Acta Geologica Polonica, Vol. 49 (1999), No. 3, pp. 215-266

Dentitions of Late Palaeozoic *Orthacanthus* species and new species of ?*Xenacanthus* (Chondrichthyes: Xenacanthiformes) from North America

GARY D. JOHNSON

Department of Earth Sciences and Physics, University of South Dakota; 414 East Clark Street, Vermillion, SD 57069-2390, USA. E-mail: gjohnson@usd.edu

ABSTRACT:

JOHNSON, G.D. 1999. Dentitions of Late Palaeozoic *Orthacanthus* species and new species of ?*Xenacanthus* (Chondrichthyes: Xenacanthiformes) from North America. *Acta Geologica Polonica*, **49** (3), 215-266. Warszawa.

Orthacanthus lateral teeth have paired, variably divergent, smooth, usually carinated labio-lingually compressed principal cusps separated by a central foramen; one or more intermediate cusps; and an apical button on the base isolated from the cusps. Several thousand isolated teeth from Texas Artinskian bulk samples are used to define the heterodont dentitions of *O. texensis* and *O. platypternus*. The *O. texensis* tooth base has a labio-lingual width greater than the anteromedial-posterolateral length, the basal tubercle is restricted to the thick labial margin, the principal cusps are serrated to varying degrees, and the posterior cusp is larger. The *O. platypternus* tooth base is longer than wide, its basal tubercle extends to the center, the labial margin is thin, serrations are absent on the principal cusps, the anterior cusp is larger, and a single intermediate cusp is present. More than two hundred isolated teeth from Nebraska (Gzhelian) and Pennsylvania (Asselian) provide a preliminary description of the heterodont dentition of *O. compressus*. The principal cusps are similar to *O. texensis* but usually(?) are not serrated, and the base is usually wider than long but has a thin or sometimes thick labial margin beneath a single intermediate cusp.

A few dozen very small isolated teeth define two ?*Xenacanthus* dentitions. ?*X. ossiani* sp. nov. (Gzhelian, Nebraska) teeth have a thin, longer than wide base with a flange at one end, an isolated apical button, a centrally extended basal tubercle, and a central foramen; the principal and intermediate cusps are recumbent, divergent, highly compressed, smooth, and lack serrations. ?*X. slaughteri* sp. nov. (Artinskian, Texas) teeth have nearly parallel, smooth, carinated, nonserrated, compressed principal cusps and intermediate cusp; the base is thin, longer than wide, with the apical button often in contact with the principal cusps, present or absent central foramen, and basal tubercle restricted to the labial margin.

The new species of ?*Xenacanthus*, as well as *O. platypternus* and other xenacanth species, appear to be endemic to North America. Other upper Palaeozoic species are endemic to Europe. However, *O. compressus* and possibly *O. texensis* are similar to some European species. Despite the Appalachian-Hercynian barrier, dispersal may have occurred in coastal marine waters during a migration phase of the reproductive cycle of some *Orthacanthus* species.

Keywords: Xenacanthiformes, Permian, Upper Carboniferous.

INTRODUCTION

Recovery of large numbers of teeth from the Lower Permian (Artinskian, Leonardian) Wichita and Clear Fork Groups in north-central Texas by bulk-sampling techniques (JOHNSON *& al.* 1994) allows for the first time a critical analysis of Early Permian xenacanth species. It is then possible to determine the biostratigraphic usefulness of xenacanth teeth. The results of this analysis, coupled with the analyses of much smaller collections of Late Carboniferous and earliest Permian (Wolfcampian = Asselian) teeth, permit the determination of taxonomically useful characters which may eventually be used to aid in interpretation of xenacanth phylogeny. Xenacanth taxonomy is confusing, and additional work is required before it can be reconciled. A preliminary attempt was made (JOHNSON 1979, pp. 237-286) based on the literature dealing with teeth; some of the assumptions were incorrect, but the annotated bibliography (JOHNSON 1979, pp. 271-286) may prove useful.

This study, together with another study on "*Xenacanthus*" [probably a new genus encompassing "*X.*" *luedersensis* (JOHNSON 1995, 1996), not to be confused with the ?*Xenacanthus* teeth described below] to be published later, reveals that considerable morphologic variation exists within individual xenacanth dentitions. The hazard of naming a new species based on a few isolated teeth will be made apparent. The detailed descriptions and inferred dentition analyses given here are intended to serve as the basis for subsequent taxonomic and biostratigraphical studies, moderated by rare discoveries of complete specimens described by others.

The Permian teeth, which serve as the primary basis for this study, are part of the Waggoner Ranch Collection (JOHNSON 1979, MURRY & JOHNSON 1987) which is reposited in the Shuler Museum of Paleontology at Southern Methodist University (SMU). The stratigraphic positions of the local faunas in the collection, their taxonomic constituents, and methods of recovery and processing are listed in JOHNSON (1979, pp. 580-632) and MURRY & JOHNSON (1987). Exact locality descriptions are housed with the collection.

Additional teeth used in this study are from the Upper Pennsylvanian (uppermost Carboniferous) Conemaugh and Monongahela Groups and Lower Permian Dunkard Group of the Dunkard Basin. They are reposited in the Carnegie Museum of Natural History (CM). Teeth from the Upper Pennsylvanian Towle Shale of Nebraska (Peru local fauna, OSSIAN 1974) were also examined. They are deposited in the Texas Memorial Museum (TMM), University of Texas, Austin. Xenacanth teeth reposited in the Museum of Natural History, University of Kansas (KUVP), Field Museum of Natural History (FMNH), and American Museum of Natural History (AMNH) were also studied. Study of the Fritsch collection at the National Museum, Prague, and additional specimens at the Czech Geological Survey helped resolve many of the taxonomic problems encountered by JOHNSON (1979).

The use of shark dentitions in determining their taxonomic relationships is not a pleasant alternative to using more complete specimens, especially when only isolated teeth are available. It is the only choice available in most instances. Only rarely have cartilaginous structures such as chondrocrania and fin elements been preserved for study. Among isolated elements, only the teeth can be easily studied. Dermal denticles may be more numerous, but many are not easily identified with certainty and have never been used to define taxa. Occipital spines have often been used to define taxa, but are far less common than teeth and may not be any more reliable for taxonomic purposes (JOHNSON 1979, pp. 78-80; see ZIDEK 1993a, for an opposing view).

Early workers often referred all xenacanth teeth to *Diplodus* if they were generally similar in morphology to the teeth figured by AGASSIZ (1843): teeth with a large base bearing lateral cusps (cones, denticles, etc.) larger than the median cusp(s), if present; in other words, not having the "cladodont" configuration. In attempts to demonstrate that "*Diplodus*" teeth belonged to the same shark that possessed either the *Xenacanthus* (*Pleuracanthus*) or *Orthacanthus* type of spine configuration (LUND 1970), paleontologists in North America only tended to confuse the taxonomic problem. *Orthacanthus* teeth bear compressed cusps which are often carinated and may be serrated (Text-fig. 1). In *Orthacanthus* the apical button (Text-fig. 1) is always in a lingual position, distinctly isolated from the cusps. Unfortunately, very few illustrations of xenacanth teeth in the literature show them in lingual ("posterior") view; they were almost always shown from the opposite side as early workers tended to stress the importance of the development of the intermediate cusps–sometimes a character of dubious value. Other distinguishing characters will become apparent as the various species are reviewed.

The pattern of the foramina on the aboral surface of the tooth base is not significant in distinguishing species (JOHNSON 1979, pp. 87-88, 1980, p. 930, 1984, p. 180). Each tooth has a unique pattern and can be individually identified by its pattern. Examples are included here to show variations in patterns. HAMPE (1993) provided a summary of an extensive study of the foramina presented in earlier papers. He did not rely so much on patterns of foramina as he did on their number on the oral and aboral surfaces of the tooth base. Although he could not distinguish individual species, he was able to demonstrate that *Xenacanthus* (in the strict sense) lateral teeth contain many more foramina (up to about 20 on each of the oral and aboral surfaces) than any teeth of *Orthacanthus* or *Triodus* (<10 foramina). The *Xenacanthus* medials, however, are about comparable with the other two genera. SCHNEIDER (1988) attempted to place various xenacanth species into morphologic groups. He included patterns of foramina as part of his analysis.

The xenacanths are generally considered to have been most diverse during the Late Carboniferous, based on numbers of both specimens (especially cephalic spines) and taxa. They were also common during the Early Permian, but the number of taxa (valid or invalid) is considerably lower. Differences in depositional environments between the European and North American Upper Carboniferous and the North American Lower Permian may be responsible (ROMER 1945; see a parallel example given by ZIDEK 1966).

GENERAL COMMENTS ON THE XENACANTHS FROM THE LOWER PERMIAN OF TEXAS

Three species of xenacanths have been recognized from the Lower Permian of mid-continental North America. An additional new species is described later in this report. Two species have traditionally been placed in the same genus; the generic name has undergone various changes, but *Orthacanthus* is generally accepted as being correct (LUND 1970). The two species, *O. texensis* and *O. platypternus*, are recognized mainly by differences in tooth morphology, as the teeth are usually the only preserved elements; minor differences have also been recognized in rarely preserved chondrocrania and lower jaws (HOTTON 1952). *Orthacanthus platypternus* may belong to a different genus, according to some, but is retained in *Orthacanthus* for reasons given below. Although occipital spines belonging to *Orthacanthus* are occasionally found, none have ever been identified to species until recently. Spines that definitely belong to *O. platypternus* (DONELAN & JOHNSON 1997) are being studied.

The third species of xenacanth, *Xenacanthus luedersensis*, was first described on the basis of teeth by BERMAN (1970). The generic assignment was accepted by JOHNSON (1979, and subsequent papers), but is probably incorrect. Similar teeth have been recognized from the Dunkard Basin (LUND 1970, 1976), but have not been described. This species will be discussed in a subsequent study. Fragments of spines from the Wichita Group (Table 1) that probably belong to "*X.*" *luedersensis* and *Orthacanthus* sp. are present in the Waggoner Ranch Collection (JOHNSON 1979, pp. 270, 287-289).

The xenacanths represent one of the most common groups of vertebrates in the Waggoner Ranch Collection. About 51,400 teeth (including discrete fragments) were recovered from more than 75 sites where the matrix was sampled; a few of these teeth were recovered by surface collecting. Numbers of teeth may be misleading, as xenacanths apparently shed their teeth in typical shark fashion, but their occurrence in nearly every sample of fossiliferous matrix collected attests to their abundance (see JOHNSON 1981a, p. 20, for comparison to abundances of other chondrichthyans). Their occipital spines might give a better indication of their relative abundance compared to other taxa, but the paucity of these spines in the geologic section would be misleading.

Orthacanthus texensis teeth are the most common in the Wichita Group with 25,700 counted compared to 19,450 for "*Xenacanthus*" *luedersensis* and nearly 2,300 for *O. platypternus*. However, because "*X.*" *luedersensis* teeth are smaller than the others, and as the 30-mesh fraction of washed matrix in some faunas was not fully sorted (see JOHNSON 1979, pp. 580-632), that species might be the most common. *O. platypternus* is represented by over 3,900 teeth in the Clear Fork Group. "*X.*" *luedersensis*? (JOHNSON 1996) is present only at the base of this unit, represented by only 40 teeth. *O. texensis* is absent in the Clear Fork Group.

	O. texensis	*O. platypternus*	*O. compressus*	?*X. slaughteri* sp. nov.	?*X. ossiani* sp. nov.
LOWER PERMIAN					
Clear Fork Group (Leonardian), Texas					
lower Choza					
Ignorant Ridge 100		65			
upper Vale					
Ignorant Ridge 94		50*			
middle Vale					
Crooked Creek 80		1367			
Crooked Creek 81		887			
lower Vale					
Crooked Creek 72		6			
Crooked Creek 70		136			
Rose Hollow Creek 67		14			
Fish Creek 61		13			
Fish Creek 60		28			
Fish Creek 59					
upper Arroyo					
Lost Lake 57		91			
West Coffee Creek 56		264			
middle Arroyo					
Indian Creek 52		5			
lower Arroyo					
East Coffee Creek 47		228			
East Coffee Creek 39		6			
East Coffee Creek 38		2			
East Coffee Creek 37		749			
East Coffee Creek 36		26			
Wichita Group (Leonardian), Texas					
middle Lueders (l. upper Waggoner Ranch)					
southwest Butte/ac (+88 m)	10	1		1	
Tit Butte/ac (+88 m)	144	25		1	
Lake Kemp B (+87 m)	330	105		5	
Lake Kemp B/ac (+87 m)	98	27		7	
Lake Kemp A (+86 m)	443	179, 1(?)		0	
Lake Electra/ac	51	1		0	
lower Lueders (u. mid. Waggoner Ranch)					
Mitchell Creek H (+72 m)	400	4		1	
Mitchell Creek G (+70 m)	17	12		0	
Mitchell Creek F/ac (+67 m)	6	0		0	
upper Clyde (mid. Waggoner Ranch)					
Mitchell Creek E (+60 m)	3	0		0	
Mitchell Creek E/ac (+60 m)	104	30		0	
Mitchell Creek D (+60 m)	0	0		0	
Mitchell Creek C (+59 m)	125	8		1	
Mitchell Creek B (+56 m)	17	9		0	
Mitchell Creek B/ac (+56 m)	1531	459, 12(?), 2[a]		1	
Mitchell Creek A (+56 m)	193	236, 1(?)		1	
Bluff Creek C	12	1		0	
Bluff Creek B	2	0		0	
Bluff Creek A	274	3		0	
Spring Creek B/ac (+53 m)	338	70		0	
La Paloma/ac (+50 m)	593	119, 2(?)		0	

	O. texensis	*O. platypternus*	*O. compressus*	?*X. slaughteri* sp. nov.	?*X. ossiani* sp. nov.
Spring Creek A/ac (+48 m)	199	52		0	
Spring Creek/ac (+48 m)	67	14		0	
Old Military Crossing (+44 m)	1	0		0	
middle Clyde (l. mid. Waggoner Ranch)					
West Franklin Bend C (+40 m)	1395	59, 1(?)		0	
West Franklin Bend C/ac (+40 m)	659	42		0	
Hackberry Creek C (+37 m)	1130	141		0	
West Franklin Bend B/ac (+36 m)	34	0		0	
West Franklin Bend A/ac (+34 m)	9	1		0	
Hackberry Creek B (+32 m)	1	0		0	
Hackberry Creek A/ac (+32 m)	49	2		0	
Franklin Bend A/ac (+24 m)	992	21		3	
Franklin Bend A (+24 m)	4614	42		0	
lower Clyde (lower Waggoner Ranch)					
Cottonwood Creek (+6 m)	4	0		0	
Brushy Creek O (+2 m)	11	0		0	
Brushy Creek N (+1 m)	1	0		0	
upper Belle Plains (upper Petrolia)					
Wolf Creek B/ac (–8 m)	32	10		0	
Wolf Creek B (–8 m)	1296	69		0	
Wolf Creek A (–8 m)	917	65, 1(?)		2	
Wolf Creek/ac (–8 m)	3664	172, 1(?)		0	
Brushy Creek M/ac (–9 m)	17	1		2	
Brushy Creek L/ac (–10 m)	3	1		26	
Brushy Creek K/ac (–10 m)	487	31		1(?)	
Brushy Creek J/ac (–10 m)	138	25, 1(?), 1[b]		6	
Brushy Creek I (–10 m)	200	90		2	
Brushy Creek H (–10 m)	25	6		0	
Brushy Creek G (–11 m)	2	0		0	
Brushy Creek F (–11 m)	510	29		1	
Brushy Creek E (–12 m)	626	14		2	
Brushy Creek D (–12 m)	80	8		0	
Brushy Creek C (–12 m)	2335	48		0	
Brushy Creek C/ac (–12 m)	1067	35		5	
Brushy Creek B (–12 m)	14	0		0	
upper Admiral (u. Nocona; Wolfcampian)					
Rattlesnake Canyon (?–100 m)	427	3		6	
Dunkard Group (Wolfcampian), Dunkard Basin					
Greene Formation					
Windy Gap Limestone					
Fairview Ridge	1	0			
upper Greene					
Postlewaithe Ridge	0	2			
lower Rockport Member					
Dallas Pike	5	49			
lower Greene					
Belpre	0	6			
Washington Formation					
upper Washington					
Powhattan Point	0	0			
Waynesburg Formation					
Colvin Limestone					
Franklin Mall	0	0	28[c]		
UPPER PENNSYLVANIAN					
Admire Group (Virgilian), Nebraska					
Towle Shale					

	O. texensis	*O. platypternus*	*O. compressus*	?*X. slaughteri* sp. nov.	?*X. ossiani* sp. nov.
Peru Site 2	0	0	50		22
Peru Site 3	1?	0	92		1
Monongahela Group (Virgilian), Dunkard Basin					
Pittsburgh Formation					
lower Pittsburgh					
Kennard Playground	0	3[a]	23		1[d]
Conemaugh Group (Virgilian), Dunkard Basin					
Conemaugh Formation					
Duquesne Limestone Bed No. 6					
Fort Pitt Tunnel-6	0	2[a]	21		1[d]
Duquesne Limestone Bed No. 2A					
Fort Pitt Tunnel-2A	0	0	14		0

[a] *Orthacanthus* aff. *platypternus;* [b] *Orthacanthus* cf. platypternus; [c] 13 teeth are *Orthacanthus* aff. *compressus*; [d] ?*Xenacanthus* cf. *ossiani*

Table 1. List of local faunas containing *Orthacanthus* and ?*Xenacanthus* teeth obtained by bulk sampling. Stratigraphic order is maintained as closely as possible. Numbers following the Clear Fork local fauna names are SMU locality numbers. Numbers in parentheses following the Wichita local fauna names are thicknesses in meters from the Belle Plains–Clyde contact (uncertain for Lake Electra/ac and especially Bluff Creek local faunas; horizons estimated from field notes and HENTZ and BROWN, 1987). Permian stratigraphic nomenclature in Texas based on JOHNSON (1979, Wichita Group) and JOHNSON (1996) with approximate equivalent names based on HENTZ (1988) in parentheses, and on MURRY & JOHNSON (1987, Clear Fork Group). Dunkard Basin stratigraphic nomenclature based on CMNH catalogue data, modified by U.S. Geological Survey stratigraphic nomenclature where possible. Age of the Admire Group is based on OSSIAN (1974) and BAARS (1991). Sample sizes vary considerably; see JOHNSON (1979, Wichita Group) and MURRY & JOHNSON (1987, Clear Fork Group); unknown for Peru and Dunkard Basin local faunas. * Surface collection; see JOHNSON (1979) and MURRY & JOHNSON (1987) for other, smaller surface collections from the Wichita and Clear Fork groups. Local faunas with no record of *Orthacanthus* teeth contain "*Xenacanthus*" teeth (probably a new genus; JOHNSON, in prep.). ? = teeth that are questionably identified.

The Waggoner Ranch Collection disproves the suggestions of DAVIS (1892) and WOODWARD (1891), among others, that all types of xenacanth teeth can occur in a single species. Only *Xenacanthus* teeth occur in the Upper Triassic (JOHNSON 1980; identified as *Triodus* by HAMPE 1989) and only *Orthacanthus* teeth occur throughout the Clear Fork Group except in the lower part (MURRY & JOHNSON 1987, JOHNSON 1996).

STRATIGRAPHIC NOMENCLATURE

The presence of marine and nonmarine facies of equivalent age in the Lower Permian of north-central Texas has produced a variety of schemes and resultant names in attempts to clarify the stratigraphy of that region. The older literature is reviewed by JOHNSON (1979), MURRY & JOHNSON (1987), and HENTZ (1988). A new approach to the problem was undertaken by HENTZ & BROWN (1987) and HENTZ (1988). This necessarily requires the introduction of several new names, but is clearly satisfactory, especially for the terrestrial facies ("classic area" of OLSON 1989).

As the presently described fossils from the Texas Permian are catalogued using the "old" (in part) stratigraphic nomenclature, that nomenclature will be largely used here in an informal sense. The terrestrial facies of the Clear Fork Group cannot be divided into formations. It is undifferentiated by HENTZ & BROWN (1987), MURRY & JOHNSON (1987), and OLSON (1989); for reasons described in MURRY & JOHNSON (1987), formation names are used informally (Table 1).

Thin marine limestones, some of which are persistent throughout the area containing the local faunas below the Clear Fork Group, provide excellent stratigraphic control (Table 1). For reasons stated by JOHNSON (1979), the designation Wichita-Albany Group was used. HENTZ & BROWN (1987), and HENTZ (1988), favored going back to the old system (in revised form) of designating the marine-nonmarine facies in the north as the Wichita Group and equivalent marine facies to the south as the Albany Group. That dichotomy is used here; hence, the Wichita-Albany local faunas in Johnson (1979, 1987) are presently assigned to the Wichita Group.

The informally used formation names in the Wichita Group in Table 1 include in parentheses their approximate equivalents assigned by Hentz & Brown (1987) and described by Hentz (1988). The contact between the Belle Plains and Clyde was placed at the Beaverburk Limestone by Johnson (1979), which differs from Hentz & Brown (1987). Hentz & Brown (1987) placed the contact between the Wolfcamp Series and Leonard Series in the upper Admiral. The Rattlesnake Canyon local fauna was questionably assigned a Wolfcampian (Sakmarian) age (Johnson 1981b), and is now accepted (Sander 1989). The Lueders Formation (Albany Group) extends northward to encompass the area on both sides of the Wichita River, which was prospected for fossils (Johnson 1979). Hentz & Brown (1987) and Hentz (1988) restricted the formation (as part of the Albany Group) to strata between the base of the Maybelle Limestone and top of the Lake Kemp Limestone; this is the upper Lueders in Johnson (1979, pp. 17-18), which did not yield any fossils until recently (Johnson 1996).

METHODS

Terminology

The terms used here to describe xenacanth teeth are taken from Hotton (1952) with some modifications (Text-fig. 1). The two large "lateral" cusps are here termed the principal cusps; if they are not of equal size, as in most *Orthacanthus* teeth, then the larger cusp is called major and the small cusp minor. The intervening, usually smaller cusps, if present, are called intermediate. If more than one intermediate cusp is present, then the largest is the primary and the others secondary. Labio–lingual and anteromedial–posterolateral (Compagno 1970) are used for basal width and length, respectively, of Hotton (1952). These terms are abbreviated l–l and am–pl in the descriptions below. Because the anteromedial and posterolateral ends of many teeth cannot be distinguished, the abbreviation am/pl is used in such instances, especially for the cusp margins. The inner margin of the principal cusps is here termed the medial margin. The enlarged foramen that occurs between the principal cusps in most species is termed the central foramen, to distinguish it from other foramina in the base.

The proximal portion of the principal cusps in all xenacanth teeth is compressed. The angle between the major transverse axis of this part of the cusp and a line parallel to the labial margin of the tooth base between the principal cusps is often

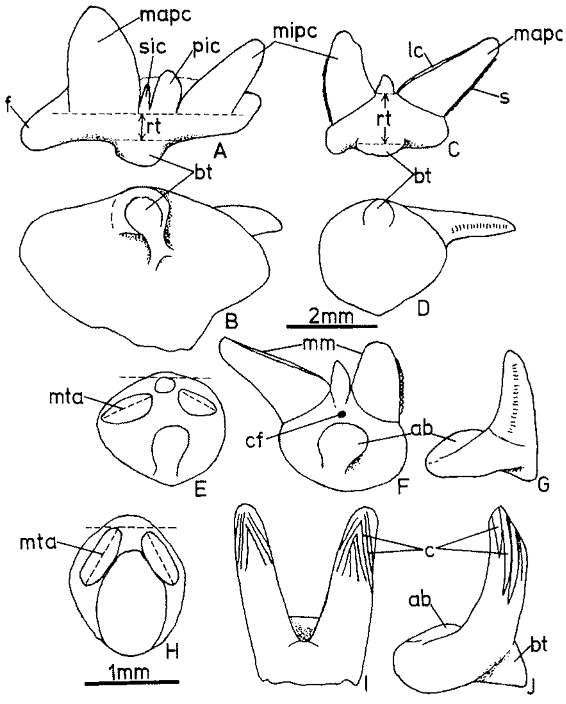

Fig. 1. Tooth morphological nomenclature used in this paper; A – labial, and B – aboral, views of *Orthacanthus platypternus*; C – labial, D – aboral, E – occlusal (oral, coronal), F – lingual-occlusal, and G – anteromedial, views of *O. texensis*; H – occlusal (oral, coronal), I – labial, and J – anteromedial or posterolateral, views of "*Xenacanthus*" *luedersensis* (see text); the serrations and cristae are slightly exaggerated; upper scale bar for A–G; lower scale bar for H–J; ab = apical button; bt = basal tubercle; c = cristae; cf = central foramen; f = flange; lc = lateral carina; mapc = major principal cusp; mipc = minor principal cusp; mm = medial margin of cusp; mta = major transverse axis of base of cusp; pic = primary intermediate cusp; rt = thickness of tooth base ("root" thickness); s = serrations; sic = secondary intermediate cusp; this terminology also applies to *O. compressus* and ?*Xenacanthus* teeth; dashed lines in E and H demonstrate differences in the angle between the major transverse axis of the principal cusps and the labial margin of the base

diagnostic. The relationship is shown in Text-fig. 1 E, H.

The terms used by APPLEGATE (1965) and COMPAGNO (1970) to describe tooth position and heterodonty are used in this study. Not all of the types of teeth they describe (such as intermediates and anteriors) seem to apply to xenacanth dentitions. Three terms used by APPLEGATE (1965) apply to *Orthacanthus* teeth: medials, laterals, and posteriors; each constitutes a suite (JOHNSON 1981a).

Adequate jaw material with attached teeth that would clarify the nature of the heterodonty in North American *Orthacanthus* specimens has not been described. Only a gradient monognathic heterodonty (COMPAGNO 1970) apparently exists in the dentition; a statistical analysis was not attempted to demonstrate this, however. Evidence of dignathic heterodonty and dental sexual dimorphism is not apparent. Ontogenetic heterodonty may occur, but this would be difficult to demonstrate using isolated teeth; however, it may exist and is discussed below.

