

# Two new iniopterygians (Chondrichthyes) from the Mississippian (Serpukhovian) Bear Gulch Limestone of Montana with evidence of a new form of chondrichthyan neurocranium

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## Abstract

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The Iniopterygia are Palaeozoic chondrichthyans whose morphology and relationships are poorly understood. The morphology of two new taxa of Iniopterygidae, *Rainerichthys zangerli* and *Papilionichthys stahlae*, from the Upper Mississippian of Montana is now described. They exhibit the iniopterygian synapomorphy of dorsolaterally placed pectoral fins. They also display a laterally compressed head and body, a homocercal tail, and a single aspinous dorsal fin originating at approximately mid-body. These taxa differ in upper dental elements, bony cranial plates, body squamation, buccopharyngeal denticles, cranial linking cartilages, palatoquadrate shape, pterygoid articulation, pectoral axis and pectoral girdle shape, and in the robustness of branchial and suprascapular cartilages. The neurocranium is unique among known chondrichthyans in presenting anterior ethmosphenoid and posterior otico-occipital units separated by an intracranial joint. A complete otico-occipital fissure is found posteriorly. One to two pairs of upper parasymphysial whorls and one median lower premandibular symphysial whorl are present. Symphysial whorls were mobile and the cranial complex appears to have been kinetic. Cladistic assessment places these new taxa as basal chondrichthyans below the divergence of the Elasmobranchii and the Euchondrocephali. The range of morphology within known iniopterygians supports rapid diversification and niche specialization in this group of atypical chondrichthyans.

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## Introduction

Chondrichthyan fishes of the Order Iniopterygia were initially described as holocephalans from the Pennsylvanian marine mid-continental black shales of Indiana, Illinois, Iowa, Missouri and Nebraska, USA (Zangerl and Case 1973). They included the genera *Iniopteryx*, *Promexylele*, *Sibyrrhynchus*, *Iniopera* and *Inioxylele*. Stahl (1980) re-evaluated the palatoquadrates of *Iniopteryx rushlaui* and *Promexylele peyeri* to be free, rather than fused to the cranium

and discussed further a putative relationship between the iniopterygians and holocephalans, and the alliance of holocephalans with elasmobranchs (rather than having independent origins in the placoderms). Zangerl subsequently updated and revised his original descriptions (Zangerl 1981, 1997) and, reported on a new, nonholocephalic form, *Cervifurca*, from the same quarry localities (Zangerl 1997). To date, these are the only published reports of iniopterygian fishes. However, there is evidence of up to six taxa from the Serpukhovian Upper Mississippian Bear Gulch Limestone

lens, Heath Formation, of Fergus County Montana. This report now describes two new taxa of Iniopterygia from the Bear Gulch Limestone, material that provides the first evidence of chondrichthyan neurocrania with an intracranial joint (generated by a ventral ethmosphenoid fissure and a dorsal joint between the orbital and otic cartilages), modification of the suprascapular cartilage into a kinetic linkage of elements between the cranium and pectoral girdle, and evidence of a passively mobile lower symphyseal cartilage supporting a dental whorl that sheared, in occlusion, between paired, upper premandibular whorls.

In describing these fish, we acknowledge the scientific contributions of Rainer Zangerl and Barbara Stahl to the study of Palaeozoic chondrichthyans and especially the Iniopterygii.

'In view of the discovery, in recent years, of new Palaeozoic fish faunas that include much unstudied chondrichthyan material, we may confidently look forward to a much better understanding of the above-mentioned relationships (sic chondrichthyan, holocephalan, and iniopterygian) as these new materials are described. Moreover, the fact that it is still possible to discover whole groups of vertebrates that have escaped our notice should once again focus attention on the probability that the fossil record is far from adequately known.' (Zangerl and Case 1973, p. 66)

## Materials and methods

### Imaging

Specimens were imaged in RGB colour with a Microtek 6000 4800 ppi colour flatbed scanner and corrected for colour casts, levels (white and black points), brightness and contrast with Adobe Photoshop, version 7.0. Images were rendered into black and white and, when necessary, reduced to the resolution required for publication, also with Adobe Photoshop software. Drawings were prepared with Adobe Illustrator, version 10.0.3, from drawings rendered with a microscope drawing tube as well as prepared from overlays of scanned fossil images. Boundaries of individual neurocranial cartilages are delineated by tessellate mineralization and, where evident, overlapping flanges of adjacent cartilages.

### Cladistic analyses

Analyses were performed upon a matrix of 31 characters (numbered 0–30), 42 Bear Gulch and non-Bear Gulch taxa, and a theoretical outgroup. Characters and character states are presented in Appendix A. Characters by taxon are presented in Appendix B. Taxa represented by codename (ElWeir, Iniopterygian1, L2SP, Chom2 and Cochliodont1) are, as yet, undescribed Bear Gulch chondrichthyans. Thrinacodont species refers to a Bear Gulch elasmobranch with thrinacodont-style teeth (Grogan and Lund, 2008). Analyses were performed using HENNIG86 (Farris 1988) and

WINCLADA (Nixon 2002) and employed slow optimization (also known as delayed or slow transformation; Kitching *et al.* 1998). Character states were treated as unordered (nonadditive).

### Institutional abbreviations

CM, Carnegie Museum of Natural History, Section of Vertebrate Palaeontology, Pittsburgh, PA; MV, University of Montana Geological Museum, Missoula, MT, ROM, Royal Ontario Museum, Toronto, Ontario, Canada.

## SYSTEMATIC PALAEONTOLOGY

CLASS CHONDRICHTHYES Huxley 1880

ORDER INIOPTERYGIA Zangerl and Case 1973

FAMILY INIOPTERYGIDAE Zangerl and Case 1973

*Typical genus.* *Iniopteryx*, Zangerl and Case 1973.

*Diagnosis.* The Iniopterygidae have been defined by Zangerl and Case (1973) and officially revised by Zangerl (1981) as nonholostylic Iniopterygia, with Meckel's cartilages not fused at the symphysis. Buccopharyngeal denticles along the margins of the jaws are unicuspid or, otherwise, simple. Enlarged symphyseal whorls are present (Zangerl 1981, p. 43). External cranial plates are absent. The Iniopterygidae are thus distinguished from the Family Sibyrhynchidae, stated to be holostylic and with mandibles fused at the symphysis.

*Included genera.* *Promexyle* Zangerl and Case 1973; *Cervifurca* Zangerl 1997.

*Geological range* – The genera *Iniopteryx*, *Promexyle*, and *Cervifurca* are Westphalian Upper Pennsylvanian of the mid-continent United States.

*Genus* *Rainerichthys*, new genus

*Type species.* *Rainerichthys zangerli*, new

*Holotype.* CM 46097, male.

*Referred specimens.* CM 27352, 35518, 41039–41041, 41089, 46093, 48525, 48526, 48677, 48835, 62858, 62862, 78515 – 78520; MV 6174, 7681; ROM 41128, 43153.

*Provenance.* Upper Mississippian (Namurian E2b, Serpukhovian) Bear Gulch Limestone lens, Bear Gulch Member of the Heath Formation, SW of Becket, Fergus County Montana, USA.

*Derivation of name.* In honor of Rainer Zangerl for his work on the iniopterygian fishes.

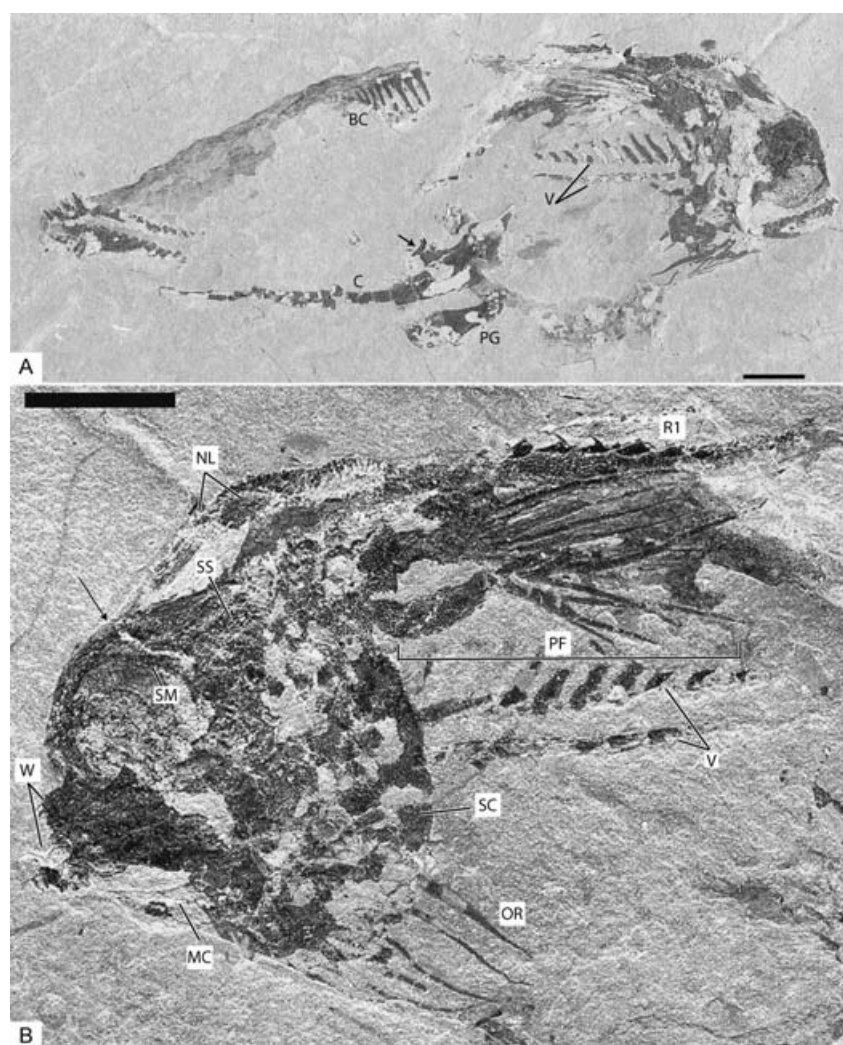
*Diagnosis.* Laterally compressed body, orbits not bound dorsally by a supraorbital cartilage. Small delicate mesial

palatal dentigerous plates, buccal plates otherwise absent; palato-buccal dentition of rows of small teeth with lateral cusplets; enlarged parasymphysial upper and median symphysial lower whorls; slim palatoquadrate with tall arcuate pterygoid process articulating with antotic process of anterior, ethmosphenoid moiety of neurocranium; neurocranium with ethmosphenoid and otico-occipital portions articulated by functional intracranial joint, plus a complete otico-occipital fissure; two small lateral and one median rostral processes; rounded slope of occipital surface down to foramen magnum; pectoral girdle linked to cranium by two paired series of cartilages; pectoral metapterygium moderately large, bearing thick first radial plus 11 others, and a multielement axis bearing four free rays; pelvic girdle with dorsal cartilage articulated with small block-like girdle element that supports the elongate triangular basipterygium laterally and the mixopterygium mesially; pelvic girdles articulate in midline; caudal endoskeleton homocercal; dorsal fin plate supports about 12 radials capable of antero-posterior mobility.

