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EARLY CONIACIAN (LATE CRETACEOUS) SELACHIAN FAUNA FROM THE BASAL ATCO FORMATION, LOWER AUSTIN GROUP, NORTH CENTRAL TEXAS

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ABSTRACT

Twenty-nine elasmobranch taxa were recovered from a phosphatic lag deposit at the base of the Atco Formation (Austin Group) in Collin, Dallas and Ellis counties, Texas. Although the lag disconformably overlies upper Turonian Eagle Ford Group strata, invertebrate taxa associated with the elasmobranchs indicate that it formed during the early Coniacian. Elasmobranch taxa we recovered include cf. *Meristodonoides* sp., *Ptychodus atcoensis* n. sp**.**, *P. latissimus*, *P. mammillaris*, *P. martini*, *P. whipplei*, *Heterodontus* sp., *Chiloscyllium greeni*, *Cantioscyllium decipiens*, cf. *Ginglymostoma* sp., *Scapanorhynchus raphiodon*, *Cretodus crassidens*, *Cretoxyrhina mantelli*, *Cretalamna appendiculata*, *Protolamna compressidens*, *Dallasiella willistoni*, cf. *Paraisurus* sp., *Johnlongia parvidens*, *Squalicorax falcatus*, *Pseudocorax laevis*, cf. *Microcorax* sp., *Sclerorhynchus* sp. cf. *S. priscus*, *Ischyrhiza schneideri*, *Ptychotrygon triangularis*, *Texatrygon hooveri*, *Kiestus texanus*, *Rhinobatos lobatus*, and *Pseudohypolophus* sp. The basal Atco Formation may have formed within an inner neritic environment (water depth < 30 m) during initial transgression of the Niobrara Sea.

INTRODUCTION

The Atco Formation, located at the base of the Austin Chalk, is a 60-meter-thick package of rock that represents marine sedimentation within the southern end of the North American Western Interior Seaway that occurred approximately 89 million years ago (upper Cretaceous, Coniacian Stage). In general, strata of the Austin Chalk, including the Atco Formation, are fine-grained and consist of chalk, marl and limestone throughout their lateral extent in Texas (Hovorka and Nance, 1994). The Atco Formation crops out in an arcuate belt (Alshuaibi, 2006) that extends from the Rio Grande River northward to San Antonio, through Dallas County and into Red River County (Figure1). The name “Atco” was proposed by Durham (1957) and utilized as an informal term by Murray (1961), but Pessagno (1969) formally identified the unit as the Atco Chalk Member of the Austin Group. A persistent phosphatic, fossiliferous conglomerate, once referred to as the “fish bed conglomerate”, occurs within the contact zone of the Eagle Ford and Austin groups (i.e., Adkins, 1933; McNulty, 1962; also Young, 1985). Pessagno (1969) included the conglomerate within his Atco Member. Smith (1981) later raised the Atco Chalk Member to formational status and retained it as the stratigraphically lowest formation within the Austin Group. Larson et al. (1991) placed the conglomerate at the base of the Atco Formation because the unit differed lithologically from Eagle Ford shales (Figure 2).

Fossils occurring within the basal Atco Formation conglomerate have received attention in the past, and Meyer (1974) was the first to conduct a comprehensive study of elasmobranchs from this horizon. Larson et al. (1991) presented a short list of elasmobranch species, compiled by Bruce Welton, that were recovered from this same interval. Welton and Farish (1993) later illustrated 21 species of elasmobranchs occurring in Austin Group strata, and 15 of these were specifically listed as originating from the Atco Formation. Cappetta and Case (1999) more recently published an account that included 25 elasmobranch taxa occurring within the “limite Tunonien-Coniacien” (Eagle Ford/Austin Chalk contact zone), and although a few additional taxa were discussed, their report generally presented taxonomic revisions to Meyer’s (1974) and Welton and Farish’s (1993) work. Cappetta and Case (1999) did not provide information regarding accession or catalogue numbers, nor did they mention an institution where the material from their study resides.

Herein we report elasmobranch fossils recovered from the basal conglomerate of Atco Formation at four different sites in northern Texas. In addition to identifying the elasmobranch taxa we discovered during our study, we discuss the biogeographic and

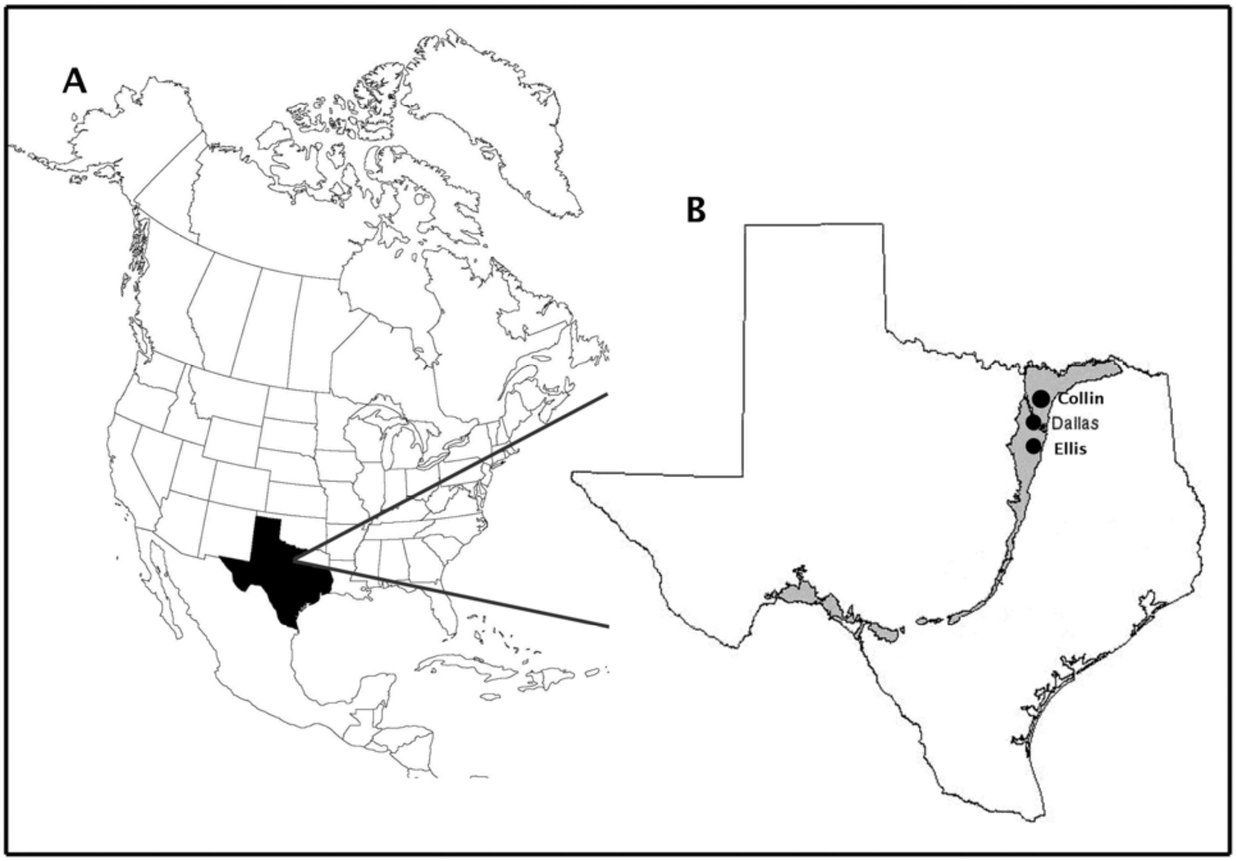

FIGURE 1. A, geo-political map of North America showing the location of Texas (black silhouette); B, enlargement of Texas showing Atco Formation outcrop belt and counties from which fossils discussed in this report were collected.

temporal distributions of these species. We also compare the basal Atco Formation assemblage with other Coniacian records from the Western Interior Seaway, and we touch upon potential differences in elasmobranch species compositions between the Turonian and Coniacian ages. Lastly, we present several paleoenvironmental scenarios that could have resulted in the formation of the "fish bed conglomerate".

AGE

The inoceramid *Cremnoceramus deformis erectus* occurs in the lower Atco Formation, and this species is a primary marker taxon for the early Coniacian (International Subcommission on Cretaceous Stratigraphy, 2004; see also Kauffman et al. 1994; Lamolda and Hancock, 1996; Walaszczyk and Cobban, 2000). In the Dallas area, Hancock and Walaszczyk (2004) found that this inoceramid occurs within a 0.92 m thick zone less than 0.5 m above the base of the Atco Formation. Although no inoceramids were recovered during our study, fragments of the ammonites *Peroniceras lepeei* and *Allocrioceras hazzardi*, two taxa indicative of an early Coniacian age (Cobban et al., 2008), were found.

The Atco Formation can be correlated with the Ernst Member of the Boquillas Formation in Texas based on the occurrences of *Allocrioceras hazzardi* and *Peroniceras lepeei* (Kennedy and Cobban, 1991), and with the Fort Hays Limestone Member of the Niobrara Formation in Kansas based on occurrences of *Cremnoceramus deformis erectus*, *Allocrioceras hazzardi*, and the foraminiferan *Marginotruncana pseudolinneiana* (Frerichs and Deiss, 1987; Hattin et al., 1987; Kennedy and Cobban, 1991; Alshuaibia, 2006).

