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MORPHOLOGICAL VARIATIONS IN THE AMMONITE SCAPHITES
OF THE BLUE HILL MEMBER, CARLILE SHALE,
UPPER CRETACEOUS, KANSAS¹

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ABSTRACT

The heteromorphic ammonite genus, *Scaphites*, is investigated with respect to its occurrence, diversity, and morphological variations in the Blue Hill Shale Member of the Carlile Shale in Kansas. The genus is not abundant and ubiquitous throughout the stratigraphic range of the member as previously reported. Accordingly, the genus is rare in the Blue Hill Shale Member except in the upper part where it is common in a three-meter zone. Morphological variations within the genus are investigated using descriptive techniques and cluster analysis. The majority of the variation is due to the presence of five species of *Scaphites* (*Scaphites*) and one species of *Scaphites* (*Hoploscaphites*) instead of the single species of *Scaphites* (*Scaphites*) previously reported. Four of the six species are new, *S. (S.) hattini*, *S. (S.) inflexus*, *S. (S.) mitchellensis*, and *S. (H.) kansiensis*. *Scaphites (S.) carlilensis* Morrow, previously the only scaphite reported from the Blue Hill Shale Member, and *S. (S.) arcadiensis* Moreman comprise the remainder of the known scaphite fauna of the member. The remaining variation is attributable to sexual dimorphism with each species consisting of dimorphic pairs represented by macroconchs and microconchs. The seemingly large number of congeneric taxa from the same province may be explained by a high degree of endemism resulting from the environmental conditions that accompanied the Cretaceous epeiric sea on the North American continent.

INTRODUCTION

Studies of the megafauna of the Turonian Carlile Shale are many and varied (Meek, 1876; Stanton, 1893; Logan, 1897, 1898; Reeside, 1927a, 1927b, 1927c; Morrow, 1931, 1935; Cobban, 1951; Hattin, 1952, 1962). These workers consistently recognized that morphological variations exist within *Scaphites*, which cause problems with its taxonomy. Four interpretations were used by

these workers to explain the observed variations:

- 1) both large and small forms were placed in the same species but smaller forms were considered to be juveniles (Stanton, 1893; Logan, 1898; Hattin, 1952, 1962),
- 2) different specific names were assigned

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- to large and small forms (Morrow, 1931, 1935),
- 3) both large and small forms were placed in the same species and a subspecific name was assigned to one of the forms (Meek, 1876; Whitfield, 1880; Reeside, 1927b; Cobban, 1951), and
 - 4) morphological variation was determined to be continuous within one species and all forms were assigned to the same species (Hattin, 1952, 1962).

The taxonomic confusion resulting from the above inconsistencies suggested that new research aided by quantitative analysis of the data might uncover subtle causes for the observed morphological variations and subsequently lead to a better understanding of the taxonomy of *Scaphites*. Two principal hypotheses were tested to determine: 1) if size variations are attributable to sexual dimorphism, and 2) if more than one species of *Scaphites* existed in the member. Both hypotheses were found to be valid for the genus. In addition much was learned of the mode of occurrence and stratigraphic placement of *Scaphites* in the Blue Hill Shale Member.

The possibility that sexual dimorphism existed in ammonites was first discussed by de Blainville (1840, p. 8) and later supported by the works of d'Orbigny (1847), Waagen (1869), Reynès (1879), Douvillé (1881), Quenstedt (1886-87), Munier-Chalmas (1892), Foord and Crick (1897), Glangeaud (1897), and Rollier (1913). The role of sexual dimorphism in ammonite studies attained its historical height of popularity at the beginning of the present century, after which it suffered a decline until the early 1940's when it was independently resurrected by Makowski (1962a, 1962b) and Callomon (1963). Since then, studies of sexual dimorphism have grown in popularity, but the application to fossil cephalopods has been restricted almost exclusively to Jurassic Ammonoidea, which generally have morphology more easily interpretable in terms of dimorphism. For a summary of these and other works pertaining to sexual dimorphism in ammonites, see Makowski (1962a), Callomon (1963, 1969), and Crick (1976).

Knowledge of ammonoid ontogeny offers the key to recognition of sexual dimorphism. It is essential to note that ammonites did not grow indefinitely and all forms which attained a well-

defined adult state show evidence of deceleration and final cessation of growth. Analogous to many other animals, the sexes can only be determined from the examination of adult specimens. Lack of knowledge of ammonite soft-part morphology requires that this determination be based on features recognizable in the morphology of the preserved shell. To determine the maturity of an ammonite the following general features are used:

- 1) Approximation, or crowding, of the final few septa ("*Lobendrangung*"), caused by diminished growth rates (Arkell, 1957; Makowski, 1962a; Callomon, 1963; Lehmann, 1971). This feature usually appears abruptly in males in the last two to three septa. Female forms usually have this approximation spread out over the final dozen or more septa with the distance between them diminishing gradually adaperturally. Mangold and Fioroni (1966), on the basis of work on recent coleoids, concluded that cessation of growth in females is much more gradual than in males, suggesting that the difference is attributable to a slower growth of the gonads.
- 2) Modification of sculpture near the peristome (Arkell, 1957; Makowski, 1962a; Callomon, 1963; Lehmann, 1971). This feature usually manifests itself in the form of coarsening and regeneration or approximation of ribbing. In addition, terminal constrictions and ventral collars are indicative of maturity.
- 3) Marked internal thickening of the test in the immediate vicinity of the aperture, causing a constriction of the aperture (Makowski, 1962a; Westermann, 1971).
- 4) Abnormal shape of the body chamber, uncoiling (scaphitoid) and other modifications (Arkell, 1957; Callomon, 1963; Cobban, 1969; Lehmann, 1971).

Application of the above criteria has convinced most workers that the majority of ammonites represent adults and constitute what Callomon (1963, p. 26) considered to be "nor-

mal faunas." In fact, faunas with more than a few juveniles are rare (Westermann, 1954; Brinkmann, 1929; Lehmann, 1971). In many normal faunas two groups of adults are recognizable, being indistinguishable in their inner whorls and differing only in size. These large and small forms were labeled by Callomon (1955, 1963) as *macroconch* and *microconch*, respectively, without regard to sex. Other authors, particularly Makowski (1962a, 1962b), Westermann (1964, 1969), Cobban (1969), and Lehmann (1966, 1971) have regarded the large forms (macroconchs) as females and the small forms (microconchs) as males. This assumption seems to be reasonable, since in recent extant dibranchiate cephalopods—in fact in almost all recent invertebrates with pronounced sexual dimorphism—it is the female that is larger (Westermann, 1969). In addition, Lehmann (1966) found what he considered to be a cluster of eggs in the body chamber of a macroconch of the Liassic ammonite *Eleganticeras* and Müller (1969) found a similar structure in the body chamber of a Triassic *Ceratites*.

General criteria have been developed to determine the existence of dimorphism in fossil cephalopods. The major points that establish dimorphism over other interpretations are:

- 1) Identical initial stages of ontogeny in macroconchs and microconchs, and identity of their phylogeny (Makowski, 1962a; Callomon, 1963; Westermann, 1964; Cobban, 1969; Lehmann, 1971). Makowski (1962a, p. 13) asserted that this "prerequisite must be applied in order to eliminate cases of far advanced convergence, most commonly observable in the adult stages."
- 2) Lack of intermediate forms in adult stages (Makowski, 1962a). This criterion is essential because the presence of intermediates among supposed males and females of an extinct taxon would prevent the gathering of conclusive supporting data.
- 3) Presence of both forms in the same strata (Makowski, 1962a; Westermann, 1964; Lehmann, 1971).
- 4) Numerical ratio of the two supposed sexes, comparable to that observed in extant forms (Makowski, 1962a). Makowski reported that the average sex

ratio for a large number of extant forms is approximately 1:1 and considered this figure to be representative. Mangold-Wirz (1963) and Westermann (1969) reported a variable sex ratio in extant cephalopods but believed the deviations to be due to sampling errors or sex segregation within the populations or both. In an investigation of 16 species, Mangold-Wirz (1963, p. 185) observed females to outnumber males in 5 species, whereas males had a numerical superiority in 2 species. The nine remaining species had a sex ratio of 1:1. Mangold-Wirz favored the hypothesis that a numerical equality exists between sexes in most cephalopod species.

- 5) New characters of ornamentation appear in macroconchs and microconchs of a genus more or less simultaneously (Callomon, 1963; Cobban, 1969; Lehmann, 1971).

All of these criteria should be considered in the description and definition of ammonite taxa.

Scaphites, long a subject of investigations in the western interior of the United States (Meek, 1876; Stanton, 1893; Logan, 1898; Reeside, 1927a, 1927b; Morrow, 1931, 1935; Cobban, 1951; Hattin, 1952, 1962), has only recently been shown to be dimorphic (Cobban, 1969; Crick, 1976). The documentation of dimorphism in the genus substantially clarifies the taxonomy resulting from conflicting interpretations of its different morphologies. The genus is characterized by two forms in almost every collection: a large form, which is involute and usually possesses an umbilical swelling, and a smaller, more evolute form. In conformance with the interpretation of similar ammonite faunas by Makowski (1962a) and others, the larger form is considered to be the female and the smaller form the male. Because changes in size and ornamentation affect both forms simultaneously, male and female forms of the same species of *Scaphites* can be distinguished only by the following criteria:

<i>Criterion</i>	<i>Male</i>	<i>Female</i>
Whorl growth :	evolute	involute
Size :	small	large

Criterion	Male	Female
Form	slender	robust
	no umbilical swelling	umbilical swelling
	slightly depressed whorls	depressed whorls
Ornamentation:	males tend to have more ventral ribs	

My investigation was limited stratigraphically to the two outcrop areas of the Blue Hill Shale Member of the Carlile Shale in Kansas. The larger of the two outcrops extends in a southwest-trending belt, approximately 320 km (200 mi) from the southernmost part of central Nebraska to Finney and Ford counties in Kansas. The smaller belt of outcrops lies in Hamilton County, near the Colorado-Kansas border, and was not studied because exposures are poor (Fig. 1,a).

The stratigraphic horizon for all collecting localities (see Fig. 1,b) is the lower part of the

upper Blue Hill Shale Member, Carlile Shale, Colorado Group of early Turonian age. Precise descriptions of numbered localities are:

1. NE $\frac{1}{4}$ sec. 9, T. 9 S., R. 10 W., Mitchell County. Gullies in slopes of Blue Hills, approximately 5.6 km (3.5 mi) south-southeast of Tipton.
2. SE $\frac{1}{4}$ sec. 4, T. 9 S., R. 10 W., Mitchell County. Gullies in slopes of Blue Hills, approximately 4.8 km (3 mi) south-southeast of Tipton.
3. NE $\frac{1}{4}$ sec. 20, T. 9 S., R. 10 W., Mitchell County. Gullies in north face of conspicuous butte in Blue Hills, 8.9 km (5.5 mi) south and 1.6 km (1 mi) east of Tipton.
4. SW $\frac{1}{4}$ sec. 25, T. 8 S., R. 12 W., Osborne County. Gullies near base of bluffs on north side of county road, approximately 13.7 km (8.5 mi) south-southwest of Osborne.
5. SW $\frac{1}{4}$ sec. 24, T. 8 S., R. 12 W., Osborne County. Gullies on south end of prominent mesa, 14.5 km (9 mi) south-southeast of Osborne.
6. SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 3 and NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 10, T. 7 S., R. 13 W., Osborne County. Bluff on north valley wall of South Fork of Solomon River, approximately 3.2 km (2 mi) north-northwest of Osborne.
7. NW $\frac{1}{4}$ sec. 2 and NE $\frac{1}{4}$ sec. 3, T. 10 S., R. 11 W., Osborne County. Gullies on south face of Blue Hills, 24.1 km (15 mi) south and 14.5 km (9 mi) east of Osborne.
8. W $\frac{1}{2}$ sec. 10, T. 9 S., R. 10 W., Mitchell County. Gullies in slopes of Blue Hills, approximately 6.4 km (4 mi) south-southeast of Tipton.
9. NE $\frac{1}{4}$ sec. 4, T. 9 S., R. 10 W., Mitchell County. Gullies in slopes of Blue Hills, approximately 3.2 km (2 mi) south-southeast of Tipton.

Three members are recognized in the Carlile Shale, the Fairport Chalk, Blue Hill Shale, and Codell Sandstone (Fig. 2). Of these, only the Blue Hill Shale Member contains scaphitids suitable for this study. Field studies were limited to Mitchell and Osborne counties because the stratigraphic horizon containing scaphitids is exposed and easily accessible in those areas. For a review of the stratigraphy, paleontology, and paleoecology of the Carlile Shale, see Hattin (1962, 1965).

Reports by Hattin (1952, 1962), Morrow

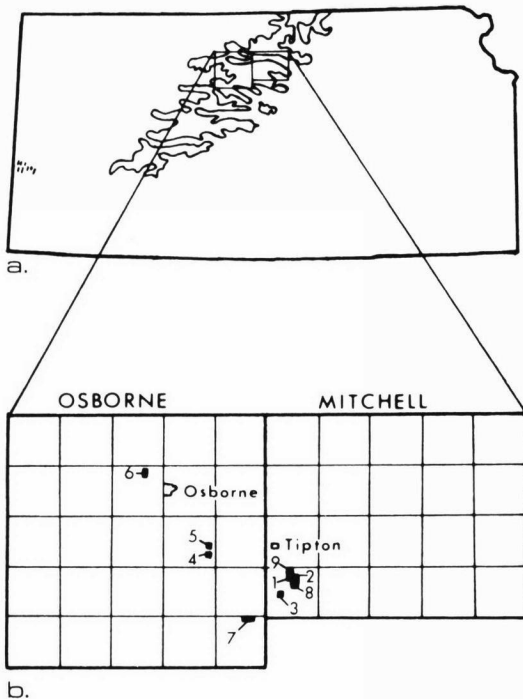


FIG. 1. Outcrop pattern of Carlile Shale in Kansas (1,a), and collecting localities (1,b).

