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PYKNOTYLACANTHUS SPATHIANUS GEN. ET SP. NOV., A NEW CTENACANTHOID FROM THE EARLY TRIASSIC OF BEAR LAKE (IDAHO, USA)

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ABSTRACT – A fairly completely preserved finspine recovered in association with dermal denticles from the Early Triassic of Bear Lake County (Idaho, USA) represents the youngest unequivocal record of a *Bythiacanthus*-like shark (Ctenacanthoidea *incertae sedis*). The accompanying invertebrate fauna indicates a late Early Spathian age (Early Triassic). Comparison of the finspine with sparse Late Paleozoic records allows identification of predominantly plesiomorphic, "ctenacanthoid" characters such as shape and cross-section of the finspine, the concave posterior wall, and the stellate morphology of the tubercles. One presumably derived character, the large and densely spaced tubercles with reduced ornament, distinguishes *Pyknotylacanthus* gen. nov. from its Carboniferous predecessors. It is suggested that "*Cosmacanthus humboldtensis*" from the Middle Triassic West Humboldt range (Nevada, USA) may represent an even younger member of the same lineage. The sample of associated dermal denticles is difficult to interpret but believed to belong at least in part to the same individual. The variability of denticles exceeds the range of expected individual variation, and is discussed in detail.

Key words: Shark, finspine, dermal denticles, Early Triassic.

RESUMO – Um espinho de nadadeira relativamente completo do Triássico inferior do condado de Bear Lake (Idaho, USA), coletado em associação com dentículos dérmicos, representa o registro inequívoco mais recente de um tubarão do tipo *Bythiacanthus* (Ctenacanthoidea *incertae sedis*). A fauna de invertebrados acompanhante indica uma idade equivalente ao final do Spathiano inferior (Triássico inferior). Comparação do espinho com escassos registros do Palaeozóico superior permite a identificação de caracteres predominantemente plesiomórficos, 'ctenacantóides', tais como a forma e secção transversal do espinho, a face posterior côncave e a morfologia estrelar dos tuberculos. Um caráter presumivelmente derivado, tubérculos grandes e densamente espaçados com reduzida ornamentação, distingue *Pyknotylacanthus* gen. nov. dos predecessores carboníferos. Sugere-se que "*Cosmacanthus humboldtensis*" das montanhas West Humboldt, Triássico médio (Nevada, USA) possa representar um representante ainda mais jovem da mesma linhagem. A amostra de dentículos dérmicos é difícil de interpretar, mas acredita-se que pertençam, pelo menos em parte, ao mesmo indivíduo. A variabilidade dos dentículos excede a variação individual esperada e é discutida em detalhe.

Palavras-chave: Tubarão, espinho de nadadeira, dentículos dérmicos, Triássico inferior.

INTRODUCTION

In 1995, the almost completely preserved finspine described here was retrieved from a nodule containing invertebrates found in the Bear Lake section about 3 miles northeast of Hot Springs (southeastern Idaho). This locality is more or less equivalent to the "locality 5" in Smith (1932). The ammonoids retrieved from the nodule containing the finspine and from adjoining nodules of the same horizon are *Columbites parisianus*, *Bajarunia* (formerly *Nordophiceras*) *pilatum*, *Bajarunia jacksoni*, *Boreoceras* (formerly *Dieneroceras*) *apostolicus*, *Xenoceltites spencei*, and *Pseudosageceras multilobatum*. Beside these ammonoids, two specimens probably belonging to the genus *Enoploceras* (Nautilida, Tainocerataceae) are preserved. In the Middle Shale unit of the Thaynes Formation of the Hot Springs locality occurs only one concretion horizon that contains *Columbites parisianus*. Because of the presence of *Columbites parisianus*, the nodule with the finspine belongs to the *Columbites parisianus* Zone, late Early Spathian.

Several remains complement the finspine: numerous dermal denticles were recovered from a thin layer within the

same nodule, along with one unidentifiable gill raker-like fragment, two undetermined, tiny actinopterygian scales showing pitted scale surfaces, and a few fragmentary, unidentified conodonts. Because this sample of shark denticles comes from a thin layer associated with the finspine in the nodule, it is likely that it belongs at least in part to the same individual of shark as the finspine, albeit found together with the other "non-shark" remains. We attempt to assess the variation (?individual variation) and compare the types of denticles with other finds and utilitarian systems.

MATERIAL AND METHODS

In the process of reducing the thickness of the nodule (containing ammonoids) using a rock saw, the finspine was discovered in the sectional plane (plane x-x in Figures 2, 3 and 5). The finspine and the denticles were released from the calcareous nodule using formic acid, and a few tubercles on the finspine had to be restored on the lateral walls of the finspine. All material is stored at Paläontologisches Institut und Museum der Universität Zürich (PIMUZ), Switzerland, with inventory number A/I 3730. Several dermal denticles and one tubercle of the finspine were subjected to SEM microscopy (PIMUZ specimens A/I 3730/1-9).

Terminology and identification of denticles follows mainly the code developed by Tway (1979, 1984) and as applied by Johns (1996). An attempt is made to assess the variation by comparing it to extant and fossil shark species and to the framework of formal taxa introduced by Johns *et al.* (1997).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Order EUSELACHII Hay, 1902
Superfamily CTENACANTHOIDEA Cappetta, 1987
Family *incertae sedis*

Pyknotylacanthus gen. nov.

Etymology. *Pykno-* Greek (dense, thick); *tyl-* (knob, hardened skin); *acanth-* (spine). The name refers to the large, densely spaced tubercles on the finspine.

Diagnosis. Finspine laterally compressed and triangular in cross-section; approximately upper third of lateral walls of finspine fringed by longitudinal or slightly curved rows of densely spaced, large and stellate tubercles (tubercles smaller and less densely spaced in both *Bythiacanthus* and *Glymmatacanthus*); tubercles with broad basal plate (less pronounced or even absent in *Glymmatacanthus*); both edges of posterior wall internally fringed by longitudinal series of very small tubercles, some recurved at their tips; posterior wall devoid of tubercles; occasionally very small tubercles with recurved tips present (absent in both *Bythiacanthus* and *Glymmatacanthus*) .

