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(WITH FIVE PLATES)

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# CRETACEOUS THYASIRA FROM THE WESTERN INTERIOR OF NORTH AMERICA

By ERLE G. KAUFFMAN

*U. S. National Museum*
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(With Five Plates)

## ABSTRACT

The unique lucinoid *Thyasira* is represented in the Western Interior Cretaceous by 7 new species and 10 new subspecies distributed through 11 Campanian ammonite zones. Two species complexes are recognized, containing five evolving lineages with Atlantic Realm affinities. Early Campanian radiation of one stock occurs prior to introduction of *Thyasira* into the Interior with southern migration of arctic waters; abrupt Late Campanian radiation of the second stock accompanies replacement of the initial complex. Southern migration of *Thyasira* proceeds through the Campanian; it disappears from the Interior during the Late Campanian, having attained maximum southern migration. The morphology, ecology, and anatomy of *Thyasira* are similar in Cretaceous and living species; evolution has been conservative since the Cretaceous. The initial phylogenetic derivation of *Thyasira* is not documented in the fossil record but may lie in deep-water deposits. Primary evolutionary trends in Cretaceous lineages are: (1) reduction of convexity; (2) elongation of the height (burrowing) axis; (3) reduction of projecting flanks; and (4) size restriction, straightening, and posterior migration of the primary sulcus. These are adaptive trends for more rapid, efficient burrowing, or reflect anatomical modifications related to change in shell form. Living *Thyasira* are anatomically unique, and adapted to life in cool waters of low productivity, usually on the outer shelf and slope, commonly in dark mud, oxygen-poor, hydrogen sulfide-rich substrate supporting a restricted molluscan assemblage. Creta-

ceous species show similar substrate and molluscan associations, adaptive features, and latitude distribution. They are excellent paleoecologic indicators of the restricted habitat preferred by contemporary species.

## INTRODUCTION

The lucinoid genus *Thyasira* contains anatomically unique bivalves adapted to restricted cool water, infaunal habitats, including oxygen-poor and/or hydrogen sulfide-rich environments with a limited food supply and an otherwise impoverished molluscan assemblage. The shell is relatively simple—thin, fragile, edentulous or pseudodentate, normally with two posterior folds and sulci, and lacking in ornamentation other than growth lines. Generic and subgeneric classification is based entirely on the shell, and is a matter of controversy among malacologists. The anatomy and ecology of living *Thyasira* have been of considerable interest to biologists and are well documented. Conversely, the fossil *Thyasira,* and in particular the ancestral Mesozoic forms, are poorly known.

In North America, the genus *Thyasira* has been recorded only from Cretaceous and younger rocks, and the fossil record is sparse. The Cretaceous Pacific Coast Thyasiridae are generally distinct from those in the Western Interior and Atlantic Provinces, a condition which generally has persisted to the present. The Cretaceous Indo-Pacific forms (group of *"Thyasira" cretacea* Whiteaves) have been generally treated taxonomically, but no species have been previously described from the Western Interior and only scattered reports of thyasirid genera have been published from this area.

In recent years, numerous well-preserved specimens of *Thyasira* have been found in middle Lower through middle Upper Campanian rocks of the Western Interior United States and Canada (Pierre Shale and equivalents), distributed through nine *Baculites* zones (as established by W.A. Cobban, 1958, p. 660; 1962, p. 704-706; 1964, fig. 2; personal communication), with a total range transgressing 11 ammonite zones, at 20 distinct stratigraphic levels. Many of these were discovered in conjunction with the U.S. Geological Survey's Pierre Shale Project. These collections, which contain good adult populations from several levels, form the basis for this study.

The Western Interior Cretaceous *Thyasira* belong to 7 new species and 10 new subspecies which are distributed into 2 principal species complexes with predominantly Atlantic Realm affinities. Inasmuch as the shell is not complex and the primary radiation of *Thyasira* apparently took place prior to the Upper Cretaceous, evolution within the genus has been demonstrably conservative from Cretaceous to Recent times. The differences between species and subspecies within any lineage are not dramatic, and can best be recognized through basic biometric analysis of ontogentic and adult variation suites of specimens. Each species group exhibits small-scale evolutionary change in the Cretaceous, primarily in the outline and measured angles of the shell, in the development, position and curvature of the beaks, umbos, and sulci, in convexity, and in the development of the lunule and escutcheon. The expected variation within fossil species, and the taxonomic and evolutionary significance of differences shown by chronologically successive populations of Cretaceous *Thyasira* are in part defined here by studies in variation of the large, morphologically similar living species, *Thyasira sarsi* (Phillipi) (=*C. insignis* Verrill and Bush; fide Ockelmann, 1961, p. 51). Based on radiometric dating the average evolutionary rate of Upper Cretaceous species of *Thyasira* is 2.3 million years, and of subspecies 0.86 million years (text fig. 1). These are coincident or slightly longer periods than found for species of ammonites (primarily *Baculites*) during the same period, but are restricted enough to make *Thyasira* useful in dating and biostratigraphic correlation of Cretaceous units. Evolutionary changes in the morphology of *Thyasira* are primarily concerned with better adaptation of the shell for rapid, efficient burrowing and anatomical modifications resulting from changes in shell morphology.

The conservative evolution of the shell in *Thyasira* observed since the Cretaceous is also demonstrated by the anatomy of the animal. The many unusual anatomical features of living *Thyasira* are reflected wholly or in part by the interior morphology of the shell (muscle impressions, pallial line, etc.), forming a basis for the interpretation of paleoanatomy, and the study of functional morphology in the Cretaceous species. A thorough study of Recent species was necessary before paleontologic interpretation could be attempted. Among the outstanding anatomical modifications of Recent *Thyasira* are: (a) loss of posterior siphons, and abnormal development and function of posterior exhalent and inhalent apertures; (b) a highly modified foot approximately 10 times the length of the body; (c) an anterior inhalent tube of mucous cemented sediment formed by the foot; (d) a modified anterior adductor muscle; and (e) modifications of the stomach, and reduction of the palps and sorting mechanisms of the gills as an adaptation for feeding on larger particles; and many other diversions from the normal pattern of infaunal bivalve anatomy.

The interior morphology of Cretaceous *Thyasira* strongly indicates that by the Late Cretaceous, the Thyasiridae had already developed most of the unusual anatomical features which characterize the modern species. Little basic change took place in the genus during the Tertiary. The early steps in the development of the Thyasiridae from primitive Lucinacea are not yet known and apparently took place in the Early Cretaceous or prior to the Cretaceous.

The study of Cretaceous *Thyasira* is of additional significance because of its potential contribution to paleoecologic interpretations in Western Interior strata. Inasmuch as structural analysis indicates that Cretaceous and Recent species were similarly adapted for infaunal living, and the anatomy and ecology of living forms is well known, it is logical to assume that rather precise paleoecologic interpretations can be based on the form and inferred anatomy, and faunal associates of the fossil species. Living species of *Thyasira* are widespread in both the Indo-Pacific and Atlantic Realms. Their distribution is predominantly controlled by substrate and water temperature; most living *Thyasira* display a marked preference for dark organic clay mud and sandy clay substrate in cool waters. The bathymetric range of many species deepens toward the southern end of their geographic range in response to temperature control on distribution. Some close parallels can be drawn with the distribution of Cretaceous *Thyasira* of the Western Interior of North America.

The collections used in this study comprise the great majority of Cretaceous *Thyasira* found to date in the Western Interior of North America and represent the entire collection of the Geological Survey of Canada, the Denver and Washington offices of the United States Geological Survey, and the Smithsonian Institution. Several major universities were canvassed but had no specimens in their collections. Type specimens are deposited in the collections of the United States National Museum (USNM) and the Geological Survey of Canada (GSC).

## ACKNOWLEDGMENTS

Dr. William A. Cobban of the United States Geological Survey first brought the problem of the Western Interior Cretaceous *Thyasira* to my attention, made available the bulk of the collections used in this study, and was an invaluable source of information concerning stratigraphic position of collections, and faunal and lithologic asso-

ciates of *Thyasira.* Dr. J.A. Jeletzky of the Geological Survey of Canada arranged for the loan of Canadian Cretaceous *Thyasira* and provided much useful information on their stratigraphic position. Dr. Alfred Rosenkrantz, Mineralogisk Museum, Copenhagen, Denmark, graciously furnished me with information regarding the Greenland Thyasiridae. Conversations with Dr. A. Lee McAlester of Yale University, Dr. Kenneth Boss of the Museum of Comparative Zoology, Harvard University, and Dr. David Nicol of the University of Florida proved highly rewarding. Drs. Cobban, Boss, and Richard E. Grant of the U.S. Geological Survey reviewed the manuscript and offered valuable criticism.

I am grateful to Robert Beauchamp, research assistant on the project, for the many hours he spent in cleaning and measuring specimens and plotting data, to Lawrence B. Isham, who did the drawings and drafting, and to Jack Scott and Andrew Wynn for their assistance in photography. All of these men are members of the U.S. National Museum staff.

## HISTORY OF WORK ON NORTH AMERICAN CRETACEOUS THYASIRIDAE

The Cretaceous Thyasiridae of the Pacific Coast were generally studied long before the family was known to be represented in rocks of the Western Interior. Whiteaves (1873, 1874, p. 266, figs. 2, 2a on fossil plate) described the first Indo-Pacific species, *Conchocele cretacea,* from the Cretaceous of Vancouver Island, assigning the same specimens in 1904 (p. 383) to the genus *Thyasira.* Anderson (1958, p. 133) noted *T. cretacea* at several localities in the "Coniacian" of California, associated with *Metaplacenticeras pacificum.* Matsumoto (1959, p. 136) has subsequently established the age of this zone as Late Campanian. Restudy of this material will probably show that more than one species occurs under the broad concept of *T. cretacea.*

Forms closely related to *T. cretacea* and in the same species group were subsequently described by White (1890, p. 14, pl. 3, figs. 1, 2) from Brazil as *Lucina? townsendi.* Wilckens (1910, p. 53, pl. 2, figs. 31a, 32; pl. 3, fig. 1) noted this species, which he assigned to *Thyasira,* and *T. excentrica* (1920, p. 11) from the Cretaceous of the Antarctic. Wetzel (1930, p. 77) noted a *Thyasira* sp. in the Cretaceous of Chile which appears to belong to this lineage. No species in this group have been found in the Western Interior Cretaceous and there is some doubt as to whether the Pacific and

Interior Thyasiridae even belong to the same genus or subgenus. Although many modern workers place species of the *T. cretacea* type in *Thyasira* (see Keen, 1963, p. 56), there is justifiable recent trend to split off some of the basic morphologic groups of sulcate Thyasiridae which have been well established through the Tertiary into distinct genera or subgenera (see Iredale, 1930). Restudy of the family following this taxonomic philosophy will probably result in the *T. cretacea* lineage of the Pacific Coast being assigned to either one of the old generic names no longer in use (i.e., *Conchocele*) or to one of Iredale's finely split genera (1930, p. 393), such as *Prothyasira*.

The first report of Cretaceous Thyasiridae in the Western Interior of North America and faunally related areas of the Western Hemisphere was by Ravn (1918, p. 348, pl. 7, fig. 19) who noted *Axinus* n. sp. from the Senonian of West Greenland. This strongly bisulcate form belongs to a species group which is distinct from those developed in the Western Interior of Canada and the United States, and seems to combine characters of *Thyasira* s.s. and *Prothyasira* Iredale, 1930. Rosenkrantz (1942, p. 277, 278) discussed some Cenozoic *Thyasira* from Greenland and noted that the oldest representatives in this hemisphere were found in the Santonian and Campanian of the Antarctic. R.A.C. Brown (1942, p. 147) did the most extensive previous work with the Western Interior Thyasiridae, noting that new species had been found in the Late Upper Cretaceous of southwestern Manitoba, east-central Alberta, and northern Alberta, Canada. Although Brown apparently described the species in an address to the Royal Society of Canada (1942), and assigned manuscript names to a new species and two subspecies, this work was never published. According to Jeletzky (personal communication, 1964) the specimens were left in the collections of the Geological Survey of Canada by Brown, who stated no intent to publish on them. Attempts to locate Brown through the Geological Survey of Canada to confirm this have not been successful. His specimens are included in this study, but his manuscript names have been discarded.

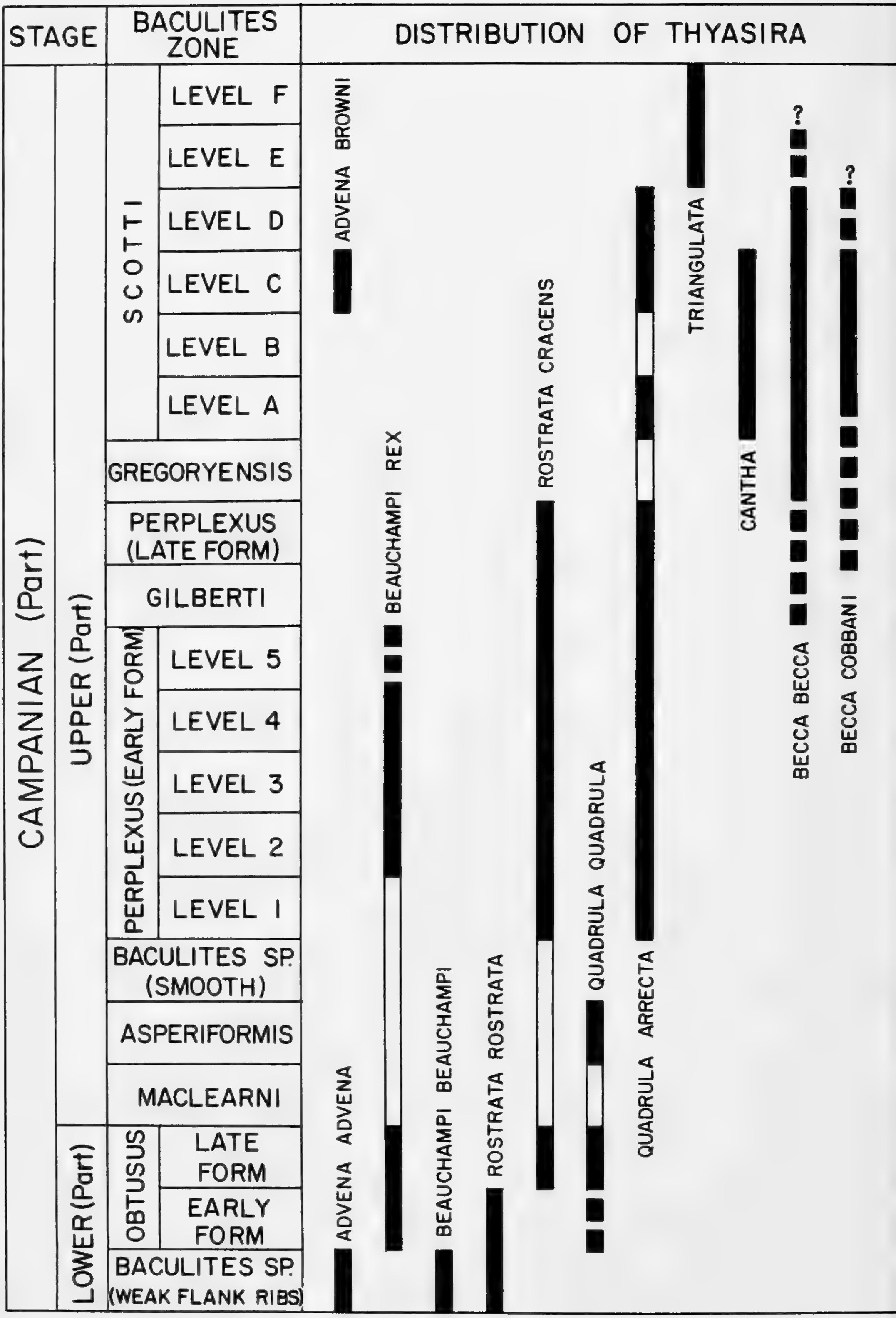
## BIOSTRATIGRAPHY

A primary objective in detailed evolutionary studies of fossils is the application of these data to dating, faunal zonation, and correlation of rock units. Experience has shown that refined and widely applicable faunal zonation is best accomplished through study centered around the phylogenetic development of select groups through time, rather than through formation by formation, whole-fauna studies which generally take a considerably greater amount of time before they are complete enough for the development of detailed biostratigraphic zonation. The historically early development of meaningful zonal criteria for the widespread correlation of Mesozoic rocks, which has long served as a model of biostratigraphic methodology, owes much to the efforts of European and subsequently American paleontologists in phylogenetic studies of important groups such as the ammonites and inoceramid bivalves.

Initial efforts using ammonites produced refined faunal zones based on single species, or only the acme of development of single species. This method eventually proved unreliable owing to faunal crossover of key species, ecologic control on range and occurrence of zonal indices, and numerous other factors. Its failure pointed out the need for faunal zonation based on isochronous assemblages of fossils rather than single species, and this is the prevalent practice of modern biostratigraphy.

By themselves, *Thyasira* and poorly represented groups like them have little stratigraphic value, regardless of how finely the ranges of species and subspecies can be restricted. Cretaceous Thyasiridae are not common in the Western Interior, and at best occur at relatively few levels in any one section. Occurrences of the genus are geographically widespread and would be difficult to relate chronologically were it not for their association with biostratigraphically critical ammonites like *Baculites*. Canadian occurrences of *Thyasira* are even fewer and are not as precisely dated; the ranges of known Canadian forms however do appear to be generally compatible with those in the United States.

*Thyasira* can be employed in the assemblage zone concept, however, where the short-ranging species and subspecies described here are effectively used in combination with other forms to define restricted time zones. *Thyasira* ranges through 11 established ammonite zones and is known from at least 20 stratigraphic levels in the Western Interior (text fig. 1). Individual species have an average time range extending through about 5.5 established ammonite zones. Subspecies of *Thyasira,* which individually have more restricted ranges than the species, have a known average time span of 2.1 ammonite zones (text fig. 1) or approximately 0.86 million years; if the long-ranging subspecies *T. rostrata cracens* n. subsp., *T. beauchampi rex,* n. subsp., and *T. quadrula arrecta,* n. subsp. are omitted, the average range of all other subspecies of *Thyasira* is through 1.5 ammonite zones,



Text Figure 1.

or 0.63 million years. These time spans were calculated by plotting the amount of time represented between the Early Campanian (from a Western Interior radiometric date) and the top of the Campanian (from a German radiometric date), dividing this figure by the number of recognized Western Interior ammonite zones in this part of the Cretaceous, and multiplying the result by the number of ammonite zones transgressed by an average species or subspecies of *Thyasira*. As indicated by the above figures, subspecies of *Thyasira* are sufficiently restricted in their time-stratigraphic range to be valuable additions to the construction of faunal assemblage zones.

In the Cretaceous of the Western Interior, assemblage zones are primarily based at present on ammonites and bivalves of the family Inoceramidae (Cobban and Reeside, 1952, chart 10b; Cobban, 1958, 1962, 1964; Kauffman 1966). Other bivalves have been used sparingly, and gastropods rarely in the construction of assemblage zones because many species within these groups are broadly defined and most genera have not been subjected to phylogenetically oriented studies. Many families have considerable biostratigraphic potential, such as the Turritellidae, Cardiidae, Ostreidae, Mactridae, Pteriidae, and others. At present, the Campanian assemblage zones encompassing the known range of Cretaceous Thyasiridae in the Western Interior, and including species and subspecies of *Thyasira* herein described, might be constructed as follows (all species used as zonal name-bearers range exclusively within each named zone; some data below furnished by W.A. Cobban, personal communication, 1964, 1965):

1. Zone of *Baculites* sp. with weak flank ribs (oldest); also exclusive known range of *Inoceramus vancouverensis* Shumard, *Thyasira advena advena,* n. subsp., and *T. beauchampi beauchampi,* n. subsp. Lower half of the range of *Trachyscaphites praespiniger* Cobban and Scott and *Thyasira rostrata rostrata,* n. subsp. Middle Early Campanian.

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Text Figure 1.—Time-stratigraphic distribution of Cretaceous *Thyasira* from the Western Interior, relative to established ammonite zones. Solid line encloses definitely established range; dark portion shows levels from which species of *Thyasira* have been obtained, light areas are levels which have not yielded a particular species but which are bounded by known occurrences of that species. Dashed lines denote possible extension of species ranges due to uncertainty of particular ammonite zones from which some *Thyasira* were collected. Ammonite zonation and its relationship to European stages taken from Cobban (1958, 1962, personal communication 1964, 1965), Cobban and Scott (1964).

2. Zone of *Baculites obtusus* Meek, early form (Cobban and Scott, 1964, fig. 2). Associated with *Delawarella danei* Young. Upper half of the range of *Trachyscaphites praespiniger* and *Thyasira rostrata rostrata*. Lower third of the range of *Inoceramus agdjakendensis* Aliev and *I. pertenuis* Meek and Hayden (early form). First appearance of *Thyasira beauchampi rex,* n. subsp. and *T. quadrula quadrula,* n. subsp. Late Early Campanian.
3. Zone of *Baculites obtusus* Meek, late form (Cobban and Scott, 1964, fig. 2). Middle part of the range of *Inoceramus agdjakendensis* and *I. pertenuis* (early form). First appearance of *Thyasira rostrata cracens,* n. subsp. Late Early Campanian.
4. Zone of *Baculites mclearni* Landes, also exclusive known range of *Inoceramus azerbaidjanensis* Aliev. Lower half of the range of *Trachyscaphites spiniger porchi* Adkins. Upper third of the range of *I. agdjakendensis.* First occurrence of "noded scaphite n. sp." (Cobban and Scott, 1964, fig. 2), and *I. subcompressus* Meek and Hayden. No *Thyasira* have been reported from this zone although the ranges of *T. rostrata cracens, T. beauchampi rex,* and *T. quadrula quadrula* span it. Early Late Campanian.
5. Zone of *Baculites asperiformis* Meek; also exclusive known range of *Hoplitoplacenticeras* sp. in the Western Interior. Upper half of the range of *Trachyscaphites spiniger porchi.* Last occurrence of *Thyasira quadrula quadrula* and *Inoceramus pertenuis* (early form). Early Late Campanian.
6. Zone of *Baculites* sp. (smooth) (see Cobban, 1962, p. 705). No other diagnostic ranges. No *Thyasira* have been found at this level although the ranges of *T. beauchampi rex* and *T. rostrata cracens* span it. Early Late Campanian.
7. Zone of *Baculites perplexus* Cobban, early form (Cobban, personal communication, 1964). First occurrence of *Thyasira quadrula arrecta,* n. subsp. Middle part of the range of *T. rostrata cracens, T. beauchampi rex,* and *Inoceramus compressus. Thyasira* distributed through five distinct levels. Early Late Campanian.
8. Zone of *Baculites gilberti* Cobban. Contains forms transitional between the early and late forms (subspecies?) of *B. perplexus.* First occurrence of *Scaphites (Hoploscaphites) gilli* Cobban and Jeletzky, and possibly of *Trachyscaphites redbirdensis*

Cobban and Scott, and *Thyasira becca becca,* n. subsp. Contains *T. rostrata cracens* and *T. beauchampi rex* in the upper part of their range, and *T. quadrula arrecta* in the middle part of its range. Early Late Campanian.

9. Zone of *Baculites perplexus* Cobban, late form (Cobban, personal communication, 1964). First definite occurrence of *Trachyscaphites redbirdensis.* First possible occurrence of *Thyasira becca cobbani,* n. subsp. Last occurrence of *T. beauchampi rex* and *T. rostrata cracens.* Early Late Campanian.
10. Zone of *Baculites gregoryensis* Cobban. Associated with *Pachydiscus complexus* (Hall and Meek). Last occurrence of *Trachyscaphites redbirdensis* (in lower third of zone), noded scaphite (n. sp.) of Cobban and Scott (1964, fig. 2). First occurrence of *Solenoceras* sp., *Didymoceras* sp., *Ostrea glabra* Meek and Hayden, *Inoceramus tenuilineatus* (lower half of its range), and the lineages of *I. barabini* Morton and *I. proximus* Toumey. First definite occurrence of *Thyasira becca becca* and *T. becca cobbani.* Early Late Campanian.
11. Zone of *Baculites scotti* Cobban, containing a fauna from six distinct levels possibly divisible into two faunal subzones; subzone of *Thyasira cantha,* n. sp. (oldest), and subzone of *T. triangulata,* n. sp. (youngest). Zone of *B. scotti* contains exclusive occurrence of *Menuites* sp., *Anapachydiscus* sp., *Inoceramus buguntaensis* Dobrov and Pavlova, *I. sublaevis* Hall and Meek, and *I. convexus* Hall and Meek. Highest occurrence of *I. tenuilineatus.* Middle Late Campanian.

    A. Subzone of *Thyasira cantha.* Contains also the exclusive range of *T. advena browni* Kauffman, n. subsp. in its upper part, and the bulk of the range (upper $\frac{3}{4}$ to $\frac{4}{5}$) of *T. becca becca* and *T. becca cobbani.* Highest occurrence of *T. quadrula arrecta.*

    B. Subzone of *Thyasira triangulata,* exclusive known occurrence.

Among the other mollusks occurring with *Thyasira,* none, as presently defined, have restricted enough stratigraphic ranges to be useful assemblage zone markers. These have been omitted from the above lists, which are composed exclusively of stratigraphically restricted genera, species, and subspecies. The assemblage zones constructed by Cobban and Reeside (1952, chart 10b, p. 1016-1026) have been greatly refined with subsequent studies of the ammonites by Cobban and his associates. Many other mollusk groups employed by these authors, however, have not been similarly studied and certain species and genera used by them to define broad assemblage zones have been here dropped in the more detailed treatment of zones.

## GENERAL ANATOMY; FUNCTIONAL MORPHOLOGY

The Lucinacea are an anatomically unique group of bivalves in which the soft-part construction deviates strikingly from that of more normal infaunal bivalves. These anatomical modifications, primarily concerned with the foot, mantle fusion, posterior inhalent and exhalent apertures, and feeding or sorting mechanisms, are closely related to the living habits of the animal, and are in part reflected by the interior shell morphology. Inasmuch as Recent and Cretaceous *Thyasira* have very similar interior shell features, it is possible to make critical comparisons of their general anatomy and to infer the ecology of the Cretaceous forms by comparative study of their functional morphology. An anatomical and morphologic review of living *Thyasira* for the purpose of interpreting fossil specimens constitutes a necessary and rewarding part of this study.

Fortunately, the anatomy of living *Thyasira* (text fig. 2), in particular the genotype *T. flexuosa* (Montagu), has been extensively studied (Allen, 1953, 1958a and b; Chavan, 1937, 1938, and others), and much of this information is applicable to the anatomical interpretation of fossil species. For details, the reader is referred to the excellent study of *T. flexuosa* by Allen (1958b). The purpose of the following discussion is only to outline the general anatomy of *Thyasira* and discuss in detail those features which are (a) unusual, (b) environmentally adaptive and have bearing on paleoecologic interpretation, or (c) are reflected in the shell structures and form a basis for the study of functional morphology and partial anatomical reconstruction of Cretaceous species. The general living habit and principal anatomical features of *T. flexuosa* are illustrated in text figure 2 (after Allen, 1958a).

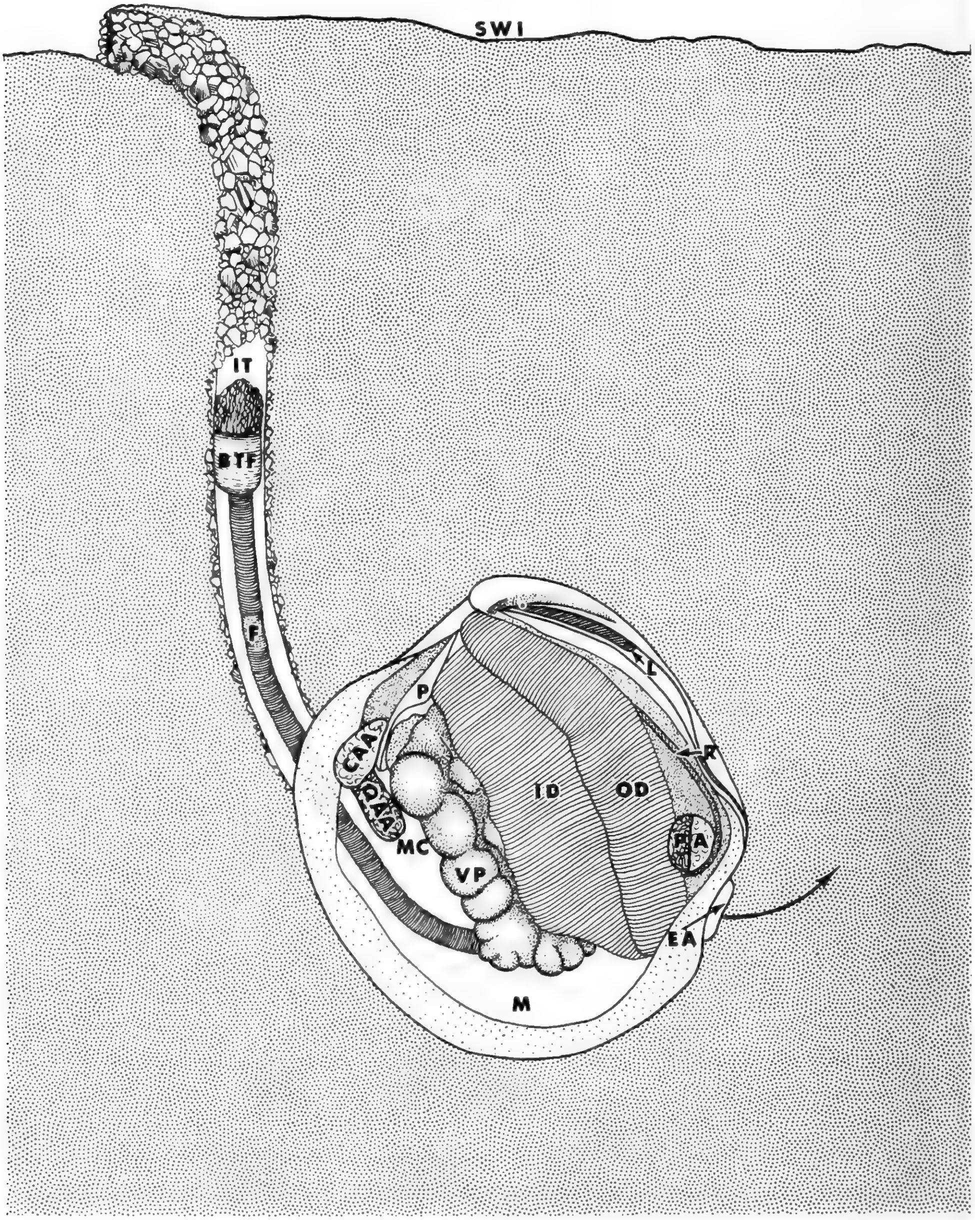
### THE FOOT AND ANTERIOR INHALENT TUBE

One of the most unusual features of the animal is the modified foot, which is slender, up to 10 times as long as the shell and terminates in a distinct, bulbous, expandable tip bearing mucous-secreting glands but lacking a byssal gland and the prominent heel developed in the Lucinidae. The tip is bipartite, with the proximal portion transversely corrugated and the distal portion longitudinally corrugated. The foot has three functions: burrowing, locomotion, and formation of an elongate anterior agglutinated tube leading from the substrate-water interface to the midanterior portion of the shell and carrying the principal inhalent currents used in feeding and respiration. The anterior tube replaces the posterior inhalent aperture for this purpose in the Thyasiridae.

The anterior inhalent tube is formed in the following manner: The foot is extended through the anterior pedal gape and forced slowly upward through the substrate by means of a series of expansions and contractions. Periodically, particles of substrate are concentrated at the distal margin of the foot through the action of terminal cilia and there become entwined in mucous secreted by the foot's glands, forming an agglutinated collar around the tip. This collar is then attached to the preceding one and another is begun. The anterior tube is therefore a series of these collars piled on top of one another and cemented. The tube extends vertically up through the substrate, but is bent horizontally at the water-substrate interface. It is cleaned and repaired by periodic protrusion of the foot. When retracted, the foot is loosely coiled in the mantle cavity with the tip close to the posterior edge of the anterior adductor muscle; the mantle cavity is somewhat expanded to accommodate this large structure.

## THE MANTLE CAVITY

Development of a large, highly specialized foot in the Thyasiridae is accompanied by other major anatomical modifications directly related to the size of the foot and the inhalent function of the anterior tube it produces. Expansion of the mantle cavity to accommodate the coiled foot when retracted is produced in three ways: the line of attachment of the gills, which in *Thyasira* is marked by the interior fold formed by the primary external sulcus, is dorsoposterior rather than dorsal and the gills themselves are reduced in size; secondly, lateral body pouches are developed on either side of the mantle cavity; finally the anterior adductor muscle, which is elongate, narrow, and somewhat constricted near its center, has been laterally compressed so as to provide more space in the anterior portion of the mantle cavity. Lateral compression and dorsoanterior-ventroposterior elongation of the anterior adductor muscle serves a dual adaptive role in respect to the function of the foot. Not only does it provide more space in the mantle cavity for coiling of the foot, but also forms a trough between the anterior edge of the muscle and the anterior attachment of the mantle lobe for the outward passage of the foot when



Text Figure 2.—General anatomy and living habit of *Thyasira flexuosa* (Montagu), modified after Allen, 1958b. Animal shown in living position with shallower than normal burial (capable of burial 6 to 10 times the length of the shell). Anterior inhalent tube broken away in center to show elongate projected, and for the inward passage of inhalent currents between the proximal end of the anterior inhalent tube and the mantle cavity. The posterior adductor is subround and terminates on the interior fold of the shell, which acts as a buttress for attachment.

## POSTERIOR APERTURES

A second important anatomical modification of *Thyasira* is the development of nonsiphonate posterior inhalent and exhalent apertures, despite the deep infaunal habit of the animal, and the functional change of the inhalent aperture. Since the main feeding currents in *Thyasira* come in through the anterior inhalent tube formed by the foot, the posterior inhalent aperture loses its primary function, developed in other infaunal bivalves, and is greatly modified. No siphon is formed, and the aperture itself is poorly defined, being formed only by partial cuticular fusion of the inner mantle lobe rather than by tissue fusion. A slight inhalent current flows through the aperture, but its only function is to create vortices in the main current flowing along the rejection track for the sorting and cementing of pseudofeces. The posterior exhalent aperture is also nonsiphonate but retains its function of voiding feces and pseudofeces and is well developed, being formed by tissue fusion of the inner muscular lobe of the mantle, a unique situation among the bivalves. Waste is deposited in the sediment adjacent to the shell; because the inhalent currents are drawn from the sediment-water interface through the anterior tube, this does not have a deleterious effect on the animal. Inasmuch as no siphons are formed in *Thyasira,* the mantle is attached to the shell in a continuous arc across the area of the posterior apertures, and no sinus is formed in the trace of the pallial line. In addition, no large siphonal retractor and protractor muscles are developed.

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vermiform foot with bulbous tip. Grains of tube enlarged to accentuate structure and no sediment size selection implied. Posterior arrow shows direction of current flow from exhalent, nonsiphonate aperture, here somewhat extruded to show its position.

Key to anatomy: **BTF**—Bulbous tip of foot; **CAA**—Catch portion of anterior adductor muscle; **EA**—Exhalent aperture; **F**—Foot; **ID**—Inner demibranch; **IT**—Inhalant tube; **L**—Ligament; **M**—Mantle lobe; **MC**—Mantle cavity; **OD**—Outer demibranch; **P**—Palps; **PA**—Posterior adductor muscle showing inner, densely shaded quick portion, and outer catch portion; **QAA**—Quick portion of anterior adductor muscle; **R**—Rectum; **SWI**—Sediment-water interface; **VP**—Visceral pouch.

## REFLECTION OF ANATOMY ON SHELL

These anatomical innovations related to the modified foot, anterior adductor muscle, and posterior apertures are well marked on the interior shell morphology of Recent and fossil species of *Thyasira*. The anterior adductor insertion area, though only weakly to moderately impressed, reflects the laterally compressed shape of the muscle (text figs. 2, 3) caused by development of a larger mantle cavity and an anterior trough for the passage of the foot and feeding currents. The central constriction of the anterior adductor, which marks the point of separation between the catch and quick portions of the muscle (text figs. 2, 3), is reflected in the insertion area of many species. The trough between the anterior edge of the adductor and the anterior attachment of the mantle is reflected in the shell morphology by a marked separation of the anteroventral edge of the adductor insertion area from the inner edge of the pallial line (text fig. 3) producing a sharp re-entrant of the inner shell layer between them. The position of the interior fold of the valve marks not only the position of gill attachment but also forms the buttress for the attachment of the rounded posterior adductor muscle, which is moderately well impressed. The entire, nonsinused pallial line demonstrates the absence of inhalent or exhalent siphons ventroposteriorly, as does the lack of observable insertion areas for siphonal protractor and retractor muscles.

This precise reflection of major anatomical features in living Thyasiridae by the interior morphology of the shell provides a firm basis for the interpretation of the anatomy of fossil species whose interiors are known. It is significant to note that whenever the interior shell morphology of Cretaceous *Thyasira* could be determined (text figs. 17, 18), it was found to be nearly identical in all respects to that of similar living species. This suggests that by Cretaceous time, the unique anatomical features which characterize Recent Thyasiridae had already developed in the major lines of descent; the Cretaceous *Thyasira* were anatomically similar to living forms in regard to the foot, musculature, posterior apertures, mantle attachment, mantle cavity, and the anterior inhalent passageway between the adductor and the mantle edge. It further implies the ecology and living habitat of *Thyasira*, for which the anatomy is unusually adapted, has not changed significantly from Cretaceous to Recent time.

## ADDITIONAL MODIFICATIONS OF THE ANATOMY

In addition to modifications of the foot, adductor muscle, mantle cavity, and posterior apertures, living *Thyasira* have other unusual anatomical features which, although not reflected in the interior morphology of the shell, are equally adaptive to the peculiar infaunal living habit of the animal. The development of a long, rigid, anterior inhalent tube in *Thyasira* permits the animal to burrow deeply into soft sediments, some of which are chemically deleterious (i.e., oxygen-poor and/or hydrogen sulfide-rich) to many other infaunal elements, while still drawing food and nourishment from overlying waters without siphons. Many environments inhabited by Thyasiridae are not only chemically unsuitable for potential competitor mollusks, but also are characterized by a limited food supply.

To adapt to these conditions, the sorting mechanisms in *Thyasira* are greatly reduced, concentrated anteriorly, and the food-selectivity of the animal is diminished considerably from that of non-Lucinacean, infaunal bivalves. The gills are reduced in size, have lost most of their particle-sorting structures, and are positioned abnormally toward the anterior part of the shell in response to the shift in the main incurrent water system from the posterior inhalent aperture to the anterior inhalent tube. The palps are similarly reduced and less selective in their food sorting ability. The principal sorting mechanisms, ciliated surfaces, are situated anteriorly near the incurrent track on the anterior adductor muscle and mantle lobes. As a result of these modifications, the Thyasiridae are adapted to accept many suitable foods including relatively large particles, that are introduced through the inhalent aperture. The initial and principal sorting mechanisms of the adductor muscle and mantle are primarily concerned with discriminating between inorganic or overly large particles and organic particles of acceptable size.

Allen (1958b) and others have assumed *Thyasira* is a filter feeder, but the mechanics of feeding have not been well documented. Since the inhalent tube is not ciliated, and cilia are restricted in the mantle cavity, it is hard to envision a powerful feeding current being created by the animal, thus sucking water in through the tube. Possibly the tube is built to face into existing currents, which force water into it, but currents in the deeper water environments preferred by many *Thyasira* are probably not very great. Dr. Kenneth Boss (1966, personal communication) has raised the question of whether or not the foot, with its ciliated adhesive tip, could play a detrital feeding role by being extruded and groping around on the bottom for chance organic debris. This is a good possibility, although no authors have documented it (i.e., Allen, 1958b, who observed living specimens). If this were the principal means of feeding, it would mean the foot is less often coiled in the mantle cavity than suspected, but does not detract from the need for an enlarged mantle cavity to accommodate it. Certainly the foot is withdrawn during periods of turbidity, fouling waters, and rest. It may actually act as a plug for the inhalent tube during periods when fouling conditions are maximum.

The mantle of *Thyasira* is basically similar to that of other bivalves and consists of three lobes: (a) an outer lobe which secretes calcareous shell material; (b) a middle sensory lobe which is represented by a double fringe, lacks tentacles in the region of the apertures, and is generally not well developed; and (c) an inner muscular lobe which internally forms a shelf or trough along which runs the main rejection track of the mantle. Glandular cells are concentrated on the upper edge of the inner mantle lobe below the rejection track. These are in part responsible for the secretion of agglutinated material for the formation of pseudofeces.

Mantle musculature consists of concentric muscle strands in the inner lobe below the outer edge of the rejection track and inside of this two main groups of longitudinal muscle strands: (a) one group inserted on the hinge side of the pallial line and connecting with the sensory and outer mantle lobes; and (b) a second group inserted on the lower half of the pallial line and connected to the outer mantle lobe. These appear as weakly impressed bands of muscles on the insertion area (pallial line) of Recent shells and not as discrete scars. These individual bands cannot be separately discerned in the pallial line of Cretaceous *Thyasira* shells, although the breadth of the entire pallial band in fossil species suggests both were present.

Other features of *Thyasira* anatomy, shown in part on figure 2 and discussed in detail by Allen (1958b), are similar to or deviate only slightly from the normal infaunal plan of non-Lucinacean bivalves. Since these have little bearing on the study of the Cretaceous Thyasiridae, they are not treated here and the reader is referred especially to the work of Allen (1958b), and for additional information to Allen (1953, 1958a), Chavan (1937, 1938), and Dall (1901).

## SHELL MORPHOLOGY

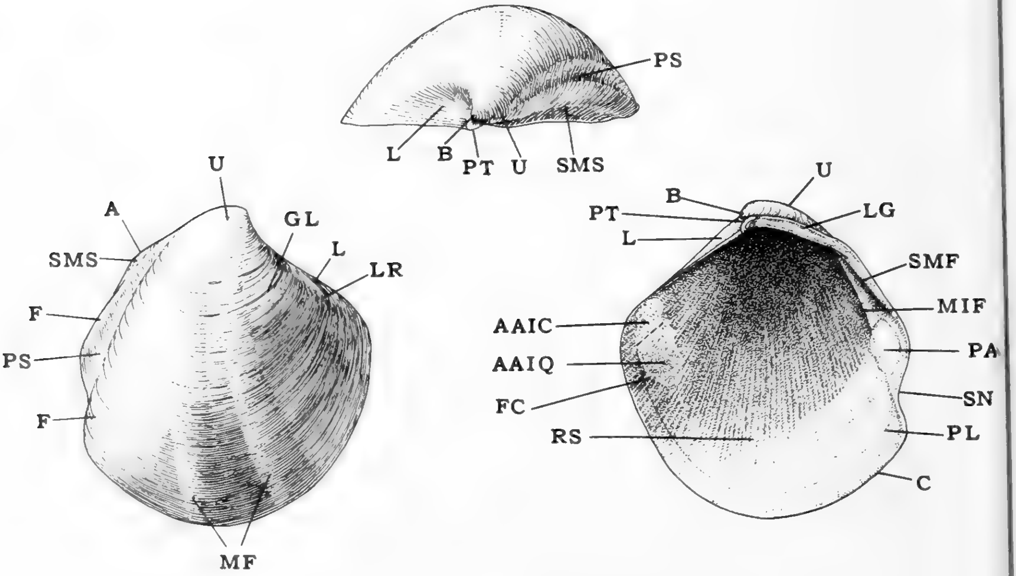
The shell of Recent and fossil *Thyasira* is basically simple and has evolved little since the Cretaceous. Consequently, morphologic distinctions between related contemporary species and subspecies are slight, as they are between the steps of chronologically successive taxa within an evolving lineage. These factors complicate subgeneric taxonomic treatment of the Thyasiridae, and the difficulties are compounded by the moderate variation in shell morphology shown by individual species of *Thyasira* (text figs. 6, 7, 8, 17, 18). Variation plots comparing structures of similar, closely related Cretaceous species may therefore be expected to exhibit a considerable amount of overlap (text figs. 14, 15), in some cases masking small-scale evolutionary changes.

Meaningful taxonomic interpretation of fossil *Thyasira* seems best achieved by: (a) analysis of variation within, and differences between related living species as a guide to the degree of morphologic separation to be expected in chronologically successive fossil species and subspecies, and (b) application of these criteria, where possible, to analysis of fossil populations. In this study, specific variation was tested biometrically on a population of the large living species, *Thyasira sarsi* (Phillipi) (=*Cryptodon insignis* Verrill and Bush; see Ockelmann, 1961, p. 51), and differences between closely related species subjectively evaluated on species in the *T. flexuosa* lineage. These data form the basis for evaluating the taxonomic significance of biometric variation and differences shown by plots of chronologically successive populations of Cretaceous *Thyasira*. Despite the rarity of Cretaceous *Thyasira*, analyzable populations from single concretions or concretion levels are available from several stratigraphic levels. In their absence, significant collections from several localities in time-contemporaneous rocks (as determined by ammonite zones) were substituted for populations and proved satisfactory for variation analysis and comparison with older and younger fossil suites.

## FEATURES OF THE SHELL MORPHOLOGY

The shell of Cretaceous and Recent *Thyasira* s.s (text fig. 3) is characteristically equivalve, moderately biconvex, prosocline, and subround, subovate, or subtriangular in outline, with the margin slightly to moderately recessed anterior to the beak. The pointed beak and inflated umbo curves inward and forward to varying degrees. The shell surface bears fine, closely and irregularly to subregularly spaced growth lines. A broad but prominent sulcus extends along the posterodorsal slope of the rounded umbonal ridge from the umbo to the posteroventral margin. A prominent fold is developed between this sulcus and the posterodorsal margin, and is commonly separated from this margin by a small, narrow submarginal sulcus. A flat to slightly excavated lunule bounded by moderately well defined, low ridges is developed on some species. The escutcheon is narrow, deep to moderately excavated, and lanceolate.

Structures of the shell interior (text figs. 3, 4) are also similarly developed in Recent and Cretaceous *Thyasira.* The hinge area is not appreciably thickened; the hinge is edentulous, or else bears a weakly defined pseudocardinal tooth or swelling just below or anterior to the incurved beak (text fig. 4). This feature is variable even within



Text Figure 3.—Morphology of *Thyasira flexuosa* (Montagu), right valve.

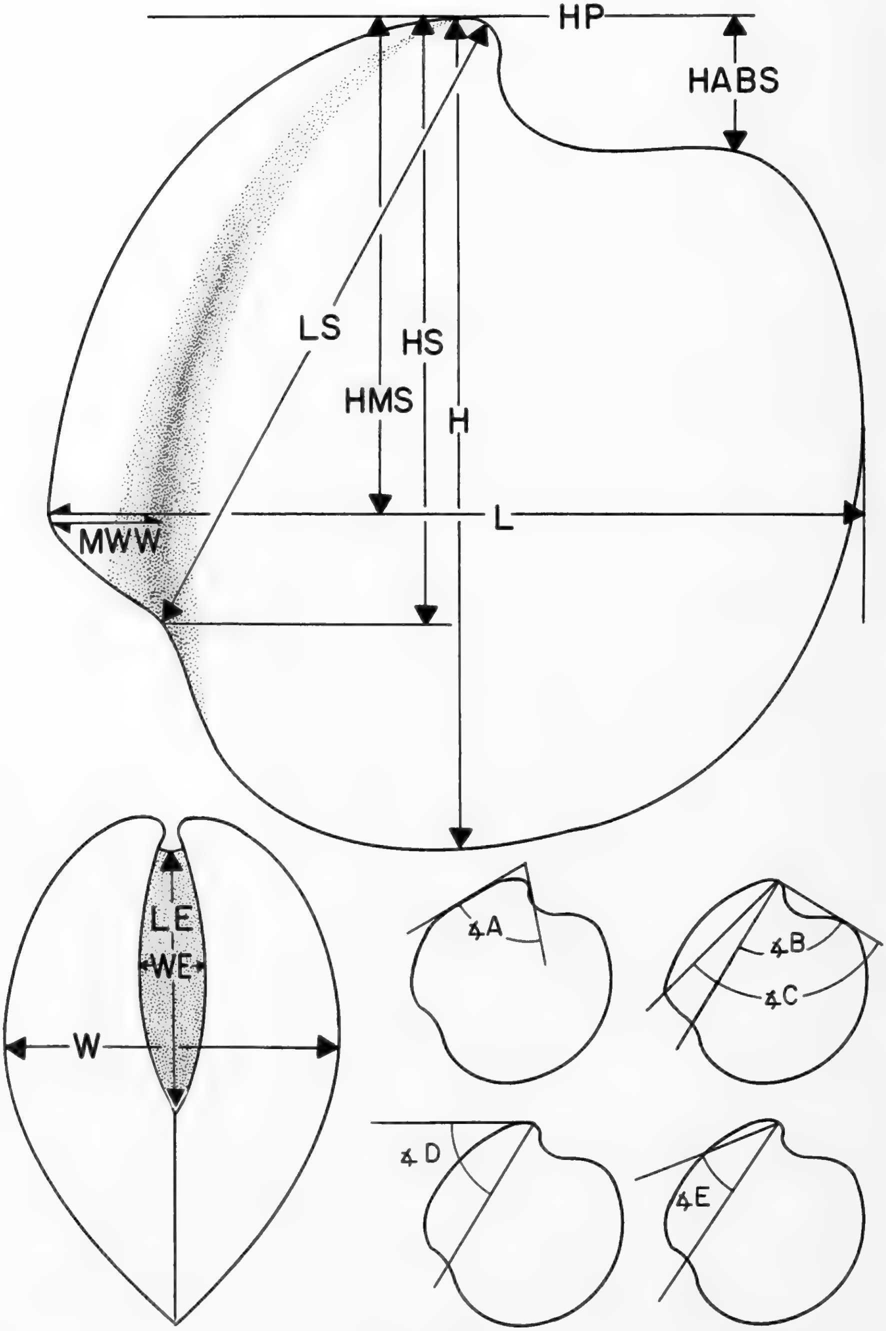
Key to symbols in alphabetical order: **A**—Posterior auricle; **AAIC**—Anterior adductor insertion area for the catch portion of the muscle; **AAIQ**—Anterior adductor insertion area for the quick portion of the muscle; **B**—Beak; **C**—Commissure; **F**—Fold on valve exterior; **FC**—Foot canal, the reentrant formed by the inner shell layer between the anteroventral edge of the adductor muscle scar and the inner edge of the pallial line, marking the position of the canal or opening in the mantle leading from the proximal end of the anterior inhalent tube to the mantle cavity (the foot projects outward, and feeding currents flow inward through this canal); **GL**—Growth line; **L**—Lunule; **LG**—Ligamental groove; **LR**—Marginal ridge of the lunule; **MF**—Medial flattened areas on the shell exterior; **MIF**—Main or primary interior fold; **PAI**—Posterior adductor muscle insertion area; **PL**—Pallial line; **PS**—Primary sulcus of the valve exterior; **PT**—Pseudocardinal tooth; **RS**—Radiating interior striae; **SMF**—Submarginal fold of the valve interior; **SMS**—Submarginal sulcus of the valve exterior; **SN**—Notch in marginal outline formed by its intersection with the primary sulcus; **U**—Umbo.

single species. A moderately deep, narrow, gently curved ligamental groove extends from behind the umbo to the dorsoposterior corner. The ridge bounding the lower part of the groove is the interior expression of the submarginal sulcus. The main sulcus is expressed internally as a broad fold, which bears the subround, slightly depressed, posterior adductor muscle insertion area near its posteroventral termination. The anterior adductor insertion area is also weakly impressed, but large and elongate, extending from near the salient dorsoanterior corner posteroventrally, becoming narrowly separated from the pallial line. The pallial line is entire. Irregular boundaries mark the margins of the adductor insertion areas, and to a lesser extent, the pallial line. Shallow, fine grooves which radiate out from the umbonal area cover much of the shell interior. The shell of *Thyasira* is characteristically thin and fragile, opaque to translucent, and polished to chalky. Some living and fossil Indo-Pacific species, and certain Cretaceous forms from the Western Interior have comparatively thick, strong valves.

