

The unusual atrypide brachiopod *Qilianotryma suspectum* (Popov, 1982) from the Upper Ordovician of the South China paleoplate

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Abstract.—The atrypide brachiopod *Qilianotryma* Xu in Jin et al., 1979 is an early member of the subfamily Spirigerinae initially described from the Katian (Upper Ordovician) Koumenzi Formation of the Qilian Mountains, Qaidam terrane, Northwest China. *Qilianotryma suspectum* (Popov in Nikiforova et al., 1982) is described for the first time from the Upper Ordovician of South China paleoplate. Serial sectioning in this study revealed the typical spiralia and other internal structures of early atrypides. The rephotographing of type material and discriminant analysis support that *Qilianotryma* and broadly similar *Euroatrypa* can be differentiated in terms of external morphology. The distribution of *Qilianotryma* across the South China paleoplate, Qaidam terrane, and a few Kazakh terranes (i.e., Chu-Ili, Boshchekul, and Chingiz-Tarbagatai) supports a low-latitude faunal province separate from that of Laurentia and Baltica during the Katian, but further work describing and reviewing additional fossil material from these plates and terranes may improve our understanding of the position of these plates and the role that paleogeography played in increasing biodiversity during the Ordovician Radiation.

Introduction

Qilianotryma Xu in Jin et al., 1979 is a mid-Katian (Ka2–3, Late Ordovician) atrypide brachiopod of the subfamily Spirigerinae first reported from Qilian Mountains of Qaidam terrane that is now part of Northwest China. *Qilianotryma* features a biconvex to dorsibiconvex profile and uniplicate anterior commissure typical of many early atrypides in this region (e.g., *Eospirigerina*, *Rongatrypa*, and *Sulcatospira*) but is distinctive in featuring an elliptical transverse outline and fine multicostellate ornamentation unlike the subpentagonal to subtriangular outline and coarse costae of most other atrypides from this region in the Upper Ordovician. The internal shell morphology of *Qilianotryma mirabile* Xu in Jin et al., 1979, the type species, is poorly known although the internal morphologies of other species (e.g., *Qilianotryma suspectum*) have been described (Popov et al., 1999).

Qilianotryma has previously been reported from the Koumenzi Formation (Katian of the Upper Ordovician) in Qilian Mountains, Qinghai Province, Northwest China. *Qilianotryma suspectum* from Henan Province represents the first occurrence of this species in South China, however, and is illustrated herein. The holotype of the type species *Qilianotryma mirabile* from the Koumenzi Formation of Qilian Mountains was rephotographed to illustrate diagnostic features of the species and genus more clearly and restudied to emend the diagnosis for this genus.

Cocks and Modzalevskaya (1997) first reported *Qilianotryma* outside of China on the basis of fossils initially described as *Euroatrypa tajmyrica* Nikiforova in Nikiforova et al., 1982 collected from the Katian of Russian central Taimyr (Popov in Nikiforova et al., 1982). Since then, there has been some debate as to whether *Euroatrypa* is a valid genus or should be accepted as a junior synonym of *Qilianotryma* (e.g., Cocks and Modzalevskaya, 1997; Popov et al., 1999; Nikitin et al., 2006; Rong et al., 2017). Species assigned to *Euroatrypa* have been differentiated from *Qilianotryma* on the basis of a more globose outline, a shorter hinge line, and a fold and sulcus not originating from the beak (Nikitin et al., 2006). Figured specimens reveal considerable morphological variation in *Euroatrypa* through its ontogeny (Nikiforova et al., 1982), however, so there is still some uncertainty as to the validity of *Euroatrypa*.

By more clearly defining the characteristics and range of this important early atrypide brachiopod genus, this study will contribute to an ongoing effort to better understand brachiopod evolution and biogeography in the plates that now comprise China and central Asia during the Early Paleozoic as new lineages were evolving during the Ordovician Radiation. A better understanding of the evolution and distribution of *Qilianotryma* and other atrypide lineages will be key to understanding the evolution and dispersal of brachiopods in this region. Given the poor paleomagnetic coverage in these regions, fossils are a particularly useful tool available to plot the location of these plates and terranes through time.

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Geological setting

The study area is located in Xichuan County, southwestern Henan Province, central China (Fig. 1). This region was part of a shallow-water platform on the north margin (present orientation) of South China paleoplate during the Late Ordovician (e.g., Ma et al., 2009; Dong et al., 2011; Rong et al., 2015; Jing et al., 2017). South China is thought to have been located in the tropical latitudes to the west of Gondwana at this time (Popov and Cocks, 2017; Torsvik and Cocks, 2017; Jin et al., 2018). Several paleoplates (e.g., North China, Tarim) and terranes (e.g., Chu-Ili, Chingiz-Tarbagatai, Atasu-Zhamshi) were also located in the tropical region and adjacent to South China west to Gondwana in the Late Ordovician.

The Shiyuanhe Formation is composed mainly of a series of gray thick-bedded grainstones interbedded with yellow thin-bedded siltstone and greenish mudstones. Macrofossils (e.g., brachiopods, corals, trilobites, bryozoans, and bivalves) are diverse and abundant (e.g., Yan et al., 1983; Deng, 1987; Liu et al., 1991; Zeng et al., 1993; Xu, 1996; Zhang et al., 2019b). The coral fauna is dominated by *Agetolites* and *Agetolitella* (Deng, 1987), two genera that are found in shallow-water settings across South China and North China during the Late Ordovician. Conodonts collected from the Shiyuanhe Formation belong to, ascendingly, the *Oulodus ulrichi*, *Oulodus robustus*, *Aphelognathus grandis*, and *Aphelognathus divergens* biozones, indicating a Katian (Late Ordovician) age (Ka2–Ka4) (Jing et al., 2017). The Shiyuanhe Formation unconformably underlies the Zhangwan Formation (Llandovery, Silurian).

Brachiopod shells are abundant in grainstones and siltstone interbeds at the locality, and loose specimens can be easily collected from weathered surfaces. Internal molds are also well preserved in siltstone and silty mudstone. This brachiopod fauna consists of 18 species within 18 genera. The strophomenide *Sowerbyella* (*Sowerbyella*) *sinensis* Wang, Jin, and Fang, 1964 and atrypide *Rongatrypa xichuanensis* (Xu, 1996) are the most abundant species in this fauna, while spiriferide, lingu- lide, and protorthide brachiopods are very rare from our collection.

Materials and methods

Specimens examined in this study were collected from the Shiyuanhe Formation at the Yaziwu section (33°07'50"N, 111° 18'32"E, WGS84) in southwestern Xichuan County, China. More than 1,000 brachiopod specimens were collected from this formation; however, only two specimens have been confidently identified as *Qilianotrypa*. Both valves were collected from the reddish massive carbonate rocks in the upper part of the formation.

