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The structure and stratigraphy of *Speonesydrion* from New South Wales, Australia, and the dentition of primitive dipnoans

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with 6 figures

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Abstract: New material of *Speonesydrion iani*, an Early Devonian dipnoan from New South Wales, has provided additional information on the dentition and jaws. Two new partial palates have been found, and X-rays of the parasphenoid shows that the structure is well preserved. The palatal teeth are well worn even in partly grown material, and they do not originate at a growth point, but at a thickening of the palate. More mandibles have been collected, and thin sections have been prepared to allow a discussion of their histology. On the mandible the teeth are clear, and they are much more defined than they are on the palate. The dental heel is variably developed, and grows in phases by thickening of the dentine at the contact with the bone. Dentine forms on the bone at the base of the heel, partly by solution of the bone and the addition of dentine from the pulp canals, but also by direct growth from the pulp canals dorsal to the bone. In the latter case the dentine and bone are in contact, and the two tissues intermingle. The teeth are also formed on a thickened bone and consist of dentine capped with enamel making a crest. Dentine and bone are related as in the heel. We conclude that the teeth in *Speonesydrion* are not homologous with the teeth in other dipnoans, and are formed by a different process involving the aggregation of denticles.

Keywords: Emsian • dipnoan • dental heel • dentition • teeth • evolutionary lineage • gene regulation

Kurzfassung: Neues Material des unterdevonischen Dipnoers *Speonesydrion iani* aus New South Wales bringt neue Information über die Struktur der Kiefer und Zähne. Zwei Teile von Palatina wurden gefunden, und Röntgenaufnahmen zeigen, dass das Parasphenoid gut erhalten ist. Die Palatinum-Zähne sind selbst bei unausgewachsenen Exemplaren schon deutlich abgenutzt, und sie stammen nicht aus einem Wachstums-Zentrum, sondern von einer Verdickung des Palatinums. Einige neue Unterkiefer wurden gefunden, und Dünnschliffe wurden angefertigt zur Untersuchung der Histologie. Die Unterkieferzähne sind sehr viel deutlicher definiert als jene auf dem Palatinum. Die Zahnbasis ist unterschiedlich ausgebildet und wächst in Phasen durch eine Verdickung des Dentins an dem Kontakt zum Knochen. Dentin entsteht auf dem Knochen an der Basis der Zahnbasis zum Teil durch die Auflösung des Knochens und Abscheidung von Dentin aus den Pulpa-Kanälen, zum Teil aber auch durch direktes Wachstum von den Pulpa-Kanälen dorsal des Knochens. Im letzteren Fall sind Knochen und Dentin im Kontakt, und die beiden Gewebe sind vermischt. Die Zähne werden ebenfalls auf verdicktem Knochen gebildet und bestehen aus Dentin mit einer Schmelzkappe, die einen Grat bildet. Dabei sind Dentin und Knochen wie in der Basis miteinander verbunden. Wir kommen daher zu dem Schluss, dass die Zähne von *Speonesydrion* nicht mit jenen anderen Dipnoer homolog sind, sondern durch einen unterschiedlichen Prozess gebildet werden, wobei verschiedene Dentikel aggregiert werden.

Schlüsselwörter: Emsium • Dipnoi • Zahnbasis • Bezahnung • Zähne • Evolutionsreihe • Gen-Regulierung

Introduction

Speonesydrion is a genus of Dipnoi first found near the junction of the Bloomfield and *Receptaculites* Limestones of the Taemas Formation at Wee Jasper. In the accompanying map (Fig. 1) we have used the limestone boundaries mapped by LINDLEY (2002), and our specimens all fall within the top of the Bloomfield Limestone. The genus was established by CAMPBELL & BARWICK (1983) using several specimens, mainly man-

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28. Supra-acetabular area smooth (0) with buttress (1) or with anterior crest-flange (2) (modified from PARRISH 1993).
29. Acetabulum imperforate (0) or with incipient perforation (1) (modified from GAUTHIER 1986).
30. 4th trochanter crest-like (0) knob-like (1) or inverted/shelf-like (2) (modified from GAUTHIER 1986).
31. Pubis length subequal to ischium (0) longer than ischium (1) (BENTON & CLARK 1988).
32. Pubic foot absent (0) or present (1) (GAUTHIER 1986).
33. Osteoderms present (0) absent (1) (GAUTHIER 1986).
34. Femur head inline with shaft (0) or offset from shaft (1) (GAUTHIER 1986; CLARK et al. 2000).

Appendix 2

Abbreviations

a.na	articulation for nasal
a.pal	articulation for palatine
a.pmx	articulation for premaxilla
ac	acetabulum
antf	antorbital fossa
a.par	accessory parapophysis
bf	brevis fossa
dia	diapophysis
f	foramen
g	groove
idp	interdental plate
ip	ischial process
ipt	ischial pit
lc	lateral crest
mf	mental foramina
ns	neural spine
of	obturator foramen
pal.p	palatal process
pap	preacetabular process
par	parapophysis
pb	pubic boot
poap	postacetabular process
pp	pubic process
s	sacral vertebra
sac	supra-acetabular crest
sr	sacral rib

