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Early Pennsylvanian xenacanth chondrichthyans from the Swisshelm Mountains, Arizona, USA

GARY D. JOHNSON and DAVID W. THAYER

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Three genera of xenacanths, based on isolated teeth, occur in the lepospondyl (amphibian)-dominated fauna from the upper Black Prince Limestone (late Bashkirian). *Orthacanthus donnelljohnsi* sp. nov. teeth, with carinae lacking serrations on the compressed principal cusps, and only one intermediate cusp, represent both adult and juvenile teeth. Heterodonty occurs in both adult and juvenile dentitions. The absence of serrations is unique among Pennsylvanian species of *Orthacanthus*. Teeth with often highly asymmetrical bases with an aborally-flexed lingual marginal flange (= antero-lingual shelf) and a single intermediate cusp are assigned to *Triodus elpia* sp. nov. A central foramen occurs in the base, unlike most other species; the moderately compressed principal cusps bear generally straight cristae. They represent the first reported occurrence of *Triodus* in the Paleozoic of North America. Five teeth, with cristae extending from the cusps onto their bases, belong to *Bransonella*. Two are questionably assigned to *Bransonella nebraskensis*, one to *B.* ?*lingulata* with its labio-lingually elongated apical button and smaller than normal intermediate cusp, and one each to *Bransonella* sp. "A" and "B". *Bransonella* sp. "A" has a base wider (labio-lingual) than long, the reverse of the other *Bransonella* teeth. *Bransonella* sp. "B" is distinctly different, as it lacks an intermediate cusp (as in some *B. lingulata* teeth), and the basal tubercle is beneath one of the cusps (with no evidence of deformity).

Key words: Chondrichthyes, Xenacanthiformes, Bransonelliformes, *Orthacanthus*, *Triodus*, *Bransonella*, Bashkirian, Arizona.

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Introduction

A vertebrate fauna dominated by lepospondyl amphibians was reported by Thayer (1985) to also contain xenacanths, lungfish (*Gnathorhiza*), possible helodontids, petalodonts, and cladoselachians. The fauna is from one meter below the top of the Black Prince Limestone at the north end of the Swisshelm Mountains in southeastern Arizona. The fauna occurs in an oncolitic limestone containing a variety of teeth, scales, and skeletal elements, which Thayer (1985) interpreted to represent an estaurine environment. Its age, based on fusulinids and conodonts, was determined by Thayer (1985) to be equivalent to the boundary between Westphalian A and B (latest Morowan). Based on Menning et al. (2006), the age is late Bashkirian (~314 Ma). This paper focuses on several taxa of xenacanth sharks present in the fauna. Their classification follows Hampe (2003: table 2) and Hampe and Ivanov (2007a), but with reservations discussed below.

Institutional abbreviation.—UAPL, University of Arizona Laboratory of Paleontology, Tucson, AZ, USA.

Other abbreviations.—am-pl, anteromedial-posterolateral (length); l-l, and labio-lingual (width); s.d., standard deviation.

Materials and methods

All specimens are reposited in the UAPL. Additional terminology is self-explanatory; otherwise, see Johnson (1999: 221–222). Teeth with complete bases, i.e., intact margins, were measured as seen in aboral view using a camera lucida. As differences in heterodonty are based on cusp orientation, and as no consistent differences could be recognized in tooth bases between teeth throughout the dental arcade, they were combined for purposes of measurement analyses. The most reliable measurement is used as the independent variable in regression analyses. Angles were estimated.

Systematic paleontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Superorder Xenacanthimorpha Berg, 1940

Order Xenacanthiformes Berg, 1940
[= Xenacanthida Glikman, 1964]

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Family Diplodoselachidae Dick, 1981

Remarks.—Hampe's (2003: 197) taxonomic review included five genera, including *Orthacanthus*, in this primitive family. Schneider and Zajíc (1994: 132) and Schneider (1996: 333–334) also placed this genus in the diplodoselachids. Soler-Gijón (1997: 166) placed *Orthacanthus* in the Xenacanthidae based on occipital spine similarities to *Xenacanthus* and *Triodus*. Schultze and Soler-Gijón (2004) follow this assignment, but without comment. Rodrigo Soler-Gijón (personal communication, October 2007) further argued that *Orthacanthus* shares many features in occipital spine and postcranial morphology with *Xenacanthus*, *Triodus*, and *Plicatodus*, which are highly derived xenacanths. His point is well taken and may be correct that *Orthacanthus* should be in the Xenacanthidae.

Genus *Orthacanthus* Agassiz, 1843

Type species: *Orthacanthus cylindricus* (Agassiz, 1843) (= *O. gibbosus*), Late Carboniferous, Coal Measures, Manchester, England. Spine figured in Agassiz (1843: pl. 45: 7–9), but its whereabouts is unknown (Hampe 2003: 205).

1843 *Diplodus* Agassiz, 1843: 204, pl. 22B: 1.
1883 *Didymodus* Cope, 1883: 108.
1885 *Diacranodus* Garman, 1885: 30.
1889 *Diplodus*; Woodward 1889: 10.
1889 *Orthacanthus*; Fritsch 1889: 100–112, pls. 81–90.
1946 *Xenacanthus* Beyrich, 1848; Olson 1946: 286–288, fig. 1.
1952 *Xenacanthus*; Hotton 1952: 489–500, pl. 58.
1970 *Xenacanthus*; Berman 1970: 19–20.

Diagnosis.—Limited to dentition. Heterodont; teeth with minimum of three cusps, two principal cusps and an intermediate cusp; secondary intermediate cusps sometimes present. Principal cusps labio-lingually compressed, often with edges developed into carinae that are usually serrated; cristae absent; major transverse axes of proximal ends <45° to, and often nearly parallel to, the labial margin of the base between these cusps. Apical button isolated from cusps; central (median) foramen present. Basal tubercle with flat or convex surface. See Hampe (2003: 205).

Orthacanthus donnelljohnsi sp. nov.

Figs. 1–9.

Etymology: In honor of the late Donnell F. Johns (1934–2002), who was professor of surgery, clinical professor of otolarynology and director of clinical research for the Department of Plastic Surgery at The University of Texas Southwestern Medical Center at Dallas. He was awarded the 2002 Frank R. Kleffner Clinical Career Award of the American Speech Language-Hearing Foundation, the most prestigious award in his profession, particularly for developing the pharyngeal flap procedure. The lives of hundreds of people were greatly improved by his direct intervention, particularly children.

Type material: Holotype: UAPL 23384, lateral tooth (Fig. 1). Paratypes include 59 measured adult teeth comprising UAPL 5269 (one lateral), 23382 (42 laterals), 23383 (one lateral), 23386 (four posteriors), 23387 (one posterior), 23388 (one posterolateral), 23490 (tooth with convergent cusps), 23491 (one medial), 23492 (three posterolaterals), 23493 (three germinal laterals), and 23498 (one ?medial); and 39 measured juvenile teeth comprising UAPL 23389 (33 teeth), 23390–23393 (four laterals), 23396 (one posterolateral), and 23497 (one ?posterolateral). Other material includes UAPL 5270 (incomplete lateral tooth), 6335

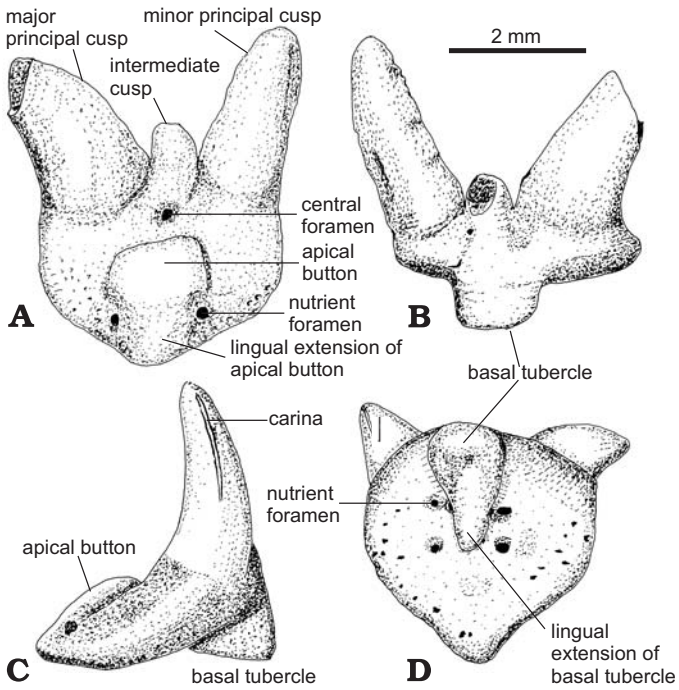

Fig. 1. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., holotype, adult lateral tooth, UAPL 23384, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), labial (**B**), anteromedial (**C**), and aboral (**D**) views. Compare with Hampe (2003: fig. 2).

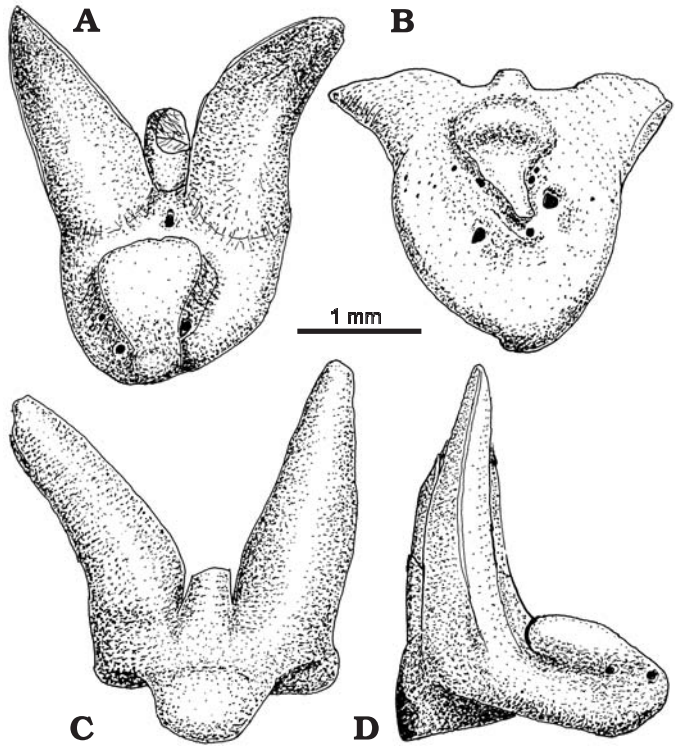

Fig. 2. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., adult medial tooth, UAPL 23491, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), aboral (**B**), labial (**C**), and anterior (**D**) views.

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(tooth fragments), 23385 (31 incomplete teeth, 30 laterals and one posterior), 23394 (six incomplete juvenile teeth, one is germinal), 23488 (three posteriors, two incomplete, one in matrix), 23489 (two incomplete germinal teeth), 23499 (juvenile ?medial or ?posterolateral), and 23500 (juvenile ?germinal lateral).

Type locality: UAPL locality 7205, Swisshelm Mountains, southeastern Arizona, USA.

Type horizon: Upper Black Prince Limestone, Lower Pennsylvanian (upper Bashkirian), equivalent to the Westphalian A and B boundary (Thayer 1985).

Diagnosis.—Teeth small to moderate size (<10 mm). Principal cusps compressed throughout with carinae lacking serrations; larger (major) cusp is posterior and more divergent than minor cusp. Single intermediate cusp present; none in posterior teeth. Labial margin of base usually thin. Lingual extension of basal tubercle usually extends to, and beyond center of base. Juvenile teeth with consistently thinner base, otherwise similar (but smaller) to adult teeth.

Description.—Based on adult teeth throughout the dental arcade; differences from lateral teeth noted below. Presumed juvenile nonsegregated teeth (see below) are compared in Table 1. Tooth base generally slightly wider (l-l) than long, probably equidimensional if the influence of the basal tubercle and lingual extension of the apical button is neglected (Fig. 1C, D). About 1/4 (Table 1) have a thick base as seen in labial view (Fig. 1B), comparable to *Orthacanthus texensis* (Johnson 1999), whereas about 1/2 have a thin base, comparable to *O. platypternus* (Johnson 1999); remaining teeth intermediate in thickness. Larger teeth tend to have a thicker base, but some are thin-based, and some small teeth have a thick base. Aboral surface flat or slightly concave in 3/4 of the teeth or distinctly concave (Table 1). Four to six nutrient foramina occur on the aboral surface (Fig. 1D), >6 in about 10% where a determination could be made; pattern random (Johnson 1999). Basal tubercle round in most teeth, or elongated (am-pl), with a convex surface or flat surface (Table 1); nearly all with a lingual extension (Fig. 1D), which is short or reaches the center of the base in half the teeth, or extends beyond the center. Apical button (Fig. 1A) always isolated from cusps; shape is round, irregular, pear- or heart-shaped, nearly always has a lingual extension that is narrow to broad, reaching the lingual margin of the base (Fig. 1A). Oral surface usually with three or four nutrient foramina (Fig. 1A, Table 1).

Principal cusps not equal. Major cusp largest by definition (Fig. 1A), always leans (or curves) posteriorly, as in *Orthacanthus texensis* (Johnson 1999: 231), always bears carinae on both edges where a determination can be made (Table 1). Minor cusp straight (near vertical) or leans slightly anteriorly (Table 1). Both cusps usually 90–105° to the base (crown-base angle, Table 1), but not always equally. Major transverse axis in a plane passing through the cusp bases (Johnson 1999: fig. 1E) forms an angle <45° with the labial margin of the base between the cusps, usually <30° for both cusps, often much less for the minor cusp (Table 1), 45° for major cusp in only one tooth.

