APPARATUS STRUCTURE OF THE LATEST SILURIAN TO EARLY DEVONIAN CONODONT *ICRIODUS WOSCHMIDTI HESPERIUS* KLAPPER *ET* MURPHY, AND SOME COMMENTS ON PHYLOGENY

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The apparatus structure of the latest Silurian to Early Devonian conodont *Icriodus woschmidti hesperius* from sequences in north Queensland, Australia, consists of **Pa**, **Pb** and **M** elements with a symmetry transition series of distinct, but variable, coniform elements. A similar complex of cones was recovered from Ludlow (*siluricus* Zone) strata; although the apparatus structure is incomplete, the results indicate the existence of a likely ancestral form of the genus *Icriodus*. The cryptic origin of the genus is discussed in general terms. A distomodontid or icriodellid origin is considered possible. The former is supported by some morphological simmilarities of the symmetry transition series and stratigraphic considerations. The documentation of a **Pa** element with morphology apparently transitional between *Icriodella* and *Icriodus* supports the second possibility.

Key words: Conodonta, *Icriodus*, evolution, taxonomy, Silurian, Devonian, Queensland, Australia.

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INTRODUCTION

Conodonts reported here were recovered from carbonate sequences of the Jack Formation, a complex unit of mixed clastics and carbonates, in northern Queensland, Australia. The formation is the uppermost unit of the Graveyard Creek Group in the Broken River Region (WITHNALL *et al.* 1993). This report is concerned only with the oldest examples of the genus *Icriodus* and closely related genera. More information about Silurian conodont faunas from the Graveyard Creek Group of the Broken River region can be found in SIMPSON (1994, 1995a, 1995b, in press) and SLOAN *et al.* (1995).

The specimens discussed here come primarily from sections through the Jack Formation in two areas. One area, where the Broken River cuts through the Jack Hills Gorge (section BR8) on the western limb of the Broken River Anticline (WITHNALL *et al.* 1993), is the type section of the Jack Formation. In this area the formation consists of a lower carbonate unit overlain by a clastic interval. The clastics underlie an upper carbonate sequence consisting of a unit of thinly interbedded shales and lithologically variable carbonates with abundant coral heads in growth positions, known informally as the "coral gardens" sequence. This is, in turn, is overlain by thickly bedded to massive limestone, the uppermost unit of the Jack Formation. The carbonate unit beneath the clastic interval is Wenlock in age. The upper carbonate sequence is Ludlow in age. The section includes one sample, (BR8-31) within the "coral gardens" from the *Polygnathoides siluricus* Zone (SIMPSON, unpublished data), yielding the icriodontid cones. In this region the top of the Jack Formation does not extend beyond the Ludlow.

The other principal area is located 5 km to the east downstream from the type section near the Broken River Crossing. In this area, the formation consists only of the upper carbonate sequence ("coral gardens" and overlying thickly bedded limestones) folded into an unnamed syncline. A detailed section (BR18) was collected along the axis of this syncline. Data indicates a Ludlow age in the lower parts, including a sample of *P. siluricus* Zone age (BR18-180) also yielding icriodontid cones. Approximately 50 m stratigraphically higher within the thickly bedded carbonates, samples yield abundant **Pa** elements of *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY, indicating that in this area the Jack Formation extends through into the latest Pridolian to Early Devonian. Associated conodonts support this age interpretation (SIMPSON 1995a). A detailed supplementary section (BRH) was collected through the uppermost carbonates.

These samples, high in the Jack Formation, also yielded an abundant suite of very small but distinctive coniform elements interpreted as part of the apparatus of *Icriodus woschmidti hesperius*. These elements differ from those of the related genera *Pedavis* and *Pelekysgnathus* as discussed below. One specifically indeterminate *Pelekysgnathus* **Pa** element was recovered from these uppermost Jack Formation samples; no *Pedavis* **Pa** elements were recovered, indicating the suite of cones could only be associated with the *Icriodus* apparatus.

A third area of relevance to this report is the Jessey Creek-Arch Creek area of the Jack Formation approximately 5 km north-east of the type section. Although this area is currently interpreted as the Jack Formation (WITHNALL *et al.* 1993), as it is generally along strike from the better exposures to the south-west, SLOAN *et al.* (1995) have reinterpreted this area as consisting of an admixture of carbonate lithologies cannibalised from the autochthonous carbonates in the region of Jack Hills Gorge. This is supported by conodont data (SLOAN *et al.* 1995; SIMPSON 1995a) where single samples contain conodont elements of Ludlow, Pridoli and Early Devonian aspect. One of these samples (CON6) yielded the element herein interpreted as transitional between *Icriodella* and *Icriodus*.

Despite the poor nature of these collections, the conodont faunas suggest a number of possible scenarios for the evolution of the genus *Icriodus*. These must be considered highly speculative at present until a more complete sequence of faunas is recovered. In the following systematic descriptions and discussion the supra-generic taxonomy of SWEET (1988) is adopted. Specimens are housed in the microfossil collection of the Geology Museum, University of Queensland, St. Lucia, Australia, for which the abbreviation UQY is used.

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SYSTEMATIC PALEONTOLOGY

Class **Conodonti** BRANSON, 1938
Order **Prioniodontida** DZIK, 1976
Family **Icriodontidae** MÜLLER *et* MÜLLER, 1957

Remarks. — SWEET (1988) separated the genera *Icriodella*, *Pedavis*, *Sannemannia*, and *Steptotaxis* from the Icriodontidae to establish the Icriodellidae. SWEET (1988) interpreted the non-**Pa** elements of *Icriodella* as substantially morphologically removed from those of the earliest Icriodontidae and, therefore, an unlikely precursor for this group.

SWEET (1988: p. 68) favored an origin for this family from distomodontid stock based, in part, on stratigraphic criteria due to the many well documented examples of Late Silurian Distomodontidae. SWEET (1988: fig. 5.17) indicated that derivation of the Icriodontidae from the icriodellid genus *Pedavis* was a possibility, but did not favor this scenario. This contention is supported here as differences in the ramiform complex of *Icriodus* and *Pedavis* are highlighted. Furthermore, this report identifies the existence of Ludlow elements of probable icriodontid affinities.

Despite the dangers inherent in according phylogenetic significance to morphological similarities in **Pa** elements, as illustrated by SWEET (1988) in comparing *Distomodus pseudopesavis* and *Pedavis pesavis*, a third possibility can not be entirely discounted. A **Pa** element with morphology transitional between *Icriodella* and *Icriodus* suggests the possibility of derivation of the Icriodontidae from cryptic taxa closely related to *Icriodella*. The vast differences in the morphology of **S** elements, and the lack of other transitional forms throughout most of the Silurian is, however, conflicting evidence.