Measurements

Selected samples of teeth from the Waggoner Ranch Collection along with those from the Peru

			Range		Mean ±1 s. d.		Linear Regression	
Local Fauna	N	n	am–pl	l–l	am–pl	l–l	m	b
				O. texensis				
(a) Lake Kemp B	330	87	0.9- 5.2	1.0-5.5	2.6±0.8	2.6±0.9	1.06±.06	–0.21±.16
(b) Mitchell Creek H	400	84	1.2- 6.4	1.1-6.7	3.4±1.1	3.6±1.4	1.15±.07	–0.26±.24
(c) Mitchell Creek B/ac	1531	98	1.3- 6.7	1.4-6.9	3.2±1.0	3.4±1.2	1.07±.06	–0.06±.21
(d) Hackberry Creek C	1130	96	1.2- 6.4	1.2-7.7	2.8±1.1	2.9±1.2	1.12±.06	–0.23±.18
(e1) Wolf Creek/ac	3664	98	1.2- 7.9	1.1-8.5	3.4±1.4	3.7±1.6	1.07±.06	+0.02±.21
(e2) Wolf Creek/ac		99	0.9- 6.6	0.7-7.1	3.3±1.3	3.7±1.4	1.04±.07	+0.22±.24
(f) Brushy Creek I	200	35	1.0- 6.5	1.1-6.6	3.0±1.3	3.2±1.3	0.97±.09	+0.24±.29
(g) Rattlesnake Canyon	427	80	1.0- 6.2	1.1-8.0	3.2±1.3	3.4±1.5	1.12±.08	–0.13±.27
				O. compressus				
(h) Peru Site 3	94	73	0.8- 3.0	0.9-3.3	2.0±0.5	1.9±0.5	0.97±.13	+0.03±.26
				O. platypternus				
(i) Ignorant Ridge 100	65	20	2.3- 9.1	2.3-8.1	5.3±2.1	4.6±1.6	0.73±.13	+0.77±.73
(j) Ignorant Ridge 94	50	17	3.9-13.2	4.0-9.3	8.0±2.7	6.4±1.7	0.59±.09	+1.62±.75
(k) Crooked Creek 81	887	76	0.9- 7.4	1.1-5.9	3.3±1.5	3.0±1.1	0.74±.05	+0.52±.17
(l) Crooked Creek 80	1367	98	1.6- 8.2	1.3-6.6	3.8±1.4	3.3±1.2	0.78±.05	+0.38±.19
(m) Crooked Creek 70	136	43	1.9- 7.6	2.1-5.8	3.7±1.2	3.2±0.8	0.61±.09	+0.97±.34
(n) Lost Lake 57	91	27	1.5-10.0	1.8-7.6	4.3±2.0	3.5±1.3	0.65±.05	+0.69±.23
(o) West Coffee Creek 56	264	39	1.4- 7.5	1.0-5.2	4.2±1.5	3.0±0.9	0.60±.05	+0.47±.22
(p) East Coffee Creek 47	228	55	2.0-13.0	1.5-9.5	5.2±2.6	4.1±1.8	0.66±.05	+0.70±.26
(q) East Coffee Creek 37	749	91	1.4- 8.2	1.3-5.8	4.0±1.4	3.1±1.0	0.69±.05	+0.32±.20
(r) Lake Kemp B	105	21	0.9- 7.8	0.6-6.0	3.0±1.7	2.3±1.3	0.74±.05	+0.11±.22
(s) Mitchell Creek B/ac	473	89	0.9-10.0	0.8-6.4	3.7±1.6	2.6±1.1	0.62±.04	+0.28±.16
(t) Hackberry Creek C	141	27	1.1- 8.7	0.8-6.0	3.9±1.9	2.8±1.2	0.64±.07	+0.28±.30
(u) Wolf Creek/ac	173	30	1.2- 6.4	0.6-3.9	3.2±1.4	2.1±0.9	0.60±.07	+0.16±.23
(v) Brushy Creek I	90	24	0.9- 5.4	0.7-3.7	2.6±1.3	1.8±0.9	0.60±.10	+0.28±.29
(w) Brushy Creek C	48	20	1.1- 7.5	0.8-5.2	3.4±1.4	2.3±1.0	0.68±.06	+0.05±.22
				?*X. slaughteri* n. sp.				
(x) Brushy Creek L/ac	26	23	0.41-1.09	0.36-0.66	0.67±.18	0.49±.09	0.36±.13	+0.24±.09
				?*X. ossiani* n. sp.				
(y) Peru Site 2	19	13	0.93-1.26	0.45-1.03	1.12±.13	0.69±.17	0.88±.56	–0.29±.63

Table 2. Summary of *Orthacanthus* and ?*Xenacanthus* tooth measurements (in millimeters). N = number of teeth in the local fauna and n = number of measured teeth; am–pl = anteromedial–posterolateral, l–l = labio–lingual, s.d. = standard deviation; m = slope and b = y–intercept, with 95% confidence intervals determined by method given in Simpson & *al.* (1960).

local faunas were measured for three reasons: (1) to attempt to better define *Orthacanthus* species for purposes of future comparisons with other collections; (2) to determine the usefulness of these measurements for comparison between valid species of this genus; and (3) to determine if any intraspecific changes occurred stratigraphically in the sampled section represented by the Waggoner Ranch Collection. Sampling procedures, method of measurement, and the accuracy of the measurements are discussed in JOHNSON (1979, pp. 90–94). Two measurements were taken for each tooth, maximum labio–lingual (l–l) width and maximum anteromedial–posterolateral (am–pl) length of the tooth base. The am–pl measurements were more easily determined, so they are considered the independent variable and used as the abscissas in plotting the measurements (scatter diagrams) and calculating respective linear regressions (JOHNSON 1979, pp. 152–155, 174–176, 189).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Order Xenacanthiformes (= Pleuracanthodii) BERG, 1940
Family Xenacanthidae FRITSCH, 1889

REMARKS: Taxonomic nomenclature follows that of CAPPETTA & *al.* (1993); see ZIDEK (1993a, b) for further discussion. All xenacanth teeth consist of a single base ("root") bearing a single lingual apical (oral) button and a single labial basal (aboral) tubercle. The crown consists of two principal cusps protruding from the labial margin of the oral basal surface. One or more smaller cusps may occur between the principal cusps. See HOTTON (1952) for a description of their mode of replacement.

Genus *Orthacanthus* AGASSIZ, 1843

TYPE SPECIES: *O. cylindricus* AGASSIZ, 1843.

1843. *O. gibbosus* (AGASSIZ); see WOODWARD 1889, JOHNSON 1979, pp. 251–252, 271, 276–277.
1843. *Diplodus* AGASSIZ, p. 204, Pl. 22B, Fig. 1; WOODWARD 1889, p. 10.
1889. *Orthacanthus* FRITSCH, pp. 100–112, Pls. 81–90; LUND 1970, pp. 239–240, Fig. 3.
1946. *Xenacanthus* OLSON, pp. 286–288, 291–292, Fig. 1; HOTTON 1952, pp. 489–500, Pl. 58; BERMAN 1970, pp. 19–20.
1952. *Dittodus* ROMER 1952, pp. 50–52.

REMARKS: The holotype of *Orthacanthus* is based on an isolated occipital spine (AGASSIZ 1843). Following WOODWARD (1889), JOHNSON (1979) argued that *O. gibbosus* should be the type species. Teeth associated with incomplete specimens of sharks bearing this type of spine are considerably larger, on the average, than other xenacanth teeth. Consequently, more of these teeth have been discovered and have served as the basis of several species. *Orthacanthus* teeth are readily distinguished from "*Xenacanthus*" teeth, as LUND (1970) pointed out. Examination of the teeth from the Waggoner Ranch Collection (especially), Peru local faunas, and some of the Carnegie Museum specimens suggests the following tentative dental diagnosis: Principal cusps normally lack cristae and are labio–lingually compressed with edges usually developed into carinae that may or may not be serrated; major transverse axes of proximal ends are nearly parallel with the labial margin of the base between these cusps. One or more intermediate cusps are usually present. Apical button is distinctly isolated from cusps; central foramen is present. Dentition is heterodont.

The most obvious and distinguishing feature of these teeth is the lenticular cross section of the principal cusps (lanceolate cusps; HAMPE 1988a). HAMPE (1988a), SCHNEIDER (1988), and SOLER-GIJÓN (1997a) stated that essentially all *Orthacanthus* teeth have serrated (crenulated) carinae. However, it is demonstrated below that otherwise typical *Orthacanthus* teeth (*i.e.*, *O. compressus*) may have cusps that lack serrations. Whether any species of *Orthacanthus* has teeth that consistently bear multiple cristae as in "*Xenacanthus*" and other genera has yet to be demonstrated. Teeth of the Permian species are very rarely cristate (discussed below). *Orthacanthus* species have heterodont dentitions which cause considerable difficulty in summarizing their characteristics and distinguishing between species, especially if only a small number of teeth is available. The lingual margin of the base is occasionally bifurcate in certain *Orthacanthus* teeth. The surface of the base tends to be rough or even punctate.

Orthacanthus texensis (Cope, 1888)
(Text-figs 1-8, Tables 1-3)

1884b. *Didymodus compressus* (Newberry); E. Cope, p. 573.
1885. *Diacranodus compressus* (Newberry); S. Garman, p. 30.
1888. *Didymodus texensis* n.sp.; E. Cope, p. 285.
1889. *Diacranodus texensis* (Cope); A. Woodward, p. 15.
1908. *Pleuracanthus texensis* (Cope); L. Hussakof, p. 28.
1911. *Diacranodus texensis* (Cope); L. Hussakof, p. 159.
1952. *Xenacanthus texensis* (Cope); N. Hotton, pp. 497, 498, Fig. 4.

MATERIAL: All of the teeth used in this study are from the Waggoner Ranch Collection and are catalogued as SMU 64120–64238. Included in that collection are several deformed teeth (Johnson 1987). Catalogued specimens listed by Johnson (1979) bear the prefix "SMP–SMU," but that designation is no longer used.

OCCURRENCE: *Orthacanthus* teeth have been identified to species only occasionally in the literature. *Orthacanthus texensis* has been reported from beds of Wolfcampian (Asselian–Sakmarian) and questionably earlier age in the Dunkard Basin by Lund (1975; see also Johnson 1992a). Hotton (1952) reported the species in Texas to be confined to the Wichita Group, including the Lueders Formation (as now defined; Johnson 1996), but it is also present in the underlying Archer City Formation, Bowie Group (= Cisco Group), which is Wolfcampian (Sakmarian) (Hentz & Brown 1987, Sander 1989, Johnson 1992a,b). Teeth from the Archer City Formation are currently being studied. Occurrences in Oklahoma are summarized in Johnson (1979, pp. 168–169). Some of these may be younger than any found thus far in Texas, as they come from beds that may be equivalent to the Arroyo (Clear Fork Group). *O. texensis* is not present in the Clear Fork Group in north-central Texas (Johnson 1987, Murry & Johnson 1987; Table 1). Studies of teeth obtained by bulk sampling from Oklahoma localities have been initiated in order to resolve this problem. Other North American occurrences, either Early Permian or Late Pennsylvanian, include New Mexico, possibly Kansas, and Prince Edward Island (Johnson 1992a). Occurrences of *O. texensis* outside of North America have not been reported, but it may be present in the Lower Permian of Europe, notwithstanding taxonomic problems (Johnson 1979, pp. 170–171) and other factors discussed below.

REMARKS: As Hotton (1952, p. 496) noted, Cope did not describe the teeth of this species, but had earlier (Cope 1884a), and again in a subsequent paper (Cope 1884b), referred them to *Didymodus compressus*. Cope (1884b) described the species (using the name *D. compressus*) on the basis of several chondrocrania and one set of jaws, but did not refer this Texas material to *D. texensis* until four years later without comment (Cope 1888). Hussakof (1908) designated a type [under "*Pleuracanthus texensis* (Cope) 1883"; however, Cope (1883) was referring to fossils from Illinois (probably from the Upper Carboniferous; Olson 1946) and did not describe any xenacanth fossils except to replace the preoccupied name, *Diplodus*], AMNH 7117, consisting of "Facial portion of one skull and roof portions of two others; two teeth." He later (Hussakof 1911) revised Cope's (1884b) diagnosis (using *Diacranodus* Garman 1885) and listed Cope's illustrated crania as cotypes (AMNH 7117, 7928–7930). AMNH 7117 then consisted of the facial portion of the chondrocranium (as above) and the two teeth; examination of the two isolated teeth clearly demonstrates, as he suspected, that they are not associated with the chondrocranium.

Both of the isolated teeth are incomplete. The smaller of the two is here designated the holotype, AMNH 7117. Being surface-collected, AMNH 7117 is typically larger than average (see below), with an am–pl length of about 10.5 mm and l–l width of 9.9 mm. (Most *O. texensis* teeth are wider than long.) The apical button is isolated from the central foramen (Text-fig. 1) and is flush with the lingual margin of the base. Other foramina are absent from the oral (coronal) surface, although very small ones might occur beneath the rim of the apical button. Five or six prominent foramina occur on the aboral surface along with nearly two dozen smaller ones closely associated with the lingual and am/pl margins of the well developed basal tubercle; three additional prominent foramina occur along the lingual margin of the base. A small part of the base is missing because one of the principal cusps is broken off. The remaining principal cusp is complete and bears faint serrations on both marginal carinae; this cusp is slightly twisted owing to a somewhat sigmoidal shape, which is normal. Two intermediate cusps were present, but are now broken.

The second isolated tooth, AMNH 19604, is larger than the holotype, about 15 mm long and 15–17 mm wide, but the base is incomplete. The area of the central foramen is covered by matrix. The apical button is well developed and is isolated from both the cusps and the lingual margin of the base, which is bifurcated. The basal tubercle is broken away. Both principal cusps are broken; serrated medial carinae are present, but the am/pl carinae are badly worn. A single intermediate cusp was present, but is broken at its base. This tooth served as a model for COPE's (1884b) Figure 5, which is clearly a composite of the base and incomplete cusp of AMNH 19604 and the complete cusp of AMNH 7117 (holotype).

The chondrocranium, with naturally articulated hyomandibula and "showing upper and lower jaws from right side" (HUSSAKOF 1911), is now designated as AMNH 19605 (without the isolated teeth). Further preparation of AMNH 19605 to expose two teeth reveals the principal cusps to be weakly serrated: ". . . we were able to find evidence of a faint serration, or more properly a scalloped margin as the serrations are not usually pointed but low and rounded. These are found on both the inner and outer cutting margins of the cusps. Both the teeth we cleaned seem to be from the upper jaw and are from the left side." (John G. MAISEY, *pers. comm.*). The specimen was sagitally sectioned at some time in the past, but neither HUSSAKOF (1911) nor SCHAEFFER (1981), who did not use this specimen in his description, mentioned this. AMNH 19605 cannot serve as the holotype because the teeth cannot be confirmed as belonging to *O. texensis* in the sense of HOTTON (1952) and this study, whereas AMNH 7117 (the newly designated holotype) and AMNH 19604 do fit this concept. The teeth in AMNH 19605 are considerably smaller than the holotype, but do not differ significantly from the average sizes in Table 2. Not enough detail about them is known, and as the geographic and stratigraphic information is vague [Permian beds of Texas, COPE 1884b; Wichita (Permian), HUSSAKOF 1908], the possibility that AMNH 19605 belongs to *O. compressus* cannot be ignored. The collector, JACOB BOLL, worked throughout Baylor and Archer Counties (GEISER 1948); *O. compressus* probably occurs in Archer County (JOHNSON 1992b).

HOTTON (1952) described some skeletal material (palatoqudrates and Meckel's cartilages) and associated teeth. Because the number of available teeth was limited, it seems appropriate to revise that part of the diagnosis. The criteria listed by HOTTON to differentiate between *O. texensis* and *O. platypternus* teeth are straightforward. Unfortunately, the large number of teeth for these species now available tends to diminish the value of these criteria, although they are useful in identifying a majority of the teeth. Most of the problems in identification arise when the smaller teeth are encountered. Also, as HOTTON (1952) pointed out (and alluded to by LUND 1976), distinguishing *O. texensis* and *O. compressus* teeth is difficult at best.

Orthacanthus texensis teeth may be defined as follows: base with labio–lingual dimension usually greater than anteromedial–posterolateral dimension; basal tubercle usually restricted to labial portion of tooth base, only occasionally extending to the center; labial margin between basal tubercle and oral surface of base thicker between principal cusps than at am/pl margins of the cusps. Major principal cusp more divergent and often more coarsely serrated than the minor principal cusp. One or more intermediate cusps usually present.

Unfortunately, exceptions to nearly every one of these criteria can be found in the Waggoner Ranch Collection owing to the heterodont nature of these teeth. The most consistent criterion is the thick labial margin of the base (rt in Text-fig. 1), which distinguishes these teeth from *O. platypternus* teeth. Some *Orthacanthus compressus* teeth possess this character, however.

DESCRIPTION

Measurements: Samples of teeth from seven local faunas ranging from the upper Admiral to the middle Lueders were measured (Table 2). Measured teeth from higher in the Lueders (JOHNSON 1996) do not differ from these measurements. The Mitchell Creek H and Rattlesnake Canyon local faunas were included because they have a higher than average number of *O. texensis* teeth and very few *O. platypternus* teeth. Analysis of the *O. texensis* teeth does not elucidate what inhibited the occurrence of *O. platypternus* in these faunas. *O. texensis* teeth from Rattlesnake Canyon do not show any characteristics of *O. compressus*, which had been suspected because of their stratigraphic position (see above). There is very little change throughout the sampled section. As READ (1943) interpreted the sedimentary environment of the Mitchell Creek H locality, the additional data may prove useful in future paleoecologic interpretations.

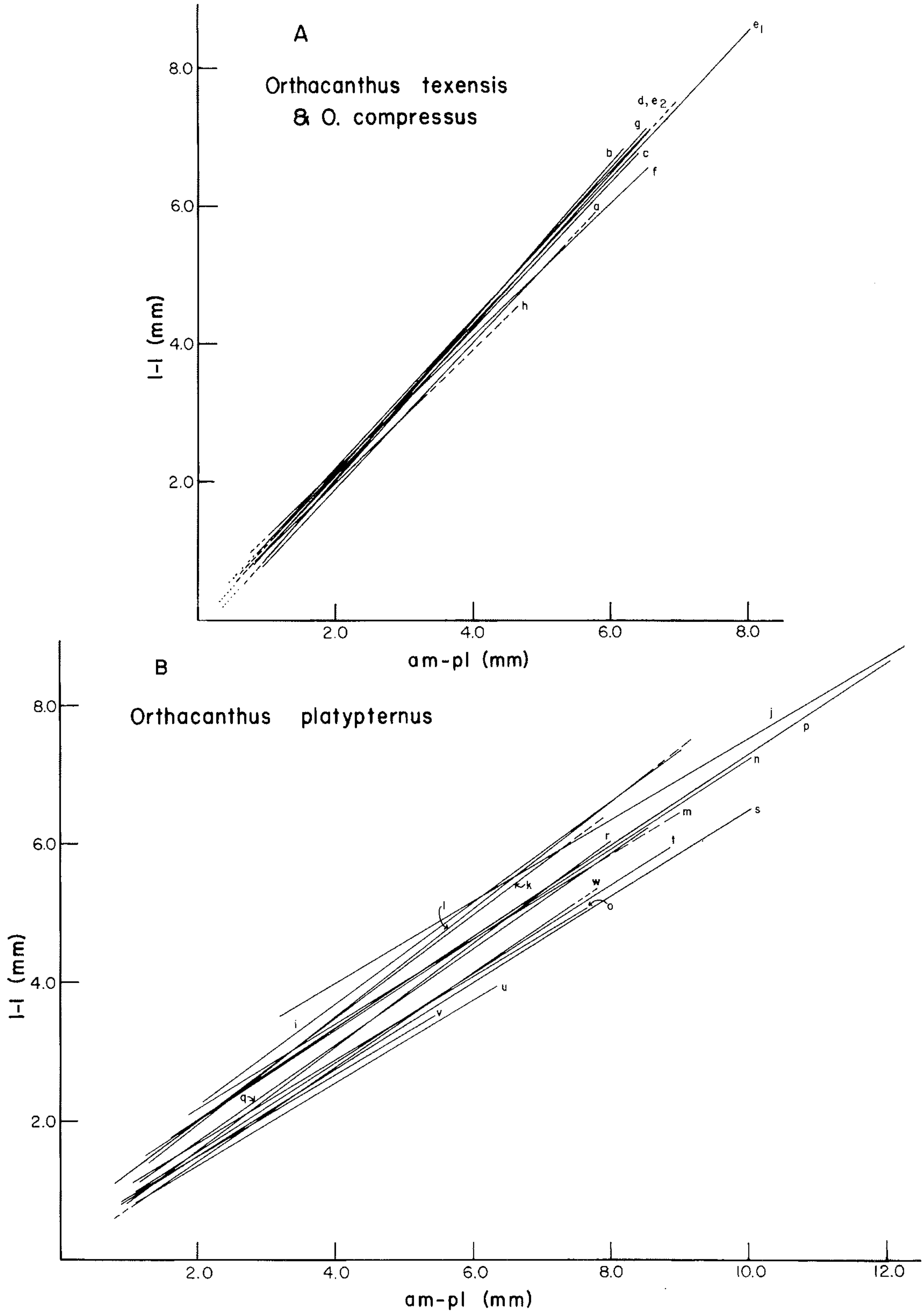

Fig. 2. Regression of labio–lingual (l–l) tooth-base dimension on anteromedial–posterolateral (am–pl) dimension for A, *Orthacanthus texensis* (a–g) and *O. compressus* (h), and B, *O. platypternus* (i–w) teeth; letters refer to faunas in Table 2; lengths of lines approximately represent the respective ranges of measurements; dashes and dots are for clarity

Although about 65 % of the fine-grained (less than 1.2 mm) concentrate was not utilized in producing the Mitchell Creek B/ac and Wolf Creek/ac local faunas, the calculated means in Table 2 for both *O. texensis* and *O. platypternus* are only slightly affected, less than 1/4 standard deviation, by using split samples (JOHNSON 1979, p. 151).

As shown in Table 2 and Text-figs 2 and 3, the measurements of *O. texensis* teeth remain fairly uniform throughout the section. The largest teeth were recovered from the upper Belle Plains (most notably Brushy Creek D and F local faunas); they have anteromedial–posterolateral and labio–lingual dimensions in the 15 to 18 mm range.

The relationship between the am–pl and l–l dimensions remains virtually unchanged throughout the section (Text-fig. 2), with variation little greater than between the two samples of the Wolf Creek/ac local fauna. The slopes of the regression lines are nearly = 1 (Table 2), demonstrating that HOTTON's (1952) criterion of tooth bases "wider than long" is far from universal. However, they are significantly different from those of *O. platypternus*.

Tooth base: HOTTON (1952) noted that the tooth base of *O. texensis* is massive. However, as will be discussed later, some of the teeth (medials) lack this appearance. He also noted that it bears a "strong basal tubercle" compared to *O. platypternus*. In the Waggoner Ranch Collection, *O. texensis* teeth generally have a pronounced basal tubercle, but there is considerable variation. In large teeth it may be protuberant and rounded. In most teeth its articular surface faces lingually and forms a distinct angle with the aboral surface, often as much as 45°. It is usually restricted to the labial portion of the base (Text-fig. 4), unlike *O. platypternus* and *O. compressus* where it often extends to the center of the base. In the latter two species, but especially *O. platypternus*, the articular surface of the basal tubercle generally forms only a shallow angle with the base.

The apical button is usually in contact with the lingual margin. It may form a shelf on either am/pl side under which one or more foramina usually occur. It is generally more prominent in the larger teeth. The central foramen is always

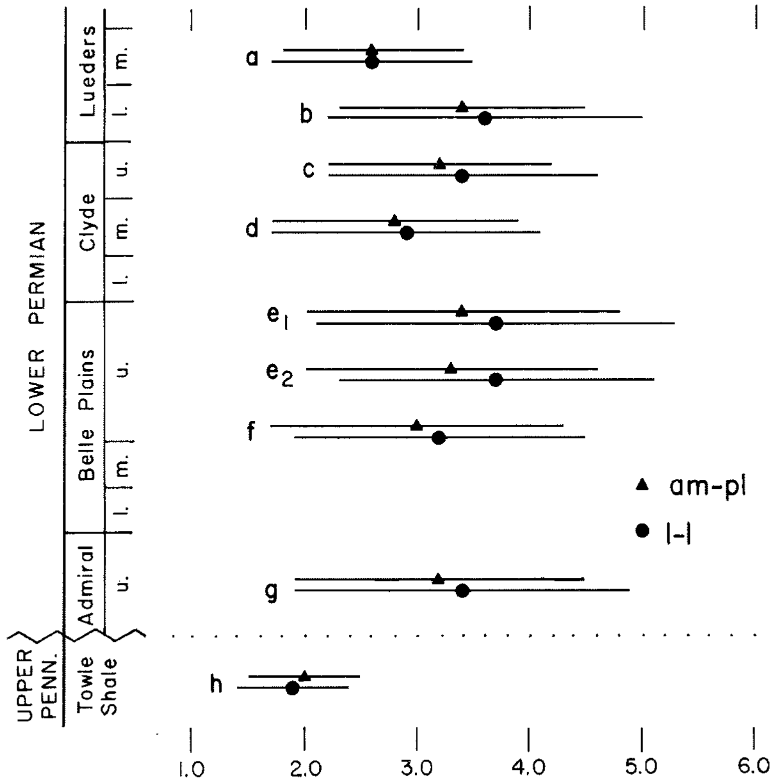

Fig. 3. Tooth-base dimensions (in millimeters) of *Orthacanthus*: Mean ±1std. dev. a–g, *O. texensis*; h, *O. compressus*; letters refer to faunas in Table 2; am–pl = anteromedial–posterolateral, l–l = labio–lingual

present and may be accentuated by occurring in a pronounced depression. Rarely, two foramina are present in its place. Other foramina tend to be scattered about the surface of the base of many of the teeth, especially the laterals. SCHNEIDER 1988, 1996 (both Fig. 3) illustrates a pattern of foramina on the aboral surface of an *O. texensis* tooth base diagram (and incorrectly assigns the species to Newberry). He shows three lingually placed foramina, quite unlike the sketches in Text-fig. 4.

The lingual margin of the base may be bifurcated, especially in the larger teeth (Text-fig. 4).

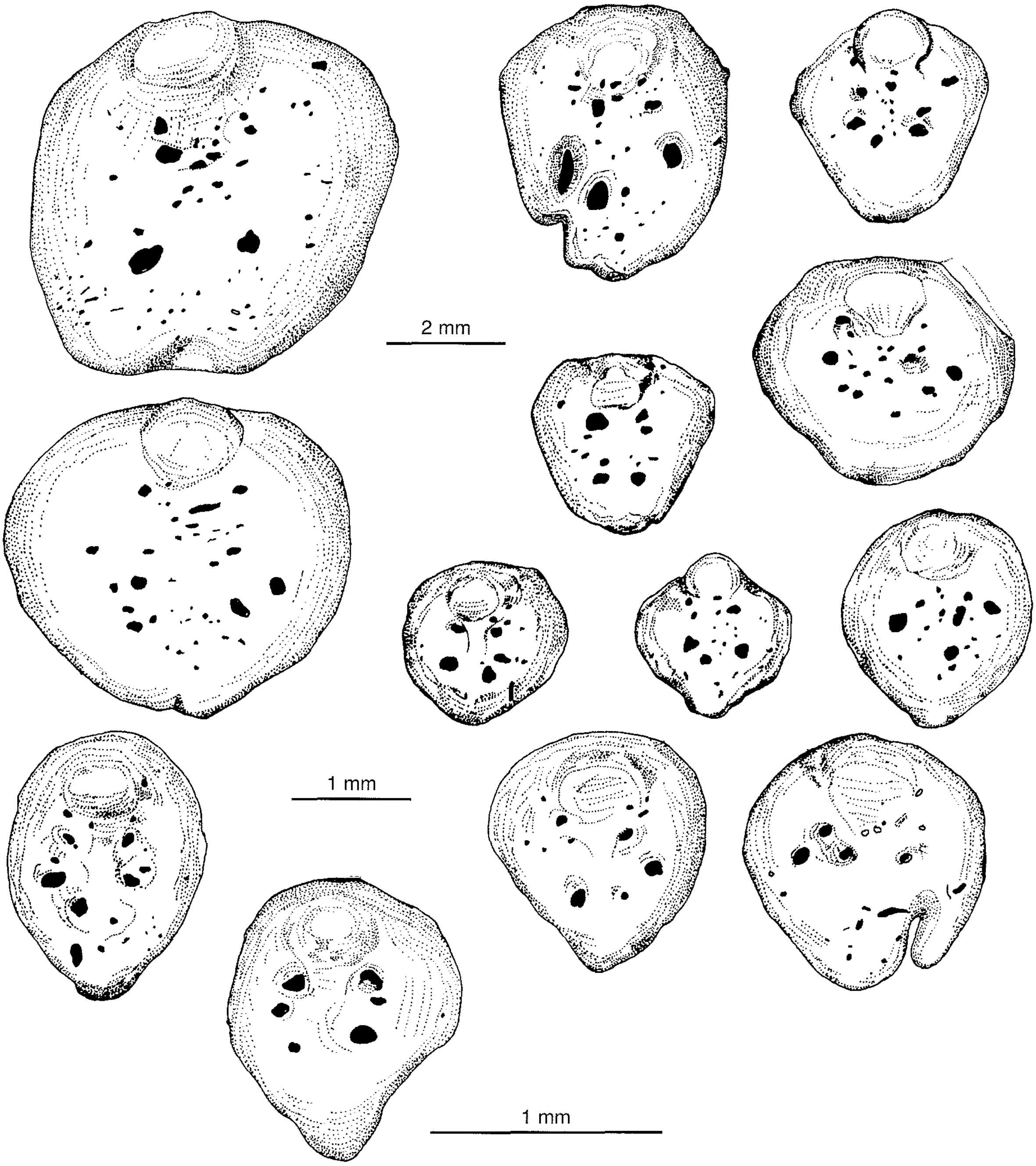

Fig. 4. Sketches of *Orthacanthus texensis* aboral tooth surfaces from the Brushy Creek I local fauna, upper Belle Plains; upper scale bar is for the upper nine sketches; the middle scale bar is for the next three sketches, and the lower scale bar is for the remaining sketch

