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Albian infaunal Pholadomyida (Cretaceous Bivalvia), Comanchean Carbonate Shelf, Texas

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Abstract.—Species of the megaorder Poromyata, although common and relatively diverse in Albian–lower Cenomanian Comanchean strata in Texas and northern Mexico, have been neglected as biostratigraphic markers and paleoecological indicators. Since 1852, more than a dozen species have been identified as *Homomya* Agassiz, order Pholadomyida, superfamily Pholadomyoidea or *Pleuromya* Agassiz, order Pholadida, superfamily Pleuromyoidea. Because valve morphologies of the two genera are similar in many ways, casts are difficult to separate. Statistical analysis of key morphological properties objectively defines species concepts and assesses synonymies. Eight species are retained in *Homomya*; four are synonymized with these. Two species are provisionally retained in "*Homomya*" although they differ significantly. One species is reassigned to *Liopistha (Sergipemya) alta* (Roemer, 1852). *Pleuromya henselli* (Hill, 1893) is reassigned to *Panopea*.

Homomyid species range from upper Aptian to lower Cenomanian of the Comanchean Series in Texas and Mexico. Their ranges vary in duration from one million years up to eight million years. These infaunal suspension feeders occupied calcareous mud and carbonate shelf substrates. Two sets of species are distinct morphotypes: a smaller-sized set of *H. knowltoni* Hill, 1895; *H. tarrantensis* Perkins, 1961; *H. tlahualiloensis* Perkins, 1961; and *H. kellumi* Perkins, 1961 and a larger-sized set of *H. cymbiformis* Perkins, 1961; *H. austinensis* Shattuck, 1903; *H. vulgaris* Shattuck, 1903; *H. budaensis* Whitney, 1911; and *H. auroraensis* Perkins, 1961. Two end-member morphotypes are represented by the "streamlined" *Homomya knowltoni*, which is an elongate, slightly inflated form with a relatively high umbo, and the cylindrical *Homomya budaensis*, which is a very elongate, tubular, inflated form with a very low umbo.

Introduction

Mesozoic soft, muddy, carbonate marine shelf substrates hosted a variety of infaunal suspension-feeding bivalves similar to the modern *Pholadomya candida* (Sowerby, 1823), which burrows in shallow muddy shelves. These large, elongate, thin-shelled bivalves feed by extending the foot through the anterior gape in search of detritus, pedal feeding (Morton, 1981). Pholadomyidae survived the end-Permian mass extinction (Stanley, 2015). Beginning in the Triassic and expanding in the Jurassic, this family evolved into several different clades. The more common Cretaceous genera were *Pholadomya* Sowerby, 1823; *Homomya* Agassiz, 1843; *Pachymya* J. de C. Sowerby, 1826 (in Sowerby and Sowerby, 1812–1846); and *Pleuromya* Agassiz, 1843, whose species generally were long ranging within and even across more than one stage.

Two common and relatively diverse Albian genera reported from Comanchean strata are *Homomya*, order Pholadomyoida Newell (1965), superfamily Pholadomyoidea King (1844), and *Pleuromya*, order Pholadida Gray (1854), superfamily Pleuromyoidea Zittel (1895). The valve morphologies of the two groups are similar in many ways and casts are difficult to distinguish. Both groups have edentulous hinges although some Pholadomyidae King, 1844 species have small knobs at the hinge line. Pholadomyoidae differ from Pleuromyoidae by the ligament structure, which is rarely preserved in external casts. Genera of Pholadomyoidae have an external opisthodetic, parivincular ligament and some have ligamental pseudonymphs. *Homomya* in the family Pholadomyidae has no lunule, but its escutcheon has marginal ridges that fade anteriorly. The external posterior ligament of Pleuromyoidea is opisthodetic, and the anterior ligament becomes subumbonal supported by weak chondrophores. *Pleuromya* species have no lunule or escutcheon and the right valve (RV) slightly overlaps the left valve (LV). The posterior shell outline of *Homomya* tends to be straight and sloping either toward the posteroventral corner or toward the dorsal margin, whereas the posterior margin of *Pleuromya* is evenly rounded. Consequently, Comanchean species previously assigned to *Pleuromya* are here reassigned to *Homomya*.

The order Pholadomyoida and the superfamily Pholadomyoidea contain Pholadomyidae King (1844), Margaritariidae Vokes (1964), Ucumariidae Sánchez (2003), and Arenigomyidae Carter (Carter et al., 2011). The superfamily Pholadomyoidea ranges from Early Ordovician to Holocene. Its common Cretaceous genus *Homomya* first appeared in Early Triassic and became extinct in middle Eocene but possibly continued into late Oligocene (personal communication, J.G. Carter, University of North Carolina at Chapel Hill, 2016). Carter et al. (2011) placed the family Pleuromyidae in the order Pholadida in the superfamily Pleuromyoidea with the families Ceratomyidae Arkell 1934 and Vacunellidae Astafieva-Urbajtis 1973. This

classification places Pleuromyidae phylogenetically distant from Pholadomyidae, which is counter to molecular data (Harper et al., 2006; Bieler et al., 2014). Pleuromyidae ranged from Early Triassic to the end of the Cretaceous (Carter et al., 2011) as did *Pleuromya* (Global Biodiversity Information Facility [GBIF], 2016). *Pleuromya* diversified during the Jurassic, especially during Middle and Late Jurassic (Duff, 1991) and became widespread latitudinally from Antarctica to Russia and Greenland (GBIF, 2016); it was less common during the Early Cretaceous. These families are grouped in the megaorder Poromyata Ridewood, 1903 by Carter et al. (2011) and in the subclass Anomalodesmata Dall, 1889 by Newell (1965), Cox et al. (1969), Morton (1981), Harper et al. (2006), and Bieler et al. (2014).

Albian–lower Cenomanian Comanchean Series species of Pholadomyoidea have been neglected as biostratigraphic markers and paleoecological indicators. Some 22 fossil species have been described (Akers and Akers, 2002). These species have been classed with *Pholadomya*, *Homomya*, *Pachymya*, *Myopholas* Douvillé (1907), *Panopea* Ménard de Groye (1807), and *Pleuromya*. Species of these genera are rather large and readily collected. Specimens are generally preserved as external casts that show external features of their uncomplicated shell morphology; internal features are rarely preserved.

These Comanchean infaunal suspension feeders (Stanley, 1970, 2015) are found in lime mud carbonate strata that represent muddy calcareous substrates in shallow shelf environments (Fig. 1). Modern *Pholadomya* occupies inshore waters and is a passive deep burrower that feeds on sediment detritus by extending its foot through the anterior gape, pedal feeding (Morton, 1981, 1985).

Ferdinand Roemer discovered and named the first species, *Homomya alta*, from the Fredericksburg Group during his exploration travels along the Texas Balcones escarpment and up the transecting rivers (Roemer, 1852). Roemer also noted a specimen that he placed in *H. Panopea* sp. and compared it to the European species *Panopea regularis* d'Orbigny (1843, v. 3, pl. 360, figs. 1, 2). Roemer (1852) named *Pholadomya pedernalis* from Fredericksburg strata. Subsequent explorers discovered similar specimens in west Texas (Conrad, 1857; Shumard, 1860), in the El Paso area (Böse, 1910), and in north Texas (Cragin, 1893, 1894, 1905; Hill, 1893), and central Texas (Whitney, 1937). This species group ranges from the upper Aptian–lower Albian Glen Rose Formation of the Trinity Group

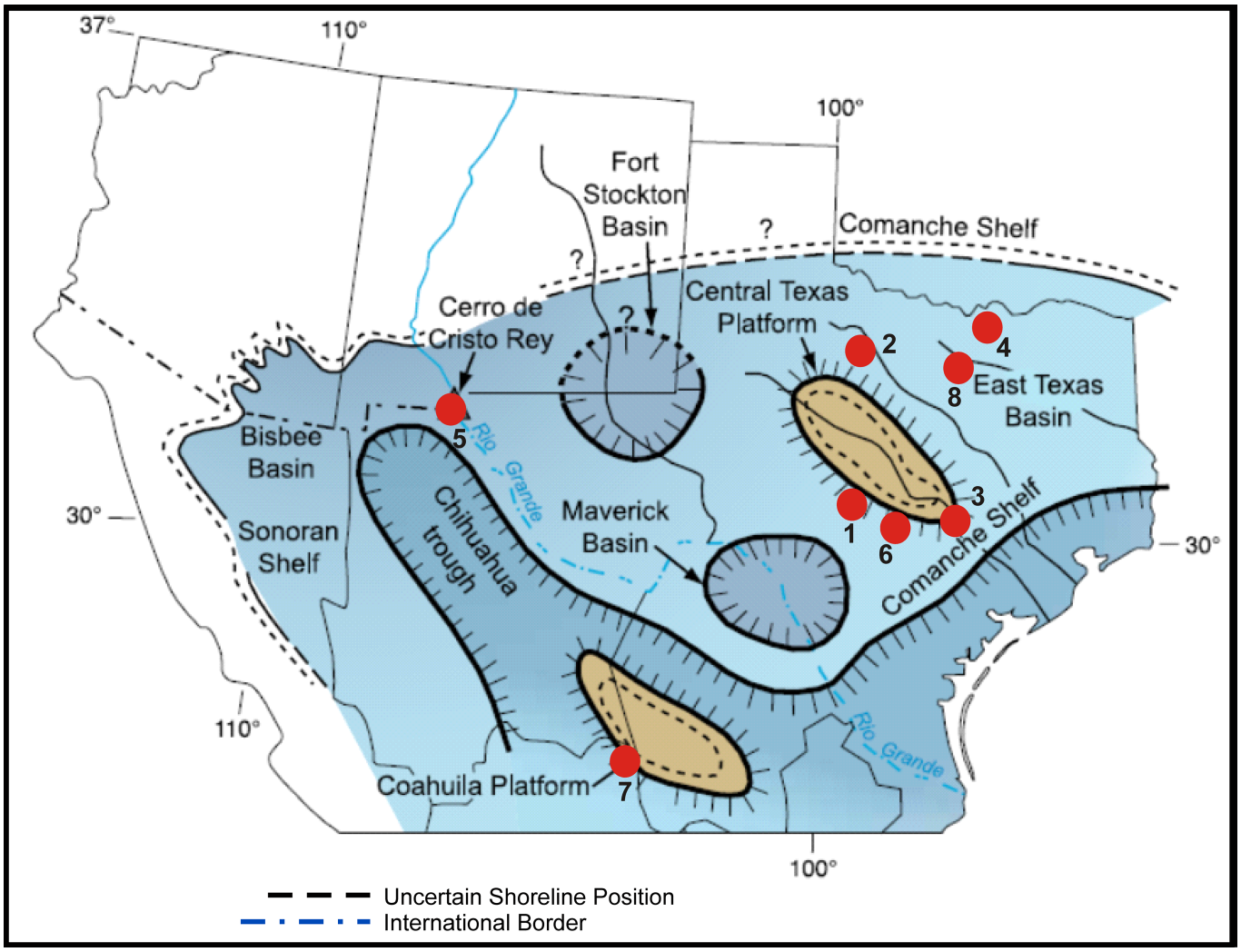

Figure 1. Middle Albian paleogeographic map of the Comanche Shelf, Texas, and surrounding areas (from Scott, 2007). Tan areas represent shallow-water carbonate; light blue is shelf carbonate; dark blue is intrashelf basin or deeper-water carbonate. Location of type localities of Homomyid species: 1. Burnett County; 2. Parker County; 3. Travis County; 4. Grayson County; 5. El Paso County; 6. Comal County; 7. Coahuila, Mexico; 8. Tarrant County.

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and into the lower Cenomanian Buda Formation at the top of the Washita Group (Fig. 2). A similar diverse assemblage of shallow-water carbonate-shelf bivalves occupied the Albian Coahuila platform in northwestern Coahuila, Mexico (Perkins, 1961). The Albian Aurora Limestone was deposited on this carbonate platform as fringing buildups and is now exposed in the Sierra de Tlahualilo (Padilla y Sanchez, 1986). The Albian species, *Pleuromya knowltoni* (Hill, 1893), has been proposed as a "guide fossil" of the informal Regional Dense Member (RDM) in the basal part of the Person Formation in central Texas (Small et al., 1996). However, it occurs in both older and younger units; instead, *Homomya comalensis* Whitney, 1937 is the distinctive species of the RDM.

This report intends to: (1) review the known Comanchean species of the families Poromyidae Dall (1889), Pholadomyidae, and Hiatellidae Gray, 1824; (2) present distinctive criteria to identify these taxa consistently; (3) show their stratigraphic utility; and (4) propose paleoecological inferences.