METHODS

The material discussed in this report was collected from four different localities in north-central Texas (Figure 1), including the Ash Grove Cement Company (formerly North Texas Cement) in Ellis County (N 32° 31'33.38 W 96° 59' 40.42), a housing construction site (no longer exposed) in Prosper, Collin

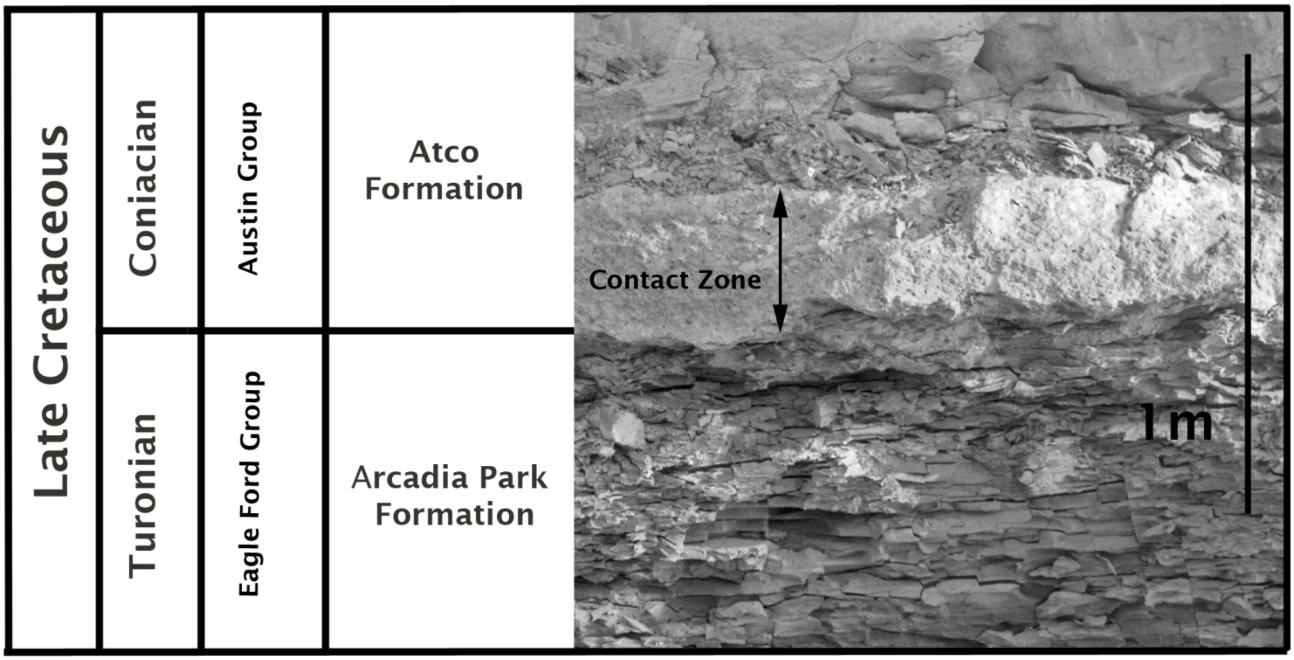

FIGURE 2. Photograph showing the stratigraphic relationships between the Eagle Ford and Austin groups in north-central Texas. The contact zone refers to the fossiliferous conglomeratic unit located at the base of the Atco Formation.

Co. (N 33° 14'54.93 W 96° 47'41.16), a housing construction site (no longer exposed) in Carrollton, Dallas Co. (N 33° 01' 30.10 W 96° 55'45.58), and a construction site (no longer exposed) in Hebron, Denton Co. (N 33° 02' 09.89 W 96° 51'21.71). In addition to surface material that was collected as float, in situ bulk matrix was obtained from all of the sites by the senior author (SAH). Approximately 158 kg of matrix was taken from the Ash Grove Cement site, and two to four kilograms from each of the construction sites. Matrix was disaggregated in water, screen-washed down to 0.25 mm particle size, and the remaining concentrates were hand-picked under a microscope.

In addition to the elasmobranch teeth reported herein, we also recovered some dermal denticles (Figure 6, H1 and H2) and vertebral centra. Associated vertebrate species include the osteichthyan fish *Enchodus petrosus* (Enchodontidae), *Hadrodus* sp. and *Anomoeodus barberi* (Pycnodontidae), *Protosphyraena perniciosa* (Pachycormidae), and *Xiphactinus audax* (Ichthyodectidae). Reptilian remains include chelonioid turtle carapace fragments and isolated mosasaur teeth and vertebrae. Specimens are housed at Southern Methodist University (SMU) in Dallas, Texas and at the Campbell Geology Museum (BCGM) at Clemson University, Clemson, South Carolina. We also examined specimens collected by Meyer (1974) that are housed at SMU, as well as several private collections containing fossils from the basal Atco Formation. Species taxonomy primarily follows Cappetta (2006).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Order HYBODONTIFORMES Maisey, 1987
Family HYBODONTIDAE Owen, 1846
Genus *MERISTODONOIDES* Underwood and Cumbaa, 2010
cf. *Meristodonoides* sp.
Figure 3A

Material—SMU 76492, (two incomplete teeth); BCGM 9323, (four incomplete teeth).

Remarks—All of the specimens are incomplete, with the largest measuring 3 mm meso-distally as preserved. The crowns consist of a rather tall central cusp flanked by at least one pair of widely separated lateral cusplets. A cutting edge is smooth and continuous across the central cusp and cusplets, and both the labial and lingual faces of these components bear elongated longitudinal ridges (originating at the

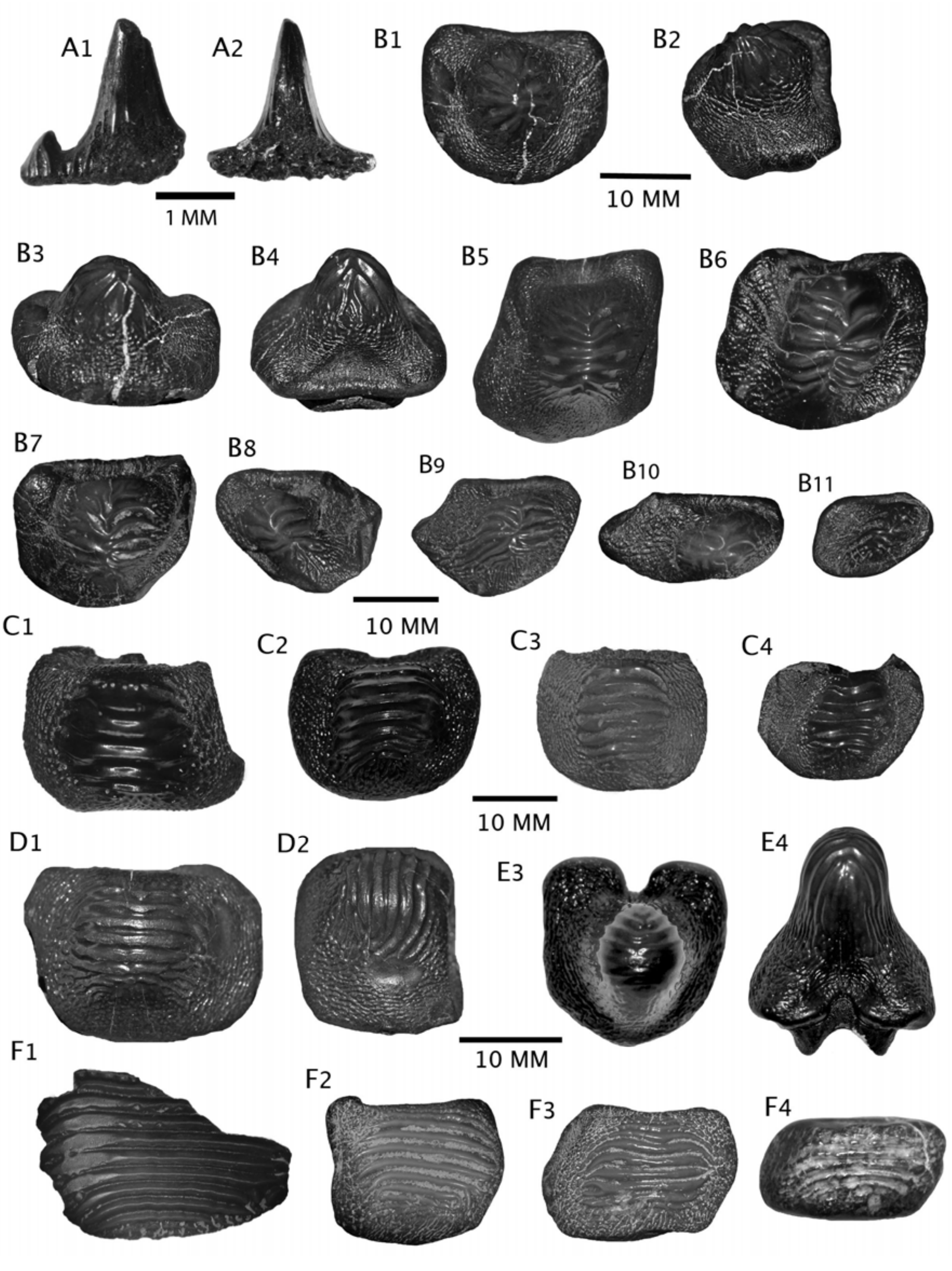

FIGURE 3. Elasmobranch species from the basal Atco Formation, north-central Texas. A, *Meristodonoides* sp., SMU 76492, A1, labial view, A2, lingual view. B, *Ptychodus atcoensis*, B1 occlusal, B2 lateral, B3, labial, B4 lingual views of SMU 75598 (anterior tooth; holotype); B5-B9, lateral teeth in occlusal view, B10-B11, posterior teeth in occlusal view. SMU 76435 includes B5, B7 and B8; SMU 76436 includes B6 and B9; SMU 76437 includes B10 and B11. C, *P. latissimus*, C1, anterior tooth in occlusal view (SMU 75590); C2 anterior tooth in occlusal view (SMU 75591); C3 anterior tooth in occlusal view; C4 lateral tooth in occlusal view (SMU 76431). D, *P. mammillaris*, SMU 75592, D1, occlusal, D2, lingual views. E, *P. whipplei*, SMU 75597, E1, occlusal, E2, lingual views. F. *P. martini*, F1, anterior tooth (SMU 76264) in occlusal view; F2 and F3, lateral teeth in occlusal view (SMU 76250); F4, posterior tooth (SMU 76265) in occlusal view.