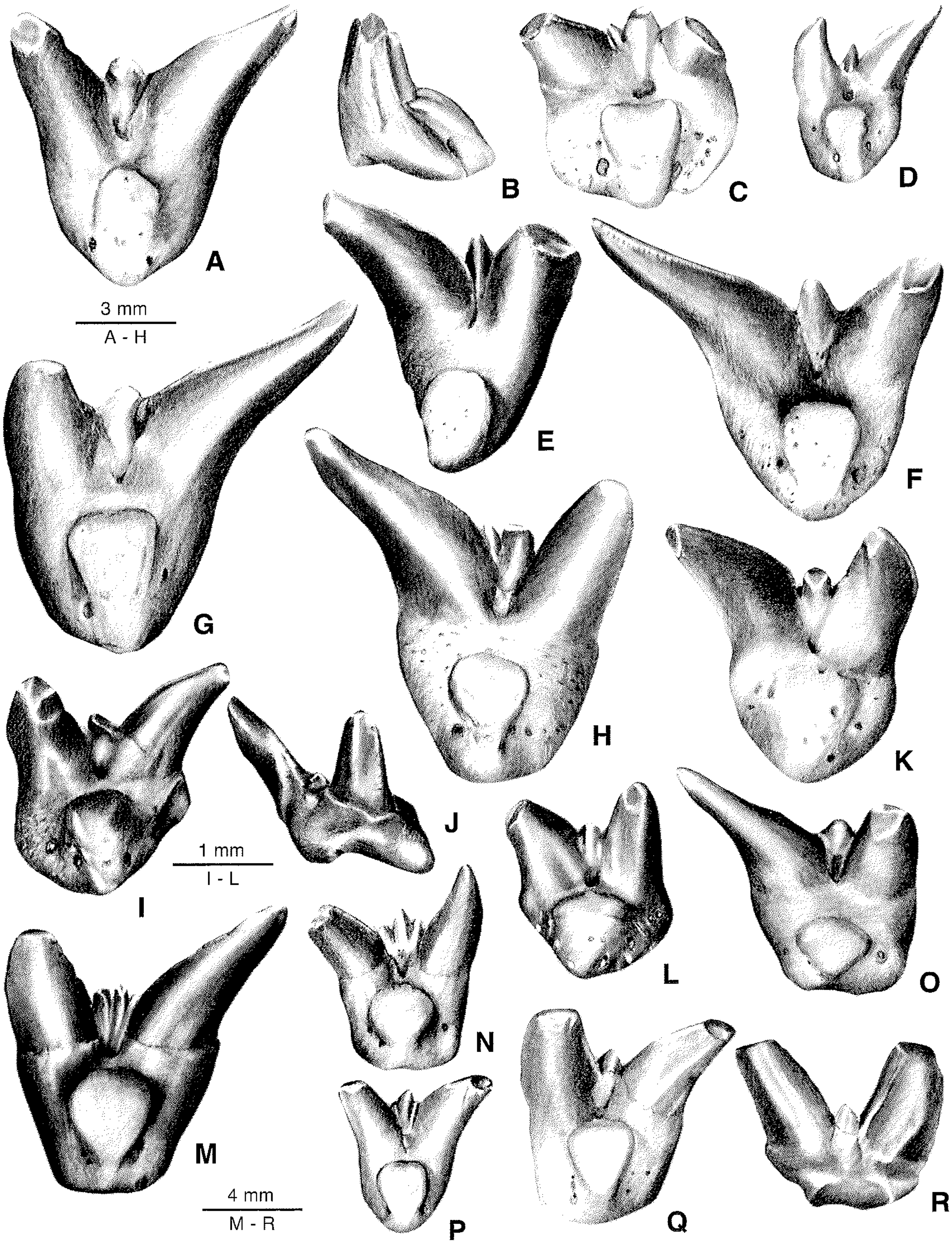

Fig. 5. *Orthacanthus texensis* lateral teeth from the Wolf Creek/ac local fauna, upper Belle Plains; A – lingual-occlusal view of SMU 64225; B – anterior, and C – lingual-occlusal, views of SMU 64224; D-H – lingual-occlusal views of SMU 64231, 64222, 64220, 64218, and 64221, respectively; I – lingual-occlusal, and J – anterolabial, views of SMU 64232; K-P – lingual-occlusal views of SMU 64233, 64234, 64214, 64216, 64215, and 64219, respectively; and Q – lingual-occlusal, and R – labial, views of SMU 64217; note the subdued serrations on the medial lateral carina of the major principal cusp in F. D could be considered a posterolateral tooth; the major principal cusp in O is twisted so that the medial margin is facing lingually, but does not appear to be an actual deformity

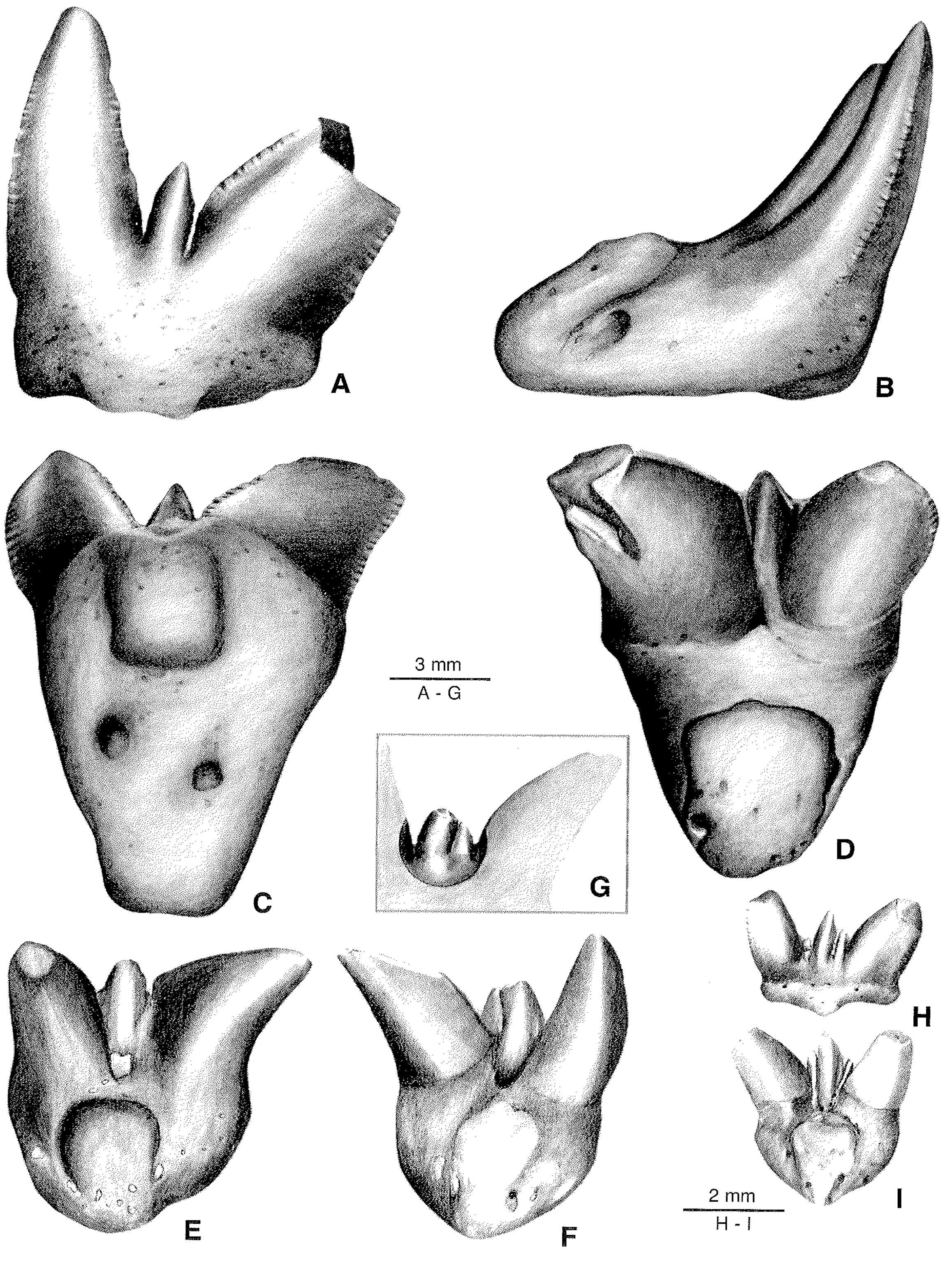

Fig. 6. *Orthacanthus texensis* lateral teeth; A – labial, B – anterior, C – aboral, and D – occlusal, views of SMU 64187 from the Mitchell Creek H local fauna, lower Lueders; E-G, teeth from the Lake Kemp B/ac local fauna, middle Lueders; E – lingual-occlusal view of SMU 64184; and F – lingual-occlusal, and G – partial labial, views of SMU 64185; H – labial and I – lingual-occlusal, views of SMU 64212 from the Tit Butte/ac local fauna, middle Lueders

In many of the smaller teeth it tends to protrude because of a prominent apical button, giving the base a triangular or trapezoidal shape (Text-figs 4, 5E, 6I). The aboral surface tends to be slightly concave, or less commonly is flat.

Principal cusps: The principal cusps of *O. texensis* are generally dissimilar. The major cusp (Text-fig. 1) tends to be more divergent, and so is presumably on the posterior side of the tooth. The minor cusp is usually rather straight, or leans

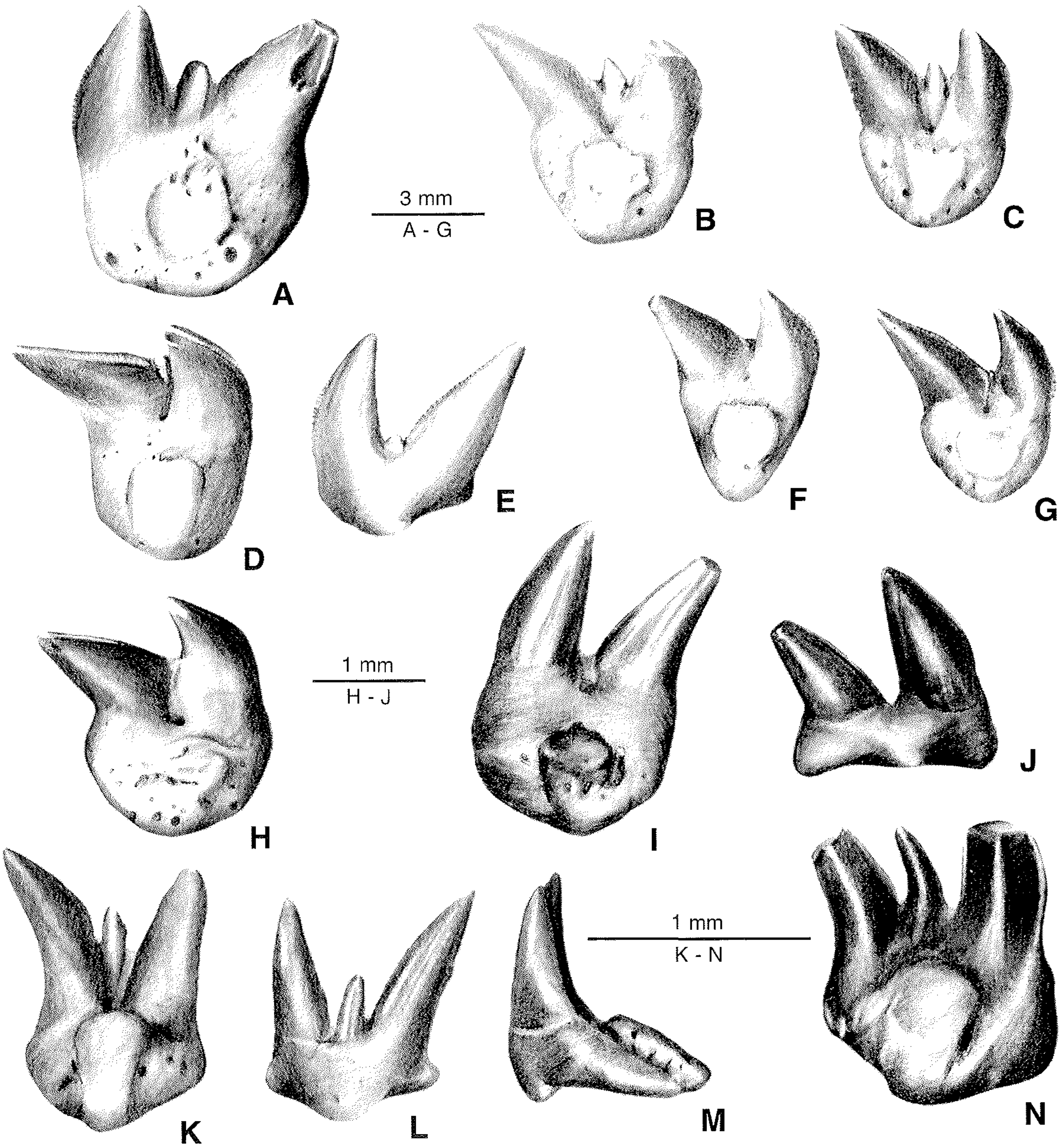

Fig. 7. *Orthacanthus texensis*; A-E – posterolateral teeth from the Wolf Creek/ac local fauna, upper Belle Plains; A-C – lingual-occlusal views of SMU 64223, 64226, and 64227, respectively; and D – lingual-occlusal, and E – labial, views of SMU 64228; F-H – posterior teeth from the Wolf Creek/ac local fauna; lingual-occlusal views of SMU 64230, 64229, and 64235, respectively; *Orthacanthus ?texensis* posterior tooth (SMU 64188) from the Wolf Creek B local fauna, upper Belle Plains; I – lingual-occlusal, and J – labial, views; note the thin base in J; medial tooth (SMU 64213) from the Wolf Creek B local fauna; K – lingual-occlusal, L – labial, and M – posterolateral, views; N – *Orthacanthus ?texensis* medial tooth (SMU 64183) from the Brushy Creek K/ac local fauna, upper Belle Plains; oblique lingual-occlusal view

toward the major cusp to varying degrees, presumably depending on the position of the tooth in the jaw. A similar arrangement of the cusps occurs in *O. senkenbergianus* (HAMPE 1988a), *O. gracilis* and *O. kounoviensis* (HAMPE 1994), and *O. meridionalis* (SOLER-GIJÓN 1997a). Both cusps are serrated, especially on the am/pl margins; only in some of the larger teeth are serrations present on the medial margins (Text-figs 5F, 6A). There appears to be no pattern to the serrations (see FRITSCH 1889, Pl. 85, Figs 10 and 18, for a similar example) except that they are coarsest (fewer per mm) at the proximal ends of the cusps, and are coarser on the major cusp.

In many of the smaller teeth the principal cusps are of similar size and appearance, or nearly so. They are divided into two groups, interpreted as posteriors and medials (Text-fig. 7F–N). The posteriors bear cusps which lean in the posterior direction and are essentially parallel to one another. They tend to be rather stout-looking and rise from a relatively massive base. They are often not serrated. In the medials, the principal cusps are more slender and originate from a base with a thin lingual margin. The cusps may be slightly apically divergent, or nearly parallel to one another; or one may be slightly divergent and the other nearly straight or leaning toward it (but is usually not parallel to it). Only the larger teeth tend to have serrated cusps.

Intermediate cusps: HOTTON's (1952) assessment of the intermediate cusp ("cuspule") in *O. texensis* teeth agrees closely with my observations of the teeth in the Waggoner Ranch Collection. The frequency of occurrences of these cusps in the teeth used for measurements is given in Table 3. The number of observations is less than the number of teeth measured because cusps were broken and a few teeth were not fully developed (JOHNSON 1979, p. 163). If more than one intermediate cusp is present, one (primary intermediate cusp) is almost always larger than the secondary intermediate cusps (Text-fig. 1A). HOTTON's (1952) estimate that about 10 % of the teeth lack an intermediate cusp is valid throughout the sampled section. His estimate that about 20–25 % of the teeth have multiple cusps is higher than my observations, as the average size of the teeth he examined from surface collections was greater than that in the Waggoner Ranch Collection. Multiple intermediate cusps tend to occur in larger teeth, but there are many exceptions (Text-fig. 6H, I). Teeth with two secondary intermediate cusps are probably more common in the lower part of the section, because larger teeth are more common there. One tooth in the Rattlesnake Canyon local fauna has four secondary intermediate cusps (three are smaller than the fourth) – five intermediate cusps in all. A tooth in the Brushy Creek C local fauna has four intermediate cusps of equal size; another has three.

If a single secondary intermediate cusp is present, it usually occurs between the primary and the major principal cusp and leans in the same direction (Text-fig. 5H). Multiple secondary cusps generally occur on both sides of the primary cusp, but other combinations rarely occur.

The intermediate cusps are not as compressed as the principal cusps nor are any serrated. Also, as HOTTON (1952) pointed out, they are always small. However, in some of the medials the single intermediate cusp may be slightly more compressed than usual, rather long, and slender. This is more typical of *O. platypternus* teeth, but in the examples considered here the tooth base is of the *O. texensis* type (Text-fig. 1C). This condition occurs in other teeth (JOHNSON 1979, p. 164), but their identification is questionable because the labial margin of the base is rather thin (Text-fig. 7N).

Unusual teeth: Besides the extreme variants of otherwise average teeth and obviously abnormal teeth (JOHNSON 1979, pp. 216–218) and deformed teeth (JOHNSON 1987), there are some *O. texensis* teeth in the Waggoner Ranch Collection that are quite unusual. As they probably did not occur in a functional dentition, their description is omitted here; see JOHNSON (1979, pp. 164–167). They are very likely not fully developed teeth (tooth embryos of HAMPE 1997a).

Local Fauna	No. of teeth observed	% with intermediate cusps		
		primary	1 secondary	2 secondaries
Lake Kemp B	85	92	6	0
Mitchell Creek H	76	88	4*	0
Mitchell Creek B/ac	83	89	10*	0
Hackberry Creek	89	91	0	0
Wolf Creek/ac	192	86	8*	2
Brushy Creek I	34	91	3	3
Rattlesnake Canyon	77	92	10	4

Table 3. Frequency of occurrence of intermediate cusps in *Orthacanthus texensis* teeth.
*one tooth present with a secondary cusp equal in size to the primary cusp

Remarks: The teeth in the uppermost part of the sampled section tend to be slightly smaller than elsewhere. There is no evidence to suggest that this is indicative of any ecological change that might be relevant to the disappearance of *O. texensis* at the end of Wichita time. A comparable size reduction in "*X.*" *luedersensis* teeth occurs in the middle Lueders (Johnson 1979). However, *O. platypternus* was not affected.

HETERODONTY

Lateral teeth: The typical teeth of *O. texensis*, with the serrated, divergent major principal cusp, are here termed laterals (Text-figs 5, 6, 8). Because the major cusp is presumably at the posterior end of the tooth, then it follows that the teeth with the more divergent major cusp were situated correspondingly closer to the commissure, accompanied by a decrease in size (Text-fig. 8). No attempt was made to correlate tooth size with cusp divergence to determine the pattern of tooth size in the arcade, but presumably the larger teeth would occur in about the middle of the lateral suite (Text-figs 5G, M–O, Q, R; 6A–O). Those laterals with the minor principal cusp leaning toward the major cusp (Text-fig. 7A–E) were positioned closer to the posterior end of the lateral suite. Smaller laterals with highly divergent major principal cusps that might occur closer to the posterior end of the lateral suite are not common. Laterals with divergent principal cusps probably occupied the anterior portion of the suite, presumably decreasing in size toward the symphysis (Text-figs 5F, H, P; 6H, I).

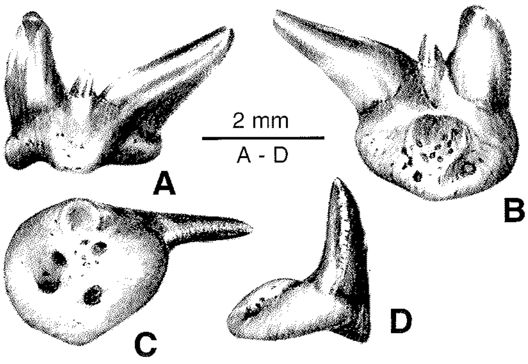

Fig. 8. *Orthacanthus texensis* lateral tooth (SMU 64211) from the Rattlesnake Canyon local fauna, upper Admiral; A – labial, B – lingual-occlusal, C – aboral, and D – anterior, views

The base of the laterals displays an asymmetry corresponding to the principal cusps. The larger part of the base, lying to one side of an imaginary line from the midpoint between the principal cusps through the center of the apical button, almost always underlies the minor cusp (Text-fig. 1, E–F).

Posterior teeth: As noted in the description of the principal cusps, the smaller teeth can be divided into posteriors and medials. They occur in about equal numbers. The posteriors (Text-fig. 7F–J) often lack an intermediate cusp. A sharp demarcation in size probably does not occur between them and the laterals. The main gradational effect is that the presumed anteriorly placed posteriors have serrated cusps, whereas those nearest the posterior end of the suite do not. No attempt was made to determine if any relationships exist between the extent of the serrations, presence of an intermediate cusp, and the size of the posteriors.

Medial teeth: The typical medials of *O. texensis* (Text-fig. 7K–N) appear to be gradational with the laterals. Those having the greatest degree of bilateral symmetry are presumably closest to the symphysis. Only the larger medials have serrated principal cusps; any correlation between presence of serrations and symmetry was not determined. The correspondence between the major cusp and smaller supporting part of the base seen in the laterals of *O. texensis* is sometimes reversed in the asymmetrical medials.

Remarks: The laterals account for a large majority of the teeth in the arcade. Although they include the largest teeth in *O. texensis*, they seldom, if ever, include teeth of smaller sizes. The laterals always have serrated cusps. Also, they are the only teeth in this species to have multiple intermediate cusps. Many of the posteriors and smaller medials lack serrated cusps.

The presumed positions in the dental arcade of the varying forms of laterals described above (and in Johnson 1979) are largely supported by Hampe's (1988a) Fig. 2 for *O. senkenbergianus* and Soler-Gijón's (1997a) Fig. 8A for *O. meridionalis*. Exceptions appear to be restricted to *O. meridionalis* which lacks teeth with the minor principal cusp leaning toward the major cusp and has smaller laterals with a highly divergent major principal cusp.

The medials tend to be similar to the corresponding *O. platypternus* teeth, except for the generally thicker labial margin of the base in *O. texensis*. They probably cannot be distinguished from the typical *O. compressus* medial teeth, despite the tendency of those teeth to have a thin base. The lingual basal margin of the *O. texensis* medials tends to be quite thin (Text-fig. 7M), and therefore easily misidentified as *O. platypternus* teeth unless the labial margin is also examined.

Orthacanthus platypternus (COPE, 1884)
(Text-figs 1-2, 9-14; Tables 1-2)

1884a. *Didymodus platypternus* n.sp.; E. COPE, p. 818, Pl. 23.
1884b. *Didymodus platypternus* COPE; E. COPE, p. 586–587, Figs 8–9.
1885. *Diacranodus platypternus* (COPE); S. GARMAN, p. 30.
1908. *Pleuracanthus platypternus* (COPE); L. HUSSAKOF, p. 28.
1911. *Diacranodus platypternus* (COPE); L. HUSSAKOF, p. 160–161.
1952. *Xenacanthus platypternus* (COPE); N. HOTTON, p. 495–498, Fig. 2.

REMARKS: HUSSAKOF (1911) listed the holotype as AMNH 7243, consisting of numerous fragments of a pair of large jaws and two incomplete and isolated teeth, and quoted COPE's (1884b) original description of the lower jaw. However, the fragments consist mostly of ceratohyals and are not diagnostic (John G. MAISEY, *pers. comm.*). The diagnostic parts are the incomplete teeth. One of these teeth has a complete base (aboral view *in* COPE 1884b, Fig. 9) and is regarded as the holotype, AMNH 7243. The remainder of the material is catalogued as AMNH 19602 (second isolated tooth) and 19603 (jaw fragments). There is no doubt that these teeth fit HOTTON's (1952, p. 498) description of *X. platypternus* teeth. However, the base of the holotype is more symmetrical than most teeth, as it lacks a flange at the anterior end (see below). The base is 11.6 mm long and 8.6 mm wide and slightly thicker at the presumed anterior end. A central foramen cannot be confirmed because of matrix interference. A small part of the apical button is broken off; it is isolated from the cusps and lingual margin of the base. There are three or four foramina on the coronal surface; a more precise determination is complicated by a pitted lingual margin. Four or five prominent foramina and a few smaller ones occur on the aboral surface. The subdued basal tubercle has a flat surface. Both principal cusps are broken; the left one, as seen in lingual view, may be posterolateral. A single intermediate cusp was present.

The second tooth, AMNH 19602, is larger than the holotype, but has a broken base and cusps. It is 10.2 mm wide and 13.0 mm long as preserved, with an estimated complete length of 14.2 mm. There is no evidence of a flange, but it could have been broken off. The base is thin, with a very platelike lingual margin. The coronal surface has about nine prominent foramina and several smaller ones (complicated by pitting). The aboral surface has four or five prominent foramina, but the total number cannot be determined because of pitting (this type of preservation is common in the larger teeth of this species). The apical button and basal tubercle are similar to the holotype. The cusps are completely broken off; an intermediate cusp was present.

MATERIAL: The teeth in the Waggoner Ranch Collection serve as the basis for the study of *O. platypternus*. They are catalogued in the Shuler Museum as SMU 64240–64318, 69146–69156, 69162–69212. Included in this collection are several deformed teeth (JOHNSON 1987). In addition, teeth were examined from the Lower Rockport Member of the Greene Formation in Ohio County, West Virginia (CM 26485; 49 teeth plus fragments; 5 teeth plus fragments are *O. texensis*), the upper part of the Greene Formation (Postlewaithe Ridge) at Wileyville, West Virginia (CM 25678, 2 teeth) and the lower Greene Formation at Belpre, Ohio (CM 25665, 6 teeth).

OCCURRENCE: Thus far, *O. platypternus* has been reported only from Texas, Oklahoma, and the Dunkard Basin (JOHNSON 1992a), except for a remarkably preserved skeleton from Kansas (ZIDEK 1993b). HOTTON (1952) thought it was restricted to the Clear Fork Group, as it had been found only in the Arroyo. BERMAN (1970) reported the occurrence of *O. platypternus* teeth in the Lueders, thereby extending it down into the Wichita Group, where they are present throughout the sampled portion of the Wichita (JOHNSON 1981a). They are present throughout the Clear Fork Group (MURRY & JOHNSON 1987; JOHNSON 1987). OLSON (1956) recovered skeletal material from the Vale. The teeth are considerably less common than those of *O. texensis* in the Wichita Group, with the Mitchell Creek A local fauna being the only significant exception (Table 1). *O. platypternus* is probably present below the upper Admiral, although only three teeth were recovered from the Rattlesnake Canyon locality.

OLSON & BEERBOWER (1953) recovered two broken teeth (FMNH UF508) from the Upper Permian San Angelo Formation in the Double Mountain Group, but refrained from making a specific identification. Both teeth are enclosed in matrix. One is exposed in anteromedial–posterolateral section through the principal cusps and base. It is probably *Orthacanthus*, based on size (larger than "*Xenacanthus*"). The second specimen appears to be a partial base of a large *O. platypternus* tooth. OLSON (1962) mentioned additional teeth recovered from the San Angelo Formation that were similar to teeth from the Clear Fork Group. These San Angelo teeth presumably belong to *O. platypternus*, but I did not see them in the Field Museum collection.

OLSON (1965) recovered a tooth and a spine in Oklahoma from different localities in the Upper Permian Chickasha Formation. He considered the tooth (UF 974) to be most similar to *O.* (*X.*) *platypternus*. The posterolateral margin is broken away and the base is dorsoventrally crushed, but is similar to *O. platypternus* teeth from the Clear Fork Group.

O. platypternus teeth have been reported from the Lower Permian of Oklahoma by SIMPSON (1979), who referred to them as *X. platypternus*. I have collected them at the Waurika locality (OLSON, 1967; included in SMU 68562).

LUND (1975, 1976) reported *O. platypternus* teeth from the Lower Permian (Wolfcampian = Sakmarian), but not the Upper Carboniferous, of the Dunkard Basin. A few teeth from the Gzhelian (Virgilian, Table 1) may be closely related to *O. platypternus*; they are discussed below. The only reported Upper Carboniferous occurrence of this species is the skeleton of a juvenile from the Hamilton Quarry in Kansas; its age is also Gzhelian (ZIDEK 1993b). CHORN & SCHULTZE (1990) reported *Orthacanthus* sp. teeth from the Robinson locality (Soldier Creek Shale Member of the Bern Limestone, Gzhelian); at least one of them (KUVP 72341) is *O. platypternus*.

O. platypternus has not been reported from outside of North America, but it may be present in the Upper Permian of Russia (OLSON 1962; JOHNSON 1979, p. 170).

