Bajocian (Middle Jurassic) ammonites of stratigraphical and palaeobiogeographical importance from Mombasa, Kenya, East Africa

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ABSTRACT
Collections of Middle Jurassic ammonites made at the Mwachi River locality, near Mombasa in the late 1980's and early 1990's are described. They support previous research concluding a Late Bajocian age for the major or the upper part of the 'Posidonia shales', immediately below and above the dividing Massive (Coral) Limestone. The ammonite species are figured and briefly described. Two Upper Bajocian ammonite zones are evidenced: a lower assemblage indicates the Strenoceras niortense Zone and a higher one belonging to the Garantiana garantiana Zone. Most of the ammonites are Tethyan forms with abundant phylloceratids and lytoceratids, some indicating connections with coeval Arabian and Sinai faunas. Palaeobiogeographically the assemblages suggest a deep-water position on the East-African Gondwana margin, with strong faunistic influence from the open Tethys and very restricted connections with the Arabian shallow water regions.

KEY WORDS
Kenya,
Middle Jurassic,
Bajocian,
ammonite zones,
faunal compositions,
phylloceratids,
lytoceratids,
palaeogeography.

RÉSUMÉ
Ammonites d'importance stratigraphique et paléogéographique du Bajocien de Mombasa (Kenya).
Des ammonites jurassiques récoltées dans les années 80 et 90 dans la localité de Mwachi River, près de Mombasa (Kenya) sont étudiées. Les espèces sont figurées et brièvement décrites. Cette étude confirme les conclusions de travaux anciens donnant un âge Bajoicien supérieur pour les « Posidonia shales » intercalés dans le « Massive Coral Limestone » [calcaire corallien massif]. Deux zones d'ammonites du Jurassique supérieur sont mises en évidence : à la base un assemblage indique la zone à Strenoceras niortense et au sommet un autre assemblage appartient à la zone à Garantiana garantiana. La plupart de ces ammonites sont des formes téthysiennes comprenant d'abondants phylloceratidés et lytoceratidé, certains indiquant des communications avec les faunes d'Arabie et du Sinai. D'un point de vue paléobiogéographique, les assemblages suggèrent une position dans des eaux profondes de la marge gondwanienne de l'Afrique de l'Est, avec une forte influence téthysienne de mer ouverte, et des communications restreintes avec les eaux peu profondes des régions arabes.

MOTS CLÉS
Kenya,
Jurassique moyen,
Bajocien,
zones à ammonite,
compositions fauniques,
phyllocératidés,
lytocératidés,
paléogéographie.

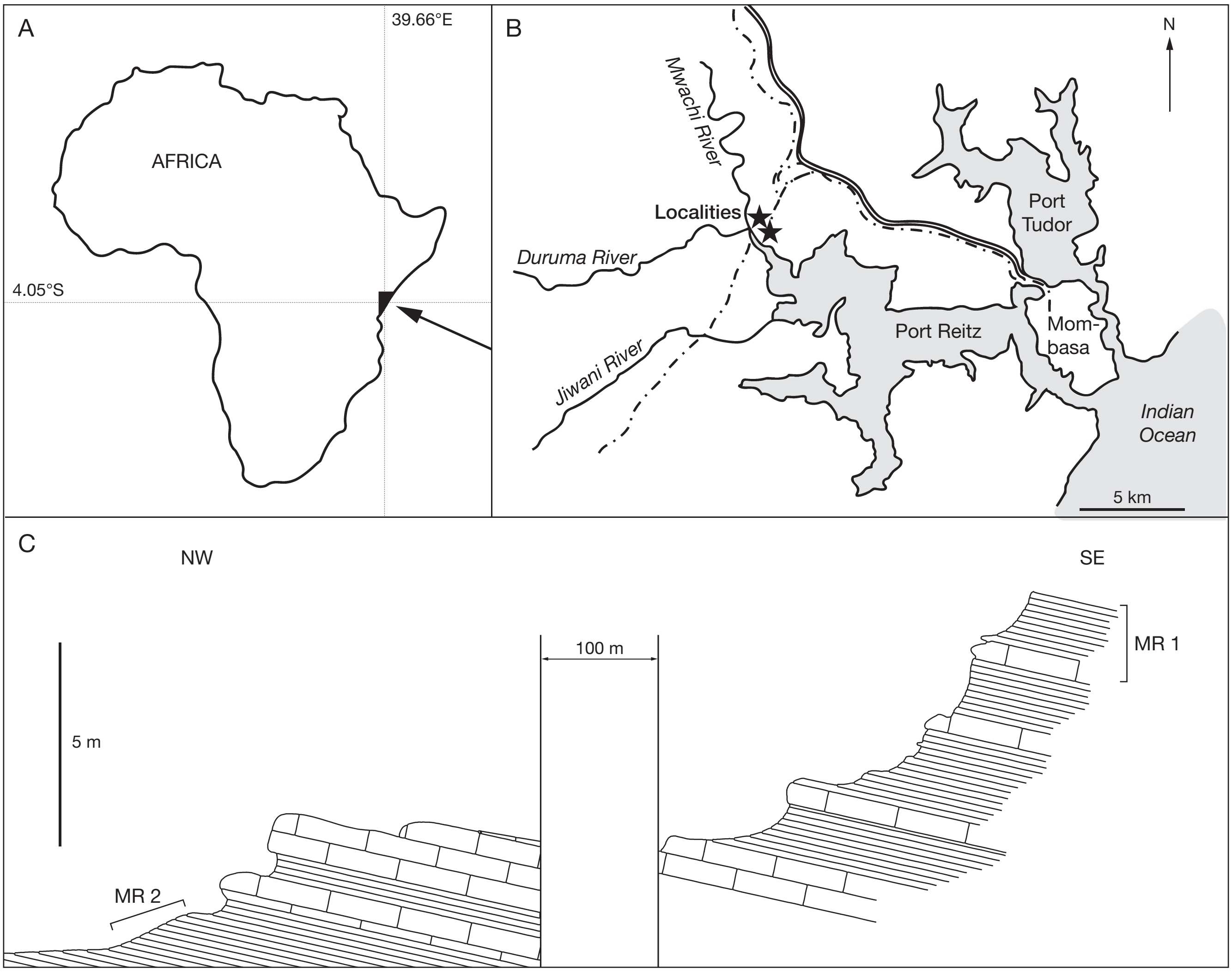

Fig. 1. — The Upper Bajocian ammonite locality in East Africa (**A**), near Mombasa (**B**), where the Garantiana garantiana Zone elements (at MR 1) and the Strenoceras niortense Zone ammonites (at MR 2) were collected from the shales respectively above and below the dividing limestone of the Kambe Formation.

