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THE MANDIBLE OF THE PRIMITIVE TETRAPOD *GREERERPETON,* AND THE EARLY EVOLUTION OF THE TETRAPOD LOWER JAW

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ABSTRACT—Exceptionally well-preserved Late Mississippian colosteid amphibian specimens occur in southern Illinois; the mandible is described here. Unexpectedly primitive features include toothed adsymphysial and intercoronoid fossa with fenestrate floor. The large adsymphysial bears teeth, forms 50 percent of the symphysis, and meets its antimere in a very coarsely rugose suture. These and other characters are shown to occur also in *Greererpeton burkemorani,* to which we refer the Illinois specimens. Colosteid mandibles from a Late Mississippian locality in southern Iowa resemble *G. burkemorani* closely, although they are not conspecific. Our findings are summarized in a PRESERVE-format data table containing 226 characters. *G. burkemorani*'s adsymphysial suture morphology is shared with the baphetid *Megalocephalus pachycephalus.* However, the relationship of colosteids to other Paleozoic amphibian groups remains unclear, beyond their position as stem tetrapods. The single elongate Meckelian fenestra of colosteids is likely primitive for tetrapods. A three-stage model is proposed for the evolution of Meckelian fenestrae in tetrapods. Based on sutural morphology, *G. burkemorani* is considered to have a kinetic joint between skull table and cheek. A functional hypothesis is outlined in which movements at this joint are accommodated at the symphysis. A phylogenetically based test of this hypothesis is proposed.

INTRODUCTION

THE MANDIBLE of osteolepiform fish and primitive tetrapods is a morphologically complex structure composed of numerous bones, both endochondral and dermal. It is relatively durable, so that even in collections of mostly fragmentary material the mandible, and especially the symphysial region, is often recovered in at least partly articulated condition. The mandible is thus increasingly being recognized as an important source of characters for deciphering the early history of tetrapods (Clack, 1988; Ahlberg, 1991; Ahlberg et al., 1994; Ahlberg and Clack, 1998). This paper deals with mandibles of recently collected and well-preserved colosteid amphibian specimens from the Late Mississippian of Iowa and Illinois.

Colosteus scutellatus, Greererpeton burkemorani, and *Pholidogaster pisciformis,* comprising the amphibian family Colosteidae, are united inter alia by the easily recognized and unequivocal autapomorphy of a deep notch on the outer surface of the mandible, which received a large premaxillary fang. Ranging from the mid-Viséan to Westphalian D, the group includes some of the earliest tetrapods known. Two of the genera, *Colosteus* and *Greererpeton,* are represented by numerous specimens. Monographs by Panchen (1975), Smithson (1982), Hook (1983), and Godfrey (1989) showed that, as expected from their time of appearance, the colosteids are quite primitive but nonetheless derived in some respects relative to Devonian tetrapods.

A number of colosteid specimens have been collected from the Mississippian of southern Illinois and southeastern Iowa (Bolt et al., 1988; Bolt, 1990; Schultze and Bolt, 1996). Schultze and Bolt referred the Illinois specimens to "*Greererpeton* sp." pending further study. Preparation of the best of the skulls from this well-preserved but difficult material is now much more complete. We now consider these specimens to be conspecific with *G. burkemorani* from the long-known Greer locality in West Virginia. The best preserved Iowa colosteid material apparently represents a new taxon and will be the subject of a separate paper; the mandible, which closely resembles that of *Greererpeton,* is considered in the present study.

We compare our findings to our and others' observations on *Greererpeton* from Greer, West Virginia. We do not consider either *Pholidogaster* or *Colosteus. Pholidogaster* is known from two specimens from the Lower Carboniferous of the Scottish Midland Valley (Panchen, 1975), in neither of which is the lower jaw well preserved. *Colosteus* is represented by numerous specimens, mostly from the well-known Middle Pennsylvanian locality at Linton, Ohio, where they are preserved as impressions in channel coal (Hook, 1983; Hook and Baird, 1993). These impressions are often remarkably detailed, and can provide reliable information about suture patterns as well as surface details and tooth morphology. However, *Colosteus* was recently monographed by Hook (1983), and our own examination of some of the specimens he figured indicates that it might be difficult to significantly extend his description of the lower jaw.

Abbreviations for institutions: CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FM, Field Museum, Chicago, Illinois; KUVP, Museum of Natural History, The University of Kansas, Lawrence, Kansas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

MATERIALS AND METHODS

Goreville specimens.—This locality in southern Illinois is Late Chesterian (Elvirian) in age, correlative with the Namurian E_2 of European terminology (Swann, 1963; Schultze and Bolt, 1996). It has produced some 50 specimens of a colosteid, as well as large numbers of the lungfish *Tranodis castrensis* and a few specimens of other vertebrate taxa, including the earliest microsaur (Lombard and Bolt, 1999). Colosteid specimens are preserved in three dimensions, often with very little crushing, and many of them represent substantial portions of articulated skeletons.

All Goreville specimens are housed at the University of Kansas Museum of Natural History. The best cranial material had been prepared to varying degrees, some extensively, before we began our study. We selected partly prepared specimens that included mandibles and carried the preparation further. Original preparation was by a combination of mechanical (pin vise) and chemical methods (dilute acetic acid), which in some cases resulted in damage. The Goreville specimens prepared at the Field Museum were developed mostly with a pin vise. KUVP 87695 and 87862 were prepared both mechanically and chemically, alternately using dilute acetic acid and the "Waller Method," a technique for converting ferric iron to the more soluble ferrous state (Blum et al., 1989).

Goreville *G. burkemorani* specimens examined are: KUVP 126313, anterior one-quarter of left mandible; KUVP 126314, anterior one-third of left mandible missing the distal symphysial region; KUVP 126315, skull with mandibles in place; KUVP

TABLE *1*—Conditions of characters for selected *Greererpeton burkemorani* specimens from the Greer and Goreville localities, and of FM PR 1653 and FM PR 1637, colosteids of uncertain identification from the Delta locality. For each Goreville and Delta specimen we have scored all characters that are both applicable and determinable with a high degree of confidence. By "applicable" we mean that the character is logically expected to be present—the degree of closure of a lateral line canal is not an applicable character if the lateral line canal is not present in the first place. A blank cell thus indicates that, for that character, the specimen in question did not meet one or both of these criteria. The conditions for Goreville and Delta specimens are extracted from the description in the text, which is intended to be complete. For these specimens, this table is therefore also an indirect guide to their preservation and completeness. This is not the case for specimens from the Greer locality, which were examined and scored only in order to elucidate selected points. All characters in the list (anatomical part + feature of the part + states of the feature) are not mutually exclusive. This means that care must be exercised in selecting characters for use. For example, MANDIBLE number of infradentary bones *0*, *1*, *2*, *3*, *4*, *5* is useful for certain types of studies, but overlaps with SPLENIAL bone *absent*, *present*; POSTSPLENIAL bone *absent*, *present*, etc., that are useful for others.

		Greer				Goreville								Delta		
Composite condition (PART + feature + *state*)	Composite	CMNH 11079	CMNH 11129	MCZ 9006	USNM 22576	KUVP 87694	KUVP 87695	KUVP 87862-1	KUVP 87862-2	KUVP 87862-3	KUVP 126313	KUVP 126314	KUVP 126315	FM PR 1637	FM PR 1653	STATE SET
SKULL																
1. SKULL dentary marginal teeth size relative to maxillary teeth *larger*	**2**						2	2						2		(0) *smaller*; (1) *same size*; (2) *larger*
2. EXOCCIPITAL joint with postparietal *absent*	**0**						0									(0) *absent*; (1) *present*
MANDIBLE																
3. ADSYMPHYSIAL bone *present*	**1**	1	1	1		1	1			1	1	1	1	1	1	(0) *absent*; (1) *present*
4. ADSYMPHYSIAL joint with antimere at symphysis *present*	**1**	1		1			1			1	1	1	1	1	1	(0) *absent*; (1) *present*
5. ADSYMPHYSIAL joint with antimere at symphysis surface relief *brassicate*	**2**	2					2			2	2			2	2	(0) *flat*; (1) *interdigitated*; (2) *brassicate*
6. ADSYMPHYSIAL joint with antimere at symphysis projects posteriorly into intermandibular space *present*	**1**	1		1			1				1		1			(0) *absent*; (1) *present*
7. ADSYMPHYSIAL joint with antimere at symphysis contribution to symphysis area *50%–74%*	**2**	2									2				2	(0) *<25%*; (1) *25%–49%*; (2) *50%–74%* (3) *>75%*
8. ADSYMPHYSIAL joint with coronoid 1 *present*	**1**	1	1			1					1	1			1	(0) *absent*; (1) *present*
9. ADSYMPHYSIAL joint with coronoid 1 type *syndesmosis*	**1**		1								1	1			1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
10. ADSYMPHYSIAL joint with dentary *present*	**1**	1	1			1					1	1		1	1	(0) *diarthrosis*; (1) *syndesmosis*; (2)
11. ADSYMPHYSIAL joint with dentary type *syndesmosis*	**1**	1	1			1					1	1			1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
12. ADSYMPHYSIAL joint with dentary overlap/underlap relationship *a butt joint*;	**1**										1	1				(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
13. ADSYMPHYSIAL joint with splenial *present*	**1**	1	1			1	1				1	1	1		1	(0) *absent*; (1) *present*
14. ADSYMPHYSIAL joint with splenial type *syndesmosis*	**1**	1	1			1	1				1	1	1		1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
15. ADSYMPHYSIAL joint with splenial overlap/underlap relationships *underlaps*	**0**	0									0	0				(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
16. ADSYMPHYSIAL fang (basal diameter and/or height >25% that of average adjacent marginal dentary teeth) *absent*	**0**	0								0	0			0		(0) *absent*; (1) *present*
17. ADSYMPHYSIAL teeth (basal diameter and/or height ≥10% and ≤25% that of average adjacent marginal dentary teeth) *present*	**1**	1								1	1			1		(0) *absent*; (1) *present*
18. ADSYMPHYSIAL teeth count *2*	**1**	1								1	1			1		(0) 1; (1) 2; (2) ≥ 3

TABLE 1—Continued.

Composite condition (PART + feature + *state*)	Com-pos-ite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
19. ADSYMPHYSIAL denticles (basal diameter and/or height <10% that of average adjacent marginal dentary teeth) *absent*	**0**	0								0	0					(0) *absent*; (1) *present*
20. ANGULAR bone *present*	**1**			1			1	1	1				1	1		(0) *absent*; (1) *present*
21. ANGULAR surface sculpture *present*	**1**			1			1	1	1				1	1		(0) *absent*; (1) *present*
22. ANGULAR surface sculpture type *"temnospondyl-like"*	**0**			0			0	0	0				0	0		(0) *"temnospondyl-like"*; (1) *"anthracosaur-like"*
23. ANGULAR joint with dentary *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
24. ANGULAR joint with dentary on labial surface of mandible *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
25. ANGULAR joint with dentary on labial surface of mandible type *syndesmosis*	**1**						1	1	1				1	1		(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
26. ANGULAR joint with dentary on labial surface of mandible overlap/underlap relationship *overlaps*	**2**						2	2	2				2	2		(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
27. ANGULAR joint with dentary on labial surface of mandible exterior appearance is *straight*	**0**						0	0					0	0		(0) *straight*; (1) *interdigitated*
28. ANGULAR medial lamina *present*	**1**			1			1	1	1				1			(0) *absent*; (1) *present*
29. ANGULAR relative exposure on labial and lingual surfaces of mandible *>75% labial*	3						3	3								(0) *<25% labial*; (1) *25%–49% labial*; (2) *50%–74% labial*; (3) *>75% labial*
30. ANGULAR joint with postsplenial *present*	**1**			1			1	1	1				1	1		(0) *absent*; (1) *present*
31. ANGULAR joint with postsplenial on lingual surface of mandible *present*	**1**			1			1	1	1				1			(0) *absent*; (1) *present*
32. ANGULAR joint with postsplenial on lingual surface of mandible type *syndesmosis*	**1**			1			1	1	1				1			(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
33. ANGULAR joint with postsplenial on labial surface of mandible *present*	**1**						1		1					1		(0) *absent*; (1) *present*
34. ANGULAR joint with prearticular *present*	**1**						1	1	1				1			(0) *absent*; (1) *present*
35. ANGULAR joint with prearticular on lingual surface of mandible *present*	**1**						1	1	1				1			(0) *absent*; (1) *present*
36. ANGULAR joint with prearticular on lingual surface on mandible type *syndesmosis*	**1**						1	1	1				1			(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
37. ANGULAR joint with surangular *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
38. ANGULAR joint with surangular on labial surface of mandible *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*

TABLE *1*—Continued.

Composite condition (PART + feature + *state*)	Com-pos-ite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
39. ANGULAR joint with surangular on labial surface of mandible type *syndesmosis*	**1**						1	1	1				1	1		(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
40. ANGULAR joint with surangular on labial surface of mandible anterior part overlap/underlap relationship *overlaps*	**2**							2								(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
41. ANGULAR border to exomeckelian fenestra *present*	**1**			1			1		1							(0) *absent*; (1) *present*
42. ANGULAR border to angular foramen *present*	**1**						1	1	1							(0) *absent*; (1) *present*
43. ANGULAR indication of mandibular lateral line *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
44. ANGULAR mandibular lateral line enclosure *completely enclosed with communicating foramina*; or *partly enclosed, with bone bridges*; or *open*	**0/1/2**						0/1		2				0/1			(0) *completely enclosed with communicating foramina*; (1) *partly enclosed, with bone bridges* (2) *open*
45. ARTICULAR bone *present*	**1**						1	1	1				1			(0) *absent* (1) *present*
46. ARTICULAR joint with prearticular *present*	**1**						1	1	1							
47. ARTICULAR joint with prearticular on lingual surface of mandible *present*	**1**						1	1	1							(0) *absent*; (1) *present*
48. ARTICULAR joint with prearticular on lingual surface of mandible type *syndesmosis*	**1**						1	1	1							(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
49. ARTICULAR border to adductor fossa *present*	**1**								1							(0) *absent*; *present*
50. ARTICULAR contribution to retroarticular process *present*	**1**						1		1				1			(0) *absent*; (1) *present*
51. ARTICULAR contribution to retroarticular process exposed dorsally *present*	**1**						1									(0) *absent*; (1) *present*
52. ARTICULAR contribution to glenoid *present*	**1**						1		1							(0) *absent*; (1) *present*
53. ARTICULAR glenoid shape with *central anteroposterior ridge, lateral depressions* (*"saddle-shaped"*)	**0**						0									(0) *central anteroposterior ridge, lateral depressions ("saddle-shaped")*; (1) *trough between condyloid processes*
54. ARTICULAR mandibular lateral line *absent*	**0**						0	0					0			
55. ARTICULAR border to "paraarticular foramen" (=presumed chorda tympani foramen) *present*	**1**						1	1	1							(0) *absent*; (1) *present*
56. CORONOID 1 bone *present*	**1**	1	1			1					1	1		1	1	(0) *absent*; (1) *present*
57. CORONOID 1 joint with coronoid 2 *present*	**1**										1	1			1	(0) *absent*; (1) *present*
58. CORONOID 1 joint with coronoid 2 type *syndesmosis*	**1**										1	1			1	(0) *diarthrosis*; (1) *syndesmosis* (2) *synchondrosis*; (3) *synostosis*
59. CORONOID 1 joint with coronoid 2 exterior appearance *interdigitated*	**1**										1	1				(0) *straight*; (1) *interdigitated*

TABLE 1—Continued.

