Journal of Paleontology, 86(4), 2012, p. 595–604

0022-3360/12/0086-0595$03.00

EARLY ORDOVICIAN MITRATES AND A POSSIBLE SOLUTE (ECHINODERMATA) FROM THE WESTERN UNITED STATES

COLIN D. SUMRALL,[1] JAMES SPRINKLE,[2] THOMAS E. GUENSBURG,[3] AND BENJAMIN F. DATTILO[4]

[1]Department of Earth and Planetary Sciences, University of Tennessee, Knoxville 37996-1410, USA, <csumrall@utk.edu>; [2]Department of Geological Sciences, Jackson School of Geosciences, University of Texas, Austin 78712-0254, USA, <echino@mail.utexas.edu>; [3]Physical Science Division, Rock Valley College, Rockford, Illinois 61114, USA, <t.guensburg@rockvalleycollege.edu>; and [4]Department of Geosciences, Indiana University–Purdue University Fort Wayne, Fort Wayne, Indiana 46805, USA, <dattilob@ipfw.edu>

ABSTRACT—Two new kirkocystid mitrate stylophorans (Echinodermata, Homalozoa) and a new possible solute (Echinodermata, Homalozoa) are described from the Early Ordovician of the western United States. The mitrates are among the earliest members of their clade to appear near the beginning of the Ordovician Radiation. *Anatifopsis ninemilensis* new species comes from the Ninemile Shale in central Nevada and the McKelligon Canyon Formation in west Texas. *Anatifopsis fillmorensis* new species comes from the middle Fillmore Formation in western Utah and a Ninemile Shale equivalent limestone bed in southern Nevada. The possible solute *Drepanocystis dubius* new genus new species from the lower Wah Wah Limestone in western Utah, shows unusual morphology with an elongate theca and a long arm shaped like a sickle.

INTRODUCTION

ALTHOUGH THE kirkocystid mitrate *Anatifopsis* is among the most common and successful stylophorans in the Ordovician, to date none have been described from the western United States. This genus is known from deposits ranging throughout the Ordovician from the Tremadocian to the Hirnantian with species recorded from various parts of Laurentia, Perigondwanan Europe, North Africa, and Korea (Lee et al., 2004; Lefebvre et al., in press). Presently, none are recorded from Baltica. Here we describe two new species of *Anatifopsis* and a very unusual possible solute from Early Ordovician faunas from Nevada and Utah, with a few additional mitrate specimens included from the McKelligon Canyon Formation in west Texas. Unlike most of the crinoids, eocrinoids, parablastoids, and edrioasteroids in these faunas, which attached to hard substrates such as hardgrounds and lithified mounds, these homalozoan groups were free-living on soft muddy or micritic sediments.

Early Ordovician echinoderm faunas from the Fillmore Formation, Wah Wah Limestone, and Ninemile Shale show previously unexpected levels of diversity. These faunas indicate that the Ordovician echinoderm radiation was well under way earlier than formerly expected including: edrioasteroids (Guensburg and Sprinkle, 1994), eocrinoids (Sumrall et al., 2001), protocrinoid, camerate, and disparid crinoids (Guensburg and Sprinkle, 2003; Guensburg, 2010), asteroids (Blake and Guensburg, 2005; Blake et al., 2007), and parablastoids (Sprinkle and Sumrall, 2008). Further information on the depositional environments, collection, distribution, diversity, and evolutionary history of the echinoderms in these faunas can be reviewed in Guensburg and Sprinkle (1992, 2000, 2001, 2003), Sprinkle and Guensburg (1995, 1997) and Sprinkle et al. (2008).

PREVIOUS WORK

Kirkocystid mitrate stylophorans are the most abundant and diverse clade of peltocystid mitrates found throughout Europe, Korea, North America, and Morocco (for a review see Parsley, 1991; Lee et al., 2004; and Lefebvre, 2007). The general morphology of kirkocystids is congruent with other mitrate stylophorans. The main body comprises a small, globular to flattened theca with distinctly different surfaces. The upper surface is domed and convex, dominated by two large adoral plates. The lower surface is flat to slightly concave with the edges of the adorals and several additional smaller plates. These plates largely overlap and some are not visible from the thecal exterior but can be seen in serial sections and disarticulated material (Jefferies, 1981, 1986; Lefebvre, 1999, 2001, 2003). The aulacophore appendage is tripartite with a highly flexible proximal region, a stylocone interpreted as the position of the mouth, and a distal feeding portion with uniserial ossicles and biserial cover plates. At the opposite end of the theca is a single, small, movable spine.

The western U.S. kirkocystid fauna was included in the Lower to Middle Ordovician kirkocystid biofacies by Lefebvre (2007). Localities where these specimens occur, however, vary widely in their depositional environment. The Ninemile Shale was deposited on the outer shelf in deep water below storm wave base. Although echinoderms and echinoderm fragments are generally in low abundance in the Ninemile Shale, kirkocystids are among the most common elements of this fauna. In contrast, the Fillmore Formation was deposited in shallow water environment associated with storm beds. Kirkocystids include isolated specimens buried by obrution events as well as small storm beds made of disarticulated plates in high abundance. Similarly, material from "Unit O_{pd}" in the Arrow Canyon Range includes numerous specimens preserved in a storm bed that is a 2.5 to 3 cm thick kirkocystid grainstone. The McKelligon Canyon Formation has produced only a few complete specimens and one small slab of plates but appears to be similar to the Fillmore Formation in having a generally shallow depositional environment.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE

The specimens reported in this paper come from three different geographic areas and four zones in the Early Ordovician. About 20 mitrate specimens along with several slabs of fragments (Sprinkle and Guensburg, 1995, fig. 10) have been collected from seven localities of the Fillmore Formation in the Ibex area of western Utah. These mitrates come from near the middle of the Fillmore Formation in Zones G-1 and G-2 (*Hintzeia celsaora* and *Protopliomerella contracta* Zones) which are middle Ibexian (latest Tremadocian to early Floian or Arenigian) in age. The possible solute was collected in the overlying basal Wah Wah Limestone in

Zone J (*Pseudocybele nasuta* Zone) which is latest Ibexian (late Floian or middle Arenigian) in age.

About 400 mitrate specimens come from the Ninemile Shale of central and southwestern Nevada and an equivalent unit in southern Nevada. About 30 specimens have been found fairly high in this formation at two nearby central Nevada localities in the Monitor Range and are from Zone J (*Pseudocybele nasuta* Zone); one specimen collected from a southwestern Nevada Ninemile locality has also been dated as Zone J. A large slab with abundant mitrates was collected along a measured section of a unit equivalent to the Ninemile Shale at a locality in the Arrow Canyon Range in southern Nevada (Langenheim et al., 1962). This shell bed is a mitrate grainstone up to 3 cm thick developed as a possible megaripple. At least 365 mitrates, some with nearly complete attached aulacophores, and a single ophiuroid were exposed on the shaley but highly lithified top surface of this grainstone bed. This bed also appears to be from Zone J (*Pseudocybele nasuta* Zone) so that all of these Ninemile and equivalent occurrences are latest Ibexian (late Floian or middle Arenigian) in age.

Two mitrates and a small slab of adoral plates were found at a single locality on the north side of El Paso, west Texas, in the upper McKelligon Canyon Formation of the El Paso Group from Zones G-2 and H (*Protopliomerella contracta* and *Trigonocerca typica* Zones). This part of the formation is considered to be of middle-late Ibexian (early Floian or Arenigian) age.

TEMPORAL AND PALEOBIOGEOGRAPHICAL SIGNIFICANCE

Anatifopsis ninemilensis and *A. fillmorensis* are among the earliest kirkocystids known. They seem closely related to the kirkocystid *Anatifopsis trapeziiformis* from the late Tremadocian to middle Arenigian of Montagne Noire, southern France, and Shropshire, U.K. (B. Lefebvre, personal commun., 2007). The earliest known mitrate (originally described as a cornute) is now considered to be *Lobocarpus vizcainoi* Ubaghs, 1998 from the Furongian of the Montagne Noire (Ubaghs, 1998).