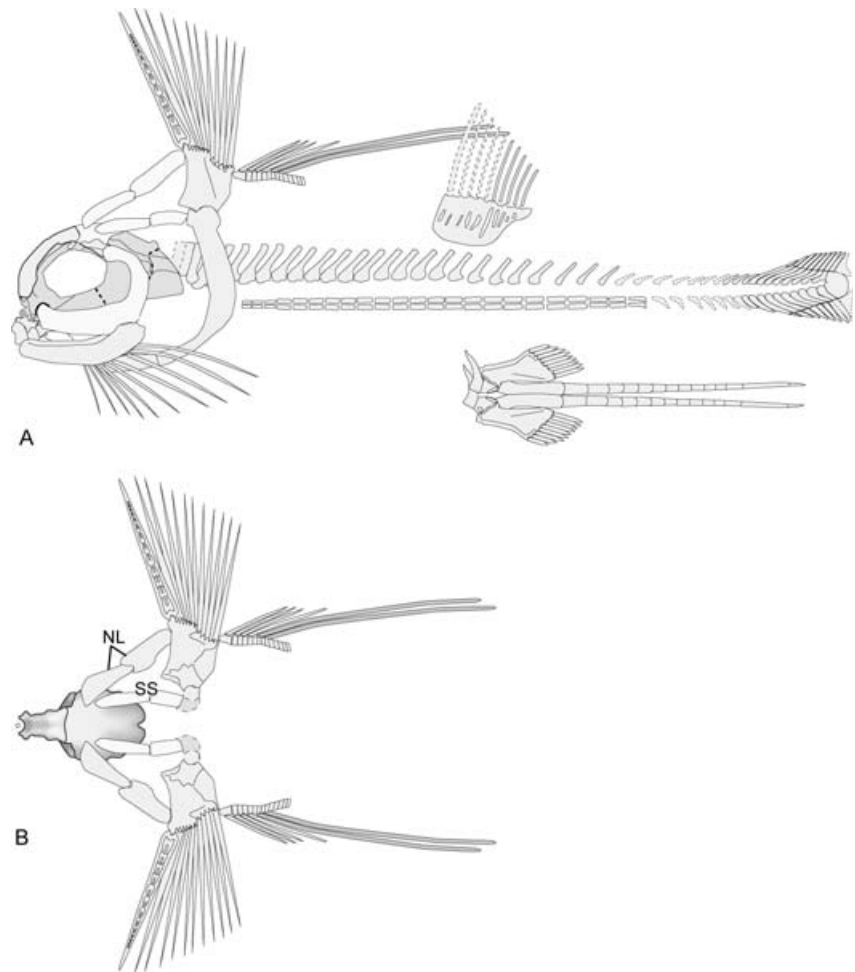
### Description

**Body form.** Operculate chondrichthyan fish with laterally compressed head and body, and homocercal tail (Figs 1 and 2). Pectoral fins articulate along the dorsolateral margins of the trunk immediately behind the head and project dorsolaterally (Figs 1–3). A single aspinous dorsal fin originates at approximately the middle of the body, at the level of the pelvic fins (Figs 1 and 2). There is virtually no caudal fin known distal to the caudal endoskeleton. Squamation is absent except along the dorsal pectoral cartilages, and anterior pectoral fin margins, of males. *Rainierichthys zangerli* sizes and proportions are: Head length 11.4–21.3 mm ( $n = 8$ , 7 specimens); Snout to dorsal fin origin 43.2–69.5 mm ( $n = 5$ , 5 specimens); Total length 95.85–128.9 mm ( $n = 4$ , 4 specimens); average head length/total length ratio 15.8.

**Neurocranium.** Neurocranial proportions relative to entire neurocranium are (average of three specimens) ethmoid



**Fig. 1**—*Rainierichthys zangerli*, holotype, CM 46097. —**A**. Whole body scan of part (side A); —**B**. Head and anterior body of counterpart (side B). Abbreviations: BC, basal cartilage of dorsal fin; C, clasper; MC, Meckel's cartilage; NL, neomorphic linking cartilage; OR, opercular rays; PF, pectoral fin; PG, pelvic girdle; R1, first ray of pectoral fin; SC, scapulocoracoid; SM, sclerotic mineralizations; SS, suprascapular cartilage; V, vertebral elements; W, whorl. Arrow, position of flanged dorsal joint. Scale bars = 1 cm.



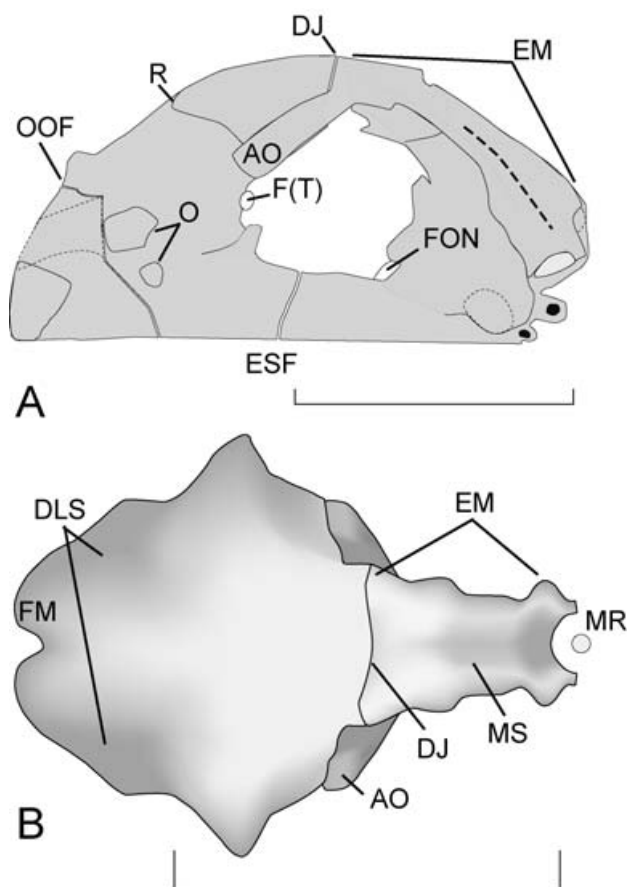
**Fig. 2**—*Rainerichthys zangerli*, restoration. —**A.** lateral view; —**B.** dorsal view of neurocranium, pectoral girdle and fin, and intervening series of kinetic cartilages. Abbreviations: NL, neomorphic linking cartilages; SS, suprascapular linking cartilages.

10.5%; orbit 45.2%; postorbital 44%. The rim of the orbit is lined by numerous small but heavy sclerotic mineralizations (Fig. 1). The margins of cranial sensory canals are merely indicated by stronger development of mineralization in underlying cranial cartilages. Many neurocrania either show midcranial post-mortem disarticulation or differ strongly in the angles between the anterior preorbital and more posterior postorbital portions of the cranium. This occurs as the neurocranium is calcified into two principal units; an anterior ethmosphenoid and a posterior otico-occipital moiety separated by an intracranial joint that is generated by a ventral ethmosphenoid fissure and a dorsal orbital joint (Figs 3–5). The overlap of the otic cartilage over the posterior edge of the ethmoid moiety forms a bevel (lap) joint. The ventral ethmosphenoid fissure presents as a discontinuity in the mineralization of the ventral neurocranium. A complete otico-occipital fissure occurs within the otico-occipital moiety, appreciably posterior to the ventral ethmosphenoid fissure (Figs 3 and 4).

The ethmoid neurocranial cartilage (akin to the tegmen cranii of *Protopterus* illustrated by Bemis (1987) is irregularly hour-glass shaped (Figs 3 and 4), widened dramatically at

the point of the intracranial joint and nasal region but generally narrowed in between, and bears a midline depression or sulcus (Figs 3B and 4B). It descends anteriorly to frame a small precerebral fontanelle along with two short dorsolateral rostral processes and a small, vertical median rostral process. Anterolaterally the cartilage is continuous with the orbitonasal lamina. A prominent articular (ethmoid) facet for the anterior end of the palatoquadrate is immediately below and behind the olfactory capsule. The floor of the orbital region narrows sharply toward a very narrow anterior ventral ethmoid. A distinct posterior dorsal process, arising posterolaterally from the ethmoid cartilage and in the position of the antotic process of coelacanth projects beyond and below the intracranial joint to lie lateral to the postorbital wall and receive the dorsal articular (pterygoid) process of the palatoquadrate (Figs 3–5).

The occipital moiety of the neurocranium is derived from the elements of 4–5 anteriormost vertebrae (Fig. 4A,B). The entire unit is approximately dome-shaped (semicircular) in lateral view, as high as it is long (Fig. 3A). Viewed from above, it presents an inflated postorbital area and a moderately broad otic wall that rises and narrows to form dorsolateral



**Fig. 3**—*Rainerichthys zangerli*, Neurocranium. —**A.** CM 41041a, anatomical illustration (specimen somewhat distorted) in lateral view; —**B.** dorsal view reconstruction, after CM 48526. Abbreviations: AO, antotic process; EM, ethmoid moiety; ESF, ventral ethmosphenoid fissure; DJ, Dorsal flanged joint of intracranial fissure; DLS, dorsolateral sulci; FM, foramen magnum; F(T), trigeminal (?) foramen; FON, orbitonasal foramen; M, midline; MR, medial rostral rod; MS, median sulcus; O, otic region with preservation of some internal features; OOF, complete oticooccipital fissure; R, ridge. Scale bars = 1 cm.

sulci (Fig. 3B). The latter accommodate a bilateral chain of cartilages that link this moiety of the neurocranium to the pectoral girdle (Figs 1B, 2B and 4). The ventral occipital surface is moderately broad.

*Jaws, other visceral cartilages and associated feeding elements.* Denticular whorls, generated by a lingual–labial fusion of individual elements, are supported by two pairs of upper premandibular parasymphysial and one median lower symphyseal cartilages (Figs 1B, 4C,D and 5). The anterior upper whorl is supported by a labial cartilage with a mesial articular facet; the location of this articulation is not clear but some specimens (CM 46097, ROM 43153) indicate that the articulation may be to rostral or other labial cartilages. The whorl bears a series of progressively posteriorly enlarged

sharp cusps. The second whorl is supported upon a narrow cartilage set into a notch in the anterolateral edge of the palatoquadrate and bears one to two robust cusps. The lower median symphyseal whorl is conspicuously larger than the anterior upper whorls. This whorl is formed by 4–5 cusps progressively increased in size posteriorly and with the bases of the cusps fused. The whorl is mounted on an anteriorly elongate cartilage that is posteriorly articulated between the anterior tips of the mandibular cartilages. This lower symphyseal whorl and supporting cartilage are evidently (passively) mobile, being found in extended position in specimens with the lower jaws depressed and rotated posterodorsally into shearing occlusion between the pair of upper whorls in specimens where the lower jaws have been elevated into the closed position (Fig. 5).