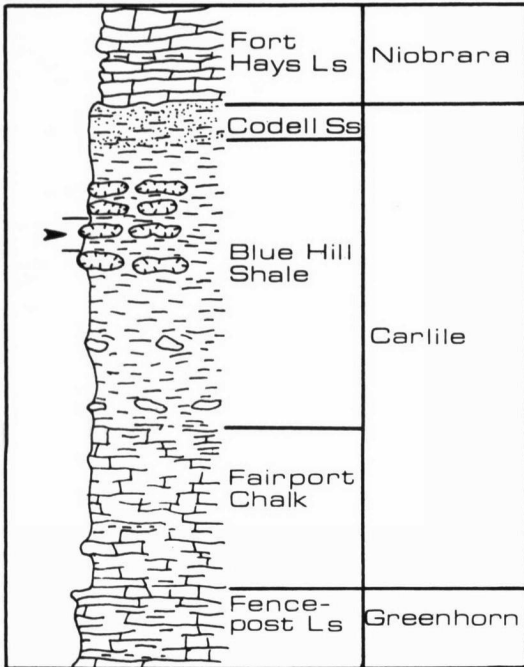


FIG. 2. Stratigraphic position of the Upper Cretaceous Carlile Shale (late Turonian) and associated formations of the Colorado Group (*Scaphites* zone indicated by arrow) (mod. from Zeller, 1968).

(1935), and Stanton (1893) that the fauna is abundant are misleading. These reports were based on collections biased by the substantial numbers of specimens that accumulated on the outcrops between the years of collection.

The single most distinguishing feature of the Blue Hill Shale is the occurrence of numerous large concretions. These can be grouped into three types: 1) calcareous septarian concretions; 2) noncalcareous clay-ironstone concretions; and 3) sandstone concretions. *Scaphites* occurs with the first type in the upper part of the Blue Hill Shale Member of Osborne and Mitchell counties. Four stratigraphic levels of calcareous septarian concretions exist at localities where the genus occurs. Although *Scaphites* had previously been reported to be ubiquitous in the Blue Hill Member, it was found to occur only within a zone 3 m (10 ft) in thickness. The base of this zone is

immediately above the basal level of large calcareous septarian concretions and terminates approximately half the distance between concretion levels 2 and 3 (Fig. 2). This zone contains specimens of the genus in two modes of occurrence: those in the shale itself, with preservation ranging from internal casts of body chambers to reasonably well-preserved body chambers, and rare complete specimens, and those in small shale nodules with a diameter of 3 to 6 cm (1.2 to 2.5 in). The preservation in these small nodules is superb, with nearly perfect to perfectly preserved body chambers and complete specimens. The majority of specimens in the collection were taken from these nodules, which themselves occur in a horizon midway in the zone described above. Specimens are rarely contained within the large septarian concretions.

The Codell Sandstone is not always present and measurements used to place specimens stratigraphically incorporate the base of the overlying Fort Hays Limestone for control. The base of the *Scaphites* zone is placed approximately 37 m (123 ft) below the base of the Fort Hays Limestone in the study area.

The repository for this collection is the Museum of Invertebrate Paleontology, the University of Kansas, herein designated KUMIP.

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MEASUREMENT OF SCAPHITES

Preservation of *Scaphites* ranges from complete specimens possessing original aragonitic shell

(pers. commun., G. E. G. Westermann) to incomplete individuals that require estimation of

size by comparison with other parameters. The bulk of the collection, however, consists of well-preserved, complete body chambers. The general lack of fossilized phragmocones and the poor condition of those that are preserved results from the differential infilling of body chambers and phragmocones by matrix. An unfavorable combination of sediment particle size and siphuncle diameter prevented infilling of most phragmocones. Those not filled with matrix were subsequently crushed and destroyed during compaction of the shale. Where loss of the phragmocone eliminates the possibility of making certain measurements, dimensions can be estimated by using the body chamber to reconstruct the missing or damaged phragmocone. This is warranted because of the strong positive correlation in *Scaphites* between the size ($LC + D_s$) of a body chamber and that of its phragmocone. The predictability of this allometry makes it possible to arrive at a reasonable estimate for at least the maximum diameter of a specimen (D_g). Estimates of other measurements may or may not be possible, depending on the condition of each specimen. The use of body chambers as substitutes for complete specimens greatly increased the size of the sample and aided significantly in understanding specific differences in morphology (shape and ornamentation) and in the recognition of dimorphism within species. This practice is acceptable because observations of complete forms by Morrow (1935), Cobban (1951, 1969), and myself support the premise that the body chamber contains all significant taxonomic information at the species level. Therefore, taxonomic assignments at the species level based on complete body chambers are valid for *Scaphites*. Estimated values are indicated by an asterisk in the measurements.

Abbreviations used throughout the remainder of the paper are listed below with an explanation of each symbol. The majority of these symbols and their applications are illustrated in Figure 3.

- LC —body chamber length
 D_g —maximum diameter of conch
 D_s —minimum diameter of conch
 m —microconch (male)
 nB —number of bullae on body chamber
 nIR —number of intercalatory ribs

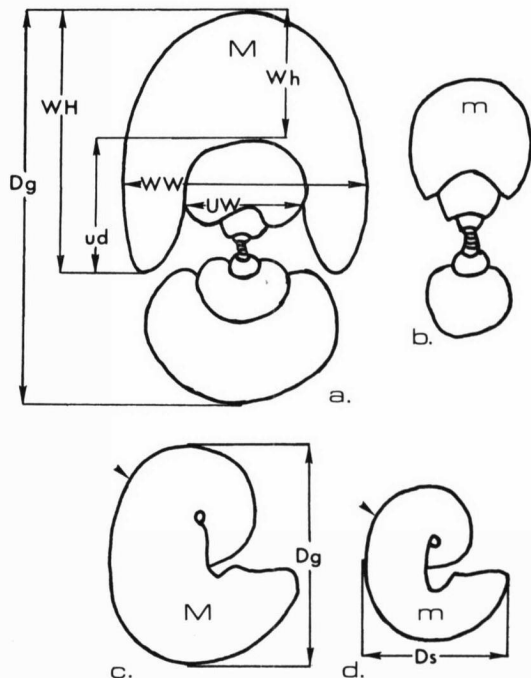


FIG. 3. Transverse and dorsoventral illustrations of typical macroconchs and microconchs; 3,a, transverse section of a macroconch with positions of measurements; 3,b, transverse section of microconch; 3,c, dorsoventral view of macroconch; 3,d, dorsoventral view of microconch.

- nN —number of nodes and tubercles on body chamber
 nUR —number of umbilical ribs on body chamber
 nVR —number of ventral ribs on body chamber
 ud —umbilical depth at base of chamber
 UW —umbilical width at base of chamber
 Wh —body chamber opening at base of chamber ($Wh-ud$)
 WH —whorl height at base of chamber
 WW —whorl width at base of chamber

Specialized terminology is necessary to describe the conch of *Scaphites*. The majority of these terms are defined in Part L of the *Treatise on Invertebrate Paleontology* (Arkell, Kummel, Miller, & Wright, 1957, p. L2-L6). Other terms, including two new terms for unusual scaphitid shell morphology, are briefly defined below. New terms are indicated by an asterisk.

- **contracted* (rib)—swung backward (ad-

apically) at or near venter.

lateral flanks—convex or flat area between dorsolateral and ventrolateral margins of the conch.

macroconch (*M*)—female designation; large involute partner of dimorphic pair.

microconch (*m*)—male designation; small evolute partner of dimorphic pair.

**point of recurvature*—apex of recurvature of the body chamber.

scaphitoid body chamber—heteromorphic body chamber recurved toward phragmocone; peristome nearly in contact with earlier whorls.

shaft—portion of body chamber extending from the base to the beginning of recurvature.

MAJOR MORPHOLOGICAL FEATURES

The 10 major morphological categories listed below contain 27 morphological characters used to describe and distinguish species of *Scaphites*. Each species described in this study has, as a formula, a unique combination of 10 characters taken from these major categories.

1. Body chamber loosely (1) or tightly (2) recurved.
2. Shaft of the body chamber slightly (3) or well (4) curved.
3. Umbilical ribs slightly (5), moderately (6), or greatly (7) pronounced.
4. Umbilical ribs rursiradiate (8) or recirradiate (9).
5. Ventral and intercalatory ribs straight (10), projected (11), or straight and then projected (12) adaperturally.
6. Ventral and intercalatory ribs distantly equispaced to the point of recurvature then approximated adaperturally (13); moderately equispaced to the point of recurvature, then approximated adaperturally (14); closely equispaced, then approximated adaperturally (15); or approximated adaperturally (16) over the length of the body chamber.
7. Body chamber without bullae (17), with greatly pronounced bullae (18), or moderately pronounced bullae (19).
8. Body chamber with very distantly spaced bullae (20), moderately spaced bullae (21), or normally spaced bullae (22).
9. Body chamber without nodes (23), with nodes (24), or a combination of nodes and bullae (25).
10. Aperture normal (26) for the genus or depressed (27). A normal aperture is defined as one that has a height equal or nearly equal to its width.

DIMORPHIC CHARACTERS

Dimorphic characters pertaining to size, form, and sculpture used in the distinction of sexes are summarized here to avoid repetition in the systematic descriptions.

Size.—For a particular species, each group of specimens shows a distinguishable range in size of forms classed as males and females. The range in size is such that a few of the largest males are larger than the smallest females. Cobban (1969) reported such an overlap in the size range of *Scaphites*. Weighed against other evidence of dimorphism, the slight overlap does not seem significant.

The ratio of maximum diameters (*Dg*) of the

largest and smallest adults of each sex within each species is commonly from 1:1.3 to 1:1.5. Few individuals of extraordinarily large or small size were found to be present. For incomplete or damaged specimens estimates of their original size were based on known ratios of existing measurements.

Within the sexes, size of the whorls is highly variable. Where preserved, the protoconch and first two whorls are nearly identical in all specimens, but subsequent whorls vary greatly in size (Cobban, 1969, p. 9). Males remain slender, whereas females tend toward robustness.

Form.—The forms herein designated as male

and female both have a wide umbilicus at the base of the body chamber relative to their overall size. At that point, the distinction between the sexes is based on the depth of the umbilicus. Shells of females, known to be involute, have a deep umbilicus relative to their whorl height (*WH*) (Fig. 3,*a*). The macroconchs have a more inflated body chamber than the microconchs and have a tendency to possess an umbilical swelling at the base of that chamber. The macroconch has a more robust form in comparison to the less robust or slender form of the microconch (Fig. 3,*c*; also, Cobban, 1969, fig. 6). In addition, phragmocones of macroconchs, with the exception of the innermost whorls, are more depressed than those of the microconchs (Fig. 3,*a*; also Cobban, 1969, fig. 7).

Ornamentation.—The macroconchs and microconchs of each species described have the same general ornamental features. All specimens possess umbilical, ventral, and intercalatory ribs on the phragmocone and body chamber. One species possesses umbilical and ventrolateral nodes; one possesses both ventrolateral nodes and bullae, some possess either ventrolateral nodes and bullae, and still others possess no nodes or bullae. Macroconchs differ from microconchs mainly in the number of nodes, bullae, or ribs on the body chamber. Cobban (1969) showed considerable differences in ornamentation between males and females.

Umbilical ribs crossing the umbilical shoulder are either rectiradiate or rursiradiate. At or before approaching the ventrolateral margin the umbilical ribs may develop into biplicate or triplicate nodes or bullae. In some species the umbilical ribs do not carry nodes or bullae, but remain simple, biplicate, or triplicate, becoming ventral ribs at the ventrolateral margin. Nodes and bullae always produce at least two, but no more than three, ventral ribs. Situated between the ventral ribs are the intercalatory ribs that appear to be randomly interspersed without formula. With the exception of *S. (H.) kansiensis*, all nodes and bullae begin at the base of the body chamber. In some species the nodes or bullae are developed over the length of the body chamber, but in the majority of the species, nodes or bullae terminate at the point of recurvature.

Orientation of ventral and intercalatory ribs is often quite distinctive between species. These

ribs may be contracted on early portions of the body chamber, changing to straight ribs toward the point of recurvature, then straight or projected adaperturally, or they may be initially straight to the point of recurvature then either straight or projected beyond this point to the aperture. This orientation does not assist in determining sexes. Macroconchs and microconchs of the same species have the same general pattern of ornamentation; however, the number and location of ornamental features (nodes, bullae, and ribs) may vary from individual to individual regardless of size or sex.

Adult and gerontic features.—The importance of determining if a specimen is an adult form has been covered in the introduction. Cobban (1951, 1969) considered a scaphite to be mature when the body chamber is scaphitoid and his definition is accepted here. In the collection made for this study, all but two specimens are adult forms. The two specimens in question consist of what normally would be considered the inner whorls of the phragmocone, and to these whorls are attached a few millimeters of body chamber. The absence of septal approximation and the reduced number of whorls in the phragmocone suggests that they may be immature forms; however, the lack of a complete body chamber leaves their status questionable. Such immature forms are rare but do exist, as shown by Cobban (1951, pl. 18, fig. 16-19), who illustrated an immature *Clioscaphtes vermiformis* (Meek & Hayden) with a body chamber that is not heteromorphous. In addition, three juvenile *Scaphites* were found within the body chambers of two adult macroconchs. Each juvenile had completed approximately one and one-half whorls before death. The body chamber of each juvenile is three-fourths of the last whorl and not scaphitoid. All complete specimens were sectioned longitudinally to determine if approximation of septa was observable; it was, and all were considered to be adult forms.

A summation of criteria useful in the recognition of dimorphism in *Scaphites* leads to the conclusion that individuals occurring in the same stratum, bearing identical ornamentation, and exhibiting a definite grouping by size into two groups are dimorphic pairs of the same species.