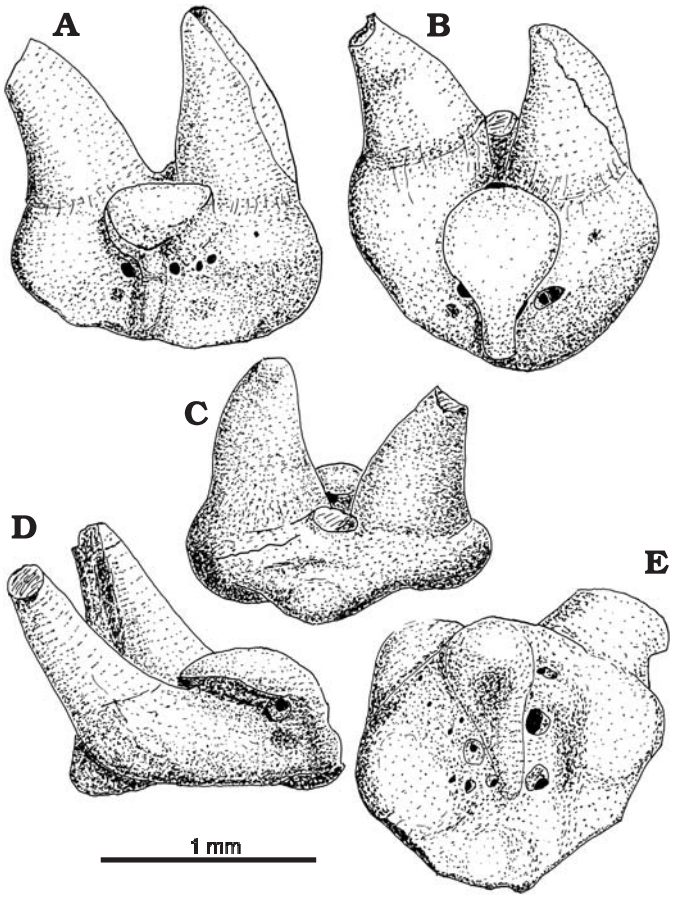

Fig. 3. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., adult posterolateral tooth (broken intermediate cusp), UAPL 23388, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual (**A**), lingual-occlusal (**B**), labial (**C**), posterior (**D**), and aboral (**E**) views.

Intermediate cusp less than half the length of the principal cusps (Table 1), tends to be straight or lean slightly toward the posterior (major) principal cusp (Table 1); all but one with "reversed compression", in which the base is am-pl compressed, but the distal two-thirds is l-l compressed.

Principal cusps of medial teeth are equal in size and somewhat divergent (Fig. 2). Both principal cusps in posterolateral teeth lean toward the posterior; intermediate cusp present (Fig. 3); minor cusp may be proximally straight, with only the distal half leaning posteriorly. Principal cusps in posterior teeth lean posteriorly (Fig. 4); the teeth are small (an exception is discussed below), lack an intermediate cusp, and sometimes lack a central foramen.

Measurements.—The adult teeth range in size from 0.75 mm (am-pl) × 1.16 mm (l-l) (a posterior tooth; the smallest lateral is 1.01 mm × 0.81 mm) to 8.06 mm × 7.76 mm (Fig. 5); a second lateral is 7.71 mm × 8.70 mm; the former is about 9 mm high. Their mean dimensions ± one standard deviation are 3.67 ± 1.64 mm (am-pl) and 3.79 ± 1.71 mm (l-l) based on 60 measured teeth (holotype plus paratypes). A linear regression of l-l on am-pl with 95% confidence intervals yields a slope of 1.00 ± 0.08 and y-intercept of 0.11 ± 0.30 mm (Fig. 6A).

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Table 1. Comparison of adult and juvenile teeth of *Orthacanthus donnelljohnsi* sp. nov.; n = sample sizes, respectively. Abbreviations: lab., labial; ling., lingual; princ., principal.

morphological feature	adult	juvenile
Base dimensions (lateral teeth), am-pl × l-l (range, mm)	1.01 × 0.81– 8.06 × 7.76	(0.91 × 0.70)?, 1.01 × 0.94 – 2.21 × 1.68
Base thickness, n = 79, 38	1/4 thick 1/2 thin	80% thin
Aboral nutrient foramina, n = 43, 36	4– ≥ 6, 100%	2–5, 90%
Aboral surface, n = 38, 35	3/4 flat, 1/4 concave	2/3 flat, 1/3 concave
Basal tubercle shape, n = 45, 34	80% round	80% round
Basal tubercle surface, n = 45, 33	1/2 convex, 1/2 flat	1/2 convex, 1/2 flat
Basal tubercle lingual extension, n = 47, 34	1/2 reach ≤ center, 1/2 beyond center	80% reach ≤ center, 20% beyond center
Apical button	isolated from cusps	isolated from cusps
Apical button shape, n = 38, 33	variable, all with lingual extension	variable, all with lingual extension
Oral nutrient foramina, n = 50, 37	2–4, 80% of teeth	2–4, 90% of teeth
Principal cusps		
carinae, n = 39, 36	always present	present in 70%
major cusp attitude	all lean posteriorly	all lean posteriorly
minor cusp attitude, n = 35, 34	1/2 lean anteriorly, 40% straight	1/2 lean anteriorly, 40% straight
crown-base angle, n = 44, 38	90% ≤ 105°, none > 120°	70% ≤ 105°, 10% ≥ 120°
major cusp transverse axis to labial margin, n = 46, 35	85% < 30°	60% < 30°
minor cusp transverse axis to labial margin, n = 46, 32	3/4 < 15°, 80% < 30°	2/3 < 15°, 90% < 30°
Intermediate cusp		
transverse shape, n = 24, 18	all "reversed compression"	1/2 lab.-ling. compressed, 1/2 variable
relative length, n = 22, 20	all ≤ 1/2 princ. cusps	3/4 ≤ 1/2 princ. cusps
attitude, n = 22, 22	2/3 straight, 1/3 lean posteriorly	3/4 straight, 1/4 lean posteriorly
carinae (sample too small)	present?	present?, some absent

The presumed juvenile teeth range in size from 0.84 mm (am-pl) × 0.81 mm (l-l) to 2.21 mm × 1.68 mm. Another tooth is 2.05 mm × 2.01 mm; the l-l dimension is relatively large because of a prominent basal tubercle (Fig. 6B). The am-pl mean ± 1 s.d. is 1.32 ± 0.36 mm and the l-l mean ± 1 s.d. is 1.21 ± 0.31 mm based on 39 measured teeth. A linear regression of l-l on am-pl with 95% confidence intervals yields a slope of 0.80 ± 0.11 and y-intercept of 0.15 ± 0.16 mm (Fig. 6B).

Discussion

All available teeth with complete bases were initially divided into two categories. Teeth in the first category were assigned by Johnson and Thayer (1999) to *Orthacanthus compressus*, and the second category, consisting of small teeth with thin bases, was thought to represent a different species (*Xenacanthus* cf. *X. decheni*) or possibly *O.* ?*compressus* medials or juvenile teeth. Detailed examination and description of each tooth revealed no significant differences in morphology, because many teeth in the first category also have thin bases, and a few are as small as those in the second category. Rodrigo Soler-Gijón (personal communication, May 1999) agreed that the second category may consist of juvenile teeth. Both categories contain medial and posterolateral as well as lateral teeth, but no juvenile posterior teeth have been identified. Segregation of juvenile teeth by position within the dental arcade is problematic, as described below. For purposes of discussion, and to facilitate future studies, the teeth remain segregated as adult and juvenile categories, although differentiation is sometimes subjective.

Adult teeth.—The diagnosis and most of the description are based on adult lateral teeth. Other teeth from the dental arcade, presumed to be adult, are less common. Whether the lingual extension of the apical button (Fig. 1A) is ever responsible for the protuberance on the base is uncertain, but generally it seems to be independent of the shape of the lingual margin. Attempts to observe carinae on the intermediate cusps of adult lateral teeth were largely unsuccessful because they were usually broken, covered by matrix, or possibly worn. Where they are reasonably complete, it was estimated that none exceeded half the length of the principal cusps (Table 1).

Symphyseal teeth have not been recognized, nor were they by Johnson (1999). However, a single large tooth (UAPL 23490) has convergent principal cusps, not typical of *Orthacanthus* teeth, and the central foramen is offset beneath the primary principal cusp. All other features are normal in this tooth, including a complete intermediate cusp about half the length of the principal cusps, which suggest it is not deformed. And one of the posterior teeth (part of UALP 23386) with a broken cusp, discussed below, might actually have occurred near the symphysis.

Medial teeth are anterior to the laterals and typically occur in *Orthacanthus* dentitions (Johnson 1999). But only one Swisshelm medial tooth (Fig. 2) is considered as adult, because it is at least 4mm high and has a moderately thick base. Other than the attitude of the principal cusps, no other morphological features are unusual, and it is included in Table 1 and the adult-tooth measurement database.

Posterolateral teeth are transitional between the lateral and posterior teeth. Johnson (1999: 233, 241) did not recognize them as a separate suite of teeth, but instead included them with the lateral teeth (but see Johnson 1999: figs. 5D, 7A–E, 18K–L). They are similar to lateral teeth, and the

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somewhat variable attitude of the minor cusp suggests a smooth transition between the two suites. Only four teeth (UAPL 23388 and 23492) from among those considered to be adult were recognized. All were measured and included in that database as their bases are not unique, although their labial margins range from "thin" to "thick". UAPL 23388 (Fig. 3) does not possess carinae on its cusps, but carinae do occur on two of the other teeth and the fourth has questionably worn highly compressed principal cusps.

Posterior teeth are the most unusual of those in the *Orthacanthus donnelljohnsi* sp. nov. dental arcade. There is no doubt these teeth belong to *O. donnelljohnsi*. The isolated apical button is not in contact with the lingual margin in UAPL 23387 (Fig. 4), its cusp-base angle is about 120°, and its cusp-labial margin angle is about 45° (unusual for *O. donnelljohnsi*; compare with Table 1); but its cusps possess carinae (Fig. 4B) and the base is normal, including a central foramen, so its identity is not questioned. Four additional teeth (UAPL 23386) are posteriors; a central foramen is present in one, absent in the second, very small in the third, and may be absent or very small in the fourth. A broken cusp in the second tooth may have been divergent from the preserved cusp, so it may not be a posterior. Also, its thick base is compressed more than usual (0.75 mm long, 1.16 mm wide), suggesting the possibility it is not a posterior, but perhaps occurred near the symphysis, although Fig. 6A suggests it is not significantly unusual. Hampe (2003: 206, fig. 10c) described a commissural, i.e., posterior, bicusped tooth of *O. gibbosus* and suggested it might have instead occupied a symphyseal position. Measurements of the five teeth were used in the database; they are the smallest teeth in Fig. 6A. None have a thin base. Three additional posteriors (UAPL 23488) are fragmentary or in matrix. Among the tooth fragments in UAPL 23385 is one that lacks a central foramen and intermediate cusp and has a minor cusp that leans toward the posterior; if complete, it would have been significantly larger than the five measured teeth.

Juvenile teeth.—Thirty-nine measured small teeth lacking a thick base (Table 1; 20% have an intermediate thickness) may be teeth from juvenile sharks. On the basis of the orientation of the principal cusps, 13 may be medial teeth (six are questioned), 18 are laterals (five questioned), eight are posterolaterals (five questioned), and one is indeterminate. One germinal tooth was not measured. Although no posterior teeth are identified, and as an inordinate number of medial teeth are present compared to the teeth from adult sharks, it is clear that these teeth demonstrate a gradual change in cusp orientation in the dental arcade. Other than possessing slightly divergent cusps, the medials are similar to the laterals, as suggested by the number of teeth with questioned position in the arcade. The teeth illustrated in Fig. 7 are considered laterals, although one is questionable (Fig. 7C), as the distal half of the minor cusp and the intermediate cusp lean toward the posterior, and might be considered a posterolateral, but the principal cusps in general have an attitude more similar to typical laterals. Another tooth, interpreted as a posterolateral, has all three cusps leaning posteriorly, but even this is subjective, depending on

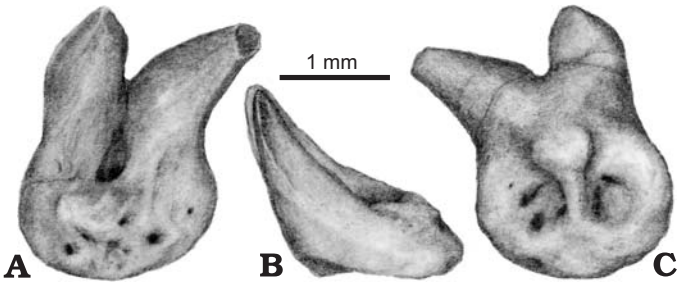

Fig. 4. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., adult posterior tooth, UAPL 23387, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**) anterior (**B**), and aboral (**C**) views.

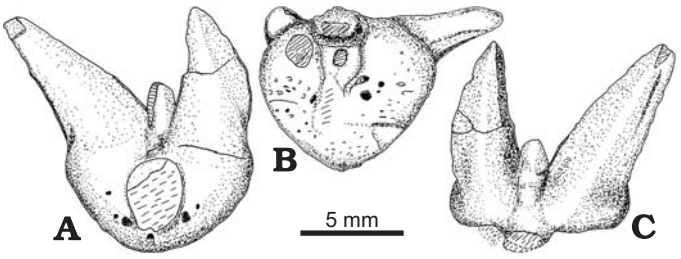

Fig. 5. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., adult lateral tooth, UAPL 23383, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), aboral (**B**), and labial (**C**) views.

the point of reference from which the tooth is viewed (Fig. 8; compare the lingual-occlusal and labial views). This apparent dilemma arose following the drawing of the initial illustrations (Fig. 8A–D); additional illustrations (Fig. 8E–H) made independently nearly three years later confirmed that no error was involved (slightly differing orientations between similar views emphasize difficulties in accurately depicting characters, e.g., minor foramina, in very small teeth). Yet another tooth, questionably a posterolateral (Fig. 9), is significantly different in cusp attitude and length:width (am-pl : l-l) ratio of the base. The proximal half of the minor cusp leans slightly anteriorly (Fig. 9C), but the distal half leans slightly posteriorly toward the major cusp; the intermediate cusp leans slightly posteriorly (barely discernable in Fig. 9A, C). But more disconcerting is the length:width ratio of about 1.37, considerably greater than the tooth in Fig. 8. As seen in Fig. 6B, UAPL 23497 (Fig. 9) is not unique (note the four values below the lower end of the trend line; the ratio of the am-pl and l-l means in Fig. 6B is 1.09), but suggests that in reality base length:width ratio may be a factor in tooth placement within the dental arcade, not just cusp attitude. Even if UAPL 23497 were considered a lateral, it would be still distinctive (compare with Fig. 8). All other characters deem it to be *Orthacanthus donnelljohnsi* sp. nov. Some other aspect of heterodonty (dignathic, sexual) might be reflected.