Comanchean Series stratigraphy

The Comanchean Series on the U.S. Gulf Coast and in northern Mexico is a mixed carbonate-siliciclastic interval interbedded with localized evaporate units that spans upper Aptian to lower Cenomanian substages. The Comanchean is composed of three groups: upper Aptian to lower Albian Trinity Group, the middle

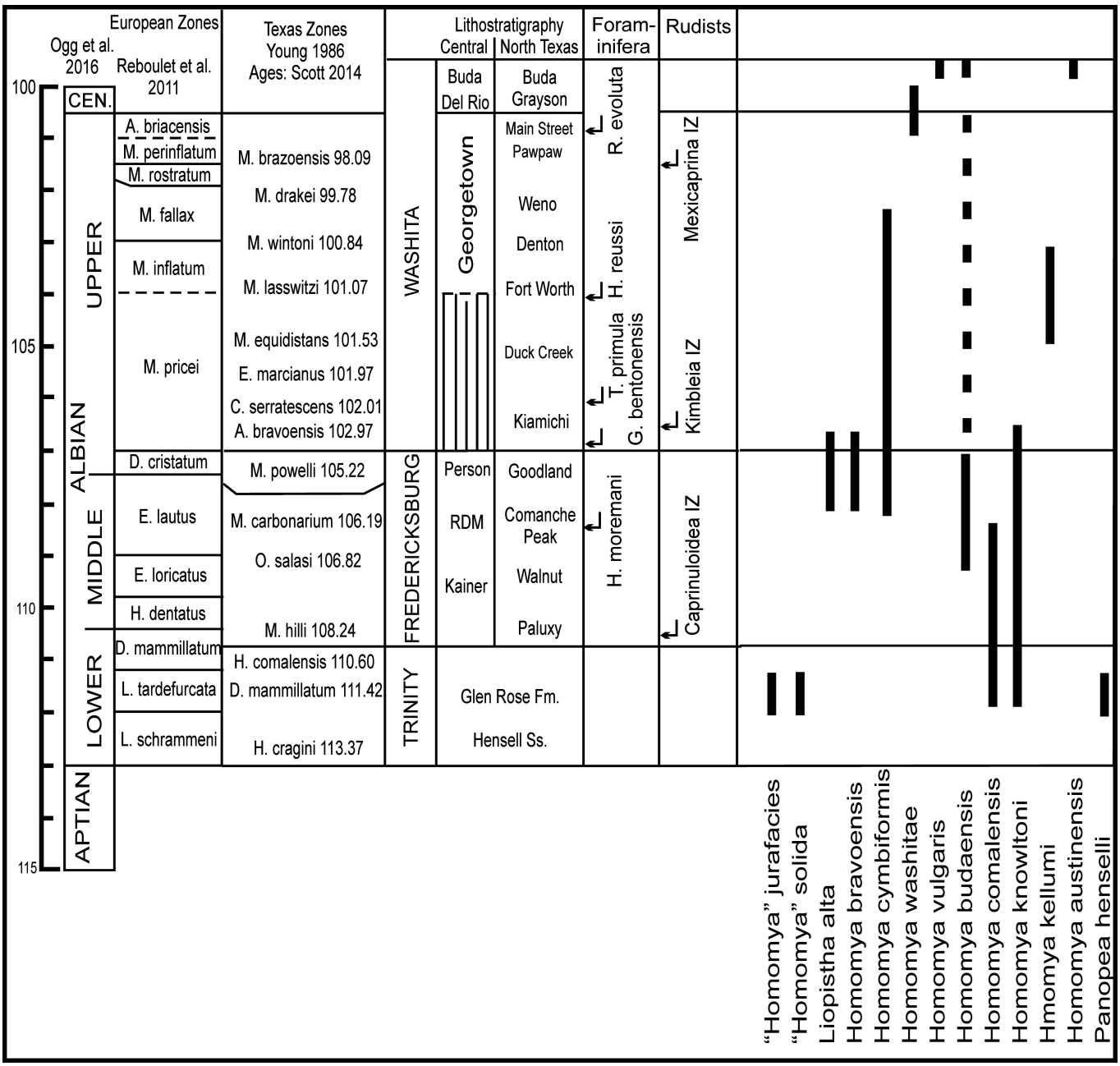

Figure 2. Biostratigraphy of Comanchean Series, Texas (Scott et al., 2003), with ranges of Albian Pholadomyidae bivalves. Planktic Foraminifera from Reichelt (2005, fig. 51). Rudist zones from Scott and Filkorn (2007).

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to basal upper Albian Fredericksburg Group, and the upper Albian to lower Cenomanian Washita Group (Scott et al., 2003). Different subdivisions into formations reflect regional lithological changes from North Texas, south to the San Marcos Arch, and to West Texas (Fig. 2). Homomyid species occur in each group in Texas and northern Mexico (Fig. 2) and evolved across this time span. Ranges are relatively long, some up to eight million years and others only one to two million years. The Trinity Group is characterized by the first appearances of *Homomya knowltoni* (Hill, 1895) and *Homomya comalensis* Whitney 1937; two other species are known only from the Trinity, but their generic assignment is uncertain. Four new *Homomya* species diversified in the middle-lower upper Albian Fredericksburg Group. One Trinity species, *H. comalensis*, ranges into the Fredericksburg basal marl member of the Person Formation on the San Marcos Arch, and *H. knowltoni* persisted into the basal formation of the Washita Group. *Homomya washitae* Cragin, 1894 spans the Albian/Cenomanian boundary, and three species are found only in the lower Cenomanian Buda Limestone (Fig. 2).

Homomya specimens are diverse and abundant in the Aurora Limestone in the Sierra de Tlahualilo in western Coahuila, Mexico (Perkins, 1961). The upper member of the Aurora is composed of fossiliferous, interbedded thick-bedded and nodular marly limestone up to 110 m (365 ft) thick. Perkins correlated the upper member with the middle-upper Albian Fredericksburg and Washita groups in North Texas. Perkins recognized an older *Texigryphaea mucronata* Zone and a younger *Homomya kellumi* Zone. The former species is characteristic of the Fredericksburg, which correlates the lower part of the upper Aurora member with middle-upper Albian. The *H. kellumi* Zone correlates the upper part of the upper Aurora member with the upper Albian Washita Group. In Texas, this species is in the Fort Worth Formation in the middle part of the Washita, which is characterized by the upper Albian ammonite species *Mortoniceras lasswitzi* (Young, 1957) (Fig. 2). Also in the *H. kellumi* Zone is the caprinid rudist *Kimbleia albrittoni* (Perkins, 1961), which ranges throughout the upper part of the upper Albian Washita in Texas (Fig. 2) (Scott et al., 2016). Thus, the *H. kellumi* Zone in the Aurora correlates with the middle part of the Washita up to the Albian/Cenomanian contact.

Statistical comparison of species

To identify consistently Comanchean species of *Homomya*, *Liopistha* (*Sergipemya*), and *Panopea*, dimensions of key morphological properties were measured (Fig. 3; Table 1). Because most specimens are preserved as internal or composite molds and most are broken, shell heights are more commonly complete than lengths. Two sets of species are compared, a smaller-sized set of *H. knowltoni*; *H. tarrantensis* Perkins, 1961; *H. tlahualiloensis* Perkins, 1961; *H. kellumi* Perkins, 1961; and *H. comalensis* (Fig. 4) and a larger-sized set of *H. cymbiformis* Perkins, 1961; *H. austinensis* Shattuck, 1903; *H. vulgaris* Shattuck, 1903; *H. budaensis* Whitnet, 1911; and *H. auroraensis* Perkins, 1961 (Fig. 5).

The difference between heights of populations of *H. knowltoni* and *H. tarrantensis* are statistically insignificant (two-tailed, paired Student's t test is 0.3001), and their stratigraphic ranges overlap in the Fredericksburg Group (Fig. 4).

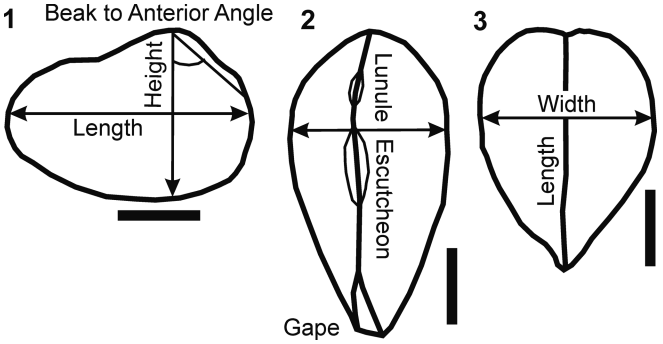

Figure 3. Outlines of a typical Comanchean homomyid showing measured dimensions on Table 1. (**1**) Right valve lateral view; (**2**) dorsal view; (**3**) anterior view. Scale bars = 1 cm.

Likewise, the difference between heights of populations of *H. kellumi* and *H. tlahualiloensis* are statistically insignificant (two-tailed, paired p = .1195, CI = 4.637) and both are in the Fort Worth Formation in the middle part of the Washita Group (Fig. 5). Heights of populations of *H. cymbiformis, H. austinensis, H. vulgaris,* and *H. budaensis-auroraensis* are also significantly different (Fig. 6). Statistical analyses were performed using equations in Excel spreadsheets and GraphPad software (www.graphpad.com/quickcalcs/ttest2/). Taxonomic implications will be discussed in the Systematic Paleontology section.

Five species appear to be quite similar, so they are compared on X/Y plots (Fig. 7): length/height (L/H) and height/width (H/W). The difference between the L/H ratios of *H. knowltoni* and *H. tarrantensis* is statistically insignificant (two-tailed p = .2004, CI = 0.0686), but the H/W ratio is significantly different (two-tailed p = .0230, CI = –0.1040). This statistic indicates that *H. knowltoni* is significantly wider than *H. tarrantensis*; however, this difference is not a practical criterion on which to base a species concept. The H/W data points of *H. knowltoni* overlap those of *H. tarrantensis* in the Fredericksburg Group (Fig. 7). The difference between H/W ratios of the two younger species in the Washita Group, *H. kellumi* and *H. tlahualiloensis*, is also statistically insignificant (two-tailed p = .0097, CI = –0.18229); the lengths of too few specimens were available to form significant populations. These two species are very similar to each other and are distinctly larger than the two Trinity and Fredericksburg group species (Fig. 7). The lower Cenomanian species, *H. austinensis*, is relatively longer and higher than the other species. This group of Comanchean *Homomya* species became larger during the early Albian to early Cenomanian time span, approximately 16 million years.

Evolution of homomyid functional morphotypes

Two end-member morphotypes are represented by the "streamlined" *Homomya knowltoni*, which is an elongate, slightly inflated form with a relatively high umbo, and the cylindrical *Homomya budaensis*, which is a very elongate, tubular, inflated form with a very low umbo. The geometry of these shell forms is approximated by a cylindrical outline, the volume of which is [$\pi \times \text{radius}^2 \times \text{length}$]; the radius is taken as half the width. The inflation of the valves is

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Table 1. Species of *Homomya* and *Panopea* reported from Albian Strata, Comanche Shelf, Texas and Mexico.

Species	Author	Date	Formation	Location (Map number)	Number of specimens	Mean Length	Mean Height	Length/ Height	Mean Width	Height/ Width	Mean Beak Distance	Beak/ Length	Beak/ Height
"Homomya" jurafacies	Cragin	1893	Glen Rose Formation	Burnett County, Texas (1)	4	79.8	60.2	1.27	53.8	1.12	21	0.265	0.349
"Homomya" solida	Cragin	1893	Glen Rose Formation	Parker County, Texas (2)	1	81.7	69	1.18	57.2	1.21	29	0.355	0.42
Bucardiomya [Homomya] alta	Roemer	1852	Fredericksburg Group (1)	Gillespie County Texas	1	45	52	1.45	39	1.33	12	0.267	0.231
Homomya [Pholadomya] knowltoni	Hill	1893	Glen Rose Formation	Travis County, Texas (3)	8	50	31.2	1.6	25.8	1.21	15	0.328	1.87
Homomya comalensis	Whitney	1937	Glen Rose Formation	Comal County, Texas (6)	1	55	35	1.57	29	1.21	11	0.2	0.314
Homomya tarrantensis	Perkins	1961	Fredericksburg Group	Tarrant County, Texas (8)	11	46.7	32.4	1.48	24	1.33	14.9	0.311	0.469
Homomya austinensis	Shattuck	1903	Buda Limestone	Travis County, Texas (3)	4	64.8	45.9	1.44	33.1	1.34	16.67	0.25	0.38
Homomya kellumi	Perkins	1961	Aurora Formation	Coahuila, Mexico (7)	7	68	46.7	1.31	32.5	1.45	17.2	0.254	0.364
Homomya tlahualiloensis	Perkins	1961	Aurora Formation	Coahuila, Mexico (7)	10	57.9	43.5	1.37	33.7	1.27	17.3	0.28	0.39
Homomya vulgaris	Shattuck	1903	Buda Limestone	Travis County, Texas (3)	3	90	51.5	1.84	49	1.1	14.5	0.167	0.29
Homomya bravoensis	Böse	1910	Fredericksburg Group	El Paso County, Texas (5)	1	77.3	52	1.5	57.3	1.01	6	0.068	0.09
Homomya auroraensis	Perkins	1961	Aurora Formation	Coahuila, Mexico (7)	2	85.8	46.9	1.83	44.1	1.07	19	0.223	0.385
Homomya budaensis	Whitney	1911	Buda and Aurora Formations	Tx (3), Coahuila, Mexico (7)	8	88.4	52.5	1.89	52.1	0.86	10.8	0.12	0.24
Homomya cymbiformis	Perkins	1961	Fredericksburg Group	Tarrant County, Texas (8)	4	63.5	41.7	1.54	36.1	1.18	16.3	0.07	0.08
Homomya washitae	Cragin	1894	Main Street and Grayson fm.	Grayson County Texas (4)	2	116.5	85	1.38	79.5	1.07	na		
Panopea [Pleuromya] henselli	Hill	1893	Glen Rose Formation	Travis County, Texas (3)	2	76.1	46.9	1.62	33.1	1.42	36	0.475	0.765

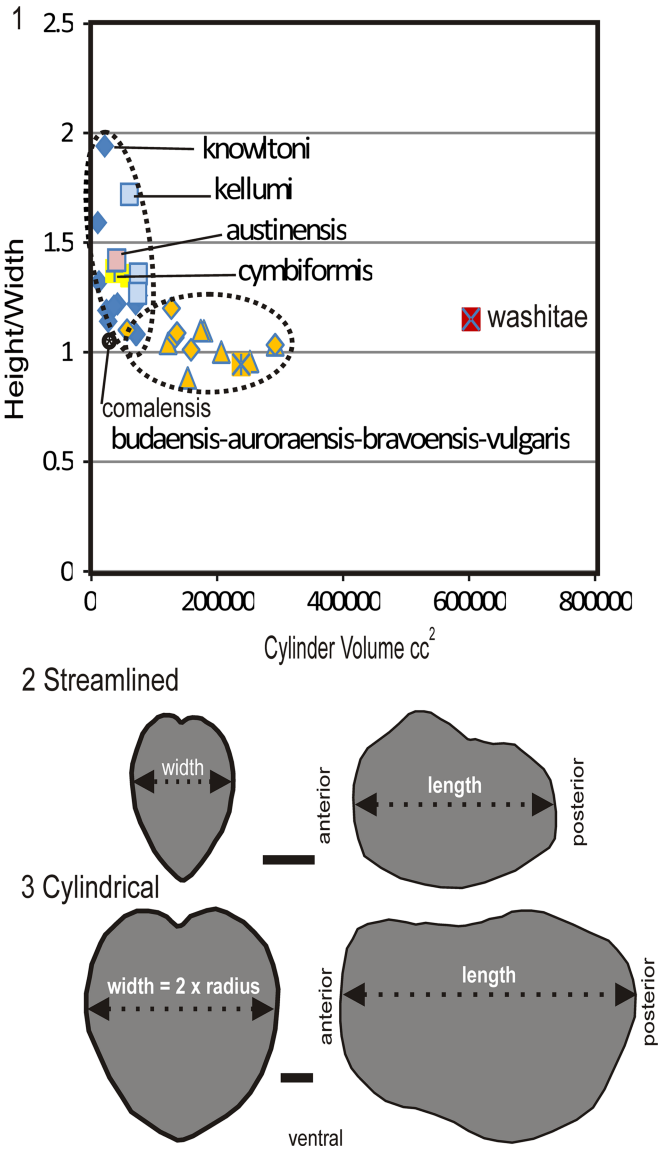

Figure 4. End-member Comanchean homomyid morphotypes. (**1**) Plot of height/width to valve volume of nine species shows two fields that overlap slightly: streamlined field in which valves are higher than wide and cylindrical field in which valves are as wide as or wider than high. (**2, 3**) Outlines of morphotype anterior and lateral left valve views: (**2**) *H. knowltoni* lectotype NMNH 145652; (**3**) cylindrical morphotype of *H. budaensis* hypotype UMMP 32854 (based on Perkins, 1961, pl. 24, figs. 6, 7). Scale bars = 1 cm.

approximated by the height-to-thickness (width) ratio. The X/Y plot of these parameters (Fig. 8) separates the "streamlined" morphotype of *H. knowltoni* and *H. cymbiformis* from the cylindrical form of *H. budaensis* and *H. auroraensis*. The volume of the valves is related to the volume of the interior visceral mass, which includes foot, gills, and stomach. Comanchean *Homomya* species valves increased in size as the visceral mass increased, suggesting that the amount of sediment processed for organic matter increased. The two shape paradigms, streamlined and cylindrical, may reflect a difference in burrowing activity, which may have responded to substrate stability and fluidity.

