CASTEROLIMULUS: A NEW LATE CRETACEOUS GENERIC LINK IN LIMULID LINEAGE

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ABSTRACT

An olive gray siltstone near the top of the Fox Hills Formation (Maestrichtian) of North Dakota, has yielded a well-preserved prosoma of a new limulid merostome arthropod. The new genus *Casterolimulus* is interpreted as an advanced Mesozoic representative of the main Tethyan limulid lineage leading to modern genera of the Tachypleinae. Although the limulid was found in strata containing abundant floral remains, known stratigraphic relationships indicate burial in an estuarine environment far from shore. The fundamental marine nature of limulids should be honored rather more than their occurrence with detrital plant remains.

INTRODUCTION

A considerable knowledge of the occurrence of fossil limulids based on ichnology has accumulated due, in no small part, to the work of Caster (1938, 1939, 1940, 1941, 1944, 1957). Yet the only known record of a limulid body fossil from North American Mesozoic strata is *Limulus coffini* Reeside and Harris (1952) from the Pierre Shale of Colorado. Thus a well-preserved specimen of a limulid xiphosuran from an unnamed member of the Fox Hills Formation (Maestrichtian) in North Dakota (Text-figure 1) is described herein even though it is known only from the prosoma. We place this specimen in a new genus, *Casterolimulus,* named in honor of Kenneth E. Caster of the University of Cincinnati.

During the past decade, the Late Cretaceous Fox Hills Formation in North Dakota has been undergoing thorough paleontologic and stratigraphic scrutiny (Feldmann, 1964, 1966, 1967, 1968, 1972; Holland and Feldmann, 1967; Artzner, 1973; Erickson, 1973, 1974; Bailey and Erickson, 1973; Chayes and Erickson, 1973). The formation represents a complex of marginal marine facies which records the waning regressive fluctuations of the late Maestrichtian seaway in the Williston Basin. It was during further detailed stratigraphic and sedimentologic studies conducted by Erickson and his students (Klett and Erickson, 1974) that the discovery here reported was made. Field relationships of Fox Hills lithofacies resulting from these studies are illustrated schematically in Text-figure 2.

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA Siebold and Stannius
Subphylum CHELICERATA Heymons
Class MEROSTOMATA Dana
Subclass XIPHOSURA Latreille
Order XIPHOSURIDA Latreille
Suborder LIMULINA Richter and Richter

Superfamily **LIMULACEA** Zittel

Family **LIMULIDAE** Zittel

Subfamily **TACHYPLEINAE** Pocock

Genus **CASTEROLIMULUS** Holland, Erickson, and O'Brien, n. gen.

Type species: *Casterolimulus kletti* Holland, Erickson, and O'Brien, n. sp.

Generic diagnosis. — Prosoma low, gently vaulted, of medium size; well-developed doublure parallel-sided through most of its arc, widening rapidly past a position anterior to the eyes. Ophthalmic ridges low but well developed, waning in strength forward from the eyes, arcing toward the median crest of the cardiac lobe but not joining it anteriorly. Axial furrows deep, angled obliquely toward the anterior end of the median crest from their origin on the posterior margin of the prosoma. Axis possessing a well-defined ridge lacking spines or protuberances. Margins of genal spines subparallel to central axis and becoming laterally more oblique toward their tips. Ocelli not defined. Opisthosoma, telson, and appendages unknown.

Etymology. — The new genus is named in honor of Kenneth E. Caster, student of the Xiphosura.

Discussion. — The new genus is a conservative limulid and combines characteristics of several fossil and extant genera, in a manner that, from published descriptions, appears to be common to none previously known. The axial furrows are distinct and converging. The ophthalmic ridges extend well toward the anterior of the prosoma and curve toward the axis though they do not meet there. In addition, the genal spines are gently but definitely directed laterally. These are traits which Størmer (1952, p. 638; 1955, p. P22) assigned to the Mesolimulidae. Yet Riek and Gill (1971, p. 207) pointed out

that there are indications that the ophthalmic ridges of *Limulitella* Størmer, placed in the Mesolimulidae by Størmer, meet in front of the cardiac lobe; this is a characteristic of the Paleolimulidae, so they transferred *Limulitella* to the Paleolimulidae. They also described *Victalimulus,* a genus from the Lower Cretaceous of Australia, as intermediate in some characters between *Mesolimulus* and modern limulids. Based on this and their judgment that the characters ascribed to the Mesolimulidae are quantitative and not qualitative they denuded Størmer's Mesolimulidae by assignment of *Psammolimulus* Lange and *Mesolimulus* Størmer to the Limulidae. Størmer (written communication, 1973) has tended to agree with this position.