crown foot and extending nearly to the apex of the central cusp and to the apex of the lateral cusplets). This species appears to be conspecific with *Hybodus* sp. that Cappetta and Case (1999) identified in the basal Atco Formation conglomerate. However, *Hybodus* may be a "wastebasket" taxon that includes tooth morphologies representing other genera. For example, Underwood and Cumbaa (2010) have assigned several species formerly attributed to *Hybodus* to their new taxon *Meristodonoides*. Within the Atco sample (including the material discussed by Cappetta and Case [1999: 8]), there is no indication of multiple pairs of lateral cusplets as in *Egertonodus* (Maisey, 1987; also Bermúdez-Rochas, 2009), and teeth of *Planohybodus* are labio-lingually thinner and the cutting edges much better developed (see Rees and Underwood, 2008; also Bermúdez-Rochas, 2009). The Atco hybodontoid teeth appear to fall within the range of variation of *Meristodonoides*, but we do not attribute them to any particular species due to the fragmentary nature of our material (see also Thurmond, 1971; Case, 1978; 2001; Case and Cappetta, 2004).

Subcohort NEOSELACHII Compagno, 1977
Order incertae sedis
Family PTYCHODONTIDAE Jaekel, 1898
Genus *PTYCHODUS* Agassiz, 1839
Ptychodus atcoensis n. sp.
Figure 3B

Material—Type specimen SMU 75598, (one tooth); Paratypes: SMU 75594, (one tooth); SMU 75595, (one tooth); SMU 75599, (one tooth); SMU 76434, (two teeth); SMU 76435, (three teeth); SMU 76436, (five teeth); SMU 76437, (three teeth); BCGM 9319, (four incomplete teeth).

Description—Anterior tooth crowns are high and bulbous, with straight sides that meet at a nearly 90 degree angle with the margin. There are between five and ten prominently raised and clearly delineated, parallel transverse ridges that extend across the apex and down the sides of the crown. The ridges are thick at the base and thin at the apex, creating a sharp cutting edge. The labial- and lingual-most ridges often converge apically towards the center of the crown, sometimes meeting at the center-most ridges and creating a distinctive chevron pattern. Each ridge maintains its thick and sharp edge as it extends down the side of the cusp and terminates at a wide and shelf-like margin. The crown margin is ornamented with coarse granulation and concentric ridges. Lateral and posterior file teeth are polygonal and irregularly shaped, with a raised crown and similar ridge and marginal ornamentation as seen on anterior teeth..

Remarks—Hamm (2009) described and figured *P. atcoensis* in an article for the Occasional Papers Volume 8 of the Dallas Paleontological Society. However, because this volume of Occasional Paper was not distributed through a publication house, according to ICZN code 8 regarding the dissemination of works where new taxa are named, herein we formally establish the taxon *P. atcoensis*.

Welton and Farish (1993) considered the *P. atcoensis* morphology to superficially resemble *P. mortoni*, and Meyer (1974) suggested that the taxon was transitional between *P. anonymus* and *P. mortoni*. The crown cusps of *P. anonymus* and *P. mammillaris* are much more inflated and bulbous with all of the ridges being transverse and parallel; whereas in *P. occidentalis* the crowns have more numerous and finer transverse ridges that nearly reach the lateral margins (Williston, 1900; Dibley, 1911). *Ptychodus mortoni* is readily distinguishable from *P. atcoensis* in that the tooth crown is more conical, with ridges that are finer, consistently radiating from the apex, and distally bifurcating. *Ptychodus whipplei* has a very high and rounded cusp with fewer and weaker ridges compared to *P. atcoensis*. *Ptychodus rugosus* is a very large species that has fewer transverse ridges, many of which have a beaded appearance (Macleod, 1982). *Ptychodus latissimus*, *P. martini*, and *P. polygyrus* can easily be distinguished from *P. atcoensis* in having rather flat crowns that lack an inflated cusp that is distinct from the marginal area. *Ptychodus atcoensis* is an uncommon species that is thus far only known to occur in the basal Atco Formation lag.

Ptychodus latissimus (Agassiz 1843)
Figure 3C

Material—SMU 75590, (one tooth); SMU 75591, (one tooth); SMU 76431, (one tooth); BCGM 9318, (one tooth).

Remarks—*Ptychodus latissimus* teeth have a moderately domed occlusal surface that is crossed by thick transverse ridges restricted to the central portion of the tooth crown, and the marginal area is wide and bears rugose or concentric and granular texture. The anterior crown face is flat with fine longitudinal ridges forming a dendritic pattern, whereas the posterior face has granular ornamentation. The teeth in our sample are represented by a single left lateral tooth (Figure3, C1) and three right lateral teeth (Figure3, C2-C4).

Ptychodus latissimus is thus far only known to occur in lower Coniacian rocks within the Western Interior Seaway, including the Sage Breaks Member of the Carlile Shale in South Dakota (Cicimurri, 2004) and the basal Atco Formation in Texas (Welton and

Farish, 1993; Hamm, 2004). Although our reported sample size is small, we observed 57 teeth of *P. latissimus* between multiple private collections from the Atco Formation. This larger sample may indicate that *P. latissimus* preferred shallow, warm water environments in the southern end of the seaway. This species has also been reported from the Coniacian of Europe (Dibley, 1911; Woodward, 1889).

Ptychodus mammillaris (Agassiz, 1838)
Figure 3D

Material—SMU 75992, (anterior tooth).

Remarks—Teeth of *P. mammillaris* differ from other ptychodontids in the Atco sample in having a large globular cusp and short marginal area. The cusp of the tooth is crossed by seven thick and robust transverse ridges that extend down the sides of the cusp but terminate sharply at the marginal area. The marginal area is clearly differentiated from the crown and ornamented with coarse beaded and concentric enameloid ridges. Although the transverse ridges of *P. martini* are similar, the crowns are flat (see below) and easily distinguished from *P. mammillaris*.

Only a single tooth of *P. mammillaris* was recovered in our sample. Welton and Farish (1993) noted that *P. mammillaris* is rare component of the Atco fauna, and a review of multiple private collections confirms this observation. The only other Coniacian report of *P. mammillaris* is based on a single tooth from the Fort Hays Limestone in Kansas (Everhart and Darnell, 2004). The species has also been reported from the Coniacian of Europe (Dibley, 1911; Woodward, 1889).

Ptychodus martini (Williston, 1900)
Figure 3F

Material—SMU 76250, (7 teeth); SMU 76264, (one tooth); SMU 76265, (one tooth); SMU 76427, (one tooth); SMU 76428, (one tooth); SMU 76429, (one tooth).

Remarks—The medial teeth of *P. martini* are unique among ptychodontids in that they are rectangular with an extremely flat occlusal surface that is crossed by eight to nine parallel and slightly undulating ridges that extend to the crown margins (Figure3, F1). The ridges are closely spaced, thick at the base but thinning apically to form sharp cutting edges. Teeth could be confused with those of *P. latissimus*, but they can be differentiated on the basis of smaller marginal area bearing coarser granular ornamentation, nearly flat as opposed to inflated crown, and less robust transverse ridges that extend further towards the lateral crown margins.

Ptychodus whipplei (Marcou, 1858)
Figure 3E

Material—SMU 75996 (single tooth), SMU 75597 (single tooth), SMU 76416 (composite dentition, 170 teeth); BCGM 9261, (four teeth); BCGM 9316, (seven teeth), BCGM 9317 (six teeth).

Remarks—Teeth of *P. whipplei* are distinctive among the Atco ptychodontids in having a very tall but narrow cusp, and the three to five transverse ridges are virtually restricted to the cusp apex. Lateral teeth are strongly asymmetrical and the cusp becomes conspicuously distally inclined. This species was widely distributed in the Western Interior Seaway from the Turonian to the Coniacian, and in terms of relative abundance, *P. whipplei* is the most common ptychodontid in the Atco sample. This species was also found to be abundant in late Turonian rocks of South Dakota (Cicimurri, 2004). *Ptychodus whipplei* is currently only known from rocks that were deposited within the Western Interior Seaway (Mexico to South Dakota).

Order HETERODONTIFORMES Blainville, 1816
Family HETERODONTIDAE Gray, 1851
Genus *HETERODONTUS* Blainville, 1816
Heterodontus sp.
Figure 4A

Material—BCGM 9320, (one incomplete tooth).

