The new Actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA)

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ABSTRACT
The new order Guildayichthyiformes n. ord. (Actinopterygii) is erected for *Guildayichthys carnegiei* n. gen. n. sp. and *Discoserra pectinodon* n. gen. n. sp. from the Upper Chesterian Bear Gulch Limestone of Montana. These marine fish have highly compressed, discoidal bodies, tall rhombic "ganoid" scales with peg-and-socket joints, fins supported by well-jointed and well-spaced rays, small mouths and specialized bones of the operculo-gular series. The skull roof features several large median bones extending from the rostrum to the occiput, three bones in the otic canal series, and several longitudinal series of pre-frontal elements. The cheek and antorbital areas are equally unique. The cheek has highly variable numbers of suborbitals, tall narrow dorsal and ventral preopercular lateral line canal bones, and a series of interopercular rays (*Guildayichthys carnegiei* n. gen. n. sp.) or bones (*Discoserra pectinodo* n. gen. n. sp.) between the ventral preopercular bone and the branchiostegal series. There are several small postspiracular bones and eight to ten sclerotic bones in the orbit. The extensive development of median skull roofing bones in the Guildayichthyiformes n. ord. compares to patterns seen in Dipnoi and Placodermi, that also concentrate biting forces anterior to the orbits, suggesting similar adaptive responses to similar types of cranial stress regimes. Cladistic analysis involving 72 characters results in a very stable sister group relationship between *Polypterus* and the Guildayichthyiformes n. ord. as a crown group within the tested Paleozoic Actinopterygii. The Cladistia are rediagnosed as a superorder to reflect this relationship. The Cladistia appear to be the sister group of *Platysomus* and *Amphicentrum*.

KEY WORDS
Guildayichthys carnegiei n. gen. n. sp.,
Discoserra pectinodon n. gen. n. sp.,
Osteichthyes,
new order,
Guildayichthyiformes n. ord.,
Cladistia,
Namurian,
Montana,
osteichthyan skulls.

RÉSUMÉ
Guildayichthyiformes, un nouvel ordre d'Actinopterygii du Carbonifère inférieur du Montana (États-Unis).
Le nouvel ordre des Guildayichthyiformes n. ord. (Actinopterygii) est créé pour *Guildayichthys carnegeiei* n. gen. n. sp. et *Discoserra pectinodon* n. gen. n. sp. du calcaire de Bear Gulch, Chesterien supérieur, du Montana. Ces poissons marins ont le corps fortement comprimé et discoïde, les écailles hautes et rhombiques avec des articulations en tenon et mortaise, les rayons des nageoires segmentés et espacés, la bouche petite et la série operculo-gulaire avec des os spécialisée. Le toit crânien comporte plusieurs grands os médians depuis le rostre jusqu'à l'occiput, trois os dans la série du canal otique et plusieurs séries longitudinales d'éléments préfrontaux. Les régions préorbitaire et de la joue sont également singulières. La joue a un nombre très variable de sousorbitaux, des os du canal préoperculaire, dorsal et ventral, hauts et étroits et une série de rayons (*Guildayichthys carnegiei* n. gen. n. sp.) ou d'os (*Discoserra pectinodon* n. gen. n. sp.) interoperculaires entre l'os préoperculaire ventral et la série branchiostège. Il y a plusieurs os postspiraculaires et huit à dix os sclérotiques dans l'œil. Le grand développement des os médians du toit crânien chez les Guildayichthyiformes n. ord. est comparable aux dispositions rencontrées chez les Dipneustes et les Placodermes, qui concentrent également en avant de l'orbite les forces de préhension, suggérant ainsi des réponses adaptatives similaires à des types semblables de stress crâniens. Une étude cladistique impliquant 72 caractères implique une relation de groupes frères très stable entre *Polypterus* et les Guildayichthyiformes n. ord., qui constituent un groupe coronal (*crown group*) au sein des Actinopterygii paléozoïques analysés. Les Cladistia sont redéfinis en un super ordre pour exprimer cette parenté. Les Cladistia apparaissent comme le groupe frère de *Platysomus* et d'*Amphicentrum*.

MOTS CLÉS
Guildayichthys carnegiei n. gen. n. sp.,
Discoserra pectinodon n. gen. n. sp.,
Osteichthyes,
nouvel ordre,
Guildayichthyiformes n. ord.,
Cladistia,
Namurien,
Montana,
morphologie crânienne.

INTRODUCTION

The Bear Gulch Limestone lens is contained within the Bear Gulch Limestone member of the Heath Formation (Upper Chesterian, Namurian E2b). It was deposited in a shallow, tropical marine bay lacking any significant traces of fresh-water fossils (Ziegler *et al.* 1979; Williams 1981, 1983; Horner 1985; Horner & Lund 1985; Lund *et al.* 1993; Feldman *et al.* 1994; Grogan & Lund ms.).

The Bear Gulch Limestone contains over 110 species of fish, including approximately 45 osteichthyan species. Only three of the approximately 34 species of actinopterygians from the Bear Gulch Limestone have strongly compressed discoidal body forms. The two species that are the subjects of this article raise difficult phylogenetic questions, because while they are specialized in propulsive and feeding adaptations, they possess many features of cranial osteology that are unique among Paleozoic actinopterygians (Lund, Poplin & McCarthy 1995) or that can best be understood by reference to sarcopterygian characters.

ABBREVIATIONS

Specimens have been deposited in the collections of:

MV	University of Montana Museum, Missoula, Montana;
CM	Section of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania;
ROM	Royal Ontario Museum, Toronto, Ontario;
FMNH	Field Museum of Natural History, Chicago, Illinois.

MATERIAL AND METHODS

There are 110 specimens collected that pertain to the taxa described herein. All collection data are archived with the Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pa. (USA).

Specimens were prepared manually and studied either from the original bones or from latex peels (Baird 1955). The courses of the calcite filled lateral line canals were determined by viewing the bones under alcohol. Peels were shadowed with magnesium oxide. Images were acquired using a high-resolution color flatbed scanner. Illustrations were prepared with Adobe Photoshop and Adobe Illustrator software packages.

Cladistic analyses were performed using the Hennig86 and Clados programs.

BONE NOMENCLATURE

The bone terminology used in these descriptions attempts to favor that used for Actinopterygii. Certain elements, series of elements and arrangements of elements, however, are more readily comparable with those of primitive Sarcopterygii, and others with Neopterygii, and those names are used. The names in question are applied topographically, but there are ample reasons to suggest, as have Arratia & Cloutier (1996), that probable homologies could exist.

SYSTEMATIC PALAEONTOLOGY

Superorder CLADISTIA Cope, 1871

Order GUILDAYICHTHYIFORMES n. ord.

DIAGNOSIS. — Paired premaxillae not sutured in midline, maxilla does not extend posterior to midorbital level. Small rostral, paired lateral postrostrals followed by a large median second postrostral. Supraoccipital prominent in skull roof. Two to three rows of paired bones, including supraorbitals, over orbits. Three bones in anteroposterior otic series. Infraorbital series of six to ten bones lacking a specialized posterodorsal infraorbital or "postorbital". Suborbitals numerous, variable, extending under orbit. Narrow dorsal and ventral preoperculars. Interopercular rays or interopercular bones present, that may carry a branch of the preopercular lateral line canal. Single large opercular bone ventral to two to for smaller postspiraculars; branchiostegal rays few, not extending forward under mandible. Braincase ossified as several bones; parasphenoid extends entire length of braincase. Presupracleithrum large. Body laterally compressed, discoidal; squamation complete, deepened peg-and-socket scales on anterior flank. Caudal hemiheterocercal; fin rays well spaced.

Family GUILDAYICHTHYIDAE n. fam.

TYPE GENUS. — *Guildayichthys* n. gen. by original designation.

DIAGNOSIS. — As for order, only family.

Genus *Guildayichthys* n. gen.

TYPE SPECIES. — *Guildayichthys carnegiei* n. gen. n. sp.

ETYMOLOGY. — Named after John Guilday, late Curator of Fossil Mammals of Carnegie Museum, Pittsburgh, for his unique appreciation of the beauty of life.

DIAGNOSIS. — Teeth short, and absent posterior to mid-maxillary and mid-dentary level. Posterior end of maxillary extending to midorbital level. Parietals meet in dorsal midline. Three rows paired bones over orbits. Five to six interopercular rays extending posterior to quadrate. Seven to eight branchiostegals, two dorsally concave, one expanded posteriorly and four to five ventrally concave, plus two lateral gulars. Dorsal ridge scales from occiput to dorsal fin bear posteriorly projecting spines; imperceptible transition from dorsal ridge scales to dorsal fin rays. Rays of leading edges of dorsal and anal fins closely spaced, following rays of other fins well spaced; all fin rays jointed and unbranched. Anal fin with two to three short leading spines, caudal fin slightly forked.

Guildayichthys carnegiei n. gen. n. sp.
(Figs 1-4; 14A)

HOLOTYPE. — CM 41071.

REFERRED SPECIMENS. — MV 6045, 6046, 6932, 7671, 7758, 7795. CM 27293, 27297, 35217, 37548, 37549-37550, 41010, 46091, 46095, 46131, 46293, 46294, 46295, 46296, 46297. ROM 36560, 41039, 41042, 41047, 43012. FMNH PF10026.

ETYMOLOGY. — Named in honor of Andrew Carnegie, founder of Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

HORIZON AND LOCALITY. — Bear Gulch Limestone lens, Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

DIAGNOSIS. — For meristics see Table 1. Diagnosis as for genus, only species.

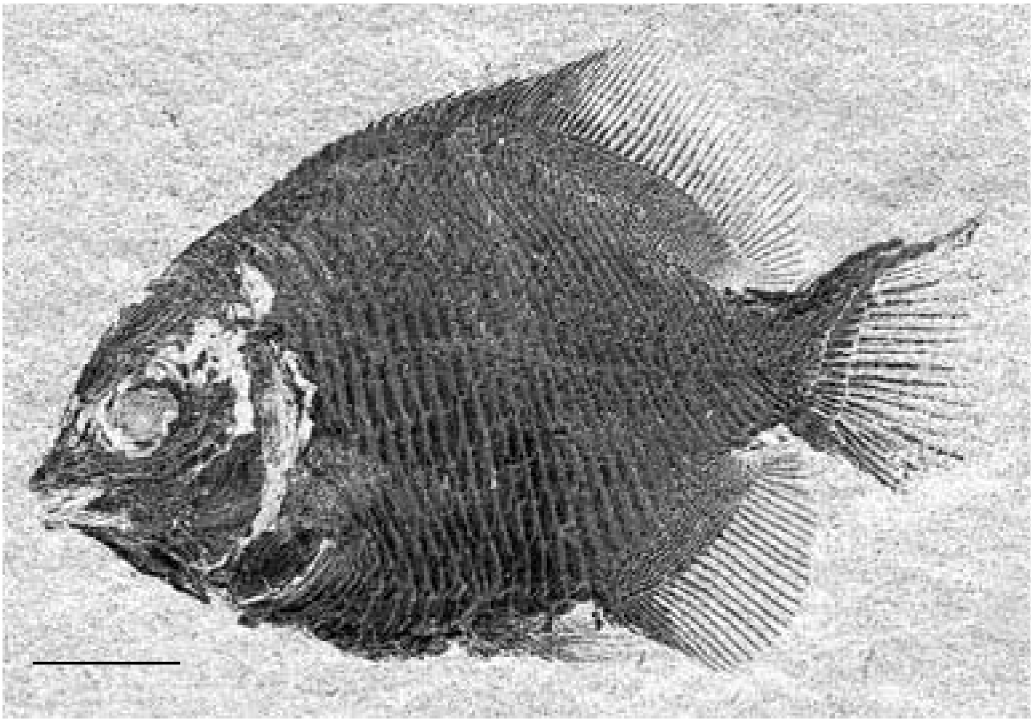

FIG. 1. — *Guildayichthys carnegiei* n. gen. n. sp., holotype (CM 41071A), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Scale: 9 mm.

REMARKS

All skull bones have ganoine sculpturing of long ridges; either the mesial or the anterior face of each ridge lies at a low angle to the plane of the bone while the opposite face meets the bone approximately perpendicularly. Ganoine ridges on the gulars are of the reverse orientation (Fig. 2). Scales of the anterior trunk have peg-and-socket joints and have ganoine sculpturing of faint marginal vertical lines; all trunk scales are pectinated and the deepened ventral abdominal scales are particularly strongly pectinated. Only the central flank scale rows are markedly deepened (rows 2-5 below the lateral line). The anterior scales of these rows average 3.85 times deeper than wide. Squamation at the bases of dorsal and anal fins is of small thin scales, extending as lobes over and under the caudal peduncle.

The statistics of *Guildayichthys* (Tables 1; 2) are based upon an inadequate sample size and may be misleading. Standard length-maximum height correlation is strong, and caudal peduncle proportions also correlate. No other recorded parameters show meaningful correlations.

DESCRIPTION

Lateral aspect of skull (Figs 2-4)

The paired premaxillae (P, Figs 3; 4) are high, narrow and separated posteriorly in the midline where they meet the rostral. They are firmly attached only to the first infraorbital posteriorly. Short styliform to conical teeth are borne in a narrow band along the oral margin. The maxilla is elongate and narrow (height one seventh of length), extends to midorbital level and overlaps the posterodorsal rim of the mandible. Short teeth are borne only upon the anterior half of the maxilla.

There are five to six bones in the infraorbital lateral line canal series (IO, Figs 3; 4). The most

TABLE 1. — Meristics of *Discoserra pectinodon* n. gen. n. sp and *Guildayichthys carnegiei* n. gen. n. sp. Abbreviations: **AFP**, anal fin position; **CFP**, caudal fin position; **CANG**, caudal angle; **BCL**, braincase length; **CPL**, caudal peduncle length; **CPW**, caudal peduncle width; **DFP**, dorsal fin position; **GL**, gape length; **HDL**, predorsal length; **HMAX**, maximum height; **NANAL**, number of anal rays; **NCAUD**, number of caudal rays; **NDORS**, number of dorsal rays; **NPECT**, number of pectoral rays; **NPELV**, number of pelvic rays; **PCR**, precaudal ridge scales; **PELPO**, pelvic fin position; **PDR**, predorsal ridge scales; **SL**, standard length; **SRALL**, scale rows from lateral line to dorsal fin origin; **SRBLL**, scale rows from lateral line to anal fin origin. Fin positions are in numbers of scale rows along the lateral line canal-bearing scales.

	***Discoserra pectinodon* n. gen. n. sp.**				***Guildayichthys carnegiei* n. gen. n. sp.**			
	n	**range**	**mean**	**SD**	**n**	**range**	**mean**	**SD**
DFP	19	17-23	19.95	1.62	8	16-20	18.38	1.51
NDORS	16	41-54	46.38	2.8	7	33-40	37.29	2.69
AFP	19	13-21	16.53	1.93	8	11-18	14.63	2.44
NANAL	15	28-43	34.53	4.17	9	26-34	29.78	2.78
CFP	21	34-48	43.05	2.87	8	33-38	35.75	1.67
NCAUD	19	22-27	24.26	1.37	7	20-21	20.14	0.38
NPECT	7	11-16	14.43	1.62	–	–	–	–
PELPO	10	9-12	10.80	0.92	6	8-9	8.83	.04
NPELV	5	3-5	4.20	0.84	4	13-16	13.75	2.22
PDR	18	19-29	24.00	3.27	7	14-21	16.29	2.29
PCR	11	2-5	3.00	1.91	5	4-7	5.40	1.52
SRALL	13	8-11	9.46	0.97	8	10-15	11.88	1.64
SRBLL	19	8-13	9.89	1.19	8	9-12	10.63	1.06
SL	26	46-57	51.50	3.63	7	49-56	55.89	2.94
HDL	20	36-43	39.79	2.67	6	36-43	39.42	2.86
GL	20	7-10	8.51	0.69	5	8-11	9.39	1.05
BCL	26	16-20	17.97	0.99	7	17-19	17.57	0.69
CPL	23	3-6	4.55	0.56	8	2-7	5.08	1.68
CPW	23	7-10	8.27	0.65	8	8-10	9.27	0.60
HMAX	25	34-44	38.04	2.45	8	34-40	36.64	2.20
CANG	22	30-44	38.59	4.58	8	28-34	31.25	2.76

TABLE 2. — Pearson correlation matrix, *Guildayichthys carnegiei* n. gen. n. sp. Numbers are correlation coefficient/number of specimens/significance. Abbreviations: **AFP**, anal fin position; **BCL**, braincase length; **CANG**, caudal angle; **CFP**, caudal fin position; **CPL**, caudal peduncle length; **CPW**, caudal peduncle width; **GL**, gape length; **HDL**, predorsal length; **HMAX**, maximum height; **NCAU**, number of caudal; **PCR**, precaudal ridge scales; **PDR**, predorsal ridge scales; **SL**, standard length; *, significant at 5% level; **, significant at 1% level.

