

SPECIAL ISSUE ARTICLE

Malayacyclus gen. nov., the first Southeast Asian Cyclida (Crustacea) from the Early Carboniferous of Terengganu, Malaysia

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Malayacyclus terengganuensis, a new genus and species of the Cyclida (Crustacea), is reported from the Early Carboniferous (Visean) of Terengganu, eastern Peninsular Malaysia (East Malaya Block). The new genus possesses diagnostic features of both families Cyclidae and Americlidae. Plus, it develops the trifurcate posterior spines: a unique morphology that was not previously known for any cyclidan genera. Based on the possession of an anterior rostrum and optic notches, it is tentatively included in the Americlidae. This represents the first find of the Cyclida from Southeast Asia and the second from the Carboniferous of Asia (eastern Tethys).

KEYWORDS

Carboniferous, Crustacea, Cyclida, Malaysia, Southeast Asia, Terengganu, Tethys

1 | INTRODUCTION

The Cyclida is an enigmatic crustacean group that existed from the Carboniferous to the Cretaceous. It has been nearly two centuries since the first Cyclida, *Agnostus? radialis* [now the type species of *Cyclus*], was reported by Phillips (1836) but erroneously as a species of an agnostid trilobite. de Koninck (1841) disagreed with the view that this animal was a trilobite and erected the genus *Cyclus*, even though he was unable to suggest its clear taxonomic position. von Meyer (1838) also considered a cyclidan fossil as a trilobite and named it *Limulus agnotus* [now the type species of the cyclidan genus *Halicyné*]. Note that *Limulus* is a genus of

horseshoe crab today. von Meyer (1844) concluded that it belonged to a unique crustacean group. During the early establishment of cyclidan taxonomy, most species were placed in *Cyclus* de Koninck, 1841, and some in *Halicyné* von Meyer, 1847. In the latest revisions of the order Cyclida (see Feldmann & Schweitzer, 2019; Mychko & Alekseev, 2018; Schweitzer, Mychko, & Feldmann, 2020), a total of 26 genera and 52 species were reviewed and grouped into six families.

In this article, we describe a new Carboniferous genus and species of the family Americlidae from the East Malaya Block of Terengganu, Peninsular Malaysia. This is the first record of the Cyclida for Southeast Asia and the second for the Carboniferous of Asia. The new

genus provides additional morphological information for the Americlidae and extends the palaeobiogeographic distributions of cyclidan animals in the eastern Tethys (Asian Tethys).

2 | REGIONAL GEOLOGY AND AGE

Peninsular Malaysia is comprised of two tectonic blocks, namely, the West Malaya Block (=Sibumasu) and the East Malaya Block (Figure 1a). Note that the Sibumasu Block of Metcalfe (1984) is a junior synonym of the West Malaya Block of Stauffer (1974) and, hence, is invalid, as there is no difference in concepts between the two names (see the fuller descriptions of this terrane under the name of the West Malaya Block given by Metcalfe, 1983).

The East Malaya Block is believed to be a Permo-Triassic volcanic arc (the southern equivalent of the Sukhothai Arc in Thailand) (see, e.g., Ng et al., 2015; Sone et al., 2012; Sone & Metcalfe, 2008; Stauffer, 1974); nevertheless, Carboniferous arc magmatism is not evident in East Malaya. Carboniferous plant deposits are found in the eastern part of the East Malaya Block, as they include the Kuantan flora, which has a typical affinity to the Euramerican flora (e.g., Laveine & Hussin, 2003). Similar Carboniferous plant deposits are found in the Indochina Block in Thailand (see Asama et al., 1975). Carboniferous marine sediments are widely distributed in the eastern part of the East Malaya Block (see Gobbett, 1973; Lee, 2009; Metcalfe, 1983; Figure 1b). They are dominantly siliciclastics, and some are deepwater and turbiditic in facies (e.g., the Mersing Beds in Johor), with the exception of the shallow-marine Panching Limestone in Pahang. We presume that the East Malaya Block was on the (offshore) margin of the Indochina Block and was located within the eastern Tethys Sea, not a part of Gondwana, during the Carboniferous.

The Panching Limestone is known to consist of four limestone hills, namely, Bukit Charas, Bukit Sagu, Bukit Tenggek, and Bukit Panching: they are massive, partly recrystallized limestones and are richly fossiliferous with various shallow-marine faunules from warm reefal environments (Fontaine, Ibrahim, & Vachard, 2003; Metcalfe, Idris, & Tan, 1980). The Panching Limestone overlies the siliciclastic Charu Formation of a Visean age (Metcalfe et al., 1980; Muir-Wood, 1948; Yanagida, 1971).

The geological age of the Panching Limestone is a matter of contention because the suggested fossil ages differ from author to author and straddle across the mid-Carboniferous boundary. Muir-Wood (1948) initially examined the brachiopods and suggested a late Visean age, based on the correlation with the European fauna. This late Visean age was supported with the foraminifers by Mamet and Saurin (1970) and by Ozawa (1976) based on the fusulinoid assemblage dominated by species of *Eostaffella*. However, Igo and Koike (1968), Metcalfe (1980), and Metcalfe et al. (1980) suggested a younger age of the Namurian A (Bashkirian, basal Pennsylvanian) for the Panching Limestone. This was based on the occurrence of a conodont assemblage that those authors interpreted to include the basal Bashkirian index species *Declinognathodus noduliferus* (Ellison & Graves).

