THOUGHTS ON LATE PRAGIAN–EMSIAN POLYGNATHID EVOLUTION: DOCUMENTATION AND DISCUSSION

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Conodont faunas from Australia and central Asia suggest that the genus *Polygnathus* stemmed from an eognathodontan lineage rather than an ozarkodinan lineage. It is proposed that narrow forms of *Eognathodus sulcatus* Philip, 1965 including *E. sulcatus kindlei* Lane *et* Ormiston, 1979 gave rise to *Polygnathus zeravshanicus* (Bardashev *et* Ziegler, 1992) from which the lineage *Polygnathus pireneae–dehiscens–nothoperbonus–inversus–serotinus* was derived. A wide form of *Eognathodus sulcatus*, *E. sulcatus secus* Philip, 1965 was the praecursor of the "*Polygnathus*" *trilinearis–hindei* lineage, one that failed to give rise to further forms.

Key words: conodonts, evolution, Pragian, Emsian, Devonian, Australia, Uzbekistan, Tajikistan.

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INTRODUCTION

As has been summarised elsewhere (e.g., SWEET 1988; MAWSON 1995), two competing theories regarding the derivation of polygnathids have been proposed. KLAPPER and PHILIP (1972), COOPER (1973), and KLAPPER and JOHNSON (1975) suggested evolution of *Polygnathus* from eognathodontans whereas LANE and ORMISTON (1979) argued against this on the grounds that their collections from Alaska failed to include forms intermediate between *Eognathodus sulcatus* and what was thought to be the first true polygnathid, *Polygnathus pireneae* BOERSMA, 1974. SWEET (1988), following LANE and ORMISTON's argument, retained *Eognathodus* in the family Spathognathodontidae and because it appeared that *Polygnathus* was an independent development, referred it to a separate family, the Polygnathidae.

In an attempt to confirm or refute derivation of polygnathids from eognathodontans, collections of conodonts were obtained from several Pragian–early Emsian localities in south-eastern Australia (Fig. 1A, B), especially from Boulder Flat (Fig. 1C), the Tyers and Boola quarries (Fig. 1D) and the Wee Jasper area (Fig. 1E) where it was known that conodonts that might help solve the problem had been previously recorded (e.g., PICKETT 1984; PHILIP 1965). Large collections of conodonts were made from Boola and Tyers quarries, especially from the latter because it is the type locality for *Eognathodus sulcatus*. The fauna from Boulder Flat was described by MAWSON *et al.* (1992); conodonts from Tyers and Boola quarries were documented by MAWSON and TALENT (1994). Type and figured specimens are housed in the invertebrate paleontological collections of the Museum of Victoria (NMV P). The type specimen of *Polygnathus dehiscens dehiscens* PHILIP *et* JACKSON, 1967 is housed in the collections of the Geology Department, University of New England, Armidale.

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THE *EOGNATHODUS* QUESTION

According to PHILIP (1965), CLARK *et al.* (1981) and SWEET (1988), *Eognathodus* is characterized by having, on its upper surface, a double row of nodes with a trough-like depression formed between the rows. On the basis of collections from Central Nevada, USA and the Frankenwald, Germany, MURPHY *et al.* (1981) described six morphotypes of *Eognathodus sulcatus*, three of which (eta, theta and iota morphs) are recognised as "wide" forms (e.g., Pl. 1: 7) and three (kappa, lambda and mu morphs) as "narrow" forms (e.g., Pl. 1: 1–6). A seventh morph was recognised by MAWSON and TALENT (1994) as nu morph but is regarded herein as a subspecies, *E. sulcatus secus* (e.g., Pl. 1: 8–15), (see section on SYSTEMATIC PALEONTOLOGY).

COOPER (1973), in describing *"Spathognathodus" trilinearis* COOPER, 1973 noted that this form is distinguished by having a third row of nodes running along the trough. He also noted the "continuity of the anterior blade with one of the outer rows of nodes on the platform" regarding this as a distinguishing feature of his new species. COOPER (1973) made these observations on just four specimens from Loyola, Victoria. Sampling at Boulder Flat (MAWSON *et al.* 1992) have shown the latter characteristic to be an unstable feature. Illustrations herein (Pl. 2: 2, 3) bear this out. *"S." trilinearis* is therefore referred to *Polygnathus* rather than to *Eognathodus* as suggested by LANE and ORMISTON (1979). The introduction of a 3rd row of denticles is taken as the novel feature distinguishing a polygnathid from an eognathodontan.

