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Orthacanthus platypternus (Cope, 1883) (Chondrichthyes: Xenacanthiformes) teeth and other isolated vertebrate remains from a single horizon in the early Permian (Artinskian) Craddock Bonebed, lower Clear Fork Group, Baylor County, Texas, USA

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ABSTRACT:

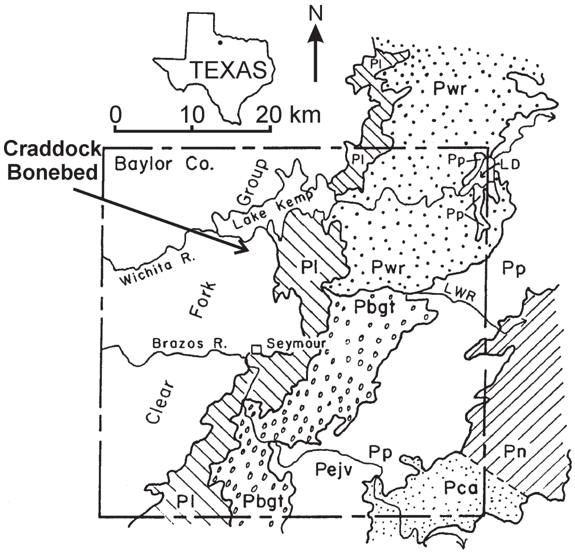
Johnson, G.D. 2018. *Orthacanthus platypternus* (Cope, 1883) (Chondrichthyes: Xenacanthiformes) teeth and other isolated vertebrate remains from a single horizon in the early Permian (Artinskian) Craddock Bonebed, lower Clear Fork Group, Baylor County, Texas, USA. *Acta Geologica Polonica*, **68** (3), 421–436. Warszawa.

An unusual 6–8 cm layer of prismatic cartilage and matrix containing some 8,800 teeth, coprolites, incomplete occipital spines, and denticles of *Orthacanthus platypternus* (Cope, 1883) occurs in the lower Permian (Artinskian) Craddock Bonebed in Texas, USA. It is the only species of shark present in the Clear Fork Group except for three worn *Xenacanthus* Beyrich, 1848 occipital spine fragments and two teeth of ?*Lissodus* (*Polyacrodus*) *zideki* (Johnson, 1981) (Hybodontoidei), both being the first occurrences in this unit. Analysis of measurements of teeth with complete bases randomly selected from 3,050 initially available teeth failed to reveal the presence of sexual dimorphism or the discrete presence of juveniles as expected, based on an independent study which identified the presence of *Orthacanthus* juvenile occipital spines. A few highly symmetrical small teeth are present, which had not been previously observed in the Texas lower Permian. They may be symphyseals and restricted only to juveniles. Other unusual teeth include germinal teeth and deformed teeth, both of which occur in the Clear Fork and underlying Wichita groups. One tooth displays an apparent example of the equivalent of an “enamel pearl” on one of its cusps. The most unusual teeth are those that appear to have undergone various stages of resorption. Only the lingual margin of the base is affected in which the apical button is resorbed to varying degrees until only the labial margin with the basal tubercle and the three cusps are all that remain. If the teeth were undergoing resorption, then the perplexing problem is why the apical button is resorbed and not the superjacent basal tubercle. Other vertebrate remains include palaeoniscoid scales and teeth and unidentified tetrapod bone fragments, jaw fragments, and teeth. Rare fragments of bones (scales?) bear a “comb edge” which have not been previously observed in the Texas lower Permian.

Key words: *Orthacanthus platypternus*; Early Permian; Craddock Bonebed; Texas.

INTRODUCTION

The Craddock Bonebed is best known for its wealth of amphibian and reptilian remains (Bakker *et al.* 2015). It is located in the lower Clear Fork Group south of Lake Kemp in north-central Baylor County, Texas, USA (Text-fig. 1; a complete stratigraphic section is given in Johnson 2013; see also Beck *et*



Text-fig. 1. Location of the Craddock Bonebed, Texas, USA. The formations below (east of) the Clear Fork Group (undifferentiated) occur in the underlying Wichita Group (Hentz 1988)

al. 2016). A bed of unknown size containing shark prismatic cartilage, which is mostly disseminated in reddish-brown calcareous mudstone that contains xenacanthid teeth and occipital spine fragments, as well as isolated vertebrate remains of other taxa, near the top of the Bonebed. About two square meters of this 6–8 cm thick bed was excavated in 1996 (Text-fig. 2). Intact pieces of cartilage represent unknown skeletal portions; none show evidence of palatoquadrate or meckelian cartilage with *in situ* teeth. This study represents a more comprehensive conclusion than given earlier by Johnson (2015a, b).

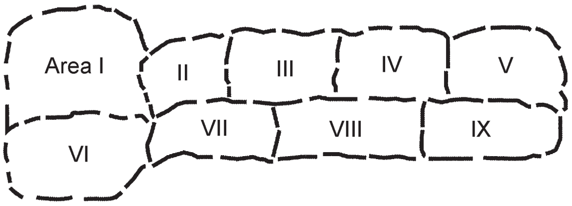
Williston (1911) reported the presence of two types of sharks in the Craddock Bonebed, on the basis of occipital spines, but did not mention teeth. A preliminary study by Donelan and Johnson (1997) of teeth recovered by bulk sampling suggested only one species of shark, *Orthacanthus platypternus* (Cope, 1883), is present. Analysis of the occipital spines by Donelan and Johnson (1997) suggested that juvenile spines (Text-fig. 3) predominated, and that the larger spines could be separated by gender. A much more complete analysis by Beck *et al.* (2015) supports this conclusion. The smallest teeth (≤1 mm in greatest dimension) resemble the larger teeth and are unlike those described by Zidek (1993). Murry and Johnson (1987) reported only *O. platypternus* from the Clear Fork Group except at the base where one other xenacanthid species occurs (Johnson 2003). Schneider and Zajic (1994) regarded the species as being a representative of *Xenacanthus* Beyrich, 1848; this opinion, however, is not followed here, based on Agassiz (1843) and Lund (1970).

Text-fig. 2. Appearance of the Craddock Bonebed site following excavation in 1996. Bed of concentrated shark remains occurs at level of shovel handle (50 cm long)

MATERIAL AND METHODS

Nine samples of the shark layer were screen-washed, with some fractions treated with ≤10% acetic acid, and concentrate sorted, but only completely so for Areas I, III, and V (Text-fig. 4). The remaining areas continue to be processed for small remains, but to date have not added significant information. Area IV yielded the largest (11 cm) piece of cartilage. Compared to the numbers of *O. platypternus* teeth obtained by bulk sampling from other Clear

Text-fig. 3. Three views of the distal end of a presumed juvenile occipital spine of *Orthacanthus platypternus* (Cope, 1883) (SMU 77016) from Area V in the Craddock Bonebed shark layer, Texas, USA (see Text-fig. 4); six pairs of ventral denticles are present; compare with Beck *et al.* (2016, fig. 3A, D). Scale bar equals to 1 mm



Text-fig. 4. Sketch of the excavated portion of the Craddock Bonebed shark layer (see Text-fig. 2) covering about two square meters showing the nine sample areas

Text-fig. 5. Two examples of *Orthacanthus platypternus* (Cope, 1883) coprolites from Area I (left, SMU 77314) and from Area V (right, SMU 77315), from the Craddock Bonebed shark layer, Texas, USA. Fragments of palaeoniscoid scales and bone fragments occur in SMU 77314 and a scale (lower left) and prismatic cartilage occur in SMU 77315

	Area I	Area III	Area V
Teeth with incomplete bases	1618	875	964
Teeth with complete(?) bases in matrix	398	296*	104
Teeth with complete bases	1441	923	1088
Measured teeth	130	89	124
Teeth with resorbed(?) lingual margins	237	166	109
Deformed teeth	20	17	17
Germinal teeth	120	56	45
Totals	3964	2422	2451

Table 1. Numbers of *Orthacanthus platypternus* (Cope, 1883) teeth collected from three of the nine sample areas (Text-fig. 4) in the shark layer (Text-fig. 2) at the Craddock Bonebed, Texas, USA; total number of teeth = 8,837. *30 teeth are instead associated with cartilage

	Area I	Area III	Area V
Approximate number of broken tooth cusps	1680	1225	1890
Approximate number of tooth fragments	1249	563	753
Approximate number of cartilage fragments*	400	475	550
Mucous-membrane denticles	837	689**	828
Dermal denticles	60	23	48
Discrete occipital spine fragments	284	13	44
Approximate number of coprolite fragments	180	72	400