Structures which were considered, and measurements which were taken in biometric analysis of the Cretaceous *Thyasira* are shown in text figures 3 and 4, respectively. Features which were found to be most useful in differentiation of species and subspecies of *Thyasira*, and in plotting evolutionary trends are: size, marginal outline, relative convexity (especially in the lower umbonal area); trace and relative development of the posterior sulci and where they intersect the margin; presence or absence of an anterior sulcus and its reflection in the marginal outline; width and outline of the valve flank posterior to the primary sulcus; development and inclination of the anterodorsal flank; projection and degree of incurving and inclination of the beaks and umbos; development, width, depth, and prominence of the lunule and its bounding ridges or folds; and nature of the cardinal area. In addition to analysis of absolute values measured on these structures, the relationship of one to the other (i.e., height vs. length, height of beak vs. height, etc.) proved useful in many cases for taxonomically separating populations and plotting ontogenetic trends within populations.

## VARIATION IN ADULT POPULATIONS OF THYASIRA

The living species *Thyasira sarsi* (Phillipi) was selected to test the expected morphologic variation in *Thyasira* because it compares closely in size and morphology with species from the Cretaceous of the Western Interior. The analysis was based on 29 adult left



Text Figure 4.

and right valves from the vicinity of the Grand Banks (USNM 52556, 52557, and 52733 in the collections of the Mollusk Division, U.S. National Museum). Variation plots based on this population are shown in text figures 6 and 7, and are here compared with similar charts, plotted at the same scale, for Cretaceous *Thyasira* populations. These comparisons indicate: (1) that the fossil and Recent populations are basically comparable in regard to all measured morphologic features and that Recent data can be used as guidelines to the analysis of variation within, and differences between time-successive fossil populations; (2) in most cases the range of variation demonstrated for each character by the Recent population is slightly less than that shown by fossil populations. This may be due either to less restricted genetic limits in fossil populations or to mechanical alteration of true character variation through post-depositional compression and deformation within the sediment. The fracturing seen on many specimens suggests the latter is most plausible; (3) in view of the close correlation between variation limits of Recent and fossil populations, the biometric discontinuities observed by analysis of shell characters on chronologically successive populations within any Cretaceous lineage of *Thyasira* are probably taxonomically significant and reflect evolutionary modification of the stocks rather than intraspecific variation. Shell characters which show only slight variability in the *T. sarsi* population are: relative height and length

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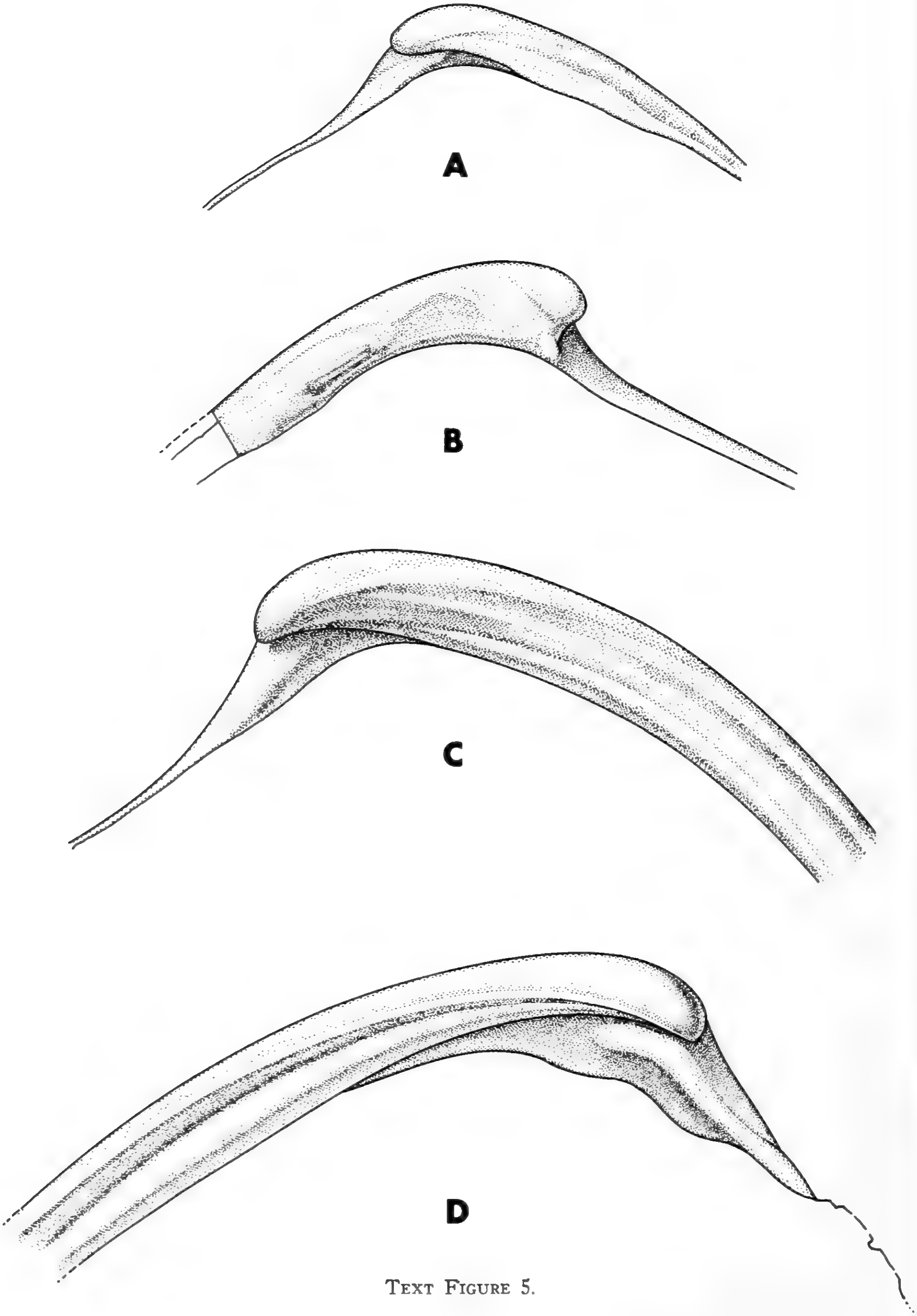
Text Figure 4.—Definition of measurements used in biometric analysis of Recent and Cretaceous *Thyasira,* in alphabetical order: **Angle A,** the angle between the posterodorsal margin and the anterior flank of the projecting beak and umbo; **Angle B,** the angle between lines connecting the center of the primary sulcus notch with the beak, and the dorsoanterior corner with the beak; **Angle C,** the angle between lines connecting the midposterior projection (corner) with the beak and the dorsoanterior corner with the beak; **Angle D,** the angle formed by a line which connects the center of the primary sulcus notch and the beak, and the horizontal plane (**HP**) of the hinge line; **Angle E,** the angle between lines connecting the center of the primary sulcus notch with the beak and the most projecting point of the posterodorsal margin with the beak; **H,** height; **HABS,** height to the point of the anterior break in slope at the dorsoanterior corner; **HMS,** height to the level of the midposterior break in slope at the dorsal margin of the primary sulcus notch; **HS,** height to the level of the middle primary sulcus notch; **L,** length; **LE,** length of the escutcheon; **LS,** length of a line connecting the beak and the middle of the primary sulcus notch, representing the approximate length of the primary sulcus; **MWW,** maximum width of the flank or fold ("wing") posterior to the primary sulcus; **W,** width of both valves; **WE,** width of the escutcheon.



Text Figure 5.

of the valves; degree and distribution of convexity; terminal nature, curvature, and degree of projection of the beaks and umbos; development of the recess in marginal outline below and anterior to the beaks; the position, curvature, and depth of the sulci; development of the notch in the marginal outline at the intersection of the primary sulcus and the commissure; surface ornamentation; development of flattened areas on the shell just posterior to the midline; size, depth, and definition of the lunule at any single developmental stage (becomes less distinct with age); development of the escutcheon; the edentulous hinge; shape, size, and position of the adductor muscle insertion areas; trace and development of the pallial line; trace, development, and position of the ligamental groove; development of faint radiating grooves on the valve interior; and the thickness and degree of luster of the shell material.

Certain angles and plots relating linear measurements (text figs. 6, 7) also show a narrow range of variability. These are: the sulcus angle, the modified apical angle, length relative to width of the escutcheon, width of the posterodorsal flank relative to shell length, length of the sulcus relative to shell height; height of the sulcus relative to shell height, and valve height relative to length.

The most variable characters of the shell on adult *T. sarsi* are associated with the marginal outline and the relative development of the anterior flank. Even in regard to shape, certain parts of the commissure are consistently formed, in particular the broad rounded posterodorsal-posterior margin, the flattened midventral margin, the recessed anterodorsal edge, and the recess formed at the termination

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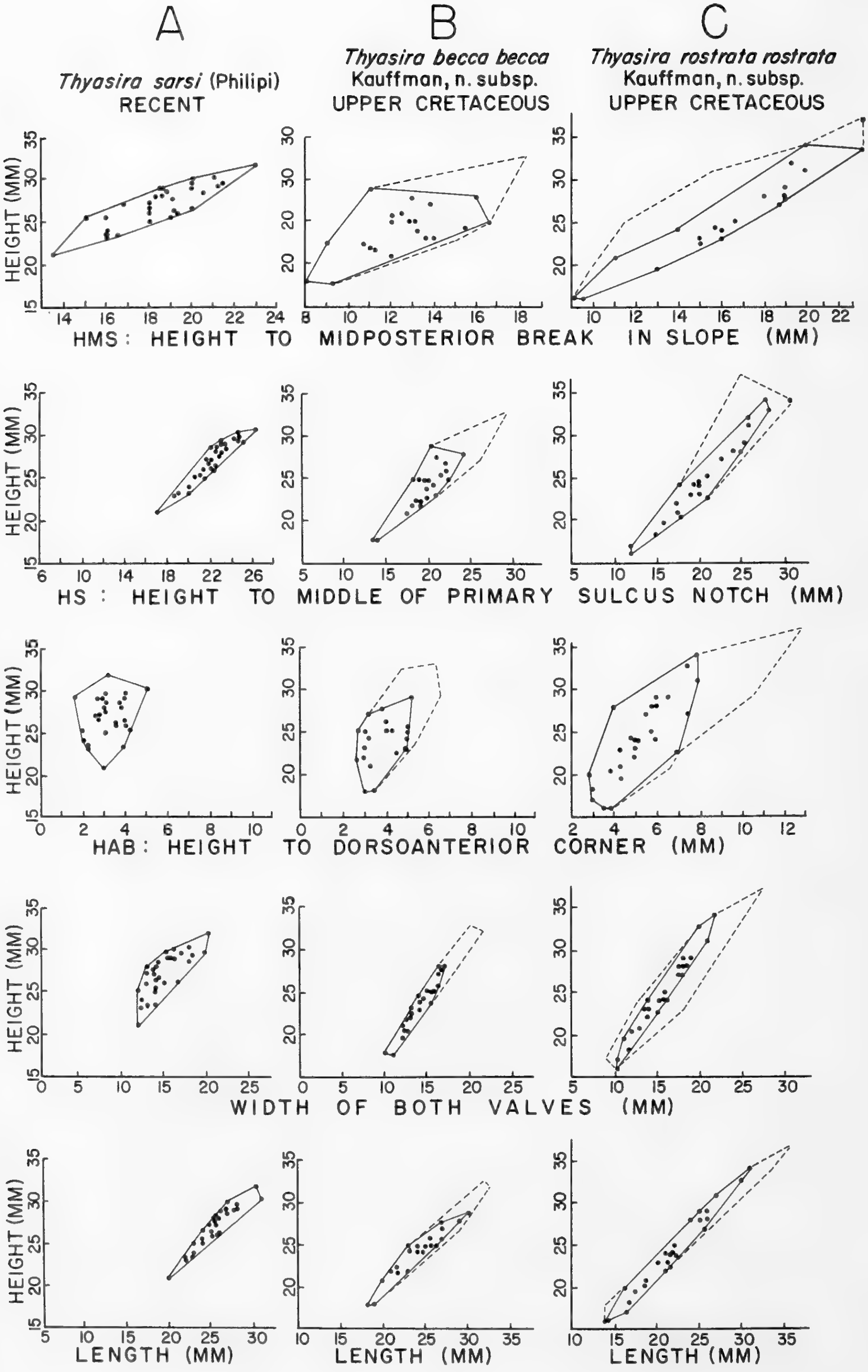
TEXT FIGURE 5.—Typical hinge areas of Upper Cretaceous *Thyasira* from the Western Interior of North America. **A**—*Thyasira quadrula arrecta,* n, subsp., interior of right valve (× 8), paratype, USNM 153451, USGS Mesozoic locality D1564. Note edentulous hinge and relatively shallow anterior portion of the ligamental groove. **B**—*Thyasira quadrula arrecta,* n. subsp., left valve (× 10); paratype, USNM 153457, from USGS Mesozoic locality D1866. A small pseudocardinal swelling occurs at inner edge of the ridge forming the ventral margin of the ligamental groove. Hinge line partially eroded posterior to beak. **C**—*Thyasira quadrula arrecta* n. subsp., right valve (× 10), paratype, USNM 153447, USGS Mesozoic locality D1865. Specimen exhibits edentulous hinge and shallow ligamental groove posteriorly. **D**—*Thyasira becca becca* Kauffman, n. subsp., left valve (× 10), paratype, USNM 153524, from USGS Mesozoic locality 22840. An unusual pseudocardinal swelling is formed by inflection of the anterodorsal margin, the inner margin of the lunule, beneath the beak. Ligamental groove is prominent and deep, becoming overhung by dorsal shell margin near beak.



Text Figure 6.

of the primary sulcus. It is expected that other more variable aspects of the marginal outline and anterior portion of the valve, however, would be of limited use in differentiating Recent and fossil species.

The variation in the development of the anterior flank and margin in *T. sarsi* is striking (text fig. 8) and most other morphologic variables in the species appear to be directly related to the relative development of this one structure. Terminal members at one end of the variation series have the margin moderately salient and rounded at its junction with the dorsal margin (text fig. 8), at the other extreme the margin is projecting and subangulate to blunt at the corner. Where the margin projects only moderately, the anterodorsal edge slopes downward away from the beak; where the anterior margin is strongly projecting, the anterodorsal edge is nearly horizontal, elongate, and straight. A very shallow anterodorsal sulcus is developed near the dorsal margin in all shells, regardless of modification of

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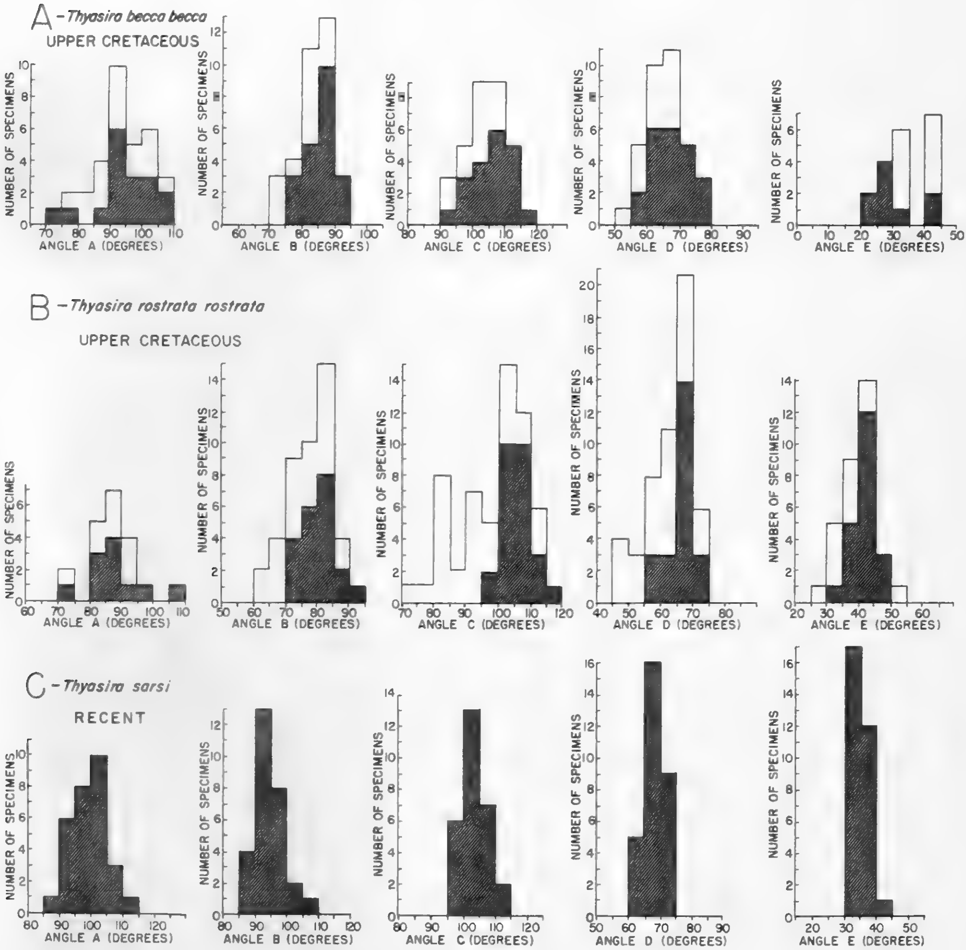
Text Figure 6.—Comparative population variation in Recent and Cretaceous *Thyasira*. **A**—*Thyasira sarsi* (Phillipi), a population of 30 valves (USNM 52733: Division of Mollusks), part of the paratype lot of *Cryptodon insignis* Verrill and Bush from the Grand Banks, U.S. Fisheries Commission Station 2499, dredged at 130 fathoms. **B**—*Thyasira becca becca* Kauffman, n. subsp. Solid dark line and all points plotted represent a single population (23 specimens) from a concretion or series of concretions in a single layer at USGS Mesozoic locality D1410, Pierre Shale, middle part of the *Baculites scotti* zone, Fall River County, South Dakota. Dashed line shows boundaries of scattergram based on measurements of all known specimens of the subspecies from all different localities. **C**—*Thyasira rostrata rostrata* Kauffman, n. subsp., variation plots on a single population (26 specimens) represented by plotted points and solid line around scattergram, from USGS Mesozoic locality 10459, a zone of limestone concretions in the Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Dashed line represents boundary of scattergram for measurements of all known specimens of the subspecies from all known localities.

The charts show very close comparison in range of variation of each character-pair for single populations of living and Cretaceous species, providing a comparative basis for species and subspecies concepts. Slightly variable characters such as height-length ratios, relative inflation of the valves, and position of the primary sulcus notch, and broadly variable characters such as the development of the dorsoanterior flank are approximately the same on Recent and Cretaceous species of the same general size. The slightly greater variation shown by fossil species in some cases is attributed to preservation factors. The range of variation for all specimens of the fossil subspecies, regardless of locality and relative position within their known stratigraphic range, is closely comparable to that of single populations with the exception of size range.

the anterior, and forms a slight recess or flattened area in the shell outline just above the junction of the anterior and dorsal margins. This sulcus appears to be a useful taxonomic character.

The ventroanterior and anteroventral margins are also highly variable in outline (text fig. 8), ranging from moderately rounded and projecting, giving the whole valve a subrounded outline, to slightly convex and steeply slanting between the dorsoanterior and midventral margins. The latter condition is produced on shells with a strongly projecting anterior flank.

A final variable character is the maximum width of the dorsoposterior flank. Although both the primary sulcus and the dorsoposterior margin are consistent in their outline, trace, and degree of



TEXT FIGURE 7.

curvature, the distance between them varies from a narrow area about as wide as the primary sulcus, to a broader flank nearly twice as wide as the sulcus. This variation may in part be a product of wear on the projecting margins during burrowing.

A broad range of variation in many single-character and bivariate plots used in this study reflects the morphologic variability discussed above. The whole apical angle (20° range), and the sulcus-anterior angle (25° range) are moderately variable in response to the variation in the development of the anterior margin, the dorsoanterior corner being a reference point for both measurements. The beak angle (30° range) varies with change in slope of the dorsoanterior margin. Scattergrams obtained by plotting the whole apical angle against valve height, and the sulcus-anterior angle against valve height showed such a wide spread of points that they were not usable.

## ONTOGENETIC VARIATION

In addition to genetic variation noted above in adult specimens of *T. sarsi,* some ontogenetic variation can be discerned between the

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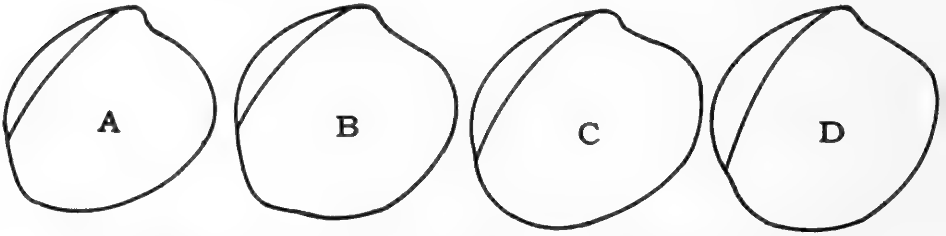
Text Figure 7.—Comparative population variation in measured angles (see text figure 4) on adult specimens of Recent and Cretaceous *Thyasira.* **A**—*Thyasira becca becca,* n. subsp. Black portion of histogram represents a single population of 23 specimens from one concretion zone at USGS Mesozoic locality D1410, Pierre Shale, middle part of the *Baculites scotti* zone, Fall River County, South Dakota. Unshaded portion of histogram represents data for all other known specimens of the subspecies, regardless of geographic or stratigraphic position within its total range. **B**—*Thyasira rostrata rostrata,* n. subsp., a population of 26 specimens (black portion of histograms) from a single concretion zone at USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Unshaded portion of histogram represents data for all other known specimens of the subspecies regardless of geographic or stratigraphic position within their total range. **C**—*Thyasira sarsi* (Phillipi), histograms representing a population of 30 valves (USNM 52733; Division of Mollusks), part of the paratype lot of *Cryptodon insignis* Verrill and Bush from the Grand Banks at U.S. Fisheries Commission Station 2499, dredged at 130 fathoms. Note the generally close approximation of variation limits and relative peaks of fossil and Recent forms, especially between populations of *T. sarsi* and *T. rostrata rostrata.* The greater variation shown by some populations may be due to angle distortion as a result of postdepositional compression of the shell. A much greater range of variation is shown by the whole sample of any fossil subspecies, especially to the left of the peak, when compared to the single test population. This could reflect geographic variation, though this is not borne out by character pairs plotted in figure 6.

early and late adult stages of this species. Unfortunately, the sample population does not contain immature individuals. Recognition of the developmental steps of the adult shell provides a means of sorting out some of the variable characters noted in the *T. sarsi* population and a basis for camparing fossil species at similar developmental stages for taxonomic purposes.

The beak of young adult shells of *T. sarsi* is more pointed, the umbo more acute, the anterior flank shorter and less projecting, and the primary sulcus and midventral flattening of the valve more prominently developed than found at later developmental stages (smallest specimen: height 38 mm., length 39 mm.; largest specimen: height 58 mm., length 63 mm.). These changes are gradually developed. In addition, the indentations in the marginal outline of the shell formed by the lunule just below and anterior to the beak, and by the intersection of the primary sulcus with the margin, are deeper and better defined in young than in old adult specimens. This could be a product, in part, of wear. Growth lines and raised concentric ridges are better defined and somewhat more evenly developed in the early than in the late adult stages.



TEXT FIGURE 8.—Variation in adult specimens of *Thyasira sarsi* (Phillipi) from the Grand Banks. Note consistency in outline and dimensions of the structures on the posterior half of the shell, the primary sulcus, and the beak and umbonal area. Most variability in marginal outline occurs on the dorsoanterior flank of the shell, and the degree to which it projects, as well as in the outline and inclination of the ventroanterior margin. All shells from collection USNM 52733 (Division of Mollusks) at U.S. Fisheries Commission Station 2499, 130 fathoms depth. Part of the paratype lot of *Cryptodon insignis* Verrill and Bush.

Similar trends were found in Cretaceous species of *Thyasira,* and these are discussed in detail under "Ontogeny" for each species.

## ECOLOGY AND PALEOECOLOGY OF THYASIRA

The unusual anatomical modification of *Thyasira* reflects also a somewhat unique ecology which appears to be similar in fossil and living species. Living species are highly specialized for habitats which exclude many other infaunal elements and which are characterized by molluscan faunas of restricted scope. Some of these habitats present chemically severe conditions of life. Temperature, depth, substrate type, sediment and water chemistry, and the amount of competition from other filter-feeding organisms seem to be the main controlling factors on the distribution of species. The ecologic summary presented below is drawn from over 100 general mollusk surveys in various parts of the world and from data on Recent collections at the U.S. National Museum.

## LIVING HABIT

The most important adaptation of *Thyasira* to its environment is the long vermiform foot and the agglutinated inhalent tube which it secretes. Species of *Thyasira* are infaunal burrowers. The animal, unlike most other infaunal bivalves, lives in the sediment with the hinge line oriented approximately parallel to the sediment-water interface (text fig. 2), and the plane of the commissure vertical. Allen (1958b, p. 447, 448, fig. 25) describes and illustrates the burrowing habit in detail. Basically, the animal burrows in the following manner, beginning from a position resting on the side of one valve at the sediment-water interface: (a) the foot is projected midventrally and pushed into the substrate a distance approximately equal to the length of the shell; (b) the bulbous tip of the foot expands, anchoring the foot in the substrate; (c) the pedal muscles contract, lifting the shell to a vertical position; (d) using the foot as an anchor, the animal burrows into the sand with a seesaw rocking motion of the shell produced by alternating contractions of the anterior and posterior adductor muscles while the pedal retractor keeps tension on the foot; (e) the tip of the foot contracts to normal size, the foot is thrust another shell length into the substrate, and the process is repeated. Periodically there is a sharp contraction of the shell, forcing water downward so that some sediment at the ventral margin is washed away. Living *Thyasira* burrow commonly to depths of 6 to 8 cm., and are capable of burrowing up to, but not more than the maximum length of the foot (about 10 times the length of the shell). This limit is imposed because the feeding and respiration currents enter through an agglutinated tube formed by the foot after the animal has burrowed to the depth at which it will live for any extended period.

Because of their burrowing habit, shells of dead *Thyasira* are commonly preserved as bivalved specimens and in living position in the substrate. The valves are easily separated once the shell is exposed to substrate surface conditions after being scoured out by currents or waves. Neither the ligament or hinge structures are strong enough to prevent this, and the shell itself is fragile. Cretaceous *Thyasira,* anatomically and morphologically similar to living species, show the same relationship to the substrate. Over 95 percent of those examined are bivalved specimens with the valves in normal apposition. The few shells whose orientation could be related to bedding planes appeared to be approximately in living position. Most single valves, on the other hand, lie in the bedding plane of containing rocks with their convex surface upward.

The anterior inhalent tube formed by the foot has a profound effect on the ecology of *Thyasira.* Its length permits *Thyasira* to be a deep burrower without development of massive siphons. The stability of the agglutinated tube makes it an effective, lasting incurrent structure which does not require continual energy output by some part of the anatomy, and can be easily repaired by the foot if damaged. The tube represents a closed incurrent system between the overlying water and the animal and its presence, in addition to an apparently broad tolerance of water and sediment chemistry, permits many species of *Thyasira* to live in chemically unfavorable substrates as long as the overlying water conditions are normal enough to sustain them. A possible tube filling was noted adjacent to one Cretaceous specimen of *Thyasira.*

*Thyasira* has also become adapted to habitats where it is not in severe competition for food with other filter feeders, such as environments where particulate food is not abundant. The reduction of sorting mechanisms in many areas, reduction of palps, and consequently the ability to accept and to utilize a large size range of food particles allow species of *Thyasira* to occupy successfully food-poor habitats. These are commonly areas of low biotic productivity (Table 1).

The thyasiridae are so well adapted to these adverse environmental conditions that they commonly occur in great numbers in such habitats, to the near exclusion of other mollusks. They are so highly specialized, however, that they apparently cannot compete successfully in similar but more normal marine habitats which support more diverse molluscan assemblages, even though depth, substrate, and water temperature conditions may be the same as those in food-poor or chemically adverse areas preferred by *Thyasira.* This ecologic distribution with restricted assemblages of associated mollusks is reflected in both the Recent and fossil record (Tables 1, 2). It is not clear, however, whether it is predominately controlled by specialization of the Thyasiridae to adverse habitats, or by their inability to compete with diverse molluscan assemblages, or equally by both factors (the most probable explanation).

## COMMUNITY RELATIONSHIPS

A survey of works dealing with marine bottom communities clearly demonstrates the limited scope and generally uniform composition of living molluscan assemblages associated with well-developed populations of *Thyasira,* as well as the preference of *Thyasira* for cool waters and soft mud substrate in areas of low biotic productivity (Table 1). Infaunal elements dominate due to the soft nature of the substrate and general lack of firm surfaces for cementation or byssal attachment of epifaunal bivalves.

Because many of these data are taken from studies in North Temperate and Subarctic latitudes, the depth ranges indicated in Table 1 are somewhat shallower than the average for species over their entire range (text figs. 10, 11). Data listed in Table 1 are taken only from communities in which *Thyasira* is a numerically significant element, and include only common associated mollusks. *Thyasira* occurs rarely in other types of communities, and conversely in communities listed in Table 1 a few additional mollusk species are sparsely and insignificantly represented.

Ten genera and fourteen species of mollusks represent the most diverse assemblage associated with abundant living *Thyasira* (the Arctic *Macoma* community of Ockelmann, 1958, p. 225, 226). The average number of associated mollusks is normally smaller, five genera, and the majority of communities have four or fewer commonly associated genera and species (Table 1). In the boreal Foraminifera community of Thorson (1957, p. 461-534), *Thyasira* is the only mollusk which occurs in any abundance. In general, the diversity of Recent molluscan assemblages associated with abundant *Thyasira* decreases with increasing depth at which the community is commonly found, the outstanding exception being the *Maldane sarsi-Ophiura sarsi* community described by Thorson (1957, p. 461-534), which has six commonly associated molluscan species at depths of 200 to 600 meters.

In all marine communities studied, a total of 27 genera (22 families) of mollusks were found to be commonly associated with large *Thyasira* populations (Table 1). Many of these are restricted in their association to a single community. Five families and one superfamily, all bivalves, comprise the most consistent ecologic asso-

TABLE 1.—*Communities, biotic association of mollusks, and environmental characteristics summarized for living* Thyasira. *Families arranged in order of number of recorded mollusk associations.*

| COMMUNITY | | SHALLOWER | | | | | | | | | | DEEPER | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Arctic Macoma* community Ocklemann, 1958 | *Amphiura filiformis* comm. Petersen, 1913, 1916 | *Amphiura chiaji* community Petersen, 1913, 1916 | North Atlantic-Mediterranean assemblages Allen, 1958b | | *Astarte crenata* community Ockelmann, 1958 | *Arca glacialis-Astarte crenata* community Sparck, 1933 | Boreal Foraminifera community Thompson, 1957 | *Maldane sarsi-Ophiura sarsi* community Thorson, 1957 | Foraminifera community Ockelmann 1958 | *Amphilepis norvegica-Pecten vitreus* Petersen, 1913, 1915 | Total for genus | Total for family |
| DEPTH RANGE IN METERS | | 4-50 | 15-100 | 15-100 | 11-140 | 11-140 | 25-550 | 30-550 | 100 + | 200-600 | 200-780 | 300 + | | |
| SUBSTRATE | | Clay;<br>Sandy clay | Soft mud | Soft clay;<br>Silty clay | Soft mud | Soft mud | Soft clay | Soft mud | Soft mud | Soft mud | Soft clay | Soft mud | | |
| TEMPERATURE | | Cold | Cool | Cool | Cool | Cool | Cold | Constant negative | Cold | Cold | Cold | Cold | | |
| PRODUCTIVITY | | Low | Low-Mod. | Low | Low? | Low? | Low? | Low | Low | Low? | Low? | Low | | |
| COMMONLY ASSOCIATED GENERA OF MOLLUSKS | | 11 | 7 | 4 | 3 | 4 | 9 | 4 | 1 | 6 | 5 | 2 | 56 | |
| **Bivalvia** | **Total** | 11 | 5 | 4 | 3 | 3 | 9 | 4 | 1 | 4 | 5 | 2 | 51 | |
| Thyasiridae | Thyasira | X | X | X | X | X | X | X | X | X | X | X | 11 | 12 |
| | Axinopsis | X | | | | | | | | | | | 1 | |
| Nuculidae | Nucula | X | X | X | X | | X | | | X | | | 6 | 6 |
| Semelidae | Syndosmya | | X | X | X | | | | | X | | | 4 | 5 |
| | Theora | | | | | | | | | X | | | 1 | |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nuculanidae | Leda | X | | X | | | | | | | | | 2 | 4 |
| | Portlandia | | | | | | X | | | | X | | 2 | |
| Astartidae | Astarte | X | | | | | X | X | | | X | | 4 | 4 |
| Pectinidae | Pecten | | | | | | | X | | | | X | 2 | 4 |
| | Propeamussium | X | | | | | X | | | | | | 2 | |
| Arcidae | Arca | | | | | | X | X | | | X | | 3 | 3 |
| Lucinidae | Phacoides | | | | | X | | | | | | | 1 | 2 |
| | Myrtea | | | | | X | | | | | | | 1 | |
| Cuspidariidae | Cuspidaria | X | | | | | X | | | | | | 2 | 2 |
| Hiatellidae | Hiatella | X | | | | | X | | | | | | 2 | 2 |
| Tellinidae | Macoma | X | | | | | | | | | | | 1 | 1 |
| Arcticidae | Cyprina | | X | | | | | | | | | | 1 | 1 |
| Cardiidae | Cardium | X | | | | | | | | | | | 1 | 1 |
| Corbulidae | Corbula | | X | | | | | | | | | | 1 | 1 |
| Myacidae | Mya | X | | | | | | | | | | | 1 | 1 |
| Limidae | Lima | | | | | | | | | | X | | 1 | 1 |
| Mytilidae | Dacrydium | | | | | | X | | | | | | 1 | 1 |
| **Gastropoda** | **Total** | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 4 | |
| Turritellidae | Turritella | | X | | | | | | | | | | 1 | 1 |
| Aporrhaidae | Aporrhais | | X | | | | | | | | | | 1 | 1 |
| Philinidae | Philine | | | | | | | | | X | | | 1 | 1 |
| Acteocinidae | Cylichna | | | | | | | | | X | | | 1 | 1 |
| **Scaphopoda** | **Total** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Dentaliidae | Dentalium | | | | | X | | | | | | | 1 | 1 |

ciates of *Thyasira*: the Lucinacea (besides *Thyasira,* the genera *Axinopsis, Phacoides, Myrtea*) ; the Nuculanidae (*Leda, Portlandia*) ; the Nuculidae (*Nucula*) ; the Semelidae (*Syndosmya=Abra, Theora*) ; the Pectinidae (*Pecten, Propeamussium*) ; and the *Astartidae* (*Astarte*). With the exception of the pectinoids, these are all infaunal bivalves and predominantly filter feeders (*Nucula* being a partial detritus feeder in the loose sense), which show a strong preference for soft mud substrate. Their association reflects very similar environmental demands. This basic "assemblage" of bivalves commonly inhabiting environments preferred by *Thyasira* is not uncommonly supplemented by the infaunal *Cuspidaria* and the epifaunal *Arca*. The general absence of numerous gastropods, scaphopods, and attached epifaunal bivalves is striking in modern *Thyasira*-rich assemblages. These are commonly associated with *Thyasira* only in particular niches. *Arca* (usually *A. glacialis*), *Dacrydium* (Mytilidae) and possibly *Lima* (Limidae) are the only attached epifaunal elements.

Molluscan assemblages associated with Cretaceous *Thyasira* from the Western Interior show both similarities and differences when compared with Recent communities containing abundant Thyasiridae. These fossil assemblages are considered representative of actual living associations for the following reasons: (a) many of the shells have coattached valves and are oriented in living position; (b) the shells do not show signs of wear or breakage due to transport; (c) the shells occur predominantly in limestone concretions in finely, evenly laminated shale where they have been enclosed and protected from crushing and reworking before or shortly after the beginning of diagenesis, at or near the water-sediment interface (see Kauffman, 1965, p. 177, 178). There is no evidence of active current or wave action that would destroy lamination or erode the exposed shells on the substrate; and (d) the fossil assemblage, within the limits of comparison to modern communities, does not appear to contain abnormal ecologic elements.

Among the similarities between Cretaceous and Recent assemblages supporting large *Thyasira* populations are: (a) the restricted scope of the assemblage, (b) the dominance of bivalves over gastropods and scaphopods, (c) the dominance of infaunal over epifaunal bivalves, (d) specific taxonomic associations, and (e) the predominant association of the assemblage with fine clay sediments in mid-Temperate latitudes (text fig. 12).

Differences between fossil and Recent assemblages are: (a) the more restricted scope of Cretaceous mollusk assemblages, particularly in regard to still extant genera; (b) the relatively greater representation of attached epifaunal bivalves; and (c) specific differences regarding associated genera.

As shown in Table 2, only 18 genera of mollusks, 10 of them extinct, have been found associated with Cretaceous *Thyasira,* the maximum in any one assemblage being 10 (including *Thyasira*), the minimum 2, and the average assemblage consisting of 4.6 genera (and species). This itself is comparable with restricted modern assemblages occurring with *Thyasira,* but if *Cymbophora* (Cretaceous only), the extinct, mobile, pelagic to benthonic cephalopods and the ubiquitous epifaunal *Inoceramus* are removed from the list, the remaining assemblage, modern in aspect, has a maximum diversity of five genera, minimum of one (*Thyasira*) and average of two genera. This is significantly more restricted than Recent community counterparts, perhaps owing to collecting or preservation factors, as well as to ecologic substitution of living for extinct groups in the same niche. It reflects, however, equally restricted habitat preference and community association for Recent and fossil *Thyasira.* As in Recent assemblages, bivalves outnumber gastropods in diversity (seven genera compared to two) and number of occurrences. Gastropods have been observed at only one locality in association with *Thyasira* (USGS 10459). Although infaunal bivalves outnumber epifaunal elements in the fossil assemblages, (four genera compared to three), epifaunal bivalves are relatively much more important in the Cretaceous. This does not denote a distinctly different habitat for Cretaceous *Thyasira,* for all other evidence points to closely similar habitats for Recent and fossil species. It is instead directly attributable to the presence of the extinct genus *Inoceramus* and numerous cephalopods. As pointed out by Kauffman (1966, in press) the Inoceramidae were ubiquitous Mesozoic bivalves, widely spread in Cretaceous epicontinental seas without being tightly restricted by marine environments. Many species adapted to epifaunal living on soft mud bottoms in deep, moderately cool waters by development of broad, flat, thin, light-weight shells providing considerable surface area for effective support on unstable substrate. Establishment of large Inoceramids in soft mud substrate occupied by *Thyasira* in turn provided broad areas on the upper valves of *Inoceramus* for attachment of smaller epifaunal bivalves, accounting for the presence of *Pteria* and small *"Ostrea"* in Cretaceous assemblages and their absence in Recent associations with *Thyasira.* Numerous dead cephalopod shells, especially those of extinct ammonites, apparently

TABLE 2.—*Abundance of* Thyasira *and faunal associates, structure of mollusk assemblages, and dominant lithology at localities yielding* Thyasira *from the Upper Cretaceous of the Western Interior United States.*

Key to lithology: IC, ironstone concretions (siderite- limonite probably); LC, limestone concretions, usually argillaceous; S, Shaley; SC, siderite concretions; SH, Shale, usually dark, noncalcareous, thin bedded; SS, sandstone, usually fine- to medium-grained, argillaceous; TB, Tepee Butte limestone masses, irregular light colored argillaceous limestone bodies.

Key to fossil assemblages: H, *Hoploscaphites* assemblage; DO, *Didymoceras, Oxybeloceras* assemblage; question mark indicates not enough data available to define principle assemblages.

Key to abundance: R, rare, five or less specimens; C, common, more than five specimens per collection.

| USGS LOCALITIES | D5 | D65 | D255 | D709 | D714 | D1012 | D1215 | D1216 | D1410 | D1564 | D1864 | D1865 | D1866 | D2909 | D2910 | D3256 | D3260 | D3332 | D3933 | D3945 | D4162 | D4747 | 3763 | 3779 | 10459 | 10666 | 22838 | 22840 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LITHOLOGY | SH<br>TB | SH<br>SC | SH<br>IC | SH<br>LC | SH<br>LC | SH<br>TB | SH<br>TB | SH<br>IC | SH<br>LC | SH<br>TB | SH<br>IC | SH<br>IC | SH<br>IC | SH<br>IC | SH<br>TB | SH<br>LC | SH<br>IC | SH<br>LC | SH<br>TB | SH<br>LC | SH<br>IC | SH<br>SC | SS | SS<br>S | SH<br>LC | SH<br>SC | SH<br>LC | SH<br>IC |
| COMMUNITY | H | | | DO | | | DO? | DO | | ? | H | | | ? | ? | ? | ? | ? | ? | DO | ? | ? | ? | ? | ? | ? | DO | DO? |
| **BIVALVIA** | 1 | 3 | 6 | 2 | 3 | 3 | 4 | 4 | 4 | 3 | 2 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 4 | 2 | 2 | 3 | 1 | 1 | 2 | 2 | 5 | 4 |
| Thyasira | R | R | C | C | R | R | R | R | C | R | R | C | C | R | R | C | R | R | R | R | C | R | R | C | C | R | R | R |
| *Inoceramus | | R | C | | R | | R | C | C | | R | | | R | R | R | | | C | | | R | | | | C | R | R |
| Lucina | | | R | R | R | C | C | C | C | R | | | | | | C | | | C | R | C | | | | | | R | C |
| *Cymbophora | | | R | | | R | | | R | | | | | | | | | | | | | R | | | | | R | |
| Pteria | | | R | | | | | | | | | | | | | | | | R | | | | | | R | | | R |
| "Ostrea" | | | R | | | | R | R | | R | | | | | | | | | | | | | | | | | | |
| Nucula | | R | | | | | | | | | | | | | | | | | | | | | | | | | R | |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **GASTROPODA** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Aporrhais? | | | | | | | | | | | | | | | | | | | | | | | | | R | | | |
| Lunatia? | | | | | | | | | | | | | | | | | | | | | | | | | R | | | |
| **CEPHALOPODA** | 2 | 2 | 3 | 3 | 3 | 4 | 3 | 2 | 5 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 2 |
| *Baculites | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | R | C | C | R | C | C | C | C | C |
| *Hoploscaphites | R | R | R | | | | | | | | R | R | R | | | | | | | | | | | | | | | |
| *Didymoceras | | | | C | C | C | | C | C | | | | | | | | | | | | | | | | | | R | |
| *Oxybeloceras | | | | R | R | C | | | R | | | | | | | | | | | R | | | | | | | R | |
| *Anapachydiscus | | | | | | R | C | | | | | | | | | | | | | | | | | | | | | R |
| *Placenticeras | | | R | | | | | | R | | | | | | | | | | | | | | | | | | | |
| *Menuites | | | | | | | R | | | | | | | | | | | | | | | | | | | | | |
| *Scaphites | | | | | | | | | | | | | | | | | | | | | | | | | R | | | |
| *Eutrephoceras | | | | | | | | | R | | | | | | | | | | | | | | | | | | | |
| **SCAPHOPODA** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dentalium | | | R | | | | | | | | | | | | | | | | | | | R | | | | | | |
| **TOTAL MOLLUSKS** | 3 | 5 | 10 | 5 | 6 | 7 | 7 | 6 | 9 | 4 | 4 | 3 | 3 | 3 | 3 | 4 | 2 | 2 | 5 | 4 | 3 | 5 | 2 | 2 | 6 | 3 | 8 | 6 |

* Extinct genus.

littered the bottom of Cretaceous seas, providing additional firm substrate for attachment of epifaunal organisms.

Specific associations of extant molluscan genera with abundant Cretaceous *Thyasira* are closely comparable with modern assemblages. *Nucula, Aporrhais, Dentalium,* and Lucinidae (*Lucina* in the Cretaceous; *Phacoides, Myrtea* in the Recent) occur with *Thyasira* in both living and Cretaceous associations. This represents five-eighths of the genera associated with Cretaceous assemblages, and their presence strongly supports the theory that Cretaceous and Recent *Thyasira* lived under nearly identical environmental conditions and were specifically adapted to these niches. The remaining extant genera associated with Cretaceous but not Recent *Thyasira* do not detract from the validity of this argument since they are predominantly epifaunal elements (*Pteria, "Ostrea"*) whose presence has been explained in Cretaceous assemblages by the existence of firm substrate for byssal attachment and cementation (*Inoceramus* and dead cephalopod shells). The only other extant genus found in Cretaceous assemblages but not represented in Recent *Thyasira*-rich communities is *Lunatia*? sp., represented by a single occurrence in which specimens are rare. This occurrence has little significance for paleoecologic interpretation.

The preceding data indicates that *Thyasira*-rich communities of the Cretaceous were closely comparable in basic composition and environmental requirements to those of Recent seas. It is interesting to note that the Cretaceous mollusks associated with *Thyasira* clearly fall into two basic molluscan paleoassemblages which can best be recognized and defined on the basis of ammonite associations and relative abundance of the infaunal *Lucina*, whose anatomical, morphological, and ecologic characteristics are closely comparable with those of *Thyasira*. These are here tentatively designated the *Hoploscaphites* assemblage and the *Didymoceras-Oxybeloceras* assemblage. Identification of the two assemblages on the basis of ammonites is done with reservation, because (1) they are vagrant nektonic or benthonic elements and not as dependent on a particular bottom environment as most bivalves or gastropods, and (2) the three ammonite genera are known to occur together elsewhere, but not with *Thyasira*. Ammonites nevertheless form the most consistently diagnostic elements of each assemblage and it seems most logical to use them here until more extensive studies allow identification of molluscan assemblages based on infaunal or attached epifaunal elements.

Since paleocommunity studies of Cretaceous organisms are virtually nonexistent, a great deal of work must be done before the regional constancy of these two assemblages can be tested, their components clearly defined, and their applicability to Cretaceous paleoecology evaluated.

The *Hoploscaphites* paleoassemblage is characterized by the presence of this ammonite and *Baculites* to the exclusion of all other cephalopods, a single occurrence of *Placenticeras* (USGS D255) being the only exception. *Inoceramus* and *Thyasira* are the only abundantly associated bivalves. *Lucina* occurs sparingly with *Hoploscaphites* at several localities, but is not common in this assemblage as it is with the *Didymoceras-Oxybeloceras* paleoassemblage. A diverse association of additional mollusks is not developed in this assemblage except at one locality (USGS D255). Scaphopods, gastropods and *Pteria* are known sparingly but exclusively with *Hoploscaphites.* The *Hoploscaphites* assemblage is typically developed at localities D5 (zone of *Baculites asperiformis*), D65 (zone of *B. scotti;* upper part) D255, D1864 (zone of *B. perplexus,* early form; lower part), D1865 (zone of *B. perplexus,* early form; middle part); and D1866 (zone *B. perplexus,* early form; late part).

The *Didymoceras-Oxybeloceras* paleoassemblage is characterized not only by one or both of these ammonite genera but also by (a) a diverse assemblage of other cephalopods (*Baculites, Anapachydiscus, Placenticeras, Menuites,* and *Eutrephoceras,* singly or in association), (b) consistently occurring and generally abundant *Lucina, Inoceramus,* and *Thyasira* and (c) a locally diverse associated mollusk fauna (*Cymbophora, Ostrea, Nucula*). *Hoploscaphites, Pteria,* gastropods, and scaphopods have not yet been found associated with this assemblage. The *Didymoceras-Oxybeloceras* paleoassemblage is typically developed in the zone of *Baculites scotti* at the following localities: D709, D714, D1012, D1216, D1410, D3945, and 22838.