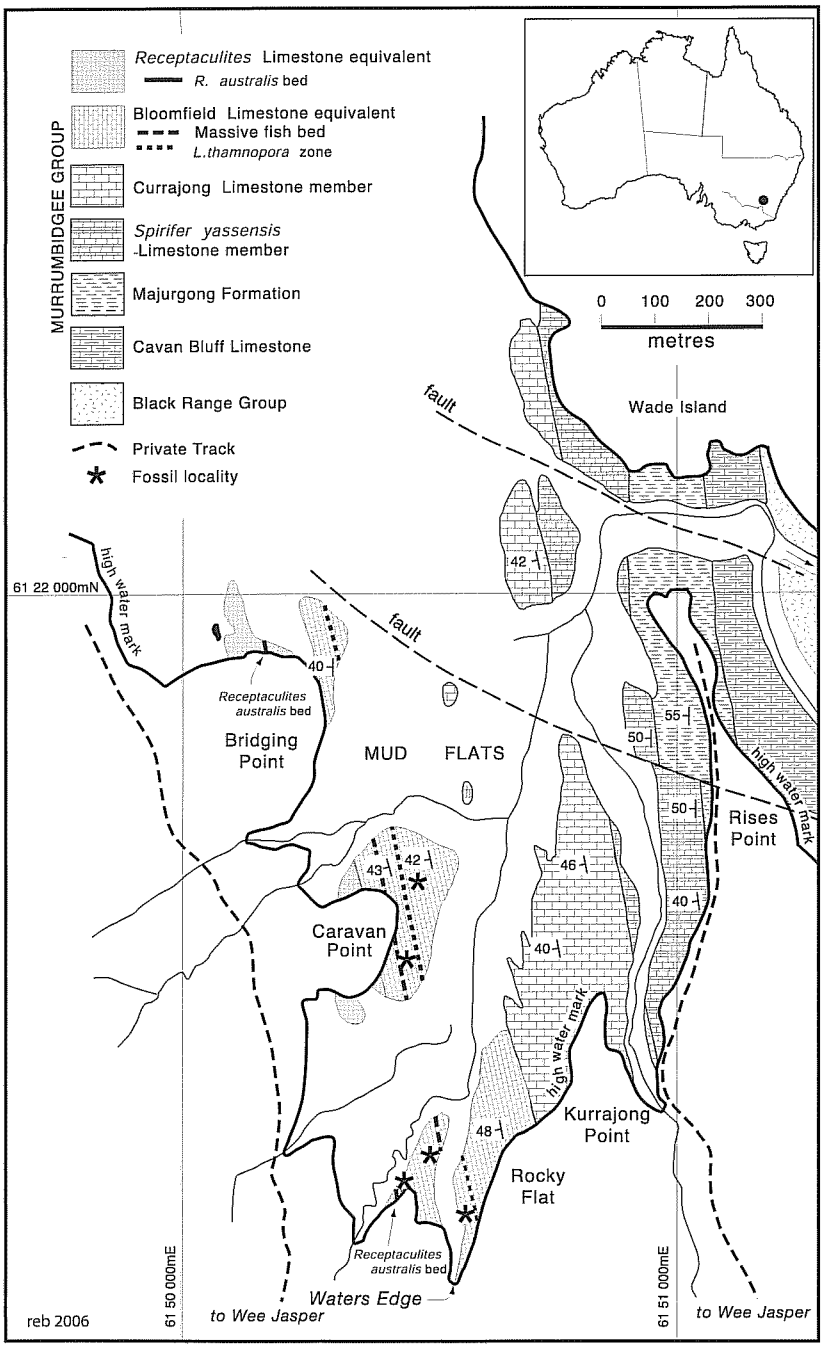

Fig. 1. Map of the area at Wee Jasper from which the specimens were collected (map modified from LINDLEY 2002). In this map the *Receptaculites australis* bed is marked, and the boundary between the Bloomfield and the *Receptaculites* limestones is placed at a slightly higher position than previously. Our specimens were previously labeled as from the *Receptaculites* Limestone or the top of the Bloomfield Limestone, whereas now they may be from the top of the Bloomfield Limestone.

dibles. Thin sections of the tooth plates were described, especially showing the heel (cushion) of dentine on the mandible in vertical and horizontal sections. Recent collecting at the type locality has produced more individuals, almost entirely mandibles, and two posterior palates. Another fragmentary skull roof showing the snout has been found at the same horizon further south. All except the last mentioned specimen come from the same stratigraphic unit as the holotype. The roof and palate come from the same horizon further to the north.

Conodont dating of the sequence by PEDDER et al. (1970) and MAWSON et al. (1992), shows that it comes from the *perbonus-gronbergi* Zone of the Emsian.

Material

All of the specimens used for the descriptions below are numbered with the Australian National University Collection Numbers. Most come from the Caravan Point area (Fig. 1) and to the area further south. ANU35646 comes from the area north of the map at Cave Island. ANU 49340 is on loan from the collection of Ian and Helen Cathles, of 'Cookbundoon', Wee Jasper, and comes from the area south of the map.

ANU 36520, mandible. ANU 35646, palate. ANU 35647, mandible

ANU 35648, mandible. ANU 35649, heel of namdible. ANU 49336, partial palate.

ANU 49337, partial mandible. ANU 49340, snout of skull. ANU 49369, partial palate.

ANU 60031, mandible.

Previous discussion of relationships

There is confusion regarding the genus *Speonesydrion*. SMITH (1988), has formally recognised three lineages of Early Devonian dentitions – (1) those based on tooth plates; (2) on denticulation scattered over bone; (3) and those on dentine plates formed from the retention of fused marginal denticles. These were then discussed in terms of the origin of each type. AHLBERG, SMITH & JOHANSON (2006: 331) have supported this view as follows '....all the major types of lungfish dentitions had appeared by the end of the Early Devonian...'. In terms of the current thinking at that time, SMITH (1988) attempted to understand which of these was the primitive type. SMITH (1988: 192) concluded that *Speonesydrion* represents, 'the primitive condition for all genera with radiate tooth plates, as suggested by CAMPBELL & BARWICK (1984), and may also lead to the type of dentition in *Holodipterus*. It is also probable that it is also primitive for those with dentine plates, such as *Dipnorhynchus suessmilchi,* although CAMPBELL & BARWICK (1984: 46) do not think this is true'. When this was written, little was known of the histology of the heel and the teeth of *Speonesydrion*. The present paper uses histological data based on new sections. Also, we do not consider that there is a primitive condition for all the types she recognized, but rather that they have arisen as a result of gene regulation, and they are independent entities. Presumably they arose from some sarcopterygian, the nature of which we cannot specify.

SCHULTZE (2001) in a paper on the genus *Melanognathus*, refers to *Speonesydrion* as a synonym of *Dipnorhynchus*. He concluded that *Speonesydrion iani* (2001: 786) 'represents a deviation from an early ontogenetic state of *Dipnorhynchus* ('transformation' of dentine plate into a tooth plate in ontogeny)'. No evidence for this view was presented. The data now available to us requires this view be reinterpreted.

Systematic palaeontology

Class Osteichthyes HUXLEY, 1880
Subslass Sarcopterygii ROMER, 1955
Infaclass Dipnoi MÜLLER, 1845
Family Speonesydrionidae CAMPBELL & BARWICK, 1990

Speonesydrion CAMPBELL & BARWICK, 1983

Type locality: Wee Jasper, New SouthWales.
Type stratum: Bloomfield Limestone, *perbonus-gronbergi* Zone, Emsian.

Diagnosis: Dipnoan with a broad snout; bones "I" joining posterior to "B"; lateral lines not connected between "X" and "K"; teeth present on four or five rows on the pterygoids; heel on the pterygoids becomes prominent in the adults; teeth in adults poorly shown because of wear and the expansion of the heel; parasphenoid extends ca. half the length of the pterygoids; hypophysial pit ca. one third the length of the pterygoids. Mandible with broad dentary; on the ventral surface, cosmine forms a continuous boundary between the dentary and the infradentaries; four infradentaries; anterior furrow well developed and containing many foramina connected with canals in the Meckelian cavity; pair of pits between posterior of the dentary and the prearticular; heel present from early growth stages; adults with expanded dental heel, showing several periods of lateral growth; teeth variable- some as simple cones and others made up of a group of denticles; valleys between the rows of teeth and in the lingual space filled with irregular rows of linear denticles; glenoid fossa small; multiple tubules in the median cavity and beneath the anterior cavity.

Discussion: This genus is easily separated from *Dipnorhynchus* by its weaker ossification, the structure of the teeth, the presence of the dental heel increasing in size during the growth of the dental plate; the breadth of the snout and the dentary; the presence of the two pits posterior to the dentary; the weakness of the glenoid; the opening of the buccohypophysial pit in a more anterior position; the parasphenoid posteriorly.

The features of *Speonesydrion* that recall the structure of *Dipnorhynchus* are the skull roof patterns of bone "I" and the lateral lines between "X" and "K", the abundance of small bones anterior to "I", the narrow dentine canals found in the heel of the mandible (CAMPBELL & BARWICK 1983: fig. 8), and the overlap of the palatoquadrate onto the process on the lateral part of the pterygoids.

Speonesydrion is also referred to by REISZ et al. (2004) in the discussion of a Russian specimen of *Ichnomylax*. They place this latter genus in the Speonesydrionidae, because *Ichnomylax* and *Speonesydrion* have a similar heel on the mandibular tooth plate, similar teeth in short rows, small denticles in the lingual furrow and between the tooth rows, and judging from the sections figured by REISZ et al., the heel and the teeth are composed of closely spaced parallel pulp canals. The types of the two genera come from Early Devonian rocks from southeastern Australia.