Genus *Icriodus* BRANSON *et* MEHL, 1938

Type species: *Icriodus expansus* BRANSON *et* MEHL, 1938.

1938. *Icriodus* BRANSON *et* MEHL: pp. 156–166.
1940. *Acodina* STAUFFER: p. 418.
1962. *Latericriodus* MÜLLER: p. 114.
1976. *Caudicriodus* BULTYNCK: pp. 19–20.
1976. *Praelatericriodus* BULTYNCK: pp. 40–41.

Remarks. — Varying interpretations of the apparatus structure of this genus have been summarised by SERPAGLI (1983). KLAPPER and PHILIP (1972) considered *Icriodus* and *Pedavis* as bielemental and trielemental Group 4 apparatuses respectively. *Icriodus* consisted of the distinctive **Pa** (= **I**) element and a large broad-based cone often referred to as "*Acodina*". The association of these two forms was first suggested by LANGE (1968) and subsequently employed by ZIEGLER (1972) and most other authors. BULTYNCK (1972), VAN DEN BOOGAARD and KUHRY (1979) considered the association of the two in a single apparatus unlikely. A third element similar to the $\mathbf{M_2}$ element of *Pelekysgnathus* was recognised by KLAPPER and ZIEGLER (1975), NICOLL (1977), and JOHNSON and KLAPPER (1981). NICOLL (1982) reconstructed a Late Devonian apparatus with 6 distinct cone elements. SERPAGLI (1983) reconstructed a seximembrate Early Devonian apparatus with two transition series equating it with Type IVA Ordovician apparatuses of BARNES *et al.* (1979). A similar apparatus structure can be interpreted from the Jack Formation material, but unlike SERPAGLI's (1983) reconstruction, the apparatus is dominated by adenticulate cones that were reported as rare in the Sardinian collections (SERPAGLI 1983: p. 157). BROADHEAD and MCCOMB (1983: fig. 3C, D) group complex cones, similar to the $\mathbf{M_{2b}}$ element of *Pedavis*, in the apparatus of *Icriodus*. NICOLL (1982) discussed the similar nature of coniform elements in *Icriodus*, *Pelekysgnathus*, and *Pedavis*.

A number of suggestions concerning the phylogeny of *Icriodus* have been advanced. KLAPPER and PHILIP (1972: p. 103) considered the *Icriodus* lineage as distinctly different from *Pedavis*. KLAPPER and MURPHY (1975) suggested the early Pridolian *Pelekysgnathus index* as a possible precursor for *Icriodus woschmidti*, but noted the lack of transitional forms. NICOLL (1982) suggested that the early Ludlow form *Pelekysgnathus dubius* was the earliest species of the Icriodontidae (excluding *Icriodella*). CHATTERTON and PERRY (1977) noted a close relationship between *Pelekysgnathus* and *Icriodus* and suggested a polyphyletic origin for the former from species of *Icriodus*. SANDBERG and DREESEN (1984) noted Late

Devonian examples of *Pelekysgnathus* with **Pa** elements similar to *Icriodus*, on which SWEET (1988: p. 70) commented that not only is *Icriodus* polyphyletic it may be its own "grandpa". BROADHEAD and MCCOMB (1983) suggested *Icriodus* evolved from *Pedavis* by paedomorphic loss during neoteny. FORDHAM (1991) groups *Icriodus woschmidti* with *Pedavis thorsteinssoni* suggesting the latter to be derived from the same ancestor as *Pedavis latialata*. SWEET (1988), while noting that the phylogeny was difficult to interpret on available data, suggested *Rotundacodina dubia* as a likely ancestor for *Icriodus*. This study identifies differences between the coniform elements of *Icriodus* and *Pedavis* and suggests a new Late Silurian species, *Icriodus*? sp. n. A, recovered in small numbers, and assigned to this genus because of the nature of the ramiform complex, is a likely ancestor for *Icriodus woschmidti*.

Icriodus woschmidti ZIEGLER, 1960

Remarks. — This species has been divided into 4 subspecies at various times. These are *Icriodus woschmidti woschmidti* ZIEGLER, *I. w. postwoschmidti* MASHKOVA, *I. w. transiens* CARLS *et* GANDL, 1969, and *I. w. hesperius* KLAPPER *et* MURPHY, 1975. *I. w. transiens* is considered a junior synonym for *I. w. woschmidti*. Some authors (e.g., MAWSON 1986) consider *I. w. postwoschmidti* to have features distinctive enough to allow separation at species level. All specimens recovered in this study, with one exception, are referable to *I. w. hesperius* and elements of the ramiform complex are therefore grouped within this subspecies.

A distinct element notation, for what were then considered bielemental and trielemental icriodontid apparatuses, was first proposed by KLAPPER and PHILIP (1971). NICOLL (1982) noted that, as the species concept expanded and more elements were recognised as part of the apparatus, the notational scheme has consisted of modifications to the original notation of KLAPPER and PHILIP (1971). NICOLL (1982) devised a new notational system as the original was considered inadequate to cover the variety of elements, and he saw little in the way of positional or functional analogy between the coniform *Icriodus* elements and the widely adopted scheme of SWEET and SCHÖNLAUB (1975) which was based on genera with platform and ramiform complexes. NICOLL (1982) saw 4 of his coniform elements (**Ca–Cd**) as analogous to the $\mathbf{S_2}$ element and two (**Ce** and **Cf**) to the $\mathbf{M_2}$ element. Despite the possibility that Late Devonian species of *Icriodus* may have a different apparatus architecture from Early Devonian species, the recognition of the ramiform complex in *I. woschmidti* (SERPAGLI 1983) now appears to obviate the need to modify the scheme of KLAPPER and PHILIP (1971) or construct new schemes (NICOLL 1982).

In SERPAGLI's (1983) reconstruction, the Type IVA apparatus of BARNES *et al.* (1979) is broadly analogous to the scheme of SWEET and SCHÖNLAUB (1975). It is comprised of two transition series, the first, morphotypes **a**, **b**, and **c** can be equated with the **Sc**, **Sb**, and **Sa** elements respectively of the symmetry transition series. The second, morphotypes **e**, **f**, and **g**, can be equated with the **M**, **Pb**, and **Pa** elements respectively. Despite the difficulties with homology that have driven others to construct new schemes, the **Sa** to **Sc** notation clearly indicate an increasing degree of element asymmetry dependent on apparatus position and, for the purposes of this study, SWEET and SCHÖNLAUB's (1975) notational scheme is employed herein without prejudice. Element morphologies within the symmetry transition series include a variety of forms and some may intergrade. Different morphotypes of elements thought to occupy the same or a similar position within the apparatus is accounted for by using numeric subscripts. Some of this variety may be attributable to ontogenetic factors. Juvenile coniform elements not readily attributable to an apparatus position are described as "cones".