These two paleoassemblages overlap only in the zone of *Baculites scotti* so that their differences may be due in part to time, expressed in single group as well as community evolution, or migration rates and patterns. Their primary distinction, however, is thought to be environmental, owing both to lateral variation within the basin at any given time (as in the zone of *B. scotti*) and to broad environmental shifts through time. Based on comparison with modern communities, the greater numbers and diversity of mollusks associated with the *Didymoceras-Oxybeloceras* paleoassemblage probably indicates shallower water conditions with more normal marine water and substrate chemistry, and higher productivity, than does the *Hoploscaphites* paleoassemblage. The presence of the mactrid bivalve

*Cymbophora* and the greater abundance of oysters in the former assemblage would support this conclusion. The lack of any pattern of differentiation regarding substrate characteristics and relative abundance of important faunal elements such as *Thyasira, Inoceramus,* and *Baculites* in the two assemblages, however, suggests environmental distinctions between them were not great and prohibits more detailed interpretation of their differences.

## SUBSTRATE RELATIONSHIPS

Living *Thyasira* inhabit a broad range of substrate types (text fig. 9), but are predominantly found in clay, ooze, or mud with or without accessory silt, sand, and coarser clastic debris (pebbles, gravel, cobbles). They are most common in sediment without any coarse detritus, and prefer soft mud to hard, plastic clays, although they will inhabit either in preference to coarse material. *Thyasira* has been reported in association with many types and colors of clay-size substrate (red, brown, gray, yellow) but there is no indication of preference for one over the other. Species are only moderately abundant in sand, and uncommon on pebble, gravel, and cobble bottoms. A few species are sediment selective, preferring soft to hard clay bottoms (or vice versa), or silty and sandy clay to purer clay substrate. Some Recent *Thyasira,* at least, prefer clay substrate in areas low in particulate food and chemically unfavorable to many other infaunal mollusks over normal marine bottom conditions supporting a rich molluscan infauna in a physically identical substrate.

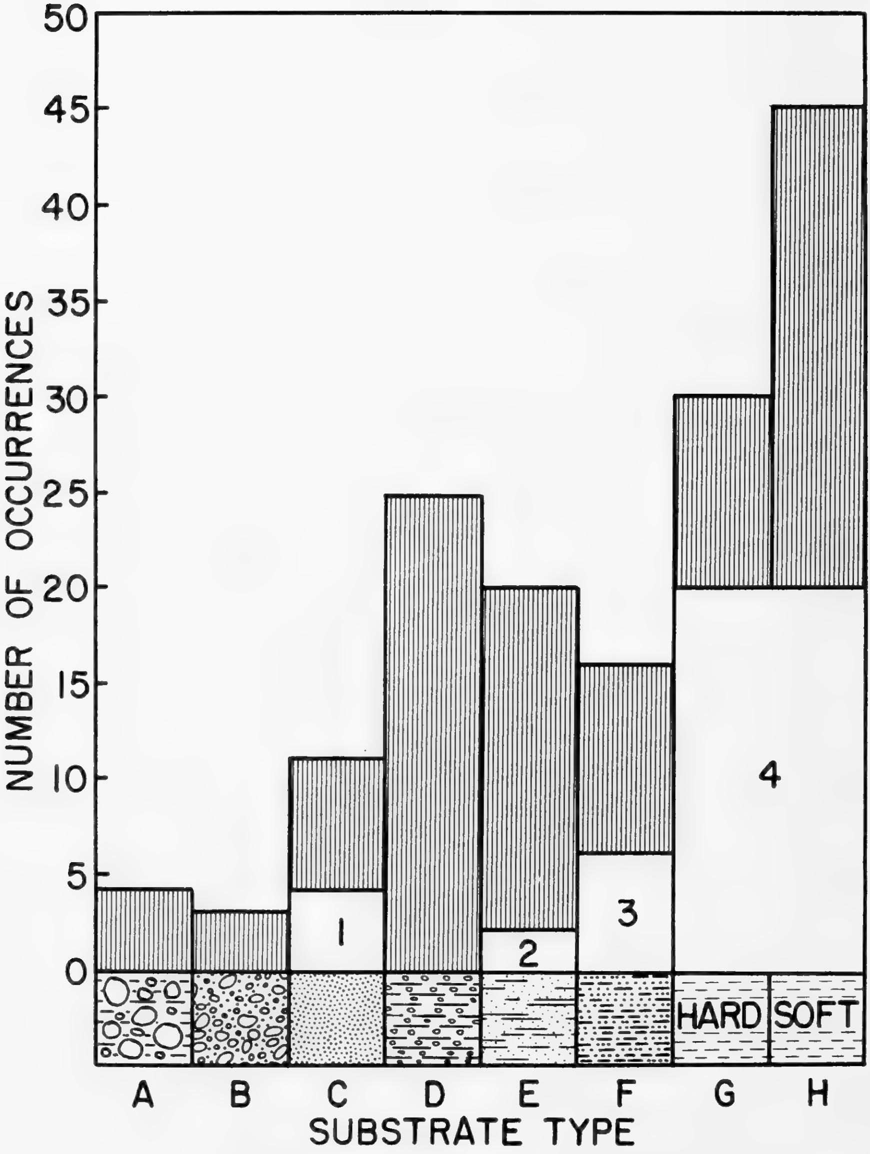
Cretaceous *Thyasira* display the same substrate relationships as their living counterparts (text fig. 9). The majority of specimens (65 percent) come from limestone concretions, probably formed at or near the water-substrate interface during early diagenesis, embedded in dark, relatively pure clay shale. Many shells from this lithology are bivalved and in or near living position. Most of the other occurrences are in silty and sandy shale cemented secondarily by calcium carbonate (commonly as concretions), or in silty, light-colored limestone of "Tepee buttes," thought by Dane, Pierce and Reeside (1937, p. 228, 229) to be deposits of precipitated calcium carbonate mixed with normal substrate material at the sites of low-volume submarine springs. A few localities yielded *Thyasira* from fine-grained, calcareous and argillaceous sandstones. At least half of the latter occurrences contained mainly single valves, reworked at the sediment-water interface, and lying in the plane of the bedding with the convex surface upward. No Cretaceous Thyasiridae have been found associated with clastics coarser than fine-grained sand.

## GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION

Living *Thyasira* are distributed throughout the world, from the Arctic to the Antarctic (text fig. 10). Individual species are generally restricted to a single broad geographic province such as the North Atlantic or Indo-Pacific regions. Allen's statement that the Lucinacea are predominantly Tropical and Subtropical faunal elements (1958, p. 423) does not apply specifically to the Thyasiridae, and especially not to the genus *Thyasira*. The greatest number and diversity of living *Thyasira* is in the mid-Temperate latitudes (text fig. 10): the genus is common in warm Temperate, cool Temperate, Subarctic, and Subantarctic waters. *Thyasira* is rare and locally absent in Arctic, Antarctic, and Tropical waters. They apparently show strong preference for cool-water conditions, therefore, although data on specific bottom temperatures at collecting sites is practically nonexistent in the literature. This preference is further indicated by the fact that species with a broad latitude distribution are found in progressively deeper and cooler waters toward the southern part of their geographic range (text fig. 11). This same trend is less clearly reflected, but persistent, in a cumulative depth-range analysis of numerous living species relative to latitude (text fig. 11). In this analysis, the overall depth range of the genus does not change appreciably from north to south, but the greatest density of species diversity moves progressively deeper from cool Temperate toward equatorial waters.

Depth, therefore, in conjunction with temperature are additional critical factors controlling the ecologic distribution of living and presumably fossil *Thyasira*. Most large assemblages of *Thyasira* occur in outer sublittoral and outer edge of the inner sublittoral bottom zones. In addition, species occur commonly at bathyal and abyssal depths, to at least 7500 feet, and in the inner sublittoral zone, but generally deeper than the near-shore environments which are so characteristically rich in mollusks. The depth distribution of living *Thyasira* is summarized in figures 10 and 11.

The geographic distribution and general diversity gradient of Cretaceous *Thyasira* from the Western Interior is strikingly similar to that of Recent species (text fig. 12). The greatest concentration of species is found between 38° and 44° north latitude, somewhat south of the zone of maximum development in modern seas, but

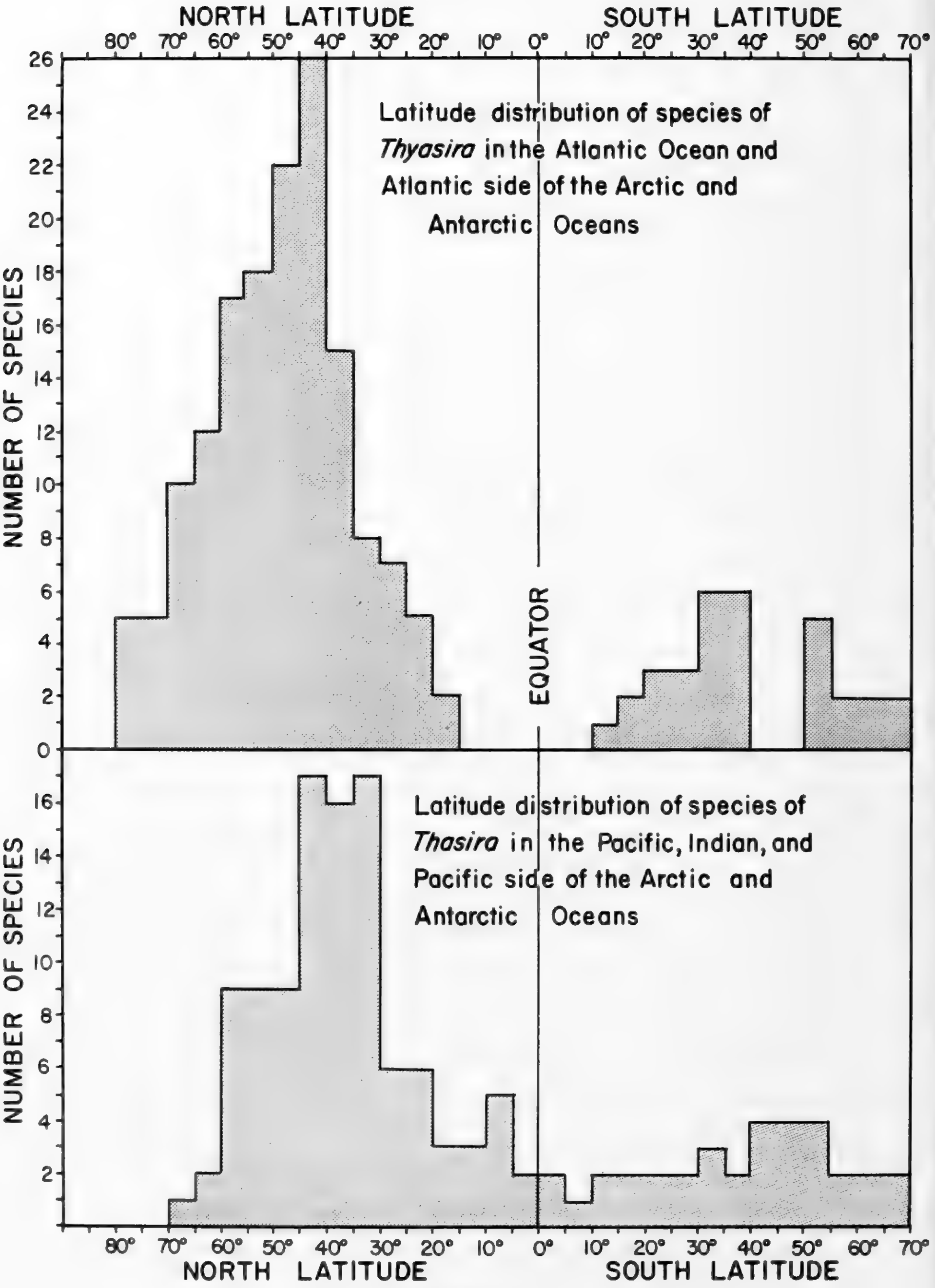


Text Figure 9.

nevertheless within the mid-Temperate region. No species are known to the south of this area. *Thyasira* occurs sparingly in Canada (three subspecies at three localities in Alberta), and only one specimen has been reported from the Cretaceous of Greenland. These data, although skewed by the relative amount of collecting in different areas, the geography of the Cretaceous outcrop area, and other factors are generally indicative of similar geographic and environmental distribution in Cretaceous and Recent *Thyasira.*

Within the zone of maximum abundance (38° to 44° north latitude), Cretaceous *Thyasira* display some interesting distribution patterns. Most obviously, the diversity gradient increases from north to south in each restricted span of time (as defined by ammonite zones) during which large populations of *Thyasira* developed, with the maximum subspecies diversity at the southern edge of the range (text fig. 12). A total plot of species and subspecies for the entire span of Cretaceous time from which *Thyasira* is known in the interior shows the same distribution pattern (text fig. 12, column 1). This is difficult to explain in terms of modern distribution, where the maximum diversity gradient occurs near the middle of the total range in each hemisphere (text fig. 10), but may indicate a relatively sharp change in temperature or depth conditions in the Western Interior basin between central Colorado and northern New Mexico so that the southern tail of the diversity gradient curve did not develop. A restriction of the seaway in this area demonstrated by Reeside (1957, fig. 17) during the time when *Thyasira* was most abundant, may have produced relatively

TEXT FIGURE 9.—Distribution of living and Cretaceous *Thyasira* (Western Interior species only) relative to substrate type, showing primary preference for clay without coarser material (especially where soft), strong secondary distribution in clay containing sand, silt, or pebbles, and poor representation of the genus in coarse clastics. There is very close agreement between Cretaceous (white areas with numbers) and Recent (vertically lined areas) substrate distribution. Key to substrate for Recent occurrences: **A**—coarse cobbles in a pebble-clay-sand matrix; **B**—pebbly sand; **C**—coarse to fine sand, silty sand, and sandy silt; **D**—pebbly clay; **E**—sandy clay; **F**—silty clay; **G**—firm clay (usually dark) without coarser clastic material; **H**—soft clay without coarser clastic material. Key to fossil substrate distribution: 1—sandstone, usually with calcareous cement and little clay; 2—sandy shale, usually cemented secondarily into concretionary masses by calcium carbonate; 3—silty shale, usually cemented secondarily into concretionary masses by calcium carbonate; 4—clay shale cemented secondarily into concretionary masses by calcium carbonate. The fossil distribution, in white, is *superimposed* onto living distribution (vertical dark lines); the two sets of data are not stacked.



Text Figure 10.

abrupt shallowing with coarser-grained substrate and created unsuitable habitats to the south of central Colorado.

A second significant distribution pattern shown by Cretaceous *Thyasira* is the gradual shifting of the southern limit of their range to the south from the time of their apparent introduction into the interior seaway (zone of *Baculites* sp. with weak flank ribs; Early Campanian), to the time of their disappearance (zone of *B. scotti;* Late Campanian). This southern migration apparently took place in three spurts, an initial one at the time of introduction, a second one during the early Late Campanian (zone of *B. asperiformis*), and a final one during the middle Late Campanian (zone of *B. scotti*). The latter two shifts were of 1 or 2 degrees latitude. The most logical explanation of this pattern would be that *Thyasira* was following a gradual southern migration of cool Boreal waters into the Western Interior basin. Because of the limited number and scope of collections involved, however, this will have to be substantiated from studies of other invertebrates before the validity of a major temperature fluctuation can be established.

## CONCLUSIONS

Living *Thyasira* are most severely restricted in their ecologic distribution by water temperature, depth, water and substrate chemistry, sediment type and firmness, amount of particulate food in suspension, and competition from other filter-feeding organisms. Most living species prefer deep inner or outer sublittoral and bathyal environments in cool to cold waters where the substrate is soft mud without coarse clastic material. Many species live at shallower depths in the northern part of their range than in the southern part, suggesting temperature is a principal controlling factor

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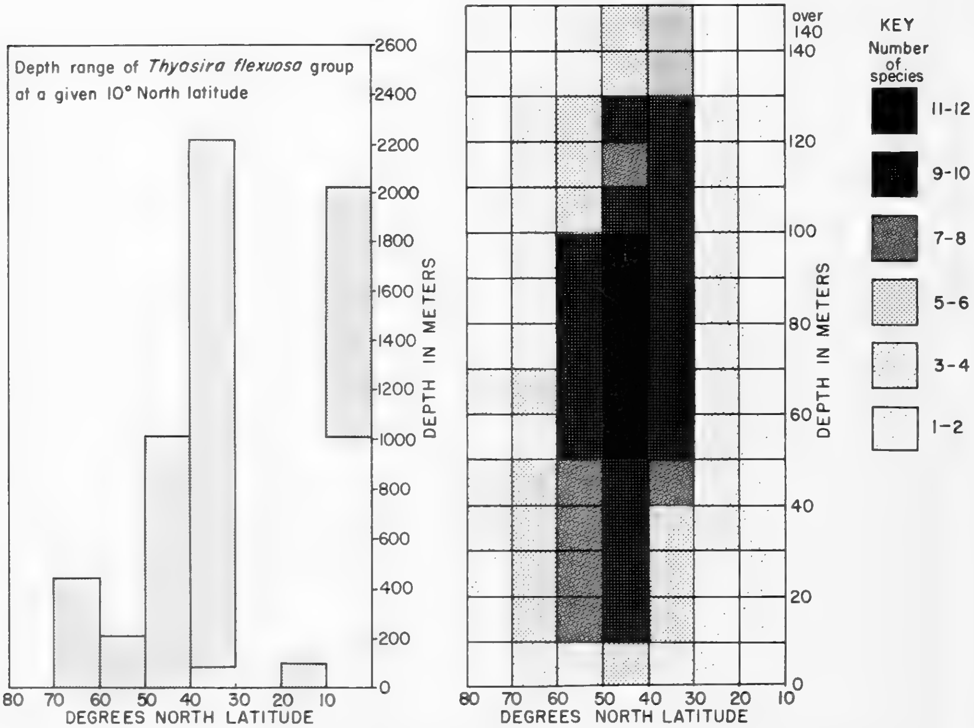
Text Figure 10.—Species diversity of living *Thyasira* relative to degrees latitude, generally reflecting water temperature. Note maximum diversity in both hemispheres, and in both major ocean basins, between 30 and 55 degrees latitude (cool-temperate), and especially between 30 and 45 degrees. Small number of species in Southern Hemisphere compared with the Northern Hemisphere probably reflects the relative amount of collecting and research in the two areas rather than an environmental distribution factor. Southern shift of maximum diversity in the Indo-Pacific area as compared with the Atlantic may be due to colder marginal currents and upwellings along the steep eastern Pacific margin, with its narrow shelf, than found along the shallow broad Atlantic shelf affected by the Gulf Stream. Note the close correlation of species diversity gradients relative to latitude between living and Cretaceous *Thyasira* by comparing this chart with text figure 12.



TEXT FIGURE 11.—Depth distribution of living *Thyasira* demonstrating general shift of bathymetric range from shallow water in the north to progressively deeper waters in the southern part of the Northern Hemisphere, in response to temperature control on species distribution. Graph on left drawn only from forms in the *Thyasira flexuosa* species complex; data sparse and ranges not significant between 10 and 30 degrees north latitude. Graph on right drawn on all species for which records were available; density of stippling reflects numbers of species occurring within any depth range at a given 10 degrees north latitude. Although the total bathymetric range of the genus is nearly equivalent in all areas between 10 and 80 degrees north latitude, the maximum diversity of species for any 10 degrees latitude shifts to deeper and cooler waters in the south. Overall maximum species diversity occurs between 40 and 50 degrees north latitude at depths of 50-100 meters, defining optimum environmental conditions for *Thyasira*. Data drawn from approximately 100 general surveys of Atlantic and Pacific mollusks, and from collections at the U.S. National Museum.

in their distribution. Some environmental niches supporting large populations of *Thyasira* are characterized by adverse chemical conditions (low in oxygen, high in hydrogen sulfide) and/or by a sparse food supply and low biotic productivity. Most niches preferred by *Thyasira* support molluscan assemblages of restricted scope, five or fewer genera and species. Lucinacea, Nuculidae, Nuculanidae, Semelidae, Astartidae, and Pectinidae are the most consistently associated molluscan elements. These are predominantly infaunal filter feeders or mobile epifaunal bivalves (Pectinidae). A paucity of attached epifaunal mollusks is characteristic of many *Thyasira*-rich communities. Living *Thyasira* are peculiarly adapted to these niches, especially in the formation of an anterior inhalent tube for feeding and respiration, and in their ability to accept and utilize large food particles.

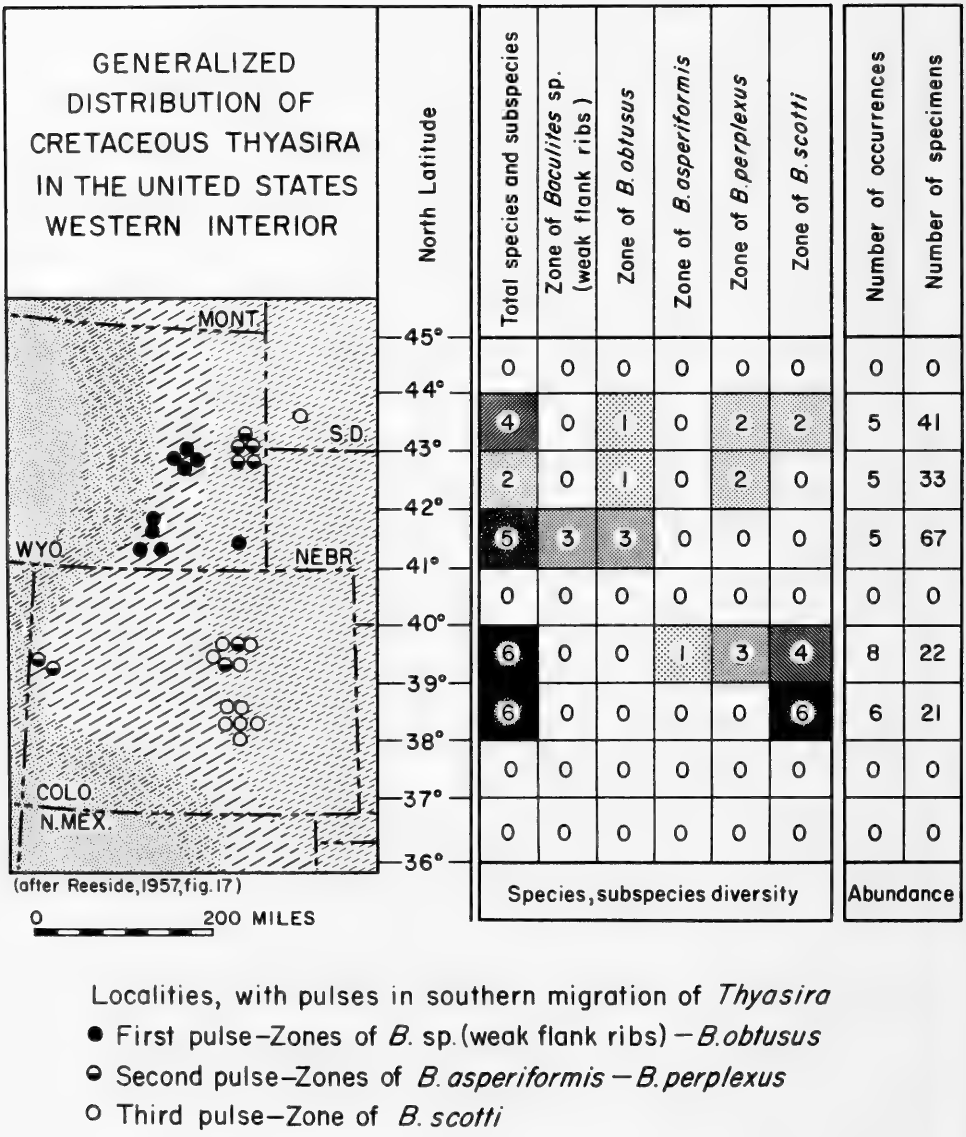
Cretaceous *Thyasira* from the Western Interior of North America apparently had environmental requirements similar to those of Recent species and displayed preference for the same ecologic niches. The following lines of evidence support this: (a) careful study of the interior morphology of Cretaceous shells indicates anatomical modifications to cope with particular environmental situations were nearly identical in Cretaceous and Recent species; (b) the molluscan faunas associated with Cretaceous and Recent *Thyasira* are closely comparable in diversity and, with the exception of extinct groups, composition; (c) Cretaceous and Recent species demonstrate the same substrate preferences; (d) the geographic distribution and species diversity gradients are similar for Cretaceous and Recent *Thyasira*.

The presence of abundant *Thyasira* and the diversity of the mollusks associated with them in Cretaceous rocks of the Western Interior should be useful indicators of substrate conditions, water depth, and temperature in paleoecologic interpretation. The abrupt appearance of *Thyasira* in the northern and central parts of the Western Interior basin during the Campanian probably indicates establishment of a connection with boreal waters and subsequent cooling of the northern half of the interior sea, possibly accompanied by deepening of parts of the basin.

## PHYLOGENY AND EVOLUTION

### INTRODUCTION

Two factors limit interpretation of the phylogeny and evolution of Cretaceous *Thyasira* in the Western Interior. (1) They are



| North Latitude | Total species and subspecies | Zone of *Baculites* sp. (weak flank ribs) | Zone of *B. obtusus* | Zone of *B. asperiformis* | Zone of *B. perplexus* | Zone of *B. scotti* | Number of occurrences | Number of specimens |
|---|---|---|---|---|---|---|---|---|
| 45°–44° | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 44°–43° | 4 | 0 | 1 | 0 | 2 | 2 | 5 | 41 |
| 43°–42° | 2 | 0 | 1 | 0 | 2 | 0 | 5 | 33 |
| 42°–41° | 5 | 3 | 3 | 0 | 0 | 0 | 5 | 67 |
| 41°–40° | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 40°–39° | 6 | 0 | 0 | 1 | 3 | 4 | 8 | 22 |
| 39°–38° | 6 | 0 | 0 | 0 | 0 | 6 | 6 | 21 |
| 38°–37° | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 37°–36° | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Species, subspecies diversity | | | | | | Abundance | |

Text Figure 12.—Generalized lithologic and latitude distribution of Cretaceous *Thyasira* in the Western Interior United States (on map), in addition to species diversity gradients and pulses of migration during the Cretaceous (chart to right of map). Map taken from J. B. Reeside, Jr. (1957, fig. 17), highly generalized for the Early Campanian and generally applicable to the early part of the Middle Campanian (zone of *Baculites scotti*). From west to east, lithologic types indicated by patterns are: sand, sandy mud, fine known from a restricted part of the stratigraphic column, representing a relatively short period of geologic time (approximately 4.6 million years) in which environmental conditions favorable for their habitation persisted. (2) Their evolution has been relatively conservative within this time period, and for that matter from the Cretaceous to the Recent. The phylogenetic roots of the species complexes are not wholly known and must be inferred primarily from morphologic similarity of species and subspecies which characterize the earliest migration of *Thyasira* into the Western Interior trough. The degree of morphologic similarity between marginal population variants of species and the average morphologic expression of contemporary taxa had to be relied upon as an indicator of (a) degree of phylogenetic relationship, and (b) the chronologic sequence of phylogenetic splitting. The early history of the species complexes represented in the Western Interior—their origin and initial radiation—is probably buried in pre-Campanian or earliest Campanian rocks, representing moderately deep cool water environments, which are not yet known in the exposed Cretaceous rocks of the Northern Hemisphere.

The following remarks on phylogeny are therefore generalized and speculative, and little can be said about broad evolutionary trends. Instead, interpretation of the evolution in particular lineages deals with specific features, some of which can be explained as adaptive mechanisms, others of which cannot be interpreted even though a thorough knowledge of the anatomy of the animal is available. Text figure 13 shows the inferred phylogenetic relationships and general evolutionary trends in shell morphology observed in this study.

Two major thyasirid species complexes appear to be present in the Cretaceous rocks of the Western Interior (text fig. 13), one centered around the lineage of *Thyasira rostrata*, the other around

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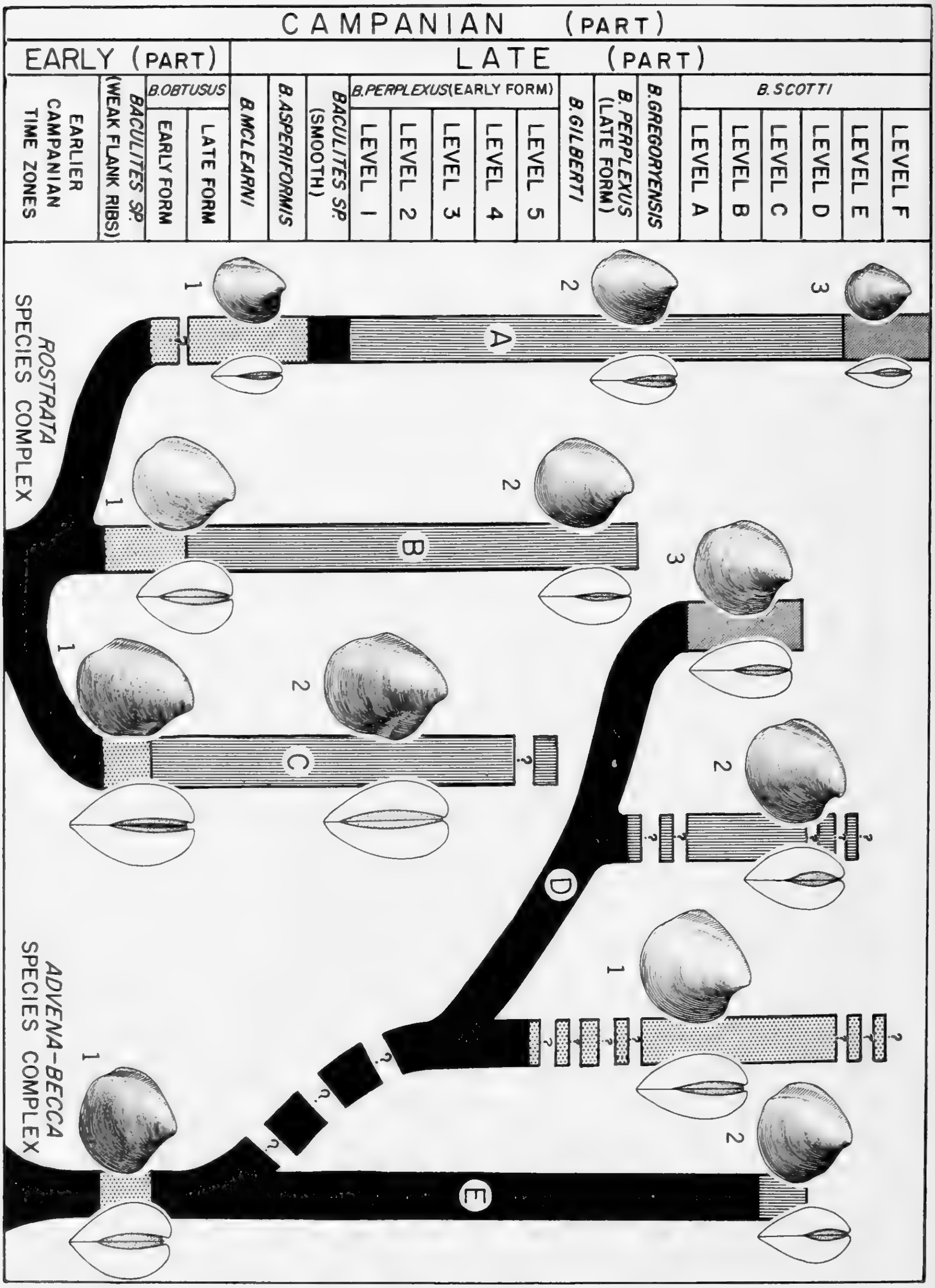
gray mud, and fine black mud (after Reeside, 1957, p. 514). A strong preference is indicated in Cretaceous *Thyasira* for fine muds without coarser clastic material, as in living species. The chart shows a shift in southernmost occurrence of *Thyasira* in progressively younger ammonite zones, implying migratory pulses (keyed to locality points on map), with the maximum species diversity occurring at southern end of the genus range during each pulse. A close correlation exists between data on latitude distribution of total range and maximum diversity range of Cretaceous *Thyasira* with that of Recent species (text fig. 10). Constriction of seaway at southern end of map may account for elimination of southern tail of distribution curve in fossil species that normally occurs on Recent species distribution charts (see text fig. 10).



Text Figure 13.

TEXT FIGURE 13.—Phylogeny and evolution of Cretaceous *Thyasira* in the Western Interior of North America. Black lines show hypothetical phylogenetic relationships, questionable where dashed, in time intervals for which no specimens representing the lineages have been found. Coarse dotted pattern designates range of oldest subspecies in each species group; vertical lines designate youngest subspecies in each species group; fine dotted pattern represents distinct species phylogenetically arranged with the species groups from which they were derived. Dashed and queried portions of these ranges denote possible extension of established ranges based on vague stratigraphic data. The following major evolutionary trends are apparent:

1. In the *T. quadrula* species group (**column A**) reduction of the dorsoanterior flank, increase in inclination of the anterodorsal slope, decrease in convexity and the apical angle, posterior migration and straightening of the primary sulcus, and dorsal migration of the primary sulcus notch. Key: 1, *T. quadrula quadrula; 2, T. quadrula arrecta; 3, T. triangulata.*

2. In the *T. rostrata* species group (**column B**), decrease in convexity, and in relative size of the escutcheon, decrease in relative height and projection of the beaks, increase in the apical angle with expansion of the dorsoanterior flank and decrease of the anterodorsal slope. Key: 1, *T. rostrata rostrata; 2, T. rostrata cracens.*

3. In the *T. beauchampi* species group (**column C**) decrease in convexity, expansion of dorsoanterior auricle and anterior sulcus, decrease in curvature and prominence of beak and umbo, and straightening of primary sulcus with dorsal migration of the notch. Key: 1, *T. beauchampi beauchampi; 2, T. beauchampi rex.*

4. In the *T. advena* species group (**column E**), decrease in convexity, posterior migration of the primary sulcus, decrease in inclination of the beaks, increase in relative projection of the beaks and depth of concave notch anterior to them. Key: *T. advena advena; 2, T. advena browni.*

5. In the *T. becca* species group (**column D**), increase in relative length, projection of the dorsoanterior flank, convexity, and beak inclination, accentuation of the anterodorsal notch below the beaks, posterior migration of the primary sulcus and decrease in the projection and angularity of the midposterior marginal beak in slope. If *T. cantha* (no. 3) is a branch of this lineage it shows further posterior migration of the primary sulcus and reduction of the flank posterior to it, as well as reduction of the beaks. Key: 1, *T. becca becca; 2, T. becca cobbani.*

All specimens except *T. triangulata* (× 1) illustrated one-half actual size. Illustrated specimens: *T. triangulata,* USNM 153418; *T. quadrula arrecta,* USNM 153456; *T. quadrula quadrula,* USNM 153470; *T. rostrata rostrata* USNM 153488; *T. rostrata cracens,* USNM 153429; *T. beauchampi beauchampi,* USNM 153412; *T. beauchampi rex,* USNM 153409; *T. advena advena,* USNM 153417; *T. advena browni,* USNM 153416; *T. becca becca,* USNM 153522; *T. becca cobbani,* GSC 18758 (reduced 20 percent); *T. cantha,* USNM 153477 (image reversed). Shell material and broken margins restored in drawings; refer to photographs of same specimens on plates.

*T. advena* and *T. becca*. The *T. rostrata* species complex includes generally erect, vertically subovate, subtriangular, or subquadrate shells with the height greater than the length, the beaks suberect to moderately prosogyrate, the notch anterior to the beaks shallow to moderately deep, and the dorsoanterior flank weakly to moderately projecting (text fig. 13, left). In most the primary sulcus is narrow to moderately broad, shallow, and the fold posterior to it is narrow. Two lineages have a well-defined anterior sulcus in one or all of the included taxa. Were it not for the presence of marginal variants in *T. rostrata rostrata* populations with an expanded dorsoanterior flank, somewhat reduced beaks, and a generally subquadrate outline suggesting affinities to *T. quadrula* (pl. 3, figs. 1-6), the subquadrate to subtriangular shells of the *T. quadrula* lineage might well have been considered a distinct species complex.

The *T. advena-T. becca* complex is characterized by species and subspecies with round to horizontally subovate shells, in which the length is equal to or greater than the height, and the beaks moderately to strongly prosogyrate, in some cases overhanging the anterodorsal margin, forming a deep notch below them. The primary sulcus is broad, prominent, moderately incised, and strongly curved. The flank or fold posterior to it is normally prominent—broad, posteriorly angulate or auriculate, and moderately arched.

## THE THYASIRA ROSTRATA SPECIES COMPLEX

*General phylogeny.*—Three distinct lineages form the *T. rostrata* species complex. Two of them, the lineage of *T. rostrata* (text fig. 13, B) and that of *T. beauchampi* (text fig. 13, C) are morphologically similar in having large erect, moderately prosogyrate and prosocline, inflated shells with strongly projecting beaks and curved shell margins. The third lineage, that of *T. quadrula* is more distinct in having small, slightly to moderately inflated shells with reduced beaks, a straight posterior margin and primary sulcus, subquadrate to subtriangular outline, and an expanded dorsoanterior flank (text fig. 13, A). The three lineages are arranged into a single species complex on the basis of morphologic variation shown by large populations of *T. rostrata rostrata*, considered to represent the main parent stock of the complex. In these populations, especially that from USGS Mesozoic locality 10459 (zone of *Baculites* sp. with weak flank ribs, the earliest occurrence of any thyasirid lineage in the Western Interior), variants of *T. rostrata rostrata* at one end of the spectrum display characters similar to, but not entirely overlapping the typical morphology of *T. beauchampi,* and at the other extreme show more distant morphologic affinities to *T. quadrula* and its descendents. These transitional forms are illustrated on plate 3, figures 1-11.

The lineages of *T. rostrata* and *T. beauchampi* both appear in the Western Interior, already distinctly separated, in the first wave of thyasirid migration during the Cretaceous (zone of *Baculites* sp. with weak flank ribs). Based on a high degree of morphologic similarity between species groups, it would appear that the *T. beauchampi* lineage represents a relatively young split from the main *T. rostrata* lineage, possibly branching off from this main line of evolution in the earliest Campanian just prior to the introduction of *Thyasira* into the Western Interior seas. The lineages probably had a North Atlantic origin, based on modern distribution of similar thyasirid bivalves. The *T. quadrula* lineage appears in the Western Interior after the first introduction of the genus in this area, and based on this would appear to be possibly a later derivative from the main stock of *T. rostrata,* as shown in text figure 13. The greater morphologic separation of *T. quadrula* from *T. rostrata,* however, would indicate just the opposite relationship, that the *T. quadrula* lineage was an older branch of the *T. rostrata* stock than that represented by *T. beauchampi,* and had become more distinct genetically by the time *Thyasira* first appeared in the Western Interior than had *T. beauchampi.* The present collections and lack of knowledge on the earlier phylogeny of the species complex does not permit this conflicting evidence to be resolved either as (1) rapid genetic differentiation of the *T. quadrula* lineage during the Late Campanian or as (2) incomplete representation of the range of *T. quadrula* in the fossil record.

Unfortunately the principal causes for the initial differentiation of the *T. rostrata* stock into three distinct lineages cannot be properly evaluated with the evidence at hand. All three forms predominantly inhabited the same substrate, dark clay muds, and no differentiation of sediment types or structures, possibly indicative of different sedimentary environments, could be made. *Thyasira rostrata rostrata* and *T. beauchampi beauchampi* occur together at USGS Mesozoic locality 10459 in a single zone of concretions, and apparently lived within close proximity. If the radiation of the lineage into three species groups was in response to the availability of different environmental niches for habitation, these were probably chemical or depth niches and cannot be ascertained at present from the known gross physical aspects of the substrate.

Following the initial radiation of the *T. rostrata* lineage (text fig. 13), the various species groups, closely related at first (zones of *Baculites* sp. with weak flank ribs; zone of *B. obtusus*), subsequently each gave rise to younger and morphologically more distinct subspecies which do not show any significant overlap in numerous morphologic features, even in the marginal variants of their populations. These are illustrated in text figure 13. Their individual evolutionary trends are discussed below.

*The Thyasira quadrula lineage.*—Three successively derived species and subspecies constitute the *T. quadrula* lineage (text fig. 13, A), in ascending order, *T. quadrula quadrula,* n. subsp., *T. quadrula arrecta,* n. subsp., and *T. triangulata* n. sp. This is the best defined evolutionary sequence among the Cretaceous *Thyasira* of the Western Interior, and many of the observed changes through time are chronoclinal. The outstanding evolutionary trends (see text figs. 13, 14) in the lineage are: (a) reduction of the apical angle (Angle C) (text fig. 14, D), (b) reduction of the dorsoanterior flank of the shell and increase in the slope of the anterodorsal margin (text fig. 13), (c) increase in the relative projection of the beaks (text fig. 13), (d) slight decrease in the prosogyre inclination of the beaks and umbos (text fig. 13), and (e) modification of the primary sulcus as follows—ventral shift of the primary sulcus notch relative to overall height (text fig. 14, C), and decrease in curvature and relative width of the primary sulcus (text fig. 13) as its ventral one-half attains a position progressively closer to the straight posterior margin in time-successive taxa. There is, in addition, a trend toward decreasing valve convexity (text fig. 14, A), ventral shift of the midposterior break in slope at the dorsal margin of the primary sulcus notch (text fig. 14, B), and increase, then subsequent decrease of angle D (text fig. 14, E). Observations on the shell interior indicate possibly a slight decrease in the relative size of the adductor muscle insertion areas in progressively younger species and subspecies of the lineage (text fig. 18).

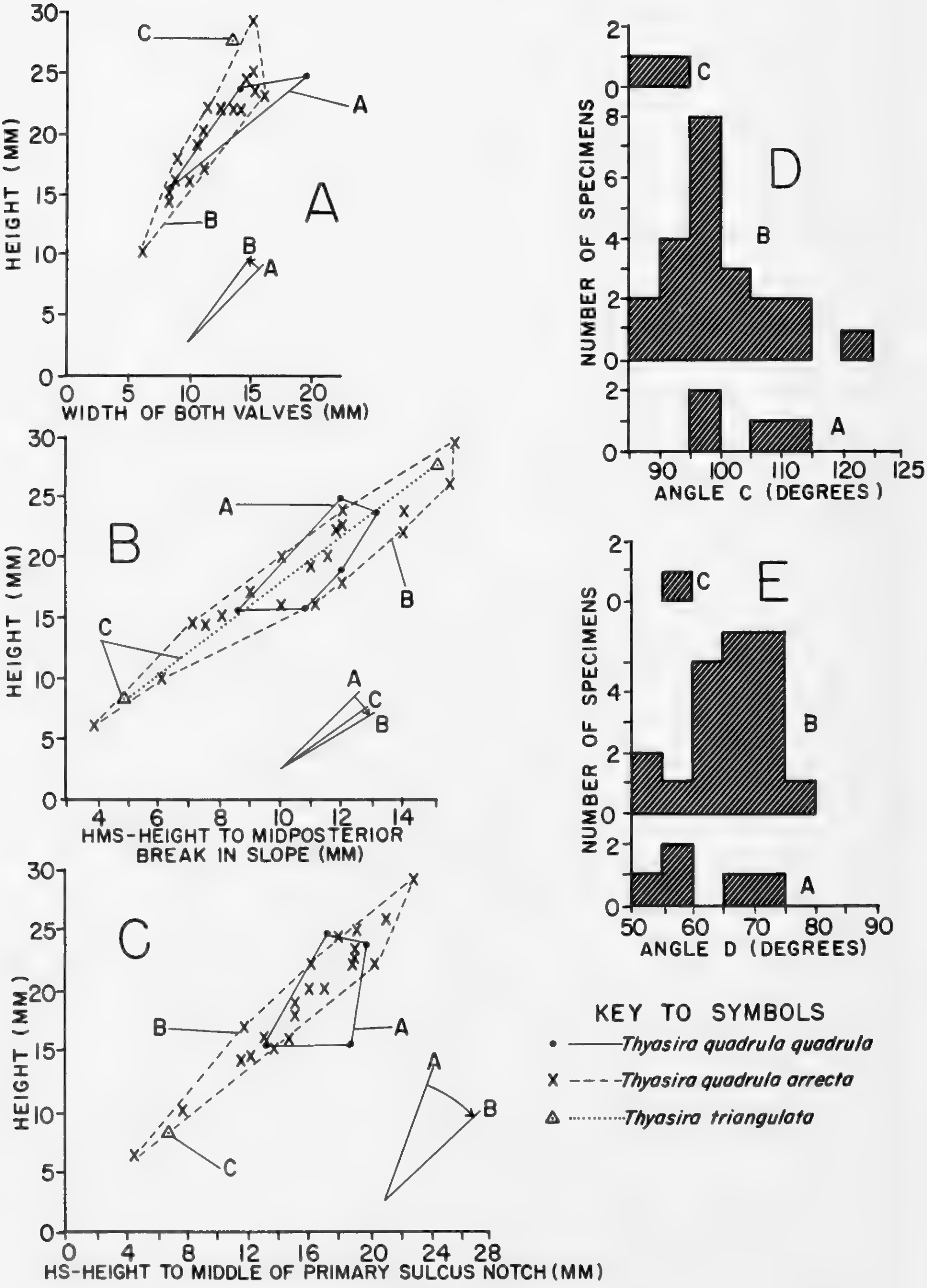
The adaptive value of these trends is difficult to interpret separately, especially in view of the apparent uniformity of substrate and sedimentary environment occupied by all members of the lineage during the Upper Cretaceous. Most of the trends, however, can be interrelated with streamlining of the shell for more rapid, efficient, burrowing. Most burrowing bivalves are elongate and slender, with the long axis parallel to the direction of burrowing. The shell has become adapted in this way in many unrelated groups to reduce friction between shell and substrate during burrowing. Yet in the

*T. quadrula* and *T. rostrata* lineages, the oldest shells are nearly equidimensional, and in all three lineages, the oldest species have the most inflated shells. Both of these characteristics are detrimental to rapid, easy burrowing.

Reduction of the projecting dorsoanterior flank and shell convexity in the *T. quadrula* lineage and shift from a subquadrate to a subtriangular shell with the long axis parallel to the direction of burrowing could be considered adaptive streamlining for more effective and rapid burrowing, which is accomplished in *Thyasira* by a rocking motion with the ventral edge facing downward as described in the ecology section of this paper. Changes in the shell angles and relative projection of the beaks are directly tied to this change in overall shell outline. Other evolutionary changes in the lineage involving change in the adductor muscle size and modification of the primary sulcus can be directly related to change in shell shape and convexity for more efficient burrowing if one considers the spatial relationships of various parts of the anatomy in typical *Thyasira* (text fig. 2).

A large mantle cavity is necessary for storage of the loosely coiled vermiform foot, which must be retracted before the agglutinated tube can become an effective incurrent structure for feeding and respiration. This was accomplished in the initial anatomical radiation of *Thyasira* by modification (lateral compression and elongation) of the anterior adductor muscle and size and position of the gills, and possibly by lateral expansion or out-pouching of the cavity itself. The position of the gills is marked by the primary sulcus, which forms an interior fold against which the gills are buttressed. A second important relationship to consider is that between the gills and the anterior incurrent opening. The orientation and position of the gills has become modified in *Thyasira* to adapt to an anterior rather than a posteroventral source of current for feeding and respiration, and it may be assumed that these two structures have a delicate spatial balance.

The modification of shell outline in the *T. quadrula* takes place primarily by reduction of the dorsoanterior and anterodorsal flanks and increase in the anterodorsal slope. This in turn shifts the position of the large anterior adductor muscle, and the incurrent channel also used by the vermiform foot, downward to a more central position. This shift, plus the decrease in convexity through time, would potentially restrict the amount of space availabe in the mantle cavity for the loosely coiled vermiform foot when completely retracted and bring the incurrent channel much closer to the original position of the gills. This loss of necessary space in the mantle



TEXT FIGURE 14.

cavity and retention of the gill-incurrent canal spatial relationship is apparently compensated in the evolution of the lineage by a posterior shift and reorientation of the gills, as indicated by posterior migration and straightening of the primary sulcus, against which the gills buttress.