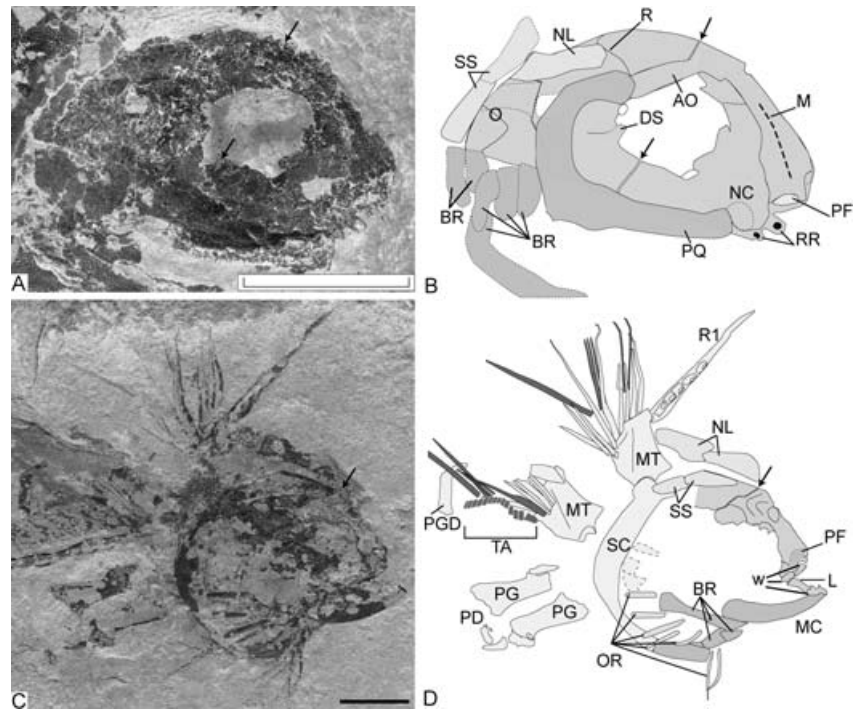
Small unicuspid to tricuspid denticles are restricted to the margins of the jaws (e.g. CM 41041, 46093, 48677) and also mark the position of the uncalcified labial cartilages (CM 46093, 62862); these delimit a small gap of the mouth at relatively closed mouth postures.

Contralateral halves of the palatoquadrate and Meckel's cartilages remain separate anteriorly (CM 48526, 62862, 78518, MV 76800). Neither bear teeth; only fine denticles, as noted above. The palatoquadrate consists of a tall, thin, pterygoid process, a thin palatine process, and a quadrate area that bears a double jaw joint with Meckel's cartilage and is suspended from the neurocranium via ethmoid and pterygoid articulations (Fig. 6). The cartilage exhibits high dimensionality and ridging, especially in suborbital span where the palatine process bears a mesial shelf that supports a small radially denticulated palatine plate (Fig. 6A,B). The pterygoid process arches and curves anterodorsally to end in a strong, rounded condyle for articulation with the antotic process of the ethmosphenoid neurocranial moiety. Meckel's cartilage is slim and of uniform height from its symphysis to the articular region, which is significantly elevated above the occlusal margin of the jaw (Fig. 6C,D). The hyoid arch supports a soft operculum; there is no evidence of a hyomandibular (Figs 1 and 6C,D).

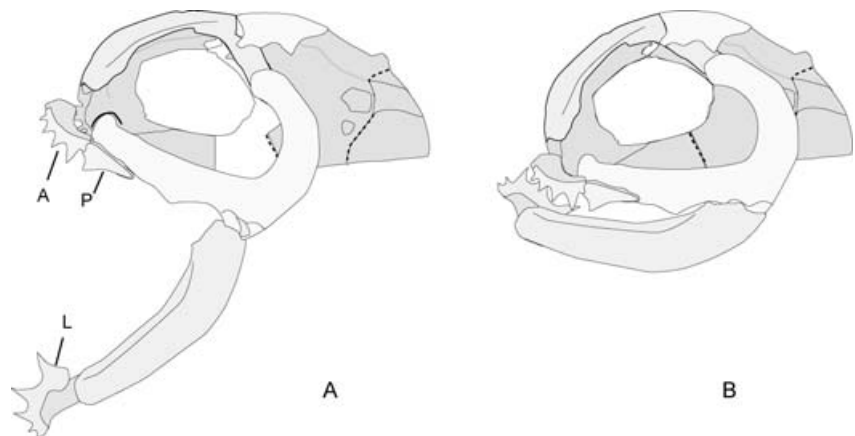
A few rows of diminutive unicuspid–tricuspid denticles of the same shape and size as those fringing the labial, palatoquadrate and Meckel's cartilages (Fig. 7) extend posteriorly into the buccal cavity. These denticles line the first branchial arches as well, and occasionally fuse basally to generate larger, more robust elements.

Traces of the branchial skeleton are preserved in most specimens (e.g. Figs 4 and 6C,D). The hyoid arch is positioned mesial to the posterior edge of the mandibular arch. The epihyal appears to be vertically oriented and independent of the palatoquadrate. At its most dorsal aspect the epihyal supports an opercular cartilage of significant size and also bears 4–5 broad, long, posterior to posteroventrally directed branchiostegal rays. Eight to nine smaller, thinner, dorsally concave rays are borne along the anterior ventral margin of the ceratohyal. Each successive branchial arch is nearly subequal

**Fig. 4**—*Rainerichthys zangerli*, Features of neurocranial, branchial pectoral, and pelvic anatomy. —**A**. Scan of CM41041a; —**B**. Anatomical rendering of CM41041a; —**C**. Scan of CM46093; —**D**. Anatomical rendering of CM46093. Abbreviations: AO, antotic process; BR, branchial elements; DS, dorsum sellae; PF, precerebral fontanelle; PQ, palatoquadrate; L, labial cartilages; M, midline; MC, Meckel's cartilage; MT, metapterygium; NC, nasal capsule; NL, neomorphic linking cartilage; O, occipital cartilages; OR, opercular rays; PD, pelvic denticle; PG, anteriorly displaced pelvic girdle; PGD, dorsal process of pelvic girdle; R, ridge; R1, first pectoral ray (denticulated); RR, rostral rods; SS, suprascapular cartilages; TA, trailing axis of pectoral fin; W, whorl and whorl cartilages. Arrows indicate the dorsal flanged neurocranial joint and ventral ethmosphenoid fissure; unlabeled dashed lines, poorly preserved margins of cartilages. Scale bars = 1 cm.



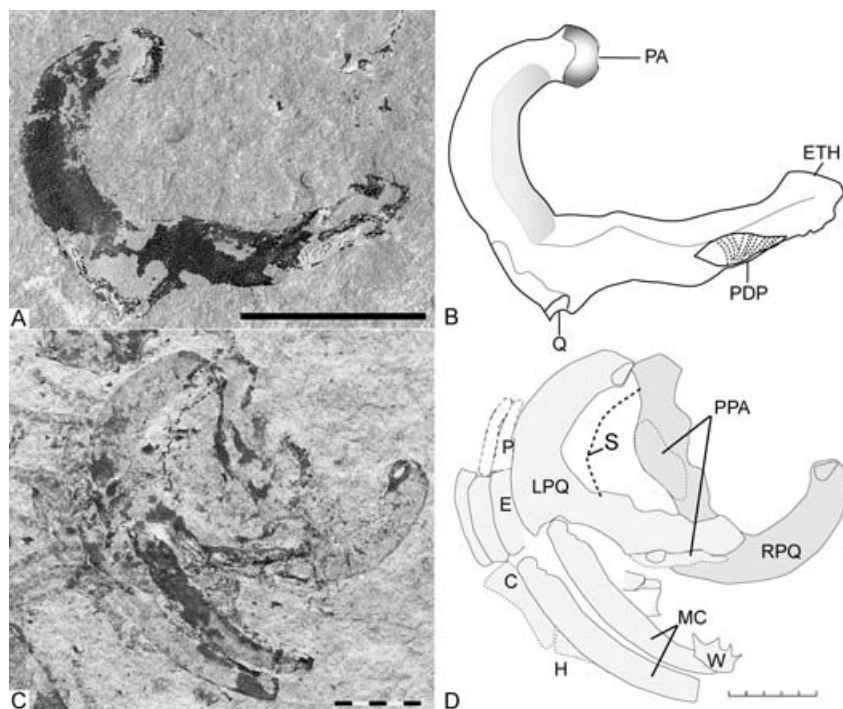
**Fig. 5**—*Rainerichthys zangerli*, reconstruction of neurocranium during jaw adduction and closure. —**A**. anterior moiety of neurocranium rotated up 150, mandible rotated down; —**B**. Head and jaws rotated closed. Abbreviations: A, anterior upper tooth whorl; L, lower, symphyseal tooth whorl; P, posterior upper tooth whorl.



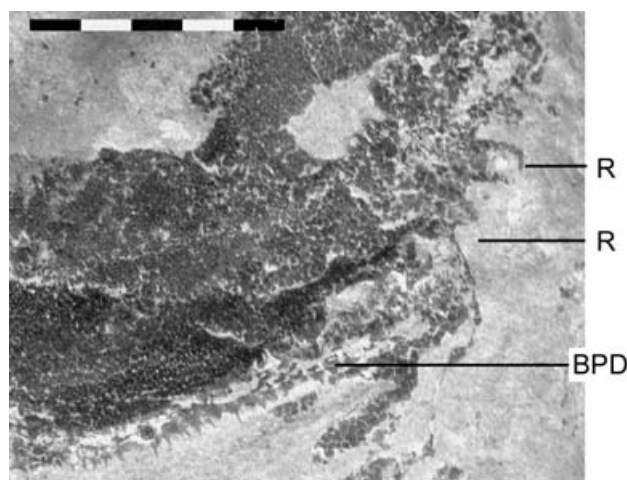
in size (neither nested in chimaeroid fashion nor miniaturizing posteriorly as in most selachians) and is positioned under the neurocranium. Within each, the ceratobranchial elements are the most prominent, presenting as broad curved elements that articulate ventrally with anteriorly elongate hypobranchials. The latter are occasionally preserved in association with chevron-shaped basibranchials. The epibranchials ( $n = 4$ ) are thin, vertically oriented elements. Thin, short saber to y-shaped pharyngobranchials are also suggested. The ventral aspect of the shoulder girdles articulates with enlarged cartilages (presumably derived from hypobranchials) which, in turn, articulate in the midline with an element likely derived from the fusion of a pair of anteriorly elongate basibranchials (CM 41041, 48677, 78518). A large foramen pierces each

side of this latter element immediately anterior to its postero-lateral articular surface. This arrangement of modified branchial cartilages thereby translated or anchored movements between the lower jaws and pectoral girdle.

**Postcranial skeleton.** The postaxial skeleton is composed of 3–4 paired occipital neurals and basals, 25 paired cervical plus abdominal neurals, six poorly calcified and diminutive precaudal neurals and haemals, 11 caudal haemal arches and spines and 10 caudal neural arches and spines (Fig. 2). The cervical and abdominal neurals are well-developed elements generally inclined in a posterodorsal direction. The cervical neurals, however, appear to be somewhat less inclined in attitude and are more closely spaced together compared to the

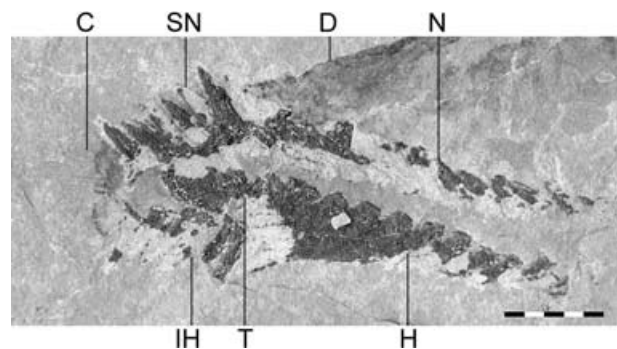


**Fig. 6**—*Rainerichthys zangerli*, scans and illustrations of splanchnocranial elements. —**A, B**, disarticulated palatoquadrate of CM 48526a; —**C, D**, jaws, palatoquadrate articular surfaces, and branchial elements of CM 62862. Abbreviations: C, Ceratal element; PA, pterygoid articulation; Q, quadratic articulation; E, epal element; ETH, ethmoid articulation; H, hypal element; LPQ, left palatoquadrate; MC, Meckel's cartilage; P, pharyngeal element; PDP, palatine denticular plate; PPA, palatine plate attachment surface; RPQ, right palatoquadrate; S, sclerotic mineralizations; W, whorl. Solid scale in cm, dashed scale = 0.5 cm.



