

CAMBRIAN RHYNCHONELLIFORM NISUSIOID BRACHIOPODS: PHYLOGENY AND DISTRIBUTION

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Abstract: A comprehensive review and phylogenetic analysis of genera and species presently assigned to the rhynchonelliform superfamily Nisusioida and family Nisusiidae suggests that this short-lived but important group of brachiopods first appeared in peri-Gondwana during the second half of the Cambrian Series 2, before going extinct by the end of Drumian times. Nisusiids achieved their maximum morphological disparity and geographical distribution during the Wuliuan Age, and Laurentia was probably the major centre of their dispersal. A new phylogenetic analysis suggests

an early separation of the lineages of spinose and non-spinose nisusiids. The non-spinose nisusiids probably evolved in Laurentia by the end of Cambrian Series 4. The new nisusiid genus *Bellistrophia* is described. The new species *Nisusia multicostata* represents the first documented rhynchonelliform (kutorginide) brachiopod from the Miaolingian (Drumian) of the Alborz Mountains, Iran.

Key words: Brachiopoda, Kutorginata, Drumian, phylogeny, taxonomy, Gondwana.

NISUSIA is one of the most common early to mid-Cambrian rhynchonelliform brachiopods, with a stratigraphic range from the unnamed Cambrian Stage 3 to the Miaolingian (Drumian). *Nisusia* has been recorded from most major Cambrian palaeo-continents except Baltica, and there are only unconfirmed reports from North China. Although it is generally common, *Nisusia* and the entire Nisusiidae is in need of taxonomic revision due to the fact that most species were described more than half a century ago, and the most significant latest review of the genus is that of Walcott (1912). Mao *et al.* (2017) listed 39 species assigned by them to the genus, but in the present review only 19 species can be assigned to *Nisusia* with some degree of confidence, and 5 more are tentatively considered to be within the genus. Many species of *Nisusia* should presently be considered to be *nomen nuda* until they can be restudied.

The Nisusiidae is well suited for phylogenetic analysis. Although they have a relatively simple shell morphology, they exhibit a good set of distinctive morphological features which can be extracted even from relatively simple

descriptions and basic illustrations. The main problem with the phylogenetic analysis is that it proved difficult to include quantitative characters, which could have improved the resolution (Wright & Stigall 2014). Nevertheless, the new phylogeny of the Nisusiidae is mainly compatible with the stepwise stratigraphic sequence of appearance of individual taxa and general patterns of biogeography of the family.

Recent palaeontological studies in eastern Alborz Mountains, northern Iran, have shown that rhynchonelliform brachiopods constituted an important component of Furongian benthic communities in eastern Gondwana (Popov *et al.* 2011, 2013). They often represent the most abundant type of skeletal debris in the extensive Furongian echinoderm–brachiopod carbonate shell beds. However, rhynchonelliform brachiopod occurrences in older rocks (Cambrian Series 2 and Miaolingian) are almost absent in Iran, with the exception of scattered occurrences of *Diraphora* and some possible *Nisusia* in the Kuhbonan Mountains, northern Kerman Province (Wolfart 1974). This is the first report of rhynchonelliform (kutorginide)

brachiopods in the Drumian (Miaolingian Series) of the Alborz Mountains.

PHYLOGENETIC ANALYSIS

Our phylogenetic analysis is based on 28 morphological characters (Table 1) identified in 22 species of the Nisusiidae, assigned to four genera (*Nisusia*, *Bellistrophia*, *Eoconcha* and *Narynella*). Two species of the closely related Kutorginidae (see also Popov *et al.* 1996), including *Agyrekia* aff. *obtusa* Koneva, 1979 and *Kutorgina cingulata* (Billings, 1861) were selected as the outgroup. The Kutorginidae are among the oldest known rhynchonelliform brachiopods and the earliest occurrences of *Kutorgina* (Ushatinskaya & Malakhovskaya 2006) predate the earliest occurrences of the Nisusiidae. *Kutorgina* is also the oldest known member of the rhynchonelliforms from the Maotianshan Chengjiang Lagerstätte of southern China, where soft-part preservation includes well preserved lophophores, digestive tracts and pedicles (Zhang *et al.* 2007, 2008; Holmer *et al.* 2018a).

The Kutorginidae and the Nisusiidae have both a ventral apical perforation as well as a posterior notothyrial and delthyrial opening between the outer margins of the notothyrium and pseudodeltidium (e.g. Bassett *et al.* 2001). Both openings have been interpreted as pedicle openings, but cannot represent homologous structures since they both occur in the same specimen, and must have been secreted by different epithelia (Holmer *et al.* 2018a,b). Soft-part preservation in *Kutorgina* from the Chengjiang Biota shows how the pedicle emerges through the ventral umbonal foramen (Zhang *et al.* 2007; Holmer *et al.* 2018a); in contrast, the pedicle of *Nisusia sulcata* Rowell & Caruso, 1985 emerges from the posterior opening, between the valves, as shown by the silicified complete valves with still-attached *in situ* pedicles (Holmer *et al.* 2018b). A pedicle of the *Nisusia*-type morphotype is apparently also present in undescribed specimens of *Bellistrophia* sp. from the Atei Formation (Miaolingian, Wuliuan) of Chingiz Range, Kazakhstan (LEP unpub. data). Therefore, while fossilization of the nisusiid and kutorginid pedicle is exceptional and could not be observed in the majority of taxa used in the analysis, the presence or absence of a certain type of the pedicle can be deduced with some degree of certainty from other morphological features.

Ushatinskaya & Malakhovskaya (2006) and Malakhovskaya (2008) described an unusual ‘prismatic’ structure in the secondary shell layer of the Kutorginidae, but the published photographs are somewhat difficult to interpret and seemingly require further detailed studies. Nevertheless, the inferred ‘prismatic’ microstructure of the kutorginid secondary shell layer described by Ushatinskaya &

TABLE 1. List of the characters and character states used in the phylogenetic analysis.

1 (out). Outline: subcircular/oval (0), subquadrate/subrectangular (1), transversely semioval (2), elongately semioval (3)
2 (hin). Hinge line: equal to the maximum width (0); shorter than maximum width (1)
3 (cex). Cardinal extremities: obtuse (0), rectangular to almost rectangular (1), acute (2), alate (3)
4 (prl). Profile (long.): subequally biconvex (0), dorsibiconvex (1), ventribiconvex (2), planoconvex (3), concavoconvex (4)
5 (prt). Profile (tras.): rectimarginate (0), unisulcate (1), uniplicate (2), emarginate (3)
6 (ror). Radial ornament: smooth (0), coarsely costellate (1), multicostellate (2), finely multicostellate (3), fascicostellate (4)
7 (hsp). Hollow spines: absent (0), present (1)
8 (hsd). Hollow spines density: faint, short, densely spaced (0), strong and relatively long (1), no spines (2), scattered and relatively few (3)
9 (cor). Concentric ornament: growth lines (0), lamellose (1)
10 (osp). Superficial ornament: absent (0), reticulate (1)
11 (att). Attachment: suproapical (0), between valves (1)
12 (pdt). Pseudodeltidium: narrow ($\frac{1}{4}$ valve width and less) (0), moderately wide ($\frac{1}{4}$ to $\frac{1}{3}$) (1), wide more than $\frac{1}{3}$ valve width (2)
13 (noc). Notothyrial cover: absent/vestigial (0), present (1)
14 (vin). Ventral interarea: orthocline (0), apsacline (1), catacline to slightly apsacline (2), procline (3)
15 (vip). Ventral interarea profile: planar (0), convex (1), with incurved umbonal area (2)
16 (din). Dorsal interarea: anacline (0), catacline (1)
17 (now). Notothyrium width: narrow ($<\frac{1}{4}$ interarea width) (0), broad ($>\frac{1}{4}$ interarea width) (1)
18 (vpr). Ventral profile anterior to umbo: evenly convex (0), concave umbonally, convex anteriorly (1), concave to almost straight anteriorly to the raised umbo (2)
19 (vhp). Ventral valve highest point: at the umbo (0), near mid-length (1), between the umbo and mid-length (2)
20 (dpr). Dorsal profile: flat to gently concave (0), convex with maximum height between umbo and mid-length (1), evenly convex with maximum height at mid-length (2)
21 (vsu). Ventral sulcus: absent (0), umbonal, fading anteriorly (1), originating at the umbo deepening anteriorly (2)
22 (dsu). Dorsal sulcus: absent (0), originating at the umbo (1), originating anterior to the umbo (2)
23 (var). Ventral articulation: hinge furrow (0), flexed cardinal margin (1)
24 (soc). Sockets: absent (0), present (1)
25 (dhf). Dorsal hinge furrow: absent (0), present (1)
26 (sbt). Socket buttress: no sockets (0), socket ridges (1)
27 (dds). Dorsal double septa: absent (0), present (1)
28 (npl). Notothyrial platform: absent/rudimentary (0), present (1)

Malakhovskaya (2006) and Malakhovskaya (2008) has some superficial resemblance with the enigmatic shell structure described for *Salanygolina* (Holmer *et al.* 2009)

and therefore may have important implications if confirmed.

