

THE SYNTHETOCERATINAE
(MAMMALIA, TYLOPODA,
PROTOCERATIDAE)

THOMAS HUDSON PATTON AND BERYL E. TAYLOR

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CONTENTS

| | |
|--|-----|
| INTRODUCTION | 123 |
| Acknowledgments | 123 |
| Abbreviations | 124 |
| STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE SYNTHETOCERATINAE | 125 |
| SYSTEMATICS | 130 |
| Order Artiodactyla Owen, 1848 | 130 |
| Suborder Tylopoda Illiger, 1811 | 130 |
| Family Protoceratidae Marsh, 1891 | 130 |
| Subfamily Synthetoceratinae Frick, 1937 | 130 |
| Genus <i>Syndyoceras</i> Barbour | 130 |
| <i>Syndyoceras cooki</i> Barbour | 131 |
| Genus <i>Prosynthetoceras</i> Frick | 138 |
| Subgenus <i>Prosynthetoceras</i> Frick, New Rank | 139 |
| <i>Prosynthetoceras (Prosynthetoceras) texanus</i> (Hay) | 140 |
| <i>Prosynthetoceras (Prosynthetoceras) francisi</i> Frick | 148 |
| Subgenus <i>Lambdoceras</i> Stirton, New Rank | 167 |
| <i>Prosynthetoceras (Lambdoceras) hessei</i> Stirton | 168 |
| <i>Prosynthetoceras (Lambdoceras) trinitiensis</i> , New Species | 172 |
| <i>Prosynthetoceras (Lambdoceras) siouxensis</i> Frick | 189 |
| cf. <i>Prosynthetoceras (Lambdoceras) siouxensis</i> | 192 |
| Genus <i>Synthetoceras</i> Stirton | 192 |
| <i>Synthetoceras tricornatus</i> Stirton | 192 |
| ZOOGEOGRAPHY | 207 |
| EVOLUTION AND PHYLOGENY | 209 |
| SUMMARY | 216 |
| REFERENCES | 216 |

INTRODUCTION

AMONG THE MANY and richly varied horned ruminants known from the great ungulate radiation of the North American middle and late Tertiary, none was so spectacularly endowed as the family Protoceratidae. Since Marsh's (1891) description of *Protoceras*, the uniquely horned members of this family have elicited much curiosity and speculation among vertebrate paleontologists. The distinctive morphologic characters of this artiodactyl group pose many interesting questions related not only to the origin and evolution of their peculiar cranial armament, but also to the relationship of the Protoceratidae with other major artiodactyl groups. The protruding bony plates on the upper surface of the maxillaries, which unite in some species to form a common-trunked rostral horn, has no parallel among other horned ruminants. Although the protoceratids are characterized by development of postorbital horns as well, it is the presence of the curious maxillary armament that distinguishes them.

Frick (1937) provided the first review of this group and included in the family Protoceratidae, under a single division, Protoceratini,¹ three subfamilies: the Protoceratinae, the Syndyoceratinae, and the Synthetoceratinae. The Protoceratinae includes the earlier more primitive taxa that are more widely known, and less troublesome systematically; as revised by Frick (1937), the Protoceratinae was composed of Marsh's genera *Protoceras* and *Calops*, the genus *Pseudoprotoceras* Cook, and a new genus, *Paratoceras*. In this classification, however, Frick reduced *Calops* to a subgenus of *Protoceras*. *Heteromeryx* Matthew (1905) is also considered by us to be a member of the Protoceratinae; this subfamily will be treated in a subsequent report.

The more advanced protoceratids, beginning with *Syndyoceras* and culminating in *Synthetoceras*,

have been less well understood than those of the Protoceratinae. Frick (1937) placed in the Synthetoceratinae the genus, *Synthetoceras* Stirton and erected a new subgenus, *Prosynthetoceras*. The Syndyoceratinae included only *Syndyoceras* Barbour. In addition, a new genus, *Lambdoceras*, was published posthumously by R. A. Stirton (1967).

In the present paper, we shall treat only those taxa comprising Frick's Synthetoceratinae and Syndyoceratinae, which we have combined into a single subfamily, the Synthetoceratinae. Because it is the most widely distributed, has the greatest temporal range, and is the most varied of the protoceratid groups, we believe that its revision affords greater insight (rather hindsight) into the evolutionary history of the entire family than could be obtained by studying the earlier members first. Determination of the course and pattern of radiation among advanced members of the lineage gives greater direction and control to the search for phylogenetic continuity within the primitive stock. The subfamily Synthetoceratinae as here revised includes the following genera: *Syndyoceras* Barbour (1905b), *Prosynthetoceras* Frick (1937), and *Synthetoceras* Stirton (1932). We have reduced Stirton's genus *Lambdoceras* to the rank of subgenus within *Prosynthetoceras*.

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We are indebted to Dr. Bobb Schaeffer, Dr. Malcolm C. McKenna, Dr. Richard H. Tedford, Messrs. Morris F. Skinner and Ted Galusha for critically reading the manuscript and giving valuable suggestions. Stimulating discussions with these gentlemen on the stratigraphy and correlation of the sedimentary Tertiary rocks of the Great Plains and Gulf Coastal Plain have aided in the presentation of the geologic data.

We acknowledge the profound contribution of the late Childs Frick for his direction of the field parties that collected most of the material described in the present report and for his systematizing of the group in 1937 in the subfamily, Synthetoceratinae.

For permission to examine and describe protoceratid material under their care, we thank

¹Frick's (1937) independent approach to taxonomic nomenclature recognized 10 interpolated categories called "Divisions," (not "groups," as attributed to him by Simpson, 1945, p. 267), which Frick regarded as being intermediate between family and subfamily. As employed by Simpson (1945) and prescribed by the International Code (1961), the ending, "...ini" is now restricted to designate a tribe, which is a family-group category between subfamily and genus.

Mr. J. Brzostoski of Redbank, New Jersey, Dr. Donald E. Savage of the University of California at Berkeley, Dr. C. B. Schultz of the University of Nebraska, Dr. Frank C. Whitmore, Jr., United States Geological Survey, and Dr. John A. Wilson, Department of Geology of the University of Texas.

We are grateful to all members of the former Frick Laboratory for their help and especially thank Mrs. Shirley M. Skinner and Mr. George Krochak of the American Museum of Natural History and Mrs. Françoise King of the Florida State Museum. The photographs are the work of Mr. Chester Tarka, the illustrations were prepared by Mr. Raymond J. Gooris, and the manuscript was typed by Mrs. Marian Galusha, all of the American Museum of Natural History.

ABBREVIATIONS

The following abbreviations of institutions and private collections are used throughout the text:

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History

F.A.M., Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History

H.C., Harold Cook Collection (now incorporated with the American Museum of Natural History Collection)

M.C.Z., Museum of Comparative Zoology, Harvard University

S.M.U., Southern Methodist University

T.A.M.U., Texas A. and M. University

U.C.M.P., University of California, Museum of Paleontology, Berkeley

U.F., University of Florida, Florida State Museum

U.N.S.M., University of Nebraska State Museum

U.S.N.M., United States National Museum, Smithsonian Institution

U.T.B.E.G., University of Texas, Bureau of Economic Geology

MEASUREMENTS AND STATISTICS

N, sample size

OR, observed range

\bar{X} , mean

S, standard deviation

V, coefficient of variation

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE SYNTHETOCERATINAE

THE SYNTHETOCERATINAE are known only from the Miocene and Pliocene of North America. They are distributed in the United States¹ in an arcuate pattern from South Dakota south through Texas, eastward through the Gulf Coastal Plain of Alabama and Florida and north into New Jersey.² Within this distribution, however, there are many long-distance gaps, as seen in figure 1. Such discontinuities, at least within the United States, are probably ascribable more to the vagaries of geologic processes involving the availability of outcrops and the preservation and recovery of fossils from them rather than to irregular dispersal and survival owing to ecological obstacles. We do not suggest that there was no isolation among these various populations, for the available evidence indicates that the distributional gaps (fig. 1) were considerably narrower than that dictated by known fossil records (see Zoogeography, p. 174).

Stratigraphically, the Synthetoceratinae range from the late Arikareean of the northern Great Plains to the early Hemphillian³ of the Gulf Coastal Plain. The earliest occurrence is represented by the genus *Syndyoceras* from the Harrison Formation, Sioux County, Nebraska, which is regarded by most workers as being of late Arikareean age. Additional specimens of *Syndyoceras* have been recovered subsequently by the Frick Laboratory of the American Museum of Natural History from the Upper Harrison of Peterson (1906); this is equivalent, in part, to

the Marsland Formation of Schultz (1938) in western Nebraska and eastern Wyoming. The genus *Prosynthetoceras* represents the earliest known protoceratid occurrence outside the upper Great Plains; it is found most abundantly in the Hemingfordian and Barstovian deposits of the Texas Coastal Plain, but occurs also in the medial Hemingfordian of north-central Florida, New Jersey, and in both the medial Hemingfordian and Barstovian of the Great Plains. The subgenus *P.* (*Prosynthetoceras*) is restricted to the Gulf and Atlantic Coastal Plains, whereas *P.* (*Lambdoceras*) is found in both the Texas Gulf Coast and the Great Plains. *Synthetoceras*, apparently the last surviving protoceratid, was first described from the Clarendonian of the Texas panhandle, but is now known from the Clarendonian of the Texas Gulf Coastal Plain, the questionable Hemphillian deposits of coastal Alabama, and the early Hemphillian of north-central Florida (fig. 1).

Because of the unusually fortunate stratigraphic configuration of the Texas Gulf Coastal Plain deposits and the abundance of synthetoceratine remains contained within them, it was this region that supplied the first real picture of the systematic relationships and evolutionary progression within the subfamily. The fossil-bearing beds in the Texas Coastal Plain treated herein occur in a vertically successive series of stratigraphic units of only slightly differing geologic age. These strata have yielded a correspondingly close succession of relatively distinct fossil vertebrate assemblages, ranging in age from medial Miocene to medial Pliocene. Quinn (1955) and Wilson (1956) considered these assemblages to be recognizable as distinct units over a large area of the Texas Coastal Plain and proposed biostratigraphic names for them. In his revision of the Miocene and Pliocene formations of this region, Wilson (1956) divided the section into three lithostratigraphic units: the Oakville, Fleming, and Goliad formations (in ascending order). Within these formations, he recognized several vertebrate "faunas" (=assemblage zones). From oldest to youngest these are the Garvin Gully, Burkeville, Cold Spring,

¹Wilson (1967) on the basis of a fragmentary tooth, tentatively recognized a protoceratid from Oaxaca, Mexico. It is presently uncertain whether this is a synthetoceratine. Dentition from the Panama Canal Zone, which was tentatively assigned to the Protoceratidae by Whitmore (1965, p. 181), is referable to the genus, *Paratoceras*.

²A *Prosynthetoceras* molar was identified by the writers in the private collection of J. Brzostowski of Redbank, New Jersey. The tooth is from the "Gravel", basal member of the Kirkwood Formation, Locality 326, Shark River, west of the Garden State Parkway, New Shrewsbury Township, Monmouth County, New Jersey.

³As this paper was going to press, a detached M² (U.F. No. 17500) of *Synthetoceras tricornatus* was found in the late Hemphillian Bone Valley deposits of Polk County, Florida. This marks the latest occurrence of the genus and species known to date.

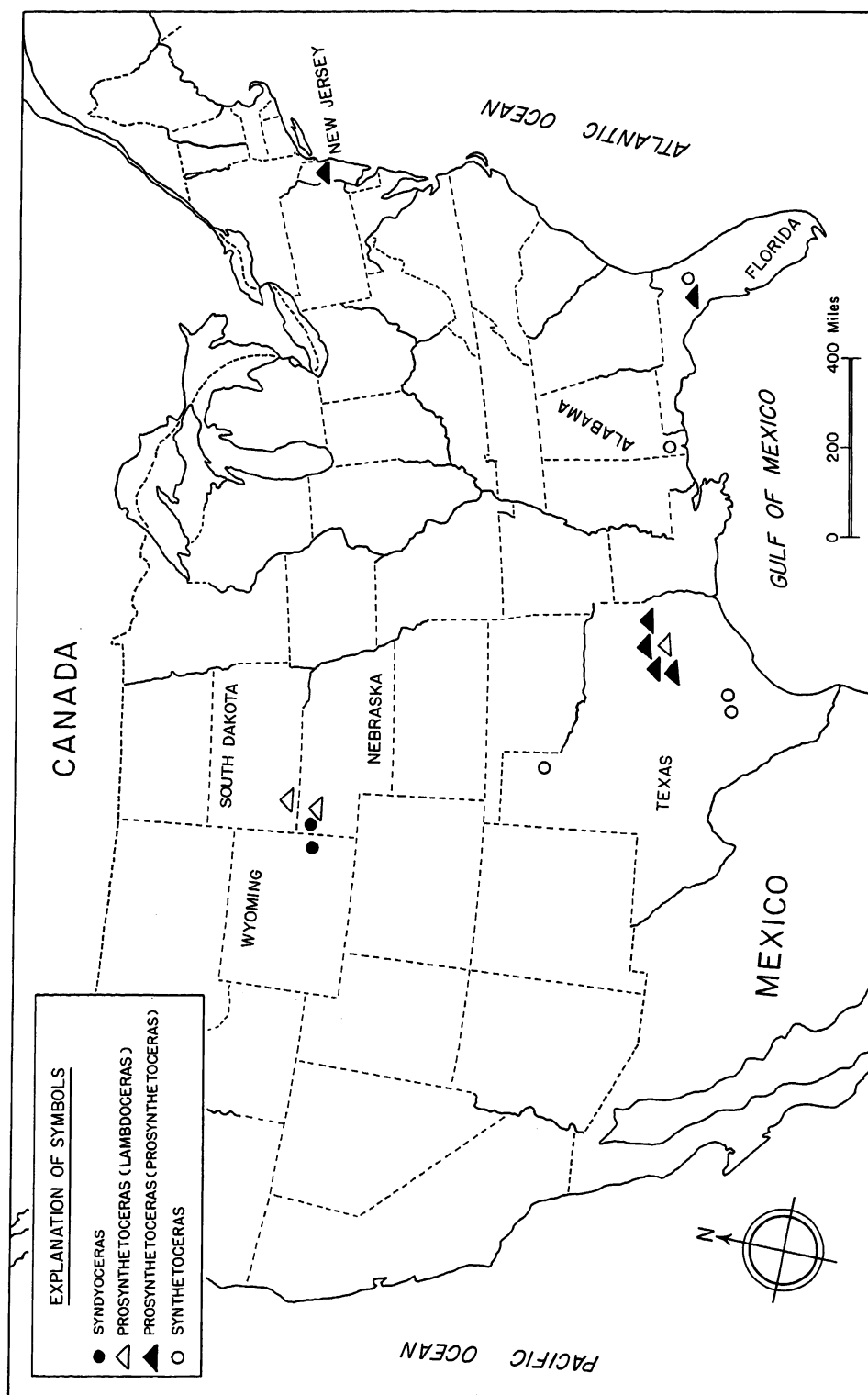


FIG. 1. Known geographic distribution of the Synthetoceratinae.

| STRATIGRAPHIC UNITS | | BIOSTRATIGRAPHIC UNITS | AGES |
|---------------------|---------------|---------------------------|---------------|
| GOLIAD FORMATION | Lapara Member | Lapara Creek Fauna | Clarendonian |
| FLEMING FORMATION | | No fossils | Barstovian |
| | | Cold Spring Fauna | |
| | | Trinity River Local Fauna | |
| | | Burkeville Fauna | Hemingfordian |
| OAKVILLE FORMATION | | Garvin Gully Fauna | |

FIG. 2. Stratigraphic framework of the Texas Coastal Plain fossil vertebrate faunas (after Wilson, 1956 and Patton, 1969b).

and Lapara Creek faunas. As a result of a study of the artiodactyls, including the synthetoceratines, from the Gulf Coast faunas, Patton (1969b) revised Wilson's age assignments for these units. Lithostratigraphic and biostratigraphic relationships of these units are graphically represented in figures 2 and 3. It should be mentioned that in addition to the above-mentioned faunas, another distinct vertebrate assemblage has been recovered by the Frick Laboratory from the Trinity River Quarry near Cold Spring, Texas. Although incompletely studied, this local fauna occupies a position intermediate between the established Burkeville and Cold Spring faunas (fig. 2). Some of the synthetoceratine material [*P. (Lambdoceras) trinitensis*, new species] from Trinity River Quarry

is described for the first time in the present paper. Another specimen, a remarkable skull of the poorly known genus *Paratoceras*, will be described by the authors in a subsequent paper.

Although Tertiary land vertebrate fossils have been found sporadically across the middle and eastern Gulf Coast, in that area only Florida has yielded a significant series of vertebrate assemblages (fig. 3). Unfortunately, in terms of classical stratigraphy, their occurrence in Florida is extremely haphazard in that they are preserved in discontinuous and widely distributed sinkhole deposits. Because the sediments are locally derived and reflect the influences of local climate, topography, and source lithology, there is no means of employing physical stratigraphy in tracing biostratigraphic "zones" or assemblages

| EPOCH | NORTH AMERICAN MAMMALIAN AGES | GREAT PLAINS | TEXAS COASTAL PLAIN and PANHANDLE | FLORIDA |
|----------|-------------------------------|---|-----------------------------------|--|
| PLIOCENE | Hemphillian | UPPER SNAKE CREEK | HEMPHILL | BONE VALLEY |
| | Clarendonian | MINNECHEDUZA BURGE | LABAHIA MISSION | Mc GEHEE |
| | | | CLARENDON LAPARA CREEK | |
| MIOCENE | Barstovian | DEVIL'S GULCH CROOKSTON BRIDGE PAWNEE BUTTES LOWER SNAKE CREEK | COLD SPRING TRINITY RIVER | ASHVILLE |
| | Hemingfordian | SHEEP CREEK BOX BUTTE RUNNINGWATER / BATESLAND MARSLAND | BURKEVILLE GARVIN GULLY | QUINCY - MIDWAY THOMAS FARM BUDA |
| | Arikarean | HARRISON MONROE CREEK GERING | | BROOKSVILLE |
| | | | | |

Fig. 3. Biostratigraphic correlation of the Panhandle and Gulf Coastal Plain faunas of Texas with those of Florida and the Great Plains. Formational names are used when no published faunal names are appropriate.

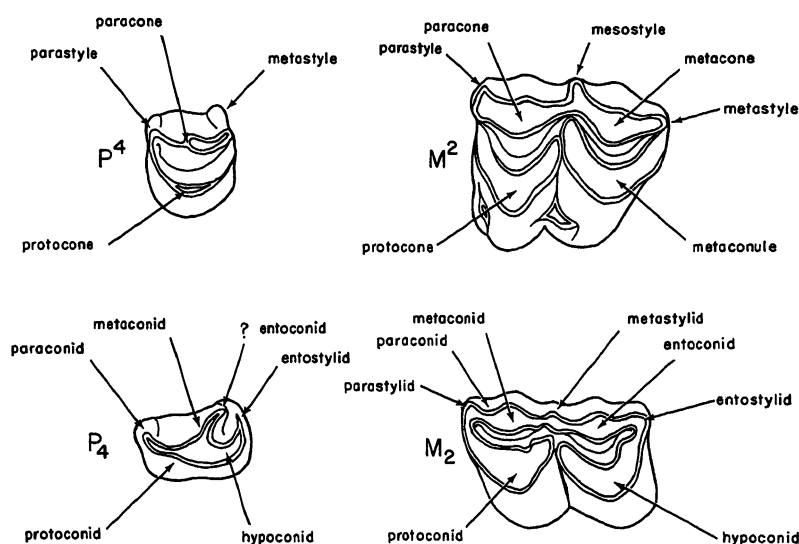


FIG. 4. Diagrammatic occlusal views of generalized synthetoceratine teeth illustrating cusp terminology used herein.

from one locality to another. In any attempt at correlation, therefore, reliance has to be placed at the outset on faunistic data. This approach is complicated, however, by the rather strong ecological bias one may encounter from one locality to another. The restricted areal extent of most of the fossil deposits favors the interment of animals representing only a single habitat and, as a consequence, makes it difficult to achieve a clear picture of the broader ecological associations of animals in one region at a given time. In bio-

stratigraphic and zoogeographic terms, this presents a dilemma wherein one must decide what associations may be attributable to ecological influences and which are the result of cumulative historical and/or evolutionary events. So far, these complications plus the need for additional geographic and stratigraphic representation have prevented formal recognition of assemblage zones in this part of the Coastal Plain.

SYSTEMATICS

ORDER *Artiodactyla* OWEN, 1848
SUBORDER *Tylopoda* ILLIGER, 1811
FAMILY *Protoceratidae* MARSH, 1891
SUBFAMILY *Synthetoceratinae* FRICK, 1937

INCLUDED GENERA: *Syndyoceras* Barbour, 1905b; *Synthetoceras* Stirton, 1932; and *Prosynthetoceras* Frick, 1937.

DISTRIBUTION: From late Arikareean to early Hemphillian of North America.

REVISED DIAGNOSIS: The *Synthetoceratinae* differ from the *Protoceratinae*, the other subfamily of the *Protoceratidae*, as follows: more elongate muzzle; relatively longer nasals; vertical fusion of the maxillary processes in male skulls to form a single shafted rostral horn that is strongly marked by surface canals; the presence of a small frontal protuberance on male skulls that arises anterior to the orbit and appears to involve the lacrimal bone; much larger orbital horns in the males that sweep outward and backward in a wide arc and are distinguished by a network of grooves and canals; the absence of parietal hornlike protuberances in the males; relatively smaller and especially less elongate premolars with the paraconid less anteriorly developed on P_2 and P_3 ; and taller-crowned molars.

GENUS *SYNDYOCERAS* BARBOUR

Table 15

Syndyoceras BARBOUR, 1905b, pp. 1-4

TYPE SPECIES: *Syndyoceras cooki* Barbour, 1905b.

INCLUDED SPECIES: Type species only.

KNOWN DISTRIBUTION: Late Arikareean and early Hemingfordian of western Nebraska and eastern Wyoming.

GENERIC DIAGNOSIS: *Syndyoceras* differs from other genera in the subfamily in that the broadly arched maxillaries are united to form a rostral horn which immediately branches into two diverging tines; the union between the two maxillary horns retains a symphyseal connection. Frontal horns extend out over the orbits and curve toward the midline of the skull, more like those of *Prosynthetoceras* (*Lambdoceras*) than the more backwardly sweeping horns of *Prosynthetoceras* (*Prosynthetoceras*). The dentition is lower crowned than that of later genera. The pre-

molars are generally larger than later forms; only those of *P. (L.) hessei* approach them in size. *Syndyoceras* differs from *Synthetoceras* in the retention of P^2 and P_{1-2} .

The limbs of *Syndyoceras* differ from those of *Prosynthetoceras* and *Synthetoceras* in tending to be shorter and heavier proportioned. Moreover, the scars and rugosities on metatarsals III and IV, which indicate the presence of vestigial laterals II and V, are more prominent and extend farther distally. In the type of *S. cooki* metatarsals III and IV show evidence indicating that the lateral metatarsals II and V extend at least two-thirds to three-fourths the length of the functional metapodials and possibly nearly their full length. In contrast vestigial laterals II and V of *Prosynthetoceras* and *Synthetoceras* are generally reduced to proximal splints. However, an occasional metatarsal III or IV of *P. (Lambdoceras) hessei* (U.C.M.P. No. 37471) and *P. (L.) trinitensis* (F.A.M. No. 34104) possesses features which suggest that vestigial laterals II and V may extend about one-half the length of the functional metatarsals.

DISCUSSION: The earliest occurring genus of the synthetoceratines, *Syndyoceras*, was also the first of this lineage to be described. It was collected by Harold Cook from the *Daemonelex* beds (=Harrison Formation) near Agate, Sioux County, Nebraska, and described in a paper by E. H. Barbour in 1905b.¹ The most striking characteristic of this new fossil was the unique arrangement and placement of the cranial horns. In addition to the two frontal horns, which extended out over the orbits and curved toward the midline, Barbour was especially astonished by the forked pair arising from the snout. Up to that time no artiodactyl, fossil or Recent, was known to possess such horns. Impressed with this remarkable animal, Barbour characterized *Syndyoceras* as "a primitive, 'four-horned antelope' with wide orbits, tapering snout, and a well-proportioned outline presaging a beast of grace and beauty equal to that of any living or extinct species." Barbour immediately recognized that the anterior, or rostral, horns were derived from two separate maxillary growths

¹A series of subsequent articles (Barbour, 1905a, 1906a, 1906b) briefly mention *Syndyoceras*.

which had united "and stand on a common trunk." He also noted its structural affinities to *Protoceras* and, although at first (1905a, p. 798) he regarded its relationship to that genus as remote, he placed it in the Protoceratidae, stating nonetheless that "it is doubtless entitled to a place in a new family." The following year (1906a, p. 288) he was apparently more convinced of this relationship and remarked on the actual derivation of the horns of *Syndyoceras* from those of *Protoceras*.

The genus is presently monospecific, being represented only by the type species, *Syndyoceras cooki*. Frick (1937, p. 607) erected a new subfamily for the genus *Syndyoceras*. Specimens upon which the new genus and species were originally based included an almost perfect skull and jaws (type: U.N.S.M. No. 1153), complete and articulated vertebral column, articulated pelvis, sacrum, hind limbs, several attached ribs and sternum, and a portion of one scapula. The only *Syndyoceras* material known other than the type includes newly available specimens from near Guernsey, Platte County, Wyoming, and from near Agate, Sioux County, Nebraska. The skull and skeleton of *Syndyoceras* never have been described adequately or illustrated. Because of its position near the beginning of synthetoceratine evolution, the skull and limbs of *Syndyoceras* are described and compared herein.

***Syndyoceras cooki* Barbour**

Figure 5; table 1

Syndyoceras cooki BARBOUR, 1905b, pp. 1-4.

TYPE¹: U.N.S.M. No. 1153, skull, mandible, and major portion of skeleton: femur, tibia, pes, 12 to 14 vertebrae in articulation, and other unprepared parts from the Harrison Formation, below the Agate Limestone, $\frac{1}{2}$ mile west of Agate, NE. $\frac{1}{4}$, sect. 12, T. 28 N., R. 56 W., in Sioux County, Nebraska. (For illustrations, see

Barbour, 1905a, pl. 1; Frick, 1937, fig. 65; present report fig. 5.)

DISTRIBUTION: Same as for the genus.

HYPODIGM: Roll Quarry (3 miles south of Guernsey) and prospects 3 miles southeast of Guernsey, Platte County, Wyoming, from rocks equivalent to the lower part of the Marsland Formation (Schultz, 1938) of western Nebraska (assigned to the Arikaree Formation, McGrew, 1963): F:A.M. No. 53511, partial skull with rostral horn; F:A.M. No. 53512, cranial saddle with orbital horns; F:A.M. No. 53510, partial skull.

Lower part of the Marsland Formation, 5 to 7 miles northeast of Agate, Sioux County, Nebraska: F:A.M. No. 53508, partial skull with P⁴-M³; F:A.M. No. 53509, left maxilla with P²-M³.

Lower part of the Marsland Formation, 4 miles south of Van Tassel, Sioux County, Nebraska: F:A.M. No. 53507, disintegrated partial skull with dentition, incomplete orbital horn and cervical vertebrae.

DIAGNOSIS: Only known species of the genus.

DESCRIPTION: Skull² and horns: The skull of *Syndyoceras* is characterized primarily by its cranial armament. A pair of large, recurved frontal horns extends over the orbits, and on the snout a maxillary pair joins above the nasal passage and diverges widely into two outwardly curving forks, or tines. The rear, or frontal, horns arise from the supraorbital region of the frontal bones and are situated mostly toward the dorso-posterior border of the orbits. Ventrally, each frontal horn is expanded to receive support from the postorbital bar. As in all synthetoceratines, the horns are highly sculptured by grooves and canals to protect ramifications of the blood vessels that supply and drain these structures. The horn tips are capped by small bulbous knobs. The front, or rostral, horns consist of two elongated, but rather flattened processes that arise from the dorsal border of the maxillae, join briefly over the open nasal passage, then continue as two separate and diverging tines. In the type, an aged individual, (U.N.S.M. No. 1153), no line of saturation is visible, but in F:A.M. No. 53511, which is broken between the forks, the presence of interspersed protuberances and

¹The type was found by the late Harold J. Cook and listed in the catalogue (archives of the Cook Collection now in the Department of Vertebrate Paleontology of the American Museum of Natural History) of his private collection as H.C. 106 and then presented to the University of Nebraska. Cook gave no stratigraphic data and to our knowledge this information has never been published. However, Cook showed Skinner and Macdonald the site and approximate stratigraphic horizon from which the types of *Syndyoceras cooki*, *Metacaenopus egregius*, *Nothocyon regulus*, *Temnocyon percussor*, and many other specimens were collected.

²For purposes of description, the synthetoceratine skulls and jaws will be oriented so that the long axis of the head is in a horizontal position.

depressions at the point of union indicates the retention of a symphyseal connection between the two maxillary processes. Moreover, the pattern of grooving along the horns does not join or cross this symphysis, further indicating the still independent development of the paired structures. In this particular configuration, *Syndyoceras* resembles *Protoceras* (that is, *P. nasutus*) more closely than it does *Prosynthetoceras*.

The nasal bones of *Syndyoceras* are retracted to a point above M_1 , much as in *Protoceras*. In later forms, as the nasal passage becomes covered by a united and increasingly large rostral horn, the retraction of the nasals becomes progressively less, and the posterior nasal opening diminishes in size. On the lateral surface of the maxilla, just above the infraorbital foramen, is a prominent knobby protuberance. Stirton (1932) believed that this structure served for origin of the levator nasolabialis muscle. We think, however, it more reasonable to assume it served as protection for the large infraorbital branch of the maxillary artery which, after its emergence from the infraorbital foramen, immediately divides into two main branches supplying the muzzle and the rostral horns. The superior (dorsal nasal) branch turns upward and runs along the dorsomedial edge of the maxilla and up the base of the horn where it diffuses into many channels. The inferior (lateral nasal) branch leads horizontally out of the infraorbital foramen to the lateral base of the horn and then continues up the side; distally, its channel remains larger, deeper, and less diffuse. In *Prosynthetoceras*, the lateral nasal is visibly forked, with the inferior branch leading over the anterior border of the maxilla into the anterior nasal passage. Although the course of this branch is not detectable in the available *Syndyoceras* specimens, it was undoubtedly present.

In contrast to the later genera, the slope of the maxilla from the base of the horn to the premaxilla is gentle; there is little distinction between the horn itself and the expanded lower portion of the maxilla. In later genera there is much greater inflection at the anterior base of the horn. At the anteroventral edge of the maxilla there is a deep alveolus for the large upper canine. The relatively small and edentulous premaxillae form two anterior "wings" which are splayed laterally to provide occlusion with the spatulate lower incisor row. The premaxillae were most probably equipped with a

horny pad such as that seen in modern ruminant artiodactyls. The premaxillary wings become more prominent in the later genera.

Other characters of the *Syndyoceras* skull¹ differ only in a minor way from those of *Prosynthetoceras* and are discussed on page 146.

UPPER DENTITION: I^0 , C^1 , P^2-4 , M^1-3 . Because of extreme wear on the teeth of the type skull and jaws of *S. cooki*, most of the tooth descriptions are based on the referred specimens.

The upper dentition of *Syndyoceras* consists of a large saber-like canine, three premolars, and three molars. As in *Protoceras*, no trace remains of the upper incisors. The upper canine is not nearly so large as that of *Protoceras*. Although no female synthetoceratines have been recovered with the muzzle region intact, we assume that, like the development of cranial horns, the growth of large upper canines is a male character, as it is in *Protoceras*.

P^1 , which persists as a small remnant in *Protoceras*, is lost in *Syndyoceras*. Only one specimen (F:A.M. No. 53509) of *Syndyoceras* allows adequate description of P^2 ; the tooth is two-rooted and very slender compared with P^3 . A prominent but low lingual cingulum extends the entire length of the tooth from the weak anterior flexus to the metastyle. P^3 is considerably wider and, except for F:A.M. No. 53509, in which P^3 and P^4 are very worn, is characterized by a thick paracone, a strong and recurved metastyle, and a smaller anterior flexus. A large cingulum buttresses the entire lingual margin of the tooth. P^4 is submolariform, the transverse diameter substantially exceeding anteroposterior length. This is accomplished by the great enlargement of the protocone. As in P^3 , there is a strong metastyle and a weaker anterior flexus. Lingually, small cingular cusps occur on either side of the protocone.

The upper molars of *Syndyoceras* are typically protoceratid in that they are relatively low crowned and possess very prominent labial styles and ribs and strong accessory cusps and cingula. The outer crests are marked by a large mesostyle and parastyle, and a somewhat smaller metastyle; the paracone and metacone are both conspicuously ribbed. On most molars there is a small cingulum on the anterior wall of the protocone. Perhaps the most characteristic feature of the *Syndyoceras* molar is the presence of a very

¹The skull and skeleton of the type of *Syndyoceras cooki* are on permanent display at the Nebraska State Museum.

large accessory cusp (intercolumnar tubercle) between the protocone and metaconule. This remains a distinctive synthetoceratine trait through the latest *Synthetoceras* species. With extreme wear, the space between the tubercle and the apex of the anterior (protocone) and posterior (metaconule) crescents becomes isolated to form a small lake or fossette.

LOWER DENTITION: I_{1-3} , C_1 , P_{1-4} , M_{1-3} . The only specimen of the lower jaw and teeth of *S. Cooki* belongs to the type (U.N.S.M. No. 1153). Because of the extreme wear on these teeth, all that can be said is that the dentition consists of three incisors, a closely appressed incisiform canine, and a caniniform P_1 separated by a diastema from P_2-P_4 and M_1-M_3 . Because the morphology of the upper dentition is closely similar to that of *P. (P.) texanus*, it is probably safe to assume the same for the lower dentition.

MANDIBLE: The mandible of *Syndyoceras* is more primitive than that of *Prosynthetoceras* (especially the later species) and *Synthetoceras*, especially in the shape of the ascending ramus. In the later genera, the ascending ramus is much slender and attenuated, virtually lacking an expanded masseteric fossa. *Syndyoceras*, on the other hand, retains a deeper, expanded masseteric region and a generally heavier horizontal ramus. The mandibular diastema of *Syndyoceras*, though considerably longer than that of *Protyloceras*, is not so lightly constructed as in *Prosynthetoceras* and *Synthetoceras*.

LIMBS¹: In addition to the skull and mandible, the known skeletal elements of the type of *Syndyoceras cooki* (U.N.S.M. No. 1153) include the vertebral column, pelvis, articulated rear limbs, ribs, sternum, and a partial scapula. The right articulated rear limb (except for the missing patella) was loaned to us for comparison with *Prosynthetoceras*. The description of the facets of the rear limb is limited in order to preserve the articulation of this exceptional exhibit material.

In *Syndyoceras cooki* the femur is short, stocky, and slightly heavier proportioned than that of *P. (P.) francisi*. Total length of the femur is 221.5 mm. From the ball of the femur to the distal extremity of the trochlea is 207.5 mm., a measurement that is bracketed by two referred

femora of *P. (P.) francisi*: F:A.M. No. 32058 is 192 mm. and F:A.M. No. 33075 214 mm. in length. The head of the femur is cylindrical, directed mesially and slightly upward. A depression for the ligamentum teres is situated slightly posterior to the midpoint of the ball of the femur. The neck is short and compressed anteroposteriorly, similar to that of *P. (P.) francisi*. Rising proximally above the level of the head, the greater trochanter is broad and massive with a slightly oblique anteroposterior alignment; its position is less oblique than in *Protyloceras* but more oblique than in *Prosynthetoceras* and *Synthetoceras*. Anteroposteriorly, the greater trochanter measures 28 mm., a measurement that is greater than the diameter of the shaft except at a point just above the trochlea. A large digital fossa extends behind the intertrochanteric ridge and undercuts the greater trochanter. The vertical extent of the digital fossa approximates that of *Prosynthetoceras*, but the transverse diameter of the fossa is proportionally less than in *Prosynthetoceras* and *Synthetoceras*. In the type of *S. cooki* the lesser trochanter is a prominent hooklike protuberance projecting posteromesially. The shaft of the femur is almost straight as in *P. (P.) francisi*, but it tends to be slightly heavier than in the latter. In shape the shaft tends to be cylindrical, except for a more flattened, rugose posterior surface. Moreover, the posterolateral part of the shaft above the lateral condyle lacks the prominent digital extensor fossa present in *Prosynthetoceras* and *Synthetoceras*. Instead, the surface is slightly elevated and rugose and resembles the opposite posteromesial ridge. The condyles of the distal trochlea project less posteriorly behind the plane of the shaft than in *Prosynthetoceras* and *Synthetoceras*. With the femur standing upright, the position of the lateral condyle is almost vertical, but the mesial condyle is more oblique relative to the shaft. The trochlear groove for the patella is wide and deep with the mesial crest, which borders the patellar groove, projecting more anteriorly than the lateral crest. In *Prosynthetoceras* and *Synthetoceras* the mesial crest also projects more anteriorly than the lateral crest and has a strong anteromesial knoblike protuberance that has not been observed in any other artiodactyl.

In the type of *S. cooki* (U.N.S.M. No. 1153) the total length of the tibia is 242 mm.; the tibia is slightly longer and proportionally heavier than that of *P. (P.) francisi* (F:A.M. No. 32058).

¹In order to facilitate and stabilize the limb descriptions and comparisons of the various taxa, all limbs, with the exception of the distal phalanx, are described from a vertical (standing) position.

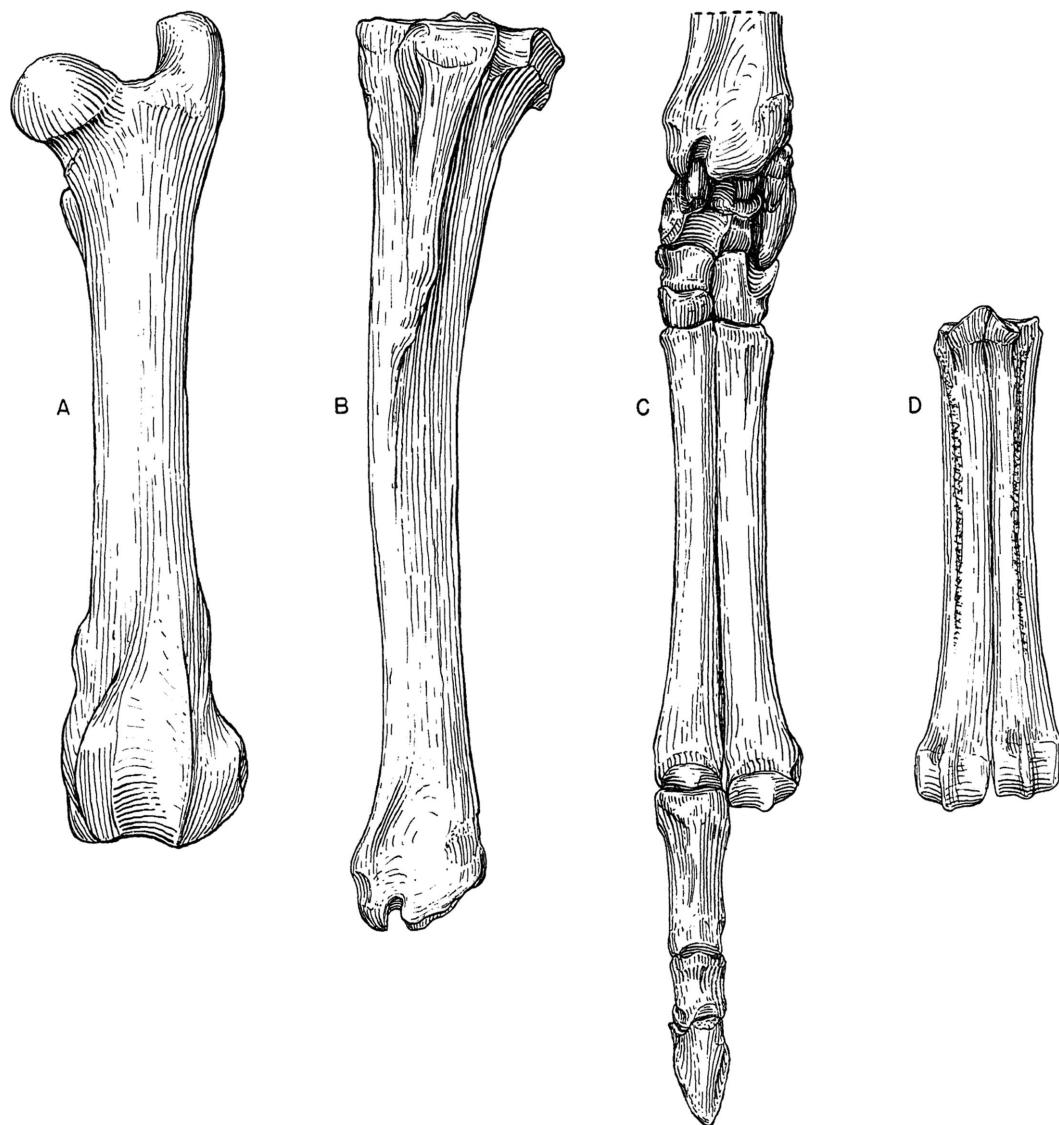


FIG. 5. *Syndyoceras cooki*. Type U.N.S.M. No. 1153, from the Harrison Formation, $\frac{1}{2}$ mile west of Agate, Sioux County, Nebraska. A. Right femur, anterior view. B. Right tibia, anterior view. C. Right articulated distal part of tibia to distal phalanx, anterior view. D. Right metatarsals III and IV, posterior view (note the rugose path for vestigial metatarsals II and V). All reversed. $\times \frac{1}{2}$.

As the tibia is mounted, only part of the proximal end can be seen, but the articular surface of the lateral condyle is larger than that of the mesial condyle. On the posterolateral edge of the lateral condyle, the presence of a fibular head is suggested, indicating a likeness in this respect to *Prosynthetoceras*. As in the latter, the anterior tubercle is moderately produced, and the anterior crest slopes gradually downward. A promi-

nent popliteal ridge marks the posteroproximal surface of the tibia. The sulcus muscularis forms a deep, somewhat semicircular notch and separates the tuberosity from the lateral condyle. Except for a slight lateral curve the shaft of the tibia is almost straight—resembling *Prosynthetoceras*. Distally, the posteromesial surface of the shaft is marked by a prominent groove extending about 50 mm. above the lower extremity. Al-

though the distal end of the tibia has been left in articulation with the astragalus, the astragalar notch is obviously deep as in *Prosynthetoceras* and the mesial malleolus is but slightly longer than the anteromedial distal process. The anterior border of the tibia slopes gradually upward from the anteromesial distal process and terminates in what appears to be a faint articular surface at the anterolateral border of the fibular facet. A prominent fibular fossa, which fades out about 13 mm. above the distal end of the tibia, is deeper than in *Prosynthetoceras*. A well-defined facet is present on the posterolateral border of the fibular fossa in contrast to a less defined articular-like surface on the anterolateral border. Except for a deeper fibular fossa, the distal end of the tibia of *S. cooki* has essentially the same characters as that of *P. (P.) francisi*.

In *S. cooki*, the articulated tarsus illustrates a primitiveness that is characteristic throughout the limbs of the synthetoceratines. The astragalus is 36 mm. in length on the mesial side, and the same measurement is 35 mm. for the partial skeleton (F:A.M. No. 32058) referred to *P. (P.) francisi*. A comparison between the astragalus of *S. cooki* and that of *P. (P.) francisi* shows that they are essentially alike; the lateral condyle in *S. cooki* is lower relative to the mesial condyle as in *P. (P.) francisi*. Viewed from an anterior upright position (fig. 5C), the distal part below the middle depression is also mesially deflected as in *Prosynthetoceras*. Moreover, the navicular fossa is moderately deep and the distal keel strong as in the *Prosynthetoceras*. The sustentacular facet is long and narrow as in *Prosynthetoceras*, and the vertical ridge on the mesial border of the sustentacular fossa is strong as in the latter. In common with all members of the Protoceratidae, the astragalus lacks the transverse process at the anterodistal end of the mesial condyle.

Total length of the calcaneum of the type of *S. cooki* is 80.5 mm. The lateral and mesial tuberosities of the tuber calcis are separated by a prominent posterior depression that fades onto the shaft about 19 mm. from the proximal end. Both the mesial and lateral sides of the shaft are slightly compressed. The facet for the fibular condyle is well developed with a gradual anteriorly sloping articular surface as in *Prosynthetoceras*, and unlike the sharply depressed notchlike feature in the camelids. Transversely, the sustentacular facet measures 15+ mm. and is proportionally narrower than that of *P. (P.) francisi*.

The mesial side of the sustentaculum is massively produced, a character shared with all other members of the Protoceratidae. The cuboid facet is broad and slightly concave.

The articulated tarsus of *S. cooki* resembles closely that of *P. (P.) francisi* and *S. tricornatus*. As in all Protoceratidae, the cuboid and the navicular are separate and the ecto-mesocuneiform is solidly fused. Although the entocuneiform is missing, the available space and articular facets on the navicular and the plantar process of metatarsal III indicate a large separate entocuneiform.

In the type of *S. cooki*, the metatarsals consist of four elements: metatarsals III and IV are large, separate, functional digits and the presence of vestigial metatarsals II and V is indicated. Metatarsal III is about 126 mm. in length from the ecto-mesocuneiform facet to the carina, approximating in size that of the skeleton (F:A.M. No. 32058) of *P. (P.) francisi*. No characters are observed that distinguish the metatarsal III of *S. cooki* from that of *P. (P.) francisi* except those that indicate a less vestigial metatarsal II. On the proximomesial surface of metatarsal III a deep depression is present, deeper than that of *P. (P.) francisi*, and more comparable with that of *P. (Lambdoceras) hessei* and *P. (L.) trinitiensis*. At the upper anterior border of the depression, a small facet is visible for vestigial metatarsal II. The depression on metatarsal III for vestigial metatarsal II is deep but fades out gradually on the shaft about 18 mm. below the proximal end. This depression is deeper and extends farther distally than in *P. (P.) francisi* but not so far distally as in the larger metatarsals of *P. (Lambdoceras) hessei* and *P. (L.) trinitiensis*. Continuing from the point of merger of the depression with the shaft, a narrow articular strip runs down the posteromesial part of metatarsal III for about two-thirds the length of the shaft. The surface of this strip is rugose and for the most part flattened, but in places slightly concave. Such a surface indicates the presence of a vestigial lateral metatarsal II, that was about two-thirds the length of metatarsal III, or even longer.