	PDR	**SL**	**HDL**	**GL**	**BCL**	**CPL**	**CANG**
AFP					.924 6 .004**		
CFP				–.940 5 .009*			
NCAU	.913 6 .005*						.912 6 .006*
PDR				–.908 5 .016*			
GL							-.952 4 .024*
CPW			.762 6 .762*			.712 8 .024*	
HMAX		.893 7 .003*		.865 5 .029*			

FIG. 2. — *Guildayichthys carnegiei* n.gen. n. sp., latex peel of the head (MV 6045B) of holotype, Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Scale: 6 mm.

anterior is narrow and forms the ventral edge of the posterior nostril. The second is large and moderately expanded anteriorly. The remaining elements are quite narrow, the most posterodorsal of which is tightly associated posteriorly with a thin and large bone. The latter two bones cover the dilator opercular fossa and articulate with the skull roof. A series of thin suborbitals extend from the skull roof to midorbital level.

There is a short dorsal and a taller ventral preoperculum, both anteroposteriorly narrow, carrying the preopercular canal from the margin of the skull roof to the posterior end of the lower jaw (POPD, POPV, Figs 3; 4). Two small postspiracular bones (see *Polypterus*, Pehrson 1958) lie dorsal to the tall, narrow, principal bone of the opercular series. The opercular is flanked ventrally by a series of branchiostegals, two dorsally concave, the next a posteriorly widened triangle, followed by 4-5 ventrally concave, deeply overlapping bones and a ventral plate (posterolateral gular). The plate is divided anteroposteriorly in one specimen (Fig. 3); a narrow lateral gular lies anterior to the plate and mesial to the mandible.

A series of five mobile, overlapping interopercular rays (Fig. 2; I, Fig. 3) extends from the posterior margin of the mandible to the anteroventral edge of the opercular. There is strong evidence in

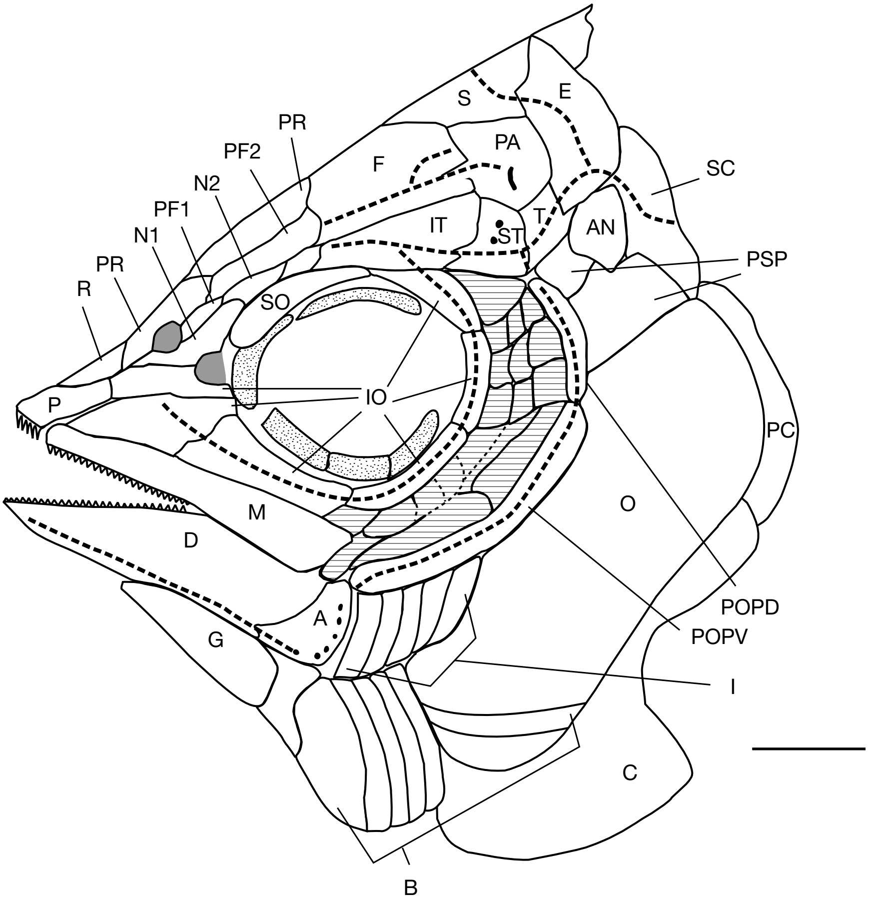

FIG. 3. — *Guildayichthys carnegiei* n. gen. n. sp., latex peel of the head (MV 6045B) of holotype, lateral aspect of skull, Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **A**, angular; **AN**, presupracleithrum; **B**, branchiostegal rays; **C**, cleithrum; **D**, dentary; **E**, extrascapular; **F**, frontal; **G**, gular; **I**, interoperculars; **IO**, infraorbital; **IT**, intertemporal; **M**, maxilla; **N1**, **N2**, nasals; **O**, opercular; **P**, premaxilla; **PA**, partietal; **PC**, postcleithrum; **PF1**, **PF2**, prefrontals; **POPD**, **POPV**, dorsal and ventral preoperculums; **PR**, postrostral; **PSP**, postspiracular; **R**, rostral; **S**, supraoccipital; **SC**, supracleithrum; **SO**, supraorbital; **ST**, supratemporal; **T**, tabular. Sclerotic bones stippled; suborbital bones hatched. Scale: 3 mm.

MV 6045 of either lateral line pores or pit-organs in the two rays closest to the mandible. The lateral surface of the mandible consists of a large dentary and smaller, posterior, angular. No surangular is visible. Short conical teeth occupy the anterior half of the oral margin of the dentary. The mandibular lateral line canal traverses the mandible near its ventral margin, and bends abruptly dorsad in the angular. The articular facet is located slightly below a projection of the dorsal margin of the jaw that presumably functioned as a coronoid process.

Skull roof (Figs 3; 4; 14A; 15C)

The small median rostral (R, Figs 3; 4) is followed by a paired postrostral that is notched for the mesial margin of the dorsal nostril. An ethmoid commissure has not been observed. A moderately large median second postrostral extends past the level of the anterior edge of the parietals. The supratemporal commissure crosses the midline anterior to the posterior margin of the supraoccipital (Figs 3; 14A).

The posterior border of the anterior (dorsal) nasal opening is formed by the most anterior of a series

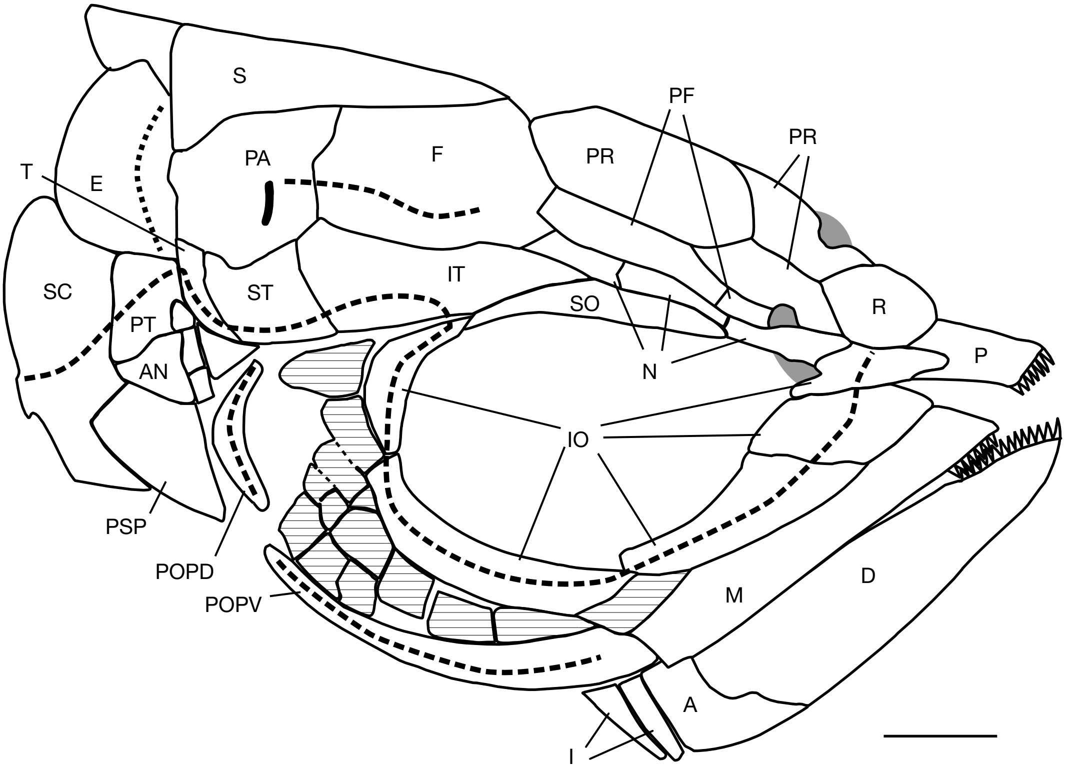

FIG. 4. — *Guildayichthys carnegiei* n. gen. n. sp., dorsolateral aspect of skull, from latex peel (CM 41010), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **A**, angular; **AN**, presupracleithrum; **D**, dentary; **E**, extrascapular; **F**, frontal; **I**, interoperculars; **IO**, infraorbital; **IT**, intertemporal; **M**, maxilla; **N**, nasals; **P**, premaxilla; **PA**, partietal; **PF**, prefrontals; **POPD**, **POPV**, dorsal and ventral preoperculums; **PR**, postrostral; **PSP**, postspiracular; **PT**, posttemporal; **R**, rostral; **S**, supraoccipital; **SC**, supracleithrum; **SO**, supraorbital; **ST**, supratemporal; **T**, tabular. Suborbital bones hatched. Scale: 3 mm.

of two to three narrow bones. This series extends lateral to the postrostrals, and mesial to the nasal and supraorbital, and abuts posteriorly against the frontal, the intertemporal, or both (Figs 3; 4). A thin nasal bone bridges the space between nostrils. The course, or even the presence of the supraorbital canal in the nasal region is uncertain; the canal can only be followed in the frontal and parietal and may lie under the suture between the pre-frontal and the more lateral series. The supraorbital canal in MV 6045 bears a short posteromesial branch in the frontal before continuing on to the parietal; the canal does not reach the transverse pit line. There are three bones in the otic canal series, the largest and most anterior, the intertemporal (IT, Figs 3; 4), receiving the infraorbital canal from the posterodorsal infraorbital. Pores associated with a profundus branch of the otic canal (Poplin 1973) extend forward within the intertemporal from the junction with the infraorbital canal in MV 6045 (Fig. 3). Two to three pores in a transverse row extend mesially across the supratemporal and parietal toward the transverse pitline but there is no evidence for an underlying canal branch. The posterior margin of the skull roof in MV 6045 is bordered by one pair of bones bearing the canal intersection characteristic of the extrascapular. In CM 41010, however, two pairs of bones are evident in the same space, posttemporal and extrascapular (Fig. 4). In neither condition do these bones extend to the dorsal midline.

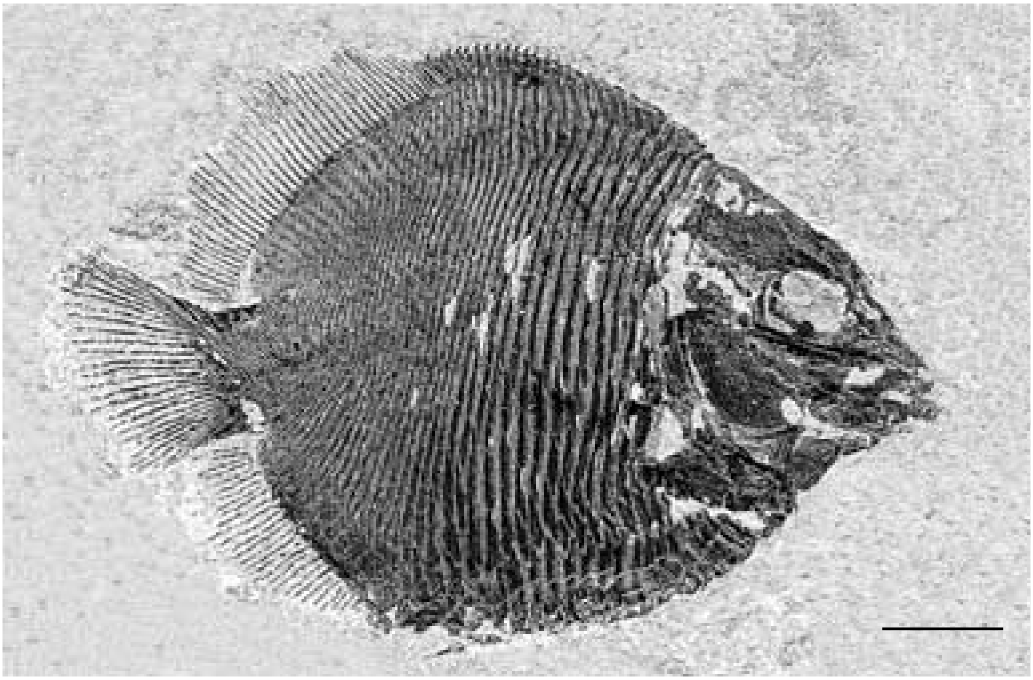

FIG. 5. — *Discoserra pectinodon* n. gen. n. sp., holotype (CM 30621A), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Scale: 8 mm.

The braincase and the floor of the olfactory cup are well ossified. Details, however, are obscured by overlying bones. A short process, possibly a palatobasal (basal) process, is visible in the orbital region of CM 41010. Neither palate nor visceral skeleton is visible.

Postcranial

Shoulder Girdle. The posttemporal is abutted anteroventrally by a presupracleithrum (Lund & Melton 1982) and posteroventrally by a large supracleithrum. The supracleithrum-cleithrum contact is masked by the operculum; a tall, thin postcleithrum is present and may have served to strengthen what appears to be a very limited area of contact. The cleithrum is deeply notched for the insertion of the pectoral fin. The scapulocoracoid is ossified in a thin sheet and supports one radial for each pectoral fin ray. Clavicles are absent.

Scales have strong peg-and-socket articulations, smooth ganoine coatings, and are slightly pectinated. Anterior flank and abdominal scales are moderated deepened. There is an abrupt caudal inversion, and the scaled body axis continues past the last caudal fin ray. A complete series of median dorsal scutes extends from the head to the origin of the dorsal fin; as the series approaches the dorsal fin, the scutes increase in height and the sharp posteriorly directed spine of each overlaps the spine of the following scute. The bases of the first jointed fin rays originate behind the last of the dorsal scutes and level with the bases of the scutes. There are two to three dorsal scutes between the end of the dorsal fin and the caudal lobe, followed by a series of dorsal caudal scutes that extend to the end of the caudal axis. There is a series of short, stout, strongly serrated abdominal scutes that extend from the shoulder girdle to the pelvic fins.

All fins are composed of well-spaced and jointed rays. The pectoral, dorsal and anal fins are supported on finely scaled lobes. The pelvic fin is moderate in length, and the caudal fin is slightly forked and slightly inequilobate. There are no fin fulcrae. No postcranial endoskeletal detail is available.

Genus *Discoserra* n. gen.

TYPE SPECIES. — *Discoserra pectinodon* n. gen. n. sp. by original designation.

ETYMOLOGY. — Discoserra, serrated disc, descriptive of the appearance of the body in lateral view.

DIAGNOSIS. — Teeth of the premaxilla, maxilla and dentary long, thin, and styliform. Posterior end of maxilla does not extend back to level of anterior margin of orbit. Parietals excluded from contact in dorsal midline by postrostral 2, which contacts supraoccipital. No transverse supratemporal commissure in supraoccipital. Two rows of paired bones over orbit. One to three interopercular bones; two to three small postspiraculars and a presupracleithrum. Branchiostegals very variable in size, number and shape. Dorsal ridge scales with small, forwardly facing hooks; two to three small anal fin hooks. Origin of anterior edge of dorsal fin set well below dorsal margin of ridge scales. All fins with well spaced rays; pelvic fin reduced, caudal fin rounded.

Discoserra pectinodon n. gen. n. sp.

(Figs 5-13; 14B)

HOLOTYPE. — CM 30621.

REFERRED SPECIMENS. — MV 2772, 2773, 2956, 2984, 3579, 3810, 3811, 7669, 7670, 7756, 7757, 7793, 7794. CM 27290-27292, 27294-27296, 27298, 27333, 35206-35216, 35409, 35547, 37545-37547, 37665, 41009, 44500, 46201-46206, 48650, 48651, 48717-48720, 48841, 62794-62802. ROM 36562, 41030, 41169, 43003, 43115, 43976.

ETYMOLOGY. — Pectinodon, in reference to the long teeth.

DIAGNOSIS. — For meristics see Table 1. Other characters as for genus, only species.

