Proceedings of the Iowa Academy of Science

Volume 93 | Number

Article 4

1986

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Proc. Iowa Acad. Sci. 93(1):07-15, 1986

Devonian Ammonoid *Manticoceras* From Iowa

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Recovery of rare, well-preserved representatives of *Manticoceras* from Upper Devonian (Frasnian) strata of north and east-central Iowa allows clarification of the poorly understood species *Manticoceras regulare* Fenton & Fenton, and marks the first recorded North American occurrence of *Manticoceras lindneri* Glenister. The faunal horizons correlate with the upper *Manticoceas cordatum* (Iγ) ammonoid zone and the *Palmatolepis gigas* conodont zone. *M. regulare* can be recognized by its narrowly discoidal conch, relatively broad sutural elements, and mature conch diameter of approximately 11 cm. Occurrences of *M. regulare* have been restricted to the "Amana Beds" of the Independence Shale and Cerro Gordo Member of the Lime Creek Formation. The larger *M. lindneri* (mature diameter of approximately 19 cm) possesses a moderately wide conch and narrow sutural elements. All known Iowa representatives are from the Owen Member of the Lime Creek Formation in the north-central portion of the state. The only other known occurrence of *M. lindneri* is from the lower Virgin Hills Formation, Fitzroy Basin, Western Australia. Recently proposed Devonian paleogeographic reconstructions suggest that such a wide distribution may be attributed to the dispersal effects of warm, equatorial currents.
INDEX DESCRIPTORS: Iowa Devonian ammonoids, biostratigraphy, paleogeography.

Manticoceras Hyatt (1884) comprises diverse Upper Devonian (almost exclusively Frasnian) ammonoids of the Family Gephurocera-tidae. The type species of the genus is *Goniatites simulator* Hall (1874) known from a single specimen from the Genesee Formation of New York. The original scheme for the zonation of the classic lower Upper Devonian sections of Germany was established by Wedekind (1913, 1918) using species of *Manticoceras* in the definition of Zonen within the *Manticoceras Stufe* (I). Many species of *Manticoceras* appear to have cosmopolitan distributions, occurring in Europe, Asia, North Africa, Australia, and North America. However, inadequate data for other species and poor quality of type material have impeded interpretation of phylogenetic relationships within the genus and precise stratigraphic implications. It has also been proposed that species recognition in *Manticoceras* is complicated by sexual dimorphism (Makowski, 1962).

Availability of well preserved specimens of *Manticoceras* from the Owen and Cerro members of the Lime Creek Formation of north-central Iowa and the "Amana Beds" of the Independence Shale of east-central Iowa has re-focused attention on the group, providing additional data on sutural detail and conch morphology of specimens from the general type area of *M. regulare* Fenton and Fenton (1924). Re-examination of the type material of *M. regulare* has convinced us that it is inadequate for species recognition. However, we have found new specimens from the Cerro Gordo Member of the Lime Creek Formation which are similar in size to the holotype of *M. regulare* (also from the Cerro Gordo Member) and are the basis of a redefinition of the species. Specimens recovered from the Owen Member of the Lime Creek Formation, which overlies the Cerro Gordo, are indistinguishable from the Australian *M. lindneri* Glenister (1958) from the Virgin Hills Formation, Fitzroy Basin. In shell morphology *M. regulare* has been compared to the widely distributed *M. intumescens* Beyrich (1837), *M. sinuosum* Hall (1843), and *M. rhynchostoma* Clarke (1899), from the *Manticoceras cordatum* I (β) γ Zone (Bogoslovskiy, 1969), but can be distinguished from these and also from *M. lindneri* by details of the suture.

The ammonoid faunas of the Cerro Gordo and Owen members and the "Amana Beds" are believed to correlate with the upper *Manticoceras cordatum* (Iγ) Zone, as defined by House and Ziegler (1977, p. 77, fig. 4).

STRATIGRAPHY

The Upper Devonian rocks of Iowa are characterized by shales, argillaceous limestones, and dolomites, of shallow marine shelf origin. Formations that have yielded *Manticoceras* are the Lime Creek Formation, Independence Shale, and the correlative "Amana Beds".

LIME CREEK FORMATION

The Lime Creek Formation crops out mainly in Cerro Gordo, Floyd and Hancock counties of north-central Iowa. It overlies the Upper Devonian Shell Rock Formation where that unit is present in the north, and succeeds largely Middle Devonian Cedar Valley Limestone to the south. Thickness for the unit (Anderson, 1966) ranges from 50 to 61 m (165 to 200 ft). Three members, in ascending order the Juniper Hill, Cerro Gordo, and Owen can be recognized in the type area around Rockford, Cerro Gordo County; elsewhere the members cannot be distinguished readily (Anderson, 1966).

Juniper Hill Member. — The Juniper Hill Member comprises 23 to 30 m (75 to 100 ft) of blue-gray shale (Anderson, 1966). It unconformably overlies the Shell Rock Formation or the Cedar Valley Limestone, and underlies the Cerro Gordo with little or no evidence of disconformity (Stainbrook, 1935). Ammonoids are absent and other fossils are generally sparse, but a variety of microfossils and brachiopods have been recovered.

Cerro Gordo Member. — The Cerro Gordo Member is an interbedded sequence of shales and argillaceous limestones with a maximum thickness of approximately 14 m (45 ft). It becomes dolomitic and less fossiliferous to the west where the unit is entirely dolomitized near Clear Lake, Iowa (Belanski in Fenton, 1931; Koch, 1963). The Cerro Gordo contains an especially abundant and diverse fauna (including corals, bryozoans, brachiopods, gastropods, bivalves, cephalopods, and crinoids) from which Fenton and Fenton (1924) described more than 100 species.

Owen Member. — The Owen Member is an approximately 15 m (50 ft) sequence of fossiliferous, interbedded dolomite and limestone. It is conformable on the Cerro Gordo and unconformable beneath the Sheffield Formation. In outcrop the Owen is typically buff colored, recessive, and soft (Stainbrook, 1935). It is similar lithologically to the dolomitic facies of the Cerro Gordo Member, but can be distinguished on stratigraphic and faunal evidence. Many fossils occur as molds.