Description:

Skulls

The skull of *Speonesydrion* is poorly represented in our material (CAMPBELL & BARWICK 1984). The specimen ANU35646 was highly distorted, but the palate is available. The margin of the specimen shows the indentations where the original teeth met the edge of the palate. Most of the teeth have been worn down, but the right side of the specimen has one tooth, on which the enamel is still preserved. The central part of the palate has a ridge on

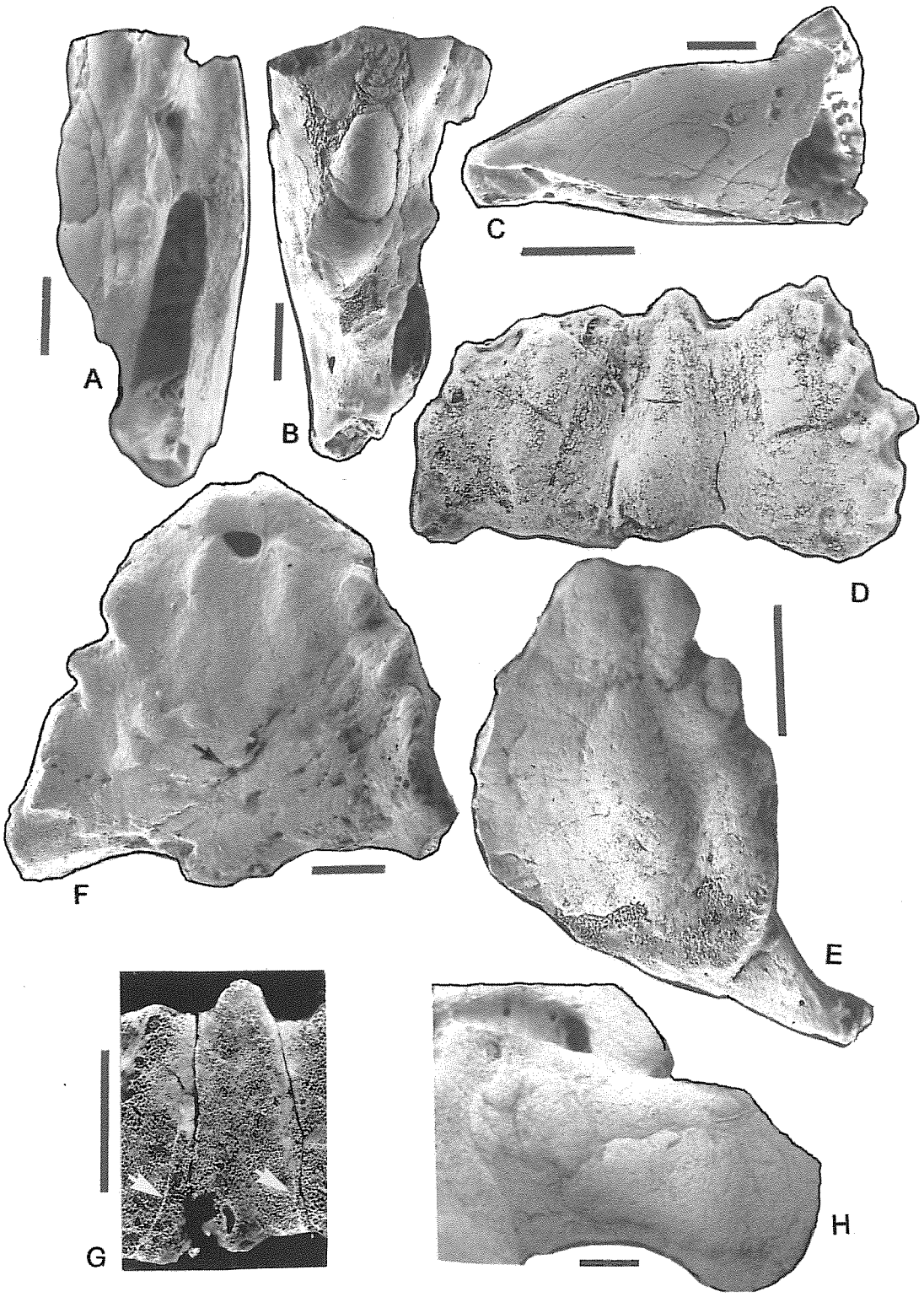

Fig. 2. *Speonesydrion iani.* **A–C**: Dorsal, medial, and lateral views of part of a mandible (ANU 49337). Note shape of the heel and the remnants of the lateral teeth in (A), and the structure of the heel in (B). (C) Note the foramina at the posterior of the mandible showing the surangular, angular and part of the postsplenial, and the Westoll Lines. **D, G**: Palate ANU 49338. D. Posterior view with teeth showing on the right side of the figure. Anterior end of the parasphenoid rounded, and the dentine in the teeth on the right well displayed. G. A deep X-ray of same showing the boundary between the pterygoid and the parasphenoid. The left boundary is clearer than the right which lies to the left of the crack. The fine structure of the dentine is shown up. White arrows indicate the boundaries of the parasphenoid. **E**: Ventral view of another palate (ANU 49336) showing the thickening medial to the teeth and denticles posteriorly. **F**: Original palate showing the thickening of the palatal plates, ANU 35646. Arrow shows the buccohypophysial opening. **H**: Posterior view of ANU 48677 showing the heel thickening, the almost complete loss of the teeth, and the large growths towards the mid-line. – Scales: A–H = 10 mm.

either side of the midline, and other areas of swelling where the palate is thickened (Fig. 2F). The posterior end of the specimen has part of the extremity of the parasphenoid preserved. Its surface is covered with dentine and it does not fall away from the level of the palate as does the parasphenoid of *Dipnorhynchus*. Thickening shows that the parasphenoid extends further posteriorly. The hypophysial pit lies at a posterior position, ca. 4 cm from the anterior boundary of the palate Fig. 2F (see also CAMPBELL & BARWICK 1984: fig. 9).

A second specimen (Fig. 2E), the left posterior end of a palate (ANU 49336) was found at the type locality. The articulation for the mandible is preserved, and it lies a little above the level of the palatal dentine. The lateral margin of the palate is preserved and is marked in places by small beads of enamel-covered dentine, indicating the growing edge of the specimen. Posteriorly, the dentine of the palate passes irregularly into a surface covered with small denticles. Remnants of the denticles can still be seen in the dentine that has grown over isolated denticles. A ridge medial to the tooth row has a thickening of the palate. The dorsal surface is made of exposed bone, but the edge of the parasphenoid is present. It is comparable with the parasphenoid on ANU 49339 (Fig. 2G) described below. Because the dentine on the palate covers the boundary between the parasphenoid and the pterygoid, the boundary only appears on the deeper sections of the bone.

A third posterior palate is also known from the top of the Bloomfield Limestone adjacent to the type locality (Figs. 2D, G). This individual (ANU49339) is smaller than either of the other two palates we have. It is approximately 45 mm across the mandibular articulation, which has had to be reconstructed. Margins of the palate are moderately preserved on the left side (Fig. 2D). The posterior lateral corner has a worn irregular group of teeth, and anterior to those there is a row of three teeth in sequence and one off centre. Three rows of teeth lie anterior to this row, the median one of which is inserted between the other two. The more anterior tooth rows also have separate teeth, but the marginal ones have been lost during preparation. Medially the tooth rows fade away against an elongate ridge of dentine, and medial to that ridge is a slight depression with weak fine denticles. The palate has a ridge along the midline over the position of the parasphenoid, and cracks appear on the specimen, but these are not the edges of the parasphenoid. The X-ray (Fig. 2G) shows the boundary of the parasphenoid as well as the crack that apparently borders the structure. Compare this with DENISON (1968: fig. 8) for *Uranolophus*. The anterior end of the parasphenoid is sub-rounded.

Finally, supplementing the material from the distorted snout (CAMPBELL & BARWICK 1984: fig. 11), a new snout of a specimen has been found at the same horizon further south, but at the same stratigraphic level (Figs. 3E, F). The external surface is smooth and does not have the large mass of bone with numerous large perforations as does *Dipnorhynchus suessmilchi*. The specimen has no thickening of the rostral plate such as occurs in *Dipnorhynchus*, and there is no sharp boundary between the rostral area and the separate roofing bones. The nerve canals that we interpret as carrying the ramus ophthalmicus NVII, and the ramus ophthalmicus profundus NV, are well preserved. One set of nerves reach the edge of the external naris, and also under the medial overhanging ridge. This is presumably the ophthalmicus profundus NV nerve. The second nerve is more dorsal in position, turns medially and makes a ramifying set of branching tubules towards the dermal bones. This is the ophthalmicus NVII nerve. These two sets are not completely separate but have many joining tubules. A small fragment of the roof of the nasal capsules is still preserved and it shows openings for some of the tubules into the bone.