REMARKS: The earlier discussion of HOTTON's (1952) study of *O. texensis* applies equally to *O. platypternus*. The number of teeth of *O. platypternus* now available suggests that a few of them may be difficult to distinguish from *O. compressus* because of heterodonty. The present collection also demonstrates that the criteria used by HOTTON to define *O. platypternus* are slightly diminished in validity. As with *O. texensis*, most of the *O. platypternus* teeth are easily recognized, but some of the smaller teeth are equivocal. BERMAN (1970) alluded to this when he stated that most of the teeth can be assigned with confidence.

Orthacanthus platypternus teeth may be defined as follows: tooth base with labio–lingual dimension less than anteromedial–posterolateral dimension; basal tubercle often flat, extending to center of base; labial margin between basal tubercle and oral surface of base between principal cusps is as thin as at the base of am/pl margins of principal cusps. Major principal cusp generally straight or leaning slightly toward minor principal cusp, which diverges posteriorly in lateral teeth; cusps always lack serrations. Intermediate cusp rarely absent and almost always single.

As with *O. texensis* teeth, there are exceptions to virtually every criterion that can be used to describe *O. platypternus* teeth. The exceptions often trend toward characters defining *O. texensis* teeth. However, COPE (1884b) very aptly named this species, for there are no teeth from the Wichita Group assigned to it that do not possess a platelike base. This character becomes less distinct in most of the teeth from the Clear Fork Group, but they all possess a thin base as seen in labial view (Text-fig. 1A). The two species can be almost always distinguished if isolated teeth are examined for a combination of characters. Unfortunately, a thin base commonly occurs also in *O. compressus* and in the new species of ?*Xenacanthus* described below.

DESCRIPTION

Measurements: The Brushy Creek C sample (Table 2) was added to the five standard Wichita samples to extend coverage as low as possible in the section. Eight samples are included from the Clear Fork Group. A ninth (from Ignorant Ridge

94 local fauna) is included in Table 2 merely to represent the upper half of the Vale and to demonstrate the bias resulting from surface collecting. As shown in Text-figs 2 and 9, in the Wichita samples the anteromedial–posterolateral length of the tooth base is consistently greater than the labio–lingual width. Of a total of 211 teeth measured, only one (JOHNSON 1979, Fig. 37) did not follow this pattern. This exception, and other deviations, involve only small teeth. More exceptions occur in the Clear Fork Group, but are uncommon; most involve smaller teeth. Teeth measured by JOHNSON (1996) from the upper Lueders (as shown in Text-fig. 9) are slightly larger than those from lower in the Wichita Group and are more comparable in size to those in the Clear Fork Group (Text-fig. 9). As Text-fig. 2 shows, the relationship of these two dimensions is significantly different from that of *O. texensis*. Casual examination of surface-collected *O. platypternus* teeth from the Wichita Group would suggest an even greater difference, as the protuberance on the lingual margin of the base (Text-fig. 10) is easily overlooked in these teeth. A similar protuberance may also occur in *O. texensis* teeth (Text-fig. 4), but this only increases their tendency toward being wider than long.

Tooth base: The usually oval-shaped thin base with its anterior extension or flange is the most striking feature of *O. platypternus* teeth, especially the larger ones (Text-figs 1; 11L, M;

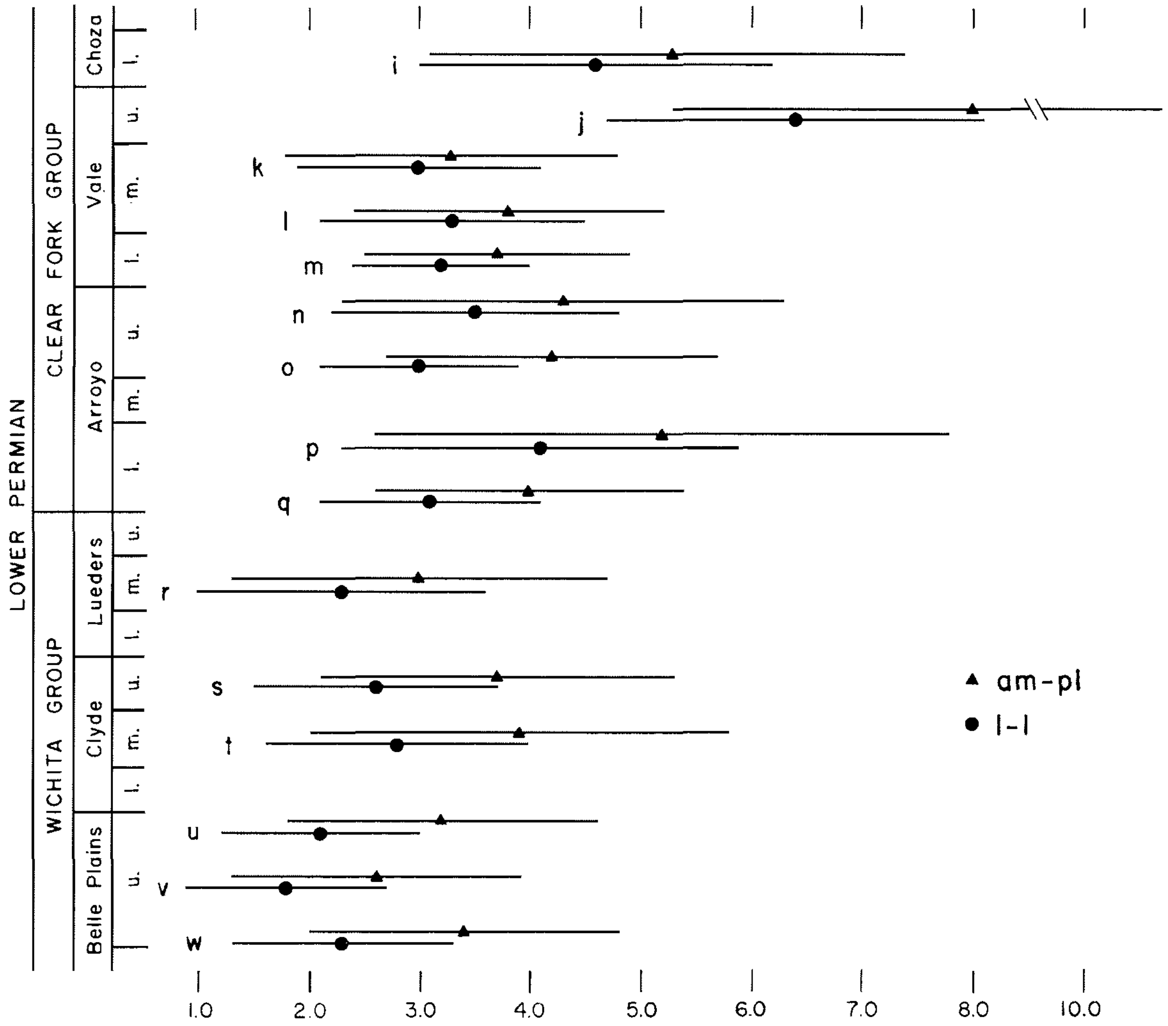

Fig. 9. Tooth-base dimensions (in millimeters) of *Orthacanthus platypternus*; mean ± 1 std. dev.; letters refer to faunas in Table 2; scale is compressed to accommodate j (surface collection; see text); am–pl = anteromedial–posterolateral, l–l = labio–lingual

12N), but some small ones as well (Text-fig. 11F, G). Although the base tends to be extended both anteriorly and posteriorly from beneath the cusps in the lateral teeth, it is the anterior extension that is most extensive. Of 204 Wichita teeth that were examined specifically for this feature (nearly all of those that were measured), half had a flange. In the other half the basal extensions were only moderate and equally developed or absent (Text-fig. 13). Only a few of the teeth from the Clear Fork Group have a well developed anterior flange. Most merely have basal extensions (Text-fig. 12J–N), or even those are absent.

The basal tubercle is generally flatter than in *O. texensis* teeth, with the articular surface nearly parallel to the aboral surface, but there is a considerable overlap between the two species. Its extension to the center of the base is often very subtle. Foramina tend to converge on the aboral surface of some teeth to produce an elongate (am–pl) groove between the basal tubercle and the center of the base; no extension of the basal tubercle occurs. Two of the measured teeth from the Crooked Creek 81 local fauna possess unusual basal tubercles. One has a secondary basal tubercle extending to the lingual margin, in addition to a normally

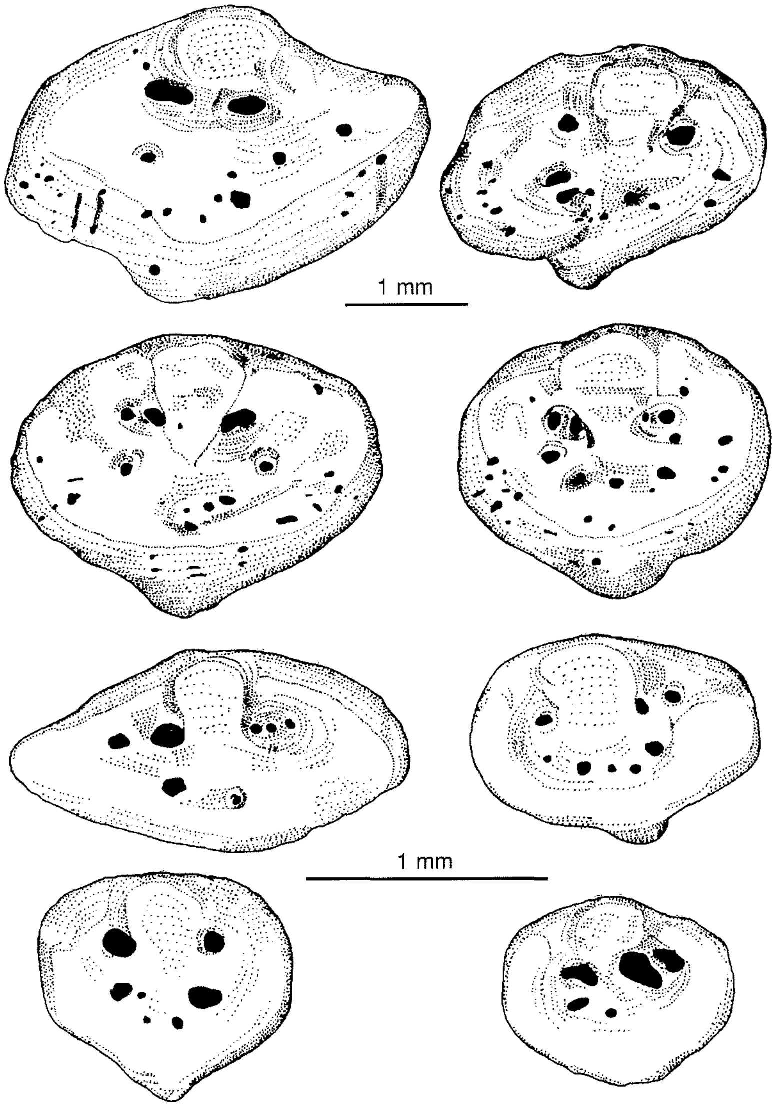

Fig. 10. Sketches of *Orthacanthus platypternus* aboral tooth surfaces from the Brushy Creek I local fauna, upper Belle Plains; upper scale bar is for the upper four sketches; lower scale bar is for the lower four sketches

positioned basal tubercle. The other has an exceptionally asymmetrical base with the basal tubercle shifted toward one of the am/pl margins. In larger teeth the aboral surface is often marked by small grooves or furrows radiating outward toward the lingual and am/pl margins. The aboral surface is slightly concave to flat.

The apical button is small and does not dominate the oral surface of the base as in *O. texensis* teeth (HOTTON 1952). However, in smaller teeth with nearly equidimensional bases no distinction can be made from *O. texensis*. The apical button and base often extend lingually to form a protuberance in the Wichita teeth. The protuberance is

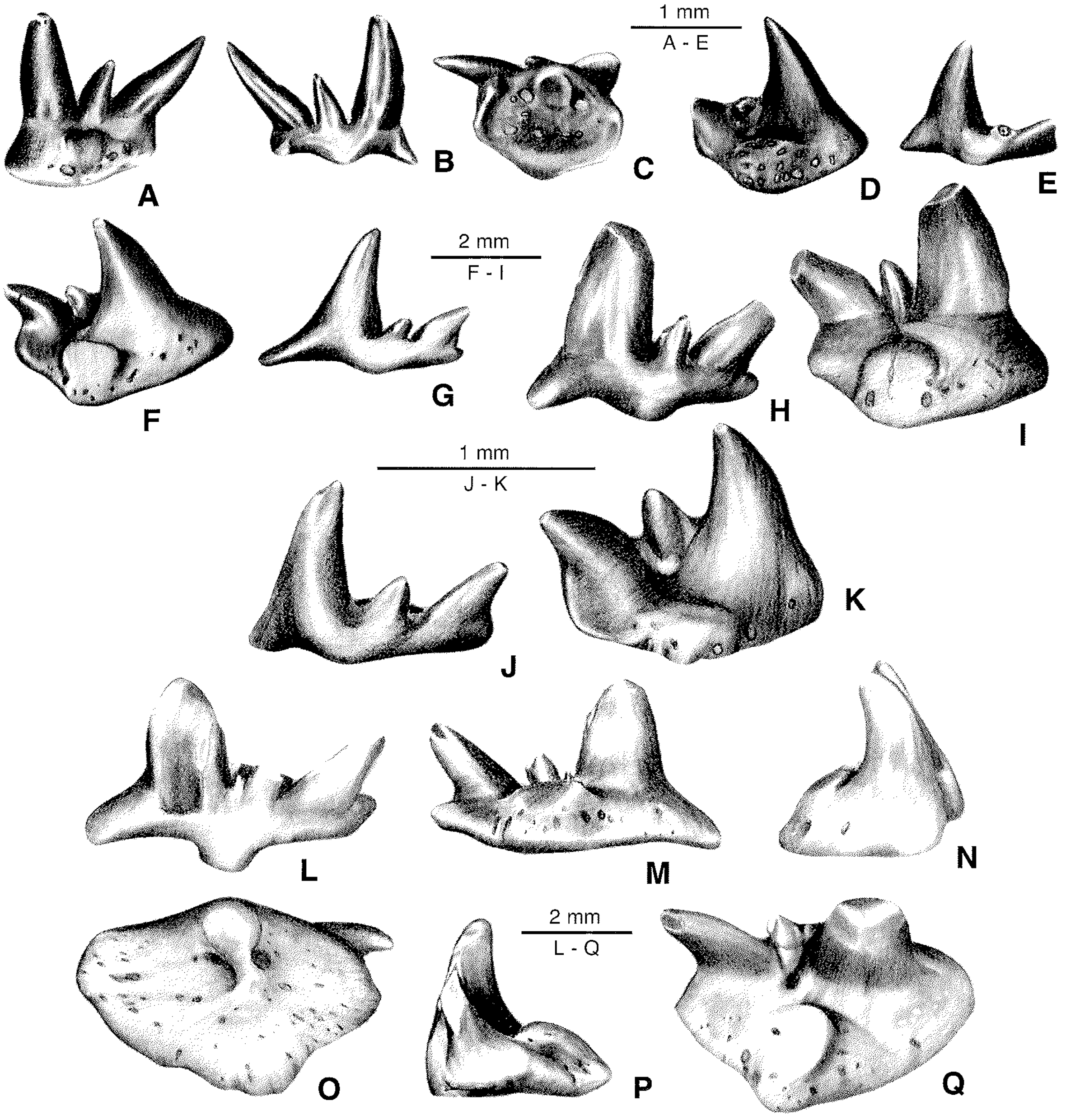

Fig. 11. *Orthacanthus platypternus* lateral teeth; A-K – from the Brushy Creek C/ac local fauna, upper Belle Plains; A – lingual-occlusal, B – labial, and C – aboral, views of SMU 64294; D – lingual-occlusal, and E – labial, views of SMU 64297; F – lingual-occlusal, and G – labial, views of SMU 64295; H – labial, and I – lingual-occlusal, views of SMU 64296; and J – labial, and K – lingual-occlusal, views of SMU 64298; L – labial, M – lingual, N – anterior, O – aboral, P – posterior, and Q – lingual-occlusal, views of SMU 64293 from the Brushy Creek F local fauna, upper Belle Plains

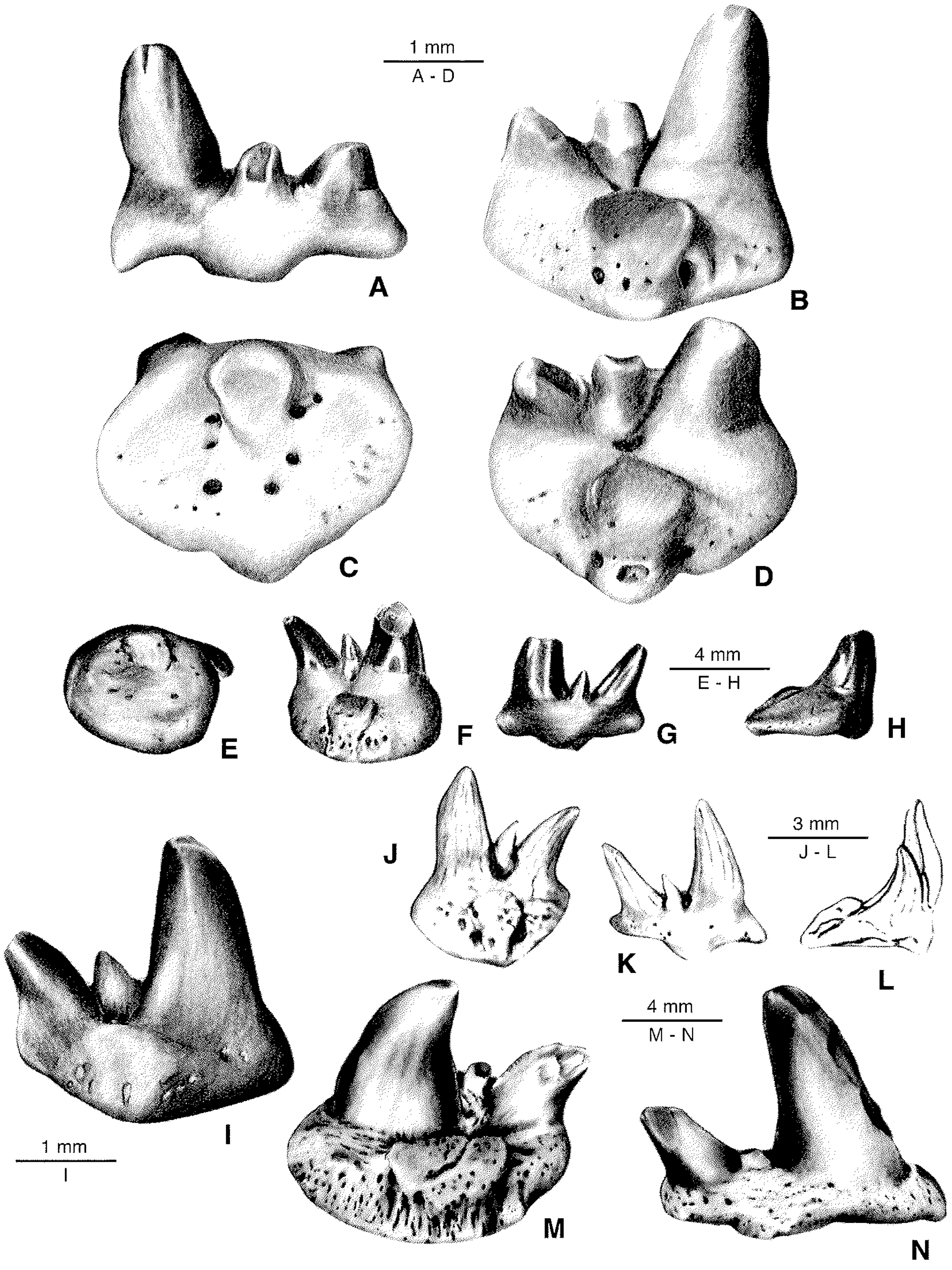

Fig. 12. *Orthacanthus platypternus* lateral teeth; A – labial, B – lingual, C – aboral, and D – nearly occlusal, views of SMU 64301 from the Wolf Creek A local fauna, upper Belle Plains; note that the major principal cusp is associated with the smaller half of the base, the opposite of what is usually observed (compare D with Text-fig. 11Q); also note the apparent change in appearance of the apical button caused by rotating the tooth from lingual to occlusal view; E – aboral, F – lingual-occlusal, G – labial, and H – anterior, views of SMU 64292 from the Mitchell Creek A local fauna, upper Clyde; I – lingual-occlusal view of SMU 64299 from the Lake Kemp B/ac local fauna, middle Lueders. J – lingual-occlusal, K – labial, and L – posterior, views of SMU 69156 from the East Coffee Creek 37 local fauna, lower Arroyo; the lines in the principal cusps are striations; they are not cristae; M – lingual-occlusal, and N – labial, views of SMU 64291 from the lower Arroyo (part of surface collection from East Coffee Creek; JOHNSON 1979, p. 630); note the incipient serrations on the medial carinae of the principal cusps

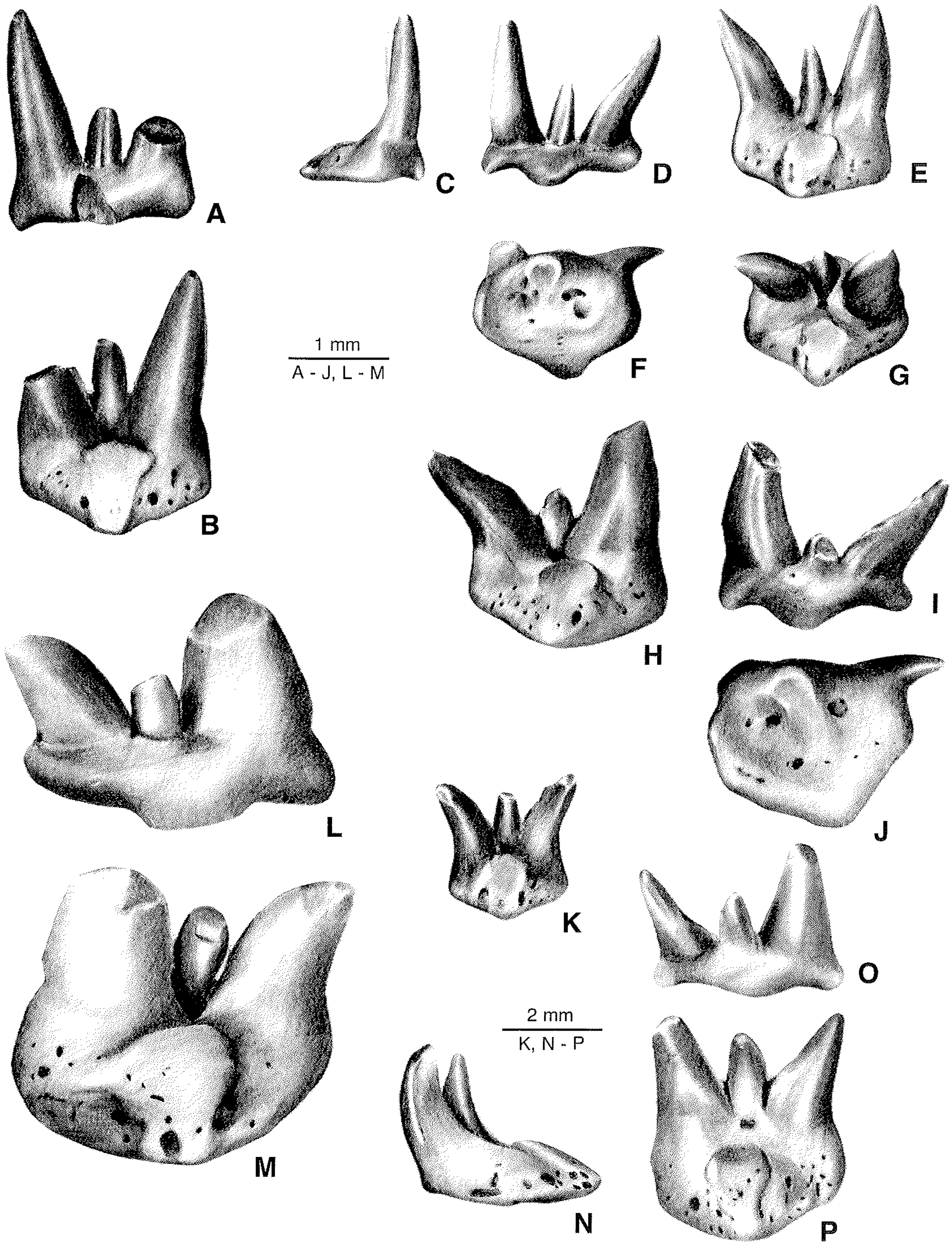

Fig. 13. *Orthacanthus platypternus* medial teeth; A-G – from the Brushy Creek J/ac local fauna, upper Belle Plains; A – labial, and B – lingual–occlusal, views of SMU 64303; and C – anteromedial, D – labial, E – lingual-occlusal, F – aboral, and G – occlusal, views of SMU 64302; H – lingual-occlusal, I – labial, and J – aboral, views of SMU 64305 from the Wolf Creek B local fauna, upper Belle Plains; K – lingual-occlusal view of SMU 64290 from the Brushy Creek C local fauna, upper Belle Plains; L – labial, and M – lingual-occlusal, views of SMU 64304 from the La Paloma/ac local fauna, upper Clyde; N-P – *Orthacanthus ?platypternus*; N – anteromedial, O – labial, and P – lingual-occlusal, views of SMU 64306 from the Mitchell Creek B/ac local fauna, upper Clyde; note that although the base is typically thin in O, the base of the intermediate cusp is relatively high compared to the anteromedial and posterolateral margins of the bases of the principal cusps as in *O. texensis* teeth

absent or slightly developed in the Clear Fork teeth (Text-fig. 12J, M). No teeth with a bifurcated lingual margin have been observed. Foramina are associated with the apical button as in *O. texensis*. They may occur along the lingual margin of the base and may be scattered about its oral surface. The central foramen is prominent.

Principal cusps: Most of the teeth of *O. platypternus* have dissimilar principal cusps. The major cusp is presumably anterior; the minor cusp is usually divergent. This combination is just the opposite of that in *O. texensis*. The major cusp is associated with the basal flange. In many of the smaller teeth the principal cusps are nearly identical. They may be nearly straight and slightly divergent, or may both lean slightly in the same direction.

The cusps of *O. platypternus* teeth are never serrated. Wrinkles or incipient serrations in the lateral carinae occur on the cusps of some of the larger teeth collected from the surface in the Arroyo (Text-fig. 12M, N). Teeth subsequently obtained by bulk sampling throughout the Clear Fork Group (MURRY & JOHNSON 1987) failed to produce any additional teeth, even the largest ones, showing this feature. A few of the Clear Fork teeth possess very fine striations on the principal cusps, especially on the labial surfaces (Text-fig. 12J, K). They are not comparable to the cristae on other xenacanth teeth.

Intermediate cusp: Nearly all the teeth of *O. platypternus* I have examined have a single intermediate cusp. It usually leans toward the divergent (minor) principal cusp. Some of the larger teeth (Text-fig. 11L, M) from the upper Belle Plains (especially the Brushy Creek F local fauna) have two intermediate cusps, one primary and one secondary. This feature becomes less common higher in the section, as none was observed in the Clyde or Arroyo. Two teeth from the Lueders (Lake Kemp A and B local faunas) have two intermediate cusps. Four teeth from the upper Vale (Ignorant Ridge 94 local fauna) also possess this feature; the intermediate cusps in one tooth are of equal size and larger than normal. A single tooth from the lower Choza (Ignorant Ridge 100 local fauna) has a pair of intermediate cusps. One of the measured teeth in the Brushy Creek I local fauna has a bifurcated intermediate cusp.

A few small teeth lack an intermediate cusp. They are not similar to typical *O. platypternus* teeth in general appearance but do have a thin base (Text-fig. 14A–D). The smaller principal cusp is divergent; the other cusp leans in the same direction.

Remarks: The Upper Permian tooth noted above with the labio–lingual width possibly greater than anteromedial–posterolateral length might not be unusual for this horizon, as this condition is more common in the Clear Fork Group than in the Wichita Group.

Tooth size tends to remain about the same throughout the Wichita Group. A slight increase in size occurs in the Clear Fork Group (Text-fig. 9). Most of the more productive Wichita local faunas contain a few large teeth (am–pl length ≥10 mm) not included in the random samples (Table 2). Only smaller teeth were recovered from the lowest part of the Clyde and subjacent Belle Plains, but this distinction is not reflected by the measured samples (Text-fig. 9).