Table 2. Additional remains of *Orthacanthus platypternus* (Cope, 1883) collected from three of the nine sample areas (Text-fig. 4) in the shark layer (Text-fig. 2) at the Craddock Bonebed, Texas, USA. * after Sampson and Johnson 2004 (some of the analyzed samples are from the Craddock Bonebed); ** includes 209 donated to another institution (Märss 2006, but without reference to these specimens)

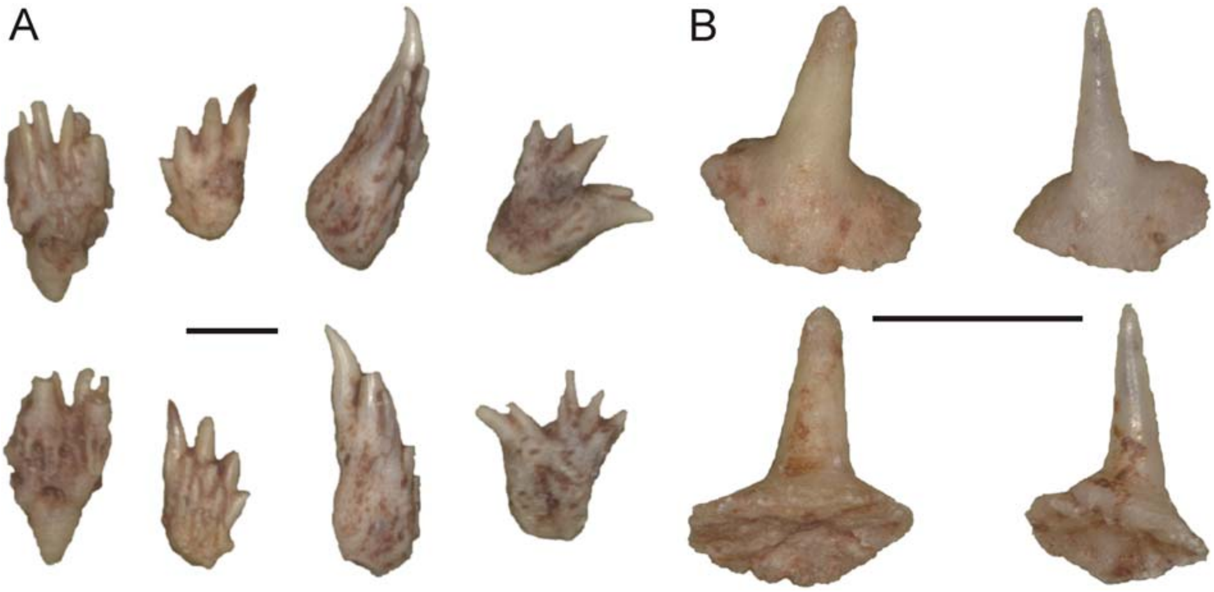
Fork localities (Murry and Johnson 1987; Johnson 1999), the total number from those three samples is staggering (Table 1). Descriptive terminology used in describing the teeth is provided by Johnson (1999). All specimens are cataloged in the Shuler Museum of Paleontology at Southern Methodist University in Dallas, Texas (abbreviated SMU).

Additional remains associated with *O. platypternus* are presented in Table 2. Occipital spine fragments in Table 2 do not include "chips" and spine denticles; it is therefore impossible to know how many spines are actually represented in these Areas. Their numbers do not include those studied by Donelan and Johnson (1997), i.e., 23, 11, and 21 from Areas I, III, and V, respectively. Also, coprolite fragments present a similar problem; but when observed in total, the collection is quite remarkable besides those few that are complete (Text-fig. 5; worth noting is their small size). They presumably could have been produced only by juveniles.

Denticles attributed to *O. platypternus* (Table 2) include mucous-membrane denticles (see Zidek *et al.* 2003 for discussion regarding a different xenacanth genus; Peyer 1968, pp. 54–60) and presumed dermal denticles (Peyer 1968, p. 54, pl. 8b), both shown in Text-fig. 6. Considerable variation in form (pattern of "cusps," for example) occurs in the mucous-membrane denticles as opposed to essentially no change in the dermal denticles.

ORTHACANTHUS PLATYPTERNUS TEETH IN THE CRADDOCK BONEBED

The original purpose of this report was to demonstrate that only teeth of one species of xenacanth shark is present in the shark layer, and to try to distinguish juvenile teeth from adult teeth. Nearly complete teeth are extremely rare; nearly all available are illustrated (Text-figs 7 and 8), a condition which seems to be universal based on illustrations in Johnson (1999) from much smaller samples. Whether these are juvenile or adult teeth is largely uncertain, as no reasonably larger teeth are available. Based on Johnson (1999), there was little doubt that only one species is present (Text-figs 7 and 8). Johnson (1999, pp. 242, 243) noted that posterior teeth occur only rarely in the Wichita and Clear Fork groups. Their common occurrence in



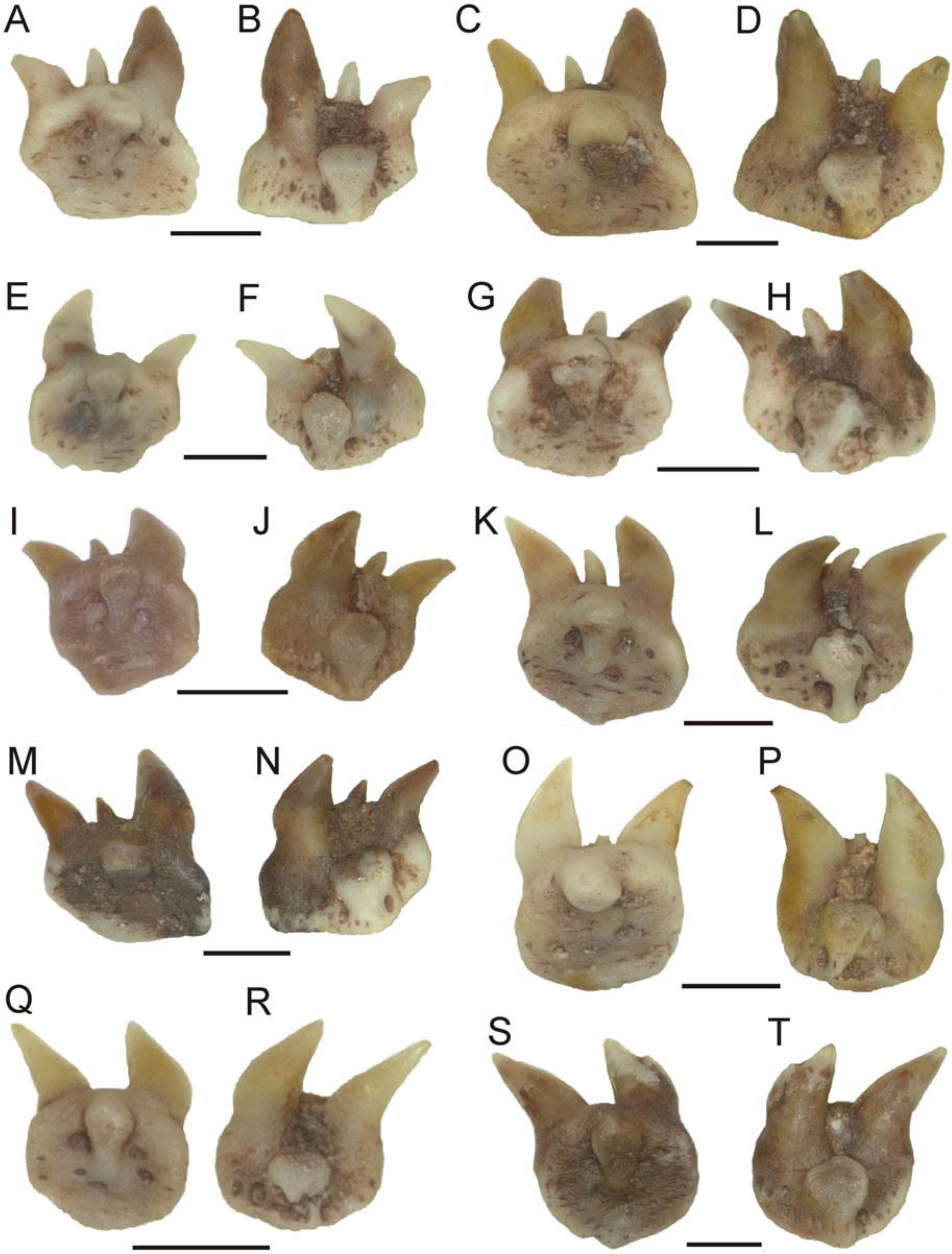
Text-fig. 6. Two views of *Orthacanthus platypternus* (Cope, 1883) mucous-membrane denticles (SMU 77316, A) and dermal denticles (SMU 77317, B), all from Area V in the Craddock Bonebed shark layer, Texas, USA. Scale bars equal to 1 mm

the Craddock Bonebed shark layer (several occur in samples Ia and IIIa, Table 3, but are not identified**)** suggests that many of these teeth represent a juvenile characteristic. This further suggests that such morphology, without an anterior extension on the base and with both principal cusps leaning posteriorly and with the intermediate cusp generally absent (Text-figs 7O–T; 8E–F), does not necessarily mean they were restricted to a posterior position in the juvenile dentition. Furthermore, dignathic and sexual dimorphism cannot be determined in any of the teeth in the samples (Johnson 1999, p. 222).

