

LATEST TRIASSIC–EARLIEST JURASSIC BIVALVES OF THE GERMIG FORMATION FROM LANONGLA (TIBET, CHINA)

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ABSTRACT—The Germig Formation of the Tethyan Himalaya of southern Tibet contains an exceptionally abundant bivalve fauna which has been found in association with choristoceratid and psiloceratid ammonoids and spans the Triassic/Jurassic boundary. The bivalve fauna consists of 25 species, including four new species: *Newaagia lanonglaensis*, *Persia hallami*, *Liostrea tibetica*, and *Ctenostreon newelli*. The fauna comprises three biostratigraphically controlled bivalve assemblages: 1) an upper Rhaetian *Palaeocardita*–*Krumbeckiella* Assemblage including seven species; 2) a high diversity transitional Rhaetian–Hettangian *Persia*–*Plagiostoma* Assemblage with many as 19 species; and 3) a low diversity lower Hettangian *Liostrea*–*Chlamys* Assemblage containing three species. The transitional Rhaetian–Hettangian Assemblage is dominated by cementing species and exhibits a high degree of endemism. A large proportion of lower latitude and cementing taxa from the lower two levels may indicate that they inhabited shallow subtidal tropic or subtropic paleoenvironments.

INTRODUCTION

THE END-TRIASSIC mass extinction remains one of the most poorly known and least understood of the five first-order Phanerozoic mass extinctions (e.g., Sepkoski, 1986). Because they are frequently the most abundant and best-preserved macrofossils in Upper Triassic and Lower Jurassic faunas, bivalves have figured prominently in assessments of the magnitude and mode of the end-Triassic mass extinction (e.g., Hallam, 1981; Johnson and Simms, 1989; McRoberts and Newton, 1995). Hallam (2002) and Tanner et al. (2004) recently suggested that the end-Triassic extinction was a more prolonged and less severe crisis, beginning as early as the middle Norian, and affecting far fewer taxa than previously realized. Although the significance of the faunal changes across the Rhaetian–Hettangian boundary at Germig in the Lanongla region of Tibet was noted briefly by Yin et al. (1999), and later Hallam et al. (2000), the bivalve fauna has yet to be documented adequately. The taxonomically and ecologically rich bivalve fauna from the Triassic–Jurassic boundary at Germig, therefore, permits a more realistic assessment of latest Triassic–earliest Jurassic bivalve diversity and extinction metrics for future analyses. We report 25 species of bivalves from these strata, making it one of the most diverse shallow-water bivalve faunas spanning the Triassic–Jurassic boundary.

Geologic and stratigraphic setting.—The bivalve fauna described herein comes from the type locality of the Upper Triassic–Lower Jurassic Germig Formation from the area around Lanongla, on the northern flanks of the Tibetan Himalaya (Fig. 1). The Germig Formation was named by Yin et al. (1999) for a nearly 30 m thick succession of thinly bedded, greenish gray, fine-grained calcareous sandstone and siltstone. According to recent investigations, the Germig Formation is likely disconformably underlain by relatively unfossiliferous Norian sediments, and disconformably overlain by unnamed clastic strata (Pliensbachian?). A sedimentologic and geochemical analysis of the type locality of the Germig Formation by Hallam et al. (2000) suggested that deposition occurred somewhat episodically in a shallow fully marine setting. Of particular note was the absence of major facies changes and geochemical evidence for widespread anoxia across the Triassic–Jurassic boundary at Germig (Hallam et al., 2000).

The Germig Formation is part of the broader Paleozoic to Early Mesozoic clastic and carbonate sequence of the Tethyan Himalayan tectonic province, situated south of the Indus–Yarlung–Zangbo Suture and Lhasa Terrane, and extending into Nepal and the Indian subcontinent (e.g., Garzanti, 1993). Most paleogeographic

reconstructions (e.g., Metcalfe, 1996) place this part of the Tethyan Himalaya near the southeastern margin of the Tethyan Sea-way at about 25° southern paleolatitude in the Triassic.

Biostratigraphy.—Although the stage names and their usage for the Upper Triassic and Lower Jurassic remain ambiguous, we follow Dagys and Dagys (1994) and consider the Rhaetian to contain the *Reticulatus*, *Sturzenbaumi*, and *Marshi* ammonoid zones (apparently equivalent to the North American *Amoenium* and *Crickmayi* ammonoid zones sensu Silberling and Tozer, 1968), and the basal Hettangian to contain one of several psiloceratid species such as *Psiloceras tillmani* Lange, 1941, *P. psilonotum* (Quenstedt, 1858), and tentatively *P. spelae* Guex et al., 1998 (see discussions in Hillebrandt, 1994, 2000; Bloos and Page, 2000; Taylor et al., 2001). It should be noted, however, that because the base of the Hettangian, and therefore the Triassic–Jurassic boundary, has not been defined, some of these ammonoid taxa may be reassigned to the latest Triassic following selection of a Global Stratigraphic Section and Point.

The primary basis for age determinations of the Germig Formation at its type locality relies mainly on the occurrence of ammonoids (see Yin et al., 1999; Yin and Enay, 2000; Hallam et al., 2000), and are corroborated by palynomorphs (determinations by J. Riding and R. Helby as cited in Hallam et al., 2000) and biostratigraphically useful bivalves (data herein). Although a systematic revision of existing ammonoid collections from the Germig section, together with new material collected by Yin in 2004, is currently in progress, preliminary taxonomic assignments are provided as our basis for age assignments of the bivalve-bearing horizons.

Figure 2 illustrates the stratigraphic position of bivalve horizons (BH-1 to BH-4) and age-significant ammonoid occurrences from sections A and B at the Germig locality. By means of correlation based on faunal similarities and ammonoid distributions, shell-bearing beds represent three distinct biostratigraphic levels ranging from the upper Rhaetian to lower Hettangian. We assign the lower bivalve horizons (BH-1 and BH-2) to the upper Rhaetian *Marshi* Zone based on the occurrence in section B, about 2 m above BH-1, of the ammonoids *Choristoceras marshi* Hauer, 1865, *C. cf. C. nobile* Mojsisovics, 1893, and *Eopsiloceras* Spath, 1930. Above this demonstrably upper Rhaetian interval, bivalve horizons BH-3a and BH-3b are closely associated with undescribed species of *Choristoceras* Hauer, 1865, *Rhacophyllites* Zittel, 1884, *Neophyllites* Lange, 1941, and *Psiloceras* Hyatt, 1867. These ammonoids, apparently representing new taxa, provide the basis for an age transitional between Rhaetian and Hettangian that

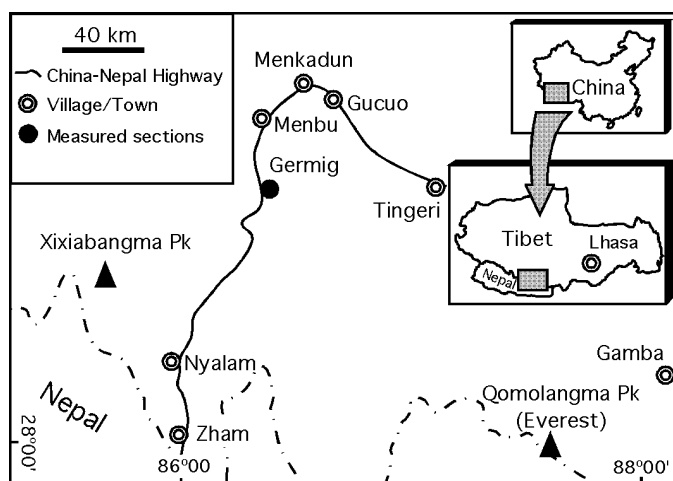


FIGURE 1—Locality map of southern Tibet showing locality at Germig along China-Nepal Highway.

may prove correlative to the *Spelae* Zone in North America (Taylor et al., 2001) at a position below the traditionally Hettangian *Planorbis* Zone of Europe (Bloos and Page, 2000) or *Tillmanni* Zone of South America (Hillebrandt, 2000). Bivalve horizon BH-4 is associated with the ammonoids *Neophyllites* cf. *N. biptychus* Lange, 1941 (illustrated as *Psiloceras* cf. *pacificum* Yin et al., 1999, fig. 3.6) and *Nevadaphyllites* sp., which we assign to the lower Hettangian and make a tentative correlation to the *Planorbis* Zone. Bivalve horizon BH-4 in section A occurs approximately 1 m below *Psiloceras calliphyllum* (Neumayr, 1879), which is the oldest Jurassic psiloceratid in northern Alps, and is now believed to be only equivalent to *P. Planorbis* Zone (s. Bloos and Page, 2000; Bloos, 2004).

OVERVIEW AND SIGNIFICANCE OF THE BIVALVE FAUNA

A summary of bivalve taxa, and their paleoautecology and stratigraphic ranges, are provided in Table 1. From the upper

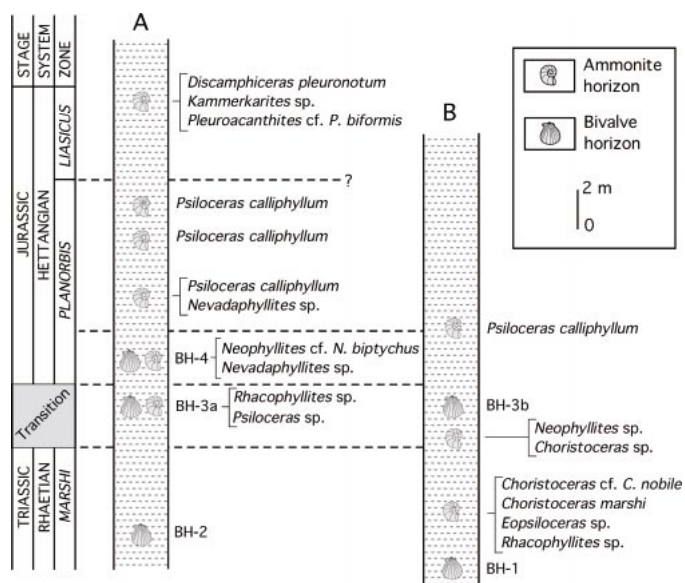


FIGURE 2—Generalized stratigraphic sections (A and B) from the Germig locality showing ammonoid occurrences and bivalve horizons. Section A, 28° 42.179'N, 86° 08.623'E; Section B, about 500 W of Section A, 28° 42.106'N, 86° 08.942'E. See text for details.

Rhaetian to Rhaetian-Hettangian transitional level, bivalve richness climbs dramatically from 7 to 19 species. There is a sharp decline in richness to the lower Hettangian to only three bivalve species, all of which are Rhaetian holdovers.