INTRODUCTION

Arkell, when treating the Jurassic formations of the world (1956), gave a comprehensive summary of the Lower, Middle and Upper Jurassic of East Africa. He discussed the Middle Jurassic formations around Mombasa as classic ammonite-bearing sequences, having been made famous by the late 19th century works of German, then mid-20th century British specialists. Most extensive are Callovian ammonite-yielding strata, but Arkell, then later Kapilima (1984) concluded that the age of the earliest Middle Jurassic beds in the hinterland of the East African coastal region is late Aalenian. Bajocian has been reported, while confirmed Bathonian ammonites have to date not been recorded from East Africa.

The Bajocian ammonite record is restricted temporally to the late Bajocian and areally to the surroundings of Mombasa. The first Bajocian ammonites (then thought to be Bathonian) were collected by J. W. Gregory and worked out and published by Spath (1920). Later Miss McKinnon Wood, the eminent geologist, collected new specimens that she sent again to Spath, who discussed and figured additional species in his later works (1930, 1933). These specimens came from the lower, shaley part of the Kambe Limestone, from different localities around, mainly southwest of Mombasa. The evaluation of Spath' data was the basis for Arkell to form his conclusion on the Bajocian of the region. Arkell made allowances for the possibility that some of the ammonites described by Spath could be Bathonian.

In 1975 Westermann published a revision of the complete Lower Kambe ammonite collection kept in the Hunterian Museum at the University of Glasgow, figuring some previously cited specimens from the collections. Ersterman was unable to contribute much new field evidence, but he checked in detail the existing local geological maps and the lithological log (Westermann 1975: figs 3, 4). He also confirmed the position of formerly mentioned localities within the series, and concluded that the Lower Kambe Limestone represents almost the whole Bajocian, while unequivocal

Fig. 2. — A rock sample from the Upper Shaley member of the Kambe Formation (locality MR 1) showing the preservation of pyritic ammonite nucleus. Scale bar: 10 mm.

evidence of the Bathonian was not found. His re-evaluation made clear that the place where the richest ammonite fauna appears is the left bank of the Mwachi River, near the bridge where the Mombasa pipeline crosses the river.

In 1988, with the Teleki Memorial Expedition, I had the opportunity to make a short visit to this locality. Modest collection of ammonites was made from two levels of the exposed shales (Galácz 1990). In 1992, in a second visit to Mombasa, I revisited the Mwachi River locality, and collected additional material from both levels.

Not long ago Italian colleagues studied the Mwachi River region, and on the left bank of the river they collected microfossil (nannoplankton) and microfacies samples (Chiocchini *et al.* 2005). The sedimentological evaluation of the sequence supported the earlier opinions. However, their conclusion on the ages of the Lower Kambe shales differs from that drawn on the basis of ammonites, their micropalaeontological material suggesting an Aalenian age. These circumstances made necessary to document the previously reported but properly never described ammonites from the Mwachi River.

LOCALITIES

The localities (Fig. 1), as stated previously (Galácz 1990) were at and near the former Mombasa pipeline bridge, on the left bank of the Mwachi River, where the pipeline service road reaches the river. Directly by the river bank, near the support of the pipeline bridge, a wall of around 8 m was visible, where at the time fresh landslide exposed the top of the Massive (Coral) Limestone (*sensu* Westermann 1975) and the shaley beds immediately above. The Upper Shaley Member ammonites collected from this location are listed under MR-1 locality in Galácz (1990), while MR-2 referred to the site where the topmost shaley beds underlying the limestone crop out by the riverside, upstream. Near the old pipeline bridge the limestone between the Lower and Upper Shaley members of the Kambe Formation seemed to be thinned out, because the generalized section of Westermann (1975: fig. 4) shows *c.* 35 m thickness. Chiocchini *et al.* (2005) indicate nearly 50 m thickness in the quarry about 2 km upstream. Nowadays the river bank changed, it was silted up, and invaded by vegetation. The water pipeline seems to be obsolete and abandoned.

Fig. 3. — Occasional preservation of big ammonite specimens (*Lytoceras eudesianum eudesianum* (d'Orbigny, 1846)), as shown here with an imprint in the Upper Shaley member of the Kambe Formation (locality MR 1). Scale bar: 10 mm.

The ammonites described here came from these two levels: one from below and another above of the Massive Limestone (see Fig. 1B, C).

AMMONITE PRESERVATION AND FAUNAL COMPOSITION

The ammonites in the shales are partial pyritic internal moulds (Fig. 2) which weather out from the matrix and can be collected at the foot of the exposures. The size of specimen is usually small, but rarely bigger specimens occur (Fig. 3).

Other faunal elements are rare. As Westermann noted, the former name 'Posidonia Shales' (Weir 1938) is misleading: pelagic bivalves traditionally called *'Posidonia'* or *'Posidonomya'* are practically absent in the shale around the Mwachi River. In the material collected only small, pyritized internal moulds of burrowing, *Nucula*-type bivalves occur.

Spath found the faunal composition of the ammonites of some interest. He gave (Spath 1933: 815) the following proportions of the total fauna (343 specimens) resulting from the sum of collecting from three Bajocian localities: phylloceratids: 70 %, lytoceratids: 22% and ammonitids: 8%. Westermann (1975: 34) repeated Spath's calculation, and interpreted the abundance of phylloceratids and lytoceratids ('leiostracans') as indication of a deep, oceanic environment.

My collections resulted in 213 specimens from the Mwachi River localities (Localities 26 and 76 of McKinnon Wood, 1938, as identified by Westermann). The respective proportions are: Phylloceratina: 65%, Lytoceratina: 31%, and Ammonitina: 4%, which are quite close to those of Spath. It is noteworthy that the comparatively high proportion of Lytoceratina is due to the representation of the genus *Nannolytoceras* Buckman, 1905, a lytoceratid off-shoot which had a short flourishing time in the late Bajocian and early Bathonian in western Tethyan regions.

STRATIGRAPHY

As it was stated earlier (Galácz 1990), the two assemblages collected from the shales below and above the limestone indicate slightly different ages, i.e. Strenoceras niortense Zone and Garantiana garantiana Zone respectively. This conclusion was based on the material collected in 1988. The subsequent collection in 1992 yielded some additional ammonitids which support these age determinations.

Strenoceras niortense Zone

The ammonites placed in this zone were weathered out from beds of the low-dipping calcareous shale in a *c.* 10 m riverside sector (MR 2).

The assemblage previously identified as of Niortense Zone contained only a few elements which were regarded as diagnostic. '?*Trimarginia* sp.' which is now determined as belonging to this genus, but with greater certainty, 'Stephanoceratinae gen. et sp. indet.' now assigned to *Normannites egyptiacus* Arkell, 1952 and *Spiroceras annulatum* (Deshayes, 1831) served as basis to identify the zone. Disregarding the phyllo- and lytoceratids, the list is now supplemented from the 1992 collection with *Leptosphinctes* cf. *schmiereri* (Bentz, 1924) and *Masckeites* cf. *psilacanthoides* (Sandoval, 1983).