Composite condition (PART + feature + *state*)	Composite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
60. CORONOID 1 joint with dentary *present*	**1**	1	1			1					1	1			1	(0) *absent*; (1) *present*
61. CORONOID 1 joint with dentary type *syndesmosis*	**1**	1	1			1					1	1			1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
62. CORONOID 1 joint with dentary exterior appearance interdigitated at and near anterior end and straight posteriorly *present*	**1**		1								1	1			1	(0) *absent*; (1) *present*
63. CORONOID 1 joint with dentary overlap/underlap relationship *underlaps*	**0**		0			0					0	0			0	(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
64. CORONOID 1 joint with prearticular *present*	**1**										1	1				(0) *absent*; (1) *present*
65. CORONOID 1 joint with prearticular type *syndesmosis*	**1**										1	1				(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; *synostosis*
66. CORONOID 1 joint with splenial *present*	**1**	1	1								1	1		1	1	(0) *absent*; (1) *present*
67. CORONOID 1 joint with splenial type *syndesmosis*	**1**	1	1								1	1			1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
68. CORONOID 1 border to intercoronoid fossa *present*	**1**					1					1	1			1	(0) *absent*; (1) *present*
69. CORONOID 1 border to intercoronoid fossa contribution *anterior and medial*	**1**											1			1	(0) *anterior and lateral*; (1) *anterior and medial*
70. CORONOID 1 fang (basal diameter and/or height >25% that of average adjacent marginal dentary teeth) *absent* or *present*	**0/1**	0	0			1					1	1		0	0	(0) *absent*; (1) *present*
71. CORONOID 1 fang number (sites for fangs plus functioning fangs) 2	**1**					1					1	1				(0) *1*; (1) 2; (2) ≥2
72. CORONOID 1 teeth (basal diameter and/or height ≥10% and ≤25% that of average adjacent marginal dentary teeth) *present*	1	1	1								1	1				(0) *absent*; (1) *present*
73. CORONOID 1 denticles (basal diameter and/or height <10% that of average adjacent marginal dentary teeth) *absent*	**0**										0	0				(0) *absent*; (1) *present*
74. CORONOID 2 bone *present*	**1**										1	1		1	1	(0) *absent*; (1) *present*
75. CORONOID 2 joint with coronoid 3 *present*	**1**								1					1		(0) *absent*; (1) *present*
76. CORONOID 2 joint with coronoid 3 type *syndesmosis* or *synostosis*	**1/3**							3						1		(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
77. CORONOID 2 joint with coronoid 3 exterior appearance *interdigitated*	**1**													1		(0) *staight*; (1) *interdigitated*
78. CORONOID 2 joint with dentary *present*	**1**											1				(0) *absent*; (1) *present*
79. CORONOID 2 joint with dentary type *syndesmosis*	**1**											1			1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
80. CORONOID 2 joint with dentary exterior appearance *straight*	**0**											0				(0) *straight*; (1) *interdigitated*

TABLE 1—Continued.

Composite condition (PART + feature + *state*)	Com-pos-ite	Greer				Goreville								Delta		STATE SET
		CMNH 11079	CMNH 11129	MCZ 9006	USNM 22576	KUVP 87694	KUVP 87695	KUVP 87862-1	KUVP 87862-2	KUVP 87862-3	KUVP 126313	KUVP 126314	KUVP 126315	FM PR 1637	FM PR 1653	
81. CORONOID 2 joint with dentary overlap/underlap relationship *underlaps*	**0**											0				(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
82. CORONOID 2 joint with prearticular *present*	**1**										1	1		1		(0) *absent*; (1) *present*
83. CORONOID 2 joint with prearticular type *syndesmosis*	**1**										1	1				(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
84. CORONOID 2 border to intercoronoid fossa *present*	**1**											1			1	(0) *absent*; (1) *present*
85. CORONOID 2 border to intercoronoid fossa contribution *posterior and medial*	**1**											1			1	(0) *posterior and lateral*; (1) *posterior and medial*
86. CORONOID 2 fang (basal diameter and/or height >25% that of average adjacent marginal dentary	**0**													0		(0) *absent*; (1) *present*
87. CORONOID 2 teeth (basal diameter and/or height ≥10% and ≤25% that of average adjacent marginal dentary teeth) *present*	**1**										1	1		1		(0) *absent*; (1) *present*
88. CORONOID 2 smallest teeth arranged in longitudinal patch which in places has >1 row *present*	**1**								1					1		(0) *absent*; (1) *present*
89. CORONOID 2 denticles (basal diametr and/or height <10% that of average adjacent marginal dentary teeth) *absent* or *present*	**0/1**								0			0		1		(0) *absent*; (1) *present*
90. CORONOID 3 bone *present*	**1**								1					1		(0) *absent*; (1) *present*
91. CORONOID 3 joint with dentary *present*	**1**								1					1		(0) *absent*; (1) *present*
92. CORONOID 3 joint with dentary overlap/underlap relationship *underlaps*	**0**								0							(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
93. CORONOID 3 joint with prearticular *present*	**1**								1							(0) *absent*; (1) *present*
94. CORONOID 3 joint with prearticular type *syndesmosis*	**1**								1							(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
95. CORONOID 3 joint with surangular *present*	**1**								1					1		(0) *absent*; (1) *present*
96. CORONOID 3 fang (basal diameter and/or height >25% that of average adjacent marginal dentary teeth) *absent*	**0**								0					0		(0) *absent*; (1) *present*
97. CORONOID 3 teeth (basal diameter and/or height ≥10% and ≤25% that of average adjacent marginal dentary teeth) *present*	**1**								1					1		(0) *absent*; *present*
98. CORONOID 3 smallest teeth arranged in longitudinal patch which in places has >1 row *present*	**1**								1					1		(0) *absent*; (1) *present*
99. CORONOID 3 denticles (basal diameter and/or height <10% that of average adjacent marginal dentary teeth) *present*	**1**								1					1		(0) *absent*; (1) *present*

TABLE 1—Continued.

Composite condition (PART + feature + *state*)	Com-pos-ite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
100. CORONOID 3 border to adductor fossa *present*	**1**								1					1		(0) *absent*; (1) *present*
101. CORONOID 3 coronoid process as vertically oriented lamina along at least part of lateral wall of adductor fossa *present*	**1**								1					1		(0) *absent*; (1) *present*
102. CORONOID 3 border to adductor fossa contribution *anterior and lateral*	**1**								1					1		(0) *anterior only*; (1) *anterior and lateral*
103. DENTARY bone *present*	**1**	1	1	1		1	1	1	1		1	1	1	1	1	(0) *absent*; (1) *present*
104. DENTARY joint with antimere at symphysis *present*	**1**	1		1	1		1	1	1		1	1	1		1	(0) *absent*; (1) *present*
105. DENTARY joint with antimere at symphysis contribution to symphysis area *25%–49%*	**1**	1									1				1	(0) *<25%*; (1) *25%–49%*; (2) *50%–74%*; (3) *>75%*
106. DENTARY joint with antimere at symphysis surface relief *flat*	**0**	0					0				0				0	(0) *flat*; (1) *interdigitated*; (2) *coarsely interdigitated*
107. DENTARY joint with antimere surface morphology detail *finely pitted*	**1**	1									1				1	(0) *smooth*; (1) *finely pitted*
108. DENTARY joint with antimere encloses an interdentary gap *present*	**1**			1			1									(0) *absent*; (1) *present*
109. DENTARY joint with postsplenial *present*	**1**						1					1	1	1	1	(0) *absent*; (1) *present*
110. DENTARY joint with postsplenial type *syndesmosis*	**1**						1					1	1	1	1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
111. DENTARY joint with postsplenial surface relief *flat*	**0**											0		0		(0) *flat*; (1) *interdigitated*
112. DENTARY joint with postsplenial exterior appearance *straight*	**0**						0					0	0	0	0	(0) *straight*; (1) *interdigitated*
113. DENTARY joint with postsplenial overlap/underlap relationship *overlaps*	**2**								2			2		2		(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
114. DENTARY joint with splenial *present*	**1**	1		1		1	1				1	1	1	1	1	(0) *absent*; (1) *present*
115. DENTARY joint with splenial on labial and/or ventral exterior surface of mandible *present*	**1**	1		1		1	1				1	1	1	1	1	(0) *absent*; (1) *present*
116. DENTARY joint with splenial on labial and/or ventral exterior surface of mandible type *syndesmosis*	**1**										1	1	1	1	1	(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
117. DENTARY joint with splenial on lingual surface of mandible exclusive of symphysis *absent*	**0**	0									0	0			0	(0) *absent*; (1) *present*
118. DENTARY joint with splenial on lingual surface within symphysis *present*	**1**	1				1	1				1				1	(0) *absent*; (1) *present*
119. DENTARY joint with splenial within symphysis type *syndesmosis*	**1**	1				1	1				1				1	(0) diarthrosis; (1) syndesmosis; (2) *synchondrosis*; (3)*synostosis*
120. DENTARY joint with splenial within symphysis exterior appearance *interdigitated*	**1**	1					1				1				1	(0) *straight*; (1) *interdigitated*

TABLE *1*—Continued.

Composite condition (PART + feature + *state*)	Composite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
121. DENTARY joint with surangular *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
122. DENTARY joint with surangular type *syndesmosis*	**1**						1	1	1				1			(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
123. DENTARY postdental process as a slender extension of dentary posterior to teeth *present*	**1**						1	1	1				1	1		(0) *absent*; (1)*present*
124. DENTARY postdental process lies in groove in surangular *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
125. DENTARY postdental process border to adductor fossa *absent*	**0**								0					0		(0) *absent*; (1) *present*
126. DENTARY postdental process posterior extent *ends within middle third of adductor fossa*	**2**						2	2	2							(0) *does not reach adductor fossa*; (1) *ends within anterior third of adductor fossa*; (2) *ends within middle third of adductor fossa*; (3) *ends within posterior third of adductor fossa*:
127. DENTARY notch for premaxillary fang *present*	**1**	1	1	1	1	1	1				1	1	1	1	1	(0) *absent*; (1) *present*
128. DENTARY lateral parasymphysial foramen *absent* or *present*	**0/1**										1	1			0	(0) *absent*; (1) *present*
129. DENTARY border to intercoronoid fossa *present*	**1**					1						1			1	(0) *absent*; (1) *present*
130. DENTARY border to adductor fossa *absent*	**0**								0							(0) *absent*; (1) present
131. DENTARY surface sculpture *present*	**1**	1	1	1		1	1		1		1	1	1	1	1	(0) *absent*; (1) *present*
132. DENTARY surface sculpture appearance "*temnospondyl-like*"	**0**	0	0	0		0	0		0		0	0	0	0		(0) "*temnospondyl-like*"; (1) "*anthracosaur-like*"
133. DENTARY unsculptured dorsal strip on labial surface *present*	**1**						1	1					1	1		(0) *absent*; (1) *present*
134. DENTARY symphysial fang (basal diameter and/or height >25% that of average adjacent marginal dentary teeth) *present*	**1**	1	1			1					1			1	1	(0) *absent*; (1) *present*
135. DENTARY symphysial fang number (sites for fangs plus functioning fangs)	**1**	1	1			1					1			1	1	(0) *1*; (1) 2; (2) ≥ 2
136. DENTARY symphysial fang position *in marginal tooth row*	**1**	1	1			1					1			1	1	(0) *lingual to marginal tooth row*; (1) *in marginal tooth row*; (2) *interrupts marginal tooth row but lies mostly lingual to it*
137. DENTARY marginal teeth *present*	**1**	1	1			1	1	1	1		1	1	1	1	1	(0) *absent*; (1) *present*
138. DENTARY marginal tooth row (exclusive of fang) begins at symphysis *absent*	**0**	0	0			0					0			0	0	(0) *absent*; (1) *present*
139. DENTARY marginal tooth attachment *pleurodont*	**0**	0	0			0			0			0	0	0	0	(0) *pleurodont*; (1) *acrodont*
140. DENTARY marginal tooth shape curved lingually	**2**					2			2			2			2	(0) *straight*; (1) *recurved posteriorly*; *2 curved lingually*
141. DENTARY marginal tooth cross section *circular* or *compressed mesiodistally*	**0/1**	1				1			0			1			1	(0) *circular*; (1) *compressed mesiodistally*; *2 compressed labiolingually*

TABLE 1—Continued.

		Greer				Goreville								Delta		
Composite condition (PART + feature + *state*)	Com-pos-ite	CMNH 11079	CMNH 11129	MCZ 9006	USNM 22576	KUVP 87694	KUVP 87695	KUVP 87862-1	KUVP 87862-2	KUVP 87862-3	KUVP 126313	KUVP 126314	KUVP 126315	FM PR 1637	FM PR 1653	STATE SET
142. DENTARY marginal tooth row exclusive of symphysial region *homodont*	**0**						0							0		(0) *homodont*; (1) *contains one or more canine peaks*
143. DENTARY marginal tooth labyrinthine folding *present*	**1**	1	1			1	1		1		1	1		1	1	(0) *absent*; (1) *present*
144. DENTARY indication of oral lateral line *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
145. DENTARY oral lateral line enclosure *open*	**2**						2		2				2	2		(0) *completely enclosed with communicating foramina*; (1) *partly enclosed, with bone bridges*; (2) *open*
146. MANDIBLE bones *present*	**1**	1	1	1	1	1	1	1	1	1	1	1	1	1	1	(0) *absent*; (1) *present*
147. MANDIBLE bones forming symphysis *dentary, splenial, adsymphysial*	**2**	2									2			2		(0) *dentary*; (1) *dentary, splenial*; (2) *dentary, splenial, adsymphysial* (3) *dentary, splenial, adsymphysial, Meckelian*
148. MANDIBLE number of coronoids exclusive of adsymphysial *three*	**2**													2		(0) *one*; (1) *two*; (2) *three*; (3) *four or more*
149. MANDIBLE surangular crest (free dorsal margin elevated above bases of the dentary teeth) *present*	**1**							1	1							(0) *absent*; (1) *present*
150. MANDIBLE precoronoid fossa *absent*	**0**	0	0			0					0	0			0	(0) *absent*; (1) *present*
151. MANDIBLE intercoronoid fossa *present*	**1**					1					1	1			1	(0) *absent*; (1) *present*
152. MANDIBLE intercoronoid fossa located *between coronoid 1 and coronoid 2*	**1**										1	1				(0) *in coronoid 1*; (1) *between coronoid 1 and coronoid 2*; (2) *in coronoid 2*
153. MANDIBLE intercoronoid fossa lateral boundary *dentary*	**1**											1			1	(0) *coronoid(s)*; (1) *dentary*
154. MANDIBLE intercoronoid fossa medial boundary *coronoid(s)*	**1**										1	1			1	(0) *prearticular*; (1) *coronoid(s)*; (2) *dentary*
155. MANDIBLE intercoronoid fossa floor is *incomplete*	**0**					0						0				(0) *incomplete*; (1) *complete*
156. MANDIBLE infradentary bones *present*	**1**	1	1		1	1	1	1	1		1	1	1	1	1	(0) *absent*; (1) *present*
157. MANDIBLE infradentary bones count *4*	**4**						4						4	4		(0) *0*; (1) *1*; (2) *2*; (3) *3*; (4) *4*; (5) *5*
158. MANDIBLE exomeckelian fenestra(e) *present*	**1**	1		1		1	1		1		1	1	1	1	1	(0) *absent*; (1) *present*
159. MANDIBLE exomeckelian fenestra(e) count *1*	**1**			1			1						1			(0) *0*; (1) *1*; (2) *2*; (3) ≥ *2*
160. MANDIBLE retroarticular process *present*	**1**						1		1				1			(0) *absent*; (1) *present*
161. MANDIBLE retroarticular process with deep pit on dorsal surface *absent* or *present*	**0/1**						1						0			(0) *absent*; (1) *present*
162. MANDIBLE surface sculpture *present*	**1**	1	1	1	1	1	1	1	1		1	1	1	1	1	(0) *absent*; (1) *present*
163. MANDIBLE surface sculpture appearance "*temnospondyl-like*"	**0**	0	0	0	0	0	0	0	0		0	0	0	0	0	(0) "*temnospondyl-like*"; (1) "*anthracosaur-like*"

TABLE *1*—Continued.

Composite condition (PART + feature + *state*)	Composite	Greer CMNH 11079	Greer CMNH 11129	Greer MCZ 9006	Greer USNM 22576	Goreville KUVP 87694	Goreville KUVP 87695	Goreville KUVP 87862-1	Goreville KUVP 87862-2	Goreville KUVP 87862-3	Goreville KUVP 126313	Goreville KUVP 126314	Goreville KUVP 126315	Delta FM PR 1637	Delta FM PR 1653	STATE SET
164. MANDIBLE adductor fossa *present*	**1**						1		1					1		(0) *absent*; (1) *present*
165. MANDIBLE adductor fossa length compared to total mandible length *25%–35%*	**1**						1									(0) < *25*; (1) *25%–35%* (2) ≥ *35%*
166. MANDIBLE level of glenoid fossa relative to dentary tooth row *approximately same horizontal plane*	**1**						1	1					1			(0) *ventral*; (*1*) *approximately same horizontal plane*; (2) *dorsal*
167. MANDIBLE angular foramen on ventromedial surface in joint between angular and prearticular *present*	**1**						1	1								(0) *absent*; (1) *present*
168. MANDIBLE para-articular foramen (= presumed chorda tympani foramen) *present*	**1**						1	1	1							(0) *absent*; (1) *present*
169. MANDIBLE "para-articular foramen" (= presumed chorda tympani foramen) location on external surface of mandible *in joint between articular and prearticular*	**1**						1	1	1							(0) *entirely in articular*; (1) *in joint between articular and prearticular*; (2) *entirely in prearticular*
170. MANDIBLE medial parasymphysial foramen *present*	**1**		1	1							1	1	1	1	1	(0) *absent*; (1) *present*
171. MANDIBLE medial parasymphysial foramen location *in splenial*	**0**		0	0							0	0	0	0	0	(0) *in splenial*; (1) *joint between adsymphysial and splenial*
172. MANDIBLE lateral parasymphysial foramen *present*	**1**										1	1			1	(0) *absent*; (1) *present*
173. MANDIBLE lateral parasymphysial foramen location *in dentary* or *in joint between adsymphysial and dentary*	**0/1**										0	0			1	(0) *in dentary*; (1) *in joint between adsymphysial and dentary*
174. MECKELIAN bone *absent*	**0**							0			0	0			0	(0) *absent*; (1) *present*
175. POSTSPLENIAL bone *present*	**1**			1			1		1			1		1	1	(0) *absent*; (1) *present*
176. POSTSPLENIAL medial lamina *absent*	**0**			0					0				0	0		(0) *absent*; (1) *present*
177. POSTSPLENIAL joint with prearticular *absent*	**0**						0	0	0				0			(0) *absent*; (1) *present*
178. POSTSPLENIAL joint with splenial *present*	**1**						1		1			1	1	1	1	
179. POSTSPLENIAL joint with splenial on labial surface of mandible *absent*	**0**						0		0			0	0	0	0	(0) *absent*; (1) *present*
180. POSTSPLENIAL joint with splenial on lingual surface of mandible *absent*	**0**						0					0	0	0		(0) *absent*; (1) *present*
181. POSTSPLENIAL joint with splenial on ventral surface of mandible *present*	**1**						1					1	1	1	1	(0) *absent*; (1) *present*
182. POSTSPLENIAL surface sculpture *present*	**1**			1			1		1			1	1	1	1	(0) *absent*; (1) *present*
183. POSTSPLENIAL surface sculpture appearance "*temnospondyl-like*"	**0**			0			0		0			0	0	0	0	(0) "*temnospondyl-like*"; (1) "*anthracosaur-like*"
184. POSTSPLENIAL border to exomeckelian fenestra(e) *present*	**1**			1			1		1				1	1		(0) *absent*; (1) *present*

TABLE 1—Continued.

