Original article

Ordovician (Caradoc) Gastropoda of the Katkoyeh Formation,
Kerman Province, IranGastéropodes ordoviciens (Caradoc) de la Formation Katkoyeh,
province du Kerman, IranJan Ove R. Ebbestad^a, Michael G. Bassett^{b,*}, Mohammad Dastanpour^c, Leonid E. Popov^b^a *Evolutionsmuseet, Uppsala Universitet, Norbyvägen 16, 752 36 Uppsala, Sweden*^b *Department of Geology, National Museum of Wales, Cathays Park, Cardiff, Wales CF10 3NP, UK*^c *AmirKabir Boulevard, P.O. Box 76185-1115, Private College, Kerman, Iran*

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Abstract

Seven taxa of gastropods are described from the Ordovician (Caradoc) upper Katkoyeh Formation of the Kerman region, east-central Iran. Three are named species and four are under open nomenclature. The most abundant is the minute bellerophontiform *Tritonophon peeli* Horný, 1977, indicative of a shallow water plectonotid community. Shell material is not preserved in this species, but a small, simple bulbous protoconch is present. Two new species are *Slehoferia pachyta* and *Nonorios kleistos*, both with prominent thick-shelled conchs. Shell repair is documented in both of these forms, interpreted as a result of failed predation. Other micromorphic species occur in the samples, but only *Tropidodiscus* sp. and *Nonorios?* sp. are named. The Kerman assemblage is comparable directly with similar, closely coeval faunas in Bohemia, France, Portugal, Morocco, and Italy, corresponding with the Palaeozoic Mediterranean Province of northern peri-Gondwana.

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Résumé

Sept taxa de gastéropodes sont ici décrits, en provenance de la partie supérieure de la Formation Katkoyeh (Ordovicien, Caradoc), région de Kerman (centre-est de l'Iran). Trois d'entre eux sont des espèces nommées, tandis que les quatre autres restent en nomenclature ouverte. Le plus abondant est le petit bellérophontiforme *Tritonophon peeli* Horný, 1977, indicateur d'une communauté plectonotide de mer peu profonde. La coquille n'est pas préservée pour cette espèce, mais une petite protoconque simple, de forme globulaire, est présente. Deux nouvelles espèces sont les *Slehoferia pachyta* et *Nonorios kleistos*, toutes les deux avec une coquille très épaisse. Une réparation de ces coquilles, observée dans les deux formes, est interprétée comme une tentative avortée de prédation. D'autres espèces micromorphiques se rencontrent dans l'échantillonnage, mais seulement *Tropidodiscus* sp. et *Nonorios ?* sp. sont nommées. L'assemblage de Kerman est comparable directement aux faunes similaires et isochrones de Bohême, France, Portugal, Maroc et Italie, ce qui correspond à la Province paléozoïque méditerranéenne du péri-Gondwana septentrional.

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Keywords: Gastropoda; Ordovician; Iran; Shell repair; Biogeography**Mots clés :** Gastéropodes ; Ordovicien ; Iran ; Réparation de coquille ; Biogéographie**1. Introduction**

Gastropods comprise the most common and most diverse elements of the molluscan biota within the upper Katkoyeh Formation to the north-west of Kerman city in east-central Iran (Fig. 1). Sparse cephalopods are restricted to a single taxon

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Fig. 1. Location of the three sections through the upper Katkoyeh Formation described in this paper.

(Dastanpour et al., 2006) and there are a few species of bivalves in limited numbers, currently under separate investigation. Other invertebrates in the sequence are mostly brachiopods, bryozoans and ostracodes (e.g. Hamed et al., 1997; Bassett et al., 1999, 2004; Ross et al., 2000).

Well over 500 gastropod specimens assigned here to seven taxa have been collected from three sections in the outcrop area along the eastern side of the Kuh Banan Fault complex (Fig. 1). The age of the upper Katkoyeh Formation is now well constrained as being within the Caradoc Series of the early Upper Ordovician, and the gastropods provide valuable evidence to allow further precision of correlation within this time span. Equally importantly, the gastropod assemblages provide clear signals of close biogeographical linkages with other regions of northern peri-Gondwana.

This is the first description of Palaeozoic gastropods from anywhere in Iran. It is not unlikely that our material incorporates the taxa reported by Huckriede et al. (1962: pp. 46, 48) as ‘indeterminate gastropod steinkern’ from west of Shabdjereh and ‘tiny *Cyrtolites* sp.’ from near Assiab; both these localities are within the region covered in this paper, and both were reported as being of Ordovician age.

All Katkoyeh material described here is housed in the National Museum of Wales, Cardiff, U.K. (NMW Accession Number 2003.8G); original field data are also housed at the Museum. Overall conclusions are the joint consensus of all authors. Most collecting was undertaken initially by Bassett and then by Bassett and Popov, following initial field guidance by Dastanpour. Sections on taxonomy and shell repair are mainly the responsibility of Ebbestad, with the authorship of the two new taxa restricted to Ebbestad and Bassett.

2. Localities and stratigraphy

As mapped by Huckriede et al. (1962: Fig. 8) and by Vahdati Daneshmand et al. (1995), Lower Palaeozoic strata crop out some 12 km east of Zarand, confined entirely to the east of the

Kuh Banan Fault complex in a series of complementary folds extending from near Dahu in the south for some 20 km towards Gischk in the north (Fig. 1).

Our gastropod faunas are from three stratigraphical sections spanning approximately the same interval through the middle-upper part of the Katkoyeh Formation as named by Hamed et al. (1997, Fig. 2) and Ross et al. (2000, Fig. 2). Older Katkoyeh rocks contain graptolites of early Ordovician (Arenig) age (Rickards et al., 1994, 2001) and are separated from the upper Katkoyeh in places by basaltic sills and then a unit of reddened maroon quartzites and micaceous sandy siltstones (so far unfossiliferous) that we take as a basal datum for each of our sections. An earlier report of a possible Llandeilo age for the oldest beds of the upper Katkoyeh Formation (Bassett et al., 1999) is now discounted, and there is good agreement that this part of the sequence begins in the Caradoc (e.g. Ross et al., 2000; Dastanpour et al., 2006); the gastropods described here strongly endorse this conclusion. A distinctive unit of green-weathering laminated and sandy siltstones everywhere forms the conformable uppermost member of the Katkoyeh Formation, and although it may well extend into the uppermost Ordovician/Ashgill (e.g. Hamed et al., 1997: Fig. 2), there is as yet no independent palaeontological evidence to confirm this. Conodonts from the succeeding Shabjereh Formation are suggestive of the Silurian (Bassett and Dastanpour, personal observations).

We are separately describing full details of this stratigraphy and faunal succession elsewhere. Here we comment on the salient points that provide the essential information for locating the three studied sections (Fig. 1) and for setting the gastropod faunas in a stratigraphical and biogeographical context.

2.1. Banestan

Coordinates 30°51′59″N, 056°39′12″E. Sequence exposed on both sides of dry river bed (wadi), c 300 m north of track and

Gs	Ts	Avalonia	Perunica	Armorica-Iberia Carnic Alps	Anti-Atlas	Iran	Baltica	Kazakhstan	Laurentia
Upper Ordovician	6c	Hi					Po		
	6b	Ashgill					Pi		
	6a	Pu	Kr				Vo		
	5d	St					Na		
	5c	Ch					Rk		
	5b	Bu					Oa		
Middle Ordovician	5a	Au					Ha		
	4c	Ll					Ku		
	4b	Ab					Uh		
							La		

Fig. 2. Distribution of Ordovician species of *Tritonophon* Öpik, 1953; *Slehoferia* Rohr and Frýda, 2001; and *Nonorios* Horný, 1997c; arranged according to terrane. Stratigraphical chart follows that of Webby et al. (2004). Gs = Global series; Ts = Time slices: Stratigraphical abbreviations of stages in descending order from left to right in the table: Hi = Hirnantian, Ra = Rawtheyan, Ca = Cautleyan, Pu = Purgillian, St = Streffordian, Ch = Cheneyan, Bu = Burrellian, Au = Aurelucian, Ll = Llandeilo, Ab = Abereiddian, Po = Porkuni, Pi = Pirgu, Vo = Vormsi, Na = Nabala, Rk = Rakvere, Oa = Oandu, Ke = Keila, Ha = Harju, Ku = Kukruuse, Uh = Uhaku, La = Lasnamägi, As = Aseri, Ku = Kunda. For Perunica, the stage abbreviation Kr = Kráľodvor. Local chronostratigraphical units are used in this figure in order to relate directly to known local stratigraphical distributions.

adjacent to the small farm approximately 0.75 km WNW of Banestan village. Measured section through some 85 m of siltstones, calcareous mudstones and argillaceous limestones, subdivided into five collecting units. Dip 45°NE from a strike of N55°W. Bassett field collections Iran 98/17A-17E, 02/11A-11E.

