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1 Late Ordovician molluscs of the central and eastern Anti-Atlas,
2 Morocco

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12
13 **Abstract:** More than 30 species of tergomyan, gastropod, bivalve and cephalopod molluscs
14 are described from the Late Ordovician of central and eastern Anti-Atlas, Morocco. For the
15 cephalopods this represent the first systematically known taxa of the region. Tergomyans and
16 gastropods are most common in the more shaly part of the Lower Ktaoua Formation, while
17 bivalves are more frequent in the sandy part of the Lower Second Bani Formation. A southern
18 Gondwana aspect is evident for the tergomyan, gastropod, and bivalve assemblages, sharing
19 many taxa with Bohemia, while no clear signal is present for the cephalopods. The latter
20 reflects insufficient knowledge of the fauna of large parts of these areas. The widely
21 recognized *Holopea? antiquata* is transferred to the genus *Radvanospira* gen. nov.; other new
22 gastropod taxa include *Allossospira* gen. nov., *Tritonophon grandis* sp. nov., *Radvanospira*
23 *baniensis* sp. nov., and *Lophospira latilabra* sp. nov. Most of the diverse bivalve fauna and
24 the few cephalopods are left in open nomenclature but new taxa include the bivalve
25 *Praenucula pojetai* sp. nov., and the cephalopods *Wadema tattai* sp. nov. and *Tafadnatoceras*

tiouririnense gen. et. sp. nov. The Late Ordovician bivalves from Morocco are dominated by pteriomorphs and protobranchs, inhabiting infaunal, semi-infaunal and epifaunal niches.

Recently, a rare, exceptionally preserved aculiferan mollusc from the Early Ordovician of Morocco provided insight into the early evolution of the Mollusca and the oldest common ancestor of the group (Vinther *et al.* 2017). The shell bearing molluscs underwent an early radiation and evolution during the Cambrian with (for example) the advent of torsion in the gastropods and the late Cambrian appearance of a cephalopod phragmocone, but also the development of true scaphopods during the Late Palaeozoic (Peel 1991, 2006; Engeser & Riedel 1996; Frýda *et al.* 2008; Landing & Kröger 2012). Although the disparity of molluscs throughout their evolutionary history is astounding, the molluscan body plan also exhibit a tendency to convergence early in their evolution (see for instance Peel 2006; Vinther *et al.* 2012). When preservation is poor, which is often the case with molluscan fossils, owing to their original aragonite composition of the shell in many groups, similar gross morphologies may make it difficult to elucidate a meaningful phylogeny.

During the Great Ordovician Biodiversification Event (GOBE) molluscs underwent a truly epic radiation and increase in diversity (Webby *et al.* 2004). Our understanding of this radiation within the molluscs remains poor. Reasons including poor preservation, a disparate and patchy record for many groups and a lack of data from several geographical areas. The present study contributes to our understanding of the latest phase of the GOBE, reviewing and updating the taxonomy and distribution of the Late Ordovician mollusc classes Tergomya, Gastropoda, Bivalvia, and Cephalopoda of the central and eastern Anti-Atlas of Morocco (Fig. 1), presenting more than 30 taxa including several new genera and species.

Termier & Termier (1950) were the first to describe and illustrate Ordovician molluscs (gastropods, bivalves, rostroconchs, and cephalopods) from Morocco and apart from a few

notable works, very few comprehensive studies have appeared since then. Most of the tergomyan, gastropod, and cephalopod specimens are from the shale and sandstone dominated Ktaoua Group (Lower Ktaoua, Upper Tiouririne and Upper Ktaoua formations) while the bivalves typically occur in the more sandy facies of the Lower Second Bani Formation (Fig. 2). For geological background and stratigraphy see Álvaro *et al.* (this volume).

Mollusc groups in the Late Ordovician

Tergomya and Gastropoda. The global diversity of Ordovician tergomyans and gastropods (TG) reflects the prevalence of records from certain palaeoareas, such as Baltica, Bohemia, Laurentia, and North China. By and large this is a consequence of monographic treatments that have focused on the faunas of these particular areas. Both tergomyans and gastropods show high endemism during the whole of the Ordovician. The lowest endemism is during the Katian, coinciding with the highest abundance of these molluscs (Frýda *et al.* 2008; Ebbestad *et al.* 2013b and references therein). With a few exceptions, Hirnantian records of these molluscs are paltry, making any new data from this time interval valuable. Four episodes of elevated radiation and origination of gastropods may be identified during the Ordovician (Frýda & Rohr 2004); the highest rate of extinction was shown to occur during the Hirnantian, although this is probably amplified by the poor fossil record noted above. Nearshore shallow water TG faunas were susceptible to sea level changes and possible habitat restrictions (Novack-Gottshall & Miller 2003), which may in part explain some of the fluctuations in the extinction rate, but increasing knowledge of deeper water assemblages will certainly modify this picture (see e.g. Ebbestad *et al.* 2013a).

Frýda *et al.* (2008) emphasized the many problems with our current understanding of e.g. gastropod phylogeny, suggesting that studies of specific shell characters as well as the development of protoconch morphologies will provide tools with which to resolve the higher

group relationships. Unfortunately, protoconchs are not preserved in the material described but the well-preserved teleoconchs provide some insight into these relationships.

Moroccan tergomyan and gastropod faunas show affinities with those of the Ibero-Armorican faunas. This is most evident for the Early Ordovician (Ebbestad 2016), while during the Late Ordovician *Sinuitopsis neglecta* Barrande in Perner, 1903, *Tritonophon peeli* Horný, 1997c, *Nonorios pater* (Barrande in Perner, 1903), and *Holopea antiquata* (Barrande in Perner, 1903) are shared with Bohemia. *Tritonophon* is otherwise widespread, while *Nonorios* can also be found in the Carnic Alps and Iran (Ebbestad *et al.* 2008).

Palaeogeographically, Bohemia did not cluster with Morocco and the Ibero-Armorican areas in the Katian-Hirnantian. This is most likely to be the consequence of the currently poor quality of the available Hirnantian data (Ebbestad *et al.* 2013b).

Bivalvia. Bivalves are well known from many parts of the Late Ordovician world; eastern Gondwana (Argentina) (Sánchez 1990, 1999), Baltica (Isberg 1934; Toni 1975), Bohemia (Barrande 1881a–d; Kříž & Steinová 2009), Britain (Tunnicliff 1982, 1987; Hind 1910; Reed 1944), Kazakhstania (Khalfin 1958; Sinicyna 1979), Laurentia (Caley 1936; Frey 1987; Bretsky 1970; Pojeta 1966), and Siberia (Krasilova 1970, 1979). According to Cope & Kříž (2014), Late Ordovician bivalves became cosmopolitan again for the first time since the early Cambrian. During the Cambrian, bivalves are known mainly from shallow carbonate ramps, where they are generally scarce, but occur in different continents. During the Early and Mid Ordovician, bivalves underwent an explosive diversification (Cope 2004), but they occur mainly around Gondwana and were mainly restricted to siliciclastic sediments (Cope & Babin 1999). The Late Ordovician bivalves occurred widespread and they are known from various habitats (Cope 2002), although their familial diversity changed a little from the Early Ordovician (only two families are new in the Late Ordovician, Cope & Kříž 2014).

Epibyssate and endobyssate forms of pteriomorphs show evidence of strong radiation (Cope & Babin 1999). Although evaluations of Late Ordovician bivalves have suffered from widespread over-splitting, Cope & Kříž (2014) demonstrated that it can yield some valuable data. A further problem results from the lack of well-described high latitude bivalve faunas from the Late Ordovician, which fetters comparison with mid-low latitude faunas.

Cephalopods. The diversity evolution and palaeogeographic differentiation of Ordovician cephalopod faunas were analysed and reviewed by Kröger & Zhang (2009) and Kröger (2013). These analyses revealed a global Ordovician diversity increase at the genus level climaxing during the Katian, accompanied by a general decrease in evolutionary rates and a reduced endemism. In the context of the Moroccan cephalopod species described herein, it is important to note that during the Late Ordovician no characteristic peri-Gondwanan fauna can be currently distinguished. This pattern is most likely to be an artefact consequent on the lack of knowledge of the faunas of large parts of eastern Gondwana in particular. Notably, *Wadema*, an actinocerid genus known predominantly from low palaeolatitude Gondwana is present in Morocco, suggesting some relationship to faunas as far away as Australia and Thailand. The only known peri-Gondwanan fauna from relatively high palaeolatitudes was described by Ghavidel-Syooki *et al.* (2015). It contained slender orthocerids, amongst them *Isorthoceras bisignatum* (Barrande, 1877), which has some similarities to *Tafadnatoceras tiouririnense* sp. nov. described herein. The former species is also known from Bohemia, which is in agreement with the general picture of a close relationship of the faunas of Armorica, Bohemia, Iberia and Morocco. Currently, too little is known of these faunas for a more detailed comparison.

Late Ordovician molluscs in the central and eastern Anti-Atlas

Tergomya and *Gastropoda* (Figs 4–25). Late Ordovician tergomyans and gastropods of Morocco are primarily known through the work of Horný (1997e), based on extensive material collected by the French geologist and palaeontologist Jacques Destombes. Material presented by Termier & Termier (1950) was shown by Horný (1997e) to be highly fragmentary and ill-determined.

The currently recognized fauna appears sparse, and of a low diversity, with a disparate stratigraphical distribution. It consists of a total of 14 species, two of which are tergomyans, five are bellerophontiform gastropods and seven are anisostrophically coiled gastropods (Fig. 2). Some new collections, especially from the Second Bani Group, add invaluable Hirnantian records, such as the large *Tritonophon grandis* sp. nov., which otherwise represents a widespread genus in the Katian. Revisions of the species *Radvanospira antiquata*, *Allossospira debganensis*, and *Deaechospira amouguerana* demonstrates more clearly the faunal differences between the cold water siliciclastic dominated realms of southern Gondwana and the warm water carbonate dominated equatorial and sub-equatorial settings of Baltica, Laurentia, and Siberia.

Most specimens in this study are preserved as internal or external moulds, very much like contemporary material from peri-Gondwanan successions in the Czech Republic, France, Portugal, and Spain. In many cases the assemblages are dominated by one species, and in certain cases, like the widespread Mid Ordovician *Tropidodiscus pusillus* Barrande in Perner, 1903, they can be extremely numerous (Horný 1999a).

Bivalvia (Figs 26–30). Ordovician Moroccan bivalves were practically unknown. Termier & Termier (1950) figured bivalve specimens from Morocco. Babin & Destombes (1990) provided a brief list of Ordovician bivalves from the Moroccan Anti-Atlas and the first

photographic illustrations of those forms. Recently, Polechová (2016) revised the evolutionary important Early Ordovician bivalves from the Fezouata Formation. In this paper, the bivalves described by Babin & Destombes (1990) are revised and compared with newly collected material from Morocco.

Bivalves from Morocco have been described from different localities and stratigraphical units. They first occur in the Early Ordovician (Tremadocian, Floian) Fezouata Formation within the central part of the Anti-Atlas (Termier & Termier 1950; Babin & Destombes 1990; Cope 2002; Cope 2004; Polechová 2016). According to Babin & Destombes (1990), after the Early Ordovician the bivalves are rare and limited to a few specimens that are very often badly preserved. Bivalves are also more widespread in the western, central and eastern Anti-Atlas. Babin & Destombes (1990) figured a few bivalves from the Late Ordovician; *Praenucula costae* (Sandbian), *Phestia?* sp. (Sandbian), *Praenucula* sp. (Hirnantian), *Myoplusia?* sp. (Sandbian), *Palaeoneilo* sp. (Hirnantian), and *Modiolopsis?* sp. (lower Katian). New material of bivalves from Morocco come from both eastern and central Anti-Atlas and originate from the upper part of the Upper Ktaoua Formation (Katian) and the Lower Second Bani Formation (latest Katian, Hirnantian) (Fig. 2).

All the bivalves studied are preserved as internal or external moulds. Some internal moulds show excellent preservation with hinge, adductor, pedal and accessory muscle scars all present (e.g. *Praenucula pojetai* sp. nov., Fig. 26o–q), but generally the preservation is mediocre. Articulated specimens are rare and specimens preserved in butterfly position are not present, suggesting some preburial transport of individuals. By contrast, two specimens of *Cleionychia prisca* (Fig. 29d–h) are probably preserved in life position. Bivalves in this study are often preserved as isolated specimens, and only the locality Aït Isioul ‘north (west of Tagounite) provides several specimens (mainly *Modiolopsis*) on one bedding plane. Kříž & Steinová (2009) described the *Modiolopsis* Community Group from the Late Ordovician of

Bohemia. The genus *Modiolopsis* is dominant in many communities from the Early Ordovician (Babin 1966; Babin & Hamman 2001) and the *Modiolopsis* Community Group is characteristic of the shallow, high energy and sandy inner shelf environments.

The Moroccan bivalve associations share some similarities to the Late Ordovician bivalve associations from Bohemia (*Praenucula*, *Sluha*, *Modiolopsis*, and *Myoplusia*), Ireland and Baltica (*Ambonychia*, *Cleionychia*, *Cyrtodonta*, and *Nuculites*).

Some internal moulds contain traces of the ichnofossil *Arachnostega*, which is often preserved in Ordovician skeletal faunas (Fatka *et al.* 2011; Lefebvre 2007; Vinn *et al.* 2014). Gil Cid & Lebrón Moreno (2010) found that *Arachnostega* is not restricted to a specific environment, as it occurs in both, shallow or deeper facies, as well as in siliciclastic and carbonate environments. They are rather indicators of firm muddy, coherent substrates.

Cephalopoda. The Late Ordovician cephalopods of Morocco and of North Africa in general are practically undescribed. The few taxa described herein, represent the first systematically known Late Ordovician cephalopods of the region. Previously, one probable Late Ordovician specimen only, an annulate orthocone, possessing a reticulate shell sculpture was figured as a schematic line drawing under the name *Pseudorthoceras?* sp. by Termier & Termier (1950, pl. 35, fig. 1–3) from the Region d'Aït Saadane-Taghbalt; no additional information is available regarding this specimen. Moreover, a regional comparison of the cephalopods, described herein, is problematic because time-equivalent assemblages from areas such as Armorica, Iberia, and Sardinia are yet to be systematically described. The Bohemian Ordovician species described by Joachim Barrande in the 19th century and listed by Marek (1999) are in need of a revision and are not yet sufficiently well figured and described to warrant a full comparison with the material described here. This is probably the main reason

why taxa closely similar to the ones described herein, are known only from relatively few regions of circum-Gondwana such as Australia and Eastern Asia (see below).

Palaeoecology

Tergomya and *Gastropoda*. Whereas several studies have investigated gastropod biofacies distribution and biocommunities (see review in Ebbestad *et al.* 2013b), fewer studies have focussed on the life habits of *Tergomya* (e.g. Horný & Vizcaïno 1995; Horný & Peel 1996; Horný 1997e). The latter work discussed life habits of all the Moroccan species of tergomyans as well as the gastropods. The Late Ordovician taxa range in size from the minute *Tritonophon* to the gigantic *Sinuities destombesi* and from planispiral to high spired conispiral shell-draggers, and a broad range of life-styles is involved. Perhaps the best studied taxon is *Sinuities*, which is inferred to have an infaunal or semi-infaunal predatory life style (see Horný 1997e). Several taxa show morphologies that are compatible with a shallow water environment and high energy, like the explanate *Bucanopsina* and the robust *Deaechospira*, *Allossospira*, *Nonorios*, and *Radvanospira*. All of these would be epibenthic browsers, scavengers or predators.

Several species show signs of shell repair, presumably from failed predation. This is particularly evident in the large *Allossospira debganensis*, where multiple repairs are seen in two specimens illustrated here (Fig. 22b & g), and in a specimens figured by Horný (1997e, pl. 14, figs 1–5). Typically this is a sign of the animal reaching a size-refuge, so that by its large size alone, it will survive more readily and thus accumulate repairs from failed predation (Ebbestad & Stott 2008). It is also shown in the present study that *Deaechospira* sp. probably was a clamper, pulling the shell down over the foot to protect the soft part from predation. Repairs are otherwise documented in *Deaechospira amouguerana* (Figs 17a, g, 18e & 19b),

223 while Horný (1997e) reported injuries in Mid Ordovician *Ptychonema marocanum* Horný,
224 1997e.

225
226 *Bivalvia*. Bivalve assemblages from the Late Ordovician of Morocco are quite diversified
227 with 13 taxa known. Most of the specimens are left in open nomenclature, because they do
228 not show enough characters for determination to the species level. According to the
229 methodology of Kříž (1999), the bivalve associations from the Early and Late Ordovician
230 were compared (Table 1). The pie diagrams (Fig. 3) follow the methodology of Cope & Kříž
231 (2014) and demonstrate a large change in faunal composition, compared with the Early
232 Ordovician assemblage of bivalves from the Fezouata Formation of Morocco (Polechová
233 2016). The Early Ordovician association of bivalves of Morocco show only infaunal feeders,
234 while epifaunal feeders are well-represented in the Late Ordovician associations.
235 Heteroconchs completely dominate the Fezouata Formation, whereas during the Late
236 Ordovician protobranchs and pteriomorphs prevail.

237 *Praenucula pojetai* sp. nov., *Myoplusia* sp., *Sluha kosoviensis*, *Nuculites* sp., *Pseudarca*?
238 sp., and *Phestia*? sp. are considered infaunal feeders. *Praenucula*, *Myoplusia* and *Sluha*
239 possess well-developed pedal muscle scars and they were probably infaunal deposit feeders.
240 *Nuculites* was probably an infaunal filter feeder. *Modiolopsis*, *Cyrtodonta* and *Dceruska* were
241 semi-infaunal, probably endobysate filter feeders but the internal morphology is not well-
242 known. They show some reduction of the anterior part, a feature characteristic of bysally
243 attached bivalves. *Cleionychia* and *Ambonychia* lived epifaunally, showing a prominent
244 byssus. According to Pojeta (1971), ambonychiids were gregarious and large numbers of
245 articulated shells on one bedding plane were described. The specimen of *Cleionychia prisca*
246 (Fig. 29d–h) is probably recorded in life position. It is associated with brachiopods and

247 bryozoans, and seems to be attached to the substrate, nestling between the brachiopods and
248 bryozoans.

249

250 **Localities**

251 The new material presented in this study comes from a number of formations and localities
252 which range from the Darriwilian to Hirnantian in the central and eastern Anti-Atlas.

253 Lithostratigraphic nomenclature follows Destombes (in Destombes *et al.* 1985; Destombes
254 2006a) and Álvaro *et al.* (this volume).

255 The oldest locality corresponds to the lower part of the Taddrist Formation (First Bani
256 Group) and lies to the SW of Alnif, about 5.8 km northeast of the town of Aachich n'Ait Azza
257 (geographic coordinates: 30° 55' 18" latitude N, 05° 14' 51" longitude W). This is the type
258 locality and horizon of two endemic trilobite and echinoderm species (Rábano *et al.* 2014;
259 Zamora *et al.* 2015; Reich *et al.* 2017) and it is the source of Endoceratidae gen. et sp. indet.
260 described below. The age of this horizon is upper Oretanian, a regional stage division roughly
261 equivalent to the upper Darriwilian 2/basal Darriwilian 3 of the global scale (Gutiérrez-Marco
262 *et al.* 2015, 2017).

263 The next location is of late Berounian regional age (= late Katian 1 to Katian 2 of the
264 global scale) and corresponds to a lenticular calcareous coquina placed in the upper part of the
265 Upper Tiouririne Formation (Ktaoua Group) represented by an isolated excavation c. 6.5 km
266 southeast of the city centre of Erfoud (= Arfoud): locality 'Erfoud 2', coordinates 31° 24' 10"
267 latitude N, 4° 10' 37" longitude W (marked E2 in Fig. 1). It contains a rich assemblage of
268 trilobites, cephalopods, gastropods and conulariids of which *Radvanospira antiquata* and
269 *Tafadnatoceras* are described here.

