy

Thelodonts have been successfully used in biostratigraphy since the 1960's (Gross 1967) with current global zonation schemes (in Gradstein *et al.* 2012) developed for the Silurian (Turner 1973; Bassett *et al.* 1982; Märss *et al.* 1995; Blom 1999; Tali-maa 2000) and Devonian, (Turner 1995a, 1999; Blom and Goujet 2002; Hairapetian *et al.*, in press). Subsequent to the Givetian–Frasnian boundary, thelodonts are restricted to the margins of northern Gondwana (Turner 1997; Trinajstic 2001; Märss *et al.* 2007) and there is a marked reduction in diversity with the Turinidae Family represented by the species *Australolepis seddoni* (Seddon 1969; Turner and Dring 1981; Trinajstic and George 2009), *Turinia hutkensis* (Blicek and Goujet 1978; Hairapetian *et al.* 2006) and a new genus and species of turiniid (Hairapetian *et al.*, in press). Of these, *A. seddoni* has been particularly useful in defining shallow water Frasnian strata in northern Gondwana (Turner *et al.* 2002). The species is known from the *falsiovalis* to *rhenana* conodont Zones (MN 1–10 CZ) in Iran and provided a lower Frasnian age constraint for the Chariseh section (Turner *et al.* 2002). Within Australia this species is now recognised as ranging from MN 6–11 CZ and has been previously used to constrain a Frasnian age for the base of the Gneudna Formation type section in the Carnarvon Basin (Turner and Dring 1981; Trinajstic and George 2009). Within the Canning Basin *A. seddoni* has been used to confirm a Frasnian age for the Hull platform (Chow *et al.* 2013). Although the increased range of *A. seddoni*, decreases the ability to obtain more finely resolved ages for strata, its confinement to the Frasnian still makes this species an important zone fossil.

The phoebodont taxa recovered in this study conform to previously established age ranges obtained for these species in the Canning Basin (Trinajstic and George 2009) with the exception of *Phoebodus latus* where the range has been extended from MN 10 CZ to MN 11 CZ. This newly extended range of *Ph. latus* in the Canning Basin brings it closer in line with the known upper age range for this species (MN 13 CZ) in the Southern Urals and South Timan in Russia as well as the Holy Cross Mountains in Poland (Ginter and Ivanov 1995b; Ivanov 1999; Ivanov and Lucas 2011). The extension of the known age ranges for *A. seddoni* and *Ph. latus* in the Canning Basin indicates further refinement of the age ranges for other phoebodont taxa such as *Ph. bifurcatus* and *Ph. fastigatus* is likely with

further collecting. Work so far undertaken describing the phoebodont fauna from the Canning Basin (Trinajstic and George 2009), has proven their utility in biostratigraphy as well as increasing the geographic distribution in which these species can be used.

A disappearance in phoebodont fauna is seen in the section at Horse Spring from MN 11 CZ and occurs too early to be attributed to the global Kellwasser Events. Despite the distinct anoxic black limestones and shales associated with the Kellwasser horizons not being recognised in the Canning Basin (Becker *et al.* 1993), perturbations are recorded in the faunas. Reductions in the species diversity and abundances are recorded within conodonts (Klapper 2007), ammonoids (Becker *et al.* 1993) and trilobites (Feist and McNamara 2013) in the Canning Basin which are also seen in the rest of the world. The absence of microvertebrates at Horse Spring above MN CZ 11 was previously noted by Trinajstic and George (2009) who suggested post depositional dolomitisation as the main factor contributing to the lack of microvertebrates. However, this does not seem to be the cause as microvertebrates are often recovered from dolomitised beds. In addition, conodonts were found in the dolomitised beds from 13–19 m (Text-fig. 2) in the section at Horse Spring where microvertebrate fossils were lacking. A global non-occurrence of the *Phoebodus bifurcatus* group from the *linguiformis* Zone (MN 13b CZ) in the Frasnian to the Famennian late *crepida* conodont Zone has been identified in the Northern Hemisphere (Ginter and Ivanov 1995b; Ginter *et al.* 2002). Ginter *et al.* (2002) suggests the disappearance mainly resulted from global cooling (Copper 1998) rather than fluctuations in sea level or anoxia. Given the much earlier disappearance of phoebodonts in the section at Horse Spring, and no evidence of major temperature excursions in sea surface temperatures during the MN 11 CZ (Joachimski *et al.* 2004), it is not likely temperature fluctuations are the reason for the disappearance of a phoebodont non-occurrence at Horse Spring.