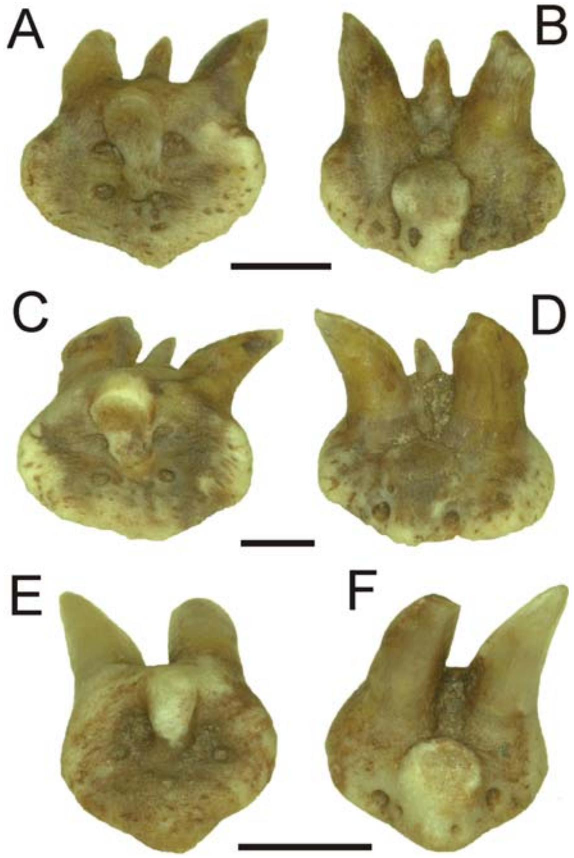
However, a new discovery in this fauna is the presence of what are interpreted as symphyseal teeth (Text-fig. 9). Because of the probable dominance of juvenile teeth in the fauna, the occipital spine occurrences (see above), and their absence from all other Wichita and Clear Fork faunas, suggest that *Orthacanthus platypternus* juvenile dentitions contained a file of symphyseal teeth (some medial teeth approach this condition, Text-fig. 8A, B; Johnson 1999, p. 243). These teeth have vertical principal cusps, or they are slightly divergent. The illustrated teeth (Text-fig. 9) suggest that the upper and lower symphyseal teeth in the dentition were different, but sexual dimorphism cannot be discounted. This singular occurrence in the Clear Fork Group can only be presently explained by the occurrence of large

	N*	n	Range [mm]		Mean ± standard deviation [mm]		Linear Regression[1]	
			am-pl	l-l	am-pl	l-l	m	b
Craddock Area Ia	1512	100	1.10–8.63	0.96–6.35	2.54±1.15	2.02±0.84	0.71±.04	0.22±.10
Craddock Area IIIa	900	69	1.30–9.00	1.16–6.67	2.77±1.32	2.24±0.93	0.69±.03	0.32±.10
Craddock Area Va	1046	99	0.94–5.67	1.06–4.75	2.93±1.12	2.40±0.83	0.72±.04	0.30±.12
Craddock Area Ib	93	30	0.78–1.36	0.72–1.20	1.04±0.16	0.99±0.13	0.51±.25	0.45±.28
Craddock Area IIIb	62	20	0.76–1.28	0.84–1.18	1.01±0.12	1.01±0.09	0.40±.28	0.60±.28
Craddock Area Vb	71	25	0.68–1.36	0.64–1.14	1.01±0.18	0.95±0.14	0.48±.24	0.46±.25
East Coffee Creek 37	749	91	1.40–8.20	1.30–5.80	4.00±1.40	3.10±1.00	0.69±.05	1.32±.20
East Coffee Creek 47	228	55	2.00–13.00	1.50–9.50	5.20±2.60	4.10±1.80	0.66±.05	0.70±.26

Table 3. Statistical data regarding the measured teeth from the Craddock Bonebed shark layer, Texas, USA (Text-fig. 4) compared with the data from two faunas at about the same stratigraphic level (data from Johnson 1999). a = teeth ≥ 20 mesh size, b = teeth ≤ 30 mesh size (see text); N = number of teeth available, n = sample size, am-pl = anteromedial-posterolateral length, l-l = labial-lingual width, m = slope, b = y intercept; *additional teeth were acquired from the shark layer after measurements were made; [1]with 95% confidence intervals



Text-fig. 7. Examples of *Orthacanthus platypternus* (Cope, 1883) teeth in the Craddock Bonebed shark layer, Texas, USA, Area I. All are labial-aboral and lingual-occlusal views. A-B – lateral tooth (SMU 76979); C-D – lateral tooth (SMU 76980); E-F – lateral tooth (SMU 76984); G-H – adult? lateral tooth (SMU 76986); I-J – adult? lateral tooth (SMU 76988); K-L – posterolateral tooth (SMU 76977; note the protruding apical button); M-N – posterolateral tooth (SMU 76978); O-P – posterior? tooth (usually the intermediate cusp is absent; SMU 76983); Q-R – adult? posterior tooth (SMU 76985); S-T – adult posterior tooth (SMU 76987). Scale bars equal to 1 mm



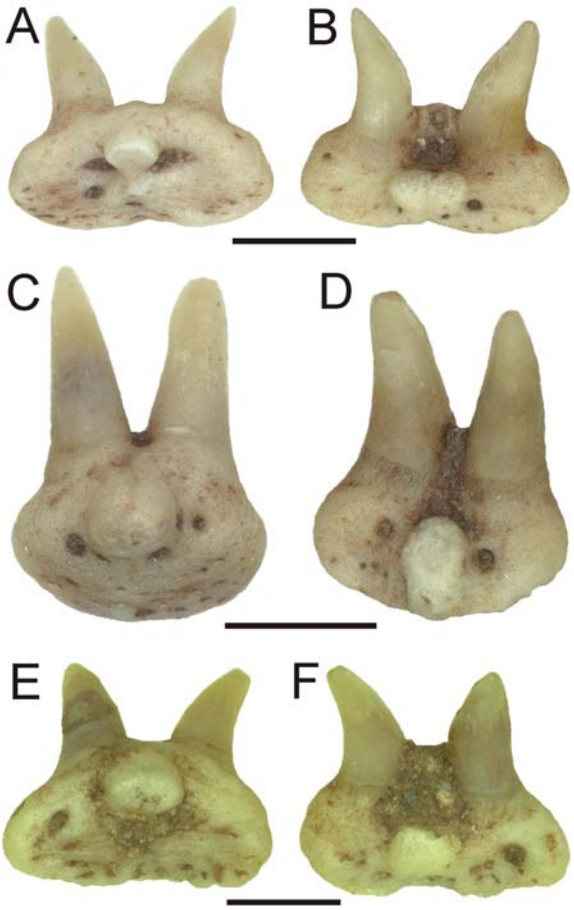
Text-fig. 8. Examples of *Orthacanthus platypternus* (Cope, 1883) teeth from the Craddock Bonebed shark layer, Texas, USA, Area V. A-B – medial tooth (SMU 77011); C-D – lateral tooth (SMU 77010); E-F – posterior tooth (SMU 77009). Scale bars equal to 1 mm

numbers of juvenile dentitions. However, their occurrence was also noted by Hampe (1997).