In *P. (P.) francisi* and *Synthetoceras tricornatus*, vestigial metatarsals II and V are confined to proximal splints. However, the vestigial metatarsals in *P. (Lambdoceras) hessei* and *P. (L.) trinitiensis* are believed to have been more distally extended. A narrow groove and rugosity sometimes appears below the deep proximal

depression on metatarsals III and IV of *P. (L.) hessei* and *P. (L.) trinitiensis*. Grooving and rugosity are highly variable and in some specimens absent, but they nevertheless indicate that the vestigial metatarsals were weak and less distally extended than in *S. cooki* but stronger than in *P. (P.) francisi* and *S. tricornatus*. Even in *Protoceras* metatarsals II and V appear to be restricted to about one-third the length of the functional metatarsals; there, a weak groove continues from the end of the vestigial lateral onto the distal one-third of the functional metatarsals but it lacks the rugosity that in recent equid metapodials indicates the actual presence of the vestigial lateral.

Metatarsal IV (about 128 mm. long) is essentially a counterpart of metatarsal III. It is nearly the size of the same bone of the partial skeleton (F.A.M. No. 32058) of *P. (P.) francisi*. No diagnostic characters are observed to distinguish the metatarsal IV of *S. cooki* from that of *P. (P.) francisi* except those characters that indicate a stronger lateral metatarsal V. Metatarsal IV has a prominent plantar process with a facet for the articulation of the cuboid. The proximolateral surface of metatarsal IV has a depression for the head of metatarsal V; the anteroproximal surface of this depression has a small facet for the attachment of the lateral metapodial. The depression for the proximal end of metatarsal V is similar to that on metatarsal III except that it tends to be shallower but longer anteroposteriorly. It also extends slightly farther distally and fades out onto the shaft about 22 mm. below the proximal end. Beneath the point of merger of the depression and the shaft, a narrow, rugose, and, at some points, slightly concave strip continues distally on the posterolateral side of metatarsal IV for about three-fourths of its length. This rugose articular surface for vestigial metatarsal V is more pronounced and slightly longer than that described for metatarsal III. Removal of the articulated proximal phalanx from the fourth metatarsal shows that the distal end of the metatarsal is similar to that of *Prosynthetoceras*. Transversely, the distal articular surface of metatarsal IV measures 17 mm.; this is identical to the measurement of the same bone of the skeleton (F.A.M. No. 32058) of *P. (P.) francisi*. As in the last named, the carina on the metatarsal is prominent and extends onto the anterior articular surface of the trochlea. Furthermore, the articular surface of the lateral condyle of the

distal trochlea of right metatarsal IV is elevated above the level of the mesial condyle as in the other synthetoceratines and the cervids.

Therefore, the scars and rugosities on metatarsals III and IV in the type of *S. cooki* (U.N.S.M. No. 1153) indicate the presence of vestigial metatarsals II and V that extend at least from two-thirds to three-fourths the length of the functional metatarsals and possibly nearly their full length. In *S. cooki*, the vestigial lateral metatarsals II and V were longer than in *P. (Prosynthetoceras) francisi* and *Synthetoceras tricornatus* and even more distally extended than in the earlier occurring *Protoceras celer*.

The proximal phalanx of the fourth digit of the pes is 44 mm. in length. Proximally, the articular surface of the first rear phalanx is divided by a deep groove for the prominent carinal ridge of the metatarsal. The carinal groove is deep posteriorly but fades out near the anterior border of the facet; a tendency toward slightly greater prominence of the groove anteriorly is found in the later synthetoceratines. The proximolateral articular surface of the first phalanx of the fourth metatarsal is smaller but more elevated than that of the mesial side. On the posterior side, the proximal part is slightly concave with well-defined lateral and mesial ridges. The distal half of the posterior surface is convex with deep perforatus scars on each side above the distal facets. The distal facet of the first phalanx is narrow and divided by a prominent groove. The groove, however, is less prominent, and the articular surface less extended dorsally than in the cervids.

Anteroposteriorly, the median phalanges of the third and fourth digits of the pes measure 22 mm. As in *Prosynthetoceras* the median phalanx is short relative to the length of the proximal phalanx. In appearance the median phalanx is short and stubby with the anteroposterior diameter of the proximal end exceeding the transverse width. The proximal articular surface is shallow, slightly concave, and divided by a faint middle ridge. The facets of the pastern joint on each side of the middle ridge are of almost equal size. Two weak proximal plantar processes are much less prominent than those of *P. (L.) hessei*. Distally, the facet of the median phalanx is distinguished from that of *Prosynthetoceras* by the anterior extension of the articular surface and a shallower median groove.

The outer volar length of the distal phalanx of

TABLE 1

SIZE RANGE AND MEAN (IN MILLIMETERS) OF THE LIMBS OF *Syndoceras*, *Prosynthetoceras* (*Prosynthetoceras*), *Prosynthetoceras* (*Lambdoceras*), AND *Synthetoceras* SPECIES

| | Humerus | | Radius | | Metacarpal III | | Femur | | Tibia | | Metatarsal III | |
|--|--------------------------|-----------------------|-----------------------|-----------------------|-------------------------|-----------------------|-----------------|------------------------|-----------------------|-------|----------------|-------|
| | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range |
| <i>S. cooki</i> Barbour | — | — | — | — | — | — | — | [1] ^a 222.0 | [1] 242.0 | — | [1] 126.0 | — |
| <i>P. (P.) francisi</i> Frick | [1] (165.0) ^b | — | [1] 185.0 | 185.0 [1] 111.5 | 111.5 [2] 192.0–214.5 | 203.2 [1] 237.0 | 237.0 [1] 125.5 | 125.5 | — | — | [1] 153.5 | — |
| <i>P. (L.) hessei</i> Stirton | — | — | — | [1] 130.0 | — | — | — | — | — | — | [1] 153.5 | — |
| <i>P. (L.) trinitensis</i> , new species | — | [3] 223.0–240.0 | 229.3 [3] 129.0–149.0 | 138.0 [4] 224.0–256.0 | 238.2 [3] 286.0–319.0 | 302.6 [6] 138.5–160.0 | 151.6 | — | — | — | — | — |
| <i>P. (L.) stouxiensis</i> Frick | — | — | — | — | — | — | — | [1] 303.0 | 303.0 [2] 143.5–149.5 | 146.5 | — | — |
| <i>S. tricornatus</i> Stirton | [2] 214.0–(225.0) | 219.5 [3] 244.0–253.0 | 249.0 [3] 133.5–138.0 | 136.1 [1] 272.0 | 272.0 [2] (283.0)–297.0 | 290.0 [3] 154.0–160.0 | 157.6 | — | — | — | — | — |

^aNumbers enclosed in brackets are the number of specimens measured.^bMeasurements enclosed in parentheses are estimated.

the pes is 30 mm. The facet of the coffin joint is deeply concave as in *Prosynthetoceras* but shallower than in the cervids. A faint median ridge divides the upper part of the facet. The facet of the coffin joint rotates mesially to form an approximate 45 degree angle to the volar plane.

GENUS *PROSYNTHETOCERAS* FRICK

Synthetoceras (*Prosynthetoceras*) FRICK, 1937, p. 602:

Prosynthetoceras: PATTON, 1967, pp. 37-38 (elevated to generic rank).

Lambdoceras STIRTON, 1967, p. 4.

TYPE SPECIES: *Prosynthetoceras francisi* Frick.

INCLUDED SPECIES: The type species and *P. texanus* (Hay, 1924), *P. hessei* (Stirton, 1967), *P. trinitensis*, new species, and *P. siouxensis* Frick, 1937.

KNOWN DISTRIBUTION: Medial Hemingfordian to approximately medial Barstovian in Nebraska, South Dakota, the Gulf Coastal Plain of Texas and Florida, and New Jersey.

DIAGNOSIS: *Prosynthetoceras* differs from *Syndyoceras* primarily in the development of a distinct, more elongate, and more anteriorly directed rostral horn shaft, in the lengthening of the maxillary and mandibular diastemata, in the reduction of premolars, and in the taller-crowned molars. Limbs of *Prosynthetoceras* differ from those of *Syndyoceras* in that they are slightly lighter proportioned, and metatarsals III and IV retain scars and rugosities that indicate vestigial metatarsals II and V are less distally extended than in *Syndyoceras* and limited to the proximal part of metatarsals III and IV.

Prosynthetoceras is separated from *Synthetoceras* on the basis of larger size, taller-crowned molars, loss of P_1 and P_2^2 , greater premolar complexity, longer diastemata, and greater length of rostral horn of the latter. Limbs of *Prosynthetoceras* differ from those of *Synthetoceras* in that they are smaller and lighter proportioned, the proximal half of the combined ulna and radius is less firmly coalesced, and metacarpals II and V are less reduced relative to metacarpals III and IV.

DISCUSSION: In his 1937 monograph, Frick (pp. 605-606) recognized two species of synthetoceratines from the Texas Gulf Coastal Plain, (?) *Synthetoceras rileyi* from Walker County (Garvin Gully Fauna) and *Synthetoceras* (*Prosynthetoceras*) *francisi* from San Jacinto County (Cold Spring Fauna). Frick (*op. cit.*) designated the latter species as the type of his new subgenus *Prosynthetoceras*, and separated it from *Syntheto-*

ceras on the basis of "smaller size, the smaller and shorter-crowned dentition and retained P_2^2 ." The concept of the latter taxon was at that time based entirely on the characters of the skull and horns collected from the Clarendon beds in the Texas Panhandle and described by Stirton in 1932 (and enlarged herein, p. 194).

Frick's concept of (?) *Synthetoceras rileyi* was founded on characters of a partial right mandible containing P_2-M_3 (F:A.M. No. 34181) and a partial left mandible with P_2 alveolus and P_3-M_3 (F:A.M. No. 34181a).¹ The questioned referral to *Synthetoceras* was predicated by lack of any specimens exhibiting characters of the subgenus *Prosynthetoceras*, as defined by Frick. Patton (1967, p. 38) later showed that a partial right maxilla discovered in the Texas A. and M. collection contains P_3-M_3 and the alveolus for P_2 and stated that (?) *Synthetoceras rileyi* Frick could then be confidently included in Frick's subgenus *Prosynthetoceras*. However, because he believed that in this phylogenetic lineage the retention or loss of P_2 is an important and useful taxonomic character most applicable at the generic level, he elevated *Prosynthetoceras* Frick to the rank of genus. Further, he (Patton, 1967, p. 38) stated that: "Examination of the types and/or casts of the Hay's (1924) *Dromomeryx texanus*, *Dromomeryx angustidens* and *Merycodus grandis* clearly demonstrates that these species are synonymous with Frick's *Prosynthetoceras rileyi*. The type dentitions of the two *Dromomeryx* species are inseparable from confidently identified *P. rileyi* specimens, whereas three horn fragments described by Hay (1924) as the type of *Merycodus grandis* correspond in size and morphology with that expected for the rostral horn of *P. rileyi* (Patton, 1966). Thus, *D. texanus* Hay, *D. angustidens* Hay, *M. grandis* Hay, and (?) *S. rileyi* Frick are synonymous under *Prosyntheto-*

¹Frick (1937, p. 605) listed the type as a "Right ramus with P_2-M_3 and left M_1-M_3 ." In examining the type material it was discovered that F:A.M. No. 34181 actually consisted of two partial mandibles, a right with P_2-M_3 and a left with P_2 alveolus (and roots) and P_3-M_3 . No left with only M_1-M_3 was found. A comparison with the illustration of the type (p. 648, fig. 66) reveals clearly that the right mandible with P_2-M_3 was the actual figured specimen. However, in keeping with Frick's format of preserving left views, the figure was reversed in press. In the present paper the holotype is designated as Frick's illustrated, but reversed, right mandible with P_2-M_3 (F:A.M. No. 34181). The left mandible with P_2 alveolus and P_3-M_3 is renumbered (F:A.M. No. 34181a) and is referred.

ceras, with *P. texanus* becoming the valid name for the species."

This conclusion is borne out by comparison of the partial horns with the associated skull of *P. texanus* (F:A.M. No. 53500) described on page 142 and illustrated in figure 6. A third species, *Prosynthetoceras siouxensis* from Sioux County, Nebraska, and a subspecies *P. siouxensis dawsonensis* from Dawes County, Nebraska, were also named by Frick (1937, p. 607). These forms have not been recognized in Gulf Coast faunas, but they do not bear on the taxonomy of the genus. *Prosynthetoceras siouxensis* was founded on characters of a partial left mandible which was originally referred to (?) *Cranioceras unicornis* by Matthew (1918). The type of *P. siouxensis* (A.M.N.H. No. 17344, fig. 27C) possesses alveoli for three incisors, an incisiform canine, and P_2 - M_3 . As mentioned above, Frick considered *Prosynthetoceras* to be separable from *Synthetoceras* partly on the basis of a retained P_2 . However, *P. siouxensis* is known only from a partial left ramus with P_2 - M_3 and a rostral horn. Frick apparently also considered the retention of P_2 as a character useful in separating the two forms, as shown by his placement of *P. siouxensis* in *Prosynthetoceras* and reflected in his generic key (Frick, 1937, p. 38). To *Prosynthetoceras francisi*, on the other hand, Frick (1937, p. 605) tentatively referred (mainly on the basis of size) a right ramus (F:A.M. No. 34180) seemingly lacking all trace of P_2 . A closer examination of this specimen, however, indicates that a single-rooted P_2 was once present, but was lost and the alveolus healed over. Another *P. francisi* specimen (U.T.B.E.G. No. 31243-5) reveals traces of a similar fate for P_2 . It is therefore possible to find adult members of the later-occurring species of *Prosynthetoceras* lacking P_2 . In view of its complete loss in the descendant of *P. francisi*, *S. tricornatus*, this is not unexpected. Other generic and specific characters are delineated below.

Lambdoceras hessei, a synthetoceratine described by Stirton (1967) from the Flint Hill Quarry local fauna (medial Hemingfordian) of South Dakota, is believed by the authors to belong more properly in the genus *Prosynthetoceras* and is herewith placed in synonymy with that genus, but is retained as a subgenus. We also propose and describe a new species, *P. (Lambdoceras) trinitiensis*, from the early Barstovian Trinity River Quarry in San Jacinto County, Texas.

On the basis of their morphology, the species

of *Prosynthetoceras* described herein fall into two distinct species groups: *P. texanus* and *P. francisi* on the one hand, and *P. hessei*, *P. trinitiensis*, and *P. siouxensis* on the other. We believe that those supraspecific traits that characterize each of the above groups reflect a natural phyletic relationship which is best expressed at the subgeneric level. Thus, we have employed two subgenera: *Prosynthetoceras* (*Prosynthetoceras*), which includes *P. (P.) texanus* and *P. (P.) francisi*, and *Prosynthetoceras* (*Lambdoceras*), which includes *P. (L.) hessei*, *P. (L.) trinitiensis*, and *P. (L.) siouxensis*. *P. (P.) texanus* occurs in the Hemingfordian Garvin Gully and Burkeville faunas of Texas and the Thomas Farm Quarry of Florida. *P. (L.) hessei* is known only from the medial Hemingfordian of South Dakota. *P. (L.) trinitiensis* and *P. (P.) francisi* have been recovered from the early to medial Barstovian deposits in Texas respectively, whereas *P. (L.) siouxensis* is so far restricted to the early Barstovian of Nebraska (fig. 3).

SUBGENUS PROSYNTHETOCERAS FRICK, NEW RANK

Table 15

Synthetoceras (*Prosynthetoceras*) FRICK, 1937, p. 602.

TYPE SPECIES: *P. (Prosynthetoceras) francisi* Frick, 1937.

INCLUDED SPECIES: Type species and *P. (Prosynthetoceras) texanus* (Hay, 1924).

KNOWN DISTRIBUTION: Medial Hemingfordian to approximately medial Barstovian of the Texas Gulf Coastal Plain and Florida.

DIAGNOSIS: The type subgenus is more progressive in most characters than *Prosynthetoceras* (*Lambdoceras*): skull and jaws more elongate and more lightly constructed; diastemata longer; frontal horns more triangular in cross section, almost directly out over the orbit in *P. (P.) texanus*, but becoming more backswept in *P. (P.) francisi*; rostral horn tending to have longer shaft with relatively longer fork; premolars more reduced, less wedge-shaped; P_2 becoming single rooted; presence of P_1 variable. Limbs of *P. (Prosynthetoceras)* differ from those of *P. (Lambdoceras)* in that they are smaller and lighter proportioned; the ulna tends to be more firmly attached to the radius with the entire distal half of the ulna and radius coossified; the median phalanx tends to be relatively longer; the posterolateral facet on the distal end of the tibia is more re-

duced, which results in a smaller articular surface for the malleolar, and the fibular fossa tends to be smaller; the calcaneal sustentaculum is less massively produced; and the depressions on the proximal ends of metatarsals III and IV for vestigial laterals II and V tend to be shallower and distally shorter.

DISCUSSION: The type subgenus of *Prosynthetoceras* is restricted to the Gulf Coastal Plain. Most of our knowledge of *P. (Prosynthetoceras)* derives from the study of successional populations comprising the Garvin Gully, Burkeville, and Cold Spring faunas of southeast Texas, although it is known also from Florida deposits. In an earlier treatment, Patton (1969b) recognized only two species in this region, *P. texanus* and *P. francisi*, which he regarded as the representatives of an essentially unbroken sequence leading to *Synthetoceras*. The little published information at the time he was working led him to regard the group as being virtually endemic to the Gulf Coastal Plain. *P. siouxensis* was based on a single partial jaw, so that not much could be said concerning its affinities to the southern populations. However, with the description of *Lambdoceras hessei* by Stirton (1967) and *P. trinitiensis* by the present authors, the interrelationships of the various *Prosynthetoceras* populations have become better understood.

The discovery of the larger and more primitive *P. trinitiensis* in deposits occurring in the stratigraphic interval between that occupied by *P. texanus* and that by *P. francisi* clouded the simple picture of the *P. texanus*-*S. tricornatus* progression. To account for *P. trinitiensis* without any indications of its (or of its relatives) presence in the otherwise relatively well-known Texas faunas and to bracket it in time was especially perplexing, in view of the lack of closely similar relatives elsewhere. Recognition of *Lambdoceras* by Stirton (1967), however, served in great measure to clarify this problem. Although we believe that *Lambdoceras* as a genus is synonymous with *Prosynthetoceras* and that its general morphology is shared by all species of that genus, those characters which serve to distinguish *Lambdoceras hessei* among existing taxa (especially *texanus* and *francisi*) also serve to link together other taxa (*trinitiensis* and *siouxensis*) that previously seemed to lack a broader association. Thus, as mentioned in the generic discussion, we regard this natural grouping to be better expressed by recognizing two subgenera: *P. (Prosynthetoceras)*

and *P. (Lambdoceras)*. This problem is discussed more fully under Zoogeography, page 207.

***Prosynthetoceras (Prosynthetoceras) texanus* (Hay)**

Figures 6, 34; tables 2, 3, 4, 10

Dromomeryx texanus HAY, 1924, pp. 15-16, pl. 2, figs. 8-12.

Dromomeryx angustidens HAY, 1924, p. 16, pl. 2, figs. 6-7.

Merycodus grandis HAY, 1924, pp. 17-18, pl. 3, figs. 9-11.

Protolabis francisi HAY, 1924, p. 13, pl. 3, figs. 5, 6 (in part).

cf. *Miolabis* sp. indet.: SIMPSON, 1932, p. 37.

?*Cranioceras texanus*: FRICK, 1937, pp. 82, 97.

?*Synthetoceras rileyi* FRICK, 1937, pp. 603, 605, fig. 66.

Blastomeryx texanus: WOOD AND WOOD, 1937, p. 137, pl. 1, figs. 5-6.

Syndoceras australis WHITE, 1941, p. 97, pl. 15, figs. 1, 1a, 2, 2a.

?*Syndoceras texanus*: HESSE, 1942, p. 163, (?*Syndoceras texanus*, p. 167, lapsus).

Nothokemas grandis WHITE, 1947, p. 508 (in part).

Synthetoceras (Prosynthetoceras) douglasi WHITE, 1947, p. 504, fig. 3a.

cf. *Miolabis tenuis*: RAY, 1957, p. 18.

Synthetoceras (Prosynthetoceras) rileyi australis: MAGLIO, 1966, p. 17 (new combination).

Prosynthetoceras texanus: PATTON, 1967, p. 37.

TYPE: T.A.M.U. No. 2387, a right M³ from the Garvin Gully locality near Navasota, Oakville Formation, Grimes County, Texas. Figured by Hay, 1924, plate 2, figures 8 and 9.

DISTRIBUTION: Medial Hemingfordian of the Gulf Coastal Plain of Texas and Florida.

HYPODIGM¹: Seven miles northeast of Huntsville (?Akin Hill), Walker County, Texas: F:A.M. No. 53500, skull, ramus (fig. 6) and skeletal elements; F:A.M. No. 34181, ramus (type of (?)*Synthetoceras rileyi*, Frick, 1937, fig. 66); F:A.M. No. 53505, detached M₃; F:A.M. No. 34078, distal end metatarsal, left cuboid, and third phalanx.

Akin Hill, Walker County, Texas: F:A.M. No. 33025, fragmentary horn.

Mann Place, San Jacinto County, Texas: F:A.M. No. 53502-A, orbital horn and horn fragments including a fragment of a rostral horn; F:A.M. No. 53503, detached M₃, P₃ and incisors; F:A.M. No. 33026, detached M²-M³; F:A.M. No. 33030, partial ramus; F:A.M. No.

¹See table 2 for a detailed location of Frick collecting localities.

33034, immature partial ramus; F:A.M. No. 33035, immature partial ramus; F:A.M. No. 53490, detached M³; F:A.M. No. 53491, immature partial mandible from locality number 2 on the Mann Farm.

Kelly Place,¹ San Jacinto County, Texas: F:A.M. No. 53504, detached M₂-M₃; F:A.M. No. 33036, partial orbital horn; F:A.M. No. 33039, partial maxilla; F:A.M. No. 33040, detached molars; F:A.M. No. 33043-D, detached molars; F:A.M. No. 33044, detached P₄-M₃; F:A.M. No. 33045, detached molars; F:A.M. No. 33046, ramal fragment; F:A.M. No. 33048, ramal fragment and detached teeth; F:A.M. No. 33051, base of rostral horn and detached teeth; F:A.M. No. 33052, fragmentary rostral and orbital horns; F:A.M. No. 33056, immature partial ramus.

Behind old Kelly Place, San Jacinto County, Texas: F:A.M. No. 33050, partial orbital and rostral horns and associated detached M₂-M₃.

Caper Place, San Jacinto County, Texas: F:A.M. No. 33024, orbital horn; F:A.M. No. 33027, detached M² and broken molar; F:A.M. No. 33028, detached M³; F:A.M. No. 33029, astragalus; F:A.M. No. 33032, partial ramus; F:A.M. No. 33033, partial ramus; F:A.M. No. 33037, fragment of orbital horn; F:A.M. No.

¹Kelly and Mann are the same place and join the Caper Place.

33041-C, three detached upper molars and astragalus; F:A.M. No. 33042, partial ramus (just below yellow line in wash, $\frac{1}{2}$ mile south of the Kelly home); F:A.M. No. 33047, immature partial ramus (just below yellow line in wash, $\frac{1}{2}$ mile south of the Kelly home).

Old Walker Place, San Jacinto County, Texas: F:A.M. No. 33038, fragmentary orbital horn.

From near Point Blank,² San Jacinto County, Texas: U.T.B.E.G. No. 31190-61, maxilla P³-M³; U.T.B.E.G. No. 31190-31, partial skull; U.T.B.E.G. No. 31190-75, partial rostral horn; U.T.B.E.G. No. 31190-95, left P₄-M₃; U.T.B.E.G. No. 31190-102, left M₁-M₃; T.A.M.U. unnumbered, right partial maxilla with P²-alveolus and P³-M³.

From an exposure on Highway 36, near Gay Hill, 11 miles northwest of Brenham, Washington County, Texas: S.M.U. No. 60898,³ left P₂-M₃.

Thomas Farm Quarry, 8 miles north of Bell, Gilchrist County, Florida: M.C.Z. No. 4065 [type of *Synthetoceras* (*Prosynthetoceras*) *douglasi*

²Directions to the U.T.B.E.G. localities are on file at the Vertebrate Paleontology Laboratory, The University of Texas at Austin.

³Although originally included in the Garvin Gully Fauna by Patton (1969b), there is some question about the exact stratigraphic level for this specimen. It may well belong in the Burkeville Fauna, as indicated by its large size.

TABLE 2
FRICK COLLECTING LOCALITIES IN SOUTHEASTERN TEXAS^a

| Localities | Quadrangle Map | County | Latitude | Longitude |
|---------------------------------|----------------|-------------|----------------|-----------------------|
| Trinity River Pit 1 | Blanchard | San Jacinto | 30° 40' 15" N. | 95° 03' 10" W. |
| McMurray Pits 1 and 2 | Cold Spring | San Jacinto | 30° 36' 45" N. | 95° 07' 56" W. |
| Love Farm | Cold Spring | San Jacinto | 30° 36' 02" N. | 95° 08' 25" W. |
| E. R. Harvey Place | Stephen Creek | San Jacinto | 30° 41' 05" N. | 95° 10' 02" W. |
| Caper Place | Stephen Creek | San Jacinto | 30° 44' 33" N. | 95° 15' 02" W. |
| Mann Place (= Kelly Place) | Oakhurst | San Jacinto | 30° 44' 37" N. | 95° 15' 10" W. |
| Old Walker Place | Oakhurst | San Jacinto | 30° 43' 12" N. | 95° 15' 58" W. |
| Three miles west of Point blank | Oakhurst | San Jacinto | 30° 44' 40" N. | 95° 15' 31" W. |
| Smith Place | Livingston | Polk | 30° 37' 10" N. | 95° 55' 50" W. |
| Windham Place | Livingston | Polk | 30° 37' 30" N. | 95° 55' 30" W. |
| Akin Hill | Riverside | Walker | 30° 46' 25" N. | 95° 27' 15" W. |
| Garvin Gully | Navasota | Grimes | 30° 24' 56" N. | 96° 05' 02" W. |
| Rush Creek; east of Woodville | Woodville | Tyler | 30° 49' 30" N. | 95° 18' 22" W. |
| pipeline, Locations 1 and 2 | | | | and 95° 18' 45" W. |

^aBecause parts of Texas are not divided into conventional land surveys, the Frick fossil localities are located by latitude and longitude. The field locations were determined by Mr. M. F. Skinner, in 1963, who was accompanied by Dr. John A. Wilson in the Navasota area and by Mr. N. Z. Ward in the Cold Spring area.

White, 1947], crushed palate with P^3 - M^3 ; M.C.Z. No. 3654 (type of *Syndyoceras australis* White, 1941), right partial ramus, P_1 and P_4 - M_3 ; M.C.Z. No. 3642, left maxilla with P^4 - M^2 ; M.C.Z. No. 4328, partial left maxilla with dP^2 - M^1 .

DIAGNOSIS: The smallest species of type subgenus, *P. (P.) texanus*, differs from *P. (P.) francisi* in that the frontal horns are situated more anteriorly and extend more directly outward over orbit; short rostral horn but with a clearly developed shaft between maxillary union and forks; P^2 two-rooted; upper and lower premolars less reduced and molars with less pronounced styles and accessory cusps. Burkeville Fauna specimens are slightly larger with longer horns and a longer diastema.

DESCRIPTION: Of the synthetoceratine species now recognized, *P. (P.) texanus* has the longest geochronologic range. In Texas it appears first in the Garvin Gully Fauna and extends through the Burkeville (see Geologic Setting, p. 125). The Burkeville specimens are characteristically larger and more advanced than those from Garvin Gully and mark an intermediate stage between the extreme occurrences of the *P. (P.) texanus*-*francisi* species group. There is no clear way to distinguish Garvin Gully and Burkeville specimens of *P. (P.) texanus* except by the dentition from the Burkeville averaging larger (fig. 7) and by the horns and dentition showing a more advanced stage of evolution. We think, however, it more instructive to describe the specimens separately so as to better establish the earliest occurring features of the group. Although Patton (1969b, fig. 27) illustrated a poorly preserved partial skull and horns of *P. (P.) texanus* from the Burkeville Fauna, the skull described below is the first to allow an adequate presentation of the general characters and proportions of the skull and cranial armament of this species.

SKULL: The skull of *P. (P.) texanus* from Garvin Gully (F.A.M. No. 53500) is partly crushed and skewed to the left. Although sutures are not detectable, gross cranial morphology can be outlined.¹ The dorsoventrally compressed (natural, not crushed) skull is characterized by a broad, low frontal region (approximately 86 mm. between the inner edges of the orbits), a short cranium, and a distinctly produced face

and muzzle. The orbits are pronounced and are placed low and well behind the tooth row. The braincase is obscured in this specimen but appears to have been small. A prominent and sturdy sagittal crest rises from the cranium at a point just back of the orbits and extends posteriorly to join with the strongly developed lambdoid crest. On each side of the braincase a prominent temporal crest extends dorsoposteriorly from the juncture of the posterior border of the zygoma and the paroccipital process to the lambdoid crest. Among the horned ruminants, only *Dromomeryx* possesses a comparable temporal crest. The posteriorly projecting external occipital protuberance is separated from the temporal region by a necklike restriction and is almost circular in outline. Posteriorly, the protuberance is highly scooped out to form a deep complexus fossa, which is further emphasized by the outwardly flaring lambdoid crest. This structure, unique among fossil and recent artiodactyls, indicates the presence of strong dorsal neck muscles necessary to lift the heavily horned skull. The large occipital condyles are directed mostly dorsoventrally and are inflected slightly mesially. The paroccipital processes are long, slender, and laterally compressed. Although obscured in this specimen, the auditory bullae appear to have been typically small—a family trait.² The wide zygomatic arch is strong and transversely flattened. Projecting downward from the base of the frontal horn, the supra-orbital process of the frontal meets the arch at the juncture of the zygomatic processes of the jugal and squamosal. The glenoid fossa is obscured in this specimen. The broad and rather flat frontals contribute elements to two important cranial structures; the posterolateral portion forms part of the widely curving frontal horn, whereas part of the supraorbital process becomes the posterior rim of the orbit. The orbits are large and rimmed with thickened bone. Just above the anterior edge of the orbit is a distinct swelling of bone. Leading from the anterior rim of the orbit is a masseteric ridge which extends to a point near the infraorbital foramen. In *P. (P.) francisi* and *S. tricornatus* this ridge never extends beyond a point about midway between the orbit and infraorbital foramen. The masseteric ridge in synthetoceratines is never so

¹A more complete description of the skull of *P. (P.) texanus* appears herein on page 149.

²The suppression of the auditory bullae is relatively greater in the Protoceratidae than in all other contemporary artiodactyls.

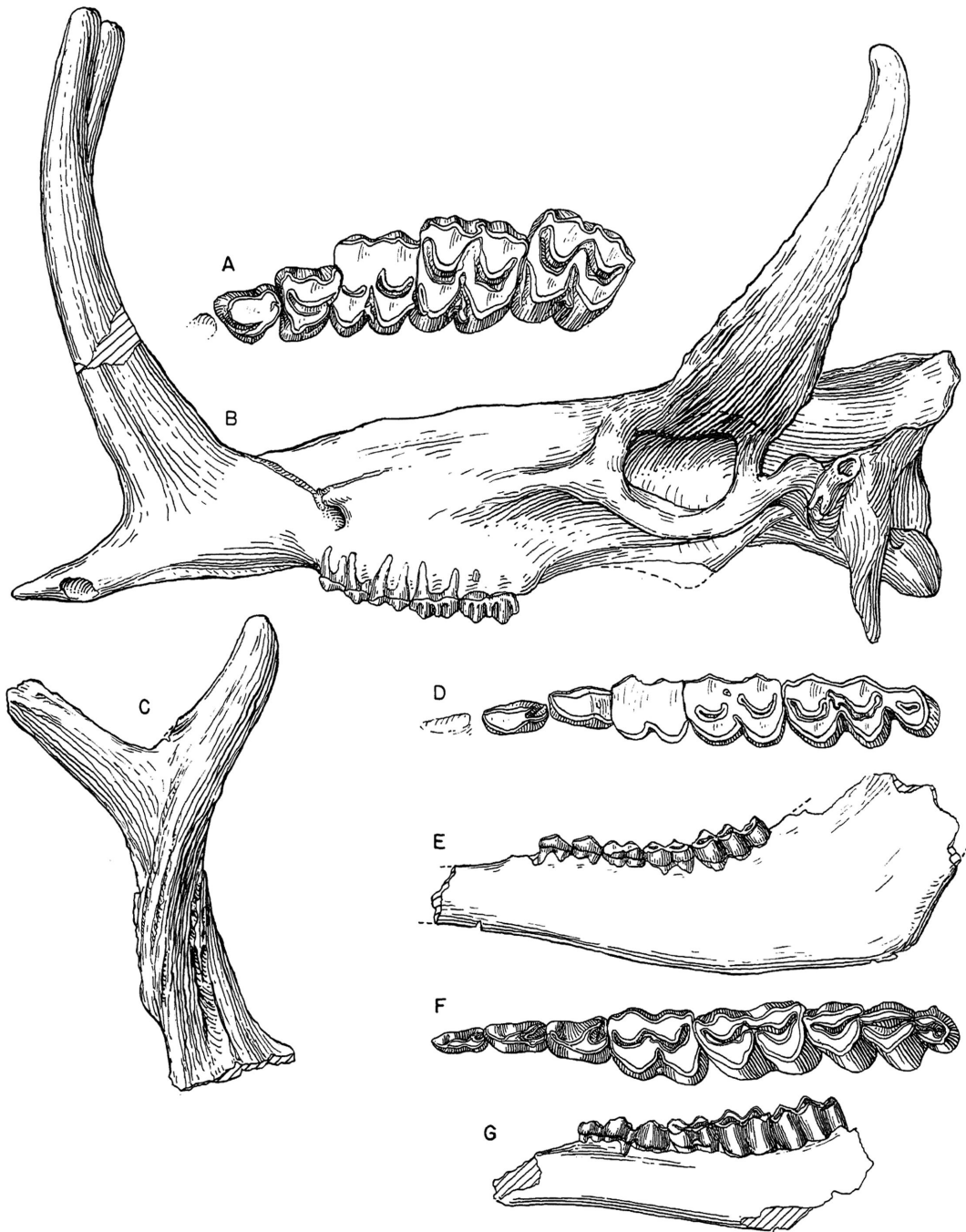


FIG. 6. *P. (Prosynthetoceras) texanus*, from 7 miles northeast of Huntsville, Walker County, Texas. A-E. Crushed skull and left ramus, F:A.M. No. 53500. A. P_2 alveolus, P_3 - M_3 , occlusal view. $\times 1$. B. Lateral view (with suggested restoration). $\times \frac{1}{2}$. C. Unrestored anterior view of twisted rostral horn. $\times \frac{1}{2}$. D. P_2 alveolus, P_3 - M_3 , occlusal view. $\times 1$. E. Lateral view (with suggested restoration). $\times \frac{1}{2}$. F, G. Right ramus, F:A.M. No. 34181. F. P_2 - M_3 , occlusal view, reversed. $\times 1$. G. Lateral view, reversed. $\times \frac{1}{2}$. (Both views of F:A.M. No. 34181 after Frick, 1937, fig. 66, in part.) See also figure 34.

strongly developed as in *Protoceras*. The knoblike tuberosity, which occurs at the end of this ridge in other synthetoceratines and in *Protoceras*, is poorly preserved in the Garvin Gully specimen, probably as a result of damage. The infraorbital foramen is above the posterior moiety of P^3 . As in *Syndyoceras cooki* and *Protoceras celer*, the nasals of *P. (P.) texanus* are retracted past the infraorbital foramen. In the Synthetoceratinae this retraction forms a large dorsal orifice that opens into the nasal passage posterior to the rostral horn, a configuration that indicates the presence of relatively large and flexible muzzle. In later synthetoceratines, the open narial region behind the rostral horn becomes progressively smaller. In *Synthetoceras*, for example, the nasals extend forward to a point halfway between the infraorbital foramen and the posterior edge of the rostral horn. The roof of the nasal passage beneath the rostral horn is the shape of an inverted "V" and it is formed by the union into a single shaft of the two maxillary protuberances as seen in *Protoceras*. Anterior to the base of the rostral horn the edentulous premaxillae form two widely flaring wings. The wings are dorso-ventrally compressed and are inflected downward and out from the anterior edge of the horn. Each maxillary portion of the wing contains a large alveolus for a caniniform tooth, the only element of the anterior upper dentition remaining. Traced from *Protoceras* and *Syndyoceras*, it can be seen that this tooth is the true upper canine. None of these large synthetoceratine canines has ever been recovered.

HORNS: The frontal horns of *P. (P.) texanus* are more like those of *Syndyoceras* than those of later synthetoceratines. They arise from a slightly more posterior position above the orbit than in *Syndyoceras* and extend perpendicular to the long axis of the skull. The proximal part of the horn is wider, more flattened, and more rugose than the rest of the horn. Although the horn is grooved along its entirety, its rear edge bears a particularly conspicuous groove which runs from the orbit over the posterior edge of the supra-orbital process and out to the bulbous tip. In later synthetoceratines, the surface of the frontal horns is more rugose and the horns arise from the dorsoposterior edge of the orbit.

The rostral horn of the Garvin Gully *P. (P.) texanus* is decidedly more advanced than that of *Syndyoceras cooki*. In *Syndyoceras* the horn lacks a distinct shaft but rather bifurcates just above

the maxillary union over the anterior nasal canal into two laterally curving tines. The base of the shaft in *Syndyoceras* is widely flared antero-posteriorly, arising from the maxillary ridge behind the infraorbital foramen at about the level of P^3 , recalling the condition of *Protoceras*. Also, the tines of the rostral horn of *Syndyoceras* are more flattened, wider, and are still rather broad at the tips. The Garvin Gully *P. (P.) texanus*, on the other hand, possesses a slender, well-defined shaft, as do all later synthetoceratines. From the point of union above the posterior nasal passage to the bifurcation the shaft is approximately 84 mm. Total length measured from the posterior base at the level of the face is approximately 180 mm. Unlike *Syndyoceras*, the tines are more noticeably tapered toward the ends and the tips usually have small bulbous swellings. The longest tine is approximately 55 mm., and although the bulbs at the tips of the tines are missing on the one complete rostral horn (F:A.M. No. 53500), the distance between them is estimated to be 65 mm. It is difficult to reconstruct the cross-sectional shape of the shaft because of its peculiar deformation (twisted clockwise in three-quarters of a turn), but the transverse diameter appears to have been the widest dimension, as is true of other synthetoceratines. The above mentioned deformation seems to have occurred during early development of the horn rather than as a result of post-burial strain in this individual. The horn is characteristically grooved and sculptured longitudinally, apparently for branches of the infraorbital artery, vein, and nerve, as described under *Syndyoceras* (p. 131). The largest grooves lead from the infraorbital foramen just below the maxillary tuberosity and continue anterodorsally along the base of the horn and up the lateral edges; they diffuse about halfway along the shaft. Another large canal extends from the area of the tuberosity to the base of the horn at its posterior edge where it turns over the dorsal edge of the maxilla into the posterior nasal opening. This canal is described more fully under the description of *P. francisi* (p. 152).

UPPER DENTITION: I^0 , C^1 , P^2-4 , M^1-3 . Characters of the upper dentition of *P. (P.) texanus* are described from two specimens, the heretofore undescribed skull and teeth (F:A.M. No. 53500) whose characters are presented herein, and a partial right maxilla (T.A.M.U. unnumbered), first described by Patton (1969b,

p. 178). The upper canine is represented by a large, deep alveolus, (approximately 11 mm. anteroposteriorly and only 6 mm. transversely), indicating a strong, laterally compressed tooth. Whereas no upper canines of *Prosynthetoceras* and *Synthetoceras* have been recovered, the alveolus indicates that the canine would be similar to that of *Protoceras* and *Syndyoceras*. In those genera the canine extends down to or below the lower level of the mandibular symphysis. P¹ is lost in *P. (P.) texanus*, as it is in *Syndyoceras cooki* and all other later synthetoceratines. P² is represented only by two alveoli in the partial maxilla (T.A.M.U. unnumbered). In comparison with P⁴, P² and P³ remain anteroposteriorly elongate, with the P³ thicker than P² and marked by a high, sharp paracone and a recurved metastyle which forms a small cusp posteriorly; no external rib is present on the paracone. Lingually, a large cingulum extends from the parastyle to join with the metastyle at the posterior border of the tooth. The more transversely produced, or submolariform P⁴ has both parastyle and metastyle well developed. The metastyle is more prominent and strongly recurved than the parastyle. Accessory cusps consist of a large cingular cusp at the base of the posterior limb of the protocone and a smaller cusp at the base of the anterior limb.

All upper molars display strong styler cusps on the anterior and posterior crests. The anterior half of each molar is offset lingually, resulting in a very prominent mesostyle and a rather deep recess anterior to it at the juncture of the paracone and metacone crests. A strong rib extends up each crest from the base of the crown to the tip of both paracone and metacone. Shape of the crescents varies from an open "V" or "U" on M³ to a more closed, slightly recurved "V" on M¹. Highly developed median pillars, characteristic of the synthetoceratines, occur between the anterior and posterior crescents and extend half the height of the crescents in unworn teeth. This relationship is generally maintained with wear, for the pillars (after some initial wear) are worn at virtually the same rate as the crescents. The apex of the double-limbed accessory pillars coincides with that of the junction of the anterior and posterior crescents. Along the anterior margin of each molar is a narrow winglike cingulum which projects from just above the base of the crown and extends labially along the anterior side. This feature is present but not so strongly developed along the posterior side of the tooth. M¹ and M² are broader than they are long, and all three molars show strong tapering toward the occlusal surface.

TABLE 3

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Prosynthetoceras* (*Prosynthetoceras*) *texanus* (GARVIN GULLY AND BURKEVILLE FAUNAS) FROM THE GULF COAST OF TEXAS

| | N | OR | \bar{X} | S | V |
|--------------------------------|----|-----------|------------|-------------|------------|
| P ³ | | | | | |
| L | 3 | 6.4- 9.7 | 8.50±1.05 | 1.825±0.745 | 21.47±8.76 |
| W | 3 | 7.2- 8.0 | 7.40±0.30 | 0.529±0.215 | 7.15±2.91 |
| P ⁴ | | | | | |
| L | 6 | 8.7- 9.7 | 9.22±0.15 | 0.387±0.112 | 4.19±1.21 |
| W | 6 | 10.0-12.2 | 11.36±0.32 | 0.791±0.229 | 6.96±2.01 |
| M ¹ | | | | | |
| L | 5 | 13.5-16.7 | 14.62±0.56 | 1.252±0.396 | 8.56±2.70 |
| W | 5 | 14.5-17.0 | 15.66±0.46 | 1.035±0.327 | 6.60±2.09 |
| M | | | | | |
| L | 10 | 16.0-18.6 | 17.36±0.24 | 0.775±0.173 | 4.46±0.99 |
| W | 10 | 16.4-19.9 | 18.14±0.34 | 1.065±0.238 | 5.87±1.31 |
| M ³ | | | | | |
| L | 11 | 16.2-20.0 | 17.86±0.35 | 1.182±0.251 | 6.63±1.41 |
| W | 11 | 15.4-22.0 | 17.91±0.49 | 1.646±0.351 | 9.19±1.96 |
| P ³ -P ⁴ | 3 | 18.3-20.6 | 19.47±0.64 | 1.151±0.470 | 5.90±2.41 |
| M ¹ -M ³ | 4 | 46.7-51.0 | 48.17±0.96 | 1.926±0.690 | 4.07±1.44 |
| P ³ -M ³ | 3 | 63.0-68.5 | 65.40±1.58 | 2.816±1.149 | 4.31±1.76 |

MANDIBLE: No *P. (P.) texanus* mandibles are sufficiently well preserved to allow an adequate description. A relatively complete description of the mandibular ramus appears under *P. (P.) francisi*.

LOWER DENTITION: I_{1-3} , C_1 , P_{1-4} , M_{1-3} . The lower premolars of *P. (P.) texanus* are reduced in comparison with those of *Syndyoceras cooki* and *Protoceras celer*. Because all of the mandibular specimens are broken away anterior to P_2 , the condition of P_1 is unknown; however, the fact that *P. (P.) texanus* is bracketed in time by two related species, *S. cooki* and *P. (P.) francisi*, that demonstrably exhibit P_1 , suggests that *P. (P.) texanus* possessed P_1 as well. The thin, elongate P_2 is two-rooted and is considerably smaller than P_3 . The primary differences between P_2 and P_3 are the more pronounced anterolingual flexid and the greater separation of hypoconid and entoconid in the latter. P_3 is elongate and is but slightly broader posteriorly than anteriorly. The hypoconid and protoconid are more distinct from the metaconid than on P_4 . As on P_4 , noticeable swellings are present at the base of the hypoconid and protoconid. P_4 is slightly wedge-shaped. Most of the reduction in this tooth has occurred in the region of the protoconid. The metaconid is high and sharp; the entoconid is narrow and blade-like. The hypoconid extends posteriorly and lingually to join the entoconid. On worn specimens the metaconid, entoconid, and hypoconid are swollen to form a bulge at the posterolabial edge of the tooth.

The lower molars of *P. (P.) texanus* are lower crowned than those of *P. (P.) francisi*. The crescents (protoconid, hypoconid) are symmetrical and show little tendency toward recurving. Stylids are reduced in comparison with those on the upper molars; the metastylid is the strongest stylid. The anterior crescent (metaconid) overlaps the posterior crescent (entoconid) slightly to form a faint stylid. A small median pillar occurs at the base of the crown between the anterior (protoconid) and posterior (hypoconid) crests of M_1 and M_2 . No accessory pillars appear on M_3 . In contrast to the median pillars on the upper molars, the lower pillars do not show wear until the teeth were worn almost to the base of the crown. No cingula are present on the lower molars. Perhaps the most significant characteristic of the lower molars is the presence of a double enamel loop on the hypoconulid of

M_3 which, with wear, encloses a fossettid. This feature, characteristic of the ruminants, is not present in the camelids (except in the problematical *Floridatragulus*), but occurs in all proto-ceratids. In this regard M_3 of *Prosynthetoceras* resembles that of the genus *Floridatragulus*, which is often found in association with it but is distinguishable on the basis of the strong anterior cingulum, the accessory pillar between the protoconid and hypoconid, and the lower crown height of the latter. Another contemporary genus, *Nothokemas*, possesses an M_3 which converges on the above-mentioned condition of *Prosynthetoceras* and *Floridatragulus*, in that it approaches the formation of a double enamel loop on the hypoconulid. In *Nothokemas*, however, this is accomplished by the posterior extension of the entoconid.