Contrariwise, Fontaine et al. (2003) questioned the reliability of the conodont age. They suggested a late Serpukhovian age for the Panching Limestone fauna, based on the occurrence of the rugose

corals *Fomichevella*, *Dibunophyllum*, and *Siphonophyllum*, and the heterocoral *Hexaphyllia*, along with the foraminifers. This criticism seems to be reasonable since the occurrence of the Heterocorallia is confined to pre-Bashkirian in age.

Chen and Shi (2003, p. 123) reviewed the Panching Limestone brachiopod assemblages of Metcalfe et al. (1980) and Muir-Wood (1948) and interpreted that there are some 45 species in 32 genera in total. They particularly compared the assemblage of Metcalfe et al. (1980), which was dominated by spiriferides, with the analogous Serpukhovian brachiopods of North America. We favour a late Serpukhovian age for the Panching Limestone fauna.

In Terengganu, the occurrence of abundant Carboniferous marine fossils has been known from siliciclastic rock layers exposed in Bukit Buchu (bukit for a hill), where the new cyclidan fossils were found (Figure 1c). Currently, there is no name for the Bukit Buchu sedimentary sequence: it is here informally called the Bukit Buchu beds. Idris and Zaki (1986) reported a small suite of macrofossils from Bukit Buchu, as the brachiopods *Brachythyrida strangwaysi* and *Chonetinella* sp., the bivalve *Edmondia* sp., the bryozoan *Fenestella retiformes*, the crinoid *Potereocrinus* sp. and the trilobite *Paladin ophistops* Kobayashi and Hamada. This fauna has never been described in detail; hence, the reliable taxonomic statuses of these fossils are still pending (currently under reinvestigation).

We can preliminarily confirm that, based on our unpublished trilobite samples from Bukit Buchu, a species of *Linguaphillipsia* Stubblefield, 1948, occurs together with the new cyclidan. It develops a tongue-shaped, anteriorly tapering, elongated glabella that extends over part of the anterior border, characteristic of *Linguaphillipsia*. Its pygidium also develops a broad marginal border with a distinct border furrow, typical for the genus. The above-mentioned trilobite of Idris and Zaki (1986) was represented only by the poorly preserved pygidia; thus, it seems difficult to assure its identification to a species of *Paladin*. The type species of *Linguaphillipsia*, *Linguaphillipsia terapaiensis* Stubblefield, 1948, was originally reported from the Charu Formation (Visean) in Pahang. This infers a possible correlation of the Bukit Buchu beds with the Charu Formation. Species of *Linguaphillipsia* are confined to the Tournaisian and Visean (Early Carboniferous) of Eurasia and Australia (see a review in Vanderlaan & Ebach, 2015). On balance, we tentatively consider the Bukit Buchu fossil assemblage including the new cyclidans to be Visean in age.

3 | SAMPLING LOCALITIES

The cyclidan fossil samples were collected from two exposures, namely locality C and locality D, on the eastern side of Bukit Buchu, Terengganu, Peninsular Malaysia (Figure 1c). Holotype UMF10942 was collected in locality C (05°26.459'N, 103°02.791'E) in the middle of the eastern hillside. Fossil-bearing beds consist of dark grey laminated siltstone (Figure 2a). These fossiliferous rock layers are overlain by cross-bedded sandstone and underlain by interbedded sandstone and shale. Complex, spirally coiled trace fossils of *Zoophycos* in siltstone and normal graded bedding in sandstone indicate stratigraphically upward orientation to the east. Locality D (05°26.848'N, 103°02.619'E) is on the northeastern part of the hill, which exposes dark grey mudstone/shale (Figure 2b). Two

paratypes UMF10943 and UMF10944 were collected from the mudstone in locality D. The bedding at the two localities strikes northwest and dips steeply to the east or almost vertically. The cyclidan fossils were preserved with many other marine invertebrates, such as brachiopods, trilobites, bryozoans, and crinoids, but bivalves are rare.

In addition, the above-mentioned fossil locality of Idris and Zaki (1986) is in between localities C and D (Figure 1c). Its stratigraphic level is about the same as that of locality C and possibly be a little higher than that of locality D. All these fossil-bearing layers occur in the eastern side of Bukit Buchu. That is, they are stratigraphically in

the upper(most) part of the entire succession of the Bukit Buchu beds, since the younging direction of the beds is consistently from the west to the east, with an average strike and dip of $340^{\circ}/80^{\circ}\text{E}$.