The "streamlined" forms of *H. knowltoni, H. kellumi, H. austinensis*, and *H. cymbiformis* first appeared on the

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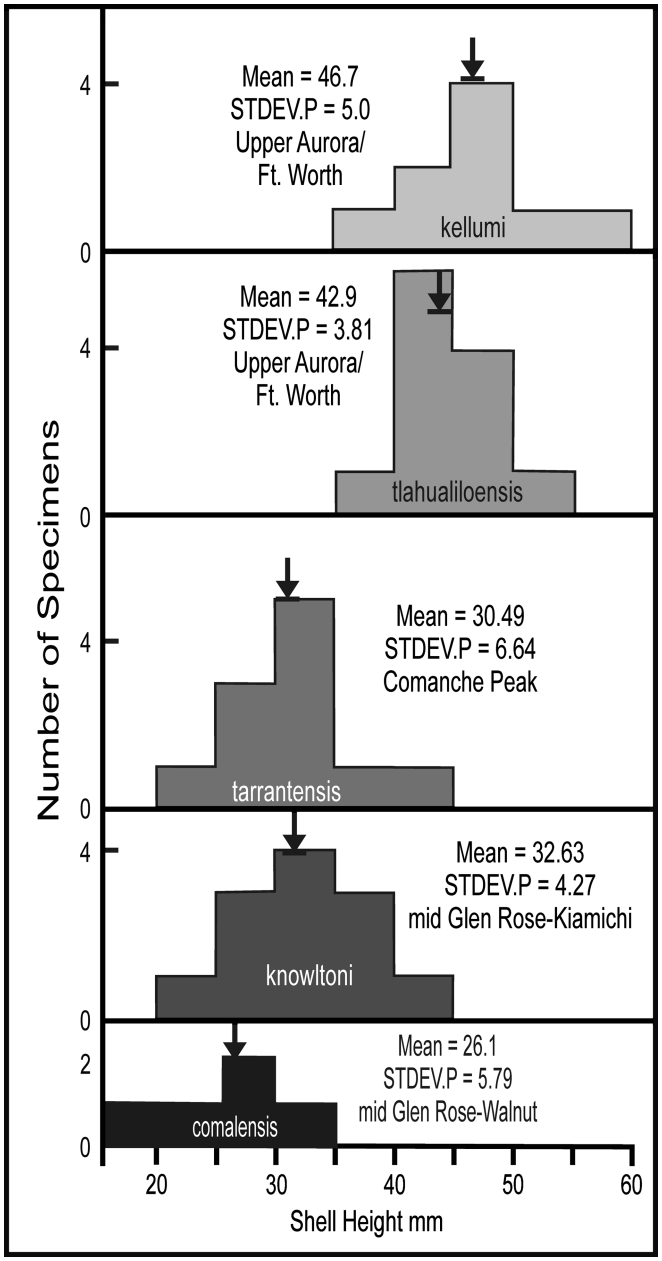

Figure 5. Histograms show the difference in shell height of five streamlined homomyid species in stratigraphic succession. STDEV.P is Excel standard deviation function.

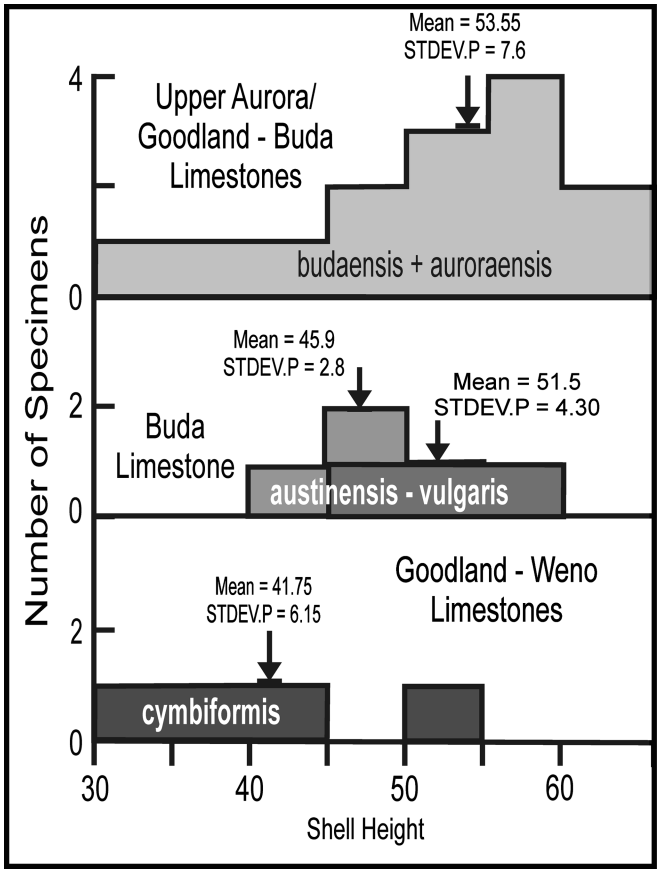

Figure 6. Histograms show the difference in shell height of five cylindrical homomyid species in stratigraphic succession. STDEV.P is Excel standard deviation function.

Comanchean shelf in early Albian in the middle part of the Glen Rose Formation. These species occupied shallow shelf marls and successive species became larger. The cylindrical forms, *H. budaensis, H. auroraensis, H. bravoensis* Böse, 1910*, H. vulgaris*, and *H. washitae*, first appeared in the late Albian in the Del Norte Formation, southwest Texas. These large species occupied both calcareous shale and muddy carbonate substrates. Future cladistics analysis of all Mesozoic Pholadomyidae is recommended.

Materials and methods

Holotypes and other specimens have been reexamined and measured with calipers and selected specimens have been photographed (Table 1); measurements of all studied specimens are available as supplemental data. Additional new specimens have been collected during numerous field seasons in Texas Comanchean Cretaceous strata since the 1970s and have been measured and used for the analyses. Most species are uncommon to rare at any one outcrop, and some are incompletely preserved so that some species are represented by a small number of specimens. The taxonomy of Carter et al. (2011) is followed.

The suprafamilial classification and thus phylogeny of Bivalvia has advanced significantly since the application of molecular phylogenetics (Harper et al., 2006; Bieler et al., 2010, 2014; Combosch et al., 2017). The resulting classification differs from that based on "all available sources of phylogenetic information, including molecular, anatomical, shell morphological, shell microstructural, bio- and paleobiogeographic as well as stratigraphic, have been integrated into the classification" (Carter et al., 2011, p. 1). The two classification positions construct different suprafamilial schemes, but the family-level schemes are similar. Analysis and critique of these two positions are beyond the scope of this paper. Because fossil bivalves in this study are preserved as composite casts, for which only rudimentary morphological features are preserved, the Carter classification is used.

Collections used in this study include the following: NMNH = National Museum of Natural History, Smithsonian

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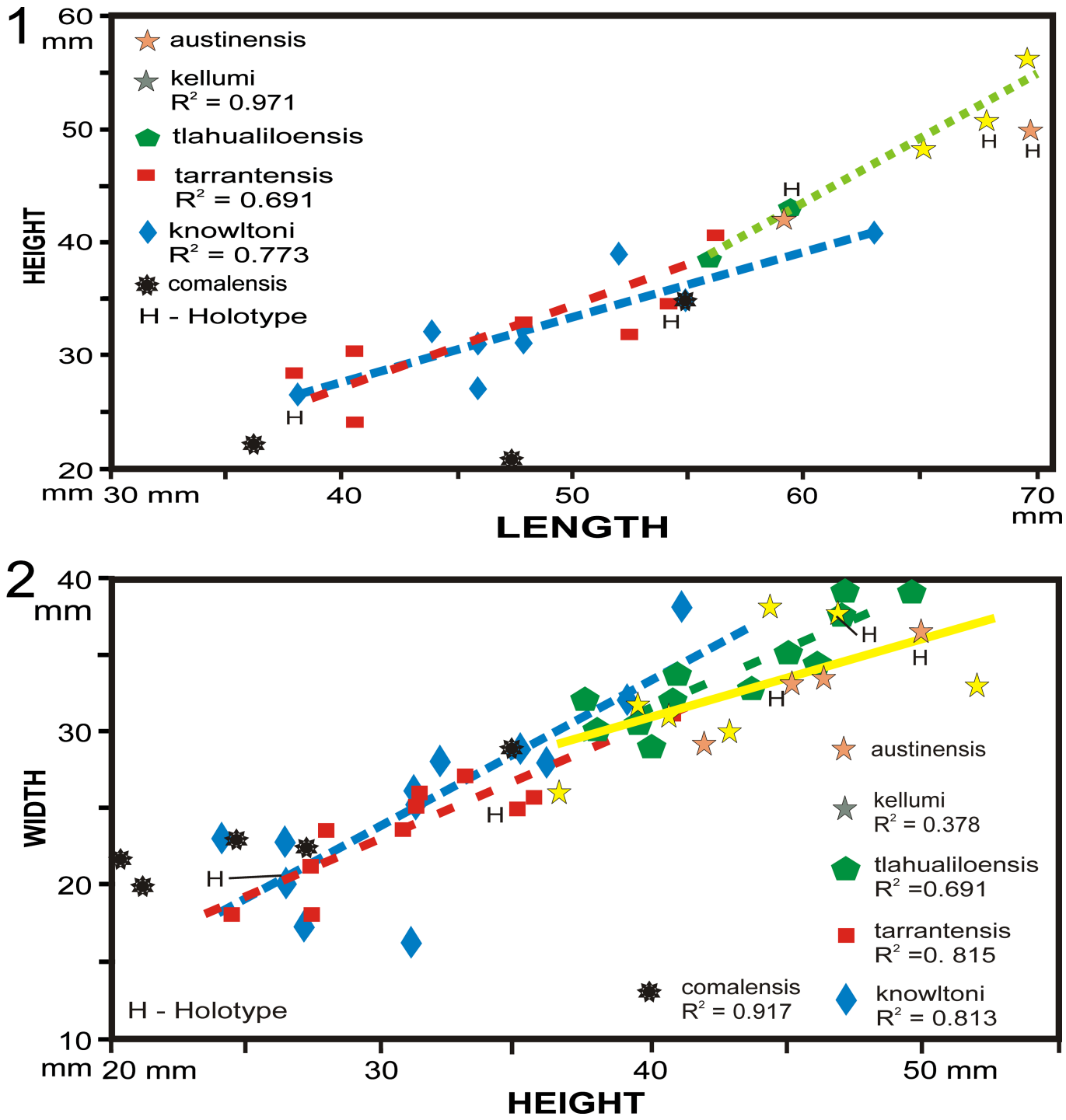

Figure 7. Cross plots of *H. knowltoni*, *H. comalensis*, and *H. kellumi* and their synonyms. (**1**) Length to height; (**2**) height to width.

Institution, Washington, D.C.; UMMP = University of Michigan Museum of Paleontology; NPL, UT, and WSA = Non-vertebrate Paleontology Laboratory, the Jackson School of Geosciences, the University of Texas at Austin. Former generic names are in brackets; accepted subgenera are in parentheses.

Repositories and institutional abbreviations.—Type specimens in the U.S. National Museum of Natural History-Smithsonian, the University of Michigan Museum of Paleontology, and the Non-vertebrate Paleontology Laboratory, the University of Texas, Austin, have been studied.