Although many of the bivalves identified also are known from, and in some cases common in, the West Tethyan and Northwest European faunal provinces, endemic taxa make up a significant proportion of the Rhaetian-Hettangian bivalve fauna from Lanongla. Taxa with known affinities to the West Tethyan and Northwest European regions include *Chlamys valoniensis* (Defrance,

TABLE 1—Faunal list of Tibetan bivalves from Germig. Abbreviations: InfMob-Det, infaunal mobile detritus feeder; EpiBys-Susp, epifaunal byssally attached suspension feeder; SmIf-Susp, semi-infaunal, byssally attached suspension feeder; EpiCem-Susp, epifaunal cementing suspension feeder; In-Susp, infaunal suspension feeder; uRha, upper Rhaetian; trans, transitional Rhaetian-Hettangian; lHet, lower Hettangian. Note that age determinations only represent species occurrence(s) in the Germig sections.

Order	Species	Living habit	Age
Nuculoidea	<i>Ryderia guangdongensis</i>	InfMob-Det	uRha-trans
Arcoida	<i>Parallelodon</i> sp.	EpiBys-Susp	trans
Pterioidea	<i>Pinna</i> cf. <i>P. octavia</i>	SmIf-Susp	trans
Pterioidea	<i>Pinna</i> cf. <i>P. meriani</i>	SmIf-Susp	trans
Pterioidea	<i>Pteria</i> sp.	EpiBys-Susp	trans-lHet
Pterioidea	<i>Gervillia (Cultrioipsis) angusta</i>	EpiBys-Susp	trans
Pterioidea	<i>Aguilerella</i> sp.	EpiBys-Susp	trans
Pterioidea	<i>Cassianella</i> sp.	EpiBys-Susp	uRha
Pterioidea	<i>Krumbeckiella timorensis</i>	EpiBys-Susp	uRha
Pectinoidea	<i>Chlamys valoniensis</i>	EpiBys-Susp	trans-lHet
Pectinoidea	<i>Newaagia lanonglaensis</i> n. sp.	EpiCem-Susp	trans
Pectinoidea	<i>Persia hallami</i> n. sp.	EpiCem-Susp	trans
Pectinoidea	? <i>Persia</i> sp.	EpiCem-Susp	trans
Pectinoidea	<i>Terquemia</i> cf. <i>T. difformis</i>	EpiCem-Susp	trans
Ostreoida	? <i>Harpax</i> sp. A	EpiCem-Susp	trans
Ostreoida	? <i>Harpax</i> sp. B	EpiCem-Susp	trans
Ostreoida	<i>Liostrea tibetica</i> n. sp.	EpiCem-Susp	trans-lHet
Ostreoida	Genus and species indeterminate	EpiCem-Susp	trans
Limoida	<i>Ctenostreon newelli</i>	EpiBys-Susp	trans
Limoida	<i>Antiquilima</i> sp.	EpiBys-Susp	uRha
Limoida	<i>Plagiostoma giganteum</i>	EpiBys-Susp	trans
Veneroida	<i>Astarte</i> sp.	In-Susp	uRha-trans
Veneroida	<i>Palaeocardita trapezoidalis</i>	In-Susp	uRha
Veneroida	? <i>Schafhaeutlia?</i> sp.	In-Susp	uRha
Unionoida	<i>Unionites griesbachi</i>	In-Susp	uRha

1825), *Plagiostoma giganteum* Sowerby, 1814, *Gervillia* (*Cultripsis*) *angusta* Münster, 1838, and *Unionites griesbachi* (Bitter, 1899). There appears to be, at least at the generic level, a high degree of similarity with the taxonomically rich fauna from central Iran (e.g., Hautmann, 2001a, 2001b). Bivalves with a more eastern Tethyan affinity include *Palaeocardita trapezoidalis* (Krumbeck, 1913), *Ryderia guangdongensis* (Zhang in Zhang et al., 1977), and *Krumbeckiella timorensis* (Krumbeck, 1924). The endemicity peak in the upper Rhaetian is followed by a more cosmopolitan low diversity, early Hettangian post-extinction bivalve assemblage.

Ecologically, the fauna is dominated by epifaunal suspension-feeding pterioids, pectinooids, limoids, and ostreooids. Of these epifaunal groups, a majority are cemented to firm substrates (e.g., plicatulids and prospondylids). Epifaunal byssally attached suspension feeders (e.g., bakevellids and limids) also contribute significantly to the fauna. The diverse epifauna, in combination with their common association with crinoids and a high degree of encrustation and bioerosion on the shells, suggest a shallow, warm, and low turbidity marine environment of normal salinity. In contrast, there are few mobile infaunal bivalves—either suspension feeders (e.g., veneroids) or detritus feeders (e.g., nuculoids)—which suggest that substrates were generally suboptimal in terms of sediment grain size, sediment mobility, and/or organic content to support an ecologically diverse infauna.

SYSTEMATIC PALEONTOLOGY

The suprageneric classification generally follows the Treatise on Invertebrate Paleontology (Cox et al., 1969) or more recent amendments (e.g., Waller, 1978; Carter, 1990), as indicated. Synonymies generally refer to type specimens and list bibliographic references to material from Tibet and adjacent areas. In a few cases, where a species has been discussed at greater length, an attempt has been made to provide a more comprehensive synonymy. All specimens have a CUGB prefix and are housed in the Museum of China University of Geosciences, Beijing.

Order NUCULOIDA Dall, 1889

Family POLIDEVCIIDAE Kumpera et al., 1960

Genus RYDERIA Wilton, 1830

RYDERIA GUANGDONGENSIS (Zhang in Zhang et al., 1977)

Figure 3.1–3.7, 3.8a

Teinonuculana guangdongensis ZHANG IN ZHANG ET AL., 1977, p. 10, pl. 1, figs. 13–15; CHEN, 1987, p. 40, pl. 2, fig. 6.

Ryderia doris CHEN, 1982, p. 407, pl. 1, figs. 8, 9.

Teinonuculana tenuistriata (PIETTE). CHEN, 1987, p. 41, pl. 1, figs. 8, 9.

Teinonuculana graphica (TATE). CHEN, 1987, p. 41, pl. 1, figs. 8, 9.

Ryderia texturata (TERQUEM AND PIETTE). CHEN, 1987, p. 41, pl. 1, fig. 2.

Description.—Shell small (maximum length = 22 mm, maximum height = 9 mm), very narrow, inequilateral, posteriorly elongated with typically narrow rostrum, anterior margin rounded; hinge consisting of central resilifer and numerous chevron-shaped taxodont denticles, anterior teeth varying between 8 and 14, posterior ones number between 8 and 16 depending on size; pallial line entire without sinus; anterior and posterior adductor scars nearly equal in size; rostrate ridge highly developed, with groove below ridge running from umbo to posterior end; central septa situated just beneath beak; ornament consisting of fine commarginal growth lines and radial ribs, forming V-shaped pattern on anterior part of shell, V-shaped pattern becomes weaker posteriorly, giving way to vertical striae that extend along entire length of rostrum.

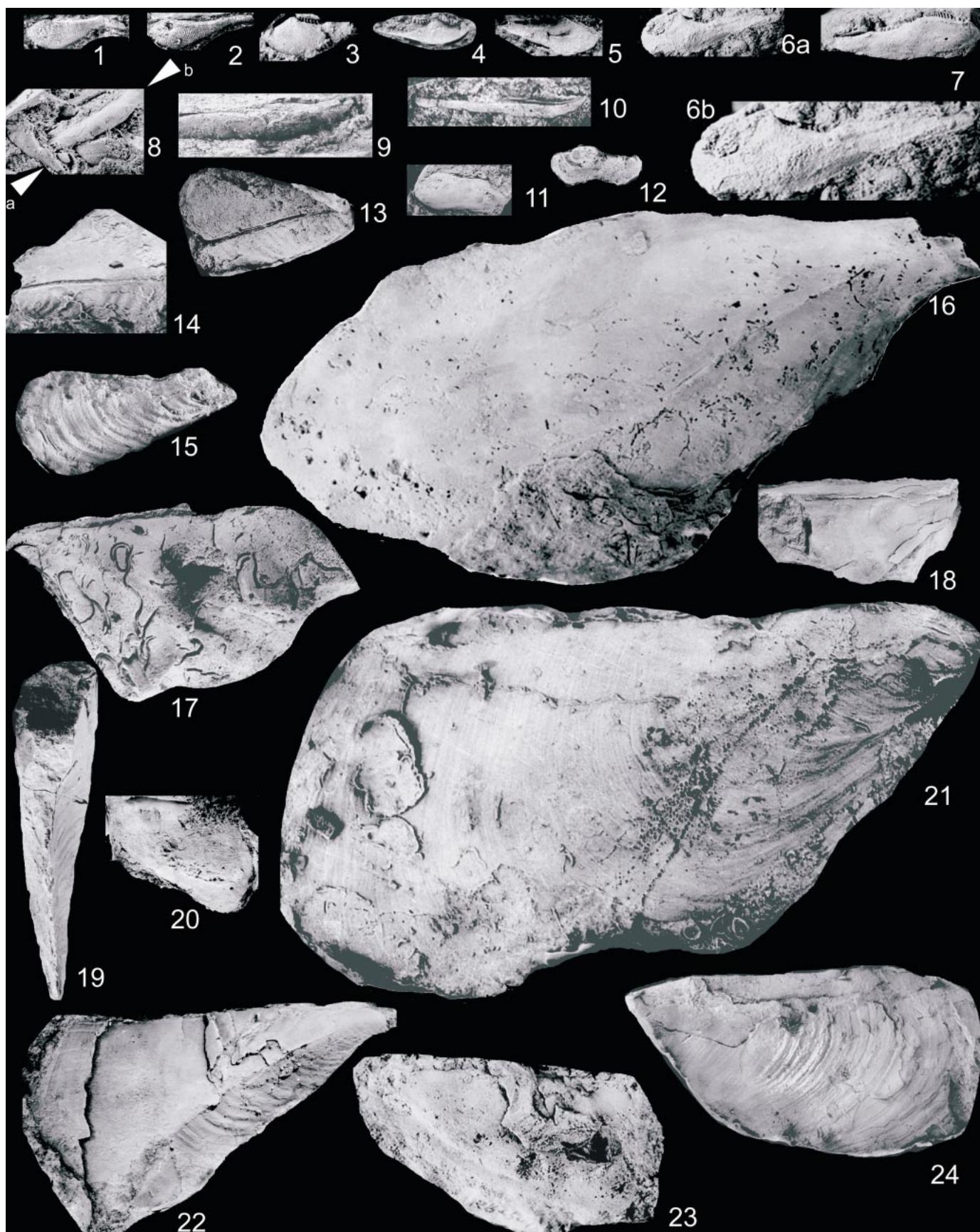
Material examined.—Fifteen specimens, including seven left and eight right valves preserved as interior and exterior molds; CUGB2002b, CUGB2004, CUGB2006b, CUGB2008, CUGB2009, CUGB2011b, CUGB20061b, CUGB2054.