4 | SYSTEMATIC PALAEOLOGY

The fossil specimens are registered with numbers prefixed UMF and are deposited in the Department of Geology, University of Malaya, Kuala Lumpur. Here, the morphological terminology and systematic

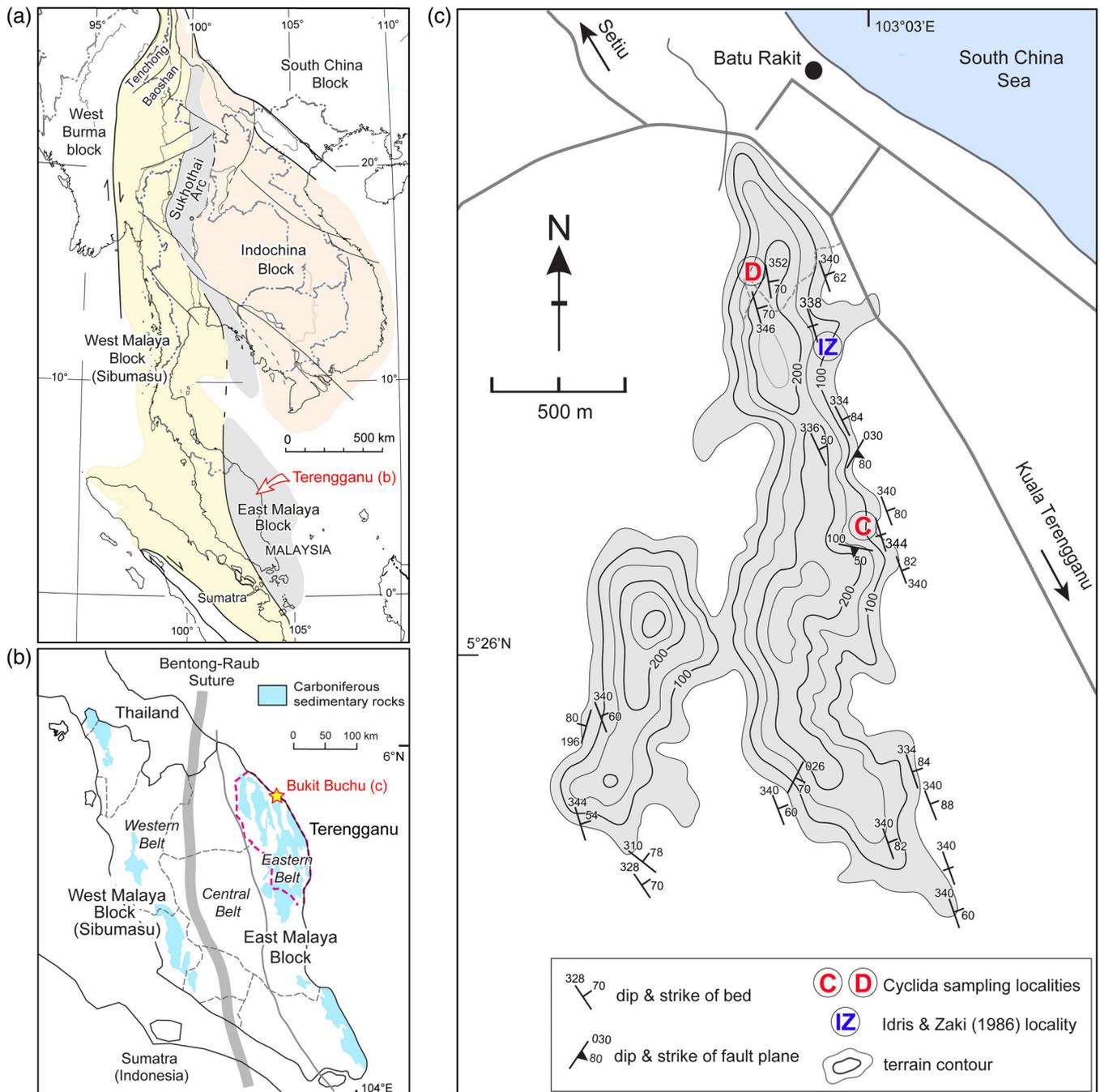


FIGURE 1 (a) Tectonic division map of Southeast Asia (in part), showing the location of Terengganu in eastern Peninsular Malaysia (East Malaya Block) (modified after Sone, Metcalfe, & Chaodumrong, 2012, fig. 1). (b) Map of Peninsular Malaysia, showing the state of Terengganu, with the local structural divisions of the Western, Central and Eastern belts and the distributions of Carboniferous sediments. (c) Simplified geological map of Bukit Buchu in Terengganu, indicating fossil localities C and D [Colour figure can be viewed at wileyonlinelibrary.com]