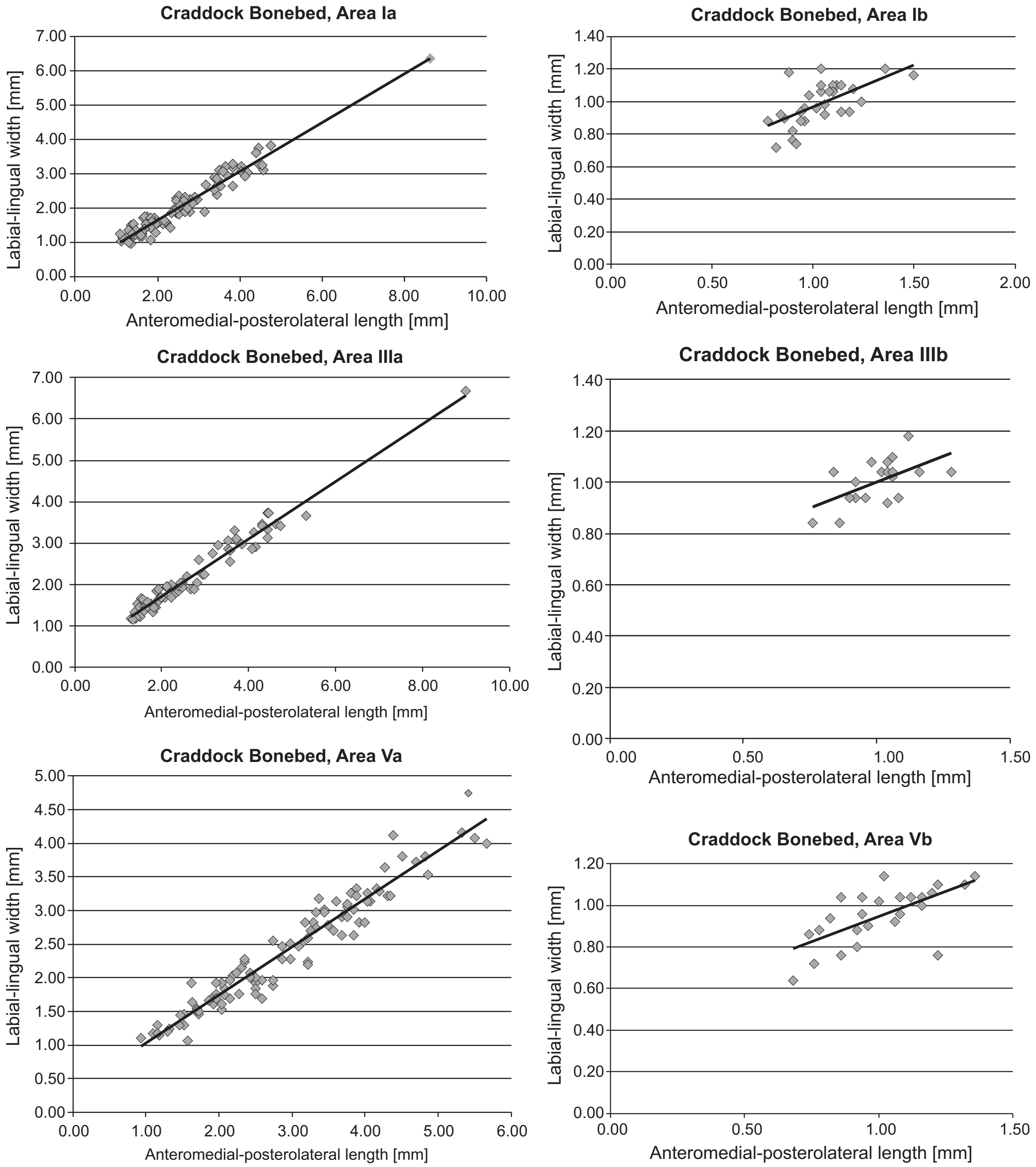
An attempt to distinguish juvenile from adult teeth using a linear regression analysis for each of the three sample areas (Text-fig. 10) is not conclusive, despite separating the samples by size (Table 3). With the presumption that juvenile teeth are abundant or even dominant in the samples, all the teeth were separated by those retained on ≥ 20 mesh (openings per inch) screens from those retained on ≤ 30 mesh screens. The resulting analyses are compared with faunas of comparable stratigraphic position in the Clear Fork Group (Table 3; Johnson 1999, table 2, figs 2, 9). One of the problems with such measurements is that the apical button (Johnson 1999, fig. 1), which is included in the labial-lingual (l-l) measurement, can influence the measurement by as much as 10% (Text-fig. 7L, for example, and is the reason l-l is chosen as the dependent variable rather than the anteromedial-posterolateral measurement in Text-fig. 10). The slopes for Areas Ia, IIIa, and Va are easily distinguished from those of the smaller teeth (Areas Ib, IIIb, and Vb) as shown in Table 3. The teeth from the two East Coffee Creek faunas (north of the east end of Lake Kemp, Text-fig. 1) may be larger than those in the Craddock Bonebed shark layer, but the slopes (m) of the linear regressions (Table 3) are comparable with those of the larger Craddock Bonebed teeth. A problem with the latter is the lack of larger measureable teeth (Text-fig. 10); fragments suggest they were present in some numbers, but not as common as in the other Clear Fork Group faunas (Johnson 1999, table 2, fig. 2B).

GERMINAL TEETH

Underdeveloped or germinal teeth (Johnson 2005; Johnson and Thayer 2009; tooth embryos in Hampe

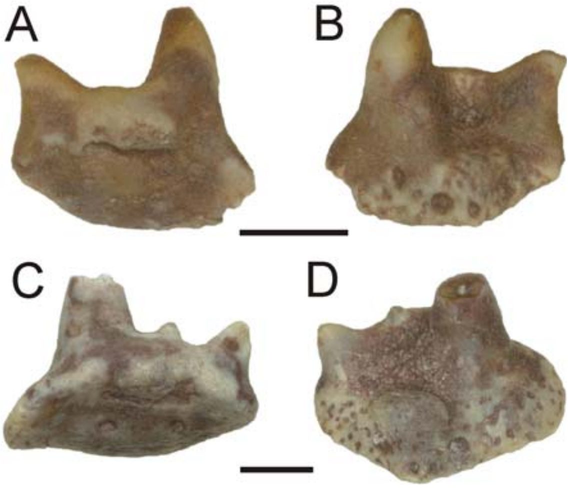


Text-fig. 9. Presumed juvenile symphyseal teeth from the Craddock Bonebed shark layer, Texas, USA. A-B and C-D are from Area I; E-F is a possible example from Area V. A-B – SMU 76981 (intermediate cusp is broken); C-D – SMU 76982 (intermediate cusp absent); E-F – SMU 77008 (presence of intermediate cusp uncertain). Scale bars equal to 1 mm



Text-fig. 10. Linear regression plots of tooth-base dimensions of *Orthacanthus platypternus* (Cope, 1883) teeth from the Craddock Bonebed shark layer, Texas, USA. Areas Ia, IIIa, and Va represent teeth retained on screens of ≥ 20 mesh size; Areas Ib, IIIb, and Vb represent teeth retained on screens of ≤ 30 mesh size. Teeth were randomly selected except for the largest teeth in Ia and IIIa (see text for details)

1997) are fairly common in the Craddock Bonebed shark layer (Table 1; Text-fig. 11; compare with Hampe 1997, fig. 2a–c). The principal cusps are not completely developed (and lack the characteristic carinae), the intermediate cusp is usually undeveloped, but the base tends to be fully developed in the shark layer teeth although Johnson (2005) noted that the apical button is often poorly developed. Teeth such as these were presumably still in the dental groove when a shark died. They constitute 2.5% of the tooth



Text-fig. 11. Germinal teeth of *Orthacanthus platypternus* (Cope, 1883) from the Craddock Bonebed shark layer, Texas, USA. Aboral-labial and occlusal-lingual views. A-B – SMU 76989 from Area I; C-D – SMU 77001 from Area III. Scale bars equal to 1 mm

sample (Table 1). This condition may be unique in xenacanth sharks. In extant sharks, the crown (equal to cusps in xenacanth teeth) develops before the base does (Peyer 1968, pp. 47–50, 63, pls 8, 9).