Mandibles

Most of our new material is of mandibles, and we now have some ten specimens. The teeth are obvious on most specimens as is the heel of the plate. The teeth fall between three extremes (1) smooth cones (Fig. 4A) which are buttressed by small denticles which make up the tooth ridge, but even here there is some evidence of duplication (CAMPBELL & BARWICK 1984: fig. 30); or (2) irregular cones made up of small denticles, one or more of which are larger than the others (Figs. 4B–D); or (3) rarely, almost completely removed teeth as the specimens reach the most adult stage (Fig. 2H). Type (1) is found in relatively young specimens; type (2) is found in young adult specimens; and type (3) is occasionally in the most adult specimens. REISZ et al. (2004: 23) have concluded that 'denticles as identified in Paleozoic dipnoans could not give rise to teeth developmentally or ontogenetically'. REIF (1982) concluded that denticles were formed 'superficially, directly at the epithelium/mesenchyme interface, without a deep invagination', and that teeth are 'formed in a deep epidermal invagination called the dental lamina'. We accept this view, and in the following we attempt to apply it to *Speonesydrion*.

There are four rows of teeth, or three in some specimens. Those with three rows often have an incipient fourth row posteriorly. The second row from the midline is continued forward towards the dentary on which there are compound tooth-like structures (Figs. 4D, E). The teeth are not always clear because wear has removed some of the structures, and the heel of the plate has expanded to cover the old teeth (Figs. 2A, B, 4C).

CAMPBELL & BARWICK (1991) have illustrated the composite form of some of these teeth. REISZ et al. (2004: 22–23) correctly comment that teeth and denticles are of different origin (following the work of REIF), and teeth cannot be derived from an accumulation of denticles as suggested by CAMPBELL & BARWICK (1995: 22). The evidence from *Speonesydrion* does not support the view of REISZ et al. Specimen ANU60031 (Fig. 4D), and ANU 35848 (Fig. 4A) have both tooth plates complete (CAMPBELL & BARWICK 1984: fig. 30).

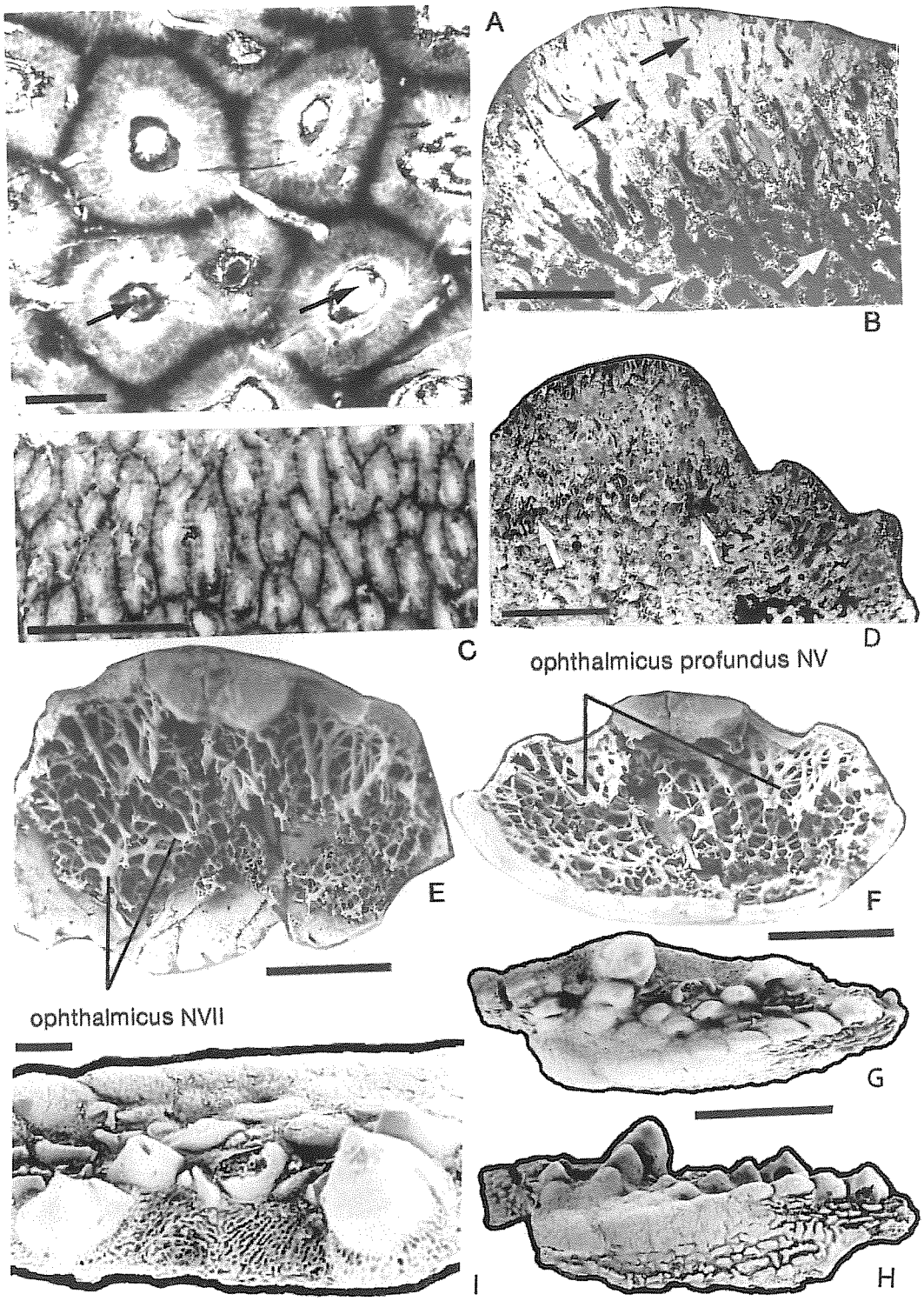

Fig. 3. *Speonesydrion iani.* **A**: Cross section of the dentine in the heel (ANU 35649). The white bands around the arrowed pulp canals are surrounded by white tissue called circumpulpal dentine, and around that are interstitial dentine with dentine tubules. These two layers are shown in vertical section in Fig. 5D. The dentine tubules are clear. **B**: Vertical section of a tooth of the same specimen with bone at the base and dentine at the top. Dentine (black arrows) and bone (white arrows). **C**: Oblique section of a heel (ANU 35649). **D**: Partially oblique section of a tooth with two denticles attached on the right. Dentine at the crest with some indication of a partial pulp cavity present shown by white arrows. **E, F**: Ventral and posteroventral views of the snout showing the large nerves of the ramus ophthalmicus NVII, and the entrance of the ramus ophthalmicus profundus NV. Note the connections between the two sets. (ANU 49340). **G–I**: Small mandible (ANU 73000) (G) dorsal, (H) median, and (I) enlarged lateral views. In I note the partly destroyed median row in which the marginal tooth has fallen out exposing the bone structure where it was attached. Note also the bone in the base of the second tooth in that row. Large teeth at each end double. – Scales: A = 0.1 mm, B, D, I = 1 mm, C = 0.5 mm, E, F = 10 mm, G, H = 5 mm.

Perhaps the most convincing specimen (Figs. 4B, C) shows the central part of the tooth made of small entities which must have been deposited first, surrounded by five smaller entities which must have been deposited on the flanks of the first group. This pattern does not agree with the concept that teeth are formed in a deep dental lamina, and should not be termed teeth. For the present we continue to use that term with reservations. The second row of teeth on the same specimen also shows a composite arrangement, and between these rows denticles like those on the teeth have been preserved. We conclude that the entities listed above are in fact denticles. A similar arrangement is illustrated on Fig. 4D.