Ammonoids

Ammonoids are known from the Cerro Gordo and Owen members, but not from the Juniper Hill Member. The first species to be recovered and described from the Lime Creek Formation was *Manticoceras regulare* Fenton & Fenton (1924) from the middle and upper Cerro Gordo Member at Hackberry Grove and Rockford, Iowa (Fig. 1, localities 1 and 3). *M. regulare* appears to range throughout the Cerro Gordo Member but not into the overlying Owen Member. Since Fenton and Fenton's report and that of Miller (1938a), additional

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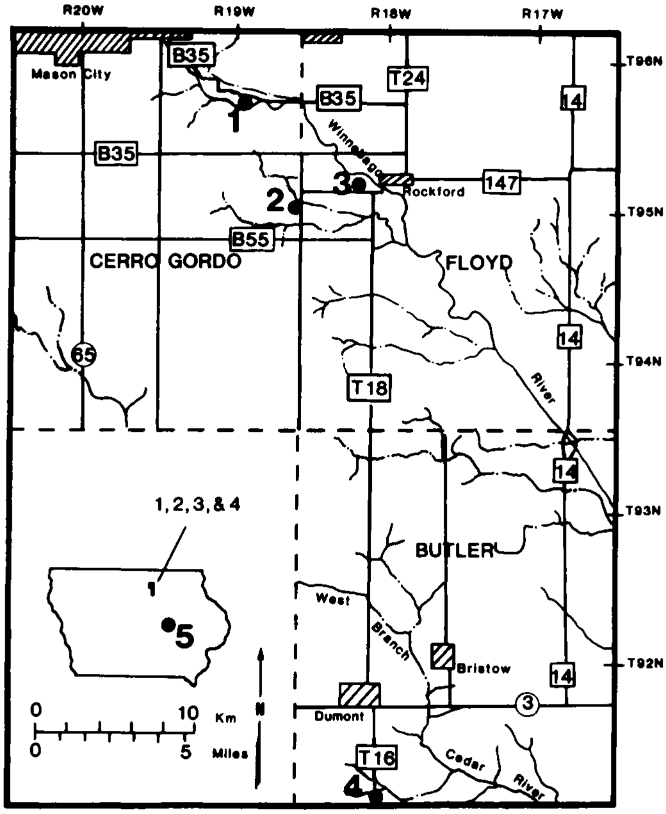

Fig. 1. Locality map showing occurrences of *Manticoceras regulare* Fenton & Fenton and *M. lindneri* Glenister from northern and east-central Iowa. Localities 1-4 (enlarged from inset) are exposures of the Upper Devonian Lime Creek Formation at Hackberry Grove, Bird Hill, Rockford Brick and Tile Quarry, and Dumont respectively. Locality 5 exposes the "Amana Beds" of the Upper Devonian Independence Shale at Middle Amana. Dashed lines represent county boundaries.

specimens of *Manticoceras* (the focus of the present study) have been recovered by one of us (Calvin O. Levorson) from the Cerro Gordo and Owen members near Rockford, Iowa, from the general type area of *M. regulare*.

Manticoceras regulare has been regarded as closely similar to *M. intumescens* Beyrich (1837), *M. sinuosum* Hall (1843), *M. lindneri* Glenister (1958), and *M. rhynchostoma* Clarke (1899) (Miller, 1938a; Glenister, 1958; Bogoslovskiy, 1969). Our intention is to demonstrate that *M. regulare* and *M. lindneri,* although similar in conch-form to *M. intumescens, M. sinuosum,* and *M. rhynchostoma,* are in fact distinct species. Occurrences of *M. intumescens* and *M. sinuosum* have been well documented (Miller, 1938a; House, 1962; House and Pedder, 1963; Bogoslovskiy, 1969; Clausen, 1969; Kirchgasser, 1975) and have been demonstrated to be restricted to the *Manticoceras cordatum* Zone I (βγ, (especially the Iγ faunas) of Wedekind (1913, 1918) by Matern (1929) and by House and Ziegler (1977). *M. regulare* and *M. lindneri* from the Lime Creek Formation of the Iowa are here shown to be most similar to gephuroceratids from the upper *M. cordatum* (Iγ) Zone (House and Ziegler, 1977) of Germany, the *M. rhynchostoma* Zone of New York, and the lower Virgin Hills Formation of Western Australia.

Conodonts

Anderson (1966) demonstrated that the Lower *Palmatolepis gigas* (*P. rhenana)* Zone of Ziegler (1962) can be recognized from the upper Juniper Hill through most of the Cerro Gordo on the presence of *P. gigas* and *P. foliacea* Youngquist (1945). Since the lower *P. gigas* and upper *M. Cordatum* (Iγ) zones correlate in the German reference section (House and Ziegler, 1977), conodont and ammonoid age-data for the Cerro Gordo Member are in agreement. The *P. gigas* Zone has been recognized elsewhere in Iowa from the Independence Shale (Klapper *et al.,* 1971) allowing correlation of the Lime Creek Formation to part of the Independence.

Conodonts are of little aid in the clarification of the precise age of the Owen Member. Identification of conodonts recovered from the Owen has been impeded by dolomitization of the unit so that no diagnostic forms have been recognized. Youngquist and Peterson (1947), Müller and Müller (1957), and Anderson (1966) described conodont faunas from the overlying Sheffield Formation, but only transitional morphotypes of *Palmatolepis* that are inconclusive for precise age assignment have been recovered from the Sheffield.

INDEPENDENCE SHALE

The term Independence refers to shales that occur in scattered areas in eastern Iowa as sink, fracture and cavern fillings, especially within the Cedar Valley and Wapsipinicon formations. The unit was named by Calvin (1878) for argillaceous, fine-grained, reportedly "bituminous" shales encountered in a well near Independence, Buchanan County, Iowa, supposedly "stratigraphically" between the Cedar Valley and Wapsipinicon formations. Stratigraphic position of the shale was debated for many years, with Stainbrook (1945) insisting that the Independence underlies the Cedar Valley. The alternative interpretation, now accepted (Cooper, 1942), is that the Independence Shale represents stratigraphic leak from a clastic unit that overlies the Cedar Valley Limestone and equivalents. The Independence Shale unit has been termed the Sweetland Creek Shale in southeastern Iowa and the Lime Creek Formation in north-central Iowa (Klapper *et al.*, 1971).