TABLE 3. — Pearson correlation coefficients, *Discoserra pectinodon* n. gen. n. sp. Abbreviations: **BCL**, braincase length; **CANG**, caudal angle; **cc**, correlation coefficient; **CFP**, caudal fin position; **CPL**, caudal peduncle length; **CPW**, caudal peduncle width; **DFP**, dorsal fin position; **HDL**, predorsal length; **HMAX**, maximum height; **n,** number; **NANAL**, number of anal rays; **NCAU**, number of caudal rays; **NDORSAL**, number of dorsal rays; **NPECT**, number of pectoral rays; **p**, Pearson coefficients; **PCR**, precaudal ridge scales; **PELPO**, pelvic fin position; **PDR**, predorsal ridge scales; **SL**, standard length; **SRALL**, scale rows from lateral line to dorsal origin; **SRBLL**, scale rows from lateral line to anal origin; *, significant at 5% level; **, significant at 1% level. Fin positions are in numbers of scale rows along the lateral line canal-bearing scales, measurements in mm.

	cc	n	p
NDORSAL			
NANAL	.648	13	.008*
NCAU	.602	14	.011*
PCR	.804	11	.001**
NCAU			
NDORSAL	.602	14	.011*
CFP	.542	17	.012*
HMAX	.564	18	.007*
CFP			
NCAU	.542	17	.012*
PCR	.653	11	.015*
PELPO	–.691	10	.013*
SRALL			
SL	.762	13	.001**
HDL	.784	13	.001**
BCL	.723	13	.003**
SRBLL			
PCR	.741	11	.003**
NPECT	–.905	07	.003**
DFP			
PDR	.710	17	.001**
BCL	.531	19	.01*
SL			
HDL	.854	20	.000**
HMAX	.807	25	.000**
CPW	.585	23	.002**
HMAX			
SL	.807	25	.000**
HDL	.748	20	.000**
BCL	.693	25	.000**
CPW	.723	22	.000**
CPL			
CANG	.515	21	.008*
CPW			
SL	.585	23	.002**
BCL	.518	23	.006
HMAX	.723	22	.000**

REMARKS

The statistics of *Discoserra* (Table 3) are remarkable. The number of dorsal fin rays correlates with the numbers of anal and caudal rays as well as those of the precaudal ridge scales. The number of caudal rays also correlates with the number of lateral line scales and a size parameter, maximum height. Pelvic position in scale rows along the lateral line negatively correlates with number of lateral line scales. Scale rows above the lateral line correlates with size parameters, while scale rows below the lateral line do not. Maximum height correlates well with most morphometrics, and excellently with caudal peduncle width. Caudal peduncle length correlates only with caudal angle. Despite these correlations, *Discoserra pectinodon* is morphologically and statistically the most variable fish in the

Bear Gulch fauna. It has not proven possible to consistently isolate variant morphologies that would suggest separate populations either through space or time; in fact several bone complexes such as branchiostegals and suborbitals are not bilaterally consistent within all individuals.

DESCRIPTION

Ganoine

Skull bones have ganoine sculpturing of coarse, irregular longitudinal to circumferential convex ridges. The central areas of broad bones such as the opercular may bear ganoine sculpturing that grades from tubercles centrally to ridges peripherally (Fig. 6).

Scales

Lateral flank scales are up to 3.6 times deeper than wide and bear strong peg-and-socket joints as well as internal anterior thickenings. Most lateral scale rows are deepened. Ganoine sculpturing varies on the flank scales from few, relatively coarse circumferential grooves near the dorsum to finer circumferential striations at midflank. The stout, deep ventral abdominal scales are strongly serrated in addition to bearing coarse circumferential grooves. Squamation at the bases of dorsal and anal fins is of small, thin scales, extended into lobes that project over and under the caudal peduncle. A significant bulk of dorsal and anal fin radial musculature is indicated.

Lateral aspect of skull (Figs 7; 8)

The premaxillae (P, Figs 7; 8) are about five times longer than wide, and are not firmly sutured either across the midline or to any other bones. There appears to have been a tendency for them to fuse, in some individuals, to the anteriormost infraorbital posteriorly. The premaxillae bear a single row of long, fine, styliform, closely set teeth. The maxilla (M, Figs 7; 8) is most often triangular in shape, varying from 1: 4 to 1: 5 in length: height ratio. It is not firmly held to any other skull bones. A mesial view of the maxilla of one specimen is available, that shows what appears to be a slight anterior articular facet (CM 27290). The single row of long, closely fit teeth diminishes abruptly in height and ends at one third of the distance to the posterior end of the bone.

The infraorbital lateral line canal bones are very variable in number (I0, Figs 7-9). The first infraorbital is short and in close contact with the premaxilla. The second element is wedge shaped, of variable length, and may either be absent or fused to the large third anterior infraorbital in some specimens. When present, it forms the anteroventral margin of the posterior nostril. The third anterior infraorbital is large and trapezoidal, with pores distributed irregularly and remote from the course of the infraorbital canal. As many as five to seven additional infraorbitals, most only surrounding the infraorbital canal, rim the orbit. Pores from the infraorbital bones below the orbit are irregularly distributed upon the suborbital bones ventrally. The most posterodorsal infraorbital is firmly associated with a large, thin bone that covers the dilator opercular fossa.

Suborbitals (Figs 7; 8) on the posterodorsal cheek are scale-like. Under the orbit, the suborbital bones vary in number and shape from one long element (CM 35215) to a series of seven (CM 27292). Normally, a trapezoidal element or elements lie dorsal to the articular region of the mandible, followed by a variable number of small posterodorsal bones; in several specimens an anterior triangular element intervenes between the third infraorbital and the trapezoidal bone or bones (CM 27294, 35206, 35211).

The dorsal of the two preopercular bones contacts the skull roof; it is shorter and thinner than the ventral element. The preopercular canal branches into an anteroventral and a ventral branch near the mandibular end of the bone (Fig. 8). There is one tall, narrow principal opercular bone, ventral to two to four considerably smaller bones and a large presupracleithrum (PSP, Figs 7; 8). The branchiostegals are very variable and are not always bilaterally symmetrical. A typical pattern is one dorsally concave ray below the opercular, followed ventrally by one that widens posteriorly, four to six ventrally concave rays and a single ventral plate (posterolateral gular). Variations are detailed in

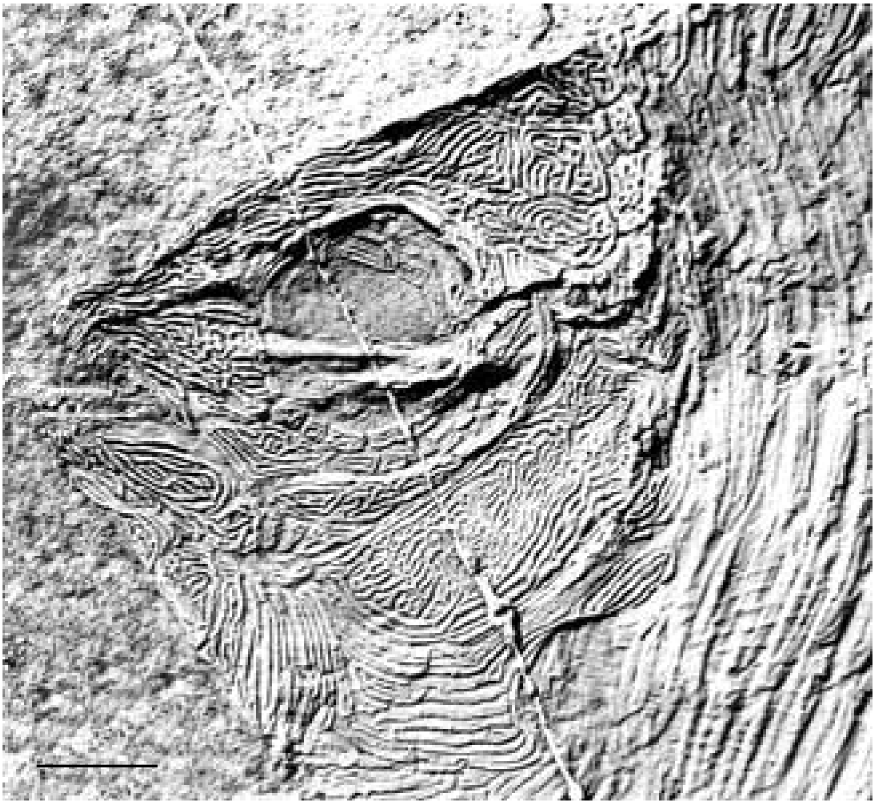

FIG. 6. — *Discoserra pectinodon* n. gen. n. sp., latex peel of skull (CM 35211B), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Scale: 4 mm.

Figure 10. One to three small interopercular bones (I, Figs 7; 8) are found between the posterior end of the mandible, the posteroventral end of the ventral preopercular and the anteroventral end of the opercular. There is clear evidence for a branch of the mandibular lateral line canal extending under the anterior of these bones, and some indication that the ventral branch of the preopercular lateral line canal extended ventrally between the interoperculars. This is best displayed in CM 35206.

The external aspect of the lower jaw consists of a large dentary and a small angular, with a single row of long, slim teeth along the anterior oral margin of the dentary. A surangular seems to be absent. The internal aspect of the mandible consists of two elements, an extensive prearticular that seems to lack teeth, and an articular with a strongly elevated anterior wall and a dorsomesial pit for adductor musculature insertion (CM 27290). The mandibular lateral line canal lies near the ventral border of the dentary; the canal is L-shaped in the angular but a posterior continuation of the canal is evident in several specimens.

Skull roof (Figs 7; 8; 14B)

The long, narrow median rostral (R, Figs 7; 8) extends back to the level of the anterior border of the nostrils. While lateral line canals enter the median rostral from either side, a complete ethmoid commissure has not been seen. The paired postrostrals extend along the dorsal midline between the nostrils, receiving the posteromedian end of the median rostral between them. The posterior median postrostral contacts the supraoccipital posteriorly and excludes the frontal and parietal bones

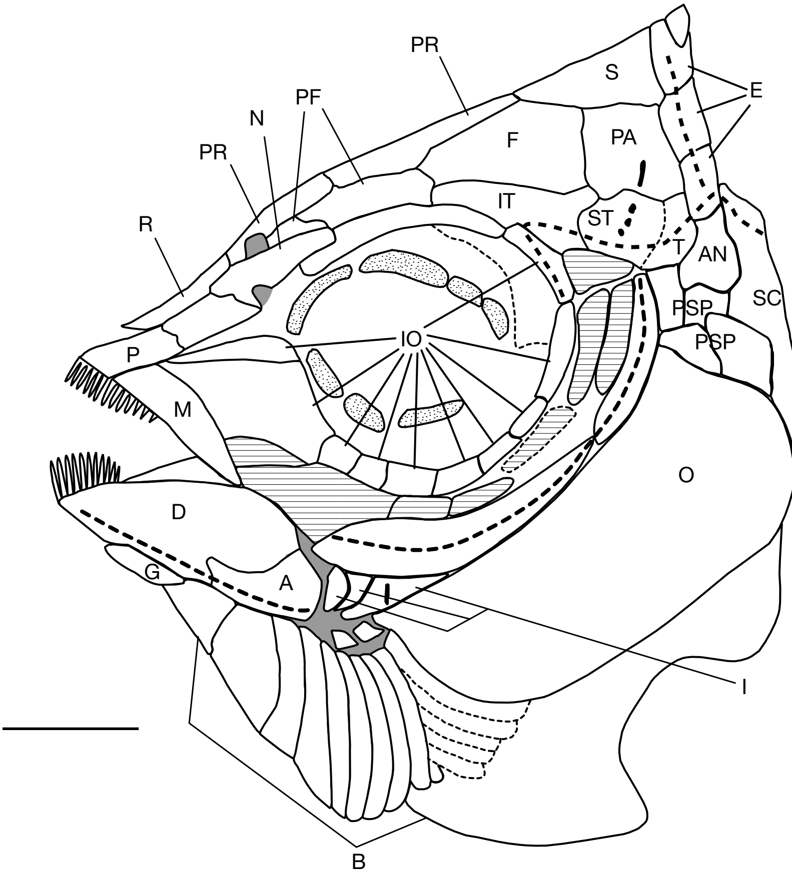

FIG. 7. — *Discoserra pectinodon* n. gen. n. sp., lateral aspect of skull (CM 35211B), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **A**, angular; **AN**, presupracleithrum; **B**, branchiostegal rays; **D**, dentary; **E**, extrascapular; **F**, frontal; **G**, gular; **I**, interoperculars; **IO**, infraorbital; **IT**, intertemporal; **M**, maxilla; **N**, nasal; **O**, opercular; **P**, premaxilla; **PA**, partietal; **PF**, prefrontals; **PR**, postrostral; **PSP**, postspiracular; **R**, rostral; **S**, supraoccipital; **SC**, supracleithrum; **ST**, supratemporal; **T**, tabular. Sclerotic bones stippled; suborbital bones hatched. Scale: 4 mm.

from the dorsal midline (Fig. 14B). The supraoccipital is a significant bone of both the braincase, the skull roof, and the posterior cranial surface, where it bears a strong posteriorly projecting crest. The supratemporal commissure does not enter the supraoccipital.

The more anterior of two pre-frontal bones (PF, Figs 7; 8) forms the posterior border of the anterior nostril, and a small nasal bone (N, Figs 7; 8) extends between the anterior and posterior nasal openings. The posterior prefrontal is narrow and flanked laterally by a single supraorbital bone. The supraorbital lateral line canal extends from the posterior pre-frontal through the frontal and parietal; the canal cannot be traced anterior to the posterior pre-frontal. The parietal bears a short transverse pitline, which may be continued laterally onto the supratemporal, the second of the three bones of the otic series, in the form of a few pores or pits. Behind the skull roof the supratemporal canal intersects with the extrascapular canal in a bone lateral to two paired extrascapulars, but there is no evidence for a complete commissure.

Visceral skeleton

The palate and suspensorium are displayed only in CM 27290 (Fig. 11). No palatal teeth can be seen.

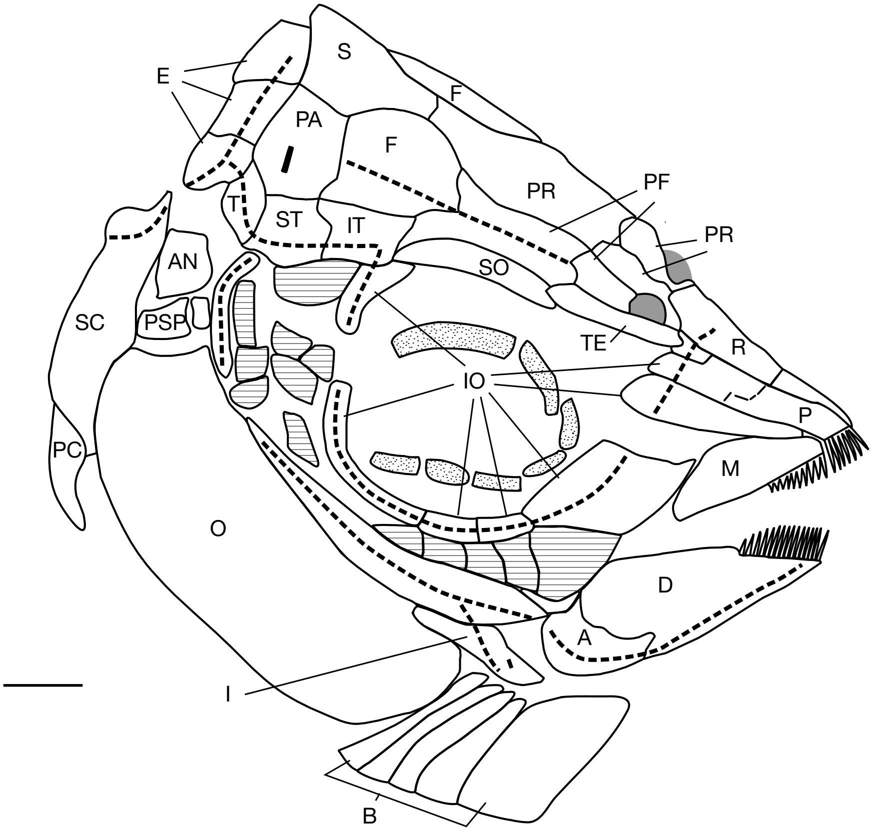

FIG. 8. — *Discoserra pectinodon* n. gen. n. sp., dorsolateral aspect of skull (CM 35214), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **A**, angular; **AN**, presupracleithrum; **B**, branchiostegal rays; **D**, dentary; **E**, extrascapular; **F**, frontal; **I**, interoperculars; **IO**, infraorbital; **IT**, intertemporal; **M**, maxilla; **O**, opercular; **P**, premaxilla; **PA**, partietal; **PC**, postcleithrum; **PF**, prefrontals; **PR**, postrostral; **PSP**, postspiracular; **R**, rostral; **S**, supraoccipital; **SC**, supracleithrum; **SO**, supraorbital; **ST**, supratemporal; **T**, tabular; **TE**, tectal. Sclerotic bones stippled; suborbital bones hatched. Scale: 2 mm.