In total, the following ammonites were identified from the Strenoceras niortense Zone:

– *Phylloceras trifoliatum* Neumayr, 1871;
– *Holcophylloceras zignodianum* (d'Orbigny, 1848);
– *Ptychophylloceras* cf. *longarae* Sturani, 1971;
– *Lytoceras eudesianum eudesianum* (d'Orbigny, 1846);
– *Nannolytoceras polyhelictum* (Böckh, 1881);
– *Lissoceras oolithicum* (d'Orbigny, 1845);
– *Trimarginia* sp.;
– *Masckeites* cf. *psilacanthoides* (Sandoval, 1983);
– *Normannites egyptiacus* Arkell, 1952;
– *Leptosphinctes* cf. *schmiereri* (Bentz, 1924);
– *Spiroceras annulatum* (Deshayes, 1831).

Garantiana garantiana Zone

The assemblage determined as belonging into this zone was collected at the Mombasa pipeline bridge (MR 1).

The identification of this zone was previously based ont the occurrence of a few ammonite species (i.e., the co-occurrence of *Ptychophylloceras haloricum* (Hauer, 1854) and *Oppelia* sp. aff. *O. subcostata* (J. Buckman, 1881) (now understood as *Ptychophylloceras lardyi* (Ooster, 1860) and *Oecotraustes* sp., respectively). These could be supplemented now by the form identified as ?*Diplesioceras* sp., representing a further indication of this zone.

The beds identified here as of Garantiana Zone yielded ammonites as follows:

– *Phylloceras trifoliatum* Neumayr, 1871;
– *Calliphylloceras disputabile* (Zittel, 1868);
– *Holcophylloceras zignodianum* (d'Orbigny, 1848);
– *Ptychophylloceras lardyi* (Ooster, 1860);
– *Lytoceras eudesianum eudesianum* (d'Orbigny, 1846);
– *Nannolytoceras polyhelictum* (Böckh, 1881);
– *Oecotraustes* sp.;
– ?*Diplesioceras* sp.;
– *Cadomites* sp.

The Garantiana Zone is the highest faunal horizon and latest fauna so far recorded in the Mombasa region within the Kambe Formation, evidenced by the fact that neither uppermost Bajocian, nor confirmed Bathonian fossils have ever been confirmed in the area.

SYSTEMATICS – SHORT DESCRIPTIONS OF THE AMMONITE SPECIES

In the descriptions below higher systematic classification is omitted and the introduction of specific morphological details is minimized. Only diagnostic features are highlighted with references to stratigraphical and geographical distributions. Synonymies are presented only with references to the original designations, to previous records of the species from East Africa (or in neighbouring palaeogeographic areas), and to works with detailed descriptive treatment.

The specimens are deposited in the collection of the Natural History Museum of the Eötvös Loránd University, Budapest (EMNH).

Phylloceras trifoliatum Neumayr, 1871
(Fig. 5 A-D)

Phylloceras trifoliatum Neumayr, 1871: 309, pl. 12, figs 2,3. — Galácz 1990: 202.

Phylloceras aff. *kudernatschi* – Spath 1920: 312, pl. 5, fig. 1a-c; 1930: 19.

Phylloceras cf. *kunthi* – Spath 1920: 316, pl. 5, fig. 3a-c.

Phylloceras cf. *P. trifoliatum* – Westermann 1975: 37, pl. 1, figs 1-4.

Phylloceras veliani – Joly 1976: 178, pl. 6, fig. 4, pl. 41, fig. 7, text-fig. 71.

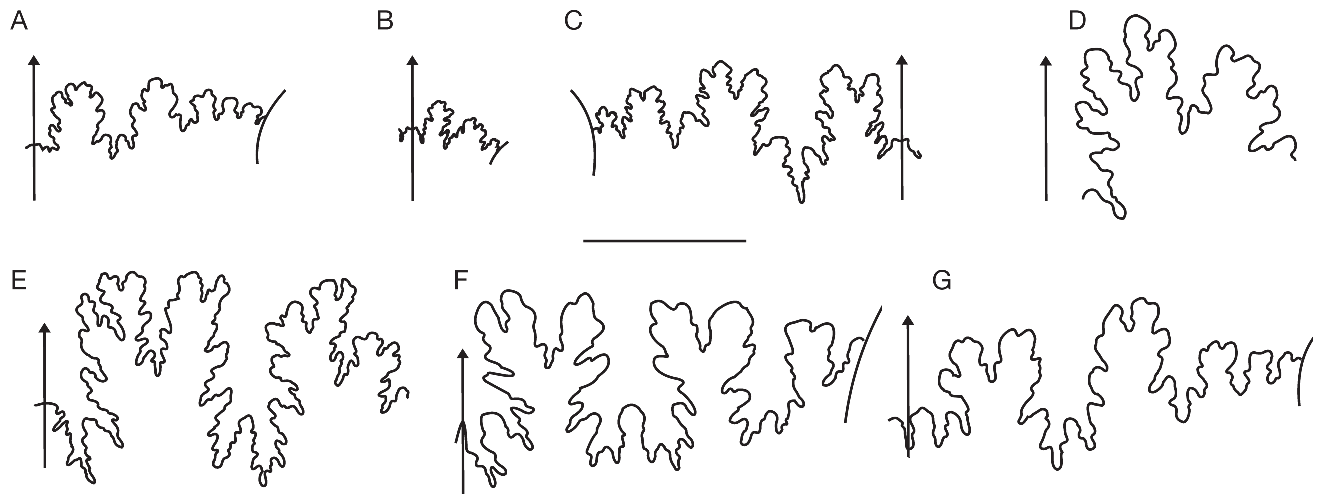

Fig. 4. — Suture lines of some important species: **A**, *Oecotraustes* sp. MR 1, EMNH.2015.249; **B**, *Cadomites* (*Cadomites*) sp. MR 1, EMNH.2015.232; **C**, ?*Diplesioceras* sp. MR 1, EMNH.2015.180; **D**, *Spiroceras annulatum* (Deshayes, 1831) MR 2, EMNH.2015.287; **E**, *Leptosphinctes* cf. *schmiereri* (Bentz, 1924) MR 2, EMNH.2015.224; **F**, *Nannolytoceras polyhelictum* (Böckh, 1881) MR 2, EMNH.2015.257; **G**, *Trimarginia* sp. MR 2, EMNH.2015.279. Scale bar: 5 mm.

Remarks

Several specimens, all are nuclei. Characteristic is the narrow umbilicus, the evenly arched, almost flattened flanks and the narrow, highly rounded venter. Lack of riblets on both the shell and the internal mould distinguishes this form from the closely similar *Phylloceras kudernatschi* (Hauer, 1854) and *P. isomorphum* Gemmellaro, 1872.

Calliphylloceras disputabile (Zittel, 1868) (Fig. 5G-H)

Phylloceras disputabile Zittel, 1868: 606.

Ammonites tatricus – Kudernatsch 1852: 4, pl. 1, figs 1-4.

non Phylloceras cf. *disputabile* – Spath 1920: 318, pl. 5, fig. 4a-d.

?*Calliphylloceras* cf. *disputabile* – Spath 1930: 22.