Systematic paleontology

Class Bivalvia Linnaeus, 1758 in Linnaeus 1758–1759
Clade Eubivalvia Carter in Carter et al., 2011
Subclass Autobranchia Grobben, 1894
Infraclass Heteroconchia Hertwig, 1895

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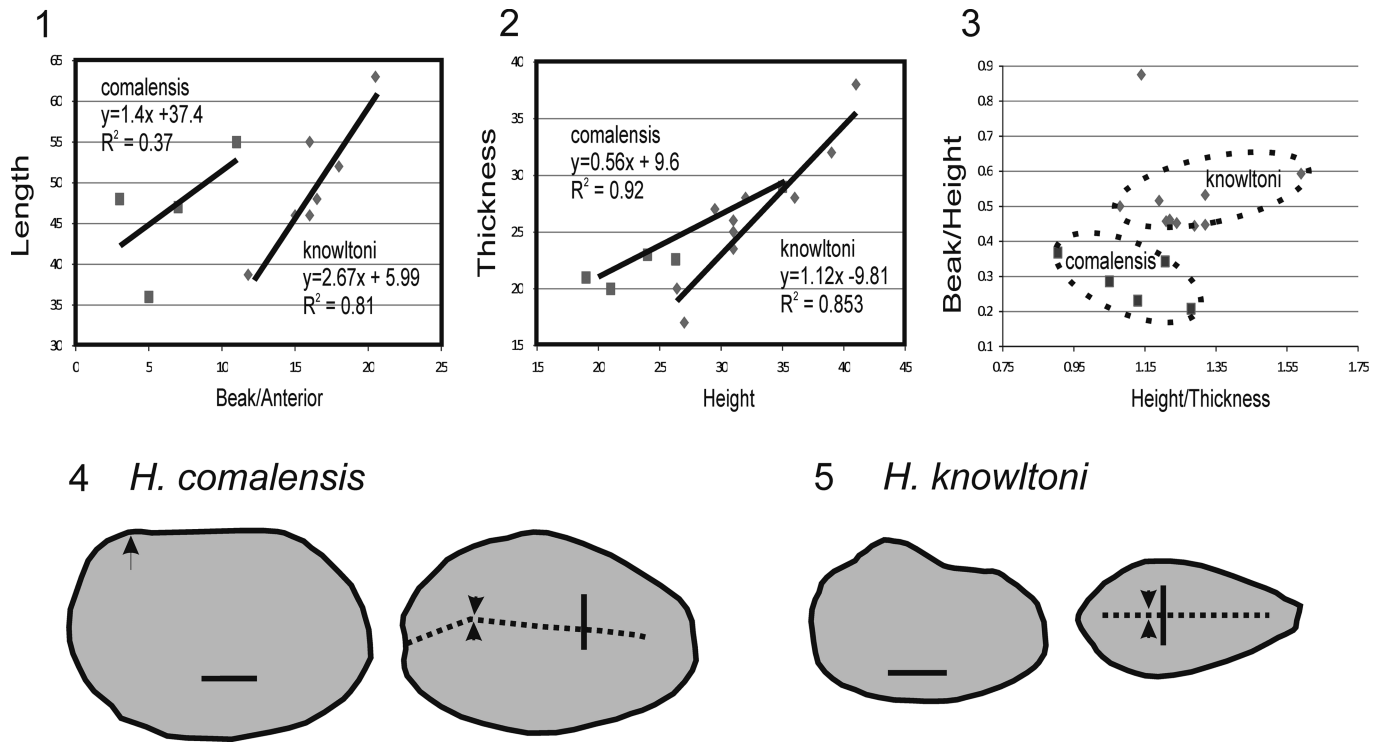

Figure 8. Comparisons of *H. comalensis* with *H. knowltoni*. (**1**) Distance of umbo from anterior margin versus valve length in millimeters. (**2**) Cross plot of valve height to thickness. (**3**) Cross plot of ratio of height to thickness versus ratio of umbo distance to height. The area of *H. comalensis* is separate from that of *H. knowltoni*. The outlier specimen is from the Comanche Peak Formation NPL44903. (**4**) Left lateral and dorsal outlines of *H. comalensis* illustrated by Whitney (1937, pl. 13, figs. 3, 4). (**5**) Left lateral and dorsal outlines of *H. knowltoni* holotype USNM145644. Scale bars = 1 cm; dashed line marks the commissure; arrows indicate beaks.

Cohort Cardiomorphi Férussac, 1822 in Férussac 1821–1822
Subcohort Cardioni Férussac, 1822 in Férussac 1821–1822
Infrasubcohort Cardiidia Férussac, 1822 in Férussac 1821–1822
Megaorder Poromyata Ridewood, 1903
Order Poromyida Ridewood, 1903
Superfamily Poromyoidea Dall, 1886

Remarks.—This superfamily is composed of two families, Poromyidae Dall (1886) and Cetoconchidae Ridewood (1903), according to Carter et al. (2011).

Family Poromyidae Dall, 1886

Remarks.—Poromyidae genera are large, rounded to quadrate, most with radial costae, external ligament without a lithodesma, and at least one cardinal tooth in one valve (Keen in Newell, 1969). Modern Poromyidae are deep-water infaunal carnivores (Morton, 1981).

Genus *Liopistha* Meek, 1864

Type species.—*Cardium elegantulum* Roemer, 1852, p. 48–49, pl. 6, figs. 5a–c.

Diagnosis.—Features of the family.

Occurrence.—Early to Late Cretaceous.

Subgenus *Sergipemya* Ayoub-Hannaa et al., 2015
Liopistha (*Sergepimya*) *alta* (Roemer, 1852)

Figure 11.5–11.8

1852 *Homomya alta* Roemer, p. 45, pl. 6, fig. 11.
1890 *Homomya alta*; Cragin, p. 76.
1895 *Homomya alta*; Cragin, p. 360.
1928 *Homomya alta*; Adkins, p. 141.
2002 *Psilomya alta*; Akers and Akers, p. 388, p. 389, fig. 372.
2015 *Liopistha (Sergipemya) alta*; Ayoub-Hannaa et al., p. 58.

Holotype.—STIPB-Roemer-79, Steinmann-Institut, Paläontologie, Geologisch-paleontologische Institute, University of Bonn.

Diagnosis.—Tall triangular shell, anterior margin truncated, posterior margin rounded; ornamented by irregular concentric ridges and grooves; minute, closely spaced nodes top concentric ridges and are vertically aligned in faint radial rows; posterior gape.

Occurrence.—Roemer (1852) collected the specimen of *L. alta* near Fredericksburg, central Texas, and Adkins (1928) reported it in the Fredericksburg Group. Cragin (1890, 1895) reported *H. alta* in the basal bed of the lower upper Albian Kiowa Formation in Kiowa County, southern Kansas. This 30 cm thick bed is a transgressive lag deposit that yields two ammonite species of the upper Goodland Formation in Texas: *Venezoliceras acutocarinatum* (Shumard, 1854) and *Venezoliceras kiowanum* (Twenhofel, 1924) (Young, 1966; Scott, 1970).

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Description.—Shell globose to inflated, heart-shaped, anterior margin truncated, posterior margin subrounded, inflated, ornamented by concentric irregular striae and growth rings; umbo prominent, enlarged, prosogyrate (Roemer, 1852, p. 45, translated from the Latin). Valve length nearly the same as height.

Valve shape triangular, angle between anterior margin and dorsal margin about 65°, posterior margin short, straight, inclined about 145° from dorsal margin; posterior-ventral corner arcuate merging with broadly curved ventral margin that curves broadly into nearly straight anterior margin, wide ovate gape. Umbo broadly curved prosogyrate. Escutcheon narrow, elongate, bordered by low ridges on either valve. Ornamented by low, rounded, concentric growth rugae wider than interspaces, topped by minute, granule-like nodes aligned forming weak indistinct lineations.

Roemer (1852) listed the length of *H. alta* as 1″ 9‴, height 1″ 9‴, width 1″ 5‴, which are translated as 1.9 inch and 1.5 inch. Converted to metric units: L = 48.26 mm; H = 48.26 mm; W = 38.10 mm.

Remarks.—Ayoub-Hannaa et al. (2015) designated *Homomya alta* Roemer (1852) the type species of their new subgenus, *Sergipemya*. Their diagnosis of *Sergipemya* includes "posterior gape lacking; numerous fine commarginal ribs covering the valves and crossed by faint radial tubercles"; however, they state in their description of *Liopistha (Sergipemya) alta* that "radial ornament is absent" (Ayoub-Hannaa et al., 2015, p. 58). They also say that a posterior gape is absent. The type specimen of *H. alta* is ornamented by irregular concentric ridges and grooves (Roemer, 1852); minute, closely spaced nodes top the concentric ridges and are vertically aligned in faint radial rows (Fig. 11.5–11.7), which is consistent with the subgeneric diagnosis. However, the diagnosis should be modified to include the presence of a posterior gape. Roemer's species is middle to upper Albian, and Ayoub-Hannaa et al. (2015) extend the range into the Cenomanian.

Roemer (1852) compared the overall form of *H. alta* to *Pholadomya ligeriensis* d'Orbigny (1843), which Ayoub-Hannaa et al. (2015, p. 50) reassigned to *Pleuromya*. The triangular shell morphology of *H. alta* is very similar to that of *Pholadomya* (*Bucardiomya*) Rollier in Cossman (1912), which, however, has distinct, even, wide radial costae. A species very similar to *H. alta* is *Pholadomya (Bucardiomya) gigantea* Jaitly (2013) in the Middle Jurassic of western India. This species is about 60 cm tall and has faint indistinct umbonal radial ribs.

A note to clarify the stratigraphic position of *Liopistha* [*Cardium*] *elegantulum* (Roemer, 1852), the type species of *Liopistha*: Roemer collected his specimen at the waterfall in the Guadalupe River beyond ("unterhalb" was Roemer's word; Roemer, 1852, p. 49) New Braunfels, Texas. In this area, either the lower Cenomanian Buda Limestone or the middle to upper Albian Edwards Limestone is exposed, so the age of *L. elegantulum* is not Santonian as suggested by Dhondt and Jagt (1988) but Albian or lower Cenomanian.

Order Pholadomyida Newell, 1965
Superfamily Pholadomyoidea King, 1844

The superfamily Pholadomyoidea is composed of four phylogenetically related families: Pholadomyidae, Arenigomyidae, Margaritariidae, and Ucumariidae (Carter et al., 2006; Carter et al., 2011).

Family Pholadomyidae King, 1844

Remarks.—The family Pholadomyidae is composed of the subfamilies Pholadomyinae and Chaenomyinae (Carter et al., 2011).

Description.—Small- to large-sized, equivalved, very inequilateral, oblong, ovate or subtrigonal, moderately to very inflated bivalves; anterior margin evenly curved, ventral margin gently curved to nearly straight, some with shallow sulcus; ventral-posterior margin curved to truncate; dorsal-posterior margin straight, inclined ventrally or dorsally. Posterior gape narrow to wide, anterior gape where present is narrow. Umbos rounded to subangular, anterior of midline; posterior umbonal carina weak or absent; lunule absent or shallow in most species; escutcheon, if present, shallow, bordered by low ridges.

Ligament external, opisthodetic, quasi-parivincular, attached to low, rounded pseudonymph in escutcheon (Carter et al., 2012, p. 148); cardinal plate extends from umbo posteriorly, with a resilium of low wave-like swellings and grooves; hinge edentulous, narrow, and straight in most, some with one or more small knob-like projections on hinge. Pallial sinus depth variable among genera; adductor and pedal muscle scars present. Radial ornament is absent or low, radial folds or ribs, some with tubercles, some with fine radial lines or radial rows of pustules, most with distinct to weak concentric growth rugae. Shell composed of aragonitic, thin, nacreous ostracum but rarely preserved (personal communication, J.G. Carter, 2016); Early Triassic to Holocene.

Subfamily Pholadomyinae King, 1844

Remarks.—Subfamily comprises 23 genera (Newell, 1969), including *Homomya* and *Pachymya*.

Genus *Homomya* Agassiz, 1843

Type species.—*Mactra gibbosa* J. Sowerby, 1813 in Sowerby and Sowerby, 1812–1846, p. 91; Herrmannsen, 1847, p. 541.

Diagnosis.—Equivalved, elongate to ovate, moderately protruding umbos situated anterior of valve midline; dorsoposterior margin straight, downwardly sloping, or slightly upturned; edentulous, opisthodetic ligament attached to pseudonymph in escutcheon; deep pallial sinus; ornamented by concentric growth rugae; radial ribs may be present only in juvenile stages.

Occurrence.—Early Triassic to middle Eocene.

Homomya knowltoni (Hill, 1893)
Figure 9.1–9.8

1893 *Pholadomya knowltoni* Hill, p. 30, pl. 2, figs. 1, 2.
1901 *Pholadomya knowltoni*; Hill, p. 232.
1940 *Pholadomya knowltoni*; Smith, p. 611.
1982 *Pholadomya knowltoni*; Offeman et al., p. 79, fig. 103.
1896 *Pleuromya knowltoni*; Stanton and Vaughan, p. 23.

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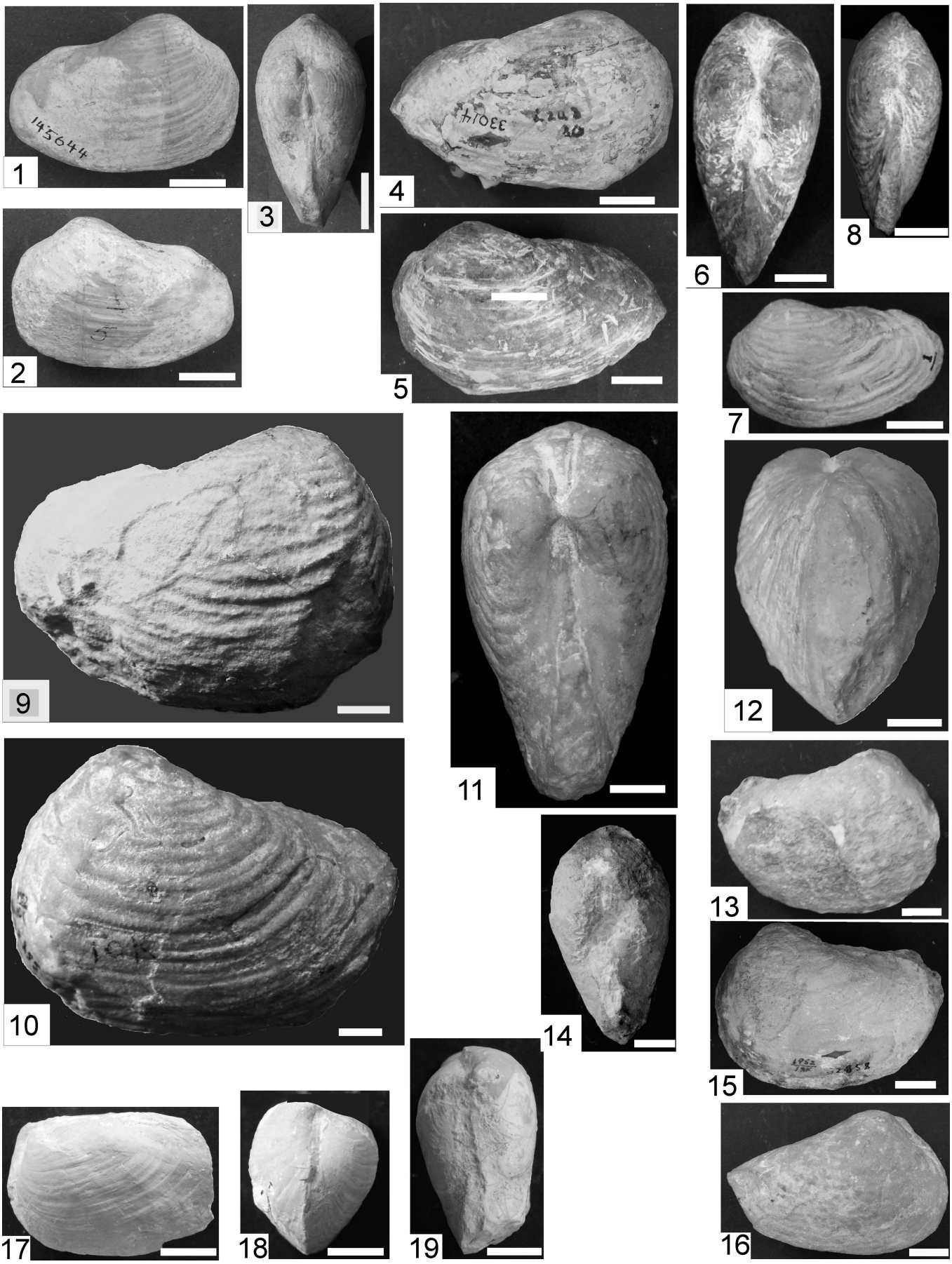

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1910 *Pleuromya knowltoni*; Böse, p. 17, 136.
1996 *Pleuromya knowltoni*; Hovorka et al., p. 16.
1996 *Pleuromya knowltoni*; Small et al., p. 4, 8, 13.
1928 *Pholadomya*(?) *knowltoni*; Adkins, p. 138.
1937 *Homomya knowltoni*; Whitney, p. 128, pl. 13, figs. 1, 2.
2002 *Homomya knowltoni*; Akers and Akers, p. 367, p. 368, fig. 350, p. 468.
1961 *Homomya tarrantensis* Perkins, p. 84, pl. 26, figs. 3, 4, 6–8.
2002 *Homomya tarrantensis*; Akers and Akers, p. 369, fig. 352, p. 468.