Criteria for recognition of sexes (macroconch vs. microconch) is summarized as follows: sexes

within a dimorphic pair of the same species (criteria may also be applied if just one member of the pair is available) may be distinguished by a robust conch in the female and a slender conch in the male; females are invariably involute whereas males are invariably evolute; females possess an umbilical swelling at, and slightly adaperturally from, the base of the body chamber, which males do not have; females typically have a more depressed body chamber than do males; females have a wide and deep umbilicus at the base of the body chamber, males a wide but shallow umbilicus; and females tend to exhibit a more prolonged approximation of septa and sutures as they approach the adult stage, whereas males tend to have rapid approximation of the last two to three septa. It should be noted that scaphites studied

and described by Cobban (1969) do not show a clear distinction between macroconchs and microconchs in terms of prolonged or rapid approximation of septa near the base of the living chamber.

The eight dimorphic characters chosen for this study are listed below in four major categories (M = macroconch; m = microconch). The use of these categories will be discussed in the data analysis section.

1. Specimen robust (M) or slender (m).
2. Specimen involute (M) or evolute (m).
3. The umbilicus swollen at the base of the body chamber (M) or not swollen (m).
4. The umbilicus deep at the base of the body chamber (M) or shallow (m).

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA Cuvier, 1797

Order AMMONOIDEA Agassiz, 1847

Family SCAPHITIDAE Meek, 1876

Genus SCAPHITES Parkinson, 1811

Subgenus SCAPHITES (SCAPHITES) Parkinson, 1811

Type species.—*Scaphites equalis* Sowerby, 1813, by subsequent designation (Meek, 1876).

Diagnosis.—Compressed to very inflated, more or less involute shell; early whorls invariably in contact; shaft short or moderately long, hook not curved over camerate whorls; aperture constricted and commonly collared, in some shells with long dorsal lappet; ribs normally branching or intercalated on coiled part, commonly single or joining at ventrolateral tubercles on shaft; umbilical and normally ventrolateral tubercles present on shaft; umbilical and normally ventrolateral tubercles present on shaft or hook. Suture ceases to be regularly lytoceratid in some geologically younger species.

Discussion.—Assignment of species to *Scaphites* (*Scaphites*) in this paper is based on the presence of scaphitoid body chambers, nature of the ribbing, and the general overall similarity to *Scaphites equalis* Sowerby (see Arkell, Kummel, & Wright, 1957, p. L228, fig. 256,3a,b).

The variability of sutures within individuals makes interspecific and intraspecific comparisons based on sutural studies impractical. This vari-

ability accounts for the absence of such an investigation in this study. The general habit of the sutural pattern of the species described below is that of the Turonian species *Scaphites nigricollensis* Cobban (1951) and can be described as less than lytoceratid in complexity. For a detailed account of the sutural pattern and its development in *Scaphites*, see Wiedmann (1965, p. 444-450, esp. text-fig. 14).

Distribution.—*Scaphites* (*Scaphites*) has a worldwide distribution in rocks of late Albian to Maastrichtian age (Cobban & Scott, 1972, p. 56).

SCAPHITES (SCAPHITES) ARCAIDIENSIS (M)

Moreman¹

Plate 1, figures 1-3

Scaphites arcadiensis MOREMAN, 1942, p. 216, pl. 34, fig. 3; COBBAN, 1951, p. 21, pl. 2, fig. 1-8.

Scaphites carlilensis MORROW; HATTIN, 1962, p. 79, pl. 23, fig. B-D, G, H.

Diagnosis.—Macroconch robust and involute with depressed subovate whorl section. Venter broad and rounded; lateral flanks short, very con-

¹In the following descriptions, the text following a regular species heading (e.g., *Scaphites* (*S.*) *hattini*) pertains to the entire species, exclusive of dimorphism. Species headings accompanied by the symbol (M) or (m) (e.g., *S.* (*S.*) *hattini* (M) or *S.* (*S.*) *hattini* (m)) refer exclusively to those forms of the species considered to be dimorphic. Accordingly, remarks contained in the discussion section of each species, except *Scaphites* (*H.*) *kansiensis*, are addressed to the species as a whole (macroconchs and microconchs). All real numbers (ratio data) in the measurements are given in millimeters.

vex, and rounded; umbilical shoulders rounded and well marked initially, weakly marked adaperturally; umbilicus wide, deep and swollen at base of body chamber.

Description.—Specimen KUMIP 108765 is incomplete, consisting of a scaphitoid body chamber loosely recurved with well-curved shaft, expanding to point of recurvature, then tapering adaperturally. Ornamentation on body chamber consists of umbilical, ventral, and intercalatory ribs and ventrolateral bullae. Umbilical ribs are moderately

pronounced and rursiradiate crossing the umbilical shoulder, gradually swelling into greatly pronounced and distant, equispaced, slightly prorsiradiate, biplicate bullae. Bullae terminate adaperturally from point of recurvature. Umbilical ribs adapertural from this point are simple and biplicate. Ventral and intercalatory ribs equispaced and straight to point of recurvature, becoming projected and approximated adaperturally. Aperture slightly depressed and arched ventrally. Measurements of macroconchs follow:

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108765	46.5*	39.0	25.0	19.0	11.0	11.0	7.0	89.0	5	8	25	4
108767	42.0*	36.0*	23.0	18.0	11.0	11.0	7.0	77.0*	5	8*	25*	6*
108768	43.0*	37.0*	25.0	17.0	9.5	10.0	6.5	75.0*	5	8*	25*	4*
108769	48.0	44.0	23.0	18.0	12.0	12.0	6.0	83.0	6	8	24	7

* Estimate.

SCAPHITES (SCAPHITES) ARCAIDIENSIS (m)

Moreman

Plate 1, figures 4, 5

Diagnosis.—Microconch slender and evolute with slightly depressed ovate whorl section. Venter broad; lateral flanks short; very convex, and rounded; umbilical shoulders rounded and well marked initially, weakly marked adaperturally; umbilicus wide and shallow at base of body chamber with no swelling.

Description.—Same as macroconch except for dimorphic characters and size. Measurements of microconchs follow section on *Occurrence*.

Discussion.—Taxonomically significant characters of the species, exclusive of dimorphism: body chamber—scaphitoid with subovate to ovate cross section, loosely recurved with well-curved shaft expanding to point of recurvature, then tapering adaperturally. Lateral flanks short and very convex. Umbilical ribs are rursiradiate at shoulder, developing into greatly pronounced and distant equispaced slightly prorsiradiate biplicate bullae that terminate at point of recurvature. Ventral and intercalatory ribs are equispaced and contracted to point of recurvature, becoming projected and approximated adaperturally.

The above described dimorphic pair is indistinguishable from the holotype of *Scaphites* (*S.*) *arcadiensis* Moreman and is placed in that species.

The combination of short and very convex lateral flanks and greatly pronounced, distant, equispaced, slightly prorsiradiate, and biplicate bullae terminating at the point of recurvature serves to distinguish *S.* (*S.*) *arcadiensis* from other species of *Scaphites*.

Comparison and correlation of morphological characteristics shared by *Scaphites* (*S.*) *arcadiensis* and the five other species described below are in the following format: numbers in parenthesis immediately following the related species refer to those shared characters explained in the section on major morphological features.

The combination of morphological characteristics shared by *Scaphites* (*S.*) *arcadiensis* with other species suggests that *S.* (*S.*) *arcadiensis* is most closely related to *S.* (*S.*) *inflexus* (13, 14, 15, 16, 17) and *S.* (*S.*) *hattini* (3, 7, 8, 15, 17), and more distantly to *S.* (*S.*) *carlilensis* (13, 14, 15, 16), and *S.* (*S.*) *mittchellensis* (1, 2, 3, 16).

Figure 4,*a*, illustrates intraspecific variations in conch size, particularly between macroconchs and microconchs.

Material.—Seven specimens; 4 macroconchs (KUMIP 108765, 108767, 108768, 108769) and 3 microconchs (KUMIP 108766, 108772, 108773).

Occurrence.—Specimens assigned to this species were collected at Localities 1, 8, and 9. Speci-

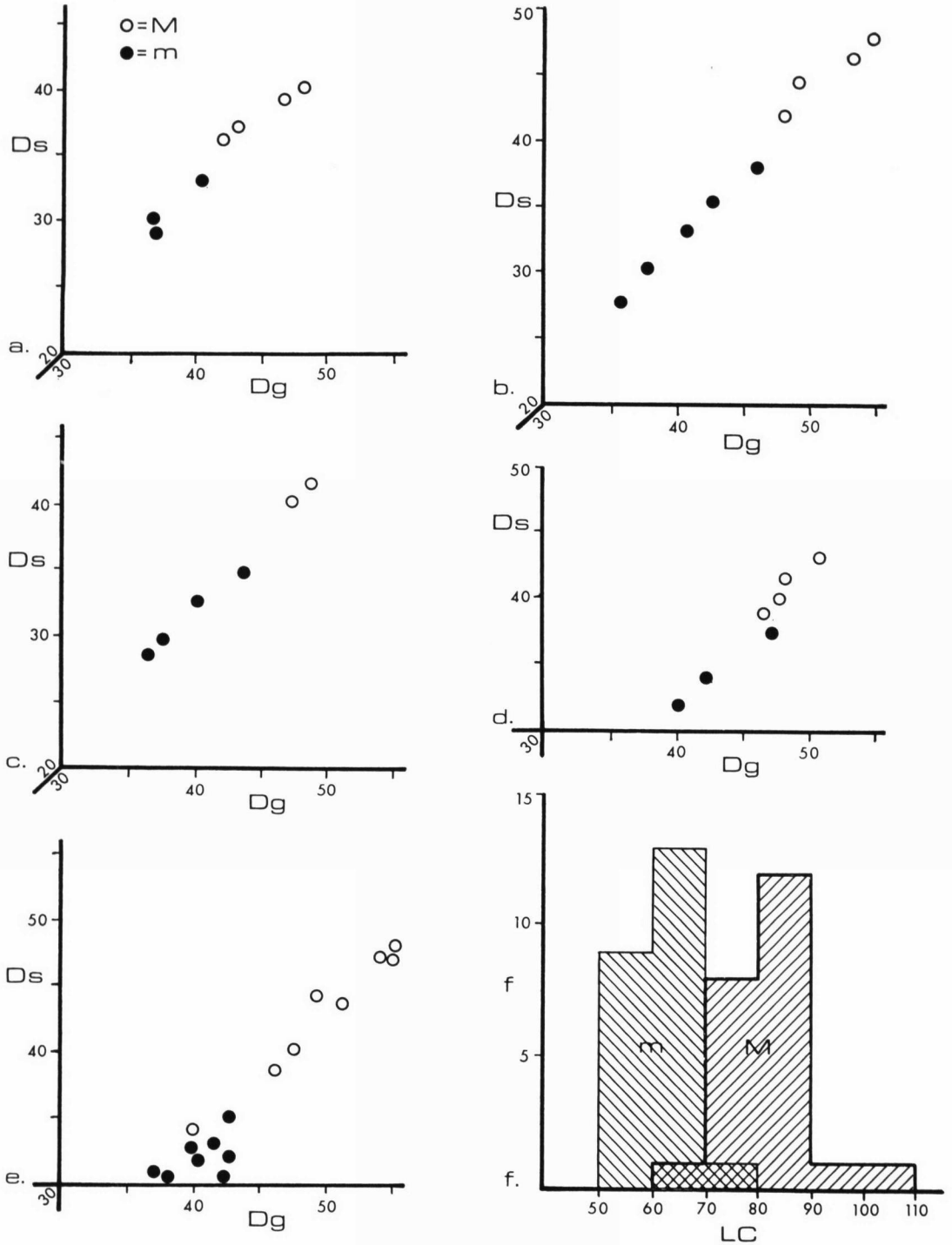


FIG. 4. Scatter diagrams of maximum diameter (D_g) vs. minimum diameter (D_s) for each species with the exception of *Scaphites (H.) kansiensis*, and a histogram of the frequency of occurrence vs. body chamber length for 46 specimens from the same 5 species (4,a-e); 4,a, *S. (S.) arcadiensis*; 4,b, *S. (S.) carlilensis*; 4,c, *S. (S.) hattini*; 4,d, *S. (S.) mitchellensis*; 4,e, *S. (S.) inflexus*; 4,f, histogram [f = frequency, LC = length of body chamber; M = macroconch; m = microconch]. All measurements in millimeters.

mens (KUMIP 108767, 108768, and 108773 taken from shale near the top of the zone; 108765, 108766, and 108769 taken from nodules midway

in the zone; and 108772 from shale near the base of the zone.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108766	37.0*	29.0	14.5	12.5	7.0	8.8	3.8	52.0	5	9	21	3
108772	40.5*	33.0	16.5	15.0	8.0	10.0	4.5	62.5	5	8	23	5
108773	37.0*	29.5	14.0	12.0	6.0	9.5	2.5	51.5	6	7	19	6

* Estimate.

SCAPHITES (SCAPHITES) CARLILENSIS (M)

Morrow

Plate 1, figures 6, 7

Scaphites carlilensis MORROW, 1935, p. 466, pl. 50, fig. 4a-d; COBBAN, 1951, p. 21, pl. 2, fig. 9-23.

Diagnosis.—Macroconch robust and involute with depressed subovate whorl section. Venter broad and well rounded; lateral flanks convex and well rounded; umbilical shoulders rounded and well marked; umbilicus wide, deep and swollen at base of body chamber.

Description.—Phragmocone is very involute, producing a markedly deep umbilicus. Flanks of the phragmocone bear distinct rectiradiate simple and biplicate umbilical ribs. The venter bears straight equispaced ventral and intercalatory ribs. Scaphitoid body chamber tightly recurved with

well-curved shaft, expanding to point of recurvature, then tapering adaperturally. Ornamentation on body chamber consists of umbilical, ventral, and intercalatory ribs and ventrolateral bullae. Umbilical ribs are moderately pronounced and slightly prorsiradiate crossing the umbilical shoulder, swelling into moderately pronounced normally equispaced and approximated prorsiradiate biplicate ventrolateral bullae. Adaperturally from point of recurvature bullae are nonexistent and umbilical ribs simple and biplicate. Moderately pronounced ventral and intercalatory ribs are straight and equispaced to point of recurvature, remaining straight beyond this point but approximated adaperturally. Aperture normal with highly arched but ventrally rounded peristome. Measurements of macroconchs follow:

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108774	54.5	47.0	26.0	21.0	13.0	13.0	7.5	89.0	7	12	27	11
108778	48.0	41.5	22.0	18.0	12.0	12.0	7.0	73.5	7	11	26	9
108779	53.0	45.5	23.0	18.5	13.0	12.0	7.5	89.0	7	12	31	13
108781	49.0*	44.0	24.0	19.5	11.5	13.0	6.5	85.0	7	13	32	7

* Estimate.