Adult vs. juvenile teeth.—Other than size differences, the ontogenetic differences in *Orthacanthus donnelljohnsi* sp. nov. teeth appear to be minor (Table 1). From a practical standpoint, the juvenile teeth were difficult to identify until

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the identities of the other xenacanth taxa in the Swisshelm fauna were established, and because of their unexpected relatively large number. Their mean base length:width (am-pl : l-l) ratios of 0.97 (adult) and 1.09 (juvenile) and linear regression slopes (1.00 and 0.80) and y-intercepts (0.11 mm and 0.15 mm) presumably reflect ontogenetic change, but the differences are not great (Fig. 6).

All of the teeth in Fig. 7 have a thin base, or at least slightly less thick than the adult laterals in Figs. 1 and 5, which are considered to be thick. This comparison suggests the difference may not be significant, as all of these teeth (adult and juvenile) have a base thickness more comparable to *Orthacanthus platypternus* than to *O. texensis* (Johnson 1999, figs. 1A, C; 6, 11). Johnson (1999: 244–245) stated that of 73 *O. compressus* teeth, 16 had thick bases, of which nine had serrated principal cusps, and the remaining teeth were thin-based, of which two had serrated principal cusps. In that group of teeth, Johnson (1999: 245) stated that some thin-based and thick-based teeth were of similar size, thus precluding the possibility that the former were juvenile teeth. The mean base length:width ratio of those nonsegregated *O. compressus* teeth is 1.05 with a linear regression slope of 0.97 and y-intercept of 0.03 mm (Johnson 1999; Table 2), not significantly different from *O. donnelljohnsi* sp. nov. The *O. donnelljohnsi* juvenile and adult teeth also overlap in size (Table 1 and Fig. 6), but the largest juvenile teeth are smaller than about 80% of the adult teeth (half of which are thin-based, Table 1). Furthermore, posteriors constitute most of the small adult teeth.

Remarks.—Assuming that tooth-base thickness is gradational and of unknown significance, then a lack of other distinguishing features would seem to preclude more than one *Orthacanthus* species present at the Swisshelm locality. Other factors such as sexual or dignathic dimorphism may be required to account for base thickness versus size during ontogeny.

Hampe (2003: 227) noted that probable juvenile teeth can display considerable intergeneric similarity. For example, *Orthacanthus bohemicus* juvenile teeth appear to be *Xenacanthus*-like (see earlier comment regarding Johnson and Thayer 1999; see also Soler-Gijón 2004 regarding juveniles of this species). And *O. gibbosus* juvenile teeth may possess both serrated and non-serrated cusps (a modification of Hampe 1988, that *Orthacanthus* juvenile teeth are serrated). He concluded that there is no unambiguous suite of characters that taxonomically segregate xenacanthid teeth. This observation appears to be confirmed by the above discussion, at least in part for *Orthacanthus*.

The lack of serrations in the Swisshelm *Orthacanthus* teeth strongly suggests that more than one species was present in Johnson's (1999) study of *O. compressus* teeth, which also possess only a single intermediate cusp, except the posterior teeth (Johnson 1999: 248). However, he was not able to delineate more than one taxon (mainly because of the base thickness problem), and had difficulty in later distinguishing some of the *O. compressus* teeth from those of geologically younger *O. texensis* and *O. platypternus* teeth (Johnson 1999: 248; see also Hampe 2003: 210). But Hampe (2003: 205, 209, 227) observed that *O. gibbosus* juvenile teeth sometimes also lack serrations. As for *O. donnelljohnsi* sp. nov., there is no doubt that most of the xenacanth teeth in the Swisshelm fauna represent adult individuals.

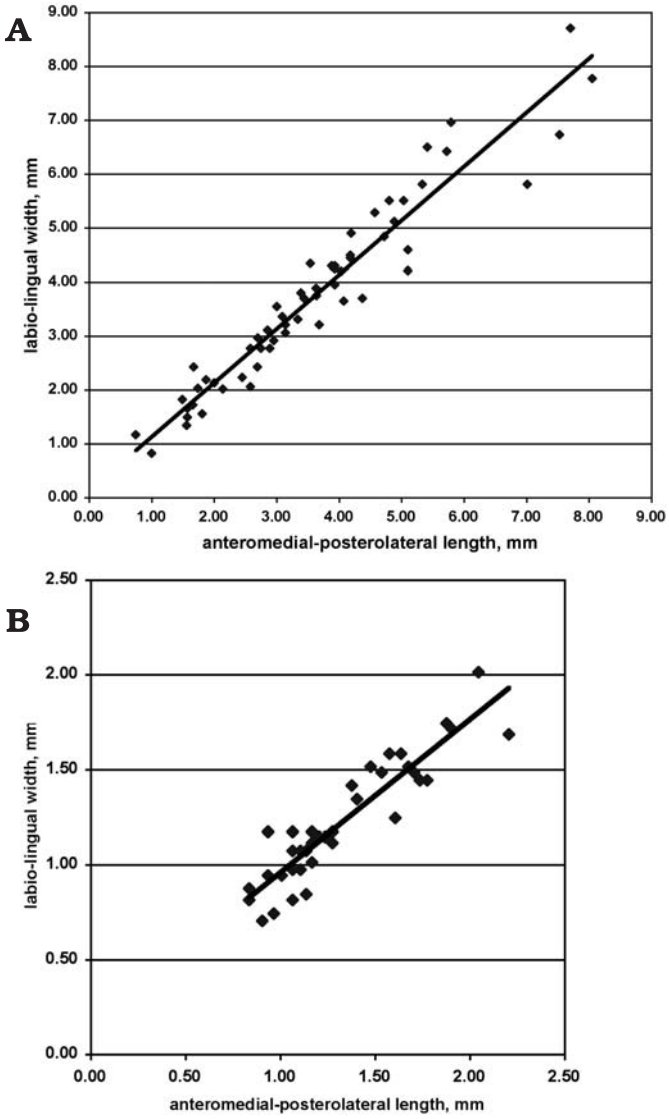

Fig. 6. Scatter diagrams of *Orthacanthus donnelljohnsi* sp. nov. tooth base dimensions; adult teeth (**A**), and juvenile teeth (**B**).

In the presumed juvenile teeth, differences with adult teeth are probably largely insignificant (Table 1). Some changes, such as increase in the number of aboral nutrient foramina, may be ontogenetic. The data suggest the same for tooth thickness, but exceptions may preclude this. It would seem reasonable that the change from thin-based to thick-based teeth was ontogenetic, because most of the observed teeth are laterals, which suggests position in the dental arcade is not responsible. But size discrepancies suggest the difference is not ontogenetic. And, as half the adult teeth are thin-based (Table 1), the possibility of sexual dimorphism or dignathic heterodonty is significant. As with other characters, such as smooth carinae and only a single intermediate cusp, tooth thickness, which is often intermediate or gradational, is not here taxonomically

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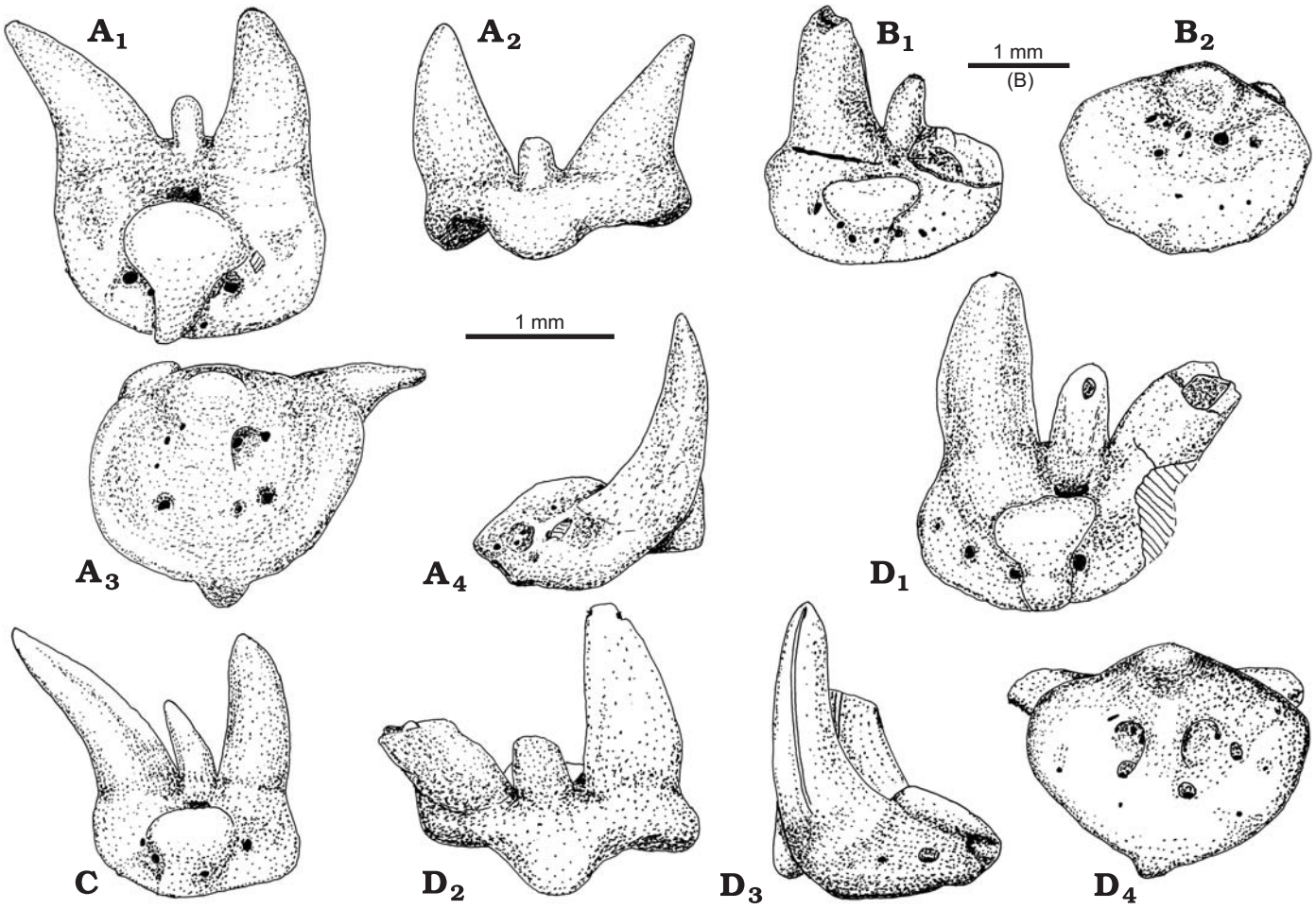

Fig. 7. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., juvenile lateral teeth, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona. **A**. UAPL 23390; lingual-occlusal (A_1) , labial (A_2), aboral (A_3), and anteromedial (A4) views. **B**. UAPL 23391; lingual-occlusal (B_1) and aboral (B_2) views. **C**. UAPL 23392; lingual-occlusal view (matrix prevented other views). **D**. UAPL 23393; lingual-occlusal (D_1), (posterior margin of oral surface covered by matrix), labial (D_2), anteromedial (D_3), and aboral (D_4) views.

discretionary, unlike the difference between *Orthacanthus texensis* and *O. platypternus* teeth.

Orthacanthus teeth from the Lower Permian of Texas (Johnson 1999) are not represented by any that could be morphologically regarded as juvenile, except by size, despite the large number available for study. This difference from the Pennsylvanian species (e.g., *O. bohemicus*, *O. gibbosus*, and *O. donnelljohnsi* sp. nov.) suggests a significant evolutionary change. *Orthacanthus donnelljohnsi* is unique among the Pennsylvanian species in lacking serrated cusps.

Germinal teeth.—Presumably unerupted teeth, but designated as germinal and generally similar to those from the Lower Permian (Johnson 2005a, designated therein as underdeveloped), are present in the Swisshelm collection. Six teeth, including UAPL 23493 (three measured adult teeth), 23489 (two adult broken teeth), and one incomplete juvenile tooth included in UAPL 23394, are not fully developed, but not in similar ways. All of the teeth with complete bases are laterals; all have thin bases. The three measured teeth are included in Fig. 6A because of their size. An additional tooth is presumably a juvenile lateral (UAPL 23500) and might be considered as germinal; the principal cusps are compressed, but show no evidence of development of carinae, and the very short but "massive" intermediate cusp is barely developed. Its apical button is normal; the basal tubercle is largely indeterminate, as the aboral surface is missing (wear from transport?).

Germinal (underdeveloped) teeth are here recognized by their lack of cusp development (Johnson 2005a). The principal cusps tend to be conical and may not be compressed (see ?*Orthacanthus* sp., UAPL 23400, below); the intermediate cusp may not be developed at all, or is merely a small conical point. Unlike many of the Lower Permian underdeveloped (germinal) teeth described by Johnson (2005a), none of the measured teeth have cusps with exposed pulp cavities, although one of the fragments does. One of the measured adult teeth has a relatively massive apical button, but in another it is completely absent, while in the third it is not fully developed and is comparable to the teeth described as "tooth embryos" by Hampe (1997).