The earliest known kirkocystids (perhaps coeval with specimens from the Fillmore Formation) include two poorly known taxa *Anatifopsis cocaban* and *A. truncata* from the Tremadocian of Korea (Kobayashi, 1960; Lee et al., 2004) and specimens of *Anatifopsis trapeziiformis.* The Korean specimens are known only from isolated plates, making species identification difficult. Lee et al. (2004) were able to distinguish two morphotypes and showed that the shape was variable within populations (more for one morphotype than the other) and that morphological variation is greater for small specimens than for large individuals. *Anatifopsis trapeziiformis* is a well-known taxon for which the full organism has been documented. Specimens from the western U.S., although not as well preserved as *A. trapeziiformis,* show complete preservation of the theca and aulacophore.

PALEOECOLOGY AND TAPHONOMY

Mitrates occur on soft substrates, usually fine clastics or micrites, which probably indicate quiet-water conditions most of the time with rare disturbances by storms or slumps. These echinoderms may have been mobile deposit feeders that likely swept the aulacophore back and forth on the substrate for deposit feeding (Sprinkle and Guensburg, 1995, fig. 8). Other ideas include holding the aulacophore up in the water column for suspension feeding (Sprinkle, 1980, fig. 2B), or living partly infaunal (Lefebvre, 2003). The organism lived flat-side down on the soft substrate (Parsley, 1988, 1991; Kolata et al., 1991; Lefebvre, 2003), although there is some disagreement on this orientation (Jefferies, 1984, 1986, 1999).

Kirkocystids in the western U.S. were living in soft substrates. One of the occurrences, the Ninemile Shale, is an offshore, deeper water environment in which mitrates were buried by storm-generated influxes of muddy sediment. The other three localities were in areas above storm wave base where kirkocystids were buried by storm-generated obrution muds. In some cases, high-density occurrences represent winnowed adorals along with other plates, and storm deposits with complete thecae or complete specimens with aulacophores.

All specimens observed in this study are preserved as original calcite unlike the more typical moldic preservation of contemporaneous deposits of Europe, North Africa, and Asia. Often specimens are weathered or incomplete, especially the appendages. When preserved on slabs, the flat side is typically oriented downwards, which is generally assumed to be the life position (Lefebvre, 2003). In these situations, only one side of the specimen is available for study except where they can be removed from the slab surface. This mode of preservation also affords the best chance for preservation of the aulocophore and glossal appendages.

Ninemile Shale specimens are preserved either freely in the shale or incorporated into small argillaceous carbonate concretions. Free specimens are typically preserved with the aulocophore and spine lost to weathering and breakage of these delicate structures. Thecae are generally in good condition and uncrushed. Specimens preserved in concretions are generally more complete but are extremely difficult to prepare beyond the exposed side because of the hardness of the matrix.

SYSTEMATIC PALEONTOLOGY

Subphylum HOMALOZOA Whitehouse, 1941

Discussion.—The Homalozoa are now recognized as either a paraphyletic (Smith, 2005) or a polyphyletic grouping of flattened, asymmetrical or partly bilaterally symmetrical, bottom-living echinoderms that are related either to blastozoan eocrinoids (solutes and perhaps cinctans because of their blastozoan-like ambulacra or single brachiole and traces of external growth lines) or apparently related to crinozoans (stylophorans because of their internal growth lines and single armlike aulacophore), with ctenocystoids unassigned at present. This flattened body form and bottom-living way-of-life have been repeatedly developed by many groups of early Paleozoic echinoderms (Sumrall, 1997; David et al., 2000; Sumrall et al., 2001; Lefebvre, 2003).

Class STYLOPHORA Gill and Caster, 1960
Order MITRATA Jaekel, 1918
Suborder PELTOCYSTIDA Jefferies, 1973
Family KIRKOCYSTIDAE Caster, 1952
Genus *ANATIFOPSIS* Barrande, 1872
ANATIFOPSIS NINEMILENSIS new species
Figures 1–3

Diagnosis.—*Anatifopsis* with short and wide thecal outline; adorals smooth, with small series of serrations forming low flange on abaxial margins; left infracentral area relatively small associated with relatively wide M′1; serrated posterior margin of both M′4 and subanal; proximal aulacophore composed of seven rings.

Description.—Theca small, flattened, rounded-triangular, slightly wider than long, greatest width one-third of way down theca; dorsal side slightly convex, ventral side nearly flat, posterior plates often depressed, anterior edge nearly flat, oblique, and indented in center for aulacophore attachment. Large holotype theca 7.1 mm long, 7.8 mm wide, 1.9 mm thick

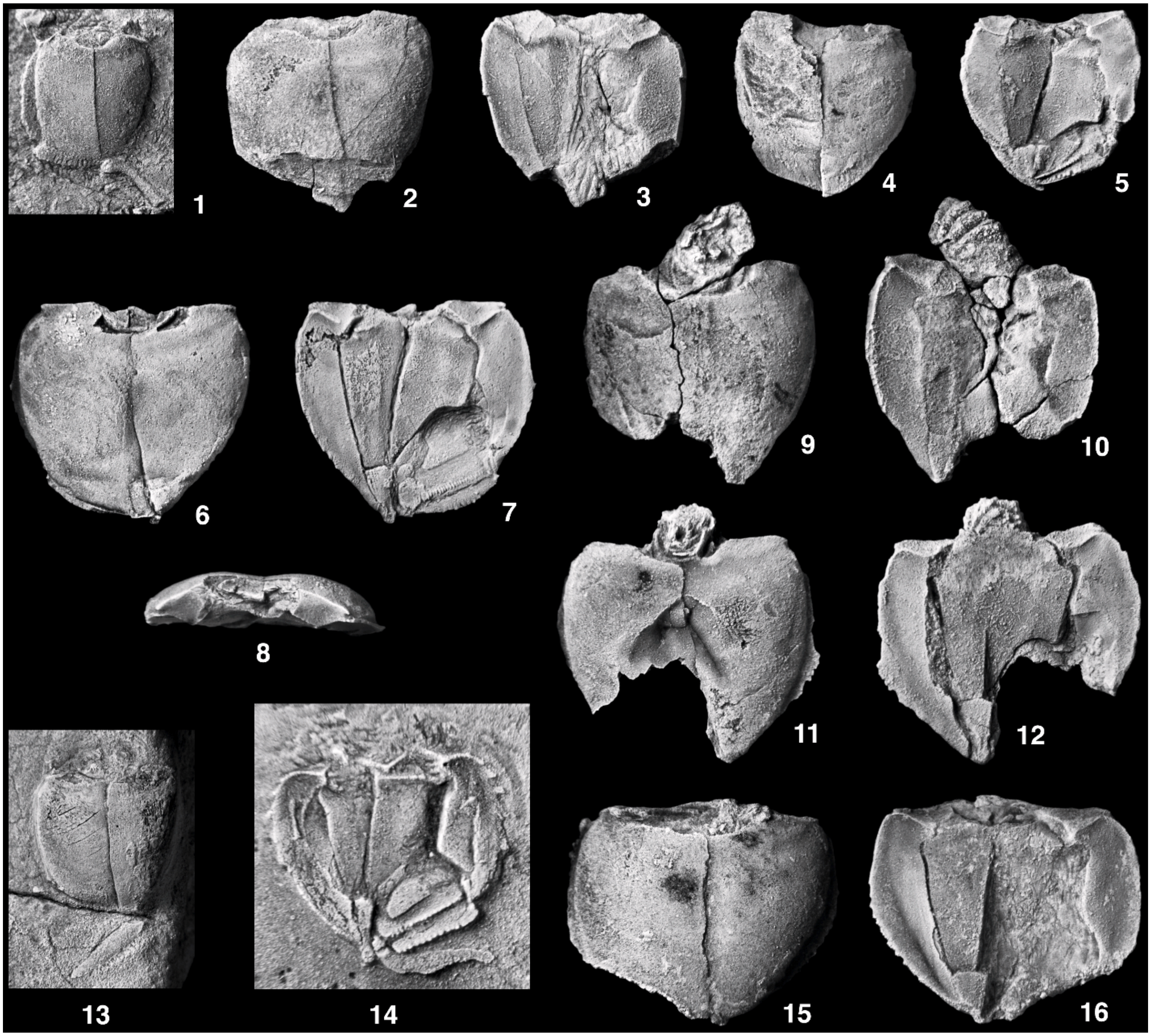

FIGURE 1—*Anatifopsis ninemilensis*, n. sp., from Ninemile Shale, central and southern Nevada, all figures whitened and ×5 unless otherwise noted. *1*, dorsal view of paratype 1780TX1 preserved on small slab showing detached glossal process; *2, 3*, dorsal and ventral views of paratype 1777TX6; *4, 5,* dorsal and ventral views of small paratype 1781TX3; note fairly good ventral plating; *6–8*, dorsal, ventral, and anterior views of holotype 1777TX7 showing most of thecal plates, slight serrations on aboral and left sides of *7*, and convex dorsal and nearly flat ventral sides in *8*; *9, 10*, dorsal and ventral views of large broken paratype 1777TX3 showing proximal aulacophore; *11, 12*, dorsal and ventral views of large damaged paratype 1777TX5 showing short proximal aulacophore; *13*, dorsal view of small paratype 1780TX2 preserved on small slab showing possibly attached glossal process; *14*, ventral view of small paratype 1968TX1 showing details of the ventral plating, serrations along lateral margins, and well-preserved, attached, glossal process, ×8; *15, 16*, dorsal and ventral views of large paratype 1781TX2; note slight serrations on left ventral edge and lower L/W ratio than other specimens.