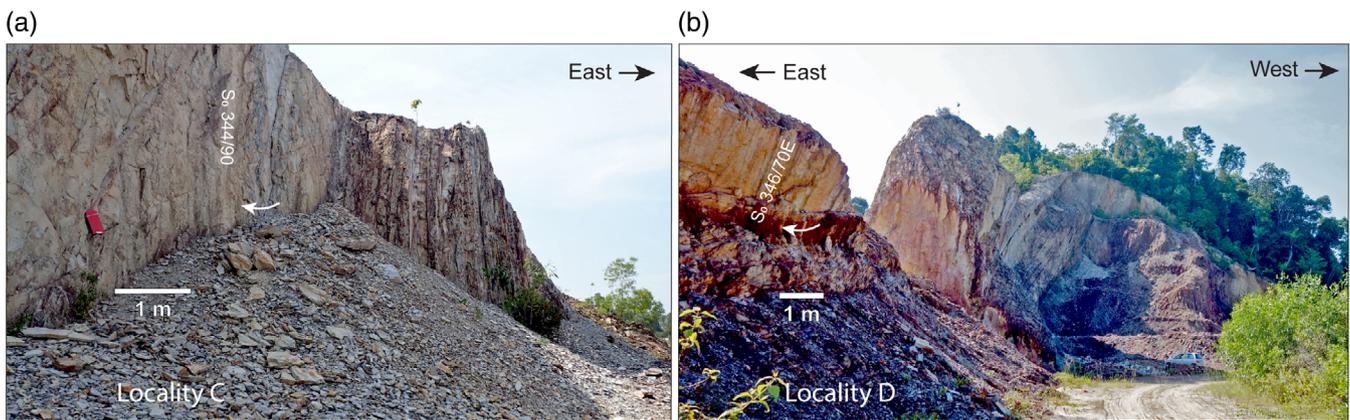


FIGURE 2 Outcrop photographs of the sampling localities in Bukit Buchu, Terengganu. (a) Locality C, showing the fossil beds of laminated siltstone. (b) Locality D, showing the fossil beds of dark grey mudstone. White arrows indicating the sampling points [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

classification follow Feldmann and Schweitzer (2019) and Schweitzer et al. (2020), respectively.

Superclass Crustacea Pennant, 1777

Class Multicrustacea Regier et al., 2010

Order Cyclida Schram, Vonk, & Hof, 1997

Family Ameriidae Dzik, 2008

Included genera. *Ameriidae* Dzik, 2008; *Brittanidae* Schweitzer et al., 2020; *Dzikidae* Schweitzer et al., 2020.

Diagnosis. As in Schweitzer et al. (2020, p. 264).

Genus *Malayacyclus* Tang, Mychko, Feldmann, and Schweitzer gen. nov.

Etymology. After Malaya, an older name for Peninsular Malaysia or West Malaysia and *Cyclidae*, the type genus of the Cyclidae.

Type species. *Malayacyclus terengganuensis* sp. nov., by monotypy.

Diagnosis. Carapace large, bilaterally symmetrical; rostrum anteriorly extended and optical notches placed at the rostral extremities; anterior regions well-defined, with a pair of strong median concentric keels extended posteriorly; marginal rim wide, with three posterior spines developed at the posterior margin.

Remarks. *Malayacyclus* gen. nov. displays unique morphological combinations of characteristics of the two families Ameriidae and Cyclidae. The well-developed anteriorly extended rostral lobes, optical notches and a flattened carapace with a broad marginal rim are typical characteristics of the Ameriidae. On the other hand, the well-developed anterior lobes and strong median concentric keels suggest affinities to the Cyclidae. A morphospace analysis—inserting *Malayacyclus* into the character matrix used by Schweitzer et al. (2020) and examined using PCO in PAST 3.25—recovers the new genus to be intermediate between Ameriidae and Cyclidae (Figure 3). Based on the possession of a flattened carapace profile and a well-developed rostrum and optical notches, we included *Malayacyclus* among the Ameriidae.

The family Ameriidae now includes the three other Carboniferous genera *Ameriidae* Dzik, 2008, *Brittanidae* Schweitzer et al., 2020

and *Dzikidae* Schweitzer et al., 2020. *Malayacyclus* gen. nov. resembles *Ameriidae* on the anteriorly extended rostral lobe and optical notches, dense tubercles on the carapace surface and the presence of a posterior axial keel. The new genus also resembles *Brittanidae* in sharing a flattened carapace, a well-developed wide marginal rim, and a rostrum extending beyond the carapace with optical notches on the rostral extremities. *Ameriidae* and *Brittanidae* also possess posterior notches but only *Malayacyclus* developed three posterior spines adjacent to the notches. *Malayacyclus* is similar to *Dzikidae* in having a flattened carapace and an anteriorly extended rostrum. Nevertheless, *Dzikidae* can be differentiated by having a broader marginal rim and an absence of posterior notches or spines.

Occurrence. Visean (Early Carboniferous) of Terengganu, Peninsular Malaysia.

Malayacyclus terengganuensis Tang, Mychko, Feldmann, and Schweitzer gen. et sp. nov.

(Figures 4 and 5)

Etymology. Named after the state of Terengganu, Malaysia, where the new species was found.

Material. Holotype UMF10942, a complete carapace from locality C; paratypes UMF10943 and UMF10944, slightly deformed carapaces, both from locality D (Table 1 for measurements).

Diagnosis. Carapace flattened to slightly vaulted in profile, bilaterally symmetrical in outline; surface heavily granulated; rostrum well-developed, extended anteriorly; optical notches placed at the rostral extremities. Anterior lobes well-developed and clearly defined; median groove defined by a pair of inner lyrate keels and an inflated posterior axial lobe. Posteriorly, the branchial regions vaulted, a pair of strong median concentric keels posteriorly extended; marginal rim broad and posterior margin with three posterior spines.