**Fig. 7**—*Rainerichthys zangerli*, Buccopharyngeal denticles (CM 41041a). Abbreviations, BPD, buccopharyngeal denticles; R, rostral rod. Anterior to right, scale in mm.

following elements. Basiventrals of rectangular lateral shape span the entire abdominal axis. The terminal axial element shows evidence of the fusion of about 6–7 haemal spines and possibly one neural spine, to form a plate with an almost perfectly semicircular posterior edge. There are nine tightly interlocked caudal supraneurals and infrahaemals; the last of each are triangular cartilages that project posterior to the edge of the terminal plate (Fig. 8). Pigmented soft tissue remnants are present in the gap between the two elements as

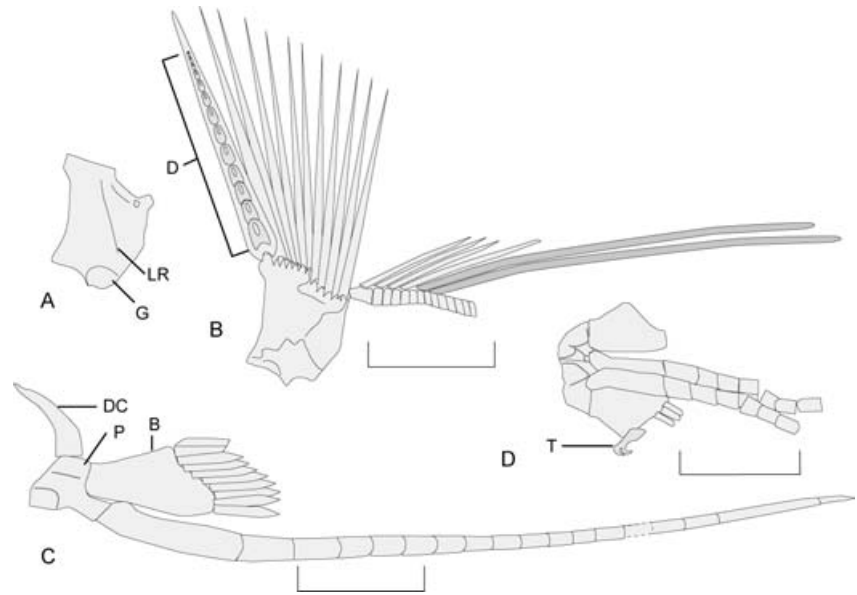


**Fig. 8**—*Rainerichthys zangerli*, Holotype, CM 46097a, caudal anatomy. Abbreviations: C, ceratotrichia; D, dorsal margin of skin; H, hemal spine; IH, infrahaemal; N, neural spine; SN, supraneural; T, terminal axial cartilage. Scale in mm.

are indications of ceratotrichia forming an externally homocercal caudal fin outline. There are no other preserved traces of skin or soft tissues beyond the caudal skeleton. The anterior edge of the dorsal fin plate falls at the level of abdominal segment 14, and the anterior extent of the pelvic girdle at approximately the level of abdominal segment 16.

**Dorsal fin.** The dorsal fin is supported upon a deeply inserted plate that bears 10 vertical calcified zones interspersed with uncalcified zones (Figs 1A and 2A). The calcified zones progressively occlude the uncalcified zones with increased size of plates. There are five serial uncalcified dorsal fin rays

**Fig. 9**—*Rainerichthys zangerli*, paired fins.  
—**A.** CM 62862, metapterygium in lateral view; —**B.** Pectoral fin in dorsal (mesial) view, principally from CM 46093; —**C.** CM 48835, pelvic girdle, fin, and clasper; —**D.** CM 78515, pelvic girdles. Abbreviations: B, basal cartilage; D, enlarged denticles of first pectoral ray; DC, dorsal cartilage; G, glenoid fossa; LR, lateral ridge; P, pelvic plate; T, tenacular denticle. Scale bars = 1 cm.



articulated with the posterior half of the dorsal fin plate of CM 35518, and articular facets that suggest an additional five anterior rays. The rays can be erected or depressed as in the first dorsal fin of chimaeroids and *Debeerius* (Grogan and Lund 2000). The anterior edge of the fin plate lies above the anterior edge of the pelvic girdle. There is no indication of an anal fin.

**Pectoral fin and girdle.** The pectoral girdle consists of a pair of tall, thin, sickle to reverse L-shaped coracoid cartilages that culminate in glenoid processes above the level of the neural arches (Figs 1B and 4C,D). The ventral ends of the coracoid cartilages articulate with paired (hypobranchial) cartilages and, more anteriorly, a median (basibranchial) cartilage. Dorsally, the coracoids articulate with two successive cartilages, the most anterior of which articulates tightly in a deep concavity of the neurocranium posterodorsal to the level of the antotic process. It is hypothesized that these two are suprascapular cartilages. Additionally, a second chain of two (neomorphic) cartilages link the anterodorsal corner of the metapterygium to the same region of the otic cartilage (Figs 1, 2 and 4).

A pectoral glenoid process articulates with the lateral surface of a transverse facet at the posteroventral corner of the metapterygium (Fig. 9A). The metapterygium is a broad, thick, robust, almost rectangular element that supports a fin of 12 tapering and distally pointed radials posterodorsally, and an axis of about 14 small blocks on a short process at its posteroventral corner (Fig. 9B). The lateral surface is divided into two fields of muscle attachment by a diagonal ridge, and the mesial surface into three fields (Fig. 9A). The axis itself supports four short, tapered, and poorly calcified rays followed by two extremely elongate, free and heavily pigmented, uncalcified rays. The elongate rays can be seen to

extend posteriorly to about the middle of the dorsal fin. The 12 fin radials are wide mesio-laterally and notched basally; the notch of each ray fitted into what appears to be a faceted groove for its reception along the edge of the metapterygium, and the rays are tightly appressed against each other basally. The bases of the first four to five rays are supported on an elevation of the edge of the metapterygium. The first ray is stout, mesiolaterally very wide at its base, and bears 11–14 large-based, anteriorly (ventrally) hooked denticles. Two successive cartilages articulate with the anterodorsal corner of the metapterygium and are anchored lateral to the suprascapular cartilage at the level of the rear of the orbit. These cartilages are thin and delicately mineralized in females. They are stout and heavily mineralized in males, and support thick pads of tightly interlocked denticles (Fig. 1B).

Independent movement of the metapterygium is severely constrained in an antero-posterior plane by its cartilaginous kinematic chain articulation with the neurocranium; movements of the neurocranium would necessarily effect movements of each metapterygium and vice-versa. There is a large expanse of surface area on the metapterygium for the origin of fin radial and axial musculature. However, as a result of the notched articulations of the pectoral rays with the metapterygium, as well as their tight basal associations, the pectoral fin rays are constrained to fore-and-aft motion upon the edge of the metapterygium. The overall relationships of neurocranial, mandibular and pectoral elements suggests a complex kinetic design.

**Pelvic fin and girdle.** Preservation demonstrates that the pelvic girdles and fins were essentially situated side-by-side on the ventral flanks (or narrow ventral surface) of the abdomen in the intact fish. Pelvic fin radials are very poorly calcified in males. Broad articular sockets suggest that there were about



six radials. Pelvic girdles of females are poorly known. It is uncertain whether they were in contact in the ventral midline, but the proximity of their ventral edges indicates that the abdomen in this region had a V-shaped cross section. Pelvic girdles of males consist of a short vertical dorsal cartilage that articulates with an angular anterior horizontal, ventral, cartilage (Fig. 9C). This element bears the articulation for the mixopterygium mesially and the unibasal cartilage (basipterygium) of the fin laterally. The basipterygium is socketed to support 9–10 short thick radials, and bears laterally a single broad-based denticle mounting two sharp, anteriorly curved distal cusps. The clasper is approximately one-third the total length of the fish, and consists of a long narrow proximal axial followed by 15 short distal axial elements and 1–2 thin tapering terminal axial elements. The shorter axial elements are each deeply concave anteriorly and strongly convex posteriorly.

**Squamation.** Secondary sexual cervical, pectoral, and pelvic patches of scales are strongly developed. The two cartilages that link the metapterygium to the neurocranium of males bear tightly packed pads of posteriorly curved single cusped denticles. A single row of 11–12 large denticles with distal, proximally curved, sharp cusps courses immediately lateral to the leading edge of the first radial of the pectoral fin. One double-cusped long-based tenacular denticle is associated with the lateral aspect of the pelvic basipterygium of males, but its precise placement is highly variable among the specimens.

While traces of the cranial lateral lines can be found impressed into cranial cartilages, there do not seem to be any scales associated with these canals and lateral line canals cannot be distinguished on the body. A few small denticles are irregularly distributed on the head. Fine, sparse, unicuspid

scales are found dorsal to the dorsal fin basal plate. Squamation is otherwise absent.

Genus *Papilionichthys*, new genus

*Type species.* *Papilionichthys stahlae*, new species.

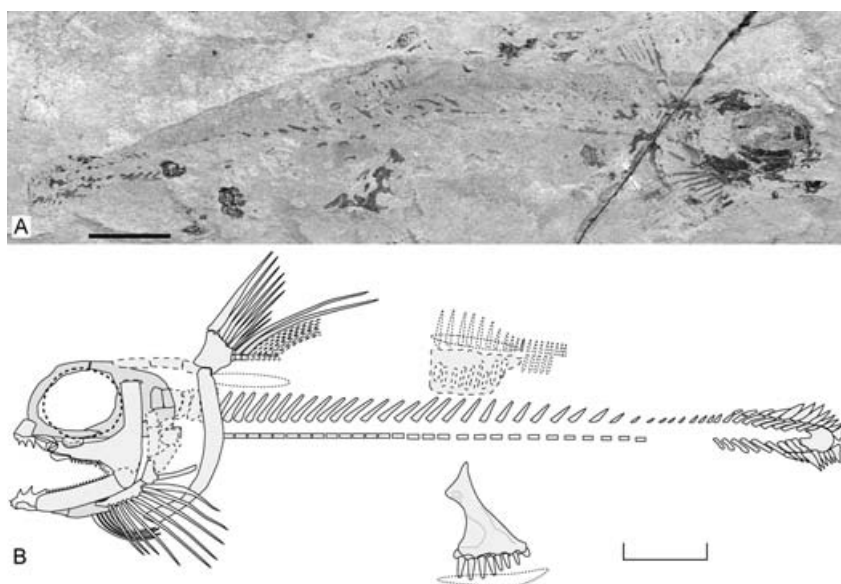
*Holotype.* MV 6170, juvenile.

*Referred specimens.* CM 62857, 62863 and MV 7680, 7682.

*Provenance.* Upper Mississippian (Namurian E2b, Serpukhovian) Bear Gulch Limestone lens, Bear Gulch Member of the Heath Formation, SW of Becket, Fergus County Montana, USA.