Comparison with other species.—There are many species of *Orthacanthus*, but only those known to possess a distinct juvenile dentition need be considered. *Orthacanthus com-*

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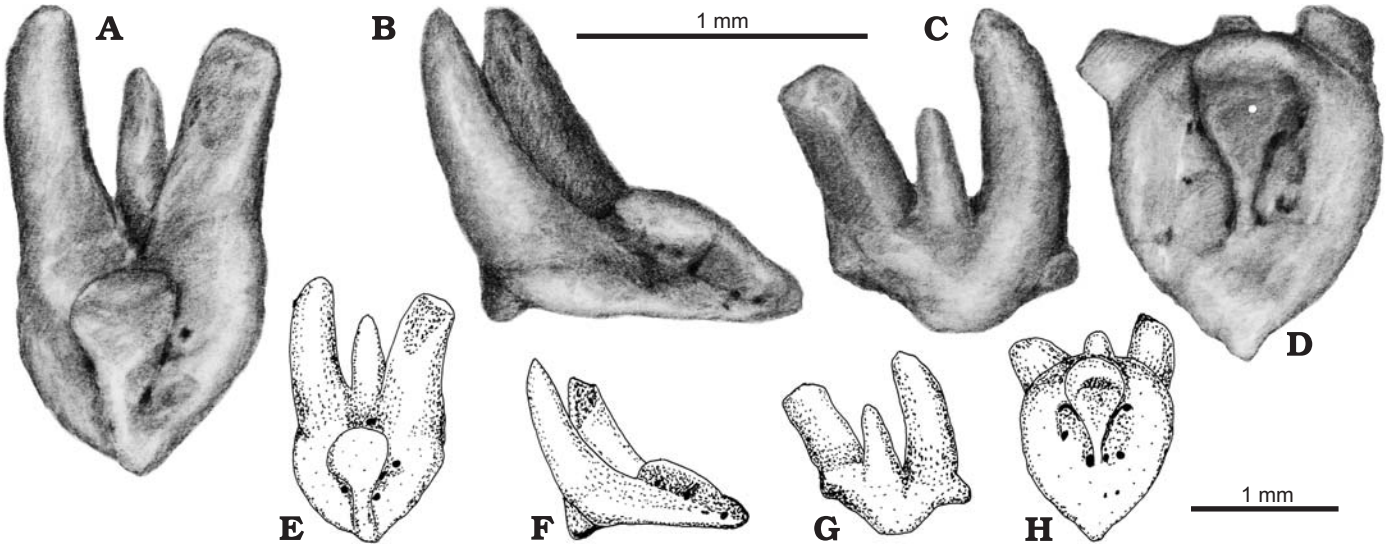

Fig. 8. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., juvenile posterolateral tooth (distal 1/4 of major principal cusp is missing), UAPL 23396, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**, **E**), anterior (**B**, **F**), labial (**C**, **G**), and aboral (**D**, **H**) views; see text for explanation.

pressus may indeed possess a juvenile dentition as commented on above [and a preliminary study (Johnson 2007) of at least one locality in the Texas Permian, that is older than those used by Johnson (1999), tends to support this]. As stated above, only two other species, *O. bohemicus* and *O. gibbosus*, possess a juvenile dentition. However, their teeth possess serrated cusps, as does *O. compressus*. The only species that does not possess serrated cusps is *O. platypternus* (Johnson 1999), but it lacks a distinct juvenile dentition. *Orthacanthus donnelljohnsi* sp. nov. is the only known species of *Orthacanthus* with a distinct juvenile dentition and whose teeth lack serrated cusps.

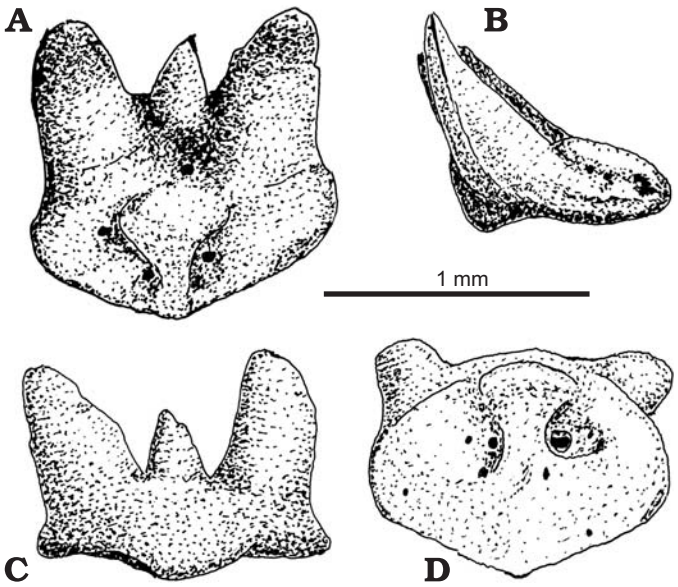

Fig. 9. Diplodoselachid chondrichthyan *Orthacanthus donnelljohnsi* sp. nov., juvenile ?posterolateral tooth, UAPL 23497, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), anterior (**B**), labial (**C**), and aboral (**D**) views.

Stratigraphic and geographic range.—Lower Pennsylvanian, southeastern Arizona, USA.

Orthacanthus ?*donnelljohnsi* sp. nov.

Fig. 10.

Material.—UAPL 23487 (two posterior teeth) and UAPL 23494 (posterolateral tooth).

Description.—Two adult posterior teeth. One with 1.47 mm (am-pl) × 1.54 mm (l-l) base, very small central foramen, extremely subdued apical button, basal tubercle less so, three prominent aboral and one prominent oral foramina; principal cusps either broken or very short, straight, "recumbent" (crown-base angle ~135°), appear to be fused at their base; intermediate cusp absent. Second tooth with 2.32 mm (am-pl) × 2.83 mm (l-l) base, central foramen ?present, subdued apical button isolated from cusps, basal tubercle subdued with convex surface, three prominent and two smaller aboral foramina, one prominent and ≥ four smaller oral foramina; principal cusps with broken bases, appear to lean posteriorly; intermediate cusp absent.

One adult posterolateral tooth (Fig. 10) with 1.54 mm (am-pl) × 1.19 mm (l-l) thin base, prominent central foramen, round apical button isolated from cusps, with prominent lingual extension, am-pl oval convex basal tubercle with subdued lingual extension reaching center of base, ≥ two prominent aboral foramina (matrix interference) and two prominent plus one or two smaller oral foramina; both principal cusps complete, labio-lingually compressed, major cusp slightly longer, leaning posteriorly, minor cusp straight, carinae present on both margins of each, transverse axis of each cusp base ≤ 15° (major) or 0° (minor) to labial margin of base; intermediate cusp complete, leans posteriorly, with carinae, reverse compressed (am-pl at base, l-l distally), relative length 1/2–2/3 of principal cusps.

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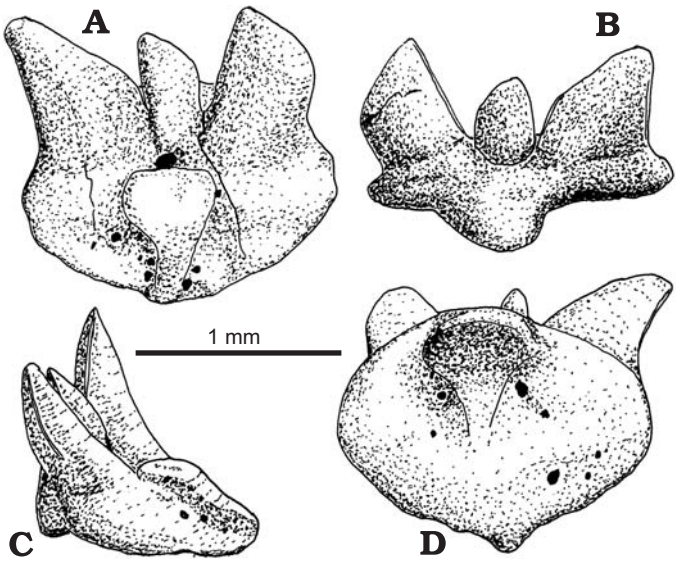

Fig. 10. Diplodoselachid chondrichthyan *Orthacanthus* ?*donnelljohnsi* sp. nov., posterolateral tooth (covered by some matrix), UAPL 23494, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), labial (**B**), posterior (**C**), and aboral (**D**) views.

Remarks.—Despite their small size, all three of the teeth appear to be adult, comparable to the smaller teeth in Fig. 6A. The smaller posterior tooth is nearly round, and even with its stubby prominent cusps, has the appearance of a pancake. The absence of an intermediate cusp and near absence of a central foramen suggests a posterior position in the dental arcade, although the straight principal cusps (as preserved) suggests otherwise. The recumbent cusps would seem to preclude it from being a medial or lateral tooth. There is no evidence that it is deformed, nor is it a germinal tooth. There may be some enclosing matrix that might influence its appearance, but surprisingly, its presence could not be identified with certainty. Because of the apparent attitude of the cusps and an overall lack of detail (probably a diagenetic effect), its identity is questioned.

The larger posterior tooth has some of the same attributes as the smaller tooth, yet they are quite different in appearance. The principal cusps may have been of equal size, and apparently leaned posteriorly. Two or three "microforamina" occupy the position of the central foramen. Both the apical button and basal tubercle may have extremely subdued lingual extensions. Matrix is present but does not contribute to problems of identification; rather, this results from the overall worn appearance and lack of information about the principal cusps.

The posterolateral tooth has a robust crown relative to its thin base. The principal cusps are unusually broad near their base, which contributes to the robust appearance. This, along with a greater than normal base length:width ratio of 1.29 compared to the mean ratio of 0.97 (Fig. 6A), is cause to question its identity.

Stratigraphic and geographic range.—Lower Pennsylvanian, southeastern Arizona, USA.

Orthacanthus sp.

Material.—UAPL 23495.

Description.—Tooth fragments: two incomplete teeth and eight isolated cusps.

Remarks.—There is little doubt about the identity of the five larger isolated cusps, as they possess carinae but no cristae. Three much smaller cusps could belong to other xenacanth taxa in the Swisshelm fauna, but lack cristae as well as carinae. One of the incomplete teeth consists of a partial base with part of a principal cusp and perhaps most of an intermediate cusp. The other incomplete tooth is represented by a partial base and may be a germinal tooth.

?*Orthacanthus* sp.

Fig. 11.

Material.—UAPL 23496, one tooth; UAPL 23401, one tooth; and UAPL 23400, germinal tooth.

Description.—Tooth (UAPL 23496) with 1.43 mm (am-pl) × 0.96 mm (l-l) base with a veneer of matrix; central foramen ?present; strongly am-pl oval apical button isolated from cusps, with a very small lingual extension producing a distinct protuberance on lingual margin of base; basal tubercle ?small, possibly with a lingual extension; aboral foramina indeterminate, ≥ two prominent oral foramina; principal cusps of ?equal size shattered near base, carinae may have been present; one intermediate cusp shattered near base.

UAPL 23401, tooth with apical button in contact with principal cusps; base with about 2 mm dimensions; both principal cusps lean posteriorly; presence of central foramen not confirmed; in matrix.

Small germinal tooth (UAPL 23400, Fig. 11). Base 1.40 mm (am-pl) × 0.68 mm (l-l); basal tubercle not centered on labial margin and lacks lingual extension; aboral surface of base deeply concave. Intermediate cusp and apical button absent; central foramen present.

Remarks.—Both the anterior and posterior ends of the base of UAPL 23496 markedly extend beyond the margins of the cusps. Its strongly oval base (length:width ratio = 1.49) is quite unlike any *Orthacanthus donnelljohnsi* sp. nov. tooth,

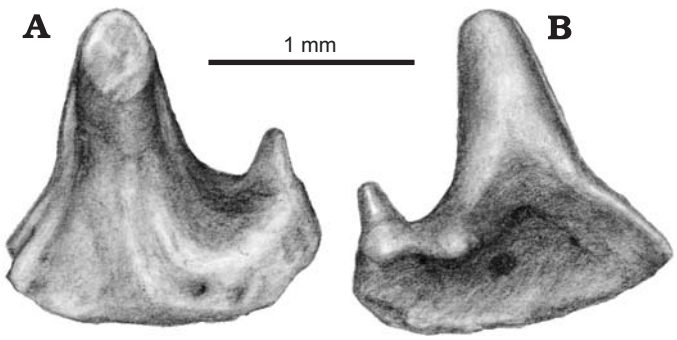

Fig. 11. Diplodoselachid chondrichthyan ?*Orthacanthus* sp., germinal and ?malformed tooth, UAPL 23400, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**) and labio-aboral (**B**) views.

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more so for *Triodus*. A lack of cristae on the labial margin of the base precludes *Bransonella* as a possibility.

UAPL 23401 is unusual because typical *Orthacanthus* teeth possess an apical button that is isolated from the cusps (Johnson 1999: 223). Otherwise, it appears to be normal, although the presence of matrix prevents determination of other characters that might confirm its identity.

UAPL 23400 (Fig. 11) is more anomalous than usual. It has an extreme length:width ratio of 2.06; its position in the dental arcade is unknown. The offset basal tubercle and deeply concave base (Fig. 11B) suggest the possibility that it is malformed as well as being germinal. Whether it represents an adult or juvenile tooth is unknown. Its identity is uncertain because of its extreme length:width ratio, as well as its other abnormal attributes.

Family Xenacanthidae Fritsch, 1889

Genus *Triodus* Jordan, 1849

Type species: *Triodus sessilis* Jordan, 1849. Early Permian, "Lebacher Toneisenstein-Layer", upper Lauterecken-Odenheim member, Lebach, Saar-Nahe basin, Germany (Hampe 2003: 221).

Diagnosis.—Limited to dentition. Slightly heterodont; teeth small. Three cusps nearly always present; lateral cusps and usually the intermediate cusp bear straight vertical cristae, sometimes bifurcated, largely limited to distal halves.