The "Amana Beds" comprise a portion of the Independence, characterized by gray shales with interbedded limestone stringers, that is exposed between the Middle and High Amana communities of Iowa County, Iowa. Lithologically, the Amana Beds are similar to the shales of the Independence in its type area, but they tend to be less calcareous (Müller and Müller, 1957).

Ammonoids

Specimens of *Manticoceras regulare* as well as a single specimen referred to *Ponticeras* have been reported from the Independence Shale (Miller, 1938). Miller named the new species *P. stainbrooki* for the single specimen collected near Brandon, Iowa. Re-examination of the type of *P. stainbrooki* has revealed it to be a specifically indeterminate juvenile (probably not a *Ponticeras,* due to the advanced character of the suture, and reasonably referred to *Manticoceras*).No ammonoid shells have been reported from the Sweetland Creek area although aptychi are abundant and have been identified as *Spathiocaris emersoni* Clarke 1884 (Weller, 1909). Occurrences of *M. regulare* in the Independence Shale would support correlation of the Independence Shale with the Cerro Gordo Member of the Lime Creek Formation and the upper *M. cordatum* Zone (Iγ).

Conodonts

The Independence Shale contains an abundant and diverse conodont assemblage. Klapper *et al.* (1971) recognized the Lower *P. gigas* Zone at a number of localities of the Independence Shale. As noted above, the *P. gigas* Zone is also recognizable in the upper Juniper Hill and most of the Cerro Gordo Member of the Lime Creek Formation, allowing correlation of those units to the upper Independence on conodont evidence as well as ammonoid occurrences.

AMMONOID LOCALITIES

All cited quadrangle maps are from the U.S. Geological Survey 7.5

Minute Series (Scale = 1:24000). Numbered localities that follow are indexed in Fig. 1. Detailed locality data for conodont occurrences in the Lime Creek Formation and Independence Shale may be obtained from Anderson (1966) and Müller and Müller (1957).

LIME CREEK FORMATION

Locality 1 — Approximately 12 m (40 ft) of the blue-gray shales of the Juniper Hill, 11 m (35 ft) of argillaceous limestones and shales of the Cerro Gordo, and 2 m (6 to 7 ft) of the Owen are exposed at the type locality of the Lime Creek Formation along the Winnebago River at Hackberry Grove in Cerro Gordo County (NE 1/4, Sec. 35, T96N, R19W, Mason City SE, Iowa, Quadrangle).

Locality 2 — Shales of the upper Cerro Gordo Member and the basal 1 m (3 ft) of the Owen Member are exposed at Bird Hill, Floyd County (Center Sec. 13, T95N, R19W, Mason City SE, Iowa, Quadrangle).

Locality 3 — Nineteen m (61 ft) exposing the Juniper Hill Shale and 11 m (35 ft) of the overlying argillaceous limestones and shales of the Cerro Gordo Member are located in Floyd County at the abandoned Rockford Brick and Tile Quarry (Center NW 1/4, Sec. 16, T95N, R18W, Rockford, Iowa, Quadrangle).

Locality 4 — Approximately 4 m (14 ft) of fossiliferous, dolomitic limestone of the Owen Member are exposed in quarries located in Butler County south of Dumont (NE 1/4, SE 1/4, Sec. 34, T91N, R18W, and SE 1/4, NE 1/4, Sec. 21, T91N, R18W, Dumont South, Iowa, Quadrangle).

INDEPENDENCE SHALE

Locality 5 — Dolomitic limestones interbedded with calcareous and non-calcareous shales of the "Amana Beds" reaching a thickness of 12 m (40 ft) are exposed approximately 1.6 km (1 mile) west of Middle Amana, Iowa, for almost a mile along Highway 220 (N 1/2, Sec. 29, T81N, R9W, Middle Amana, Iowa, Quadrangle).

ABBREVIATIONS

The following abbreviations are used throughout the remainder of the text and in plates and figures.

Measurements: Dimensions are given in millimeters.

D = Diameter measured across the center of the umbilicus.
W = Maximum whorl width.
U = Umbilical width measured between umbilical walls.
H = Whorl height measured from venter to the midpoint of a line joining corresponding umbilical seams.
Vh = Height of ventral lobe complex (Fig. 4).
Vw = Width of ventral lobe complex measured from the tips of the ventral prongs (V_2).
Sw = Width of ventral lobe complex measured from the highest point of lateral saddles.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class CEPHALOPODA Leach, 1817
Order ANARCESTIDA Miller & Furnish, 1954
Suborder GEPHUROCERATINA Frech, 1897
Superfamily GEPHUROCERATACEAE Frech, 1897
Family GEPHUROCERATIDAE Frech, 1897
Genus MANTICOCERAS Hyatt, 1884

Type species. — *Goniatites simulator* Hall, 1879, p. 2: OD.

Diagnosis. — Conch subdiscoidal to lenticular, moderately involute (U/D 0.1-0.4, Fig. 2; Glenister, 1958; House and Pedder, 1963; Bogoslovskiy, 1969), suture 6-lobed with ventral lobe deeply trifid, growth lines rectilinear to biconvex (forming a broad lateral sinus).

Description. — Conch small to very large (max. 30 cm), subdiscoidal to lenticular (W/D 0.3-0.8), moderately involute with rounded to flattened lateral sides and rounded to angular venter. The umbilicus is deep and moderate to large (U/D 0.1-0.4) with slightly rounded umbilical walls. When preserved, the body chamber comprises one-third to one-half the length of the whorl. Mature modifications comprise slight divergence and slight decrease in absolute width of the body chamber. The surface of the shell is smooth, but sometimes developed weak transverse ribs. Growth lines may range from rectilinear to biconvex, forming a deep sinus across the venter and a broader, shallower lateral sinus.