Holotype.—*Homomya tarrantensis* Perkins is UMMP 33014; paratypes: UMMP 33015, 33016, 33017, 33018, and 33019.

Lectotype.—*Homomya knowltoni* NMNH 145644 is here designated lectotype from a set of two cotypes; NMNH 145652 is a paralectotype; specimen label: "Glen Rose beds, Trinity, Cretaceous"; from "section along Colorado River between Austin and Paleozoic contact, Burnet County, Texas."

Diagnosis.—A moderately small species 30–60 mm long, equivalved, inequilateral valves, inflated, prosogyrate beaks, distance between beak and anterior margin averages 35% of the length; anterior margin broadly rounded; ventral margin very slightly arched toward truncated posterior margin; dorsal margin nearly straight; no lunule; shallow narrow escutcheon. Concentric growth rings low, rounded.

Occurrence.—The type locality of *Homomya knowltoni* is in exposures along the Colorado River valley in the Austin area. This is in middle parts of the Glen Rose Formation near the mouth of Bull Creek (Adkins, 1928). The species is reported throughout much of the Glen Rose section in north-central Texas above *Mesorbitolina texana* (Roemer, 1852) with a diverse set of bivalves and gastropods (Whitney, 1937; Rodgers, 1967). In Hays County, *H. knowltoni* is in Unit 3 of the Upper Member, Glen Rose (Watson et al., 2017). It also is in the Edwards Formation at Austin on East Bull Creek, just east of old Spice Springs Road Crossing, east of West Loop Bridge, Travis County, Texas. *H. knowltoni* is considered a marker taxon of the Regional Dense member of the Person Formation northwest and southwest of Austin (Small et al., 1996). However, collections in 2015 and 2016 discovered only *Homomya comalensis* Whitney 1937. Akers and Akers (2002, p. 367) reported *H. knowltoni* in the Glen Rose, Edwards, and Kiamichi formations, central Texas and north Texas, and in the Bluff Formation in southwest Texas (Smith, 1940). A single new specimen is from the Kiamichi Formation.

The type specimens of *Homomya tarrantensis* are from the Benbrook Member of the Goodland Formation exposed along Marys Creek in southwest Fort Worth, Tarrant County, Texas. The total range of *H. knowltoni* is from the lower Albian Upper Glen Rose to basal upper Albian Kiamichi Formation in Texas.

Description.—Specimens are external casts showing exterior shape and ornament; most are incomplete. Ornament of unequal concentric growth rugae, rounded, slightly steeper ventrally, continuous to discontinuous anteriorly to posteriorly. Length ranges from about 38 to 63 mm, height is from 24 to 41 mm, and width is from 17 to 38 mm. The distance from anterior margin to beak is from about 14 mm to about 20 mm. Opisthodetic ligament attached to pseudonymph; dentition and musculature unknown.

Remarks.—Types of *H. knowltoni*, *H. comalensis*, and *H. tarrantense* display well-defined escutcheons, in which the conjunction of the two valves forms a low pseudonymph (Fig. 4.3, 4.7–4.9). The dorsal margins of the two valves do not overlap as is the case of *Pleuromya*. Therefore, this set of species is here allocated to *Homomya*.

Hill (1893, p. 30) compared *H. knowltoni* to *Pholadomya pleuromayaeformis* Choffat (1888) in Albian deposits near Dombey, Angola, West Africa. Examination of Choffat's drawings of this African species shows that his species differs from the Texas species by having two to four low, rounded radial ribs extending from beak to ventral margin, typical of *Pholadomya*. The beaks of *P. pleuromayaeformis* appear to project higher than those of *P. knowltoni* and the lunule appears to be distinct. Because of the radial ribs, *P. pleuromayaeformis* is a separate species.

Stanton and Vaughan (1896), followed by Böse (1910), Hovorka et al. (1996), and Small et al. (1996), reassigned *Pholadomya knowltoni* to *Pleuromya* without explanation. Subsequently, no one has presented a taxonomic explanation of this generic reassignment. Stanton and Vaughan (1896) and Böse (1910) listed this species in the assemblage from the basal limestone unit at Cerro de Cristo Rey, which is the Finlay Formation and which they correlated with the Fredericksburg Group in north Texas.

Three specimens in the collections of the Non-vertebrate Paleontology Laboratory, University of Texas Austin, are labeled as "*Homomya fredericksburgensis* n. sp. W.C.I." (UT 17010, 17011, 17013). The author is identified as W.C.I. and this species name has never been published, so it is a nomen nudum. Each specimen was collected from the upper part of the Walnut Formation near Belton, Texas. These specimens are here assigned to *H. knowltoni*.

Homomya tarrantensis is here considered a junior synonym of *H. knowltoni* because it shares the same morphology and its shape and size are within the range of *H. knowltoni* (Fig. 4). The position of the umbo of *H. tarrantensis* is about 25% of the length, and that of *H. knowltoni* is about 35%. *H. tarrantensis* is common in the middle and upper parts of the Goodland Formation in the Fort Worth, Texas, area (Perkins, 1961).

Pleuromya aff. *P. inconstans* Castillo and Aguilera (1895) is quite similar to *H. knowltoni*, but the posterior-dorsal carina is distinct. This species is in dark gray limestone near Miquihuana,

Figure 9. (**1–3**) *Homomya knowltoni*; holotype USNM 145644; (**1**) right valve; (**2**) left valve; (**3**) dorsal view. (**4–8**) *Homomya tarrantense*; (**4–6**) holotype UMMP 33014; (**4**) right valve; (**5**) left valve; (**6**) dorsal view; (**7, 8**) paratype UMMP 33015; (**7**) left valve; (**8**) dorsal view. (**9–12**) *Homomya kellumi* holotype UMMP 32855; (**9**) right valve; (**10**) left valve; (**11**) dorsal view; (**12**) posterior view. (**13–16**) *Homomya tlahualiloensis*; (**13–15**) holotype UMMP 32858; (**13**) right valve; (**14**) dorsal view; (**15**) left valve; (**16**) right valve paratype UMMP 32859. (**17–19**) *Homomya comalensis* lectotype NPL85566; (**15**) left valve; (**18**) anterior view; (**19**) dorsal view. Scale bars = 1 cm.

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Tamaulipas, Mexico. Imlay (1937) tentatively correlated this limestone with the Valanginian Stage by associated ammonites, which in Cuba are Valanginian (Myczynski, 1977).

Pleuromya orbigniana (Rouillier, 1845) is in the Berriasian-Valanginian Spilsby Sandstone in northeastern England near the North Sea coast (Woods, 1909, p. 256–257). This species is much smaller than *H. knowltoni* and is ornamented by either radial striae or radial rows of nodes. A similar species, *Pleuromya peregrina* (d'Orbigny, 1845), is found in lowermost Cretaceous near Moscow. *Pleuromya hidensis* Hayami (1959) in Aptian strata of Japan and eastern China is smaller than *H. knowltoni* and taller relative to its length, with a length-to-height ratio of 1.5.

Pholadomya marcoui Cragin (1905) in the lowermost Cretaceous Malone Formation in southwest Texas is very similar in form to *H. knowltoni* except for the six faint radial ribs (Akers and Akers, 2002, p. 359–360, fig. 342). If these species are not related they are convergent morphotypes.

Pleuromya ingramensis Pampe (1975) is an internal cast from the Middle Albian Basal Nodular Member of the Fort Terrett Formation, Fredericksburg Group, north of Kerrville, Texas. It is not a pleuromyid or pholadomyid. Its raised posterodorsal margin along the hinge line and pronounced grooves along the dorsal side are characteristic of arcid taxa such as *Cucullaea*.

Homomya comalensis Whitney, 1937
Figures 9.17–9.19, 11.11

1937 *Homomya comalensis* Whitney, p. 130, pl. 13, figs. 3, 4.
2002 *Homomya comalensis*; Akers and Akers, p. 367, p. 368, fig. 350, p. 468.

Lectotype.—The single specimen illustrated by Whitney would be the holotype, but has not been found in the collections of the Non-vertebrate Laboratory, the University of Texas. Consequently, a lectotype is selected from among two specimens recovered from the Regional Dense Member of the Person Formation in the road cut at Stone Crossing, New Braunfels, Texas (Porter, 2017), Texas Memorial Museum Non-vertebrate Paleontology Laboratory NPL85566. Unnumbered paralectoypes are from the Regional Dense Member of the Person Formation at the exposures where highways Loop 1 and Loop 360 intersect in south Austin and from the basal Bee Cave Member of the Walnut Formation on the east road cut in Loop 360 at Bee Cave Road, Austin (Diehl, 2017).

Diagnosis.—A moderate-sized species 30–50 mm long equivalved, very inequilateral, ovate, globose valve, longer than high, slightly higher than wide; beaks low, slightly opisthogyrate, very close to rounded anterior margin, distance between beak and anterior margin averages 15% of the length; ventral margin broadly curved; posterior margin narrowly rounded, slightly gaping, and sloping into flat dorsal margin; no lunule, shallow wide escutcheon. Low, rounded concentric growth rings.

Occurrence.—Whitney's specimen of *Homomya comalensis* is from the middle Glen Rose Formation: "About 275 feet (84 m) above the base … 2.3 miles (3.7 km) west of Fischer Store, Comal County," Central Texas (Whitney, 1937, p. 131). Newly discovered specimens are in lime mudstone from the middle Albian Regional Dense Member at the base of the Person Formation in Travis and Hays counties and in the Bee Cave Member of the Walnut Formation in Travis County. Total known range is lower to middle Albian.

Description.—Specimens are external casts showing exterior shape and ornament; most are incomplete. Beaks wide, very low, barely projecting above the straight dorsal margin. Ornament of weak, rounded, unequal, discontinuous concentric growth rugae, slightly steeper ventrally. Length ranges from 36 to 55 mm, height is from 19 to 35 mm, and width is from 20 to 29 mm. The distance from anterior margin to beak is from about 5 mm to 11 mm. Posterior gape is slight, not flared. Interior dentition, ligament, and musculature are unknown.

Remarks.—Whitney (1937) distinguished *Homomya comalensis* from *H. knowltoni* by its greater width, by its rounded gaping posterior margin, and by posterior ridges bordering escutcheon (Akers and Akers, 2002, fig. 230). *H. comalensis* is as long as smaller specimens of *H. knowltoni*, but its height is less and it is slightly wider at the same height than *H. knowltoni* and *H. tarrantensis* (Figs. 6, 8). The distance of the beak from the anterior margin of *H. comalensis* is less than of *H. knowltoni* margin so the beak-to-length and beak-to-height ratios are lower than for *H. knowltoni* (Fig. 8).

Homomya kellumi (Perkins, 1961)
Figure 9.8–9.12

1910 *Homomya* aff. *H. ligeriensis* Böse, p. 137, pl. 29, figs. 1–4.
1928 *Homomya* aff. *H. ligeriensis*; Adkins, p. 142.
2002 *Homomya* aff. *H. ligeriensis*; Akers and Akers, p. 369, fig. 352.
1961 *Homomya kellumi* Perkins, p. 82, pl. 24, fig. 5; pl. 15, figs. 1–3, 5, 6.
1967 *Homomya kellumi*; Lokke, p. 352.
2002 *Homomya kellumi*; Akers and Akers, p. 468.
1961 *Homomya tlahualiloensis* Perkins, p. 83, pl. 25, figs. 4, 7–10.

Holotype.—*Homomya kellumi*: holotype UMMP 32855; paratypes: UMMP 32856, 32857. Type locality and age: Sierra Tlahualilo, localities 13, 14, 15, 18, 19, 31, and 51, Coahuila, Mexico, upper interval of Aurora Limestone, Lower Cretaceous. Holotype of *Homomya tlahualiloensis*: UMMP 32858; paratypes UMMP 32859. Type locality and age: Sierra Tlahualilo, localities 14, 18, 26, and 29, Coahuila, Mexico, upper interval of Aurora Limestone, Lower Cretaceous.

Diagnosis.—A large-sized, 65–70 mm long, equivalved species, very inequilateral, inflated, prosogyrate beaks 25% to 30% of the length from the anterior margin; anterior margin broadly rounded; ventral margin broadly arched toward narrowly curved posterior margin; dorsal margin nearly straight; gape extends anteriorly along dorsal commissure that merges into a low ridge up to beak.

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Occurrence.—Type specimens of *H. kellumi* and *H. tlahualiloensis* were collected from the upper part of the upper interval of the Aurora Limestone. Two specimens of *H. kellumi* were also collected from the Fort Worth Limestone near Fort Worth, Tarrant County, Texas (Perkins, 1961, p. 55). Specimens of *Homomya* aff. *H. ligeriensis* were collected at Cerro de Muleros (now Cristo de Rey), New Mexico, west of El Paso, Texas, in units 4–6 with the upper Albian ammonite *Mortoniceras equidistans* (originally *Schloenbachia trinodosa*) (Cragin, 1893). This stratigraphic interval is now composed of the upper Albian Smeltertown, Muleros and Mesilla Valley formations (Lucas et al., 2010) and correlate with the Washita Group of North Texas.