270 Higher in the succession, the next fossiliferous horizon corresponds to the upper part of the
271 Upper Ktaoua Formation (Ktaoua Group), and is represented by richly fossiliferous strata

containing a typical *Mucronaspis termieri*-*Flexicalymene ouzregui* trilobite assemblage. This occurs in nodules at two locations that lie close to each other at Jbel Bou Ingarf, north and south of the Zagora-Tazarine road (Jbel Bou Ingarf ‘north’, 30° 34’ 33” latitude N, 5° 34’ 18” longitude W; Jbel Bou Ingarf ‘south’, 30° 28’ 11” latitude N, 5° 26’ 0” longitude W). Material from the first locality comes from below the level erroneously designated as the ‘Ouzregui bed’ by Loi *et al.* (2010), which in fact corresponds to the single and discontinuous ferruginous marker horizon mentioned by Destombes (2006b, p. 35), containing ‘*Dreyfussina struvei* and *Amphitryon*. The noduliferous strata with *Flexicalymene ouzregui* and other abundant trilobites, different from the taxa mentioned above, occur in a 30–40 m stratigraphic range below this horizon marking the top of the Upper Ktaoua Formation (Gutiérrez-Marco *et al.* 2017, p. 272). Besides the trilobites, molluscs occur scarcely and other fossil groups are very rare in the nodules at these localities. *Deaechospira*, *Sinuities*, *Wadema*, and an ormoceratid are recognized from here. According to Gutiérrez-Marco *et al.* (2017, fig. 5), the age of the upper part of the Upper Ktaoua Formation is Kralodvorian, equivalent to Katian 3 – 4 of the global scale (Bergström *et al.* 2009).

The remaining material comes from different localities placed in the Lower Formation of the Second Bani Group with excellent sections to the west and south of the town of Tagounite (from 30 km southwest to 50 km southeast of the city of Zagora, Central Anti-Atlas). With the exception of a single older horizon in one section, all the other sections are regarded as being of a Hirnantian age based on the occurrence of a typical *Mucronaspis-Hirnantia* faunal assemblage. This may occur in association with the studied molluscs, or from beds immediately below or above (Destombes *et al.* 1985, figs 37 & 38; Gutiérrez-Marco & Vinn 2018). The most fossiliferous sections lie near the eastern end of the quartzitic cuesta of Aït Isioul, about 33.4 km west-north-west of Tagounite. Here and above the local outcrops of the Ktaoua Group, the sandstones and bioturbated shales of the Lower Second Bani Formation

form a prominent escarpment (*bani*= mountain), and the two main sections nearby are named Aït Isioul ‘north’ and ‘south’, being respectively placed in the eastern and western banks of the same small valley running to the north into the Oued Moulili. In the former locality (c. 30° 04’ 41” latitude N, 05° 54’ 25” longitude W), Hirnantian bivalves occur abundantly in coquinoïd sandstones belonging to bed ‘F’ of the Lower Second Bani Formation as defined by Destombes *et al.* (1985) and Destombes (1983: an unpublished version of the incompletely published manuscript of Destombes 2006b). This is well above the FAD of the *Hirnantia* Fauna (Colmenar in Gutiérrez-Marco & Vinn 2018). The bivalves *Nuculites*, *Modiolopsis*, *Dceruska*, *Ambonychia*, *Cleionychia*, and *Cyrtodonta* are known from here.

The complementary section Aït Isioul ‘south’ is located 800 m southwest of the former and also ranges from the quartzitic horizon ‘G’ (lower) to horizon ‘F’ (upper) of Destombes, lying at about 30° 04’ 27” latitude N, 5° 54’ 53” longitude W. This steeply-inclined section has been studied in detail and starts with beds of late Kralodvorian (= late Katian 4) age. These range from the base of the formation to about 6 m above horizon ‘G’, thus comprising the first studied fossiliferous beds T1 and T2 (above ‘G’) bearing some trilobites and bivalves. Fossil horizons T4 (coincident with the FAD of the *Hirnantia* brachiopod fauna) and T5 are placed respectively 11.5 and 14.8 m above the top of the horizon ‘G’, having yielded the gastropods *Tritonophon* and *Radvanospira* and the bivalves *Ambonychia*, *Cleionychia*, and *Dceruska*. Higher up in the section, several levels containing large bivalves are recorded from the quartzitic horizon ‘F’, whose base is placed about 40–60 m above the top of ‘G’ and which also bears a very abundant *Hirnantia* brachiopod fauna.

Finally, two other sections in the Hirnantian beds of the Lower Second Bani Formation also yielded remains of the large bivalve *Cyrtodonta* and the smaller bivalve *Cleionychia prisca*. The first section, provisionally designated the “Foum el Fehamiya section” is located 10.8 km west of the Foum el Fehamiya pass and 27 km northwest of Tagounite (30°

02' 55" latitude N, 5° 51' 13.4" longitude W). It was studied by Havlíček (1971), Destombes *et al.* (1985), Destombes (1983), and Mergl (1983), and was attributed to somewhat higher beds (quartzitic horizons 'D' and 'C'), but still associated with the *Hirnantia* Fauna.

The second locality lies east of the road to Mhamid on the mountain Pass south of Tagounite (29° 54' 33.5" latitude N, 5° 36' 04" longitude W), where a 'float' specimen of the large bivalve *Nuculites* sp. was recorded from strata lying below the first of the glacial unconformities recorded within the Second Bani sandstone Group. (i.e., below the base of the Upper Second Bani Formation).

Horný (1997e) referred to Destombes' localities and presented a detailed list with names and coordinates. This information is not repeated here, and only the Destombes locality number is given here.

Material and methods

The material described and discussed herein comes partly from extensive material collected by the French geologist and palaeontologist Jacques Destombes. New material has been added by J.C. Gutiérrez-Marco from several fieldtrips to Morocco. Most of the tergomyan and gastropod specimens were described by Horný (1997e), while part of the bivalve material was described by Babin & Destombes (1990). Destombes (2006a) re-illustrated some of the material described by these authors.

All the figured tergomyans, gastropods, bivalves, and some of the cephalopods were coated with ammonium chloride before being photographed. All bivalve specimens were measured (length, height, and width of the shell, and in some specimens also the angular relationship between different parts of the shells). The methodology of Stanley (1970), Kříž (1999) and Cope & Kříž (2014) was used for the palaeoecological interpretation of the bivalves. All bivalve specimens were systematically determined and statistically analysed to

find their numerical and ranked abundance. *Abbreviations Bivalvia*. V = valve, L = length of the shell, H = height of the shell, W = width of the shell, W/2 = width of one valve (Kříž 1969). Measurements of whorl parameters in tergomyans and gastropods follow Peel (1974) and Ebbestad (1999). All linear measurements are in millimetres.

Systematic Palaeontology

Naming of taxa for each systematic group is credited to the main authors of the group only; Ebbestad & Gutiérrez-Marco for Tergomya and Gastropoda, Polechová & Gutiérrez-Marco for Bivalvia, and Kröger & Gutiérrez-Marco for the Cephalopoda. The classifications used by Horný (1997b, 1997c, 2002) for the Tergomya and the bellerophonoid Gastropoda, Wagner (2002) and Frýda & Bouchet (2005) for the anisostrophic Gastropoda, and Carter *et al.* (2011) for the Bivalvia are adopted here. Synonym lists follow the recommendations by Matthews (1973). Specimens are deposited in the following collections: the University of Lyon 1, France (FSL); the Museo Geominero, Madrid, Spain (MGM); the Department of Palaeontology in the National Museum, Praha 9, Czech Republic (NM); the Cadi-Ayyad University, Marrakesh, Morocco (AA). Non-Moroccan specimens from other collections are mentioned as follows: BGS GSM (British Geological Survey, Keyworth, Nottingham), NIGP (Nanjing Institute of Geology and Palaeontology, Nanjing, China), and UM K Ulster Museum, Belfast, Ireland).

LSID: [http:// zoobank.org/###](http://zoobank.org/###)

Phylum **Mollusca** Linné, 1758

Class **Tergomya** Horný, 1965

Family **Cyrtolitidae** Miller, 1889

Genus *Sinuitopsis* Perner, 1903

Type species. By subsequent designation of Cossmann (1904, p. 108), *Sinuitopsis neglecta* Barrande in Perner, 1903, pp. 68–71, text-figs 42–46, pl. 85, fig. 11 & pl. 88, figs 28–30, 38–40, from the Upper Ordovician (Katian Stage) Zahořany Formation at Loděnice, Prague Basin, Czech Republic.

Sinuitopsis neglecta Barrande in Perner, 1903

(Fig. 4a–h)

Material. 22 specimens, listed by Horný (1997e).

Localities and horizons (Moroccan specimens only). Destombes localities 86, 88, 134, 628, 899, 1265, 1778, central and eastern Anti-Atlas, Morocco. Lower Ktaoua and Upper Tiouririne formations, Sandbian and Katian stages.

Remarks. The tergomyan *Sinuitopsis* is a characteristic element of the Mid to Late Ordovician of the Bohemia, Czech Republic, with four species known; *S. evoluta* (Perner, 1903) from the Šárka Formation (Darriwilian), *Sinuitopsis* sp. *sensu* Horný (1997b) from the Dobrotivá Formation (Darriwilian), the type species *S. neglecta* from the Zahořany Formation (Katian), and *S. hornyi* Marek, 1963 from the Kosov Formation (Hirnantian). Horný (1997e, 1999b) mentions other unnamed species of the genus in Bohemia. The species *S. nodosa* Perner, 1903 co-occurs with the type species and was considered its junior synonym by Horný (2002).

Sinuitopsis neglecta is common in the Lower Ktaoua Formation in the eastern Anti-Atlas (Horný 1997e), and the most typical specimens are re-illustrated here (Fig. 4). Villas *et al.*

(2006) reported the species in the uppermost part of the Lower Ktaoua Formation at Alnif in eastern Anti-Atlas (Katian), where it co-occurs with the (here revised) gastropods *Radvanospira antiquata* (Barrande in Perner, 1903) and *Deaechospira amouguerana* (Horný, 1997e). According to Horný (1997e) in Morocco *S. neglecta* is even associated with the gastropods *Nonorios pater* (Barrande in Perner, 1903), *Tritonophon peeli* Horný (1997c), and *Bucanopsina calypso* (Perner, 1903). In Bohemia, Czech Republic, the latter also co-occurs with *Sinuitopsis neglecta*.

Dzik (1981) figured a specimen of *S. neglecta* from an erratic boulder of Backsteinkalk found in Poland. Erratics of this type came from Sweden or Baltic states and are no younger than mid-Sandbian (Schallreuter 1970), thus this record is older than the Czech Republic and Moroccan occurrences. Horný (1997e) further discussed the possibility that *Pharetrolites?* *tumidus* (Koken, 1897) and *P.?* *elegans* (Koken in Koken & Perner, 1925) from the Dariwillian Elnes Formation, Oslo Region, Norway could be species of *Sinuitopsis*. Yochelson (1963) redescribed these species and tentatively assigned them to the Silurian *Pharetrolites* Wenz, 1943.

Bellerophon (*Sinuitopsis*) *avunculus* Hadding, 1913 from the Darriwilian Andersön Formation at Andersön, Jämtland, Sweden, belongs with *Tropidodiscus* and so is also most likely the case with the poorly preserved *B. (Sinuitopsis) consobrinus* Troedsson, 1918 from the Katian Lindegård Mudstone, Scania, Sweden. Yochelson (1964) discussed both species and although no firm generic assignment was made, he pointed out that the latter species possessed a dorsal median band thus excluding it from the sinuate *Sinuitopsis*. *Bellerophon* (*Sinuitopsis?*) *subtrilobatus* Troedsson, 1918, from the same unit, was shown to be a species of *Tritonophon* by Ebbestad *et al.* (2008).

Kobayashi (1934) described *Sinuitopsis kochiriensis* from the Darriwilian Jigunsan Formation, South Korea, showing a small, paucispiral shell with strong ribs and a V-shaped

median anterior sinus without a median dorsal band. The taxon is not readily comparable with *Sinuitopsis*, or other sinuate taxa for that matter, and may constitute a new genus. *Sinuitopsis* cf. *kochiriensis sensu* Kobayashi (1959) from the Floian La Nga Formation, Tarutao Island, southern Thailand, is most likely *Peelerophon oehlerti* (Bergeron) according to Jell *et al.* (1984).

An interesting occurrence of *Sinuitopsis* is *S. congruens* Reed, 1920 from the Sandbian Pumphouse Member of the Balclatchie Formation in Girvan, Scotland, as this would represent marginal Laurentia. However, other typical peri-Gondwanan form also make their appearance in the Girvan succession. Horný (1963, 2002) and Ebbestad (2008) discussed the presence of the characteristic peri-Gondwana genera *Carcassonnella* Horný & Peel, 1996 and *Grandostoma* Horný, 1962 in the Katian of Girvan, and Ebbestad *et al.* (2013b) speculated that this could relate to transgressive episodes that could introduce peri-Gondwanan genera to Girvan via Baltica.

Although post-Ordovician species have been named, *Sinuitopsis* is likely to be restricted to the Ordovician. Examination of *Sinuitropsis subrectangulatus* Pitcher, 1939 from the Silurian of the Welsh Borderland shows a paucispiral shell with barely contiguous whorls. Although the apertural lip is not preserved, the species is better placed with *Pharetrolites* Wenz, 1943 (see Peel 1975 for a discussion on *Pharetrolites*). The Devonian *Bellerophon acutilira* Hall, 1861 was placed with *Sinuitopsis* by Rollins & Batten (1968), a position viewed with scepticism by Horný (1991). Blodgett *et al.* (1999) eventually placed the species with *Sinuitina* Knight, 1945.

Horný (1997e, p. 2, figs 5 & 6) described two specimens of *Sinuitopsis?* sp. from the Lower Ktaoua Formation at Destombes locality 399, eastern Anti-Atlas. These differ from *S. neglecta* in having regular commarginal ribs in the early whorls instead of undulating ribs. These specimens are otherwise flattened and incomplete and are not re-illustrated here.

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Class **Gastropoda** Cuvier, 1797

Family indeterminate

Genus *Atlantophon* Horný, 1997e

Type species. By original designation, *Atlantophon maider* Horný, 1997e, p. 53, pl. 8, figs 8–11, from the Upper Ordovician (Katian Stage) Lower Ktaoua Formation at Destombes locality 882, Inakiana plain SW of Amjerane, Maïder, eastern Anti-Atlas, Morocco.

Atlantophon maider Horný, 1997e

(Fig. 5a–e)

Material. Holotype specimen only (NM S2673), figured herein as Fig. 5a–e.

Locality and horizon. Destombes locality 882, eastern Anti-Atlas, Morocco. Lower Ktaoua Formation, Katian Stage.

Remarks. This enigmatic taxon is known solely from the type species. It was described in detail by Horný (1997e) and is re-figured here, high-lighting various aspects of the morphology. The left half of the shell is almost covered by matrix. Horný (1997e) remarked that the specimen was depressed and crushed. In posterior and dorsal views (Fig. 5b & c) it is clear that the specimen is laterally compressed, which is also suggested by irregularities on the body whorl. The dorsal lobe is obscured at the posterior of the visible shell (see arrow 1 in Fig. 5b). Furthermore, the transition from the median lobe to the whorl on the left side is placed much higher than on the right side (see arrows marked 2 in Fig. 5b & c); the growth

lines are visible in the groove between the shell and the matrix. The lack of a lobe on the earlier whorls and the high placement on the left side is due to the compressional deformation of that part of the shell having been sheared and moved up (see white arrow in Fig. 5b: the compressional suture runs adaperturally, cutting across the median lobe towards the left). The compaction and deformation probably contribute to an accentuation of the median lobe, perhaps even more so than acknowledged by Horný (1997e). Furthermore, near the aperture the trilobation is less marked (see white arrow in Fig. 5c).

Atlantophon therefore seems to be less strongly trilobate than for instance *Tritonophon* and the whorls are probably more lanceolate than reniform with the shallow U-shaped sinus on the median lobe (see tentative outline drawn on specimen in Fig. 5c). The overall shell morphology would thus resemble that of *Sinuitopsis*, although with an accentuated median dorsum, a more shallow median apertural sinus, and an ornamentation of distinct tiled increments with a raised edge adaperturally.

Horný (1997e) compared *Atlantophon* with the trilobed *Bucanella* Meek from the Tremadocian of North America. The concept of *Bucanella* formulated by Koken & Perner (1925) is essentially eroded, with most of the originally assigned species that were placed in their sub-family Bucanellinae now being transferred to other genera (such as *B. quadrisulcatus* (Reed) herein being transferred to *Plectonotus*). Frýda & Bouchet (2005) elevated the Bucanellinae to family level, attributing the name to Koken (1925). However, as explained by Ebbestad (1999) that work, and in this case the family name, must be attributed to Koken & Perner (1925).

Peel (1974) showed that *Bucanella nana* Meek, the type species, may in fact have a bordered median dorsal band instead of only the dorsum being sinuated. In light of the discussion herein, similarities between *Bucanella nana* and *Atlantophon* seems merely conjectural and the trilobation also shared with the Plectonotinae should be viewed as case of

convergent morphology and *Atlantophon* can therefore neither be placed in the Plectonotinae nor the Bucanellidae.

Until new and better material of *Atlantophon* is discovered the family placement remains unresolved. Because of the trilobation, and comparison with the Plectonotinae, it is tacitly understood that this taxon had a pair of laterally placed ctenidia coinciding with the position of inhalant currents, while the median placed elevation was the site of the exhalant current and the anus as a result of torsion.

Superfamily **Bellerophontoidea** McCoy, 1852

Family **Sinuitidae** Dall in Zittel & Eastman, 1913

Genus *Sinuities* Koken, 1896

Type species. By subsequent designation of Bassler (1915, p. 1159), *Bellerophon bilobatus* Sowerby in Murchison, 1839, p. 643, pl. 19, fig. 13, from the Upper Ordovician (Sandbian Stage) Horderly Sandstone at Horderley, Shropshire, England.

Sinuities destombesi Horný, 1997e

(Figs 6a–f, 7a–f & 8)

Material. 30 specimens mentioned by Horný (1997e) and five new specimens added herein (specimens MGM-6963X– MGM-6966X).

Localities and horizons. Destombes localities 750, 885, 901, 1078, 1080, 1109, 1132, 1624, 1651, 1791 (see Horný 1997e) and Jbel Bou Ingarf ‘south’ (the MGM specimens listed under

material), central and eastern Anti-Atlas, Morocco. Upper Ktaoua and Lower Second Bani formations, Katian to Hirnantian stages.

Remarks. Horný (1997e) erected this species, based on the exceptionally large size of adult specimens (Fig. 6). It bears finely reticulated shell ornamentation (Fig. 7), which is seen in a number of species of *Sinuities* (see discussion in Horný 1997e). Records of the genus in the cold-water settings of Armorica, Iberia, and Bohemia flourish in the literature. Often they appear under the name *Sinuities bilobatus* (Sowerby in Murchison, 1839), but a number of species are named (see Horný 1963; Gutiérrez-Marco 1984; Sá 2008). Except for *Sinuities sowerbyi* Perner, 1903 from the older Tachilla Formation (Darrwilian), *S. destombesi* is the only named species of the genus in the Ordovician of Morocco.

Besides the gross morphology, specimens of *S. destombesi* preserve a number of morphological details. The reticulate shell structure shows densely spaced co marginal ribs crossed by subordinate spiral lines. The reticulation can be subdued or more distinct on the median sinus (Fig. 7a & c) and is more densely spaced on the lateral sides of the shell than towards the dorsum (Fig. 7b & d). At the umbilici the lip does not fill the space but forms a deep depression with a labro-umbilical ridge (Fig. 7e). Two deposits are seen in or close to the umbilical area. Firstly, the inductura in the umbilici, a lamellar deposit that would correspond to the parietal inductura or parietal callus at the inner part of the lip at the umbilicus in conical shells. The second type of deposit was called the subinductura by Horný (1996), and represents deposits laid on top of the original shell outside the umbilici (Fig. 7d & f). The subinductura is deposited underneath the inductura proper. Sometimes the subinductura preserves a slightly raised ring-like structure which was called the subinductural vallum by Horný (1996) pertaining to the rampart of roman fortifications (see Horný 1997e, pl. 6, fig. 2). Secondary shell deposits have been used to distinguish between sinuitid genera

(i.e. Frýda & Gutiérrez-Marco 1996) but as pointed out by Ebbestad *et al.* (2013a) secondary shell deposits may not be a derived feature, but could equally well be a broadly shared sinuitid characteristic, or even an ecological response in some sinuitid groups.