Paleolimulids are characterized by a distinctly annulated opisthosoma on which the ultimate segment is moveable, in addition to the meeting of the ophthalmic ridges anteriorly. Because our specimen lacks the opisthosoma, *Casterolimulus* is assigned to the Limulidae solely on prosomal characters. The anteriorly convergent axial furrows and the low arch of the prosoma suggest that *Casterolimulus* belongs to the subfamily Tachypleinae rather than the highly vaulted Limulinae.

The convergence of the axial furrows of *Casterolimulus* anteriorly toward the median crest or ridge is reminiscent of the Jurassic *Mesolimulus* and Early Cretaceous *Victalimulus* and indicative of relationship with the Holocene *Tachypleus* Leach. However, differences in the genera are definite. *Casterolimulus* lacks the narrow cardiac lobe and sharp, spine-bearing median keel of *Victalimulus* and has the genal angles more laterally directed than in *Mesolimulus* and slightly more so than in *Victalimulus*. *Casterolimulus* is also larger than Riek and Gill's specimen of *Victalimulus* which they regarded as adult. The anterior convergence of the axial furrows and ophthalmic ridges, lesser backward prolongation of the genal spines, and lesser arch of *Casterolimulus* readily separate it from *Limulus* Müller.

Casterolimulus kletti Holland, Erickson, and O'Brien, n. sp.
Pl. 1, 2; Text-fig. 3

Description. — Having the characters ascribed to the genus; additionally, the broad, smooth, median crest of the cardiac lobe is maintained for two-thirds the length of the prosoma and becomes

ill-defined where the axial furrows approach it. The eyes are low and lunate; the posterior of the prosoma is marked by a slightly raised border.

Etymology. — Following well-known, Casterian, pedagogical tactics (described by Caster and Macke, 1952, p. 754) the writers persuaded Mark C. Klett, finder of the specimen, to surrender it. The specific name attests to Mr. Klett's efforts and our appreciation of his diligence.

Dimensions of holotype. — The following measurements were taken from the internal mold of the prosoma:

Length at axis	5.2 cm
Width from tip-to-tip of genal spines (calculated as twice the half-width):	10.6 cm
Distance between ophthalmic ridges posterior margin:	5.0 cm
Distance between axial furrows at posterior margin:	2.2 cm
Minimum length of genal spine:	1.4 cm

Types. — Internal and external molds of the holotype are stored at the U.S. National Museum where they carry catalogue number 206801. Plastotypes of the external mold are housed in the paleontological collections of the Department of Geology and Geography, St. Lawrence University, Canton, New York (SLU 500), and in the paleontological collections of the Geology Department at the University of North Dakota in Grand Forks (UND 13,795).

Contrary to frequent patterns of limulid preservation in which the remains have been compressed by sediment loading so that characters of dorsum and venter appear superimposed in a single plane, out specimen is little compressed and the prosoma has a marked thickness.

One half of the specimen is a mold of the exterior of the prosoma (Pl. 2). The other half, which gives the prosoma in positive relief, is a mold of the interior of the dorsal carapace; when collected this exfoliated, in all but the cardiophthalmic region, revealed a mold of the exterior of the doublure and part of the wrinkled contiguous ventral membrane. (Pl. 1, fig. 2). These very fragile exfoliations were saved (shown restored to position in Pl. 1, fig. 1) but have not been permanently re-assembled because they are largely a mold of the interior of the doublure. Thus our specimen consists of the

mold of all four prosomal surfaces. The left genal spine separated along a joint plane in the rock and was not found during excavation.

As preserved, the prosoma is gently vaulted. Although there are some depressed regions and slight wrinkling on the dorsal side, the arch of the prosoma seems to be much as it was in life. Preservation at the perimeter of the prosoma indicates that there was little space between the mold surfaces. This and the slight wrinkling indicates that the cuticle was thin, delicate, and flexible compared with that of modern limulids. This flexibility is easily attained by many living marine Crustacea by withdrawing calcium from their sclerotized exoskeleton prior to ecdysis. Although we do not know of any analogous process in living Xiphosura, we see no reason why some skeletal softening, at least in the ventral region, should not occur. The cephalothorax seems to have been in this pliable state when filled and encased in sediment in such a way that crushing was largely avoided.