(slightly crushed); another large but uncrushed theca 2.4 mm thick.

Dorsal surface 98% covered by two large adoral plates, A1 on right side, A′1 on left side, roughly equal in size, meeting at midline along nearly straight suture slightly curving to right distally; A′1 slightly imbricate over A1 (left over right); A1 rounded triangular dorsally, much longer than wide, pointed at distal end; A′1 a rounded parallelogram dorsally, about twice as long as wide, with small notch on distal left side at periproctal opening; both adorals continuing onto ventral surface with thin narrow flange on lateral margins about 0.6 mm wide, tapering toward proximal and distal ends, saw-toothed with 11 to 12 teeth about 0.4 mm apart; edge of M′4 barely visible dorsally on extreme distal edge of A′1; dorsal ornament nearly smooth but with hint of growth lines.

Ventral surface having at least six flat plates visible: two adorals, three marginals, zygal, subanal and several infracentrals; anterior margin thick, beveled for central aulacophore attachment upon apophyses, curved ridge extending along entire anterior margin, with A1 and A′1 distinctly concave here; A1 forming entire left thecal margin, gradually tapering distally to point, A′1 forming two-thirds of right margin to near notch where flange ends; separate adorals rare, so interior of thecal plates rarely seen; M1 in left center, thin,

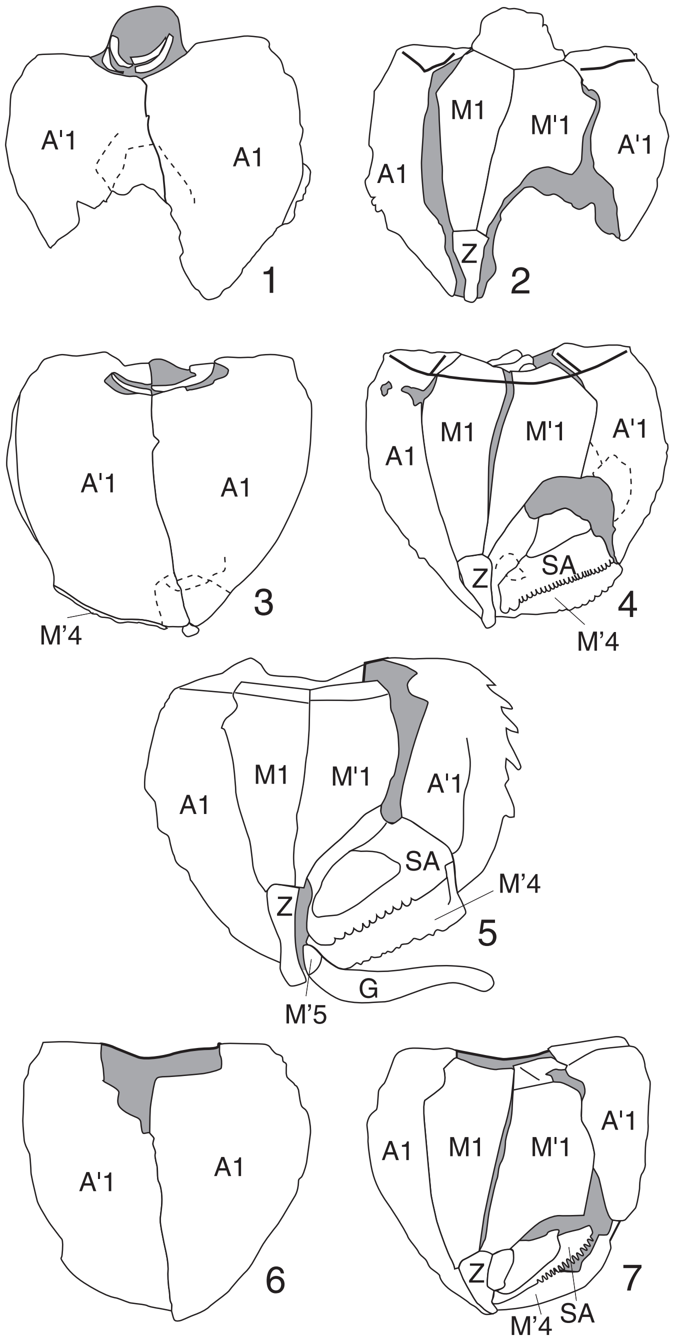

FIGURE 2—Line drawings of *Anatifopsis ninemilensis*, n. sp. *1, 2*, dorsal and ventral views of paratype 1777TX5 with damaged posterior end, ×5; *3, 4*, dorsal and ventral views of nearly complete and well preserved holotype 1777TX7, ×5; *5*, ventral surface of small paratype 1968TX1 showing glossal process and marginal serrations, ×10; *6, 7*, dorsal and ventral views of paratype 1781TX3 with fairly complete ventral plating, ×8. A1 and A′1=adorals; G=glossal; M1 and M′1=marginals; SA=subanal; Z=zygal; shaded areas=matrix or broken plate areas.

elongate, posterior end sutured to zygal plate, M′1 in right center slightly wider, pointed, curved suture along right distal corner infracentral plates, bearing very short suture with zygal plate; M′4 elongate, forming poster edge of theca along with subanal plate, serrated edge; M′5 small, positioned between M′4 and zygal, shape poorly constrained (Fig. 1.5); subanal large and elongate diagonal plate edge serrated; small number of infracentrals present filling relatively small infracentral area, but configuration unknown; zygal plate small, elongate triangular, articulates to glossal spine posteriorly.

Glossal formed into thin curved appendage about 2.6 mm long preserved in three small thecae (Fig. 1.1, 1.13, 1.14), angled to right in ventral view, and attached distally either to tip of pointed zygal or in notch between zygal and subanal.

Aulacophore poorly known; proximal portion plated with about seven, large thin-walled, tetramerous elements that imbricate proximally, circular in cross section, with large lumen; stylocone and distal aulacophore not preserved in present material.

Material.—Holotype 1777TX7; paratypes 1777TX5-6, 1780TX1-2, 1781TX2-3, and 1968TX1; other figured specimens and plates 1971TX1-17; many additional unfigured specimens in these collections.

Etymology.—Named for the Ninemile Shale in central and southwestern Nevada.

Occurrence.—Known from localities WR-1 (Front Section) and WR-2 and 2A (Narrows Section) in the upper Ninemile Shale (Zone J), about 0.25 mi. (0.4 km) and about 0.75 mi. (1.2 km), respectively, NW of end of north side dirt track into Whiterock Canyon, Monitor Range, about 35 mi. (56 km) southwest of Eureka, Eureka County, central Nevada, western U.S.A. Also from the Ninemile Shale at locality MJ-1 just east of the west gulley up to the large Antelope Valley Formation reef on Meiklejohn Peak, about 7 mi. (11.2 km) northeast of Beatty, Nye County, southwestern Nevada, western U.S.A. Also, from the upper McKelligon Canyon Formation (Zones G-2 to H), near CAMLU Retirement Apartments, between Robinson Road and Scenic Drive, south end of Franklin Mountains and near the north city limits of El Paso, west Texas, southwestern U.S.A.