*Derivation of name.* Papillon (butterfly), -ichthyes (fish), and (stahlae) in honour of Barbara Stahl who was the first to recognize the condition of the iniopterygian wing-like pectoral fin being positioned at the nape of the neck.

**Diagnosis.** Operculate chondrichthyan fishes with laterally compressed bodies entirely covered with a delicate, simple shagreen of denticular placoid scales with concentrations distal to dorsal and pelvic cartilages; pectoral fins situated at the nape of the neck, a single, low, aspinous dorsal fin, internally and externally homocercal tail (Fig. 10). Cranium comprised of separate ethmosphenoid, otic and occipital units, the latter derived from two transformed vertebral units. A chain of suprascapular cartilages ( $n = 3$ ) provide a kinetic linkage between scapula and dorsal surface of otic cartilage, approximately at a postorbital level. Pectoral metapterygium moderately large, bearing about eight radials and axis of nine basals and eight radials. Pelvic girdle a single vertical curved cartilage supporting radials laterally on the



**Fig. 10**—*Papilionichthys stahlae*. —**A.** scan of holotype, MV 6170b; —**B.** reconstruction principally based on holotype but also MV7680 (dorsal and pelvic fins and girdles) and all specimens (neurocranium and splanchnocranium). Scale bars = 1 cm.

ventral edge; girdles in close proximity in midline. Large delicate mesial palatal dentigerous plates, other buccal plates either sparse or absent; palatobuccal dentition of fine unicuspid teeth; enlarged upper parasymphysial and lower symphyseal tooth whorls supported on separate labial cartilages; broad palatoquadrate with tall vertical pterygoid process articulating dorsally on otic moiety of neurocranium.

**Comments.** Five specimens share the axial/caudal skeletal structure and basic construction of the head (including fissures, orbital joint, and occipital moiety) with *R. zangerli*. They differ, however, in a number of important morphological details. Ethmoid dorsal surfaces are shorter and significantly narrower and there is no evidence of an antotic process as found in *Rainerichthys*. The slope of the otic moiety in its descent to the occipital is steeper. The wide, cross-sectionally thin pterygoid process of the palatoquadrate articulates against the edge of the otic braincase, dorsal to the quadratic articulation. The anterior (palatine) process is significantly wider and the denticulated palatal plate is approximately double the size of that of *R. zangerli*. The ventral branchial elements appear to be more robust than those of *R. zangerli*. The coracoid cartilage is somewhat arcuate but is more vertically oriented. Both the scapular and suprascapular elements are less robust, more delicate, than in *R. zangerli*. A series of two, rather than 4–5, arcualia are tightly associated with the occiput. The pectoral metapterygium is essentially rectangular, rays are narrower and the axial extension bears more rays. Pelvic girdles of females were large, vertically orientated and extended to the level of the vertebral basiventrals, with articular facets on the ventrolateral edge of the girdles

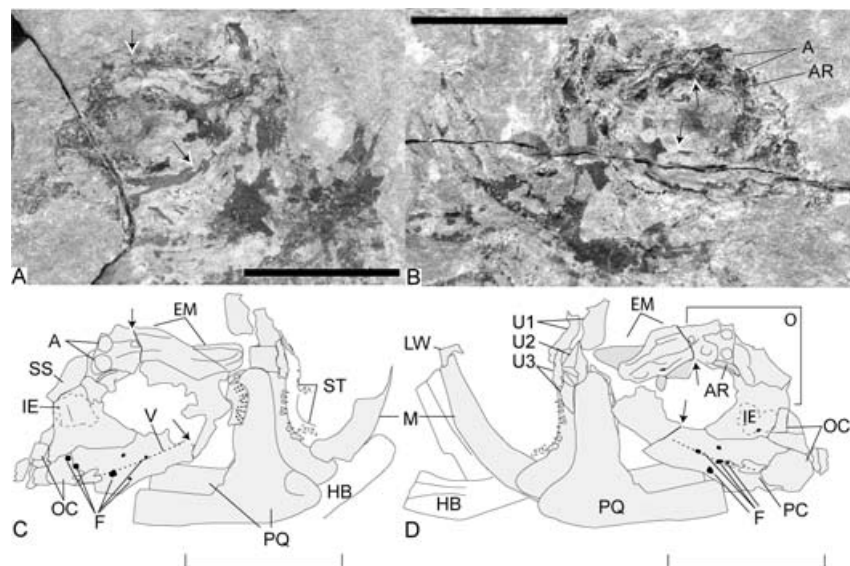
for about 6 uncalcified radials. Males are not known. The dorsal fin plates appear to have an elongate narrow posterior process and are followed by several separate basidorsals and radials. A fine shagreen of denticles covers the body.

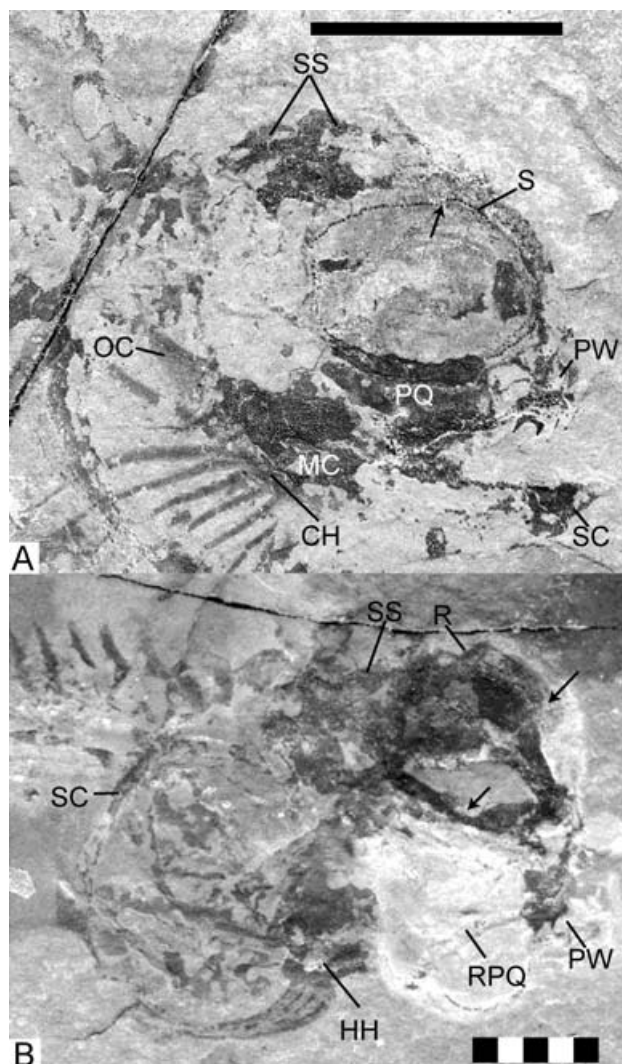
### Description

**Body form.** Overall body form generally follows that described for *R. zangerli* with the exception of denticles covering the body and males unknown. *Papilionichthys stahlae* sizes and proportions are: Head length 12.6–19.3 mm ( $n = 6$ , 4 specimens); Snout to dorsal fin origin 43–56.1 mm ( $n = 3$ , 3 specimens); Total length 94.5–103.1 mm ( $n = 2$ , 2 specimens); average head length/total length ratio 12.7.

**Neurocranium.** The cranium is comprised of ethmosphenoid, otic and occipital units (Fig. 11). The ethmosphenoid unit is broadest above the orbits, narrowing markedly anteriorly before descending ventrally and expanding to meet with the nasal capsules, located immediately anterior to the palatoquadrates. There is a narrow trabecular plate, receiving the small ethmoid articulation of the palatoquadrate, and extending to approximately midorbital level, where an ethmosphenoid fissure exists between it and the basal plate (Figs 11 and 12B). The flanged association between ethmoid and dorsal otic cartilages (dorsal cranial joint) is variably disarticulated in some specimens (CM 62857, MV 7680, 7682). An intracranial joint is generated by the combination of the dorsal joint and the ethmosphenoid fissure. Suborbital and supraorbital cartilages or shelves are absent. No preorbital or postorbital processes are developed. The dorsal margin of

**Fig. 11**—*Papilionichthys stahlae*, head, MV 7680. —A. part, and —C. illustration; —B. counterpart, and —D. illustration. Head appreciably dissociated so that the anterior of neurocranium is toward middle of page, the anterior of displaced palatoquadrates is toward top of page. Scale bars = 1 cm. Abbreviations: A, sites interpreted as articular surfaces for the suprascapular cartilage chain; AR, articular facet for pterygoid process of palatoquadrate; EM, ethmoid moiety; F, foramina in floor of neurocranium; HB, ventral hyobranchial structures; IE, features of inner ear anotomy; LW, lower symphyseal whorl; MC, Meekel's cartilage; PC, parachordal region of otic unit; PQ, palatoquadrate; O, otic moiety; OC, occipital elements; SS, suprascapular linking cartilage; ST, limit of labial soft tissue traces; U1, U2, U3, first, second, and third upper dental plates. Arrows indicate positions of the dorsal flanged joint and ventral ethmosphenoid fissure that constitute the intracranial joint.





**Fig. 12**—*Papilionichthys stahlae*. Neurocranial and splanchnocranial features. —**A**. Holotype, MV6170b; —**B**. MV 7682a.

Abbreviations: CH, ceratohyal with associated opercular rays; HH, hypohyal with associated opercular rays; OC, opercular cartilage; PW, parasymphysial whorl and supporting cartilage; R, otic ridge; RPQ, right palatoquadrate; S, sclerotic mineralizations; SS, suprascapular cartilages.

the otic cartilage is obliquely oriented as it descends to meet the occipital unit, thus accommodating bilateral chain of suprascapular cartilages and, presumably, the associated pectoral and epaxial muscles and ligaments (Figs 11 and 12). Large otic capsules are indicated, with evidence of some internal features. The anteriormost two vertebral elements are modified to form the discrete occipital unit, even as the constituent elements remain identifiable (Fig. 11).