Pyknotylacanthus spathianus gen. et sp. nov.
(Figures 1-5)

Referred specimen. PIMUZ A/I 3730, finspine and, with reservation, PMUZ Z/I 3730/1-9, a sample of dermal denticles.
Locality and horizon. Hot Springs near Bear Lake (Bear Lake County, southeastern Idaho, USA); Thaynes group, *Columbites parisianus* Zone.
Age. Late Early Spathian (Early Triassic).
Etymology. Spathian- refers to the Early Triassic Age of the specimen.
Differential diagnosis. As outlined below, the fragmentary finspine from the Middle Triassic West Humboldt range in Nevada, described by Davidson (1919; see below) as "*Cosmacanthus*" *humboldtensis*, is provisionally assigned to the genus *Pyknotylacanthus* gen. nov. due to its overall similarity with *Pyknotylacanthus spathianus* gen. et sp. nov. *Pyknotylacanthus humboldtensis* can be distinguished from *Pyknotylacanthus spathianus* gen. et sp. nov. in possessing a less slender-triangular cross-section with stronger curved lateral walls and a less deep posterior cavity.

Description

Finspine. The finspine measures 178.0 mm in height, 34.0 mm in maximum depth and 16.2 mm in maximum width. The apical half of the shaft is arched posteriad (Figure 1). Judged from the shape of the finspine and from the angle at the finspine may have been inserted in the fish body (see Maisey 1978:664), specimen PIMUZ A/I 3730 may represent an anterior rather than a posterior finspine.

At least the upper third of the striately furrowed lateral walls' surfaces are covered with roundish, usually oval-like and closely set tubercles, whereas the lower nearly two thirds are devoid of any ornament (Figure 2). The finspine is quite acute - triangular in cross-section. The anterior edge which may have originally been fringed by long, oval-shaped tubercles, which are often recurved at their tips.

The approximately equidistant arrangement of tubercles on either side differs considerably (Figures 2-3). Roughly, the tubercles are lined up in longitudinal rows but this pattern is interrupted by patches of irregular or other regular tubercle arrangement, especially on the left wall (which is not due to restoration after acid preparation of the finspine); the tubercles in antero-posterior line are closer spaced than tubercles along longitudinal lines, and there are different patterns in their arrangement on the lateral walls. The tip of the finspine is devoid of any ornament, probably due to wear; near the apex and further down the finspine, most tubercles show wear facets.

The proximal two thirds of the finspine are unornamented but longitudinally coarsely furrowed (Figure 3). In lateral view, the anterior edge is round and strongly curved, whereas the posterior wall is deeply concave, less curved in outline. The central cavity extends from the level of the line which separates the ornamented distal portion and the unornamented proximal portion right down to the basal tip. As the cavity increases in

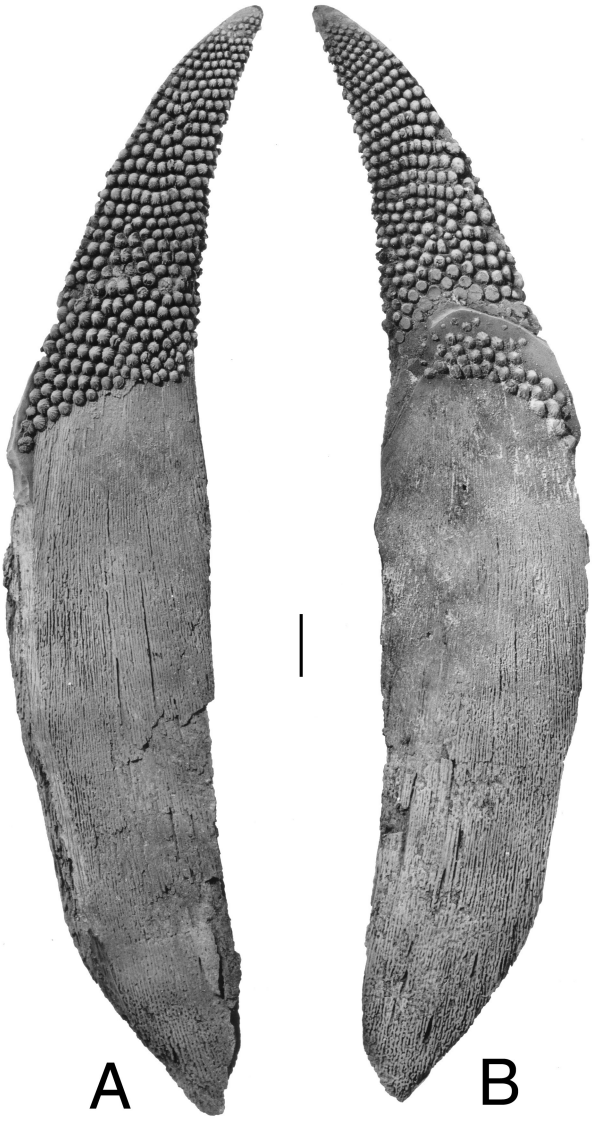

Figure 1. PIMUZ A/I 3730, finspine in left (**A**) and right (**B**) lateral views. Scale bar = 10 mm.

width basad, the posterior walls' edges taper towards the middle portion of the finspine's entire length. Only a couple of tiny tubercles are still attached to the anterior edge. Yet the kind of preservation suggests several more, very small tubercles with oval-like crowns were aligned along the anterior edge in the living animal.

The very slender posterior wall is deeply concave and devoid of any ornament except for the lateral edges which are hemmed with denticles showing a central cusp pointing basad. The tubercles vary in size from small (0.8 mm in diameter) in the apical posterior portion to large (2.5 mm) in the basal anterior portion. In the latter region small tubercles occur among larger ones.

Most crowns of tubercles consist of a simple cusp which appears to be pointed faintly basad. Approximately 8 to 14 striae run down the crown from the apex, usually bifurcating. Additional small striae may variably originate from below the apex. On the posterolateral edges, there are remains of originally probably two rows of denticles, each of which projected slightly basad. Three tubercles show a peculiar, abbreviated shape; although two joined crowns are present, there is only one basal plate to the crowns (Figures 3C, 4). The basal plate of each tubercle shows many foramina and slightly exceeds the crown in diameter.