Occurrence.—BIH-2 and BIH-3a of section A of Germig (upper Rhaetian to transitional Rhaetian-Hettangian). Elsewhere, this species occurs in the Upper Jinji Formation of eastern Guangdong (Upper Lias).

Discussion.—*Teinonuculana* was erected by Zhang et al. (1977) to accommodate polidevciids whose ornament consists of somewhat sinuous transverse lines that cross the commarginal growth lines. This genus was more recently reviewed by Chen et al. (1983) within a broader systematic treatment of the ornamented nuculanaceans. We believe, however, that the type species of *Teinonuculana* exhibits diagnostic features (e.g., posteriorly elongated form, long and narrow rostrum, and taxodont dentition consisting of numerous chevron-shaped teeth and sockets) that are consistent with *Ryderia*. Exterior ornament attributed to *Teinonuculana* is visible in English specimens, referred to as *Ryderia texturata* by Hodges (2000, p. 45, pl. 3, figs. 5, 8–11, 13–17). Liassic specimens from Guangdong, referred by Chen (1982, 1987) to *Ryderia doris*, *Ryderia texturata*, *Teinonuculana tenuistriata*, and *Teinonuculana graphica*, we believe exhibit a variation within intraspecific range of ornamentation of *Ryderia guangdongensis*.

English *Ryderia* has been reviewed recently, and the synonym of both *Ryderia doris* and *Ryderia texturata* has been compiled by Hodges (2000). However, whether V-shaped or commarginal ornamentation can be investigated on the specimens is to a great extent dependent on taphonomic destruction of surficial shell features. Some of the Tibetan specimens resemble *Ryderia texturata* if the transverse striae of the anterior shell are evidently worn away. Otherwise, the V-shaped ornament appears similar to *Teinonuculana guangdongensis* provided that the commarginal lines were too faint or too poorly preserved.

FIGURE 3—1–7, 8a, *Ryderia guangdongensis* (Zhang in Zhang et al., 1977). 1, Latex cast of right valve interior, CUGB2006b, loc. BH-3a; 2, latex cast of right valve exterior CUGB2002b, loc. BH-3a; 3, left valve, internal mold CUGB2009, loc. BH-3a; 4, right valve, internal mold, CUGB2004, loc. BH-3a; 5, right valve, internal mold, CUGB2011b, loc. BH-3a; 6a, left valve, internal mold CUGB20061b, loc. BH-3a; 6b, enlarged; 7, right valve, internal mold CUGB2008, loc. BH-3a; 8a, left valve, internal mold, CUGB2054, loc. BH-3a. 8b, 9, 10, *Gervillia* (*Cultripsis*) *angusta* Münster, 1838; 8b, internal mold, left valve, in association with *Ryderia guangdongensis*, CUGB2054, loc. BH-3a; 9, right valve, internal mold, enlarged to show multiligamental pits, CUGB2061a, loc. BH-3a; 10, external mold, right valve, CUGB2062, loc. BH-3a. 11, 12, *Parallelodon* sp.; 11, left valve, internal mold, CUGB2438a, loc. BH-3a; 12, latex cast of left valve exterior, CUGB2438b, loc. BH-3a. 13–15, 19, 22, *Pinna* cf. *P. meriani* Winkler, 1859; 13, latex cast of right valve exterior, CUGB2442, loc. BH-3a; 14, fragment showing shell sculpture, CUGB2076, loc. BH-3a; 15, latex cast of right valve exterior, CUGB2074, loc. BH-3a; 19, articulated valve pair, internal mold, CUGB3010, loc. BH-3a; 22, latex cast of right valve interior, CUGB3011b, loc. BH-3a. 16–18, 21, 24, *Pinna* cf. *P. octavia* Marwick, 1953; 16, left valve internal mold of articulated specimen, CUGB2073a, loc. BH-3b; 17, left valve internal mold, note encrusting serpulid tubes, CUGB2063, loc. BH-3b; 18, right valve external mold, CUGB2012, loc. BH-4; 21, latex cast of right valve exterior, note encrusting bivalves and fine concentric ornament with weak central carina, same individual as 16, CUGB2073b, loc. BH-3b; 24, latex cast of left valve exterior, CUGB3120, loc. BH-3b. 20, 23, *Pteria* sp., 20, left valve internal mold, CUGB2500, loc. BH-3b; 23, left valve internal mold, CUGB2501, loc. BH-3b. Magnification, 1–6a, 7, 8, 10–24, $\times 1$; 6b, 9, $\times 2.5$.



Order ARCOIDA Stoliczka, 1871
 Family PARALLELODONTIDAE Dall, 1898
 Genus PARALLELODON Meek and Worthen, 1866
 PARALLELODON sp.
 Figure 3.11, 3.12

Description.—Small-sized (maximum length = 20 mm, maximum height = 9 mm); shell elongate, trapezoidal, moderately inflated; ornament of few commarginal undulations; hinge margin long and straight with posterior lateral teeth visible; ventral margin characterized by conspicuous sulcus; posterior umbonal ridge runs from umbo to posteroventral margin.

Material examined.—Only one individual preserved as interior and exterior molds, CUGB2438.

Occurrence.—BH-3a of section A of Germig (transitional Rhaetian-Hettangian).

Discussion.—Due to small sample size and quality of the specimen, the specific determination of this specimen remains in question.

Order PTERIOIDA Newell, 1965
 Family PINNIDAE Leach, 1819
 Genus PINNA Linné, 1758
 PINNA cf. *P. OCTAVIA* Marwick, 1953
 Figure 3.16–3.18, 3.21, 3.24

cf. *Pinna octavia* MARWICK, 1953, p. 64, pl. 3, fig. 13.

Description.—Large-sized (maximum length = 140 mm, maximum height = 90 mm), equivalved and inequilateral; submedial valve carina only visible in interior mold, slightly curved and subdivides valve into two somewhat unequal lobes; mean apical angle nearly 60°; dorsal margin straight; dorsal lobe obviously larger than ventral lobe; ventral margin arched; ornament on ventral lobe consisting of commarginal growth undulations of variable strength on ventral lobe and distant, irregularly interspaced radial and growth lines on dorsal lobe.

Material examined.—Four specimens, including exterior and interior molds; CUGB2073, CUGB2063, CUGB2012, CUGB3120.

Occurrence.—From locality BH-3b of section B of Germig (transitional Rhaetian-Hettangian).

Discussion.—The studied specimens do not exhibit external features typical in *Pinna* because a pronounced median carina running from the beak to the posterior is absent on the valve exterior. However, internal molds of the specimens exhibit a median carina, double lobe, and adductor scar characteristic of *Pinna*. The irregularly interspaced commarginal lines across the shell exterior are comparable with *Pinna octavia* Marwick (Marwick, 1953, p. 64, pl. 3, fig. 13), a species that was formerly only known in New Zealand.

PINNA cf. *P. MERIANI* Winkler, 1859
 Figure 3.13–3.15, 3.19, 3.22

cf. *Pinna meriani* WINKLER, 1859, p. 14.

Description.—Medium-sized (maximum length = 110 mm, maximum height = 63 mm); wedge-shaped, equivalved, and inequilateral; valve carina submedial, extending from beak towards posteroventral margin, subdividing shell into two somewhat unequal lobes with different ornament; apical angle varying between 30° and 40°; dorsal margin straight; dorsal lobe larger than ventral lobe on which ornament consists of distantly, irregularly interspaced radials and more densely spaced growth lines; ornament on ventral lobe consists of irregular commarginal undulations.

Material examined.—Five specimens, including exterior and interior molds; CUGB2442, CUGB2076, CUGB2074, CUGB3010, CUGB3011b.

Occurrence.—BH-3a of section A and BH-3b of section B of Germig (transitional Rhaetian-Hettangian).

Discussion.—The Tibetan specimens compare well with *Pinna meriani* Winkler, 1859, which is quite common in the Rhaetian of Alpine Europe. Other Alpine species, including *P. escheri* De Stefani, 1882, *P. miliaria* Stoppani, 1860–1865, *P. papyracea* Stoppani, 1860–1865, and *P. reticularis* Benecke, 1865, differ from these Tibetan specimens in shell shape and ornament. In Southeast Asia, Healey (1908) illustrated *P. cf. P. blanfordi* (Böttger, 1880) as a Rhaetian form in the Napeng beds of Myanmar; however, the Southeast Asian form has much stronger radial ribs.

Family PTERIIDAE Gray, 1847
 Genus PTERIA Scopoli, 1777
 PTERIA sp.
 Figure 3.20, 3.23

Material examined.—Three specimens: two left and one right valve, including CUGB2500 and CUGB2501.

Occurrence.—BH-3a and BH-4 of section A (transitional Rhaetian-Hettangian to lower Hettangian).

Discussion.—Due to poor preservation, the specimens cannot be identified to specific level. Features exhibited by the specimens seem more or less diagnostic for *Pteria*, that is they have relatively low shell convexity, a terminal beak, a straight hinge line, an obtuse posterior wing, and an entire pallial line.

Family BAKEVELLIDAE King, 1850
 Genus GERVILLIA Defrance, 1820
 Subgenus CULTRIOPSIS Cossmann, 1904
 GERVILLIA (CULTRIOPSIS) ANGUSTA Münster, 1838
 Figure 3.8b, 3.9, 3.10

Gervillia angusta MÜNSTER, 1838, p. 122, pl. 65, fig. 6.

Gervilleia angusta (MÜNSTER). BITTNER, 1895, p. 85, pl. 9, figs. 7–10; BITTNER, 1901, p. 21, pl. 4, fig. 18.

Gervillia (Angustella) angusta MÜNSTER. CHEN *IN* MA ET AL., 1976, p. 142, pl. 27, figs. 11, 12.

Gervillia (Angustella) cf. rugosa HEALY. CHEN *IN* MA ET AL., 1976, p. 294, pl. 28, fig. 48.

Gervillia (Angustella) angusta elongata CHEN *IN* MA ET AL., 1976, p. 294, pl. 28, figs. 41–44, 49.

Gervillia (Angustella) angusta tumida CHEN *IN* MA ET AL., 1976, p. 294, pl. 28, figs. 46, 47.

Gervillia (Angustella) epichara CHEN *IN* WEN ET AL., 1976, p. 39, pl. 8, figs. 4–6.