The mature suture comprises 6 primary lobes: a broad, deep unequally trifid ventral lobe; an angular umbilical lobe that is generally acute; shallow, angular internal lobe; deep, narrow dorsal lobe, and rounded saddles. The umbilical lobe may be level with to shorter than the ventral prongs. Sutural formula:

$$(V_2V_1V_2)U{:}ID$$

Occurrence. — I (β) γ — IIα. Primarily Lower Upper Devonian (Frasnian) of North America (U.S.: Iowa, Missouri, Michigan, Indiana, New York, West Virginia, Utah, Arizona, New Mexico, Nevada; Canada: Alberta and Northwestern Territories), Western Europe, U.S.S.R. (Urals including Timan and Rudnyy Altay), Northern Africa (Algeria, Morocco), China, and Western Australia (Canning Basin).

Discussion. — *Manticoceras* has been compared closely to the genus *Crickites* because of similarities in shell shape and sutural detail. Wedekind (1913) established the Subfamily Crickitinae for discoidal to lenticular, moderately involute forms that differ from gephuroceratins only in the nature of the growth lines. Growth lines in *Crickites* were defined as "convex and not doubly convex" although Wedekind himself apparently assigned forms with rectilinear to slightly doubly convex growth lines to *Crickites expectatus* Wedekind (1913). Bogoslovskiy (1969) has demonstrated continuous gradation in the contours of the growth lines in representatives of both genera [*Crickites expectatus, C. holzapfeli* Wedekind (1913) which possess weakly convex growth lines; and *Manticoceras carinatum* Beyrich (1837) possessing growth lines that are rectilinear to slightly biconvex]. This apparently continuous gradation between *Manticoceras* and *Crickites* led a number of authors (Schmidt, 1921; Miller and Furnish, 1957; Glenister, 1958; Clausen, 1969) to question the taxonomic significance of growth lines. They contended that the growth lines are of secondary importance and insufficient to separate the two genera, and that the Subfamily Crickitinae as defined by Wedekind is unrecognizable.

Clausen (1969) separated transitional forms into two groups and proposed re-definition of Crickitinae based on changes in contour of the growth lines through ontogeny and on nature of the runzelschicht ("wrinkle layer"). Forms traditionally assigned to both *Manticoceras* and *Crickites* that have weakly biconvex to rectilinear growth lines in later stages and found to be biconvex in early ontogenetic stages possess "Ritzstreifung" (lines of the runzelschicht) that are nearly parallel. Forms originally assigned to *Crickites* in which growth lines remain convex throughout life possess Ritzstreifung that are discontinuous and non-parallel. Kirchgasser (personal communication 10/30/84) however, contends that just the opposite is found in some species from New York (*M. sinuosum*) and Europe (*M. cordatum*) and that "Ritzstreifung" have not been seen in the type species of *Manticoceras, M. simulator*. Additional analysis of similar *Manticoceras* and *Crickites* is needed to establish the taxonomic value of the "Ritzstreifung".

Some authors (House, 1962) have also speculated an ancestral — descendant relationship between *Manticoceras* and *Crickites*. *Manticoceras* first appears in strata of Wedekind's Iβ Zonen, whereas *Crickites* first occurs later (Iδ). The expected ontogenetic transition of biconvex to convex growth lines in *Crickites* which would support this derivation was not observed by Clausen (1969), and as a result he postulated that the similarities between the two genera resulted not from close affinity but from homeomorphy.