It now becomes apparent that we should consider the possibility that there is more than one kind of denticle, and more than one kind of tooth. There is no doubt that the denticles on *Holodipterus* and *Griphognathus* are in fact true denticles, but the large denticle group on *Speonesydrion* form the large end of a series which are small in the furrows and larger on the lateral edges of the teeth. This has been illustrated previously (CAMPBELL & BARWICK 1984: figs. 29, 30, 1995: figs. 7C–E). The teeth in *Speonesydrion* have an enamel cover, and superficially appear as in normal teeth (CAMPBELL & BARWICK 1984: fig. 30). But there are large denticles at the margin of the tooth plate, and this pattern does not occur on the other genera. What is more, as we have indicated above, the teeth in *Speonesydrion* do not form in a deep epidermal invagination, but sit on a ridge of bone with the dentine connected to the underlying bone (Figs. 3B, D). A new juvenile specimen (ANU73000, Figs. 3G–I) supports this view. A poorly developed tooth row has lost the last tooth and exposed the same basal tissue as the surrounding bone. In this row a broken tooth shows the core made of broken bone. The large teeth at the ends of the of the rows are made of two entities. We conclude that the teeth in *Speonesydrion* are of a different type from other dipnoan teeth, and that they are partly formed by a single swelling and partly from the aggregation of special denticles of a kind not found in other dipnoans. In this sense we are in agreement with REISZ et al. on the usage of the word teeth.

On Fig. 4C, the second row of teeth from the midline is aligned with the end of the dentary, and the structure of that tissue is significant in interpreting the teeth in the prearticulars. Specimen ANU60031 (Figs. 4D, E) is the best individual. The ends of the dentary are worn naturally, and so some of the detail is lost. Small denticles lie on the end of the dentary, the largest ones posteriorly (Figs. 4C–E), and the smallest ones making up lateral denticles. The surfaces of these denticles are covered with shiny tissue of enamel. On both sides of the specimen these denticles lie directly on bone. In other words, the tooth bearing capacity is carried forwards onto the dentary where composite teeth are developed.

The heel of the plate is very variable – so variable that specimens at the extremities of the range could be regarded as members of different species. The smallest specimen (Figs. 3G, H) shows that the teeth do not reach the margin of the plate, and a small heel is present. Other small individuals have lower heels that stand higher than the surrounding tissue (Fig. 4A). Surrounding these high areas are the lower levels of tissue, which were just beginning to grow. Some of these have small denticles in position and these are being overgrown by heel tissue. Small tubercles surrounding the heel are gradually engulfed by the expanding heel tissue.

One fragmentary adult specimen has been examined by serial X-rays. This specimen has two, possibly three, large central raised areas in the heel (ANU49337), surrounded by a much lower inflated area, and even more laterally by worn down teeth (Figs. 2A, B). Obviously the heel grows by phasic growth. Within the central area, the posterior unit is more highly raised and is more rounded. X-rays show that this was the second phase of deposition. Internally the surface of the Meckelian cavity is smooth and shows no sign of thickening, demonstrating that the thickening of the surface layers takes place by deposition of dentine at the bone-dentine boundary, thus pushing the external surface outwards. The X-rays show that the largest central body is more or less conical shape, and the surface slightly overlaps the anterior swelling. Anteriorly and anteromedially the heel terminates in a mass of denticles, the anterior ones being worn and the medial ones still having a thin layer of enamel on the surface because they were out of the bite.

On the same specimen, lateral to this major central heel, is a band of slightly raised material that is joined to the posterior part of the central area, and is part of the same growth phase. This lies on bone, indicating that it grew from tissue in the bone and displaced the teeth which were first formed in those areas. Its growth is clear as it has a sharp boundary on its outer edge (Figs. 2A, B).

Two adult specimens have the teeth removed by the large outgrowth of the heel, and this gives a most remarkable appearance. Specimen ANU48677 has lost most of its teeth, but the edge of the teeth are still present on the left side. It has all the characters of *Speonesydrion*. A reduced illustration of the specimen is given in Fig. 2H, and this shows the extent of the heel. This range of variation within the species will cause difficulties even though they show continuous variation. As all the specimens come from the same horizon, and some of them come from the same locality, we are sure that it is within species variation.

Histology

The prearticular plate provides the best specimens that show the histology. Thin sections of three specimens have been made, coated with gold, and examined by SEM. Of course the sections do not all run along the tooth bearing ridges, and so they show specimens not at the same level of development, and they show the histology in the valleys and the ridges

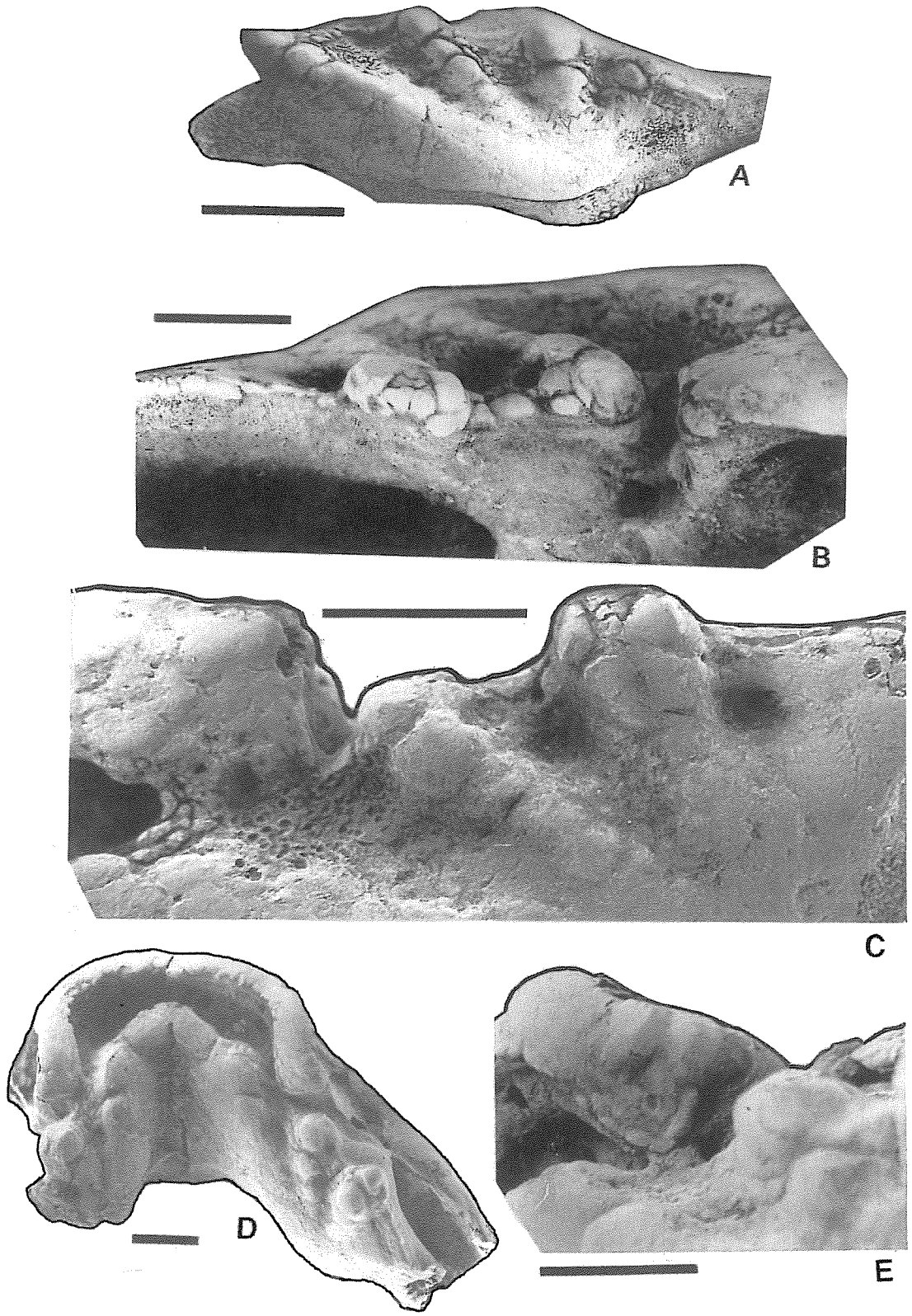

Fig. 4. *Speonesydrion iani.* **A**: The right side of a small mandible showing the multiplicity of small denticles between the tooth rows, and enlarged denticles at the margins (ANU 35648). Teeth are of single units but notice the large denticles between the teeth (see also CAMPBELL & BARWICK 1991: pl. 3 figs. A–D). **B, C**: A single specimen of a large individual showing the tooth pattern (ANU 35647); B. Lateral view showing the composite nature of the tooth in one position and the large denticles adjacent to the other tooth. C. The same individual from a median point of view showing the worn down teeth, and the larger teeth on the dentary. The second tooth in the right side is divided into two with the edge of the enamel showing. **D**: Dorsal view of ANU 60031. Note the composite nature of the teeth on both sides of the specimen. **E**: More oblique view of the same specimen again showing the composite teeth and the tooth-like structure of the posterior of the dentary. – Scales: A–E = 10 mm.