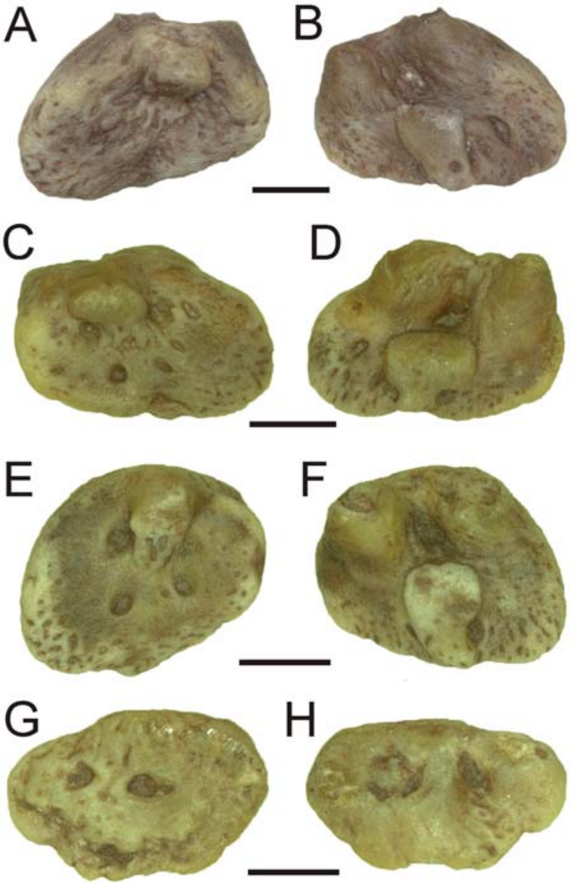
DEFORMED TEETH

Developmentally deformed teeth (Table 1) are associated with xenacanth sharks throughout the Texas lower Permian stratigraphic section (Johnson 1987, fig. 1). In a sense, this makes them unique as deformed teeth have not been observed in other sharks (in the Wichita Group; Text-fig. 1) such as hybodonts, petalodonts, cladodonts, and helodonts, despite being somewhat common (Johnson 1992; see also Hampe 1997).

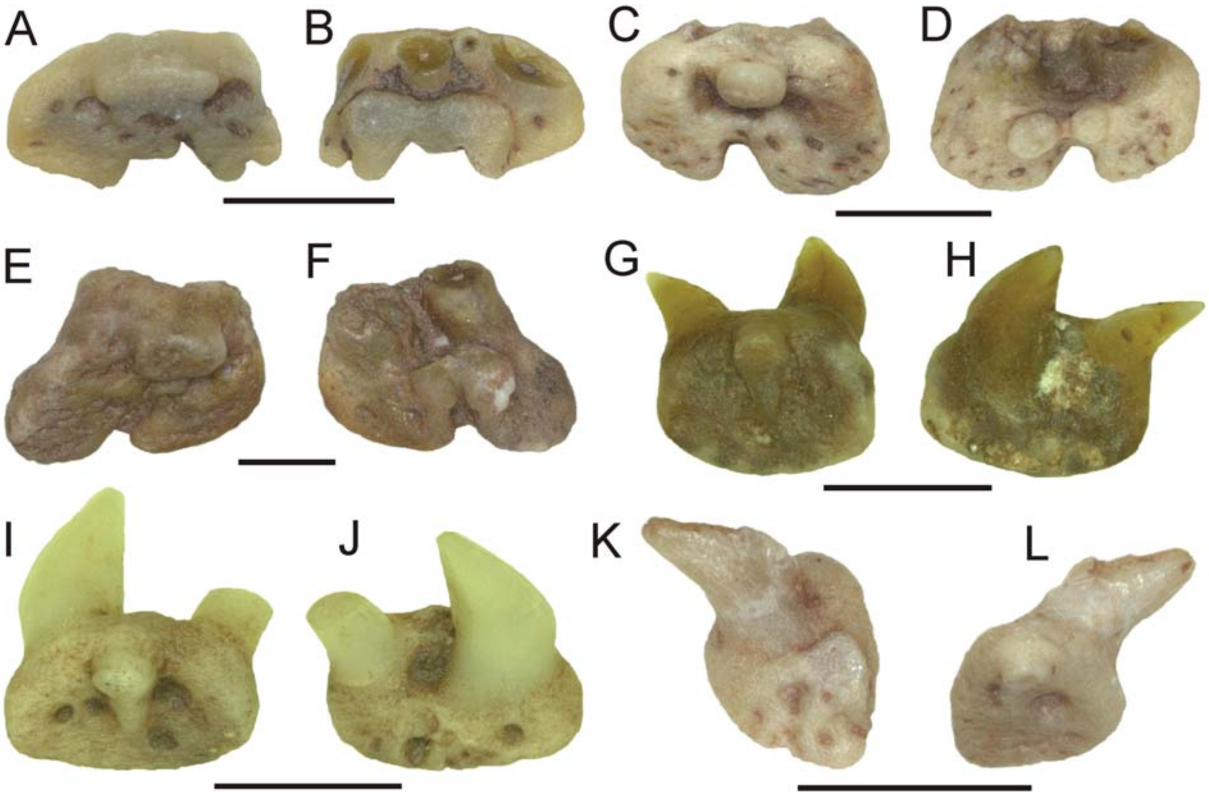
Some teeth tend to appear distorted and have principal cusps with a “knob-like” appearance (Text-fig. 12A–F), which gives the suggestion that they could be germinal teeth except that a ridge occurs between the principal cusps in place of an intermediate cusp (uncertain in Text-fig. 12A, B). The tooth in Text-fig. 12G, H may in fact be a germinal tooth, but appears badly worn, possibly by transport; its apical button (Text-fig. 12H) is absent and the basal tubercle is reduced in depth, and the original development of the three cusps is unknown.

In other deformed teeth, the apical button is distorted or apparently absent (Text-fig. 13), yet the basal tubercle is completely normal in Text-fig. 13A, C, E. As seen only in the occlusal views (Text-fig. 13B, D, F), it might appear the teeth were undergoing a form of division. But in Text-fig. 13B, where four cusps might have been present (note the strange symmetry), two teeth might have been undergoing fusion. All this is negated by the normal basal tubercle in each. The fact that the labial side of the base is not affected may be related to the occurrence of teeth with resorbed(?) lingual (but not labial) margins (see below). On the other hand, the teeth in Text-fig. 13G–J are completely normal except that the apical button in Text-fig. 13H is either mostly undeveloped or somehow distorted, while it is absent in Text-fig. 13J (note the reduced lingual margin). There is no evidence of resorption in these teeth.

No examples of fused teeth have been found in the shark layer, except for one possibility from Area III, although they do occur in the Texas lower Permian (Johnson 1987).



Text-fig. 12. Deformed *Orthacanthus platypternus* (Cope, 1883) teeth from the Craddock Bonebed shark layer, Texas, USA. Aboral-labial and lingual-occlusal views. A-B is from Area I, C-D, E-F and G-H are from Area V. A-B – SMU 76992; C-D – SMU 77006; E-F – SMU 77015; G-H – SMU 77012. Scale bars equal to 1 mm