The smaller teeth with identical principal cusps can be usually distinguished from *O. texensis* teeth, but they do tend to converge in appearance. HOTTON (1952) stated that the principal cusps of *O. texensis* teeth are more compressed than in *O. platypternus*. This is often true for the minor cusp in *O. platypternus*, but I have observed many *O. platypternus* teeth with both cusps as compressed as in *O. texensis* teeth. Teeth lacking an intermediate cusp are quite similar to the posterior teeth of *O. texensis*.

HETERODONTY

Lateral teeth: Probably nearly all the *O. platypternus* teeth identified in the past have been laterals (Text-figs 11-12). The straight or nearly straight major principal cusp is associated with the larger half of the base, the opposite of *O. texensis* teeth. In contrast with the other *Orthacanthus* species described here, the laterals range downward in size to include some of the smallest teeth in the arcade (Text-figs 11A–E, J–K). They may be from small individuals, but this condition is not reflected by the other species. These small laterals might occur at either end of the lateral suite, except the major cusp does not tend to lean toward the minor cusp as it does in the larger laterals that were presumably situated nearer the posterior end of the arcade (Text-fig. 11F,G). The largest laterals (Text-fig. 11L–Q) tend to have a straight major cusp, suggesting that they were situated nearer the middle or anterior portion of the lateral suite (but see Text-fig. 12M, N).

The lack of an anterior flange on the base of most of the Clear Fork *O. platypternus* teeth (as in the holotype) may indicate a change in the nature of the heterodonty from the Wichita. The older Wichita teeth may represent either dignathic heterodonty or sexual dimorphism, as about half of the measured teeth possess a flange. A gradient monognathic heterodonty probably occurs in the Clear Fork dentitions, and for simplicity is assumed in the Wichita dentitions as well, despite the difference between the two groups.

Posterior teeth: Teeth comparable to the *O. texensis* posteriors tend to be absent in *O.*

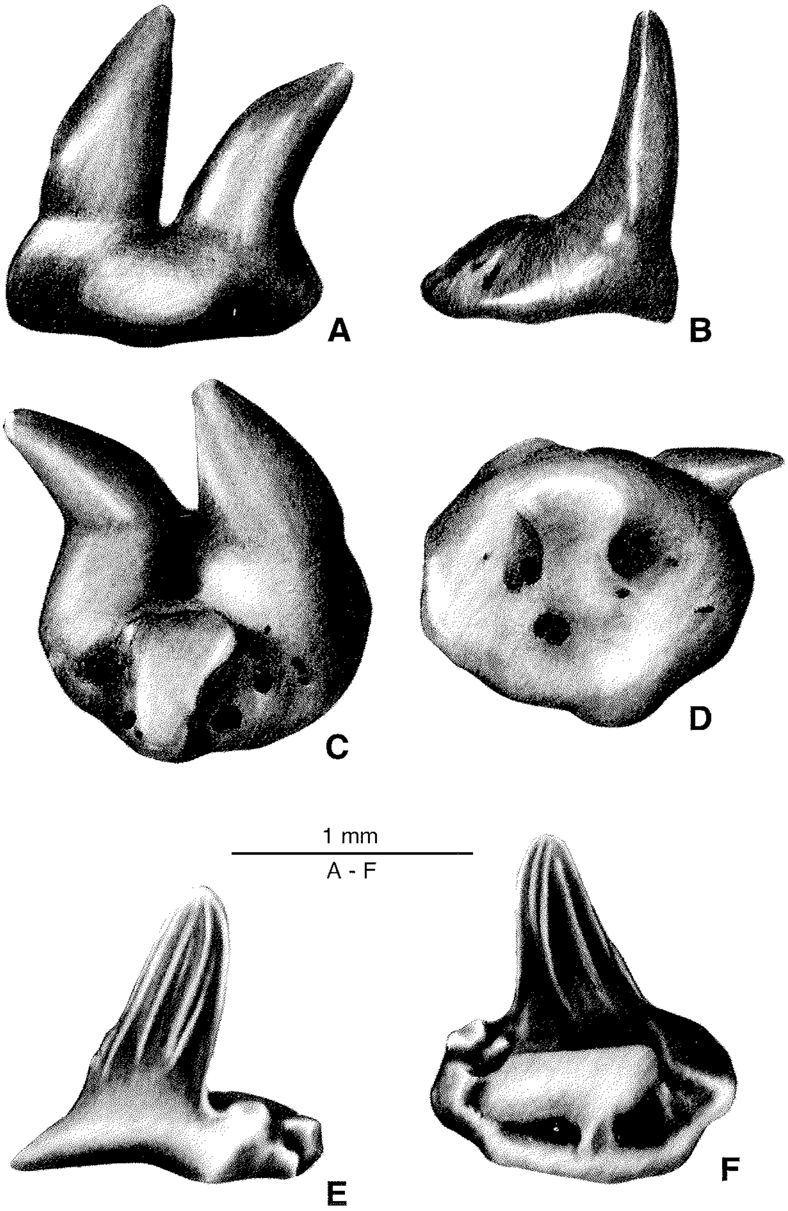

Fig. 14. A–D, *Orthacanthus ?platypternus* posterior tooth (SMU 64307) from the La Paloma/ac local fauna, upper Clyde; A – labial, B – anterior, C – lingual-occlusal, and D – aboral views; compare with Fig. 7I, J and see text; E-F – *Orthacanthus* aff. *platypternus* tooth (CM 35161) from the Fort Pitt Tunnel-6 local fauna at Pittsburgh, Pennsylvania, Duquesne Limestone Bed No. 6, Conemaugh Formation; E – labial, and F – lingual-occlusal views; minor principal cusp is broken away; intermediate cusp also broken

platypternus. Teeth with both principal cusps leaning in the same direction in parallel fashion, associated with a thin base at the labial margin, occur only rarely (Text-fig. 14A–D). They lack an intermediate cusp, and are included in *O. platypternus* with reservation.

Medial teeth: *O. platypternus* medials are the most difficult xenacanth teeth from the Wichita Group to identify. They tend to display considerable, though subtle, variation, as suggested by the examples in Text-fig. 13. The principal cusps in some medials are equally divergent (Text-fig. 13K) or nearly straight (vertical) (Text-fig. 13A,B). Presumably they occur in this order away from the symphysis, although the straight-cusped teeth could be closest to the symphysis. The teeth with asymmetrical principal cusps occupy the posterior part of the medial suite, probably grading imperceptibly into the lateral suite. The intermediate cusp is always present, is long relative to the principal cusps, and is sometimes compressed as much as the principal cusps. These medials can often be distinguished from medials of other species by the presence of slightly downturned (aborally flexed) anteromedial or posterolateral margins of the base. This feature must be used with caution, however, especially if *O. compressus* teeth should be present at the same stratigraphic horizon. As *O. platypternus* medial teeth are often difficult to identify, they have been isolated in some of the Wichita collections for reference purposes (*see* JOHNSON 1979, p. 206). Ten presumably medial teeth (SMU 64317) from the largest local fauna (Mitchell Creek B/ac, Table 1) are tentatively identified as *O. platypternus* because of their similarity to *O. texensis* teeth (Text-fig. 13N-P). Some of these teeth could belong to *O. texensis* if it should be demonstrated that the characteristics of *O. compressus* medials continue to persist through the Early Permian, as LUND (1976) suggested that *O. texensis* had descended from *O. compressus*.

Orthacanthus aff. *platypternus*
(Text-fig. 14E, F; Table 1)

Two teeth (SMU 64309) from the Wichita Group are unusual in possessing coarse cristae on their major principal cusps, which are broken. The minor principal cusps are completely broken off, as is the intermediate cusp of one tooth. The proximal end of the intermediate cusp in the other tooth is preserved and is cristated. The cristae occur only on the labial margins, besides the usual lateral carinae on the principal cusps. Both teeth are from the Mitchell Creek B/ac local fauna (Table 1). Except for the cristae, they are similar to *O. platypternus* teeth.

The presence of cristae may be an atavistic feature in the Permian teeth, as this condition is more common in older faunas. Two teeth (CM 26350, 35161) from the Duquesne Limestone (Virgilian) Fort Pitt Tunnel-6 local fauna (Table 1) bear cristae on the labial and lingual margins of the major principal cusps (Text-fig. 14E, F). The cristae are subdued on the labial margin of the major cusp of CM 26350, perhaps because of wear; none are present on the minor cusp of the same tooth. The intermediate cusps are broken in both teeth. Another tooth (CM 35154) with cristae on the cusps occurs in the Kennard Playground local fauna. It is very small, with short, stout, compressed principal cusps; it lacks an intermediate cusp. It is probably a posterior tooth. Two other teeth (CM 27256) from the same locality possess intermediate cusps, but the cristae are limited to the principal cusps. The larger of the two has two secondary intermediate cusps, one on either side of the primary cusp; the tooth is large for this fauna, with an am–pl length of about 5 mm.

LUND (1976) reported teeth from the Gzhelian (Virgilian), and described them as being different from true *O. platypternus* in having oval, cristated cusps. He referred to them as *O.* aff. *platypternus*. If enough of these teeth should be recovered in the future, it may be demonstrated that they represent a distinct species, possibly "*Pleuracanthus*" *albuquerquei* (SILVA SANTOS 1946; JOHNSON 1979, p. 261). Presence of cristae in some *Orthacanthus* teeth seems unlikely. It may be preferable to refer these teeth to a different genus, as discussed below.

Orthacanthus compressus (NEWBERRY, 1856)
(Text-figs 2-3, 15-20; Tables 1-2)

1856. *Diplodus compressus* n.sp.; J. NEWBERRY, p. 99.
1856. *Diplodus gracilis* n.sp.; J. NEWBERRY, p. 99.
1856. *Diplodus latus* n.sp.; J. NEWBERRY, p. 99.
1860. *Diplodus penetrans* n.sp.; J. DAWSON, 1868, p. 211.
1885. *Diacranodus compressus* (NEWBERRY); S. GARMAN, p. 30.
1952. *Xenacanthus compressus* (NEWBERRY); N. HOTTON, p. 495–497, Fig. 2.

1970. *Orthacanthus compressus* (NEWBERRY); R. LUND, p. 239–240.

MATERIAL: The basis for this preliminary study is the collection of 142 *O. compressus* teeth made by OSSIAN (1974) from a conglomerate at his Peru locality (Table 1): (Site 2: TMM 41647-11, 12, 318–322, 332; and Site 3: TMM 41648-5, 8, 124–131, 142; revised from JOHNSON 1979, p. 186). Additional teeth from the Dunkard Basin, also obtained by bulk-sampling techniques, were available for study (Table 1): 21 from the Duquesne Limestone No. 6 at Pittsburgh, Pennsylvania (CM 26349, 26351), 14 from the Duquesne Limestone No. 2A at Pittsburgh (CM 26337, 35162, 35163), 23 from the lower Pittsburgh Formation at Pittsburgh (CM 27257, 35156–35159), and 15 from the Colvin Limestone at Washington, Pennsylvania (CM 26426, 26436, 35142, 35146–35149).

OCCURRENCE: Most occurrences of *O. compressus* are of Late Carboniferous age. LUND (1975) indicated that it extends into the lower Greene Formation (Sakmarian), but then seemed less certain as there appeared to be a gradual phyletic change from *O. compressus* to *O. texensis* (LUND 1976). LUND (1975, 1976) listed several horizons in the Dunkard Basin where he or earlier workers had recovered teeth. One of the oldest of these horizons produced the Linton fauna (Desmoinesian = upper Westphalian) from which NEWBERRY (1856) described *O. compressus*. The youngest is apparently the Colvin Limestone Member of the Waynesburg Formation (Asselian). OLSON (1946) listed five localities from Illinois that yielded *O. compressus* specimens; their age apparently ranges from Desmoinesian to Missourian (Westphalian–Stephanian). OSSIAN (1974) determined the Peru faunas to be Gzhelian (Virgilian, Table 1). DAWSON (1868) described several teeth from the Upper Carboniferous of Nova Scotia that may belong to this species (JOHNSON 1979, p. 273). MASSON & RUST (1984) also reported teeth from the Upper Carboniferous of Nova Scotia that appear similar to some of the *O. compressus* teeth described in this study. They described them as possessing ornamentation, but none (such as cristae) is evident in their illustrations. HAMPE (1988a) refuted their assignment to *Orthacanthus* because of their small size and lack of serrations on the principal cusps. Neither of these arguments are valid based on evidence given in this study. This species may also be present on Prince Edward Island (JOHNSON 1979, p. 170). Occurrences of *O. compressus* have not been reported from western North America except Kansas (JOHNSON 1979, pp. 169–170), where *Orthacanthus* sp. has been reported from the lowermost Permian (SCHULTZE 1985) and Upper Carboniferous (SCHULTZE & CHORN 1988, CHORN & SCHULTZE 1990; the Robinson locality does contain *O. compressus* teeth, KUVP 72338, 72340, and 72344, for example). It has not been reported outside of North America, except for the occurrence of "*Diplodus latus*" teeth in Belgium (DESTINEZ 1898); this species was synonymized with *O. compressus* by HOTTON (1952). HOTTON (1952) also synonymized NEWBERRY's (1856) *D. gracilis* with *O.* (*X.*) *compressus* [not to be confused with *O.* (*Chilodus*) *gracilis* (GIEBEL, 1848) described by HAMPE (1994)].

O. compressus may be restricted to the upper half of the Upper Carboniferous and lowermost Permian. However, the xenacanth record in the lower half of the Upper Carboniferous of North America is poor. The European record of this species may be more extensive, pending taxonomic problems yet to be resolved.

REMARKS: The number of teeth available for study is too low to permit a diagnosis of *O. compressus* comparable to the diagnoses of the Permian *Orthacanthus* species from Texas. Also, larger teeth comparable to those of *O. texensis* are not present in the samples, although they are common (JOHNSON 1979, pp. 187–188; subsequent observations of FMNH and AMNH teeth). The data presented in Text-figs 2 and 3, and Table 2 probably reflect a particular population rather than the species in general; they are included for the purposes of future comparisons. *Orthacanthus* teeth recently collected by bulk-sampling of Archer City Bonebed 3 (Sakmarian; SANDER 1989) probably include *O. compressus* (JOHNSON 1992b), but additional study has not been completed.

It is difficult to distinguish many *O. compressus* teeth from *O. texensis* and *O. platypternus*. If their intact dentitions could be compared, thus allowing for heterodonty, significant differences should be apparent. If a parsimonious approach is taken using isolated teeth, some differences are apparent. *O. compressus* teeth are similar to *O. texensis* in general appearance, except that most possess a thin base (rt in Text-fig. 1) as in *O. platypternus*. Of the

73 measured *O. compressus* teeth (Table 2), 16 have thick bases and nine of these have serrated principal cusps. Two of the thin-based teeth have serrated principal cusps, an *O. texensis* character. Some of the thin-based teeth have a principal-cusp arrangement similar to that of *O. texensis*, in which the major cusp is the most divergent. Similar sizes of thin-base and thick-base teeth preclude the possibility that the former are juvenile teeth in the sense of HAMPE (1988a), where *Xenacanthus*-like, but serrated, juvenile teeth (which are thin-based in that genus) occur in *O. senkenbergianus*. Dignathic or sexual heterodonty in *O. compressus* is a possibility, but this seems unlikely as no comparable condition exists in other *Orthacanthus* dentitions. HAMPE (1994) stated that *O. gracilis* (NEWBERRY) lacks serrations, and suggested it may be a species of *Xenacanthus*. This is not correct, as NEWBERRY (1856) merely described it as less conspicuously serrated.

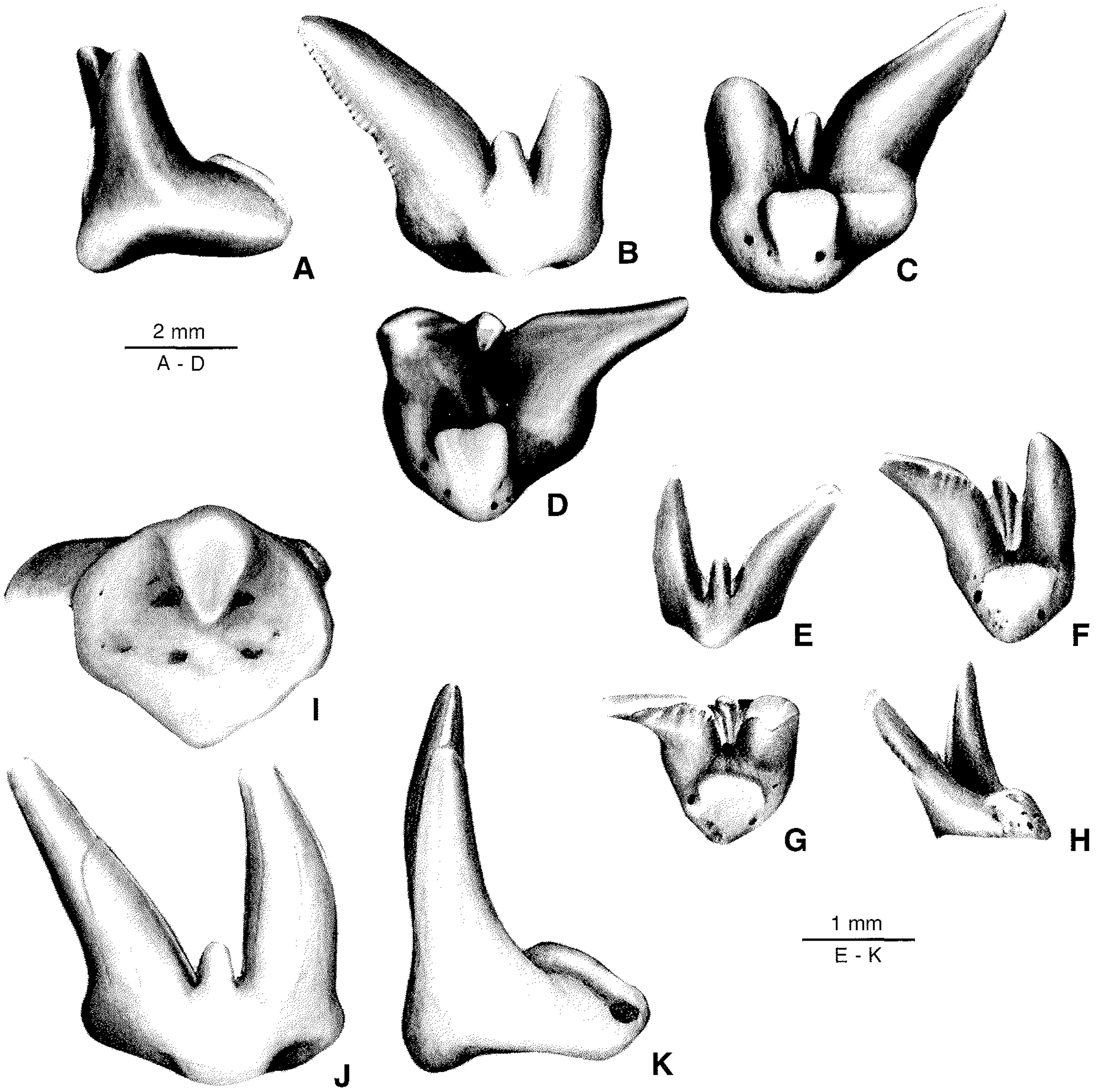

Fig. 15. *Orthacanthus compressus* lateral teeth from Site 2 of the Peru local fauna, Towle Shale; A – anterior, B – labial, C – lingual-occlusal, and D – occlusal, views of TMM 41647-12; E – labial, F – lingual-occlusal, G – occlusal, and H – posterior, views of TMM 41647-321; and I – aboral, J – labial, and K – anterior, views of TMM 41647-11

DAWSON's (1868; initially described in 1860) *D. penetrans* teeth have a thick base which is strongly lobed (probably in reference to the basal tubercle) and about 4 mm long (am–pl). The divergent principal cusps are compressed and serrated, especially on the am and pl lower margins. A short intermediate cusp is present.

HOTTON (1952) and LUND (1970) indicated that *O. compressus* teeth have a single intermediate cusp; it is absent in a few of the teeth I examined. Many *O. texensis* teeth have more than one. LUND (1970) and NEWBERRY (1856) noted that the intermediate cusp of *O. compressus* is sometimes serrated. This character does not occur in *O. texensis*, and apparently occurs only in larger *O. compressus* teeth, as it is not present in the teeth examined for this study.

HOTTON (1952) noted that *O. texensis* teeth have more coarsely serrated principal cusps, which are also more compressed, than those of comparably sized *O. compressus*. Although *O. texensis* teeth may have coarser serrations, this study indicates the medial margins of their cusps are less often serrated than in comparable *O. compressus* teeth, except in the abraded(?) Peru teeth (JOHNSON 1979, p. 187). Smaller teeth of *O. compressus* tend not to have serrated cusps, while those of *O. texensis* often do. Also, some *O. compressus* teeth have the proximal portions of their principal cusps more compressed than any of the *O. texensis* teeth I have examined (Text-fig. 15K).

Besides different basal thicknesses at the labial margin, *O. compressus* teeth also possess other combined features of the bases of *O. texensis* and *O. platypternus* teeth. In general shape, those of *O. texensis* are most similar (compare Text-figs 4, 10, 16). The aboral surface is more like *O.*

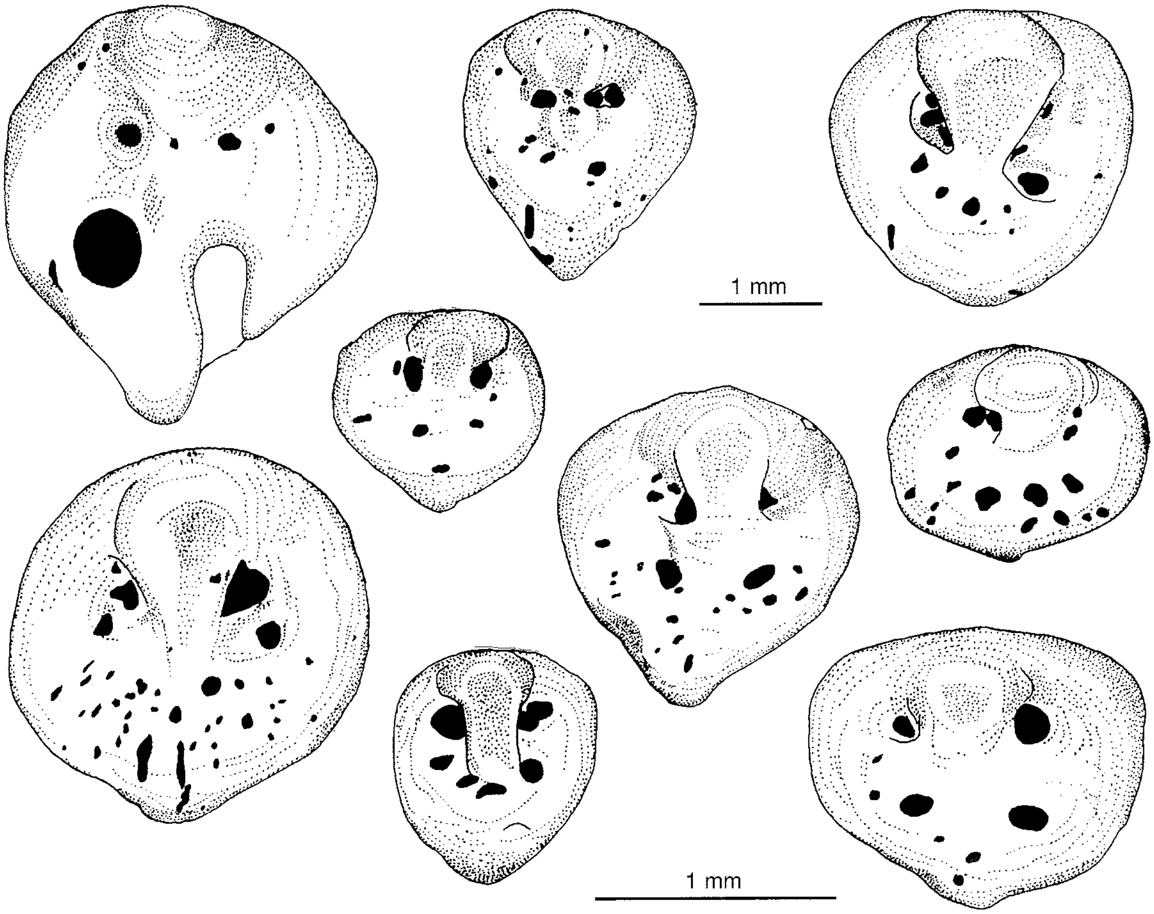

Fig. 16. Sketches of *Orthacanthus compressus* aboral tooth surfaces from Site 3 of the Peru local fauna, Towle Shale; upper scale bar is for the upper seven sketches; lower scale bar is for the two lower sketches

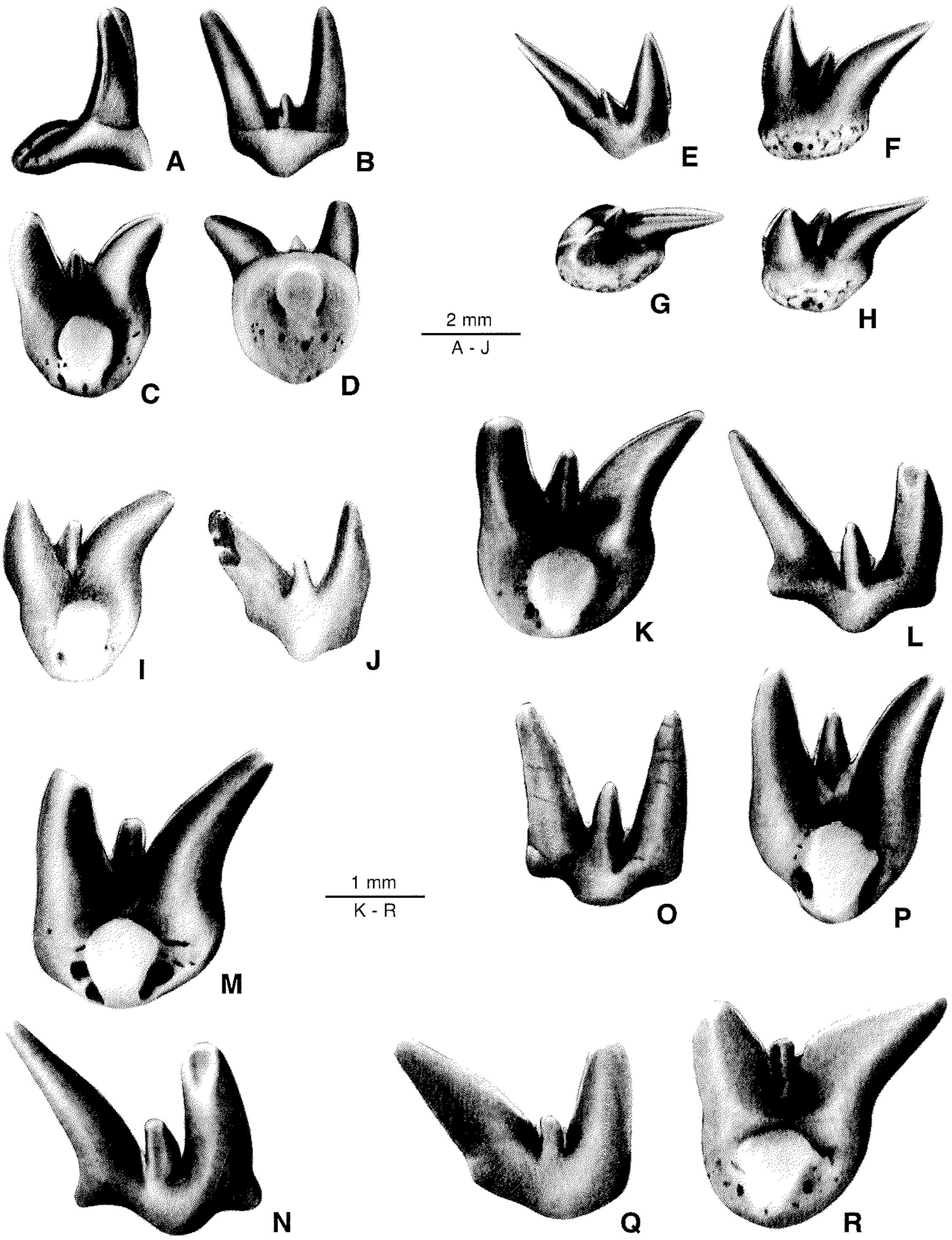

Fig. 17. *Orthacanthus compressus* lateral teeth from Site 3 of the Peru local fauna, Towle Shale; A – posterior, B – labial, C – lingual-occlusal, and D – aboral, views of TMM 41648-125; E – labial, F – lingual, G – occlusal, and H – lingual-occlusal views of TMM 41648-126; I – lingual-occlusal, and J – labial, views of TMM 41648-124; K – lingual-occlusal, and L – labial, views of TMM 41648-130; M – lingual-occlusal, and N – labial, views of TMM 41648-127; O – labial, and P – lingual-occlusal, views of TMM 41648-129; and Q – labial, and R – lingual-occlusal, views of TMM 41648-128

platypternus as it is generally flat, but may be slightly concave to slightly convex. The basal tubercle in *O. compressus* is sometimes prominent, extending outward from the labial margin, and generally extends toward the center of the base. If an anterior flange were present, the base of *O. compressus* teeth probably could not be distinguished from those of *O. platypternus* in most cases. The apical button and related foramina are not distinctive. The central foramen is always present in *O. compressus* teeth.