SERPAGLI (1983) gave four reasons for associating the ramiform complex with the other elements of this species, and, from the literature gave some examples of elements probably belonging to this or a closely related species. These included Gen. et sp. n. A and B (MASHKOVA 1971); "*Paltodus*" sp. c, "*Drepanodus*" sp. a, and *Cordylodus* sp. n. (ZIEGLER 1960); *Rotundacodina dubia* and *Acodina plicata* (CARLS and GANDL 1969); *Rotundacodina dubia*, *Acodina retracta*, and *Acodina plicata* (DRYGANT 1974); and *Neoprioniodus brevirameus*, *Oepikodus* sp., and *Acodus* sp. (BARNETT 1971). To this list *Distacodus robustus* and Gen. et sp. indet. (WANG 1981: pl. 1: 13, 14, and 15 respectively) and *Acodina triquetra* and *Rotundacodina* ssp. (DRYGANT 1984: pl. 1: 29, 30 and 36–52 respectively) can be added. JEPPSSON (1988: p. 23) noted the existence of ramiform elements in a sample with platform elements of *I. woschmidti*. DENKLER and HARRIS (1988: pl. 1: C–H) and ELBERT, HARRIS and DENKLER (1988: fig. 6D–F) illustrated coniform elements as part of the apparatus of this species.

Icriodus woschmidti hesperius KLAPPER *et* MURPHY, 1975
(Pl. 1: 1–17; Pl. 2: 1–23; Pl. 3: 1–10)

1969. *Icriodus woschmidti* ZIEGLER; KLAPPER: p. 10, pl. 2: 1, 2.
?1972. *Icriodus woschmidti* ZIEGLER; LINK and DRUCE: pp. 39–40, pl. 3: 10, 13, 14.
1975. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY: p. 48, pl. 11: 1–19.
1979. *Caudicriodus woschmidti* (ZIEGLER); UYENO in NORRIS and UYENO: p. 8, pl. 5: 10–17.
1980. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; KLAPPER and JOHNSON: p. 499, pl. 2: 11.
1981. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; UYENO: p. 43, pl. 5: 10–17.
1984. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; DRYGANT: p. 138, pl. 16: 4.
1990. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; UYENO: p. 57, pl. 16: 23, 24, 26–33.
1991. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; UYENO: pl. 1, figs 1, 2.
1991. *Icriodus woschmidti hesperius* KLAPPER *et* MURPHY; KLAPPER: pp. 71–72, *Icriodus* pl. 9: 7, 8 (with synomymy).

Material. — Thirteen **Pa** elements, 5 **Pb** elements, 3 **M** elements, 13 **Sa** elements, 20 **Sb$_1$** elements, 6 **Sb$_2$** elements, 9 **Sb** elements undifferentiated, 19 **Sc** elements, 9 undesignated cones.

Description. — **Pa** element. See KLAPPER and MURPHY (1975: p. 48 = **I** element).

Pb element. See KLAPPER and MURPHY (1975: p. 48 = **S$_2$** element).

M element. A strongly compressed, broad-based, proclined cone with sharp anterior and posterior margins. Element is lanceolate in cross section with acostate, convex lateral faces. In lateral view the posterior margin has a concave outline and the anterior margin is almost straight. Basal cavity extends two thirds to three quarters the height of the cone. Prominent flattened anterior and posterior keels are widest near the top of basal cavity and narrow basally and towards the cusp.

Sa element. An uncompressed, broad-based, reclined cone with sharp anterior and posterior margins. Two adenticulate lateral costae on opposite lateral faces are slightly asymmetrically aligned. Basal cavity, rounded and subquadrangular in outline, is widely expanded both antero-posteriorly and laterally. Cusp is slightly asymmetrically quadrangular in cross section. Element has an ornament of short discontinuous irregular striations, most abundant near posterior margin and in region of greatest curvature. Isolated, discontinuous striations in other region of cone separate unornamented regions between costae. Striations are mostly subparallel with each other and the costae but at times merge obliquely towards cusp. Cusp is normally straight but occasionally is slightly deflected to one side.

Sb$_1$ element. Slightly compressed, elongate, narrow-based, erect cones with sharp or sharply rounded anterior and posterior margins. Cusp, triangular to subtriangular in cross section, is long and straight; the basal cavity is low, one third to one half the height of the element. A prominent lateral costa extends from high on the cusp to the basal region on one lateral face; the other lateral face is broadly convex. Basal cavity has an asymmetrical quadrangular outline, "pear-shaped" in smaller specimens. Majority of specimens have the cusp deflected towards the costate lateral face (Pl. 2: 16); sometimes the deflection can be quite strong. A small number of specimens (approximately 10%) have the cusp deflected weakly towards acostate lateral face (Pl. 2: 18). The ornament varies between large, coarse striations (Pl. 2: 17) and finer striations (Pl. 2: 10) but is frequently a combination of both. Striations may merge obliquely with the anterior or posterior margin, lateral costa, or adjacent striations. The posterobasal region of the basal cavity may be extended to a sharp margin (Pl. 2: 17) or develop a small posterobasal keel (Pl. 2: 8).

Sb$_2$ element. Slightly compressed, erect, narrow-based cone with a sharp anterior margin and a sharp or sharply rounded posterior margin; both lateral faces are acostate, one is strongly convex, the other weakly convex; the cusp has a lenticular cross section. Basal cavity has an asymmetrical quadrangular outline. There is a varying degree of curvature of elements with some gently recurved (Pl. 2: 20) and others nearly straight (Pl. 2: 23). Cone has striate ornament covering most of the element and may be fine (Pl. 2: 21) or coarse (Pl. 2: 23) but often closely spaced near the posterior margin. Striations may merge obliquely with posterior margin. Cusp shows varying degrees of deflection from the anterior-posterior plane.

Sc element. Strongly compressed, broad-based, reclined to erect cones with sharp anterior and posterior margins that may be adenticulate or have one to three ancillary denticles developed along the posterior margin of the cone. Ancillary denticles are very strongly posteriorly inclined. Basal cavity is elongate and quadrangular to subelliptical in outline and strongly asymmetric sometimes with a concave or partially concave outline on one side of the basal cavity. The cusp is strongly compressed and deflected. As with all other elements, ornament is highly variable ranging from coarse subparallel striations (Pl. 3: 9) to densely packed fine striations (Pl. 3: 10) running parallel to the anterior and posterior margins. The **Sc**

element has not been separated into a denticulate and adenticulate morphotype as this difference is considered a result of ontogeny (see below).