*The Thyasira rostrata lineage.*—This appears to be the main stock of the species complex. It is also notably the most conservative in its evolution, frequently a characteristic of parental stocks in a radiating species complex. Two morphologically similar and linearly descended subspecies form the known part of the lineage, in ascending order, *T. rostrata rostrata,* n. subsp., and *T. rostrata cracens,* n. subsp. Most of the evolutionary changes shown by *T. rostrata cracens* are small-scale, but a few gross changes facilitate distinction of the subspecies. Many of the changes can be related to adaptive morphologic shifts to better cope with the burrowing habitat in clay substrate. The most obvious changes are (a) decrease in average convexity, and correspondingly, in the width of the escutcheon and lunule (text fig. 15, B), (b) loss of a well-defined lunule and the faint anterior sulcus found in *T. rostrata rostrata* (pl. 2, figs. 24,

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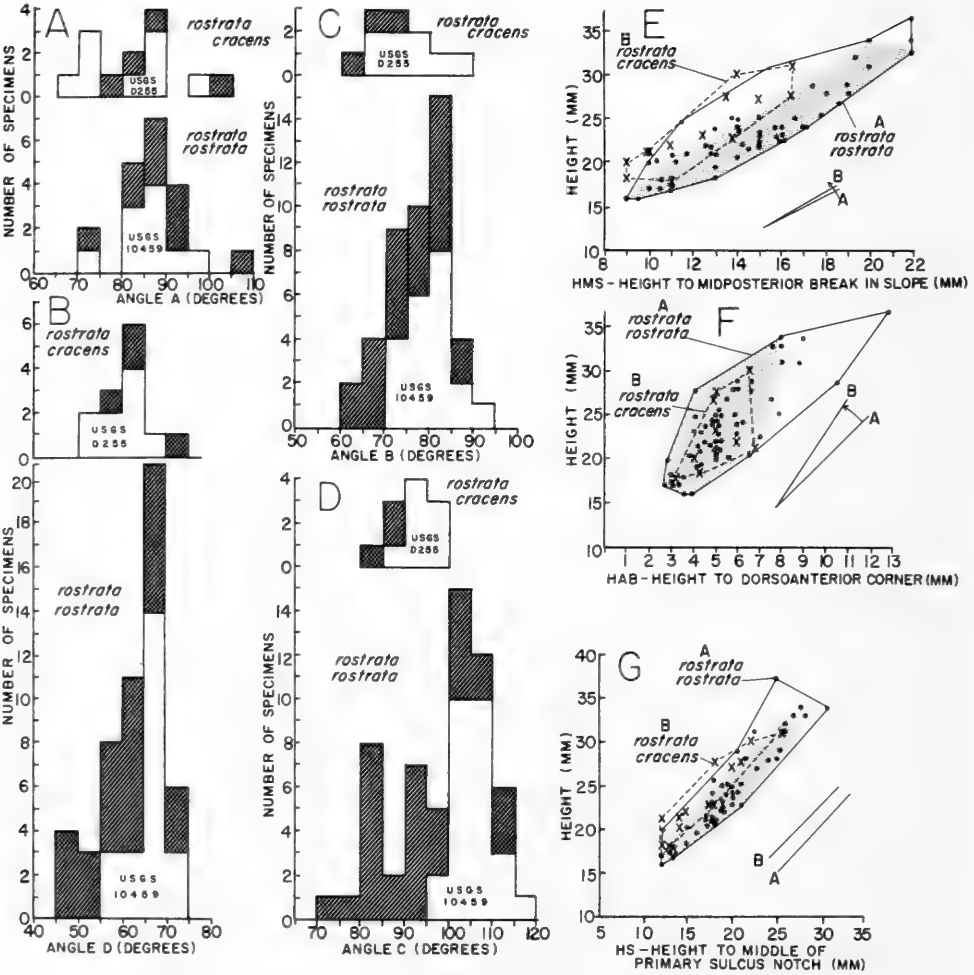
Text Figure 14.—Evolution of the *Thyasira quadrula* species group, as reflected by shifts in angles and character pairs through time. Plots include data for all available specimens that could be measured in each species or subspecies, regardless of geographic or stratigraphic position within known ranges. Individual populations are not large enough to give significant results by being plotted separately, and on other species whole plots show little variation, other than size range, from individual population plots (text figs. 6, 7). Taxa are keyed in stratigraphic order of occurrence in each plot by small letters. A being the oldest, C the youngest. Bivariate plots (charts A-C) show scattergram boundaries (solid for *T. quadrula quadrula,* dashed for *T. quadrula arrecta*), points for *T. triangulata* connected with finely dashed line where a particular character is measurable on both known specimens (as in B), and comparative slopes of approximate regression lines fitted to point clusters visually (lower right corners of charts A-C). Direction of evolutionary shift on regression lines denoted by arrow. Histograms arranged stratigraphically and plotted to the same scale. The following general trends in the lineage: chart A, decrease in width of both valves relative to height (chronoclinal); chart B, increase in the height to the posterior break in slope at the dorsal edge of the primary sulcus notch, relative to overall height (note minor reverse in trend from *arrecta* to *triangulata*); chart C, a similar increase in the relative height of the primary sulcus notch compared with overall shell height; chart D, chronoclinal decrease in angle C, the overall apical angle; and chart E, initial increase in angle D, formed by the primary sulcus notch, beak, and dorsoanterior corner (see text fig. 4), followed by an apparent decrease in this angle as *T. quadrula arrecta* gives rise to *T. triangulata.*



Text Figure 15.—Evolution in the *Thyasira rostrata* lineage, as demonstrated by shifts in the peaks of histograms depicting shell angles (see text fig. 4 for explanation), and variation in the position of polygrams and regression lines of bivariate plots for measurable shell characters. Histograms (A-D) include measurements for all specimens of the two subspecies, with the largest single populations not shaded. The scale is constant for each histogram pair. Bivariate plots show points for all measurable specimens in each subspecies, with the points for *T. rostrata rostrata* (dots enclosed with solid line) and *T. rostrata cracens* (X's enclosed with dashed line) plotted to the same scale, and the largest single population of *T. rostrata rostrata* (USGS 10459) shaded. Approximated regression lines plotted visually for each set of points shown in lower right corner of bivariate plots with direction of evolutionary shift in lineage denoted by an arrow. A very

25), slight decrease in projection of the dorsoanterior flank (pl. 3, figs. 19-27), (d) and development of more erect relatively higher shells, with somewhat less prosogyrate beaks and umbos (pl. 3, figs. 19, 20, 23-26).

As previously pointed out in the *T. quadrula* lineage, decrease in shell convexity, development of higher, more erect shells (long axis parallel to burrowing direction), decrease in projection of the dorsoanterior flank, and possibly loss of the faint anterior sulcus may all be interpreted as adaptation of the shell to more efficient, rapid burrowing by making the shell more streamlined. It is difficult to interpret other noticeable changes, such as the loss of a well-defined lunule, in terms of adaptive evolution with the very generalized evidence at hand.

*The Thyasira beauchampi lineage.*—The fossil record of this lineage is meager, and although successive subspecies of the lineage show some gross changes through time, these are only generally implied to represent the evolution of the group. This apparent evolution has not been tested by analysis of large suites of specimens.

*Thyasira beauchampi rex,* n. subsp., shows the following differentiation from the older *T. beauchampi beauchampi* (see text fig. 13, C): (a) increase in size, (b) decrease in relative convexity, (c) expansion of the dorsoanterior margin into a distinct auricle, (d) increase in length and decrease in width of the anterior sulcus, (e) migration

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small degree of shift in the variation limits and/or the peaks of the histograms occurs from the ancestral *T. rostrata rostrata* to *T. rostrata cracens* (graphs A-D), in each case the angles becoming slightly narrower. This reflects the general trend toward relatively higher, more erect shells with narrower, somewhat more projecting beaks and umbos and a steeper posterior margin in *T. rostrata cracens.* The bivariate plots show the following trends (graphs E-G): the center of the primary sulcus notch, and the point of the midposterior break in slope which forms the dorsal margin of the notch, both attain a more dorsal position on the posterior margin relative to overall height in the younger *T. rostrata cracens* than they have in *T. rostrata rostrata* (graph F). The height to the dorsoanterior corner, at the junction between the dorsal and anterior margins, becomes notably less, relative to overall height of the valve, in the younger subspecies *T. rostrata cracens.* This reflects expansion of the dorsoanterior flank in this subspecies into a flat, subquadrate, bluntly auriculate projection. All terminology used on graphs is explained in text figure 4. The population of *T. rostrata rostrata* is from a single concretion zone at USGS Mesozoic locality 10459, in the Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. The population of *T. rostrata cracens* is from USGS Mesozoic locality D255, Steele Shale, lower part of the zone of *Baculites perplexus,* early form, Converse County, Wyoming.

of the sulcus notch and midposterior break in slope dorsally along the posterior margin to a more medial position, (f) straightening of the dorsoposterior margin and primary sulcus, (g) decrease in size and prominence of the lunule (pl. 1, compare figs. 23 and 25), (h) decrease in relative height with rounding and decreasing projection of the beaks; the beaks are more erect on *T. beauchampi rex* than on the older subspecies, and (i) increase in size and extent of the anterior adductor muscle scar (text fig. 17).

Of all Cretaceous *Thyasira* in the Western Interior, the apparent evolutionary trends in the *T. beauchampi* lineage are the most difficult to interpret, and appear to be the antithesis of trends in other groups. The shell becomes less streamlined (except for reduction of valve convexity) through time, and presumably more poorly adapted to rapid, efficient burrowing. Decrease in relative height (and in elongation along the axis of burrowing), projection of the beaks, and expansion of the anterior sulcus, anterodorsal flank (auriculate), and midposterior margin all adversely affect the ability of the shell to be drawn easily into the substrate behind the burrowing vermiform foot once it is anchored. It is possible that this lineage, unlike the others, was adapting to a shallower burrowing habitat in which the larger, heavier shell, the projecting margins, and the larger sulci would serve to anchor the shell better in a shallow, possibly more mobile substrate than encountered by deep burrowing *Thyasira*. This might also explain its ability to coexist in the same substrate with the deeper burrowing *T. rostrata rostrata*.

Individually, certain of the trends in this lineage may be explained in terms of adaptive anatomical features. The anterior sulcus internally forms a fold which acts as a buttress for the large anterior adductor muscle. This muscle becomes relatively larger (text fig. 17) in the younger subspecies, and a corresponding increase in the size and extent of the anterior sulcus may reflect the need for a larger buttress to support the expanding muscle. The posterior shift, rotation, and straightening of the primary sulcus marks a reorientation of the gills (which attach along the line of the sulcus) within the mantle cavity so that their leading edges face more diagonally toward the anteroventral corner than directly toward the anterior margin, as is common to many *Thyasira*. This reorientation could well reflect a shift in the position of the incurrent canal downward toward the anteroventral margin on time successive subspecies in response to increase in size of the anterior adductor muscle and anterior sulcus, and with ventral migration of the sulcus in *T. beauchampi rex* (text fig. 13, C). Such a dual shift in the position of the gills and the anterior incurrent canal would maintain proper and probably critical spatial relationships between these two structures.

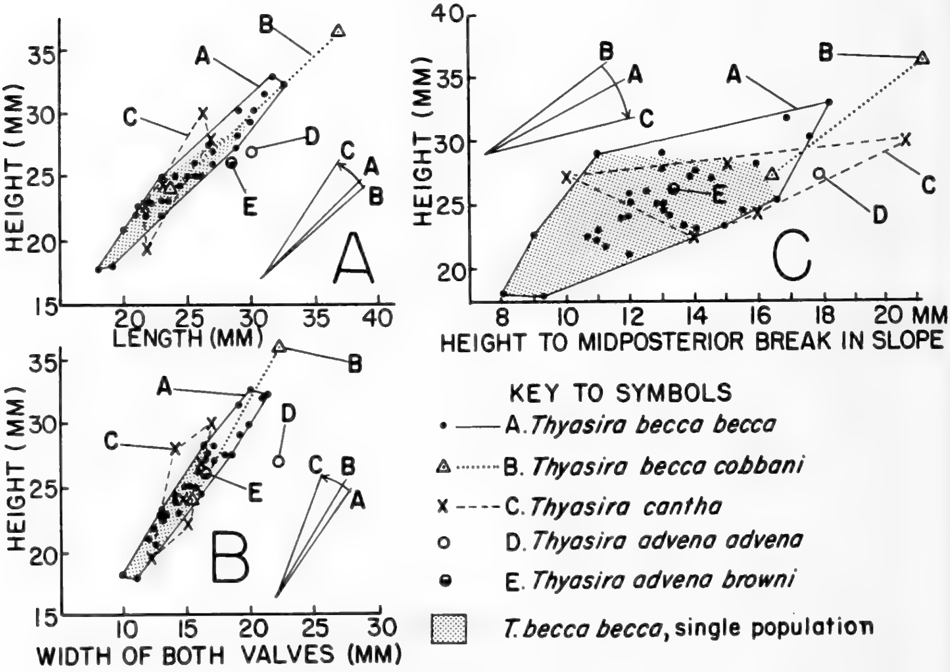
## THE THYASIRA ADVENA-THYASIRA BECCA SPECIES COMPLEX

*General phylogeny.*—The phylogenetic picture of this complex lineage is quite distinct from that of the *T. rostrata* species complex (text fig. 13). Members of the lineage are unusual thyasirids having a rounded outline with the length commonly greater than the height. They are sparsely represented in the Western Interior Cretaceous by an Early Campanian subspecies, *Thyasira advena advena,* based on a single, morphologically unique specimen, and are unknown in the early Late Campanian. The lineage undergoes a striking radiation in middle Late Campanian time however (zone of *B. scotti*) giving rise to four subspecies and species with overlapping stratigraphic ranges but distinct morphologies (text fig. 13). At this time, the lineage became dominant in the Western Interior, apparently replacing members of the *T. rostrata* complex in the same ecologic niches. The precise phylogenetic relationships of these Late Campanian forms, and their time of differentiation during the Cretaceous must be inferred from the degree of morphologic similarity between members of the complex, and is not documented by large, closely spaced collections in the fossil record. These hypothetical steps in differentiation of the lineage are shown on text figure 13. The dashed lines show where relationships are largely implied from comparative morphology of the component species and subspecies.

Two lineages are present in the species complex, the poorly represented *T. advena* lineage, apparently the parent stock, and the well-developed *T. becca* lineage of the Late Campanian, which also includes *T. cantha.*

*The Thyasira advena lineage.*—Two time-successive subspecies, widely separated stratigraphically and represented by meager collections, form this poorly known lineage. The nature of the fossil record does not permit a sequential evolutionary picture to be drawn for the lineage, but the distinct subspecies are considered to represent points of morphologic grade within an evolving sequence such as that demonstrated for other Cretaceous lineages, in particular that of *T. quadrula.*

The principal modifications shown by *T. advena browni* over the older *T. advena advena* are (see text fig. 13): (1) decrease in convexity, (2) decrease in the size and prominence of the lunule and



Text Figure 16.—Evolution in certain character pairs of the *Thyasira advena-becca* species complex. Plots of all measurable specimens for the five species and subspecies comprising the complex; scattergram boundaries delineated in *T. becca becca* (solid line) and *T. cantha* (dashed line). Single population of *T. becca becca* shown as shaded area. Two points for *T. becca cobbani* connected by dotted line. This line (B), and approximated regression lines for *T. becca becca* (A) and *T. cantha* (C), fitted to point plots visually, shown in corners of each diagram. General trends are toward greater relative height (graph A), decreasing convexity, and ventral migration of the midposterior break in slope (dorsal edge of primary sulcus notch) in successively derived species and subspecies of the complex. The trend reverses from A to B in some cases. Approximate age relationships of first appearance, in ascending order, are D, A, B, C and E.

escutcheon, (3) rounding of the midanterior and midposterior margins, (4) development of a straighter and shallower primary sulcus, and a weak anterior sulcus, and (5) decrease in beak curvature, but increase in projection of this structure.

As in most other lineages of *Thyasira,* evolutionary shifts producing decrease in convexity, rounding of the projecting margins, and elongation of the dorsal-ventral axis of the valves better adapted the shell for rapid and efficient burrowing in clay substrate by streamlining it along the axis of burrowing. Decrease in the development of the lunule and escutcheon may be similarly adaptive, especially in regard to the latter structure which shows severe restriction in the younger subspecies. Reduction of the midanterior margin in the youngest subspecies would have caused a consequent inward and downward migration of the anterior adductor muscle, thus restricting the mantle cavity (coupled with decrease in shell convexity) and shifting the position of the incurrent tube ventrally. Evolutionary trends producing straightening of the primary sulcus, marking the line of gill attachment, probably reflects a shift in the position and orientation of the gills to maintain proper spatial relationships with the incurrent canal and compensate somewhat for the restriction of space in the mantle cavity, although these changes are not as marked in the *T. advena* lineage as in, for example, the *T. quadrula* group.

Development of an anterior sulcus in the youngest subspecies of the lineage, producing a low internal fold beneath the anterior adductor muscle insertion, is considered an adaptive trend to improve the anchorage and operation of this muscle by providing a firm structure against which it could attach.

*The Thyasira becca lineage.*—Unlike all other lines of thyasirid evolution in the Cretaceous of the Western Interior, in which genetic modification produced chronoclinal relationships with successive species and subspecies replacing their ancestors in the same ecologic niches (text fig. 13), the evolution of the *T. becca* lineage appears to be one of rapid radiation during the early Late Campanian, producing coexisting, related species within the same general niche. A sequential order of derivation in the lineage is inferred from the stratigraphic ranges of the component taxa (text fig. 13), from oldest to youngest, *T. becca becca,* n. subsp.; *T. becca cobbani,* n. subsp.; and *T. cantha,* n. sp. The roots of the lineage are unknown since no fossils have been found in the early Upper Campanian or older rocks, but the general rounded form of the shell, the subcentral beaks, strongly curved and well-developed primary sulcus, and other minor features strongly suggest affinities to the parental stock of *T. advena*, with separation of the two lineages probably in the earliest Late Campanian (text fig. 13).

At two localities three morphologically distinct subspecies of *Thyasira* occur together, *T. becca becca, T. becca cobbani,* and *T. advena browni* at D709, and *T. beauchampi beauchampi, T. rostrata rostrata*, and *T. advena advena* at 10459. The association of three members of a single species complex at D709 is an unusual situation by modern ecologic standards. This is subsequently discussed in a section dealing with problems of cooccurrence. At numerous other localities two related subspecies are found together. Inasmuch as the shells characteristic of the *T. advena* species complex are not especially streamlined for rapid and deep burrowing, it is assumed that most of the component taxa were fairly shallow infaunal elements. With the evidence at hand it is not possible to explain the ability of these distinct taxa to coexist in the same substrate where they would be in direct competition with each other, unless they were depth zoned in the substrate or adapted to specific microniches which are not reflected in the physical aspects of the rock.

The cooccurrence of *T. becca becca* and *T. quadrula arrecta* at USGS Mesozoic localities D714 and D3945 is easier to comprehend because one is probably a deeper infaunal element than the other, based on the degree of adaptive streamlining of the shells, and they may have been depth zoned in the substrate.

If the inferred phylogenetic derivation of species and subspecies in the *T. becca* lineage is correct, the following evolutionary trends are expressed by the progressively younger members of the radiating sequence (text fig. 13): (1) decrease in convexity; (2) rounding of the shell in progressively younger taxa by reduction of the produced midanterior and midposterior flanks, increase in shell height relative to length, and decrease in the projection of the beaks and umbos; (3) shifting of the beaks to a more central position; and (4) reduction of the depth and width of the primary sulcus, coupled with straightening and a shift in its position toward the posterior margin, restricting the size of the posterior primary fold.

Many of these trends follow the prevalent pattern of evolution of Cretaceous thyasirid lineages; modification toward more efficient and rapid burrowing through decrease in convexity, rounding of projecting margins, elongation of the vertical shell axis (height), central migration of the beaks, and decrease in prominence of the sulci. Similarly, straightening and posterior migration of the primary sulcus are linked trends widespread in the evolutionary pattern of

Cretaceous *Thyasira* and reflect reorientation of the gills to maintain critical spatial relationships with the incurrent canal (shifted ventrally and inward with reduction of the protruding midanterior flank), and a large mantle cavity for storage of the coiled vermiform foot. The mantle cavity was restricted initially in the evolution of the lineage by decrease in convexity and reduction of the projecting midanterior and midposterior flanks.

*Thyasira* is not yet known in the Western Interior in rocks younger than the zone of *Baculites scotti,* and its disappearance is possibly tied to retreat of cool and/or deep water conditions in the interior marine trough. Had the genus persisted, it is likely that the newly radiated lineage of *T. becca* would have followed the same pattern as other longer ranging lineages, and that the best adapted form for the infaunal mud habitat, *T. cantha,* would have persisted and become the dominant and youngest form.

## CONCLUSIONS

Despite the restrictions placed on broad evolutionary interpretation by the short tenure of *Thyasira* in the Cretaceous of the Western Interior, the commonly sparse fossil record, and the conservative aspect of its evolution, an amazingly consistent pattern of evolution characterizes all but one lineage (*T. beauchampi*). As far as can be ascertained, this overall pattern is not controlled by a broadly shifting environment but rather reflects more efficient adaptation of the shell in independent lineages to an infaunal existence in the same general ecologic niche, a clay mud substrate, probably characterized by reducing conditions, in cool and possibly deep, quiet waters.

To varying degrees, nearly all of the Upper Cretaceous thyasirid lineages display evolutionary trends which cumulatively produce streamlining of the shell for more rapid and more efficient burrowing in the mud substrate. The principal trends involved are reduction of convexity, elongation of the dorsoventral shell axis which parallels the direction of burrowing, rounding and streamlining of the lateral shell margins by elimination or reduction of projecting lateral flanks, folds, and auricles, reduction in the size and extent of concave areas such as the primary sulcus, escutcheon, and lunule, and central migration of the beaks and umbos accompanied by decrease in their forward inclination. The lineage of *T. beauchampi* displays a reverse trend however, developing more projecting extremities and may actually be evolving toward a shallower infaunal habitat.

Accompanying this modification of shell form which occurred independently in most Cretaceous lineages is a marked change in the curvature and position of the primary sulcus. Progressively younger taxa of most lineages display a migration of this structure toward the posterior margin of the valve accompanied by a decrease in curvature and, generally, width and depth of the sulcus. This reflects anatomical modification linked with streamlining of the shell for burrowing, so that critical internal spatial relationships within the mantle cavity, and between the incurrent canal and the leading edge of the gills might be maintained.

Progressive reduction of shell convexity and of projecting margins would have restricted severely the size of the mantle cavity unless a compensating posterior shift of the gills had occurred. This shift is marked by the posterior migration of the primary sulcus against which the gills buttress. A large mantle cavity had to be maintained to accommodate the vermiform foot once it was withdrawn from the incurrent tube to allow water to flow through for feeding and respiration.

Posterior migration and straightening of the sulcus also reflects a reorientation of the gills to face anteroventrally instead of anteriorly, and to maintain critical spacing with the incurrent canal. This gill reorientation was in response to a ventral and inward shift of the anterior adductor muscle and the incurrent canal below it with progressive reduction of the dorsoanterior flank in younger taxa of many lineages. Anteroventral reorientation of the gills allowed them to face directly incoming currents at all stages of evolutionary development within the lineage and thus perform their functions with greatest efficiency.

It would appear that at the time of its disappearance from the Western Interior during the Cretaceous, *Thyasira* was well adapted to its particular habitat. The close similarity of Recent and terminal Cretaceous species, and the conservative evolution of Cenozoic forms would seem to indicate this. The adaptive evolution of the Cretaceous species is relatively great in contrast to the post-Cretaceous history of the genus.

## THE PROBLEM OF COOCCURRENCE

At many Western Interior localities, assemblages of *Thyasira* are moderately diverse; two and rarely three distinct species or subspecies are found along an isochronous zone at a single locality, usually in a zone of limestone concretions and less commonly in a single concretion. Inasmuch as it is rare in modern environments to have several related species coexisting, this situation merits some discussion. Cooccurring species and subspecies are listed below, and the reader is referred to figure 13 for the general morphology of these forms, which will be discussed in later paragraphs.

USGS D3945 (youngest): *T. quadrula arrecta* and *T. becca becca.*
USGS D714: *T. quadrula arrecta* and *T. becca becca.*
USGS 22838: *T. cantha* and *T. becca becca.*
USGS D709: *T. advena browni, T. becca becca,* and *T. becca cobbani.*
USGS D1410: *T. cantha* and *T. becca becca.*
USGS D1216: *T. cantha* and *T. becca becca.*
USGS 22840: *T. cantha* and *T. becca becca.*
USGS D1215: *T. quadrula arrecta* and *T. becca becca.*
USGS D2910: *T. quadrula arrecta* and *T. becca becca.*
USGS D1564: *T. quadrula arrecta* and *T. becca becca.*
USGS D1866: *T. quadrula arrecta* and *T. rostrata cracens.*
USGS D1865: *T. quadrula arrecta* and *T. rostrata cracens.*
USGS D255: *T. quadrula arrecta* and *T. rostrata cracens.*
USGS 10666: *T. quadrula quadrula* and *T. beauchampi rex.*
USGS 10459: *T. beauchampi beauchampi, T. rostrata rostrata,* and *T. advena advena.*

In addition, *T. becca becca* and *T. becca cobbani* both occur in Alberta along the Assiniboine River in the Riding Mountain Formation, but there is no data indicating whether or not they were collected from the same zone or isochronous level.

Cooccurrence of living *Thyasira* is not well documented, in particular cases where more than one species was found in a single bottom sample. Such detailed information is not commonly published. However, the Recent molluscan literature contains several accounts of numerous species of *Thyasira* cooccurring throughout a general area. For example, Ockelmann lists (1958, table 1, p. 190) three species of *Thyasira, T. gouldi, T. equalis,* and *T. croulinensis,* as generally inhabiting offshore areas of west Greenland, Spitzbergen, and Norway north of Lofoten, in association with the related thyasirid *Axinopsis orbiculata.* He reports seven species of *Thyasira* and three of *Axinopsis* or *Axinulus* along the Atlantic Coast between Newfoundland and Cape Cod (1958, p. 197). Although he infers the Greenland species are depth zoned (1958, p. 108), no detailed information is presented as to the possible overlap of species ranges or the cooccurrence of two or more *Thyasira* species in single samples. Parker (1963, p. 159, tab. 1) furnishes one of the only single station reports in which two species of *Thyasira* are present; he notes *T. barbarensis* and *T.* n. sp. cooccurring alive in 35 to 40 feet of water at Station 212 (Gulf of California), and these two species generally occurring with *T. excavata* (but not at the same station) between 27 and 40 fathoms in the intermediate shelf environment as defined by him in this area. No authors, to my knowledge, have dealt with the problem of how two or more species coexist in the sediment; whether they are depth zoned, zoned laterally in microniches, or coexist in the same niche. This is an area that needs careful study for several cases of cooccurrence can be cited (for example, four species of *Tellina* in the *Diplanthera* zone of Florida: Boss, personal communication, 1966), and in none have genetic and ecologic factors been properly evaluated.

The mass of the data suggests that it is not uncommon for two or more species of *Thyasira* to occur together in the same area at the same time. Perhaps *Thyasira* is ecologically better able to accomplish this than many infaunal bivalves, considering its niche preference. *Thyasira* does not flourish in areas where it is in direct competition with a diverse bivalve infauna, but commonly occurs in great numbers by itself, even in chemically severe substrate. The reasons for this are not clear, but the gregarious nature of certain species would indicate potentially that different species could successfully coexist in the same niche, or in microniches within the same area that are only slightly different. The effects of competition on *Thyasira* from its own kind do not seem to be the same as the detrimental effects of competition with a variety of other mollusks. Much work needs to be done on living species to confirm this. No information is now available.

It would seem more reasonable that species apparently coexisting in the same substrate were in some way zoned into distinct microniches rather than directly competing with one another, particularly in the case of *Thyasira,* which avoids competition with other mollusks and lives commonly in food-poor areas. Microniche zoning decreases competition for space, food, and oxygen. Ideally for the paleontologist, microniche differentiation would not only be reflected in slightly different substrate type or spatial occurrence of species, but also in the shell morphology by development in each species of specifically adaptive features. Interestingly, living species of *Thyasira* inhabiting the same area have different morphologies comparable to those demonstrated by Cretaceous species which cooccur in single time zones at single localities.

In the preceding section, the adaptive value of some of these shell features was discussed at length. It was proposed that vertically elongate, narrow shells with reduced auricles and sulci were better adapted to rapid and possibly deeper burrowing than rounder, or horizontally elongate, inflated shells such as *T. advena advena* and *T. becca becca,* n. subspp. It would follow from this that different species and subspecies of Cretaceous *Thyasira* probably lived at different depths in the substrate, and that these approximate or relative depths might be interpreted from the shell morphology of the species. It is probable that two species of the same genus might live together in the same area by being depth zoned in the sediment without developing a severe competitive situation. Other infaunal bivalves can apparently do this. If such a depth zonation was responsible for Recent and Cretaceous species or subspecies cooccurrence, and if the effective burrowing depth of the individual species was reflected by the shell structure, it would follow that cooccurring species would be morphologically quite distinct—some being shallow burrowers, other more streamlined and deeper burrowing.

It is significant that both living and Cretaceous *Thyasira* known to cooccur in the same area or at the same level have distinct shell forms in which the variable characters between them are specifically those which suggest a relationship to burrowing depth and efficiency —relative height, width, auricular projection, and development of sulci on the shell. By comparing the list that begins this section with figure 13 and the data from the section on phylogeny and evolution of Cretaceous *Thyasira,* it becomes evident that in almost every case the following relationships occur between coexisting Cretaceous species and subspecies: (1) they are specifically different and belong to distinct lineages; only in the late Campanian does coexistence within a single lineage commonly occur; (2) in most cases only two species occur together and, of these, one is adapted for deeper and more rapid burrowing than the other. (For example, the massive *T. beauchampi rex* or *T. rostrata cracens* is probably a shallower burrower than the delicate *T. quadrula arrecta* or *T. quadrula quadrula* with which they commonly occur. The horizontally elongate *T. becca becca* is much less adapted for burrowing than the slender, dorsoventrally lengthened shell of *T. quadrula arrecta.* Within the *T. becca* lineage, *T. cantha,* round and slender, must have been a far more efficient burrower than the massive *T. becca becca,* with which it coexists.) In one of the two localities where three species occur together, the three have distinct morphologies adapted to different burrowing rates and depths. This suggests strongly that coexisting Cretaceous *Thyasira* were predominantly depth zoned, and possibly also zoned laterally in the sediment, into distinct microniches which allowed individual species and subspecies to live together without severe competition between them.

There is only a single discrepancy in this pattern. In USGS D709, *T. advena browni*, a rounded, slender, moderate-depth burrower in all probability, coexists with the massive shallow burrowing *T. becca becca*. The two were apparently depth zoned. Occurring with these two species however is a single bivalved specimen of *T. becca cobbani*, whose morphology and probable habitat closely approximates that of the common *T. becca becca*. Two interpretations are possible, since the bivalved condition of the shell indicates that it probably lived with the two dominant species. Either (1) *T. becca becca* and *T. becca cobbani* represent sympatric species rather than related subspecies and are thus able to live in the same niche without competing severely due to some feature, anatomical or behaviorial, not preserved in the shell morphology, or (2) this is a freak occurrence in which a specimen of *T. becca cobbani* settled in a niche dominated by *T. becca becca* (the two possibly being ecologic or geographic subspecies), possibly in a range of ecologic or geographic overlap between these subspecies, but were not abundant enough to cause a competitive situation and thus were allowed to remain and grow in the area without being forced out. In view of the single occurrence of this association, I favor the latter explanation over the former.

## TAXONOMY

### NOMENCLATURAL STATUS OF THYASIRA

Contemporary mollusk workers throughout the world have accepted and widely used the taxa *Thyasira* and Thyasiridae, although the validity of these names has been questioned. *Thyasira* was originally a Leach manuscript name and was first published by Lamarck (1818, p. 492) in a synonymy list for *Amphidesma flexuosa* (Montagu). A brief description of *A. flexuosa,* which was to eventually become the type species of *Thyasira,* was presented and no other species were listed. Because the species in question obviously did not belong in *Amphidesma,* or in *Tellina* where it was originally placed (Montagu, 1803), most workers in the last 50 years have accepted this as the original generic description of *Thyasira,* in which *T. flexuosa* becomes the type-species by monotypy. The International Code of Zoological Nomenclature as revised in 1961 (Stoll, *et al.* 1961, p. 11) clearly stated, however, that a name first published as a synonym is not available (Article 11d), invalidating *Thyasira* as of 1818. The first valid designation of *Thyasira,* in view of this rule, would be that of Gray (1847, p. 195). Prior to this, however, other generic names were proposed for similar forms, and some of these are now considered synonyms of the genus *Thyasira.* These are *Axinus, Bequania,* and *Cryptodon.* Other pre-1847 names occasionally placed in synonymy with *Thyasira* are here considered distinct genera. Fortunately, the code was again revised in 1964 (Stoll, *et al,* p. 11) and Article 11d altered so that names first published in synonymy are now valid, giving *Thyasira* clear priority. Even without this, arguments can be presented which suggest *Thyasira* is valid as of Gray's 1847 designation. These will be useful should the Code again be changed and are presented below.

*Axinus* was validly proposed in 1821 (p. 351) by James Sowerby and is considered synonymous with *Thyasira* by most workers. A few scientists still use it in preference to *Thyasira.* However, the type of *Axinus* (by original designation), *A. angulatus,* is a Tertiary species characterized by (1) a prominent, greatly expanded anterior flank bearing a broad, shallow, anterodorsal sulcus and prominent fold, (2) by posteriorly situated beaks, and (3) in having a shortened, unisulcate posterior flank. If Sowerby's illustrations are even moderately accurate, it is generically distinct from *Thyasira,* and may not even belong in the Thyasiridae. The interior morphology has not been described. James Sowerby himself was in doubt as to the validity of *Axinus* as a distinct genus, as noted by G.B. Sowerby (1852, p. 80):

> The very late Mr. James Sowerby, who described this shell in the Mineral Conchology, did not consider his genus as established, not having seen the hinge (despite this, the name is validly presented). It is stated to have been previously named *Thyassira* (misspelling); but CRYPTODON, Turton, is the first name accompanied by true character. (Remarks in parentheses are mine).

*Cryptodon* Turton represented the greatest threat to the existing nomenclatural status of *Thyasira* under the 1961 Code of Nomenclature, and though not now in common usage, was possibly the most valid name for the genus under this set of rules. Some doubt, however, also surrounds its status. *Cryptodon* was first proposed by William Turton (1822, p. 121), adequately described, and illustrated (pl. 7, figs. 9, 10). Below the generic heading on the page, two species are listed with equal status, *Tellina flexuosa* Montagu, followed by its synonymy, and *Venus sinuosa* Donovan with its synonymy.

Only a single species description is presented below this, in which no species name is mentioned, and in the margin after the entry for *T. flexuosa* there appears in small letters "flexuosus 1." It has been interpreted by most workers concerned with the problem, and probably correctly, that Turton has placed *V. sinuosa* in synonymy with *T. flexuosa,* that *T. flexuosa* is the only species described, and therefore that *Cryptodon* is validly proposed as of 1822 with *T. flexuosa* its type species by monotypy. Based on the presentation of species in the synonymy, however, it could also be interpreted that two species are listed under *Cryptodon,* a general description of the species presented with no names inserted, and no type species selected. In either interpretation, the genus *Cryptodon* becomes validated as of this date. Brown (1844, p. 99) subsequently clearly defined *Cryptodon* and described *C. flexuosus* alone under this heading. In addition he indicated that *Venus sinuosa* was a synonym of this species, clearing up the doubt that prevailed in Turton's original description of the genus. Both of these works predate Gray's first valid publication of *Thyasira* (1847). In the same publication, Brown (1844, p. 99) introduced another Leach manuscript name, *Bequania,* which had been applied to *C. flexuosa,* as a synonym of *Cryptodon.* Since this name postdates both *Thyasira* and *Cryptodon,* and has the same questionable validity as *Thyasira* (under the 1961 rules) because it appears in synonymy, it need not be taken into consideration in dealing with this nomenclatural problem.

*Cryptodon's* apparent firm entrenchment as the valid name for the genus before the 1964 revision of the rules is open to question; however, under Article 65b (p. 61) of the Code of Zoological Nomenclature (1961): misidentification or altered concept. The modern concept of *Thyasira flexuosa,* well stated by Verrill and Bush (1898, p. 784; under *Cryptodon*), and by Lamy (1920, p. 289, 290) includes only edentulous specimens which may or may not have a low pseudocardinal swelling on the right valve along the hinge line. The ligament is partially internal posteriorly. Lamarck mentions no dentition in the original reference to *Thyasira flexuosa* (1818, p. 492). In his original description of *Cryptodon,* however, Turton states (1822, p. 121) that the hinge has a single, obscure, penetrating tooth and a narrow lateral cavity (the ligamental groove?), and that the ligament is entirely external. Further, in his subsequent species description he describes extremely minute "teeth" which are hardly distinguishable. Brown (1844, p. 99) in his description of *Cryptodon flexuosus* describes the dentition as, "hinge with a single, erect, triangular tooth in one valve, and a flat, nearly obsolete one in the other;" and in his generic description of *Cryptodon* notes in addition the presence of " . . . a narrow lateral cavity, for the reception of a triangular, flat, hollow, lateral tooth of the other valve, which is provided also with an ill-defined, nearly flat, primary tooth." He further describes the ligament as predominantly internal.

Thus there seems to be a serious discrepancy in the published descriptions of the dentition and ligament of *Cryptodon flexuosus* by Turton and Brown, and the original and more modern accounts of *Thyasira flexuosa,* suggesting that more than one species is involved. Until recently, *T. flexuosa* has been a general catch-all name for various species of *Thyasira* in both the Atlantic and Indo-Pacific, ranging from arctic to subtropical waters. Ockelmann (1958, p. 100) made this quite clear in dealing with the Thyasiridae of East Greenland. He pointed out that five distinct species, *T. gouldi* (Phillipi), *T. sarsi* (Phillipi) (= *T. insignis* Verrill and Bush), *T. equalis* Verrill and Bush, *T. granulosa* Monterosato, and *T.* sp. A from arctic and subarctic waters were all originally placed in *T. flexuosa,* which does not even occur in these areas. Furthermore, since many workers have pointed out that the amount of exposure of the ligament and development of the dentition are of major taxonomic importance in the Thyasiridae, it becomes highly suspect that both Turton's and Brown's identification of *T. flexuosa* as the type species of *Cryptodon* are based on misidentifications at the species level. Variation suites of *T. flexuosa* from the British Isles are edentulous, with a low pseudocardinal swelling on the right valve and a partially internal ligament. Shells with dentition and ligament characters such as those described by Turton (1822) and Brown (1844) are not within the normal range of variation of *T. flexuosa* from the type area.

Reexamination of all type species involved and a taxonomic revision of the living *Thyasira* are needed to resolve this problem, and this is well beyond the scope of this paper. If *Cryptodon* is established on misidentified specimens attributed to *C. flexuosa, Thyasira* becomes valid dating from Gray's 1847 (p. 195) publication of the name, with *T. flexuosa* as the type species. All other generic names proposed for the Thyasiridae which are listed by Vokes (unpublished, 1951-1954, p. 62) probably represent genera other than *Thyasira*, and the date of their introduction has no bearing on this problem.

In view of the wide acceptance of *Thyasira* as a generic, subgeneric, sectional, and/or family-root name in an overwhelming volume of contemporary literature (Abbott, 1954, p. 384; Keen, 1963, p. 56, 91; Ockelmann, 1958, p. 100; Lamy, 1920 (1921), p. 292-296; Habe, 1951, p. 127; Iredale, 1930, p. 392-394, Eberzin, 1960, p. 114, and many others), the almost total abandonment of *Cryptodon* by contemporary workers, the questionable validity of *Cryptodon* due to possible misidentification of the type species, the current legality of *Thyasira* under the emended 1964 rules of nomenclature, and the possible validity of *Thyasira* dating from 1847 (Gray, p. 195) should the rules be changed again, I have used *Thyasira* throughout this study and consider it the most applicable generic name based on current usage and knowledge.

## CLASSIFICATION OF THE THYASIRIDAE

Supraspecific classification of the Recent Thyasiridae is confusing, and inconsistent among contemporary workers. For example, Vokes (1951-1954, unpublished, p. 62) lists 18 generic and subgeneric names proposed for Recent and fossil members of the family; about half of these are sulcate forms similar to those in the American Cretaceous. Many malacologists and paleontologists treat all sulcate species as *Thyasira* s.l. (Thiele, 1935; Chavan, 1937, 1938; Abbott, 1954; Keen, 1963, and others). Iredale (1930, p. 392-394), on the other hand, limits *Thyasira* to edentulous forms with a small submarginal sulcus or groove, and a large, primary, posteroventrally directed sulcus bounded by two moderately broad, well-defined, primary folds (lobes of Iredale, 1930). He proposes the genus *Prothyasira* for forms with three prominent posterior folds separated by two well-defined sulci. *Parathyasira* Iredale includes forms with a single, broad sulcus posteriorly bounded by broad, low, indistinct folds. The nature of the lunule, escutcheon, ligamental groove, and the presence or absence of dentition form additional bases for Iredale's separation of the Thyasiridae. Habe (1951, p. 127, 128) accepts Iredale's divisions to some extent as subgenera of *Thyasira*. Other authors accept a taxonomic middle-ground and employ relatively fewer and less restricted genera than Iredale.

Proper evaluation of the various schemes proposed for the classification of the Thyasiridae will require anatomical and morphological reexamination of all living and fossil species, a major task in itself. It is fortunate that the Cretaceous Thyasiridae of the Western Interior all fall within the broad concept of *Thyasira*, and with only minor variance, within the restricted concept of the genus used by Iredale, whose bases for generic classification are here tentatively accepted. A cursory survey of the Mesozoic and Cenozoic fossil Thyasiridae reveals that the basic morphologic distinctions between living *Thyasira* s.s., *Parathyasira*, and *Prothyasira* are also characteristic of separate lineages of fossil species, suggesting they form a valid basis for supraspecific classification. Some of the more subtle characteristics of the dentition, ligamental groove, and lunule used by Iredale in distinguishing his genera, however, are still of questionable taxonomic value and need to be evaluated on the majority of species. Iredale's new names (1930, p. 392-394) also have questionable status and may have to be abandoned in favor of older taxa such as *Philis* Fischer, 1861, *Tauraxinus* Sacco, 1901, and/or *Ptychina* Phillipi, 1836.

Cretaceous *Thyasira* differ from typical living representatives of the genus only in lacking on some species a well-defined submarginal sulcus on the shell exterior. In this respect, some Cretaceous species are more closely comparable with *Parathyasira,* which has a single sulcus. Cretaceous *Thyasira* lack the radial ornamentation and the broad, shallow primary sulcus of *Parathyasira,* however, and exhibit a low fold internally, and on some species a shallow groove externally, in the position of the well-defined submarginal sulcus found on Recent forms of *Thyasira.* It appears, therefore, that the Cretaceous species, while most closely allied to *Thyasira* s.s., also combine some of the characteristics of *Parathyasira,* a Cenozoic and Recent genus. *Parathyasira* may have had its origin in the weakly bisulcate Cretaceous *Thyasira.* Splitting of the Cretaceous rootstock in the early Cenozoic could have given rise to two branches, one trending toward *Parathyasira* in which the submarginal sulcus was completely lost, the other producing modern bisulcate *Thyasira* by progressive accentuation of the submarginal sulcus. The Tertiary fossil record, however, is too incomplete to substantiate this phylogeny at present.

## SYSTEMATIC PALEONTOLOGY

### Family THYASIRIDAE Dall, 1901

### **Genus THYASIRA Leach 1817**

Leach, 1817; unpublished manuscript; 1847, p. 272.
Lamarck, 1818, p. 492; in synonymy with *Amphidesma flexuosa* (Montagu).
Gray, 1847, p. 195.
Lamy, 1920 (1921), p. 290-292.
Iredale, 1930, p. 392-394.
Habe, 1951, p. 127.
Abbott, 1954, p. 384.
Ockelmann, 1958, p. 100.
Allen, 1958, p. 421-484.
Eberzin, 1960, p. 114.
Keen, 1963, p. 56, 91.

*Type species.—Tellina flexuosa* Montagu, 1803 (monotypy in Lamarck, 1818, in synonymy; subsequent designation in Gray, 1847).

*Diagnosis.*—Primary sulcus prominent, extending from posterior flank of umbo to posteroventral or midposterior margin; sulcus bounded by two moderately rounded folds; submarginal sulcus or groove small, prominent to faint, in some cases expressed mainly on shell interior. Shell smooth or with fine, concentric, flat to slightly raised growth lines; no fine radial ornament. Lunule weakly to moderately developed, flat to slightly recessed; escutcheon prominent, narrow, lanceolate. Ligament partially internal posteriorly. Hinge edentulous or with subtle pseudocardinal swelling just below and anterior to beak.

*Description.*—Shell inequilateral, prosocline, small to moderate size, attaining lengths greater than 1 inch; valves thin, fragile, to moderately thick, porcellanous to chalky, normally light colored; white and pale yellow common. Outline subround, subovate, or subtriangular; margin moderately recessed below and anterior to beaks and posteriorly at intersection with sulci. Equivalve, moderately biconvex, convexity greatest dorsocentrally on ventral portion of umbo. Beaks pointed to subacute; umbo swollen; beaks, early umbo prosogyre, curved forward and inward. Primary sulcus extends from posterior flank of early umbo to midposterior or posteroventral margin; sulcus prominent, moderately deep and broad, bounded by prominent, moderately and evenly rounded folds, the most central of which is the rounded umbonal fold. Submarginal sulcus situated just below and slightly inclined downward from posterodorsal margin; sulcus short, narrow, shallow and faint to deeply impressed, on some species not obvious externally and expressed either as an interior fold or a slight notch in the marginal outline of the shell. Where submarginal sulcus deeply impressed, posterodorsal flank of valve between sulcus and dorsal margin turned up in a small, rounded, subtriangular auricle. Many species with one or two very faint, narrow, medial flattened areas extending from the middle of the umbo to the midventral margin (text fig. 3). Rare species with a narrow flattened area or very shallow sulcus extending from anterior flank of umbo, along ventral margin of lunule, to the dorsoanterior margin, in some cases creating a truncated or slightly recessed area in the margin outline at this point (pl. 1, figs. 22, 24, 26). Lunule poorly to moderately well defined, flattened to shallowly excavated, on some species bordered by a distinct, narrowly rounded but never acute margin. Escutcheon deep, narrow, lanceolate, closing posteriorly over ligament. Valves smooth, or with fine, flat, raised, crowded growth lines;

no fine radial ornament developed, except rarely in primary sulcus.

Ligament partially internal posteriorly, covered by shelf-like projection of posterodorsal margin. Ligamental groove elongate, narrow, moderately deep, broadly curved, its lower raised margin formed in part by a narrow fold which is the interior counterpart of the submarginal sulcus on the shell exterior. Primary sulcus forms a broad interior fold along which gills and posterior adductor muscle attach. Posterior adductor insertion area rounded, situated midposteriorly on flank of interior fold. Anterior adductor insertion area larger than posterior, diagonally elongate-ovate to subrectangular with somewhat irregular margins, in some cases constricted near middle, extending from pallial line midanteriorly in a posteroventral direction, becoming separated from inner edge of pallial line near center of insertion area. Pallial line entire, narrow, without sinus. Muscle insertion areas and pallial line faintly impressed. Very fine, faint, radiating striae transgress shell interior. Hinge area only slightly thickened, without distinct hinge plate, edentulous, or with weakly developed to somewhat projecting flat pseudocardinal swelling just below and anterior to beak, known on both left and right valves. Pseudocardinal formed by flaring of slightly upturned edge of dorsoanterior margin where it abuts against the early umbo below the beak. Left valve of some species with shallow depression below beak to receive pseudocardinal swelling.

### THYASIRA ROSTRATA Kauffman, new species

*Diagnosis.*—Erect, moderately prosogyrate, moderately biconvex shells with prominent projecting beaks and umbos, a shallow notch anterior to the beak, steeply inclined dorsoanterior margin, moderately curved dorsoposterior-posterodorsal margin and primary sulcus, a moderately well-defined to prominent lunule and the height greater than the length. Two subspecies are known.

### THYASIRA ROSTRATA ROSTRATA Kauffman, new subspecies

Plate 1, figures 17, 18; plate 2, figures 1-27, 30; plate 3, figures 1-11

*Diagnosis.*—Shell attaining very large size for genus, moderately to highly biconvex; lunule large and well defined with ridged margins; shallow, prominent anterior sulcus forms flat to slightly concave notch in marginal outline at its intersection with the commissure.

*Material.*—Sixty-six well-preserved and generally complete specimens, all of them bivalved with the valves in normal opposition, most of them internal molds but the complete shell is preserved on a few.

The collection includes one large single population (35 specimens) from one locality and a complete adult variation suite and an ontogenetic series from early to late adult growth stages. Specimens are available from six localities.

*General form.*—Shell attaining very large size for genus, equivalve, moderately to greatly biconvex with the greatest inflation dorsocentrally; suberect, slightly to moderately prosocline. Outline subovate to subtriangular with the basal corners rounded (pl. 2, figs. 1-27). Posterodorsal and dorsoposterior margin steeply sloping from beak, forming a continuous, gentle, and somewhat asymmetrical curve, becoming nearly flat midposteriorly. Midposterior margin moderately to narrowly rounded at dorsal edge of primary sulcus notch; notch situated ventroposteriorly, shallow and evenly concave. Ventral and ventroanterior margins forming moderate, continuous, and nearly even curve, on some large specimens slightly flattened ventrally (pl. 2, fig. 15). Dorsoanterior margin flat to slightly concave at intersection with anterior sulcus; dorsoanterior corner subangular to narrowly rounded. Anterodorsal margin broadly and subevenly concave, forming shallow notch below beak, in some variants flattened at anterior extremity on auricle. Shell moderately thick.

TABLE 3.—*Summary of measurements for* Thyasira rostrata rostrata Kauffman, new subspecies.

| Character[1] | Number of specimens | Range | Average |
|---|---|---|---|
| Height (mm.) | 62 | 16.0-37.0 | 23.9 |
| Length (mm.) | 61 | 14.3-36.0 | 21.1 |
| Width of both valves (mm.) | 61 | 9.0-27.6 | 15.2 |
| HMS (mm.) | 58 | 9.0-25.0 | 14.9 |
| HABS (mm.) | 60 | 2.6-12.8 | 5.5 |
| HS (mm.) | 54 | 12.0-31.0 | 19.3 |
| LS (mm.) | 19 | 14.7-36.0 | 23.6 |
| Length of escutcheon (mm.) | 21 | 11.0-26.2 | 17.0 |
| Maximum width of escutcheon (mm.) | 21 | 2.0- 4.5 | 3.3 |
| MWF (mm.) | 20 | 1.3- 5.8 | 3.1 |
| Angle A (degrees) | 20 | 72.0-108.0 | 87.4 |
| Angle B (degrees) | 53 | 63.0-93.0 | 78.0 |
| Angle C (degrees) | 58 | 73.0-118.5 | 99.6 |
| Angle D (degrees) | 54 | 47.0-75.0 | 63.3 |
| Angle E (degrees) | 19 | 22.0-45.0 | 34.3 |

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[1] See text figure 4 for explanation of angles and abbreviations.