The hyomandibula (H, Fig. 11) has a ventral process one half of the total height of the bone and has a prominent central foramen for the hyomandibular branch of nerve VII. The metapterygoid (ME, Fig. 11) is attached only to the anterior edge of the ventral process of the hyomandibula, leaving ample room for a large spiracle. There is an indication of a symplectic and a palatal groove for this bone near the posterior edge of the quadrate. The quadrate condyle is poorly preserved but faced forward; a prominent ventral facet posterior to the condyle may have been for attachment of a strong quadrate-mandibular ligament. A stout ceratohyal is visible, with branchiostegal rays attached, in FMNH PF10207.

There are eight to ten sclerotic bones in the eye, the largest of which are the dorsal and anterior bones.

Braincase

The braincase is well ossified and is devoid of sutures that would delineate individual bones. No occipital fissure is evident, unless the small foramina (OC, Fig. 12) are remnants of such a structure. Structures are best displayed in CM 27295, although CM 27290 and CM 35547 have also contributed information (Figs 11; 12). The parasphenoid (PS, Figs 11; 12) extends the entire length of the braincase. It has small lateral wings, no obvious palatal articulations, and is strongly V-sha-

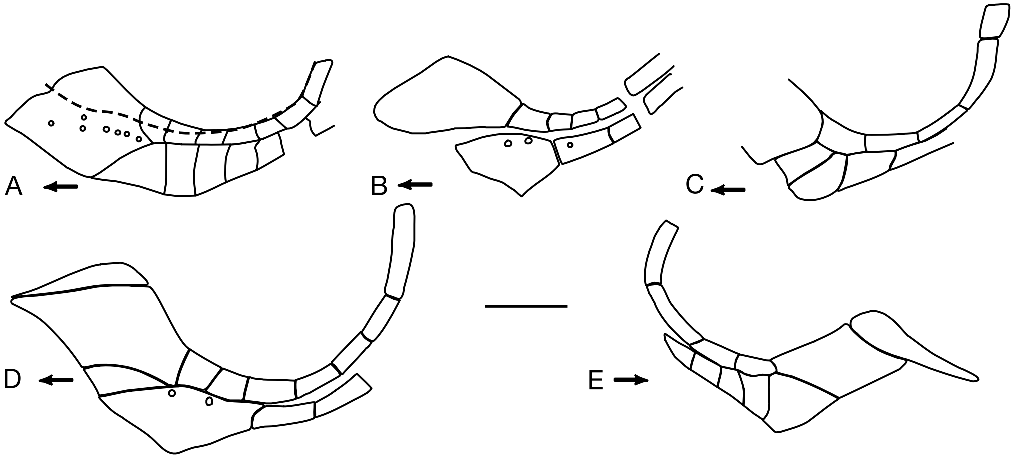

FIG. 9. — *Discoserra pectinodon* n. gen. n. sp., infraorbital bones, Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). **A**, CM 35206A; **B**, CM 35207A; **C**, CM 35209B; **D**, CM 35211B, from latex peel; **E**, CM 35214A, from latex peel. Arrow indicates anterior. Scale: 3 mm.

ped in transverse section through most of its length. The ethmoid region is sheathed by two thin ossifications, the dorsal one also forming the floor of the nasal capsule and enclosing a foramen for the olfactory nerve. The sphenoid region is strongly notched for the exit of the optic nerve (II, Fig. 12). The sphenotic ossification area projects laterally beyond the skull roofing bones and is excavated by a deep pit with an apparent narrow foramen in its floor. This pit clearly is of the form and position of the dilator opercular fossa (DO, Fig. 12) of teleosts and seems to shows no relationship to a spiracular canal as reported for some chondrosteans (Patterson 1975). Foramina for branches of cranial nerves V, VII, and X are visible (Fig. 12). A strong posteriorly directed supraoccipital crest projects beyond the posterior face of the braincase.

Postcranial

Clavicles are absent in the shoulder girdle. The cleithrum is deeply notched for the insertion of the pectoral fin and has a strong peg-and-socket articulation with the supracleithrum. The postcleithrum is small.

All scales have strong peg-and-socket articulations, smooth ganoine coatings, and have finely pectinated posterior borders (Fig. 13C, D). The anterior flank and abdominal scales are tall and narrow.There is no caudal inversion, and the unscaled body axis extends to the last caudal fin ray and bears only long, fine dorsal scutes. A complete series of median dorsal scutes extends from the head to the origin of the dorsal fin; each scute taller than the preceding one and bearing a small forwardly facing hook. The bases of the first jointed fin rays originate behind the last of the dorsal scutes and level with the bases of the scutes. There are two to three dorsal and ventral scutes between the end of the dorsal fin and the caudal lobe. There is a series of tall, thick, strongly serrated abdominal scutes that extend from the shoulder girdle to the pelvic fins, and there are two to three pre-anal scutes.

All fins are composed of well-spaced and jointed rays. The pectoral, dorsal and anal fins are supported on finely scaled lobes. The pelvic fin is very small, and the caudal fin is rounded but not dorsoventrally symmetrical. There are no fin fulcrae.

Postcranial endoskeleton (Fig. 13)

The pectoral fin base is lobed. Up to 11 to 12 radials are visible supporting the pectoral fin rays. The pelvic fin is very small and no endoskeleton is known. The axial skeleton contains 12 to 13 precaudal segments, 13 to 14 caudal segments anterior to the

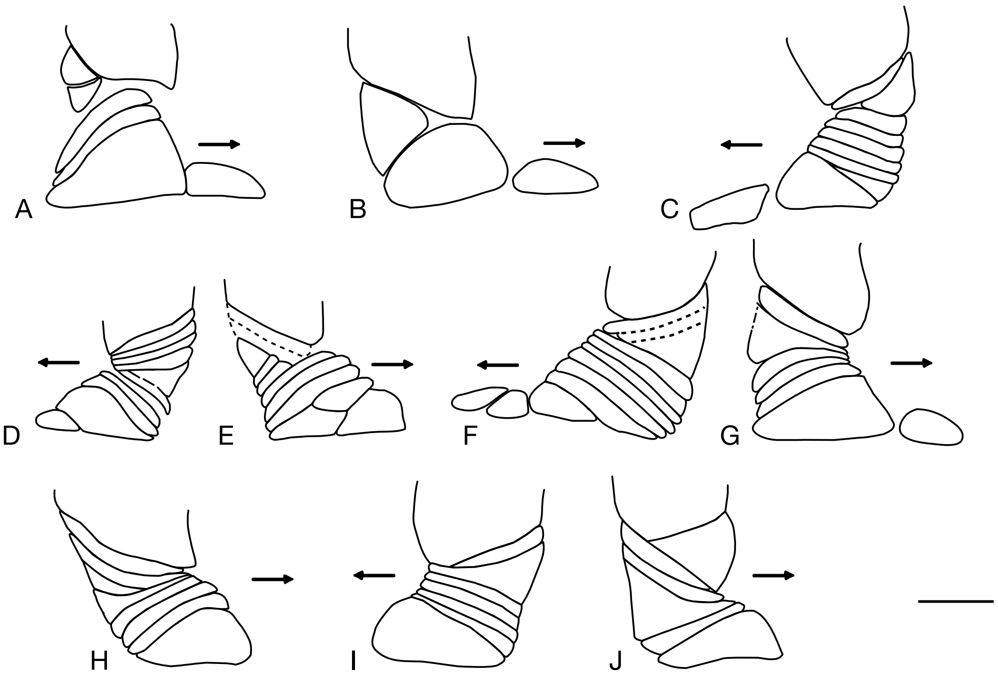

FIG. 10. — *Discoserra pectinodon* n. gen. n. sp., branchiostegal series, Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). **A**, MV 2956; **B**, MV 3811; **C**, CM 27292B; **D**, **E**, CM 44500A, B; **F**, CM 35211A; **G**, CM 35215B; **H**, FMNH PF 10207; **I**, **J**, CM 37547A, B. Scale: 3 mm.

caudal fin endoskeleton and 11 segments are visible in the sharply upturned caudal lobe. Precaudal neural arches are paired, and while there are blocky precaudal ventral arch elements, there are no ossified interarcuals. Caudal neural arches are fused across the midline. Neural spines are not fused to the arches but extend from occiput to the end of the caudal as a complete separate series. Dorsal to the neural spines, a complete supraneural series extends from the occiput to the posterior end of the dorsal fin, the predorsal supraneurals each bearing a dorsal facet for articulation with the dorsal ridge scales (Fig. 13A, B). Approximately two dorsal fin rays are supported by each supraneural (baseost); axonosts are not evident. Haemal arches are fused across the midline and articulate with separate haemal spines; these in turn support the infrahaemal series. The origin of the anal fin is supported by two haemal and infrahaemal elements. The anal fin ray: infrahaemal ratio is also approximately 2: 1.

DISCUSSION

ADAPTATIONS

Guildayichthys and *Discoserra* are clearly sister taxa, separated from all other actinopterygians by the common possession of unique skull, opercular and cheek osteology. The two genera differ subtly in body and fin form, and both are median and paired fin propulsive specialists for maneuvering in geometrically complex environments (Webb 1984). Propulsive system differences, including body and tail form, leading edges of dorsal and anal fins, size of pelvics and height of anterior flank scales, indicate subtle differences in propulsive specializations. Similarly, the two taxa differ in dentition and mouth gape, indicating differing dietary adaptations. *D. prionodon*, with a very attenuated gape and long, gracile teeth was clearly a plucking and grazing feeder, while the longer gape and shorter, well spaced teeth of *G. carnegiei* are somewhat closer to a generalized condition.

The feeding mechanisms of the Guildayichthyiformes are highly specialized for plucking and suction-feeding. The extensive alterations of the operculo-gular series are manifestly associated with great deepening of the pharyngeal region and restriction of the posterior opening of the opercular chamber and stabilizing or strengthening the opercular pumping system, and these changes are functionally associated with restrictions of the size of the gape, toward much more effective suction feeding. Loosening, extension and fragmentation of the bones of the cheek and snout, producing greater snout mobility, may well have accompanied these alterations. It is possible that the interopercular elements are also associated with these changes; similar pressures evidently resulted in the evolution of the halecostome interopercular bone (Schaeffer & Rosen 1961).

OSTEOLOGY

The most anterior bone of the rostral series of the Guildayichthyiformes is a median element, identified as the rostral because of the passage of the ethmoid commissure through it. Paired lateral postrostrals lie medial to the nasal, and a large posterior median postrostral follows posteriorly. The posterior median postrostral may be the topographical equivalent of a pineal plate (Arratia & Cloutier 1996; Pearson 1982) but is significantly larger and is not perforated for a pineal foramen.

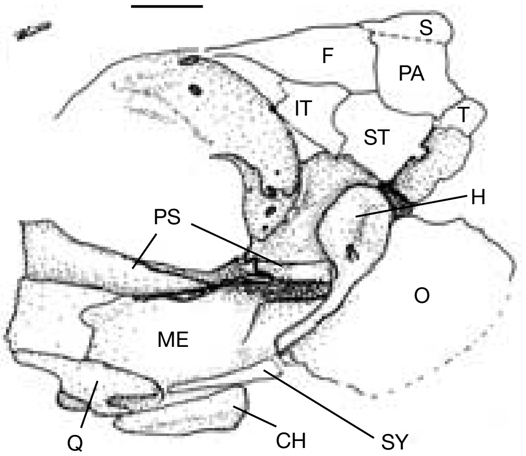

FIG. 11. — *Discoserra pectinodon* n. gen. n. sp., palate and neurocranium (CM 27290A), Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **CH**, ceratohyal; **F**, frontal; **IT**, intertemporal; **H**, hyomandibula; **ME**, metapterygoid; **O**, opercular; **PA**, parietal; **PS**, parasphenoid; **Q**, quadrate; **S**, supraoccipital; **ST**, supratemporal; **SY**, symplectic; **T**, tabular. Scale: 2mm.

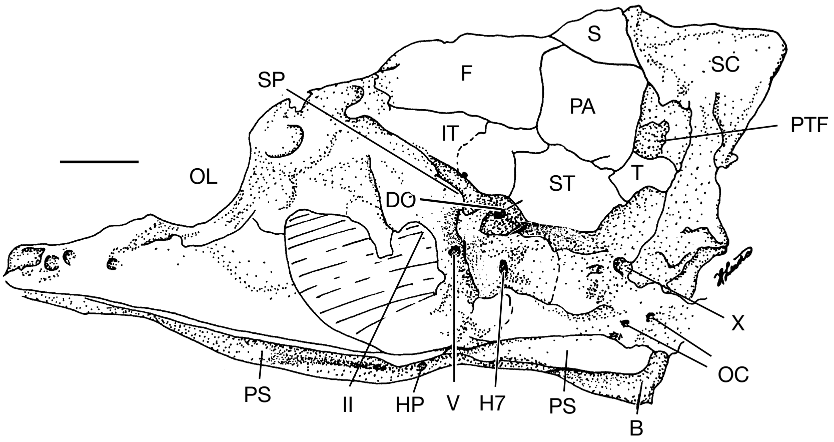

FIG. 12. — *Discoserra pectinodon* n. gen. n. sp., neurocranium (CM 27295A), from latex peels, Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). Abbreviations: **B**, basioccipital; **DO**, dilator opercular fossa; **F**, frontal; **HP**, hypophyseal foramen; **H7**, foramen for hyomandibular branch of facial nerve; **IT**, intertemporal; **OC**, foramina for occipital artery; **OL**, olfactory cup; **PA**, parietal; **PS**, parasphenoid; **PTF**, post-temporal fossa?; **S**, supraoccipital; **SC**, supraoccipital crest; **SP**, sphenotic ossification; **ST**, supratemporal; **T**, tabular; **V**, foramen for trigeminal nerve; **X**, foramen for vagus nerve; **II**, optic foramen. Scale: 2 mm.

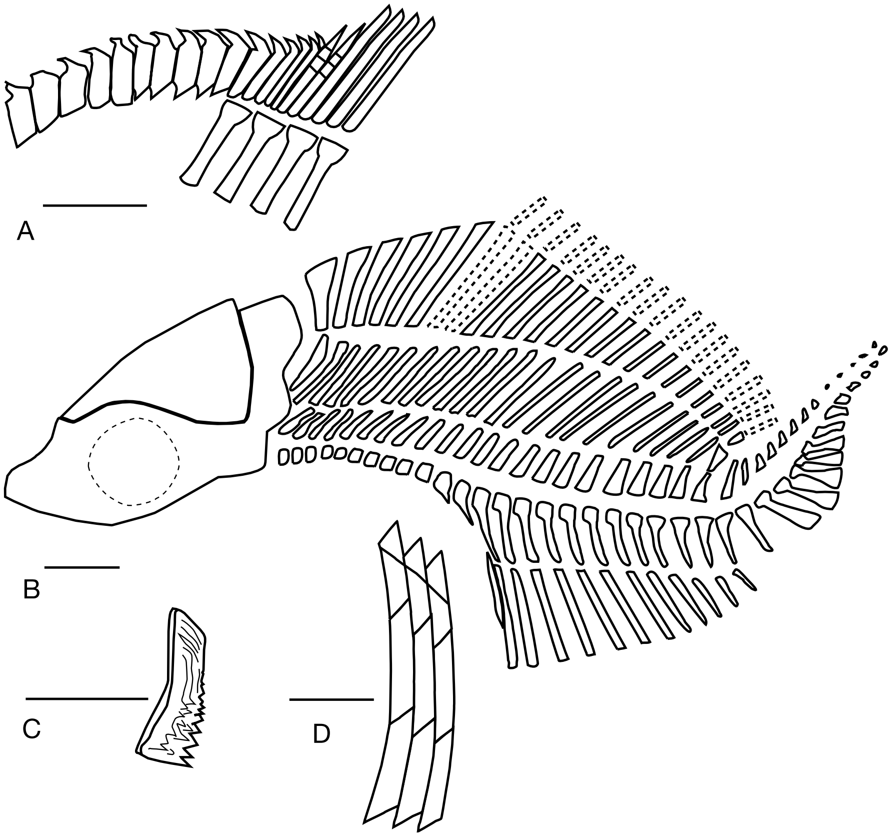

FIG. 13. — *Discoserra pectinodon* n. gen. n. sp., Lower Carboniferous Bear Gulch Limestone, Heath Formation, Fergus County, Montana (USA). **A**, origin of the dorsal fin, from MV 7756; **B**, axial skeleton, from CM 35547, with CM 27295; **C**, first enlarged abdominal scale, from ROM 43976; **D**, scale rows 9-11, from ROM 43976. Scale: A, 3 mm; B, 5 mm; C,D, 4 mm.