Horný (1997e) illustrated four specimens in which the myostracum was preserved. This appears as a thin, entire layer reflecting the area where the adductor muscle of the head-foot mass attached to the umbilical area of the shell.

A cross-section of *S. destombesi* shows a very low umbilical angle (*sensu* Ebbestad 1999) of about only 6°. Whorl height of the last whorl is slightly more than 2/3 of whorl width, while for the penultimate whorl this is slightly lower than 2/3 of whorl width. The rate of whorl expansion and whorl expansion at half whorls (*sensu* Peel 1974) is 2.7 and 4.4 respectively (Fig. 8). Thus, the shell is tightly coiled with a fairly low rate of expansion that increases slightly at maturity with a whorl that expands more dorsally than laterally.

Of the cold-water peri-Gondwanan species *S. destombesi* is most similar to *S. hispanicus* (Born, 1918) from the Darriwilian of Spain. Apart from attaining a large size, the contemporaneous species show similar reticulate ornamentation and the slight flattening of the median dorsum. Horný (1997e) pointed out that *S. destombesi* does not show constrictions across the internal mould of the body whorl, which sometimes occur in *S. hispanicus*. However, this is not a feature that seems to have phylogenetic importance.

Family **Bellerophontidae** McCoy, 1852

Subfamily **Plectonotinae** Boucot & 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 – ‘Illaenus Band’), Heathcote, Victoria, Australia.

Tritonophon peeli Horný, 1997c

(Fig. 9a & b)

Material. Five specimens mentioned by Horný (1997e).

Localities and horizon. Destombes localities 399 and 899, eastern Anti-Atlas, Morocco. Lower Ktaoua Formation, Sandbian? to Katian stages.

Remarks. The Ordovician distribution and species of this taxon was reviewed by Ebbestad *et al.* (2008). It is widespread in several peri-Gondwanan areas, Baltica, Avalonia, Kazakhstan, and Laurentia, ranging in age from Darriwilian to Hirnantian (herein). Owing to generally poor preservation, usually only the small and distinctly trilobed internal moulds are known. Although this leaves some degree of uncertainty with regards to affinity, the trilobed morphology, small size and narrow umbilici readily distinguish these kind of shells. Another trilobed Ordovician genus is *Bucanella* Meek, where the umbilical angle is greater than in *Tritonophon* or *Plectonotus* and it does not seemingly have a dorsal median band (but see discussion on *Atlantophon mairer*). As such, the species ‘*Bucaniella*’ [= *Bucanella*] *quadrisulcata* Reed, 1920 from the Silurian (Llandovery) of Wales should be transferred to *Plectonotus*, owing to the general shell morphology and the narrow outline of a dorsal median band, and it is here recombined as *Plectonotus quadrisulcatus* (Reed).

One of the Moroccan specimens of *T. peeli* Horný, 1997c shows fine prosocline growth lines curving gently back on the whorl towards the median raised keel, and the border of the median dorsal band (Fig. 9). Horný (1997e) compared it with the type material from Bohemia, Czech Republic, where the species has a long range. Horný (1997c) suggested that a specimens attributed to '*Bucaniella*' *bohemica* Perner, 1903 (now *T. bohemicus*) by Termier & Termier (1950, pl. 131, fig. 3) from a locality 3 km north of Taouz, eastern Anti-Atlas, could belong to *T. peeli*. In Bohemia *T. bohemicus* occurs in the Kralodvorian (upper Katian and lower Hirnantian).

Frýda (1999) followed Wahlman (1992) and placed the subfamily Plectonotinae in the family Bucaniidae while Horný (1997e) and Ebbestad *et al.* (2008) placed it with the family Bellerophontidae. Frýda (1999) pointed out the many uncertainties at the family-level classification within the bellerophontoidean gastropods.

Tritonophon grandis sp. nov.

(Fig. 10a–h)

Holotype. Specimen MGM-6967X figured herein as Fig. 10a–e.

Diagnosis. Large *Tritonophon* with shell nearly as wide as long, median lobe broad with median band slightly narrower than the lobe.

Derivation of name. From latin *grandis*, meaning large or grand, pertaining to the impressive size of the species.

Material. Four paratype specimens preserved as internal moulds (MGM-6968X–MGM-

618 6971X).

619

620 *Type locality and horizon.* Aït Isioul 'south', West of Tagounite, central Anti-Atlas, Morocco.

621 Lower Second Bani Formation, horizon T5, Hirnantian Stage.

622

623 *Description.* Shell large with maximum preserved shell length of ~10 mm; max shell width ~8
624 mm. Number of whorls unknown. Median lobe embraced by succeeding whorls, showing the
625 side of the whorls in the narrow umbilicus. Periphery at mid of evenly convex whorl with
626 slightly increased curvature of the umbilical wall towards the umbilici. Transition to median
627 lobe weakly concave. Height of lobe approximately the same as height of the whorl. Width of
628 median lobe 2/3 of total width, but narrower aperturally at the laterally expanding apertural
629 part of the whorl. Median band flat, outlined by grooves on the median lobe, being slightly
630 narrower than the lobe itself. Ornamentation, apertural lip and median anterior sinus
631 unknown.

632

633 *Remarks.* With a length of nearly 10 mm *Tritonophon grandis* sp. nov. is the largest species
634 of the genus hitherto known. It is also the youngest Ordovician occurrence of the taxon. The
635 shell is about as wide as it is long, and the broad median lobe bears a slightly narrower
636 median band. The shell therefore has a broadly rounded profile, compared to the narrow,
637 pointed outline of the type species and other species of the genus. Two large specimens
638 (MGM-6968X in Fig. 10f & MGM-6971X) have slightly narrower whorl widths and the
639 median lobe is more pronounced than compared to the holotype specimen. However, all five
640 known specimens of the new species are preserved in a soft decalcified coquina which
641 invariably yields different preservation of internal moulds.

The cross section of *T. peeli* from Iran shown by Ebbestad *et al.* (2008) illustrates that the median lobe is quite wide but higher than the whorl height in this species. In *T. grandis* the width of the lobe is proportionally larger and the height is proportionally lower. *Tritonophon kivitalonae* from the Silurian Stonehouse Formation, Nova Scotia, Canada, has a proportionally low median lobe compared to the height of the whorl but it is proportionally narrower than that in *T. grandis*.

Peel (1974) showed that the median band of the Silurian to Devonian *Plectonotus* occupies only part of the width of the median dorsal elevation, whereas it covers the entire width in *Tritonophon*. Generally, the trilobation in *Tritonophon* is more marked than that in *Plectonotus*. It could be argued that the narrow median dorsal band in *T. grandis* should suggest a placement with *Plectonotus*, but the marked trilobation suggests otherwise. The opposite argument was used by Peel (1974) for the Silurian *Plectonotus cherylae* Peel, 1974 that has a narrow shell with a *Tritonophon*-like median dorsal band, but a low median lobe.

Subfamily Bucaniinae Ulrich & Scofield, 1897

Genus *Bucanopsina* Horný, 1997a

Type species. By original designation of Horný (1997a, p. 7, text-figs 1–10), *Bucanopsis calypso* Perner, 1903, p. 157, text-fig. 110, from the Upper Ordovician (Katian Stage) Zahořany Formation at Praha-Libeň, Bohemia, Czech Republic.

Bucanopsina calypso (Perner, 1903)

(Fig. 11a–d)

Material. 13 specimens mentioned by Horný (1997e). Typical specimens are figured here as

Fig. 11a–d.

Localities and horizon. Destombes localities 899, 1640, and 1778, central and eastern Anti-Atlas, Morocco. Lower Ktaoua Formation, Sandbian to Katian stages.

Remarks. This explanate species is characterized by its small size, a well-bordered but low median dorsal band, short median anterior slit, and massive parietal deposits. Horný (1996, 1997a, f) discussed in detail the differences between *Bucanopsina* and the broadly comparable *Grandostoma* Horný, 1962. The latter has a median apertural sinus while *Bucanopsina* has a median apertural slit. Widely explanate gastropods are typically associated with shallow water soft substrates (Peel 1984 and references therein; Horný 1997e).

Bucanopsina calypso was first reported from the Zahořany Formation in Bohemia, and constitutes a genus that has hitherto only been found in Bohemia and Morocco. It co-occurs in Morocco with Bohemian species of *Sinuitopsis*, *Tritonophon*, and *Nonorios*, also from the Zahořany Formation, but all of these genera are found outside the peri-Gondwanan areas and have longer ranges.

Clade Neritomorpha

Superfamily **Platyceratoidea** Hall, 1879

Family **Platyceratidae** Hall, 1879

Remarks. Bouchet & Rocroi (2005) discovered that the original reference to the family-name by Knight (1934) was wrong (seemingly by *lapsus calami*). In a footnote Knight referred to Hall (1859) using Platyceridae as a heading on plates 1 to 8 in volume 3 of the ‘Palaeontology of New York’. However, Platyceridae is used in Hall (1879), on plates 1 to 8 in volume 5 of

the ‘Palaeontology of New York’. *Platyceridae* was corrected to *Platyceratidae* by Knight (1934).

Palaeozoic platyceratids have two types of protoconchs, a tightly coiled type found as far back as the Silurian and an open coiled hook-like protoconch found as far back as the Early Ordovician (Frýda 1999; Frýda & Rohr 2004; Frýda *et al.* 2009 and references therein). Note that although identifiable in the fossil record, these protoconch morphologies are rarely associated with teleoconchs. These important findings led the authors to suggest that Palaeozoic platyceratids are diphyletic and two sub-clades within the Neritimorpha, to which platyceratids have been associated (e.g. Bandel 1992), were erected; the Cyrtoneritimorpha for members with a hook-like protoconch and the Cycloneritimorpha for members with the tightly coiled protoconch. Possible patellogastropod affinities of the platyceratids suggested by Sutton *et al.* (2006) were dismissed by Frýda *et al.* (2009) owing to the uncertain affinity of the putative platyceratid from the Herefordshire Silurian lagerstätte that was the foundation for this suggestion.

Genus *Nonorios* Horný, 1997d

Type species. By original designation of Horný (1997d, p. 46); *Turbonitella pater* Barrande in Perner, 1903, pl. 51, figs 1–3; 1907, p. 288, from the Upper Ordovician (Katian Stage) Zahořany Formation at Vráž, Bohemia, Czech Republic.

Nonorios pater (Barrande in Perner, 1903)

(Fig. 12a–d)

Material (Moroccan specimens only). Three specimens mentioned by Horný (1997e).

717
718 *Localities and horizon.* Destombes localities 1266, 1270, and 1276, eastern Anti-Atlas,
719 Morocco. Lower Ktaoua Formation, Katian Stage.
720
721 *Remarks.* *Nonorios* was erected by Horný (1997d) for a number of Ordovician platyceratid
722 species discussed by Perner (1903, 1907). *Nonorios pater* is known from the Letná, Vinice,
723 and Zahořany formations in Bohemia, the Lower Ktaoua Formation in Morocco, and strata
724 contemporaneous with the Vinice Formation in Spain (undescribed) (Horný 1997d, 1997e,
725 1999b; Gutiérrez-Marco *et al.* 1999). Typically it co-occurs with *Holopea? antiquata* (now
726 placed with *Radvanospira*) in what Horný (1997e, 1999b) referred to as the *Nonorios*
727 Community; except for *Sinuitopsis* sp. none of the other co-occurring taxa in Bohemia can be
728 found in Morocco.

729 *Nonorios* is characterized by the rapidly expanding turbiniform shell, large rounded
730 aperture, an inner lip having a groove or channel and an ornamentation of both spiral and
731 commarginal components (Fig. 12).

732 Horný (1997e) noted that *N. pater* and *Holopea? [=Radvanospira] antiquata* had been
733 recognized by Romão *et al.* (1995) in Portugal under different names, and anticipated these
734 two could also be recognized in France and Sardinia (Horný 2002). With respect to the latter
735 he may have had *Craspedostoma sardoum* Vinassa de Regny, 1927 from the Late Ordovician
736 (Katian) Portixeddu Formation in mind. This is a small rotund, anomphalous species that has
737 an overall similarity with *Nonorios* but could as well be compared to *Radvanospira antiquata*.
738 Without ornamentation preserved these two species can be difficult to separate (Horný 1997e)
739 and more material is required in order to assess the degree of variation in these two species.

740 Ebbestad *et al.* (2008) recognized *Nonorios kleistos* in the Late Ordovician (Sandbian)
741 Katkoyeh Formation of the Kerman Region of east-central Iran. This is a large and thick-

shelled species that develops a massively thickened base and a closed umbilicus at maturity. The ornamentation lacks the spiral component seen in *N. pater*. Two other species tentatively assigned to *Nonorios* are known, the Late Ordovician (Katian) *Nonorios? carnicus* Vinassa de Regny of the Italian Carnic Alps and *Nonorios? transversum* Ulrich in Ulrich & Scofield, Late Ordovician (Katian) of USA (see Horný 1997d; Ebbestad *et al.* 2008).

Radvanospira gen. nov.

Type species. Designated here, *Naticopsis antiquata* Barrande in Perner, 1903, pl. 54, figs 31–33, non 34–37 from the Upper Ordovician (Sandbian to Katian) Letná to Zahořany formations, Bohemia, Czech Republic.

Diagnosis. Shell turbiniform with 4–5 evenly expanding whorls, whorl profile elongated, higher than wide. Aperture auriform to semi-circular. Width of shell up to 40 mm. Shell thick, umbilicus closed, ornamentation of fine, straight to slightly irregular and densely spaced prosocline and sharp lirae. Entire aperture weakly inclined (up to ~35°), inner lip reflexed with channel, thicker than base and outer lip.

Derivation of name. Named in honour of the late Dr Radvan J. Horný, Czech Republic, for his outstanding contributions to the understanding of Lower Palaeozoic molluscs and their evolution. The name is combined with the Latin *Spira*, a spire. The ending is feminine.

Remarks. The type species of *Radvanospira*, *H.? antiquata* (Barrande in Perner) cannot be placed with *Holopea* Hall. Species of *Holopea* are generally smaller, have thinner shells, no thickening of the inner lip and no inner lip channel, the whorls are more rounded with deeper

sutures, and the ornamentation generally consists of finer threads. The preservation of *Radvanospira*, although variable, suggests that the shell was primarily calcitic whereas that of *Holopea* spp. is seldom preserved, leaving mainly steinkerns, which is typical in taxa with an aragonitic shell (see Cherns *et al.* 2008).

Radvanospira resembles species of *Platystoma* Conrad and *Naticonema* Perner, but both of these genera have a more rapid shell expansion giving a lower, more rotund shell form (i.e. Naticiform) and have a more rounded whorl profile. Ornamentation in *Platystoma* typically has a spiral component.

Radvanospira gen. nov. is an important genus in southern Gondwana, being widely recognized through *R. antiquata* (see discussion for the species, and also discussion under *Nonorios pater*).

Perner (1903, 1907) described a number of Ordovician and Silurian species attributed to *Holopea*, and these need to be examined for comparison with *Radvanospira*. Likewise, species of *Holopea s.l.* in other collections of the southern Gondwanan areas should be carefully examined to seek for the presence of *Radvanospira*, but this is beyond the scope of this paper.

The close similarity of *R. antiquata* to the platyceratid *N. pater* was noted by Horný (1997e), and the morphological traits in *Radvanospira* discussed above also seem to warrant the placement of the genus in the family Platyceratidae.

Radvanospira antiquata (Perner, 1903)

(Figs 13a–g & 14a–h)

*1903 *Naticopsis antiquata* Barrande in Perner, pl. 54, figs 31–33, non 34–37.

1907 *Naticopsis antiquata* Barrande in Perner. – Perner, p. 289.

792 1911 *Platyostoma ferrigenum* Barrande in Perner. – Perner, p. 170.
 793 ?1975 *Holopea* sp. – Carls, p. 136.
 794 ?1995 *Holopea?* sp. – Romão *et al.*, p. 124.
 795 1997e *Holopea? antiquata* Barrande in Perner. – Horný p. 60, pl. 15, figs 1–13; pl. 16, figs 1–
 796 6.
 797 ?1997 *Holopea?* sp. – Gutiérrez-Marco *et al.*, p. 35.
 798 1999 *Holopea? antiquata* (Barrande in Perner). – Gutiérrez-Marco *et al.*, p. 490.
 799 1999b ?*Holopea* – Horný, p. 398.
 800 2000 *Holopea? antiquata* (Barrande in Perner). – Horný, p. 421.
 801 2003 *Holopea? antiquata* (Barrande). – Herranz Araújo *et al.*, p. 422.
 802 2006 *Holopea? antiquata* (Barrande). – Villas *et al.*, p. 734.
 803 2006 *Holopea? antiquata* (Barrande). – Sá, p. 618, fig. 1.
 804 2008 *Holopea? antiquata* Barrande in Perner. – Sá, p. 56, fig. 2; pl. 5, figs 11–13.
 805 ?2016 *Holopa* sp. – Montserín López *et al.*, p. 19.
 806
 807 *Lectotype*. Designated by Horný (1997e, p. 60), specimen NM L8443 figured by Perner
 808 (1903, pl. 54, fig. 33).
 809
 810 *Material* (Moroccan material). 15 specimens mentioned by Horný (1997e) and five new
 811 specimens added herein (specimens MGM-6972X– MGM-6976X).
 812
 813 *Localities and horizons*. Destombes localities 88, 1250, 1266, 1302, 1305, 1313, and 1315,
 814 eastern Anti-Atlas, Morocco. Lower Ktaoua and Upper Tiouririne formations, Katian Stage.
 815 Erfoud 2, eastern Anti-Atlas, Morocco. Upper Tiouririne Formation (MGM specimens),
 816 Katian Stage.

817
818 *Remarks.* The species was described by Horný (1997e) but some emendations and additions
819 can be made, and some typical specimens are re-figured here (Figs 13 & 14). Originally it was
820 stated that the species has three to four whorls, which would suggest very rapid whorl
821 expansion. However, the available specimens show at least three whorls preserved with the
822 spire being eroded (Figs 13d & 14e). Thus the shell had at least four whorls and most likely
823 five giving it a low turbiniform shape rather than naticiform. The whorl expansion rate W (see
824 methods) is around 2 in the comparable *R. baniensis* sp. nov. although that species has a
825 slightly higher rate of translation down the axis. The periphery is at mid-height of whorl.
826 Inclination of entire aperture in *R. antiquata* is about 35°, and there is very little posterior
827 projection of base. The inner margin of the aperture in large specimens is evenly curved but
828 parallel to the axis of coiling (Fig. 13a). In a juvenile specimen attributed to the species the
829 curvature of the inner margin is absent as it is inclined at about 15° to the axis (Fig. 14f & g).
830 The apertural edge is broken and may not show the inner margin entirely correctly, but an
831 ontogenetic change in the curvature and inclination of this feature seems likely.

832 Besides Bohemia and Morocco, *Holopea? antiquata* has been reported from the Central
833 Iberian Zone at Camada Favaçal (Buçaco), Amêndoa-Mação, and the Trás-os-Montes region
834 (see Sá 2008). In Spain a number of occurrences may relate to *R. antiquata* or *Radvanospira*
835 spp., which could be common in middle Berounian (Katian) strata. *Holopea?* has been
836 mentioned in the eastern (or Aragonian) branch of the Iberian Ranges (Carls 1975), in the
837 Western (or Castilian) branch of the same (Herranz Araújo *et al.* 2003), and is abundant in
838 other strata such as the Cantera Shales/base of the Bancos Mixtos Formation of the Viso del
839 Marqués syncline of the southern Central Iberian Zone (Monteserín López *et al.* 2016). In the
840 West Asturian-Leonese Zone (NW Spain), *Holopea?* sp. occurs within an assemblage of
841 brachiopods, trilobites, and bryozoans correlatable with those from the Iberian Ranges and the

Central Iberian Zone of Spain and Portugal (Gutiérrez-Marco *et al.* 1997). Note that the 1987 reference in the synonym list of Sá (2008) is erroneous. All of these records need to be reassessed in the light of the Bohemian and Moroccan material.