*Beaks, umbos.*—Beaks pointed, moderately prosogyrate, somewhat incurved, not touching, situated anterior to midline about one-third of the length from the anterior margin; apical angle narrow relative to other species (pl. 2, fig. 1). Umbos not well defined from rest of shell, highly inflated, prosogyrate, with faint trace of primary sulcus and fine, crowded concentric growth lines.

*Folds, sulci, auricles.*—Primary sulcus well defined, moderately and evenly curved from its origin on the posterior flank of the umbo to its termination at the ventroposterior margin, in some variants only slightly curved ventrally. Sulcus moderately deep, with a subangular base and the anterior face steeper than the posterior; becoming slightly broader with age (pl. 2, figs. 26, 27). Primary fold anterior to sulcus well defined, moderately arched, posterior flank steepest, crest subangular. Primary fold posterior to sulcus low, prominent, evenly arched. Submarginal sulcus a faint narrow groove 1-2 mm. in from margin and parallel to it, disappearing on mid-posterior flank of large shells. Shell broadly flattened between midline and primary sulcus. Anterior sulcus situated on dorsoanterior flank, originating on early adult portion of shell below umbo, extending with slight curvature and abrupt increase in width to dorsoanterior margin; sulcus broad, faintly defined, flat to slightly concave near margin. A small subtriangular auricle with blunt distal apex formed between anterior sulcus and dorsal to dorsoanterior margin (pl. 2, fig. 24).

*Lunule, escutcheon.*—Lunule large, relatively broad, heart-shaped, flat to slightly depressed and bounded by rounded ridges in small- to medium-size shells, prominently depressed and bounded by subangular ridges in large adult shells; a small, very low fold lies near the center of each side of the lunule in medium- to large-size shells (pl. 2, fig. 25). Escutcheon narrow, moderately depressed, unequally lenticular with the widest point just posterior to the middle, consisting of two shallow troughs with subangulated bases and fine, sharp peripheral ridges on either side of the deep narrow depression occupied by the ligament (pl. 2, fig. 25).

*Ornamentation.*—Entire shell surface covered with crowded, fine to moderately fine, subequally spaced, raised concentric growth lines, finer and more equally developed dorsally than ventrally, slightly coarser in primary sulcus than over rest of shell (pl. 1, fig. 17).

*Interior morphology.*—Ligamental grooves narrow, moderately depressed, with an angular base and flat interior flank, extending with slight curvature parallel to the posterodorsal margin from the beak to the edge of the dorsoposterior corner. Submarginal fold low, rounded, weakly developed, restricted to an area parallel to dorsoposterior margin. Primary interior fold prominent, moderately rounded, asymmetrical, following trace of primary sulcus on exterior.

Anterior sulcus reflected internally as a broad, very low rounded fold with coarse radial striae and ridges. Entire inner surface of shell between umbone and pallial line transgressed by fine to moderate strength radiating ridges and lines with shallow interspaces (pl. 2, fig. 17). Radial elements finely developed between pallial line and commissure. Pallial line prominent, entire without sinus, a slightly raised band about 1 mm. in width between the adductor muscle insertion areas. Anterior adductor insertion area very large, elongate-ovate in outline with irregular margins, its long axis directed from the dorsoanterior margin toward the midventral margin, its surface relatively smooth, transgressed by very fine crowded growth lines and a few coarse radial ridges (pl. 2, figs. 22, 26; text fig. 17). Anterior adductor insertion area separated from pallial line along the posterior half of its ventral margin (text fig. 17). Posterior adductor insertion area subround, midposterior in position astride the primary interior fold; margins irregular, surface marked by fine growth lines and a few radial ridges. A small, prominent, projecting pseudocardinal tooth formed beneath the beak of the left valve by flaring of the proximal edge of the ridge bounding the ligamental groove ventrally.

*Measurements.*—The range and average values of measurements on the large variation suite of *T. rostrata rostrata* are given in Table 3, and the measurements explained in text figure 4.

*Ontogeny.*—Ontogenetic development of juvenile and early adult individuals below 15 mm. height was determined from growth line traces at 5 mm. intervals of height on several specimens. Adult development above 15 mm. height was traced on an essentially complete growth suite of specimens. The primary ontogenetic changes in shell morphology are shown by the marginal outline of the shell, relative projection and apical angle of the beaks and umbos, development of the sulci, slope and projection of the anterodorsal flank (and size of the anterior auricle), and concentric ornamentation.

The marginal outline is subtriangular, much like that of *T. triangulata,* n. sp., on the juvenile shell (height 5 mm.), the anterior flank is rounded, not projecting, steeply sloping, and the apical angle is relatively narrow. Only the primary sulcus is weakly developed. At 10 mm. height (early adult stage) the shell retains many juvenile characters and is erect, higher than long, and has prominent projecting beaks. Ventral growth accelerates at this stage however, and the dorsoanterior and midposterior margins project slightly, giving the shell more of an ovate outline (text fig. 17). The anterior sulcus is faintly defined at this size.

Middle adult growth (height 10 to 25 mm.) is characterized by somewhat abrupt expansion of the anterior and dorsoanterior flanks, producing a more rounded marginal outline, shallowing of the dorsoanterior slope, widening of the apical angle, and reduction in the relative projection of the beaks and umbos. The primary sulcus becomes well defined, deep and narrow. In larger specimens (25 mm. and larger), further expansion of the anterior margin is limited, ventral growth becomes dominant, and the outline again becomes subtriangular to subovate with the height greater than the length, the beak and umbo strongly projecting, the apical angle relatively small, and the notch anterior to the beak shallower. The sulci, which gradually increase in width and depth during middle adult growth, become broader, better defined, and slightly shallower in late growth stages.

The lunule is flat and poorly defined by rounded ridges in shells from 10-15 mm. in height, slightly concave and well defined by narrowly rounded ridges in shells from 15 to 25 mm. in height, and very prominent, depressed, and sharply bounded by ridges in older shells. Finally, the concentric ornamentation is fine and subequally developed in shells below 15 mm. in height, becoming coarser and less equally developed on larger shells, and moderately coarse and more crowded on the largest valves. Small concentric undulations are limited to middle and late adult growth.

*Adult variation.*—*Thyasira rostrata rostrata,* n. subsp., is the most variable of Cretaceous *Thyasira* from the Western Interior, particularly in middle adult growth stages (height, 15 to 25 mm.). This is perhaps to be expected inasmuch as it is one of the first species to appear in the Cretaceous of the Western Interior, and apparently gave rise not only to the younger subspecies *T. rostrata cracens,* but also to the lineages of *T. beauchampi* and *T. quadrula.* Populations of adult *T. rostrata rostrata* contain numerous marginal variants which approach, but in most respects do not morphologically overlap both *T. quadrula quadrula* and *T. beauchampi beauchampi.* Compared with variation in a Recent population of the similar sized *T. sarsi* (text figs. 6, 7), *T. rostrata rostrata* is somewhat more variable in most respects, possibly due to postdepositional changes in shell form, and therefore the graphic differences shown between *T. rostrata rostrata,* the subspecies *cracens, T. beauchampi beauchampi,* and *T. quadrula quadrula* are more likely to indicate genetically distinct groups than an even broader range of intrasubspecific variation.

The primary variation in adult *T. rostrata rostrata* is expressed in the marginal outline, projection of the beaks, convexity, curvature of the posterior and anterodorsal margins and sulci, and projection and slope of the anterodorsal flank and auricle. Variation in the last feature seems to control variation in the others. In adult specimens between 15 and 25 mm. in height, the dorsoanterior flank ranges from rounded and moderately projecting with a small auricle (pl. 2, figs. 3, 19) to prominently projecting with a larger auricle, angulated dorsoanterior corner, and flattened anterodorsal and dorsoanterior margins (pl. 2, figs. 15, 24, 26). With expansion of the anterior auricle, the projection of the beak becomes relatively less, the apical angle larger, and the notch anterior to the beak shallower than found in shells without the expanded auricle. The marginal outline of shells with an expanded anterior flank ranges from subround to subovate, in normal shells from subovate to subtriangular. Most shells have a gently and evenly curved posterior margin and are moderately to highly biconvex, but some variants have the midposterior and dorsoposterior margin nearly straight (also the lower part of the primary sulcus), and much less convex shells more like those of *T. rostrata cracens.*

It is probable that the younger *T. rostrata cracens* evolved from marginal variants of *T. rostrata rostrata* with selection for and isolation of forms with low convexity, a straighter posterior margin and sulcus, and a more projected anterior and dorsal flank. Such forms exist in populations of *T. rostrata rostrata* but are not common. Subsequent evolutionary modification of this type of variant in which the anterior sulcus was eliminated and the lunule greatly reduced in prominence produced typical *T. rostrata cracens.*

*Remarks.—Thyasira rostrata rostrata* is one of the most abundant and variable of the Western Interior *Thyasira,* was among the first known to occupy the interior seaway during the Cretaceous, and based on morphologic similarities of certain variants to other species, probably was the parent stock from which arose the widely divergent lineages of *T. quadrula* and *T. beauchampi,* as well as the closely related and younger *T. rostrata cracens.* The derivation of *T. rostrata cracens* has been discussed. The *T. beauchampi* lineage is distinct from *T. rostrata rostrata* in being relatively much shorter and higher, in having a longer and more curved primary sulcus and posterior margin, in the more ventroposterior position of the primary sulcus notch, in the more prominent anterior sulcus, less well-developed lunule, and coarser concentric ornamentation. The two are morphologically related, however, having a common general erect form with projecting beaks and umbos, prominent anterior sulci, well-developed lunules, anterior auricles, and evenly curved posterodorsal and dorsoposterior margins (compare pl. 1, fig. 24 with pl. 2, fig. 24). The *T. beauchampi* lineage probably arose from more erect variants of

*T. rostrata rostrata,* though no morphologic series can be established between the two.

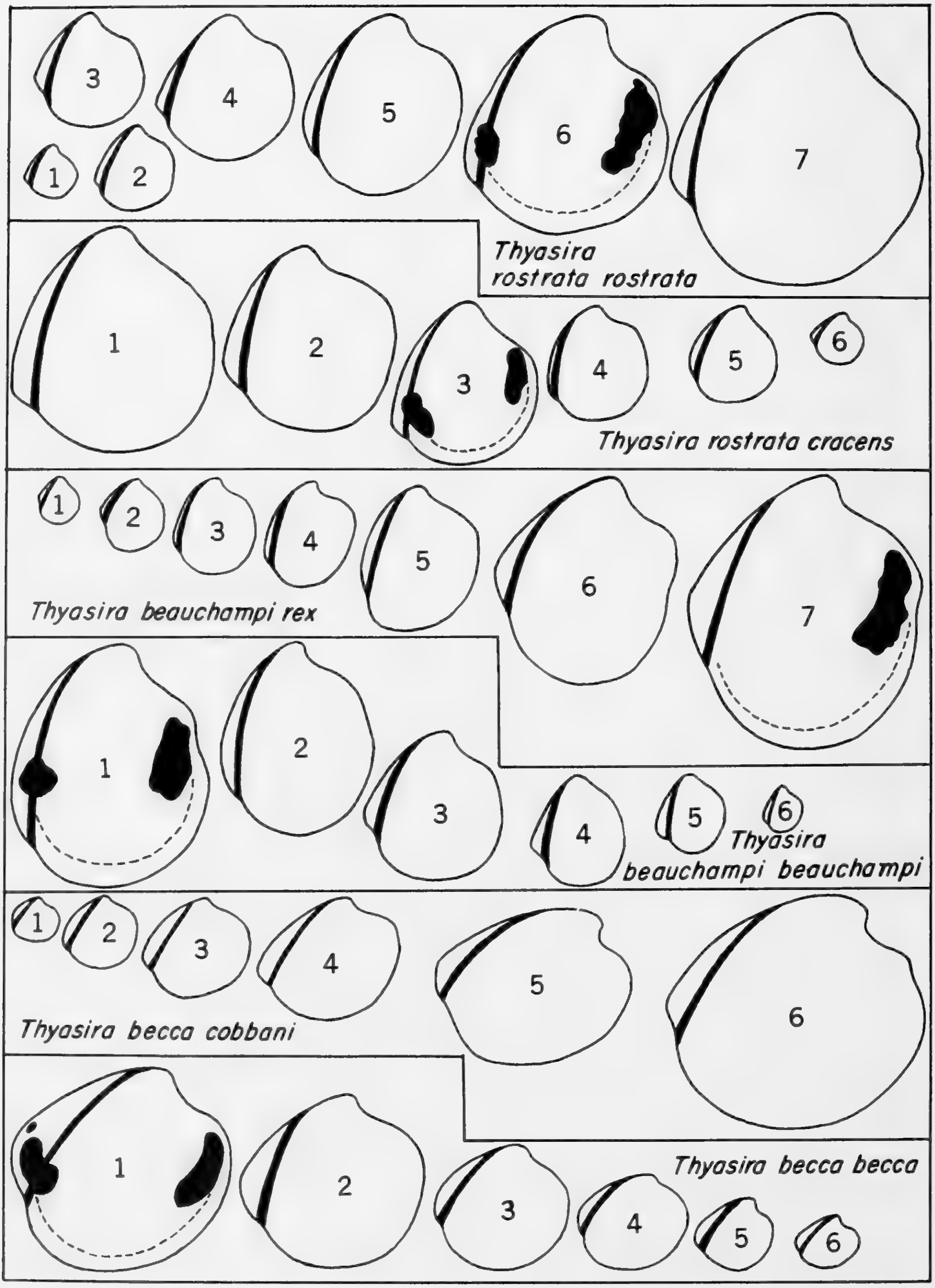
*T. rostrata rostrata* is more distantly related to the *T. quadrula* lineage; marginal variants with a round profile, projecting dorsoanterior flank, flattened posterior, anterodorsal, and dorsoanterior margins, moderately projecting beaks, and only slightly curved sulci (pl. 3, figs. 1-6) approach but do not overlap *T. quadrula quadrula,* the oldest subspecies in the lineage, in gross morphologic aspect. The two may be easily distinguished, however, by the low blunt beak and umbo, nearly horizontal anterodorsal margin, straighter posterior margin and primary sulcus, more ventroposterior position of the primary sulcus notch, and oblique, slightly curved ventroanterior margin on *T. quadrula quadrula* (compare pl. 3, figs. 1-6 with pl. 1, figs. 1, 2).

*T. rostrata cracens* is derived directly from this subspecies and most closely resembles it. Typical *cracens* however are much less convex, relatively higher with less projecting anterior and posterior margins, have a straighter posterior margin and primary sulcus, lack an anterior sulcus and well-defined lunule, have well-defined medial flattened areas on either side of the midline, and have a less projecting beak than found in *T. rostrata rostrata.*

*T. rostrata rostrata* is named from the Latin *rostratus* meaning beaked or curved, referring to the prominent projecting beaks and umbos of moderate prosogyrate curvature.

*Stratigraphic position.*—In the Western Interior of North America *T. rostrata rostrata* is one of the first major lineages to appear, occurring solely in the Early Campanian ammonite zones of *Baculites* sp. with weak flank ribs and *B. obtusus* (early form) (text fig. 1). In the zone of *B.* sp. with weak flank ribs, *T. rostrata rostrata* is known from three localities in the United States and one in Canada: USGS Mesozoic locality D3332, from the Steele Shale 200 feet below the base of the Mesaverde Formation, Carbon County, Wyoming; USGS Mesozoic locality D4162, from the Cody Shale, 150 feet below the Parkman Sandstone, Carbon County, Wyoming; USGS Mesozoic locality 10459, from the Steele Shale, Lost Soldier-Ferris District, Wyoming; and from the Lea Park Formation (zone of *Baculites* sp. with weak flank ribs or *B. obtusus,* early form) in east-central Alberta, Canada.

From the zone of *B. obtusus* (early form), the species may be represented in the Lea Park Formation of east-central Alberta, as previously cited, and in addition occurs at two localities in the United States: USGS Mesozoic locality D3256, in the Steele Shale,



Text Figure 17.

80 feet above the Ardmore Bentonite Bed, T. 40 N., R. 79 W., Wyoming; and at USGS Mesozoic locality D4747, in the Cody Shale, 1,690 feet below the top, Carbon County, Wyoming.

*Types.*—Holotype, a large adult bivalved specimen with the shells in normal apposition and the shell material intact; well preserved; from the Lea Park Formation of Alberta, GSC 18757. Paratype, a large bivalved shell from the same locality, GSC 18759. Figured paratypes from the zone of *Baculites* sp. with weak flank ribs, USNM 153481-153488, 153492-153495, 153497-153499, 153500, 153502, 153507. Figured paratypes from the zone of *B. obtusus* (early form), USNM 193490, 193505-193506. Measured, unfigured paratypes: from USGS 10459 (35 specimens), USNM 153480 (typical) 153479 (transitional variants to *T. quadrula*), 153501 (transitional to *rostrata cracens*); from USGS D4162 (4 specimens), USNM 153496; from USGS D3332, (1 specimen), USNM 153491; and from USGS D4747 (2 specimens), USNM 153489.

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TEXT FIGURE 17.—Ontogeny of the marginal outline and primary sulcus trace, and characteristics of the muscle insertion areas and pallial line, where observable, in Cretaceous species of *Thyasira* from North America. Primary sulcus trace denoted by heavy line, muscle insertion areas by black patches, pallial line by light line between insertion areas. Development of ontogeny described in detail with each species description. Illustrations based on the following, partially restored where necessary to show entire outline: *Thyasira rostrata rostrata,* n. subsp., all specimens paratypes, (1, 2) growth line traces at 5-mm. intervals, USNM 153507; (3-7), marginal outlines of adult valves as follows—(3) USNM 153497, (4) USNM 153502, (5) USNM 153490, (6) USNM 153482, (7) USNM 153483, the largest specimen. *Thyasira rostrata cracens,* n. subsp., all specimens paratypes; (1-4) marginal outlines of adult shells as follows—(1) USNM 153430a, (2) USNM 153420, (3) USNM 153425, (4) USNM 153428; (5) marginal outline and (6) 5-mm. growth line trace of USNM 153427. *Thyasira beauchampi rex,* n. subsp., (1-3) growth line traces at 5-mm. intervals, and marginal outline (5) of the holotype, USNM 153411; (4) marginal outline of a paratype, USNM 153410; (6) growth line trace at height of 30 mm., and (7) marginal outline of the largest paratype, USNM 153409. *Thyasira beauchampi beauchampi,* n. subsp., (1) marginal outline, and (3-6) growth line traces at 5-mm. intervals of the holotype, USNM 153412; (2) marginal outline of a paratype, USNM 153413. *Thyasira becca cobbani,* n. subsp., (1-4) growth line traces at 5-mm. intervals on the paratype, USNM 153478; (5) growth line trace at 23 mm. in height, and (6) marginal outline of the holotype, GSC 18758; *Thyasira becca becca,* n. subsp., (1-3) outline traces of the following—(1) USNM 153518, paratype, (2) USNM 153512, the holotype, (3) USNM 153521, a paratype; (4-6) growth line traces at 5-mm. intervals on the holotype, USNM 153512.

### THYASIRA ROSTRATA CRACENS Kauffman, new subspecies

Plate 1, figures 14-16; plate 3, figures 12-30, 32-34

*Diagnosis.*—Shell attaining moderate size, moderately biconvex, lunule poorly defined; no anterior sulcus developed on majority of specimens; flank posterior to primary sulcus narrow; dorsoanterior corner rounded and not greatly projecting; concentric growth lines fine and subequally developed; concentric undulations prominent, moderately spaced.

*Material.*—Twenty-six well-preserved specimens, most of them relatively complete, bivalved internal molds with the valves in normal apposition; some specimens with the shell completely preserved; specimens from 8 localities; a graded growth series from early to late adult stage (height, 13-35 mm.) represented; largest single population (USGS D255) consisting of 13 specimens.

*General form.*—Shell attaining moderate size for genus, equivalve, moderately biconvex with greatest inflation dorsocentrally; slightly prosocline; shell moderately thick, strong. Marginal outline subovate; shell suberect, with height greater than length (pl. 3, figs. 19-29). Posterodorsal and dorsoposterior margins forming gentle continuous curve, nearly symmetrical, somewhat flattened midposteriorly; midposterior margin at dorsal edge of primary sulcus notch moderately rounded, rarely subangular on internal molds; sulcus notch ventroposterior, very shallow and asymmetrical. Ventral and anterior margins normally forming continuous moderate curve, on some specimens slightly flattened midventrally and dorsoanteriorly (pl. 3, figs. 21, 22). Dorsoanterior corner moderately rounded, not angulated or auriculate. Anterodorsal margin flat except below beaks where it forms shallow concave notch.

*Beaks, umbos.*—Beaks pointed to acutely rounded, moderately prosogyrate, slightly incurved and nearly touching, situated subcentrally just anterior to midline (pl. 1, figs. 14-16). Umbos not well defined from rest of shell except that they lack concentric undulations (pl. 1, fig. 14); umbos slightly prosogyrate, moderately inflated, with fine subeven raised growth lines. Apical angle moderate (Table 4).

*Folds, sulcus.*—Primary sulcus well defined, shallow, slightly asymmetrical with anterior face steepest, gently and evenly curved, containing faint, fine radial lines and ridges, originating on the posterior flank of the umbo and terminating posteroventrally in a shallow notch; narrow dorsally and moderately broad ventrally, expanding uniformly. Submarginal sulcus not developed on shell exterior, represented by faint flattened area or, on one juvenile shell, a very faint groove next to the dorsoposterior margin; a small but prominent interior fold marks position of submarginal sulcus. No posterior auricle. Primary fold posterior to primary sulcus low, gently and evenly arched on large adults, more prominent and inflated on youngest adult shells (pl. 3, figs. 12-17). Primary fold anterior to sulcus moderately prominent and convex, asymmetrically rounded with posterior flank steepest. Well-defined flattened area lies between this fold and the midline, on rare specimens slightly depressed and sulcate near margin. No anterior sulcus developed, anterior flank and dorsoanterior margin commonly evenly rounded; on rare specimens a faint anterior flattened band on shell intersects dorsoanterior margin forming somewhat flattened profile at this point (pl. 3, fig. 19). No anterior auricle.

TABLE 4.—*Summary of measurements for* Thyasira rostrata cracens Kauffman, new subspecies.

| Character[1] | Number of specimens | Range | Average |
|---|---|---|---|
| Height (mm.) | 13 | 18.0-31.0 | 23.8 |
| Length (mm.) | 14 | 16.0-30.5 | 22.1 |
| Width of both valves (mm.) | 13 | 10.5-22.0 | 14.5 |
| HMS (mm.) | 14 | 9.0-19.5 | 13.0 |
| HABS (mm.) | 11 | 3.1- 8.1 | 5.3 |
| HS (mm.) | 14 | 12.0-25.5 | 17.3 |
| LS (mm.) | 13 | 15.0-30.0 | 22.1 |
| Length of escutcheon (mm.) | 11 | 10.0-20.5 | 14.0 |
| Maximum width of escutcheon (mm.) | 11 | 2.2- 4.0 | 3.1 |
| MWF (mm.) | 14 | 1.0- 4.3 | 2.9 |
| Angle A (degrees) | 13 | 68.5-102.0 | 83.3 |
| Angle B (degrees) | 11 | 65.0-81.5 | 73.5 |
| Angle C (degrees) | 11 | 82.0-100.0 | 91.8 |
| Angle D (degrees) | 13 | 51.0-72.0 | 61.7 |
| Angle E (degrees) | 13 | 22.0-44.0 | 35.2 |

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[1] See figure 4 for explanation of angles and abbreviations.

*Lunule, escutcheon.*—Lunule not distinguishable on small shells, weakly defined on large shells; moderate size, heart-shaped, flat to very slightly depressed, bounded by faint, moderately rounded ridges. Escutcheon narrow, subequally lenticular in outline with widest point just anterior to center; shallow, consisting of narrow shallow troughs about 1 mm. wide and having low sharp ridges along the outer periphery, bounding the deep, very narrow, lanceolate depression occupied by the ligament( pl. 3, fig. 28).

*Ornamentation.*—Surface of valves covered by moderately fine, subequally developed (rarely unequal as in pl. 3, fig. 23), crowded and subevenly spaced, raised concentric growth lines (pl. 3, fig. 32), in most cases superimposed on the adult part of the shell onto small, prominent, moderately spaced, low concentric undulations (pl. 3, fig. 19), the most prominent among Cretaceous representatives of the genus. Fine radial lines and fine ridges occupy the primary sulcus and rarely other parts of the shell surface.

*Interior morphology.*—No evidence of pseudocardinal dentition. Entire inner surface of shell between umbo and commissure covered with fine radial ridges with moderately broad shallow interspaces (pl. 3, figs. 19, 20); ridges more prominent anteriorly, posteriorly on flanks of primary interior fold, and over adductor insertion areas; ridges faintest on early umbo and between pallial line and commissure. Primary interior fold moderately and asymmetrically convex (anterior flank steepest), radially striate, conforming to trace of primary sulcus exteriorly. Submarginal fold narrow, moderately convex, prominent, extending between widest point of escutcheon and midposterior margin, slightly expanding in size and subparallel to commissure. Posterocentral and (rare) anterior flattened areas of shell reflected interiorly. Pallial line entire, narrow (0.5 mm. or less), slightly raised, prominent between adductor insertion areas. Posterior adductor insertion area (text fig. 17-3) weakly impressed, subovate with somewhat irregular margins, moderate size, situated midposteriorly astride the primary interior fold, and on its anterior flank; area with faint crowded growth lines and coarse radial lines. Anterior adductor insertion area weakly impressed, elongate-ovate with long axis directed from midanterior to midventral margin, moderately large, its margins irregular and ventrally separated partially from pallial line (text fig. 17-3), its surface smoother than rest of shell except where transgressed by prominent raised radial lines.

*Measurements.*—The maximum range and average values of measurements obtained from specimens of *T. rostrata cracens* are presented in Table 4, and the measurements explained in text figure 4.

*Ontogeny.*—Early to late adult growth stages are represented in the collections by an intergrading series of specimens between 17 and 35 mm. in height. Observations on the ontogeny of earlier juvenile and adult growth were obtained from growth line traces taken on several specimens at 5 mm. intervals (text fig. 17). Significant ontogenetic change in *T. rostrata cracens* is demonstrated by the marginal outline, ornamentation, sulci and flattened areas of the shell exterior, development of the lunule, and relative projection of the beaks and umbos.

The marginal outline of *T. rostrata cracens* does not change as radically with growth as does that of other Cretaceous *Thyasira* from the Western Interior. The juvenile shell (height, 5 mm.) is erect, subovate, and relatively higher than it is long. It differs primarily from the adult in having a less produced anterior flank, more anterior and more projected beak, and straighter dorsoposterior margin and primary sulcus (very faint and shallow at this growth stage). The early shell at 10 mm. in height (text fig. 17) shows acceleration of ventrally directed growth, accentuation of the primary sulcus and its marginal notch, and slight projection of the mid-posterior margin. The mature adult form of the shell develops at heights of 15 mm. and above with expansion of the anterior margin (text fig. 17). This results in a more rounded-subovate marginal outline, reduction of the beak-umbo projection and increase in apical angle, and produces greater curvature of the primary sulcus, posterior margin, and accentuation of the recess below the beaks.

The primary sulcus is shallow and poorly defined at a height of 5 mm., becomes more depressed and very prominent from 10 to 15 mm. in height with associated elevation of the posterior primary fold, and becomes shallower with more gently sloping flanks at greater vertical diameters due to broadening and relative loss of convexity of the posterior fold. The flattened areas of the shell posteromedially and anteriorly (on some specimens) appear between 10 and 15 mm. in height and become gradually more pronounced with increasing size. No lunule is defined below 10 mm. in height; the lunule is weakly delineated, small, and flat between 10 and 20 mm. in height, and becomes weakly to moderately well defined, slightly depressed, and bordered by distinct rounded ridges in larger shells. Finally, the juvenile and early adult surface sculpture at sizes smaller than 10 mm. in height is finer and more evenly developed, generally without associated undulations, than that found on later growth stages, where it is superimposed on concentric undulations. The adult ornament becomes coarser, more crowded, and more unequally developed with increasing shell size.

*Adult variation.*—Among medium to large adult shells of *T. rostrata cracens,* morphologic variation is slight with the exception of the dorsoanterior flank. This is one of the most variable parts of living *Thyasira,* such as *T. sarsi* (see previous discussion), as well. The flank of *T. rostrata cracens* varies from slightly projecting and evenly rounded (pl. 3, fig. 23), in which case the anterodorsal margin slopes steeply away from the beak and forms a very shallow notch anterior to the beak, to moderately projecting, with a more narrowly and unevenly rounded dorsoanterior corner (pl. 3, figs. 19, 29), a less steeply sloping anterodorsal margin, and a more prominent notch anterior to the beak. The height is less, relative to length, in the latter.

Minor adult variation in *T. rostrata cracens* includes the following: radial lines are variously developed on a few valves, absent on others; rare valves have a flattened band in the position of the anterior sulcus of *T. rostrata rostrata,* whereas most shells have this area evenly rounded; concentric undulations are faintly to coarsely developed on the shell; the beaks are pointed to narrowly rounded and moderately to strongly projecting. These variations are illustrated on plate 3, figures 12-30, 32-34.

*Remarks.—Thyasira rostrata cracens,* n. subsp., is the youngest member of the *T. rostrata* lineage. It has certain gross features in common with *T. triangulata,* although the two belong in separate lineages. *T. triangulata* is distinct from *T. rostrata cracens* in the more erect pointed beak, smaller apical angle, less produced and more steeply sloping anterodorsal-dorsoanterior margin, straighter posterior margin and primary sulcus, more prominent primary posterior fold, and more irregular surface sculpture (compare pl. 1, fig. 6 with pl. 1, figs. 14, 15).

The differences between *T. rostrata cracens* and its ancestor are less striking. *T. rostrata rostrata* may be distinguished from this subspecies in having a much more inflated shell, strongly developed lunule, more projected dorsoanterior flank which is auriculate, in having an anterior sulcus, in having finer concentric sculpture, more strongly prosogyrate beaks, and in lacking a strongly developed posteromedial flattened area on the shell surface. The two subspecies are very similar in gross aspect however, attesting to their close phylogenetic relationship and the conservative nature of evolutionary change in Cretaceous *Thyasira.*

The name *cracens* is drawn from the Latin *cracens, -entis,* meaning slender, graceful, and refers to the reduced width and graceful arched form of the shell.

*Stratigraphic postion.—Thyasira rostrata cracens* is one of the longest ranging Cretaceous thyasirids from the Western Interior, extending from the zone of *Baculites obtusus* (late form) through the zone of *B. perplexus* (late form). This extended stratigraphic occurrence may in part be due to the limited record and poor preservation of specimens from the upper half of the range. These specimens definitely belong in the lineage of *T. rostrata* and appear closest to the subspecies *cracens*, where I have placed them. Their numbers and preservation, however, do not allow critical morphologic comparison with the good populations at the base of the range, and slight evolutionary change in the lineage, possibly of subspecific magnitude, could have taken place in the upper part of the time span but would not be detectable on the basis of this material.

In the zone of *B. obtusus* (late form), this subspecies occurs at USGS Mesozoic locality D3260 in the middle Steele Shale, between the Stray and Parkman Sandstones, in sec. 33, T. 39 N., R. 78 W., Wyoming. *T. rostrata cracens* occurs in the zone of *B. perplexus* (early form) at four distinct levels (levels 1, 2, 3, 5 of this report; text fig. 1), from oldest to youngest: USGS Mesozoic locality D255, Steele Shale, Converse County, Wyoming (level 1); USGS Mesozoic locality D1864, Pierre Shale, 30 to 60 feet above the basal bentonite of the Mitten Black Shale Member, Niobrara County, Wyoming (level 2); D1865, Pierre Shale, 70 to 90 feet above the basal bentonite of the Mitten Black Shale Member, Niobrara County, Wyoming (level 3); USGS Mesozoic locality D1866, Pierre Shale, 695 to 714 feet above the top of the Mitten Black Shale Member, Niobrara County, Wyoming (level 5).

*T. rostrata cracens* occurs in the zone of *B. gilberti* (fig. 1) at USGS Mesozoic locality D2910, Pierre Shale, 878 feet above the base of the Mitten Black Shale Member, Niobrara County, Wyoming. It occurs in the zone of *B. perplexus* (late form), its highest stratigraphic position, at USGS Mesozoic locality D1564 in the Tepee Butte zone of the Pierre Shale, Jefferson County, Colorado. The species is also known from two localities from levels which could be defined no more precisely than the zone of *Baculites perplexus* undifferentiated: USGS Mesozoic locality 3763, Montana Group, probably lower Mount Garfield Formation or upper Mancos Shale, Book Cliff Coal Field, Mesa County, Colorado; and USGS Mesozoic locality 3779, from the same level and general area as cited above for 3763.

*Types.*—Holotype, USNM 153429, a large adult bivalved specimen with valves in normal apposition and shell material intact, from USGS Mesozoic locality D1864. Illustrated paratypes from the zone of *B. perplexus* (early form): from USGS D255, USNM 153420, 153424-153426, 153433, 153434, 153436, 153437; from USGS D1866, USNM 153432; from USGS 3779 (zone of *B. perplexus* undifferentiated), USNM 153427, 153428; illustrated paratype from the zone of *B. obtusus* (late form), USNM 153435; measured but unillustrated paratypes; from the zone of *B. perplexus* (early form), USGS D255 (5 specimens), USNM 153430; USGS D1865 (1 specimen), USNM 153421; USGS D1866 (1 specimen), USNM 153422; USGS D2910, from the zone of *B. gilberti* (1 specimen), USNM 153423; from rocks bearing *B. perplexus* undifferentiated, USGS 3763 (1 specimen), USNM 153438; USGS 3779 (unmeasured paratypes, 3), USNM 153439. Unmeasured paratype from USGS D255, USNM 153431.

### THYASIRA QUADRULA Kauffman, new species

*Diagnosis.*—Erect, medium size, moderately biconvex shells with a subquadrate outline; Posterior margin and primary sulcus straight to slightly curved, sulcus notch near junction between ventroposterior and posteroventral margins; beaks low, slightly prosogyrate, posterior of midline; beak notch shallow; anterodorsal margin straight and nearly horizontal; apical angle large. Two subspecies are known.

### THYASIRA QUADRULA QUADRULA Kauffman, new subspecies

Plate 1, figures 1, 2; plate 5, figures 1-5

*Diagnosis.*—Beak very slightly projecting and rounded, situated on posterior third of shell, suberect to slightly prosogyrate; apical angle broad; submarginal sulcus well defined; primary sulcus straight to slightly curved; no anterior sulcus developed; ventroanterior margin obliquely sloping.

*Material.*—Six specimens representing a growth series from early to late adult development, moderately well preserved; four of the specimens are bivalved internal molds with varying amounts of attached shell material; two are single valves with much of the shell retained.

*General form.*—Shell moderate size for genus, equivalve, orthocline to slightly prosocline, moderately biconvex with greatest convexity subcentral. Shell thin, fragile. Outline subquadrate to subrectangular with height slightly greater than length. Dorsoanterior margin straight to very slightly concave and nearly parallel to hinge axis (horizontal plane); shallow concave notch formed just anterior to beak. Dorsoanterior corner narrowly rounded to obtusely subangular. Anterior and ventral margins forming a continuous moderate curve, in most shells asymmetrical with slightly uneven curvature, oblique and somewhat less rounded anteroventrally (pl. 1, fig. 2), slightly more rounded posteroventrally. Primary sulcus notch weakly defined, slightly convex, flat, or slightly concave, situated near posteroventral corner.

Dorsal edge of notch moderately rounded to obtusely subangulate with posterior margin. Posterior margin very slightly curved between sulcus notch and beak, flatter ventrally than dorsally.

*Beaks, umbos.*—Beaks narrowly to moderately rounded, slightly projecting above dorsal margin, slightly prosogyrate (pl. 1, fig. 1), situated at posterior end of dorsal margin in posterior third of total length; very slightly incurved. Umbos not well defined, moderately convex, with very fine growth lines and first trace of shallow primary sulcus on posterior flank.

*Folds, sulci, auricle.*—Submarginal sulcus well defined, a narrow, moderately depressed groove extending along the middle part of the posterior margin to the edge of the primary sulcus notch (pl. 1, fig. 2); slightly curved. A narrow, flat, subtriangular auricle formed posterior to submarginal sulcus. Primary sulcus well defined, relatively narrow, shallow to moderately depressed, slightly curved, becoming broader and shallower ventrally on large shells, originating on posterior flank of umbo and extending to ventroposterior corner (pl. 1, fig. 2). Posterior primary fold very narrow, prominent, asymmetrical with posterior flank steepest; crest narrowly rounded to subangular. Anterior primary fold low, broadly rounded, asymmetrical with posterior flank steepest. Faint flattened area on shell formed between midline and anterior primary fold. No anterior sulcus.

*Lunule, escutcheon.*—Lunule poorly defined, a flat to slightly depressed heart-shaped area anterior to beaks with rounded lateral margins. Escutcheon very narrow, lenticular in outline, shallow, extending from umbo to dorsal margin of primary sulcus notch. Lunule composed of two shallow troughs 1 mm. or less at widest point on either side of narrow lenticular depression occupied by ligament. Ligament exposed over most of length. Fine ridges bound troughs.

*Ornamentation.*—Entire surface of valve covered by crowded, very fine growth lines, a few of them slightly raised and coarser than the others (pl. 5, figs. 1, 2). A few faint concentric undulations developed on ventral half of rare shells. Rare fine striae developed in primary sulcus.

*Interior morphology.*—Hinge areas poorly preserved; no evidence of pseudocardinal dentition noted. Ligamental groove shallow, with narrowly curved base, opening obliquely outward, possibly covered at anterior and posterior extremities by overlapping shell margin. Primary fold prominent, asymmetrical, anterior flank steepest, conforming to primary sulcus exteriorly. Submarginal fold prominent, more strongly developed than corresponding exterior sulcus; narrow, moderately elevated with narrowly rounded crest. Pallial line entire, weakly defined as a slightly elevated band between adductor muscle insertion areas: insertion areas not completely preserved on any specimens available for study. Anterior area large, diagonally elongate-ovate, with irregular margins, extending from midanterior toward midventral margin (text fig. 18), covered with fine growth lines and transgressed by prominent radial ridges. Posterior adductor insertion area not known. Fine, moderately and unevenly spaced, raised radial lines transgress shell interior between umbo and pallial line; lines strongest anteriorly and posteriorly, especially over muscle insertion area.

*Measurements.*—Holotype, coattached medium-size adult valves: Height, 18.7 mm.; length, 19 mm.; width of both valves, 10.8 mm.; height to posterior break in slope, dorsal edge of sulcus notch, 12 mm.; height to junction of dorsal and anterior margins, 3.5 mm.; height to middle of primary sulcus notch, 15.5 mm.; length of line connecting beak and middle of sulcus notch, 17.8 mm.; length of escutcheon, 11.5 mm.; maximum width of escutcheon, 2.5 mm.; maximum width of margin posterior to primary sulcus, 2.3 mm.; angle A, 76°; angle B, 88°; angle C, 108°; angle D, 58°; angle E, 34° (USNM 153470).

Paratype (USNM 153467), a large adult internal mold of coattached valves: height, 24.7 mm.; length, 25 mm.; width of both valves, 19.1 mm.; height to posterior break in slope at dorsal edge of sulcus notch, 12 mm.; height to junction between anterior and dorsal margins, 4 mm.; height to middle of primary sulcus notch, 17.2 mm.; length of line connecting middle of sulcus notch and beak, 22.2 mm.; maximum width of escutcheon, 3 mm.; maximum width of flank posterior to primary sulcus, 3.5 mm.; angle B, 89°; angle C, 111.5°; angle D, 54.5°; angle E, 27°. Paratype (USNM 153468), a small adult right valve: height, 15.7 mm.; length, 14 mm.; height to posterior break in slope at dorsal edge of primary sulcus notch, 10.8 mm.; length of a line connecting beak and middle of posterior sulcus notch, 15 mm.; length of escutcheon, 10.4 mm.; angle D, 55°; angle E, 33°. Paratype, small adult paired valves (USNM 153469): height, 15.5 mm.; length, 15 mm.; width of both valves, 8.2 mm.; height to posterior break in slope, dorsal edge of primary sulcus notch, 8.5 mm.; height to junction of anterior and dorsal margins, 2.4 mm.; height to middle of primary sulcus notch, 13 mm.; length of line connecting beak and middle of primary sulcus notch, 14 mm.; length of escutcheon 9.3 mm.; maximum width of escutcheon, 1.5 mm.; maximum width of flank posterior to primary sulcus, 2 mm.; angle B, 78°; angle C, 97°; angle D, 67°; angle E, 40°.

*Ontogeny.*—Observations on development at sizes less than 15 mm.

in height, the smallest individual, were taken from growth line traces at 5-mm. intervals on two specimens. A moderately complete growth series is present for larger sizes. The main ontogenetic changes noted in *Thyasira quadrula quadrula* are in the marginal outline, curvature of the primary sulcus and posterior margin, and in the ornamentation. The latter changes from fine flat early growth lines, subevenly developed, to slightly coarser growth lines, many of them raised and unequally developed on later ontogenetic stages. Weak concentric undulations are middle to late adult growth features not known on shells below 10 mm. in height.

The marginal outline changes from subrounded on juvenile shells (height, 5 mm.: text fig. 18) to subovate on young adults (height, 10 mm.), to subquadrate and subrectangular at larger sizes (pl. 5, compare fig. 2 with fig. 4; text fig. 18). These changes are tied to changes in the development of the dorsal and anteroventral margins. In small shells the anterodorsal margin slopes moderately away from the beak and is projecting. The anteroventral margin is moderately and evenly rounded and somewhat projecting. At heights of 10 to 15 mm., the dorsal margin becomes more nearly parallel to the hinge axis, producing a more quadrate outline, and above 15 mm., the anteroventral margin ceases to expand significantly, becomes more oblique in slope, and relatively less rounded. The relative projection of the anterior margin increases with shell size. The posterior margin is slightly to moderately curved in shells below 10 mm. in height, as is the primary sulcus; both straighten and become slightly curved at later growth stages. In the largest adult shells, the primary sulcus again becomes more curved near its ventral termination, whereas the posterior margin continues to straighten.

*Remarks.*—The low erect beaks, broad apical angle, and subquadrate outline of *T. quadrula quadrula* distinguish it from all other Cretaceous species in the Western Interior. Although this is one of the early species to appear in the Interior, it is not among the first wave which includes *T. rostrata rostrata, T. beauchampi beauchampi,* and *T. advena advena.* The general similarity between typical *T. quadrula quadrula* and certain marginal variants of *T. rostrata rostrata* with an abnormally expanded dorsoanterior flank and somewhat reduced beaks (pl. 3, figs. 1-6) suggests that the *T. quadrula* lineage arose as a major phylogenetic branch from the lineage of *T. rostrata* toward the end of the Early Campanian (fig. 13). No morphologic series can be established between the two species however, supporting their taxonomic division. Even marginal variants of *T. rostrata rostrata* never attain the reduced beaks, nearly horizontal dorsal margin, posterior position of the beaks, and subquadrate outline of the *T. quadrula* lineage.

*Thyasira quadrula quadrula* is morphologically most closely comparable to its direct descendent *T. quadrula arrecta.* It may be distinguished from the younger subspecies by its less projecting beaks, finer ornamentation, lack of an anterior sulcus, larger apical angle, more nearly horizontal anterodorsal margin, more obscure lunule, stronger submarginal sulcus and interior fold, and less incised primary sulcus notch. The name *quadrula* is drawn from the Latin *quadrula* meaning a small or diminutive square and refers to the subquadrate outline of the small valves.

*Stratigraphic position.—Thyasira quadrula quadrula* first appears in the Western Interior in the Early Campanian zone of *Baculites obtusus* (probably the late form) at USGS Mesozoic locality 10666, upper part of the Pierre Shale northwest of Horse Creek, Wyoming. It is not yet known from the early Late Campanian zone of *B. maclearni.* The highest occurrence of the subspecies is in the early Late Campanian zone of *B. asperiformis* at USGS Mesozoic locality D5 (text fig. 1) in the lower one-third of the Pierre Shale, Douglas County, Colorado.

*Types.*—Holotype, moderately large coattached adult valves (pl. 1, figs. 1, 2), internal mold with about half of the shell material attached, USNM 153470, USGS Mesozoic locality D5. Paratype (USGS D5), small adult coattached valves with shell intact, USNM 153469; paratype (USGS D5), large adult internal mold of coattached valves, USNM 153467; paratype, (USGS D5), a small adult internal mold of a right valve, USNM 153468; paratype, a moderately large adult right valve with most of the shell intact and ventral margin broken (USGS 10666), USNM 153466; unfigured paratype (USGS 10666), crushed, incomplete, coattached valves, USNM 153503.

### THYASIRA QUADRULA ARRECTA Kauffman, new subspecies

Plate 1, figures 3-5; plate 5, figures 6-27

*Diagnosis.*—Beaks pointed, slightly to moderately prosogyrate, more strongly projecting than in *T. quadrula quadrula,* situated just anterior to midline at anterior end of dorsal margin. Posterior margin slightly curved. Outline subquadrate with projecting, moderately rounded anteroventral margin; not oblique. Ornamentation of fine to medium size, subequal raised growth lines and low but numerous concentric undulations.

*Material.*—Thirty-five adult valves, most of them bivalved internal molds with shells in normal apposition and pieces of shell material adhering. Some valves have shell completely intact. Scattered single valves. Shells form a continuous adult growth series; largest single population 15 specimens.

*General form.*—Shell attaining moderate size for genus, equivalve, suberect, slightly prosocline, moderately biconvex with greatest inflation dorsocentrally. Shell thin, fragile. Outline subquadrate with rounded corners, to subovate (pl. 5, figs. 6-27). Dorsal margin anterior to beak flat to slightly concave, posteriorly forming shallow to moderately incised notch in front of beak. Posterior margin slightly and unevenly curved, with curvature greatest dorsally, flattening ventrally; margin slopes steeply. Primary sulcus notch near posteroventral corner, slightly to moderately indented, well defined, with moderately rounded margins, the dorsal one subangulate in some specimens. Ventral and anterior margins forming continuous moderate curve, even (pl. 1, fig. 5) to asymmetrical with the ventral and dorsoanterior margins slightly flattened (pl. 5, figs. 12, 20). Dorsoanterior margin moderately and unevenly rounded, rarely subangulate.

TABLE 5.—*Summary of measurements for* Thyasira quadrula arrecta Kauffman, new subspecies.

| Character[1] | Number of specimens | Range | Average |
|---|---|---|---|
| Height (mm.) | 23 | 6.2-29.3 | 19.5 |
| Length (mm.) | 25 | 5.0-27.0 | 18.1 |
| Width of both valves (mm.) | 23 | 6.0-15.3 | 11.9 |
| HMS (mm.) | 22 | 3.9-16.7 | 11.1 |
| HABS (mm.) | 25 | 1.0- 7.0 | 3.7 |
| HS (mm.) | 21 | 4.3-21.0 | 15.5 |
| Length of escutcheon (mm.) | 22 | 5.8-17.0 | 12.5 |
| Maximum width of escutcheon (mm.) | 18 | 1.0- 3.0 | 2.2 |
| MWF (mm.) | 19 | 0.3- 4.5 | 2.7 |
| Angle A (degrees) | 20 | 65.0-98.0 | 82.2 |
| Angle B (degrees) | 18 | 75.0-95.0 | 85.6 |
| Angle C (degrees) | 21 | 85.0-125.0 | 101.0 |
| Angle D (degrees) | 21 | 55.0-79.0 | 68.2 |
| Angle E (degrees) | 21 | 22.0-56.0 | 31.0 |

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[1] See text figure 4 for explanation of angles and abbreviations.

*Beaks, umbos.*—Beaks sharply to bluntly pointed, slightly to moderately prosogyrate, slightly incurved, nearly touching, situated subcentrally on posterior side of midline (pl. 1, fig. 5). Umbos not well defined, moderately inflated, their axis slightly prosogyrate, covered with very fine growth lines but lacking concentric undulations.

*Folds, sulci, auricles.*—A shallow, broad, slightly curved anterior sulcus formed on about half of the adult valves (pl. 5, fig. 23), most other valves having a faint flattened area on valve surface in this position; sulcus extends from ventroanterior part of umbonal area to dorsoanterior margin, commonly forming a shallow but prominent concave notch or flattened area on margin at their intersection. Valve surface slightly flatter on either side of midline than across it, but prominent medial flattened areas not developed as on *T. triangulata*. Primary sulcus slightly curved dorsally, straight ventrally, prominent, moderately excavated medially, becoming shallow dorsally near origin on posterior flank of umbo, and near ventroposterior margin of large adult shells; somewhat asymmetrical with anterior flank steepest. Anterior primary fold prominent, moderately convex, asymmetrical with posterior flank steepest, broad. Posterior primary fold narrow, moderately and subevenly arched on small shells, becoming broader and lower, less prominent at later growth stages (pl. 5, figs. 26, 27). Submarginal sulcus a shallow, indistinct, narrow groove parallel to midposterior margin, not extending dorsally to beak, better expressed internally as fold than externally (pl. 5, figs. 17, 18). A small, narrow, triangular auricle developed midposteriorly on valves with best developed submarginal sulcus (pl. 5, fig. 19). A folded, subtriangular anterior auricle with rounded apex formed in shells with strong anterior sulcus, between this sulcus and the dorsal margin (pl. 5, fig. 23).