2.2. Gezueh

Coordinates 30°50'57"N, 056°42'15"E. Low hillside section on south side of track immediately NE of Zarkhiz farmstead, c. 4.5 km NE of Gezueh village. Measured section through 12 lithological packets of heterolithic siltstones, sandstones, mudstones and calcareous sandstones/shales/sandy limestones; includes units with silicified and phosphatised faunas. Dip 85°–95°S from a strike of N81°E. Bassett field collections Iran 11A–11E, 02/6–9.

2.3. Katkoyeh

Coordinates 30°51'00"N, 056°42'40"E, section in low hillside on S side of track a few kilometres NNW of Dahu village, and repeated 50–60 m along strike to the W on the N side of track on N side of sharp curving bend. This is the type sequence for the upper Katkoyeh Formation, comprising some 43 m of calcareous and sandy siltstones, muddy limestones and argillites; some units are distinctly channeled and there are coquinoid high energy shell accumulations at some levels. Dip 70°–80°N from a strike of N94°E. Bassett field collections 98/14A–14H, 02/10A–10G.

3. Systematic palaeontology

Terminology and classification mainly follow Peel (1974) for the isostrophic planispiral *Tritonophon*, and Wagner (2002) for the anisostrophic conispiral taxa. Measurements of whorl expansion rate (W) are based on Raup (1966), and the rate of expansion at half whorl intervals (V) is measured as by Peel (1974). Inclination (E) of the whole apertural plane refers to the elevation angle of Vermeij (1971). Umbilical angle is used as defined by Ebbestad (1999).

Class GASTROPODA Cuvier, 1797

Family BELLEROPHONTIDAE M'Coy, 1851

Subfamily PLECTONOTINAE Boucot and Yochelson, 1966

Genus *Tritonophon* Öpik, 1953

Type species: By original designation; *Kokenospira* (*Tritonophon*) *trimetra* Öpik, 1953, p. 20, Pl. 7, Figs. 52–54, from the Lower Silurian (Llandovery), Wapentake Beds (lower part – 'Illanus Band'), Heathcote, Victoria, Australia.

Diagnosis emended and modified from Peel (1974) and Horný (1997b): Bellerophontid with 3–4 whorls bearing a strongly trilobed median dorsal lobe, the selenizone occupying the full width of the upper surface of the central lobe. Spiral ornamentation on entire shell common, but may be lacking in some species.

Discussion: Seven species of Ordovician *Tritonophon* are recognized currently (Fig. 2). The genus ranges from the Llanvirn through the Ashgill (Rawtheyan), mainly in shallow water siliciclastic sediments (Benthic Assemblage 1-2) of West Gondwana (see discussion of palaeogeography below). At least

Table 1

Known Ordovician and Silurian species of *Tritonophon* Öpik, 1953, arranged according to palaeocontinental distribution

Species, located by palaeogeographical terranes	Stratigraphical ages and localities
Eastern Gondwana	
<i>T. trimetra</i> Öpik, 1953	Wapentake Formation (Llandovery, Telychian), Heathcote, Victoria, Australia.
Western Gondwana	
<i>T. ? bohemica</i> (Perner, 1903; Horný (1997b) <i>T. peeli</i> Horný, 1997b; 1) Horný (1997b, d); 2) this paper	Kráľův Dvůr Formation (Kralodvor), Lejskov and Praha–Bechovice, Barrandian Area, Czech Republic 1) Letná, Zahorany and Bohdalec formations (Beroun), Praha–Vysocany, Barrandian Area, Czech Republic and Lower Ktaoua Formation (Caradoc, Aurelucian–Burrellian), Jbel Tafenna and Jbel Bou Ingart (south-east and east-north-east of Zagora), Anti-Atlas, Morocco; 2) Upper Katkoyeh Formation (Caradoc) near Gezueh, east of Zarand, Kerman Province, Iran.
<i>T. trilobata</i> (Sowerby in Murchison, 1839); 1) Tromelin and Lebesconte (1875); 2) Delgado (1897, 1908); Pillet (1992)	1) Schistes d'Angers Formation (Llanvirn), La Bouexière, Chevré, Riadan, Domfront, and Falaise, Armorican Massif, France; 2) Louredo Formation (Caradoc), Bucaco, Portugal.
Kazakhstan	
<i>T. ? sp. sensu</i> Mironova (1979)	Dulankarinsky Horizon (Upper Ordovician), Betpak–Dala, Kazakhstan.
Baltica	
<i>T. trilobata</i> (Sowerby in Murchison, 1839); 1) Lindström (1884); 2) Moberg and Grönwall (1909); 3) Peel (1974)	1, 3) Hemse Group (Ludlow, Gorstian–Ludfordian), Petesviken, and Burgsvik Sandstone (Ludlow, Ludfordian), Burgsvik, both Gotland, Sweden; 2) Öved–Ramsåsa Group (Ludlow, Ludfordian), Ramsåsa and Klinta, Scania, Sweden.
<i>T. subtrilobatus</i> (Troedsson, 1919)	Lindegård Mudstone (Harjuan–Pirgu), Röstängen, Scania, Sweden.
Avalonia	
<i>T. trilobata</i> (Sowerby in Murchison, 1839); 1) Straw (1933); 2) Pitcher (1939); 3) Peel (1974)	1) Drillcore (Přídolí) at Little Missenden, Buckinghamshire; England; 2) Purple Shales, Pentamerus. Beds (Llandovery) near Minsterley, Shropshire, England; 3) Cefn Einion Formation: (Ludlow–Ludfordian) at Felindre, Radnorshire, Wales.
<i>T. aff. bohemica</i> (Perner, 1903); Williams and Wright (1981)	Rawtheyan Siltstones (Ashgill, Rawtheyan), Chapel and Garth, SW Powys, Wales.
Laurentia	
<i>T. kivialonae</i> Peel, 1974	Stonehouse Formation (Přídolí), Arisaig, Nova Scotia, and Jones Creek Formation (Přídolí), New Brunswick, both Canada.
<i>T. trilobata</i> (Sowerby in Murchison, 1839); Peel (1974)	Green Member, Moydart Formation (Přídolí), Sutherland River, Pictou County, Arisaig, Nova Scotia, Canada. 1) Medina Sandstone, Medina Group (Llandovery), Medina, and Clinton Group (Llandovery), New Hartford, Oneida County, New York; 2) Mifflintown Formation (Ludlow) near Mifflintown, Juniata County, Pennsylvania; 3) Rose Hill and Rochester (Llandovery–Wenlock), Rose Hill, Cumberland, Six-Mile House, and Cresaptown, Maryland State; 4) Upper Ross Brook and French River formations (Llandovery–Wenlock), from Arisaig, Nova Scotia, Canada; 5) Brassfield Formation (Llandovery), Brassfield, Cleveland, Ohio. All U.S.A. unless noted otherwise.
<i>T. trilobata sensu</i> Conrad (1839), non Sowerby in Murchison (1839); 1) Hall (1843, 1852); 2) Foerste (1893); 3) Swartz and Prouty (1923); 4) Butts (1942); 5) Peel (1974); 6) Harrison and Harrison in Pojeta and Pope (1975)	Beechhill Cove, Upper Ross Brook, and French River formations (Llandovery–Wenlock), Arisaig and French River; Nova Scotia, Canada.
<i>T. sp.</i> ; Peel (1975)	Góeland Member, Jupiter Formation (Llandovery, Aeronian) at Schmitt Creek, Anticosti Island, Quebec, Canada.
<i>T. sp.</i> (pers. observation, JORE)	Reedsville Formation (Cincinnatian) at numerous localities in West Virginia, south-central Pennsylvania, U.S.A.
<i>T. sp.</i> ; Bretsky (1970)	

The Carboniferous record by Amler and Heidelberg (2003) is not shown.

a dozen Silurian species are known, distributed mainly in Laurentia, Baltica, and Avalonia (Table 1). A Carboniferous species has also been identified tentatively (Amler and Heidelberg, 2003), but these post-Ordovician forms are not considered further here in any detail.