SCAPHITES (SCAPHITES) CARLILENSIS (m)

Morrow

Plate 1, figures 8-10

Scaphites pygmaeus MORROW, 1935, p. 465, pl. 50, fig. 2a-e, 3; MOREMAN, 1942, p. 216, pl. 34, figs. 5, 6.

Scaphites morrowi JELETZKY, 1949, p. 330; COBBAN, 1951, p. 21.

Diagnosis.—Microconch slender and evolute

with slightly depressed ovate whorl section. Venter rounded and disproportionately narrower than macroconch; lateral flanks convex and well rounded; umbilical shoulder round and well marked initially, weakly marked adaperturally; umbilicus wide and shallow at base of body chamber with no swelling.

Description.—Same as macroconch except for

dimorphic characters and size. Measurements of microconchs follow section on *Occurrence*.

Discussion.—Taxonomically significant characters of the species, exclusive of dimorphism: body chamber—scaphitoid with subovate to ovate cross section, tightly recurved with well-curved shaft and expansion to point of recurvature with taper to aperture. Umbilical ribs swell into moderately pronounced equispaced and approximated biplicate ventrolateral bullae. Bullae not developed adaperturally from point of recurvature. Ventral and intercalatory ribs straight, becoming approximated adaperturally from point of recurvature. Aperture normal with peristome highly arched and rounded ventrally.

Scaphites (*S.*) *carlilensis* is distinguishable from other species of *Scaphites* by the combination of the above-mentioned taxonomically significant characters. Of these, the most distinctive are the moderately pronounced, normally equispaced, biplicate and ventrolateral bullae being somewhat approximated near the point of recurvature. Adapertural from this point the bullae are nonexistent.

The combination of morphological characteristics shared by *Scaphites* (*S.*) *carlilensis* with other species suggest that *S.* (*S.*) *carlilensis* is most closely related to *S.* (*S.*) *inflexus* (11, 12, 13, 14, 15, 16) and more distantly with *S.* (*S.*) *arcadiensis* (13, 14, 15, 16), *S.* (*S.*) *mitchellensis* (16,

29, 30, 31), and *S.* (*S.*) *hattini* (11, 15).

Designation herein of forms previously assigned to *Scaphites morrowi* as microconchs of *S.* (*S.*) *carlilensis* is warranted because these forms are indistinguishable from *S.* (*S.*) *carlilensis* (*M*) except by characters of dimorphism and size. Application of dimorphic criteria readily indicates that the forms previously identified as *S. morrowi* are microconchs of *S.* (*S.*) *carlilensis*. Morrow (1935, p. 466), in his remarks pertaining to *Scaphites morrowi* (*pygmaeus*), stated that "*Scaphites pygmaeus* and *S. carlilensis* are very much alike in many details, the principal difference being in the size."

Figure 4, *b*, represents intraspecific variations in conch size and particularly between macroconchs and microconchs. The lack of a convincing break between (*M*) and (*m*) and the linearity of (*m*) is thought to be an artifact of the scale of the figure (cf. Fig. 5, *a* and 5, *b*).

Material.—Nine specimens; 4 macroconchs (KUMIP 108774, 108778, 108779, 108781) and 5 microconchs (KUMIP 108775, 108776, 108777, 108780, 108782).

Occurrence.—Specimens assigned to this species were collected at Localities 1, 3, 7, 8, and 9. Specimens KUMIP 108777 and 108781 were taken from shale near the top of the zone. The remaining specimens are from nodules midway in the zone.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108775	42.5	35.0	16.5	14.5	9.0	10.5	4.3	64.0	6	10	26	10
108776	40.5	33.0	16.5	15.0	8.0	10.0	4.5	62.5	6	9	26	10
108777	37.5*	30.0	16.5	14.5	9.5	11.0	5.0	56.0	5	9	23	5
108780	46.0*	37.5	18.0	16.0	6.5	11.0	5.0	68.5	7	11	25	10
108782	35.5*	27.5	15.0	13.5	7.5	9.0	4.5	57.0	7	12	25	7

* Estimate.

SCAPHITES (SCAPHITES) HATTINI (M) Crick, n. sp.
Plate 2, figures 1-3

Diagnosis.—Macroconch robust and involute with depressed subovate whorl section. Venter broad and rounded; lateral flanks short, very convex and well rounded; umbilical shoulders rounded and well marked; umbilicus wide, deep

and swollen at base of body chamber.

Description.—Flanks of the phragmocone bear distinct rectiradiate simple and biplicate umbilical ribs. Venter bears straight equispaced ventral and intercalatory ribs. Scaphitoid body chamber tightly recurved with slightly curved shaft, expanding to point of recurvature then tapering

adaperturally. Ornamentation of body chamber consists of umbilical, ventral and intercalatory ribs, and ventrolateral nodes and bullae. Umbilical ribs are moderately pronounced and rursiradiate crossing the umbilical shoulder, rapidly swelling into greatly pronounced prorsiradiate and biplicate bullae and moderately pronounced rectiradiate biplicate and triplicate nodes. First five or six

umbilical ribs develop into very distant bullae and remaining three develop into three approximated nodes. Ventral and intercalatory ribs straight and distant to point of recurvature becoming slightly projected and approximated adaperturally. Aperture depressed and highly arched ventrally. Measurements of macroconchs follow:

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nN	nB	nUR	nVR	nIR
108807	48.5	41.0	23.0	17.0	12.0	10.0	7.0	85.0	3	6	9	25	7
108809	47.0	39.5	23.5	17.5	12.0	10.0	7.5	77.0	3	6	9	25	7

SCAPHITES (SCAPHITES) HATTINI (m) Crick, n. sp.
Plate 2, figures 4, 5

Diagnosis.—Microconch slender and evolute with slightly depressed ovate whorl section. Venter broad for the overall size and rounded; lateral flanks convex and well rounded; umbilical shoulders rounded and well marked initially, weakly marked adaperturally; umbilicus wide and shallow at base of body chamber with no swelling.

Description.—Same as macroconch except for dimorphic characters and size. Measurements of microconchs follow section on *Occurrence*.

Discussion.—Taxonomically significant characters of the species, exclusive of dimorphism: body chamber—scaphitoid with subovate to ovate cross section, tightly recurved with a slightly curved shaft expanding to point of recurvature then tapering adaperturally. Umbilical ribs are rursiradiate over the shoulder, swelling rapidly into greatly pronounced and very distant prorsiradiate biplicate bullae from the base of the body chamber to point of recurvature. Adaperturally from this point the umbilical ribs swell into moderately pronounced and approximated nodes. Morphology of the bullae differs from others in the collection by approaching that of nodes. Ventral and intercalatory ribs are initially straight and distant from the base of body chamber to the point of recurvature, becoming slightly projected and approximated adapertural from this point.

Scaphites (*S.*) *hattini* differs from other species of *Scaphites* by possessing the combination of a

tightly recurved body chamber, a slightly curved shaft, initial rursiradiate umbilical ribs, and the presence of both ventrolateral bullae and nodes. This type bears a strong resemblance to *S. (S.) arcadiensis* (Moreman, 1942, p. 216, pl. 34, fig. 3). Although differing in size (Moreman's illustrated specimen is a male), *S. (S.) arcadiensis* has more distant and fewer umbilical and ventral ribs, and a lack of nodes, whereas tubercles are present. Moreman did not mention the existence of intercalatory ribs on the holotype, but examination of the holotype showed them to exist.

The combination of morphological characteristics shared by *Scaphites (S.) hattini* and other species suggests that *S. (S.) hattini* is most closely related to *S. (S.) arcadiensis* (3, 7, 8, 15, 17), and more distantly with *S. (S.) inflexus* (11, 15, 17), *S. (S.) mitchellensis* (3, 4, 5), and *S. (S.) carlilensis* (11, 15).

Figure 4, *c*, illustrates intraspecific variations in conch size and particularly those between macroconchs and microconchs.

Etymology.—The species is named after Dr. Donald E. Hattin of the University of Illinois, who has for many years contributed much to the understanding of the Cretaceous strata and fauna of Kansas.

Material.—Six specimens; 2 macroconchs (KUMIP 108807, 108809) and 4 microconchs (108808, 108810, 108811, 108812).

Occurrence.—Specimens assigned to this spe-

cies were collected at Localities 1 and 9. Specimen KUMIP 108810 was taken from shale near

the base of the zone, and remaining specimens are from nodules midway in the zone.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nN	nB	nUR	nVR	nIR
108808	43.5*	34.5	22.0	16.0	10.0	11.0	5.0	65.5	3	5	8	23	7
108810	37.5*	29.5	17.5	13.0	8.0	8.5	4.5	55.5	3	6	9	25	7
108811	36.5	28.5	14.5	12.5	7.0	8.5	4.0	53.0	3	5	8	21	5
108812	40.5*	32.5	16.0	15.0	7.5	11.0	5.0	65.0	5	5	7	24	6

* Estimate.

SCAPHITES (SCAPHITES) MITCHELLENSIS (M)

Crick, n. sp.

Plate 2, figures 6, 7

Diagnosis.—Macroconch robust and involute with depressed subovate whorl section. Venter broad and rounded; lateral flanks convex and rounded; umbilical shoulders rounded and well marked; umbilicus wide, deep and swollen at base of body chamber.

Description.—Phragmocone very involute, producing a markedly deep umbilicus at the base of body chamber. Flanks of septate whorls bear distinct rectiradiate simple and biplicate umbilical ribs. Venter bears straight equispaced ventral and intercalatory ribs. Scaphitoid body chamber loosely recurved, with slightly curved shaft and no expansion. Tapering occurs adaperturally from

point of recurvature. Ornamentation on body chamber consists of umbilical, ventral and intercalatory ribs and moderately pronounced ventrolateral bullae. Umbilical ribs moderately pronounced and rectiradiate crossing the umbilical shoulder, the first nine rapidly swelling into moderately pronounced blunt but stout and elongate, slightly prorsiradiate, biplicate bullae. Bullae are moderately distant and equispaced to point of recurvature, becoming approximated adaperturally. Ventral and intercalatory ribs are straight and equispaced to point of recurvature, remaining straight but approximated adaperturally from this point. Although the aperture is crushed on the holotype and paratype, it does appear to be depressed. Measurements of macroconchs follow:

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108783	48.0*	41.5	25.0	18.0	13.5	12.5	8.0	84.5	9	11	30	10
108784	47.5*	40.0	24.0	18.0	11.5	12.0	6.0	83.0	9	11	28	8
108785	46.5*	39.0	20.0	16.0	9.0	10.0	7.0	77.0	8	11	25	8
108786	50.5*	43.0	26.0	20.0	9.0	13.0	7.0	74.0	6	11	28	9

* Estimate.

SCAPHITES (SCAPHITES) MITCHELLENSIS (m)

Crick, n. sp.

Plate 2, figures 8, 9

Diagnosis.—Microconch slender and evolute with slightly depressed ovate whorl section. Venter proportional for size and rounded; lateral flanks convex and rounded and well marked ini-

tially, weakly marked adaperturally; umbilicus wide and shallow at base of body chamber with no swelling.

Description.—Same as macroconch except for dimorphic characters and size. Measurements of microconchs follow section on *Occurrence*.

Discussion.—Taxonomically significant char-

acters of the species, exclusive of dimorphism: body chamber—scaphitoid with subovate to ovate cross section, loosely recurved with curved shaft and no expansion. Lateral flanks are convex and well rounded bearing rectiradiate umbilical ribs over the shoulder and greatly pronounced, blunt, stout, and slightly prorsiradiate, biplicate, ventrolateral bullae. Ventral and intercalatory ribs are straight and equispaced to point of recurvature, remaining straight but approximated adaperturally from that point. Morphology of the aperture is uncertain.

Scaphites (*S.*) *mittchellensis* is distinguishable from other *Scaphites* by possessing the combination of a loosely recurved chamber, curved shaft, rectiradiate umbilical ribs over the shoulder, and greatly pronounced blunt, stout, and slightly prorsiradiate, biplicate, ventrolateral bullae. This latter feature is the most distinctive.

The combination of morphological characteristics shared by *Scaphites* (*S.*) *mittchellensis* and other species suggests that *S.* (*S.*) *mittchellensis* is

most closely related to *S.* (*S.*) *arcadiensis* (1, 2, 3, 16) and *S.* (*S.*) *carlilensis* (16, 29, 30, 31), and more distantly with *S.* (*S.*) *hattini* (3, 4, 5), and *S.* (*S.*) *inflexus* (16).

Figure 4,*d*, illustrates intraspecific variations in conch size, particularly those of macroconchs and microconchs, together with a moderate size overlap. The specimen in this case has all the attributes of a male but is a large form.

Etymology.—The species name is derived from Mitchell County, Kansas, where it was collected.

Material.—Seven specimens; 4 macroconchs (KUMIP 108783, 108784, 108785, 108786) and 3 microconchs (KUMIP 108787, 108788, 108789).

Occurrence.—Specimens assigned to this species were collected at Localities 1, 8, and 9. Specimens KUMIP 108785, 108787 taken from shale near the top of the zone; 108784 taken from shale midway in the zone; and 108786 taken from shale near the base of the zone. Remaining specimens are from nodules midway in the zone.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nB	nUR	nVR	nIR
108787	47.0*	37.5	19.5	16.0	9.0	11.0	5.5	78.0	7	10	27	9
108788	42.0*	34.0	16.0	14.0	9.0	10.0	4.0	61.0	8	12	29	10
108789	40.0	32.0	16.5	13.5	9.0	10.3	3.3	56.0	6	10	26	5

* Estimate.