Remarks.—*Anatifopsis ninemilensis* n. sp. is morphologically very close to *A. fillmorensis*, and *A. trapeziiformis*. *Anatifopsis ninemilensis* is easily distinguishable from *A. trapeziiformis* by the presence of large, well-developed lateral flanges on A′1 and A1. *Anatifopsis ninemilensis* has much more subdued ornamentation of the plates especially the ridges on A′1, M′1, and A1, and the smaller left intracentral area does not extend as far anteriorly along M′1. Although subdued ornamentation has been noted to correlate with deeper, more fine-grained facies (Lefebvre, 2003), we believe these differences reflect taxonomic differences rather than ecophenotypic variation.

ANATIFOPSIS FILLMORENSIS new species
Figures 4–6

Diagnosis.—*Anatifopsis* with rounded rectangular outline with medium lateral abaxial flange with serrations; left infracentral area relatively large and elongate associated with narrow M′1; proximal aulacophore six rings long, tapering sharply.

Description.—Theca small, flattened, rounded-trapezoidal, about as wide as long with wide lateral flanges, greatest width at about 30% of length not counting wide flange; dorsal side moderately convex, ventral side nearly flat, posterior plates often depressed, anterior edge nearly flat with nearly flush aulacophore attachment; holotype theca 8.9 mm long, 8.0 mm wide (without flanges), and about 2.0 mm thick.

Dorsal surface 75 to 80% covered by two large adoral plates, A1 on right side, A′1 on left side, roughly equal in size, meeting at midline along nearly straight suture slightly curving to right, A1 slightly imbricate over A′1 (right over left); excluding lateral flanges, A1 and A′1 both rounded rectangular, 1.5 times longer than wide, M′4 and zygal typically visible from dorsal surface at posterior end of theca; both adorals

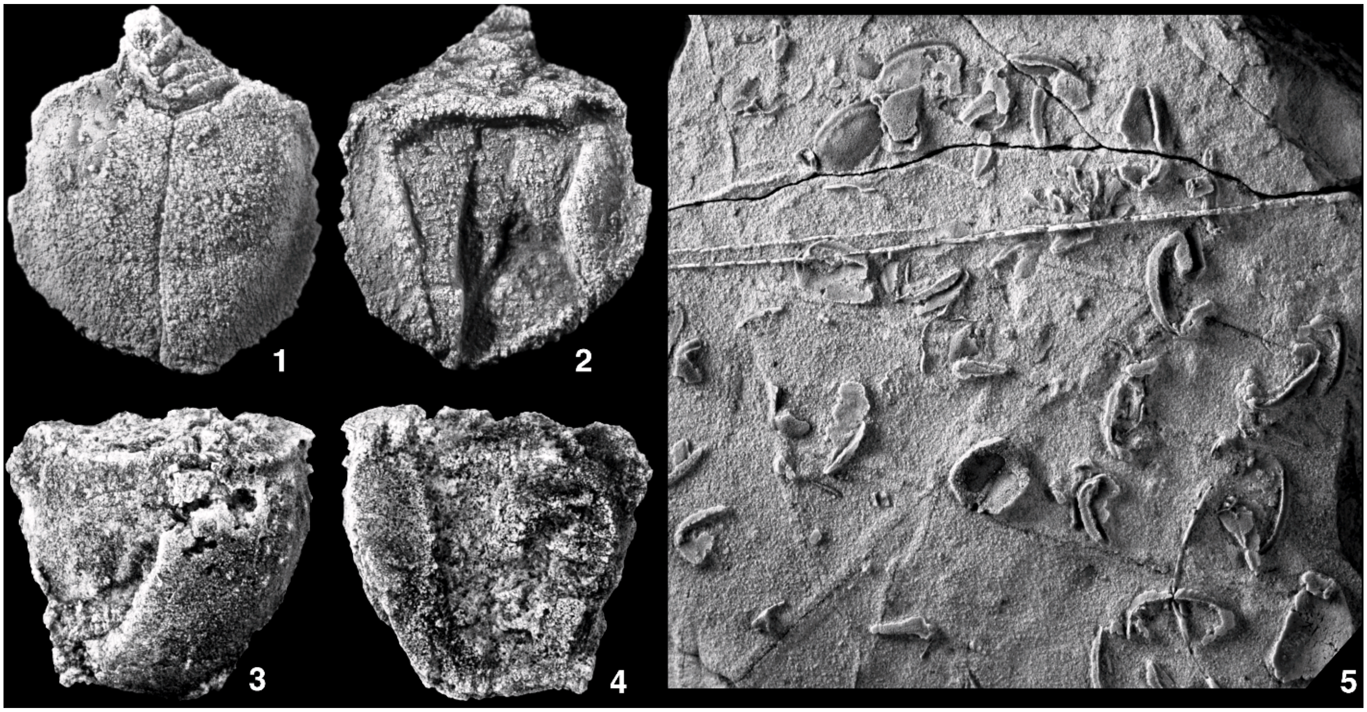

FIGURE 3—*Anatifopsis ninemilensis*, n. sp., from the McKelligon Canyon Formation, north edge of El Paso, west Texas, all figures whitened. *1, 2*, dorsal and ventral views of small figured specimen 1971TX1, whitened; general shape and plating is consistent with *A. ninemilensis*, but small size and coarse surface texture make exact species assignment difficult, ×15; *3, 4*, dorsal and ventral views of large but poorly preserved figured specimen 1971TX2, whitened, ×8.2; *5*, small slab with numerous adorals 1971TX3-17 in ventral and dorsal view, some showing serrations and internal structures, ×3.1.

continuing onto ventral surface with thin wide flange on lateral margins up to 1.2 mm wide, tapering toward proximal end, saw toothed with 11 to 12 tiny teeth about 0.4 mm apart; dorsal ornament nearly smooth with trace of curved growth lines; interiors of separate adoral plates showing distinct, concentric, growth lines (Fig. 4.7). M1 in left center, thin, elongate, posterior end sutured to zygal, M′1 in right center slightly narrower, pointed, curved suture in right distal corner to large elongate infracentral area, with very short suture to zygal plate; subanal not seen in material; several infracentral plates present but arrangement unclear in present material; glossal seen only in two slab thecae (Fig. 4.6), elongate, thin, slightly curved, about 1.3 mm long.

Proximal aulacophore attached to large facet on anterior end of theca; in 8 mm theca (Fig. 4.2), proximal aulacophore very short and conical, about 3.0 mm in diameter, 1.7 mm long with six rings folded down over stylocone, proximal rings nearly parallel to thecal surface at facet, distal rings much smaller and strongly curved concave to facet; stylocone not well exposed in this specimen, 1.7 to 1.8 mm long and about 1.0 mm wide, distal aulacophore long, gradually tapering, with high cover plates; in 8 mm theca, aulacophore at least 10 mm long, up to 14.4 mm long in other specimens, ossicles uniserial, longer than wide, one set of cover plates per floor plate; in medium-sized theca pried off large slab (Fig. 6.5), proximal aulacophore having eight rings that only taper slightly, about 1.8 mm wide and 1.7 mm long, ventral tectals smaller than dorsal ones, with stylocone about 1.5 mm long and 0.8 mm wide proximally.

Material.—Holotype 2061TX1; paratypes 2061TX2-5, 2062TX1-3, and 1965TX13; additional figured specimens 1980TX2-6 and thin section 1980TX8A; many additional unfigured specimens in these collections, especially on slab 1980TX7.

Etymology.—Named for the Fillmore Formation in western Utah.

Occurrence.—Known from the middle Fillmore Formation near Church's Reef in the Pyramid Section and low in the Giza Peak Section in the northern Ibex area north of U.S. Routes 6-50, and at C Section about 610 and 698 ft. (187 and 214 m) above the base of the Fillmore, and at nearby Mesa Section in the eastern Ibex area east of the Tule Valley Road, about 49 mi. (79 km) and 55 mi. (86 km), respectively, southwest of Delta, Millard County, western Utah, western U.S.A. Large, three-piece slab collected from a measured section through the Ninemile Shale equivalent (section O_{pd}; see Langenheim et al., 1962), in a large canyon high up in the Arrow Canyon Range directly east of milepost 73 on U.S. Route 93, about 35 mi. (56 km) northeast of Las Vegas, Clark County, southern Nevada, western U.S.A.