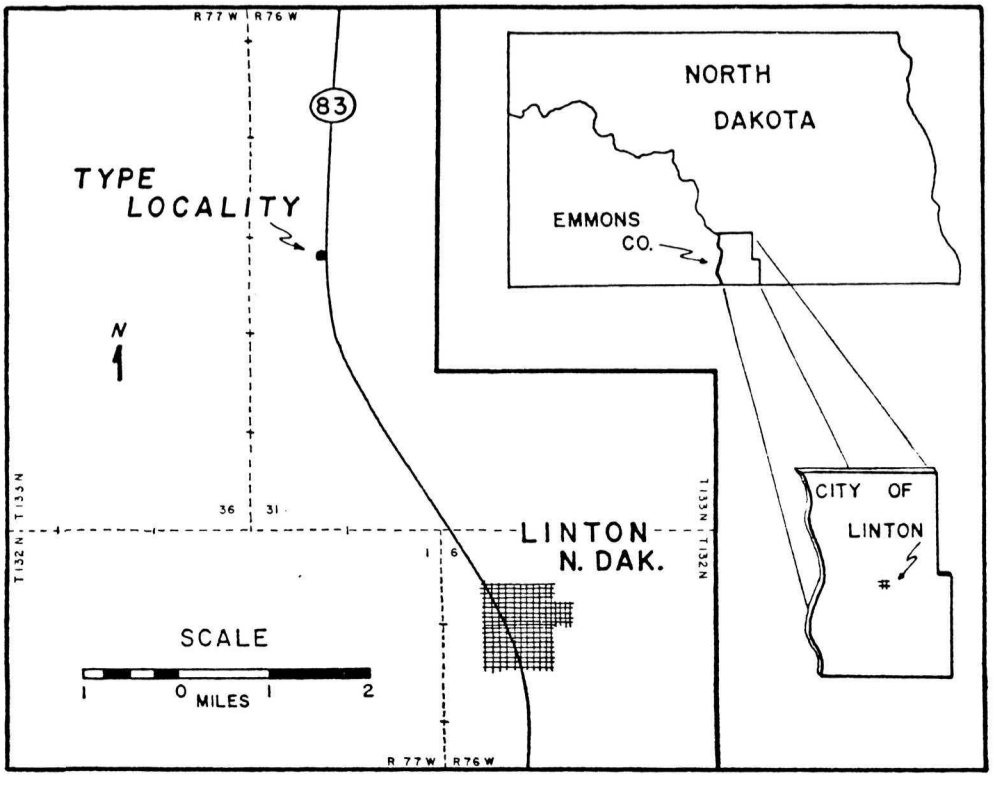
It is also possible that we have the unhardened prosoma of a newly molted individual which died of unknown causes. It might well have been dismembered by scavengers; if this occurred, they left no trace, and we feel the specimen is the disarticulated result of normal ecdysis.

Type locality. — The specimen was collected from a roadcut on the west side of North Dakota Highway 83 about 7 kilometers north of Linton; SE¼, NE¼, NE¼, sec. 19, T. 133 N., R. 76 W., Emmons County, North Dakota (Text-fig. 1).