Because of the brittle nature of the finspine, no cross-section was conducted. Part of the well-vascularized outer osteodentine layer (ol) can be seen in the single section available, obtained during preparation of the specimen (Figure 5, see discussion below). However, the section is not informative as to what degree a lamination was present.

Dermal denticles. About 40 dermal denticles (Figures 6-7, Table 1) were recovered associated with the finspine. In spite of the few other piscine remains found in association, we think it possible that at least the most abundant denticles (Figure 6A-D2 and Figure 7A-D) belong to the same individual of shark as the finspine, because all microremains were recovered from the same thin layer within the nodule as the finspine.

The sample of dermal denticles can be subdivided in groups and some can be tentatively identified either by following the coded systems of ichthyoliths (Doyle *et al.* 1974; Tway 1979, 1984; Johns *et al.* 1997) or by comparison to other reports on (more or less contemporaneous) elasmobranch denticles.

The dermal denticles found measure between 0.25 and 1.3 mm in length (Figures 6-7). The denticles consist of a basal pedicle and an apical crown usually consisting of at least a principal cusp, and some denticles posses a neck as a more or less pronounced crown-pedicle junction (see Figures 6F1, F2 and Figure 7F). The pedicles are roughly rhomboidal in basal view and are pierced by a central canal opening (and sometimes various peripheral foramina) in most denticles. The cusps may be blunt, acute, single, multiple, or subdivided ("serrated"). Few cusps are blunt, possess or lack side cusps (rare types, Figure 7E-H). Most dermal denticles possess an acuminate central cusp (abundant and common type, Figure 7A-D), which is flanked by two lateral wings, a mesial ridge (posterior) and a mesial "platform" (compare Johns *et al.,* 1997:19) that usually represents the convex anterior ridge. The lateral wings may taper to side cusps and the anterior ridge may be developed as a serrated edge showing 1 to 3 cusplets. The mesial (posterior) ridge is rather weakly developed and, if at all, faintly modified. The principal cusp may be wingless, oblong-straight, arched, pointed or blunt and broad with flat or convex surface, and the ridges may be coursely developed or faintly developed. The shape of the pedicle usually differs corresponding to the shape of the crown but the shape and size of foramina varies in the various types of denticles.

The denticles are either (rarely) stout, usually long and

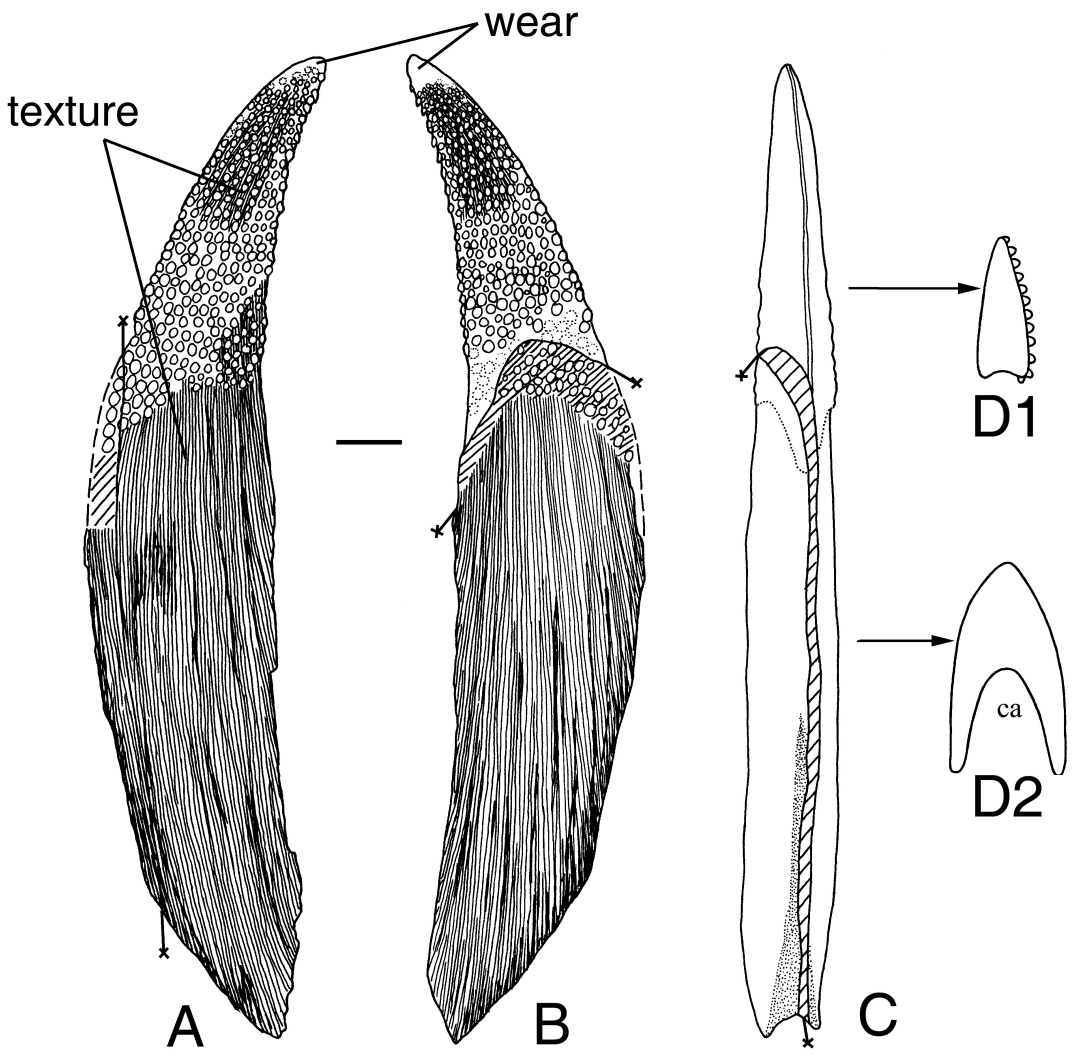

Figure 2. Sketch of the finspine (PIMUZ A/I 3730) in left lateral (**A**), right lateral (**B**), and anterior (**C**) views. The slightly enlarged cross-sections (**D**) show also the relative positions of the tubercles on one side (**D1**) and the extent of the cavity near the base (**D2**). The texture (striate furrows) of the core is clearly visible between the smaller tubercles toward the apex. The hatched streak x-x indicates the track where the finspine was cut by the rock saw. Scale bar = 10 mm.

acute lanceolate, uni- or tricuspid, rarely blunt or extremely angled, usually symmetrical and have two lateral ridges or wings (Figure 7). The mesial platform is often replaced by a central ridge, which may be serrated (Figure 7B). Two denticles are peculiar in showing a crown that is irregularly polygonal in outlines with concave sides and topped by few radiating ribs (Figure 7G).