Remarks—Welton and Farish (1993) illustrated two *Heterodontus* anterior teeth (p. 79, figs. 1 and 4) from the basal Atco Formation, and these are similar in morphology to the specimen we recovered. Our specimen also compares well to a tooth from the basal Atco Formation that was illustrated by Cappetta and Case (1999; plate 1, fig 6). Although Welton and Farish (1993) identified their material as *Heterodontus* cf. *canaliculatus*, we agree with Cappetta and Case (1999) that the species assignment is incorrect, as anterior teeth of *H. canaliculatus* have a much higher and narrower cusp, and lateral cusplets are very poorly developed (see Underwood and Mitchell, 1999). BCGM 9320 bears some similarity to *H. lonzeensis* (Herman, 1977) but our available sample does not allow for a more precise specific identification. Welton and Farish (1993) noted that *Heterodontus* is a rare component of Atco Formation elasmobranch samples from Travis County, and we recovered only one tooth despite having sampled four localities within Collin, Ellis and Dallas counties. Cappetta and Case (1999) refrained from making a specific assignment for the Atco *Heterodontus*, but they suggested that the teeth represent a new species. Unfortunately, BCGM 9320 does not provide sufficient information to warrant our naming a new species. *Heterodontus* has not been reported from Turonian or Coniacian rocks in other parts of the North American Gulf Coastal Plain or Western Interior.

Order ORECTOLOBIFORMES Applegate, 1972
Family HEMISCYLLIIDAE Gill, 1862
Genus *CHILOSCYLLIUM* Müller and Henle, 1837
Chiloscyllium greeni (Cappetta, 1973)
Figure 4C

Material—SMU 76488, (one tooth); BCGM 9322, (two incomplete teeth).

Remarks—The three teeth in our sample are identical to specimens reported by Cappetta and Case (1999) from the basal Atco Formation, and they compare well to specimens described from the Turner Sandy Member of the Carlile Shale of South Dakota and Wyoming (Cappetta, 1973; Cicimurri, 2004). Tooth crowns of *Chiloscyllium greeni* are easily distinguished from a similar taxon, *Cantioscyllium decipiens* (see below), in that they are much smaller in size and the labial crown face is devoid of ornamentation.

Family GINGLYMOSTOMATIDAE Gill, 1862
Genus *CANTIOSCYLLIUM* Woodward, 1889
Cantioscyllium decipiens (Woodward, 1889)
Figure 4D

Material—SMU 76491, (one tooth); BCGM 9321, (six teeth).

Remarks—These teeth are comparable to specimens reported from the upper Turonian Turner Sandy Member of the Carlile Shale of South Dakota (Cappetta, 1973; Cicimurri, 2004). Cappetta and Case (1999) tentatively assigned teeth from the basal Atco to *Cantioscyllium decipiens*, stating that the Texas material differed from the South Dakota specimens in having stronger labial ornamentation and often only a single pair of lateral cusplets. Cicimurri (2004) noted that teeth from the Carlile Formation generally have only one pair of lateral cusplets, and crown ornamentation is highly variable and not considered by us to be specifically diagnostic. These teeth differ from *Chiloscyllium greeni* (see above) in having distinctive longitudinal ridges on the labial crown face.

Genus *GINGLYMOSTOMA* Müller and Henle, 1837
cf. *Ginglymostoma* sp.
Figure 4B

Material—SMU 76513, (incomplete tooth).

Remarks—The crown of SMU 76513 is complete and differs from *Cantioscyllium decipiens* in lacking extensive labial crown ornamentation and from *Chiloscyllium* in being much larger in size and bearing two pairs of lateral cusplets (second pair vestigial). SMU 76513 compares well to teeth of *Ginglymostoma* and *Plicatoscyllium* (see Noubhani and Cappetta [1997] for illustrations of various species), but the latter genus is primarily distinguished by the development of labial ornamentation. The lack of crown ornamentation SMU 76513 leads us to tentatively identify the tooth as *Ginglymostoma*, but a larger sample size is needed to make a more precise species identification. The tooth is significant because it represents a previously unknown orectolobiform occurring within the basal Atco Formation.

Order LAMNIFORMES Berg, 1958
Family MITSUKURINIDAE Jordan, 1898
Genus *SCAPANORHYNCHUS* Woodward, 1889
Scapanorhynchus raphiodon (Agassiz, 1843)
Figure 4E

Material—SMU 63114-63126 (2310 teeth); SMU 76483, (2 teeth); BCGM 9263, (two teeth); BCGM 9325, (328 complete and partial teeth).

Remarks—Heterodonty is observable in the sample, as crowns of anterior teeth are narrow and sigmoidal in profile view, and with strong labial longitudinal ridges that do not reach the cusp apex. Main cusps of lateral teeth are broader and more erect, labio-lingually thinner, and ornamentation is reduced or absent. Based on the sample size, *Scapanorhynchus raphiodon* is the most common lamniform shark in the basal Atco Formation. The specimens in the sample we obtained measure between 5 to 10 mm in height, and the largest complete specimen measures 20 mm. However, we observed teeth in private collections that reach a height of 30 mm.

Family CRETOXYRHINIDAE Gluckman, 1958
Genus *CRETOXYRHINA* Gluckman, 1958
Cretoxyrhina mantelli (Agassiz, 1843)
Figure 4G

Material—SMU 76495, (three teeth).

Remarks—*Cretoxyrhina* is appears to be a rare component of the basal Atco Formation elasmobranch fauna, based on the sample we obtained in the field and our examination of private collections. Anterior teeth of *Cretoxyrhina mantelli* differ from those of *Cretodus* in lacking lateral cusplets and labial/lingual crown ornamentation. The teeth of *Cretalamna* all teeth bear a pair of lateral cusplets and the root morphologies are quite different, with lateral teeth having short, sub-rectangular lobes. Shimada (1993) suggested that *Cretoxyrhina mantelli* preferred offshore habitats, and Cicimurri (2004) noted that *Cretoxyrhina* was found in rocks that represented deeper water, offshore habitats, but the taxon was absent from rocks representing shallow water, nearshore habitats (in which *Cretodus* was common).

Family OTODONTIDAE Gluckman, 1964
Genus *CRETALAMNA* Gluckman, 1958
Cretalamna appendiculata (Agassiz, 1843)
Figure 4H

Material—SMU 76493, (one tooth); BCGM 9265, (four teeth).

Remarks—Anterior teeth have a narrow and erect triangular crown, and narrow, rounded root lobes. Teeth in more lateral positions have thinner but broader main cusps, wider lateral cusplets, and root lobes become shorter and rectangular. The specimen shown in Figure 4H conforms to a lower left lateral position (see Shimada et al. for reconstructed dentitions of *C. appendiculata*). Although of similar morphology, *Cretalamna* is distinguished from *Cretodus crassidens* by its smaller size, more gracile morphology, and lack of crown ornamentation. Teeth differ from *Cretoxyrhina* in bearing a pair of lateral cusplets. *Cretalamna appendiculata* may have been a geographically widespread and temporally long-ranging taxon, from Albian (lower Cretaceous) to Eocene (Paleogene) strata worldwide (Cappetta, 1987). Shimada et al. (2007) noted that the dentition of *C. appendiculata* was more similar to *Lamna* (Lamnidae) than to *Cretoxyrhina*, but they still questionably referred *Cretalamna* to Cretoxyrhinidae. We place *Cretalamna* in Otodontidae following Underwood et al. (2011).

Family EOPTOLAMNIDAE Kriwet et al., 2008
Genus *PROTOLAMNA* Cappetta, 1980a
Protolamna compressidens (Herman, 1977)
Figure 4I

Material—SMU 76496, (one tooth), SMU 76522, (damaged tooth); BCGM 9324, (two incomplete teeth).

Remarks—Kriwet et al. (2008) recently erected Eoptolamnidae and included two genera formerly allied with Cretoxyrhinidae, *Leptostyrax* and *Protolamna*. SMU 76496 is a small anterior tooth (13 mm in tooth height) that is morphologically consistent with Cappetta and Case's (1999) *Protolamna compressidens* from the basal Atco Formation. Anterior teeth of *P. compressidens* resemble those of *Scapanorhynchus* but can be distinguished by rather large lateral cusplets that are located anterior to the labial face of the main cusp, the lingual root boss is much larger, and the enameloid is smooth. To our knowledge, the only other record of this species outside of Texas is from the Coniacian of Belgium (Herman, 1977; Cappetta and Case, 1999).

Genus *PARAISURUS* (Sokolov, 1978)
cf. *Paraisurus* sp.
Figure 5B

Material—SMU 76522, (damaged tooth).

Remarks—SMU 76522 is a broken anterior tooth (13.5 mm in height) that appears to lack lateral cusplets, but enameloid shoulders extend basally onto the root lobes. The root is compressed and may have had very elongated lobes. In these respects the tooth is comparable to *Paraisurus*, a taxon known from Albian deposits of France (Leriche, 1902), England (Woodward, 1889), Russia (Sokolov, 1978), and Texas (Welton and Farish, 1993). The massive lingual root boss bears a nutritive groove, uncharacteristic of *Paraisurus*, but this characteristic may not be taxonomically important (see Shimada et al. 2007). Welton and Farish (1993) indicated that an undescribed species of *Paraisurus* occurs in the basal Atco Formation, and the occurrence of the genus within the basal Atco Formation would represent a significant temporal range extension.

Family ODONTASPIDIDAE Müller and Henle, 1839
Genus *JOHNLONGIA* Siverson, 1996
Johnlongia parvidens (Cappetta, 1973)
Figure 5C

Material—SMU 76524, (four teeth).

Remarks—The teeth of *Johnlongia parvidens* are easily distinguished by their sigmoidal and distally inclined central cusp, limited development of cutting edges on anterior teeth, tall and needle-like lateral cusplets, large lingual boss bisected by a deep nutritive groove and mesial root lobe obviously longer than the distal lobe. The taxon occurs in middle Cenomanian rocks of Colorado (Shimada et al., 2006), Turonian strata of South Dakota (Cappetta, 1973; Cicimurri, 2001b; 2004) and New Mexico (Wolberg, 1985;), and Shimada et al. (2004) reported a single tooth from the upper Coniacian Niobrara Chalk of Kansas. Early Coniacian material from the basal Atco Formation represents the southern-most occurrence of the taxon in North America.

