MID-CRETACEOUS RUDISTS (BIVALVIA: HIPPURITIDA) FROM THE LANGSHAN FORMATION, LHASA BLOCK, TIBET

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Abstract: The Cretaceous Langshan Formation, which crops out along the northern portion of the Lhasa block, is composed mainly of grey or grey-black fine-grained limestones, argillaceous limestones and a few thin-bedded siltstones and silty mudstones. From specimens collected and/or photographed in the field, combined with a revision of taxa previously recorded from the Langshan Formation, four rudist taxa are recognized: (1) Auroradiolites gen. nov.; (2) Eoradiolites cf. davidsoni; (3) Magallanesia rutogensis sp. nov.; and (4) Sellaea sp. We propose Auroradiolites gen. nov. for the grouping of SW Asian to Pacific radiolitid species formerly attributed to Eoradiolites and characterized by a compact (non-celluloprismatic) outer shell layer. The new genus is represented in the Langshan Formation by A. biconvexus (Yang et al., 1982), including several other synonymized taxa. Taxonomic confusion in the literature has resulted from the varied appearance of the strongly developed ligamentary infolding in such forms: in the right valve, it has a forked inner termination, but common transverse sections through both valves show the latter juxtaposed against its broad, rounded counterpart in the left valve, giving the combined terminations a bulb-shaped appearance. Associated Eoradiolites cf. davidsoni is of smaller size and, by contrast, shows the celluloprismatic structure of the outer shell layer. The recently described canaliculate polyconitid genus, Magallanesia Sano et al., 2014, is represented by M. rutogensis sp. nov., which differs from the type species in possessing more numerous and ventrally extended canals in the left valve. Possibly belonging with the latter species are isolated right valves, similar to Horiopleura, but containing tabulae. A probable Sellaea sp. is represented by poorly preserved right valves nevertheless showing typical features, including a very thin outer shell layer and an erect posterior myophoral wall, separating off a broad posterior ectomyophoral cavity. Based on the presence of Magallanesia and the orbitolinid record, this rudist fauna is probably no older than late Albian, while a younger age cannot be excluded. Both Magallanesia and Auroradiolites are characteristic of a SW Asian/central Pacific faunal province, while the other two genera are more widely distributed. 

Key words: Radiolitidae, Auroradiolites gen. nov., Polyconitidae, orbitolinids, Albian, SW Asian – Pacific province.

The elaborate morphologies of rudist bivalves (Cestari and Sartorio 1995; Skelton 2013a) enabled them to occupy shallow marine habitats in great abundance on the vast carbonate platforms that developed within the equatorially encircling Tethyan–Atlantic–tropical Pacific oceanic realm of the Late Jurassic and Cretaceous. There, they congregated in loose to dense clusters, often forming broad shelly ‘meadows’ (Gili et al. 1995) or low mounds sometimes preserved as laterally extensive biostromes to bioherms within carbonate platform successions.

One such area of rudist colonization was the Lhasa block, which was located on the northern margin of the eastern Tethys Ocean in mid-Cretaceous times (Chang et al. 1986; Zhang 2000), and is today bounded on its northern side by the Bangong–Nu Suture and on its southern side by the Indus–Yarlung Suture (XZBGM 1993; Fig. 1). Massive mid-Cretaceous carbonate deposits are exposed in the northern portion of the Lhasa block, referred to as the Langshan Formation (Leier et al. 2007). This formation is distributed in a belt encompassing...
Rutog, Gar, Geyai, Zhongba, Gerze, Coqen, Nyima, Xainza and Baingoin counties (XZBGM 1993; Fig. 1), and it contains abundant orbitolinids, gastropods, corals and rudists (Zhang 1982, 1986, 1991; Yu and Xia 1985; Lüser and Liao 2001; Scott et al. 2010).

The rudists from the Langshan Formation have been described in Rutog, Geyai, Gerze and Baingoin counties. Nineteen species have been described in the previous literature, assigned to 11 genera (Yang et al. 1982; Yang 1984; Gou 1994; Gou and Shi 1998; Scott et al. 2010). However, in most cases, the diagnostic characters of the genera or even families have not been well established in these publications, so their identification remains problematic and in need of revision according to recent advances in rudist classification. Such revision is of particular interest given the intermediate palaeogeographical position of this fauna between the classically documented rudist faunas of the Mediterranean/Middle Eastern Tethyan region and those of Pacific provenance, largely described in the last few years (Masse and Shiba 2010; Sano and Masse 2013; Skelton et al. 2013; Sano et al. 2014).

The most abundant rudists from the Langshan Formation are some radiolitids that were originally assigned to Praeradiolites (Yang et al. 1982; Gou and Shi 1998), but later to Eoradiolites and Sphaerulites (Scott et al. 2010), though possessing an entirely compact outer shell layer. Similar forms were also reported from Iran, central Afghanistan, northern Pakistan, northern India and Japan (Montenat et al. 1982; Pudsey et al. 1985; Mathur and Vogel 1988; Masse and Gallo Maresca 1997; Sano and Masse 2013; Upadhyay 2014 and see also Upadhyay 2001, fig. 4b). Yang et al. (1982) and Gou and Shi (1998) established many new species for these radiolitids based mainly on supposed differences in the form of their ligamentary infolding in transverse section. But both Masse and Gallo Maresca (1997) and Scott et al. (2010) questioned the reliability of such variation in ligament form as a diagnostic criterion. Moreover, these south-west Asian and western Pacific radiolitids differ from typical Eoradiolites (Pons et al. 2010) not only in the structure of the outer shell layer, but also in the shape of the shell and the myocardial apparatus.

Accordingly, these Lhasa block radiolitid species are revised herein based on the investigation of material newly collected and/or photographed in the field by the senior author, and revision of the previous publications. In addition, three further rudist species are also described for the first time from China and their stratigraphical and palaeogeographical significance clarified.

**FIG. 1.** Map showing the outcrop of the Langshan Formation in the Lhasa block (modified from XZBGM, 1993). BNS, Bangong–Nu Suture; IYS, Indus–Yarlung Suture.
GEOLOGICAL SETTING

The rudist bivalves described herein were collected from the limestone beds of the following three sections in Tibet: (1) the north side of Lameila Mountain at the junction of Rutog County and Gar County (N 32°42′51″, E 79°51′25″; Fig. 2A); (2) the south bank of Nyer Lake in Gegyai County (N 32°14′31.5″, E 82°07′58.9″; Fig. 2B); and (3) the south-west bank of Zabuye Lake in Zhongba County (N 31°18′16″, E 83°55′34″; Fig. 2C).

In the tectonic division of Tibet, these areas belong to the northern part of the Lhasa block, which is sandwiched between the Bangong–Nu Suture and the Indus–Yarlung Suture (Fig. 1; Yin and Harrison 2000; Zhang 2000; Leier et al. 2007). Here, thick shallow marine carbonates of mid-Cretaceous age, called the Langshan Formation, are widely distributed. This formation is interpreted to have been deposited in the Gangdese retroarc foreland basin (Zhang et al. 2011).

The Langshan Formation crops out widely along a belt encompassing Rutog, Gar, Gegyai, Zhongba, Gerze, Coqen, Nyima, Xainza and Baingoin counties, extending from Rutog County in the west to Namtsa Lake in the east (Fig. 1; XZBGM 1993). It was deposited in a relatively stable carbonate sedimentary environment and is mainly composed of grey or grey-black fine-grained limestones, argillaceous limestones and a few thin-bedded siltstones and silty mudstones (Fig. 2D; Marcoux et al. 1987; Zhang et al. 2004; Leier et al. 2007). The thickness of the Langshan Formation is poorly constrained; we regard it as about 1000 m based on Zhang et al. (1986) and Yin et al. (1988). Based on its lithological character, the Langshan Formation was separated into lower and upper parts, the former containing limestones, siltstones and marlstones, and the latter...
dominated by limestones (Zhang et al. 1986). The rudist specimens described herein were all collected from the upper part of the Langshan Formation (Fig. 2D). This formation conformably overlies the Lower Cretaceous siliciclastic Duoba Formation, and is in turn unconformably overlain by the Upper Cretaceous coarse-grained clastic Jingzhushan Formation (BGMRXAR 1997; Zhao et al. 2001).

Abundant marine fossils are present in the Langshan Formation and the main elements are orbitolinids, rudists, gastropods and corals (Zhang 1982, 1986, 1991; Liao and Xia 1985; Yu and Xia 1985; BGMRXAR 1997; Löser and Liao 2001; Scott et al. 2010; Deng and Wang 2013).

During the course of this study, RAO and IBA re-studied the orbitolinid records of Zhang (1986, 1991) in the light of the recent evolutionary and biostratigraphical scheme of the Eopalarbitolina–Palarbitolinoides and Praorbitolina–Mesorbitolina lineages (Schroeder 1975; Schroeder et al. 2010) and confirmed the age assignment of the Langshan Formation to the early Barremian to early Cenomanian according to the presence of Eopalarbitolina charollaisi, Palarbitolina lenticularis, Palarbitolina ultima, Praorbitolina cornyi, Mesorbitolina parva, M. texana, M. subconcava and M. aperta (see Stratigraphical Correlation, below).