A small nasal bone is notched both medially and laterally, presumably for anterior and posterior nostrils, in the usual pattern for Actinopterygii. Two or three anamestic "pre-frontal" bones are found in anteroposterior series lateral to the lateral postrostrals, and an additional series of two to three anamestic bones lie posterior to the nasals, lateral to the "pre-frontals" and medial to the single large supraorbital. This series seems to be the topographic equivalent of the serial nasals of *Paratarrasius* (Lund & Melton 1982) and the frontonasals of Coelacanthiformes (Lund & Lund 1985), but no lateral line canal can be detected in this area.

Parietals, bearing transverse pit-lines, carry the supraorbital canal forward onto paired frontals. Lateral to the parietals and frontals are three clearly delineated bones of the skull roof that carry the otic lateral line canal and accompanying pit-lines. Several Sarcopterygii have more than two otic canal bones, the X-Y series of certain Dipnoi, *Powichthys*, *Panderichthys*, *Barameda* and *Youngolepis* (Campbell & Barwick 1986; Chang 1982; Jessen 1975; Long 1989; Vorobyeva & Schultze 1991; Young *et al.* 1992). The relationships among the surrounding and supporting structures, canals and pit-lines, all strongly suggest that the anterior bone of the series may be homologous to the dermosphenotic, and the posterior two elements homologous to or the equivalent of the dermopterotic of actinopterygians. The terms intertemporal, supratemporal and tabular are most appropriate for these bones.

A large median bone between the parietals, extending to the posterior margin of the skull roof, is called the supraoccipital. It is in the same topographical position as bone B of Dipnoi (Campbell & Bell 1982) and quite similar to the nuchal of most dolichothoracid arthrodires (Goujet 1975), but has distinctly different relationships to underlying structures. There are no other Paleozoic Osteichthyes with this bone aside from Dipnoi, and no homology with any other named supraoccipital is intended.

There is no distinct antorbital bone in the infraorbital canal bone series, although there is an enlarged infraorbital-canal-carrying bone anterior to the orbit. The infraorbital canal itself is continuous with the ethmoid commissure; there is no detectable lateral line canal in the nasal and no visible anterior communication with the supraorbital canal. The anterior bones of the infraorbital series are variable in shape and number in the Guildayichthyiformes. Suborbitals are numerous and variable in number and shape, as in *Paratarrasius* (Lund & Melton 1982).

The single dorsal suborbital is in the same anatomical relationship to the posterodorsal infraorbital, and presumed spiracle, as the spiracular (postspiracular) of coelacanths. Several small, irregular bones are also positioned dorsal to the largest bone of the opercular series, which is designated the operculum. These smaller bones are in the position of the posterior spiraculars of *Polypterus* (Pehrson 1958) and *Bobasatrania* (Lehman 1956).

Tall, narrow, dorsal and ventral bones carry the preopercular lateral line canal ventrally from the margin of skull roof. There is no sensory line communicating between the preopercular and infraorbital lateral line canals.

A series of overlapping rays to small plates occupies a prominent area ventral to the ventral preopercular bone, posterior to the lower jaw, and anterior to the operculum and branchiostegals, and attach to the posterior edge of the palate and ventral preoperculum. A branch of the preopercular canal enters this bony series in at least one specimen. These elements occupy the positions of the preopercular canal-carrying bones "9" of early Dipnoi such as *Chirodipterus*, *Dipnorhynchus* and *Griphognathus* (Westoll 1949; Miles 1977; Campbell & Barwick 1982, 1984, 1986; Schultze & Arsenault 1987), the preopercular bone of sarcopterygians such as *Quebecius* and *Glyptolepis* (Schultze & Arsenault 1987; Jarvik 1972) and coelacanths (Lund & Lund 1985), as well as the interopercular bone of Neopterygii. They are called interoperculars for topographic reasons. Several alternative interpretations of these bones are possible:

1. The guildayichthiform interoperculars are unique neomorphs, autapomorphies of this group, with no homology to the interopercular of halecostomes. They may be derived, for instance, by fragmentation of the anteroventral end of the operculum or preoperculum for functional reasons associated with evolution of the feeding mechanism, as has been advocated for the evolution of the neopterygian interoperculum.

2. Alternatively, the guildayichthiform interoperculars have homologies with other bones in other fishes. Two possibilities ensue:

2A. the condition in the two Guildayichthyiformes represents a transformation series from many rays or bones to a single bone. This prospect leads to 3A, B or C.

2B. the reverse is the case; fragmentation of an original ventralmost preopercular bone resulted in the 9 series in the origin of the Dipnoi and in the interopercular rays in *G. carnegiei*. This yields an origin for the structures, and can conceivably lead to alternative 3.

3A. The guildayichthyiform interoperculars are homologous with the 9 a-f series of preopercular bones in primitive dipnoans (Miles 1977). The dipnoan condition of 9 a-f series is the most primitive known state of these bones, and the guildayichthyiform condition is derived from that.

3B. The guildayichthyiform interoperculars are derived from a portion of a mandibular operculum, as in the submandibular series of Jarvik (1972); the presence of a mandibular operculum would be the most primitive state known among Osteichthyes.

3C. The elements are homologous with the interoperculum of Neopterygii.

Alternative 1 is rejected on the basis of the probable homologies shown between these elements and the series 9 bones of sarcopterygians.

If alternative 2 is accepted, that there are possible homologies, alternative 2A is unsupported by any other evidence and is unlikely, and two of the character associations it would lead to, 3A and 3B, are also unlikely. Alternative 3A would require that the presence of this series of elements is a symplesiomorphy of actinopterygians and dipnoans, a prospect unsupported by any other evidence. The obviously imbricated rays of *G. carnegiei* seem to rule out any explanation that might relate to the functions of either a preoperculum or an interoperculum, and suggest only alternative 3B, branchiostegal rays of a mandibular operculum. Counter to 3B, however, Pearson (1982) has convincingly argued that the elements in question among crossopterygians are branchiostegal rays of a hyoidean operculum. Further, no other firm evidence can be demonstrated that a functional mandibular operculum or aphetohyoidean condition existed, or could have existed, among the gnathostomes.

Thus alternative 2B seems to be both the most parsimonious and the most functionally elegant thesis, that the plesiomorphous condition of the preopercular canal bone series in the cheek of Osteichthyes consisted of three bones as seen, for instance, in most Sarcopterygii, and that fragmentation of the ventral-most element resulted in both the dipnoan and the guildayichthyiform conditions.

Alternative 3C would support the concept that the Guildayichthyiformes could be the primitive sister group of the Neopterygii; this explanation seems quite plausible on other osteological grounds, and would not be excluded by the acceptance of a plesiomorphous three-preopercular state.

The acceptance of 2B as an operational hypothesis, with or without 3C, further indicates that the single squamous cleaver-shaped preopercular bone, cleaver-shaped maxilla and absence of interopercular ossifications are synapomorphies of a monophyletic group of Paleozoic-Mesozoic Actinopterygii, the Paleoniscimorpha (see Kazantseva 1981).

Extrascapulars, bearing the supratemporal commissure, lie immediately posterior to the occiput and the skull roof. A prominent element of the shoulder girdle anterior to the supracleithrum links the girdle to the skull. It does not bear a canal and it is in the same anatomical relationship and topographical position as the presupracleithrum of coelacanths, other crossopterygians, several other paleoniscoids, and tarrasiids (Lund & Melton 1982; Lund & Lund 1985). It has been termed the presupracleithrum in *Howqualepis* by Long (1988).

Cranial architecture

The cranial osteology of the Guildayichthyiformes is unique among Actinopterygii. Many of the singular features of the skull roofs of these fish had very strong structural, and consequently adaptive, value when viewed in the context of the architecture of the cranium.

Major differences in cranial architecture between the guildayichthyids and other Paleozoic Actinopterygii involve: extension of the parasphenoid to the rear of the braincase, a strong sphenotic ossification and a dilator opercular fossa, the presence of three lateral otic series skull roofing bones, the presence of numbers of loose pre-orbital snout bones, a large median posterior occipital crest and the enlargement of median skull roof bones relative to lateral bones (Figs 14; 15), to manifest, in *D. prionodon*, a virtually complete antero-posterior median shield. Moreover, the midline of the skull roof is elevated to a sharp peak, dramatically altering the cross-sectional profile of the neurocranium from the inverted isosceles triangle of typical paleoniscoids to something approaching a diamond shape.

Skull roofs of early Osteichthyes and Arthrodira seem to assemble into two basic configurations, a lateral pattern and a median pattern of paired versus median bones (Fig. 15). A median ethmo-rostral element, or chain of elements, is common to both patterns but is not universal. A lateral pattern is typical of paleoniscoids (including

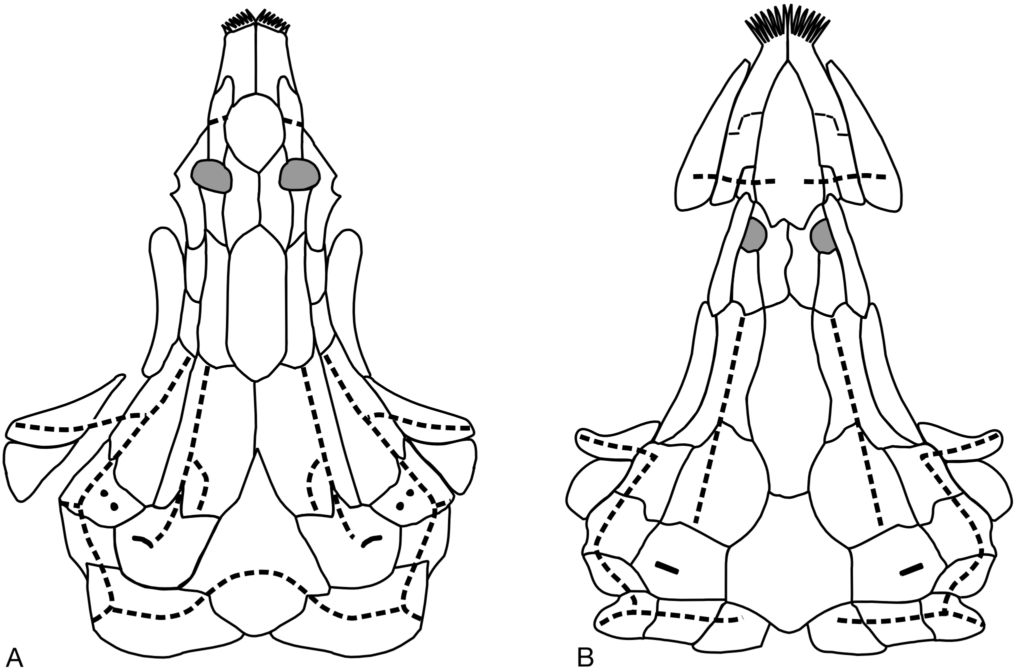

FIG. 14. — Skull roofs reconstructed in dorsal view. **A**, *Guildayichthys carnegiei* n. gen. n. sp., from MV 6045 and CMNH 41010; **B**, *Discoserra pectinodon* n. gen. n. sp., from CMNH 35211 and CMNH 35214.

Platysomidae and other deep-bodied forms), and sarcopterygians (Fig. 15D-F), where median skull roofing bones may be seen only in the ethmoid region, if present at all in the lateral pattern; the supratemporal commissure is straight and postcranial, and prominent laterally placed posttemporal bones are present. A median pattern is seen in guildayichthyids, Dipnoi, and Arthrodira (Fig. 15A-C). Median elements include an ethmo-rostral, a bone spanning the orbits, and a bone in the position of a supraoccipital. The supratemporal commissure bends onto the skull roof in one or more places. A strong posterior median vertical cranial or postcranial skeletal structure may be a feature of this pattern. It can be theorized that the two patterns reflect markedly different stress regimes upon regions of the cranium and skull roof. Some basic observations lend credibility to this conjecture.

The most extensive fusions of bones of the rostral area form a structural dome and are associated with a posteroventral olfactory capsule and a lack of firm posterior palatal support. The consequence of this dome is that strong biting stresses could be transferred to, and dissipated around, the snout from an anterior, ethmo-palatine, joint or support. Examples include the "pariea-autostylic" (Stensiö 1963) placoderms and the autostylic Dipnoi, both with anteriorly braced dental apparatus; the "endocranial autostylic" porolepids, with fangs, jaws, and palate, braced on an extensively excavated, reduced ethmo-rostral moiety; and the limited methyostylic (DeBeer 1937) guildayichthyids, where most biting stresses were concentrated preorbitally. It is noteworthy that the extent of median bones increases with the reduction of the gape from *G. carnegiei* to *D. prionodon*. More limited rostral area ossifications are associated with some posterior palatal bracing, such as an extensive methyostylic suspensorium, a basal process, or an antotic process; and the transfer of a significant proportion of feeding mechanism forces posteriorly. They

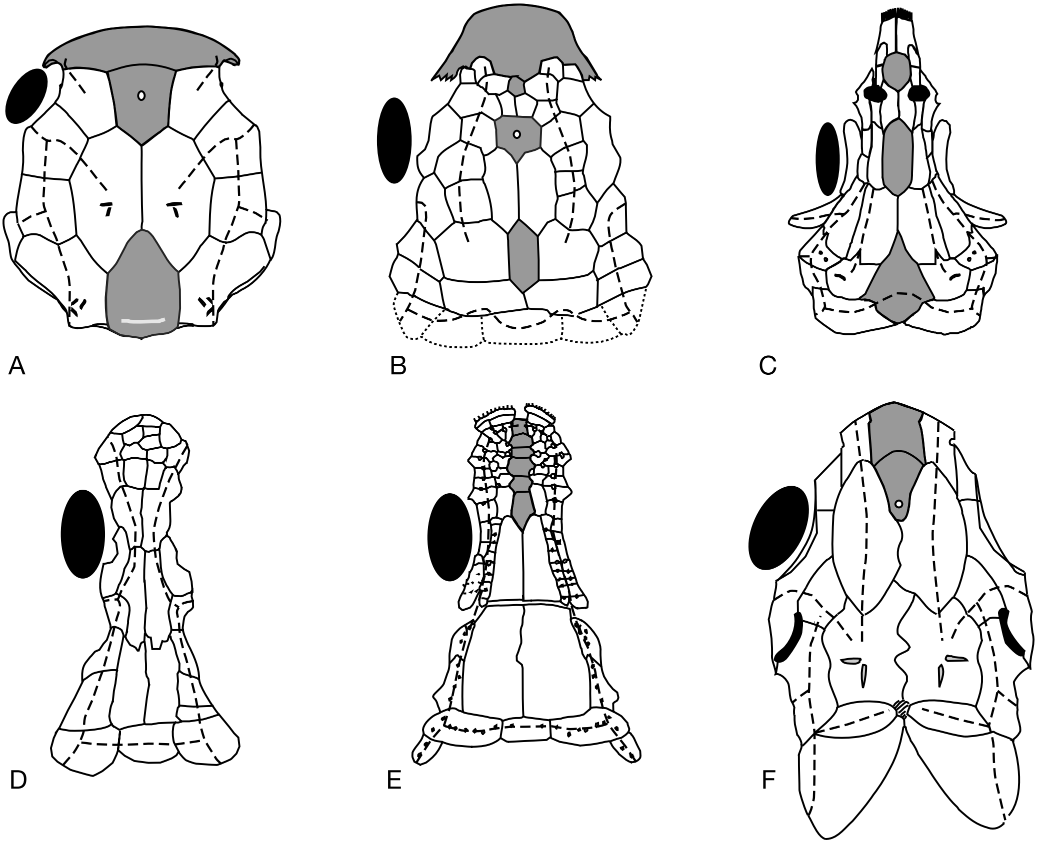

FIG. 15. — Skull roofs of fishes. **A**, *Arctolepis decipiens*, after Goujet (1975); **B**, *Dipnorhynchus kurikae*, after Campbell & Barwick (1986); **C**, *Guildayichthys carnegiei* n. gen. n. sp. ; **D**, *Panderichthys rhombolepis*, after Vorobyeva & Schultze (1991); **E**, *Hadronector donbairdi*, after Lund & Lund (1985); **F**, *Cheirolepis trailli*, after Pearson (1982). Skull roofs scaled to equal snout-occiput lengths, positions and sizes of (left) orbits approximate, median elements shaded.

may also be associated with the introduction of dorsal olfactory capsules in the Actinopterygii or rostral organs in the Coelacanthiformes. Examples include paleoniscoids, where much of the force of the bite is applied toward the rear of the palate and cheek and posterolaterally braced *via* the neurocranium; coelacanths, with very little bite force, a highly flexible snout, and posterolateral bracing via an antotic process; and osteolepid and panderichthyid sarcopterygians, with strong posteriorly directed neurocranial and endoskeletal bracing.

A paired or median supra-orbital bone acts as a bridge to transmit stresses across the orbits of the fish skull, the most structurally excavated part of the neurocranium, from ethmo-rostral to otic region. The interorbital bridge may be broadly supported by paired walls, or only underlain at each end by narrow ethmoid and sphenoid buttresses and a membranous septum. It is conceivable that maximized ethmo-rostral stress regimes will be associated with near or total fusion of the ethmo-rostral structures, as in porolepids, or with a fused median rostral dome followed by a median bone that contributed to the distribution of stresses into the otic braincase and skull roof, as in Dipnoi. Examples of a median pattern include the Dolichothoraci and Dipnoi, wide interorbitally with vertical orbital walls; and the guildayichthyids, narrow interorbitally, with dorsal sphenoid and ethmoid buttresses and a ventral parasphenoid girder.