Remarks.—Perkins (1961) characterized *H. kellumi* by "its high beaks and pronounced shoulder anterior to the beaks." He contrasted *H. tlahualiloensis* with *H. kellumi* by the "less pointed and less terminal beaks," its greater width, and by the absence of an anterior shoulder (Perkins, 1961, p. 83). However, these characters intergrade; the distance between the anterior margin and beak of the former is 17.2 ± 3.14 mm compared to 17.3 ± 2.03 mm in the latter (data of *Homomya* species described here available as Supplementary Data). The mean widths of both species are within the standard deviation: mean width of *H. tlahualiloensis* is 33.7 ± 3.23 mm; mean width of *H. kellumi* is 32.5 ± 3.921 mm. These relative proportions, however, are gradational and an insufficient basis upon which to define species among this variable group of homomyids. The "pronounced shoulder anterior to the beaks" of *P. kellumi* is a subtle and impersistent feature subject to compaction and distortion. In addition, the species occur together at the same sites in the upper part of the Aurora Limestone at Sierra de Tlahualilo, thus have no stratigraphic or geographic significance. Therefore, they are here judged to be synonyms.

Perkins compared *H. kellumi* to *Homomya bravoensis*, which has a lower height-to-thickness ratio (Fig. 4). *Homomya bravoensis* is an oblong species with a length-to-height ratio of 1.38; its anterior margin is nearly at a right angle to the dorsal margin; whereas *H. kellumi* is a low triangular form with a length-to-height ratio of 1.34 and apical angle of about 115°.

Although Perkins did not compare *H. kellumi* to the lower Cenomanian *Homomya austinensis* Shattuck (1903, pl. 16, figs. 1–3), they are quite similar in form, proportions, and size (Table 2). The gape even extends anteriorly along the posterior hinge, which merges into a low ridge, the pseudonymph beneath the beaks. However, *H. austinensis* differs from *H. kellumi* by its more broadly rounded, wider posterior margin, which reflects a wider siphon.

Perkins also compared *H. kellumi* to *Homomya* aff. *H. ligeriensis* d'Orbigny (1845), which has finer growth rugae and is less elongate than *H. kellumi*. Böse (1910) identified a species at Cerro de Muleros (now Cristo de Rey), New Mexico, west of El Paso, Texas, that he compared to *Homomya ligeriensis*:

> The average shell has an ovate form, transversally extended, somewhat convex, posteriorly extended; anterior margin arcuate passing by a curve into the ventral margin; this margin is also somewhat arcuate; posterior margin is not preserved in any of the specimens but nevertheless the outline of lines for a superficial very regular curve; dorsal margin straight; umbos strong large, prominent, prosogyrate; situated very near the anterior of the dorsal margin. The valves are gaping posteriorly. The ornament on the surface consists of very regular concentric costellae separated by relatively deep grooves.
>
> Our species is very similar to *Homomya ligerienses* of the Cenomanian at Le Mans, the differences are quite small; in the Mexican form the umbos are smaller and lower and the outline is slightly different. We cannot compare our specimens with the French species because none of our examples are complete.
>
> Number of specimens: 4.
>
> Locality: Cerro Muleros close to the monument marking the Mexican-US border.
>
> Horizon: Subdivisions 4, 5 and 6, horizon with *Schloenbachia trinodosa*, lower Cenomanian. (Böse, 1910, p. 137)

Adkins (1928, p. 142) described *Homomya* aff. *H. ligeriensis* as a "form subrectangular, beaks nearly terminal; prominent somewhat irregular growth lines." The specimen illustrated by Akers and Akers (2002, fig. 352) is incompletely preserved and is within the size range of *H. kellumi*. Because the size, shape, and stratigraphic and geographic ranges of *Homomya* aff. *H. ligeriensis* are similar to those of *H. kellumi*, it is placed in synonymy with *H. kellumi*.

Ayoub-Hannaa et al. (2015) reassigned the species *Pholadomya ligeriensis* to *Pleuromya*. *Pleuromya ligeriensis* d'Orbigny (1845) is well known from Cenomanian-Turonian strata in Europe, North Africa, Nigeria, and Brazil (Ayoub-Hannaa et al., 2015). *P. ligeriensis* is about the same size as *H. kellumi* and *H. tlahualiloensis* but the length and height of *P. ligeriensis* are nearly the same, whereas the Comanchean species are longer than high. The valve outline of *H. ligeriensis* differs from the two Albian species in having a straighter anterior margin and a more steeply inclined posterior margin, and the angle between the dorsal and anterior margins is nearly 90° whereas the same angle of the Albian species is greater than 90°. *P. ligeriensis* differs from *H. kellumi* by its strongly prosogyrate beaks and by the right angle between dorsal and anterior margins (Ayoub-Hannaa et al., 2015).

Homomya washitae Cragin, 1894
Figure 10.1–10.3

1894 *Homomya washita* (sic) Cragin, p. 59.
1928 *Homomya washita* (sic); Adkins, p. 141.
2002 *Homomya washita* (sic); Akers and Akers, p. 469.
1961 *Homomya washitae*; Perkins, p. 40.

Holotype.—NMNH PAL 32689; topotype: WSA 10444, the label reads "*Homomya washitaensis* (sic), railroad cut, 0.5 mi SE of Union Depot, Denison."

Diagnosis.—Shell elongate, broadly inflated, beak at anterior margin; escutcheon a narrow shallow depression merging posteriorly with a straight commissure line posterior to beaks; concentric rugae as flat ridges wider than the interspaces; ribs slope slightly ventrally and widen from beak to ventral margin.

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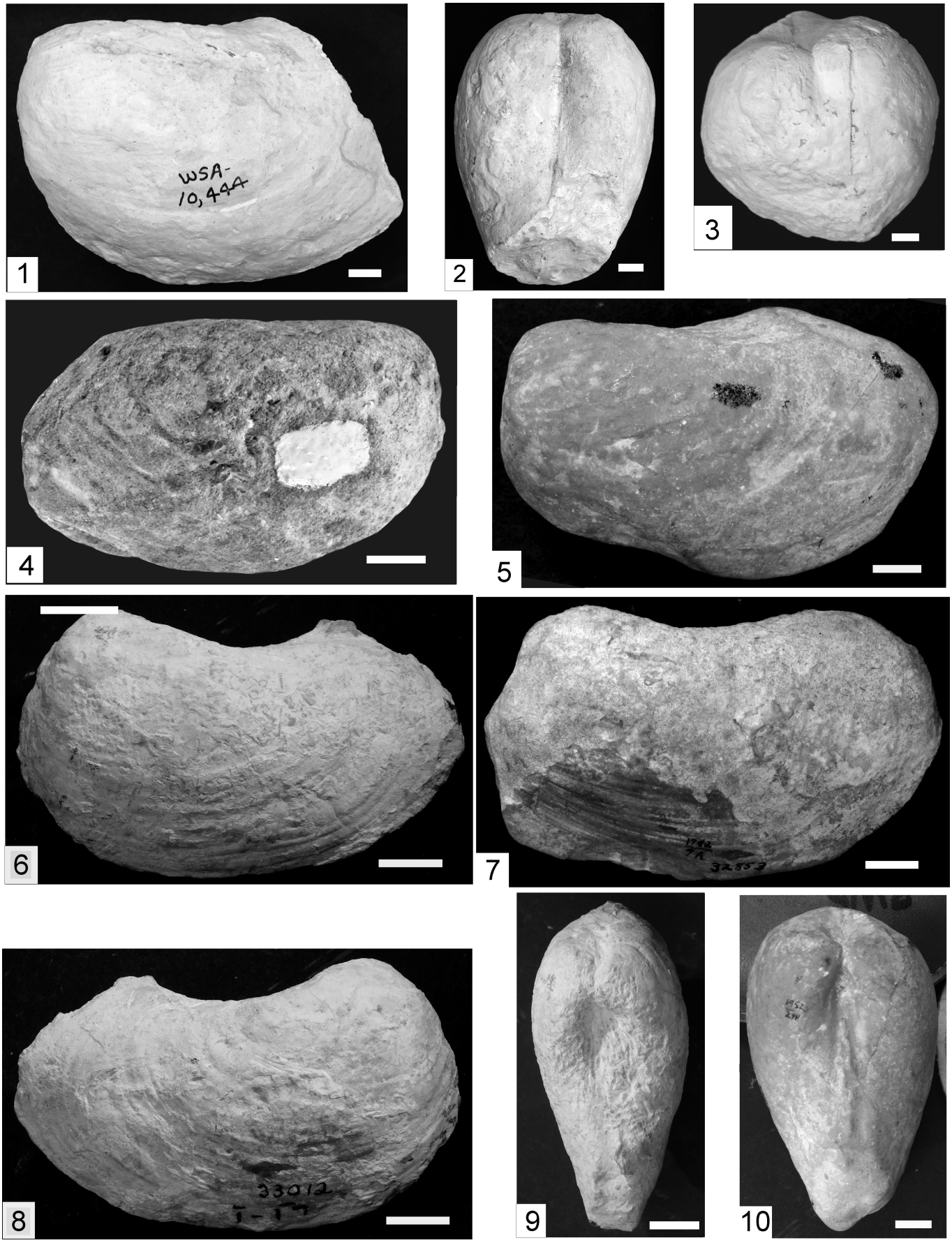

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Occurrence.—Upper Albian Main Street Limestone and lower Cenomanian Grayson Formation "in the abandoned D. B. and N. O. railway cut about half a mile southeast of the Union depot of Denison, Texas; … on summit of Pawpaw creek bluff southeast and east of Dennison" (Cragin, 1894, p. 60). Specimen WSA 10444 (Non-vertebrate Paleontology Laboratory) was collected from a railroad cut in the Grayson Formation 0.5 mi southeast of the Union Depot, Denison, Grayson County, Texas.

Cragin's Description.—"Shell large, curved-oblong, closed or nearly closed anteriorly and closed along the dorsal margin back of the beaks, obliquely truncated and gaping posteriorly, the breadth usually a little greater than the vertical dimension from hinge-margin to ventral margin, the length equal to somewhat more than one and a half times the breadth, the greatest breadth being about half way between the beaks and the mid-region; beaks nearly terminal, low, swollen, obtusely tangent, their bases long in the direction of the length of the shell and rising at a very low angle from their posterior origin to their rather broadly rounded summits; surface marked only with concentric growth-lines and undulations, and sometimes showing distally two or three broad growth-zones or stage" (Cragin, 1894, p. 59). Length 120 mm, height 92 mm, width 80 mm.

Remarks.—A plaster cast of the incomplete holotype NMNH 32689 is curated in the Non-vertebrate Paleontology Laboratory at the University of Texas (WSA10444). The posterior portion is missing and the anterior, dorsal, and ventral margins are intact. A lunule is not developed because the umbo is terminal; the escutcheon is directly posterior to the beaks and is a narrow and shallow depression merging posteriorly with a straight commissure line. The concentric rugae are incompletely preserved as flat ridges wider than the interspaces; the ribs slope slightly ventrally and widen from beak to ventral margin.

Cragin (1894) originally spelled the species name "*washita*," which is an incorrect Latinization and therefore not an inadvertent error (ICZN, 2000 Code, Article 32.5, p. 39). The correct Latinized species name is "*washitae*" as a noun in the genitive case (ICZN, 2000, Code, Article 11.9, p. 13–14).

Homomya austinensis (Shattuck, 1903)

1903 *Homomya austinensis* Shattuck, p. 28, pl. 16, figs. 1–3.
1928 *Homomya austinensis*; Adkins, p. 141.
1961 *Homomya austinensis*; Perkins, p. 42.
2002 *Homomya austinensis*; Akers and Akers, p. 468.

Holotype.—*Homomya austinensis* holotype: NMNH PAL 315995; topotypes: NPL 62211, UT 30035, UT32168, UT 32299, UT 32308, UT 32309.

Diagnosis.—A moderately large, 50–65 mm long, equivalved, inequilateral, ovate species about one and a half times long as tall, relatively narrow width, weakly inflated, prosogyrate beaks 15% to 20% of the length from the anterior margin; anterior margin broadly rounded; ventral margin merging smoothly into curved posterior margin; dorsal margin nearly straight with a distinct escutcheon.

Occurrence.—Lower Cenomanian Buda Limestone, Austin, Texas.

Description.—Inflated, equivalved, inequilateral shell; anterior margin rounded, ventral margin broadly rounded, posterior margin narrowly rounded, dorsal margin slightly inclined toward beak, beak about one-fourth the length toward the anterior. Beaks nearly touching, slightly prosogyrate; no lunule, anterior hinge margin short; posterior hinge margin a low ridge at commissure, bordered by shallow groves that are separated from umbo by faint ridges. Slightly gaping. Ornamented by low, rounded, concentric growth rugae, wider than interspaces.

Remarks.—The outline and compact thickness of this species are more similar to *H. kellumi* than to other species in the Buda Limestone. Its escutcheon is shallow, fading out into the posterior gape and with a commissural pseudonymph ridge. Shattuck (1903, p. 28) differentiated *H. austinensis* from *H. vulgaris* in "that it is much shorter and broader in proportion to its thickness. It is also much more compressed." *H. austinensis* is nearly indistinguishable from the French and Brazilian *P. ligeriensis* (d'Orbigny, 1845, in Ayoub-Hannaa et al., 2015). The length-to-height ratio of *H. austinensis* is 1.44 and that of *P. ligeriensis* is 1.52; *H. austinensis* is the larger species; the beak positions are virtually the same. *P. ligeriensis* is a cosmopolitan member of the Mediterranean to eastern South American provinces (Ayoub-Hannaa et al., 2015), and *H. austinensis* is a member of the Caribbean Province.

Homomya vulgaris Shattuck, 1903

1903 *Homomya vulgaris* Shattuck, p. 29, pl. 16, figs. 4–5.
1928 *Homomya vulgaris*; Adkins, p. 141.
2002 *Homomya vulgaris*; Akers and Akers, p. 371, 372, 469, fig. 354.

Holotype.—*H. vulgaris* holotype: NMNH PAL 315996; topotypes: NPL 62219, WSA 5013, UT 35380B.