Gervillia (Cultriopsis) angusta MÜNSTER. NEWTON ET AL., 1987, p. 21, fig. 16.13–16.21; MÜNSTER, 1995, p. 81, fig. 62.

Description.—Shell small (maximum length = 34 mm), cylinder-shaped and very narrow, longitudinally elongate; highly inflated; beak terminal; anterior auricle poorly developed or reduced; posterior auricle obtuse, well demarked by deep furrow from main body of shell; shell exterior smooth; hinge consisting of five ligamental pits and one slightly oblique posterior elongate tooth.

Material examined.—Seven specimens, preserved as interior or exterior molds including CUGB2054, CUGB2061a, CUGB2062.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—Following Cox et al. (1969, p. N308) we regard *Cultriopsis* Cossmann, 1904 as a valid subgenus for *Gervillia*. By ratio of shell length to height, Chen (*in* Ma et al., 1976) recognized four new subspecies of *Gervillia (Cultriopsis)* from the Upper Triassic of western Yunnan and one new species from southern Tibet (see synonymy). Evaluation of descriptions and illustrations of these taxa leads us to conclude that no significant difference in form or characters exist between *Gervillia (Cultriopsis) angusta* and the species or subspecies introduced by Chen (*in*

Ma et al., 1976). In general, our Tibetan specimens agree with Münster's (1838) original description based on specimens from the Carnian of the southern Alps.

Genus AGUILERELLA Chavan, 1951

AGUILERELLA sp.

Figure 4.1–4.3

Description.—Medium-sized (maximum length about 34 mm, maximum height = 5 mm); outline subrhombic, posteriorly alate, inequilateral; height slightly exceeding length; slightly curved carina running from beak to anteroventral corner of shell, anterior margin in front of ridge steep; dorsal margin straight, posterior margin at obtuse angle; posterior umbonal ridge broad, rather feeble; beak subterminal; valve exterior smooth; smooth hinge exhibiting external ligamental pattern with about 11 pits vertical to hinge margin and irregularly spaced; left valve with one oblique anterior tooth adjacent to two sockets; pallial line represented by series of discontinuous points on umbonal area; posterior adductor scar large and centrally positioned.

Material examined.—One left valve preserved as both interior and exterior mold, CUGB2050.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—The single specimen exhibits diagnostic features of *Aguilerella* although this genus was previously only known from younger Jurassic strata (e.g., Cox et al., 1969; Muster, 1995). The absence of posterior teeth in the left valve may indicate that the species would be the most primitive member of the genus. No late Triassic or early Hettangian species of *Aguilerella* are known to be comparable with the Tibetan form. Although Chen (1987) referred specimens from the Liassic of southern Hunan to *Aguilerella*, we believe these specimens to be too poorly preserved for a confident generic assignment. Other Early Jurassic *Aguilerella* are known, including *A. neuquensis* Damborenea, 1987 from the Pliensbachian of Argentina. Based on Sinemurian material from northern Chile, Aberhan (1994) considers *A. neuquensis* a junior synonym of *A. kobyi* (Loriol, 1901), the type species of the genus known primarily from Alpine Europe. Therefore, Sinemurian and Pliensbachian records for this genus along the Pacific margins are apparently older than those in Western Europe and the northern margin of the eastern Tethyan faunal realm where *Aguilerella* range mainly from Toarcian to Oxfordian (e.g., Cox et al., 1969; Yin and Fürsich, 1991).

Family CASSIANELLIDAE Ichikawa, 1958

Genus CASSIANELLA Beyrich, 1862

CASSIANELLA sp.

Figure 4.4

?*Cassianella tulongensis* CHEN *IN* WEN ET AL., 1976, p. 41, pl. 7, figs. 22–24, 27–29.

?*Cassianella* cf. *C. douzhikovi* VUKHUC. CHEN *IN* MA ET AL., 1976, p. 295, pl. 29, figs. 11–13.

Material examined.—Three left valves preserved as internal molds including CUGB3032.

Occurrence.—BH-2 of section A (upper Rhaetian).

Discussion.—The specimens exhibit diagnostic features of *Cassianella*. The Tibetan material is most comparable in shape and external form to *Cassianella tulongensis* (Chen *in* Wen et al., 1976) and to the similar, and possibly conspecific, *Cassianella* cf. *C. douzhikovi* Vukhuc from western Yunnan (Chen *in* Ma et al., 1976); however, the poor quality of the Germig material does not permit specific identification. In addition, similar shaped *Cassianella* are common throughout the Upper Triassic with significant occurrences in Alpine Europe (e.g., Bittner, 1895; Zardini, 1981), the western Pacific (e.g., Krumbeck, 1913), North America (e.g.,

McLearn, 1942; Newton et al., 1987; McRoberts and Blodgett, 2002), and South America (Körner, 1937; Riccardi et al., 1997).

Family PERGAMIDIIDAE Cox, 1969

Genus KRUMBECKIELLA Ichikawa, 1958

KRUMBECKIELLA TIMORENSIS (Krumbeck, 1924)

Figure 4.13, 4.14

Timoria timorensis KRUMBECK, 1924, p. 221, pl. 194, figs. 17–22; pl. 195, figs. 4–6.

?*Krumbeckiella timorensis* (KRUMBECK). ICHIKAWA, 1958, p. 196; SHA ET AL., 1990, p. 148, pl. 3, figs. 6, 7.

?*Krumbeckiella* cf. *K. subtimorensis* (KRUMBECK). CHEN *IN* MA ET AL., 1976, p. 337, pl. 38, figs. 11, 13.

Description.—Shell medium-sized (length = 30 mm, height = 40 mm), moderately inflated, and slightly inequilateral, vertically ovate in outline, almost equivalved, umbo prosogyrous, more or less anteriorly placed, slightly protruding; exterior surface smooth except for slightly irregularly spaced, commarginal lines. Valve interiors not observed.

Material examined.—One articulated valve pair, CUGB3099.

Occurrence.—BH-1 of section B (upper Rhaetian).

Discussion.—Although partially crushed, the single specimen compares well with the type species *Krumbeckiella timorensis*. Three species of *Krumbeckiella* were found in western Yunnan by Chen (*in* Ma et al., 1976). One of them, referred to as *Krumbeckiella* cf. *K. subtimorensis*, is close to the present specimen in size and shape and may possibly belong to the same species. *Krumbeckiella timorensis* was also reported in southern Qinghai by Sha et al. (1990); although, because this specimen exhibits a triangular outline and hinge line longer than shell length, its specific assignment is questionable.

Order PECTINOIDA Rafinesque, 1815

Family PECTINIDAE Rafinesque, 1815

Genus CHLAMYS Röding, 1798

CHLAMYS VALONIENSIS (Defrance, 1825)

Figure 4.5–4.12

Pecten valoniensis DEFRANCE, 1825, p. 507, pl. 22, fig. 6.

Chlamys (*Chlamys*) *valoniensis* (DEFRANCE). JOHNSON, 1984, p. 179, pl. 9, figs. 3, 5; ABERHAN, 1994, p. 40, pl. 19, figs. 7–9; 1998, pl. 12, figs. 14, 17, 19, 22.

Chlamys valoniensis (DEFRANCE). IVIMEY-COOK ET AL., 1999, p. 105, pl. 14, figs. 8–10.

?*Praechlamys valoniensis* (DEFRANCE). DAMBORENEA, 2002, p. 74, pl. 8, figs. 9–15.

Description.—Medium-sized (maximum length = 36 mm, maximum height = 36 mm), approximately equilateral, height exceeding length in early ontogeny, gradually becoming equal to length in adult shells; inequivalved with left valve more inflated than right; umbonal angle about 90°; right anterior auricle with large byssal notch, ornamented by four or five radial ribs, larger than obtusely pointed posterior auricle; both valves bearing large number of radial plicae that vary in strength and spacing, increasing in number by intercalation of secondary ribs, varying from 24 at 15 mm from beak to about 70 at 35 mm from beak.

Material examined.—Including the seven catalogued specimens, the collection consists of 10 specimens: four left valves, six right valves, all preserved as internal or external molds; CUGB2132, CUGB3033b, CUGB2051b, CUGB2052, CUGB2253, CUGB2154, CUGB2059.

Occurrence.—Localities BH-3a and BH-4 of section A (transitional Rhaetian-Hettangian to lower Hettangian).

Discussion.—*Chlamys valoniensis* has been reviewed at length by Johnson (1984) and more recently, as a species within *Praechlamys* Allasinaz, 1972, by Damborenea, 2002. Although the

Tibetan forms exhibit somewhat more closely spaced and finer radial plicae than some specimens attributed to this species, the rib characters fall within the limits of this highly variable species. *Chlamys valoniensis* has a cosmopolitan distribution and is found in New Zealand and South America (e.g., Damborenea and Mancaño, 1992; Aberhan, 1994; Riccardi et al., 2004), alpine and northwest Europe (e.g., Johnson, 1984; Hodges, 2000), and western Canada (e.g., Aberhan, 1998), ranging from Rhaetian to Hettangian.

Family PROSPONDYLIDAE Pchelinceva, 1960 [emend. Hautmann, 2001a]

Genus PERSIA Repin, 1996 [emend. Hautmann, 2001a]

PERSIA HALLAMI new species

Figures 5.15–5.18, 5.22–5.25, 6.1–6.7

Terquimia sp. YIN ET AL., 1999, fig. 3.4.

Diagnosis.—Medium-sized *Persia*, suborbicular in outline, height equal to or slightly exceeding length; dorsal margin almost equal to shell length; attachment area of right valve varying greatly in size and shape; radial ribs well developed, hinge area longitudinally elongated; ligamental pit pear-shaped, medially positioned, protruding beyond lower margin of cardinal area; pair of crura adjacent to ligament.

Description.—Medium-sized (maximum length = 55 mm, maximum height = 54 mm); suborbicular in outline, height equals or slightly exceeds length; hinge margin almost equal to shell length, subequilateral; right valve xenomorphic, attachment area of right valve small to nearly entire valve surface; hinge area well developed, longitudinally elongated; pear-shaped ligamental pit medially positioned, protruding from lower margin of cardinal area and positioned between a pair of crura; internal molds of right valve exhibiting large, subcircular, posteriorly placed adductor scar; left valve slightly inflated, ornament on both valves consisting of 22 and 30 coarse, radial ribs, broadly rounded, subequal in strength, occasionally intercalated by secondary ribs.

Etymology.—After A. Hallam, a significant contributor to Mesozoic paleontology.