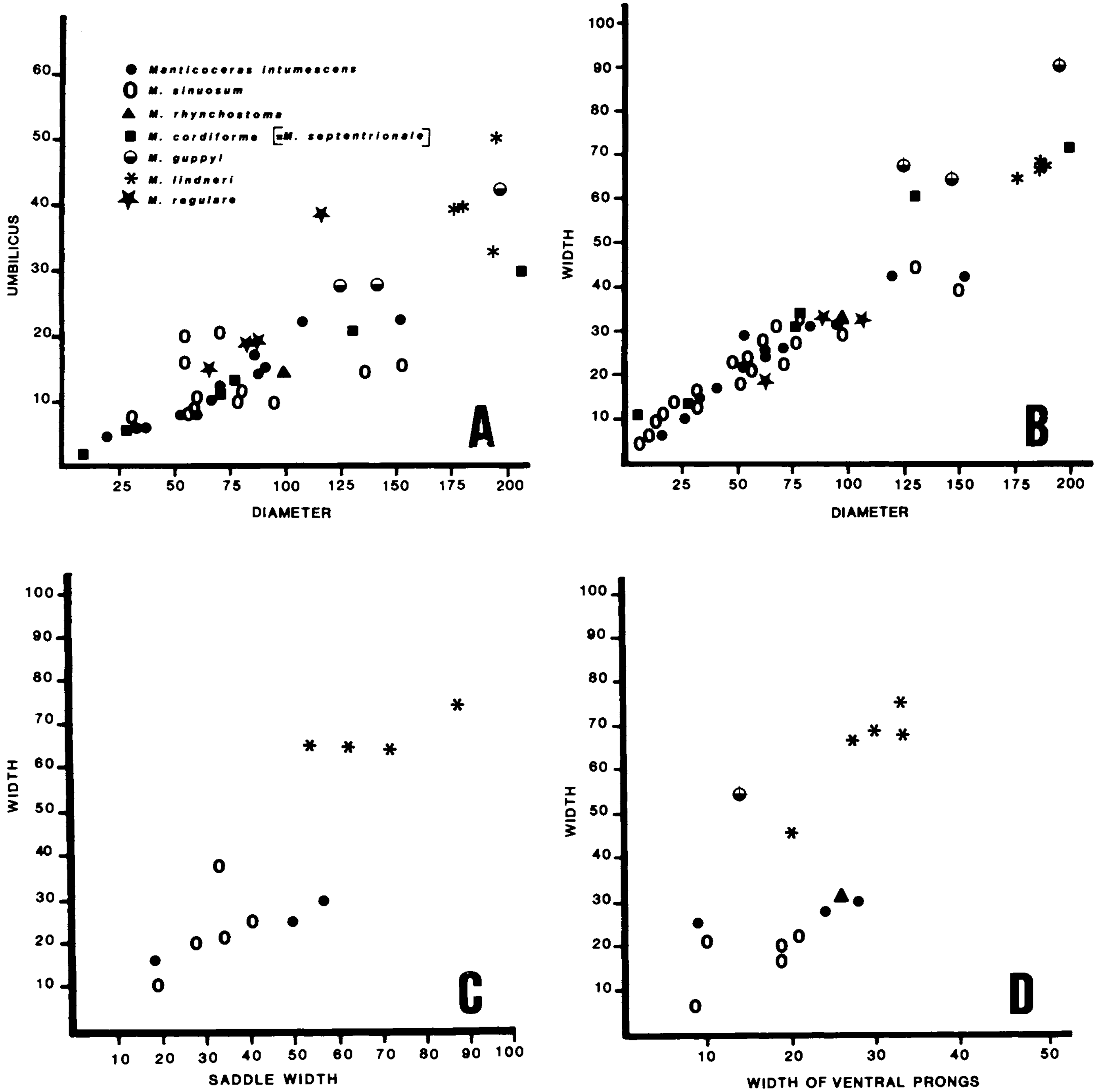

Fig. 2. Bivariate plots of morphologic characters of *Manticoceras.* Data for plots are compiled in Table 1, and from Glenister (1958), House & Pedder (1963), and Bogoslovskiy (1969).

Species recognition in *Manticoceras* has been subject recently to increasingly careful analysis (e.g. House, Kirchgasser, Bogoslovskiy). Traditionally, minor, unquantified details of the suture, including relative width and degree of constriction of the ventral prongs, width of the umbilical lobes, depth of the lobes, and conch proportions have served for specific determination. However, recent studies (House, 1962; Makowski, 1962; Bogoslovskiy, 1969; Clausen, 1969; Kirchgasser, 1975) have demonstrated considerable intraspecific variation in these features. In addition, compounding these problems, much confusion regarding specific assignments within the genus relates to inadequate type material. Many species are based on poorly preserved, crushed, or distorted specimens; some have not been described completely, and others are represented by either large or small specimens only.

Species recognition in *Manticoceras* may also be complicated by sexual dimorphism. Makowski (1962) suggested dimorphism in *Manticoceras intumescens,* citing as evidence the work of Holzapfel (1899) on the Timan materials, where large specimens of *M. intumescens* occur with the much smaller *Manticoceras ammon* Keyserling (1884). These two species can only be distinguished by the mature modifications and size.

The cosmopolitan distribution of *Manticoceras* has long been recognized (Clarke, 1899; Wedekind, 1913; Miller, 1938a) and has more recently been recounted by House (1962, 1963, 1973a, 1973b, 1979, 1981). Occurrences of *Manticoceras* in Europe, the Urals, and Novaya Zemlya are linked, via those of the Siberian coast, to western North America (Northwest Territories, Alberta, Utah, Arizona and New Mexico), the Midcontinent (Iowa, Missouri, Michigan, Indiana), and New York and the Appalachians (Miller, 1938a; House, 1962, 1973a, 1973b; Bogoslovskiy, 1969). Although the Frasnian is characterized by world-wide distribution of the genus (except South America and Antarctica), only a few species are known to be cosmopolitan on that scale (*M. sinuosum* and possibly *M. intumescens*). The European and Uralian "Old World" faunas have long been regarded as the most diverse of Frasnian ammonoid faunas. Only the Appalachian fauna approaches the Old World fauna in diversity (Clarke, 1899; Bogoslovskiy, 1969).

A number of biogeographic provinces have been postulated for the Frasnian (Boucot *et al.*, 1969; House, 1973a, 1973b; Oliver, 1976), but discovery of new biotas has re-affirmed the cosmopolitan nature of Frasnian faunas. The Appalachian or Eastern American province (Heckel and Witzke, 1979), though very similar in specific characteristics to the Old World fauna, is the only province with endemic species. Some authors (i.e. Miller, Bogoslovskiy, House) have been tempted to view the European Old World Realm as the area of origin of *Manticoceras*, with subsequent migration. House (1973a, 1973b) has viewed the landward facies to the east and northeast of the New York ammonoid-bearing facies as likely barriers to direct intermingling of Old and New World faunas. Such isolation would have favored the development of a highly diverse and distinctive Appalachian fauna.

House (1973a, 1973b) also summarized the widespread Asian occurrences from Iran, Asiatic Russia, and China, suggesting that the very wide distribution may infer a faunal link along the Paleo-Tethys and explain the remarkable European affinity of Australian Devonian faunas (House, 1973a). However, the record of the Asian part of the link is poor and documentation of this possible migration route is inadequate.

Recent Devonian paleogeographic reconstructions have been proposed by Heckel and Witzke (1979) based on lithic paleoclimatic indicators and tectonic setting. The pattern of oceanic circulation derived from Devonian world paleogeography may offer a relatively simple explanation for the biogeographic distribution of *Manticoceras* species as well as other Frasnian biotas. The wide distribution of Old World faunas (Heckel and Witzke, 1979, p. 114) can be explained by coincidence with warm equatorial currents (and their numerous associated gyres) flowing freely around the world through the Paleotethys Sea. Migration of *Manticoceras* to North America via the Uralian and Cordilleran regions would be consistent with Heckel and Witzke's paleogeographic and paleocurrent models and with migration routes proposed by House (1973a). Development of land barriers to the north and east (Transcontinental Arch and Acadian Mountains) would have effectively separated the Appalachian and Midwestern provinces from equatorial currents and prevented associated intermingling of Old World, Uralian and Cordilleran faunas. Joint occurrences in the Eastern American province and Australia of species that are unknown elsewhere (i.e. *M. lindneri*), may suggest a closer connection between these areas than between Australia and Asia. In that case it is possible to postulate an alternative route to the Paleo-tethys link of House mentioned above; that *Manticoceras* from Australia and Eastern America intermingled via warm, easterly, equatorial currents.

MANTICOCERAS REGULARE Fenton & Fenton, 1924
Figures 2;3;6B-E,G,H; Table 1

Manticoceras regulare FENTON & FENTON, 1924, p. 196-197; Pl. 39, figs. 1-3. MILLER, 1938a, p. 97-99; Pl. 21, fig. 1; Pl. 22, figs. 1-6. CLAUSEN, 1969, p. 119, 127.