DISCUSSION: The tooth lengths of the type specimen of *P. (P.) texanus* and the specimens from the Garvin Gully Fauna referred to it are within the range of published measurements of *Syndyoceras cooki* (Barbour, 1905a; Frick, 1937). Specimens from the Burkeville Fauna are clearly larger. Unfortunately, the teeth of the only specimen available of *S. cooki* are badly worn, but as far as can be determined they approach closely those of *P. (P.) texanus*. However, rostral horns of *P. (P.) texanus* from the Burkeville Fauna (U.T.B.E.G. Nos. 31190-31, 31190-72) are larger and have a longer shaft than those of either *Syndyoceras cooki* or those specimens of *P. (P.) texanus* from the Garvin Gully Fauna. In addition, the premolars of *P. (P.) texanus* appear to have undergone approximately 10 per cent greater reduction than those of *Syndyoceras cooki*, indicating that the former had developed farther along the lines characterizing the later synthetoceratines.

The Burkeville specimens (U.T.B.E.G. No. 31190-31, a partial skull with horns, left M^3 , and right M^2-M^3 ; U.T.B.E.G. No. 31190-61, maxilla with left M^1-M^3 , and right P^3-M^3) are intermediate in size, crown height, and complexity of molars between *P. (P.) texanus* from the Garvin Gully fauna and *P. (P.) francisi* from the Cold Spring fauna. The metastyle of P^4 of the Burkeville *P. (P.) texanus* is large and strongly recurved; the parastyle is small. A tiny tubercle is present at the base of the anterior limb of the protocone. This tooth is more elongate and appears slightly more wedge-shaped than that of the Garvin Gully *P. (P.) texanus*. The metastyle

TABLE 4

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Prosynthetoceras* (*Prosynthetoceras*) *texanus* (GARVIN GULLY AND BURKEVILLE FAUNAS) FROM THE GULF COAST OF TEXAS

| | N | OR | \bar{X} | S | V |
|--------------------------------|----|-----------|------------|-------------|------------|
| P ₂ | | | | | |
| L | 4 | 8.0- 8.9 | 8.35±0.20 | 0.404±0.143 | 4.83±1.70 |
| W | 3 | 3.1- 3.9 | 3.53±0.23 | 0.406±0.165 | 11.43±4.66 |
| P ₃ | | | | | |
| L | 8 | 8.9-11.0 | 9.61±0.22 | 0.649±0.162 | 6.75±1.68 |
| W | 8 | 4.3- 5.0 | 4.61±0.08 | 0.253±0.063 | 5.50±1.37 |
| P ₄ | | | | | |
| L | 8 | 9.4-10.5 | 9.86±0.13 | 0.377±0.094 | 3.90±0.78 |
| W | 7 | 5.5- 6.7 | 6.04±0.16 | 0.439±0.117 | 7.26±1.94 |
| M ₁ | | | | | |
| L | 9 | 12.5-15.5 | 13.72±0.30 | 0.920±0.217 | 6.68±1.58 |
| W | 9 | 9.3-10.3 | 9.91±0.10 | 0.318±0.075 | 3.21±0.75 |
| M ₂ | | | | | |
| L | 14 | 16.1-18.5 | 17.18±0.19 | 0.770±0.145 | 4.48±0.84 |
| W | 14 | 10.3-12.0 | 10.98±0.14 | 0.539±0.102 | 4.91±0.92 |
| M ₃ | | | | | |
| L | 16 | 21.0-27.6 | 23.42±0.51 | 2.074±0.366 | 8.87±1.56 |
| W | 16 | 10.4-12.2 | 11.48±0.13 | 0.528±0.934 | 4.60±0.81 |
| P ₃ -M ₃ | 3 | 67.0-71.5 | 69.23±1.30 | 2.250±0.918 | 3.25±1.32 |
| P ₄ -M ₃ | 3 | 59.0-62.2 | 60.40±0.91 | 1.637±0.668 | 2.71±1.10 |
| M ₁ -M ₃ | 5 | 49.0-56.1 | 53.20±1.53 | 3.430±1.085 | 6.44±2.03 |

on P₃ is also large and recurved. Cingula and intercolumnar pillars are less strongly developed than in the Garvin Gully *P. (P.) texanus*, but more so than in *P. (P.) francisi*. The shape of the crests and crescents of the molars of the Burkeville form are similar to those from Garvin Gully. The posterior cingulum, when present, is tight against the side of the tooth, relatively prominent lingually, and becomes faint as it approaches the anterior edge of the metastyle; these cingula are only faintly visible on M₁-M₂ of U.T.B.E.G. No. 31190-61. The anterior cingula are conspicuous lingually and rise over half the length of the anterior limb of the protocone for approximately one-third the width of the tooth, then dip down close to the base of the crown, becoming increasingly faint toward the parastyle. The median pillars are strong and folded into the limbs, which abut closely on their respective crescents. Wear on the pillars is proportional to the degree of wear on the primary cusps. The styles are very well developed, especially the mesostyle. The postorbital horns are laterally directed. The shaft of the rostral horns of the Burkeville *P. (P.) texanus* is longer than that of the Garvin Gully form, attaining a length of

approximately 135 mm. from the base to the point of bifurcation.

Specimens of *P. (P.) texanus* from the Burkeville Fauna mark an intermediate stage between earlier *P. (P.) texanus* and later *P. (P.) francisi* of the Cold Spring fauna. An analysis of all the comparable known features in the teeth, skulls, and jaws indicates a remarkably close relationship between the Garvin Gully and Burkeville populations. This affinity is shown by intergradation of every comparable diagnostic character available in the two series of specimens. *P. (P.) texanus* from the Burkeville Fauna more closely approximates *P. (P.) texanus* from the Garvin Gully fauna than *P. (P.) francisi* in size, as well as in evolutionary development. For example, figure 7 illustrates the distribution of lengths of M₃ of synthetoceratines from the five biostratigraphic units included in this study. The separation of *P. (P.) francisi* from the Burkeville *P. (P.) texanus* is consistent, but the length of M₃ of *P. (P.) texanus* from the Garvin Gully is equivalent in length to the smaller Burkeville individuals, with the Burkeville form averaging larger than those from Garvin Gully. This same pattern is observed in other synthetoceratine

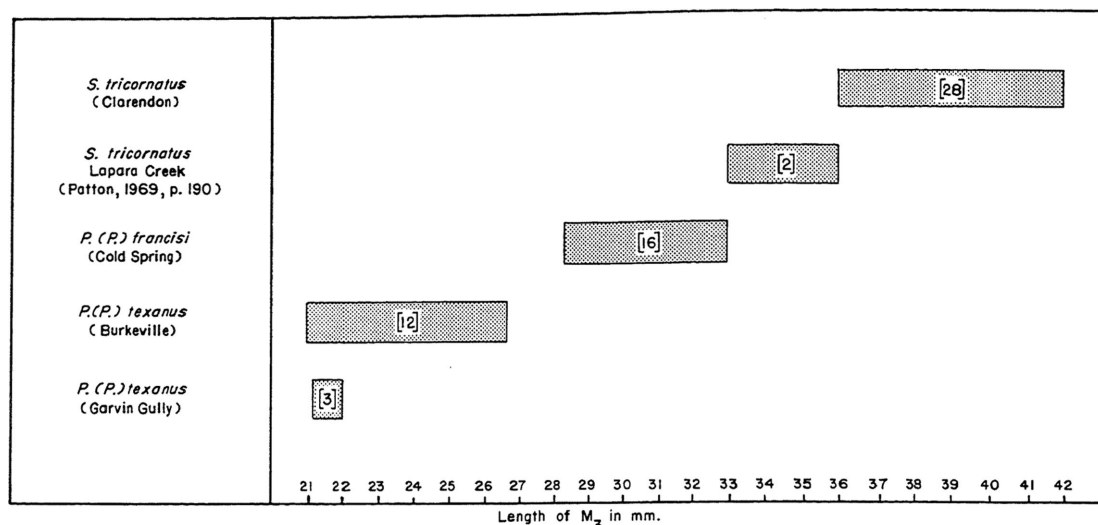


FIG. 7. Distribution of measurements of the M_3 lengths of the synthetoceratines from the Gulf Coast and the Panhandle of Texas

characters, such as the taller rostral horn, longer diastema, and taller-crowned molars. The aforementioned shifts in the patterns of synthetoceratine characters from the Garvin Gully Fauna to the Burkeville Fauna may be important in interpreting the evolution of this group of aritodactyls, and they may eventually warrant separate taxonomic status for the two forms. It is probable that the Burkeville specimens represent a temporal, or successional, subspecies of *P. (P.) texanus*. The degree of differentiation between the Garvin Gully and Burkeville populations is smaller than the sequential differences observed in other more distinct synthetoceratine species.

***Prosynthetoceras* (*Prosynthetoceras*) *francisi* Frick**

Figures 8–17, 28, 31, 34; tables 1, 5–7, 10

Procamelus leptognathus: HAY, 1924, pp. 10–11, pl. 2, fig. 5, pl. 3, fig. 4 (in part).

Synthetoceras (*Prosynthetoceras*) *francisi* FRICK, 1937, pp. 605–606, figs. 2, 2a, 60–63.

Prosynthetoceras francisi: PATTON, 1967, p. 39.

TYPE: T.A.M.U. unnumbered, skull with canine alveolus, P^2 – M^3 , rostral horn, and the bases of both orbital horns; from 1.3 miles north of the Court House in the town of Cold Spring.¹

¹"An old sand road leads north out of this town [Cold Spring] past one cemetery and ends at another small private cemetery. From the northeast corner of the latter, the exposures are easily visible. The Bur. Econ. Geol. loc. No. 31219, site 3, is 2000 ft. N. 20 E. of the N.E. corner of

San Jacinto County, Texas. (Figured by Frick 1937, figs. 2, 2a, 60–63.)

DISTRIBUTION: Cold Spring fauna from San Jacinto, Polk, and Tyler counties, Texas.

HYPODGM²: Love Place, San Jacinto County, Texas: F.A.M. No. 34180, right partial mandible; F.A.M. No. 33053, left detached M^3 .

Mann Place, San Jacinto County, Texas: F.A.M. No. 34182, right P^3 – M^3 .

McMurray Place, San Jacinto County, Texas: F.A.M. No. 33070, right immature mandible; F.A.M. No. 33070, right partial mandible; F.A.M. No. 33071, partial orbital horn; F.A.M. No. 33072, posterior part of skull with M^1 – M^3 broken and both orbital horns, Pit No. 2; F.A.M. Nos. 33074 and 33074A, right and left partial mandibles which appear to be one individual, Pit No. 2; F.A.M. No. 33075, left femur; F.A.M. No. 33076, right proximal part of metatarsal III; F.A.M. No. 33077, left proximal part of metatarsal IV; F.A.M. Nos. 33078 and 33079, two first phalanges.

Near Cold Spring, San Jacinto County, Texas: U.T.B.E.G. Nos. 31219–213 and 31219–214, two left partial mandibles; U.T.B.E.G. No. 31219–236, rostral horn; U.T.B.E.G. No.

this cemetery. Here is a small quarry, 240 specimens were obtained. The collection at the [Texas] A. & M. Mus. loc. No. 38, was made over the entire exposure. The area is on the southwestern half of the James Rankin Survey." (Hesse, 1942, p. 170–171).

²See table 2 for details of Frick collecting localities.

31219-219, partial right mandible with P_4 - M_3 .

Near Point Blank, San Jacinto County, Texas: U.T.B.E.G. No. 31243-5, right partial mandible with P_3 - M_3 .

Near Goodrich, Polk County, Texas: U.T.B.E.G. No. 31183-47, partial left mandible with M_1 - M_3 .

Windham Place,¹ Polk County, Texas: F:A.M. No. 33049, almost complete skull except for part of the right orbital horn with C/alveolus and P^2 - M^3 .

Smith Place, Polk County, Texas: F:A.M. No. 33054, right partial mandible; F:A.M. No. 33055, immature right and left partial maxillae with dP^3 - M^2 (broken), right and left partial mandibles with dP_4 - M_2 and fragmentary occiput.

Wright Farm, Polk County, Texas: F:A.M. No. 32058, associated skeletal elements of two or more individuals, including: right partial humerus; right and left radii; right lunar; left magnum; (A) right metacarpal III, right metacarpal IV, and associated two incomplete lateral metacarpals; (B) left metacarpal III and associated incomplete? metacarpal IV (proximal end missing) with articulated distal part of ?metacarpal V, a detached proximal part of a lateral metacarpal; (C) right metacarpal III and associated lateral metacarpal; proximal part of left metacarpal IV; three front first phalanges; right femur; right tibia; right calcaneum, astragalus, cuboid, navicular, ectocuneiform, metatarsal III, metatarsal IV, two rear first phalanges and one second phalanx.

East of Woodville, Tyler County, Texas: F:A.M. No. 33057, partial rostral horn; F:A.M. No. 33061, right partial mandible.

Woodville Location 1, between the pipeline and highway, Tyler County, Texas: F:A.M. No. 33059, base of right orbital horn; F:A.M. No. 33062, right partial mandible; F:A.M. No. 33066, left immature partial mandible; F:A.M. No. 33067, left immature partial mandible; F:A.M. No. 34145, partial tibia.

Woodville Location 2, Tyler County, Texas: F:A.M. No. 33060, right M^2 - M^3 ; F:A.M. No. 33063, left partial mandible; F:A.M. No. 33064, right fragmentary mandible; F:A.M. No. 33065, right fragmentary mandible.

West Doucette and northwest of Woodville, Tyler County, Texas: F:A.M. No. 34109, partial

metatarsal III; F:A.M. No. 34114, partial metatarsal IV; F:A.M. Nos. 34153, 34154, astragali.

DIAGNOSIS: Differs from *P. (P.) texanus* in being approximately 25 per cent larger; frontal horns arise from dorsoposterior edge of orbit and sweep back in a wide arc; base of frontal horns are more flattened and edges more irregular; molars taller-crowned, cingula and accessory tubercles more reduced; premolars average relatively smaller, and P_2 usually single-rooted; mandible more slender and diastema longer.

DESCRIPTION: Skull: Two skulls of *P. (Prosynthetoceras) francisi* have been recovered from the Texas Gulf Coastal Plain. The first skull (T.A.M.U. unnumbered) was found by Claude Riley in 1935 near Cold Spring, San Jacinto County, and was designated by Frick (1937, p. 605) as the type of his new subgenus *Prosynthetoceras*. This specimen, originally deposited in the Mark Francis Collection at Texas A. and M. subsequently was lost, but is represented by several good casts (at A.M.N.H., Univ. of Texas, and Univ. of Florida). A well-preserved second skull, also found by Riley, was recovered from the Windham Place, 7 miles south of Livingston, which is approximately 15 miles northeast of Cold Spring.

Because of their better and more complete preservation, the *P. (P.) francisi* specimens provide morphologic information on the skull of *Prosynthetoceras (Prosynthetoceras)* not obtainable from studying the *P. (P.) texanus* skull alone. The most notable differences between *P. (P.) texanus* and *francisi* involve over-all size and shape of the cranial armament. When mature individuals are compared we find that the skull of *P. (P.) francisi* is 25 per cent longer and the rostral horn two and one-half times longer than that of *P. (P.) texanus*.

The occipital region of *P. (P.) francisi* is much the same as that of *P. (P.) texanus*. Strong sagittal and lambdoid crests combine to form a widely flaring occipital protuberance with a deep complex fossa and a necklike constriction between it and the small braincase. As in all protoceratids there is a strong temporal ridge leading from the dorsolateral edge of the supraoccipital to the paroccipital process. Joining with it midway along the side of the braincase is a crest leading from the zygomatic process of the squamosal. The paroccipitals are larger and more widely flared than in *P. (P.) texanus*. Although laterally compressed as in the latter, the paroccipitals are

¹Windham Place, Smith Place, and Wright Farm are all one general locality.



FIG. 8. *P. (Prosynthetoceras) francisi*, type, T.A.M.U. unnumbered skull, from Cold Spring, San Jacinto County, Texas. Lateral view. $\times \frac{1}{2}$. (After Frick, 1937, fig. 60, in part.) See dorsal view, present report, figure 9.
Abbreviations: MA, auditory meatus; PP, paroccipital process; X, cross section of horn (see fig. 9BB); 7, condylar foramen.

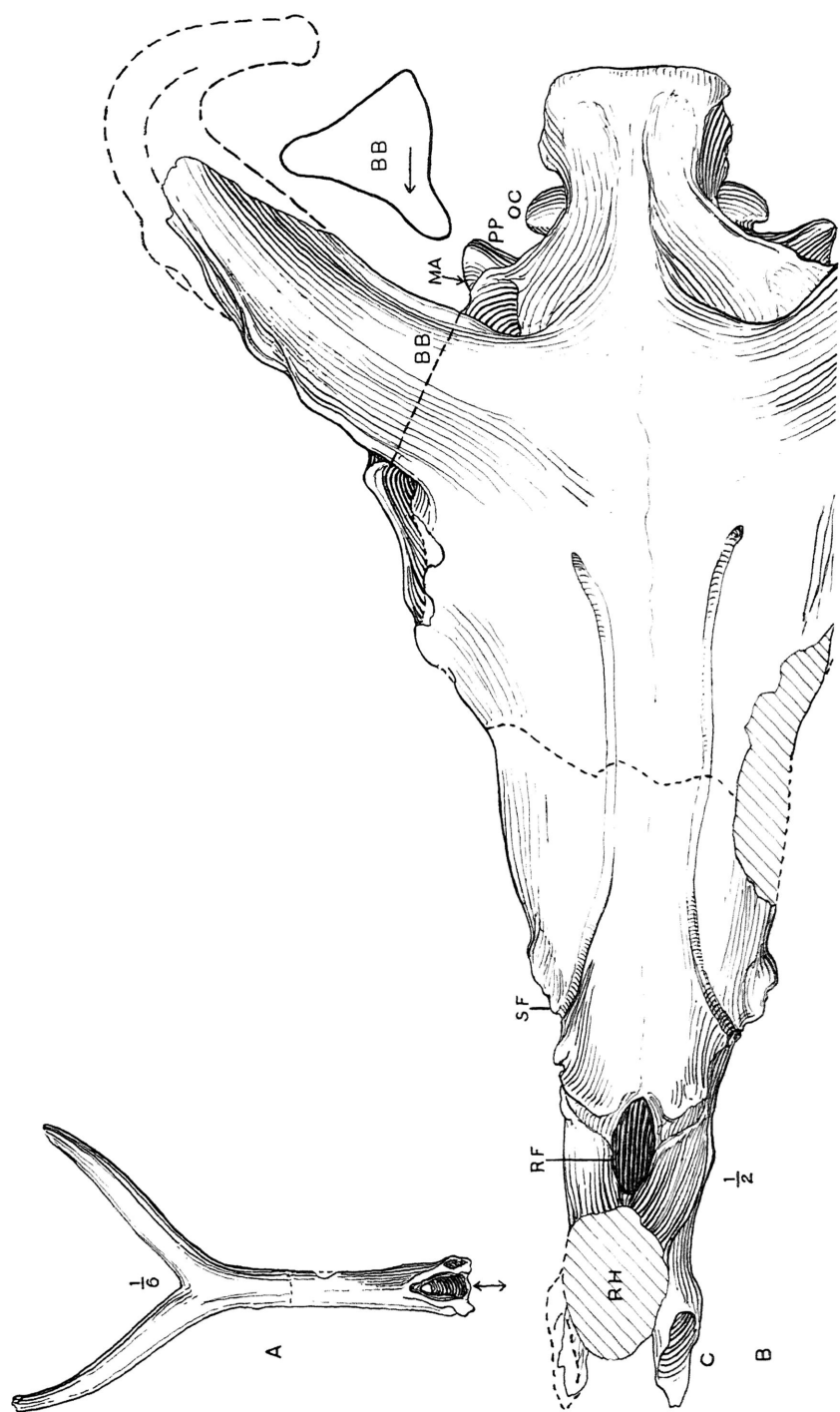


FIG. 9. *P. (Prosmilthoceras) francisi*, type T.A.M.U. unnumbered skull, from Cold Spring, San Jacinto County, Texas. A. Anterior view of rostral horn. $\times \frac{1}{6}$. B. Dorsal view. $\times \frac{1}{4}$. BB. Cross section of horn. (After Frick, 1937, fig. 63, in part.) See lateral view present report, figure 8. Abbreviations: IOF, infraorbital foramen; MA, auditory meatus; OC, occipital condyle; PP, paroccipital process; RF, rostral foramen; RH, rostral horn.

more sturdily constructed and are more swollen toward the point of descent. Between the paroccipital and the zygomatic portion of the squamosal lies a small, wedge-shaped tympanic. The bulla is not inflated and the external auditory meatus is obscured. The postglenoid portion of the squamosal, missing in the *P. (P.) texanus* specimens, is very wide and flat and is expanded posteriorly. A broad and heavy jugal extends beneath the orbit and expands into a broad, flat, transverse shelf (29 mm. wide), unlike that of the camelids and cervids. The zygomatic process of the squamosal participates only slightly in formation of the shelf. The frontals are broad and flat as in *P. (P.) texanus*, and in approximately their center occur the supraorbital foramina. From each foramen a surface groove leads anteriorly to the nasal orifice. The nasals are less retracted than in *P. (P.) texanus* and consequently the orifice is relatively smaller. In the crushed skull of *P. (P.) texanus* the masseteric ridge appears to extend from the anterior edge of the orbit to the infraorbital foramen. In *P. (P.) francisi* and *S. tricornatus*, however, two such ridges are apparent. The fainter dorsal ridge extends to the infraorbital foramen, whereas the other and more prominent one curves down the side of the maxilla and disappears above the middle of M_2 at about the level of the infraorbital foramen. It is unlikely that the dorsal ridge is an artifact of preservation because it is present in five skulls of *S. tricornatus*. The region below the masseteric ridge is scooped to form a rather large fossa.

As in all synthetoceratines, there is a conspicuous knoblike tuberosity on the side of the maxilla above the infraorbital foramen. Immediately anterior to this maxillary tuberosity is a small depression, representing the point of flexure of the prominent supraorbital groove on the top of the skull leading from the supraorbital foramen on the frontal and continuing over the superior edge of the maxilla and into the nasal opening behind the rostral horn. The upper edge of this groove is rimmed by thickened bone and a few small tuberosities, which vary in size. Another large groove leads from the infraorbital foramen to the base of the rostral horn, at which point one branch travels up the side of the horn where it eventually diffuses, and the other continues along the base of the horn and turns over the premaxillary wing and into the anterior nasal opening. The winglike premaxillae extend

forward and slightly downward from the base of the rostral horn. A large alveolus for a caniniform tooth occurs at the anterior edge of the maxillary portion of each wing, as in all synthetoceratines.

HORNS: In contrast to *P. (P.) texanus*, the frontal horns of *P. (P.) francisi* arise at the dorso-posterior edge of the orbit and sweep more posteriorly in a wide arc. They differ from *P. (P.) texanus* also in the greater flattening of the dorsal surface of the horn base and in the more prominent irregularity of the anterior and posterior edges. Although broken away in some specimens, small bulbous knobs occur at the tips of the frontal horns. Surface grooving for blood vessels and nerves is like that in all synthetoceratines.

The rostral horn of *P. (P.) francisi* is considerably larger than that of *P. (P.) texanus*. In addition, it is characterized by a relatively, as well as absolutely, longer shaft and a proportionally longer fork (table 10). The length of the fork varies but is always at least one-third the total length of the horn. In *P. (P.) francisi* and later synthetoceratines, the shaft of the rostral horn is tilted slightly forward whereas the forked segment is swept gently to the rear.

As in *P. (P.) texanus* and all later synthetoceratines, conspicuous grooving leads up the base of the rostral horn from the infraorbital foramen and diffuses along its entire surface. Another and even more prominent surface canal extends from each side of the posterior nasal cavity down to a point just above the infraorbital foramen where it shifts dorsally and leads along the top of the skull to the supraorbital foramen. As this horn has increased in bulk from *P. (P.) texanus* to *P. (P.) francisi* (and still later forms), there has been a corresponding increase in the size of the surface canals leading to and from it, reflecting the additional demands of nutrition and enervation. In further response to this, these canals have become more protected from possible injury by the growth of bony rims and knobs along part of their course.

UPPER DENTITION: I^0 , C^1 , P^2-4 , M^1-3 . The upper molars of *P. (P.) francisi* are approximately 20 per cent larger than those of the earlier Burkeville *P. (P.) texanus*. Although the teeth of both the type and the most complete specimens (U.T.B.E.G. No. 31219-213 and F.A.M. No. 33049) are worn, they appear to have been taller crowned than earlier forms.



FIG. 10. *P. (Prosyntheloceras) francisi*, referred skull, F.A.M. No. 33049. Lateral view. $\times 0.485$. (See figs. 11 and 12.)



FIG. 11. *P. (Prosynthetoceras) francisi*, referred skull, F.A.M. No. 33049, from Windham Place, Polk County, Texas. Dorsal view. $\times 0.485$. (See figs. 10 and 12.)

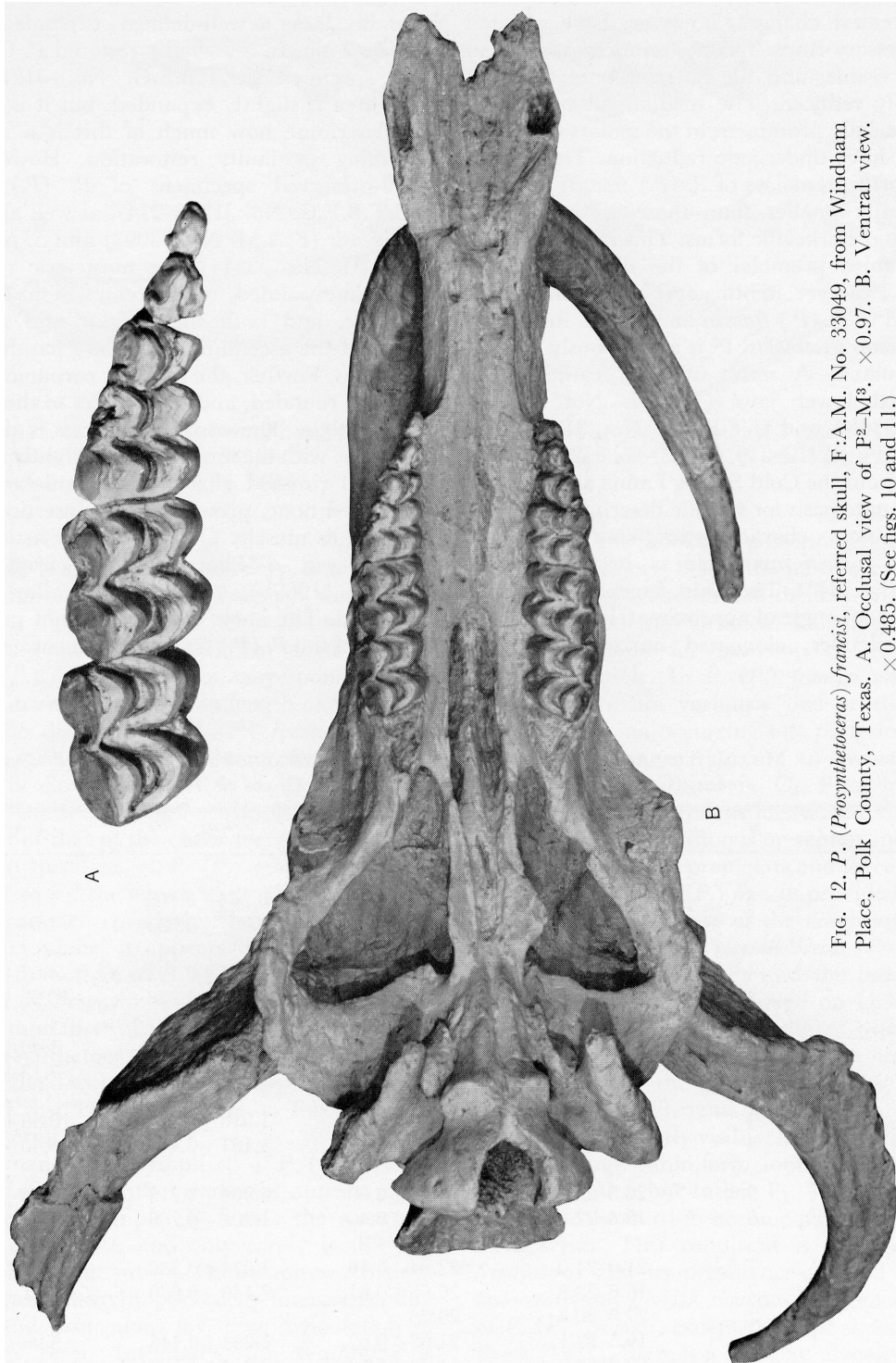


FIG. 12. *P. (Prosynthetoceras) francisi*, referred skull, F.A.M. No. 33049, from Windham Place, Polk County, Texas. A. Occlusal view of P₂-M₃. $\times 0.97$. B. Ventral view. $\times 0.485$. (See figs. 10 and 11.)

The greatest changes, however, have affected the accessory cusps. The posterior cingula are no longer visible, and the anterior ones are considerably reduced. The median pillars, which are especially prominent in the molars of *P. (P.) texanus*, have undergone reduction. The second and fourth premolars of *P. (P.) francisi* are proportionally smaller than those of the Garvin Gully and Burkeville forms. This is equally true of the third premolar of the type of *P. (P.) francisi*. However, in other specimens confidently assigned to *P. (P.) francisi* and also in the larger *Synthetoceras tricornatus*, P³ is anomalously robust.

MANDIBLE: A series of eight rather well-preserved lower jaws (F:A.M. Nos. 33180, 33060, 33062, and U.T.B.E.G. Nos. 31219-213, 31219-214, 31219-219, 31183-47, 31243-5) are known from the Cold Spring Fauna and provide an adequate basis for specific description.

The most characteristic feature of the *P. (P.) francisi* mandible is its remarkable shape (fig. 13). The thin ascending ramus, canted at an angle of approximately 140 degrees to the slender, elongated horizontal ramus,

notably lacks a well-defined, expanded masseteric region. In a partially restored *P. (P.) francisi* specimen (U.T.B.E.G. No. 31219-213), this area is slightly expanded, but it is difficult to determine how much of this is a result of crushing or faulty restoration. However, in well-preserved specimens of *P. (P.) francisi* (U.T.B.E.G. No. 31219-214), as well as *P. (L.) trinitiensis* (F:A.M. No. 33093) and *S. tricornatus* (F:A.M. No. 53444), the masseteric region is thin, unexpanded, and attenuated toward the condyle, and both the inferior and superior edges of the ascending ramus are parallel to its long axis. Further, the peculiar coronoid process is short, rounded, and barely rises to the level of the condyle. The coronoid process is deflected laterally, with the mesial surface slightly scooped out and rimmed along the ventral border by thickened bone, presumably for insertion of the temporalis muscle. Only one other artiodactyl, *Nothotylopus*, a Pliocene camel from Texas (Patton, 1969b), possesses a similarly short coronoid. The angle of the jaw is not preserved in any of the *P. (P.) francisi* specimens.

TABLE 5

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Prosynthetoceras* (*Prosynthetoceras*) *francisi* (COLD SPRING FAUNA) FROM THE GULF COAST OF TEXAS

| | N | OR | \bar{X} | S | V |
|--------------------------------|---|-----------|------------|-------------|------------|
| P ² | | | | | |
| L | 3 | 9.0- 9.5 | 9.20±0.15 | 0.264±0.108 | 2.87±1.17 |
| W | 3 | 5.5- 5.6 | 5.53±0.04 | 0.057±0.023 | 1.04±0.42 |
| P ³ | | | | | |
| L | 4 | 10.2-11.5 | 10.95±0.27 | 0.545±0.193 | 4.97±1.75 |
| W | 4 | 6.5- 8.3 | 7.20±0.31 | 0.787±0.278 | 10.93±3.86 |
| P ⁴ | | | | | |
| L | 4 | 10.7-11.0 | 10.95±0.07 | 0.152±0.054 | 1.40±0.49 |
| W | 4 | 11.3-13.2 | 12.65±0.45 | 0.903±0.320 | 7.13±2.52 |
| M ¹ | | | | | |
| L | 4 | 16.1-20.8 | 18.47±0.97 | 1.918±0.678 | 10.38±3.67 |
| W | 4 | 16.8-19.6 | 18.45±0.59 | 1.181±0.417 | 6.40±2.26 |
| M ² | | | | | |
| L | 9 | 20.5-23.3 | 22.13±0.30 | 0.904±0.213 | 4.08±0.96 |
| W | 9 | 18.4-22.8 | 20.47±0.40 | 1.202±0.283 | 5.87±1.38 |
| M ³ | | | | | |
| L | 7 | 21.0-24.0 | 22.94±0.40 | 1.074±0.330 | 4.68±1.43 |
| W | 7 | 16.6-23.8 | 20.66±0.81 | 2.150±0.660 | 10.21±2.72 |
| P ² -P ⁴ | 2 | 27.8-30.7 | 29.25 | — | — |
| P ³ -P ⁴ | 4 | 19.5-22.1 | 21.02±0.62 | 1.253±0.443 | 5.96±2.10 |
| M ¹ -M ³ | 3 | 58.3-63.0 | 61.43±1.53 | 2.714±1.108 | 4.41±1.80 |
| P ² -M ³ | 2 | 84.0-94.6 | 89.30 | — | — |
| P ³ -M ³ | 3 | 76.3-84.4 | 81.23±2.44 | 4.330±1.767 | 5.33±2.17 |

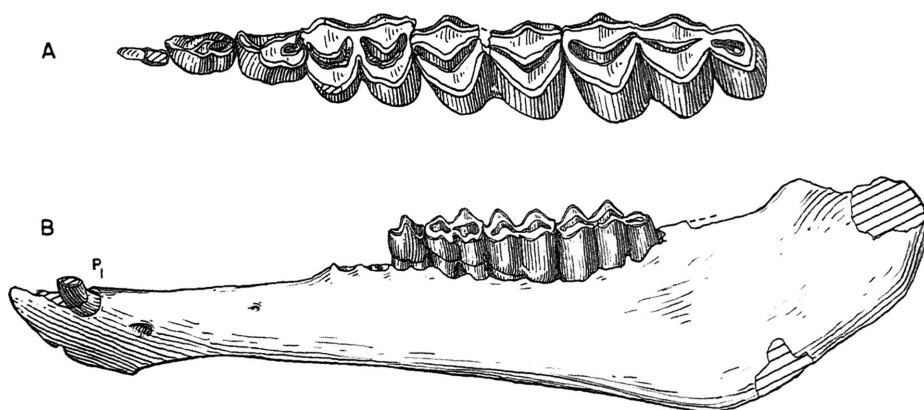


FIG. 13. *P. (Prosynthetoceras) francisi*, from near Cold Spring, San Jacinto County, Texas. A. Left ramus, U.T.B.E.G. No. 31219-213, occlusal view. $\times 1$. B. Left ramus, U.T.B.E.G. No. 31219-214, lateral view. $\times \frac{1}{2}$. (See fig. 34B.)

The horizontal ramus of the *P. (P.) francisi* mandible is slender and less deep than that of *Syndyoceras cooki* and *P. (P.) texanus*; the lingual surface is slightly concave below the tooth row. There also has been a significant lengthening of the *P. (P.) francisi* diastema, corresponding to a similar increase in diastema length of the upper jaw. The diastema of *P. (P.) francisi* extends from P_2 to the rather prominent caniniform P_1 , which is closely appressed to the incisiform canine. Diastema length varies from 75 to 100 per cent of that of the cheek teeth row. Because the type specimen of *P. (P.) texanus* is broken anterior to P_2 , the length of its diastema cannot be determined precisely, but judging from symmetry alone, it appears to be significantly shorter than that of *P. (P.) francisi*. The diastemata of *Protoceras* and *Syndyoceras* are much shorter than those of any of the succeeding forms. In most synthetoceratine specimens, the superior edge of the diastema is quite sharp and most are pinched just below the edge to form a well-defined crest.

The mandibular symphysis of *P. (P.) francisi*, like that of other synthetoceratines, appears never to have been completely fused; the suture is always detectable, and only rarely is the jaw broken across the suture. The symphyseal articular surface is heavily pocked by interconnecting facets and projections for loose articulation of the two rami. Internally, the symphysis is hollowed by sinuses. From a point just posterior to the symphysis the anterior lingual surface of the mandible becomes slightly concave and

spatulate. The hooklike posterior edge of the symphysis projects below the inferior contour of the mandible at the level of the forward edge of the anterior mental foramen. This large process probably served for insertion of the genio-hyoideus muscle. In *P. (P.) francisi* and other species, there are variously one or two other mental foramina occurring just posterior to the large anterior one.

LOWER DENTITION: I_1-3 , C_1 , P_1-4 , M_1-3 . In six of the eight specimens mentioned above the complete cheek dentition is present or indicated, and consists of three premolars and three molars. The fossil jaws of *P. (P.) francisi* provide the first, if only partial, glimpse of the condition of the anterior dentition of *Prosynthetoceras* (*Prosynthetoceras*). The caniniform P_1 and the base of the incisiform canine are preserved on U.T.B.E.G. No. 31219-214, a left mandible, whereas on U.T.B.E.G. No. 31219-213, also a left mandible, most of the diastema and symphysis remain intact. Whereas the alveoli for the incisors are only partly visible, there is no question that the large caniniform tooth represents not the true canine but rather P_1 . The true canine has shifted forward to become part of the incisiform series. This condition is anticipated in *Syndyoceras* and its persistence verified by *Synthetoceras* [and *P. (L.) siouxensis*]. In each ramus of *P. (P.) francisi*, except the type described by Frick (1937), there is a P_2 or an alveolus for P_2 . However, this tooth when present is much reduced. In F.A.M. No. 33063 and U.T.B.E.G. No. 31219-213, two small alveoli for P_2 are

present, whereas in U.T.B.E.G. No. 31219-214 only one alveolus is present. In all other respects, the specimens are virtually identical, affording no reason for taxonomic separation. In view of the gradual reduction of P_2 in earlier proto-ceratids, and its complete loss in *Synthetoceras tricornatus*, variation in occurrences of this tooth among individuals within any one population is not surprising; it is indeed, to be expected. P_3 of *P. (P.) francisi* is almost indistinguishable from that of the earlier forms. With the exception of the greater recurving of the protoconid, which forms a distinct recess lingually between it and the metaconid, no significant differences in morphology are noted in P_4 . In one specimen (F:A.M. No. 33063), however, the metaconid is expanded anteroposteriorly, anticipating the greater development of that trend in some *S. tricornatus*. It is not certain if the posterior part of this expansion corresponds to the metastylid, for wear has obscured whatever cusp differentiation might have existed. M_2 has a small accessory tubercle at the base of the posterior limb of the protoconid. M_3 of *P. (P.) francisi* is high crowned and lacks any trace of accessory cusps. Except for a distinct parastylid, the other stylids on M_3 are only faintly developed.

LIMBS: The following description of the skeletal elements of *Prosynthetoceras francisi* (F:A.M. No. 32058) from the Wright Farm, Polk County, Texas is based on two or more individuals associated in one field block. F:A.M. No. 32058 covers all associated elements from this block.

FRONT LIMB: A crushed right humerus, lacking the proximal end, is short, stocky, and proportionally more similar to the cervids (e.g. *Cranioceras*) than it is to the camelids. The humerus measures 151 mm. from a point just below the missing head to the distal end of the trochlea. Even though the proximal half of the humerus is distorted because of crushing, the deltoid ridge appears weak and the lateral condyloid crest is faint. The greatest width (35.5 mm.) of the distal half of the humerus is across the trochlea. A prominent ridge on the anterolateral condyle of the trochlea runs straight to the proximal edge of the trochlea as in camelids. In the cervids, this condylar ridge is equally prominent, but it is directed more laterally and terminates at the anterolateral edge of the trochlea. In *P. (P.) francisi* the olecranon fossa is deep, and the internal wall is thin but unperforated. Posteriorly, the trochlear surface does not extend the entire depth of the olecranon

TABLE 6

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Prosynthetoceras (Prosynthetoceras) francisi* (COLD SPRING FAUNA) FROM THE GULF COAST OF TEXAS

| | N | OR | \bar{X} | S | V |
|-----------|----|-----------|------------------|-------------------|------------------|
| P_2 | | | | | |
| L | 1 | 9.0 | — | — | — |
| W | 1 | 4.6 | — | — | — |
| P_3 | | | | | |
| L | 5 | 8.6-10.5 | 9.80 ± 0.31 | 0.710 ± 0.225 | 7.25 ± 2.29 |
| W | 5 | 4.9- 6.3 | 5.30 ± 0.25 | 0.570 ± 0.180 | 10.75 ± 3.40 |
| P_4 | | | | | |
| L | 8 | 9.0-12.0 | 10.81 ± 0.30 | 0.876 ± 0.219 | 8.10 ± 2.02 |
| W | 7 | 6.5- 8.1 | 7.43 ± 0.24 | 0.643 ± 0.171 | 8.64 ± 2.31 |
| M_1 | | | | | |
| L | 8 | 15.5-18.5 | 16.82 ± 0.37 | 1.060 ± 0.265 | 6.30 ± 1.57 |
| W | 9 | 10.7-13.0 | 11.69 ± 0.28 | 0.852 ± 0.201 | 7.28 ± 1.71 |
| M_2 | | | | | |
| L | 14 | 20.0-23.8 | 21.30 ± 0.29 | 1.089 ± 0.205 | 5.11 ± 0.96 |
| W | 14 | 12.0-15.0 | 13.50 ± 0.26 | 0.997 ± 0.188 | 7.39 ± 1.39 |
| M_3 | | | | | |
| L | 16 | 28.3-33.0 | 30.05 ± 0.31 | 1.245 ± 0.220 | 4.14 ± 0.73 |
| W | 15 | 11.6-16.4 | 13.74 ± 0.33 | 1.296 ± 0.237 | 9.43 ± 1.72 |
| P_3-M_3 | 6 | 80.0-90.5 | 85.78 ± 1.62 | 3.970 ± 1.146 | 4.62 ± 1.33 |
| P_4-M_3 | 5 | 71.0-76.5 | 74.56 ± 1.12 | 2.190 ± 0.692 | 2.93 ± 0.92 |
| M_1-M_3 | 6 | 62.0-69.4 | 66.08 ± 1.03 | 2.540 ± 0.733 | 3.84 ± 1.10 |

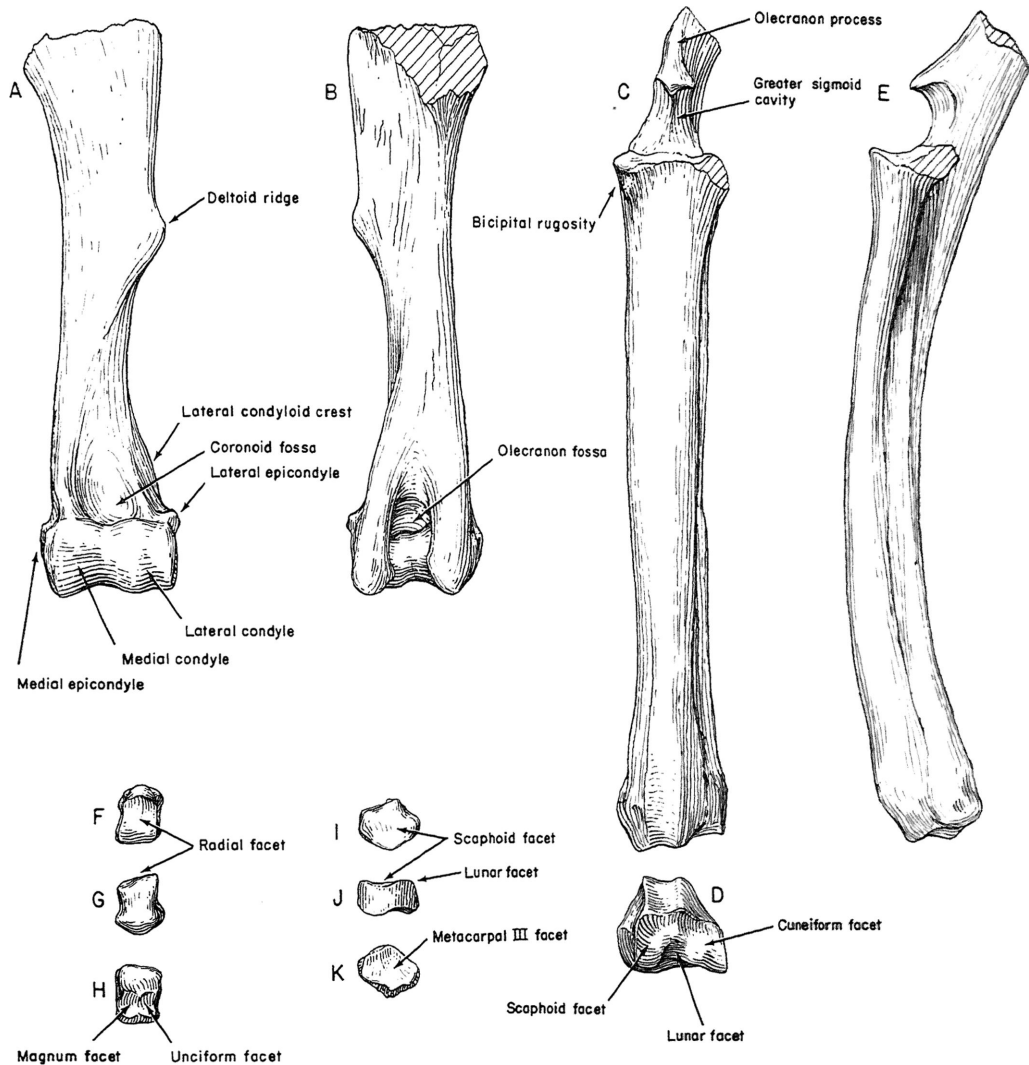


FIG. 14. *P. (Prosynthetoceras) francisi*, from the Wright Farm, Polk County, Texas. Partial skeleton, F:A.M. No. 32058. A, B. Right humerus. A. Anterior view, reversed. B. Posterior view, reversed. C-E. Left and right radii. C. Left radius, anterior view, partly restored from opposite side. D. Right radius, distal view, reversed. E. Left radius, lateral view, partly restored from opposite side. F-H. Right lunar, reversed. F. Proximal view. G. Anterior view. H. Distal view. I-K. Left magnum. I. Proximal view. J. Anterior view. K. Distal view. (For additional skeletal elements of F:A.M. No. 32058, see figs. 15-17.) All $\times \frac{1}{2}$.

fossa. A prominent internal epicondyle is present on the mesial surface.