Composite condition (PART + feature + *state*)	Composite	Greer				Goreville								Delta		STATE SET
		CMNH 11079	CMNH 11129	MCZ 9006	USNM 22576	KUVP 87694	KUVP 87695	KUVP 87862-1	KUVP 87862-2	KUVP 87862-3	KUVP 126313	KUVP 126314	KUVP 126315	FM PR 1637	FM PR 1653	
185. POSTSPLENIAL indication of mandibular lateral line *present*	**1**			1			1		1			1	1	1	1	(0) *absent*; (1) *present*
186. POSTSPLENIAL mandibular lateral line enclosure *partly enclosed, with bone bridges*, or *open*	**1/2**			1			1		2				1		1	(0) *completely enclosed with communicating foramina*; (1) *partly enclosed, with bone bridges*; (2) *open*
187. PREARTICULAR bone *present*	**1**	1	1	1			1	1	1		1	1	1	1		(0) *absent*; (1) *present*
188. PREARTICULAR joint with splenial *present*	**1**	1	1	1			1		1		1	1				(0) *absent*; (1) *present*
189. PREARTICULAR joint with splenial type *syndesmosis*	**1**	1	1	1			1		1		1	1				(0) *diarthrosis*; (1) *syndesmosis*; (2) *synchondrosis*; (3) *synostosis*
190. PREARTICULAR joint with splenial overlap/underlap relationship *underlaps*	**0**			0			0				0	0				(0) *underlaps*; (1) *a butt joint*; (2) *overlaps*
191. PREARTICULAR joint with surangular *absent*	**0**						0	0	0				0			(0) *absent*; (1) *present*
192. PREARTICULAR length from posterior edge of glenoid to anteriormost externally visible extent, relative to total length of mandible as measured from posterior edge of glenoid *80–89%*	**7**										7	7				(0) *<20%*; (1) *20–29%*; (2) *30–39%*; (3) *40–49%*; (4) *50–59%* (5) *60–69%*; (6) *70–79%*; (7) *80–89%*; (8) *90–100%*
193. PREARTICULAR border of adductor fossa *present*	**1**			1			1	1	1					1		(0) *absent*; (1) *present*
194. PREARTICULAR border of adductor fossa shape in profile *concave upward*	**0**			0			0	0	0					0		(0) *concave upward*; (1) *straight*; (2) *convex upward*
195. PREARTICULAR participation in glenoid fossa *absent*	**0**						0	0	0							(0) *absent*; (1) *present*
196. PREARTICULAR border of "para-articular foramen" (=presumed chorda tympani foramen) *present*	**1**						1	1	1							(0) *absent*; (1) *present*
197. PREARTICULAR border of angular foramen *present*	**1**						1	1								(0) *absent*; (1) *present*
198. PREARTICULAR contribution to retroarticular process *absent*	**0**						0		0							(0) *absent*; (1) *present*
199. PREARTICULAR border to exomeckelian fenestra(e) *present*	**1**			1			1		1				1	1		(0) *absent*; (1) *present*
200. PREARTICULAR border of exomeckelian fenestra(e) count *1*	**1**			1			1						1			(0) *0*; 1 *1*; (2) *2*; (3) *≥ 3*
201. PREARTICULAR teeth (basal diameter and/or height ≥10% and ≤25% that of average adjacent marginal dentary teeth) *present*	**1**											1				(0) *absent*; (1) *present*
202. SPLENIAL bone *present*	**1**	1	1	1			1		1		1	1	1	1	1	(0) *absent*; (1) *present*
203. SPLENIAL joint with antimere at symphysis *present*	**1**	1					1				1		1		1	(0) *absent*; (1) *present*
204. SPLENIAL joint with antimere at symphysis contribution to symphysis area *<25%*	**0**	0									0				0	(0) *<25%*; (1) *25%–50%*; (2) *51%–75%*, (3) *>75%*
205. SPLENIAL joint with antimere surface morphology detail *finely pitted*	**1**	1									1				1	(0) *smooth*; (1) *finely pitted*
206. SPLENIAL medially directed free ventral flange *absent* or *present*	**0/1**						0				1		0	0	1	(0) *absent*; (1) *present*

TABLE *1*—Continued.

Composite condition (PART + feature + *state*)	Composite	Greer: CMNH 11079	Greer: CMNH 11129	Greer: MCZ 9006	Greer: USNM 22576	Goreville: KUVP 87694	Goreville: KUVP 87695	Goreville: KUVP 87862-1	Goreville: KUVP 87862-2	Goreville: KUVP 87862-3	Goreville: KUVP 126313	Goreville: KUVP 126314	Goreville: KUVP 126315	Delta: FM PR 1637	Delta: FM PR 1653	STATE SET
207. SPLENIAL length on ventral surface of mandible relative to total mandible length *35%–45%*	**3**						3									(0) *<15%*; (1) *15%–24%*; (2) *25%–34%*; (3) *35%–45%*
208. SPLENIAL relative exposure on labial and lingual surfaces of mandible *<25% labial*	**0**						0					0				(0) *<25% labial*; (1) *25%–49% labial*; (2) *50%–74% labial*; (3) *>75% labial*
209. SPLENIAL surface sculpture *present*	**1**	1	1	1		1	1				1	1	1		1	(0) *absent*; (1) *present*
210. SPLENIAL surface sculpture appearance *"temnospondyl-like"*	**0**	0	0	0		0	0				0	0	0		0	(0) *"temnospondyl-like"*; (1) *"anthracosaur-like"*
211. SPLENIAL border to exomeckelian fenestra(e) *present*	**1**			1			1				1	1	1	1	1	(0) *absent*; (1) *present*
212. SPLENIAL border to anterior end of exomeckelian fenestra(e) contribution *ventral and dorsal*	**1**						1				1	1				(0) *ventral*; (1) *ventral and dorsal*; (2) *dorsal*
213. SPLENIAL indication of mandibular lateral line *present*	**1**			1			1				1	1	1		1	(0) *absent*; (1) *present*
214. SPLENIAL mandibular lateral line enclosure *partly enclosed, with bone bridges*	**1**			1			1				1				1	(0) *completely enclosed, with communicating foramina*; (1) *partly enclosed, with bone bridges*; (2) *open*
215. SPLENIAL medial parasymphysial foramen in lingual surface between symphysis and exomeckelian fenestra *present*	**1**		1	1			1				1	1	1	1	1	(0) *absent*; (1) *present*
216. SURANGULAR bone *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
217. SURANGULAR contribution to apex of surangular crest *present*	**1**							1	1				1			(0) *absent*; (1) *present*
218. SURANGULAR contribution to retroarticular process *absent*	**0**						0						0			(0) *absent*; (1) *present*
219. SURANGULAR border to adductor fossa *present*	**1**								1					1		(0) *absent*; (1) *present*
220. SURANGULAR surface sculpture *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
221. SURANGULAR surface sculpture appearance *"temnospondyl-like"*	**0**						0	0	0				0	0		(0) *"temnospondyl-like"*; (1) *"anthracosaur-like"*
222. SURANGULAR unsculptured dorsal strip on lateral surface *present*	**1**						1	1	1				1	1		(0) *absent*; (1) *present*
223. SURANGULAR indication of mandibular lateral line *present*	**1**						1	1	1				1			(0) *absent*; (1) *present*
224. SURANGULAR mandibular lateral line enclosure *completely enclosed, with communicating foramina* or *partly enclosed, with bone bridges*, or *open*	**0/1/2**						1/2	2	2				0/1			(0) *completely enclosed, with communicating foramina*; (1) *partly enclosed, with bone bridges*; (2) *open*
225. SURANGULAR indicating of oral lateral line *present*	**1**						1	1	1				1			(0) *absent*; (1) *present*
226. SURANGULAR oral lateral line enclosure *open*	**2**						2	2	2				2			(0) *completely enclosed, with communicating foramina*; (1) *partly enclosed, with bone bridges*; (2) *open*

87694, anterior one-half of left mandible, damaged by acid preparation; KUVP 87695, skull with both mandibles in place; KUVP 87862-1, posterior half of skull including partial shoulder girdle, with rear of right mandible; KUVP 87862-2, posterior half of left mandible from same individual; KUVP 87862-3, incomplete anteriormost region of snout from same individual, extending back to about midlength of the palatines; and KUVP 87697, a large crushed and deformed skull with both mandibles in place.

Delta specimens.—This locality in southeastern Iowa has yielded numerous vertebrate specimens, including both fish and tetrapods, from two adjacent sinkholes. The most likely age for these fills is Early Chesterian, correlative with the Viséan V3b, Asbian, of Europe (Witzke et al., 1990; R. M. McKay, personal commun., 1993; Lombard and Bolt, 1995a). Colosteids are rare at Delta, being represented by only two specimens compared to many hundreds representing the stem amniote *Whatcheeria deltae* (Lombard and Bolt, 1995a).

The two colosteid specimens are from different stratigraphic levels. They may or may not represent the same species, though both preserve the dentary notch and are clearly colosteids. The more complete specimen, from lower in the section, may represent a new colosteid taxon based mostly on characters of the skull roof. A complete description of this specimen is in preparation. The preserved elements of the mandibles are described and illustrated here.

Delta colosteid specimens examined are: FM PR 1653, anterior one-third of a left mandible preserved with some, but not severe, crushing; FM PR 1637, skull in association with both mandibles. This specimen was illustrated in a color photograph in Bolt (1990). The skull is dorsoventrally flattened, and partly disarticulated. Both mandibles have been mediolaterally crushed. A complete left mandible, preserved in mostly lingual view, is severely crushed and significantly distorted. The right mandible, preserved in labial view, is present but separated into anterior and posterior halves.

Greer specimens.—This site in central West Virginia has produced some 50 specimens of the colosteid *Greererpeton burkemorani* (Romer, 1969), plus other tetrapods and fish including the lungfish *Tranodis castrensis* (Smithson, 1982; Schultze and Bolt, 1996). Age of the locality is uncertain; Smithson (1982) quotes estimates from the literature that range from Late Viséan to Namurian A.

We have examined all of the known *G. burkemorani* specimens from the Greer locality that preserve lower jaws. Most are housed in the Cleveland Museum of Natural History, although significant specimens are also in the collections of the Museum of Comparative Zoology at Harvard University, and the U.S. National Museum. Nearly all available *G. burkemorani* jaws are associated with skulls and are in closed position. The specimens listed below are those selected for inclusion in this work either because of their completeness or because they preserve fine details in some region.

Greer *G. burkemorani* specimens examined are: CMNH 11079, right one-half of a skull, symphysial region of right lower jaw prepared free at Field Museum, figured by Smithson (1982) in figures 10a and 14e; CMNH 11093, skull, right side reasonably complete and with lower jaw in situ, left lower jaw represented by anterior one-quarter; CMNH 11129, anterior third of left lower jaw, broken just behind the posteriormost of two fangs preserved on coronoid 1; CMNH 11133, left lower jaw, exposed in medial view, crushed and broken, symphysial surface badly battered, much of dorsal surface mostly matrix-covered and part of it obviously damaged; MCZ 9006 (partim), almost-uncrushed skull with both mandibles in place, (formerly CMNH 11068; figured as such by Smithson (1982) in figs. 1, 2, 5, and 6); USNM 22576 (partim), small skull with both mandibles in place, somewhat dorsoventrally crushed and incompletely prepared.

Characters.—Mandibular characters are summarized in the Appendix. The condition of each of the new specimens from Goreville and Delta was determined for each of the characters. In cases where our findings were inconsistent with previous descriptions, the condition of some characters was determined for selected specimens from Greer. The characters are presented in a format consistent with the PRESERVE database character protocol (available at URL at http://www.phyla.org). An introduction to the PRESERVE character format was published by Lombard and Bolt (1999) and a full description and rationale is part of the instructions for use of the PRESERVE web site. In outline, the protocol is as follows: each character is expressed in terms of three elements: a body part, a feature of that part, and states of that feature. By convention, the part is in upper case, the feature in lower case and the states in italics. For example: TABULAR horn *absent, present.* The intent in developing this standard format was to improve the accuracy and usefulness of individual characters, facilitate retrieval and comparison of characters from the rapidly growing literature, and help researchers to keep track of characters both within their own databases and when using the abbreviated naming format required by such phylogenetic analysis programs as PAUP. In this paper we use the term "condition" to refer to the combination of part, feature, and state actually observed in a given taxon; for example, TABULAR horn *absent.*

GREERERPETON BURKEMORANI MANDIBLES FROM GOREVILLE

The specimens are essentially uncrushed and undistorted, though the dermal sculpturing of some is poorly preserved. Overall, however, this material presents an unusually clear and complete picture of the lower jaw. The Goreville specimens are the only ones available that permit a secure interpretation of both the occlusal view and the symphysial region. The description below is organized alphabetically by individual bone and, for each, the specimens used for that description are noted. We follow the same protocol for description of Delta and Greer material.

Adsymphysial.—The adsymphysial is best seen in KUVP 126313 (Fig. 1), where it is intact and has been acid-prepared so that its bordering sutures are clear. Its posterior portion is also well preserved in KUVP 126314 (Fig. 2), although in that specimen the anterior tip of the jaw had been removed. In partial compensation for this loss, KUVP 126314 now shows a cross-section through the adsymphysial and surrounding bones (Figs. 3.1, 4). The adsymphysial is visible to some extent in all of the other Goreville specimens that preserve the symphysial area. A right adsymphysial is preserved as an isolated bone, broken off posteriorly and ventrally and cemented by matrix to the anterior end of the right vomer in snout fragment KUVP 87862-3. This occurrence preserves an adsymphysial nearly in life position with respect to the skull, and is the only example available of intact adsymphysial dentition.