Radvanospira baniensis sp. nov.

(Figs 15a–i & 16)

Types. Holotype (MGM-6977X) and paratype (partial steinkern) (MGM-6978X) (Figs 15 & 16).

Diagnosis. A species of *Radvanospira* with a shell of sub-equal width and height, an apical angle of $\sim 85^\circ$, inclination of aperture around 30° , width of aperture less than height, periphery slightly below mid-height of whorl. Ornamentation consisting of gently prosocline lira without undulations or bifurcations.

Derivation of name. After the Upper Bani Group in which this species occur.

Type locality and horizon. Aït Isioul ‘south’, West of Tagounite, central Anti-Atlas, Morocco. Lower Second Bani Formation, horizon T4, Hirnantian Stage.

Description. Shell ~ 20 mm wide with at least four whorls. Height slightly greater than width. Whorl profile auriform with evenly and gently convex upper and lower whorl surfaces, but with periphery slightly below mid-height of whorl. Whorl expansion rate is about 2. Whorls overlap slightly below periphery with sharp suture line but without being incised. Apical angle is $\sim 85^\circ$. Earliest whorl(s) and protoconch unknown. Aperture tangential, simple,

867 inclined about $\sim 30^\circ$. Outer lip entire, without a sinus, base rounded with an angle of about 60°
868 to inner margin. Shell thick with thickening of inner margin which is gently curved, nearly
869 straight, broad, flat and slightly recurved, bearing a shallow groove along most of its length.
870 Ornamentation consists of fine, sharp lirae that are straight without undulations or
871 bifurcations. In early ontogeny there are as many as $\sim 10/\text{mm}$ and $\sim 5/\text{mm}$ in later ontogeny.
872

873 *Remarks.* *Radvanospira baniensis* sp. nov. is smaller than *R. antiquata*, with a more
874 pronounced auriform aperture that is slightly less inclined. The periphery of the whorls is a
875 little lower and the translation down the axis is greater than in *R. antiquata*. In both species
876 the ornamentation is equally dense and the lirae are sharp, but in *R. baniensis* they are straight
877 without the undulations and bifurcation seen in *R. antiquata*.

878

879 Superfamily **Eotomarioidea** Ulrich & Scofield, 1897

880 Family **Gosseletinidae** Wenz, 1938

881 Subfamily **Euryzoninae** Wagner, 2002

882

883 *Deaechospira* Wagner, 2002

884

885 *Type species.* – By original designation of Wagner (2002, p. 85), *Trochus ellipticus* Hisinger,
886 1831, p. 11, pl. 2, fig. 2. From the Upper Ordovician (Sandbian) Dalby Limestone at Furudal
887 in the Siljan District, Sweden.

888

889 *Remarks.* The type species of *Deaechospira* Wagner was discussed by Frisk & Ebbestad
890 (2007). The type material is poorly preserved, but well-preserved exemplars of the species are
891 known from both Sweden and Norway (see also Yochelson 1963). This predominantly

Baltoscandian genus differs from the North American *Clathrospira* Ulrich & Sofield, 1897 in a more convex whorl profile, a peripheral band that is broader and symmetrical placed on the periphery, between the upper and lower whorl, rather than more on the upper whorl surface. The upper whorl of *Clathrospira* is higher (adapically) than the lower part, so that the band appears to sit low on the whorl. The bordering lirae of the band are less prominent in *Deaechospira*, and there is a greater symmetry between the upper and lower parts of the whorl than in *Clathrospira*.

Identifying this genus in southern Gondwana is not unreasonable. A number of gastropod and tergomyan taxa first identified in, and specific to, Bohemia have later been found in Baltica, such as *Sarkanella* Horný, *Laeogyra* Perner, *Grandostoma* Horný, and *Carcassonnella* Horný & Peel (see Ebbestad 2008; Stewart 2012; Ebbestad *et al.* 2013b). There is an obvious similarity between the wider Mediterranean faunas (e.g. Gutiérrez-Marco *et al.* 2017), although of the mentioned taxa only *Carcassonnella* has hitherto be found in Baltica, Bohemia, and Morocco (Ebbestad 2016).

Deaechospira amouguerana (Horný, 1997e)

(Figs 17a–h, 18a–k & 19a–e)

Holotype. Specimen NM S2564, re-illustrated here in Fig. 17a–h.

Material. 47 specimens mentioned by Horný (1997e).

Localities and horizons. Destombes localities 86, 88, 882, 1100, 1266, 1652, and 1778, eastern Anti-Atlas, Morocco (except locality 1652 from the High Atlas north of Ouarzazate). Lower Ktaoua Formation, Katian Stage except for the Sandbian Stage localities 1100 and

917 1778. Localities 585, 1134, and 1282, eastern Anti-Atlas, Morocco. Upper Tiouririne
918 Formation, Katian Stage.

919

920 *Remarks.* The species was described by Horný (1997e), and previously illustrated and non-
921 illustrated material is presented here (Figs 17–19). Additional observations on the
922 morphology can be added here. Most likely the species has more than six whorls, as this is the
923 number of observable preserved whorls and the spire is missing. The apertural sinus is well-
924 developed and easy to follow, but does not seem to generate a slit. In specimen NM S2686,
925 not illustrated by Horný (1997e), the course of the sinus and development of the peripheral
926 band suggest development of a short sinus at the sinus apex (Fig. 18g–h); the sides of the
927 sinus are not sub-parallel. A portion of the band in specimen NM S2685 (Fig. 18f) is lacking
928 lirae and the apex sinus is clearly seen. On the internal mould of NM S2684 the impression of
929 the peripheral band is raised medially and flanked by shallow spiral depressions (Fig. 18k).

930 In the juvenile specimen (Fig. 19) the peripheral band is flush with the whorl and the
931 bordering lirae are very faint. The band may even be positioned slightly higher on the whorl,
932 as in *Clathrospira*, although the roundness and symmetry of the whorls in *Deaechospira*
933 clearly set these genera apart.

934 Horný (1997e) compared the Moroccan species closely to *Clathrospira egens* (Barrande in
935 Perner, 1907) from the Zahořany Formation in Bohemia. This appears to be a smaller species,
936 with a more convex whorl profile, deeper sutures, stronger lirae bordering the peripheral
937 band, and less prosocline growth lines giving a shallower apertural sinus. The Bohemian
938 species is also transferred to *Deaechospira*.

939 *D. amouguerana* is similar to the type species *D. elliptica* (Hisinger) in its large size and
940 high number of whorls. The base in the type species is flatter, the upper whorl profile is less

convex, the lirae bordering the peripheral band are stronger, the lunulae of the band are asymmetrical, and the band has a spiral thread that is lacking in the Moroccan species.

Deaechospira sp.

(Fig. 20a–i)

Material. Four specimens mentioned by Horný (1997e), of which three have been studied here (NM S2687–NM S2689).

Locality and horizon. Destombes locality 134, eastern Anti-Atlas, Morocco. Upper Tiouririne Formation, Katian Stage.

Remarks. Horný (1997e) described the species in detail, but some additions can be made. The species has at least four whorls preserved, and most likely had five to six whorls. The peripheral band is broad, straight and slightly sunken between the upper and lower border so that bordering lirae are not really standing out from the shell but forming a ledge. Horný (1997e) recorded a faint angulation on the lower whorl surface of the internal mould of NM S 2689, but this cannot be substantiated (Fig. 20a, c & d). A muscle impression is present on the base of the same specimen (Fig. 20d). It is crescent-shaped, with a well-defined outer edge, positioned on the umbilical wall and encroaching slightly onto the base of the whorl. It starts quarter of a whorl back from the aperture and extends nearly three quarters of a whorl back abaperturally where it disappears under the matrix. The surface is textured with fine irregular and wrinkled, discontinuous lines.

The position of the muscle impression close to the aperture and sinus suggest that the snail was not capable of deep withdrawal of the body. Instead the near-aperture position of the scar,

the rounded and straight aperture would suggest clamping behaviour of this species (see discussion on clamping behaviour in Ebbestad & Peel 2001 and references therein).

Horný (1997e) placed these specimens with the true *Lophospira* Miller, which is not supported here. The general shell shape, great symmetry of the apertural sinus and its symmetrical placement on the periphery, the broad peripheral band with well-defined lirae, and the median spiral lira on the band support a placement with *Deaechospira*. Although the material seems well-enough preserved to define a species, a new name is not put forward. This is because one gets the sense that Horný (1997e) may have compared these specimens with contemporaneous Bohemian material and expected similarities. Most of the original Perner material has not been examined for this project, and a designation will have to await a thorough revision of that material.

Deaechospira sp. is smaller than *D. amouguerana* but both share a similar shell shape, a broad peripheral band and a symmetrical and short apertural sinus (for the latter character compare Fig. 18g–i with Fig. 20c & e). The development of the peripheral band is different in the two, where the peripheral band of *Deaechospira* sp. has distinct upper and lower lirae and a lira placed low on the peripheral band, whereas in *D. amouguerana* the band is slightly raised with more indistinct bordering lirae and no lira on the band (compare Fig. 17g & h with Fig. 20f).

Genus *Allossospira* gen. nov.

Type species. Designated here, *Lophospira? debganensis* Horný, 1997e, p. 58, pl. 13, figs 7–10, pl. 14, figs 1–9, from the Upper Ordovician (Katian) Upper Ktaoua Formation, central and eastern Anti-Atlas, Morocco.

Diagnosis. (Modified from the diagnosis of *Lophospira? debganensis* by Horný 1997e). Shell trochiform but slightly coeloconical at maturity, upper whorl surface of earliest whorls weakly convex. Shell up to 35 mm wide, with at least six whorls, with increasing translation during ontogeny. Aperture with a deep, narrow asymmetrical sinus. Peripheral band vertical in early ontogeny with sharp upper edge, changing to a slightly inflated band with raised weakly defined median keel at apex of asymmetrical lunulae. At maturity band extend out from shell, curving slightly adapically.

Derivation of name. From Greek *Allosso*, meaning change, changeable, referring to the marked ontogenetic changes in the shell of this taxon. The name is combined with the Latin *Spira*, a spire. The ending is feminine.

Remarks. The original placement of this genus with the Lophospirids is not upheld, and by comparison with *Deaechospira* it is being placed in the subfamily Euryzoninae Wagner. Horný (1997e) discussed a number of species attributed to *Pleurotomaria (Lophospira) s.l.* by Perner (1903, 1907), and while some of these (especially *L. infausta* Perner) may be close to *Allossospira* they have not been studied in the present work.

Allossospira debganensis (Horný, 1997e)

(Figs 21a–i, 22a–h, 23a–c & 24a, b)

Holotype. Specimen NM S2466, figured here as Fig. 21a–i.

Diagnosis. Same as for genus.

1016 *Material.* 37 specimens reported by Horný (1997e) and 16 new specimens added here (MGM-
1017 6979X–MGM-6991X; the number MGM-6985X includes three specimens and number
1018 MGM-6991X includes two specimens).

1019
1020 *Localities and horizon.* Destombes localities 49, 757, 901, 1077, 1078, 1109, 1125, 1132
1021 (holotype), 1146, 1649 (marked as 1149 in Horný 1997e), 1791, and Jbel Bou Ingarf ‘south’
1022 (MGM specimens listed under material), central and eastern Anti-Atlas, Morocco. Upper
1023 Ktaoua Formation, Katian Stage.

1024
1025 *Description* (modified and emended from Horný 1997e). Shell trochiform, anomphalous, with
1026 at least six whorls. Spire angle of $\sim 80^\circ$, whorl expansion rate ~ 1.7 . Whorls embraced just
1027 below periphery, obscuring the lower part of the peripheral sinus, but rate of translation
1028 increases during ontogeny so that lower part of peripheral sinus becomes visible. Suture is
1029 shallow. Upper whorl surface on initial three to four whorls nearly straight or slightly convex,
1030 bulging slightly at upper margin of peripheral sinus, becoming gradually weakly concave and
1031 finally strongly concave at maturity, giving a coeloconical appearance. Peripheral band
1032 vertical in early ontogeny, slightly concave with sharp upper edge, changing to a slightly
1033 inflated band with raised, weakly defined median keel from fourth whorl onwards and with
1034 gradually increased convexity. At maturity peripheral band carina-like, extending out from
1035 shell, rounded and curving slightly adapically. Growth lines consist of fine, dense, slightly
1036 irregular prosocline lines above periphery, but curving slightly anteriorly close to suture
1037 before turning backwards with increased curvature near periphery. Below periphery growth
1038 lines run anteriorly and slightly abapically, at the upper third of the whorl, thereafter turning
1039 in a wide convex arch back towards the umbilicus. Base projecting anteriorly in umbilical
1040 view. Aperture inclined about 15° , with lower side being more inclined than upper side.

1041 Apertural sinus forms wide and deep V-shape, asymmetrical with lower side being wider.
1042 Apex of sinus coincides with spiral keel. Upper part of sinus and lunulae sub-parallel owing
1043 to the increased curvature of the growth lines at the periphery, defining the sharp edge in early
1044 ontogeny. Lunulae open below periphery. Upper edge of lunulae lost during ontogeny as
1045 peripheral band becomes convex and protruding from shell. Protoconch not preserved, but
1046 possibly simple and bulbous.

1047

1048 *Remarks.* *Allossospira* gen. nov. is a taxon that displays a number of major ontogenetic
1049 changes; the convexity of the upper whorl surfaces goes from slightly convex to strongly
1050 concave and almost perpendicular to the axis of coiling, the peripheral band goes from flat
1051 with a sharp upper edge to bulging and upturned with a weak median carina so that the growth
1052 lines continue uninterruptedly across the periphery, and the rate of translation increases during
1053 ontogeny. The aperture is slightly inclined with greater inclination of the lower half, reflecting
1054 the asymmetric and deep V-shaped sinus and the anterior projection of the base. Although the
1055 initial part of the spire and the protoconch is missing, specimen MGM-6982X (arrow in Fig.
1056 22f) preserves an external impression of what may be the protoconch. The structure is about
1057 250µm across, and would be simple, openly coiled.

1058 The concave upper whorl surface and upturned peripheral band at maturity is reminiscent
1059 of similar features in some raphistomiid species of *Raphistoma* Hall and *Scalites* Emmons,
1060 and the eotomariid *Phanerotrema* Fischer, but in these forms these characters are continuous.
1061 Most of these taxa has spiral ornamentation and *Raphistoma* and *Scalites* generally has a basal
1062 carina which is absent in the anomphalous *Allossospira*.

1063 It is clear that there are no peripheral lirae in *Allossospira*. The sharp upper line in early
1064 ontogeny is purely a result of the growth lines sweeping strongly backwards and aligning

(Fig. 21g). As the periphery starts to bulge the growth lines are pulled out and the tight congregation seen at the flat band is lost (arrows in Fig. 21e).

Originally the genus was tentatively placed with *Lophospira* Whitfield. The lophospiroids, including the lophospirids and the trochonematids, are a species rich group that was revised by Wagner (1995, 1999). The group as a whole contain species with both comarginal and spiral ornamentation, many exhibiting a carina on the lower whorl surface, a basal carina, a phaneromphalus umbilicus, and deep sutures. Typically, the peripheral band is bordered by lirae and it contains one or more spiral components or a keel. Most of these characters are not seen in *Allossospira*, although the anterior projection of the base is shared with many lophospirids. The peripheral band keel in *Allossospira* is an indistinct feature and develops late in the ontogeny, and is somewhat reminiscent of the structure seen in *Lophospira milleri* (Miller), the type species of *Lophospira*. Both Knight (1941) and Horný (1997e) used the term pseudo-selenizone to describe the nature of the peripheral band in *L. milleri* and *L. debganensis* respectively. A broadly similar situation is seen in the eotomarid genus *Semizona* Ebbestad & Peel, 2001 from the Late Ordovician of Sweden, where the curvature of growth lines of the upper whorl surface are almost horizontal at the periphery and creates the impression of a border on the upper part of the peripheral band; *Semizona* lacks a peripheral keel (Ebbestad & Peel 2001). It is considered important that these characters together with the convex upper whorl surface and protruding peripheral band, are a gerontic development in *Allossospira*. Together with the other characters discussed above, this separates the genus from the lophospirids.

Three juvenile specimens of *Allossospira debganensis*, all on the same block of matrix, appear very similar to the juvenile *Deaechospira amouguerana* (compare Figs 19 & 23). Growth lines of the upper whorl surface of *Allossospira debganensis* curve more strongly abaperturally, and while the peripheral band is not bordered by lirae, it is horizontal with a

1090 sharp and distinct edge on the upper whorl surface. *Allossospira* is also similar to
 1091 *Deaechospira ellpitica*, the type specis of the latter genus, in the asymmetrical development
 1092 of the apertural sinus. While *D. elliptica* has a bordered peripheral band, the lunulae are
 1093 asymmetrical, with the lower half being the widest. In *D. elliptica* the peripheral band has a
 1094 spiral lira, which is absent in *Allossospira*. Although both are quite large, the two differ in the
 1095 convexity of the upper whorl surface of the last whorl, but have a similar inclination of the
 1096 aperture owing to the asymmetrical apertural sinus. In *Deaechospira* the sinus is not very
 1097 deep, and as seen in *D. amouguerana* the sinus dos not generate a proper slit. The latter
 1098 species has a peripheral band bordered by lirae, lacking in *Allossospira*.

1099

1100 Superfamily **Lophospiroidea** Wenz, 1938

1101 Family **Lophospiridae** Wenz, 1938

1102 Genus *Lophospira* Whitfield, 1886

1103

1104 *Type species*. By subsequent designation of Oehlert (1888, p. 23), *Murchisonia bicincta* Hall,
 1105 1847, now considered a junior synonym of *Murchisonia milleri* Miller, 1877. Upper
 1106 Ordovician (Katian Stage) Trenton Limestone at Waterstown, New York State, USA.

1107

1108 *Lophospira latilabra* sp. nov.

1109 (Fig. 25a–k)

1110

1111 *Holotype*. Specimen MGM-6992X, figured here as Fig. 25a–d, f–h, i & k.

1112

1113 *Paratypes*. Two specimen MGM-6993X-1 and MGM-6993X-2 (not figured), from the same
 1114 locality as the holotype (Fig. 25e & j).

1115

1116 *Diagnosis.* A species of *Lophospira* with seven non-disjunct whorls, a sharp wedge-shaped –
1117 and from the fourth whorl – continuous peripheral band, deep shovel-like base and inner
1118 margin.

1119

1120 *Derivation of name.* From Latin *Lata*, Wide and *Labrum*, giving the meaning wide-lipped,
1121 pertaining to the large prominent inner margin and base in this species.

1122

1123 *Type locality and horizon.* Jbel Bou Ingarf ‘south’, central Anti-Atlas, Morocco. Upper
1124 Ktaoua Formation, Katian Stage.

1125

1126 *Description.* Shell moderately high spired, with seven whorls. Height of holotype 12 mm,
1127 width 7 mm. Spire angle is 60°. Umbilicus anomphalus, the base curving sharply toward the
1128 umbilicus. Upper whorl surface steeply inclined (30° relative to axis of coiling), evenly
1129 concave with a sharp upper angulation (sutural shelf) that is nearly horizontal and at the
1130 height of the suture. Suture simple, not incised. Thin peripheral band placed symmetrical on
1131 periphery, slightly sunken and bordered by fine, thin ledge-like edges that are not raised as
1132 lirae but flush with upper and lower whorl surfaces. Band bluntly wedge-shaped without
1133 visible lunulae. Band is first manifested on the fourth whorl. Apertural sinus broad, V-shaped
1134 and short. Inclination of aperture slight, nearly vertical. Base nearly straight, abapertural
1135 projection gentle. Upper part of lower whorl surface nearly vertical and weakly concave
1136 above low, blunt spiral carina, and gently convex below carina with an angle of about 50°
1137 relative to axis of coiling. Upper surface and lower surface down to carina symmetrical in
1138 shape. Whorls embrace at carina, obscuring this in earlier whorls. Aperture of similar height
1139 and width (sub-rounded in outline). Outer margin thin above periphery, gradually widening

1140 into wide and broad shovel-like base and inner margin. Angle between base and inner margin
1141 about 15°. Inner margin straight, gently curved with faint longitudinal groove, reflected
1142 around axis of coiling. Apex of sinus nearly perpendicular relative to axis of coiling (angles
1143 about 80° adapically). Protoconch not preserved in detail, but seemingly simple, open coiled.
1144 Ornamentation consists of fine gently prosocline growth lines on upper whorl surface. Below
1145 the peripheral band the growth lines are of same strength as above, curving gently convex to
1146 carina before turning sharply abaperturally towards umbilicus.