A significant number of species used in the phylogenetic analysis have not been re-studied since their original publication. Nevertheless, the original descriptions and illustrations are good enough to recognize key morphological characters and states used for the specific discrimination of taxa (e.g. Walcott 1912; Bell 1941; Nikitin 1956). With the exception of the pseudodeltidium and notothyrium width, only discrete characters are used, because continuous (quantitative) characters are not available for a significant number of the species. Pinnate mantle canals are present in the ventral valve of some *Nisusia* species; however, the mantle canals are still poorly unknown in the Kutorginidae. Therefore, this potentially important character is not included in the matrix.

NISUSIOID PHYLOGENY AND DISTRIBUTION

Method

The inferred phylogeny of the family Nisusiidae presented in the paper (Fig. 1) is based on the outcomes of phylogenetic analysis of 24 taxa, including 22 species assigned to the family, characterized by 28 unordered and unweighted characters (Tables 2, 3; Holmer *et al.* 2019). The Willi Hennig Society edition of TNT (Tree Analysis Using Traditional Search) parsimony program version 1.5-beta (Goloboff *et al.* 2008) was applied using new technology method. The analysis resulted in a single tree 123 steps long (consistency index 0.413, retention index 0.545).

A significant number of nisusiid species, including some used in the analysis, still require revision; nevertheless, the analysed matrix gives a satisfactory representation of the family and makes it possible to trace its evolutionary history from the first occurrence in the unnamed Cambrian Stage 2 to its extinction at the end of the Drumian. It gives also useful information for understanding the biogeographical dispersal of nisusiids during the early to mid-Cambrian.

Results and discussion

Together, the Nisusioidea and Nisusiidae represent a monophyletic group (Node 2; Fig. 1) defined by their multicostellate ornament (char. 6, state 2; expressed as 6.2 in the following text), attachment by pedicle protruding between valves (11.1), articulation characterized by flexed cardinal margin (23.1), the presence of sockets (24.1), dorsal hinge furrow (25.1) and socket ridges (26.1).

Two main clades can be recognized within the Nisusiidae. The first, Node 3 (Fig. 1), comprises the majority of *Nisusia* species (excluding *Nisusia sulcata*), which are characterized by having a ventral valve profile that is concave umbonally, convex anteriorly (18.1), and with maximum height at the umbo (19.0). The second clade, Node 18 (Fig. 1), is distinguished only by having a subequally biconvex shell (4.0) and includes almost all nisusiids lacking spines along with the finely spinose *Nisusia sulcata*. At Node 19 (Fig. 1) the non-spinose nisusiids are united only by the presence of a dorsal sulcus originating at the umbo (22.1), while the absence of hollow spines is not recognized as a synapomorphy in the analysis. This may be an effect of the apparent absence of spines in *Nisusia? guizhouensis* from the Kaili Formation (Mao *et al.* 2017) and while a secondary loss of spines is possible, the absence of spines in the Chinese species may also simply represent poor preservation, since it is preserved as internal/external moulds in an argillaceous matrix. In other characters, *Nisusia? guizhouensis* shows typical features of the spinose nisusiids and constitutes a sister taxon to *Nisusia granosa* (Node 8; Fig. 1), another species from the Kaili Formation. In the latter species, the bases of hollow spines were observed by Mao *et al.* (2017). Rowell & Caruso (1985) described *Nisusia sulcata* as lacking spines, but the presence of minute spines on silicified shells were described by Holmer *et al.* (2018b). Nevertheless, our analysis placed *Nisusia sulcata* within the group of non-spinose nisusiids, including *Bellistrophia*.

Eoconcha austini from the upper part of the Shady Formation, Austinville (VA), which contains a trilobite fauna characteristic of the *Bonnina–Olenellus* Zone (Resser 1938; Cooper 1951), is the earliest documented representative of the group including non-spinose nisusiids. The monotaxic *Narynella* from the Miaolingian of the Alai peri-Gondwana terrane (Popov *et al.* 2015) is a sister taxon to *Bellistrophia* sp. from the Miaolingian (Wuliuan) of the Chingiz–Tarbagatay island arc system which, according to Popov & Cocks (2017), was located in low southern latitudes in proximity of western margin of Australasian Gondwana during the Cambrian (Fig. 2). These are the only species of non-spinose nisusiids yet recorded outside Laurentia, and our phylogenetic analysis indicates that the non-spinose nisusiids first appeared and diversified in Laurentia early in the unnamed Cambrian Epoch 4. Their migration towards equatorial peri-Gondwana probably occurred at the beginning of the Wuliuan, which also coincides with a time of major turnover in the biogeographical patterns of linguliform brachiopods (Popov *et al.* 2015; Fig. 2).

The early divergence of the spinose nisusiid clade (Node 3; Fig. 1) is obscured by the inadequate early Cambrian fossil record of this group. There are some possible early records of nisusiids in the *Fallotaspis* Zone of Laurentia (Rowell 1977) as well as in the *Pagetiellus*

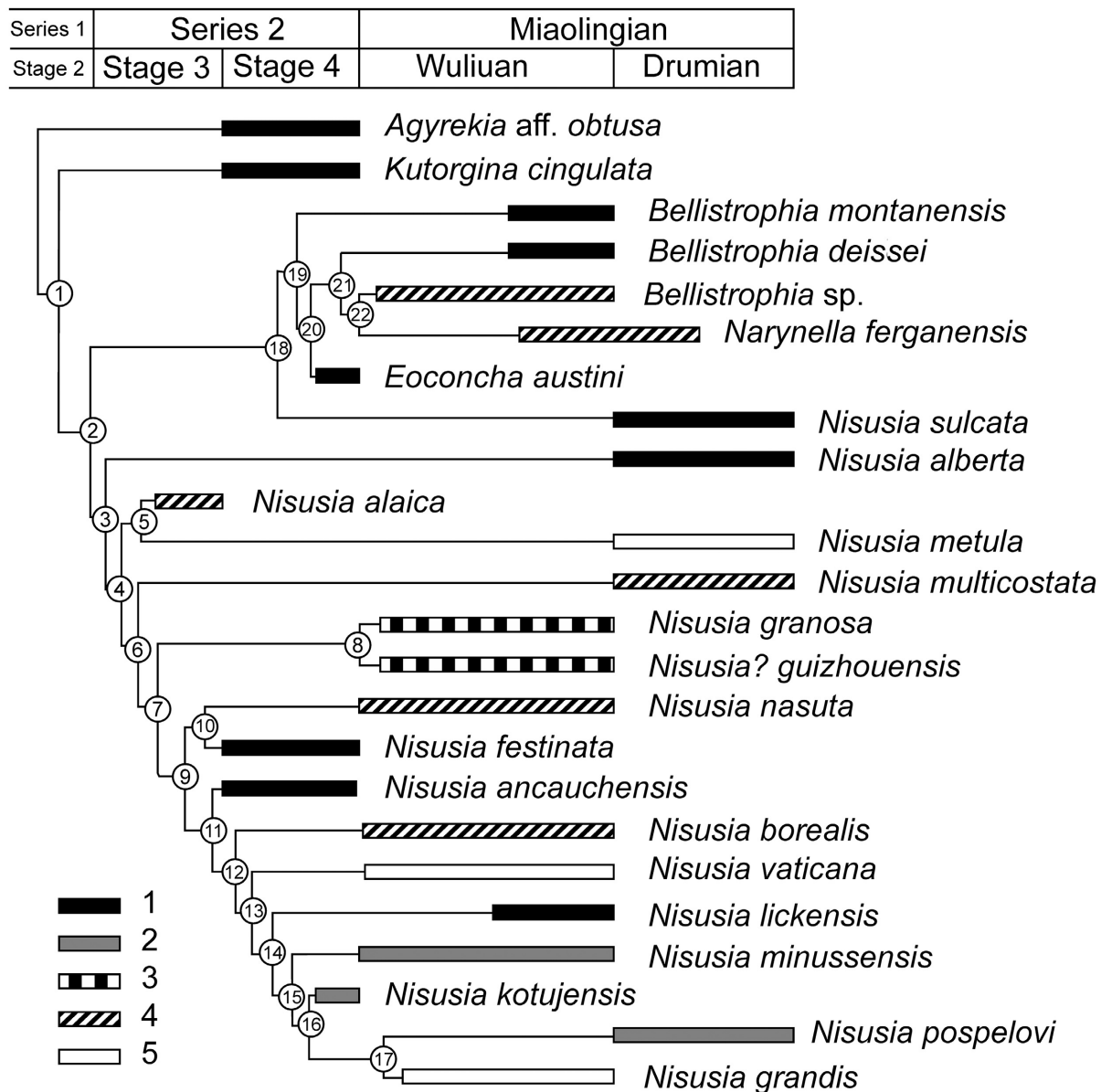


FIG. 1. Inferred phylogenetic relationships for species of Nisusiidae obtained from a single most parsimonious tree generated from TNT v. 1.5-beta (Goloboff *et al.* 2008). Numbered nodes (in circles) supported by character states listed in the text, and Tables 2 and 3. Geographical occurrences of analysed species are shown as: 1, Laurentia; 2, Siberia and associated terranes; 3, South China; 4, peri-Gondwana terranes and microcontinents; 5, Gondwana.

anabaricus Zone of Siberia (Ushatinskaya 1986), both from the lower part of the unnamed Cambrian Stage 3. However, the taxonomic position of the possible nisusiid specimens in these two reports cannot be evaluated, because the cardinalia and umbonal part of the ventral valves, key for their taxonomic affiliation, could not be observed. Nevertheless, three of five nisusiid species documented from the unnamed Cambrian Series 2, including *Eoconcha austini*, *Nisusia festinata* and *Nisusia ancauchensis*, are from Laurentia, suggesting that this continent was

probably the major centre of the early Cambrian nisusiid dispersal.