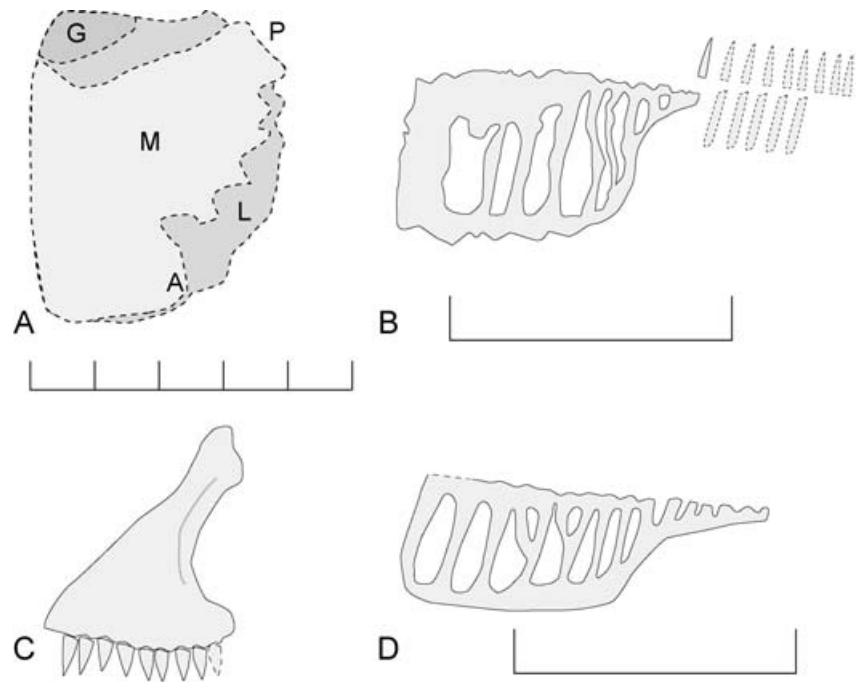
*Jaws, other visceral cartilages and associated feeding elements.* There are three paired upper dental units and paired palatal

plates (Fig. 11). The anteriormost, immediately anterior to the palatoquadrate and at the tip of the ethmoid, is a denticular whorl supported on a vertically oriented cartilage with an expanded base to accommodate the whorl (Fig. 12A). The whorl bears cusps that increase in size posteriorly. The second and third dental units are thick plates with undetermined occlusal surfaces, supported by labial cartilages. Of these the second is located anterior to the palatoquadrate, the second occurs lateral to the palatine portion of the palatoquadrate. The overall shapes are narrow, elliptical and oblong, ovoid, respectively. A radially tuberculated thin plate is located on the mesial aspect of the palatoquadrate at midorbital level. The anterior upper denticular whorls have a shearing occlusion with a median lower whorl, which is supported by a relatively small symphyseal cartilage located between and projecting anterior to the anterior ends of the lower jaw cartilages (Figs 10 and 12). Cusps increase in size posteriorly. Upper and lower jaw margins are lined by minute unicuspid denticles, tending to aggregate or fuse at the rear margins of the jaws as illustrated in Fig. 11. The denticles are not attached to the jaws but appear to be borne in soft tissue anterior to the rims of the jaw cartilages.

Palatoquadrates are not fused to the neurocranium (Figs 11 and 12). The highly contoured palatine process has a narrow ethmoid articulation, expanding to a broad, tall pterygoid process. The oral margin curves downward to the quadrate at a 35–45° angle. The quadrate–mandibular articulation is borne upon the internal face of the quadrate lamina. Mandibles are slender and uniform in height throughout.

The hyoid closely approximates the rear mandibular arch margin and supports a membranous opercular covering through numerous cartilaginous rays; 8–9 robust rays arising from the ceratohyal, 4–5 thinner and strongly posteriorly recurved from the hypohyal (Figs 10 and 12). An indeterminate number of additional supports are associated with a pharyngohyal or opercular cartilage. Four branchial arches follow, decreasing in size posteriorly but not nested in chimaeroid fashion. Arrays of stout basibranchials and hypobranchials are indicated. Some basibranchials present as a roughly triangular median elements with their apex posteriorly directed. The posteriormost hypobranchials articulate posteriorly with the ventral aspect of the coracoid cartilage and remain separate anteriorly. The branchial region is devoid of buccopharyngeal denticles, tuberculated plates or whorls.

*Postcranial skeleton.* The vertebral axis is composed of 37 trunk, 3 occipital and 10–11 caudal vertebral segments (Fig. 10). Neurals are robust, elongate and posterodorsally inclined. Those of the occipital series are broad and adopt a more anterodorsal inclination. A series of 5 neural elements are associated with the dorsal fin basal plate. Rectangular shaped, paired basiventral elements can be traced posteriorly, to body segment 33. The internally homocercal caudal fin skeleton is made up of 10 neurals and 10–11 supraneurals,



**Fig. 13**—*Papilionichthys stahlae*. —**A**. MV 7682, pectoral metapterygium, mesial view. —**B**. MV 7680, dorsal plate and fin radials. —**C**. CM 62857, left pelvic girdle and radials in lateral view. —**D**. CM 62857, dorsal fin plate. A, scale in mm; B–D, scale = 1 cm; anterior to left. Abbreviations: A, axial articular face; G, glenoid facet; L, lateral lamina; M, mesial lamina; P, articulation for first pectoral ray.

9 haemals, 9 infrahemals and a terminal plate with a circular posterior margin.

**Dorsal fin.** The basal plate of the dorsal fin consists of a minimum of 8–10 irregularly vertical mineralized zones interspersed with nonmineralized zones (Figs 10 and 13B,D). The basal plates of the different specimens terminate in a variably extended process, and are followed by a minimum of eight faintly mineralized or unmineralized separate basidorsals and radials.

**Pectoral fin and girdle.** The pectoral girdle is comprised of separate suprascapular ( $n = 3$ ) and scapulocoracoid elements. The suprascapulars form a kinetic linkage to the cranium, articulating anteriorly along the dorsal surface of the otic cartilage, in close proximity to the dorsal aspect of the ethmosphenoid joint (Figs 11 and 12). The scapular articulation to the pectoral fin forms a ball-shaped condyle, received by a corresponding fossa in a rhomboidal, enlarged metapterygium. The metapterygium has broad lateral laminae that project over the articular surfaces for the eight robust, distally tapering fin radials, the glenoid condyle and the attachment of the pectoral axis (Fig. 13A). The postmetapterygial axis has a minimum of nine basal cartilages that support two large proximal free rays and at least six thin short radials. Whether the last six rays are free or support a fin web is not known. The ventral aspect of each pectoral girdle is linked to the branchial apparatus through paired, elongate cartilages interpreted as modified hypobranchials.

**Pelvic fin and girdle.** The pelvic girdles are vertically oriented in the lateral body wall and in tight proximity ventrally, but separate from each other (Fig. 10A). No reliable evidence of claspers is preserved. The ventral edges of the girdles are sculpted to accommodate articulations for approximately eight weakly mineralized rays (Fig. 13C). No other features of the fin are preserved.

**Squamation.** The type specimen reveals an even distribution of very fine, stellate-based placoid scales. Other specimens reveal slightly enlarged scales along the dorsal and ventral body margins in proximity to the pectoral, dorsal and pelvic fins.

## Discussion

Iniopterygians are, by definition, chondrichthyans given their possession of a tesserate-mineralized cartilaginous endoskeleton and pelvic claspers in mature males. Iniopterygian synapomorphies are pectoral fin at nape of the neck, specialized pectoral metapterygium, all rays of the main body of the pectoral fin borne upon a large rhomboidal metapterygium, a postmetapterygial axis with free trailing rays, absence of a first dorsal fin; absence of lateral line canal scales, sexually dimorphic squamation, and articulation of all pelvic radials to the pelvic plate.

To date, the Iniopterygiformes (Zangerl and Case 1973; Zangerl 1997) have been comprised of six genera (eight species), all of which are Pennsylvanian in age. The Bear Gulch Limestone of Montana has yielded at least seven different forms of iniopterygians over the past 39 years of field work.

The description of two new forms, *R. zangerli* and *P. stahlae*, now extends the range of these fishes to the upper Mississippian.

All of the *R. zangerli* identified in this study are either mature males or juveniles, the latter for which anatomical information is inconclusive for sex. All of the specimens of *P. stahlae* are either females or juveniles. The authors are confident that the differences between the two taxa cannot be attributed to sexual dimorphism. The degree of difference in cranial, palatoquadrate, and branchial morphology and pectoral and suprascapular elements argues against sexual dimorphism as an explanation for the observed variation. The balance of observations justifies taxonomic distinction between the two forms.

These new taxa, as well as the other specimens of Bear Gulch iniopterygians, show similarity with the Pennsylvanian taxa with regard to general body form, disposition and general design of the pectoral fin and girdle, dorsal fin support, sexually dimorphic squamation, early calcification of the endoskeleton and, to the best of our knowledge, the branchial arch elements. There is appreciable variation between and within the Mississippian and Pennsylvanian forms with regard to neurocranial design, specialized scales, buccopharyngeal elements and the relation of the palatoquadrate to the cranium.

*Rainerichthys zangerli* and *P. stahlae*, as the other members of the family Iniopterygidae, are unique among the known iniopterygians in the absence of external denticles that take on the appearance of greatly enlarged plates, cones, or other tuberculated variants of dermal/epidermal elements that can armour the head and body of these fishes. They do not exhibit any jaw-associated teeth or tooth plates, only unicuspid or tricuspid jaw-fringing denticles, labial denticles, buccopharyngeal denticles, a denticulated palatine plate, and symphyseal and parasymphyseal denticular whorls. Unlike the Sibyrhynchidae (Zangerl 1981, 1997), the Iniopterygidae, including these new taxa, exhibit a basal plate of the dorsal fin and an internally homocercal caudal fin that includes a terminal plate formed from the fusion of several neural and haemal elements.

The jaw suspension shows a range of variation in the Bear Gulch and non-Bear Gulch iniopterygians alike. Most notable is that none of the Bear Gulch forms recovered to date are holocephalic. Rather the suspensorium ranges from autodiastyle (Grogan 1993; Grogan *et al.* 1999; Grogan and Lund 2000) to that illustrated by the new taxa. Details of this variation and that of the corresponding branchial arch design are the subject of a more comprehensive analysis to be discussed elsewhere. Yet, to the extent that the new taxa document some of this variation they are discussed below.

The general morphology of the ethmoid cranium and palatoquadrate suggest that the palatine aspect of the palatoquadrate may have accommodated a preorbitalis muscle originating on the lateral surface of the ethmoid. Beyond this, there are bold differences in the palatoquadrates. The palatoquadrate of *R. zangerli* bears a tall, narrow pterygoid process capped by a strongly mineralized and rounded condyle

that articulates with a posterior (antotic) process on the ethmosphenoid moiety of the braincase. This articulation appears to have provided some lateral rotation of the palatoquadrate during feeding. Comparatively, *P. stahlae* exhibits a broader palatal component of the palatoquadrate and a plate-like pterygoid that engages in a much more reduced articulation subject to little mobility. That this articulation occurs on the otic moiety (in contrast to an antotic process) and that the number and robustness of the cartilages linking the shoulder girdle and cranium are also reduced in this taxon relative to the former also suggests significant differences in the kinetics of the mandibular–cranial–pectoral linkages between the two taxa (see Discussion below).

The disposition of the upper whorl-bearing elements suggests that they are premandibular arch cartilages that served as the principal feeding apparatus. Such vertically inclined, whorl-supporting cartilages are not unique to the new taxa, as they have been identified in other Bear Gulch chondrichthyans and are components of a premandibular feeding apparatus that does not rely upon the mandibular arch for support of the dentition (Grogan and Lund, in prep.). It is notable that separate paired mandibular symphyseal cartilages and a rotating lower symphyseal whorl (tusk) have also been reported in *Onychodus* (Andrews *et al.* 2006).

The feeding mechanism of *R. zangerli* presents a design that is entirely new for chondrichthyans. It is one that relies on the apparent mobility provided by the symphyseal and parasymphyseal whorls, and the intracranial joint. The potential for cranial kinesis may have been further enhanced by linkage of the otic cranial moiety to the pectoral girdle by a jointed series of modified suprascapular (and, in *R. zangerli*, additional neomorphic) cartilages and, so, influenced the efficiency of prey capture. Our preliminary biomechanical assessment of this design also suggests a jaw and lower symphyseal mechanism specialized for speed and shearing action. Limited palatoquadrate mobility and opercular movements would have principally influenced changes in buccopharyngeal volume and pressure. With regard to other gnathostomes, it would appear that kinetic linkage system described here is convergent with that of coelacanth and onychodontids, although more complex in the number of components involved.