Both ulnae and radii are represented, but the ulnae lack the proximal part of the olecranon process. Compared with *Protolabis* and *Procamelus*, the radius is proportionally shorter (185 mm.) relative to the estimated length of the humerus, and the ulna is heavier than in both

the cervids and camelids. The proximal part of the ulna is separate from the radius, with the distal part, coossified with the radius as in *Protoceras*. Although the olecranon process is incomplete, enough is present to indicate that it slopes less posteriorly than in the later camelids (e.g. *Procamelus*, *Camelops*), but similar to *Poebrotherium* and the cervids. The articular surface of

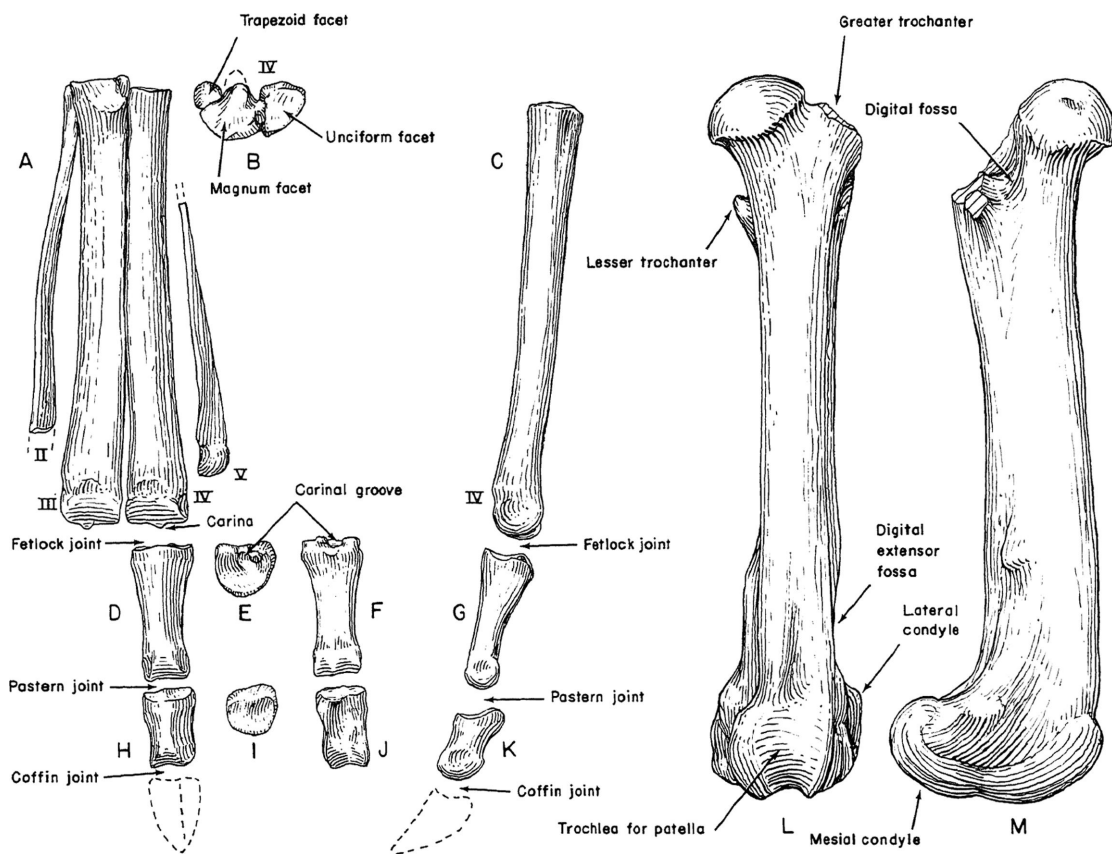


FIG. 15. *P. (Prosynthetoceras) francisi*, from the Wright Farm, Polk County, Texas. Partial skeleton, F:A.M. No. 32058. A. Right partial manus (metacarpals II-V). B. Right metacarpals II-IV, proximal view. C. Right metacarpal IV, lateral view. D-G. Right proximal phalanx. D. Anterior view. E. Proximal view. F. Posterior view. G. Lateral view. H-K. Right median phalanx. H. Anterior view. I. Proximal view. J. Posterior view. K. Lateral view. L, M. Right femur. L. Anterior view. M. Mesial view. (For additional skeletal elements of F:A.M. No. 32058, see figs. 14, 16, 17.) All reversed. $\times \frac{1}{2}$.

the sigmoid notch of the ulna is not divided by a sharp ridge as in *Protolabis* and *Procamelus*. The bicipital rugosity is relatively smaller and less excavated than in *Oxydactylus*, *Procamelus*, and *Camelops*. Distally, the radius resembles that of the equids, and is unlike that of the camelids and other ruminants in the greater distal projection of the facet for the scaphoid, and in the lack of a sharp dividing crest between the articular surface of the cuneiform and the lunar. Despite the prominence of the distal end of the ulna, the articular surface for the lunar is still larger than that for the cuneiform. The largest articular surface is for the scaphoid, with the dividing ridge between it and the lunar facets less prominent than in the camelids and the cervids.

Anteriorly, the lunar is vertically elongate, resembling that of a camelid. Total vertical height of the lunar is 16 mm.; the greatest transverse measurement is 11 mm., and the antero-posterior length is 15.2 mm.; the length is proportionally less than in the camelids. Unlike the camelids, the synthetoceratine lunar lacks the posterior production that articulates with the posterolateral surface of the scaphoid, and the radial articular surface is less convex anteriorly. The posterior half of the radial facet is concave with the posterior border elevated. Posteriorly, the surface of the lunar resembles that of the cervids in having two small basal tuberosities instead of two prominent basal projections as in the camelids. A sharp crest on the distal end of

the lunar divides the two articular surfaces for the unciform and the magnum. A description of both sides of the lunar is based on specimens referred to *P. (L.) trinitiensis* (p. 184).

Metacarpals III and IV are not coossified. Among the associated skeletal elements (F:A.M. No. 32058), are two right and one left metacarpals III. It is assumed that one individual is represented by one right and one left metacarpal III in which the length of both is approximately 111.5 mm. Another larger individual is represented by a right metacarpal III that measures 119 mm. The proximal articular surface of metacarpal III is higher than that of metacarpal IV, and the magnum facet is slightly concave. When the proximal surface of metacarpal III is viewed from above, the lateral and the mesial sides appear strongly compressed posterior to the magnum facet, and the posterior articular surface is narrowed accordingly. The lateral side of metacarpal III has two articular surfaces for metacarpal IV and a small facet on the antero-lateral surface for the unciform. The antero-lateral facet for metacarpal IV is a small concave surface beneath the facet for the unciform; the posterior facet is a small round articular surface on the proximolateral border. A well-defined depression for metacarpal II is also present on the proximomesial surface of metacarpal III; this depression gradually disappears about halfway down the shaft. One fragile but complete lateral metacarpal and several incomplete laterals are present. Lack of evidence prevents us from determining whether the lateral metacarpal is II or V. This lateral metacarpal is 97 mm. in length and would extend almost the full length of either of the associated metacarpals III or IV. On the distal end, the carina is well defined, indicating the presence of lateral phalanges. The distal trochlea of metacarpal III is slightly more expanded than the shaft; transversely, the diameter of the trochlea is 15.3 mm. A prominent carina, which is restricted almost entirely to the posterior surface, projects slightly below the distal articular surface of the trochlea. It is difficult to determine left from right because the width of the distal trochlea on each side of the carina is almost equal. However, the mesial articular surface tends to be more concave than that of the lateral.

One right metacarpal IV (length, 116 mm.) is represented. The posterior portion of the proximal end is broken away, and the mesial side

is damaged so that the articular facets for metacarpal III are obscure. (See a supplementary description of the metacarpal IV of *P. (L.) trinitiensis* on p. 185). A well-defined depression on the proximolateral side of metacarpal IV indicates the presence of metacarpal V. This depression is smaller than the corresponding depression on metacarpal III for metacarpal II. Below the depression on the proximal part of metacarpal IV, the shaft is flattened slightly beyond the midpoint, indicating a closely appressed metacarpal V. In other respects, the distal end resembles that of metacarpal III. Compared to the unconsolidated metacarpals of the earlier occurring *Poebrotherium* in which metacarpals II and V are reduced to rudimentary nodules, metacarpals III and IV of *P. (P.) francisi* have a deeper depression on the proximomesial and proximolateral surfaces and the associated lateral metacarpals extend almost the full length of the central metacarpals.

Of five associated proximal phalanges, the three shortest (35 mm.) are assumed to belong to the manus, and the two longer (43.2 mm.) to the pes. In addition to their shorter length, the proximal phalanx of the manus has a shallower groove for the carina which is less prominent on the metacarpal than the metatarsal. In *P. (P.) francisi* the proximal phalanx is proportionally shorter with the posterior surface less grooved than in the camelids. Compared with that of the cervids, the proximal end of the first phalanx has a shallower carinal groove which also extends less anteriorly on the facet. Furthermore, in *P. (P.) francisi* the proximal articular surfaces on each side of the carinal groove are about the same level, whereas in the cervids the articular surface for the mesial condyle of the metacarpal is much lower. Interestingly enough, the general proportion of the proximal phalanx resembles that of the equids, but the distal half is relatively more slender and the distal articular surface is transversely narrower. In *P. (P.) francisi*, the carinal groove on the proximal end of the first phalanx is not centrally situated, and the articular surfaces on each side of the groove are less symmetrical than in the equids. The proximo-posterior half of the first phalanx is slightly concave in *Prosynthetoceras* and convex in the equids.

A median phalanx of either digit three or four is questionably assigned to the manus because of its short length (21.5 mm.). The proximal width is 13.5 mm., slightly more than the width

(13 mm.) of the distal end of the proximal phalanx. The proportional length of the median phalanx is short compared to that of the proximal phalanx, as in *Protoceras*. Both sides of the pastern facet are shallow and the middle ridge is faint, weaker than in *Cranioceras*, and more like that of the camelids. The middle ridge is weaker than that of *P. (L.) hessei* and similar to that of *Synthetoceras*. As in *P. (L.) hessei*, the two proximo-posterior processes are not separated by a deep groove as they are in *Cranioceras*. The median groove of the coffin facet is shallower than in *Cranioceras* and more like that of the camelids, but the anterior surface of the coffin facet does not extend as far dorsally as in the camelids and the cervids.

REAR LIMBS: Associated remains of *P. (P.) francisi* also include a right femur, which is proportionally short and stocky, with a shaft that is less curved than that of the camelids. It is similar in proportion to that of *Protoceras* but slightly longer; total length, excluding the missing greater trochanter, is 192 mm. The oval depression for the ligamentum teres is situated about midway on the posterior half of the well-rounded head. The greater trochanter has been broken, but the ridge between it and the head is anteroposteriorly compressed, and the underlying digital fossa is large. Although the posterior intertrochanteric ridge connecting the greater and lesser trochanters is also broken, enough is present to show that this ridge is strong. On the lower mesial border of the digital fossa is a prominent hooklike lesser trochanter. The shaft is almost straight and somewhat laterally compressed; it is less cylindrical and lacks the curvature typical of the camelids. Above the lateral condyle is a small, deep digital extensor fossa; expression of this feature varies considerably in both the camelids and the ruminants. Although the lateral condyle is broken, it appears to be almost vertical, in contrast to the mesial condyle which is placed obliquely to the shaft. The trochlea for the patella is wide and deep with the mesial crest projecting much more anteriorly than the lateral crest. The conspicuous prominence of the mesial crest is similar to that of *Cranioceras* and greater than that of the camelids.

Only a single tibia (length, 237 mm.) can confidently be assigned to *P. (Prosynthetoceras)*. The tibia is shorter and heavier proportioned than that of *Poebrotherium*, *Protolabis*, or *Procamelus*, and similar in proportion to *Protoceras*

and *Miolabis*. The latter has unconsolidated metatarsals III and IV, similar to those of the protoceratids. Although the proximomesial condyle in *P. (P.) francisi* is broken, it appears to be slightly smaller than the lateral one. The outer edge of this lateral condyle is eroded, but a weak distal projection suggests the presence of a fibular rudiment that is also present in *Protoceras* but absent in the camelids. Although somewhat crushed, it is evident that the anterior tubercle and crest are less anteriorly produced than in *Poebrotherium*, *Protolabis*, or *Procamelus*; again, similar to *Miolabis*. The anterolateral border of the distal end of the tibia slopes gradually upward from the anteromedial distal process as in *Protoceras*, and unlike that of the camelids in which the anterior border dips sharply downward. Stirton (1967, p. 14) observed that *Lambdoceras* has "no anterolateral distal process at the edge of the fibular facet as in *Paratylopus* and the later camels in that lineage." In *P. (P.) francisi* (F.A.M. No. 32058), a small upward sloping articular-like surface is interpreted as being an anterolateral distal process at the edge of the fibular fossa. This articular surface projects well beyond the fibular fossa and beyond the contour of the shaft of the tibia and is larger than the posterolateral distal process. This is in contrast to the camelids, where both the anterior and posterior lateral distal processes of the fibular fossa are present (i.e. *Gentilicamelus* and *Procamelus*), but the posterior process is the larger. The fibular groove is narrow but deep and disappears about 10 mm. above the fibular facet. On the posteromesial surface, a prominent flexor digitalis groove gradually fades out about 60 mm. above the distal end. The mesial malleolus is slightly longer than the anteromedial distal process as in the camelids. The ridge connecting the anteromedial distal process and the posteromedial process is not straight as in the camelids and cervids but runs in a more posteromesial direction which reduces the articular surface for the mesial condyle of the astragalus.

Also present is a right astragalus, which is 35 mm. in length on the mesial side (the distal portion of the lateral side is broken). The astragalus is similar to that of *Miolabis*, in which the metatarsals III and IV are also unfused. However, in *P. (Prosynthetoceras)* the lateral condyle of the astragalus is lower relative to the mesial condyle than in *Miolabis*. Furthermore, the

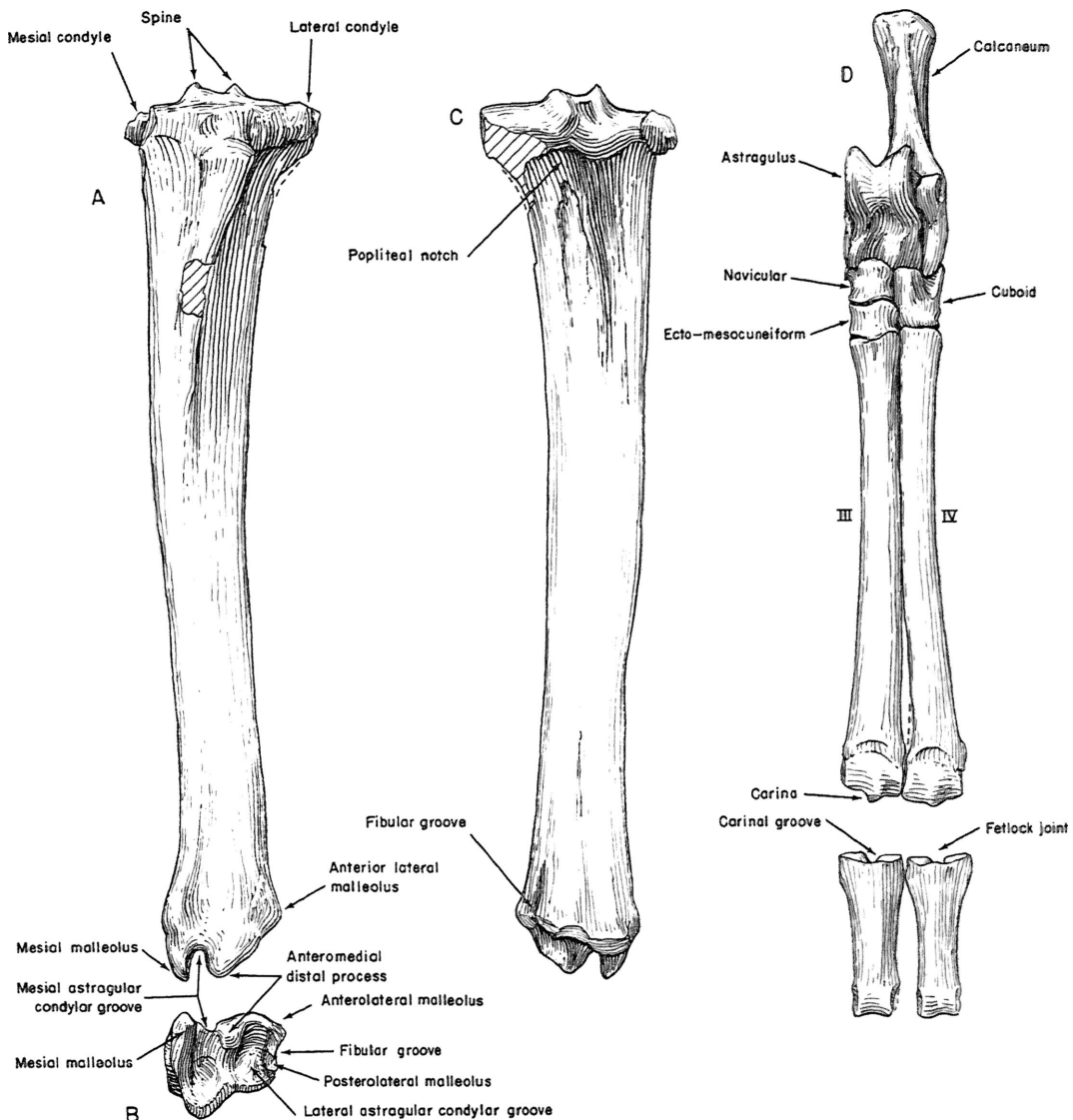


FIG. 16. *P. (Prosynthetoceras) francisi*, from the Wright Farm, Polk County, Texas. Partial skeleton, F:A.M. No. 32058. A-C. Right tibia. A. Anterior view. B. Distal view. C. Posterior view. D. Right pes, anterior view. (For additional skeletal elements of F:A.M. No. 32058, see figs. 14, 15, 17.) All reversed. $\times \frac{1}{2}$.

distal keel on the lateral side is more prominent than in *Miolabis*. When the right astragulus is viewed anteriorly (fig. 17H), the entire distal part below the middle depression is more mesially deflected than in *Miolabis*, and the condyles of the distal trochlea tend more mesially deflected than in *Lambdoceras* [= *P. (Lambdoceras)*], as figured by Stirton (1967, fig. 2a). When the astragulus of *Prosynthetoceras* is compared with

that of *Poebrotherium*, the condyles of the distal trochlear are also more mesially deflected and the astragulus is proportionally longer and narrower, with a more prominent distal keel. The astragulus of *Prosynthetoceras* is similar to that of *Protoceras*, but is longer and narrower than that of the camelids. The sustentacular facet tends to be relatively longer and transversely narrower, and the vertical groove on the facet is

situated nearer the mesial side than in the camelids. In *P. (P.) francisi* the proximal lateral and mesial tuberosities of the condyles are proportionally lower and the connecting transverse bridge is relatively stronger than in *Protoceras celer*. As observed by Stirton (1967, p. 16), *P. (Prosynthetoceras)*, and *P. (Lambdoceras)*, differ from *Protoceras* and the camelids in the absence of the short transverse process at the antero-distal end of the mesial condyle.

A right calcaneum articulates with the astragalus described above. Its total length is 72.5 mm. and it measures 51.5 mm. from the edge of the sustentacular facet to the top of the tuber calcis. In *P. (Prosynthetoceras)*, the lateral and mesial tuberosities of the tuber calcis are less produced, and the plantar sulcus separating the tuberosities is slightly deeper and extends farther onto the shaft than in *Paratylopus*, *Miolabis*, and *Procamelus*. In *P. (Prosynthetoceras)* the greater extension of the plantar sulcus also differs from *Protoceras*. Stirton (1967, p. 16) observed that the mesial surface of the shaft of *P. (L.) hessei* is more depressed than in the camelids; this is especially evident when compared with *Procamelus*. In *P. (P.) francisi*, the mesial facet of the fibular condyle slopes gradually downward; in the camelids this facet is so sharply depressed that it forms a definite notch. The mesial side of the sustentaculum is enlarged and projects posteriorly, similar to that of *Protoceras*, and is larger and more massive than in the camelids. In the description of the calcaneum of *Lambdoceras hessei* [= *P. (L.) hessei*], Stirton (1967, p. 17) stated, "The flexor hallucis longus groove behind the sustentaculum . . . is conspicuously deeper, as is the sustentaculum much larger, than in the cameloids and ruminants." The sustentaculum is comparatively larger in the cervids than in the camelids, and the massive development of the sustentaculum in the protoceratids is similar to that of the cervids. The astragalar-capitulum facet is almost flat, as in *Cramioceras* and *Poebrotherium*. The mesial border of the cuboid facet is almost straight, and the proximal part of the cuboid articular surface slopes inwardly, as in *Protoceras* and the camelids.

In contrast to the cervids, the cuboid and navicular are separate in both the Protoceratidae and the Camelidae. A right navicular articulates almost perfectly with the cuboid and ectocuneiform. Anteriorly, the navicular is transversely narrow and vertically deep (10.8

mm.), with a prominent horizontal groove on the anteromesial surface. When viewed from the mesial side (the plantar process is broken), the astragalar facet of the navicular projects upward to form a prominent posterior tuberosity. The distal mesial surface has a V-shaped spur which marks the posterior extent of the ectocuneiform. On the lateral side, are four articular facets for the cuboid. The anteroproximal facet is small and tends to be oval in shape (the anterodistal facet is broken). The proximal posterior facet is by far the largest, tending to be rectangular and slightly concave near the center. Enough of the posterior distal cuboid facet is present to indicate a relatively small, flat surface. Most of the dorsal surface of the cuboid is a large and deeply concave facet for reception of the mesial condyle of the astragalus; the anteromesial surface slopes downward and near the center the lateral side is marked by a small notchlike opening. Distally, the navicular appears at first to have three separate articular surfaces. The anterodistal two-thirds of the navicular tends to be divided into two articular facets. Stirton (1967, p. 18) surmised that in *P. (Lambdoceras)* these facets might receive both the ectocuneiform and the smaller mesocuneiform, but he pointed out that the tarsals might also be fused as in *Protoceras*. In *P. (P.) francisi* an associated right ecto-mesocuneiform articulates perfectly with the navicular and occupies the entire articular surface for the ectocuneiform and the space believed to be for the mesocuneiform. No entocuneiform has been identified. The facets for the ecto-mesocuneiform and entocuneiform are separated by a sharp spur. No diagnostic characters are observed that distinguish the navicular of *Prosynthetoceras* from that of the camelids.

A right ecto-mesocuneiform articulates with the navicular and the metatarsal III. When the ecto-mesocuneiform is viewed from the proximal end, it projects more posteriorly and has a deeper posteromesial notch than that of the camelids.

A right incomplete cuboid lacks the posteromesial part. Anteriorly, the cuboid is transversely narrow (14 mm.) in comparison to the greater depth (16.5 mm.) between the facets of the astragalus and metatarsal IV. The anterior view shows that the calcaneal facet extends farther distally than in *Protoceras* and most camelids. Anteriorly, the cuboid is slightly depressed between the calcaneal facet and the distal border. A lateral view shows that not only

is the calcaneal facet extended more distally than in the camelids, but also the plantar process is more distally extended than in most cervids and camelids. In the camelids, the plantar process is produced more posteriorly than in *Prosynthetoceras*. Stirton (1967, p. 19) observed that in *Lambdoceras* the peroneus longus groove, which runs diagonally from the anterior part of the calcaneal facet to the anterolateral base of the plantar process, is more clearly defined than in the camelids. This is not true in *P. (P.) francisi* (F.A.M. No. 32058) in which the peroneus longus groove is only a shallow depression that is less prominent than in *Protolabis* and *Miolabis*. The posteromesial part of the cuboid is missing, and the anterior half of the mesial surface has articular facets for the navicular and the ectomesocuneiform. A dorsal view of the cuboid shows that the posteromesial part is broken, including the rear part of the facet for the lateral condyle of the astragalus and the calcaneal facet. The astragalar facet is deeply concave; the narrow elongate calcaneal facet slopes anterodistally and ends 6.5 mm. above the facet for metatarsal IV. Distally, the cuboid bears a large facet for metatarsal IV and a plantar process which projects sharply downward below the level of the facet. A definite facet for metatarsal V is not recognized, but as in *Protoceras* adequate space for a fifth metatarsal occurs at the distal border where the peroneus longus groove terminates between the facet for metatarsal IV and the plantar process.

The third and fourth metatarsals are unfused, as in *Poebrotherium*, *Miolabis*, and *Homocamelus*. Metatarsal III, which measures 125.5 mm. from the facet for the entocuneiform to the carina, is slightly shorter than metatarsal IV. The ectomesocuneiform facet is centrally concave with the mesial border slightly elevated and anteroposteriorly convex; the lateral border is less elevated and narrowed posteriorly by the interosseous fossa. When viewed from the mesial side, the plantar process of the right third metatarsal appears slightly elevated above the level of the ectocuneiform facet with a sharp mesial sloping facet for the entocuneiform. A deep depression, which fades out on the shaft about 15 mm. below the proximal border, is present on the proximomesial surface of the third metatarsal. This depression bears a small facet for a vestigial metatarsal II on the anteroproximal border. In *Prosynthetoceras* the depression for metatarsal II

on the proximomesial surface of metatarsal III indicates that metatarsal II is situated less posteriorly than is its counterpart in the articulated pes of *Protoceras*. Two facets are present on the proximolateral surface of metatarsal III for the articulation of metatarsal IV. A small concave facet is situated anteriorly about 4 mm. below the ecto-mesocuneiform facet, and a larger vertically elongate facet is situated on the plantar process. Transversely, the distal trochlea of metatarsal III measures 17 mm. The carina on the metatarsals is more prominent and extends more anteriorly on the distal surface of the trochlea than on the metacarpals. The carinae of metatarsals III and IV are more prominent and less restricted to the posterior surface of the trochlea than in the camelids (*Poebrotherium*, *Oxydactylus*, and *Miolabis*) that also have unfused metatarsals. Furthermore, protoceratids differ from the camelids in having the lateral condyle of metatarsal III and the mesial condyle of metatarsal IV more distally extended (see fig. 16D) than on their counterparts, the mesial condyle of metatarsal III and the lateral condyle of metatarsal IV.

The length of metatarsal IV from the cuboid facet to the carina (129.5 mm.) is slightly greater than that of metatarsal III. Both the posterior edge of the cuboid facet and the plantar process are broken but enough remains to show that the cuboid facet is concave and the anteromesial and posterolateral borders slightly elevated. On the anteromesial surface of metatarsal IV a small projecting facet articulates with the concave facet on opposing metatarsal III. The proximolateral surface of metatarsal IV has a deep depression that gradually disappears onto the shaft about 16 mm. below the proximal end. This depression is similar to that on metatarsal III and indicates the presence of a vestigial metatarsal V, as in *Protoceras*. The distal trochlea of metatarsal IV resembles that of the previously described metatarsal III, except that on metatarsal IV the mesial condyle is more distally produced than the lateral one.

Two proximal phalanges articulate almost perfectly with metatarsals III and IV. The total length of each is 43.2 mm., both being longer than the first phalanges of the manus. In addition to their greater length, the proximal phalanges of the pes can be distinguished from those of the manus by the presence of a deeper groove for the more prominent carinae of the

metatarsals. As in the cervids, the proximal facet of the rear first phalanx in *Prosynthetoceras* is higher on the lateral side than on the mesial side. The carinal groove is deep posteriorly as in the cervids, and it extends more anteriorly than in the camelids. In *Prosynthetoceras* and *Protoceras* the distal end of the proximal rear phalanx is less expanded transversely relative to the diameter of the shaft, and the posteroproximal surface is flatter and less grooved than in the camelids.

TABLE 7

COMPARATIVE LIMB LENGTHS (IN MILLIMETERS) OF A
PARTIAL SKELETON OF *P. (Prosynthetoceras) francisi*
F:A.M. No. 32058 AND *Synthetoceras tricornatus*
F:A.M. No. 40229

| | F:A.M. No. 32058 | F:A.M. No. 40229 |
|----------------|----------------------|---------------------|
| Humerus | (165.0) ^a | 214.0 |
| Radius | 185.0 | — |
| Metacarpal III | 111.5 | 138.0 |
| Femur | 192.0 | — |
| Tibia | 237.0 | (283.0) |
| Metatarsal III | 125.5 | (154.0) |

^aMeasurements in parentheses are estimated.

SUBGENUS **LAMBDOCERAS** STIRTON, NEW RANK

Table 15

Lambdoceras STIRTON, 1967, p. 4.

TYPE SPECIES: *Prosynthetoceras (Lambdoceras) hessei* Stirton, 1967.

DISTRIBUTION: Medial Hemingfordian to early Barstovian of Nebraska, South Dakota, and Texas Coastal Plain.

INCLUDED SPECIES: The type species, *P. (L.) trinitensis*, new species, and *P. (L.) siouxensis* Frick.

DIAGNOSIS: *P. (Lambdoceras)* differs from the type subgenus in that nearly contemporaneously occurring species are relatively larger, have less elongate skull and jaws, shorter diastemata, and more flattened frontal horns. The frontal horns, which are backswept in *P. (P.) francisi*, are more perpendicularly directed in *P. (Lambdoceras)*. The rostral horn of the more advanced species of *P. (Lambdoceras)*, i.e., *P. (L.) trinitensis* and *P. (L.) siouxensis*, never attains the length of that of *P. (P.) francisi* (and its descendant, *S. tricornatus*). Further, the rostral horn of *P. (Lambdoceras)* retains a relatively short fork in comparison

with that of *P. (Prosynthetoceras)*. Dentition is less advanced than in *P. (Prosynthetoceras)*; premolars more wedge-shaped and less reduced; P_1 invariably present and P_2 invariably double-rooted.

Limbs of *P. (Lambdoceras)* differ from those of *P. (Prosynthetoceras)* in that they average larger and are heavier proportioned, and the ulna is less firmly coalesced with the radius. The medial phalanx of the manus in *P. (Lambdoceras)* is shorter and heavier proportioned, and the calcaneal sustentaculum is more massive than in *Prosynthetoceras*. Deeper and more distally extended depressions occur on the proximal ends of metatarsals III and IV in *P. (Lambdoceras)* for proportionately larger metatarsals II and V.

DISCUSSION: In a paper published posthumously, the late R. A. Stirton described a new genus and species of the Protoceratidae, *Lambdoceras hessei*, from the Hemingfordian Flint Hill local fauna of South Dakota and concluded that it was most closely related to *Syndyoceras* and *Synthetoceras*. Separation of *Lambdoceras* from those genera was based primarily on characters of the teeth and rostral horn. Limb elements were described, but because very little information was then available on the post-cranial skeleton of other synthetoceratine taxa, few substantive comparisons could be made. Stirton correctly recognized that the Flint Hill specimens differed significantly from either *Syndyoceras* or *Synthetoceras* as those genera were then constituted. Although rather closely related, *Syndyoceras* and *Synthetoceras* differed substantially in morphology and were of different geologic age. The development of the unique cranial armament that characterizes the Synthetoceratinae was in an early stage in the skull of the Arikareean and early Hemphillian *Syndyoceras* and was culminated in the fantastic horns of the Clarendonian *Synthetoceras*. This morphologic (and taxonomic) disparity was shown also in the extreme reduction of the anterior dentition from *Syndyoceras* to *Synthetoceras*. Unfortunately, the genus *Prosynthetoceras*, which Frick (1937) originally erected as a subgenus of *Synthetoceras*, was poorly known until recently and its importance in bridging the morphological (and again, taxonomic) gap between the two genera only dimly perceived. Thus, Stirton justifiably regarded the Flint Hill specimens as generically distinct from the only other synthetoceratine genera then recognized, *Syndyoceras* and *Synthetoceras*. Stirton was aware, however, that delineation

tion of the more precise affinities of the Synthetoceratinae would depend on eventual clarification of the relationships of the many Gulf Coast taxa known at that time. Such a study was in fact in progress at the time Stirton wrote, and the first report on the results of this work (Patton, 1967) actually preceded Stirton's delayed publication. Many of the problematical taxa Stirton regarded as preventing fuller understanding of the systematic placement of *Lambdoceras* have been demonstrated to be synonyms of just two species of *Prosynthetoceras*, *P. texanus* and *P. francisi*, and these forms represent a virtually unbroken sequence leading to *Synthetoceras* (Patton, 1966, 1967). In addition to the confusion surrounding the taxonomy and nomenclature of Gulf Coast artiodactyls known at that time, Stirton was unaware of undescribed specimens of a new Gulf Coast species, *P. (Lambdoceras) trinitiensis*, which occupies a stratigraphic position intermediate between *P. texanus* and *P. francisi*. We consider *P. (L.) trinitiensis* to be the coastal plain representative of a species group [including *P. (L.) siouxensis*] distributed primarily in the Great Plains region (see Zoogeography on p. 208). Recognition of this species group removes more of the doubt Stirton expressed with regard to the affinities of *Lambdoceras* to *Prosynthetoceras* by demonstrating that the concept of the latter taxon does not rest entirely on the characters of *P. (P.) texanus* and *francisi* but includes as well a group whose features closely resemble *L. hessei*. Thus, because we regard those criteria employed by Stirton in erecting the genus *Lambdoceras* as being insufficient to separate that taxon from *Prosynthetoceras*, we have put it into synonymy with the latter. Furthermore, we consider those characters that are shared by and tend to unify the species *P. hessei*, *P. trinitiensis*, and *P. siouxensis* sufficient to warrant grouping them as a subgenus, *Prosynthetoceras* (*Lambdoceras*).

***Prosynthetoceras* (*Lambdoceras*) *hessei* Stirton**
Tables 1, 8, 9

Lambdoceras hessei STIRTON, 1967, p. 5, figs. 1-3, pls. 1-3.

TYPE: U.C.M.P. No. 32372, maxillary rostral horn from the Flint Hill Quarry deposits (U.C.M.P. location V-3417) Batesland Formation, Bennett County, South Dakota. Illustrated by Stirton, 1967, pl. 1.

HYPODIGM: U.C.M.P. No. 32377, right

maxillary dP²-4-M¹; U.C.M.P. No. 32380, right maxillary, dP²-M¹; U.C.M.P. No. 23282, left maxillary, dP³-4-M¹; U.C.M.P. Nos. 37467, 73168, 73169, three dP³s; U.C.M.P. Nos. 37669, 73164, 73165, three M¹s; U.C.M.P. Nos. 37670, 73166, 73167, three M²s; U.C.M.P. No. 32381, part of right mandible, P₃-M₃ well worn; U.C.M.P. No. 68696, fragment of mandible at posterior end of symphysis; U.C.M.P. No. 53523, P₂; U.C.M.P. No. 37674, P₃; U.C.M.P. No. 37675, M₁; U.C.M.P. No. 37676, M₂; U.C.M.P. No. 37677, dP₄-M₁; U.C.M.P. Nos. 37671, 73170, 73171, three dP₃s; U.C.M.P. No. 37672, dP₃; U.C.M.P. No. 37673, dP₄; U.C.M.P. No. 37682, scapula; U.C.M.P. No. 37679, lunar; U.C.M.P. No. 37683, unciform; U.C.M.P. No. 37681, trapezoid; U.C.M.P. No. 37678, metacarpal III; U.C.M.P. No. 68695, three proximal phalanges of manus; U.C.M.P. No. 53517, five median phalanges of manus; U.C.M.P. No. 68692, two distal phalanges; U.C.M.P. No. 73172, distal end tibia; U.C.M.P. No. 68691, calcaneum; U.C.M.P. No. 37438, seven astragali; U.C.M.P. Nos. 37468, 53519, cuboids; U.C.M.P. No. 68693, two naviculars; U.C.M.P. No. 37471, metatarsals III and IV; U.C.M.P. No. 68694, proximal end of metatarsal IV; U.C.M.P. No. 37474, 12 proximal phalanges of pes; U.C.M.P. No. 53520, median phalanx of pes; U.C.M.P. No. 68697, distal phalanx of pes.

DIAGNOSIS: The smallest species of the subgenus, *P. (L.) hessei*, differs from *P. (L.) trinitiensis* and *P. (L.) siouxensis* in having: a wider and more transversely flattened rostral horn; relatively larger and more distinctly lobed lower premolars; P₃ anteroposteriorly longer than P₄ and relatively longer than in the other species; relatively lower-crowned molars; a smaller M₃ relative to the size of the other molars; and smaller and lighter proportioned limbs.

DISCUSSION: In terms of geologic age, *P. (L.) hessei* most closely approaches *P. (P.) texanus* from the medial Hemingfordian Garvin Gully Fauna of the Texas Coastal Plain. Morphologically, however, the two species differ considerably: *P. (L.) hessei* is approximately 23 per cent larger than *P. (P.) texanus* and possesses a lower crowned and more complex dentition. This is especially true of the lower premolars (no upper premolars of *P. (L.) hessei* have been recovered). P₂ of *P. (L.) hessei* has a higher protoconid and more strongly developed hypoconid; the poste-

TABLE 8

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Prosynthetoceras* (*Lambdoceras*) *hessei*, *Prosynthetoceras* (*Lambdoceras*) *trinitensis*, AND *Prosynthetoceras* (*Lambdoceras*) *siouxensis*

| | N | OR | \bar{X} | S | V |
|--------------------------------|---|------------|------------|-------------|------------|
| <i>P. (L.) hessei</i> | | | | | |
| M ³ | | | | | |
| L | 1 | 22.4 | — | — | — |
| W | 1 | 22.7 | — | — | — |
| <i>P. (L.) trinitensis</i> | | | | | |
| P ² | | | | | |
| L | 5 | 9.8–11.2 | 10.50±0.47 | 1.632±0.516 | 6.02±1.90 |
| W | 5 | 6.0– 8.6 | 6.94±0.46 | 1.040±0.329 | 14.98±4.73 |
| P ³ | | | | | |
| L | 7 | 11.3–12.8 | 12.11±0.19 | 0.515±0.137 | 4.25±1.13 |
| W | 7 | 8.0–11.7 | 9.86±0.43 | 1.160±0.310 | 11.62±3.10 |
| P ⁴ | | | | | |
| L | 6 | 11.5–12.6 | 12.18±0.17 | 0.427±0.123 | 3.50±1.01 |
| W | 6 | 14.3–15.5 | 14.80±0.17 | 0.419±0.121 | 2.83±0.81 |
| M ¹ | | | | | |
| L | 5 | 18.0–20.8 | 18.96±0.53 | 1.197±0.378 | 6.31±1.99 |
| W | 5 | 20.0–21.0 | 20.50±0.19 | 0.436±0.138 | 2.12±0.67 |
| M ² | | | | | |
| L | 8 | 21.5–28.0 | 24.45±0.78 | 2.219±0.555 | 9.07±2.26 |
| W | 8 | 22.2–25.3 | 23.51±0.23 | 1.017±0.254 | 4.32±1.08 |
| M ³ | | | | | |
| L | 7 | 22.5– 25.5 | 24.11±0.36 | 0.962±0.257 | 3.99±1.06 |
| W | 5 | 21.0– 24.5 | 22.90±0.59 | 1.321±0.418 | 5.76±1.82 |
| P ² –P ⁴ | 5 | 34.0– 36.5 | 35.28±0.50 | 1.120±0.354 | 3.18±1.00 |
| P ³ –P ⁴ | 5 | 23.0– 26.0 | 24.62±0.52 | 1.175±0.372 | 4.77±1.50 |
| M ¹ –M ³ | 5 | 60.6– 69.2 | 65.08±1.54 | 3.450±1.090 | 5.30±1.67 |
| P ² –M ³ | 5 | 94.0–102.8 | 98.42±1.67 | 3.750±1.186 | 3.81±1.20 |
| <i>P. (L.) siouxensis</i> | | | | | |
| P ³ | | | | | |
| L | 1 | 12.2 | — | — | — |
| W | 1 | 11.0 | — | — | — |
| P ⁴ | | | | | |
| L | 1 | 12.2 | — | — | — |
| W | 1 | 16.5 | — | — | — |
| M ¹ | | | | | |
| L | 1 | 22.0 | — | — | — |
| W | 1 | 21.8 | — | — | — |
| M ² | | | | | |
| L | 1 | 27.0 | — | — | — |
| W | 1 | 25.2 | — | — | — |
| M ³ | | | | | |
| L | 1 | 26.0 | — | — | — |
| W | 1 | 24.0 | — | — | — |
| P ² –P ⁴ | 1 | 33.2 | — | — | — |
| P ³ –P ⁴ | 1 | 25.0 | — | — | — |
| M ¹ –M ³ | 1 | 73.0 | — | — | — |
| P ² –M ³ | 1 | 104.0 | — | — | — |

TABLE 9

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Prosynthetoceras* (*Lambdoceras*) *hessei*, *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, AND *Prosynthetoceras* (*Lambdoceras*) *siouxensis*

| | N | OR | \bar{X} | S | V |
|--------------------------------|---|------------|-------------|-------------|-----------|
| <i>P. (L.) hessei</i> | | | | | |
| P ₃ | | | | | |
| L | 1 | 12.3 | — | — | — |
| W | 1 | 6.4 | — | — | — |
| P ₄ | | | | | |
| L | 1 | 11.5 | — | — | — |
| W | 1 | 8.9 | — | — | — |
| M ₁ | | | | | |
| L | 1 | 16.0 | — | — | — |
| W | 1 | 13.4 | — | — | — |
| M ₂ | | | | | |
| L | 1 | 19.5 | — | — | — |
| W | 1 | 15.6 | — | — | — |
| M ₃ | | | | | |
| L | 1 | 28.0 | — | — | — |
| W | 1 | 15.0 | — | — | — |
| P ₂ -M ₃ | 1 | 94.0 | — | — | — |
| P ₂ -P ₄ | 1 | 33.0 | — | — | — |
| P ₄ -M ₃ | 1 | 71.0 | — | — | — |
| M ₁ -M ₃ | 1 | 61.0 | — | — | — |
| <i>P. (L.) trinitiensis</i> | | | | | |
| P ₂ | | | | | |
| L | 4 | 8.5- 9.5 | 9.07±0.21 | 0.436±0.154 | 4.80±1.69 |
| W | 4 | 4.4- 5.2 | 4.80±0.16 | 0.337±0.119 | 7.02±2.48 |
| P ₃ | | | | | |
| L | 4 | 10.0- 11.0 | 10.45±0.20 | 0.525±0.186 | 5.03±1.77 |
| W | 4 | 5.5- 7.7 | 6.80±0.54 | 1.089±0.385 | 1.60±0.56 |
| P ₄ | | | | | |
| L | 9 | 11.9- 13.0 | 12.27±0.11 | 0.339±0.080 | 2.76±0.65 |
| W | 9 | 7.5- 10.0 | 8.87±0.29 | 0.715±0.175 | 8.40±1.98 |
| M ₁ | | | | | |
| L | 4 | 18.0- 19.0 | 18.37±0.24 | 0.480±0.170 | 2.61±0.92 |
| W | 5 | 13.0- 14.5 | 13.68±0.30 | 0.684±0.216 | 5.00±1.58 |
| M ₂ | | | | | |
| L | 7 | 21.0- 23.5 | 22.36±0.37 | 0.988±0.264 | 4.41±1.18 |
| W | 6 | 14.7- 17.0 | 15.70±0.43 | 1.040±0.300 | 6.61±1.41 |
| M ₃ | | | | | |
| L | 9 | 30.0- 35.5 | 31.85±0.56 | 1.692±0.399 | 5.31±1.25 |
| W | 8 | 15.2- 18.0 | 16.50±0.20 | 1.209±0.302 | 7.33±1.83 |
| P ₂ -M ₃ | 4 | 99.0-107.0 | 102.87±1.87 | 3.750±1.325 | 3.64±1.28 |
| P ₂ -P ₄ | 3 | 29.5- 32.5 | 31.33±0.92 | 1.610±0.657 | 5.13±2.04 |
| P ₄ -M ₃ | 5 | 77.5- 88.0 | 82.40±2.04 | 4.490±1.421 | 5.45±1.72 |
| M ₁ -M ₃ | 5 | 66.0- 75.5 | 70.10±1.88 | 4.231±1.339 | 6.04±1.91 |
| <i>P. (L.) siouxensis</i> | | | | | |
| P ₂ | | | | | |
| L | 2 | 10.2- 10.2 | 10.20 | — | — |
| W | 2 | 5.3- 6.2 | 5.75 | — | — |
| P ₃ | | | | | |
| L | 3 | 11.5- 12.1 | 11.76 | — | — |
| W | 3 | 6.8- 7.8 | 7.33 | — | — |

TABLE 9—(Continued)

| | N | OR | \bar{X} | S | V |
|--------------------------------|---|------------|-----------|---|---|
| P ₄ | | | | | |
| L | 3 | 13.9– 14.2 | 14.03 | — | — |
| W | 2 | 8.5– 11.1 | 9.80 | — | — |
| M ₁ | | | | | |
| L | 3 | 17.5– 19.5 | 18.66 | — | — |
| W | 2 | 14.0– 14.5 | 14.25 | — | — |
| M ₂ | | | | | |
| L | 2 | 23.5– 27.0 | 25.25 | — | — |
| W | 2 | 16.4– 25.7 | 21.05 | — | — |
| M ₃ | | | | | |
| L | 2 | 34.5– 35.0 | 34.75 | — | — |
| W | 1 | 17.5 | — | — | — |
| P ₂ –M ₃ | 1 | 109.0 | — | — | — |
| P ₂ –P ₄ | 1 | 34.0 | — | — | — |
| P ₄ –M ₃ | 1 | 88.8 | — | — | — |
| M ₁ –M ₃ | 1 | 75.0 | — | — | — |
| C–P ₂ | 1 | 94.5 | — | — | — |

rior moiety of P₃ of *P. (L.) hessei* is wider, whereas P₃ of *P. (P.) texanus* is more evenly compressed laterally. The greatest difference in premolar construction, however, is in P₄. That of *P. (L.) hessei* is a considerably more blocky, or "squared," tooth than that of *P. (P.) texanus*, even considering wear differences in the only comparable specimens. It is distinctly three-lobed, with the posterior lobe being approximately 18 per cent wider than the anterior lobe. In *P. (P.) texanus* the middle lobe (protoconid) is not pinched off from the others, as in *P. (L.) hessei*; the greatest width of the tooth with respect to total length is about 11 per cent less than that of *P. (L.) hessei*. Molar configuration of the two species is similar, but the molars of *P. (P.) texanus* are taller crowned. Those differences described between *P. (L.) hessei* and *P. (P.) texanus* are even more pronounced between *P. (L.) hessei* and the immediate descendant of *P. (P.) texanus*, *P. (P.) francisi*. The greatest similarities to the dentition of *P. (L.) hessei* are found in *P. (L.) trinitiensis* and *P. (L.) siouxensis*. In contrast to the progressively reduced premolars of the *texanus-francisi-tricornatus* lineage, those of *hessei*, *trinitiensis*, and *siouxensis* have undergone relatively little reduction and retain a more conservative configuration in cusp morphology. This is evident in their greater posterior width and in their more distinctly lobed construction. The molars of the latter group are similar but are shorter crowned than those of the former. However, *P. (L.) hessei* differs from *P. (L.) trinitiensis* and *P. (L.) siouxensis* primarily in

its smaller size, deeper jaw, and larger premolars.