1147

1148 *Remarks.* The holotype is an external mould preserved in two halves of a nodule. Silicone
1149 casts were made for each half, completing the specimen (Fig. 25a–d, k shows one half and
1150 25f–i the other half). The paratypes are preserved with the impression of one side only,
1151 allowing a silicon cast to be made.

1152 This species is similar to North American Ordovician species of angular *Lophospira*
1153 (major differences given in parentheses behind each species); for instance *L. perangulata*
1154 (Hall) (taller, steeper spire angle, lower carina not embraced by subsequent whorls), *L.*
1155 *sorocula* (Billings) (fewer whorls?, less prominent sutural shelf, more prominent carina on
1156 lower surface, stronger ornamentation, more incised suture at maturity), and *Lophospira*
1157 *milleri* Miller (less distinct and sloping sutural shelf, less distinct peripheral band lacking the
1158 sharp wedge-shape, coarser ornamentation). The Moroccan species resembles even some
1159 species of *Paupospira* Wagner, recognized by its thick columnella and the shovel-like
1160 aperture, but the nature of the columella is unknown in *L. latilabra* and the trilineation of the
1161 peripheral band is continuous.

1162 Some similar taxa from other Ordovician deposits are (in alphabetical order): *L. acuta*
1163 Grabau (Korea, North China: more narrow and taller, more curved inner margin, whorls
1164 embrace below carina on lower whorl surface), *L. argenta* Tassel (Australia: narrower and

1165 taller, lacking sutural shelf, whorls embrace below carina on lower whorl surface), *L. jaekeli*
1166 (Koken in Koken & Perner) (drift material in Germany, originating from Scandinavia. Too
1167 little is known of this species to compare),

1168 *Lophospira* is a wide-spread taxon in the Ordovician, mostly in the warm water realms, but
1169 also unequivocally present in cold-water southern Gondwana. The specimen from Morocco
1170 attributed to *Lophospira* by Horný (1997e) is here placed differently, while the affinity of *L.*
1171 *latilabra* is more certain. Several Bohemian taxa need to be considered to be able to
1172 understand the distribution of this genus, but that is beyond the scope of this study.

1173

1174 Gastropoda indet.

1175

1176 *Remarks.* A poorly featureless external mould of a high-spired gastropod with ten whorls was
1177 tentatively attributed to *Loxonema?* sp. by Horný (1997e, pl. 16, figs 14 & 15). The poor state
1178 of the specimen (latex cast) does not allow identification of its affinity and it is here treated as
1179 indeterminable. The specimen comes from Destombes locality 1791, Upper Ktaoua Formation
1180 (Katian), eastern Anti-Atlas, Morocco.

1181

1182 Class **Bivalvia** Linné, 1758

1183 Subclass **Protobranchia** Pelseneer, 1889

1184 Superorder **Nuculiformii** Gray, 1824

1185 Order **Nuculoida** Dall, 1889

1186 Superfamily **Nuculoidea** Gray, 1824

1187 Family **Praenuculidae** McAlester, 1969

1188 Genus *Praenucula* Pfab, 1934

1189

1190 *Type species.* By subsequent designation of Pfab (1934, p. 235), *Nucula dispar* Barrande,
 1191 1881d, pl. 273, from the Mid Ordovician (early and mid Darriwilian Stage) Šárka Formation
 1192 at Osek, Bohemia, Czech Republic.

1193

1194

1195 *Remarks.* The similarity between the genera *Praenucula*, *Praeleda*, and *Deceptrix* were
 1196 previously discussed in many papers (Bradshaw 1970; Pojeta 1978; Tunnicliff 1982; Babin &
 1197 Gutiérrez-Marco 1991; Cope 1997, 1999; Babin & Beaulieu 2003; Kříž & Steinová 2009;
 1198 Polechová 2013). Here only the main opinions regarding these genera are discussed, as this is
 1199 otherwise beyond the scope of the paper. According to Cope (1997), the genus *Deceptrix* is
 1200 valid, but it is characteristic of the Devonian while *Praeleda* and *Praenucula* are
 1201 characteristic of the Ordovician. Tunnicliff (1982) suggested the following main differences
 1202 between *Praenucula* and *Praeleda* (in his concept *Deceptrix*): 1) the posterior teeth in
 1203 *Praeleda* (=‘*Deceptrix*’) are smaller and more numerous than the anterior teeth while in
 1204 *Praenucula* the posterior and anterior teeth are similar in size and number; 2) umbos in
 1205 *Praenucula* lie in the posterior half while in ‘*Deceptrix*’ they generally lie in the anterior half;
 1206 3) in ‘*Deceptrix*’ the adductor muscle scars are larger and in a more ventral position, in
 1207 *Praenucula* they are close to the dorsal margin. Cope (1999) added another character:
 1208 between the anterior and posterior hinge range it is possible (but not always) to find the
 1209 discordance). In conclusion, all these authors noted the similarity between these two genera
 1210 and they could be congeneric. In the Late Ordovician of Bohemia these two genera are very
 1211 common and their species show a mixture of the characters, which should be characteristic
 1212 only for one genus. On the other hand, there are species which correspond perfectly only with
 1213 the diagnose of *Praenucula* or *Praeleda* (e.g. *Praenucula dispar*, *Praeleda pulchra*).
 1214 Moroccan specimens of *Praenucula* show a mixture of these characters: posterior teeth are

1215 smaller and more numerous, the anterior adductor is more ventral (characteristic for
1216 *Praeleda*); the hinge ranges do not show any discordance or disruption, and umbos lie in the
1217 posterior half (characteristic of *Praenucula*).

1218

1219 *Praenucula pojetai* sp. nov.

1220 (Fig. 26b, c & k–q)

1221

1222 1990 *Praenucula costae* Sharpe. – Babin & Destombes, pl. 1, fig. 6.

1223

1224 *Holotype*. Internal mould of the left valve, MGM-6845X, figured herein as Fig. 26o, p & q.

1225

1226 *Paratypes*. Five right valves, two left valves, one articulated specimen (specimens FSL

1227 550113, FSL 550118, FSL 550161, MGM-6843X, MGM-6844X, MGM-6846X, MGM-

1228 6848X, MGM-6849X). Measurements are given in Table 2. MGM-6846X is figured herein as

1229 Fig. 26b & m.

1230

1231 *Diagnosis*. *Praenucula* with broadly subelliptic to ovate shells, with nine to 11 teeth in the

1232 anterior part of the hinge and with 15–20 smaller teeth in the posterior part of the hinge. Three

1233 pairs of accessory muscle scars constitute row in the umbonal region, toward to the anterior

1234 part of the shell they are smaller.

1235

1236 *Derivation of name*. In honour of John Pojeta, Jr. (1935–2017), who devoted his research

1237 mainly to Palaeozoic bivalves and rostroconchs.

1238

1239 *Type locality and horizons.* North slope of the Jbel Amouguer, south of the eastern Sarhro
1240 Massif, Jbel Bou Isidane, south of Alnif, eastern Anti-Atlas, Morocco. Lower Ktaoua
1241 Formation, Sandbian Stage. Jbel Bou Ingarf ‘south’ (holotype) and Jbel Bou Ingarf ‘north’,
1242 central Anti-Atlas, Morocco. Upper Ktaoua Formation, Katian Stage. Near the Tizi n’Takrit, 7
1243 km southwest of Tazarine (Maïder), eastern Anti-Atlas, Morocco. Lower Member of the
1244 Lower Second Bani Formation, upper Katian Stage.

1245
1246 *Description.* Small, equivalve, inequilateral, and broadly subelliptic to ovate shell. Anterior
1247 margin evenly rounded, posterior margin more straight, ventral margin convex. Anterior part
1248 constitutes larger part of the shell. Umbos are situated in the posterior half of the shell length.
1249 Dorsal margin in the anterior part of the shell is slightly concave. Posterior part of the shell is
1250 slightly convex or straight. The hinge is taxodont, the posterior part with small numerous
1251 teeth (15–20 in number), and the anterior part of the shell with abruptly larger teeth (9–11 in
1252 number). Teeth in the posterior part are slightly convexodont or orthomorphodont, in the
1253 anterior part convexodont. Teeth row between the umbos is not interrupted. Anterior adductor
1254 muscle scar elliptic and slightly larger than elliptic posterior adductor muscle scar. One pair of
1255 elliptic pedal muscle scars (protractors) is developed posterodorsally from the anterior
1256 adductor muscle scars, one pair of slightly elliptic pedal muscle scars (retractors) is developed
1257 anterodorsally from the posterior adductor muscle scar, and three pairs of rounded accessory
1258 muscle scars are developed in the umbonal region. The accessory muscle scars toward the
1259 anterior part of the shell are smaller, the largest one is the closest to the umbo. Inner surface
1260 sculpture is smooth. Outer surface sculpture consists of numerous, regularly spaced growth
1261 bands and furrows.

1262
1263 *Remarks.* *Praenucula dispar* (Barrande, 1881d) from the Hirnantian of Bohemia differs from
1264 *Praenucula pojetai* in more rounded shape, prominent umbos and less numerous teeth, which

1265 show almost similar size. *Praenucula abrupta* Kříž & Polechová, 2009 from the Hirnantian of
1266 Bohemia has triangular shape and prominent umbos and less numerous teeth. *Praenucula*
1267 *dispersa* Tunncliff, 1982 from the Katian of Ireland has a more dorsally placed adductor
1268 muscle scars and teeth of almost similar size. *Praenucula infirma* Tunncliff, 1982 from the
1269 Katian of Ireland, is distinguished from *Praenucula pojetai* on its more dorsally placed
1270 adductor muscle scars and prominent umbos. *Praenucula praetermissa* Tunncliff, 1982 from
1271 the Katian of Ireland are characterised in more centrally placed umbos and more numerous
1272 teeth than *Praenucula pojetai* sp. nov. *Praenucula* sp. from the Sandbian of Argentina
1273 (Sánchez 1999) differs in having umbos in a central position and less numerous teeth in the
1274 posterior and anterior hinge lines. *Ctenodonta dubia* Hall, 1847 from the mid Katian
1275 (probably Katian 2) of Norway is similar to *P. pojetai* sp. nov. in shape, but other characters
1276 are unknown.

1277

1278

1279 Family **Nuculitidae** Bradshaw, 1999

1280 Genus *Nuculites* Conrad, 1841

1281

1282 *Type species.* By original designation, *Nuculites oblongatus* Conrad, 1841, p. 49, from the
1283 Mid Devonian Hamilton Group near Smyrna, Chenango County, New York, USA.

1284

1285 *Nuculites* sp.

1286 (Fig. 27d, m & o)

1287

1288 *Material.* One articulated specimen, one left valve (specimens MGM-6860X, MGM-6862X).

1289 Measurements are given in Table 3.

1290

1291 *Description.* Shell of very large size, equivalved, inequilateral, ovate or longitudinally
1292 elongated. Umbos inconspicuous, in the anterior part of shell, prosogyrate. Anterior margin
1293 rather straight, posterior margin rounded. Dorsal margin very slightly convex and ventral
1294 margin rather straight. The septum in the anterior part is relatively long and extends from
1295 anterior part of the hinge line towards the ventral margin of the shell, constituting an arc
1296 around the anterior adductor muscle scar. Posterior hinge line straight, the anterior hinge line
1297 curved ventrally. Hinge unknown, hinge line is preserved but seems to be without teeth,
1298 edentulous. The anterior adductor muscle scar badly preserved, occupying much of the
1299 portion of the shell anteriorly to the septum. Posterior adductor muscle scar unknown, outer
1300 surface sculpture with growth wrinkles.

1301

1302 *Remarks.* The genus *Nuculites* show very high variability of the shell, as it was demonstrated
1303 by Bretsky & Bretsky (1977) for *Nuculites planulatus* and by Tunnicliff (1982) for *Nuculites*
1304 *cylindricus*. *Nuculites* sp. from the Late Ordovician of Morocco shows a key character for this
1305 genus, the septum. It is very characteristic in its dimensions, being a very large shell.

1306

1307 *Locality and horizon.* Mountain Pass south of Tagounite, central Anti-Atlas, Morocco. Lower
1308 Second Bani Formation, Hirnantian Stage.

1309

1310 Superfamily **Nuculanoidea** Adams & Adams, 1858

1311 Family **Malletidae** Adams & Adams, 1858

1312 Genus *Myoplusia* Neumayr, 1884

1313

1314 *Type species.* By subsequent designation of McAlester (1968), *Leda bilunata* Barrande,
1315 1881a, d, p. 153, pl. 270, fig. 3 from the Upper Ordovician (Katian Stage) Zahořany
1316 Formation at Štěrboholy, Bohemia, Czech Republic.

1317

1318 *Myoplusia* sp.

1319 (Fig. 26a, d, e, g & j)

1320

1321 *Material.* Two right valves, three left valves (specimens FSL 550117, MGM-6850X– MGM-
1322 6853X). Measurements are given in Table 4.

1323

1324 *Description.* Shell small, equivalve, inequilateral, ovate, and longitudinally elongated. Umbos
1325 are placed at two thirds of the shell length, prosogyrate. Anterior part of the shell is smaller
1326 than posterior part of the shell. Anterior part and posterior part rounded, posterior part slightly
1327 truncate. Dorsal margin straight, ventral margin convex. Hinge preserved only in the anterior
1328 part, with numerous taxodont teeth (MGM-6852X). Anterior adductor muscle scar slightly
1329 ovate, posterior adductor muscle scar unknown. Inner surface sculpture smooth, outer surface
1330 sculpture unknown.

1331

1332 *Remarks.* Specimens from the Late Ordovician of Morocco are poorly preserved, so only the
1333 shape of the shell, prosogyrate umbos and taxodont teeth permit the determination to

1334 *Myoplusia*. The specimen MGM-6853X from the central Anti-Atlas differs from other
1335 *Myoplusia* in shape of the shell and very probably it represents a new species. It is very
1336 similar to *Myoplusia incisa* (Barrande, 1881d) from the Late Ordovician of Bohemia.

1337

1338 *Localities and horizons.* Slope of the Jbel Amouguer, south of the eastern Sarhro Massif,
1339 eastern Anti-Atlas, Morocco. Lower Ktaoua Formation, Sandbian Stage. Jbel Bou Ingarf
1340 ‘south’, central Anti-Atlas, Morocco. Upper Ktaoua Formation, Katian Stage. Aït Isioul
1341 ‘north’, central Anti-Atlas, Morocco. Lower Second Bani Formation, Hirnantian Stage.

1342

1343 Genus *Sluha* Barrande, 1881a

1344

1345 *Type species.* By original designation, *Sluha expansus* Barrande, 1881a, p. 159, pl. 267 from
1346 the Upper Ordovician (upper Katian Stage) Králův Dvůr Formation at Lejškov Hill, Bohemia,
1347 Czech Republic.

1348

1349 *Sluha kosoviensis* (Barrande, 1881d)

1350 (Fig. 26f, h & i)

1351

1352 *1881d *Arca? kosoviensis* Barrande, pl. 265, figs III/1–12.

1353 1881d *Arca? disputabilis* Barrande, pl. 265, figs I/13–15.

1354 1881d *Arca? innotata* Barrande, pl. 265, figs II/1–20.

1355 1891 *Praearca kosoviensis* (Barrande). – Neumayr, p. 755.

1356 1934 *Praearca kosoviensis* (Barrande). – Pfab, p. 220, pl. 3, fig. 21.

1357 1934 *Ctenodonta praecox* (Barrande). – Pfab, p. 228, pl. 2, fig. 14.

1358 1934 *Ctenodonta disputabilis* (Barrande). – Pfab, p. 228, pl. 2, fig. 15.

1359 1934 *Ctenodonta (Palaeoneilo) flectens* (Barrande). – Pfab, p. 230, pl. 2, fig. 18.

1360 1934 *Ctenodonta (Palaeoneilo) magna* (Barrande). – Pfab, p. 231, pl. 2, fig. 19.

1361 1968 *Praearca kosoviensis* (Barrande). – McAlester, pp. 44, 45, pl. 30, figs 1–8.

1362 1969 *Sluha kosoviensis* (Barrande). – McAlester, p. N235.

1363 2009 *Sluha kosoviensis* (Barrande). – Kříž & Steinová, p. 420, pl. 3, fig. L–M & pl. 5, fig. A–
1364 C, E–L.

1365

1366 *Material.* Two left valves (specimens FSL 550162, MGM-6847X). Measurements are given
1367 in Table 5.

1368

1369 *Types.* Lectotype, designated by Pfab (1934), internal mould of a right valve figured by
1370 Barrande (1881d, pl. 265, figs III/9 & 10), NM L 27070. Paralectotypes, internal mould of the
1371 shell with articulated and opened valves figured by Barrande (1881d, pl. 265, fig. III/1), NM
1372 L27072; internal mould of the shell with articulated and opened valves figured by Barrande
1373 (1881d, pl. 265, fig. III/2), NML27071; internal mould of the left valve figured by Barrande
1374 (1881d, pl. 265, figs III/3–5), NML27073; internal mould of the right valve figured by
1375 Barrande (1881d, pl. 265, figs III/6–8), NM L27069; internal mould of a left valve figured by
1376 Barrande (1881d, pl. 265, figs III/11 & 12), NM L27068.

1377

1378 *Type locality.* Kosov Hill near Beroun, Bohemia, Czech Republic.

1379

1380 *Type horizon.* Late Ordovician, late Katian Stage, uppermost Králův Dvůr Formation.

1381

1382 *Diagnosis.* *Sluha* without prominent umbo, small orthomorphodont teeth in the anterior and
1383 posterior part of the shell and with the anterior smaller than the posterior portion of the shell.

1384

1385 *Description.* Shell medium size, equivalved, inequilateral, broadly ovate. Anterior part of the
1386 shell is smaller than posterior part. Anterior margin evenly rounded, posterior margin rather
1387 straight, ventral slightly convex, and dorsal margin convex. Umbos not prominent, in anterior

1388 half of the shell. Ligament external. Hinge line in anterior part of the shell slightly curved
1389 ventrally, in posterior part slightly convex. Taxodont teeth orthomorphodont. In anterior range
1390 of the hinge probably 6–7 teeth, in posterior hinge line probably 18–20 teeth. Posterior
1391 adductor muscle scar large and rounded, close to the hinge line and posterior margin. Anterior
1392 adductor muscle scar smaller, also rounded, distant from the anterior hinge line. Inner surface
1393 smooth. Outer surface sculpture of fine growth wrinkles.

1394

1395 *Remarks.* *Sluha kosoviensis* is well known from the Late Ordovician of Bohemia (Barrande
1396 1881a; Kříž & Steinová 2009) and it is probably a direct descendant of *Sluha expansus*
1397 Barrande, 1881a, from the mid Katian of Bohemia. Moroccan specimens of *Sluha* are very
1398 similar to the Bohemian species, differing slightly in the more rounded shape of the shell.

1399

1400 *Localities and horizons.* Morocco: Jbel Bou Ingarf ‘south’, central Anti-Atlas. Upper part of
1401 the Upper Ktaoua Formation, Katian Stage. Near the Tizi n’Takrit, 7 km southwest of
1402 Tazarine (Maïder), eastern Anti-Atlas. Lower Member of the Lower Second Bani Formation,
1403 upper Katian. Bohemia, Czech Republic: Králův Dvůr Formation, Katian Stage.

1404

1405 Superfamily **Nuculanoidea** Adams & Adams, 1858

1406 Family **Nuculanidae** Adams & Adams, 1858

1407 Genus *Phestia* Chernyshev, 1951

1408

1409 *Type species.* By original designation of Chernyshev (1951), p. 9, *Leda inflatiformis*
1410 Chernyshev, 1939, p. 116, from the Carboniferous Formation C₂ at Volchya River, Don
1411 Basin, Ukraine.