The sutures between the adsymphysial and all of the bones which it contacts—coronoid 1, dentary and splenial—are interdigitated at least in part. The adsymphysial forms 50 percent of the total area of the symphysis in plan view, as measured on KUVP 126313. Its symphysial surface is highly complex, consisting of an irregular network of interconnected ridges bounding deep pits. It is clear from the well-preserved articulated mandibles of KUVP that the sutural surfaces of the apposed adsymphysials did interpenetrate. However, this suture exhibits neither the scale nor the morphology of most interdigitated sutures: the projections and recesses are on a much coarser scale than usual, and the projecting elements are mostly ridges rather than pointed spicules. This type of sutural articular surface bears some resemblance to

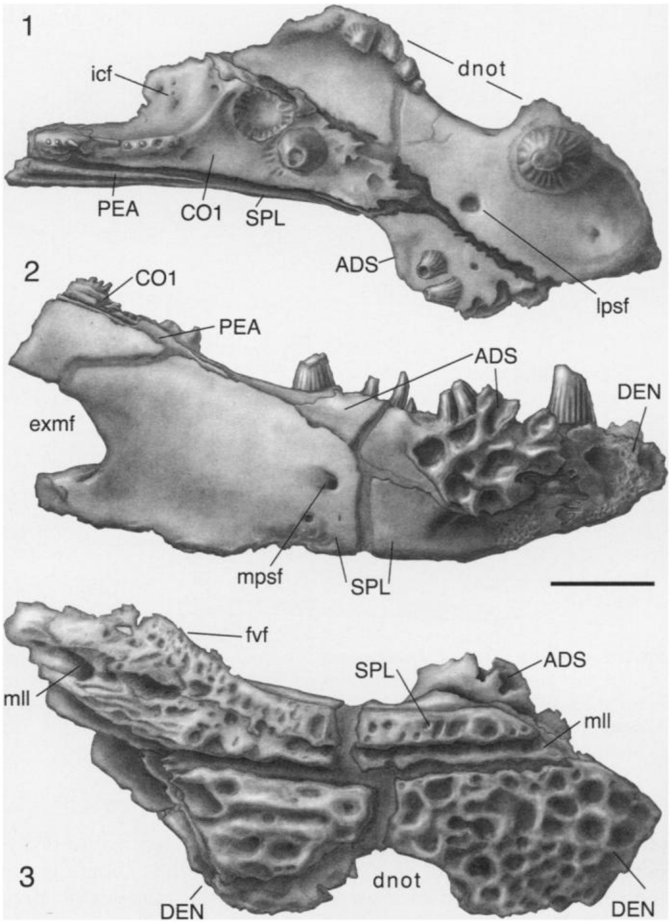

FIGURE 1—*Greererpeton burkemorani* KUVP 126313, anterior portion of left mandible. Scale = 1 cm. *1,* Dorsal (occlusal) view. *2,* Medial view. *3,* Ventral view. Abbreviations for this and subsequent figures: * = unsculptured area marking dentary attachment, ADS = adsymphysial, ANG = angular, angf = angular foramen, ART = articular, CO1 = coronoid 1, CO2 = coronoid 2, CO3 = coronoid 3, ctf = chorda tympani foramen, DEN = dentary, dnot = dentary notch, dnot1 = anterior dentary notch, dnot2 = posterior dentary notch, exmf = exomeckelian fenestra, fvf = free ventral flange, icf = intercoronoid fossa, lpsf = lateral parasymphysial foramen, mc = Meckelian canal, mll = mandibular lateral line canal, mpsf = medial parasymphysial foramen, ors = oral sulcus, PEA = prearticular, PTS = postsplenial, SPL = splenial, SRA = surangular.

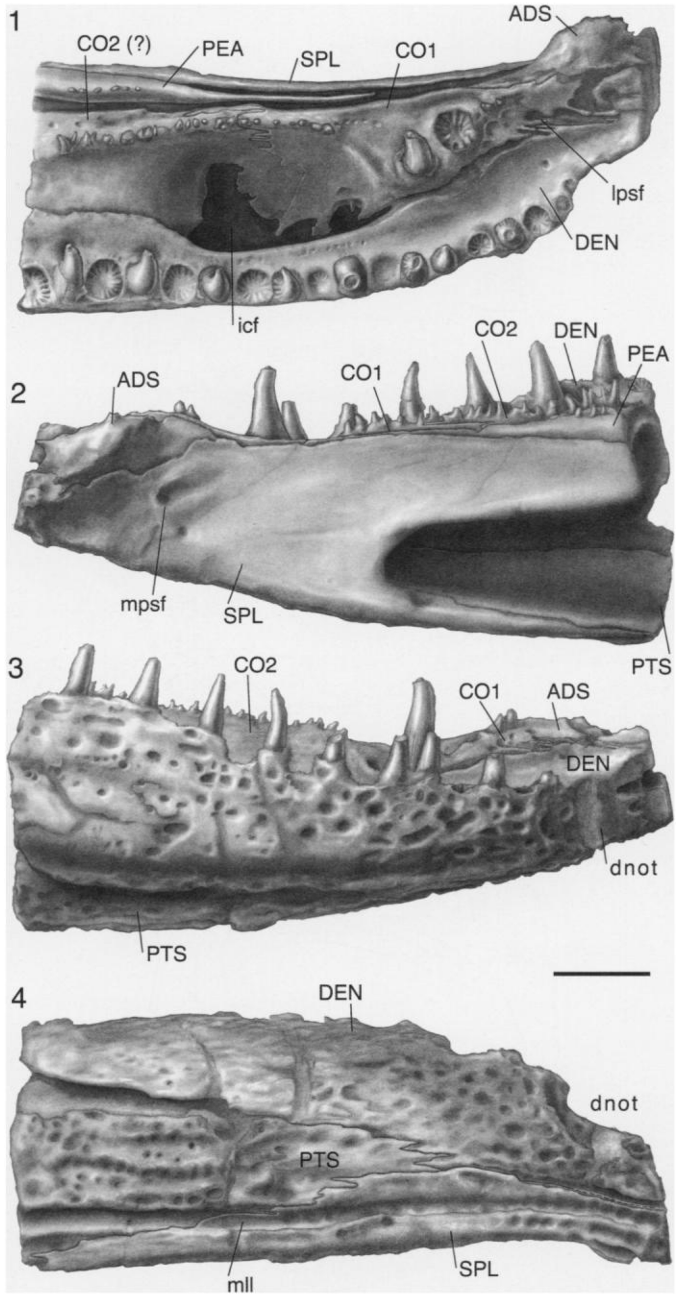

FIGURE 2—*Greererpeton burkemorani* KUVP 126314, anterior portion of right mandible missing the tip and with dorsal part of adsymphysial broken off. Scale = 1 cm. *1,* Dorsal (occlusal) view. *2,* Medial view. *3,* Lateral view. *4,* Ventral view. Abbreviations: see Figure 1.

a cauliflower head; the resemblance to a mold of the head's surface is even stronger. P. Ahlberg and J. Clack (personal commun.) independently noted the same resemblance in a baphetid amphibian, and informally referred to this type of suture articular surface as "brassicate" after the family (Brassicaceae) and genus to which cauliflower belongs. We will use this aptly descriptive term throughout this paper.

The two adsymphysials together form a bulbous mass that projects posteriorly into the intermandibular area, interrupting the V shape formed by the ventromedial margins of the splenials. The adsymphysial is excluded from the ventral edge of the symphysial region by the splenial, which overlaps its medial side and extends forward ventral to the adsymphysial to contact the dentary in an interdigitated suture (Fig. 1.2). The adsymphysial forms part of the wall of the Meckelian canal, as seen in cross section in KUVP 126314 (Fig. 3.1).

Some of the earliest tetrapods have lateral and medial parasymphysial foramina; in a few taxa, only the medial foramen is present (Ahlberg et al., 1994; Ahlberg and Clack, 1998). Most often, the parasymphysial foramina lie respectively in the lateral and medial bordering sutures of the adsymphysial, although in *Acanthostega* the medial foramen lies entirely within the adsymphysial (Ahlberg and Clack, 1998). *Greererpeton* has no precisely comparable foramina associated with the adsymphysial. However, we suggest that the lateral foramen is represented by one seen in the dentary just lateral to the adsymphysial-dentary suture in KUVP 125313 (Fig. 1.1); the same foramen is apparently present in

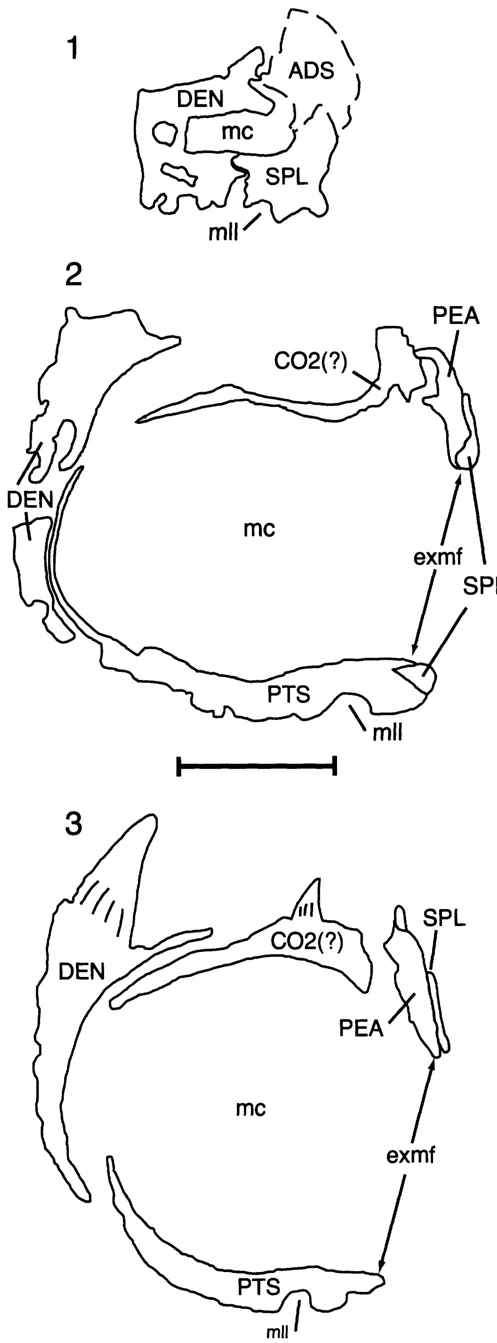

FIGURE 3—*Greererpeton burkemorani* from Goreville. Cross-sections through the mandible. Re-oriented as necessary for consistency. Location of each section indicated on Figure 4. Sections are ordered from front to back. Scale = 1 cm. *1,* from KUVP 126314. *2,* from KUVP 87862-2. *3,* from KUVP 126314. Abbreviations: see Figure 1.

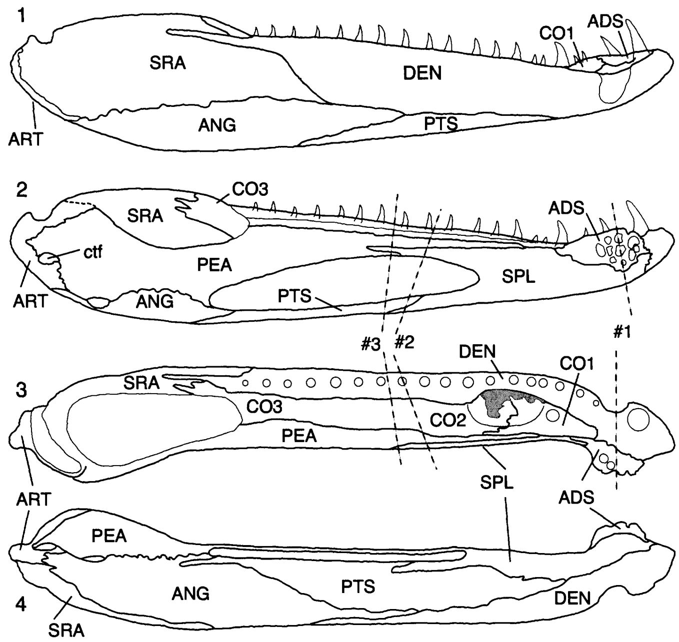

FIGURE 4—*Greererpeton burkemorani* from Goreville. Outline drawings of whole mandible reconstructions in Figure 5, with lateral view re-oriented so that all drawings have anterior end to right. Numbered dashed lines indicate positions of the cross-sections in Figure 3. Abbreviations: see Figure 1.

KUVP 126314, although the symphysial area is missing just anterior to this point. Similarly, we suggest that the medial foramen is represented by a large foramen in the splenial, just ventral to its contact with the adsymphysial. This foramen is visible in both KUVP 125313 and 126314 (Figs. 1.2, 2.2).

The adsymphysial dentition in KUVP 126313 consists of two adjacent teeth with missing crowns (Fig. 1.1). These teeth have a basal diameter comparable to that of anterior members of the dentary tooth row. The isolated (from the rest of the mandible) adsymphysial in KUVP 87862-3 preserves two closely set intact teeth, whose crown morphology appears to be identical to that of dentary teeth. The most accessible of these teeth is about 6.6 mm long from base to tip of crown, with a basal diameter of about 2.5 mm. These dimensions are comparable to those of the (small) vomerine fangs in KUVP 87862-3, and to the basal diameter of maxillary teeth in the same specimen. No other teeth, or denticles, are visible on any of the available adsymphysials.

Angular.—The lateral and ventral surfaces of the angular are strongly sculptured. The angular-dentary suture is beveled and not interdigitated along its externally visible course. The angular-surangular suture is highly interdigitated posteriorly. Anteriorly, it appears to be beveled, with the surangular overlapping the angular (right mandible of KUVP 87862), but not interdigitated.

The angular has a small unsculptured exposure, the medial lamina, on the medial surface of the mandible. The medial lamina forms a small postero-ventral portion of the border of the large Meckelian fenestra; where it borders the foramen, its edge is smoothly rounded. The medial lamina also forms the ventral margin of an elongate foramen that lies within the angular-prearticular suture (Fig. 5.2). The homology and function of this foramen is unknown; we will refer to it as the angular foramen. The angular portion of the mandibular lateral line canal runs partly within open sulci, partly within canals that open onto the bone surface via foramina. As usual, the exact pattern varies from specimen to specimen.

Articular.—KUVP 87862-2 provides the only unobstructed dorsal view of the articular, including its relationships within the adductor fossa. Unfortunately, this specimen is damaged, and matrix could not be completely removed from the adductor fossa because it provides support for the crushed and fractured posterior end of the mandible. Several other specimens provide good views of the articular from other perspectives.

The articular forms a short, blunt retroarticular process, which is best seen in KUVP 87695. The most notable feature of this area is a pronounced pit on the dorsal surface, which can be

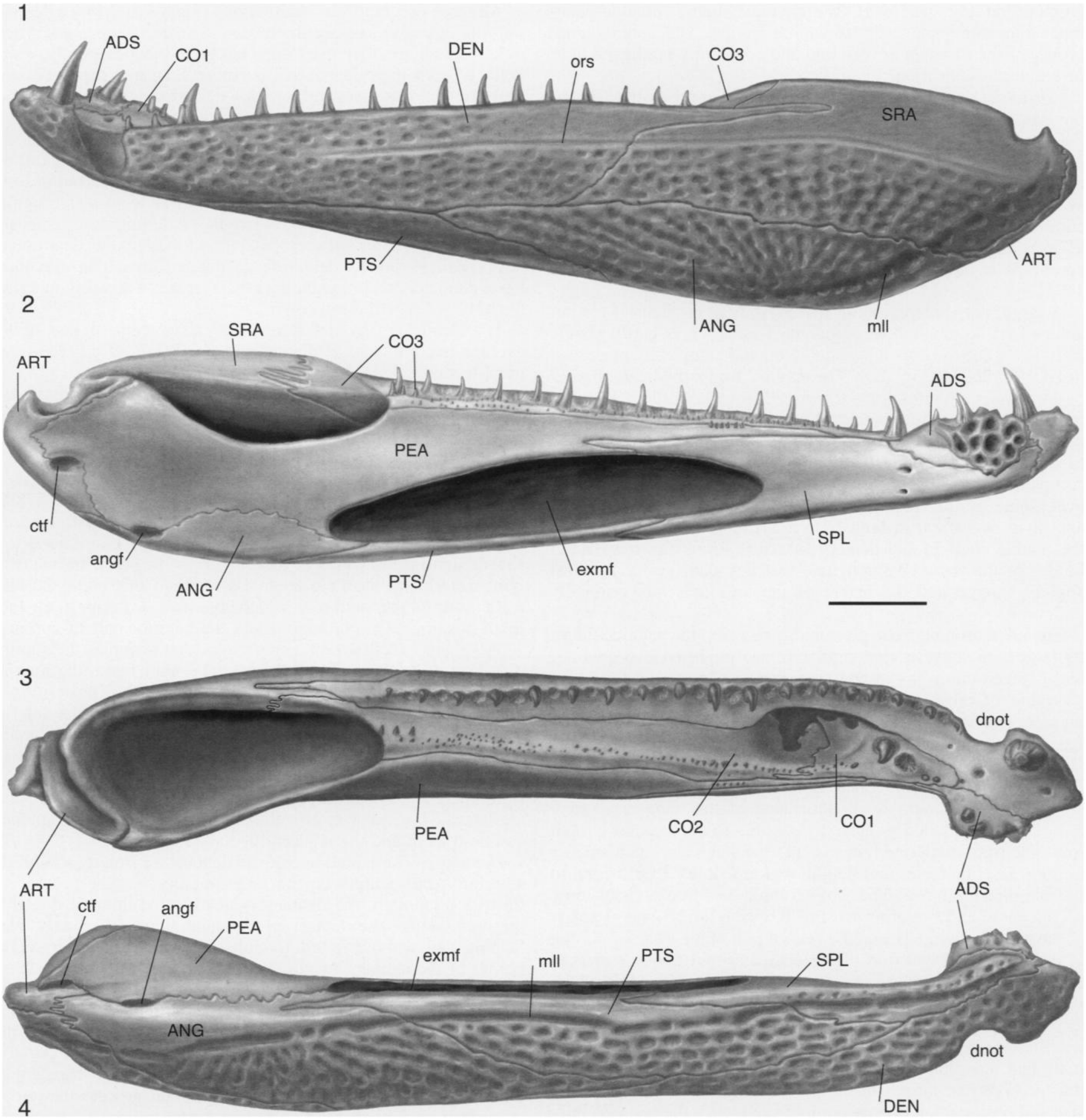

FIGURE 5—*Greererpeton burkemorani*; reconstruction of left lower jaw based on Goreville specimens. Overall shape is based on KUVP 126315, which also contributed much of the detailed information in all views except dorsal. Additional details from other specimens cited in the text. Scale = 2 cm. *1*, Lateral view. *2*, Medial view. *3*, Dorsal (occlusal) view. *4*, Ventral view. Abbreviations: see Figure 1.

referred to as the retroarticular pit and presumably represents the insertion of jaw depressor musculature. The retroarticular process and pit are less well developed on the left mandible of KUVP 126315, which is a smaller individual; on the right mandible of the same specimen, both the retroarticular process and pit are practically nonexistent.