Calliphylloceras cf. *C. disputabile* – Westermann 1975: 38, pl. 1, fig. 6.

Calliphylloceras disputabile – Galácz 1990: 202.

Remarks

The specimens are easy to recognise by the wide-oval cross-section of the swollen whorls, especially at small sizes. The other characteristic feature is the straight, slightly projected constrictions. The form determined by Spath as close to *C. disputabile* (Spath 1920: pl. 5, fig. 4) most probably belongs to *Ptychophylloceras longarae* (see Westermann 1975: 37, and below). Genus *Calliphylloceras* Spath, 1927 is common in East Africa, in Madagascar (Joly 1976) and in Kachchh (Spath 1927), in the latter two regions with the same species.

Holcophylloceras zignodianum (d'Orbigny, 1848) (Fig. 5I-J)

Ammonites zignodianus d'Orbigny, 1842: 493, pl. 182, figs 1-2.

Holcophylloceras mediterraneum – Spath 1930: 23.

Holcophylloceras zignodianum – Galácz 1980: 41, pl. 5, figs 4-5; pl. 6, fig. 1; pl. 7, fig. 1; text-figs 30-32 (*cum syn.*); 1990: 202.

Remarks

H. zignodianum has characteristic inner whorls and nuclei with proportionally wide umbilicus and very strong, unmistakable constrictions. The Mombasa specimens are nuclei or fragments of middle whorls, those phragmocone parts where the otherwise characteristic high-lateral and ventral ribs are not developed ont he available specimens.

Holcophylloceras Spath, 1927, similarly as *Calliphylloceras*, is widely distributed in the later Middle Jurassic through the Upper Jurassic of East Africa and of the wider Indo-Malgashi area.

Ptychophylloceras lardyi (Ooster, 1860) (Fig. 5E-F)

Ammonites lardyi Oooster, 1860: 71, pl. 19, figs 7-9.

Ptychophylloceras (*P.*) *lardyi* – Pavia 1983: 16, pl. 3, fig. 4, pl. 4, figs 10, 11, 13, 14, text-figs 4, 6, 9 (*cum syn.*)

Ptychophylloceras lardyi – Parnes 1988: 713, pl. 1, figs 8-11.

Ptychophylloceras haloricum – Galácz 1990: 202.

Remarks

These nuclei were determined previously as *Ptychophylloceras haloricum* (see Galácz 1990: 202). Better specimens from the new collection show the suture-line which is consistent with those figured by Pavia (1983: text-fig. 4). The specimens represent the innermost whorls which show only the funnel-shaped periumbilical area but just under the size where the first characteristic ventral constrictions and ridges appear. Pavia (1983: 16) restricted the stratigraphic distribution of the species to the Garantiana Zone.

Lytoceras eudesianum eudesianum (d'Orbigny, 1846)
(Figs 3; 6A, B)

Ammonites eudesianus d'Orbigny, 1846: 386, pl. 128, figs 1-3.

Lytoceras adeloides – Douvillé 1916: 13, pl. 2, fig. 1. — Parnes 1988: 713, pl. 1, fig. 29.

Lytoceras eudesianum eudesianum – Galácz 1980: 48, pl. 9 (*cum syn.*)

Lytoceras eudesianum – Galácz 1990: 202.

Remarks

The impression of a large specimen (Fig. 3) and the small pyritic moulds (Fig. 6A, B) displaying clearly the thin crinkled collars which appear periodically among the straight riblets. The geographically closest record is the '*L. adeloides*' from the Sinai (Douvillé 1916: 13, pl. 2, fig. 1; Parnes 1988: 713, pl. 1, fig. 29). Both figured forms are too old (i.e., Late Bajocian) to be *L. adeloides* (Kudernatsch, 1852), and are most probably *L. eudesianum*.

Nannolytoceras polyhelictum (Böckh, 1881)
(Figs 4F; 5K, L)

Lytoceras polyhelictum Böckh, 1881: 35, pl. 1, figs 2, 3.

Protetragonites cf. *tripartitus* – Spath 1920: 355, pl. 5, fig. 6a-c.

Nannolytoceras aff. *N. polyhelictum* – Westermann 1975: 36, pl. 1, fig. 7.

Nannolytoceras polyhelictum – Galácz 1990: 202. — Galácz & Kassai 2012: 291, figs 7a-d, 8e, 9g-h.

Remarks

Several specimens of this characteristic Upper Bajocian *Nannolytoceras*. They differ from other, much rarer species with their high-oval whorl-section and constrictions: there are four on these inner whorls and they are narrow and prorsiradiate on the flanks. Spath, and later Westermann also described and figured the species (see synonymy above). A lectotype was designated and figured recently from the original material of Böckh (see Galácz & Kassai 2012).

Lissoceras oolithicum (d'Orbigny, 1845)
(Fig. 5O-P)

Ammonites oolithicus d'Orbigny, 1845: 383, pl. 126, figs 1-4.

Lissoceras oolithicum – Douvillé 1916: 17, pl. 3, fig. 9. — Galácz 1980: 57, pl. 11, figs 5,6, text-figs 43, 44 (*cum syn.*); 1990: 202.

Lissoceras sp. cf. *L.* (*L.*) *oolithicum* – Parnes 1988: 721, pl. 2, figs 13-17.

Remarks

A small fragment of a wholly septate internal cast. Characteristic is the oval whorl-section with convex flanks and highly-arched venter. The suture-line is very poorly preserved, but the details of the typical haploceratid suture are discernible.

This is a Bajocian Ammonitina species with extremely wide north-south geographic range. This Mombasa locality is almost on the equator, and the northernmost record is from Isle of Skye, Scotland (Morton 1971: 40, figs 1,2). It is also recorded from the Sinai (Douvillé 1916: 17, pl. 3, fig. 9 and Parnes 1988: 721, pl. 2, figs 13-17).

Oecotraustes sp.
(Figs 4A; 5Q, R)

Hecticoceras sp. juv. – Spath 1920: 359, pl. 5, fig. 7.

(?) Oppeliidae indet [? *Oecotraustes*] – Westermann 1975: 40, pl. 2, fig. 3.

Oppelia sp. aff. *O. subcostata* – Galácz 1990: 202.

Remarks

Half-whorl of a phragmocone showing a narrow, sharp keel and almost smooth flanks. The only discernible sculptural elements are faint, forwardly bent crinkles on the middle of the whorl-sides. The suture-line (Fig. 4A) is simple with low saddles and short lobes.

Most of the Bajocian *Oecotraustes* species have weakly sculptured and keeled nucleus, but closer determination is not possible.

This morphology seems to agree with that figured previously by Spath (1920), then refigured by Westermann (1975).

Trimarginia sp.
(Figs 4G; 5M, N)

? *Oecotraustes*? (*Limoxyites*?) aff. *O. nivernensis* – Westermann 1975: 42, pl. 2, figs 5, 6.

? *Trimarginia* sp. – Galácz 1990: 202.