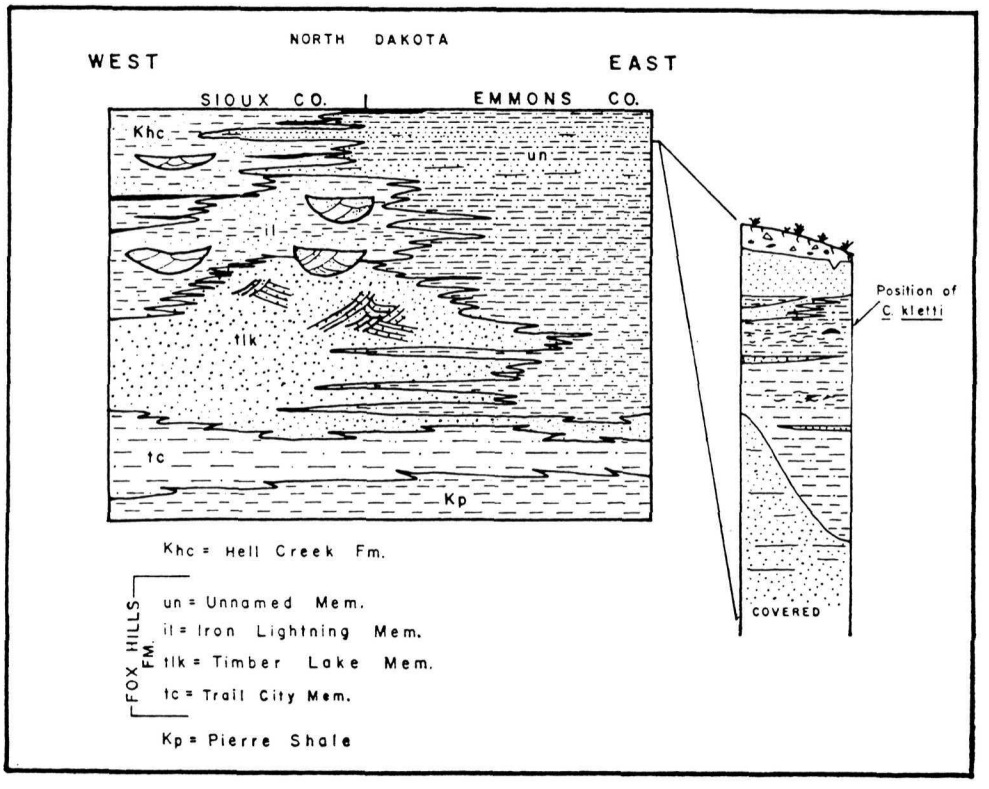
Lithologic relationships in the roadcut are intricate and difficult to determine due to vegetational overgrowth and slope creep. The new limulid was excavated from a moderate olive brown (5Y 4/4, wet) to light olive gray (5Y 6/2, dry) siltstone which apparently fills a channel cut in an olive gray, fine-grained sandstone of unknown thickness. Upward the siltstone grades abruptly into another fine-grained sandstone truncated by weathering and by glacial erosion at the top of the roadcut. This channel in an unnamed member of the Fox Hills Formation occurs within 10 meters of the top of the formation.

The siltstone channel contains plant material; this fact led Fisher (1952) to suggest that the siltstone was the basal unit of the overlying Hell Creek Formation. But it is not. The manner of

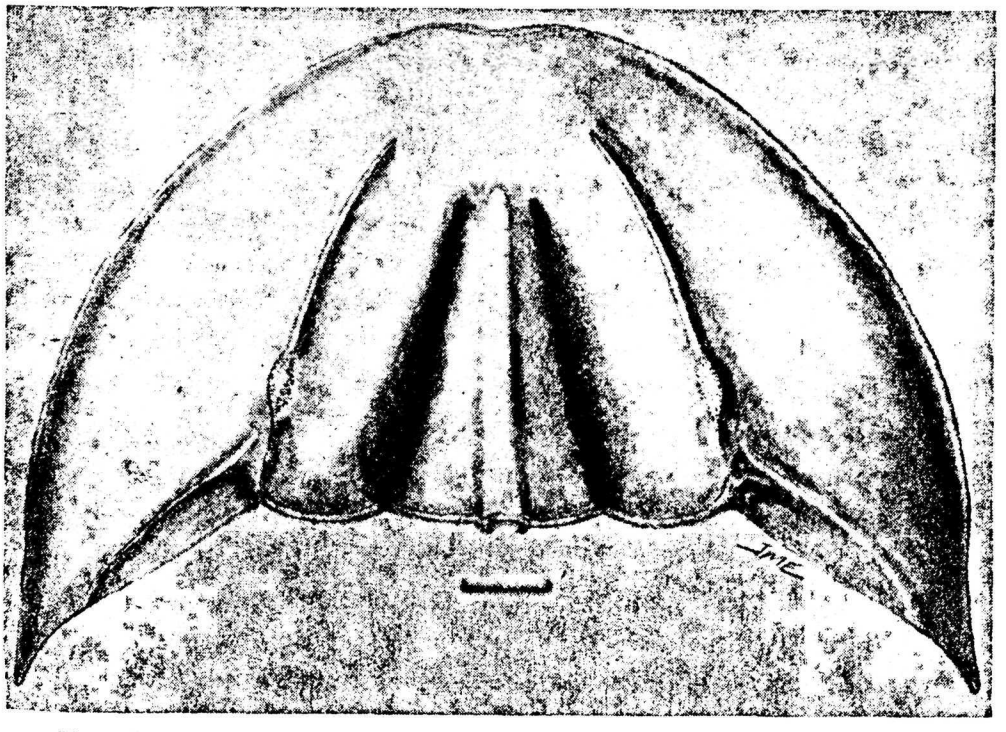
occurrence and preservation of the plants indicates that they were wafted to the depositional site by gentle currents but under conditions of rapid silt deposition relatively far from the estuarine shore. The channel is well within the unnamed member which is marine at its base and is overlain by the widespread Linton Member of the Fox Hills (Klett and Erickson, 1974, and in press) that is responsible for the butte caps in the vicinity. The fine-grained sandstone lithofacies of the unnamed member intertongues with units in both the Fox Hills Formation and Hell Creek Formation to the west and this makes location of the contact between the formations difficult where visible sections are short and incomplete. We are defining the contact at the lowest indications of truly terrestrial or fresh-water depositional facies — for example, paleo-soil zones, presence of abundant lignite or presence of non-transported fresh-water fauna. We do not regard the presence of plant fossils in the siltstone associated with the limulid as diagnostic of the Hell Creek