Fossil materials were prepared, measured with digital calipers, coated with ammonium chloride powder (Teichert, 1948), and photographed under an optical microscope. One conjoined shell was serially sectioned with a refined Croft parallel grinder (Zhang et al., 2019a). Serial sections were produced on acetate peels, photographed under an optical microscope, and manually traced to illustrate the internal morphology of the shell. The software PAST 3.20 (Hammer et al., 2001) was used to plot scatter charts and run discriminant analysis on the dataset of measurements.

Repository and institutional abbreviation.—Two conjoined valves and 80 acetate peel replications of transverse sections examined in this study are deposited at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China (NIGP 173727–173728). The holotype of *Qilianotrypa mirabile* was collected by Hankui Xu in the Koumenzi Formation at the upstream of Tianbao river, Qilian Mountains, Qaidam terrane, Northwest China. The remains of the serial sectioned holotype specimen and a complete epoxy replica are deposited at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP 42574).

Systematic paleontology

Order Atrypida Rzhonsnitskaia, 1960

Suborder Atrypidina Rzhonsnitskaia, 1960

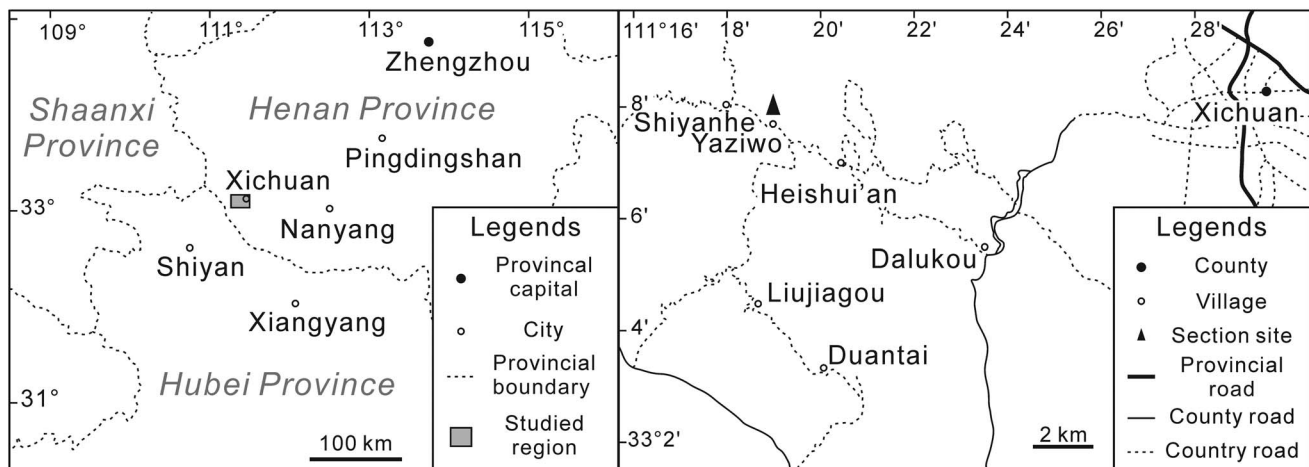


Figure 1. Simplified geographical maps of central China and the study area in Xichuan County, southwestern Henan Province, central China, modified from Zhang et al., 2019b.

Superfamily Atrypoidea Gill, 1871
 Family Atrypinidae McEwan, 1939
 Subfamily Spirigerininae Rzhonsnitskaia, 1974
 Genus *Qilianotryma* Xu in Jin et al., 1979

Type species.—*Qilianotryma mirabile* Xu in Jin et al., 1979 (p. 97, 98, in-text fig. 40, pl. 20, figs. 23, 24); collected from the Koumenzi Formation (Katian, Upper Ordovician), Qilian Mountains, Northwest China.

Other species.—*Qilianotryma suspectum* (Popov in Nikiforova et al., 1982) (p. 57, pl. 6, figs. 9–12); type specimens initially identified as *Euroatrypa suspecta* in Nikiforova et al. (1982); collected from the Katian of the Chu-Ili terrane, Kazakhstan. *Qilianotryma* cf. *Q. suspectum* Popov in Nikiforova et al., 1982 (p. 67, pl. 6, figs. 9–12) from the Degeres Member of the Dulankara Formation, Chu Ili terrane, Kazakhstan; see also Popov and Cocks (2021, p. 94–95, pl. 10, fig. 19) from an unnamed formation in southern Kazakhstan. *Qilianotryma* sp. Popov and Cocks, 2014 (p. 749, fig. 25X, Y), collected from the Akdombak Formation of the Chingiz Terrane, Kazakhstan.

Diagnosis.—See Rong et al., 2017.

Occurrence.—Koumenzi Formation (Katian, Upper Ordovician) of the Qilian Mountains, Qaidam terrane, Northwest China; Shiyanhe Formation (Katian, Upper Ordovician) of Xichuan County, Henan Province, South China; Degeres and Akkol Members, Dulankara Formation (Katian, Upper Ordovician) of the Dulankara Mountains and

an unnamed formation (Katian, Upper Ordovician) of the Ergeneky Mountains, southern Chu-Ili Range, Kazakhstan; Odak Beds of the Angrenor Formation (Katian, Upper Ordovician), central Kazakhstan; Akdombak Formation (Katian, Upper Ordovician), Mount Akdombak area, Chingiz, Kazakhstan.

Remarks.—*Qilianotryma* and its type species *Qilianotryma mirabile* was established on the basis of a single specimen found in the Koumenzi Formation (Katian, Upper Ordovician) of Qilian Mountains, Northwest China (Xu in Jin et al., 1979). This genus was previously assigned to the family Ancistrorhynchidae within the Rhynchonellida because of its similarity to *Ancistrorhyncha* Ulrich and Cooper, 1942 in terms of external morphology (Xu in Jin et al., 1979). However, the presence of jugal processes in the mantle cavity (Xu in Jin et al., 1979, in-text fig. 40) indicates this genus should instead be assigned to the Atrypida and with affinities to the Atrypidae, although spiralia are not illustrated in the initial description of the species and are not visible in the holotype specimen. It also represents a major difference compared with other Late Ordovician early atrypide lineages such as the Anazygidae that have a solid jugum rather than jugal processes (see Copper, 1977; Sproat and McLeod, 2023) although the function of these structures remains poorly understood.