The denticles have been tentatively grouped and compared to types described in the literature (compare Figures 6-7 and Table 1). Since individual variability in the squamation of similar ctenacathoid sharks but also more derived Triassic sharks is completely unknown, we used utilitarian systems coded for identification of Paleozoic and Mesozoic ichthyoliths (Tway, 1979; Tway & Zidek, 1982) as well as denticles of taxa known as "biological entities". In particular, the morphological range was compared to the best known formal genera described from the Middle/Late Triassic Liard Formation of the Peace River area (British Columbia) (Johns 1996, Johns *et al.* 1997). Where in conformity, cross-reference to specialist literature is given in Table 1.

Short characterization. Dermal denticles of diverse outlines; pedicles often tetrahedroid (less often truncate); crowns often acuminate (seldom blunt), mesial platform with ornament, usually well developed, often serrated, lateral cuspid wings normally present, ridges andcusps present, and profile of crown very variably developed.

DISCUSSION

Finspine. Triassic finspines possessing stellate tubercles are known to occur in several hybodont form-genera: *Nemacanthus* Agassiz, 1837 (see Agassiz, 1833-44), *Asteracanthus* Agassiz, 1837 (see Agassiz, 1833-44), and *Acronemus* Rieppel, 1982. Although similarity in Mesozoic

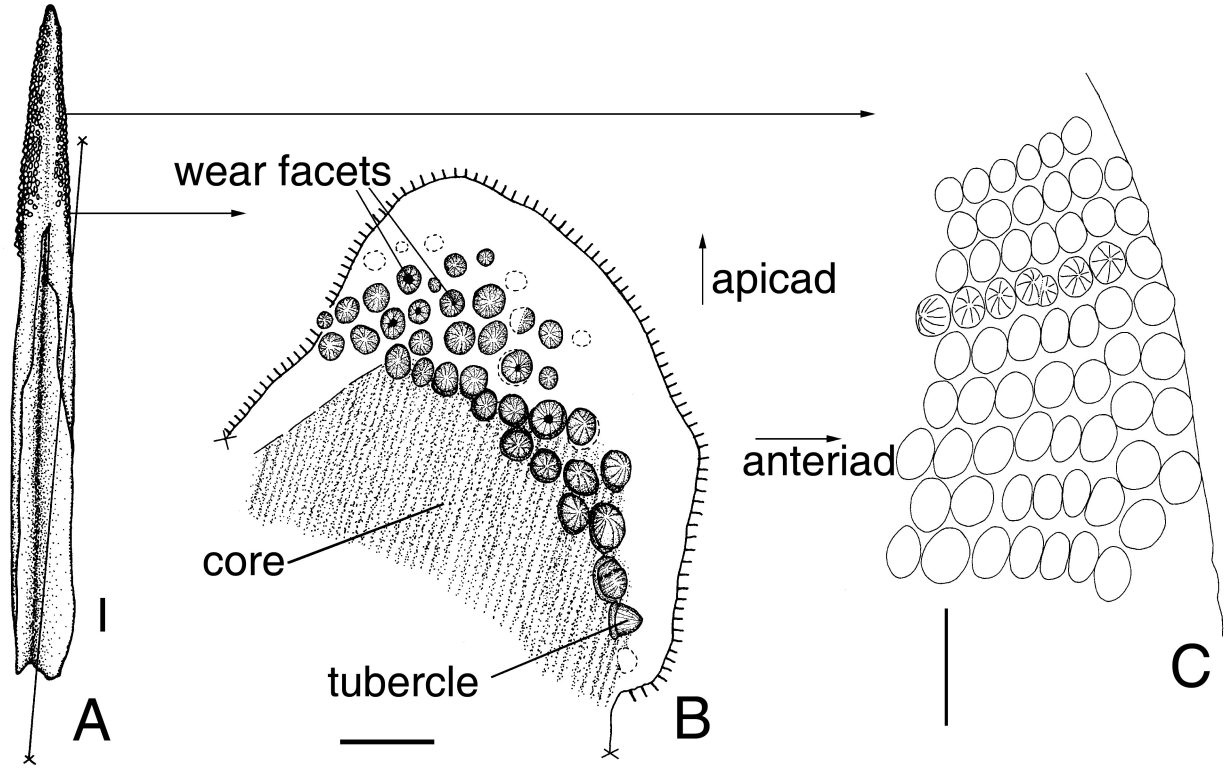

Figure 3. Finspine (PIMUZ A/I 3730). **A**, posterior view; **B**, close-up of the stellate ornamentation of tubercles at the level of finspine insertion; **C**, sketch of the finspine's middle portion, showing the regular arrangement of tubercles on the right lateral wall. Note the "merged" tubercles in the center of a transversal row. Scale bars = 10 mm.

selachian finspines does not necessarily reflect their close relationships, their morphology correlates with family-level or larger systematics (Maisey, 1977) and is conservative at the genus level (pers. comm. John Maisey, 2004). Very few features are available for appropriate characterization and diagnoses below the genus level. For instance, the finspine's size, curvature and length/width ratio are generally regarded features of little taxonomic importance. It is also believed there is a considerable variation in the overall shape of the crown and in the arrangement of tubercles within a single species (e.g. Rieppel, 1982:pl. 43, figs. 6-8).