Remarks.—*Anatifopsis fillmorensis* n. sp. is morphologically very close to *A. ninemilensis*, and *A. trapeziiformis*. *Anatifopsis fillmorensis* is easily distinguishable from *A. trapeziiformis* by the presence of large well-developed lateral flanges on A′1 and A1. *Anatifopsis fillmorensis* has much stronger ornamentation of the plates especially the ridges on A′1, M′1, and A1, and a larger left intracentral area that extends farther anteriorly along M′1. As with the previous species, we believe these differences in ornament reflect taxonomic differences rather than ecophenotypic variation.

Class HOMOIOSTELEA? Gill and Caster, 1960
Order SOLUTA? Jaekel, 1901
Family UNKNOWN
DREPANOCYSTIS new genus

Diagnosis.—Same as for species.

Type species.—*Drepanocystis dubius* new species

Occurrence.—Latest Ibexian (middle Arenigian), late Early Ordovician, western Utah.

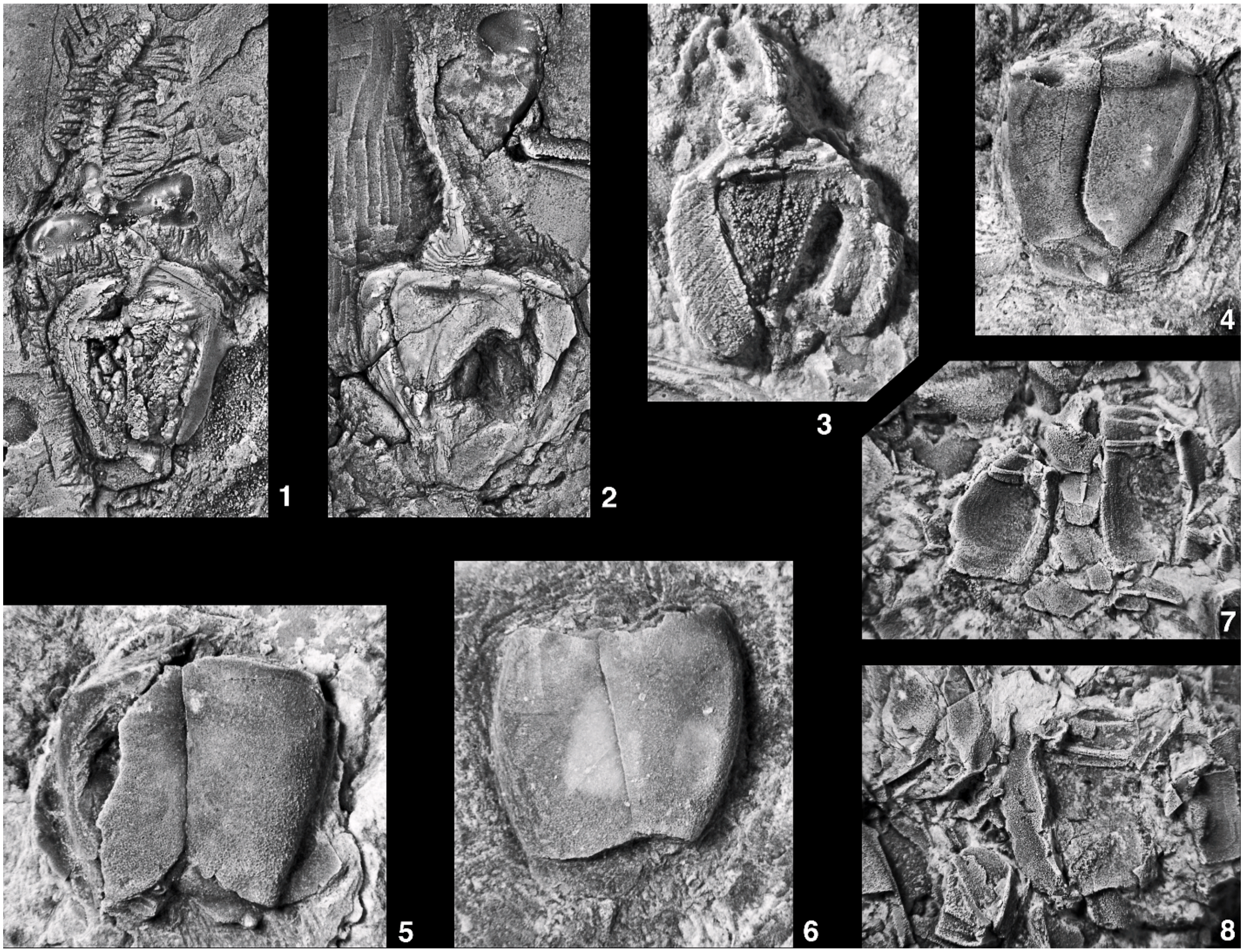

FIGURE 4—*Anatifopsis fillmorensis*, n. sp., from the middle Fillmore Formation and basal Wah Wah Formation, Ibex area, western Utah, all figures whitened and ×5 unless otherwise noted. *1*, dorsal view of poorly preserved paratype 2062TX1 showing nearly complete aulacophore; apparent smaller central plates are calcite crystals growing in exposed thecal interior; *2*, ventral view of poorly preserved paratype 2062TX2 showing nearly complete aulacophore; note that proximal aulacophore is wrapped around stylocone; *3*, ventral view of small paratype 2062TX3 showing poorly preserved proximal aulacophore, ×10; *4*, dorsal view of paratype 1965TX13; note that small posterior plates extend beyond A1 and A′1; *5*, dorsal view of large paratype 2061TX2; *6*, dorsal view of large holotype 2061TX1 showing barely visible posterior plates and glossal attachment; *7*, two interior views of isolated A′1 plates preserved on small slab, 2061TX3-4; note two internal horizontal ridges and small process along proximal lateral margin bearing deep pit, plus presence of internal growth lines on adorals; *8*, interior view of isolated A1 plate preserved on small slab, 2061TX5; note two internal horizontal ridges and small process along proximal lateral margin bearing deep pit.

Etymology.—From the Greek drepanon, sickle, scimitar, and cystis, sac for the large sickle-shaped appendage attached to this unusual homalozoan.

DREPANOCYSTIS DUBIUS new species
Figure 7

Diagnosis.—Theca elongate, cylindrical, with few large plates on each side, small pyramid alongside attachment of larger appendage; large appendage long, sickle-shaped feeding structure, bearing uniserial, ridged brachiolars, constricted somewhat at attachment, with very high imbricate cover plates; smaller appendage medium-sized, relatively short, proximal part bearing rings.

Description.—Medium-sized specimen at least 47 mm long with medium-sized theca, incomplete stele, and very long, robust, sickle-shaped, feeding appendage; theca elongate, cylindrical, 9.7 mm long, maximum width 3.0 mm just above base, slightly wider at apparent base than at top; entire right side of theca damaged and crushed; left side fairly well preserved with approximately seven plates in three circlets; best preserved thecal plates moderately curved along length; two plates in lower left showing coarse pitting or stereom where surface weathered; attachment facets for both stele and brachiole oblique to apparent thecal axis; large, wide facet for stele tilted about 25° from 'horizontal', feeding appendage attached to small, highly oblique facet (60 to 65° from 'horizontal') on left side of apparent summit, 0.8 mm below top; pyramid just to right of where feeding appendage attached also subterminal, roughly circular, about 1.0 mm across, high-conical, composed of 12 to 13 tooth-shaped plates.