Family ANACORACIDAE Casier, 1947
Genus *SQUALICORAX* Whitley, 1939
Squalicorax sp. aff. *S. falcatus* (Agassiz, 1843)
Figure 5D

Material—SMU 76484, (two teeth); BCGM 9262, (four teeth).

Remarks—Although the number of teeth in our sample is small, there is some degree of morphological variation based on our review of Meyer's (1974) Atco

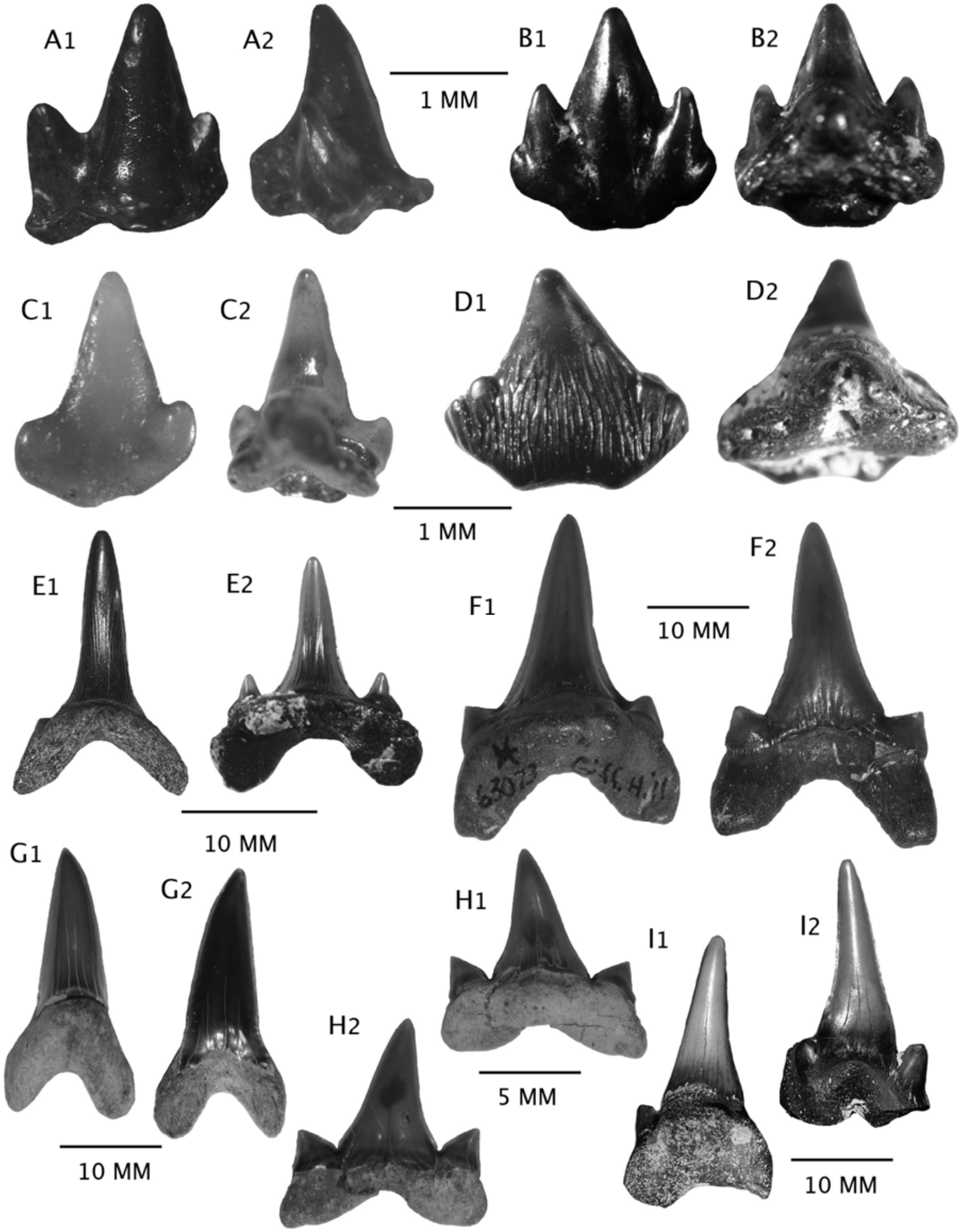

FIGURE 4. Elasmobranch species from the basal Atco Formation, north-central Texas. A, *Heterodontus* sp., BCGM 9320, A1, labial. A2, lateral views. B, cf. *Ginglymostoma* sp., SMU 76513, B1, labial, B2, lingual views. C, *Chiloscyllium greeni*, SMU 76488, C1, labial, C2, lingual views. D, *Cantioscyllium decipiens*, SMU 76491, D1, labial, D2, lingual views. E, *Scapanorhynchus raphiodon*, SMU 76483, E1, lingual view of anterior tooth; E2, lingual view of lateral tooth. F, *Cretodus crassidens*, SMU 63073, F1, lingual, F2, labial views. G, *Cretoxyrhina mantelli*, SMU 76495, G1, lingual, G2, labial views. H, *Cretalamna appendiculata*, SMU 76493, H1, lingual, H2, labial views. I, *Protolamna compressidens*, SMU 76496, I1, lingual, I2, labial views.

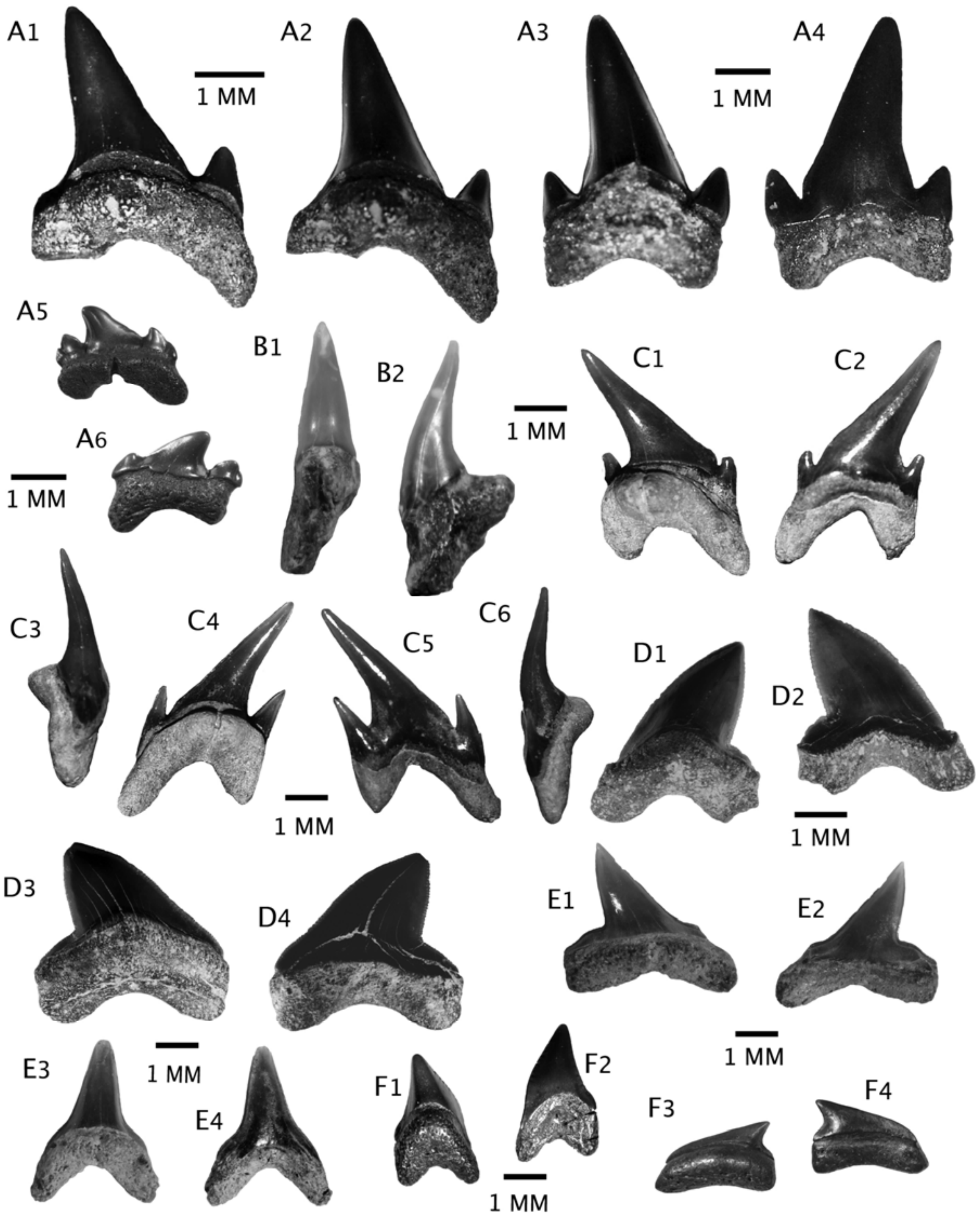

FIGURE 5. Elasmobranch species from the basal Atco Formation, north-central Texas. A. SMU 76518, *Dallasiella willistoni*: A1-A4, anterior teeth, A1-labial view, A2-lingual view; A3, anterior tooth, labial view, A4, lingual view; A5-A6, posterior teeth, A5- lingual view, A6-labial view. B, cf. *Paraisurus* sp. SMU 76522, B1, lingual, B2, lateral views. C, *Johnlongia parvidens*, SMU 76524, lateral tooth in C1, lingual and C2, labial views; lateral tooth in C3 distal, C4 lingual, C5 labial, and C6 mesial views. D, *Squalicorax falcatus*, SMU 76484, anterior tooth in D1, lingual and D2, labial views; anterolateral tooth in D3, lingual and D4, labial views. E, *Pseudocorax laevis*, SMU 76486, lateral tooth in E1, lingual and E2, labial views; anterior tooth in E3, lingual and E4, labial views. F, cf. *Microcorax* sp., SMU 76485, anterior tooth in F1, lingual and F2, labial views; lateral tooth in F3, lingual and F4 labial views.