The published sections (CAMPBELL & BARWICK 1983: figs. 12A–C) were produced by an optical microscope, and they show long thin vertical pulp canals overlying the bone in the heel. The horizontal section of the heel shows bounded units of dentine with lighter coloured layer around the pulp canals, referred to as the circumpulpal layer, surrounded by darker coloured layer, referred to as the interstitial layer. This differentiation is not always clear, but the vertical section on Fig. 5D shows bands of material around the pulp canals indicating that the division is real. The nomenclature of the bands as interstitial and circumpulpal layers are topographically correct. Dentine tubules lie within the bands as very fine branching canals, which are now filled with sediment (Fig. 3A).

The heel is a distinct mass which is quite thick in the centre and fades out laterally. Our sections of this specimen (ANU36549), include one through the tooth ridge (Fig. 5A) and obliquely through the marginal tooth (Fig. 6C); others through the heel and partly along the tooth ridges with relics of old teeth showing poorly developed dentine (Fig. 6A); and another obliquely along a tooth ridge showing the relics of worn down teeth (Fig. 6B). These sections have been examined by SEM and optically. The section in Figs. 6A, B includes the edge of the tooth ridge lying on bone. This indicates that the spaces between the tooth rows are partly floored by bone. This is what we would expect from an examination of the hand specimens in which the bone in the valleys is covered with denticles. The heel is made of dentine which is easily distinguished because it follows the parallel pulp canals standing vertically, and the bone contains many osteocyte spaces and forms around irregular trabeculae.

The vertical sections show the units of dentine surrounding the pulp canals; some of these units show weak differentiation into inner and outer layers. On both optical and SEM sections the bone is obvious because it contains many osteocyte spaces, and the dentine has no open spaces. Despite the difference between the two tissues, the boundary between them is well marked. In some places the layers of bone and the layers of dentine are directly in contact without any sharp boundary changes (Figs. 5C, 6B). What is more, in some specimens the layers of bone and the dentine seem to grade into one another (Figs. 5D, 6D). The trabeculae in the bone have irregular multiple shapes, whereas the dentine layers are in vertical lines between the closely spaced pulp canals. These features make the generation of dentine difficult to understand.

Further along the junction, the same specimens show that there is no continuity between the dentine and the bone. On Fig. 5A and part of Fig. 6A there is little continuity between the bone and the dentine. We conclude that the gap appears in some places where resorption has taken place. In other places the bone and the dentine are in direct contact (Figs. 5C, D, 6D).

The following points have to be taken into account in developing an hypothesis: (1) New dentine is added to the heel at its base. (2) The dentine must be deposited from cells in the pulp canals. (3) The change in shape between trabeculae in the bone layers and the columns in the dentine layers requires a deposition of new layers in the dentine independent of the shape of trabeculae in the bone. (4) The continuity between the bone layers and the dentine layers in an intermingled way requires the addition of dentine from the pulp canals onto bone tissue.

These requirements indicate there are two methods of dentine deposition. (1) The gap between the dentine and the bone indicates that the bone may be removed by solution and dentine deposited in the pulp canals dorsal to it. (2) Elsewhere the intermingled contact between the bone and the dentine (Fig. 5D) indicates that the dentine was deposited from the cells in the pulp canals against the bone which was partly removed. The shape of the bone layers has no control on the shape of the vertical dentine layers because the dentine is deposited from the pulp canals overlying the bone, and adopts the shape of the newly grown vertical pulp canals. The heel gets higher because the addition of dentine takes place at the bone-dentine boundary. We have not found this mode of growth in any other dipnoan, and it certainly is in no way comparable with petrodentine (KEMP 2001).

REISZ et al. (2004: 21) in their description of *Ichnomylax* comment that 'Some of this growth may infill existing trabeculae of bone in a process described as pleromic (ØRVIG 1967; SMITH 1977; SMITH & SANSOM 2000). This occurs if the process of resorption in the remodelling of the tooth plate, does not completely remove the bone'. The first use of the term pleromic dentine was in a paper by TARLO & TARLO (1961) in relation to ostracoderm skeletons in which secondary dentine filled 'in the vascular spaces of the spongy bone' after wear. What we see in *Speonesydrion* is the dentine lying on bone, or on a gap on the surface of the bone, and it does not fill up the spaces in the bone trabeculae. Pleromic dentine is formed by the invasion of spaces in bone left after solution. It does not replace bone, but it fills up spaces left in bone either by wear, or by basal dentine in a tooth plate invading bone. Thus it is not possible that the dentine in *Speonesydrion* could be referred to as pleromic dentine. The dentine and the bone of *Speonesydrion* are closely related, and the dentine and bone are intermingled in some places. The new growth of dentine in vertical columns in association with bone, should have a new name, but one is careful about introducing new names into the already complex nomenclature.

The teeth themselves have been sectioned in several directions. Essentially they show the same features as the heel. The tip of the tooth is made of enamel covered dentine which lies on bone. Figs. 5A, 6C show a tooth on the end of a tooth row in ordinary section and as an enlargement, and Fig. 3B shows an isolated tooth. There is no break at the bone-dentine boundary, and the bone-dentine contact consists of the intermingling of the two substances as was evident in the heel. Deposition of the