The type species *Qilianotryma mirabile* is poorly known due to the ambiguity of the original figure and the hard access to the initial fossil locality in northern Tibet (Jin et al., 1979). The holotype is rephotographed in this study (Fig. 2), indicating a less globose and longer hinge line compared with *Euroatrypa*

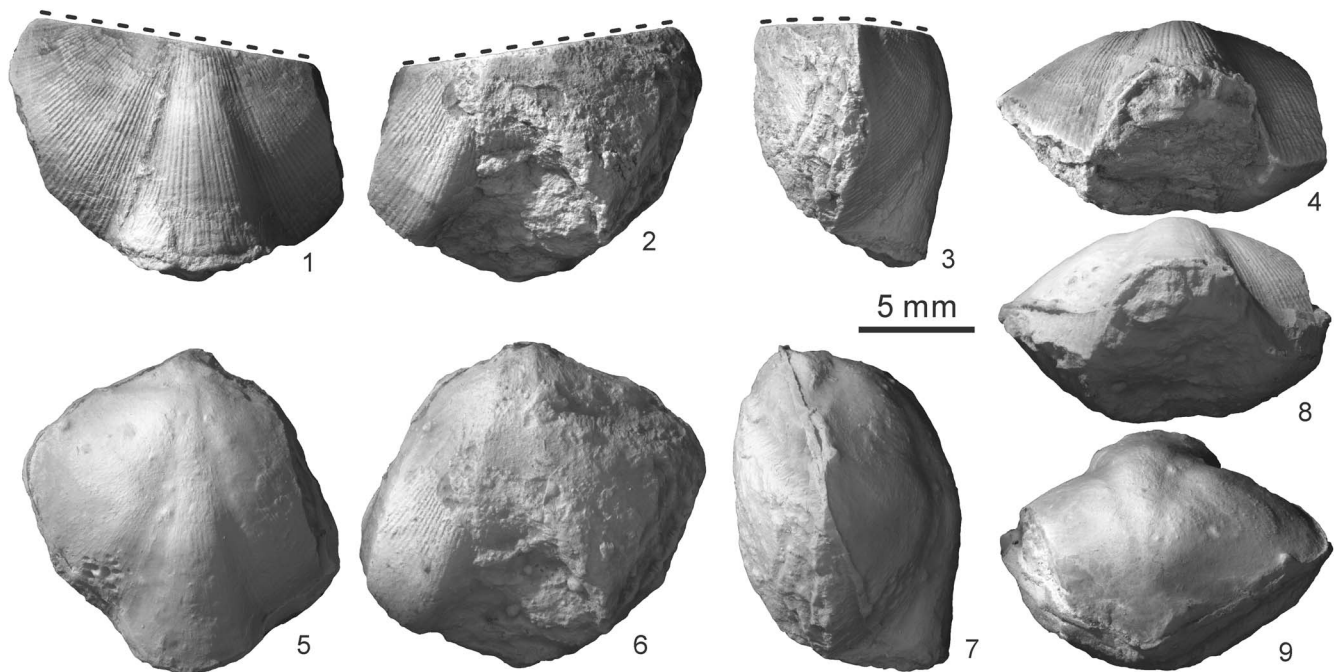


Figure 2. Holotype of *Qilianotryma mirabile* Xu in Jin et al., 1979 from the Koumenzi Formation at Tianbaohe upper stream section, Qilian County, Qinghai Province, northwestern China. (1–4) Holotype, NIGP 42575: (1) dorsal view; (2) ventral view; (3) lateral view; (4) anterior view. (5–9) Epoxy cast representing the complete holotype, NIGP 42575: (5) dorsal view; (6) ventral view; (7) lateral view; (8) anterior view; (9) posterior view. Dashed lines represent the surface that the shell was ground down to. Scale bar = 5 mm.

type species (i.e., *Euroatrypa tajmyrica*, Nikiforova et al., 1982, pl. 6, figs. 3, 4) and other species (e.g., *Euroatrypa aitenensis*, Nikitin et al., 2006, fig. 35.1, 35.3).

A parasulcate commissure and lateral furrows (and plications) on either side of the dorsal fold and ventral sulcus are known in some species of *Qilianotryma* (e.g., *Qilianotryma suspectum*, Popov et al., 1999), but these characteristics are not common in species of the genus. Other species have a more subtle division between the fold and sulcus and the flanks of each valve (e.g., *Qilianotryma mirabile*).

Some shells can be only questionably assigned to the genus. *Qilianotryma* cf. *Q. suspectum* Popov and Cocks, 2021 resemble *Q. suspectum* in overall character, but only a single dorsal valve interior mold was available for study, and thus the shell can be assigned only tentatively to the genus. Similarly, *Qilianotryma* sp. Popov and Cocks, 2014 is similar to the type species, *Q. mirabile*, in the exterior features of the shell, such as the fine ribs and uniplicate anterior. Given that no shell interiors or serial sections have been made to study the internal morphology of the shells and that only a few deformed shells are known from the locality, its definitive assignment to the genus will be possible only with study of additional material.

Qilianotryma differs from *Spirigerina* and *Eospirigerina* in its finely, evenly multicostellate radial ornamentation and transverse outline. *Qilianotryma* also has fewer spiralia whorls (usually fewer than seven) than typically found in *Eospirigerina* (fewer than 12 whorls). *Qilianotryma* differs from *Anabaria* and *Rongatrypa* in its fine radial ornamentation, thin dental plates in the ventral interior, and lack of a vertical myophragm and a cardinal process at the end of notothyrial cavity.

Euroatrypa Oradovskaya in Nikiforova et al., 1982 and its type species, *Euroatrypa tajmyrica*, are broadly similar to *Qilianotryma* and were established on the basis of materials from the Korotkaya Formation (Katian), central Taimyr of northern Siberia, Russia (Nikiforova et al., 1982). Additional specimens of *Euroatrypa* have been also found in the Tirekhtyakh horizon (Katian), Northeast Russia (Nikiforova et al., 1982) and the Odak Beds (Katian), central Kazakhstan (Nikitin et al., 2006). *Euroatrypa* was considered a subjective synonym of *Qilianotryma* by Cocks and Modzalevskaya (1997) and Copper (2002).

Nikitin et al. (2006) maintained *Euroatrypa* as a separate taxon based on examination of new material of both *Qilianotryma* and *Euroatrypa* from the Angrenor Formation (Katian) from further collections at the Odak Beds in central Kazakhstan, suggesting these two genera should be treated as different taxa since *Euroatrypa* has a more globose shell, a shorter hinge line, and a ventral sulcus and dorsal fold that do not originate from the beak.

Available measurable specimens of *Euroatrypa* (Table 1) appear to be broadly similar to those of *Qilianotryma* in terms of length, width, and thickness (Fig. 3). Discriminant analysis, however, shows that the taxa can be readily differentiated, with a 77.3% correct classification based on shell dimensions alone (Fig. 4). With some hesitation, we accept these two genera are different in shell outline. The length of the hinge line and development of the dorsal fold and ventral sulcus are also essential in discriminating *Qilianotryma* from *Euroatrypa*. *Euroatrypa* is herein able to be differentiated from *Qilianotryma* as a valid genus.

