

The occurrence of *Polygnathus tuberculatus* in lag deposits near the Middle-Upper Devonian boundary and its stratigraphic range in the conodont zonation

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ABSTRACT: The conodont species *Polygnathus tuberculatus* Hinde is best known in condensed conodont-bone bed lag deposits in western New York and southern Indiana. These occurrences, containing conodonts ranging from zones of the Middle Givetian Middle *varcus* (= *ansatus*) Zone to Lower Frasnian Zone 2, have influenced a postulated range extension above the *varcus* Zone. However, the occurrence in the Kentucky New Albany Shale zonal succession indicates that *P. tuberculatus* may be confined to the Middle *varcus* Zone. This is supported by the occurrence in the Tully Limestone in Pennsylvania. The species appears to be endemic to eastern North America, with the exception of occurrences in southwest England and the Rhenish Slate Mountains of Germany of a somewhat different morphotype.

INTRODUCTION AND ENDEMISM OF *POLYGNATHUS TUBERCULATUS*

The Devonian conodont species *Polygnathus tuberculatus* was named by G. J. Hinde (1879) from Eighteenmile Creek near the village of North Evans, a short distance south of Buffalo, NY, in the first paper describing North American conodonts. Although Hinde described conodonts of varying age from other localities and horizons in New York State and Ohio, as well as Ontario and Quebec, Canada, *P. tuberculatus* along with many other species was found in the 'conodont bed' of Hinde (Bryant 1921, p. 6; Orr and Klapper 1968, p. 10). This stratigraphic unit was later formalized as the North Evans Limestone (J. W. Wells in Rickard 1964). The North Evans has been recognized for many years as a highly condensed conodont-bone bed lag deposit that contains species whose first occurrences are diagnostic of numerous Middle Devonian (Givetian) and Upper Devonian (Frasnian) conodont zones (e.g., Orr and Klapper 1968; Baird et al. 2006, p. 373, fig. 10; Klapper and Kirchgasser 2016, p. 527, fig. 3, NE). Among these are *Polygnathus ansatus* Ziegler and Klapper, in Ziegler, Klapper and Johnson 1976 and *Tortodus caelatus* (Bryant 1921) (Middle *varcus* or *ansatus* Zone), *Schmidtognathus wittekindti* Ziegler 1966 (*hermanni* Zone), *Klapperina disparalvea* (Orr and Klapper 1968) (*disparilis* Zone), all in the Givetian, and *Ancyrodella rotundiloba* (Hinde 1879) s.s. and *A. recta* Kralick 1994 (first occurrences, respectively, at the lower boundary and in the uppermost part of lower Frasnian Zone 2).

Polygnathus tuberculatus is one of the most prominent and characteristic species found in the North Evans Limestone. It is highly distinctive morphologically and is endemic to eastern North America, occurring in western New York (Hinde 1879; Bryant 1921; Huddle 1981), Pennsylvania and West Virginia (Weary and Harris 1994, p. 217–218), Indiana [Huddle 1934; Orr and Klapper 1968, in both references identified as the junior synonym *P. bryanti* Huddle 1934 (Sandberg, Hasenmueller and Rexroad 1994)], and Kentucky (Work, Mason and Klapper 2007). There are only two known exceptions to this highly en-

demically restriction of *P. tuberculatus*, and that is southwest England in Cornwall (Kirchgasser 1970) and Devon (Orchard 1978) and the Rhenish Slate Mountains, Germany (Wittekindt 1966). These at least partly represent somewhat different morphotypes of the species (see Taxonomy). In a 'splitter's' taxonomy, which seems to be gaining traction in some current conodont literature, these European specimens might well be considered a different species (see discussion of intraspecific variation in Klapper and Votr  zkov   2013).