Following from the argument above it appears that the specimens bearing three rows of denticles described by BARDASHEV and ZIEGLER (1992) as *Eognathodus trilinearis zeravshanicus* should be considered to be polygnathids. Several specimens from Boulder Flat have three rows of denticles but, being much narrower than *Polygnathus trilinearis* (COOPER, 1973), were identified by MAWSON *et al.* (1992) as *P.* cf. *pireneae* BOERSMA. These are now referred to *P. zeravshanicus* (BARDASHEV and ZIEGLER) (see Pl. 2: 4 and section on SYSTEMATIC PALEONTOLOGY).

DERIVATION OF *POLYGNATHUS*

From the argument developed above, it appears that the most likely line of evolution for the genus *Polygnathus* is via narrow forms of *E. sulcatus* such as *E. sulcatus kindlei* (= *E. sulcatus* lambda morph of MURPHY *et al.* 1981). Wide forms of *E. sulcatus* such as *E. sulcatus secus* gave rise to *"P." trilinearis* from which *"P." hindei* was derived. In Australia, at least, it appears that the latter failed to give rise to a successful lineage.

Circumstantial evidence involving abundance of specimens and localities from which faunas have come, suggests that the lineage from *E. sulcatus sulcatus–E. sulcatus kindlei–P. zeravshanicus–P. pireneae* may have originated on the Gondwana continental margin. Localities which have yielded representatives of the lineage include Australia (e.g., PHILIP 1965; MAWSON and TALENT 1994; WALL *et al.* 1995), Europe (e.g., BOERSMA 1974; AL-RAWI 1977; VALENZUELA-RIOS 1994), and parts of central Asia (MASHKOVA and APEKINA 1980; YOLKIN *et al.* 1989; BARDASHEV and ZIEGLER 1992). The lineage from *P. pireneae* to *P. dehiscens–P. nothoperbonus–P. inversus–P. serotinus* similarly appears to be Gondwana-derived. The last four species have been documented for continuous sections (e.g., MAWSON 1987) and exhibit a "Y-branched" evolutionary pattern wherein the lineage splitting is "characterized by an interval of stratigraphic overlap of the ancestral and descendent species" (KLAPPER and JOHNSON 1975: p. 65). For more than 20 years, this evolutionary sequence of polygnathids has been the basis for the zonation of most of Emsian time and has been able to be recognised with ease globally. An alternative zonal scheme for this interval was recently proposed by YOLKIN *et al.* (1994). They assumed that there is a problem with the type specimen of *P. dehiscens*. MAWSON (1995) has addressed their concerns. The type specimen of *P. dehiscens dehiscens* is re-illustrated herein (Pl. 2: 8) for the reader's convenience.

SYSTEMATIC PALEONTOLOGY

As most of the conodont faunas referred to herein have been documented in earlier papers (MAWSON 1987; MAWSON *et al.* 1992; MAWSON and TALENT 1994; WALL *et al.* 1995), only specimens relevant to the argument proffered have been illustrated and/or otherwise documented.

Genus *Eognathodus* PHILIP, 1965

Remarks. — In the Catalogue of Conodonts, Part III (KLAPPER *in* ZIEGLER ed. 1977), *Eognathodus* was shown to be represented by four species: *E. sulcatus*, *E. secus*, *E. bipennatus*, and *E. trilinearis*. MAWSON *et al.* (1992) reassigned the last of these, *E. trilinearis*, to *Polygnathus*. On the basis of recent extensive collections from Tyers, Victoria, the type locality for *E. sulcatus* and *E. secus*, it now seems logical on grounds of evolutionary pathways, that *E. secus* be considered a subspecies of *E. sulcatus* (see below). With the species *E. bipennatus* (BISCHOFF *et* ZIEGLER, 1957) having been assigned a new genus, *Bipennatus* (MAWSON, 1993), *Eognathodus* became monospecific. Within this species, here is a general tendency for the basal cavity of *E. sulcatus* to decrease in size with time: *E. sulcatus sulcatus* to *E. sulcatus juliae* LANE *et* ORMISTON, 1979 to *E. sulcatus kindlei* or, in terms of MURPHY *et al.* (1981), *E. sulcatus* eta to kappa to mu morphs.