Text-figure 1. — Location of the type locality of *Casterolimulus kletti,* n. gen., n. sp., Fox Hills Formation, Upper Cretaceous.



Text-figure 2. — Generalized stratigraphic relationships of unnamed member of the Fox Hills Formation (Upper Cretaceous) in North Dakota, which has yielded *Casterolimulus kletti,* n. gen., n. sp. Diagrammatic stratigraphic column at the type locality (see Text-figure 1) of *C. kletti* indicates the approximate position of occurrence of the holotype.



Text-figure 3. — Reconstruction of prosoma of *Casterolimulus kletti,* n. gen., n. sp., from the Fox Hills Formation, Upper Maestrichtian, of North Dakota. Bar is 1 cm long.

for plant remains are common throughout much of the Fox Hills sequence; this is analogous to a situation which Caster (1938, p. 51) pointed out with regard to depositional environments of *"Paramphibius"* as follows:

> Plant remains occur everywhere in the Upper Devonian of the [Penn-York] embayment and, in the absence of a soil zone, cannot by themselves be used to judge conditions of sedimentation.

The stratigraphy has been diagrammed as well as is currently practicable in Text-figure 2. Further details are now in preparation and will be the subject of later publication.

Geologic age. — Maestrichtian, Late Cretaceous.

LIMULID PHYLOGENY

Conservatism in limulid form through time (Størmer, 1944, p. 73) combined with a sparse fossil record makes phylogenetic reconstruction difficult. The rare, discrete glimpses we get of this lineage indicate that it is, indeed, a modest, conservative one in which major morphologic modification is the exception. Størmer (1952, pp. 632, 637) outlined certain trends in general phylogenetic development of the dorsal skeleton of limulaceans: gradual increase in size, gradual reduction in depth of the axial furrows, backward extension and prolongation of the genal angles, increasing sharpness of an axial keel, and backward migration of the movable lateral spines of the abdomen.

Extant limulid genera are three in number: *Limulus* Müller, *Tachypleus* Leach, and *Carcinoscorpius* Pocock. *Limulus* is the limulid inhabitant of the Atlantic Ocean and Gulf of Mexico today; the other genera are southwestern Pacific Ocean forms. The Pacific forms belong to the Tachypleinae Pocock, whereas *Limulus* stands by itself in a monogeneric subfamily, the Limulinae Zittel. Most of the Mesozoic occurrences of limulids are in rocks bordering the Tethys seaway or near seas with access to Tethys. Because of similarities in their morphology *Mesolimulus, Victalimulus,* and *Casterolimulus* are probably all on the main line of limulid evolution leading to *Tachypleus.* Modern *Limulus* seems an isolate from this main lineage. In terms of the prosoma, it alone possesses axial furrows which are nearly parallel to the median crest rather than being uniformly converging toward the anterior as in all other Mesozoic and

Cenozoic forms. The cephalothorax is highly vaulted as well. It remains to explain this isolation and the inland North American occurrence of the tachyplein genus *Casterolimulus*.