To date, the earliest documented species of the genus is *Nisusia alaica* from the Cambrian (probably the upper part of the unnamed Cambrian Stage 3) of the Alai terrane, where it occurs in association with unidentified archaeocyaths and a highly endemic brachiopod fauna including *Chile*, *Naukat*, *Oina* and *Kutorgina* (Popov & Tikhonov 1990). In the phylogenetic analysis it is placed close to the base of the major *Nisusia* clade together with

TABLE 2. Matrix of 28 morphological characters recognized in 22 species of the Nisusiidae and two species of the Kutorginidae listed in the text (Holmer *et al.* 2019).

	1234567891111111122222222
	0123456789012345678
<i>Agyrekia obtusa</i>	010200002?010300101100001000
<i>Kutorgina cingulata</i>	1103000211020020101010001001
<i>Bellistrophia aitenensis</i>	1100230200100120012112110100
<i>Bellistrophia deissei</i>	110132020011012001112211010?
<i>Bellistrophia montanensis</i>	110033020011112010112111010?
<i>Eoconcha austini</i>	2020110200100100001201110110
<i>Narynella ferganensis</i>	1102120200120120012122110111
<i>Nisusia alaica</i>	1112021110110310110100110101
<i>Nisusia alberta</i>	01020211001112201101001101?1
<i>Nisusia ancauchensis</i>	103202130012?2001101101101??
<i>Nisusia borealis</i>	1012121000110200110112110111
<i>Nisusia festinata</i>	2012021100110121112110110111
<i>Nisusia grandis</i>	1032221010121200120122110111
<i>Nisusia granosa</i>	101112100011?2001201101101??
<i>Nisusia kotujensis</i>	10323310001002000201211101?1
<i>Nisusia lickensis</i>	110034100011?1011101221101??
<i>Nisusia metula</i>	1112011100110301110100110101
<i>Nisusia minussensis</i>	10123210001112111101211101?1
<i>Nisusia multicostata</i>	10100210001102011102001101??
<i>Nisusia nasuta</i>	20120210001?0220?201101101??
<i>Nisusia pospelovi</i>	1001221000120220120121110101
<i>Nisusia sulcata</i>	1100121000110110101120110111
<i>Nisusia vaticina</i>	00121110101101011101121101??
<i>Nisusia? guizhouensis</i>	1012020200110200120111110101

the Laurentian species *Nisusia alberta* from the Stephen Formation (Miaolingian, Drumian), Alberta, Canada. *Nisusia alberta* formed a small, but long-lived Gondwanan clade, together with *Nisusia metula* Brock, 1998 from the Murrawong Creek Formation (Miaolingian, Drumian) (Node 5; Figs 1, 2).

Nisusia multicostata from the Miaolingian (Drumian) of the peri-Gondwana Alborz platform appears to be an early offshoot that separated from the major *Nisusia* clade (Node 6; Figs 1, 2), before its major radiation in the unnamed Cambrian Epoch 4 had occurred. This group is characterized by a subequally biconvex shell (4.0), a catacline dorsal interarea (16.1) and an evenly biconvex dorsal valve sagittal profile with maximum height at mid-length (20.2).

A significant proportion of the Miaolingian *Nisusia* species from Siberia and Gondwana appears in the analysis as a monophyletic clade with Laurentian roots (Node 11; Figs 1, 2). An early Cambrian (unnamed Cambrian Epoch 4) Laurentian species *Nisusia ancauchensis* forms a sister taxon of that clade. It occurs in allochthonous setting within the Cuyania terrane at Argentinian Precordillera (Fig. 2). The Laurentian origin of that terrane is well supported by data given by Benedetto *et al.* (2009), including an associated trilobite assemblage of the *Bonnina*–*Olenellus* Zone with strong Laurentian signature. Another species at the base of

TABLE 3. Character transformations and synapomorphy scheme for internal nodes shown on Fig. 1.

<i>Agyrekia</i> aff. <i>obtusa</i> : no autapomorphies
<i>Kutorgina cingulata</i> : 4(2→3); 12(1→2); 20(1→0); 21(0→1)
<i>Bellistrophia</i> sp.: 5(1→2); 6(2→3); 21(2→1)
<i>Bellistrophia deissei</i> : 4(0→1), 5(1→3)
<i>Bellistrophia montanensis</i> : 5 (1→3); 6(2→3)
<i>Eoconcha austini</i> : 1(1→2); 2(1→2); 3(0→1)
<i>Nisusia? guizhouensis</i> : 7(1→0), 8(0→2), 22(0→1)
<i>Narynella ferganensis</i> : 4(0→2); 27(0→1)
<i>Nisusia sulcata</i> : 15(0→1); 27(0→1)
<i>Nisusia alaica</i> : 9(0→1); 15(0→1)
<i>Nisusia ancauchensis</i> : 3(1→3); 8(0→3); 12(1→2)
<i>N. alberta</i> : 1(1→0)
<i>Nisusia borealis</i> (no autapomorphies)
<i>Nisusia festinata</i> : 8(0→1); 14(2→1); 16(0→1); 19(0→2)
<i>Nisusia grandis</i> : 9(0→1); 13(0→1); 22(1→2)
<i>Nisusia granosa</i> : 4(2→1); 5(0→1)
<i>Nisusia kotujensis</i> : 6(2→3); 17(1→0)
<i>Nisusia lickensis</i> : 2(1→1); 3(1→0)
<i>Nisusia metula</i> : 6(2→1); 16(0→1)
<i>Nisusia minussensis</i> : 13(0→1), 15(0→1)
<i>Nisusia multicostata</i> : 4(2→0); 16(0→1); 20(1→2)
<i>Nisusia nasuta</i> : 18(1→2)
<i>Nisusia pospelovi</i> : 3(3→0); 4(2→1); 15(0→2); 27(1→0)
<i>Nisusia vaticina</i> : 1(1→0); 6(2→1); 9(0→1)
Node 1: (no synapomorphies)
Node 2: 6(0→2); 11(0→1); 23(0→1); 24(0→1), 25(1→0); 26 (0→1)
Node 3: 18(0→1); 19(1→0)
Node 4: 3(0→1); 15(2→0)
Node 5: (no synapomorphies)
Node 6: 2(1→0)
Node 7: 27(0→1)
Node 8: 18(1→2)
Node 9: 21(0→1)
Node 10: 1(1→2); 15(0→2)
Node 11: (no synapomorphies)
Node 12: 5(0→1); 22(0→2)
Node 13: 16(0→1)
Node 14: 5(1→3); 21(1→2)
Node 15: 22(2→1)
Node 16: 3(1→3); 16(1→0); 17(1→2)
Node 17: 4(3→2)
Node 18: 4(2→0)
Node 19: 22(0→1)
Node 20: 17(1→0)
Node 21: 18(0→1)
Node 22: 19(1→2)

the clade is *Nisusia borealis*, a Miaolingian species from the vicinity of Eagle, Alaska, where it occurs together with *Arctohedra* (Cooper 1936). As demonstrated by Bassett *et al.* (2002), the Cambrian protorthides and clitambonitoids (Arctohedridae) were restricted in their geographical distribution to Gondwana and associated terranes. Therefore, this *Nisusia* species is probably derived from an exotic peri-