Eognathodus sulcatus sulcatus PHILIP, 1965

1965. *Eognathodus sulcatus* sp. nov.; PHILIP: p. 100; fig. 1; pl. 10: 17, 18, 20, 21, 24, 25.
1981. *Eognathodus sulcatus* PHILIP 1965; MURPHY *et al.*: *q.v.* for morphs and synonymy to 1981.
1991. *Eognathodus sulcatus* PHILIP 1965; BISCHOFF and ARGENT 1991: pp. 454–456; pl. 2: 1–31, pl. 3: 1–13, 15–19.
1991. *Polygnathus pireneae* BOERSMA 1974; BISCHOFF and ARGENT: p. 459; pl. 3: 14.

Remarks. — MAWSON and TALENT (1994) studied conodont faunas from two quarries located in eastern Victoria, the old Tyers Limestone Quarry, the type locality of *E. sulcatus* (PHILIP, 1965), and Boola Quarry approximately 1 km north of Tyers Quarry (Fig. 1B, D), both within the Cooper's Creek Limestone. They reconsidered variation within the species, noting that although the holotype of *E. sulcatus* is large and obviously gerontic compared to the designated paratypes illustrated by PHILIP (1965), workers globally

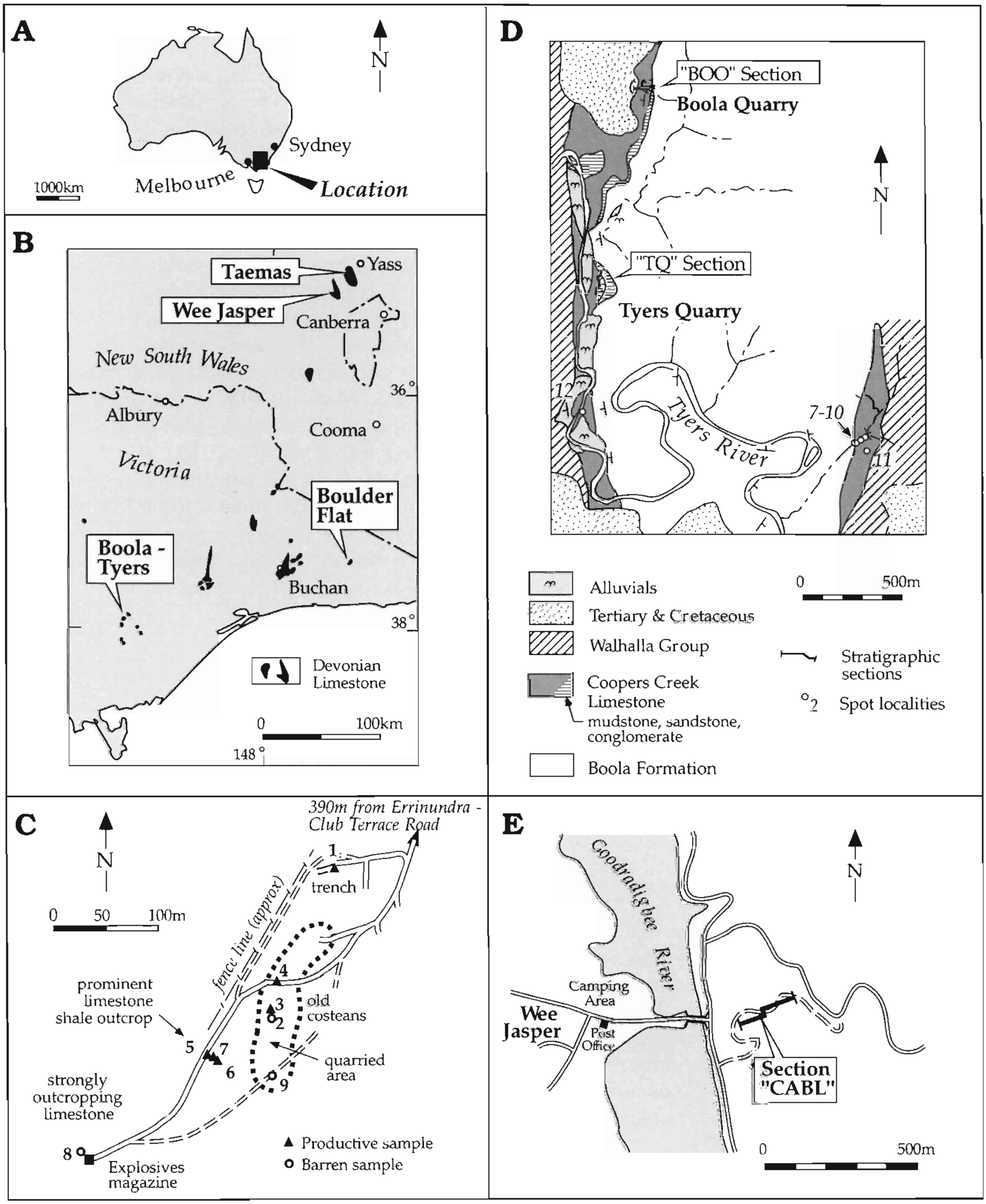

Fig. 1
General map of Australia (**A**) and map of southeast Australia (**B**) showing principal localities mentioned in the text, and details of main collecting sites: Boulder Flat (**C**), the Boola-Tyers area (**D**) and the Wee Jasper area (**E**).

have been able to recognise *E. sulcatus* (e.g., KLAPPER 1969; FÅHRÆUS 1971; MCGREGOR and UYENO 1972; KLAPPER 1977; SAVAGE 1977; SAVAGE *et al.* 1977; AL-RAWI 1977; LANE and ORMISTON 1979; WANG *et al.* 1979; MURPHY *et al.* 1981; SAVAGE and GEHRELS 1984; SCHÖNLAUB 1985; WEDDIGE 1987; MURPHY 1989; SORENTINO 1989 and WILSON 1989). In order to allay concern regarding the relative stratigraphic position of the holotype of *E. sulcatus* and its paratypes expressed in recent years at meetings of the