Types.—Holotype, CUGB3080c; Paratypes, CUGB1099, CUGB2042, CUGB2460, CUGB2466b, CUGB2477, CUGB2449b, CUGB2333, CUGB2449a, CUGB2304, CUGB2309, CUGB2079, CUGB3011, CUGB3081. See Table 2 for measurements.

Material examined.—Including types, the collection consists of 15 specimens.

Occurrence.—BH-3a of section A and BH-3b of section B (transitional Rhaetian-Hettangian).

Discussion.—Morphologic details of the hinge of this Tibetan species exhibit features transitional between *Enantiostreon* Bittner, 1901, *Terquemia* Tate, 1868, and *Persia*. This new species possesses a narrow triangular cardinal area and broad resilifer characteristic of *Enantiostreon*, but also has a pair of crura, which have not previously been observed in *Enantiostreon* nor in *Terquemia*. However, crura have been shown to be weakly developed in *Persia*, and are more pronounced in plicatulids such as *Eoplicatula* Carter, 1990 (see Hautmann, 2001b). According to Hautmann (2001b) *Persia* is characterized by distinct ears, a deep and narrow resilifer, and weak crura; but in *Persia hallami*, the resilifer is somewhat broader and extends below the lower hinge margin. Although crura in *Persia hallami* are well developed, they are only placed in the lower ligamental pit, which is different from *Eoplicatula*, a genus characteristic of well-developed crura. *Persia hallami* appears more oysterlike than other Prospondylidae such as *Enantiostreon*. However, based on the nature of ligament, we tentatively place this new species in *Persia*. Morphologically, *Persia hallami* differs from *Persia monstrosa* Repin, 1996 (Repin, 1996; Hautmann, 2001b) by possessing longer and more numerous and bifurcated riblets. Our new species can be easily distinguished from the Upper Triassic *Enantiostreon hungaricum* of German Rhaetian deposits (illustrated by Frech, 1907). *Enantiostreon hungaricum* Bittner, 1901, the type species from the Carnian of Alpine Europe, has a thicker shell and more pronounced costae than *Persia hallami*. Other poorly known *Enantiostreon*, mostly from the Muschelkalk, such as *E. spondyloides* (Schlotheim, 1823) and *E. multicostratum* (Münster, 1838), need to be compared with the new species. Another externally similar form, such as “*Enantiostreon difformis*” (illustrated by Schmidt, 1928, p. 166, fig. 361a–d), is better placed in *Terquemia* based on the nature of ligament.

?PERSIA sp.
Figure 4.17

Description.—Medium-sized (length = 45 mm, height = 48 mm); rounded, nearly equivalved, and subequilateral, umbonal area moderately inflated; exterior ornament of right valve consisting of coarse, sinuous, radial ribs; commarginal growth lines absent.

Material examined.—One articulated specimen, CUGB3121.

Occurrence.—Locality BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—The specimen is comparable with Iranian specimens (Hautmann, 2001b, pl. 18, figs. 1–5) in shape and ribbing; however, with only one specimen available in which details of

FIGURE 4—1–3, *Aguilerella* sp. indet., CUGB2050, loc. BH-3a; 1, left valve external mold; 2, internal mold of same specimen; 3, enlarged ligamental area of same specimen. 4, *Cassianella* sp. indeterminate, right valve internal mold, CUGB3032, loc. BH-2. 5–12, *Chlamys valoniensis* (Defrance, 1825); 5, latex cast of left valve exterior, showing anterior auricle, CUGB3033b, loc. BH-3a; 6, latex cast of left valve exterior, CUGB2051b, loc. BH-4; 7, left valve external mold, CUGB2059, loc. BH-4; 8, left valve external mold, CUGB2154, loc. BH-3a; 9, right valve internal mold showing large auricle, CUGB2253, loc. BH-3a; 10, right valve, internal mold, CUGB2052, loc. BH-4; 11, latex cast of right valve exterior, CUGB2053b, loc. BH-4; 12, right valve external mold, CUGB2132, loc. BH-3a. 13, 14, *Krumbeckiella timorensis* (Krumbeck, 1924), CUGB3099, loc. BH-1; 13, right valve of articulated specimen; 14, posterior view of left valve of same specimen. 15, ?*Harpax* sp. B, latex cast of left valve exterior, CUGB3035b, loc. BH-3a. 16, 18, 19, Ostreoid gen et sp. indeterminate, all from loc. BH-3a; 16, right valve internal mold showing attachment area, CUGB30213; 18, latex cast of left valve exterior, CUGB3128; 19, latex cast of left valve exterior, CUGB2177. 17, ?*Persia* sp., right valve of articulated specimen, CUGB3121, loc. BH-3a. 20, 21, ?*Harpax* sp. A, all from loc. BH-3a; 20, latex cast of right valve exterior, CUGB2093; 21, latex cast of left valve exterior, CUGB3036b. 22–32, *Ctenostreon newelli* n. sp., all from loc. BH-3a; 22, right valve, internal mold showing large resilifer and cardinal area, paratype, CUGB2021; 23, latex cast of right valve exterior showing spines along dorsal and ventral margins, paratype, CUGB2044b; 24, latex cast of left(?) valve exterior showing concentric lamellae and spines, paratype, CUGB3039b; 25, latex cast of left(?) valve exterior, paratype, CUGB2059b; 26, latex cast of left valve exterior showing anterior and posterior auricles, CUGB3049, paratype; 27, left valve, external mold, holotype, CUGB2026; 28, right valve, internal mold, paratype, CUGB3040; 29, right valve, internal mold, paratype, CUGB2049; 30, left valve, internal mold, paratype, CUGB2048; 31, left valve, internal mold, CUGB2511a; 32, left or right valve, internal mold, paratype, CUGB3038. Magnification, 1, 2, 4, 6, 7, 9–32, $\times 1$; 5, $\times 1.5$; 3, 8, $\times 2$.



hinge area and ligament are indeterminable, assignment to the genus remains questionable.

Genus *NEWAAGIA* Hertlein, 1952 [emend. Hautmann, 2001a]
NEWAAGIA LANONGLAENSIS new species
 Figure 5.14, 5.19–5.21

Diagnosis.—*Newaagia* with an orbicular outline, flat shell, short dorsal margin, and highly transverse lamellae with spines and discontinuous radial ribs.

Description.—Medium-sized (maximum length = 40 mm, maximum height = 50 mm); obliquely ovate in outline, height slightly exceeding length; shell compressed; attachment area varying greatly from small and near umbo to nearly entire surface of right valve; ornament consists of strong transverse lamellae and radial ribs; about 20 ribs almost regularly interspaced, commonly interrupted by lamellae especially towards ventral margin so that ribs become short, tubular spines; commarginal lamellae irregular in strength, more distant, and stronger towards ventral margin.

Etymology.—After Lanongla, the region in southern Tibet where the species occurs.

Types.—Holotype, CUGB2081a; Paratypes, CUGB3079b, CUGB3081, CUGB2084, CUGB2081b. See Table 3 for measurements.

Material examined.—Including the types, the collection consists of six specimens, including four right and two left valves.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—This form is associated with *Persia hallami* n. sp., but it is distinguishable from the latter in its distinct ornament consisting of strong lamellae and discontinuous radial ribs, whereas *Persia hallami* exhibits stronger radial costae that diverge at the shell margin. *Newaagia* (*Latinewaagia*) *qilianensis* Yin and Yin, 1983 from the Middle Triassic of Qinghai province, China (Yin and Yin, 1983, p. 109, pl. 20, figs. 1–9), is easily distinguished from the Tibetan form by strong radial ribs. *Newaagia stocklini* (Repin, 1996) of eastern central Iran (Hautmann, 2001b, p. 80, pl. 17, figs. 1, 2) is somewhat similar to the Tibetan form in its ornament, but differs in its stronger radial riblets.

Family UNCERTAIN

Genus *TERQUEMIA* Tate, 1868

TERQUEMIA cf. *T. DIFFORMIS* (Schlotheim, 1820)

Figure 6.8–6.11

cf. *Enantiostreon difformis* (SCHLOTHEIM). SCHMIDT, 1928, p. 166, fig. 361a–d.

cf. *Terquemia difformis* (SCHLOTHEIM). IVIMEY-COOK ET AL., 1999, p. 102, pl. 14, fig. 3.

Description.—Medium-sized (maximum length = 34 mm,

maximum height = 30 mm); xenomorphic, shape variable but mostly subtriangular in outline; attachment area on right valve small; left valve moderately inflated, with 6–10 radial costae, irregularly interspaced, sometimes slightly sinuous and bifurcated, strong near umbo, but fade towards shell margin, intersected by feebly commarginal growth lines.

Material examined.—Four fragmented specimens; CUGB3201, CUGB3203, CUGB3208, CUGB3209.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—Based on the poor quality of our specimens and definitive characterization of hinge and shell structure of *Terquemia*, we leave unresolved the suprageneric classification of this genus. We assign these specimens to *Terquemia* because distinct auricles, known in other prospannids, were not observed. The features of our Tibetan specimens are similar to those of German and English specimens of *Terquemia difformis* (Schmidt, 1928; Ivimey-Cook et al., 1999). In absence of well-preserved specimens, however, a more precise assignment remains impossible.

Order OSTREOIDA Férussac, 1822

Ostreoid genus and species indeterminate

Figure 4.16, 4.18, 4.19

Material examined.—The collection consists of three specimens, all are left valves; CUGB2177, CUGB3128, CUGB30213.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—The left valves are slightly convex, ornament consists of sinuous radial lines and commarginal lamellae that differ from associated cementing forms in the collection. Due to the absence of a right valve, and details of the attachment area, the generic determination is questionable and specific assignment is withheld until better material becomes available.