Feeding appendage sickle-shaped, very long and robust, about 32 mm long with at least 70 uniserial, ridged, arm plates visible on exposed side, arm plates forming outside of curve over most of length with cover plates on inside; proximal region 3 mm long, highly reflexed to right with arm plates

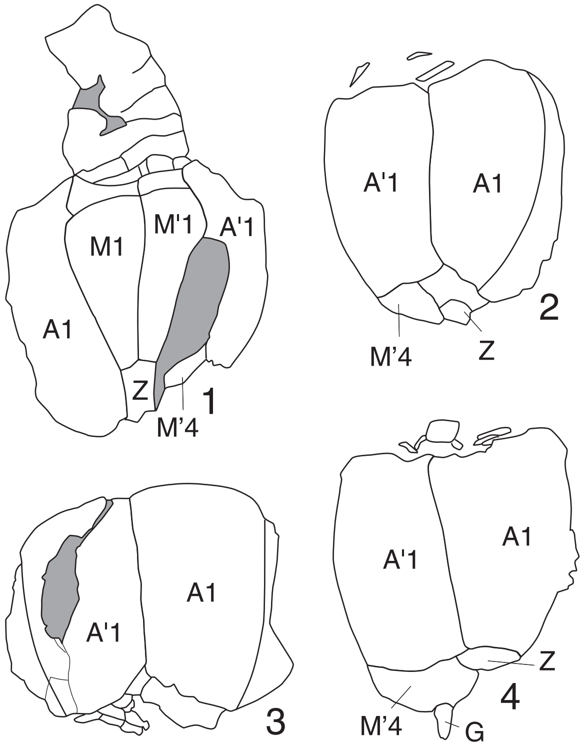

FIGURE 5—Line drawings of *Anatifopsis fillmorensis*, n. sp. *1*, small paratype 2062TX3 showing the ventral surface and proximal aulachophore, ×10; *2*, dorsal surface of paratype 1965TX13, ×5; *3*, dorsal surface of paratype 2061TX2, ×4; *4*, dorsal surface of holotype 2061TX1, ×4.3. A1 and A′1=adorals; G=glossal; Z=zygal; shaded areas=matrix or broken plate areas.

becoming larger, better organized distally; middle region gradually curving to left with largest and most highly ridged arm plates; distal region long, slightly curved to nearly straight, with arm and cover plates gradually becoming smaller; about 20 small, short, arm plates in proximal region, strongly curved, lacking ridges, cover plates low, imbricate, about two cover plates per arm plate, cover plates clearly in biseries; medial region having about 25 large arm plates, slightly arcuate with low lip along food groove, largest arm plates about 1.1 mm deep, 0.6 mm long, 1.0 mm wide, central ridge high, slightly expanding away from food groove and extending across entire back; cover plates in depressed single biseries, imbricate orally, 0.6 mm deep, 0.2 to 0.25 mm long, about two and a half cover plates per arm plate; distal region long, with about 32 arm plates and ridges gradually decreasing in size (especially depth and width) distally, about two cover plates per arm plate, cover plates not as deep, imbrication gradually decreasing; distal tip of appendage apparently not preserved.

Preserved stele relatively short, about 5 mm long with 19 plate circlets, all from proximal stele? (broken off distally), tetrameric, slightly tapering distally, width about 1.8 mm proximally, 0.9 mm distally, plates rounded, slightly imbricating distally.

Material.—Only holotype 1966TX13 is known.

Etymology.—Named for the puzzling morphology shown by this echinoderm.

Occurrence.—Float from a few meters above the base of the Wah Wah Limestone at the top of the Square Top North Section, on the front of Square Top, just east of the Tule Valley Road, eastern Ibex area, about 55 mi. (88 km) southwest of Delta, Millard County, western Utah, western U.S.A. (for section descriptions see Hintze, 1973).

Remarks.—This fossil has many confusing morphological features. The theca is poorly preserved but appears to have an elongate cylindrical shape, with only a few, large, curved plates on the exposed side. One appendage is long, heavily plated with ridges and cover plates, and curved into a sickle shape; the second appendage at the opposite end of the theca is smaller, thinner plated without any cover plates, and is incomplete.

The sickle-shaped appendage is definitely an erect ambulacrum as shown by the presence of large brachiolar elements that apparently carry a food groove that is covered by a cover plate series. The presence of uniserial arm plate elements is puzzling. It does not appear to be an aulacophore because the cover plates are more numerous than the floor plates rather than a one-to-one ratio as seen in most derived stylophorans, there is no stylocone, and the proximal portion is smaller and differently plated. It does not appear to be a brachiole because it is heavily plated, and the arm plate elements are uniserial. Likewise it does not appear to be a solute arm in the typical sense because of the uniserial arm plate elements. The plating of the smaller appendage is clearly different suggesting it is a stem derivative. Its multiplated and organized nature is similar to the proximal portion of a stele, suggesting a solute. However, the striking dissimilarity between the two appendages is difficult to explain in terms of their function, life habits, and classification of the animal.

Kraig Derstler (personal commun., 2010) suggested that this organism would make more sense as a solute if it were oriented opposite to the way we have presented it, with the large sickle-shaped appendage being the stele attached to the base of theca and the smaller appendage being the brachiole attached over the mouth near the thecal summit. The pyramid near the attachment of the large appendage would then be in a nearly normal position for an anal pyramid low on the theca, compared to other solutes. We do not agree with this interpretation because this would make the stele plated as in an arm and the arm plated as in a stele.

It has also been suggested that this organism is a chimera composed of a flattened theca of one organism and an appendage from a second organism. The specimen was carefully prepared on the slab surface by CDS and it is clear in hand that both the appendages are articulated to the theca. During preparation, only tan shale covering the specimen in places was removed from the slab surface. Furthermore, there was no evidence in this material that a disarticulated second specimen bearing appendages was draped over the preserved theca thereby making a chimera specimen. Although we are by no means fully confident that the specimen is a solute, we are certain that all described anatomy is derived from a single animal.

ACKNOWLEDGMENTS

We thank F. Siewers, Western Kentucky College; R. Johns, Austin Community College; and M. McKinzie, Grapevine, TX, for field assistance and collecting specimens. K. Derstler, University of New Orleans; B. Lefebvre, Université Claude Bernard, Lyon, France; and D. Kolata, Illinois Geological Survey, Champaign, reviewed the manuscript and made many helpful suggestions. Research was funded by National Science Foundation Grants BSR 89-06568 (Sprinkle) and EAR 93-04253 (Sprinkle, Guensburg), and CRDF Grant RG1-242 (Sprinkle, Guensburg, Rozhnov). The Geology Foundation, University of Texas at Austin (Sprinkle, Sumrall), Rock Valley College, Rockford, IL (Guensburg), and the University