Description. The carapace is subcircular in shape, bilaterally symmetrical, wider than long (width/length = 1.25 for holotype) as the widest at the midpoint. It is gently vaulted, as the highest at the mid-length in cross-section. A rostrum is extended anteriorly. At the rostral

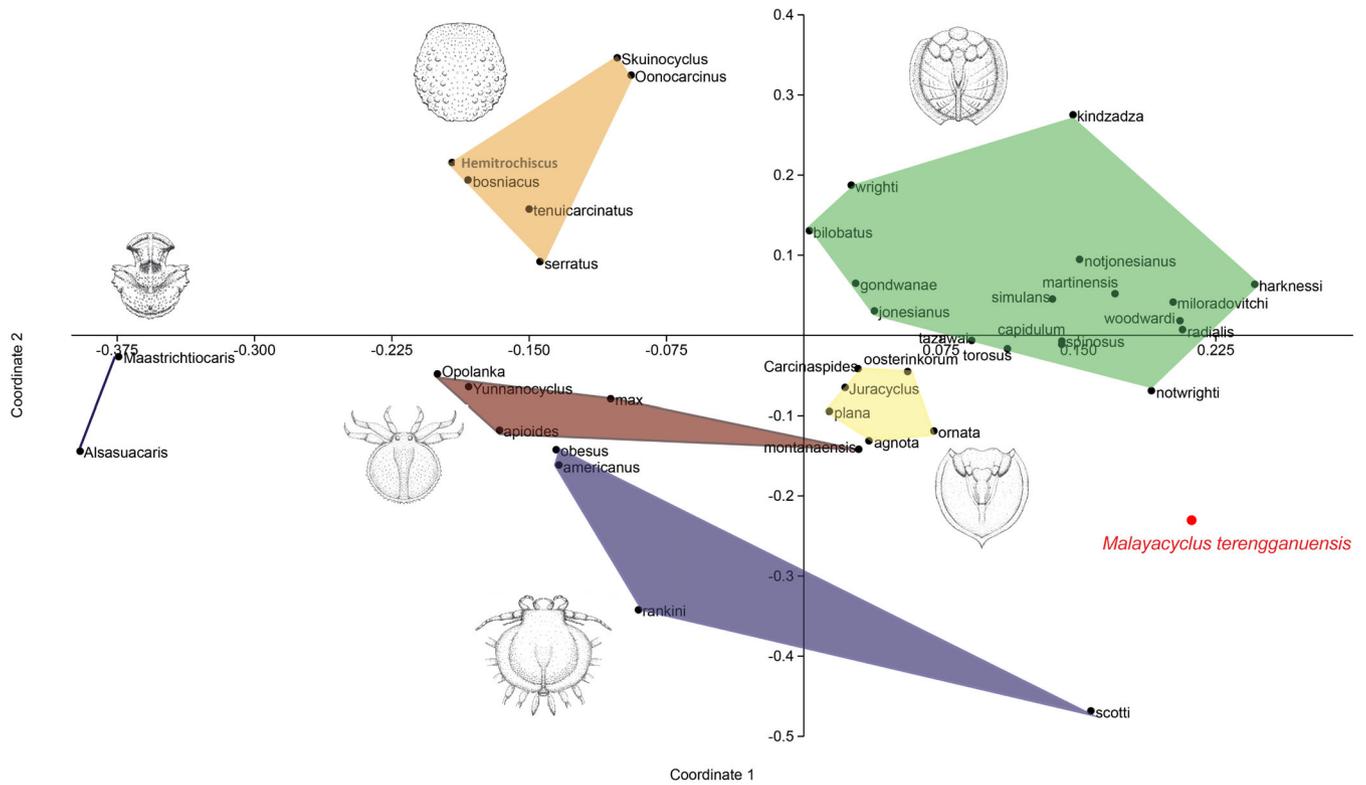


FIGURE 3 PCO morphospace analysis (PAST 3.25 of Hammer, Hammer, & Ryan, 2001), following the character matrix used by Schweitzer et al. (2020). *Malayacyclus terengganuensis* gen. et sp. nov. plotted with the red mark. The base diagram from Schweitzer et al. (2020, fig. 26) reproduced with permission of Schweizerbart science publishers (www.schweizerbart.de/journals/njgpa) [Colour figure can be viewed at wileyonlinelibrary.com]

extremities, the optic notches form concave re-entrants that are continuous to the marginal rim laterally. The marginal rim is wide, flattened to slightly depressed, not uniform in size and posteriorly narrower. Three posterior spines are developed as framing two posterior notches. The entire surface of the carapace is heavily granulated.

The anterior lobes are bilaterally symmetrical. The first axial lobe and two second axial lobes are lozenge-shaped, closely attached, elevated and appear as a large V-shaped lobe. The third axial lobe is broadly triangular. The first lateral lobe is a pair of rhomboid lobes attached at the lower edges of the second axial lobes, laterally at the same level as the first axial lobe. The first lateral lobe is connected to the median concentric keel, which extends posteriorly as ridges are covered by tubercles. The second lateral lobe is a pair of rounded pentagonal lobes adjacent to the first lateral lobe and the marginal rim. The third lateral lobe is a pair of the broad rectangular lobe, gently inflated. Two third lateral lobes and a third axial lobe define the rostrum.