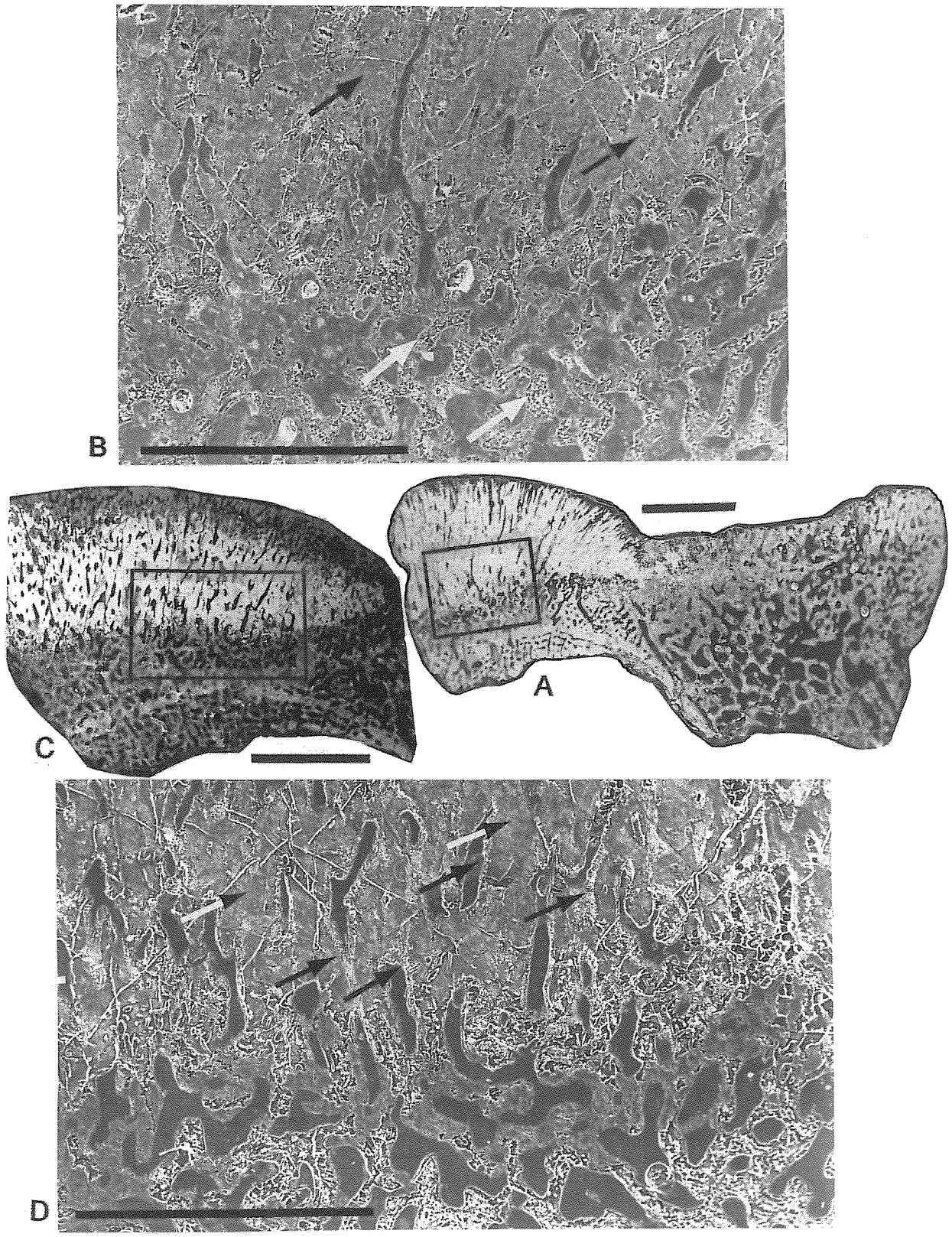

Fig. 5. *Speonesydrion iani*. **A**: SEM of a section of a tooth plate showing the heel on the left and the tooth on the right. The junction between the dentine and the bone structure shows that the bone is not always in connection with the dentine (ANU 36549 K). **B**: Enlargement of part of this junction outlined in Fig. A, with the bone at its base and dentine at the top. Intermingling of the two structures is well shown. Dentine = black arrows and bone = white arrows. **C, D**: C. Section across the heel. Note that the bone and dentine are in contact throughout the length of the specimen (ANU 35649 L). D. SEM enlargement of the bone dentine contact outlined in Fig. C, again showing the details of the relationship between the bone and the dentine. Dentine = white shafted black arrowheads. Circumpulpal dentine = black shafted arrows. – Scales: A, C = 2 mm; B, D = 1 mm.

tooth is the same as deposition of the heel. Cross sections of the tooth with the denticles still attached show the same arrangement as the teeth (Fig. 3D), but there are signs of a weak basal cavity. In *Speonesydrion* the denticles have the same structure as the teeth, and we see no argument (REISZ et al. 2004: 23) that the structure of the denticles 'argues against one giving rise to the other developmentally', as suggested by CAMPBELL & BARWICK (1995: 22).

Relationships with primitive dipnoans

Comparison with *Ichnomylax*

The obvious comparison with another genus is with *Ichnomylax*. The original description of *Ichnomylax* was based on a single specimen (LONG et al. 1994) that could not be sectioned. Our present interpretation of that genus is based on the work of REISZ et al. (2004) in which the thin sections of the teeth and the heel have been recorded. The heel and the teeth have the same general form as those in *Speonesydrion*, and the histology of the heel and teeth are comparable. The images produced by REISZ et al. (2004) show a break at the dentine bone boundary as shown in their figs. 3A–C, and this they refer to as the 'formative dental surface'. They do not use the term basal pulp cavity in their description. Their images on figs. 3E, F do not show a clear break, but the spaces between dentine and bone is filled with irregular tissue. The magnification of the images does not allow us to determine if these fragments contain osteocyte spaces, but we assume that they did. REISZ et al. (2004) comment on the possible resorption of the bone, and subsequent remodelling of the tooth plate to produce a pleromic feature. This indicates that they thought the bone was resorbed, and dentine was deposited above the resorbed bone surface. This is comparable with the situation in *Speonesydrion* in places where there is a gap between the dentine and the bone. As indicated above, this is not pleromic formation, as dentine is not formed in gaps in the bone produced by resorption.

The published images of *Ichnomylax* do not show any detail of the fine structure of the dentine, and so we are not convinced that the structure has the characteristics of petrodentine. REISZ et al. (2004: 21) comment that the 'microstructure of this kind of dentine (petrodentine) consists of nine features'. Unfortunately, item 3, 'few cell-process tubules, or if present below resolution of the light microscope'; item 5, 'birefringence due to mineral component, zones alternating at right angles'; and item 6, crystals arranged in parallel in groups as alternating interwoven bundles'; cannot be found in our specimens of *Speonesydrion*. Neither do the illustrations of *Ichnomylax*, show such features. For these reasons, we cannot accept that the dentine in these genera are related in any way to petrodentine. REISZ et al. have commented that the evolutionary history of petrodentine can be evaluated only in a phylogenetic context. But we state that petrodentine has to be recognized by its structural and morphological characters. In our view the presence of petrodentine in various forms has not been justified.

Comparison between the histology of *Ichnomylax* and *Speonesydrion* is of great value. The heel of the two is closely comparable, being made of dentine formed around closely spaced parallel pulp canals lying on bone. In some places, the boundary between the two tissues is modified by solution, allowing new growth of the dentine to take place, and has intergrowth of the two tissues (see above). This has not been described in *Ichnomylax*, but further study of the specimens is required, especially the enlarged illustrations of the dentine-bone contact. In *Speonesydrion*, where the bone-dentine occurs, it seems that the intermingled bone and dentine indicates that the bone is replaced by dentine deposited from the pulp canals.

The pattern of the dentine shows that *Ichnomylax* and *Speonesydrion* have comparable structure, but that this is not found in any other dipnoan. We conclude that these two genera are closely related in general structure and histology, and that they belong to a separate lineage which evolved shortly after the origin of the dipnoans.

CAMPBELL & BARWICK (1984: 46) comment that *Speonesydrion* could have given rise to *Dipterus*, but this statement was made before the histology of *Speonesydrion* was understood. We do not accept this statement at present. *Speonesydrion* did not give rise to the other dipnoans such as *Tarachomylax* or *Dipterus*. These two genera have no heel on the dental plates, have the teeth continued back to the point of origin of the dental plates, they have teeth that are added to the margins, they have teeth in which the pallial dentine and similar core dentine make up the mass of the tooth, and they have distinctive growth patterns around the margins of the plates. The dentine structure of *Dipterus valenciennesi* has been discussed in a recent paper by DEN BLAAUWEN et al. (2006).

Other primitive dipnoans

The discovery of yet another type of palatal biting increases the number of types of palatal dentition in the Early Devonian dipnoans to four from three (CAMPBELL & BARWICK 1990). Changes in the mandibular dentition are related to modification of the pterygoid and prearticular tooth plates, and we note the large development of the heel on the pterygoids.