The origin and considerable expansion of a supraoccipital bone and occipital crest, as well as the posterior extension of the parasphenoid of the Guildayichthyidae, suggest the development of significant stresses upon the occiput and posterior median skull roof by trunk musculature. They also recall the development of bone B of Dipnoi (Campbell & Barwick 1986) and the nuchal bone of Arthrodira (Goujet 1975). Guildayichthyids also have a continuous series of enlarged thoracic supraneurals articulated with deeply imbricated, immobilizing median dorsal scales; the supraneural series would function as a median dorsal keel for musculo-skeletal origins that insert on the occiput. A sharply peaked roof and an otically wide skull also strongly suggests vertical and lateral complexity of trunk-cranial musculature. The occipital surfaces of arthrodire skull roofs have a large median nuchal, followed posteriorly by a median dorsal girdle element, usually with a ventral keel for muscle origin; cranio-thoracic joints, with active mobility; prominent posttemporal fossae for trunk muscular insertion; and strong occipital articulations (see for instance Goujet 1975). The posterodorsal surfaces of lungfish skulls have a large median bone B; extensive lateral cranial vaults (adductor mandibular fossae); a median cranial vault (median temporal fossa, with a median internal keel supporting the median dorsal roofing bone); and complex lateral trunk muscular insertions (Miles 1977; Campbell & Barwick 1982). A posterodorsal median skull roof element, whether called supraoccipital, nuchal, or “B”, is associated with evidence of complex stress regimes transmitted from the trunk as well as from lateral and anterior directions.

Instances of median skull roof bone patterns accordingly involve areas of the cranium of members of several classes of fish. The skulls of the osteichthyan fish with median skull roof bone patterns, such as the Guildayichthyiformes, have evidently been extensively altered to shift stresses drastically away from the plesiomorphous lateral bone pattern of, for instance, a typical chondrostean-level fish, for very strong mechanical, adaptive, and therefore positively selected ends.

CHARACTER ANALYSIS

The Guildayichthyiformes are clearly Actinopterygii but differ strongly from other Paleozoic actinopterygians in many cranial characters. The cladistic characters utilized were drawn from the following sources:

– *Polypterus*: Allis (1922); DeBeer (1937); Pehrson (1947, 1958) and specimens of *Polypterus palmas*.

– Fusiform Actinopterygii: Arratia & Cloutier (1996); Gardiner (1984); Long (1989); Lund & Poplin (1997); Lund, Poplin & McCarthy (1995); Moy-Thomas & Dyne (1938); Pearson (1982); Pearson & Westoll (1979).

– Platysomiformes: Campbell & Le Duy Phuoc (1983); Lehman (1956); Moy-Thomas & Dyne (1938); Traquair (1879); Zidek (1992) and specimens.

– Additional information on coelacanths: Lund & Lund (1985).

Comments on the interpretation of certain of the characters follow:

3. Premaxillary condition and relationships with other bones. Paired, toothed, tightly sutured premaxillae, without an included lateral line canal, are plesiomorphous for Osteichthyes. Premaxillae with an included ethmoid commissure of the lateral line canal system are a derived state representing fusion with rostral bony components; premaxillae including a bony territory with tripartite canal are a separately derived state representing fusion with the antorbital bone.

4, 6. Rostral. The outgroup condition in sarcopterygians is a micromeric/mesomeric bone pattern, with the canal carried by a rostral bone or bones (Pearson 1982; Lund & Lund 1985). This condition of multiple median and paired rostrals is not unusual among the Actinopterygii (Lund & Melton 1982; Pearson & Westoll 1979) and is considered plesiomorphous for the Osteichthyes (Lund & Lund 1985). The rostral series of *Cheirolepis trailli* (Pearson 1982; Arratia & Cloutier 1996) also consists of multiple bones, but a correspondence of bone pattern or numbers of bones with the Guildayichthyiformes cannot be established. The extension of the rostral series over much of the skull roof, and the precise

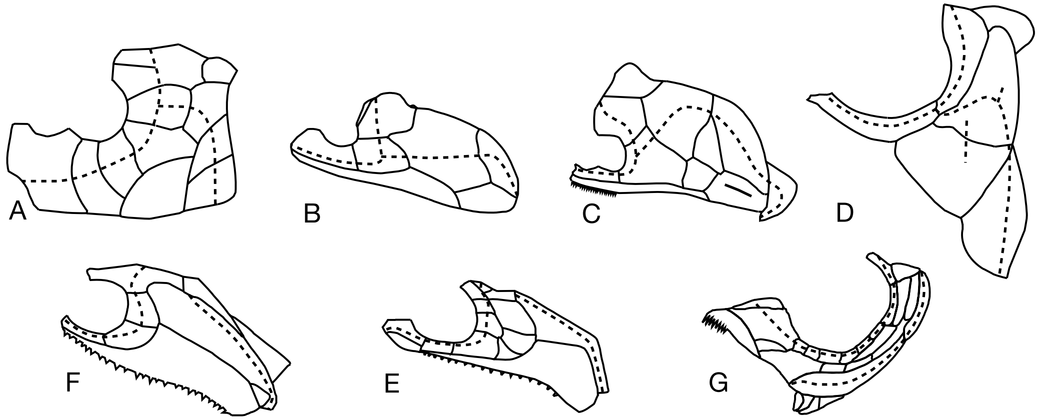

FIG. 16. — Cheek bones of Osteichthyes. **A**, *Chirodipterus australis*, after Campbell & Barwick (1982); **B**, *Eusthenopteron foordi*, after Jarvik (1972); **C**, *Glyptolepis leptopterus*, after Schultze & Arsenault (1987); **D**, *Hadronector donbairdi*, after Lund & Lund (1985); **E**, *Paleoniscus frieislebeni*, after Pearson (1982); **F**, *Cheirolepis trailli*, after Pearson (1982); **G**, *Discoserra pectinodon* n. gen. n. sp.

combination of paired first postrostrals and median second postrostral, is autapomorphous for the Guildayichthyiformes.

11, 13. The series of small pre-frontals, anterior to the frontals and lateral to the postrostrals (Fig. 15), is quite similar to, if simpler than, the frontonasal series of bones in coelacanths (Lund & Lund 1985), porolepids (Jarvik 1972; Young *et al.* 1992) and dipnoans (Campbell & Barwick 1986; Miles 1977; Denison 1968). *Paratarrasius hibbardi* has three pairs of lateral-line-carrying bones anterior to the frontals (Lund & Melton 1982); it has also tectals, absent in Guildayichthyidae. *Cheirolepis trailli* has a pair of anamestic pre-frontals and serial nasals (Pearson 1982). Other Actinopterygii have only three pairs of bones in the series; parietals, frontals, and nasals. The "mosaic" condition of many small pre-frontals is plesiomorphous for the Actinopterygii and for the Osteichthyes.

15. Bones carrying the otic portion of the infraorbital canal. The presence of three lateral line canal bones in the otic series, accompanied by the lateral transverse pit-line on the supratemporal, is not known from any published actinopterygians. A trace of this condition can be inferred in the 24 mm stage of *Polypterus* (Pehrson 1947). Primitive Dipnoi (Miles 1977; Campbell & Barwick 1986; Campbell & Bell 1982; Denison 1968) also show three bones (X, Y1, Y2) in the otic series as do *Powichthys*, *Panderichthys*, *Barameda* (Jessen 1975; Vorobyeva & Schultze 1991; Young *et al.* 1992) and early tetrapods (Jarvik 1972) where they are named intertemporal, supratemporal and tabular. Coelacanths, osteolepids and other early actinopterygians have two canal-carrying bones in the otic series, while porolepids have only one. *Tarrasius* and *Paratarrasius* change ontogenetically from two bones to one (Lund & Melton 1982). Commonality suggests that two bones would be the plesiomorphous state. This is supported by the observation that those fishes with three otic series bones share very few other synapomorphies. Three bones in the otic series would be considered as a derived condition, and the reduction to one in some Actinopterygii, later coelacanths, and porolepids, is a separately derived state that has occurred several times among the subclasses. The derived condition in this character appears to be the retention into adulthood of an early developmental condition that is common to the development of early Osteichthyes.

38, 39. Preoperculum. Two bones commonly carry the preopercular canal across the cheek of primitive coelacanths to join the infraorbital canal (Lund & Lund 1985). Three bones carry the preopercular lateral line canal in *Glyptolepis leptopterus*, other porolepids, and primitive lungfish (Jarvik 1948; Schultze & Arsenault 1987; Young *et al.* 1992; Campbell & Barwick 1984, 1986). Two bones also carry the preopercular canal in *Moythomasia* and *Howqualepis*, some platysomids, and bobasatraniids (Zidek 1992). The larger, ventral preoperculum of the Guildayichthiformes is of the same form and anatomical relationship to the palate and hyomandibula as that of *Acentrophorus*, halecomorphs and their relatives (Moy-Thomas & Miles 1971; Daget 1964). Dorsal (suprapreoperculum) and ventral preoperculae are well-known among teleosts (Daget 1964). They bear little resemblance to the cleaver-shaped or diamond-shaped squamous preoperculum or preopercular bones of the Paleoniscimorpha or other Paleozoic Actinopterygii (Lund & Melton 1982; Lowney 1980; Kazantseva 1981). The latter condition is considered a synapomorphy of certain Paleozoic Actinopterygii, the Paleoniscimorpha.

44. Anteoperculum [dermohyal]. There is no indication of an element with the tight anatomical relationship to the hyomandibular bone and operculum that could be interpreted as a dermohyal or anteopercular bone in sarcopterygians or guildayichthyids. *Polypterus* has a single anteopercular element dorsal to the preoperculum as do most paleoniscoids; *Paratarrasius* has a series of anteopercular elements dorsal to the preoperculum. An anteopercular or anteopercular series is therefore regarded as a derived condition among Actinopterygii.

45-47. Suboperculum and branchiostegals. The opercular-gular series of the guildayichthyids is autapomorphous in lacking a clear subopercular, in the discontinuous and complex branchiostegal series, and in the branchiostegals not extending behind or below the lower jaw.

53. Postspiraculars. Several small elements, the postspiraculars, are located between the principal opercular bone and the rear of the skull in both *G. carnegiei* and *D. pectinodon*. They are equivalent to, and probably homologous to, that portion of the spiracular series of *Polypterus* located posterior to the dermohyal (Pehrson 1947). The prespiraculars, anterior to the dermohyal of *Polypterus*, are probably homologous to the suborbitals of paleoniscoids and evidently to the spiracular or postspiracular bone of coelacanths and other crossopterygians.

55. Sclerotic bones. The guildayichthyids have sclerotic numbers that are higher than the normal condition of two to four found among other Actinopterygii. Higher numbers of sclerotics characterize many arthrodires, Chondrichthyes (Lund 1985, 1986) and Sarcopterygii (Lund & Lund 1984). The plesiomorphous condition for the gnathostomes is considered here to be many sclerotics, although precise numbers can not be arrived at.

56. Parasphenoid. A parasphenoid extending the length of the braincase is derived relative to Sarcopterygii, most Paleoniscimorpha (Gardiner 1973; Lowney 1980; Pearson 1982), Acanthodii (Miles 1973) and Placodermi (Denison 1975). Guildayichthyiformes share this derived character with Neopterygii.

57. Suspensorium. An autodiastylic suspensorium is plesiomorphous for gnathostomes (DeBeer 1937; Grogan 1993; Lund & Grogan 1997); all known Osteichthyes have a hyomandibular bone, an enlarged epihyal articulated to the braincase. The sarcopterygian non-suspensory amphistyly is plesiomorphous for Osteichthyes (Grogan 1993). In *Polypterus*, there is limited osteological and ligamentous contact between the hyomandibula and the palate, although a portion of the adductor mandibularis musculature originates upon the hyomandibula (Allis 1922). The guildayichthyid palate contacts the hyomandibula only along its ventral process and by means of a symplectic element. The typical actinopterygian condition is a methyostylic suspensorium, the metapterygoid and hyomandibula being in extensive osteological contact.

Cladistic analysis was performed using the mhennig procedure of Hennig86. The data matrix used for the analysis employed 72 characters of 13 fusiform Paleozoic Actinopterygii and platysomoid fish plus *Polypterus*. Of the characters used, 50 were multi-state and the remainder were two-state characters (Appendix 1). *Cheirolepis* was used as the outgroup. The analysis resulted in one tree of length 196, ci 64, and ri 63 (Fig. 17). All

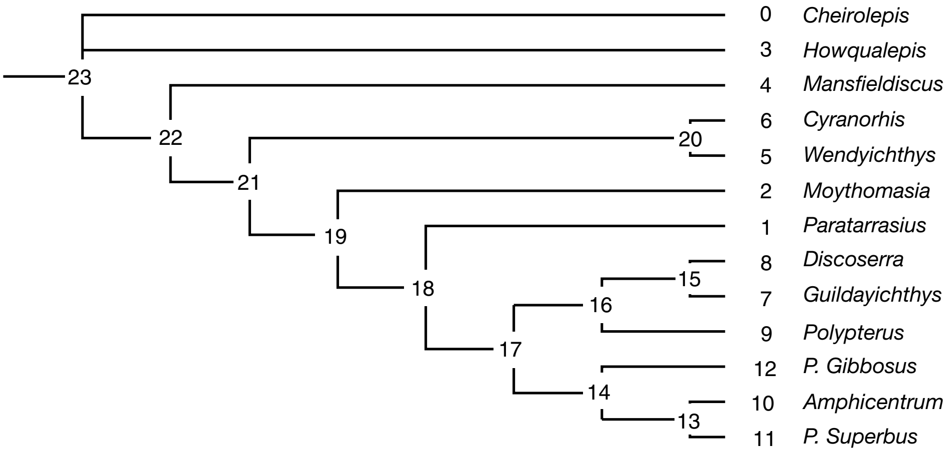

FIG. 17. — Relationships of the Guildayichthyiformes n. ord. Characters were treated non-additively using the procedure mhennig; 72 characters resulted in one tree of length 196, ci 64, and ri 64. The characters and character states used in the analyses are given as Appendix 1, the characters supporting each node are listed in Appendix 2, and the data matrix is given in Appendix 3. The characters have been arrived at from Allis (1922); Arratia & Cloutier (1996); Campbell & Le Duy Phuoc 1983; DeBeer (1937); Gardiner 1984; Lehman 1956; Long 1988; Lund & Lund (1985); Lund & Poplin (1997); Lund, Poplin & McCarthy (1995); Moy-Thomas & Dyne (1938); Pearson (1982); Pehrson (1947, 1958) and Zidek 1992, as well as from unpublished Bear Gulch Limestone taxa.

treatments result in the placement of *Polypterus* as the sister taxon of the Guildayichthyidae; node 16 is supported by 16 character states (Appendix 2; data matrix in Appendix 3). These results were unaffected by alternative interpretations of the condition of the antorbital area, preoperculum, suborbital series, or the condition of the premaxilla, the numbers or identities of included taxa, or the choice of outgroup or outgroups. The strength of the *Polypterus-Guildayichthyidae* association is remarkable considering the long history of debate on the relationships of the Polypteriformes. The resulting clade, the Cladistia, is placed as a crown group among the actinopterygians tested in this specific analysis. Perhaps more importantly, the Cladistia emerges as the sister clade of the included members of the Platysomidae and Amphicentridae at node 17, supported by 15 characters.

CONCLUSION

The Guildayichthyiformes are characterized by discoidal body forms, lobed pectorals set high on the flank, and well-webbed fins, adaptations for swimming in geometrically complex habitats. The feeding mechanisms of these fishes feature pointed snouts, reduced gapes, reduced maxillae, and loosened snout bones, as well as restricted and modified opercular bones. They are also characterized by a unique assemblage of characters, including an extended rostral and postrostral series, multiple prefrontal ossifications, three bones in the otic series, an interopercular series, and an opercular bone surmounted by postspiraculars and followed ventrally not by a suboperculum but by a short, highly modified and very variable branchiostegal series. There is also evidence that, in *Discoserra pectinodon*, the reduced maxilla had a limited ability to passively rotate around an anteromesial articulation in association with mandibular opening. There are eight to ten sclerotics of unequal size.

A brief architectural analysis supports the thesis that the guildayichthyiform skull is median-bone oriented, and is highly modified for structural reasons from the typical lateral-bone oriented actinopterygian skull.

Aspects of the rostral-postrostral series, the supraorbital bones, the interopercular series, preoperculae, and sclerotics are readily comparable to features of the osteology of Polypteriformes, primitive Dipnoi, and Sarcopterygii. Cladistic analysis results in a strong alignment of the Guildayichthyiformes as the sister taxon of *Polypterus* within the Cladistia. The Cladistia in turn are indicated by the cladistic analysis as the sister group of *Platysomus* and *Amphicentrum*.