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://www.zoobank.org/References/A00A7D9A-58D2-403B-8836-06B790A2DE5B

All numbered specimens are conserved in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China (NIGP).

The suprageneric classification and morphological terminology used herein follow Skelton (2013a, b).

Abbreviations. am, anterior myophore; ab, anterior radial band; at, anterior tooth; ats, anterior tooth socket; bc, body cavity; ct, central tooth; cts, central tooth socket; ecto, ectomyophoral cavity; ib, interband; Llv, ligamentary infolding in left valve; Lrv, ligamentary infolding in right valve; LV, left valve; ol, outer (calcitic) shell layer; pm, posterior myophore; pb, posterior radial band; pt, posterior tooth; pts, posterior tooth socket; RV, right valve.


Suborder HIPPURITIDINA Newell, 1965 (Skelton, 2013b)

Superfamily RADIOLITOIDEA d’Orbigny, 1847
Family RADIOLITIDAE d’Orbigny, 1847

Genus AURORADIOLITES gen. nov.

LSID. urn:lsid:zoobank.org:act:AC0FD0E6-2E5C-4249-A935-77B57B7A0AA3

Type species. Praeradiolites gilgitensis Douvillé, 1926a; from the upper Aptian of Kohistan, northern Pakistan.

Derivation of name. From the Roman goddess of dawn, ‘Aurora’, contracted with Radiolites, in reference both to the oriental provenance of the new genus, and to its early evolutionary appearance within the radiation of the family Radiolitidae.


Diagnosis. Moderate- to large-sized radiolitid (adult commissural diameters from 2 to over 10 cm). LV externally almost flat to strongly domed; RV subcylindrical to obtusely conical with thick (0.5 to several cm), entirely compact (non-celluloprismatic) ol, forming projecting laminar growth rugae and ornamented externally by coarse rounded to subangular costae. Radial bands weakly to moderately protruding from posteroventral flank of RV, separated by relatively narrower, indented ib. Ligamentary infolding strongly developed, producing elongate inward extension of ol with widely forked inner termination in RV, although transverse sections across the two articulated valves show the Lrv inner termination juxtaposed against its broad, rounded counterpart in the LV giving the combined inner terminations a bulb-shaped appearance. LV teeth prominent, straddling elongate ridge-like ct in RV, which is separated from Lrv by small accessory cavity. LV myophores robust, facing outwards onto inner wall of RV. LV pm a protruding plate attached via embayed neck to pt, am somewhat less protruding.

Remarks. This new genus is proposed to embrace the distinctive grouping of south-west Asian to Japanese radiolitid species that are characterized by a compact (non-celluloprismatic) outer shell layer and which were formerly attributed to Eoradiolites by Masse and Gallo Maresca (1997) and Sano and Masse (2013). Despite showing a similar configuration of radial bands to that in Eoradiolites, Auroradiolites differs from the former genus in its possession of the following characters: (1) an entirely compact fibrous prismatic, as opposed to cellu-
loprismatic ol in the RV (contrary to the erroneous description of polygonal cells in a specimen of *A. gilgitensis* by Skelton, in Pudsey et al. (1985), as confirmed here by Fig. 3A–C); (2) an almost flat to strongly convex LV (e.g. Fig. 4A), contrasting with the externally concave form of that in *Eoradiolites* (*with nearly flat centre and inwards inclined margin* in the diagnosis of the latter genus given by Pons et al. (2010)); and (3) a more robust myocardinal apparatus, with a much more strongly developed ligamentary infolding (e.g. Figs 3, 4B–C). The compact outer shell layer, in particular, suggests the possibility that this endemic north-eastern Tethyan to western Pacific genus arose independently from the ancestral radiolitid genus *Agriopleura* in the late Aptian, while the first celluloprismatic forms, *Archaeoradiolites* and *Eoradiolites*, were evolving in the Mediterranean Tethyan region at almost same time (Fenerci-Masse et al. 2006).

Published photographic figures of *Radiolites abraensis* Coogan, 1973, from the upper Albian of Mexico, also appear to show an entirely compact ol (Coogan 1973, pl. 7, fig. 1b; Alencáster and García-Barrera 2008, figs 3.4 and 8.3), despite the somewhat ambiguous text descriptions of the ol by those authors (‘...composed of finely reticulate vertical and radial funnel plates’ (Coogan 1973, p. 63), and ‘...polygonal cells of less than 0.5 mm’ (Alencáster and García-Barrera 2008, p. 579)). Moreover, the ol microstructure in the closely similar *R. costata* Scott, 1990, is described as ‘...prismatic rather than coarsely cellular as in most other radiolitids’ (Scott 1990, p. 78). Nevertheless, we exclude both these Mexican species from *Auroradiolites*, as

**FIG. 3.** *Auroradiolites* gen. nov.; transverse sections of RV in adumbonal view plus myocardinal elements of LV. A–C, *A. gilgitensis* from Kohistan (see Pudsey et al. 1985; specimen re-photographed by PWS); A, transverse section passing through ligamentary infoldings of both valves; B, detail from white square in (A); C, transverse section cut at a lower level in a neighbouring RV. D, *A. biconvexus* (= paratype of *Praeradiolites ngariensis* Yang et al., 1982, copied from Scott et al. 2010, fig. 9.1). All scale bars represent 10 mm. Abbreviations: at, anterior tooth; ct, central tooth; Llv, ligamentary infolding in left valve; Lrv, ligamentary infolding in right valve; LV, left valve; pm, posterior myophore; pt, posterior tooth; RV, right valve.
they differ from the latter in the following respects: (1) the radial bands of *Auroradiolites* are weak to moderate protrusions (Figs 4D, 5A), as opposed to the smooth indented furrows in *R. abraensis* and *R. costata*; (2) the ligamentary infolding of *Auroradiolites* is much more strongly developed than that in the Mexican species.

Another New World Albian genus possessing a relatively thick, compact *Pseudopetalodontia* (Masse et al., 2007) that invites comparison is *Pseudopetalodontia* (Masse et al., 2007). Yet this genus is again distinguished from *Auroradiolites* by its markedly less pronounced ligamentary infolding and externally indented radial bands (Masse et al. 2007, fig. 6), as well by its robust *ct* in the *RV*, which projects inwards past the ligamentary infolding with no intervening dorsal accessory cavity, in our view justifying its attribution to the Monopleuridae by Masse et al. (2007). Thus, we judge its similarities with *Auroradiolites* to be convergent.

At the species level, a number of similar radiolitid species from the Langshan Formation erected by Gou and Shi (1998) and attributed by them to *Praeradiolites* (*P. geqyainensis*, *P. daxungensis*, *P. bangoinensis*, *P. perbellus* and *P. coquenensis*) were distinguished on the basis of apparent differences in the form of their ligamentary infoldings in transverse section. As noted by Scott *et al.* (2010), however, lack of information concerning the developmental variability of this shell feature renders these distinctions open to question. Indeed, Masse and Gallo Maresca (1997, fig. 2) had already pointed out in their figured transverse sections of ‘*Praeradiolites* sp.’ from Afghanistan, and ‘*Eoradiolites gilgitensis* (Douvillé)’, from Iran, that ‘the ligamental crest appears bulbous: a feature linked with the position of the section, close to the upper valve with the ligamental crest inside in the anterior/dorsal part of the posterior tooth. Sections cut further down, away from the commissure, exhibit the typical triangular pediculate shape of the ligamental crest of the lower valve’. This critical observation is confirmed here in newly photographed transverse sections of ‘*P. gilgitensis* Douvillé’ from Kohistan, N. Pakistan, described by Pudsey *et al.* (1985) that show both the bulbous appearance of the opposed ligamentary infoldings of both valves in a transverse section close to the commissure (Fig. 3A–B) and the broadly Y-shaped inner termination of the infolding seen in a *RV* sectioned at a lower level (Fig. 3C). Hence, the ‘bulb-shaped’ transverse section of the ligamentary infolding supposed to be characteristic of ‘*P. ngariensis*’ by Yang *et al.* (1982), but likewise shown only in a section containing the opposed ligamentary infoldings of both valves (Fig. 3D), can no longer be regarded as a diagnostic character. Synonymy of the latter

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**FIG. 4.** *Auroradiolites biconvexus* specimens from Langshan Formation in Zhongba County (A) and Rutog County (B–D), Tibet. A, polished radial section of articulated shell (NIGP no. 160500), showing the myophore of *LV*; it is unclear whether the myophore shown in this section is the anterior or posterior one. B, polished transverse section of two conjoined *RV*s (NIGP no. 160502). C, broken transverse section of *RV* (NIGP no. 160507). D, detail from white rectangle in (C). All scale bars represent 10 mm. Abbreviations: *ab*, anterior radial band; *bc*, body cavity; *ib*, interband; *Lrv*, ligamentary infolding in right valve; *LV*, left valve; *pb*, posterior radial band; *RV*, right valve.
species with ‘P. biconvexus’ Yang et al. (1982), stated by its authors to have a narrow ligament ridge, is accordingly proposed below.