Casterolimulus kletti was taken from rocks deposited at the end of the Late Cretaceous seaway in the Western Interior of the United States. Recent paleogeographic studies (Sohl, 1971; Jeletzky, 1971; Erickson, 1973; Kauffman, 1973) have documented biogeographic units in the Upper Cretaceous of the Western Interior. This seaway joined the Atlantic, *via* the Gulf Coast, with the northeast Pacific allowing mixing of their faunas on a large scale, perhaps for the last time. Although these dual faunal sources were present during the time of the Fox Hills deposition in North Dakota, the major source contributing to the molluscan fauna of North Dakota was Tethyan from the Gulf Coast (Erickson, 1973). For these reasons, we believe it likely that *Casterolimulus* immigrated to North Dakota *via* the Gulf Coast seaway rather than by a route from the Pacific. In like manner, *Limulus* probably originated in Tethyan (Gulf Coast) waters prior to the Campanian following the opening of the Atlantic (Dietz and Holden, 1970; Smith, Briden, and Drewry, 1973), and *Limulus coffini* Reeside and Harris appears in Upper Campanian marine strata in Colorado. Thus, only in the Cenozoic, as Tethys closed and the Atlantic opened further, did the Tachypleinae become confined to the Eurasian side of the Atlantic, and eventually to the Pacific. *Casterolimulus* was likely the last of the Tethyan Tachypleinae in North America.

LIMULID PALEOECOLOGY

We believe that the stratigraphic relationships indicate that the final resting place of *Casterolimulus kletti* was in the brackish-water or marine portion of a Late Cretaceous estuary. We think that Størmer (1955, p. P9) implied over-simplification of the limulid habitat when he said:

> Inasmuch as most older-than-Recent merostomes are nonmarine forms, fossil remains of these arthropods are chiefly confined to the less common fresh-water and brackish-water sediments and are not common.

Caster (1938) expressed apprehension regarding use of floral evidence in assigning a fresh-water origin to rocks containing limulids.

He further said (1957, p. 1026):

> There is equally sound logic in the assumption that the habits of the present day [xiphosuran] descendants are very ancient, and that a remarkable vitality made them tolerant of considerable freshening of the water, perhaps even making occasional or seasonal incursions into estuaries or coastal plain swamps feasible, while they nevertheless remained fundamentally marine.

It seems only an application of Occam's razor that in most cases limulid remains should be taken as an indication of marine deposition or of proximity to the marine environment. The consideration of so many species as "freshwater", in a conservative group with such persistence in the rock record and with such global distribution of similar forms, raises many phylogenetic questions. To such consideration logical answers are most readily provided (not by suggestions of numerous evolutionary experiments with the freshwater environments, which in turn would mean paleontologists are seeing remains of many endemic forms) by simply honoring the fact that these animals have always exhibited a wide tolerance of salinities and that they have always roamed the nearshore zones of the seas. Our view of limulid evolution would be far more punctuated and far more inconsistent, due to all the fresh-water "dead ends", were this not the case. Caster's (1957, p. 1025) repeated warning might well bear remembering in the future: "The Xiphosura, as well as merostomes in general, bespeak the sea."