*Lunule, escutcheon.*—Lunule not differentiated on small adult shells, weakly defined on large adults, consisting of a small, flat to slightly depressed, heart-shaped area between beaks and anterodorsal corner of valve, bounded by a single, broad, moderately rounded ridge, or a pair of low rounded ridges on each side (pl. 1, fig. 4). Escutcheon prominent, relatively broad for Cretaceous species, lanceolate, broadest posterior to middle, moderately depressed, consisting of shallow asymmetrical troughs bounded laterally by sharp, elevated dorsoposterior margins and medially by low raised ridges on either side of the very narrow lenticular depression occupied by the ligament. Ligament about two-thirds exposed to exterior, covered slightly at anterior end, and about a third of its length posteriorly by inward projecting dorsoposterior shell margins in escutcheon. Lunule and escutcheon more strongly defined on internal molds in most growth stages.

*Ornamentation.*—Entire surface covered by fine to medium size, crowded, subevenly spaced, raised growth lines which are equally developed on dorsal half of shell, unequally developed ventrally with some becoming moderately coarse. Growth lines strongly developed in sulci and on folds and auricles, weakly developed in escutcheon, coarse in lunule. Low, broad, unequally developed, moderately spaced concentric undulations formed over ventral two-thirds to three-quarters of shell (pl. 1, fig. 5).

*Interior morphology.*—Hinge of three small- to medium-size adults edentulate (text fig. 5); one large adult with trace of slight pseudocardinal swelling below beak, not well defined. Submarginal fold prominent, narrow, slightly expanding ventrally, moderately elevated. Primary interior fold prominent, moderately elevated, asymmetrical and conforming to primary sulcus exteriorly. A low broad dorsoanterior fold marks the position of the anterior sulcus (pl. 1, fig. 3). Fine, moderately spaced, raised radial ridges transgress shell interior between umbo and pallial line; faintly developed beyond pallial line. Ridges coarser anteriorly and posteriorly than medially (pl. 5, fig. 26). Pallial line entire, a prominent raised band about 1 mm. wide between the adductor muscle insertion areas (pl. 5, fig. 26). Posterior adductor insertion area (text fig. 18) well defined, subovate with long axis inclined toward posteroventral margin, small with somewhat irregular margins, situated astride the primary interior fold midposteriorly, opposite dorsal edge of primary sulcus notch; scar transgressed by coarse radial lines. Anterior adductor insertion area prominent (pl. 1, fig. 3), well impressed, elongate-ovate in outline with irregular margins, its long axis nearly perpendicular to the hinge axis (text fig. 18), its margin partially separated from the pallial line along the anterior margin; area constricted irregularly, transgressed by a few radial ridges and very fine growth lines. Ligamental groove arcuate, narrow, moderately deep, with angular base and flat ventral slope, extending from posterior area of umbo to midposterior margin just dorsad to primary sulcus notch, opening inward toward center of escutcheon, its posterior third covered by inflected margins of valve.

*Measurements.*—A summary of measurements for *T. quadrula arrecta* is presented in Table 6 and the measurements explained in text figure 4.

*Ontogeny.*—A relatively complete adult growth suite is available for study from 10 mm. height to the largest valve. Observations on earlier (juvenile) growth are based on growth line traces at 5 mm. intervals on USNM 153454 (paratype). Significant ontogenetic changes occur in the marginal outline of the valve, development and curvature of the posterior sulci and the anterior sulcus or flattened area, ornamentation, development of the lunule, and relative projection and curvature of the beaks and umbos.

The juvenile shell (5 mm.; see text fig. 18) has a subovate outline with an evenly rounded ventral and anterior margin, rounded and nonprojecting dorsoanterior corner, and sloping dorsal margin. The posterior margin, especially at the edge of the umbo, is slightly to moderately curved and the concave notches dorsoanteriorly and ventroposteriorly very weakly defined. The ultimate adult outline begins to develop in the early adult growth stages between 5 and 15 mm. (text fig. 18) with attainment of a subquadrate profile through acceleration of ventral and dorsoanterior growth of the margins relative to growth elsewhere on the shell, and flattening of the posterior margin. The subquadrate adult outline becomes accentuated in larger shells as the posterior margin continues to flatten and the flattened areas of the ventral and anterior margins develop (pl. 5, fig. 20).

The primary sulcus trace compliments changes in the curvature of the posterior margin with growth, being faint, shallow, and moderately to slightly curved on the juvenile shell, moderately deep, prominent, and slightly curved during early adult growth, becoming straighter at heights of 10 to 20 mm., and shallower, broader, and more curved near the ventral margin of larger shells. The anterior sulcus is strictly an adult feature first appearing at heights of 15 mm. as a flattened area and abruptly expanding and becoming slightly concave during late adult growth. The lunule is also an adult feature, becoming first defined during middle adult growth (15-20 mm.) and becoming depressed only on large shells. Beaks of young shells (5-15 mm.) are sharper, but more erect and relatively less projecting than those of larger and presumably older shells. Finally, juvenile ornamentation consists of fine evenly developed growth lines. These become less equally developed, more unevenly spaced, and coarser with further growth, and in shells larger than 15 mm. are superimposed on low concentric undulations.

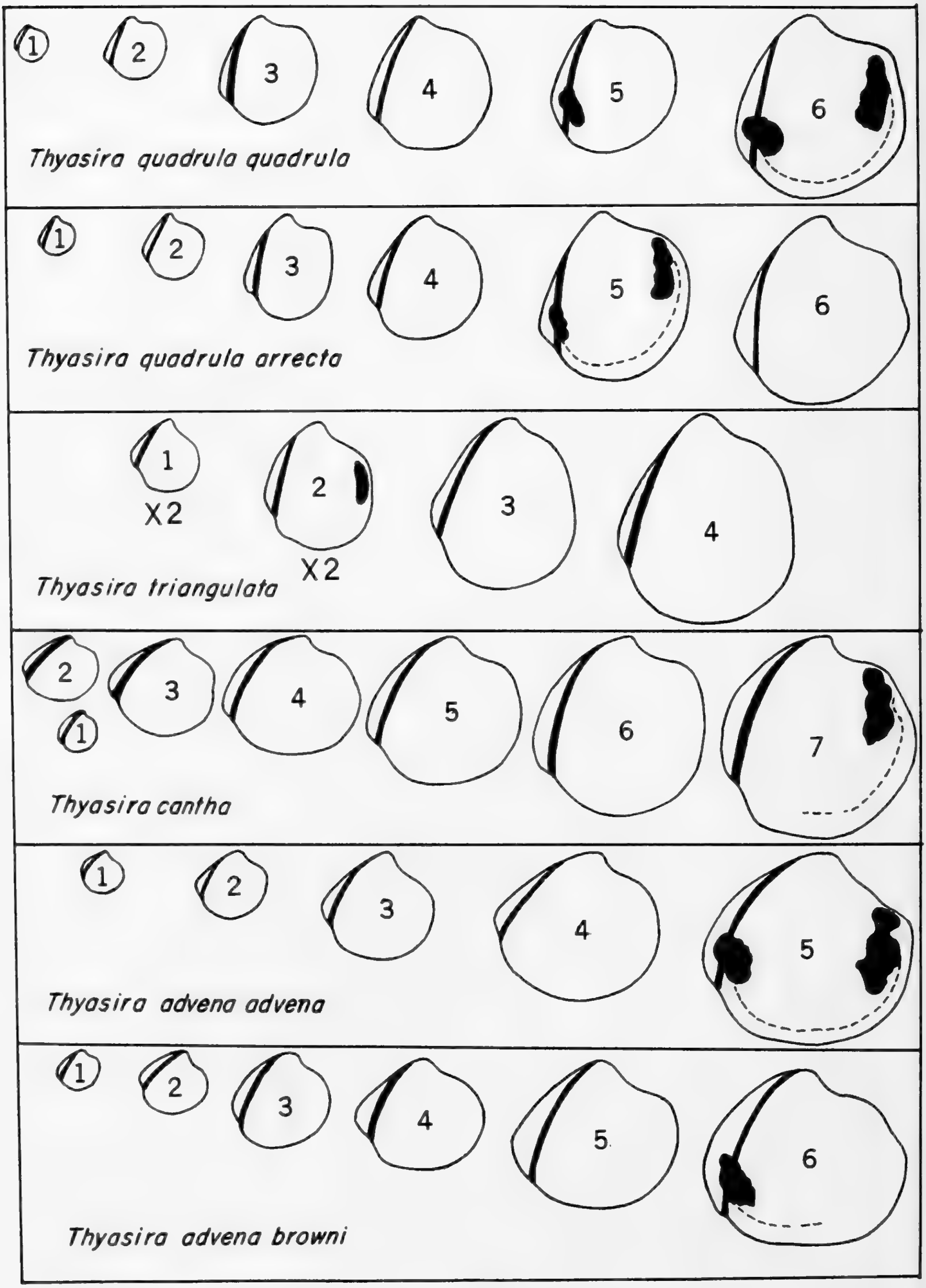
*Adult variation.*—The adult shell of *T. quadrula arrecta* is remarkably uniform in regard to most characteristics. Significant variation occurs in the following features. Normally a shallow anterior sulcus, or dorsoanterior flattened area of the shell is developed, but on a few valves there is no trace of either between the anterior part of the umbo and the dorsoanterior margin. Concentric undulations, which cover much of the adult shell, range from faint (pl. 5, fig. 10) to moderately coarse (pl. 1, fig. 3). The dorsoanterior corner may be subangular or sharply rounded and auriculate, but on rare valves (pl. 5, fig. 18) is moderately rounded, nonauriculate, and the anterodorsal margin less nearly parallel to the hinge axis. The primary sulcus notch ranges from slightly to moderately concave. The ventral margin is flattened on some valves, rounded on others, and the anteroventral margin is oblique and not projecting on a few specimens (pl. 1, fig. 3). Finally, the beaks show slight variation in the amount of projection above the dorsal margin, and range from sharply to bluntly pointed.

*Remarks.—Thyasira quadrula arrecta* is the middle member of the major lineage of *T. quadrula,* and differs from the ancestral subspecies *T. quadrula quadrula* in having more pointed, projecting, and slightly more prosogyrate beaks, a smaller apical angle, in having the dorsal margin somewhat more inclined to the hinge axis, and in having an anterior sulcus, coarser concentric ornamentation, and a more prominent primary sulcus notch. The ancestry of the younger *T. triangulata,* n. sp., probably lies in the lineage of *T. quadrula* but no gradation between the two can be established. The two forms are similar in the straight nature of the posterior margin and primary sulcus, the ventroposterior position of the sulcus notch, the well-defined primary fold, the suberect beaks, and the ornamentation. *T. triangulata* is quite distinct however in the narrow apical angle, steeply sloping anterior margin which is not auriculate or projecting, the greater relative height of the shell, and in the well-defined flattened areas on the shell flanking the midline. Some of these characters are found in the lineage of *T. rostrata.*

*T. quadrula arrecta* is an unusually long ranging subspecies (text fig. 1). It is rather sparsely represented in the upper part of its range by scattered, commonly poorly preserved specimens. Some variants from the upper part of the range (pl. 5, fig. 16) develop a few morphologic characteristics not found in populations near the base of the range, although most of the younger representatives of the subspecies are identical to the earliest forms. Differences shown by these variants include an erect, much reduced beak, larger apical angle, more evenly rounded margins, slightly greater relative length, and a broader flank posterior to the primary sulcus. In many respects these variants approach the older *T. quadrula quadrula,* though the two can be easily differentiated. This would suggest the possibility that a third subspecies can be defined in the lineage above the typical *T. quadrula arrecta.* The scope and preservation of the material from these younger levels is not sufficient at present to ascertain the magnitude of these differences or to attempt formal naming of a new subspecies, and the younger variants are best grouped at present with *T. quadrula arrecta.*

The subspecific name is drawn from the Latin, *arrectus,* meaning upright or steep, and refers to the erect posture of the shell and beaks, and its steeply sloping posterior margin.

*Stratigraphic position.—T. quadrula arrecta* has an extended Late



Text Figure 18.

Campanian range from the lower part of the *Baculites perplexus* (early form) zone to the middle of the *B. scotti* zone (text fig. 1). It is best represented in the lower part of its range. In the zone of *B. perplexus* (early form), *T. quadrula arrecta* occurs at several distinct levels designated levels 1 through 5 in this report and shown on text figure 1. At level 1 it occurs in the Steele Shale at USGS Mesozoic locality D255, Converse County, Wyoming. At level 2 it occurs in the Pierre Shale 30 to 60 feet above the basal bentonite of the Mitten Black Shale Member at USGS Mesozoic locality D1864, Niobrara County, Wyoming. At level 3, *T. quadrula arrecta* occurs in the same area 70 to 90 feet above the bentonite mentioned above (USGS Mesozoic locality D1865). At level 4 it occurs questionably (fragment of shell) at USGS Mesozoic locality D2909 in the Pierre Shale 695 feet above the base of the Mitten Black Shale Member, Niobrara County, Wyoming. At level 5 the subspecies occurs 695 to 714 feet above the top of the Mitten Black Shale Member, Pierre Shale at USGS Mesozoic locality D1866, Niobrara County, Wyoming.

In the zone of *B. gilberti* (text fig. 1), *Thyasira quadrula arrecta* occurs in the Pierre Shale 878 feet above the base of the Mitten Black Shale Member at USGS Mesozoic locality D2910, Niobrara County,

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TEXT FIGURE 18.—Ontogeny of the marginal outline and primary sulcus trace, and characteristics of the muscle insertion areas, where observable, in Cretaceous species of *Thyasira* from North America. Primary sulcus denoted by heavy line, muscle insertion areas by black patches, pallial line by thin dark line between insertion areas. Development of ontogeny described in detail with each species description. Illustrations based on the following, partially restored where necessary to show whole outline: *Thyasira quadrula quadrula*, n. subsp., (1,2) growth line traces at 5-mm. intervals, and (3) marginal outline of a paratype, USNM 153469; (4) marginal outline of a paratype, USNM 153468; (5) marginal outline of the holotype, USNM 153470; (6) marginal outline of a paratype, USNM 153467. *Thyasira quadrula arrecta*, n. subsp., (1,2) growth line traces at 5-mm. intervals, and (3) marginal outline of a paratype, USNM 153454; (4) marginal outline of a paratype, USNM 153446; (5) marginal outline of a paratype, USNM 153456; (6) marginal outline of the largest paratype, USNM 153440. *Thyasira triangulata*, n. sp., (1) growth line trace at 2.5 mm. (× 2), and (2) marginal outline (× 2) of the holotype, USNM 153418; (3) growth line trace at 25 mm. and (4) marginal outline (restored) of a paratype, USNM 153419. *Thyasira cantha* n. sp., (1-5) growth line traces at 5-mm. intervals, and (7) marginal outline of the holotype, USNM 153477; (6) marginal outline of a paratype, restored, USNM 153472. *Thyasira advena advena* n. subsp., (1-5) growth line traces at 5-mm. intervals, and (6) marginal outline of the holotype, USNM 153417. *Thyasira advena browni*, n. subsp., (1-5) growth line traces at 5-mm. intervals, and (6) marginal outline of the holotype, USNM 153416.

Wyoming. In the zone of *B. perplexus* (late form) it occurs in Tepee Butte limestone masses of the Pierre Shale at USGS Mesozoic locality D1564, Jefferson County, Colorado. A large specimen questionably belonging to the subspecies occurs in the lowest level of the *Baculites scotti* zone (level A, text fig. 1) at USGS Mesozoic locality D1215 in concretions and Tepee Butte limestone masses of the Pierre Shale, Pueblo County, Colorado. In the middle part of the *B. scotti* zone *T. quadrula arrecta* occurs at level C in Tepee Butte limestone of the Pierre Shale, Douglas County, Colorado (USGS Mesozoic locality D1012) and at level D at two localities: USGS Mesozoic locality D714, Tepee Butte zone of the Pierre Shale, Pueblo County, Colorado, and USGS Mesozoic locality D3945, also in the Pierre Shale of Pueblo County.

In Canada, *T. quadrula arrecta* occurs in concretions probably from the Riding Mountain Formation along the Assiniboine River 1 mile south of Millwood. As explained in the "stratigraphic position" section of *Thyasira becca cobbani*, it probably occurs here in the zone of *Baculites scotti*, although the formation may contain levels as old as Earliest Campanian (just above the *Scaphites hippocrepis* zone), and as young as the zone of *Baculites eliasi*, in the Late Campanian.

*Types.*—Holotype, a bivalved adult shell of moderate size with the shell material intact, right valve broken (USGS D1865; pl. 1, fig. 5), USNM 153464; illustrated paratypes from USGS D255, bivalved internal molds of small- to large-size adult shells, USNM 153440-153442, 153445, 153446, 153456, 153458; illustrated paratypes from USGS D1865, small- to medium-size bivalved specimens with the shell intact, USNM 153445, 153454, 153455; illustrated paratype from USGS D1866, bivalved specimen, shell intact, posterior and posteroventral margin broken, USNM 153457; illustrated specimen (text fig. 5) from USGS D1864, incomplete bivalve specimen with hinge of right valve excavated, USNM 153451; illustrated paratype from USGS D1012, a small adult right valve, USNM 153459; illustrated paratype from USGS D714, bivalved internal mold of small adult shell, USNM 153460; paratype from Millwood, Canada, GSC 18761, bivalved specimen with shell intact and posterior margin broken.

Measured paratypes, not illustrated: From USGS D255 (6 specimens), USNM 153448; from USGS D1864 (1 specimen), USNM 153444; from USGS D1866 (2 specimens), USNM 153453; from USGS D1564 (2 specimens), USNM 153449; from USGS D1012, (1 specimen), USNM 153452; from USGS D3945 (1 specimen), USNM 153463. Paratypes not illustrated or measured: from USGS

D255 (1 specimen), USNM 153443; from USGS D2910 (1 specimen), USNM 153450; Specimens assigned to species with question due to preservation: from USGS D2909, 1 specimen, USNM 153462; from USGS D1215 (1 specimen), USNM 153461; from USGS D1410 (2 specimens), USNM 155430.

### THYASIRA TRIANGULATA Kauffman, new species

Plate 1, figure 6; plate 3, figures 31, 35

*Diagnosis.*—Shell erect, height greater than length, outline subtriangular. Apical angle relatively small, dorsoposterior margin nearly straight, notch anterior to beak shallow, dorsoanterior flank steeply sloping. Primary sulcus straight to slightly curved, submarginal, prominent; two median flattened areas are developed, separated and bordered by low folds; primary posterior fold well defined.

*Material.*—Two nearly complete specimens: a young adult right valve (holotype), a well-preserved internal mold with some shell attached: a large adult specimen with coattached valves in normal apposition and shell material on both valves; anteroventral flanks crushed, and portions of the anteroventral and posteroventral margins missing.

*General form.*—Shell attaining large size for genus, equivalve, slightly to moderately biconvex with greatest inflation medially, slightly prosocline, suberect. Outline subtriangular with slightly curved posterodorsal and dorsoposterior margins, slightly concave anterodorsal margin (even below beak), moderately rounded midanterior and midposterior margins, a relatively narrow, shallow concave notch ventroposteriorly at interesection with primary sulcus, moderately rounded ventroposterior and anteroventral borders, and straight to slightly convex ventral and ventroanterior margins (pl. 1, fig. 6). Shell thin and delicate.

*Beaks, umbos.*—Beaks central, narrowly rounded to pointed, moderately prosogyrate, not incurved or projecting prominently above dorsal margin, close together in normal apposition but not touching. Umbos not well defined, moderately convex, with early expression of medial flattened areas and bounding low folds found on adult valves. Ornamentation similar to rest of shell.

*Folds, sulci, auricle.*—Posterior auricle small, subtriangular, not greatly projecting, consisting of a low, rounded, flat projection in the center of the posterodorsal margin (pl. 1, fig. 6). Primary sulcus well defined, narrow, moderately deep, with rounded base and moderately inclined flanks; slightly curved dorsally, straight ventrally, originating just posterior to early umbo and extending nearly parallel to the posterior margin, intersecting the ventroposterior margin and forming a shallow notch (pl. 1, fig. 6). Folds prominent on either side of primary sulcus; posterior fold narrow, moderately convex, strongly developed; anterior fold broader, moderately convex. Submarginal sulcus narrow, rounded, moderately deep, relatively short, extending halfway along combined posterodorsal-dorsoposterior margin, separating small posterior auricle from prominent posterior fold. Two broad, flat to very slightly concave medial flattened areas lie between anterior fold on edge of primary sulcus and midline. Flat areas originate on umbo and extend to ventral margin without altering curvature of that margin; flat areas separated and bounded anteriorly by very low, narrow, radiating folds (pl. 1, fig. 6).

*Lunule, escutcheon.*—Lunule small, narrow, subtriangular, poorly defined, flat to slightly depressed, bounded by rounded folds. Escutcheon very narrow, lanceolate, extending along entire posterodorsal and dorsoposterior margin; well defined, moderately deep, bounded by steep upturned posterior auricles. Escutcheon consisting of two narrow, rounded grooves on either side of deep depression occupied by ligament.

*Ornamentation.*—Entire surface of shell uniformly covered with fine, irregularly to subregularly arranged growth lines. Coarser, irregular, incomplete undulations scattered over shell, especially on anterior flank (pl. 1, fig. 6). Extremely fine radiating lines noted on umbo of adult specimen .

*Interior morphology.*—Ligamental grooves narrow with moderately rounded bases, predominantly opening inward, into escutcheon. Grooves completely covered over by dorsal valve margins along posterior half of escutcheon and ligament internal, partially covered and narrowly opening to exterior along anterior half of escutcheon. Interior surface of valve covered with extremely fine, crowded and subequally spaced radiating grooves between umbo and pallial line. Pallial line narrow, not completely observed. Adductor muscle impression areas very weakly defined, not completely observed. Anterior adductor situated near margin, elongate, diagonally inclined from ventroanterior margin toward anteroventral border.

*Measurements.*—Holotype, USNM 153418, a small, young adult right valve: height, 8.7 mm.; length 7.5 mm.; width (single valve), 2.1 mm.; height to midposterior break in slope where the margin turns into primary sulcus notch, 4.8 mm.; height to a point in the center of the notch in marginal outline made by intersection of the primary sulcus, 6 mm.; height to break in slope between anterodorsal and midanterior margin, 2.8 mm.; length of line connecting beak and primary sulcus notch, 6.5 mm.; maximum width of posterior flank posterior to primary sulcus, 1 mm.; angle A, 74°; angle B, 77°; angle C, 92.5°; angle D, 60°; angle E, 38° (see text fig. 4 for definition of measurements and angles).

Paratype, USNM 153419, a large adult pair of coattached valves, incomplete; height, 27.5 mm.; length 25.3 mm.; width (both valves), 13.3 mm.; height to midposterior break in slope where the margin turns into the primary sulcus notch, 15 mm.; maximum width of the escutcheon, 2.8 mm.; angle A, 87°; angle C, 87°; other measurements not possible due to poor preservation of specimen.

*Ontogeny.*—Ontogenetic changes are mainly expressed in the development of the marginal outline and adult morphologic features such as the folds, sulci, and auricle. Since only two specimens, a young and an old adult shell, are available, the following remarks are drawn mainly from studies of growth line traces at 5-mm. intervals (text fig. 18), taken from both specimens.

The late juvenile to early adult shell (height, 5 mm.) is much more rounded than the adult, with the height slightly greater than the length and the midanterior and midposterior slopes relatively more projecting. The ventral margin is rounded and the primary sulcus notch relatively broader and more ventral in position than in later stages. There is no evidence of a posterior auricle, and the primary sulcus is slightly to moderately curved.

The early to middle adult stage (height, 10 mm.) demonstrates acceleration of ventral growth, producing a relatively higher, more erect shell, straight to very slightly curved primary sulcus, and a narrower primary sulcus notch which is more dorsally situated on the ventroposterior margin than in earlier stages. A small posterior auricle is also formed.

The late adult stage seems to be characterized by growth trends similar to those of the middle adult stage with the exception that continued expansion of the anterodorsal flank and margin makes the concave notch anterior to the beak shallower, and the beaks and umbos consequently appear to be less projecting.

*Remarks.*—*Thyasira triangulata* Kauffman, n. sp., is the youngest known member of the genus in the Western Interior Cretaceous. It is clearly distinct from its ancestors in its subtriangular outline, low apical angle, steeply inclined and nonprojecting dorsoanterior and anterodorsal flanks, and especially in the exceptional development of median flattened areas and adjacent folds on the central and posterior parts of the shell.

The species is most closely allied to, and probably descended from, *Thyasira quadrula arrecta,* n. subsp. The stratigraphic range of this species extends to the base of, but does not overlap that of *T. triangulata* (text fig. 1). *T. triangulata* is easily distinguished from *T. quadrula arrecta* in being less convex, relatively higher, in having a more steeply inclined and less alate anterodorsal flank, in the development of median flattened areas and adjacent low folds, in having a more expanded anteroventral margin, more projecting beaks in the early adult stage, and in lacking any evidence of a dorsoanterior sulcus and marginal notch. No other species closely approaches *T. triangulata* in morphology.

The species name refers to the subtriangular marginal outline of the valve and is derived from the Latin, *triangulus.*

*Stratigraphic position.—Thyasira triangulata* Kauffman, n. sp., is known only from the upper part of the zone of *Baculites scotti* Cobban at levels E and F (text fig. 1). It was found in level E at USGS Mesozoic locality D3933, in the Pierre Shale of Pueblo County, Colorado. The specimen from level F comes from the Pierre Shale in the Littleton Quadrangle, Jefferson County, Colorado (USGS Mesozoic locality D65).

*Types.*—Holotype, a small, young adult right valve; a well-preserved internal mold of the entire valve with some shell material attached, USNM 153418 (locality D65). Paratype, large coattached adult valves with most of the shell material preserved but with the ventral and anterior flanks crushed (locality D3933), USNM 153419.

### THYASIRA BEAUCHAMPI Kauffman, new species

*Diagnosis.*—Adult shell exceptionally large, elevated and erect for genus, moderately biconvex; apical angle narrow, beaks, umbos projecting. Anterior flank not much expanded, moderately to steeply sloping away from beak in adult valves, with a prominent dorsoanterior sulcus forming a concave notch at its intersection with the commissure. Lunule moderately well defined, with rounded margins; escutcheon narrow, lanceolate.

### THYASIRA BEAUCHAMPI BEAUCHAMPI Kauffman, new subspecies

Plate 1, figures 24-26; plate 2, figures 28, 29, 31-33

*Diagnosis.*—Moderately biconvex, large, with height considerably greater than length and apical angle narrow. Anterior flank greatly restricted and steeply sloping in adult. Anterior sulcus prominent, broad, forming strong notch at intersection with dorsoanterior margin. Posterior and posterodorsal margin moderately curved. Growth lines coarse and unevenly spaced.

*Material.*—Four specimens, all well preserved, nearly complete, with valves coattached in normal apposition. Holotype a large, complete specimen with most of the shell material attached and ligament partially preserved. Three paratypes are internal molds of medium-size adult shells showing interior morphology.

*General form.*—Shell large for genus, equivalve, prosocline, moderately biconvex, with point of greatest inflation dorsocentral. Outline modified elongate-ovate (pl. 1, fig. 24); height significantly greater than length, especially in late adult stage. Posterior and posterodorsal margins forming continuous, moderately convex curve; ventral and ventroanterior margins forming continuous, moderately convex curve, with curvature somewhat greater than that posteriorly. Anterodorsal margin steeply sloping away from beak, slightly to moderately and unevenly concave, with curvature greatest just anterior to beak, but not forming prominent notch. Broad, shallow, concave reentrants in marginal outline formed ventroposteriorly and dorsoanteriorly at intersection of commissure and major sulci. Margins narrowly curved at peripheries of these reentrants. Segments of shell flanks narrow anterior and posterior to the anterior and primary sulci, respectively. Dorsoanterior flank relatively more expanded in early than in late adult growth stages.

*Beaks, umbos.*—Beaks pointed, prosogyrate, slightly incurved in early to middle adult stages, situated somewhat anterior to midline (pl. 1, fig. 26). Umbos not well differentiated, highly inflated, prosogyrate, with finer concentric ornamentation than found over rest of shell surface.

*Folds, sulci.*—Primary sulcus prominent, narrow, moderately deep, (pl. 1, fig. 26) with curved base and sides inclined at 15 to 20 degrees; primary sulcus originating on posterior flank of early umbo and extending with moderate to slight curvature (dorsal to ventral), nearly parallel to the posterior margin, to the ventroposterior corner, forming broad concave notch in commissure. Strong, relatively narrow, low rounded folds lie adjacent to primary sulcus. Submarginal sulcus weakly and poorly defined, narrow and shallow, incompletely developed, originating on posterior flank of the ventral umbonal area, and extending parallel to posterodorsal and dorsoposterior margins to the midposterior margin, where it disappears in large adult valves. A narrow fold lies posterior to submarginal sulcus, but no auricle is developed. Shell surface flat between midline and anterior primary fold, but no prominent medial flattened areas and folds developed as in *Thyasira triangulata,* n. sp. (pl. 1, fig. 6). Anterior sulcus prominent, bounded by prominent, narrowly to moderately rounded folds (pl. 1, fig. 26), the best developed sulcus of any Cretaceous species here described. Sulcus originates as flattened area on anteroventral part of umbonal area and extends, with moderate, even curvature, to dorsoanterior margin, forming a prominent reentrant at intersection with commissure; sulcus expands strongly and becomes depressed as adult shell increases in size.

*Lunule, escutcheon.*—Lunule of moderate size for genus, relatively broad, situated entirely on anterodorsal flank. In early to middle adult growth stages, lunule poorly defined, flat to very slightly convex and bounded on each side by a low rounded fold which bifurcates near its termination at the dorsoanterior corner (pl. 2, fig. 31). In late adult growth stage, on largest valve (pl. 1, fig. 25), lunule prominent, depressed and bounded by two low, moderately rounded folds. Escutcheon narrow, well defined, lanceolate, broadest near junction of posterodorsal and dorsoposterior margins, bounded by very narrowly rounded to acute ridges, not deeply excavated (pl. 1, fig. 25). Escutcheon consisting of two narrow, nearly flat-bottomed depressions bounded distally by a steep slope and sharp ridge, and medially by a fine sharp ridge at edge of ligamental groove.

*Ornamentation.*—Entire surface covered with crowded, irregularly spaced and unequally developed growth lines, fine on umbo and early adult growth stage of shell, becoming coarser and sublamellate ventrally; somewhat accentuated in main sulci (pl. 1, fig. 26). Low, narrow, broadly rounded, unevenly and widely spaced concentric undulations developed on middle and late adult parts of shell.

*Interior morphology.*—Ligamental groove narrow, moderately deep, with an acute base, extending parallel to posterodorsal margin, opening medially into escutcheon, overhung by dorsoposterior margin only at its posterior extremity; ligament otherwise external. Ligamental material partially preserved on largest shell, resinous-brown, fibrous, calcified, about 0.25 mm. thick. Submarginal fold very narrow, moderately rounded, low, extending parallel to the dorsoposterior margin from a point one-third the length of the escutcheon from its apical origin, to the mid-posterior corner, becoming lower and slightly broader posteriorly. Primary interior fold prominent, broad, low, rounded, the internal expression of the primary sulcus and having the same trace. Anterior sulcus of shell exterior not well expressed internally, represented by a broad, slightly elevated, flat to rounded area near the dorsoanterior margin. Fine, subequally to unevenly spaced radiating grooves cover shell interior between the umbo, where they are very weakly developed, and the pallial line; grooves and broadly rounded interspaces more strongly developed anteriorly and posteriorly, around adductor muscle scars and interior folds, than they are medially. Pallial line entire, without sinus, consisting of a narrow (0.75 mm.), slightly raised band between the adductor insertion areas. Posterior adductor insertion area subround with somewhat irregular margins, weakly impressed, situated astride the primary interior fold just below midshell (text fig. 17). Anterior adductor insertion area large, weakly impressed, elongate-ovate with finely irregular margins (text fig. 17), situated midanteriorly and inclined toward midventral margin; dorsal part of insertion area overlaps low fold which is the internal expression of the anterior sulcus; anteroventral part of area separated from pallial line, forming narrow reentrant of inner shell surface between them, marking anterior incurrent passage. Attachment areas with strongly developed radiating grooves and rounded interspaces. Neither the shell nor internal molds show any trace of pseudocardinal dentition.

TABLE 6.—*Measurements for* Thyasira beauchampi beauchampi Kauffman, new subspecies.

| CHARACTER | USNM 153412 | USNM 153415 | USNM 153414 | USNM 153413 |
|---|---|---|---|---|
| Height (mm.) | 33.0 | 25.0 | 23.3 | 23.0 |
| Length (mm.) | 27.5 | 21.5 | 20.0 | 21.0 |
| Width, both valves (mm.) | 22.0 | 15.5 | 14.0 | 16.0 |
| Height to edge of posterior break in slope at edge of primary sulcus (mm.) | 25.0 | 17.8 | 14.3 | — |
| Height to dorsoanterior break in slope (mm.) | 6.8 | 5.0 | 6.0 | 4.0 |
| Height to middle of primary sulcus at intersection with commissure (mm.) | 29.0 | 21.5 | 19.7 | — |
| Angle B (degrees) | 72.5 | 78.0 | 68.0 | — |
| Angle C (degrees) | 101.0 | 107.0 | 92.5 | — |
| Angle D (degrees) | 73.0 | 70.0 | 70.0 | — |

*Measurements.*—Measurements for the four primary types of *T. beauchampi beauchampi,* n. subsp., are given in Table 6.

*Ontogeny.*—The four known specimens of this subspecies comprise an adult growth suite which demonstrates some notable ontogenetic development. No juvenile or early adult shells are present in the series and remarks concerning the early ontogenetic development of the subspecies are based on growth line traces at 5-mm. intervals on the holotype (text fig. 17) up to the smallest size represented by a single specimen. Significant ontogenetic change is shown by the following: marginal outline, development of the sulci and folds, strength of the ornamentation, development of the lunule, and relative development of the flank posterior to the primary sulcus. In the following discussion, the umbonal area is considered representative of the juvenile shell, valves to 15 mm. in height the early adult growth stage, to 30 mm. in height, the middle adult growth stage, and larger valves are considered old (late) adults.

The marginal outline changes radically during ontogenetic development of *T. beauchampi beauchampi* (text fig. 17; pl. 1, fig. 24; pl. 2, figs. 28, 33). The juvenile and early adult shells are subround to subovate and not as erect or prosocline as the mature adult valve. At heights of 15 to 20 mm. ventrally directed growth starts to accelerate and is decidedly greater than lateral expansion throughout the rest of the adult growth stage, producing a more erect, relatively higher shell (pl. 1, fig. 24). During the juvenile and early adult stages the anterior and posterior flanks are more produced than at later growth stages, and the flank posterior to the primary sulcus is considerably wider relative to the width of the sulcus. Both flanks become gradually more rounded and less produced with age. The primary sulcus becomes deeper and slowly widens from juvenile to late adult growth stages. The submarginal sulcus and anterior sulcus appear to be exclusively middle and late adult growth features and are not developed on the juvenile shell (represented by part or all of the umbo). The anterior sulcus is flat and poorly defined during middle adult growth (pl. 2, fig. 33) and becomes concave and prominently defined only during late adult growth (pl. 1, fig. 26). All folds are weakly developed in juvenile through middle adult growth stages, and become more prominent and narrowly rounded in later growth.

The lunule is not easily definable in the juvenile shell, poorly defined in the early and middle adult stages (to 30 mm. in height), being flat and bounded with broadly rounded, low folds. The lunule is depressed, well defined, and bordered with two prominent, narrowly to moderately rounded folds in large adult shells. Finally, concentric growth lines become progressively larger, coarser, and more crowded with increasing shell size. Low concentric undulations and sublamellate growth lines are known only from the largest adult valve.

*Remarks.*—The lineage of *Thyasira beauchampi* is distinct in its erect, relatively high shell and in the strong development of the anterior sulcus. No other Cretaceous species closely resembles it. It is generally similar to *Thyasira rostrata cracens,* n. subsp., especially in the juvenile and early adult growth stages before the shell acquires its great relative height, and is thought to be derived from the lineage of *T. rostrata,* n. sp.

*Thyasira beauchampi beauchampi,* n. subsp., is easily distinguished from *T. rostrata rostrata,* n. subsp., with which it occurs, by the following features: the shell of *T. beauchampi beauchampi* is shorter, relatively higher, less convex, and more coarsely ornamented. The primary sulcus is longer, deeper, and intersects the margin at a more ventral position. The anterior sulcus is more strongly developed, larger, and much more depressed; it forms a larger anterior notch at the commissure. The midanterior and midposterior flanks are much less projecting, especially the latter on the posterior side of the primary sulcus, and the beak is more projecting with a narrower apical angle in *T. beauchampi beauchampi.* Finally, the lunule is smaller, narrower, and not as well defined in this subspecies as it is in *T. rostrata rostrata.*

In form, *T. beauchampi beauchampi* is closer to the younger *T. rostrata cracens,* n. subsp., but is distinguished from this subspecies in being relatively higher, more convex, in having a less produced dorsoanterior flank, a much more prominent anterior sulcus, and a better defined lunule.

*Thyasira beauchampi rex,* n. subsp., is a direct descendent of this subspecies which can be distinguished by its relatively greater length, more produced anterodorsal flank, shallower primary and anterior sulci, midanterior position of the notch formed by the intersection of the anterior sulcus and the commissure, less projecting beak and larger apical angle, and finer, more evenly developed growth lines. The lunule is less pronounced and smaller in *T. beauchampi rex.*

*T. beauchampi* is named in honor of Robert G. Beauchamp, research assistant in the project, who was responsible for cleaning and measuring specimens used in this study and who first noted the distinctive character of the species.

*Stratigraphic position.—Thyasira beauchampi beauchampi,* n. subsp., is known only from the zone of *Baculites* sp. with weak flank ribs in the Steele Shale, Lost Soldier-Ferris District, Wyoming (USGS Mesozoic locality 10459).

*Types.*—Holotype, a very large bivalved specimen, late adult growth stage, with the valves in normal apposition and most of the shell preserved, USNM 153412. Paratypes, three nearly complete bivalved internal molds, valves in normal apposition, middle adult growth stage, USNM 153413 through 153415.

### THYASIRA BEAUCHAMPI REX Kauffman, new subspecies

Plate 1, figures 19-23

*Diagnosis.*—Shell attaining large size, erect, height significantly greater than length. Well-defined anterior sulcus forming shallow notch in dorsoanterior margin. Dorsoanterior flank somewhat projected. No posterior auricle. Lunule poorly defined. Beaks moderately projecting, apical angle about 90° ; anterodorsal margin not greatly recessed below beak. Surface covered with fine subequal growth lines.

*Material.*—Three well-preserved bivalved specimens with the valves in normal apposition; small, medium size, and exceptionally large adult valves with part or all of the shell material intact. Largest shell with dorsocentral portion of the left valve missing and shell layers partially peeled off; posterior margin of both valves chipped and damaged.

*General form.*—Shell attaining exceptionally large size for genus (pl. 1, fig. 22), moderately biconvex, greatest inflation dorsocentrally, suberect, slightly prosocline. Outline elongate-ovate with height significantly greater than length; apical angle approximately 90°. Anterior, ventroposterior, and posterodorsal-dorsoposterior margins gently and evenly curved. Ventral margin slightly and evenly curved in young adult shells, moderately curved in large adults. Anterodorsal margin slightly concave, not deeply recessed below beak. Junction between ventroposterior and dorsoposterior margins moderately rounded to subangular, between anterodorsal and dorsoanterior margins narrowly to moderately rounded on large and small adult shells, respectively. Broad, shallow, concave notches in marginal outline formed by intersection of primary and anterior sulci with commissure.

*Beaks, umbos.*—Beaks subangular on young shells, narrowly rounded on large adults, slightly prosogyrate and incurved, nearly touching in normal apposition, situated just anterior to midline. Umbos not clearly defined, inflated, slightly prosogyrate, bearing ornamentation similar to, but finer than found over rest of shell.

*Folds, sulci, auricle.*—Primary sulcus narrow, moderately depressed, with rounded asymmetrical base, extending with slight curvature from posterior flank of umbo to ventroposterior margin where it forms a broad shallow notch in commissure at their intersection (pl. 1, fig. 21). Anterior primary fold moderately low, rounded, prominent; posterior fold broad and low. Submarginal sulcus not developed in young adult shells up to 15 mm. in height; sulcus represented by a flat to very slightly depressed area midposteriorly on adults of 20 mm.; on largest shells submarginal sulcus a very shallow, narrow groove parallel to and just below the posterior margin, poorly defined. No posterior auricle or median flattened areas developed. Anterior sulcus developed only on large adult valves on midanterior flank, originating about one-half the length from the midline to the midanterior margin, expanding abruptly, broad and shallow but prominent near the margin, forming a wide concave reentrant in the commissure at their intersection (pl. 1, fig. 22). Dorsoanterior flank somewhat projecting and rounded into a subtle auricle dorsal to anterior sulcus.

*Lunule, escutcheon.*—No distinct lunule developed at 15 mm. in height; lunule poorly defined at 20 mm. in height; a small flat, heart-shaped area anterior to beaks with or without very low rounded folds at the margin. Lunule of large shells relatively small, slightly depressed, bounded by low rounded ridges; not prominent. Escutcheon very narrow, shallow, prominent, lenticular, with greatest width just anterior to its center. Escutcheon composed of a concave, narrow trough on either side of the depression occupied by the ligament; troughs bounded distally by the sharp raised dorsoposterior margin of the shell and medially by low sharp ridges at the edge of the ligamental groove, itself very narrow, deep, and lenticular as viewed externally.

*Ornamentation.*—Entire outer valve surface covered by extremely fine, raised, crowded, subequally developed and subevenly spaced concentric growth lines, becoming slightly larger and more prominent on the adult portion of the shell (pl. 1, fig. 21). A few low, broad, undulations are scattered over the shell.

*Interior morphology.*—Ligamental groove not exposed on any specimens. Ligament mainly external, covered over by valve margins only on the posterior end of the escutcheon. Fine radiating striae, shallow grooves, and broad rounded interspaces cover entire inner surface of valve between the umbonal area and the pallial line; radiating structures more strongly developed laterally, ventrally, and in adductor insertion areas than elsewhere on valve. Submarginal fold parallel to dorsoposterior margin; faint, low, rounded, narrow, not extending as far dorsally as the umbo. Primary interior fold low, moderately narrow, broadly rounded, having the same trace as the primary sulcus exteriorly. Anterior sulcus expressed internally as a very broad, low fold on the midanterior flank near the commissure. Pallial line, dentition, and posterior adductor insertion area not observed. Anterior adductor insertion area well defined, impressed, moderately large, elongate-ovate, situated midanteriorly astride and marginal to the anterior fold (interior reflection of the sulcus), with irregular margins and strong radial and concentric surface markings; axis of area inclined toward the midventral margin; area separated ventroanteriorly from the pallial line (text fig. 17).

*Measurements.*—See text figure 4 for explanation of measurements. Largest adult valve (USNM 153409): height, 35.5 mm.; length, 30.8 mm.; width (both valves), 21.5 mm.; height to anterior break in slope, the junction between the dorsal and anterior margins, 9.2 mm.; height to midposterior break in slope, dorsal to the notch formed by the intersection of the primary sulcus and commissure, 12.8 mm.; height to middle of the primary sulcus where it intersects the ventroposterior margin, 21.2 mm.; length, beak to middle of primary sulcus notch, 28.7 mm.; angle A, 98°; angle B, 91°; angle C, 105°; angle D, 51°; angle E, 37°.

Holotype, medium-size adult valve (USNM 153411): height, 18.2 mm.; length, 15.8 mm.; width (both valves), 11.2 mm.; height to anterior break in slope, 4.2 mm.; height to midposterior break in slope, 10.4 mm.; height to middle of primary sulcus at intersection with ventroposterior margin, 14.5 mm.; length, beak to middle of primary sulcus notch, 15.7 mm.; angle A, 70°; angle B, 79°; angle C, 90°; angle D, 57°; angle E, 36°.

Paratype, the smallest adult valve (USNM 153410): height 12.8 mm.; length, 10.5 mm.; width (both valves), 6.7 mm.; height to anterior break in slope, 41 mm.; height to midposterior break in slope, 5.3 mm.; height to middle of primary sulcus at intersection with ventroposterior margin, 6.9 mm.; length, beak to middle of primary sulcus notch, 8.9 mm.; angle A, 82°; angle B, 91°; angle C, 99°; angle D, 57°; angle E, 22°.

*Ontogeny.*—The principal ontogenetic changes that can be noted on the growth series (three specimens between 12 and 36 mm. in height), and in growth line traces on the specimens at 5 mm. intervals (text fig. 17) are in the marginal outline, relative height and projection of the beak, development of the sulci, and width and projection of the flank posterior to the primary sulcus. The ornamentation becomes somewhat coarser with increasing size but does not change in character.

The marginal outline changes from ovate or subround in the juvenile and early adult growth stages (to heights of 15 mm.), to vertically ovate and elongate-ovate as ventral growth accelerates relative to lateral growth in the middle and late adult growth stages (about 20 to 35 mm.). The dorsoanterior flank is projected into a triangular auricle sloping gently away from the beak in the early adult growth stage, and becomes progressively smaller (relative to overall size), more rounded, and slopes more steeply away from the beak at later growth stages. The beak and umbo, not greatly projecting in early to middle adult growth stages, become more prominent and project more in large adults in response to size reduction and increase in slope of the dorsoanterior flank. The midposterior flank which lies posterior to the primary sulcus becomes progressively broader with increasing shell size and more angular in the midposterior region (text fig. 17). The primary sulcus becomes less curved, deeper, and gradually broader with age. The submarginal and anterior sulci are strictly features of the late adult growth stage and the anterior sulcus becomes abruptly more expanded and deeper during late adult growth. The lunule does not become depressed or bounded by distinct folds until the late adult growth stage.

*Remarks.*—*Thyasira beauchampi rex,* n. subsp., is the terminal member of the *T. beauchampi* lineage, and is distinct in its large size, relatively great height, and the development and midanterior position of its anterior sulcus. It is possible that the three specimens assigned to this subspecies will prove to be two distinct subspecies, since they occur at two widely separated stratigraphic levels and cannot be compared at equivalent growth stages. All specimens are closely related, however, and possess many characters in common. It seems best at present to group them within a single subspecies and consider the few differences between them as being ontogenetically controlled.

*Thyasira beauchampi rex* can be distinguished from *T. beauchampi beauchampi,* n. subsp., by its relatively longer shell, more projecting midposterior and dorsoanterior flanks, less projecting beaks and umbos, larger adult size, finer and more regular ornamentation, less convex valves, smaller and less prominent lunule, and broader, less recessed notches at the intersection of the primary and anterior sulci with the commissure. No other species is closely comparable to *T. beauchampi rex.* The subspecific name is from the Latin *regis,* meaning king, and refers to the great size of the adult valve.

*Stratigraphic position.*—*Thyasira beauchampi rex,* n. subsp., is known from the zone of *Baculites obtusus* (late Early Campanian) in the upper Pierre Shale near Horse Creek, Wyoming (USGS Mesozoic locality 10666), and from the younger zone of *B. perplexus* (early form; Late Campanian), either in the uppermost Mancos Shale or lower Mount Garfield Formation at the Book Cliff Coal Field, Mesa County, Colorado (USGS Mesozoic locality 3779).

*Types.*—Holotype, a small, complete, adult shell with valves in normal apposition and shell material intact (zone of *B. perplexus*), USNM 153411. Paratype, a very small early adult shell from the same locality, coattached valves in normal apposition; a complete internal mold with some of the shell attached, USNM 153410. Paratype, a very large adult shell, coattached valves in normal apposition, damaged, with much shell attached (zone of *B. obtusus*), USNM 153409.

### THYASIRA ADVENA Kauffman, new species

*Diagnosis.*—Subovate, moderately to highly biconvex, anterior flank expanded; outline of ventral margin truncate, margin not deeply recessed anterior to beak. Beak subcentral, slightly to moderately prosogyrate. Primary sulcus straight to slightly curved. Two subspecies are recognized.

### THYASIRA ADVENA ADVENA Kauffman, new subspecies

Plate 1, figures 11-13

*Diagnosis.*—Highly biconvex; beaks moderately prosogyrate and incurved; primary sulcus slightly curved, broad, shallow; lunule, escutcheon broad, depressed, well defined, with ridged periphery.

*Material.*—A single well-preserved internal mold of an adult shell with the valves coattached and in normal apposition; beak, umbo of right valve moderately crushed, umbo of left valve slightly depressed.

*General form.*—Shell large for genus, equivalve, prosocline, biconvex and highly inflated; greatest convexity dorsocentrally. Outline subovate, with length slightly greater than height (pl. 1, fig. 11). Posterodorsal, posterior margins forming moderate, continuous curve; midposterior margin strongly rounded at edge of notch in marginal outline formed by intersection of commissure and primary sulcus; sulcus notch broad, gently concave; anteroventral, posteroventral margins moderately and evenly rounded; midventral margin flattened; midanterior margin strongly rounded; anterodorsal margin slightly and unevenly concave in front of beak, with greatest curvature just below beak.

*Beaks, umbos.*—Beaks narrowly rounded, subcentral, slightly anterior to midline, prosogyrate and slightly incurved, directly opposed and nearly touching; umbos highly convex, broad, not well differentiated.

*Sulci, auricle.*—Primary sulcus originates on posterior margin of umbo at proximal end of escutcheon and extends with slight to moderate curvature to ventroposterior margin, becoming progressively broader; sulcus shallow, with gently sloping flanks throughout length, relatively broad for genus at distal termination. Submarginal sulcus very shallow, narrow, poorly defined on internal mold, extending nearly parallel to escutcheon along posterior third of shell. Posterior auricle very narrow, poorly defined, curved, not projecting significantly.

*Lunule, escutcheon.*—Lunule heart-shaped (pl. 1, fig. 12), very broad for genus, well defined, depressed, slightly concave, bounded by narrowly rounded ridges. Escutcheon lanceolate, with greatest width posteriorly, moderately depressed and well defined, with steep flanks bounded by sharp ridges (the edges of the posterior auricles); width greater than in majority of Cretaceous species.