Subcommission on Devonian Stratigraphy and by individual researchers (e.g., MURPHY 1989), MAWSON and TALENT (1994) published the results of bed-by-bed collection of sequences in the old Tyers and Boola Limestone quarries. From their study of over 400 specimens of *E. sulcatus* classified according to the morphs of MURPHY *et al.* (1981), they were able to pinpoint the boundary between the *sulcatus* and *kindlei* zones in both sections. They also noted that the various morphs could be separated into narrow forms and wide forms. The narrow form tended to retain the 'normal' ornamentation of a parallel row of nodes on the upper surface whereas ornament of the wide form varied greatly, ranging from parallel rows of nodes and ladder-like arrangement of horizontal ridges to irregular arrangement of nodes on either side of a sulcus, or irregular arrangement of nodes without a sulcus. The wide form, presumably because of the geometry involved, showed less reduction in size of the basal cavity.

Based on the investigations of MURPHY *et al.* (1981), MAWSON and TALENT (1994) referred to a seventh form as the nu morph. This morph embraced forms of *E. sulcatus* that had developed a specific pattern of ornament on their upper surface; included in it were the two specimens identified by PHILIP (1965) as *E. secus*. From further deliberations concerning evolution of the polygnathid lineage, it now seems appropriate for this form to be recognised as a subspecies of *E. sulcatus*.

Material. — 38 specimens of eta morph; 65 specimens of theta morph; 98 specimens of iota morph; 21 specimens of kappa morph.

Occurrence. — Coopers Creek Limestone, TQ section at Tyres Quarry and BOO section at Boola Quarry.

Stratigraphic range. — Pragian (*sulcatus* and *kindlei* zones).

Eognathodus sulcatus secus PHILIP, 1965
(Pl. 1: 8–15)

1965. *Eognathodus secus* sp. nov.; PHILIP: pp. 100–101; pl. 10: 22, 23.