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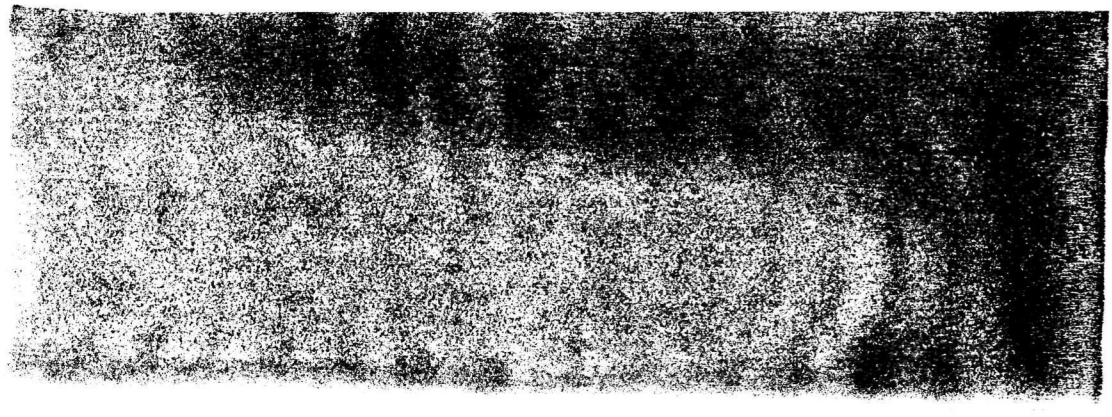
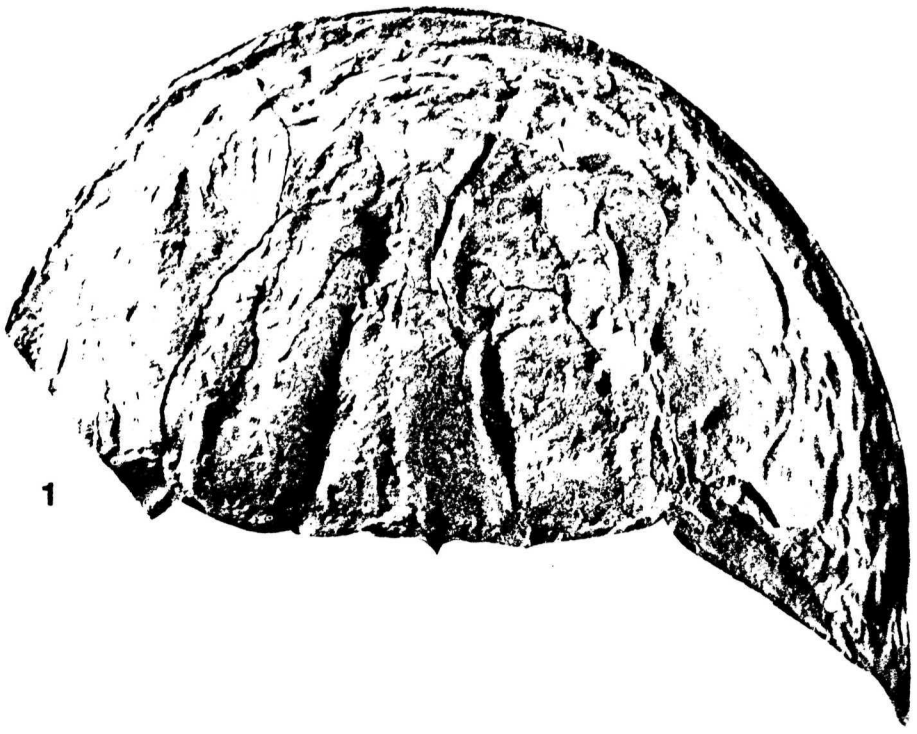
EXPLANATION OF PLATE 1

Both figures approximately natural size.

Figure

1-2. **Casterolimulus kletti** Holland, Erickson, and O'Brien, n. gen., n. sp.
Holotype (USNM 206801). 1. Mold of the interior of prosoma with exfoliated portions (note cracks) restored to their natural positions. Note, on impression of the slightly wrinkled carapace, the deep converging axial furrows, the moderately developed ophthalmic ridges, and the mold of the exterior of the right genal spine extending from below a broken exfoliation. 2. Exfoliated portions removed to expose the mold of the exterior of the doublure and part of the wrinkled ventral integument. The internal boundary of the doublure on the right side is difficult to trace because its impression blends with that of the thin, wrinkled, ventral membrane. Neither this wrinkling nor the plant fossil near the left limb of the doublure should be construed as the remains of an appendage.