Auroradiolites biconvexus (Yang et al., 1982)
Figures 3D, 4A–D, 5, 6A (pars), B–D, 7A

1982 Praeradiolites biconvexus Yang et al., p. 299, pl. 1, fig. 4a–c.
1982 Praeradiolites ngariensis Yang et al., p. 299, pl. 1, figs 2, 3.
1998 Praeradiolites gegyainensis Gou and Shi, p. 261, pl. 1, figs 1, 2.
1998 Praeradiolites bangoinensis Gou and Shi, p. 263, pl. 2, fig. 1.
1998 Praeradiolites perbellus Gou and Shi, p. 263, pl. 2, fig. 2.
2010 Eoradiolites gilgitensis (Douvillé, 1926b); Scott et al., pp. 455–457, fig. 9.1–9.3 (= types of P. ngariensis Yang et al., 1982, re-photographed; non Auroradiolites gilgitensis (Douvillé, 1926a)).
2010 Sphaerulites biconvexus (Yang et al., 1982); Scott et al., p. 457, fig. 9.4–9.7 (= holotype of P. biconvexus Yang et al., 1982, re-photographed, together with copy of the latter authors’ fig. 6).

Revised diagnosis. Relatively large species of Auroradiolites (commissural diameter may exceed 100 mm) with markedly convex LV and radially oriented undulations on the inner margin of the ol.

Material. All specimens are preserved in section in indurated dark grey limestone: one polished radial section of both valves (NIGP no. 160500, Fig. 4A); 11 RVs in transverse section, either polished (NIGP no. 160501, NIGP no. 160502 (2 specimens, Fig. 4B), NIGP no. 160503, NIGP no. 160504 (Fig. 6A–B)) or natural sections (NIGP no. 160505 (Fig. 6C–D), NIGP no. 160506 (two mutually attached specimens, of which one is shown in Fig. 5D), NIGP no. 160507 (Fig. 4C–D), NIGP no. 160508 (Fig. 5A–C), NIGP no. 160509); plus some other RV fragments (including NIGP no. 160510 (Fig. 5E)); together with a number of specimens photographed in the field by the first author.

Localities. The north side of Lameila Mountain at the junction of Rutog County and Gar County (N 32°42′31″, E 79°51′25″), the south bank of Nyer Lake in Geggai County (N 32°14′31.5″, E 82°07′58.9″) and the south-west bank of Zabuye Lake in Zhongba County (N 31°18′16″, E 83°55′34″).

Description. The external shell form of specimens that are unambiguously attributable to this species shows a markedly domed LV and a RV of broadly conical form with widely flared, laminar growth rugae (Figs 4–6, 7A). Commissural diameters may exceed 100 mm (Fig. 5A). Some radiolitid specimens with flared growth rugae, but with an almost flat LV and slender conical RV, were also photographed in the field (Fig. 7B–C), but their relatively small size and uncertainty as to whether their ol structure is compact or cellular makes their attribution to this species questionable; alternatively, they may represent another species, or – if their ol is cellulosprismatic – they might belong to Eoradiolites, which is also described herein from the Langshan Formation.

The ol of A. biconvexus is moderately thick (up to 5 mm) over the LV (Figs 4A, 7A) and, in the RV, may extend from the junction with the inner shell for over 40 mm to the perimeter of the valve in larger specimens (Fig. 5A). Externally, it is ornamented by coarse subangular costae (Fig. 5C) that are matched on the inner margin of the ol by radial undulations (Fig. 5D), which frequently give rise to ‘zigzag’ growth lines in transverse sections of the RV (Fig. 4B). The radial bands are situated ventrally, ab being a little wider than pb (Fig. 5A), and are separated by a narrow, indented ib (Figs 4D, 5A). However, the relative protrusion of the radial bands is quite variable, such that they cannot always be clearly identified in transverse sections (e.g. Fig. 6B). The compact fibrous prismatic microstructure of the ol is visible on close inspection of clean broken surfaces even to the naked eye (Figs 4D, 5E) and lacks any signs of the cellulosprismatic mesostructure that characterizes most other radiolitid taxa: that this lack of cells is not merely an effect of diagenetic alteration is confirmed by the clear preservation of cellulosprismatic mesostructure in nearby specimens of Eoradiolites (Figs 6A, 8A–B).

The inner shell of the specimens inspected by us – originally aragonitic, but now replaced by white sparry calcite – is thickly developed, especially in the myocardinal area, though naturally appearing thinner in transverse sections close to the margin of the RV (e.g. Fig. 6C). The ol infoldings associated with the invaginated ligament are strongly developed, in transverse section showing either the bulbous form of the opposed infoldings of both valves in sections close to the commissural plane (Fig. 5B and partially shown in Fig. 6D) or an asymmetrically Y-shaped form in sections at lower levels in the RV (Fig. 6B), as discussed above.

The two projecting LV teeth (at and pt) straddle the narrow cr in the RV, which appears in transverse section as an elongate ridge with a swollen inner termination and is separated from the ligamentary infolding by a small accessory cavity (Figs 3D, 6C–D). The myophores are not well displayed in the material inspected by us, but, as in the original specimens of Yang et al. (1982; e.g. Fig. 3D herein), the robust pm appears to project more strongly than the am, judging from its preferential appearance in some transverse sections (Fig. 5A–B).

Remarks. As its name suggests, the most striking character of A. biconvexus is its strongly domed LV (Yang et al. 1982, pl. 1, fig. 4a–c; see also Figs 4A, 7A herein) – if the smaller specimens with an almost flat LV shown in Fig. 7B–C can be excluded from the species as suggested
Above. In this respect, *A. biconvexus* also differs from the type species of the genus, *A. gilgitensis* (Douvillé, 1926a), in which the LV is considered to be ‘not strongly convex’ (Sano and Masse 2013, p. 320). The latter species, moreover, lacks any clear indication of the radial undulations of the ol inner margin seen in *A. biconvexus* (Sano and Masse 2013; see also Fig. 3A herein). In contrast, not only are these marginal undulations clearly shown in the holotype of *A. biconvexus* (refigured by Scott et al. 2010, fig. 9, 4–7), but they are also visible in the original holotype and paratype of ‘*P. ngariensis*’ of Yang et al. (1982; refigured by Scott et al. 2010, fig. 9, 1–3), which is here regarded as a synonym of *A. biconvexus*. As ‘*P. biconvexus*’ was established before ‘*P. ngariensis*’ on p. 299 of Yang et al. (1982), we designate it as the senior synonym.

*Auroradiolites griesbachi*, which was described from the region of Herat, in Afghanistan, is very similar to *A. gilgitensis* (see Sano and Masse 2013), although Scott et al. (2010) mentioned some slight differences between these two species in the shapes of the central tooth and myophores. The ligamentary infolding of specimens assigned to *A. griesbachi* is narrower and longer than that of *A. gilgitensis* (see Montenat et al. 1982, pl. 1, fig. 4). However, similar variation is seen in *A. biconvexus*: for example, a specimen with a distinctly narrow, elongate ligamentary infolding is illustrated by Gou and Shi (1998, pl. 2, fig. 2b). As noted previously, we do not regard such variation in the shape of the ligamentary infolding as a reliable diagnostic criterion for distinguishing species in *Auroradiolites*. In conclusion, the specific status of *A. griesbachi*, as well as its age, remains uncertain. So, pending further study, the species is provisionally retained herein.

The descriptions and figures of the rudist species erected by Gou and Shi (1998) are not sufficiently informative for a clear understanding of their taxonomic status. Nevertheless, the five new species from the Langshan Formation proposed by them and attributed to *Praeradiolites* are here regarded as likely junior synonyms of *A. biconvexus*, as tentatively indicated in our synonymy list above. Notably, the descriptions all refer to well-
FIG. 6. *Auroradiolites biconvexus* specimens from Langshan Formation in Zhongba County (A–B) and Rutog County (C–D), Tibet. A, polished cut slab showing transverse sections of RVs, in abumonal view, of *A. biconvexus* (white rectangle) together with smaller *Eoradiolites cf. davidsoni* (NIGP no. 160504). B, detail of *A. biconvexus* RV section from white rectangle in (A). C, natural broken transverse section of RV in abumonal view (NIGP no. 160505). D, detail of ligamentary infolding and dentition from white rectangle in (C). All scale bars represent 10 mm. Abbreviations: *ats*, anterior tooth socket; *ct*, central tooth; *Lrv*, ligamentary infolding in right valve; *pts*, posterior tooth socket.