Another notable global change recorded towards the end of the Frasnian is the *semichatovae* Transgression (Sandberg *et al.* 1997). This event occurs at the base of the MN 11 Zone and coincides with the absence of phoebodont taxa in the Canning Basin. Despite reported localised tectonic overprinting (Southgate *et al.* 1993; George and Chow 2002; Chow *et al.* 2013), evidence of a longer-term 2nd order transgressive event is observable in these sections. The effect of these localised and global events may be highly influential in the faunal changes and extinctions seen in the basin (George and Chow 2002). The phoebodont group has been previously noted as niche sensitive (Ginter

and Turner 1999), which may explain their apparent confinement to specific sites in the Canning Basin. Following any ecological disturbance within the Horse Spring area, a migration of phoebodont taxa may have occurred. In this scenario, the disappearance in MN 11 CZ would reflect a movement of these sharks rather than the extinction seen in other areas of the world, such as Poland at the *linguiformis* CZ (13b) (Ginter *et al.* 2002). It is important to note that a re-emergence of the phoebodont group in the Famennian is present along both the North and Eastern margins of Gondwana as well as Laurussia (Ginter and Turner 1999; Ginter and Ivanov 2000; Ginter *et al.* 2002). Interestingly, this re-emergence is not reflected in the studied sections here and could indicate the factor or factors influencing the non-occurrence of phoebodonts in the Canning Basin were potentially long lasting and perhaps localised. A collecting bias can also not be ignored as there have only been limited studies in the Canning Basin focusing on Frasnian microvertebrate faunas.

The current phoebodont based zonation established for the Famennian (Ginter and Ivanov 1995b; Gradstein *et al.* 2012) has not yet been correlated in the Canning Basin and this is partly due to the study of Famennian vertebrates being in its infancy. The sections described also do not encompass the open shelf environment where this scheme is most applicable (Ginter *et al.* 2002) and may account for the lack of *Phoebodus* teeth in the Famennian dated intervals. Despite a lack of *Phoebodus* species in the Bugle Gap Limestone, the recovered shark species exhibit comparable ages for the same species found in other areas of the world. Of these, *Thrinacodus tranquilus* has been recorded as occurring from the Middle to Late Devonian in Laurussia and North Gondwana (Ginter and Turner 2010). The presence of this species in the Canning Basin makes it one of the oldest global occurrences (Upper *marginifera* CZ) with similar ages recorded in Morocco, South China and Iran (Lelièvre and Derycke 1998; Hairapetian and Long 2000; Ginter *et al.* 2002). The oldest report of the protacrodont *Deihim mansureae* is from the Late Frasnian, *rhenana* (MN 11 CZ) in Kale Sardar area of Iran (Hairapetian and Ginter 2010). This species is far more wide spread in the Famennian, extending from the east of Laurussia (Ivanov and Lucas 2011) to the north-west of Gondwana. An Upper *crepida* conodont Zone is recorded as the upper range of *D. mansureae* in both Iran and Armenia. In the Canning Basin, Australia the range extends further, from Upper *marginifera* CZ, into the lower Tournaisian (Burrow *et al.* 2010). Two other shallow water shark species, *Protacrodus serra*

and *Lissodus lusavorichi*, been recorded from the *expansa* CZ of the Khor Virap region in Armenia and Dalmeh in Iran (Ginter *et al.* 2011). The presence of both *P. serra* and *L. lusavorichi* in the Canning Basin extends the lower age range of these species from the *expansa* conodont Zone to Upper *marginifera*. Like *D. mansureae*, an increased Famennian distribution of *Th. tranquilus*, *L. lusavorichi* and *P. serra* in Northern Gondwana is established. The presence of small, shallow water genera such as *Deihim*, *Lissodus* and *Protacrodus* across the margins of North Gondwana, would support the presence of a continuous shallow platform and reef environmental (Golonka 2007) suitable for faunal exchange.

Biogeography and chondrichthyan assemblages

Chondrichthyan biofacies present in the depauperate Famennian intervals of the Virgin Hills and Napier formations are often difficult to determine. These intervals often comprise largely shallow water and slope derived material. This results in the microvertebrate remains often not representing an original environment of habitation. In contrast to the described sections, samples taken from the shallow fore-reef deposits of the Bugle Gap Limestone (Guppy *et al.* 1958; Playford and Lowry 1966; Playford *et al.* 2009) preserve a more original chondrichthyan biofacies. A diverse shark genera including *Thrinacodus*, *Stethacanthus*, *Protacrodus*, *Deihim* and *Lissodus* were present in these shallow water facies. Despite the low numbers of teeth recovered from the Bugle Gap Limestone, the proportionally higher number of protacrodont and hybodont type sharks as well as the absence of *Phoebodus* and *Jalodus*, is indicative of a shallow water *Protacrodus* biofacies (Ginter 2000, 2001). Similar assemblages have also been recorded in Famennian strata from both Dalmeh and Chahriseh, Iran (Ginter *et al.* 2002; Hairapetian and Ginter 2010).