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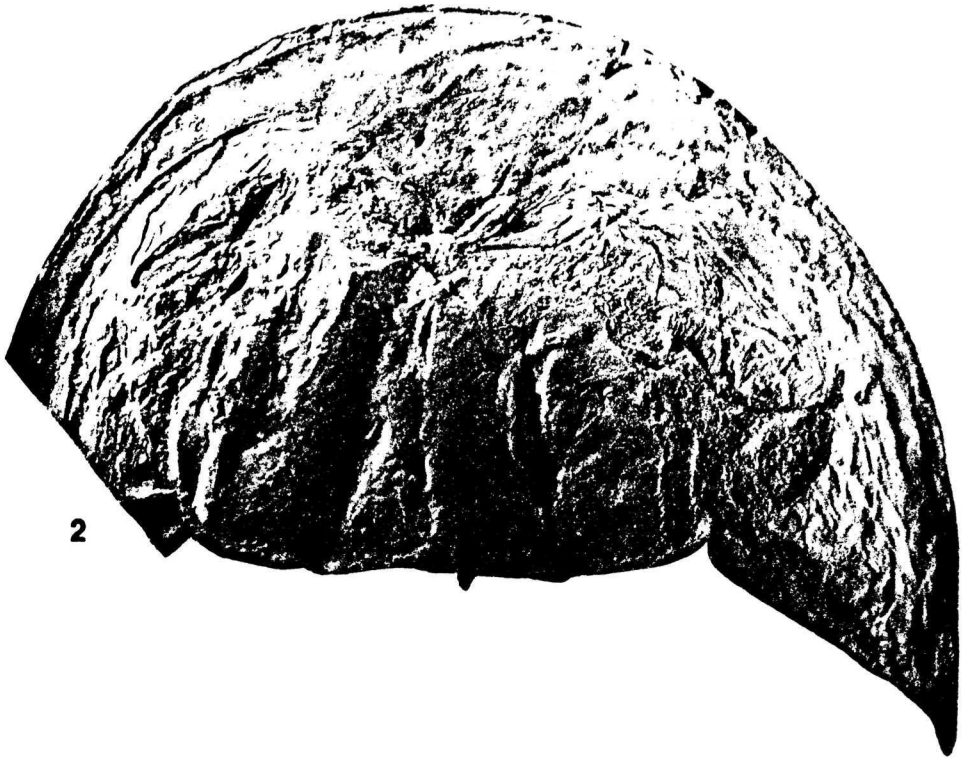

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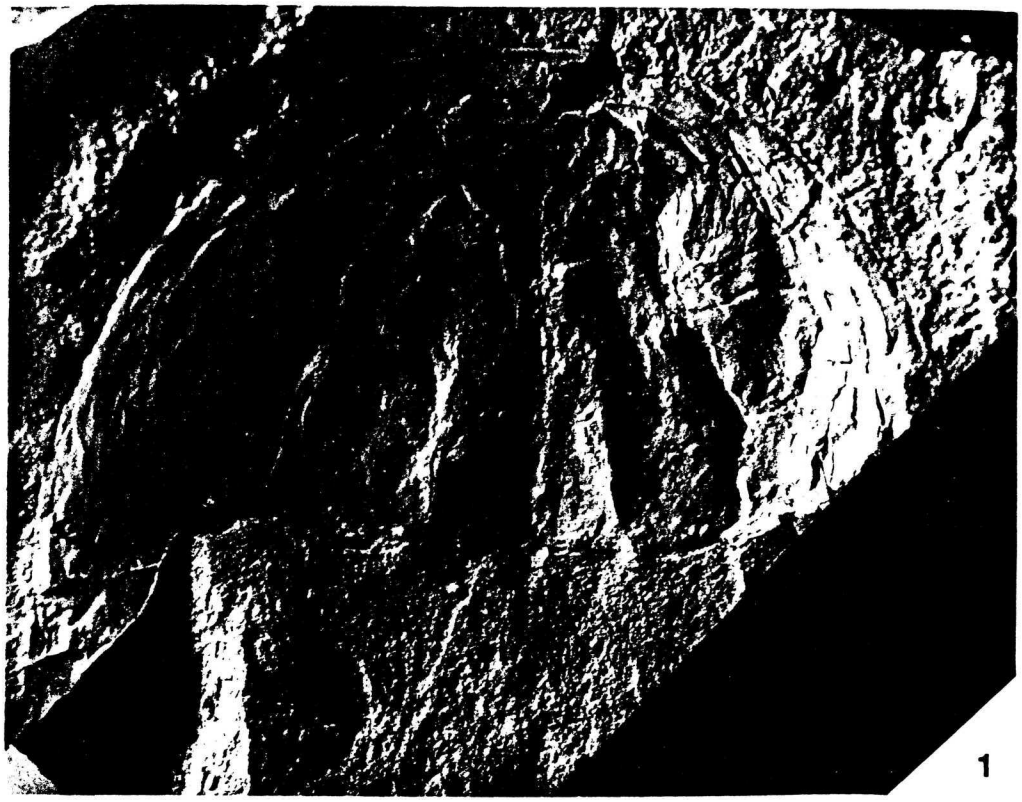

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EXPLANATION OF PLATE 2

Figure

1. **Casterolimulus kletti** Holland, Erickson, and O'Brien, n. gen., n. sp.
Holotype (USNM 206801). × 1. Mold of the exterior.