Remarks. — Characteristics of the **Pa** (= **I**) element of this subspecies listed by KLAPPER and MURPHY (1975) include the long posteriorly directed lateral process bearing a single row of denticles, and the narrow transverse ridges along the main process. Although most specimens conform to the original subspecific diagnosis, there is some minor variation in the collection from the Jack Formation. On some specimens, the longitudinal ridge running along the main process and bisecting the transverse ridges can be clearly seen (Pl. 1: 1, 2, 8). As originally noted by KLAPPER and MURPHY (1975), the anteriorly directed lateral lobes are better developed on the inner side and may have a prominent ridge. This is seen in most Jack Formation specimens (Pl. 1: 4), however some specimens have a prominent ridge on both anteriorly directed lobes (Pl. 1: 8, 10).

Specimens illustrated by LINK and DRUCE (1972: pl. 3: 10, 13, 14) from the Elmside Formation of the Yass Basin, have a long posteriorly directed process bearing a single row of denticles, it is therefore close to this subspecies in morphology. The transverse ridges are broader than in the Jack Formation specimens and are comprised of three distinct rows of nodes. KLAPPER and MURPHY (1975: p. 49) noted that the three rows of denticles on the main process were not seen in later growth stages, and the Yass Basin specimens are large. Despite this, KLAPPER and MURPHY (1975: p. 49) suggested these specimens may be examples of this subspecies, whereas ZIEGLER (1975: 161) indicated an affinity to *Icriodus postwoschmidti*. They are included tentatively in the synonymy because of the long posterior process.

The **Pb** element is broad-based with a quadrangular outline as described by KLAPPER and MURPHY (1975: p. 48). Some have sharp (Pl. 1: 13) or rounded (Pl. 1: 12) costae on the outer lateral face. A prominent well rounded costa (Pl. 1: 14) may be present on the inner lateral face. There is some variation in the width of the base relative to the height of the cone. **M** elements and **Pb** elements are close in morphology but can be separated on the following criteria: **M** elements are more strongly compressed and have acostate lateral faces, whereas **Pb** elements are less compressed, broader-based, and have a number of costae; the basal cavity of the **Pb** element is deeper and the cusp is not strongly deflected as it is in the **M** element.

The ornament of the symmetry transition series and its variable nature are noteworthy features of the apparatus. The same combination of a laterally unornamented platform complex and an ornamented symmetry transition series is seen in the genus *Pedavis*. The variable ornament described here initially suggested that a number of apparatuses may be present in the collection. Coarsely and finely striate elements occur throughout the symmetry transition series. These have not been separated because of the significant number of elements, also occurring throughout the symmetry transition series with a combination of coarse and fine ornament. A more reasonable interpretation in the light of this is that the variable ornament is a diagnostic feature and the three forms, coarse, fine, and a combination thereof, represent intraspecific variability. Alternatively, the variation could be due to a wide range of element morphotypes within an apparatus. A collection of elements a degree of magnitude larger would be required to test these hypotheses. Faint, striate ornament is observable on some of the elements of the ramiform complex of *Icriodus woschmidti woschmidti* illustrated by SERPAGLI (1983: fig. 7A, B, E).

The coniform elements with coarse ornament are superficially similar to those of *Pedavis*. The two genera can be separated on the following criteria: the outline of the basal cavity in all *Pedavis* cones is bilaterally symmetrical around the anterior-posterior plane of the element; *Icriodus* cones are asymmetrical around this axis, with the exception of very small juvenile cones with a rounded cavity outline; *Icriodus* cones are striate, the ornament is subdued in comparison with *Pedavis*; most *Pedavis* cones (with the exception of Type 5 cones of SIMPSON *et al.* 1993: fig. 8) have gently rounded posterior and anterior margins; *Icriodus* cones have sharp or sharply rounded margins; ancillary denticles of *Icriodus* cones (**Sc** element this study) are more posteriorly inclined than the erect ancillary denticles on the complex cones of *Pedavis*. It is possible that some Early Devonian cones illustrated in the literature as *Pedavis* are in fact elements of *Icriodus*. Whilst it is obvious that the holotype of "*Scolopodus devonicus*" (BISCHOFF and SANNEMAN 1958: pl. 15: 19) is part of a *Pedavis* apparatus, some elements with this name may also be better placed within *Icriodus*. Examination of the specimens with respect to the above features would be required to separate them; a synonymy based on examination of photographs would not necessarily be conclusive and has not been attempted.

The apparatus structure of *Icriodus woschmidti hesperius*, as reconstructed here, is very similar to that of *Coryssognathus dubius*, a possible progenitor of *Icriodus*. One **Sc** element of *I. w. hesperius* (Pl. 3: 9) has an ancillary denticle that appears misaligned. This suggests the mode of growth of these elements involved the accretion of coniform elements into the ramiform complex during ontogeny. This feature was recognised in *C. dubius* by VAN DEN BOOGAARD (1990) and MILLER and ALDRIDGE (1993). Another similarity between the ramiform complex of these two species is the slightly asymmetric nature of the Sa element; MILLER and ALDRIDGE (1993) divided *C. dubius* into three morphotypes of elements of the "**Sa/Sb**" position. Except for the abundance of coniform elements referred to the symmetry transition series in this reconstruction, the morphology of the ramiform complex of *I. w. hesperius* is close to an ornamented version of the ramiform complex of *C. dubius*. MILLER and ALDRIDGE (1993) reconstructed *C. dubius* as a septimembrate apparatus consisting of 4 elements in one transition series.

A similar plexus of elements was described and illustrated as 6 different species of *Rotundacodina* by DRYGANT (1984). All of them were recovered from samples yielding **Pa** elements of *Icriodus woschmidti transiens* (DRYGANT 1984: table 15, p. 175). Both *R. noguerensis* (DRYGANT 1984: pl. 1: 36, 37) and *R. carlsi* (DRYGANT 1984: pl. 1: 38, 39) appear to be adenticulate **Sc** elements, *R. elegans* (DRYGANT 1984: pl. 1: 40–42) are **Sb** elements, *R. quadratibasis* (DRYGANT 1984: pl. 1: 43–45) are slightly asymmetrical **Sa** elements or **Sa/Sb** transitional elements, *R. rotunda* (DRYGANT 1984: pl. 1: 46) is an undifferentiated cone and *R. dubia* (DRYGANT 1984: pl. 1: 47–52) are denticulate **Sc** elements.

An unillustrated record of *Dentacodina* sp. from Silurian–Devonian boundary strata in east Yunnan, China (FANG *et al.* 1994) possibly represents an **Sc** element of this, or a closely related, unreconstructed subspecies.