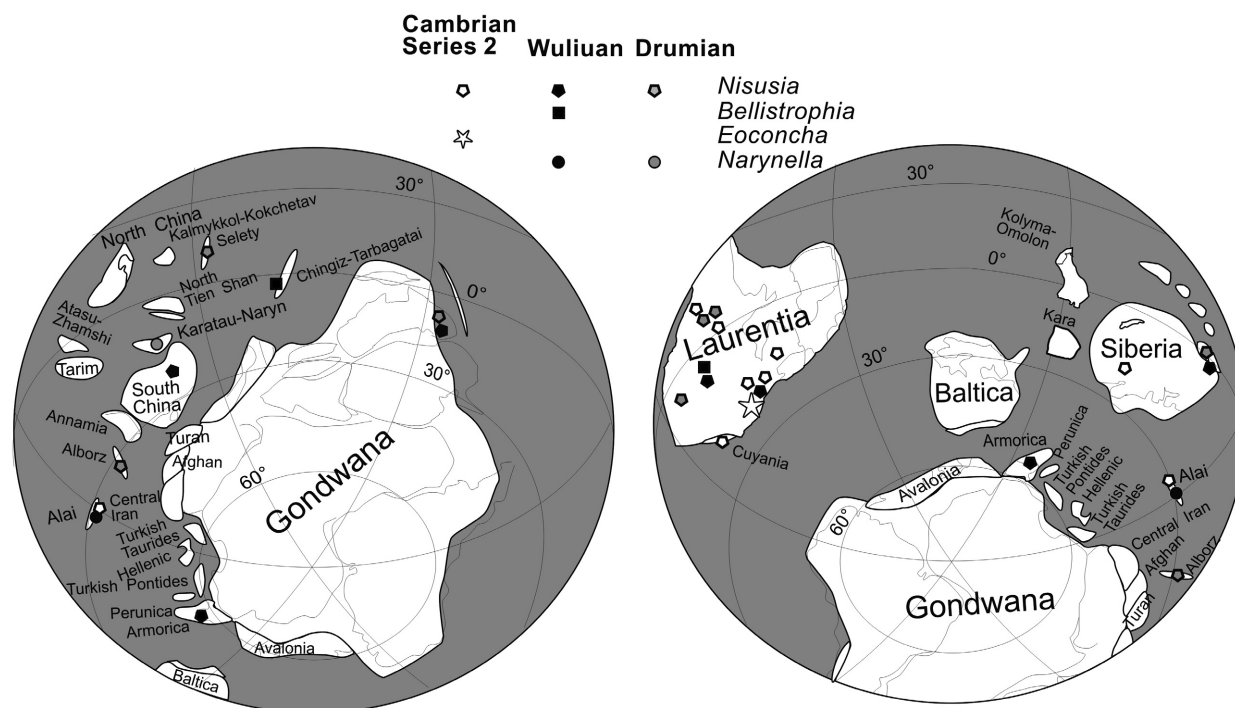


FIG. 2. Palaeogeographical reconstruction showing geographical distribution of Nisusiidae. Relative position of major Early Palaeozoic continents (e.g. Laurentia, Baltica, Gondwana and Siberia) for Cambrian, Wuliuan (e.g. Torsvik & Cocks 2017) with emendations for Australasian peri-Gondwana mainly after Popov & Cocks (2017).

Gondwana terrane that was later accreted to Laurentia. Dispersal of that clade and its radiation outside Laurentia probably occurred sometime in the unnamed Cambrian Epoch 4; the Siberian *Nisusia kotujensis* occurs in deposits dated as pre-Wuliuan. In the analysis it appears as a derived member of the clade together with two other Siberian species including *Nisusia minussensis* and *Nisusia paspelovi* (Node 15; Fig. 1). The Australian species *Nisusia grandis* and its sister taxon *Nisusia paspelovi* constitute the most derived members of the clade.

The Wuliuan nisusiids show a significant increase in morphological disparity with three genera documented. Among them, 11 species can be confidently assigned to *Nisusia* at present. Most of the species were confined to low-latitude palaeogeographical settings, including Laurentia (*Nisusia burgessensis* Walcott, 1924, *Nisusia claudi* Shaw, 1957 and *Nisusia sulcata* Rowell & Caruso, 1985), Siberia and associated microplates of the Sayany–Altai region (*Nisusia kotujensis* Andreeva, 1962 and *Nisusia paspelovi* Aksarina, 1960), South China (*Nisusia granosa* Mao *et al.*, 2014), Kazakhstani island arcs (*Nisusia nasuta* Nikitin, 1956) and the Australasian margin of Gondwana (*Nisusia grandis grandis* Roberts & Jell, 1990 and *Nisusia metula* Brock, 1998). *Nisusia vaticina* (de Verneuil & Barande, 1860) from the Mediterranean peri-Gondwana is the only record of this genus in temperate latitudes, while the Alborz platform was crossing subtropical waters

during the Furongian due to the counter-clockwise rotation of Gondwana during Cambrian times (Scotese & Barrett 1990; Álvaro *et al.* 2000; Mitchell *et al.* 2010). The generic assignment of four brachiopod species to *Nisusia* by Endo & Resser (1937) cannot be confirmed due to inadequate description and illustration. Thus, the presence of nisusiids in North China is uncertain.

During the Drumian nisusiids went through a considerable decline, with only six species known, while among non-spinose nisusiids only *Narynella* crossed the Wuliuan–Drumian boundary. However, they were present in Laurentia, Siberia and Australasian Gondwana (Fig. 2). The geographical distribution of nisusiids is confined almost exclusively to the low latitudes. They are unknown in Baltica and outside the Australasian segment of Gondwana. All nisusiids became extinct by the end of the Drumian time.

SYSTEMATIC PALAEOONTOLOGY

by Lars. E. Holmer, Mohammad-Reza Kebria-ee Zadeh, Leonid E. Popov and Mansoureh Ghobadi Pour

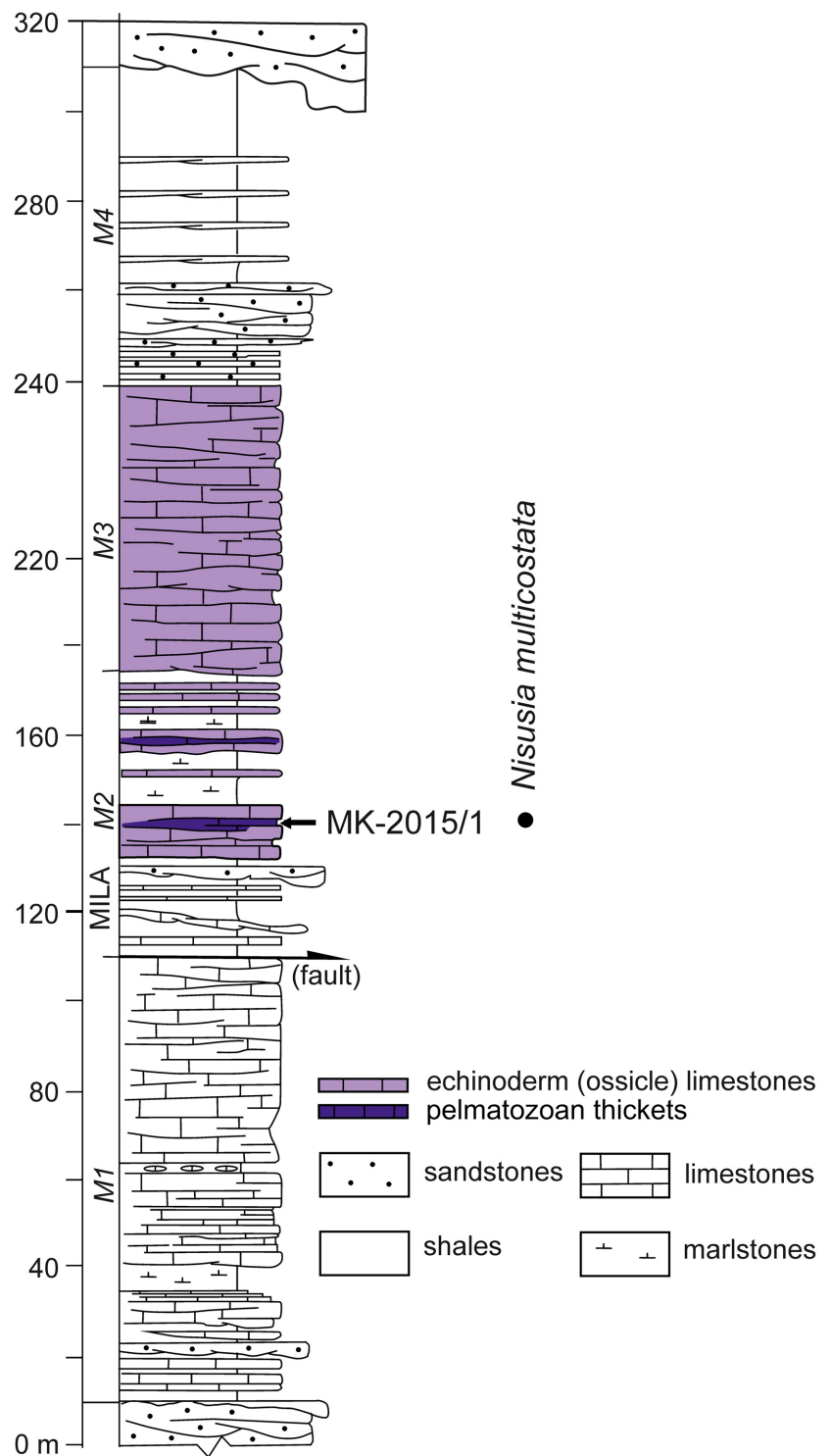
All types and illustrated specimens discussed in the paper are deposited in the National Museum of Wales, Cardiff under the accession number NMW 2018.4G and in the Central Geological Research and Exploration

Tschernyshev Museum (St Petersburg), collection no. *Geological setting*
CNIGR 8202.