An increase in cosmopolitanism is seen in many Late Devonian marine groups, including brachiopods (Copper 1998), ammonoids (House 1973), trilobites (McNamara and Feist 2006), crustaceans (Rode and Lieberman 2005), conodonts (Girard *et al.* 2010) and fish (Ginter and Turner 1999; Burrow *et al.* 2010). This faunal exchange between areas was likely driven by the closure of the Rheic Ocean (Nance *et al.* 2012; Domeier and Torsvik 2014) during the Late Devonian, culminating in an increased proximity of Laurussia and Gondwana (Young 2003; Burrow *et al.* 2010; Young *et al.* 2010). This period also saw the rifting of the Palaeotethys resulting in a separation of the north

China, Indochina, Tarim and South China blocks from Gondwana (Metcalf 1984, 2011). Connections between South China and north-west Australia were maintained in the Late Devonian by the occurrence of an extensive, shallow water shelf (Golonka 2007; Metcalfe 2011; Golonka and Gaweda 2012). Previous work on Late Devonian conodonts (Burrett *et al.* 1990; Girard *et al.* 2010) and fish (Long 1993) support a close relationship between the two areas. In addition, Trinajstić and George (2009) had previously shown close affinities, in regards to the temporal ranges, of the Frasnian phoebodonts *Ph. fastigatus* and *Ph. bifurcatus* in the Canning Basin and South China. The presence of a likely shallow water taxon, *Deihim* sp.1 (Text-fig. 6G₁₋₃) in both the Canning Basin and Menggongao Formation of South China (Lelièvre and Derycke 1998, fig. 7B), would support the presence of a shallow water platform between the two areas into the middle part of the Famennian. Determining the extent of faunal exchange further into the Famennian or even Carboniferous is difficult, as studies into shark faunas of these ages are limited for the north west of Australia. However *Th. ferox* has been reported in the late Famennian in both South China and Australia (Long and Burrett 1989). The similarities between the tooth identified here as Protacrodontidae sp. 1 (Text-fig. 7A₁₋₂) found in a middle Famennian of the Virgin Hills Formation and a tooth from the middle Tournaisian in Muhua, South China (Ginter and Sun 2007, fig. E₁₋₂) provides further support for a close connection between China and Australia (Metcalf 2001) however, further data from microvertebrates are required.

Clear links between the shark taxa in the north-west of Australia and other parts of Laurussia, South China and Northern areas of Gondwana are demonstrated here. Despite the similarities, there is also a degree of endemism amongst some of the shark species present in the Canning Basin. This is not unusual as endemism in some conodont (Klapper 1995, 2007) and many placoderm (Long 2006) species has also been noted. Of the Frasnian taxa *Diademodus dominicus* sp. nov. had not been previously recorded outside of Laurussia. The presence of this species along the eastern margins of North Gondwana would also suggest a greater distribution of this genus than previously recognised. Of the other phoebodonts, *Phoebodus* tooth forms found in the Horse Spring section often possess unusual features. These include the tricuspid form of *Ph. bifurcatus* which appear relatively common in the Canning Basin but rare in other areas of the world. The teeth of *Ph. fastigatus* also differ from the diagnostic smooth cusps, often possessing cusps with heavy ornament on

the labial face. In addition to the Frasnian taxa, there are two types of ctenacanthiform and a species of *Stethacanthus* that have not been found anywhere else. Despite an increased cosmopolitanism in Devonian shark faunas, a considerable endemic component is present in the Canning Basin. The mechanisms for this are difficult to determine and may be the result of lack of sampling, although unique palaeoenvironmental conditions or environmental niches might have existed in this part of East Gondwana (north-western Australia) at this time.

CONCLUSIONS

A largely undescribed chondrichthyan fauna ranging in age from MN 11 CZ in the late Frasnian to the late *marginifera* Zone in the middle Famennian was recorded from the Virgin Hills Formation, and the Bugle Gap Limestone, and Napier Formation in the Canning Basin. The section at Horse Springs reveals a similar diversity of phoebodonts to that previously described by Trinajstić and George (2009). A new species of diademodont, *Diademodus dominicus* sp. nov., a genus which until now had only previously been described from Laurussia was recovered from the phoebodont-rich beds. This species, in addition to variation in *Phoebodus fastigatus*, as well as newly described cladodont and stethacanthid teeth, reveals a potentially endemic Frasnian component to the Canning Basin.

The Famennian Bugle Gap limestone and uppermost beds of the section at Casey Falls reveals a diverse shark fauna that had not been previously described from the Canning Basin. Many of these, including *Th. tranquilus*, *C. wildungensis*, *P. serra*, *D. mansureae* and *L. lusavorichi*, represent ages similar to or the same as those previously described for these species. The presence of this shark fauna in the Canning Basin also allows for a more comprehensive understanding of species distribution in the Famennian. A number of genera including *Phoebodus* and *Protocrodus* occur in both eastern Australia and Western Australia (Turner and Young 2000), however, these new reports on chondrichthyans from the Canning Basin indicate stronger faunal links between the Canning Basin and other areas of Gondwana such as Iran and Morocco as well as Poland and the United States of America in Laurussia. In addition, faunal similarities between South China and the Canning Basin are present, with some shark species indicating potential faunal exchange extending into the Late Famennian and possible Early Carboniferous.

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