The posterior axial lobe is rounded and arched anteriorly, tapered posteriorly, bounded on both sides by a pair of inner lyrate keels. Posterior parts of the posterior axial lobe and the inner lyrate keels are depressed, forming a median groove. The axial keel was elevated, uniform in width and extended towards the posterior margin. Outer branchial regions are large, elongated lobes, and raised; inner branchial regions are characterized by elongated lobes, strongly raised, and densely covered by large tubercles. A pair of prominent median concentric keels mark the boundaries between the outer and inner branchial

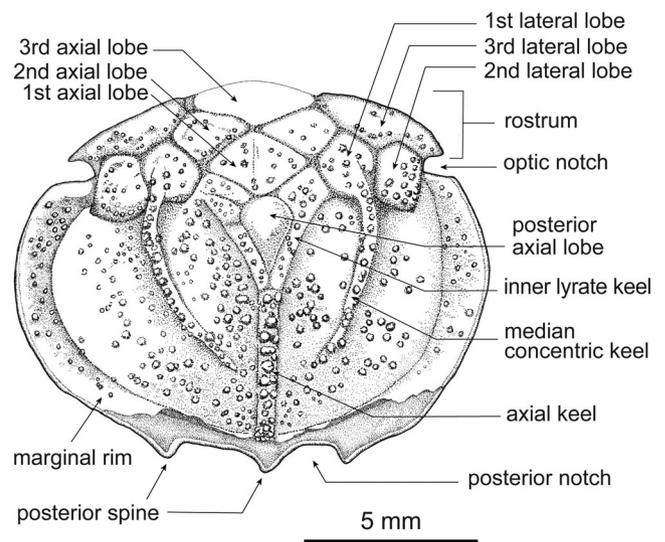


FIGURE 4 Line drawing of *Malayacyclus terengganuensis* gen. et sp. nov. (based on holotype UMF10942) with each morphology labelled

regions. The external mould of the carapace UMF10944 reveals the presence of an axial keel and median concentric keels (Figure 5d–e). The surface of the carapace is entirely ornamented with various sizes of granules. Three posterior spines are large and pointing.