Remarks

This is a septate whorl fragment with flattened and smooth flanks and trimarginate venter. The suture-line is slightly displaced on this specimen (see Fig. 4G). The actual size of the specimen could have been about 12-14 mm, a diameter at which Arkell (1952: 308) states the presence of tertiary ribbing on the type species. However, *Trimarginia iberica* Fernández-López, 1985 (Fernández-López (1985: 241, pl. 16, figs 11,12) does not show development of ribs at these sizes.

The specimens figured by Westermann (1975: pl. 2, figs 5,6) are similar by the shape of the venter but differ in having faint ribs and a suture-line with better developed first lateral saddle.

T. sinaitica Arkell, 1952 (the type re-figured in Parnes 1988: pl. 2, figs 35, 36), possibly of Late Bajocian age, is associated with *Normannites egyptiacus* in the Sinai (see Arkell 1952: 308).

There are some similar oppeliids in the Upper Bathonian previously described as *Trimarginia* (see '*Oppelia* [*Trimarginia*] *sinaitica*' in Wendt [1963: 123], and '*Trimarginia sylviae*' in Mangold & Gygi [1997: 502]). They are similar, but regarded here as Bathonian homoeomorphs.

Fig. 5. — **A**, **B**, *Phylloceras trifoliatum* Neumayr, 1871 MR 1, EMNH.2015.286; **C**, **D**, *Phylloceras trifoliatum* Neumayr, 1871 MR 2, EMNH.2015.285; **E**, **F**, *Ptychophylloceras lardyi* (Ooster, 1860) MR 1, EMNH.2015.303; **G**, **H**, *Calliphylloceras disputabile* (Zittel, 1868) MR 1, EMNH.2015.304; **I**, **J**, *Holcophylloceras zignodianum* (d'Orbigny, 1848) MR 1, EMNH.2015.259; **K**, **L**, *Nannolytoceras polyhelictum* (Böckh, 1881) MR 2, EMNH.2015.257; **M**, **N**, *Trimarginia* sp. MR 2, EMNH.2015.279; **O**, **P**, *Lissoceras oolithicum* (d'Orbigny, 1845) MR 2, EMNH.2015.268; **Q**, **R**, *Oecotraustes* sp. MR 1, EMNH.2015.249; **S**, ?*Diplesioceras* sp. MR 1, EMNH.2015.180; **T**, **U**, *Cadomites* (*Cadomites*) sp. MR 1, EMNH.2015.232; **V**, **W**, *Normannites egyptiacus* Arkell, 1952 MR 2, EMNH.2015.288; **X**, **Y**, *Spiroceras annulatum* (Deshayes, 1831) MR 2, EMNH.2015.287. Scale bar: 10 mm.

?*Diplesioceras* sp.
(Figs 4C; 5S)

Remarks

This is a half-whorl phragmocone fragment of an ammonite with flattish flanks, relatively wide venter with low, blunt keel on it and weak, rounded, biplicate ribs.

The only similar specimen is the *Diplesioceras* sp. nov. 1 in Fernández-López (1985: 204, pl. 17, fig. 8), a small specimen from the Garantiana Zone of the Iberian Cordilleras. The Mombasa ammonite has comparable size proportions and shows the same style of ribbing. Its suture-line is very similar to that of the *Diplesioceras diplesium* Buckman, 1920 figured by Dietl (1974: text-fig. 7).

Diplesioceras is a strange genus regarded *incertae sedis* by Donovan *et al.* (1981: 118) and grouped together with the haploceratid *Poecilomorphus* by Fernández-López (1985: 204). Recently Howarth (2013: 121) ranged the genus into the Hildoceratoidea, as *incertae sedis*.

Cadomites (*Cadomites*) sp.
(Figs 4B; 5T, U)

Remarks

Very small nuclei of which one is figured here.

Cadomites Munier-Chalmas, 1892 was also documented from the Kambe limestone by Westermann (1975) with a beautiful specimen (Westermann 1975: pl. 2, fig. 8), and probably with his '?*Torrensia* sp. nov.' (Westermann 1975: pl. 2, fig. 10). The latter is a nucleus, a fragment that is difficult to determine correctly, however shows a suture-line (Westermann 1975: text-fig. 6A) which is close to that observed on small *Cadomites*, including the one figured here (Fig. 4B). Ventral weakening of the ribbing and constrictions are uncommon but do occur on the inner whorls of *Cadomites*.

Masckeites cf. ***psilacanthoides*** (Sandoval, 1983)
(Fig. 6C)

cf. *Cadomites* (*Polyplectites*) *psilacanthoides* Sandoval, 1983: 295, pl. 21, figs 3, 5, 7, text-fig. 109.

cf. *Polyplectites psilacanthoides* – Sandoval 1990: 158, pl. 3, fig. 7.

cf. *Masckeites psilacanthoides* – Galácz 1994: 168, pl. 3, fig. 2.

Remarks

A small (33 mm) specimen, showing only the lateral and ventral side of the last whorl. The identification was based on the sculpture that is typically stephanoceratid with short inner ribs ending in rounded tubercles where the radial secondary ribs arise in threes and fours. Closest form is *Masckeites psilacanthoides*, described originally from the Niortense Zone (Sandoval 1983: 295). *Masckeites* Buckman, 1920 was suggested as the microconch pair for macroconchiate *Lokuticeras* Galácz, 1994 (see Galácz 1994). Remarkable is that a *Lokuticeras*-type stephanoceratid, the similarly Niortense Zone *'Cadomites* aff. *C. lissajousi'* Roché, 1939 was figured from a nearby locality by Westermann (1975: pl. 2, fig. 8).

Normannites egyptiacus Arkell, 1952
(Fig. 5V, W)

Normannites egyptiacus Arkell, 1952: 309, pl. 30, fig. 4. — Parnes 1981: 47, pl. 7, figs 27-29.

Coeloceras braikenridgei – Douvillé 1916: 28, pl. 1, figs 11-12.

Normannites (*Normannites* ?) *aegyptiacus* – Westermann 1954: 204, pl. 32, fig. 2.

? *Normannites*? sp. – Imlay 1970: D11, pl. 1, figs 9-12.

Normannites cf. *braikenridgei ventriplanus* Enay *et al.*, 1987a: 38, pl. 2, fig. 6.

Stephanoceratinae gen. et sp. indet. – Galácz 1990: 202.

REMARKS

A single, minute, crushed phragmocone fragment.

The possible presence of *Normannites egyptiacus* was indicated by Westermann (1975: 46), who reported fragments from the Lower Posidonia shale which could be identified as belonging to this species.

Normannites Munier-Chalmas, 1892 is generally regarded as the microconchiate partner of *Skirroceras*-like *Stephanoceras*. These present collections did not yield representatives of *Skirroceras*, but Westermann figured a beautiful macroconch under the name *Stephanoceras* (*Skirroceras*) cf. *S. macrum* (Quenstedt) (Westermann 1975: pl. 2, fig. 7). This is the specimen identified earlier by Spath (1930: 66) as *Stephanoceras* cf. *tenuicostatum* Hochstetter, 1898. This specimen likely belongs to a group of *Stephanoceras* which survives into the basal Niortense Zone (e.g. '*Cadomites*' *humphriesiformis* Roché, 1939 [Roché 1939: pl. 2, figs 3 and 4]).