Occurrence. — Jack Formation, upper limestone unit, Broken River Crossing.

Icriodus? sp.
(Pl. 3: 11)

Material. — One **Pa** element.

Description. — Pastinoscaphate **Pa** element with a long anterior process, short posterior process and two adenticulate lateral processes. The anterior process narrows close to the cusp in upper view; it is twice the length of the posterior process with three rows of nodes connected by 7 strongly developed transverse ridges. Transverse ridges are closely spaced adjacent to the cusp and more widely spaced in distal regions. Nodes of the central row are weakly developed and connected by a thin, weakly developed longitudinal ridge. The longitudinal ridge is gently arcuate in upper view. Nodes flanking this central longitudinal ridge, on both the outer and the inner sides of the anterior process are better developed than those of the central row. They are also better developed in distal parts of the process. The posterior process has 4 nodose denticles and, is slightly offset towards the inner side of the element from the longitudinal axis of the anterior process in upper view. The lateral processes are adenticulate. The outer lateral process is straight and directed anteriorly. The inner lateral process is directed posteriorly close to the cusp and sharply deflected anteriorly at mid-length. The cusp is a raised ridge joining the two lateral processes. There is a weak platform developed between both lateral processes and the anterior process.

Remarks. — The specimen (Pl. 3: 11) has relatively broad transverse ridges, a narrow basal cavity beneath the main process and three rows of nodes along this process. These characteristics are usually associated with the genus *Icriodus*. The thin longitudinal ridge along the anterior process was also cited as a diagnostic generic characteristic (KLAPPER 1969). The ornament on this specimen does bear a superficial resemblance to *Icriodus woschmidti*. It is, however, much more subdued than typical examples of *I. woschmidti* and the spacing between the transverse ridges is more varied. This same specimen has been previously identified and illustrated as *Icriodus* cf. *woschmidti woschmidti* (SLOAN *et al.* 1995: pl. 12: 7); a more careful examination and consideration of morphology and diagnostic features has led to the reinterpretation presented here.

The orientation and relative lengths of the anterior and posterior processes and the development of the two adenticulate lateral processes is similar to the **Pa** element of *Icriodella*. These features are seen in the Ordovician species *Icriodella superba*, in particular, the specimens from the Lexington Limestone illustrated by BERGSTRÖM and SWEET (1966: pl. 29: 1–3). As noted by Treatise authors (KLAPPER and BERGSTRÖM 1981), this genus is characterised by only two rows of nodes on the anterior process.

This element is therefore not readily classifiable within either genus. As it has characteristics of both genera it is provisionally identified as a transitional form pending the recovery of further specimens.

The single **Pa** (= **I**) element recovered came from a sample, with a conodont fauna of discordant age, interpreted here as a deeper water allochthonous debris flow, cannibalised from a range of autochthonous limestones of the Jack Formation of various ages. The age of other elements from the same sample ranges from Ludlow to Early Devonian. No other elements that could be grouped with this specimen were recovered from the same sample. Morphological differences between **Pb** elements are particularly useful in discriminating genera of the Icriodontidae, but none were recovered.

No comparable elements were recovered from autochthonous sequences. A small collection of ramiform elements grouped herein as *Icriodus*? sp. n. A (described below) were recovered from Ludlow autochthonous sequences. As no **Pa** element was recovered with these, it is possible that this specimen represents the unrecovered **Pa** element of this new species. Until the two are recovered in some abundance in the same samples they are treated as separate taxa. An alternative speculation concerning a possible coryssognathid **Pa** element with the icriodontid cones from the autochthonous sequences is discussed below.

Occurrence. — Jack Formation undifferentiated, lower Arch Creek/lower Jessey Creek area.

Icriodus? sp. n. A
(Pl. 3: 12–19)

Material. — One **Pb** element, 2 **Sa** elements, 6 **Sb** elements, 3 **Sc** elements, 2 undesignated cones.

Description. — **Pa** element. Not recovered in this study.

Pb element. Broad-based, erect cone with sharp posterior and anterior margins and a prominent lateral costa on one face. Costa is sharp and extends for the entire length of the cone and is located close to the anterior margin. Basal cavity is low, tapers sharply and occupies lower half of cone; it has a triangular outline. Cusp is elongate, narrow, and strongly compressed. Surface of cone between costa and margins is smooth.

Sa element. Broad-based cone with sharp to sharply rounded posterior and anterior margins with two sharp lateral costa on either side of cone, slightly asymmetrically aligned. Basal cavity is shallow, tapers sharply and occupies lower third of cone. Basal cavity, subquadrangular in outline, is expanded laterally and antero-posteriorly. Cusp is elongate, narrow and has a quadrangular cross-section. Entire surface of element is covered by fine subparallel striations sometimes merging obliquely with the posterior margin.

Sb element. Broad-based, slightly compressed element with a sharp posterior margin and a rounded anterior margin in unkeeled areas. Anterobasal (Pl. 3: 15) or posterobasal (Pl. 3: 16) keels may develop with sharply rounded margins. Basal cavity is low and subtriangular in outline. Cusp is elongate, deflected and twisted to one side; in cross section it is "tear-drop" shaped. Ornament may be finely striate (Pl. 3: 14) or a mixture of coarse and fine striae (Pl. 3: 16).

Sc element. Strongly compressed, broad-based, erect cones with a sharp keeled anterior margin and a sharp denticulate posterior margin. Basal cavity is shallow extending approximately one half height of cone and the basal cavity outline is an asymmetrically compressed ellipsoid with one convex side and a flat, gently sinuous or concave side. Cusp is elongate, strongly compressed resulting in a compressed lenticular cross-section. Two or three ancillary denticles along posterior margin of cone occur at varying positions (compare Pl. 3: 18 with 19). These denticles are inclined subparallel to the cusp when proximal to cusp and inclined more strongly with increasing distance from cusp. Anterior margin is characterised by a prominent keel very well developed anterobasally. Fine striate ornament over entire surface of cone excluding keels and ancillary denticles.

Remarks. — All the elements grouped here have basal cavities more squat and cusps more elongate than is seen in homologous elements of the younger *Icriodus woschmidti hesperius*. Other differences include the prominent anterior keel of the **Sc** element and the keels of the **Sb** element. In all other respects the two apparatuses are closely comparable, in particular the nature of the micro-ornament in the symmetry transition series.

Elements were recovered, in small numbers, from two *siluricus* Zone samples yielding abundant faunas consisting primarily of *Ozarkodina excavata excavata*. As no **Pa** element was recovered with this collection, these elements are tentatively referred to *Icriodus* because of the nature of the symmetry transition series. This implies the existence of an icriodontid species in strata of Ludlow age which would therefore represent the oldest examples of this genus.