*Ornamentation.*—Exterior surface of shell apparently marked by subequally developed, evenly spaced, moderately fine, rounded concentric ridges on dorsal one-third of valve and by fine, widely and unevenly spaced ridges and very fine growth lines over ventral two-thirds of valves (pl. 1, fig. 13). Ornament as defined from sculpture impressed on internal mold.

*Interior morphology.*—Ligamental grooves narrow, maximum width near posterior third of trace, partially or wholly closed over along anterior third by dorsal margins of shell (ligament thus "internal" here), open to exterior along posterior two-thirds of length; base of grooves narrowly rounded. Submarginal fold low, narrow, rounded, extending nearly parallel to commissure along posterior two-thirds of posterodorsal margin. Main interior fold broad, rounded, moderately low, the interior reflection of the primary sulcus. Radiating interior striae fine, low, rounded, crowded, separated by narrow grooves, extending from umbo to pallial line; striae strongest on ventral half of valves, weakly developed in umbonal area. Pallial line entire, without sinus, slightly raised, rounded, well defined (pl. 1, fig. 11), moderately broad (1 mm.). Adductor muscle impression areas weakly defined. Posterior adductor area subovate, with height greater than length, situated in center of main interior fold. Anterior adductor impression elongate-ovate, with long axis extending diagonally toward ventral margin from midanterior margin; inner edge of anterior adductor impression irregular, outer edge subregular and separated from pallial line along ventral half of its length. Both impression areas marked by stronger, coarser radiating interior striae, especially along their inner portions, than found over rest of shell. Internal mold shows no trace of pseudocardinal dentition.

*Measurements.*—Height, 28 mm.; length, 30.4 mm.; width (both valves), 22.5 mm.; height to the dorsal margin of the primary sulcus at its intersection with the commissure, 18 mm.; height to the midpoint of the sulcus at its intersection with the commissure, 23.5 mm.; height to the anterior break in slope, 8 mm.; angle B, 86.5°; angle C, 119°; angle D, 56°. Refer to text figure 4 for definition of measurements and angles.

*Ontogeny.*—Individual growth stages (i.e., nepionic, neanic, ephebic, gerontic) are not definable on this species by changes in the shell morphology. Shape and ornamentation are the only two characters that demonstrate significant ontogenetic changes. The juvenile and early adult concentric ornamentation is stronger, more evenly developed, and more closely spaced than that characterizing late adulthood, where the concentric ridges become irregularly and widely scattered (pl. 1, fig. 13). Growth line traces were made at given diameters to determine change in marginal outline at different stages of development (text fig. 18). These traces suggest that the juvenile shell was equidimensional and round. In early adult growth, ventral expansion of the valve margin predominated over lateral growth, producing an erect shell with the height slightly greater than the length. Middle adult growth was marked by approximately even expansion in all directions and by development of more acute midanterior and midposterior margins. In the late adult stage (assuming the single large valve is an old specimen) lateral growth becomes dominant over ventral expansion and many of the features characteristic of the species become strongly developed; the projected anterior flank, the truncated ventral margin, and increase in curvature of the posterodorsal and dorsoposterior margins and the primary sulcus.

*Remarks.*—The lineage of *Thyasira advena* is poorly represented in the Cretaceous of the Western Interior, but is so distinct from other species groups that the individual subspecies, represented by two, stratigraphically separated specimens, warrant recognition. Only *Thyasira cantha*, n. sp., approaches this lineage in the ovate form of the shell and the central beaks. Members of the *T. advena* lineage are easily distinguished from *T. cantha* however in having much more projecting, curved beaks and umbos, in the much greater projection of the anterior flank, in having the height less than the length, in having less rounded anterodorsal and posterodorsal margins, in the truncated ventral margin, and by the shallower, broader, and less curved primary sulcus.

*Thyasira advena advena* can be distinguished from the younger *T. advena browni, n. subsp.,* by its much greater convexity, much broader, and more depressed lunule, by having sharp ridges bounding the lunule, by the broader escutcheon, by its more curved, prosogyrate beaks and umbos, by its broader, shallower, and more curved primary sulcus, by its narrower fold and overall flank dorsal to the primary sulcus, by its more acute midanterior and midposterior margins and shallower recess below the beak, and in having a relatively higher shell. In addition, the early adult ornamentation appears stronger and more evenly developed on *T. advena advena.*

The derivation of the species and subspecies name is from the Latin *advena,* meaning stranger, and refers to the unusual morphology of this species as compared with the other, more important lineages of *Thyasira* found in the Cretaceous of the Western Interior.

*Stratigraphic position.*—Known only from the zone of *Baculites* sp. with weak flank ribs, middle Early Campanian, in the Steele Shale, Lost Soldier-Ferris district, Wyoming (USGS Mesozoic Locality 10459). This is the time of first appearance of *Thyasira* in the Western Interior.

*Types.*—Holotype, an internal mold of coattached valves, USNM 153417.

## THYASIRA ADVENA BROWNI Kauffman, new subspecies

Plate 1, figures 9, 10

*Diagnosis.*—Moderately biconvex, midanterior and midposterior margins moderately rounded; margin recessed anterior to beak. Flank broad posterior and dorsal to primary sulcus. Beak slightly prosogyrate, not greatly incurved. Lunule narrow, poorly defined, flat, with rounded margins; escutcheon narrow; primary sulcus narrow, moderately depressed, nearly straight. Faint posteromedial flattened area and dorsoanterior sulcus developed.

*Material.*—A single adult specimen, coattached valves nearly in normal apposition, moderately well preserved. Right valve nearly complete; left valve crushed; both valves with shell preserved over two-thirds of surface.

*General form.*—Shell large for genus, probably equivalve, slightly prosocline, probably biconvex, valve inflation moderate, greatest convexity dorsocentrally. Outline subovate, length significantly greater than height (pl. 1, fig. 10). Posterodorsal margin slightly curved, moderately inclined to hinge axis; midposterior, posteroventral, and entire anterior margins moderately and evenly curved; midventral margin flat; anterodorsal margin moderately recessed, concave below beak, becoming flat and parallel to hinge axis anteriorly, forming auricle (pl. 1, fig. 10). Sulcus notch ventroposterior, narrow, slightly concave. Flank area broad posterior and dorsal to primary sulcus, subtriangular in shape.

*Beaks, umbos.*—Beaks bluntly pointed, subcentral, slightly prosogyrate, with minor inward curvature. Beaks opposed and probably touching in complete shells. Umbos broad, moderately convex, not well defined. Umbonal angle obtuse.

*Sulci, folds, auricles.*—Primary sulcus extending from just behind beak to posteroventral margin with very slight curvature; sulcus moderately narrow and deep, well defined, with flanks sloping at around 30° to 45°, about twice as wide posteroventrally as it is on flanks of umbo. Folds low and broad bounding the primary sulcus. A faint broad, flattened area present anterior to inner fold. Submarginal sulcus very narrow, shallow, parallel to posterodorsal margin, peculiarly situated along the dorsal flank of the shell and even partly on the inward sloping flank of the escutcheon next to the ligamental groove. No posterior auricle developed. Anterior auricle of moderate size, with rounded margins, situated just anterior to recess in marginal outline below beak, separated from main body of shell by a narrow flattened area on the dorsoanterior flank which becomes abruptly broader and slightly depressed near margin, forming a weak dorsoanterior sulcus. Dorsoanterior margin faintly recessed at junction with this sulcus (pl. 1, fig. 10).

*Lunule, escutcheon.*—Lunule poorly defined, small, narrow, flat to slightly convex, bordered by low, rounded ridges. Escutcheon lanceolate, very narrow, deeply excavated, bordered by narrowly rounded ridges, practically filled with ligament area.

*Ornamentation.*—Concentric ornamentation consisting of fine, crowded, subequal growth lines on dorsal half of shell, becoming coarser and more irregular in size and distribution on ventral half (pl. 1, fig. 10). No radial elements.

*Interior morphology.*—Ligamental groove extending along escutcheon, moderately narrow and deep, with angulated base, situated beneath overhanging dorsal margin of valve near beak and opening inward (ligament partially internal in this area), twisting outward slightly toward the posterior where it is situated on flank of escutcheon and faces inward and upward, but is not covered. Main interior fold moderately rounded and elevated, narrow, the internal reflection of the primary sulcus. Submarginal ridge very narrow, low, sharp, parallel to dorsal margin of ligamental groove. Pallial line entire, well defined (text fig. 18), 1 mm. wide, slightly raised and rounded. Interior radiating striae and intervening ridges fine, crowded, irregularly spaced, faintly defined dorsally, becoming larger and coarser ventrally, near pallial line, and in adductor muscle insertion areas. Anterior adductor insertion area unknown; posterior adductor insertion area subovate, recessed and well defined, situated on posterior flank and posterior to the main interior fold (text fig. 18). Dentition, if any, unknown.

*Measurements.*—See text figure 4 for definition and orientation of measurements. Height, 25.5 mm.; length, 28.6 mm.; width (both valves), 17 mm.; height to the midposterior margin, where it breaks slope and trends toward the primary sulcus, 11.2 mm.; height to the middle of the primary sulcus at its interesection with the ventroposterior margin, 19.7 mm.; height to the dorsoanterior break in slope, at the dorsolateral edge of the anterior auricle, 5.1 mm.; angle A, 100°; angle B, 78°; angle C, 102°; angle D, 75°; angle E, 34°.

*Ontogeny.*—Individual growth stages (i.e., nepionic, neanic, etc.) are not definable on this species by changes in the shell morphology. Ornamentation and marginal outline illustrate some general ontogenetic trends. The concentric ornamentation becomes coarser and more irregularly distributed from early to late adult growth stages (pl. 1, fig. 10). Adult features of the outline become better developed with age, as demonstrated by growth line traces at 5 mm. intervals (text fig. 18). The juvenile and early adult shell (umbo) is subround, nearly equidimensional, and does not have an expanded anterior flank. During early adult growth (midshell) ventral and lateral expansion are about equal, and the projected, more narrowly rounded midanterior and midposterior parts of the flank become defined. These are accentuated in the late adult stage where lateral growth is somewhat greater than ventral growth, and the ventral margin becomes flattened. The recessed anterior sulcus is strictly a late adult feature.

*Remarks.—Thyasira advena browni,* n. subsp., is the youngest known member of the *T. advena* lineage. It can be distinguished from its ancestor, *T. advena advena,* n. subsp., by its less inflated valves, relatively greater length, more rounded midanterior and midposterior margins, narrower, smaller, and more poorly defined lunule, narrow escutcheon, straighter and narrower primary sulcus and more dorsally situated submarginal sulcus. It possesses in addition a posterior median flattening of the shell and a shallow dorsoanterior sulcus forming a notch in the marginal outline. The posterior flank of the shell between the primary sulcus and the commissure is much broader in this subspecies, the anterodorsal margin more recessed beneath the beak, the beak more erect and less curved, and the early adult ornamentation less prominent.

The subspecies is named in honor of R.A.C. Brown, who first noted the presence of *Thyasira* in Cretaceous rocks of the Western Interior of North America.

*Stratigraphic position.*—The subspecies has been reported only from the middle part of the *Baculites scotti* zone, Late Campanian, in limestone concretions of the Pierre Shale, Pueblo County, Colorado (USGS Mesozoic loc. D709).

*Type.*—Holotype, coattached, nearly complete valves with much of the shell preserved and the left valve crushed, USNM 153416.

### THYASIRA BECCA Kauffman, new species

*Diagnosis.*—Shell outline ovate to subtrapezoidal; length slightly greater than height; beaks projecting and strongly prosogyrate; anterodorsal notch below beaks relatively deep; sulcus notch strong; dorsoanterior flank projecting, in some cases auriculate, narrowly rounded; flank broad, subtriangular posterior to well-defined primary sulcus; anterior sulcus present in one subspecies; concentric growth lines relatively coarse; shell large for genus and relatively thick, strong. Two subspecies are known.

### THYASIRA BECCA BECCA Kauffman, new subspecies

Plate 1, figures 27, 29, 30; plate 4, figures 1-21; plate 5, figures 28, 33, 37, 38

*Diagnosis.*—Subovate, beaks strongly projecting, moderately prosogyrate (45° to 50°); notch anterior to beaks well defined, moderately and subevenly concave; dorsoanterior and midposterior margins projecting and strongly rounded, not auriculate; primary sulcus notch ventroposterior. Beak subcentral, anterior to midline; concentric growth lines of medium strength.

*Material.*—Forty-one well-preserved bivalved shells and internal molds of adult individuals from 9 localities; largest variation suite from a single locality, 23 specimens (D1410).

*General form.*—Shell attaining large size for genus, equivalve, moderately biconvex, greatest convexity dorsocentral; moderately prosocline. Outline subround (early to middle adult growth stage) to subovate (large adults) with length slightly greater than height consistently. Posterodorsal and dorsoposterior margins continuously and slightly curved. Dorsoanterior and midposterior margins strongly rounded. Primary sulcus notch ventroposterior, moderately broad and deep, nearly symmetrical. Ventral and anterior margins moderately rounded in continuous curve, becoming slightly flattened at dorsoanterior extremity. Anterodorsal margin flat, slightly convex, or slightly concave anterior to moderately deep, asymmetrical notch beneath beak. Shell moderately thick, strong. Typical specimens on plate 4, figures 1-21.

*Beaks, umbos.*—Beaks bluntly pointed, moderately (small shells) to strongly (large shells) projecting, beak angle obtuse; beaks moderately prosogyrate, situated subcentrally just anterior to midline (pl. 4, fig. 14). Beaks slightly incurved on large specimens. Umbos not well differentiated from rest of shell, strongly convex, with concentric sculpture similar to that over rest of shell but finer; first development of primary sulcus on umbo.

*Folds, sulci, auricles.*—Primary sulcus moderately deep, asymmetrical, with anterior flank steep, curvature medium, extending from posterior flank of umbo to ventroposterior margin, forming prominent notch (pl. 4, fig. 20). Concentric sculpture equally developed in sulcus and at midshell; in some specimens subtle fine radial ridges transgress sulcus. Primary fold anterior to sulcus well defined, moderately rounded, asymmetrical with steep posterior flank, in some cases with fine radial ridge at its crest. Posterior primary fold prominent, broad, evenly rounded, moderately low, occupying most of shell flank posterior to primary sulcus (pl. 4, fig. 13). No submarginal sulcus clearly defined on shell exterior, but area where sulcus normally developed occupied by a narrow flat to very slightly concave band adjacent to dorsoposterior margin; submarginal sulcus strongly reflected internally however as a narrow fold. No clear auricles developed anteriorly or posteriorly; no anterior sulcus developed, its position occupied by a narrow flattened area forming truncate zone in anterior margin at

TABLE 7.—*Summary of measurements for* Thyasira becca becca Kauffman, new subspecies.

| CHARACTER[1] | NUMBER OF SPECIMENS | RANGE | AVERAGE |
|---|---|---|---|
| Height (mm.) | 34 | 17.8-32.5 | 25.3 |
| Length (mm.) | 34 | 18.0-32.5 | 25.6 |
| Width, both valves (mm.) | 34 | 10.0-21.1 | 15.5 |
| HMS (mm.) | 33 | 8.0-18.3 | 12.6 |
| HABS (mm.) | 36 | 2.6- 9.0 | 4.6 |
| HS (mm.) | 33 | 13.5-29.0 | 20.6 |
| LS (mm.) | 33 | 15.5-30.5 | 22.4 |
| Length of escutcheon (mm.) | 28 | 10.0-21.0 | 15.2 |
| Maximum width of escutcheon (mm.) | 33 | 1.0- 5.0 | 3.1 |
| MWF (mm.) | 29 | 3.0-6.5 | 4.6 |
| Angle A (degrees) | 31 | 75-110 | 94.2 |
| Angle B (degrees) | 32 | 73-92.5 | 84.7 |
| Angle C (degrees) | 32 | 93-116 | 104.5 |
| Angle D (degrees) | 33 | 55.5-78.5 | 66.9 |
| Angle E (degrees) | 32 | 27.5-51.0 | 40.4 |

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[1] See text figure 4 for explanation of angles and abbreviations.

their intersection. Shell surface slightly flattened anterior and posterior to broadly rounded at midline. In some large valves the posterior flattened area becomes broadly sulcate near the posteroventral margin.

*Lunule, escutcheon.*—Lunule small for genus, broadly lanceolate in outline, not quite extending to dorsoanterior corner, slightly concave, with narrowly rounded, semiprominent bounding ridges (pl. 4, fig. 16). Escutcheon shallow, narrow, lanceolate, broadest near posterior flank of umbo, consisting of two very narrow, shallow depressions bordered by sharp low ridges on either side of deep depression occupied by ligament (pl. 4, fig. 19).

*Ornamentation.*—Entire surface of shell covered by very crowded, fine, subevenly spaced, unequally developed, raised concentric growth lines, finer on umbo and coarser near ventral margin than found elsewhere (pl. 1, fig. 27). Fine radial ridges noted in and adjacent to primary sulcus of some specimens.

*Interior morphology.*—Thin, low pseudocardinal swelling formed beneath beaks of left valve by expansion of ridge forming lower edge of ligamental groove; apparently not developed on all specimens. Ligamental groove paralleling posterior part of dorsal-dorsoposterior margin, broadly curved, narrow, deep, asymmetrical with flat ventral shelf, subangulated at base. Submarginal fold prominent, very narrow, with narrowly rounded crest (pl. 4, fig. 15), extending from middle posterodorsal margin to upper dorsoposterior margin, delineating on internal molds only a small, triangular posterior auricle (pl. 4, fig. 20). Primary interior fold following trace of primary sulcus exteriorly, well defined, moderately convex, narrow, asymmetrical with anterior flank steepest. Central and posterior part of fold occupied midposteriorly by well impressed, relatively large, subovate posterior adductor insertion area (pl. 4, fig. 20); surface of area moderately smooth, transgressed by fine radial grooves. In numerous large adult specimens a prominent, deeply incised, narrow, elongate-ovate muscle scar, possibly an isolated portion of the posterior adductor area, is situated on the submarginal fold midposteriorly (pl. 4, fig. 20; text fig. 17). Anterior adductor insertion area very large, elongate-ovate, its long axis inclined from the midanterior toward the midposterior margin; insertion area well impressed, with irregular margins, bipartite with small subovate anterior part separated from main area by a small fold (pl. 4, figs. 6, 12; text fig. 17), separated ventrally from pallial line (text fig. 17) in position of incurrent channel; surface of area marked by strong radial grooves, low ridges, and fine, closely spaced growth lines. Pallial line entire, well defined, a narrow slightly raised band between adductor insertion areas. Entire inner surface of valve marked by moderately crowded, narrow raised lines and grooves with broad interspaces between them; most strongly developed ventrally and laterally.

*Measurements.*—A summary of measurements for the large variation suite of *Thyasira becca becca,* n. subsp., is presented in Table 7.

*Ontogeny.*—Remarks on early adult and preadult development (less than 17 mm. in height) are based on growth line traces at 5 mm. intervals on typical adult valves (text fig. 17). A complete ontogenetic suite of adult specimens is available for larger sizes. The principal ontogenetic changes noted were in the development of the marginal valve outline and particularly the profile of the anterior and posterior margins, in the relative projection of the beaks and umbos, the apical (beak) angle, the development of the notch anterior to the beaks, definition of the sulci and flattened areas of the valve, and the development of the lunule. The ornamentation becomes coarser with increasing size but does not change in character except that small concentric undulations appear only in middle to late adult growth stages, above 20 mm. in height.

The general outline of the valve undergoes slight change with growth, being subrectangular at the juvenile growth stage (height, around 5 mm.), becoming ovate, with the length slightly greater than the height in early adulthood (around 10 mm.), and achieving its general adult form, subovate to subrounded, at heights of 15 mm. and greater. The beak is blunt and not greatly projecting in juvenile and early adult growth stages (to heights of 20 mm.) and the concave notch anterior to the beak is shallow and broad. In larger shells the beak gradually becomes more prominent, angular, and projecting, the apical angle becomes less, and the notch deeper and more accentuated (see growth series on pl. 4, figs. 1-21; pl. 5, figs. 28-33, 37, 38). The dorsoanterior corner is more angular and relatively more projecting in early growth stages than in large adults, where it becomes rounded. Conversely, the midposterior break in slope and the primary sulcus notch become better defined with increased size of adult shells. The primary sulcus is broad and shallow to heights of 10 mm., and becomes deeper and more prominent with continued growth; the submarginal flattened area and the internal fold in this position are not defined until heights of 15 mm. (middle adult growth stage) and become better developed with increasing size. The flattened areas of the shell on either side of the midline are strictly middle to late adult features and were not observed on shells smaller than 15 mm. in height. The posterior flattened area is first to develop.

*Adult variation.*—The large suite of well-preserved adult specimens representing this subspecies provide an opportunity to make some pertinent observation on adult morphological variation which can be compared directly to variation studies on similar Recent species such as *T. sarsi* (see earlier discussion of variation in this species). In almost every species of Cretaceous *Thyasira,* adult morphogenetic variation is not as great at any single growth stage as is ontogenetic variation within a single species. The principal adult variations in shell morphology are shown on plate 4, figures 1, 5, 8, 9, 12, 14, 15, 20.

Significant morphologic variation in adult shells of *Thyasira becca becca,* n. subsp., is expressed in the general marginal outline of the shell, the projection and apical angle of the beaks and umbos, the development of the marginal notch anterior to the beaks, the curvature of the posterodorsal-dorsoposterior margin, the trace of the primary sulcus, the position and concavity of the primary sulcus notch, and markedly in the projection and outline of the dorsoanterior flank. As discussed in an earlier section on shell variation, several of these structures show significant variation in adult shells of the living *T. sarsi* (Philipi). Comparison of variation plots of living and Cretaceous species shows that the amount of variation is comparable in populations from the two ages (text figs. 6, 7).

The marginal outline varies from subcircular (pl. 4, fig. 14) to subovate with the length slightly greater than the height (pl. 4, fig. 12). Subcircular valves have more projecting beaks and umbos, a smaller apical angle, and more rounded, less projecting dorsoanterior flanks than valves which are subovate. On the latter, the notch anterior to the beak is shallower than on the former. The curvature of the posterodorsal-dorsoposterior margin ranges from slight (pl. 4, fig. 20) to moderate (pl. 4, fig. 14). On valves where the curvature is slight, the flank posterior to the primary sulcus is broader and more narrowly rounded midventrally than on valves with moderate marginal curvature. The curvature of the primary sulcus varies in the middle to late adult stages from slight to moderate, but is constant in earlier growth stages. Valves with a moderately curved ventral half of the primary sulcus have a relatively broader flank posterior to the sulcus, and a more ventrally situated primary sulcus notch than those with a slightly curved primary sulcus (pl. 4, compare fig. 20 with fig. 9). Development of the dorsoanterior flank is one of the most variable adult characters in *T. becca becca* as it is in living *T. sarsi.* The flank ranges from moderately projecting with an evenly rounded margin (pl. 4, fig. 20) to prominently projecting with flattened dorsal and anterior margins intersecting at a narrowly rounded dorsoanterior corner (pl. 4, fig. 14). In no case does the adult morphogenetic variation in *T. becca becca* exceed that which might be expected for an adult population, using the population of living *T. sarsi* as a guide (text figs. 6, 7). The range of adult variation in *T. becca becca* does not overlap that of similar species or subspecies in regard to the characters mentioned above.

*Remarks.—Thyasira becca becca* is morphologically similar to *T. becca cobbani,* n. subsp., with which it occurs in the middle part of its range (lower part of the *Baculites scotti* zone). Since no morphologic gradient can be established between the two, they are here considered distinct subspecies, with *T. becca cobbani* being a phylogenetic branch of the earliest *T. becca becca* (text fig. 13).

*Thyasira becca becca* may be distinguished from the subspecies *cobbani* by its more rounded to ovate marginal outline, less prosogyrate beaks and umbos, shallower notch anterior to the beaks, less projecting and more rounded dorsoanterior flank which is not auriculate, lack of an anterior sulcus in the adult shell, development of flattened areas on large shells on either side of the midline, ventroposterior position of the primary sulcus notch, broader escutcheon, and finer, more regular concentric growth lines.

The species and subspecies name *becca* is taken from the Latin *beccus* meaning nose, beak, or bill, and refers to the prominent, projecting beak and umbonal area of the adult shell.

*Stratigraphic position.*—In the Western Interior of the United States, *Thyasira becca becca* is known only from the zone of *Baculites scotti,* in the lower and middle part (levels A through D of this report; text fig. 1). In the lower part of the zone it occurs at level A at USGS Mesozoic locality D1215 in the "Tepee Butte" zone of the Pierre Shale, Pueblo County, Colorado, and at USGS Mesozoic locality 22840 in the Pierre Shale of the Kassler Quadrangle, northern Front Range foothills, Colorado. At level B, *T. becca becca* occurs at USGS Mesozoic locality D1216, Pierre Shale, Pueblo County, Colorado. In the middle part of the *B. scotti* zone, *T. becca becca* occurs in level C at 3 localities: USGS Mesozoic locality D1410 (possibly includes level B), Pierre Shale, Fall River County, South Dakota; USGS Mesozoic locality D709, Pierre Shale, Pueblo County, Colorado; and USGS Mesozoic locality 22838, Pierre Shale, Kassler Quadrangle, northern Front Range foothills, Colorado. In level D the subspecies is known only from USGS Mesozoic localities D714 and D3945, Pierre Shale, Pueblo County, Colorado.

The range of *T. becca becca* is less certain and may include younger or older beds in Canada, as explained in detail under the "stratigraphic position" section of *T. becca cobbani.* The extension of the range downward and possibly upward from the lower to middle *B. scotti* zone on text figure 1 is based on the fact that the Riding Mountain Formation along the Assiniboine River in Canada may include beds anywhere from the top of the *Scaphites hippocrepis* zone (Early Campanian) to the top of the *Baculites eliasi* zone (Late Campanian), and the precise level at which the specimens of *Thyasira* were collected in the formation is not known.

*Types.*—Holotype, a medium-size adult shell with valves in normal apposition and most of the shell material intact; the beaks are not strongly projecting as in later adult stages, USNM 153512 (USGS D1410).

Illustrated paratypes: from the Riding Mountain Formation on the Assiniboine River, Canada, zone of *Baculites scotti* (lower part) and questionably *B. gregoryensis* and *B. perplexus,* GSC 18760; from level A, zone of *B. scotti* (lower part), USGS Mesozoic locality 22840 (2 specimens), USNM 153514, 153524; from level B, lower part of *B. scotti* zone, USGS Mesozoic locality D1216 (1 specimen), USNM 153517; from level B or C, lower part of *B. scotti* zone, USGS Mesozoic locality D1410 (8 specimens), USNM 153510-153513, 153516, 153520, 153521, 153525; from level C, middle *B. scotti* zone, USGS Mesozoic locality D709 (4 specimens) USNM 153509, 153515, 153518, 153519; from level D, middle *B. scotti* zone, USGS Mesozoic locality D714 (1 specimen), USNM 153522. Measured paratype suites, not illustrated: from USGS D1215, USNM 153528 (1 specimen); from USGS D1410, USNM 153508 (13 specimens); from USGS D709, USNM 153526 (3 specimens); from USGS 22838, USNM 153523 (1 specimen); from USGS D714, USNM 153471 (1 specimen); from USGS D3945, USNM 153527 (1 specimen); and from the Riding Mountain Formation of Canada, GSC 18762 (1 specimen).

### THYASIRA BECCA COBBANI Kauffman, new subspecies

Plate 1, figure 28; plate 5, figures 34-36

*Diagnosis.*—Outline subrectangular to subtrapezoidal, shell attaining large size for genus, strongly prosocline and prosogyrate; deep notch in outline formed beneath beak and at intersection of primary sulcus and commissure. Length significantly greater than height, midanterior and midposterior flanks strongly projected, beak situated in anterior third of length. Lunule poorly defined. Concentric ornamentation moderately coarse.

*Material.*—A very large adult shell with valves in normal apposition, complete with most of the shell attached (holotype, GSC 18758). A moderately large adult shell with valves in normal apposition, most of the shell attached, left valve crushed, part of anteroventral margin missing.

*General form.*—Shell attaining very large size for genus, equivalved, strongly prosocline, moderately biconvex, with greatest inflation dorsocentrally. Outline subrectangular to subtrapezoidal (pl. 1, fig. 28). Posterodorsal margin long and gently curved; dorsoposterior and dorsoanterior margins narrowly rounded and projecting at margins of primary sulcus notch and notch below beak, respectively. Primary sulcus notch midposterior, prominent, moderately broad and recessed. Ventroposterior, ventral, and ventroanterior margins forming continuous moderate curve except for slight flattening in outline midventrally (pl. 1, fig. 28). Area below beak deeply recessed and asymmetrical, with greatest concavity just below beak. Shell thick, strong.

*Beaks, umbos.*—Beaks blunt, narrowly rounded, strongly prosogyrate, directed anteriorly nearly parallel to hinge axis, very slightly incurved, situated one-third the total shell length from the anterior margin. Umbos highly inflated, poorly defined, merging with adult part of shell, strongly prosogyrate, with ornamentation similar to that over rest of shell but finer and having weakly defined primary sulcus.

*Folds, sulci, auricles.*—Primary sulcus broadly curved, prominent, moderately narrow and shallow, asymmetrical, with anterior flank steepest, originating on posterior flank of umbo and terminating in a prominent concave notch at the midposterior margin (pl. 1, fig. 28; pl. 5, fig. 36). Shell flank posterior to primary sulcus broad, angulated posteriorly, forming subtriangular auricle with projecting posterior apex, broadly arched into primary fold. Submarginal sulcus not preserved on either specimen. Anterior primary fold broad, moderately convex, asymmetrical with steepest flank posterior. On largest adult shell, a shallow sulcus formed anterior to this fold, between it and midline; this secondary sulcus represented by semiflattened part of shell flank in moderate-size adults, and bounded anteriorly by a very broad low secondary fold. Narrow, shallow, moderately curved anterior sulcus developed on large adult shells, extending from anterior flank of late umbo in an arc to the dorsoanterior margin, which is somewhat flattened at their intersection. Area between anterior sulcus and margin forms a subtle subtriangular auricle with an angular, projecting, dorsoanterior apex.

*Lunule, escutcheon.*—Lunule small, heart-shaped, poorly defined, flat to depressed (on largest valves), bounded by broadly rounded folds, situated in prominent notch below beak and terminating at distal angular margin of anterior auricle. Escutcheon narrow, lanceolate, broadest medially, moderately depressed, with steep flanks bearing shallow grooves on either side of narrow central groove occupied by ligament. Escutcheon margins subangular, narrow, ridged. Lunule, escutcheon illustrated on plate 5, figure 35.

*Ornamentation.*—Entire shell surface covered with coarse, raised, crowded, irregularly developed and subregularly spaced growth lines; lines coarser ventrally than dorsally, well developed in sulci, lunule, and over folds. Small, closely spaced undulations bearing several lines occur over ventral two-thirds of shell.

*Interior morphology.*—Dentition unknown. Small to medium size, narrow, irregularly and closely spaced interior grooves with broad to narrow, low rounded interspaces radiate from umbo to pallial line, becoming coarser ventrally, laterally, and in adductor muscle insertion areas. Pallial line weakly impressed, entire, a slightly elevated band about 1 mm. in thickness. Posterior adductor insertion area subround, well impressed, situated astride the low, moderately broad, primary interior fold, marked by crowded concentric growth striae and lines, and by coarse to fine radial grooves. Anterior adductor insertion area well impressed, large, elongate-ovate in outline, incompletely known, its long axis inclined from the midanterior margin toward the midposterior margin, and its ventral margin separated partially from the pallial line. Margins of insertion area irregular, and surface marked by strong to fine radial grooves and fine concentric lines. Other interior structures of shell not known.

*Measurements.*—Holotype, a very large adult shell with valves in normal apposition and shell material attached, GSC 18758: height, 36 mm.; length 37 mm.; width of both valves, 22.2 mm.; height to midposterior break in slope, dorsal edge of primary sulcus notch, 22 mm.; height to angulate distal edge of anterior auricle, 7 mm.; height to middle of primary sulcus notch, 24 mm.; length of a line connecting beak and middle of primary sulcus notch, 31.5 mm.; length of escutcheon, 20 mm.; width of escutcheon, 5.3 mm.; maximum width of posterior auricle, 6.5 mm.; angle A, 81°; angle B, 95°; angle C, 108°; angle D, 39.5°; angle E, 30.5°.

Paratype, an incomplete moderate-size adult shell, USNM 153478: height, 27.2 mm.; length, 29 mm.; width of both valves, 17 mm.; height to midposterior break in slope at dorsal edge of primary sulcus notch, 16.5 mm.; height to junction between dorsal and anterior margin, angulate edge of auricle, 2.4 mm.; height to middle of primary sulcus notch, 24 mm.; length of a line connecting beak and middle of primary sulcus notch, 25 mm.; length of the escutcheon, 18.5 mm.; maximum width of escutcheon, 3 mm.; maximum width of posterior auricle, 5.5 mm.; angle A, 102°; angle B, 95.5°; angle C, 115.5°; angle D, 73°; angle E, 38°. See figure 4 for explanation of measurements.

*Ontogeny.*—Only two adult shells are known for this subspecies, and therefore the ontogenetic development of the shell morphology is known primarily from growth line traces taken at 5-mm. intervals on both specimens (text fig. 17). The valve outline is subround in juvenile and early adult growth stages (height, up to 10 mm.); anterior and posterior growth accelerates relative to ventral expansion in later growth stages forming a more elongate shell with the midanterior and midposterior margins becoming more projected with increasing size. The concave notches beneath the beak and at the intersection of the margin and the primary sulcus are slightly recessed in young shells (height, to 15 mm.) and become gradually deeper and more prominent in later growth stages; they are strongly indented in old adult shells (text fig. 17). The primary sulcus is shallow and weakly defined in small shells to 10 mm. height, becomes significantly deeper, more prominent, and slightly broader in middle adult growth stages (height, 10-20 mm.), and relatively shallower and broader in larger shells. The anterior sulcus is strictly a late adult feature first expressed at heights of 15 to 20 mm. and becoming distinctly concave and more prominent at later growth stages. Finally, the strength of the growth lines increases as the shell becomes larger, but the general nature of the surface sculpture does not change. The curvature of various parts of the shell margin does not change appreciably through adult growth except for slight flattening of the anteroventral and dorsoanterior margins in middle to late adult growth (height, 20 mm. and greater).

*Remarks.*—The stratigraphic and geographic cooccurrence of *Thyasira becca becca* Kauffman, n. subsp., and *T. becca cobbani,* n. subsp., suggests that they are not only closely related but also only ecologic subspecies of the same stock or varieties of the same species. In the collections at hand, no morphologic gradient can be established between the two however, even though *T. becca becca* is represented by a large suite of specimens, and it seems logical at present to separate the two forms as subspecies.

*Thyasira becca cobbani* is unique in its subtrapezoidal outline, strongly prosogyrate beaks, the deep anterior notch below the beaks, and the strongly projecting, auriculate anterior flank with its late adult sulcus. This subspecies may be distinguished from *T. becca becca,* the only Western Interior thyasirid which closely resembles it, by the following features: less rounded outline; more projecting, auriculate anterior flank; possession of an anterior sulcus; more strongly prosogyrate beaks and umbos; deeper notch anterior to beaks; midposterior position of the primary sulcus notch in the marginal outline; more evenly convex shell without median flattenings; narrower escutcheon; and coarser concentric growth lines.

This subspecies was given the manuscript name "*T. albertensis* var. *proxima*" by R.A.C. Brown (on labels only), who first discovered it in the Riding Mountain Formation of Canada, and reported the presence of the genus in Canada (1942, p. 147), but never completed a manuscript on species of *Thyasira* and has now abandoned the problem.

The subspecies is named in honor of Dr. William A. Cobban of the United States Geological Survey, who suggested this problem, provided much of the material used, and has been of considerable assistance in furnishing faunal and stratigraphic data throughout the study.

*Stratigraphic position.*—In the Western Interior of the United States, *Thyasira becca cobbani* occurs only in the middle part of the *Baculites scotti* zone (level C of this report; text fig. 1) at USGS Mesozoic locality D709, in the Pierre Shale of Pueblo County, Colorado. In Canada, the stratigraphic position of the subspecies is not precisely known. It has been found in the Riding Mountain Formation on the Assiniboine River, above Qu'appelle River, from a stratigraphic level probably somewhere in the zone of *Baculites compressus* s.l. (Cobban and Reeside, 1952, chart 10b). J.A. Jeletzky (written communication, October 8, 1964) states:

> The age limits of the Riding Mountain Formation are even more vague. All that can be said is that the bulk of it is in the *Baculites compressus* s. lato zone as used by Cobban and Reeside (1952). It may well extend somewhat beyond this zone both upward and downward, however, and I could not tell how far, except that the *Scaphites hippocrepis* is probably beneath it. . . . I did not see any *Scaphites* referable to *S. nicolletii* or other Maestrichtian forms from it. . . .

*Baculites compressus,* as broadly defined, has subsequently been subdivided by Cobban (1958, p. 660) into three species, in ascending order, *Baculites scotti, B. compressus* s.s., and *B. eliasi.* In view of its occurrence in the United States, I am inclined to tentatively place the Canadian specimen also from the zone of *B. scotti,* though as shown above, it could certainly be younger, and if *Scaphites hippo-*

*crepis* is the next known ammonite zone below the Riding Mountain Formation, *Thyasira becca cobbani* could have come from Early and Late Campanian levels considerably below the *B. scotti* zone (text fig. 1).

*Types.*—Holotype, a very large adult shell with the valves in normal apposition and most of the shell material attached. The dorsal third is covered by caliche and the median part of the right valve is missing, GSC (Geological Survey of Canada) 18758. Paratype, a medium-size adult shell, valves in normal apposition, anteroventral margin broken off, and most of the shell material preserved, USNM 153478.

## THYASIRA CANTHA Kauffman, new species

Plate 1, figures 7, 8; plate 3, figures 36-41

*Diagnosis.*—Outline round, beaks blunt, not greatly projecting, strongly prosogyrate, centrally situated. Posterior margin moderately curved; anterodorsal margin blunt at intersection with anterior flattened area on shell surface. Ornamentation consisting of fine, subeven, raised growth lines. Edentulous.

*Material.*—Five bivalved specimens, four with much of the shell material preserved. Four of the specimens have the valves in normal apposition; four are nearly complete with only parts of the margins missing.

*General form.*—Shell attaining moderately large size for genus (pl. 1, fig. 7), moderately biconvex, equivalved, convexity greatest dorsocentrally, slightly prosocline. Outline subround, height and length approximately equal. Posterodorsal and dorsoposterior margins forming continuous moderate curve; midposterior margin above sulcus notch narrowly rounded; sulcus notch ventroposterior, broad, slightly concave. Midventral and ventroanterior margins flat to slightly rounded, the junction between them moderately rounded. Midanterior margin moderately rounded; dorsoanterior margin flat to slightly rounded at intersection with anterior flattened area of shell surface. Dorsoanterior corner obtusely angulate. Anterodorsal margin flat anteriorly on auricle, gently concave beneath beaks; no deep notch formed below beaks. Shell moderately thin, fragile.

*Beaks, umbos.*—Beaks bluntly pointed, strongly prosogyrate and moderately incurved, nearly touching; apical angle 90° or more. Umbos not well defined, merging with adult portion of shell, moderately convex, prosogyrate, with ornamentation similar to, but finer than that covering rest of shell. Beaks subcentral, just anterior to midline.

*Folds, sulci, auricles.*—Primary sulcus very well defined, strongly curved between posterior flank of umbo and ventroposterior margin; shallow, with a gently sloping posterior flank and a moderately steep anterior flank. Sulcus becoming broader and shallower as size of shell increases. Anterior primary fold bordering sulcus moderately prominent, rounded, asymmetrical, with steep posterior flank and very shallowly sloping anterior flank. Posterior primary fold moderately broad, gently convex, evenly rounded, filling nearly the entire flank area posterior to the primary sulcus. No distinct submarginal sulcus developed on shell exterior; area where it occurs in other species subtly flattened. No posterior auricle developed, and median flattened areas not formed on shell surface. A broad, flat, triangular area developed between anterior edge of umbo and dorsoanterior margin; margin flattened in profile at their intersection. A subtle, moderately projecting anterior auricle, triangular in outline, is formed on and above the anterior flattened area of the shell (pl. 1, fig. 7).

*Lunule, escutcheon.*—Lunule small, heart-shaped, lying between beaks and angulated edge of anterior auricle, flat, poorly defined, and bounded by broad rounded ridges in moderate-size adult shells (pl. 3, fig. 38), slightly depressed, prominent, and bounded by narrowly rounded ridges in large adults. Ornamentation well defined in lunule. Escutcheon very narrow, lanceolate, broadest on posterodorsal slope one-third its total length from the beak; most of escutcheon area occupied by narrow ligamental area (pl. 3, fig. 38), which is bounded laterally by narrow, shallow depressions on moderately sloping flanks of escutcheon. Troughs bounded by very narrow, low, sharp ridges. Ligament exposed externally over most of length.

*Ornamentation.*—Entire shell surface covered with fine, subequally developed, subequally to unequally spaced, raised growth lines and narrow grooved interspaces. Ornamentation fine on umbo, more crowded and coarser near perimeter, than found over rest of shell. A few narrow, small constrictions occur between growth lines that are larger than normal interspaces. One specimen with fine radiating lines on umbo.

*Interior morphology.*—A subtle pseudocardinal swelling present just below beak; incompletely known. Ligamental groove narrow, arcuate, on flank of escutcheon and facing inward, asymmetrical with broadest flank dorsad; base angular; groove partially covered over with dorsal valve margins just posterior to beaks and possibly at posterior end of escutcheon. Fine, crowded, radiating grooves with low, rounded interspaces covering valve interior between umbo and pallial line. Pallial line entire, poorly known, weakly impressed, submarginal. Primary interior fold following trace of primary sulcus, moderately arched, prominent, relatively narrow for Cretaceous species; radial striae strong on and adjacent to fold. Submarginal fold and internal expression of anterior flattened area not observed. Adductor muscle insertion areas not preserved on available internal molds of specimens.

*Measurements.*—See figure 4 for explanation of measurements. Holotype, USNM 153477, a moderately large adult shell: height, 28 mm.; length, 26.6 mm.; width (both valves), 14 mm.; height to midposterior break in slope at dorsal edge of primary sulcus notch, 15.2 mm.; height to junction of dorsal and anterior margins at angulate edge of anterior auricle, 5 mm.; height to middle of primary sulcus at its intersection with ventroposterior margin, 24.5 mm.; length, line connecting beak and center of primary sulcus notch, 25.5 mm; width of escutcheon (maximum), 2 mm.; maximum width of posterior "wing" or portion of flank posterior to primary sulcus, 4.5 mm.; angle A, 98.5°; angle B, 79.5°; angle C, 101°; angle D, 74.5°; angle E, 43°.

Paratype, USNM 153472, a medium-size adult shell, incomplete; height, 22.1 mm.; length, 21.5 mm.; width (both valves) 15 mm.; height to midposterior break in slope at dorsal edge of primary sulcus notch, 14 mm.; height to junction of dorsal and anterior margins, 3.2 mm.; height to middle of primary sulcus at its intersection with ventroposterior margin, 22 mm.; length of a line connecting beak with center of primary sulcus notch, 22.8 mm.; length of escutcheon, 15 mm.; maximum width of escutcheon, 3 mm.; maximum width of posterior flank posterior to primary sulcus, 4.5 mm.; angle A, 92°; angle B, 80.5°; angle C, 104°; angle D, 75°; angle E, 42.5°.

Paratype, USNM 153474, incomplete large adult valves, coattached; measurements on left valve; height, 27.2 mm.; width of both valves, 16 mm.; height to midposterior break in slope, edge of primary sulcus, 10 mm.; height to junction between anterior and dorsal margins, 5 mm.; height to middle of primary sulcus at its intersection with the ventroposterior margin, 17 mm.; length of a line connecting the beak and the center of the primary sulcus notch, 20 mm.; angle B, 96°; angle C, 111°; angle D, 55°; angle E, 35°. Paratype, USNM 153476, poorly preserved, moderately large internal mold of coattached valves: height, 29.7 mm.; length, 27.7 mm.; width of both valves, 16.8 mm.; height to midposterior break in slope, 19.6 mm; height to middle of primary sulcus notch, 24.5 mm.; length of line connecting beak and middle of primary sulcus notch, 27.8 mm.; maximum width of flank posterior to primary sulcus, 4 mm.

Paratype, a medium-size adult, internal mold of coattached valves, USNM 153473: height, 24.4 mm.; length, 23.5 mm.; width of both valves, 14.3 mm.; height to midposterior break in slope, 13.6 mm.; height to junction of dorsal and anterior margins, 4 mm.; height to middle of primary sulcus notch, 20 mm.; length of line from beak to middle of primary sulcus notch, 22.1 mm.; length of escutcheon, 16.1 mm.; maximum width of escutcheon, 3.9 mm.; maximum width of flank posterior to primary sulcus, 3.8 mm.; angle A, 104°; angle B, 89°; angle C, 104°; angle D, 62°; angle E, 49°.

*Ontogeny.*—Observations on juvenile through middle adult growth stages (20 mm. and greater in height) were made by taking growth line traces at 5-mm. intervals on the holotype and paratype USNM 153472 (text fig. 18). Significant ontogenetic variation in the species is demonstrated by the marginal outline, prominence and curvature of the beaks and umbos, development of the sulci and flattened areas on the valve, and development of the lunule. The concentric ornamentation does not change significantly except for becoming somewhat coarser with increasing size of the shell.

Two basic ontogenetic changes characterize the development of the marginal outline. The juvenile and early adult growth stages (heights, 5-10 mm.) are characterized by subrounded shells without greatly projecting midanterior and midposterior margins, no anterior auricle, and with the primary sulcus and dorsoposterior margin only slightly curved (text fig. 18). During the middle adult growth stage (height, 10-20 mm.), posterior and ventral expansion accelerate, anterior growth decreases, and the valve outline becomes more ovate to subtrapezoidal, with the midposterior margin projecting and narrowly rounded. The dorsoposterior margin and primary sulcus become slightly more curved and the primary sulcus notch becomes prominent for the first time (text fig. 18). A dominance of ventral and anterior expansion over posterior growth characterize the late adult growth stages, producing a more rounded, equidimensional shell, considerable curvature of the dorsoposterior margin and primary sulcus, broadening and shallowing of the primary sulcus notch, and expansion of the dorsoanterior margin into a subtle auricle. The flattened midventral and ventroanterior margins are strictly late adult features, as is the dorsoanterior flattening of the shell flank and margin. The beak is more prosogyrate, incurved, and more projecting in large adult shells than at earlier growth stages.

The primary sulcus is slightly curved and prominent, narrow and moderately deep, in early to middle adult shells (10 to 20 mm.), and becomes gradually broader, more curved, and shallower at later growth stages. The lunule is poorly defined, flat and bounded by broad rounded ridges in all growth stages except large adults, where it becomes well defined, depressed, and bounded by narrowly rounded ridges.

*Remarks.—Thyasira cantha,* n. sp., is unique in its round outline, blunt, weakly projecting beaks, moderately rounded dorsoposterior margin, and flattened midventral, ventroanterior, and dorsoanterior margins. It appears to be most closely related to *Thyasira becca becca,* n. subsp., especially when young adult shells are compared. The mature adult shell of *T. cantha* may be distinguished from *T. becca becca,* however, by its more rounded outline, relatively higher, less convex shell, by the greater curvature of its dorsoposterior margin, its more flattened midventral, ventroanterior, and dorsoanterior margins, by the narrower, less projecting and less angular posterior flank behind the primary sulcus, and the relatively more dorsal position of the primary sulcus notch. The beaks of *T. cantha* are less projecting and more strongly prosogyrate, the anterior flattened area of the flank better defined, and the lunule smaller and better defined than on *T. becca becca.* The two species have overlapping ranges and may have been derived from a common stock. The name *cantha* is derived from the Latin *canthus,* meaning wheel, and referring to the circular outline of the mature adult shell.

*Stratigraphic position.—Thyasira cantha* occurs in the lower to middle part of the *Baculites scotti* zone, at levels A, B, and C of this report (text fig. 1). In the lower part of the *B. scotti* zone it occurs in level A at USGS Mesozoic locality 22840, Pierre Shale, Kassler Quadrangle, along the northern Front Range foothills of Colorado. At level B, *T. cantha* occurs at USGS Mesozoic locality D1216, in the Pierre Shale 2 miles northeast of Pueblo, Colorado. *T. cantha* occurs at level C in the middle part of the *B. scotti* zone at two localities: USGS Mesozoic locality D1410, in the Pierre Shale of Fall River County, South Dakota, and USGS Mesozoic locality 22838, in the Pierre Shale, Kassler Quadrangle, northern Front Range foothills, Colorado. The specimen from USGS D470 comes from middle Upper Campanian rocks with *Inoceramus vanuxemi,* probably in the zone of *B. scotti.*

*Types.*—Holotype, a moderately large adult shell with valves in normal apposition and the shell preserved: beak and umbo of the left valve slightly crushed (USGS D1216), USNM 153477; paratype, a pair of large adult valves not in normal apposition, with parts of the anterior and posterior margins missing and shell attached, (USGS D1410) USNM 153474; paratype, moderately large adult valves in normal apposition with the shell attached and much of the ventral margin missing (USGS 22840), USNM 153472; paratype, large adult valves in normal apposition, poorly preserved and partly embedded in matrix (USGS 22838), USNM 153476; paratype, moderate-size adult coattached valves, internal mold with some shell adhering (USGS 22838), USNM 153473. Measured, unillustrated paratype, internal mold of moderate-size adult with shell adhering (USGS D470), USNM 153475.

## REGISTER OF LOCALITIES

The localities and stratigraphic data listed below are cited as they appear in the catalogs of the U.S. Geological Survey Mesozoic Unit of the Paleontology and Stratigraphy Branch, and on labels accompanying specimens sent from the Geological Survey of Canada. All data supplemental to the original labels has been placed in parenthesis.