Normannites egyptiacus is another species which occurs also in Jebel Moghara. It was described by Arkell in 1952 and previously by Douvillé in 1916, on the basis of a specimen which was later re-figured by Westermann (1954: pl. 32, fig. 2). Parnes (1981: pl. 7, figs 27-29) figured an *ex situ* example from the Negev (South Israel) which he placed in a slightly lower horizon.

Leptosphinctes cf. ***schmiereri*** (Bentz, 1924)
(Figs 4E; 6D)

cf. *Bigotites schmiereri* Bentz, 1924: 181, pl. 9, fig. 7 (only).

cf. *Perisphinctes tenuiplicatus* Douvillé, 1916: 23, pl. 1, fig. 1 (only)

cf. *Leptosphinctes*? (*L.*?) *subcoronatus* – Pavia 1973: 130, pl. 27, fig. 4 (only).

cf. *Leptosphinctes* (*Leptosphinctes*) *schmiereri* – Dietl 1980: 10, pl. 1, fig. 2 (only).

cf. ?*Leptosphinctes* (*L.*) sp. – Parnes 1988: 732, pl. 6, figs 4-5.

REMARKS

The specimen is a fragment of a phragmocone with one side in good preservation. The short and moderately strong inner ribs and the rounded secondaries indicate early, Niortense Zone forms, such as the small-size specimens of *L. schmiereri* in Dietl (1980: pl. 1, fig. 3), or *L. subcoronatus* in Pavia (1973: pl. 27, fig. 4). The suture-line (Fig. 4E) with wide, deeply dissected first lateral saddle also indicates *Leptosphinctes*. A very similar form was figured by Douvillé (1916: pl. 1, fig. 2) from the Upper Bajocian fauna of the Sinai. Arkell (1952: 296, 307) supported the Late Bajocian age of this form in the Jebel Moghara. Parnes (1988) also documented the genus with a very similar form from Moghara.

This is the first record of early, i.e., pre-Callovian perisphinctids from East Africa.

Spiroceras annulatum (Deshayes, 1831)
(Figs 4D; 5X, Y)

Hamites annulatus Deshayes, 1831: 228, pl. 6, fig. 5.

Ancyloceras tenue – Douvillé 1916: 26, pl. 3, figs 10-14.

Spiroceras annulatum – Dietl 1978: 40, pl. 6, figs 1-5, pl. 7, figs 1-6, pl. 10, fig. 5, text-figs 6d, 6f, 7c, 8. (*cum syn.*). — Imlay 1970: 1, D11, figs 7,8. — Enay *et al.* 1987a: 43, pl. 4, fig. 5. — Galácz 1990: 202.

REMARKS

This is a second heteromorph from the Kambe Limestone. The one described and figured by Westermann (1975: 45, pl. 2, fig. 9) as *Spiroceras* cf. *bifurcati* (Quenstedt, 1843) (regarded as *S. orbignyi* by Dietl [1978: 19]) is certainly different, because he mentioned the characteristic two rows of tubercles on the ribs. That is probably the same specimen what Spath (1933: 815) mentioned as *Spiroceras*. The here figured example is a short, crushed fragment showing a very slight curve and straight, somewhat prorsiradiate ribs without tubercles. In this respect it is similar to the specimen figured under the same name by Imlay from Arabia (Imlay 1970: D11, pl. 1, figs 7, 8). The "*Ancyloceras tenue*" specimens from the Sinai figured by Douvillé (1916: pl. 3, figs 10-14) are also close. Parnes (1988: 732) recorded the species also from Gebel Maghara of the Sinai. Most of the well-localized specimens discussed by Dietl (1978) came from the Niortense and some from the Garantiana Zone.

CONCLUSIONS

The Mwachi River locality is probably the richest Upper Bajocian ammonite collecting site of the Kambe Limestone. The two collections reported as from above and below the Massive (Coral) Limestone (*sensu* Westermann 1975) or Conglomeratic Member (*in* Chiocchini *et al.* 2005) dividing the shales of the Kambe Formation provided assemblages poor in diagnostic ammonites. It is concluded that the lower level is of Niortense Zone age, and the upper unit is younger, referable to the Garantiana Zone. These conclusions were also made in an earlier study (Galácz 1990). These stratigraphical results were recently challenged by Chiocchini *et al.* (2005), who had concluded, on the basis of nannofossils, that the Lower Shaley Member (i.e., the shales below the dividing limestones) are Aalenian, and the Upper Shaley Member (i.e., the Upper Posidonia Shales *auctt.*) is Late Aalenian-Early Bajocian in age.

The obscured outcrops near the pipeline bridge on the Mwachi River near the here mentioned localities restrict significantly the possibilities of identifying faulting or if the limestone beds between the shales at the collecting sites belong to the Massive (Coral) Limestone (Conglomeratic Member) or are merely limestone interbeds within the calcareous shales. Nevertheless, the ammonites described herein and previously figured and described specimens from the Mwachi River localities firmly establish Late Bajocian ages for the higher or major part of the Posidonia shales. Aalenian ammonites are hitherto unknown from the area.

The faunal composition of the ammonites, with the great majority of 'leiostracans' unequivocally indicates a pelagic, open oceanic environment (see Lukeneder 2015). While water depth cannot be calculated, the abundant phylloceratids in the Tethys suggest mesopelagic (i.e., 250-800 m) depths (Westermann 1990). Taking into account that the resurgence of the rifting of the Kenyan and Tanzanian coastal region have begun in the early Middle Jurassic (Raiss-Assa 1988; Hankel 1994), this is regarded as extremely rapid subsidence.

As shortly discussed in the earlier paper (Galácz 1990), the Upper Bajocian faunas from Mombasa present a problematic pattern from the viewpoint of palaeobiogeography. The high percentage of phylloceratids unequivocally renders these assemblages into the Tethyan pelagic, deep-water realm, the Ammonitina elements show affinity to the Arabian-Sinai faunas. *Trimarginia* Arkell, 1952 and *Normannites egyptiacus* are recorded from Gebel Maghara of the Sinai, from the Negev and from central Saudi Arabia also, where the cosmopolitan *Spiroceras* and *Lissoceras* also occur. However, phylloceratids were never reported from the Arabian Peninsula, but are richly represented in the Upper Bajocian in the Sinai (Parnes 1988). The Jurassic faunas of the Arabian Peninsula (practically from Jabal Tuwaiq, see Enay *et al.* 1987a) were influenced by transgressions and regressions (i.e., by global sea level changes), however their development remained independent for a long time. According to recent suggestions (e.g. El-Sorogy *et al.* 2014) the Jabal Tuwaiq Middle Jurassic was developed on a shallow margin of the nearby, north-easterly lying open sea region of the Tethys. The sea level highstands made possible, if only intermittent, faunal element exchanges with other areas, e.g. with Gebel Moghara or East Africa or even beyond. These exchanges were apparently selective, as in the Bajocian, neither lytoceratids nor phylloceratids reached the central Arabian region, and from there a few groups (e.g. *Thambites* Arkell, 1952, *Ermoceras* H. Douvillé, 1916) accessed North African or European regions (see Enay *et al.* 1987b; Galácz 1999).