Conspicuously, *P. tuberculatus* has not been reported from the intensively studied Devonian sections in Belgium, the Montagne Noire in southern France, nor in southern Morocco. Its erroneous reported occurrences in the Himalayas (Kashmir and Nepal, Gupta 1975a and b, in addition to other papers by him) led to skepticism about the source of V. J. Gupta's material that was questioned by Klapper and Ziegler (1979, p. 220). One of their unstated reasons was the illustration in both the Kashmir and Nepal papers of specimens identical to those of North Evans *P. tuberculatus* and the knowledge at that time of the endemic distribution of the species in eastern North America. Full exposure of Gupta's fraudulent methodology was accomplished by Talent et al. (1988) and subsequent, numerous articles by John Talent and various co-authors (e.g., Webster, Rexroad and Talent 1993). Noteworthy is a paper by Wyatt (1990, p. 590), who raised the distinct possibility that a collection of North Evans conodonts housed at the University College of Wales in Aberystwyth was purloined by Gupta when he spent a postdoctoral period there. It is known that the Buffalo, NY, amateur collector, Raymond R. Hibbard, had mined a highly weathered lens of North Evans Limestone at Amsdell Creek, a short distance north of the type locality at Eighteenmile Creek, and in the late 1940s to early 1950s had distributed jars of concentrated residues of conodonts and fish plates to conodont workers and museums in many parts of the world. While I was a student of Walter Youngquist at the University of Kansas in 1957, a small jar of Amsdell Creek North Evans conodonts given by Mr. Hibbard to Professor Youngquist provided the source of a graduate seminar project.

STRATIGRAPHIC RANGE IN NEW ALBANY SHALE, KENTUCKY

Polygnathus tuberculatus occurs in the Portwood Member of the New Albany Shale in the J. K. Smith Power Plant section in Clark County, east-central Kentucky (Work, Mason and Klapper 2007, fig. 1; text-fig. 1 herein). The species ranges from Beds 2–4 in the lower Portwood, which in terms of the conodont succession are in the Middle *varcus* Zone as identified by Work, Mason and Klapper (2007, p. 1510, following the original definition of Ziegler, Klapper and Johnson 1976 = subzone in that paper). However, Beds 2 and 3 fall within the *P. rhenanus/varcus* Zone in the revised zonation of Bultynck (1987, fig. 9), which is equivalent to the upper part of the Lower *varcus* Zone of the earlier terminology. Bed 4 is within the *P. ansatus* Zone of the revised zonation. *Polygnathus tuberculatus* is especially abundant in Bed 3, which is the source of the illustrations in Plate 1. The specimens in this sample are well preserved; in contrast with many previous illustrations the free blade is preserved in many specimens and immature specimens occur as well. Most of the literature references illustrate adult specimens with the free blade unpreserved. In terms of the New Albany conodont succession in Kentucky, *P. tuberculatus* is not younger than the *ansatus* Zone (= Middle *varcus* Zone of the earlier terminology). This conclusion is in agreement with the inference about the range of the species suggested by Orchard (1978, p. 917) regarding the Plymouth Limestone occurrence in south Devon.