The glenoid, apparently formed entirely by the articular, is roughly saddle-shaped with a low central eminence, and is bounded on all sides by a low ridge. The shape of the glenoid is best seen on the left side of KUVP 87695, where it is slightly separated from the quadrate even though the mandibles are in adducted position. Within the adductor fossa, the articular appears to be a thin plate of bone that is confined to the posterior wall (although as noted above, this region has not been completely prepared on any specimen). The chorda tympani foramen penetrates this thin plate near its ventral border. The anteroventral border of the foramen is very thin and apparently marks the limit of articular ossification.

Coronoid series.—The coronoid series comprises the adsymphysial, described above, plus two suturally outlined coronoids that we identify as coronoid 1 (anteriormost) and coronoid 2 plus 3. We follow Smithson (1982) in assuming that both coronoid 2 and coronoid 3 are present, but the suture between them has fused. We base this assumption on the widespread occurrence of three coronoids in other early tetrapods and in tetrapodomorph (see Fig. 8) fish, as well as one of the Delta colosteids. The number of coronoids is indeterminate in *Colosteus* (Hook, 1983; Panchen, 1975).

A large, deep intercoronoid fossa (Ahlberg et al., 1994) is developed at the junction of coronoids 1 and 2. It is partly visible in KUVP 126313 (Fig. 1.1) and 87694, and completely preserved in KUVP 126314 (Fig. 2.1). The dentary forms the lateral border of the fossa; coronoids 1 and 2 form all its other borders. Keeping in mind the fact that coronoids 1 and 2 are thin where they form the floor and that all of these specimens have been acid-prepared to some degree, it might be thought that the floor was originally complete and its absence is a result of preparation damage. However, some of the free edges of the coronoids within the floor appear to be natural in both KUVP 87694 and 126314, as does the medial shelf of the dentary where it forms the free lateral border of the fossa. We conclude that any damage has at most slightly exaggerated the extent of the area that was originally unfloored.

The intercoronoid fossa presumably received the palatine fangs. Its large size suggests that similar fossae might be expected anterior (precoronoid fossa) and posterior to it (coronoid fossa) for reception of other palatal fangs. However, no other fossae are present. This is correlated with the position and size of the palatal fangs. The palatine fang positions are visible in KUVP 87862-3 (snout), where they were occupied by an alternately replacing pair of large fangs, one of which is in place and missing only its crown. The maximum basal dimension of this fang is about 9 mm, and it is situated as close as possible to the maxillary tooth row. The right vomerine fangs in this specimen are much smaller in both basal diameter and height, and are situated far medial to the marginal tooth row. The ectopterygoid dentition is visible only on the snout and posterior skull of KUVP 87862-3 and -1 (parts of the same individual), and the central part of the bone is missing at the break. The position of the ectopterygoid fangs is marked in KUVP 87862-1 by a large pit, as for the palatine fangs, which is occupied by the single largest tooth base in the ectopterygoid tooth row as preserved. This tooth base, which is set close to the maxilla, has a maximum diameter of about 5.25 mm—substantially less than that of the palatine fangs. The intercoronoid fossa thus receives the largest of the palatal fangs, which due to their size and position had to be accommodated when the jaw was fully adducted by a pit in the occlusal surface.

Toothed areas of the coronoids are confined to the occlusal surface. In KUVP 87862-2, the only specimen where the region is visible, the toothless posterolateral extremity of coronoid 3 twists through 90 degrees to form an interdigitated suture with the inner surface of the surangular to bound the anterolateral part of the adductor fossa. This is the common condition of coronoid 3 in temnospondyl amphibians. In contrast, Smithson (1982, p. 69) states that in the Greer specimens "Unlike some later temnospondyls . . . , the posterior coronoid is not incorporated into the lateral wall of the adductor fossa." Coronoid 3 also has a small lateral exposure that forms the leading edge of the surangular crest.

All three coronoids are dentigerous (Figs. 1.1, 2.1). In describing this dentition, we use the terms "tooth," "fang," and "denticle." These are often used imprecisely and inconsistently, which detracts from their descriptive usefulness. In this paper, we employ the following conventions for describing the dentition present on any bone.

1) Marginal teeth of the skull and mandible represent the size standard for "tooth" of the upper and lower dentition, respectively. In most cases this will be practically identical, but in some groups such as Colosteidae upper and lower teeth differ significantly in size. Thus the relative-size-based definition of fangs and denticles may differ between palatal and mandibular dentitions.

2) "Fangs" are by definition 25 percent greater in maximum basal diameter and/or height than the average of adjacent marginal teeth.

3) "Denticles" by definition have 10 percent or less of the average maximum basal diameter and/or height of adjacent marginal teeth.

Under these definitions coronoid 1 has a pair of alternately replacing fangs, which are emplaced within a poorly defined common pit that is reminiscent of the much better defined pit for the palatine fangs. Coronoids 2 and 3 apparently have neither fang teeth nor marginal-sized teeth, assuming that the short segment of jaw not represented by either KUVP 126314 or KUVP 87862-2 does not include either tooth type. We have reconstructed the jaw on this assumption. The fangs on coronoid 1 lie lateral to a row of small teeth, which in KUVP 126314 begins with two teeth lying anterior to the fang teeth. Posterior to this point the fang teeth interrupt the tooth row, which continues posterior to the fang tooth positions. On coronoid 1 and the anterior part of coronoid 2, these small teeth are in a single row that occupies the summit of a low ridge. Posterior to the intercoronoid fossa, the number of tooth rows increases to as many as three to four posteriorly in coronoid 3, then declines again to one to two rows just anterior to the adductor fossa. Most of the posterior teeth are considerably smaller than the anterior, and some denticles are present among them. At the posterior end of coronoid 3, and lateral to these small teeth, there is a row of three larger teeth in KUVP 87862-2. These are intermediate in size, as well as position, between the smallest coronoid teeth and the adjacent dentary teeth.

Dentary.—The labial face of the dentary is strongly sculptured anteriorly, but sculpturing becomes rapidly weaker posteriorly. Past its midlength, the dentary is nearly unsculptured dorsal to the oral sulcus. The dentary-postsplenial suture is broadly overlapping and without interdigitations (Fig. 3.2, 3.3). The ventral border of the dentary curves sharply upward at its joint with the surangular. This curved part of the ventral border has a ragged appearance in some specimens, but is a continuous smooth curve in the well-preserved KUVP 126315. The dentary is thin in this region, and consequently easily damaged post mortem, possibly explaining its ragged appearance in some specimens. The dentary terminates posteriorly in a slender postdental process that tapers posteriorly to a blunt point. The postdental process is deeply incised into a smooth-surfaced groove in the surangular, and extends through about the anterior one-third of the adductor fossa. In both KUVP 126215 and KUVP 87695 (large skulls), this process is about 25 mm long.

The dentary constitutes about 33 percent of the total area of the symphysis as measured on KUVP 126313. Its symphysial surface as preserved in KUVP 126313 is slightly rugose (Fig. 1.2). Within the symphysis, the dentary-splenial suture is interdigitated in cross section (Fig. 3.1); no available cross sections show the morphology of this suture posterior to the symphysis.

The occlusal surface of the dentary is comprised of the very thin lateral wall and the medial shelf. The marginal teeth attach to the inner face of the lateral wall and the adjacent occlusal surface of the medial shelf (Figs. 1.1, 2.1, 3.2, 3.3). The medial shelf narrows markedly where it forms the lateral border of the intercoronoid fossa. It overlaps coronoid 1 in an interdigitated and moderately beveled suture. Posterior to the intercoronoid fossa, the medial shelf overlaps coronoids 2 and 3 in a broad, flat joint without interdigitations. The dentary lateral wall is high opposite the symphysial fangs, especially in KUVP 87694. It is absent adjacent to the dentary notch, but everywhere else is well above the level of the medial shelf. The height of the wall has clearly been reduced post mortem in most specimens by weathering or preparation.

Dentary teeth are markedly larger than the maxillary teeth. The separated pieces of KUVP 87862 indicate that the maximum diameter of the dentary teeth may be at least twice that of the maxillary teeth, although precisely matching regions cannot be compared. The dentary has a continuous row of teeth between the dentary notch and the anterior end of the adductor fossa. Teeth are curved and point inward. Bases of most dentary teeth are somewhat compressed proximodistally. Compression is strongest in the anterior part of the tooth row. This is particularly marked in KUVP 87694, where the ratio of proximodistal:labiolingual diameters can be 2:1 or greater. Posterior dentary tooth bases are progressively less compressed (roughly circular) and the teeth are smaller. Based mostly on KUVP 126314, tooth crowns are sharp and slightly compressed in an approximately parasagittal plane.

Between the anterior end of the dentary notch and the symphysis, the dentition consists only of a large fang and an adjacent pit for its replacement. The fang(s) is unfortunately not preserved intact in any of the three specimens where the dorsal surface of the symphysial region could be fully prepared. Greatest basal diameter of the fang appears to be nearly twice the greatest basal diameter of the next-largest marginal tooth. Adjacent to the notch, the dentary is either edentulous (KUVP 126313), or there is at least one small tooth at the midpoint of the notch (KUVP 87694; this specimen is damaged).

None of the available specimens preserves a complete tooth row, but using a composite of well-preserved specimens we estimate a total of about 30 dentary teeth plus tooth spaces. Replacement was active and approximately alternate. Replaced teeth are represented by: tooth bases alone, which may retain labyrinthine structure of bone plus dentine or of bone only; pits which show little or no trace of infolding, and are apparently formed only of bone; and semicircular areas of punctate bone, flush with the surface of the medial shelf ("plugged" pits). The first two presumably represent successive stages in the replacement cycle; plugged pits likely represent termination of replacement at that locus.

The dentary notch is smooth-surfaced, and large enough to accommodate two premaxillary fangs simultaneously to judge by KUVP 87695, where, however, only a single fang is present in each notch. In KUVP 87694 at least one and possibly two plugged replacement pits are visible in the medial shelf adjacent to the dentary notch and anterior to the isolated first functional tooth. In both KUVP 126313 and 126314 the tooth row begins with a plugged replacement pit at the posterior end of the dentary notch. In KUVP 126313 the bases of the first two functioning teeth partly overhang the dentary notch, and the first tooth is very small. Clearly, replacement was no longer taking place posterior to the first functioning teeth; presumably it was suppressed as the dentary notch encroached onto the anterior end of the marginal tooth row during growth of the individual.

Prearticular.—Where it borders the posterior half of the Meckelian fenestra, the prearticular often has an irregular or "ragged" margin, which we interpret as damage. The prearticular extends forward to about the level of the anterior end of the intercoronoid fossa or slightly beyond (Figs. 1.1, 2.1). Dorsal to the anterior part of the Meckelian fenestra, the prearticular is clasped between the overlapping splenial medially and the coronoid series laterally so that only a small dentigerous ridge of prearticular is visible in medial and occlusal view (Figs. 1.1, 2.1, 3.2, 3.3). The prearticular, however, where it is overlapped by the splenial forms most of the thickness of the mandibular wall.

Posteriorly, the prearticular forms the dorsal and anterior borders of a large chorda tympani foramen. Posteroventrally, it forms the dorsal border of the angular foramen. The dorsal articular-prearticular suture is clear in KUVP 87695 and 87862, but the exact course of other parts of this suture is not clear on any specimen.

At the level of the posterior edge of the intercoronoid fossa, the dorsal edge of the prearticular carries a short single row of very small teeth in KUVP 126314 (Figs. 2.1, 3.3). These teeth are attached both to the rounded dorsal surface of the prearticular and to the lateral side of a low, thin flange that extends dorsally above the general dorsal surface. Only one specimen (KUVP 87862) provides an occlusal view of the jaw posterior to KUVP 126314, and the two specimens do not overlap—a short central segment of the jaw is not represented in either. With the possible exception of this small missing portion of the jaw, there are no other teeth or denticles on the prearticular.

Splenial and postsplenial.—The splenial forms about 17 percent of the total symphysial area, as measured in KUVP 126313. The splenial has an extensive medial lamina, which is oriented at nearly a right angle to the ventral surface. In most specimens, the transition between these surfaces is through a slightly rounded edge. In KUVP 126313 a distinct free ventral flange, with sculptured ventral surface, projects medially from this edge for a short distance anterior to the Meckelian fenestra (Fig. 1.3). This is apparently an individual variant. Dorsal and ventral to the Meckelian fenestra, the medial lamina tapers gradually and terminates in each case as a thin, pointed and posteriorly-directed process. Posterior to the adsymphysial, the medial lamina contains two foramina in KUVP 126313 (Fig. 1.2) and KUVP 126314 (Fig. 2.2), with the dorsal one being considerably larger. Both foramina are present in the left mandible of KUVP 126315. The larger foramen is present in both mandibles of KUVP 87695; the presence of the smaller one is uncertain. As noted in the description of the adsymphysial, we suggest that the larger, dorsal foramen is the medial parasymphysial foramen.

The postsplenial is strongly sculptured on its ventral and lateral faces. On its lateral surface, the postsplenial forms a joint with the dentary. At the level of Section 2 (Fig. 3.2), a thin flange of the postsplenial extensively underlies the dentary. The less extensive overlap seen in Section 3, immediately posterior to Section 2 (Fig. 3.3), may be due to damage. The postsplenial forms most of the ventral border of the Meckelian fenestra. It lacks any indication of a medial lamina or free ventral flange.

The mandibular lateral line canal runs anteriorly along the ventral surface of the splenial and postsplenial to open onto the symphysis. In most specimens, the canal runs partly within the bone, partly in an open sulcus. It appears to be entirely open in KUVP 126314 and 87862-2. Neither of these, however, preserves the complete postsplenial, although 87862-2 preserves most of it. In this specimen, the open sulcus could be secondary and due to excessive preparation, but if so there is no obvious trace of the bony bridges between foramina that are seen in other specimens. We have scored it in the Appendix as having an open sulcus, although with some hesitation.

Surangular.—The surangular forms most of the lateral margin of the adductor fossa, and most of the low surangular crest. Dermal sculpturing on the surangular is confined to the area ventral to the oral sulcus; dorsal to the sulcus, the surangular is smooth and unsculptured. In the anterior portion of this smooth area is the groove into which the postdental process of the dentary fits. The oral sulcus itself is open, broad, and shallow for most of its course. Posteriorly, at its junction with the mandibular sulcus, the oral sulcus disappears before it meets the mandibular sulcus in some specimens (e.g., the right mandible of KUVP 87862). In these cases it likely runs within the bone, as suggested in the right mandible of KUVP 87862 by a short, curved line of foramina along its likely course. The surangular portion of the mandibular sulcus runs partly within open sulci and partly within the bone, in which case it opens onto the surface via prominent foramina. As usual, the degree of enclosure appears to vary from specimen to specimen.

Details of the articular-surangular contact are difficult to trace externally. The location of the suture as reconstructed in lateral view (Fig. 5.1) is plausible but not certain. As reconstructed, the angular-surangular suture produces a small exposure of the articular in lateral view. In occlusal view and within the adductor fossa, we are unable to find any sign of the articular-surangular suture on any specimen. We are thus unable to test in Goreville specimens Smithson's (1982) claim, based on Greer specimens, that the surangular participates in the jaw joint.

Reconstruction of the Greererpeton *mandible.*—Our reconstruction of the mandible, based entirely on Goreville specimens, is shown in Figure 5. The mandible consists of 10 bones: dentary; four infradentaries; adsymphysial; two coronoids; prearticular; and articular. This is two less than the 12 found in the most primitive tetrapod jaws and those of related sarcopterygian fish. Missing are: a symphysial ossification of the Meckelian; and coronoid 3, the latter due to either loss of coronoid 3 or fusion with coronoid 2.