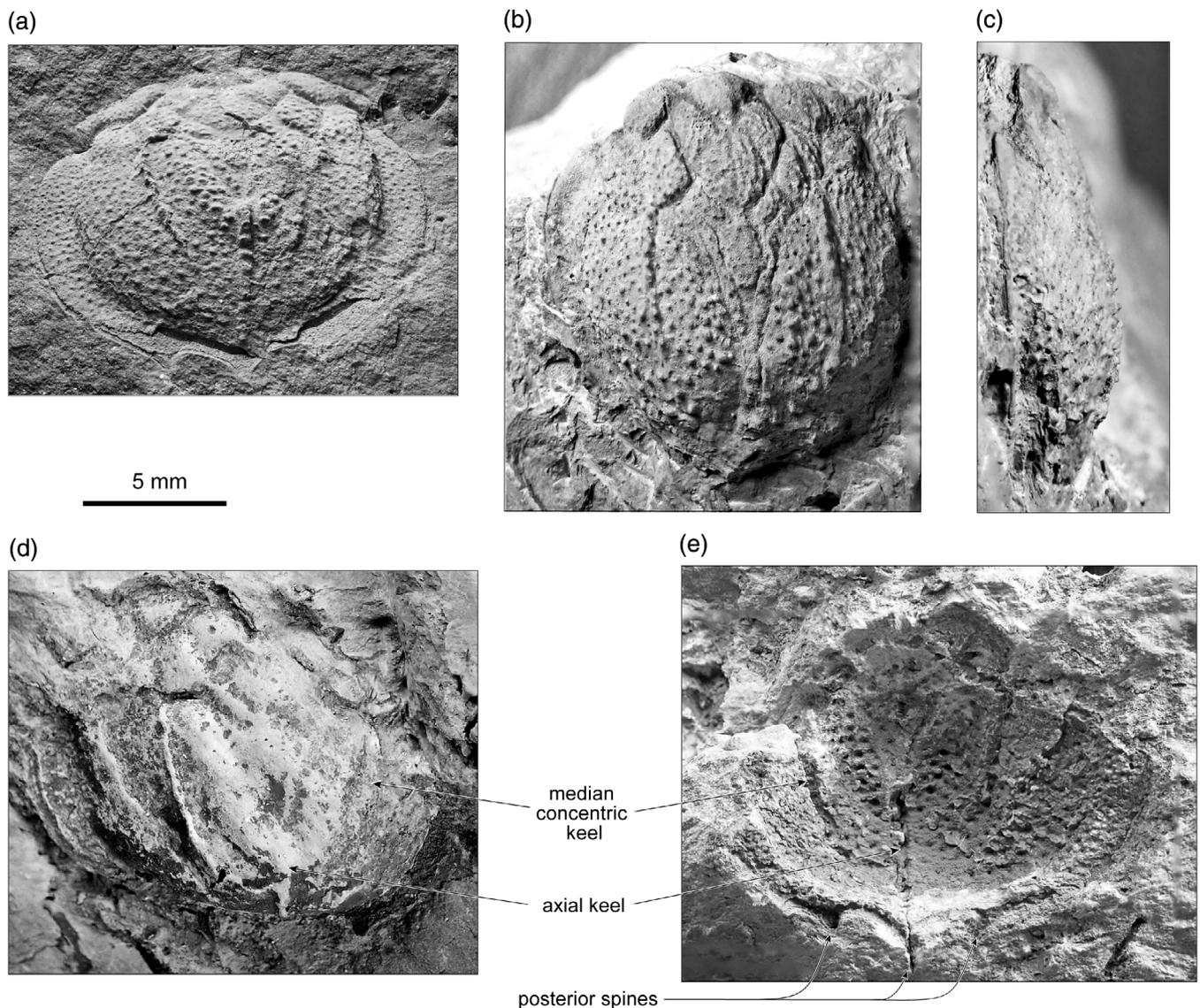


FIGURE 5 *Malayacyclus terengganuensis* gen. et sp. nov. (a) Holotype UMF10942 from locality C, carapace in dorsal view. (b,c) Paratype UMF10943 from locality D, carapace in dorsal view (b) and lateral view (c). (d,e) Paratype UMF10944 from locality D, exfoliated carapace in dorsal view (d) and external mould of the carapace (e)

TABLE 1 Measurements of the carapaces of the type specimens of *Malayacyclus terengganuensis* gen. et sp. nov. from Malaysia (in mm)

Specimen No.	Width	Length	Width/Length	Height
UMF10942 holotype	13.8	11	1.25	1
UMF10943 paratype	(15)	(14.5)	(1.03)	(4)
UMF10944 paratype	(14.3)	—	—	(4.5)

Note: Values in brackets based on the deformed specimens.

Remarks. *Malayacyclus terengganuensis* sp. nov. is comparable to *Americlus americanus* (Packard, 1885), the type species of *Americlus* from the Moscovian (Pennsylvanian) of North America, in having a flattened carapace and the well-developed axial keel. However, the rostrum and the anterior region of *A. americanus* are poorly bilobate, unlike the new species. *Americlus? packardi* (Rogers, 1902) [originally in *Cyclus*] from the Kasimovian (Pennsylvanian) of North America is

tentatively assigned to *Americlus*, the view shared with Schweitzer et al. (2020, p. 266). It has the granulated carapace with well-defined anterior lobes and is perhaps most closely comparable with the Malaysian species, although its possession of posterior spines is unknown.

Brittaniclus testudo (Peach, 1882) and *Brittaniclus rankini* (Woodward, 1869) from the Visean and Serpukhovian of Scotland, respectively, are among the earliest species of the Americlidae. Both

FIGURE 6 Total numbers of cyclidan species by family by geological time intervals. Data compiled from Schweitzer et al. (2020), plus a new Early Carboniferous species of the Americlidae in this report [Colour figure can be viewed at wileyonlinelibrary.com]

Period	Carboniferous			Permian			Triassic			Jurassic			Cretaceous	
Total species	27			5			21			1			3	
Family \ Epoch	Miss.	Penn.	Cis.	Gua.	Lop.	E	M	L	E	M	L	E	L	
Cyclidae	13	3	1											
Americlidae	3	5												
Schraminidae		3	1			3	2							
Hemitrochiscidae				2	1			6						
Halicynidae						2	6	1	1					
<i>incertae sedis</i>							1							
Alsasuacaridae												1	2	
Total species	16	11	2	2	1	5	9	7	1	0	0	1	2	

Early Carboniferous (Mississippian)