Table 1. Dimensions of measurable specimens of *Qilianotryma* and *Euroatrypa* from China and central Asia. L/W = length divided by width; D/W = depth divided by width; D/W = depth divided by width. Specimens are measured in millimeters.

Serial number	Catalog number	Originally described species	Length	Width	Depth	L/W	D/W	Occurrence	Reference
1	NIGP 173727	<i>Qilianotryma suspectum</i>	19.6	25.0	13.1	0.78	0.52	Xichuan, S China	This study
2	NIGP 173728	<i>Qilianotryma suspectum</i>	17.8	25.2	11.3	0.71	0.45	Xichuan, S China	This study
3	—	<i>Cliftonia</i> ex gr. <i>spiriferoides</i>	16.5	19.5	6.0	0.85	0.31	Chu-Ili, Kazakhstan	Rukavishnikova, 1956
4	NIGP 42575 (holotype of type species)	<i>Qilianotryma mirabile</i>	17.0	18.0	10.3	0.94	0.57	Qinghai, NW China	Xu in Jin et al., 1979
5	NIGP 42574	<i>Qilianotryma mirabile</i>	11.7	15.4	7.5	0.76	0.64	Qinghai, NW China	Xu in Jin et al., 1979
6	CNIGR 25/11943	<i>Euroatrypa suspecta</i>	12.8	18.2	8.7	0.70	0.48	Chu-Ili, Kazakhstan	Popov in Nikiforova et al., 1982
7	CNIGR 25/11943	<i>Qilianotryma suspectum</i>	12.8	18.2	8.7	0.70	0.48	Chu-Ili, Kazakhstan	Popov et al., 1999
8	NMW 98.65G.1751	<i>Qilianotryma suspectum</i>	14.2	16.5	7.1	0.86	0.43	Boshchekul, Kazakhstan	Nikitin et al., 2006
9	NMW 98.65G.1750	<i>Qilianotryma suspectum</i>	11.6	13.9	6.6	0.83	0.47	Boshchekul, Kazakhstan	Nikitin et al., 2006
10	NMW 98.65G.1753	<i>Qilianotryma suspectum</i>	14.0	18.6	10.0	0.75	0.54	Boshchekul, Kazakhstan	Nikitin et al., 2006
11	CNIGR 10/11943	<i>Euroatrypa tajmyrica</i>	16.2	20.8	12.0	0.78	0.58	Central Taimyr, Russia	Nikiforova in Nikiforova et al., 1982
12	CNIGR 14/11943	<i>Euroatrypa tajmyrica</i>	12.2	15.0	7.5	0.82	0.50	Central Taimyr, Russia	Nikiforova in Nikiforova et al., 1982
13	CNIGR 10/11943	<i>Euroatrypa tajmyrica</i>	18.5	21.5	12.5	0.86	0.58	Central Taimyr, Russia	Nikiforova in Nikiforova et al., 1982
14	CNIGR 1/11943	<i>Euroatrypa kolymica</i>	18.6	21.5	12.8	0.87	0.60	Tirekhtyakh zone, Northeast Russia	Oradovskaya in Nikiforova et al., 1982
15	CNIGR 2/11943	<i>Euroatrypa kolymica</i>	16.0	18.7	9.7	0.86	0.52	Tirekhtyakh zone, Northeast Russia	Oradovskaya in Nikiforova et al., 1982
16	CNIGR 3/11943	<i>Euroatrypa kolymica</i>	17.6	21.0	10.3	0.84	0.49	Tirekhtyakh zone, Northeast Russia	Oradovskaya in Nikiforova et al., 1982
17	CNIGR 4/11943	<i>Euroatrypa kolymica</i>	17.9	24.1	10.8	0.74	0.44	Tirekhtyakh zone, Northeast Russia	Oradovskaya in Nikiforova et al., 1982
18	CNIGR 5/11943	<i>Euroatrypa kolymica</i>	13.9	16.1	7.7	0.86	0.47	Tirekhtyakh zone, Northeast Russia	Oradovskaya in Nikiforova et al., 1982
19	NMW 98.65G.1688	<i>Euroatrypa aitenensis</i>	15.3	17.4	10.9	0.88	0.63	Odak, central Kazakhstan	Nikitin et al., 2006
20	NMW 98.65G.1689	<i>Euroatrypa aitenensis</i>	12.5	15.1	8.7	0.83	0.58	Odak, central Kazakhstan	Nikitin et al., 2006
21	NMW 98.65G.1690	<i>Euroatrypa aitenensis</i>	11.4	13.2	8.6	0.86	0.65	Odak, central Kazakhstan	Nikitin et al., 2006
22	NMW 98.65G.1691	<i>Euroatrypa aitenensis</i>	11.4	14.1	8.4	0.81	0.60	Odak, central Kazakhstan	Nikitin et al., 2006