SCAPHITES (SCAPHITES) INFLEXUS (M) Crick, n. sp.
Plate 2, figures 10, 11

Diagnosis.—Macroconch robust and involute with depressed, subovate whorl section. Venter broad and well rounded; lateral flanks convex and well rounded; umbilical shoulders rounded and well marked; umbilicus wide, deep, and swollen at base of body chamber.

Description.—Flanks of the phragmocone bear distinct rectiradiate simple and biplicate umbilical ribs. Venter bears straight, equispaced ventral and intercalatory ribs. Scaphitoid body chamber tightly recurved with well-curved shaft and no expansion adaperturally, tapering toward aperture.

Ornamentation on body chamber consists of umbilical, ventral, and intercalatory ribs. Umbilical ribs are moderately pronounced and rursiradiate, crossing the umbilical shoulder and becoming greatly pronounced toward the ventrolateral margin where they are simple and biplicate. In addition, the umbilical ribs form an adaperturally projected inflection (Pl. 2, fig. 10, 12) at the ventrolateral margin. Ventral and intercalatory ribs straight and approximated to point of recurvature, becoming slightly projected and approximated adaperturally. Aperture normal, but slightly depressed. Measurements of macroconchs follow:

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nUR	nVR	nIR
108790	54.5	47.0	28.0	22.0	13.0	13.0	9.0	87.5	13	33	9
108791	51.0*	43.5	24.5	19.0	12.0	11.0	8.0	86.0	13	30	6
108792	49.0*	44.0	24.0	19.5	12.0	12.0	8.0	86.0	14	35	10
108794	75.5*	66.5	32.0	26.0	14.0	16.0	10.0	105.0	21*	57*	15*
108795	54.5*	47.0	28.5	22.5	15.5	13.0	9.5	95.5	13	35	9
108801	55.0*	47.5	25.0	20.0	14.0	12.0	8.0	87.5	11	27	6
108804	47.5*	20.0	26.0	20.0	10.0	11.0	6.0	78.0	13	28	6
108805	46.0*	38.5	21.0	17.0	9.5	9.0	8.0	69.0	8	24	8
108806	40.0	34.0	21.0	15.5	10.0	9.5	5.5	72.0	13	30	6

* Estimate.

SCAPHITES (SCAPHITES) INFLEXUS (m) Crick, n. sp.
Plate 2, figures 12, 13

Diagnosis.—Microconch slender and evolute with slightly depressed ovate whorl section. Venter more round and narrow than macroconch; lateral flanks convex and well rounded; umbilical shoulders rounded and well marked initially, weakly marked aperturally; umbilicus wide and shallow at base of body chamber with no swelling.

Description.—Same as macroconch except for dimorphic characters and size. Measurements of microconchs follow section on *Occurrence*.

Discussion.—Taxonomically significant characters of the species, exclusive of dimorphism: body chamber—scaphitoid with subovate to ovate cross section, tightly recurved with well-curved shaft and no expansion. Chamber tapers adaperturally from point of recurvature. Umbilical ribs are greatly pronounced, prorsiradiate, simple and biplicate, rursiradiate at the shoulder, inflected adaperturally at ventrolateral margin. Ventral and intercalatory ribs are greatly pronounced, straight to point of recurvature, continuing straight then becoming projected and approximated adaperturally. Ventrolateral nodes and bullae are lacking.

Scaphites (S.) inflexus differs from other species of *Scaphites* by possessing the combination of a well-curved shaft, very convex and well-rounded venter, rursiradiate ribs over the shoulder, greatly pronounced umbilical, ventral, and intercalatory ribs. The former is inflected adaperturally at the ventrolateral margin. Lack of nodes or bullae is the most distinctive feature. Hattin (1962, p. 29, pl. 23, figs. C, F-H) mistakenly identified speci-

mens of *S. (S.) inflexus* as *S. (S.) carlilensis*. Comparison with Morrow's (1935) holotype of *S. (S.) carlilensis* shows sufficient dissimilarities in the type and nature of ornamentation to prevent confusion of the two.

The combination of morphological characteristics shared by *Scaphites (S.) inflexus* with other species suggests that *S. (S.) inflexus* is most closely related to *S. (S.) carlilensis* (11, 12, 13, 14, 15, 16), and more distantly with *S. (S.) arcadiensis* (13, 14, 15, 16, 17), *S. (S.) hattini* (11, 15, 17), and *S. (S.) mitchellensis* (16).

Figure 4,e, illustrates the intraspecific variation of conch size, particularly those of macroconchs and microconchs. The one case of overlap is the reverse of Figure 4,d. The specimen has all the attributes of a female, but is of small size. The distinction between (*M*) and (*m*) in this plot is due to the large sample size.

Etymology.—The name *inflexus* alludes to the existence of inflected points in the umbilical ribs at the ventrolateral margin.

Material.—Seventeen specimens; 9 macroconchs (KUMIP 108790, 108791, 108792, 108794, 108795, 108801, 108804, 108805, 108806) and 8 microconchs (108793, 108796, 108797, 108798, 108799, 108800, 108802, 108803).

Occurrence.—Specimens assigned to this species were collected at Localities 1, 3, 7, 8, and 9. Specimens KUMIP 108792, 108802, 108803, 108804 taken from shale near the top of the zone; 108794, 108795, 108805 taken from shale midway in the zone; 108791, 108798, 108804 taken from shale near the base of the zone. Remaining specimens are from nodules midway in the zone.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nUR	nVR	nIR
108793	42.5*	32.0	17.5	14.5	7.0	11.0	3.5	57.5	11	25	9
108796	41.5*	33.0	17.5	15.0	10.0	11.5	4.0	61.0	10	28	10
108797	40.0	32.0*	16.0*	14.0	10.0*	11.5	3.4	64.0	11	26	4
108798	42.5*	35.0*	21.0	18.0*	10.0*	12.0	6.0	64.0	9	24	8
108799	37.5*	30.0	14.5	12.0	7.0	9.5	4.5	62.5	12	30	4
108800	40.0*	32.0	17.0	14.0	8.5	10.5	3.5	61.0	11	25	6
108802	37.5*	30.0	16.0	14.5	9.0	10.0	4.5	58.0	12	27	8
108803	42.5*	35.0	16.5	14.0	10.0	9.5	4.0	64.0	14	30	10

* Estimate.

Subgenus SCAPHITES (HOPLOSCAPHITES) Nowak, 1912

Type species.—*Ammonites constrictus* Sowerby, 1818.

Diagnosis.—*Scaphites* with a slightly involute to evolute phragmocone (degree of volution dependent on dimorphic status); phragmocone compressed with flattened flanks and rounded venter; scaphitoid body chamber with a short, well-curved shaft and a slightly recurved hook; flanks flattened and venter well rounded; ribs flexous with weak lateral and ventral projections; with or without circular to subcircular umbilical and ventrolateral nodes; suture with a symmetric to slightly asymmetric bifid lateral lobe.

Discussion.—Assignment of the following new species to the subgenus *Scaphites* (*Hoploscaphites*) is based on the specimen's general similarity to the type species and other members of the subgenus, particularly the North American species *S. (H.) gilli* (Cobban & Jeletzky, 1965, p. 796, pl. 96, fig. 1A, 1B, 3B, 8B).

Retention of *Hoploscaphites* as a subgenus of *Scaphites* continues the practice of experienced scaphite workers who question whether the phylogeny of the genus is sufficiently understood to allow the recognition of new genera with many of the same basic characteristics (Birkelund, 1965; Cobban & Jeletzky, 1965). Others have recognized the difficulties of generic distinction among the scaphitids, but have preferred to treat *Hoploscaphites* and other potential subgenera as valid genera (for a summary, see Wiedmann, 1965).

The most important emendation to the subgenus is the expanded stratigraphic and geographic range documented by the occurrence of *Scaphites* (*Hoploscaphites*) *kansiensis*, n. sp., in

strata of Turonian age from northcentral Kansas. *Scaphites* (*Hoploscaphites*) is reported worldwide from strata of Campanian and Maastrichtian age. North American occurrences have been reported from Manitoba and Saskatchewan in Canada, and from Colorado and Wyoming in the United States.

SCAPHITES (HOPLOSCAPHITES) KANSIENSIS (m) Crick, n. sp.

Plate 1, figures 11, 12

Diagnosis.—Microconch slender and evolute with compressed whorl section. Venter narrow and rounded; lateral flanks slightly convex on phragmocone and flattened on body chamber; umbilical shoulders rounded and not well marked; umbilicus narrow and shallow at base of body chamber with no swelling. Umbilical and ventrolateral nodes on body chamber and youngest part of the phragmocone.

Description.—Flanks and venter of exposed phragmocone bear distinct umbilical and ventral ribs. Circular to subcircular umbilical and ventrolateral nodes begin on last septate whorl, becoming progressively larger toward body chamber. Two umbilical and three ventrolateral nodes occur on the phragmocone. Scaphitoid body chamber loosely recurved with well-curved shaft expanding to point of recurvature then tapering aperturally. Ornamentation on body chamber consists of flexous umbilical, ventral, and intercalatory ribs, and circular to subcircular umbilical and ventrolateral nodes. Umbilical ribs are slightly pronounced, rectiradiate crossing the umbilical shoulder, then prorsiradiate. Four umbilical nodes on the body chamber become progressively larger to point of recurvature, then decrease in size

adaperturally; none occur on last 12 mm of body chamber. Six ventrolateral nodes also become progressively larger to point of recurvature, then decrease in size adaperturally; none occur in last 25 mm of body chamber. Ventral ribs are projected as they cross venter, becoming approximated adaperturally. Aperture is not lappeted, but is thickened dorsally and ventrally. Measurements of the microconch follow section on *Occurrence*.

Discussion.—Taxonomically significant characters of the species, exclusive of dimorphism: phragmocone—flanks are slightly convex or flattened and bear distinct umbilical ribs adapically arched at the shoulder, then rectiradiate, becoming simple and biplicate to the ventrolateral margin. Venter bears distinct and straight ventral and intercalatory ribs. Several evenly spaced umbilical and ventrolateral, circular to subcircular nodes appear on the final one-third volution. Body chamber—flanks are flattened and bear distinct umbilical ribs, which are rectiradiate at the shoulder, then prorsiradiate, equispaced, simple, and biplicate to the ventrolateral margin. Venter bears distinct and projected ventral and intercalatory ribs that are approximated adaperturally. Development of evenly spaced umbilical and ventrolateral circular to subcircular nodes continues on the body chamber and ceases 12 mm umbilically and 25 mm ventrally from aperture, which is thickened, but is without lappets or other projections.

The species is monotypic and is placed in the subgenus *Scaphites* (*Hoploscaphites*) instead of *S.* (*Scaphites*) because it possesses both umbilical and ventrolateral nodes on the phragmocone and

the body chamber, a highly compressed conch (slightly convex to flattened flanks), and other hoploscaphitid characteristics.

Scaphites (*Hoploscaphites*) *kansiensis* exhibits only the most superficial resemblance to other scaphitids in the collection. Scaphitids that are most similar to *S.* (*H.*) *kansiensis* are hoploscaphitids, which occur in younger strata of Campanian to Maastrichtian age. Cobban and Jeletzky (1965) described *S.* (*H.*) *gilli* from Campanian and Maastrichtian formations of central Canada and north-central United States with a range of morphology that includes a few forms similar to *S.* (*H.*) *kansiensis* by possessing convex flanks, a row of slightly pronounced ventrolateral nodes on the body chamber, an absence of umbilical nodes, and a dorsal lappet. In addition to the considerable stratigraphic separations, these differences are sufficient to distinguish *S.* (*H.*) *kansiensis* from *S.* (*H.*) *gilli*. Birkelund (1965) described three hoploscaphitids from Upper Campanian strata of West Greenland. Of those illustrated, *S.* (*H.*) *ikorfatensis* (p. 102, pl. 24, 25, 26) and *S.* (*H.*) *ravni* (p. 106, pl. 26, 27, 28, 29) show the closest relationship to *S.* (*H.*) *kansiensis*, but are distinct by having ventrolateral nodes only on the body chamber, an absence of umbilical nodes, finer and more flexuous ribbing, and an inflated body chamber.

Etymology.—The species name is derived from the State of Kansas where it was collected.

Material.—One specimen (microconch); holotype KUMIP 108770.

Occurrence.—Collected from a nodule midway in the zone at Locality 1.