Abbreviations. Lv, Ld, sagittal ventral and dorsal valve length; T, maximum thickness; W, maximum width.

The Iranian specimens of the Nisusiidae come from a single locality (Fig. 3) at the Mila-Kuh hill (MK-2015/1, at 53°48'45"E and 35°59'5"N coordinates), 6.5 km north

FIG. 3. Schematic stratigraphical column of the Mila-Kuh Formation at Mila-Kuh showing the position of the brachiopod locality. Colour online.



of the highway connecting Semnan with Damgan, and about 6.5 km south-west of the village of Tuyeh. The Cambrian succession in Mila-Kuh was first described by Stöcklin *et al.* (1964), who introduced the Mila Formation for the middle Cambrian to Lower Ordovician strata exposed in the area, which was subdivided it into five informal members. The Cambrian fossil faunas and trilobite-based biostratigraphy of the Mila-Kuh section were described by Kushan (1973, 1978) and Wittke (1984). The traditional views of the Mila lithostratigraphy in the Alborz Mountains were criticized by Geyer *et al.* (2014a), who introduced the Deh-Sufian and Deh-Molla formations as a replacement for the Cambrian Series 2 (members 1 and 2) and Furongian (members 3 and 4) parts of the Mila Formation, respectively. However, due to the fact that a detailed revision of the Mila-Kuh section was not attempted by Geyer *et al.* (2014a), their proposed nomenclature has not been accepted by the Geological Survey of Iran. For this paper, we provisionally keep the traditional subdivision of the Mila Formation (Stöcklin *et al.* 1964).

The section studied (Fig. 3) is situated somewhat to the east of the section described by Stöcklin *et al.* (1964). Here the lower boundary of the Mila-2 Member is faulted and only the upper part of the unit is preserved (Fig. 1). The brachiopod sample MK-2015/1 was collected 34 m below the base of the Mila-3 Member, which coincides with the upper part of Unit 4 (Kushan 1978, p. 14). It is located on the flank of a decimetre-thick echinoderm-rich bioaccumulation. The background deposits through this interval are represented by intercalating argillaceous limestones and calcareous argillites, which contain a monotaxic trilobite association with *Iranolesia pisiformis* (King, 1937). The presence of this trilobite allows an attribution to the *Iranolesia* Zone of Kushan (1973) that, according to the correlation proposed by Geyer *et al.* (2014a), corresponds to the upper part of the Drumian Stage (Miaolingian Series).

The studied specimens of *Narynella ferganensis* (Andreeva, 1962) are most probably paratypes (donated by Andreeva to the late Alwyn Williams, Glasgow). They were sampled from a Cambrian olistolith (probably *Sdzuyella*–*Aegunaspis* beds, Miaolingian Series) at Madygen, northern slopes of eastern Turkestan Range, Kyrgyzstan. No detailed locality data were presented in the original publication and the age of the sample was erroneously presented as ‘Lower Cambrian’. It is likely that an allochthonous limestone block at Sauk Tanga gorge, Madygen, which represents the major source of the Cambrian (Miaolingian) fossils described by Geyer *et al.* (2014b), is the type locality of *Narynella ferganensis*.

Order KUTORGINIDA Kuhn, 1949

Superfamily NISUSOIDEA Walcott & Schuchert *in* Walcott, 1908

Family NISUSIDAE Walcott & Schuchert *in* Walcott, 1908

Genus NISUSIA Walcott, 1905

Type species. By original designation *Orthisina festinata* Billings, 1861.

Remarks. Until recently *Nisusia* was regarded as a poorly defined ‘waste basket’ taxon, due to the fact that the morphology of many species described in the first half of the previous century are inadequately known. Here we restrict *Nisusia* to comprise only species with hollow spines. It is likely that most of the taxa (mainly from Laurentia) from the lower Cambrian (unnamed stages 3–4) that have been assigned to *Nisusia*, neither belong to *Nisusia* nor to Nisusioidea (see below). Presently only 19 taxa, plus one described under open nomenclature, can be assigned to *Nisusia* with some degree of confidence, while the generic affinity of five more species requires further study.

Species assigned. Taxa described under open nomenclature are mostly not considered in the list due to the inadequate information and illustrations that are usually provided.

Nisusia alaica Popov & Tikhonov, 1990, from olistolith (unnamed Cambrian Stage 3) in the Silurian Pulgon Formation, Alai Range, Kyrgyzstan.

Nisusia ancauchensis Benedetto & Foglia, 2012, from olistolith (unnamed Cambrian Stage 4, *Bonnina*–*Olenellus* Zone), Quebrada Ancaucha, Argentine Precordillera.

Nisusia borealis Cooper, 1936, from unnamed limestone unit (Miaolingian, Wuliuan?) in the vicinity of Eagle, Alaska, USA.

Nisusia burgessensis Walcott, 1924, from Burgess Shale Formation (Miaolingian, Drumian), British Columbia, Canada. Represented by flattened material and not included in the analysis.

Nisusia claudi Shaw, 1957, from upper Parker Slate (Miaolingian) of Vermont, USA. While attribution of this species to *Nisusia* is likely, an imperfect description and poor illustrations in the original publication make difficult to recognize this taxon outside the type locality. Not included in the analysis.

Nisusia grandis Roberts & Jell, 1990, from ‘First Discovery Limestone’ Member of the Coonigan Formation (Miaolingian, Wuliuan) of western New South Wales, Australia.

Nisusia granosa Mao *et al.*, 2014, from Kaili Formation (Miaolingian, Wuliuan) of Guizhou, South China.

Nisusia lickensis Bell, 1941, from Pentagon Shale (Miaolingian, Wuliuan), Montana, USA.

Nisusia kotujensis Andreeva, 1962, from Ust'-Dzhar Formation (unnamed Cambrian Stage 4) of north-central Siberia, Russia.

Nisusia metula Brock, 1998, from Murrawong Creek Formation (Miaolingian, Drumian), southern New England Fold Belt, north-eastern New South Wales, Australia.

Nisusia minussensis Lermontova, 1940, from Suyaryk Regional Stage (Miaolingian, Wuliuan) of Gornyi Altai, Russia.

Nisusia multicostata sp. nov., from Mila Formation (Miaolingian, Drumian), eastern Alborz Mountains, Iran.

Nisusia nasuta Nikitin, 1956 (including *Nisusia nasuta* var. *ramosa* Nikitin 1956), from Maidan Formation (Miaolingian) of Selety river basin, north-central Kazakhstan.

Nisusia paspelovi Aksarina, 1960, from Mundybash Regional Stage (Miaolingian, Drumian) of Gornaya Shoriya, Russia.

Nisusia sulcata Rowell & Caruso, 1985, from the Marjum Formation (Miaolingian, Drumian), western Utah, USA.

Orthisina alberta Walcott, 1889, from Stephen Formation (Miaolingian, Drumian), Alberta, Canada.

Orthisina festinata Billings, 1861, from unnamed Cambrian Stage 4 (*Bonnina*–*Olenellus* Zone) of USA and Canada.

Orthisina pellico de Verneuil & Barrande, 1860 is synonymous with *Nisusia vaticina* de Verneuil & Barrande, 1860 according to Wotte & Mergl (2007).

Orthisina vaticina de Verneuil & Barrande, 1860 (= *Orthisina pellico* de Verneuil & Barrande, 1860), from upper member of Láncara Formation (Miaolingian, Wuliuan) from Cantabrian Mountains, north-west Spain (Wotte & Mergl 2007).

Nisusia sp., from Murero Formation (Miaolingian, Wuliuan) of Iberian Chains, Spain (Mergl & Zamora 2012).

Species questionably assigned. *Nisusia grandis glabara* Roberts & Jell, 1990, from 'First Discovery Limestone' member of the Coonigan Formation (Miaolingian, Wuliuan) of western New South Wales, Australia. The taxon has radial ornament of coarse ribs without spines, unlike other species of *Nisusia*. Occasional presence of spines reported, but not illustrated in the original publication. Probably represents a different genus and it is not conspecific with *Nisusia grandis*.

Nisusia guizhouensis Mao et al., 2017, from Kaili Formation (Miaolingian, Wuliuan) of Guizhou, South China. The absence of spines reported from the original publication may represent a preservation artefact and requires further verification.

Nisusia liantoensis Zeng, 1987, from Shipai Formation (unnamed Cambrian Series 2) of Lianto, Yichang City, western Hubei Province, South China. While generic assignment of this taxon is likely, the species requires revision, in particular, the presence of spinose ornament is not confirmed.