FIG. 7. Radiolitids in the Langshan Formation, photographed in the field by the first author. A, *Auroradiolites biconvexus* (Zhongba County). B–C, undetermined small radiolitids with flat *LV* (Rutog County). All scale bars represent 10 mm. Abbreviations: *at*, anterior tooth; *Llv*, ligamentary infolding in left valve; *LV*, left valve; *RV*, right valve.
developed ligamentary infoldings, albeit with differences in appearance in transverse section that are here regarded as diagnostically invalid, as discussed above. In addition, the descriptions of Gou and Shi (1998) variously share mentions of growth rugae and radial undulations of the ol inner margin (in those cases where that shell layer is preserved); thus, ‘Funnel plates overlapping unevenly and wavy’ (‘P. gegyainensis’, p. 261); ‘Outer ostracum consisting of irregular lamellar structure; wavy layers appear in transverse section’ (‘P. daxungensis’, p. 261); ‘Outer ostracum consisting of thin, wavy funnel plates’ (‘P. bangoinensis’, p. 263); ‘Funnel plates... appearing as slightly wavy circular structures’ (‘P. coquenensis’, p. 265). Although none of the original plate figures is sufficiently clear to show whether or not any cellulopristmatic mesostructure is present in the ol, the oblique section of that in ‘P. bangoinensis’ (Gou and Shi, 1998, pl. 2, fig. 1c) appears to be compact, contrary to those authors’ assertion of a ‘fine quadrangular network’ being present (p. 263). Moreover, the myocardinal apparatus of ‘P. gegyainensis’ (Gou and Shi, 1998, pl. 1, figs 1b, 2b), which is the only form in which it is adequately illustrated, is essentially identical to that in A. biconvexus. Meanwhile, the shape of the LV is illustrated only for ‘P. bangoinensis’ (Gou and Shi, 1998, pl. 2, fig. 2a), albeit with the ol missing, but is distinctly convex. Finally, mention should also be made of the confused account of another new species, ‘Lapeirousia lomata’, given by Gou and Shi (1998, p. 265), which is stated in their text description to come from the ‘Upper Zongshan Formation (Campanian–Maastrichtian), Zongshan, Gamba County, Tibet’, but in the plate figure captions, it is attributed to the Langshan Formation of the Zhilongashan area, Gegyai, Tibet. While the specimens illustrated by Gou and Shi (1998, pl. 1, figs 5, 6 and pl. 2, fig. 6) clearly show marginal undulations of the ol, it is not possible from these figures to confirm the absence of a ligament, as asserted in the text. Consequently, the taxonomic status and age of this last form remains unclear. Hence, careful revisionary study of the taxa erected by Gou and Shi (1998) is evidently necessary.

In addition, Sano and Masse (2013) mentioned a possible new record of A. biconvexus from Kandahar region, Afghanistan, which was previously assigned to Praeradiolites? sp. by Masse and Gallo Maresca (1997, fig. 2a). The relevant specimen has a strongly convex LV as in the Tibetan specimens. Current stratigraphical data suggest that A. biconvexus is most probably of late Albian age (see Stratigraphical Correlation, below), hence somewhat younger than A. gilgitensis, which is of late Aptian – Albian age, based on the accompanying orbitolinids (Pudsey et al. 1985; Sano and Masse 2013). So, based on present data, it seems most likely that A. biconvexus is an evolutionary descendant of A. gilgitensis.

**Genus EORADIOLITES Douvillé, 1909**

*Type species.* Radiolites davidsoni Hill, 1893.

**Eoradiolites cf. davidsoni** (Hill, 1893)

*Figures 6A (pars), 8*

*Material.* Three cut and polished slabs of indurated grey limestone: one containing several RV specimens in transverse section (NIGP no. 160504, Figs 6A, 8A); one with a small RV in transverse section, contained within a RV of A. biconvexus (NIGP no.
160501, Fig. 8B); and a slab containing several RV specimens and fragments in random orientations (NIGP no. 160511).

**Localities.** The north side of Lameila Mountain at the junction of Rutog County and Gar County (N 32°42′51″, E 79°51′25″) and the south-west bank of Zabuye Lake in Zhongba County (N 31°18′16″, E 83°55′34″).

**Description.** In transverse section, the RV is relatively small (commissural diameters generally reach around 20 mm) with a rounded to subquadrate outline. A slight dorsal indentation marks the position of the short ligamentary infolding, which is of broad triangular cross-sectional form. Weakly projecting, flat-faced radial bands are present on the posteroventral flank, *ab* being slightly broader than *pb*, separated by a narrow, indented *ib* (Fig. 8A). Otherwise, much of the outer valve surface is shown in section to be ornamented by rounded ribs, 2–3 mm wide (Fig. 8A), although these may be lacking in smaller specimens (Fig. 8B).

The *ol* is mostly celluloprismatic, although the outer rim of the layer may be compact locally, particularly around the radial bands (Fig. 8A). The cellular mesostructure is well preserved, even in small specimens, which thus contrast distinctly with the wholly compact structure of associated specimens of *A. biconcavus* (Fig. 8B). The side walls of the cells have a strongly radial pattern, traversed by frequent commarginal intersections with the floors of the cell layers, reflecting a relatively steep inward marginal inclination of the *ol* in the RV. The inner shell is largely missing from the specimens we have studied, although relics of it, replaced by white to colourless calcite spar, are locally preserved.

**Remarks.** The size and external form of the RV, particularly of the radial bands, and the inner marginal inclination and radially dominated cell wall pattern of the *ol* in the Tibetan specimens are consistent with *Eoradiolites*, while the ribbing on the remaining parts of the outer valve surface suggests *E. davidsoni*, according to the revision of Pons et al. (2010). *Eoradiolites davidsoni* is an externally highly variable species, as illustrated by Steuber (1999) and Pons et al. (2010). Although relatively small for the species, our specimens nevertheless overlap with the size range for specimens of *E. davidsoni* illustrated from the Albian of Boeotia, Greece, by Steuber (1999). We therefore tentatively assign our specimens to the species, an alternative possibility being that they represent a distinct small species with wavy radial walls.

**Family POLYCONITIDAE Mac Gillavry, 1937**

**Genus MAGALLANESIA Sano et al., 2014**

Type species. *Magallanesia canaliculata* Sano et al., 2014.

![FIG. 9. Magallanesia rutogensis sp. nov., LV specimens collected from Langshan Formation (all in adumbonal view) in Rutog County, Tibet. A, holotype LV (NIGP no. 160512). B–C, paratype LV in natural transverse section (B) and in polished section (C) a few mm below (NIGP no. 160513). D, interpretative sketch of section shown in (B); ‘biocl.’ is a bioclastic fragment unconnected with the rudist specimen. All scale bars represent 10 mm. Abbreviations: *am*, anterior myophore; *at*, anterior tooth; *bc*, body cavity; *cts*, central tooth socket; *Llv*, ligamentary infolding in left valve; *ol*, outer (calcitic) shell layer; *pm*, posterior myophore; *pt*, posterior tooth.](image-url)
**Magallanesia rutogensis** sp. nov.  
Figures 9, 10, 11?

**LSID.** urn:lsid:zoobank.org:act:CC8BE863-5D2F-41E8-BDEB-7525D721F4D5

**Derivation of name.** From Rutog County, in northern Tibet, in which the type locality for the new species is situated.

**Material.** All specimens are preserved in section in indurated dark grey limestone.

**Holotype.** LV in oblique transverse section in block (NIGP no. 160512, Fig. 9A).

**Paratypes.** One incomplete LV in block, also shown in polished section (NIGP no. 160513, Fig. 9B–D) and a small rounded LV fragment displaying canals (NIGP no. 160514); plus two possible RVs in transverse section (NIGP no. 160515 and NIGP no. 160516, Fig. 11A–C). Also, several specimens photographed in the field by the first author.

**Localities.** The north side of Lamela Mountain at the junction of Rutog County and Gar County (N 32°42′51″, E 79°51′25″) and the south-west bank of Zabuye Lake in Zhongba County (N 31°18′16″, E 83°55′34″).

**Diagnosis.** *Magallanesia* with a single row of numerous (usually more than 12) posteroventral pallial canals in the LV that continue for some distance around the ventral margin beyond the base of the pm.

**Description.** The holotype (NIGP no. 160512, Fig. 9A) is a partially preserved LV, of about 40 mm anteroposterior diameter, exposed in an oblique adumbonal natural transverse section. The section shows the valve to be of low capuloid shape and to possess a relatively thick (~2 mm), dark calcitic ol. The posterior part of the valve is well displayed, with a single row of at least 15 narrow pallial canals that decrease in size towards the ventral margin, where they stop a small distance ventrally from the base of the pm (Fig. 9A). The apparent extreme radial elongation of the canals in this specimen is due to the obliquely inward orientation of the plane of section. The partially exposed teeth (at and pt) are likewise shown in extended oblique section.