Remarks.—Schneider (1996: 330) described *Bohemiacanthus* in a manuscript that remained in press for at least two years, as Schneider and Zajíc (1994: 123) had already recognized this taxon. They and Schneider (1996: 325–326, fig. 2) assigned to *Bohemiacanthus* those species with teeth showing cristae on the principal cusps that are simple and straight (as in Hampe 1989: fig. 3), although they may be bifurcated (Schneider and Zajíc 1994: fig. 21); and they restricted *Triodus* to those species that possess cristae restricted to the labial side of the principal cusps, or at most, one lingual crista as well. Furthermore, the labial cristae in *Triodus* possess an inverted Y-shaped bifurcation below the apex of the principal cusps (Schneider and Zajíc 1994: 125, 133). Thus, *Triodus* would include only *T. sessilis* and *T. kraetschmeri*. *Triodus* species assigned to *Bohemiacanthus* by Schneider and Zajíc (1994) include *T. carinatus*, *T. lauterensis*, *T. palatinus*, and *T. obscurus*, with the latter three species, in this order, showing a stratigraphically older to younger decrease in the number of labial and lingual cristae (Schneider 1996: fig. 8). Other morphological features in *Triodus* and *Bohemiacanthus* teeth are not significantly different (compare characteristics in Schneider 1996: 326) and their histology is the same (Schneider 1996: table 1). Soler-Gijón and Hampe (1998: 343 and table 2) and Hampe (2003: 221) argued that *Bohemiacanthus* is a junior synonym of *Triodus* for these reasons, and also because both Y-shaped bifurcations of the cristae and straight cristae appear together in *T.* ?*frossardi* teeth (Soler-Gijón and Hampe 1998: fig. 4). This combination is approached in *T. obscurus* (Hampe 1989: fig. 5d) and *T. serratus* (Hampe 2003: fig. 20); and Schneider and Zajíc (1994: figs. 21.1, 5a, 9, 12) show cristae with straight and Y-shaped bifurcations in "*Bohemiacanthus*" *carinatus*. Schneider (1996: 326) mentioned that *Bohemiacanthus* teeth possess "simple to occasionally forked carinae". Given the variability in the pattern and number of cristae in *Triodus* teeth, Soler-Gijón and Hampe's (1998) argument is valid. However, *Bohemiacanthus* has continued to be used (Werneburg et al. 2007).

Triodus elpia sp. nov.

Figs. 12–17.

Etymology: After the acronym, LPIA, late Paleozoic ice age, utilized by Stanley and Powell (2003), and others (Montañez et al. 2007, for example). Despite the Swisshelm locality being equatorial, this ice age influence may have been much closer at hand later in the Pennsylvanian (Soreghan et al. 2008). Perhaps the data from xenacanths and other vertebrates influenced by changing marine environments will be sufficient enough in the future to be added to the invertebrate database.

Type material: Holotype: UAPL 23397, lateral tooth (Figs. 12, 14). Paratypes include 29 measured teeth comprising UAPL 23395 (21 laterals), plus three additional laterals (UAPL 23398, 23505, 23506), UAPL 23501 (one posterolateral), UAPL 23503 (one "anteromedial"), UAPL 23504 (one posterior), and UAPL 23502 (one ?posterolateral).

Type locality: UAPL locality 7205, Swisshelm Mountains, southeastern Arizona, USA.

Type horizon: Upper Black Prince Limestone, Lower Pennsylvanian (upper Bashkirian), equivalent to the Westphalian A and B boundary (Thayer 1985).

Referred material.—Includes nine incomplete teeth plus tooth fragments and isolated cusps (all in UAPL 23399) which provide no additional descriptive information and exhibit no anomalies.

Diagnosis.—Teeth with principal cusps moderately labiolingually compressed; cristae present on lingual and labial sides, often with one that is carina-like; minor cusp leans posteriorly, major cusp straight. Crown-base angle 90–105°, sometimes greater; angle between minor cusp base transverse axis and labial side of base variable, averaging about

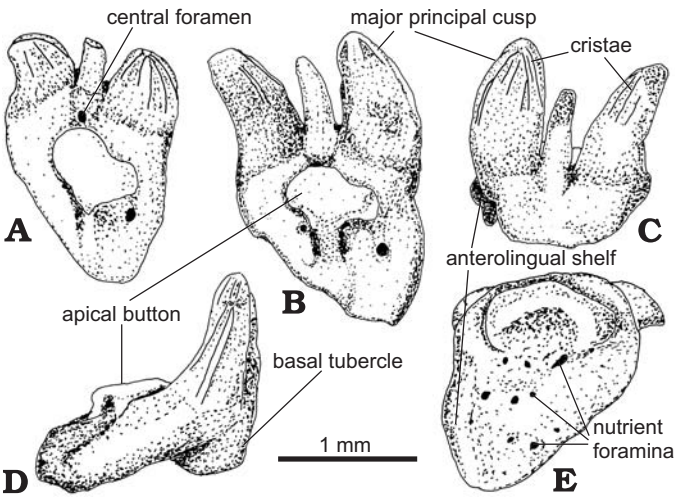

Fig. 12. Xenacanthid chondrichthyan *Triodus elpia* sp. nov., lateral tooth, holotype, UAPL 23397, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; occlusal (**A**), lingual-occlusal (**B**), labial (**C**), anteromedial (**D**), and aboral (**E**) views; note the lingual extension on the apical button in B.

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30°, about 15° for major cusp. Base asymmetrical with an anterolingual shelf, sometimes reduced, absent in some nonlaterals; central foramen present. Basal tubercle with concave surface; lingual extension absent. Apical button isolated from cusps and usually from base margin; lingual extension reduced or absent. Maximum dimension < 2 mm. Heterodont dentition probable.

Description.—Based on 25 (= n) mostly complete lateral teeth (others discussed below); n < 25 (< 100%) noted for many features. Labial side of base (Fig. 12C) thin (84%). Anterolingual shelf (Fig. 12) always present, aborally flexed; in oral view, 44% on left side, 56% right side; may be subdued; base nearly always asymmetrical. Aboral nutrient foramina range from two to five (88%), but up to eight. Basal tubercle nearly always concave, rarely flat; shape equally round, semicircular, or anteroposteriorly oval; lingual extension absent (80%) or defined principally by foramina. Aboral side of base concave (92%) or flat. Apical button isolated from cusps (92%) and margin of base (80%); shape irregularly round or pear-shaped, but generally oval or rectangular with one long side parallel to the posterolateral base margin; lingual extension present (20%), abbreviated and usually defined only by foramina (48%), or absent. Central (medial) foramen present (76%), questionably absent (8%) or indeterminate (matrix). Two to four oral nutrient foramina most common (88%), otherwise five or six, with one indeterminate.

Principal cusps unequal in size (breadth, not length; see Fig. 12), except in one tooth (n = 20); minor cusp posterior (one questionable), longer than major cusp (n = 7; all others indeterminate). Base of both minor and major cusps compressed in all teeth, more or less labio-lingually, increasing distally. Cristae (Fig. 12) generally straight, converging at the tips, may proximally bifurcate, restricted to the distal half (n = 11), sometimes extending onto the proximal half (n = 6), especially where adjacent to the carina-like cristae; one to four on labial side, one to three on lingual side of minor cusp, and most often three to five on labial side, two to five on lingual side of major cusp. Carina-like cristae usually present on both cusps (minor, n = 14 with 3 questionable; major, n = 18, with 2 questionable), but often indeterminate, presumably because of wear or poor preservation. Minor cusp leans in posterior direction (n = 20 with 2 questionable); major cusp straight (n = 16 with 1 questionable), or leans posteriorly (n = 3) or anteriorly (n = 1). Crown-base angle (angle between the cusps and oral side of the base) 90° to 105° (n = 15), >105° to 120° (n = 6); angle between transverse axis of minor cusp base and base labial margin 15° to 30° (n = 13), 30° to 45° (n = 8), and major cusp 0° to 15° (n = 19), >15° to 45° (n = 5).

Intermediate cusp always present, but nearly always broken at or near its base (n = 23), leaving only two teeth where it is more than half complete. Base antero-posteriorly compressed (n = 15) or round to labio-lingually compressed (n = 7); cusp straight (n = 2), cristae may be absent (n = 2).

Measurements.—Twenty-nine teeth with complete bases were measured (Fig. 13). All are included in a single data-

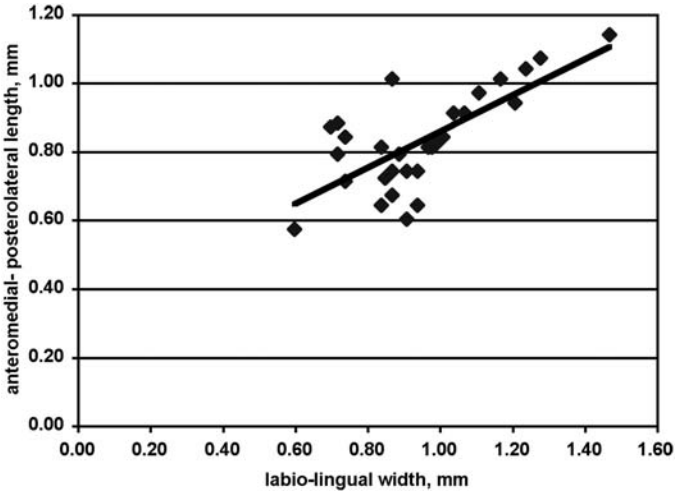

Fig. 13. Scatter diagram of *Triodus elpia* sp. nov. tooth base dimensions.

base. The teeth range in size from 0.60 mm (l-l) × 0.57 mm (am-pl) to 1.47 mm × 1.14 mm (holotype); both are laterals. The height of the holotype is 1.4 mm. Their mean dimensions ± one standard deviation (n = 29) are 0.95 ±0.20 mm (l-l) and 0.83 ±0.15 mm (am-pl). A linear regression of am-pl on l-l with 95% confidence intervals yields a slope of 0.53 ±0.20 and y-intercept of 0.33 ±0.20 mm (Fig. 13). The labio-lingual measurements were considered to be more reliable and therefore the independent variable, the reverse of *Orthacanthus donnelljohnsi* sp. nov. measurements. The anteromedial-posterolateral measurements were sometimes rather subjective because of asymmetry (Fig. 12A). The labio-lingual measurements were taken from the lingual tip of the anterolingual shelf (Fig. 12E) to the opposite margin of the basal tubercle in the more asymmetrical teeth so as to emphasize the l-l > am-pl ratio. This ratio is reversed in five teeth (Fig. 13).

Discussion

Remarks.—The holotype (Figs. 12, 14) is the only essentially complete tooth available and coincidently the largest of all the teeth assigned to this species, and one of the 20% to possess an apical button with a lingual extension (Figs. 12B, 14B). The am-pl measurements are not as precise as those normally acquired for other species (this report; Johnson 1999, 2003). Estimates based on Figs. 12E (1.59 mm) and 14E (1.57 mm) exceed the actual measurement (1.47 mm). This is probably caused by the highly flexed anterolingual shelf (Fig. 12) in the holotype and the unusual asymmetry exhibited by most of the lateral teeth. The anterolingual shelf is sometimes subdued or it is mostly on the anterior margin, but is distinctly aborally flexed, similar to the anterior end of the base in *Orthacanthus platypternus* teeth (Johnson 1999). Figures 12 (which is more schematic) and 14 illustrate the subjective appearances of the cristae, some of which tend to be emphasized by differing angles of view and light sources.

Figure 15 illustrates a lateral tooth with reversed asymmetry compared to the holotype (Fig. 12). Of the 25 measured laterals, the anterolingual shelf is on the left side

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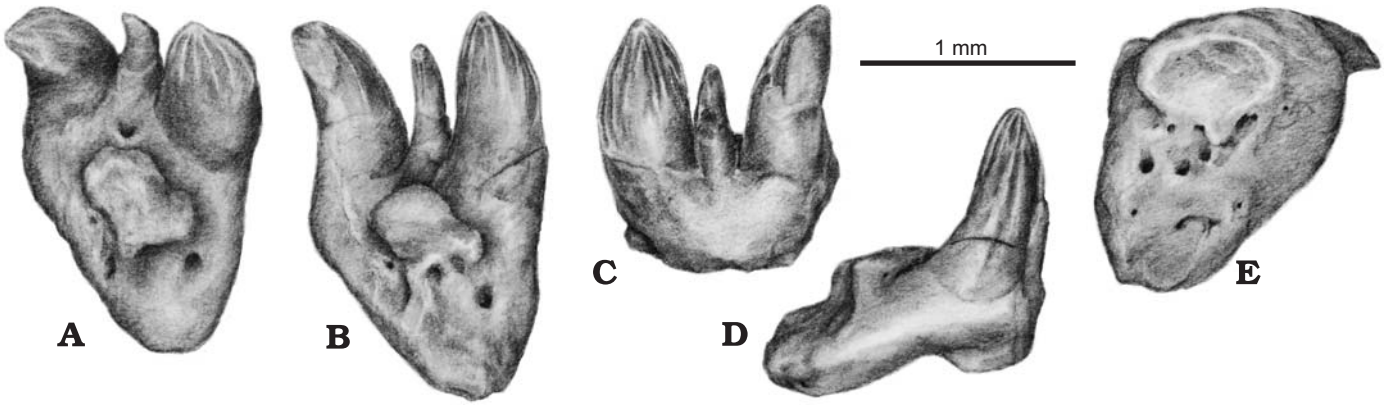

Fig. 14. Xenacanthid chondrichthyan *Triodus elpia* sp. nov., lateral tooth, holotype, UAPL 23397, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; compare with Fig. 12 and see text for explanation. Occlusal (**A**), lingual-occlusal (**B**), labial (**C**), anteromedial (**D**), and aboral (**E**) views.