Although only distantly reminiscent, several form-genera share superficial similarities with *Pyknotylacanthus* gen. nov.: *Acronemus* is established on the basis of Middle Triassic finspines and teeth, a fairly complete dentition, and a few cranial and postcranial remains (Rieppel, 1982). Compared with *Pyknotylacanthus* gen. nov., the finspines of *Acronemus* are much deeper, possess a prominent anterior ridge, a broad and stout basal trunk and an apical curvature of quite variable degree.

Asteracanthus finspines are the largest and least curved of all hybodont finspines. The posterior wall shows a double series of recurved tubercles, and the posterolateral edges are devoid of any ornament. First occurrence known is the Middle Triassic Besano Formation in Italy and southern Switzerland (Rieppel, 1981). *Pyknotylacanthus* gen. nov. lacks the conspicuous double series of recurved tubercles in the posterior wall.

Nemacanthus finspines are more slender than finspines of *Acronemus* or *Asteracanthus*, rather small and faintly arched; they reveal a conspicuous anterior ridge which is round in cross-section, and the tuberculate ornament is quite variably developed. Triassic finspines are reported from East Greenland (Stensiö, 1932) and from Spitzbergen but Stensiö (1921:pl. I, figure 19) declined assigning the single specimen from Spitzbergen to any taxon more specific than hybodont (see also Maisey, 1977).

Evans (1904) described a finspine under the name *Cosmacanthus elegans*, which was found in a nodule in Paris near Bear Lake (southeastern Idaho). According to Smith (1932), Paris represents the most prolific outcrop of the *Columbites parisianus* Zone - the same well-defined interregional correlation zone below the Middle of the Thaynes group *Pyknotylacanthus* gen. nov. comes from - a zone which also occurs in Utah, western Wyoming, Nevada, and southeastern California. The locality "Paris" of Evans (1904) is situated about ten miles northwest of the northern end of Bear Lake and may be equivalent to "locality 4" of Smith (1932). However, lacking more detailed information on fossils which accompanied the finspine in the same nodule, it is difficult to determine the horizon of the finspine described by Evans (1904).

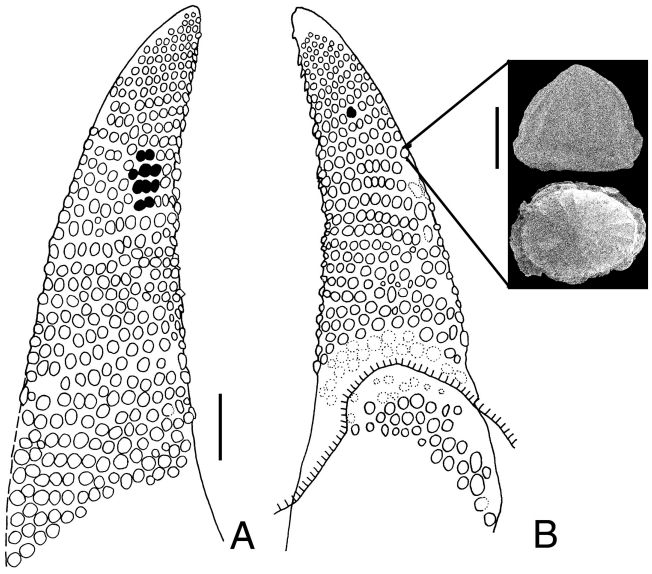

Figure 4. Sketch of arrangement of tubercles on fin spine PIMUZ A/I 3730 (occurrence of "merged" tubercles in full circles) on the left side (**A**) and the right side (**B**). Tubercle is displayed in lateral (top) and in occlusal views. The shown tubercle is SEM specimen PIMUZ A/I 3730/2. Scale bars are as follows: A= 10 mm; B= 1 mm

Yet Evan's specimen closely resembles *Nemacanthus monilifer* from the Rhaetian of southern England except for details of ornamentation of tubercles that may have also been caused by abrasion. Evans (1904) mentioned close resemblance of his finspine to *Asteracanthus* but found differences in the morphology of its tubercles and in the presence of a "sharply defined enamel keel". We agree with Maisey (1977:271) who suggested that the finspine may better be included in the genus *Nemacanthus,* because of its conspicuous keel (see also Cappetta, 1987).

Although *Pyknotylacanthus spathianus* gen. et sp. nov. shows a few elongate and backward curved tubercles aligned along the anterior rim, it lacks an anterior enameloid rim, and also differs from all three abovementioned form-genera in overall shape, morphology and arrangement of tubercles and in their restriction to the upper third of the spine (all plesiomorphic features).

Another finspine formally assigned to "*Cosmacanthus*" is the single preserved proximal portion of a finspine from the West Humboldt range (Middle Triassic) of Nevada, described by Davidson (1919) as *Cosmacanthus humboldtensis*. Although the finspine is very fragmentarily preserved, it shows tubercles with distinctive basal plates, and relatively densely spaced similar to the arrangement in *Pyknotylacanthus spathianus* gen. et sp. nov. We suggest to provisionally include the species "*C.*" *humboldtensis* in the genus *Pyknotylacanthus* gen. nov., because the finspine also resembles *Pyknotylacanthus spathianus* gen. et sp. nov. in the relative width of the lateral wall and in the fairly deep and far extension of the cavity in the posterior wall. The tubercles also have similar, large basal plates. The cross-section, however, is less triangular and the lateral walls are more convex in *P. humboldtensis*.

Apart from the Triassic species *Pyknotylacanthus humboldtensis* (Davidson, 1919), the general morphology of *Pyknotylacanthus gen. nov.* more closely resembles in particular a couple of enigmatic ctenacanthoids, both known from the Upper Carboniferous, including *Glymmatacanthus* St. John & Worthen, 1875, from Iowa and in particular *Bythiacanthus* St. John & Worthen, 1875, from Illinois. This group of ctenacanthoid sharks is currently under revision by Maisey (pers. comm. 2004), and may also include *Heslerodus divergens* (Trautschold, 1879).