The vertically oriented pelvic girdles of *P. stahlae* are unique among known Iniopterygiformes, although separate dorsal cartilages are known from *Iniopteryx* (Zangerl and Case 1973) and *Rainerichthys*. The great height, orientation, mineralization, and massive size of the pelvic girdles of these juvenile and female individuals relative to the pelvic fins argue against the vertical girdle being specialized specifically for pelvic fin or clasper control. Rather, the posterior concavity and the orientation of the girdles suggest they serve as the site of origin for caudal musculature of considerable size.

Tenacular hooks are associated with the pelvic fins of males of *Iniopteryx*, *Promexyle* and *Rainerichthys*, but are not borne on pelvic or prepelvic tenacular cartilages as in

Chimaeriformes (Didier 1995). Rather, they are reminiscent of the tenacular plates of ptyctodont arthrodires (Young 1986).

The evidence from the weakly mineralized pelvic and unmineralized dorsal radials of *Rainerichthys* and *Papilionichthys* suggests that the fins of the Iniopertygiformes were all aplesodic, and that there was a considerable extent of unmineralized and unpigmented caudal fin beyond the short, strong, homocercal caudal endoskeleton (Fig. 8).

The terminal caudal axial plates are similar among the Iniopertygidae; the preceding dorsal and ventral vertebral elements are more robust and closely associated in *Rainerichthys* than in *Papilionichthys*. Sibyrhynchidae apparently lack a terminal axial plate.

The Iniopertygidae share noteworthy adaptive specializations. The sclerotic ring of mineralizations, referred to by Zangerl and Case (1973) as significantly enlarged prisms of calcified cartilage in *Iniopertyx*, delineates of very large eyes. The premandibular whorls of sharp bladed cusps are in shearing occlusion and supported on small mobile cartilages. The proportions of whorls and jaws indicate that speed of closure was the primary mechanical adaptation. This was coupled with kinetic arrangements of neurocranium and pectoral girdle to present a gracile feeding mechanism adapted for shearing of rather soft materials. The axially stiffened homocercal caudal endoskeleton suggests specialization for acceleration, emphasized in *Papilionichthys* by the vertical pelvic girdle. The primary propulsive thrust for normal swimming would have been provided by the pectoral fins. Aplesodic fins (Wilga and Lauder 2004) and weakly to unmineralized postpectoral fins also suggest specialization for manoeuvrability and acceleration. Long free trailing rays of the pectoral fins parallel those of the modern teleostean family Triglidae, where they have touch and chemosensory functions (Lagler *et al.* 1962). Compressed bodies and the absence of or much reduced squamation suggest upper water column habitats.

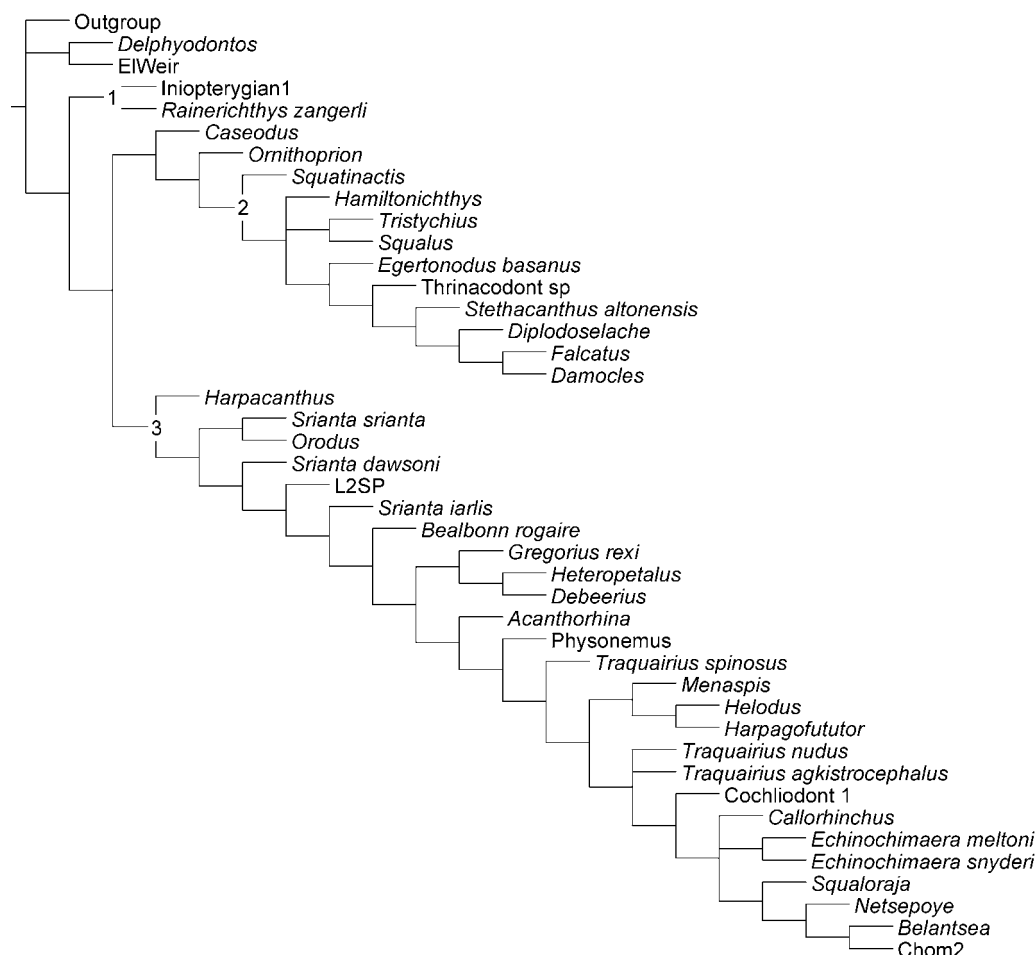
#### *Iniopertygian morphology relative to other fishes*

With their description of the first iniopertygian fishes, Zangerl and Case (1973) listed putative structural affinities between the iniopertygians and the elasmobranchs and chimaeroid holocephalans, respectively. The elasmobranchian features that we can confirm (aplesodic fin design and terminal mouth) are generalized for Palaeozoic elasmobranchs. Of the latter, they cite an autostylic jaw suspension, the membranous operculum, tenacular hooks, general absence of skin denticles, elaborate male claspers, and tendency to form fused dental elements as features that support a closer relationship of the iniopertygians to chimaeroid holocephalans. Thus, Zangerl and Case (1973) proposed the iniopertygians to be the sister taxon to the holocephalans, united on the presumption that autostyly (holostyly) is synapomorphic for the two. Despite her discovery that two of the five genera of iniopertygians described by Zangerl were nonholocephalic,

Stahl (1980) argued for the retention of the iniopertygians within a holocephalan assemblage (later identified by Zangerl (1981) as the Subterbranchialia given similarities in general body form and possession of an opercular flap. The nonholostylic forms (*Iniopertyx* and *Promexylele*) were considered by Stahl to represent primitive holocephalans which retained the unfused palatoquadrate condition from elasmobranch ancestors.

Certainly, the new, and older, iniopertygian taxa described in this paper emphasize that early iniopertygian jaws were nonholostylic and that variation existed in the extent of skin denticulation and possession of 'tenacular hooks'. Furthermore, research subsequent to the first introduction of the iniopertygians has illustrated that the chimaeroids holocephalan features cited above, the basis for a putative iniopertygian-holocephalan sister relationship, are shared by a greater range of non-elasmobranchian chondrichthyans or gnathostomes in general, and subject to convergence or parallelism. Holostyly, the suspensorial state of holocephalic chondrichthyans (Gregory 1904), has arisen multiple times within the chondrichthyan lineage (Gregory 1904; Stahl 1980; Zangerl 1981; Lund 1990; Grogan 1993) and the operculate condition is interpreted as plesiomorphic for gnathostomes (Grogan 1993). Structures identified as ptyctodont claspers (Miles and Young 1977; Young 1986) suggest affinity to the iniopertygian pelvic tenacular denticles. The ability to form tooth whorls or other fused dental elements appears to be plesiomorphic for gnathostomes (present in placoderm, chondrichthyan, acanthodian, sarcopterygian and actinopterygian groupings). Therefore, despite some similarity in overt appearance, the balance of morphological characters does not support a closer affinity of the iniopertygians with either elasmobranchian or holocephalan chondrichthyans *per se*.

Rather, the data suggest that a broader perspective is more appropriate in assessing the relationship of iniopertygians to other chondrichthyans and to gnathostomes at large. This is further substantiated by the following observations. A premandibular feeding apparatus (whether mobile or not) and a cranium that can be resolved into ethmosphenoid and otico-occipital units are features not traditionally associated with the chondrichthyan condition. These features and the association of the pectoral girdle to the cranium, albeit through the intervention of a kinetic linkage of cartilages in the new iniopertygians, generally parallels the osteichthyan condition. The information available on the branchial architecture presents a style that is somewhat distinctive from the elasmobranchian or holocephalan plans. The branchial arches are effectively constrained beneath the cranium and covered by a membranous operculum. However, they do not appear to be nested, as in holocephalans, and a coracoid-hypobranchial association is suggested. The ceratohyal either occurs in two parts or, as is interpreted here, the hypohyal bears rays reminiscent in position to gular rays of actinopterygians.



**Fig. 14**—Cladistic analysis of the relationships of Iniopterygia, based on 31 cranial characters and 44 taxa. Numbered nodes: 1, Iniopterygia; 2, Elasmobranchii; 3, Euchondrocephali. The positions of *Caseodus* and *Ornithoprion* appear to be an artifact of missing data for each taxa in this character assemblage. This matrix is coded as C53Z in the database of Bear Gulch files.

**Cladistic analysis** A more comprehensive and robust assessment of iniopterygian interrelationships is anticipated with the description of several additional taxa of Bear Gulch Limestone Iniopterygiformes, forms which are older than those currently described in the literature. In the interim, however, a preliminary analysis of iniopterygians relative to other chondrichthyans was performed with HENNIG86 (Farris 1988) and WINCLADA (Nixon 2002) using a matrix of 31 cranial characters and 42 taxa and a theoretical outgroup (Appendices A and B). We specifically note that this matrix was not constructed to discriminate between *R. zangerli* and *P. stahlae*, as they are best discriminated by inclusion of details of the postcranial anatomy. Rather, the design employs two well preserved, well documented and distinct Bear Gulch iniopterygian taxa (*R. zangerli* and an undescribed form code named Iniop 1) to reassess the position of iniopterygians relative to other chondrichthyans on the basis of cranial information that is available for a number of taxa.

The analysis yields two trees that vary in the relationships of the menaspid Holocephali alone, one of which is presented (Fig. 14). Using these particular characters places two taxa (*Delphyodontos* and *ElWeir*) basal to all other Chondrichthyes, and one clade, the Iniopterygiformes containing *R. zangerli* and Bear Gulch Iniopterygian 1 (Fig. 14, node 1), that falls as sister group to both the Elasmobranchii and the Euchondrocephali (Fig. 14, nodes 2 and 3, respectively).