The morphologically similar genus *Plectonotus* Clarke, 1899 appears to be restricted to the Silurian and Devonian (Boucot and Yochelson, 1966; Peel, 1974). Uncertainties remain concerning the affinity of the unfigured and undescribed Portuguese and French Ordovician specimens referred to *Bellerophon trilobatus* Sowerby in Murchison, 1839 (Tromelin and Lebesconte, 1875; Delgado, 1897, 1908; Pillet, 1992; Table 1). The North American *Plectonotus*? sp. of Bretsky (1970) was assigned to *Tritonophon* by Horný (1997b: p. 337). The Kazakhstan *Plectonotus*? sp. from

the Ashgill Dulankarinsky Regional Stage (Mironova, 1979) is also reassigned here tentatively to *Tritonophon*.

The species *T. peeli* Horný, 1997b, from the Ordovician of Bohemia (Horný, 1997b), and the North American Silurian *T. trilobata sensu* Conrad, 1839 non Sowerby in Murchison, 1839 (unfigured specimen from Pennsylvania discussed by Foerste, 1893; United States National Museum 88544) are both unusual in lacking spiral ornamentation. Horný (1997b) suggested emendation of the generic diagnosis to encompass this difference, a recommendation adopted here.

Several specimens of *Tritonophon* from Kerman preserve the internal mould of the protoconch. This is simple, short and bulbous, with space for shell material on the ventral side of the abutting second whorl (Fig. 3 (15)). Few protoconchs of early

Fig. 3. 1–17. *Tritonophon peeli* Horný, 1997b. 1–6, silicified specimen (2003.8G.72) with partially preserved apertural margin. All $\times 10$. 7, lateral view of 2003.8G.74, $\times 20$, the typical form in the samples. 8, 12, lateral and dorsal views of 2003.8G.82, $\times 20$, a narrow form. 9, 10, posterior and lateral views of 2003.8G.86, silicified, $\times 12.5$. 11, 16, 17, lateral, anterior oblique, and dorsal views of typical phosphatic infilling, 2003.8G.75, $\times 20$. 13, internal mould, dorsal view, 2003.8G.76, $\times 20$. 14, internal mould, ventral view, 2003.8G.77, $\times 20$. 15, internal mould with detail of left umbilicus with protoconch, 2003.8G.78, $\times 55$. 18–20. *Tropidodiscus* sp. 18, internal mould, ventral view, 2003.8G.69, $\times 10$, showing distinct heart-shaped whorl profile. 19, lateral view of small internal mould, 2003.8G.70, $\times 20$. 20, lateral view of internal mould, 2003.8G.71, $\times 10$.

bellerophonitiform molluscs are available for comparison, but the *Tritonophon* protoconch is less expanded than that in *Bellerophon* cf. *scaber* (Perner, 1903), as described by Frýda (1999) from the Silurian of Bohemia. The minute specimens of *B.* cf. *scaber* were interpreted as multiwhorled protoconch stages, and they are significantly smaller than the *Tritonophon* specimens described in this paper.

Tritonophon peeli Horný, 1997b

Figs. 3(1–17) and Fig. 4.

Material: About 240 specimens are present in the fauna, from which 13 were selected for closer examination (NMW 2003.8G.72, 74, 75–80, 82–84, 86, 88). Most are phosphatic internal moulds, but silicified specimens are also present

(NMW 2003.8G.72; see Fig. 3(1–6)). Samples Iran 11A–E (Gezueh), 98/14C, F (Katkoyeh).

Discussion: The Iranian specimens compare closely in overall morphology with *T. peeli* as described originally from Bohemia and Morocco, both as internal moulds and silicified shells. Ornamentation in the type material of *T. peeli* differs markedly from most other species of *Tritonophon* where these features are known, in lacking a spiral component but having a sharp delineation of the presumed selenizone (Horný, 1997b). Unfortunately, ornamentation is not preserved in the Kerman samples, which therefore does not exclude affinity with the closely related but younger *T?* *bohémica* (Perner, 1903). However, the latter is a rare species restricted to the Ashgill (see discussion by Horný, 1997b), and other faunal evidence is

Fig. 4. Cross section of *Tritonophon peeli* Horný, 1997b; (2003.8G.88). Black indicates matrix filled areas.

clearly indicative of an older age for the Kerman sequences (Bassett et al., 2004; Dastanpour et al., 2006). The presence of *T. peeli* suggests a correlation with the Letná through to Bohdalec formations of the Beroun Regional Stage, Bohemia (Fig. 2).

Full description of our Kerman material is not necessary because Horný's original description is comprehensive, but some features require comment. Whorl expansion rate in this species is high ($W = 4.9$; $V = 2.14$; Fig. 4). Few other cross-sections of *Tritonophon* species are illustrated in the literature (Peel, 1974) to allow numerical comparison, although it is clear that a number of species have high whorl expansion (W) of the last whorl. For example, the last whorl of the Silurian *T. kivitalonae* from Arisaig, Nova Scotia ($W = 5.48$; $V = 2.17$) is even more rapidly expanding than that of *T. peeli*. Expansion at half whorl intervals is the same in the two species. The whorls of the widely distributed Silurian *T. trilobata* are more slowly expanding ($W = 2.88$; $V = 1.69$) and narrow. Umbilical angles in *T. peeli* and *T. trilobata* are both moderate (75°), while that of *T. kivitalonae* is narrow at 30° (see Peel, 1974 for the latter two species). The shell of *T. peeli* therefore appears to be less laterally compressed than that of *T. trilobata* (compare Fig. 4 with Peel, 1974, fig. 12), although there appears to be intraspecific variation in the Iranian material (compare Fig. 3(12) with Fig. 3(13)). In NMW 2003.8G.72 (Fig. 3(2, 3)) a posterior and posterolateral apertural edge is present, which has not been observed in other species of *Tritonophon* in which the apertural margin is preserved (for example in USNM 88544, *T. trilobata* sensu Conrad as noted above).

The Swedish late Ordovician species *T. subtrilobatus* (Troedsson, 1919) has a distinct trilobation but the vaulting is less prominent and the upper surface of the median lobe is more flattened than in *T. peeli*. The Avalonian Ashgill species

T. aff. bohémica (Perner, 1903) sensu Williams and Wright (1981) is similar to the contemporaneous Swedish species in the expression of the median dorsal lobe, but appears to have a faster rate of whorl expansion. Compared with most other species, the median dorsal trilobation in both *T. sp. sensu Bretsky* (1970) from the late Ordovician of the U.S.A. and *T? sp. sensu Mironova* (1979) from the late Ordovician of Kazakhstan, although distinct, appears to be broad and very low with narrow lateral lobes.

Family TROPIDODISCIDAE Knight, 1956

Genus *Tropidodiscus* Meek and Worthen, 1866

Type species: By original designation of Meek and Worthen (1866: p. 160); *Bellerophon curvilineatus* Conrad, 1842, p. 269, Pl. 16, Fig. 7, from the Lower Devonian (Eifelian) Onondaga Limestone at Schoharie, New York, U.S.A.

Tropidodiscus sp.

Fig. 3(18–20).

Material: Three internal moulds (NMW 2003.8G.69–71). Sample Iran 11E (Gezueh).