The identity of the adsymphysial was not obvious on first inspection, primarily because, as in *Greererpeton burkemorani* from Greer, only two of the coronoids are outlined by sutures. However, as shown below, a colosteid from the Delta locality has a suture between coronoids 2 and 3, plus an adsymphysial. Moreover, the large and coarsely rugose symphysial surface of the adsymphysial is matched among early tetrapods and osteolepiform fish in the baphetid *Megalocephalus pachycephalus,* which has the usual early-tetrapod complement of three coronoids (Ahlberg and Clack, 1998). All lines of evidence combined now show beyond doubt that this bone is an adsymphysial.

For the most part, our reconstruction agrees with Smithson's (1982), which he based on the numerous specimens from Greer. Based on our examination of Greer specimens, however, we conclude that some of his dorsal view was hypothetical. Nearly all available *G. burkemorani* jaws are associated with skulls in which they are in closed position, and the few separated specimens are either inadequately preserved or would require unacceptably destructive preparation to expose the symphysial region. Our reconstruction includes details of the symphysial region based on several excellent Goreville specimens that provide an occlusal view of the intercoronoid fossa and both the adsymphysial and coronoid dentitions. Finally, the new material from Goreville has allowed a better understanding of the joints among bones, both superficial and deep.

In lateral view (Fig. 5.1), the mandible is deepest in the angular region, tapering anteriorly to less than one-half of that depth near the symphysis. The toothed margin is nearly straight, with the articular condyle at about the same level as the tooth row. The dentary shows the diagnostic notch on its outer face for reception of the premaxillary fang(s). The lateral and ventral (Fig. 5.1, 5.4) surfaces of the dentary and the four infradentaries are covered with dermal ornament of early tetrapod type as described by Ahlberg et al. (1994; see also references therein). From their description, we consider "early tetrapod" ornament to be that typical of many temnospondyl amphibians, such as *Eryops* spp. Ornament is particularly strongly developed on the angular. The mandibular lateral line system is prominent on the labial and ventral surface also, running partly in open sulci and partly in closed canals whose roof is penetrated by a row of foramina. The distribution of open sulci versus canals is somewhat variable. A short, poorly defined oral sulcus runs anterodorsally within the surangular, beginning near the posterior end of the mandibular lateral line.

In medial view (Fig. 5.2), the large, elongate Meckelian fenestra extends over a distance equal to almost one-half of the total jaw length. This type of Meckelian fenestra is present in all colosteids in which this region has been described. The splenial forms the border for the anterior one-third of the Meckelian fenestra. The postsplenial forms joints with the splenial and angular and together they form the ventral border of the fenestra. The remainder of the border, primarily the posterior two-thirds of the dorsal edge, is formed by the prearticular.

In both medial and ventral views, the mandible shows three remarkable features of the symphysis. The first is the brassicate symphysial suture, already mentioned. Second is a massive expansion of the adsymphysial compared to other early tetrapods and tetrapodomorph fish, which extends for about one-half of the anteroposterior length of the symphysis and, most visibly when the mandibles are in articulation, projects markedly backward into the intermandibular area. The third, obvious only when the mandibles are in articulation, is a gap between the dentaries anterior to this adsymphysial expansion. This gap extends over the anterior half of the anteroposterior length of the symphysis. In KUVP 87695 it is at least 5 mm wide at its anterior end. Given the nearly undistorted preservation of much of the material available and the fact that this morphology can be seen on several specimens, this interdentary gap must be natural.

In occlusal (Fig. 5.3) or ventral (Fig. 5.4) view, the middle one-half of the mandibular ramus is almost perfectly straight. The posterior one-quarter of the ramus is slightly inflected medially, with a stronger but still modest medial inflection in the anterior one-quarter. When in articulation, the two mandibles form an outline that is more V- than U-shaped, as shown particularly well in KUVP 87695 where they are in articulation in an exceptionally well preserved skull.

In occlusal view, the prominent adductor fossa occupies the posterior one-third of the ramus and the anterior occlusal surface is marked by a prominent intercoronoid fossa between coronoid 1 and coronoid 2. The intercoronoid fossa is bounded labially by the dentary and lingually by coronoids 1 and 2. The floor of the fossa is incomplete. The fossa lies lateral to the row of small coronoid teeth and posterior to and in line with the fang pair on coronoid 1.

COLOSTEID MANDIBLE FM PR 1653 FROM DELTA

FM PR 1653 comprises the anterior one-third of the left mandible of a colosteid amphibian. This identification is confirmed by the dentary notch and strengthened by the presence of both an intercoronoid fossa and an adsymphysial like that of *Greererpeton burkemorani.* The specimen is three-dimensionally preserved, although it is somewhat dorsoventrally crushed with the coronoids posterior to the anterior border of the intercoronoid fossa displaced laterally. When found, the specimen was broken across at the level of the dentary notch, just behind the symphysis. Although it has been repaired, there was some bone loss ventral to the dentary notch and at the posterior tip of the adsymphysial. Preparation has allowed the identification of most sutures.

The external surfaces of the dentary, splenial, and postsplenial bear temnospondyl-type pit and ridge dermal ornament, although it is very weakly expressed. The sculptured surfaces of these bones appear eroded, and the same is true of other bone surfaces as well as teeth. This eroded appearance might be due to a period

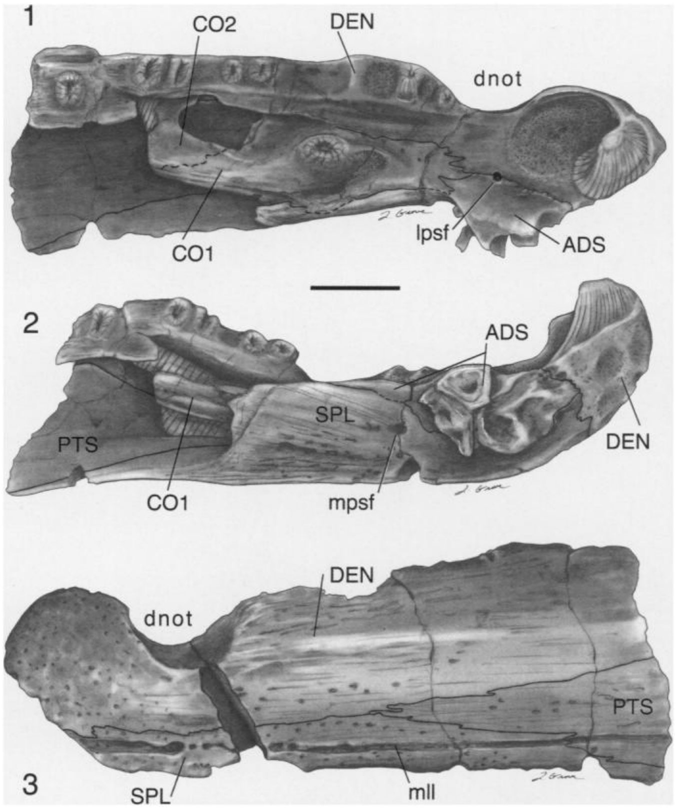

FIGURE 6—Colosteid cf. *Greererpeton burkemorani*, FM PR 1653, anterior one-third of left mandible from Delta locality. Scale = 1 cm. *1*, Dorsal (occlusal) view. *2*, Medial view. *3*, Lateral view. Abbreviations: see Figure 1.

of exposure before burial; alternatively, it might have been produced by passage through the alimentary tract of some predator or scavenger. Whatever its cause, its effects must be kept in mind when comparing FM PR 1653 to *Greererpeton burkemorani.*

Adsymphysial.—Except at its posterior tip, the adsymphysial is very similar to that of *Greererpeton burkemorani,* including brassicate symphysial suture. The small discrepancies shown in Figure 6.1 and 6.2 reflect uncertainty due to damage or individual variation, rather than any demonstrable difference from *G. burkemorani.* The lateral parasymphysial foramen is in the adsymphysial-dentary suture, rather than entirely within the dentary as in KUVP 126313. There is no sign of an adsymphysial dentition, but this is of questionable significance given the condition of the dentary teeth and the fact that the entire surface of the specimen is more or less eroded.

Coronoid series.—Coronoids 1 and 2 are apparently present and bound an intercoronoid fossa. The joint separating these coronoids is indistinct, and its general course only is indicated with a dashed line in Figure 6.1. The intercoronoid fossa as preserved differs from that of *Greererpeton burkemorani* (Figs. 1.1, 2.1) in size and in the borders of the coronoids, where they floor the intercoronoid fenestra (apparently partly open here as in *G. burkemorani*). However, this is a smaller specimen, and it is obvious that the margins of the fenestra have been displaced and damaged by crushing. Detailed comparison with the intercoronoid fenestra of *G. burkemorani* is thus not possible, and the significance of the differences between FM PR 1653 and the better known *G. burkemorani* is unclear.

Dentary.—The symphysial portion of the dentary resembles that of *Greerereton burkemorani* within the limits of their differing preservation. Posterior to the dentary notch, the dorsal margin is scalloped opposite the tooth bases, in places quite deeply. Thus, whatever lateral wall was originally present in this area is missing. Anterior to the notch the dorsal margin of the dentary is thin and straight where it forms the lateral wall of the replacement pit for a fang. The notch is deeply incised and, as in *G. burkemorani,* involves the dentary alone. The dentary sutures with the splenial and postsplenial do not differ from those seen in *G. burkemorani.*

In dorsal view, the dentary is eroded but unbroken except for the fact that the posteriormost preserved tooth and the adjacent bone have been slightly displaced medially and anteriorly. The dentary sutures with the adsymphysial and coronoid 1 resemble the same sutures in *Greererpeton burkemorani,* allowing for the fact that, beginning at the level of the intercoronoid fossa, the coronoids have been displaced laterally by crushing. As in that genus, the medial shelf narrows markedly where it forms the lateral margin of the intercoronoid fossa.

The anteriormost dentary tooth is a large fang, broken off level with the adjacent lateral wall. Greatest basal diameter of this fang is nearly twice the greatest basal diameter of the next-largest marginal tooth preserved. Immediately posterior to the fang is a semicircular area, including what appears to be eroded bone of attachment, that marks the former position of a second fang. The lateral wall is high opposite the fangs, although its crest is visibly broken. Aside from the fang, none of the other dentary teeth is preserved as more than a base. In occlusal view, some tooth bases are semicircular, and most, including the fang, are proximodistally compressed as in *Greererpeton burkemorani.* Some of the tooth bases are exposed and somewhat eroded laterally; this is particularly clear in the two teeth lying just posterior to the level of the coronoid tooth.

Taking into account regional variations in tooth base diameter, there is room for about 15 teeth posterior to the fangs. Seven loci show cross sections through complex "labyrinthine" dentine, and thus were likely occupied by functioning teeth. Replacement pits are represented mostly by subcircular areas floored by bone of attachment or by the underlying bone of the dentary. At its deepest point, the dentary notch bisects a "plugged" replacement pit, suggesting that, as in *Greererpeton burkemorani,* replacement was suppressed in this area.

Proceeding posteriorly from approximately the anterior end of the coronoid tooth, coronoid 2 is progressively more displaced, mostly medially but also ventrally. This displacement has opened up the coronoid 1-dentary suture and reveals that the dentary overlaps (lies external to) coronoid 1 along the suture.

Splenial and postsplenial.—With allowance for surficial erosion, these bones agree with the splenial series in *Greererpeton burkemorani.* The canal for the mandibular lateral line runs in an open sulcus posteriorly, and anteriorly it is partly within a sulcus and partly within a closed canal (Fig. 6.3). The anterior margin of the Meckelian fenestra is preserved on the splenial, and the lower border of the fenestra is rounded and clearly natural (Fig. 6.2). This is all consistent with the presence of an elongate Meckelian fenestra like that of *G. burkemorani* and *Colosteus scutellatus* (see Hook, 1983). This area is unknown in *Pholidogaster pisciformis* (see Panchen, 1975).

COLOSTEID MANDIBLES FM PR 1637 FROM DELTA

Adsymphysial.—The adsymphysial region is visible only on the left mandible. The region has been strongly crushed mediolaterally, as has the jaw as a whole. Despite this crushing, part of the adsymphysial region stands well above the surrounding area. This area corresponds in size and position to the symphysial suture in the colosteid jaws described above. Its surface is irregular and undulating, though broken in places. Based on this evidence, we

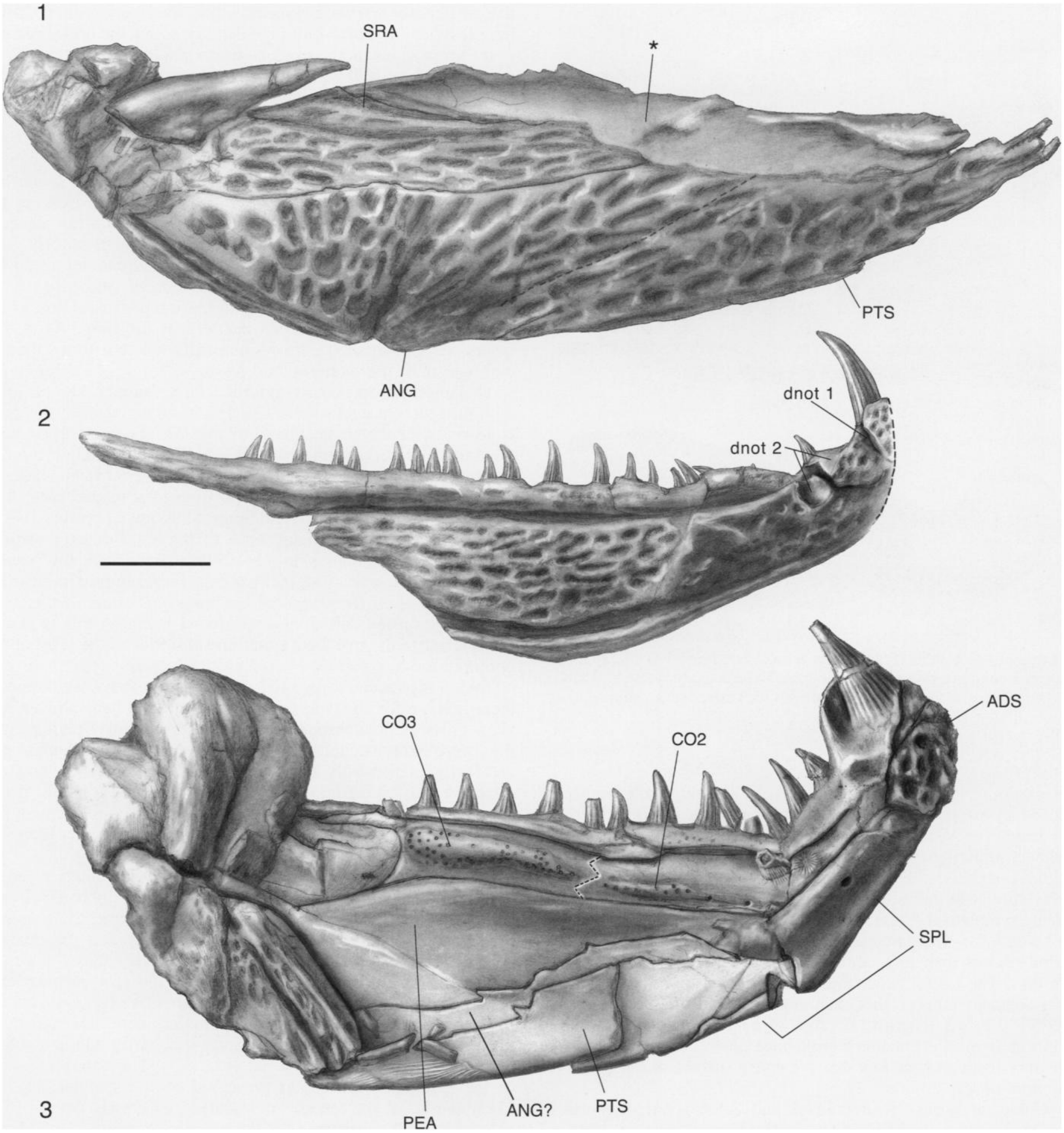

FIGURE 7—Unidentified colosteid, FM PR 1637, left and right mandibles only figured here; from Delta locality, different horizon than FM PR 1653. Scale = 2 cm. *1,* Posterior portion of right mandible, lateral view. *2,* Anterior portion of right mandible, lateral view. *3,* Left mandible, medial view. Some of the sutures shown, particularly in the medial view, pass through badly cracked areas where their course is a matter of interpretation. For the sake of clarity, in such cases we show only the suture and do not include details of the cracked areas. As indicated in the text, the brassicate morphology of the symphysial surface of the adsymphysial is reconstructed, based on the suggestive but imperfectly preserved symphysial surface of the specimen. Abbreviations: see Figure 1.

suggest that a large adsymphysial is present in this taxon, and have reconstructed a *Greererpeton burkemorani*-like brassicate surface on the symphysial articular area in Figure 7.3. Neither the sutures bounding the adsymphysial nor the presence of adsymphysial teeth can be determined.