We emphasize that the cladistic analysis presented herein of the iniopterygians is preliminary as it does not include the complete suite of information presented by Bear Gulch and non-Bear Gulch forms. Nevertheless, the following statements may be made given the data at hand. The Iniopterygians and other select Devonian-Carboniferous chondrichthyans are separated from the rest of the cartilaginous fishes by virtue of the neurocranial moieties, fissures and/or joints that they exhibit and by the linkage of pectoral girdle to the neurocranium through the intervention of a

series of cartilages, presumably of suprascapular derivation. The plesiomorphic condition of the Iniopterygian neurocranium is a structure principally comprised of ethmosphenoid and otico-occipital units delimited by an intracranial joint. A complete otico-occipital fissure divides the latter unit into otic and occipital moieties. The data suggests that the Iniopterygian cranial condition is plesiomorphously closer to the actinopterygian, acanthodian and sarcopterygian conditions than previously considered, despite the question of homology regarding the intracranial joint and ventral fissure of the iniopterygians relative to other major gnathostome groups. Similarly, within the Iniopterygiformes, the plesiomorphic condition is for an unfused palatoquadrate. Further, the functional feeding apparatus is composed of both premandibular and mandibular arch elements. These new data are important to consider as we continue to explore the primitive gnathostome condition and the evolution of gnathostome cranial designs. That withstanding, the palaeoecological (Zangerl and Richardson 1963; Grogan and Lund 2002) and morphological data presented thus far suggests that the iniopterygians are likely to represent a basal chondrichthyan group that has secondarily achieved a range of niche specializations within the Carboniferous.

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**Appendix A** Characters and states for the cladogram of Fig. 14

N	Character	State 0	State 1	State 2	State 3	State 4
0	Mineralized endoskeletal tissue	Perichondral bone	Tessellate mineralization			
1	Frontal clasper	Absent	Median	Median, very long	Single pair	Multiple pairs
2	Extended neurocranial rostrum	Absent	Present			
3	Anterior braincase opening	Large/precerebral fontanelle	Closed/small opening			
4	Rostrum:basal plane	Greater than 180 degrees	180 degrees			
5	Ethmoid % of neurocranium	< 25%	25–40%	40–50%	> 50%	
6	Orbital % of neurocranium	35–46%	< 35%	> 46%		
7	Postorbital % of neurocranium	25–40%	15–25%	> 40%	< 15%	
8	Anterior ventral braincase (X-section)	Narrow v-shaped	Platybasic, narrow	Platybasic wide		
9	Posterior ventral braincase (X-section)	Narrow v-shaped	Narrow shelf	Wide shelf		
10	Palatoquadrate-basitrabecular articulation	Present	Fused	Absent		
11	Palatoquadrate-postorbital articulation	Absent	Under PO process	Posterior to PO process		
12	Basitrabecular process attitude	In line with postorbital edge	Ventrolateral to postorbital	Anteroventrolateral	Absent	
13	Basitrabecular-palatoquadrate articulation	Postorbital	Orbital	Antorbital	Absent	
14	Chondrocranial construction (adult)	3 moieties	2 moieties	Continuous vault		
15	Occipital moiety	Separate vertebral elements	Fused vertebral elements	Single separate unit	Fused to otic moiety	
16	Occipital joint/fissure	Open fissure	Immobile/fusion			
17	Ethmo-sphenoid joint/fissure	Open fissure	Immobile/fusion	Mobile joint		
18	Suspensorium	Autodiastyly	Hyostyly	Amphistlyly	Holostyly	Methyostyly
19	Extravisceral cephalic cartilages	Premandibular feeding element	Prominent labials	Few/reduced labials	None	
20	Palatoquadrate anteriad	Separate	Parallel (parasymphysial) extension	Median symphysis		
21	Palatoquadrate-pterygoid process shape	Slight/postorbital	Dorsally recurved	Posteriorly extended	Dorsally expanded	
22	Meckel's-quadrangle articulation	Postorbital	Orbital	preorbital		
23	Mandibular mineralization	Bone	Spheritic	Random tesserae	Solid fibrocartilage	Prismatic calcified cartilage
24	Upper parasymphysial/cartilage(s)	Multiple	Small	Anteriorly extended	Absent	
25	Lower symphysial element(s)	Multiple	Present between mandibles	Extended anteriad	Absent	
26	Gill openings	Single opercular valve	Separate gill openings			
27	Epil hyoid	Opercular support	Mandibular arch support			
28	Buccopharyngeal/palatal denticles	Simple to compound odontodes	Absent			
29	Branchial basket	Subotic to postcranial	Subcranial	Principally postcranial		
30	Tooth row/jaw length	Absent/NA	> 50%	< 40%		

## Appendix B Character scores for the taxa of Fig. 14 and Appendix A

Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Delphyodontos</i>	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	?	1	0
Iniopterygian 1	1	0	0	1	0	0	0	0	0	0	?	0	1	0	?	2	1	1	0	0	?	0	0	1	?	1	0	0	0	1	0
<i>Rainerichthys</i>	1	0	0	1	0	0	1	0	0	0	?	0	1	0	1	2	1	2	0	0	?	0	0	1	2	1	0	0	0	1	0
<i>Belantsea</i>	1	0	0	1	1	3	1	1	2	2	?	0	2	?	2	3	1	1	3	3	1	0	1	?	3	3	0	0	1	1	1
<i>Netsepoye</i>	1	0	0	1	1	2	0	3	2	2	1	0	2	?	2	3	1	1	3	3	1	0	2	?	3	?	0	0	1	1	1
ElWeir	1	1	0	0	0	0	2	1	0	2	0	0	0	1	0	?	?	?	0	0	0	0	1	1	0	0	0	0	0	0	0
L2SP	1	0	0	1	1	1	0	1	1	2	0	0	2	1	2	3	1	1	0	2	0	3	1	?	1	1	0	0	1	1	2
<i>Gregorius rexi</i>	1	0	0	1	0	3	1	0	1	2	0	0	2	0	2	3	1	1	0	?	2	0	2	?	1	1	0	0	1	1	1
<i>Srianta dawsoni</i>	1	0	0	1	1	1	1	2	2	2	0	0	0	1	2	3	1	1	0	?	0	0	1	?	1	1	0	0	?	1	1
<i>Srianta iarlis</i>	1	0	0	1	1	3	1	0	1	2	0	0	2	1	2	3	1	1	0	2	0	0	2	?	2	2	0	0	1	1	1
<i>Srianta srianta</i>	1	0	0	1	1	2	1	0	1	2	0	0	1	1	2	3	1	1	0	2	0	0	1	?	1	1	0	0	0	0	1
<i>Bealbonn rogaire</i>	1	0	0	1	1	3	1	1	1	2	0	0	2	2	2	3	1	1	0	1	0	0	2	?	1	1	0	0	?	1	1
<i>Heteropetalus</i>	1	0	0	1	0	1	1	0	1	2	0	0	1	0	2	3	1	1	0	1	2	0	0	?	1	1	0	0	1	0	2
<i>Debeerius</i>	1	0	0	1	0	3	1	1	1	2	0	0	2	0	2	3	1	1	0	1	2	0	2	4	1	1	0	0	1	1	2
<i>Orodus</i>	1	0	0	?	?	2	0	0	2	2	0	0	2	1	2	3	1	1	0	?	?	0	1	?	1	1	?	0	1	0	1
Chom2	1	0	0	1	1	2	0	1	2	2	1	0	0	0	2	3	1	1	3	3	1	0	0	?	3	3	0	0	0	1	1
<i>Helodus</i>	1	0	0	1	1	1	1	0	2	2	1	0	2	2	2	3	1	1	3	3	1	0	2	?	2	2	0	0	1	0	1
<i>Callorhinchus</i>	1	1	0	1	1	2	0	1	2	2	1	0	2	2	2	3	1	1	3	1	2	0	2	?	0	3	0	0	1	1	1
<i>Physonemus</i>	1	0	0	1	1	3	1	2	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	?	2	?	0	0	1	1	1
<i>Echinochimaera meltoni</i>	1	0	0	1	1	2	2	1	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	3	2	3	0	0	1	1	1
<i>Echinochimaera snyderi</i>	1	0	0	1	1	2	2	1	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	3	2	3	0	0	1	1	1
<i>Squaloraja</i>	1	2	1	1	0	2	0	3	2	2	1	0	1	0	2	3	1	1	3	1	2	0	2	?	2	3	0	0	1	1	1
<i>Harpagofututor</i>	1	3	0	1	0	2	1	0	2	2	1	0	1	0	2	3	1	1	3	?	2	0	0	?	2	2	0	0	1	0	1
<i>Traquairius nudus</i>	1	0	0	1	?	2	1	1	2	2	1	0	2	2	2	3	1	1	3	1	2	0	2	?	2	2	?	0	?	?	1
<i>Traquairius spinosus</i>	1	0	0	1	1	2	1	3	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	?	2	2	0	0	1	1	1
<i>T. agkistrocephalus</i>	1	0	0	1	?	2	1	1	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	?	2	2	0	0	1	1	1
<i>Menaspis</i>	1	0	0	1	1	2	1	3	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	?	2	2	0	0	1	1	1
<i>Cochliodont1</i>	1	0	0	1	1	2	0	1	2	2	1	0	2	2	2	3	1	1	3	?	2	0	2	3	2	2	0	0	1	1	1
<i>Acanthorhina</i>	1	1	0	1	1	3	1	3	?	2	1	0	2	2	2	3	1	1	3	1	2	0	1	?	2	1	0	0	?	1	1
<i>Harpacanthus</i>	1	4	0	1	0	1	1	0	2	2	0	0	2	1	2	3	1	1	0	?	0	0	1	?	2	2	0	0	0	0	1
<i>Caseodus</i>	1	0	0	1	0	2	1	1	2	2	0	0	0	1	2	3	1	1	0	?	0	0	0	?	3	2	0	0	1	?	1
<i>Ornithoprion</i>	1	0	1	1	0	3	1	1	1	1	0	0	0	3	2	3	1	1	0	2	0	0	0	?	3	2	0	0	1	?	1
<i>Stethacanthus altonensis</i>	1	0	0	0	0	0	0	0	2	2	2	2	3	3	2	3	1	1	2	2	0	3	0	4	3	3	1	1	0	2	1
<i>Falcatus</i>	1	0	0	0	0	0	0	2	1	2	2	2	3	3	2	3	1	1	2	2	0	3	0	4	3	3	1	1	0	2	1
<i>Damocles</i>	1	0	0	0	0	0	0	1	1	2	2	2	3	3	2	3	1	1	2	2	0	3	0	4	3	3	1	1	0	2	1
<i>Tristychius</i>	1	0	0	0	0	0	1	2	2	2	2	1	?	3	2	3	1	1	1	1	1	0	1	4	3	3	1	1	0	2	1
<i>Squalus</i>	1	0	0	0	0	0	0	2	2	2	2	0	3	3	2	3	1	1	1	2	1	0	0	4	3	3	1	1	0	2	1
<i>Diplodoselache</i>	1	0	0	0	?	?	?	?	2	2	2	2	1	1	2	3	1	1	2	2	0	3	0	?	3	3	1	1	?	2	1
<i>Squatinactis</i>	1	0	0	0	0	0	1	2	2	2	2	0	3	3	2	3	1	1	1	2	0	0	0	4	3	3	1	1	1	2	1
<i>Hamiltonichthys</i>	1	0	0	0	0	0	0	2	2	2	2	0	3	3	2	3	1	1	1	?	0	0	0	4	3	?	1	1	0	2	1
<i>Thrinacodont sp</i>	1	0	1	0	0	1	1	0	?	2	?	2	?	?	1	0	1	1	1	3	0	3	0	2	3	3	1	1	0	2	1
<i>Egertonodus basanus</i>	1	0	0	0	0	0	1	2	1	2	2	0	3	4	2	3	1	1	1	1	0	3	0	4	3	3	1	1	0	2	1