Discussion: The three available specimens are a minute species (1.2–3.5 mm) with three whorls. Apart from *Tritonophon*, this genus is the most widely distributed in the Mediterranean Province, although specific taxonomy is again largely unresolved. The minute *Tropidodiscus pusillus* (Barande in Perner, 1903) is the most common gastropod in the Ordovician Šárka Formation of Bohemia and the Tachilla Formation of Morocco, where hundreds of specimens have been recovered from siliceous and silty concretions (Horný, 1997a, 1997d, 2002). Two unnamed and less common younger species occur in the Bohemian Zahořany and Králův Dvůr formations respectively (Horný, 1997a, 2002). Pillet (1992) reported *T. acutus* (Sowerby in Murchison, 1839) from concretions in the Llanvirn Schistes d'Angers Formation of the Armorican Massif, France. This species name seems to be a widely used collective name for different species, making it difficult to interpret its true distribution.

Comparison of the Iranian species with any of these four taxa is further hampered by the poor state of preservation, except that they are all small (less than 7 mm maximum length).

Superfamily LOPHOSPIROIDEA Wenz, 1938

Family TROCHONEMATIDAE Zittel, 1895

Genus *Slehoferia* Rohr and Frýda, 2001

Type species: By monotypy; *Trochonema excavatum* Barrande in Perner, 1903, Pl. 71, Figs. 1–4; 1907, pp. 216–217, from the late Ordovician (Caradoc; Beroun) Zahořany Formation at Dubeč, Barrandian basin, Bohemia, Czech Republic.

Discussion: Rohr and Frýda (2001) proposed the operculate monotypic genus *Slehoferia* for a minute Barrandian species (Perner, 1907: p. 216), earlier allied with *Trochonema* Salter, 1859. The new genus was justified by the size and position of its sinus and the angulation on the upper whorl of the teleoconch. The left and right sides of the sinus of *Slehoferia* curve symmetrically and continuously back across the periphery, forming a sinus of moderate depth. A sinus keel is developed,

emphasizing the distinct angulated upper whorl surface. The base and inner margin of the aperture are thickened, but this does not fill the narrow umbilicus. *Slehoferia* was distinguished from species of *Trochonema* mainly by the lack of a lower spiral angulation (left ramp carina of Wagner, 2002), but placed in the Trochonematidae Zittel, 1895 based on the overall similarity of the teleoconch shape with members of this family. The Trochonematidae was allied with the Lophospiroidea Wenz, 1938, by Wagner (1999).

The two previously recognized species of *Slehoferia* are closely comparable with the monotypic stone-dweller *Kiviasukkaan nelsonae* Peel, 1975, from the Silurian (late Llandovery) Manistique Formation at Ashford, Wisconsin, U.S.A. This genus is characterized by the lack of a well-defined sinus, gradate upper whorl profile, a narrowly phaneromphalous shell, and disjunct coiling of the final apertural part of the whorl. It differs from *Slehoferia* in the latter respect, but also in lacking a thickened inner margin. The base in both genera is wide, but in *Slehoferia* the shell is substantially more thickened.

In *Kiviasukkaan*, only an incipient sinus is recognized, as is the case with the Iranian *Slehoferia*. The Bohemian type species of *Slehoferia* has a well-developed symmetrical sinus. In all these three forms, a peripheral sinus keel is developed. Wagner (1996, 1999) demonstrated a morphological trend in reduction of sinus depth in lophospiroids and, at the same time, a reduction in the expression of the sinus keel, such as in derived *Trochonema* and the *Loxoplocus* Fischer, 1885 clade (Caradoc–Ashgill). These characters were interpreted by Wagner (1999) as independent homologues, the development of which was unrelated in time and space. Characters of *K. nelsonae* were considered by Wagner (1999) to conform to this trend, and the genus was synonymized with *Loxoplocus*. Peel (1975) discussed affinities of *Kiviasukkaan* with members of the trochonematoids (*sensu* Knight et al., 1960), such as *Globonema* Wenz, 1938 and *Trochonema*, emphasising the shallow emarginations and somewhat similar peripheral angulation.

The inclusion of our Iranian species in *Slehoferia* suggests that the genus has reduced peripheral keels, but at the same time includes species with both a shallow and a well-developed sinus. This combination of characters within species of the genus can be interpreted as trends of independent sinus and keel reduction in lophospiroids as demonstrated by Wagner (1996). At the same time, the most common model of speciation in the lophospiroids occurred with ancestors and descendants coexisting (budding cladogenesis). Homoplasy through convergence was more prominent in stratigraphically younger species (Wagner, 1999), which is evident in the broadly similar shell morphology of *Slehoferia* and *Kiviasukkaan*.

Slehoferia pachyta Ebbestad and Bassett sp. nov.

Figs. 5(1–12), 6, 7(1–14) and 8(1–9).

Derivation of name: From the Greek *pachys* (thick), referring to the marked sutural thickening of the shell.

Holotype: NMW 2003.8G.13; sample 98/14E (Katkoyeh); a large, complete specimen with well-preserved aperture and base. The upper part of the spire is obscured by bryozoan overgrowth.

Paratypes: An additional 34 specimens (NMW 2003.8G.14–47); samples 98/14A, 14E, 02/10A, 10B (Katkoyeh), 02/11D (Banestan). The largest specimen (NMW 2003.8G.26) is 3.8 cm high, while the smallest (NMW 2003.8G.45) is 1 cm high (incomplete spire and base).

Diagnosis: Large species of *Slehoferia* with an anomphalous shell at maturity, a thick columella, thick shell in the basal part, transverse growth-lines for much of ontogeny, and an incipient sinus at the apertural margin at maturity.

Description: Five whorls of moderate whorl expansion ($W = 1.74$). Shell width almost 66% of shell height. Apical angle about 105° . Whorl embracement is at the periphery of the previous whorl, with weak suture indentation. Shell thickened greatly at suture, producing a subsutural welt, falsely emphasising sutural indentation. Upper whorl surface therefore has a prominent convex profile near the suture, with a concave transition to conspicuous marginal band or keel. The band appears as a thickening of the shell, thus forming a distinct shoulder at about 75% of the height of the whorl profile (as seen in apertural view). The profile of the left ramp below the carina is horizontal to broadly and evenly convex, placing the periphery at midwhorl. Shell thick, with additional thickening of the basal part. Aperture tangential, the inclination of the whole apertural plane (E) being 38° . In axial cross-section the aperture is elongated in early ontogeny, about twice as high as wide, but becomes more rounded at maturity (width/height ratio $\sim 66\%$); in the apertural plane the aperture opening is round. At maturity, a shallow, V-shaped, symmetrical apertural sinus forms, giving different inclination of left and right apertural margins ($\sim 30^\circ$ and $\sim 50^\circ$, respectively). The deepest point of the sinus coincides with the position of peripheral keel. Apertural lip thickened at both inner margin and base. The angle between the inner margin and base is $\sim 75^\circ$. Shell principally anomphalous in early ontogeny, but the umbilicus is so narrow that during ontogeny the inner margin fills it, creating a thick columella. Shape of inner margin of the base slightly excavated (in ventral view). Ornamentation consists of near-transverse growth lines throughout most of ontogeny. At the suture, the growth lines arch aperturally, their prosocline curvature enhanced partly when crossing the subsutural welt. This curvature is enhanced with the development of a peripheral sinus at maturity. Adumbilically, the growth-lines continue straight across the periphery.

Discussion: The most prominent feature of the heavy shell of this species is the almost undeflected traversing of the peripheral angulation by the growth lines, followed by development of a shallow median sinus in large, presumably mature shells. The sinus culminates at the peripheral angulation, where the supposed exhalant current from the mantle cavity would be located. There are no emarginations near the suture nor at the periphery in younger shells (evident from the transverse growth-lines). Younger shells have a proportionally thinner apertural margin and lack a sinus even in small specimens (e.g. NMW 2003.8G.45). Only toward maturity is the outer shell margin thickened and a sinus developed. It can be speculated that a change in mode of life in late ontogeny may have necessitated this type of reentrant. The

Fig. 5. 1–12. *Slehoferia pachyta* sp. nov. All $\times 1.4$ except Fig. 10, which is $\times 3.0$. 1–7, 10, holotype, 2003.8G.13, apertural, lateral, dorsal, ventral, dorsal oblique and various lateral views; specimen shows well preserved aperture with incipient sinus and thickened inner margin and base. 8, 9, 11, 12, lateral, dorsal oblique, dorsal, and further dorsal oblique views of 2003.8G.23; specimen shows well preserved growth lines.

anomalphous condition of the shell seems to be persistent through ontogeny. However, in cross-section the earliest whorls are separated, although abutting (see Fig. 6(1, 2)); thickening of the inner margin and base is evident at the onset of the teleoconch.