What produces these changes in palatal biting early in dipnoan evolution? We do not think it was a series of small mutational changes in the genes, because it seems unlikely that such a large number of functionally unrelated changes could have occurred almost simultaneously. We note that *Dipnorhynchus* has a thick skeleton and thick pterygoid and prearticular tooth plates, and has no separate teeth, and no denticles. It had the capacity to grind hard tissues such a nautiloids and brachiopods that

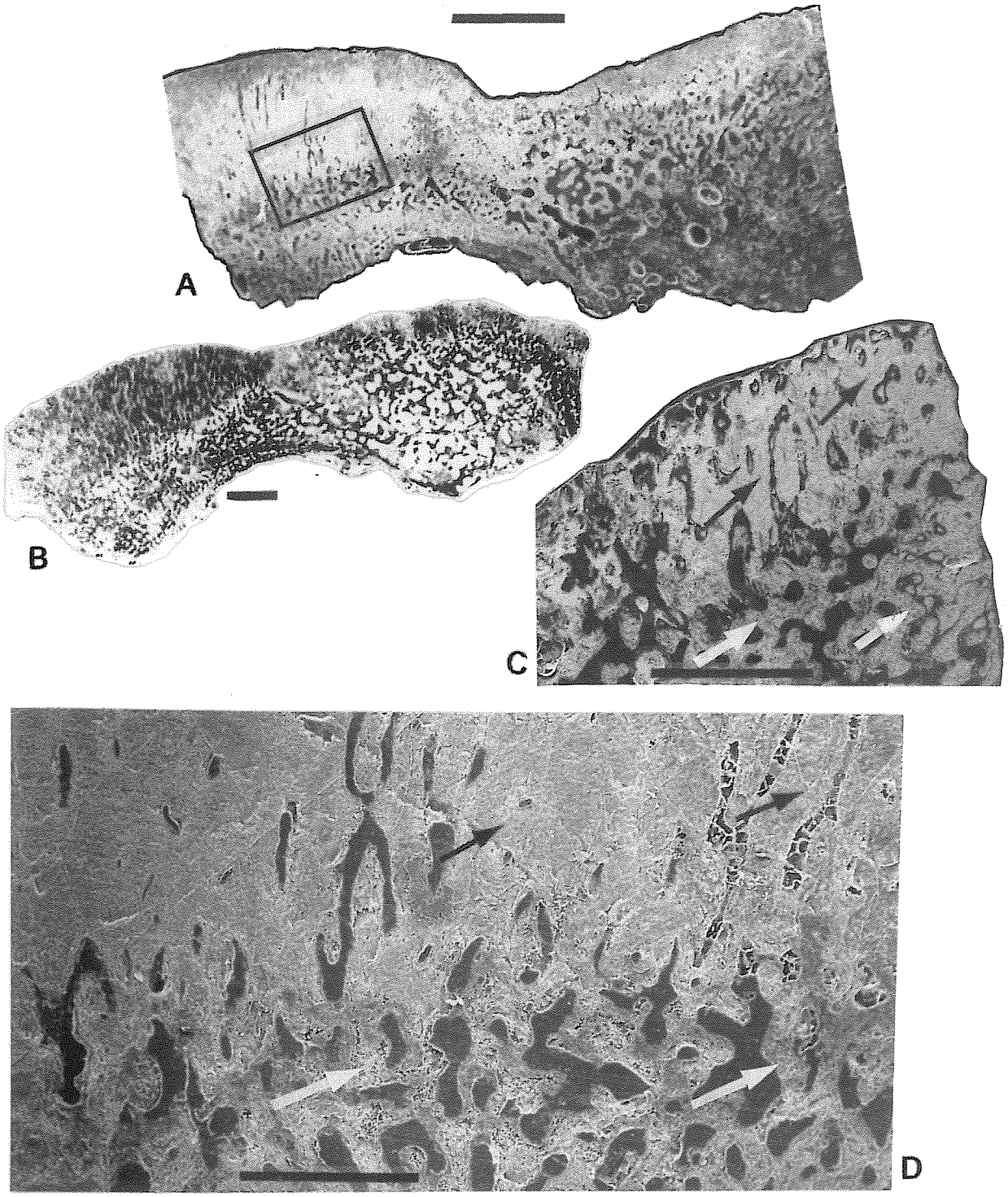

Fig. 6. *Speonesydrion iani.* **A, D**: SEM of an oblique cross section through the heel and the margins of a tooth ridge (ANU 36549 L). A. The distal end of the ridge is lost. Dentine lying on the bone along the margins of the tooth ridge. Note the lack of continuity between the dentine and the bone in places. D. SEM of the heel of the same specimen outlined on Fig. A showing the oblique sections of the pulp canals and the contact between the bone and the dentine. Dentine with black arrows and bone with white arrows. **B**: Optical illustration of another section. This runs along the tooth ridge and shows the remains of the old teeth made of dentine and the broken tooth at the end of the series (ANU 36549 C). **C**: Enlargement of the tooth in Fig. 5A, with bone at the base (white arrows) and the dentine at the top (black arrows) (ANU 36549 K). – Scales: A = 2 mm, B, C = 1 mm, D = 500 μm.

occur in abundance with them. *Uranolophus* has multiple denticles surrounded by marginal structures which do not have the structure of teeth. Growth took place by the addition of new denticles on the body of the palate, and the outward movement of the marginal structures which were modified by growth. Biting took place by using the marginal structures to break down hard prey, and rasping the results using the basihyal tooth plates against the denticles on the palate, as was well illustrated by *Griphognathus*. As would be expected, the adductor furrows in the mandible, are much smaller than those of *Dipnorhynchus*. *Tarachomylax* had marginal teeth which were added to by the growth of new teeth at the palatal margin. Denticles were present, but they were distributed close to the mid-line, and were related to mid-line growth of the palate. Our specimens do not show the size of the adductor cavities. And now we have the complex structures of *Speonesydrion*, as a type of organism that grew by the addition of tooth-like structures at the margin partly by the aggregation of denticles, the development of a heel which gradually increased in size displacing older teeth, used the teeth for breaking down soft food, and the heel for grinding hard tissues. Its adductor pits are comparable in size to those of *Dipnorhynchus*, as would have been expected from the grinding heel on the tooth plates.

It seems that these four types of teeth could not be evolved from one base form by gradual changes. Rather there must have been a change to produce a structure that could use the palate/prearticular grinding surface, and from this the types we observe independently evolved. There is no evidence of any groups of changes intermediate between the different groups of dentitions. The record suggests that the changes took place by some rapid means. All we can say is that this basic stock must have been a sarcopterygian organism.

Recent work on the effects of changes in gene regulation, and the capacity of new gene-circuitry to produce new designs in organisms (BRITTEN 1996), has given us the clue of how organisms can develop new structures around an older body plan. Most of this work has been based on extant organisms. CARROLL (2000) has commented that evidence on regulatory genes 'suggests that evolutionary changes in developmental gene regulation have shaped large scale changes in animal body plans and body parts'. SHUBIN & MARSHALL (2000) note that 'major evolutionary changes may not be due to changes in the number or structure of genes per se, but may be due to changes in their regulation.... Indeed, changes in the spatial pattern and timing of gene activity play an important role in generating variation at both small and large phylogenetic scales...'. An account of the range of changes is given by DAVIDSON (2001) in a book on development and evolution caused by changes in gene regulation. CAMPBELL & BARWICK (2006) have given an account of the hypothesis of the changes in gene regulation in sarcopterygian development, that has been given rise to onychodontiform fish. A more extensive account of this process in the development of sarcopterygian fishes is given by CAMPBELL & BARWICK (in press).

This discussion supports the statements of CAMPBELL & BARWICK (1990), who divided the Early Devonian genera into groups on the basis of their dentitions. All of these have different biting mechanisms, and apart from *Speonesydrion*, all can be continued on into the later Devonian. The *Dipnorhynchus* type is represented by *Sorbitorhynchus* from China; *Tarachomylax* continues through to the dipterid types of the Old Red Sandstone, and to the more developed Palaeozoic and later dipnoans; and *Uranolophus* type is represented by the much more evolved *Griphognathus*, *Soederbergia,* and the holodiopterids. We consider that the dental characters outlined above define the lineages evolved in the later Devonian and Palaeozoic. The genetic changes that produced these designs were continued on controlling the subsequent evolution of the group. Note that the *Speonesydrion* type died out in the Early Devonian, and it represents a failed attempt to make a new design.

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