STRATIGRAPHIC RANGE IN TULLY LIMESTONE, PENNSYLVANIA

Weary and Harris (1994, p. 217, fig. 7 and pl. 1, figs. 5, 6) illustrated *Polygnathus tuberculatus* from a level 1.3 m above the base of the Tully Limestone at Newry, Pennsylvania. It occurs in this one sample at Newry together with *P. timorensis* Klapper, Philip and Jackson, 1970 and *P. linguiformis linguiformis* Hinde 1879 gamma morphotype, a very long-ranging species that is zonally undiagnostic. *P. tuberculatus* has not been found in the Tully Limestone in New York. However, *P. timorensis* occurs in the New York Tully in the Middle *varcus* Zone below the entry of *Schmidtognathus latifossatus* (Wirth 1967) (the defining species of the Upper *varcus* Zone) in all recorded instances (Ziegler, Klapper and Johnson, 1976, tables 1–3) and below the first occurrence of ‘*Ozarkodina*’ *semialternans* (Wirth 1967) with one exception where it overlaps the latter species in one sample (Ziegler, Klapper and Johnson, 1976, table 2). Thus the highest range of *P. timorensis* within the New York Tully is in the lowest interval of the *latifossatus/semialternans* Zone in the zonation of Bultynck (1987, fig. 9; Narkiewicz and Bultynck 2010, fig. 10), but not as high as the Upper *varcus* Zone in its original definition (Ziegler, Klapper and Johnson 1976). ‘*Ozarkodina*’ *semialternans* typically enters the New York Tully sequence just below or with *S. latifossatus* (Ziegler, Klapper and Johnson 1976, tables 1–3). The difference in the first occurrences of these two species in terms of graphic correlation as represented by the Ardennes, Belgium, and Moroccan Composite Standard is trivial, less than one Composite Standard Unit (Gouwpy and Bultynck 2002, table 1). Thus, the *P. tuberculatus* occurrence in the Tully at Newry can be interpreted as not zonally higher than its range in the Kentucky New Albany Portwood Member (text-fig. 1).

LAG BED OCCURRENCES IN NEW YORK AND INDIANA

As noted above, *Polygnathus tuberculatus* is well represented in the North Evans Limestone at Eighteenmile Creek, the type locality of the formation (Baird et al. 2006, fig. 9 and p. 386, locality 3). The species is also abundant at two nearby localities in Erie County: Amsdell Creek (Baird et al. 2006, p. 387, locality 4), and the unnamed creek south of Big Tree Road and the WKBW radio towers (Klapper 2000, p. 158, locality information for pl. 1, figs. 6, 7 in that paper; Baird et al. 2006, p. 387, locality 6). As noted previously, the North Evans represents a highly condensed conodont-fish plate lag bed spanning numerous Givetian through Lower Frasnian conodont zones. These North Evans Limestone occurrences have probably led to hypothesized upward range extensions of *P. tuberculatus* (discussed below), much higher than the Upper *varcus* Zone (or the *latifossatus/semialternans* Zone) of the Middle Givetian in the substage terminology now in use (Narkiewicz and Bultynck 2010, fig. 10).