Nisusia rara Walcott, 1908, from Led Shale Member (formerly Spence Shale Member) of Langston Formation (Miaolingian, Wuliuan), of Idaho, USA. While affiliation of this taxon to *Nisusia* looks likely, it is inadequately known and requires revision.

Orthisina? transversa Walcott, 1886, from Parker Formation (Cambrian Series 2) of Vermont, USA. While affiliation of this species to *Nisusia* is likely, it remains inadequately known and requires revision.

Species rejected (selected). *Nisusia deseii* Bell, 1941, from the Meagher Limestone, *Ehmania* Zone (Miaolingian, Wuliuan), Montana, USA. Here it is reassigned to *Bel-listrophia*.

Nisusia ferganensis Andreeva, 1962. This is the type species of *Narynella* discussed below.

Nisusia fulleri Mount, 1981, from the Latham Shale Formation (unnamed Cambrian Series 3) of California. Generic affiliation of the species cannot be proved due to insufficient description and illustrations (no data on interareas, pseudodeltidium, foramen and interiors of both valves). The taxon should be considered to be a *nomen dubium*.

Nisusia hayasakai Sun, 1924, from the Changhsia Formation (Miaolingian) of Luanxian County, northeastern Hebei Province, North China. Taxon was not revised since its formal designations, although the type material (J.-Y. Rong, pers. comm. 2018) was probably lost. Until topotypes are available and revised, this taxon should be considered to be a *nomen dubium*.

Nisusia? howelli Shaw, 1957, from the lower Parker Slate (unnamed Cambrian Stage 4) of Vermont, USA. The taxon is known from a single imperfectly preserved ventral valve, while a very short description in the original publication does not provide necessary information for the generic discrimination of the species and it should be considered to be a *nomen dubium*.

Nisusia montanensis Bell, 1941, from the Meagher Limestone, *Ehmania* Zone (Miaolingian, Wuliuan), Montana, USA. Here reassigned *Bel-listrophia*.

Nisusia spinigera Walcott, 1924, from the Ottetail Formation (Furongian) of British Columbia. The species has an open delthyrium and the original report on a presence of spines looks unsupported. The taxon definitely does not represent *Nisusia* or Nisusioidea, while its generic affiliation cannot be defined without data on cardinalia, thus it is here considered to be a *nomen dubium*.

Nisusia? sp., from the Campito Formation, Montenegro Member (unnamed Cambrian Stage 3, *Fallotaspis* Zone). According to Rowell (1977), specimens may belong to a new, as yet formally undescribed genus. No data on the interior and characters of the delthyrial opening were presented in the original description, although specimens apparently lack hollow spines. They are unlikely to belong to *Nisusia* or *Nisusioidea*.

Nisusia? sp., from the *Pagetiellus anabaricus* Zone (unnamed Cambrian Stage 3) west side of the Lena River near Sailyk village, Central Siberia, Russia (Ushatinskaya 1986). This unnamed taxon is known from a single dorsal valve showing straight hinge line and distinct radial ornament with possible bases of 12 spines on the ribs. While assignation of this shell to *Nisusioidea* is possible, in the absence of data on the interior and characters of posterior margin in both valves its generic attribution remains uncertain.

Nisusia (Jamesella) amii Walcott, 1905, from a boulder in the Saint-Nicolas Formation (Cambrian Series 2), eastern Quebec, Canada. The species is known from a single ventral valve which is high, subconical, with a high, planar interarea bearing a convex pseudodeltidium. The umbonal area was described by Walcott (1912) as broken, but it may represent a partly preserved foramen similar to those of chileides (e.g. *Acareorthis*).

Nisusia (Jamesella) argenta Walcott, 1908, from the Silver Peak Group (unnamed Cambrian Series 2) of Nevada. The species is characterized by an open delthyrium, paucicostate radial ornament and a lack of spines. Its generic affiliation is uncertain, although it does not represent *Nisusioidea*. The species should be considered to be a *nomen dubium*.

Nisusia concentrica Endo & Resser, 1937, from the Taitzu Formation (Miaolingian) of north-east China. The taxon is based on two dorsal valves and a single incomplete shell. Brief descriptions and inadequate illustrations do not provide sufficient information on the interior of either valve, characters of delthyrial opening, or the presence or absence of spines; therefore taxonomic affiliation to the family or genus level is impossible. The species name should be considered to be a *nomen dubium*.

Nisusia (Jamesella) erecta Walcott, 1908, from middle Cambrian of Nevada, USA. While the holotype definitely possesses a pseudodeltidium, it is characterized by radial ornament of simple coarse ribs unusual for *Nisusia*, although a presence of hollow spines was not reported and interior of both valves is unknown. The generic assignation of the species is uncertain and it should be considered to be a *nomen dubium*.

Nisusia (Jamesella?) kanabensis Walcott, 1908, based on a single incomplete ventral internal mould from the Tonto Group (Furongian) exposed at the mouth of Kanab Canyon, Grand Canyon of the Colorado, Arizona,

USA. While the generic affiliation of the specimen is impossible to determine, it definitely does not belong to either *Nisusia* or *Nisusioidea* and should be considered to be a *nomen dubium*.

Nisusia (Jamesella) lowei Walcott, 1908, from Led Shale Member (formerly Spence Shale Member) of the Langston Formation (Miaolingian, Wuliuan), of Idaho, USA. Description and illustrations given by Walcott (1912) are not satisfactory to assign this taxon to either *Nisusia* or to *Nisusiidae* and it should be considered to be a *nomen dubium*.

Nisusia mantouensis Endo & Resser, 1937, from the Taitzu Formation (Miaolingian) of north-east China. The taxon is based on a single ventral valve which does not exhibit features helpful for its generic and species affiliation. The taxon should be considered to be a *nomen dubium*.

Nisusia (Jamesella?) nautes Walcott, 1905, from the Led Shale Member (formerly Spence Shale Member) of the Langston Formation (Miaolingian, Wuliuan), of Idaho, USA. In the absence of data on the foramen, pseudodeltidium and cardinalia, generic affiliation of the species cannot be proved. Also, it apparently lack spines and therefore does not represent a species of *Nisusia*; it is here considered to be a *nomen dubium*.

Nisusia (Jamesella) oriens Walcott, 1924, from the Forteau Formation (*Bonnina*–*Olenellus* Zone; unnamed Cambrian Series 2). Species requires revision, it may represent a paterinate.

Nisusia orientalis Endo & Resser, 1937, from the Taitzu Formation (Miaolingian) of north-east China. No data on characters of the delthyrial opening or interior of either valve were presented; the specimens apparently lack spines. The species should be considered to be a *nomen dubium*.

Nisusia salebroza Endo & Resser, 1937, from Taitzu Formation (Miaolingian) of north-east China. The taxon is based on a few fragmented shells, which are inadequate for determining family or generic affiliation; also interior of both valves remains unknown. The species should be considered to be a *nomen dubium*.

Nisusia (Jamesella) utahensis Walcott, 1905, from the Wuliuan of Utah. The taxon is known from two imperfectly preserved specimens and could not be identified outside the type locality until new material is available. It should be considered to be a *nomen dubium*.

Orthosina compta Tate, 1892 is based on a single specimen from the Kulpara Limestone (unnamed Cambrian Stage 3) of Yorke Peninsula. Brock (1998, p. 608), rejected it as a species of *Nisusia*. In view of the limited material presently available this taxon should be considered to be a *nomen dubium*.

Protorthis spencei Walcott, 1905, from the Led Shale Member (formerly Spence Shale Member) of the

Langston Formation (Miaolingian, Wuliuan), of Idaho, USA. Species requiring revision. It was reassigned to *Nisusia* by Walcott (1912, p. 737). Bell (1941), who studied the types, noted the absence of spines and a general similarity to *Nisusia* (= *Bellistrophia*) *desei*, but the original description and illustrations are not satisfactory for its precise generic discrimination.

Nisusia multicostata sp. nov.

Figure 4A–G

LSID. urn:lsid:zoobank.org:act: 0078127E-9469-4FA4-8434-E540A5F409AB

Derivation of name. After characteristic radial ornament of numerous delicate ribs.

Holotype. NMW 2018.4G.1 (Lv = 9.4 mm, W = 12.8 mm; Fig. 4A, B), from the Mila Formation Member 2, *Iranolesia* Zone (Drumian), sample MK2015/1, Mila-Kuh, eastern Alborz Mountains, Semnan Province, Iran.

Paratypes. Ventral valves: NMW 2018.4G.2 (Fig. 4C), NMW 2018.4G.3 (Lv = 7.8 mm, W = 10.3 mm; Fig. 4D), NMW 2018.4G.4 (Fig. 4G), NMW 2018.4G.6–8; dorsal valve, NMW 2018.4G.9 (Ld = 7.0 mm, W = 11.5 mm, T = 2.0 mm; Fig. 4E, F). Locality and horizon as for the holotype. Other material includes more than 30 variably preserved ventral and dorsal valves housed in Department of Geology, Faculty of Sciences, Payame Noor University, Tehran, Iran.