HETERODONTY: *O. compressus* teeth are generally similar to *O. texensis* teeth in their heterodont tendencies, despite having some *O. platypternus* characters, except for one or two significant differences. The large laterals are of the *O. texensis* type, with thick bases (Text-figs 15A–O, 18A–E). The smaller laterals may have either thick (Text-fig. 17Q, R) or thin (Text-fig. 17A–H, K–P) bases. No attempt has been made to correlate this difference with the degree of cusp divergence, extent of serrations, or relationship between the minor principal cusp and largest anteromedial or posterolateral half of the base, which are factors that might be used in determining tooth position in the lateral suite.

Posterior teeth similar to those of *O. texensis* are present (Text-fig. 18K, L), but they are considerably fewer in number. They lack an intermediate cusp.

Typical medial teeth (Text-fig. 19) are thin-based and similar to those of *O. platypternus* in this sense; Text-fig. 19R, S illustrates a possible

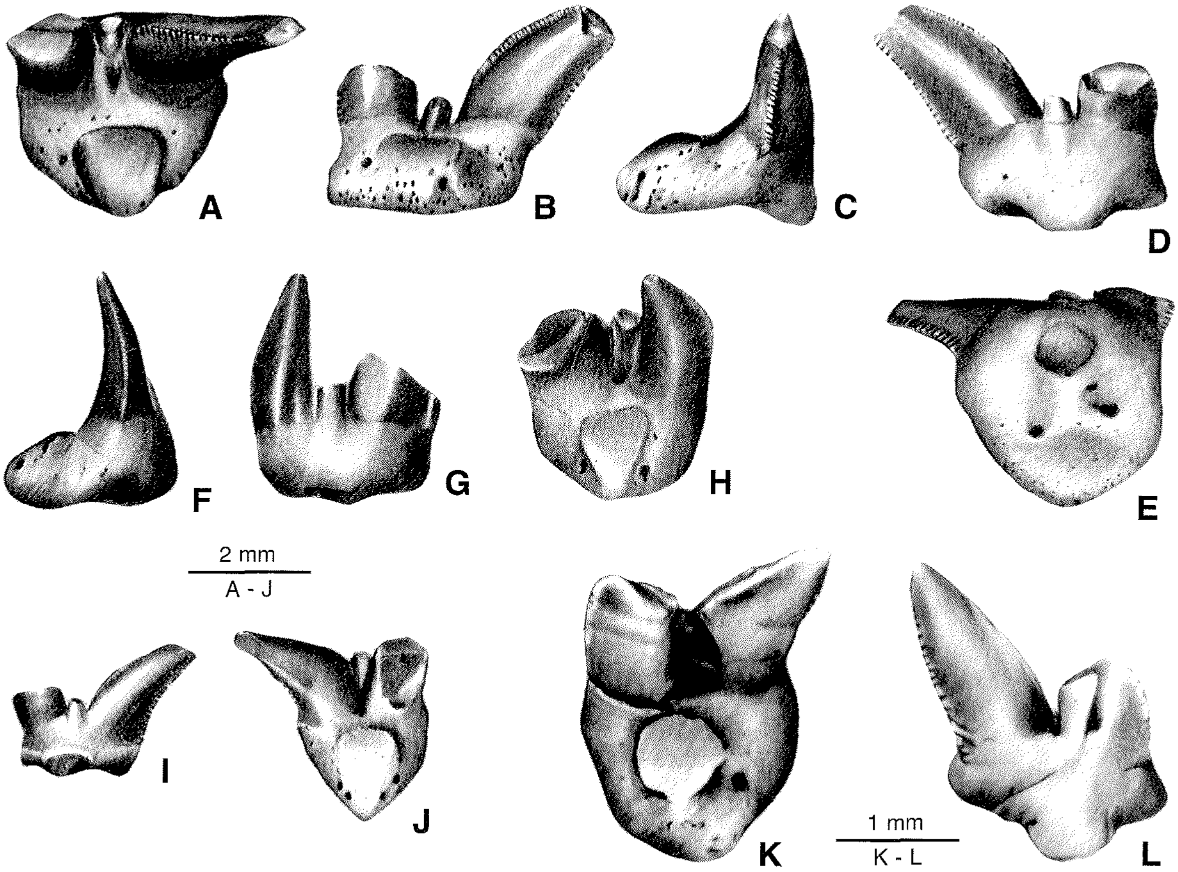

Fig. 18. *Orthacanthus compressus*; A-H – lateral teeth from the Fort Pitt Tunnel-2A local fauna at Pittsburgh, Pennsylvania, Duquesne Limestone Bed No. 2A, Conemaugh Formation; A – occlusal, B – lingual, C – posterior, D – labial, and E – aboral, views of CM 35162; and F – anterior, G – labial, and H – lingual-occlusal, views of CM 35163; basal tubercle is broken, and base of intermediate cusp is obscured by matrix. I – labial, and J – lingual-occlusal, views of lateral tooth (CM 35149) from the Franklin Mall local fauna at Washington, Pennsylvania, Colvin Limestone, Waynesburg Formation; K-L – posterior or posterolateral tooth (CM 35156) from the Kennard Playground local fauna at Pittsburgh, Pennsylvania, lower Pittsburgh Formation; K – lingual-occlusal, and L – labial views

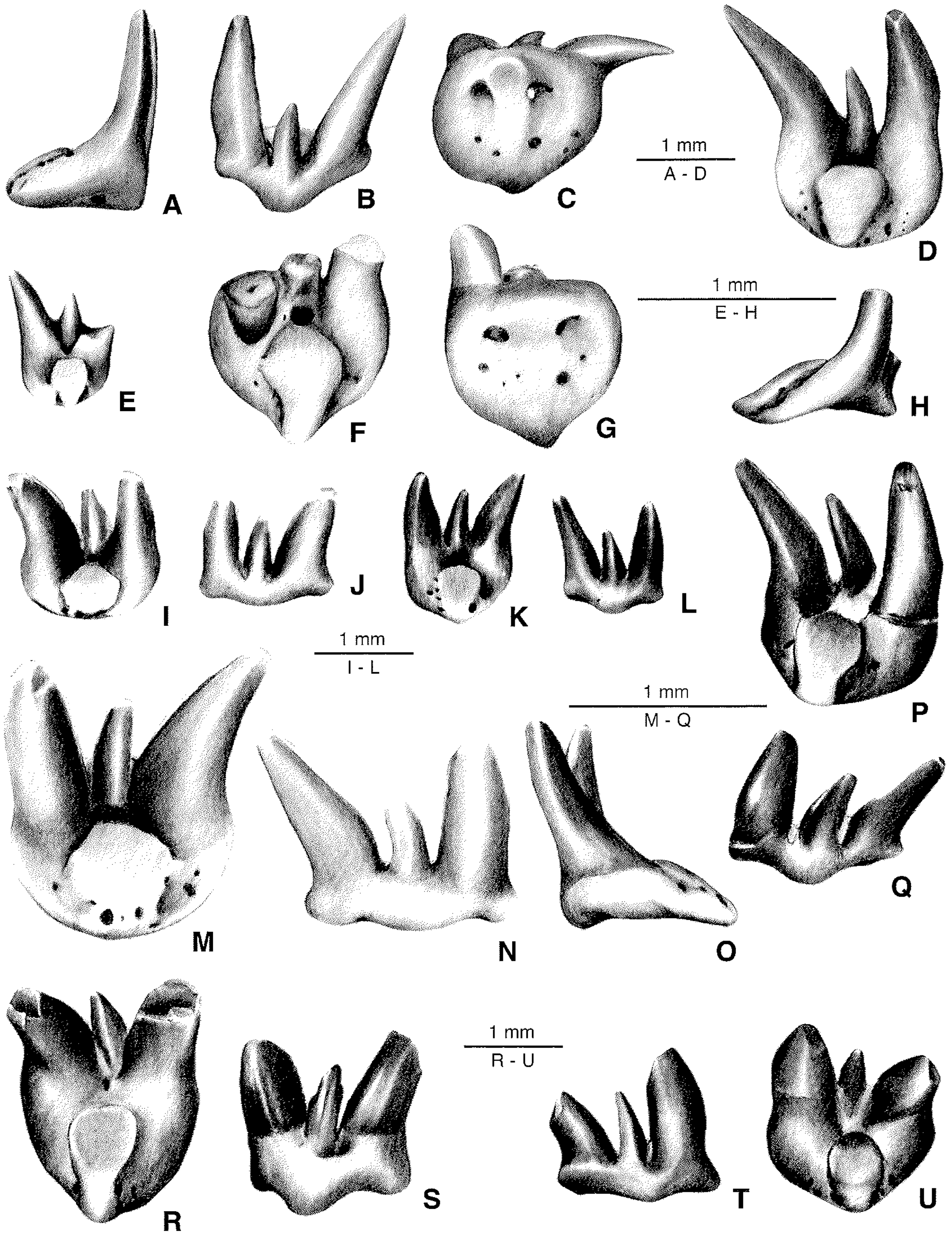

Fig. 19. *Orthacanthus compressus* medial teeth; A-H – from the Kennard Playground local fauna at Pittsburgh, Pennsylvania, lower Pittsburgh Formation; A – anteromedial, B – labial, C – aboral and D – lingual-occlusal, views of CM 35159; E – lingual-occlusal view of CM 35157; and F – lingual-occlusal, G – aboral, and H – anteromedial or posterolateral, views of CM 35158; I-O – from Site 2 of the Peru local fauna, Towle Shale; I – lingual-occlusal, and J – labial, views of TMM 41647-318; K – lingual-occlusal, and L – labial, views of TMM 41647-320; and M – lingual-occlusal, N – labial, and O – anteromedial, views of TMM 41647-319; P-U – from the Franklin Mall local fauna at Washington, Pennsylvania, Colvin Limestone, Waynesburg Formation; P – lingual-occlusal, and Q – labial, views of CM 35146 (central foramen covered by matrix); R – lingual-occlusal, and S – labial, views of CM 35148 (could be considered a lateral tooth); and T – labial, and U – lingual-occlusal, views of CM 35147

exception. They are similar to *O. texensis* medials in other respects.

Orthacanthus aff. *compressus*
(Text-fig. 20, Table 1)

Thirteen teeth (CM 35143–35145, 35150) from the Colvin Limestone (Wolfcampian = Asselian) have varying numbers of coarse cristae on their principal cusps in addition to the lateral carinae, which are not serrated. The cristae tend to occur mostly on the lingual or mediolingual margins where they may extend almost to the proximal end of the cusps. The teeth are small, comparable to the smallest normal *O. compressus* teeth that are associated with them. Except for the cristae, these teeth are identical with *O. compressus* teeth.

A somewhat comparable tooth was described by FRITSCH (1889) as *O. plicatus* (considered a species of *Xenacanthus* by SCHNEIDER 1988, and assigned to a new genus by HAMPE 1995; see discussion below). It has more cristae on each principal cusp that more or less extend their full length. Two very short, blunt intermediate cusps are present.

Upper Carboniferous teeth described by DAWSON (1868) in 1860 as *Diplodus acinaces* may be similar to the Colvin Limestone teeth (JOHNSON 1979, p. 273). However, *D. acinaces* teeth are much larger, with a thick base and an am–pl base length of about 8 mm, and an intermediate cusp is absent. The principal cusps are compressed, with unserrated carinae (WOODWARD 1889) and cristae(?) ["scarcely crenulated" (DAWSON 1868); faint striae are present, but the cusps are definitely not plicate according to Christopher J. DUFFIN (*pers. comm.*)].

More of the teeth described here must be recovered before it can be determined to which species they belong.

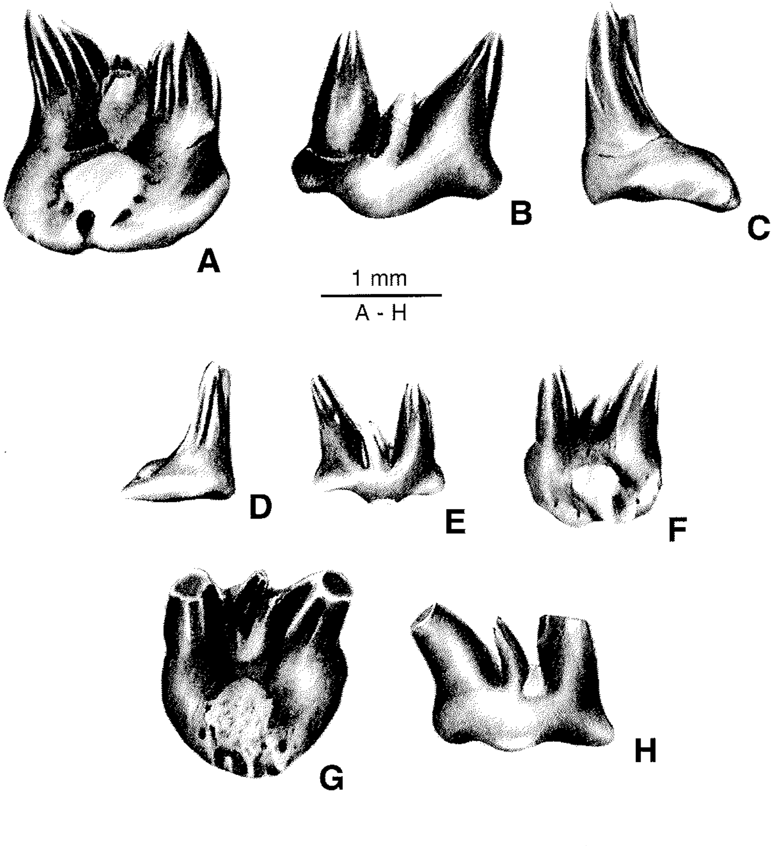

Fig. 20. *Orthacanthus* aff. *compressus* teeth from the Franklin Mall local fauna at Washington, Pennsylvania, Colvin Limestone, Waynesburg Formation; A – lingual-occlusal, B – labial, and C – anteromedial or posterolateral, views of CM 35143 (intermediate cusp obscured by matrix in A); D – anteromedial or posterolateral, E – labial, and F – lingual-occlusal, views of CM 35144; and G – lingual-occlusal, and H – labial, views of CM 35145 (matrix covers base of intermediate cusp in G)

DISCUSSION OF *ORTHACANTHUS* DENTITIONS

Morphological convergences

The three species described above are differentiated on the basis of their teeth. HOTTON (1952) noted only a slight difference between *O. texensis* and *O. platypternus* in their Meckel's cartilages, but made no reference to any different characters in the chondrocranium or Meckel's cartilage in *O. compressus*. Differentiation of these species on the basis of mucous membrane denticles, dermal denticles (scales), or occipital spines has not been attempted, although a study of *O. platypternus* spines is in progress (DONELAN & JOHNSON 1997).

The principal cusps in *O. platypternus* and *O. compressus* teeth display as much variability as in *O. texensis*. The pattern of the cusps in *O. platypternus* can usually be used, along with the structure of the base, to distinguish its teeth from those of *O. texensis*. Differences between *O. texensis* and *O. compressus* are not as apparent.

The convergence of corresponding basal dimensions in the smaller teeth of the three species of *Orthacanthus* causes the slopes of the regression lines in Text-fig. 2 to be more similar than if only teeth in surface collections were measured. The number of foramina on the aboral surfaces of *O. texensis*, *O. platypternus,* and *O. compressus* tooth bases (Text-figs 4, 10, and 15) is about the same. However, SCHNEIDER (1996) uses the number of foramina to differentiate *Orthacanthus* from *Xenacanthus* while maintaining that *O. platypternus* belongs to *Xenacanthus* (as does HAMPE 1994).

Examination of *O. compressus* teeth in the FMNH collections and from the Archer City bonebed (JOHNSON 1992a; study in progress) suggests that the occurrence of a highly prominent basal tubercle may be more common than indicated by the teeth in this study. Some of the *O. gracilis* (GIEBEL, 1848) teeth illustrated by HAMPE (1994) closely resemble some *O. compressus* teeth. Direct comparisons should be made in the future to determine if they are conspecific; if the result is positive, then *O. gracilis* will have taxonomic priority, as HAMPE notes.

I have found very few posteriors in this study of *O. compressus* teeth, and, as they are rare in *O. platypternus*, it appears they are largely a characteristic of *O. texensis*.

Cristated teeth in *Orthacanthus*?

Teeth bearing cristae on the principal cusps, described above as *O.* aff. *platypternus*, are similar to typical teeth of that species except for the cristae. "*Pleuracanthus*" *albuquerquei* (SILVA SANTOS, 1946) teeth possess a thin base with compressed, unserrated principal cusps and isolated apical button. These cusps bear cristae only on the lingual surface; their labial surfaces are smooth. The age of these teeth is probably Early Permian (SILVA SANTOS & SARDENBERG SALGADO 1970). The Texas Permian *O.* aff. *platypternus* teeth bear cristae only on the labial surfaces of the principal cusps, while those from the Upper Carboniferous bear cristae on both lingual and labial surfaces. This distribution of cristae suggests three species belonging to the same genus, although too few teeth are known to ensure the validity of this many species. Known genera with cristated compressed principal cusps include *Plicatodus* (HAMPE 1995) and possibly *Bohemiacanthus* (SCHNEIDER & ZAJÍC 1994, Fig. 21), although SCHNEIDER (1996) described its cusps as round to polygonal in cross-section (SOLER-GIJÓN & HAMPE 1998 consider this genus to be a junior synonym of *Triodus*). *Plicatodus jordani* teeth have a thin base with a posterior flange, and bifurcated cristae on the lingual and labial surfaces of the compressed principal cusps of the laterals (HAMPE 1995). *P. plicatus* has a greater number and extent of bifurcated cristae on both lingual and labial principal cusp surfaces and a thin base with an anteromedial flange that appears similar to *O. platypternus* (HAMPE 1995, and SCHNEIDER & ZAJÍC 1994; their illustrations differ from FRITSCH's, 1889, illustration of the same tooth). *Bohemiacanthus* teeth bear cristae on both lingual and labial cusp surfaces, but they are only sometimes bifurcated (SCHNEIDER 1996); the tooth bases appear to be variable in thickness (SCHNEIDER & ZAJÍC 1994, Fig. 21).

WÜRDIG-MACIEL (1975) described two Upper Permian species of "*Xenacanthus*" that bear cristae on the principal cusps. "*X.*" *santosi* has slightly compressed cusps with unserrated carinae and straight as well as bifurcated cristae on both lingual and sometimes labial surfaces. She compares these teeth, especially their base, with *Orthacanthus* (*Xenacanthus*) *platypternus*, but it is evident that she meant *O. texensis* in reference to the thick base (and see her Plates 8 and 9). HAMPE (1995) suggested that this species might belong to *Plicatodus*, but the differences in their bases appear too great, unless the extent of the differences in the bases of the *O. compressus* teeth described above is accepted. WÜRDIG-MACIEL's (1975) other species, "*X.*" *pricei*, has teeth with cusps round in cross-section, but with a single unserrated carina and a single short crista on each of the labial and lingual surfaces.

None of the above taxa compare favourably with *O.* aff. *compressus* teeth, which have straight, nonbifurcated cristae. Except for the pattern of the cristae, it could be a species of *Plicatodus* (HAMPE 1995) because of its rather thin base, but is unlike *O.* aff. *platypternus* which has cristae only on the labial side of its cusps.

Nonserrated *Orthacanthus* teeth

One of the most commonly described features of *Orthacanthus* teeth is the serrations on the principal cusps and sometimes on the intermediate cusp as well. HAMPE (1988a, 1993, 1994, 1995) and SCHNEIDER (1988, 1996) use this feature as a character defining the genus; SOLER-GIJÓN (1997b) does also, except that he includes *Lebachacanthus* (*O.*) *senkenbergianus*. HAMPE (1988b, 1994), SCHNEIDER (1988, 1996), and SCHNEIDER & ZAJÍC (1994) refer *O. platypternus* to *Xenacanthus* because that species lacks serrated cusps. However, the posteriors and small medials in *O. texensis* often lack serrations, as do smaller *O. compressus* teeth. Although the largest *O. platypternus* teeth have wrinkles or incipient serrations on their carinae, it is probably incorrect to interpret them as potentially possessing serrations. Unfortunately, on the basis of JOHNSON (1979) and after confirming with JOHNSON the presence of "incipient serrations" in some teeth, ZIDEK (1993b, p. 62) used this character in arguing that *O. platypternus* is not a species *Xenacanthus*. But ZIDEK's remaining arguments using tooth morphology are persuasive (as are the similarities among the smaller teeth and number of foramina, as noted above), and the differences between *Xenacanthus* and *O. platypternus* in the chondrocranium, jaws, and hyoid elements (ZIDEK 1993b) suggest there is no affinity. ZIDEK (1993b) noted that the holotype of *O. bohemicus* is a juvenile. Examination of M1145 and M1147 (illustrated by FRITSCH 1889, Pls. 81, 81b; M1145 is the holotype; M1146 is the counterpart to M1145 and M1147 is a galvanic copy of M1146) reveals that the teeth lack serrations. Finally, the occipital spines associated with *O. platypternus* teeth (DONELAN & JOHNSON 1997) belong to *Orthacanthus* as defined by ZIDEK (1993b) and SOLER-GIJÓN (1997a). Therefore, the inclusion of *O. platypternus* in *Xenacanthus* is not warranted, nor can the occurrence of serrated cusps be used as a distinguishing character of *Orthacanthus*.

DENTITION, DIET, AND HABITAT OF *ORTHACANTHUS*

APPLEGATE (1965) summarized the functions of euselachian teeth; that summary serves as a basis for this discussion. The medial teeth of *Orthacanthus* were probably used for grasping smaller prey. These small teeth may have been largely restricted to juveniles, thereby implying ontogenetic heterodonty. However, HAMPE (1988a) stated that juvenile teeth of *O. senkenbergianus* (*Lebachacanthus* of SOLER-GIJÓN 1997b) are similar to *Xenacanthus* teeth, although the former are serrated at this early stage. Comparable teeth have not been found in the Texas Permian. The laterals, especially those in *O. texensis* and *O. compressus* with their serrated, posteriorly divergent major cusp, must have been very effective in slicing (the "grip and rip" hypothesis of ABLER 1992). These teeth would have permitted the capture of larger than bite-size prey. Movement by the captured prey attempting to escape or by the shark turning its head or body would cause the prey to become impaled on the cusps. The greater development of the posteriors in *O. texensis* may have permitted additional holding and perhaps even crushing power. However, these teeth are not heavily worn as in comparable teeth of some modern sharks described by APPLEGATE (1965). Although the laterals of *O. platypternus* may be as large as those of *O. texensis* (but not *O. compressus*), the former could not accommodate as large a prey as the latter because the posteriorly divergent cusp in *O. platypternus* is smaller and unserrated. It may have swallowed its prey whole.

The laterals in all three species of *Orthacanthus* have the same basic tooth-base construction. The design of the base indicates that considerable force may have been applied to the posteriorly divergent cusp as the prey was impaled. The components of this force would be directed anteriorly and toward the tooth base. To accommodate this force, the anterior part of the base is nearly always larger (bearing surface) than the posterior part, especially in *O. platypternus* laterals. The anterior principal and intermediate cusps presumably acted to resist the lateral forces produced by the shark and/or prey movements during the biting process.

The functions of the intermediate cusp(s) in *Orthacanthus* are difficult to assess. These cusps tend to be relatively shorter and more massive in *O. texensis* lateral teeth, suggesting they served primarily in the manner just mentioned. The usually single cusp in *O. platypternus* laterals tends to be longer and may have been more important in assisting in occlusion. Examination of *Orthacanthus* teeth from the Wichita Group for wear facets offered no evidence of occlusal patterns, however (JOHNSON 1979).

OLSON (1971, Fig. 151) suggested possible food sources for *Orthacanthus* (his *Xenacanthus*) in an attempt to assess the feeding relationships among known and inferred organisms from the Arroyo. Besides fishes, he suggested amphibians (*Trimerorhachis*) and reptiles such as the large *Dimetrodon*, which, though considerably adapted to a terrestrial life, may have preyed upon fish and amphibians in ponds and streams. Although *O. texensis* may have been dentally equipped to handle prey as large as *Dimetrodon*, it appears that *O. platypternus* (with teeth lacking serrations) would have been restricted to smaller prey. It seems likely that fishes were the main food source for both species. Later interpretations by OLSON (1977, 1984) excluded reptiles as potential prey. As both species probably exceeded 2 m in length, based on *O. senkenbergianus* (HEIDTKE 1982), nearly any animal that ventured into the water may have been potential prey, especially for *O. texensis*.

WILLIAMS (1972) analyzed Wolfcampian (Sakmarian) spiral coprolites and interpreted them as fossilized spiral valves (enterospirae) of xenacanths; MCALLISTER (1985) reinterpreted them as cololitic coprolites. WILLIAMS (1972) found them to contain mostly palaeoniscoid and lungfish scales, but also arthropod limbs, a *Helodus* tooth, a xenacanth tooth, and calcified cartilage. If xenacanths did prey on larger tetrapods, it might not be evident from the coprolites. WILLIAMS (1972) referred to the xenacanth teeth in the Wymore Shale fauna as *Xenacanthus*, probably following the standard procedure established by OLSON (1946), but they are *Orthacanthus* (JOHNSON 1992a; the Wymore Shale is a member of the Matfield Shale). Cursory examination of similar coprolites in the Texas Permian shows the presence of palaeoniscoid scales in the few where a determination can be made. HAMPE (1988) described the diet of *O. senkenbergianus*, the largest (3 m) known xenacanth, based on coprolite contents. He identified palaeoniscoids, acanthodians, other xenacanths (*Triodus*), and possibly smaller amphibians. This shark probably had the capability to take even larger prey, as it could have bitten it into pieces before ingesting it. SOLER-GIJÓN (1995) provided direct evidence of predation on *Triodus* by *O. meridionalis* (SOLER-GIJÓN, 1997a). *Orthacanthus* (nor other xenacanth genera) apparently did not utilize its occipital spine for capture of prey, as it was used only defensively (HAMPE 1997b).

HOTTON's (1952) suggestion that *O. platypternus* may have been a stream dweller is probably correct. It occurs throughout the Clear Fork Group, which is largely a stream channel-floodplain complex (MURRY & JOHNSON 1987). It is the least abundant of the three xenacanth species in the Wichita Group, which is characterized mostly by a deltaic-tidal flat complex (PARRISH 1978), suggesting that it may have preferred more inland waters. However, OLSON (1989) recovered numerous teeth of *O. platypternus* from marine facies in the Arroyo. It may have been diadromous, possibly catadromous, based on the low paleolatitude of the Texas Permian deposits (GROSS & *al.* 1988, ZIEGLER & *al.* 1997).

Orthacanthus texensis was probably a pond-dweller, according to HOTTON (1952) and SANDER (1989). Based on its occurrence in the Wichita section I have sampled, the water must have been brackish or even approaching normal marine salinity. Many of the local faunas appear to be similar to the type described by PARRISH (1978), in which animal remains were buried by storm-driven tidal waters. Examples are listed in JOHNSON (1979, p. 229). The absence of *O. texensis* in the terrestrial facies of the Clear Fork Group would suggest that it did not inhabit fresh water, but preliminary study of Oklahoma faunas refute this (JOHNSON 1994), as does its presence in freshwater deposits in the Archer City Bonebeds (SANDER 1989, JOHNSON 1992b). *O. texensis* must have been extinct by the beginning of Clear Fork time (JOHNSON 1996), notwithstanding presumed post-Wichita occurrences in Oklahoma (*O. compressus* of SIMPSON 1979).