JEPPSSON (1983: p. 136) noted the occurrence of a fragmentary icriodontid from the Eke Beds of Gotland and considered it possibly part of a *Pedavis* apparatus. The same was noted by JEPPSSON *et al.* (1994); coniform elements similar to those described here have also been recovered (JEPPSSON personal communication 1996) at this level. The Eke Beds of Gotland are slightly younger than the samples yielding *Icriodus*? sp. n. A in the Jack Formation occurring just above the *siluricus* Zone on Gotland.

The sample from the type section of the Jack Formation yielded a small number of elements of *Coryssognathus dubius*. This included 3 **Pa** elements, but no symmetry transition elements. An intriguing possibility is that, in the Late Silurian, these elements occurred together in the same apparatus with a symmetry transition series with *Icriodus* characteristics and other elements having *Coryssognathus* characteristics. Such an hypothesis would represent an intermediate form between two suprageneric groups of conodonts, the Distomodontidae and the Icriodontidae. As the number of specimens is low, these elements are treated as two separate taxa until larger collections are available to resolve the conflicting interpretations.

Occurrence. — Jack Formation "coral gardens" unit, Broken River Crossing, *siluricus* Zone; Jack Formation "coral gardens" unit, Jack Hills Gorge, *siluricus* Zone.

Genus *Pelekysgnathus* THOMAS, 1949

Type species: *Pelekysgnathus inclinatus* THOMAS, 1949.

Pelekysgnathus sp.
(Pl. 3: 20, 21)

Material. — One **Pa** element, 1 "coniform" element.

Remarks. — Two elements referable to this species were recovered. Illustrations have been included for comparative purposes.

Occurrence. — Jack Formation, upper limestone unit, Broken River Crossing, *woschmidti* Zone.

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APPARATUS STRUCTURE OF THE LATEST SILURIAN TO EARLY DEVONIAN CONODONT *ICRIODUS WOSCHMIDTI HESPERIUS* KLAPPER *ET* MURPHY, AND SOME COMMENTS ON PHYLOGENY

PLATE 1

Some **Pa** elements were obliquely oriented for photography to highlight the variable nature of the lateral processes. All specimens from Broken River Crossing sections (BR18 and BRH), Jack Formation, upper limestone unit, *woschmidti* Zone.

1. **Pa** element UQY7374, sample BRH 14, upper view, × 60.
2. **Pa** element UQY7375, sample BR18 255.5, upper view, × 30.
3. **Pa** element UQY7376, sample BRH 14, upper view, × 45.
4. **Pa** element UQY7377, sample BRH 14, upper view, × 30.
5. **Pa** element UQY7378, sample BRH 9, oblique upper view, × 45.
6. **Pa** element UQY7379, sample BRH 14, oblique upper view, × 45.
7. **Pa** element UQY7380, sample BRH 14, upper view, × 90.
8. **Pa** element UQY7381, sample BR18 262.5, upper view, × 45.
9. **Pa** element UQY7382, sample BR18 290.6, oblique upper view, × 60.
10. **Pa** element UQY7383, sample BRH 3, upper view, × 30.
11. **Pb** element UQY7384, sample BRH 14, lateral view, × 45.
12. **Pb** element UQY7385, sample BRH 12, lateral view, × 60.
13. **Pb** element UQY7386, sample BRH 12, lateral view, × 90.
14. **Pb** element UQY7387, sample BRH 14, lateral view, × 45.
15. **M** element UQY7388, sample BRH 14, lateral view, × 90.
16. **M** element UQY7389, sample BRH 3, lateral view, × 60.
17. **M** element UQY7390, sample BRH 4, lateral view, × 90.

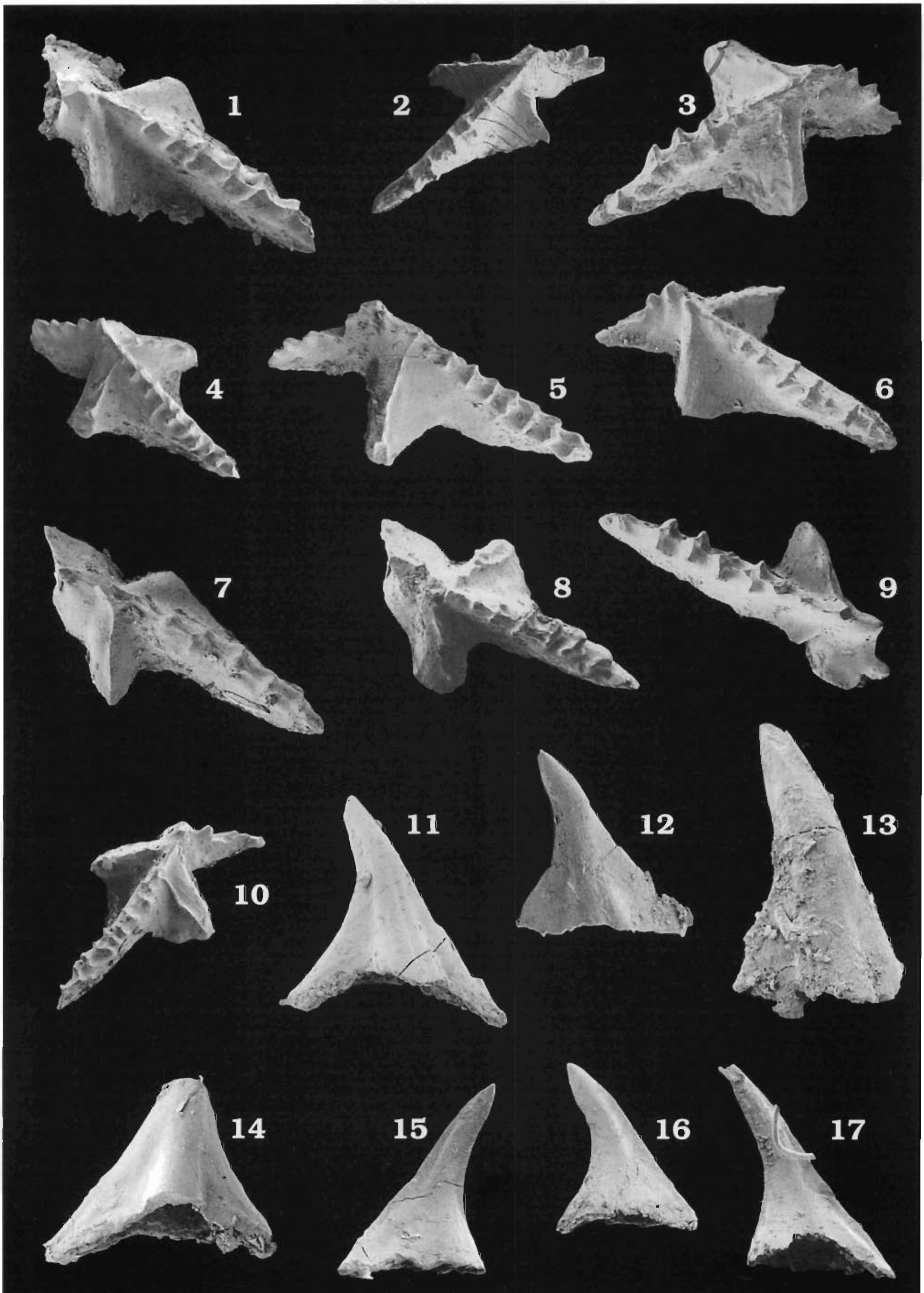
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PLATE 2