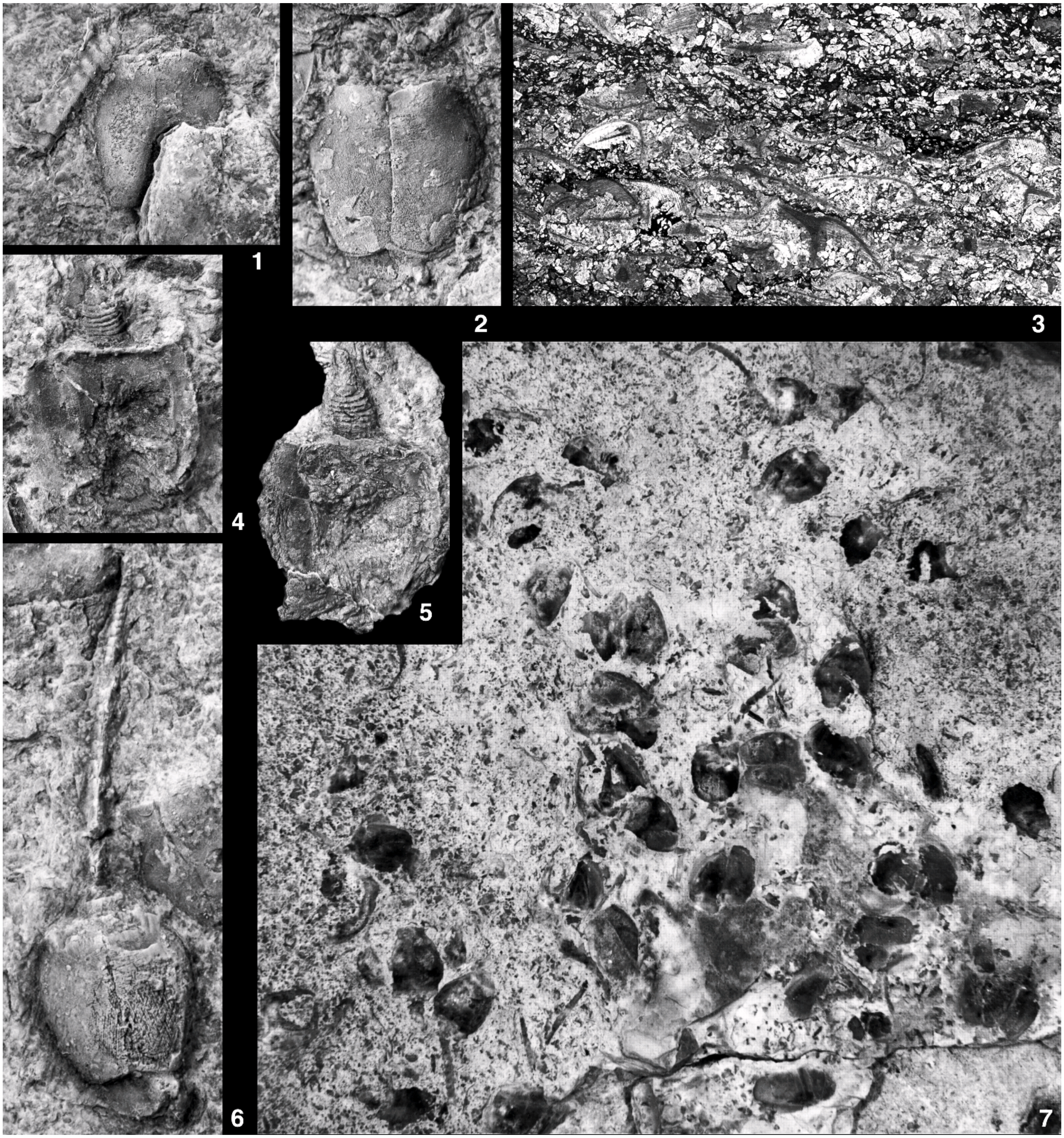

FIGURE 6—Slab specimens of *Anatifopsis fillmorensis*, n. sp. from Ninemile Shale equivalent, Arrow Canyon Range, southern Nevada, whitened and ×4 unless otherwise noted. *1*, dorsal view of specimen 1980TX2 with strongly recurved, incomplete aulacophore showing cover plates proximally on the right side; note that posterior right corner of theca is covered by second poorly preserved specimen; *2*, dorsal view of large theca 1980TX3 showing posterior plates extending beyond A1 and A′1; *3*, thin section 1980TX8A of mitrate slab 1 edge in crossed-polarized light; note that slab is a mitrate grainstone bed showing dozens of curved adoral plates in thecae overlying spar- or matrix-filled sheltered areas, ×4.75; *4*, ventral view of theca 1980TX4 showing proximal aulacophore; *5*, ventral view of theca 1980TX5 removed from slab showing proximal aulacophore and stylocone; note that proximal aulacophore does not wrap around stylocone as in some Fillmore specimens; *6*, complete specimen 1980TX6 showing posterior thecal elements extending beyond A1 and A′1, short proximal aulacophore, and long, slender, distal aulacophore; *7*, uncoated upper surface of 1980TX7 mitrate slab 2 showing about 45 thecae with some articulated aulacophores; nearly all illustrated specimens are dorsal side up, approximately the same size, and showing no consistent orientation, ×1.75.

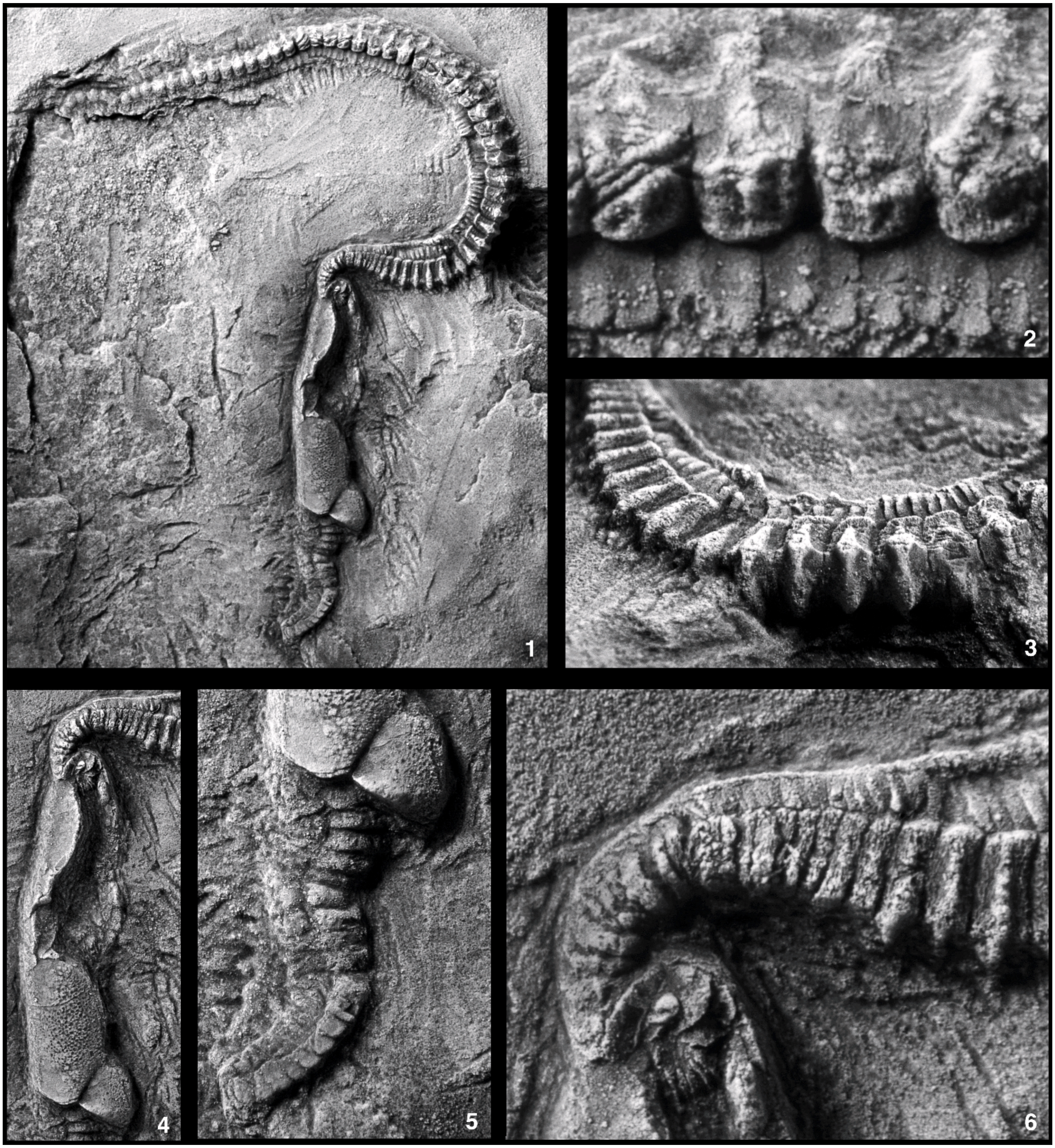

FIGURE 7—*Drepanocystis dubius* n. gen. n. sp., lower Wah Wah Formation, Ibex area, western Utah, all figures whitened. *1*, complete holotype 1966TX13 showing crushed theca of large plates, medium-sized proxistele (below), and long, heteromorphic, sickle-shaped brachiole at top, ×5; *2*, detail of distal portion of brachiole showing ridged brachiolar plates and slightly imbricate cover plates below, ×45; *3*, detail of medial portion of brachiole showing extremely well developed ridges on brachiolar plates and highly imbricate cover plates, ×15; *4*, detail of theca showing large plates and coarse stereom on two lower left plates, ×7.5; *5*, detail of proxistele; note tetrameric plating and relatively large number of rings, ×14; *6*, detail of proximal end of theca, anal pyramid, and proximal portion of brachiole. Note that brachiole attaches to left side of exposed face below top of theca and transitions from tightly spaced brachiolar plates with low cover plates to more robust ridged brachiolar plates with high cover plates; adjacent periproct is covered by slightly disrupted anal pyramid, ×25.

of Nevada, Las Vegas (Dattilo) supported travel, research, and some publication expenses.

REFERENCES

BARRANDE, J. 1872. Système silurien du centre de la Bohême. Supplément au. volume 1. Trilobites, crustacés divers et poissons. Rivnác, Prague, 647 p.