Genus HARPAX Parkinson, 1811

?*HARPAX* sp. A

Figure 4.20, 4.21

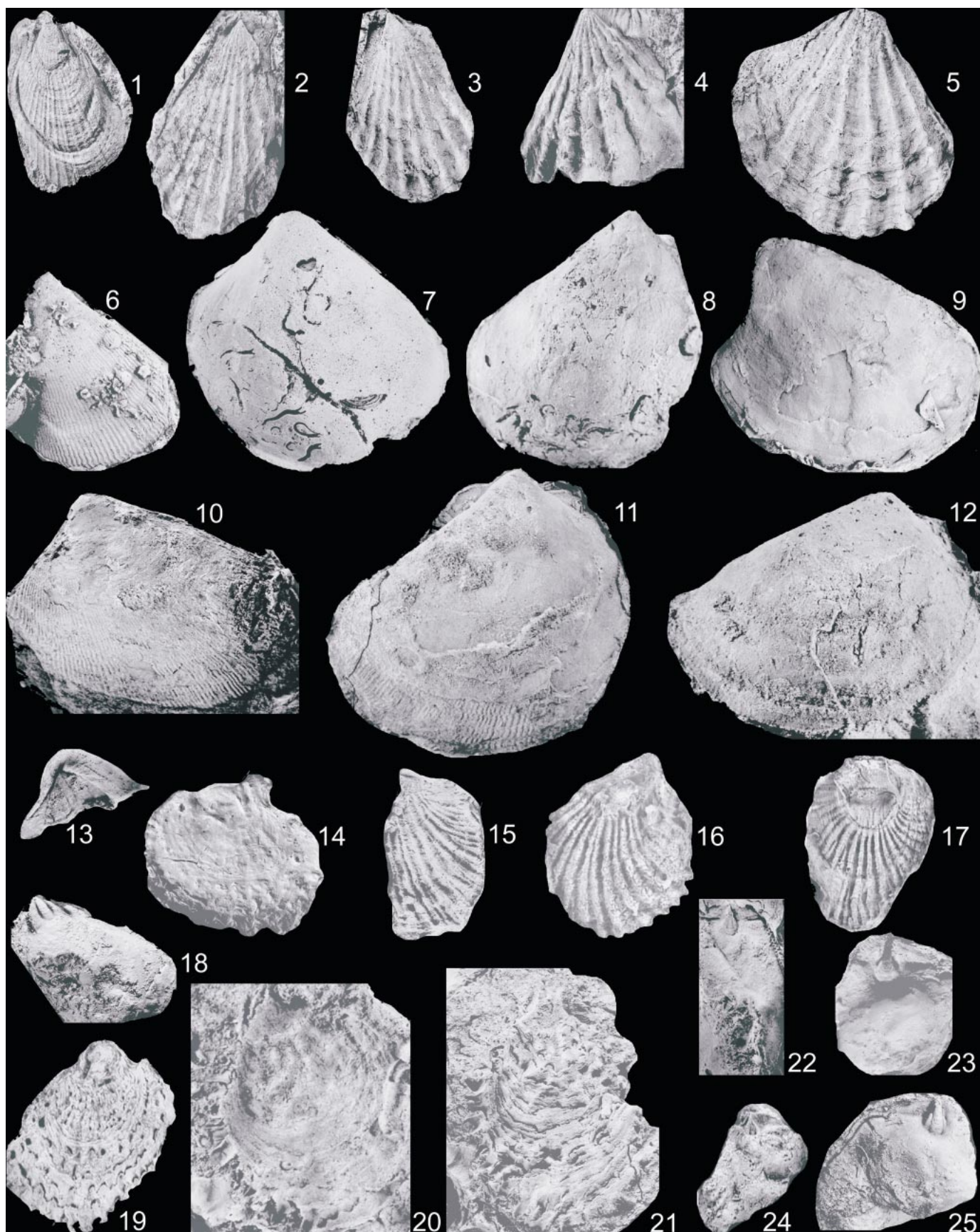
Description.—Medium-sized, moderately inflated, length exceeding height, dorsal margin horizontally elongated, right valve possessing large attachment area; longitudinally ovate in outline, ornamentation consists of stout tubular spines which occur along commarginal lamellae and increase in strength towards ventral margin; valve interior not observed.

Material examined.—The collection consists of two external molds; CUGB2093, CUGB3036b.

Occurrence.—BH-3b of section B (transitional Rhaetian-Hettangian).

Discussion.—Cox et al. (1969) regarded *Harpax* as a junior

FIGURE 5—1, *Antiquilima* sp., left valve of articulated valve pair, CUGB3200, loc. BH-1. 2–5, *Ctenostreon newelli* n. sp., all from loc. BH-3a; 2, left valve, internal mold, paratype, CUGB2028; 3, right valve, internal mold, paratype, CUGB1205. 4, left valve, internal mold, paratype, CUGB2035; 5, right valve, internal mold, CUGB2061c. 6–13, *Plagiostoma giganteum* Sowerby, 1814, all from loc. BH-3a; 6, latex cast of right valve exterior, CUGB2441b; 7, right valve internal mold showing extensive serpulid encrustation, CUGB2403; 8, left valve internal mold, CUGB2405; 9, latex cast of right valve exterior, CUGB20628; 10, latex cast of right valve exterior, CUGB2466a; 11, left valve external mold showing radial ribs along ventral margin, CUGB2402; 12, left valve external mold, CUGB2422; 13, latex cast of right valve cardinal area, CUGB2412. 14, 19–21, *Newaagia lanonglaensis* n. sp., all from loc. BH-3a; 14, right valve external mold, paratype, CUGB3079a; 19, right valve external mold showing sculpture, paratype, CUGB3079b; 20, right valve external mold with large xenomorphic impression, holotype, CUGB2081a; 21, right valve external mold showing ornament on internal layer whereas external layer retains xenomorphic impression, paratype, CUGB2081b. 15–18, 22–25, *Persia hallami* n. sp., all from loc. BH-3a; 15, left valve external mold, paratype, CUGB2460; 16, latex cast of right valve exterior showing attachment area, paratype, CUGB1099; 17, latex cast of right valve exterior showing attachment area, paratype, CUGB2466b; 18, left(?) valve internal mold, paratype, the cardinal area not fully preserved but note crura and resilifer, paratype, CUGB3081; 22, latex cast of right valve(?) cardinal area, paratype, CUGB2477; 23, latex cast of internal mold of same specimen as 25 showing large resilifer and triangular cardinal area, paratype, CUGB2449b; 24, internal mold of cardinal area with well defined resilifer and crura, paratype, CUGB2333; 25, internal mold of cardinal area with well defined resilifer between crura, paratype, CUGB2449a. Magnification, $\times 1$.



synonym of *Plicatula* Lamark, 1801. Based on ornamentation and hinge structure, however, it has recently been revived as a valid taxon (e.g., Poulton, 1991; Damborenea, 1993, 2002; Aberhan, 1994). These two Tibetan specimens show a straight, long hinge margin and commarginal growth rugae with irregularly stout, short knobs. Specific assignment is withheld until more material becomes available.

?HARPAX sp. B
Figure 4.15

Description.—Left valve horizontally ovate, oblique; beak anteriorly situated, umbonal area moderately inflated; valve exterior with commarginal growth lines, radial ribs towards ventral margin, and irregularly spaced but densely packed spines.

Material examined.—One exterior mold which was used to make the figured latex cast, CUGB3035b.

Occurrence.—BH-3b of section B (transitional Rhaetian-Hettangian).

Discussion.—The Tibetan specimen with its more oval shape differs from *Harpax rapa* (Bayle and Coquand, 1851) known from North and South America (e.g., Aberhan, 1994, 1998; Damborenea, 2002). Although the Tibetan specimen may represent a new species, additional material is needed for an adequate diagnosis and description.

Family GRYPHAEIDAE Vyalov, 1936
Genus LIOSTREA Douvillé, 1904
LIOSTREA TIBETICA new species
Figure 6.19, 6.22–6.29, 6.30b, 6.31–6.33

Diagnosis.—Smooth-shelled *Liostrea*, small-sized for genus, with left valve highly inflated and right valve flat or slightly concave, shape subtriangular to ovate, height well exceeding length; left valve adductor scar, orbicular in outline, situated just below posterior hinge; attachment area of left valve varying greatly.

Description.—Small-sized (maximum length = 24 mm, maximum height = 32 mm), orbicular to subtriangular, varied in outline, height generally exceeding length; valve exterior smooth except for irregularly interspaced concentric growth lines in both valves; left valve variably inflated, mostly capacious and highly convex in dorsoventral direction, maximum of convexity at one-fourth to one-third of height from cardinal line; right valve flat or slightly concave, cardinal area small, adductor muscle scar somewhat longer than high, relatively large, and slightly concave at dorsal margin, situated closely to upper posterodorsal margin.

Etymology.—After its only known occurrence in Tibet.

Types.—Holotype, CUGB3090; Paratypes, CUGB2600–2604, CUGB2607, CUGB2609, CUGB2610, CUGB2611, CUGB2614, CUGB2617, CUGB2618, CUGB2620, CUGB3088. See Table 4 for measurements.

Material examined.—Including the types, the collection consists of 15 specimens, mostly left valves.

Occurrence.—BH-3b and BH-4 of section A (transitional Rhaetian-Hettangian to lower Hettangian).

Discussion.—Although the specimens can be confidently placed in *Liostrea*, valve morphology is highly variable due to the nature of attachment surfaces. Most Rhaetian *Liostrea* in Europe, such as *Liostrea bristovi* (Richardson, 1905) and *Liostrea hisinggeri* (Nilsson, 1832), possess lower convexity than the present Tibetan species. In addition, *Liostrea tibetica* is distinguishable from these European species in possessing strong valve inflation and an adductor scar in a more posterodorsal position.

Order LIMOIDA Waller, 1978
Family LIMIDAE Rafinesque, 1815
Genus CTENOSTREON Eichwald, 1862
CTENOSTREON NEWELLI new species
Figures 4.22–4.32, 5.2–5.5

Diagnosis.—Slightly inequivalved *Ctenostreon*, inequilateral, suborbicular shell with low convexity, height exceeding length, auricles well defined, anterior auricle shorter than posterior, poorly developed byssal notch on right valve; ornamentation consisting of squamose surface with eight or nine rounded spinose ribs on both right and left valves, rib width less than interspaces; ligament area wide with large central resilifer lacking cardinal crura.

Description.—Shell medium-sized (maximum length = 41 mm, maximum height = 51 mm); slightly inequilateral and inequivalved; height generally exceeds length; both right and left valves weakly inflated, ornament consisting of eight or nine regularly interspaced, rounded, radial ribs with tubular spines, spines occasionally well preserved in ventral and posterodorsal margins, width of ribs slightly less than interspaces; irregularly spaced, commarginal growth lamellae; hinge margin relatively long, beak centrally situated; anterior auricle larger than posterior auricle in juveniles, becoming more or less shorter than posterior auricle in adult shells; posterior auricle well differentiated from body of shell; umbonal area weakly inflated, hinge structure consisting of broad, flat ligamental area and large central resilifer.

Etymology.—After the late Norman D. Newell, specialist of Permian and Lower Triassic bivalves.