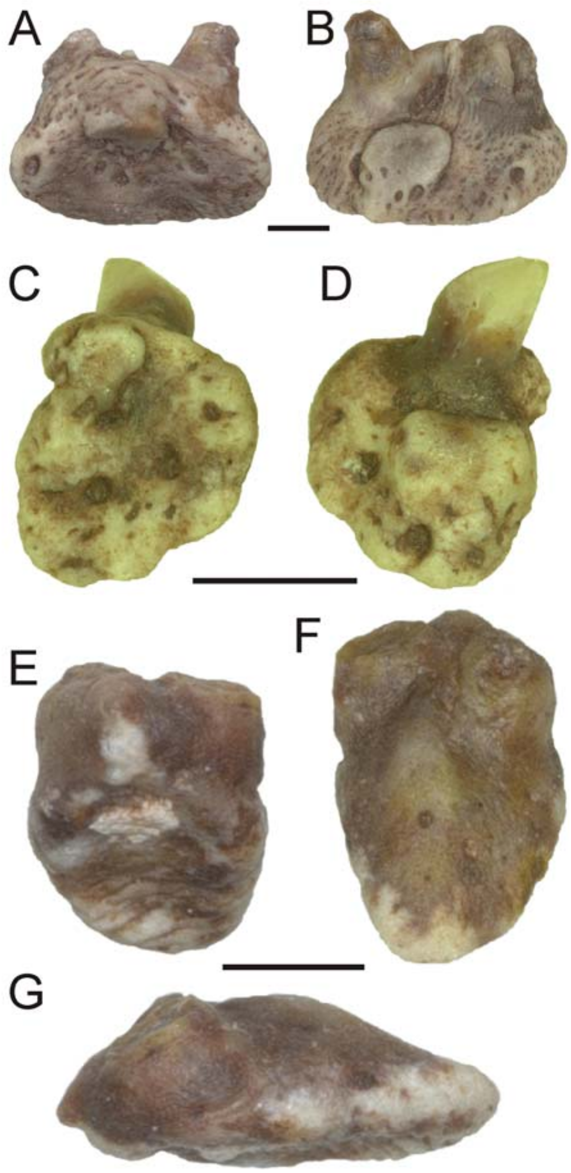


Text-fig. 13. Deformed *Orthacanthus platypternus* (Cope, 1883) teeth from the Craddock Bonebed shark layer, Texas, USA. Aboral-labial and labial-occlusal views. A-B, C-D, E-F and K-L are from Area I, G-H and I-J are from Area V. A-B – SMU 76991, one end is broken; C-D – SMU 76993; E-F – SMU 76994; G-H – SMU 77013, posterior tooth; I-J – SMU 77014, posterolateral tooth, intermediate cusp is broken; K-L – SMU 76990. Scale bars equal to 1 mm

Other deformed teeth (Text-figs 13K, L, 14) include three with only one principal cusp or nearly so. The tooth in Text-fig. 13K, L is complete, with a normal apical button and basal tubercle but only one principal cusp (the intermediate cusp is apparently absent). The tooth in Text-fig. 14A, B has a broken normal cusp, but the second principal cusp is apparently underdeveloped and fused to what might be an intermediate cusp; otherwise it appears to be normal. The second tooth (Text-fig. 14C, D) has only one principal cusp; the second, and the intermediate cusp, are not developed, with only the central **(**median**)** foramen (possibly) appearing on the left side of the apical button in Text-fig. 14D.

Other examples, isolated but not separately cataloged, of deformed teeth include two examples in which all three cusps appear to be fused, another with the basal tubercle essentially absent although the apical button is normal, and one that is completely deformed in which the cusps, apical button, and basal tubercle cannot be distinguished, all from Area I. One undistorted-appearing very small (≈ 1 mm) tooth, also from Area I, possesses only one cusp positioned at one end of the labial margin, while the well-developed basal tubercle is at the opposite end; the poorly-developed apical button is normally positioned. Another very small tooth has two basal tubercles and with an underdeveloped principal cusp, and a possible symphyseal tooth with the apical button replaced with a foramen, are from Area V. Further examples occur in all three sampled Areas, which suggest that it is not probable that all the deformed teeth can be conveniently placed into categories that would suggest discrete causes of deformation.

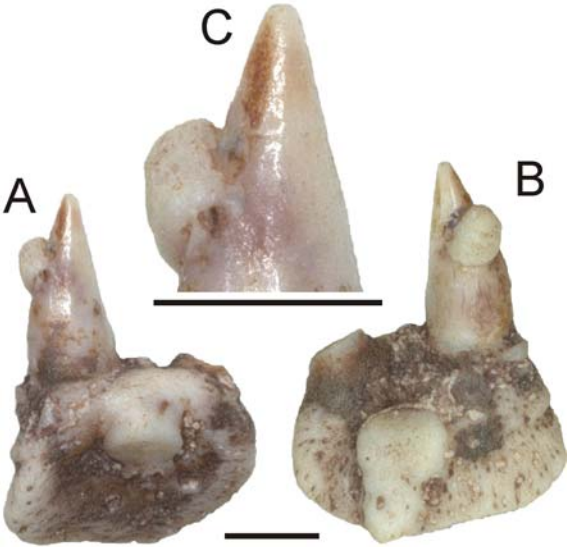
Finally, a sign of extreme compression seems best to describe the tooth in Text-fig. 14E–G. The principal cusps are broken and the intermediate cusp is not developed or is absent. The antero-posterior compression also applies to the enlarged apical button (note its height in Text-fig. 14G) and to the basal tubercle (the bulge is difficult to distinguish because of poor contrast in Text-fig. 14E).



Text-fig. 14. Deformed *Orthacanthus platypternus* (Cope, 1883) teeth from the Craddock Bonebed shark layer, Texas, USA. Aboral-labial and occlusal-labial views in A-F, side view in G. A-B and E-G are from Area III, C-D is from Area V. A-B – SMU 77002; C-D – SMU 77007; E-G – SMU 77005 (lingual end at right in G). Scale bars equal to 1 mm

“ENAMEL” PEARL?

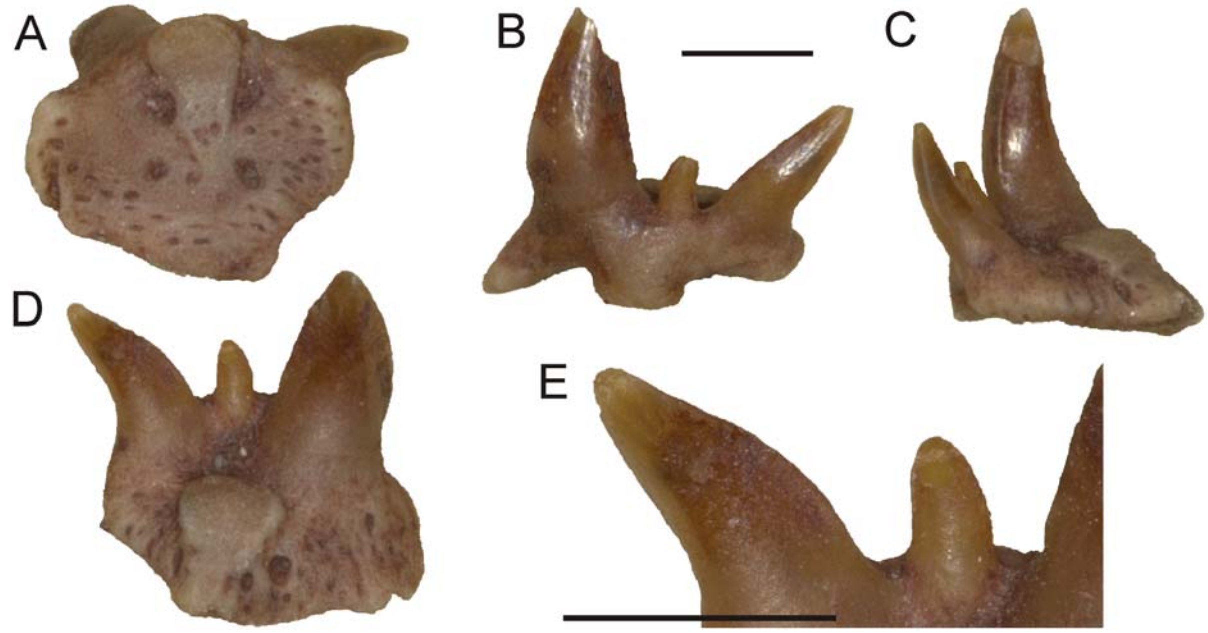
The tooth in Text-fig. 15 is normal except for the outgrowth on the complete principal cusp; the enlargement (Text-fig. 15C) clearly shows that it is not merely a fragment cemented to the cusp. It is similar to “enamel pearls” that occur in human teeth (Langlais *et al.* 2009). A similar condition (enamel pearls, M.R. Whitney, pers. comm.) was reported to occur in a late Permian (Lopingian) gorgonopsian synapsid (Whitney *et al.* 2016). The problem is that *Orthacanthus* teeth do not possess enamel or enameloid (Ginter *et al.* 2010). However, in a study by Stiernagle and Johnson (2006), evidence from SEM views of *O. platypternus* tooth cusps (from the Craddock Bonebed, SMU 69442, 69446) suggested that the identification of the tissue in the carinae is equivocal (the serrations in the carinae of *O. texensis* teeth contain pallial dentine, based on thin-sections). In a well-preserved tooth of *O. platypternus* (Text-fig. 16) the tip of the cusp and associated carina are translucent, suggesting the orthodentine may be modified. Furthermore, this outgrowth should not be confused with an overgrowth of orthodentine formed as a result of a healed fracture in an unerupted tooth (Text-fig. 17).