The slightly larger paratype LV (Fig. 9B–D) is again shown in adumbonal transverse section, as demonstrated by the decrease in diameter of the body cavity in the polished section (Fig. 9C) that was made a short distance beneath the natural section exposed on the surface of the block (Fig. 9B, D). The two sections are relatively dorsally situated in the valve, so cutting across the two teeth (Fig. 9D). The anterior part of the valve as well as most of the ol has been lost as a result of boring and/or erosion, but the single row of posteroventral pallial canals is again well displayed. At least 21 canals of more or less elliptical cross-sectional outline are here visible, passing in this example around the larger part of the ventral margin.

A number of sections of articulated shells photographed in the field by XR (Zhongba County). All scale bars represent 10 mm. **Abbreviations:** am, anterior myophore; at, anterior tooth; bc, body cavity; ct, central tooth; ecto, ectomyophoral cavity; ol, outer (calcitic) shell layer; pm, posterior myophore; pt, posterior tooth.

**FIG. 10.** *Magallanesia rutogensis* sp. nov., specimens in Langshan Formation photographed in the field by XR (Zhongba County). All scale bars represent 10 mm. **Abbreviations:** am, anterior myophore; at, anterior tooth; bc, body cavity; ct, central tooth; ecto, ectomyophoral cavity; ol, outer (calcitic) shell layer; pm, posterior myophore; pt, posterior tooth.
cavity (Fig. 10A), while the am forms a broad, flat shelf, opposed by its counterpart in the LV (Fig. 10B).

Lacking canals, isolated specimens of the RV are naturally harder to identify as such, but a number of strikingly thick-shelled specimens of polyconitid affinity (Fig. 11A–C) – with subequal sockets for the LV teeth (ats and pts; Fig. 11A–B), and again, a thickened ol – are here considered to be likely candidates. Notable features of these specimens include the presence of tabulae within at least the ats (Fig. 11B) and the bc (Fig. 11C) and paired indentations of the posteroventral margin corresponding to radial bands (Fig. 11A). One articulated specimen photographed in the field (Fig. 11D), although lacking most of the canaliculate part of the LV in the visible section, similarly shows subequal LV teeth and greatly thickened shell walls with broad, platform-like am surfaces.

Remarks. With their diagnostic combination of simple pallial canals around the posteroventral flank, subequal teeth and relatively thickened ol, the LV specimens described here can be attributed without doubt to the recently described canaliculate polyconitid genus Magallanesia Sano et al., 2014. As with the type species of that genus, M. canaliculata Sano et al., 2014, the subequal LV teeth and thickened ol exclude the attribution of the present material to any caprinoid or caprinulid taxa (sensu Skelton 2013a). By contrast, Sano et al. (2014) explained how the simple subdivision by radial laminae of the LV ectomyophoral cavity in a polyconitid such as Praecaprotina Yabe and Nagao, 1926, probably gave rise to Magallanesia. Nevertheless, the present specimens – despite constituting only a small sample – can be distinguished from the type species by their more numerous canals, which extend relatively further along the ventral valve margin: whereas M. canaliculata has up to 12 canals, only, situated behind the posterior myophore (Sano et al. 2014), the holotype of the species described here has at least 15 (Fig. 9A) canals and the paratype, at least 21 (Fig. 9B), while specimens observed in the field (Fig. 10) appear to attain similar numbers. Moreover, the canals in the Langshan specimens continue for some distance beyond the base of the pm around part of the ventral margin – so apparently representing a further advance towards the condition seen in the plagioptychids, as postulated by Sano et al. (2014). As M. canaliculata is currently considered to be of late Albian age, based on accompanying orbitolinids at the type locality in Cebu Island, in the Philippines, the age of M. rutogensis, with its slightly more derived development of canals, is thus considered here to be probably not older than late Albian.

With their thickened ol, subequal sockets for the LV teeth and prominent pm, the RV specimens illustrated in Figure 11A–C at first suggest affinity with Horiopleura...
Douvillé, 1889, but tabulae are unknown in that well-studied genus. Given their co-occurrence with the undisputed specimens of *Magallanesia* described above, and their similar size, attribution to the new species of the latter genus described herein thus seems most probable at present. As information on the RV of the type species of *Magallanesia* was somewhat limited by the state of preservation of the material studied by Sano et al. (2014), the additional features noted here – the tabulae and the two indented radial bands – are of special interest. In particular, the indented radial bands, together with a ligamentary infolding (as well as tabulae), are shared by another, as yet unnamed form, 'Polyconitid new taxon 3', recently described from the Japanese seamounts by Skelton et al. (2013), although the latter taxon lacks canals in the LV. Nevertheless, the similarities noted here between these Albian polyconitids of the NE Tethyan to central Pacific region further strengthen the case for close relationships between them and thus for an endemic radiation of polyconitids in the region at that time, as postulated by Skelton et al. (2013).

Finally, the identification of this recently recognized canalicate polyconitid genus in northern Tibet casts doubt on the un-illustrated reports of some other canalicate rudist taxa from the Langshan and/or likely equivalent formations by Gou and Shi (1998), which were already dubious on stratigraphical grounds. Such suspect identifications include those of *Caprina* d’Orbigny, 1822, *Pracaprina* Paquier, 1905 and *Amphitriscocelus* Harris and Hodson, 1922 (the last two genera being of early Aptian age), in the Chenba Formation of the Zedang region, and of *Plagiopychus* Matheron, 1842 (a Late Cretaceous genus) in Langshan limestones of the Coqen-Gerze region. Careful taxonomic revision of those specimens is therefore needed, as with the radiolitids described by Gou and Shi (1998) discussed above.

**FIG. 12.** *Sellaea* sp., RVs from Langshan Formation in Rutog County, Tibet. A, transverse section in abumbonal view (NIGP no. 160517). B, transverse section in adumbonal view, with position of broken-away posterior valve wall indicated by dashed white lines (NIGP no. 160518). C, external mould with thin, faintly ribbed outer shell layer locally attached (NIGP no. 160519). D, posteroventral flank of valve, showing ventral sulcus (NIGP no. 160520). E, partial radial section showing apparent tabulae in unidentified accessory cavity (NIGP no. 160521). F, specimens closely associated with RV fragment of *Auroradiolites* (NIGP no. 160519). All scale bars represent 10 mm. Abbreviations: am, anterior myophore; ats, anterior tooth socket; bc, body cavity; ct, central tooth; ecto, ectomyophoral cavity; Lrv, ligamentary infolding in right valve; ol, outer (calcitic) shell layer; pm, posterior myophore; pts, posterior tooth socket.
Family CAPRINULIDAE Yanin, 1990

Genus SELLAEA Di Stefano, 1889

Type species. *Caprotina (Sellaea) zitteli* Di Stefano, 1889.

**Sellaea sp.**

**Figures 12–13**

**Material.** All specimens from the Langshan Formation are preserved in section in indurated pink to pale grey limestone, from the north side of Lameila Mountain at the junction of Rutog County and Gar County (N 32°42'51", E 79°31'23"), and include two RV specimens in polished transverse section, NIGP no. 160517 (Fig. 12A) and NIGP no. 160518 (Fig. 12B), a cut block containing several fragments, NIGP no. 160519 (Fig. 12C, F), plus other loose RV fragments NIGP no. 160520, NIGP no. 160521 (Fig. 12D–E). In addition, a partial articulated specimen was photographed in the field by the first author (Fig. 13A), in the Sangzugang Formation, which is regarded as time equivalent to the Langshan Formation (see below).

**Description.** The slender cylindrical RV specimens have a rounded subquadrate cross-sectional form, of between 30 and 40 mm anteroposterior diameter, with a dorsal indentation marking the site of ligamentary infolding and a broad but shallow ventral sulcus (Fig. 12A–B, D). Preservation of the shell material is poor, with the thick inner shell (originally aragonitic) replaced by white to transparent cavity-filling calcite spar, and the ol almost entirely missing. However, a relic of the ol adhering to part of an external mould (Fig. 12C), shows it to have been very thin (<1 mm) with an external ornamentation of fine mm-scale riblets.

Internally, the robust ct is flanked by apparently subequal sockets for the LV teeth (Fig. 12A). The pm forms a thick vertical wall connecting the ct to the posteroventral margin of the valve and is separated from the posterior valve wall by a relatively broad ectomyophoral cavity (Fig. 12A–B). The am is less distinct, but is presumed to be represented by a slight thickening of the anterior valve wall (Fig. 12B). No clear evidence of pallial canals is visible in the anterior valve wall, although the poor preservation of the material makes it impossible to decide whether they were completely absent. A longitudinal section of a RV fragment (Fig. 12E), however, shows indeterminate tabulæ-like structures in some unidentified small internal cavities.

In addition to the specimens collected from the Langshan Formation, described above, the first author also photographed in the field a natural section of a partial articulated specimen in the Sangzugang Formation (Fig. 13A). The Aptian–Albian Sangzugang Formation crops out in the area of Xigaze region in the Lhasa block. It was deposited in the northern margin of the Xigaze Forearc Basin of the Indus Arc and is regarded as time equivalent to the Langshan Formation (Wan et al. 2003; Scott et al. 2010). This specimen provides further valuable information on the myocardial organization of the LV and particularly its accessory cavities, including a prominent posterior ectomyophoral cavity.