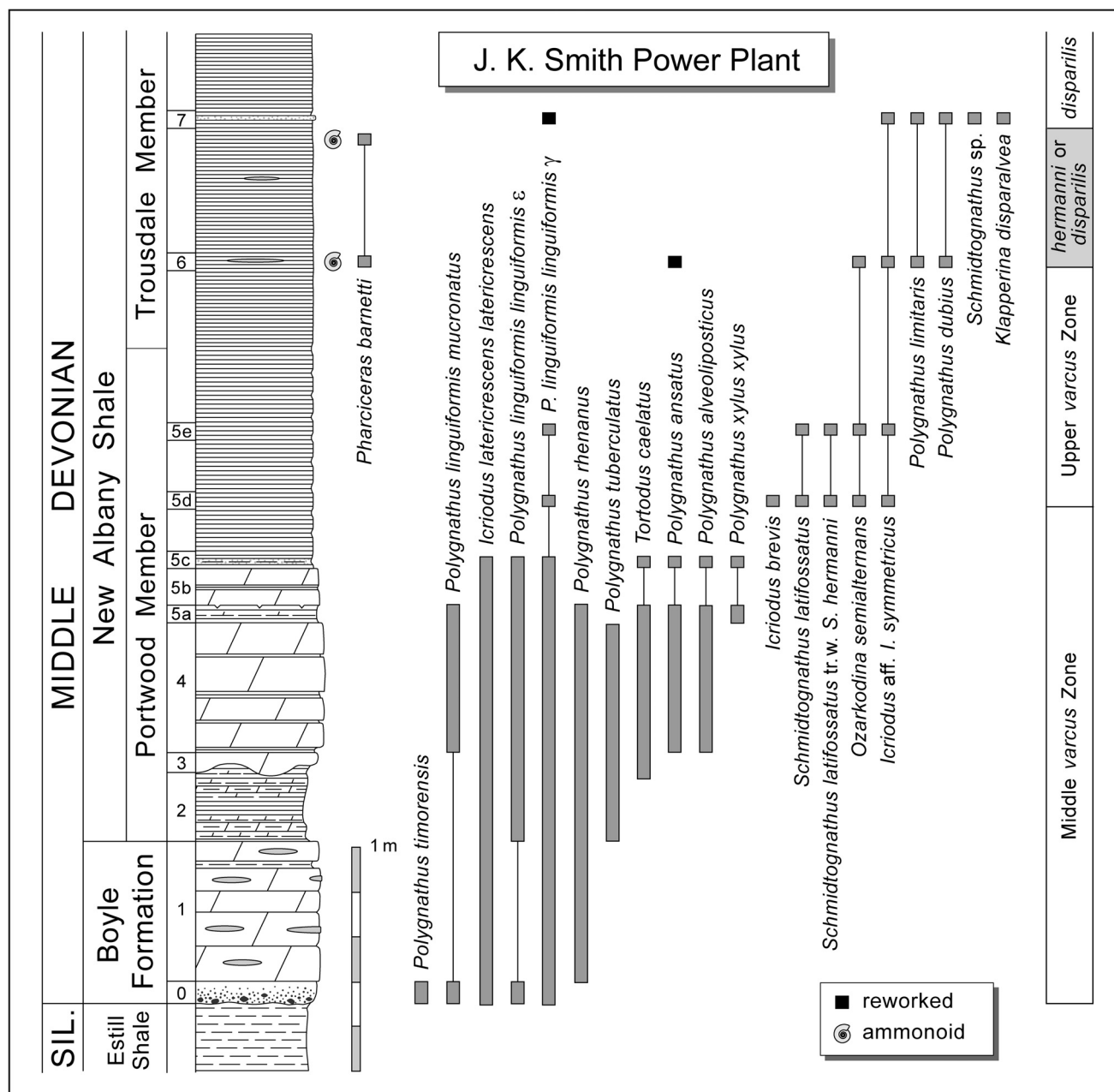
In addition to the North Evans, *Polygnathus tuberculatus* occurs in a white crinoidal limestone-conodont lag bed at the base of the New Albany Shale at the Meshberger Quarry in southern Indiana (Orr and Klapper 1968; Klapper and Johnson 1980, p. 427, table 12). “Within the white limestone and at its base, a few extremely thin streaks of black shale are visible, which suggests interfingering and gradation upward with the characteristic black shale of the New Albany” (Orr and Klapper 1968, p. 1069). The Meshberger lag bed is thus interpreted as the initial deposit of the New Albany and should not be attributed to the underlying Beechwood Member of the North Vernon Limestone as represented by Sandberg, Hasenmueller and Rexroad (1994, fig. 2, their lower and upper encrinurites beds).

Orr and Klapper (1968, p. 1068) listed many species of the Upper *hermanni* Zone from the basal lag bed of the New Albany at Meshberger Quarry, but also such species as *Polygnathus caelatus* [now placed in *Tortodus* = *T. beckmanni* (Bischoff and Ziegler, 1957)], *Icriodus latericrescens latericrescens* Branson and Mehl 1938, *P. varcus*, Stauffer 1940 and *P. tuberculatus* (as *P. bryanti*, see synonymy). All of these latter species are characteristic of the Middle *varcus* Zone. Sandberg, Hasenmueller and Rexroad (1994, p. 233 and fig. 2) indicate that *P. tuberculatus* occurs in the Upper *hermanni* Zone (or Late *hermanni-cristatus* Zone of their usage) in southern Indiana, but such an interpretation does not consider the difficulty of inferring accurate zonal ranges from such complex lag beds as the North Evans and the Meshberger white crinoidal limestone.