Spec.	Dg	Ds	WW	WH	UW	Wh	ud	LC	nN	nUR	nVR	nIR
108770	56.0	53.5	8.5	18.5	5.0	15.0	3.5	100.0	15	15	70	20

DATA ANALYSIS

The histogram in Figure 4,f, is bimodal and shows an overlap in size range less than that observed by Birkelund (1965) and Cobban (1969). Makowski (1962a) did not find an overlap in size of male and female specimens. It seems

reasonable, considering normal growth patterns, to expect a size overlap of sexes within and between congeneric species. The size overlap in Figure 4,f, is explained by comparing whorl height (*WH*) and width (*WW*) (Fig. 5,b) and maxi-

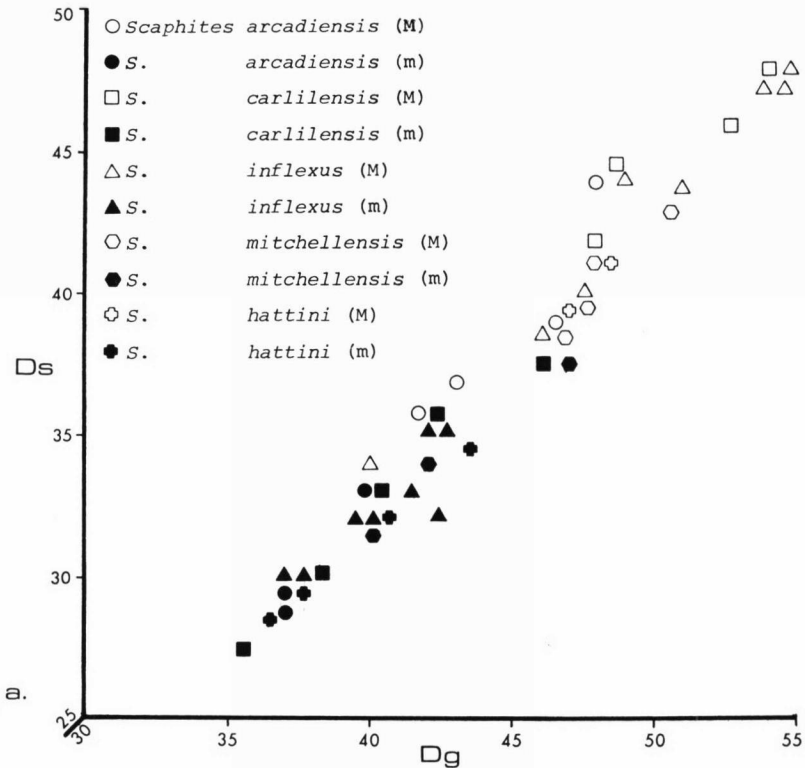
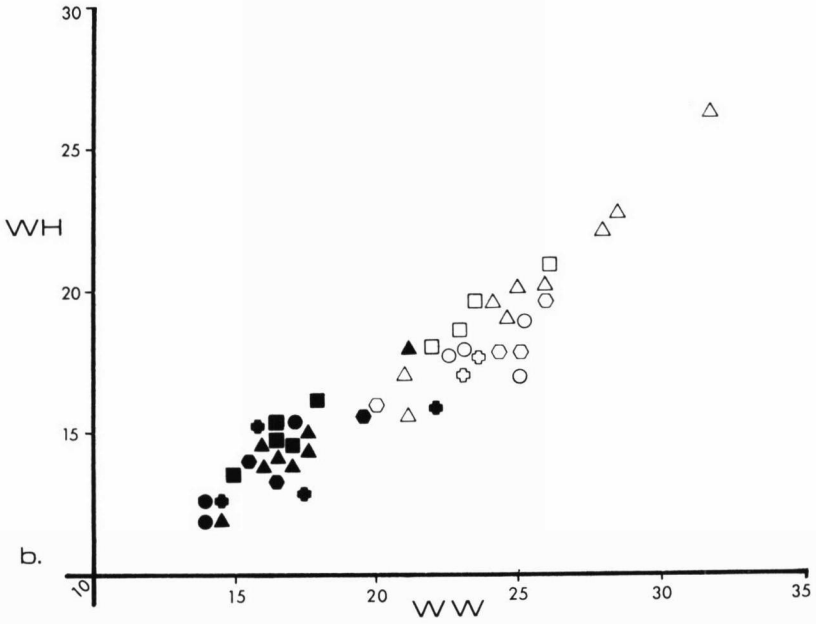


FIG. 5. Scatter diagrams combining the 5 species of Figure 4 and showing a separation of macroconch and microconchs for the genus; 5,a, plot of maximum diameters (D_g) vs. minimum diameter (D_s); 5,b, plot of whorl width (WW) vs. whorl height (WH). Symbols for 5,b, are the same as 5,a. All measurements in millimeters.

mum conch diameter (D_g) and minimum conch diameter (D_s) (Fig. 5,a). It is a function of relative overall size differences between sexes. *Scaphites* (*S.*) *inflexus* and *S.* (*S.*) *arcadiensis* have a greater size variation in macroconchs than other species and contribute disproportionately to the overlap.

Considerable variation occurs in the size of the whorls within macroconchs and microconchs. The protoconch and the initial two whorls, where preserved, are of nearly the same size in all specimens, whereas the subsequent whorls vary greatly in size. Unlike Makowski (1962a) and Cobban (1969), I did not find macroconchs to have an additional whorl when comparing sagittal sections of macroconchs and microconchs.

The nominal, ratio, and ordinal data were analyzed quantitatively by NT-SYS (Numerical Taxonomy SYStem), a collection of multivariate statistical routines that have been organized to form a compatible system of programs. The system was developed by Rohlf et al. (1974), with the computational methods described in Sokal and Sneath (1963). Programs and data matrices used in this investigation are listed in Crick (1976) and are available upon request from the author.

The Dice Coefficient of similarity (Dice,

$$\frac{2A}{2A + B + C}$$

1945) was chosen because of the desired effect of matched pairs (A) of nominal or presence-absence data carrying twice the weight of unmatched pairs (B and C), whereas negative matches carry no weight at all.

The combined operations performed on the nominal data, which are nothing more than binary sorts, provided a clear picture of the relationships within and between species without the negative matches as illustrated in Figure 6.

The Unweighted Pair-Group Method using arithmetic averages (UPGMA) was chosen to deal with the nominal data. The choice of the UPGMA method of clustering in the dendrogram was made because test runs with the data indicated that the clusters would be small. The small size of the clusters negated the weakness of UPGMA, that is, that late entries into large clusters have significantly less influence on the similarity measures of that cluster.

Cosine theta was chosen as the measure of

similarity because it gives reliable measures of proportional similarity when working with ratio data and may be the best measure of shape. In computations using this measure each variable is considered to be a vector going from the origin to a point given by coordinates taken from the input data. The actual measure is the angle between two vectors in "n" dimensional space.

The cophenetic correlation coefficients are 0.815 in Q-mode and 0.841 in R-mode for the nominal data, and 0.852 in Q-mode and 0.793 in R-mode for the ratio and ordinal data. A cophenetic correlation below 0.8 is usually interpreted as an indicator of severe distortion in the dendrogram at the lower linkages. This distortion may be such that the dendrogram is misleading; however, because only one of the above values falls slightly below 0.8, this suggests that the coefficients are slightly above average, but not superior.

The results of the quantitative analyses discussed above are presented in Figures 6, 7,a, and 7,b. The first of these, Figure 6, is a two-way cluster analysis of nominal data. Thirty-six characters are listed in R-mode. Twenty-seven of these are morphological characters, eight are dimorphic characters, and one is the character necessary to balance the binary coding of the nominal data set. This method of presenting data offers rapid comparison of the relationships between the species and the characters that describe them (for further explanation of this method, see Sepkoski & Rex, 1974). The Q-mode dendrogram groups those specimens with identical characters into specific categories A,a; B,b; . . . F,f, with macroconch and microconch having slightly different levels of association. Relationships at the subgeneric level are shown by lower levels of association. *Scaphites* (*H.*) *kansiensis*, indicated by "e," shows only the microconch category because it is monotypic. Each dot represents the presence of that character in R-mode for a specimen in Q-mode. The relationship of species at the subgeneric level can easily be seen with this method of representation. *S.* (*S.*) *inflexus* (B,b) is more closely related to *S.* (*S.*) *carlilensis* (A,a) than it is to *S.* (*S.*) *arcadiensis* (C,c) not only because they share six of the same characters (11-16) but because *S.* (*S.*) *arcadiensis*, in addition to sharing five of the same characters (13-17) as *S.* (*S.*) *inflexus*, possesses five additional characters (1-3, 7-8), which are in a different subgroup at a much lower level of association. Categories 21-28 are dimorphic characters

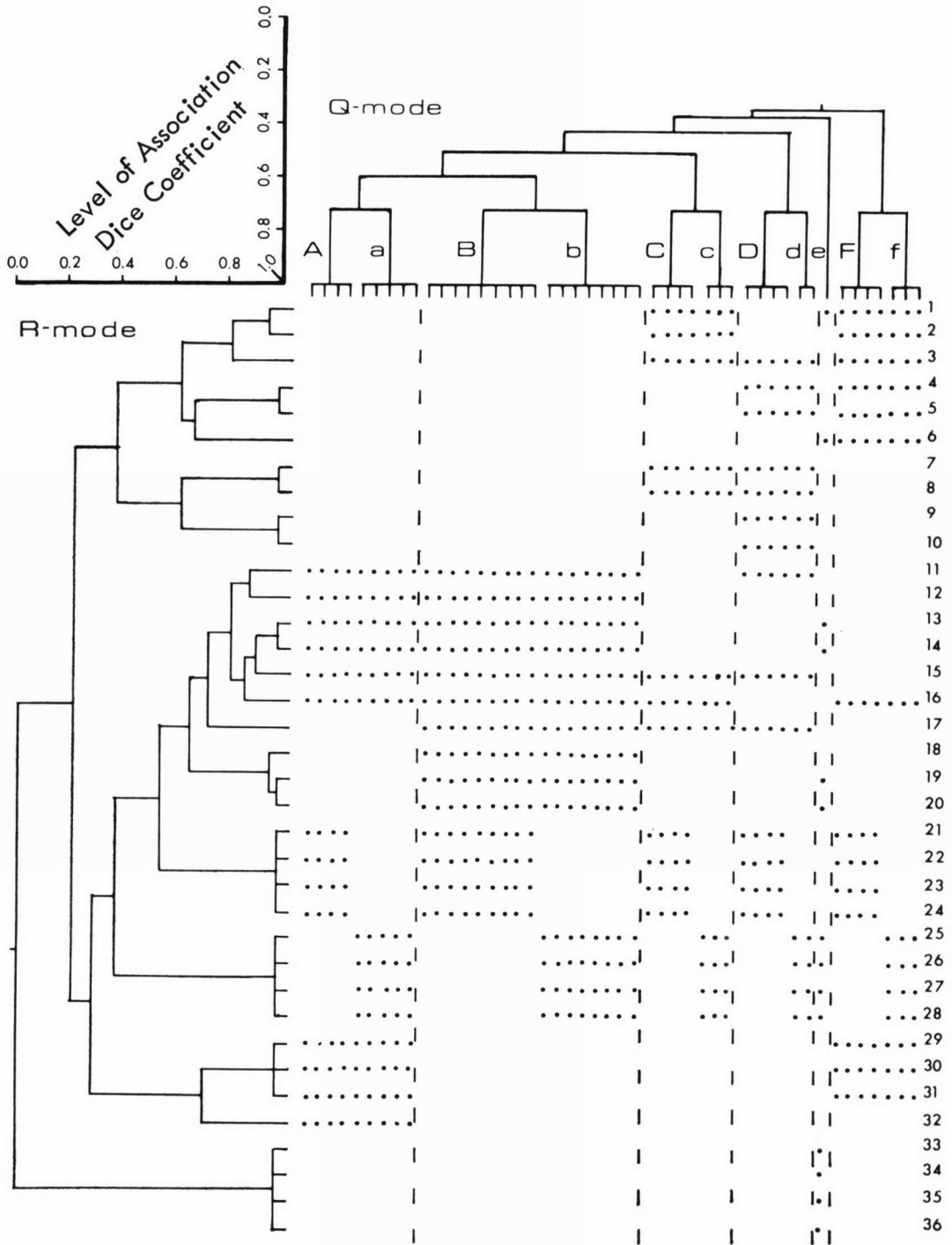


FIG. 6. Two-way cluster analysis of the nominal data of the 6 species of *Scaphites*. The degree with which each species is related to the other five, in terms of morphologic similarity, is illustrated by the dot pattern and represented by the hierarchical Q-mode dendrogram. An interdependence among variables is suggested by the R-mode dendrogram. Explanation of alphanumeric symbols on facing page.

and, because they occur in each species, are not useful in this comparison.

The overriding influence of the maximum and minimum diameter of the specimens suggests a strong growth factor connected to size and shape. The somewhat random grouping of the specimens in Figure 7*a*, is explained as a function of similar or near similar size, analogous to those seen in Figure 5*a*, and 5*b*. The R-mode dendrogram clusters those individuals with similar overall measurements. Consequently, there are differences in the levels of association between specimens of the same species. The mixing of a few microconchs with macroconchs and vice versa is expected on the basis of previous bivariate plots (see Fig. 5*a,b*). Separation of the genus into dimorphic groups is reasonably accurate. In R-mode, the most strongly correlated characters are maximum and minimum diameter of each specimen, and length of body chamber (1-3) and whorl width and height (5 and 6). The measurement of only these five characters would have been sufficient to produce the same results, particularly regarding dimorphism. The counting of characters of ornamentation (11, 14-17) was only marginally important in the distinction of species as evidenced by the levels of association. Because the ornamentation of both sexes of the same species is

generally the same, these characters were not useful in the recognition of dimorphism.

Representation of the correlation between modes as in Figure 6 is not practical with ratio and ordinal data. The analysis illustrates that this type of data is decidedly inadequate for discerning species with the techniques employed, but reasonably reliable for determining dimorphism. Separation of specimens into two almost mutually exclusive groups based on size supports the hypothesis that relative size differences within ammonite genera and species can be used as a rough estimation of sexual dimorphism.

Finally, a disclaimer is added with reference to the occurrence in the ratio data of redundant variables such as a few of the dimorphic variables in the nominal data, and especially maximum (Dg) and minimum (Ds) specimen diameter and length of body chamber (LC). It is known that the existence of redundant or repetitious variables will influence the similarity coefficients and tend to inflate them. These variables affect the Dice Coefficient more than other measures of similarity because the Dice algorithm puts the greatest emphasis on positive matches. A subsequent analysis without the redundant variables reduced the value of all similarity coefficients, but did not alter the basic structure of the dendrogram.

CONCLUSIONS

The 47 well-preserved body chambers and conchs of *Scaphites* examined in this study yielded the following information:

1) Five species of the subgenus *Scaphites* (*Scaphites*) were found to exist in the Blue Hill

Shale Member of the Carlile Shale. Two of these have previously been described as *Scaphites* (*S.*) *arcadiensis* Moreman and *Scaphites* (*S.*) *carlilensis* Morrow, but only the latter had been reported from this member. The three remaining taxa,

Q-mode

A. *carlilensis* (M). a. *carlilensis* (m). B. *inflexus* (M). b. *inflexus* (m). C. *arcadiensis* (M). c. *arcadiensis* (m). D. *hattini* (M). d. *hattini* (m). e. *kansiensis* (m). F. *mittchellensis* (M). f. *mittchellensis* (m).