Icriodus woschmidti hesperius KLAPPER *et* MURPHY 157

All specimens from Broken River Crossing sections (BR18 and BRH), Jack Formation, upper limestone unit, *woschmidti* Zone.

1. **Sa** element UQY7391, sample BRH 14, oblique posterior view, × 120.
2. **Sa** element UQY7392, sample BRH 14, lateral view, × 90.
3. **Sa** element UQY7393, sample BRH 13, lateral view, × 90.
4. **Sa** element UQY7394, sample BRH 14, posterior view, × 120.
5. **Sb$_1$** element UQY7395, sample BRH 14, lateral view, × 90.
6. **Sb$_1$** element UQY7396, sample (BR18 290, lateral view, × 120.
7. **Sb$_1$** element UQY7397, sample BRH 14, lateral view, × 120.
8. **Sb$_1$** element UQY7398, sample BRH 14, lateral view, × 90.
9. **Sb$_1$** element UQY7399, sample BRH 9, lateral view, × 120.
10. **Sb$_1$** element UQY7400, sample BRH 14, lateral view, × 120.
11. **Sb$_1$** element UQY7401, sample BR18 291.5, lateral view, × 150.
12. **Sb$_1$** element UQY7402, sample BRH 2, lateral view, × 120.
13. **Sb$_1$** element UQY7403, sample BRH 12, oblique anterior view, × 120.
14. **Sb$_1$** element UQY7404, sample BR18 260.6, lateral view, × 120.
15. **Sb1** element UQY7405, sample BRH 12, posterior view, × 90.
16. **Sb$_1$** element UQY7406, sample BRH 12, lateral view, × 120.
17. **Sb$_1$** element UQY7407, sample BRH 14, lateral view, × 90.
18. **Sb$_1$** element UQY7408, sample BRH 14, lateral view, × 120.
19. **Sb$_1$** element UQY7409, sample BRH 14, oblique lower view, × 90.
20. **Sb$_2$** element UQY7410, sample BRH 14, lateral view, × 120.
21. **Sb$_2$** element UQY7411, sample BRH 14, lateral view, × 90.
22. **Sb$_2$** element UQY7412, sample BRH 3, lateral view, × 90.
23. **Sb$_2$** element UQY7413, sample BRH 14, lateral view, × 90.

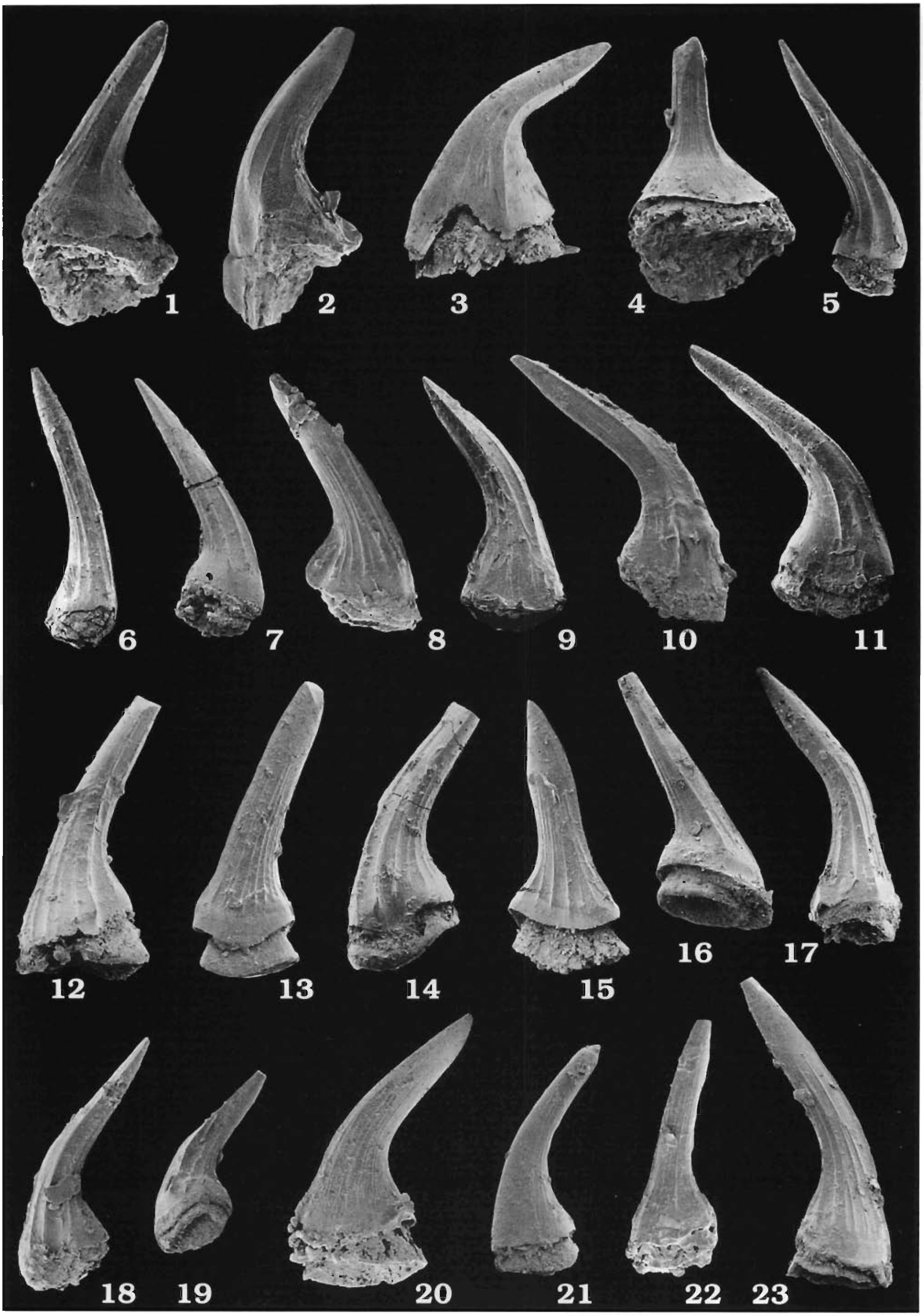
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PLATE 3

Icriodus woschmidti hesperius Klapper *et* Murphy 157

All specimens from Broken River Crossing sections (BR18 and BRH), Jack Formation, upper limestone unit, *woschmidti* Zone.