Diagnosis.—An equivalved, very inflated, elongate shell much longer than tall, with subparallel dorsal and ventral margins; with a shallow, elongate escutcheon.

Occurrence.—Uppermost interval of the lower Cenomanian Buda Limestone, upper Washita Group in the Austin, Texas, area; in northern Mexico it is in the upper part of the upper Albian Aurora Limestone.

Figure 10. (**1–3**) *Homomya washitae* Cragin, 1894; plaster cast of WSA 10,444, incomplete specimen, Grayson Marl, Denison, Texas; (**1**) left valve; (**2**) dorsal view; (**3**) anterior view. (**4**) *Homomya bravoensis* Böse, holotype IGM 384, RV; (2017 image available at: http://www.unipaleo.unam.mx/public/consulta_publica.php). (**5, 10**) *Homomya budaensis* Whitney, 1911, hypotype UMMP 32854, collected by Perkins (1961); (**5**) left valve; (**10**) dorsal view. (**6, 8, 9**) *Homomya cymbiformis* Perkins, 1961; holotype UMMP 33012; (**6**) left valve; (**8**) right valve; (**9**) dorsal view. (**7**) *Homomya auroraensis* Perkins, 1961, holotype UMMP 32853, left valve. Scale bars = 1 cm.

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Description.—Large-sized, 70–100 mm long elongate shell, widely inflated; anterior margin broadly rounded, ventral margin broadly curved, posterior margin narrowly rounded, merging with dorsal margin that slopes up to umbo. Umbos broadly incurved, slightly prosogyrate; no lunule; escutcheon wide, shallow, merging smoothly with valve margins. Ornamented by rounded growth rugae wider than interspaces, widening and diverging posteriorly.

Remarks.—Perkins (1961) distinguished *H. vulgaris* from his new species *Homomya auroraensis* by several relative differences in shape: (1) the dorsal margin of *H. auroraensis* is more concave than *H. vulgaris*; (2) the posterior margin of *H. auroraensis* is more rounded; (3) beaks of *H. auroraensis* are more posterior from the anterior margin and less prosogyrate; and (4) the height-to-thickness ratio of *H. auroraensis* is less. These differences are subject to compaction and distortion. Only the latter two properties can be quantified and the differences are slight based on the small number of specimens. In a subsequent section, *H. auroraensis* is considered a junior synonym of *Homomya budaensis*.

H. vulgaris occurs with *Homomya budaensis* in the Buda Limestone in the Austin, Texas, area. They differ, however, by the valve outlines. *H. vulgaris* is an elongate shell and its dorsal margin is subparallel with the ventral margin. *H. budaensis* has a concave dorsal margin and its posterior is expanded and flares dorsally. This difference suggests that soft parts such as siphons or gills were larger in *H. budaensis*.

Homomya bravoensis Böse, 1910
Figure 10.4

1910 *Homomya bravoensis* Böse, p. 136, pl. 29, figs. 5, 6.
1928 *Homomya bravoensis*; Adkins, p. 141.
1961 *Homomya bravoensis*; Perkins, p. 83.
2002 *Homomya bravoensis*; Akers and Akers, p. 367, p. 368, fig. 350.

Holotype.—*Homomya bravoensis* holotype IGM 384, Colección Nacional de Paleontología (IGM), Universidad Nacional Autónoma de México; upper Albian, Böse's unit 3 with *Ceratostreon* [*Exogyra*] *texana*, along the Southern Pacific and Bisbee Railroad, near Rio Bravo, Chihuahua, Mexico (source: http://documents.mx/documents/fosiles-tipo-mexicanos.html; image available at: http://www.unipaleo.unam.mx/public/consulta_publica.php).

Diagnosis.—Elongate, ovate shell, beaks at anterior margin, posterior margin truncate, inclined, rounded, gaping; ornament of low, rounded concentric rugae.

Occurrence.—Type specimens were collected at Cerro de Muleros (now Cerro de Cristo Rey) next to the Southern Pacific and Bisbee railroad near the Rio Bravo, New Mexico, west of El Paso, Texas, in the Del Norte Formation. It is also known in the Edwards Formation west of Round Rock, Williamson, and in Bell and Parker counties, Texas, in Walnut to Goodland formations, Fredericksburg Group (Adkins, 1928). It is reported in the Benevides Formation in the southern part of the Quitman Mountains (Albritton and Smith, 1965). It also was collected from the University Mesa Marl near Fort Stockton, I-10, Pecos County, Texas (NPL 74414). In Mexico, it is in the lower part of the Upper Aurora Limestone. It ranges from middle Albian to lower upper Albian.

Description.—According to Böse:

> Shell moderately oval, transversally extended, very convex, posteriorly extended; anterior margin short, obliquely curved ventrally, posterior margin longer, regularly curved; dorsal margin nearly straight, long, subparallel with ventral margin which is slightly arcuate; umbo strong, elevated, globose, curved towards anterior and below; positioned nearly at the extreme anterior of the valve. The valves are open at the posterior margin. The ornament consists of undulations and concentric grooves. Dimensions: length 55 mm, height 40 mm, width of one valve 18.2 mm.
>
> Our species rather resembles *Homomya vulgaris* Shattuck in its general form, but is distinguished by the position of the umbos, which in our species are positioned very near the anterior margin and by the less extended form. The species is rather rare and is encountered only in the lower part of the Cretaceous deposits at Cerro Muleros; Stanton and Vaughan cited the same horizon of *Pleuromya knowltoni* Hill; we have not found this species at Cerro Muleros. (Freely translated from Böse, 1910, p. 136.)

According to Adkins:

> Form roughly elongate rectangular, rounded, oblique, quite inflated, beaks subterminal, proportionately less tall and more inflated than *H* aff. *ligeriensis*; reduced concentric lines. (Adkins, 1928, p. 142)

Remarks.—Böse noted that the overall form of *H. bravoensis* is similar to that of *Homomya vulgaris* Shattuck, but distinguished it by the position of the umbo, which is flush with the anterior margin. The escutcheon is elongate, ovate, but covered in lime mud (personal communication, J. Alvarado Ortega, 2017, Nacional de Paleontología del Instituto de Geología de la UNAM). *H. bravoensis* is from strata of the same age as *L.* (*Sergipemya*) *alta* but differs by its low umbo and oblong form; *L. alta* is characterized by a tall umbo very close to the anterior margin. The length and height of *L. alta* are subequal but the types of *H. bravoensis* are longer than high. *H. bravoensis* is similar to *H. budaensis* but tends to be shorter relative to its height, and the distance of the beak to the anterior margin of *H. bravoensis* is less than 10% and that of *H. budaensis* is nearly 30%.

Homomya budaensis Whitney, 1911
Figure 10.5, 10.7, 10.10

1911 *Homomya budaensis* Whitney, p. 15, pl. 3, figs. 1, 2, pl. 4, figs. 1, 2.
1928 *Homomya budaensis*; Adkins, p. 141.
1961 *Homomya budaensis*; Perkins, p. 81, pl. 24, figs. 4, 6, 7.

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2002 *Homomya budaensis*; Akers and Akers, p. 369, 468, fig. 352.
1961 *Homomya auroraensis* Perkins, p. 81, pl. 24, figs. 1–3.
2002 *Homomya auroraensis*; Akers and Akers, p. 468.

Holotype.—*Homomya auroraensis* holotype UMMP 32853. Reference specimens in the Non-vertebrate Paleontology Laboratory: UT 32300, UT 30019, UT 32298, UT 32294.

Lectotype.—*Homomya budaensis* lectotype UT 32300; topotypes: UT 30019, UT 32298, UT 32294.

Diagnosis.—Medium to large, 75–100 mm long, equivalved, greatly inflated shell; prosogyrate beaks nearly even with anterior margin, anterior margin truncated, ventral margin concave, posterior margin expanded, dorsal margin concave, dorsal-posterior corner inclined upward, higher than anterior margin.

Occurrence.—Whitney's specimens are from the upper 2 m of the Buda Limestone at Shoal Creek, Austin, Travis County, Texas. Perkins's specimens of *H. budaensis* are from seven sites in the upper Aurora Limestone in the *P. kellumi* zone, which correlates with the Washita Group of north Texas (Scott et al., 2003). The holotype of *H. auroraensis* co-occurs with *H. budaensis* at Perkins's site 18 in the *H. kellumi* zone of the upper Albian Aurora Limestone, Ojo de Agua, Sierra de Tlahualilo, Coahuila, Mexico. The total known range of *H. budaensis* is middle Albian to lower Cenomanian.

Description.—"Shell large, globose, equivalved, inequilateral, greatly produced and broadened posteriorly; anterior margin short, curved; ventral margin deeply curved; posterior margin broadly rounded; dorsal margin curved, subparallel with ventral; umbos globose, approximate, elevated, curved inward and slightly forward, situated anteriorly; shell closed anteriorly, gaping posteriorly. Surface marked by lines of growth, which vary considerably in size" (Whitney, 1911, p. 15–16). The valves gape posteriorly; beaks are low, large, subterminal in position; surface ornament of irregular, coarse, concentric growth lines (Perkins, 1961, p. 81–82).

H. budaensis: length = ~110 mm; height = 60 mm; width = 61 mm (Buda Formation; Whitney, 1911, p. 16); mean length = 88.37 mm; mean height = 48.0 mm; mean width = 52.1 mm; mean beak distance to anterior margin 10.8 mm (Aurora Limestone). *H. auroraensis*: length = 85.8 mm; height = 46.9 mm; width = 44 mm (Table 1).

Remarks.—Whitney distinguished *H. budaensis* from *H. vulgaris* by its overall shape, the more curved dorsal and ventral margins, the more expanded, flaring posterior margin, the greater width, and the variable growth rings. The dorsal-posterior corner flares up and the posterior margin is straight and tilted upward. Perkins (1961, p. 81) distinguished *H. auroraensis* from *H. budaensis* by its "more concave dorsal border, a greater height in relation to the thickness of the shell and in not having the broad posterior, vertical expansion." Perkins also noted that the growth rings of *H. auroraensis* seemed less coarse. The height-to-width ratio of the holotype of *H. auroraensis* is 1.2 and that of eight specimens of *H. budaensis* is 0.923 ± 0.066 (Fig. 6). Furthermore, the shapes and dimensions are very similar except that the beak-to-anterior-margin distance is greater in *H. auroraensis*, 19 mm compared to 10.8 mm in *budaensis*. Because these two species are morphologically similar and because *H. auroraensis* occurs together with *H. budaensis* in the *H. kellumi* zone, Aurora Limestone, the species are synonymized.

Perkins (1961) identified four specimens as *Homomya budaensis* from the *Texigryphaea mucronata* Zone in the lower part of the upper member of the Aurora Limestone, Coahuila, Mexico: UMMP 32972, 32974, 32976, and 32977. Two relatively complete specimens are indistinguishable from the holotype. This extends the range of *H. budaensis* from the upper part of the Washita Group–equivalent Aurora Limestone into the lower part of the Fredericksburg Group–equivalent.

Homomya cymbiformis Perkins, 1961
Figure 10.6, 10.8, 10.9

1961 *Homomya cymbiformis* Perkins, p. 83, pl. 26, figs. 1, 2, 5.
2002 *Homomya cymbiformis*; Akers and Akers, p. 367, 468, fig. 350.

Holotype.—*Homomya cymbiformis* holotype UMMP 33012, an external cast; paratype: UMMP 33013, cast of incomplete specimen.

Diagnosis.—"A *Homomya* distinguished by the strong central concavity of the dorsal border and its cymbiform profile" (Perkins, 1961, p. 83).

Occurrence.—The type locality of *H. cymbiformis* is the lower part of the Marys Creek Member of the Goodland Formation in Fort Worth, Tarrant County, Texas, Fredericksburg Group, middle Albian. An additional specimen in the Non-vertebrate Paleontological Laboratory, University of Texas, is from the Weno Formation, Washita Group on Old Mansfield Road, Tarrant County, Texas (UT 35247), which extends the species range into the middle part of the upper Albian Washita.

Description.—A medium-sized, 60–70 mm long, equivalved, elongate, compressed shell characterized by a concave dorsal margin and dorsally arched, expanded posterior margin resulting in the so-called cymbiform margin. Prosogyrate umbos close to the anterior margin, distance about 25% of length. Ornament of simple concentric, co-marginal, rounded growth rugae.

Remarks.—*H. cymbiformis* is similar in outline to *H. budaensis* and their ranges overlap from uppermost middle Albian to middle upper Albian. The valves of *H. cymbiformis* are more equidimensional than *H. budaensis*; the length-to-height ratio is 1.48 versus 1.69. *H. cymbiformis* is higher than wide, 1.25 versus 1.08, and its volume is less than half of the volume of *H. budaensis*: 73,419 mm^3 versus 164,760 mm^3.

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Species doubtfully attributed to *Homomya*

Three Comanchean species were placed in the genus *Homomya* by their authors. However, their valve morphologies differ substantially from species of *Homomya*, and their internal features are not known because the type specimens are preserved as external molds. Therefore, these species are provisionally retained in "*Homomya*."

"Homomya" jurafacies Cragin, 1893
Figure 11.1, 11.2

1893 *Homomya jurafacies* Cragin, p. 191, pl. 39, figs. 1, 2.
1928 *Homomya jurafacies*; Adkins, p. 140.
1937 *Liopistha* (*Psilomya*) *jurafacies;* Whitney, p. 143, pl. 28, figs. 1, 2.
1952 *Liopistha* (*Psilomya*) *jurafacies;* Whitney, p. 68.
2002 *Psilomya jurafacies*; Akers and Akers, p. 388, 389, figs. 371, 372.

Lectotype.—Two syntypes collected by J. Taff are cataloged as UT 17236, Non-vertebrate Paleontology Laboratory, which are from Hickory Creek, Burnet County, Texas. The smaller specimen is better preserved and is here designated the lectotype, and the larger specimen becomes the paralectotype. Topotypes are UT 8307, UT 8309, UT 17236.

Occurrence.—Lower Albian Glen Rose Formation in Burnet and Bosque counties, central Texas.

Description.—A large, equivalved, ovate-trapezoidal shell with a tall, angular, prosogyrate umbo, average length-to-height ratio 1.27 ± 0.106; umbo close to anterior margin about 27% of the length; anterior margin evenly rounded, ventral margin broadly curved, posterior margin nearly straight, inclined about 150° to the dorsal margin; lunule short, narrow; escutcheon longer, shallow; pallial line a faint shallow groove at both anterior-ventral and posterior-dorsal margins. Dentition not evident on type specimens.