R-mode

1. Body chamber loosely recurved. 2. Bullae distantly spaced. 3. Umbilical ribs moderately pronounced. 4. Body chamber shaft slightly curved. 5. Aperture depressed. 6. Umbilical ribs rectiradial. 7. Ventral ribs distantly equispaced then approximated. 8. Bullae greatly pronounced. 9. Bullae very distantly spaced. 10. Both nodes and bullae present. 11. Body chamber tightly recurved. 12. Umbilical ribs greatly pronounced. 13. Body chamber shaft well curved. 14. Aperture normal. 15. Umbilical

ribs rursiradial. 16. No nodes on body chamber. 17. Ventral intercalary ribs straight and then projected. 18. Ventral and intercalary ribs approximated from base of body chamber. 19,20. No bullae present on body chamber. 21. Specimen robust. 22. Specimen involute. 23. Umbilical swelling present. 24. Umbilicus deep. 25. Specimen slender. 26. Specimen evolute. 27. No umbilical swelling. 28. Umbilicus shallow. 29. Ventral and intercalary ribs straight. 30. Ventral and intercalary ribs moderately equispaced and then approximated. 31. Bullae moderately pronounced. 32. Bullae normally spaced. 33. Umbilical ribs slightly pronounced. 34. Ventral and intercalary ribs projected. 35. Closely equispaced and then approximated. 36. Nodes present on body chamber. [Note: 21-28 are dimorphic characters.]

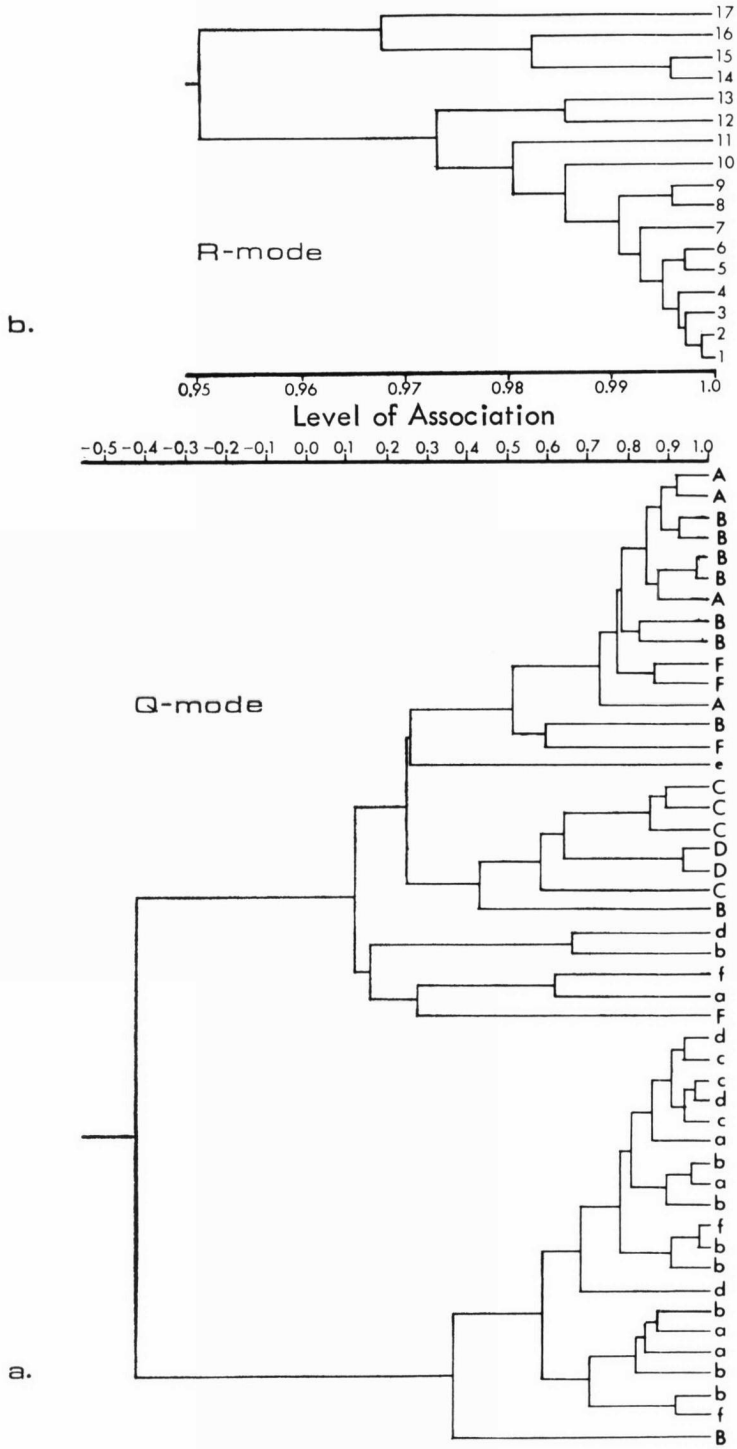


FIG. 7. (See facing page.)

Scaphites (*S.*) *inflexus*, *S.* (*S.*) *mitchellensis*, and *S.* (*S.*) *hattini*, are new species.

2) A new species of the subgenus *Scaphites* (*Hoploscaphites*) can be distinguished from *S.* (*Scaphites*). The occurrence of *S.* (*H.*) *kansiensis* in strata of Turonian age in north-central Kansas significantly expands the stratigraphic and geographic range of the subgenus.

3) All members of the six species were observed to be adult and dimorphic, possessing characteristics attributable to either female or male forms. Specimens so observed are designated either macroconchs for female or microconchs for male. A few submacroscopic juveniles were found in *Scaphites* (*Scaphites*) macroconch body chambers.

4) Specimens of *Scaphites* were found to be limited to a narrow zone between two horizons of large septarian concretions and not ubiquitous throughout the member as previously reported.

Although the recognition of two previously described species and the establishment of four new species is based primarily on the 47 specimens listed and described above, nearly 200 additional specimens ranging from fragmental body chambers to incomplete phragmocones were collected and examined. Whereas the majority of these fragmental or incomplete body chambers can be identified as belonging to five of the six species named above (*S.* (*H.*) *kansiensis* excluded), the incomplete or fragmental phragmocones are useless for reasons already outlined. The fragmental body chambers did not form an integral part of this study because neither accurate measurements nor reasonable estimates could be made.

The occurrence of six congeneric species dis-

tributed randomly throughout the stratigraphic range of the zone is defended on the basis of sympatry and endemism. The existence of a broad, shallow, epeiric sea extending through the Western Interior of North America is well documented and widely accepted (for a recent comprehensive discussion, see Kennedy & Cobban, 1976, p. 60). The reduced salinities of this seaway, resulting from restricted connections with the open sea, presumably led to hyposaline groups with low diversities and high degrees of intrageneric variability. Young (1972) has summarized the causal factors of these restrictions and suggested several evolutionary pathways by which groups of ammonites, such as *Scaphites*, could have developed endemic faunas. Endemism is further supported when contrasting scaphitids of the Western Interior of North America with those outside this province. The endemic forms of the late Cretaceous seaway developed progressively in terms of mode of recoiling and suture complexity, those outside of this center of endemism remained simple in terms of sutural complexity and mode of recoiling (Wiedmann, 1965).

Quantitative analysis of the data presented herein supports the descriptive methods in the assignment of the scaphite forms to six species and the placement of the large and small forms of each species in macroconch (female) and microconch (male) categories, respectively. Previously observed variations within *Scaphites* in the Blue Hill Shale Member are shown to be attributable to the presence of five species of *S.* (*Scaphites*), one species of *S.* (*Hoploscaphites*), and the existence of sexual dimorphism in each species.

FIG. 7. Dendrograms produced from correlation matrices of ratio and ordinal data; 7,a, Q-mode. Generally a clean separation is illustrated between macroconchs in the top half of the dendrogram and microconchs in the bottom half. Mixing of macroconchs and microconchs near the point of separation is explained in the text (also, see Fig. 5,a, b). Appearance of *Scaphites* (*H.*) *kansiensis* (c) high in the macroconchs is similarly explained; 7,b, R-mode. Variables 1-10, 12, 13 are ratio data, variables 11, 14-17 are ordinal data. Explanation of the Q-mode symbols is given in caption to Figure 6. [Explanation of numeric symbols: 1, *Dg*; 2, *Ds*; 3, *LC*; 4, radius of septate whorls; 5, *WW*; 6, *WH*; 7, *Wh* ($Wh - ud = Wh$); 8, radius of body chamber; 9, height of aperture; 10, width of aperture; 11, *nUR*; 12, *UW*; 13, *ud*; 14, *nN*; 15, *nB*; 16, *nVR*; 17, *nIR*. See Fig. 3,a, c and d for the location of ratio measurements.]

REFERENCES

- Agassiz, Louis, 1847, An introduction to the study of natural history: 58 p., Greeley & McElrath (New York).
- Arkell, W. J., 1957, Introduction to Mesozoic Ammonoidea: in Treatise on invertebrate paleontology, R. C. Moore (ed.), Part L, Mollusca 4, p. L81-L129, Geol. Soc. America and Univ. Kansas Press (New York and Lawrence, Kans.).
- , Kummel, Bernhard, Miller, A. K., & Wright, C. W., 1957, Morphological terms applied to Ammonoidea: in Treatise on invertebrate paleontology, R. C. Moore (ed.), Part L, Mollusca 4, L2-L6, Geol. Soc. America and Univ. Kansas Press (New York and Lawrence, Kans.).
- , ———, & Wright, C. W., 1957, Systematic descriptions: in Treatise on invertebrate paleontology, R. C. Moore (ed.), Part L, Mollusca 4, p. L180-L436, Geol. Soc. America and Univ. Kansas Press (New York and Lawrence, Kans.).
- Birkelund, Tove, 1965, Ammonites from the Upper Cretaceous of West Greenland: Medd. om Grønland, v. 179, no. 7, 192 p., 49 pl.
- Blainville, M. H. D. de, 1840, Prodrôme d'une monographie des ammonites: Extrait du Supplément du Dictionnaire des Sciences Naturelles, 34 p., Bertrand (Paris).
- Brinkmann, Roland, 1929, Statistisch-biostratigraphische Untersuchungen an mitteljurassischen Ammoniten über Artbegriff und Stammesentwicklung: Ges. Wiss. Göttingen, Abh., Math.-phys. Kl., n. ser., no. 13, p. 1-249, pl. 1-5.
- Callomon, J. H., 1955, The ammonite succession in the Lower Oxford Clay and Kellaway beds at Kidlington, Oxfordshire, and the zones of the Callovian Stage: Roy. Soc. London, Philos. Trans., ser. B, v. 239, p. 215-264, pl. 3, 4.———1963, Sexual dimorphism in Jurassic ammonites: Leicester Lit. Philos. Soc., Trans., no. 57, 56 p., 1 pl.———1969, Dimorphism in Jurassic ammonites; some reflections: in Sexual dimorphism in fossil Metazoa and taxonomic implications, G.E.G. Westermann (ed.), Internat. Union Geol. Sci., ser. A, no. 1, p. 111-121.
- Cobban, W. A., 1951, Scaphitoid cephalopods of the Colorado Group: U.S. Geol. Surv., Prof. Paper 239, 42 p., 21 pl.———1969, The Late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (Dekay) in the western interior of the United States: U.S. Geol. Surv., Prof. Pap. 619, 29 p., 5 pl.
- , & Jeletzky, J. A., 1965, A new scaphite from the Campanian rocks of the Western Interior of North America: J. Paleontol., v. 39, no. 5, p. 794-801, pl. 95, 96.
- , & Scott, G. R., 1972, Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, Colorado: U.S. Geol. Survey, Prof. Pap. 645, 108 p., 49 pl.
- Crick, R. C., 1976, Morphological variations in the ammonite genus *Scaphites* of the Blue Hill Member, Carlile Shale, Upper Cretaceous, Kansas: unpub. master's thesis, Univ. Kansas, 87 p., 4 pl.
- Cuvier, Georges, 1797, Tableau élémentaire de l'histoire naturelle des animaux: xvi + 710 p., 14 pl., Boudouin (Paris).
- Dice, L. R., 1945, Measures of the amount of ecologic association between species: Ecology, v. 26, p. 297-302.
- Douvillé, Henri, 1881, Note sur l'Ammonite pseudo-anceps et sur la forme de son ouverture: Soc. Géol. Fr., Bull., sér. 3, v. 8, p. 239-246.
- Foord, A. H., & Crick, G. C., 1897, Catalogue of the fossil Cephalopoda in the British Museum (Natural History): pt. 3, 303 p., printed by order of the Trustees (London).
- Glandgeaud, Philippe, 1897, Sur la forme de l'ouverture de quelques ammonites: Soc. Géol. Fr., Bull., sér. 3, v. 25, p. 99-107.
- Hattin, D. E., 1952, The megascopic invertebrate fossils of the Carlile Shale of Kansas: unpub. master's thesis, Univ. Kansas, 112 p., 10 pl.———1962, Stratigraphy of the Carlile Shale (Upper Cretaceous) in Kansas: Kansas Geol. Surv., Bull. 156, 155 p., 27 pl.———1965, Upper Cretaceous stratigraphy, paleontology, and paleoecology of western Kansas: in Geol. Soc. Am., Field Conf. Guidebook (1965), 69 p., 18 fig.
- Jeletzky, J. A., 1949, *Scaphites morrowi*, new name for *Scaphites pygmaeus* Morrow 1935, non Holzapfel, 1888: J. Paleontol., v. 23, no. 3, p. 330.
- Kennedy, W. J., & Cobban, W. A., 1976, Aspects of ammonite biology, biogeography, and biostratigraphy: Spec. Pap. Paleontology, no. 12, 94 p., 17 pl.
- Lehmann, Ulrich, 1966, Dimorphismus bei Ammoniten der Ahrensburger Lias-Geschiebe: Paläontol. Z., no. 40, p. 26-55.———1971, New aspects in ammonite biology: North Am. Paleontol. Conv. (1969), Proc., E. L. Yochelson (ed.), pt. 1, p. 1251-1269, Allen Press, Inc. (Lawrence, Kans.).
- Logan, W. N., 1897, The Upper Cretaceous of Kansas: Kansas Geol. Survey, v. 2, p. 195-234, pl. 29-34.———1898, The invertebrates of the Benton, Niobrara, and Fort Pierre Groups: Kansas Geol. Surv., v. 4, Paleontol., pt. 1 (pt. 8), p. 433-518, pl. 86-120.
- Makowski, Henryk, 1962a, Problem of sexual dimorphism in ammonites: Palaeontol. Polonica, no. 12, 92 p., 20 pl.———1962b, Recherches sur le dimorphisme sexuel chez les Ammonoïdes: in Księga Pamiatkowa ku czci Profesora Jana Samsonowicza (Book in memory of Professor Jan Samsonowicz), Polska Akad. Nauk, Kom. Geol., p. 31-55, pl. 8-11 (Warsaw).
- Mangold, Kaethi, & Fioroni, P., 1966, Morphologie et biométrie des mandibules de quelques céphalopodes Méditerranéens: Vie et Milieu, v. 17, no. 3, sér. A, p. 1139-1196.
- Mangold-Wirz, Kaethi, 1963, Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane: Vie et Milieu, suppl. no. 13, 225 p.
- Meeq, F. B., 1876, A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country: in U.S. Geol. Survey Terr., Rept., v. 9, 629 p., 45 pl.
- Moreman, W. L., 1942, Paleontology of the Eagle Ford Group of north and central Texas: J. Paleontol., v. 16, no. 2, p. 192-220, pl. 31-34.
- Morrow, A. L., 1931, A study of the invertebrate fauna of the Colorado Group: unpub. master's thesis, Univ.