1412

1413 *Remarks.* McAlester (*in Cox et al.* 1969) suggested that the widely used name *Nuculana*
1414 (*Leda* in older bibliography) should be restricted to Triassic-Recent forms with a rostrum and
1415 commarginal sculpture. *Phestia* should be used for stratigraphically older forms.

1416

1417 *Phestia?* sp.

1418 (Fig. 30c)

1419

1420 *Material.* One right valve (specimen FSL 550115). Measurements are given in Table 6.

1421

1422 *Description.* The single right valve of an internal mould. Small, longitudinally elongated,
1423 equivalve, inequilateral. Umbos in the middle of the shell, rather orthogyrate. Anterior margin
1424 rounded, dorsal margin in the posterior part slightly concave, ventral margin convex. Posterior
1425 part of the shell extends into rostrum. Dentition and muscle scars unknown, and sculpture of
1426 inner surface smooth.

1427

1428 *Remarks.* *Phestia?* sp. from the Mid Ordovician of China is preserved as an external mould,
1429 so any comparison is difficult. *Phestia rostellata* (Hall, 1883) and *Phestia diversa* (Conrad,
1430 1841) are stratigraphically younger (Devonian) than the taxon described here.

1431

1432 *Locality and horizon.* Plain between Jbel Tafenna and Ikhf n'Ouzerg, 60 km south east of
1433 Zagora, eastern Anti-Atlas, Morocco. Lower Ktaoua Formation, Sandbian Stage.

1434

1435 Subclass **Autobranchia** Grobben, 1894

1436 Infraclass **Pteriomorpha** Beurlen, 1944

1437 Cohort **Mytilomorphi** Férussac, 1822 (*in Férussac & Audebard* 1822)

1438 Order **Mytilida** Férussac, 1822 (in Férussac & Audebard 1822)

1439 Superfamily **Modiolopsoidea** Fischer, 1886

1440 Family **Modiolopsidae** Fischer, 1886

1441 Genus *Modiolopsis* Hall, 1847

1442

1443 *Type species.* By original designation of Hall, 1847, p. 157, *Pterinea modiolaris* Conrad, 1838,

1444 p. 118, from the Upper Ordovician (Katian Stage) Pulaski Formation, New York State, USA.

1445

1446 *Modiolopsis* sp.

1447 (Fig. 30a, d & e–k)

1448

1449 *Material.* Seven left valves, three right valves (specimens MGM-6854X, MGM-6855X,

1450 MGM-6857X, MGM-6865X, MGM-6867X, MGM-6870X– MGM-6874X. Measurements

1451 are given in Table 7.

1452

1453 *Description.* Large shells, posteriorly elongated, modioliform, equivalve, inequilateral.

1454 Anterior part smaller, slightly lobate, evenly rounded, posterior part larger and rounded.

1455 Ventral margin convex, dorsal margin prominently convex. Umbos inconspicuous, situated

1456 very slightly above the hinge line, prosogyrate. Ligament opisthodetic. Outer surface

1457 sculpture composed of irregularly spaced growth wrinkles. Hinge plate edentulous, muscle

1458 scars and pallial line unknown.

1459

1460 *Remarks.* Pojeta (1971) reported that more than 163 species belong to *Modiolopsis*. Very

1461 often taxa have been determined only on the basis of the modioliform shape, edentulous

1462 hinge and growth ornamentation, so the determination to the species level may be very

1463 difficult. It is preferred to leave the Moroccan *Modiolopsis* in open nomenclature, because the
1464 whole concept of *Modiolopsis* requires revision.

1465

1466 *Localities and horizon.* Aït Isioul ‘north’ and ‘south’, central Anti-Atlas, Morocco. Lower
1467 Second Bani Formation, Hirnantian Stage.

1468

1469 Genus *Dceruska* Barrande, 1881a

1470

1471 *Type species.* By original designation, *Dceruska primula* Barrande, 1881a, d, p. 77, pl. 275,
1472 fig. 2, from the Upper Ordovician (middle and upper Katian Stage) Králův Dvůr Formation at
1473 Lejškov Hill, Barrandian Area, Czech Republic.

1474

1475 *Remarks.* Some species of *Modiolopsis* are similar to *Dceruska*. The significant character of
1476 *Dceruska* noted by Kříž (2005) is the anterior lobe. Other significant characters may include
1477 the posteroventrally elongation of the shell and a prominently higher posterior part.

1478

1479 *Dceruska* sp.

1480 (Fig. 27a, e & h)

1481

1482 *Material.* One articulated specimen, one left valve (MGM-6842X, MGM-6861X).

1483 Measurements are given in Table 8.

1484

1485 *Description.* Shell medium size, equivalved, inequilateral, modioliform, expanding postero-
1486 ventrally, posterior part is prominently higher. Anterior part of the shell is smaller than
1487 posterior part. Anterior and posterior margins are evenly rounded, ventral margin convex, and

1488 dorsal margin straight. Umbos not prominent, in anterior half of the shell, not terminal,
1489 prosogyrate. Hinge edentulous. Opisthodontic ligament. Anterior adductor muscle scar small,
1490 evenly rounded, closed to the anterior margin. Inner surface with prominent growth bands in
1491 the ventral part. Outer surface sculpture unknown.

1492
1493 *Remarks.* *Dceruska* was described from the Late Ordovician of Bohemia by Barrande (1881a)
1494 and from the Telychian (Silurian) of Spain (Kříž 2005). *Dceruska primula* from the Katian of
1495 Bohemia has a prominent anterior lobe. *Dceruska hispanica* from the Telychian of Spain has
1496 a generally shorter shell and its shape is more pteriiform.

1497
1498 *Locality and horizon.* Aït Isioul ‘south’, central Anti-Atlas, Morocco. Lower Second Bani
1499 Formation, Hirnantian Stage.

1500

1501 Cohort **Ostreomorphi** Férussac, 1822

1502 Order **Myalinida** Paul, 1939

1503 Superfamily **Ambonychioidea** Miller, 1877

1504 Family **Ambonychiidae** Miller, 1877

1505 Genus *Ambonychia* Hall, 1847

1506

1507 *Type species.* By original designation, *Ambonychia radiata* Hall, 1847, p. 163, from the Upper
1508 Ordovician (Katian Stage) Lorraine Formation of USA.

1509

1510 *Ambonychia* aff. *magna* Isberg, 1934

1511 (Fig. 29i)

1512

1513 *Material.* One left valve (specimen MGM-6858X). Measurements are given in Table 9.

1514

1515 *Description.* – Shell large, inflated, equivalved, strongly inequilateral, longitudinally
1516 elongated. Umbos prominent, in the anterior part of shell, prosogyrate, rising above the hinge
1517 line. Posterior margin rounded. Ventral margin straight, curving rapidly up to the anterior
1518 margin. Angle alpha about 40°, angle gamma about 100°, angle beta about 150° (see Fig. 28).
1519 Hinge line straight, dentition unknown. Muscle scars unknown. Inner surface sculpture is
1520 smooth. Outer surface sculpture of coarse rugae.

1521

1522 *Remarks.* Ambonychiids are a well known group of the Late Ordovician bivalves mainly
1523 because of the systematic work of Pojeta (1966). They were widespread; many species have
1524 been described from North America, Baltica, Avalonia, Australia, and China. They are typical
1525 representatives of epibyssate bivalves of this age. *Ambonychia magna* originally described
1526 from the Late Ordovician of Sweden is preserved as an external mould, while the present
1527 Moroccan species interpreted as *Ambonychia* aff. *magna* is preserved as an internal mould. In
1528 spite of the different aspects of preservation they seem to be very similar in shape and
1529 dimensions.

1530

1531 *Locality and horizon.* Aït Isioul ‘south’, central Anti-Atlas, Morocco. Lower Second Bani
1532 Formation, Hirnantian Stage.

1533

1534 *Ambonychia* sp.

1535 (Fig. 29b & j)

1536

1537 *Material.* One articulated specimen (MGM-6866X). Measurements are given in Table 10.

1538

1539 *Description.* Shell small, equivalved, strongly inequilateral, longitudinally elongated. Umbos
1540 terminal, probably prosogyrate. Posterior part rounded dorsal part rather straight, slightly
1541 convex in posterior part, ventral margin convex. Anterior part without lobation. Hinge
1542 unknown. Dorsal part with very prominent escutcheon delimited by ridges. Outer surface
1543 sculpture of growth lines and rugae, inner surface sculpture with one prominent ridge visible
1544 from escutcheon, directed posteroventrally. Muscle scars unknown.

1545

1546 *Locality and horizon.* Aït Isioul ‘south’, central Anti-Atlas, Morocco, Lower Second Bani
1547 Formation, Hirnantian Stage.

1548

1549 Genus *Cleionychia* Ulrich, 1892

1550

1551 *Type species.* By subsequent designation of Ulrich (1892, p. 97), *Ambonychia lamellosa* Hall,
1552 1861 from the Upper Ordovician (Katian Stage) Platteville Formation at Mineral Point,
1553 opposite to Dubuque, State of Wisconsin, USA.

1554

1555 *Cleionychia transversa* (Portlock, 1843)

1556 (Fig. 27f & g)

1557

1558 *1843 *Inoceramus transversus* Portlock, p. 423, pl. 33, fig. 11.

1559 1843 *Inoceramus vetustus* Portlock, p. 423, pl. 33, figs 2 & 3.

1560 1952 *Clionychia subovalis* Reed, p. 76, pl. 4, fig. 7.

1561 1952 *Clionychia subquadrata* Reed, pp. 76–77, pl. 4, fig. 8.

1562 1982 *Cleionychia transversa* (Portlock). – Tunnicliff, p. 73, pl. 12, figs 1–6.

1563

1564 *Material.* One left valve (MGM-6841X). Measurements are given in Table 11.

1565

1566 *Types.* Lectotype, internal mould of the left valve figured by Tunnicliff (1982, pl. 12, fig. 1),
1567 BGS GSM 12439. Paralectotypes: internal mould of the right valve figured by Tunnicliff
1568 (1982, pl. 12, fig. 3), BGS GSM 12440; internal mould of the left figured by Tunnicliff (1982,
1569 pl. 12, fig. 5), BGS GSM 24304.

1570

1571 *Type locality and horizon.* Exact locality unknown but south of the Craigbardahessiagh,
1572 Pomeroy, Ireland. Bardahessiagh Formation, Katian Stage.

1573

1574 *Diagnosis.* *Cleionychia* with long, straight dorsal margin, angle gamma about 90°.

1575

1576 *Description.* Shell equivalve, strongly inequilateral, transversally elongate. Umbos not
1577 prominent, in the anterior part of shell, terminal, prosogyrate, rising slightly the hinge line.
1578 Anterior margin straight, posterior margin rounded. Ventral margin convex, curving rapidly
1579 up to the anterior margin. Angle gamma about 90°, angle beta about 145° (see Fig. 28). Hinge
1580 line straight, dentition unknown. The anterior adductor muscle scar rounded, far from the
1581 hinge line and very closed to the anterior margin. Inner surface sculpture is smooth. Outer
1582 surface sculpture is characterized by coarse rugae.

1583

1584 *Remarks.* *Cleionychia transversa* was described by Tunnicliff (1982) from the Late
1585 Ordovician of Ireland. Other species from Ireland (*Cleionychia Prisca* and *Cleionychia*
1586 *incognita*) were revised by Tunnicliff (1982). The main differences between these species are
1587 in the shape of the shell and the angles alpha and gamma.

1588

1589 *Locality and horizon* (Moroccan material). Aït Isioul ‘south’, above bed G, central Anti-Atlas,
1590 Morocco. Lower Second Bani Formation, Hirnantian Stage.

1591

1592 *Cleionychia prisca* (Portlock, 1843)

1593 (Fig. 29a, c & d–h)

1594

1595 *1843 *Inoceramus vetustus* Sowerby var. *priscus* Portlock. – Portlock, p. 423, pl. 33, fig. 1.

1596 1878 *Ambonychia undata* Hall. – Baily, p. 28.

1597 1952 *Ambonychia prisca* (Portlock). – Reed, p. 73.

1598 1982 *Cleionychia prisca* (Portlock). – Tunnicliff, p. 74, pl. 12, figs 8 & 12.

1599

1600

1601 *Material*. Two left valves, one articulated specimen, one right valve (specimens MGM-
1602 6856X, MGM-6864X, MGM-6875X). Measurements are given in Table 12.

1603

1604 *Types*. Lectotype, external mould of the right valve figured by Tunnicliff (1982, pl. 12, fig.
1605 11), BGS GSM 12438. Paralectotype: external mould of the right valve figured by Tunnicliff
1606 (1982, pl. 12, fig. 8), UM K 4200.

1607

1608 *Type locality and horizon*. Portlock’s (1843) locality, sheet 37, no. 6, south of
1609 Craighbardahessiagh, Pomeroy, Ireland. Bardahessiagh Formation, Katian Stage.

1610

1611 *Diagnosis*. *Cleionychia* with oblique and narrow shell, more inflated, angle gamma more
1612 acute (80°).

1613

1614 *Description.* Shell equivalved, strongly inequilateral, ovate and inflated. Umbos
1615 inconspicuous, in the anterior part of shell, terminal, prosogyrate, rising above the hinge line.
1616 Posterior margin rounded. Ventral margin convex, curving rapidly up to the anterior margin.
1617 Angle alpha about 50°, angle gamma about 80° and angle beta about 120° (see Fig. 28).
1618 Hinge line straight, two cardinal teeth in the anterior part (Fig. 29g). Muscle scars unknown.
1619 Inner surface of the shell is smooth. Outer surface sculpture consists of coarse rugae.

1620

1621 *Remarks.* *Cleionychia prisca* was originally described from the Late Ordovician of Ireland,
1622 Tunnicliff (1982) revised this species. *Cleionychia prisca* from Ireland also shows strong
1623 growth rugae and in this feature it differs from *C. incognita* Tunnicliff, 1982. In Moroccan
1624 specimens this character is not preserved. *Cleionychia transversa* is less oblique and less
1625 inflated while angle gamma is about 90°.

1626

1627 *Localities and horizon* (Moroccan material). Foum el Fehamya section, Aït Isioul ‘north’,
1628 central Anti-Atlas, Morocco. Lower Second Bani Formation, Hirnantian Stage.

1629

1630 Order **Cyrtodontida** Nevesskaya *et al.*, 1971

1631 Superfamily **Cyrtodontoidea** Ulrich, 1894 (in Ulrich & Scofield, 1894)

1632 Family **Cyrtodontidae** Ulrich, 1894 (in Ulrich & Scofield, 1894)

1633 Genus *Cyrtodonta* Billings, 1858

1634

1635 *Type species.* By original designation, *Cyrtodonta rugosa* Billings, 1858 from the Upper
1636 Ordovician (Sandbian Stage) Chaumont Formation at the Paquette Rapids near Ottawa,
1637 Canada.

Cyrtodonta sp.

(Fig. 27b, c, i–k & l)

Material. Two articulated specimens, one left valve, one right valve (specimens MGM-6859X, MGM-6863X, MGM-6868X, MGM-6869X). Measurements are given in Table 13.

Description. Shell large, ovate, equivalve, very inequilateral, becoming broader towards the posterior. Anterior part smaller than posterior, posterior part rounded. Dorsal and ventral margins convex. Umbos not prominent, terminal, prosogyrate. Ligament external, probably duplivincular. Muscle scars and pallial line not developed. Hinge unknown. Inner surface sculpture smooth. Outer surface sculpture unknown.

Remarks. *Cyrtodonta* is well known from a variety of areas throughout the Ordovician (Canada, Wales, Ireland, Sweden, China, Canada, United States, and the Czech Republic). Identification to the species level is difficult, as in most species only the shape of the shell is known, while the other characters are rarely preserved.

Localities and horizon. Aït Isioul ‘north’ and ‘south’, and the Foug el Fehamya section, central Anti-Atlas, Morocco. Lower Second Bani Formation, Hirnantian Stage.

Infraclass **Heteroconchia** Hertwig, 1895

Cohort **Uniomorpha** Gray, 1854

Superfamily **Lyrodesmatoidea** Fischer, 1886

Family **Pseudarcidae** Scarlato & Starobogatov, 1979

1663 Genus *Pseudarca* Tromelin & Lebesconte, 1875

1664

1665 *Type species.* By original designation, *Pseudarca typa* Tromelin & Lebesconte, 1875, p. 5,

1666 from the Upper Ordovician (Sandbian Stage) Grés de May Formation at Bouexière in the

1667 Armorican Massif, France.

1668

1669 *Pseudarca?* sp.

1670 (Fig. 30b)

1671

1672 *Material.* One right valve (FSL 550155). Measurements are given in Table 14.

1673

1674 *Description.* Shell medium size, very elongated longitudinally, equivalve, strongly

1675 inequilateral. Umbo in the middle of the shell, rather orthogyrate. Anterior margin rounded,

1676 posterior margin truncate, dorsal margin in the posterior part slightly concave, ventral margin

1677 convex. Dentition and muscle scars are not visible. Inner surface is smooth.

1678

1679 *Remarks.* Babin & Destombes (1990) figured this specimen and determined it as

1680 *Modiolopsis?* sp. It differs substantially from *Modiolopsis* in having very narrow and

1681 elongated shell, which is characteristic of *Pseudarca*. *Pseudarca typa* Tromelin &

1682 Lebesconte, 1875 is known from the Late Ordovician (Katian) of France and *Pseudarca*

1683 *celtica* Tunnicliff, 1987 from the Late Ordovician (Katian) of North Wales. The specimen

1684 from Morocco has the characteristic shape of *Pseudarca*, but the other characters are

1685 unknown in this specimen.

1686

1687 *Locality and horizon.* West of Akka Akka, Jbel Bani, western Anti-Atlas, Morocco. Lower
1688 Ktaoua Formation, Katian Stage.

1689

1690 Class **Cephalopoda** Cuvier, 1797

1691 Order **Actinocerida** Teichert, 1933

1692 Family **Wademidae** Özdikmen, 2008

1693 Genus *Wadema* Özdikmen, 2008

1694

1695 *Type species.* By original designation of Özdikmen (2008, p. 595), *Georgina taylori* (Wade,
1696 1977), p 8, figs 3, 4, 6h–p, pl. 2, fig. 7, pl. 3 figs 1–6 & pl 4, fig. 1, from the Lower
1697 Ordovician (Floian Stage) Coolibah Formation of the Georgina Basin, northern Australia.

1698

1699 *Diagnosis.* Orthocones with subcentral siphuncle; siphuncle expanded within chambers with
1700 adnate area at septa and small septal perforation; septal necks suborthochoantic in early
1701 growth stages to cyrtochoanitic and recumbent in later stages; siphuncular segments non-
1702 adnate to adnate; siphuncular deposits with variable number of engrafts and radial lamellae of
1703 annuli, endocameral deposits not known (after Wade 1977).

1704

1705 *Wadema tattai* sp. nov.

1706 (Fig. 31a)

1707

1708 *Holotype.* Specimen AA.ABT.OS 38 figured herein as Fig. 31a.

1709

1710 *Diagnosis.* *Wadema* with relatively wide chamber distance of 0.45 of corresponding conch
1711 cross section; suborthochoantic septal necks, and relatively thin barrel-shaped siphuncular

1712 segments; siphuncle with maximum diameter c. 0.25 that of corresponding conch diameter.

1713

1714 *Derivation of name.* Referring to the type locality.

1715

1716 *Material.* Holotype only.

1717

1718 *Type locality and horizon.* SSE de Abdi bou Tatta, locality 6 of Destombes (2006b), west of
1719 Tazarine, east-central Anti-Atlas, Morocco. Upper Ktaoua Formation, Katian Stage.

1720

1721 *Description.* The holotype is a portion of a phragmocone with four chambers, 37 mm long and
1722 with a diameter of 24–29 mm. The siphuncle is subcentral, with a distance of the septal
1723 perforation of c. 11 mm from the conch margin at a corresponding conch cross section of 27
1724 mm. The septal necks are suborthochoanitic. The siphuncular segments are barrel-shaped
1725 expanded within the chambers to a maximum diameter of 5.5 mm where the corresponding
1726 septal perforation is 2.8 mm and the corresponding conch cross section is 25 mm. The
1727 siphuncular annuli are elongated with convex adapical and adoral margins and have well
1728 preserved lamellae. Siphuncular engrafts are preserved at mid-length between the septa (Fig.
1729 31a), they are shallow with a length of 2 mm and a thickness of c. 0.7 mm at corresponding
1730 siphuncular diameter of 6.7 mm. Endocameral deposits are not present. The conch surface is
1731 not preserved.