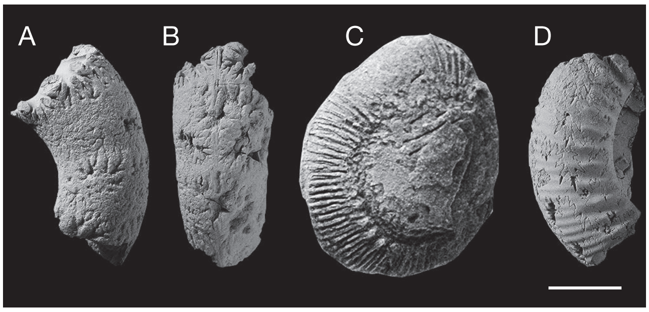

Fig. 6. — **A**, **B**, *Lytoceras eudesianum eudesianum* (d'Orbigny, 1846) MR 1, EMNH.2015.184; **C**, *Masckeites* cf. *psilacanthoides* (Sandoval, 1983) MR 2, EMNH.2015.278; **D**, *Leptosphinctes* cf. *schmiereri* (Bentz, 1924) MR 2, EMNH.2015.224. Scale bar: 10 mm.

In conclusion, the Middle Jurassic coastal region of this part of East Africa could be best understood as a pelagic Tethyan area between cratonic Africa and the more or less restricted, shallow-water Arabian basin. The palaeogeographic setting of Gebel Maghara may have been similar, but connecting rock sequences between the two areas were probably destroyed by erosion on the north-eastern corner of the Afro-Arabian plate.

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REFERENCES

Arkell W. J. 1952. — Jurassic ammonites from Jebel Tuwaiq, Central Arabia. *Philosophical Transactions of the Royal Society, London, Ser. B*, 633, 236: 241-316. https://doi.org/10.1098/rstb.1952.0003

Arkell W. J. 1956. — *Jurassic Geology of the World*. Oliver & Boyd, Edinburgh, London. i-xv + 806 p.

Bentz A. 1924. — Die Garantianen-Schichten von Norddeutschland mit besonderer Berücksichtung des Brauneisenoolit-Horizontes von Harzburg. *Jahrbuch des preussischen geologischen Landesanstalt* 45: 119-193.

Böckh J. 1881. — [Data to the knowledge on the Jurassic deposits of the Mecsek Mountains and adjacent areas. II. Palaeontology]. *Értekezések a Természettudományok Köréből, Budapest* 11 (9): 1-107. (in Hungarian).

Chiocchini M., Fazzuoli M. & Reale V. 2005. — The Mid-Jurassic marine transgression in East Africa: New data on the depositional environment and age of the Lower Kambe Formation (Aalenian to Bajocian) in the Mombasa area (S. E. Kenya). *Rivista Italiana di Paleontologia e Stratigrafia* 111 (3): 439-454. https://doi.org/10.13130/2039-4942/6330

Deshayes M. G. P. 1831. — *Description de coquilles caractéristiques des terrains*. Levraut, Paris, 264 p. http://gallica.bnf.fr/ark:/12148/bpt6k990705/f3.image

Dietl G. 1974. — Zur Stratigraphie und Ammonitenfauna des Dogger, insbesondere des Oberbajocium des westlichen Keltiberischen Ketten (Spanien). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 14: 1-217.

Dietl G. 1978. — Die heteromorphen Ammoniten des Dogger. *Stuttgarter Beiträge zur Naturkunde, Serie B*, 33: 1-97.

Dietl G. 1980. — Die Ammoniten-Gattung *Leptosphinctes* aus dem südwestdeutschen Subfurcaten-Oolith (Bajocium, Mittl. Jura). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 66: 1-49.

Donovan D. T., Callomon J. H. & Howarth M. K. 1981. — Classification of the Jurassic Ammonitina, *in* House M. R. & Senior J. R. (eds), *The Ammonoidea : the Evolution, Classification, Mode of Life, and Geological Usefulness of a Major Fossil Group*. The Systematics Association special volume no. 18. Academic Press, London and New York: 101-155.

Douvillé H. 1916. — Les terrains secondaires dans le Massif du Moghara à l'est de l'isthme de Suez : Paléontologie. *Mémoires de l'Académie des Sciences de l'Institut de France, série 2,* 54: 1-184. http://gallica.bnf.fr/ark:/12148/bpt6k3269h/f3.item

El-Sorogy A. S., Al-Kahtany K. M. & El-Asmar H. M. 2014. — Marine benthic invertebrates of the upper Jurassic Tuwaiq Mountain Limestone, Khashm A-Qaddiyah, central Saudi Arabia. *Journal of African Earth Sciences* 97: 161-172. https://doi.org/10.1016/j.jafrearsci.2014.04.004

Enay R., Le Nindre Y. M., Mangold C., Manivit J. & Vaslet D. 1987a. — Le Jurassique d'Arabie saoudite centrale : nouvelles données sur la lithostratigraphie, les paléoenvironements, les faunes d'Ammonites, les âges et les corrélations, *in* Enay R. (ed.), Le Jurassique d'Arabie Saoudite centrale. *Geobios, Mém. Spec*. 9: 13-65. https://doi.org/10.1016/S0016-6995(87)80071-2

Enay R., Mangold C., Du Dresnay R. & Rakús M. 1987b. — Arrivals of Arabian origin among the ammonite faunas of Morocco during the Bajocian-Bathonian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 61: 107-120. https://doi.org/10.1016/0031-0182(87)90043-5

Fernández-López S. 1985. — *El Bajociense en la Cordillera Ibérica*. Universidad Complutense de Madrid, Facultad de Ciencias Geologicas, 850 p.

Galácz A. 1980. — Bajocian and Bathonian ammonites of Gyenespuszta, Bakony Mts., Hungary. *Geologica Hungarica, Ser. Palaeontologica* 39: 1-227.

Galácz A. 1990. — New collection of successive ammonite faunas from the Bajocian of Mombasa (Kenya, East Africa). *Memorie Descrittive della Carta Geologica d'Italia* 40: 199-204.

Galácz A. 1994. — *Lokuticeras* nov. gen. – a new genus for a Mediterranean Bajocian (Middle Jurassic) stephanoceratid group. *Miscellanea del Servizio Geologico Nazionale* 5: 161-175.

Galácz A. 1999. — Middle Jurassic ammonites of Arabian origin in Western Sicily. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1999 (10): 605-613.