1965. *Eognathodus* sp.; PHILIP: p. 102; pl. 10: 19.

1994. *Eognathodus sulcatus* PHILIP nu morph MAWSON and TALENT: p. 55; figs 8I–P, 9A–C.

Emended diagnosis. — A subspecies *E. sulcatus* characterized by a relatively wide basal cavity and variable ornament of the blade ranging from parallel rows of variably sized nodes, ladder-like arrangement of horizontal ridges, irregular arrangement of nodes on either sides of a sulcus, or irregular arrangement of nodes without a sulcus, and, commonly, with nodes additional to the normal two rows.

Remarks. — *E. sulcatus secus* differs from *E. sulcatus sulcatus* in that the denticle pattern is highly variable and extends from the central part of the blade to the posterior end of the unit. MAWSON and TALENT (1994: tables 3–4) show *E. sulcatus secus* (identified as nu on the Tables) appearing close to the boundary between the *sulcatus* Zone and the *kindlei* Zone in both sections (indicated by the incoming of lambda morph in both instances), 2.4 m below the boundary in the Boola Quarry section and 1.8 m above the boundary in the Tyers Quarry section.

Material. — 38 specimens.

Occurrence. — Coopers Creek Limestone, TQ section at Tyres Quarry and BOO section at Boola Quarry.

Stratigraphic range. — Pragian (latest *sulcatus* Zone and *kindlei* Zone).

Genus *Polygnathus* HINDE, 1879
Polygnathus hindei MASHKOVA *et* APEKINA, 1980

1980. *Polygnathus hindei* n. sp. MASHKOVA and APEKINA: p. 136; fig. 2a, b.

1995. *Polygnathus hindei* MASHKOVA *et* APEKINA; WALL *et al.*: pp. 378–379; pl. 2: 6, 7.

(See also for synonymy to 1995).

Remarks. — *P. hindei*, first described from Uzbekistan by MASHKOVA and APEKINA (1980) has also been documented by YOLKIN *et al.* (1989). BARDASHEV and ZIEGLER (1992) illustrated specimens from Tajikistan. Faunas from the Lilydale Limestone Quarry, approximately 40 km north of Melbourne (Fig. 1A) included the first specimens of *P. hindei* (WALL *et al.* 1995) to be documented outside central Asia. BARDASHEV and ZIEGLER (1992) suggested that this form was derived from *"P." trilinearis* and that the former is "the representative of a polygnathid blind branch" (BARDASHEV and ZIEGLER 1992: p. 5). Data gleaned from Australian sections is consistent with this summation.

Material. — Four specimens.

Occurrence. — Lilydale Limestone, at Cave Hill Quarry, Lilydale.

Stratigraphic range. — Late Pragian (*pireneae* Zone).

Polygnathus zeravshanicus (BARDASHEV *et* ZIEGLER, 1992)
(Pl. 2: 4–5)

1992. *Eognathodus trilinearis zeravshanicus* subsp. nov.; BARDASHEV and ZIEGLER: p. 14; pl. 4: 1–6.

1992. *Polygnathus* cf. *pireneae* BOERSMA; MAWSON *et al.*: p. 51; fig. 9H (re-illustrated herein).

Emended diagnosis. — A species of *Polygnathus* with relatively deep, narrow and gently curved platform lacking adcarinal grooves.

Remarks. — *Polygnathus zeravshanicus* differs from *P. pireneae* in having a deeper and almost straight platform. It is suggested that the narrow form, *E. sulcatus kindlei* LANE *et* ORMISTON, 1979 (= *E. sulcatus* lambda morph), gave rise to *P. zeravshanicus* with development centrally of a third row of denticles along the platform.

Material. — Five specimens.

Occurrence. — Boulder Flat Limestone, Boulder Flat (possible equivalent of Buchan Caves Limestone at Buchan).

Stratigraphic range. — Late Pragian (*pireneae* Zone).