**Remarks.** The elongate cylindrical shape of the RV, with its ventral sulcus, and the thick pm wall, apparent lack of pallial canals, at least around most of the valve walls, and thin ol are all consistent with the characters of both the primitive caprinid *Pachytraga* and the caprinulid *Sellaea* (taken here to include the forms assigned to *Caprotina* by Di Stefano (1889); see Skelton (2013a)). However, both the relatively wide ectomyophoral cavity (Fig. 12A) and the apparently subequal LV teeth argue in favour of *Sellaea* and against *Pachytraga*, which is characterized by

![Fig. 13.](image-url)
a narrow ectomyophoral cavity in the RV and a pt that is distinctly smaller than the at in the LV (Skelton and Masse 1998). Moreover, Pachytraga has not been recorded above the lower Aptian (Skelton and Masse 1998), whereas the presence of a fragment of Auroradiolites in close association with the specimens described here (Fig. 12F) indicates a higher stratigraphical level, consistent with the Aptian–Albian stratigraphical range of Sellaea (Skelton and Gili 2012; PWS unpub. data). Further evidence in favour of the identification of Sellaea in Tibet comes from the partial articulated specimen observed in the Sangzugang Formation (Fig. 13A). Comparison with an oblique transverse section of a LV of S. ciafaloi (Di Stefano, 1889) in the type collection from Termini Imerese, Sicily (Fig. 13B), reveals the same basic myocardial organization and arrangement of accessory cavities, including a broad posterior ectomyophoral cavity typical of Sellaea, in contrast to Pachytraga (Skelton and Masse 1998).

Di Stefano (1889) erected several nominal species in two subgenera that he assigned to the genus Caprotina (namely Caprotina `sensu stricto’, and Sellaea) although none of his species in fact compare closely with the type species of the genus, Caprotina striata d’Orbigny, 1840. Di Stefano (1889) distinguished his two ‘subgenera’ only on the basis of possession, or not, of pallial canals outside the RV am – a feature that could nevertheless be subject to intraspecific variation, by analogy with that seen in Pachytraga paradoxa (Skelton and Masse 1998). Pending much needed modern revision of Di Stefano’s (1889) Sicilian material, the Tibetan specimens described here are thus placed without specific assignment in the genus Sellaea, taken to include those forms attributed to Caprotina by Di Stefano (1889). In any case, the poor state of preservation of our specimens precludes certainty as to whether or not canals were present outside the RV am.

Coralliochama anomalusa Gou and Shi, 1998, was described from the Langshan Formation in Gegyai County, but only the external form of one articulated shell and a RV were figured. Not only is the attribution to that relatively derived Campanian–Maastrichtian plagioptychid genus (Mac Gillavry 1937) extremely doubtful on stratigraphical grounds, but no mention was made of fine pallial canals in the inner shell, which are diagnostic of Coralliochama. The external shell form of the RV is similar to that of the Tibetan Sellaea, both having a slender cylindrical RV and a shallow ligamentary groove. Another important similarity is that their external surfaces both show fine vertical riblets and circular growth lines (Fig. 12C). Although Gou and Shi (1998, p. 265) state ‘Outer ostracum 3–4 mm in thickness; inner ostracum 2 mm in thickness’, it is unclear how their so-called outer and inner ostraca relate to the calcitic outer (ol), and originally aragonitic inner shell layers of rudists recognized herein. Indeed, the uppermost part of the RV of the articulated specimen figured by Gou and Shi (1998, pl. 2, fig. 7) appears to show a thin ol that has partly spalled off and is quite similar in appearance to that seen in the Tibetan Sellaea sp. (Fig. 12C). As Gou and Shi (1998) did not figure a transverse section of C. anomalusa, the form of its myocardial apparatus, which is crucial in the classification of rudists, remains obscure. To summarize, although C. anomalusa is externally similar to Sellaea, sp., resolution of its taxonomic status must await further revision of the type material.

**STRATIGRAPHICAL CORRELATION**

The Langshan Formation has been dated mainly using foraminifers (Zhang 1982, 1986, 1991), but its age remains controversial. The most abundant foraminifers of this formation are orbitolinids. Zhang (1986, 1991) described and clearly illustrated the orbitolinids of the Langshan Formation from Tibet and established many new genera and species, which we nevertheless regard as very similar to some previously established species as we discuss below. So revision and correct identification of these forms is of paramount importance for determining the age of the Langshan Formation.

The structure and size of the embryonic apparatus is the most important factor for generic- and species-level classification of orbitolinids ( Schroeder 1975; Schroeder et al. 2010), and several phylogenetic lineages were established based on the detailed study on the development pattern of the embryonic apparatus ( Schroeder 1975; Schroeder et al. 2002, 2010). The first author therefore measured the maximum diameters of embryonic apparatuses and protoconchs on the published photographs of median sections from Zhang (1986, 1991). Our revision is mainly based on these data together with the structures of the embryonic apparatuses. Nine species have been recognized for age determination (Fig. 14), eight of them belong to the Eopolarbitolina pertenuis – Palorbitolinoides hedini lineage ( Schroeder et al. 2002, 2010) and Praeorbitolina cornyi – Mesorbitolina aperta lineage ( Schroeder 1975; Schroeder et al. 2010), and the last one is Mesorbitolina birmicana. M. birmicana, which was characterized by a biconvex embryonic apparatus and plane convex to triangular protoconch, was revised recently by Schlagintweit and Wilmsen (2014). It has been reported from Myanmar, Iran and Tibet and probably Ladakh, India and Tunisia ( Zhang 1982, 1986, 1991; Cherchi et al. 1984; Schlagintweit and Wilmsen 2014), and a possible upper Aptian to upper Albian stratigraphic range could be assumed based on these occurrences.
Zhang (1986) described the orbitolinids from Xainza and Baingoin counties. In this area, the Langshan Formation was divided into lower and upper parts (Zhang et al. 1986). According to our revision of the orbitolinids, the lower part contains two species: *Eopalorbitolina charollaisi* and *Palorbitolina lenticularis* which was formerly described as *Eorbitolina lentiformis* by Zhang (1986; Table 1). On the basis of the two species recognized herein, the lower part of the Langshan Formation should thus be lower Barremian to lower Aptian (Schroeder et al. 2010).

Zhang (1986) described 15 species from upper part of the Langshan Formation in the same area including 10 new species. We recognized five species that are useful for age-dating: *Eopalarbitolina parva*, *M. texana*, *M. subconcava*, *M. birmanica* and *M. aperta* (Table 2). It should be mentioned that the *M. birmanica* specimens from Zhang (1986) may represent the advanced form of this species, as the size of their embryo is bigger and the structure of their subembryonic zone is more complicated compared with the Myanmar and Iran records (Schlagintweit and Wilmsen 2014). In Zhang (1986), *Palorbitolina lenticularis* was also reported from the upper Langshan Formation, but only one transverse section was illustrated, in which the structure of the embryonic apparatus was not shown, so this record was discounted. According to the species cited above, we bracket the upper Langshan Formation within the upper Aptian to lower Cenomanian interval (Schroeder 1962, 1979; Schroeder and Neumann 1985; Schroeder et al. 2010).

Zhang (1991) described 25 species collected from the Langshan Formation in western Tibet (including Gerze, Gegyai, Rutog and Gar counties). Nine species are recognized herein for the age determination: *Eopalarbitolina charollaisi*, *Palorbitolina lenticularis*, *P. ultima*, *Praeorbitolina cornyi*, *Mesorbitolina parva*, *M. texana*, *

TABLE 1. Revised orbitoline species from the lower part of the Langshan Formation, Lhasa block, Tibet (Zhang, 1986).

<table>
<thead>
<tr>
<th>Species</th>
<th>Synonyms in Zhang (1986)</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Palorbitolina</em></td>
<td><em>Palorbitolina lentiformis</em></td>
<td>(pl. 6, figs 2–3)</td>
</tr>
</tbody>
</table>

Species

*Eopalorbitolina* charollaisi (Schroeder 1962, 1979; Schroeder and Neumann 1985; Table 1, fig. 1)

TABLE 2. Revised orbitoline species from the upper part of the Langshan Formation, Lhasa block, Tibet (Zhang, 1986).