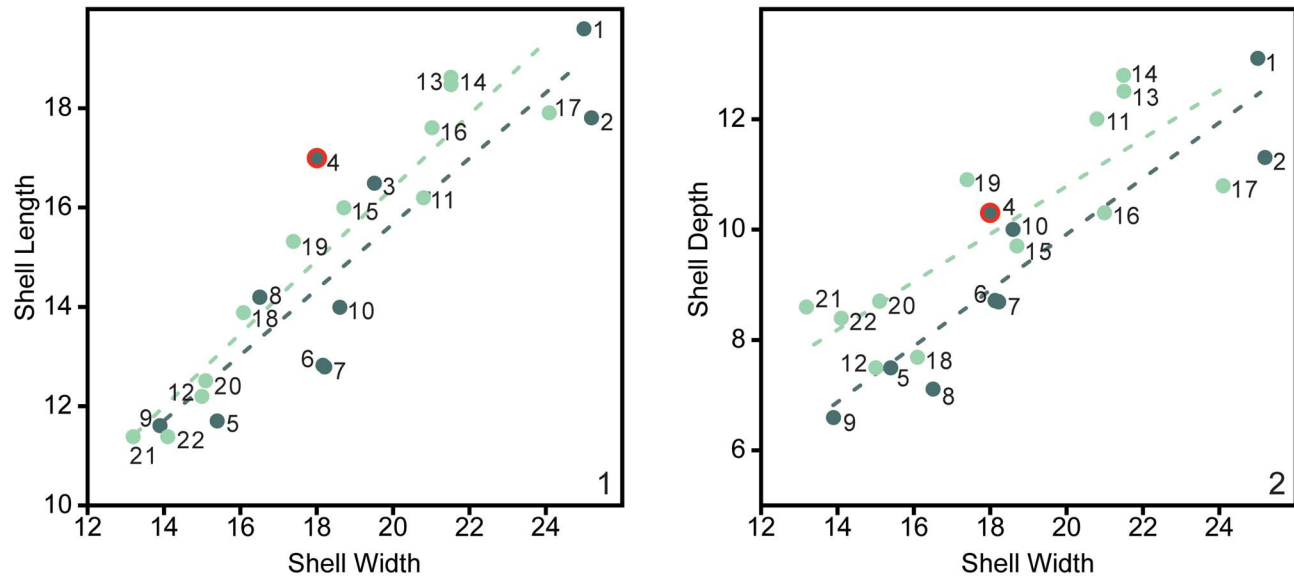


Figure 3. (1, 2) Linear regression plots of width versus length and width versus depth of measurable specimens of *Qilianotryma* and previously identified *Euroatrypa*: (1) $k = 0.64$ and 0.75 , $r^2 = 0.74$ and 0.91 , respectively; (2) $k = 0.50$ and 0.42 , $r^2 = 0.84$ and 0.65 , respectively. Points in dark green and light green represent specimens previously described *Qilianotryma* and *Euroatrypa*, respectively. The data point with a red outline represents the holotype of the type species, *Qilianotryma mirabile* Xu in Jin et al., 1979. Each point corresponds with specimens presented in Table 1.

Qilianotryma suspectum (Popov in Nikiforova et al., 1982)
Figures 5, 6

- 1956 *Cliftonia* ex gr. *spirigeroides* (M'Coy, 1851); Rukavishnikova, p. 151, pl. 4, figs. 14, 15.
1982 *Euroatrypa suspecta* Popov in Nikiforova et al., p. 57, pl. 6, figs. 9–12.
1999 *Qilianotryma suspectum*; Popov et al., p. 634, pl. 1, figs. 11–15.

- 2006 *Qilianotryma suspectum*; Nikitin et al., p. 270, figs. 35 12a–e, 38 1–3, 39.
2006 *Qilianotryma suspectum*; Popov and Cocks, p. 279, fig. 6G–H, J.

Holotype.—A conjoined valve (CNIGR 25/11943) from Akkol Beds, upper Dulankara Formation (Katian) of the Dulankara Mountains, southern Chu-Ili Range, Kazakhstan (Nikiforova et al., 1982, p. 57, pl. 6, figs. 9–12).

Occurrence.—Shiyanhe Formation (mid–upper Katian) in the Yaziwo section, Xichuan County, Henan Province, South China.

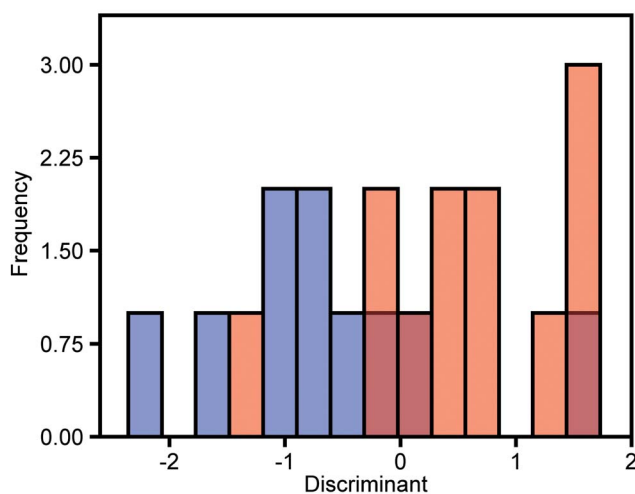


Figure 4. Histogram of discriminant projection values for reported measurable specimens of *Qilianotryma* and *Euroatrypa* (Table 1). The cutoff point is set to zero. Blue, pink, and red zones represent *Qilianotryma*, *Euroatrypa*, and the mixture of two genera, respectively.

Description.—Shell moderate in size, dorsibiconvex, elliptical transverse to subpentagonal in outline, about 70–80% as long as wide, and 45–67% as thick as wide (Fig. 5; Table 1). Anterior commissure uniplicate. Hinge line wide and astrophic, about four-fifths as long as shell width. Cardinal extremities rounded. Radial ornament finely and evenly multicostellate with 20–24 costellae on fold and sulcus and 31–44 costellae on lateral flanks; 5–6 costellae per 3 mm in anterior commissure of adult specimens (Fig. 5.1, 5.2).

Ventral valve slightly convex, with the maximum height at one-third length from beak (Fig. 5.5, 5.10). Beak incurved and pointed, apsacline interarea with open delthyrium. Ventral sulcus originating from the beak, becoming prominent and wide anteriorly (Fig. 5.2, 5.7). Semioval tongue-shaped sulcus taking up one-half to three-fifths of the shell width.

Dorsal valve moderately to strongly convex, with maximum height at two-thirds length from the beak (Fig. 5.5, 5.10). Median fold originating from the beak and forming a uniplicate commissure at anterior. Lateral furrows very weak, originating from the beak (Fig. 5.8).