Types.—Holotype: CUGB2026; Paratypes: CUGB2021,

FIGURE 6—1–7, *Persia hallami* n. sp., all from loc. BH-3a; 1, latex cast of left valve exterior, paratype, CUGB2079; 2, latex cast of right valve interior, holotype, same specimen as 3, CUGB3080b; 3, right valve internal mold, holotype, CUGB3080a; 4, right valve external mold, of holotype, CUGB3080c; 5, right valve external mold showing xenomorphic impression and large attachment area, paratype, CUGB2304; 6, right valve external mold, paratype, CUGB2309; 7, right valve external mold, paratype, CUGB2042. 8–11, *Terquemia* cf. *T. difformis* (Schlotheim, 1820), all from loc. BH-3a; 8, fragment of left(?) valve exterior, CUGB3201; 9, left valve external mold, CUGB3208; 10, right valve external mold, CUGB3209; 11, right valve external mold, CUGB3203. 12–18, 35, *Palaeocardita trapezoidalis* (Krumbeck, 1913), all from loc. BH-1; 12, posterior view of articulated valve pair internal mold, CUGB3332; 13, anterior view of same specimen CUGB3332; 14, dorsal view of a latex cast of articulated valve exterior, CUGB3333; 15, left valve internal mold, CUGB3321; 16, left valve internal mold, CUGB3338; 17, left valve internal mold, CUGB3332; 18, latex cast of left valve exterior, same specimen as 14, CUGB3321; 35, latex cast of left(?) valve exterior, CUGB3575. 19, 22–29, 30b (30a: associated brachiopods), 31–33, *Liostrea tibetica* n. sp., all from loc. BH-3a; 19, latex cast of left valve exterior, paratype, CUGB2600; 22, left valve internal mold, paratype, CUGB2601; 23, latex cast of right valve interior, paratype, CUGB2603; 24, latex cast of left valve exterior, holotype, CUGB3090; 25, left valve internal mold, paratype, CUGB2604; 26, left valve internal mold, paratype, CUGB2611; 27, left valve internal mold, CUGB2607; 28, left valve internal mold, paratype, CUGB2614; 29, left valve internal mold, paratype, CUGB2618; 30b, left valve internal mold, paratype, CUGB2617; 31, left valve internal mold, paratype, CUGB3088; 32, latex cast of right valve, paratype, CUGB2620; 33, left valve internal mold, paratype, CUGB2609. 20, 21, ?*Schafhaeulia* sp. indet., from loc. BH-1; 20, articulated valve pair, CUGB3337; 21, right valve internal mold, CUGB3307. 34, 36–41, *Astarte* sp., all from loc. BH-2; 34, left valve external mold, CUGB2444; 36, right valve internal mold, CUGB2440; 37, left valve internal mold, CUGB2445; 38, latex cast of right valve exterior, CUGB3309b; 39, latex cast of right valve exterior, CUGB2447b; 40, latex cast of right valve exterior, CUGB3304b; 41, left valve hinge area, internal mold, CUGB3338. 42, *Unionites griesbachi* (Bittner, 1899), left valve internal mold, loc. BH-1, CUGB3331. Magnification, 1, 34, ×2; 2–13, 15–33, 35–40, 42, ×1; 14, ×1.2; 41, ×5.

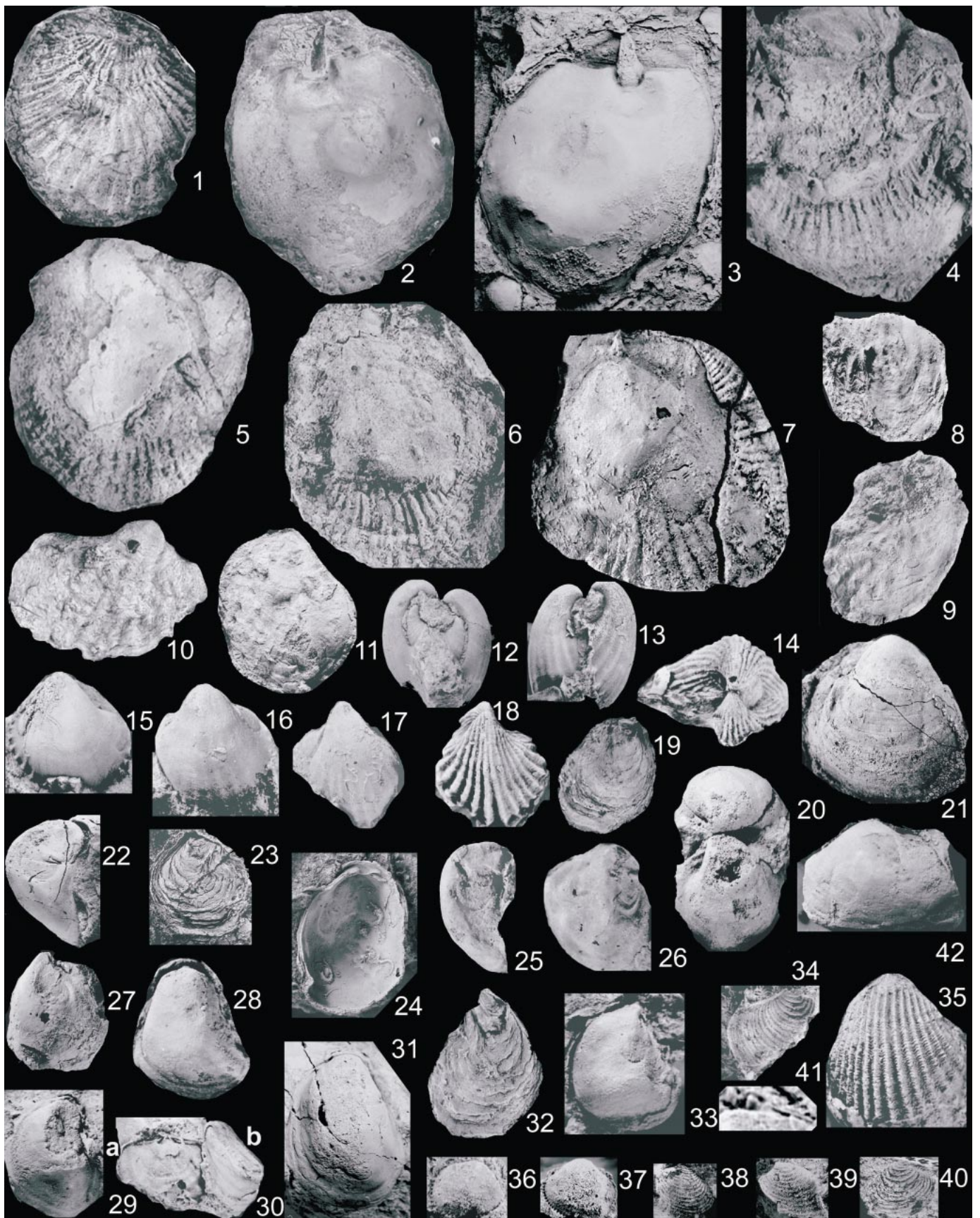


TABLE 2—Measurements in mm of *Persia hallami* n. sp. Abbreviations: AA, attachment area; RR, radial rib count; RV, right valve; LV, left valve. * indicates holotype, (??) indicates measurement estimated.

Specimen	Length	Height	AA		RR	Valve
			L	H		
CUGB2460	20(??)	30	—	—	20	LV
CUGB2466b	33	25(??)	11	15	25	RV
CUGB3011	38	40	—	—	28	LV
CUGB3080*	55	46	35	40	23(??)	RV
CUGB2304	47	54	34	34	25	RV
CUGB2309	24	32	13	12	23	RV
CUGB2042	50	50?	30	35	34	RV
CUGB2314	53	53	43	39	—	RV
CUGB2317	46	49	32	33	—	RV
CUGB2308	25(??)	31	17	21	12	RV
CUGB2302a	37	37	18	24	34	RV
CUGB2303	34	39	15	19	18	RV
CUGB2302b	32	32	14	10	18	RV
CUGB2305	35	33	31	33	33	RV
CUGB2307	—	33	13	17	17	RV
CUGB2301	42	44	—	—	30	LV
CUGB2306	—	33	—	—	24	LV
CUGB2302c	40	37	—	—	28	LV
CUGB2313	48(??)	42	—	—	30	LV

CUGB2028, CUGB2044b, CUGB1205, CUGB2035, CUGB3039b, CUGB2059b, CUGB2061c, CUGB3049, CUGB3040, CUGB2048, CUGB2049, CUGB2511a, CUGB3038. See Table 5 for measurements.

Material examined.—Including the types, the collection consists of 22 specimens, mostly exterior and interior molds.

Occurrence.—BH-3a of section A and BH-3b of section B (transitional Rhaetian-Hettangian).

Discussion.—*Ctenostreon* has previously been reported from Lower Jurassic to Lower Cretaceous in the Europe, Asia, and North and South America (e.g., Cox, 1952; Yamani, 1975; Aberhan, 1994, 1998). The oldest Jurassic species, *Ctenostreon wrighti* Bayle, 1878, occurs in France (Bayle, 1878) and northern Chile (Aberhan, 1994) and apparently, like other species of this genus, exhibits great variability in rib density and shell form (e.g., Cox, 1952; Yamani, 1975). The Tibetan form is most similar to *Ctenostreon wrighti*, but is characterized by having fewer ribs (between 9 and 11) and tubular spines at wider and more irregularly spaced intervals. Other species of *Ctenostreon*, such as *C. rugosum* (Smith, 1817), have broader valves, less prominent ribs, and narrower rib interspaces. The specimen referred to as "*Lima terquimi*" from the pre-*Planorbis* beds of South England (see Arkell, 1933, p. 602, pl. 29, fig. 3) is somewhat similar to *Ctenostreon newelli*, but possess fewer ribs. Other *Ctenostreon*, including *Ctenostreon tuberculatum* (Terquem, 1855), *C. rariocostatum* (Bayle and Coquand, 1851), and *C. terquemi* (Tate, 1867), are too poorly known for meaningful comparison with the new species from Germig.

TABLE 3—Measurements in mm of *Newaagia lanonglaensis* n. sp. Abbreviations: AA, attachment area; L, length; H, height; LV, left valve; RV, right valve. * indicates holotype, (??) indicates measurement estimated.

Specimen	Length	Height	AA		Valve
			L	H	
CUGB3079b	35	26	26	20	RV
CUGB3081	35(??)	23?	—	—	LV?
CUGB2084	35	35	—	—	LV
CUGB2081a*	40	50	30	30	RV
CUGB2081b	40(??)	50	—	—	RV
CUGB3080d	22	—	—	—	—
CUGB3071	15	12	—	—	RV

TABLE 4—Measurements in mm of *Liostrea tibetica* n. sp. Abbreviations: LV, left valve; RV, right valve. * indicates holotype, (??) indicates measurement estimated.