Except for the infilling of the umbilicus by the thickened inner margin, the Iranian species compares closely with the type species *S. excavata* (Barrande in Perner, 1903) in the shape of the apertural lip, the rounded inner whorl, the gradate profile

of the upper whorl surface, and the peripheral keel. The subsutural welt in *S. pachyta* is similar to that in *Kiviasukkaan nelsonae* (see discussion above), but it is less well developed in *S. excavata*. This may be attributed partly to the diminutive size of the type specimen of *S. excavata*. Although the height of specimens of *S. excavata* is variable (R. Horný, personal communication 2004), the main differences lie in the size of the two *Slehoferia* species. Differences in presence/absence of a sinus can be explained by the morphological trends observed in

Fig. 6. 1, 2. Cross sections of *Slehoferia pachyta* sp. nov. Scale bars = 0.5 cm. Black indicates shell material, white indicates space or matrix filled areas, white lines indicate where shell contours can be made out, grey indicates recrystallized areas. 1, large, mature specimen (2003.8G.24) demonstrating the greatly thickened inner margin and base. 2, young specimen (2003.8G.44) with the earliest whorls of the teleoconch preserved; although abutting, the whorls are separated.

the family of these gastropods (Wagner, 1996, 1999, see discussion above).

Our Iranian species compares equally well with the monotypic *Kiviasukkaan*, except for the phaneromphalous condition and the disjunct coiling in the latter. The seemingly increased whorl translation in the *S. pachyta* specimen in Fig. 7(14) is an artefact of shell repair and preservation (see section on shell repair). There are also differences in the shape, direction and development of the inner margin, which is upright and much thinner in *Kiviasukkaan*. The thick columella seen in the Iranian species invites comparison with the lophospiroid genus *Paupospira* Wagner, 1999, from Laurentia. Species of this genus are distinguished from *Slehoferia* by the presence of a deep and wide sinus and a prominent sinus keel that is usually trilineate on early whorls.

Rohr and Frýda (2001) described an occurrence of *Slehoferia excavata* with a plug-like operculum in place.

Opercula have not been found in the Kerman samples, although the shape of the inner whorl profile strongly suggests the original presence of a well-developed operculum.

Superfamily PLATYCERATOIDEA Hall, 1859

Family PLATYCERATIDAE Hall, 1859

Genus *Nonorios* Horný, 1997c

Type species: By original designation of Horný (1997c, p. 46); *Turbonitella pater* Barrande in Perner, 1903, Pl. 51, Figs. 1–3; 1907, p. 288, from the late Ordovician (Caradoc; Beroun) Zahořany Formation at Vráž, Barrandian basin, Bohemia, Czech Republic.

Discussion: In erecting the genus *Nonorios*, Horný (1997c) included an additional five species described by Perner (1903, 1907), which he placed in synonymy with the type species. In Bohemia the genus is restricted to the Beroun Regional Stage, ranging from the Letná through the Zahořany formations. It has also been recognized in the lower Ktaoua Formation (lowermost Beroun) of the Anti-Atlas, Morocco (Horný, 1997c, 1997d). A more extensive distribution in the Palaeozoic Mediterranean Province was later anticipated by Horný (2000, pp. 421–422), who considered this genus to be a characteristic element of the region. In this regard, we tentatively refer *Strophostylus carnicus* Vinassa de Regny, 1914 from the Ashgill Uggwa Limestone of the Italian Carnic Alps, to *Nonorios* (Table 2). One additional species was also referred tentatively to the genus by Horný (1997c), namely *Nonorios? transversum* Ulrich in Ulrich and Scofield, 1897, from the Cincinnati Fairmount Member, Fairview Formation of Cincinnati and Kentucky (see Thompson, 1970), which would then represent the youngest species of *Nonorios*.

The genus is characterised by having an almost closed umbilicus, which is completely closed at maturity in our Iranian species, with a large and heavy shell. The type species shows variation in both shell form and ornamentation, with both naticiform and turbiniform shells occurring with or without cancellate ornamentation. Horný (1997d; personal communication 2004) pointed out that the highly variable morphology causes problems with taxonomic determination, which is also a well known factor in the related genus *Cyclonema* Hall, 1852.

Nonorios kleistos Ebbestad and Bassett sp. nov.

Figs. 9(1–15), 10 and 11(1–7).

Derivation of name: From the Greek *kleistos* (closed or shut), referring to the complete closure of the umbilicus in mature specimens.

Holotype: NMW 2003.8G.48; sample 02/10C (Katkoeyeh); a medium size (2.7 cm high), almost complete specimen with only the uppermost spire and outer apertural margin missing.

Paratypes: Eight additional specimens (NMW 2003.8G.49–56); samples 98/14E, 02/10A, 10C (Katkoeyeh). The largest specimen (NMW 2003.8G.53) is 4.3 cm high, while the smallest (NMW 2003.8G.52) is 1 cm high (incomplete spire and base).

Diagnosis: Large species of *Nonorios* with low naticiform shell having a thickened base and inner margin that completely fills the umbilicus in late ontogeny.

Fig. 7. 1–14. *Slehoferia pachyta* sp. nov. 1–6, 11, various lateral, dorsal oblique, dorsal and ventral views of 2003.8G.14. All $\times 2.0$, except Fig. 11, which is $\times 5.0$. Well preserved growth lines run transversely across the whorl from the suture and adumbilically. 8, apertural view of 2003.8G.15, $\times 2.0$, demonstrating the massive development of the inner margin and the section of the shell at the peripheral thickening (white arrow). 7, 9, 10, ventral, apertural and lateral views of 2003.8G.16, all $\times 1.5$. 12–14, dorsal, dorsal oblique and lateral views of 2003.8G.27, $\times 1.5$. This is the largest specimen. Repaired shell injury is marked by disturbed growth of the whorl (at white arrow).

Description: Shell large, slightly higher than wide, low spired, naticiform with apical angle of 130° . Four rapidly expanding whorls ($W = 2.58$) with a circular inner cross section (axial section). Outer whorl profile evenly rounded, convex, with about 80% of the height of a whorl embraced by the following whorl. Shell generally thick with apertural lip thickened additionally at the base and inner margin to more

than twice the other shell thickness. Shell narrowly phaneromphalous in early ontogeny, but the thickened inner margin fills the umbilicus and provides a thick columella in late maturity. The greatly thickened shell at the base and the broad, excavated inner margin with a columellar excavation, create a distinct scoop-shaped transition between the inner margin and base. This is marked by a concave depression low on the outer

Fig. 8. 1–9. *Slehoferia pachyta* sp. nov. with shell repairs. All $\times 2.0$. 1, 4, 7–9, dorsal oblique, ventral oblique, lateral, dorsal, and further lateral view of 2003.8G.29. Distinct transverse repair on the last whorl. 2, 3, 5, 6, lateral, dorsal oblique, dorsal, and further dorsal oblique view of NMGW 2003.8G.28. This is the most substantial injury to specimens of this species.