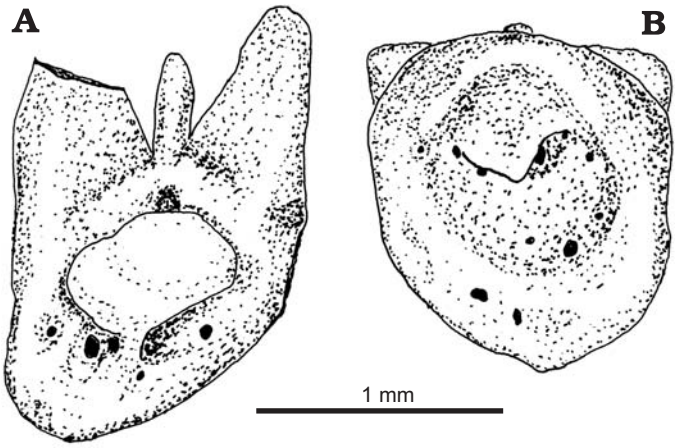

Fig. 15. Xenacanthid chondrichthyan *Triodus elpia* sp. nov., lateral tooth, UAPL 23398, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**) and aboral (**B**) views. Left cusp in A is presumably the major (anterior) cusp; compare with Fig. 12.

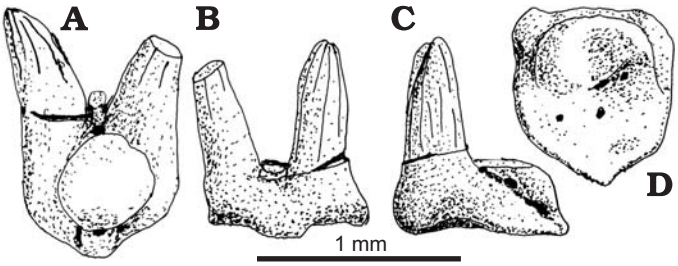

Fig. 16. Xenacanthid chondrichthyan *Triodus elpia* sp. nov., "anteromedial" tooth, UAPL 23503, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), labial (**B**), anteromedial (**C**), and aboral (**D**) views. B–D drawn following reattachment of major cusp to the base after A was drawn.

(occlusal view) in 11 teeth and right side in 14. This difference would probably diminish in larger samples. Another chondrichthyan that possesses an asymmetric tooth base is *Thrinacodus* (a Devonian phoebodontiform, Ginter et al. 2002), although its crown also displays asymmetry. Ginter et al. (2002: 201–203, fig. 14) suggested a possible arrangement of the teeth in a *Th. tranquillus* dentition, which may be applicable to the *Triodus elpia* sp. nov. dentition. The dental asymmetry displayed in these two species may have a bearing on the relationship between the phoebodontiforms and xenacanths (see *Bransonella* comments below). Although other Paleozoic sharks, such as *Denaea wangi* (Wang et al. 2004), have asymmetrical teeth (mainly the crown), it is the similarity of the tooth bases in *T. elpia* and *Thrinacodus* that appears to be significant. The lateral tooth in Fig. 15 also illustrates the problem in determining the major and minor principal cusps in teeth with incomplete cusps, although it is nearly always less ambiguous than in this example.

As noted above, five of the measured 29 tooth bases (Fig. 13) have reversed l-l and am-pl dimensions. Two are included in UAPL 23395 with 0.74 mm × 0.84 mm and 0.72 mm × 0.79 mm dimensions, and two additional laterals measure 0.70 mm × 0.87 mm (UAPL 23505) and 0.87 mm × 1.01 mm (UAPL 23506). The fifth tooth may be a posterolateral (UAPL 23502, described below) with 0.72 mm × 0.88 mm dimensions. These differences, all within one standard deviation, are probably insignificant (Fig. 13).

Evidence of heterodonty.—Five of the measured teeth are not laterals. One (Fig. 16) is considered an "anteromedial" tooth, and is closer to being a true medial than any other tooth in the available sample. Its base is 0.85 (l-l) × 0.72 (am-pl) mm, nearly symmetrical, without an anterolingual shelf. The apical button is in contact with the central foramen and minor (posterior) cusp (Fig. 16A).

Two teeth are interpreted as posterolaterals. The first (UAPL 23501) has complete principal cusps; the minor cusp is longest, curves posteriorly with a conical distal half. The major cusp is straight, but leans posteriorly. The intermediate cusp is broken and partly obscured by matrix. In all other aspects, it is similar to the lateral teeth. The second posterolateral (UAPL 23502) may be questionable only because the distal half of the major cusp is missing; the preserved portion is

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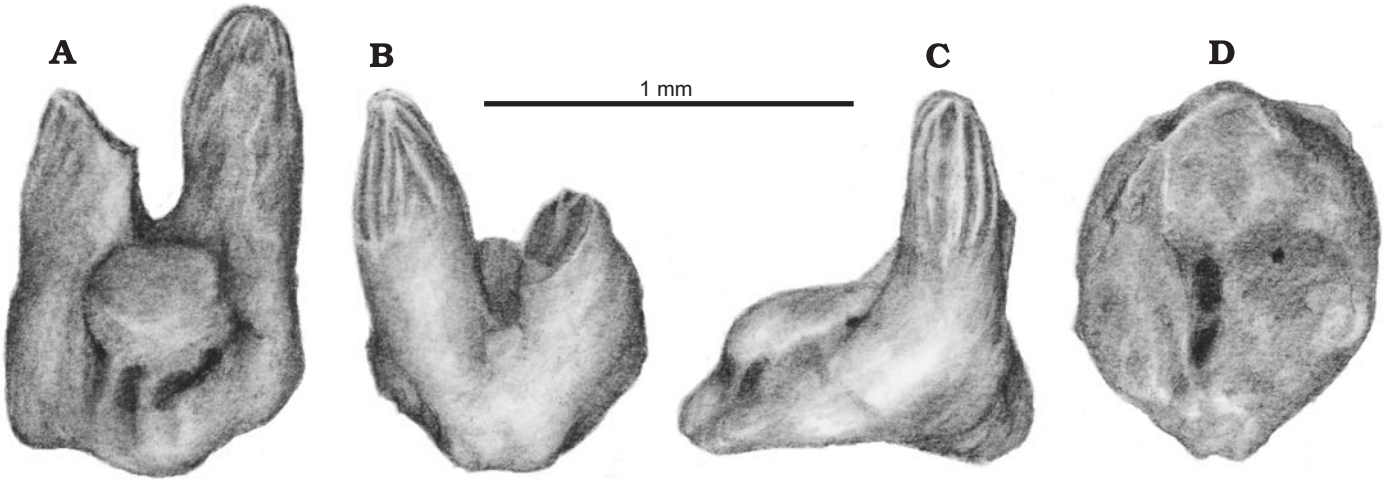

Fig. 17. Xenacanthid chondrichthyan *Triodus elpia* sp. nov., posterior tooth, UAPL 23504, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; lingual-occlusal (**A**), labial (**B**), ?anterior (**C**), and aboral (**D**) views. Cristae on the broken (?minor) cusp extend proximally to the base; there is the slightest hint that the central crista shown in C extends to the base, but is not shown. The right half of the aboral surface (D), lingual of the basal tubercle, is largely covered by matrix; the small foramen shown is probably valid. There is no evidence of an intermediate cusp.

straight and appears to have leaned posteriorly. The minor cusp leans posteriorly. Both cusps are labio-lingually compressed as preserved. This tooth, also with a broken intermediate cusp, is otherwise similar to the laterals, except there is no anterolingual shelf, but the base is extended more anteriorly than usual (reversed l-l and am-pl dimensions, see above).

The last nonlateral tooth is interpreted to be a posterior tooth (Fig. 17). The principal cusps, as preserved, are nearly equal in size. The presumably major (anterior) cusp is slightly labio-lingually compressed (Fig. 17C), but the minor cusp, as preserved, is nearly round to slightly antero-posteriorly compressed. The intermediate cusp appears to be absent. The tooth is similar to laterals in other aspects, but with a reduced anterolingual shelf; the apical button is isolated from the principal cusps (not evident in Fig. 17A), and there is a prominent central foramen (compare Fig. 17A with Fig. 12A, B). The presence of an anterolingual shelf, which is absent in one of the posterolaterals, as interpreted, suggests a more complex heterodonty.

Comparison with other species.—Triodus elpia sp. nov. is different from all other described species of *Triodus*, as its lateral teeth possess a somewhat to highly asymmetrical base with an anterolingual shelf, and all of the teeth, where a determination can be made (matrix interference), possess a central foramen, although it is sometimes very small. Hampe (1989, 2003) has provided the most comprehensive reviews of most of the other species. *Triodus sessilis* (Hampe 1989) teeth are comparable in size to those of *T. elpia*, but they lack an asymmetrical base, the crown-base angle is always 90°, and represent a homodont dentition. *Triodus lauterensis* teeth (Hampe 1989) are also small and have a comparable crown-base angle, and have a variably asymmetrical base suggesting heterodonty; but, the asymmetry is quite unlike the *T. elpia* teeth with their anterolingual shelf, and Hampe (1989) did not mention the presence of a central foramen. *Triodus palatinus* teeth (Hampe 1989) represent a heterodont dentition, are slightly larger than *T. elpia* teeth, and have a comparable crown-base angle; but, although the bases are sometimes asymmetrical, their asymmetry is quite unlike that of *T. elpia* teeth, and Hampe (1989) did not mention the presence of a central foramen. *Triodus obscurus* teeth (Hampe 1989) are of similar crown-base angle and size to *T. elpia*, and questionably represent a heterodont dentition, but they lack lingual cristae and show little base asymmetry. *Triodus kraetschmeri* teeth (Hampe 1989) are smaller than *T. elpia* teeth, and although Hampe (1989) described them as representing a homodont dentition, distinctive posterior teeth lacking an intermediate cusp are present; their crown-base angle is constantly 100°, and the intermediate cusp is positioned labially relative to the principal cusps which are rounded and not compressed; the tooth bases show little asymmetry, and Hampe (1989) does not mention the presence of a central foramen.

Hampe (1993) provided a summary description of the *Triodus* species he described earlier (Hampe 1989). He did not mention the presence or absence of a central foramen in any of them. However, in his summary description of *Orthacanthus* (Hampe 1993), he did mention its presence (median aperture). Therefore, a central foramen is very likely absent in *T. sessilis*, *T. kraetschmeri*, *T. palatinus*, *T. obscurus*, and *T. lauterensis*. However, *T. sessilis* does possess a central foramen (Oliver Hampe, personal communication, October 2007). The age of these species collectively range from Gzhelian to perhaps as late as Kungurian (Hampe 1989; Menning et al. 2006), so all are younger than *T. elpia* sp. nov.

Triodus serratus teeth (Westphalian A-C, Hampe 2003; or Bashkirian-Moscovian, in part) are generally significantly larger than *T. elpia* sp. nov., have a distinctive aboral depression on the oval base, and lack a central foramen (median foramen of Hampe 2003). Its dentition is largely homodont, with some teeth showing some asymmetry in the base. Other than having a similar crown-base angle, *T. serratus* is quite unlike *T. elpia*.

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Teeth assigned by Soler-Gijón and Hampe (1998) to *Triodus* ?*frossardi* (Asselian; type specimen is a spine; species not questioned by Hampe and Ivanov 2007b) are similar in size to *T. elpia* sp. nov. teeth; the crown-base angle is smaller in the former. The tooth base in *T.* ?*frossardi* is asymmetrical (Soler-Gijón and Hampe 1998: fig. 4D, E), but is unlike that in *T. elpia*, in lacking an anterolingual shelf. Curiously, the lingual extension of the apical button curves toward one side of the base and not to the tip of the base (their fig. 4E), similar to a tooth of *T. serratus* illustrated by Hampe (2003: fig. 20c) and the holotype of *T. elpia* (Fig. 12). Soler-Gijón and Hampe (1998) did not state whether *T.* ?*frossardi* teeth possess a central foramen. They did, however, provide a summary (their table 2) of tooth characteristics of most *Triodus* species. Parenthetically, they suggested (Soler-Gijón and Hampe 1998: 342, 345) that *Triodus* should occur in the Lower Permian of Texas, based on neurocrania; there is no evidence of the occurrence of *Triodus* teeth in the Texas Permian, based on extensive collections (Johnson 1999, 2003).

Schindler and Hampe (1996) assigned three teeth from the Gzhelian [lowermost Permian of Central Europe (Menning et al. 2006: fig. 4), but now uppermost Carboniferous in standard usage] to *Triodus* sp. ZÖ. They are similar in size to *T. elpia* sp. nov., and they possess a central foramen. However, the tooth base is quite symmetrical. Schindler and Hampe (1996) also provided a summary description of the species mentioned above, and also of *T. carinatus* teeth (also Asselian), but there is no mention of the presence of a central foramen or an asymmetrical base with an anterolingual shelf in the latter.

Hampe and Ivanov (2007b) assigned three very small teeth from Pennsylvanian (Moscovian) marine sediments of the Northern Caucasus to a new species, *Triodus teberdaensis*. They possess a central (median) foramen and prominent aboral and lingual foramina in the base, which is fairly symmetrical. The cusps are rather round in cross-section and possess four or five straight cristae, some of which may be carina-like (lateral cutting edges, Hampe and Ivanov 2007b: 182). Hampe and Ivanov (2007b) successfully delineated their new species from all other previously described species mentioned above, and confirmed the absence of a central foramen in all but two species (*T. teberdaensis* and *Triodus* sp. ZÖ; plus *T. sessilis* as noted above).

The teeth of *Hagenoselache sippeli*, based on a nearly complete articulated (and only) xenacanth specimen (Hampe and Heidtke 1997) from the Namurian B (lower Bashkirian, Menning et al. 2006), possess a central foramen and show evidence of variable symmetry in their lingually extended base. Although the principal cusps possess cristae, the overall morphology of *H. sippeli* teeth (Hampe and Heidtke 1997: fig. 4) is quite unlike those of *Triodus elpia* sp. nov.