Specimen	Length	Height	Thickness	Valve
CUGB2600	20	22	—	LV
CUGB2601	22	23	16	LV
CUGB2603	20	22	—	RV
CUGB2604	22	28	—	LV
CUGB2610	18	20	15	LV
CUGB2611	20	24	10	LV
CUGB2607	19	23	12	LV
CUGB2614	23	25	9	LV
CUGB2618	20	23	8	LV
CUGB3088	34	25	15(??)	LV
CUGB3090*	30	26	17	LV
CUGB2617	15	17	12	LV
CUGB2620	24	32	16	RV
CUGB2609	22	24	15	LV

Genus ANTIQUILIMA Cox, 1943

ANTIQUILIMA sp.

Figure 5.1

Description.—Medium-sized (length = 21 mm, height > 30 mm), oblique ovate; umbo small, moderately inflated, well demarcated from body of shell; beak sharply pointed, protruding above hinge line; anterior margin straight, meeting smoothly with ventral margin; posterior margin convex, joining dorsal margin at right or obtuse angle; ornament consisting of about 20 broad, flat-topped, irregularly spaced radial ribs, occasionally intercalated by secondary ribs.

Material examined.—The collection consists of a single articulated valve pair, CUGB3200.

Occurrence.—BH-0 of section B (upper Rhaetian).

Discussion.—*Antiquilima* is a genus ranging from between the Early to Middle Jurassic, according to Cox et al. (1969, N386). Recently, this genus has been found in the Upper Triassic of Northeast Russia (e.g., Kiparisova et al., 1966; Milova, 1976), North and South America (Hayami et al., 1977; Newton et al., 1987), and Iran (Hautmann, 2001b). This Tibetan specimen has a distinctive ornamentation pattern, but with one specimen it is impossible to evaluate the range of morphological variation and to provide a precise specific designation.

TABLE 5—Measurements in mm of *Ctenostreon newelli* n. sp. Abbreviations: AA, attachment area; LAA, length of anterior attachment area; LPA, length of posterior attachment area; RR, radial rib count; RV, right valve; LV, left valve. * indicates holotype, (??) indicates measurement estimated.

Specimen	Length	Height	RR	AA		Valve
				LAA	LPA	
CUGB2044b	25	32	9	—	8	RV
CUGB3039b	30(??)	45	8	—	9	LV?
CUGB2059b	37	45	9	—	—	LV?
CUGB3049	—	—	9	4	6	LV
CUGB2026*	35	41	9	8	5	LV
CUGB3040	—	—	8	9	6	RV
CUGB2049	36	51	8	8	9	RV
CUGB2048	41	47(??)	9	—	—	LV
CUGB2511a	40(??)	47	8	10	9(??)	LV
CUGB3038	40(??)	45	8	?	?	?
CUGB2031	31	37	8(??)	—	—	LV
CUGB2042	38	47	9	—	11	RV
CUGB2028	33	42	9	—	9	LV
CUGB2046	30	34	—	9	9	RV
CUGB2035	37	44(??)	9	—	10	LV
CUGB2034	32	34	9	—	—	?

Genus PLAGIOSTOMA SOWERBY, 1814
 PLAGIOSTOMA GIGANTEUM SOWERBY, 1814
 Figure 5.6–5.13

Plagiostoma gigantea SOWERBY, 1814, p. 176, pl. 77.
Lima (Plagiostoma) gigantea SOWERBY. COX, 1935, p. 4, pl. 1, fig. 6.
Plagiostoma giganteum SOWERBY. ABERHAN, 1994, p. 25, pl. 9, figs. 8–10; IVIMEY-COOK ET AL., 1999, p. 95, pl. 12, figs. 9, 10.
 ?*Plagiostoma subpunctatoides* KRUMBECK. CHEN IN MA ET AL., 1976, p. 318, pl. 35, figs. 36, 37.

Description.—Shells moderately large (maximum length = 60 mm, maximum height = 54 mm), obliquely ovate, opisthocline, length commonly exceeding height in adult shell; inflation moderate to strong; posterior and ventral margins well rounded, beak protruding over hinge line, auricles obtuse, almost equal; poorly developed posterior umbonal ridge, anterior umbonal ridge well defined with excavated lunule; cardinal area long with triangular ligamental pit; surface smooth except for commarginal striae and regular, flat-topped riblets; riblets well developed in small shells or towards ventral margin of adult shells where they become slightly sinuous.

Material examined.—The collection consists of more than 50 specimens; Cataloged specimens, CUGB20628, CUGB2402, CUGB2403, CUGB2405, CUGB2412, CUGB2422, CUGB2441b, CUGB2466a.

Occurrence.—BH-3a of section A (transitional Rhaetian-Hettangian).

Discussion.—This form is the most abundant in the collection and therefore exhibits a large variability in shell shape. In general, small individuals frequently exhibit a greater height to length ratio and have finer riblets. Some medium-sized individuals are only ornamented by fine commarginal growth lines without riblets. Larger individuals possess the diagnostic features of *Plagiostoma giganteum*, that is, length well exceeding height, radial riblets more strongly developed towards the shell margin and becoming slightly sinuous near the posterior and anterior margins. Most likely, the variation in shell shape and ornamentation only suggests an intraspecific range of ontogenetic variation for this species. However, the Hettangian specimens in Dorset, southern England (e.g., Sowerby, 1814; Cox, 1935; Ivimey-Cook et al., 1999), can attain a very large size.

Two specimens from late Triassic deposits of western Yunnan referred to as *Plagiostoma subpunctatoides* Krumbeck (Chen in Ma et al., 1976) may be conspecific. As the Yunnan specimens are only preserved as interior molds, it is difficult to confirm their specific identification because information on their ornament is absent.

Order VENEROIDA Adams and Adams, 1854–1858
 Family ASTARTIDAE d'Orbigny, 1844
 Genus ASTARTE SOWERBY, 1816
 ASTARTE sp.
 Figure 6.34, 6.36–6.41

?*Astarte* sp. IVIMEY-COOK ET AL., 1999, p. 116, pl. 16, figs. 14, 15.

Description.—Shells small (maximum length = 15 mm, maximum height = 11 mm), obliquely subtriangular shell; length commonly exceeding height, beak situated at one-third of shell length from anterior margin; umbonal area inflated, anterior umbonal ridge broad, prominent, running from umbo to posteroventral corner of shell. Posterodorsal margin gently convex, forming a rounded, very obtuse angle with the posteroventral margin; shell ornament consisting of between 15 and 20 regularly spaced, commarginal ribs that may fade out laterally; inner ventral and posterior margins denticular.

Material examined.—More than 20 specimens available; Cataloged specimens, CUGB2440, CUGB2444, CUGB2445, CUGB2445, CUGB3304b.

Occurrence.—BH-2 and BH-3b of section A (upper Rhaetian to transitional Rhaetian-Hettangian).

Discussion.—This small astartid is commonly found as external or internal molds in which the strong cardinal teeth may be visible. The specimens resemble in shape, small size, and ornamentation English Rhaetian *Astarte* sp. as figured by Hodges (in Ivimey-Cook et al., 1999), yet differ in having more numerous concentric growth lines.

Family CARDITIDAE Fleming, 1828
 Genus PALAEOCARDITA Conrad, 1867
 PALAEOCARDITA TRAPEZOIDALIS (Krumbeck, 1913)
 Figure 6.12–6.18, 6.35

Cardita trapezoidalis KRUMBECK, 1913, p. 147, pl. 4, fig. 15, text-fig. 5.

Description.—Shell small to medium-sized (maximum length = 26 mm, maximum height = 28 mm), subtriangular to trapezoidal in shape, equivalved, highly convex, height slightly exceeding length, umbonal area well inflated, beak projected over hinge line; ornament consisting of strongly granulose radial ribs and commarginal growth lines, ribs varying between 14 and 19, internal mold with denticular ventral margin and well-developed ridge of posterior adductor.

Material examined.—The collection consists of nine specimens, including CUGB3321, CUGB3332, CUGB3333, and CUGB3338.

Occurrence.—BH-1 of section B (upper Rhaetian).

Discussion.—Although *Palaocardita* is distributed widely in the Upper Triassic (Middle Norian to Rhaetian deposits) of the Himalayan Tibet and western Yunnan, we question the reported diversity of 15 species (Chen in Wen et al., 1976; Chen in Ma et al., 1976) as most are represented by either internal molds or single specimens. The Chinese species we attribute to *P. trapezoidalis* varies from trapezoidal to subquadrate in outline and has between 14 to 20 ribs and, therefore, likely represents intraspecific variation. A revision of this genus, based on detailed morphologic study, will likely resolve questions of variation and species diversity of *Palaocardita*.

Family FIMBRIIDAE Nicol, 1950
 Genus SCHAFHAEUTLIA Cossmann, 1897
 ?SCHAFHAEUTLIA sp.
 Figure 6.20, 6.21

Description.—Shells small to medium in size (maximum length = 31 mm, maximum height = 32 mm); subtriangular in outline, very thick, slightly inequilateral; ornament smooth; umbo inflated, well demarcated by umbonal ridges from shell body, posterior ridge extending from umbo to posteroventral corner forming slightly truncated posterior slope.

Material examined.—Two specimens, both internal molds; CUGB3307, CUGB3337.

Occurrence.—BH-1 of section B (upper Rhaetian).

Discussion.—Preserved as internal molds, these specimens exhibit a high valve convexity suggesting affinity to *Schafhaeutlia*; however, the assignment of this specimens at the genetic level remains to be confirmed with more material.

Order UNIONOIDA Stoliczka, 1871
 Family PACHYCARDIIDAE Cox, 1961
 Genus UNIONITES Wislizenus, 1841
 UNIONITES GRIESBACHI (Bittner, 1899)
 Figure 6.42

Anodotophora griesbachi BITTNER, 1899, p. 60, pl. 8, figs. 14–16; KRUMBECK, 1913, p. 55, pl. 3, figs. 21–23; VU KHUC ET AL., 1965, p. 49, pl. 18, figs. 3, 4.

Unionites griesbachi (BITTNER). CHEN *IN* MA ET AL., 1976, p. 223, pl. 14, figs. 3, 5; HAUTMANN, 2001b, p. 110, pl. 26, figs. 6–9.
Unionites griesbachi brevis (VU KHUC ET AL.). WEN ET AL., 1976, p. 28, pl. 2, figs. 16–23.

Material examined.—One internal mold of a left valve; CUGB3331.

Occurrence.—BH-1 of section B (upper Rhaetian).

Discussion.—This species has been repeatedly reported from the Late Triassic deposits of western Yunnan and the Tibetan Himalayas. There is another associated subspecies, *Unionites griesbachi brevis*, which is slightly more elongate than the present species. Due to the small amount of material available, it is not confirmed that these two forms represent intraspecific variation, but it is clear that they range up into the Rhaetian.

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