Formation sample. The variation could be taken to reflect multiple species within the basal Atco Formation (i.e., Welton and Farish, 1993), or as representing intraspecific variation (i.e., dignathic, ontogenetic, or gynandric heterodonty) within a species as suggested Shimada and Cicimurri (2006), who considered *S. falcatus* to include Cappetta and Case's (1999) "*Squalicorax* sp. 1" and "*Squalicorax* sp. 2". Cappetta and Case (1999) stated that the species "*falcatus*" was in need of revision (also Siverson, 1992), and more recent discussion by Siverson et al. (2007) indicated that teeth traditionally referred to as *S. falcatus* from the North American Turonian may not represent the same taxon as the *S. falcatus* originally reported from England. Agassiz's (1843) type specimen was illustrated by Siverson et al. (2007; text Figure5) and Leidy (1873; pl. 18, Figure43), and it does bear similarities to middle and late Turonian teeth identified as *S. falcatus* by Cicimurri (2001b, 2004). Some of the confusion in the application of the name "*falcatus*" comes from older literature, in which what might be now considered multiple other species are listed together as *S. falcatus* (i.e., Williston, 1900: pl. 31, figs. 1-40 and pl. 32, Figure1; Leidy, 1873: pl. 18, figs. 29-42). Future statistical analyses of the North American and English material may eventually elucidate these problems of taxonomy, but for the purposes of this report we tentatively assign the Atco Formation teeth to *S. falcatus*.

Genus *PSEUDOCORAX* Priem, 1897
Pseudocorax laevis (Leriche, 1906)
Figure 5E

Material—SMU 76486, (two teeth).

Remarks—Cappetta and Case (1975) described the teeth of *Pseudocorax granti* as being smaller and having more slender crowns than *P. laevis*, and these Cappetta and Case (1999) later referred teeth from the basal Atco Formation to *P.* aff. *granti*. However, examination of thousands of *Pseudocorax* teeth from Texas led Hamm and Shimada (2007) to conclude that the criteria used to separate *P. granti* from *P. laevis* were insufficient to distinguish two species, and they considered *P. granti* to be conspecific with *P. laevis*. Teeth of *Pseudocorax laevis* are easy to distinguish from similarly shaped *Squalicorax falcatus* in being much smaller in overall size, having more gracile morphology, lacking serrations on cutting edges, and bearing a nutritive groove.

Genus *MICROCORAX* Cappetta and Case, 1975
cf. *Microcorax* sp.
Figure 5F

Material—SMU 76485, (six teeth).

Remarks—These small teeth measure only 4 mm in width but can be differentiated from *Pseudocorax laevis* in having shorter distal heels and lack of a lingual nutritive groove. Morphologically, these teeth could represent symphyseal/parasymphyseal and posterior teeth of *Squalicorax*, but all of our specimens lack serrated cutting edges. All of the Turonian teeth attributed to *S. falcatus* by Cicimurri (2004), including those from symphyseal and posterior positions, have serrated cutting edges. *Microcorax* is predominantly known from Cenomanian deposits (Welton and Farish, 1993; Cappetta and Case, 1975; Shimada et al., 2006), but the genus has also been reported from the Santonian portion of the Niobrara Formation of South Dakota (Schumacher; 1997; Cicimurri, 1998; Martin et al., 1998) and tentatively from the Albian of France (Biddle, 1993).

LAMNIFORMES Family incertae cedis
Genus *CRETODUS* Sokolov, 1965
Cretodus crassidens (Dixon, 1850)
Figure 4F

Material—SMU 63070, (one tooth); SMU 63073, (two teeth); SMU 76482, (one tooth); BCGM 9264, (one tooth).

Remarks—Schwimmer et al. (2002) argued that *Cretodus crassidens* and *C. semiplicatus* were conspecific (= *C. semiplicatus*). We concur with Welton and Farish (1993) that compared to *C. semiplicatus*, teeth of *C. crassidens* are larger with more robust crowns and roots, and crown ornamentation is less well developed. These differences are sufficient to treat the morphologies as separate species, and in South Dakota *C. semiplicatus* is known from Cenomanian rocks (Cicimurri, 2001a), whereas *C. crassidens* occurs in Turonian rocks (Cicimurri, 2001b, 2004). Welton and Farish (1993) reported that the largest *C. crassidens* teeth from Texas occur in the basal Atco Formation, and specimens we observed in private collections attain sizes up to 70 mm in tooth height.

Cretodus has been placed within Cretoxyrhinidae, but it has been suggested that only *Cretoxyrhina* be included within the family (i.e., Siverson, 1999; Siverson and Lundgren, 2005). Other genera previously identified as Cretoxyrhinidae have subsequently been reassigned to other genera (i.e., Kriwet et al., 2008). Underwood et al. (2011) listed the familial placement of *Cretodus* as uncertain, and this position is followed herein.

Family incertae cedis
Genus *DALLASIELLA* Cappetta and Case, 1999

Dallasiella willistoni (Cappetta and Case, 1999)
Figure 5A

Material—SMU 63138-63147 (620 teeth); SMU 76518, (3 teeth).

Remarks—This tooth morphology was originally recognized from Turonian and Coniacian deposits by Meyer (1974), who considered the material to be referable to Odontaspididae and tentatively assigned them *Odontaspis subulata*. Cappetta and Case (1999) believed that the teeth are inconsistent with the odontaspidid dentition and assigned them instead to Cretoxyrhinidae, while at the same time erecting a new taxonomic name, *Dallasiella willistoni*. Cicimurri (1998) identified identical teeth from the middle Turonian of South Dakota as *Odontaspis* sp. cf. *O. subulata*, following Meyer's (1974) designation. The taxon was again reported from the middle Turonian of South Dakota (Cicimurri, 2001b, 2004), this time under the name *Carcharias* sp. Cicimurri (2004) argued for assignment to Odontaspididae based on the development of a lingual nutritive groove, which is a characteristic not typically seen in other cretoxyrhinid sharks (Cappetta, 1987). However, Shimada (2007) reported teeth of *Cretalamna appendiculata* with and without a nutritive groove, and this characteristic may be of little taxonomic importance. The taxonomic assignment of this morphology has not been satisfactorily resolved, and although we utilize the name *Dallasiella willistoni*, we leave the familial placement open.

Superorder BATOMORPHII Cappetta, 1980b
Order SCLERORHYNCHIFORMES Kriwet, 2004
Family SCLERORHYNCHIDAE Cappetta, 1974
Genus *SCLERORHYNCHUS* Woodward, 1889
Sclerorhynchus sp. cf. *S. priscus* (Cappetta and Case, 1999)
Figure 6A

Material—SMU 76514 (one tooth); BCGM 9328, (four incomplete rostral spines).

Remarks—The rostral spines lack most or all of the peduncle. The crowns are similar to *Ischyrhiza schneideri* rostral spines (also part of our assemblage), but they differ in being more dorso-ventrally flattened, with sharper, sinuous anterior and posterior edges. We did not recover *Sclerorhynchus* teeth during our study, and we tentatively assign our rostral spines to *S. priscus* based on similarities in morphology. *Sclerorhynchus priscus* is also the only pre-Campanian species that has been reported from Texas (Cappetta and Case, 1999). Campanian specimens have been referred to *S. atavus* (i.e., Slaughter and Steiner, 1968; Meyer, 1974), but the Texas material was deemed to be different from the type *S. atavus* by Cappetta and Case (1999), who referred Texas Campanian spines to their new taxon, *S. fanninensis*. Rostral spines of *S. priscus* differ from *S. fanninensis* in being smaller in overall size and lacking a distinctive enameloid lip at the base of the crown.

Genus *ISCHYRHIZA* Leidy, 1856
Ischyrhiza schneideri (Slaughter and Steiner, 1968)
Figure 6, B1-B3

Material—SMU 76487, (2 complete rostral spines); BCGM 9326, (11 incomplete rostral spines), BCGM 9327, (six rostral spines).

Remarks—We assign two rostral spine morphologies to *I. schneideri*, one of which is similar to *I. mira* (Figure6, B1) and the other similar to *I. avonicola* (see Estes, 1964). The former morphology was originally considered as a subspecies of *I. mira* (*I. m. schneideri*) by Slaughter and Steiner (1968), but Welton and Farish (1993) considered the Coniacian morphology to represent a species distinct from Campanian and younger *I. mira*, which was later advocated by Cappetta and Case (1999). The latter spine morphology, similar to *I. avonicola*, consists of a short, rather conical crown that bears longitudinal enameloid ridge of various lengths (Figure6, B2-B3). The peduncle is also quite different, being short, and quickly flaring into dorsal and ventral processes that lack finger-like projections.