Galácz A. & Kassai P. 2012. — New species and stratigraphic data on Lower Bajocian (Middle Jurassic) lytoceratids (Ammonoidea) from Lókút, Bakony Mts, Hungary. *Paläontologische Zeitschrift* 86: 281-295. https://doi.org/10.1007/s12542-011-0128-7

Hankel O. 1994. — Early Permian to Middle Jurassic rifting and sedimentation in East Africa and Madagascar. *Geologische Rundschau* 83: 703-710. https://doi.org/10.1007/BF00251069

Howarth M. K. 2013. — *Treatise Online No. 57. Part L, Revised, Volume 3B, Chapter 4: Psiloceratoidea, Eoderoceratoidea, Hildoceratoidea*. The University of Kansas, Lawrence, Kansas, 137 p.

Imlay R. W. 1970. — Some Jurassic ammonites from Central Saudi Arabia. *Geological Survey Professional Paper* 643-D: D1-17.

Joly B. 1976. — Les Phylloceratidae malgaches au Jurassique. Generalites sur les Phylloceratidae et quelques Juraphyllitidae. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 67: 1-471.

Kapilima S. 1984. — Stratigraphische und paläontologische Untersuchungen im Jura und der Kreide des tansanischen Küstenstreifens im Hinterland von Dar-Es-Salaam und Bagamoyo. *Berliner geowissenschaftliche Abhandlungen* A: 57, 1-77.

Kudernatsch J. 1852. — Die Ammoniten von Swinitza. *Abhandlungen der k. k. geologischen Reichsanstalt*: 1/2, 1-16.

Lukeneder A. 2015. — Ammonoid habitats and life history, *in* Klug C., Korn D., De Baets K., Kruta I. & Mapes R. H. (eds), *Ammonoid Paleobiology. From Anatomy to Ecology*. Topics in Geobiology, vol. 43. Springer Netherlands: 689-792. https://doi.org/10.1007/978-94-017-9630-9_18

McKinnon Wood M. 1938. — Some further geological observations on the coastlands of Kenya. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* 49: 1-11.

Mangold C. & Gygi R. A. 1997. — Bathonian ammonites from Canton Aargau, northern Switzerland: Stratigraphy, taxonomy and biogeography. *Geobios* 30 (4): 497-518. https://doi.org/10.1016/S0016-6995(97)80119-2

Morton N. 1971. — Some Bajocian ammonites from western Scotland. *Palaeontology* 14 (2): 266-293. http://go.palass.org/3sk

Neumayr M. 1871. — Die Phylloceraten des Dogger und Malm. *Jahrbuch der k. k. Geologischen Reichsanstalt* 21 (3): 297-354. http://ir.nmu.org.ua/handle/GenofondUA/17708

Ooster W. A. 1858. — Pétrifactions rémarquables des Alpes suisses. *Neue Denkschriften der allgemeine schweizerische Gesellschaft für die gesammten Naturwissenschaften* 18: 1-6.

Orbigny A. d' 1842-51 — *Paléontologie Française, Terrains jurassiques, I. Céphalopodes*. Masson, Paris, 642 p. https://doi.org/10.5962/bhl.title.50510

Parnes A. 1981. — Biostratigraphy of the Mahmal Formation (Middle and Upper Bajocian) in Makhtesh Ramon (Negev, Southern Israel). *Geological Survey of Israel, Bulletin* 74: 1-55.

Parnes A. 1988. — Middle Jurassic (Middle Bajocian-Middle Bathonian) ammonites from Gebel Maghara, Sinai, Egypt. *Journal of African Earth Sciences* 7 (4): 707-733. https://doi.org/10.1016/0899-5362(88)90120-0

Pavia G. 1973. — Ammoniti del Bajociano superiore di Digne (Francia SE, Dip. Basses-Alpes). *Bollettino della Società Paleontologica Italiana* 10 (2): 75-142.

Pavia G. 1983. — Il genere *Ptychophylloceras* Spath, 1927 (Ammonoidea, Phyllocerataceae) nel Baiociano sudeuropeo. *Memorie della Accademia Nazionale dei Lincei* VIII, 17 (1): 5-31.

Raiss-Assa R. 1988. — Stratigraphy and geodynamics of the Mombasa Basin (Kenya) in relation to the genesis of the proto-Indian Ocean. *Geological Magazine* 125 (2): 141-147. https://doi.org/10.1017/S0016756800009547

Roché P. 1939. — Aalénien et Bajocien du Maconnais et de quelques régions voisines. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* XXV, 29: 1-355.

Sandoval J. 1983. — *Bioestratigrafia y Paleontologia (Stephanocerataceae y Perisphinctaceae) del Bajocense y Bathonense en las Cordilleras Béticas*. Doctoral Thesis, Universidad de Granada, 613 p.

Sandoval J. 1990. — A revision of the Bajocian divisions in the Subbetic Domain (southern Spain). *Memorie Descrittive della Carta Geologica d'Italia* 40: 141-162.

Spath L. F. 1920. — On Jurassic ammonites from East Africa, collected by Prof. J. W. Gregory. *Geological Magazine* 57: 311-320; 351-362. https://doi.org/10.1017/S0016756800101906

Spath L. F. 1927. — Revision of the Jurassic cephalopod fauna of Kachh (Cutch), Part I. *Palaeontologia Indica, N.S.* 9 (2): 1-71.

Spath L. F. 1930. — The Jurassic faunas of the neighbourhood of Mombasa. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* 4: 13-71.

Spath L. F. 1933. — Revision of the Jurassic cephalopod fauna of Kachh (Cutch), Part VI. *Palaeontologia Indica, N.S.* 9 (2): 659-945.

WEIR J. 1938. — The Jurassic faunas of Kenya with description of some Brachiopoda and Mollusca. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* 5 (3): 17-60.

WENDT J. 1963. — Stratigraphisch-paläontologische Untersuchungen im Dogger Westsiziliens. *Bollettino della Società Paleontologica Italiana* 2 (1): 57-145.

WESTERMANN G. 1954. — Monographie der Otoitidae (Ammonoidea). *Beihefte zum Geologischen Jahrbuch* 15: 1-364.

WESTERMANN G. E. G. 1975. — Bajocian ammonoid fauna of Tethyan affinities from the Kambe Limestone Series of Kenya and implications to plate tectonics. *Newsletters on Stratigraphy* 4 (1): 23-48. https://doi.org/10.1127/nos/4/1975/23

WESTERMANN G. E. G. 1990. — New developments in ecology of Jurassic-Cretaceous ammonites, *in* PALLINI G., CECCA F., CRESTA S. & SANTANTONIO M. (eds), *Atti del secondo convegno internationale Fossili, Evoluzione, Ambiente, Pergola, 25-30 October, 1987*: 459-478.

ZITTEL K. A. 1868. — Paläontologische Notizen über Lias-, Jura- und Kreide-Schichten in den baierischen und österreichischen Alpen. *Jahrbuch der k. k. geologischen Reichsanstalt* 18: 599-610.

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