Table 2
Known species of *Slehoferia* Rohr and Frýda, 2001, and *Nonorios* Horný, 1997c, arranged according to palaeocontinental distribution

Species, located by palaeogeographical terranes	Stratigraphical ages and localities
Laurentia	
<i>Nonorios? transversum</i> Ulrich in Ulrich and Scofield (1897); Thompson (1970); Horný (1997c)	Fairmount Member, Fairview Formation (Cincinnati) near Cincinnati, Ohio, and Covington and Newport, Kentucky, U.S.A.
Western Gondwana	
<i>Slehoferia excavata</i> (Barrande in Perner (1903), Rohr and Frýda (2001); Frýda and Rohr (2004)	Zahořany Formation (Beroun), Dubeč, Barrandian area, Czech Republic.
<i>S. pachyta</i> sp. nov.	Lower Katkoyeh Formation (Caradoc), near Gezeuh, east of Zarand, Kerman Province.
<i>N? carnica</i> (Vinassa de Regny, 1914)	Uggwa Limestone (Ashgill–Rawtheyan), Carnic Alps, Italy.
<i>N. pater</i> (Barrande in Perner, 1903); 1) Horný (1997c); 2) Horný (1997d)	1) Zahořany Formation (Beroun), Vráz, Barrandian area Czech Republic; 2) Lower Ktaoua Formation (Caradoc, Aurelucian/Burrellian), Bou el Koualb, Tizi ou Mekhazni and Isthou (east of Alnifa), Anti-Atlas, Morocco.
<i>N. kleistos</i> sp. nov.	Lower Katkoyeh Formation (Caradoc), near Gezeuh, east of Zarand, Kerman Province, Iran.

Fig. 9. 1–15. *Nonorios kleistos* sp. nov. 1–8, dorsal, lateral, lateral oblique, and ventral views of holotype (2003.8G.48). All $\times 1.5$. 9–15, dorsal, various lateral, lateral oblique and ventral views of largest specimen (2003.8G.53). All $\times 1.0$. Fractions of missing shell demonstrate its substantial thickness.

whorl profile in the anterior-most part of the last whorl. Aperture tangential, about twice as high as wide (in apertural view), with an inclination (E) of about 40° . Shape of inner margin base (viewed from base) slightly excavated (curved). A possible emargination is formed at the intersection of the suture and outer lip. Ornamentation consists of simple, transverse growth-lines throughout ontogeny.

Discussion: The substantially thickened naticiform shell of this species is striking in its appearance. The other noticeable feature is the elongated aperture with a columellar excavation and a scoop-shaped basal part of the inner margin. The excavation is similar, but not so pronounced, as that on the inner margin of some species of *Cyclonema* Hall, 1852 (see

Thompson, 1970). What appears to be an emargination occurs where the outer lip meets the suture (Fig. 11(4)); the shell margin is turned up and slightly hollowed out. The aperture is about twice as high as wide (apertural view). This elongated aperture will inevitably give a low inclination of the apertural plane, a low degree of tilting upwards of the axis of coiling and a rotation of the long axis of the shell (regulatory detorsion of Linsley, 1977) so that during life it would have almost paralleled the long axis of the foot. The elongated base of the shell would thus point anteriorly to the left of the gastropod's head and represents the point for the inhalant current. Waste water would be expelled at the emargination near the suture, and thus pass nearly straight through the mantle cavity.

Fig. 10. Cross section of *Nonorios kleistos* sp. nov. (2003.8G.54). Black indicates shell material, white indicates space or matrix filled areas. White lines indicate where shell contours can be made out. Scale bar = 0.5 cm.

The Iranian species differs from the type species of *Nonorios* in having a naticiform shell and the extremely thickened shell of the inner margin and base. As a result, the umbilicus is closed at maturity in *N. kleistos* (cross-section Fig. 10, and unfigured cross section NMW 2003.8G.56), while it remains open in the Bohemian and Moroccan specimens. In these forms the shell

ornamentation can be cancellate, with or without spiral component, while only regular growth lines are observable in *N. kleistos*. However, both shell shape and ornamentation vary considerably in the type species, making it difficult to delimit species within this genus (Horný, 1997c, 1997d, 2000; personal communication 2004).

The Italian late Ordovician *N.?* *carnicus* from the Carnic Alps is a small globose naticiform species, slightly wider than high, with sutures that are not pronounced, transverse growth lines, an oval aperture, and an umbilicus that is closed by a thickened inner margin (Vinassa de Regny, 1914). It appears to be more globose than either *N. pater* and especially *N. kleistos*, and in this respect is closer to *Holopea? antiquata* (Barrande in Perner, 1903) from the Zahořany and Bohdalec formations of Bohemia and the Lower Ktaoua Formation of Morocco (Horný, 1997c). Problems related to preservation give considerable variation in the appearance of the type species *Nonorios pater* and *H. antiquata*, which makes it difficult to distinguish these (Horný, 1997c; personal communication 2004). However, description of the thickened inner margin in the Italian specimen (Vinassa de Regny, 1914) suggests affinity with *Nonorios*, but further evaluation of the material is needed. This is also the case with material from the Ordovician of Sardinia (Vinassa de Regny, 1927), which is currently under revision (Horný, personal communication 2004).

Spiral ornamentation may also be present in *Nonorios? transversum* from the late Ordovician of Cincinnati and Kentucky, U.S.A. (see Table 2). This taxon has a low turbiniform shell with an elongated aperture with thickened inner margin, although not developed to the same degree as the

Fig. 11. 1–7. Specimens of *Nonorios kleistos* sp. nov. with shell repairs. 1–5, dorsal, lateral oblique, lateral, detail upper part of outer lip, and apertural views of 2003.8G.49. All $\times 2.0$, except Fig. 5 which is $\times 5.0$. White arrows on Fig. 1 point to the two injuries. 6, 7, dorsal and lateral views of 2003.8G.55, with substantial repaired arcuate break. All $\times 1.5$.

Fig. 12. 1–13. *Nonorios?* sp. 1–5, dorsal, various lateral, ventral oblique, and ventral views of 2003.8G.57, with preserved apertural margins. 6–8, lateral, ventral oblique, and ventral views of 2003.8G.58, showing thin inner margin and anomphalous condition. 9, 10, ventral and lateral views of 2003.8G.59, showing growth lines. 11–13, dorsal oblique, and lateral views of 2003.8G.60. 14, 15. Gen and sp. indet. 1. Dorsal oblique and dorsal views of 2003.8G.67. 16–19. Gen. and sp. indet. 2. Lateral dorsal, lateral and dorsal oblique views of NMGW 2003.8G.68. All images $\times 12$.

Iranian species. The North American form also lacks the thickened base that is so prominent in *N. kleistos*.

Nonorios? sp.

Fig. 12(1–13).

Material: Eight well preserved, silicified specimens were selected for examination (NMW 2003.8G.57–62, 64, 65; samples 98/14B,F (Katkoyeh), Iran 11E (Gezueh). Additionally, there are about 260 poorly preserved silicified specimens (Iran 11E, Gezueh; 98/14C, Katkoyeh; 2003.8G.63, 66). Maximum height of the specimens is about 0.25 cm.

Discussion: These minute gastropods resemble the larger *Nonorios kleistos* in their overall shape. The shell is wider than high, with 3.5 whorls of moderate whorl expansion, and a low spire (apical angle 130 – 115° ; compare Fig. 12(2) with 12(10)). This is equal to or slightly smaller than that of *N. kleistos*. Inclination of the aperture in both species is similar, as is the whorl expansion rate. Aperture nearly circular or slightly higher than wide. Lower 75% of previous whorl is embraced by the succeeding whorl. The main difference from *N. kleistos*, apart from the size, is that the micromorphic shells appear

anomphalous (Fig. 12(4, 5, 7, 9)). The inner margin in *Nonorios?* sp. also has a steeper angle, and is of similar thickness as the remainder of shell. Moreover, the base (as seen in ventral view) seems not to be excavated. In many respects, this species is similar to the minute *N? carnicus* from the Italian Carnic Alps in the overall proportions of the shell, development of growth lines and the thin apertural margin. However, in the Italian species the inner margin is slightly thickened so that it fills the umbilicus (Vinassa de Regny, 1914).

Family indet.

Gen. and sp. indet. 1.

Fig. 12(14, 15).

Material: One silicified specimen (NMW 2003.8G.67; sample Iran 11E (Gezueh).

Discussion: This microgastropod is preserved with a partial, large (0.4 mm width) bulbous protoconch and three subsequent whorls. The outer whorl profile is steeply curved with an incised suture. Early whorls are embraced at the periphery, which is at mid-whorl or slightly above. Growth lines on the upper whorl surface are transverse. The ventral part of the shell is missing.

The species is clearly distinct from material of *Nonorios?* sp. in having an incised suture, a higher spire, a steeper whorl profile, slower whorl expansion rate, and thus the number of whorls at this size. The bulbous protoconch is not preserved completely, but appears to be typical of archaeogastropods (see Frýda and Bandel, 1997).