Diagnosis. *Nisusia* with subequally biconvex shell, hinge line shorter than maximum width at mid-length and rectimarginate anterior commissure. Ventral valve sagittal profile concave in umbonal area, evenly convex posteriorly with maximum height at umbo; ventral interarea slightly apsacline. Dorsal valve with catacline interarea. No ventral or dorsal sulcus. Radial ornament finely multicostellate, with 60–70 ribs; hollow spines minute, densely spaced.

Description. Shell subequally biconvex, transverse, subrectangular to trapezoidal in outline, length about three-quarters of width, with maximum width at hinge line. Cardinal extremities slightly acute to almost rectangular; anterior commissure rectimarginate. Ventral valve lateral profile concave anterior to umbo, becoming almost straight in middle part and moderately convex in anterior third of valve length in mature individuals. Ventral umbo strongly raised, with small suproapical foramen. Ventral interarea high, slightly apsacline with convex pseudodeltidium occupying about one-third of interarea width. Dorsal valve

moderately and evenly convex, depth slightly more than quarter of length, with small pointed beak facing posteriorly. Dorsal interarea high, catacline with broad, subtriangular open notothyrium. Radial ornament multicostellate with faint, rounded ribs increasing mainly by intercalation and separated by narrow interspaces; in total, 60–70 ribs with 9–11 ribs per 3 mm along anterior margin of mature individuals. Rib crests bearing faint, hollow spines. Ventral interior lacking distinct features. Dorsal interior not observed.

Remarks. *Nisusia multicostata* sp. nov. is distinct from most of the species assigned to the genus in having a finely multicostellate ornament with minute, densely placed spines on the rib crests, and in the complete absence of the ventral sulcus and dorsal median fold. In these characters, as well as in having a relatively low, slightly apsacline ventral interarea and maximum shell width along the hinge line it recalls *Nisusia kotujensis* Andreeva, 1962 from the unnamed Cambrian Series 3 of north-central Siberia, Russia, but can be distinguished in having a wider pseudodeltidium approaching one-third interarea width, a rectimarginate (not emarginate) anterior commissure, a sagittal profile of the ventral valve concave umbonally and evenly convex anterior to the umbo, and in the absence of the dorsal and ventral sulcus. Among other species of the genus documented from the unnamed Cambrian Series 3, *Nisusia nasuta* Nikitin, 1956 is another similar species, which has similar radial ornament and a rectimarginate anterior commissure; however, *Nisusia multicostata* can be readily distinguished from the former taxon in having a ventral valve sagittal profile with maximum height at the umbo, a catacline dorsal interarea and a complete absence of the ventral sulcus.

A very finely spinose shell is also characteristic for *Nisusia sulcata* Rowell & Caruso, 1985, from the Marjum Formation (Drumian) of western Utah, USA; however, *Nisusia multicostata* differs readily from that taxon in having a rectimarginate (not sulcate) anterior commissure, in the complete absence of ventral sulcus, maximum shell width at the hinge line, rectangular (not obtuse) cardinal extremities and fine radial ornament.

Nisusia multicostata differs from *Nisusia metula* Brock, 1998, from Murrawong Creek Formation (Drumian) of the southern New England Fold Belt, north-eastern New South Wales, Australia in having a subequally biconvex (not ventribiconvex) shell, maximum shell width at the hinge line and finely multicostellate ornament with minute spines,

Nisusia multicostata differs from *Nisusia grandis grandis* Roberts & Jell, 1990, from the ‘first discovery limestone’ member of the Coonigan Formation (Wuliuan) of western New South Wales, Australia in having a subequally biconvex (not ventribiconvex) shell, rectimarginate (not

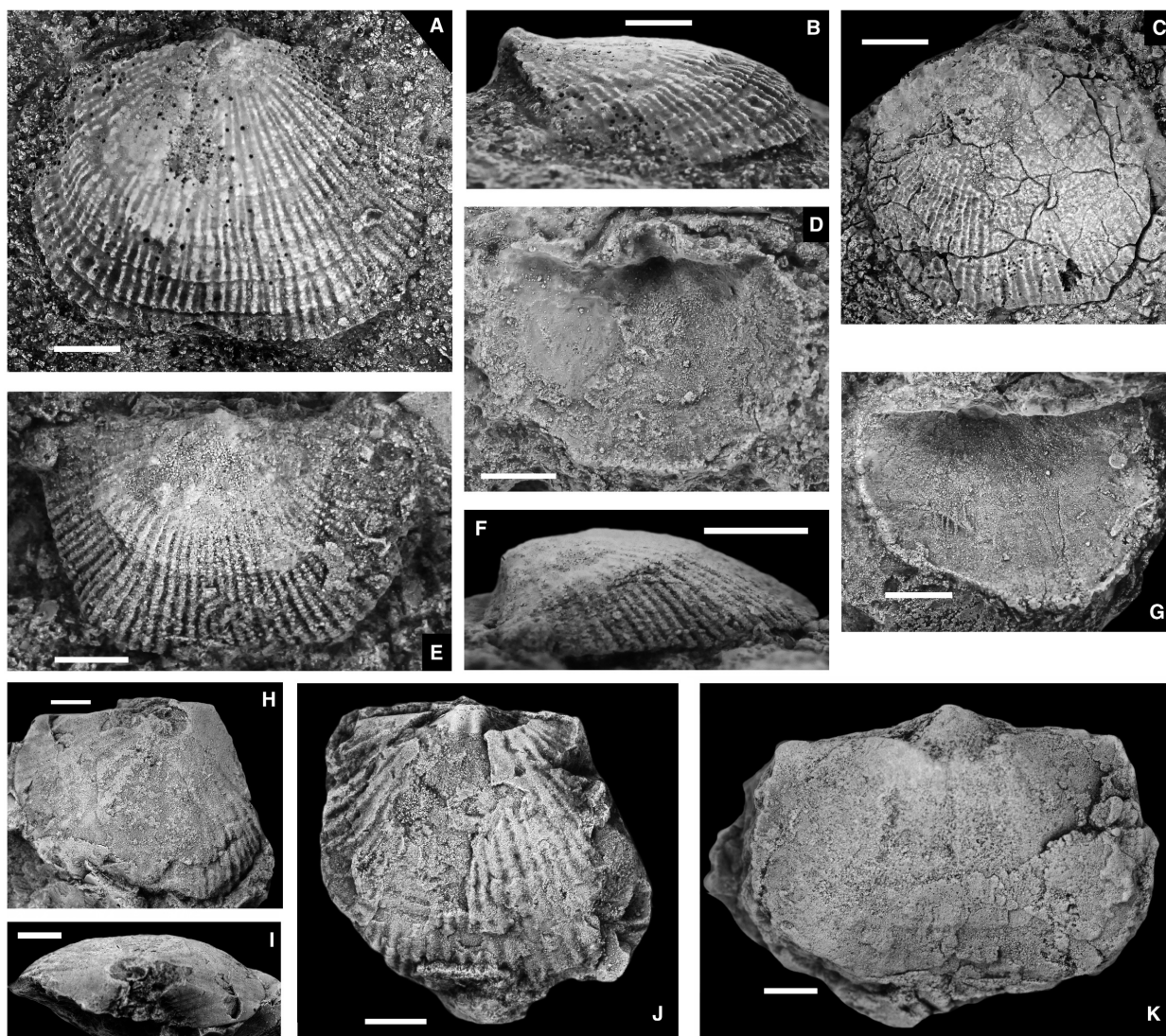


FIG. 4. A–G, *Nisusia multicostata* sp. nov., Mila Formation Member 2, *Iranolesia* Zone (Drumian), sample MK2015/1, Mila-Kuh, eastern Alborz Mountains, Semnan Province, Iran: A–B, NMW 2018.4G.1, ventral valve, holotype, exterior and side view; C, 2018.4G.2, ventral valve exterior; D, NMW 2018.4G.3, ventral valve interior; E–F, NMW 2018.4G.9, dorsal valve exterior and side view; G, NMW 2018.4G.4, ventral valve interior. H–K, *Narynella ferganensis* (Andreeva, 1962), Cambrian (Wuliuan) olistolith, Madygen, northern footsteps of eastern Turkestan Range, Kyrgyzstan: H–I, NMW 2018.4G.10, exfoliated ventral valve exterior and posterior view; J, NMW 2018.4G.11, dorsal valve exterior; K, NMW 2018.4G.12, strongly exfoliated dorsal valve exterior showing notothyrial platform. All scale bars represent 2 mm.

uniplicate) anterior commissure, an absence of well-defined concentric lamellae, a narrow pseudodeltidium not exceeding one-quarter of maximum shell width, and a complete absence of the dorsal and ventral sulcus.