1732

1733 *Remarks.* The presence of siphuncular engrafts and the shape of the siphuncle and septal
1734 necks justifies the assignment of this species to *Wadema*. The Australasian specimens are all
1735 considerably older (late Floian Stage).

1736 Mid Ordovician occurrences of wademids are reported from northern China (Wade 1988),
1737 Thailand (Stait & Burrett 1984), and tentatively from Saudi Arabia and Bolivia (Evans 2000),
1738 suggesting a circum-Gondwana distribution of this group during the Mid Ordovician. The
1739 Moroccan occurrence is the youngest report of a wademid cephalopod so far.

1740

1741 *Wadema* sp.

1742 (Fig. 32e)

1743

1744 *Material.* Specimen MGM-7013X.

1745

1746 *Locality and horizon.* Locality Jbel Bou Ingarf ‘north’, eastern Anti-Atlas, Morocco. Upper

1747 Ktaoua Formation, Katian Stage.

1748

1749 *Description.* The specimen is an internal mould of a portion of a phragmocone with two
1750 chambers. The specimen is 37 mm long and with a diameter of 51–52 mm. The siphuncle is
1751 subcentral, with a distance of the septal perforation of c. 14 mm from the conch margin and a
1752 diameter of 9 mm at a corresponding conch cross section of 51 mm. The septal necks are
1753 suborthochoantic. The siphuncular segments are expanded within the chambers. The
1754 endosiphuncular annuli have convex adoral margins and well preserved lamellae. The conch
1755 surface is not preserved.

1756

1757 *Remarks.* The general conch morphology (distance of chambers, position of siphuncle,
1758 presence of annuli with lamellae) is similar to *Wadema tattai* sp. nov. but internal characters,
1759 such as connecting ring shape and engrafts are not preserved, and do not permit more specific
1760 determination of this specimen.

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Family **Ormoceratidae** Saemann, 1852

Ormoceratidae gen. et sp. indet.

(Fig. 31b)

Material. Specimen MGM-7014X.

Locality and horizon. Jbel Bou Ingarf ‘north’, eastern Anti-Atlas, Morocco. Uppermost beds of the Upper Ktaoua Formation, Katian Stage.

Description. The specimen is a fragmentary internal mould of a portion of a phragmocone with three chambers, 20 mm long and with a diameter of 44 mm. The siphuncle is subcentral, with a distance of the centre of the septal perforation of c. 17 mm from the conch margin and a maximum siphuncular diameter of 16 mm. The shape of the septal necks is not preserved. The siphuncular segments are expanded within the chambers. The siphuncular annuli have convex adoral and adapical margins and well preserved lamellae. The conch surface is not preserved.

Remarks. The general conch morphology (distance of chambers, position of siphuncle, presence of annuli with lamellae) is similar to other ormoceratids, but internal characters, such as septal neck shape and conch surface are not preserved, not permitting a determination at genus level or higher.

Order **Orthocerida** Kuhn, 1940

Family **Stereoplasmoceratidae** Kobayashi, 1934

1811 ornamentation and non-adnate cyrtchoanitic septal necks.

1812

1813 *Tafadnatoceras tiouririnense* sp. nov.

1814 (Figs 32a, b, 33a & 34a–d)

1815

1816 *Holotype*. Specimen MGM-7005X figured herein as Figs 32b & 34d.

1817

1818 *Diagnosis*. Slightly curved orthocones, with angle of expansion of up to c. 7°, smooth conch
1819 surface or ornamented with very fine irregularly spaced rugae or growth lines; conch cross
1820 section circular; siphuncle centrally positioned, with septal perforation diameter of c. 0.07 mm
1821 of corresponding conch diameter; siphuncular segments expanded, barrel-shaped; maximum
1822 expansion of siphuncle at mid-length with diameter of c. 0.2 of corresponding conch diameter,
1823 connecting ring adnate at septa, septal necks cyrtchoanitic, adnate, except in earliest growth
1824 stage; siphuncular deposits form continuous lining; massive episeptal and hyposeptal deposits.

1825

1826 *Derivation of name*. Referring to type horizon.

1827

1828 *Material*. Nine additional specimen, MGM-7003X & MGM-7006X–MGM-7012X, and one
1829 specimen MGM-7004X from locality Erfoud 2; all from the Upper Tiouririne Formation,
1830 Katian Stage.

1831

1832 *Type locality and horizon*. Erfoud 2, Tafilalt, eastern Anti-Atlas, Morocco. Upper Tiouririne
1833 Formation, Katian Stage.

1834

1835 *Description.* The holotype is a portion of a phragmocone with a length of 22 mm and a
1836 diameter of 5.5–6.8 mm (angle of expansion 6°). The conch cross section is circular. The
1837 chamber height varies between 1.8–2.5 mm (0.33–0.38 of the corresponding conch cross
1838 section). The conch surface is nearly smooth with very fine irregularly spaced transverse
1839 rugae or growth lines. The siphuncle is central with very narrow septal perforation (c. 0.7 of
1840 corresponding conch cross section), barrel-shaped outline in median section, adnate in adoral
1841 part of the specimen, less expanded in adapical parts. Septal necks cyrtchoanitic and adnate
1842 in adoral part of specimen. Parietal siphuncular deposits form thin continuous lining, which is
1843 thicker on the “ventral” side (Figs 33a & 34d). Massive, irregular episepal and hyposepal
1844 deposits occur.

1845 Specimen MGM-7003X is a portion of a slightly curved phragmocone with a length of 25
1846 mm and a conch diameter of 2.6–5.4 mm with circular conch cross section. The adapical
1847 chamber spacing is wider than the adoral spacing with a chamber distance of 0.3–0.6 of the
1848 corresponding conch cross section (Fig. 34c). The siphuncle is central and is nearly tubular in
1849 its extreme adapical part, becoming more expanded and barrel-shaped within the adapical 10
1850 mm (Fig. 34a). The septal necks are cyrtchoanitic, they are adnate only in the adoral part of
1851 the specimen. The siphuncle is empty. Episepal and hyposepal deposits are irregular and
1852 mural deposits are more massive in the adapical part of the specimen. The largest specimen in
1853 the collection is MGM-7009X with a maximum diameter of 19 mm, and a length of 58 mm.
1854 The fragment of the phragmocone has an angle of expansion of 6.5° , and a chamber distance
1855 of up to 0.35 of the corresponding conch cross section.

1856

1857 *Remarks.* The adult size of this species is not known. The available fragments reveal a change
1858 in siphuncle shape in the earliest growth stages toward a diameter of c. 3 mm, with a more
1859 tubular siphuncle and non-adnate connecting rings and septal necks.

1860 The early growth stages with nearly tubular connecting rings and less curved septal necks,
1861 preserved in one of the specimens described herein, are important because they link
1862 cyrtochoanitic stereoplasmoceratids morphologically with other suborthochoanitic orthocerids
1863 with more discontinuous parietal deposits. This new link and the presence of a continuous
1864 siphuncular lining, formed by stacked layers of parietal deposits justifies a classification of
1865 the Stereoplasmoceridae within the Orthocerida.

1866

1867 Order **Endocerida** Teichert, 1933

1868 Family **Endoceratidae** Hyatt, 1884

1869 Endoceratidae gen. et sp. indet.

1870 Figures 32c & d

1871

1872 *Material.* Nine specimens MGM-6994X– MGM-7002X.

1873

1874 *Locality and horizon.* SW of Alnif, about 5.8 km northeast from the town of Aachich n'Ait
1875 Azza, eastern Anti-Atlas, Morocco. Taddrist Formation (First Bani), Sandbian Stage.

1876

1877 *Description.* The specimens are all fragmentary inner moulds of phragmocones with
1878 apparently smooth conch surface, circular conch cross section and marginal siphuncles. The
1879 siphuncles, if preserved are nearly tubular or slightly concavo-convex with holchoanitic
1880 septal necks (Fig. 32c). Specimen MGM-6994X is a fragment with a length of 35 mm and a
1881 diameter of 36–38 mm.; it has a chamber distance of 7 mm and a siphuncular diameter of 17
1882 mm at a corresponding conch cross section of 38 mm. Specimen MGM-6997X is a fragment
1883 with a diameter of 47 mm and a corresponding siphuncular diameter of 20 mm and a chamber
1884 distance of 8 mm. Specimen MGM-7001X has a length of 54 mm is 45–48 mm wide and has

1885 a diameter of 21 mm and a chamber distance of 10 mm at a corresponding conch cross section
1886 of 48 mm. No siphuncular deposits are preserved in these specimens.

1887

1888 *Remarks.* The general conch morphology (smooth conch surface, depth of chambers, position
1889 of siphuncle, presence of holochonitic septal necks) are similar to other endoceratids, but
1890 internal characters, such as the endosiphicone shape and early ontogenetic growth stages are
1891 not preserved, negating a determination at genus level or higher.

1892

1893 **Discussion**

1894 The mollusc assemblage of the Late Ordovician of central and eastern Morocco is diverse
1895 with more than 30 taxa documented. Most taxa are from the Sandbian to Katian Lower
1896 Ktaoua Group and the Hirnantian portion of the Lower Second Bani Formation. Tergomyan
1897 and gastropods are represented by 14 species, two which are tergomyans, four are
1898 bellerophonitiform gastropods, and eight are anisostrophically coiled gastropods. The widely
1899 recognized *Holopea? antiquata* is transferred to the genus *Radvanospira* gen. nov.; other new
1900 gastropod taxa include *Allossospira* gen. nov., *Tritonophon grandis* sp. nov., *Radvanospira*
1901 *baniensis* sp. nov., and *Lophospira latilabra* sp. nov.

1902 The bivalve assemblage is relatively diverse, including 13 taxa, although most of them are
1903 left in open nomenclature: *Ambonychia* aff. *magna*, *Ambonychia* sp., *Praenucula pojetai* sp.
1904 nov., *Cleionychia prisca*, *Cleionychia transversa*, *Cyrtodonta* sp., *Dceruska* sp., *Modiolopsis*
1905 sp., *Myoplusia* sp., *Nuculites* sp., *Phestia?* sp., *Pseudarca?* sp., and *Sluha kosoviensis*. They
1906 are mostly preserved as isolated valves and articulated specimens are rare. There is a clear
1907 dominance of pteriomorphs and protobranchs, while the dominating elements in the Early
1908 Ordovician bivalves from Morocco are heteroconchs. The life habits of Moroccan Late

1909 Ordovician bivalves are varied, from infaunal and semi-infaunal to epifaunal. In contrast, the
1910 Early Ordovician bivalves from Morocco were entirely infaunal.

1911 Five cephalopod taxa are recognized but except for two taxa they are left in open
1912 nomenclature. *Tafadnatoceras tiouririnense* gen. et. sp. nov. from the Upper Tiouririne
1913 Formation is similar to the late Palaeozoic *Adnatoceras* Flower, 1939 and the Mid Ordovician
1914 *Paradnatoceras* Chen & Liu (1974).

1915 The cool-water, high-latitude Mediterranean province of southern Gondwana is well-
1916 established (Gutierrez-Marco et al. 2017). Widespread Late Ordovician shallow water benthic
1917 assemblages dominate but the knowledge of many groups are still sketchy, as demonstrated
1918 by the molluscan fauna described herein. The bivalve fauna, which shows strong affinities
1919 with contemporaneous bivalve faunas in Bohemia, Ireland, and Baltica, was until now
1920 practically unknown and the cephalopods described herein represent the first systematically
1921 known from the region. A surprising result is the presence of the actinocerid genus *Wadema*
1922 in Morocco otherwise known from low palaeolatitude Gondwana faunas as far away as
1923 Australia and Thailand. Characteristic peri-Gondwanan faunal elements are lacking in
1924 Morocco but this may be an artefact because of insufficient knowledge of the cephalopod
1925 fauna of large parts of especially eastern Gondwana (Kröger 2013).

1926 The tergomyan and gastropod faunas are better known. Late Ordovician records from
1927 Morocco showed prior to the present work a high percentage of widespread genera (Ebbestad
1928 et al. 2013b), but the new definitions of *Radvanospira* and *Allossospira* emphasises better the
1929 southern Gondwana aspect of the assemblage. Genera like *Sinuitopsis*, *Bucanopsis*, and
1930 *Nonorios* are in common with Bohemia, *Deaechospira* is shared with Baltica and Bohemia,
1931 while *Tritonophon* and *Lophospira* are more widely spread genera. The latter taxon, e.g.
1932 *Lophospira latilabra*, is a representative of a generally warm-water genus.

1933

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1948

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Figure captions

Fig. 1. (a) Map of Morocco showing inset of enlarged area in (b). (b) Simplified geological map of the Moroccan Anti-Atlas, showing the distribution of Ordovician rocks and localities. The numbered localities refer to tergomyan and gastropod material, while E2 refers to the Erfoud 2 locality. Modified from Horný (1997e) and Álvaro *et al.* (this volume).

Fig. 2. Range and distribution of molluscs discussed herein. The stratigraphy is based on Álvaro *et al.* (this volume).

Fig. 3. (a) Pie diagram illustrating the composition of the Early Ordovician bivalve fauna from Morocco, Polechová (2016). (b) Pie diagram illustrating the composition of the Late Ordovician bivalve fauna from Morocco.

Fig. 4. *Sinuitopsis neglecta* Barrande in Perner, 1903 from the Lower Ktaoua Formation. (a) & (b) NM S7574, right lateral and dorsal views showing fine sculpture (latex cast). Destombes locality 1778. (c) NM S2664, cross-section and growth lines on umbilical wall. (d) NM S2573, right lateral view of mature specimen showing overall morphology. Destombes locality 88. (e)–(h) NM S2572, dorsal, left lateral, posterior, and detail views of internal mould showing muscle impression (arrows). Destombes locality 88. Scale bars for (a)–(c) = 5 mm, (d)–(g) = 10 mm, (h) = 1 mm.

Fig. 5. *Atlantophon maider* Horný, 1997e from the Lower Ktaoua Formation. (a)–(e) Holotype (NM S2673). Left lateral, anterior, dorsal, posterior oblique, and detailed views respectively. Destombes locality 882. Scale bars = 5 mm.

2550 **Fig. 6.** *Sinuities destombesi* Horný, 1997e from the Upper Ktaoua Formation. (a)–(d) Holotype
2551 specimen (NM S2560) showing characteristic shape and ornamentation. Destombes locality
2552 1624. (e) One of the largest specimens (NM S2569), showing sculpture and subinductural
2553 vallum (arrow) (see also Fig. 6b & 6d). Destombes locality 1651. (f) Anterior view of large
2554 specimen (NM S2562) showing the shape of the median apertural sinus. Upper arrow points
2555 to sinus apex. Lower arrow points to edge of lateral shield. Destombes locality 1624. Scale
2556 bars = 10 mm.

2557
2558 **Fig. 7.** *Sinuities destombesi* Horný, 1997e from the Upper Ktaoua Formation. Details of
2559 ornamentation. (a) NM S2566, median sinus with comarginal ribs only. Destombes locality
2560 1080. (b) NM S2569, sub-dorsum of left flank of last whorl with commarginal ribs and fainter
2561 spiral lirae (see Fig. 5e for left lateral view of specimen). Destombes locality 1651. (c) NM
2562 S2560 (Holotype), median sinus with comarginal ribs and spiral lirae. Destombes
2563 locality 1624. (d) NM S2569 showing subinductural deposits (si) on the lower left side of the
2564 last whorl (see Fig. 5e for left lateral view of specimen). Destombes locality 1651. (e) NM
2565 S2560 (Holotype), showing labroumbilical depression (lud) and labroumbilical ridge (lur).
2566 Destombes locality 1624. (f) NM S2563 showing subinductural deposits (si). Destombes
2567 locality 1624. Scale bars = 1 mm.

2568
2569 **Fig. 8.** *Sinuities destombesi* Horný, 1997e from the Upper Ktaoua Formation. Cross section of
2570 specimen MGM-6963X. Locality Jbel Bou Ingarf ‘South’. Scale bar = 10 mm.

2571
2572 **Fig. 9.** *Tritonophon peeli* Horný, 1997d from the Lower Ktaoua Formation. NM S2668, right
2573 side and posterior views illustrating ornamentation and the high median lobe. Destombes
2574 locality 399. Scale bars = 1 mm.

2575

2576 **Fig. 10.** *Tritonophon grandis* sp. nov., from the Lower Second Bani Formation. (a)–(e)

2577 Holotype (MGM-6967X), right lateral, left lateral, posterior, dorsal, and anterior views

2578 respectively. (f) Posterior view of paratype (MGM-6968X). (g) & (h) Posterior and right

2579 lateral views of paratype (MGM-6969X). Locality Aït Isioul ‘south’. Scale bar in (a) is same

2580 for (a)–(e). Scale bars = 5 mm.

2581

2582 **Fig. 11.** *Bucanopsina calypso* (Perner, 1903) from the Lower Ktaoua Formation. (a) & (b)

2583 Specimen NM S2659, dorsally compressed. Dorsal view and detail of median sinus

2584 respectively. (b) is a latex cast. Destombes locality 1640. (c) & (d) Right lateral and posterior

2585 view of well-preserved, uncompressed specimen (NM S2660). Latex cast. Destombes locality

2586 1778. Scale bars for (a) = 10 mm, (b) = 1 mm, (c) & (d) = 5 mm.

2587

2588 **Fig. 12.** *Nonorios pater* (Barrande in Perner, 1903) from the Lower Ktaoua Formation. (a) &

2589 (b) Specimen NM S2631, dorsal and lateral oblique views of typical internal mould.

2590 Destombes locality 1270. (c) & (d) Specimen NM S2632, latex cast of umbilicus and dorsal

2591 view of same specimen showing ornamentation. Destombes locality 1276. Scale bars = 10

2592 mm.

2593

2594 **Fig. 13.** *Radvanospira antiquata* (Perner, 1903) from the Lower Ktaoua Formation. (a) & (b)

2595 Specimen NM S2702, apertural and lateral views of internal mould. Destombes locality 1305.

2596 (c) Specimen NM S2627, dorsal view of steinkern. Destombes locality 1305. (d) & (e) Dorsal

2597 and lateral oblique views of steinkern (NM S2698). Destombes locality 88. (f) & (g) Dorsal

2598 and lateral oblique views showing ornamentation (NM S2628). Destombes locality 1315.

2599 Scale bars = 10 mm.

2600

2601 **Fig. 14.** *Radvanospira antiquata* (Perner, 1903) from the Lower Ktaoua Formation. **(a) & (b)**
2602 Specimen NM S2700, dorsal view of internal mould and latex cast of the umbilicus of the
2603 same showing fine growth lines. Destombes locality 88. **(c)–(e)** NM S2626, lateral, lateral
2604 oblique, and dorsal views of well-preserved specimen showing partially preserved
2605 ornamentation. Destombes locality 1313. **(f)–(h)** NM S2629, apertural, lateral, and ventral
2606 views of small specimen. Destombes locality 1315. **(i)** NM S2701, lateral view of large
2607 internal mould. Scale bars = 5 mm.

2608

2609 **Fig. 15.** *Radvanospira baniensis* sp. nov. from the Lower Second Bani Formation at the
2610 locality Aït Isioul ‘south’. **(a)–(f)** Holotype (MGM-6977X), apertural, dorsal, lateral, ventral,
2611 lateral, and ventral oblique views respectively. **(g)–(i)** Internal mould (MGM-6978X),
2612 apertural, lateral and dorsal views respectively. Specimen was sectioned (see Fig. 16). Scale
2613 bars = 10 mm.

2614

2615 **Fig. 16.** *Radvanospira baniensis* sp. nov. from the Lower Second Bani Formation at the
2616 locality Aït Isioul ‘south’. Cross section of specimen MGM-6978X (see also Fig. 15**(g)–(i)**).
2617 Scale bar = 10 mm.