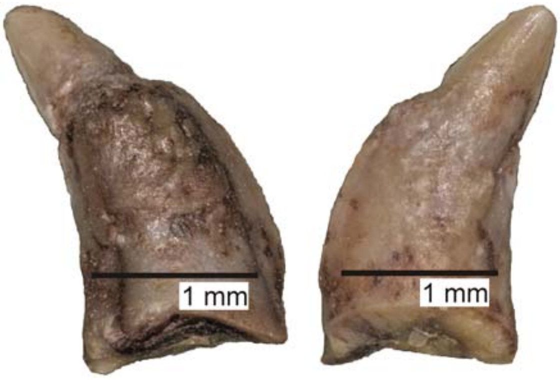
Text-fig. 15. *Orthacanthus platypternus* (Cope, 1883) tooth with an “enamel pearl” from Area III of the Craddock Bonebed shark layer, Texas, USA in aboral-labial (A), lingual-occlusal (B) and close-up (C) views. Scale bars equal to 1 mm

TEETH SHOWING EVIDENCE OF RESORPTION

The most unusual teeth, in that they have not been previously observed in other faunas in the Wichita and Clear Fork groups (Text fig. 1), are those that appear to have undergone various stages of resorption. They represent nearly 6% of the total sample (Table 1). Only the lingual margin of the base is affected. Some merely have an etched margin, but in others the apical button is resorbed to varying



Text-fig. 16. *Orthacanthus platypternus* (Cope, 1883) tooth (SMU 77318) recovered from matrix just above the nine sampled areas of the Craddock Bonebed shark layer, Texas, USA (Text-fig. 4; Field No. 6-2-95A, matrix still being processed and yielding yet more significant specimens). A – aboral view; B – labial view; C – lateral view; D – lingual view; E – posterior principal cusp. Scale bars equal to 1 mm



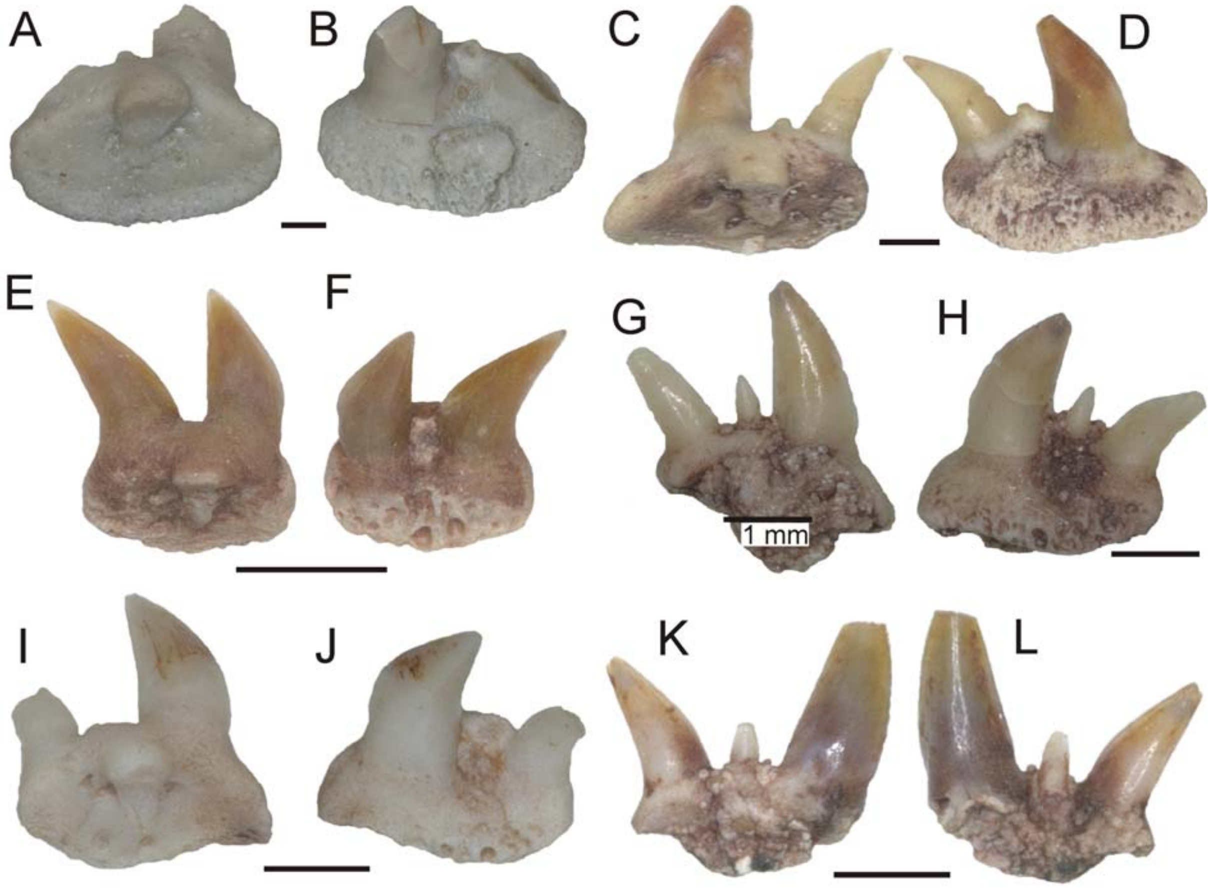
Text-fig. 17. Two views of a healed fractured cusp of an *Orthacanthus platypternus* (Cope, 1883) (SMU 77326) tooth from matrix just above the nine sampled areas of the Craddock Bonebed shark layer, Texas, USA (see caption to Text-fig. 16); the fracture is only visible on the edges of the cusp, which possesses prominent carinae

Locality (name and SMU number)	SMU No.	Sample size	Resorbed[1] teeth
Clear Fork Group			
Crooked Creek 80	69197	468	0
Crooked Creek 80	69198	798*	1
Crooked Creek 81	69204	222	3
Crooked Creek 81	69205	586*	1
Lost Lake 57	69183	64*	0
West Coffee Creek 56	69180	73	4
West Coffee Creek 56	69181	150*	3
East Coffee Creek 47	69175	103	2
East Coffee Creek 47	69176	70*	1
East Coffee Creek 37	69164	287	7
East Coffee Creek 37	69167	246	3
East Coffee Creek 36	69172	26*	1
Wichtita Group			
Lake Kemp A 340	64274	179*	0
Mitchell Creek A 653	64267	236*	11
Hackberry Creek C 339	64260	141*	7

Table 4. Survey of faunas in the Clear Fork and Wichita groups, in stratigraphic order (Johnson 1999) used to identify possible *Orthacanthus platypternus* (Cope, 1883) teeth showing evidence of resorption. Measured samples of teeth and faunas obtained by acid-treatment of matrix not used. [1]Teeth were not isolated; *some teeth with incomplete lingual margin

degrees until only the labial margin with the basal tubercle and the three cusps are all that remain. In a few instances, only the cusps remain, held in place by matrix. For the sake of convenience, examples are divided into four stages, ranging from an etched margin to only the labial margin containing the cusps and basal tubercle (Text-fig. 18).

In a typical tooth file, the basal tubercle rests upon the apical button of the underlying tooth. If the teeth were undergoing resorption, then the perplexing problem is why the apical button is resorbed and not the superjacent basal tubercle. Some other, but unknown, pathological process may have been occurring. In chondrichthyans, complete teeth are shed



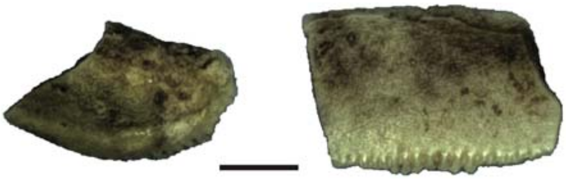
Text-fig. 18. Examples of four stages of presumed progressive tooth resorption; all are from Area I in the Craddock Bonebed shark layer, Texas, USA (Text-fig. 4, Table 1). A-B – SMU 76995 (image electronically darkened, as it is nearly pure white), an example of Stage 1, in which the lingual margin is merely etched; C-D – SMU 76996 (lateral tooth), an example of Stage 2, in which part of the apical button has been resorbed; E-F – SMU 76997 (posterior tooth); G-H – SMU 76998 (lateral tooth) and I-J – SMU 76999 (lateral tooth, electronically darkened), examples of Stage 3, in which the lingual margin and essentially all of the apical button have been resorbed; K-L – SMU 77000 (medial tooth), an example of Stage 4, in which all but the labial one-third of the tooth has been resorbed. Scale bars equal to 1 mm

and no resorption occurs (see Chen *et al.* 2016 who provided an informative general review of the process in fishes, less so in tetrapods; see also Rücklin *et al.* 2017 and Trinajstic *et al.* 2017). Chen *et al.* (2016) do not discuss pathological processes or occurrences involving resorption, but presumably they occur, just as in humans (Langlais *et al.* 2009).