- Kansas, 70 p., 60 pl.—1935, Cephalopods from the Upper Cretaceous of Kansas: *J. Paleontol.*, v. 9, no. 6, p. 463-473, pl. 49-53.
- Müller, A. H., 1969, Ammoniten mit "Eierbeutel" und die Frage nach dem Sexual-Dimorphism der Ceratitiden (Cephalopoda): *Dtsch. Akad. Wiss. Berlin, Monatsber.*, no. 11, p. 411-420.
- Munier-Chalmas, E. C. P. A., 1892, Sur la possibilité d'admettre un dimorphisme sexuel chez les Ammonitides: *Soc. Géol. Fr., Bull., Compte Rendu, sér. 3*, v. 20, p. 170-174.
- Nowak, Jan, 1912, Die Skaphiten, Part 2 of Untersuchungen über die Cephalopoden der oberen Kreide in Polen: *Acad. Sci. Cracovie, Bull. Internat.*, 1911, ser. B, p. 547-589.
- Orbigny, Alcide d', 1847, Paléontologie Française, Terrain jurassique: T. Premier, Céphalopodes, 642 p., 234 pl., Masson et Cie (Paris).
- Parkinson, James, 1811, Organic remains of a former world: v. 3, 479 p., 22 pl., Benjamin Meredith (London).
- Quenstedt, F. A., 1886-87, Die Ammoniten des Schwäbischen Jura: v. 2, Der Braune Jura, p. 441-815, E. Schweizerbart (Stuttgart).
- Reeside, J. B., 1927a, Cephalopods from the lower part of the Cody Shale of Oregon Basin, Wyoming: *U.S. Geol. Surv., Prof. Pap. 150-A*, p. 1-10, pl. 1-8.—1927b, The scaphites, an Upper Cretaceous ammonite group: *U.S. Geol. Surv., Prof. Pap. 150-B*, p. 21-39, pl. 9-11.—1927c, The cephalopods of the Eagle Sandstone and related formations in the Western Interior of the United States: *U.S. Geol. Surv., Prof. Pap. 151*, 87 p., 45 pl.
- Reynès, Paul, 1879, Monographie des ammonites, avec une introduction par M. Le Dr. P. de Rouville: 72 p., Atlas, J.-B. Baillière (Paris).
- Rohlf, F. J., Kishpaugh, J., & Kirk, D., 1974, Numerical taxonomy system of multivariate statistical programs: State Univ. New York at Stony Brook, Tech. Rept., p. 95 (New York).
- Rollier, Louis, 1913, Sur quelques Ammonitoides jurassiques et leur dimorphisme sexuel: *Arch. Sci. phys. nat., sér. 4*, v. 35, p. 263-288.
- Sepkoski, J. J., Jr., & Rex, M. A., 1974, Distribution of freshwater mussels: Coastal rivers as biogeographic islands: *Syst. Zool.*, v. 23, no. 2, p. 165-188.
- Sokal, R. R., & Sneath, P. H. A., 1963, Principles of numerical taxonomy: 359 p., W. H. Freeman & Company (San Francisco).
- Sowerby, James, 1813, The mineral conchology of Great Britain: vol. I, 243 p., 102 pl., Benjamin Meredith (London).—1818, The mineral conchology of Great Britain: vol. II, 251 p., pl. 103-203, Benjamin Meredith (London).
- Stanton, T. W., 1893, The Colorado Formation and its invertebrate fauna: *U.S. Geol. Surv., Bull. 106*, 282 p., 45 pl.
- Waagen, Wilhelm, 1869, Über die Formenreihe des Ammonites subradiatus: *Geogn.-Paläontol., Beitr.*, v. 2, p. 181-256, pl. 16-20.
- Westermann, G. E. G., 1954, Monographie der Otoitidae: *Geol. Jahrb., Beih. no. 15*, 364 p., 33 pl.—1964, Sexual-Dimorphismus bei Ammonoitiden und seine Bedeutung für die Taxonomie der Otoitidae: *Palaeontogr.*, v. 124, pt. A, p. 33-74, pl. 6-9.—1969, Supplement: Sexual dimorphism, migration, and segregation in living cephalopods: in Sexual dimorphism in fossil metazoa and taxonomic implications, G. E. G. Westermann (ed.), *Internat. Union Geol. Sci., ser. A*, no. 1, p. 18-20.—1971, Form, structure and function of shell and siphuncle in coiled Mesozoic ammonoids: *Roy. Ontario Mus., Life Sci. Contrib.* 78, 39 p.
- Whitfield, R. P., 1880, Paleontology of the Black Hills of Dakota: in Report on the geology and resources of the Black Hills of Dakota, Henry Newton & W. P. Jenny, *U.S. Geol. Surv. Rocky Mtn. Reg.*, p. 325-468.
- Wiedmann, Jost, 1965, Origin, limits, and systematic position of *Scaphites*: *Palaeontol.*, v. 8, no. 3, p. 397-453, pl. 53-60.
- Young, Keith, 1972, Cretaceous paleogeography: Implications of endemic ammonite faunas: *Univ. Texas, Bur. Econ. Geol., Geol. Circ. no. 72-2*, 13 p.
- Zeller, D. E., 1968, The stratigraphic succession in Kansas: *Kansas State Geol. Surv., Bull. 189*, 81 p.

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EXPLANATION OF PLATES

[All figures natural size. Arrows indicate base of body chambers.]

PLATE 1

FIGURE

- 1-5. *Scaphites (Scaphites) arcadiensis* Moreman.—1. Side view of complete macroconch, KUMIP 108769.—2. Side view of macroconch body chamber, KUMIP 108765.—3. View of base of macroconch body chamber, KUMIP 108768.—4,5. Views of side and base of microconch body chamber, KUMIP 108772.
6-10. *Scaphites (Scaphites) carlilensis* Morrow.—6.

FIGURE

- Side view of complete macroconch, KUMIP 108774.—7. View of base of macroconch body chamber, KUMIP 108781.—8,9. Side views of complete microconch, KUMIP 108776.—10. View of base of microconch body chamber, KUMIP 108780.
11-12. *Scaphites (Hoploscaphites) kansiensis* Crick, n. sp.—11,12. Side views of complete microconch holotype, KUMIP 108770.

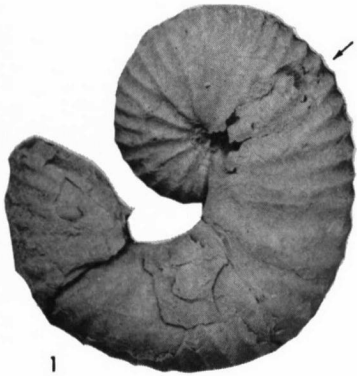
PLATE 2

FIGURE

- 1-5. *Scaphites (Scaphites) hattini* Crick, n. sp.—1,3. Side views of the complete macroconch holotype, KUMIP 108807.—2. View of base of macroconch body chamber, KUMIP 108818.—4,5. Views of side and base of microconch body chamber, KUMIP 108811.
6-9. *Scaphites (Scaphites) mitchellensis* Crick, n. sp.—6. Side view of complete macroconch holotype, KUMIP 108784.—7. View of base of macroconch body chamber, KUMIP 108784.—8. Side view of

FIGURE

- microconch body chamber, KUMIP 108787.—9. View of base of microconch body chamber, KUMIP 108815.
10-13. *Scaphites (Scaphites) inflexus* Crick, n. sp.—10. Side view of the body chamber of the macroconch, KUMIP 108790.—11. View of base of macroconch body chamber, KUMIP 108792.—12. Side view of microconch body chamber, KUMIP 108793.—13. View of base of microconch body chamber, KUMIP 108796.



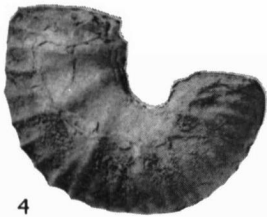
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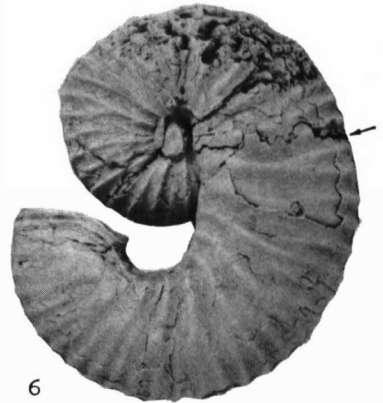
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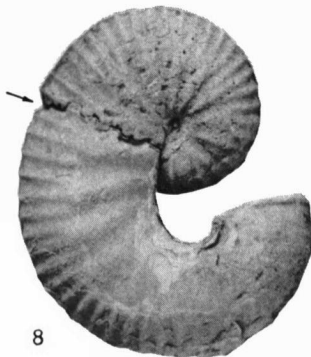
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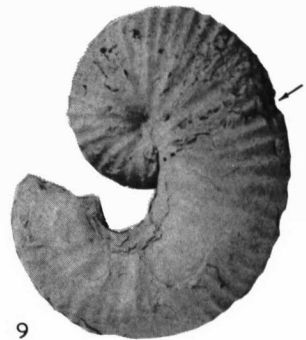
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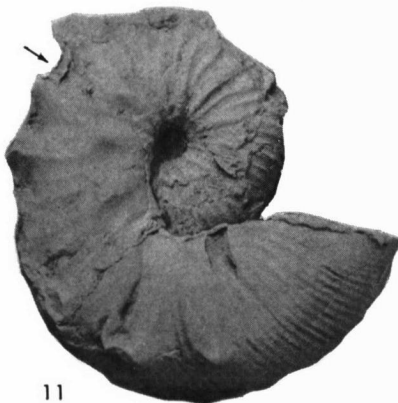
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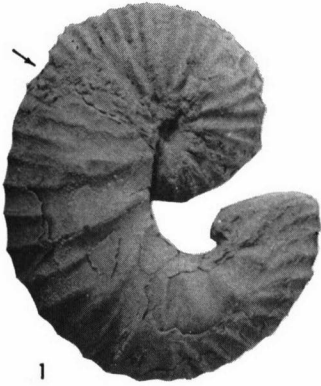
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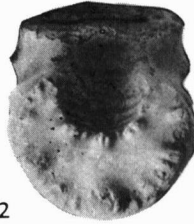
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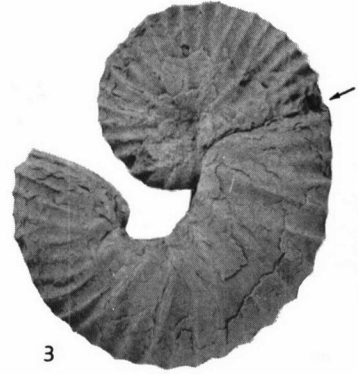
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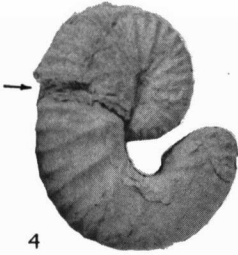
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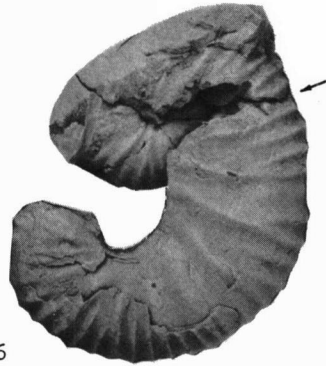
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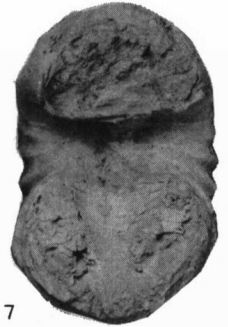
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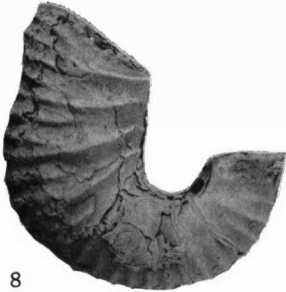
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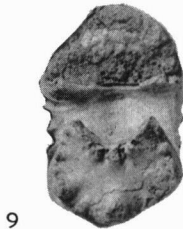
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