PALAEOBIOGEOGRAPHY

Comparison between the xenacanth teeth found in North America and Europe seems to indicate a dilemma. Teeth of some taxa in the two regions seem remarkably similar, while other taxa appear to be endemic to one or the other region. Discovery of better skeletal material in North America and (perhaps) larger collections obtained by bulk sampling (if possible) of European deposits would better define their true distribution. From a North American perspective, it would be interesting to know whether *O. compressus* and possibly *O. texensis* occur in Europe. Although convergent evolution may be responsible, there appear to be close similarities between some *O. compressus* and *O. bohemicus* (and perhaps to an equal extent, *O. kounoviensis*) teeth based on examination of the collections at the National Museum in Prague. This similarity can be extended to the Lower Permian *Orthacanthus* tooth illustrated by HEYLER & POPLIN (1990, Fig. 2a). The similarity between some *O. compressus* and *O. gracilis* (GIEBEL) teeth was noted earlier. HAMPE (1988a, p. 292) concluded that *Orthacanthus* species from the European Permo-Carboniferous cannot yet be clearly distinguished by means of their teeth, but then (p. 294) gave a more optimistic opinion and included *O. texensis* among the species that can be differentiated. If there was an interchange of some of these species between these adjoining continents (HAMPE 1993, Fig. 1; see ZIEGLER & *al.* 1997 for a more recent palaeogeographic reconstruction), then why is there such a disparity between other species easily recognized by only their teeth? For example, *X. decheni*, "*X.*" *luedersensis,* and *O. platypternus* should be expected in both North America and Europe. Perhaps there was no interchange of any xenacanth species during the Late Carboniferous and Early Permian because of the Appalachian–Hercynian mountain barrier. OLSON (1979) noted there are fewer resemblances among fishes and aquatic tetrapods than strictly terrestrial tetrapods (BERMAN & MARTENS 1993, for example) between the two continents.

SCHNEIDER & ZAJÍC (1994) and SCHNEIDER (1996) discussed the environments, mostly lacustrine and some fluviatile, of the European xenacanth genera. They also discussed the dispersal of sharks between the Late Carboniferous and Early Permian European basins, noting the complications resulting from tectonic activity. Stable basins maintain a relatively high diversity, whereas short-lived basins have a low diversity, depending on migration opportunities. Although tectonic activity may not be responsible, other (unknown) abiotic factors may account for faunal differences between Nebraska and Pennsylvania. However, habitat preference may be responsible, as HAMPE (1994) noted that contemporaneous species of *Orthacanthus* and *Xenacanthus* are not found together in the Saar-Nahe basin. Pre-Artinskian faunas in Texas must be discovered and studied to explain the differences from the earlier North American faunas. Also, complications may arise from changing environmental preferences of some species during ontogeny (SCHNEIDER 1996). This might explain why large *O. compressus* teeth are absent from the Nebraska and Pennsylvania faunas. Perhaps most noteworthy is SCHNEIDER'S (1996) suggestion, accompanied by some evidence based on the distribution of egg capsules, of the migratory behaviour during reproductive cycles of as yet unidentified xenacanth genera. This could presumably include migration through coastal marine waters, which might account for the marine occurrence of *O. platypternus* described earlier. Although this species is unknown in Europe, it might explain the possible dispersal of other species of *Orthacanthus* and isolation of the more endemic species.

Genus *Xenacanthus* BEYRICH, 1848

TYPE SPECIES: *Orthacanthus decheni* GOLDFUSS, 1847.

REMARKS: See JOHNSON (1979) and HAMPE (1988a, 1994) for historical details concerning *Xenacanthus*, which originally referred to an occipital spine. Although spines identified as *Xenacanthus*, based on LUND'S (1970) description, occur in the Wichita Group of Texas and were presumably associated with "*X.*" *luedersensis* teeth (JOHNSON 1979), JOHNSON (1995) concluded that this association is not correct. Very small teeth from the Upper Carboniferous and Lower Permian were considered by JOHNSON (1979) to possibly be *Orthacanthus* "parasymphysial" teeth. Based on HAMPE'S (1994) study, these teeth are now tentatively assigned to *Xenacanthus*.

?*Xenacanthus slaughteri* sp. nov.
(Text-figs 21 and 22A-I; Tables 1-2)

HOLOTYPE: SMU 64345 (Text-fig. 21 R–V)

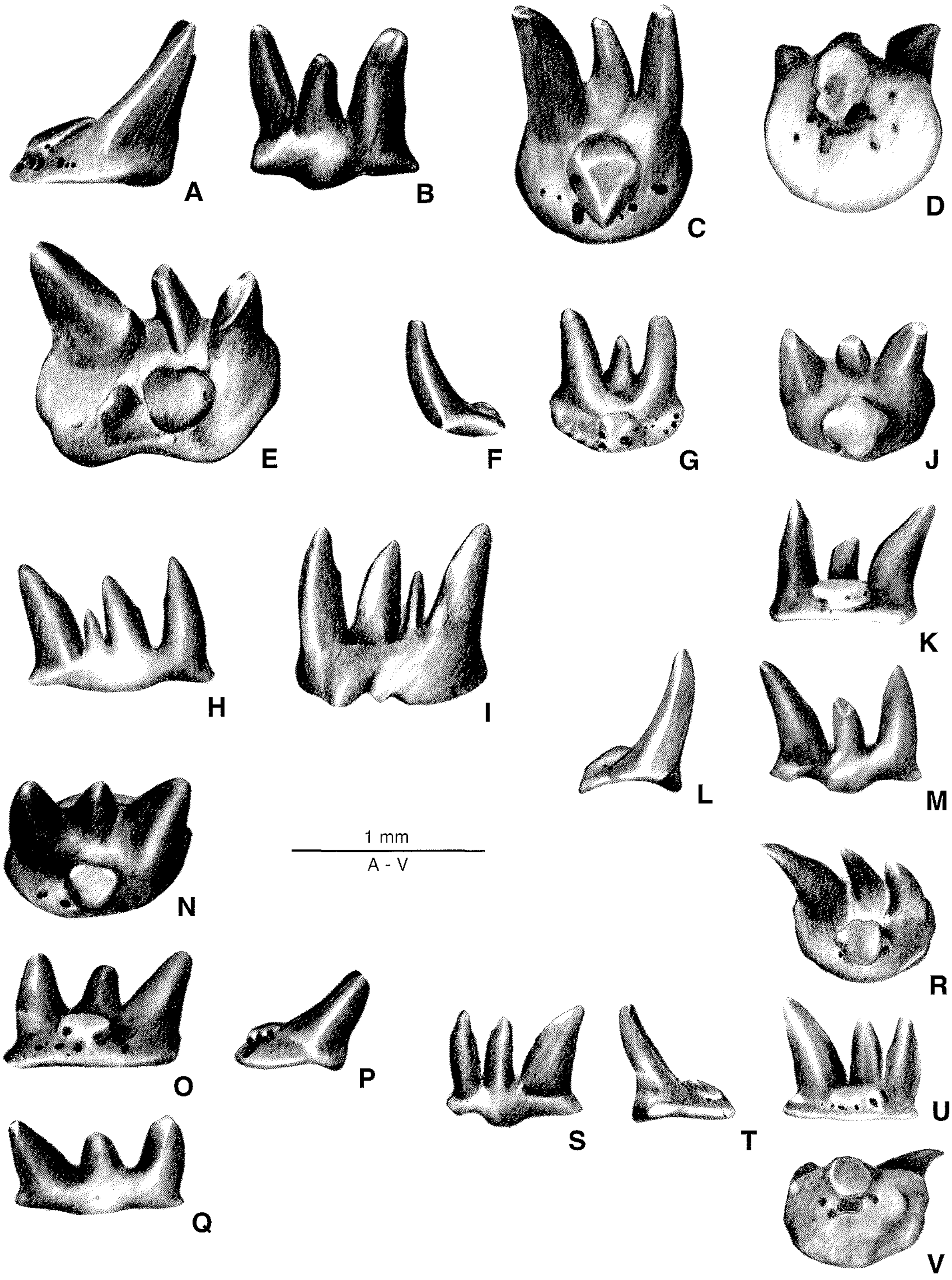

Fig. 21. ?*Xenacanthus slaughteri* sp. nov.; A-G – teeth from the Brushy Creek C/ac local fauna, upper Belle Plains; A – anteromedial or posterolateral, B – labial, C – lingual-occlusal, and D – aboral, views of SMU 64341; E – lingual-occlusal view of SMU 64342 (partly covered by matrix); and F – anteromedial or posterolateral, and G – lingual-occlusal, views of SMU 64343; H – labial, and I – lingual-occlusal, views of SMU 64319 from the Brushy Creek L/ac local fauna, upper Belle Plains; J-Q – teeth from the Wolf Creek A local fauna, upper Belle Plains; J – lingual-occlusal, K – lingual, L – posterolateral, and M – labial, views of SMU 64339; and N – lingual-occlusal, O – lingual, P – posterolateral, and Q – labial, views of SMU 64340; R – lingual-occlusal, S – labial, T – posterolateral, U – lingual, and V – aboral, views of SMU 64345 (holotype) from the Lake Kemp B/ac local fauna, middle Lueders

from the Lake Kemp B/ac local fauna, Lueders Formation, Lower Permian (Leonardian = Artinskian). This locality is in the Albany Group, whereas the remaining localities in the Lueders Formation (Table 1) away from Lake Kemp, even at the same horizon, are in the upper Waggoner Ranch Formation (Wichita Group); see JOHNSON 1996, HENTZ & BROWN 1987, and HENTZ 1988, for a stratigraphic explanation.

HYPODIGM: SMU 64345 (holotype); SMU 64339–64344, 64346 (Text-figs 21A–G, J–V; 22A–I).

ETYMOLOGY: Named in honour of Professor Bob H. Slaughter, former Director of the Shuler Museum of Paleontology, Southern Methodist University.

MATERIAL: Isolated teeth from the Wichita Group (SMU 64319–64346; Table 1). Three additional teeth have been recovered from the Lueders Formation (JOHNSON 1996, p. 375, lists four, but one may belong to *Orthacanthus*); one is complete (SMU 68787) and the other two are mostly complete (SMU 68788).

OCCURRENCE AND AGE: Known only from the Lueders, Waggoner Ranch [= Lueders (in part) + Clyde], and upper Petrolia (upper Belle Plains) formations (Leonardian = Artinskian) and upper Nocona (upper Admiral) Formation (Wolfcampian = Sakmarian) in north-central Texas, USA; see Table 1.

DIAGNOSIS: Principal cusps slightly divergent and compressed; carinae usually present, serrations always absent. Intermediate cusp present. Base thin and platelike. Apical button well developed, often in contact with the principal cusps. Central foramen usually present. Basal tubercle restricted to labial margin.

DESCRIPTION

Measurements: Only one local fauna has an adequate number of teeth for a suitable sample (Tables 1 and 2). The lack of larger samples may be a result of a procedural error, as explained below. The am–pl length of the base is greater than its l–l width, although a few teeth are nearly equidimensional (Text-fig. 21D; see scatter diagram in JOHNSON 1979, Fig. 45B). The ratio (slope, Table 2) of these dimensions is significantly less than in *O. platypternus*.

Tooth base: The base has the general shape of the *O. platypternus* base. The close proximity of the apical button to the principal cusps is a major character of "*X.*" *luedersensis* teeth (Text-fig. 1H), and it may reach the intermediate cusp (SMU 64331). The apical button is usually small relative to the size of the base (Text-fig. 21N); it is often isolated from the lingual margin. In a few teeth it is large, giving the base a massive appearance (Text-fig. 21C). The central foramen may occur to one side of the intruding apical button. It is not nearly as pronounced as in *Orthacanthus* teeth (Text-fig. 1F). Additional foramina may occur along the lingual, anteromedial, and posterolateral margins of the apical button. The basal tubercle is usually well developed. It does not extend to the center of the base (Text-figs 21D, V; 22A). The aboral surface of the base may be nearly flat, but is usually concave, sometimes noticeably so.

Principal cusps: These cusps are nearly parallel to one another, showing only slight divergence, and are often compressed throughout their length. They may diverge equally, giving a symmetrical appearance, or only one may be divergent. If only one cusp is divergent, as in the holotype, it is the major cusp (larger of the two; Text-figs 21E, K, S; 22D, H). Cristae are absent.

Intermediate cusp: A single long (relative to the principal cusps) and slender intermediate cusp is always present. It is straight in the symmetrical teeth or may lean in the direction of the divergent major cusp. It may be as long as the minor principal cusp (Text-figs 21S, 22D); all three cusps are of equal length in a tooth from the Brushy Creek L/ac measured sample (Table 2).

Unusual teeth: Two of the teeth have four cusps; both are from the Brushy Creek L/ac local fauna (Table 1). Three of the cusps are of nearly equal size in one of these teeth (Text-fig. 21H, I) and carinae are absent. The tooth has an elongated (am–pl) basal tubercle and the lingual margin is doubly bifurcated. The apical button is not developed. The other tooth is broken, but appears to have had four cusps. One of the principal cusps is smaller than the intermediate cusp next to it. Another tooth has a protruding rim on the labial

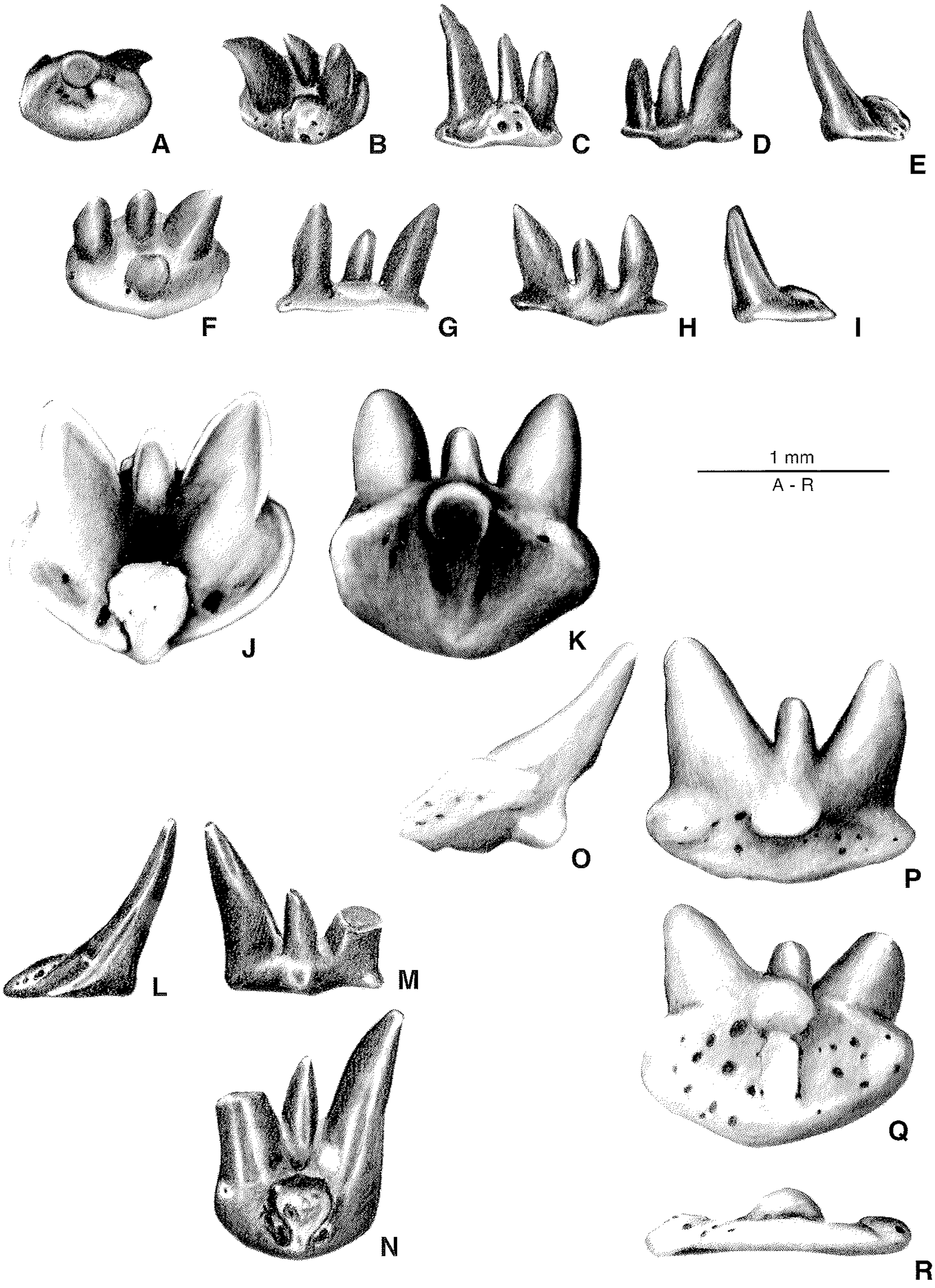

Fig. 22. A–I, ?*Xenacanthus slaughteri* sp. nov. teeth from the Lake Kemp B/ac local fauna, middle Lueders; A – aboral, B – lingual-occlusal, C – lingual, D – labial, and E – posterolateral, views of SMU 64344; and F – lingual-occlusal, G – lingual, H – labial, and I – anteromedial, views of SMU 64346; J-R – ?*Xenacanthus ossiani* sp. nov. teeth from Site 2 of the Peru local fauna, Towle Shale; J – lingual-occlusal, and K – labio-aboral, views of TMM 41647-23 (holotype); L – anteromedial or posterolateral, M – labial, and N – lingual–occlusal views of TMM 41647-317; and O – anteromedial or posterolateral, P – labial, Q – aboral, and R – lingual, views of TMM 41647-24 (all but the basal tubercle is hidden by the base in R)

margin of the base and an apical button offset toward the major principal cusp (Text-fig. 21E). The rim occurs in a few other teeth (SMU 64345, Lake Kemp B/ac local fauna, for example), but its significance is unknown. The tooth (SMU 64326) from the Brushy Creek K/ac local fuana (Table 1) has principal cusps that are nearly circular in cross section, although the major cusp has a weakly developed carina on the inner margin; its identity is questionable. A few teeth (SMU 64332, Mitchell Creek C, and SMU 64334, Lake Kemp B, for example) have highly compressed or spatulate cusps, but otherwise are normal.

Remarks: All the teeth are very small and distinctive in appearance. As only 77 were recovered, the extent of variation is not well known. They do not exhibit a heterodont dentition comparable to the *Orthacanthus* species described above, but they indicate more variation than any of the "*Xenacanthus*" species (JOHNSON 1979, 1980, 1984). Therefore, it remains unclear whether this species had a heterodont dentition.

DISCUSSION: These teeth represent a new species, although JOHNSON (1979) argued they do not. JOHNSON (1979) thought it reasonable that they functioned as "parasymphysials" and assigned them to *Orthacanthus* cf. *O. texensis*. Their distribution from one local fauna to the next in the Wichita Group appears to be independent of the other xenacanth species. For example, none of these teeth occur in the Wolf Creek/ac local fauna which contains large numbers of identified teeth (Table 1), although two of these teeth occur in the Wolf Creek A local fauna at the same locality. Twenty-six of these teeth occur in the Brushy Creek L/ac local fauna which contains only eight "*X.*" *luedersensis* and four *Orthacanthus* teeth. Their size range (Table 2) suggests a different species, but this is diminished by heterodonty (small teeth) in the *Orthacanthus* dentitions. There is a sufficient overlap in size (BERMAN 1970) with the *Orthacanthus* species so that immature individuals need not be considered in the sense of HAMPE's (1988a) juvenile teeth. However, SCHNEIDER (1996, p. 325) rejected HAMPE's (1994) *X. remigiusbergensis* apparently based partly on size, and also because the teeth are typical of juvenile *Xenacanthus*. This is not in agreement with ZIDEK's (1993b) assessment of *Orthacanthus* juvenile teeth; undisputed juvenile *Xenacanthus* teeth have not been described to my knowledge.

Review of the 18 local faunas (Table 1 and JOHNSON 1979, pp. 580–632) that produced these teeth reveals that 54 of the 74 known teeth come from local faunas obtained by acidizing rock. Concentrate obtained by this method was available for processing through a 40-mesh screen, whereas this was not practical for the remaining local faunas, including those from the Clear Fork Group. Only a small amount of 40-mesh concentrate was sorted because of the time required, for example 4% of the Wolf Creek/ac local fauna (used in earlier example). The exceptionally large number of teeth in the Brushy Creek L/ac local fauna, which is unusual in other ways (JOHNSON 1979, pp. 592–593), was obtained by sorting all of the 40-mesh concentrate (only 100 mL).

Teeth of ?*X. slaughteri* sp. nov. are most similar to those of *X. remigiusbergensis* from the lowermost Permian (HAMPE 1994), which is also described on the basis of very small isolated teeth. In the latter species the base is thin, with length > width; the principal cusps are compressed except near the base and bear carinae which are not serrated; the apical button is small, reduced, or even absent in presumed posterior teeth, isolated from the cusps, and sometimes has a lingual extension to the base margin; the basal tubercle is largely restricted (apparently) to the labial portion of the base; a prominent central foramen is always present, as is an intermediate cusp which has a length > 1/2 – 4/5 the principal cusp length. The dentition of *X. remigiusbergensis* is heterodont, based on the presence of bicusped symphysial teeth (presumably valid, unless another species is present). ?*X. slaughteri* sp. nov. teeth differ from this species in 1) often having the principal cusps compressed throughout their length; 2) apical button always present (except in one unusual tooth), often in contact with the cusps; 3) central foramen subdued or absent; 4) intermediate cusp often as long, or nearly as long, as the minor principal cusp; and 5) despite a larger sample [more than 70 teeth compared to HAMPE's (1994) 17 teeth], there is no evidence of symphysial teeth.

HAMPE (1994) compared his teeth with those of all other known species of *Xenacanthus*. Although the use of the number of foramina on the base is sometimes of dubious value, other characters such as shape of the tooth base, morphology of the apical button and basal tubercle, and usually the relative length of the intermediate cusp, collectively show significant differences.

?*X. slaughteri* sp. nov. is not similar to any of the species reviewed by HAMPE (1994).

The platelike base of ?*X. slaughteri* sp. nov. teeth suggests an *O. platypternus* affinity, as perhaps does the presence of the intermediate cusp. An affinity with *O. texensis* is suggested by a slightly divergent (although not persistently) major principal cusp and restriction of the basal tubercle to the labial portion of the base. Despite the thinness of the base (rt in Text-fig. 1), it is slightly thicker below the intermediate cusp than below the am/pl margins of the principal cusps, as in *O. texensis*. However, an affinity with *Xenacanthus* (HAMPE 1994) is much more compelling.

?*Xenacanthus ossiani* sp. nov.
(Text-figs 22J-R, 23, and 24; Tables 1-2)

HOLOTYPE: TMM 41647-23 (Text-fig. 22J, K) from Site 2 of the Peru local fauna (OSSIAN 1974), Towle Shale, Upper Carboniferous (Pennsylvanian), Gzhelian (Virgilian).

HYPODIGM: TMM 41647-23 (holotype); TMM 41647-317, 41647-24 (Text-fig. 22J–R).

ETYMOLOGY: Named in honour of Dr. Clair R. Ossian, who graciously permitted me to describe the xenacanths from his Peru locality (JOHNSON 1984, and this study).

MATERIAL: Isolated teeth from the Peru local fauna, Towle Shale (Site 2: TMM 41647-23, 24, 26, 317, 333; Site 3: TMM 41648-135), and Pittsburgh (CM 35160) and Conemaugh (one tooth in CM 26349) formations (Table 1).

OCCURRENCE AND AGE: Known only from the Peru local fauna in southeastern Nebraska and questionably from the Kennard Playground and Fort Pitt Tunnel-6 local faunas at Pittsburgh, Pennsylvania, USA. All occurrences are of Late Carboniferous (Pennsylvanian), Gzhelian (Virgilian), age (Table1).

DIAGNOSIS: Principal cusps highly compressed, labially inclined, smooth, without serrations; usually divergent. Single intermediate cusp present and compressed. Base thin. Apical button isolated from cusps. Prominent central foramen present. Basal tubercle generally extends to center of base.

DESCRIPTION

Measurements: Teeth from OSSIAN's Peru Site 2 (Tables 1 and 2) were measured, but the sample size (n = 13) may not be significant. However, it suggests that these teeth are generally larger than ?*X. slaughteri* sp. nov. teeth and noticeably smaller than *Orthacanthus* teeth. The base dimensions are more equidimensional (slope, Table 2; Text-fig. 23) than ?*X. slaughteri* sp. nov., approaching that of *O. compressus*. A scatter diagram is provided by JOHNSON (1979, Fig. 45A).

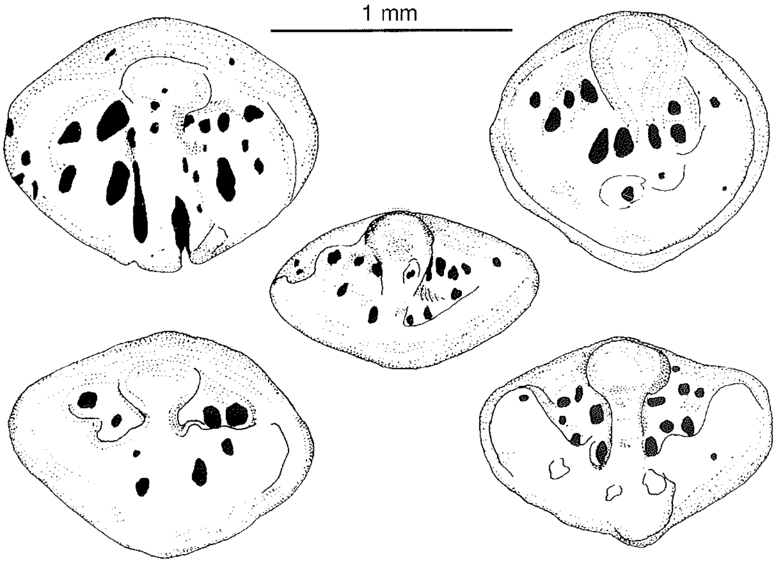

Fig. 23. Sketches of ?*Xenacanthus ossiani* sp. nov. aboral tooth surfaces from Site 2 of the Peru local fauna, Towle Shale. Comparable sketches of the measured teeth of ?*X. slaughteri* n. sp. from the Brushy Creek L/ac local fauna (upper Belle Plains) could not be made because of interference from matrix; but see Text-figs 21D, V and 22A

Tooth base: The thin appearance results mostly from a distinct flange that may be present at either the anteromedial or posterolateral end of the base; this flange does not resemble the one typical of *O. platypternus* laterals. Most of these teeth have a considerably thicker labial margin (rt in Text-fig. 1) between the basal tubercle and intermediate cusp than below the base of the am/pl margin of one of the principal cusps. The apical button is sometimes isolated from the lingual margin of the base. A single row of small foramina is present along the lingual margin. The basal tubercle (Text-fig. 23) is often subdued, possibly due to transport. The foramina on the aboral surface (Text-fig. 23) do not form any particular pattern, except for being generally absent from the lingual portion.

Principal cusps: They are nearly always divergent, either equally or unequally. The larger cusp is usually more divergent, but because the principal cusps are often of equal stature (or one is broken), major and minor cusps cannot be distinguished. Some bear carinae and are spatulate, and always lack cristae.

Intermediate cusp: It is usually about half the length of the principal cusps. It lacks cristae and serrations.

Unusual tooth: One tooth (TMM 41647-333) is comparable to the two unusual ?*X. slaughteri* sp. nov. teeth, as it also has four cusps. One of the intermediate cusps is broken; its base is labial to the other cusps. Its proximal diameter suggests that it may have been nearly as large as the other intermediate cusp, which is nearly as long as the principal cusps.

Remarks: The cusps are always labially inclined from the base. Ossian (1974) noted that the cusps and bases are often nearly in the same plane, so that the angle between them approaches 180° (Text-fig. 22O–R). This far exceeds the maximum angle of 140° given by Hampe (1994) for *X. remigiusbergensis*. Too few teeth are available to determine if ?*X. ossiani* sp. nov. possessed a heterodont dentition, but the illustrated teeth (Text-fig. 22J–R) suggest this possibility.

DISCUSSION: Ossian (1974) listed some of the fossils from the Peru locality as possibly "gill raker denticles," based on Fritsch (1889). However, they must be teeth from the jaw margin, as they possess well developed apical buttons and basal tubercles.