In a chart said to represent global ranges, Weary and Harris (1994, p. 209, fig. 6) show the range of *Polygnathus tuberculatus* entering at the lower boundary of the Middle *varcus* Zone, based on their evidence from the Tully at Newry, Pennsylvania. But the higher range through the *hermanni* Zone into the *disparilis* Zone was not based on evidence presented in their paper but rather on a personal communication from C. A. Sandberg. The same doubt expressed about the Sandberg, Hasenmueller and Rexroad (1994) interpretation of the species range above the *varcus* Zone in southern Indiana can be suggested for the Weary and Harris range chart.

SUMMARY ON THE RANGE OF *P. TUBERCULATUS*

The established range of *Polygnathus tuberculatus*, as well as the associated species *Tortodus caelatus* and *Icriodus latericrescens latericrescens*, is not higher than the Middle



TEXT-FIGURE 1

Stratigraphic section, showing distribution of Middle Devonian (Givetian) conodont and ammonoid species in the J. K. Smith Power Plant section, Clark County, Kentucky, from Work, Mason and Klapper (2007, fig. 1). David Work (April 2016) provided a slight modification for this paper making the 'hermanni or disparilis' zones in the right column more readable.

varcus Zone (= *ansatus* Zone in the later terminology of Bultynck 1987). Hypothesized ranges above this zonal level are speculative, appearing to be based on occurrences in lag deposits such as the North Evans Limestone.

TAXONOMY

Illustrated conodont specimens are in the fossil repository of The University of Iowa, Iowa City, under the SUI designation. Conventional orientation terminology used for many years is

also used herein. The equivalence with the terminology proposed by Purnell, Donoghue and Aldridge (2000) is as follows: anterior = ventral, posterior = dorsal, and inner = caudal.

Polygnathus tuberculatus Hinde 1879

Plate 1, figures 1–9

Polygnathus tuberculatus HINDE 1879, p. 366, pl.17, fig. 9 [lectotype selected by Bryant 1921, p. 25; not fig. 10 = a species of *Ancyrodella*, probably *A. recta* Kralick 1994]. – BRYANT 1921, p. 25–26, pl. 12, figs. 7–9.

– BRANSON and MEHL 1933, p. 148, 165, pl. 11, fig. 2 [= reillustration of Hinde 1879, fig. 9], not pl. 11, fig. 9 [= reillustration of Hinde 1879, fig. 10]. – FAY 1952, p. 161 [further synonymy]. – GLENISTER and KLAPPER 1966, p. 799. – ORCHARD 1978, p. 949–950, pl. 113, figs. 1–4 [regarding fig. 4, see text]. – HUDDLE 1981, p. B32, pl. 11, figs. 8–14; pl. 12, figs. 19–21; pl. 13, figs. 9, 10. – WEARY and HARRIS 1994, p. 217–218, figs. 5, 6 [further synonymy]. – SANDBERG, HASENMUELLER and REXROAD 1994, p. 233, 235, fig. 2.42.

Polygnathus bryanti HUDDLE 1934, p. 97–98, pl. 8, figs. 9, 10. – WITTEKINDT 1966, p. 632–633, pl. 1, figs. 22–25 [see text]. – ORR and KLAPPER 1968, p. 1068. – KIRCHGASSER 1970, p. 349, fig. 4.

Diagnosis: Pa elements of *Polygnathus tuberculatus* have a distinctive platform outline, at least two prominent rostral ridges, and a wide and deep groove in the broad keel from the basal pit to the anterior end of the platform.

Discussion: There can be two to four rostral ridges in the anterior part of the platform in the Pa (or P₁) element. The groove in the keel narrows under the free blade. As stated previously in the introductory part of the paper, many of the specimens illustrated in the literature lack preservation of the free blade. But the original specimen of Hinde (1879, pl. 17, fig. 9, as well as those illustrated by Orchard (1978, pl. 113, figs. 1–4) and Huddle (1981, pl. 11, figs. 8–10, pl. 12, figs. 19–21) have a complete free blade as do the Kentucky New Albany specimens herein. Nodes on the platform are typically large and widely spaced.