Angular.—The right angular is preserved in lateral view on the separated posterior half mandible, though damaged posteriorly (Fig. 7.1). It is strongly sculptured, with a temnospondyl type of sculpturing radiating from its ventral margin. The position of the angular-surangular suture is indicated by an abrupt change in

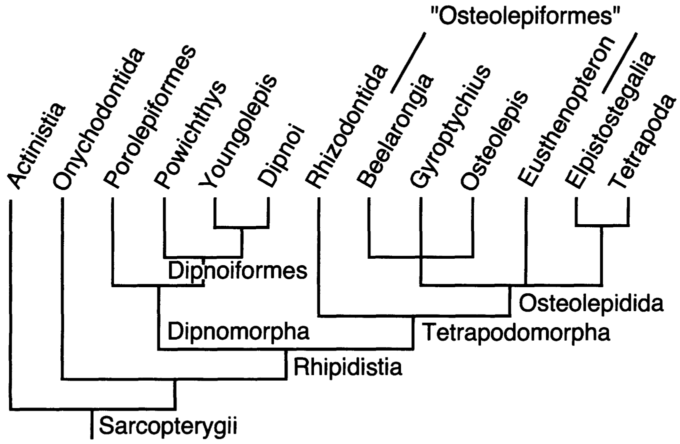

FIGURE 8—Interrelationships of sarcopterygian higher taxa, modified from Cloutier and Ahlberg (1996). Note that "Osteolepiformes," one of the taxa most commonly cited by systematists working near the fish-tetrapod transition, is not a monophyletic group. Note also that Cloutier and Ahlberg defined Tetrapoda as a clade possessing limbs with digits rather than fins, plus a few other characters. This is the "traditional" definition of the group.

sculpture orientation, and the suture itself is visible in the central part of the contact. The surface expression does not show interdigitation. We were not able to follow the suture onto the unsculptured portion of the surangular, and damage to the articular region of the jaw has obscured the bounding sutures of the angular in this area. The angular-dentary suture is an incised area whose surface is smooth except for some weakly developed striae. The course of the mandibular lateral line as preserved is represented entirely by an open sulcus. The significance of this is unclear. The strong crushing that this specimen has obviously experienced might have broken some of the bony bridges covering parts of the canal. This suggestion is supported by the short section of this lateral line canal that is visible on the small, folded-over portion of the left angular, where there appear to be several short (but damaged) bony bridges over part of the canal. It does seem that in PR 1637 this canal was partly covered, but still more open than in *Greererpeton burkemorani* from either Greer or Goreville.

Articular.—The surface of the "articular" glenoid is partly visible, but no description of the shape or bounding sutures of the articular is possible. Strictly speaking, therefore, presence or absence of the articular cannot be demonstrated.

Coronoid series.—The coronoid series of PR 1637 is exposed in dorsomedial view on the left mandible (Fig. 7.3). The suture between the coronoid series and the prearticular/splenial is reasonably clear, as indicated in the figure. The base of a tooth, about the same diameter as adjacent marginal teeth, is in place in the coronoid 1 region, and immediately anterior to it is the attachment site of a second tooth. The area that in *Greererpeton burkemorani* is occupied by the intercoronoid fossa is uninterpretable in this specimen: this is the site of the break between the anterior and middle parts of the mandible, and bone is shattered and displaced. For this reason, we cannot tell if there is an intercoronoid fossa and likewise cannot detect the suture between coronoids 1 and 2, which in *G. burkemorani* is visible in the floor of the fossa. At about midlength of the coronoid series, there is an indication of a suture, which we interpret as that between coronoids 2 and 3 based on its anteroposterior position. The very short surface expression of this suture shows long, narrow loops; it is drawn schematically in Figure 7.3. Coronoid 3 appears to form part of the lateral wall of the adductor fossa as an edentulous extension along the inner face of surangular similar to that seen in *G. burkemorani.* Because of damage in this area, the sutural boundaries of this extension cannot be precisely determined. The sutures between coronoids 2 and 3 and the prearticular are visible (Fig. 7.3), but no details can be discerned other than the fact that they are not interdigitated. The nature of the coronoid-dentary joint is indeterminable due to damage.

No marginal-sized or fang teeth are present on coronoid 2 or 3. Both coronoids 2 and 3 bear very small teeth (the average size is slightly larger than our definition of denticles) and some denticles. These teeth plus denticles are arranged in a nearly continuous strip that is first visible at the position of the break between anterior and middle parts of the mandible. Presence of small teeth or denticles, and details of their attachment, are uncertain anterior to this point because of damage. At its anteriormost visible point on coronoid 2(?), the tooth-bearing area is a distinct ridge, wide enough anteriorly for one tooth, and broadening posteriorly to carry two side by side. At the level of the coronoid 2-coronoid 3 suture, the ridge is briefly interrupted. Running posteriorly on coronoid 3, the ridge quickly broadens to an elevated patch some seven to eight teeth wide in places, with a distinctively punctate surface that contrasts with the smooth surface of the coronoid on either side.

Dentary.—The external surface of the dentary is sculptured similarly to that of Goreville *Greererpeton burkemorani* including weaker sculpturing posteriorly, dorsal to the oral sulcus (Fig. 7.1). The dentary notch is bipartite. The posterior portion is most strongly developed, but it is shallower and dorsoventrally shorter than in *G. burkemorani* and slants strongly posteriorly from top to bottom. The anterior portion is less strongly developed, shorter, and less markedly slanted. This type of dentary notch has not previously been reported among colosteids. The dentary terminates posteriorly in a slender postdental process approximately 30 mm long posterior to the last dentary tooth. The condition of the specimen does not permit us to determine whether or not the postdental process participates in the lateral wall of the adductor fossa. The symphysial end of the dentary is too crushed to permit estimation of its proportional participation in the symphysis. The suture between the dentary and postsplenial and splenial is partly visible on the latter, where it is marked by striae. The dentary-surangular suture is featureless except for weak striae.

There are 20 functional teeth in place on the right dentary posterior to the notch, and an estimated eight to nine empty tooth spaces. The total number of estimated tooth positions is thus about 28–29, practically identical to the 30 estimated in *Greererpeton burkemorani.* The largest tooth in mid-length of the right dentary rises about 3 mm above the lateral wall in lateral view. The largest tooth in the same region of the right maxilla rises about 1.7 mm in lateral view. The basal diameter of the upper and lower teeth is in proportion, so it is clear that, as in colosteids generally, the dentary teeth are much larger than the maxillary. Dentary tooth morphology is similar to that described for *G. burkemorani.* A large fang is present on both right and left dentaries (Fig. 7.2, 7.3). On the left dentary, there is a large replacement pit for a second fang immediately posterior to the functional one. The marginal tooth row begins immediately posterior to the fang replacement pit and continues without interruption. On the right dentary, where the anterior tip of the jaw is covered by the skull, there is a gap posterior to the fang and above the second part of the dentary notch. From the center of the notch posteriorly, the marginal tooth row apparently continues without interruption.

Prearticular.—The prearticular is visible only on the left mandible, between the anterior break and the posterior folded-over part of the angular region (Fig. 7.3). Posteriorly, it forms the medial wall of the adductor fossa. By comparison with *Greererpeton burkemorani*, it should form the dorsal border of the Meckelian fenestra over its entire visible extent. What might be the dorsal border is clearly visible in places. However, it is very thin and lacks the sort of rounded edge that would mark it as a free edge rather than a break or a suture. A narrow band of broken bone ventral to the definitive prearticular area cannot be assigned definitely to either the prearticular or one of the splenial series. There is no sign of the multiple small Meckelian fenestrae found in some other early tetrapods.

Splenial and postsplenial.—A small strip of the postsplenial plus splenial is visible in lateral view on the right mandible (Fig. 7.2). The postsplenial-splenial suture is not evident. These bones display sculpturing like that of the other dermal bones of PR 1637. In medial view, the splenial is identifiable anterior to the break. Its surface is smooth and unsculptured. Despite crushing, it is evident that the ventrolateral surface meets the medial lamina at a high angle as in *Greererpeton burkemorani*. The ventral edge of the splenial is rounded and without the free ventral flange seen in one specimen of *G. burkemorani*. At the break in the jaw, a rounded edge indicates the anterior border of a large Meckelian fenestra in the splenial. The small preserved portion of this border is indistinguishable in position, size, and shape from that of *G. burkemorani*. Anterior and dorsal to the border of the Meckelian fenestra, there a medial parasymphysial foramen in the same position as that described above in *G. burkemorani* (Fig. 7.3). The prearticular-splenial suture above the Meckelian fenestra is not determinable. The ventral postsplenial-splenial suture is visible in medial view, posterior to the break line.

The postsplenial shows in medial view a thickened, smoothly rounded ventral edge. There is no sign of sutural contact along this edge or along the ventromedial surface of the postsplenial until a point just anterior to the folded-over jaw angle. Here the medial surface shows a small patch of parallel striae. We interpret this as a sutural area for the medial flange of the angular, as seen in *Greererpeton burkemorani*. Most of the ventral margin of the postsplenial thus appears to be a free edge, with no medial flange. This and other features described above strongly suggest that the mandible of PR 1637 resembled that of other colosteids in having a single long Meckelian fenestra.

Surangular.—The surangular is exposed mostly in lateral view, on the separated right posterior half of the mandible (Fig. 7.1), although a small area of its medial surface within the adductor fossa is exposed in the left mandible. Relationships of the posterior part of the surangular are obscured by damage or are covered. On the right side, the anterior part of the surangular crest is missing, and the posterior part is broken off and somewhat displaced. On the left mandible, the surangular crest is clearly damaged as well as mostly covered. The preserved portions of the surangular crest suggest that it was low and resembled closely that of *Greererpeton burkemorani*. As in *G. burkemorani*, the surangular is unsculptured for a short distance ventral to the crest. The course of the mandibular lateral line cannot be seen because this area of the surangular is damaged. The surangular part of the oral sulcus is not identifiable. This may be due to damage because the oral sulcus is identifiable in the dentary.

GREERERPETON BURKEMORANI FROM GREER

There is general agreement between our description of the mandible in the Goreville *Greererpeton* and Smithson's (1982) description of Greer specimens. Some of the differences, however, are striking, such as the presence of an adsymphysial and intercoronoid fossa in the Goreville material and the apparent absence of these elements in specimens from Greer. Our intent in this section is to present the results of our re-determination of the discrepant characters in Greer specimens. We have not attempted a complete redescription of the lower jaw.

Adsymphysial.—Based on what we now know from several well-preserved and well-prepared Goreville specimens, the presence of an adsymphysial in the Greer specimens is evident even if details of its bounding sutures are obscure. Thus, in several skulls with lower jaws in situ (CMNH 11093; MCZ 9006; USNM 22576), the posterior part of the mandibular symphysis is formed by a backwardly-bulging mass of bone identical to that described for the specimens from Goreville. Also as in these specimens, the symphysial surfaces of the dentaries are not in contact anterior to the adsymphysial (MCZ 9006; USNM 22576; CMNH 11093 is damaged in this area). Apparently, the only free symphysial region available to Smithson was in CMNH 11129. The sutures bounding the adsymphysial are partly visible in this specimen, but the sutural surface of the adsymphysial is badly damaged. A much better specimen is the anterior tip of a right jaw, which we have prepared free from the partial skull of CMNH 11079. The sutures outlining the adsymphysial are almost completely visible here, and agree perfectly with the description of Goreville *Greererpeton.* The symphysial sutural surface is brassicate.

Articular.—We were unable to determine whether the surangular forms part of the glenoid, as claimed by Smithson. Unfortunately, as noted above we were also unable to completely determine the sutural relationships of the articular and surangular in the Goreville specimens.

Coronoid series.—CMNH 11079 and 11129 preserve only coronoid 1, and in both it is damaged posteriorly. CMNH 11079 preserves what might be the anterior part of the medial border of the intercoronoid fossa, but the specimen is sufficiently damaged in this area that we cannot be certain that the fossa was present. In both specimens, the prearticular extends forward to a point midway between the two large coronoid teeth. This is visible in CMNH 11079; in CMNH 11129, the anterior tip of the prearticular is visible only as a tiny wedge of bone. The contact of coronoid 1 with the prearticular is thus identical to that seen in the Goreville *Greererpeton burkemorani.*

As scored in the Appendix, the dentition of coronoid 1 seems to differ from that of the Goreville *Greererpeton* in having coronoid teeth rather than fangs. The apparent difference is due entirely to our size-based definition of "fang" and "tooth." In reality, the Greer specimens have a pair of teeth in the same position as the fang pair seen in the Goreville specimens. The difference may be related to individual age and therefore size; CMNH 11079 and 11129 are considerably smaller than the Goreville specimens on which our description is based.

Dentary.—The symphysial surfaces of the dentaries are separated by an interdentary gap. This condition is as described above for Goreville *Greererpeton burkemorani,* and is seen well in the articulated skull with jaws MCZ 9006.

Prearticular.—As described above, the anterior extent of the prearticular is identical to that of the Goreville *Greererpeton burkemorani.* Smithson (1982) described the prearticular-splenial contact dorsal to the Meckelian fenestra as a "vertical interdigitating suture" (p. 69), and his reconstruction (fig. 19) shows the splenial completely covering the prearticular in medial view as far posteriorly as the suture. We have not been able to find a Greer specimen showing these conditions. On the contrary, the right mandible of MCZ 9006 shows prearticular-splenial sutural relationships much like those of the Goreville *G. burkemorani.* The splenial appears to lie superficial to the prearticular in lingual view, and to gradually decrease in height posteriorly so that the prearticular is visible both dorsal and ventral to it. Although details of the termination of the splenial are obscure due to damage, it was incorrectly reconstructed by Smithson.

DISCUSSION

Classification.—Group names such as "osteolepiform," "rhipidistian," and even "tetrapod" as used in many recent papers on early tetrapods do not necessarily refer to taxa with the same content. To avoid confusion, we follow the usage proposed by Cloutier and Ahlberg (1996) in their cladistic study of the interrelationships of basal sarcopterygians and illustrated in our Figure 8. It is important to emphasize that "Osteolepiformes" is not monophyletic according to Cloutier and Ahlberg; we use the term informally in the following discussion. Note also that their Tetrapoda is the "traditional" apomorphy-based one, which defines the group as a clade which possesses limbs with digits rather than paired fins, plus a few other characters.

Cranial kinesis and the "third joint" in the lower jaw.—Cranial kinesis in osteolepiform fishes and early tetrapods—its existence, operation, and functional significance—has long been a vexed subject. The majority of lower-vertebrate paleontologists today believe that osteolepiform fishes had a highly kinetic skull, that most of this kinesis was lost early in tetrapod history, and that its remnant joints and functions often are identifiable in the earliest tetrapods. Thomson (1967) exemplified this point of view, using linkage diagrams to analyze the operation of cranial kinesis and the effect on kinesis of proportional changes in the skull during the fish-tetrapod transition. Jarvik (1996, p. 39) expressed a very different opinion: "The skull in ichthyostegids, as in osteolepiforms, is thus akinetic. . . . The widespread view about intracranial kinetism in osteolepiforms is a delusion unsupported by reliable data."

Romer (1969) considered *Greererpeton burkemorani* to have a kinetic skull, although he did not present any detailed analysis of its operation. He apparently suspected the existence of a mobile linkage between skull table and cheek, noting that in the holotype skull "the suturing was not too tight between the two regions" (p. 8). Smithson (1982) denied the presence of a mobile skull table-cheek joint in *G. burkemorani,* and indeed of any cranial kinesis whatever. Although they reached opposite conclusions about cranial kinesis in *G. burkemorani,* both Romer and Smithson were actually consistent with the majority view of the evolution of cranial kinesis. Thus for Romer, kinesis in *G. burkemorani* was partly retained; for Smithson, it was completely lost, rather than primitively absent.

Recently, Schultze and Bolt (1996) noted that, in *Greererpeton* from both Goreville and Greer, the joint line between skull table and cheek is gently sinuous and non-interdigitating in contrast to sutures between other dermal bones in the cheek and skull table. This observation confirmed Romer's description, which was based solely on the holotype skull. Romer had also accurately noted that the skull table rests partly on an inward-projecting flange from the squamosal. After further preparation of KUVP 87695, we can add that this flange is continued anteriorly by the jugal, and extends to a point just posterior to the orbit. Schultze and Bolt concluded that the skull table-cheek junction was likely a mobile joint, as implied by Romer. Their conclusion was based entirely on the distinctive morphology of the joint, independent of assumptions about the history and function of cranial kinesis in either osteolepiform fish or tetrapods.