2618

2619 **Fig. 17.** *Deaechospira amouguerana* (Horný, 1997b) from the Upper Tiouririne Formation.
2620 **(a)–(h)** Holotype (NM S2654) in various views. Destombes locality 585. **(g) & (h)** are latex
2621 cast showing details of the peripheral band. Arrows in **(a) & (g)** points to a repaired injury.
2622 Scale bars in **(a)–(f)** = 5 mm, **(g) & (h)** = 1 mm

2623

Fig. 18. *Deaechospira amouguerana* (Horný, 1997b) from the Lower Ktaoua Formation. (a)–(c) NM S2656, latex cast of base of mature specimen showing inner margin. Destombes locality 1778. (d)–(f) NM S2655, lateral, ventral, and apertural view showing ornamentation and shell repair (arrows). Destombes locality 585. (g)–(i) NM S2686 Lateral, ventral oblique and detail views of specimen showing the apertural sinus. Destombes locality 86. (j) NM S2685, detail of peripheral band. Destombes locality 86. (k) NM S2684, internal mould with some shell, showing the course of the peripheral band. Destombes locality 86. Scale bars for (a)–(h) & (k) = 5 mm, (i) & (j) = 1 mm.

Fig. 19. *Deaechospira amouguerana* (Horný, 1997b) from the Lower Ktaoua Formation. (a)–(e) NM S2657, latex cast of juvenile specimen showing ornamentation and peripheral band. Arrow in (b) points to shell repair. Destombes locality 1778. Scale bars = 1 mm.

Fig. 20. *Deaechospira* sp. from the Upper Tiouririne Formation. Destombes locality 134. (a)–(f) NM S2689, various views of specimen with partial shell preserved. S = sinus. Arrow in (d) points to muscle scar. (e) & (f) are latex cast from external mould, showing apertural sinus and peripheral band respectively. (g)–(i) NM S2687, lateral, dorsal and detail of partial specimen. Scale bars of (a)–(e) = 5 mm, (f)–(i) = 1 mm.

Fig. 21. *Allossospira debganensis* (Horný, 1997e) from the Upper Ktaoua Formation. (a)–(i) NM S2644, holotype, various views showing morphological details. Arrows in (e) show the transition from a flat peripheral band with sharp upper margin to protruding peripheral band aperturally. Destombes locality 1132. Scale bars for (a)–(f) & (h) = 5 mm, (g) & (i) = 1 mm.

Fig. 22. *Allossospira debganensis* (Horný, 1997e) from the Upper Ktaoua Formation at the locality Jbel Bou Ingarf ‘South’. (a) & (b) MGM-6979X, large specimen showing development of spire and peripheral band. Arrows in (a) point to the different convexity of the left and right sides of the whorl. Arrows in (b) point to shell repair. (c) MGM-6980X showing protruding peripheral band. (d) MGM-6981X showing several shell layers. (e) MGM-6982X, dorsal view of small specimen. Arrow points to possible impression of the protoconch. (f) MGM-6983X, detail of un-bordered peripheral band. (g) & (h) MGM-6984X, lateral and ventral views of shell respectively, showing the turn of the growth lines on the lower whorl surface and base. Arrows point to shell repair. All specimens are silicon casts. Scale bars for (a)–(d), (g) & (h) = 10 mm, (e) = 5 mm, (f) = 1 mm.

Fig. 23. *Allossospira debganensis* (Horný, 1997e) from the Upper Ktaoua Formation at the locality Jbel Bou Ingarf ‘South’. (a) & (b) MGM-6985X-1, small specimen showing development of whorl curvature, peripheral band and ornamentation. (c) MGM-6985X-2, apertural view of small specimen occurring with MGM-6985X-1. Both specimens are silicon casts. Scale bars = 1 mm.

Fig. 24. *Allossospira debganensis* (Horný, 1997e) from the Upper Ktaoua Formation at the locality Jbel Bou Ingarf ‘South’. (a) MGM-6986X, steinker in place in the external mould. (b) MGM-6987, cross section showing the development of the whorls. Scale bars = 10 mm.

Fig. 25. *Lophospira latilabra* sp. nov. From the Upper Ktaoua Formation at the locality Jbel Bou Ingarf ‘South’. (a)–(d), (f)–(h), (i) & (k) MGM-6992X, holotype. Silicon casts of both halves of the external mould. (e) & (j) MGM-6993X, paratype. Apertural view and detail of spire showing possible protoconch. Scale bars = 5 mm.

2674

2675 **Fig. 26.** (a), (d), (e), (g) & (j) *Myoplusia* sp. (a), (j) MGM-6853X, right valve, dorsolateral
2676 view. (j) Lateral view. (d) MGM-6852X, right valve, lateral view. (e) FSL 550117, left valve,
2677 lateral view. (g) MGM-6851X, left valve, lateral view. (b), (c) & (k)–(q) *Praenucula pojetai*
2678 sp. nov. (b) & (m) MGM-6846X, paratype, left valve, external mould, lateral view. (m)
2679 Paratype, left valve, internal mould, lateral view. (c) FSL 550161, right valve, lateral view.
2680 (k) & (n) MGM-6843X, articulated specimen. (k) Dorsolateral view. (n) Dorsal view. (l) FSL
2681 550118, right valve, lateral view. (o)–(q) MGM-6845X, holotype, left valve. (o) Lateral view.
2682 (p) Dorsal view. (q) Dorsolateral view. (f), (h) & (i) *Sluha kosoviensis* (Barrande, 1881d). (f)
2683 & (h) MGM-6847X, left valve. (f) Dorsolateral view. (h) Lateral view. (i) FSL 550162,
2684 external mould, lateral view. Scale bars = 5mm.

2685

2686 **Fig. 27.** (a), (e) & (h) *Dceruska* sp. (a) MGM-6861X, left valve, lateral view. (e) & (h)
2687 MGM-6842X, articulated specimen. (e) Lateral view. (h) Dorsal view. (b), (c), (i)–(k) & (l)
2688 *Cyrtodonta* sp. (b) MGM-6863X, left valve, lateral view. (c) MGM-6859X, right valve,
2689 lateral view. (i) & (k) MGM-6869X, articulated specimen. (i) Right valve, lateral view. (k)
2690 Dorsal view. (j) & (l) MGM-6868X, articulated specimen. (j) Dorsal view. (l) Left valve,
2691 lateral view. (d) & (m)–(o) *Nuculites* sp. (d) MGM-6860X, right valve, lateral view. (m)–(o)
2692 MGM-6862X, left valve. (m) Part of the external mould. (n) Dorsolateral view. (o) Lateral
2693 view. (f) & (g) *Cleionychia transversa* (Portlock, 1843). MGM-6841X, left valve. (f) Detail
2694 of the anterior part with anterior adductor muscle scar. (g) Lateral view. Scale bars for (b)–(d)
2695 = 20 mm, (a) & (e)–(m) = 10 mm.

2696

2697 **Fig. 28.** Angular measurements (angles alpha, beta, gamma) used in describing Ambonychiids
2698 (after Pojeta 1966).

2699

2700 **Fig. 29.** (a), (c) & (d)–(h) *Cleionychia prisca* (Portlock, 1843). (a) MGM-6875X, left valve,
2701 lateral view. (c) MGM-6856X, right valve, lateral view. (d)–(h), MGM-6864X, two
2702 specimens in life position. (d) Two articulated specimens, lateral view. (e) One articulated
2703 specimen (MGM-6864X a) showing hinge line. (f) One articulated specimen, posterior view.
2704 (g) Anterior view with beaks into the substrate, brachiopods and bryozoans. (h) Lateral view
2705 on two articulated specimens. (b) & (j) *Ambonychia* sp., MGM-6866X, articulated specimen.
2706 (b) Dorsal view with prominent escutcheon. (j) Left valve, lateral view. (i) *Ambonychia* aff.
2707 *magna* Isberg, 1934. MGM-6858X, left valve, dorsal view. Scale bars = 10 mm.

2708

2709 **Fig. 30.** (a), (d) & (e)–(k) *Modiolopsis* sp. (a) MGM-6873X, left valve, lateral view (d)
2710 MGM-6857X, left valve, lateral view (e) MGM-6874X, right valve, lateral view. (f) MGM-
2711 6871X, left valve, lateral view (g) MGM-6867X, left valve, lateral view. (h) & (j) MGM-
2712 6872X, right valve. (h) Lateral view. (j) Detail of the right valve, lateral view. (i) & (k)
2713 MGM-6870X, right valve. (i) Lateral view. (k) Detail of the right valve, lateral view. (b)
2714 *Pseudarca?* sp., FSL 550155, left valve, lateral view. (c) *Phestia?* sp., FSL 550115, right
2715 valve, lateral view. Scale bars for (c) & (g) = 5 mm, (a), (b), (d)–(f) & (h)–(k) = 10 mm.

2716

2717 **Fig. 31.** Actinocerids of the Upper Ktaoua Formation, Katian Stage, Morocco. (a) *Wadema*
2718 *tattai* sp. nov., specimen AA.ABT.OS 38, holotype. Naturally weathered median section.
2719 Note the thin siphuncular engrafts (arrow) and lamellar annuli, and note also the bryozoan
2720 overgrowth (left side). (b) Ormoceratidae gen. et sp. indet., specimen MGM-7014X, natural
2721 cut of internal mold, with massive remains of siphuncular annuli. Scale bars = 10 mm.

2722

2723 **Fig. 32.** Late Ordovician cephalopods of Morocco. (a) & (b) *Tafadnatoceras tiouririnense*

2724 gen. et sp. nov. from the Upper Tiouririne Formation, Katian; **(a)** MGM-7009X; **(b)** MGM-
2725 7005X, holotype. **(c)** & **(d)** Endoceratidae gen. et sp. indet. from the Taddrist Formation. **(c)**
2726 MGM-6997X, adoral view; **(d)** MGM-7001X, lateral view of internal mold of siphuncle. **(e)**
2727 *Wadema* sp., MGM-7013X, adoral view of internal mold. Scale bars for **(a)** & **(c)**–**(e)** = 10
2728 mm, **(b)** = 5 mm.

2729

2730 **Fig. 33.** Interpretation of septal neck, siphuncular tube structures. **(a)** *Tafadnatoceras*
2731 *tiouririnense* gen et sp. nov., holotype. **(b)** *Paradnatoceras tubiforme* Chen & Liu, 1974,
2732 NIGP 15395–15653, holotype. Camera lucida drawing from median polished sections, not to
2733 scale. Black lines, septa; stippled lines, connecting ring; grey areas, siphuncular deposits.
2734 Endocameral deposits omitted.

2735

2736 **Fig. 34.** Polished median sections of siphuncle and septal neck details *Tafadnatoceras*
2737 *tiouririnense* gen et sp. nov. from the Upper Tiouririne Formation, Katian. **(a)** MGM-7003X,
2738 adoral part of specimen with barrel-shaped siphuncular segments. **(b)** MGM-7009X, part of
2739 section with of adnate barrel-shaped siphuncular segments; **(c)** same specimen as in **(a)**,
2740 adapical part with nearly tubular siphuncular segments; **(d)** MGM-7005X, holotype, with
2741 stacked parietal siphuncular deposits, which form continuous lining, note also heavy
2742 endocameral deposits. Scale bars = 3 mm.

MO		Upper Ordovician		Global Series/ Stages
Dw	Sandbian	Katian	Hirnantian	Lithostratigraphy
First Bani Group	Ktaoua Group	Ktaoua Group	Second Bani Group	Upper Second Bani Formation Lower Second Bani Formation
			Upper Ktaoua Formation Upper Tiouririne Formation Lower Ktaoua Formation	
	<i>Sinuitopsis</i> sp.	<i>Tritonophon grandis</i> sp. nov.	<i>Radvanospira banienensis</i> gen. et sp. nov.	
	<i>Sinuitopsis neglecta</i>	<i>Lophospira latilabra</i> sp. nov.		
	<i>Atlantophon maider</i>	<i>Sinuites destombesi</i>		
	<i>Tritonophon peeli</i>	<i>Allossospira debganensis</i>	<i>Nuculites</i> sp.	
	<i>Bucanopsina calypso</i>		<i>Modiolopsis</i> sp.	
	<i>Nonorios pater</i>		<i>Deerуска</i> sp.	
	<i>Deaechospira amouguerana</i>	<i>Ambonychia aff. magna</i>		
	<i>Radvanopsira antiquata</i>	<i>Sluha kosoviensis</i>		
	<i>Phestia?</i> sp.	<i>Cleionychia transversa</i>		
	<i>Pseudarca?</i> sp.	<i>Cleionychia prisca</i>		
	<i>Praenucula pojetai</i> sp. nov.			
	<i>Myoplusia</i> sp.			
			<i>Ambonychia</i> sp.	
			<i>Cyrtodonta</i> sp.	
		<i>Wadema tattai</i> sp. nov.		
		<i>Wadema</i> sp.		
		<i>Ormoceratidae</i> gen. et sp. indet.		
		<i>Tafadnatoceras tiourinense</i> gen. et sp. nov.		
		<i>Endoceratidae</i> gen. et sp. indet.		

Fig. 2

Figure-04.psd @ 41,5% (Gray/8) *

Figure-05.psd @ 66,7% (Gray/8) *

Figure-06.psd @ 33,3% (Gray/8) *

Figure-07.psd @ 33,3% (Gray/8) *

Figure-09.psd @ 100% (RGB/8) *

Figure-10.psd @ 142% (Gray/8) *

Figure-11.psd @ 50% (Gray/8) *

Figure-12.psd @ 62,4% (Gray/8) *

Figure-13.psd @ 33,3% (Gray/8) *

Figure-14.psd @ 33,3% (Gray/8) *

Figure-15.psd @ 33,3% (Gray/8) *

Figure-17.psd @ 2050% (Layer 0, Gray/8) *

Figure-18.psd @ 33,3% (Gray/8) *

Figure-19.psd @ 66,7% (Gray/8) *

Figure-20.psd @ 33,3% (Gray/8) *

Figure-21.psd @ 33,3% (Gray/8) *

Figure-22.psd @ 33,3% (Gray/8) *

Figure-23.psd @ 66,7% (Gray/8) *

Figure-24.psd @ 100% (Gray/8) *

Figure-25.psd @ 33,3% (Gray/8) *

Figure-26.TIF @ 33,3% (Layer 0, RGB/8#) *

Figure-27.TIF @ 33,3% (Layer 0, RGB/8#) *

gamma

beta

alpha

Figure-29.TIF @ 33,3% (RGB/8#) *

Figure-30.TIF @ 33,3% (RGB/8#) *

Table 1. Numerical and ranked abundance of bivalves, based on the collections of bivalves from Morocco (Early and Late Ordovician). RV and LV – right and left valves (disarticulated specimens); A – shells with conjoined valves (articulated specimens); RA – percentage relative abundance; AA – percentage relative abundance of shells with conjoined valves; R – ranked abundance.

Morocco - Early Ordovician

Species	Life habits	RV	LV	A	RA	AA	R
<i>Redonia michelae</i>	infaunal	42	46	5	66.2	6.76	1
<i>Babinka prima</i>	infaunal	7	10	-	11.50	0.00	2
<i>Coxiconchia guiraudi</i>	infaunal	10	3	-	8.80	0.00	3
<i>Ekaterodonta courtessolei</i>	infaunal	6	2	1	6.8	1.35	4
<i>Aloconcha?</i>	infaunal	3	-	-	2.03	0.00	5
<i>Cardiolaria?</i>	infaunal	2	1	-	2.03	0.00	6
<i>Glyptarca</i> sp.	infaunal	-	-	1	1.40	1.35	7
<i>Cienagomya?</i>	infaunal	-	1	-	0.68	0.00	8
<i>Praenucula?</i>	infaunal	1	-	-	0.68	0.00	9
Totals		71	63	7	100.12%	9.46%	

Morocco - Late Ordovician

Species	Life habits	RV	LV	A	RA	AA	R
<i>Praenucula pojetai</i>	infaunal	5	3	1	20.0	20.0	1
<i>Modiolopsis</i> sp.	semi-infaunal	3	7	-	20.0	-	1
<i>Cyrtodonta</i> sp.	semi-infaunal	1	1	2	12.0	66.7	2
<i>Cleionychia prisca</i>	epifaunal	1	2	1	10.0	40.0	3
<i>Myoplusia</i> sp.	infaunal	2	3	-	10.0	-	3
<i>Dceruska</i> sp.	semi-infaunal	-	1	1	6.0	66.7	4
<i>Nuculites</i> sp.	infaunal	-	1	1	6.0	66.7	4
<i>Sluha kosoviensis</i>	infaunal	-	2	-	4.0	-	4
<i>Ambonychia</i> sp.	epifaunal	-	-	1	4.0	100.0	4
<i>Phestia?</i> sp.	infaunal	1	-	-	2.0	-	5
<i>Pseudarca?</i> sp.	infaunal	1	-	-	2.0	-	5
<i>Cleionychia transversa</i>	epifaunal	-	1	-	2.0	-	5
<i>Ambonychia</i> aff. <i>magna</i>	epifaunal	-	1	-	2.0	-	5
Totals		14	22	7	100.0%	28.0%	

Table 2. Dimensions and type of the valve in *Praenucula pojetai* sp. nov.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
FSL 550118	R	22.5	14.2	2.0
MGM-6845X	L	22.2	15.0	2.1
MGM-6844X	R	20.1	14.8	2.5
FSL 550113	R	15.5	11.1	1.5
FSL 550161	R	12.5	7.7	1.0
MGM-6849X	R	–	18.4	–
MGM-6846X	L	–	12.1	1.9
MGM-6843X	A	–	–	4.0
MGM-6848X	L	–	–	1.5

Table 3. Dimensions and type of the valve in *Nuculites* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6860X	A	96.5	48.7	16.1
MGM-6862X	L	59.2	32.2	7.2

Table 4. Dimensions and type of the valve in *Myoplusia* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6853X	R	26.2	18.5	3.9
MGM-6850X	L	13.0	11.1	1.5
MGM-6851X	L	11.6	76.0	1.1
FSL 550117	L	9.8	7.3	1.0
MGM-6852X	R	8.2	4.9	1.2

Table 5. Dimensions and type of the valve in *Sluha kosoviensis* (Barrande, 1881d).

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
FSL 550162	L	24.4	17.2	1.2
MGM-6847X	L	22.2	18.5	3.1

Table 6. Dimensions and type of the valve in *Phestia?* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
FSL 550115	R	20.2	10.4	1.5

Table 7. Dimensions and type of the valve in *Modiolopsis* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6871X	L	51.2	30.8	8.4
MGM-6873X	L	249.1	28.4	7.1
MGM-6854X	L	44.8	23.9	6.0
MGM-6874X	R	39.7	22.0	4.1
MGM-6855X	R	37.2	26.0	3.2
MGM-6870X	R	35.0	19.1	1.9
MGM-6872X	L	231.5	17.2	1.9
MGM-6865X	L	26.2	14.7	2
MGM-6867X	L	21.0	16.1	2.5
MGM-6857X	L	–	25.2	5.0

Table 8. Dimensions and type of the valve in *Dceruska* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6842X	A	51.2	26.3	7.7
MGM-6861X	L	41.2	–	–

Table 9. Dimensions and type of the valve in *Ambonychia* aff. *magna*.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6858X	L	92.1	56.8	10.2

Table 10. Dimensions and type of the valve in *Ambonychia* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6866X	A	45.8	22.2	11.0

Table 11. Dimensions and type of the valve in *Cleionychia transversa* (Portlock, 1843)

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6841X	L	–	–	10.0

Table 12. Dimensions and type of the valve in *Cleionychia prisca* (Portlock, 1843).

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6864X b	L	–	34.8	–
MGM-6864X a	A	–	–	19.1
MGM-6875X	L	–	–	10.2
MGM-6856X	R	–	–	9.0

Table 13. Dimensions and type of the valve in *Cyrtodonta* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
MGM-6863X	L	89.4	53.8	15.1
MGM-6859X	R	73.1	52.9	18.2
MGM-6869X	A	–	54	17
MGM-6868X	A	–	53	22

Table 14. Dimensions and type of the valve in *Pseudarca?* sp.

Abbreviations: V = valve (R= right valve, L= left valve, A= articulated specimen), L = length of the valve, H = height of the valve, W= width of the valve.

<i>Dimensions.</i>	V	L	H	W/2
FSL 550155	R	82.1	19.8	?