In describing *Lambdoceras*, Stirton was impressed with the marked difference in size and shape of the frontal horn in comparison with those of *Syndyoceras* and *Synthetoceras*. Because the skull and horns of *P. (P.) texanus* (then ?*S. rileyi*) and *P. (L.) trinitiensis* were then unknown, Stirton believed the Flint Hill horn to be sufficiently distinct from those of the two then known genera to warrant separate generic status.

Now, however, with the description of *P. (L.) hessei*, *P. (L.) trinitiensis*, and *P. (L.) siouxensis*, the presumed disparity in relationship between the various synthetoceratine horn types is more easily resolved. The progression in size and shape of the horns of the *texanus-francisi-tricornatus* lineage is now readily apparent. The specimen of *P. (P.) texanus* from the Garvin Gully fauna is seen to have a small but distinctly shafted rostral horn, a condition which clearly demonstrates its advance over that of *Syndyoceras*. Moreover, trends in size and shape of the rostral horn through the Burkeville and Cold Spring faunas relate the Garvin Gully *P. (P.) texanus* firmly (and ancestrally) to *P. (P.) francisi* and, ultimately, *Synthetoceras tricornatus*. Thus, the horn condition of the early Gulf Coast species, *P. (P.) texanus* (then ?*S. rileyi*), which was a major concern to Stirton, is established as being intermediate between *Syndyoceras* and *Synthetoceras*. Quite importantly, it is also closely similar to that of *P. (Lambdoceras) hessei* and is a significant

factor in assigning the two species to the same genus. In addition, those horn characters that distinguish *P. (L.) hessei* from the *P. (P.) texanus-francisi* group are found not to be unique to *hessei* but serve rather to unite it with *P. (L.) trinitiensis* and *P. (L.) siouxensis* and have contributed to the assessment of the three species as comprising a distinct subgenus. The primary difference in the rostral horn between the two groups is the shorter forks and generally more flattened cross-section of the *P. (L.) hessei* group. Never does the horn of the *P. (L.) hessei* group attain the sweeping dimensions reached by the later members of the *P. (P.) texanus-francisi* group. Further, the forks of the rostral horns in the *P. (L.) hessei* group are relatively shorter than those of the *P. (P.) texanus* group. Of the three *Lambdoceras* species, only *P. (L.) trinitiensis* differs in any significant way from the others. Whereas fork length in *P. (L.) trinitiensis* closely approximates that found in *P. (L.) hessei* and *siouxensis*, shaft length is proportionally greater. Also, and perhaps most significantly, cross-sectional shapes of the shaft in *P. (L.) hessei* and *siouxensis*, both Great Plains forms, are very similar, whereas that of the Gulf Coastal Plain, *P. (L.) trinitiensis*, diverges from the former two. The shaft of both *P. (L.) hessei* and *siouxensis* is flattened and broadened posteriorly, and the anterior end is narrower and rounder. In *P. (L.) trinitiensis* the shaft cross-section is ovate, with the long dimension directed anteroposteriorly. The two Great Plains species resemble each other also in the size and depth of surface grooving; in these forms the rostral horn is marked by large channels running up the anterolateral edges. Whereas other surface grooving corresponds to the characteristic synthetoceratine patterns, no other species possesses such deep channeling as that which appears on *P. (L.) hessei* and *siouxensis*. There is no readily apparent functional explanation for the larger channels, considering the rather small size of the horns.

***Prosynthetoceras (Lambdoceras) trinitiensis*,
new species**

Figures 18–26, 31, 34; tables 1, 8, 9, 10

TYPE: F:A.M. No. 33073, complete skull, except for the premaxilla and anterior part of maxilla, with rostral and orbital horns and P^2-M^3 (figs. 18–21). The type is from Trinity River Pit 1, 7 miles northeast of Cold Spring, San Jacinto County, Texas (see table 2). The quarry

is situated on the south bank of the Trinity River, about 1000 feet downstream from the mouth of Prayer Creek directly below a high point or bluff known locally as Pine Island Hill. Trinity River Pit 1 is in the upper part of the Fleming Formation and lithologically 225 to 300 feet below the lithic zone from which the published Cold Spring fauna of Wilson (1956) was derived, according to the unpublished stratigraphic data of Skinner on file in the American Museum of Natural History; see discussion on page 207. The type was collected by N. Z. Ward in 1954.

DISTRIBUTION: Known only from the type locality.

HYPODIGM: Trinity River Pit 1, upper part of the Fleming Formation, San Jacinto County, Texas: Type and F:A.M. No. 33080, anterior part of skull with rostral horn, C alveolus, and P^2-M^3 ; F:A.M. No. 33081, partial female skull, lacking the rostral horn and postorbital regions, with P^2-M^3 ; F:A.M. No. 33082, crushed partial female skull, lacking the premaxilla and rostral horn area, with P^2-M^3 and a postorbital protuberance indicating restrained horn development; F:A.M. No. 33083, postorbital part of skull; F:A.M. No. 33084, incomplete maxillary region with C alveolus and base of rostral horn; F:A.M. No. 33085, rostral horn fragment; F:A.M. No. 33086, posterior part of skull with right orbital horn and associated detached maxillary region with rostral horn; F:A.M. No. 33087, partial female skull with P^2-M^3 ; F:A.M. No. 33088, posterior part of skull with right orbital horn; F:A.M. No. 33089, anterior maxillary region with rostral horn; F:A.M. No. 33090, partial rostral horn; F:A.M. No. 33091, right orbital horn; F:A.M. No. 33092, left partial orbital horn; F:A.M. No. 33093, left mandible with broken symphysis, P_1 , P_2-P_3 alveolus, and P_4-M_3 ; F:A.M. No. 33094, right partial mandible with P_2 alveolus- M_3 ; F:A.M. Nos. 33095, 33096, 33097, partial rami; F:A.M. Nos. 33098, 33099, partial rami with P_2-M_3 ; F:A.M. Nos. 32037, 32038, partial rami; F:A.M. Nos. 32048, 32049, 32052, partial ramus and detached teeth; F:A.M. Nos. 32053, 32054, 32055, 32056, partial maxillae and upper dentition; F:A.M. No. 32057, immature partial maxilla with dP^2-dP^4 ; F:A.M. Nos. 34123, 34124, distal part humeri; F:A.M. Nos. 34125–34128, three complete and one partial radii; F:A.M. No. 34129, partial radius, Trinity River Pit 1 dump;

F:A.M. No. 34130, partial ulna; F:A.M. No. 34065, scaphoid; F:A.M. Nos. 34066, 34066A, 34066B, three lunars; F:A.M. No. 34068, magnum; F:A.M. Nos. 32198, 32273, 32274, three metacarpals III; F:A.M. Nos. 32275–32277, three metacarpals IV; F:A.M. Nos. 32279, 34111, 34112, 34113, incomplete metacarpals; F:A.M. No. 34118, lateral metapodial (metacarpal ?II or V); F:A.M. No. 34119, lateral metapodial (metacarpal ?II or V); F:A.M. Nos. 34120–34122, three distal part lateral metapodials; F:A.M. Nos. 34176–34179 inclusive and 34055, 34056, 34056-A, seven proximal phalanges belonging to digits III or IV of the manus; F:A.M. Nos. 34057–34061, 34061-A, 34061-B, seven medial phalanges of the manus; F:A.M. Nos. 34173–34175, 34175B, four distal phalanges of the manus; F:A.M. Nos. 34110, 34131–34133, four femurs; F:A.M. Nos. 34134, 34135, distal part femurs; F:A.M. Nos. 34159, 34160, broken patellae; F:A.M. Nos. 34136–34144, three complete and six partial tibiae; F:A.M. Nos. 34146–34152, seven astragali; F:A.M. Nos. 34155–34158, four calcanea; F:A.M. Nos. 34069–34072, four naviculars; F:A.M. Nos. 34073–34077, five cuboids; F:A.M. Nos. 32280–32282 and 34100–34102, six metatarsals III; F:A.M. No. 34103, immature metatarsal III; F:A.M. Nos. 34104, 34105, metatarsals IV; F:A.M. No. 34106, immature metatarsal IV; F:A.M. Nos. 34107, 34108, 34115, 34115A, 34116, distal part of metatarsals III and IV; F:A.M. Nos. 34161–34165, five proximal phalanges belonging to digits III or IV of the pes; F:A.M. Nos. 34166–34172, seven medial phalanges of the pes; F:A.M. Nos. 34175A, 34062, distal phalanges of the pes.

E. R. Harvey No. 1, 1 and $\frac{2}{16}$ miles on road 224 on Stephens Creek, San Jacinto County, Texas: F:A.M. No. 34117, immature metatarsal III; F:A.M. No. 34063, partial rostral horn; F:A.M. No. 34064, proximal phalanx of digit III or IV of the pes.

DIAGNOSIS: *P. (L.) trinitiensis* differs from *P. (L.) hessei* in having a narrower and less transversely flattened rostral horn; relatively smaller and less distinctly lobed premolars; P_3 anteroposteriorly shorter than P_4 , relatively taller-crowned molars; a larger M_3 relative to the size of the other molars; and larger and heavier proportioned limbs.

P. (L.) trinitiensis differs from *P. (L.) siouxensis* in having: a larger but less prominently grooved

rostral horn; a less elongate mandibular diastema; a relatively larger P_1 ; and a relatively smaller and lower-crowned M_3 .

DESCRIPTION: Skull: In contrast to the slim, elongated skull of *P. (P.) francisi*, that of *P. (L.) trinitiensis* is stout, rather wide, and foreshortened. Although there are differences in proportions throughout the skull, the most notable occur in the region of the snout. In this species, snout length is significantly shorter relative to maxillary breadth than in *P. (P.) francisi* or *S. tricornatus*. There is also a notable decrease in the length of the muzzle anterior to the cheek teeth. Part of this foreshortening of the skull has taken place in the posterior half of the skull as well. The distance between the anterior edge of the foramen magnum to the posterior edge of M^3 measures 120 mm. in *P. (L.) trinitiensis*, 141 mm. in *P. (P.) francisi*; the distance between the posterior edge of M^3 to a point below the middle of the rostral horn measures 120.2 mm. in *P. (L.) trinitiensis*, 137 mm. in *P. (P.) francisi*. In contrast to the shorter skull of *P. (L.) trinitiensis*, the cheek tooth row of the latter measures approximately 95 mm., that of *P. (P.) francisi* 84 mm. Thus while there has been a shortening of the skull of *P. (L.) trinitiensis*, there also has been an actual relative increase in length of the cheek dentition (fig. 31).

The skull profile of *P. (L.) trinitiensis* is low and relatively flat with a slight flexure of the level of the postorbital rim. A strong sagittal crest extends anteriorly from the lambdoidal ridge and bifurcates into two less distinct ridges leading to the posterior edges of the frontal horns. This feature is more prominent in *P. (L.) trinitiensis* than in *P. (P.) texanus* or *P. (P.) francisi*. Bones surrounding the orbit, especially the postorbital bar, of *P. (L.) trinitiensis* tend to be more thickly constructed than in *P. (P.) texanus* or *P. (P.) francisi*. As in *P. (P.) francisi*, the strong masseteric ridge extends to a point above the anterior edge of M^2 . However, the bony knob that protects vessels leading to the rostral horn, and which is placed above the infraorbital foramen in *P. (P.) francisi*, is situated more posteriorly in *P. (L.) trinitiensis*; in the former it occurs above P^4 , in the latter, above M^1 . Except for the aforementioned differences in proportion and increased sturdiness, the configuration of the male skull of *P. (L.) trinitiensis* is in most respects virtually indistinguishable from that of *P. (P.) francisi* and *S. tricornatus*.

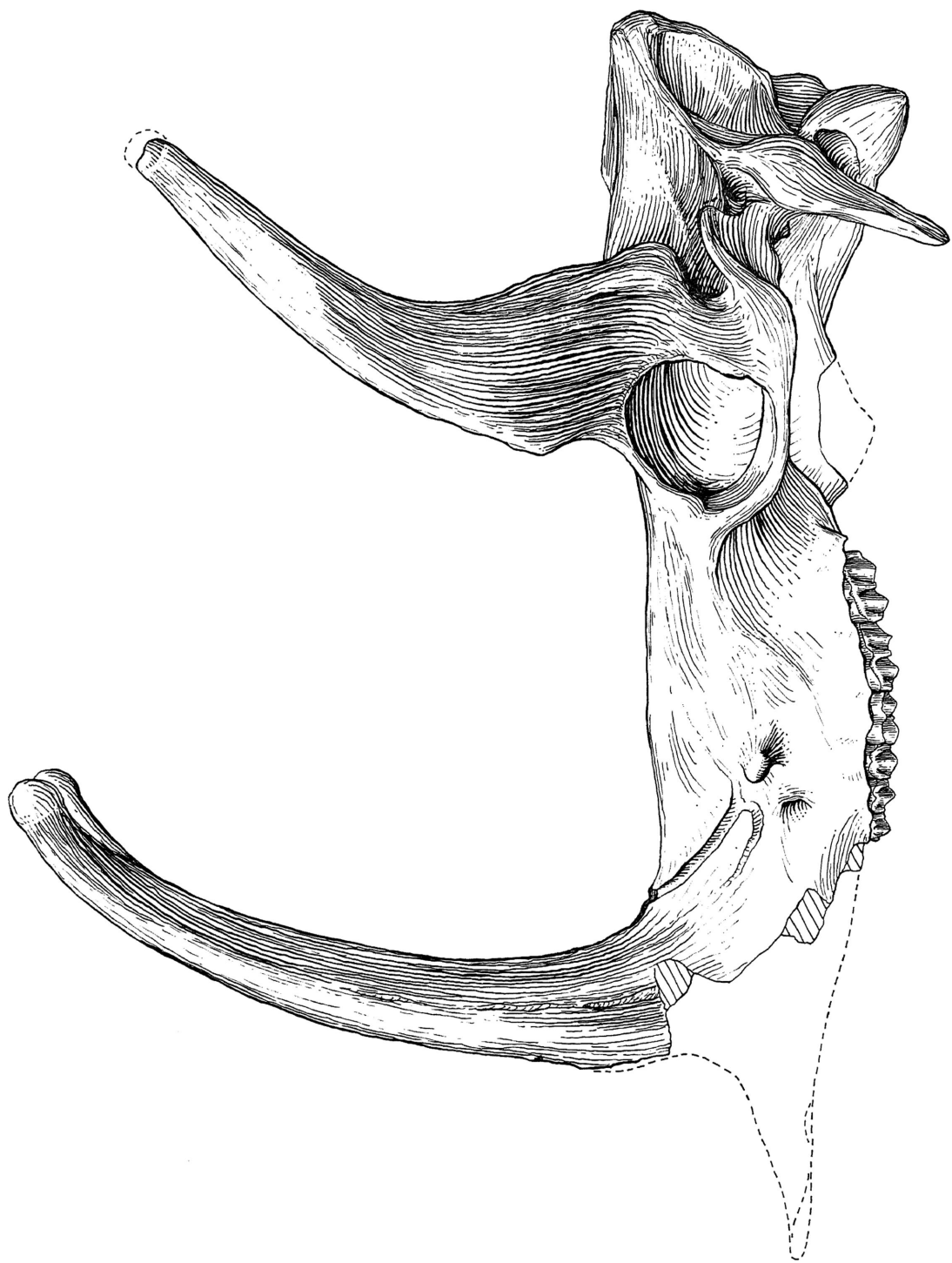


FIG. 18. *Prosyntheloceras* (*Lambdoceras*) *trinitensis*, new species, type, F.A.M. No. 33073, from Trinity River Pit 1, San Jacinto County, Texas. Lateral view (P₂ restored from right side). $\times \frac{1}{2}$. [See lateral and ventral views, figs. 19 and 20 (photographs) and occlusal view of dentition and posterior view of skull, fig. 21.]



FIG. 19. *Prosynthetoceras* (*Lambdoceras*) *trinitensis*, new species, type, F.A.M. No. 33073. Lateral view. $\times 0.60$. (See figs. 18, 20, and 21.)

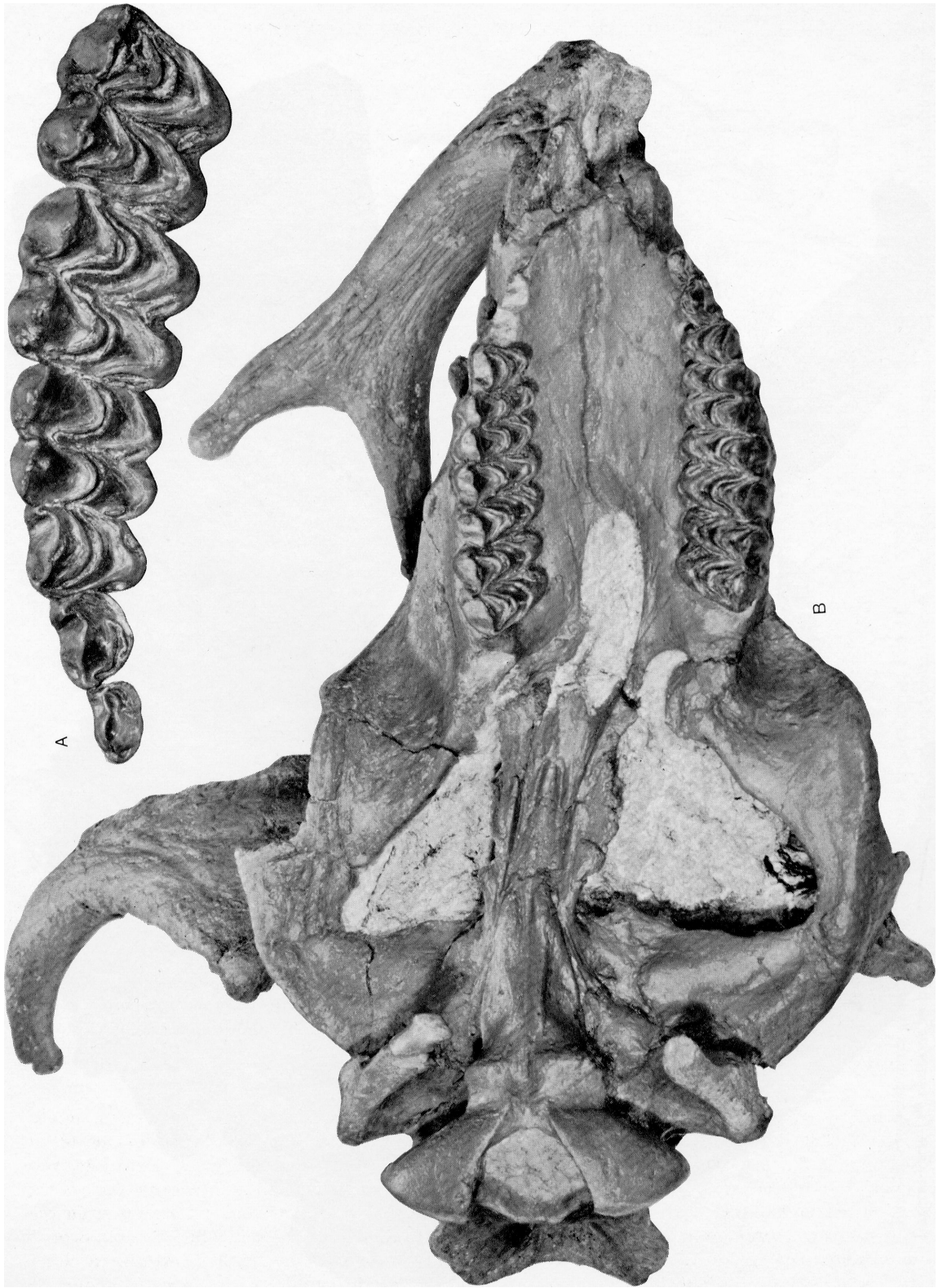


FIG. 20. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, type, F.A.M. No. 33073. A. Occlusal view. $\times 1.20$. B. Ventral view. $\times 0.60$. (See figs. 18, 19, 21.

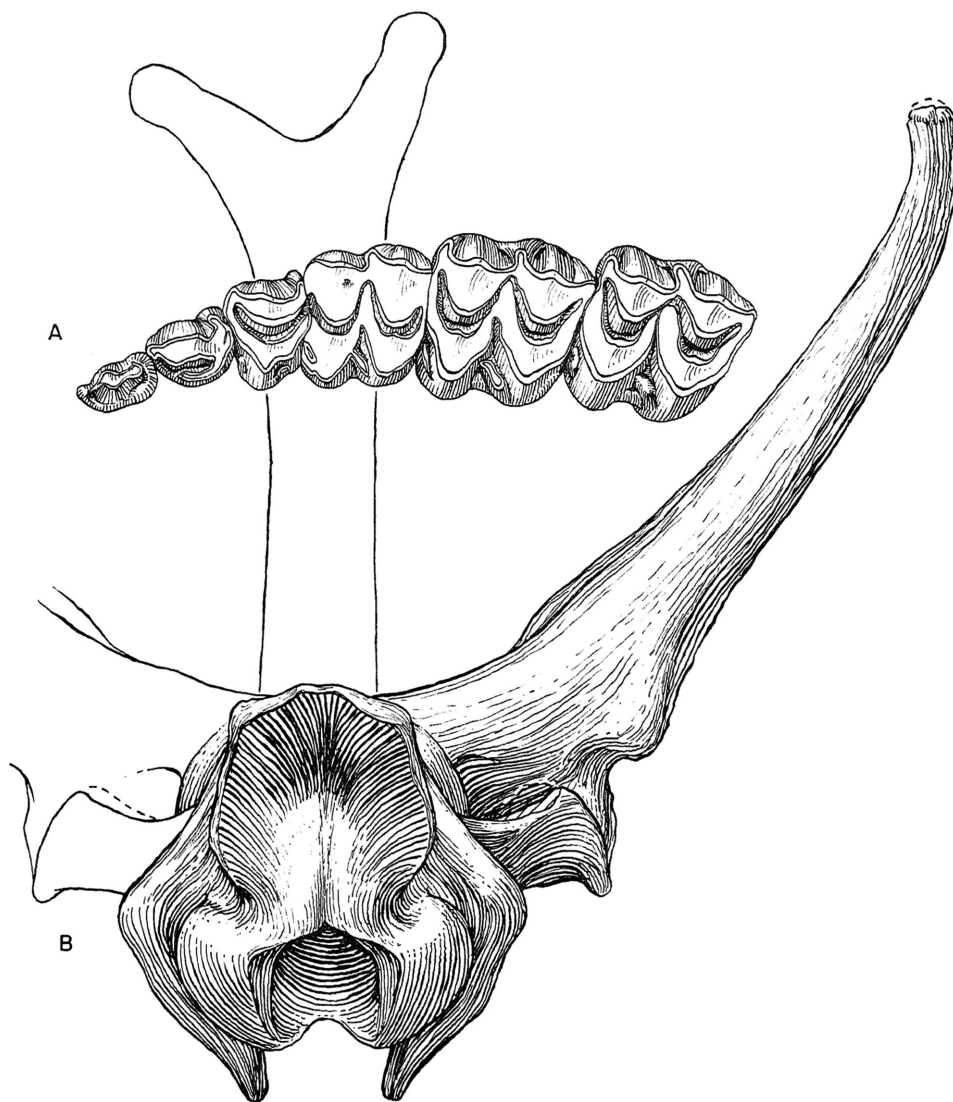


FIG. 21. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, type, F:A.M. No. 33073, from Trinity River Pit 1, San Jacinto County, Texas. A. Occlusal view. $\times 1$. B. Posterior view with outline of rostral horn. $\times \frac{1}{2}$. (For lateral views, see figs. 18 and 19 and occlusion of dentition and ventral view of skull, fig. 20.)

The first recognizable female skulls (F:A.M. Nos. 33082, 33087) in the synthetoceratine lineage belong to *P. (L.) trinitiensis*. Other female specimens include one partial skull of *Synthetoceras* from Clarendon, Texas and another of the same genus from Florida (see below). The most obvious difference between the male and female skull is the absence of comparable cranial armament in the latter. The large, recurved frontal

horns of the male are reduced to small triangular projections extending from the dorsoposterior rim of the orbit, just above the postorbital bar (fig. 23C). This portion of the frontal bone is not thickened for support and protection as in the male skull. The orbit itself, which juts out prominently in the males, is smaller and placed closer to the lateral profile of the face. Although all female synthetoceratine skulls lack preserved



FIG. 22. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, referred partial skull, F:A.M. No. 33080, from Trinity River Pit 1, San Jacinto County, Texas. Lateral view. $\times \frac{1}{2}$.

muzzles, it seems most reasonable to assume they had no rostral horns. *Protoceras* females lacked both frontal protuberances and the arched maxillaries antecedent to the synthetoceratine rostral horn. Furthermore, of all the cranial armament, the rostral horn appears to be most certainly the specialized offensive weapon of the male. Bones in the rostral region of the female

skull are more lightly constructed than in the male, undoubtedly because of the absence of a rostral horn. Nasal bones of the female skull are retracted to above the level of P³, as in the males; however, the nares are not divided into anterior and posterior openings like those of the males.

HORNS: The horns of male *P. (L.) trinitiensis*

differ significantly from those of *P. (P.) texanus*, *P. (P.) francisi*, and *S. tricornatus*. Trends in horn size, shape, and direction noted in the *P. (P.) texanus-francisi* group are not maintained in *P. (L.) trinitiensis*, which in these and other characters bears more resemblance to *P. (L.) hessei* and *P. (L.) siouxensis* from Great Plains faunas. Similar to *P. (P.) texanus*, and unlike *P. (P.) francisi* and *S. tricornatus*, the frontal horns of *P. (L.) trinitiensis* extend out over the orbit perpendicular to the long axis of the skull. The horn is triangular in cross section at the base and is widely expanded anteroposteriorly just beyond the base. In *P. (P.) francisi*, the base of the frontal horn is thick and about the shape of an equilateral triangle, with the ventral apex an acute angle; the posterior edge is declined ventrally and roughened by small knobs. In *P. (L.) trinitiensis*, on the other hand, it is much wider and flatter at the base and is shaped more in the form of a scalene triangle with the ventral apex an obtuse angle. There is also less ventral inclination on the posterior edge. Distally, the frontal horn becomes circular and tapers toward the tip, which is capped by a small bulb. Except for the rather symmetrical flare at the base, the edges of the frontal horn of *P. (L.) trinitiensis* are relatively smooth, especially in comparison with those of *P. (P.) francisi* and *S. tricornatus*.

The rostral horn of *P. (L.) trinitiensis* differs from that of other Gulf Coast synthetoceratines in size and in the proportional lengths of the shaft and the forks. Circumference of the shaft of the rostral horn (measured about halfway between the base and the fork) of the type (F:A.M. No. 33073) of *P. (L.) trinitiensis* measures 97 mm., approximately the same as that of the type of the more fragile *P. (P.) francisi*. In *S. tricornatus*, this figure reaches 138 mm. In cross section, the *P. (L.) trinitiensis* shaft tends to be circular, whereas those of *P. (P.) francisi* and *S. tricornatus* are more oval, the flattening taking place in the sagittal plane. The most notable difference of the rostral horn between *P. (L.) trinitiensis* and the other Coastal Plain species is its shorter over-all length and the generally shorter fork relative to length of shaft. In *P. (P.) texanus-francisi*, and *S. tricornatus*, the fork is at least one-third (usually one-half) of the total length of the horn, but in *P. (L.) trinitiensis* it is commonly no more than one-fifth of the total length (fig. 21). Only in one specimen (F:A.M. No. 33080, fig. 22) does the fork attain

any appreciable length. Like *P. (P.) texanus* and *P. (L.) siouxensis*, the base of each fork is flattened transversely; in *P. (P.) francisi* and *S. tricornatus* the direction of flattening is variable. In all other characters, the morphology of the *P. (L.) trinitiensis* rostral horn compares closely to that of other synthetoceratines. It is interesting to note that of all the many synthetoceratine horns recovered, only one (F:A.M. No. 33089) appears to have suffered any noticeable injury. In this specimen, the left tine of the rostral horn barely extends beyond the point of bifurcation. The tip is capped by a small bulb as in normal specimens. Even in this instance it is questionable whether this deformation is truly due to an injury or to an accident of development.

UPPER DENTITION: I^0 , C^1 , P^2-4 , M^1-3 . In none of the *P. (L.) trinitiensis* specimens available for study is the anterior dentition preserved. When judged from the condition of the incisors and canine in taxa, which *P. (L.) trinitiensis* resembles in all other respects and which occur above and below it in the stratigraphic section, there is no reason to suppose that *P. (L.) trinitiensis* differed in any major way.

The premolars of *P. (L.) trinitiensis* are less reduced than those of *P. (P.) francisi*; relative to the M^1-M^2 length, P^2-P^4 of *P. (L.) trinitiensis* is 7 per cent longer than in *P. (P.) francisi*. P^2 is two-rooted and is relatively larger and more complicated than that of *P. (P.) francisi*. It is characterized by a high paracone, a lower metacone, and a relatively prominent and flexed metastyle. The parastyle is pinched off from the principal cusp (paracone), but is not flexed labially. However, the parastyle does extend lingually to merge with a short but distinct anterolingual cingulum. Posteriorly, P^2 is marked by a strong anterolingual cingulum that leads from the metastyle to near the base of the paracone. A small basal cingulum connects this cingulum with the anterior one mentioned above. In contrast to those of *P. (L.) trinitiensis* none of the principal or accessory cusps of the *P. (P.) francisi* P^2 are so prominent. The anterolingual cingulum in *P. (P.) francisi*, for example, is virtually absent.

P^3 of *P. (L.) trinitiensis* has lost the longitudinally compressed shape characteristic of most artiodactyl anterior premolars and has become more triangular, or "molarized." The paracone and metacone are more swollen, and the metastyle is much stronger and more recurved than

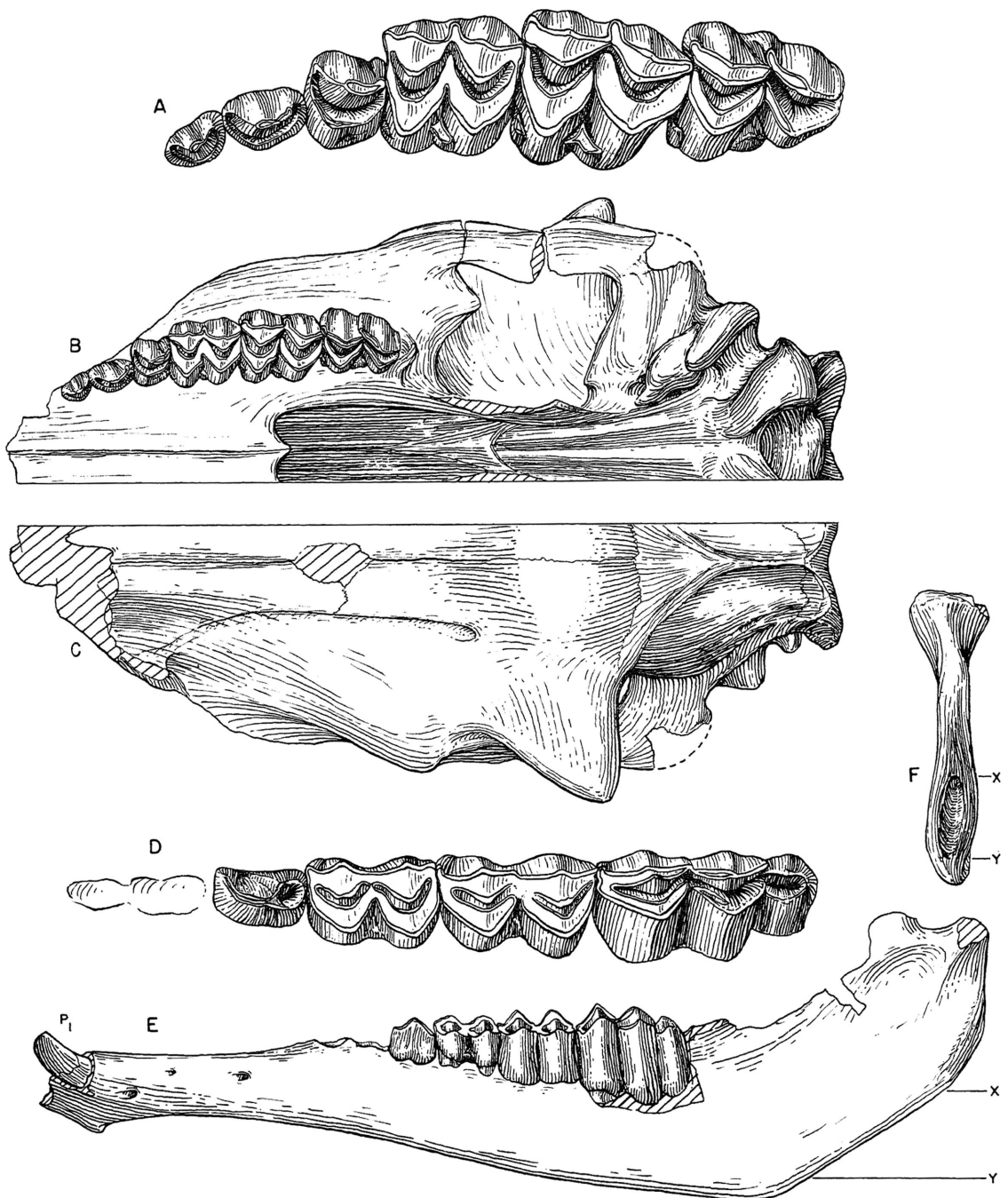


FIG. 23. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, referred, from Trinity River Pit 1, San Jacinto County, Texas. A-C. Partial female skull, F:A.M. No. 33082. A. P²-M³, occlusal view. $\times 1$. B. Palatal view. $\times \frac{1}{2}$. C. Dorsal view. $\times \frac{1}{2}$. D-F. Left mandible, F:A.M. No. 33093 (see fig. 34.). D. P₂-P₃ alveoli, P₄-M₃, occlusal view. $\times 1$. E. Lateral view. $\times \frac{1}{2}$. F. Posterior view (showing prominent fossa on the angle of the mandible.) $\times \frac{1}{2}$.

in *P. (P.) francisi*. On the labial base of the rather weak parastyle is a small accessory tubercle. The most notable difference, however, between the P^3 of *P. (L.) trinitiensis* and that of *P. (P.) texanus* and *francisi* is the extreme growth of the posterolingual cingulum in the former. Arising from the exaggerated metastyle, it extends virtually undiminished around the lingual border of the tooth to abut on the parastyle. The only other *Prosynthetoceras* species with a comparable P^3 is *P. (L.) siouxensis* from Nebraska, a species with which *P. (L.) trinitiensis* is grouped taxonomically. P^3 of *P. (P.) texanus* and *francisi* is more like that of *Syndyoceras cooki* in shape and size.

P^4 of *P. (L.) trinitiensis* is large and trenchant; the protocone is deepened lingually and is flanked by a small cingular cusp posteriorly and an accessory tubercle anteriorly. The metastyle is pronounced and recurved; the parastyle is much more weakly expressed.

The upper molars of *P. (L.) trinitiensis* resemble closely those of other synthetoceratines in the strong development of styles and accessory cusps. In contrast to a rather weak metastyle, the parastyle and mesostyle are very prominent. Both the paracone and metacone are distinctly ribbed. Lingually, the molars are characterized by large intercolumnar tubercles between the protocone and metacone and a bladed cingulum along the anterior limb of the protocone. With wear, each of these accessory cusps forms a fossettid between it and the adjacent primary cusp. In crown height, *P. (L.) trinitiensis* molars compare more closely with *P. (P.) texanus* and *francisi* than with *S. tricornatus*.

MANDIBLE: The unique shape and configuration (morphology) of the synthetoceratine mandible as expressed in specimens of *P. (P.) francisi* and *S. tricornatus* are seen clearly in *P. (L.) trinitiensis*. As in the first two species, the mandible is characterized by an elongate, slender, horizontal ramus with a long diastema and by a peculiarly nonexpanding ascending ramus. The latter structure was only partially preserved in the *P. (P.) francisi* specimens; however, in at least one specimen (F:A.M. No. 33093) of *P. (L.) trinitiensis*, the complete ramus is available for description. The tiny laterally deflected coronoid process noted in *P. (P.) francisi* and *S. tricornatus* is characteristic also of *P. (L.) trinitiensis*. Although the very tip is broken away, this thin, rounded structure rises hardly above the level of



FIG. 24. *Prosynthetoceras (Lambdoceras) trinitiensis*, new species, referred immature partial maxilla, F:A.M. No. 32057, from Trinity River Pit 1, San Jacinto County, Texas. DP²-dP⁴, occlusal view. $\times 1$.

the condyle. Its lateral surfaces are marked by scars for attachment of the temporalis muscle. The articular surface of the condyle is not preserved but appears to have been level and undifferentiated, as in *S. tricornatus*.

The ventral part of the ascending ramus is remarkable for its lack of an expanded masseteric (fossa) region. This feature was first mentioned in the description of *P. (P.) francisi*, but because of poor preservation, was not fully observable in that species. It is, however, fully described under *S. tricornatus*. Whereas the angle of the mandible in almost all other artiodactyls is widely curved toward the condyle, that of *P. (L.) trinitiensis* (and other synthetoceratines) turns rather abruptly from the horizontal and continues obliquely in a straight line parallel to the anterior border of the ascending ramus. This straight border is approximately 75 mm. long. At a point roughly level to the molar row, the border becomes vertical and continues to the condyle. This unusual shape is not anticipated in either *Protoceras* or *Syndyoceras*, but must have evolved in early *P. (P.) texanus* and *P. (L.) hessei* populations. On the other hand, the low coronoid can be traced back to the *Protoceras* stage of proto-ceratid evolution.

The inferior border of the ascending ramus is marked by a rather deep sulcus, (fig. 23F) presumed earlier to serve for insertion of the occipito-mandibularis muscle. This structure is unique in artiodactyls. As in *S. tricornatus*, the inferior border of the horizontal ramus flattens below the molar row, probably for insertion of the digastric.

The mandibular diastema of *P. (L.) trinitiensis* is not so long as that of *S. tricornatus*, partially because *P. (L.) trinitiensis* retains P_1 and P_2 . The diastemal crest is sharp, but not pinched as in *P. (P.) francisi* and *S. tricornatus*. Large mental foramina occur at the base of the root of the

caniniform P_1 and about midway along the side of the diastema.

LOWER DENTITION: None of the incisiform teeth of *P. (L.) trinitiensis* has been recovered, but because of the consistency of their expression throughout the subfamily, they are presumed to be about the same as in other species. The large caniniform P_1 (F:A.M. No. 33093) is laterally compressed into more of a blade than in *P. (P.) francisi*. [P_1 is not represented among the *P. (P.) texanus* specimens.] It is tilted anteriorly and flares laterally. In contrast to the single-rooted P_2 of *P. (P.) francisi*, P_2 of *P. (L.) trinitiensis* possesses two distinct roots. It is, however, a small and simple tooth; the paraconid is in line with the protoconid, and only a slight distinction exists between the hypoconid and entoconid. P_3 , on the other hand, is much larger and more heavily constructed. In comparison with *P. (P.) texanus* and *P. (P.) francisi*, the posterior half of the tooth is considerably wider than the front. P_3 has a small anterolingual flexid (paraconid), a high and thick protoconid, and a posterolingually flexid (entoconid). The entoconid varies in degree of expression, but usually reaches the hypoconid posteriorly. P_4 of *P. (L.) trinitiensis* is a relatively larger and more wedge-shaped tooth than that possessed by either *P. (P.) texanus* or *P. (P.) francisi*. The paraconid is more strongly flexed and the separation of the entoconid and hypoconid is more conspicuous than on P_3 . Lingually, the hypoconid curves to contact the posterior border of the entoconid; with wear, however, the two cuspids enclose a large fossettid.

The lower molars of *P. (L.) trinitiensis* are morphologically inseparable from those of *P. (P.) texanus*, *P. (P.) francisi*, and *S. tricornatus*, but are taller crowned than the first two of these species. Only M_1 has an accessory tubercle between hypoconid and protoconid.

LIMBS: The limbs of *P. (L.) trinitiensis* (figs. 25, 26) are described and compared with those of *P. (P.) francisi*. This description is restricted primarily to supplementing the description of the partial skeleton (F:A.M. No. 32058) of *P. (P.) francisi* and describing skeletal elements unrepresented by this skeleton. Differences between the two taxa are noted.

FRONT LIMB: The broken distal half of a right humerus (F:A.M. No. 34123) is tentatively referred to *P. (L.) trinitiensis*. Except for its larger size, it is comparable with that of *P. (P.) francisi*. The

transverse diameter of the distal trochlea of the humerus is 44.5 mm. versus 35.5 mm. for that of *P. (P.) francisi* (F:A.M. No. 32058).

Three radii (F:A.M. Nos. 34125–34127), ranging in length from 223 mm. to 240 mm., are referred to *P. (L.) trinitiensis*. The proximal part of the radius and ulna are unfused as in the cervids. In all three, the rugose posterior surface indicates that almost the entire ulna was loosely attached to the radius, and only the distal ends of the radius and ulna are coossified. In *P. (P.) francisi*, the entire distal half of the radius and ulna tend to be coalesced, and the bicipital rugosity is less marked than in *P. (L.) trinitiensis*. The diameter of the proximolateral facet of the radius, which articulates with the lateral condyle of the humerus, is transversely wider than the facet for the mesial condyle, and relatively larger than in *Cranioceras*. Furthermore, the articular facet for the lateral condyle of the humerus is less concave, and the posterior border is less notched for the prominent lateral condylar ridge of the humerus than in the cervids. The articular facet of the radius for the mesial condyle of the humerus is more notched on the posterior mesial border than in the cervids and equids. This notch is for the attachment of the strong ulna so characteristic of the protoceratids. When viewed anteriorly, the lateral border of the proximal end of the radius flares less outwardly in *Prosynthetoceras* than in both the cervids and equids.