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PLATE 1

Eognathodus sulcatus kindlei LANE *et* ORMISTON, 1979

1. Specimen NMV P143160, **Pa** element, upper view, BOO73 loose, × 45.
3. Specimen NMV P143088, **Pa** element, upper view, BOO21, × 75. Originally illustrated in MAWSON and TALENT 1994: fig. 7O.
5. Specimen NMV P143164, **Pa** element, upper view, BOO14.5, × 60.
6. Specimen NMV P143165, **Pa** element, upper view, BOO7.8, × 60.

Eognathodus sulcatus PHILIP kappa morph MURPHY, MATTI *et* WALLISER, 1981 . . 203

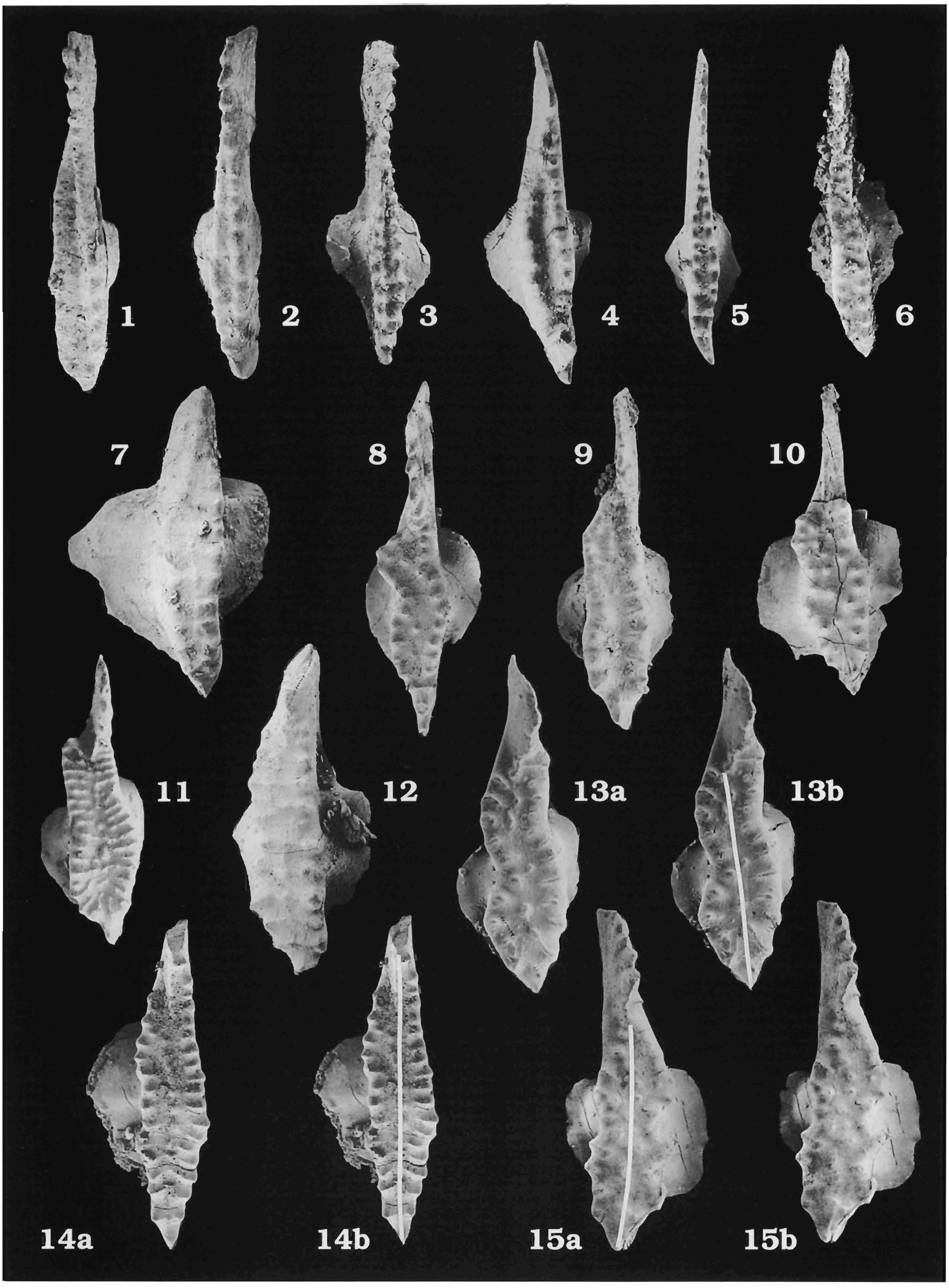
2. Specimen NMV P143161, **Pa** element, upper view, TQ2.0–2.1, × 75.
4. Specimen NMV P143163, **Pa** element, upper view, TQ11.8–11.9, × 30.