Gen. and sp. indet. 2.

Fig. 12(16–19).

Material: One silicified specimen (NMW 2003.8G.68; sample 98/14F (Katkoeyeh). Maximum height 0.3 cm.

Discussion: The shell of this microgastropod is trochiform with only two whorls preserved, and the protoconch missing. Whorl profile is evenly convex, with periphery at mid-whorl. On the upper whorl surface, what appears to be a bilineate peripheral band is present, giving asymmetrical right and left ramps. Just below the periphery on the left ramp, what appears to be a basal carina is present. On the other hand, this feature may be an artefact of the sutural contact with the next whorl.

4. Preservation and shell repair

Within the Katkoeyeh specimens there are three types of preservation: silica replacement, silica impregnation, and phosphatic infilling. The bulk of the small specimens of *Tritonophon* and the three specimens of *Tropidodiscus* are phosphatic internal moulds. In a few specimens of *Tritonophon* and the minute *Nonorios?* sp. the shells are preserved as silica replacements. The large specimens of *Slehoferia* and *Nonorios* are both thick shelled and internal moulds are not preserved for either species, so that the specimens are mostly complete, except for deterioration due to weathering. However, these specimens are not easy to prepare because of silica impregnation of the shell and matrix, but replacement of the shell is only superficial. Preparation by acid treatment was therefore unsuccessful, although ultrasonic bath and mechanical preparation using an engraver tool proved efficient in removing adhering matrix.

Specimens of *Slehoferia* and *Nonorios* display rather severe shell injuries. Preservation usually does not allow the finer details of the repairs to be discerned, although the severity of the injuries is well demarcated by the repairs. Three specimens out of 37 (about 8%) of *Slehoferia* have clear shell repairs. The first example (NMW 2003.8G.27; Fig. 7(12–14)) is one of the largest specimens available (3.5 cm high). Here, the injury occurs half a whorl back, and has resulted in the last part of the whorl being translated markedly down the axis of coiling. Normal growth of the shell seems to have commenced only a quarter of a whorl back from the aperture. In specimen NMW 2003.8G.29 (Fig. 8(1, 4, 7–9)), which is about 2.7 cm high, a straight break transversely across the shell occurs almost half a whorl back from the aperture, seemingly following the shell ornamentation. New shell was developed from underneath the break, but the new growth does not seem to have disfigured the whorl beyond the repair. Specimen NMW 2003.8G.28 (Fig. 8(2, 3, 5, 6)), shows the most severe injury. This specimen is smaller than the others noted above (about 2.1 cm

high as preserved), with the injury occurring three-quarters of a whorl back from the aperture. A deep U-shaped cut exists back on the whorl at the periphery, with breakage trailing the shell edge on both upper and lower whorl surfaces. The repaired area and new whorl were severely deformed, leaving a dent in the shell for about a quarter of a whorl adapturally before normal shell growth was reestablished.

In *Nonorios*, three specimens out of eight have been injured (37.5%). The first (NMW 2003.8G.53) is the largest available of the species (4.3 cm high). On the lower whorl surface close to the aperture, a small but distinct, arcuate scar is visible, with an uneven shell margin below and above (Fig. 9(12)). The upper surface is obscured, so the injury cannot be followed adapically. The second specimen (NMW 2003.8G.49; Fig. 1(1, 2); 2.2 cm high) displays two injuries, one three-quarters of a whorl back, and a subsequent injury nearly half a whorl back. Both breaks seem to traverse the whorl, more or less following the shell ornamentation. However, preservation obscures the path of the injuries abaxially. Three-quarters of a whorl back from the aperture of the third specimen (NMW 2003.8G.55; Fig. 11(6, 7); 3 cm high) a wide and deep cut crosses the whorl from the suture to the base of the shell. New shell was developed from underneath the thick shell edge, and normal shell growth was reestablished rapidly.

It can be difficult to discriminate breakages in fossil shells as being naturally mechanical or as biologically induced (see Ebbestad and Peel, 1997). The transverse breaks in the Iranian material may have had natural causes, for instance resulting from tumbling as a result of storms or currents. However, rocky bottom conditions or hard substrates that could cause breakage have not been identified in the Kerman deposits, which are generally of relatively low energy environments. Furthermore, in some modern gastropods, storm-induced injuries only result in minor chipping along the apertural margin (Savazzi, 1991), and not breakage of the entire lip. Heavy shells also protect against physical damage. The form of the deep arcuate injuries is therefore interpreted more readily as predatory. The high frequency of shell repair in *Nonorios* may not be representative for the assemblage owing to the low number of specimens available, although the low percentage of failed predation in the large sample size of *Slehoferia* is what would be expected in Palaeozoic assemblages (Vermeij et al., 1981). However, the specimens were collected at five different levels, covering about 20 m of section, making the sample size from each level too small for statistical analysis.

5. Ecology and biogeography

The Kerman gastropods described here form a low diversity, shallow water community dominated by the minute *Tritonophon*. Typically, species of this genus and related trilobed bellerophonitoideans are numerically dominant in many areas in near shore argillaceous, siltstone facies within Benthic Assemblage 1 or 2 (Boucot, 1975; Bretsky, 1970; Peel, 1974, 1977, 1978; Williams and Wright, 1981; Rohr, 1999). Rohr (1999) proposed the recognition of a plectonotid community for assemblages of this type. Although involving

mainly Silurian and Devonian species of *Tritonophon* and the related *Plectonotus*, this community concept can be extended comfortably to include mid to late Ordovician assemblages (Rohr, 1999). Nevertheless, the benthic community concept cannot be invoked uncritically where *Tritonophon* is found. Peel (1978) pointed out that the abundance of Silurian plectonotids at Arisaig, Nova Scotia was related to proximity to shore (=depth), and not necessarily bottom conditions, and Rohr (1999) emphasized that it is the predominance of the plectonotid genera that characterizes the assemblage. Further, Jin (2003) demonstrated that interpreted water depth of the classic *Eocoelia* brachiopod community varied in the reef and interreef facies of the Silurian of Hudson Bay, Canada. This could parallel the occurrence of *Tritonophon* in similar settings, as for instance in the Silurian of Gotland, Sweden, where this genus and the related plectonotids are present (Lindström, 1884; Moberg and Grönwall, 1909; Peel, 1974).

The Katkoyeh Formation gastropods show close affinities with taxa occurring in the Lower Palaeozoic Mediterranean Province (PMP) as recognised by Spjeldnæs (1961) and Havlíček (1989). Gastropods and tergomyans from this region are known historically mainly from the Bohemian region of the Czech Republic (Perner, 1903, 1907, 1911). Coeval assemblages of similar univalved molluscs occur throughout other regions of Armorica and the Anti-Atlas of North Africa, although they are as yet less well resolved taxonomically, and preservation is sometimes poor (see reviews by Yochelson, 1982; Horný, 1997d). In most of these areas the gastropod and tergomyan assemblages appear to be more diverse than that from the Kerman area (see distribution lists in Horný, 1997d, 2002).

Apart from our new data recorded here from Iran, information on gastropod distribution in the north-western areas of Gondwana and peri-Gondwana is somewhat sparse (e.g. Turkey, Annamia (Indochina), Apulia and Hellenic terranes, Arabia, Himalaya Region; terrane names and palaeopositions East, West and Intermediate palaeolatitude Gondwana mainly follow those of Fortey and Cocks, 2003; Cocks and Torsvik, 2004; Fig. 13). Ordovician gastropods are fairly well known from North China and Korea (Grabau, 1922; Kobayashi, 1930, 1931, 1934, 1958a, 1959; Endo, 1932). However, these areas were in the northern hemisphere during the Ordovician (Cocks and Torsvik, 2002, 2004), and show a distinct faunal separation from East Gondwana (here considering Sibumasu (Shan–Thai), South China, and Himalayan terranes). A few gastropods are described from Malaysia (Kobayashi, 1958b), and there are a number of interesting interterrane similarities with Laurentia, such as the distribution of *Malayaspira* Kobayashi, 1958b (see Rohr et al., 1995). Well-preserved Ordovician gastropods are also known from the Himalaya (Reed, 1912). None of these faunas, however, compares with those of the Palaeozoic Mediterranean Province or Iran, which supports the distinct faunal integrity of East and West Gondwana during the Ordovician (Fortey and Cocks, 2003).