Despite the platelike appearance of the base with its flanges in ?*X. ossiani* sp. nov. teeth, and although all three cusps are considerably compressed, the general characteristics of these teeth match those of *O. compressus*. A few of the medial teeth of *O. compressus* are noticeably convergent in appearance with these teeth (Text-figs 19F, G, M–O; 24). The medial teeth of *O.*

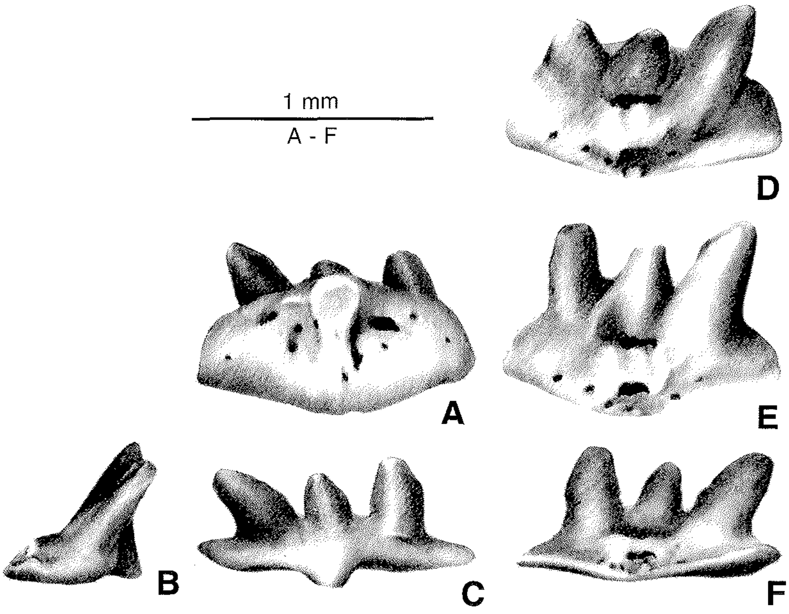

Fig. 24. ?*Xenacanthus* cf. ?*X. ossiani* sp. nov. tooth (CM 35160) from the Kennard Playground local fauna at Pittsburgh, Pennsylvania, lower Pittsburgh Formation; A – aboral, B – posterolateral, C – labial, D – occlusal, E – lingual-occlusal, and F – lingual, views

compressus tend to lack the flanges and the pattern of the foramina is not the same, but the angle between the cusps and the platelike base is distinctly obtuse.

As *O. platypternus* is not known from the Peru locality, that species need not be considered. Similar teeth referred to as ?*Xenacanthus* cf. ?*X. ossiani* occur in the Dunkard Basin faunas (Table 1; Text-fig. 24, and one tooth in CM 26349). JOHNSON (1979) regarded CM 35160 (Text-fig. 24) as either a medial or parasymphysial of *O. compressus*; subsequent examination of this tooth suggests the present interpretation.

These teeth were thought by JOHNSON (1979) to belong to *O. compressus*. As they are not typical of what JOHNSON (1979) regarded as medial teeth in this species, he called them "parasymphysial" teeth. As both symmetrical and asymmetrical teeth are present, they cannot be considered symphysial teeth (APPLEGATE 1965). If they should be demonstrated to belong to *O. compressus*, they may represent an example of dignathic or ontogenetic heterodonty or sexual dimorphism. Despite convergence with the medials of that species, there are enough discrepancies to warrant the conclusion that they belong to a separate and probably new species of *Xenacanthus*, unlike any of those reviewed by HAMPE (1994).

CONCLUSIONS

The attempt made by JOHNSON (1979) to solve taxonomic problems associated with upper Palaeozoic North American xenacanths was only partly successful because he thought European genera must have been similar to those in North America (and did not utilize all the information provided by Chris DUFFIN, *pers. comm.*) and was probably too conservative in identifications of isolated teeth. Although the analysis of collections of *O. compressus* teeth is judged to be preliminary, the concept of what North American *Orthacanthus* dentitions must have been like is now fairly well understood, although ontogenetic heterodonty may be a problem. Certainly there is less confusion than two decades ago, aided to a great degree by European studies. This presumed success in understanding *Orthacanthus* taxonomy in North America may result from blissful ignorance of more complete skeletal evidence and relationships to European species; as SCHNEIDER (1996) noted, there is still a great deal of confusion in the general classification of xenacanths.

The occurrence of ?*X. slaughteri* sp. nov. and ?*X. ossiani* sp. nov. along with poorly known *Xenacanthus*-like occipital-spine fragments (JOHNSON 1979) (which may or may not belong to these species) suggests *Xenacanthus* was present in North America. The occurrence of these species, together with *O.* aff. *platypternus*, *O.* aff. *compressus*, "*X.*" *luedersensis*, and *Bransonella (X.?) nebraskensis*, suggests strongly endemic populations. Endemic populations of other more numerous taxa occur in Europe. In contrast to these taxa are apparently very closely related species of *Orthacanthus* in the upper Palaeozoic.

Future research into palaeogeographic distributions of xenacanths should be beneficial after more success in identifying valid taxa and understanding their relationships is attained. Meanwhile, the biostratigraphic usefulness of isolated xenacanth teeth in the upper Palaeozoic is now approaching reality in North America as well as in Europe (SCHNEIDER 1996, HAMPE 1994).

Acknowledgments

This paper is dedicated to the late Bob H. SLAUGHTER, an exemplary mentor. Support was provided by the Dallas Geological Society, the National Park Service, the National Science Foundation (EAR-8216472, with Phillip A. MURRY), and the University of South Dakota College of Arts and Sciences and Office of Research for release time, travel, and research funds. Nearly all of the field work was done on the Waggoner Ranch; the hospitality and cooperation of several people, especially Gene WILLINGHAM and the late Glen COLLIER, is appreciated. The illustrations in Text-figures 4–8 and 10–24 were drawn by Pat GASSER, except those in Text-fig. 12J–L, which were drawn by April GAWBOY. Colleen ODENBRETT, South Dakota Geological Survey, typed the manuscript. Dennis JOHNSON, South Dakota Geological Survey, provided assistance with some figures. Field assistance was provided by Phillip MURRY and several of our students; and by Ronald RITCHIE, Robert MEYER, Rex SHEPPERD, and David GILLETTE. Logistical support in the field was provided by the Army Corps of Engineers, Fort Worth Office. Several people assisted in the initial phase of this study, including Bryce BELL, Elizabeth GWYN, Rose MALONEY, and Nanci MAYNES. Conversations and/or correpondence with the late Everett C. OLSON, Jiri ZIDEK, Chris DUFFIN, John MAISEY, Richard LUND, and Clair OSSIAN have been most helpful. Assistance in translating papers was provided by Werner KITZLER, Michael LEHR, and Mary Anne GARNETT. Loans of specimens and/or permission and assistance to study specimens were provided by Mary DAWSON and David BERMAN, Carnegie Museum of Natural History; Carolyn GOOD, Vertebrate Paleontology Laboratory, University of Texas at Austin; John BOLT and Catherine FORSTER, Field Museum of Natural History; John MAISEY and Ivy RUTZKY, American Museum of Natural History; John CHORN and Desui MIAO, Museum of Natural History, University of Kansas; V. TUREK, National Museum, Prague, Czech Republic; and Jaroslav ZAJÍC, Czech Geological Survey. Jiri ZIDEK, Oliver HAMPE, and Rodrigo SOLER-GIJÓN provided useful comments on the initial manuscript submitted to the editor. Their efforts are greatly appreciated. This is a contribution to the International Geological Correlation Programme Nos. 328 and 406.

REFERENCES

ABLER, W. L. 1992. The serrated teeth of tyrannosaurid dinosaurs and biting structures in other animals. *Paleobiology*, **18**, 161-183. Lawrence.

AGASSIZ, L. 1843. Recherches sur les poissons fossiles. Volume 3. Contenant l'Histoire de l'Ordre des Placoides, pp. 1-422. Neuchâtel.

APPLEGATE, S. P. 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. *Los Angeles County Museum Contributions in Science*, **87**, 3-18. Los Angeles.

BAARS, D. L. 1991. Permian chronostratigraphy in Kansas: Reply. *Geology*, **19**, 665-666. Boulder.

BERMAN, D. S. 1970. Vertebrate fossils from the Lueders Formation, Lower Permian of north-central Texas. *University of California, Publications in Geological Sciences*, **86**, 1-61. Berkeley.

BERMAN, D. S. & MARTENS, T. 1993. First occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of central Germany. *Annals of Carnegie Museum*, **62**, 63-79. Pittsburgh.

BEYRICH, E. 1848. Über *Xenacanthus decheni* und *Holacanthus gracilis*, zwei Fische aus der Formation des Rothliegenden in Nord Deutschland. *Preussische Akademie der Wissenschaften, Berlin*, **1848**, 24-33. Berlin.

CAPPETA, H., DUFFIN, C. & ZIDEK, J. 1993. Chondrichthyes. *In*: M. J. BENTON (*Ed.*), The Fossil Record 2. *Chapman & Hall*, pp. 593-609. London.

CHORN, J. & SCHULTZE, H.-P. 1990. The Robinson locality: fauna and depositional environment. *In*: C. R. CUNNINGHAM & C. G. MAPLES (*Eds*), 1990 Society of Vertebrate Paleontology Upper Paleozoic of Eastern Kansas Excursion Guidebook. *Kansas Geological Survey Open-file Report*, **90-24**, 17-24. Lawrence.

COMPAGNO, L. J. V. 1970. Systematics of the genus *Henritriakis* (Selachii; Carcharhinidae) and related genera. *California Academy of Sciences Proceedings*, **38** (4), 63-98. San Francisco.

COPE, E. D. 1883. On some Vertebrata from the Permian of Illinois. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1883**, 108-110. Philadelphia.

— 1884a. The genus *Pleuracanthus*. *The American Naturalist*, **18**, 818. Philadelphia.

— 1884b. On the structure of the skull in the elasmobranch *Didymodus*. *Proceedings of the American Philosophical Society*, **21**, 572-590. Philadelphia.

— 1888. Systematic catalogue of species of Vertebrata found in beds of the Permian epoch in N. America with notes and descriptions. *American Philosophical Society Transactions (N. S.)*, **16**, 285-297. Philadelphia.

DAVIS, J. W. 1892. On the fossil fish-remains of the Coal Measures of the British Islands, Part I. Pleuracanthidae. *Royal Dublin Society Scientific Transactions*, **4** (2), 703-748, pls. 65-73. Dublin.

DAWSON, J. W. 1868. Acadian Geology, 2nd ed., pp. 1-694. *Macmillan*; London.

DESTINEZ, P. 1898. Sur deux *Diplodus* et un *Chomatodus* de l'Ampélite à unifère de Chopier, et deux *Cladodus* de Visé. *Annales de la Société Geologique de Belgique*, **24**, 219-223. Liége.

DONELAN, C. & JOHNSON, G. D. 1997. *Orthacanthus platypternus* (Chondrichthyes: Xenacanthida) occipital spines from the Lower Permian Craddock bonebed, Baylor County, Texas. *Journal of Vertebrate Paleontology*, **17** (Supplement to No. 3, Abstracts), 43A. Chicago.

FRITSCH, A. 1889. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, v. 2, pp. 1-114 + 42 pls. *F. Řivnáč*; Praha.

GARMAN, S. 1885. *Chlamydoselachus anguineus* Garm.– a living species of cladodont shark. *Bulletin of the Museum of Comparative Zoology*, **12**, 1-35. Cambridge.

GEISER, S. W. 1948. Naturalists of the Frontier, 2nd ed., pp. 1-296. *University Press, Southern Methodist University*; Dallas.

GOLDFUSS, G. A. 1847. Über das älteste der mit Bestimimtheit erkannten Reptilien, einen Krokodilier, und einige neue fossile Fische aus der steinkohlen-Formation. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1847**, 400-404. Stuttgart.

GROSS, M. R., COLEMAN, R. M. & MCDOWALL, R. M.

1988. Aquatic productivity and the evolution of diadromous fish migration. *Science*, **239**, 1291-1293. Washington.

HAMPE, O. 1988a. Über die Bezahnung des *Orthacanthus* (Chondrichthyes: Xenacanthida; Oberkarbon–Unterperm). *Paläontologische Zeitschrift*, **62**, 285-296. Stuttgart.

— 1988b. Über die Bezahnung des *Xenacanthus* (Chondrichthyes: Xenacanthida; Unterperm, SW-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1988**, 743-756. Stuttgart.

— 1989. Revision der *Triodus*-Arten (Chondrichthyes: Xenacanthida) aus dem saarpfälzischen Rotliegenden (Oberkarbon–Perm, SW-Deutschland) aufgrund ihrer Bezahnung. *Paläontologische Zeitschrift*, **63**, 79-101. Stuttgart.

— 1993. Variation of xenacanthid teeth in the Permo-Carboniferous deposits of the Saar-Nahe Basin (SW-Germany). *In*: U. HEIDTKE (*compiler*), New Research on Permo-Carboniferous Faunas. POLLICHIA–Buch, **29**, 37-51. Bad Dürkheim.

— 1994. Neue Erkenntnisse zur permokarbonischen Xenacanthiden-Fauna (Chondrichthyes: Elasmobranchii) und deren Verbreitung im südwestdeutschen Saar-Nahe-Becken. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **192**, 53-87. Stuttgart.

— 1995. *Plicatodus jordani* n. g., n. sp., a new xenacanthid shark from the Lower Permian of Europe (Saar-Nahe Basin, Germany). *In*: M. ARSENAULT, H. LELIEVRE, & P. JANVIER (*Eds*), Studies on Early Vertebrates. *Bulletin du Muséum National d'Histoire Naturelle, Section C, Sciences de la Terre; Paléontologie, Géologie, Minéralogie*, **17**, 209-226. Paris.

— 1997a. Dental growth anomalies and morphological changes in the teeth of the Xenacanthida (Lower Permian; Saar-Nahe Basin, SW Germany). *Modern Geology*, **21**, 121-135. Amsterdam.

— 1997b. Zur funktionellen Deutung des Dorsalstachels und der Placoidschuppen der Xenacanthida (Chondrichthyes: Elasmobranchii; Unterperm). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **206**, 29-51. Stuttgart.

HEIDTKE, U. 1982. Der Xenacanthide *Orthacanthus senckenbergianus* aus dem pfälzischen Rotliegenden (Unter-Perm). *Mitteilungen der POLLICHIA*, **70**, 65-86. Bad Dürkheim.

HENTZ, T. F. 1988. Lithostratigraphy and paleoenvironments of upper Paleozoic continental red beds, North-Central Texas: Bowie (new) and Wichita (revised) Groups. *The University of Texas at Austin, Bureau of Economic Geology Report of Investigations*, **170**, 1-55. Austin.

HENTZ, T. F. & BROWN, JR., L. F. 1987. Wichita Falls–Lawton sheet. *In* V. E. BARNES (*project director*), Geologic Atlas of Texas. *The University of Texas at Austin, Bureau of Economic Geology*, scale 1:250,000. Austin.

HEYLER, D. & POPLIN, C. 1990. Les vertébrés autuniens de Buxiéres-les-Mines (Allier, France). *Bulletin du Muséum National d'Histoire Naturelle. Section C, Sciences de la Terre; Paléontologie, Géologie, Minéralogie [Série 4]*, **12**, 225-239. Paris.

HOTTON, N. 1952. Jaws and teeth of American xenacanth sharks. *Journal of Paleontology*, **26**, 489-500. Tulsa.

HUSSAKOF, L. 1908. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. Part I. Fishes. *Bulletin of the American Museum of Natural History*, **25**, 1-103. New York.

— 1911. The Permian fishes of North America. *Carnegie Institution of Washington Publications*, **146**, 155-175. Washington.

JOHNSON, G. D. 1979. Early Permian vertebrates from Texas: Actinopterygii (*Schaefferichthys*), Chondrichthyes (including North American Pennsylvanian and Triassic Xenacanthodii), and Acanthodii, pp. 1-653. *Unpublished Ph.D. dissertation, Southern Methodist University*; Dallas. [available from University Microfilms International, Ann Arbor and London (listed as 1980)]

— 1980. Xenacanthodii (Chondrichthyes) from the Tecovas Formation (Late Triassic) of West Texas. *Journal of Paleontology*, **54**, 923-932. Tulsa.

— 1981a. Hybodontoidei (Chondrichthyes) from the Wichita–Albany Group (Early Permian) of Texas. *Journal of Vertebrate Paleontology*, **1**, 1-41. Norman.

— 1981b. A Permian–?Pennsylvanian chondrichthyan microfauna from lowermost Wichita–Albany Group in north-central Texas. *Bulletin, American Association of Petroleum Geologists*, **65**, 941-942 (abstract). Tulsa.

— 1984. A new species of Xenacanthodii (Chondrichthyes, Elasmobrachii) from the Late Pennsylvanian of Nebraska. *In*: R. M. MENGEL (*Ed.*), Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. *Special Publication of Carnegie Museum of Natural History*, **9**, 178-186. Pittsburgh.

— 1987. Deformed xenacanthodiid shark teeth from the Permian of Texas. *In*: J. E. MARTIN & G. E. OSTRANDER (*Eds*), Papers in Vertebrate Paleontology Honoring Morton Green. *Dakoterra*, **3**, 22-27. Rapid City.

— 1992a. Chondrichthyan biostratigraphy of the North American Permian System. *In*: A.E.M. NAIRN & V.

KOROTEEV (*Eds*), Contributions to Eurasian Geology. Papers Presented at the International Congress on the Permian System of the World, Perm, Russia, 1991–Part 1. *Occasional Publications ESRI, New Series*, **8B**, 41-50. Columbia.

— 1992b. Early Permian vertebrate microfossils from Archer City Bonebed 3, Archer County, Texas. *Journal of Vertebrate Paleontology*, **12** (Supplement to No. 3, Abstracts), 35A-36A. Lincoln.

— 1994. Microfossils from the Lower Permian (Wellington Formation) Orlando Site, Noble County, Oklahoma. *Journal of Vertebrate Paleontology*, **14** (Supplement to No. 3, Abstracts), 31A. Chicago.

— 1995. Does *Xenacanthus* (Chondrichthyes, Xenacanthiformes) occur in the upper Paleozoic of North America? *Journal of Vertebrate Paleontology*, **15** (Supplement to No. 3, Abstracts), 38A. Chicago.

— 1996. Vertebrate microfossils from the Lueders Formation, Albany Group, and the faunal transition from the Wichita Group into the Clear Fork Group, Lower Permian of Texas. *Modern Geology*, **20**, 371-382. Amsterdam.

JOHNSON, G. D., MURRY, P. A. & STORER, J. E. 1994. Recovery of vertebrate microfossils. *Proceedings of the South Dakota Academy of Science*, **73**, 211-230. Vermillion.

LUND, R. 1970. Fishes from the Duquesne Limestone (Conemaugh, Pennsylvanian), Part I: Fossil fishes from southwestern Pennsylvania. *Annals of Carnegie Museum*, **41**, 231-261. Pittsburgh.

— 1975. Vertebrate-fossil zonation and correlation of the Dunkard Basin. *In*: J. A. BARLOW (*Ed.*), The Age of the Dunkard. Proceedings of the First I. C. White Memorial Symposium, pp. 171-182. *West Virginia Geological and Economic Survey*. Morgantown.

— 1976. General geology and vertebrate biostratigraphy of the Dunkard Basin. *In*: H. FALKE (*Ed.*), The Continental Permian in Central, West, and South Europe, pp. 225-239. *D. Reidel Co.*; Dordrecht.

MASSON, A. G. & RUST, B. R. 1984. Freshwater shark teeth as paleoenvironmental indicators in the Upper Pennsylvanian Morien Group of the Sydney Basin, Nova Scotia. *Canadian Journal of Earth Sciences*, **21**, 1151-1155. Ottawa.

MCALLISTER, J. A. 1985. Reevaluation of the formation of spiral coprolites. *University of Kansas Paleontological Contributions, Paper*, **114**, 1-12. Lawrence.

MURRY, P. A. & JOHNSON, G. D. 1987. Clear Fork vertebrates and environments from the Lower Permian of north-central Texas. *Texas Journal of Science*, **39**, 253-266. San Angelo.

NEWBERRY, J. S. 1856. Description of several new genera and species of fossil fishes, from the Carboniferous strata of Ohio. *Philadelphia Academy of Natural Science Proceedings*, **1858**, 96-100. Philadelphia.

OLSON, E. C. 1946. Fresh- and brackish-water vertebrate-bearing deposits of the Pennsylvanian of Illinois. *The Journal of Geology*, **54**, 281-305. Chicago.

— 1956. Fauna of the Vale and Choza. 13. *Diadectes, Xenacanthus*, and specimens of uncertain affinities. *Fieldiana, Geology*, **10**, 329-334. Chicago.

— 1962. Late Permian terrestrial vertebrates. U.S.A. and U.S.S.R. *American Philosophical Society Transactions (N.S.)*, **52**(2), 1-224. Philadelphia.

— 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. *Oklahoma Geological Survey Circular*, **70**, 1-70. Norman.

— 1967. Early Permian vertebrates of Oklahoma. *Oklahoma Geological Survey Circular*, **74**, 1-111. Norman.

— 1971. Vertebrate Paleozoology, pp. 1-839. *John Wiley and Sons, Inc.*; New York.

— 1977. Permian lake faunas: A study in community evolution. *In*: S. N. SINGH (*Ed.*), Jurij Alexandrovich Orlov Memorial Volume. *Journal of the Paleontological Society of India*, **20**, 146-163. Lucknow.

— 1979. Biological and physical factors in the dispersal of Permo-Carboniferous terrestrial vertebrates. *In*: J. GRAY & A. J. BOUCOT (*Eds*), Historical Biogeography, Plate Tectonics, and the Changing Environment. *Proceedings of the Annual Biology Colloquium and Selected Papers*, No. 37, pp. 227-238. *Oregon State University Press*; Corvallis.

— 1984. Permo-Carboniferous vertebrate communities. *In*: J. T. DUTRO, JR. (*Ed.*), Neuviéme Congrés International de Stratigraphie et de Géologie du Carbonifére. Compte Rendu. Volume 5. Paleontology, Paleoecology, Paleogeography, pp. 331-345. *Southern Illinois Press*; Carbondale.

— 1989. The Arroyo Formation (Leonardian: Lower Permian) and its vertebrate fossils. *Texas Memorial Museum Bulletin*, **35**, pp. 1-25. Austin.

OLSON, E. C. & BEERBOWER, J. R. 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. *The Journal of Geology*, **61**, 389-423. Chicago.

OSSIAN, C. R. 1974. Paleontology, paleobotany, and facies characteristics of a Pennsylvanian delta in southeastern Nebraska, *Unpublished Ph.D. dissertation, University of Texas, Austin*; pp. 1-393. Austin.

PARRISH, W. C. 1978. Paleoenvironmental analysis of a Lower Permian bonebed and adjacent sediments, Wichita County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **24**, 209-237. Amsterdam.

READ, W. F. 1943. Environmental significance of a small deposit in the Texas Permian. *The Journal of Geology*, **51**, 473-487. Chicago.

ROMER, A. S. 1945. The Late Carboniferous vertebrate fauna of Kounova (Bohemia) compared with that of the Texas redbeds. *American Journal of Science*, **243**, 417-442. New Haven.

— 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh–West Virginia region. *Annals of the Carnegie Museum*, **33**, 47-112. Pittsburgh.

SANDER, P. M. 1989. Early Permian depositional environments and pond bonebeds in central Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **69**, 1-21. Amsterdam.

SCHAEFFER, B. 1981. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *American Museum of Natural History Bulletin*, **169**(1), 1-66. New York.

SCHNEIDER, J. 1988. Grundlagen der Morphogenie, Taxonomie, und Biostratigraphie isolieter Xenacanthodier-Zähne (Elasmobranchii). *Freiberger Forschungshefte*, C **419**, 71-80. Leipzig.

— 1996. Xenacanth teeth-a key for taxonomy and biostratigraphy. *Modern Geology*, **20**, 321-340. Amsterdam.

SCHNEIDER, J. W. & ZAJÍC, J. 1994. Xenacanthiden (Pisces, Chondrichthyes) des mitteleuropäischen Oberkarbon und Perm – Revision der Originale zu Goldfuss 1847, Beyrich 1848, Kner 1867 und Fritsch 1879–1890. *Freiberger Forschungshefte*, **C452**, 101-151. Leipzig.

SCHULTZE, H.-P. 1985. Marine to onshore vertebrates in the Lower Permian of Kansas and their paleoenvironmental implications. *University of Kansas Paleontological Contributions*, *Paper*, **113**, 1-18. Lawrence.

SCHULTZE, H.-P. & CHORN, J. 1988. The Upper Pennsylvanian vertebrate fauna of Hamilton, Kansas. *In*: G. MAPES & R. H. MAPES (*Eds*), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas, pp. 147-154. *Kansas Geological Survey Guidebook* 6. Lawrence.

SILVA SANTOS, R. 1946. Duas novas formas de elasmobranquios do Paleozoico do Meio do Norte, Brasil. *Anais da Academia Brasileira de Ciências*, **18**, 281-285. Rio de Janeiro.

SILVA SANTOS, R. & SARDENBERG SALGADO, M. 1970. Um espinho de *Xenacanthus* do Carbonífero do estado de Maranhão. *Anais da Academia Brasileira de Ciências*, **42**, 223-227. Rio de Janeiro.

SIMPSON, G. G., ROE, A. & LEWONTIN, R. C. 1960. Quantitative Zoology, rev. ed., pp. 1-440. *Harcourt Brace and Co.*; New York.

SIMPSON, L. C. 1979. Upper Gearyan and Lower Leondardian terrestrial vertebrate faunas of Oklahoma. *Oklahoma Geology Notes*, **39**, 3-21. Norman.

SOLER-GIJÓN, R. 1995. Evidence of predator–prey relationsip in xenacanth sharks of the Upper Carboniferous (Stephanian C) from Puertollano, Spain. *In:* H. LELIEVRE, S. WENZ, A. BLIECK, & R. CLOUTIER (*Eds*), Premiers vertébrés et vertébrés inférieurs. *Géobios Mémoire Spécial*, **19**, 151-156. Lyon.

— 1997a. *Orthacanthus meridionalis*, a new xenacanth shark (Elasmobranchii) from the Upper Carboniferous of the Puertollano basin, Spain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **205**, 141-169. Stuttgart.

— 1997b. New discoveries of xenacanth sharks from the Late Carboniferous of Spain (Puertollano Basin) and Early Permian of Germany (Saar-Nahe Basin): Implications for the phylogeny of xenacanthiform and anacanthous sharks. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **205**, 1-31. Stuttgart.

SOLER-GIJÓN, R. & HAMPE, O. 1998. Evidence of *Triodus* Jordan 1849 (Elasmobranchii: Xenacanthidae) in the Lower Permian of the Autun basin (Muse, France). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1998**, 335-348. Stuttgart.

WILLIAMS, M. E. 1972. The origin of "spiral coprolites." *The University of Kansas Paleontological Contributions*, **59**, 1-19. Lawrence.

WOODWARD, A. S. 1889. Catalogue of the fossil fishes in the British Museum (Nat. Hist.); Part 1, Containing the Elasmobranchii, pp. 1-474. *Taylor and Francis*; London.

— 1891. Dr. Anton Fritsch on Paleozoic elasmobranch fishes. *The Geological Magazine*, **8** (3), 375-378. London.

WÜRDIG-MACIEL, N. L. 1975. Ichtiodontes e ichtiodurlites (Pisces) da Formação Estrada Nova e sua aplicação na estratigrafia do Grupo Passa Dois. *Pesquisas*, **5**, 7-83. Porto Alegre.

ZIDEK, J. 1966. Nové nálezy žralokovitých ryb skupiny Xenacanthodii ve spodním permu Boskovické brázdy na Moravě. *Časopsis Národního Muzea, Přírodovědecké oddělení*, **135**, 74-80. Praha.

— 1993a. Xenacanth genera: How many and how to tell them apart. *In*: U. HEIDKE (*compiler*), New Research on Permo-Carboniferous Faunas. *POLLICHIA*-Buch, **29**, 23-25. Bad Dürkheim.

— 1993b. Juvenile *Orthacanthus platypternus* (COPE 1883) (Elasmobranchii: Xenacanthiformes) from the Upper Carboniferous near Hamilton, Kansas, U.S.A. *In*: U. HEIDTKE (*compiler*), New Research on Permo-

Carboniferous Faunas. *POLLICHIA*–Buch, **29**, 53-65. Bad Dürkheim.

ZIEGLER, A. M., HULVER, M. L. & ROWLEY, D. B. 1997. Permian world topography and climate. *In*: I. P. MARTINI (*Ed.*), Late Glacial and Postglacial Environmental Changes–Quaternary, Carboniferous-Permian, and Proterozoic, pp. 111-146. *Oxford University Press*; New York.

Manuscript submitted: 15th October 1998
Revised version accepted: 20th January 1999