Eognathodus sulcatus PHILIP iota morph MURPHY, MATTI *et* WALLISER, 1981 . . . 203

7. Specimen NMV P143171, **Pa** element, upper view, TQ6.8–6.9, × 30.

Eognathodus sulcatus secus PHILIP, 1965 205

8. Specimen NMV P143054, **Pa** element, upper view, BOO6.2, × 60. Originally illustrated in MAWSON and TALENT 1994: fig. 8I.
9. Specimen NMV P143172, **Pa** element, upper view, BOO13.5, × 45.
10. Specimen NMV P143058, **Pa** element, upper view, TQ11.8–11.9, × 45. Originally illustrated in MAWSON and TALENT 1994: fig. 8M.
11. Specimen NMV P143060, **Pa** element, upper view, BOO13.1, × 40. Originally illustrated in MAWSON and TALENT 1994: fig. 8P.
12. Specimen NMV P143166, **Pa** element, upper view, TQ9.1 south, × 45.
13. Specimen NMV P143167, **Pa** element, *a* upper view, *b* upper view – note the marked centre row of denticles forming the blade, BOO13.1, × 45.
14. Specimen NMV P143168, **Pa** element, *a* upper view, *b* upper view – note the marked centre row of denticles forming the blade, TQ9.1 south, × 45.
15. Specimen NMV P143169, **Pa** element, *a* upper view – note the marked centre row of denticles forming the blade, *b* upper view, BOO6.2, × 60.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THOUGHTS ON LATE PRAGIAN–EMSIAN POLYGNATHID EVOLUTION: DOCUMENTATION AND DISCUSSION

PLATE 2

Polygnathus trilinearis (COOPER, 1973) 202

1. Specimen NMV P142101, **Pa** element, *a* upper view, *b* lower view, BY7, × 65. Originally illustrated in MAWSON *et al.* 1992: fig. 9F, G.
2. Specimen NMV P142100, **Pa** element, *a* upper view, *b* upper view – note the marked centre row of denticles continuing to form the blade, BF4, × 45. Originally illustrated in MAWSON *et al.* 1992: fig. 9E.
3. Specimen NMV P142098, **Pa** element, *a* upper view – note the marked centre row of denticles forming the carina and blade, *b* lower view, BF3, × 60. Originally illustrated in MAWSON *et al.* 1992: fig. 9A, B.