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REFERENCES

Allis E. P. Jr. 1922. — The cranial anatomy of *Polypterus*. *Journal of Morphology* 12: 489-809.

Arratia G. & Cloutier R. 1996. — Reassessment of the morphology of *Cheirolepis canadensis* (Cheirolepididae: Actinopterygii): 165-197, *in* Schultze H.-P., Cloutier R. & Veziná D. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Pfeil., München.

Baird D. 1955. — Latex micro-molding and latex-plaster molding mixture. *Science* 122: 202.

Campbell K. S. W. & Barwick R. E. 1982. — A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* 25: 509-527.

Campbell K. S. W. & Barwick R. E. 1984. — *Speonesydrion*, an early Devonian dipnoan with primitive toothplates. *Paleo Ichthyologica* 2: 1-48.

Campbell K. S. W. & Barwick R. E. 1986. — Paleozoic lungfishes, a review. *Journal of Morphology* supplement 1: 93-131.

Campbell K. S. W. & Bell M. W. 1982. — Soederberghia (Dipnoi) from the Late Devonian of New South Wales. *Alcheringa* 6: 143-149.

Campbell K. S. W. & Le Duy Phuoc 1983. — A late Permian actinopterygian fish from Australia. *Palaeontology* 26: 33-70.

Chang M.-M. 1982. — *The Braincase of* Youngolepis, *a Lower Devonian Crossopterygian from Yunnan, South-Western China.* Swedish Museum of Natural History, The Hague, 113 p. + 13 pls.

Cope E. D. 1871. — Contributions to the ichthyology of the Lesser Antilles. *Transactions of the American Philosophical Society* 14: 445-483.

Daget J. 1964. — Le crâne des téleostéens. *Mémoires du Muséum national d'Histoire Naturelle*, N. S. Zoologie 31: 1-341.

DeBeer G. R. 1937. — *The Development of the Vertebrate Skull.* Oxford University Press, London, 552 p.

Denison R. H. 1968a. — Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana*, *Geology* 17: 353-409.

Denison R. H. 1968b. — The evolutionary significance of the earliest known lungfish *Uranolophus. Nobel Symposium* 4: 247-257.

Denison R. H. 1975. — Evolution and classification of placoderm fishes. *Breviora* 432: 1-24.

Feldman H., Lund R., Maples C. & Archer A. 1994. — Origin of the Bear Gulch beds (Namurian, Montana, USA). *Geobios* M.S. 16: 283-291.

Fierstine H. L. 1968. — Swollen dorsal fin elements in living and fossil *Caranx* (Teleostei, Carangidae). *Los Angeles County Museum*, *Contributions in Science* 137: 1-10.

Gardiner B. G. 1973. — Interrelationships of teleostomes: 105-135, *in* Greenwood P. H., Miles R. & Patterson C. (eds), *Interrelationships of Fishes.* Academic Press, London.

Gardiner B. G. 1984. — The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History* 37 (4): 173-428.

Goujet D. 1975. — *Dicksonosteus,* un nouvel arthrodire du Dévonien du Spitzberg. Remarques sur le squelette viscéral des Dolichthoraci : 81-99, *in* Lehman J.-P. (éd.), *Problèmes Actuels de Paléontologie : Évolution des Vertébrés, Actes du*

Colloque International CNRS, Paris 4-9 juin 1973. CNRS, Colloques internationaux du Centre national de la recherche scientifique 218, Paris.

Grogan E. D. 1993. — *The Structure of the Holocephalan Head and the Relationships of the Chondrichthyes.* Ph.D. dissertation, School of Marine Science, College of William and Mary, Gloucester Point, Virginia, USA.

Grogan E. D. & Lund R. — The Environment of the Bear Gulch Limestone (Mississippian of Montana). 31 pp, 3 figs; submitted ms for Annals of Carnegie Museum.

Horner J. R. 1985. — The stratigraphic position of the Bear Gulch Limestone (Lower Carboniferous) of central Montana. *Compte Rendu, IX^e Congrès international de Stratigraphie et de Géologie du Carbonifère* 5 : 427-436.

Horner J. R. & Lund R. 1985. — Biotic distribution and diversity in the Bear Gulch Limestone of central Montana. *Compte-Rendu, IX^e Congrès international de Stratigraphie et de Géologie du Carbonifère* 5 : 437-442.

Jarvik E. 1948. — On the morphology and taxonomy of the Middle Devonian osteolepid fishes. *Kunglica svenska Vetenskapsakademiens,* Handlingar Ser. 3, 25: 1-301.

Jarvik E. 1972. — Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. and a discussion on the structure of the head in Porolepiformes. *Meddelelser om Gronland* 187: 1-307.

Jessen H. 1975. — *A New Choanate fish,* Powichthys thorsteinssoni, *n. g., n. sp., from the Early Lower Devonian of the Canadian Arctic Archipelago.* Colloques Internationaux du Centre national de la recherche scientifique 218 : 213-225.

Kazantseva A. R. 1981. — The phylogeny of the lower actinopterygians. *Journal of Ichthyology* 21: 579-594; English translation 1982, 21: 1-16, Scripta Publishing, Silver Spring, Md.

Lehman J. P. 1956. — Compléments à l'étude des genres *Ecrinesomus* et *Bobasatrania* de l'Éotrias de Madagascar. *Annales de Paléontologie* 42 : 67-94.

Long J. A. 1989. — New palaeoniscoid fishes from the Late Devonian and Early Carboniferous of Victoria: 1-64, *in* Jell P. A. (ed.), Devonian and Carboniferous Fish Studies, *Memoir 7 of the Association of Australasian Paleontologists.*

Lowney K. A. 1980. — *Certain Bear Gulch (Namurian A, Montana) Actinopterygii (Osteichthyes) and a Reevaluation of the Evolution of the Paleozoic Actinopterygians.* Ph.D. thesis, New York University, New York, USA.

Lowney K. A. 1985. — The morphology of *Falcatus falcatus* (St John & Worthen), a Mississippian stethacanthid chondrichthyan from the Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* 5: 1-19.

Lowney K. A. 1986. — On *Damocles serratus* nov. gen. et sp. (Elasmobranchii: Cladodontida) from the Upper Mississippian Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* 6: 12-19.

Lund R., Feldman H., Lund W. & Maples C. 1993. — The depositional environment of the Bear Gulch Limestone, Fergus County Montana: 87-96, *in Energy and Mineral Resources of Central Montana*, Montana Geological Society Guidebook 1993, Billings.

Lund R. & Grogan E. D.1997. — Relationships of the Chimaeriformes and the basal radiation of the Chondrichthyes. *Reviews of Fish Biology and Fisheries* 7: 1-59.

Lund R. & Lund W. 1984. — New genera and species of coelacanths from the Bear Gulch Limestone of Montana. *Geobios* 17: 237-244.

Lund R. & Lund W. 1985. — Coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bulletin of Carnegie Museum of Natural History* 25: 1-74.

Lund R. & Melton W. G. Jr. 1982. — A new actinopterygian fish from the Mississippian Bear Gulch Limestone of Montana. *Palaeontology* 25: 485-498.

Lund R., Poplin C. & McCarthy K. 1995. — Preliminary analysis of the interrelationships of some Paleozoic actinopterygians, *in* Lelièvre H., Wenz S., Blieck A. & Cloutier R. (eds), Premiers Vertébrés et Vertébrés inférieurs. *Geobios* M.S. 19 : 215-220.

Lund R. & Poplin C. 1997. — The rhadinichthyids (paleoniscoid actinopterygians) from the Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* 17: 466-486.

Miles R. S. 1977. — Dipnoan (lungfish) skulls and relationships of the group: a study based on a new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61: 1-328.

Moy-Thomas J. A. & Dyne M. B. 1938. — The actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Transactions of the Royal Society of Edinburgh* 59: 437-480.

Moy-Thomas J. A. & Miles R. S. 1971. — *Paleozoic Fishes.* Saunders, Philadelphia, 259 p.

Patterson C. 1975. — The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London*, 269 (B): 275-579.

Pearson D. M. 1982. — Primitive bony fishes, with a special reference to *Cheirolepis* and paleonisciform actinopterygians. *Zoological Journal of the Linnaean Society* 74: 35-67.

Pearson D. M. & Westoll T. S. 1979. — The Devonian actinopterygian *Cheirolepis* Agassiz. *Transactions of the Royal Society of Edinburgh* 70: 337-399.

Pehrson T. 1947. — Some new interpretations of the skull in *Polypterus*. *Acta Zoologica* 28: 400-455.

Pehrson T. 1958. — The early ontogeny of the sensory lines and the dermal skull in *Polypterus*. *Acta Zoologica* 39: 241-258.

Poplin C. 1973. — Survivance de la “ligne épibranchiale”, en particulier du “canal dorso-latéral-antérieur” (ligne profonde) chez les vertébrés inférieurs. *Bulletin du Muséum national d'Histoire naturelle* 175 : 117-140.

Schaeffer B. & Rosen D. E. 1961. — Major adaptive levels in the evolution of theactinopterygian feeding mechanism. *American Zoologist* 1: 187-204.

Schultze H.-P. & Arsenault M. 1987. — Quebecius quebecensis (Whiteaves), a porolepiform crossopterygian (Pisces) from the Late Devonian of Quebec, Canada. *Canadian Journal of Earth Sciences* 24: 2351-2361.

Stensiö E. (1963). — Anatomical studies on the Arthrodiran head. Part 1. *Kunglica Svenska Vetenskapsakademiens* 9: 1-419.

Traquair R. H. 1879. — On the structure and affinities of the Platysomidae. *Transactions of the Royal Society of Edinburgh* 29: 343-391, 6 pls.

Vorobyeva E. & Schultze H.-P. 1991. — Description and systematics of panderichthyid fishes with comments on their relationships to tetrapods: 68-109, *in* Schultze H.-P. & Trueb L. (eds), *Origins of the Higher Groups of Tetrapods*, Cornell University Press, Ithaca.

Webb P. W. 1984. — Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* 24: 107-120.

Westoll T. S. 1949. — On the evolution of the Dipnoi: 121-184, *in* Jepsen G. L., Mayr E. & Simpson G. G. (eds), *Genetics, Paleontology and Evolution*. Princeton University Press, Princeton.

Williams L. A. 1981. — *The Sedimentational History of the Bear Gulch Limestone (Middle Carboniferous, Central Montana).* Ph.D. dissertation, Princeton University, Princeton, USA.

Williams L. A. 1983. — Deposition of the Bear Gulch Limestone: a Carboniferous Plattenkalk from central Montana. *Sedimentology* 30: 843-860.

Young G. C., Long J. A. & Ritchie A. 1992. — Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum* Suppl. 14: 1-77.

Zidek J. 1992. — Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines and Mineral Resources Bulletin* 138: 145-182.

Ziegler A. M., Scotese G. R., McKerron W., Johnson M. & Barnbach R. K. 1979. — Paleozoic paleogeography. *Annual Review of Earth and Planetary Sciences* 7: 473-502.

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APPENDIX 1

Characters and character states for the cladogram of Fig. 17. The characters have been arrived at from Allis (1922); Arratia & Cloutier (1996); Campbell & Le Duy Phuoc (1983); DeBeer (1937); Gardiner (1984); Lehman (1956); Long (1988); Lund & Lund (1985); Lund & Poplin (1997); Lund, Poplin & McCarthy (1995); Moy-Thomas & Dyne (1938); Pearson (1982); Pehrson (1947, 1958) and Zidek (1992), as well as from unpublished Bear Gulch Limestone taxa.

	Character	**State 0**	**State 1**	**State 2**	**State 3**	**States 4 and 5**
0	Body form	0 - fusiform/elongate	1 - high dorsum, flatter venter	2 - round	3 - angulated	
1	Highest point of body profile	0 - no specializations	1 - ridge scutes	2 - few specialized scales		
2	Premaxillary position	0 - sutured in midline	1 - lateral, under antorbital	2 - absent as distinct bone		
3	Premaxillary condition	0 - sutured	1 - loose	2 - premaxilla field fused to other bones	3 - absent as distinct bone	
4	Rostral	0 - separate bone or bones	1 - fused to postrostral	2 - fused to premaxilla	3 - fused to premaxilla and postrostral	4 - absent as distinct bone
5	Ethmoid commissure	0 - across midline	1 - not across midline	2 - absent		
6	Postrostrals	0 - several median	1 - single median	2 - median and paired	3 - paired	4 - absent as distinct bone
7	Mouth	0 - mouth subterminal	1 - mouth terminal			
8	Snout shape	0 - rounded	1 - sharp bump	2 - pointed snout		
9	Rostral notch	0 - absent	1 - vertical	2 - keyhole-shape		
10	Nasals	0 - serial	1 - single bone			
11	Supraorbitals	0 - absent	1 - single series	2 - double series		
12	Tectals	0 - present	1 - absent			
13	Frontals	0 - two pairs	1 - one pair			
14	Parietal/frontal ratio	0 - subequal	1 - much smaller parietal			
15	Otic canal bones	0 - dermosphenotic and dermopterotic	1 - dermopterotic only	2 - three bones		
16	Infraorbital canal	0 - to dermosphenotic	1 - to dermopterotic	2 - to fused dpt-parietal		
17	Dsphenotic/nasal contact	0 - absent	1 - present			
18	Supraoccipital	0 - absent	1 - only on braincase	2 - on skull roof		
19	Supratemporal commissure	0 - across midline	1 - not across midline	2 - loop to skull roof		
20	Extrascapulars	0 - three	1 - one pair	2 - two pairs	3 - absent	
21	Posteroventral IO is #	0 - two	1 - one	2 - > two		
22	Posterodorsal IO is #	0 - three	1 - two (< three)	2 - > three		
23	Posterodorsal IO shape	0 - simple	1 - T-shaped	2 - rev-L shaped		
24	Antorbital presence	0 - absent as distinct bone	1 - differentiated	2 - fused		
25	Antorbital shape	0 - rhombic	1 - inverted L	2 - vertical pillar	3 - fused to premaxilla	4 - absent as distinct bone
26	Suborbital numbers	0 - none	1 - one row	2 - more than one row	3 - large one with canal	
27	Suborbital fit	0 - absent	1 - sutured	2 - loose, gaps		
28	Suborbital thickness	0 - absent	1 - thick	2 - thin, no ganoine		
29	Suborbital fit	0 - not between maxilla and infraorbital	1 - between maxilla and infraorbital	2 - separate maxilla and infraorbital		
30	Maxilla length	0 - posterior to orbit	1 - orbital	2 - preorbital	3 - absent	

31	Maxilla posterior end	0 - moderate rectangular plate	1 - high rounded	2 - high triangle	3 - narrow	
32	Maxilla mandibularfossa	0 - rear of mandible	1 - absent	2 - most of mandible		
33	Maxilla posteroventral angle	0 - not projecting	1 - projecting			
34	Mandible coronoid process	0 - absent	1 - present			
35	Maxilla-preopercular ganoine	0 - circumferential ridges	1 - vertical ridges	2 - tuberculations	3 - absent	
36	Marginal teeth	0 - vertical	1 - forward	2 - posteriad	3 - absent	
37	Dentition	0 - marginal	1 - marginal-palatal	2 - phyllodont		
38	Preoperculum numbers	0 - one bone	1 - two bones			
39	Preoperculum shape	0 - «hatchet-shape»	1 - trapezoidal	2 - tall, narrow	3 - polygonal plate	
40	Preopercular canal	0 - to mid-otic region	1 - to postorbital corner	2 - to postotic region		
41	Preopercular canal ventrally	0 - to mandible	1 - ends blindly in preoperculum	2 - absent		
42	Vertical preopercular pit line	0 - short on preoperculum	1 - on preoperculum, long	2 - absent		
43	Horizontal preopercular pit line	0 - short on preoperculum	1 - absent			
44	Anteoperculum [dermohyal]	0 - absent	1 - single	2 - series		
45	Suboperculum	0 - shorter than opercular	1 - taller than opercular	2 - absent as distinct bone		
46	Anterior branchiostegals	0 - numerous	1 - absent below mandible			
47	Posterior branchiostegals	0 - uniform	1 - short behind mandible	2 - complex	3 - absent	
48	Extralateral gular	0 - absent	1 - present			
49	Gular, median	0 - present	1 - absent			
50	Gular, lateral	0 - like branchiostegals	1 - absent	2 - extended		
51	Clavicles	0 - present	1 - rudimentary	2 - absent		
52	Clavicle length	0 - short	1 - elongate	2 - absent		
53	Postspiraculars	0 - absent	1 - present			
54	Presupracleithrum	0 - present	1 - absent			
55	Sclerotics	0 - many	1 - four	2 - two		
56	Parasphenoid	0 - short	1 - length of braincase			
57	Suspensorium	0 - limited methyostyly	1 - extensive methyostyly			
58	Dorsal fin length	0 - short	1 - slight extension	2 - rear close to caudal	3 - merged with caudal	
59	Dorsal fin shape	0 - Triangular	1 - sigmoidal	2 - long, acuminate	3 - very high and long	4 - long, low (> 60 rays) 5 - short rounded
60	Dorsal fin base	0 - no specializations	1 - scaled lobe	2 - guard scales		
61	Pectoral extended lobe	0 - absent	1 - present			
62	Pelvic fin	0 - normal proportions	1 - reduced or absent	2 - elongate		
63	Caudal axis	0 - heterocercal past last ray	1 - hemiheterocercal			
64	Caudal outline	0 - cleft equilobate	1 - strongly inequilobate	2 - rounded	3 - pointed	
65	Predorsal scutes	0 - absent	1 - few	2 - many	3 - complete to occiput	
66	Anal fin base length	0 - short	1 - anal ends close to caudal	2 - merged with caudal		
67	Caudal fin rays	0 - not webbed	1 - webbed			
68	Scale row inversion	0 - progressive	1 - abrupt	2 - absent		
69	Fin fulcrae	0 - present	1 - absent			
70	Flank scales	0 - same size as others	1 - very high	2 - high, cristate		
71	Ventrolateral flank scales	0 - same proportions as others	1 - very narrow			

APPENDIX 2

Characters and character states at nodes and terminals for Fig. 17. The characters have been arrived at from Allis (1922); Arratia & Cloutier (1996); Campbell & Le Duy Phuoc (1983); DeBeer (1937); Gardiner (1984); Lehman (1956); Long (1988); Lund & Lund (1985); Lund & Poplin (1997); Lund, Poplin & McCarthy (1995); Moy-Thomas & Dyne (1938); Pearson (1982); Pehrson (1947, 1958) and Zidek (1992), as well as from unpublished Bear Gulch Limestone taxa.