1. **Sc** element UQY7414, sample BRH 1, lateral view, × 120.
2. **Sc** element UQY7415, sample BRH 12, lateral view, × 120.
3. **Sc** element UQY7416, sample BRHD 10, lateral view, × 90.
4. **Sc** element UQY7417, sample BRH 15, lateral view, × 90.
5. **Sc** element UQY7418, sample BRH 14, lateral view, × 90.
6. **Sc** element UQY7419, sample BRH 12, lateral view, × 150.
7. **Sc** element UQY7420, sample BRH 14, lateral view, × 60.
8. **Sc** element UQY7421, sample BR18 261, lateral view, × 60.
9. **Sc** element UQY7422, sample BRH 12, lateral view, × 90.
10. **Sc** element UQY7423, sample BRH 17, lateral view, × 120.

Icriodus? sp. 159

11. **Pa** element UQY7615, Jack Formation, lower Arch Creek/lower Jessey Creek area, sample CON 6, upper view, × 45.

Icriodus? sp. n. A 160

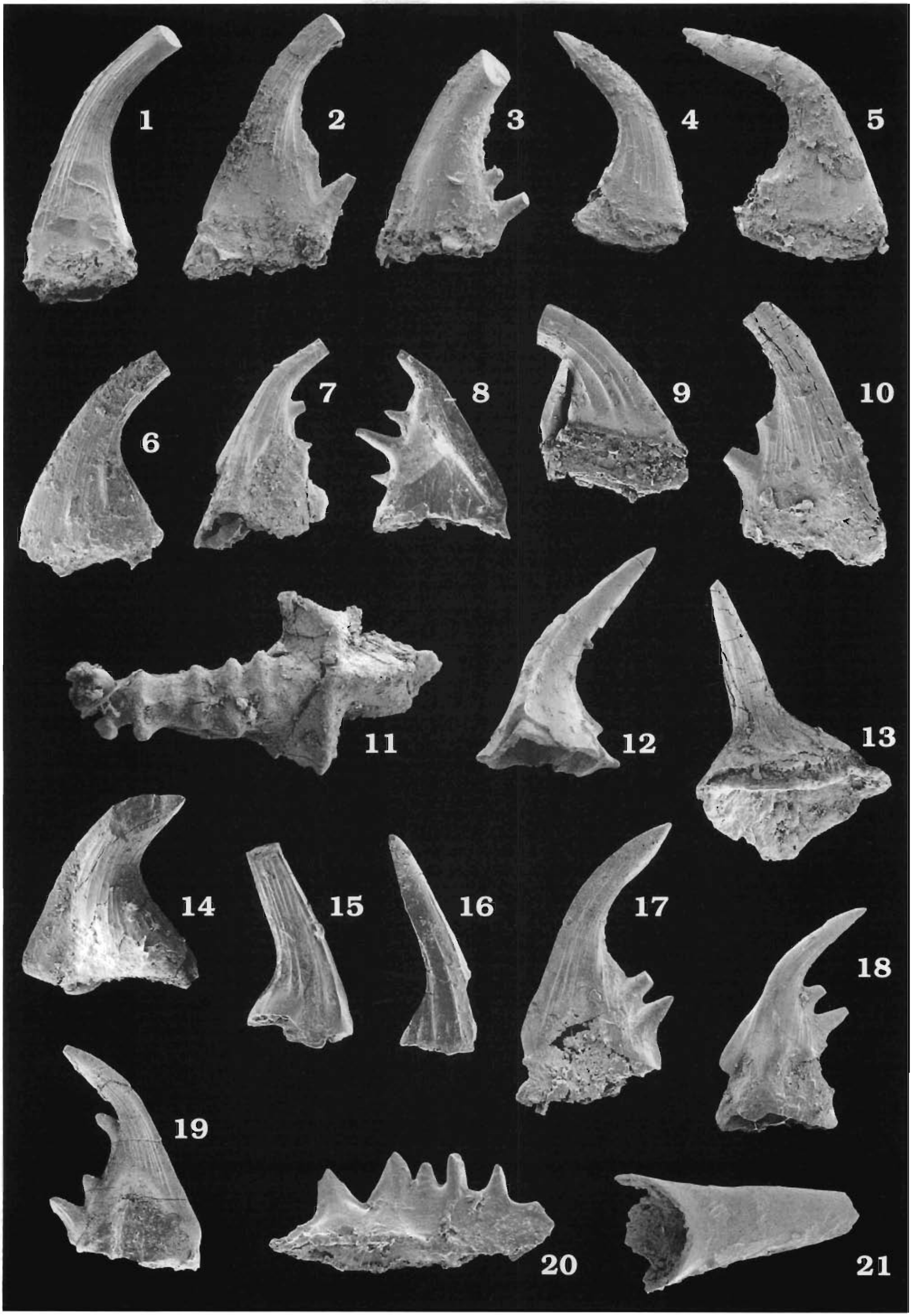
All specimens from Broken River Crossing section (BR18) or Jack Hills Gorge section (BR8), Jack Formation, coral gardens unit, *siluricus* Zone.

12. **Pb** element, (BR8 31), UQY7424 lateral view, × 60.
13. **Sa** element, (BR8 31), UQY7425 posterior view, × 90.
14. **Sb** element UQY7426, sample BR8 31, lateral view, × 90.
15. **Sb** element UQY7427, sample BR8 31, lateral view, × 90.
16. **Sb** element UQY7428, sample BR8 31, lateral view, × 120.
17. **Sc** element UQY7429, sample BR18 180, lateral view, × 90.
18. **Sc** element UQY7430, sample BR8 31, lateral view, × 60.
19. **Sc** element UQY7431, sample BR18 180, lateral view, × 60.

Pelekysgnathus sp. 161

Both specimens from sample BRH 14, Broken River Crossing section, Jack Formation, upper limestone unit, *woschmidti* Zone.

20. **Pa** element UQY7432, lateral view, × 120.
21. "Coniform" element UQY7433, posterior view, × 60.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