Polygnathus zeravshanicus (BARDASHEV *et* ZIEGLER, 1992) 206

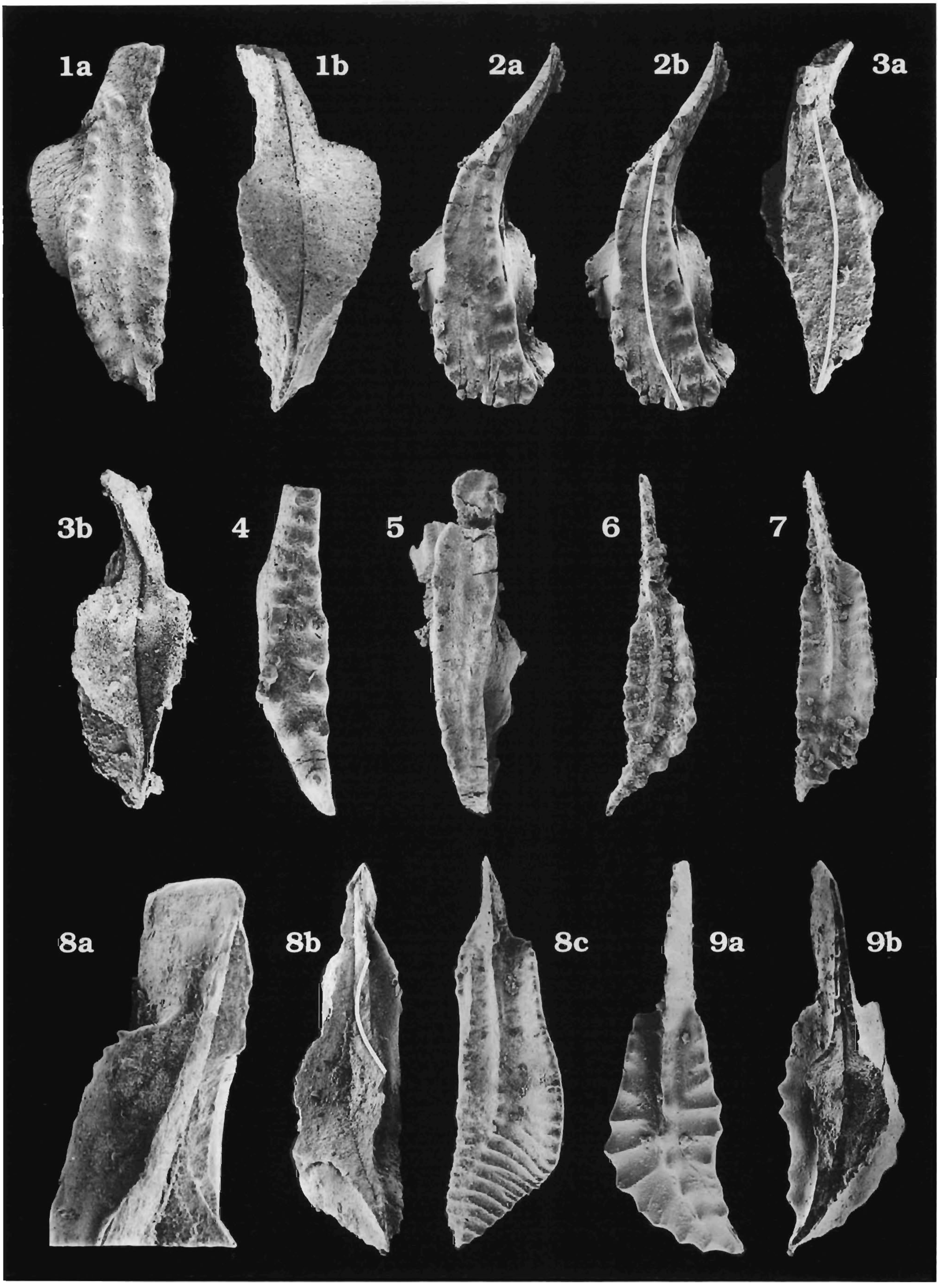
4. Specimen NMV P143170, **Pa** element, transitional, BF4C, × 120.
5. Specimen NMV P142102, **Pa** element, upper view of broken specimen, BF4, × 70. Originally illustrated in MAWSON *et al.* 1992: fig. 9H.

Polygnathus pireneae BOERSMA, 1994

6. Specimen NMV P142080, **Pa** element, upper view, CABL67.6, × 70. Originally illustrated in MAWSON *et al.* 1992: fig. 7B.
7. Specimen NMV P142083, **Pa** element, upper view, CABL75, × 70. Originally illustrated in MAWSON *et al.* 1992: fig. 7F.

Polygnathus dehiscens dehiscens PHILIP *et* JACKSON, 1967 203

8. Specimen F9173/1, **Pa** element, *a* lateral view, *b* lower view, *c* upper view. Note the damaged basal cavity in *8a* and *8b*. From the Cavan Formation in road cutting ca. 350 yards W. of Taemas Bridge, Taemas, southern N.S.W." (PHILIP *et* JACKSON, 1967); *8a* × 100, *8b, 8c* × 55. New photographs of the holotype, originally illustrated in MAWSON and TALENT 1994: fig. 16H–K.
9. Specimen NMV P143159, **Pa** element, *a* upper view, *b* lower view, Loc. 12, × 55. Originally illustrated in MAWSON and TALENT 1994: fig. 16F, G.


1a
1b
2a
2b
3a
3b
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7
8a
8b
8c
9a
9b