Specimens from the Rhenish Slate Mountains illustrated by Wittekindt (1966, pl. 1, figs. 23–25) represent a slightly different morphotype of the species. In these, the posterior carina is incurved such that the inner margin projects strongly inward posteriorly. Although the posterior carina is also strongly incurved in the eastern North American morphotype, the inner margin is straight. One of Orchard's specimens (1978, pl. 113, fig. 4) is similar to the Rhenish morphotype. This morphotype is regarded herein as an intraspecific variant of *P. tuberculatus*. Additionally, Wittekindt (1966, pl. 1, fig. 22) illustrated the only immature specimen of the species until now.

Hinde (1879, pl. 17, figs. 9, 10) illustrated two specimens of the species, both embedded in matrix so that only one view of each is available. It is clear from Branson and Mehl's (1933, pl. 11, figs. 2, 9, respectively) re-illustrations that the second specimen is a species of *Ancyrodella*, probably *A. recta*, as stated in the synonymy above. The lectotype (Hinde, 1879, pl. 17, fig. 9) has two prominent rostral ridges and large, widely spaced nodes on the platform. This is well shown by Branson and Mehl (1933, pl. 11, fig. 2; the lectotype was coated in their photo) and by Giles Miller who provided a color photo with the lectotype uncoated. In terms of the rostral ridges and widely spaced nodes, the lectotype is similar to many specimens identified with the species. However, the platform outline of the lectotype is essentially a half-ellipse in shape, and the straight carina does not reach the posterior tip. In these respects, the lectotype differs from most later identified specimens, which have a squarish outline and a complete, strongly incurved carina. Thus, the lectotype does not correspond in all details exactly with later attributed specimens. If *P. tuberculatus* is later regarded as a *nomen dubium* (which I do not recommend), the name *P. bryanti* Huddle 1934, the type specimens of which do match most identified specimens, can be used instead. Also I do not recommend splitting *P. tuberculatus* from *P. bryanti*, because

these cited slight differences are best interpreted as intraspecific variation and the main morphologic features coincide.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of my long-time friend and colleague, Rich Lane. We met for the first time in 1963 when he was an undergraduate student at the University of Illinois and was working as Charlie Collinson's lab assistant at the Illinois State Geological Survey, where I was doing a postdoctoral year with Charlie. Rich was my assistant for several summers at the Amoco Research Center in Tulsa during the 1960s, while he was doing graduate work at the University of Iowa. He then was my first PhD student in his final year of graduate work at Iowa. We were close friends and colleagues for many years thereafter.

Photography was done at the University of Iowa, using the optical Visionary Digital BK Lab System, referenced in Klapper and Kirchgasser (2016, p. 543). Thanks to Giles Miller who in 2009 sent a good optical color photograph of the *Polygnathus tuberculatus* lectotype, from the Natural History Museum of London's type collection. I would like to thank David Work and Charles Mason for collecting and processing the specimens from the Portwood Member of the New Albany Shale of Kentucky and providing the detailed stratigraphic context for the specimens illustrated in this paper. Thanks to W. T. Kirchgasser and T. T. Uyeno for reviews of an earlier version of the manuscript.