Bythiacanthus is known by fragmentary, laterally compressed finspines from the Pennsylvanian (Leidy, 1873; St. John & Worthen, 1875). The tubercles on the finspine *Bythiacanthus vanhornei* St. John & Worthen, 1875, from the Carboniferous of Illinois (1875:pl. 17), resemble those in *Pyknotylacanthus* gen. nov. in possessing basal plates and

Table 1. Comparison of types of denticles (as in Figure 6) in specimen PIMUZ A/I 3730/1-9 with utilitarian systems, binomial form-taxa, and other identified remains.

Denticle type Abundance	A common	B common	C common	D abundant	E 1 scale	F rare	G 2 scales	H rare	reference
PIMUZ A/I 3730/nr:	7	9	8	4	5	3	1	6	
identification				fig. 33					Peyer, 1946
identification			fig. 2 (N1-N3)						Stensiö, 1961
coded system 1	a4/b2/c2/d5/e0/ f6/g2/h1/h1	a4/b2/c2/d5/ e0/ f6/g2/h1/i1	a4/b2/c2/d5/ e0/ f6/g2/h2/i2	a4/b2/c2/d5/e 0,1/ f6/g2,3/h1/i1	a5/b1/c1/d2 /e1/f2	a5/b2/c1/d1 /e2/f2	a5/b2/c1/d0/e 4/f2	a5/b1/c1/d0 /e0/f1	Tway, 1979; 1984
coded utilitarian system 2	9	-	4, 10	18, 39	(22)	23	70(II)	4	Tway & Zidek, 1982; 1983 (II), figures
coded system 2, subtypes	191	-	062, 199	002, 158	(028)	029	(140)	062	Tway & Zidek, 1982
identification			fig. 34A	fig. 34B			(fig. 34D)		Maisey, 1989
comparison to binomial form-taxa	Indet.	Indet.	cf. *Fragilicorona* -Labrilancea	cf. *Fragilicorona* sp.	Indet.	cf. *Carina subcorona* sp.	cf. *Lobaticorona* sp.	cf. *Proprigalea* ?	Johns *et al.*, 1997

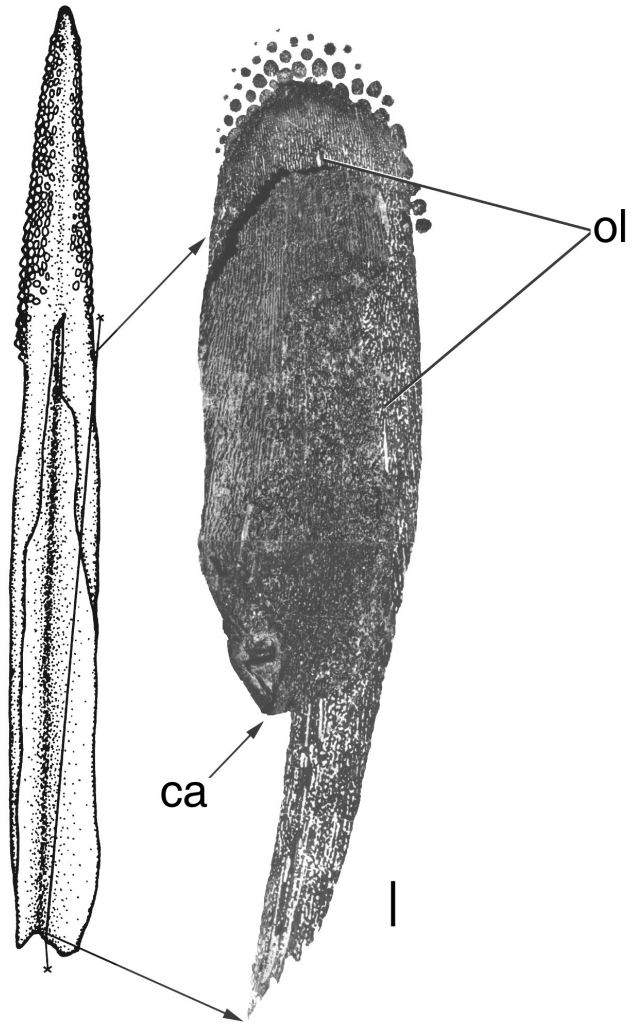

Figure 5. Longitudinal section through fin spine: only central cavity (**ca**) and spongy outer osteodentine layer (**ol**) are visible. Scale bar = 10 mm.

a similar stellate ornament. However, the tubercles on the finspine of *Pyknotylacanthus* gen. nov. have fewer ridges running down straight from the apex of the crown and the basal plates are reduced. *Bythiacanthus* has a very deep posterior cavity and the finspine is also waisted in the uppermost portion of the finspine being devoid of ornament.

Only one small fragment of a finspine is known of *Glymmatacanthus irishii* St. John & Worthen, 1875. In *Pyknotylacanthus* gen. nov. some tubercles seem to have become fused during growth similar to the condition in *Glymmatacanthus irishii* (compare Figures 3C, 4 with St. John & Worthen, 1875:pl. 17, figure 2c). *Glymmatacanthus* resembles *Pyknotylacanthus* gen. nov. in the morphology of the tubercles, although they possess a more distinctive apical cap and they lack the basal plates. The tubercles are also much less densely spaced and resemble *Bythiacanthus* much more in this respect. In the triangular cross-section, however, and in the extent of the cavity in the posterior wall, *Glymmatacanthus* is not distinguishable from *Pyknotylacanthus* gen. nov. The cross-sections of *Pyknotylacanthus* gen. nov. matches both genera (see Figure 2 and St. John & Worthen, 1875:pl. 17, figs. 1h, i, and 2b).

The histology of the finspine and the diameter at the mid-cross-section are diagnostic at a higher hierarchical level (Maisey, 1977; Zangerl, 1981). Unfortunately, the only section available is the snapshot taken before acid preparation (Figure 5): as can be seen from the section - obliquely cut nearly parallel to the lateral wall (Figure 4) - only informs on the histology of the outer osteodentine layer. A lamination in the osteodentine, distinctive of the anterior portion of hybodont finspines, is absent but since this structure can only be discerned using thin sections (Maisey, 1978, pers. comm. Maisey, 2004), this section is not informative in this respect. However, the deep and extensive cavity and the concave posterior wall together with the triangular outline of the midportion of the finspine in cross-section clearly suggest ctencanthoid affinities.