The possible existence of resorbed teeth elsewhere in the Wichita and Clear Fork groups was not recognized by Johnson (1999). However, a review of appropriate faunas (Table 4) reveals their existence, but generally their occurrence is rather limited. The reason for their relatively greater occurrence in the lowest two examples from the Wichita Group (Table 4; middle Waggoner Ranch Formation, Johnson 1999, table 1) is unknown.

OTHER VERTEBRATE REMAINS

A summary of other fossils in Areas I, III, and V (Text-fig. 4) is presented in Table 5. No attempt was made to identify the tetrapod remains except for *Diplocaulus*?. Some of the teeth belong to unknown



Text-fig. 19. Two examples of bones (scales?) with a "comb edge" (SMU 77305) from Area V in the Craddock Bonebed shark layer, Texas, USA. Scale bar equals to 1 mm

Microvertebrates present	Area I	Area III	Area V
Partial palaeoniscoid scales*	2540	1225	1890
Complete palaeoniscoid scales	545	303	357
Palaeoniscoid teeth	60	4	9
Unidentified bones (scales?) with "comb edge"	5	3	11
Tetrapod bone fragments (some identifiable)*	795	170	327
Unidentified partial tetrapod jaws	7	0	2
Tetrapod teeth (some identifiable)**	25	21	9
Diplocanthus? fragments	0	3	2
Xenacanthus occipital spine fragments	1	1	1
?*Lissodus* (*Polyacrodus*) *zideki* teeth	1	0	1

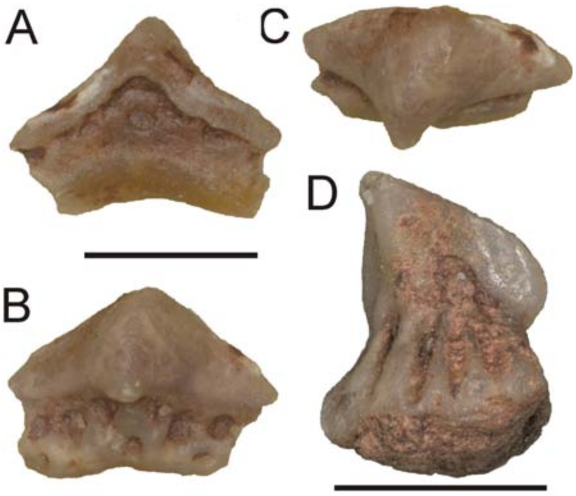
Table 5. Vertebrate remains ("microvertebrates") obtained by wet-screening samples from the Craddock Bonebed shark layer, Texas, USA (Text-fig. 4) used in an attempt to demonstrate consistency between samples, complicated by the fact that the Area I sample is some three times the size (by weight) of the Areas III and V samples. Obvious inconsistencies occur (also in Tables 1 and 2); their significance cannot be determined. * approximate numbers; ** fragments not counted

labyrinthodonts. The partial bones (scales?) with a "comb edge" (Text-fig. 19) are presumably identifiable; they may occur in other faunas (Johnson 1979), but if so, were not deemed significant.

Of greater interest, partly from a stratigraphic viewpoint, is the occurrence of two other chondrichthyan taxa in the Craddock Bonebed (Table 5). This is their first occurrence in the Clear Fork Group. Several *Xenacanthus* worn occipital spine fragments (Text-fig. 20A) have also been recovered from matrix above the sampled areas (SMU 77325; Text-fig. 16 caption). However, *Xenacanthus* teeth have not been recovered from the Craddock Bonebed. A similar situation occurs in the Archer City Formation (Bowie Group underlying the Wichita Group; see Hentz, 1989, for an explanation of this discrepancy in stratigraphic nomenclature, as this formation is also considered to be part of the Cisco Group, Johnson 2013, fig. 1). The presence of very small incomplete occipital spines (Text-fig. 20) coupled with the absence of teeth was discussed by Johnson (2012). A similar occurrence of *Xenacanthus* occipital spines but no teeth was reported by Johnson (2013) from the overlying Nocona Formation (Wichita Group, Pn, Text-fig. 1). *Xenacanthus* has not been reported from the stratigraphic record above the Nocona Formation. Teeth that were questionably assigned to this genus were reassigned to a new genus (Johnson 2003) and interestingly, occipital spines have not been recovered (if they existed) from faunas containing those teeth.

The other first occurrence in the Clear Fork Group is the hybodont ?*Lissodus* (*Polyacrodus*) *zideki* (Table 5, Text-fig. 21; its taxonomic problems are discussed in Duffin 1985; Rees and Underwood 2002; Fischer 2008, and updated in Fischer *et al.* 2010 and Ginter *et al.* 2010). Previously, its last known occurrence was in the middle Lueders Formation (Johnson 1981; Tit Butte and Southwest Butte local faunas in Johnson 1979, pp. 629, 630), now the lower upper Waggoner Ranch Formation, Wichita Group (Johnson 2003, table 1; Pwr in Text-fig. 1). The tooth in Text-fig. 21 shows little sign of wear, as does a

Text-fig. 20. *Xenacanthus* Beyrich, 1848 occipital spine fragments. A – SMU 77060 from Area III in the Craddock Bonebed shark layer, Texas, USA; B – SMU 77319 from the Archer City Formation, Texas, USA (see text). Scale bars equal to 1 mm



Text-fig. 21. **A-C** – ?*Lissodus* (*Polyacrodus*) *zideki* (Johnson, 1981) tooth (SMU 77312) from Area V in the Craddock Bonebed shark layer, Texas, USA. A – labial view; B – lingual view; C – occlusal view. **D** – hybodont? dermal denticle (SMU 77322) from Area I in the Craddock Bonebed shark layer, Texas, USA. Scale bars equal to 1 mm mostly complete tooth from Area I (SMU 77320). Also recovered from Area I is a single, presumably hybodont, dermal denticle (Text-fig. 21D; or scale, A. Ivanov, pers. comm.; compare with fig. 8, pl. 7 in Ivanov 1999). This implies another curiosity, as fossils similar to this were not reported by Johnson (1981) and apparently only xenacanth denticles were recovered by Johnson (1979, p. 581).

The presence of these two taxa after a hiatus in the stratigraphic record may suggest they were nearshore marine, as suggested by Johnson (1981, p. 19; 2012, p. 370). Furthermore, reports of possible occurrences of ?*Lissodus* (*Polyacrodus*) *zideki* from outside North America (Ginter *et al.* 2010, pp. 95, 96) support this suggestion.

CONCLUSIONS

The Craddock Bonebed shark layer, near the base of the Clear Fork Group in Texas, USA, probably contains the greatest concentration (based on examination of three out of nine collected samples) of xenacanth teeth, in this case those of *Orthacanthus platypternus*, of any known locality. There is no doubt that both adult and juvenile teeth (and occipital spines) are present. However, no success has been achieved in morphologically distinguishing the teeth (unlike the spines). It is quite likely that the shark layer represents the preservation of the remains of a shark nursery, something not previously observed in the Texas lower Permian stratigraphic succession. Based on previously studied xenacanth localities in the Texas lower Permian, it is not surprising that a variety of unusual (deformed, germinal) teeth are present, which seems to be characteristic of the xenacanth sharks. Even more so is that new varieties of these unusual teeth, symphyseals and teeth showing presumed evidence of resorption, are present. Moreover, one tooth bears evidence of the equivalent of an "enamel pearl."

The presence of *Xenacanthus* worn occipital spines presents a conundrum. Their previously last known occurrence was near the base of the underlying Wichita Group, where a lack of teeth also occurred. They may have been reworked, but it is not clear from where. The rare presence of unworn hybodont shark teeth belonging to ?*Lissodus* (*Polyacrodus*) *zideki*, last known from the upper Wichita Group, may not be unexpected. Evidence from earlier studies suggests these two taxa may have spent at least part of their life history in the marine realm, which was in near geographic proximity to the Craddock Bonebed.

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