Remarks.—*"Homomya" jurafacies* is very similar to *"Homomya" solida*. The type specimens of *"H." jurafacies* were collected from the Glen Rose Formation in 'the Alternating beds' from central Texas in Burnet and Bosque counties and the types of *"H." solida* are from the Glen Rose formation in Parker, Hood, Erath, and Travis counties, north Texas. The small number of available specimens is not a statistically significant population; however, their measurements are quite similar: the length of four specimens of *"H." jurafacies* ranges 73–88 mm, height 53–69 mm, articulated thickness 51–57.2 mm, and the ratio of umbo distance from anterior margin to length is 0.18–0.32; a single specimen of *"H." solida* is 81.7 mm long, height 69 mm, thickness 57.2 mm, with the ratio of umbo distance to length 0.35. The posterior margin of *"H." jurafacies* is straighter and more truncate than that of *"H." solida.*

Whitney (1937, 1952) reclassified this species as well as "*H." solida* in *Psilomya* White; however, *Psilomya* is a member of Poromyidae Dall, which is characterized by radial striae, a single cardinal tooth, an external ligament, and no posterior gape. Neither *"H." jurafacies* nor *"H." solida* bears these features. Although Whitney (1937) described two cardinal teeth in both valves of *"H." jurafacies*, these are not visible on the internal mold she illustrated (Whitney, 1937, pl. 28, fig. 2). Molds of teeth are not visible in specimens UT 8307, UT 8309, and UT 17236. Thus, both species are here provisionally retained in the genus "*Homomya*."

'Homomya' solida Cragin, 1893
Figure 11.3, 11.4

1893 *Homomya solida* Cragin, p. 191, pl. 39, figs. 3, 4.
1928 *Homomya solida*; Adkins, p. 141.
1937 *Liopistha* (*Psilomya*) *solida*; Whitney, p. 141, pl. 25, figs. 1, 2; 1952, p. 69.
1952 *Liopistha (Psilomya) fletcheri* Whitney, p. 68, pl. 16, figs. 3, 4.
2002 *Psilomya solida*; Akers and Akers, p. 390, 471, figs. 373, 374.

Holotype.—*"Homomya" solida* holotype BEG-UT 21724; this single specimen becomes the holotype by original designation. Three additional specimens in the Non-vertebrate Paleontology Laboratory collections are: UT 38950, "not illustrated, Granbury, Brazos bluffs at railroad bridge, Texas, Stone collector"; UT 34126, Parker County; and UT 17296. The type specimen of *Liopistha fletcheri* is unknown.

Occurrence.—Lower Albian Glen Rose Formation in north and central Texas. The holotype specimen label states: "syntype, Hinor, Parker Co., Tx, Glen Rose, Taff collector." Whitney collected *L. fletcheri* from the *Salenia texana* zone, Lower Member, Glen Rose Formation at Julian Creek, Bandera, Texas.

Remarks.—The posterior margin of this large, ovate shell is rounded in contrast to the straight margin inclined toward dorsal margin of *'Homomya' jurafacies*. Whitney (1952) distinguished *Liopistha fletcheri* from *"H." solida* by the overall shape: "a more prolonged posterior, a concave posterior cardinal margin and a more rounded ventral margin" (p. 69). These subtle differences are evident by comparing photographed specimens but have not been substantiated by statistical analysis. *L. fletcheri* is larger but the length-to-height and height-to-width ratios are close to those of *"H." solida* and do not support the definition of a separate species. The generic assignment of *"H." solida* is indeterminate because dentition of this species is unknown and radial ornament is not evident.

Figure 11. (**1, 2**) *Homomya jurafacies* Cragin, 1893; lectoparatype UT 17236, left valve, right valve. (**3, 4**) *Homomya solida*, holotype UT 21724; (**3**) right valve; (**4**) dorsal view. (**5–8**) *Liopistha* (*Sergipemya*) *alta* (Roemer, 1852), holotype STIPB-Roemer-79, Bonn Museum; (**5**) drawing of right valve (Roemer, 1852, pl. 6, fig. 11); (**6**) right valve, note minute nodes on concentric rugae (photo by Georg Heumann, Steinmann-Institut, Paläontologie); (**7**) left valve, minute granule-like nodes on concentric rugae create a granular texture; (**8**) posterior view showing gape and elongate oval escutcheon on dorsal margin. (**9, 10**) *Panopea henselli*; (**9**) left valve; (**10**) dorsal views. (**11**) *Homomya comalensis* in situ, Regional Dense member, basal Person Formation, Stone Crossing outcrop, New Braunfels, Texas; dotted lines approximate bedding. (**1–10**) Scale bar = 1 cm; (**11**) scale bar = 5 cm.

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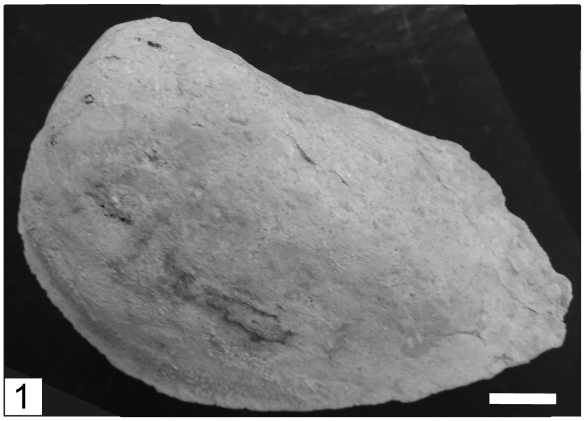
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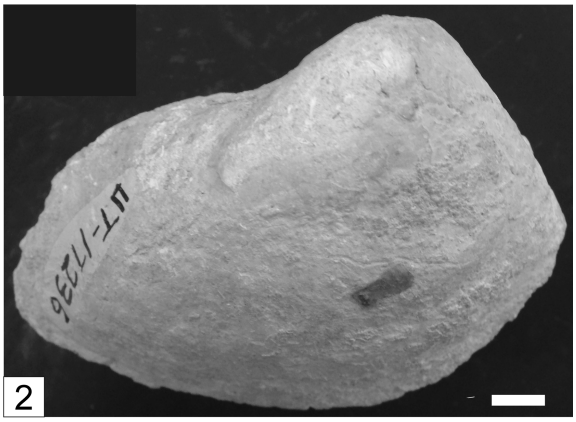

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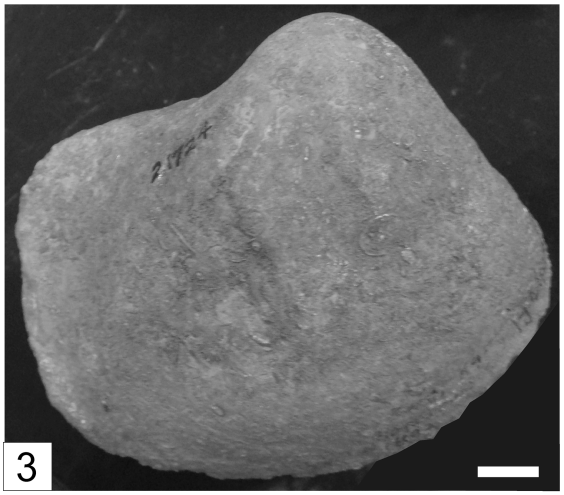
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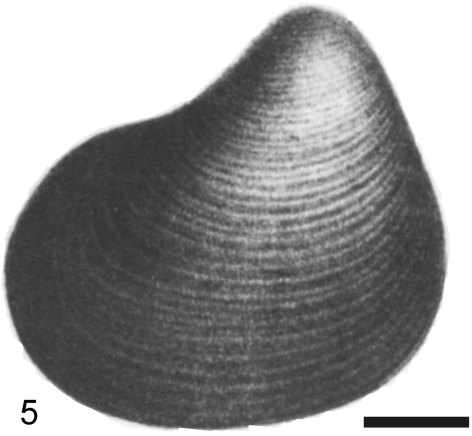
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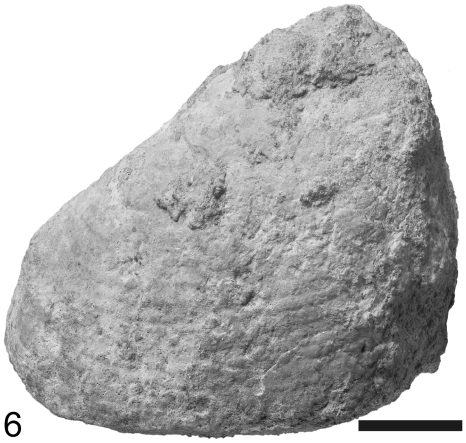
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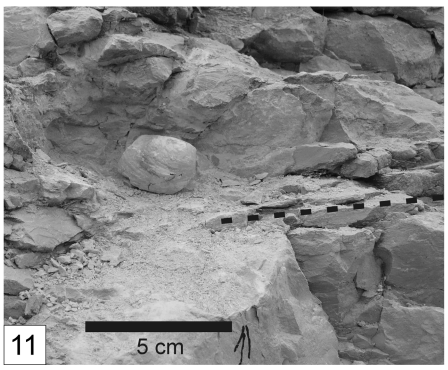

11

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Megaorder Solenata Dall, 1889
Order Hiatellida Carter in Carter et al., 2011
Superfamily Hiatelloidea Gray, 1824
Family Hiatellidae Gray, 1824
Subfamily Panopeinae Bronn, 1862
Genus *Panopea* Ménard de la Groye, 1807

Type species.—*Mya glycimeris* Born, 1778 (ICZN, 1986).

Description.—Medium to large, equivalved, quadrate to trapezoidal, elongate, gaping valves; ligamental nymphs tall; one or two small cardinal teeth; wide pallial sinus. The generic name, *Panopea*, has been conserved (ICZN, 1986).

Panopea henselli (Hill, 1893)
Figure 11.9, 11.10

1893 *Pleuromya* (?) *henselli* Hill, p. 31, pl. 4, figs. 1, 2.
1967 *Pleuromya* (?) *henselli*; Rodgers in Lokke, p. 127.
1928 *Panope* (sic) *henselli*; Adkins, p. 170.
1924 *Panopea henselli*; Gillet, p. 233.
2002 *Panopea henselli*; Akers and Akers, p. 473.
1901 *Pholadomya henselli*; Hill, p. 161.
1937 *Panopea hilli*; Whitney p. 172, pl. 15, figs. 2, 3.

Lectotype.—*Panopea henselli* two cotypes NMNH 145646; here the smaller is designated the lectotype.

Diagnosis.—An elongate shell, subcentral beaks, anterior and posterior margins evenly rounded, slight posterior gape; ornament of low, rounded commarginal growth rugae.

Occurrence.—Lower Albian, Somervell County, Texas, about 12 m below top of Glen Rose.

Description.—Equivalved, elliptical, elongate valve, umbo subcentral, not prominent; anterior margin rounded, posterior margin subrounded, gaping slightly; angle around beak between dorsal anterior and posterior margins 135°–140°. Ornamented by simple rounded commarginal growth rugae. The average length of the two specimens is 76.1 mm; height is 46.95 mm; thickness is 33.1 mm.

Remarks.—Hill (1893) questioned the generic assignment of this species but created this species because it is characteristic of the Glen Rose Formation. Hill noted the similarities between *P. henselli* and *Thracia myaeformis* White (1880). Similar species in Texas Comanchean strata are *Panopea texana* Shumard 1854 at 'camp 4 Cross Timbers,' and *Panopea newberryi* Shumard 1860 from the Edwards Limestone in north Texas. Both species are illustrated by hand drawings; both are relatively higher than *P. henselli*. Roemer (1852, p. 45) noted an indeterminate *Panopaea* (sic) sp. together with *Mesorbitolina texana* (Roemer) near Pedernales that he compared to *Panopea regularis* d'Orbigny (1843). *Panopea sellardsi* Whitney 1952 from the middle part of the Glen Rose Formation in central Texas is much smaller than *P. henselli*, narrower posteriorly, and relatively more inflated.

Panopea is a common genus in pre-Albian strata in Switzerland and in Argentina (Weaver, 1931). *Panopea dupiana* d'Orbigny 1843 is about twice as long as high and the umbo is closer to the anterior margin than in *P. henselli*. *Panopea neocomiensis* (Leymerie, 1842) is ornamented by very fine radial striae. Modern *Panopea* bivalves have aragonite shells that dissolve quickly following death, leaving external molds, which are filled with fine crystalline carbonate. Because of this taphonomy, the resulting casts show mainly external characters.

Conclusions

Species of Pholadomyidea are common and relatively diverse in Albian–lower Cenomanian Comanchean strata in Texas and northern Mexico. Some 22 species have been classed with *Pholadomya*, *Homomya*, *Pachymya*, *Myopholas*, *Panopea*, and *Pleuromya*. Two genera most commonly reported are *Homomya*, order Pholadomyoida, superfamily Pholadomyoidea and *Pleuromya*, order Pholadida, superfamily Pleuromyoidea. Since 1852, more than a dozen species have been identified as either *Homomya* or *Pleuromya*. Because valve morphologies of the two genera are similar in many ways, casts are difficult to separate. Statistical analysis of height and width objectively differentiates species. Eight species are retained in *Homomya*, four are synonymized with these; two species are provisionally retained in "*Homomya*" although they differ significantly.

Homomyid species in Texas and Mexico range from lower Albian to lower Cenomanian. They are found in each of three Gulf Coast Comanchean Series groups: upper Aptian to lower Albian Trinity Group, middle to basal upper Albian Fredericksburg Group, and upper Albian to lower Cenomanian Washita Group. They evolved across this interval, and their ranges vary from one to two million years to up to eight million years. Two sets of species form two clades, the smaller-sized *H. knowltoni, H. tarrantensis, H. tlahualiloensis, H. kellumi* (Fig. 4) and the larger-sized set of *H. cymbiformis, H. austinensis, H. vulgaris, H. budaensis*, and *H. auroraensis*. Two end-member morphotypes are represented by the 'streamlined' *Homomya knowltoni*, which is an elongate, slightly inflated form with a relatively high umbo, and the cylindrical *Homomya budaensis*, which is a very elongate, tubular, inflated form with a very low umbo. These infaunal suspension feeders occupied offshore calcareous mud and carbonate shelf substrates.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.40s3m.

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