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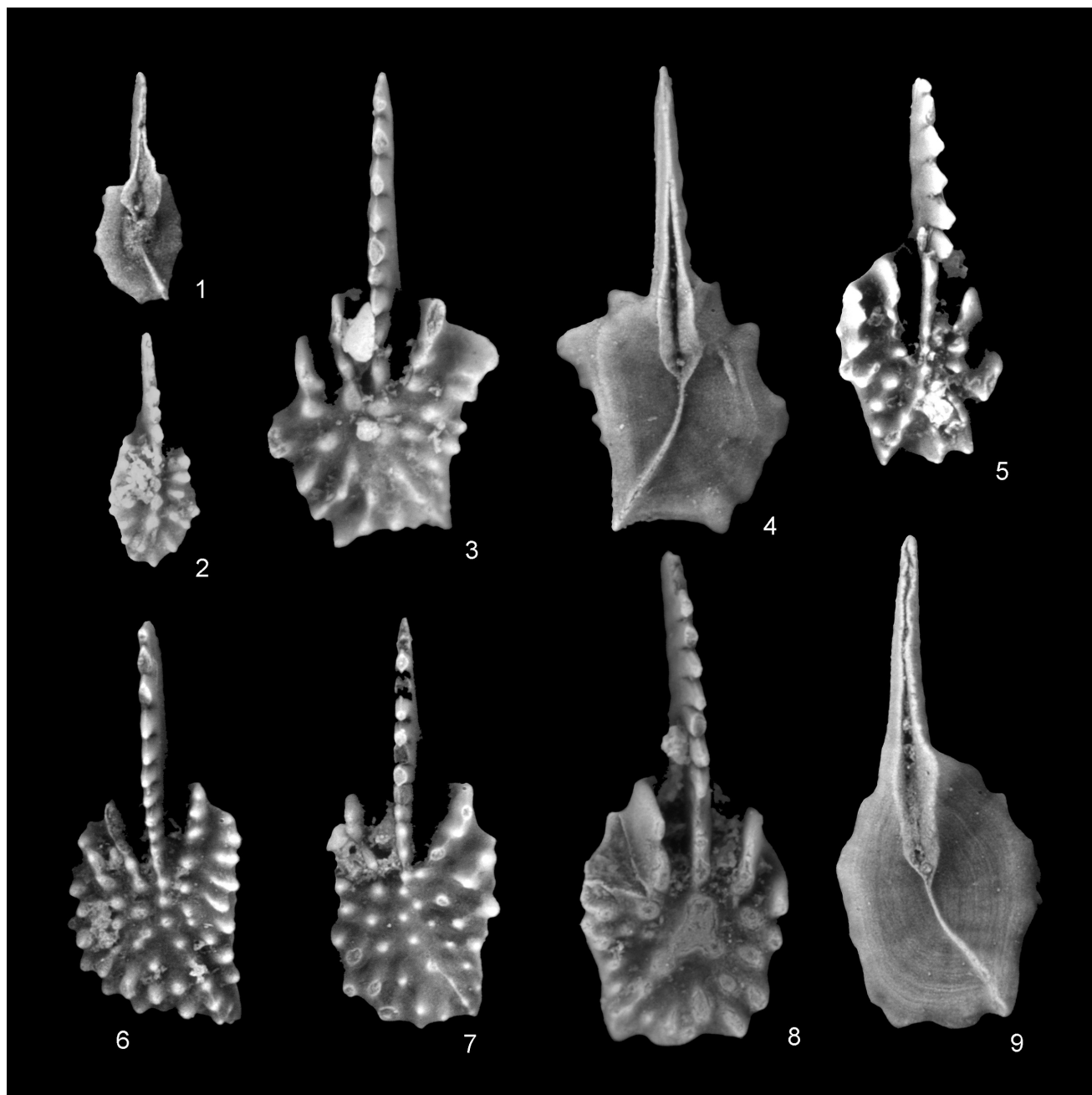


PLATE 1

All magnifications $\sim \times 40$. All are illustrations of Pa (P_1) elements of *Polygnathus tuberculatus* Hinde 1879, and all are from Bed 3 of the Portwood Member of the New Albany Shale in the J. K. Smith Power Plant section, Clark County, Kentucky (Work et al. 2007, fig. 1; text-fig. 1 herein). In figures 4 and 9, note especially the wide and deep groove in the broad keel from the basal pit to the anterior end of the platform. Note the obvious wear on the denticles in the center of the platform in the specimen in figure 8.

1,2 Lower and upper views of SUI 142245.

5-7 Upper views of SUI 142247-142249

3,4 Upper and lower views of SUI 142246

8,9 Upper and lower views of SUI 142250

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