Like the dermal denticles, the tubercles of the finspine can be compared to other ichthyoliths. Applying the utilitarian system suggested by Tway & Zidek (1982, 1983), the tubercles are type 64 (II) and subtype 200 (see Table 1).

Dermal denticles. If this sample of dermal denticles truly belongs to a single individual, it seems questionable whether single denticle morphology is distinctive enough to separate out characters at a lower taxonomic level in primitive sharks. For instance, type D, the most abundant type of denticles identified here, oblong-lanceolate, is found in *Asteracanthus*, and also in *Hamiltonichthys mapesi* (Peyer, 1946, Maisey, 1989). Furthermore, type C, fairly common in *Pyknotylacanthus spathianus* gen. et sp. nov., is referred to as the lepto-columnar type and is reported to occur abundantly among extant selachians (Stensiö, 1961). Maisey (1977) noted the occurrence of similar spatulate scales in *Palaeospinax priscus*, *Squalus acanthias*, *Squalus latidens*, *Entoxychirus uyatus*, and *Centrosqualus primaevus* but lacked comparative data for assessment of specific or generic variation.

The types of denticles identified in specimen *Pyknotylacanthus spathianus* gen. et sp. nov. include very stout, mostly lanceolate shapes (types B, C, D) but also elliptical shapes (type E) and intermediates (types F, H). Type G resembles denticles found above the eye of extant *Heterodontus philippi* (Peyer, 1946:fig. 33).

In contrast, some hybodont scales such as those of *Hybodus fraasi* (Maisey, 1986:figs.6B, C; 7B, C) and *Egertonodus* (Maisey, 1983:Figure 23A-F) bear more ridges and do not resemble any of the denticles in this sample. Type A is indistinguishable from type B according to the system provided by Tway (1979, 1984) because of the lack of codes for the accessory 1-3 cusplets on the mesial platform (ridge). These cusplets may rarely preserve and may therefore be

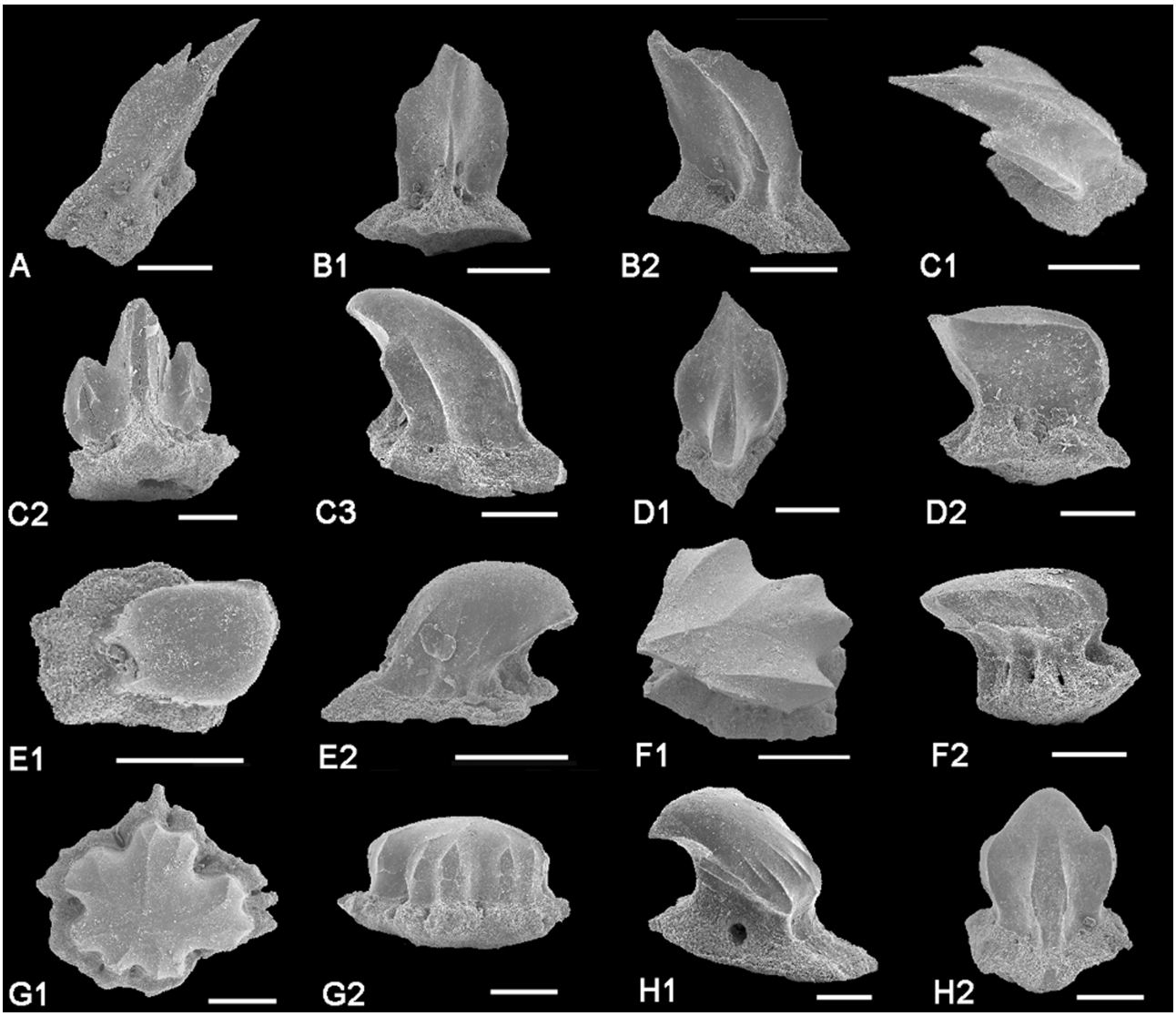

Figure 6. Types of dermal denticles (as in Figure 7) as found associated with the finspine PIMUZ A/I 3730 in various views. **A**, PIMUZ A/I 3730/7 (type A); **B**1-2, PIMUZ A/I 3730/9 (type B); **C**1-3, PIMUZ A/I 3730/8 (type C); **D**1-2, PIMUZ A/I 3730/4 (type D); **E**1-2, PIMUZ A/I 3730/5 (type E); **F**1-2, PIMUZ A/I 3730/3 (type F); **G**1-2, PIMUZ A/I 3730/1 (type G); **H**1-2, PIMUZ A/I 3730/6 (type H). Scale bars = 200 µm.

unreported in the literature. The flat mesial platform and the serrated mesial ridge ("platform") constitute the two extremes of crown morphology. The pedicle morphology is commonly "multiforaminate" and "cruciform" (described as "tetrahedroid" in Johns, 1996; Johns *et al.,* 1997). This type of pedicle may, in comparison to Middle-Late Triassic ichthyolith remains from northeastern British Columbia, be tentatively interpreted as rather modern or "derived". Yet the individual variation cannot be compared to any other records of more complete shark squamations.