The proximal half of a right detached ulna (F:A.M. No. 34130, fig. 25C) is tentatively referred to *P. (L.) trinitiensis*. This allocation appears to be almost certain because the anterior part articulates almost perfectly with the distinctive contour and marked rugosity on the posterior part of a right radius (F:A.M. No. 34127). This is the only known synthetoceratine radius with a complete olecranon process. The olecranon process is long and slopes more posteriorly than that of *P. (P.) francisi* (F:A.M. No. 32058). In *P. (L.) trinitiensis* (F:A.M. No. 34130) the olecranon process is longer than that of the equids. The length and the posterior sloping of the olecranon process corresponds more closely to that of the camelids, but the anterior border curves more mesially than in either the equids or the camelids. In *P. (L.) trinitiensis*, the strong mesial curve of the olecranon process terminates about midway, in contrast to the equids, in which a more gradual

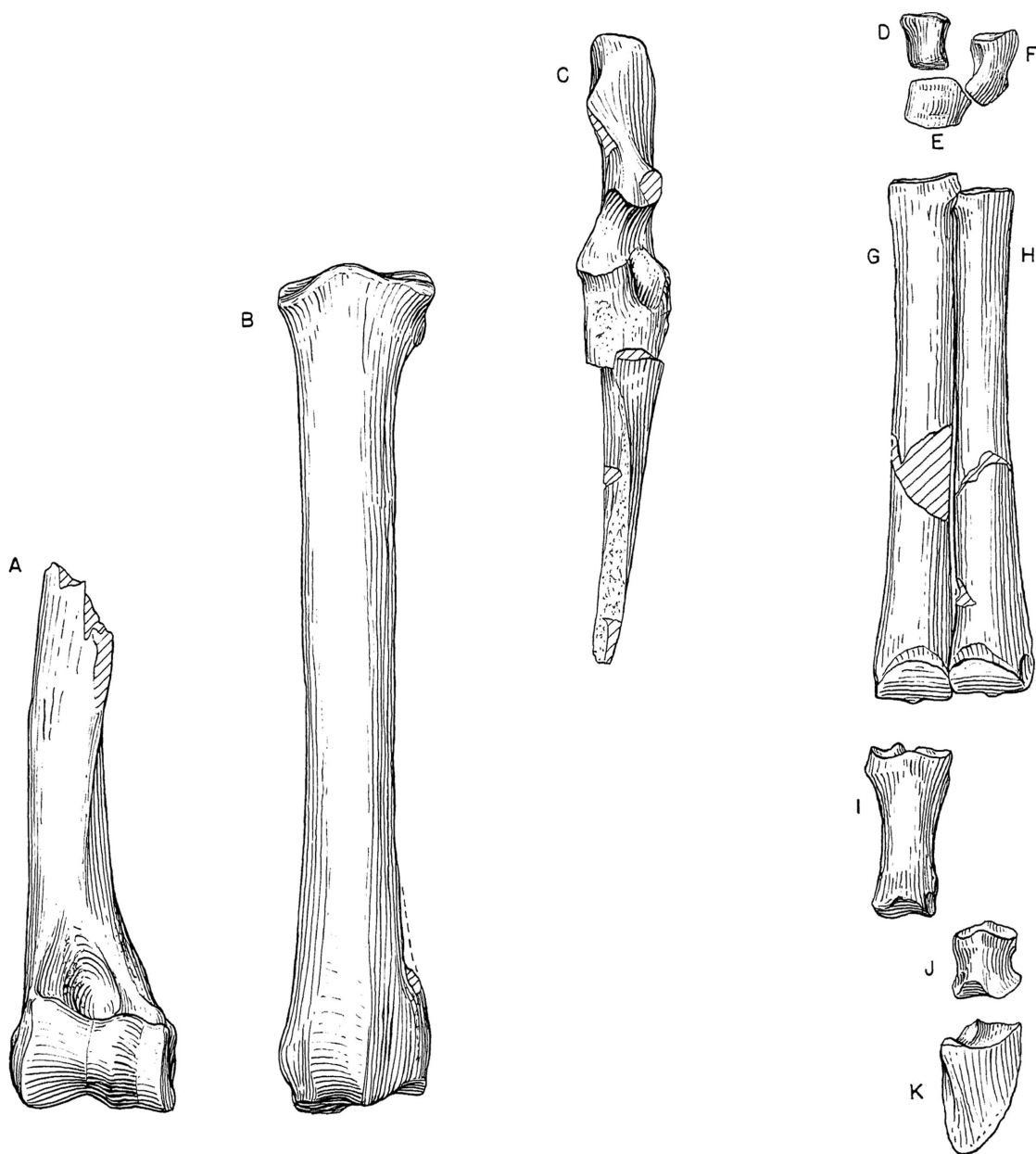


FIG. 25. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, from Trinity River Pit 1, San Jacinto County, Texas. A. Right partial humerus, F:A.M. No. 34123, anterior view, reversed. B. Right radius, F:A.M. No. 34127, anterior view, reversed. C. Right partial ulna, F:A.M. No. 34130, anterior view, reversed. D. Left scaphoid, F:A.M. No. 34065, anterior view. E. Right magnum, F:A.M. No. 34068, anterior view, reversed. F. Right lunar, F:A.M. No. 34066A, anterior view, reversed. G. Right metacarpal III, F:A.M. No. 32274, anterior view, reversed. H. Right metacarpal IV, F:A.M. No. 32277, anterior view, reversed. I. Right proximal phalanx, F:A.M. No. 34055, anterior view, reversed. J. Right medial phalanx, F:A.M. No. 34061B, anterior view, reversed. K. Right distal phalanx, F:A.M. No. 34174, anterior view, reversed. All $\times \frac{1}{2}$.

mesial curve extends nearly the full length of the process. Furthermore, in *Prosynthetoceras* the mesial articular surface of the greater sigmoid cavity is relatively larger and distally wider than in the equids.

A left scaphoid (F:A.M. No. 34065, fig. 25D) is tentatively referred to *P. (L.) trinitiensis*. The greatest anterior vertical height is 14.5 mm.; the width is 12.8 mm. Most of the proximal surface of the scaphoid is a large concave facet for attachment to the mesial condyle of the radius. However, the eminence just anterior of the concavity slopes anterodistally. When viewed from the mesial side, the scaphoid narrows sharply near the middle, and the posterior half is approximately 25 per cent narrower than the anterior part and transversely narrower than in the camelids. Both the anterior and mesial surfaces of the left scaphoid resemble those of the camelids. The posterior surface is narrower than in the camelids with the proximoposterior border less elevated than in the cervids. On the lateral surface, both the anterolateral and anterodistal facets for the lunar are indistinct because of abrasion. The posterolateral facet for the lunar is very small, much smaller than in the camelids, in which the lunar is more posteriorly produced. The anterodistal facet of the scaphoid for the magnum is a slightly convex surface that narrows and terminates about midway between the anterior and posterior borders of the scaphoid. Posterior to this magnum facet is a narrow concave facet for the trapezoid. The magnum and trapezoid facets are not separated by so prominent a ridge as in the camelids. Associated skeletal evidence (F:A.M. No. 32058) of *P. (P.) francisi* shows the magnum is separate from the trapezoid as in the camelids, whereas these bones are confluent in the ruminants.

Three lunars (F:A.M. Nos. 34066, 34066A, 34066B) are tentatively referred to *P. (L.) trinitiensis* and differ from that of *P. (P.) francisi* (F:A.M. No. 32058) in being about one-third larger. The lunar of *P. (L.) trinitiensis* also differs from that of *P. (P.) francisi* in the more elevated proximoposterior border, in a more prominent ridge separating the unciform and magnum facets, and the less horizontal position of both the unciform and magnum articular surfaces, which lie at an approximate 45 degree angle to the vertical axis of the lunar. Because some of the facets on both the lateral and mesial sides of the lunar of *P. (P.) francisi* are obscured by abrasion,

a supplementary description is given here. Total vertical height of the three lunars ranges from 20.8 mm. to 24.5 mm. On the mesial side, the upper scaphoid facet is elongate, slightly concave, and extends posteriorly to near the plantar surface. The lower scaphoid facet is smaller, almost flat anteriorly, and slightly concave posteriorly. Between the upper and lower facets is a wide fossa. The upper cuneiform facet on the lateral side of the lunar is vertically elongate and gradually narrows posteriorly before terminating prior to the proximoposterior border. The anterodistal surface lacks a distinct facet for the cuneiform, but the posterodistal corner of the lateral side has a small tubercle with a somewhat rounded facet. The position of this facet is at an approximate 45 degree angle to the anteroposterior axis of the lunar, which helped to hold the cuneiform in place when the foot was in motion.

A right broken magnum (F:A.M. No. 34068, fig. 25E) articulates almost perfectly with the anteroproximal half of a right third metacarpal (F:A.M. No. 32274) which is referred to *P. (L.) trinitiensis*. The total height (14 mm.) is almost equal to the transverse diameter (17 mm.) and the magnum is similar in proportion to that of *Protoceras*. It resembles the magnum of *Homo-camelus*, which also has unfused metacarpals III and IV, except for the proportionally greater vertical height, the more concave facet for the scaphoid, and the less-produced and less-elevated posterior facet. The posterodistal surface of the magnum is broken away and only the anterior facet, which articulates with metacarpal III, remains. The anteromesial side of the magnum is also broken. Behind the facet for the scaphoid, the mesial side is excavated as in the camelids, in which the trapezoid is also separate. The facet for the lunar on the proximolateral surface of the magnum is anteroposteriorly elongate, narrow, and similar to that of the camelids. The anterodistal facet for the unciform is not distinct because of abrasion, and the posterolateral facet is small and rounded.

Three third and three fourth metacarpals are referred to *P. (L.) trinitiensis*. The third metacarpals range in length from 129 mm. (F:A.M. No. 32198) to 149 mm. (F:A.M. No. 32274) and the fourth metacarpals from 124.5 mm. (F:A.M. No. 32275) to 144.3 mm. (F:A.M. No. 32277). The metacarpals average about 20 per cent larger than those of *P. (P.) francisi* (F:A.M. No.

32058). Except for their larger size, the metacarpals of *P. (L.) trinitiensis* are comparable with those of *P. (P.) francisi* described on page 161. The description of the fourth metacarpal of *P. (P.) francisi* is incomplete because the posterior and mesial surfaces of the proximal end are broken and abraded. In *P. (L.) trinitiensis* the proximal width of two right metacarpals is 16 mm. (F:A.M. No. 32275) and 18 mm. (F:A.M. No. 32277). A proximal view of metacarpal IV shows that the anterior part of the unciform facet is slightly concave with the lateral border of the facet slightly the higher. The proximomesial part of the facet is lower with the mesial border strongly indented and the posterior part narrow. On the anteromesial surface of metacarpal IV is a small, narrow, anteroposteriorly elongate facet that articulates with the concave facet on metacarpal III beneath the anterolateral lunar facet. The proximal posteromesial facet for metacarpal III is an oval, almost flat articular surface that is larger than the anterior facet. A well-defined depression on the proximolateral side of metacarpal IV with a small facet on the proximal border indicates the presence of metacarpal V. This depression extends about one-fourth the length of metacarpal IV with both the depression and the lateral surface below showing a marked rugosity to nearly the middle of the metapodial.

Two detached metacarpals of either digits II or V are tentatively referred to *P. (L.) trinitiensis*. The smaller metacarpal (F:A.M. No. 34118) measures 119.5 mm., and the length of the larger (F:A.M. No. 34119) is 134.5 mm. It is not known if the metacarpals represent digits II or V. The shape of the proximal end of the metacarpals and the facets differ; neither agree with the associated metacarpals of *P. (P.) francisi* (F:A.M. No. 32058) or those of an associated manus of *Synthetoceras tricornatus* (F:A.M. No. 40229). A definite allocation as to which digit is represented cannot be made. The anteroproximal surface of the larger metacarpal (F:A.M. No. 34119) is rugose, slightly concave and slopes anteriorly; the posteroproximal part is a smooth articular-like backward sloping surface. An anteroposteriorly, elongate, narrow facet is present on one side for attachment to the central metacarpal. The proximal end of the smaller metacarpal (F:A.M. No. 34118) narrows to almost a point and unlike F:A.M. No. 34119, the anterior surface is convex and lacks

the rugosity that is evident in the latter. Posteriorly, the proximal surface is almost smooth and slopes backward as in F:A.M. No. 34119, but the facet is more triangular in shape. On one side, a semicircular shaped facet extends anteroposteriorly the full length of the proximal end of the metacarpal and is relatively larger than that of the other digit (F:A.M. No. 34119). No differences are noted on the distal ends of these metacarpals; both have a well-developed carina, which, for the most part, is confined to the posterior surface. The distal end of both metacarpals is offset so that the articular surface on the lateral side of the carina is smaller and less distally extended than that of the mesial side.

Seven proximal and seven median phalanges are referred to the manus of *P. (L.) trinitiensis*. The lengths range from 38.7 mm. to 46 mm. for the proximal phalanges and 18.5 to 22.5 mm. for the median phalanges. The proximal phalanges are larger than that of *P. (P.) francisi* (F:A.M. No. 32058), whereas the length of the median phalanx of *P. (P.) francisi* is within the size range of those referred to *P. (L.) trinitiensis*. Based upon the unassociated referred phalanges, the median phalanx of *P. (L.) trinitiensis* is proportionally shorter and heavier than that of *P. (P.) francisi*, and the groove on the posterodistal side of the coffin facet is also deeper.

Four distal phalanges of digits III and IV are allocated to the manus. The lateral palmar length ranges from 33 mm. (F:A.M. No. 34175-B) to 42 mm. (F:A.M. No. 34175). The distal phalanx of the manus differs from that of the pes in the mesial part of the coffin facet being more concave and the lower part of the facet projecting more posteriorly with a stronger median ridge. Furthermore, the coffin facet rotates more mesially than that of the ungual phalanx of the pes and because of this rotation the vertical height is proportionally less. Compared with the cervids, the mesial palmar border of the distal phalanx of *P. (L.) trinitiensis* is nearly straight as in the cervids, but the transverse dimension is much greater and the lateral palmar border is more circular. In *P. (L.) trinitiensis*, the coffin facet rotates more mesially and is more concave than in the cervids.

REAR LIMB: Four femora ranging in length from 224 mm. (F:A.M. No. 34133) to 256 mm. (F:A.M. No. 34110) are referred to *P. (L.) trinitiensis*. From these specimens the greater trochanter [missing in *P. (P.) francisi*] is observed

to be large and stands well above the head of the femur. The anteroposterior diameter of the trochanter is 35 mm. (F:A.M. No. 34131), longer than the diameter of the shaft except at a point just above the condyles. A large digital fossa extends deeply behind the intertrochanteric ridge. The lesser trochanter is a strong hooklike process that projects in a posteromesial direction and tends to be more prominent than in *P. (P.) francisi*. The trochlea for the patella is wide with the mesial crest projecting anteriorly but less anteriorly extended than in *P. (P.) francisi* and the cervids. Moreover, the mesial crest has a strong mesial knoblike protuberance which is absent in the camelids and the cervids. This unusual protuberance is reflected by a unique hook on the patella.

Two patellae of *P. (L.) trinitiensis* are recognized because comparison is possible with an associated patella and partial femur (F:A.M. No. 40229) of *S. tricornatus*. Where it is viewed anteriorly, the outline of the patella tends to be triangular except for a proximal mesial projection which is broken in both referred specimens. Except for this mesial projection, the shape of the patella is similar to that of the cervids and unlike the more oval-shaped patella of the camelids. Anteroposteriorly, the proximal end is thick (23.5 mm., F:A.M. No. 34159) but gradually narrows to a blunt distal end. Anteriorly, the surface is strongly convex and rough for muscular and ligamentous attachments. The posterior articular surface is elongate and transversely convex to fit the patellar groove. A prominent groove runs from the distal end onto the mesial side and ends at the mesial projection. An eroded, posteriorly curved projection is present on the proximomesial side of the patella; this projection articulates with the prominent mesial knoblike protuberance on the mesial crest of the trochlea of the femur. The posterior hook on the patella is unlike that of any other artiodactyl known to us.

Three complete tibiae that range in length from 288.5 mm. (F:A.M. No. 34138) to 319 mm. (F:A.M. No. 34136) and several partial tibiae are referred to *P. (L.) trinitiensis*. As we surmised in the description of the somewhat crushed tibia (F:A.M. No. 32058) of *P. (P.) francisi*, the articular surface of the mesial condyle is smaller than that of the lateral condyle, and the outer border of the lateral condyle has an attached rudimentary fibula as in *Protoceras*. The anterior

tubercle is smaller, and the crest slopes less abruptly downward than in the camelids and cervids. Posteriorly, the proximal surface is marked by a strong popliteal scar, which is more prominent than in the camelids. The distal end of the tibia conforms with that of *P. (P.) francisi* except for a larger posterolateral distal facet at the edge of the fibular fossa. Distally, this process has a small, round articular surface for the attachment of the malleolus. In *P. (L.) trinitiensis* the fibular fossa varies from a slightly concave depression (F:A.M. No. 34138) to an anteroposteriorly long, deep, rugose groove (F:A.M. No. 34136).

Seven astragali, with the length of the lateral side ranging from 43 mm. (F:A.M. No. 34151) to 51 mm. (F:A.M. No. 34152) are referred to *P. (L.) trinitiensis*. The length of the mesial side averages 3 to 4 mm. less than the lateral side. Aside from its larger size, the astragalus of *P. (L.) trinitiensis* is similar to that of *P. (P.) francisi* (F:A.M. No. 32158). Stirton (1967, p. 15) observed that despite abrasion in all the astragali of *Lambdoceras*, the small tuberosity on the posteromesial end of the mesial tibial condyle appears not to have been as prominent as in the camelids. This tuberosity was broken in *P. (P.) francisi* but is present in three of the astragali of *P. (L.) trinitiensis* and is equally as prominent as in the camelids. In *P. (L.) trinitiensis* the distal facet on the lateral condyle is relatively short (11 mm.) and its depth is approximately equal to its length. Anteroposteriorly, it is shorter and relatively deeper than in *Lambdoceras*. Stirton (p. 15) also observed that in *Lambdoceras* there is a nearly vertical ridge on the upper mesial surface of the astragalus. In *P. (P.) francisi*, this ridge is broken, but it is very prominent in *P. (L.) trinitiensis* and would restrict the mesial movement of the tibia as postulated by Stirton. In *Prosyntheloceras*, the astragalus lacks the transverse process at the end of the mesial condyle that is so evident in the camelids and the cervids. The absence of this transverse ridge would permit a greater fore and aft movement of the foot. On the distal part of the astragalus, the navicular facet is deeper and the lateral surface, which articulates with the cuboid, is narrower than in the camelids.

Three calcanea (F:A.M. Nos. 34155-34157) have been assigned to *P. (L.) trinitiensis*. The total length varies from 89 mm. to 91.5 mm., and the length from the sustentacular facet to

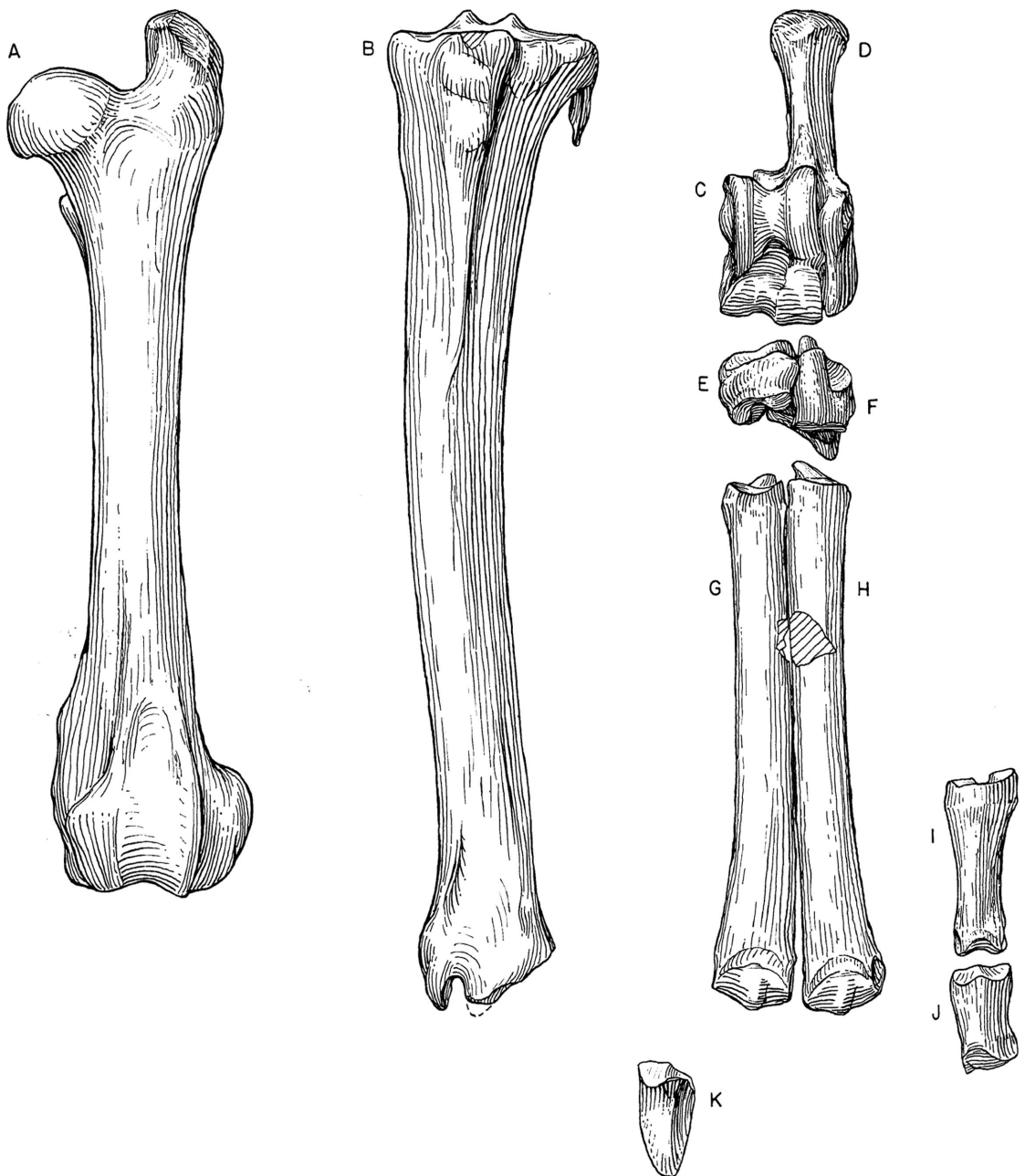


FIG. 26. *Prosynthetoceras* (*Lambdoceras*) *trinitiensis*, new species, from the Trinity River Pit 1, San Jacinto County, Texas. A. Right femur, F:A.M. No. 34131. B. Right tibia, F:A.M. No. 34138. C. Right astragalus, F:A.M. No. 34138. D. Right calcaneum, F:A.M. No. 34156. E. Right navicular, F:A.M. No. 34070. F. Right cuboid, F:A.M. No. 34077. G. Right metatarsal III, F:A.M. No. 32282. H. Right metatarsal IV, F:A.M. No. 34105. I. Right proximal phalanx, F:A.M. No. 34162. J. Right medial phalanx, F:A.M. No. 34172. K. Right distal phalanx, F:A.M. No. 34175A. All anterior views, reversed. $\times \frac{1}{2}$.

the top of the tuber calcis ranges from 63.5 mm. to 66 mm. In addition to their larger size, the calcanea referred to *P. (L.) trinitiensis* differ from that of *P. (P.) francisi* (F:A.M. No. 32058) in the relatively narrower transverse dimension of the sustentacular facet and the more massive sustentaculum. In *P. (P.) francisi*, the transverse measurement of the sustentacular facet is 15.5 mm. versus only 16 mm. in the much larger *P. (L.) trinitiensis* (F:A.M. No. 34156) but anteroposteriorly, the sustentacular facet, including the cuboidal facet, measures 18 mm. and 22 mm. respectively. This proportionally more elongate sustentacular facet in *P. (L.) trinitiensis* should permit greater fore and aft movement of the foot.

Four naviculars are identified as belonging to *P. (L.) trinitiensis*. Although larger, they are essentially the same as that of *P. (P.) francisi*. The plantar process and the anterolateral distal facet for the cuboid, which are broken in the latter, are preserved. In *P. (L.) trinitiensis*, the plantar process is a prominent spur that projects distally below the "V"-shaped spur on the mesial side which marks the posterior extent of the ectocuneiform. The anterodistal facet for the cuboid, which is broken in *P. (P.) francisi*, is an extremely small articular surface that tends to be oval and slightly concave.

Five cuboids are allocated to *P. (L.) trinitiensis*. The dimensions of the cuboids vary transversely from 17 mm. to 19 mm., and the antero-vertical measurement ranges from 17.5 mm. to 23.5 mm. The three facets on the mesial side, which are damaged or missing in *P. (P.) francisi*, are preserved. The anterior facet is anteroposteriorly elongate and narrow; the posterior facet is much larger, almost erect, and concave. These two proximal facets for the navicular are separated by an interosseous fossa. The third posterior distal facet for the navicular is a large, almost square flat surface. In addition to the navicular facets, an anterodistal facet for the ectocuneiform is also present.

Six third metatarsals ranging in length from 138.5 mm. (F:A.M. No. 32280) to 160 mm. (F:A.M. No. 34103) and two fourth metatarsals measuring 143.3 mm. (F:A.M. No. 34104) and 155.5 mm. (F:A.M. No. 34105) are referred to *P. (L.) trinitiensis*. The third metatarsal corresponds to the description for *P. (P.) francisi* (F:A.M. No. 32058) except that the depression on the proximomesial surface is even deeper, and

the facet for the vestigial metatarsal II at the anterior border of the depression is definitely more concave and undercut. The description of the fourth metatarsal of *P. (P.) francisi* is incomplete because the posterior edge of the cuboid facet and the plantar process are broken. In *P. (L.) trinitiensis*, the cuboid facet is concave, and the posterior border is elevated and joins the base of the plantar process. On the mesial side of metatarsal IV, a large, flat, vertical facet on the plantar process contacts the lateral side of the plantar process of metatarsal III. The lateral side of the plantar process of metatarsal IV has a mesial sloping facet which contacts the mesial side of the plantar process of the cuboid. A deep depression similar to that on the mesial side of metatarsal III is present on the proximolateral surface of metatarsal IV. A small facet is situated on the anteroproximal part of the depression for a vestigial metatarsal V.

Five proximal phalanges of digit III or IV of the pes are referred to *P. (L.) trinitiensis*. The total length ranges from 51 mm. (F:A.M. No. 34161) to 60 mm. (F:A.M. No. 34165). The former is slender and similar in proportion to that of *P. (P.) francisi* (F:A.M. No. 32058), whereas the latter is more massive. Except for their larger size, no morphological characters are observed to distinguish the proximal phalanges of *P. (L.) trinitiensis* from those of *P. (P.) francisi*.

Seven medial phalanges of digits III and IV are assigned to the pes. Over-all length of the median phalanges ranges from 23.5 mm. (F:A.M. No. 34166) to 30 mm. (F:A.M. No. 34172). The median phalanx of the pes is longer proportioned than that of the manus. In the median phalanx of *P. (L.) trinitiensis*, the middle ridge of the pastern facet is weak; it is, however, stronger than in the later camelids but weaker than in the cervids. Both sides of the pastern facet are of almost equal width, but the facet is shallower than in both the cervids and camelids, and the posterior part of the facet does not extend so near the posterior surface as in the latter. Posteriorly, the two proximal plantar processes are much smaller and are not separated by a deep groove as in the cervids. The most distinguishing feature on the anterior side of the median phalanx is the failure of the articular surface of the coffin facet to extend as far anteriorly as it does in the cervids. This would restrict the forward flexion of the distal phalanx.

On the distal end, the dimension of the mesial part of the facet exceeds that of the lateral part. The median groove of the coffin facet is deep. Stirton (1967, p. 22) observed that this groove is much deeper in *Lambdoceras hessei* than in *Synthetoceras*, but the depth of the groove in *P. (L.) trinitiensis* is comparable to that of the *Synthetoceras*.

Two distal phalanges of digits III and IV are assigned to the pes. One is broken; the lateral plantar length of the other is 33.5 mm. Characters distinguishing the distal phalanx of the manus from that of the pes and a comparison of the distal phalanx of *Prosynthetoceras* with the cervids can be found under the description of the manus, page 185.

Prosynthetoceras (Lambdoceras) siouxensis

Frick

Figure 27; tables 1, 8-10

Cranioceras unicornis MATTHEW, 1918, p. 224, fig. 20 [ramus referred to *C. unicornis* was later selected by Frick as the type of *P. siouxensis*].

Prosynthetoceras siouxensis FRICK, 1937, p. 607.

Prosynthetoceras siouxensis dawesensis FRICK, 1937, p. 607, fig. 20.

TYPE: A.M.N.H. No. 17344, left mandibular ramus with I_1 - I_3 alveoli, C, and P_2 - M_3 from the undifferentiated Snake Creek beds of Matthew (1918), 23 miles south of Agate, Sioux County, Nebraska. The type was collected by Whitford and Stoll in 1916 and was figured by Matthew, 1918 (fig. 20, under A.M.N.H. No. 17144). According to Morris F. Skinner, the expedition of 1916 collected from the Lower Snake Creek beds in Sinclair Draw and from deposits on Olcott Hill which are Upper Snake Creek (fide McKenna, 1965). At this time, Whitford and Stoll called both of these localities the Snake Creek beds. From a study of Whitford's annual report and conversations with Stoll, Skinner learned that most of the material that was collected in 1916 came from the Lower Snake Creek beds in East Sinclair Draw including all the remains referred to *P. (L.) siouxensis*.

DISTRIBUTION: Early Barstovian in Sioux and Dawes counties, Nebraska.

HYPODGM: Lower Snake Creek beds,¹ Sioux County, Nebraska: F:A.M. No. 53493, partial skull with orbital horns and F:A.M. No. 34079,

tibia, *Prosynthetoceras* Quarry; F:A.M. No. 53494, orbital horn and F:A.M. No. 53498, ramal fragment, Quarry No. 2; F:A.M. No. 53495, incomplete orbital horn, F:A.M. No. 53499, detached P_4 and F:A.M. No. 34080, metatarsal III, Echo Quarry; F:A.M. No. 53496, left partial mandible, West Sand Quarry; F:A.M. No. 53497, right partial mandible, Version Quarry.

Observation Quarry,² Dawes County, Nebraska: F:A.M. No. 34022,³ rostral horn; F:A.M. No. 32059, right maxilla with P^2 (alveolus)- M^3 ; F:A.M. No. 53506, left maxilla with M^1 - M^2 ; F:A.M. No. 34081, left partial mandible with P_2 - M_3 ; F:A.M. No. 34028,⁴ left metacarpal IV; F:A.M. No. 34086, median phalanx of digits III or IV of the manus; F:A.M. No. 34083, metatarsal III; F:A.M. No. 34084, partial metatarsal IV; F:A.M. No. 34085, lateral metapodial; F:A.M. Nos. 34087-34090, four proximal phalanges of digits III or IV.

SPECIFIC DIAGNOSIS: Largest species of the subgenus; rostral horn relatively small and deeply grooved, more similar to that of *P. (L.) hessei* than *P. (L.) trinitiensis*; mandibular diastema longest; P_1 most reduced, M_3 relatively larger than in *P. (L.) hessei* and *trinitiensis*.

DESCRIPTION: Skull and horns: The only cranial material available representing *P. (L.) siouxensis* consists of a partial skull with frontal horns and an isolated rostral horn. Little can be said of the skull other than its interorbital breadth (158 mm.) indicates a large animal approximating the size of the southern *Synthetoceras tricornatus*. The more anterior position of the frontal horns over the orbit corresponds to a similar condition in *P. (P.) texanus* and *P. (L.) trinitiensis*. Although not so flattened, the base of the *P. (L.) siouxensis* frontal horn is flared like that of *P. (L.) trinitiensis*. Other characters of the skull and frontal horns do not differ significantly from those of other members of the subgenus. The rostral horn of *P. (L.) siouxensis* is small, transversely flattened, and very widely and deeply grooved, verifying its close relationship

²A report on the geology and stratigraphy of the Hay Springs, Nebraska area, which will include Observation Quarry, is being prepared by Ted Galusha.

³F:A.M. No. 34022 is the type of *Prosynthetoceras siouxensis-dawesensis* Frick, 1937.

⁴F:A.M. No. 34028 was listed by Frick (1937, p. 607) as a right metacarpal III.

¹Stratigraphy and biostratigraphy of the late Cenozoic deposits in central Sioux County, Nebraska is being prepared for publication by Morris F. Skinner.

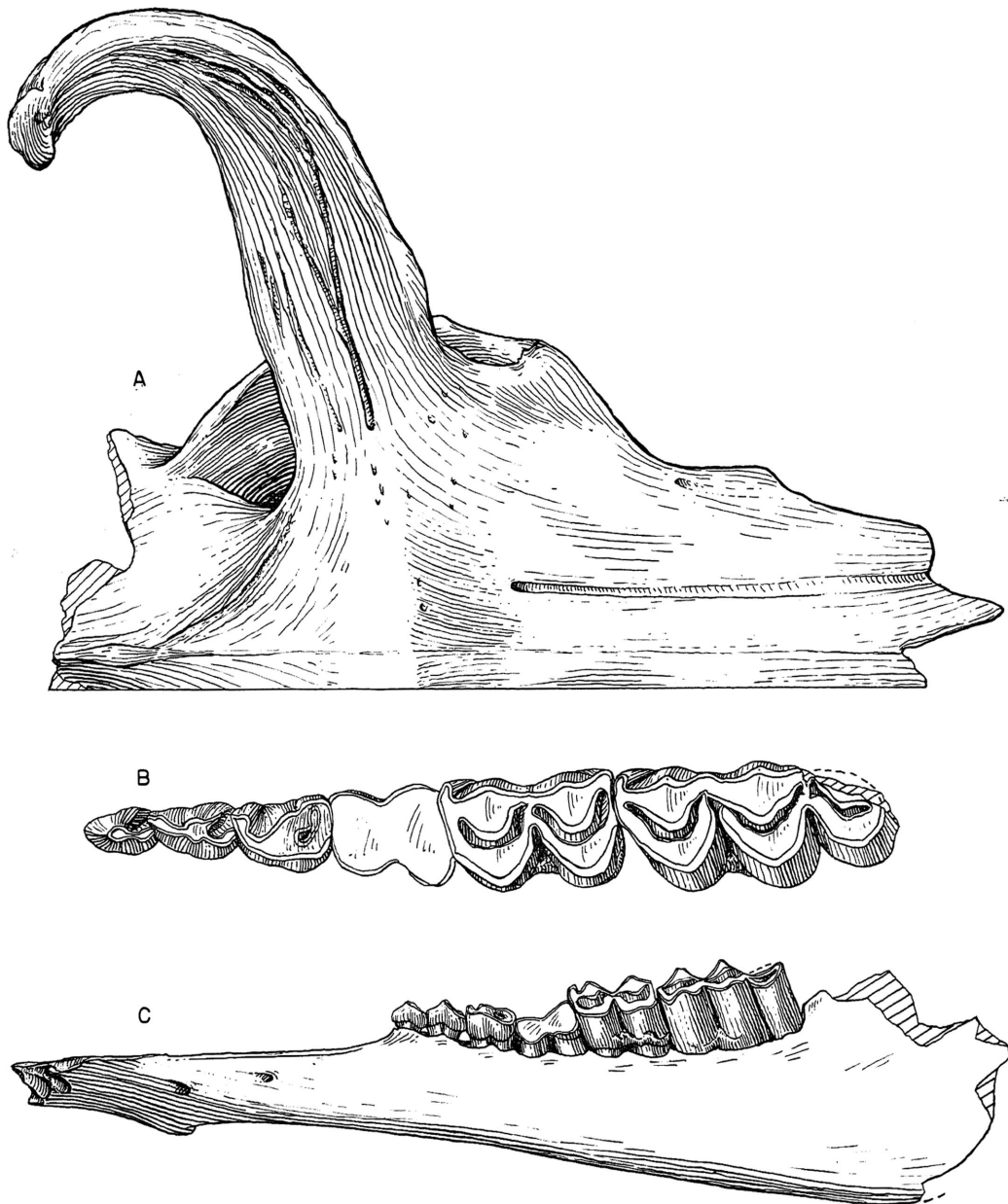


FIG. 27. *Prosynthetoceras* (*Lambdoceras*) *siouxensis*, from the Lower Snake Creek beds, Sioux County, Nebraska. A. F:A.M. No. 53493, dorsal view. $\times \frac{1}{2}$. B, C. Type, A.M.N.H. No. 17344. B. P_2-M_3 , occlusal view. $\times 1$. C. Lateral view. $\times \frac{1}{2}$.

to *P. (L.) hessei*. In no other members of the subfamily is this grooving so pronounced. Why blood vessels supplying and draining the smaller rostral horn of these two species should be distinctly larger than in other species is not clear; however, the presence of such grooves and

canals in *P. (L.) hessei* and *siouxensis* versus smaller grooves in *P. (P.) texanus*, *francisi*, and *P. (L.) trinitiensis* suggests that in the latter species the distribution of these blood vessels is simply more diffuse and does not necessarily mean that nutrient demands were any less.

One interesting and apparently diagnostic feature of the rostral horn is its cross-sectional shape. As in *P. (L.) hessei*, the posterior half of the middle part of the shaft becomes transversely flattened, whereas the anterior, or leading edge, remains slightly rounded at this point but flattens progressively toward the fork.

DENTITION: Unfortunately, the incisiform teeth were not preserved in the type mandibular ramus (A.M.N.H. No. 17344) of *P. (L.) siouxensis*. In the type, the symphysis contains the alveoli for three incisors plus a more cylindrical alveolus for the incisiform lower canine. The canine alveolus is adjacent to that of I_3 , the four alveoli forming a parallel row at the anterior border of the symphysis. Immediately adjacent but slightly above the level of the alveolus is a small alveolus for P_1 . The size and shape of this alveolus indicates a small compressed caniniform P_1 which is similar to, but much smaller than, that of *P. (L.) trinitiensis*. Thus, as in all other synthetoceratines, *P. (L.) siouxensis* possesses an anterior lower battery of five closely appressed teeth: three incisors, an incisiform canine, and a much reduced caniniform P_1 . Whether the extremely small size of the caniniform P_1 indicates a female specimen is for the present indeterminable.

Unlike the single-rooted P_2 of *P. (P.) francisi*, P_2 of *P. (L.) siouxensis* is double-rooted, short, and heavy. P_2 is characterized by a tall lingually rounded protoconid, the absence of a metaconid, and a short paraconid. The protoconid is joined to the hypoconid and the reduced entoconid by a low crest. Enclosed between the hypoconid and the entoconid is a small posterior fossettid. P_3 differs from P_2 by its larger size, greater transverse thickness, slightly more anterolingually flexed paraconid, and a larger posterior fossettid. Those characters which distinguish P_3 from P_2 are even more emphasized in P_4 . P_4 is notably heavy with the transverse width increasing to form a triangular outline. The paraconid of P_4 is directed lingually.

In the type, M_1 is greatly worn; M_2 is marked by a median style and cingulum on the hypoconid and M_2 and M_3 possess a large recurved parastylid. Although the M_3 is worn, it appears to have been taller crowned than *P. (L.) trinitiensis*.

A partial maxilla (F:A.M. No. 32059) from Dawes County closely resembles those of *P. (L.) trinitiensis*. The P^3 has a swollen paracone, a

weakly recurved parastyle, and a pronounced strongly recurved metastyle. A strong lingual cingulum extends posteriorly from the parastyle to the metastyle. P^4 is larger than P^3 and more triangular in shape. It is distinguished by a stronger protocone and an extremely large and recurved metastyle. The upper molars are marked by strong styles emerging from the anterior base of the protocone and between the protocone and metaconule.

DISCUSSION: Frick (1937, p. 607) originally erected the species *Prosynthetoceras siouxensis* on the basis of a mandibular ramus that Matthew (1918, p. 224) had questionably referred to *Cranioceras unicornis*, which he founded on a partial occipital horn. In describing his new genus and species from the Lower Snake Creek beds, Matthew fretted over the fact that of the "five very distinct types of horned ruminants . . . known from the Snake Creek beds, only two . . ., *Merycodus* and *Dromomeryx*, can be correlated with the dentition." The other three were *Neotragoceras* (see below), *Drepanomeryx*, and, of course, *Cranioceras*. Matthew's tentative referral to *Cranioceras* (which he believed to be a bovid) of "a remarkable lower jaw . . ." was predicated by "the breadth and pattern of the premolars, the moderate height and width and smooth surface of the molar crowns, and the character of the heel of M_3 , as well as by the form of the front of the jaw and arrangement of the front teeth and entire lack of caniniform teeth. It is distinguished by the great reduction of the premolars. I can find no near relative or parallel among existing Bovidae or the known extinct forms, and the aberrant character of the jaw may well have been correlated with the aberrant skull characters of the type of *Cranioceras*."

As Stirton (1967, p. 4) remarked, Matthew was then unaware of the later synthetoceratines yet to be found and described and could not possibly have made the protoceratid correlation. Matthew was aware, however, of the difficulty and confusion in the artiodactyl systematics at the time and prophetically stated (1918, p. 224) that "until the discovery of skulls of these various ruminant genera serves to correlate definitely their teeth and horns, it will be impossible to determine their association." It is also ironic that in mentioning his friends' lighthearted suggestion that *Cranioceras* possibly "represents the legendary unicorn," Matthew was totally unaware of the truly bizarre nature of the cranial

armament of the creature to which this jaw actually belonged.

The type of *Prosynthetoceras siouxensis dawesensis* Frick exhibits no important differences to distinguish it from *P. (Lambdoceras) siouxensis* except the smaller than expected size of the rostral horn. The size of this horn is subject to wide individual variation, judging by the variation in size of the rostral horns referred to *Synthetoceras tricornatus*. Moreover, since Frick described *P. siouxensis dawesensis*, dentitions of this taxon have been found from the type locality, and they are approximate in size to those of *P. (Lambdoceras) siouxensis*. It is therefore unlikely that the smaller size of the type rostral horn constitutes a valid subspecific difference, and the subspecies *P. siouxensis dawesensis* is synonymous with *P. (L.) siouxensis*.

cf. *Prosynthetoceras (Lambdoceras)*
siouxensis

A right metatarsal IV (F:A.M. No. 34082) was collected by Jack Wilson in 1937, from Hill-top Quarry, Sheep Creek beds, Sioux County, Nebraska. It is not so large as the smallest third metatarsal (F:A.M. No. 34088) referred to *P. (L.) siouxensis* from the later Lower Snake Creek beds. The length of the fourth metatarsal from the Sheep Creek beds is 123 mm. and the greatest transverse width of the distal trochlea is 18 mm. versus 143 mm. and 21 mm. respectively, for the smallest third metatarsal referred to *P. (L.) siouxensis*.

The occurrence of this metatarsal in the earlier Sheep Creek beds is of biostratigraphic significance. It is approximately equivalent in size to examples of *P. (P.) francisi* and smaller than examples of both *P. (L.) siouxensis* and *P. (L.) trinitiensis*.

GENUS *SYNTHETOCERAS* STIRTON

Table 15

Synthetoceras STIRTON, 1932, p. 147.

TYPE SPECIES: *Synthetoceras tricornatus* Stirton, 1932.

INCLUDED SPECIES: Type species only.

KNOWN DISTRIBUTION: Clarendonian of the Panhandle and Gulf Coastal Plain of Texas, Hemphillian of Florida, and ?Hemphillian of Alabama Coastal Plain.

DIAGNOSIS: *Synthetoceras* differs from its nearest relative, *Prosynthetoceras*, in its larger size and in the loss of P_1 - P_2^3 ; longer diastemata; taller rostral

horn; greater complications of cusp morphology of both the upper and lower premolars, correlating with the loss of the anterior premolars; taller-crowned dentition; larger and heavier proportioned limbs; more firmly coalesced radius and ulna; relatively slenderer metacarpals II and V and more reduced vestigial metatarsals II and V.

DISCUSSION: The genus *Synthetoceras* was initially described by Stirton (1932) from a skull collected in the Clarendon beds, Donley County, Texas. At the time of its discovery, it was the first indication of synthetoceratine horn progression beyond that attained by *Syndyoceras*. Although there were intermediate steps in this progression, represented by the horns of *Prosynthetoceras*, *Synthetoceras* represents the culmination of horn evolution anticipated by *Syndyoceras*.

The great majority of specimens assignable to *Synthetoceras* have been recovered from the type Clarendon deposits, and it is from these beds that the only skull material was found. This includes at least seven relatively well-preserved skulls with intact cranial armament. Aside from the Clarendon locality, the only other *Synthetoceras* specimens known include two upper molars from the Clarendonian Lapara Creek Fauna of the Texas Coastal Plain, a partial maxilla and dentition from undifferentiated Pliocene deposits near Mobile, Alabama, and a partial female skull and jaw from the early Hemphillian McGehee Locality of north-central Florida. The Hemphillian occurrence marks the latest known extension of its geochronologic range. The Lapara Creek Fauna is regarded by Patton (1969b) as being temporally equivalent to the Burge Fauna of Nebraska, which in turn is considered earliest Clarendonian by most workers. Thus, the known range of *Synthetoceras* extends from earliest Clarendonian to early Hemphillian (Webb, 1964, p. 27; Hirschfeld and Webb, 1968, p. 249).¹

Synthetoceras tricornatus Stirton

Figures 28-33, 35, 36; tables 1, 7, 10, 11-14

Synthetoceras tricornatus STIRTON, 1932, p. 147, figs. 1-3, pls. 6-11,

TYPE: U.C.M.P. No. 31520, skull with incomplete rostral and orbital horns, broken C alveolus, P^3 - M^1 alveoli, and M^2 - M^3 . The type

¹The McGehee specimens that Hirschfeld and Webb (1968) referred to the Protoceratidae have been identified by us as *Synthetoceras tricornatus*.

was collected by Stirton on the Bromley Ranch¹ between Turkey and Barton creeks, Donley County, Texas.

DISTRIBUTION: Same as for the genus.

HYPODIGM: MacAdams Quarry,² 10 miles north of Clarendon on the east side of Carrol Creek in the NW. $\frac{1}{4}$, NE. $\frac{1}{4}$, sect. 7, Blk. C-3, G. C. and Santa Fe Railway Survey, Donley County, Texas: F:A.M. No. 33407, complete skull with rostral and orbital horns, premaxilla, C alveolus, and P³-M³; F:A.M. No. 33408, complete skull with rostral and orbital horns, premaxilla, C alveolus, and P³-M³; F:A.M. No. 53412, almost complete skull, except for the left side of the premaxilla and one orbital horn, with P³-M³ and atlas; F:A.M. No. 53409, crushed skull, lacking premaxilla, with rostral and orbital horns and P³-M³; F:A.M. No. 53411, crushed skull, lacking premaxilla, with rostral and badly crushed orbital horns and P³-M³; F:A.M. No. 53410, crushed skull, lacking premaxilla, with rostral and orbital horns and M²-M³; F:A.M. No. 53413, lacking premaxilla, with orbital and rostral horns and P³-M³; F:A.M. No. 33405, partial skull with premaxilla missing, rostral horn with tips broken, right orbital horn and base of left, and P³-M³; F:A.M. No. 33406, skull with premaxilla missing, rostral horn, incomplete orbital horns and P³-M³; F:A.M. No. 33413, skull with premaxilla missing, incomplete rostral horn, orbital horns and P³-M³; F:A.M. No. 34091, skull with premaxilla missing, rostral horn with tips missing, orbital horns and P³-M³; F:A.M. No. 34092, partial skull with rostral and orbital horns; F:A.M. No. 34093, anterior part of skull with rostral horn and P³-M³; F:A.M. No. 53414A, anterior part of skull with incomplete rostral horn and P³-M³; F:A.M. No. 53421,

crushed partial female skull with a small protuberance on the upper posterior rim of the orbit and P³-M³; F:A.M. No. 53416, anterior part of skull with rostral horn and P³-M³; F:A.M. No. 53415, anterior part of skull with incomplete rostral horn and P³-M³; F:A.M. Nos. 53414, 53419, 53417, 53417A, 53418, posterior part of skulls with orbital horns; F:A.M. Nos. 53420, 53420A, right orbital horn with attached cranial fragment and associated left partial orbital horn; F:A.M. No. 34094, palate with base of rostral horn and P³-M³; F:A.M. No. 32467, palate with P³-M³; F:A.M. Nos. 34095, 34096, 34097, 40214, 53422, maxillae with P³-M³; F:A.M. Nos. 34098, 34099, 40213, 40215, 53423, 53424, 53425, partial maxillae; F:A.M. No. 32465, mandible with I₂₋₃ and P₃-M₃; F:A.M. No. 53428, right and left mandibles with symphysis I₁-C alveolus and P₃-M₃; F:A.M. No. 33401, right and left mandibles with broken symphysis and P₃-M₃; F:A.M. No. 53426, right and left mandibles with I₁-C alveolus and P₃-M₃; F:A.M. No. 53427, left and right partial mandibles with I₁-C alveolus and P₃-M₃; F:A.M. No. 53444, left mandible with symphysis, I₁-C and P₃-M₃; F:A.M. Nos. 53447, 53429, 53436, 53445, 53448, rami with symphysis, I₁-C alveolus and P₃-M₃; F:A.M. Nos. 32464, 53430, 53451, 53452, 53439, 53433, 53450, 53453, 53454, 40220, 40221, 40222, rami with diastema and P₃-M₃; F:A.M. Nos. 32468, 33408, 53434, 53435, 53446, 53449, 40218, rami with diastema and P₄-M₃; F:A.M. Nos. 53437, 53438, 53440, 53455, 53456, 40223, 40224, 40225, 40226, 40227, 40228, 40105, 53441, 53442, partial rami; F:A.M. No. 40216, immature anterior fragment of skull with dP²-M² broken and part mandible with incisors broken and dP₂-dP₄; F:A.M. No. 53477, right immature maxilla, dP²-M¹; F:A.M. No. 32467A, right immature maxilla, dP²(br.)-M²; F:A.M. Nos. 53476, 53478-53481, 53483-53487, 40217, partial immature maxillae; F:A.M. No. 33420, right immature ramus with dP₂-M₁ (germ); F:A.M. No. 40101, right immature partial ramus with dP₄-M₃ (germ) (P₃-P₄ germs); F:A.M. Nos. 33421, 39977, 39978, 39987, 39992, 39994, 53457-53475, immature rami and partial rami; F:A.M. No. 40230, left associated humerus, radius and ulna; F:A.M. Nos. 33410, 33410A, 33410B, radius and ulnae; F:A.M. No. 40235, articulated distal part of radius to proximal phalanx; F:A.M. Nos. 33403,

¹Stirton (1932, p. 147) recorded the type locality as "Barton Creek locality—Site 1, Blk. 6-7, Sec. 15, Bromley Ranch, Donley County, Texas." Skinner related that according to Will Chamberlain, who worked with Stirton and knew the site, the type of *Synthetoceras tricornatus* was found in about the center of the NE. $\frac{1}{4}$, sect. 58, Blk. C-7, D. and P. Railway Co., Survey on the north side of Turkey Creek, about 5 $\frac{1}{4}$ miles east and $\frac{1}{2}$ mile south of MacAdams Quarry. According to Skinner, there is no Blk. 6-7; it must be C-7. The Bromley Ranch did not include a section 15 at that time or now and the section number should have been 58.