Node	Character	State
23 Basal node		
	3 Premaxillary condition	2 - premaxilla field fused to other bones
	6 Postrostrals	1 - single median
	10 Nasals	1 - single bone
	12 Tectals	1 - absent
	20 Extrascapulars	1 - 1 pair
	23 Posterodorsal IO shape	1 - T-shaped
	33 Maxilla posteroventral angle	1 - projecting
	35 Maxilla-preopercular ganoine	2 - tuberculations
	44 Anteoperculum [dermohyal]	2 - series
	52 Clavicle	1 - elongate
	55 Sclerotics	1 - 4
	57 Suspensorium	1 - extensive methyostyly
	65 Predorsal scutes	1 - few
0 *Cheirolepis*		
	0 Body form	0 - fusiform/elongate
	12 Tectals	1 - absent
	14 Parietal/frontal ratio	0 - subequal
	25 Antorbital shape	4 - absent as distinct bone
	40 Preoperculum	1 - to postorbital corner
	50 Gular, lateral	2 - extended
	54 Presupracleithrum	1 - absent
3 *Howqualepis*		
	2 Premaxillary position	2 - absent as distinct bone
	4 Rostral	3 - fused to premaxilla & postrostral
	25 Antorbital shape	3 - fused to premaxilla
	38 Preoperculum numbers	1 - 2 bones
	44 Anteoperculum [dermohyal]	1 - single
	47 Posterior branchiostegals	1 - short behind mandible
	62 Pelvic fin	2 - elongate
22		
	4 Rostral	1 - fused to postrostral
	26 Suborbital numbers	1 - 1 row
	27 Suborbital fit	1 - sutured
	28 Suborbital thickness	1 - thick
	65 Predorsal scutes	3 - complete to occiput
4 *Mansfieldiscus*		
	3 Premaxillary condition	0 - sutured
	15 Otic canal bones	1 - dermopterotic only
	16 Infraorbital canal	1 - to dermopterotic
	24 Antorbital presence	1 - differentiated
	27 Suborbital fit	2 - loose, gaps
	40 Preopercular canal	1 - to postorbital corner
21		
	20 Extrascapulars	2 - 2 pairs
	29 Suborbital fit	1 - between maxilla & infraorbital
	68 Scale row inversion	1 - abrupt
20 Rhadinichthyidae		
	2 Premaxillary position	2 - absent as distinct bone
	3 Premaxillary condition	3 - absent as distinct bone
	19 Supratemporal commissure	1 - not across midline

Node	Character	State
	36 Marginal teeth	1 - forward
	44 Anteoperculum [dermohyal]	1 - single
	48 Extralateral gular	1 - present
	60 Dorsal fin base	2 - guard scales
	65 Predorsal scutes	1 - few
	71 Ventrolateral flank scales	1 - very narrow
5 *Wendyichthys*		
	9 Rostral notch	2 - keyhole-shaped
	17 Dermosphenotic/ nasal contact	1 - present
	25 Antorbital shape	1 - inverted L
	27 Suborbital	2 - loose, gaps
	35 Maxilla-preopercular ganoine	3 - absent
	47 Posterior branchiostegals	1 - short behind mandible
6 *Cyranorhis*		
	8 Snout shape	1 - sharp bump
	68 Scale row inversion	0 - progressive
19		
	35 Maxilla-preopercular ganoine	0 - circumferential ridges
	69 Fin fulcrae	1 - absent
2 *Moythomasia*		
	5 Ethmoid commissure	1 - not across midline
	7 Mouth	1 - terminal
	14 Parietal/frontal ratio	0 - subequal
	24 Antorbital presence	2 - fused
	25 Antorbital shape	3 - fused to premaxilla
	38 Preoperculum numbers	1 - 2 bones
	60 Dorsal fin base	2 - guard scales
	64 Caudal outline	1 - strongly inequilobate
18		
	33 Maxilla posteroventral angle	0 - not projecting
	55 Sclerotics	0 - many
	58 Dorsal fin length	2 - rear close to caudal
	59 Dorsal fin shape	2 - long, acuminate
1 *Paratarrasius*		
	3 Premaxillary condition	0 - sutured
	4 Rostral	0 - separate bone or bones
	10 Nasals	0 - serial
	11 Supraorbitals	2 - double series
	12 Tectals	0 - present
	13 Frontals	0 - two pairs
	18 Supraoccipital	1 - only on braincase
	26 Suborbital numbers	2 - more than 1 row
	42 Vertical preopercular pit line	1 - long
	52 Clavicle length	0 - short
	58 Dorsal fin length	3 - merged with caudal
	61 Pectoral extended lobe	1 - present
	62 Pelvic fin	1 - reduced or absent
	63 Caudal axis	2 - diphycercal
	64 Caudal outline	3 - pointed
	65 Predorsal scutes	0 - absent
	66 Anal fin base length	2 - merged with caudal
17		
	7 Mouth	1 - terminal
	8 Snout shape	2 - pointed snout
	15 Otic canal bones	1 - dermopterotic only
	22 Posterodorsal IO is #	1 - 2 (<3)
	23 Posterodorsal IO shape	0 - simple
	24 Antorbital presence	0 - absent as distinct bone
	25 Antorbital shape	4 - absent as distinct bone

Node	Character	State
	27 Suborbital fit	2 - loose, gaps
	30 Maxilla length	1 - orbital
	31 Maxilla posterior end	2 - high triangle
	39 Preoperculum shape	2 - tall, narrow
	44 Anteoperculum [dermohyal]	0 - absent
	46 Anterior branchiostegals	1 - absent below mandible
	57 Suspensorium	0 - limited methyostyly
	66 Anal fin base length	1 - anal ends close to caudal
16 Cladistia		
	0 Body form	2 - round
	4 Rostral	0 - separate bone or bones
	6 Postrostrals	2 - median & paired
	10 Nasals	0 - serial
	21 Posteroventral 10 is #	1 - 1
	31 Maxilla posterior end	3 - narrow
	32 Maxilla mandibular fossa	1 - absent
	49 Gular, median	1 - absent
	50 Gular, lateral	2 - extended
	51 Clavicles	1 - rudimentary
	52 Clavicle length	2 - absent
	53 Postspiraculars	1 - present
	56 Parasphenoid	1 - length of braincase
	61 Pectoral extended lobe	1 - present
	64 Caudal outline	2 - rounded
	67 Caudal fin rays	1 - webbed
15 Guildayichthyidae		
	1 Highest point of body profile	1 - ridge scutes
	3 Premaxillary condition	1 - loose
	11 Supraorbitals	2 - double series
	13 Frontals	0 - two pairs
	14 Parietal/frontal ratio	0 - subequal
	15 Otic canal bones	2 - 3 bones
	18 Supraoccipital	2 - on skull roof
	19 Supratemporal commissure	1 - not across midline
	21 Posteroventral IO is #	2 - >2
	22 Posterodorsal IO is #	2 - >3
	26 Suborbital numbers	2 - more than 1 row
	32 Maxilla mandibular fossa	2 - most of mandible
	38 Preoperculum numbers	1 - 2 bones
	45 Suboperculum	2 - absent as distinct bone
	51 Clavicles	2 - absent
	59 Dorsal fin shape	4 - long, low (>60 rays)
	60 Dorsal fin base	1 - scaled lobe
	70 Flank scales	1 - very high
8 *Discoserra*		
	5 Ethmoid commissure	1 - not across midline
	30 Maxilla length	2 - preorbital
	42 Vertical preopercular pit line	2 - absent
	43 Horizontal preopercular pit line	1 - absent
	47 Posterior branchiostegals	2 - complex
	62 Pelvic fin	1 - reduced or absent
7 *Guildayichthys*		
	17 Dermosphenotic/nasal contact	1 - present
	19 Supratemporal commissure	2 - loop to skull roof
	20 Extrascapulars	1 - 1 pair
9 *Polypterus*		
	6 Postrostrals	4 - absent as distinct bone
	8 Snout shape	0 - rounded
	16 Infraorbital canal	2 - to fused dermopterotic-parietal

Node	Character	State
	29 Suborbital fit	0 - not between maxilla & infraorbital
	30 Maxilla length	3 - absent
	34 Mandible coronoid process	1 - present
	35 Maxilla-preopercular ganoine	2 - tuberculations
	39 Preoperculum shape	3 - polygonal plate
	44 Anteoperculum [dermohyal]	1 - single
	47 Posterior branchiostegal	3 - absent
	58 Dorsal fin length	3 - merged with caudal
	59 Dorsal fin shape	5 - polypteriform
	63 Caudal axis	1 - hemiheterocercal
	66 Anal fin base length	0 - short
	68 Scale row inversion	2 - absent
14 “Platysomidae”		
	0 Body form	3 - angulated
	2 Premaxillary position	2 - absent as distinct bone
	3 Premaxillary condition	3 - absent as distinct bone
	29 Suborbital fit	0 - not between maxilla & infraorbital
	36 Marginal teeth	3 - absent
	37 Dentition	2 - phyllodont
	43 Horizontal preopercular pit line	1 - absent
	70 Flank scales	2 - high, cristate
12 *P. gibbosus*		
	1 Highest point of body profile	1 - ridge scutes
	4 Rostral	4 - absent as distinct bone
	5 Ethmoid commissure	2 - absent
	21 Posteroventral IO is	2 - >2
	22 Posterodorsal IO is	2 - >3
	26 Suborbital numbers	3 - large one with canal
	30 Maxilla length	2 - preorbital
	34 Mandible coronoid process	1 - present
	35 Maxilla-preopercular ganoine	1 - vertical ridges
	38 Preoperculum numbers	1 - 2 bones
	40 Preoperculum	2 - to postotic region
	41 Preopercular canal ventrally	2 - absent
	42 Vertical preopercular pit line	2 - absent
	47 Posterior branchiostegals	3 - absent
	53 Postspiraculars	1 - present
13		
	22 Posterodorsal IO is #	0 - 3
	26 Suborbital numbers	0 - none
	27 Suborbital fit	0 - absent
	28 Suborbital thickness	0 - absent
	45 Suboperculum	1 - taller than opercular
	46 Anterior branchiostegals	0 - numerous
	54 Presupracleithrum	1 - absent
10 *Amphicentrum*		
	1 Highest point of body profile	2 - few specialized scales
	14 Parietal/frontal ratio	0 - subequal
	20 Extrascapulars	1 - 1 pair
	23 Posterodorsal IO shape	1 - T-shaped
	30 Maxilla length	0 - posterior to orbit
	35 Maxilla-preopercular ganoine	2 - tuberculations
	37 Dentition	1 - marginal- palatal
	62 Pelvic fin	1 - reduced or absent
	70 Flank scales	1 - very high
11 *“P.” superbus*		
	5 Ethmoid commissure	2 - absent
	59 Dorsal fin shape	3 - very high & long
	65 Predorsal scutes	0 - absent
	69 Fin fulcrae	0 - present

APPENDIX 3

Data matrix for cladogram of Fig. 17.

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
Cheirolepis	0	0	0	2	?	?	0	0	0	0	?	0	0	1	0	0	0	0	0	0	1	0	0	1
Paratarrasius	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	0	0	0	1	0	1	0	0	1
Moythomasia	0	0	0	2	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	2	0	0	1
Howqualepis	0	0	2	2	3	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	1
Mansfieldiscus	0	0	0	0	?	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1
Wendyichthys	0	0	2	3	1	0	1	0	0	2	1	0	1	1	1	0	0	1	0	1	2	0	0	1
Cyranorhis	0	0	2	3	1	0	1	0	1	1	1	0	1	1	1	0	0	0	0	1	2	0	0	1
Guildayichthys	2	1	0	1	0	?	2	1	2	0	0	2	1	0	0	2	0	1	2	2	1	2	2	0
Discoserra	2	1	0	1	0	1	2	1	2	0	0	2	1	0	0	2	0	0	2	1	2	2	2	0
Polypterus	0	0	0	2	0	0	4	1	0	0	0	0	1	1	1	1	2	0	0	0	2	1	1	0
Amphicentrum	3	2	2	3	1	0	1	1	2	0	1	0	1	1	0	1	1	0	0	0	1	0	0	1
P. superbus	3	0	2	3	?	2	1	1	2	0	1	0	1	1	1	1	1	0	0	0	2	0	0	0
P. gibbosus	3	1	2	3	4	2	1	1	2	0	1	0	1	1	1	1	1	0	0	0	2	2	2	0

Character	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Cheirolepis	0	4	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	2	0	0	0
Paratarrasius	1	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0
Moythomasia	2	3	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	?	0	2	0	0	0
Howqualepis	0	3	0	0	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	1	0	0	1
Mansfieldiscus	1	0	1	2	1	0	0	0	0	1	0	?	0	0	0	0	1	0	?	?	2	0	0	0
Wendyichthys	1	1	1	2	2	1	0	0	0	1	0	3	1	0	0	0	0	0	0	0	1	0	0	1
Cyranorhis	1	0	1	1	1	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	1	0	0	0
Guildayichthys	0	4	2	2	1	1	1	3	2	0	0	0	0	0	1	2	0	0	0	0	0	2	1	0
Discoserra	0	4	2	2	1	1	2	3	2	0	0	3	0	0	1	2	0	0	2	1	0	2	1	2
Polypterus	0	4	1	2	1	0	3	3	1	0	1	2	0	0	0	3	0	0	0	0	1	0	1	3
Amphicentrum	0	4	0	0	0	0	0	2	?	0	?	2	3	1	0	2	0	0	?	?	0	1	0	0
P. superbus	0	4	0	0	0	0	1	2	?	0	0	0	?	2	0	2	0	0	?	1	0	1	0	0
P. gibbosus	0	4	3	2	1	0	2	2	0	0	1	1	3	2	1	2	2	2	2	1	0	0	1	3

Character	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Cheirolepis	0	0	2	0	?	0	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratarrasius	0	0	0	0	0	0	0	0	0	1	3	2	0	1	1	2	3	0	2	0	1	1	0	0
Moythomasia	0	0	0	0	1	0	0	1	0	?	0	0	2	0	0	0	1	3	0	0	1	1	0	0
Howqualepis	0	0	0	0	1	0	0	1	0	1	0	0	0	0	2	0	0	1	0	0	0	0	0	0
Mansfieldiscus	0	0	0	0	?	0	0	1	?	?	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Wendyichthys	1	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	1	0	0	1	0	0	1
Cyranorhis	1	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	1
Guildayichthys	0	1	2	2	2	1	0	0	1	0	2	4	1	1	0	0	2	3	1	1	1	1	1	0
Discoserra	0	1	2	2	2	1	0	0	1	0	2	4	1	1	1	0	2	3	1	1	1	1	1	0
Polypterus	0	1	2	1	2	1	?	?	1	0	3	5	0	1	0	1	2	3	0	1	2	1	0	0
Amphicentrum	0	?	0	0	1	0	1	?	?	?	2	2	0	0	1	0	0	3	1	0	1	1	1	0
P. superbus	0	0	0	0	?	0	1	?	0	?	2	3	0	0	0	0	0	0	1	0	1	0	2	0
P. gibbosus	0	?	?	?	?	1	0	?	?	?	2	2	0	0	0	0	0	3	1	0	?	?	2	0