Diagnosis. — A species of *Manticoceras* characterized by combination of proportionally narrow conch (W/D 0.3 at 11 cm diameter) and a suture with broad ventral prongs and broad, nearly symmetrical lateral saddle.

Description. — Knowledge of *Manticoceras regulare* is based on 28 poorly preserved molds from the Lime Creek Formation of eastern Iowa. Holotype USNM 78694 is an abraded internal mold that achieves a conch diameter of 11 cm and includes one-third volution of body chamber; neither the conch proportions nor sutural detail are sufficiently well-preserved to provide the basis for confident specific comparison. However, two similar-sized specimens (SUI 50158, 50160; Fig. 6D, G, H) from the same general horizon and area as well as 26 phragmocone fragments of comparable morphology (topotypes

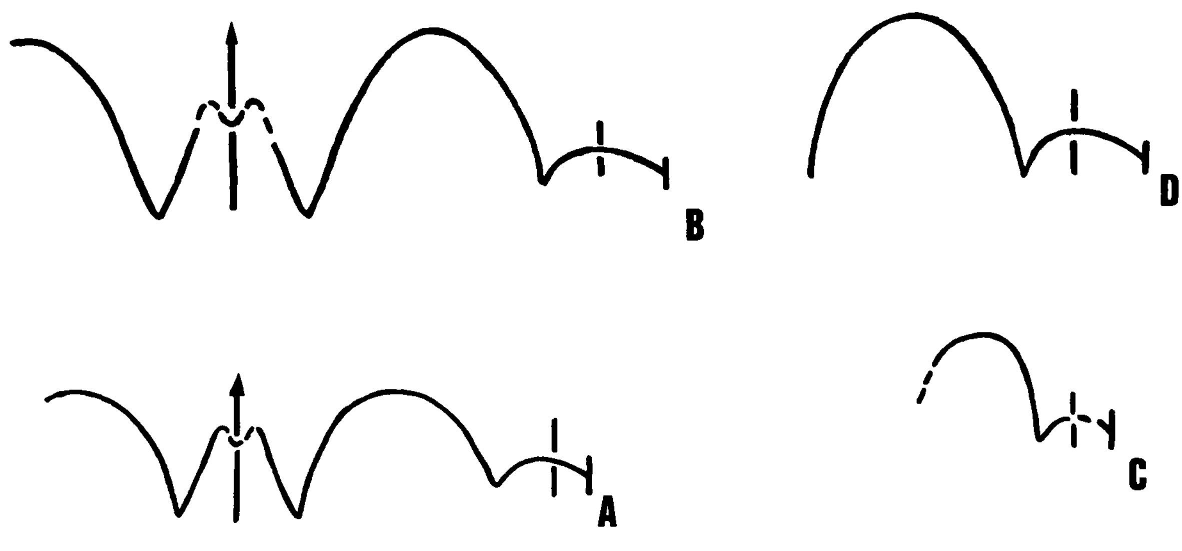

Fig. 3. Sutural outlines of *Manticoceras regulare* Fenton & Fenton. All specimens are figured at approximately x0.7. A, topotype SUI 50158 at approximately 11 cm diameter from Locality 5. B, topotype SUI 9631 from Locality 2. C, partial suture from topotype SUI 726 from Locality 3. D, partial suture topotype SUI 725 from Locality 1.

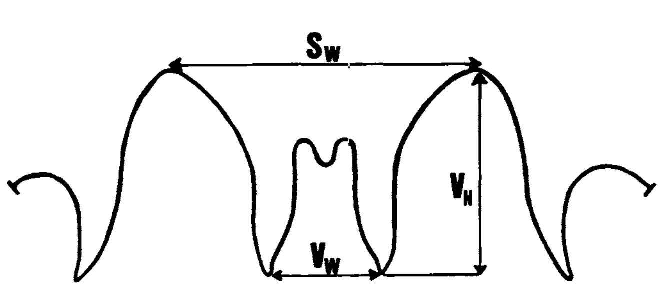

Fig. 4. Diagram explaining measurement of sutural parameters of *Manticoceras*. Vh = depth of ventral lobe; Vw = width of ventral lobe measured from the tips of the ventral prongs; and Sw = width of the ventral lobe measured from the highest points of the lateral saddle.

SUI 723-728, 9631, 50158-50164) collectively provide a fairly satisfactory basis for species recognition. Approximate coincidence of the conch diameter of the holotype and other large specimens at 11 cm, and of the base of the living chamber at 9 cm suggest that these figures represent mature dimensions. In addition, SUI 50158 preserves an apparent mature modification in slight divergence of the body chamber (Fig. 6D).

The conch of *M. regulare* (Fig. 6H; Table 1) appears narrowly discoidal (W/D 0.3 at 11 cm diameter) and has a proportionally large umbilicus (U/D 0.35 at 11 cm diameter).

Two representations of the suture (SUI 50158, 9631) and partial sutures (SUI 726, 725) are shown in Fig. 3. Prominent features include the width of the ventral prongs and nearly symmetrical lateral lobe.

Comparison. — Close similarities of *Manticoceras regulare* with the widely distributed *M. intumescens* Beyrich (1837) and *M. sinuosum* Hall (1843); the Canadian *M. cordiforme* Miller (1938a) [= *M. septentrionale* Miller (1938a)]; and the Australian *M. lindneri* Glenister (1958) and *M. quppyi* Glenister (1958) have been noted by a number of authors (Miller, 1938a; Glenister, 1958; House & Pedder, 1963; Bogoslovskiy, 1969; Clausen, 1969). Conch similarities among these species are especially striking (Fig. 2A, B), but the large umbilicus of *M. regulare* combined with narrow conch and distinctive suture serve to distinguish the species.