*USGS Mesozoic locality numbers:* (D = Denver office numbers; no letter preceding number = Washington office number)

D5. Lower third of the Pierre Shale (Zone of *Baculites asperiformis*), in a gully 5 miles southeast of Kassler, SE ¼ SE ¼ sec. 19, T. 7 S., R. 68 W., Kassler Quadrangle, Douglas County, Colorado. Collected by Scott, Van Horn, and Cobban, 1954.

D65. Pierre Shale (upper part of the zone of *Baculites scotti*), west side of the South Platte Valley, 1.5 miles north of Kassler, NE ¼ NE ¼ SE ¼ sec. 22, T. 6 S., R. 69 W., Littleton Quadrangle, Jefferson County, Colorado. Collected by G.R. Scott, 1954.

D255. Steele Shale (lower part of the zone of *Baculites perplexus;* early form), 4.3 miles west-southwest of the Continental Oil Company refinery at Glenrock, NW ¼ SE ¼ NE ¼ sec. 9, T. 33 N., R. 76 W., Parkerton Quadrangle, Converse County, Wyoming. Collected by W.A. Cobban, 1954.

D470. Gray-brown limestone concretions, Pierre Shale, with *Inoceramus vanuxemi,* possibly in the *Baculites scotti* zone, NW ¼, NE ¼ SW ¼ NE ¼ sec. 29, T 2 S., R. 70 W., Colorado. Collected by R. Van Horn, 1955.

D709. Gray limestone concretions in the Pierre Shale (middle of the *Baculites scotti* zone), from sec. 10, T. 20 S., R. 64 W., Pueblo County, Colorado. Collected by G.R. Scott, 1955.

D714. Pierre Shale (middle part of the *Baculites scotti* zone), from a "Tepee Butte" (in dense limestone) 0.5 miles west of the road in sec. 9. T. 20 S., R. 64 W., Pueblo County, Colorado. Collected by G.R. Scott, 1955.

D1012. From gray, sandy, "Tepee Butte" limestone in the Pierre Shale (middle part of the *Baculites scotti* zone), with *Didymoceras* sp. and about 12 feet above an occurrence of *Menuites* sp., NE ¼ NW ¼ SE ¼ sec. 35 T. 6 S., R. 69 W., Kassler Quadrangle, Douglas County, Colorado. Collected by G.R. Scott, 1956.

D1215. From gray sandy limestone concretions and "Tepee Butte" limestone masses in the Pierre Shale (lower part of the *Baculites scotti* zone), east side of a road 2 miles northeast of Pueblo, in SE ¼ NW ¼ SE ¼ sec. 16, T. 20 S., R. 64 W., Pueblo County, Colorado. Collected by G.R. Scott and W.A. Cobban, 1956.

D1216. From ironstone (siderite) concretions in the Pierre Shale (lower to middle part of the *Baculites scotti* zone), top of ridge 2 miles northeast of Pueblo, NE ¼ SE ¼ sec. 16, T. 20 S., R. 64 W., Pueblo County, Colorado. Collected by G.R. Scott and W.A. Cobban, 1956.

D1410. (Same locality as D903) From gray calcareous concretions in the Pierre Shale, 13 feet above D1409 (containing *Didymoceras* sp.), (middle part of the *Baculites scotti* zone), north side of the Cheyenne River, 4.7 miles southeast of Buffalo Gap, in the SE ¼ NW ¼ NW ¼ sec. 23, T. 7 S., R. 7 E., Buffalo Gap Quadrangle, Fall River County, South Dakota. Collected by G.R. Scott and W.A. Cobban, 1957.

D1564. "Tepee Butte" limestone mass in the Pierre Shale (zone of *Baculites perplexus;* late form), NW ¼ NE ¼ NE ¼ sec. 9, T. 6 S., R. 69 W., Littleton Quadrangle, Jefferson County, Colorado. Collected by G.R. Scott, 1957.

D1864. Pierre Shale, 30 to 60 feet above the basal bentonite of the Mitten Black Shale Member (lower part of the zone of *Baculites perplexus;* early form), from drainage divide in NE ¼ NE ¼ NE ¼ sec. 23, T. 38 N., R. 62 W., Niobrara County, Wyoming. Collected by W.A. Cobban, 1958.

D1865. Pierre Shale, 70 to 90 feet above the basal bentonite of the Mitten Black Shale Member (middle part of the zone of *Baculites perplexus;* early form), SW ¼ NE ¼ NE ¼ sec. 23, T. 38 N., R. 62 W., Niobrara County, Wyoming. Collected by W.A. Cobban and W.J. Mapel, 1958.

D1866. Pierre Shale, 695 to 714 feet above the top of the Mitten Black Shale Member (upper part of the zone of *Baculites perplexus;* early form), NE ¼ SW ¼ NE ¼ NE ¼ sec. 23, T. 38 N., R. 62 W., Redbird section, Niobrara County, Wyoming. Collected by J.R. Gill, W.J. Mapel, C.S. Robinson, and H.A. Tourtelot, 1958.

D2909. Pierre Shale, 695 feet above the base of the Mitten Black Shale Member (middle to upper part of the zone of *Baculites perplexus;* early form), S ½ NE ¼ NW ¼ SW ¼ sec. 13, T. 38 N., R. 62 W., Redbird section, Niobrara County, Wyoming. Collected by J.R. Gill, W.S. Mapel, C.S. Robinson, H.A. Tourtelot, 1958.

D2910. Pierre Shale, 878 feet above the base of the Mitten Black Shale Member (zone of *Baculites perplexus;* middle form, and *B. gilberti*), NW ¼ NW ¼ SW ¼ sec. 13, T. 38 N., R. 62 W., Niobrara County, Wyoming. Collected by W.A. Cobban, 1960.

D3256. Limestone concretions in the Steele Shale about 80 feet above the Ardmore Bentonite Bed (zone of *Baculites obtusus;* early form), highway cut in E ½ sec. 17, T. 40 N., R. 79 W., Wyoming. Collected by W.A. Cobban, 1960.

D3260. Middle part of Steele Shale, between Stray and Parkman Sandstones (zone of *Baculites obtusus;* late form), ravine in SW ¼ sec. 33, T. 39 N., R. 78 W., Wyoming. Collected by J.R. Gill, L.G. Schultz, and W.A. Cobban, 1960.

D3332. Steele Shale, about 200 feet below the base of "Kmv-1" of Weimer and Guyton (1961 Wyoming Geological Association Guidebook) (zone of *Baculites* sp. with weak flank ribs), SE ¼ SE ¼ SE ¼ sec. 1, T. 26 N., R. 89 W., Carbon County, Wyoming. Collected by A.D. Zapp, 1961.

D3933. Pierre Shale (upper part of the *Baculites scotti* zone), NE ¼ SW ¼ NW ¼ sec. 10, T. 20 S., R. 64 W., northeast Pueblo Quadrangle, Pueblo County, Colorado. Collected by G.R. Scott and Juanita Scott.

D3945. Pierre Shale (middle part of the *Baculites scotti* zone), SW ¼ SE ¼ SE ¼ sec. 29, T. 19 S., R. 64 W., Pueblo 1 Southeast Quadrangle, Pueblo County, Colorado. Collected by G.R. Scott, 1962.

D4162. Cody Shale, about 150 feet below the Parkman Sandstone (zone of *Baculites* sp. with weak flank ribs), SE ¼ sec. 1, T. 24 N., R. 83 W., Carbon County, Wyoming. Collected by J.R. Gill and R. Vaughn, 1962.

D4747. Cody Shale, 1,690 feet below the top of the formation (zone of *Baculites obtusus;* early form), SW ¼ NE ¼ sec. 14, T. 22 N., R. 79 W., Carbon County, Wyoming. Collected by J.R. Gill and Givens, 1964.

3763. (Original No. 2) Montana Group (zone of *Baculites perplexus*) in a band of limestone in shale (lower Mount Garfield Formation or upper Mancos Shale), about 1 mile southwest of the Book Cliff Mine, Book Cliff Coal Field (Mesa County), Colorado. Collected by N.D. Neal and C.D. Perrin, 1906.

3779. (Original No. 9) Montana Group (zone of *Baculites perplexus*), in lenses of sandstone and limestone in shale below the coal measures (either lower Mount Garfield Formation or uppermost Mancos Shale), 1 mile south of the mine in a bed of a ravine below the bungalow, Book Cliff Coal Field (Mesa County), Colorado. Collected by W.D. Neal, 1906.

10459. Steele Shale (zone of *Baculites* sp. with weak flank ribs), Lost Soldier-Ferris District, on state highway 46, Wyoming. Collected by Fath and C.T. Usieh, 1920.

10666. "Well up in the Pierre Shale" (zone of *Baculites obtusus*), at the water tank northwest of Horse Creek, Wyoming. Collected by W.T. Lee, 1921.

22838. Pierre Shale (middle part of the *Baculites scotti* zone), NW ¼ NW ¼ sec. 32, T. 7 S., R. 68 W., Kassler Quadrangle, northern foothills of the Front Range, Colorado. Collected by G.R. Scott, 1950.

22840. Pierre Shale (lower part of the *Baculites scotti* zone), NE ¼ NE ¼ sec. 19, T. 7 S., R. 68 W., Kassler Quadrangle, northern foothills of the Front Range, Colorado. Collected by G.R. Scott, 1950.

*Canadian localities*

1. Lea Park Formation (zone of *Baculites* sp. with weak flank ribs or lower *B. obtusus* zone), NW 11, 54, 3W4, east-central Alberta, Canada. Collected by C.O. Hage.
2. Riding Mountain Formation (probably zones of *Baculites gilberti* and *B. perplexus,* middle form; *B. perplexus,* late form; and/or *B. gregoryensis*), Assiniboine River above Qu'appelle River, Canada. Collected by J.B. Tyrrell.
3. A limestone concretion presumably from the Riding Mountain Formation (probably the zones of *Baculites gilberti* and B. *perplexus,* middle form; *B. perplexus,* late form; and/or *B. gregoryensis*), right bank of the Assiniboine River, 1 mile south of Millwood, Canada. Collected by S.R. Kirk.

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## Plate 1

All figures × 1 except figure 6 (× 2)

***Thyasira quadrula quadrula*** **Kauffman, new subspecies**

Figs. 1, 2. Right- and left-lateral views of the holotype, USNM 153470, an average-size adult valve from USGS Mesozoic locality D5, Pierre Shale, zone of *Baculites asperiformis,* Douglas County, Colorado.

***Thyasira quadrula arrecta*** **Kauffman, new subspecies**

Fig. 3. Lateral view, right valve, internal mold of a typical adult specimen showing anterior adductor muscle scar; paratype, USNM 153456, from USGS Mesozoic locality D255, Steele Shale, zone of *Baculites perplexus,* lower part, Converse County, Wyoming.

Fig. 4. Dorsal view, internal mold of a bivalved adult paratype, USNM 153440, same locality as figure 3. Note low convexity, weakly developed lunule.

Fig. 5. Lateral view, left valve of the holotype, USNM 153464, an average-size adult valve with typical ornamentation, form, and development of sulci; from USGS Mesozoic locality D1865, Pierre Shale, Mitten Black Shale Member, Niobrara County, Wyoming.

***Thyasira triangulata*** **Kauffman, new species**

Fig. 6. Lateral view of a small right valve (× 2), the holotype, USNM 153418, showing typical triangular outline, sharp erect beaks, straight primary sulcus and posterior margin, prominent flattened areas and low folds on middle of shell. USGS Mesozoic locality D65, Pierre Shale, upper part of *Baculites scotti* zone, Jefferson County, Colorado.

***Thyasira cantha*** **Kauffman, new species**

Figs. 7, 8. Lateral views, right and left valves of holotype, USNM 153477, a large adult shell with typical round outline, low, blunt, central beaks, and strongly curved posterior margin and primary sulcus; from USGS Mesozoic locality D1216, Pierre Shale, lower to middle *Baculites scotti* zone, Pueblo County, Colorado.

***Thyasira advena browni*** **Kauffman, new subspecies**

Figs. 9, 10. Dorsal and right-lateral views of the holotype, USNM 153416, an adult shell from USGS Mesozoic locality D709, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado. Shows low convexity absence of lunule, slight curvature of primary sulcus, suberect rounded beaks, and expanded dorsoanterior margin.

***Thyasira advena advena*** **Kauffman, new subspecies**

Figs. 11-13. Right-lateral, dorsal, and left-lateral views of the holotype, USNM 153417, an internal mold of an adult shell from USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Wyoming. Specimen shows typical high convexity, well-defined lunule, moderately prosogyrate beaks and umbos, curved primary sulcus, and trace of anterior adductor muscle scar.

***Thyasira rostrata cracens*** **Kauffman, new subspecies**

Figs. 14-16. Left-lateral, right-lateral, and dorsal views of the holotype, USNM 153429, a moderate-size adult shell typical of the species, exhibiting especially well the moderate convexity, weakly defined lunule, moderately projecting beaks, and somewhat expanded anterodorsal flank compared to *T. rostrata rostrata* (figs. 17, 18). From USGS Mesozoic locality D1864, Pierre Shale, Mitten Black Shale Member, lower part of the zone of *Baculites perplexus,* Niobrara County, Wyoming.

***Thyasira rostrata rostrata*** **Kauffman, new subspecies**

Fig. 17. Lateral view of a large left valve, the holotype, GSC 18757, typical of the species except for slightly greater than normal expansion of the anterior auricle. From the Lea Park Formation, probably the zone of *Baculites* sp. with weak flank ribs or the lower *B. obtusus* zone, east-central Alberta, Canada.

Fig. 18. Dorsal view, internal mold of a large adult shell showing well-defined lunule, escutcheon, and great convexity compared to *T. rostrata cracens* (fig. 16). A paratype, USNM 153482, from USGS Mesozoic locality D4162, Cody Shale, zone of *Baculites* sp. with weak flank ribs, Carbon County, Wyoming.

***Thyasira beauchampi rex*** **Kauffman, new subspecies**

Fig. 19. Lateral view of a juvenile left valve, a paratype, USNM 153410, from USGS Mesozoic locality 10666, upper Pierre Shale, zone of *Baculites obtusus,* Wyoming. Expanded dorsoanterior flank and mid-posterior position of primary sulcus notch even at this stage of development are well illustrated.

Figs. 20, 21. Dorsal and left-lateral views of the holotype, USNM 153411, a small adult valve showing characteristic features of the subspecies except that anterior sulcus has not yet developed. Locality as figure 19.

Figs. 22, 23. Right-lateral and dorsal views of the largest adult valve, a paratype, USNM 153409, showing weakly defined anterior sulcus, depressed beak and umbo, expanded anterodorsal flank, and relatively high position of intersection between posterior margin and primary sulcus. From USGS Mesozoic locality 3779, upper Mancos Shale or lower Mount Garfield Formation, zone of *Baculites perplexus* (early form), Mesa County, Colorado.

***Thyasira beauchampi beauchampi*** **Kauffman, new subspecies**

Figs. 24-26. Right-lateral, dorsal, and left-lateral views of a typical large adult shell, the holotype, USNM 153412, from USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Compare with figures 22, 23, the narrow erect beaks, steeply sloping anterodorsal margin, prominent anterior sulcus, and posteroventral position of the primary sulcus notch.

***Thyasira becca becca*** **Kauffman, new subspecies**

Figs. 27, 30. Lateral views, right and left valves of the holotype, USNM 153512, a medium-size adult valve with slightly more depressed beak than typical for the species at this stage of development. From USGS Mesozoic locality D1410, Pierre Shale, middle *Baculites scotti* zone, Fall River County, South Dakota.

Fig. 29. Lateral view, left valve, internal mold of a large adult valve showing characteristic development of beak, dorsoanterior flank, sulci, and radial ridges (shown as depressions) at this stage of development. Compare with figure 28. Paratype, USNM 153518, from USGS Mesozoic locality D709, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado.

***Thyasira becca cobbani*** **Kauffman, new subspecies**

Fig. 28. Lateral view, right valve of the holotype, GSC 18758, a large adult shell showing strongly prosogyrate beaks and umbos, deep notch below beaks, projecting angulated anterior auricle, faint anterior sulcus, and midposterior position of primary sulcus notch. From the Riding Mountain Formation on the Assiniboine River, Canada, probably between the zones of *Baculites gilberti* and *B. gregoryensis.*

## Plate 2

All figures × 1

***Thyasira rostrata rostrata*** **Kauffman, new subspecies**

Figs. 1-3. Right-lateral, dorsal, and left-lateral views, internal mold of a paratype, a small adult, USNM 153493, USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Wyoming.

Fig. 4. Lateral view, left valve, small adult internal mold with well-defined submarginal sulcus and small auricle, paratype, USNM 153504, from USGS Mesozoic locality D4162, Cody Shale, zone as figures 1-3, Carbon County, Wyoming.

Figs. 5, 7. Right- and left-lateral views, respectively, internal mold of coattached valves, a paratype, USNM 153502, locality and zone as figure 4.

Figs. 6, 15, 16. Dorsal, right-lateral, and left-lateral views, respectively, as well-preserved internal mold of coattached adult valves, a paratype, USNM 153490, USGS Mesozoic locality D3256, Steele Shale, zone of *Baculites obtusus,* early form, Wyoming. Note well-defined lunule, radial interior ornament, and unusually expanded dorsoanterior flank.

Figs. 8, 10. Right-lateral and left-lateral views, internal mold of coattached, typical adult valves, paratype, USNM 153495, locality and zone as in figures 1-3.

Figs. 9, 14. Dorsal and right-lateral views, internal mold of coattached adult valves, anteroventral margin broken; paratype, USNM 153487, from USGS Mesozoic locality D4162, Cody Shale, zone of *Baculites* sp. with weak flank ribs, Carbon County, Wyoming. Specimen exhibits strong convexity, prominent lunule, and well-defined anterior adductor insertion area (fig. 14).

Fig. 11. Lateral view, internal mold of right valve, an adult paratype faintly showing the adductor insertion areas, USNM 153494, from same zone and locality as figures 1-3.

Fig. 12. Dorsal view of coattached adult valves showing strong convexity, paratype, USNM 153507, from same zone and locality as figures 9, 14.

Fig. 13. Lateral view, right valve of an adult paratype, USNM 153506, USGS Mesozoic locality D3256, Steele Shale, zone of *B. obtusus,* early form, Wyoming. Inner shell layer preserved only; pallial line well defined and anterior sulcus producing notch in margin.

Figs. 17, 18. Right-lateral and left-lateral views, internal mold of a typical moderate-size adult shell, paratype, USNM 153488, locality and zone as in figures 9, 14. Specimen shows faint pallial line, radial internal ornament, well-defined anterior and faint posterior adductor insertion areas, and faint anterior sulcus and notch.

Figs. 19-21. Right-lateral, left-lateral, and dorsal views respectively of an internal mold, coattached adult valves, showing abnormally reduced beaks, umbos, clearly defined muscle insertion areas and pallial line; paratype, USNM 153484, locality and zone same as figures 1-3.

Figs. 22, 23. Right-lateral and left-lateral views of a large, typical, internal mold of an adult shell; paratype, USNM 153482, locality and zone as in figures 9, 14, showing well-defined muscle insertion areas, pallial line, separation between anterior adductor insertion area and pallial line, small posterior auricle, and faint dorsoanterior notch at intersection with shallow anterior sulcus.

Figs. 24, 25, 27. Right-lateral, dorsal, and left-lateral views, respectively, internal mold of the largest adult shell with the inner shell layer mostly intact; paratype, USNM 153483, USGS Mesozoic locality D3332, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Carbon County, Wyoming. Specimen exhibits typical outline, great convexity, prominent lunule, shallow anterior sulcus and dorsoanterior marginal notch.

Fig. 26. Lateral view, internal mold of a typical adult left valve; paratype, USNM 153481, locality and zone as in figures 9, 14, with well-defined anterior adductor insertion area and dorsoanterior sulcus notch.

Fig. 30. Lateral view, left valve of a large adult preserving the shell and showing typical ornamentation of close, coarse growth lines. Paratype, GSC 18759, from the Lea Park Formation, east-central Alberta, Canada.

### ***Thyasira beauchampi beauchampi*** **Kauffman, new subspecies**

Fig. 28. Lateral view, internal mold of a right valve, part of coattached pair, with ventroanterior margin broken; paratype, USNM 153413, from USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Faint axial fold and posterocentral flattened area between it and primary sulcus developed on specimen.

Fig. 29. Lateral view, right valve, internal mold of coattached pair, ventroposterior margin broken; paratype, USNM 153415, from the same locality and level as figure 28, showing faintly defined anterior adductor insertion area.

Figs. 31-33. Dorsal, left-lateral, and right-lateral views, respectively, of a bivalved internal mold, a moderate-size adult; paratype, USNM 153414, from the same locality and zone as figure 28. Mold typical of subspecies; with well-defined dorsoanterior sulcus notch, weakly defined lunule.

## Plate 3

All figures × 1

***Thyasira rostrata rostrata*** **Kauffman, new subspecies;** marginal variants possibly transitional with the lineage of *T. quadrula,* new species.

Figs. 1, 2. Right-lateral and left-lateral views, internal mold of a small adult shell; paratype, USNM 153497, from USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Depressed beak, expanded dorsoanterior flank, truncate ventral margin, and slightly curved posterior margin of this and other specimens suggest affinities with the *T. quadrula* lineage.

Fig. 3. Lateral view of left valve, internal mold of coattached valves; paratype, USNM 153485, locality and zone as in figures 1, 2. Shows similarity to *T. quadrula* in expansion of dorsoanterior flank; curved posterior margin and sulcus distinguishes it from the *T. quadrula* lineage.

Fig. 4. Lateral view, right valve of a coattached pair, internal mold; paratype, USNM 153486, locality and zone as in figures 1, 2.

Figs. 5, 6. Right-lateral and left-lateral views, internal mold of coattached valves with greatly reduced beak compared to normal individuals. Paratype, USNM 153498, locality and zone as in figs. 1, 2.

***Thyasira rostrata rostrata*** **Kauffman, new subspecies,** variants of this subspecies transitional to *T. rostrata cracens,* new subspecies.

Fig. 7. Right-lateral view, internal mold of coattached valves with unusually coarse concentric undulations; paratype, USNM 153505. Specimen exhibits affinities to the subspecies *cracens* in regard to the narrow, erect shell, reduction of dorsoanterior flank (partially broken), and more erect beaks and umbos. Note also prominent adductor insertion areas and pallial line.

Figs. 8, 9. Right-lateral and left-lateral views of an adult, internal mold of coattached valves; paratype, USNM 153499, USGS Mesozoic locality 10459, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Lost Soldier-Ferris District, Wyoming. Expanded dorsoanterior flank well defined; compare with typical adult *T. rostrata cracens* in figures 19-31.

Fig. 10. Lateral view, right valve of coattached pair, internal mold; a paratype, USNM 153500, from USGS Mesozoic locality D3332, Steele Shale, zone of *Baculites* sp. with weak flank ribs, Carbon County, Wyoming. Specimen has reduced, rounded beak and well-defined anterior adductor insertion area.

Fig. 11. Lateral view, right valve of coattached pair, internal mold showing well-defined muscle insertion areas, high erect shell as found in the subspecies *cracens;* paratype, USNM 153492, locality and zone as in figure 10.

***Thyasira rostrata cracens* Kauffman, new subspecies**

Figs. 12, 13. Right-lateral and left-lateral views of coattached valves, a juvenile without the dorsoanterior flank expanded as in adults, and showing characteristic ornamentation; paratype, USNM 153427, from USGS Mesozoic locality 3779, lower Mount Garfield Formation or upper Mancos Shale, zone of *Baculites perplexus,* Mesa County, Colorado.

Figs. 14-16. Right-lateral, dorsal, and left-lateral views, respectively, of a typical small adult shell with expanded dorsoanterior flank, reduced beaks, and straight posterior margin. Note that outline still resembles the subspecies *rostrata* in regard to height-length ratio at this growth stage. Paratype, USNM 153428, locality and zone as in figures 12, 13.

Fig. 17. Lateral view, right valve of coattached pair, internal mold, typical small adult; paratype, USNM 153434, USGS Mesozoic locality D255, Steele Shale, lower part, zone of *Baculites perplexus* (early form), Converse County, Wyoming.

Fig. 18. Lateral view, left valve of coattached pair, internal mold, ventroposterior margin broken; paratype, USNM 153435, USGS Mesozoic locality D3260, Steele Shale, zone of *Baculites obtusus* (late form), Wyoming.

Figs. 19, 20. Right-lateral and left-lateral views, coattached valves, internal mold, typical moderate-size adult except for trace of anterior sulcus (a *T. rostrata rostrata* character); coarse concentric undulations well defined. Paratype, USNM 153426, locality and zone as in figure 17.

Figs. 21, 22. Right-lateral and left-lateral views, coattached valves, internal mold, moderate-size adult shell with abnormally truncated ventral margin, well-defined pallial line, posterior auricle, anterior adductor insertion area, and medial flattened area. Paratype, USNM 153433, locality and zone as in figure 17.

Fig. 23. Lateral view, right valve of coattached pair, typical erect adult shell with well-defined anterior adductor insertion area, coarse shell sculpture; paratype, USNM 153437, locality and zone as in figure 17.

Fig. 24. Lateral view, left valve of coattached pair, internal mold with part of dorsoanterior margin broken, but showing erect adult form; paratype, USNM 153436, locality and zone as in figure 17. Specimen with well-defined posterior auricle, submarginal sulcus, medial low fold and flattened area posterior to it.

Figs. 25, 26. Right-lateral and left-lateral views, internal mold of coattached valves, adult with characteristic features, well-defined pallial line; paratype, USNM 153425, locality and zone as in figure 17.

Figs. 27-29. Right-lateral, dorsal, and left-lateral views, respectively, internal mold of coattached adult valves characteristic of subspecies; paratype, USNM 153424, locality and zone as in figure 17. Posterior auricle, submarginal sulcus, and reflection of interior shell markings are well defined. In comparison with typical *T. rostrata rostrata,* note weakly defined lunule, relatively low convexity of valves, erect posture and reduced beaks.

Fig. 30. Lateral view, right valve of coattached pair, internal mold, with characteristic adult outline, shell ornamentation on isolated adhering patches. Paratype, USNM 153432, USGS Mesozoic locality D1866,

Pierre Shale, middle of *Baculites perplexus* (early form) zone, Niobrara County, Wyoming.

Figs. 32-34. Right-lateral, dorsal, and left-lateral views, respectively, of a typical, well-preserved, large adult shell; paratype, USNM 153420, locality and zone as in figure 17. Specimen shows characteristic outline with depressed suberect beaks and umbos, expanded dorsoanterior flank, relatively moderate convexity, poorly defined lunule, and subregular surface ornamentation.

***Thyasira triangulata* Kauffman, new species**

Figs. 31, 35. Right-lateral and left-lateral views of the largest adult shell, crushed and poorly preserved, but showing straight posterior margin and primary sulcus, faint concentric ornament, pointed erect beaks, and subtriangular outline; paratype, USNM 153419, USGS Mesozoic locality D3933, Pierre Shale, upper part of the *Baculites scotti* zone, Pueblo County, Colorado.

***Thyasira cantha* Kauffman, new species**

Figs. 36-38. Left-lateral, right-lateral, and dorsal views, respectively, moderate size, incomplete, bivalved adult shell typical of the species. Paratype, USNM 153472, USGS Mesozoic locality 22840, Pierre Shale, lower *Baculites scotti* zone, Kassler Quadrangle, Colorado. Specimen exhibits rounded outline, strongly curved posterior margin and primary sulcus, and depressed, strongly prosogyrate beaks.

Figs. 39, 40. Right-lateral and left-lateral views of a pair of incomplete, large adult valves. Specimen shows strongly curved posterior margin, sulcus, and reduced, strongly prosogyrate beaks typical of species. Angulate nature of expanded dorsoanterior flank not characteristic (fig. 39). Paratype, USNM 153474, USGS Mesozoic locality D1410, Pierre Shale, middle *Baculites scotti* zone, Fall River County, South Dakota.

Fig. 41. Lateral view, left valve of coattached pair, inner shell layer adhering to internal mold, showing characteristic rounded outline, curved posterior margin and sulcus, and low prosogyrate beaks. Paratype, USNM 153473, USGS Mesozoic locality 22838, Pierre Shale, middle *Baculites scotti* zone, Kassler Quadrangle, Colorado.

## Plate 4

All Figures × 1

***Thyasira becca becca* Kauffman, new subspecies**

Figs. 1, 2. Right-lateral and left-lateral views of a moderate-size adult showing characteristic outline and surface ornamentation; paratype, USNM 153510, from USGS Mesozoic locality D1410, Pierre Shale, middle of the *Baculites scotti* zone, Fall River County, South Dakota.

Fig. 3. Lateral view, left valve of coattached pair showing characteristic ornamentation, outline, radial markings of shell interior; paratype, USNM 153511, from same locality and zone as figures 1, 2.

Figs. 4, 5. Right-lateral and left-lateral views of coattached adult valves, a marginal variant of the population transitional to *T. cantha* in having small depressed beaks and in the general marginal outline; margin incomplete in area of primary sulcus notch and along dorsoanterior border. Paratype, USNM 153514; USGS Mesozoic locality 22840, Pierre Shale, lower *Baculites scotti* zone, Kassler Quadrangle, Colorado.

Figs. 6-8. Right-lateral, dorsal, and left-lateral views, respectively, internal mold of coattached valves, a moderate-size adult shell characteristic of the subspecies. Specimen exhibits typical outline, blunt prosogyrate beaks, broad fold posterior to moderately curved primary sulcus, low convexity, poorly defined lunule, and well-defined pallial line and anterior adductor insertion area. Paratype, USNM 153516, locality and zone as in figures 1, 2.

Fig. 9. Lateral view, left valve of coattached pair, internal mold of a typical moderate-size adult shell showing well-defined posterior adductor insertion area; paratype, USNM 153513, locality and zone as in figures 1, 2.

Figs. 10, 11. Right-lateral and left-lateral views of coattached valves with the beak area crushed downward and abnormally depressed. Specimen shows the well-defined concentric ornamentation, traces of the radial interior ridges, typical primary sulcus and well-developed fold posterior to it. Paratype, GSC 18760, from the Riding Mountain Formation on the Assiniboine River, Canada.

Figs. 12, 13. Right-lateral and left-lateral views, internal mold of typical coattached adult valves showing characteristic outline at this growth stage and reflection of interior shell markings. Paratype, USNM 153519, USGS Mesozoic locality D709, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado.

Figs. 14, 21. Right-lateral and left-lateral views of coattached valves, internal mold with part of shell adhering; paratype, USNM 153517, USGS Mesozoic locality D1216, Pierre Shale, lower to middle *Baculites scotti* zone, Pueblo County, Colorado. This is a variant of *T. becca becca* transitional to *T. cantha*, n. sp., in regard to curvature of the posterior margin and width of the fold or flank posterior to the primary sulcus.

Figs. 15, 16. Right-lateral and dorsal views, internal mold of coattached valves, characteristic of the subspecies in outline, convexity, development of beaks, sulci, lunule, and interior shell markings. Note well-defined pallial line. Paratype, USNM 153518, locality and zone as in figures 12, 13.

Fig. 17. Lateral view, left valve of coattached pair with ventroanterior and ventroposterior margins slightly broken to give rounded outline. Note characteristic ornamentation. Paratype, USNM 153515, locality and zone as in figures 12, 13.

Figs. 18-20. Right-lateral, dorsal, and left-lateral views, respectively, internal mold of a large, typical adult shell. Specimen exhibits poorly defined lunule bordered by two low folds, well-defined pallial line, and posterior adductor insertion area (fig. 20). Paratype, USNM 153522, USGS Mesozoic locality D714, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado,

## Plate 5

All Figures × 1

***Thyasira quadrula quadrula*** **Kauffman, new subspecies**

Figs. 1, 2. Right-lateral and left-lateral views of a small adult shell, valves in normal apposition, characteristic of the subspecies in outline, ornamentation, development of the beaks, straight primary sulcus and posterior margin, and expanded dorsoanterior flank. Paratype, USNM 153469, USGS Mesozoic locality D5, Pierre Shale, *Baculites asperiformis* zone, Douglas County, Colorado.

Fig. 3. Lateral view, right valve, poorly preserved internal mold of a typical, moderate-size adult shell; paratype, USNM 153468, locality and zone as in figures 1, 2.

Fig. 4. Lateral view, right valve of coattached pair, internal mold of the largest adult shell with characteristically depressed blunt beaks, subquadrate outline, straight posterior margin and primary sulcus, and expanded dorsoanterior margin; paratype, USNM 153467, locality and zone as in figures 1, 2.

Fig. 5. Lateral view, incomplete right valve with ventral margin broken off, showing typical outline and fine concentric exterior ornamentation; paratype, USNM 153466, USGS Mesozoic locality 10666, Pierre Shale, *Baculites obtusus* zone, northwest of Horse Creek, Wyoming.

***Thyasira quadrula arrecta*** **Kauffman, new subspecies**

Figs. 6, 7. Right-lateral and left-lateral views, internal mold of coattached juvenile valves with typical early characters of subspecies. Note especially greater projection of beak compared to the subspecies *quadrula*. Paratype, USNM 153458, USGS Mesozoic locality D255, Steele Shale, lower *Baculites perplexus* (early form) zone, Converse County, Wyoming.

Fig. 8. Lateral view, right valve, a juvenile shell with characters more closely resembling the subspecies *quadrula* than subspecies *arrecta* (broad apical angle, depressed beaks), a marginal variant of an *arrecta* population; paratype, USNM 153459, USGS Mesozoic locality D1012, Pierre Shale, middle *Baculites scotti* zone, Douglas County, Colorado.

Figs. 9, 10. Right-lateral and left-lateral views, internal mold of coattached young adult valves; paratype, USNM 153441, locality and zone as in figures 6, 7. Medial flattened area, straight posterior margin and sulcus, and fine interior radial lines characteristic of the subspecies are well illustrated here.

Figs. 11, 14, 15. Dorsal, right-lateral, and left-lateral views, respectively, coattached valves of a small adult, internal mold; paratype, USNM 153446, locality and zone as in figures 6, 7. Specimen shows low convexity, poorly defined lunule, erect projecting pointed beaks, and interior sculpture typical of the subspecies.

Figs. 12, 13. Right-lateral and left-lateral views of coattached valves; a small adult showing characteristic form, exterior morphology, and surface sculpture of the subspecies. Compare with subspecies *quadrula* at same size in figures 1, 2. Paratype, USNM 153454, USGS Mesozoic locality D1865, Pierre Shale, middle *Baculites perplexus* (early form) zone, Niobrara County, Wyoming.

Fig. 16. Lateral view, left valve, internal mold of a coattached pair; paratype, USNM 153460, from USGS Mesozoic locality D714, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado. This marginal variant resembles the older subspecies *quadrula* in the expanded anterodorsal margin and slightly projecting beak.

Figs. 17, 18. Right-lateral and left-lateral views, internal mold of coattached valves; a characteristic moderate-size adult specimen; paratype USNM 153442 locality and zone as in figures 6, 7.

Fig. 19. Lateral view, left valve, internal mold of coattached pair, a medium-size adult characteristic of the subspecies except for blunt beak; paratype, USNM 153445, locality and zone as in figures 6, 7.

Figs. 20-22. Right-lateral, dorsal, and left-lateral views, respectively, of a typical moderate-size adult shell; paratype, USNM 153455, locality and zone as in figures 12, 13, showing characteristically coarse uneven concentric growth lines, suberect projecting beaks, relatively straight anterior and posterior margins, poorly defined lunule, moderate convexity, and height to length relationship.

Figs. 23, 24. Right-lateral and left-lateral views of the largest adult shell with posterior margin broken off; paratype, GSC 18761, from the Riding Mountain Formation?, Assiniboine River, Canada. Note the unusually developed anterior sulcus and notched dorsoanterior margin.

Fig. 25. Lateral view, incomplete left valve of a coattached pair, a moderate-size adult shell with typical surface sculpture and quadrate outline; paratype, USNM 153457, USGS Mesozoic locality D1866, Pierre Shale, upper *Baculites perplexus* (early form) zone, Niobrara County, Wyoming.

Fig. 26. Lateral view, internal mold of a left valve with the beak broken off, part of coattached pair characteristic of subspecies. Pallial line and anterior adductor insertion area are well defined. Paratype, USNM 153440, locality and zone as in figures 6, 7.

Fig. 27. Lateral view, left valve, internal mold of coattached pair typical of subspecies. Specimen illustrates adductor insertion areas and pallial line. Paratype, USNM 153456, locality and zone as in figures 6, 7.

### *Thyasira becca becca* Kauffman, new subspecies

Figs. 28-30. Right-lateral, dorsal, and left-lateral views, respectively, of a young adult shell with atypically expanded dorsoanterior flank but otherwise characteristic of the subspecies; paratype, USNM 153525, USGS Mesozoic locality D1410, Pierre Shale, middle *Baculites scotti* zone, Fall River County, South Dakota.

Fig. 31. Lateral view, right valve, internal mold of coattached pair, early adult specimen with typical characters. Beak depressed at this growth stage. Paratype, USNM 153509, USGS Mesozoic locality D709, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado.

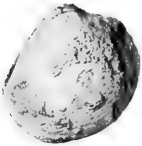
Figs. 32, 33. Right-lateral and left-lateral views, internal mold of coattached valves typical of early adult growth stage in all respects. Paratype, USNM 153521, locality and zone as in figures 28-30.

Fig. 37. Lateral view, left valve, internal mold of coattached pair with pieces of shell adhering and beaks somewhat blunter than normal at this growth stage; paratype, USNM 153520, locality and zone as in figures 28-30.

Fig. 38. Lateral view, incomplete left valve of coattached pair showing characteristic adult ornamentation, development of primary sulcus and flank posterior to it; paratype, USNM 153524, USGS Mesozoic locality 22840, Pierre Shale, lower *Baculites scotti* zone, Kassler Quadrangle, Douglas County, Colorado.

***Thyasira becca cobbani* Kauffman, new subspecies**

Figs. 34-36. Right-lateral, dorsal, and left-lateral views, respectively, of a crushed, incomplete bivalved paratype, USNM 153478, from USGS Mesozoic locality D709, Pierre Shale, middle *Baculites scotti* zone, Pueblo County, Colorado. Strongly prosogyrate beaks and umbos, auriculate dorsoanterior flank, elongate shell, and fine growth lines characteristic of the subspecies are well defined.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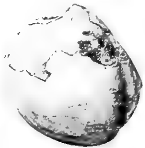
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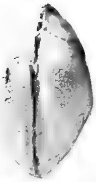
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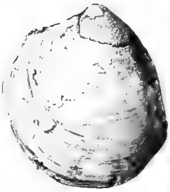
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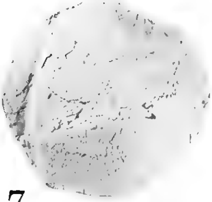
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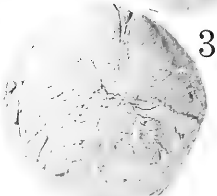
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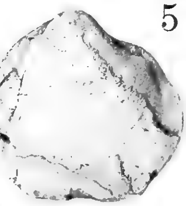
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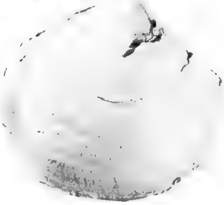
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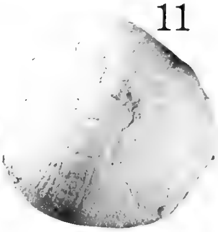
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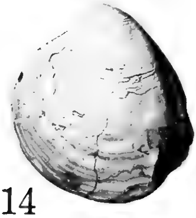
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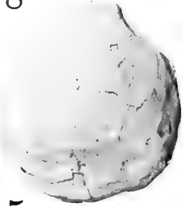
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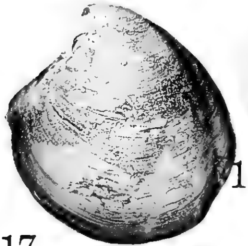
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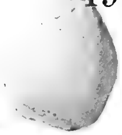
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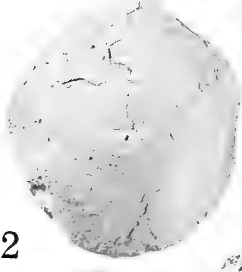
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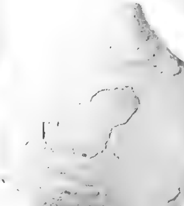
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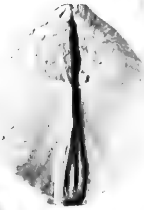
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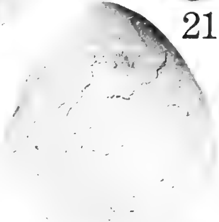
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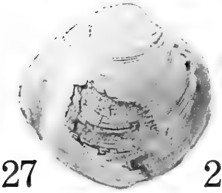
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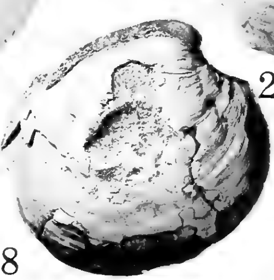
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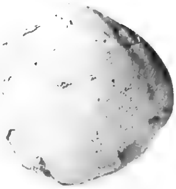
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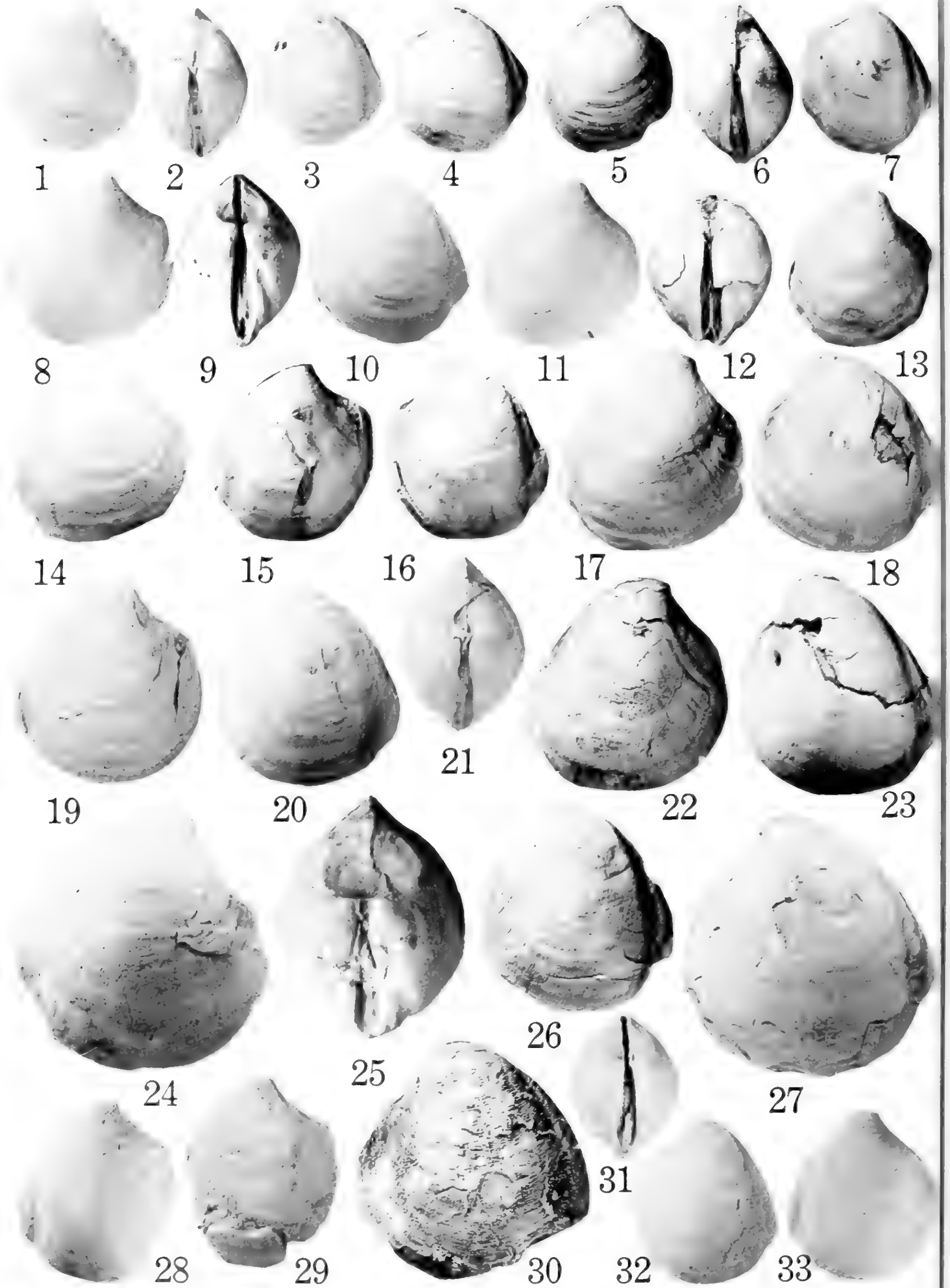
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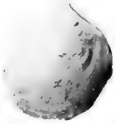
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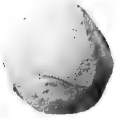
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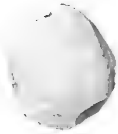
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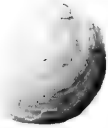
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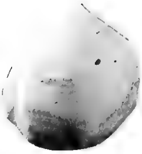
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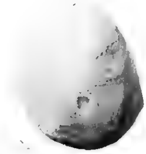
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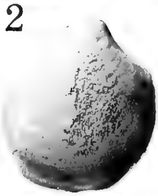
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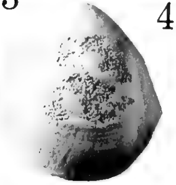
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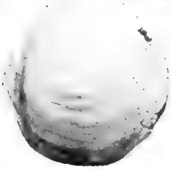
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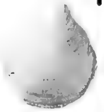
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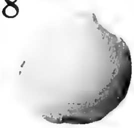
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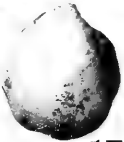
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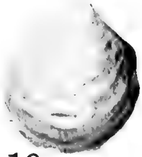
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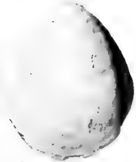
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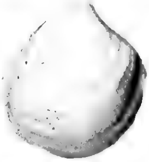
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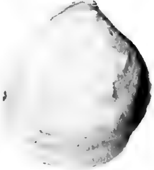
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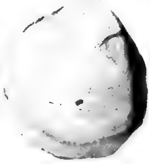
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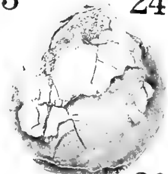
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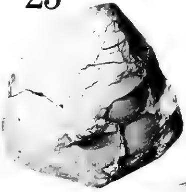
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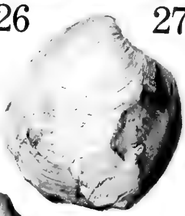
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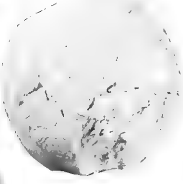
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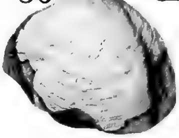
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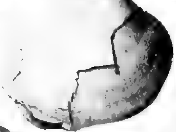
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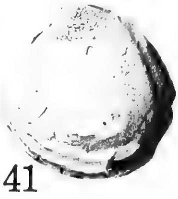
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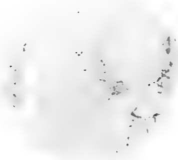
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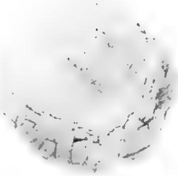
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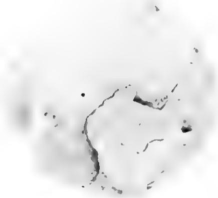
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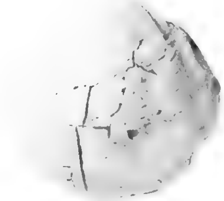
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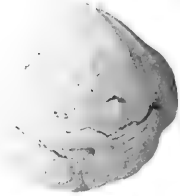
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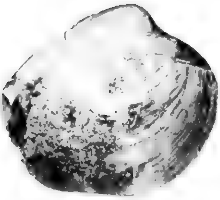
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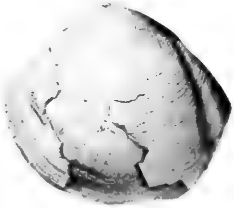
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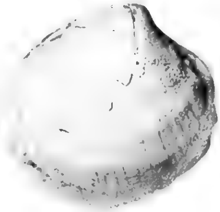
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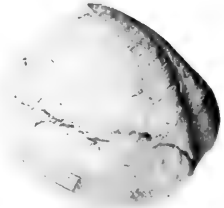
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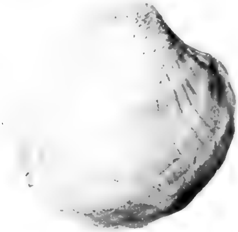
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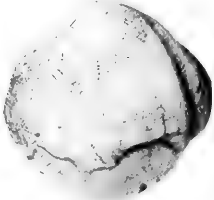
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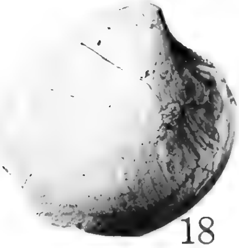
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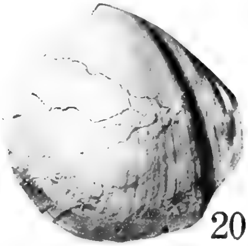
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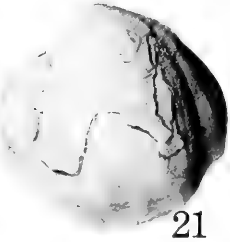
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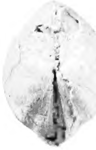
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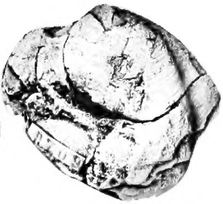
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