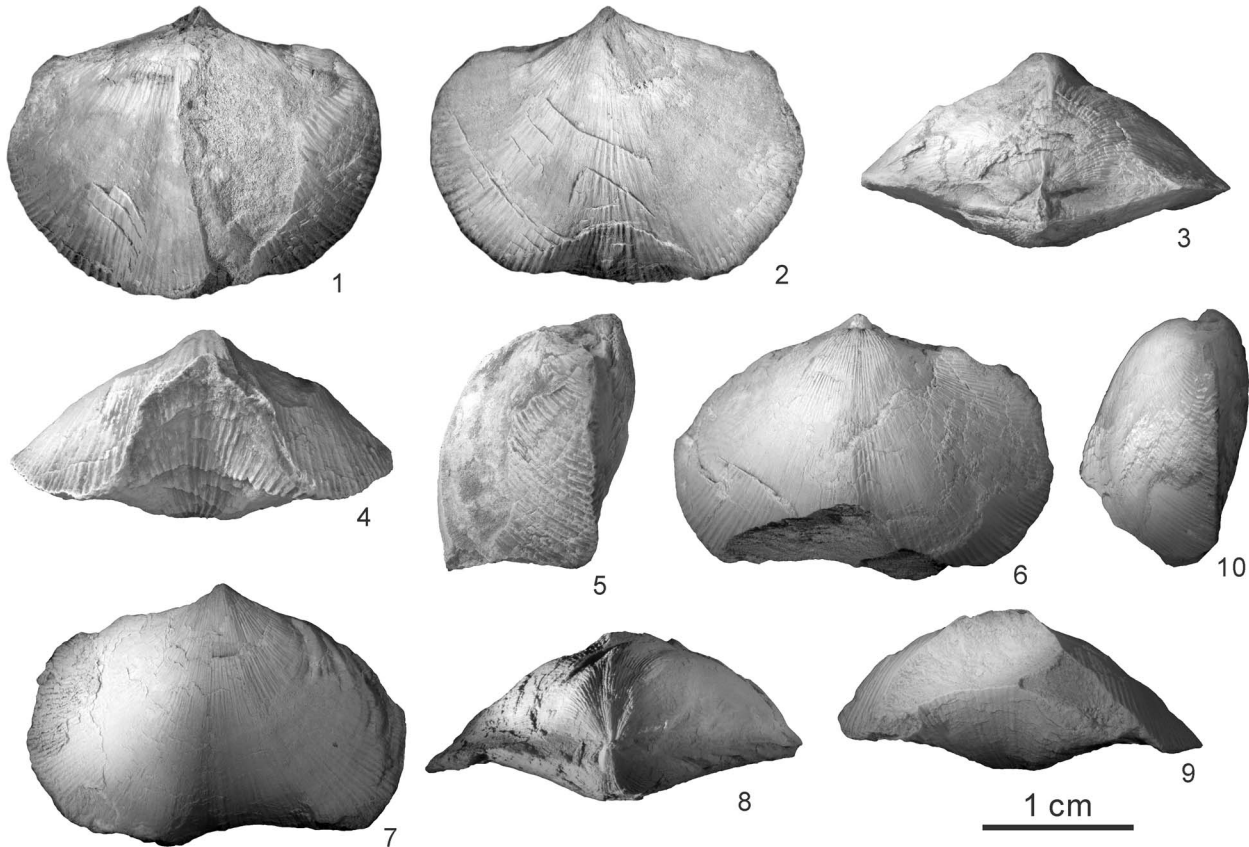


Figure 5. Two specimens of *Qilianotryma suspectum* (Popov in Nikiforova et al., 1982) from the upper part of the Shiyuhe Formation at Yaziwo section, Xichuan County, southwestern Henan Province, central China. (1–5) Specimen NIGP 173727: (1) dorsal view; (2) ventral view; (3) posterior view; (4) anterior view; (5) lateral view. (6–10) Specimen NIGP 173728: (6) dorsal view; (7) ventral view; (8) posterior view; (9) anterior view; (10) lateral view. Scale bar = 1 cm.

Teeth simple and strong in ventral valve (Fig. 6, 1.2–1.9). Dental plates thin (Fig. 6, 1.2–2.05), slightly diverging dorsally, and thinning toward the anterior (Fig. 6, 1.2–2.05). Dental cavities subtriangular (Fig. 6, 1.5–1.8) to ellipsoid (Fig. 6, 2.05) in transverse sections. Delthyrial cavity wide, taking up one-sixth of the shell width and one-third of shell depth.

Socket plates strong in dorsal valve. Crural bases long and weak (Fig. 6, 1.8–2.0). Ventral median ridge with a pair of weak oblique submedian ridges present in dorsal valve. Spiralia delicate, with up to seven whorls (Fig. 6, 5.1–9.1). Jugal processes short, located ventroposteriorly (Fig. 6, 2.7). Muscle scars poorly impressed.

Materials.—Two conjoined shells. Specimens NIGP 173727 and NIGP 173728 are figured in Figure 5. Internal morphology of specimen NIGP 173728 is illustrated in Figure 6.

Remarks.—This species differs from the type species, *Qilianotryma mirabile* Xu in Jin et al., 1979, in its larger size, less-elliptical outline, and more-dorsibiconvex lateral profile with lateral furrows on the dorsal valve. *Qilianotryma suspectum* from Chu-Ili, Kazakhstan, differs from this species in having 16–20 costellae on fold and sulcus and

more-prominent lateral plications on ventral valves (Popov et al., 1999). *Euroatrypa kolymica* Oradovskaya in Nikiforova et al., 1982 is smaller, equally biconvex in lateral profile, and has a stronger rectangular anterior commissure, taking up two-thirds of shell length and width. *Euroatrypa tajmyrica* Nikiforova in Nikiforova et al., 1982 is more ventribiconvex in some junior shells, with a prominent carination in the ventral umbonal region. The dorsal fold and ventral sulcus are weaker without any lateral furrows or plications and take up four-fifths of the width and two-thirds of the depth of the shell. *Qilianotryma* cf. *Q. suspectum* Popov and Cocks, 2021 has a less-elevated but wider dorsal fold compared with the specimens in this study.

Paleobiogeographic implications

Qilianotryma was first described from Qilian Mountains, Northwest China (Xu in Jin et al., 1979) located on the northern Tibet Plateau and regarded as a part of the Qaidam terrane in the Late Ordovician. The Qaidam terrane was inferred to have been close to the Lhasa (or Qiangtang) terrane in the midlatitudes off the margin of western Gondwana and the neighboring South China paleoplate and Kazakh terranes during the Late Ordovician. However, the precise paleogeographic location of the Qaidam terrane is still uncertain due to poor paleomagnetic