The most abundant gastropod in the Kerman sections is *Tritonophon peeli*. Species of the genus are usually minute (less than 2 mm), but represent adult stages of a micromorphic

gastropod and not juveniles. The origin and early radiation of *Tritonophon* seems to be linked with inner shelf biofacies in Armorica, although currently details are masked by imprecision of stratigraphical resolution, systematic descriptions and/or studies of the appropriate biofacies (Figs. 1 and 2; Table 1). In older literature, trilobed bellerophontiform species have been referred commonly to *Bellerophon trilobatus* Sowerby in Murchison, 1839 (see Horný, 1997d for review of some of these). Although other trilobed Ordovician bellerophontoids occur (Peel, 1974; Horný, 1997b: p. 336), many of the so-called ‘*trilobatus*’ are likely to be *Tritonophon* spp. Mis-identifications are also to be expected, as indicated by the stratigraphically oldest ‘*trilobatus*’, reported from Lower Ordovician (Kunda) limestone at Pulkova, near St. Petersburg, Russia by Eichwald (1856: p. 588; 1860: p. 1078). A number of micromorphic planispiral and conispiral snails occur in these beds (Ebbestad and Isakar, 2004), in which the numerically dominant bellerophontiform genus bears some resemblance to *Tropidodiscus* Meek and Worthen, 1866, but with a more pronounced elevation of the median dorsal band (Ebbestad personal observation 2004). It is highly likely that this represents the ‘*trilobatus*’ species of Eichwald (1856, 1860).

In France ‘*trilobatus*’ was reported from the Llanvirn Schistes d’Angers Formation of Anjou, in the Armorican Massif (Tromelin and Lebesconte, 1875; Pillet, 1992). It is listed further from the Caradoc Louredo Formation (Schistes à *Dalmanites dujardini*) in Bucaco, Portugal (Delgado, 1897, 1908). In Bohemia, the widely distributed *T. peeli* is well documented from the Letná, Zahořany, and Bohdalec formations. The species also occurs in the Caradoc (Aurelucian–Burrellian) lower Ktaoua Formation of the Anti-Atlas, Morocco (Horný, 1997d), and now in the Caradoc Katkoyeh Formation of the Kerman Region, Iran. A later species *T.?* *bohémica* (Perner, 1903), from the Králův Dvůr and Kosov formations of Bohemia is less well known (Horný, 1997d, 2002), but Williams and Wright (1981) reported *T. sp.* and *T. aff. bohémica* from late Rawtheyan siltstones in the Garth area of South Wales, on Avalonia. By Caradoc times Avalonia was separated from Gondwana and in a warm temperate position (Cocks and Torsvik, 2002, 2004; Fortey and Cocks, 2003). Because of the transitional drift history of Avalonia, the faunal assemblage (i.e. brachiopods and trilobites) included a combination of former endemics from Baltica, Gondwana, and Laurentia (Lees et al., 2002), so that finding *Tritonophon* here is not surprising.

Outside Gondwana, *Tritonophon subtrilobatus* (Troedsson, 1919) occurs in the upper Ordovician Harjuan (Pirgu Stage) Lindegård Mudstone at Röstänga in Tommarp, Sweden (Baltica). Another occurrence outside Gondwana is the Kazakhstani *Tritonophon?* sp. from the Dulankarinskaya Formation in the Betpak–Dala region (Mironov, 1979). We here include this form only tentatively in the genus, but the occurrence in this terrane is unexpected. Kazakhstan has been divided into at least four separate terranes (Sengor et al., 1993; Holmer et al., 2001), although there are currently no palaeomagnetic constraints on these (Cocks and Torsvik, 2002, 2004; Fortey and Cocks, 2003). The North American

Fig. 13. Late Ordovician (mid Caradoc; approx. 455 Ma) palaeogeographical reconstruction showing known distribution of gastropod genera discussed in the text; all genera are located within shallow water biofacies (map modified from various sources).

Ordovician occurrence of *Tritonophon*? in the Cincinnati Reedsville Formation (Bretsky, 1970) is more enigmatic. Morphologically the species is similar to the Kazakhstanian material, with a low, rounded dorsal median trilobation, which could imply a lineage different from the typically strongly trilobed *Tritonophon* species.

It is interesting to note that *Tritonophon* survived the end-Ordovician extinction to diversify and spread in the Silurian (Table 1), when the genus was widespread in Baltica, Avalonia, and Laurentia (Peel, 1974). It seems to be missing from most of Gondwana at this time, with the exception of the type species *Tritonophon trimetra* from the late Llandovery in Victoria, Australia.

A general lack of investigations of molluscs in shallow water biofacies may explain why *Tritonophon* is not known more widely in peri-Gondwanan terranes during the Ordovician, and the genus could be expected to have a wider distributional pattern in shelf biofacies of East Gondwana than hitherto recognized. The genus seems to be lacking in intermediate palaeolatitudes of Gondwana (e.g. Argentina; D.M. Rohr, personal communication 2004). The close proximity in time and space of the known Ordovician *Tritonophon* species (Table 1), coupled with poorly known taxonomy and low stratigraphical resolution, also raise questions of synonymy. If these factors were better constrained, *Tritonophon* may

potentially become a highly useful tool in interterrane correlation.

Another planispiral genus with promising potential for correlation within the Palaeozoic Mediterranean Province is *Tropidodiscus* Meek and Worthen, 1866. Various species of this genus dominate in the Berounian deposits of Bohemia and Morocco (Horný, 1997d, 2002). Unfortunately, the poor preservation of the three available Kerman specimens limits their usefulness.

Perhaps the strongest gastropod faunal link between the Katkoyeh Formation of Kerman and in particular the Zahořany Formation of Bohemia is *Slehoferia*. This previously monotypic taxon is represented by numerous specimens in Iran. The Bohemian species *S. excavata* (Barrande in Perner, 1903) is minute, and occurs in carbonate concretions in a unit dominated by siltstone. It is found together with *T. peeli* and *Tropidodiscus*, which further strengthen the correlation with the Katkoyeh Formation. The appearance of *Slehoferia* with its gradate upper whorl profile, and the thickened basal and inner margin is striking, which holds promise for identification of this taxon in other comparable palaeoterranes within the Mediterranean Province (Figs. 1 and 2; Table 2).

Nonorios pater (Barrande in Perner, 1903) is restricted to Berounian arenaceous deposits of Bohemia (Letná to Zahořany formations) and the Caradoc of Morocco (Lower Ktaoua

Formation) (Horný, 1997c, 1997d, 2000), where it occurs commonly with the platyceratoidean *Holopea? antiquata* (Barrande in Perner, 1903); both are possibly recognized in Portugal (Horný, 1997d: p. 64), and could be expected to be recognized also in France and Sardinia (Vinassa de Regny, 1927; Horný, 2000: pp. 421–422). Our record of *Nonorios* in Iran also further corroborates the Caradoc age of the Kerman deposits, and again the strong link with the Mediterranean Province (Figs. 1 and 2; Table 2). *Nonorios* may also be present in the Italian Carnic Alps, represented by the species *N.? carnicus* (Vinassa de Regny, 1914), described from the Upper Ordovician (Ashgill) Uggwa Limestone in a tectonic setting representing Gondwana or peri-Gondwana fragments (Cocks, 2000). Outside the Mediterranean Province, the North American Cincinnati *Nonorios? transversum* Ulrich in Ulrich and Scofield (1897) was included tentatively in the genus by Horný (1997c), which could suggest a much wider distribution.

Nonorios is still not well understood, especially with regards to variation in form and ornamentation (Horný, 1997c, 1997d and personal communication 2004). However, as is the case with *Tritonophon*, it is not unlikely that future studies will demonstrate a much wider distribution in the Palaeozoic Mediterranean Province, and thus a wider usefulness in stratigraphical and palaeogeographical applications.

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