Nisusia multicostata differs from *Nisusia paspelovi* Aksarina, 1960, from the Mundybash Regional Stage (Wuliuan) of Gornaya Shoriya, Russia in having a maximum shell width at the hinge line, rectangular (not obtuse) cardinal extremities, a subequally biconvex (not dorsibiconvex) shell, a rectimarginate (not emarginate)

anterior commissure, a narrow pseudodeltidium not exceeding one-quarter of maximum shell width, planar, not umbonally incurved ventral interarea, a concave umbonally, convex anteriorly sagittal profile of the ventral valve, and a complete absence of the dorsal and ventral sulcus.

Nisusia multicostata differs from *Nisusia granosa* Mao *et al.*, 2014, from the Kaili Formation (Wuliuan) of Guizhou, South China in having a subequally biconvex shell, a complete absence of the ventral sulcus, and a concave

umbonally, becoming convex anteriorly (not straight) sagittal profile of the ventral valve.

Nisusia multicostrata differs from *Nisusia vaticina* (de Verneuil & Barrande, 1860), from the upper member of the Láncara Formation (Wuliuan) from Cantabrian Mountains, north-west Spain (Wotte & Mergl 2007) in having a subequally convex (not ventribiconvex shell with a rectimarginate (not uniplicate) anterior commissure, a narrow pseudodeltidium not exceeding one-quarter of maximum shell width, and a complete absence of the dorsal sulcus.

Genus NARYNELLA Andreeva, 1987

Type species. By original designation *Nisusia ferganensis* Andreeva, 1962.

Diagnosis (emended). Shell ventribiconvex to subequally biconvex with gently unisulcate anterior commissure; ventral valve sagittal profile moderately convex with maximum height anterior to umbo. Ventral interarea planar, catacline; low ventral median fold and dorsal sulcus originating at mid-length. Dorsal interior with low notothyrial platform, faint double septa and radially arranged adductor scars; mantle canals pinnate in both valves.

Species assigned. *Nisusia ferganensis* Andreeva, 1962, Miaolingian, Wuliuan (probably *Sdzuyella-Aegunaspis* Beds), Madygen, northern footsteps of eastern Turkestan Range, Kyrgyzstan; *Narynella* cf. *ferganensis* Andreeva, 1962, Miaolingian, Drumian, *Ptychagnostus attavus* Zone, Kyrshabakty, Malyi Karatau Range, Kazakhstan (Holmer *et al.* 2001).

Remarks. The generic diagnosis is emended here mainly due to inconsistencies spotted by Geyer *et al.* (2014b) in the previous diagnosis of the genus given by Popov & Williams (2000).

Narynella ferganensis (Andreeva, 1962)

Figure 4H–K

- 1962 *Nisusia ferganensis* Andreeva; p. 89, fig. 2.
- 1975 *Nisusia nasuta* var. *ramosa* Nikitin; Aksarina, p. 97, pl. 5 figs 10–15.
- 2014b *Narynella* cf. *ferganensis* (Andreeva); Geyer *et al.*, p. 390, fig. 8A–J.

Holotype. CNIGR 6/8202, exfoliated ventral valve, Miaolingian, Wuliuan (probably *Sdzuyella-Aegunaspis*

Beds), Madygen, northern footsteps of eastern Turkestan Range, Kyrgyzstan.

Material. NMW 2018.4G.10 (Fig. 4H, I), CNIGR 7/8202, ventral valves; NMW 2018.4G.11 (Fig. 4J), NMW 2018.4G.12 (Ld = 11.1 mm, W = 15.4 mm; Fig. 4K), NMW 2018.4G.13, CNIGR 9/8202 (Ld = 14 mm; W = 17 mm), dorsal valves. Locality as for holotype.

Description. Shell slightly ventribiconvex, transverse, subrectangular in outline with hinge line slightly shorter than maximum shell width at mid-length. Cardinal extremities obtuse. Anterior commissure sulcate. Ventral valve lateral profile gently concave immediately anterior to umbo, then moderately convex, with maximum height slightly anterior to umbo. Pseudodeltidium broad, convex, slightly exceeding one-third of ventral interarea width. Umbo raised, pointed ventrally and terminated with circular foramen. Poorly defined median fold present anterior to mid-length of mature individuals. Dorsal valve evenly convex with maximum height between umbo and mid-length. Dorsal interarea apsacline with broad, open notothyrium. Radial ornament multicostellate with 6–9 rounded ribs per 3 mm along anterior margin of mature individuals. Ribs increasing in number both by intercalation and bifurcation and separated by interspaces slightly narrower than ribs.

Ventral interior without distinctive characters. Dorsal interior with transverse socket plates bounding anteriorly narrow and shallow sockets, low notothyrial platform bisected medially weakly defined ridge and variably developed double septum bisecting weakly impressed adductor muscle field.

Remarks. The revised description of *Narynella ferganensis* presented here is based on the study of four specimens (most probably paratypes) donated to the late Alwyn Williams. The material is now housed in the National Museum of Wales, Cardiff, and illustrated types deposited in the CNIGR Museum (St Petersburg). In the original description of the species (Andreeva 1962) there is no precise data on the fossil locality at Madygen, while the 'lower' Cambrian age of the source rock was misleading as pointed out by Geyer *et al.* (2014b). The description of Andreeva (1962) unfortunately provided illustrations that are of poor quality, and no data on the interior of either valve was given. Andreeva's specimens of *Narynella* cf. *ferganensis* came from an allochthonous limestone block at the Sauk Tanga gorge. It is most probably the type locality and the illustrated specimens are topotypes. As shown by detailed geological mapping performed in the Turkestan and Alai ranges by the South Kyrgyz Geological Survey shortly before the collapse of the USSR, the Cambrian rocks in the area occur exclusively as olistoliths and olistostromes in the Silurian Pulgon Formation (Koren *et al.* 1993; Holmer *et al.* 2000), which were shown, probably erroneously, on the schematic map presented by Geyer *et al.* (2014b) as the 'Ordovician

siliceous shale'. The Cambrian outcrops of the Sauk Tanga gorge were also briefly described by Repina *et al.* (1975), and this publication contains a description of *Narynella ferganensis*, which was erroneously identified by Aksarina as *Nisusia nasuta* var. *ramosa* Nikitin, 1956 (see also Geyer *et al.* 2014b). While these specimens came from a different fossil locality at Sulukty Gorge, they represent a useful addition to Andreeva's (1962) original description of the species, because the dorsal internal mould illustrated by Aksarina (1975, pl. 5, fig. 15) shows a distinct dorsal double septa. The specimens from Sulukty occur in the *Sdzuyella–Aegunaspis* Beds as defined by associated trilobites, so they are approximately contemporaneous with those from Madygen (Geyer *et al.* 2014b).

Genus BELLISTROPHIA nov.

LSID. urn:lsid:zoobank.org:act:34C5D2A7-EC71-40F7-876D-7682D55B39A5

Derivation of name. After Charles Bell in appreciation of his studies of the Cambrian brachiopods and biostratigraphy of North America.

Type species. *Nisusia deissei* Bell, 1941.

Diagnosis. Shell subequally biconvex to slightly dorsibiconvex, with hinge line shorter than maximum shell width at mid-length, variably emarginate anterior commissure and sulcus present in both valves. Ventral valve lateral profile moderately convex with maximum height between umbo and mid-length. Ventral interarea apsacline with broad, convex pseudodeltidium. Dorsal valve evenly convex with anacline interarea. Radial ornament multicostellate with rounded ribs increasing in number mainly by intercalation. Impressions of muscle scars undiscernible in both valves.

Species assigned. In addition to the type species, the genus includes *Nisusia montanensis* Bell, 1941, from the Meagher Limestone, *Ehmania* Zone (Miaolingian, Wuliuan) of Montana, USA and *Bellistrophia* sp. from the Atei Formation (Miaolingian, Wuliuan) of the Chingiz Range, Kazakhstan.

Species questionably assigned. *Protorthis spencei* Walcott, 1905, from Led Shale Member (formerly Spence Shale Member) of Langston Formation (Miaolingian, Wuliuan), of Idaho, USA. Species is inadequately known. Its provisional generic affiliation is mainly due to assessment of Bell (1941) who recognized a general similarity of the

taxon to *Nisusia* (= *Bellistrophia*) *desei* and reported a complete absence of spines.

Remarks. *Bellistrophia* differs from *Nisusia* Walcott, 1905, in the complete absence of hollow spines, as well as in having an apsacline ventral interarea and an emarginate anterior commissure. It differs from *Narynella* Andreeva, 1987 in having emarginate (not unisulcate) anterior commissure, apsacline (not catacline) ventral interarea, and in the absence of a ventral median fold and dorsal double septa; although *Bellistrophia* has an emarginate (not uniplicate) anterior commissure, a dorsal sulcus and multicostellate radial ornament unlike *Eoconcha* Cooper, 1951.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/18CD19D5-EDF4-40D0-A657-6411CAB05BBE>.

The character matrix is also available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q80p8j4>.

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