<table>
<thead>
<tr>
<th>Species</th>
<th>Synonyms in Zhang (1986)</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mesorbitolina</em></td>
<td><em>Mesorbitolina parva</em></td>
<td>Late Aptian</td>
</tr>
<tr>
<td></td>
<td><em>Columnorbitolina</em></td>
<td>(pl. 3, figs 13, 15–16)</td>
</tr>
<tr>
<td><em>Mesorbitolina</em></td>
<td><em>Mesorbitolina texana</em></td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td><em>Eopalorbitolina</em></td>
<td><em>Eopalorbitolina lentiformis</em></td>
<td>(pl. 6, figs 2–3)</td>
</tr>
</tbody>
</table>

Species

*Eopalorbitolina charollaisi* (pl. 1, fig. 1)

M. subconcava, M. birmanica and M. aperta (Table 3). According to these species, it can be concluded that the Langshan Formation in this region can be assigned to the lower Barremian to lower Cenomanian interval (Schroeder 1962, 1979; Schroeder and Neumann 1985; Schroeder et al. 2010).

In conclusion, we consider the Langshan Formation to have been deposited during the early Barremian to early Cenomanian interval. The lower part of this formation is of early Barremian to early Aptian age, while the upper part is of late Aptian to early Cenomanian age.

The age of the rudist fauna

*Eoradiolites davidsoni* has a cosmopolitan distribution (in both the Old and New worlds) and ranges stratigraphically from the Alban to the Cenomanian – lower Turonian (Steuber 1999; Alencaster and García-Barrera 2008), but is mainly reported from Alban strata in Texas, Mexico, Egypt, Iran, Hungary, Apulia and Somalia (Pons et al. 2010).

*Sellaea* was first reported from Sicily by Di Stefano (1889, 1898), who assigned a Cenomanian age to his specimens based on other rudists and nerineid gastropods from the type locality at Termini Imerese. However, the latter section exposes slope deposits containing blocks of rudist-bearing limestone of different ages. In contrast, *Sellaea*, as well as *Himeraelites* and *Caprotina* sensu Di Stefano (1889), are all preserved in situ in platform limestones of early Aptian age (including *Offneria* and *Glossomyophorus*). Exposure further east, at Cefalù (Camoin 1983; PWS pers. obs. May 2011). Nevertheless, *Sellaea* has also been reported from the Alban of southern Italy, based on micropaleontological assemblages (Chiocchini et al. 1994; Masse et al. 1998), as well as Oman (Masse et al. 1997) and Sinai (Steuber and Bachmann 2002). Whether or not specimens from the Alban of Texas that were referred to the genus by Coogan (1977) truly belong to the genus remains an open question. In any case, *Sellaea* thus appears to have an Aptian to Albanian range, on present evidence.

*Magallanesia* was recently established by Sano et al. (2014), who described a new species, *M. canaliculata*, from the Aptian–Albian of Takuyo-Daini Seamount in the Japanese seamounts and the upper Alban of Cebu Island, Philippines. These two localities were both located in the central Pacific in Aptian–Albian times. The age of the Takuyo specimens is only roughly estimated, but given the relatively derived characters of *M. canaliculata* compared with other Aptian–Albian polycotids, the authors considered that *M. canaliculata* was most likely of late Albanian age (Sano et al. 2014). As discussed in Systematic Palaeontology above, the Tibetan *M. rutogensis* is yet more derived than *M. canaliculata*, according to the quantity and distribution of the canals, and is thus considered to be probably not older than late Albanian.

In summary, the age of the rudist fauna here described is most likely late Albanian.

THE DISTRIBUTION AND ORIGIN OF AURORADIOLITES

Stratigraphical and geographical distribution of Auroradiolites

*Auroradiolites gigitensis* has been recorded in upper Aptian – Albian limestones from Iran, central Afghanistan, northern Pakistan, northern India and Japan (Montenat et al. 1982; Pudsey et al. 1985; Mathur and Vogel 1988; Masse and Gallo Maresca 1997; Sano and Masse 2013; Upadhyay 2014 and see also Upadhyay 2001, fig. 4b).
Auroradiolites griesbachi, previously referred to Sphaerulites griesbachi, was reported from Herat, in northern Afghanistan (Montenat et al. 1982; Masse and Gallo Maresca 1997). The age of this species is poorly constrained, although Masse and Gallo Maresca (1997) envisaged that it could be late Aptian.

Auroradiolites biconvexus is distributed in the Lhasa block of Tibet and Kandahar region, Afghanistan (Sano and Masse 2013). The stratigraphical data suggest that this species is most probably of late Albian age (see Stratigraphical Correlation, above).

To conclude, our data indicate that Auroradiolites was restricted to those parts of south-west Asia that pertained to the northern margin of Tethys and to the western Pacific margin. The geological age of this genus is late Aptian to Albian.

The origin of Auroradiolites

The most primitive genus of the Radiolitidae is Hauterivian – lower Aptian Agriopleura (Sano and Masse 2013; Skelton 2013a; Masse and Fenerci-Masse 2015), and the compact nature of its outer shell layer makes it a natural candidate for the ancestry of Auroradiolites (see Systematic Palaeontology, above). Agriopleura is distributed in the Mediterranean and Middle East regions, but questionably also in Mexico (Masse and Fenerci-Masse 2008, 2015).

The Mediterranean to Middle Eastern lower Aptian species A. libanica (Astre, 1930), recently reviewed by Masse and Fenerci-Masse (2015), is both stratigraphically and palaeobiogeographically closest to the south-west Asian examples of Auroradiolites. It is characterized by a concave LV, a relatively thick, entirely compact outer shell layer, and the presence in the LV of downwardly projected myophoral bulges (distinct from true plates; Skelton and Masse 2000; Fenerci-Masse et al. 2006; Masse and Fenerci-Masse 2015). The differences between Auroradiolites and Agriopleura are as follows: (1) the LV of Auroradiolites is almost flat to strongly convex, contrasting with the concave, lid-like LV of Agriopleura; (2) the LV myophores of Auroradiolites are more robust, looking like protruding plates as in other radiolitids, while the LV myophores of Agriopleura project only as low buttresses; (3) the ligamentary infolding of Auroradiolites is more strongly developed, producing an elongate inward extension of the ol with a widely forked inner termination in the RV, whereas the ligamentary infolding of Agriopleura is much shorter and is triangular in transverse section. In other words, the myocardial apparatus of Auroradiolites is notably more robust than that of Agriopleura, possibly to ensure stronger attachment between the two valves (see Skelton 1979).

For each of the three character-state differences cited above, the primitive condition is apparent in Agriopleura, its depressed LV (1) and relatively weak ligamentary infolding (3) both being retained in Archaeoradiolites and Eoradiolites, while its relatively less prominent myophores reflect its monopleurid ancestry. Based on present data, Auroradiolites is thus most parsimoniously interpreted as having descended directly from Agriopleura, with progressive convex projection of the LV and strengthening of its myocardial anchorage in the RV. An alternative phylogenetic hypothesis would be the derivation of Auroradiolites from Archaeoradiolites or Eoradiolites, but that is less parsimonious as it would involve the secondary loss of the

### TABLE 3. Revised orbitoline species from the Langshan Formation in western Tibet, Lhasa block, Tibet (Zhang 1991).

<table>
<thead>
<tr>
<th>Species</th>
<th>Synonyms in Zhang (1991)</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eoporalbitolina charollaisi</td>
<td>Eoporalbitolina charollaisi (pl. 2, figs 3–4)</td>
<td>Early Barremian</td>
</tr>
<tr>
<td>Palorbitolina lenticularis</td>
<td>Palorbitolina nannembryona (pl. 1, figs 11–14)</td>
<td>Late Barremian – early Aptian</td>
</tr>
<tr>
<td>Palorbitolina ultima</td>
<td>Palorbitolina lenticularis (pl. 1, figs 4–5, 9)</td>
<td>Early Aptian</td>
</tr>
<tr>
<td>Praeorbitolina cornyi</td>
<td>Praeorbitolina cornyi (pl. 2, figs 7–9)</td>
<td>Early Aptian</td>
</tr>
<tr>
<td>Mesorbitolina parva</td>
<td>Mesorbitolina lhianzhubensis (pl. 2, figs 10–12)</td>
<td>Late Aptian</td>
</tr>
<tr>
<td></td>
<td>Mesorbitolina tibetica (pl. 2, fig. 19)</td>
<td>Late Aptian</td>
</tr>
<tr>
<td></td>
<td>Mesorbitolina minascula (pl. 3, fig. 15)</td>
<td>Late Aptian</td>
</tr>
<tr>
<td>Mesorbitolina parva</td>
<td>Mesorbitolina gregaria (pl. 5, figs 6, 8–10)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina texana</td>
<td>Mesorbitolina pengboensis (pl. 2, fig. 21)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina texana</td>
<td>Mesorbitolina texana (pl. 3, figs 17, 19, 21–22)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina subconcava</td>
<td>Mesorbitolina subconcava (pl. 4, figs 8, 11)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina subconcava</td>
<td>Mesorbitolina confusa (pl. 5, figs 20–21)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina birmanica</td>
<td>Mesorbitolina birmanica (pl. 4, figs 1–7, 13–18)</td>
<td>Late Aptian – late Albian</td>
</tr>
<tr>
<td>Mesorbitolina aperta</td>
<td>Mesorbitolina aperta (pl. 3, figs 1–5, 8)</td>
<td>Late Albian – early Cenomanian</td>
</tr>
<tr>
<td>Mesorbitolina gregaria</td>
<td>Mesorbitolina gregaria (pl. 5, figs 13–16)</td>
<td>Late Albian – early Cenomanian</td>
</tr>
</tbody>
</table>
celluloprismatic structure of the outer shell layer seen in the last two genera. Nevertheless, some additional radiolitid specimens containing mixed compact and celluloprismatic structure in the outer shell layer were collected from the Langshan Formation by the first author in 2014. From our initial analysis, however, we regard these specimens as most probably belonging to *Eoradiolites* (in which it is known that some compact structure may be locally present) and not connected with *Auroradiolites*. Full description of this latest material and discussion of its significance will follow in a later study.