We consider that our description of the *Greererpeton* mandible strengthens the evidence for a mobile joint between skull table and cheek. Specifically, we propose that mediolateral excursions of the cheek were accommodated within the symphysis at the inter-adsymphysial suture. In this view, soft tissues that permitted, and presumably helped to control, these inter-mandibular movements would have occupied the gap between the symphysial surfaces of the dentaries and splenials. The symphysis was thus the third joint of the jaw in *Greererpeton,* as it is in extant canids (Scapino, 1965). In canids, the complex arrangement of soft tissues could not possibly have been deduced from sutural osteology alone. We are thus certain both that (1) the unusual topography of the adsymphysial sutural surface reflects some unusual feature(s) of the symphysial soft tissues in *Greererpeton*; and (2) we cannot determine with any precision what such feature(s) may have been.

Hypotheses about function in extinct taxa are notoriously difficult to test (see, e.g., Lauder, 1995), and the above is no exception. At the moment, we can propose only one feasible test: Our hypothesis predicts that where a large adsymphysial with brassicate symphysial suture is present, it will occur in conjunction with morphological evidence for a mobile joint between skull table and cheek. This prediction can be tested for the skull table-cheek suture in the *Megalocephalus* specimen mentioned above that is known to have a large adsymphysial with a brassicate symphysial suture. If more (and more distantly related) taxa with similar adsymphysials are discovered, they will provide the basis for an increasingly stringent, phylogenetically based test.

Evolutionary history of Meckelian bone or cartilage and fenestrae in tetrapods.—Students of non-tetrapod sarcopterygians have long had to distinguish carefully between features of the cranial exo- and endoskeleton. However, the rapid evolutionary recession of the endoskeleton in tetrapods has rendered the distinction almost trivial for the majority of workers on that group. With discovery of diverse truly primitive tetrapods, the endoskeleton is now assuming greater significance, and this applies to the lower jaw as well as to the skull.

It has long been known (e.g., Gross, 1941) that Meckel's cartilage in rhipidistians was extensive and often ossified over much of its extent. This is true also of the "fish" now generally considered most closely related to tetrapods, notably the elpistostegalian *Panderichthys* (Gross, 1941). On comparative-anatomical grounds alone, it would be expected that the earliest tetrapods had an extensive Meckel's cartilage and that substantial portions of this may have been ossified. Until recently, however, in the majority of known early tetrapods, only the articular portion of Meckel's was known to be ossified. Recent descriptions of very early tetrapods have changed that picture. Thus mandibles of Upper Devonian and Lower Carboniferous tetrapods have been described that show ossification in Meckel's cartilage outside of the articular area; examples include *Obruchevichthys* (Vorobyeva, 1977; Ahlberg, 1995), *Elginerpeton* (Ahlberg, 1995), and *Ichthyostega* (Jarvik, 1996). Scattered observations on the mandibles of the earliest tetrapods were recently collected and significantly extended by Ahlberg and Clack (1998). The new data have implications for the evolutionary history of two of the most striking features of the *Greererpeton* lower jaw—the intercoronoid fossa and the single large Meckelian fenestra—and for the evolution of these features in tetrapods in general.

In many fish-grade rhipidistians, the Meckelian bone or cartilage is extensively exposed ventral to the prearticular. This is the case in porolepiforms (Gross, 1941; Ahlberg, 1992), osteolepiforms (e.g., the osteolepidid *Medoevia*; Lebedev, 1995), and elpistostegalians (*Panderichthys*; Gross, 1941 and Ahlberg and Clack, 1998). The condition in *Panderichthys* is of particular interest because of this taxon's close relationship to tetrapods. Gross (1941) published 12 serial cross-sections through the lower jaw of *Panderichthys rhombolepis,* which clearly indicated a large exoskeletal fenestra between the prearticular dorsally and the postsplenial ventrally. Gross' description was greatly extended by Ahlberg and Clack (1998), who produced the first complete description of the *Panderichthys* mandible. Involvement of the splenial and angular in the border of the Meckelian fenestra is conjectural in Gross' description because of the long interval between the cross sections. Ahlberg and Clack showed that both bones have a small involvement in the ventral margin of that border. The size, position, and bordering bones of this exoskeletal opening are closely comparable to that of the single long Meckelian fenestra of *Greererpeton.* The fenestra in *Panderichthys* is underlain by the Meckelian ossification. Ahlberg and Clack (1998, fig. 1) showed two "Meckelian foramina" penetrating the Meckelian bone within the exoskeletal Meckelian fenestra. To facilitate description and discussion, we will hereafter refer to any Meckelian fenestrae developed within dermal bones as "exomeckelian fenestrae." Meckelian fenestrae developed within the endoskeleton, whether cartilage or bone, will be referred to as "endomeckelian fenestrae."

Thanks to a number of recent studies, the early history of the Meckelian bone or cartilage and the Meckelian fenestrae in tetrapods is now reasonably clear. We suggest that the following evolutionary scenario best fits the current evidence.

In the primitive condition, the Meckelian bone or cartilage is exposed on the medial surface of the jaw, between the prearticular and the infradentaries. The exomeckelian fenestra is a single elongate opening without notched borders that would indicate the position of an endomeckelian fenestra. The endomeckelian fenestrae are small and multiple—five to seven or more in some cases. Ahlberg and Clack (1998) demonstrated this condition in the Late Devonian *Elginerpeton pancheni* and *Ichthyostega stensioei* (*contra* Jarvik, 1996) based on adequately preserved material in which there is a Meckelian ossification. The Late Mississippian *Whatcheeria deltae* also appears to represent this stage.

In the intermediate condition, the Meckelian bone or cartilage is still exposed on the medial surface of the jaw within a single elongate exomeckelian fenestra. However, the borders of this fenestra include some notches that indicate the positions of endomeckelian fenestrae. In taxa without a medial lamina of the postsplenial, the exoskeletal openings are confined to the ventral border of the prearticular. There are multiple endomeckelian fenestrae. Ahlberg and Clack (1998) demonstrated this condition in the Late Devonian *Ventastega curonica,* in which there is an extensive Meckelian ossification. The Late Devonian *Acanthostega gunnari* is likely in the early phases of this stage; the prearticular shows some shallow notches, reasonably interpreted by Ahlberg and Clack as representing the borders of exomeckelian fenestrae, but there is almost no Meckelian ossification.

In the most advanced stage, the exomeckelian fenestra(e) are roughly circular rather than elongate, and are completely surrounded by dermal bone. The presence and morphology of any possible endomeckelian fenestra(e) is conjectural, as there is little or no Meckelian ossification other than the articular. This is the general condition in later Carboniferous and Permian tetrapods.

This is a very generalized model; we expect that subsequent morphological and phylogenetic studies will test it and indicate necessary refinements. But if it is correct even at this level of generality, it strongly suggests that the single, long exomeckelian fenestra is primitive for tetrapods, and that the condition in colosteids is a retention of this primitive state as implied by Ahlberg and Clack (1998). This is a radical reversal of the usual view of the fenestra in colosteids. For example, Hook (1983) listed the elongate single (exo)Meckelian fenestra as a colosteid synapomorphy. Smithson (1982) considered the colosteid fenestra as a synapomorphy of *Greererpeton* and suggested that its development may have been correlated with expansion of part of the adductor jaw musculature, following Heaton (1980) who suggested this for some more advanced tetrapods with large single exomeckelian fenestrae (*Diadectes* and *Tseajaia*). We are fairly confident that no such explanation is either necessary for or applicable to colosteids.

The intercoronoid fossa in Greererpeton.—Ahlberg et al. (1994) pointed out that members of several rhipidistian "fish" groups (porolepiforms, elpistostegalians, and osteolepiforms) have a lower jaw in which Meckelian bone is exposed in the floor of the precoronoid, intercoronoid, and/or coronoid fossae, often in all three. According to Ahlberg and Clack (1998), *Panderichthys* has all three fossae, but only the anterior (precoronoid) fossa is floored by Meckelian bone. Only a few, very early, tetrapods were heretofore known to preserve any trace of even one of the primitive three "coronoid" fossae. Where one or more fossae are present, as in *Ventastega,* they are very shallow and completely floored by bones of the coronoid series (e.g., Ahlberg et al., 1994, fig. 16).

Greererpeton provides the first known example of a tetrapod with a deep "coronoid" fossa (the intercoronoid fossa in this case), and the first one with a fossa whose exoskeletal floor is incomplete and thus may have been partly formed by Meckelian bone or cartilage. The intercoronoid fossa in *Greererpeton* differs from that of other rhipidistian groups in having a lateral border formed by the dentary rather than the coronoids, and a medial border formed by the coronoids rather than the prearticular. These are very likely derived conditions, as is the relatively large size of the *Greererpeton* intercoronoid fossa. But this does not necessarily mean that the fossa itself is derived and homoplastic as suggested by Ahlberg and Clack (1998). They commented (p. 35) that "the intercoronoid fossa [in *Greererpeton*] is *lateral* to the tooth row, and thus probably not homologous with the mesially placed intercoronoid fossae of sarcopterygians. . . ." This comparison is somewhat misleading because irrespective of the presence or absence of an intercoronoid fossa, the mediolateral position of coronoid teeth cannot be assumed to be invariate. It is clear from the literature that the arrangement of the coronoid dentition and the position of the intercoronoid fossa relative to that dentition vary widely among rhipidistian and tetrapodomorph fishes. Thus despite *Greererpeton*'s late-Mississippian age, we see no justification for denying homology of the intercoronoid fossa *a priori.* Retention of the intercoronoid fossa would be consistent with *Greererpeton*'s other primitive features. In any case, this assumption will ultimately have to be tested against an appropriate cladogram.

Ahlberg et al. (1994) noted that exposure of Meckelian bone in the floor of one or more of the "coronoid" fossae was widespread in non-tetrapod rhipidistians, and suggested that the absence of such exposure in tetrapods was synapomorphous. We agree, but consider that the condition of the floor should be characterized first by the presence or absence of fenestration. Presence or absence of Meckelian ossification in a fenestrated floor is a separate character. As argued above for presence of an intercoronoid fossa, we suggest that the fenestra in the floor of the fossa is also homologous with that in other rhipidistians, and therefore primitive.

Identification of the Goreville Greererpeton, *and relationships of* G. burkemorani.—Schultze and Bolt's (1996) cautious referral of the Goreville *Greererpeton* to "Greererpeton sp." can now legitimately be replaced by its identification as *Greererpeton burkemorani.* Every feature of the Goreville *Greererpeton* that at first sight appeared novel has been found in *G. burkemorani* when adequately preserved material has been examined. The larger question of *Greererpeton*'s phylogenetic relationships to other early tetrapod groups is best investigated as part of a cladistic study that includes the entire skeleton, not the mandible alone. We have in preparation such a study of colosteids, which will include all of the described species and will be presented in our description of the colosteid skull from Iowa. For the present, short of a detailed cladistic study the general systematic position of *G. burkemorani* will be briefly considered here.

The major question regarding *Greererpeton*'s affinities is the relationship of colosteids to the Temnospondyli, which is by far the largest group of Paleozoic amphibians. With one partial exception, there is little evidence for relationship to any of the other major early tetrapod groups, such as nectrideans or microsaurs. Unfortunately there is no satisfactory definition of the Temnospondyli, which is often and probably correctly referred to as a paraphyletic group. *Greererpeton* and other colosteids are sometimes considered to be primitive temnospondyls (e.g., Smithson, 1982; Hook, 1983; Godfrey, 1989), apparently based on Smithson's (1982) definition of Temnospondyli. Without Smithson's claim for "fundamental" ontogenetic significance, this amounts to a suggested single but at least unambiguously stated character: a contact between the exoccipitals and the postparietals. Smithson considered *Greererpeton* to meet this criterion based on his study of the Greer specimens. Our observations render this conclusion doubtful: preparation of skull KUVP 87695 shows that, in this large Goreville specimen, the otic capsule interposes between the postparietals and the dorsal extremity of the exoccipital. By Smithson's criterion, *Greererpeton* is thus not a temnospondyl. Milner (1990) diagnosed Temnospondyli using four characters that we consider poorly formulated and ambiguous. He did, however, conclude that colosteids are not temnospondyls. Panchen and Smithson (1988) proposed a two-character diagnosis, also ambiguously stated, that likewise excluded colosteids from Temnospondyli.

We conclude that the most that can be said at present is that colosteids are a tetrapod stem group—a position quite compatible with their surprisingly primitive morphology. The only evidence for a more restricted sister taxon relationship to any other group of early tetrapods is provided by the adsymphysial. The relationship between baphetids and colosteids that this implies remains to be tested, preferably with a data set that includes characters from all regions of the skeleton. Other than this character of the adsymphysial, the morphology of the two groups as now known does not suggest close relationship.

SUMMARY AND CONCLUSIONS

"*Greererpeton* sp." from Goreville, Illinois is indistinguishable from *G. burkemorani* from the holotype locality near Greer, West Virginia, and should be referred to that species. On the basis of the Goreville *G. burkemorani* material alone, we have been able to determine the condition of numerous mandibular characters. Many of these character conditions were not previously known in *G. burkemorani*, or were mentioned only in abstract form (e.g., Bolt and Lombard, 1994, 1996; Lombard and Bolt, 1995b). Among them are many that are likely primitive for tetrapods, by comparison with non-tetrapod rhipidistians and especially elpistostegalians, as well as very early tetrapods (cf. Ahlberg et al., 1994; Ahlberg and Clack, 1998). Character conditions previously unknown, or mentioned only in abstract form, include:

(1) MANDIBLE intercoronoid fossa *present*; (2) MANDIBLE intercoronoid fossa floor is *incomplete*; (3) MANDIBLE lateral parasymphysial foramen *present*; (4) MANDIBLE medial parasymphysial foramen *present*; (5) MANDIBLE angular foramen on ventromedial surface in joint between angular and prearticular *present*; (6) ADSYMPHYSIAL bone *present*; (7) ADSYMPHYSIAL joint with antimere at symphysis joint surface *brassicate*; (8) ADSYMPHYSIAL joint with antimere at symphysis contribution to symphysis area *50–74 percent*; (9) ADSYMPHYSIAL teeth *present*; (10) DENTARY postdental process as a slender extension of dentary posterior to teeth *present*; (11) DENTARY postdental process lies in longitudinal groove in surangular *present*; (12) DENTARY postdental process posterior extent *ends within middle third of adductor fossa*; (13) DENTARY indication of oral lateral line *present*; (14) DENTARY postdental process border to adductor fossa *absent*; (15) PREARTICULAR teeth *present*; (16) PREARTICULAR length from posterior edge of glenoid to anteriormost externally visible extent, relative to total length of mandible as measured from posterior edge of glenoid *80–89* percent; (17) SURANGULAR indication of oral lateral line *present*; (18) EXOCCIPITAL joint with postparietal *absent*. Although 18 does not pertain to the mandible, it is included here because it is a further indication of the status of *Greererpeton burkemorani* as a very primitive tetrapod.

While presence of an adsymphysial is primitive for tetrapods, some conditions are shared only with the baphetid *Megalocephalus pachycephalus,* and are most likely derived within early tetrapods: (1) ADSYMPHYSIAL joint with antimere at symphysis contribution to symphysis area *50–74 percent*; 2) ADSYMPHYSIAL joint with antimere at symphysis surface relief *brassicate*.

Most of the above conditions of Goreville *Greererpeton burkemorani*, as well as some others mentioned in the description, were not observed in Greer *G. burkemorani* by Smithson (1982). When it was possible to check any of these features against adequately preserved Greer specimens, however, all proved to be present. The same was true for colosteid mandibular specimens from the Delta locality. One of these, FM PR1637, is indistinguishable from *G. burkemorani* and is referred to as "cf. *G. burkemorani*," although the identity of such a fragmentary specimen cannot be conclusively established. The other Delta specimens described were two damaged mandibles associated with a colosteid skull that represents a taxon different from *G. burkemorani*. These agreed in most respects with *G. burkemorani,* although differing in having a visible suture between coronoids 2 and 3 and in having a smaller and bipartite dentary notch.

We have proposed a three-stage scenario for the evolution of the Meckelian bone or cartilage, and the exo- and endomeckelian fenestrae. At the moment this is a "grade" rather than phylogenetic scheme, as its applicability to and history within various tetrapod clades remains to be tested. We believe that our proposal will foster a search for the mandibular characters that are required for such a test.

Based solely on joint morphology, we propose that the skull table-cheek suture in *Greererpeton burkemorani* was a kinetic joint. We further propose that movements at this joint were accommodated at the symphysis, and that the brassicate structure of the interadsymphysial suture is associated with these movements. As one test of this hypothesis, we predict that *Megalocephalus pachycephalus,* in which the interadsymphysial suture is now known to be brassicate, also has a kinetic skull table-cheek joint.

The excellent preservation of Goreville *Greererpeton burkemorani* enabled us to formulate and determine states for characters of the mandible. These are listed in PRESERVE format (Lombard and Bolt, 1999) in Table 1. Table 1 also incorporates a few of the mandibular characters utilized by Ahlberg and Clack (1998), which we have expressed in PRESERVE format. The resulting data table makes available 226 mandibular characters in a consistent format. The table includes many new characters, representing a large addition to the character set currently available for early tetrapods.

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