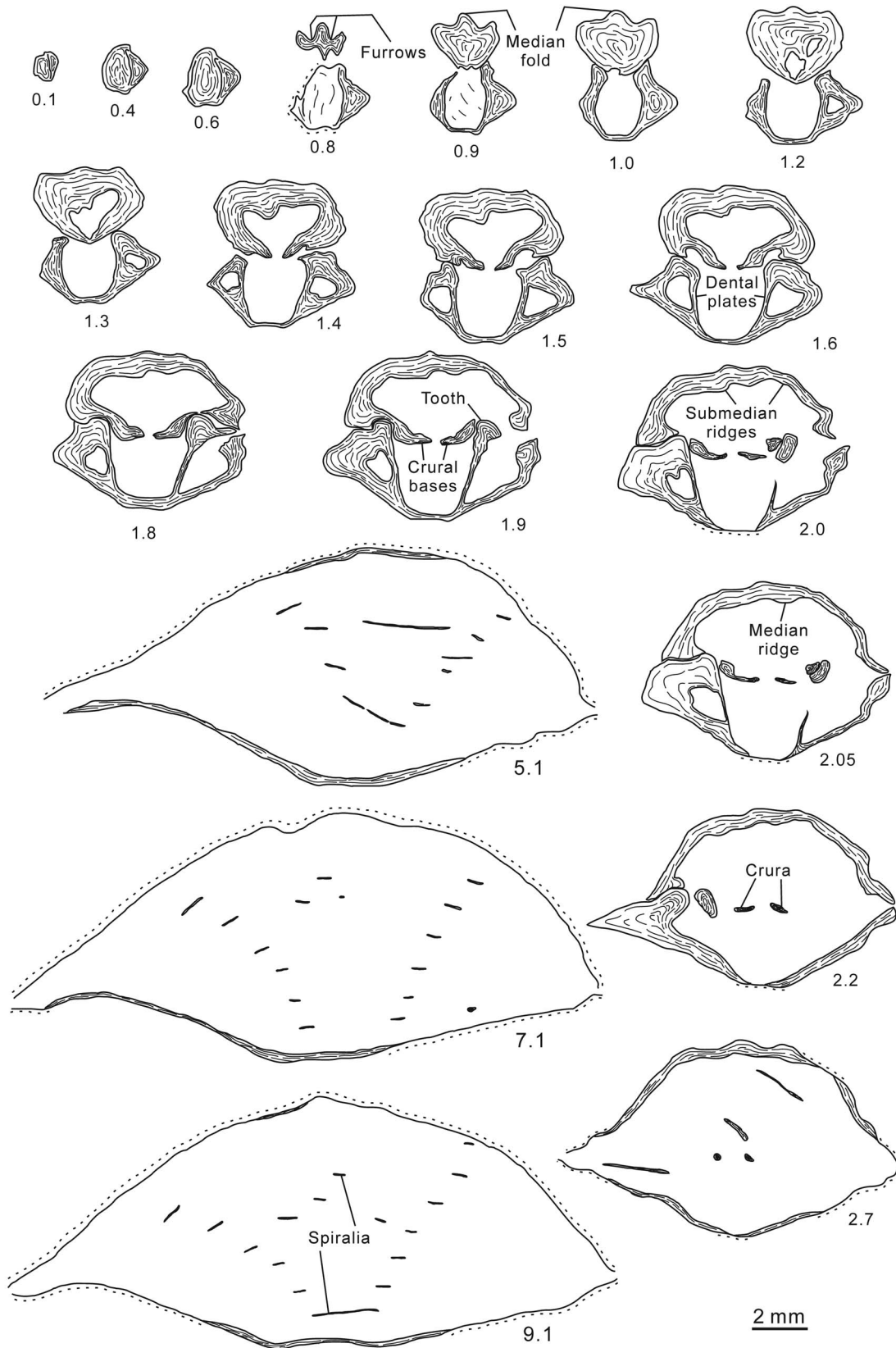


Figure 6. Sketches of internal structures of brachiopod *Qilianotryma suspectum* (Popov in Nikiforova et al., 1982) from the upper part of the Shiyanhe Formation at Yaziwu section, Xichuan County, southwestern Henan Province, central China. Numbers below each sketch indicate the distance, in millimeters, of each section from the posterior of the shell. One spiralia on the right is broken and likely displaced from its position during life inside the shell. The catalog number of the studied cellulose acetate peels is NIGP 173728. Scale bar = 2 mm.

coverage. Recent studies reported the discoveries of Middle–Late Ordovician volcanic rocks in the Halahu of this region, perhaps indicating an active margin (Li et al., 2019, 2020).

Qilianotryma is known from a brachiopod fauna in the Koumenzi Formation of this region. This fauna consists of *Altaethyrella*, *Bokorthis*, *Eospirigerina*, *Liostrongia*, ? *Mimella*, *Porambonites*, *Ptychoglyptus*, *Qilianotryma*, *Sowerbyella*, *Strophomena*, *Sulcatospira*, and *Triplesia* (Xu in Jin et al., 1979; Rong et al., 2017), indicating a shallow-water, mid-shelf environmental setting (Rong et al., 2017).

Outside China, *Qilianotryma* is known from the Chu-Ili, Boshchekul, and Chingiz-Tarbagatai terranes of Kazakhstan (Fig. 7; Nikiforova et al., 1982; Popov et al., 1999; Nikitin et al., 2006; Popov and Cocks, 2006, 2014, 2021). *Qilianotryma* sp. was noted from Akdombak Formation (upper Katian) of Chingiz, Kazakhstan (Popov and Cocks, 2014). *Qilianotryma* cf. *Q. suspectum* (Popov in Nikiforova et al., 1982) is known from an unnamed formation (early to mid-Katian) of Chu-Ili, Kazakhstan (Popov and Cocks, 2021). *Qilianotryma suspectum* has a wide distribution compared with other species. It has been noted in the *Platymena*–*Strophomena*, *Strophomena*–*Christiania*, *Metambonites*–*Plectrothis*, and *Parastrophina*–*Kellerella* associations in the Akkol Member, Dulankara Formation, Chu-Ili of Kazakhstan (Popov and Cocks, 2006) and Odak of Kazakhstan (Nikitin et al., 2006). Brachiopod fauna in the Shiyanhe Formation in this study is also characteristic of *Altaethyrella* and

Schachriomonia, showing a faunal similarity with those in Kazakhstan.

Altaethyrella is the most widely spread genus in the faunas where *Qilianotryma* was found. These faunas were named *Altaethyrella* Fauna (Rong and Zhan, 2004), which flourished mainly in the well-oxygenated shallow-water marine setting with high faunal richness and diversity. *Altaethyrella* Fauna has been known to distribute in different paleoplates or terranes of the Russian Altai Mountains, Kyrgyzstan, Turkmenistan, Kazakhstan, South China, North China, and Northwest China (e.g., Severgina, 1978; Zhan and Li, 1998; Popov and Cocks, 2017; Rong et al., 2017; Sproat and Zhan, 2018). These localities are widely accepted to have been located in the tropical region west to Gondwana during the Late Ordovician (e.g., Chen et al., 2013; Harper et al., 2013; Popov and Cocks, 2017; Torsvik and Cocks, 2017).

The limited geographic range of *Qilianotryma* reaffirms that Chu-Ili, Boshchekul, and Chingiz-Tarbagatai terranes of Kazakhstan, Qaidam terrane of Northwest China, and South China Paleoplate were located close to each other. The co-occurrence of *Qilianotryma suspectum* in Chu-Ili terrane and South China matches the recent paleogeographic reconstruction (Popov and Cocks, 2017), supporting the interpretation that Chu-Ili and South China were adjacent to each other during the Late Ordovician. The relationship to these plates will become increasingly clear as more of the shallow-water brachiopod fauna of these plates is documented and described.