Therefore, the only *Triodus* species to possess a central foramen is *T. sessilis* from the Asselian, *Triodus* sp. ZÖ from the Gzhelian, and *T. teberdaensis* from the Moscovian, besides *T. elpia* sp. nov. from the upper Bashkirian. *Triodus serratus* is the only species, for which teeth are known (Hampe 2003), that is of similar age to *T. elpia*, but they differ in this fundamental morphologic feature. And, while some *T. serratus* teeth have an asymmetrical base, only *T. elpia* lateral teeth are generally asymmetrical with an anterolingual shelf.

The number of cristae and their patterns demonstrate enough variability within species of *Triodus* to be of questionable significance (e.g., "*Bohemiacanthus*" *carinatus* in Schneider and Zajíc 1994: fig. 21), except the lack of lingual cristae in *T. obscurus* and that, in general, they are straight in this genus. However, the efforts of Soler-Gijón and Hampe (1998: table 2) and Hampe (2003: 223–225) are useful in delineating species, despite the variability of the cristae in each one.

To summarize, *Triodus elpia* sp. nov. is similar in one major aspect only to *T. lauterensis*, *T. palatinus*, and possibly *T. obscurus* and *T.* ?*frossardi*, in possessing a heterodont dentition; but those species lack a central foramen. *Triodus teberdaensis*, *T. sessilis*, and *Triodus* sp. ZÖ possess a central foramen, but otherwise are unlike *T. elpia*. Some of the *T.* ?*frossardi* teeth are more similar to *T. elpia* teeth than any other species, except for their lack of an anterolingual shelf (and central foramen). *Triodus serratus* and *Hagenoselache sippeli* (with a central foramen), the only species of comparable age to *T. elpia*, are quite different, as noted above. The combination of a central foramen and an anterolingual shelf on an asymmetrical base distinguish the teeth of *T. elpia* from all other species. Hampe and Ivanov (2007b) provided a phylogenetic analysis of the *Triodus* species, based on 13 tooth morphology characters. Unfortunately, the absence or presence of a central (median) foramen is not among them. This might help resolve Hampe and Ivanov's (2007b: 185) comment that *Triodus* may not be monophyletic; but Schneider's (1996) *Bohemiacanthus* is not the solution.

Age, distribution and habitat.—*Triodus* occurrences in the Pennsylvanian and Permian are limited to Europe and North America (Hampe 1989, 2003), and South America (Johnson et al. 2002). If the Triassic species questionably assigned to this genus (reviewed by Hampe 2003: 225) are included, then its ultimate distribution would be significantly greater (India, Australia, as well as European and North American Upper Triassic). It should be noted that the South American occurrence (Upper Permian) is represented by teeth similar to those from the Upper Triassic.

Occurrences of *Triodus* are typically in nonmarine facies. However, Hampe and Ivanov (2007b) stated that *Triodus teberdaensis* was very likely a marine xenacanth, as the teeth and associated fossils were recovered from a marine carbonate facies (plant remains at the locality were found in clastic facies; Alexander Ivanov, personal communication, December 2008). It is possible that *T. elpia* sp. nov. was also a marine xenacanth, but because of the associated lepospondyl amphibian remains (Thayer 1985), its habitat remains uncertain.

Order Bransonelliformes Hampe and Ivanov, 2007a

Remarks.—Hampe and Ivanov (2007a) suggested this taxon to include *Bransonella* and *Barbclabornia*, both known only

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from isolated teeth. The teeth in these genera are quite dissimilar (compare fig. 1 A–D with fig. 1 E–H in Hampe and Ivanov 2007a), despite their attempt to draw analogies. It is beyond the scope of this paper to deconstruct their reasoning (e.g., their choice of character-states; Rodrigo Soler-Gijón, personal communication, October 2007), because analysis of other genera would be necessary. And until skeletal information (even dorsal spines) is discovered, such an assignment may be premature. However, for the present, Hampe and Ivanov's (2007a) taxonomy is followed here and discussed further below.

Family insertae sedis

Genus *Bransonella* Harlton, 1933

Type species: *Bransonella tridentata* Harlton, 1933. Lower Pennsylvanian Johns Valley Shale; Zidek (1972: 175; 1973: 94, fig. 3) stated the horizon is slightly below the Johns Valley, but no reason was provided; Bashkirian (Morrowan) age.

Diagnosis.—Relatively long intermediate cusp, often nearly equal to principal cusps; crown large relative to base; prominent straight to sigmoidal cristae forming chevrons on labial side of all three cusps that usually extend onto base; dominant apical button; central foramen absent. See Ivanov and Ginter (1996) and Ivanov (2005).

Stratigraphic and geographic range.—Upper Devonian (Famennian)?, Mississippian (Tournasian) to Early Permian (Sakmarian); North and South America, Europe, and Asia.

Bransonella ?*nebraskensis* (Johnson, 1984)

Material.—Two teeth, UAPL 23508 and UAPL 23509.

Description.—Base of UAPL 23508 wider (l-l) than long (am-pl; Table 2), apical button in contact with intermediate and principal cusps, with smooth transition between lingual margin and base, appearing to reach lingual bifurcation of base; both principal cusps broken near base, intermediate cusp broken at base. Base of UAPL 23509 wider (l-l) than long (am-pl; Table 2), apical button in contact with one principal cusp and with intermediate cusp, otherwise similar to UAPL 23508; principal and intermediate cusps broken near base. Semicircular basal tubercle in both teeth; both with two aboral foramina; oral foramina absent in both teeth.

Remarks.—Both teeth are questionably assigned to *Bransonella nebraskensis*, largely because of incompleteness and interference from matrix. They are well within the size range of *B*. (*Xenacanthus*) *nebraskensis* teeth (Johnson 1984), in which the apical button is always in contact with the intermediate cusp and nearly so with the principal cusps (Johnson 1984: figs. 3–14). However, the small number of aboral foramina (Table 2) is unusual for *B*. (*X*.) *nebraskensis* (Johnson 1984: fig. 1). Besides its occurrence in the Pennsylvanian of North America, Gzhelian age (Johnson 1984), Bashkirian (this paper), it also occurs in the Mississippian of Europe, Viséan age (Ivanov and Ginter 1996; Ivanov 1999; Hampe and Ivanov 2007a) and Asia (Siberia) (Rodina and Ivanov 2002). Hampe (2003: 236) mentioned two other occurrences from Kansas in North America: one is Late Pennsylvanian (Bell Limestone Member, Lecompton Limestone, Shawnee Group, middle Gzhelian; Tway and Zidek 1983: fig. 52, as "Subtype 173"; West 1990: fig. 1; Hills and Kottlowski 1983); the second is Early Permian (Schultze 1985: fig. 4.1), as *Xenacanthus luedersensis*, Funston Limestone, Council Grove Group, middle Sakmarian (Wardlaw et al. 2004). The tooth mentioned by Schultze (1985) is the only known Permian occurrence.

Bransonella ?*lingulata* Ivanov and Ginter, 1996

Fig. 18A.

Material.—Single tooth, UAPL 23510.

Description.—Base wider (l-l) than long (am-pl; Table 2); lingual margin bifurcated (Fig. 18A_1); basal tubercle round with prominent labial rim with no distinct lingual margin; apical button slightly isolated from principal cusps but in contact with intermediate cusp, oval shape (Fig. 18A_1), labio-lingually elongated with slightly bifurcated lingual margin (Table 2); prominent aboral foramen at labial end of groove associated with lingual bifurcation plus about six smaller but significant foramina; significant oral foramina absent. Principal cusps with distal tips missing, approximately equal in size with posterior cusp (left side in Fig. 18 A_1) possibly longer if cusps restored; both compressed, forming a transverse axis (Table 2); posterior cusp with at least three cristae on labial side (Fig. 18A_2), one of which curves down along posterior margin, some with a tendency to proximally bifurcate onto base, and three on lingual side (Fig. 18A_1); anterior cusp with two labial cristae, one of which bifurcates onto base, and possibly four on lingual side. Single intermediate cusp, distal 1/3 missing, antero-posteriorly compressed throughout, with labial, lingual, and marginal cristae (Table 2), leans posteriorly (Fig. 18 A_1), probably 2/3 length of posterior principal cusp. Distinct groove between crown and base on labial side (Fig. 18A_2) extends onto anterior and posterior margins.

Remarks.—The attitude of the three cusps suggests UAPL 23510 was in a posterolateral position in the dental arcade. This tooth may belong to *Bransonella lingulata*, as the apical button extends to the lingual margin of the base (also similar to *B. tridentata*, Johnson 1984, although the apical button is not in contact with the intermediate cusp in that species). Its identity is questioned because of the presence of a bifurcated lingual margin; but the aboral lingual groove is similar to fig. 3H in Ivanov and Ginter (1996), although it may also be present in *B. nebraskensis* (Johnson 1984: fig. 10a). The shape of the apical button (Fig. 18 A_1) is similar to one illustrated by Ivanov and Ginter (1996: fig. 4I), and is quite unlike that in *B. nebraskensis* (Johnson 1984; Ivanov and Ginter 1996), although there is considerable overlap in shape between the two species (Ivanov and Ginter 1996: figs. 1, 3, 4). The greatest difference between UAPL 23510 and *B. lingulata* is the presence of cristae on the lingual side of the cusps in the former, while they are apparently absent on the lingual side of the latter; however, they are on the edges of the lingual side (Ivanov and Ginter 1996: fig. 5C; Alexander Ivanov, personal commu-

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Table 2. Morphological features of Swisshelm *Bransonella* teeth. Angles are estimated; features questioned where matrix interferes, worn, or broken; l-l = labio-lingual, am-pl = anteromedial-posterolateral; left and right cusps in lingual view.

Morphologic feature	*B.* ?*nebraskensis*	*B.* ?*nebraskensis*	*B.* ?*lingulata*	*Bransonella* sp. "A"	*Bransonella* sp. "B"
	UAPL 23508	UAPL 23509	UAPL 23510	UAPL 23511	UAPL 23512
Tooth base dimensions (l-l × am-pl)	1.19 × 1.09 mm	1.23 × 1.13 mm	0.92 × 0.75 mm	0.82 × 0.99 mm	≈ 0.78 × ≈ 0.91 mm
lingual bifurcation	present	present	present	present	present
aboral surface	concave	concave	flat to concave	flat	flat?, concave
basal tubercle	lunate, flat, ≈ offset	lunate to semicircular, flat	round, no lingual margin	semicircular, flat	asymmetrical, offset, flat
apical button in contact with principal cusps?	yes	one isolated	≈ isolated	≈ isolated	isolated
in contact with intermediate cusp?	yes	yes	yes	yes	–
isolated from lingual margin?	yes, but blends into bifurcation	yes	yes	yes	no
apical button shape	irregularly round	irregularly round, protuberance close to intermediate cusp	oval, with lingual end bifurcated	broad l-l oval	irregular, subdued
central foramen	absent	absent	absent	absent	present?
aboral foramina	2?	2	≤ 7	2	4?
oral foramina	0?	0	1?	0	≥ 2
Crown					
principal cusps	broken, ≈ divergent?	incomplete, divergent	distal 1/4–1/3 missing, divergent	left cusp incomplete, divergent	distal 1/4 missing, ≈ divergent
transverse axis to labial margin	both 45°	both 45°?	left 60°, right ≥ 45°	both 45°	left ≤ 15°, right 30°
proximal cross-section of principal cusps	≈ compressed	≈compressed	compressed	compressed	≈ compressed, larger cusp nearly round
distal cross-section	?	?	no change	no change	nearly round
crown-base angle	90°?	90°	90°, one ≈ recumbent	≤ 90°, ≈ recumbent	90°, ≈ recumbent
labial cristae (cusps not distinguished)	present, indet.	?	≥ 3, 2	4, ≤ 6	5, 5
labial cristae on base	present	present	present	absent	present
lingual cristae	present, indet.	?	3, 4?	1?, 2?	0?, 0?
intermediate cusp	present, broken	present, broken	present, incomplete	present	absent
intermediate cusp cross-section	?	?	am-pl compressed throughout	am-pl compressed; distally l-l compressed to equidimensional	–
intermediate cusp cristae	?	?	3 lingual, 3 labial, 2 marginal	4? lingual, ≈ 5 labial	–

nication, December 2008, claims they are on the lingual side, but certainly not to the extent as seen in UAPL 23510, based on fig. 5C). Cristae sometimes occur on the lingual side in *B. nebraskensis* (Johnson 1984: 183; Ivanov and Ginter 1996: fig. 1J), but not as extensively as in UAPL 23510. The intermediate cusp in *B. lingulata* teeth tends to be shorter than that in UAPL 23510, although it is antero-posteriorly compressed in both, as in *B. nebraskensis* (Johnson 1984: 180). UAPL 23510 could questionably be assigned to *B. nebraskensis*, but the nature of the apical button prevents this.

Bransonella sp. "A"

Fig. 18C.

Material.—Single tooth, UAPL 23511.