Closest similarities are between *M. regulare* and *M. cordiforme* (= *M. septentrionale*). The conchs of the holotypes of *M. cordiforme* (Geological Survey of Canada, GSC 2393) and *M. septentrionale* (GSC 5139) is subdiscoidal with sharply rounded venter (W/D 0.4 at 8 and 20 cm diameter). The diameter of approximately 20 cm for mature specimens (*M. septentionale*) would suggest that this species obtained a much larger size at maturity than *M. regulare*. The greater widths of the elements of the suture of *M. regulare* also serve to distinguish it from *M. cordiforme*.

Occurrence. — All known representatives of *M. regulare* are from the Cerro Gordo Member of the Lime Creek Formation of north-central Iowa and the correlative "Amana Beds" of the Independence Shale in eastern Iowa, and are referable to the Upper Devonian (Iγ).

Repository. — Holotype USNM 78694 (Fenton & Fenton, 1924, p. 196-197; Pl. 39, figs. 1-3) is in the United States National Museum, Washington. Topotype SUI 723 (Miller, 1938a, Pl. 22, figs. 1,2) and topotypes SUI 724-727, 9631, 50158-50164) and a plaster cast of the holotype (SUI 728) are housed in the Repository at The University of Iowa.

MANTICOCERAS LINDNERI Glenister, 1958
Figures 2;5;6A,F,J,K; Table 1

Manticoceras lindneri GLENISTER, 1958, Pl. 6, figs. 1,2; Pl. 7, fig. 2; Pl. 9, figs. 1,2; Text-figs. 4,5B,C; CLAUSEN, 1969, p. 119,127.

Diagnosis. — A species of *Manticoceras* characterized by combination of moderately wide conch (W/D 0.4 at 19 cm diameter) and a suture with proportionally long, narrow ventral prongs (Vh/Vw 1.4 at 19 cm diameter), narrow lateral saddle, and deep umbilical lobe.

Description. — Knowledge of *Manticoceras lindneri* is based on the holotype (UWA 35765), a mature internal mold preserving one-third volution of body chamber that achieves a diameter of 19 cm, and paratypes of comparable morphology (UWA 35766,35774,35775, and BMR 1728) all from the lower Virgin Hills Formation, Fitzroy Basin, Western Australia. In addition, 5 previously undescribed specimens, whose conch morphology and diameter are comparable to those of the holotype, have been recovered from the Owen Member of the Lime Creek Formation of north-central Iowa. Three are well preserved specimens with coincident, probably mature diameters of approximately 19 cm (SUI 31835,50154,50155); the remaining specimens are a fragmentary phragmocone (SUI 50156) and a large,

Table 1. Measurements (in mm) of suture and conch proportions for *Manticoceras regulare* Fenton & Fenton and *Manticoceras lindneri* Glenister. D = diameter, W = width, H = height, U = size of umbilicus. Methods of suture measurements are explained in Fig. 4. Asterisk denotes estimation of conch parameters. Hyphen denotes preservation too poor to determine parameters.

SPECIMEN	D	H/D	W/D	U/D	Vw	Vh	Sw
Manticoceras lindneri							
UWA 35765 (Holotype)	192.0	.53	.47	.22	—	—	—
	130.0	—	—	—	26.0	33.0	66.0
UWA 35766 (Paratype)	140.0	.49	.46	.20	—	—	—
BMR 1728 (Paratype)	123.0	.51	.54	.22	—	—	—
UWA 35774, 35775	75.0	—	—	—	12.0	23.0	38.0
SUI 31835	179.0	.50	.37	.23	27.0	46.0	71.0
SUI 50155	172.0	.49	.39	.23	33.0	40.0	62.0
SUI 50154	192.8	.44	.35	.24	29.0	40.0	53.0
SUI 50156	*191.0	*.46	*.39	*.17	33.0	57.0	88.0
SUI 50156	—	—	—	—	20.0	30.0	50.0
Manticoceras regulare							
SUI 50158	*106.0	*.35	*.29	*.35	—	—	—
SUI 50160	89.5	.49	.37	.26	—	—	—
SUI 50159	* 82.3	*.46	—	*.24	—	—	—
SUI 724	* 61.2	*.50	*.29	*.24	—	—	—