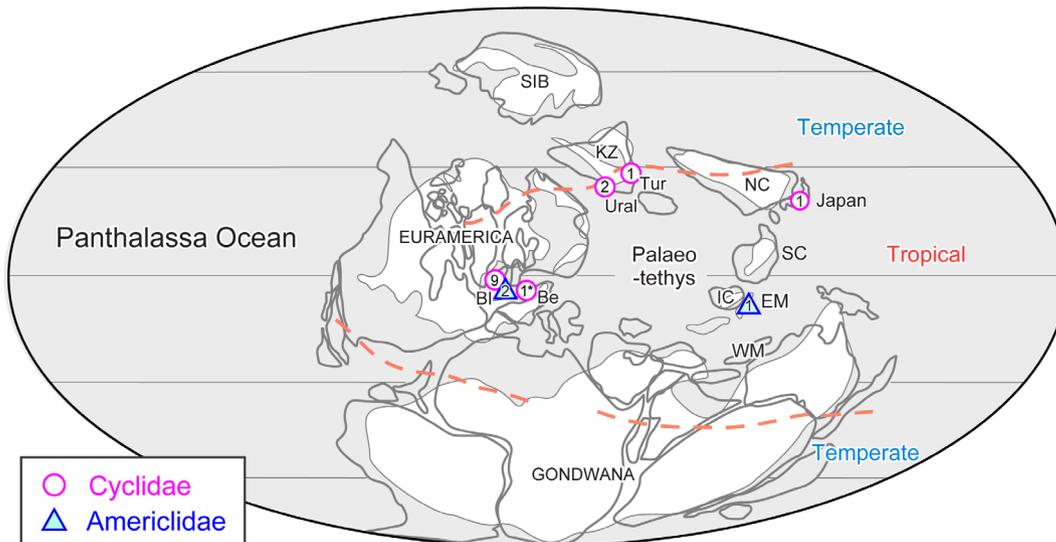


FIGURE 7 Early Carboniferous distributions of the Cyclidae and Americlidae plotted on the global palaeogeographical reconstruction map (modified after the Visean map of Qiao & Shen, 2014, fig. 3). Numbers inside each family's symbol represent the number of species that occurred in each palaeogeographical region (information from Schweitzer et al., 2020). *Cyclus radialis* was reported also from Belgium, besides the British Isles (see Schweitzer et al., 2020), and both occurrences are included in this figure (1* for the Belgian cyclid occurrence). Palaeoclimatic zonation was with dashed lines adopted from Map 10 of Boucot, Scotese, Chen, and Morley (2013). Be, Belgium; BI, British Isles for both Ireland and Great Britain; EM, East Malaya Block; IC, Indochina Block; KZ, Kazakhstan Block; NC, North China Block; SC, South China Block; SIB, Siberian Block; Tur, Turkestan Range, Tajikistan; Ural, Ural Mountains; WM, West Malaya Block (Sibumasu) [Colour figure can be viewed at wileyonlinelibrary.com]

species are clearly separable from the new species by lacking prominent posterior spines. *Brittanicus scotti* (Woodward, 1893) from the Moscovian of England is comparable on well-developed median concentric keels, axial keel, and posterior notches. Nevertheless, the anterior region and the rostrum of *B. scotti* are unlike those of *M. terengganuensis*. Note that these classic British species, formerly in *Cyclus* then in *Americlus*, have been re-transferred to the newly proposed *Brittanicus* by Schweitzer et al. (2020).

5 | EARLY CARBONIFEROUS CYCLIDA

Cyclidan crustaceans lived from the Carboniferous to the Cretaceous, and they have already reached the acme of their diversity during the Early Carboniferous (Mississippian), most likely in the Visean (Figure 6; Schweitzer et al., 2020). The family Cyclidae was the earliest

cyclidan group. Nine species are known from the Tournaisian–Visean limestones of the British Isles (Ireland and Great Britain) and Belgium. They are *Cyclus radialis*, *Ambocyclus simulans*, *Prolatocyclus martinensis*, *Carabicyclus wrighti*, *Litocyclus bilobatus*, *Litocyclus torosus*, *Litocyclus jonesianus*, *Uralocyclus harknessi*, and *Uralocyclus woodwardi*. Three other species of the Cyclidae, *Ambocyclus capidulum*, *Chernyshevine spinosus*, and *Prolatocyclus kindzadza*, are also known from the Mississippian of Russia and Tajikistan (Schweitzer et al., 2020). *Tazawacyclus tazawai* (Niko & Ibaraki, 2011) [originally in *Cyclus*] from the Serpukhovian of the Hida Gaian Belt, Japan, is the sole occurrence of Asian Cyclidae in the Carboniferous. The Cyclidae dominated with 81% of all the cyclidan diversity during the Mississippian time (13 out of 16 species in total) (Figure 6).

The family Americlidae was the second earliest group, as the three species, *Brittanicus rankini*, *Brittanicus testudo*, and *Malayacyclus terengganuensis* sp. nov., are now known from the Visean–

Serpukhovian interval of Scotland and Malaysia, respectively (Figure 6; Schweitzer et al., 2020). *M. terengganuensis* from the possible Visean of Malaysia now represents the first occurrence of Asian Americlidae.

The two Asian species *T. tazawai* and *M. terengganuensis* are the only examples of Carboniferous cyclidans in the eastern Tethys region (Figure 7). Note that Schweitzer et al. (2020, fig. 28) plotted *T. tazawai* to northern Gondwana, but this must be in error as the Hida Gaian Belt of Japan is supposed to have been located in the northeastern side of the Tethys Sea during the Carboniferous (e.g., Niko & Ibaraki, 2011). No cyclidan occurrence is yet confirmed in the Mississippian of North America: this is a puzzle. Its earliest appearance in North America is known to be the Bashkirian *Schramine montanaensis* (Schram, Boere, & Thomas, 2006) of the long-ranging family Schraminidae (see Schweitzer et al., 2020).

6 | SUMMARY

Malacyclus terengganuensis gen. et sp. nov. is reported from the possible Visean (middle Early Carboniferous) of Terengganu, eastern Peninsular Malaysia (East Malaya Block). The new genus is referred to as a member of the family Americlidae. Nevertheless, it possesses some characteristics of both Americlidae and Cyclidae, the two earliest groups of the Cyclida. Plus, it exhibits trifurcate posterior spines: a unique morphology that was not previously known for other cyclidan genera. This is the first record of the Cyclida for Southeast Asia, and it marks the second occurrence in the Carboniferous of Asia, only following the report of Niko and Ibaraki (2011) from Japan. The new find implies extended distributions of this rare crustacean group in the eastern Tethys Sea (Asian Tethys) during the Early Carboniferous.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/gj.4128>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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