²Location 17, Quarry 1 is synonymous with MacAdams Quarry, and Location 17, Quarry 2 and Canyon, Texas, Museum's Grant Quarry are a continuation of the same channel deposit.

33404, left third metacarpals; F:A.M. No. 40231 left metacarpals III and IV; F:A.M. No. 40232, left metacarpals III and IV; F:A.M. No. 40233, right metacarpal III; F:A.M. No. 40234, left metacarpal IV; F:A.M. No. 40236, right femur; F:A.M. No. 40237, right tibia; F:A.M. No. 40239, left metatarsal III; F:A.M. No. 40240, right astragalus; F:A.M. No. 40241, proximal phalanx of the pes; F:A.M. Nos. 40243, 40244, medial phalanges; F:A.M. No. 40245, distal phalanx of the pes.

McMurty Ranch, east side of Saddler Creek, 4 miles east and $\frac{1}{4}$ mile north of MacAdams Quarry, Donley County, Texas: F:A.M. No. 40219, left and right partial mandibles with P_3 - M_3 .

Location 5, Quarry 2, Lewis Place, Spade Flats, SE. $\frac{1}{4}$, NW. $\frac{1}{4}$, sect. 26, G. C. and S. F. Railway Co., Blk. C-8, Donley County, Texas: F:A.M. No. 40229, incomplete articulated front and rear limbs including; humerus, partial radius and ulna, scaphoid, lunar, cuneiform, metacarpals II, III, IV, and incomplete V, broken proximal phalanx, lateral proximal, medial and distal phalanges, partial femur, patella, tibia, partial calcaneum, broken astragalus, cuboid, navicular, ectocuneiform, pisiform, metatarsals III and IV, one proximal, medial and distal phalanx for the pes, broken thoracic vertebra and fragments.

Quarry 3, Lewis Place, $\frac{1}{4}$ mile northeast of Spade Flats, east central side of NW. $\frac{1}{4}$, NE. $\frac{1}{4}$, sect. 30, G. C. and S. F. Railway Co., Blk. C-8, Donley County, Texas: F:A.M. No. 40238, articulated distal part of tibia to distal phalanx.

Dilli Place, Turkey Creek, SE. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 20, Block C-3, T. T. Railway Survey, Donley County, Texas: F:A.M. No. 40242, proximal phalanx of the pes.

Lapara Creek Fauna, Live Oak County, Texas: U.T.B.E.G. No. 30936-214, detached M^3 . Lapara Creek Fauna, Bee County, Texas: U.T.B.E.G. No. 31132-563, detached M^2 .

About 135 feet below base of Citronelle Formation, Chickasaw Creek, sect. 27, T. 2 S., R. 2 W., Kushla 7.5' quadrangle, Mobile County, Alabama; 30°50'N. latitude, 88°10'W. longitude: U.S.N.M. No. 25687, left maxilla, P^3 (br.)- M^3 .

McGehee Farm Quarry, near Newberry, sect. 22, T. 9 S., R. 17 E., Alachua County, Florida: U.F. No. 16154, partial female skull, P^3 - M^3 ; U.F. No. 9542, left M^3 ; U.F. No. 9504,

right broken M^2 ; U.F. No. 9529, worn broken upper molar; U.F. No. 16155, right M^2 ; U.F. No. 16158, left P^3 ; U.F. No. 16157, right M_3 ; U.F. No. 16156, right detached M_1 (br.), M_2 and M_3 ; U.F. No. 16159, right partial ramus, M_2 - M_3 ; U.F. No. 9558, left tibia; U.F. No. 11021, right tibia; U.F. No. 9522, rear first phalanx; U.F. No. 9532, right metatarsal III; U.F. No. 9512, right metatarsal III; and U.F. No. 16160, right incomplete symphysis and diastema.

DIAGNOSIS: Same as for the genus; only known species of the genus.

DESCRIPTION: Skull: The skull of *Synthetoceras* is longer and more slender than that of *Prosynthetoceras* (table 10), culminating a trend begun by the *P. (P.) texanus-francisi* species group. The superior surface of the skull is quite flat, lacking any kind of a cranial flexure, in contrast to *P. (P.) texanus*, *P. (P.) francisi*, and *P. (L.) trinitiensis* in which there is a slight rise posterior to the antorbital rim. As in *Prosynthetoceras*, this frontal region is broad and flat, but the orbits are placed slightly lower than in that genus. The supraoccipital region is similar to *Prosynthetoceras*, but with a smaller sagittal crest. Temporal ridges and paroccipital processes are as strongly developed as in *P. (P.) francisi*. The basicranium is like that of *Prosynthetoceras*. The orbits are large, rimmed with thickened bone, and are situated below the dorsal surface of the cranium. At the anterior edge of the orbit, just below the antorbital tuberosity, is a prominent foramen from which a small groove leads on to the antorbital rim. This probably is the lacrimal foramen and groove. Rostral grooves and foramina are similar to those of *P. (P.) francisi*. Retraction of nasals is also comparable with that of *P. (P.) francisi*. The premaxillary-maxillary wings anterior to the rostral horn are longer and more widely flared than in any other synthetoceratine. These bones are also more flattened dorsoventrally than in *Prosynthetoceras*. The contact of the premaxilla with the maxilla extends from within the anterior nares to a point just anterior to the canine. The alveolus for the large canine is present, but, as in *Prosynthetoceras*, none of these teeth has been recovered.

A partial skull with dentition (F:A.M. No. 53421) from MacAdams Quarry, serves to illustrate the cranial characters of the female *Synthetoceras*. Aside from a partial skull from the early Hemphillian McGehee deposit of Florida,

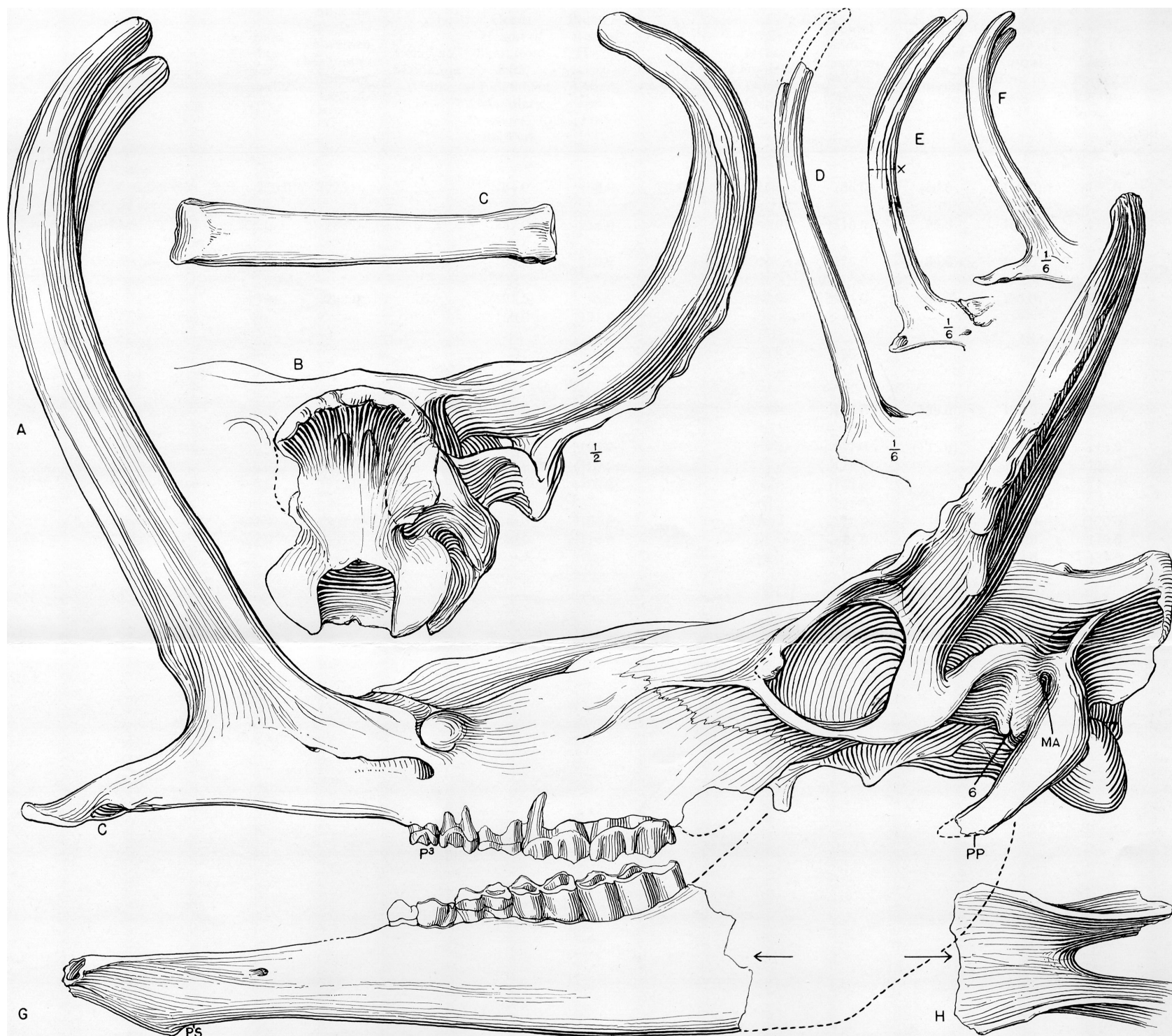


FIG. 28. *Synthetoceras tricornatus* and *P. (Prosynthetoceras) francisi*. A–D. *Synthetoceras tricornatus*, from MacAdams Quarry, Donley County, Texas. A, B. F:A.M. No. 33407. A. Lateral view. $\times \frac{1}{2}$. B. Posterior view. $\times \frac{1}{2}$. (See dorsal and ventral views, figs. 29 and 30). C. F:A.M. No. 33404, anterior view of metacarpal III. $\times \frac{1}{2}$. D. F:A.M. No. 33405, lateral view of rostral horn. $\times \frac{1}{2}$. E. *P. (Prosynthetoceras) francisi*, type, T.A.M.U. unnumbered skull, from Cold Spring, San Jacinto County, Texas. Lateral view of rostral horn. $\times \frac{1}{6}$. (X=point where horn is cut off on fig. 8.) F–H. *Synthetoceras tricornatus*, from MacAdams Quarry, Donley County, Texas. F. F:A.M. No. 33407. Lateral view of rostral horn. $\times \frac{1}{6}$. G, H. F:A.M. No. 32468. G. Lateral view. $\times \frac{1}{2}$. H. Dorsal view of symphysis. $\times \frac{1}{2}$. (After Frick, 1937, fig. 61.)

TABLE 10
MEASUREMENTS (IN MILLIMETERS) OF THE SKULLS AND HORNS OF THE SPECIES OF *Prosynthetoceras* (*Prosynthetoceras*), *Prosynthetoceras* (*Lambdoceras*) AND *Synthetoceras*

| | Occipital Crest to Tip of Prenaxilla (Vertex) | Anterior Border of Foramen Magnum to Anterior Face of Rostral Horn | Condyles, Maximum Width | Rostral Horn: Height of Shaft from Base (Junction of Maxillary Processes) to the Fork | Prong of Rostral Horn, Maximum Length above Fork | Rostral Horn: Total Length on Anterior Curve above Palate | Orbital Horn: Length on Outer Curve | Frontal Width, Maximum Width between Orbits | Posterior Border of C to Anterior P ² or P ³ | Anterior Border of Rostral Horn to Posterior M ³ | Posterior M ³ to Anterior Border of Foramen Magnum |
|-------------------------------------|---|---|-------------------------------|---|--|--|---|--|--|--|--|
| <i>P. (P.) texanus</i> | | | | | | | | | | | |
| F:A.M. No. 53500 | (275.0-280.0) ^a | (225.0) | 52.5 | (84.0) | (58.0) | (180.0) | 225.0 | (86.0) | (60.0) | (120.0) | (108.0) |
| <i>P. (P.) francisi</i> | | | | | | | | | | | |
| F:A.M. No. 33049 | 366.0 | 286.0 | 61.5 | 137.0 | 214.0 | 412.0 | (295.0) | (118.0) | 85.0 | 166.0 | 118.0 |
| T.A.M.U. unnumbered ^b | (385.0) | 300.0 | 70.0 | 198.0 | 210.0 | (450.0) | — | 128.0 | (85.0) | 155.0 | 143.0 |
| <i>P. (L.) trinitensis</i> | | | | | | | | | | | |
| F:A.M. No. 33073 ^c | (378.0) | 289.0 | 76.0 | (197.5) | 55.0 | (290.0) | (240.0) | 124.0 | (87.0) | (166.0) | (125.0) |
| F:A.M. No. 33080 | — | — | — | 150.0 | 121.0 | 330.0 | — | — | — | — | — |
| <i>P. (L.) siouxensis</i> | | | | | | | | | | | |
| F:A.M. No. 53493 | — | — | — | — | — | — | 260.0 | 158.0 | — | — | — |
| <i>S. tricornatus</i> | | | | | | | | | | | |
| U.C.M.P. No. 31520 ^d | (466.0) | 357.0 | 73.0 | 317.0 | (147.0) | (525.0) | (310.0) | 177.0 | 139.0 | 198.0 | 145.0 |
| [A.M. cast] | | | | | | | | | | | |
| F:A.M. No. 53412 | 442.0 | 354.0 | 75.5 | 185.0 | 188.0 | 440.0 | 285.0 | 147.0 | (125.0) | 204.0 | 143.0 |
| F:A.M. No. 53409 | (420.0) | 315.0 | 67.0 | 202.0 | (120.0) | (385.0) | 295.0 | (128.0) | — | 195.0 | 125.0 |
| F:A.M. No. 53410 | (525.0) | (375.0) | 76.0 | 230.0 | (160.0) | (465.0) | 330.0 | 175.0 | — | 223.0 | 177.0 |
| F:A.M. No. 53414 | — | — | — | — | — | — | 335.0 | 154.0 | — | — | — |
| F:A.M. No. 33405 | (490.0) | (367.0) | — | 308.0 | (104.0) | (513.0) | 310.0 | (170.0) | — | 202.0 | (170.0) |
| F:A.M. No. 33407 | 448.0 | 332.0 | 73.0 | 199.0 | 114.0 | 373.0 | 262.0 | 136.5 | 112.0 | 190.0 | 149.0 |
| F:A.M. No. 53408 | 462.0 | 345.0 | 78.0 | 190.0 | 168.0 | 410.0 | 230.0 | (136.0) | 112.0 | 188.0 | 153.0 |

^aMeasurements enclosed in parentheses are approximate.

^bType (T.A.M.U. unnumbered) of *P. (Prosynthetoceras) francisi* Frick from Cold Spring, Texas.

^cType (F.A.M. No. 33073) of *P. (Lambdoceras) trinitensis*, new species, from Trinity River, Texas.

^dType (U.C.M.P. No. 31520) of *Synthetoceras tricornatus* Stirton from Clarendon, Texas.



FIG. 30. *Synthetoceras tricornatus*, referred skull, F.A.M. No. 33407, Donley County, Texas. A. Occlusal view. $\times 0.98$. B. Ventral view. $\times 0.49$. (See figs. 28 and 29.)

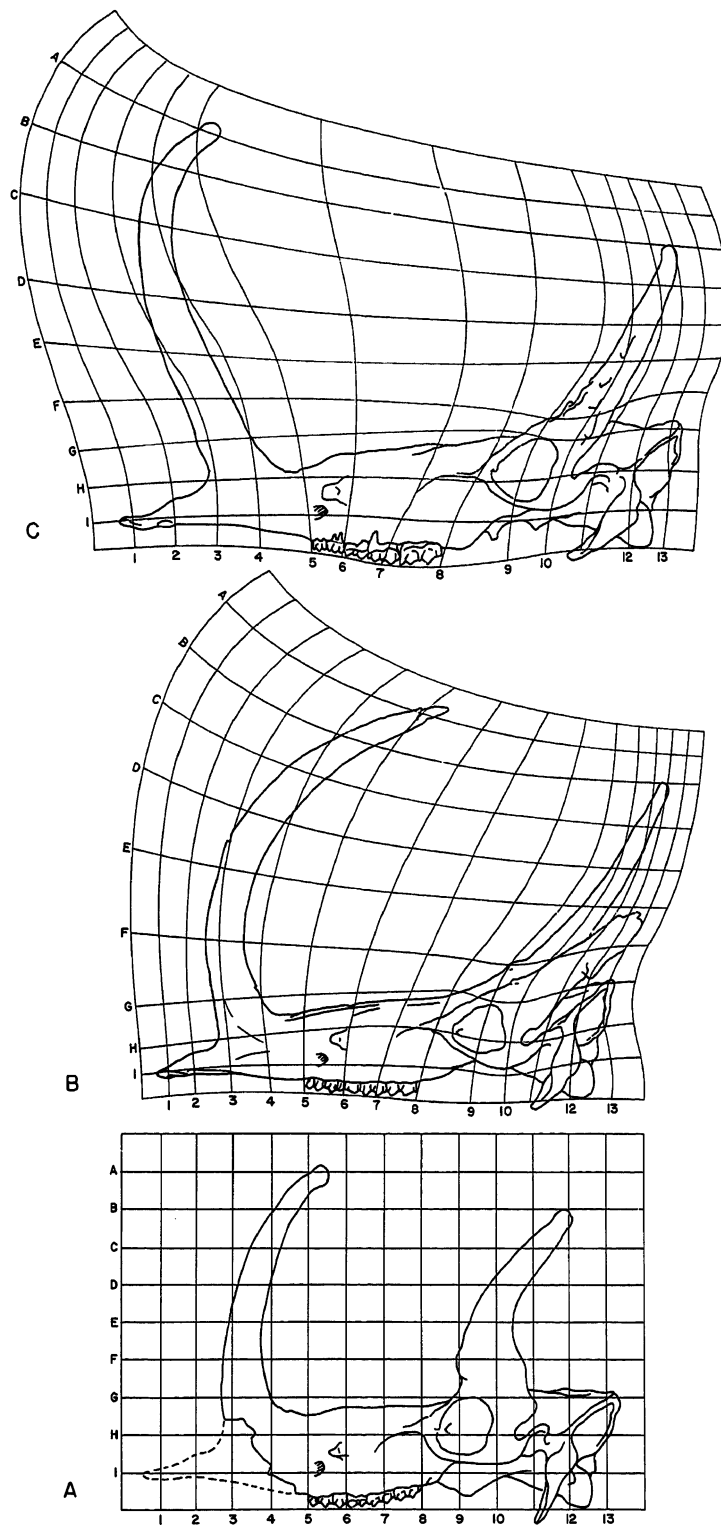


FIG. 31. Changing skull and horn proportions are shown by the deformed coordinates. A. *Prosynthetoceras* (*Lambdoceras*) *trinitensis*, new species, type, F:A.M. No. 33073, from Trinity River Pit 1, San Jacinto County, Texas. B. *Prosynthetoceras* (*Prosynthetoceras*) *francis*, F:A.M. No. 33049, from Windham Place, Polk County, Texas. C. *Synthetoceras* *tricornatus*, F:A.M. No. 33407, from MacAdams Quarry, Donley County, Texas.

the only other female synthetoceratine specimens known are of *P. (L.) trinitiensis*.

HORNS: The frontal horns of *S. tricornatus* are much more similar to those of *P. (P.) francisi* than to those of any other synthetoceratine species. In all other species these horns extend out over the orbit almost perpendicular to the long axis of the skull. In *P. (P.) francisi* and *S. tricornatus*, however, the horns sweep more backward from the dorsoposterior edge of the orbit with less flattening of the proximal part of the frontal horn than in other species. In cross section, the base of the horn is posteriorly broad and anteriorly narrow. The horns are marked with prominent longitudinal grooves and are swollen into small bulbs at their tips. Some horns have conspicuous knobbing along the anterolateral edges.

The rostral horn of *S. tricornatus* is relatively longer and stouter than that of other synthetoceratines, but noticeable individual variation occurs in this character (table 10). Some variation also occurs in the length of the shaft in proportion to the total length of the horn; however, the length of the horn past the point of bifurcation is always relatively great (at least one-third of the total length). This is true also of *P. (P.) francisi*. In contrast, the rostral horn of the *P. (L.) siouxensis-trinitiensis* group is comparatively short, and the length of the prongs above the fork is considerably smaller (fig. 21). The shaft of the rostral horn in *S. tricornatus* is tilted anteriorly, but at the point of bifurcation the forks usually become swept toward the rear. Surface morphological characters of this horn correspond to those of *Prosynthetoceras*.

UPPER DENTITION: I^0 , C^1 , P^3-4 , M^1-3 . The upper canine alveolus of *Synthetoceras tricornatus* is less prominent than that of *P. (Prosynthetoceras) francisi*, but, because of the small sample size of the latter, this is for the present uncertain as a diagnostic character. P^2 is absent in this genus. P^3 and P^4 are relatively larger than those of *Prosynthetoceras* and exhibit a greater degree of "molarization." This is accomplished by an increase in the size of the tooth and by greater development of the parastyle and metastyle. In *S. tricornatus*, P^4 is remarkably uniform in construction; it is much less variable than P_4 . The P^4 s of all *S. tricornatus* specimens are molarized and not one resembles P^3 . P^4 tends to be triangular in shape and has a well-developed and recurved parastyle, an even stronger and anterior-

ly curved metastyle, and a large protocone. P^4 differs from P^3 primarily in having a larger protocone, whereas P^3 possesses a strong lingual cingulum. Although this condition was anticipated in the P^4 of *P. (P.) francisi*, P^3 of *Synthetoceras* has evolved even farther than in any of the preceding taxa.

The upper molars of *tricornatus* are substantially larger and taller crowned than those of *P. (P.) francisi*, but are virtually identical in cusp morphology. As in all protoceratids, they are characterized by salient styles, ribs, and accessory tubercles. Strong, bladelike cingula mark the anterolingual border of the molars. The anterior edge of M^3 occurs a few millimeters anterior to the posterior nares. In *P. (P.) texanus* and *P. (P.) francisi*, the leading edge of the posterior nares extends more anteriorly, so that it is on line with or forward of M^3 .

LOWER DENTITION: I_{1-3} , C_1 , P_{3-4} , M_{1-3} . The teeth of the lower jaw of *Synthetoceras* are divided into two distinct functional batteries separated by a long diastema: the incisors and the cheek teeth. In addition to the normal three incisors, the C_1 has become incisiform and joins the others to form an almost parallel row at the edge of the splayed-out symphysis. I_1 is wide, spatulate, and more symmetrically constructed than the other incisors, which tend to be oriented *en echelon* with respect to one another and which show both asymmetrical construction and wear. All have long roots, usually three times the length of the exposed crown.

The mandibular diastema of *S. tricornatus* is even longer than that of *P. (P.) francisi*, both relatively and absolutely. As in *P. (P.) francisi*, the diastemal crest is sharp and pinched just below the edge. P_1 and P_2 are lost in *Synthetoceras*, culminating a trend in premolar reduction begun in earlier synthetoceratines. There is, however, apparently more variation in the degree of reduction and complexity of cusps development in *S. tricornatus* (at least from MacAdams Quarry) premolars than in *P. (P.) texanus* and *P. (P.) francisi*. Because of the inadequate sample representing the earlier species, this is, unfortunately, statistically unverifiable. Nevertheless, the trend in reduction and loss of the anterior premolars is evident. Concomitant with this trend is a correlated one involving increasing size and complexity of P_4 , a progression toward molarization noted also in the upper dentition.

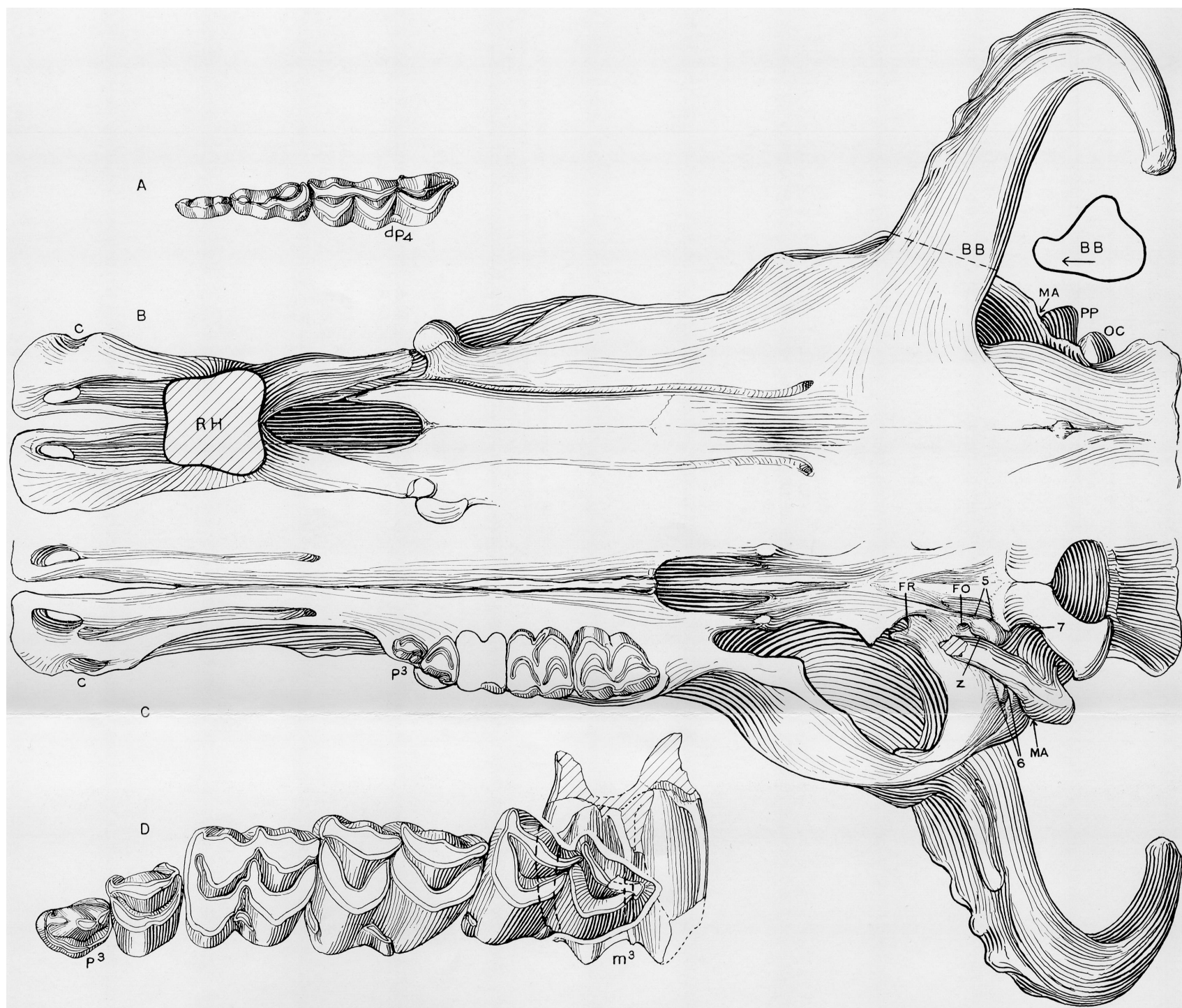


FIG. 29. *Synthetoceras tricornatus*, from MacAdams Quarry, Donley County, Texas. A. F:A.M. No. 33420, dP₂-dP₄, occlusal view, reversed. $\times 1$. (After Frick, 1937 fig. 62, in part; letters and numbers as used in legend.) B, C. F:A.M. No. 33407. B. Dorsal view. $\times \frac{1}{2}$. C. Ventral view. $\times \frac{1}{2}$. (See lateral, ventral, and posterior views figs. 28 and 30.) D. Palate, F:A.M. No. 32467, P³-M³, occlusal view and M³, buccal view. $\times 1$. BB. Cross section of horn.

Abbreviations: FO, foramen ovale; FR, foramen rotundum; MA, auditory meatus; OC, occipital condyle; PP, paroccipital process; RH, rostral horn; Z, depression for tympanohyal; 5, lacerated foramina; 6, glenoid foramina; 7, condylar foramen.

TABLE 11
MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Synthetoceras tricornatus*

| | N | OR | \bar{X} | S | V |
|--------------------------------|----|-------------|-------------|-------------|-----------|
| P ³ | | | | | |
| L | 15 | 12.7- 15.5 | 13.71±0.20 | 0.779±0.146 | 5.83±1.06 |
| W | 15 | 8.7- 12.1 | 10.40±0.22 | 0.882±0.161 | 8.47±1.55 |
| P ⁴ | | | | | |
| L | 15 | 14.0- 16.0 | 15.20±0.18 | 0.711±0.130 | 4.67±0.85 |
| W | 15 | 15.0- 19.0 | 16.80±0.31 | 1.200±0.220 | 7.24±1.32 |
| M ¹ | | | | | |
| L | 13 | 21.0- 27.3 | 23.95±0.45 | 1.640±0.322 | 6.84±1.34 |
| W | 13 | 21.8- 24.5 | 23.27±0.20 | 0.728±0.143 | 3.12±0.61 |
| M ² | | | | | |
| L | 17 | 25.0- 32.0 | 29.10±0.52 | 2.170±0.372 | 7.45±1.27 |
| W | 17 | 23.0- 27.0 | 25.59±0.27 | 1.140±0.195 | 4.45±0.76 |
| M ³ | | | | | |
| L | 17 | 28.8- 32.8 | 30.85±0.26 | 1.100±0.187 | 3.56±0.61 |
| W | 15 | 24.0- 27.3 | 25.23±0.29 | 1.130±0.206 | 4.47±0.81 |
| P ³ -P ⁴ | 15 | 27.5- 30.5 | 28.82±0.27 | 1.050±0.192 | 3.64±0.66 |
| M ¹ -M ³ | 15 | 74.5- 89.0 | 82.40±0.98 | 3.820±0.698 | 4.63±0.84 |
| P ³ -M ³ | 15 | 100.0-116.0 | 109.20±1.22 | 4.760±0.870 | 4.35±0.79 |

TABLE 12
MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Synthetoceras tricornatus*

| | N | OR | \bar{X} | S | V |
|--------------------------------|----|-------------|-------------|-------------|------------|
| P ₃ | | | | | |
| L | 19 | 11.0- 12.5 | 11.95±0.31 | 1.412±0.229 | 3.45±0.55 |
| W | 18 | 5.6- 8.1 | 6.62±0.15 | 0.623±0.104 | 9.35±1.55 |
| P ₄ | | | | | |
| L | 25 | 13.0- 16.3 | 14.57±2.91 | 1.000±0.141 | 6.90±0.97 |
| W | 25 | 8.2- 10.9 | 9.48±0.11 | 0.579±0.082 | 6.07±0.85 |
| M ₁ | | | | | |
| L | 27 | 18.0- 24.5 | 20.18±0.29 | 1.620±0.220 | 8.02±1.09 |
| W | 23 | 13.0- 16.5 | 14.43±0.16 | 0.799±0.118 | 5.53±0.81 |
| M ₂ | | | | | |
| L | 29 | 23.0- 31.5 | 27.28±0.33 | 1.800±0.236 | 6.59±0.86 |
| W | 28 | 13.5- 18.5 | 16.36±0.23 | 1.175±0.157 | 7.18±0.95 |
| M ₃ | | | | | |
| L | 28 | 36.0- 42.0 | 39.15±0.28 | 1.525±0.209 | 13.89±1.51 |
| W | 26 | 13.5- 18.6 | 16.62±0.25 | 1.300±0.180 | 7.82±1.08 |
| P ₃ -P ₄ | 17 | 23.0- 27.5 | 25.50±0.28 | 1.130±0.193 | 4.45±0.76 |
| M ₁ -M ₃ | 26 | 79.0- 94.0 | 85.07±0.72 | 3.700±0.513 | 4.34±0.60 |
| P ₃ -M ₃ | 23 | 104.0-118.0 | 109.97±0.70 | 3.370±0.497 | 3.06±0.45 |
| C-P ₃ | 10 | 114.0-137.0 | 120.10±0.69 | 7.010±1.567 | 5.84±1.30 |

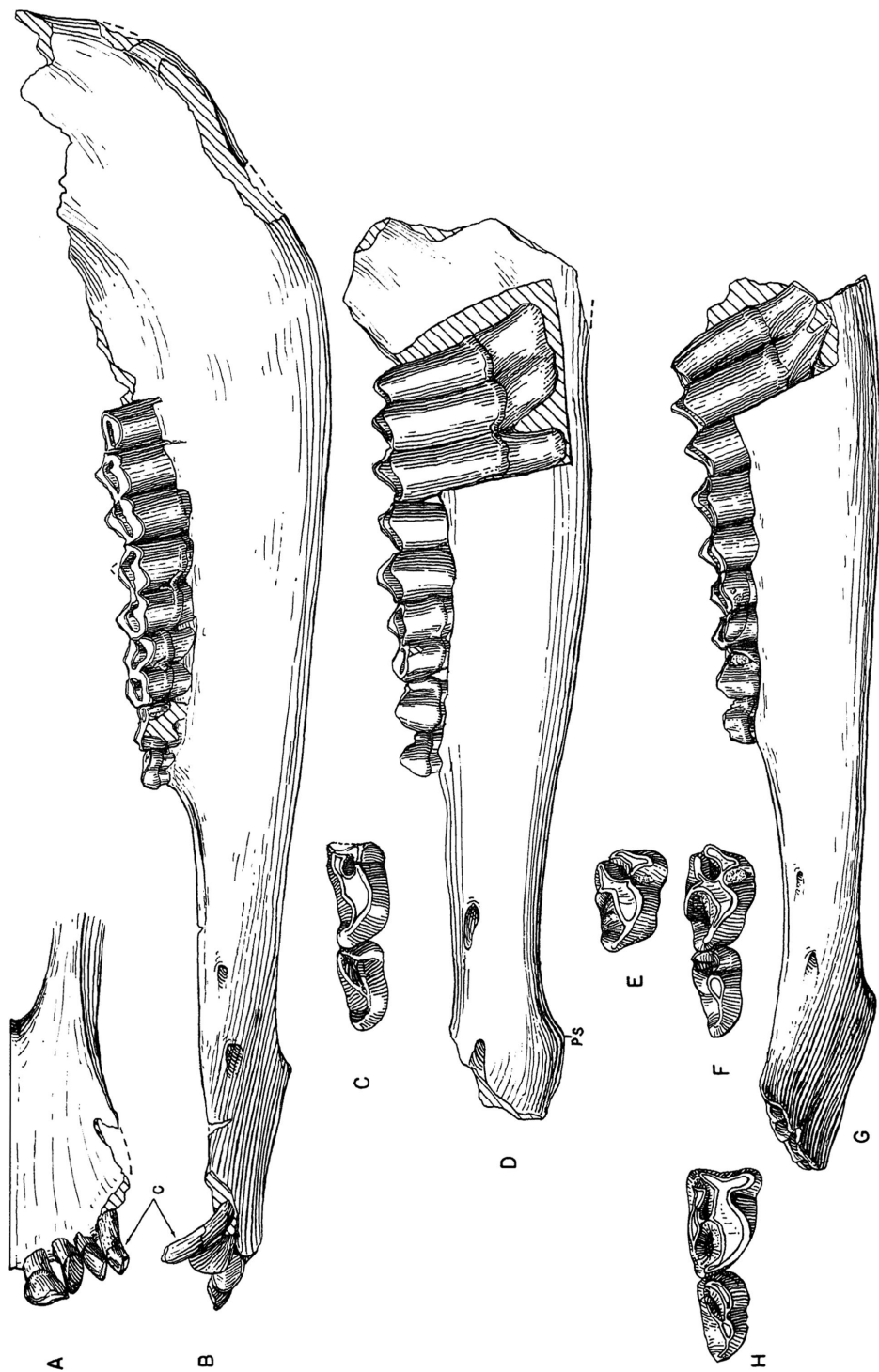


FIG. 32. *Synheloceras tricornatus*, from MacAdams Quarry, Donley County, Texas. A, B. F.A.M. No. 53444. A. Dorsal view of symphysis. $\times \frac{1}{2}$. B. Lateral view. $\times \frac{1}{2}$. C, D. F.A.M. No. 32464. C. Occlusal view of P₃-P₄. $\times 1$. D. Lateral view. $\times \frac{1}{2}$. (Both views after Frick, 1937, fig. 65; M₃ root exposed.) E-G. F.A.M. No. 53426, partial mandible. E. Occlusal view of right P₄, reversed. $\times 1$. F. Occlusal view of left P₃-P₄. $\times 1$. G. Lateral view. $\times \frac{1}{2}$. H. Right ramus with P₃-M₃, F.A.M. No. 53430, occlusal view of P₃-P₄, reversed. $\times 1$.

P₃ of *S. tricornatus* does not differ substantially from that of *P. (P.) francisi*. It is characterized by a high median protoconid, an anterolingual flexid (paraconid), which is swollen distally to form a distinct stylid, and an "L"-shaped hypoconid that is flexed labially. In contrast to *P. (P.) francisi*, the entoconid of *S. tricornatus* does not extend so far posteriorly. With wear, the hypoconid and entoconid enclose a small fossettid. P₄ is morphologically the most variable tooth in the *S. tricornatus* dentition. This variability obtains between opposite halves of the same jaw, as well as among individuals of the same population. Most of it is expressed by various complications in the formation of the metaconid, entoconid, and hypoconid. The anterolingual flexid is much the same as in *P. (P.) francisi* and is connected to the high protocone by a rather sharp ridge. Although the most variable cuspid on the *S. tricornatus* P₄, the metaconid is usually characterized by a bladelike forward extension which in some specimens almost reaches the anterolingual flexid. (This is by far the most complicated tooth in the synthetoceratine lineage and

represents the greatest "molarization" of premolars in this group; see fig. 32.) In other P₄s, this extension is not so strongly expressed. The hypoconid of the *S. tricornatus* P₄, like that of *P. (P.) francisi*, makes a "dog-leg" lingually; however, in most specimens there is pronounced labial extension which serves to form a prominent labial stylid on this tooth. Again, the hypoconid and entoconid enclose a posterior fossettid in later stages of wear.

Except for their greater hypsodonty, the lower molars of *S. tricornatus* do not differ substantially from those of *P. (P.) texanus* or *P. (P.) francisi*. Although prominent, stylids are not so well developed as the corresponding styles on the upper molars; accessory tubercles appear between the protoconid and hypoconid of M₁ and occasionally M₂.

MANDIBLE: Numerous and well-preserved fossil specimens assigned to *S. tricornatus* provide the basis for a more complete description of the synthetoceratine mandible. The trends observed in shape and proportions of the mandible from *Syndyoceras* through *P. (P.) texanus* and *P. (P.)*

TABLE 13

MEASUREMENTS (IN MILLIMETERS) OF THE IMMATURE UPPER DENTITION OF *Synthetoceras tricornatus* STIRTON

| | dP ² | | dP ³ | | dP ⁴ | | M ¹ | | M ² | |
|------------------|-----------------|-------|-----------------|--------|------------------------------|--------|----------------|--------|----------------|-----|
| | L | W | L | W | L | W | L | W | L | W |
| F:A.M. No. 53478 | 11.0 | × 5.5 | 20.0 | × 14.8 | 22.3 | × 16.5 | — | — | — | — |
| F:A.M. No. 53487 | 12.0 | × 5.8 | 21.4 | × 14.9 | (23.5) ^a × (17.5) | — | — | — | — | — |
| F:A.M. No. 53477 | 10.5 | × 4.7 | 20.0 | × 13.9 | 20.9 | × 19.0 | 27.0 | × 20.5 | — | — |
| F:A.M. No. 53485 | — | — | 19.5 | × 13.6 | 22.2 | × 15.6 | 26.5 | × 19.0 | — | — |
| F:A.M. No. 53483 | — | — | (19.+) × — | — | 19.5+ × 19.0+ | — | 28.2 | × 19.5 | 31.0 | × — |

^aMeasurements enclosed in parentheses are approximate.

TABLE 14

MEASUREMENTS (IN MILLIMETERS) OF THE IMMATURE LOWER DENTITION OF *Synthetoceras tricornatus* STIRTON

| | dP ₂ | | dP ₃ | | dP ₄ | | M ₁ | | M ₂ | |
|------------------|-----------------|-------|-----------------------------|---------|-----------------|--------|----------------|--------|----------------|-----|
| | L | W | L | W | L | W | L | W | L | W |
| F:A.M. No. 33420 | 11.0 | × 3.9 | 14.9 | × 7.0 | 28.8 | × 9.9 | — | — | — | — |
| F:A.M. No. 53474 | 9.5 | × 4.0 | 13.0 | × 6.3 | 26.5 | × 11.5 | — | — | — | — |
| F:A.M. No. 33421 | 10.2 | × 3.8 | 13.0 | × 7.0 | 28.6 | × 11.0 | — | — | — | — |
| F:A.M. No. 39994 | 10.1 | × 4.4 | (14.3) ^a × (7.8) | — | 28.5 | × 12.8 | 26.5 | × — | — | — |
| F:A.M. No. 53459 | — | — | 15.5 | × (7.0) | 29.0 | × 12.5 | 27.4 | × 12.+ | — | — |
| F:A.M. No. 53470 | 11.3 | × 4.0 | 15.5 | × 7.8 | 29.0 | × 12.0 | (26.8) × — | — | — | — |
| F:A.M. No. 53457 | 10.1 | × 4.0 | 14.8 | × 7.4 | 25.8 | × 12.3 | 25.3 | × 12.5 | (29.0) | × — |
| F:A.M. No. 53467 | 11.9 | × 4.9 | 16.3 | × (8.2) | 27.5 | × 13.9 | 27.5 | × 13.5 | 34.0 | × — |

^aMeasurements in parentheses are approximate.



FIG. 33. *Syntheloceras tricornatus*, referred right and left mandibular rami, F.A.M. No. 53428, from MacAdams Quarry, Donley County, Texas.
 A. Occlusal view. B. Lateral view. All $\times 0.50$.