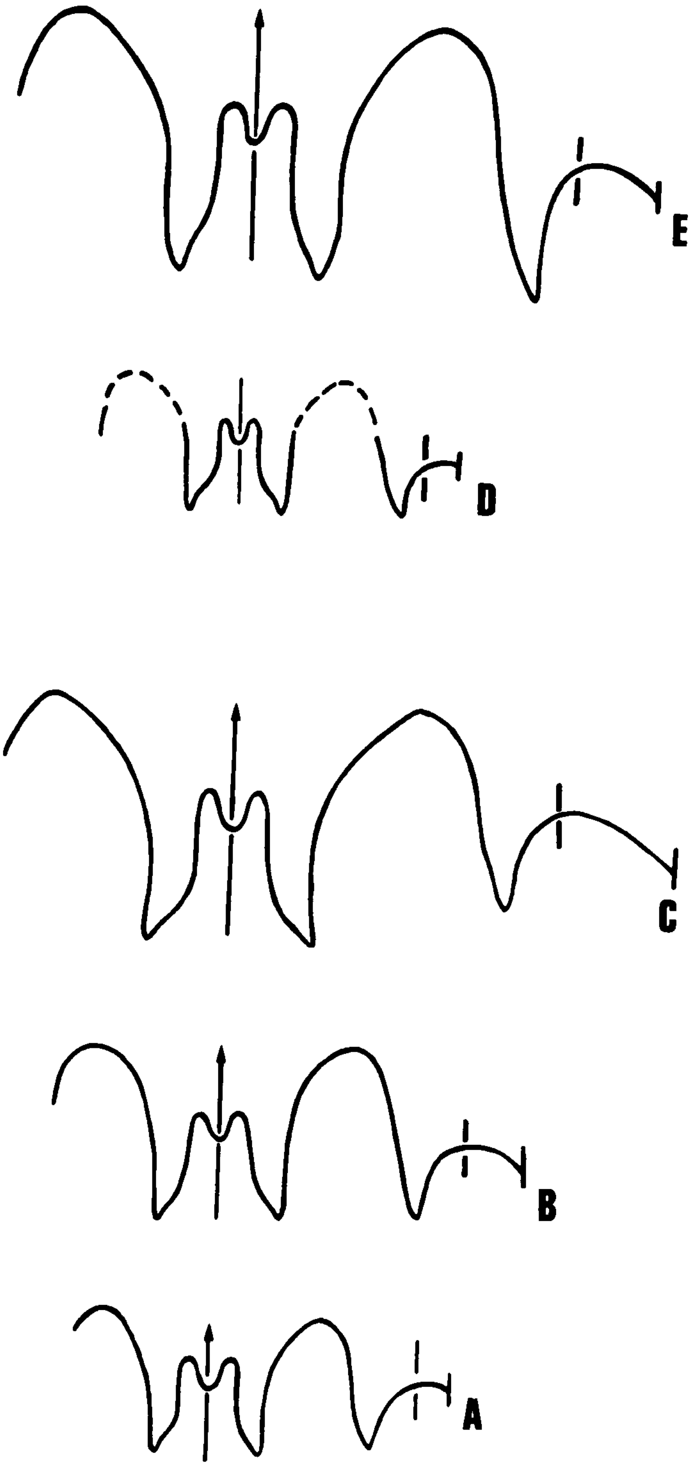

Fig. 5. Sutural outline of *Manticoceras lindneri* Glenister. All specimens are pictured at approximately x0.7 and are all from the Owen Member, Lime Creek Formation at Locality 4. A, topotype SUI 50155 at 17 cm diameter. B, topotype SUI 31835 at 19 cm diameter. C, topotype SUI 50154 at approximately 19 cm diameter. D,E, topotype SUI 50156; D, diameter = approximately 19 cm and width 74 = mm. E, width = 47 mm.

compressed phragmocone (SUI 50157) approximately 23 cm in diameter.

The conch of both the Australian and North American representatives of *M. lindneri* (Fig. 6A,F,J,K; Table 1) appear wide for the genus (W/D 0.4 at 19 cm diameter) and have a moderate to small umbilicus (U/D 0.2 at 18 cm diameter). Mature modifications include slight decrease in absolute width and slight coiling divergence of the body chamber (Fig. 6F,K).

The suture is illustrated in Fig. 5. Proportions of the suture (Explanation Fig. 4) prove useful in distinguishing *M. Lindneri* from other members of the genus (Table 1). The most conspicuous features are the relatively deep, narrow ventral lobe (Vh/Vw 1.4 at 19 cm diameter) and the adjoining high, narrow lateral saddle (Fig. 2C,D). Major trends in sutural ontogeny are proportional increase in length and angularity of lobes and height of the lateral saddle (Fig. 5D,E).

Comparison. — The closest overall affinity of *Manticoceras lindneri* is with *Manticoceras guppyi* Glenister (1958), also from the Virgin Hills Formation. Sutural similarities are striking (Glenister, 1958), especially in the depth of the ventral lobe and narrowness of the lateral saddle. The depth and acuteness of the umbilical lobe of *M. lindneri* and its larger, proportionally greater mature diameter (*M. guppyi* maximum diameter 135 mm) serve to distinguish the two species.

Two North American species of *Manticoceras* are sufficiently close in conch and sutural morphology to warrant comparison (Fig. 2A,B). *Manticoceras cordiforme* and *M. rhynchostoma* Clarke (1899) are like *M. lindneri* in attaining large diameters at maturity. The mature diameters of 19 cm for *M. lindneri* and 20 cm for *M. cordiforme* are almost coincident; however, the mature diameter of *M. rhynchostoma* is even larger — approximately 29 cm. These North American species can be distinguished from *M. lindneri* by their shallower and relatively wider ventral lobes (Vh/Vw is approximately 40 percent less than in *M. lindneri*) (Fig. 2D).

A single compressed phragmocone (SUI 50157) from the Owen Member of the Lime Creek Formation (Fig. 6I) reaches a phragmocone diameter of 23 cm — larger than any *M. lindneri* from that horizon or from Australia. Although inadequately preserved, the sutural elements appear shallower than those of *M. lindneri*. They are more reminiscent of the suture of *M. rhynchostoma,* and the specimen may be assigned questionably to that species.

Occurrence. — All known representatives of *M. lindneri* are from the Owen Member of the Lime Creek Formation of north-central Iowa, and from the lower Virgin Hills Formation, Fitzroy Basin, Western Australia.

Repository. — Holotype UWA 35765 and paratypes UWA 35766, 35774, and 35775 are deposited in the Department of Geology of the University of Western Australia at Perth and Paratype BMR 1728 is deposited at the Australian Bureau of Mineral Resources in Canberra. Hypotypes SUI 31835, 50154-50157 are housed in the Repository at The University of Iowa.

ACKNOWLEDGEMENTS

Ed Landing, New York State Museum, Albany, made available key collections of New York *Manticoceras;* and Julia Golden, The University of Iowa, helped with loans and location of specimens. M. R. House, University of Hull, England, discussed paleozoology and biostratigraphy of Devonian ammonoids. Bill Bunker and Brian Witzke, Iowa Geological Survey, shared new data on Upper Devonian stratigraphy of Iowa. William Kirchgasser, State University College Potsdam, and Wayne I. Anderson, University of Northern Iowa, offered many valuable suggestions in reviewing the manuscript.

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Fig. 6. All specimens are pictured at approximately x0.7 unless otherwise indicated. A,F,J,K, *Manticoceras lindneri* Glenister, all specimens are from Locality 4. A,J,K, hypotype SUI 50155 at 17 cm diameter. F, hypotype SUI 50154 at 19 cm diameter.
B-E,G,H, *Manticoceras regulare* Fenton & Fenton. B, topotype SUI 724 at approximately 6 cm diameter from Locality 3. C, topotype SUI 726 phragmocone fragment from Locality 3. D, SUI 50158 at 11 cm diameter from Locality 5. E, topotype SUI 9631 fragment from Locality 2. G,H, topotype SUI 50160 at 9 cm diameter from Locality 5. I, *Manticoceras rhynchostoma* (?) Clarke (1899) at approximately 23 cm diameter, shown at approximately x0.4 from Locality 4.