In conclusion, the fossil record shows that *Agriopleura* persisted in the Mediterranean to Middle Eastern region until (at least) the end of the early Aptian, while *Auroradiolites* spread along the northern Tethyan margin of south-west Asia to the Pacific rim from the late Aptian to the late Albian. The most parsimonious interpretation of the morphological evidence suggests that the latter genus evolved directly from the former, with the modification of the LV but retention of the primitively compact outer shell layer.

**PALAEOBIOGEOGRAPHICAL IMPLICATIONS**

Of the four rudist genera described from the Langshan Formation herein, one (*Eoradiolites*) is cosmopolitan, with widespread Albian records from both the New World and the Old World (Pons et al. 2010); two more (*Auroradiolites* and *Magallanesia*), by contrast, are considered endemic to the NE Tethyan – Pacific region (Masse and Gallo Maresca 1997; Sano and Masse 2013; Sano et al. 2014); finally, a fourth genus (*Sellaea*) presents a palaeobiogeographical puzzle, having previously been unquestionably recorded only from central to southern Tethyan carbonate platforms (Steuber and Bachmann 2002).

As the most easterly Tethyan material referred (tentatively) to the species so far reported, the Tibetan specimens of *Eoradiolites* cf. *davidsoni* narrow the palaeobiogeographical gap between Tethyan populations of the species to the west and those of the New World to the east. On the basis of current knowledge, the Tibetan population could have been derived from either the east (via the Pacific) or the west according to the Albian dispersal routes discussed by Skelton et al. (2013).

In this respect, it is interesting to note van Waasbergen’s (1995) record of radiolitid fragments with typical celluloprismatic of mesostructure from the central Pacific. These samples were thought also to be Albian in age (van Waasbergen 1995; Sano and Masse 2013). At the very least, this record together with that of the Tibetan *Eoradiolites* cf. *davidsoni* confirms the already cosmopolitan distribution of radiolitids with celluloprismatic of in Albian times.

The presence of *Auroradiolites* in the Lhasa block clearly associates this terrane with the south-west Asian to western Pacific palaeobiogeographical province. *Auroradiolites* is an endemic genus that was distributed along the northern margin of eastern Tethys and around to the western Pacific (Japan) during the late Aptian to Albian, according to records from Iran, central Afghanistan, northern Pakistan, northern India (Ladakh) and Japan (Montenat et al. 1982; Pudsey et al. 1985; Mathur and Vogel 1988; Masse and Gallo Maresca 1997; Upadhyay 2001, 2014; Sano and Masse 2013), besides those from Tibet. Masse and Gallo Maresca (1997) summarized the distribution of late Aptian radiolitids and proposed the concept of a south-west Asian palaeobiogeographical province based on the acellular forms here placed in the new genus *Auroradiolites*. Sano and Masse (2013) reported further examples attributable to the genus from Hokkaido, Japan, thereby expanding the province from south-west Asia to the western Pacific. The latter authors also mentioned the corresponding palaeobiogeographical links demonstrated by the late Aptian polyconitid probable sister taxa *Praecaprotina yaegashii* Yabe and Nagao, 1926, from northern Japan, and *Horiopleura haydeni* Douville, 1926a from Pakistan, both of which are found with *Auroradiolites giglitensis*. Moreover, in the Lhasa block of Tibet, *Auroradiolites biconvexus* is accompanied by *Magallanesia rutogensis*. As discussed in Systematic Palaeontology above, *Magallanesia* is probably the descendant of *Praecaprotina*. Thus, both the *Auroradiolites* and the *Horiopleura haydeni–Praecaprotina–Magallanesia* lineages can be said to characterize the south-west Asian – western Pacific province.

Given the context above, the presence also of the genus *Sellaea* in the Langshan Formation, otherwise regarded as characteristic of the central to southern Tethyan region, is intriguing. Coogan’s (1977) attribution of some specimens from the Albian of Texas to *Sellaea* was based on his evident confusion of borings in the shell wall outside the anterior myophore of the RV for pallial canals (Coogan 1977, pl. 3, fig. 6). However, if the Sicilian specimens that likewise lack such canals, which were attributed by Di Stefano (1889) to *Caprotina*, can also be included in *Sellaea* (see Systematic Palaeontology, above), then the presence or absence of these canals may be taxonomically immaterial, after all. Pending revision of the Texan material, the case for *Sellaea* in the New World thus remains open, hinting at the further possibility of trans-Pacific derivation of the Langshan examples, as for *Eoradiolites* cf. *davidsoni*. However, testing of that hypothesis requires a lot more revision of relevant material, going beyond the scope of the present study.

Sano et al. (2014) discussed the systematic relationship of *Sellaea*, *Praecaprotina* and *Magallanesia* using cladistic analysis. They concluded that *Sellaea* and...
Ma
gallanesia could be sister taxa, both possibly derived from Praecaprotina or some allied form. If correct, this phylogenetic hypothesis would strengthen the evidence for a palaeobiogeographical relationship between Tibet and the Pacific. A corollary of this hypothesis would be that Sellaea would thus originally have spread from the NW Pacific to the central and southern Tethyan platforms, possibly via the Lhasa block, and then situated on the northern margin of the eastern part of the Tethys. Countering this hypothesis, however, is our current knowledge of the stratigraphical distribution of Sellaea, the earliest records of which come from the early Aptian of the central and southern Tethyan regions, as previously discussed (see The age of the rudist fauna, above). Hence, further testing of the hypothesis is evidently required.

In this context, it should also be mentioned that Löser and Liao (2001) revised the spatial and temporal distribution of Cretaceous coral faunas from Tibet. They concluded that the mid-Cretaceous coral fauna from the Langshan Formation and the equivalent Jaggang Formation in the Lhasa block has a closer relationship with Tethyan faunas in Asia and Europe than with Caribbean faunas. Although this conclusion likewise still needs future confirmation, it again hints at an intimate palaeobiogeographical link between the Asian/Pacific and European regions.

CONCLUSIONS

Based on the investigation of newly collected material and specimens photographed in the field, together with the revision of some previously recorded taxa, four rudist genera and species are recognized from the upper part of the Langshan Formation in the Lhasa block:

1. Auroradiolites gen. nov. is a new radiolitid genus proposed for the grouping of south-west Asian to western Pacific radiolitid species that are characterized by an entirely compact outer shell layer and which were formerly attributed to Eoradiolites. The Tibetan Auroradiolites is attributed to A. biconvexus (Yang et al., 1982), which differs from the type species A. gigi
tensis (Douvillé, 1926a) by its strongly domed LV and the radially ‘wavy’ structure in the outer shell layer.

Auroradiolites most likely evolved directly from the most primitive radiolitid genus Agriopleura, which also has a completely compact outer shell layer and persisted in the Mediterranean to Middle Eastern region until (at least) the end of the early Aptian, while Auroradiolites then spread around the northern Tethyan margin of south-west Asia and the western Pacific from the late Aptian to the late Albian.

2. Eoradiolites cf. davidsoni (Hill, 1893) is of smaller size, with celluloprismatic structure in its outer shell layer as well as the typical ribbing of the species.

3. Magallanesia rutogensis sp. nov., a new species of the canaliculate polyconitid, Magallanesia Sano et al., 2014, differs from the type species in possessing more numerous and ventrally extended canals in the left valves.

4. Sellaea sp., represented by poorly preserved right valves from the Langshan Formation together with a partial articulated specimen observed in the correlative Sangzuzang Formation, shows typical features of this genus, including a very thin outer shell layer and an erect posterior myophoral wall in the RV, separating off a broad posterior ectomyophoral cavity.

The revision of the orbitolinids from the Langshan Formation confirms that it was deposited during the early Barremian to early Cenomanian interval. The rudist fauna described herein from the upper part of the formation indicates most probably a late Albian age, based mainly on the presence of Magallanesia rutogensis.

Both Auroradiolites biconvexus and Magallanesia rutogensis are characteristic of a south-west Asian – Pacific faunal province. Eoradiolites davidsoni and Sellaea are more widely distributed, and their likely presence in Tibet could imply derivation either from the East (via the Pacific) or from the West, along the northern Tethyan margin.

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