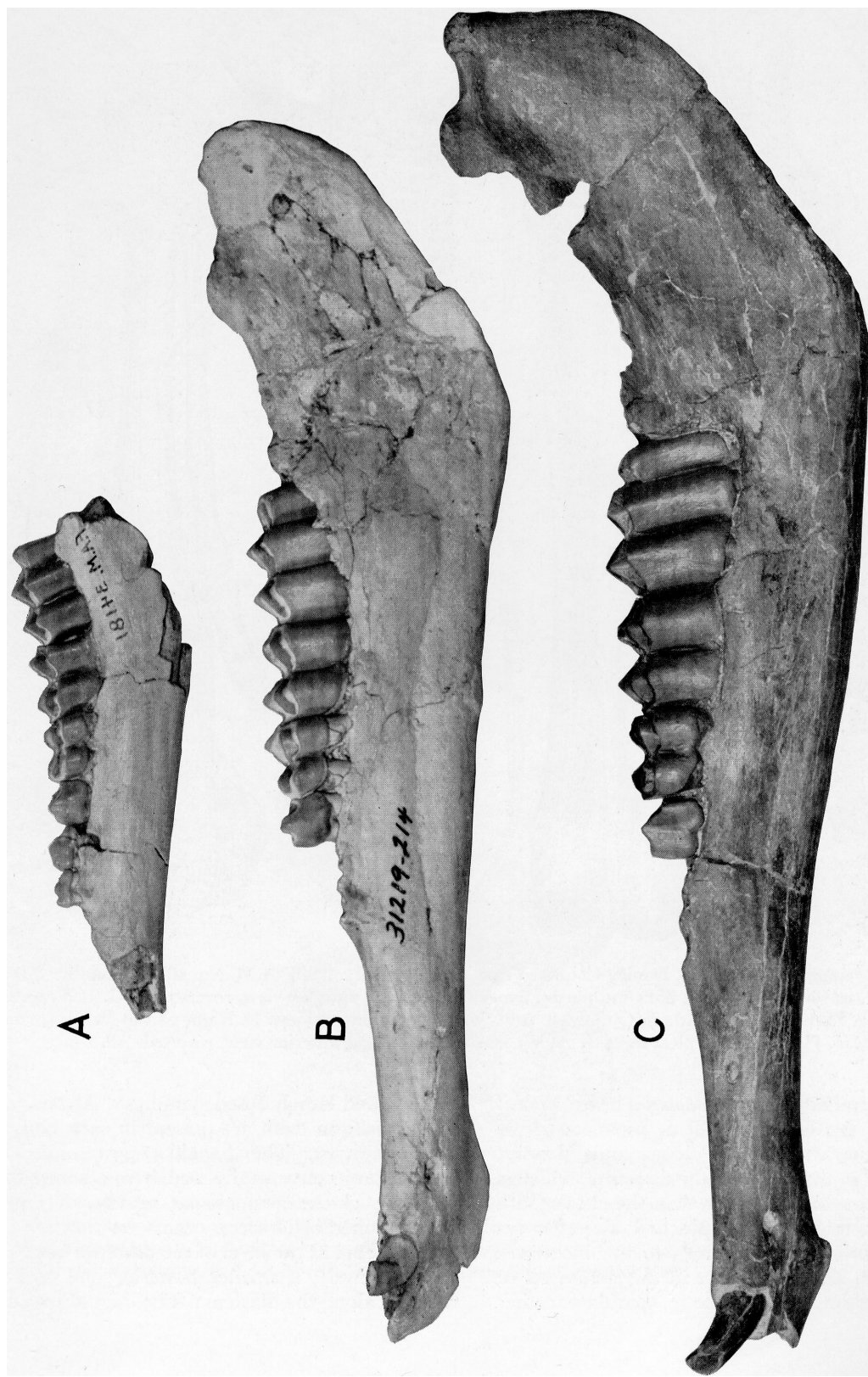


FIG. 34. A. *Prosyntheloceras* (*Prosyntheloceras*) *texanus*, referred right partial ramus, F.A.M. No. 34181, from 7 miles northeast of Huntsville, Walker County, Texas [type of (?) *Syntheloceras rileyi* Frick, 1937, fig. 66] (see fig. 6). B. *Prosyntheloceras* (*Prosyntheloceras*) *francisi*, left ramus, U.T.B.E.G. No. 31219-214, from near Cold Spring, San Jacinto County, Texas. Lateral view (see fig. 13). C. *Prosyntheloceras* (*Lambdoceras*) *trinitensis*, new species, referred left ramus, F.A.M. No. 33093, from Trinity River, San Jacinto County, Texas. Lateral view (see fig. 23). All $\times 0.75$.

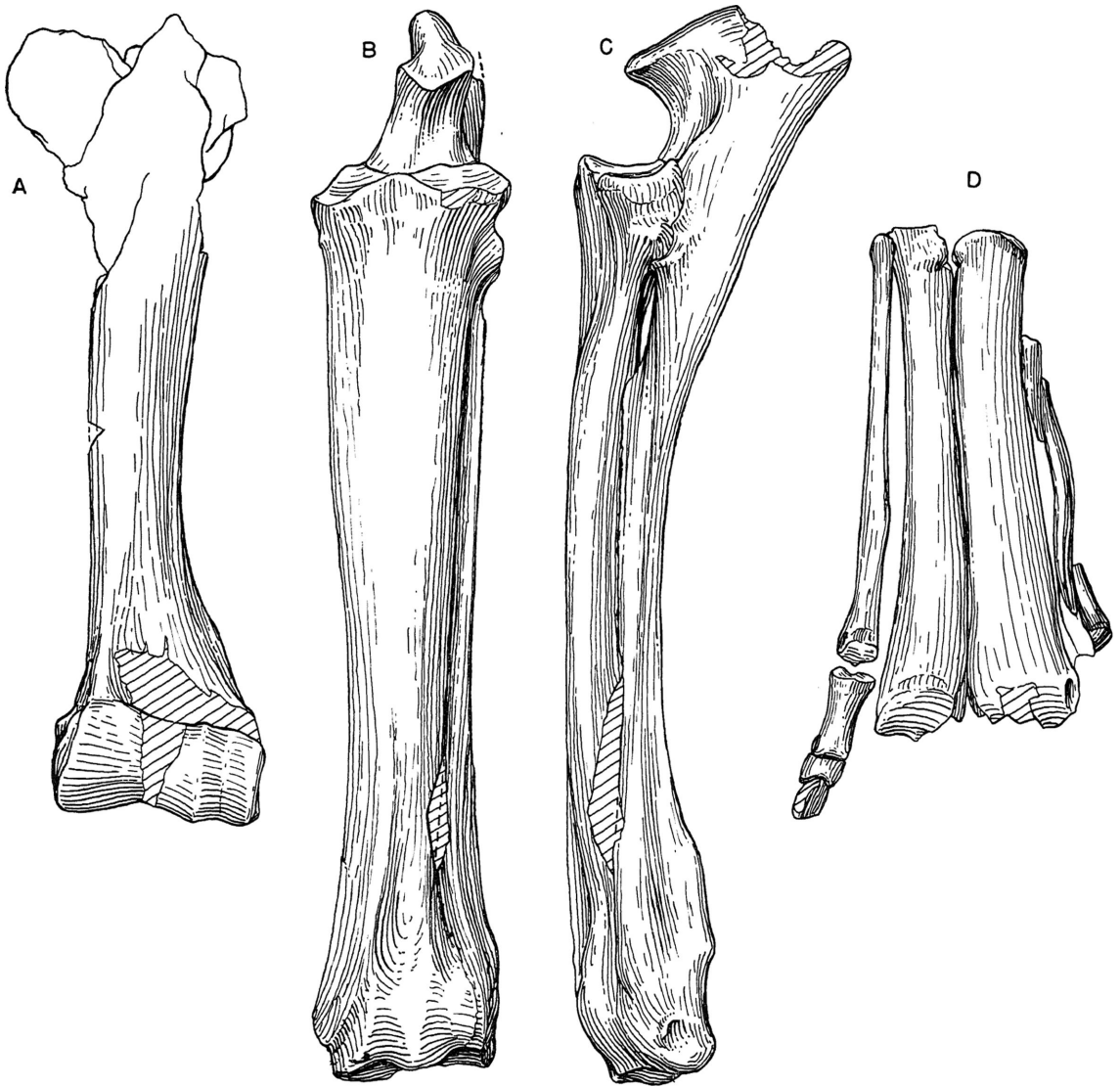


FIG. 35. *Synthetoceras tricornatus*, Donley County, Texas. A. Right humerus, F:A.M. No. 40229, from the Lewis Place (see associated manus fig. 35D and partial femur fig. 36B, C), anterior view, reversed. B, C. Left radius, F:A.M. No. 33410, from MacAdams Quarry. B. Anterior view. C. Lateral view. D. Right partial manus (metacarpals II, III, IV, and incomplete metacarpal V), F:A.M. No. 40229, anterior view, reversed. All $\times \frac{1}{2}$.

francisi culminate in *S. tricornatus*. The horizontal ramus of the lower jaw of *S. tricornatus* is, as noted, characteristically long and slender, especially in the region of the diastema, which is now proportionally longer than the cheek tooth row. The thin, dorsally pinched diastema extends uninterrupted from P_3 to the incisiform canine; P_1 and P_2 are lost in this genus. As in *P. (P.) francisi*, there is a large, spatulate, rather

hollow, and loosely fused symphysis. Alveoli for four incisiform teeth are present in each half of the symphysis. The hooklike posteroinferior border projects ventrally and is roughened for insertion of the genioglossus muscle. A large anterior mental foramen occurs on the side of the diastema at the level of the posterior edge of the symphysis; a smaller posterior one occurs midway along the diastema. The lingual surface

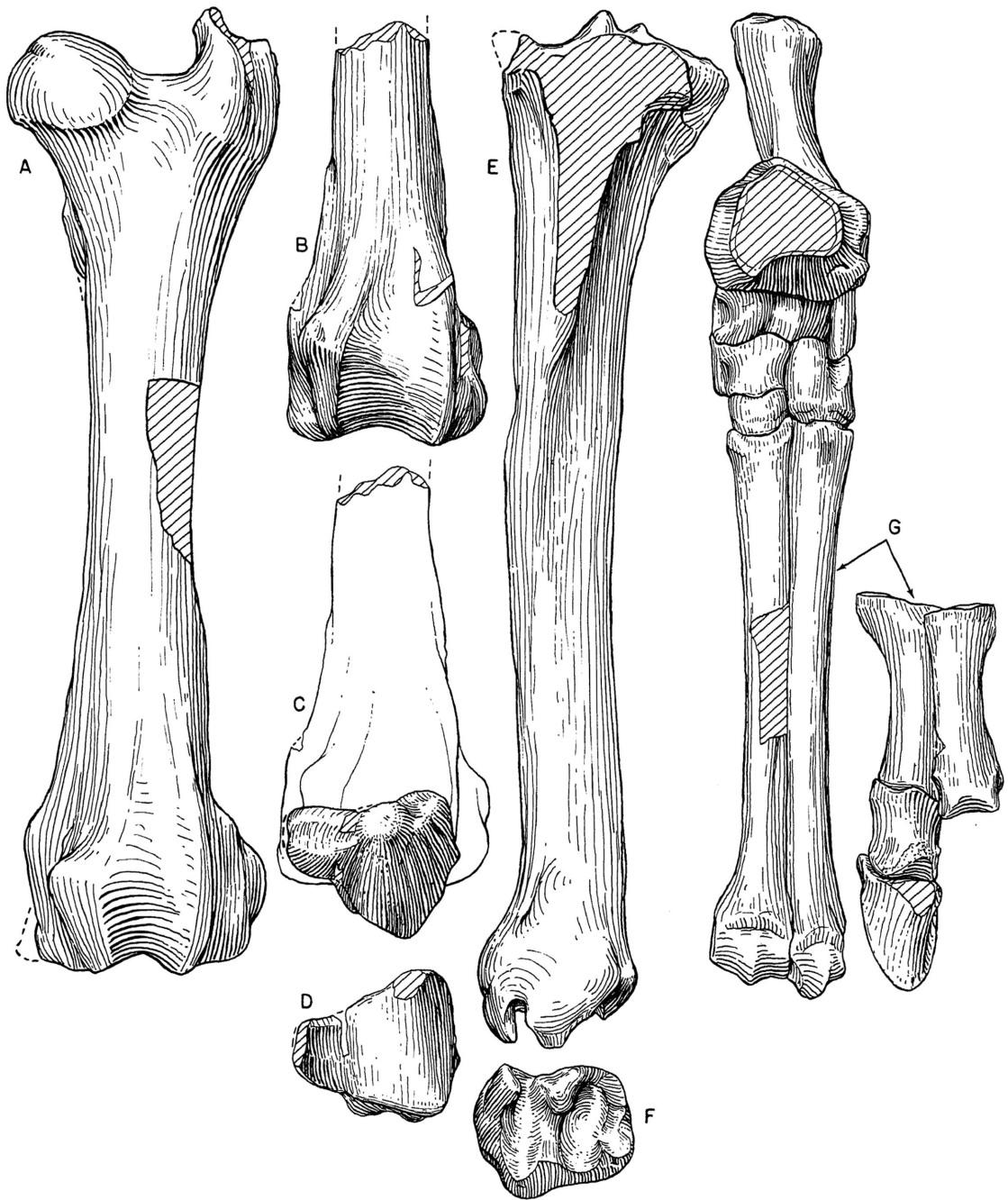


FIG. 36. *Synthetoceras tricornatus*, from Donley County, Texas. A. Right Femur, F:A.M. No. 40236, from MacAdams Quarry, anterior view, reversed. B-D. Right distal part of femur and patella, F:A.M. No. 40229, from the Lewis Place, (see humerus and manus, fig. 35A, D). B. Anterior view, reversed. C. Outline of femur and patella, anterior view, reversed. D. Patella, posterior view, reversed. E, F. Right tibia, F:A.M. No. 40237, from MacAdams Quarry. E. Anterior view, reversed. F. Distal view, reversed. G. Left articulated pes including the distal end of the tibia. F:A.M. No. 40238, from the Lewis Place, anterior view. All $\times \frac{1}{2}$.

of the body of the mandible is concave below the level of the molar roots; the bulge above this concavity apparently results not only from accommodation of the teeth but also for insertion of the mylohyoideus muscle. Labially, the inferior border of the horizontal ramus is flattened for insertion of the digastric muscle.

For the first time in this synthetoceratine lineage a full description of the morphological features of the ascending ramus can be made. The remarkably low and reduced coronoid process is similar to that described under *P. (P.) francisi*. In the earlier species, however, muscular attachments on the ascending ramus were missing or obscured. In the *S. tricornatus* specimens they are well in evidence. Again as in *P. (P.) francisi*, there is a small temporalis fossa labially and a larger masseter medialis fossa lingually. The most distinctive characteristic of the ascending ramus is the shape and reduction of the masseteric fossa. Unlike most other mammals, there is little or no expansion or excavation of the ramus for reception of the masseter muscle; rugosities for insertion of the masseter surround a shallow, elongated oval parallel to the long axis of the ramus. The lateral edge of the inferior rim of the ramus is also thickened for this purpose. Just below the stubby coronoid process is a small (30 mm. long) oval fossa, presumably for insertion of the masseter medialis. The depressor labii inferioris muscle inserts in a large scar on the labial base of the ascending ramus, just posterior to M_3 . This peculiar ramus is further distinguished by the presence of a long, scooped-out sulcus running along the middle of the inferior surface, which presumably served for insertion of an enlarged occipito-mandibularis muscle.

The condyle, which was not fully preserved in previously described forms, is seen in this species to be quite wide transversely and level along its dorsal, or articular, surface. Differentiation of the articular surface into separate planes is very slight; the labial half is flattened parallel to the axis of the horizontal ramus, and the posterior edge of the lingual half is ventrally expanded and slightly flattened at approximately 90 degrees to the labial half. The condition of the mandibular condyle correlates with that of the glenoid surface of the squamosal to indicate a very loose and motile articulation of the mandible.

LIMBS: Because the principal morphological

features of the synthetoceratine limbs have been described under *P. (P.) francisi* and *P. (L.) trinitiensis*, the description of the *Synthetoceras tricornatus* limbs (figs. 35, 36) will be limited primarily to a comparison with these taxa. The limbs and foot bones of *Synthetoceras tricornatus* are heavier proportioned than those of *Prosynthetoceras*. Limb elements (radius, F:A.M. No. 34127; metacarpals III and IV, F:A.M. Nos. 32274 and 32277; tibia, F:A.M. No. 41436; and metatarsals III and IV, F:A.M. Nos. 32282 and 34105) referred to *P. (L.) trinitiensis* approximate the length of the corresponding limbs referred to *S. tricornatus* but are slenderer proportioned (table 1). Furthermore, the ulna of *S. tricornatus* is proportionally heavier and more firmly coalesced with the radius than that of *P. (L.) trinitiensis*. Compared with the latter, the proximomesial facet of the *S. tricornatus* radius, which articulates with the inner condyle of the humerus, is relatively longer anteroposteriorly and the posteromesial border is more deeply notched for the articulation of the heavier ulna. Compared with *P. (L.) trinitiensis*, the medial facet for the lunar in *S. tricornatus* tends to be proportionally smaller than the ulnar facet for the unciform.

In the rear limb, the femur (fig. 36A, B) of *S. tricornatus* has a deeper patellar groove and the mesial ridge of the trochlea projects more anteriorly relative to the lateral ridge than in *P. (L.) trinitiensis*. The mesial ridge also, has a more prominent internal knoblike protuberance than does the latter. In *S. tricornatus*, the vestigial metatarsals II and V (F:A.M. No. 40238) are short nodules measuring 16 mm. and 13 mm., respectively. Further evidence corroborating the reduction in length of the vestigial metatarsals in *S. tricornatus* is seen in the pes of a partial skeleton (F:A.M. No. 40229) in which the depressions on the proximal parts of metatarsals III and IV for accommodation of the vestigial metatarsals do not extend as far distally as they do on metatarsals III and IV (F:A.M. Nos. 32282 and 34105) of the earlier occurring *P. (L.) trinitiensis*.

Thus, the limbs of *Synthetoceras* differ primarily from those of *Prosynthetoceras* in being heavier proportioned and in having a relatively stronger ulna, which is more firmly coalesced with the radius. Metacarpals II and V are relatively more slender than in *Prosynthetoceras* and vestigial metatarsals II and V are proportionally smaller and less distally extended than in the latter.

ZOOGEOGRAPHY

ALTHOUGH THE VERY EARLIEST HISTORY of the Protoceratidae has not been firmly established, it seems most likely that the oldest members of the family were distributed primarily in the Great Plains. More certainly designated protoceratids, such as *Pseudoprotoceras* from the Chadronian of Nebraska and *Heteromeryx* from the middle *Titanotherium* beds of the Chadronian of South Dakota are known only from this region, although a *Pseudoprotoceras*-like animal recently has been reported from Oligocene beds in the Sierra Vieja region of west Texas (J. A. Wilson, personal commun.). In view of later protoceratid occurrences in Texas, Mexico, and Central America, it is quite possible that the initial spread southward took place as early as the early Oligocene. The next morphological stage of protoceratid evolution is represented by *Protoceras*, which is known only from the Whitneyan of South Dakota.¹ No evidence exists that *Protoceras* ever ranged beyond the upper Great Plains, possibly because the Whitneyan is so poorly represented in the sedimentary record elsewhere.

A gap of some four and a half million years, the largest break in the entire history of the group, separates *Protoceras* from the next known protoceratid, *Syndyoceras*. From the latest occurrence of *Protoceras* in the upper part of the Pole-slide Member of the Brule Formation (Whitneyan), no published record of a protoceratid is known until we find *Syndyoceras* in the upper part of the Harrison Formation (Late Arikarean). By that time most of the morphological changes that later characterized the Synthetoceratinae had already accumulated. The exact distribution of the protoceratids during that time is not now definitely known. Certainly some of them remained in the Great Plains, while others may have dispersed into the Texas Coastal Plain as early as that. Those that remained gave rise to *Syndyoceras*, which in turn probably provided the basal stock of the *Prosynthetoceras* lineage.²

¹Fossil remains of *Protoceras* have been recovered only from channel deposits, suggesting a preference for open, floodplain habitat.

²Still another genus, *Paratoceras*, which is treated in a subsequent paper, was distributed over a region extending from the southern Great Plains (Texas panhandle) through

Two mostly allopatric subgenera of *Prosynthetoceras*, *P. (Prosynthetoceras)* and *P. (Lambdoceras)*, are recognized in the present report. The former is distributed entirely in the Gulf Coastal Plain, but the latter is found in both the Great Plains and in the Texas Coastal Plain. The ancestral population of both subgenera was probably restricted to the upper Great Plains; just when the initial southward dispersal reached the Texas Coastal Plain is not known, but probably took place during the early Hemingfordian. The subgenus *P. (Lambdoceras)* seems to have undergone most of its evolution in the Great Plains; it is distributed primarily in that region and is closest in many ways to *Syndyoceras* and its ancestral protoceratid stock. *Prosynthetoceras (L.) siouxensis* from the early Barstovian of Nebraska is similar to the medial Hemingfordian *P. (L.) hessei* of South Dakota and is most likely a direct descendant of it. At some point in this transition, however, probably during the latest Hemingfordian, an offshoot of this lineage reached the Gulf Coastal Plain and probably lived sympatrically alongside the earlier established *P. (Prosynthetoceras) texanus*. The second southward dispersal is represented by *P. (Lambdoceras) trinitiensis* from the Texas Trinity River Quarry. This, as yet, undescribed assemblage lies stratigraphically between the medial to late Hemingfordian Burkeville fauna and the medial Barstovian Cold Spring fauna and most probably will prove correlative with the early Barstovian Lower Snake Creek fauna of Nebraska. Although no *P. (Prosynthetoceras)* specimens have been recovered from the Trinity River Quarry, its position between a virtually unbroken evolutionary sequence from *P. (P.) texanus* to *P. (P.) francisi* testifies to the probable sympatry of members of the two subgenera. It is, of course, possible that *P. (L.) trinitiensis* temporarily displaced *P. (Prosynthetoceras)* from that particular region of the Texas Coastal Plain, but in any event the success of *P. (Lambdoceras)* was apparently short-lived, for no remains of *P. (L.) trinitiensis* have been found in deposits younger than those of early Barstovian age.

the Texas Coastal Plain and down into Central America as far as Panama. Its history is poorly known.

The first member of the *P. (Prosynthetoceras)* lineage, *P. (P.) texanus*, is found in the medial Hemingfordian Garvin Gully fauna of Texas. Apparently very shortly after it had become established in the Texas Coastal Plain it also dispersed to Florida, where it is found in the slightly younger Thomas Farm deposits. In Texas, this species persists into the medial to late Hemingfordian Burkeville fauna, undergoing only minor changes during the transition. In the as yet poorly known Trinity River assemblage, this lineage is apparently displaced by the immigrant, *P. (L.) trinitiensis* from the Great Plains, but this may be attributable to differential ecological sampling, possibly indicating only partial or incomplete allopatry. In the long run, this species seems to have been relatively unsuccessful in the Coastal Plain compared with those species comprising the *P. (Prosynthetoceras)* group, for it is not found outside of Texas and apparently became extinct some time before the medial Barstovian. At that time, the Cold Spring fauna reveals the continuing existence in Texas of the *P. (Prosynthetoceras)* lineage in the form of *P. (P.) francisi*. This species shows considerable advancement over its Burkeville predecessor and at the same time clearly demonstrates its phylogenetic importance as the ancestor to *Synthetoceras*. All evidence indicates that this transition took place in the Coastal Plain, as a result of direct, sustained inheritance, not as a consequence of replacement by adaptively superior allochthonous populations moving into the coastal region.

The genus *Synthetoceras* first appears in the early Clarendonian Lapara Creek Fauna of the Texas Coastal Plain. The same species is found next in the later Clarendonian of the Texas panhandle and still later in the early Hemphillian of Alabama¹ and Florida. We emphasize that al-

though neither the advanced *P. (P.) texanus* and *P. (P.) francisi* have been recovered outside Texas, we believe them to have had a trans-Gulf distribution, as have the early *P. (P.) texanus* and *S. tricornatus*. In view of the persistence of synthetoceratines and other forms into the Hemphillian of Florida, these distributional gaps, both chronologic and geographic, are probably a reflection of the poor fossil record of that period in this part of the coastal plain.

In sum, we suggest that the early synthetoceratine ancestors were distributed primarily in the Great Plains. An early dispersal, probably during the early Hemingfordian, brought the ancestors of the (*Prosynthetoceras*) lineage to the Texas Gulf Coastal Plain where they eventually spread eastward into Florida and northeastward along the Atlantic Coastal Plain.² The (*Lambdoceras*) group, on the other hand, had remained in the Great Plains during the course of most of its evolutionary history. During the late Hemingfordian, however, members of this group reached the Texas coast where they lived for a relatively short time through the early Barstovian. *Synthetoceras*, the direct descendant of *P. (Prosynthetoceras)*, flourished throughout the Gulf Coastal Plain and persisted, at least in Florida, until the early Hemphillian. Some of its representatives also spread back into the southern Great Plains, where they are preserved in the Clarendonian of the Texas panhandle.

tricornatus and those from the more definitely placed early Hemphillian McGehee fauna of Florida. Frank Whitmore of the United States Geological Survey is currently studying the rest of the newly discovered Hemphillian Alabama assemblage; this age designation is, therefore, subject to reinterpretation.

²Almost nothing is known of the Tertiary vertebrate history of the central interior of the United States, therefore it is obviously difficult to speculate on the historical and/or ecological zoogeography of this region until more evidence is forthcoming. The interpretation presented here is considered to be the most likely one based on presently available evidence.

¹Our Alabama age assignment is based on the close similarity between the Mobile specimen referred to *S.*

EVOLUTION AND PHYLOGENY

THE PHYLOGENETIC HISTORY of the Synthetoceratinae is relatively clear. Although certain critical evolutionary steps are not so well represented by fossils as others, morphological, and presumably genetic, continuity from one taxon to the next is rather well documented. Until the Protoceratinae are restudied, it would be premature to conjecture just which, if any, of the presently recognized species of that subfamily gave rise to the later subfamilies, but it is apparent that the Protoceratinae provided the basal stock for further protoceratid evolution.

The earliest known protoceratid, *Pseudoprotoceras*, is known from the Chadron Formation of western Nebraska. Described by Cook in 1934 as *Pseudoprotoceras longinaris*, it apparently lacks the cranial protuberances of *Protoceras*. The type skull (H.C. No. 507=A.M.N.H. No. 81000) contains alveoli for large canine tusks, indicating its male gender, but absence of a preserved cranial region precludes definite determination of the presence of parietal horns. However, just above and anterior to the orbit occurs an elongate and slightly rugose convexity. The convexity apparently extended at least part way over the orbit. The frontal area between the two convexities is also rugose. The open nasal passage formed by the extremely retracted nasal bones is bordered by gently arched maxillaries, but, in all, this form exhibits very few of the specialized characters possessed by *Protoceras*. It does, however, provide the probable ancestral condition for *Protoceras*. Members of the genus *Protoceras*, brought to light by Marsh (1897), display the most primitive development of the unusually distributed bony protuberances that characterize the skull of all later protoceratids. Although there is considerable variation in their expression, the bony processes of *Protoceras* males fall into two major groups: rostral and cranial. The cranial processes rise from the temporal crests of the parietals and from the supraorbital borders of the frontals. The rostral ones arise from the dorsal borders of the maxillaries. These processes are represented in each species of *Protoceras*, but are suppressed in females. It is interesting to note that the skull of *Protoceras* females and those of females of later genera are remarkably similar, especially when contrasted with the

striking differences observed in the male skulls. A third and smaller set of protuberances occurs on the male skull at the anterolateral borders of the frontals near the suture with the nasals and lacrimals. These are only faintly indicated in the female and do not persist in any of the later protoceratids.

The skull of *Protoceras*, irrespective of the horns, was described by Scott (1940) as being highly modernized with respect to other Oligocene artiodactyls: "The modernization of the skull . . . consists in the following characters: (1) the shortening and rounding of the cranium; (2) the backward shifting of the orbit, which is removed entirely behind the line of the molar teeth; (3) the great elongation of the facial region, due not only to the shifting of the orbit, but also the lengthening of the muzzle; (4) the bending downward of the face on the facio-cranial axis, which does not occur in the Cervidae." These characters for the most part are carried on in the later forms; however, the evolution of the more generalized features of the protoceratid skull is overshadowed by the more dramatic specializations in cranial armament.

Except for the lack of upper incisors, *Protoceras* possesses a full dentition. In the upper jaw there are no traces of alveoli in the premaxillaries. The canine of the male is a large curved tusk, comparable in development to that of *Hydropotes*, *Moschus*, and *Tragulus*. The premolars are unreduced and the molars are quite brachydont, robust, and complicated by accessory styles and tubercles. The lower jaw of *Protoceras* is relatively deep and robust, possesses a normal rounded and expanded angle and has a relatively short diastema. The lower dentition consists of three incisors, an incisiform canine, a caniniform P_1 , P_2 - P_4 , and M_1 - M_3 . As is true of the upper dentition, the lower molars are unreduced and primitively constructed, with both accessory styliids and tubercles.

The limbs of *Protoceras* are short, stout, and decidedly primitive. In the forelimb the ulna is heavy and only the distal end is coalesced with the radius; the magnum, trapezoid, and trapezium are all separate. In the manus there are four complete, separate, and functional metapodials. The hind foot is characterized by two functional

TABLE 15
SUMMARY OF DIAGNOSTIC CHARACTERS OF MEMBERS OF THE SYNTHETOCERATINAE

| | <i>Syndyoceras</i> | <i>P. (Lambdoceras)</i> | <i>P. (Prosynthetoceras)</i> | <i>Synthetoceras</i> |
|---|--|---|---|---|
| Rostral horn | Consists of two maxillary processes that join for a short distance to form an extremely short-shafted horn with relatively long and widely divergent forks | Elongate shaft with relatively shorter fork than in <i>Syndyoceras</i> and <i>P. (Prosynthetoceras)</i> | Longer and more anteriorly directed shaft than in <i>Syndyoceras</i> and <i>P. (Lambdoceras)</i> | Relatively longer and stouter |
| Frontal horns | Arise almost vertically from supraorbital region of frontal bone with posteroventral basal part of horn only slightly expanded | Extend more directly out over orbit with basal part less triangular in cross section than in <i>P. (Prosynthetoceras)</i> | Arise from a more posterior position on orbit and sweep more outward and backward, with basal part of horn more triangular in cross section, especially in later occurring species | Similar to those of <i>P. (Prosynthetoceras)</i> but with more conspicuous knobbing |
| Length of P ₁ -P ₄ diastema | Moderately long | Long | Long; longest in <i>P. (P.) francisi</i> | Extremely long |
| P ₁ | Caniniform | Caniniform | Caniniform | Lost |
| P ₂ | Double rooted and relatively large | Double rooted and relatively large in <i>P. (L.) hessei</i> to reduced in <i>P. (L.) trinitiensis</i> | Double rooted and moderately large in <i>P. (P.) texanus</i> to single rooted and reduced in <i>P. (P.) francisi</i> | Lost |
| P ₃ -P ₄ | Worn, but appear relatively large | Relatively heavier, posteriorly wider and more wedge-shaped than in <i>P. (Prosynthetoceras)</i> | Elongate in <i>P. (P.) texanus</i> to moderately reduced in <i>P. (P.) francisi</i> ; more laterally compressed than in <i>P. (Lambdoceras)</i> | Proportionally smaller relative to size of molars and characterized by a high median protoconid; P ₄ is more variable in development of metaconid than in other taxa |
| Upper molars | Low crowned with prominent labial styles and ribs and strong accessory cusps and cingula | Lower crowned and more complex molars than those of contemporaneous <i>P. (Prosynthetoceras)</i> species | Taller crowned than in <i>Syndyoceras</i> with prominent styles, ribs, accessory cusps and cingula | Larger and taller crowned with stronger anterolingual cingula than in <i>Prosynthetoceras</i> |
| Lower molars | Only known mandible is the type, with badly worn molars | Similar to those of <i>P. (Prosynthetoceras)</i> | Moderate in crown height with stylids reduced in comparison with upper molars; small median pillar at base of crown between protoconid and hypoconid on M ₁ and M ₂ | Taller crowned with an occasional median pillar at base of crown between protoconid and hypoconid on M ₁ and M ₂ |

TABLE 15—(Continued)

| | <i>Syndyoceras</i> | <i>P. (Lambdoceras)</i> | <i>P. (Prosynthetoceras)</i> | <i>Synthetoceras</i> |
|-------------|--|---|---|--|
| Metacarpals | Unknown | Four separate functional digits | Four separate functional digits | Four separate functional digits with lateral metacarpals II and V tending to be proportionally smaller than in <i>Prosynthetoceras</i> |
| Metatarsals | III and IV are separate; II and V extend distally about three-quarters of length of functional metatarsals | III and IV are separate; deeper depressions on proximal part of metatarsals III and IV for laterals II and V than in <i>P. (Prosynthetoceras)</i> | III and IV are separate; II and V are reduced to proximal splints | III and IV are separate; II and V tend relatively smaller than in <i>Prosynthetoceras</i> |

and separate metatarsals, lateral toes II and V being reduced to proximal splints. The cuboid and navicular are separate, the ecto- and mesocuneiforms are fused and the entocuneiform is separate. The proximal end of the fibula is co-ossified with the tibia; the fibula shaft is reduced or incomplete, and the malleolar is not fused with the tibia.

The greatest gap in our knowledge of proto-ceratid evolution lies between that morphological stage represented by *Protoceras* and that attained by *Syndyoceras*. In terms of absolute chronology, this corresponds to approximately four and a half million years. Although there is considerable variation among *Protoceras* species in the late Whitneyan (Scott, 1940), no single species truly anticipates *Syndyoceras*. In *P. celer* the maxillary protuberances are broad and platelike, curve outward, and are widely separated at the base. Those of *P. nasutus*, on the other hand, are much narrower, more rodlike, and unite suturally over the nasal canal. It is especially in this character that, among all the *Protoceras* species, *P. nasutus* anticipates *Syndyoceras*. *Syndyoceras* has progressed in horn development much beyond the condition observed in *Protoceras*. The rostral or maxillary pair join over the nasal canal to form a common trunk, then bifurcate just above the juncture to form two outwardly flaring tines. The frontal pair rise from the dorsal and posterior rim of the orbits, extend directly out over the orbits, then curve in a gentle arc toward the midline of the skull.

The kind of rostral horn seen in *Syndyoceras* certainly evolved from the union of the two maxillary protuberances of the type seen in *P. nasutus*, but this does not mean that *P. nasutus* was a direct ancestor, or even that the genus *Protoceras* provided the basal stock for *Syndyoceras*. The above-mentioned time gap between the two undoubtedly contained the true progenitor of the synthetoceratines; however, it is obvious that the evolution of the synthetoceratine rostral horn had to pass through a morphological stage like that represented by *Protoceras*. Tracing the evolution of the frontal horns of *Syndyoceras* from the cranial protuberances of *Protoceras* is more uncertain. Patton (1969b, p. 191) postulated that they were derived "from the union of the bony processes on the supraorbital borders of the frontals and those on the temporal crests of the parietals, forming a single beam." Now, however, we think it just as likely that they developed from the supraorbital processes alone. In any event, the ancestors of *Syndyoceras* either suppressed the parietal processes of the *Protoceras* stage or represent a lineage that paralleled *Protoceras* but never developed the other cranial processes.

Previously, the lack of significant numbers of frontal and rostral horns in any of the available collections prevented assessment of microevolutionary trends in these structures. Only three skulls, one each of *Syndyoceras cooki*, *Prosynthetoceras francisi*, and *Synthetoceras tricornatus*, were preserved sufficiently intact to allow accurate

correlation of skull and horn characters. Other fragmentary horns, housed mainly in the University of Texas collections, were used by Patton (1969b) to fill in some of the morphological gaps, but with the specimens available for the present study, these trends are now confidently established. As with the rostral horn, the ancestral frontal horn condition seems discernible in *Syndyoceras*.¹ These horns extend laterally out over the orbits at nearly right angles to the sagittal plane and then curve upward and toward the midline in a wide semicircle. The bases of the horns tend to be slightly flared and flattened, but distally, the horns become more rounded. Except for the typical vascular grooving, the edges of the horns are smooth.

The dentition of *Syndyoceras* is advanced over that of *Protoceras* in that the upper canine is relatively smaller, P¹ is lost, the premolars are more reduced in size, and the accessory cusps of the molars are generally less complex. This trend of tooth reduction and simplification is continued throughout the synthetoceratine lineage. *Syndyoceras* limbs, like those of all protoceratids, remain primitively constructed, and in some ways are even less advanced than in *Protoceras*. The forelimb of *Syndyoceras* is unknown, but in the hind limb, metatarsals II and V are even longer than those of *Protoceras* and their length is about three-fourths that of metatarsals III and IV. In *Protoceras* these toes are reduced to proximal splints.

In the medial Hemingfordian of the Great Plains and the Gulf Coastal Plain, *Syndyoceras* is replaced by *Prosynthetoceras*. The two populations of *Prosynthetoceras* are considered to belong to a single genus; however, those differences accumulated during their geographic separation have proved to be sufficient to warrant subgeneric grouping. It must be emphasized that this is a "natural" phylogenetic divergence sharing close common descent, not an instance of a synchronous polyphyletic step over a morphological threshold. Of the two subgenera, *Prosynthetoceras* (*Prosynthetoceras*) and *Prosynthetoceras* (*Lambdoceras*), the latter apparently led to an evolutionary dead end, whereas the former eventually gave rise to *Synthetoceras*. At the ge-

neric level, *Prosynthetoceras* has advanced over *Syndyoceras* primarily in the lengthening of the shaft of the rostral horn. Other differences, which are accentuated in later species of the genus, include increase in size, reduction in size of the premolars, lengthening of diastemata, and reduction of lateral metapodials. In all of these features, however, *P. (Lambdoceras)* was evolving more conservatively than *P. (Prosynthetoceras)*, so that contemporaneous species of each subgenus differ significantly. In fact, most of these features are incorporated in the subgeneric diagnosis. Although *P. (Lambdoceras)* probably evolved from the same ancestor as *P. (Prosynthetoceras)*, it retained more of the conservative *Syndyoceras* features. The most important of these taxonomically are the more primitive dentition, the more perpendicularly directed frontal horns, and the relatively shorter shaft on the rostral horn. In *P. (Lambdoceras)* the premolars remain quite large and complex in comparison to those of the type subgenus. This is continued from the earliest species, *P. (L.) hessei* of the Hemingfordian Flint Hill Quarry of South Dakota, to the early Barstovian *P. (L.) siouxensis* from western Nebraska. *Prosynthetoceras (L.) trinitiensis* from the early Barstovian of the Texas Coastal Plain also retains relatively large premolars and a rostral horn with a proportionally short fork, but has departed from its Great Plains relatives in other less taxonomically significant ways.

The subgenus *P. (Prosynthetoceras)* was apparently a true coastal plain² endemic, as no representatives have ever been found outside of this region. The earliest species, *P. (P.) texanus*, appeared in the medial Hemingfordian Garvin Gully fauna of Texas and evidently spread rapidly into other parts of the Gulf Coast. It is found in deposits of similar age in Florida and possibly New Jersey. At this stage of its evolution *P. (Prosynthetoceras)* possesses a rostral horn with a shaft not much longer than that of *P. (Lambdoceras)* but with a characteristically different shape. The rostral horns of all the Gulf Coast species are oval in cross section and show none of the posterior flattening typical of *P. (Lambdoceras)*. In successively higher stratigraphic units,

¹An undescribed skull of *Paratoceras* from the Miocene of Texas serves to illustrate still another variation in the development of cranial processes of early horned protoceratids. Although in other ways similar to *Protoceras*, in addition to supraorbital horns it has developed occipital rather than parietal horns.

²If the specimen from New Jersey is indeed *P. (Prosynthetoceras)*, then the term "coastal plain," as used herein, should be extended to include the Atlantic Coastal Plain, which, of course, is confluent with the Gulf Coastal Plain in Florida and Georgia.

the *P. (Prosynthetoceras)* horn is increasingly longer.

Temporally later and morphologically similar populations of *P. (P.) texanus* occur also in the Texas Burkeville Fauna. These individuals, however, are larger with taller-crowned molars, and possess longer-shafted rostral horns than do those from the Garvin Gully; little difference is noted in other characters. In the medial Barstovian Cold Spring fauna several important changes, mostly continuations of previously established trends, are discernible. The shaft of the rostral horn has attained much greater length and the fork is proportionally much longer; the frontal horns have become longer and sweep out toward the rear. The base of the frontal horns has widened and the lateral edges have become much more rugose. Changes in the dentition include reduction in size, occasional loss of P_2 and increased crown height of the molars. Concomitant with dentitional changes has been a general stretching of the snout region and lengthening the mandibular diastema resulting in a thinner and more elongated mandible.

Culmination of evolutionary progression within the Gulf Coast lineage is seen in the genus *Synthetoceras*. This remarkable animal, the largest and most advanced of all protoceratids, was characterized primarily by its exceptionally long rostral horn, its widely curved and knobby frontal horns, and its elongated snout and highly reduced dentition. From a total rostral horn length of 180 mm. in *P. (P.) texanus*, that of *Synthetoceras tricornatus* has attained a maximum length of 525 mm. In addition to its greater length, it is also stouter, generally longer forked, and more curved than in *P. (Prosynthetoceras) francisi*. The frontal horns, though not much larger than those of *P. (P.) francisi*, are much knobbier along the lateral edges (fig. 28). Changes in the jaws and dentition from *Prosynthetoceras* to *Synthetoceras* are especially significant. The already lengthened muzzle of later *Prosynthetoceras* becomes even more extended in *Synthetoceras*. The anterior half of the long, distally spatulate mandible is as slender as that of a giraffe, which it closely resembles. The mandibular diastema extends from the incisiform row to the third premolar, *Synthetoceras* having lost both P_2 and the caniniform P_1 . P_2 is also lost in *Synthetoceras*. The premolars have become more complex and molariform, and the molars are taller crowned. In the limbs, the ulna is rela-

tively stronger and more firmly coalesced with the radius, and the lateral metapodials are even more reduced than those of *Prosynthetoceras*.

Evolution of *Synthetoceras* from *Prosynthetoceras* was evidently gradual and probably occurred not in a single local population but rather within a large, gulf-wide population throughout which gene flow was relatively open. The presence of previously established *Prosynthetoceras* populations and the conspecificity of members of the genus over its entire distribution is persuasive in this regard. Thus, the morphologic stage represented by the taxon *Synthetoceras* was probably reached virtually simultaneously throughout the Gulf Coastal Plain and Texas panhandle. The occurrence of *Synthetoceras* in the early Clarendonian of the Texas Coastal Plain, the medial Clarendonian of the panhandle (type Clarendonian), and the early Hemphillian of Alabama and Florida is more a reflection of geological accident than of differential dispersal. Early Clarendonian deposits are not preserved in the panhandle, no Clarendonian deposits at all are recognized in Florida and Alabama, and the Hemphillian of the Texas Coastal Plain is poorly known.

Because the whole family has not been studied in detail, we are following Stirton's (1967) taxonomic arrangement and leaving the Protoceratidae in the suborder Tylopoda. Concerning the classification of the Protoceratidae with the Tylopoda, Stirton (1967, p. 25) stated, "Perhaps the most informative character in this regard is their retention of a separate navicular and cuboid, which is united in the earliest known ruminants. . . ." He further noted that "Characters in the dentition also support this conclusion."

A study of the various taxa of the Protoceratidae shows that the limbs and especially the foot structure of the most advanced member, *Synthetoceras*, remain primitive. The small degree of structural change observed in the limbs from the Oligocene protoceratids to the Pliocene synthetoceratines, shows that the limbs were subject to less adaptational change than the dentition and are therefore very useful for classification. In addition to the separated cuboid and navicular observed by Stirton, the limbs of the protoceratids have the following in common with the camelids: (1) separate magnum and trapezoid, (2) unfused metacarpals III and IV as in *Poebrotherium* and certain late occurring

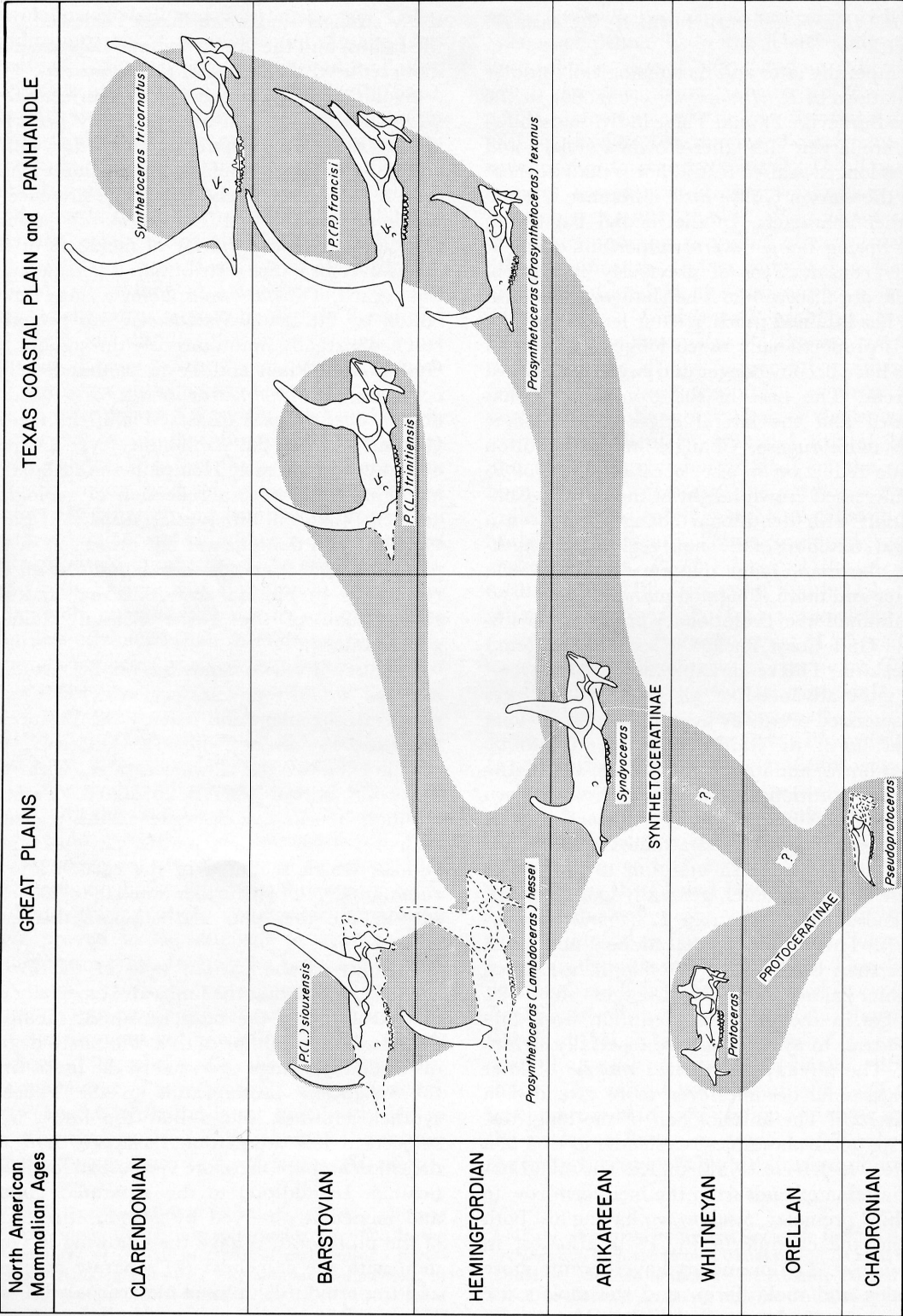


FIG. 37. Suggested phylogeny of the Synthetoceratinae.

camelids, (3) lack of carina on the anterior surface of the distal trochlea of the metacarpals, (4) strong distal keel on the astragalus, (5) united ecto-mesocuneiform, and (6) unfused metatarsals III and IV as in *Poebrotherium*.

Further, limbs of the protoceratids differ from those of the ruminants in the presence of a strong

distal keel and unparallelled upper and lower ginglymi of the astragalus and a separate cuboid and navicular. Distinct differences are also observed in the skull and dentition. The relationship of the various taxa of the Protoceratidae and the taxonomic position of the family will be treated more fully in a subsequent report.