The taxonomic placement of the latter rostral spine morphology has been problematical. Similar spines have been variously identified as *I. texana* (Welton and Farish, 1993), *I. schneideri* (Cicimurri, 2004), and *I. mira* (Cappetta and Case, 1999). The material reported by Welton and Farish (1993) from the basal Atco Formation is a mixture of *Ischyrhiza* and *Ptychotrygon*, and their taxonomic designation is invalid (see discussion under *Kiestus* below). Cappetta and Case (1999), referring to the same material, considered the morphology to represent spines located in a proximal position on the rostrum, but they identified them as *I. mira* instead of *I. schneideri* (possibly in error). We interpret spines of this type to represent either a more proximal location on the rostrum or possibly juvenile individuals of *I. schneideri* (see also Meyer, 1974; p. 88, Figure21). Several denticles have been recovered that are similar to those illustrated by Welton and Farish (1993; p. 142, Figure2), and these consist of a short, somewhat conical, posteriorly pointed crown that bears several longitudinal ridges. The base is dorso-ventrally flattened, with numerous finger-like projections emanating from the margins. It is possible that these denticles were located on the dorsal and/or ventral surfaces of the *I. schneideri* rostrum.

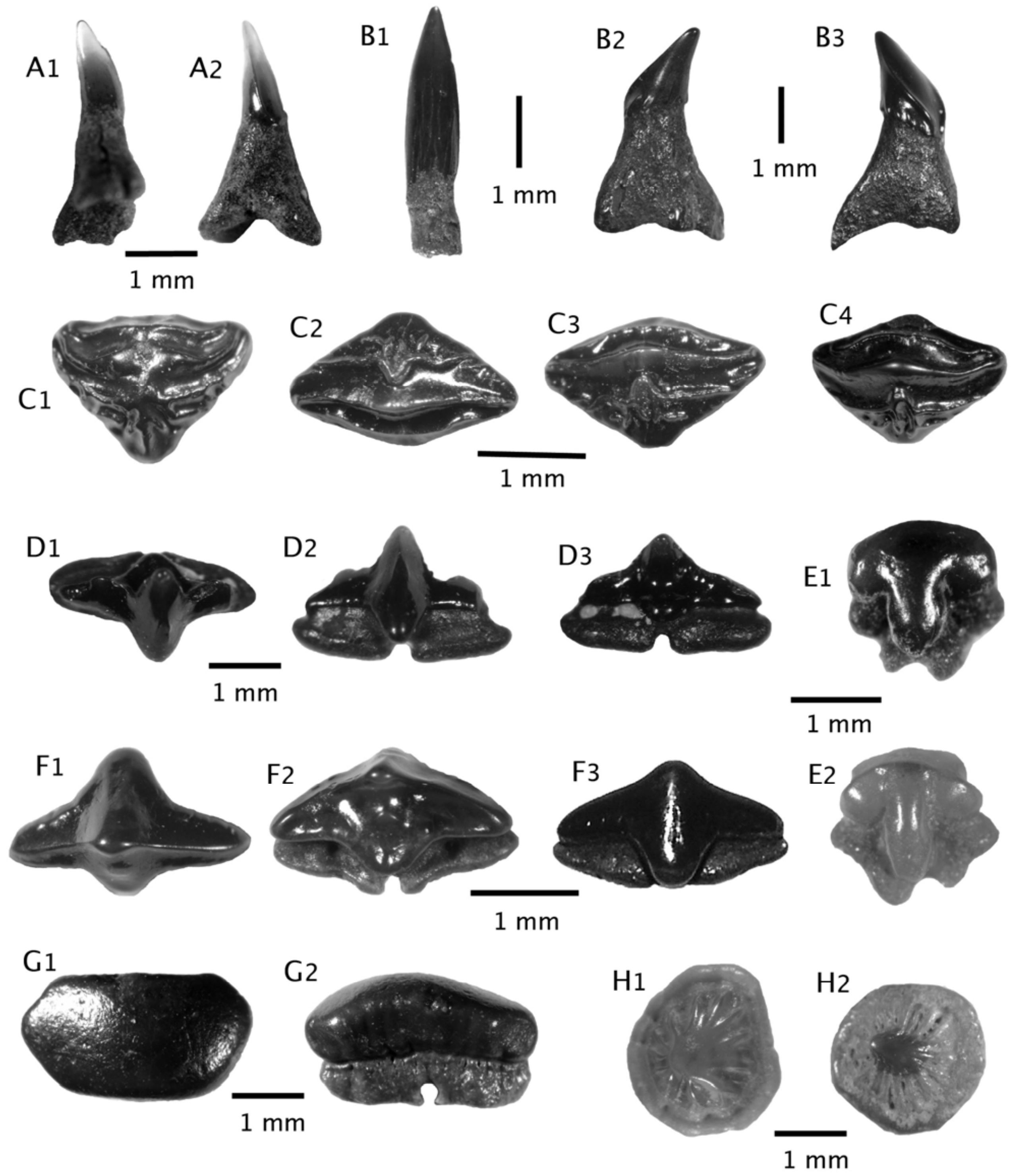

FIGURE 6. Elasmobranch species from the basal Atco Formation, north-central Texas. A, *Sclerorhynchus* sp. cf. *S. priscus*, SMU 76514, rostral spine in A1, dorsal and A2, posterior views. B, *Ischyrhiza schneideri*, SMU 76487, rostral spines, B1 dorsal or ventral view; B2, postero-ventral, B3, antero-dorsal views. C, *Ptychotrygon triangularis*, SMU 76490, four different teeth in occlusal views (labial at bottom in C1, C3, C4). D, *Kiestus texanus*, SMU 76251, D1, occlusal, D2, labial, D3, lingual views. E, *Rhinobatos lobatus*, SMU 76494, two teeth in occlusal view. F, *Texatrygon hooveri*, SMU 76525, F1, occlusal, F2, lingual oblique, F3, labial views. G, *Psuedohypolophus* sp., SMU 76515, G1, occlusal, G2, lingual views. H, dermal denticles in dorsal view.

Genus *PTYCHOTRYGON* Jaekel, 1894
Ptychotrygon triangularis (Reuss, 1845)
Figure 6C

Material—SMU 76490, (5 teeth); BCGM 9329, (126 teeth).

Remarks—These sclerorhynchid teeth are quite distinctive in the extensive development of transverse ridges and lack of a cusp. Only one other similar sclerorhynchid taxon has been reported from the basal Atco Formation, *Texatrygon hooveri* (Welton and Farish, 1993; Cappetta and Case, 1999), but this taxon is easily distinguished from *P. triangularis* (see below) in having a distinctive cusp and lacking transverse ridges. *Ptychotrygon triangularis* is the most common batomorph taxon in our Atco Formation sample.

Genus TEXATRYGON Cappetta and Case, 1999
Texatrygon hooveri (McNulty and Slaughter, 1972)
Figure 6F

Material—SMU 76525, (4 teeth); BCGM 9330, (two teeth), BCGM 9366, (one tooth).

Remarks—These teeth are comparable in morphology to *Ptychotrygon*, but Cappetta and Case (1999) erected a new genus, *Texatrygon*, for *Ptychotrygon*-like teeth that are cuspidate, lack transverse ridges, and have smooth or weakly ornamented enameloid. Teeth listed above possess these characteristics and are therefore referred to *Texatrygon*. Of three species placed in *Texatrygon* by Cappetta and Case (1999), *T. copei*, *T. hooveri*, and *T. greybullensis*, the latter two were formerly placed within *Ptychotrygon* (see McNulty and Slaughter, 1972; Case, 1987). Only *T. hooveri* is known from pre-Campanian rocks, and the basal Atco Formation specimens are comparable to this species (see McNulty and Slaughter, 1972; Meyer, 1974; Welton and Farish, 1993). *Ptychotrygon rubyae* from the Turonian of Arizona (see Williamson et al., 1993) was considered to be synonymous with *T. hooveri* (Cappetta and Case, 1999).

Genus *KIESTUS* Cappetta and Case, 1999
Kiestus texanus (Cappetta and Case, 1975)
Figure 6D

Material—SMU 76251 (one tooth); BCGM 9345, (seven teeth); BCGM 9351, (one tooth).

Remarks—These teeth are similar in overall morphology to those attributed to *Ischyrhiza schneideri*, but the cusp is lower and broader, the lateral shoulders are often developed into weak cusplets, and the labial basal protuberance is much shorter but wider. *Kiestus texanus* was identified as *Ptychotrygon triangularis* by McNulty and Slaughter (1972), *P. ritchei* by Meyer (1974), and *Ischyrhiza texana* by Cappetta and Case (1975). Using the name *I. texana*, Welton and Farish (1993) associated *I. avonicola*-like rostral spines with teeth of *Ptychotrygon*, and their designation is invalid because of the incorrect association of remains belonging to more than one species. *Kiestus texanus* is unknown outside of Texas.

Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838
Genus *RHINOBATOS* Linck, 1790
Rhinobatos lobatus (Cappetta and Case, 1999)
Figure 6E

Material—SMU 76494, (2 teeth).