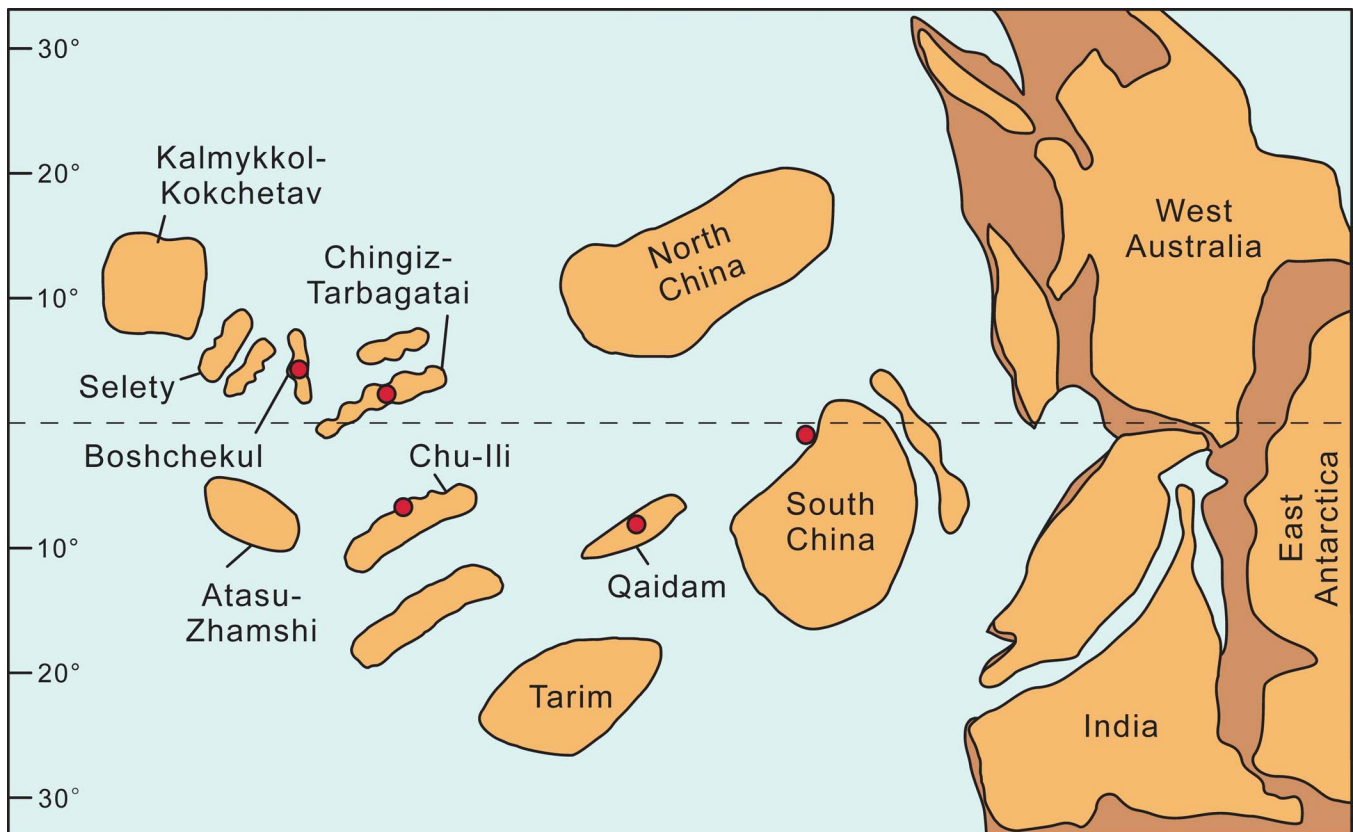


Figure 7. The distribution of *Qilianotryma* in the tropical region west to Gondwana during the Late Ordovician. Paleogeographical map is modified from Popov and Cocks, 2017. The individual localities of *Qilianotryma* are from Rukavishnikov, 1956, Jin et al., 1979, Nikiforova et al., 1982, Popov et al., 1999, Nikitin et al., 2006, and Popov and Cocks, 2006.

Evolutionary significance

Qilianotryma, like many atrypides in these regions, belongs to the subfamily Spirigerininae Rzhonsnitskaia, 1974. Brachiopods in this subfamily lack frills, have fewer whorls in the spiralia, and are typically more equally biconvex than later atrypides in the Silurian and Devonian (e.g., Copper, 1967, 1977, 1978); they also possess jugal processes rather than a solid jugum or jugal plates. Almost all *Qilianotryma* are Late Ordovician in age, with only one species questionably assigned to *Qilianotryma* from the Silurian (Baarli, 2021). *Qilianotryma? sigridi* Baarli, 2021 was collected from Padda and Leangen members of the Solvik Formation (Aeronian, Silurian) in Norway (Baltica; Baarli, 2021) and is similar to the type species of *Qilianotryma* in external morphology but distinct in some key diagnostic characters (e.g., medium-coarse ribs, fibrous crura, and the presence of a cardinal process). No definitive *Qilianotryma* are known to have survived the first pulse of the End-Ordovician Mass Extinction.

Beitaia Rong, Xu, and Yang, 1974 from the upper Rhuddanian and Aeronian of Llandovery, Silurian in South China, and western Tarim (Rong et al., 2017) may represent the successor to *Qilianotryma*. This genus is similar to *Qilianotryma* in having fine and continuous costellate ornamentation, dorsibiconvex lateral profile in adult shells, and the presence of jugal process in the transverse section. *Beitaia* differs from *Qilianotryma* in its subquadrate outline, shorter hinge line, ventral sulcus originated from half of the shell, and distinct concentric filae on the full shell.

Qilianotryma is very different from the atrypides that dominated other paleoequatorial plates during the Late Ordovician. The most common and well known of Late Ordovician atrypides from Laurentia are the Anazygidina. *Anazyga* and *Zygospira* appear to look similar to their counterparts from Asia, but their external morphologies differ in terms of their reversed fold and sulcus and the structure of the spiralia compared with most atrypides from mid- and East Asia (Copper, 1977; Sproat and McLeod, 2023). Most shallow-marine North American atrypides possess a jugum rather than separate jugal processes typical of Asian lineages, indicating that they likely evolved along different evolutionary pathways (see Popov et al., 1999; Baarli et al., 2022). The evolutionary pressures driving the divergence of these forms remain uncertain, but these differences hint at different evolutionary pressures acting on brachiopods in each of these equatorial zones.

Conclusions

This first report of *Qilianotryma suspectum* (Popov in Nikiforova et al., 1982) from the Shiyanhe Formation of Henan Province, central China, significantly expands the geographical range of the genus. The rephotograph of type material and discriminant analysis support that *Qilianotryma* and broadly similar *Euroatrypa* can be differentiated in terms of external morphology, the length of the hinge line, and the development of the median fold and sulcus. The presence of *Qilianotryma* in shallow-marine communities across the South China paleo-plate, Qaidam terrane, and several Kazakh terranes (i.e., Chu-Ili, Boshchekul, and Chingiz-Tarbagatai) suggests that the

low-latitude brachiopod province once thought to stretch across these plates and North America may not be as homogeneous as once thought although further analysis of other lineages is needed to confirm this. Perhaps this provincialism was a consequence of either underlying paleogeographic factors or the evolution of different novel characteristics in brachiopods during the Ordovician Radiation.

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Declaration of competing interests

The authors declare none.

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