BLAKE, D. B. AND T. E. GUENSBURG. 2005. Implications of a new Early Ordovician asteroid (Echinodermata) for the phylogeny of Asterozoans. Journal of Paleontology, 79:395–399.

BLAKE, D. B., T. E. GUENSBURG, J. SPRINKLE, AND C. D. SUMRALL. 2007. A new, phylogenetically significant Early Ordovician asteroid (Echinodermata). Journal of Paleontology, 81:1257–1265.

CASTER, K. E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology, 34:5–56.

DAVID, B., B. LEFEBVRE, R. MOOI, AND R. L. PARSLEY. 2000. Are homalozoans echinoderms? An answer from the extraxial-axial theory. Paleobiology, 26:529–555.

GILL, E. D. AND K. E. CASTER. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology, 41:7–43.

GUENSBURG, T. E. 2010. *Alphacrinus* new genus and origin of the disparid clade. Journal of Paleontology, 84:1209–1216.

GUENSBURG, T. E. AND J. SPRINKLE. 1992. Rise of echinoderms in the Paleozoic Evolutionary Fauna: significance of paleoenvironmental controls. Geology, 20:407–410.

GUENSBURG, T. E. AND J. SPRINKLE. 1994. Revised phylogeny and functional interpretation of the Edrioasteroidea based on new taxa from the Early and Middle Ordovician of western Utah. Fieldiana (Geology), N. S., 29:1–43.

GUENSBURG, T. E. AND J. SPRINKLE. 2000 (2001). Ecologic radiation of Cambro–Ordovician echinoderms, p. 428–444. *In* A. Y. Zhuravlev and R. Riding (eds.), The Ecology of the Cambrian Radiation. Columbia University Press, New York.

GUENSBURG, T. E. AND J. SPRINKLE. 2001. Earliest crinoids: new evidence for the origin of the dominant Paleozoic echinoderms. Geology, 29:131–134.

GUENSBURG, T. E. AND J. SPRINKLE. 2003. The oldest known crinoids (Early Ordovician, Utah) and a new crinoid plate homology system. Bulletins of American Paleontology, 364:1–43.

HINTZE, L. F. 1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard, County, Utah. Brigham Young University Geology Studies, 20:3–36.

JAEKEL, O. 1901. Über Carpoideen: eine neus Klasse von Pelmatozoen. Zeitschrift der deutschen geologischen Gesellschaft, 52:661–677.

JAEKEL, O. 1918. Phylogenie und system der Pelmatozoen. Paläontologische Zeitschrift, 3:1–128.

JEFFERIES, R. P. S. 1973. The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of *Amphioxus*. Philosophical Transactions of the Royal Society, Series B, 265:409–469.

JEFFERIES, R. P. S. 1981. In defence of the Calcichordates. Zoological Journal of the Linnean Society, 73:351–396.

JEFFERIES, R. P. S. 1984. Locomotion, shape, ornament, and external ontogeny in some mitrate calcichordates. Journal of Vertebrate Paleontology, 4:292–319.

JEFFERIES, R. P. S. 1986. The Ancestry of the Vertebrates. British Museum (Natural History), London, 376 p.

JEFFERIES, R. P. S. 1999. Which way is up in mitrates? – Flat surface up, p. 550. *In* M. D. Candia Carnevali and F. Bonasoro (eds.), Echinoderm Research 1998. A. A. Balkema, Rotterdam.

KOBAYASHI, T. 1960. The Cambro–Ordivician formations and faunas of South Korea. Part 6. Palaeontology 5. Journal of the Faculty of Science. University of Tokyo, Section 2, 12:217–275.

KOLATA, D., T. J. FREST, AND R. H. MAPES. 1991. The youngest carpoid: occurrence, affinities and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. Journal of Paleontology 65:844–855.

LANGENHEIM, R. L., B. W. CARSS, J. B. KENNERLY, V. A. MCCUTCHEON, AND R. H. WAINES. 1962. Paleozoic section in Arrow Canyon Range, Clark County, Nevada. American Association of Petroleum Geologists Bulletin, 46:592–609.

LEE, S.-B., B. LEFEBVRE, AND D. K. CHOI. 2004. Morphometric analysis of Tremodocian (earliest Ordovician) kirkocystid mitrates (Echinodermata, Stylophora) from the Taebaeksan Basin, Korea. Geobios, 37:731–748.

LEFEBVRE, B. 1999. Stylophores (Cornuta, Mitrata): situation au sein du phylum des échinodermes et phylogenèse. Unpublished Ph.D. thesis, Lyon, 630 p.

LEFEBVRE, B. 2001. Some critical comments on ''ankyroids''. *Geobios*, 34:597–627.

LEFEBVRE, B. 2003. Functional morphology of stylophoran echinoderms. Palaeontology, 46:511–555.

LEFEBVRE, B. 2007. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. Palaeogeography, Palaeoclimatology, Palaeoecology, 245:159–199.

LEFEBVRE, B., C. D. SUMRALL, R. A. SHROAT-LEWIS, M. REICH, G. D. WEBSTER, A. W. HUNTER, E. NARDIN, S. V. ROZHNOV, T. E. GUENSBURG, A. TOUZEAU, F. NOAILLES AND J. SPRINKLE. In Press. Palaeobiogeography of Ordovician Echinoderms. *In* D. A. T. Harper and T. Servais (eds.), Early Palaeozoic Palaeobiogeography and Palaeogeography. Geological Society of London, Memoir.

PARSLEY, R. L. 1988. Feeding and respiration strategies in Stylophora, p. 347–351. *In* C. R. C. Paul and A. B. Smith (eds.), Echinoderm Phylogeny and Evolutionary Biology. Clarendon Press, Oxford.

PARSLEY, R. L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology, 100:1–57.

SMITH, A. B. 2005. The pre-radial history of echinoderms. Geological Journal, 40:255–280.

SPRINKLE, J. 1980. An overview of the fossil record, p. 15–26. *In* T. W. Broadhead and J. A. Waters (eds.), Echinoderms, Notes for a Short Course. University of Tennessee Department of Geological Sciences, Studies in Geology 3.

SPRINKLE, J. AND T. E. GUENSBURG. 1995. Origin of echinoderms in the Paleozoic Evolutionary Fauna: the role of substrates. Palaios, 10:437–453.

SPRINKLE, J. AND T. E. GUENSBURG. 1997. Appendix D—echinoderm biostratigraphy, p. 49–50, and pl. 1, chart C. *In* R. J. Ross Jr., L. F. Hintze, R. L. Ethington, J. F. Miller, M. E. Taylor, and J. E. Repetski (eds.), The Ibexian, lowermost series in the North American Ordovician. U.S. Geological Survey Professional Paper 1579A.

SPRINKLE, J. AND C. D. SUMRALL. 2008. New parablastoids from the western United States. University of Kansas Paleontological Contributions, New Series, 16:1–14.

SPRINKLE, J., T. E. GUENSBURG, AND F. J. GAHN. 2008. Overview of Early Ordovician crinoid diversity from the western and southwestern United States, p. 313–330. *In* W. I. Ausich and G. D. Webster (eds.), Echinoderm Paleobiology. Indiana University Press, Bloomington.

SUMRALL, C. D. 1997. The role of fossils in the phylogenetic reconstruction of Echinodermata, p. 267–288. *In* J. A. Waters and C. G. Maples (eds.), Paleontological Society Papers Vol. 3, Geobiology of Echinoderms. The Paleontological Society, Pittsburgh.

SUMRALL, C. D., J. SPRINKLE, AND T. E. GUENSBURG. 2001. Comparison of flattened blastozoan echinoderms: insights from the new Early Ordovician eocrinoid *Haimacystis rozhnovi*. Journal of Paleontology, 75:985–992.

UBAGHS, G. 1998. Echinodermes nouveaux du Cambrien supérieur de la Montagne Noire (France méridionale). Geobios, 31:809–829.

WHITEHOUSE, F. W. 1941. The Cambrian faunas of north-eastern Australia. Part 4: Early Cambrian echinoderms similar to the larval stages of recent forms. Memoirs of the Queensland Museum, 12:1–28.

ACCEPTED 21 JANUARY 2012