Remarks—Welton and Farish (1993) reported that *R. incertus* is found in the basal Atco Formation, but Cappetta and Case (1999) later differentiated the Atco Formation guitarfish sample into *R. kiestensis* and *R. lobatus*. Cappetta and Case (1999) considered the possibility that the varied morphologies represented gynandric heterodonty within a single species, but they went on to differentiate two species based on the development of a cusp and the shapes of a transverse crest, the labial face, and lingual crown protuberances. In these respects, our two specimens lack cusps, have dull transverse crests, and bulbous labial crown foot with lateral concavities, and we therefore assign them to *R. lobatus*. Some species previously assigned to *Rhinobatos* have subsequently been allied with other genera, and it is possible that other teeth, like *R. incertus* and *R. lobatus*, will also be found to represent a genus other than *Rhinobatos*. However, for the purposes of this report we assign the teeth to *Rhinobatos*. Although guitarfish have been reported from other locations from within the Western Interior Seaway, including Kansas (Everhart, 2009), South Dakota (Cappetta, 1973; Cicimurri, 2001b, 2004), Arizona (Williamson et al., 1993), and Canada (Underwood and Cumbaa, 2010), the *lobatus* morphology has not yet been reported outside of Texas.

Family incertae sedis
Genus *PSEUDOHYPOLOPHUS* Cappetta and Case, 1975
Pseudohypolophus sp.
Figure 6G

Material—SMU 76515, (one tooth).

Remarks—This tooth, measuring only 3 mm in maximum crown dimension, is easily distinguished from all other batoid taxa in our basal Atco Formation sample in having a simple crown that is oval in outline, having a nearly flat occlusal surface, and covered with a thin layer of unornamented enameloid. SMU 76515 is morphologically similar to *Pseudohypolophus mcnultyi* and *P. ellipsis*, the latter taxon being based on a single late Santonian specimen from Georgia (Case et al., 2001). The Atco tooth is similar to *P. ellipsis* in having a thicker crown and lacking a low transverse ridge as seen on *P. mcnultyi*, but we hesitate to assign SMU 76515 to *P. ellipsis* because of the lack of knowledge regarding morphological/histological variation. *Pseudohypolophus* was geographically widely distributed and temporally wide ranging, having been reported from strata of Albian to Campanian age in the US Western Interior, Gulf Coastal Plain, and Atlantic Coastal Plain (Meyer, 1974; Williamson et al., 1993; Cicimurri, 2000, 2007).

DISCUSSION

Turonian/Coniacian Elasmobranch Faunal Turnover?—Johnson and Lucas (2002) reported a “substantial” faunal turnover and reduction in *Ptychodus* species from the Turonian to the Coniacian, and their listing of the temporal ranges of the eight species that they recognized indicates that only four of these are found in post-Turonian rocks. However, the number of *Ptychodus* species occurring in North America was greater than these authors indicate (see Hamm, 2008). Assuming no reworking (see additional discussion below), the basal Atco Formation sample shows that ptychodontid diversity was still high post-Turonian, at least in Texas, with five species occurring in the early Coniacian (*P. martini*, *P. mammillaris*, *P. latissimus*, *P. whipplei*, and *P. atcoensis*). By the end of the Coniacian only four species are known in North America (*P. rugosus*, *P. martini*, *P. mortoni* and *P. polygyrus*).

When evaluated as a whole, interpreting species differences in elasmobranch assemblages between the Turonian and Coniacian ages in North America is difficult because of the limited number of late Turonian and early Coniacian records, and the wide geographic separation between these localities. The best documented late Turonian elasmobranch assemblage is from the Turner Sandy Member of the Carlile Shale of South Dakota and Wyoming (Cappetta, 1973; Evetts, 1979; Cicimurri, 2004). In contrast, the depauperate Coniacian fauna of South Dakota includes only *Ptychodus latissimus* from the Sage Breaks Shale Member of the Carlile Shale (Cicimurri, 2004), and *P. mortoni*, *Squalicorax falcatus*, *Microcorax* sp., and *Cretoxyrhina mantelli* from the Niobrara Chalk (Martin et al., 1998). Additional taxa reported from the Coniacian Fort Hays Limestone Member of the Niobrara Chalk of Kansas include *P. mammillaris*; cf. *Scapanorhynchus* sp., *Cretalamna appendiculata*, and *Paranomotodon* sp. (see Shimada, 1996; Everhart and Darnell, 2004; Shimada and Everhart, 2003). The taxa listed above are generally characterized by large teeth that are easy to see in the field. Perhaps the record is biased towards material visible to the naked eye, and bulk sampling may reveal a more diverse microfauna. Alternatively, differences could be related to changing environments, with the shift from Turonian shoreface sand facies to Coniacian offshore shale and chalk facies influencing species distributions (i.e., a high number of nearshore, benthic taxa in the Turonian).

The most diverse Coniacian elasmobranch assemblage in North America occurs within the basal Atco Formation of Texas, and at least 15 taxa within this lithostratigraphic unit also occur in Turonian rocks elsewhere (i.e., Williamson et al., 1993; Cicimurri, 2004; Becker and others, 2010). The contact between the Atco Formation and underlying Eagle Ford Group is disconformable, and Pessagno (1969) reported up to 1.5 m of erosional relief at the contact. In addition, Hancock and Walaszczyk (1994) suggested that the entire upper Turonian section of the Eagle Ford Group is missing in Dallas County. At this time we cannot rule out the possibility that the basal Atco Formation elasmobranch assemblage represents a mixing of Turonian and Coniacian remains that resulted from erosion of older Eagle Ford Group strata and roughly coeval deposition of younger Atco Formation material (see additional discussion below). Thus far only invertebrates indicative of a Coniacian age have been found within the conglomerate, which is in contrast to a fossiliferous conglomerate located at the base of the Tombigbee Sand further to the east in the Mississippi Embayment, where Santonian and Campanian ammonites occur together (i.e., Becker et al., 1998). Additionally, elasmobranch teeth from the basal Atco Formation are generally complete and relatively unabraded.

An alternative interpretation for the basal Atco Formation conglomerate is that it contains species that have a Turonian to Coniacian (or longer) temporal distribution. With half of the Atco Formation elasmobranch species also occurring in the Turonian, the Turonian/Coniacian faunal turnover does not appear to be significant, and differences in species compositions could be indicative of geographic/environmental provincialism.

Formation of the Basal Atco Formation Lag—Hancock and Walaszczyk (2004) considered the basal Atco Formation conglomerate to be the product of a deep regressive trough (major sea-level drop) during the late Turonian, with a fast rise in sea level during the early Coniacian, before chalk sedimentation began. Larson et al. (1991) believed that the conglomerate represents a condensed section, and they suggested that the nature of the conglomerate was characteristic of hardgrounds (Kennedy and Garrison, 1975) related to maximum transgression (see Loutit et al., 1988). The fine-grained carbonate rocks higher in the Atco Formation and within the Austin Chalk Group in general are thought to represent deep water deposits that accumulated later in the Niobrara Cyclothem (i.e., Hovorka and Nance, 1994).

Haq et al. (1988) noted a major sequence boundary at 90 Ma, between the Upper Zuni A-2 and UZA-3 supercyles, that marks the transgressive phase at the beginning of the third order cycle UZA-3.1. We believe that the conglomerate at the base of the Atco Formation represents the major sequence boundary as identified by Haq et al. (1988). Assuming that transgression of the Niobrara Sea began from the south, the age of the rocks at the base of UZA-3.1 should be older in Texas than they are further north, and a relative age of 90 Ma for the basal Atco Formation conglomerate is close to the 89.3 Ma age of lower Coniacian strata disconformably overlying Turonian rocks in southeastern Colorado and northeastern New Mexico (Merewether et al., 2007). Interestingly, Merewether et al. (2007) also found that the ages of the transgressive strata above the disconformity decrease northwestward and toward the northeast, about 88.7 Ma in northwestern-most Wyoming and 87.6 Ma in northeastern-most Nebraska. The Niobrara Sea would therefore have transgressed about 805 km from southeastern Colorado to northwestern Wyoming in about 0.6 million years, and 772 km from southeastern Colorado to northeastern Nebraska in about 1.7 million years.

Becker et al. (1998) presented a model for the formation of a transgressive lag deposit located at the base of the Tombigbee Sand Member of the Eutaw Formation. In their model, chondrichthyan remains are reworked from older strata during initial transgression, and these older remains are subsequently mixed together with younger remains. Such a model, where material from different stratigraphic intervals (and potentially significantly different temporal ages and depositional environments) is mixed together, could account for the breakage and/or abrasion of some remains, and the association of taxa that may have been nearshore inhabitants with those that may have been offshore inhabitants. This hypothesis is supported by the co-occurrence of Santonian and Campanian mollusk taxa.

Alternatively, the basal Atco Formation lag could simply represent an accumulation of remains within an inner neritic environment that existed early in the transgressive phase of the Niobrara Cyclothem, with no reworking of fossil-rich underlying strata. Cicimurri (2004) found that the greatest diversity of benthic taxa (i.e., orectolobiforms and batoids) occurred in lower shoreface deposits of the Turner Sandy Member of the Carlile Shale, and many of these same taxa also occur in the younger Atco Formation. *Hybodus* and *Pseudohypolophus* are generally found in rocks representing brackish and other nearshore marine environments (i.e., Thurmond, 1971; Welton and Farish, 1993). The apparent scarcity of presumed offshore, pelagic inhabitants like *Cretoxyrhina mantelli* (see Shimada, 1997), protostegid turtles and mosasaurs suggests that these taxa occasionally ventured closer to shore. Only mollusk taxa of Coniacian age have been reported from the basal Atco Formation.

An additional hypothesis for the formation of the basal Atco Formation conglomerate is that the majority of vertebrate remains accumulated closer to shore, but were later transported shoreward by storm deposits, similar to an interpretation proposed by Becker and others (2010) for a middle Turonian elasmobranch assemblage from Utah. This scenario could also explain the mixing of nearshore and offshore taxa. However, the Atco Formation fossils, although broken, are not rounded and polished as might be expected to have occurred during post-mortem transport.

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