Identifications of binomial form-taxa are summarized in Table 1. Translated in codes according to Johns *et al.* (1997), the range of denticle morphology is: >a4/b2/c2/d5/e0,1/f6/g2,3/h1,2/i1,2< and >a5/b1,2/c1/d0,1,2/e0,1,2,4/f1,2<. This range of morphotypes exceeds the range of 4 form-genera established on the basis of isolated dermal denticles (Figures 6-7).

CONCLUSIONS

This find is a remarkable record of an "archaic" ctenacanthoid shark in association with dermal denticles and implies survival of an enigmatic group of ctenacanthoids across the Permian-Triassic boundary, previously known from the Pennsylvanian. The nicely preserved specimen is particularly important because its Spathian age is well-supported by the ammonoid fauna, that comes from the *Columbites parisianus* Zone, and which is suitable for interregional correlation.

The range of individual dermal denticle morphology is surprisingly wide and suggests that individual variation of the squamation in many fossil and extant sharks in general is not well enough known to separate out diagnostic features at a lower taxonomic level.

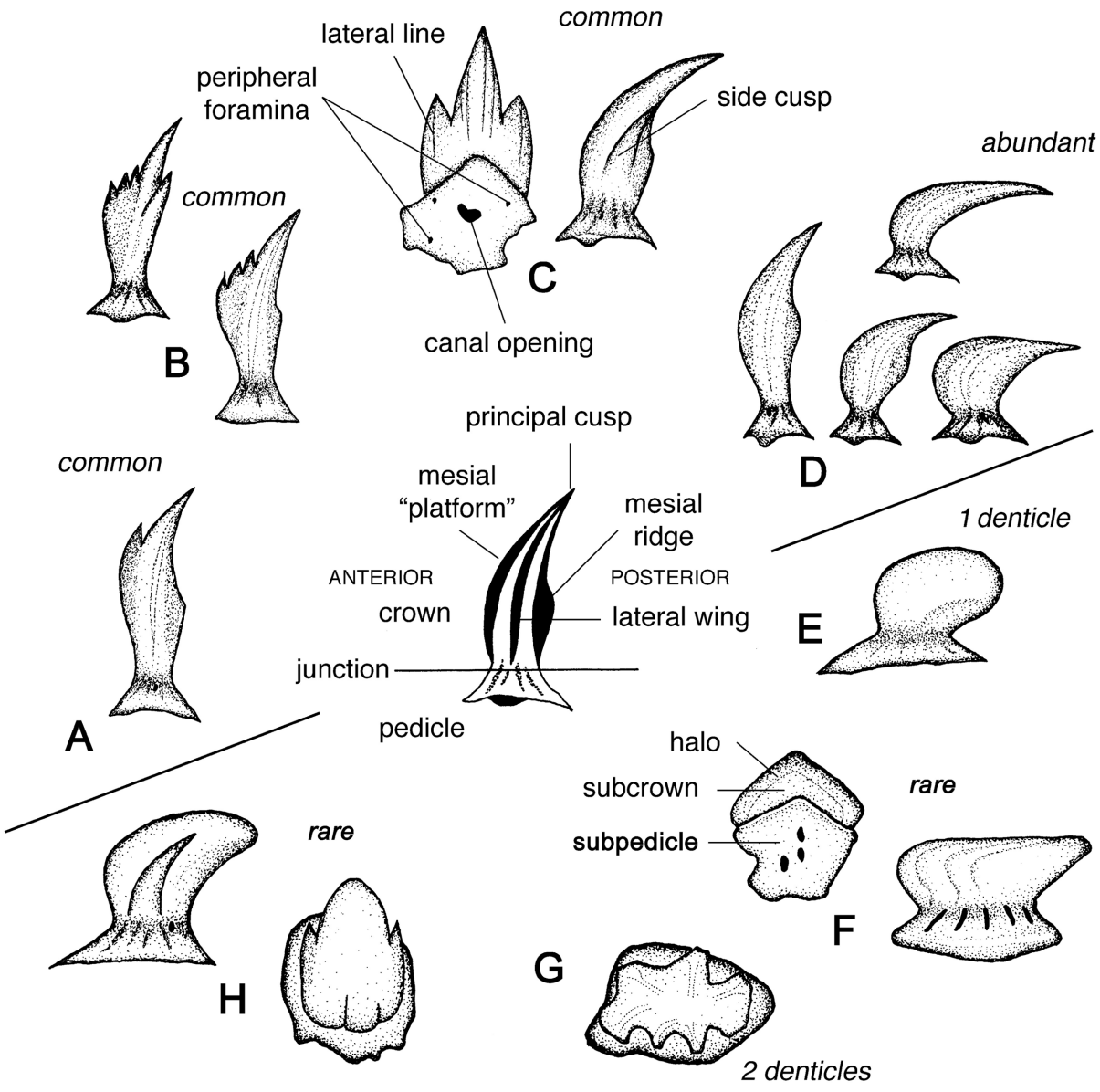

Figure 7. Overview of dermal denticles found associated with the finspine of *Pyknotylacanthus spathianus* gen. et sp. nov.: the types of denticles (**A**-**H**) differ in morphology and in abundance. The most abundant denticles (**A**-**D**) may belong to the same individual. Not to scale; width of crowns is up to 0.5 mm (see Figure 6).

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