Description.—Base longer (am-pl) than wide (l-l; Table 2); lingual margin bifurcated (Fig. 18C_1, C_4); basal tubercle semicircular with nearly straight lingual margin (Fig. 18C_4); apical button subdued with flat surface, in contact with intermediate cusp but slightly isolated from principal cusps, isolated from base lingual margin (Fig. 18C_1); only two significant aboral foramina (Fig. 18C_4), oral foramina absent. Principal cusps equally divergent; left cusp (Fig. 18C_1) incomplete and worn, right cusp largely complete (but see Fig. 18C_1); both compressed with longest transverse axis 45° to labial margin (Table 2); left cusp (Fig. 18C_1) with about four labial cristae and possibly one on lingual side, right cusp with about six labial cristae and possibly one or two lingual cristae on proximal half. Intermediate cusp complete, straight, perhaps 3/4 length

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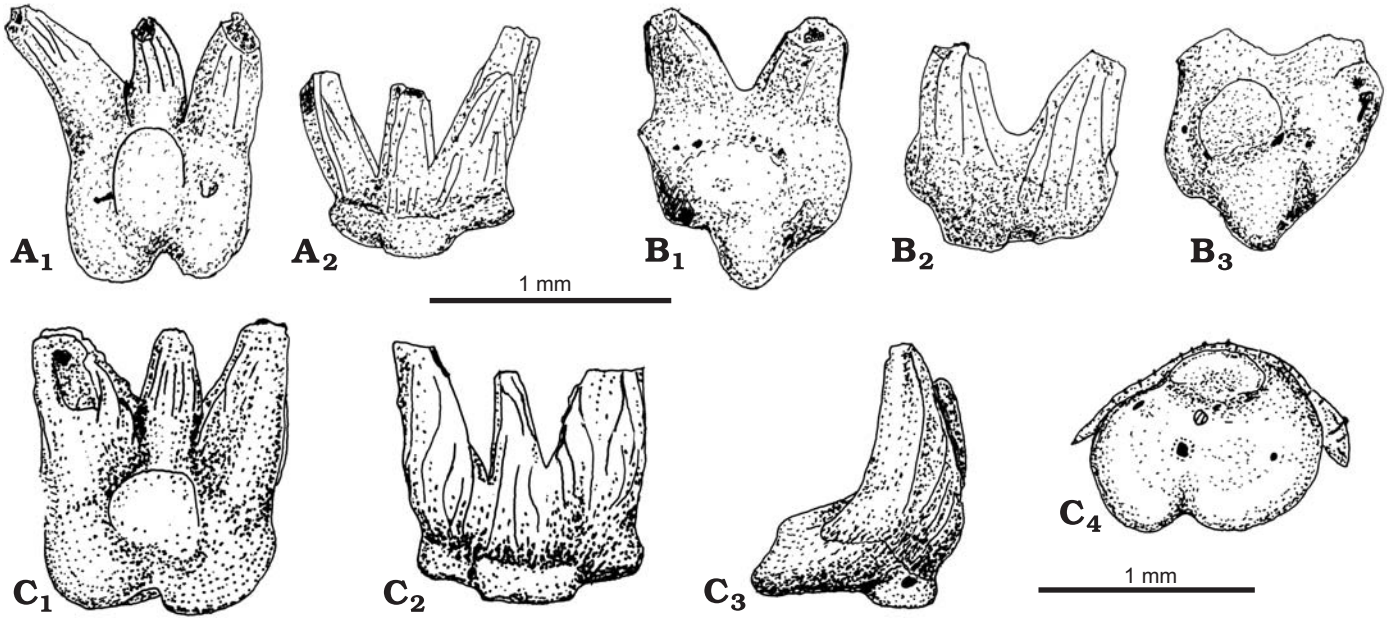

Fig. 18. Bransonelliform chondrichthyan teeth of *Bransonella*, Lower Pennsylvanian, Black Prince Limestone, Swisshelm Mountains, Arizona; **A**. *Bransonella* ?*lingulata*, UAPL 23510; lingual-occlusal (A_1, ?posterior cusp on left) and labial (A_2) views. **B**. *Bransonella* sp. "B" with broken bifurcated base, UAPL 23512; lingual-occlusal (B_1), labial (B_2), and aboral (B_3) views. **C**. *Bransonella* sp. "A", UAPL 23511; lingual-occlusal (C_1, left cusp obscured by matrix; distal portion of right cusp lost after illustration completed), labial (C_2), annteromedial or posterolateral (B_3), and aboral (B_4) views.

of principal cusps if complete, base practically fused to principal cusps; proximally compressed antero-posteriorly, distally slightly compressed labio-lingually or equidimensional (not conical); possibly two distal and three or four proximal cristae extending onto base on labial side, ?four faint distal cristae on lingual side, proximally absent.

Remarks.—Tooth wear, probably from transport, precludes a full assessment of the cristae in UAPL 23511 (Table 2). They appear finer than is typical for *Bransonella*; on both principal cusps, they appear not to extend onto the base on the labial side, but this may be from wear. If the cristae did not extend onto the base, then the tooth would be unlike others assigned to *Bransonella*, although Johnson (1984: 183, fig. 8b) noted an exception. The base dimensions are reversed (am-pl > l-l, Table 2) from UAPL 23508–23510, but this is normal for most *B. nebraskensis* teeth (Johnson 1984: fig. 2) and not unusual for *B. lingulata* (Ivanov and Ginter 1996: fig. 2). The apical button is in contact with the intermediate cusp and isolated from the base lingual margin, as in *B. nebraskensis* (Johnson 1984); it is nevertheless much smaller and more subdued than in this and other species. The small apical button, coupled with the low number of aboral foramina (compare Fig. 18C_4 with Johnson 1984: fig. 1), suggests UAPL 23511 is probably not *B. nebraskensis*, nor is it *B. lingulata*, which has a dominant apical button in contact with the lingual margin of the base. However, Alexander Ivanov (personal communication, December 2008) thinks it does belong to *B. nebraskensis*; compare with Ivanov and Ginter (1996: fig. 1 N–R).

Bransonella sp. "B"

Fig. 18B.

Material.—Single incomplete tooth, UAPL 23512.

Description.—Base longer (am-pl) than wide (l-l; Table 2), lingual margin bifurcated, but one side of bifurcation and associated anterior/posterior margin missing (Fig. 18B_1, B_3); asymmetrically-positioned basal tubercle flat to slightly concave, mostly below one principal cusp; apical button subdued with irregular shape, isolated from cusps, with even more subdued lingual extension reaching preserved portion of lingual margin of base; one prominent aboral foramen centrally positioned next to margin of basal tubercle (Fig. 18B_3) plus three smaller foramina; insignificant oral foramina associated with labial margin of apical button, two small foramina on lateral (am/pl) side of lingual extension of base, and one prominent foramen on broken margin of base (Fig. 18B_1) associated with lingual aboral groove (Fig. 18B_3); central foramen may be present. Principal cusps slightly unequal, with distal 1/4 missing in both; both slightly labio-lingually compressed at base and nearly round at distal ends; slightly larger cusp (right side in Fig. 18B_1) with longest transverse axis 30° to labial margin, smaller (?posterior) cusp ≤ 15°; larger cusp with three labial cristae plus one each on lateral and medial margins, smaller cusp with four cristae plus one medial crista (right cusp in Fig. 18B_2), most extending onto base, with two on base between cusps (some are too faint to show in Fig. 18B_2); lingual cristae absent or faint (Fig. 18B_1, Table 2). Intermediate cusp absent.

Remarks.—Two anomalies are obvious in UAPL 23512, the offset basal tubercle and lack of an intermediate cusp. The absence of an intermediate cusp is unknown in *Bransonella nebraskensis* (Johnson 1984) but its absence sometimes occurs in *B. lingulata* (Ivanov and Ginter 1996: 654). This ab-

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sence is often associated with posterior teeth in *Orthacanthus* (Hampe 1988: fig. 2; 2003: fig. 10d; Johnson 1999) and possibly symphyseal teeth (Hampe 2003: 206). There is no evidence UAPL 23512 is malformed, despite the position of the basal tubercle; perhaps it is associated with position in the dental arcade, i.e., perhaps posterior, which may also explain the unusual angles between the proximal transverse axes of the cusps relative to the labial margin (Table 2). The deeply bifurcated (although incomplete) base precludes UAPL 23512 from belonging to *B. lingulata*. Although matrix obscures a slight concavity in the position of a central foramen, it is almost certainly present, unlike any known *Bransonella* tooth; tooth size and fragility precluded any opportunity to remove the matrix. But, despite this uncertainty, and given its other features, UAPL 23512 very likely belongs to *Bransonella*.

Discussion of Bransonella.—Hampe (2003: 226) suggested *Bransonella* may not be a xenacanthid because of the chevron pattern of the cristae on the labial side, including the base, and the presence of a kidney-shaped basal tubercle and labial foramina on the base of the teeth. The shape of the basal tubercle is too variable (Fig. 18, Table 2; Johnson 1984: figs. 1, 3c, 10a) to be of much taxonomic use, although in a majority of *Bransonella* teeth it probably is lunate (or kidney) shaped (Ivanov 2005). However, the generally distinct labial rim on the basal tubercle (Ivanov and Ginter 1996: 652, 656) is unlike that in other xenacanthid genera. This, along with some resemblance of the cristae to *Jalodus* (Ginter 1999), which has a chevron (en echelon) cristae pattern on its three cusps, suggests a close relationship between the Xenacanthida and Phoebodontiformes (Ginter 1999; Ginter et al. 2002; Ivanov 2005). Hampe (2003: 226) suggested that there is a consistent similarity between the patterns of the cristae between *Bransonella* and certain nonxenacanthid sharks, which he considered as phoebodontids (*Adamantina*; see also Ivanov 1999). Ivanov and Ginter (1996) and Ivanov (2005) were probably correct in suggesting that *Bransonella* is a xenacanthid, but probably in a new family (Ivanov and Ginter 1996: 656), and probably in a new suborder within the Xenacanthida. Hampe and Ivanov (2007a) proposed that *Bransonella* and *Barbclabornia* (Johnson 2003) be placed in a new order, Bransonelliformes. Their primary reason was that both genera possess chevron (inverted "V"-nested) cristae as opposed to all other xenacanthimorphs (Hampe and Ivanov 2007a) that either possess more-or-less straight (vertical) cristae (as in *Triodus*) or no cristae (e.g., *Orthacanthus*). They also cite the presence of foramina on the labial margin of the tooth base, but these foramina often appear to be absent in *Barbclabornia* (Johnson 2003: figs. 8–11). However, when viewed at higher magnification, a foramen the size of a "microdot" is often observed in these teeth. Hampe and Ivanov (2007a: fig. 1E) indicate one in SMU 64112 (Johnson 2003: fig. 9M); in the remainder of the illustrated teeth from the same fauna (Johnson 2003: figs. 8K–N, 9), a labial foramen was confirmed in all but one (SMU 64110), and indeterminate in one (SMU 64108). Near the top of the Texas section, in the Little Moonshine Creek fauna, the 99 measured teeth (Johnson 1996, 2003: tables 1, 2) were reexamined for the presence of labial foramina; they are present in 69, absent in 24, with six indeterminate. Some had several foramina, and some slightly larger than the "microdot" variety, but still smaller than those shown in illustrations by Johnson (2003: figs. 4–11) except for the very smallest (e.g., Johnson 2003: fig. 10A). The labial foramina are usually on the basal tubercle, but sometimes below one of the cusps. Therefore, although not universal, the presence of labial foramina in *Barbclabornia* might be considered as a significant character.

Finally, Hampe and Ivanov (2007a) cite the frequent occurrence of a large central lingual foramen leading to a main nutrient canal, which may be a valid character. However, it can also occur in phoebodonts (*Phoebodus gothicus*; Hampe 2000: 358) and in a tooth of uncertain but related affinity (Johnson 2005b: fig. 1 D, F), and in *Diplodoselache parvulus* (Hampe 2003: fig. 6a), *Orthacanthus platypternus* (Johnson 1999: fig. 13 M). *Orthacanthus donnelljohnsi* sp. nov. also has a lingual foramen (Fig. 5A), but its size is insignificant relative to Hampe and Ivanov's (2007a) character.

Hampe and Ivanov (2007a) established the priority of Xenacanthiformes Berg, 1940, over Xenacanthida Glickman, 1964, ordinal names used interchangeably by various authors; both names are used in this report to reflect usage by various authors.

Bransonella may be the only exclusively marine xenacanth genus. It occurs in marine faunas [Harlton 1933 (Zidek 1972, 1973; Suneson and Hemish 1994: 74–82, 103–107); Kozur 1984: 143, pl. 9; Duffin et al. 1996: 238; Ginter et al. 2002: 189; Ivanov 2005] and mixed marine and nonmarine faunas [Johnson 1984 (Ossian 1974); Thayer 1985], otherwise not explicitly stated in other references given here, but is associated with other presumably marine chondrichthyans. *Bransonella* was not present among a variety of marine chondrichthyans described from the Middle Pennsylvanian (upper Moscovian) of central Arizona (Elliott et al. 2004), suggesting its habitat may have been restricted, perhaps to shallow marine water (Alexander Ivanov, personal communication December 2008).

The nearly cosmopolitan distribution of *Bransonella* also suggests a marine habitat (Rodrigo Soler-Gijón, personal communication, August 1999). It is known from North America (see *B. nebraskensis* above), Europe (see *B. nebraskensis* and *B. lingulata* above; *Bransonella* also occurs in Hungary [Kozur 1984; Hampe and Ivanov 2007a]), Siberia (Rodina and Ivanov 2002), Iran (*Bransonella*? sp., Devonian, Ginter et al. 2002), South America (Duffin et al. 1996 reported the presence of ?*Triodus*, but is actually *Bransonella*: Rodrigo Soler-Gijón, personal communication August 1999; Martha Richter, personal communication, October 2002; and Hampe 2003: 226), and China (Wang et al. 2004; Wang 2006). Wang (2006: table 3) reported the occurrence of three undescribed (Nian-Zhong Wang, personal communication, April 2007) species from the Tournasian (also Wang et al. 2004), Moscovian-Kasimovian, and Gzhelian.

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Conclusions

The Swisshelm *Orthacanthus* teeth represent dentitions of juvenile and adult sharks, as in *O. bohemicus* and *O. gibbosus*. But, unlike these European species, *O. donnelljohnsi* sp. nov. lacks serrated carinae, resulting in a combination of characters that is unique among *Orthacanthus* species. The presence of *Triodus* is the first reported occurrence in the North American Paleozoic; and the teeth, with their aborally-flexed anterolingual shelf, represent a new species, *T. elpia*, one of the oldest species in that genus. The occurrence of *Bransonella* teeth increases the likelihood that this geographically widespread genus was a marine xenacanth.

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